

A new host and range record for the gall crab *Fungicola fagei* as a symbiont of the mushroom coral *Lobactis scutaria* in Hawai'i

By Bert W. Hoeksema*, Roland Butôt and Jaaziel E. García-Hernández

Abstract

The coral crab *Fungicola fagei* (Decapoda: Brachyura: Cryptochiridae) is recorded for the first time from the Hawaiian Islands, where it was discovered in a previously unknown association with the solitary, free-living mushroom coral *Lobactis scutaria* (Anthozoa: Scleractinia: Fungiidae). The associated crab species was discovered off Hilo on the island of Hawai'i, where it appeared to be relatively common. It could have been previously overlooked because of its small size (max. ca. 1 cm long) and its hidden life style inside the host coral. Species identification is based on the morphology of the carapace and use of the cytochrome oxidase subunit I (COI) barcode gene as molecular marker. *Fungicola fagei* is known from other localities in the Indo-West Pacific region, where it is only hosted by mushroom coral species of the genera *Podabacia* and *Sandalolitha*. The record of *F. fagei* from the Hawaiian Islands represents a northeastward extension of its known geographical distribution range, 6,000 km away from its nearest locality in Vanuatu, despite the availability of host species as eastward as the Cook Islands and French Polynesia. Since these other host species do not occur in the Hawaiian Islands, *F. fagei*'s occurrence here is only possible because of its association with *L. scutaria*, uniquely recorded from Hawai'i.

*Corresponding Author E-mail: bert.hoeksema@naturalis.nl

This **early view** paper has been peer-reviewed and accepted for publication in *Pacific Science*. However, it has not been copy-edited nor has it undergone typesetting for *Pacific Science*. The final published paper will look different due to formatting changes, but scientific content will remain the same.

Introduction

Lobactis scutaria (Lamarck, 1801) is a solitary, free-living scleractinian coral of the family Fungiidae, which shows a wide distribution range in the Indo-West Pacific region, from the Red Sea to the Hawaiian Islands, and French Polynesia (Hoeksema 1989, Gittenberger et al. 2011). It is the largest and most common mushroom coral in the Hawaiian Archipelago, where it was traditionally known as *Fungia scutaria* (Edmondson 1946, Maragos 1977, Hoover 1999, Fenner 2005). This species has been used in coral reef research in Kaneohe Bay and Waikiki Reef (O'ahu Island) or in laboratory experiments with specimens taken from these localities, which has resulted in numerous publications on its ecology and physiology over a long period of time (a.o. Edmondson 1929, Stephens 1962, Bosch 1976, Yamazato 1970, Pearse 1971, Jokiel and Cowdin 1976, Krupp 1982, 1983, 1984, 1985, Chadwick 1988, Romano 1988, Krupp et al. 1993, 2006, Jokiel and Bigger 1994, Schwarz et al. 1999, Weis et al. 2001, Hagedorn et al. 2006, Concepcion et al. 2010, Schnitzer et al. 2012). Additional references can be found in the work by Coles et al. (2002).

Despite all the research on *Lobactis scutaria* in the Hawaiian Islands, limited attention has been given to its associated fauna. For example, Bosch (1965) and Bell (1985) reported on epitoniid snails and their egg capsules found on the undersurface of several *L. scutaria* corals in Kaneohe Bay, O'ahu, which probably feeds on its host's tissue and can be considered parasitic. They were described as *Epitonium ulu* Pilsbry, 1921, with Hilo at Hawai'i as type locality (Pilsbry 1921, Edmondson 1946). Now, this gastropod is classified as *Epifungium ulu* and considered widespread in the Indo-West Pacific region, where it has been recorded from 11 mushroom coral species (Gittenberger and Gittenberger 2005, Gittenberger and Hoeksema 2013).

Furthermore, Maragos (1977) mentions that small xanthid crabs find shelter underneath mushroom corals in the Hawaiian Islands. Finally, Van der Meij et al. (2015a) reported on empty galls of cryptochirids found in museum specimens of *L. scutaria* from Hawai'i, which were assigned to *Fungicola* sp. In an earlier review paper, Hoeksema et al. (2012) reported on two gall crab species, *Fungicola fagei* (Fize and Serène, 1956) and *F. utinomi* (Fize and Serène, 1956) in association with *L. scutaria*, but they did not give specific locality data or references. In a successive, more elaborate study on cryptochirids associated with mushroom corals, Van der Meij (2015a) mentioned that *F. fagei* crabs were only known to dwell in corals of *Podabacia* and *Sandalolitha* and that *F. utinomi* crabs were hosted by corals of *Ctenactis*, *Danafungia*, *Fungia*, *Halomitra*, *Lithophyllon*, and *Sandalolitha*, whereas *F. syzygia* Van der Meij, 2015, was predominantly associated with *Cycloseris* and *Pleuractis*. Hence, there was no certainty about which gall crab species lived in association with *Lobactis* in the Hawaiian Islands and no occurrence records of this association are known from elsewhere.

During exploratory dives at the reef off Leleiwi Beach, Hilo, Hawai'i in July 2016, the last author (JEGH) came across numerous mushroom corals of *Lobactis scutaria* and of another solitary, free-living mushroom coral species, *Pleuractis granulosa* (Klunzinger, 1879). Individuals of *L. scutaria* were very common and many of them contained visible injuries (Figure 1). Closer inspection revealed that these injuries were gall crab dwellings and that most of them contained living crabs. This finding offered the opportunity to investigate the identity of the gall crab species associated with *L. scutaria*, which so far has remained unknown.

<<Fig. 1 near here>>

MATERIALS AND METHODS

Mushroom corals off Leleiwi Beach, Hilo, Island of Hawai'i (19°44'05.6"N, 155°01'00.1"W) were observed and photographed *in situ* at ca. 10-15 m depth (July 4th, 2016). Individuals

containing galls of cryptochirids were investigated more closely. A total of six crabs (two females and four males) were extracted from the corals with the help of a forceps and stored in 96% ethanol. The crabs were brought to the laboratory for identification by morphological examination and molecular analyses based on the cytochrome oxidase subunit I (COI) barcoding gene as marker. Close-up photographs of the crabs were made with a Carl Zeiss Discovery V20 stereo microscope equipped with a Axiocam Mrc5 camera for stacking photography.

