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ORIGINAL PAPER

Anthopleura dalyae sp. nov. (Cnidaria: Actiniaria), a new species of sea anemone from the southern Gulf of Mexico

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Abstract

Anthopleura dalyae sp. nov, a new species of sea anemone (Actiniaria: Actiniidae) from the rocky intertidal zone of La Gallega reef, Veracruz, Mexico, is described and illustrated. This species is characterized by a column that is pale yellow proximally and dark-orange to bright-orange distally, longitudinal rows of verrucae from margin to limbus, and a series of marginal projections with acrorhagi. *Anthopleura dalyae* sp. nov. is distinguished from other species of *Anthopleura* from the Gulf of Mexico by several taxonomic characters, such as column coloration, number of tentacles, variable number of directive mesenteries and siphonoglyphs, as well as some differences on cnidae. *Anthopleura dalyae* sp. nov. is the fourth species of the genus occurring in shallow intertidal waters associated to coastal and coral reef environments of the region, and the third species of the genus *Anthopleura* recorded in the southern Gulf of Mexico.

Keywords Actinioidea · Actiniidae · Coral reef · Taxonomy · Intertidal fauna · Benthic invertebrates

Introduction

The genus *Anthopleura* Duchassaing de Fonbressin & Michelotti, 1860 is one of the best known genera of sea anemones, and its members can be typically found inhabiting the intertidal and shallow subtidal ecosystems from both tropical and temperate regions (Daly et al. 2017; Spano and Häussermann 2017). This genus comprises about 45 valid species (Fautin 2016; Spano and Häussermann 2017), and can be differentiated from other members of Actiniidae Rafinesque, 1815 in having both acrorhagi and adhesive verrucae arranged in longitudinal endocoelic rows on the column (see Daly et al. 2017).

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There are currently three known valid species of *Anthopleura* inhabiting coastal and coral reef environments of the Gulf of Mexico and the Caribbean Sea: *Anthopleura krebsi* Duchassaing de Fonbressin & Michelotti, 1860, *Anthopleura pallida* Duchassaing de Fonbressin & Michelotti, 1864, and *Anthopleura texaensis* (Carlgren & Hedgepeth, 1952) (Daly and den Hartog 2004).

In 1922, Watzl (1922) described the species *Anthopleura varioarmata* from specimens collected in the Bahamas, and Carlgren (1952) and Belém and Monteiro (1981) applied the name *A. varioarmata* to specimens from North Florida, USA, and Rio de Janeiro, Brazil, respectively. However, Cairns et al. (1986) and Daly and den Hartog (2004) recognized that the specimens of Watzl from the Bahamas actually belongs to *A. krebsi*. In addition, Daly and den Hartog (2004) provisionally refer the specimens identified by Carlgren (1952) and Belém and Monteiro (1981) to *A. texaensis*, but recognized that those specimens may belong to a different, as yet unnamed, species.

In the present study, we describe a new species of sea anemone, *Anthopleura dalyae* sp. nov., from specimens collected in the rocky intertidal zone of La Gallega reef, one of the 25 coral reef formations of the Veracruz Reef System, in Mexico (Tunnel 2007).

The taxonomic features of *A. dalyae* sp. nov. resembles, in many respects, to those of the specimens identified as *A. varioarmata* by Carlgren (1952) and Belém and Monteiro

(1981). However, some differences are discussed, as well as the distinctions of *A. dalyae* sp. nov. from other species of *Anthopleura* from the region. *Anthopleura dalyae* sp. nov. is the fourth species of the genus reported in the Gulf of Mexico, and the third species of the genus reported in the coral reef environments of the southern Gulf of Mexico.

