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Anthopleura radians, a new species of sea anemone (Cnidaria: Actiniaria: Actiniidae) from northern Chile, with comments on other species of the genus from the South Pacific Ocean

Anthopleura radians, una nueva especie de anémona de mar (Cnidaria: Actiniaria: Actiniidae) del norte de Chile, con comentarios sobre las otras especies del género del Océano Pacifico Sur

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Abstract

A new species of sea anemone, *Anthopleura radians* n. sp., is described from the intertidal zone of northern Chile and the taxonomic status of the other *Anthopleura* species from the South Pacific are discussed. *A. radians* n. sp. is characterized by a yellow-whitish and brown checkerboard-like pattern on the oral disc, adhesive verrucae along the entire column and a series of marginal projections, each bearing a brightly-colored acrorhagus on the oral surface. This is the seventh species of *Anthopleura* described from the South Pacific Ocean; each one distinguished by a particular combination of differences related to their coloration pattern, presence of zooxanthellae, cnidae, and mode of reproduction. Some of these species have not been reported since their original description and thus require to be taxonomically validated. *A. hermaphroditica* and *A. aureoradiata* are synonyms considering the lack of differences seen between live specimens, museum collections and published records. *A. radians* could also be a junior synonym of *A. minima*, however, no type material was found for testing this hypothesis. Furthermore, it is crucial to designate neotypes for *A. inconspicua*, *A. rosea* and *A. minima* since there are no name-bearing types reported for these species.

Key words: New Zealand, intertidal, *Anthopleura aureoradiata*, *Anthopleura hermaphroditica*, synonyms, taxonomy.

Resumen

Una nueva especie de anémona de mar, *Anthopleura radians* n. sp., es descrita para la zona intermareal del norte de Chile y el estatus taxonómico de las otras especies de *Anthopleura* del Pacifico Sur es discutido. *A. radians* n. sp. se caracteriza por el patrón de coloración amarillo-blanquecino y café tipo tablero de ajedrez del disco oral, las verrugas adhesivas a lo largo de toda la columna y una serie de proyecciones marginales, cada una provista de un notorio acroragio en la superficie oral. Esta es la séptima especie de *Anthopleura* descrita para el Océano Pacifico Austral; cada una se distingue a través de una combinación particular de diferencias relacionadas al patrón de coloración, presencia de zooxantelas, cnidocistos y modo de reproducción. Varias de estas especies no han vuelto a ser reportadas desde su descripción original y, por lo tanto, requieren ser taxonómicamente validadas. *A. hermaphroditica* y *A. aureoradiata* son sinónimos considerando la falta de diferencias observadas entre especímenes vivos, colecciones de museo y registros publicados. *A. radians* podría ser también un sinónimo moderno de *A. minima*, no obstante, no se encontró material tipo de esta especie para poner a prueba dicha hipótesis. Más aun, es crucial designar neotipos para *A. inconspicua*, *A. rosea* y *A. minima* dado que no hay tipos portanombres reportados para estas especies.

Palabras clave: Nueva Zelanda, intermareal, *Anthopleura aureoradiata*, *Anthopleura hermaphroditica*, sinónimos, taxonomía.

INTRODUCTION

The genus *Anthopleura* Duchassaing & Michelotti, 1860 comprises some of the most familiar and well-known sea anemones from the intertidal and shallow subtidal ecosystems. This group is present in all oceans except polar seas, and some species can be locally abundant in hard-bottom communities (Daly, 2004). Through different body features such as adhesive verrucae or acrorhagi, members of *Anthopleura* have been able to colonize diverse habitats by better withstanding desiccation, predation, and competition for space (Hart & Crowe, 1977; Bigger 1980, 1982). In fact, the development of these structures seems to respond to environmental condition and thus, the taxonomic use of such diagnostic features has been

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extensively debated in the past decades (*e.g.* Belem & Pinto, 1990; Daly & den Hartog 2004; Spano *et al.*, 2013).

There are currently 45 described species of *Anthopleura*, and it is the second largest genus of the family Actiniidae after *Actinia* (Fautin, 2016). Most members of *Anthopleura* are especially abundant in temperate regions, even though phylogenetic studies suggest a tropical origin of the clade (Daly, 2004). Carlgren (1949) listed four species for the South Pacific: *Anthopleura kohli* Carlgren, 1930, *Anthopleura aureoradiata* (Stuckey, 1909) and *Anthopleura inconspicua* (Hutton, 1879) from New Zealand and *Anthopleura hermaphroditica* (Carlgren, 1899) from the coast of Chile. Additionally, Stuckey & Walton (1910) described *Anthopleura rosea* and *Anthopleura minima* from Manukau Harbour in New Zealand. Most of these descriptions were later completed by Parry (1951), who added information on size, coloration, cnidae, and habitat of the species. Since then, few reports have reassessed the diversity of *Anthopleura* fauna in the South Pacific, of which the vast majority seems to be endemic of New Zealand (Dawson, 1992).

In the present article a new species of sea anemone –*Anthopleura radians* n. sp.– is described from the intertidal of northern Chile. While in several aspects it resembles some of the species from New Zealand, *A. radians* can be distinguished by the coloration pattern and body dimensions. In addition, the diversity and taxonomic validity of the other *Anthopleura* species described from the South Pacific Ocean are further discussed.

