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# Four new species of Tubastraea (Scleractinia, Dendrophylliidae) from the Brazilian Coast, Southwestern Atlantic

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**Abstract:** In Brazil, two species of exotic 'sun corals' have been cited, majorly in ecological studies, over the last two decades. In Bahia State, colonies were registered for the first time in 2008 in a shipwreck in the Todos-os-Santos Bay. Since then, these species have spread locally across artificial and natural environments comprising variable patterns of interspecific morphologies. However, the identifications of these dendrophylliids have been circumstantially influenced by a single morphological aspect, the development of corallites: plocoid colonies have been referred to as *Tubastraea coccinea*, and dendroid morphotypes as *Tubastraea tagusensis*. Thus, the main goal of this study was to analyze the patterns of the morphological variation of sun corals from the Bahia State (12ºS, Southwestern Atlantic), inferring their interspecific limits. Skeleton macro and micromorphology analyses provided evidence for the presence of seven species in this coastal section. As a result, we describe four new *Tubastraea* species: *Tubastraea ramosa* sp. nov., *Tubastraea columnata* sp. nov., *Tubastraea.grandidentata* sp. nov., and *Tubastraea megalostoma* sp. nov. A new distribution record is reported for *Tubastraea faulkneri* in Brazil. A morphological diagnosis was developed for all seven Brazilian sun coral species. Finally, two identification keys, the worldwide and the Brazilian *Tubastraea* species are provided.

**Key words:** Sun corals, taxonomy, micromorphology, identification keys, Tropical Atlantic.

**Quatro novas espécies de *Tubastraea* (Scleractinia, Dendrophylliidae) do litoral brasileiro, Atlântico Sudoeste. Resumo:** No Brasil, duas espécies exóticas de 'coral sol' têm sido citadas, principalmente em estudos ecológicos, nas últimas duas décadas. Na Bahia, as colônias foram registradas pela primeira vez em 2008, em um naufrágio na Baía de Todos-os-Santos. Desde então, estas espécies tem dispersado localmente por ambientes artificiais e naturais, compreendendo em padrões morfológicos interespecíficos variáveis. Todavia, as identificações desses dendrofilídeos têm sido circunstancialmente influenciadas por um único aspecto morfológico, o desenvolvimento dos coralitos: as colônias plocoides têm sido referidas como *Tubastraea coccinea*, e os morfotipos dendroides como *Tubastraea tagusensis*. Assim, o objetivo principal deste estudo foi analisar os padrões de variação morfológica dos corais-sol do estado da Bahia (12ºS, Atlântico Sudoeste), inferindo seus limites interespecíficos. Análises macro e micromorfológicas do esqueleto forneceram evidências da presença de sete espécies para este setor da costa. Como resultado, descrevemos quatro novas espécies de *Tubastraea*:

*Tubastraea ramosa* sp. nov., *Tubastraea columnata* sp. nov., *Tubastraea.grandidentata* sp. nov. e *Tubastraea megalostoma* sp. nov.. Um novo registro de distribuição é relatado para *Tubastraea faulkneri* no Brasil. Uma diagnose morfológica foi desenvolvida para todas as sete espécies brasileiras de coral-sol. Por fim, são fornecidas duas chaves de identificação, para as espécies de *Tubastraea* do mundo e do Brasil.

**Palavras-chave:** Coral-sol, taxonomia, micromorfologia, chave de identificação, Atlântico Tropical.

**Introduction**

The family Dendrophyllidae (Gray, 1847) is the third largest family of extant scleractinian corals, comprising 24 genera and 187 valid species, mainly represented by azooxanthellate corals, including *Tubastraea* Lesson, 1830 and *Atlantia* López & Capel, 2020 (Hoeksema & Cairns 2024a), both occurring in the Atlantic Ocean.

*Tubastraea* is distributed along a wide bathymetric range, from shallow water environments to the mesophotic zone (Cairns 2001, Glynn *et al*. 2008). The Indo-Pacific *Tubastraea* consists of 12 accepted species: *Tubastraea coccinea* Lesson, 1830; *T. aurea* (Quoy & Gaimard, 1833); *T. micranthus* (Ehrenberg, 1834); *T. diaphana* (Dana, 1846); *T. stimpsonii* (Verrill, 1866); *T. faulkneri* Wells, 1982; *T. tagusensis* Wells, 1982; *T. floreana* Wells, 1982; *T. megacorallita* Yiu, Chung & Qiu, 2021; *T. dendroida* Yiu & Qiu, 2022; *T. chloromura* Yiu & Qiu, 2022 and *T. violacea* Yiu & Qiu, 2022 (Hoeksema & Cairns 2024b)

In the Eastern Atlantic, Laborel (1974) registered two morphotypes of *Tubastraea* in islands of the Gulf of Guinea and on some regions of the coast of Gabon, Sierra Leone, and Cape Verde Islands, also suggesting '*They certainly pertain to T. aurea-T. tenuilamellosa group found in the Indo-Pacific and in Tropical Atlantic (with exception of the Brazilian region)*' (p. 435, author *op. cit.*). Originally from Bora-Bora Is. (Southern Pacific Ocean), *Tubastraea coccinea* was the first 'sun coral' recorded out of its natural geographical border, being early identified in Porto Rico, Caribbean, in the 1940s (Vaughan & Wells 1943, Sammarco *et al*. 2010). According to Fenner & Banks (2004), *Tubastraea* colonies were first seen in the Southeastern Gulf of Mexico in 1977, dispersing in a clockwise way to the western, northwestern, and north, probably due to natural larval drift by the currents.

A few hypotheses have supported the presence of the *Tubastraea* in the Atlantic Ocean. In Brazil, it was first attributed to anthropic activities (Castro & Pires 2001, Sampaio *et al*. 2012), while Laborel (1974) suggested a scenario based on a recent dispersion from the Indo-Pacific through the Panama Channel. Nowadays this genus has achieved a much wider distribution, becoming widespread along the North and Southwestern Tropical Atlantic (Soares *et al*. 2020).

Sun corals were, for the first time, identified in Southwestern Brazil by the late 1980s, observed on offshore oil platforms in the Campos Basin (22ºS), Rio de Janeiro (Castro & Pires 2001). In the Northeastern Coast, colonies were first reported in 2008, established on a shipwreck in the Todos-os-Santos Bay (12ºS), Bahia State (Sampaio *et al*. 2012). These exotic corals have spread across natural and man-made environments, regularly established on columns and decks of piers and shipyards (Sampaio *et al*. 2012, Soares *et al*. 2020). Moreover, *Tubastraea* has adapted to the local biofouling, and the benthic communities of coral reefs and rocky outcrops (Sampaio *et al.* 2012, Miranda *et al*. 2016a), usually fixed on biogenic substrates, such as mollusk and barnacle shells (authors *pers. obs*.).

In the latest taxonomic contributions to the *Tubastraea* genus, four new species were described from the China Sea between 2021 and 2022 (Yiu *et al*. 2021, Yiu & Qiu 2022). This sudden increase in *Tubastraea* inventory for the Western Pacific points out a high diversity of species, and the possibility of discoveries for science.

Since de Paula & Creed (2004), the identification of the Atlantic sun corals became 'dichotomized', relying on the distinction of two morphotypes: plocoid and dendroid forms (i.e., short corallites *vs.* elongated corallites, respectively). This identification protocol has been indiscriminately adopted, and two species, *T. coccinea* (plocoid) and *T. tagusensis* (dendroid) have been referenced, mainly in local ecological studies (Sampaio *et al*. 2012, Miranda *et al*. 2016a, Miranda *et al*. 2016b, Soares *et al*. 2018, Capel *et al*. 2019). Another traditional character considered is based on tissue colors, with colonies ranging from regular yellow (*T. tagusensis*), orange-red (*T. coccinea*), and dark green/black (*T. micranthus*) (de Paula & Creed 2004, Sammarco *et al.* 2010).

