



The scleractinian *Agaricia undata* as a new host for the coral-gall crab *Opecarcinus hypostegus* at Bonaire, southern Caribbean

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Abstract

The Caribbean scleractinian reef coral *Agaricia undata* (Agariciidae) is recorded for the first time as a host of the coral-gall crab *Opecarcinus hypostegus* (Cryptochiridae). The identity of the crab was confirmed with the help of DNA barcoding. The association has been documented with photographs taken in situ at 25 m depth and in the laboratory. The predominantly mesophotic depth range of the host species suggests this association to be present also at greater depths. With this record, all seven *Agaricia* species are now listed as gall-crab hosts, together with the agariciid *Helioseris cucullata*. Within the phylogeny of Agariciidae, *Helioseris* is not closely related to *Agaricia*. Therefore, the association between Caribbean agariciids and their gall-crab symbionts may either have originated early in their shared evolutionary history or later as a result of host range expansion. New information on coral-associated fauna, such as what is presented here, leads to a better insight on the diversity, evolution, and ecology of coral reef biota, particularly in the Caribbean, where cryptochirids have rarely been studied.

Keywords Associated fauna · Brachyura · Coral reefs · Cryptochiridae · Marine biodiversity · Symbiosis

1 Introduction

Reef coral species of various scleractinian families are known to host coral-gall crabs of the brachyuran family Cryptochiridae. These crabs dwell inside pits or galls inside the coral skeleton (Castro 1976, 2015; Klompmaker et al. 2016; Chan et al. 2020). In addition to Cryptochiridae, species of some other brachyuran families live inside scleractinian corals and modify their skeletons, such as the domeciid crab *Domecia acanthophora* (Desbonne and Schramm, 1867)

living in association with species of the genus *Acropora* (Acroporidae) in the western Atlantic (Hoeksema and García-Hernández 2020). Although there is disagreement on whether to consider coral-gall crabs parasites or commensals, they are known to feed on their hosts and hinder their growth, and therefore the argument for parasitism is strongest (Simon-Blecher and Achituv 1997; Simon-Blecher et al. 1999; Klompmaker and Boxshall 2015).

Since much of the biodiversity of coral reefs consists of coral-associated fauna, from an evolutionary point of view, it is important to examine host-specificity in coral-dwelling crabs and whether they display specific host-dependent genetic divergence (van Tienderen and van der Meij 2017). With over 1600 scleractinian species on record (Hoeksema and Cairns 2020a), however, it is far from clear which coral taxa actually host gall crabs. This information would help to clarify which coral species are inhabited by cryptochirids and which ones are not, and whether such presence-absence patterns have the same evolutionary origin. The latter may, however, be less obvious when host switching is taken into consideration (Hoeksema et al. 2018). Furthermore, since some closely related coral species have different bathymetric ranges (Hoeksema 2012; Bongaerts et al. 2013; Muir et al. 2015; Roberts et al. 2019), the presence-absence of crab inhabitation may also depend on particular depth limits of their hosts, like for Christmas tree worms (Polychaeta, Serpulidae,

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Spirobranchus) ranging from 2 to 39 m depth (Hoeksema and ten Hove 2017; Hoeksema et al. 2020).

It is unclear whether zooxanthellate coral species common in the surf zone or at mesophotic depths (>30 m) possess crab galls. Only a few examples from deep water are known and these are limited to the family Agariciidae, such as the cryptochirid *Luciades agana* Kropp and Manning, 1996 in the coral *Leptoseris papyracea* (Dana, 1846) at 128–137 m depth off Guam (Kropp and Manning 1996) and at 34 m depth in Tonga (Komatsu and Takeda 2013). Another example is *Opecarcinus hypostegus* (Shaw and Hopkins 1977) in *Agaricia lamarecki* Milne Edwards and Haime, 1851 at 60 m depth off Curaçao (van der Meij et al. 2015). Cryptochirids are also known to live in azooxanthellate deep-sea corals, such as *Cecidocarcinus brychius* Kropp and Manning, 1987 at 512–686 m depth in a dendrophyliid off Namibia, SE Atlantic (Zibrowius and Gili 1990), and *Cecidocarcinus zibrowii* Manning, 1991 off New Caledonia at 425–440 m depth in the West Pacific (Manning 1991). In order to increase our understanding of the evolutionary history of these associations, it is relevant to expand our knowledge regarding cryptochirids in relation to the bathymetrical ranges and phylogenetic relationships of their host taxa. This is crucial since our knowledge of these associations could be biased by depth limitations set by SCUBA diving limits. This could particularly be true in the Caribbean, where few records are known in comparison with the Indo-West Pacific region (van der Meij and Nieman 2016; Chan et al. 2020).

