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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, pontoniine shrimps, mytilid bivalves, epitoniid 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).

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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;

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

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

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 wellsi* 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, epitoniid 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).

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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: *Anchimolgus 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; *Odontomolgus decens* Humes, 1978; *O. flammeus* Kim, 2007; *O. fultus* Humes, 1978; *O. scitulus* Humes, 1973; *Paramarda aculeata* Humes, 1978; *Schedomolgus dumbensis* Kim, 2003; *S. tener* (Humes, 1973); *Temanus halmaherensis* Humes, 1997; *Tondua tholincola* Humes, 1997; *Xarifia* sp.; and *Zazaranus fungicolus* Humes & Dojiri, 1983. *Anchimolgus* 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: *Anchimolgus pandus* and *Schedomolgus tener*. Four copepods have been recorded from two host species: *A. notatus*, *A. punctilis*, *Paramarda aculata* and *Schedomolgus 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* (Kolosvary, 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), *Galkina 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

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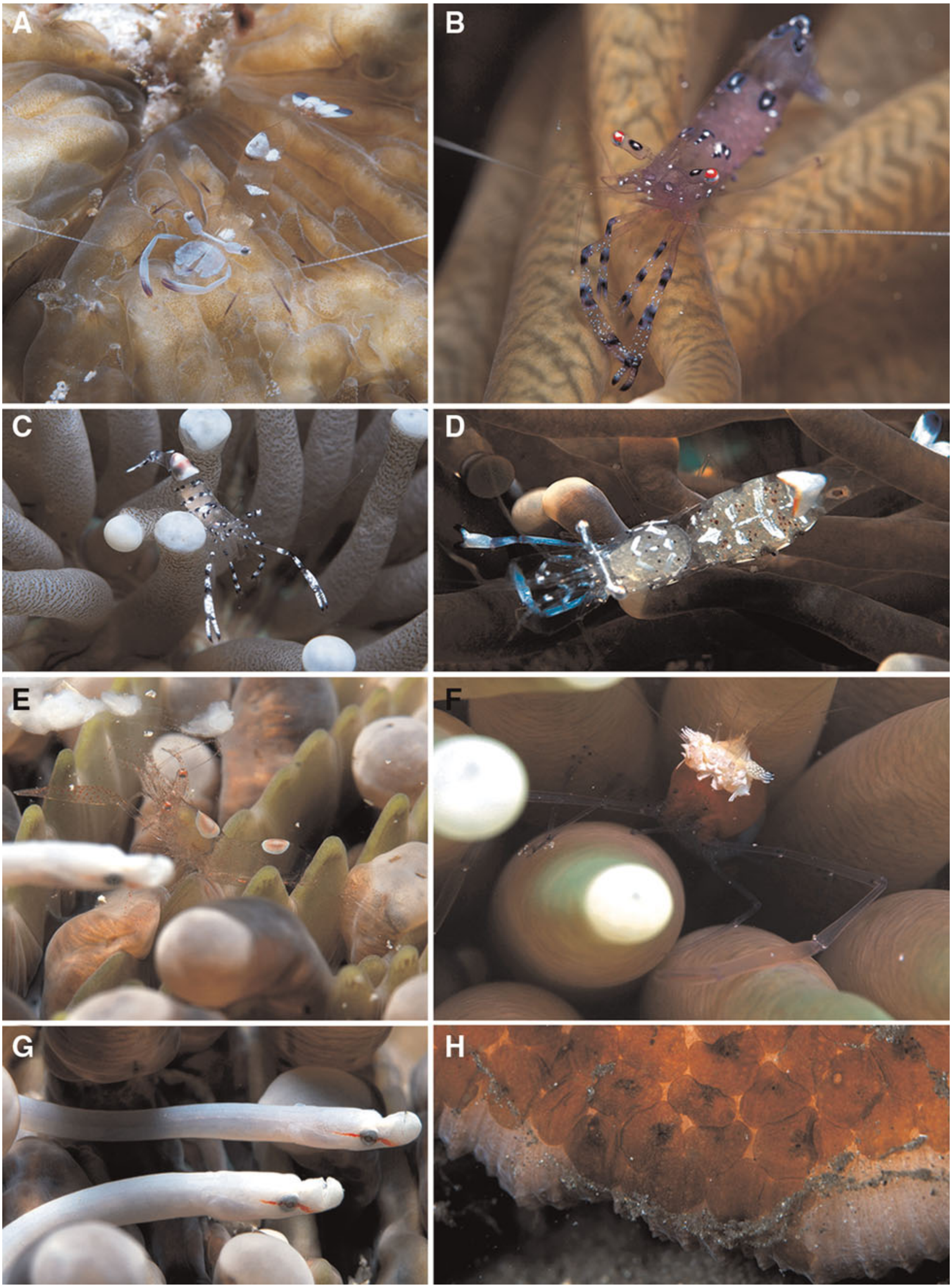

