Bull Mar Sci. 90(4):1001–1010. 2014
http://dx.doi.org/10.5343/bms.2014.1017

coral reef paper

# Host species, range extensions, and an observation of the mating system of Atlantic shallow-water gall crabs (Decapoda: Cryptochiridae)

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ABSTRACT.—Coral-associated invertebrates dominate the biodiversity of coral reefs. Some of the associations involving symbiotic invertebrates remain unknown or little studied. This holds true even for relatively well-studied coral reefs, like those in the Caribbean Sea. Coral gall crabs (Cryptochiridae), obligate symbionts of stony corals, form a much-overlooked component of coral reef communities. Most recent studies on the Atlantic members of Cryptochiridae have been conducted off Brazil and little recent data have become available from the Caribbean region. During fieldwork off Curaçao (southern Caribbean Sea), eight new host coral species, belonging to four coral families, were recorded for three cryptochirid species. *Kroppcarcinus siderastreicola* Badaro, Neves, Castro and Johnsson, 2012, previously only known from Brazil, and *Opecarcinus hypostegus* (Shaw and Hopkins, 1977) are new additions to the fauna of Curaçao. Besides the new hosts and geographic range extensions, a free-living male *Troglocarcinus corallicola* Verrill, 1908 was observed visiting a female of the same species lodged in her gall in an *Orbicella annularis* (Ellis and Solander, 1786) colony. This is the first photodocumented record of the "visiting" mating system in Cryptochiridae.

Date Submitted: 5 March, 2014.
Date Accepted: 3 June, 2014.
Available Online: 2 September, 2014.

The biodiversity of coral reefs is predominantly composed of invertebrates, many of which live in close association with sponges, molluscs, echinoderms, ascidians, and coelenterates like sea anemones, and soft and stony corals. About 870 invertebrate species are known to be associated with stony corals (Scleractinia) alone, but the extent of these associations is only partially known (Stella et al. 2011, Hoeksema et al. 2012). Species that live in obligate symbioses with a host depend on it for their survival and, hence, are more vulnerable to extinction (McKinney 1997). This is a concern in the light of the ongoing degradation of coral reefs, especially given that the coral-associated fauna is relatively unknown. Such associated fauna has not been subject of many surveys, even in relatively well-studied regions like the Caribbean Sea. With the exception of the overview provided by Zlatarski and Martínez-Estalella (1982), most published studies have focused on a particular geographical area, host, or symbiont (Reed et al. 1982, Scott 1985, 1987, 1988).

Gall crabs (Cryptochiridae; also known as pit crabs) are obligate symbionts of stony corals (see Castro 1988) worldwide, but many regions still need to be monitored for their occurrence. Research on Atlantic gall crabs has also been sparse. Kropp and

Manning (1987) studied both deep and shallow-water Atlantic cryptochirids and included many new host corals based on museum collections. All published research on Cryptochiridae conducted after 1987 has been carried out in Brazil (Noguiera 2003, Johnsson et al. 2006, Oigman-Pszczol and Creed 2006, Badaro et al. 2012, Noguiera et al. 2014), except for one publication from Mexico (Carricart-Ganivet et al. 2004). For the three Atlantic species of shallow-water gall crabs recognized to date, a total of 23 host species have been recorded (Kropp and Manning 1987, Badaro et al. 2012). One gall crab species, *Kroppcarcinus siderastreicola* Badaro, Neves, Castro and Johnsson, 2012, is so far only known from Brazil, whereas *Troglocarcinus corallicola* Verrill, 1908 and *Opecarcinus hypostegus* (Shaw and Hopkins, 1977) have amphi-Atlantic distributions (Kropp and Manning 1987).

The present study focuses on the gall crab fauna off Curaçao, for which previously only one gall crab had been recorded (Kropp and Manning 1987). The present study uses the "reversed" approach, which is to investigate the associated fauna from the perspective of the host by collecting specimens from as many coral species as possible.

## Material and Methods

Between 16 October and 9 November, 2013, fieldwork was conducted around Curaçao (Dutch Caribbean, Leeward Islands) in the southern Caribbean Sea. A total of 23 localities were visited, 22 on the leeward side and one on the windward side of the island. Cryptochirids were sampled from a wide range of corals to a maximum depth of 40 m. After in situ photography, crabs were collected from their coral hosts and taken to the CARMABI research station for further processing. All cryptochirids were photographed in vivo with a digital SLR camera with 50/60 mm macro lens, and subsequently fixed in 80% ethanol. The crab specimens were stored in the scientific collections of Naturalis Biodiversity Center in Leiden, the Netherlands.