The Agariciidae is one of only a few coral families with cryptochirid records from the Caribbean, Indo-West Pacific, and Eastern Pacific. These records are represented by cryptochirid species of *Opecarcinus* Kropp and Manning, 1987 (Kropp 1989; van der Meij 2014a, 2014b; Chan et al. 2020) and two monospecific cryptochirid genera in the Indo-West Pacific. The latter are *Luciades* Kropp and Manning, 1996, represented by *L. agana* in association with *Leptoseris papyracea* (mentioned above) and *Pseudohapalocarcinus* Fize and Serène, 1956, represented by *P. ransonii* Fize and Serène, 1956, in association with *Pavona frondifera* (Lamarck, 1816) (Fize and Serène 1956; Takeda and Tamura 1980) and *Pavona cactus* (Forskål, 1775) (van der Meij and Nieman 2016). Although information on *Opecarcinus* distributions seems to be scarce, apart from host and depth records, only the Indo-West Pacific *O. cathyae* van der Meij, 2014, has received special attention. This species is reported to show a wide geographical distribution and extremely high abundances (Hoeksema and van der Meij 2013; van der Meij et al. 2018). Because cryptochirids are small and usually hide inside their dwellings, they are easily overlooked and their prevalence on coral reefs may be commonly underestimated (Simon-Blecher and Achituv 1997; Nogueira et al. 2014).

The first record of gall crabs associated with Caribbean agariciids dates to 1977, with the description of *Opecarcinus hypostegus* in Florida (Shaw and Hopkins 1977) from *Agaricia*

fragilis (Table 1). Additional host-coral species were discovered, especially within the last five years, including *Helioseris cucullata* in 2017 and *Agaricia tenuifolia* in 2018, both in the Caribbean Netherlands (Table 1). *Agaricia* consists of seven species (Hoeksema and Cairns 2020b), with only one species, *A. undata*, not previously recorded as a host. This coral is best known for its predominantly mesophotic bathymetrical range, from 17 to 87 m in the Colombian Caribbean (Gonzalez-Zapata et al. 2018), from 60 to 90 m at Curaçao (Bongaerts et al. 2015), and from 70 to 90 m at Puerto Rico (Appeldoorn et al. 2016, 2019). Here we report the first record of *A. undata* as host for the gall crab *Opecarcinus hypostegus* and discuss its possible evolutionary and ecological relevance.

2 Material and methods

During a marine biodiversity survey at Bonaire (22 October – 9 November 2019), Caribbean Netherlands (previously known as Netherlands Antilles, see Hoeksema et al. 2017a), we studied the occurrence of corals and associated fauna at 35 stations using the roving diver technique (Hoeksema and Koh 2009). Scuba diving was performed to a maximum depth of 30 m. Special attention was given to coral species and their interspecific interactions with other benthic fauna, particularly rarely recorded species. Stony corals were identified using Wells (1973) and Reyes et al. (2010).

Three specimens of cryptochirids were collected for identification, one female and two males. Published illustrations of type material only consist of line drawings (Shaw and Hopkins 1977; Kropp and Manning 1987) and a previously published photograph shows a crab without host and locality data (Santana et al. 2016). Photographs of a male and a female collected from the Brazilian endemic scleractinian *Siderastrea stellata* Verrill, 1868 (Johnsson et al. 2006: Fig. 3), probably concern *Kropparcinus siderastreicola* Badaró et al., 2012, a common species in Brazil (Badaró et al. 2012; Nogueira et al. 2014), which also occurs in the Caribbean (van der Meij et al. 2014b). Therefore, in order to obtain a reliable identification for the crab associated with *Agaricia undata* in Bonaire, DNA barcoding was applied.

