

A new blue astrangiid coral from the Southwestern Atlantic: coral diversity under globalization

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Abstract

Two *Astrangia* Milne Edwards & Haime, 1848 species have been identified in shallow water environments along the Brazilian coast: *A. solitaria* (Le Sueur, 1817) and *A. rathbuni* Vaughan, 1906. *Astrangia woodsi* Wells, 1955 is an incrusting coral with blue-gray polyps, and a darker skeleton originally described to the Eastern Coast of Australia. This species was for the first time identified out of its natural border in 2021, on a rocky reef in the Arabian Sea. In the last decades, Indo-Pacific dendrophylliids belonging to the genus *Tubastraea* Lesson 1830 became widespread in the Atlantic. Indeed, two other exotic marine cnidarians have been recently introduced in the Tropical Atlantic, the octocorals *Sarcothelia* sp. Verrill, 1928 and *Briareum hamrum* (Gohar, 1948). Here, we describe a new *Astrangia* species to the Northeastern Brazilian coast. Scanning electron microscopy images of the corallites supported the taxonomic analysis and description of the new astrangiid. Early confounded with the *A. woodsi*, this new coral may be promptly recognized in biofouling because of its color and solitary development. Indeed, the incorporation of iron salts into the aragonite fibers may result in blue carbonate skeletons – an exquisite condition observed in a small group of reef-building octocorals, the Helioporidae Moseley, 1876. Scleractinians have usually white aragonite skeletons. However, like the helioporids, *Astrangia* sp. nov. has also a blue skeleton, a natural camouflage that is likely to prevent it to be noticed somewhere else. Finally, a key of the world *Astrangia* species is provided for the first time.

Introduction

Astrangia Milne Edwards & Haime 1848 is a scleractinian genus, being alternatively solitary or colonial, azooxanthellate or facultative zooxanthellate, usually found on natural, and artificial substrates, usually in biofouling communities, from deep to shallow water environments, and adapted to a wide range of temperatures. According to WoRMS database (Hoeksema and Cairns 2022), there are 15 valid *Astrangia* species.

Previously mentioned within the Rhizangiidae d'Orbigny, 1851, a family of the 'Robust' clade that comprises five extant genera (*Siderastrea*, de Blainville 1830, *Culicia*, Dana 1846 and *Oulangia*, Milne Edwards and Haime 1848, *Cladangia*, Milne Edwards & Haime, 1851 and *Pseudosiderastrea* Yabe & Sugiyama 1935), *Astrangia* has been recently replaced in the Astrangiidae Milne Edwards & Haime, 1857 (Romano and Palumbi 1996, Löser et al. 2021). Indeed, based on the microstructures of the corallites, Rhizangiidae was redefined by Löser et al. (2021) – prevailing over Astrangiidae, the synonymization between these two families was also refuted by the authors.

Another remarkable change in this group was the exclusion of the three 19th century subgenera – *Astrangia* (*Astrangia*) Milne Edwards and Haime, 1848, *Astrangia* (*Phyllangia*) Milne Edwards and Haime, 1848 and *Astrangia* (*Coenangia*) Verrill, 1870. Although being cited in the species key of Durham and Barnard (1952), during the 1950's all subgenera disappeared from the literature. Among the accepted valid species, *Astrangia* (*Astrangia*) was mostly synonymized as *Astrangia haimeii* Verrill, 1866, while *Astrangia* (*Coenangia*) became *A. conferta* Verrill, 1870. In turn, *Astrangia* (*Phyllangia*) was transferred to

another genus, *Phyllangia* Milne Edwards and Haime, 1948. The distinction of these three subgenera occurred majorly in the Eastern Pacific, where the diversity of *Astrangia* was attributed by Durham and Barnard (*op. cit.*) to the coral's early life: '*the planulae may have a very short motile stage, with the consequent development of numerous local endemic species*' (p. 4)

In 1906, two astrangiid corals were described by Vaughan to Brazil: *Astrangia brasiliensis* and *Astrangia rathbuni*. However, *A. brasiliensis* has been suggested as a synonym of *A. solitaria* (Lesueur, 1817) (Kitahara 2007). *Astrangia solitaria* and *A. rathbuni* are distinct species, promptly separated by colonial development and corallite size. Following Vaughan's original diagnosis (*op.cit.*), *Astrangia brasiliensis* (= *A. solitaria*) has reptoid, irregular incrusting colonies, with smaller calice size (2.0–4.0 mm), and three complete septa cycles. *Astrangia rathbuni* form small, rounded clumps, with larger calices (4.0–7.0 mm) and four complete septa cycles. The congeners have also clear geographical limits, the former from warmer environments in the Northeastern (type locality: Periperi beach, Bahia State), while the latter from colder waters in the Southeastern (type locality: Paquetá Island, Rio de Janeiro) (Vaughan 1906). No other species has been so far recognized for the genus along the Brazilian coast.

Hoeksema et al. (2018) mentioned the dispersion of *A. poculata* (Ellis & Solander 1786) on marine debris by a mechanism of long-distance rafting from the Gulf of Mexico to Normandy (France) – a colony on a fragment of flotsam apparently rafted across the entire Atlantic. Another introduction has been attributed to an astrangiid coral: *A. woodsi* Wells, 1955. Considered endemic to Eastern Australia, this species can be easily identified *in situ* by its deep blue-gray polyps with transparent tentacles, and a darker skeleton. In 2021, *A. woodsi* was for the first time reported out of its natural range in the Eastern Arabian Sea (Indian coast) (Viswambharan et al. 2021).