Materials and methods

Seven specimens were collected in the rocky intertidal zone of La Gallega reef (19°13′19.91″ N, 96°07′38.74″ W) (Fig. 1). Collections were made by hand, using a hammer and a chisel. Collected specimens were transferred to the laboratory and maintained in an aquarium to photograph their color while alive. Specimens were relaxed in 5% $MgCl_2$ seawater solution, subsequently fixed in 10% seawater formalin, and stored in 70% ethanol. Squash preparations of small amounts of tissue (approximately 1 mm^2) from tentacles, actinopharynx, filaments, column, and acrorhagi were made from five preserved specimens to study the cnidom. From each squash, the length and width of 40 undischarged capsules of each cnidae type present were haphazardly measured using a Nikon Labophot-2 light microscope (1000× oil immersion). Cnidae terminology follows Östman (2000). Measurements were obtained from living specimens. Longitudinal and cross-sectional serial sections 6–8 mm were made from two specimens dehydrated in ethanol and embedded in Paraplast (Fisher Scientific). Sections were stained with hematoxylin and eosin (Estrada-Flores et al. 1982). Type and voucher specimens were deposited in the Cnidarian Collection of the Gulf of Mexico and Mexican Caribbean Sea (registration code: YUC-CC-254-11) of Unidad Multidisciplinaria de Docencia e Investigación en Sisal (UMDI-Sisal) at the Universidad Nacional Autónoma de México (UNAM). Taxonomic classification follows Rodríguez et al. (2014).

Results

Suborder **Enthemonae** Rodríguez & Daly, 2014 in Rodríguez et al. (2014).

Superfamily **Actinioidea** Rafinesque, 1815.

Family **Actiniidae** Rafinesque, 1815.

Genus *Anthopleura* Duchassaing de Fonbressin & Michelotti, 1860.

Anthopleura dalyae sp. nov.

(Figs. 2 and 3)

non *Anthopleura varioarmata*: Watzl, 1922: 33–36, 75.

? *Anthopleura vario-armata* [sic]: Carlgren, 1952: 373–374.

Anthopleura varioarmata: Belém and Monteiro, 1981: 193–203.

Anthopleura variarmata [sic]: Zamponi et al., 1998: 36, 38, 40.

Anthopleura texaensis: González-Muñoz, Tello-Musi and Simões, 2015: 101–118.

Type material: Holotype: one specimen (YUC-CC-254-11-000329), La Gallega reef, Veracruz, Mexico, (19°13′19.91″ N, 96°07′38.74″ W), 0.5 m depth, 6 January 2012, coll. R. González-Muñoz; paratypes: four specimens (YUC-CC-254-

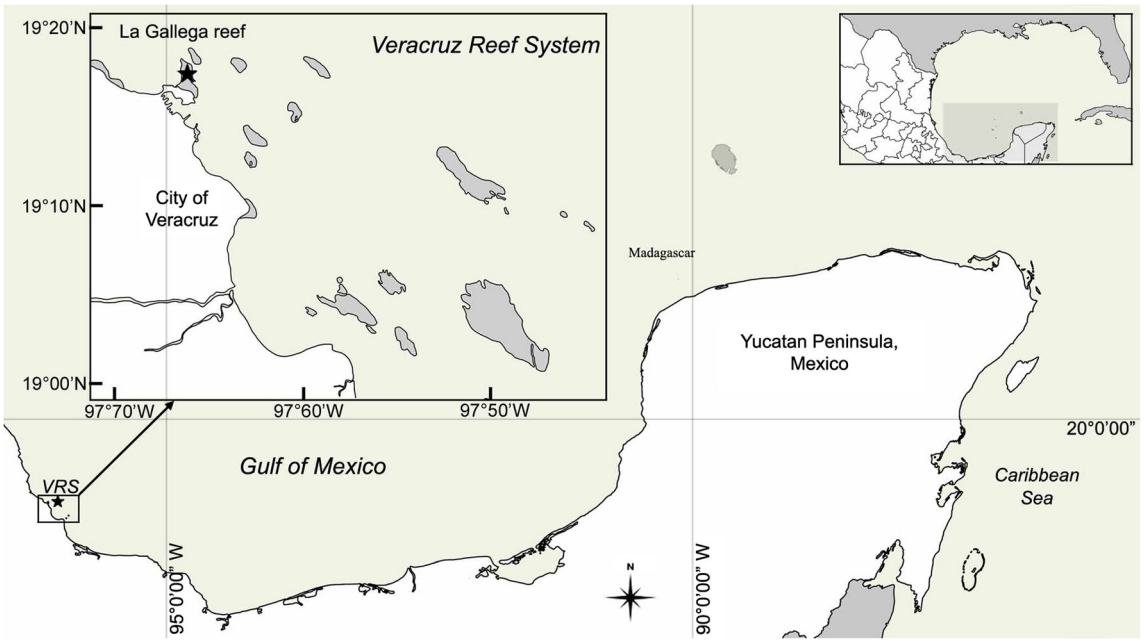

Fig. 1 Map indicating the location of La Gallega reef in the Veracruz Reef System, southern Gulf of Mexico

