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Published in:
Cahiers de biologie marine

DOI:
10.21411/CBM.A.946E2CEE

Cah. Biol. Mar. (2022) 63-3 : 239-246
DOI: 10.21411/CBM.A.946E2CEE

Host use of the elkhorn coral crab *Domecia acanthophora* (Brachyura : Domeciidae), with a phylogeny of the genus

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Abstract: Coral-dwelling crabs form a diverse community on coral reefs, and various families independently colonised scleractinian corals. Species of *Domecia* have a circumtropical distribution, with two known species in the Indo-Pacific, one in the West Atlantic and one in the East Atlantic. New host records for the West Atlantic species *D. acanthophora* are recorded from Guadeloupe, as well as the first dwellings in *Acropora prolifera* from Curaçao. Here we provide an overview of all known hosts of *Domecia* species and, based on COI mtDNA, the first phylogeny of the genus. The coral *Orbicella faveolata* and the sponge *Callyspongia* sp. are recorded as new hosts for *D. acanthophora.* Host records for this species now include eight scleractinian hosts, *Millepora* fire corals and records on sponges. Our phylogenetic reconstruction shows that *D. acanthophora* is closest to the wide-ranging Indo-Pacific species *D. hispida*, and more distantly related to *D. glabra*. *Domecia acanthophora* appears to be less host specific than its congeners *D. hispida* and *D. glabra* that predominantly associate with *Pocillopora* and *Acropora* corals, respectively. Differences in host-specificity between Indo-Pacific and Atlantic species are briefly discussed in the light of similar observations on other coral-dwelling crab species.

Résumé : *Hôtes utilisés par le crabe de coraux corne d'élan* Domecia acanthophora *(Brachyura: Domeciidae), avec une phylogénie du genre.* Les crabes vivant sur les récifs coralliens forment une communauté diversifiée et de nombreuses familles colonisent les coraux scléractiniaires. Les espèces du genre *Domecia* ont une distribution circumtropicale, avec deux espèces connues dans la région Indo-Pacifique, une espèce dans l'Atlantique ouest et une espèce dans l'Atlantique est. De nouvelles espèces de coraux hôtes ont été recensées en Guadeloupe pour *D. acanthophora*, l'espèce inféodée à la région de l'Atlantique ouest. Cette espèce a également été observée pour la première fois dans des colonies d'*Acropora prolifera* sur l'île de Curaçao. Nous présentons ici une liste des hôtes connus pour les espèces de *Domecia* ainsi que la première phylogénie du genre, réalisée à partir de séquences du gène mitochondrial codant pour la sous-unité 1 de la cytochrome oxydase (COI). Le corail *Orbicella faveolata* et les éponges *Callyspongia* sp. ont été observés comme nouveaux hôtes de *D. acanthophora*. Le recensement des espèces hôtes pour cette espèce comprend à présent huit espèces de scléractiniaires, les coraux de feu du genre *Millepora* ainsi que des éponges. La reconstruction phylogénétique montre que *D. hispida*, l'espèce indo-pacifique à large répartition est l'espèce la plus proche de *D. acanthophora*

Reçu le 9 novembre 2021 ; accepté après révision le 13 mars 2022.
Received 9 November 2021; accepted in revised form 13 March 2022.

tandis que *D. glabra* est l'espèce la plus éloignée. *Domecia acanthophora* semble choisir des hôtes moins spécifiques que ses congénères *D. hispida* et *D. glabra* qui s'associent respectivement aux coraux *Pocillopora* et *Acropora* en priorité. Les différences de spécificité vis-à-vis des hôtes entre les espèces de l'Indo-Pacifique et celles de l'Atlantique sont brièvement discutées à la lumière d'observations similaires sur d'autres espèces de crabes inféodés au milieu corallien.

