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Chapter 9

Phylogenetic ecology of gall crabs (Brachyura: Cryptochiridae) and their mushroom host corals (Scleractinia: Fungiidae)

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Abstract

Coral-associated fauna is a relatively understudied topic, hence the nature of the relationship between an associated organism and its host is frequently unknown. In the present study the obligate associations between gall crabs (Cryptochiridae) and mushroom corals (Fungiidae) are reviewed from a phylogenetic perspective. Based on field surveys, examination of museum material and a literature review, a total of 35 fungiid species have been found that act as hosts for four gall crab species. Fungiid-associated gall crabs appear to be more geographically widespread than previously known, with new records showing their occurrences from the Red Sea and western Indian Ocean all the way to the central Pacific Ocean. The obligate nature of the association between cryptochirids and their hosts makes them an ideal model taxon to test for possible cospeciation events. The congruence between their phylogenies was tested by using the programme Jane 4.0, resulting in cospeciation and duplication events between the crabs and their host corals. The sharing of several closely related coral host species by a gall crab species or genus may provide support to models indicating phylogenetic relationships within the Scleractinia.

Manuscript under review

Introduction

The integration of molecular analyses with skeleton microstructure data in recent phylogeny reconstructions of stony corals (Scleractinia), has initiated large changes in scleractinian systematics (i.e. Benzoni *et al.,* 2007; Budd *et al.,* 2012; Huang *et al.,* 2014). For the mushroom coral family Fungiidae this approach has resulted in various changes at genus level and the inclusion of two additional species (Gittenberger *et al.,* 2011; Benzoni *et al.,* 2012a). Fungiidae occur in the Indo-Pacific with a distribution ranging from the Red Sea and eastern Africa to the west coast of central America (Hoeksema, 1989). Several species have been recorded to live in association with fungiids. Most of the associated fauna consists of crustaceans and molluscs, but also includes acoel flatworms and fishes (e.g., Hoeksema *et al.,* 2012; van der Meij, 2015a; Bos and Hoeksema, in press).

Gall crabs (Brachyura: Cryptochiridae) are obligate associates of stony corals, living in dwellings inside their coral hosts. They are common inhabitants of coral reefs, but are easily overlooked because of their small size and hidden life inside their coral hosts (Hoeksema and van der Meij, 2013). Gall crab genera used to be defined by host specificity (Fize and Serène, 1957), a scheme that worked for some crab genera but proved to be unreliable for other genera (Kropp and Manning, 1987).

According to the last taxonomic revision of Indo-Pacific gall crabs (Kropp, 1990a), two species are known to live in association with mushroom corals: *Fungicola fagei* (Fize and Serène, 1956) and *F. utinomi* (Fize and Serène, 1956). Hoeksema *et al*. (2012) reported on a *Dacryomaia* species as a third cryptochirid species associated with Fungiidae, whereas Van der Meij and Hoeksema (2013) reported on the fourth. The latter concerned a cryptic species closely related to *F. fagei*, described as *Fungicola syzygia* van der Meij, 2015.

The obligate nature of the association between cryptochirids and their hosts raises questions about possible cospeciation between the two. Studies on the associated fauna of stony corals, however, have so far largely been focused on the symbiont. In this study the following questions are addressed. Is there an overlap between the geographical distribution of the corals and their associated gall crabs? Are common coral species more likely to be inhabited by gall crabs than less commonly occurring corals? Are the phylogenetic relationships of the host corals reflected in the phylogenetic relationships of the crabs, hence is there some kind of cospeciation between the two?

To answer these questions fungiid-associated gall crabs were studied from the perspective of the host by collecting crabs from as many coral species as possible. Fieldwork in various parts of the Indo-Pacific, examination of museum collections, and a review of available literature were carried out in order to obtain host, distribution and occurrence records. The gall crab-coral associations and occurrence rates were projected on a cladogram of the Fungiidae in order to reconstruct the evolutionary history of the associations of the crabs and their host species. The congruence between the fungiid and gall crab phylogenies was tested for cospeciation events with the help of the programme Jane 4.0.