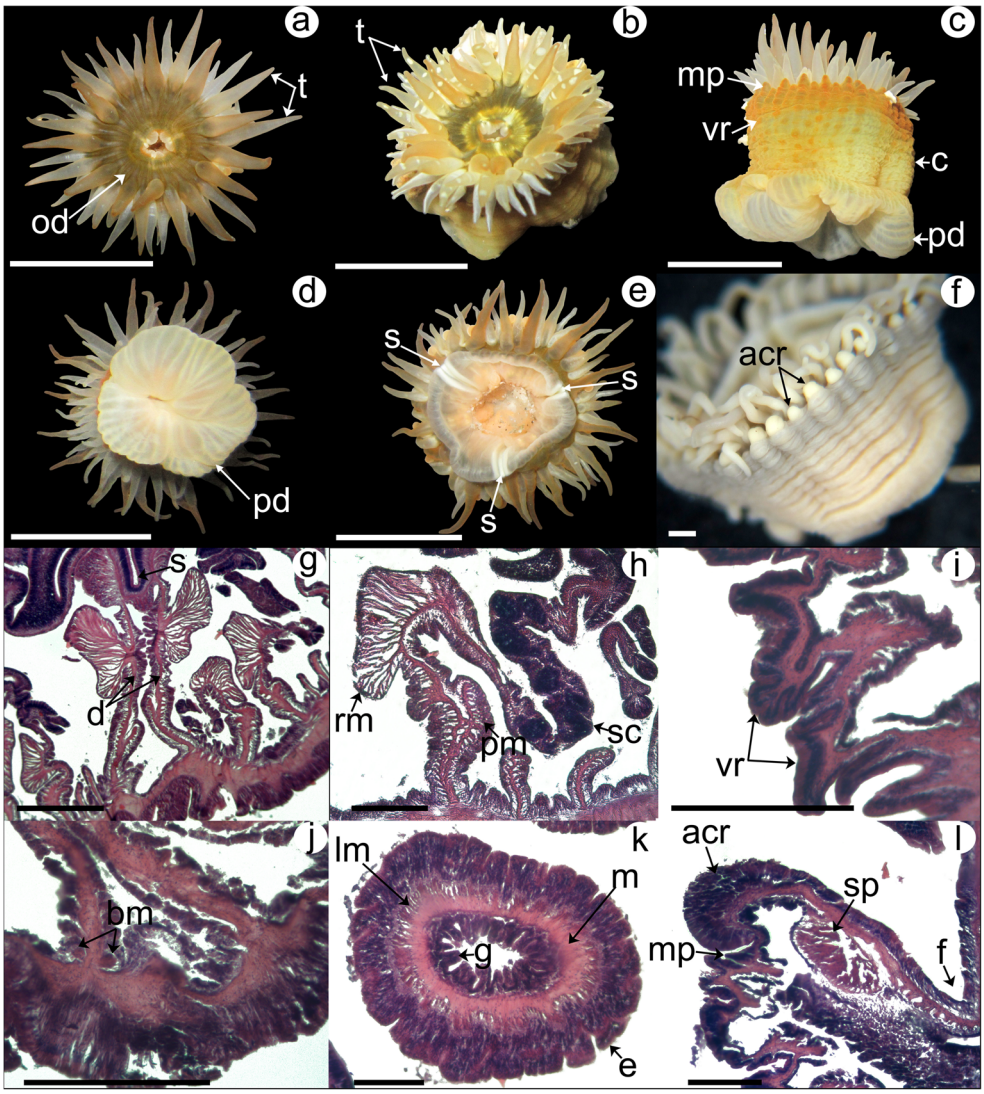

Fig. 2 *Anthopleura dalyae* sp. nov. **a** Oral disk view. **b** Oral disk view: detail of the tentacle color variation. **c** Lateral view. **d** Pedal disk view. **e** Oral disk view: detail of the wide open mouth showing the siphonoglyphs. **a**–**e** Living specimen. **f** Preserved specimen: detail of marginal projections with acrorhagi. **g** Transversal section through distal column showing siphonoglyph. **h** Transversal section through proximal column showing mesenteric muscles. **i** Longitudinal section through distal column showing verrucae. **j** Longitudinal section through pedal disk showing basilar muscles. **k** Transversal section through tentacle showing longitudinal muscles from a tentacle. **l** Longitudinal section through margin showing marginal sphincter. Scale bars: **a**–**e** = 10 mm; **f** = 1 mm; **g**–**l** = 200 μm). Abbreviations: acr: acrorhagi, bm: basilar muscles, c: column, d: directive mesenteries, e: epidermis, f: fosse, g: gastrodermis, lm: longitudinal muscles, m: mesoglea, mp: marginal projection, od: oral disk, pd: pedal disk, pm: parietobasilar muscle, rm: retractor muscle, s: siphonoglyph, sc: spermatic cysts, sp: sphincter, t: tentacles, vr: verrucae

11-000317, 000330, 000331, 000332), with the same sampling data as the holotype; voucher of longitudinal and transversal histological sections from two more specimens (YUC-CC-254-11-000055, 000056), with the same sampling data as the holotype.

Diagnosis

Actiniidae with endocoelic adhesive verrucae from margin to just above the limbus. Column pale yellow proximally, dark-orange or bright-orange distally. Margin with endocoelic projections with acrorhagi (containing basitrichs and holotrichs) on the oral surface and settled in the fosse. Acrorhagi sometimes appear only on the marginal projections relative to the first and second cycles, but sometimes appear in those from almost all marginal projections.

Description

External anatomy

Fully expanded oral disk and tentacles 11–27 mm in diameter in living specimens (8–10 when preserved). Oral disk flat, smooth, 5–10 mm in diameter, olive-green to dark-green, sometimes with white spots marking the siphonoglyphs (Fig. 2a, b). Tentacles irregularly arranged in four to five cycles (between 64 and 82 in number in the specimens examined) (Fig. 2a, b, e). Tentacles short (3–8 mm in diameter in living specimens), conical, tapering distally, smooth, inner cycles longer than outer ones, contractile, pale-gray with orange flashes, sometimes with small white rounded spots (Fig. 2a, b). Fosse well marked. Column cylindrical, stout, 8–14 mm in diameter and 6–11 mm in height in living specimens (8–10 in diameter and 5–7 in height when preserved), pale yellow proximally and dark-orange or bright-orange