Here we describe a new *Astrangia* species to Brazil, and the type locality is the Todos-os-Santos Bay (TSB) (12°S, Bahia State). Solitary polyps were observed settled on live barnacles and oysters in a biofouling community established negatively on a deck pier together with other exotic invertebrates, as the bryozoan *Triphyllozoon arcuatum* (MacGillivray, 1889) and the 'sun corals' (*Tubastraea* spp. Lesson 1830). It is noteworthy that two exotic octocorals from the Indo-Pacific have been recently identified in the TSB: the blue *Sarcothelia* sp. Verrill, 1928 and *Briareum hamrum* (Gohar, 1948) – capable to form extensive mats they are rapidly spreading on natural substrates (Menezes et al. 2022).

'Blue corals' are a small group of Helioporidae Moseley, 1876, the only known reef-building octocorals with blue aragonite fibers, a condition attributed to the incorporation of iron salts into the skeleton (Courtney et al. 2021). Scleractinians have white aragonite skeletons covered superficially by transparent tissues. Among shallow and deep-water corals, variable color patterns usually occur due to the presence of the endosymbiotic microalgae, the zooxanthellae, and/or the carotenoid pigments.

Because of the blue color, the new astrangiid was early cofounded with Wells' species. In contrast with *A. solitaria* and *A. rathbuni*, the new species is somewhat difficult to detect in its natural habitat – being

darker is a perfect camouflage for keeping the polyps unnoticed, and, probably, dispersing somewhere else.

In the last two decades, it is surprising that, in a scenario gradually dominated by the orange of the sun coral colonies, blue has apparently become a new trend among introduced organisms on the Brazilian Coast. Actually, a few questions remain puzzling this new finding: How many 'blue' *Astrangia* have not been described yet? How many species have been 'at a glance' misinterpreted as *A. woodsi*? As result, we provide the diagnosis of a new blue Atlantic *Astrangia*. Furthermore, a key to the world species is provided for the first time.

Material & Methods

Study area

The material analyzed was collected in the Todos-os-Santos Bay (TSB), Bahia State, Northeastern Brazil (Fig. 1). TSB is the second largest navigable bay in Brazil (Hatje and Andrade 2009). It harbors 56 islands, and the estuaries of the rivers Paraguaçu, Jaguaripe, and Subaé (Cirano and Lessa 2007; Caroso et al. 2011). TSB has two of the largest ports of the Bahia State, the Port of Aratu and the Port of Salvador, attending international commercial ships, and playing an important role in the regional economy (Faria 2011). Among several other risk vectors, touristic and commercial activities in the waters of the TSB are probably related to the introduction of exotic organisms - and the inventory is increasing over the last two decades, including the crab *Charybdis hellerii* (A. Milne-Edwards, 1867) (Carqueija and Gouveia 1996; Silva and Barros 2011), the sun corals *Tubastraea* spp. (Castro and Pires 2001; de Paula and Creed 2004; Sampaio et al. 2012), the bryozoan *Triphyllozoon arcuatum* (Almeida et al. 2015), the calcareous sponge *Heteropia* sp. Carter, 1886 (Chagas and Cavalcanti 2017; Barros et al. 2018; Chagas et al. 2020) and the soft corals *Sarcothelia* sp. and *Briareum hamrum* (Menezes et al. 2022).

Sampling

Between August 2021 and June 2022, colonies were sampled from Bom Jesus dos Passos Island (12°45'S, 38°38'W). The new species was majorly found settled on other fouling organisms in a pier deck, such as barnacles and oysters (less commonly observed on polystyrene floats). A second population was found on another pier (Marina de Itaparica Pier), Itaparica Island (12°53'S, 38°41'W), in November 2022. At this site, the new coral was identified only on bivalves. Larger polyps were visualized during SCUBA diving at 0 to 2 m depth, and specimens were collected with the basibionts. Samples were separated individually in plastic bags with seawater and kept alive. The material was transferred to the boat where it was examined and photographed with a Canon PowerShot SX30 IS. In the laboratory, samples were fixed in 96% ethanol. For corallite analyses, the specimens were treated with a 4% sodium hypochlorite solution to remove all organic fractions. After 24 hours, the skeleton was washed in running water and placed to dry.

Morphological analysis

In the laboratory, corallites were photographed under a stereomicroscope supplied with a digital camera, model ZEISS Stereo Discovery.V20. The identification was supported by specialized literature, following Vaughan (1906), Wells (1955), and Cairns (2000). SEM images were developed for the analysis of the corallite microstructures, including columella and septa ornamentation. The corallites were submitted to an ultrasonic bath for complete cleaning and then left to dry for 30 minutes inside a stove at 70°C. Measurements of corallite structures were taken by caliper (model Mitutoyo 500-143B) or using ZEISS software under a stereo microscope. Each sample was fixed with carbon adhesive tabs on pin stubs. For SEM analysis, the samples were coated with a thin layer of gold, 10/20 Å, for 2 min, and images were captured using the JOEL JSM-6390LV equipment (Oswaldo Cruz Foundation, FIOCRUZ-BA). Type series are deposited in the Cnidaria Collection at the 'Museu de Historia Natural da Bahia' (acronym: UFBA), at the Universidade Federal da Bahia. For the infographic, data on the taxonomy and ecology of the genus *Astrangia* were compiled from the available published literature and based on Spalding et al. (2007)

Results

Taxonomy

Class: Anthozoa Ehrenberg, 1834

Order: Scleractinia Bourne, 1900

Family: Astrangiidae Milne Edwards & Haime, 1857

Genus: *Astrangia* Milne Edwards & Haime, 1848

Diagnosis of *Astrangia* genus (*sensu* Cairns 2000): colony development by extracalicular budding, incrusting or subplocoid corallum, thin tissue layer of coenosteum connecting basally the corallites (reptoid development with stolonial structures), costae granular, axial and distal edges of all septa regularly dentate, paliform lobes around the columella, columella papillose.

