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Research article

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First record of the genus *Staurocladia* (Hydrozoa: Cladonematidae) in the Gulf of Mexico with the description of *Staurocladia dzilamensis* sp. nov., a new species of crawling hydromedusa

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Abstract. The Cladonematidae are a family of hydrozoans with a worldwide distribution and morphological adaptations for a benthic mode of life. Species of this family are characterized by high morphological variability, which has caused many taxonomical debates, mainly for the species of the genera *Eleutheria* Quatrefages, 1842 and *Staurocladia* Hartlaub, 1917. Herein, we describe *Staurocladia dzilamensis* sp. nov., a new species of crawling hydromedusa from the southern Gulf of Mexico. This finding also constitutes the first record of the genus *Staurocladia* for the Gulf of Mexico. The presence of additional nematocyst clusters, supplementing the apical one on the upper branch of the tentacles, places it within *Staurocladia*. The presence of exumbrellar buds, a conspicuous marginal ring of nematocysts, 6–11 bifid tentacles with lower branches longer than their upper counterpart, the cnidome with stenoteles of two size classes, and two nematocyst clusters on the upper branch supplementing the apical one, opposite placed alternately on its aboral and oral sides permits to differentiate *S. dzilamensis* from its congeners. A taxonomic key for the species of *Staurocladia* is provided.

Keywords. Medusozoa, Mexico, Anthoathecata, Yucatan.

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Introduction

Medusae of the family Cladonematidae Gegenbaur, 1857 are characterized by having adaptations for a benthic mode of life. The individuals often show extensive morphological variability, which has generated much uncertainty in their taxonomy (Brinckmann-Voss 1970; Bouillon *et al.* 2006; Schuchert 2006; Ahuatzin-Hernández *et al.* 2022). Three genera are currently recognized within this family: *Cladonema* Dujardin, 1843, *Eleutheria* Quatrefages, 1842 and *Staurocladia* Hartlaub, 1917 (Schuchert 2023). The polyphyletic origin of some of its members (i.e., *Staurocladia*, *Eleutheria*), together with the limited morphological studies, have caused the taxonomic boundaries of the group to be uncertain (Nawrocki *et al.* 2010; Fang *et al.* 2022; Zhou *et al.* 2022). The main taxonomic debates have been on the genus level, mainly focusing on members of *Eleutheria* and *Staurocladia,* which show adaptations for a fully benthic lifestyle. Among these adaptations are a flattened umbrella, mesoglea reduction, and bifid tentacles with adhesive pads (Mayer 1910; Russell 1953; Nawrocki *et al.* 2010). Currently, both genera are separated based on the number of nematocyst clusters on their tentacles, i.e., one for *Eleutheria* and more than one for *Staurocladia* (Nawrocki *et al.* 2010).

Hartlaub (1917) established the genus *Staurocladia* to separate *Eleutheria vallentini* Browne, 1902, *E. claparedii* Hartlaub, 1889 and others from *E. dichotoma* Quatrefages, 1842, due to the hermaphroditism, the presence of a brood chamber, and the gonostyle in the polyp stage in the latter (Schuchert 2006). Hartlaub therefore used the combination *Staurocladia claparedii* (Hartlaub, 1889) since, like the other members of *Staurocladia*, this species lacks a brood chamber (Schuchert 2006). Gilchrist (1919) suggested the genus *Cnidonema* Gilchrist, 1919 for all the species of *Eleutheria* of the southern hemisphere due to the need to introduce a new genus for *E. claparedii*, which lacks a brood chamber (Schuchert 2006). Later studies (Browne & Kramp 1939; Kramp 1959, 1961, 1968; Brinckman-Voss 1970) modified this taxonomy and differentiated *Eleutheria* from *Staurocladia* by the number of nematocyst clusters on the tentacles (Schuchert 2006). *Staurocladia* currently comprises 11 valid species (Schuchert 2023), which can be distinguished mainly by the arrangement of their nematocyst clusters on the upper branch. Additional features to distinguish among the species of this genus are the presence/absence of exumbrellar buds, the number of tentacles and the length of their branches, and the features of the manubrium (Kramp 1961, 1968; Bouillon 1978). The hydroid of few species of *Staurocladia* is known, and the characteristics of the known species are very similar to each other (3–4 oral capitate tentacles and 4–6 aboral filiform tentacles) (Briggs 1920; Kakinuma 1963; Brinckmann-Voss 1970), so it seems there are not reliably diagnostics features to differentiate species only with this stage.

The genus *Staurocladia* is mainly distributed in temperate waters around the world (GBIF 2023), being less frequent in tropical seas (Bouillon 1978; Canché-Canché & Castellanos-Osorio 2005). Among the most documented species, we can mention *S. charcoti* (Bedot, 1908) from Antarctic and Subantarctic localities (i.e., Wilhelm Archipelago, McMurdo Sound, Graham Land, the South Shetland Islands, South Georgia and Kerguelen) (Galea & Schories 2012a), *S. portmanni* Brinckmann, 1964 from the Mediterranean Sea (Schuchert 2006), *S. vallentini* (Browne, 1902) from Chile, and Falkland Islands (Galea & Schories 2012b), *S. alternata* (Edmonson, 1930) from Hawaii and Papua New Guinea, and *S. acuminata* (Edmonson, 1930) from Japan, Hawaii, and Papua New Guinea. Other species less documented around the world are *S. schizogena* Bouillon, 1978, *S. ulvae* Bouillon, 1978, and *S. wellingtoni* Schuchert, 1996 (Bouillon *et al.* 1978, 1991; Schuchert 1996; Hirano *et al.* 2006) (Fig. 1).

Studies on hydrozoans from the southern Gulf of Mexico have been scarce and dispersed throughout history (e.g., Segura-Puertas 1992; Segura-Puertas & Ordóñez-López 1994; Mendoza-Becerril *et al.* 2018; Ahuatzin-Hernández *et al.* 2020, 2022). These have focused mainly on describing ecological aspects of planktonic organisms (e.g., Segura-Puertas 1992; Segura-Puertas & Ordóñez-López 1994; Loman-Ramos *et al.* 2007; Martell-Hernández *et al.* 2014; Flores-Coto *et al.* 2016; Puente-Tapia *et al.* 2022), so the taxonomy and biodiversity of benthic groups, such as hydroids (i.e., De la Cruz-Francisco *et al.* 2016; Mendoza-Becerril *et al.* 2018) and some Hydromedusae (e.g., Cortés-Lacomba *et al.* 2013; Ahuatzin-Hernández et al. 2020, 2022; López-Torres *et al.* 2023) are poor. Currently, there are no type species described for the southern Gulf of Mexico, and *Cladonema radiatum* Dujardin, 1843 is the only member of the Cladonematidae family reported in the region (Ahuatzin-Hernández *et al.* 2020, 2022). This contrasts with the efforts conducted in the Mexican Caribbean, an adjacent zone where several studies have been conducted, even describing new hydrozoan species (e.g., Bogle 1984; Cairns 1986; Zamponi *et al.* 1999). In this sense, the present work describes *S. dzilamensis* sp. nov., a new species of crawling hydromedusa, based on morphological, histological, and geographical grounds and provides the first record of the genus *Staurocladia* in the Gulf of Mexico.

Material and methods

Collection site

The town of Dzilam de Bravo is located in the north-central region of the Yucatan coast in the southern Gulf of Mexico. The region is characterized by diverse ecosystems, such as coastal lagoons, grass beds, and mangrove areas (Herrera-Silveira & Morales-Ojeda 2010). The depth of the zone ranges from 2 to 8.7 m (Marina *et al.* 2017). On average, the values of temperature (28.4°C) and salinity (36.1 PSU) show tropical features, being relatively homogeneous temporarily (Marina *et al.* 2017), although they can be sharply heterogeneous spatially (i.e., with sharp changes in the physicochemical characteristics of the water column over a relatively short distance, regardless of seasonality) due to the presence of freshwater outcrops (Herrera-Silveira 2006; Marina *et al.* 2017). The substratum is diverse, which can be sandy, sandy with shells, covered by grasses and macroalgae, or hard bottom of flagstones and rocks