Genomic DNA of gall crabs was extracted with the DNeasy Blood and Tissue Isolation Kit (QIAGEN) using the manufacturer's instructions. Two walking legs per specimen were lysed overnight in lysis buffer ATL and Proteinase K at 56 °C. First and second elution steps were done with 200 µl and 50 µl AE buffer respectively. A polymerase chain reaction (PCR) was carried out by using a cocktail of two primer mixes (M13F-LepFolF mix: 5'– TGT AAA ACG ACG GCC AGT RKT CAA CMA ATC ATA AAG ATA TTG G – 3' and M13R-LepFolR mix: 5' – CAG GAA ACA GCT ATG ACT AAA CTT CWG GRT GWC CAA AAA ATC – 3') with an amplification product between the primers

Table 1 Records of Caribbean Agariciidae as host corals for gall crabs

Species	Localities [references]
<i>Agaricia agaricites</i> (Linnaeus, 1758)	Puerto Rico [2], Jamaica [3], Curaçao [4,6]
<i>Agaricia fragilis</i> Dana, 1846	Florida [1,2], Curaçao [4,6]
<i>Agaricia grahamae</i> Wells, 1973	Jamaica [3], Curaçao [4,6]
<i>Agaricia humilis</i> Verrill, 1902	Curaçao [4,6]
<i>Agaricia lamarcki</i> Milne Edwards and Haime, 1851	Jamaica [3], Curaçao [4,5,6]
<i>Agaricia tenuifolia</i> Dana, 1846	Bonaire [8]
<i>Agaricia undata</i> (Ellis and Solander, 1786)	Bonaire [present study]
<i>Helioseris cucullata</i> (Ellis and Solander, 1786)	St. Eustatius [7]
<i>Leptoseris cailleti</i> (Duchassaing and Michelotti, 1864)	no record

References: [1] Shaw and Hopkins (1977); [2] Kropp and Manning (1987); [3] Scott (1987); [4] van der Meij (2014b); [5] van der Meij et al. (2015a); [6] van Tienderen and van der Meij (2016, 2017); [7] Hoeksema et al. (2017a); [8] van Moorsel and van der Meij et al. (2018)

of 658 base pairs (bp). The M13F-LepFolF primer mix was a combination of M13F-LepF1 and M13F-LCO1490, and the M13R-LepFolR primer mix was a combination of M13R-LepR1 and M13R-HCO2198 (Folmer et al. 1994; Herbert et al. 2004). A PCR amplification of the mitochondrial COI was performed in a volume of 25 µl containing 2 µl DNA template, 2.5 µl of 10x PCR Coraload PCR buffer (Qiagen), 0.5 µl of 10 µM of all four primers, 0.5 µl of 2.5 mM dNTP, and 0.25 µl of 5 U/µl Taq DNA polymerase (Qiagen). Standard PCR conditions were used: initial denaturation at 96 °C for 3 min, 40 cycles of: denaturation at 96 °C for 15 s, annealing at 50 °C for 1 min, elongation at 72 °C for 1 min, and a final elongation step at 72 °C for 5 min). PCR

products were visualized by agarose gel electrophoresis (1% agarose gel). Suitable amplicons were sequenced by BaseClear Leiden using the M13-tailed primers (forward and reverse sequencing).

Raw sequences were edited by using MEGA X (v. 10.0.5; Kumar et al. 2018) and trimmed to 623 bp for analysis. For the purpose of molecular identification, a Maximum Likelihood (ML) tree with 500 bootstrap replicates was constructed to show the phylogenetic affinities to three other crab species from the same genus, along with two outgroup species (Table 2). Newly obtained sequences of COI were deposited in NCBI under the accession numbers MT488422–MT488424 (Table 2).