Based on early identifications of the sun corals in colder environments at higher latitudes (22ºS), Sampaio *et al*. (2012) also attested the occurrence of *T. coccinea* and *T. tagusensis* in warm waters of the Todos-os-Santos Bay (12ºS). Monitoring across distinct geographical scales has focused on the expansion and new occurrences of sun corals, with all studies reinforcing the identity of the two congeners along the Brazilian littoral (Capel *et al*. 2019, Soares *et al*. 2020). Guided by the same dichotomous trend, Figueroa *et al*. (2019) have expanded the occurrence of *T. tagusensis* in the Gulf of Mexico.

In Brazil, Bastos *et al*. (2022) attested the occurrence of a dendroid *Tubastraea* incompatible with *T. tagusensis*. Taxonomic divergences due to variable morphologies of the sun corals from the Bahia State have put in check species identities early established by Sampaio *et al*. (2012). Indeed, the dichotomic models established for *Tubastraea* (plocoid/red-orange *vs.* dendroid/yellow) are unfeasible, neglecting major patterns of budding and colonial development, as well as micro and macromorphological characteristics of the corallites. Although trends in *Tubastraea* have confounded the identifications worldwide, undoubtedly, this is a highly diverse coral genus (Yiu *et al*. 2021, Yiu & Qiu 2022).

Therefore, based on valuable tools of the traditional Scleractinia taxonomy, here we describe four new species of *Tubastraea*, and the first record of *Tubastraea faulkneri* in the Southwestern Atlantic. Finally, two identification keys, one to worldwide *Tubastraea* species and another to Brazilian sun corals are provided. These findings are expected to contribute to the development of public policies for the conservation and management of the biodiversity and reef environments, such as the 'Sun Coral National Plan for Prevention, Control, and Monitoring' (Do, CEM; 2018).

## Material and methods

*Sampling:* Samples were collected by SCUBA diving between 0 to 10 m depth. Colonies were selected by morphotypes (plocoid *vs*. dendroid), and to avoid fragmentation and larvae release, they were carefully removed with a hammer and a spatula, being immediately separated in plastic bags. In the field, before fixation in 96% ethanol, each colony was photographed with a Canon PowerShot SX30 IS to record tissue color.

Fieldwork was majorly carried out in diverse artificial environments, including pier decks and columns, and columns of a shipyard structure, in six distinct localities in the Todos-os-Santos Bay (TSB), Bahia State, Northeastern Brazil, from 2019 to 2023 (Fig. 1, Table I). The first colonies were obtained from a decommissioned oil platform, neighboring the Paraguaçu estuary between 2016 and 2018.

The TSB is the second largest navigable bay on the Brazilian Coast with approximately 1,200 $km^2$ (Hatje & Andrade 2009). It comprises 56 islands, and pristine natural ecosystems such as reefs, mangroves, and three important estuaries: Paraguaçu, Jaguaripe, and Subaé rivers (Cirano & Lessa 2007, Caroso *et al*. 2011). Two of the largest ports in Bahia State are in TSB: the Port of Aratu and the Port of Salvador, being a very important trade route for the country's economy (Faria 2011). These commercial routes attend national and international ships, and this activity may represent a potential route for the introduction of exotic organisms. Moreover, due to the calm waters and the natural scenic beauty, small tourist boats from international harbors also used to visit the TSB.

The inventory of non-native invertebrates in the TSB has increased in the last decades, including the bryozoan *Triphyllozoon arcuatum* (MacGillivray, 1889) (Almeida *et al*. 2015), the calcareous sponge *Heteropia* sp. Carter, 1886 (Chagas & Cavalcantti 2017, Barros *et al*. 2018, Chagas *et al*. 2020), the crab *Charybdis hellerii* (A. Milne-Edwards, 1867) (Carqueija & Gouvêa 1996, Silva & Barros 2011), the soft corals *Briareum hamrum* (Gohar, 1948) and *Sarcothelia* sp. Verrill, 1928 (Menezes *et al*. 2022), and the sun corals of the genus *Tubastraea* (Sampaio *et al*. 2012).

*Morphological analysis:* For skeleton analysis, the specimens were bleached in a 2,5% sodium hypochlorite solution. After 72 hours, the skeleton was washed in running water and dried at room temperature.

The skeletons were photographed with a Canon PowerShot SX30 IS, to record the BTS morphotypes based on the corallite growth pattern. A total of 300 colonies were identified, and from this material, 43 were separated and morphometrically analyzed. Two corallites from each colony were randomly selected for analysis under a stereo microscope with a digital camera (model ZEISS SteREO Discovery.V20). Measurements of the

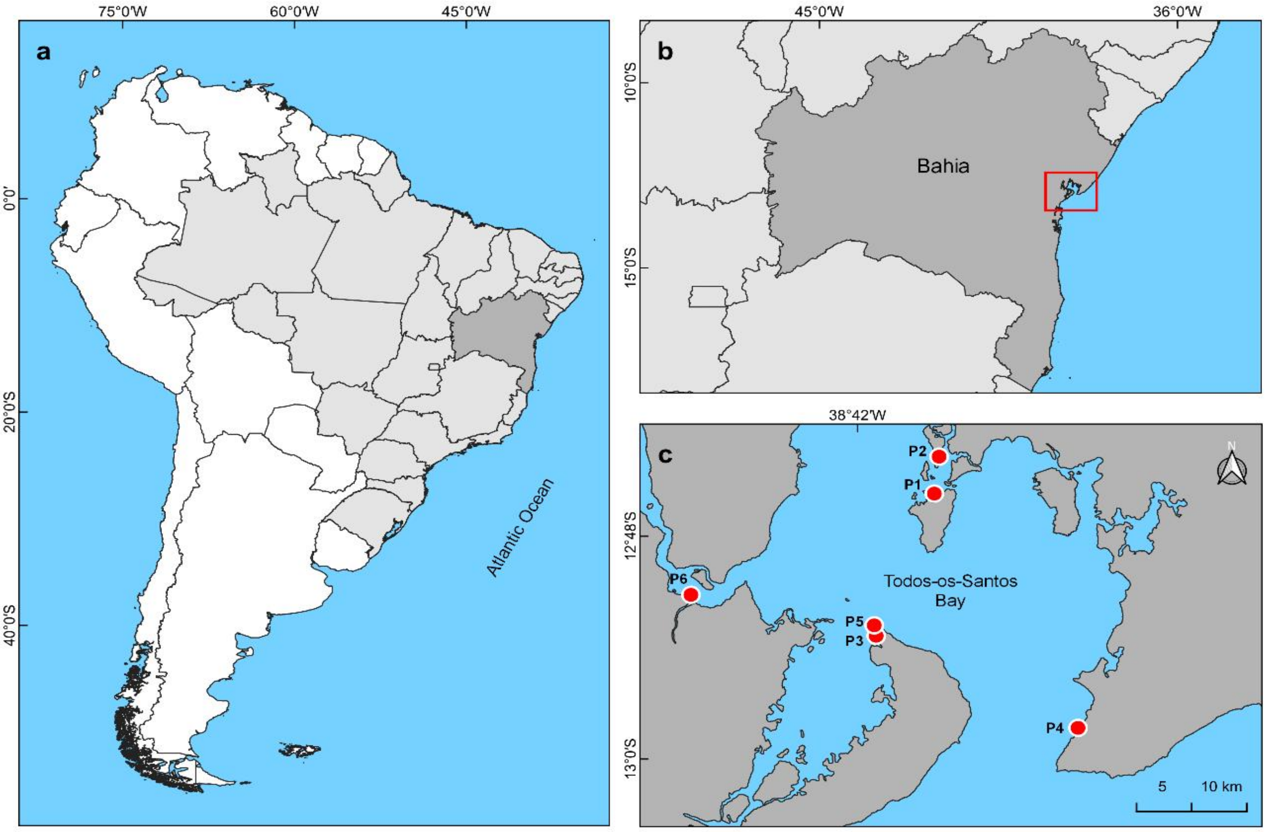


**Figure 1** Distribution of sun coral populations analyzed in Todos-os-Santos Bay (TSB). P1 Bom Jesus dos Passos Island; P2 Maria Guarda Is.; P3 Marina de Itaparica, Itaparica Is.; P4 Private Terminal, Salvador Capital; P5 Magnetic Measurement Station, Itaparica Is.; P6 Decommissioned oil platform, Paraguaçu estuary.