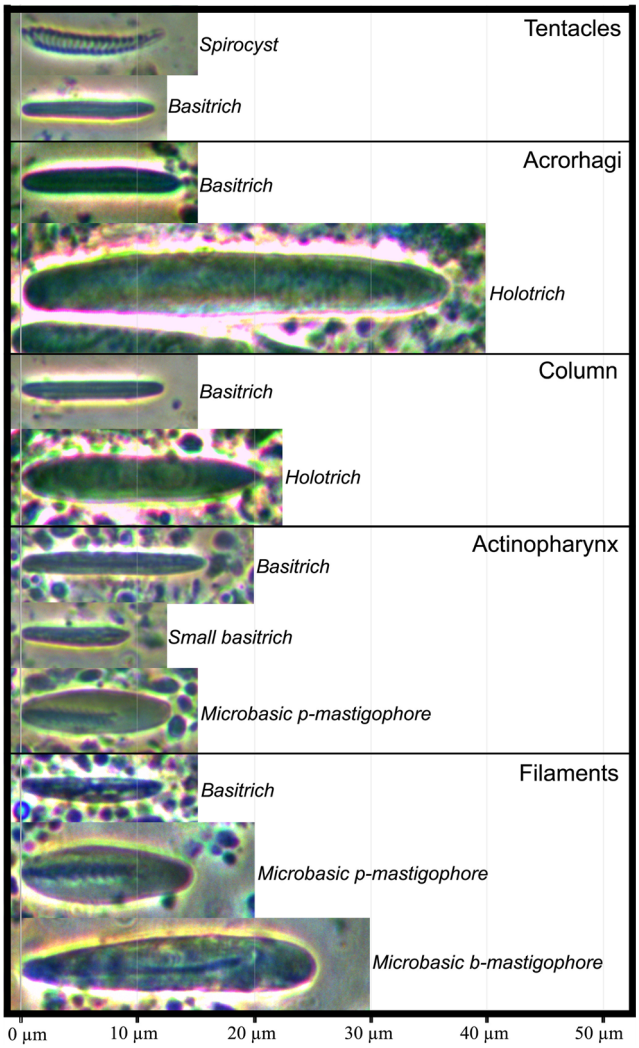

Fig. 3 Cnidom from *Anthopleura dalyae* sp. nov.

distally in living specimens (Fig. 2c), beige proximally and gray distally when preserved. Column covered from margin to just above limbus with simple, endocoelic, adhesive verrucae arranged in 42–48 longitudinal series (Fig. 2c). Verrucae cup-shaped, more prominent distally than proximally, same color as column in live specimens (Fig. 2c, i). Margin with endocoelic marginal projections (29–41 in number in specimens examined); acrorhagi (containing basitrichs and holotrichs) attached to the oral face of the marginal projections and settled in the fosse; acrorhagi sometimes appear only on the marginal projections corresponding to the first and second cycles (Fig. 2f), but sometimes appear in those from almost all marginal projections. Pedal disk well-developed, 8–14 mm in diameter in living specimens (7–10 when preserved), slightly wider than column, pale yellow to beige (Fig. 2d). Acrorhagi pale orange while alive, milky-white in preservation.

Internal anatomy

Mesenteries irregularly arranged in four cycles (40–52 pairs in the specimens examined): mesenteries of the first, second, and some of the third cycles perfect, others imperfect; same number of mesenteries distally and proximally. Directive mesenteries in variable number (2–4 pairs in specimens examined), each attached to a well-developed siphonoglyph (Fig. 2e, g). Stronger mesenteries of the first three cycles fertile, except directives; gonochoric (?), only spermatic cysts were observed in specimens examined (Fig. 2h). Retractor muscles well-developed, restricted; parietobasilar muscles developed with short mesogleal pennon (Fig. 2h). Basilar muscles well-developed (Fig. 2j). Longitudinal muscles of tentacles and oral disk ectodermal (Fig. 2k). Marginal sphincter endodermal, strong, circumscribed, and palmate (Fig. 2l).

Cnidom

Basitrichs, spirocysts, holotrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores (Fig. 3). See Table 1 for size and cnidom distribution.

Natural history

Anthopleura dalyae sp. nov. lives attached to rocks, inside cracks and crevices, in the intertidal and subtidal zone. Azooxanthellate.

Known distribution

La Gallega reef, Veracruz Reef System, Gulf of Mexico; coast of Rio de Janeiro, Brazil (Belém and Monteiro 1981).

Etymology

Anthopleura dalyae sp. nov. is named after Dr. Marymegan Daly, in recognition of her valuable contributions to the taxonomic and phylogenetic study of cnidarians, particularly on sea anemones.

Differential diagnosis

Anthopleura dalyae sp. nov. is easily distinguished from other species of the genus *Anthopleura* from the Gulf of Mexico by its column coloration pattern. In addition, *A. krebsi* and *A. pallida* possess 24–48 tentacles and verrucae arranged in up to 24 longitudinal rows on the column, while *A. dalyae* sp. nov. and *A. texaensis* have a greater number of tentacles (about 64–82 in the former and up to 100 in the latter) and verrucae arranged in up to 48 longitudinal rows on the column (Daly and den Hartog 2004).