Table 2 Information on sequences used in the phylogenetic analysis of coral-gall crabs in relation to their host corals

Species	Genbank nr.	Host coral	Locality (reference)
<i>Opecarcinus hypostegus</i> (female)	MT488423	<i>Agaricia undata</i>	Bonaire, Caribbean [1]
<i>O. hypostegus</i> (male)	MT488424	<i>A. undata</i>	Bonaire, Caribbean [1]
<i>O. hypostegus</i> (male)	MT488422	<i>A. undata</i>	Bonaire, Caribbean [1]
<i>O. hypostegus</i>	KY026324	<i>Agaricia agaricites</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026344	<i>A. agaricites</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026355	<i>A. agaricites</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026400	<i>Agaricia fragilis</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026230	<i>Agaricia grahamae</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026249	<i>Agaricia humilis</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026296	<i>Agaricia lamarcki</i>	Curaçao, Caribbean [2]
<i>O. hypostegus</i>	KY026380	<i>A. lamarcki</i>	Curaçao, Caribbean [2]
<i>Opecarcinus cathyae</i>	KY013342	<i>Pavona</i> sp.	Malaysia, Pacific Ocean [3]
<i>O. cathyae</i>	KY013334	<i>Pavona</i> sp.	Saudi Arabia, Red Sea [3]
<i>Opecarcinus lobifrons</i>	KJ923666	<i>Gardineroseris planulata</i>	Malaysia, Pacific Ocean [4]
<i>O. lobifrons</i>	KJ923670	<i>G. planulata</i>	Indonesia, Pacific Ocean [4]
<i>Opecarcinus pholeter</i>	KU041833	<i>Pavona explanulata</i>	Indonesia, Pacific Ocean [5]
<i>Pseudohapalocarcinus ransonii</i>	KJ923668	<i>Pavona cactus</i>	Malaysia, Pacific Ocean [5]
<i>Kroppcarcinus siderastreicola</i>	KU041837	<i>Siderastrea siderea</i>	Curaçao, Caribbean [5]

References: [1] this study; [2] van Tienderen and van der Meij (2017); [3] van der Meij et al. (2018); [4] van der Meij and Reijnen (2014); [5] van der Meij and Nieman (2016)