Fig. 1. Associated organisms on mushroom corals at Raja Ampat Islands, West Papua, Indonesia (November 2007). (A–F) Pontoniine shrimps: (A) *Ancylomenes magnificus* on *Cycloseris costulata*; (B) *A. sarasvati* on *Heliofungia actiniformis*; (C) *A. venustus* on *H. actiniformis*; (D) *A. holthuisi* on *H. actiniformis*; (E) *Hamopontonia corallicola* on *H. actiniformis*; (F) *Cuapates kororensis* on *H. actiniformis*; (G) pipefish *Siokunichtys nigrolineatus* on *H. actiniformis*; (H) acoel 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
Ctenactis echinata	*Anchimolgus latens*
	Anchimolgus pandus
	Mycoxynus fungianus
	Schedomolgus tener
	Xarifia sp.
Danafungia scruposa, *Fungia fungites*	*Asteropontius latioriger*
	Anchimolgus latens
	Anchimolgus punctilis
	Odontomolgus scitulus
	Schedomolgus dumbensis
Fungia sp.	*Anchimolgus hastatus*
	Anchimolgus orectus
	Asteropontius fungicola
	Odontomolgus flammeus
	Zazaranus fungicolus
Halomitra pileus	*Odontomolgus fultus*
	Paramarda aculeata
Heliofungia actiniformis	*Anchimolgus notatus*
	Anchimolgus pandus
	Odontomolgus decens
Herpolitha limax	*Anchimolgus latens*
	Mycoxynus villosus
Lithophyllon concinna	*Anchimolgus maximus*
Pleuractis paumotensis	*Anchimolgus latens*
	Anchimolgus notatus
	Anchimolgus orectus
	Anchimolgus pandus
	Anchimolgus punctilis
	Paramarda aculata
Polyphyllia novaehiberniae	*Anchimolgus gratus*
Polyphyllia talpina	*Anchimolgus pandus*
Sandalolitha robusta	*Anchimolgus convexus*
	Mycoxynus longicauda
	Schedomolgus tener
	Temanus halmaherensis
	Tondua tholincola

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. gonioporae* 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* (Jousseaume 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

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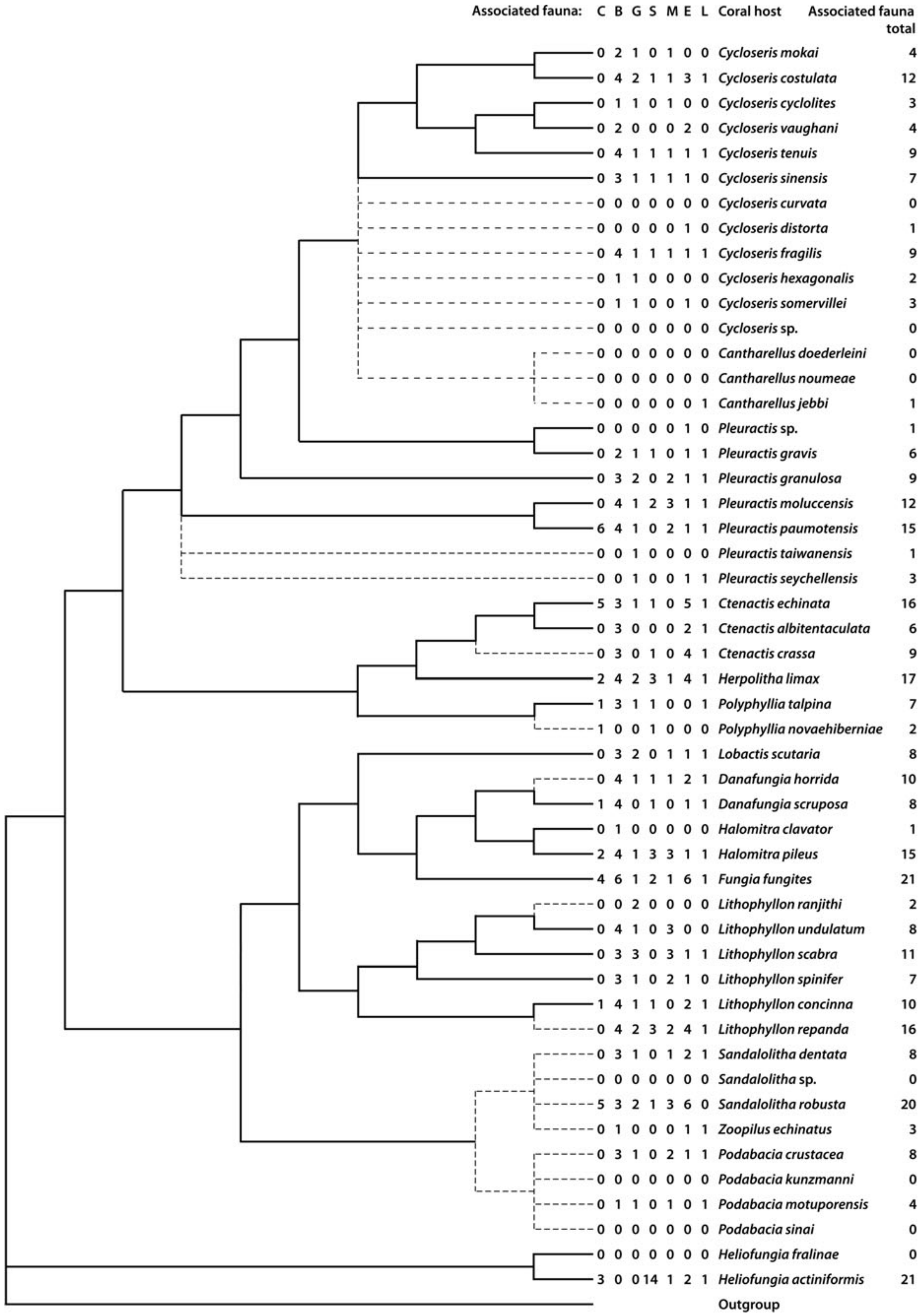