**Table I** Sample localities in Todos-os-Santos Bay, Bahia State, Brazil

| Locality | Coordinates |
|---|---|
| Bom Jesus dos Passos Island | 12°45'S, 38°38'W |
| Maria Guarda Is. | 12°43'S, 38°37'W |
| Marina de Itaparica, Itaparica Is. | 12°53'S, 38°41'W |
| Private Terminal, Salvador Capital | 12°58'S, 38°30'W |
| Magnetic Measurement Station, Itaparica Is. | 12°52'S, 38°41'W |
| Decommissioned oil platform, Paraguaçu estuary | 12°51'S, 38°50'W |

colony and corallites (e.g., calice and corallite diameter, theca height, columellar depth) were taken by an automatic caliper (model Mitutoyo 500-143B). In the case of some small corallite structures (e.g., columella diameter), an ocular eye lens micrometer was used under a stereo microscope. The identifications and comparisons were based on Boschma (1953), Cairns (1991, 1994, 2000, 2001, 2004), Cairns & Kitahara (2012), Cairns & Zibrowius (1997), Lam *et al*. (2008), Ocaña *et al*. (2015) and Wells (1982).

Corallite fragments (5.0 mm – 10.0 mm) were analyzed under scanning electron microscopy (SEM) for characterization of the micromorphology (e.g., septa and theca ornamentation) and the porosity. First, the fragments underwent ultrasonic baths (42 kHz) for 8 minutes and were dried into a drying oven for 30 minutes at 70°C. Each one was fixed on a pin stub with carbon adhesive. For SEM analysis, all material was coated with a thin layer of gold, 10/20 Å, for 2 min, and images were captured with a JEOL JSM-6390LV equipment, at the Oswaldo Cruz Foundation (FIOCRUZ-BA).

The following abbreviations were applied in this study: GCD, greater calicular diameter; LCD, lesser calicular diameter; S, septa. All voucher specimens and type material were deposited in the Museum of Natural History of Bahia, at the Federal University of Bahia (acronym: UFBA).

## Results

*Systematics*

Class: Anthozoa Ehrenberg, 1834
Order: Scleractinia Bourne, 1900
Family: Dendrophylliidae Gray, 1847

*Tubastraea* Lesson, 1830

*Diagnosis* (adapted from Cairns 2001, and Cairns & Kitahara 2012): Encrusting corallum, plocoid to dendroid corallites, extracalicinal budding, new polyps from the polyp basis adjacent to coenosteum; plocoid forms with short corallites, aligned to coenosteum, or slightly projected over the colony surface; dendroid forms with erect colonies; corallites rarely with anastomosis in acute angle; porous theca; septa arranged hexamerally or in Pourtalès plan; three to five septa cycles; columella conspicuous, medium to small size with spongy or trabecular aspect.

Type species: *Tubastraea coccinea* Lesson, 1830, by monotypy (see Wells, 1936)

Type locality: Bora-Bora, Society Is., unknown depth.

***Tubastraea ramosa* sp. nov**. Serra, Neves & Johnsson, 2024 (Fig. 2a-d; Fig. 4a-c)

*Tubastraea tagusensis* – de Paula & Creed 2004, Figure 2a,b, Sampaio *et al*. 2012: Figure 3, Figure 5, Mantelatto *et al*. 2015: Fig. 1G-L, Miranda *et al*. 2016a: Fig. 2a, Miranda *et al*. 2016b: Fig. 3.

Type material: Holotype (length x height): UFBA 1436, 74.2 x 56.1 mm, 37 corallites, collected at 1 meter deep, in an artificial environment. Paratypes (length x height): UFBA 1424, 63.8 x 45.5 mm, 29 corallites; UFBA 1373, 76.3 x 54.6 mm, 31 corallites; UFBA 1405, 104.6 x 55.2 mm, 90 corallites; UFBA 1434, 57.0 x 37.0 mm, 39 corallites; UFBA 1435, 59.6 x 55.5 mm, 37 corallites.

*Type locality*: Private Terminal, Salvador Capital (12°58’S, 38°30’W), Todos-os-Santos Bay, Bahia State, Brazil.

*Etymology*: The specific epithet is attributed to the colonial growth pattern, with branches budding from the axial polyps. In Latin, *ramosa* = branched.

*Diagnosis*: Branching colonies with irregular monopodial growth; branches interspersed or in opposite distribution, with arborescent growth; dendroid corallites; extracalicinal budding; coenosarc and polyps yellow to intense orange, polyps with tentacles yellow to orange; corallite cylindrical and high (up to 39.1 mm height) with circular to elliptical calices; corallites closely spaced basally and spaced distally; synapticulotheca eventually with irregular calcification near theca edge; medium to large pores (130.0–450.0 µm) along costa and intercostal grooves; septa arranged hexamerally (21–51 septa), four cycles non-exsert (S1>S2>S3>S4), S1–S3 complete, S4 rudimentary; septal faces ornamented with rounded and slightly pointed granules, septal edge regular and smooth in S1 and S2, and irregular, with laciniate projections, in S3; columella moderately developed (1.1–7.1 mm), elliptical and spongy, fossa columellar deep (4.9–12.9 mm).

*Description*: Branching adult colonies, with irregular monopodial growth – more than one main axis, branches interspersed or in opposite distribution, with peculiar arborescent growth; dendroid corallites (Fig. 2a-b); extracalicinal budding with new individuals emerging from polyp basis, adjacent to a porous and costate coenosteum, from ½ of polyp column, and/or near margin of oral disc; larger corallites may undergo fission. Basis pedunculated (majorly on biogenic substrates), or wider and flattened. Coenosarc and polyps ranging from yellow to intense orange, polyps with yellow to orange tentacles (Fig. 2a). Corallum and corallites porous, corallite cylindrical, slender, and high (10.4–39.1 mm height), with circular to elliptical calices (LCD: 6.0–7.8 mm; GCD: 9.5–12.4 mm), closely spaced at the basis and spaced distally (Fig. 2b). Synapticulotheca porous and granular, some corallites with irregular calcification near thecal edge, resulting in a thickened or double-walled appearance. Costae with shallow intercostal grooves between each striae pair. Numerous, medium to large pores, (130.0–450.0 µm) distributed along coastae and intercostal grooves (Table II), 1–3 adjacent pores appear to be inserted within groove depressions (Fig. 4a). Septa arranged hexamerally, number of septa varying from 21 to 51, organized in four cycles non-exsert (S1>S2>S3>S4) (Table III), S1-S3 complete, S4 rudimentary (Fig. 2c), S1 and S2 similar in size and width, S3 eventually not fused to S2, S4 incomplete occasionally not fused to S3. Septal faces ornamented with rounded and slightly pointed granules (Fig. 4b-c); septal edge regular and smooth in S1 and S2, and irregular, with laciniate projections, in S3 (Fig. 2d; Fig. 4b-c). Columella moderately developed (LCD: 1.1–2.6 mm; GCD: 5.0-7.1 mm), elliptical and spongy (Fig. 2c); fossa columellar deep (4.9–12.9 mm).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State – Localities in the TSB: Bom Jesus dos Passos Is. (12°45'S, 38°38'W), Marina de Itaparica, Itaparica Is. (12°53'S, 38°41'W), Private Terminal, Salvador Capital (12°58’S, 38°30’W), Magnetic Measurement Station, Itaparica Is. (12°52'S, 38°41'W), Maria Guarda Is. (12°43’S, 38°37’W), decommissioned oil platform, Paraguaçu estuary (12°51’S, 38°50’W);