Genomic DNA was extracted using the Macherey-Nagel NucleoMag® 96 Tissue Kit and the KingFisher Flex (Thermo Scientific). One leg of a gall crab was used for the DNA extraction and was lysed overnight in Lysis buffer T1 and Proteinase K at 56°C. A PCR was carried out by using a M13-LepFol primer mix (M13F-LepFolF mix and M13R-LepFolR mix) with an amplification product between the primers of 658 bp M13-LepfolF primer mix was a mix of M13F-LepF1 and M13F-LCO1490 and M13-LepFolR primer mix was a mix of M13R-LepR1 and M13R-HCO2198 (Folmer et al. 1994, Herbert et al. 2004). A PCR amplification of the mitochondrial cytochrome oxidation subunit I was performed in a volume of 25 µl containing 2 µl DNA template, 2.5 µl of 10x PCR Coraload buffer (Qiagen), 0.5 µl of 10 µM of each primer, 0.5 µl of 2.5 mM dNTP and 0.25 µl of 5 U/µl Taq DNA polymerase (Qiagen) under standard PCR conditions (initial denaturation at 94°C for 3 min, 40 cycles of: denaturation at 94°C for 15 sec, annealing at 50°C for 30 sec and elongation at 72°C for 40 sec and a final elongation step at 72°C for 5 min). PCR products were visualized by agarose gel electrophoresis (2% agarose E-Gel, Invitrogen) and suitable amplicons were sequenced by Baseclear Leiden using the M13 primers (forward and reverse sequencing). Four out of six sequences were successful. The raw sequences were edited by using Geneious software (version 8.1.8). For the purpose of molecular identification, a Neighbor-Joining tree was constructed to show the phylogenetic affinities of the crabs from Hawai'i, along with all three *Fungicola* species recognized so far (Van der Meij et. al.

2015a). Data are derived from GenBank (NCBI) based on specimens from Southeast Asia and the West Pacific (Van der Meij 2015a). Since *Fungicola fagei* and *F. syzygia* together form a sister group of *F. utinomi* (Van der Meij 2015a), the latter was selected as outgroup.

The six specimens have been deposited in the collections of the Bernice B. Bishop Museum in Honolulu (BPBM) and Naturalis Biodiversity Center (previously known as Rijksmuseum van Natuurlijke Historie) in Leiden (RMNH). The following catalog numbers were assigned, BPBM-S17057 (one female and one male), RMNH.CRUS.D.57237 (one female), RMNH.CRUS.D.57238 (one male), RMNH.CRUS.D.57239 (one male), RMNH.CRUS.D.57240 (one male). The latter four had sequences that were deposited in Genbank (NCBI) under accession numbers MF973150-MF973153.

RESULTS

Based on the association with mushroom corals (Figure 1), the crabs could be identified at family level as belonging to the Cryptochiridae. The elongated pits were wedged in between the host's septa, with the crabs themselves in perpendicular position (Figure 1f). These dwellings were similar to those made by *Fungicola* crabs in corals of *Cycloseris* and *Pleuractis* (Van der Meij et al. 2015a: Figure 1). Most crabs lived as a pair consisting of a large female and a small male (Figure 1a, c, d, f), whereas others lived alone (Figure 1b, e). The females were about 8–11 mm long and the males 3–4 mm, a ratio of ca. 3:1 (Figure 2). The upper surface of the female carapace shows a keyhole-shaped sculpture (Figures 2a, c), which is also seen in *Fungicola fagei* (Van der Meij 2015a: Figures 1A, 4A) but not in its congeners.

<<Fig. 2 near here>>

In the COI-based phylogenetic tree, all four crabs from Hawai'i clustered with specimens of *F. fagei* found in corals of the fungiid genera *Podabacia* and *Sandalolitha*, which were collected from Indonesia, Malaysia and New Caledonia (Figure 3). Hence, results of the

molecular analysis are consistent with those of the morphological examination, confirming the crab's identity as *F. fagei*.
<<Fig. 3 near here>>

DISCUSSION

Gall crabs belonging to the genus *Fungicola* were previously unknown from the Hawaiian Islands, except for the listing by Hoeksema et al. (2012). Until now, only four gall crab species (family Cryptochiridae) were previously recognized from the Hawaiian Islands (Kropp 1989, 1990, Castro 2011): (1) *Hapalocarcinus marsupialis* Stimpson, 1859, associated with corals of the scleractinian family Pocilloporidae, (2) *Opecarcinus crescentus* (Edmondson, 1925), known from corals of the genus *Pavona* (Agariciidae), (3) *Pelycomaia minuta* (Edmondson, 1933), found in corals of the scleractinian genera *Cyphastrea* (family Merulinidae) and *Leptastrea* (family incertae sedis), and (4) *Utinomiella dimorpha* (Henderson, 1906) in association with pocilloporid corals. Hence, *F. fagei* is the fifth cryptochirid species recorded from the Hawaiian Islands.

The new record is also an addition to the known associated fauna of *L. scutaria*. Besides the parasitic snail *Epifungium ulu*, *L. scutaria* is known to host various other invertebrates. It has been observed to host three barnacle species, an excavating mytilid bivalve, a coralliophiliid snail, and a hydroid (Gittenberger and Gittenberger 2011, Hoeksema et al. 2012, Montano et al. 2015).