Identifications of cryptochirids were based on Kropp and Manning (1987) and Badaro et al. (2012), whereas coral identifications were based on Wells (1973), Zlatarski and Martínez-Estalella (1982), Humann and DeLoach (2002), Coralpedia (http://coralpedia.bio.warwick.ac.uk), and the reference collections of Naturalis Biodiversity Center. Coral nomenclature was updated following Budd et al. (2012).

## Results

In total, 21 coral species were recorded hosting three cryptochirid species off Curaçao. Eight of these 21 coral species represent new records as cryptochirid hosts (Fig. 1A–H). With an additional 10 host records based on literature, the number of Atlantic host coral species for gall crabs is now 31 (Table 1). The majority of the coral species housing gall crabs belong to the coral families Agariciidae and Mussidae, the latter being the Atlantic coral family with most species. *Favia fragum* (see Table 1 for species authorities), *Manicina areolata,* and *Mussa angulosa* were only recorded in low densities, yet they were found inhabited by cryptochirids on two different occasions. Some common coral species (e.g., *Colpophyllia natans* and *Meandrina meandrites*) were frequently found inhabited by gall crabs. *Mycetophyllia* sp. was previously recorded as a host in Kropp and Manning (1987), but despite extensive searches, no cryptochirid was found associated with *Mycetophyllia* off Curaçao.