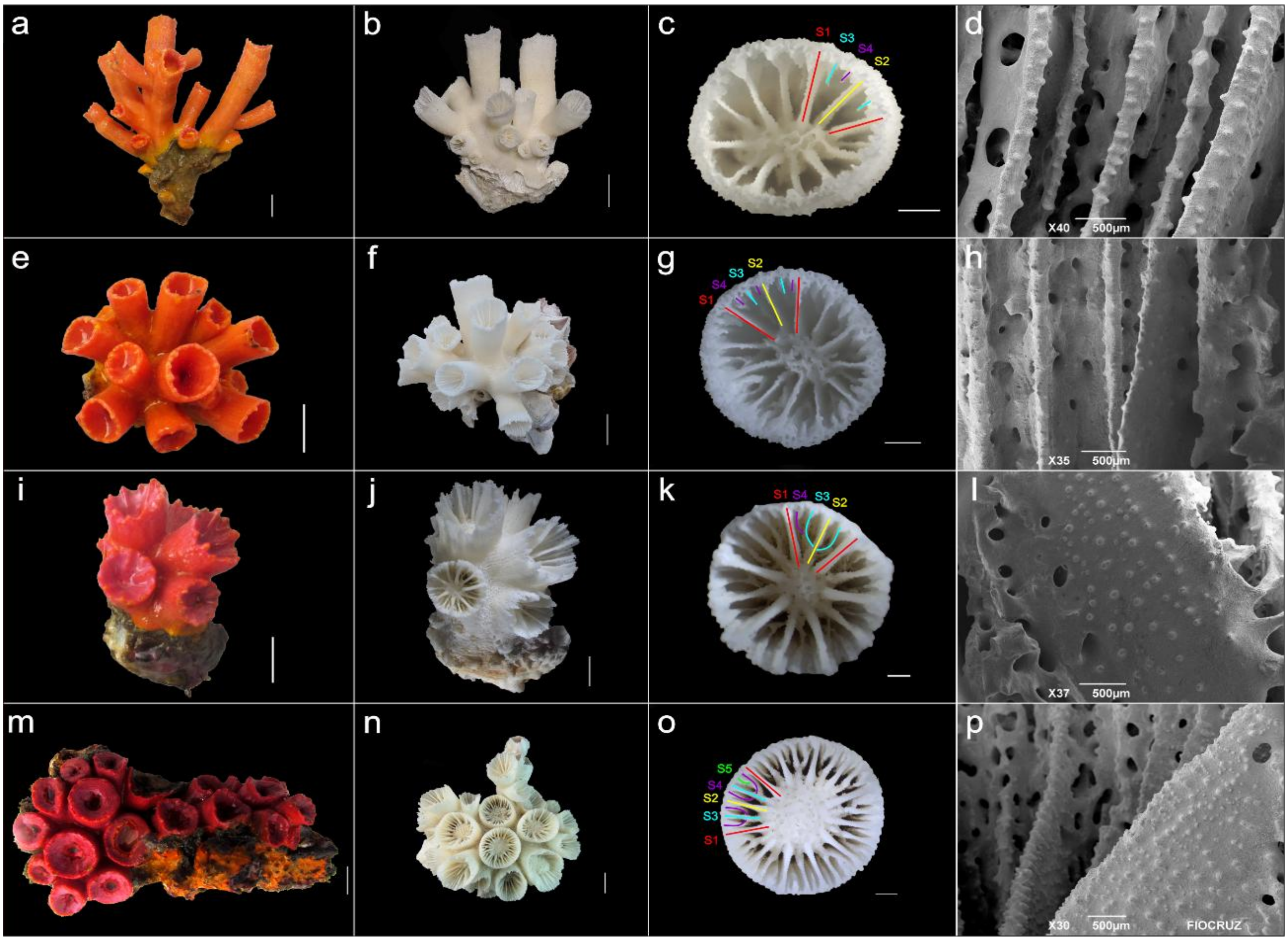


**Figure 2.** New species of sun corals in the Todos-os-Santos Bay. **a-d**: *Tubastraea ramosa* sp. nov., **a** and **b**: dendroid corallum with anastomosis (scale bar: 1 cm), **c**: calicular view of septa (scale bar: 2 mm), **d**: septa face ornamentation; **e-h**: *Tubastraea columnata* sp. nov., **e** and **f**: dendroid corallum, corallites closely spaced at base and widely spaced distally (scale bar: 1 cm), **g**: septa cycles and spongy columella (scale bar: 2 mm), **h**: septa face ornamentation; **i-l**: *Tubastraea grandidentata* sp. nov., **i** and **j**: plocoid corallite, remarkable dentate projections along the calicular edge (scale bar: 1 cm), **k**: radial structures details (columella aspect, number of septa, septa cycles) (scale bar: 1 cm), **l**: septa face ornamentation; **m-p**: *Tubastraea megalostoma* sp. nov., **m** and **n**: massive and encrusting corallum, plocoid development, with large corallites (scale bar: 1 cm), **o**: calicular view of radial elements, numerous septa distributed in five cycles and a well-developed columella (scale bar: 2 mm), **p**: rounded granules in septa face.

Buzios Is. São Paulo (23°48'S, 45°08'W ) (*in* Mizrahi *et al*. 2023).

*Ecology*: This species was found in all six localities in this study (Table I, Fig 1), probably being the most widely distributed species in artificial environments of the TSB. *Tubastraea ramosa* sp. nov. is usually settled negatively and/or vertically on the columns and decks of piers and touristic harbors, on three types of substrates, polystyrene, concrete, and biogenic, such as mollusk and barnacle shells. Because of its arborescent skeleton, this species may be easily fragmented, and pieces of *T. ramosa* sp. nov. may cover the natural bottom. In TSB, colonies of *T. ramosa* sp. nov. occur syntopically with other *Tubastraea* species (Fig 6, c-d).

*Remarks*: Despite the branchy development and the extracalicinal budding, as also observed in *T. dendroida*, *T. diaphana* and *T. micranthus* (Cairns & Zibrowius 1997, Cairns 2001, Arrigoni *et al*. 2014, Yiu & Qiu 2022), *T. ramosa* sp. nov. is easily distinguished from the three former species due to its irregular monopodial growth pattern. Phaceloid corallite development has been attributed to *T. diaphana*, however, it is important to point out that tissue usually covers all the column polyp, and most areas of the skeleton, being not restricted to the corallite theca and calice – as observed, for instance, in the Brazilian phaceloid coral *Mussismilia harttii* (Verrill, 1868). In the endemic mussid, the corallites have dichotomous development with anastomosis. In turn, *T. ramosa* sp. nov. follows a peculiar trend in the monopodial growth, alternating one to more