Type species: *Astrangia michelinii* Milne Edwards & Haime, 1848 [= *A. poculata* (Ellis & Solander, 1786)].

Type locality: Recent - off Atlantic City, New Jersey

Astrangia pichoni sp. nov Serra, Neves, Alves & Johnsson 2023

(Figs. 2, 3, 4)

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Type material: Holotype: UFBA 1680, metalized corallite (6.5 mm diameter, 5.2 mm high)

Paratypes: UFBA 1426, three solitary corallites, two encrusted in a barnacle, one encrusted in a mussel; UFBA 1544, three solitary corallites encrusted in a mussel; UFBA 1545, one corallite sitting on bivalve

mollusk; UFBA 1546, one corallite sitting on bivalve mollusk; UFBA 1549, one corallite in a mussel; UFBA 1550, one corallite in a mussel; UFBA 1551, one corallite in a mussel.

Type locality: Bom Jesus dos Passos Island (12°45'S, 38°38'W), Brazil (Southwestern Atlantic).

Etymology: *Astrangia pichoni* sp. nov. is named after renowned researcher and coral taxonomist, Dr. Michel Pichon (Museum of Tropical Queensland, Townsville, Australia).

Diagnosis: Solitary corallum, tympanoid to cylindrical shape; polyp color ranging from discrete blue to brownish at the tip of the tentacles; base polycyclic; epitheca inconspicuous; theca externally white, calice and septa structures blue; septo-costae equally distributed, low and granular; septa exerted, and arranged hexamerally; 4 to 5 septa cycles, S1>S2>S3>S4>S5, S4-S5 poorly developed; columella papillose with well-developed paliform lobes, fossa moderately deep.

Description: Tympanoid to cylindrical solitary corallum with an encrusting, polycyclic base formed by concentric thecal rings, base weakly calcified. Two or three individuals forming small aggregates; asexual reproduction by fission. Corallum externally white with calice, septa and columella dark blue. Polyps discretely bluish with brownish tentacle tips. Calicular diameter 4.0 mm on average (4.1 mm to 6.5 mm). Mature and well-developed corallites 2.3 mm high on average (0.7 mm to 5.2 mm). Low and granular costae, corresponding to all septa, discrete towards the theca base. Costae extending from the calicular edge to the base in shorter corallites, and from the calicular edge to ½ theca in the highest ones. Costae are separated by thin, shallow intercostal grooves. Epitheca discrete. Septa number varying from 42 to 53 (46 on average), arranged hexamerally (irregular arrangement rare), 4 to 5 cycles (S1>S2>S3>S4>S5), S1 to S4 complete, S1 and S2 exerted and reaching the columella, S1 slightly larger with distal margins projecting above calicular edge, S2 with regular distal margins and slightly projected, axial margins dentate, S4 poorly developed eventually fused to S3; S5 incomplete and rudimentary. Septal face granulated with distal ornamentation fused, forming raised striations extending towards the septa edge. Paliform lobes around the columella, columella papillose (about 2.5 mm in diameter), columellar fossa moderately deep (ranging from 1.0 mm to 2.9 mm in depth).

Distribution: Todos-os-Santos Bay, Bahia, Brazil (Southwestern Atlantic): Bom Jesus dos Passos I. (12°45'S, 38°38'W), and Marina de Itaparica (Itaparica I.) (12°53'S, 38°41'W)

Ecology: This species has an epibiotic behavior, being predominantly observed encrusted on carbonate shells (bivalves and barnacles) (**Fig. 2C; Fig. 3B-C**). One single coral, or groups of two, three, or more individuals can establish on the same basibiont (**Fig. 2A-B, D; Fig 3A**). Only a few coralla were observed growing directly attached to artificial substrates, such as polystyrene floats.

Remarks: The new species from the TSB belongs to *Astrangia* genus because (1) the encrusting corallum; (2) the axial septal margin dentate; (3) the paliform lobes, and (4) the columella papillose. However, it has other characteristics hitherto not mentioned in the genus diagnosis (Milne Edwards & Haime 1848; Cairns 2000), specifically the solitary development and the asexual reproduction by fissiparity (**Fig. 2A**).

Astrangia pichoni sp. nov. differs from the other Brazilian astrangiids due to the exquisite color of its skeleton, with calice structures in dark blue tones (theca being white outside) (**Fig. 3A-C**), while *Astrangia rathbuni* has reddish-brown corallites, and *A. solitaria* has a gradient from completely white to light brown corallites (Cairns 2000). Other characteristics are also distinguishable among the congeners: *A. rathbuni* has higher and larger corallites than *A. pichoni* sp. nov. which is the smaller astrangiid of the Brazilian group (Vaughan 1906; Cairns 2000). Indeed, the maximum height observed in the new species is almost equivalent to the minimum recorded in the two other species (**Table 1**) (Cairns 2000). The septal organization of *A. pichoni* sp. nov. should be also highlighted: it may have five cycles (the two others have only four cycles), with an average number of septa around 46 (sometimes a total of 53 septa is observed in a single corallite) (**Fig. 4A**). A fourth species, *A. poculata* (Ellis & Solander, 1786), also occurs in the Western Atlantic, but it has not been reported to Brazil yet (Peters 1988; Cairns 2000). *Astrangia poculata* has a reduced number of septa (30-36), but the calice diameter of the corallites may vary enormously, from the smallest size among the congeners (1.0 mm), it may be bigger than in *A. rathbuni* (7.0 mm). In addition, the corallites of *A. poculata* are closer, with a poorly developed coenosteum, sometimes completely absent. The absence of coenosteum between nearby polyps reinforces the diagnosis of solitary and/or colonial development in *Astrangia*. However, because of reproduction by fissiparity, two or three corals can be eventually observed side by side, in close contact. Recruits are usually whitish with light shadows of blue color.