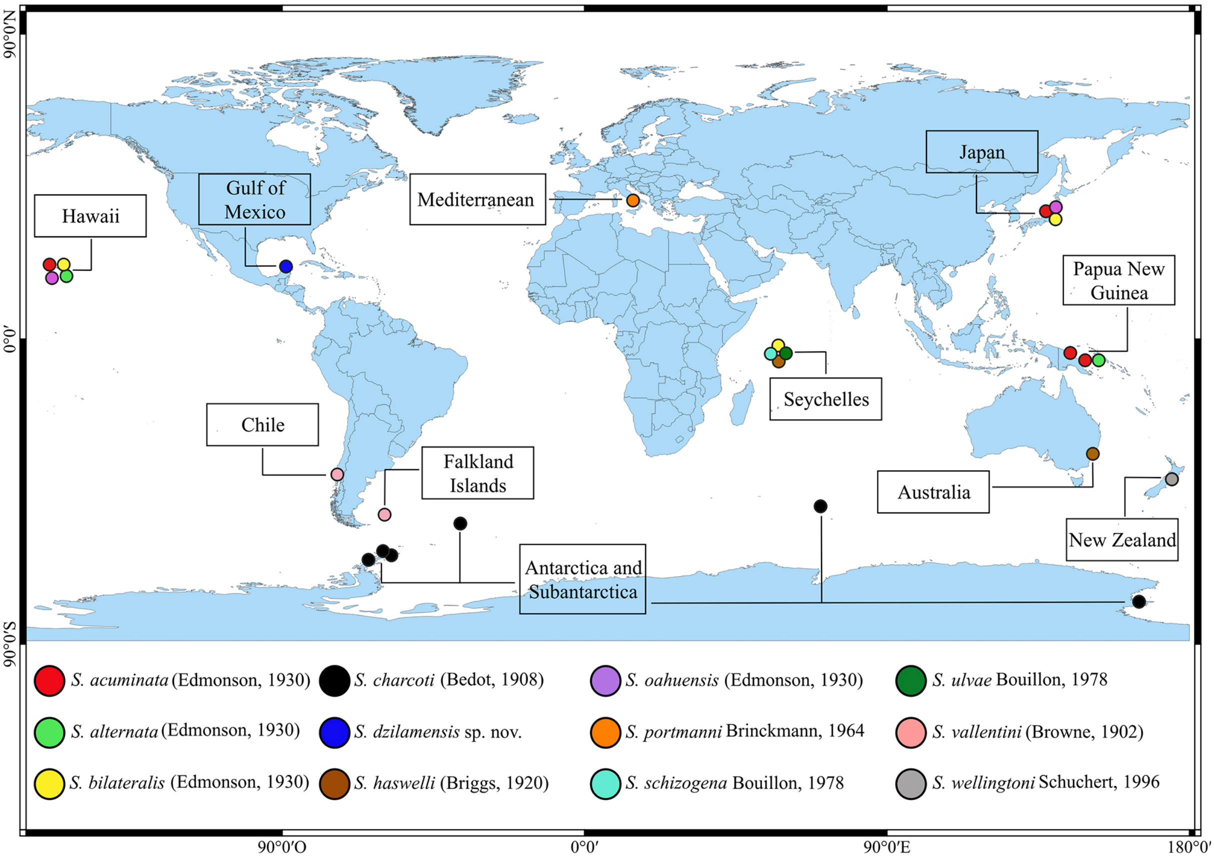

Fig. 1. Worldwide distribution of the nominal species of *Staurocladia* Hartlaub, 1917.

(Rosado-Espinosa *et al.* 2012). The ocean circulation is mainly due to the influence of the Caribbean Current System, which enters the Gulf through the Yucatan Channel and plays an important role in the distribution of various organisms (Candela *et al.* 2002; Manzanilla-Domínguez & Gasca 2004; Sanvicente-Añorve *et al.* 2018).

Field work

Hydromedusae were collected on May 7, 14 and 28, 2022, by snorkeling and manually off the coast of Dzilam de Bravo (21°23.7′ N, 88°53.1′ W). The collection site was of the rocky intertidal type, with freshwater influence and a maximum depth of 1.5 m. The substratum was covered by macroalgae

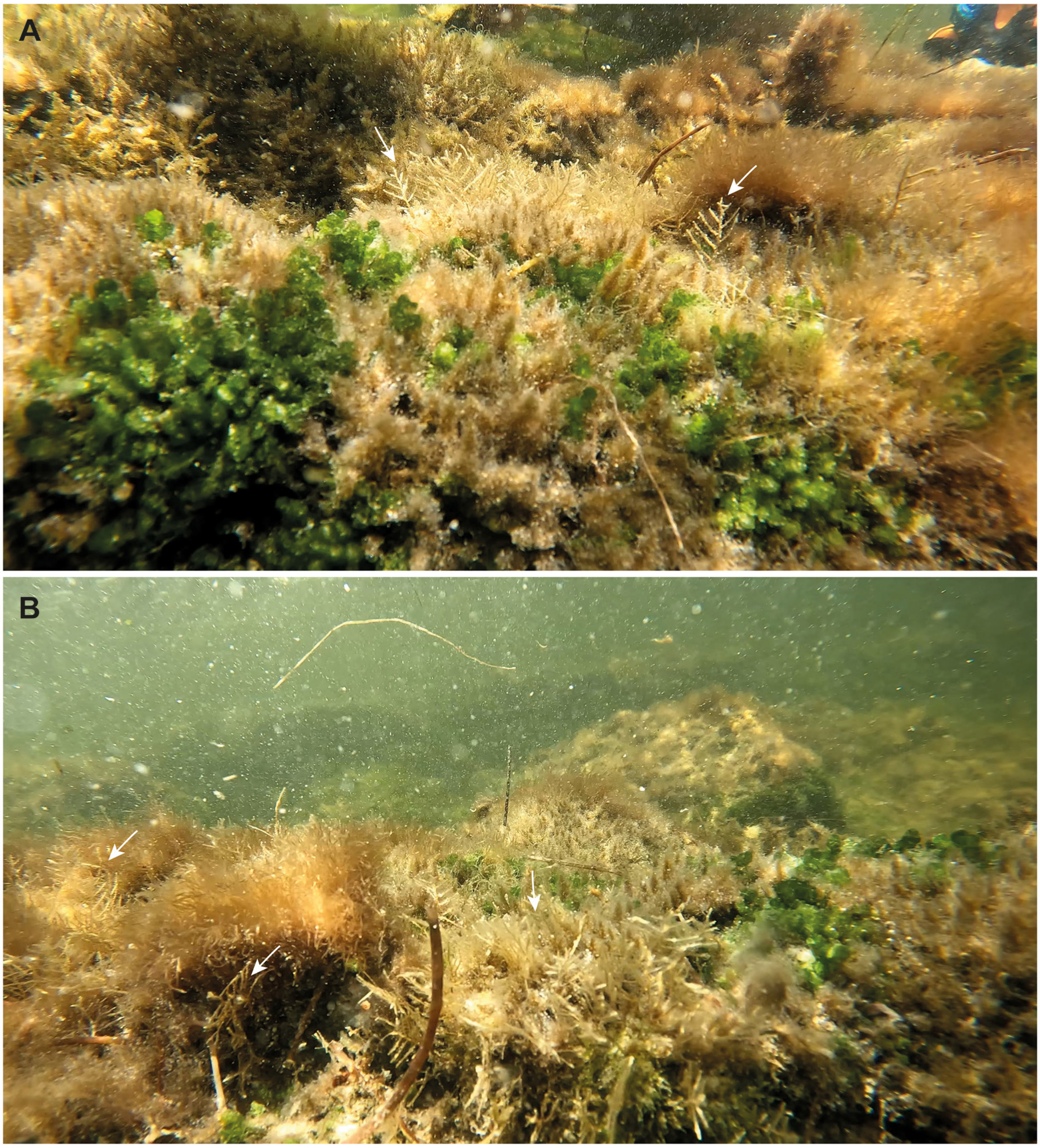

Fig. 2. Photographs of the collection site. White arrows indicate colonies of *Dynamena* sp.

with the presence of hydroids of *Dynamena* sp. (Fig. 2, photo taken with a Go Pro10 Black camera). The collected samples (one 250 mL bottle per day, full of algae and hydroids) were transferred to the Aquatic Pathology Laboratory at CINVESTAV-Mérida for further analysis. Salinity (ppt), dissolved oxygen (mg/L), and temperature (°C) values were recorded at points adjacent to the collection site.

Laboratory analysis

Samples were observed under a Motic SMZ-168 stereoscopic microscope. Hydromedusae were sorted from the rest of the material and fixed in a 4% formalin solution. In total, 110 specimens were analyzed, of which only 100 were in an optimal state of preservation to be measured. The umbrella diameter of specimens was measured with an ocular micrometer mounted on an Olympus BX50 optical microscope. Photographs were taken with a Leica DM2500 microscope equipped with a Leica MC170 HD camera. Squash preparations of tissue from tentacles and subumbrella were made from five specimens to observe their cnidae types. All measurements, observations, and taxonomic drawings were made on preserved specimens. Type material was deposited in the Regional Collection of Cnidarians of the Yucatán Peninsula 'Lourdes Segura', based at the Universidad Nacional Autónoma de México: Facultad de Ciencias, Unidad Multidisciplinaria de Docencia e Investigación-Sisal, Yucatán (YUC-CC-254-11). The organization of the material examined section follows the Darwin Core terms. A map with the distribution of nominal species of *Staurocladia* was made with QGIS ver. 3.28.2, considering the published literature (i.e., Brinckmann-Voss 1970; Bouillon 1978, 1991; Schuchert 1996, 2006; Hirano *et al.* 2006; Galea & Schories 2012a, 2012b), and occurrences from the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS) databases. We only retrieved occurrences coming from the basis of record "preserved specimen" and "material citation". Doubtful records were removed.