MATERIAL AND METHODS

In 1997, V. Häussermann and G. Försterra collected a few specimens of an unknown morph of *Anthopleura* at Pan de Azucar (26°11'S; 70°39'W) and Totoralillo (30°3'S; 71°24'W), in northern Chile. They originally listed them as a morphological variation of *A. hermaphroditica* (Häussermann, 1998), assignment that persisted since then (*e.g.* Yanagi & Daly, 2004). More recently, many more individuals were found in Coquimbo, being especially abundant in sector Bucanero of La Herradura (29°58'S; 71°21'W). This material was reexamined by Spano *et al.* (2013), who detailed its description and expanded the anatomical differences between this morph and the *Anthopleura* species already known. Several dozen specimens have been photographed in the field during this time, from which approximately 35 were collected, relaxed with menthol crystal, and fixed in 8-10% seawater formalin for morphological analysis. For histological examination, longitudinal and cross-sectional segments of 10 specimens were embedded in paraffin, sectioned at 5-9 µm, and stained with Masson's trichrome modified by Spano & Flores (2013).

Fired and unfired cnidae from living and preserved specimens were observed, photographed and measured per type (*i.e.* of cnidae) and per tissue (*i.e.* tentacle, column, acrorhagi, actinopharynx, and mesenterial filament) using a light microscope (1000X oil immersion) connected to an image analysis software. The largest and smallest cnidae of a particular type were sought for each tissue sample (Hand, 1955; England, 1987). Nematocyst terminology follows that of Schmidt (1972) and England (1991).

Type and voucher specimens were deposited at the Museo Nacional de Historia Natural de Chile (MNHNCL), Sala de Colecciones Biológicas de la Universidad Católica del Norte (SCBUCN), Museo de Zoología de la Universidad de Concepción (MZUC-UCCC) and the Zoologische Staatssammlung München (ZSM).

RESULTS

Suborder Enthemonae Rodríguez & Daly, 2014
Superfamily Actinioidea Rafinesque, 1815
Family Actiniidae Rafinesque, 1815
Genus *Anthopleura* Duchassaing & Michelotti, 1860
Anthopleura radians n. sp. (Figs. 1-3)

Material examined

All specimens from intertidal, preserved in formalin and stored in 70% ethanol: Holotype: 1 specimen (MNHNCL CNID-15008), Playa La Herradura (29°58'S; 71°21'W), 1 May 2012, Coll. C. Spano; Paratypes: 3 specimens (MZUC-UCCC 45078), Escollo El Pulpo (27°01'S; 70°49'W), 18 May 2012, Coll. C. Spano; 2 specimens (MZUC-UCCC 45079), Punta Teatinos (29°49'S; 71°17'W), 30 April 2012, Coll. C. Spano; 4 specimens (MZUC-UCCC 45080), Playa La Herradura (29°58'S; 71°21'W), 1 May 2012, Coll. C. Spano; 2 specimens (SCBUCN-4117), Playa La Herradura (29°58'S; 71°21'W), 28 May 2015; 1 specimen (ZSM 20060554), Playa Totoralillo (30°03'S; 71°24'W), 30 December 1997, Coll. V. Häussermann; 3 specimens (MZUC-UCCC 45081), Puerto Aldea (30°17'S; 71°36'W), 28 April 2012, Coll. C. Spano.

Diagnosis

Orange to pink, small cylinder-shaped actiniid with marginal projections, acrorhagi, and endocoelic adhesive verrucae fully covering the column with particles from surrounding environment. Oral disc with yellow-whitish and brown checkerboard-like pattern radiating from the mouth towards the base of the tentacles, which typically present a row of white spots on oral surface. Marginal sphincter circumscript, retractor muscles diffuse and mesenteries more numerous proximally than distally. Gonochoric; azooxan-thellate.

External anatomy

Size: Pedal disc diameter up to 17 mm, typically 9 mm (S.D = 3; n = 30); Oral disc diameter up to 16 mm, typically 9 mm (S.D = 3; n = 30). Column about a centimeter long and contracted specimens generally dome-shaped. Tentacles *in vivo* usually as long as oral disc diameter; about 8 mm long in preserved specimens.

Coloration: Column very variable in color, ranging from grayish or purple ochre to brick orange or light pink.

Tentacles paler than column, usually in more purplish tones towards inner cycles. Oral disc with a very noticeable yellow-whitish and brown checkerboard-like pattern radiating from a typically pink mouth towards the dark brown-base of the tentacles. Most specimens also present a straight row of white spots on the oral surface of some or all of the tentacles (Fig. 1A). In preservation, a column turns pale yellow or light brown and tentacles usually translucent gray with white marks.

Column: Covered from margin to just above the limbus with numerous small, endocoelic, adhesive verrucae, generally arranged in several fairly distinguishable longitudinal rows (Fig. 1A). Verrucae may be more or less developed and either distinctly pigmented or slightly paler in color than the column; holding small stones and shell debris in life. Each row ends distally in a marginal projection that can bear up to four verrucae on its outer surface and a single swollen brightly-colored acrorhagus on the inner edge (Figs. 1B, 2A). On larger specimens, the acrorhagus can be very prominent (over 2 mm in diameter), widely protruding outside the denticulate margin even under contraction.

Oral disc and tentacles: Mouth prominent, rounded, and may be elevated on oral cone in center of disc. In life, tentacles slender, conical with rounded and, occasionally, perforated tip. Tentacles number 40-70 depending on size of animal, usually hexamerously arranged in 4 to 5 cycles (last one never complete). Inner tentacles longer than outer one, typically held erect and all can be fully covered by the column during contraction (Fig. 1C).

Pedal disc: Distinct limbus; usually arcuate inwards in preserved organisms. Pedal disc roughly circular, adherent and well-developed.

