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Sponges (Porifera) associated with the decorator crab *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867): three new records for Mexican waters

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Abstract. Sponges and decapods share diverse ecological interactions, including epibiosis in which sponges colonize crab carapaces. We report three sponge species—*Stelletta kallitetilla* (Laubenfels, 1936), *Hymeniacidon heliophila* (Wilson, 1911), and *Haliclona (Reniera) manglaris* Alcolado, 1984—on the decorator crab *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) collected from the Campeche Bank (southern Gulf of Mexico), presenting new records for Mexican waters. Our research highlights the importance of describing ecologically associated species and offers insights into the presence of sponge species not previously reported in Mexico.

Key words. Campeche Bank, ecological associations, epibiosis, Gulf of Mexico

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INTRODUCTION

Sponges (Porifera) and decapods (Arthropoda, Crustacea) share a diverse array of ecological interactions (Wulff 2006; Hultgren and Stachowicz 2008, 2009; Özcan and Katağan 2011). One of these is epibiosis, a facultative interaction in which one organism (the epibiont) adheres to the living surface of another (the basibiont) (Wahl et al. 1997). In specific sponge–crab associations, the sponges act as epibionts, settling and growing on the carapace of crabs. This interaction is often promoted by the decorating behavior of certain crab species, particularly within the superfamilies Majoidea Samouelle, 1819 and Dromioidea De Haan, 1833 (Cruz-Rivera 2001; Bedini et al. 2003), where crabs use specific sponge species as natural carapace ornaments (Maldonado and Uriz 1992; Parapar et al. 1997; Poore and Ahyong 2023).

Numerous studies have shown that decorator crabs of the superfamily Majoidea are often associated with sponges from orders Suberitida Chombard & Boury-Esnault, 1999, Haplosclerida Topsent, 1928, and Poecilosclerida Topsent, 1928 (Maldonado and Uriz 1992; Parapar et al. 1997; Martinelli et al. 2007). Although it is difficult to determine the precise functional relationships (Bell 2008), evidence suggests sponges can provide several crucial benefits to their associates such as chemical and physical defenses against predation (Woods and Page 1999; Stachowicz and Hay 2000), as well as camouflage through cryptic coloration and textures, which help crabs avoid detection by predators or preys (Hultgren and Stachowicz 2011).

Among majoid crabs, the genus *Macrocoeloma* Miers, 1879 of the family Epialtidae (MacLeay, 1838) is well documented for its decorating behavior (Humann et al. 2013; Colavite et al. 2016). This genus has 12 recognized species, mostly found in the Western Atlantic (Felder et al. 2009). However, detailed information about sponge associations is only available for one species from the Caribbean, *Macrocoeloma trispinosum* (Latreille, 1825), where the sponge *Lissondendoryx* (*Lissodendoryx*) *colombiensis* Zea & van Soest, 1986 is the only documented species used in its decorating repertoire (Rebolledo and Collin 2018; Cabrera-Guerrero and Jover-Capote 2019). Therefore, although the genus *Macrocoeloma* is recognized for its decorating ability, we have limited knowledge about the sponge taxa involved in these associations.

We present the first records of three sponges species inhabiting the carapace of the crab *Macrocoeloma nodipes*, a widely distributed species in the Western Atlantic, from the Bahamas to Brazil (Rodrigues-Alves et al. 2012). In the Gulf of Mexico, *M. nodipes* is commonly found in coastal habitats inhabiting shallow ar-

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eas, such as coral reefs, sand bottoms, shells, rocks, mangrove roots, grass-covered surfaces, and even in floating masses of *Sargassum* C.Agardh (Álvarez-Noguera and Villalobos-Hiriart 2002; Hermoso-Salazar and Arvizu-Coyotzi 2015; Carmona-Suárez and Poupin 2016). Our findings contribute to understanding sponge species potentially associated with the crab genus *Macrocoeloma*. Furthermore, our study introduces novel records for Mexican waters in the Gulf of Mexico, highlighting the importance of documenting interspecific associations between taxonomic groups. Such investigations can unveil species previously undocumented in an area or a region, emphasizing the importance of identifying and describing taxonomic species involved in these interactions.