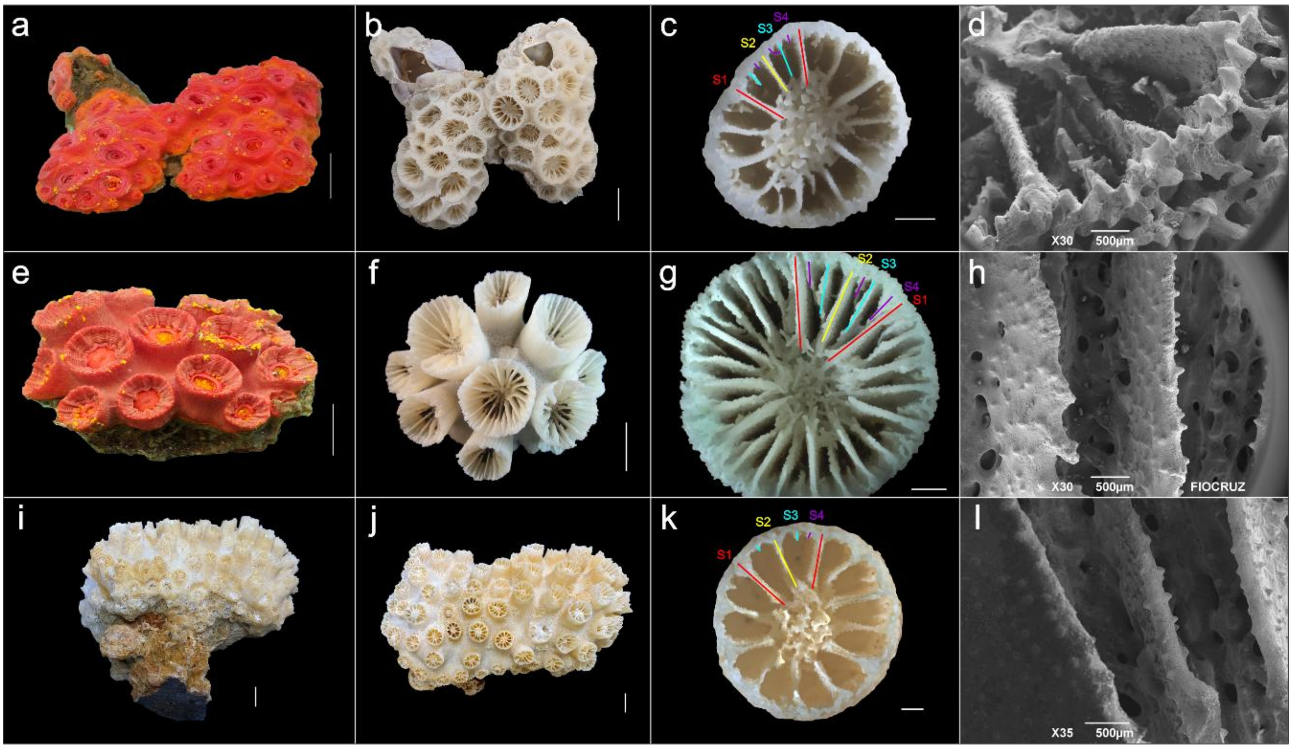


**Figure 3.** Diversity of plocoid sun corals species in Todos-os-Santos Bay. **a-d**: *Tubastraea coccinea*, **a** and **b**: corallum with corallites closely spaced (scale bar: 1 cm), **c**: calicular view, septa organization, spongy columella (scale bar: 2 mm), **d**: septa face and margin ornamentation; **e-h**: *Tubastraea aurea*, **e** and **f**: corallum with a flattened base, subdendroid and conical corallites (scale bar: 1 cm), **g**: calicular view, spongy and irregular columella (scale bar: 2 mm), **h**: septa face ornamentation; **i-l**: *Tubastraea faulkneri*, **i** and **j**: corallum with a pedunculated base (scale bar: 1 cm), **k**: calicular view, spongy columella (scale bar: 2 mm), **l**: septa face ornamentation.

axial polyps which undergo multiple lateral budding, looking like an arborescent development. New polyps may emerge from three distinct sites: the polyp basis (adjacent to the coenosteum), the polyp column, and the margin of the oral disc. Indeed, this may promptly distinguish *T. ramosa* from the dendroid colonies of *Tubastraea*, including *T. tagusensis*, on the Southern and Northern Brazilian Coast. Colonies of *T. ramosa* from the TSB have thicker theca, incomplete S4, and a more developed columella.

***Tubastraea columnata* sp. nov**. Serra, Neves & Johnsson, 2024 (Fig. 2e-h; Fig. 4d-f)

*Tubastraea tagusensis* – Luz *et al*. 2018: Fig. 1c;

*Tubastraea* sp. - Bastos *et al.* 2022: Fig. 2i-l

*Type material*: Holotype (length x height): UFBA 1423, yellow-orange colony, 49 x 33 mm, 28 corallites, in the artificial substrate at 1 meter deep. Paratypes (length x height): UFBA 1352, 53 x 28 mm, 28 corallites, in association with *T. coccinea*; UFBA 1354, 51 x 37 mm, 25 corallites; UFBA 1427, 51 x 35 mm, 22 corallites; UFBA 1552, 39 x 32 mm, 24 corallites.

*Type locality*: Private Terminal, Salvador Capital (12°58'S, 38°30'W), Todos-os-Santos Bay, Bahia State, Brazil.

*Etymology*: The specific epithet is attributed to the colonial growth supported by elongated corallites, as the columns of classical Greek architecture. In Greek, *columnata* = columns.

*Diagnosis*: Massive colonies, bushy growth, flattened basis, dendroid corallites, extracalicinal budding, costate coenosteum; coenosarc and polyps yellow to light orange, polyps with yellow tentacles; corallite cylindrical and high (up to 25.4 mm height) with circular to elliptical calices, corallite base closely spaced and widely apart distally; synapticulotheca thick, small pores (80.0–138.0 µm) along the intercostal grooves; septa arranged hexamerally (23–48 septa), four cycles non-exsert (S1≥S2>S3≥S4), S1–S3 complete, S4 incomplete, S3 thinner, deeply fused to S2, eventually with free axial margins, S4 rudimentary; septal faces ornamented with small slightly pointed granules, S1 and S2 with small dentate projections near to columella, S3 septal margin irregularly dentate; columella small (0.8–5.7 mm), spongy, fossa columellar deep (4.4–14.7 mm).