Internal anatomy

General: Actinopharynx no longer than half length of the column, deeply sulcated, with two well-developed aborally prolonged siphonoglyphs, each attached to a pair of directives. Marginal stoma slightly larger than oral stoma. Mesenteries hexamerously arranged in three perfect cycles; occasionally individuals with less than 24 pairs or with a fourth cycle in early development were found (Fig. 2C). Mesenteries grow from the pedal disc upward (with more mesenteries proximally than distally). Gonochoric; Reproductive tissue only observed in perfect mesenteries (Fig. 2E). Azooxanthellate.

Musculature: Marginal sphincter muscle endodermal, circumscribed and generally palmate; with numerous secondary mesogleal branches (Fig. 2B). Mesoglea of the body wall at least as thick as the epidermis and circular endodermal musculature frequently visible. Longitudinal muscles of tentacles ectodermal (Fig. 2D). Retractor muscles diffuse, highly branched and occasionally reniform. Parietal muscle may span as much as half the distance between the column and the free edge of the mesentery. Basilar and parietobasilar muscles well-defined and usually strong (Fig. 2F).

Cnidom: Spirocysts, basitrichs, rod-like basitrichs, holotrichs, microbasic *b*-mastigophores and microbasic p-mastigophores (Fig. 3). See Table 1 for size and distribution of cnidae.

Distribution and habitat

Anthopleura radians can be found in the rocky intertidal of protected or semi-protected beaches from Pan de Azucar (26°11'S; 70°39'W) to Puerto Aldea (30°17'S; 71°36'W). This species typically lives in rock crevices and buried in gravel, with only the tentacles visible during high tide. It can be locally abundant, apparently in clonal populations (Fig. 1D). Individuals usually live in close physical proximity and may share habitat with other sea anemones such as *Anthopleura hermaphroditica* (Carlgren, 1899) and *Anemonia alicemartinae* Häussermann & Försterra, 2001.

Table 1: Capsules size and distribution of cnidae of *Anthopleura radians*. '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 respective type of cnidae present and '*n*' is the number of capsules measured.

Tabla 1: Tamaño de las cápsulas y distribución de los cnidocistos en *Anthopleura radians*. 'm_l' y 'm_w' son los promedios, 'd_l' y 'd_w' son las desviaciones estándar (todo en µm), '*N*' es la proporción de animales examinados con el respectivo tipo de cnidocisto presente y '*n*' es el número de capsulas medidas.

Tissue	Cnida	Length	m_l	d_l	Width	m_w	d_w	*N*	*n*
Tentacle	Spirocyst (A)	9.2-24.0	17.3	3.3	1.4-3.0	2.3	0.3	9/9	220
	Basitrich 2 (B)	11.2-20.6	17.0	1.4	1.5-3.2	2.2	0.3	9/9	280
Acrorhagus	Holotrich (C)	22.3-38.4	32.1	3.2	2.8-6.2	4.5	0.6	4/4	220
Column	Basitrich 1 (D)	8.3-10.0	9.3	0.4	1.4-2.1	1.7	0.2	4/10	11
	Basitrich 2 (E)	10.5-20.4	14.6	1.6	1.5-2.6	2.1	0.2	10/10	340
	Holotrich (F)	11.7-26.7	15.8	2.5	1.6-5.0	4.0	0.4	10/10	220
Actinopharynx	Basitrich 2 (G)	11.6-23.9	19.7	2.1	1.7-3.1	2.4	0.3	6/6	220
	Microbasic *p*-mastigophore A2 (H)	13.3-21.1	17.9	1.8	3.0-5.6	4.1	0.5	5/6	56
Filament	Basitrich 1 (I)	8.2-12.5	10.4	0.9	1.6-2.9	2.3	0.2	3/6	110
	Basitrich 2 (J)	11.9-23.3	18.7	3.1	1.8-3.3	2.5	0.3	4/6	48
	Rod-like basitrich (K)	17.5-42.0	26.6	9.8	1.2-2.2	1.6	0.4	4/6	8
	Microbasic *b*-mastigophore (L)	18.0-35.0	24.6	3.5	2.6-6.3	4.6	0.7	6/6	185
	Microbasic *p*-mastigophore A1 (M)	12.3-17.9	14.9	0.9	2.1-3.7	2.8	0.3	6/6	100
	Microbasic *p*-mastigophore A2 (N)	14.0-22.4	18.2	1.6	2.7-6.8	4.3	0.7	6/6	240

Etymology

Anthopleura radians receive its name based on the radiated pattern of the oral disc. The epithet radians means sun in Latin and refers to the concentric warm-colored marks around the mouth.