Keywords: Associated fauna ● Caribbean ● Coral ● Decapoda ● Scleractinia ● Symbiosis

Introduction

Brachyuran crabs represent one of the most diverse components of coral reefs, and many of these species associate with sessile hosts. Scleractinian corals in particular are inhabited by brachyuran crabs and the obligate commensal relationship between coral-dwelling crabs and scleractinian corals has long been recognised by marine biologists (Castro, 1976). The majority of these crabs associate with branching corals of the genera *Acropora* and *Pocillopora*, where they move freely among the branches of their hosts (Lai et al., 2009; Stella et al., 2011). These crabs belong to several families (e.g. Tetraliidae, Trapeziidae, Domeciidae) within Xanthoidea that have independently colonised scleractinians on several occasions (Lai et al., 2009). The circumtropical genus *Domecia* (Domeciidae) is comprised of four species: *Domecia acanthophora* (Desbonne in Desbonne & Schramm, 1867) in the West Atlantic, *D. africana* Holthuis, Edwards & Lubbock, 1980 in the East Atlantic, and *D. glabra* Alcock, 1899 and *D. hispida* Eydoux & Souleyet, 1842 both widely distributed in the Indo-West Pacific (Castro, 1976). The latter two species are thought to associate with *Acropora* and *Pocillopora*, respectively, whereas the most well-known host of *D. acanthophora* is the Caribbean acroporid *A. palmata* (Lamarck, 1816), hence its vernacular name "elkhorn coral crab". Like gall crabs (Cryptochiridae), domeciid crabs live in a dwelling on their host, however, they are not closely related (Lai et al., 2009, Van der Meij & Schubart, 2014). Patton (1967) recorded three *Acropora* species as hosts for *D. acanthophora* in the Caribbean, of which one, *A. prolifera* Lamarck, 1816, is now considered a F1 hybrid of *A. cervicornis* (Lamarck, 1816) and *A. palmata* (Oppen et al., 2000). *Domecia acanthophora* produces structural modifications in *A. palmata*, dubbed 'resting places' by Patton (1967), which are found in the upper portions of the corals and between branches. According to Grajal & Laughlin (1984) no structural deformations were observed in *A. cervicornis* and *A. prolifera* and they suggested that mostly dwellings in *A. palmata* are used as reproductive shelters for reproduction and brood care by ovigerous females, because *A. palmata* hosts higher ratios of ovigerous/non-ovigerous females than *A. prolifera* or *A. cervicornis*. High abundances of *D. acanthophora* are linked to reefs with high cover of *A. palmata* and *Millepora* fire corals, another common host of this crab (Garcia et al., 2008; Gonzalez-Gomez et al., 2018). Here we report on new host records of *D. acanthophora* from Guadeloupe and Curaçao in the Caribbean, provide the first phylogeny of the genus, an overview of host records in literature and a discussion of host use for species in *Domecia*.

Material and Methods

Fieldwork was conducted in Guadeloupe (April-June 2021), where *D. acanthophora* was observed at six sites and collected from two sites. Moreover, observations and collections of *D. acanthophora* from Curaçao (July-September 2021) are included (Table 1). Additionally, we provide literature records of all recorded hosts for *D. acanthophora* and its congeners *D. africana*, *D. glabra* and *D. hispida*. Two specimens of *D. acanthophora* sampled from *Millepora alcicornis* Linnaeus, 1758 in Guadeloupe, as well as two specimens of *D. acanthophora* sampled from *Acropora palmata* and *A. prolifera* in Curaçao were barcoded for COI using standard Folmer primers, following the protocols in van der Meij (2015). Sequences were submitted to GenBank under accession numbers OM669764-7 (Table 2). We obtained sequences from *D. glabra* and *D. hispida* from GenBank, and added the domeciid *Cherusius triunguiculatus* (Borradaile, 1902) and a species in the family Tetraliidae as outgroups based on Lai et al., (2009) (Table 2). The resulting dataset was aligned using clustalw in Seaview (Gouy et al., 2010), and a maximum likelihood analysis was performed in IQ-tree (Nguyen et al., 2015) after performing a test of the best-fit model for nucleotide substitution in ModelFinder (Kalyaanamoorthy et al., 2017). One thousand ultrafast bootstraps were performed using UFBoot (Hoang et al., 2018). The tree was visualised

Table 1. *Domecia acanthophora* .Site data where the species was observed and collected in Guadeloupe (G) and Curaçao (C).