Table 1. Major diagnostic characteristics of Western Atlantic *Astrangia* species. Data supported by Vaughan (1906)^a, Peters (1988)^b, and Cairns (2000)^c

Species/ Character	<i>Astrangia poculata</i> (Ellis & Solander, 1786) ^{b, c}	<i>Astrangia rathbuni</i> Vaughan 1906 ^{a, c}	<i>Astrangia solitaria</i> (Lesueur 1817) ^c	<i>Astrangia pichoni</i> sp. nov. Freitas et al., 2022
tissue color	translucent white (azooxanthellate) to brown (zooxanthellate)	whitish to pale brown	orangish to pale brown	translucent to brownish, at the tentacles
skeleton color	white	reddish-brown	completely white to light brown	outside wall white; deep blue-gray calice (whitish recruits)
corallum	encrusting, cerioid or plocoid, branching	colonial, encrusting, forming round clumps	colonial, encrusting, cerioid or reptoid	solitary, encrusting
budding	extracalicular	extracalicular, basal from stolons	extracalicular, basal from stolons	fissiparity
corallite height	2.0 – 10.0 mm	4.0 – 9.0 mm	4.0 – 8.0 mm	0.7 – 5.2 mm
calice diameter	1.0 – 7.0 mm	4.0 – 6.5 mm	2.5 – 6.0 mm	4.1 – 6.5 mm
corallite distances	0.5 – 2.0 mm; coenosteum poorly developed to absent	not crowded, slightly tufted	1.5 – 4.0 mm	solitary polyps
costa	usually not present; eventually granular	indistinct	alternating in size	granular
number of septa	24 – 36, S4 rarely complete	~ 48; S4 complete	commonly 36 (rarely reaching 48); S4 rudimentary	42 – 53; S5 rudimentary
septal margins	strongly dentate	dentate	dentate, slightly exsert	distal margin moderately regular, axial margin with dentate to truncated projections, slightly exsert
calicular fossa	shallow to moderately deep	very deep	deep	moderately deep (1.0 – 2.9 mm)
columella	Papillose	weak, papillate above	papillate surface	papillose

paliform lobes

-

not differentiate

present

present

Discussion

The diversity of astrangiids in the Western Atlantic has been probably biased by the life trends of the corals, including the small coralla, the reptoid incrusting colonial development (polyps usually connected by discrete stolons), and the cryptic habit. Indeed, because of the assessment and monitoring project of the exotic sun corals in the TSB (coordinators: E. Neves & R. Johnsson), two species, *A. solitaria* and *A. pichoni* n. sp., have been identified in the same artificial environments, the latter regularly found in epibiosis with other sessile and calcifying organisms, as components of the biofouling. In fact, considering all *Astrangia* species there is an apparent selective behavior of the planulae for solid and biogenic substrates, principally mollusk shells and rocks (Fig. 5). However, in the oldest literature, the nature of the 'rocks' is not well defined – it could be limestone, sandstone or granite, or even another kind of boulder found in the marine environment. It is important to point out that in the major Southwestern Atlantic Provinces (the Tropical and Warm-Temperate, *in* Spalding et al. 2009), the inventory has been updated, comprising now three species: *A. solitaria*, *A. rathbuni* and *A. pichoni* n. sp.

Originally described by Milne Edwards & Haime (1848), and redescribed by Cairns (2000), no other record has been added to the species list of *Astrangia* in recent years. Thus, the description of *Astrangia pichoni* sp. nov. in addition to supporting the inventory of the worldwide Astrangiidae, also highlights two peculiar characteristics of the group, (1) the solitary development of the adults, and (2) the ability of the polyps to reproduce asexually by fission. Verrill (1866) has also reported solitary polyps of *A. costata* Verrill, 1866 from Tropical East Pacific, but it is unclear whether this is an attribute of primary development preceding the colonial stage, or an alternative growth pattern of adult corals. Moreover, we suspect that *A. costata* may form small polyp aggregates with inconspicuous coenosteum, once based on Verrill's (*op. cit*) description this species may vary from 1 to 4 polyps.

The blue color of *A. pichoni* sp. nov. also draws attention, as this color pattern is quite uncommon among corals. Scleractinian skeleton is white with tissues naturally transparent, being colorful because of the presence of carotenoids and/or due to the pigmentation from the endosymbiotic microalgae (e.g., zooxanthellate species). However, in the new species, the impregnation of the aragonite fibers apparently occurs during early development, once recruits are regularly whitish, with light shadows of blue color (getting bluer as they get older). Blue skeletons have been recorded only in octocorals of the family Helioporidae, a condition attributed to the incorporation of iron salts from the seawater into the aragonite fibers (Hill 1960; Richards et al. 2018). Iron is a micronutrient usually found at low rates in the seas, but recent studies have pointed out its influence on phytoplankton productivity and consequent effects on greenhouse gases (Cooper 1935, Blaustein 2011, Tagliabue et al. 2017). Therefore, whether (and how) *A. pichoni* sp. nov. is incorporating iron salts (or another element) along its development, is an interesting gap that should be answered in future studies.