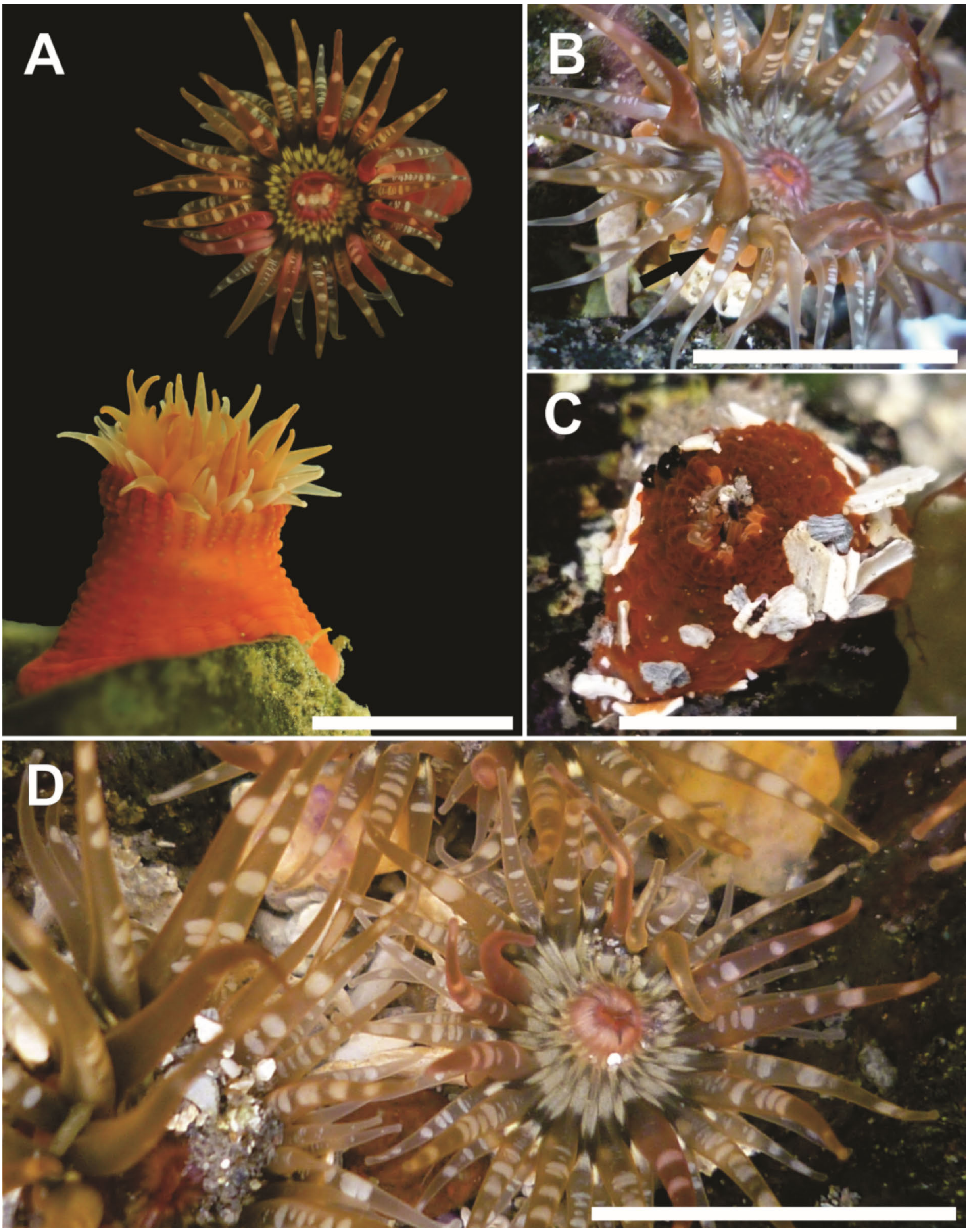

Figure 1: *Anthopleura radians*. A) Oral and lateral view; B) Specimen displaying its acrorhagi outside tentacle crown (see arrow); C) Oral view of contracted specimen; D) *In situ* photograph of several specimens from La Herradura, Chile. Scale bar: 1 cm.

Figura 1: *Anthopleura radians*. A) Vista oral y lateral; B) Espécimen exhibiendo sus acroragios por fuera de la corona de tentáculos (ver flecha); C) Vista oral de un espécimen contraído; D) Fotografía *in situ* de varios especímenes de La Herradura, Chile. Escala: 1 cm.