Location	Host	Coordinates		Date	Depth (m)
Observation					
La Pointe de l'Hermitage (G)	*Acropora palmata*	61°46'33.3''W	16°07'34.0"N	29/04/2021	5
Sainte-Anne (G)	*Millepora alcicornis*	61°23'02.4''W	16°13'13.4''N	03/05/2021	6
Anse Marigot (G)	*Orbicella faveolata*	61°47'43.8''W	16°14'06.9''N	09/05/2021	5
Pointe Malendure (G)	*Orbicella faveolata*	61°47'03.4''W	6°10'30.4''N	18/05/2021	5
Pointe Malendure (G)	*Millepora alcicornis*	61°47'03.4''W	6°10'30.4''N	18/05/2021	5
Petite-Anse (Pointe-Noire) (G)	*Callyspongia* sp.	61°48'34.0''W	16°16'10.3''N	22/05/2021	6
Anse à Jacques (G)	*Millepora alcicornis*	61°25'22.1''W	16°12'29.4''N	26/05/2021	3
Double Reef (C)	*Acropora palmata*	68°56'57.3''W	12°06'27.1''N	21/09/2021	4-5
Double Reef (C)	*Acropora prolifera*	68°56'57.3''W	12°06'27.1''N	21/09/2021	4-5
Water Factory (C)	*Acropora prolifera*	68°57'06.7''W	12°06'26.7''N	18/09/2021	5-6
Collection					
Sainte-Anne (G)	*Millepora alcicornis*	61°23'02.4''W	16°13'13.4''N	03/05/2021	6
Anse à Jacques (G)	*Millepora alcicornis*	61°25'22.1''W	16°12'29.4''N	26/05/2021	3-4
Anse à Jacques (G)	*Millepora alcicornis*	61°25'22.1''W	16°12'29.4''N	02/06/2021	3-4
Double Reef (C)	*Acropora palmata*	68°56'57.3''W	12°06'27.1''N	21/09/2021	4-5
Double Reef (C)	*Acropora prolifera*	68°56'57.3''W	12°06'27.1''N	21/09/2021	4-5
Double Reef (C)	*Acropora prolifera*	68°56'57.3''W	12°06'27.1''N	21/09/2021	4-5

Table 2. GenBank accession numbers (COI) of specimens used in this study.

Species	Locality	Genbank	Reference
Domecia acanthophora	**Curaçao**	**OM669764**	**This study**
Domecia acanthophora	**Curaçao**	**OM669765**	**This study**
Domecia acanthophora	**Guadeloupe**	**OM669766**	**This study**
Domecia acanthophora	**Guadeloupe**	**OM669767**	**This study**
Domecia glabra	Hawaii, USA	MW278665	Paulay et al.,
Domecia hispida	Hawaii, USA	MW278069	Paulay et al.,
Domecia hispida	Line Islands / Moorea	GQ260916	Plaisance et al., 2009
Domecia hispida	Palmyra Island	MT413353	Servis et al., 2020
Domecia hispida	Palmyra Island	MT169692	Servis et al., 2020
Domecia sp. C	Central Red Sea	KY262716	Kandler et al., 2019
Cherusius triunguiculatus	New Caledonia	KJ923688	Van der Meij & Reijnen, 2014
Tetraliidae sp.	Central Red Sea	MH339088	Pearman et al., 2018

and rooted in FigTree v 1.4.0. Evolutionary divergence over sequence pairs (p-distance) between *a priori* determined groups were obtained using MEGA 7 (Kumar et al., 2016).