METHODS

The crab specimens were collected from a depth of 16 m within the Campeche Bank, a broad shallow carbonate platform extending up to 120 m deep and forming part of the submerged Yucatan Peninsula (Johnston and Bernard 2017; Hübscher et al. 2023). The sampling site is located approximately 45 km west of the Yucatán Peninsula, offshore from the Celestún coast, at 20°48′14.4″ N, 090°50′10.32″ W (Figure 1). The Campeche Bank is characterized by hard bottoms and warm waters (Sanvicente-Añorve et al. 2014; Guzmán-Hidalgo et al. 2021), harboring numerous reef systems (Tunnell et al. 2007) as well as adjacent habitats such as mangroves and seagrass beds (typically *Thalassia thestudinum* Banks & Sol. ex K.D.Koenig (Durán-García et al. 2016). These auxiliary coastal environments represent vital ecosystems that support a wide diversity of marine and estuarine species (Robertson et al. 2019).

The crabs were obtained as bycatch during artisanal octopus fishing activities conducted on seagrass beds, using the traditional fishing method known locally as "jimbas", which are described in detail by López-Rocha et al. (2021). Post-collection, the crabs were promptly separated, frozen, and subsequently fixed in 90% ethanol before being preserved in 70% ethanol for long-term storage. Two crab specimens of *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) were collected; their carapaces measured 3.3–3.7 cm in length and 2.9–3.5 cm in width. These specimens were identified in the laboratory using the taxonomic keys provided by Abele and Kim (1986) and Ortiz (2022).

We follow the taxonomic identification of sponge specimens using the standard procedures outlined by Hajdu et al. (2011). The spicules were cleaned with nitric acid, allowing for detailed examination. Sponge frag-