Until now, the easternmost record of *F. fagei* is from New Caledonia and Vanuatu (Figure 4), where it was reported from the corals *Podabacia motuporensis* Veron, 1990 and *Sandalolitha robusta* (Quelch, 1886), respectively (Van der Meij 2015a, Van der Meij et al. 2015a). Hawai'i is about 6,000 km away from the nearest locality of *F. fagei* at Vanuatu (Figure 4). Other *F. fagei* host records concern *Podabacia crustacea* (Pallas, 1766) from eastern Indonesia and northeast Borneo (Malaysia), *Podabacia sinai* Veron, 2000 from Palau, and *Sandalolitha dentata* Quelch,

1884, also from northeast Borneo. Some of the coral species themselves have more eastward distribution localities, such as *P. crustacea* in French Polynesia (Hoeksema 1989), *S. dentata* in the Marshall Islands, Caroline Islands and French Polynesia (Hoeksema 1989, Hoeksema and Benzoni 2013), and *S. robusta* in the Cook Islands (Hoeksema 1989). *Fungicola fagei* may occur at these localities, in which case it has been overlooked, like previously in Hawai'i. Other easternmost records for *Fungicola* concern *F. syzygia* from French Polynesia (Van der Meij et al. 2015a) and *F. utinomi* from Guam and Palau (Kropp 1990, Paulay et al. 2003).

<<Fig. 4 near here>>

The present record for *F. fagei* is not only unique because of the eastward extension of its known distribution range, but also because *L. scutaria* is documented as newly recorded host coral (Figure 1). Extensive surveys of the mushroom coral fauna have been performed in various localities in eastern Indonesia and eastern Malaysia, where *L. scutaria* is most common on offshore reefs: the Spermonde Archipelago, South Sulawesi (Hoeksema 2012a,b), Ternate, Moluccas (Gittenberger et al. 2015), Kudat and Semporna, Sabah (Waheed and Hoeksema 2013, Waheed et al. 2015). Corals at the same localities were also searched for cryptochirids, which did not result in host records for *L. scutaria* (Van der Meij and Hoeksema 2013, Van der Meij et al. 2015a). Unfortunately, we have no occurrence data on *F. fagei* from localities between Palau/Vanuatu and Hawai'i. Nevertheless, the Hawaiian crabs appear closely related to those from remote localities (Figure 3), which indicates that they may have been introduced relatively recently.

It is important to note that the population of *F. fagei* would not have been able to establish and maintain itself at Hawai'i without a host switch to *L. scutaria* from *Podabacia/Sandalolitha* spp., which are absent in the Hawaiian Islands. The reverse is unlikely because then *L. scutaria* would also have been found as host in other investigated areas. Because *Lobactis* is not directly related to *Podabacia/Sandalolitha*, and elsewhere it is unknown to serve as host for *F. fagei*, it is

also not likely that this association originated in a shared ancestral host taxon. A host switch is therefore more probable but it is unclear when and where this could have happened, either in the Hawaiian Islands or in localities more westward. Host switches have also been reported from other crustacean taxa, such as pea crabs (Becker and Turkey 2017), xanthid crabs (García-Hernández et al. 2016), and palaemonid shrimps (Brinkmann and Fransen 2016, Horká et al. 2016, Hoeksema and Fransen 2017).

Since *F. fagei* appears to be common at Hawai'i, it is likely that this association also occurs at other islands throughout the Hawaiian Archipelago. The absence of field records despite a long research history concerning its host at O'ahu is probably due to a lack of focus on coral-associated fauna. Cryptochirid crabs are small and live concealed inside their pits and therefore they are usually not easily noticed (Hoeksema 2017), except perhaps when they appear in extremely high densities (Hoeksema and Van der Meij 2013). Recent research targeting coral gall crabs resulted in the discovery of various new species (Badaro et al. 2012, Zayas et al. 2013, Van der Meij 2014a, 2015b, 2017, Van der Meij et al. 2015b) and new host records (Van der Meij 2012, 2014b, Hoeksema et al. 2017). Likewise, recent surveys on mushroom coral hosts have also led to new discoveries of associated fauna, including some undescribed species, such as a benthic ctenophore (Hoeksema et al. 2013, Alamaru et al. 2016), a serpulid worm (Hoeksema and Ten Hove 2014), a hydroid (Montano et al. 2015), and cryptobenthic fishes (Bos and Hoeksema 2015, 2017). The present discovery, will undoubtedly be succeeded by new observation records of *F. fagei* and perhaps of other coral-associated fauna within the Hawaiian Archipelago. Because of its common occurrence in Hawai'i, the abundance of the association between *F. fagei* and *L. scutaria* could become the subject of in-depth ecological studies.

ACKNOWLEDGMENTS

JEGH is grateful to SeaGrant Puerto Rico for providing travel funds to attend and present at the 13th International Coral Reef Symposium in Honolulu, which also allowed for field work to take place on the Island of Hawai'i. JEGH thanks Anna Baker Mikkelsen, Jean Devine, Nick Vanderzyl, and Zac Higgins, for assisting in SCUBA diving. Lastly, and wholeheartedly, JEGH thanks the Ogata family (Crystal, Skyler, Shani, and Royce) for hosting him at their home, and would like to dedicate this work to Skyler Ogata, a true Hawaiian warrior who left us unexpectedly too soon. Holly Bollick (BPBM) and Karen van Dorp (RMNH) assigned museum catalog numbers. Charles Fransen constructed the phylogenetic tree. Kees van den Berg assisted with the microscopic photography. Erik-Jan Bosch made the final version of the distribution map. Three anonymous reviewers provided constructive comments, which helped to improve the manuscript.