Results & Discussion

Domecia acanthophora was reported from Guadeloupe by Poupin (2018: Fig. 235). Here we report on new observations of *D. acanthophora* from Guadeloupe associated with the coral *Orbicella faveolata* (Ellis & Solander, 1786) at Anse Marigot and Pointe Malendure reef and the sponge *Callyspongia* sp. at Petite-Anse (Pointe-Noire) reef (Table 1, Fig.1C-D, F), at depths between three and six metres. Moreover, on Double Reef and Water Factory (Curaçao) multiple dwellings of *D. acanthophora* were observed in *A. prolifera* colonies (Fig. 1B). A large *A. prolifera*

colony on Double Reef, from which specimens were collected (Table 1), contained 20 dwellings and 15 crabs; these dwellings were observed in all parts of the colony. A juvenile colony was inhabited by two crabs, but no clear dwellings were observed.

List of new and recorded hosts of *Domecia* spp.

Domecia acanthophora (Desbonne in Desbonne & Schramm, 1867)

Distribution

West Atlantic (Guinot, 1964: Fig. 17)

Host corals

Acropora cervicornis, *A. palmata*, *A. prolifera* (Patton, 1967); *Oculina arbuscula* Agassiz, 1880 and *O. varicosa* Le Sueur, 1820 (Reed et al., 1982); and the fire corals *Millepora* spp. (Garcia et al., 2008; Gonzalez-Gomez et al., 2018). A list of specimens is discussed in Rathbun (1930) and includes material collected from sponges and among branches of corals, but also specifically lists *Porites furcata* Lamarck, 1816, and *Meandrina* as hosts. Given the status of coral taxonomy at the time *Meandrina* could refer to a variety of species currently known under other genus names, however, it likely refers to a species commonly grouped under the 'brain corals'. Here we report on the presence of *D. acanthophora* in crevices on *Orbicella faveolata* (Fig. 1C-D), on *Millepora alcicornis* (Fig. 1E), and on *Callyspongia* sp. (possibly *C. plicifera* (Lamarck, 1814), Fig. 1F) in Guadeloupe. Humann & DeLoach (2013: 127) provided a photograph of a specimen sitting on top of an *Orbicella* sp. coral, however, no further information was provided. Additionally, we observed *D. acanthophora* in dwellings in the hybrid acroporid *A. prolifera* at Curaçao (Fig. 1B).

Domecia africana Holthuis, Edwards & Lubbock, 1980 (Guinot, 1964: Fig. 17 as *D. acanthophora forma africana)*

Distribution

West Africa, Saint Peter and Saint Paul Archipelago (central equatorial Atlantic) (Guinot, 1964; Holthuis et al., 1980).

Host corals

among coral, and between rocks and calcareous algae (Guinot, 1964).

Domecia glabra Alcock, 1899

Distribution

Indo-West Pacific, from East Africa to the Central Pacific, absent from the East Pacific (Guinot, 1964: Fig. 17).

Host corals

Acropora spp. (Garth 1964 & 1974; Castro 1976 and references therein).

Domecia hispida Eydoux & Souleyet, 1842

Distribution

Indo-West Pacific, from the Red Sea to the East Pacific (Guinot, 1964: Fig. 17).

Host corals

Pocillopora spp. (Garth, 1964 & 1974; Guinot, 1964; Castro, 1976, and references therein). There is also a record of *Domecia* sp. C reported from the sponge *Stylissa carteri* (Dendy, 1889) in the Red Sea, which clusters with the sequences of *Domecia hispida* (Kandler et al., 2019, Fig. 2), and a record obtained from an Autonomous Reef Monitoring Structure (ARMS) (Servis et al., 2020).

Discussion

Erroneous identification

In some field guides *D. acanthophora* is confused with *Batodaeus urinator* (A. Milne-Edwards, 1880) (Humann & DeLoach 2003: 208-209, as *Micropane urinator*). Humann & DeLoach (2013: 127) corrected their identification to *D. acanthophora*. In a different field guide specimens specifically occurring on *Millepora* sp. are referred to as *B. urinator* (Charteris, 2017: 236), however, this is a deep-water species belonging to the crab family Xanthidae and not known to associate with corals.