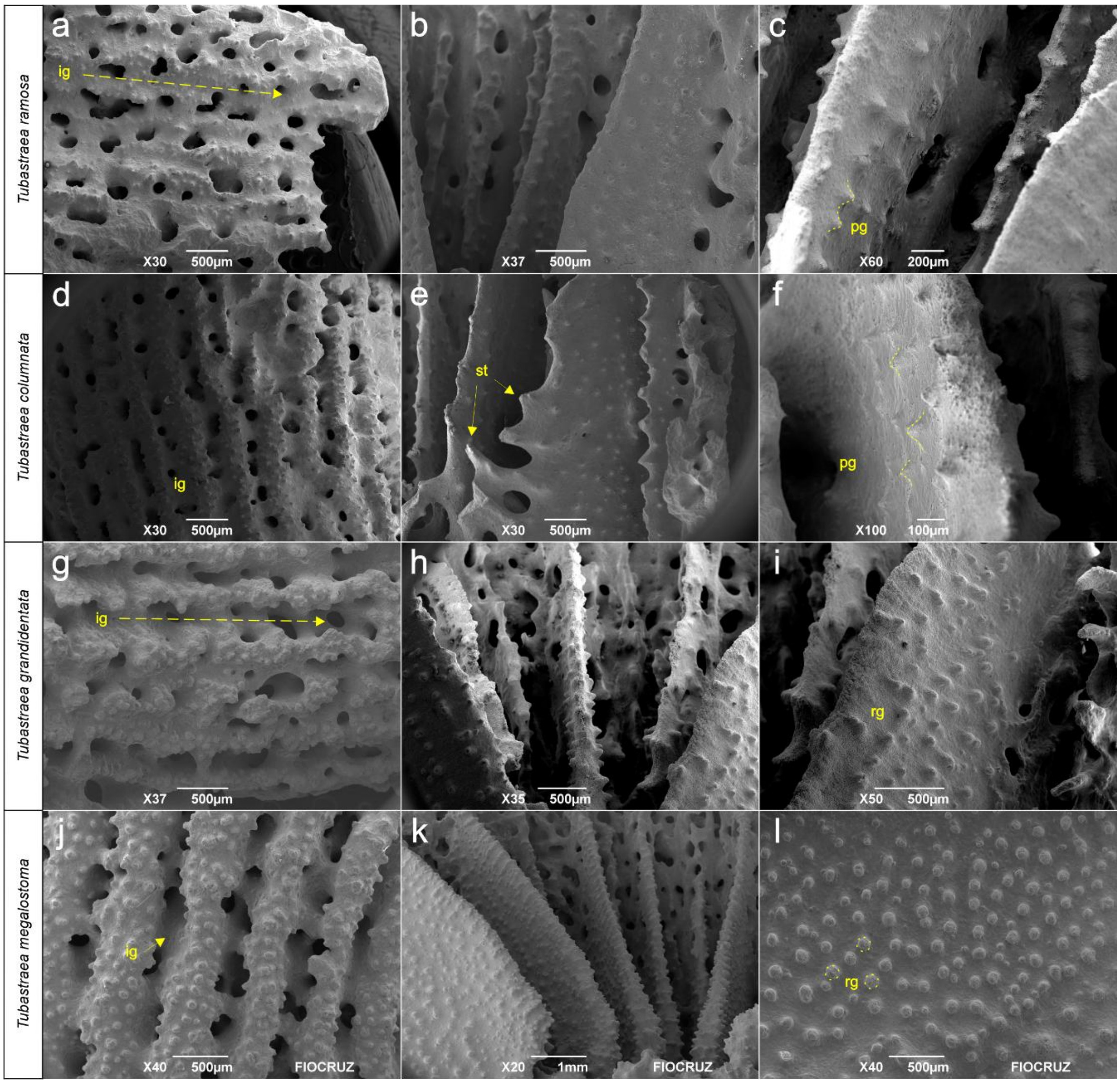


**Figure 4.** SEM images showing the micromorphology of *Tubastraea ramosa* sp. nov. (**a-c**), *Tubastraea columnata* sp. nov. (**d-f**), *Tubastraea grandidentata* sp. nov. (**g-i**) and *Tubastraea megalostoma* sp. nov. (**j-l**). First column (**a**, **d**, **g**, **j**): the outer face of the theca, including theca ornamentation, costae striation and pores. Second column (**b**, **e**, **h**, **k**): ornamentation in septa faces and margins. Third column (**c**, **f**, **i**, **l**): details of the septa ornamentation (ig: intercostal groove, st: septal teeth, pg: pointed granules, rg: rounded granules).

*Description*: Massive adult colonies, with a bushy growth, and flattened basis, dendroid corallites (Fig. 2e-f), extracalicinal budding, with new polyps emerging from the polyp basis, adjacent to a porous and costate coenosteum. Coenosarc and polyps yellow to light orange, polyps with yellow tentacles, mouth distinctly bright orange or red (Fig. 2e). Corallum and corallites porous, corallite cylindrical, and high (11.1–25.4 mm height), with circular to elliptical calices (LCD: 6.1–6.7 mm; GCD: 9.0–10.8 mm), corallite basis closely spaced and widely apart at thecal margins (Fig. 2e-f). Synapticulotheca porous, thick, and granular. Costae with narrow and shallow intercostal grooves. Numerous small pores (80.0–138.0 µm) distributed along the intercostal grooves (Table II) (Fig. 4d). Septa arranged hexamerally, number of septa varying from 23 to 48, organized in four cycles non-exsert (S1≥S2>S3≥S4) (Table III), S1–S3 complete, S4 incomplete (Fig. 2g), S1 and S2 similar in thickness, S3 thinner, deeply fused to S2, and eventually with free axial margins, S4 rudimentary occasionally not fused to S3. Septal faces ornamented with small slightly pointed granules (Fig. 4e-f). S1 and S2 with small dentate projections near to columella, smooth towards the distal edge, S3 septal margin irregularly dentate (Fig. 2h; Fig. 4e). Columella small (LCD: 0.8–2.3 mm; GCD: 3.6–5.7 mm), spongy (Fig. 2g),

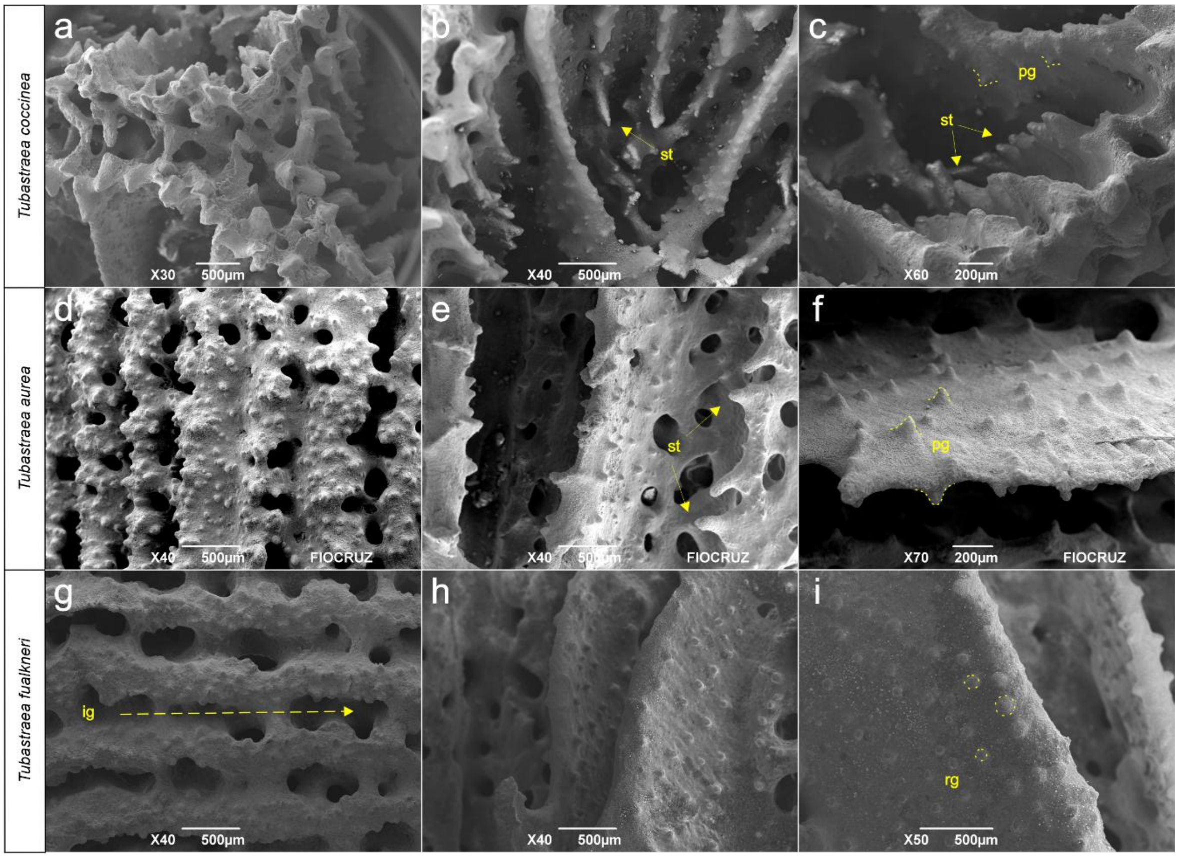


**Fig. 5** SEM images showing the micromorphology of *Tubastraea coccinea* (**a-c**), *Tubastraea aurea* (**d-f**) and *Tubastraea faulkneri* (**g-i**). First column (**a**, **d**, **g**): the outer face of the theca, including theca ornamentation, costae striation and pores. Second column (**b**, **e**, **h**): ornamentation in septa faces and margins. Third column (**c**, **f**, **i**): details of the septa ornamentation (ig: intercostal groove, st: septal teeth, pg: pointed granules, rg: rounded granules).

fossa columellar deep (4.4–14.7 mm).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State. Localities in the TSB: Bom Jesus dos Passos Is. (12°45'S, 38°38'W), Marina de Itaparica, Itaparica Is. (12°53'S, 38°41'W), Private Terminal, Salvador Capital (12°58'S, 38°30'W); Arraial do Cabo, Rio de Janeiro (*in* Bastos *et al*. 2022), Buzios Is., São Paulo (23°49'S, 45°08'W) (*in* Luz *et al*. 2018)

*Ecology*: In the TSB, colonies of *T. columnata* sp. nov. were found settled negatively and/or vertically on three different types of substrates: polystyrene, concrete, and biogenic, such as mollusk and barnacle shells (Fig 6, a-b). *Tubastraea columnata* sp. nov. also occurs synoptically with other sun coral species (Fig 6, d).