Histological sections were obtained in the sagittal plane from eight specimens. The tissues were dehydrated in a Histokinette Reichert-Jung and embedded in paraffin (melting point ~56°C). Serial thin sections of 5 µm were obtained using a Kedee microtome, model KD-3358, and then stained with hematoxylin and eosin, following the standard criteria proposed by Estrada-Flores *et al.* (1982) and Roberts (2012). Histological measurements (i.e., width of the marginal ring of nematocysts, width of the subumbrellar and gastric cavities, and width of the gastrodermis layer) were made with the Leica Application Suite software ver. 4.13.0.

Results

Taxonomic account

Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Superorder Anthoathecata Cornelius, 1992
Order Capitata Kühn, 1913
Family Cladonematidae Gegenbaur, 1857
Genus *Staurocladia* Hartlaub, 1917

Staurocladia dzilamensis sp. nov.
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Figs 3–5

Diagnosis

Staurocladia medusae with flattened-hemispherical to occasionally dome-shaped umbrella, with medusa buds on exumbrella, dorsally placed. A thickened and continuous marginal nematocyst ring on subumbrella; 6–11 bifid tentacles, branching proximally, with lower branch up to two times as long as

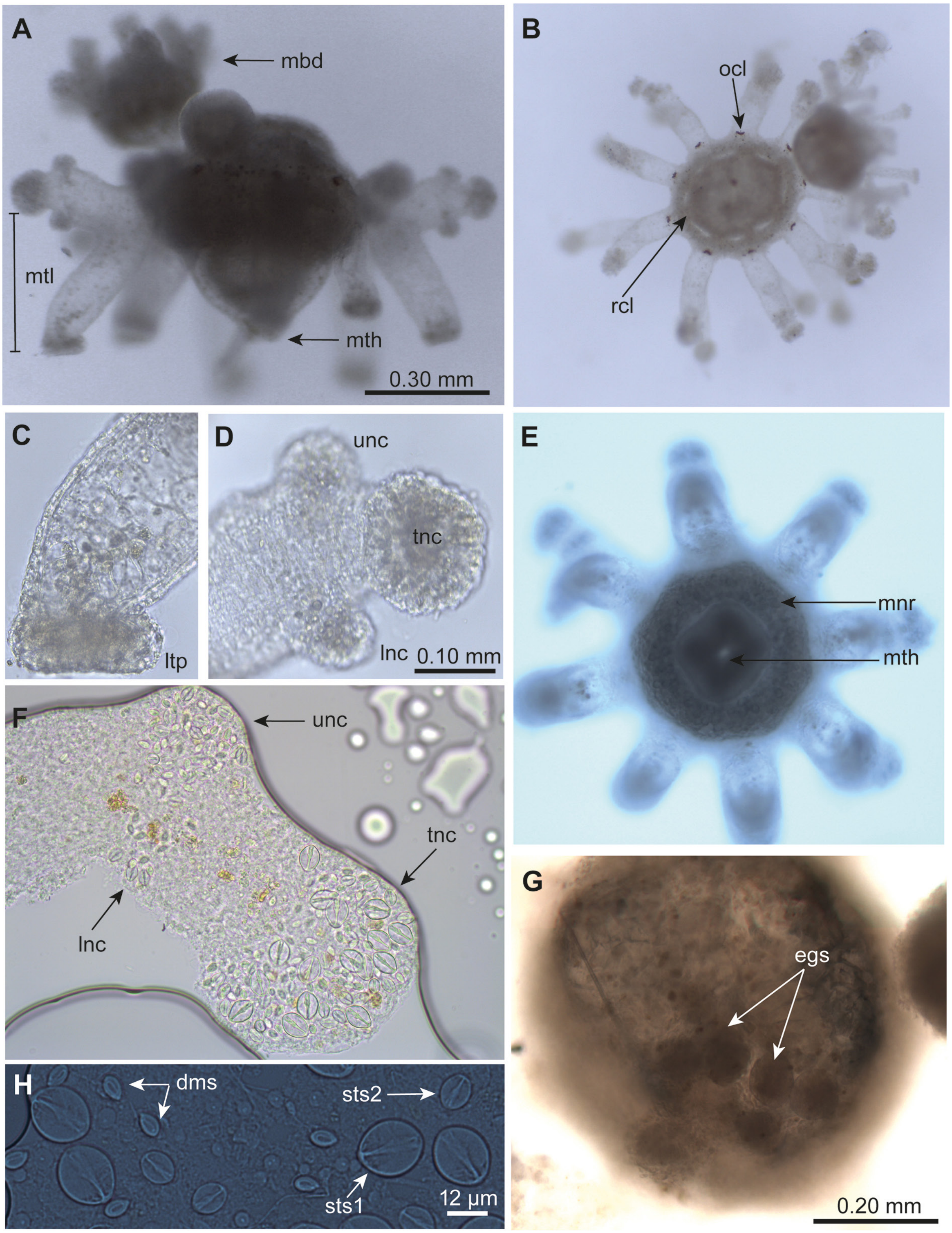

Fig. 3. Diagnostic features of *Staurocladia dzilamensis* sp. nov. **A**. Lateral view. **B, G**. Aboral view. **C**. Tentacle lower branch. **D, F**. Tentacle upper branch. **E**. Oral view. **H**. Cnidome. Abbreviations: dms = desmonemes; egs = eggs; lnc = lower nematocyst cluster; ltp = adhesive pad; mbd = medusa bud; mnr = marginal nematocyst ring; mth = mouth; mtl = bifid marginal tentacles; ocl = ocellus; rcl = radial canal; sts1 = stenoteles class 1; sts2 = stenoteles class 2; tnc = terminal nematocyst cluster; unc = upper nematocyst cluster.

upper one. Upper branch with three nematocyst clusters, one apical, and two opposite placed alternately on its aboral and oral sides. Lower branch with terminal adhesive pad. Cnidome composed of stenoteles (two size classes) and desmonemes.

Etymology

The name is derived from the type locality, Dzilam de Bravo.

Material examined

Holotype

MEXICO • Yucatán, Dzilam de Bravo; 21°23.7′ N, 88°53.1′ W; depth 1 m; 14 May 2022; José María Ahuatzin Hernández leg.; macroalgae; YUC-CC-254-11-001655.

Paratypes

MEXICO • 1 spec.; same collection data as for holotype; 7 May 2022; YUC-CC-254-11-001656 • 1 spec.; same collection data as for holotype; 7 May 2022; YUC-CC-254-11-001657 • 1 spec.; same collection data as for holotype; YUC-CC-254-11-001658.