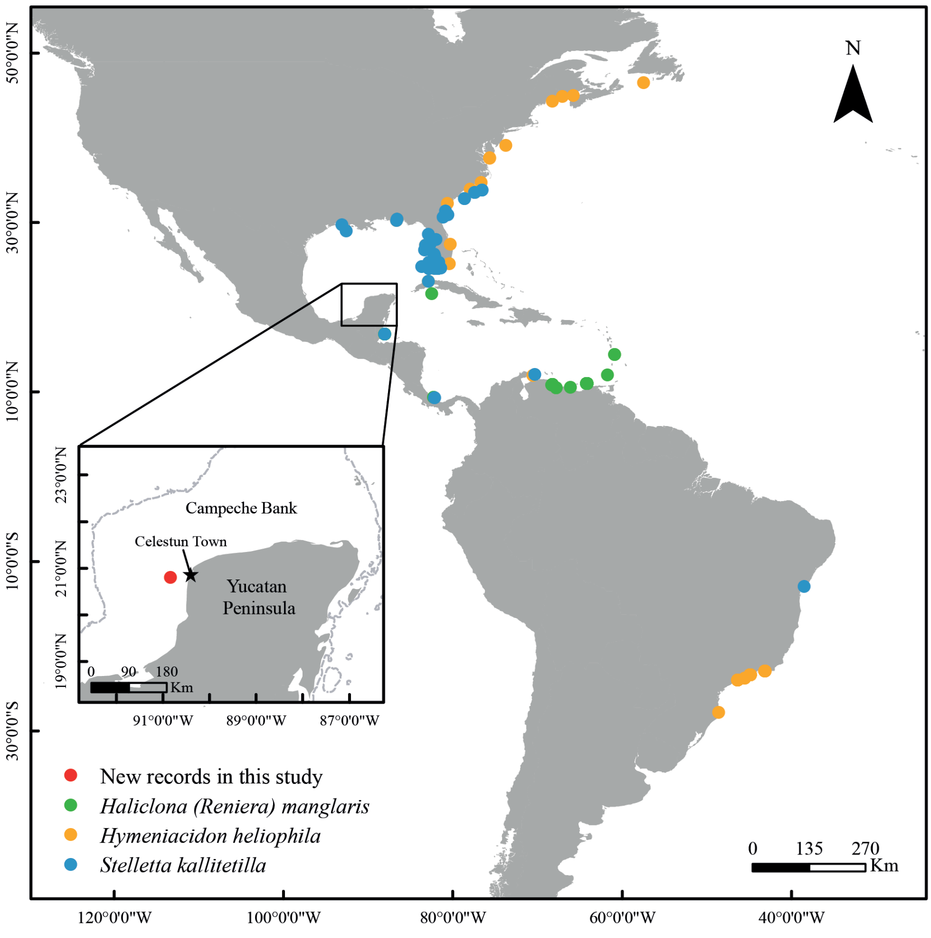

Figure 1. Distribution of *Haliclona (Reniera) manglaris*, *Hymeniacidon heliophila*, and *Stelletta kallitetilla* in the Western Atlantic. The sampling site for *Macrocoeloma nodipes* crabs is marked with a red dot. The gray dotted line indicates the 200-m bathymetric boundary of the Campeche Bank region. Data sourced from the Ocean Biodiversity Information System (OBIS 2024).

ments were hand-sectioned for analysis of the arrangement of the spicules within the skeletal architecture. To ensure permanent preservation, the cleaned spicules were mounted in Canada balsam, while the skeletal arrangements were embedded in Entellan® resin. We measured spicule size of 15 representative spicules from each spicule category, reported in the format: average (minimum–maximum) for length and width. Our Species-level identification of the sponges adhere to the classification system established by Morrow and Cárdenas (2015) and the authoritative World Porifera Database (de Voogd et al. 2024). Higher taxonomic ranks, including order, family, and genus, were assigned based on the comprehensive reference work of Hooper and Van Soest (2002). Supplementary literature consulted for species-level determinations included de Weerdt (2000), Cosme and Peixinho (2007), and Van Soest (2017).

The intact crab specimens, with sponges remaining attached to their carapaces, were accessioned into the regional "Crustáceos de Yucatán" (YUC-CC) collection housed at the Unidad Multidisciplinaria de Docencia e Investigación" (UMDI), Universidad Nacional Autónoma de México (UNAM), Sisal, Yucatan, Mexico. Additionally, as the recorded sponges represent new distributional records for Mexican waters, a small fragment from each specimen, accompanied by permanent microscope slide preparations of the corresponding spicules and skeletal architectures, were deposited in the National Collection "Colección Nacional del Phylum Porifera – Gerardo Green" (CNPGG) at the Instituto de Ciencias del Mar y Limnología, UNAM, Mexico City.

RESULTS

Three sponge species were found in association with the decorator crab *Macrocoeloma nodipes*, expanding the current knowledge of the sponges associated with these crabs. In addition, these sponge species are reported from Mexican waters for the first time.

Phylum Porifera Grant, 1836
Class Demospongiae Sollas, 1885
Subclass Heteroscleromorpha Cárdenas, Perez & Boury-Esnault, 2012
Order Haplosclerida Topsent, 1928
Family Chalinidae Gray, 1867
Genus *Haliclona* Grant, 1841
Subgenus *Haliclona* (*Reniera*) Schmidt, 1862

***Haliclona* (*Reniera*) *manglaris* Alcolado, 1984**
Figures 2A, 3A, B

Material examined. MEXICO – Yucatán • Celestún; 20°48′14.4″N, 090°50′10.32″W; 16 m depth; 11 Aug. 2022; Carlos A. Jiménez Flores leg.; on carapace of a female *Macrocoeloma nodipes*; YUC-CC-255-11-007387, CNPGG-2522.

Identification. External morphology: thickly encrusting to cushion shaped, elongated. Texture soft, fragile, and compressible, with 0.9 cm long × 0.47 cm wide. Surface smooth. Pale brown coloration in ethanol. Oscules not visible (Figure 2A). **Skeleton:** choanosomal skeleton is a well-defined isotropic net, comprising by an unispicular isotropic polygonal mesh with abundant spongin nodes. Spongin coating spicules, not abundant (Figure 3A). **Spicules:** megascleres only homogeneous and fusiform oxeas, slightly curved in the center and pointed. Spicules very uniform in size, 99.84 (82.05–118.08) × 3.82 (2.74–6.36) µm (Figure 3B).

Distribution. Caribbean Sea (Díaz 2005), Florida (de Weerdt 2000), Brazil (Cedro et al. 2007; Hajdu et al. 2011; Muricy et al. 2011).