Host use of coral-dwelling crabs.

Domecia acanthophora predominantly associates with species in the genera *Acropora* and *Millepora* in the West Atlantic (Patton, 1967; Garcia et al., 2008), however, the list of host organisms is growing and currently includes eight scleractinian coral species in five genera, fire corals and two sponge records. It is likely that multiple *Millepora* species are inhabited by *D. acanthophora*, but there is some uncertainty about the

identification of these species, especially *M. alcicornis* and *M. complanata* Lamarck, 1816 (Ruiz-Ramos et al., 2014). It appears that *D. acanthophora* inhabits natural crevices in *O. faveolata*, and does not create dwellings similar to those observed in *Acropora* (Fig. 1A-B). Clearly *D. acanthophora* is not as host specific as its vernacular name suggests, however *A. palmata* appears to be of special importance for ovigerous females (Grajal & Laughlin, 1984). No information is available on sex ratios or the presence of ovigerous

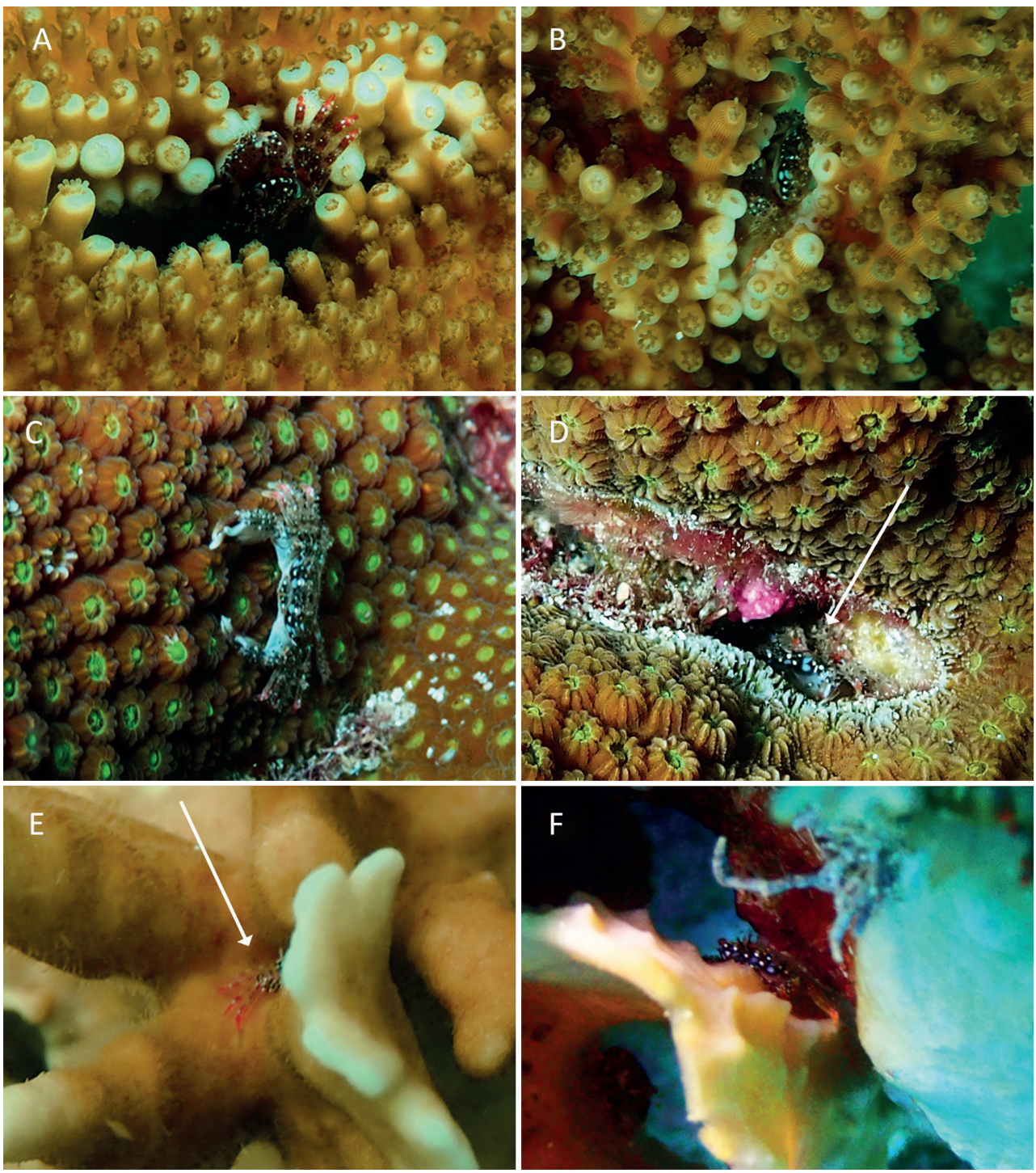

Figure 1. *Domecia acanthophora* Hosts. **A.** *Acropora palmata*. **B.** *A. prolifera*. **C.** *Orbicella faveolata*. **D.** natural crevice in *O. faveolata* inhabited by *D. acanthophora* (arrow) **E.** *Millepora alcicornis* with crab (arrow), but without dwelling. **F.** *Callyspongia* sp. Photos A, C-F by H. Bravo from Guadeloupe and B by Y. Scholten from Curaçao.