Table 1 Capsule sizes and distribution of cnidae of *Anthopleura dalyae* sp. nov.: m_l and m_w are the means, d_l and d_w are the standard deviations (all in μm), N is the proportion of animals examined with the respective type of cnidae present, and n is the number of capsules measured

Tissue	Cnidae type	Length	m_l	d_l	Width	m_w	d_w	N	n
Tentacle	Spirocyst	11.5–26.0	18.5	3.3	2.1–4.7	3.2	0.5	5/5	200
	Basitrich	14.0–20.3	17.5	1.2	1.9–3.6	2.5	0.3	5/5	200
Acrorhagi	Basitrich	11.6–17.9	14.4	1.3	1.7–2.9	2.2	0.2	5/5	200
	Holotrich	23.4–44.8	35.7	3.9	4.1–7.1	5.5	0.6	5/5	200
Upper column	Basitrich	12.4–21.2	16.2	1.7	2.0–3.3	2.4	0.3	5/5	200
	Holotrich	13.3–21.6	17.2	1.7	2.3–5.2	4.0	0.4	5/5	200
Limbus	Basitrich	11.7–22.9	17.6	2.3	2.0–3.8	2.6	0.4	4/5	160
	Holotrich	13.5–29.4	20.1	3.7	3.5–5.8	4.7	0.5	4/5	160
Actinopharynx	Basitrich	15.1–24.6	21.0	1.5	2.3–3.6	2.9	0.2	5/5	200
	Small basitrich	11.1–15.3	13.0	0.8	1.5–3.0	2.4	0.2	5/5	200
	Microbasic *p*-mastigophore	13.0–22.3	16.9	1.3	4.1–6.7	5.2	0.4	5/5	200
Mesenterial filament	Small basitrich	10.8–17.1	12.7	0.9	1.9–3.3	2.4	0.3	5/5	200
	Microbasic *p*-mastigophore	12.2–19.6	15.9	1.1	3.2–6.4	4.8	0.5	5/5	200
	Microbasic *b*-mastigophore	16.8–28.8	21.7	2.7	3.0–5.4	3.9	0.5	5/5	200

Capsules from limbus were only measured in four specimens. The pedal disk diameters of each of the five specimens measured are as follows (all in mm): 7, 7, 8, 9, 10

Aside from column coloration and number of tentacles, other differences between *A. dalyae* sp. nov. and *A. texaensis* lie on the type of the retractor muscle, being restricted in the former and diffuse in the latter (Table 2). Furthermore, two size categories of holotrichs from acrorhagi have been reported from *A. krebsi*, *A. pallida*, and *A. texaensis* (Daly and den Hartog 2004), while only one was observed from *A. dalyae* sp. nov., which is smaller, particularly compared with those of *A. texaensis* (Table 3).

In addition, the whole body size reported for the specimens of *A. texaensis* is somewhat greater than those reported from specimens of the other three species, and *A. krebsi* is the only of these four species reported as zooxanthellate (Daly and den Hartog 2004). Differences in anatomy and cnidae between these four species could also be observed in Tables 2 and 3, respectively.

Discussion

The anatomic features of the specimens examined by Carlgren (1952) and Belém and Monteiro (1981) fit well with those observed in *A. dalyae* sp. nov. Carlgren (1952) reported specimens with up to 100 tentacles, 2–4 siphonoglyphs, several pairs of directive mesenteries and mesenteries irregularly arranged, all strongest mesenteries fertile, band-like retractor muscles, and a marginal sphincter circumscribed. The specimens described by Carlgren (1952) only differ to those of *A. dalyae* sp. nov. in the column coloration, being reported as cream below and olive above, and in the number of tentacles (64–82 in *A. dalyae* sp. nov., while up to 100 are present in *A. texaensis*). In addition, Carlgren (1952) did not report basitrichs in the marginal projections, spirocysts in the tentacles, nor the microbasic *b*-mastigophores in the filaments, which were observed in *A. dalyae* sp. nov.

Specimens reported by Belém and Monteiro (1981) only differ from those of *A. dalyae* sp. nov. in some aspects of the cnidom. They did not report the microbasic *b*-mastigophores from the filaments that were found in *A. dalyae* sp. nov. Instead, they report a long curved type of basitrich, which was not observed in *A. dalyae* sp. nov.