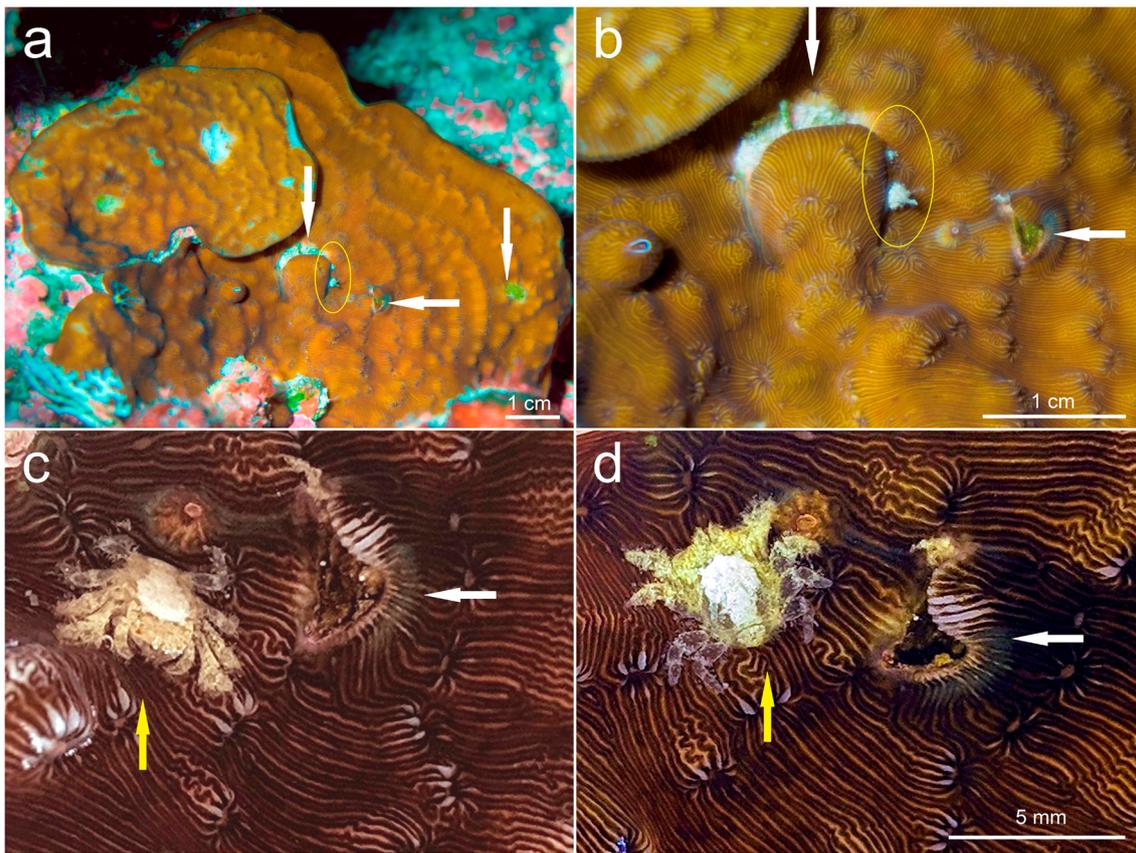


Fig. 1 *Agaricia undata* at 25 m depth, Willemstoren Lighthouse, Bonaire, with gall crabs (yellow ellipses and arrows) and their pits (white arrows). a. Overall view of the host coral; b. Close-up showing calice pattern and position of gall crab pits, and one pair of crabs leaving

the pit (yellow ellipse; RMNH.CRUS.D.57958, 57959); c,d. One male crab inside a pit (white arrow; RMNH.CRUS.D.57960) and the female walking around after capture and release (yellow arrow; RMNH.CRUS.D.57958)

One female and one male specimen were photographed (Figs. 1c, 2) to be used as reference for future studies. The three specimens were deposited in the Crustacea collection of Naturalis Biodiversity Center, Leiden as reference material (catalogue numbers RMNH.CRUS.D.57958, 57959, 57960, respectively).

3 Results

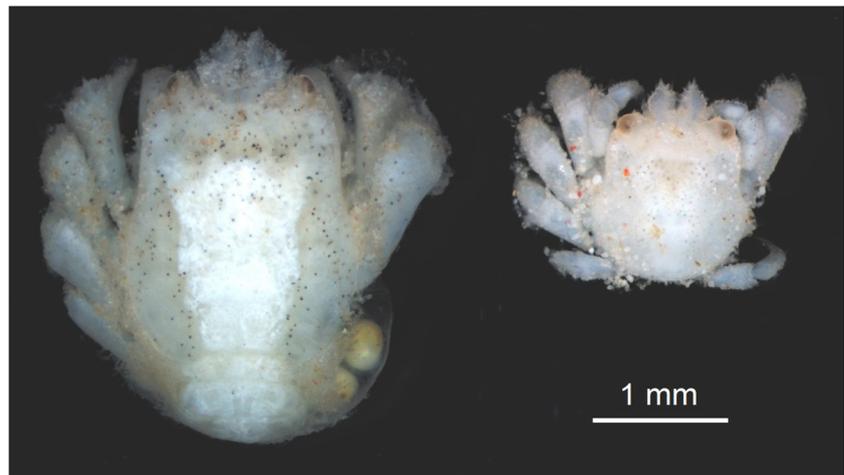
A shore dive on the wave-exposed reef in front of Willemstoren Lighthouse (12°01'39"N 68°14'12"W) on the southern coast of Bonaire (29 October 2019) resulted in the discovery of one specimen of *Agaricia undata* at ca. 25 m depth (Fig. 1a, b). This particular colony was occupied by three coral crabs (Fig. 1c, d), one female and two males (Fig. 2). The dwellings were typical for *Opecarcinus hypostegus* as encountered in various *Agaricia* spp. hosts (Kropp 1989; van der Meij et al. 2015; van Tienderen and van der Meij 2017; van Moorsel and van der Meij 2018). We provisionally assumed that it concerned *Opecarcinus hypostegus*, based on the crab's dwelling as in previous

studies (van der Meij et al. 2015; Hoeksema et al. 2017c; van Moorsel and van der Meij 2018). *Agaricia undata* was observed and documented at two other sites around Bonaire, but in these cases no associates were found.