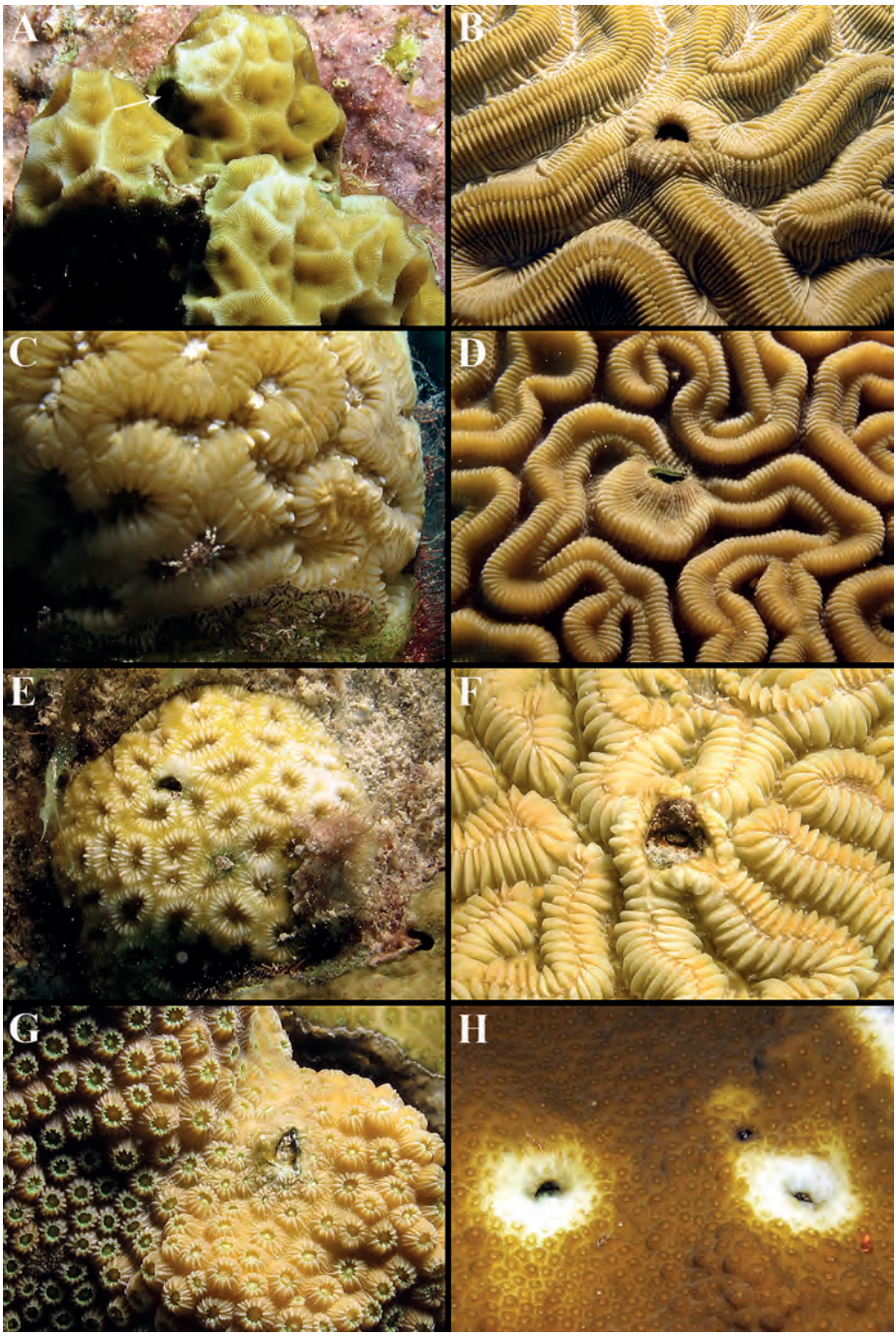


Figure 1. Gall crab dwellings in the newly reported coral hosts. (A) *Agaricia humilis*, (B) *Colpophyllia natans*, (C) *Dendrogyra cylindrus* (free-living male), (D) *Diploria labyrinthiformis*, (E) *Favia fragum*, (F) *Meandrina meandrites*, (G) *Orbicella faveolata*, (H) *Orbicella franksi*. For the associated gall crab species, see Table 1.

Table 1. Overview of the reef coral species hosting shallow-water Atlantic cryptochirids. Names of coral species indicated **in bold** represent new host records. Tcor = *Troglocarcinus corallicola* Verrill, 1908, Ohyp = *Opecarcinus hypostegus* (Shaw and Hopkins, 1977), Ksid = *Kroppcarcinus siderastreicola* Badaro et al., 2012.

| Coral family/species | Crab | Present study | References earlier records | Remarks |
|---|---|---|---|---|
| Agariciidae | | | | |
| *Agaricia agaricites* (Linnaeus, 1758) | Ohyp | *n* = 5 | Kropp and Manning 1987, Scott 1987 | |
| *Agaricia fragilis* Dana, 1846 | Ohyp | *n* = 1 | Shaw and Hopkins 1977, Kropp and Manning 1987 | |
| *Agaricia grahamae* Wells, 1973 | Ohyp | *n* = 1 | Kropp and Manning 1987, Scott 1987 | |
| ***Agaricia humilis* Verrill, 1901** | Ohyp | *n* = 1 | | New host for *O. hypostegus*. |
| *Agaricia lamarcki* Milne-Edwards and Haime, 1851 | Ohyp | *n* = 11 | Kropp and Manning 1987, Scott 1987 | |
| Astrocoeniidae | | | | |
| *Stephanocoenia intersepta* (Lamarck, 1816) | Tcor | — | Scott 1985 | As *S. michellini* by Scott (1985), considered a j.s. of *S. intersepta* (see Zlatarski and Martínez-Estalella 1982). There is no material available to check if this record should possibly be attributed to *K. siderastreicola.* |
| *S. intersepta* | Ksid | *n* = 4 | | First record outside of Brazil, new host for *K. siderastreicola.* |
| Caryophylliidae | | | | |
| *Polycyathus* sp. | Tcor | — | Kropp and Manning 1987 | |
| Meandrinidae | | | | |
| ***? Dendrogyra cylindrus* Ehrenberg, 1834** | Tcor | *n* = 1 | | This is a tentative new host record. One male was collected from a *D. cylindrus* colony, but no dwelling was found (see Fig. 1). |
| *Dichocoenia stokesii* Milne-Edwards and Haime, 1848 | Tcor | *n* = 2 | Verrill 1908, Shaw and Hopkins 1977 | As *Dichocoenia* sp. by Verrill (1908) and Shaw and Hopkins (1977). |
| ***Meandrina meandrites* (Linnaeus, 1758)** | Tcor | *n* = 7 | | New host for *T. corallicola.* |
| Merulinidae | | | | |
| *Orbicella annularis* (Ellis and Solander, 1786) | Tcor | *n* = 2 | Scott 1985, 1987, Kropp and Manning 1987 | |
| ***Orbicella faveolata* (Ellis and Solander, 1786)** | Tcor | *n* = 3 | | New host for *T. corallicola.* |
| ***Orbicella franksi* (Gregory, 1895)** | Tcor | *n* = 4 | | New host for *T. corallicola.* |