Fig. 2. Phylogeny reconstruction of the Fungiidae (after Gittenberger *et al.*, 2011), with an indication of numbers of associated fauna per mushroom coral species. Only well investigated taxa are included, while taxa with low or uncertain numbers of associated species are excluded. C, copepods; B, barnacles; 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
Ctenactis albitentaculata	*Cantellius tredecimus*
	Galkinia indica
	Megatrema oulastreae
Ctenactis crassa	*Cantellius tredecimus*
	Galkinia indica
	Megatrema oulastreae
Ctenactis echinata	*Cantellius tredecimus*
	Galkinia indica
	Megatrema oulastreae
Cycloseris costulata	*Cantellius pallidus*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Cycloseris cyclolites	*Megatrema oulastreae*
Cycloseris fragilis	*Cantellius pallidus*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Cycloseris hexagonalis	*Cantellius tredecimus*
Cycloseris mokai	*Cantellius tredecimus*
	Galkinia indica
Cycloseris sinensis	*Cantellius pallidus*
	Cantellius tredecimus
	Megatrema oulastreae
Cycloseris somervillei	*Cantellius tredecimus*
Cycloseris tenuis	*Cantellius pallidus*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Cycloseris vaughani	*Cantellius tredecimus*
	Megatrema oulastreae
Danafungia horrida	*Armatobalanus allium*
	Cantellius pallidus
	Cantellius tredecimus
	Galkinia indica
Danafungia scruposa	*Armatobalanus allium*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Fungia fungites	*Armatobalanus allium*
	Cantellius euspinulosus
	Cantellius pallidus
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Halomitra clavator	*Galkinia indica*
Halomitra pileus	*Darwiniella conjugatum*
	Galkinia indica
	Megatrema oulastreae
	Nobia halomitrae
	Herpolitha limax
	Cantellius euspinulosus
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Lithophyllon concinna	*Cantellius pallidus*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae
Lithophyllon repanda	*Cantellius pallidus*
	Cantellius tredecimus
	Galkinia indica
	Megatrema oulastreae

Continued

Table 3. Continued

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

(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 crassicostatum* Gittenberger & Gittenberger, 2005; *E. graviarmatum* Gittenberger & Gittenberger, 2005; *Surrepifungium costulatum* (Kiener, 1838); *S. ingridae* (Gittenberger & Goud, 2000); *S. oliverioi* (Bonfitto & Sabelli, 2001); and *S. patamakanthini* 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
Ctenactis echinata	*Fungicola utinomi*
Cycloseris costulata	*Dacryomaia* sp.
	Fungicola fagei
Cycloseris cyclolites	Cryptochirid sp.
Cycloseris fragilis	*Fungicola fagei*
Cycloseris hexagonalis	*Fungicola fagei*
Cycloseris mokai	Cryptochirid sp.
Cycloseris sinensis	Cryptochirid sp.
Cycloseris somervillei	*Fungicola fagei*
Cycloseris tenuis	*Fungicola fagei*
Danafungia horrida	*Fungicola utinomi*
Fungia fungites	*Fungicola utinomi*
Halomitra pileus	*Fungicola utinomi*
Herpolitha limax	*Fungicola fagei*
	Fungicola utinomi
Lithophyllon concinna	*Fungicola utinomi*
Lithophyllon ranjithi	*Fungicola fagei*
	Cryptochirid sp.
Lithophyllon repanda	*Fungicola fagei*
	Fungicola utinomi
Lithophyllon scabra	*Dacryomaia* sp.
	Fungicola fagei
	Fungicola utinomi
Lithophyllon spinifer	Cryptochirid sp.
Lithophyllon undulatum	*Dacryomaia* sp.
Lobactis scutaria	*Fungicola fagei*
	Fungicola utinomi
Pleuractis granulosa	*Dacryomaia* sp.
	Fungicola fagei
Pleuractis gravis	*Fungicola fagei*
Pleuractis moluccensis	*Fungicola fagei*
Pleuractis paumotensis	*Fungicola fagei*
Pleuractis seychellensis	*Fungicola fagei*
Pleuractis taiwanensis	*Fungicola fagei*
Podabacia crustacea	*Fungicola fagei*
Podabacia motuporensis	Cryptochirid sp.
Polyphyllia talpina	Cryptochirid sp.
Sandalolitha dentata	*Fungicola fagei*
Sandalolitha robusta	*Fungicola fagei*
	Fungicola utinomi