Material and methods

Historical records

In order to examine the distribution of fungiid associated gall crabs the coral collections of Naturalis Biodiversity Center (RMNH) in Leiden, the Netherlands, and the Royal Belgian Institute of Natural Sciences (IRSNB) in Brussels, Belgium, were searched for the presence of gall crabs or their vacated pits. Additional records were obtained from the coral collections of the

Table 1. Distribution of gall crab species based on museum records of Fungiidae containing coral gall crabs (indicated by species name) or their pits (+), literature, and incidental observations (photo vouchers). Coral names updated according to Gittenberger *et al*. (2011). Localities of the listed host species: A = Israel (Eilat, Red Sea); B = Kenya (western Indian Ocean); C = Gulf of Aden, Yemen; D = Seychelles (western Indian Ocean); E = Maldives (central Indian Ocean); F = Thailand (Phuket); G = Indonesia; H = Vietnam (Nha Trang); I = Malaysia (Tioman Isl.).; J = Malaysia (Sabah); K = Taiwan; L = Palau; M = Papua New Guinea (Bismarck Sea); N = Japan (Yaeyama Isl.,); O = Australia (GBR, off Cairns); P = Samoa Isl. (western Pacific Ocean); Q = Tahiti (central Pacific Ocean); R = Hawaii; S = Vanuatu. Museum records: [1] = RMNH, [2] = IRSNB, [3] = UNIMIB, [4] = AMNH. In bold, localities based on literature references and/or incidental observations. **Fungicola utinomi* without host record was reported from Indonesia (Moluccas – Kropp, 1994) and Micronesia (Mariana Isl. – Paulay *et al.,* 2003).

Coral host	Museum records	Localities	Reference for locality data
Cycloseris costulata (Ortmann, 1889)	*Fungicola syzygia*[1]	B, G, J, S	
C. curvata (Hoeksema, 1989)	+[3]	C	
C. cyclolites (Lamarck, 1815)	+[1]	F, G	
C. fragilis (Alcock, 1893)	+[1]	G	
C. mokai (Hoeksema, 1989)	+[1]	G	
C. sinensis (M. Edwards & Haime, 1851)	+[1]	G	
C. tenuis (Dana, 1846)	+[1]	F, K	
Danafungia horrida (Dana, 1846)	-	**H**	Fize and Serène, 1957 (*F. utinomi*)
Fungia fungites (Linnaeus, 1758)	+[1], *F. utinomi*[2]	G, **H**, M	Fize and Serène, 1957 (*F. utinomi*)
Herpolitha limax (Esper, 1797)	-	**O**	
Lithophyllon concinna (Verrill, 1864)	+[1]	G, K	
L. ranjithi Ditlev, 2003	+[1]	J	
L. repanda (Dana, 1846)	+[1], *F. utinomi*[2]	**H**, K, M, **N**, **O**	Takeda and Tamura, 1979 (*F. utinomi*); Fize and Serène, 1957 (*F. utinomi*)
L. scabra (Döderlein, 1901)	*Dacryomaia* sp., *Fungicola* sp.	G	
L. undulatum Rehberg, 1892	*Dacryomaia* sp.	G, **I**	
Lobactis scutaria (Lamarck, 1801)	*Fungicola* sp.[4]	R	
Pleuractis granulosa (Klunzinger, 1879)	*Fungicola syzygia* [1, 2]	A, E, G, L, P, S	
P. gravis (Nemenzo, 1956)	*Fungicola syzygia* [1]	G	
P. moluccensis (Van der Horst, 1919)	+[1]	G, K	
P. paumotensis (Stutchbury, 1833)	*Fungicola syzygia* [1, 2]	E, G, **H**, **N**, **O**, Q, S	Fize and Serène, 1957 (? *F. syzygia*); Takeda and Tamura, 1979 (? *F. syzygia*)
P. seychellensis (Hoeksema, 1993)	*Fungicola syzygia* [1]	D	
P. taiwanensis (Hoeksema & Dai, 1991)	+[1]	G	
Podabacia crustacea (Pallas, 1766)	*F. fagei*[1]	G	
P. motuporensis Veron, 1990	+[1]	L	
P. sinai Veron, 2000	*F. fagei*[1]	L	
Sandalolitha dentata Quelch, 1884	+[1]	G, **H**	Fize and Serène, 1957 (*F. fagei*)
S. robusta (Quelch, 1886)	*F. fagei*[1, 2]	M, S	