Table 1. Continued.

| Coral family/species | Crab | Present study | References earlier records | Remarks |
|---|---|---|---|---|
| Montastraeidae | | | | |
| *Montastraea cavernosa* (Linnaeus, 1766) | Tcor | *n* = 4 | Scott 1985, Kropp and Manning 1987 | |
| Mussidae | | | | |
| ***Colpophyllia natans* (Houttuyn, 1772)** | Tcor | *n* = 6 | | New host for *T. corallicola.* |
| ***Diploria labyrinthiformis* (Linnaeus, 1758)** | Tcor | *n* = 5 | | New host for *T. corallicola.* |
| ***Favia fragum* (Esper, 1795)** | Tcor | *n* = 2 | | New host for *T. corallicola.* |
| *Favia gravida* Verrill, 1868 | Tcor | — | Kropp and Manning 1987 | *Favia gravida*'s distribution range includes Brazil and the eastern Atlantic (Laborel 1969, 1974). |
| *Isophyllia sinuosa* (Ellis and Solander, 1786) | Tcor | — | Scott 1985, Kropp and Manning 1987 | |
| *Manicina areolata* (Linnaeus, 1758) | Tcor | *n* = 2 | Rathbun 1937, Utinomi 1944, Shaw and Hopkins 1977, Scott 1985, Kropp and Manning 1987, Carricart-Ganivet 2004 | As *Meandra areolata* by Rathbun (1937), as *Meandra areolata* and *Meandrea areolata* var. *hispida* by Utinomi (1944). |
| *Mussa angulosa* (Pallas, 1766) | Tcor | *n* = 2 | Shaw and Hopkins 1977 | |
| *Mussismilia hispida* (Verrill, 1901) | Tcor | — | Utinomi 1944, Coelho 1966 in Kropp and Manning 1987 | As *Mussa (Isophyllia) dipsacea*, *Mussa (Symphyllia) hispida*, and *Mussa Harrttii* var. *conferta* by Utinomi (1944), as *M. hispida tenuisepta* by Coelho (1966). Genus endemic for Brazil. |
| *M. hispida* | ? Ohyp | — | Noguiera 2003 | *Opecarcinus hypostegus* has only been recorded from *M. hispida* by Noguiera (2003). Because no other records exist, I tentatively include it here. |
| *Mycetophyllia* sp. | Tcor | — | Kropp and Manning 1987 | |
| *Pseudodiploria clivosa* (Ellis and Solander, 1786) | Tcor | *n* = 3 | Verrill 1908, Scott 1985 | As *Meandra clivosa* by Verrill (1908), as *Diploria clivosa* by Scott (1985). |
| *Pseudodiploria strigosa* (Dana, 1846) | Tcor | *n* = 4 | Scott 1985, Kropp and Manning 1987 | As *Diploria strigosa* by Scott (1985) and Kropp and Manning (1987). |
| *Scolymia lacera* (Pallas, 1766) | Tcor | — | Shaw and Hopkins 1977, Martínez-Estalella 1982 | |

Table 1. Continued.

| Coral family/species | Crab | Present study | References earlier records | Remarks |
|---|---|---|---|---|
| Oculinidae | | | | |
| *Oculina* sp. | Tcor | — | Kropp and Manning 1987 | |
| *Oculina varicosa* Lesueur, 1821 | Tcor | — | Scotto and Gore 1981 | |
| *Sclerhelia hirtella* (Pallas, 1766) | Tcor | — | Kropp and Manning 1987, den Hartog 1989 | |
| Siderastreidae | | | | |
| *Siderastrea siderea* (Ellis and Solander, 1786) | Tcor | — | Kropp and Manning 1987 | |
| *S. siderea* | Ohyp | — | Scott 1985, 1987 | |
| *S. siderea* | Ksid | *n* = 8 | | First record outside of Brazil, new host for *K. siderastreicola*. |
| *Siderastrea stellata* (Verrill, 1868) | Tcor / Ohyp | — | Johnsson et al. 2006 | |
| *S. stellata* | Ksid | — | Noguiera et al. 2014 | Records from Bahia State: Tinharé-Boipeba Archipel, Todos-os-Santos Bay, and the North Shore. |
| *Siderastrea* sp. | Ksid | — | Badaro et al. 2012 | Described from Guarajuba (type locality) and Praia do Forte (Brazil) in northern Bahia State. |


Figure 2. A female *Troglocarcinus corallicola* (A) in her lodge inside a colony of the coral *Orbicella annularis*, with a free-living male (B) residing closely.