LITERATURE CITED

- Alamaru, A, E. Brokovich, and Y. Loya. 2016. Four new species and three new records of benthic ctenophores (Family: Coeloplanidae) from the Red Sea. *Mar. Biodivers.* 46:261–279.
- Badaro, M. F. S., E. G. Neves, P. Castro, and R. Johnsson. 2012. Description of a new genus of Cryptochiridae (Decapoda: Brachyura) associated with *Siderastrea* (Anthozoa: Scleractinia), with notes on feeding habits. *Sci. Mar.* 76:517–526.
- Becker, C., and M. Turkey. 2017. Host specificity and feeding in European pea crabs (Brachyura: Pinnotheridae). *Crustaceana* 90:819–844.
- Bell, J. L. 1985. Larval growth and metamorphosis of a prosobranch gastropod associated with a solitary coral. *Proc. 5th Intern. Coral Reef Congr.* 5:159–164.
- Bos, A. R., and B. W. Hoeksema. 2015. Cryptobenthic fishes and co-inhabiting shrimps associated with the mushroom coral *Heliofungia actiniformis* (Fungiidae) in the Davao Gulf, Philippines. *Environ. Biol. Fish.* 98:1479–1489.

- Bos, A. R., and B. W. Hoeksema. 2017. Mushroom corals (Fungiidae) in the Davao Gulf, Philippines, with records of associated fish and other cryptofauna. *Raffles Bull. Zool.* 65:198–206.
- Bosch, H. F. 1965. A gastropod parasite of solitary corals in Hawaii. *Pac. Sci.* 19:267–268.
- . 1967. Growth rate of *Fungia scutaria* in Kaneohe Bay, Oahu. M.Sc. thesis, University of Hawaii, Honolulu.
- Brinkmann, B. W., and C. H. J. M. Fransen. 2016. Identification of a new stony coral host for the anemone shrimp *Periclimenes rathbunae* Schmitt, 1924 with notes on the host-use pattern. *Contrib. Zool.* 85:437–456.
- Castro, P. 2011. Catalog of the anomuran and brachyuran crabs (Crustacea: Decapoda: Anomura, Brachyura) of the Hawaiian Islands. *Zootaxa* 2947:1–154.
- Chadwick, N. E. 1988. Competition and locomotion in a free-living fungiid coral. *J. Exp. Mar. Biol. Ecol.* 123:189–200.
- Coles, S. L., R. C. DeFelice, and L. G. Eldredge. 2002. Nonindigenous marine species in Kaneohe Bay, O’ahu, Hawai’i. Bishop Mus. Tech. Rep. 24.
- Concepcion, G. T., N. R. Polato, I. B. Baums, R. J. Toonen. 2010. Development of microsatellite markers from four Hawaiian corals: *Acropora cytherea*, *Fungia scutaria*, *Montipora capitata* and *Porites lobata*. *Conserv. Genet. Resour.* 2:11–15.
- Edmondson, C. H. 1929. Growth of Hawaiian corals. Bishop Mus. Bull. 58:1–38, pls. 1–5.
- . 1946. Reef and shore fauna of Hawaii. Bishop Mus. Spec. Pub. 22:1–381.
- Fenner, D. 2005. Corals of Hawai’i. A fieldguide to the hard, black and soft corals of Hawai’i and the Northwest Hawaiian islands, including Midway. Mutual Publishing, Honolulu.
- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol* 3:294–299.
- García-Hernández, J. E., J. D. Reimer, and B. W. Hoeksema. 2016. Sponges hosting the zoantharia-associated crab *Platypodiella spectabilis* at St. Eustatius, Dutch Caribbean. *Coral Reefs* 35:209.
- Gittenberger, A., and E. Gittenberger. 2005. A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated-with corals (Scleractinia). *Contrib. Zool.* 74:125–203.

- Gittenberger, A., and E. Gittenberger. 2011. Cryptic, adaptive radiation of parasitic snails: sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. *Org. Divers. Evol.* 11:21–41.
- Gittenberger, A., and B. W. Hoeksema. 2013. Habitat preferences of coral-associated wentletrap snails (Gastropoda: Epitoniidae). *Contrib. Zool.* 82:1–25
- Gittenberger, A., B. T. Reijnen, and B. W. Hoeksema. 2011. A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contrib. Zool.* 80:107–132.
- Gittenberger, A., S. G. A. Draisma, U. Y. Arbi, V. Langenberg, P. L. A. Erftemeijer, Y. Tuti, and B. W. Hoeksema. 2015. Coral reef organisms as bioregion indicators off Halmahera, Moluccas, Indonesia. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 25:743–755.
- Hagedorn, M., V. L. Carter, R. A. Steyn, D. Krupp, J.C. Leong, R.P. Lang, and T.R. Tiersch. 2006. Preliminary studies of sperm cryopreservation in the mushroom coral, *Fungia scutaria*. *Cryobiology* 52:454–458.
- Herbert, P. D. N., E. H. Penton, J. M. Burns, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Natl Acad. Sci. U.S.A.* 101:14812–14817.
- Hoeksema, B. W. 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zool. Verh.* 254:1–295.
- . 2012a. Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. *Raffles Bull. Zool.* 60:183–212.
- . 2012b. Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). *Contrib. Zool.* 81:199–221.
- . 2017. The hidden biodiversity of tropical coral reefs. *Biodiversity* 18:8–12.
- Hoeksema, B. W., and F. Benzoni. 2013. Multispecies aggregations of mushroom corals in the Gambier Islands, French Polynesia. *Coral Reefs* 32:1041.
- Hoeksema, B. W., and C.-F. Dai. 1991. Scleractinia of Taiwan: II. Family Fungiidae (including a new species). *Bull. Inst. Zool. Acad. Sin.* 30:203–228.
- Hoeksema, B. W., and C. H. J. M. Franssen. 2017. Host switch by the Caribbean anemone shrimp *Periclimenes rathbunae* in Curaçao. *Coral Reefs* 36:607.