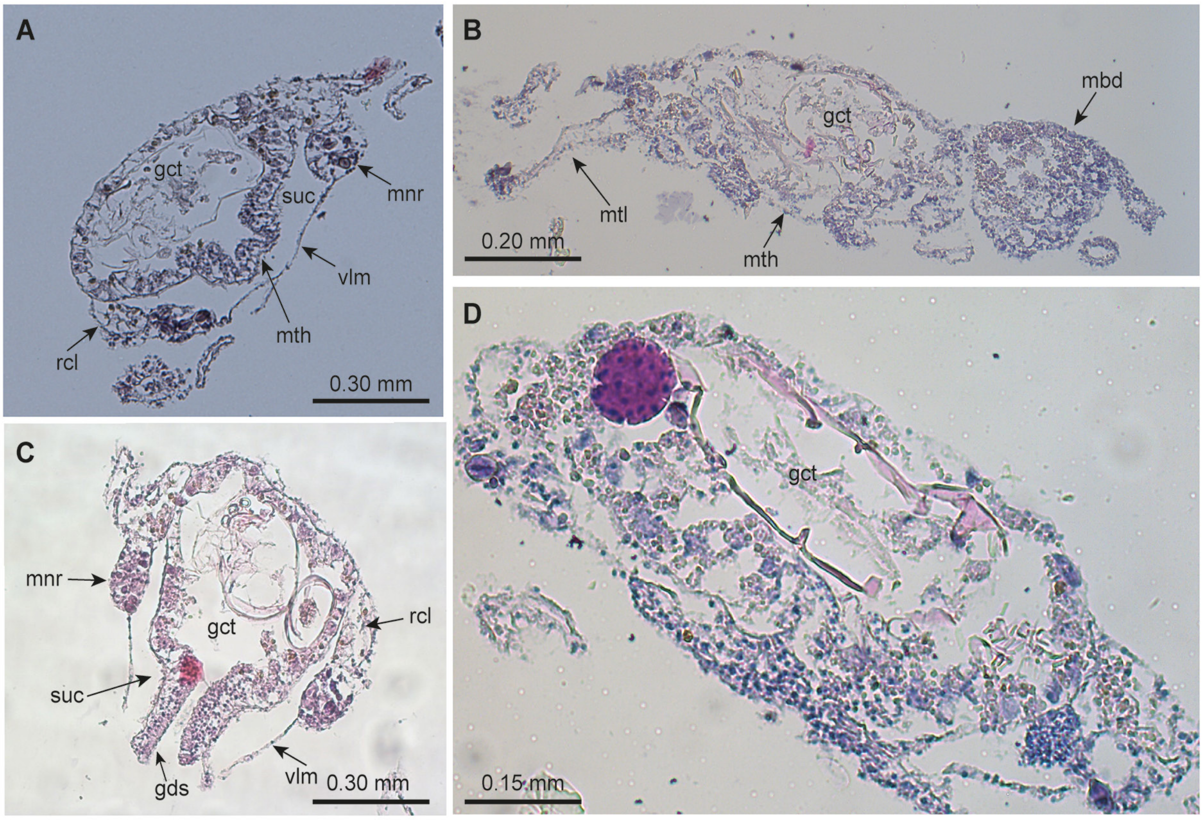

Fig. 4. Sagittal histological sections from different specimens of *Staurocladia dzilamensis* sp. nov. Abbreviations: gct = gastric cavity with a prey; gds = gastrodermis; mbd = medusa bud; mnr = marginal nematocyst ring; mth = mouth; mtl = marginal tentacle; rcl = radial canal; suc = subumbrellar cavity; vlm = velum.

Description

Medusa bell flattened-hemispherical to dome-shaped, ca 0.43 mm wide (0.25 ± 0.60 mm, n = 100); brown-olive coloured, commonly with medusa buds on exumbrella, dorsally located; manubrium conical, extending beyond the margin, occupying a great part of the subumbrellar cavity, distally with simple, circular mouth; gonads surrounding the upper part of manubrium; neither pouches nor nematocyst knobs were observed on the manubrium; some specimens with visible eggs; a continuous and thickened nematocyst ring present on subumbrella; velum fully closing subumbrella; 5–7 short,

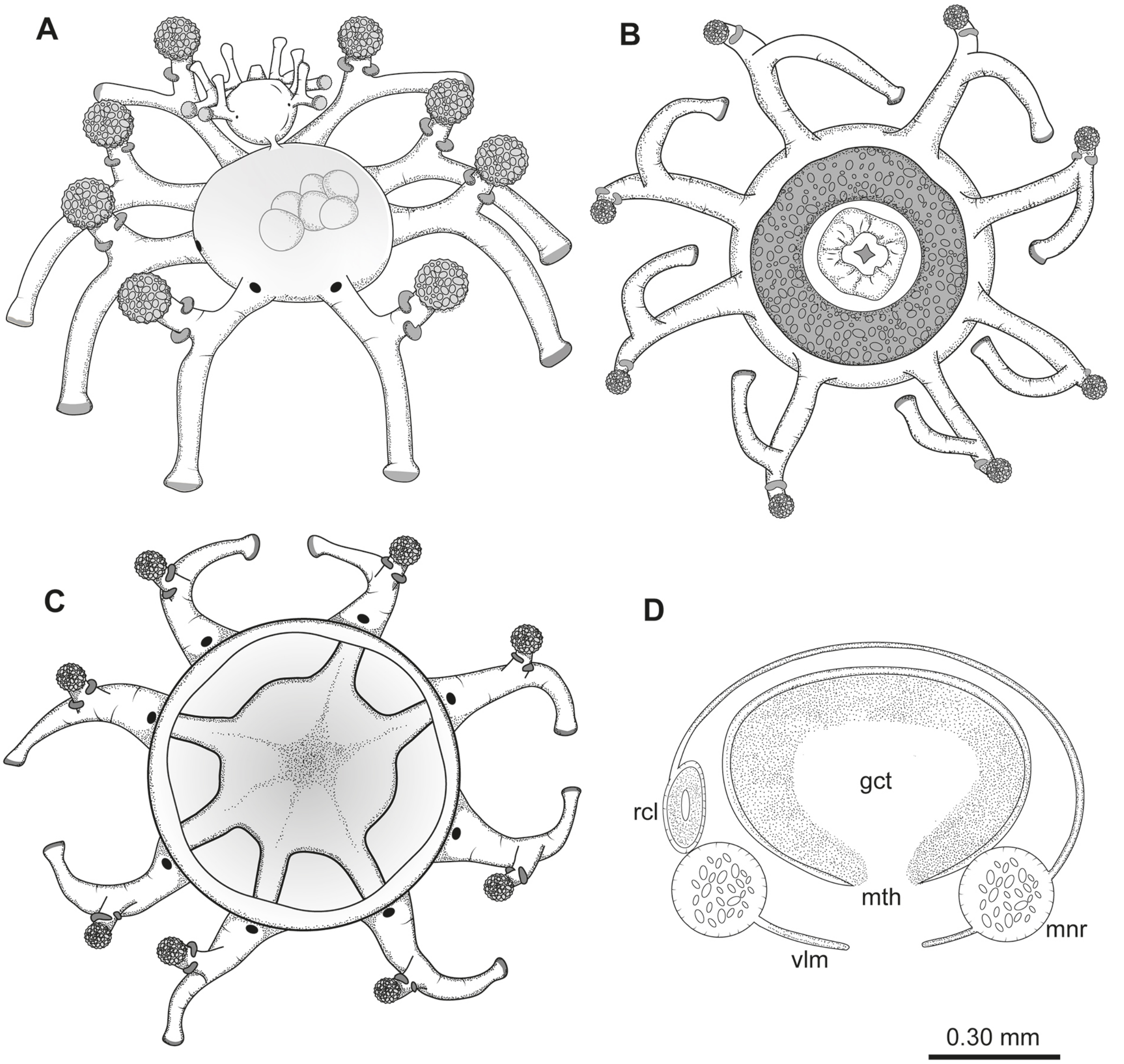

Fig. 5. *Staurocladia dzilamensis* sp. nov. **A**. Lateral view. **B**. Oral view. **C**. Aboral view. **D**. Sagittal section. Abbreviations: gct = gastric cavity; mnr = marginal nematocyst ring; mth = mouth; rcl = radial canal; vlm = velum.

unbranched radial canals, hard to see in most specimens and rarely corresponding to the number of marginal tentacles; 6–11 (usually 8) bifid tentacles with a black-reddish ocellus at their aboral base; tentacles branching a short distance after their origin, with the lower branch up to 2 times as long as the upper one, the former with a terminal adhesive pad; upper branch short, with 3 nematocyst clusters, one apical, knob-like shaped, and 2 additional, crescent-shaped, placed alternately on the aboral and oral sides of the branch. Cnidome: stenoteles of two size classes, class 1 = (15.00–17.50) × (12.50–15.00) µm, class 2 = 10.00 × 7.50 µm, and desmonemes = 7.50 × 5.00 µm, all in the upper branch, capsules restricted to both the terminal knob and the crescent-shaped clusters; no nematocysts were observed in the adhesive pad of the lower branch; marginal ring with stenoteles and desmonemes.

Histology: mesoglea reduced, not noticeable; velum evident, fully closing subumbrella; subumbrellar cavity wide, ca 149.18 µm (SD = 33.60); gonads like an external thin layer that surrounds the upper part of the manubrium, without any apparent division; radial canals short and broad, originating laterally from the gastric cavity, ending in a ring canal located immediately above the thickened continuous nematocysts ring; nematocysts ring ca 38.30 µm wide (SD = 3.92); internal walls of the manubrium with a layer of gastrodermis, gastrodermis ca 6.34 µm wide (SD = 0.72); gastric cavity wide, occupying ⅔ of subumbrella, ca 110.46 µm (SD = 22.31).

Remarks

A large cover of filamentous algae and *Dynamena* sp. hydroids occurred at the site, so a possible association between *S. dzilamensis* sp. nov. and *Dynamena* hydroids must be studied in the future. Of the 110 specimens, most were observed alive, and their morphology did not considerably change post-fixation. Most specimens had eight tentacles (n = 57), followed by nine (n = 25), seven (n = 22), six (n = 3), ten (n = 2), and eleven (n = 1). Two specimens showed tentacles with two aboral crescent-shaped nematocyst clusters on the upper branch of some tentacles. Two specimens presented a trifid tentacle. The origin of the third bifurcation was on the distal part of the lower branch, with both lower branches of equal length and with adhesive pads. Most specimens had exumbrellar medusa buds (n = 61). Thirty-eight specimens had one medusa bud, twenty had two buds, and only three specimens had three buds. Budding was the only way of asexual reproduction observed.