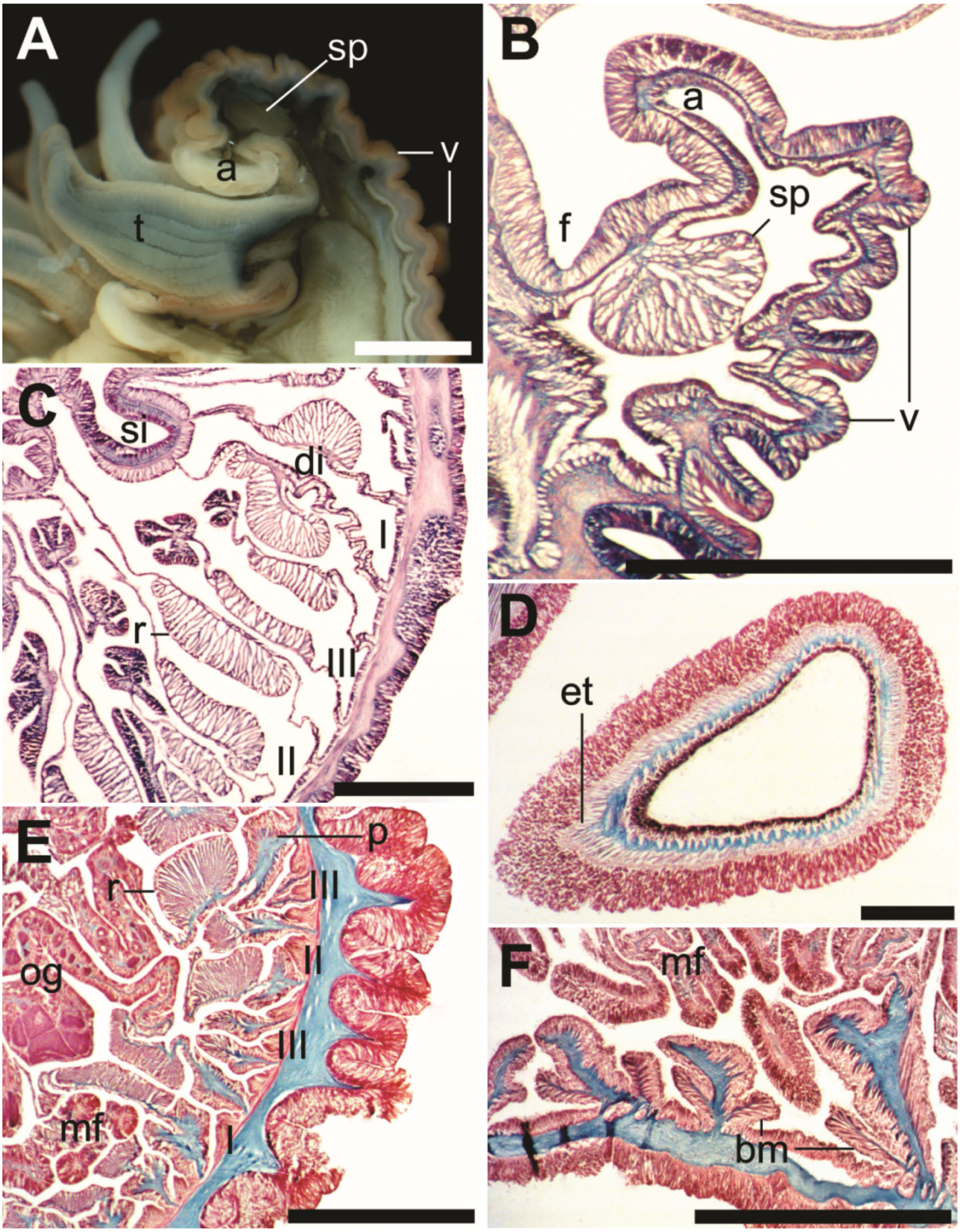

Figure 2. *Anthopleura radians* anatomy. A-B) Longitudinal section of margin, scale: 1 mm; C) Cross section of upper column, scale: 1 mm; D) Cross section of tentacle, scale: 0.1 mm; E) Cross section of lower column, scale: 1 mm; F) Longitudinal section of pedal disc, scale: 0.5 mm. I, II and III: 1^{st} to 3^{rd} cycle of mesenteries, a: acrorhagus, bm: basilar muscle, di: directives, et: ectodermal longitudinal muscle of tentacle, f: fosse, mf: mesenterial filaments, og: oogonia, p: parietal muscle, r: retractor muscle, si: siphonoglyph, sp: sphincter, v: verruca.

Figura 2. Anatomía de *Anthopleura radians*. A-B) Corte longitudinal del margen, escala: 1 mm; C) Corte transversal de la columna superior, escala: 1 mm; D) Corte transversal de un tentáculo, escala: 0.1 mm; E) Corte transversal de la columna inferior; escala: 1 mm; F) Corte longitudinal del disco pedio, escala: 0.5 mm. I, II y III: 1^{er} a 3^{er} ciclo de mesenterios, a: acroragio, bm: músculo basilar, di: directivos, et: músculo longitudinal ectodérmico del tentáculo, f: fosa, mf: filamentos mesenteriales, og: ovogonia, p: músculo parietal, r: músculo retractor, si: sifonoglifo, sp: esfínter, v: verruga.

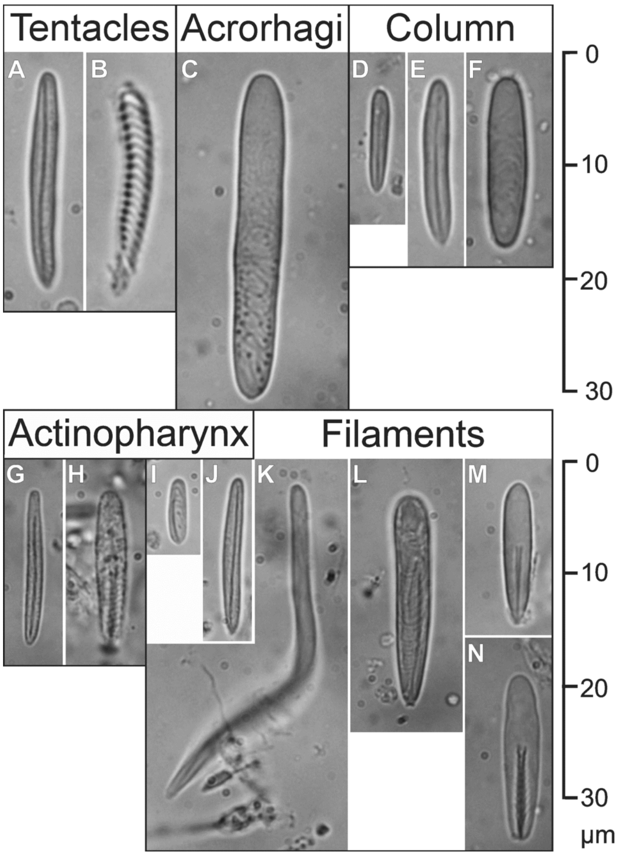

Figure 3. Cnidae of *Anthopleura radians.* Letters A-N refer to Table 1.

Figura 3. Cnidocistos de *Anthopleura radians.* Letras A-N referidas a la Tabla 1.

Remarks

The species described here possess some similarities to other intertidal sea anemones; however, *Anthopleura radians* n. sp. can be readily identified by both external and internal features. The only congeneric species which occurs in the same habitat across its distribution is *A. hermaphroditica*, a widespread intertidal and shallow subtidal species in the southeastern Pacific coast (Spano *et al.*, 2013). In the field, *A. radians* can be distinguished from *A. hermaphroditica* by coloration, especially by the particular checkerboard-like pattern of its oral disc. *A. radians* also typically has a thicker musculature with a distinctive parietal muscle, whereas *A. hermaphroditica* tends to present thinner longitudinal muscles and the coelenteron usually contains one or several embryos. Additionally, unlike *A. radians*, *A. hermaphroditica* is zooxanthellate.