Remarks. The spicular measurements provided for *Haliclona (Reniera) manglaris* in this study coincide remarkably with those reported in other studies in the Caribbean Sea region (de Weerdt et al. 1991; de Weerdt 2000). This species exhibits remarkable uniformity in oxeas length, ranging from 50 to 100 µm. The spicules are the smallest among *Haliclona* species of the subgenus *Reniera* in the Caribbean region. There are other species of *Haliclona* with small oxeas (up to 150 µm) in the Western Atlantic, most of which belong to subgenera other than *Reniera*. According to Bispo et al. (2014) and Muricy et al. (2015) these species are *H.* (*Haliclona*) *epiphytica* Zea & de Weerdt, 1999, *H.* (*Haliclona*) *lilacea* Mothes & Lerner, 1994, *H.* (*Rhizoniera*) *fugidia* Muricy, Esteves, Monteiro, Rodrigues & Albano, 2015, *H.* (*Halichoclona*) *pulitzerfinalii* Van Soest & Hooper, 2020, *H.* (*Rhizoniera*) *curacaoensis* (van Soest, 1980), *H. (Soestella) peixinhoae* Bispo, Correia & Hajdu, 2016, and *H. (Reniera) chlorilla* Bispo, Correia & Hajdu, 2016.

The subgenera of *Haliclona* are distinguished by their skeletons (de Weerdt 2000). For example, the subgenus *Reniera*, which includes our specimen, is characterized by a choanosomal skeleton with delicate, regular, unispicular, and isotropic reticulation, with spongin present at spicule nodes (de Weerdt 2000). These characteristics in the choanosomal skeleton distinguish our specimen from other subgenera with small oxeas in the Western Atlantic. The species most like *H. (Reniera) manglaris* in its spicule dimensions is *H. (Reniera) chlorilla*. However, *Haliclona* species may exhibit cushion-shaped forms when the specimens are small (Bispo et al. 2014). Despite these similarities, there are subtle differences in their oxeas. Specifically, *H. (Reniera)*

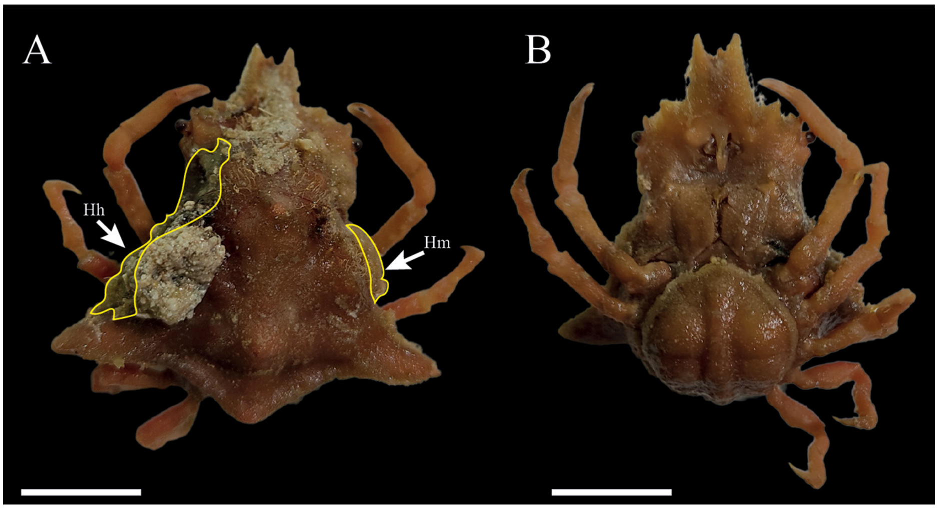

Figure 2. External morphology of *Haliclona (Reniera) manglaris* and *Hymeniacidon heliophila* associated with *Macrocoeloma nodipes*. **A.** Dorsal view of *M. nodipes* carapace showing the embedding of *H. (Reniera) manglaris* (Hm) and *H. heliophila* (Hh), with a yellow line delineating the sponge-covered area. **B.** Anterior view of *M. nodipes*. Scale bars: 1 cm.