The third day of sampling (May 28) recorded the highest values of the measured variables and their greatest variation. The average temperature showed the highest values on the first day of sampling, ranging between 28.25 and 29.35°C. Dissolved oxygen recorded the highest values on the third day of sampling; this variable ranged between 0.10 and 0.67 mg/L. Salinity showed euhaline characteristics, since its values ranged from 36.07 to 38.94 ppt. Finally, the pH showed a higher acidity during the first two days, while on the third day, it showed alkaline (Table 1). Unfortunately, the polyp stage was not found in the samples (Appendices).

Key for the nominal medusae of Staurocladia

1. Tentacles without nematocyst clusters on their proximal, unbranched portion................................ 2
– Tentacles with an occasional nematocyst cluster on their proximal, unbranched portion. One apical cluster, 2–3 aboral, and 1 oral, cnidome composed of stenoteles (23.00–25.00) × (17.00–19.00) µm and desmonemes (8.00 × 4.00) µm.. ***S. haswelli*** (Briggs, 1920)

2. Tentacles with lateral nematocyst clusters... 3
– Tentacles without lateral nematocyst clusters.. 6

3. Tentacles with up to 6 lateral, alternating clusters per side, cnidome composed of stenoteles of four size classes: class one (28.00–30.50) × (20.00–21.00), class two (17.50–24.00) × (13.00–15.00), class three (9.50–14.50) × (7.00–9.50), class four (7.00–9.00) × (5.50–6.50) µm and desmonemes (10.50–14.50) × (4.00–6.00) µm.. ***S. wellingtoni*** Schuchert, 1996
– Tentacles with 1 nematocyst cluster laterally placed slightly before the branching point or on the lateral side of the upper branch.. 4

4. Tentacles with 2–5 aboral and 2–4 oral clusters. Medusa able to swim, cnidome composed of stenoteles of two size classes: class one (15.00 × 12.00), class two (25.00 × 21.00) µm and desmonemes (14.00–16.00) × (4.00–7.00) µm.. ***S. portmanni*** Brinckmann, 1964
– Tentacles with up to 2 aboral clusters.. 5

5. Tentacles with 2 aboral and 1 oral clusters alternately placed, 11–25 tentacles. Umbrella pearl-white (reflected light), brown (transmitted light), cnidome composed of stenoteles of two size classes: class one (24.90 × 17.30), class two (14.30 × 9.50) µm and desmonemes (9.70 × 4.80) µm .... ***S. acuminata*** (Edmonson, 1930)
– Tentacles with 1 single nematocyst cluster on the aboral side, up to 12 tentacles. Umbrella brown coloured .... ***S. bilateralis*** (Edmonson, 1930)

6. Tentacles with clusters restricted to the aboral side.. 7
– Tentacles with clusters present on both aboral and oral sides 10

7. Tentacles with clusters alternating left and right along a median line.. 8
– Tentacles with clusters in a single row 9

8. Bell flattened, 0.8 mm wide, with densely granulate, central area, clear at periphery, up to 13 tentacles, upper branch with 6 alternating clusters along a median, aboral line...... ***S. alternata*** (Edmonson, 1930)
– Bell nearly hemispherical, up to 8 mm wide, manubrium, endoderm of ring canal and tentacles orange, up to 65 tentacles, upper branch with 32 alternating clusters along a median, aboral line..... .... ***S. charcoti*** (Bedot, 1908)

9. Bell 0.5 mm wide, brown or reddish brown, up to 20 tentacles, upper branch longer than lower one, with 2 aboral clusters, cnidome apparently composed of a single type of stenoteles......................... .... ***S. oahuensis*** (Edmonson, 1930)
– Bell 0.7–1.2 mm wide, mostly transparent, 16–30 tentacles, upper branch shorter than lower one, 3–4 aboral, collinear clusters, cnidome composed of stenoteles of two size classes: class one (18.60 × 12.60), class two (10.80 × 6.60) µm and desmonemes (9.60 × 4.20) µm................. ***S. schizogena*** Bouillon, 1978

10. Bell 0.25–0.60 mm wide, up to 11 (usually 8) tentacles, upper branch shorter than lower one, clusters alternately placed, 1 aboral and 1 oral, cnidome composed of stenoteles of two size classes: class one (15.00–17.50) × (12.50–15.00), class two (10.00 × 7.50) µm and desmonemes (7.50 × 5.00) µm .... ***S. dzilamensis*** sp. nov.
– Tentacles with upper branch longer than lower one 11

11. Bell 0.2–0.8 mm wide, up to 16 tentacles, upper branch with 2–3 aboral and 1–2 oral clusters, cnidome composed of stenoteles of two size classes: class one (20.00 × 16.00), class two (12.00 × 8.50) µm and desmonemes (8.00 × 2.00) µm .... ***S. ulvae*** Bouillon, 1978
– Bell up to 3 mm wide, up to 42 tentacles, upper branch with up to 4 aboral and up to 3 oral clusters, cnidome composed of stenoteles of three size classes: class one (19.00–25.00) × (12.00–16.00), class two (14.00–15.50) × (8.50–10.50), class three (11.00–13.00) × (7.00–9.00) µm and desmonemes (10.00–11.00) × (4.50–5.50) µm... ***S. vallentini*** (Browne, 1902)

Discussion

The average umbrella size of *S. dzilamensis* sp. nov. is smaller than usually reported for the genus but matches the known range for species of *Staurocladia* and *Eleutheria* (Russell 1953; Kramp 1961; Schuchert 2006, 2012). Both genera are polyphyletic and are currently separated based on the number of their nematocyst clusters (Schuchert 2006; Zhou *et al.* 2022). This character, however, is currently considered uninformative in the definition of the taxonomy of this group at the genus level, and more analyses considering more taxa are suggested to redefine it (Nawrocki *et al.* 2010). Yet, as long as the taxonomic boundaries of both genera remain unclear, their separation should be maintained, and the number of nematocyst clusters on the tentacles considered as diagnostic for *Staurocladia*. Thus, we decided to assign the specimens from the coast of Dzilam to that genus.

Staurocladia dzilamensis sp. nov. can be distinguished from its congeners mainly by the arrangement of the nematocyst clusters on the upper branch of the tentacles, which bears one apical and two opposite clusters, placed alternately on its aboral and oral sides, in addition to the presence of dorsally-placed, exumbrellar buds, a conspicuous nematocyst ring, the features of the manubrium, the number of tentacles and the length of their branches (Table 2).

Among the valid species of *Staurocladia*, only five display a similar pattern in the arrangement of the nematocyst clusters regarding *S. dzilamensis* sp. nov. (alternately placed in aboral and oral sides), i.e., *S. haswelli*, *S. portmanni*, *S. acuminata*, *S. ulvae*, and *S. vallentini* (Fig. 6). Of these five species, *S. portmanni* and *S. acuminata* are easily distinguishable from *S. dzilamensis* due to the presence of nematocyst clusters on the lateral sides, either at the branching point, or a short distance after it, respectively. In addition, *S. portmanni* has a manubrium armed with nematocyst clusters, an umbrella able to swim, and larger desmonemes, and in *S. acuminata*, the upper branch of the tentacles is longer than its lower counterpart, and its cnidome is composed of larger stenoteles and desmonemes (Table 2). Both species differ from *S. dzilamensis* in the number of nematocyst clusters (Edmonson 1930; Brinckmann-Voss 1964) (Fig. 6). *Staurocladia haswelli* has a nematocyst cluster on the aboral side of the main stem of tentacles behind the branching point, yet this cluster can be absent in adult specimens (Briggs 1920; Kramp 1961). Despite this, *S. haswelli* has an umbrella of up to 1.2 mm, up to 31 tentacles with up to five nematocyst clusters on their upper branch, and larger stenoteles of one size class, features that allow us to differentiate it from *S. dzilamensis*. Between *S. vallentini* and *S. ulvae,* the former is easy to differentiate from *S. dzilamensis* due to the number of tentacles, the number of nematocyst clusters, and the cnidome, which is composed of stenoteles of three size classes and larger desmonemes (Table 2). Additionally, in *S. vallentini,* the upper branch of the tentacles is longer than the lower one, and the exumbrellar buds are orally placed, originating between the velum and bell margin (Schuchert 1996; Galea & Schories 2012b) (Table 2). *Staurocladia ulvae* matches *S. dzilamensis* in the umbrella size, the number of tentacles, and by having stenoteles of two size classes (Bouillon 1978). Nonetheless, *S. dzilamensis* has only three nematocyst clusters on the tentacles, one apical and two extra oppositely arranged, placed on aboral and oral sides, and a cnidome composed of stenoteles of two size classes, class one (15.00–17.50) × (12.50–15.00) µm, class two 10.00 × 7.50 µm, and desmonemes 7.50 × 5.00 µm, whereas *S. ulvae* presents up to six nematocyst clusters on the tentacles, one apical, two to three aboral, and one to two oral clusters, and the capsules of its cnidome are larger, i.e., stenoteles class one 20.00 × 16.00, stenoteles class two 12.00 × 8.50, and desmonemes 8.00 × 2.00 (Table 2). In addition, the length of the tentacular branches differs between both species.