DNA barcoding confirmed the identification of the specimens as *O. hypostegus* (Fig. 3). In the phylogenetic tree, the three crab specimens were distributed over various branches, mixing with crabs collected from other *Agaricia* spp. Therefore, our molecular data confirm the first record of a cryptochirid symbiont of *A. undata*, implying that all *Agaricia* species are known to host gall crabs, together with *Helioseris cucullata* (Table 1). *Leptoseris cailleti* remains as the only Caribbean agariciid without a record of a cryptochirid symbiont (Table 1) or any other associated invertebrate (see Scott 1985, 1987).

The identification of the coral as *Agaricia undata* was confirmed after the descriptions in Wells (1973) and Reyes et al. (2010). To the untrained eye, *A. undata* can be easily confused with *A. grahamae*. Both species occur predominantly in the mesophotic zone (Sherman et al. 2010; Bongaerts et al. 2015; Appeldoorn et al. 2016; Hoeksema et al. 2017b; Sánchez et al. 2019). The calices of *A. undata* are mostly arranged in rows

Fig. 2 Female and male gall crab specimens of *Opecarcinus hypostegus* (RMNH.CRUS.D.57958, 57959, respectively) collected from the host coral *Agaricia undata* at Bonaire



underneath ridges with rounded tops, directing in outward direction, but starting more or less separated (Fig. 1b), whereas those of *A. grahamae* are positioned on the bottom of long v-shaped valleys (Wells 1973; Reyes et al. 2010). These distinguishing characters are not clear in relatively young specimens.

4 Discussion

Based on previous records and the present observations, it appears that all *Agaricia* spp. in the Caribbean, along with the agariciid *Helioseris cucullata* (Table 1), share the same cryptochirid species, *O. hypostegus*. In Brazil, *O. hypostegus* has been reported from *Agaricia fragilis* and *A. agaricites* (Johnsson et al. 2006; Badaró et al. 2012; Santana et al. 2016). Older records of *O. hypostegus* from non-agariciid hosts (e.g. Scott 1985; Nogueira 2003) are doubtful and

probably concern misidentified crabs of recently discovered species (Badaró et al. 2012; Canário et al. 2015; Hoeksema et al. 2017c).

Few cryptochirids in these associations have had their identities verified with the help of barcoding. It should be noted that the other species of *Opecarcinus*, including *O. lobifrons* in the widespread coral *Gardineroseris planulata* as the sister species of *O. hypostegus* (Table 2), are from the Indo-West Pacific, and some of these are also from the Eastern Pacific (Kropp 1989; Wei et al. 2005; van der Meij and Nieman 2016). Within the phylogeny of the Agariciidae, however, *Agaricia* and *Helioseris* are not closely related (Huang 2012; Kitahara et al. 2012). Furthermore, the identity of the crab species in *A. tenuifolia* and *H. cucullata* still needs to be verified, since their preliminary identifications are based on the morphology of their dwellings. The Caribbean agariciid genera are thus not monophyletic and a shared cryptochirid symbiont should be either the result of a very early evolutionary