Finally, based on a hypothetical scenario where *A. woodsi* and *A. pichoni* sp. nov. could live syntopically, they would be easily misidentified. Indeed, the hypothesis that these blue astrangiids could select the same environment must be considered. And, the idea that other blue astrangiids may be dispersed and confounded with *A. woodsi* is also highly plausible. Among other possible vectors, and considering the intense commercial and tourist services of port areas in the TSB, which may be contributing to the introduction of foreign benthic fauna in the littoral, we are unsure if *A. pichoni* sp. nov. is 'truly' a native new coral, or a case of exotic organism described out its natural limits. At this moment we are unable to answer this puzzling question, but a case of a 'pseudoindivigenous' (*sensu* Carlton 2009) *Astrangia* species in Brazil deserves further reflection.

Conclusion

Named after Dr. Michel Pichon (Museum of Tropical Queensland, Australia) and contributing to the worldwide inventory of Astrangiidae corals, a new blue scleractinian, *Astrangia pichoni* sp. nov. Serra, Neves, Alves & Johnsson, 2023, is described in the Southwestern Atlantic.

Declarations

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Authors contribution: All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Saulo Freitas and Elizabeth Gerardo Neves, as well as the first draft of the manuscript. Jessika Alves contributed to the text, and the species key, and developed the graphs. Rodrigo Johnsson supervised the study and revised the manuscript.

Consent: All authors read and approved the final manuscript, and agreed to publish the paper.

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Figures

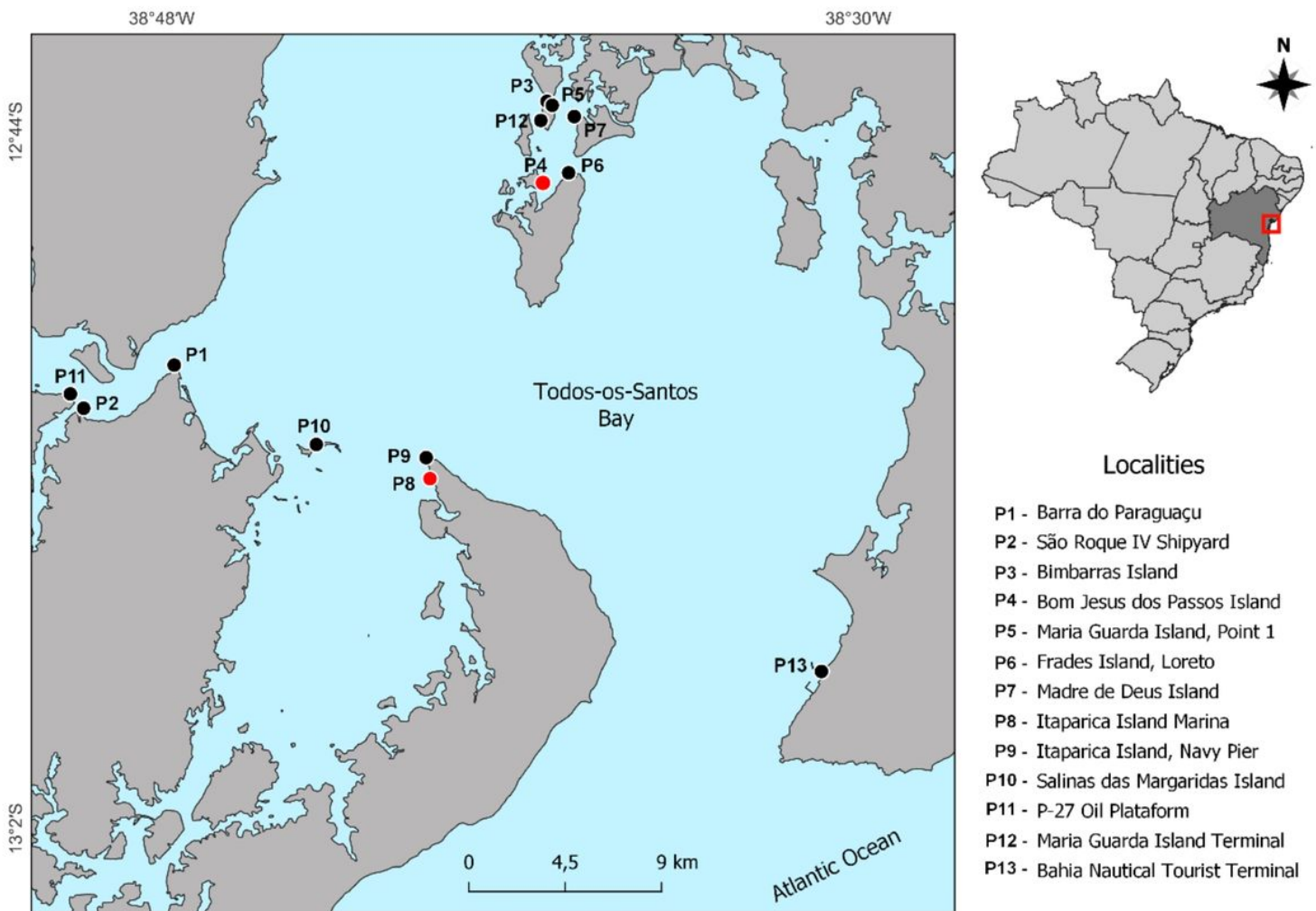


Figure 1

Map of the study area with the localities of occurrence of *Astrangia pichonisp.* nov. in the Todos-os-Santos Bay