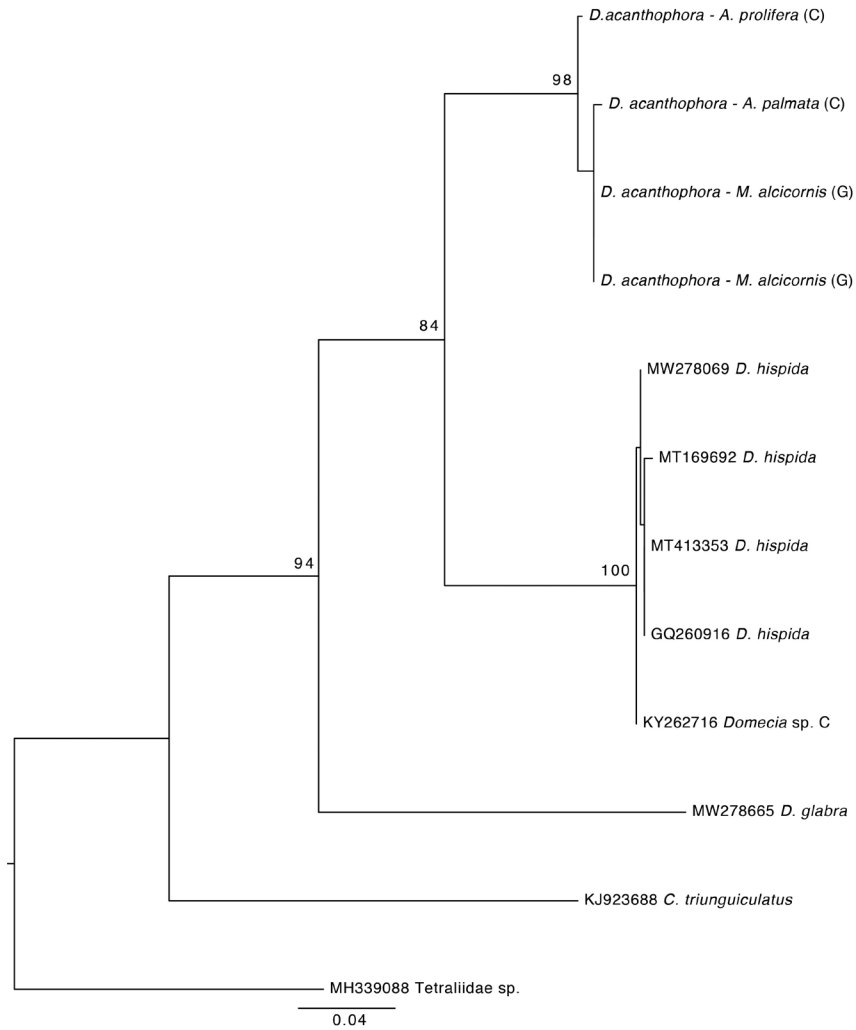

Figure 2. Maximum likelihood tree (1000 ultrafast bootstraps), with *C. triunguiculatus* and Tetrallidae sp. as outgroups. The best-fit model according to the AIC was GTR+F+G4. The genus *Domecia* has a support value of 94, however, we have no material of the East Atlantic species *D. africana* to ensure monophyly. Divergence over COI between *D. acanthophora* and *D. hispida* is 12%, and divergence with *D. glabra* is 18.4%. (C) is a sample from Curaçao, (G) is a sample from Guadeloupe.

females in *Millepora* sp. to draw any conclusions on the relative importance of this host for *D. acanthophora*. The dwellings observed in *A. prolifera* (Fig. 1B) are new records, as Castro (1976) and Grajal & Laughlin (1984) specifically stated that they did not observe dwellings in *Acropora* species other than *A. palmata*. The two Indo-Pacific *Domecia* species do not appear to induce the formation of dwellings in their hosts (Castro, 1976).

Domeciidae, represented by *D. acanthophora*, were found to be closely related to coral-dwelling species of Tetraliidae (Lai et al., 2009) but no other domeciids were included in their study, hence monophyly of the genus and family was not previously established using genetic data. Here we included three out of four described *Domecia* species, as no fresh material of *D. africana* was available for study nor are sequences present on GenBank. The phylogeny reconstruction of the species of *Domecia* shows that the West Atlantic species *D. acanthophora* is closest to the wide-ranging Indo-Pacific species *D. hispida* (Fig. 2). *Domecia glabra* has a narrower Indo-Pacific distribution than *D. hispida* and has not been recorded from the East Pacific, likely due to the absence of its *Acropora* hosts (Castro, 1976). The inclusion of fresh *D. africana* material would address the question raised by Guinot (1964) as to whether *D. africana* is a separate species or a phenotypic variety of *D. acanthophora*. The circumtropical distribution of *Domecia* and the species' association with scleractinian corals is interesting from a diversification and host specificity perspective. *Domecia acanthophora* is associated with eight scleractinian hosts to date, as well as *Millepora* spp. fire corals and sponges, whereas *D. glabra* and