University of Milano-Bicocca (UNIMIB) in Milan, Italy, and the American Museum of Natural History (AMNH) in New York, USA. Some pits contained (dried) gall crab carapaces which were examined for identification (Table 1). Gall crab identifications were based on Fize and Serène (1957), Kropp (1990a) and van der Meij (2015a), whereas coral identifications were based on Hoeksema (1989), Gittenberger *et al.* (2011) and Benzoni *et al.* (2012a). Literature was studied to obtain further distribution records. Host species data provided by Fize and Serène (1957) were taken from the main text (p. 122, 130, 134, 156, 171) because these were assumed to be more correct than those listed on p. 13. In addition, a few field observations are included (photo vouchered).

Fieldwork

A large part of the fieldwork was carried out in Spermonde Archipelago – SW Sulawesi, in the southern part of the Makassar Strait (1994), where belt quadrats of 50 × 2m^2 were used to study gall crab – fungiid occurrences. Per quadrat the density of mushroom coral species and the percentage of inhabited corals was recorded. Transect work was mostly carried out on the western reef slopes as mushroom coral species are most abundant at these sides of the reefs, which are the most exposed to wind and wave action. Additionally, inhabited mushroom corals were collected to obtain the gall crab specimens. The corals were split by use of a hammer and chisel and coral fragments containing the gall crabs were immersed in 80% ethanol for at least one hour to immobilize the crabs, which were subsequently transferred to labelled vials. All specimens are deposited in the collections of Naturalis in Leiden, The Netherlands (collection coded as RMNH.Crus.D).

Further data on fungiid-gall crab associations were collected during fieldwork (2007-2012) in Indonesia (Raja Ampat – W Papua, Bunaken – N Sulawesi, Ternate – N Moluccas, Lembeh Strait – N Sulawesi) and Malaysia (Semporna – N Borneo, Kudat – N Borneo). Mushroom corals from various reef sites were sampled for gall crabs, attempting to sample as many host species as possible from deep to shallow reef zones. Mushroom corals containing gall crabs were collected until a representative collection of the Fungiidae species was reached. The corals were sampled in the same way as described above after being photographed with a Canon 400D camera equipped with a 50 mm Sigma macro-lens.

Additional records were obtained from Vietnam (Nha Trang – 2006), Australia (Great Barrier Reef – off Cairns (2010), New Caledonia (2012, Loyalty Is. – 2013), Malaysia (Payar Isl, Tioman Isl – 2013), and the Maldives (2014).

Cophylogenetic analyses based on host preference data

The phylogenetic congruence of hosts and associates was tested by using the programme Jane 4.0 (Conow *et al.,* 2010), based on the phylogenies in Gittenberger *et al.* (2011), Benzoni *et al.* (2012a), and Van der Meij (2015a). The programme is based on an event-based model which considers cospeciation as the most parsimonious explanation for congruence between host and associate trees. Detection of coevolutionary relationships are easily obstructed by the complex interplay of events, i.e., cospeciation, duplication (intrahost speciation), host switching, sorting (extinction) and inertia (lack of parasite speciation). For definitions we refer to Paterson and Banks (2001) and Conow *et al.* (2010). The evolutionary events are used to superimpose phylogeny reconstruction of the associated taxon on that of the host taxon. Jane 4.0 assigns a cost to each evolutionary event, after which it seeks to find mappings minimizing the total cost. The default costs settings of Jane were used, as follows: cospeciation (0), duplication (1), duplication – host switching (2), loss (1) and failure to diverge (1). Statistical analyses are performed by comparing the best (minimum) costs found for the host parasite data set against randomized data sets (Cruaud *et al.*, 2012).