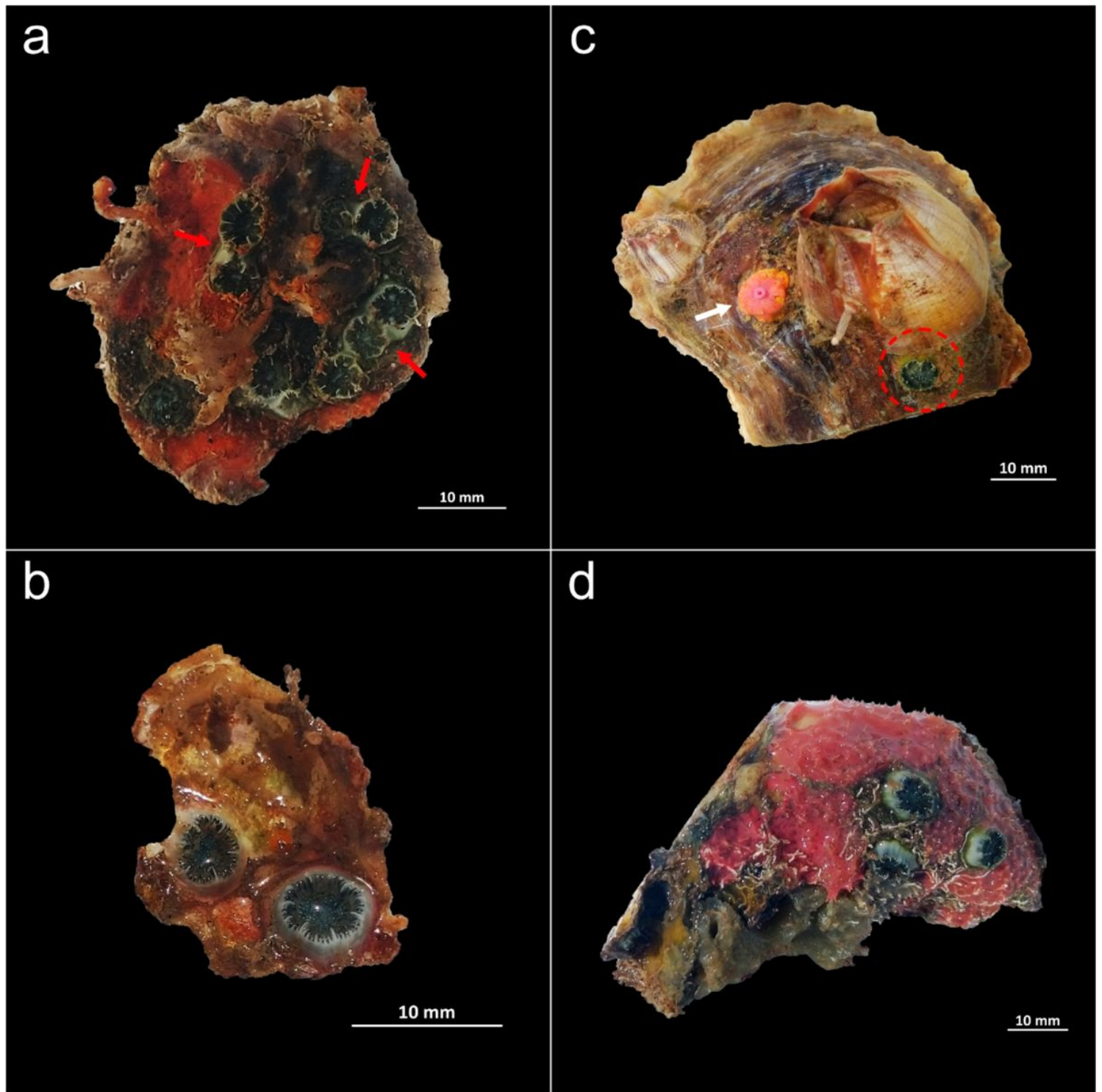


Figure 2

A, Live polyps of *A. pichoni* sp. nov. settled on a bivalve shell (family Ostreidae) and in contact with a sponge species (*Mycale* aff. *microsigmatosa* Arndt, 1927); red arrows indicating polyps undergoing fission. **B**, Two adult polyps on a bivalve shell. **C**, A polyp on a shell of *Pinctada imbricata* Röding, 1798, and in contact with a barnacle (*Striatoballanus* sp.); arrow indicating a recruit of sun coral (*Tubastraea*

sp. Lesson 1830). **D**, Three polyps on a bivalve shell and in contact with a sponge species *Aplysilla* aff. *rosea* (Barrois, 1876)