Based on the descriptions by Carlgren (1952) and Belém and Monteiro (1981), it is most probable that those specimens are the same that here described as *A. dalyae* sp. nov. However, because the type specimen assigned to *A. varioamata* by Watzl (1922) was synonymized with *A. krebsi* (Daly and den Hartog 2004), according to the International Code of Zoological Nomenclature (Article 49, ICZN 1999), the name *Anthopleura varioarmata* becomes unavailable. The species *A. dalyae* sp. nov. is here described according to the standard morphological features currently used in actiniarian taxonomy. In addition, the specimens of Belém and Monteiro (1981) are here recognized as synonyms of *A. dalyae* sp. nov., but those specimens named by Carlgren (1952) as *A. varioarmata* need to be examined in order to corroborate its synonymy with *A. dalyae* sp. nov.

Due to the observation of an irregular number of directive mesenteries, siphonoglyphs (one specimen with two siphonoglyphs, five with three, and one with four), and tentacles, it maybe that *A. dalyae* sp. nov. undergoes asexual reproduction by longitudinal fission, which has also been reported for *A. krebsi* and *A. texaensis* (Belém and Pinto 1990; Daly and den Hartog 2004). Although the specimens of *A. dalyae*

Table 2 Comparison of the diagnostic anatomic features of the species of *Anthopleura* from the Gulf of Mexico

Species	No. of tentacles	Column color	Verrucae arrangement	No. of siphonoglyphs and directive pairs of mesenteries	Retractor muscle	Sphincter muscle	Gametogenic tissue	Reproduction	Zooxanthellae
Anthopleura krebsi	24–48	Pale pink to white, with red spots	In 18–24 rows, from margin to limbus	2 siphonoglyphs and 2 pairs of directive mesenteries	Diffuse	Diffuse to circumscript	All mesenteries of first two cycles fertile (directives of small specimens may be sterile)	Sexual and asexual (undergoes longitudinal fission)	Present
Anthopleura pallida	24–48	Pale green to white	In 12–24 rows, from margin to mid-column	2 siphonoglyphs and 2 pairs of directive mesenteries	Restricted, reniform	Circumscript-diffuse	First two cycles of mesenteries fertile, except directives	Sexual, broadcast spawns, no asexual reproduction evidence	Absent
Anthopleura texaensis	80–100	Gray to pale pink	In approximately 48 rows, from margin to limbus	2 siphonoglyphs and 2 pairs of directive mesenteries	Diffuse	Circumscript-palmate	First three cycles of mesenteries fertile, except directives	Sexual and asexual (undergoes longitudinal fission)	Absent
Anthopleura dalyae sp. nov.	64–82	Pale-yellow below, dark to bright orange above	In 42–48 rows, from margin to limbus	2–4 siphonoglyphs and 2–4 pairs of directive mesenteries	Restricted	Circumscript strong	Strong mesenteries of first three cycles fertile, except directives	Sexual and asexual (undergoes longitudinal fission)	Absent

Data of the species *A. krebsi*, *A. pallida*, and *A. texaensis* come from Daly and den Hartog (2004)

Table 3 Comparison of the capsule sizes (all in μm) and distribution of cnidae between the species of *Anthopleura* from the Gulf of Mexico