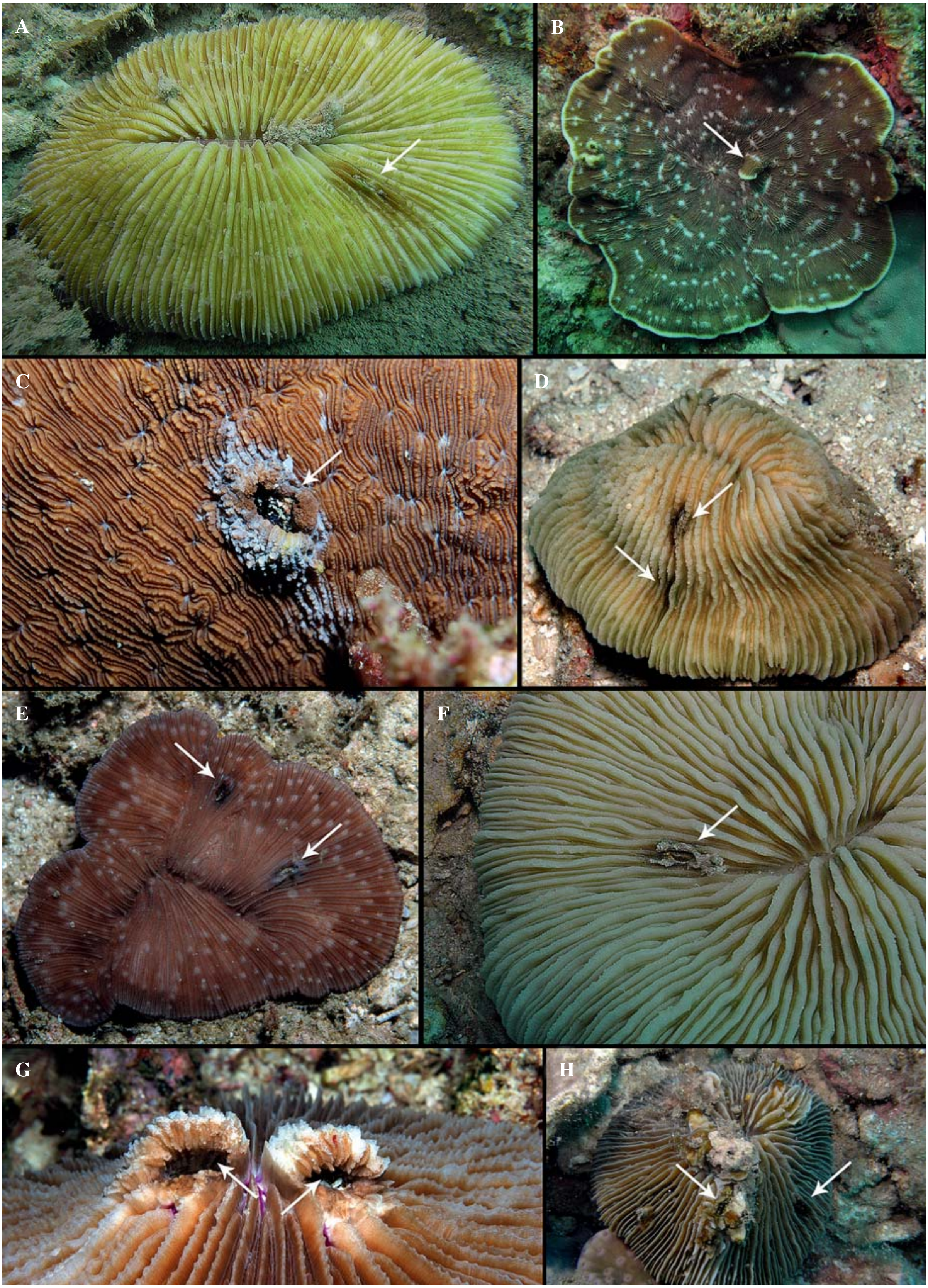

Fig. 1. Mushroom coral hosts with crab galls and their pits (arrows). **A**, *Pleuractis paumotensis* (Nha Trang, Vietnam); **B**, *Lithophyllon undulatum* (Nha Trang, Vietnam); **C**, *Podabacia crustacea* (Raja Ampat, Indonesia); **D**, *Pleuractis moluccensis* (Nha Trang, Vietnam); **E**, *Cycloseris sinensis* (Raja Ampat, Indonesia); **F**, *Pleuractis granulosa* (Ternate, Indonesia); **G**, *Lithophyllon repanda* (Raja Ampat, Indonesia); **H**, *L. scabra* (Nha Trang, Vietnam). Photographs not to scale.