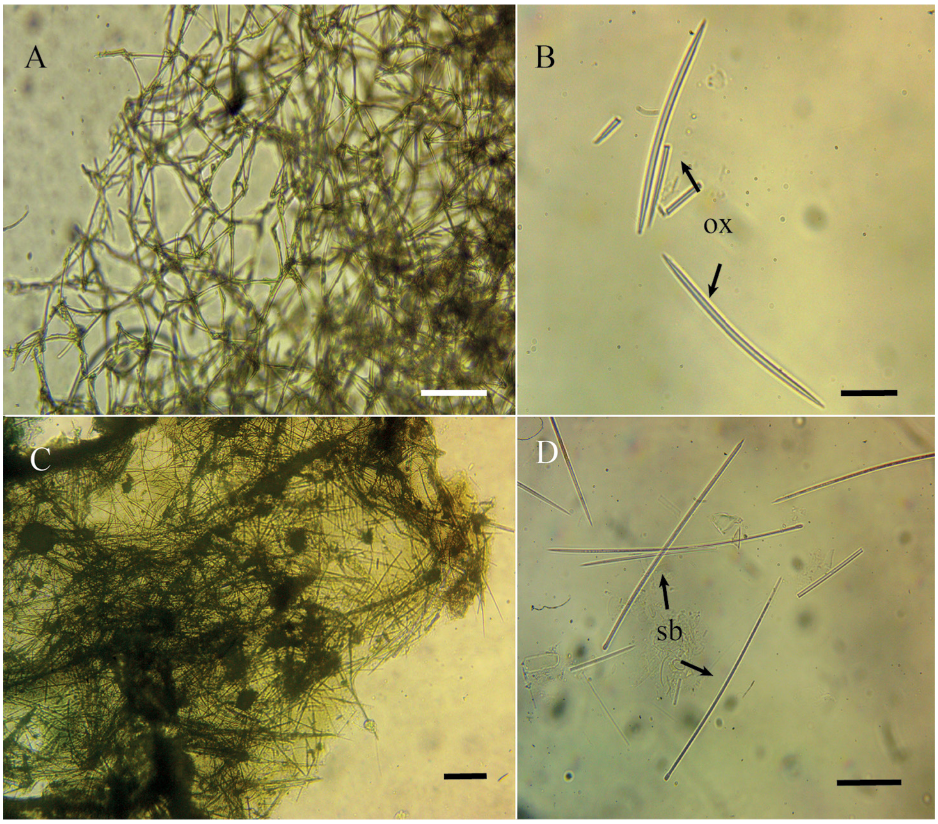

Figure 3. Skeleton and spicules of *Haliclona (Reniera) manglaris* and *Hymeniacidon heliophila*. **A, B.** Cross section of the choanosomal skeleton and oxeas (ox) of *H. (Reniera) manglaris* respectively. **C, D.** Cross section of the choanosomal skeleton and subtylostyles (sb) of *H. heliophila* respectively. Scale bars: A, B = 100 µm; C = 20 µm; D = 50 µm.

chlorilla possesses wider, robust oxeas (5–7.5 µm) that are either straight or curved (Bispo et al. 2014), while *H. (Reniera) manglaris* features slender fusiform oxeas (3–5 µm) with long, sharp points and varying degrees of curvature (Hajdu et al. 2011). Our specimen corresponds to *H. (Reniera) manglaris*, consistently displaying curved oxeas with no straight forms (Figure 3B).

Order Suberitida Chombard & Boury-Esnault, 1999
Family Halichondriidae Gray, 1867
Genus *Hymeniacidon* Bowerbank, 1858

Hymeniacidon heliophila **Wilson, 1911**
Figures 2A, 3C, D

Material examined. MEXICO – Yucatán • Celestún; 20°48′14.4″N, 090°50′10.32″W; 16 m depth; 11 Aug. 2022; Carlos A. Jiménez Flores leg.; on carapace of female *Macrocoeloma nodipes*; YUC-CC-255-11-007387, CNPGG-2523.

Identification. External morphology: thin encrusting, texture soft, 1.5 cm long. Smooth surface. Greenish brown in ethanol. Oscules not visible (Figure 2A). **Skeleton:** choanosomal region presents a disorganized matrix of spicules, with some bundles of styles without organization. Some free styles intersect with the bundles (Figure 3C). **Spicules:** only megascleres styles thin and slightly curved, often with faint tyle, 192.27 (123.74–233.45) µm × 2.45 (0.76–5.43) µm (Figure 3D).