Tissue	Cnidae type	*Anthopleura krebsi*	*Anthopleura pallida*	*Anthopleura texaensis*	*Anthopleura dalyae* sp. nov.
Tentacle	Spirocyst	10.5–29.8 × 1.7–4.2 (4.7)	10.2–22.3 × 1.4–4.4	12.9–24.0 × 1.8–3.4	11.5–26.0 × 2.1–4.7
	Basitrich	11.7–21.4 (28.2) × 2.0–4.4	10.2–20.1 × 2.0–3.8	17.0–26.0 × 2.0–3.1	14.0–20.3 × 1.9–3.6
Acrorhagi ("Spherule" in Daly and den Hartog 2004)	Small basitrich	–	10.5–14.4 × 1.9–3.3	–	–
	Basitrich	7.3–16.8 × 1.5–3.6	13.5–25.1 × 2.5–3.6	11.6–18.5 × 1.2–2.5	11.6–17.9 × 1.7–2.9
	Holotrich I	32.2–59.7 × 4.6–6.9	32.4–68.8 × 4.0–7.5	46.04–59.6 × 4.8–7.4	**23.4–44.8 × 4.1–7.1**
	Holotrich II	20.0–39.9 × 2.6–4.2 (5.9)	30.4–53.1 × 3.6–5.2	40.9–54.1 × 2.1–3.4	–
Upper column	Basitrich	(7.0) 12.3–20.0 × (1.7) 2.0–3.8	12.2–25.1 × 1.7–3.6	12.1–21.1 × 1.8–3.0	12.4–21.2 × 2.0–3.3
	Small basitrich	–	5.0–12.4 × 1.1–2.4	–	–
	Holotrich III	12.8–19.6 × 2.8–5.5	13.8–22.4 × 2.7–5.0	16.0–26.7 × (1.8) 2.7–5.2	13.3–21.6 × 2.3–5.2
Limbus	Small basitrich	–	–	6.0–13.8 × 1.6–3.0	–
	Basitrich	8.0–18.2 × 1.8–3.7	14.9–22.4 × 3.1–3.9	14.0–23.6 × 1.7–3.0	11.7–22.9 × 2.0–3.8
	Long, curved basitrich	–	26.1–42.8 × 1.7–3.0	–	–
	Holotrich III	(9.9) 11.4–21.1 × 2.1–5.7	13.2–22.4 × 3.1–5.4	16.2–25.8 × 3.2–5.6	13.5–29.4 × 3.5–5.8
Actinopharynx	Basitrich	19.1–25 × 2.9–4.7	16.6–26.2 × 2.3–3.6	16.2–33.3 × 2.4–3.8	15.1–24.6 × 2.3–3.6
	Small basitrich	–	9.1–13.1 × 2.1–2.4	7.3–14.5 × 1.3–2.9	11.1–15.3 × 1.5–3.0
	Microbasic *p*-mastigophore	16.5–20.4 × 3.7–5.7 (6.5)	15.4–26.3 × 3.3–5.6	19.8–26.1 × 3.6–6.6	13.0–22.3 × 4.1–6.7
	Microbasic *b*-mastigophore	–	21.4–27.5 × 3.1–5.4	–	–
	Microbasic *b*-mastigophore II	–	13.8–17.6 × 2.7–3.6	–	–
Mesenterial filament	Small basitrich	10.3–16.4 × 2.3–3.8	–	8.1–19.21 × 1.5–3.4	10.8–17.1 × 1.9–3.3
	Basitrich	–	9.4–17.7 × 1.9–3.4	28.8–40.3 × 4.2–6.7	–
	Long, curved basitrich	–	27.0–46.1 × 1.9–2.5	–	–
	Microbasic *p*-mastigophore	14.4–21.0 × (2.3) 3.9–5.1	14.3–24.7 × 3.0–5.4	17.0–25.8 × 3.5–6.0	12.2–19.6 × 3.2–6.4
	Microbasic *b*-mastigophore	17.7–26.8 × 3.6–4.7	22.4–30.1 × 3.9–5.0 (6.2)	–	–
	Microbasic *b*-mastigophore II	12.3–8.9 × 2.2–4.1	14.0–19.5 × 2.4–3.9	15.0–21.5 × 2.2–3.6	16.8–28.8 × 3.0–5.4

Data of the species *A. krebsi*, *A. pallida*, and *A. texaensis* come from Daly and den Hartog (2004). The main differences between *A. dalyae* sp. nov. and other *Anthopleura* species marked in bold

sp. nov. collected in La Gallega reef were previously reported as *A. texaensis* by González-Muñoz et al. (2015), the finding of a new species was apparent under a more thorough revision. The species *A. krebsi* has been previously reported in the Veracruz Reef System (González-Muñoz et al. 2015) and in the Mexican Caribbean (Instituto Nacional de Ecología, INE 1998), and *A. pallida* has been reported in Alacranes reef (González-Muñoz et al. 2013). *Anthopleura dalyae* sp. nov. is the third species of the genus reported from the coastal coral reef environments in the Mexican Atlantic.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

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