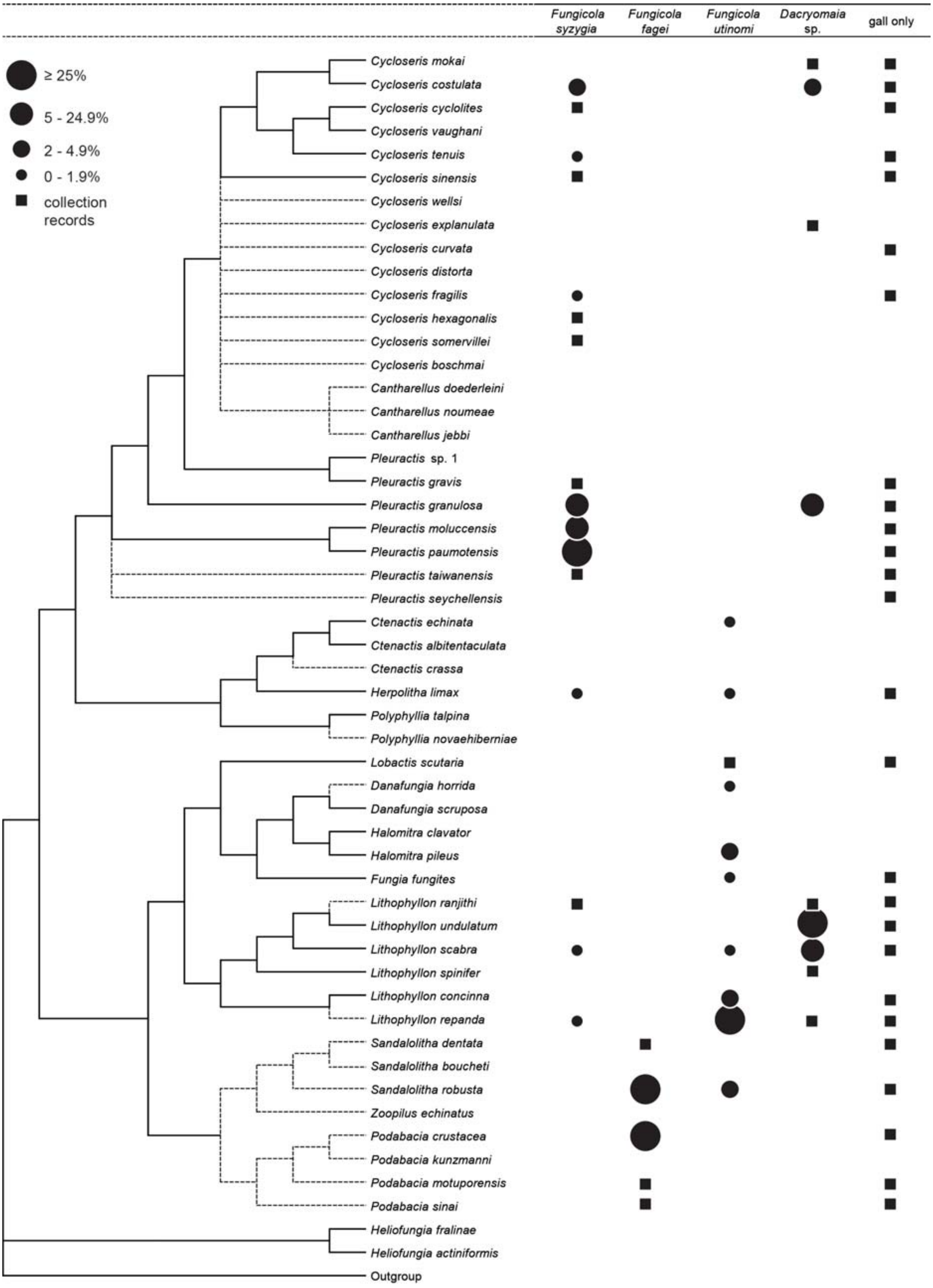

Fig. 2. Cladogram of the Fungiidae (based on Gittenberger *et al.,* 2011; Benzoni *et al.,* 2012), combined with gall crab associations. Percentages portray how the gall crabs are distributed over their coral hosts: *Fungicola syzygia* (n = 316), *F. fagei* (n = 4), *F. utinomi* (n = 82), and *Dacryomaia* sp. (n = 29). Other records based on collection data (Table 1) and fieldwork other than SW Sulawesi. All fungiid-gall crab associations resulting from fieldwork after 1994 are included as squares.