- Hoeksema, B. W., and H. A. ten Hove. 2014. First record of a christmas tree worm in a mushroom coral (Loyalty Islands, Southwest Pacific). *Coral Reefs* 33:717.
- Hoeksema, B. W., and S. E. T. van der Meij. 2013. Gall crab city: an aggregation of endosymbiotic crabs inhabiting a colossal colony of *Pavona clavus*. *Coral Reefs* 32:59.
- Hoeksema, B. W., S. E. T. van der Meij, and C. H. J. M. Fransen. 2012. The mushroom coral as a habitat. *J. Mar. Biol. Assoc. U.K.* 92:647–663.
- Hoeksema, B. W., Z. Waheed, and A. Alamaru. 2013. Out of sight: aggregations of epizoic comb jellies underneath mushroom corals. *Coral Reefs* 32:1065.
- Hoeksema, B. W., M. van Beusekom, H. A. ten Hove, V. N. Ivanenko, S. E. T. van der Meij, and G. W. N. M. van Moorsel. 2017. *Helioseris cucullata* as a host coral at St. Eustatius, Dutch Caribbean. *Mar. Biodivers.* 47:71–78.
- Horká, I., S. de Grave, C. H. J. M. Fransen, A. Petrusek, and Z. Ďuriš. 2016. Multiple host switching events shape the evolution of symbiotic palaemonid shrimps (Crustacea: Decapoda). *Sci. Rep.* 6:26486.
- Hoover, J. P. 1999. Hawai'i's sea creatures. A guide to Hawai'i's marine invertebrates. Mutual Publishing, Honolulu.
- Jokiel, P. L., and C. H. Bigger. 1994. Aspects of histocompatibility and regeneration in the solitary reef coral *Fungia scutaria*. *Biol. Bull.* 186:72–80.
- Jokiel, P. L., and H. P. Cowdin, 1976. Hydromechanical adaptation in the solitary free-living coral *Fungia scutaria*. *Nature* 262:212–213.
- Kropp, R. K. 1989. A revision of the Pacific species of gall crabs, genus *Opecarcinus* (Crustacea: Cryptochiridae). *Bull. Mar. Sci.* 45:98–129.
- . 1990. Revision of the genera of gall crabs (Crustacea: Cryptochiridae) occurring in the Pacific Ocean. *Pac. Sci.* 44:417–448.
- Krupp, D. A. 1982. The composition of the mucus from the mushroom coral *Fungia scutaria*. *Proc. 4th Int. Coral Reef Symp.* 2:9–73.
- . 1983. Sexual reproduction and early development of the solitary coral *Fungia scutaria* (Anthozoa: Scleractinia). *Coral Reefs* 2:159–164.
- . 1984. Mucus production by corals exposed during an extreme low tide. *Pac. Sci.* 38:1–11.
- . 1985. An immunochemical study of the mucus from the solitary coral *Fungia scutaria* (Scleractinia, Fungiidae). *Bull. Mar. Sci.* 36:163–176.

- Krupp, D. A., P. L. Jokiel, and T. S. Chartrand. 1993. Asexual reproduction by the solitary scleractinian coral *Fungia scutaria* on dead parent coralla in Kaneohe Bay, Oahu, Hawaiian Islands. Proc. 7th Int. Coral Reef Symp. 1:527–534.
- Krupp, D., L. Hollingsworth, and J. Peterka. 2006. Elevated temperature sensitivity of fertilization and early development in the mushroom coral *Fungia scutaria* Lamarck 1801. Proc. 10th Int. Coral Reef Symp. 1:71–77.
- Maragos, J. E. 1977. Order Scleractinia. Stony corals. Pages 158–241 in D. M. Devenay and L. G. Eldredge, eds. Reef and shore fauna of Hawaii, Section 1: Protozoa through Ctenophora. Bishop Mus. Spec. Publ. 64 (1).
- Montano, S., D. Seveso, P. Galli, S. Puce, and B. W. Hoeksema. 2015. Mushroom corals as newly recorded hosts of the hydrozoan symbiont *Zanclaea* sp. Mar. Biol. Res. 11:773–779.
- Paulay, G., R. Kropp, P. K. L. Ng, and L. G. Eldredge. 2003. The crustaceans and pycnogonids of the Mariana Islands. Micronesica 35–36:456–513.
- Pearse, V. B. 1971. Sources of carbon in the skeleton of the coral *Fungia scutaria*. Pages 239–245 in H. M. Lenhof, L. Muscatine, and L. V. Davis, eds. Experimental Coelenterate Biology. University of Hawai‘i Press, Honolulu.
- Pilsbry, H. A. 1921. The marine molluscs of Hawaii XIV, XV. Proc. Acad. Nat. Sci. Phila. 72:360–382.
- Romano, S. L. 1988. Evolutionary game theory applied to interspecific aggression among corals: Are corals really bullies? Pac. Sci. 42:131.
- Schnitzler, C. E., L. L. Hollingsworth, D. A. Krupp, and V. M. Weis. 2012. Elevated temperature impairs onset of symbiosis and reduces survivorship in larvae of the Hawaiian coral, *Fungia scutaria*. Mar. Biol. 159:633–642.
- Schwarz, J. A., D. A. Krupp, and V. M. Weis. 1999. Late larval development and onset of symbiosis in the scleractinian coral *Fungia scutaria*. Mar. Biol. 196:70–79.
- Stephens, G. C. 1962. Uptake of organic material by aquatic invertebrates. I. Uptake of glucose by the solitary coral, *Fungia scutaria*. Biol. Bull. 123:648–659.
- van der Meij, S. E. T. 2012. Host preferences, colour patterns and distribution records of *Pseudocryptochirus viridis* Hiro, 1938 (Decapoda, Cryptochiridae). Crustaceana 85:769–777.