*Kroppcarcinus siderastreicola* is recorded here outside of Brazil for the first time, with *Siderastrea siderea* and *Stephanocoenia intersepta* as new hosts. *Opecarcinus hypostegus*, representing a new record for Curaçao, was found in association with five *Agaricia* species, of which *Agaricia humilis* is a new record. The agariciid *Helioseris cucullata* was encountered on a few reefs, but was not found inhabited by cryptochirids. *Troglocarcinus corallicola* was associated with a wide range of hosts, but did not occur in association with Agariciidae (Table 1).

Male "Visiting" Female Gall Crab.—During a dive in Slangenbaai (Snake Bay) a male *T. corallicola* was observed residing close to the dwelling of a female (Fig. 2A–B). The female was partially extended from her lodge, an uncommon sight for cryptochirids. The male was observed for approximately 5 min during which he did not move. This immobility could have been caused by the presence of the diver and/or the flashes of the camera strobe.

In the present study, cryptochirid males were collected mainly from their own dwelling on a host coral, with the exception of this record of *T. corallicola* from *Orbicella annularis*, a free-living male *T. corallicola* from *Dendrogyra cylindrus* and a free-living male *T. corallicola* from *Pseudodiploria clivosa* (Table 1).

## Discussion

Previously only one published record was available for the gall crab fauna of Curaçao; LB Holthuis collected *Troglocarcinus corallicola* in 1957 from unknown coral hosts in Piscadera Baai (Piscadera Bay, record in Kropp and Manning 1987). This record was also the only available record from the southern Caribbean Sea. The results of the present study increase the gall crab fauna of Curaçao from one to three

species, and it now has the highest number of recorded cryptochirid-coral associations. *Opecarcinus hypostegus* and *T. corallicola* were already known from various localities in the Caribbean region, but the recently described *K. siderastreicola* was so far only known from off Bahia State, Brazil (Badaro et al. 2012, Noguiera et al. 2014). *Kroppcarcinus siderastreicola* is now also documented from the Caribbean Sea. It is possible that *K. siderastreicola* also occurs in the central Atlantic Ocean, like *T. corallicola* and *O. hypostegus*, because its host coral genus *Siderastrea* has a distribution range that includes western off Africa (Laborel 1974, Neves et al. 2010, Nunes et al. 2011). *Siderastrea siderea* is now recorded to host *K. siderastreicola*, a new host for the species. This coral species was previously considered restricted to the Caribbean Sea, but was recently recorded off Brazil (Neves et al. 2010).

Eight new coral hosts were recorded for gall crabs, which increases the number of Atlantic host coral species from 23 to 31 (Table 1). The new host records include common coral species like *Colpohyllia natans, Diploria labyrinthiformis,* and *Meandrina meandrites*, all of which are inhabited by *T. corallicola*, a generalist that occurs in association with a wide variety of Atlantic coral species (Verrill 1908, Kropp and Manning 1987). *Opecarcinus hypostegus* is associated with Atlantic species of the coral families Agariciidae (Kropp and Manning 1987, present study) and Siderastreidae (Scott 1985, 1987, Johnsson et al. 2006), whereas *K. siderastreicola* is now known from Siderastreidae and the astrocoeniid *S. intersepta.* Consistent with previous collections, no gall crabs were encountered in corals belonging to the families Acroporidae and Poritidae (Kropp and Manning 1987, Kropp 1990).

One of the newly recorded hosts, *Dendrogyra cylindrus,* is possibly not a true host of cryptochirids. A male *T. corallicola* was found on the surface of a colony, among the coral tentacles, but no dwelling was found. No other gall crabs were found on *D. cylindrus* colonies despite further searching. This single observation, also based on the fact that there are no other records of gall crabs associated with long-tentacled coral species, may reflect the wanderlust of a free-living male.