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 wentletrap 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*' (Kuiter, 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 (Kuiter, 2000 p. 119, 2009 p. 203). There are also records on pygmy seahorses that have been seen moving over fungiids (Lourie & Kuiter, 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
Ctenactis crassa	*Periclimenes diverspes*	RMNH D 50723
Ctenactis echinata	*Periclimenes gonioporae*	RMNH D 54528
Cycloseris costulata	*Ancylomenes magnificus*	B.W.H., personal observation
Cycloseris fragilis	*Ancylomenes magnificus*	B.W.H., personal observation
Cycloseris sinensis	*Ancylomenes magnificus*	B.W.H., personal observation
Cycloseris tenuis	*Ancylomenes magnificus*	B.W.H., personal observation, RMNH D 54532
Danafungia horrida	*Ancylomenes magnificus*	B.W.H., personal observation
Danafungia scruposa	*Hamopontonia corallicola*	RMNH D 54531
Fungia fungites	*Ancylomenes magnificus*	B.W.H., personal observation
	Periclimenes gonioporae	RMNH D 54529
Halomitra pileus	*Periclimenes* sp.	RMNH D 48495
	Metapontonia fungiacola	Bruce, 1976
	Periclimenes watamuae	RMNH D 46471
Heliofungia actiniformis	*Ancylomenes grandidens*	RMNH D 50413
	Ancylomenes holthuisi	Bruce, 1978; De Grave, 1998; RMNH D 37390
	Ancylomenes kobayashii	RMNH D 54540
	Ancylomenes luteomaculatus	RMNH D 48478
	Ancylomenes magnificus	B.W.H., personal observation, RMNH D 54533
	Ancylomenes sarasvati	RMNH D 48478, 50413, 50414
	Ancylomenes venustus	De Grave, 1998; Bruce, 2005; Hoeksema & Fransen, 2011; RMNH D 47539, 48120
	Cuapetes lacertae	RMNH D 48449, 50398
	Cuapetes kororensis	Bruce, 1977, 1983; Bruce & Svoboda, 1984; Chace & Bruce, 1993; De Grave, 1998; RMNH D 47687, 48444
	Cuapetes tenuipes	De Grave, 1998; Hoeksema & Fransen, 2011; RMNH D 46347, 47514
	Hamopontonia corallicola	Bruce, 1978; 1981; De Grave, 1998; RMNH D 48373, 50170
	Periclimenes jugalis	RMNH D 54527
	Periclimenes watamuae	De Grave, 1998
	Thor amboinensis	De Grave, 1998; Hoeksema & Fransen, 2011
Herpolitha limax	*Ancylomenes magnificus*	B.W.H., personal observation
	Metapontonia fungiacola	Yamashiro, 1999
	Periclimenes watamuae	RMNH D 54537, 54538
Lithophyllon concinna	*Metapontonia fungiacola*	Yamashiro, 1999
Lithophyllon repanda	*Cuapetes tenuipes*	RMNH D 54539
	Metapontonia fungiacola	Yamashiro, 1999
	Periclimenes gonioporae	RMNH D 54530
Pleuractis gravis	*Ancylomenes magnificus*	RMNH D 54534
Pleuractis moluccensis	*Ancylomenes holthuisi*	B.W.H., personal observation
	Ancylomenes magnificus	B.W.H., personal observation
Polyphyllia novaehiberniae	*Ancylomenes kobayashii*	RMNH D 54541
Polyphyllia talpina	*Periclimenes watamuae*	RMNH D 54535, 54536
Sandalolitha robusta	*Periclimenes gonioporae*	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

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

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

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

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

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

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 pontoniine 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

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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 pontoniine 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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