- . 2014a. A new species of *Opecarcinus* Kropp & Manning, 1987 (Crustacea: Brachyura: Cryptochiridae) associated with the stony corals *Pavona clavus* (Dana, 1846) and *P. bipartita* Nemenzo, 1980 (Scleractinia: Agariciidae). *Zootaxa* 3869:44–52.
- . 2014b. Host species, range extensions, and an observation of the mating system of Atlantic shallow-water gall crabs (Decapoda: Cryptochiridae). *Bull. Mar. Sci.* 90:1001–1010.
- . 2015a. Host relations and DNA reveal a cryptic gall crab species (Crustacea: Decapoda: Cryptochiridae) associated with mushroom corals (Scleractinia: Fungiidae). *Contrib. Zool.* 84:39–57.
- . 2015b. A new gall crab species (Brachyura, Cryptochiridae) associated with the free-living coral *Trachyphyllia geoffroyi* (Scleractinia, Merulinidae). *ZooKeys* 500:61–72.
- . 2017. The coral genus *Caulastraea* Dana, 1846 (Scleractinia, Merulinidae) as a new host for gall crabs (Decapoda, Cryptochiridae), with the description of *Lithoscaptus tuerkayi* sp. nov. *Crustaceana* 90:1027–1038.
- van der Meij, S. E. T., and B. W. Hoeksema. 2013. Distribution of gall crabs inhabiting mushroom corals on Semporna reefs, Malaysia. *Mar. Biodivers.* 43:53–59.
- van der Meij, S. E. T., C. H. J. M. Franssen, L. R. Pasman, and B. W. Hoeksema. 2015a. Phylogenetic ecology of gall crabs (Cryptochiridae) as associates of mushroom corals (Fungiidae). *Ecol. Evol.* 5:5770–5780.
- van der Meij, S. E. T., M. L. Berumen, and G. Paulay. 2015b. A new species of *Fizesereneia* Takeda & Tamura, 1980 (Crustacea: Brachyura: Cryptochiridae) from the Red Sea and Oman. *Zootaxa* 3931:585–595.
- Waheed, Z., and B. W. Hoeksema. 2013. A tale of two winds: Species richness patterns of reef corals around the Semporna peninsula, Malaysia. *Mar. Biodivers.* 43:37–51.
- Waheed, Z., H. G. J. van Mil, M. A. S. Hussein, R. Jumin, B. G. Ahad, and B. W. Hoeksema. 2015. Coral reefs at the northernmost tip of Borneo: An assessment of scleractinian species richness patterns and benthic reef assemblages. *PLoS ONE* 10:e0146006.

- Weis, V. M., W. S. Reynolds, and D. A. Krupp. 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.
- Yamazato, K. 1970. Calcification in a solitary coral, *Fungia scutaria* Lamarck in relation to environmental factors. *Bull. Sci. Eng. Div. Univ. Ryukyus (Math. Nat. Sci.)* 13:57–122.
- Zayasu, Y., K. Nomura, K. Seno, and A. Asakura. 2013. A new species of *Fizesereneia* Takeda & Tamura, 1980 (Crustacea: Decapoda: Brachyura: Cryptochiridae) from Japan. *Zootaxa*, 3681:257–269.