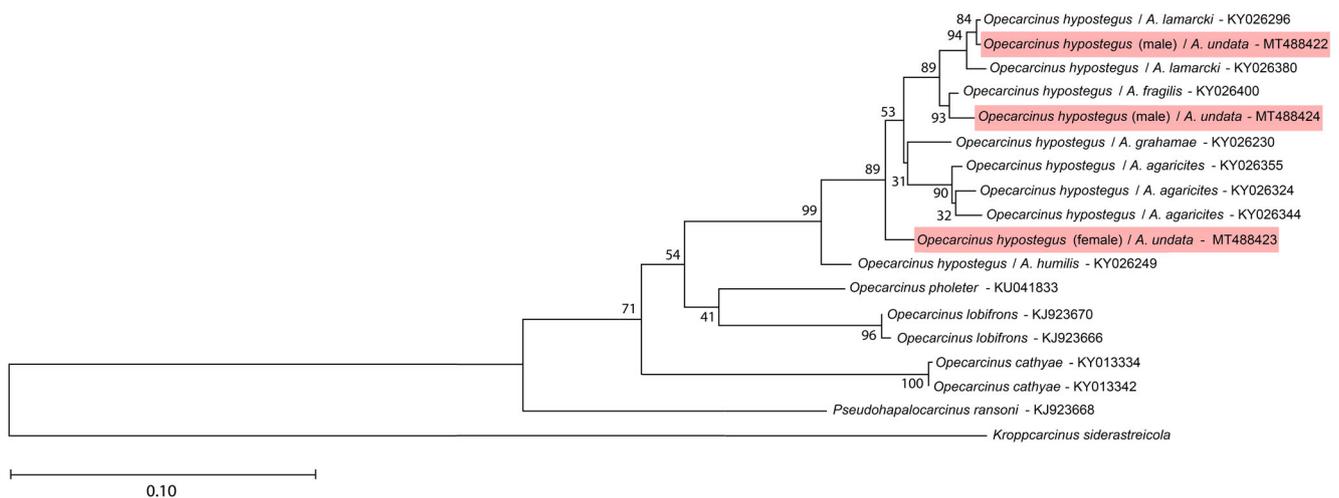


Fig. 3 Phylogenetic analysis based on the COI mitochondrial gene of a subset of *Opecarcinus* species and two related outgroup species (Table 2). Host coral species of the Caribbean reef coral genus *Agaricia* are

specified. Maximum Likelihood (ML) tree with Bootstrap values. Specimens from this study are highlighted in red

origin of the cryptochirid coral association or of a more recent host range expansion.

That all *Agaricia* spp. share a common cryptochirid symbiont is perhaps not surprising. There are also examples of scleractinian genera in other families, e.g. Fungiidae (see Gittenberger et al. 2011; Benzoni et al. 2012; Hoeksema 2014), in which cryptochirid symbionts have been found in only a limited number of species (*Centactis*, *Cycloseris*) or in none at all (*Cantharellus*, *Heliofungia*) (van der Meij et al. 2015b). The present finding and other recently discovered crab-coral associations (van der Meij 2015, 2017; Hoeksema et al. 2017c; van Moorsel and van der Meij 2018) suggest that missing host records are partly due to insufficient sampling.

Because *A. undata* is most abundant at depths >25 m (Fenner 1999), the present discovery contributes to our understanding of similarities in reef faunas among the mesophotic and shallower parts of the reef slopes (<30 m depth). *Opecarcinus hypostegus* was previously reported from 60 m depth in association with *A. lamarcki* (van der Meij et al. 2015a). If mesophotic zones are potential refugia for coral reef fauna (Rooney et al. 2010; Slattey et al. 2011; Semmler et al. 2017; Baldwin et al. 2018), future surveys of mesophotic reefs should not only focus on the occurrence of deep-living corals but also on the occurrence of other coral-associated organisms (Hoeksema et al. 2017c; Veglia et al. 2018; Korzhavina et al. 2019).

Leptoseris cailleti is the only Caribbean agariciid in need of investigation of its associated fauna (Table 1). This deep-water species has only been recorded from depths >33 m (Dinesen 1980; Fenner 2001; Garcia-Sais et al. 2007, 2011) and is the only *Leptoseris* species in the Caribbean (Muir and Pichon 2019), whereas all of its presently known congeners are from the Indo-West Pacific (Waheed et al. 2015) and some from the Eastern Pacific (Glynn et al. 2017). A possible candidate gall-crab associate could belong to an undescribed species of *Luciades*, the only cryptochirid genus known to be represented in Indo-West Pacific *Leptoseris* corals (Kropp and Manning 1996; Wetzler et al. 2009). *Leptoseris papyracea* (Dana, 1846), host of *Luciades agana* at Guam and Tonga (Komatsu and Takeda 2013), also occurs in the Eastern Pacific, but here it is not yet known to host cryptochirids. Crabs of the genus *Opecarcinus* would require a host expansion in order to become associated with Caribbean *Leptoseris*. The latter genus is phylogenetically more closely related to the Indo-Pacific agariciid genus *Pavona* than to the West Atlantic / Caribbean genus *Agaricia* (Huang 2012). Because the family Agariciidae is widespread in tropical areas and is represented in a wide depth range (Muir et al. 2018; Muir and Pichon 2019), it is well suited for studies on the evolution and biogeography of coral-associated faunas.

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