Distribution. Virginia (Parker 1910), Florida (Laubenfels 1936), Bermudas (Laubenfels 1950), northern Gulf of Mexico (Little 1963), southeastern Caribbean (Van Soest 1981), Greater Antilles (Pulitzer-Finali 1986), Brazil (Muricy et al. 2011), Suriname, Guyana (Van Soest 2017).

Remarks. *Hymeniacidon heliophila* has been documented in United States waters in the northern Gulf of Mexico by Little (1963). Fortunato et al. (2020) identified *H. heliophila* as possessing the smallest styles among all congeneric species reported from the Western Atlantic region, with these diagnostic spicules never exceeding 500 µm in length. The style measurements obtained by us are consistent with Fortunato et al., corroborating the species identification. Remarkably, *H. heliophila* exhibits a propensity for a relationship with decorator crabs and has been previously reported living on species of the family Epialtidae (Stachowicz and Hay 2000).

Order Tetractinellida Marshall, 1876
Suborder Astrophorina Sollas, 1887
Family Ancorinidae Schmidt, 1870
Genus *Stelletta* Schmidt, 1862

Stelletta kallitetilla **(Laubenfels, 1936)**
Figure 4A–E

Material examined. MEXICO – Yucatán • Celestún; 20°48′14.4″N, 090°50′10.32″W; 16 m depth; 11 Aug. 2022; Carlos A. Jiménez Flores leg.; on carapace of *Macrocoeloma nodipes*, sex of crab unknown due to lack of anterior part of carapace; YUC-CC-255-11-007389, CNPGG-25225.

Identification. External morphology: encrusting, cushion-shaped. With a soft but firm consistency, slightly rough surface, 1.88 cm long × 0.5 cm wide. The ectosome is approximately 1 mm thick and easily visible. In etha-