The rest of the species are easy to distinguish solely by the arrangement of the nematocyst clusters since they either present clusters only on the lateral sides of the upper branches or are restricted to their aboral side (Fig. 6, Table 2). It is worth mentioning that the number and arrangement of the nematocyst clusters in *S. dzilamensis* sp. nov. were consistent through different stages of development (specimens with different umbrella sizes presented the same number and arrangement of clusters),

Table 1. Physicochemical variables recorded in adjacent areas to the collection site. Abbreviations: DO = Dissolved oxygen; Sal = Salinity; Tem = Temperature.

		Tem °C		**DO mg/L**		**Sal ppt**		**pH**	
	N	Mean	SD	Mean	SD	Mean	SD	Mean	SD
7 May 22	28	28.72	0.24	0.10	0.00	36.07	0.42	5.98	0.06
14 May 22	19	28.25	0.40	0.24	0.05	36.36	0.17	6.99	0.08
28 May 22	9	29.35	0.38	0.67	0.08	38.94	2.11	11.70	2.35

unlike other species such as *S. portmanni*, *S. haswelli*, *S. wellingtoni* or *S. oahuensis*, where these features varied through the ontogenetic development (Briggs 1920; Edmonson 1930; Schuchert 1996). This fact encourages more research on the ontogeny of the species of *Staurocladia*, including *S. dzilamensis*, which could provide more information about the morphological boundaries of the genus.

There are few ecological studies on the medusae of *Staurocladia* compared to those of *Eleutheria*. The hydroid of *S. portmanni* was reared at lower temperatures (13–20°C) than those recorded in this study, budding medusae from January to March that were subsequently found between May and July (Brinckmann-Voss 1970), which matches the period in which the specimens dealt with in this work were collected. Brinckmann-Voss (1970) suggests that the high occurrence of the medusa between May and July might be due to the medusae dying after their sexual reproduction by the end of June, and the species occurs in the hydroid stage only from then on. Two populations of *S. oahuensis* and *S. bilateralis* did not perform asexual reproduction at 12°C, while at 17°C and higher temperatures, both species reproduced asexually by fission at a high rate, proving low temperatures as a critical inhibitory factor for their asexual reproduction and growth (Hirano *et al.* 2000). This behaviour is also reported in *Eleutheria dichotoma* but through budding (Schierwater & Hadrys 1998; Dánko *et al.* 2020). The population analysed in this study showed a high rate of medusa budding, which can be associated with the high temperatures of a tropical region such as the southern Gulf of Mexico. The influence of temperature, observed in the populations mentioned above, and other variables such as salinity, dissolved oxygen, and pH must be tested in the specimens described in this study.

On the other hand, the high occurrence observed in this study and usually reported in *Staurocladia* and *Eleutheria* populations may be due to an ecological strategy (Hirano *et al.* 2000; Fraser *et al.* 2006). In *E. dichotoma*, sexual reproduction occurs at high rates when the population density is medium, favouring survival probability, which results in the production of motile larvae that can escape unfavorable conditions and settle in environments with better ones (Dańko *et al.* 2018). Moreover, this type of reproduction leads to the generation of a polyp stage, which is more resistant to environmental stress (Dánko *et al.* 2020). *Eleutheria dichotoma* and *S. dzilamensis* sp. nov. show a high rate of asexual reproduction through budding, responding similarly to temperature, and occurring in similar environments, such as intertidal pools with the presence of macroalgae, so the previously mentioned strategy likely applies to populations of *S. dzilamensis* sp. nov. In this sense, freshwater outcrops along the coast of Dzilam carry colder water masses with low salinities (Marina *et al.* 2017), which can conduce to physiological stress for some species. This can be associated with the factors previously mentioned and may explain the high abundances of *S. dzilamensis* sp. nov., the high rates of medusa budding, small umbrella sizes, and the absence of the polyp stage.

The record of *S. dzilamensis* sp. nov. in the southern Gulf of Mexico extends the geographic distribution range reported for the genus. Species of *Staurocladia* are common in temperate zones, mainly in the

Table 2 (continued on next two pages)**.** Comparison of the diagnostic characters of the medusae of *Staurocladia* Hartlaub, 1917. Data compiled from: Browne (1902), Bedot (1908), Briggs (1920), Edmonson (1930), Kramp (1959, 1961, 1968), Brinckmann-Voss (1964), Bouillon (1978), Schuchert (1996, 2006), Hirano *et al*. (2000, 2006), Galea & Schories (2012a, 2012b).

Taxa	**Umbrella**	**Manubrium**	**Nematocysts ring**	**Medusa buds**	**Brood chamber**	**Tentacles**	**Nematocyst clusters**	**Cnidome (μm)**	**Distribution**
S. dzilamensis sp. nov.	0.2–0.6 mm; brown-olive coloured	Conical, occupying a great part of the subumbrellar cavity, lacking either nematocyst knobs or pouches	Present. Continuous and thickened	Exumbrellar, dorsally located	Absent	6–11 (usually 8). Lower branch about 2 times as long as the upper one	Apical + two extra crescent-shaped, oppositely arranged, placed on both oral and aboral sides	Stenoteles of two size classes (15.00–17.50) × (12.50–15.00), and 10.00 × 7.50. Desmonemes 7.50 × 5.00	Gulf of Mexico
S. acuminata (Edmonson, 1930)	0.8 mm; pearl-white (reflected light), brown (transmitted light)	Tubular, extensible, apparently lacking either nematocyst knobs or pouches; gonads on surface	"A marginal ring of thickened epidermis that contained many nematocysts on the oral surface"	Absent	"A dorsal brood pouch that opens into the bell-cavity by a variable number of pores"	11-25. Upper branch as long or slightly longer than the lower one	Apical + 2 aboral + 1 oral + 1 pair of laterals	Large stenoteles 24.90 ± 0.80 × 17.30 ± 0.40; small stenoteles 14.30 ± 0.40 × 9.50 ± 0.20; desmonemes 9.70 ± 0.20 × 4.80 ± 0.10	Hawaii, Papua New Guinea, Japan
S. alternata (Edmonson, 1930)	0.8 mm; center dark-brown, clear elsewhere	Not documented	Not documented	Absent	No data	Up to 13. Upper branch longer than the lower one	Apical + 6 alternating along a median, aboral line	Not available	Hawaii, Papua New Guinea
S. bilateralis (Edmonson, 1930)	0.6 mm; brown coloured	Not documented	Not documented	Absent; asexual reproduction by fission	"Dorsal to the stomach"	As much as 20. Upper branch longer than the lower one	Apical + 1 aboral + 1 pair of laterals	Not documented	Hawaii, Japan, Seychelles
S. charcoti (Bedot, 1908)	Up to 8 mm; manubrium, endoderm of ring canals and tentacles orange	With longitudinal creases, terminally crowded with nematocysts	Discontinuous. On the proximal-most oral side of the main stem of the lower tentacular branches, conspicuous pads of nematocysts clasping around for a certain distance of the circumference of the tentacles, not fused laterally to form a continuous ring	Absent	Absent	Up to at least 65; upper branch longer than the lower one	Apical + up to 32 alternating along a median, aboral line	Not documented	Antarctica, South Georgia, and Kerguelen

Table 2 (continued)**.** Comparison of diagnostic characters of the medusae of *Staurocladia* Hartlaub, 1917. Data compiled from: Browne (1902), Bedot (1908), Briggs (1920), Edmonson (1930), Kramp (1959, 1961, 1968), Brinckmann-Voss (1964), Bouillon (1978), Schuchert (1996, 2006), Hirano *et al*. (2000, 2006), Galea & Schories (2012a, 2012b).