Further north from the current distribution limits of *Anthopleura radians* is *A. mariscali* Daly & Fautin, 2004. This species was originally described from the Galapagos Islands, but recent surveys found it up to Puntarenas in Costa Rica (Quesada *et al.*, 2016). While similar in size and habitat, *A. mariscali* can be distinguished by its coloration pattern and especially the frosted white markings in the distal column (Daly & Fautin, 2004). *A. mariscali* has also been described with a much larger number of tentacles and acrorhagus holotrichs that can be twice as long as in *A. radians*. This type of variation also distinguishes *A. radians* from other South Pacific *Anthopleura* species (Table 2); nevertheless, since several of these diagnostic differences are currently under debate and there is a noticeable similarity between some species descriptions from Australia and New Zealand to those from Chile, this comparison will be further detailed in the following discussion.

DISCUSSION

Anthopleura radians shows all features that characterize the genus (see Spano *et al.*, 2013 for revised diagnosis). Unfortunately this cannot be said for many other *Anthopleura* species since this taxon has undergone several taxonomic rearrangements that have made it increasingly difficult to determine specific membership in the genus. The generic definition is mainly debated nowadays based upon the acrorhagi and holotrich cnidae, whose presence coarsely brings together all *Anthopleura* species and distinguish the genus from *Bunodactis* Verrill, 1899, *Aulactinia* Verrill, 1864, and *Gyractis* Boveri, 1893 (Daly & den Hartog, 2004). Some of these characters, however, are highly variable and quite inconsistent among populations (see, for instance, Fautin, 1988). This problem (which is not exclusive of *Anthopleura* or cnidarians for that matter) has been resolved either by splitting the description to new taxa (*e.g.* England, 1987) or by expanding the original diagnosis to include all morphological variations (*e.g.* Dunn *et al.*, 1980). Each approach leads to rather different conclusions about generic diversity, for which lower-level phylogenies are still unresolved at least based on current taxonomic classifications (Daly *et al.*, 2008). Progressively more traits are needed in an integrated framework not only for discovering new species but first and foremost, to demonstrate that they have not been already described.

The main characteristics that distinguish the species of *Anthopleura* in the South Pacific are summarized in Table 2. Only *Anthopleura aureoradiata* and *A. hermaphroditica* have been reported frequently since their description, although Parry (1951) mentioned that the other species from New Zealand are also common 'if one knows its usual environment'. They were all depicted with typically large marginal spherules on the edge of the oral disc, supporting their original assignment to the genus *Bunodes* Gosse, 1855 and later to *Anthopleura*. Nevertheless, this wide-ranging character (as originally defined) does not necessarily correspond with the acrorhagial structure that currently characterizes the genus. Daly (2003) analyzed different marginal structures and concluded that they are basically composed of two parts: a projection of the column and a holotrich-dense pad (= acrorhagus) that is histologically differentiated from the surrounding tissues. From this perspective, the affiliation of *A. inconspicua* and *A. rosea* has yet to be confirmed.

It is noteworthy that not all specimens may exhibit fully developed acrorhagi (*e.g. Anthopleura hermaphroditica*; Schories *et al.*, 2011). Larger individuals of *A. radians*

TABLE 2: Comparison of the diagnostic features of *Anthopleura* species from the South Pacific Ocean based on the literature. Nematocysts terminology from early references was updated based on Mariscal (1974) and was consistent with Bigger's (1982) observation about acrorhagial "atrichs". *Abundance is taken from author's description.

TABLA 2: Comparación de los caracteres diagnósticos de las especies de *Anthopleura* para el Pacifico Sur de acuerdo a la literatura. La terminología de los nematocistos proveniente de referencias antiguas fue actualizada según Mariscal (1974) y acorde a las observaciones de Bigger (1982) sobre los "atricos" acrorágicos. *Abundancia tomada de la descripción del autor.