*Remarks*: Among the dendroid *Tubastraea* species, *T. dendroida*, *T. diaphana*, *T. micranthus*, and *T. ramosa* sp. nov. are easily distinguished from *T. columnata* sp. nov. because of their erect, branchy development, and the extracalicinal budding on the corallite walls (Cairns & Zibrowius 1997, Cairns 2001, Arrigoni *et al*. 2014 – Fig. 1 E: *T. micranthus*, Fig. 11 G-I: *T. micranthus*, Fig. 11 J-L: *T. diaphana*, Yiu & Qiu 2022 – Fig. 2 A-D: *T. dendorida*). The septa arrangement can still divide this group in two: the species with a regular septa distribution (*T. chloromura*, *T. diaphana*, *T. floreana*, *T. micranthus*, *T. tagusensis*, *T. columnata* sp. nov., and *T. ramosa* sp. nov.), and those with a Pourtalès plan (*T. dendroida*, *T. megacorallita*, *T. violacea* and *T. stimpsonii*). Although having a regular septal arrangement, *Tubastraea floreana* undergoes extracalicinal budding on the corallite walls and has smaller corallites (2.0-10.0 mm) (Wells 1982 – Figure 4, 5,6, Cairns 1991 – Plate 12 h, i). Following Wells (1982), *T. tagusensis* has plocoid to subdendroid corallites, while *T. columnata* sp. nov. has dendroid development with slender corallites, up to 25.4 mm in height. Indeed, Cairns (1991) has described *T. tagusensis* with higher corallites from Galapagos and Cocos Is., up to 20.0 mm, contrasting with the shorter corallites (3.0 to 15.0 mm) of the Wells' species. However, the new species from the TSB has a peculiar colony growth (bushy, not spherical) and distinct aspects related to S3: septa are thinner, and deeply fused to S2. Finally, *T. chloromura* is an olive-green sun coral, with the septal organization following the formula S1>S2>S3=S4 (Yiu & Qiu 2022 – Fig.3 A-F) – *T. columnata* sp. nov. is a typical yellow-orange dendrophylliid and has a distinct formula: S1≥S2>S3≥S4.

***Tubastraea grandidentata*** **sp. nov**. Serra, Neves & Johnsson, 2024 (Fig. 2i-l; Fig. 4g-i)

*Type material*: Holotype (length x height): UFBA 1361, colony with orange polyps, 28.5 x 23.9 mm, 7 corallites, collected at 3 meters deep in an artificial environment. Paratypes (length x height): UFBA 1360, 29.2 x 19.0 mm, 9 corallites; UFBA 1379, 40.2 x 26.6 mm, 13 corallites; UFBA 1443, 67.1 x 30.7 mm, 19 corallites; UFBA 1437, 64.1 x 45.9 mm, 33 corallites; UFBA 1438, 61.3 x 28.9 mm, 28 corallites.

*Type locality*: Marina de Itaparica (12°53'S, 38°41'W), Itaparica Is., Todos-os-Santos Bay, Bahia State, Brazil.

*Etymology*: The epithet refers to the irregular edge of the corallite theca, which alternates deep grooves and prominent projections. Two Latin terms were used to create the specific epithet: *grandis* – large or great, and *dentata* – toothed or pointed.

*Diagnosis*: Massive, hemispherical to irregular encrusting colonies, plocoid corallites, extracalicinal budding, non-costate coenosteum; coenosarc and polyps bright yellow, pink or orangish-pink, polyps with yellow tentacles; cylindrical and short corallites (up to 15.0 mm height), circular to elliptical calices, corallites closer basally and spaced distally; synapticulotheca thick basally and fragile at calice margins, theca margins deeply dentate; medium-sized pores (80-0-300.0 µm) along costae and intercostal grooves; septa arranged hexamerally (25-44), four cycles non-exsert (S1>S2>S3>S4); S1-S3 complete, S4 rudimentary, S1 and S2 markedly thicker; septal faces strongly ornamented with small and rounded granules; columella small (1.2-6.1 mm), solid to spongy, fossa columellar moderately deep (3.5-8.4 mm).

*Description*: Massive, hemispherical to irregular encrusting adult colonies, plocoid corallites (Fig. 2i-j), young colonies (3-5 corallites) usually with a stalk-like basis, heavily calcified and resembling a peduncle; extracalicinal budding, with new individuals emerging from polyp base, adjacent to a porous, non-costate coenosteum; larger corallites may undergo fission. Coenosarc and polyps bright yellow to orange at the colony margins, gradually changing into pink, or an orangish-pink along polyp column and oral disc, polyps with yellow tentacles (Fig. 2i). Corallum and corallites very porous, cylindrical, and short corallites (5.5-15.0 mm height), with circular to elliptical calices (LCD: 6.9-9.2 mm; GCD: 10.0-12.8 mm), corallites closer basally and spaced distally, forming bouquet-like colonies (Fig. 2j). Synapticulotheca porous and granular, thick at the basal plate, and fragile and very porous at the calice margins; theca margins deeply dentate between S1 and S2, forming typical grooves. Costae with narrow and shallow to moderately deep intercostal grooves, striae width about 250 µm. Numerous medium size pores (80-300 µm), distributed along costae and intercostal grooves (Table II), 1-2 adjacent pores appear to be inserted within depressions in grooves (Fig. 4g). Septa arranged hexamerally, number of septa varying from 25 to 44, organized in four cycles non-exsert (S1>S2>S3>S4) (Table III), S1-S3 complete, S4 rudimentary (Fig. 2k), S1 and S2 markedly thicker, projecting under the soft tissue, S3 eventually not fused to S2, S4 poorly developed, occasionally not fused to S3. Septal faces strongly ornamented with small and rounded granules (Fig. 2l; Fig. 4h-i), axial margins poorly ornamented (Fig. 4h). Columella small (LCD: 1.2-2.5 mm; GCD: 3.1-6.1 mm), varying from solid to spongy (Fig. 2k), fossa columellar moderately deep (3.5-8.4 mm).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State. Localities in the TSB: Bom Jesus dos Passos Is. (12°45'S, 38°38'W), Marina de Itaparica, Itaparica Is. (12°53'S, 38°41'W), Private Terminal, Salvador (12°58'S, 38°30'W), Magnetic Measurement Station, Itaparica Is. (12°52'S, 38°41'W).

*Ecology*: Colonies of *Tubastraea grandidentata* sp. nov. were found in artificial environments, including columns and decks of piers and touristic harbors, settled negatively and/or vertically on at least three types of substrates, polystyrene, concrete, and biogenic, as mollusk and barnacle shells. In TSB, the new species occurs synoptically with other congeners (Fig 6, c-d).

*Remarks*: Among the group of the 'sun corals' from the TSB, *Tubastraea grandidentata* sp. nov. may be readily recognized in the field due to two aspects: (1) this species has thecal margins strongly dentate, and (2) the two primary cycles are visible just beneath the tissue of the oral disc. Moreover, pink tissues usually prevail over all other color patterns, being the color also a distinguishable characteristic of the new species – particularly, when the biofouling comprises a community of sun corals.

Indeed, this is one of the most identifiable dendrophylliids in the field. Compared with plocoid congeners (e.g., *T. coccinea*, *T. aurea*, *T. faulkneri*, *T. megalostoma* sp. nov.), its diagnostic characteristics do not allow any type of inaccuracy in the identification – all other plocoid *Tubastraea* species have no such grooved theca margins, and the septa are usually slender (see Table S.I and S.II).

***Tubastraea megalostoma* sp. nov**. Serra, Neves & Johnsson, 2024 (Fig. 2m-p; Fig. 4j-l)

*Type material*: Holotype (length x height): UFBA 1348, 65.2 x 41.3 mm, 33 corallites, in the artificial substrate at 1 meter deep. Paratypes (length x height): UFBA 1358, 84.5 x 59.2 mm, 29 corallites; UFBA 1364, 84.8 x 47.3 mm, 27 corallites; UFBA 1439, 67.3 x 53,6 mm, 21 corallites; UFBA 1440, 108.1 x 55,3 mm, 73 corallites; UFBA 1441, 98.5 x 36,7 mm, 27 corallites.

*Type locality*: Private Terminal, Salvador (12°58'S, 38°30'W), Todos-os-Santos Bay, Bahia State, Brazil.