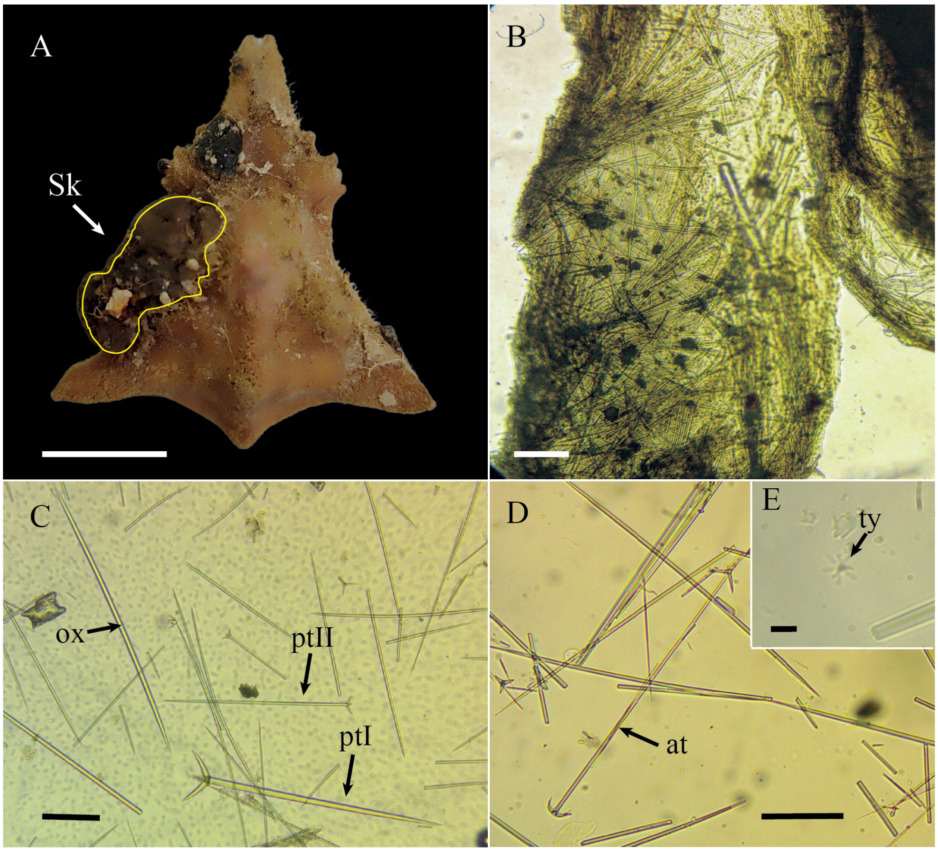

Figure 4. External morphology, skeleton and spicules of *Stelletta kallitetilla* embedded in *Macrocoeloma nodipes*. **A.** Dorsal view of the carapace of *M. nodipes* with the embedding of *S. kallitetilla* (Sk), yellow line delimits the area covered by the sponge. **B.** Cross section of the choanosomal skeleton. **C.** Oxeas (ox) and Plagiotriaenes in the two size ranges found (ptI, ptII). **D**. Anatriaene (at). **E.** Tylaster. Scale bars: A = 1.5 cm; B–D = 100 µm; E = 10 µm.

nol, it exhibits a dark purple color on the exterior and a grayish-brown hue on the interior. Oscules not visible (Figure 4A). **Skeleton:** choanosomal skeleton not radial; skeleton dominated by oxeas that intersect paratangentially, that forms bouquets reaching surface. Anatriaenes and plagiotriaenes scarce and scattered, without clear orientation in the choanosoma. (Figure 4B). **Spicules:** megascleres. Oxeas: thin and straight (some slightly curved), with pointed ends, 480.51 (378.45–595.6) × 5.94 (4.27–6.81) µm (Figure 4C); plagiotriaenes I: longer and thicker rhabdome than type II, measuring 596.37 (588.17–604.57) × 16.81 (16.46–17.15) µm, clads arranged at an angle of 45°, with a cladome width 111.34 (103.04–119.63) µm (Figure 4C); plagiotriaenes II: with a short and thinner rhabdome than previous one, 465.02 (361.41–577.49) × 8.17 (6.81–10.06) µm, cladome width 44.23 (41.05–52) µm (Figure 4C); anatriaenes: thin and straight rhabdome measuring 447.61 (286.78–637.51) × 4.38 (2.44–5.4) µm, forward curved clads 18.37 (10.12–27.09) µm and cladome width 33.58 (32.49–35.26) µm (Figure 4D). Microscleres are tylaster with slender rays, 12.05 (10.75–14.65) µm in diameter, with rays 4.82 (3.92–5.59) µm long and with 6–7 distinguishable rays (Figure 4E).

Distribution. Bahamas (Wiedenmayer 1977); Caribbean Sea (Van Soest 1981; Rützler et al. 2000); Greater Antilles (Alcolado 1980); Eastern Brazil (Cosme and Peixinho 2007).

Remarks: Within the sponge diversity of *Stelletta* in the Western Atlantic, two species stand out for their spicule assemblage comprising oxeas, plagiotriaenes, anatriaenes, and tylasters: *S. fibrosa* (Schmidt,1870) and *S. kallitetilla* (Cárdenas et al. 2009; Cosme and Peixinho 2007). However, a critical diagnostic feature distinguishes these two species. The large oxeas and plagiotriaenes of *S. fibrosa* exceed 1000 µm in length, while those of *S. kallitetilla* remain confined below this threshold across all its spicule types. The spicule dimensions of our specimen unambiguously align with the latter species: *S. kallitetilla*, although these were shorter than documented by Wiedenmayer (1977) and Cosme and Peixinho (2007). Cosme and Peixinho (2007) documented the distinctive acanthotylaster morphology of this species' tylasters, describing them as exhibiting spiny rays radiating from their spherical cores. Although we did not observe this ornamentation, the dimensions of the tylasters remained consistent with the range documented for *S. kallitetilla*.

DISCUSSION

Our study represents the first effort to describe sponge species associated with *Macrocoeloma nodipes* and expands current knowledge of sponge species related to this genus. The sponge *Hymeniacidon heliophila* has been reported in other decorator crabs of the family Epialtidae. The record of Stachowicz and Hay (2000) revealed a marked preference by the crab *Libinia dubia* H. Milne Edwards, 1834, to adorn itself with *H. heliophila* as a camouflaging agent. However, this association offers more than mere camouflage. Investigations into the chemical repertoire of *H. heliophila* have unveiled its potent defensive capabilities (Meneses-Ribeiro et al. 2010). Extracts from this sponge have demonstrated remarkable repellent properties against the predator *Logodon rhomboides* (Linnaeus, 1766) (Stachowicz and Hay 2000). In addition, chemical defensive properties, documenting the sponge extract's ability to repel the crab *Calcinus tibicen* (Herbst, 1791) and the sea urchin *Lytechinus variegatus* (Lamarck, 1816) (Meneses-Ribeiro et al. 2010). Therefore, this sponge could also provide chemical defense against decorator crab predators in addition to camouflage.