Species	N° of tentacles	Coloration	Verrucae arrangement	Zooxanthellae	Reproduction	Cnidae	Distribution and habitat	Abundance	Main references
Anthopleura inconspicua (Hutton, 1879)	Up to 4 cycles (120 tentacles)	**Column:** Olive brown to yellowish white **Oral Disc:** Marked with darker lines along the mesenteries **Tentacles:** Olive brown margined with white, and often white-spotted	In rows, from margin to mid-column; Non-prominent	Present	Not reported	Spirocysts, basitrichs, holotrichs and microbasic *p*-mastigophores	New Zealand; In mudflats	Occasional*	Stuckey 1909b, Parry 1951
Anthopleura hermaphroditica (Carlgren, 1899)	Up to 4 cycles (68 tentacles)	**Column:** Brown, from olive green to grayish ochre **Oral Disc:** With opaque marks in a stellate pattern of radial stripes around mouth **Tentacles:** Idem as column, with greenish-white spots	In rows, from margin to limbus; Distally prominent	Present	Hermaphrodite; Brood internally	Spirocysts, basitrichs, rod-like basitrichs, holotrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores	Chile; In rocky intertidal, shallow subtidal and mudflats	Abundant	Spano *et al.* 2013
Anthopleura aureoradiata (Stuckey, 1909)	Up to 4 cycles (70 tentacles)	**Column:** Brown, yellow, and white **Oral Disc:** With yellow mark on the peristome, corresponding to the primary endocoels **Tentacles:** Brown, mottled with irregular patches of silvery white	In rows, from margin to limbus; Distally prominent	Present	Gonochoric; Brood internally	Basitrichs, holotrichs and microbasic *p*-mastigophores	South Australia New Zealand; In rocky intertidal and mudflats	Abundant	Carlgren 1924, Parry 1951
Anthopleura minima (Stuckey & Walton, 1910)	In 3 cycles (36 tentacles)	**Column:** Dark pink or red, to orange or brick **Oral Disc:** With radiating gold marks running from the peristome towards the bases of the tentacles **Tentacles:** Mottled with silver and brown in a complex pattern	Not reported; Non-prominent	Absent	Not reported	Spirocysts, holotrichs and microbasic *p*-mastigophores	New Zealand; In mussel beds and serpulid tubes	Common*	Parry 1951
Anthopleura rosea (Stuckey & Walton, 1910)	In 3 cycles (50 tentacles)	**Column:** From white or grey to bright orange or olive green **Oral Disc:** Creamy white with 12 dark brown rays running out from the peristome **Tentacles:** Rosy pink and marked with brown and white spots	In rows, from margin to limbus	Absent	Gonochoric	Spirocysts, basitrichs and microbasic *p*-mastigophores	New Zealand; Under stones and buried in gravel or mud	Common	Parry 1951
Anthopleura kohli Carlgren, 1930	Up to 4 cycles (54 tentacles)	Reddish or white (in alcohol)	Not reported	Present	Not reported	Spirocysts and nematocysts	New Zealand; Under stones	Common*	Carlgren 1924 (as *Anthopleura* sp.?)
Anthopleura radians n. sp.	Up to 4 cycles (70 tentacles)	**Column:** From grayish or purple ocher to brick orange or light pink **Oral Disc:** With yellow-white checkerboard-like pattern running from the peristome towards the base of the tentacles **Tentacles:** Paler than column, with white spots on upper surface	In rows, from margin to limbus; Distally prominent	Absent	Gonochoric	Spirocysts, basitrichs, rod-like basitrichs, holotrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores	Chile; In rocky intertidal and buried in gravel	Common	This paper

typically showed this feature, probably because they were often found in very dense populations. Francis (1973, 1976) established that competition for space is possibly the main cause for the acrorhagial response of actiniid species. In *A. elegantissima* (Brandt, 1835), for example, differences in the number and size of acrorhagi have been related to the division of labour in clonal aggregations, being far more developed in those polyps that live along the boundaries of the population (Ayre & Grosberg, 2005). Although no such pattern nor clonal division was observed in *A. radians*, its gregarious nature together with sporadic siphonoglyph asymmetries and column scars does suggest that this species might reproduce asexually. This was already confirmed for *A. rosea* by Stuckey & Walton (1910) and has been also suggested by Parry (1951) for *A. minima*.

Anthopleura hermaphroditica* and *A. aureoradiata

One of the first things that emerges from the species comparison in Table 2 is the striking similarity between *Anthopleura hermaphroditica* and *A. aureoradiata*. They are not only the most abundant members of the genus in the South Pacific Ocean but also inhabit virtually the same environments (see also Schories *et al.*, 2011). Moreover, *A. hermaphroditica* and *A. aureoradiata* are the only southern *Anthopleura* species that have been reported to brood their young internally (Carlgren, 1899; Carlgren, 1950), being one of the few cases that expresses this reproductive mode within the genus (the others are *A. atodai* Yanagi & Daly, 2004, from Japan and *A. handi* Dunn, 1978, from the Philippines, Hong Kong and Malaysia).

The body size as well as the coloration pattern are also extremely similar. Stuckey (1909a: 369) characterized *Anthopleura aureoradiata* by having a 'broken circle of yellow around the peristome, from which extend 6 groups, each consisting of 3 radiating yellow lines with a shorter yellow line between each 2 groups'. This "stellate pattern" is commonly observed in *A. hermaphroditica* (see Fig. 2A in Spano *et al.*, 2013), although it should be noted that it is not always present and appears independently from the silvery white patches of the tentacles that were included in Parry's (1951) description (*i.e.* specimens may either show an oral stellate pattern with white patches on their tentacles or only the pattern or tentacles markings).

Examination of preserved and *in situ* material from both species revealed no differences that could distinguish them beyond what it is expected from intraspecific variability. We verify the cnidom of *Anthopleura aureoradiata* and additionally found spirocysts and microbasic *b*-mastigophores profusely spread in the tentacles and mesenterial filaments, respectively. No rod-like basitrichs were seen, however, that does not mean that they are absent given the scarce occurrence of this type of nematocyst in *A. hermaphroditica*. Cnidae measurements were relatively similar and in both cases zooxanthellae were visibly present throughout the body. Carlgren (1924) indicated that *A. aureoradiata* is dioecious, which so far would be the only remaining difference between the two species. We do have seen some degree of asynchrony in the gonadal development of *A. hermaphroditica* (see also Jennison, 1979); therefore, when gametogenic follicles rip out during spawning, individuals are found with a lower proportion of residual, usually single-sex gametes. Furthermore, the occurrence of males, females and hermaphrodites within a local population is not rare (*e.g.* Dunn *et al.*, 1980; Jennison, 1981; Van Praët, 1990; Rodríguez *et al.*, 2013) and has been recently described as 'trioecy' in the sea anemone *Aiptasia diaphana* (Armoza-Zvuloni *et al.*, 2014). Whether or not this is the case here has yet to be demonstrated, but overall we did not find sufficient evidence to argue that *A. aureoradiata* and *A. hermaphroditica* are different species and hence, we suggest that they should be formally synonymized.