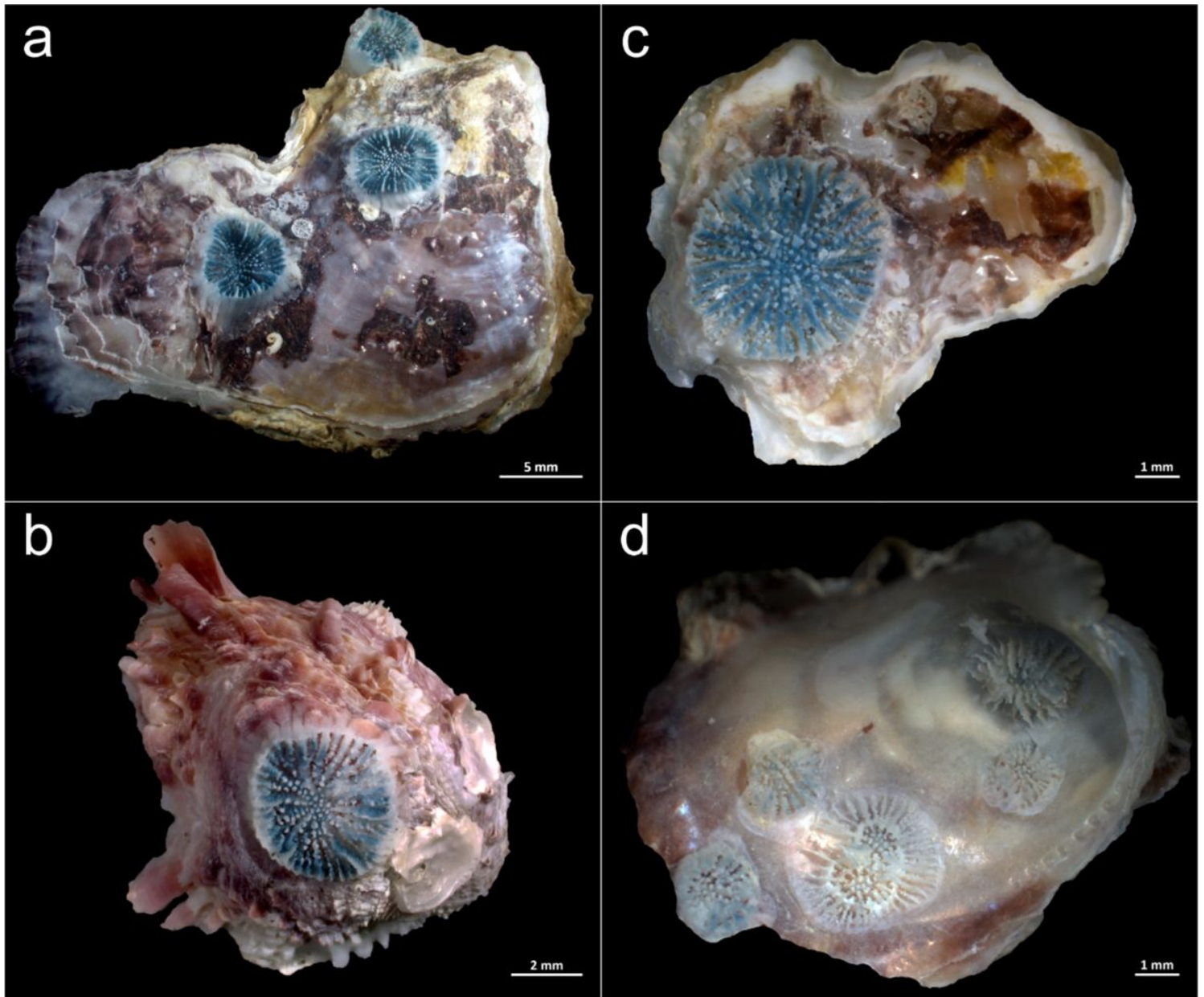


Figure 3

Blue-gray adult corallites and whitish recruits of *Astrangia pichoni* sp. nov. **A**, **C** and **D**, corallites on Ostreidae. **B**, corallite on *Chama* sp. Linnaeus, 1758