Furthermore, *H. heliophila* and other sponges have been reported in the family Epialtidae. Bonfi and Carvacho (1989) documented the presence of the genus *Mycale* Gray 1867 on the crab *Pelia pacifica* A. Milne-Edwards, 1875. Calcareous sponges of the genus *Grantia* Fleming, 1828 were also found on the crabs *Herbstia parvifrons* Randall, 1840, and *Scyra acutifrons* Dana, 1851. Finally, these authors identified the sponge *Halichondria* (*Halichondria*) *panicea* (Pallas, 1766) on the carapace of *Pelia tumida* (Lockington, 1877) and *Scyra acutifrons* Dana, 1851. Our study adds two more species to the list of sponges associated with the crab family Epialtidae: *Haliclona (Reniera) manglaris* and *Stelletta kallitetilla*.

While the genus *Haliclona* has been one of the genera most frequently found in crabs of other families in the superfamily Majoidea, specifically in the crab *Pitho sexdentata* Bell, 1836 of the family Mithracidae MacLeay, 1838 (Sánchez-Vargas and Hendricx 1987), *Maja squinado* (Herbst, 1788) of the family Majidae (Parapar et al. 1997), and *Inachus aguiarii* de Brito Capello, 1876 of the family Inachidae MacLeay, 1838 (Maldonado and Uriz 1992), the discovery of *Stelletta kallitettilla* in a crab–sponge association represents a remarkable first to science. The genus *Stelletta* is renowned for its vast biochemical wealth, with a vast number of metabolites and diverse biological activities (Wu et al. 2019). This chemical property raises the possibility that like the defensive virtues given by *H. heliophila*, *S. kallitetilla* may possess chemical compounds with predator-repellent properties.

The three sponge species found in this study have a wide distribution in the Western Atlantic (Figure 1). However, only *S. kallitetilla* and *H. heliophila* had been recorded in the northern Gulf of Mexico in United States waters (Rützler et al. 2009), while *H. (Reniera) manglaris* has records mainly within the Caribbean Sea, from Belize to the Lesser Antilles (de Weerdt 2000). Therefore, our findings represent the first formal record of this species, with their respective morphological and spicular description in the Mexican waters of the Gulf of Mexico. The discovery of these previously undocumented sponge species highlights the vast biodiversity that remains uncovered in this region, even in relatively well-studied coastal environments (Ugalde et al. 2015, 2021; Ávila et al. 2022).

Studies on the fauna associated with decorator crabs can contribute to regional biodiversity data (Williams and McDermott 2004). Due to the large number of species within the superfamily Majoidea—approximately 930 in the Indo-Pacific and 125 in the Atlantic (Boschi 2000; Cruz-Castaño and Campos 2003; Poore and Ahyong 2023)—it is essential to record and describe epibionts decorator crab species. Besides providing new information about the biology of these species, describing decorating behavior can potentially result in the description of new species (McLay and Hosie 2022) or new records (like in this study). Furthermore, these discoveries emphasize the ongoing need for extensive taxonomic investigations in epibiotic relations, as they can reveal novel insights into the complex inter specific relations within marine environments.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

Author contributions

Conceptualization: PAHS, LVLD. Data curation: PAHS, IPM. Formal analysis: PAHS, IPM. Funding acquisition: LVLD, DU. Investigation: PAHS, IPM, DU. Methodology: PAHS, IPM, DU. Resources: LVLD. Supervision: LVLD, DU. Validation: DU. Visualization: PAHS. Project administration: LVLD, DU. Software: DU. Writing – original draft: PAHS. Writing – review and editing: DU, LVLD, IPM

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Data availability

All data that support the findings of this study are available in the main text.

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