Table 2. Mushroom coral species (Fungiidae) acting as host for gall crab species in the Spermonde Archipelago, SW Sulawesi The number of collected coral specimens hosting specified gall crab species is given.

Coral host	*Fungicola syzygia*	*Fungicola fagei*	*Fungicola utinomi*	*Dacryomaia* sp.
Ctenactis echinata (Pallas, 1766)			1	
Cycloseris costulata (Ortmann, 1889)	8			1
C. fragilis (Alcock, 1893)	2			
C. tenuis (Dana, 1846)	1			
Danafungia horrida (Dana, 1846)			1	
Fungia fungites (Linnaeus, 1758)			1	
Halomitra pileus (Linnaeus, 1758)			3	
Herpolitha limax (Esper, 1797)	1		1	
Lithophyllon concinna (Verrill, 1864)			4	
L. repanda (Dana, 1846)	1		68	
L. scabra (Döderlein, 1901)	1		1	7
L. undulatum Rehberg, 1892				15
Pleuractis granulosa (Klunzinger, 1879)	49			6
P. moluccensis (Van der Horst, 1919)	40			
P. paumotensis (Stutchbury, 1833)	213			
Podabacia crustacea (Pallas, 1766)		1		
Sandalolitha robusta (Quelch, 1886)		3	2	

The programme can take multiple host associations into account, but occurrence levels are not supported, and therefore it was run twice: 1) on the complete dataset including all host specificity data, 2) on a dataset comprising only the common hosts (see Norton and Carpenter, 1998). In this second dataset sporadic host occurrences (singletons) were removed. In both runs the following settings were used (stats mode): 100 generations, population size 500, sample size 100. All other settings were left unchanged.

Results

Distribution based on historical records

Based on museum and literature records, distributions of Fungiidae-associated gall crabs range from Eilat in the Red Sea, and Kenya in the western Indian Ocean, towards Hawaii and Tahiti in the central Pacific Ocean (Table 1).

Occurrence records

Data on crab occurrences obtained from the belt quadrats in the Spermonde Archipelago, are projected on a cladogram of the Fungiidae (Table 2, Fig. 2). Percentages per host species are based on the number of encountered coral specimens per gall crab species. Fig. 1 shows gall crab dwellings in eight of their common gall crab hosts. *Fungicola fagei* was only found inhabiting corals belonging to the genera *Podabacia* and *Sandalolitha*, *F. syzygia* was predominantly found in corals of the genus *Pleuractis* and to a lesser extent in *Cycloseris*, whereas *Fungicola utinomi* was predominantly found in *Lithophyllon repanda*. *Dacryomaia* sp. mainly inhabits corals of the genera *Lithophyllon*, and was primarily associated with *L. undulatum*. It also occurs in the genera *Cycloseris* and *Pleuractis*. In the belt quadrats only one specimen of *Dacryomaia* sp. was recorded from the genus *Cycloseris*.

Host preferences and cophylogenetic analyses

The total number of Fungiidae associated with gall crabs is 35 (Fig. 2, Table S1). *Fungicola utinomi* is found to be associated with 10 mushroom corals species, *F. fagei* with five fungiids, and *F. syzygia* with 15 hosts. *Dacryomaia* sp., appears to be associated with nine fungiid species (Fig. 2, Table 2). *Cycloseris curvata* and *C. explanulata* are new host records. Hoeksema *et al*. (2012) recorded *Polyphyllia talpina* as a gall crab host. Further inspection of the material in the Naturalis collections revealed that this is likely not a gall crab dwelling, because the two pits in the host coral are interconnected and the surface of the dwelling is not smooth. These characteristics argue against a gall crab dwelling, and we therefore remove this coral species from the list of fungiid gall crab hosts until more evidence becomes available.

Based on the analysis in Jane 4.0 the complete dataset (Fig. S2) shows two duplication events, one cospeciation event, 34 losses and 37 failures to diverges. The smaller dataset (Fig. S4), comprised of only the common hosts, resulted in one duplication event, one duplication plus host switch event, one cospeciation event, 20 losses and 11 failures to diverge. Both results show that the costs of the random sample solutions are higher than the optimal [= cospeciation] solution (Figs S3, 5).