The observation of a free-living male *T. corallicola* close to the lodged female in an *Orbicella annularis* colony is consistent with Asakura (2009), who, based on anecdotal evidence and observations (see McCain and Coles 1979, and references in Asakura 2009), used the term "visiting" for the mating system in which cryptochirid males "visit" females inhabiting separate galls or pits. Baeza and Thiel (2007) used the term "visiting" or "pure-search polygynandry of sedentary females," and Guinot et al. (2013) used "visiting" for the mating system in which males of symbiotic species of crabs move from host to host in search of potential female mates. Baeza and Thiel (2007) presume that a "pure-search polygynandry of sedentary females" evolves when hosts are extremely small, which is (mostly) not the case in cryptochirids. Asakura (2009) specifically mentioned *T. corallicola*: "… the male crab normally resides outside the gall, which was constructed by the female, and is thought to visit the gall of the female for mating." The fact that almost all other males were collected from their own dwelling, as well as the close proximity to the female, suggests that this male was indeed "visiting." This is the first photodocumented observation of this mating system in cryptochirids.

## Acknowledgments

The fieldwork was funded by KNAW (Schure-Beijerinck-Poppingfonds) and the TREUB-maatschappij (Society for the Advancement of Research in the Tropics), and supported by the CARMABI Research Station and DiveVersity Curaçao. Two reviewers provided constructive comments on an earlier version of this manuscript.

## Literature Cited

Asakura A. 2009. The evolution of mating systems in decapod crustaceans. *In:* Martin JW, Crandall KA, Felder DL(eds.) Decapod Crustacean Phylogenetics. Crustacean Issues. Koenemann S. (series editor) Vol. 18. Boca Raton, London, New York: CRC Press, Taylor and Francis Group. p. 121–182.

Baeza JA, Thiel M. 2007. The mating system of symbiotic crustaceans: a conceptual model based on optimality and ecological constraints. *In:* Duffy JE, Thiel M, editors. Evolutionary ecology of social and sexual systems. Crustaceans as model organisms. Oxford, Oxford University Press. p. 250–267. http://dx.doi.org/10.1093/acprof:oso/9780195179927.003.0012

Badaro MFS, Neves EG, Castro P, Johnsson R. 2012. Description of a new genus of Cryptochiridae (Decapoda: Brachyura) associated with *Siderastrea* (Anthozoa: Scleractinia), with notes on feeding habits. Sci Mar. 76(3):517–526. http://dx.doi.org/10.3989/scimar.03538.02E

Budd AF, Fukami H, Smith ND, Knowlton N. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool J Linn Soc Lond. 166:465–529. http://dx.doi.org/10.1111/j.1096-3642.2012.00855.x

Carricart-Ganivet JP, Carrera-Parra LF, Quan-Young LI, García- Madrigal MS. 2004. Ecological note on *Troglocarcinus corallicola* (Brachyura: Cryptochiridae) living in symbiosis with *Manicina areolata* (Cnidaria: Scleractinia) in the Mexican Caribbean. Coral Reefs. 23:215–217.

Castro P. 1988. Animal symbioses in coral reef communities: a review. Symbiosis. 5:161–184.

Guinot D, Tavares M, Castro P. 2013. Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. Zootaxa. 3665:1–414. http://dx.doi.org/10.11646/zootaxa.3665.1.1

Hartog JC den. 1989. Herinneringen aan een reis naar Sint-Helena (3). Dieren 6:114–120. [in Dutch]

Hoeksema BW, van der Meij SET, Fransen CHJM. 2012. The mushroom coral as a habitat. J Mar Biol Assoc UK. 92:647–663. http://dx.doi.org/10.1017/S0025315411001445

Humann P, Deloach N. 2002. Reef coral identification: Florida, Caribbean, Bahamas. New World Publications, Florida. 278 p.

Johnsson R, Neves E, Franco GMO, da Silveira FL. 2006. The association of two gall crabs (Brachyura: Cryptochiridae) with the reef-building coral *Siderastrea stellata* Verrill, 1868. Hydrobiologia. 559:379–384. http://dx.doi.org/10.1007/s10750-005-9307-4

Kropp RK. 1990. Revision of the genera of gall crabs (Crustacea: Cryptochiridae) occurring in the Pacific Ocean. Pac Sci. 44:417–448.

Kropp RK, Manning RB. 1987. The Atlantic gall crabs, family Cryptochiridae (Crustacea: Decapoda: Brachyura). Smithsonian Contrib Zool. 462:1–21. http://dx.doi.org/10.5479/si.00810282.462

Laborel J. 1969. Madréporaires et hydrocoralliaires récifaux des côtes brésiliennes. Systématique, écologie, répartition verticale et géographique. Annales de l'Institut océanographique. 47:171–229.

Laborel J. 1974. West African reef corals: a hypothesis on their origin. Proc 2nd Int Coral Reef Symp. 1:425–442.