Taxa	**Umbrella**	**Manubrium**	**Nematocysts ring**	**Medusa buds**	**Brood chamber**	**Tentacles**	**Nematocyst clusters**	**Cnidome (µm)**	**Distribution**
S. haswelli (Briggs, 1920)	Up to 1.2 mm; reddish-yellow (transmitted light), bright red or orange (reflected light)	Lacking oral tentacles or nematocyst knobs but around the edge of the month the ectoderm forms a thickened ridge, which bears large, well-developed nematocysts	Present. Thickened, uninterrupted	Exumbrellar, “arising from the circular canal between the tentacles and the nematocyst ring”	Absent	Up to 31. Lower branch longer than the upper one	Apical + 2 aboral + 1 oral + 1 cluster on aboral side of the main stem of tentacles behind the branching point	Identity uncertain, but possibly stenoteles (23.00–25.00) × (17.00–19.00), and desmonemes 8.00 × 4.00	Australia, Seychelles
S. oahuensis (Edmonson, 1930)	Up to 0.5 mm; brown or reddish brown	Not documented	Not documented	Absent; asexual reproduction by fission	“Dorsal to the stomach communicating with the bell cavity by a series of small openings”	As much as 20. Upper branch longer than the lower one	Apical + 2 aboral	Apparently, a single type of stenoteles	Hawaii, Japan
S. portmanni Brinckmann, 1964	4–6 mm; endoderm of manubrium, ring canal and tentacles, red-orange	With five protruding stomach pouches in middle, mouth with five spherical nematocyst clusters	Present. Thickened	Absent	Absent	16–25. Upper branch as long as the lower one (based on figures of Brinckmann 1970)	Apical + 2–5 aboral + 2–4 oral + 1 pair of lateral clusters proximal to the ramification of the tentacle	Small (15.00 × 12.00) and large (25.00 × 21.00) stenoteles. Desmonemes [(14.00–16.00) × (4.00–7.00)], and a large, unidentified capsule (haploneme?) [(18.00–28.00) × (6.00–12.00)]	Mediterranean Sea
S. schizogena Bouillon, 1978	Up to 1.2 mm; mostly transparent	Not documented	Not documented	Absent. Asexual reproduction by fission	Absent	16–30. Branches of nearly the same length, lower branch slightly longer than the upper one	Apical + 3–4 collinear on aboral surface	Large (18.60 × 12.60) and small (10.80 × 6.60) stenoteles. Desmonemes (9.60 × 4.20)	Seychelles

Table 2 (continued)**.** Comparison of diagnostic characters of the medusae of *Staurocladia* Hartlaub, 1917. Data compiled from: Browne (1902), Bedot (1908), Briggs (1920), Edmonson (1930), Kramp (1959, 1961, 1968), Brinckmann-Voss (1964), Bouillon (1978), Schuchert (1996, 2006), Hirano *et al.* (2000, 2006), Galea & Schories (2012a, 2012b).

Taxa	**Umbrella**	**Manubrium**	**Nematocysts ring**	**Medusa buds**	**Brood chamber**	**Tentacles**	**Nematocyst clusters**	**Cnidome (µm)**	**Distribution**
S. ulvae Bouillon, 1978	02–0.8 mm	Not documented	Not documented	Exumbrellar	Absent	7–16. Upper branch up to twice as long as the lower one	Apical + 2–3 aboral + 1–2 oral	Stenoteles of two size classes 20.00 × 16.00 and 12.00 × 8.50. Desmonemes of one size class 8.00 × 2.00	Seychelles
S. vallentini (Browne, 1902)	Up to 3 mm; circular canal and gastric cavity orange, radial canals bright white; adhesive pads and clusters of nematocysts white	With gastric pouches as orange bodies. Lacking nematocyst knobs	Present. Continuous and thickened	Exumbrellar, between velum and bell margin	Absent	Up to 42. Upper branch longer than the lower one	Apical + up to 4 collinear aborally + up to 3 collinear orally	Stenoteles of three size classes (19.00–25.00) × (12.00–16.00), (14.00–15.50) × (8.50–10.50) and (11.00–13.00) × (7.00–9.00). Desmonemes (10.00–11.00) × (4.50–5.50)	Falkland Islands, Chile, South Africa?, Japan?, Bermuda?, New Zealand?, and Mexico (Caribbean Sea)?
S. wellingtoni Schuchert, 1996	Up to 4 mm	With 5–6 mobile protrusions, mouth with 6 nematocyst knobs. Gonads of female brown-yellow opaque, in male olive-green transparent, gonads covered with black pigment towards the centre; lumen of tentacles and radial canal dark brown to black, apex of manubrium white; sucker pads light yellow	Absent	Absent	Absent	Up to 55. Upper branch longer than the lower one	Apical + up to 6 lateral, alternating clusters per side	Stenoteles of four size classes (28.00–30.50) × (20.00–21.00), (17.50–24.00) × (13.00–15.00), (9.50–14.50) × (7.00–9.50), (7.00–9.00) × (5.50–6.50). Desmonemes (10.50–14.50) × (4.00–6.00)	New Zealand

Antarctic, Subantarctic, and Mediterranean regions (Kramp 1959, 1961, 1968; Bouillon *et al.* 2006; Schuchert 2006) (Fig. 1). Some tropical records are from Hawaii (Pacific Ocean), and Seychelles (Indian Ocean) (Edmonson 1930; Bouillon 1978). The nearest report to the Gulf of Mexico was given by Canché-Canché & Castellanos-Osorio (2005) in the Mexican Caribbean Sea (i.e., *S. vallentini* in the Ascensión Bay, Quintana Roo). That report, however, lacks morphological or molecular evidence, so the specific identity of the specimens is doubtful. Despite the proximity, the warm, nutrient-rich waters of the southern Gulf of Mexico represent a new habitat relative to the oligotrophic waters of the Caribbean and the previously mentioned regions. Thus, it is important to continue exploring the coastal environments of the southern Gulf of Mexico, which have remained poorly studied regarding hydrozoans, as they could provide new perspectives concerning the systematics and biogeography of this and other taxa.

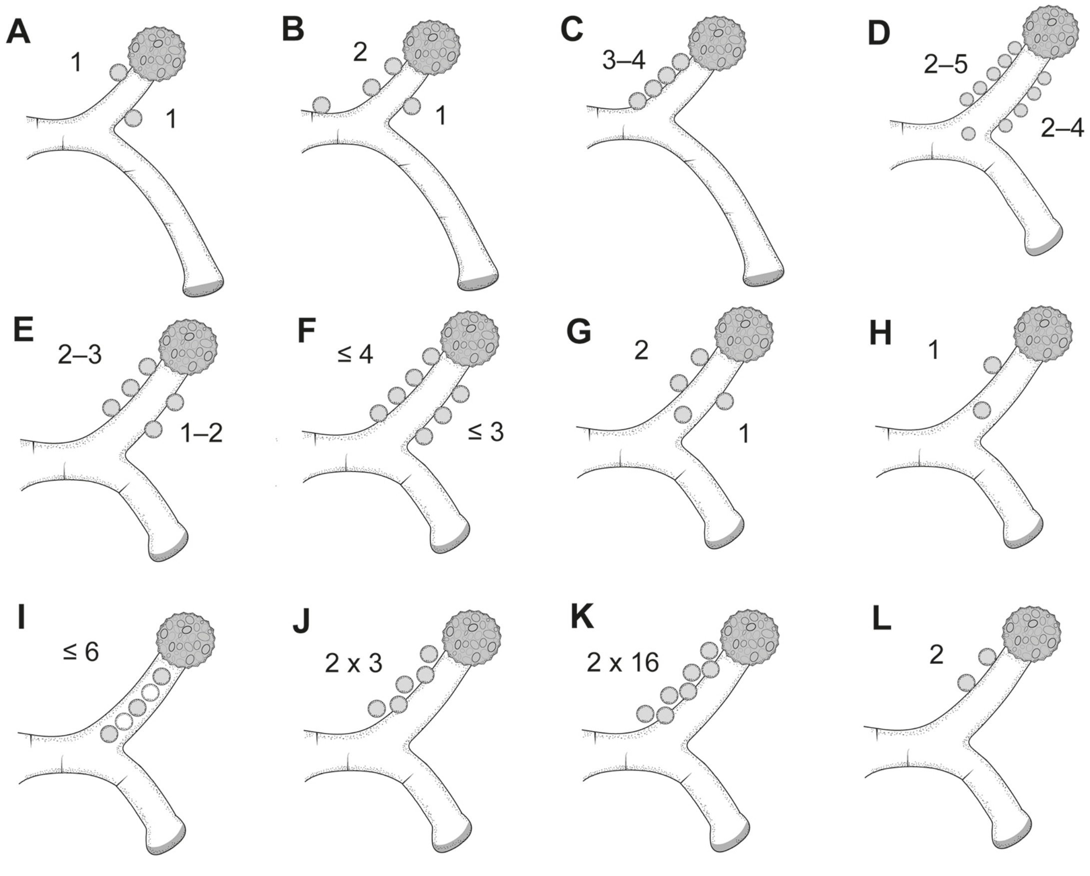

Fig. 6. A–L. Arrangement of the nematocyst clusters for each nominal species of *Staurocladia* Hartlaub, 1917. Numbers represent the number of nematocyst clusters on the oral and aboral sides. **A**. *S. dzilamensis* sp. nov. **B**. *S. haswelli* (Briggs, 1920). **C**. *S. schizogena* Bouillon, 1978. **D**. *S. portmanni* Brinckmann, 1964. **E**. *S. ulvae* Bouillon, 1978. **F**. *S. vallentini* (Browne, 1902). **G**. *S. acuminata* (Edmonson, 1930). **H**. *S. bilateralis* (Edmonson, 1930). **I**. *S. wellingtoni* Schuchert, 1996. White circles represent nematocyst clusters on the alternate side of the upper branch. **J**. *S. alternata* (Edmonson, 1930). **K**. *S. charcoti* (Bedot, 1908). **L**. *S. oahuensis* (Edmonson, 1930).