D. hispida show strong affinities for *Acropora* and *Pocillopora* corals, respectively. While there are few dedicated studies on Indo-Pacific *Domecia*, there are at least incidental records of *D. hispida* associating with other hosts (Kandler et al., 2019; Servis et al., 2020). Interestingly, a similar observation can be made for coral-dwelling gall crabs of the genus *Opecarcinus* (Cryptochiridae), obligately associated with Agariciidae corals, which, like *Domecia*, occur in both the Indo-Pacific and the Atlantic. *Opecarcinus hypostegus* (Shaw & Hopkins, 1977) is the Atlantic representative of the genus and associates with *Agaricia* and *Helioseris* corals. This species appears to be less host-specific than many of its Indo-Pacific congeners, perhaps as a result of its young age, as these crabs are thought to have migrated from the Indo-Pacific to the West Atlantic across the Eastern Pacific Barrier through the Panama Isthmus (Xu et al., 2021). These coral-dwelling crabs provide interesting avenues for research on crab-coral symbiosis and (possible) host-driven diversification, especially for those genera and families that have representatives in both basins.

Acknowledgements

The authors would like to thank Anna Schleimer for her invaluable help in the field and Tao Xu (University of Groningen) for his assistance in the lab. Samplings were authorised by the Direction de la Mer de Guadeloupe under Autorisation N°09/2021. Sampling from Curaçao was authorised by the Caribbean Research and Management of Biodiversity under Government reference 2019/021824. Fieldwork by Henrique Bravo was funded by TREUB-maatschappij (Society for the Advancement of Research in the Tropics) and Flying Sharks.

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