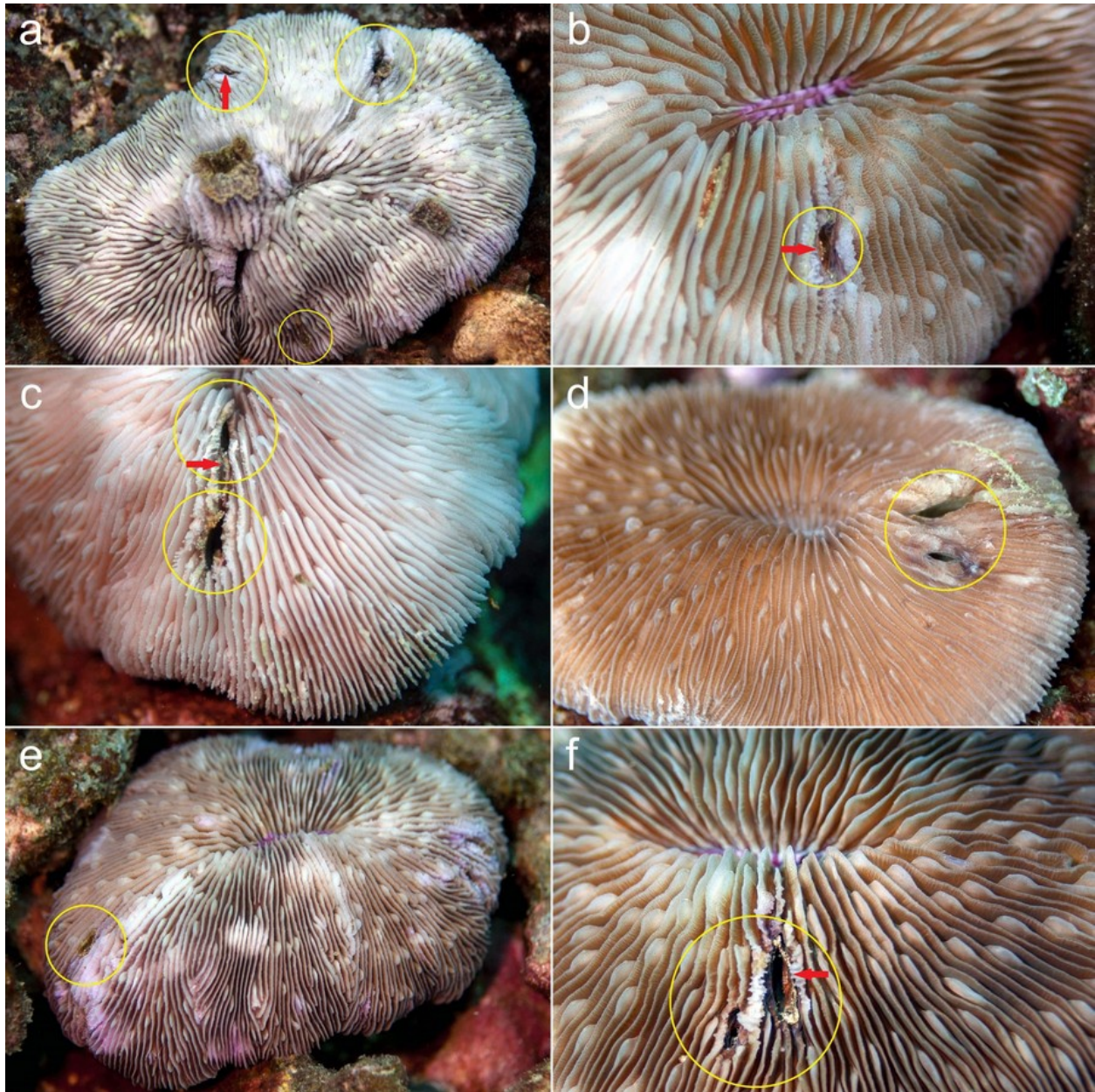


Figure 1. Gall grab dwellings (*Fungicola fagei*) in mushroom corals (*Lobactis scutaria*), Hilo, Hawai'i (marked by yellow circles). Crabs are marked by red arrows. a One coral containing two female crabs (at the top; BPBM-S17057, RMNH.CRUS.D.57237) and at least one male (bottom). b Host coral with one male crab, clearly visible (RMNH.CRUS.D.57238). c One host coral with two dwellings from which one male crab was extracted (RMNH.CRUS.D.57239). d One host coral with two pits, no visible crabs. e One coral with one crab pit, crab not visible. f One coral with two crabs, one of which is clearly visible.

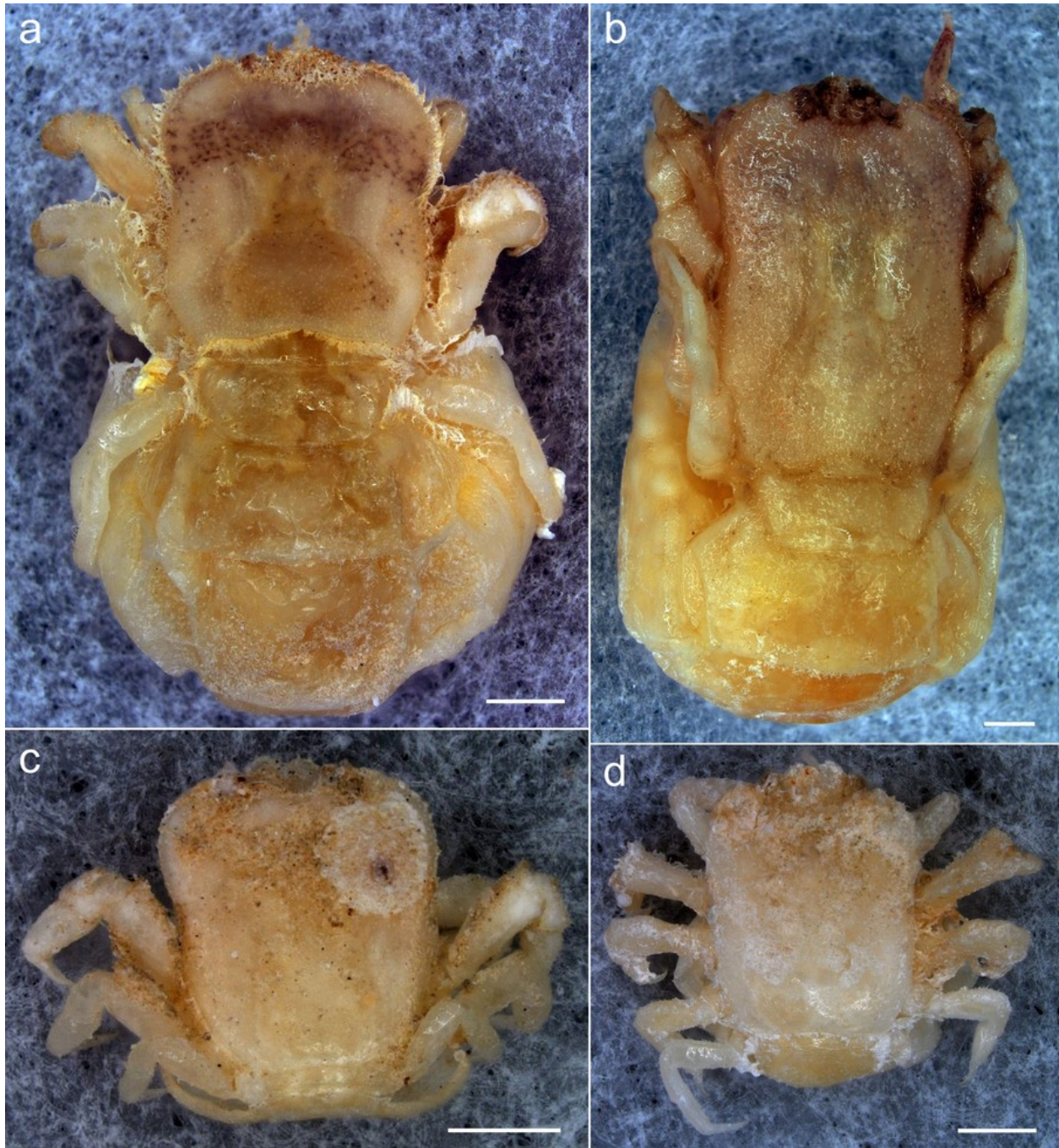


Figure 2. Microphotographs of two females and two males of *Fungicola fagei* from Hilo, Hawaii
i. Scale bars: 1 mm. a Female, BPBM-S17057. b Female, RMNH.CRUS.D.57237. c Male,
BPBM-S17057. d Male, RMNH.CRUS.D.57239.