The separation of *Eleutheria* and *Staurocladia* is still problematic due to the ambiguity relative to the number of nematocyst clusters on the tentacles as a generic diagnostic feature (Schuchert 2006; Nawrocki *et al.* 2010). This separation is probably unnecessary, yet, studies including molecular data and more taxa are required for a comprehensive analysis before a taxonomic rearrangement can be made. In addition, a global review of the morphological boundaries of Cladonematidae is necessary due to its polyphyletic nature and the high morphological variability of its species (Ahuatzin-Hernández *et al.* 2022; Fang *et al.* 2022; Zhou *et al.* 2022). Only integrative studies, which consider species morphology and molecular data, would allow us to redefine the taxonomic boundaries and clarify the systematics and evolution of this group.

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Appendices

Table S1 (continued on next two pages)**.** Medusae measurements.

ID	Collecting date	Medusa buds (n)	Tentacles (n)	Diameter (mm)
1	7 May 2022	1	8	0.42
2	7 May 2022	2	10	0.53
3	7 May 2022	0	8	0.39
4	7 May 2022	0	8	0.45
5	7 May 2022	0	9	0.56
6	7 May 2022	0	8	0.45
7	7 May 2022	2	8	0.51
8	7 May 2022	2	9	0.43
9	7 May 2022	2	8	0.41
10	7 May 2022	2	9	0.45
11	7 May 2022	0	9	0.45
12	7 May 2022	1	9	0.35
13	7 May 2022	1	9	0.40
14	7 May 2022	1	8	0.45
15	7 May 2022	0	8	0.45
16	7 May 2022	0	8	0.30
17	7 May 2022	0	8	0.35
18	7 May 2022	0	7	0.35
19	7 May 2022	0	7	0.39
20	7 May 2022	0	7	0.30
21	7 May 2022	0	6	0.29
22	7 May 2022	0	7	0.29
23	7 May 2022	0	7	0.30

Table S1 (continued)**.** Medusae measurements.

ID	Collecting date	Medusa buds (n)	Tentacles (n)	Diameter (mm)
24	7 May 2022	0	6	0.28
25	7 May 2022	0	7	0.26
26	14 May 2022	1	9	0.55
27	14 May 2022	2	8	0.54
28	14 May 2022	0	6	0.45
29	14 May 2022	0	9	0.50
30	14 May 2022	2	10	0.53
31	14 May 2022	1	8	0.52
32	14 May 2022	2	9	0.58
33	14 May 2022	2	9	0.56
34	14 May 2022	1	9	0.50
35	14 May 2022	1	8	0.46
36	14 May 2022	1	8	0.50
37	14 May 2022	1	8	0.50
38	14 May 2022	1	9	0.50
39	14 May 2022	0	9	0.53
40	14 May 2022	1	8	0.51
41	14 May 2022	2	9	0.60
42	14 May 2022	3	8	0.45
43	14 May 2022	2	8	0.55
44	14 May 2022	1	8	0.45
45	14 May 2022	1	8	0.55
46	14 May 2022	0	7	0.33
47	14 May 2022	1	9	0.45
48	14 May 2022	3	8	0.54
49	14 May 2022	2	8	0.49
50	14 May 2022	2	8	0.53
51	14 May 2022	2	11	0.60
52	14 May 2022	0	8	0.45
53	14 May 2022	3	8	0.55
54	14 May 2022	1	9	0.53
55	14 May 2022	0	8	0.50
56	14 May 2022	1	8	0.45
57	14 May 2022	0	8	0.54
58	14 May 2022	1	8	0.55
59	14 May 2022	1	8	0.45
60	14 May 2022	1	9	0.38
61	14 May 2022	0	8	0.25
62	14 May 2022	0	8	0.45
63	14 May 2022	0	8	0.39

Table S1 (continued)**.** Medusae measurements.

ID	Collecting date	Medusa buds (n)	Tentacles (n)	Diameter (mm)
64	14 May 2022	1	7	0.43
65	14 May 2022	0	9	0.36
66	14 May 2022	1	7	0.38
67	14 May 2022	1	8	0.43
68	14 May 2022	0	8	0.42
69	14 May 2022	0	8	0.38
70	14 May 2022	1	7	0.45
71	14 May 2022	0	8	0.28
72	14 May 2022	0	8	0.35
73	14 May 2022	0	9	0.35
74	14 May 2022	1	8	0.40
75	14 May 2022	1	8	0.40
76	14 May 2022	1	7	0.50
77	14 May 2022	0	9	0.33
78	14 May 2022	0	8	0.41
79	14 May 2022	0	8	0.40
80	14 May 2022	2	7	0.40
81	14 May 2022	1	7	0.40
82	14 May 2022	1	9	0.45
83	28 May 2022	0	7	0.40
84	28 May 2022	1	8	0.40
85	28 May 2022	0	9	0.43
86	28 May 2022	2	7	0.40
87	28 May 2022	1	8	0.40
88	28 May 2022	1	7	0.50
89	28 May 2022	1	7	0.48
90	28 May 2022	1	7	0.40
91	28 May 2022	2	9	0.40
92	28 May 2022	2	8	0.35
93	28 May 2022	2	9	0.50
94	28 May 2022	0	8	0.45
95	28 May 2022	2	8	0.40
96	28 May 2022	1	7	0.40
97	28 May 2022	1	8	0.45
98	28 May 2022	0	7	0.30
99	28 May 2022	1	8	0.40
100	28 May 2022	1	8	0.40

Table S2 (continued on next page)**.** Physico-chemical parameters.

Collecting date	Temperature C°	Dissolved oxygen mg/L	Salinity ppt	pH
7 May 2022	28.5	0.1	36.1	5.90
7 May 2022	28.5	0.1	36.03	5.90
7 May 2022	28.5	0.1	34.06	5.9
7 May 2022	28.5	0.1	36.18	5.91
7 May 2022	28.5	0.1	36.1	5.91
7 May 2022	28.6	0.1	36.16	5.91
7 May 2022	28.6	0.1	36.12	5.91
7 May 2022	28.6	0.1	36.04	5.91
7 May 2022	28.6	0.1	36	5.92
7 May 2022	28.6	0.1	36.06	5.92
7 May 2022	28.6	0.1	36.02	5.92
7 May 2022	28.6	0.1	35.8	5.90
7 May 2022	27.9	0.1	36.33	6.03
7 May 2022	28.9	0.1	36.27	6.03
7 May 2022	29	0.1	36.2	6.03
7 May 2022	29	0.1	36.22	6.03
7 May 2022	28.9	0.1	36.26	6.03
7 May 2022	28.9	0.1	36.32	6.03
7 May 2022	28.9	0.1	36.31	6.03
7 May 2022	28.9	0.1	36.24	6.03
7 May 2022	28.9	0.1	36.27	6.03
7 May 2022	28.9	0.1	35.61	6.02
7 May 2022	28.9	0.1	36.07	6.02
7 May 2022	28.9	0.1	36.24	6.03
7 May 2022	28.9	0.1	36.27	6.03
7 May 2022	28.9	0.1	36.31	6.03
7 May 2022	28.9	0.1	36.21	6.03
7 May 2022	28.9	0.1	36.31	6.03
14 May 2022	27.8	0.3	36.3	6.88
14 May 2022	27.8	0.3	36.12	6.89
14 May 2022	27.8	0.3	36.41	6.90
14 May 2022	27.8	0.3	36.54	6.90
14 May 2022	27.8	0.3	36.4	6.90
14 May 2022	27.8	0.3	36.5	6.90
14 May 2022	27.8	0.3	36.53	6.91
14 May 2022	27.8	0.3	36.53	6.91
14 May 2022	28.5	0.2	35.76	7.04
14 May 2022	28.6	0.2	36.3	7.04

Table S2. (continued) Physico-chemical parameters.

Collecting date	Temperature C°	Dissolved oxygen mg/L	Salinity ppt	pH
14 May 2022	28.6	0.2	36.35	7.04
14 May 2022	28.6	0.2	36.37	7.05
14 May 2022	28.6	0.2	36.46	7.05
14 May 2022	28.6	0.2	36.45	7.05
14 May 2022	28.6	0.2	36.3	7.05
14 May 2022	28.6	0.2	36.38	7.05
14 May 2022	28.6	0.2	36.3	7.05
14 May 2022	28.6	0.2	36.4	7.05
14 May 2022	28.6	0.2	36.46	7.06
28 May 2022	29.1	0.7	42.04	7.66
28 May 2022	29.1	0.8	42.3	7.61
28 May 2022	29.5	0.6	38.9	13.3
28 May 2022	28.5	0.8	38.5	12.9
28 May 2022	29.5	0.7	35.3	13.3
28 May 2022	29.6	0.7	38.2	13.2
28 May 2022	29.6	0.6	38.7	12.0
28 May 2022	29.6	0.6	38.6	12.7
28 May 2022	29.65	0.6	38	12.8