Anthopleura minima* and *A. radians

Perhaps the most distinctive similarity between these two species is the coloration pattern of the oral disc (Fig. 1A, Table 2). Stuckey & Walton (1910: 543) originally described *Anthopleura minima* with a rose-color center surrounded by a 'complicated pattern of light and dark olive-green and gray'. Parry (1951) further detailed this specific feature, including a diagram of the oral disc in her check-list of New Zealand actiniarians (see Fig. 7 in that paper). Although the distribution of the colors within this 'complicated pattern' is still unclear in Parry's description, at least the oral pattern outlined there for *A. minima* fits quite well with that of *A. radians*.

The similarity between both descriptions is also evident in the characterizations of the tentacles and column, although there are considerable differences in some measurements. *Anthopleura minima* was described as usually having 36 tentacles, few non-prominent verrucae, and only 14 pairs of mesenteries, unevenly distributed with 9 pairs on one side and 5 pairs on the other. Based on these differences, this species looks more like a juvenile of *A. radians* rather than a different taxon. Individuals of *A. minima* were commonly found in large numbers in mussel beds or among *Pomatoceros* tubes, possibly in clonal populations (Parry, 1951). Even though *A. minima* individuals seems to be smaller in size (especially if they reproduce asexually), surprisingly the overall body dimensions are larger (*i.e.* 2-3 cm in height and 1-1.5 cm in diameter) while the tentacles are somewhat shorter (*i.e.* 0.5 cm long). Furthermore, the cnidom of *A. minima* has yet to be revised, especially considering the oddly absence of any basitrich nematocyst in its description. Since no type specimen (or any specimen at all) could be found for *A. minima*, the decision whether or not it is a senior synonym of *A. radians* remains pending until new samples from its original locality are examined.

Anthopleura inconspicua*, *A. rosea*, and *A. kohli

The lack of type material is a major problem for species that are rare or have incomplete descriptions. Many sea anemone species have been determined based on their similarities with other species rather than on share derived characters (Daly *et al.*, 2008). For example, all descriptions of *Anthopleura inconspicua* stressed how similar it is to *A. aureoradiata*, but the former differs by a larger number of tentacles (as indicated by Stuckey, 1909b), less prominent verrucae and generally larger sizes (Parry, 1951). This also applies to *A. kohli*, which is endemic to Stewart Island in New Zealand. In fact, Carlgren initially thought that this species was a young form of *A. inconspicua* or *A. rosea*, but later decided to give it a different name as they were all too 'imperfectly known', particularly regarding their nematocysts (Carlgren, 1924, 1930). He was a keen proponent of the cnidom as taxonomic character, especially to distinguish closely related species (Carlgren, 1940). Today this trait is essential in sea anemones descriptions; however, its usefulness is largely discussed and should be handled carefully (Fautin, 1988). In *A. rosea*, for instance, we were able to confirm (from museum collections: NIWA 35279) much of the cnidom indicated by Parry (1951); however, we also found many basitrichs and some other basitrich-like nematocysts that could have been previously classified as microbasic *p*-mastigophores (no V-shaped notch was clearly distinguishable at the base of the unfired shafts). While the differences here were qualitative, even disparities among cnidae measurements are commonly used to identify and re-describe species (but see Williams, 1996, 1998, 2000). Even though we could verify some of the external features of *A. rosea*, accurately characterizing its cnidom was impractical since we could only examine one poorly preserved specimen whose anatomy was heavily deteriorated due to fixative solution.

Conclusion

The determination of the diversity of *Anthopleura* poses a challenging topic within sea anemone taxonomy considering the large number of species that have been historically assigned to this genus. Perhaps the most straightforward way to untangle this problem is by addressing species complexes regionally (*e.g.* Daly & den Hartog, 2004). We agree with the current diagnosis of *Anthopleura* Duchassaing and Michelotti, 1860 for the South Pacific species but do suggest that *A. hermaphroditica* and *A. aureoradiata* are synonyms. Because *A. hermaphroditica* (Carlgren, 1899) has priority over *A. aureoradiata* (Stuckey, 1909), the former should be kept as the valid name (Art. 23: International Commission on Zoological Nomenclature, 1999). With the newly described species and the synonymy of *A. aureoradiata*, the genus *Anthopleura* would retain 45 nominal species. The lack of name-bearing types prevents the verification of the validity of *A. inconspicua* (Hutton, 1879), *A. rosea* (Stuckey & Walton, 1910) and *A. minima* (Stuckey & Walton, 1910). If no such material exists, a neotype for each species must be fixed (Art. 72.2: International Commission on Zoological Nomenclature, 1999). Furthermore, the validity of several diagnostic features that have been traditionally used to recognize *Anthopleura* members has yet to be resolved. Most recent proposals point to the nematocyst ultrastructure to define the genus *Anthopleura* (England, 1987; Belem & Pinto, 1990); and a combination of other characteristics such as coloration pattern and cnidae dimensions are generally used to identify species. Nevertheless, ascertaining which variations represent phenotypic plasticity (*i.e.* changes of the phenotype in response to changes in the environment; *e.g.* Francis, 2004; Price, 2006) rather than evolutionary novelties is crucial if we want to settle species designations in Actiniaria. The lack of synapomorphies (or occurrence of character convergences; Daly, 2004) on neutral genetic markers might be highlighting the importance of local adaptations to explain the current taxonomic diversity. Only by knowing the nature of these differences will we be able to finally estimate the true richness of sea anemones.

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