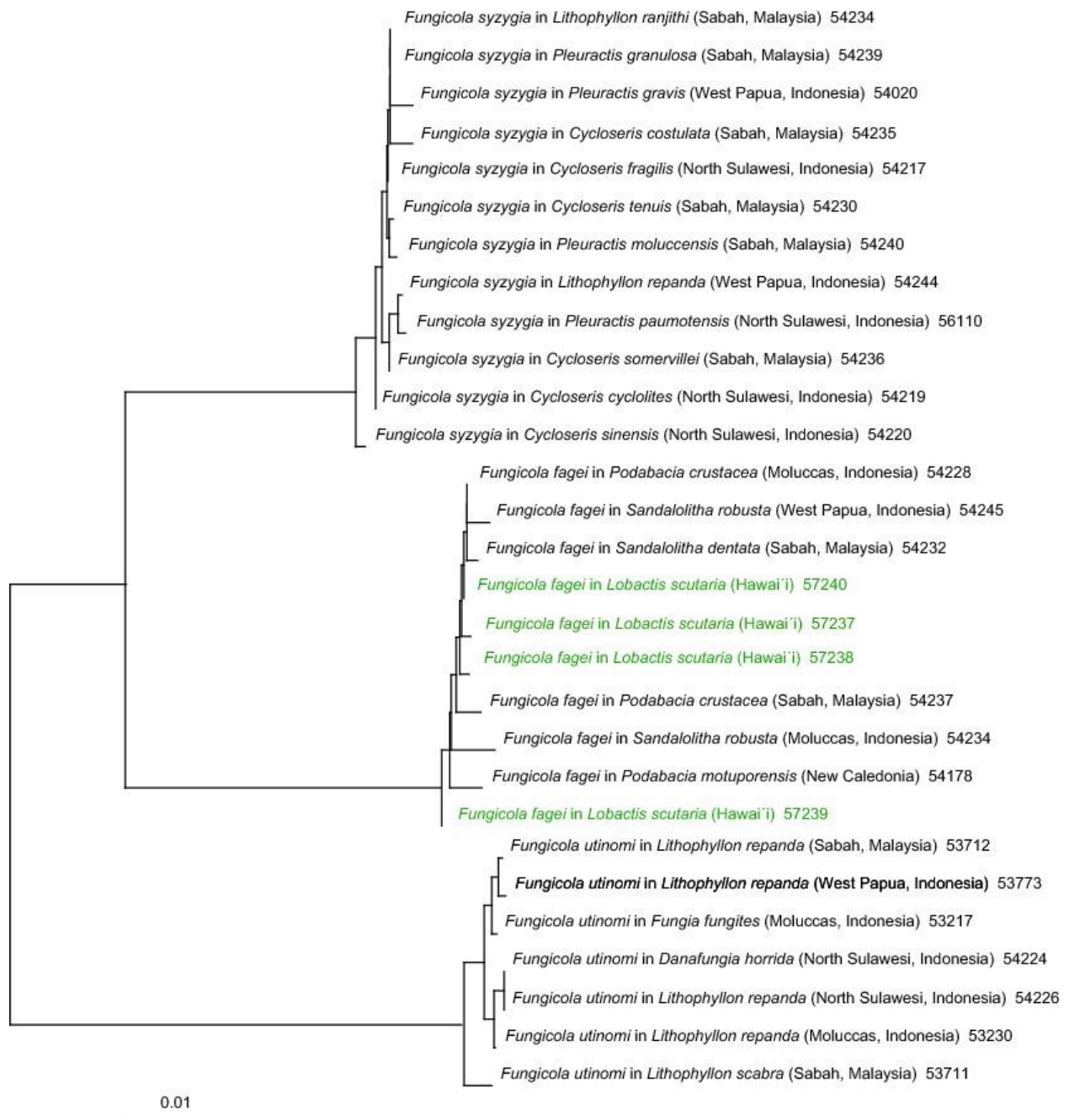


Figure 3. Neighbor-Joining tree showing the phylogenetic affinities (COI) of *Fungicola fagei* crabs from Hawai'i (green script) with *Fungicola* specimens from Southeast Asia and the West Pacific represented in GenBank (black script). Numbers refer to collection catalogue entries (RMNH.Crus.D).

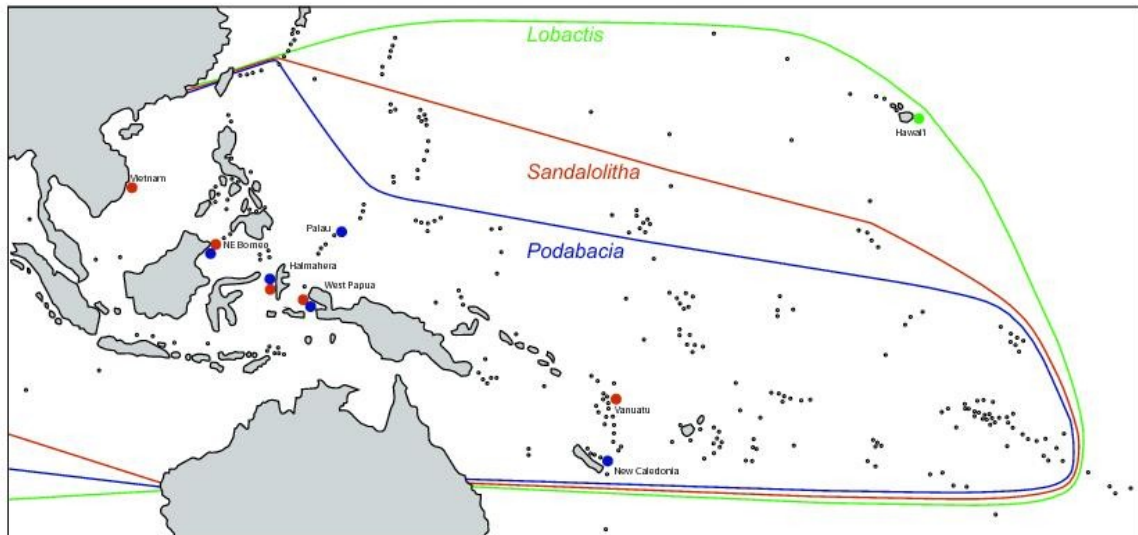


Figure 4. Distribution map of *Fungicola fagei* (host and locality records from Van der Meij 2015, Van der Meij et al. 2015, present study) and the known ranges of its host coral genera in the West and Central Pacific (Hoeksema 1989, Hoeksema and Dai 1991, Hoeksema and Benzoni 2013).