Discussion

Invertebrate taxa account for the greatest numerical abundance and diversity on coral reefs, yet have received rather little attention. Our awareness of coral reef ecosystem functioning is derived from what we know about a relative small proportion of coral reef species. Animals so closely associated with their habitat may be vital to the maintenance of critical ecological systems pertaining to coral health (Stella *et al.,* 2010), and as such could be potentially useful as environmental indicators (Thomas, 1993; Scaps and Denis, 2008).

In this study we used a phylogeny of the Fungiidae corals to map host preferences and occurrence rates. Using phylogenies to map ecologically meaningful traits of species is a fusion between ecology and evolution, also known as phylogenetic ecology or phylo-ecology (Westoby, 2006; Hoeksema, 2012a).

Distribution records

Until the late 1960s, the genus *Fungicola* was only known from Vietnam and since then just a few records became available from elsewhere (Takeda and Tamura, 1979; Kropp, 1990a, 1994). Van der Meij and Hoeksema (2013) and Van der Meij (2015a) added several new records of the genus in Indonesia and Malaysia. The present research on museum collections resulted in the availability of many additional records for all three *Fungicola* species (Table 1). During a short survey on the Great Barrier Reef off Cairns in May 2010 one specimen of *F. utinomi* was observed in *Lithophyllon repanda*, and individuals of *Fungicola* sp. were observed in *Pleuractis paumotensis* and *Herpolitha limax*. *Fungicola syzygia* is now reported from the Red Sea and Kenya in the west, to Japan and Vanuatu in the east, while *F. fagei* and *F. utinomi* are now recorded from Vietnam and Indonesia in the west, to Japan and possibly Australia (GBR) in the east. *Dacryomaia* sp. is recorded from the heart of the Coral Triangle: Indonesia and Malaysia (Table 1-2). The Indo-Pacific mushroom coral *Lobactis scutaria*, host to *Fungicola utinomi*, was brought to Jamaica from Eilat in 1966 and has established an apparently viable population (Bush *et al.,* 2004). So far no gall crabs have been reported for this population, which seems unlikely given current day ocean currents.

Hoeksema and Gittenberger (2008) report that coral gall crabs appear to be abundant in Nha Trang, Vietnam, especially in *Podabacia crustacea* and *Lithophyllon repanda*. Based on their results, the gall crab fauna in Vietnam likely consists of *Fungicola fagei* and *F. utinomi*, which is in agreement with the reports by Fize and Serène (1956a, b; 1957). According to Takeda and Tamura (1979), *F. utinomi* is more common in Japan than *F. fagei*, of which only two specimens are known. Based on Van der Meij (2015a) the identification of *F. fagei* by Takeda and Tamura (1979) should most likely be corrected to *F. syzygia*. The main hosts of *F. fagei* are, however, also present in Japan (Hoeksema, 1989). It is unclear whether the findings of Takeda and Tamura (1979) are caused by undersampling of particular species of mushroom coral hosts or by lower occurrence rates of *F. fagei* and *F. syzygia*. The genus *Dacryomaia* has been recorded from non-fungiid corals at the Ryukyu Islands (Japan), Caroline Isl. (Kiribati), Guam and other Mariana Isl. (Table 1), however, these records most likely concern *D. japonica*, *D. edmonsoni* and/or further undescribed species (Paulay *et al.,* 2003, van der Meij unpubl. data).

There appears to be much overlap in the geographical distribution of the mushroom corals and fungiid-associated gall crabs (Hoeksema, 1989; Table 2). The distribution ranges of the gall crab species is likely even more extensive. Presumably rare species, or species with a disjunct distribution, may be represented in scientific coral collections without being noticed. This confirms the value of historical collection material for biogeographical research, since museum specimens may show that species display a greater distribution range than previously assumed (Drew, 2011; Hoeksema *et al.,* 2011; van der Meij and Visser, 2011).