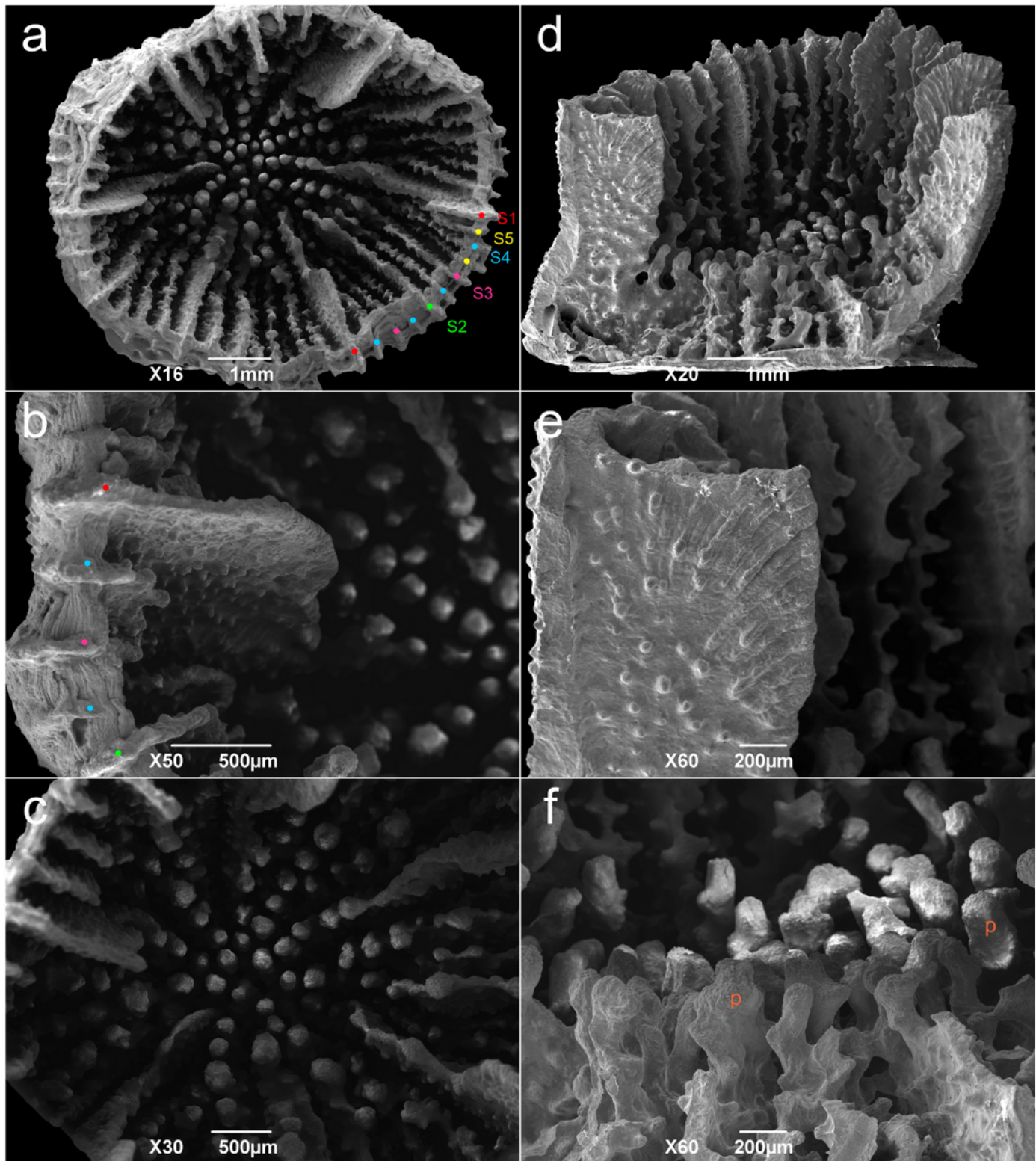


Figure 4

SEM images of the type series of *Astrangia pichoni* sp. nov. Calice, transversal view (**A-C: holotype**) and longitudinal view (**D-F: paratype**). **A**, Septa distribution - S1 projecting distally on the theca margin. **B**, Theca margin with S1, S2, S3 and S4, S1 septal face granulated. **C**, Columella papillose. **D**, Mesh of projections from septa margins form the columella papillose. **E**, S1 lateral face with ornamentation. **F**, Close view of the septa projections that form the columella (p = paliform lobe)

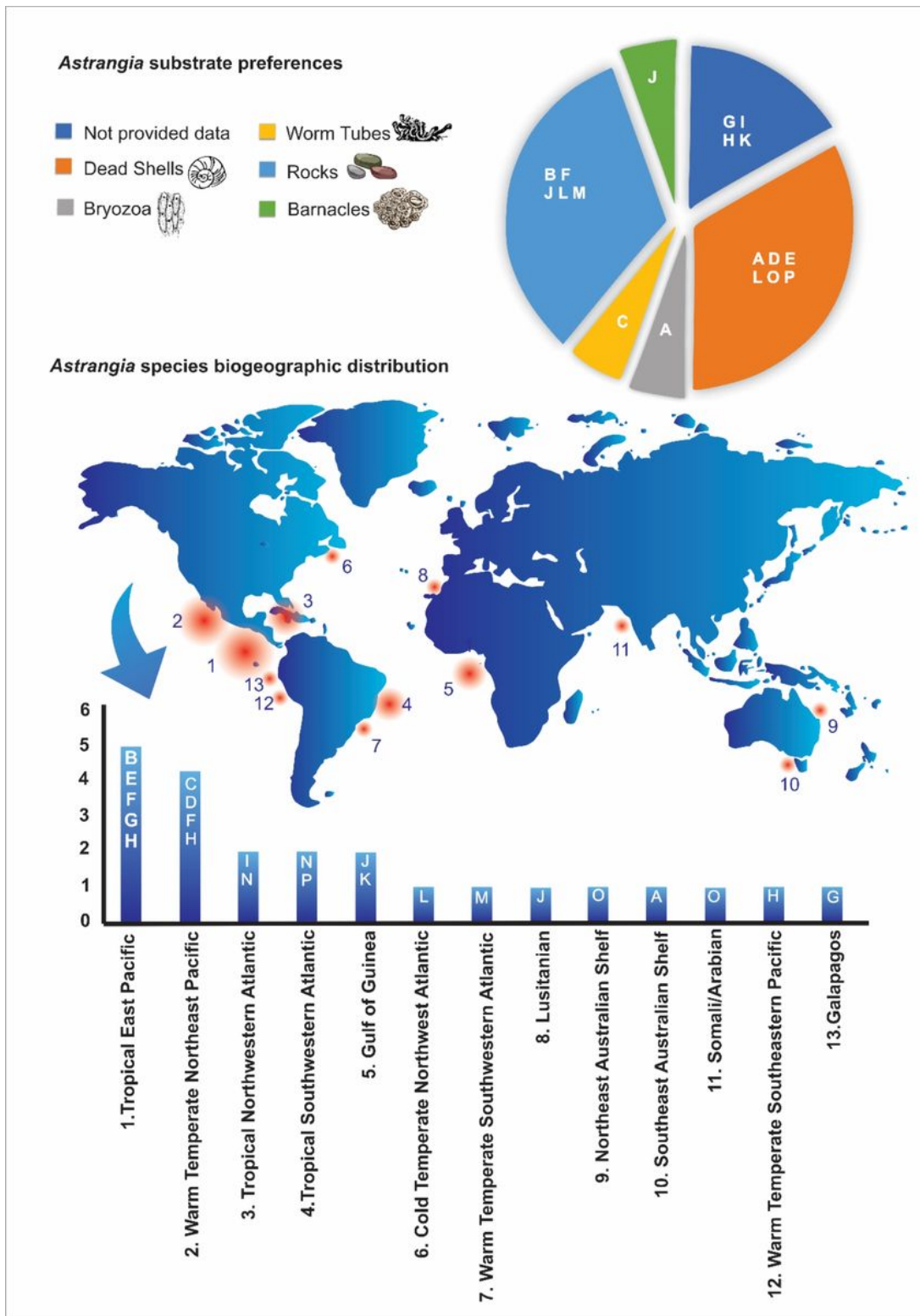


Figure 5

Infographic with compiled data from the available literature considering substrate preferences and biogeographic distribution for the worldwide *Astrangia* species. Letters in the graphs: A= *A. atrata*, B= *A. browni*, C= *A. californica*, D= *A. conferta*, E= *A. costata*, F= *A. dentata*, G= *A. equatorialis*, H= *A. haimej*, I= *A. howardi*, J= *A. macrodentata*, K= *A. mercatoris*, L= *A. poculata*, M= *A. rathbuni*, N= *A. solitaria*, O= *A. woodsii*, P= *A. pichoni* sp. nov.

Supplementary Files

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