McCain JC, Coles SL. 1979. A new species of crab (Brachyura, Hapalocarcinidae) inhabiting pocilloporid corals in Hawaii. Crustaceana. 36: 81–89. http://dx.doi.org/10.1163/156854079X00230

McKinney ML. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annu Rev Ecol Syst. 28:495–516. http://dx.doi.org/10.1146/annurev.ecolsys.28.1.495

Neves EG, da Silveira FL, Pichon M, Johnsson R. 2010. Cnidaria, Scleractinia, Siderastreidae, *Siderastrea siderea* (Ellis and Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical southwestern Atlantic. Check List. 6:505–510.

Nogueira JMM. 2003. Fauna living in colonies of *Mussismilia hispida* (Verrill) (Cnidaria: Scleractinia) in four South-eastern Brazil islands. Braz Arch Biol Tech. 46:421–432. http://dx.doi.org/10.1590/S1516-89132003000300014

Noguiera MM, Menezes NM, Johnsson R, Neves E. 2014. The adverse effects of cryptochirid crabs (Decapoda: Brachyura) on *Siderastrea stellata* Verril, 1868 (Anthozoa: Scleractinia): causes and consequences of cavity establishment. Cah Biol Mar. 55:155–162.

Nunes FLD, Norris RD, Knowlton N. 2011. Long distance dispersal and connectivity in amphi-Atlantic corals at regional and basin scales. PLoS One. 6: e22298. http://dx.doi.org/10.1371/journal.pone.0022298

Oigman-Pszczol SS, Creed JC. 2006. Distribution and abundance of fauna on living tissues of two Brazilian hermatypic corals (*Mussismilia hispida* (Verril, 1902) and *Siderastrea stellata* Verril, 1868). Hydrobiologia. 563:143–154. http://dx.doi.org/10.1007/s10750-005-0002-2

Rathbun MJ. 1937. The oxystomatous and allied crabs of America. Bull US Nat Mus. 166:1–278.

Reed JK, Gore RH, Scotto LE, Wilson KA. 1982. Community composition, structure, areal and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs. Bull Mar Sci. 32:761–786.

Scott PJB. 1985. Aspects of living coral associates in Jamaica. Proc 5th Int Coral Reef Congress, Tahiti. 5:345–350.

Scott PJB. 1987. Associations between corals and macro-infaunal invertebrates in Jamaica, with a list of Caribbean and Atlantic coral associates. Bull Mar Sci. 40(2):271–286.

Scott PJB. 1988. Distribution, habitat and morphology of the coral and rock-boring bivalve *Lithophaga bisulcata* (d'Orbigny) (Mytilidae: Lithophaginae). J Mollus Stud. 54:83–85. http://dx.doi.org/10.1093/mollus/54.1.83

Scotto LE, Gore RH.1981. Studies on decapod Crustacea from the Indian River region of Florida. XXIII. The laboratory cultured zoeal stages of the coral gall-forming crab *Troglocarcinus corallicola* Verrill, 1908 (Brachyura: Hapalocarcinidae) and its familial position. J Crustacean Biol. 1(4):486–505. http://dx.doi.org/10.2307/1548126

Shaw JK, Hopkins TS. 1977. The distribution of the family Hapalocarcinidae (Decapoda, Brachyura) on the Florida Middle Ground with a description of *Pseudocryptochirus hypostegus* new species. Proc 3rd Int Coral Reef Symp, Miami. 1:177–183.

Stella JS, Pratchett MS, Hutchings PA, Jones GP. 2011. Diversity, importance and vulnerability of coral-associated invertebrates. Oceanogr Mar Bio - Ann Rev. 49:43–104.

Utinomi H. 1944. Studies on the animals inhabiting reef corals. III. A revision of the family Hapalocarcinidae (Brachyura), with some remarks on their morphological peculiarities. Palao Tropical Biological Station Studies. 2(4):687–731, pls. 3–5.

Verrill AE. 1908. Brachyura and Anomura: their distribution, variations, and habits: Decapod Crustacea of Bermuda. I. Transactions of the Connecticut Arts and Sciences. 13:299–474.

Wells JW. 1973. New and old scleractinian corals from Jamaica. Bull Mar Sci. 23:16–58.

Zlatarski VN, Martínez-Estalella N. 1982. Les Scléractiniaires de Cuba avec des données sur les organismes associés. Editions l'Académie bulgare des Sciences, Sofia. 472 p.