Occurrence records

The results of the belt quadrats in the Spermonde Archipelago show that the percentage of encountered gall crabs appears to be linked to the relative occurrence of their host corals. The coral species for which most gall crabs are reported are also among the most commonly occurring mushroom corals, i.e. *Lithophyllon repanda*, *Pleuractis granulosa*, *P. moluccensis* and *P. paumotensis* (see Hoeksema, 2012b). However, some common mushroom corals are not frequently inhabited by gall crabs (e.g. *Halomitra pileus*, *Lobactis scutaria*, *Sandalolitha dentata*), whereas others appear to be associated with one or more species (Table 2). Small and/or thin species (e.g. *Cycloseris boschmai*, *C. distorta*, *Halomitra clavator, Zoopilus echinatus*), those with fleshy polyps and permanently extending tentacles (e.g. *Heliofungia* spp., *Polyphyllia* spp.), or rarely observed species (e.g. *Cantharellus* spp., *Podabacia kunzmanni*, *Sandalolitha boucheti*) are not yet found to be associated with gall crabs.

Host preferences and cophylogenetic analyses

The total number of fungiid species inhabited by gall crabs is now 35 (Table S1). *Cycloseris explanulata* and *C. wellsi* were not yet included in the Fungiidae (Benzoni *et al.,* 2012) during most of the present research and were therefore also not considered as potential host for fungiid-associated gall crabs. This likely lead to under-sampling of these coral hosts. *Polyphyllia talpina* is no longer considered to be a gall crab host. This is in line with previous observations that gall crabs are mostly not observed in coral species with fleshy polyps and large tentacles (e.g. Van der Meij, 2014a).

Recently the coral family Fungiidae was revised based on a molecular analysis (Gittenberger *et al.,* 2011). The majority (95%) of *Fungicola syzygia* specimens was encountered in *Pleuractis* corals, i.e. *P. paumotensis*, *P. granulosa*, and *P. moluccensis* (Fig. 2). Apart from the genus *Pleuractis*, this gall crab species also occurs in the closely related genus *Cycloseris*. *Fungicola utinomi* is in almost all cases associated with *Lithophyllon repanda*, but occurs to a lesser extent in corals belonging to other genera. None of the inhabited fungiids were simultaneously occupied by more than one gall crab species, but one host species, *Lithophyllon scabra*, was found inhabited by either one of the three gall crab species. The sporadic selection of certain corals as a host might be related to a low availability of the common or 'preferred' host species at a certain locality. It might also be the result of a collecting artefact, as it remains possible that host occurrence has geographic variability.

Dacryomaia sp. mostly targets *Lithophyllon undulatum*, and to a lesser extent *L. scabra*, and *Pleuractis granulosa*. Other species in the genus *Dacryomaia* are associated with the genera *Coscinaraea* (Coscinaraeidae), *Leptastrea* (Scleractinia *incertae sedis*), and *Psammocora* (Psammocoridae) (Kropp, 1990a, van der Meij, unpubl. data). This is likely not a coincidence, since these genera are closely related to the Fungiidae (Fukami *et al.,* 2008; Kitahara *et al.*, 2010; Huang, 2012). The genus *Dacryomaia*, which contains undescribed species, is in need of a taxonomic revision (Paulay *et al.,* 2003, van der Meij, unpubl. data). Further research on the gall crabs of this genus and their host preferences may be used to verify congruencies of the phylogenetic relationships of the associated fauna and their hosts as support for reconstructed phylogenetic relationships within the Scleractinia.

The analyses in Jane 4.0 show that there have been cospeciation and duplication events between fungiids and their gall crab inhabitants, as well as several losses and failures to diverge. Differences between the outcomes of the analysis on the complete dataset vs the common host dataset can be explained by the settings of the programme Jane. Associations between host and symbiont are not weighed, hence single recorded associations are given the same value in the analysis, obscuring the overall patterns between host and symbiont. Both analyses show that even within a moderately small coral family like the Fungiidae with just over 50 species (Gittenberger *et al.,* 2011; Benzoni *et al.,* 2012a), four gall crab associates occupy their own niche and are host-specific to a certain degree. *Fungicola fagei* appears to be more strict in its host preference than the other three species. The large-scale phylogeny reconstruction of all gall crabs and their coral hosts provides more insight in the cospeciation between these associates and their hosts. Gall crabs are mostly host specific on coral genus level, which explains the high number of losses and failures to divergence in the Jane analysis. The relationship between Scleractinia and Cryptochiridae appears to be so tight that gall crabs can be used as phylogenetic indicators of scleractinian evolution (van der Meij, 2015a), which contradicts the hypothesis of Kropp and Manning (1987) that the generic identity of coral hosts is an unreliable character for defining gall crab genera.

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Appendices S1-5 are available upon request.