*Etymology*: The specific epithet is attributed to the oversized calice and columella. Two Greek terms were used to create the species name: *megalo* – big size, *stoma* – mouth.

*Diagnosis*: Massive to encrusting colonies, plocoid corallites; extracalicinal budding; larger corallites may undergo fission, non-costate coenosteum; coenosarc and polyps dark pink to reddish, polyps with yellow-orange tentacles; corallites large, slightly conical to cylindrical (up to 15.3 mm height) with circular to elliptical calices; corallites close to moderately spaced at the base and spaced distally; synapticulotheca moderately thick and strongly granular, medium size pores (138.0-275.0 µm) along intercostal grooves; septa arranged hexamerally (32-65 septa), five cycles non-exsert (S1=S2≥S3>S4>S5); S1-S3 complete, S4 rarely incomplete, S5 incomplete, S1 and S2 with thicker axial margins, S3 occasionally free; septal face heavily ornamented with small, closely spaced rounded granules, S1-S3 with regular margins and poorly ornamented, S4 with smooth axial margin, with depressions towards the theca; columella well-developed (1.2-10.1 mm), spongy, fossa columellar moderately deep (4.4 -11.1 mm).

*Description*: Massive to encrusting adult colonies, plocoid corallites (Fig. 2m-n); extracalicinal budding, with new individuals emerging from polyp base, adjacent to a porous, non-costate coenosteum; larger corallites may undergo fission. Coenosarc and polyps dark pink to reddish, with yellow-orange tentacles (Fig. 2m). Corallum and corallites porous, corallites distinctly large, slightly conical to cylindrical (4.5-15.3 mm height), with circular to elliptical calices (LCD: 8.0-11.6 mm; GCD: 11.6-16.2 mm), corallites closely to moderately spaced basally and rather apart distally (Fig. 2n). Synapticulotheca porous, moderately thick, and strongly granular. Costae with narrow and shallow intercostal grooves. Medium size pores (138.0-275.0 µm) distributed along intercostal grooves (Table S.I) (Fig. 4j). Septa arranged hexamerally, number of septa varying from 32 to 65, organized in five cycles non-exsert (S1=S2≥S3>S4>S5) (Table S.II); S1-S3 complete, S4 rarely incomplete, S5 incomplete (Fig. 2o), S1 and S2 with thicker axial margins, S3 occasionally with free axial margins. Septal face heavily ornamented with small, closely spaced rounded granules (Fig. 2p; Fig. 4k-l), granules larger (about 100.0 µm) next to septal edge, interspersing with smaller ones (from 20.0-60.0 µm) towards theca, S1-S3 with regular margins and poorly ornamented (Fig. 2p; Fig. 4k), S4 with smooth axial margin, with depressions towards theca. Columella well-developed (LCD: 1.2-4.2 mm; GCD: 4.8-10.1 mm), ½ of calice diameter, with distinct spongy appearance in larger corallites (Fig. 2o), fossa columellar moderately deep (4.4 -11.1 mm).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State. Localities in the TSB: Maria Guarda Is. (12°43'S, 38°37'W), Marina de Itaparica, Itaparica Is. (12°53'S, 38°41'W), Private Terminal, Salvador Capital (12°58'S, 38°30'W), Magnetic Measurement Station, Itaparica Is. (12°52'S, 38°41'W).

*Ecology*: Massive and encrusting colonies of *Tubastraea megalostoma* sp. nov. were found in artificial substrates at four localities in the TSB. In all of them, the new species was growing negatively and/or vertically on biogenic substrates, such as mollusk and barnacle shells, or on skeletons of degraded sun coral colonies. *Tubastraea megalostoma* sp. nov. also occurs syntopically with other sun coral species.

*Remarks*: This species belongs to the *Tubastraea* genus by sharing the generic diagnostic characteristics such as pointed out by Cairns (2001) and Cairns & Kitahara (2012), but it differs from all other TSB congeners due to the greater corallite and columella diameter, the remarkable pattern of the ornamentation of theca and septal faces, and the five cycles of septa (it is the species with the highest number of septa described in this study). Considering the growth pattern and the corallite size, *T. megalostoma* sp. nov. may be compared to some morphotypes of *T. coccinea* and *T. aurea*, but these species do not present a large columella. In the Pacific, *Tubastraea megacorallita* also has well-developed corallites with five septal cycles but, unlike the plocoid *T. megalostoma* sp. nov. from the TSB, the Hong Kong species has dendroid corallites, and septa arranged in Pourtalès plan (Yiu *et al*. 2021).

***Tubastraea coccinea*** Lesson, 1830 (Fig. 3a-d; Fig. 5a-c)

*Lobophyllia aurea* – Quoy & Gaimard 1833: 195, pl. 15, figs 7-11.

*Dendrophyllia willeyi* – Vaughan 1918: 143-144, pl. 60, fig 4a.

*Dendrophyllia aurea* – van der Horst 1926: 46-48, pl. 2, figs 2-4, 8-9.

*Tubastraea aurea* – Boschma 1953: 119, pl. 11, figs 2,4-6, pl. 12, figs 1-6; Schuhmacher 1984: 94-95

*Material examined* (length x height): UFBA 1349, 67.4 x 41.9 mm, 35 corallites; UFBA 1351, 55.2 x 42.2 mm, 49 corallites; UFBA 1420, 74.1 x 17.9 mm, 76 corallites; UFBA 1422, 71.0 x 18.6 mm, 69 corallites; UFBA 1467, 58.6 x 19.4 mm, 51 corallites.

*Diagnosis*: Massive to encrusting colonies, plocoid corallites; extracalicinal budding, larger corallites may undergo fission; non-costate coenosteum; coenosarc and polyps in an orange gradient, from light orange to intense red, polyps with yellow-orange tentacles; corallite cylindrical, generally short (up to 15.2 mm height) with circular to elliptical calices, corallites closely spaced; synapticulotheca irregularly thick, medium size pores (116.0-280.0 µm) along the intercostal grooves; septa arranged hexamerally (13-55 septa), four cycles non-exsert (S1>S2>S3>S4); S1 and S2 complete, S3 incomplete, S4 rudimentary or absent; septal face moderately ornamented with small and slightly pointed granules, S1 septa margin smooth, S2-S4 with dentate projections; columella moderately developed (LCD: 1.2-3.0 mm; GCD: 3.4-8.0 mm), solid to spongy, fossa columellar moderately deep (3.1-8.2 mm).

*Description*: Massive to encrusting adult colonies, with a broad and flat basis, plocoid corallites (Fig. 3a-b), extracalicinal budding, with new individuals emerging from polyp base, adjacent to a porous, non-costate coenosteum, larger corallites may undergo fission. Coenosarc and polyps in an orange gradient, polyps from light orange to intense red with yellow-orange tentacles (Fig. 3a). Corallum and corallites porous, corallite cylindrical, generally short (1.8-15.2 mm height) with circular to elliptical calice (LCD: 6.3-8.0 mm; GCD: 8.9-10.7 mm), corallites closely spaced (Fig. 3b). Synapticulotheca porous, irregularly thick, and granular (Fig. 5a). Costae thick with moderately deep intercostal grooves. Medium-sized pores (116-280 µm) distributed along the intercostal grooves (Table S.I). Septa arranged hexamerally, number of septa varying from 13 to 55, organized in four cycles non-exsert (S1>S2>S3>S4) (Table S.II), S1 and S2 complete, S3 incomplete, occasionally with free axial margins, S4 rudimentary or absent (Fig. 3c). Septal face moderately ornamented with small and slightly pointed granules, S1 septa margin smooth, S2-S4 with dentate projections (Fig. 3d; Fig. 5b-c). Columella moderately developed (LCD: 1.2-3.0 mm; GCD: 3.4-8.0 mm), solid to spongy (Fig. 3c), fossa columellar moderately deep (3.1-8.2 mm).

*Distribution*: Circumtropical. Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State – Localities in this study: Marina de Itaparica, Itaparica Is. (12°53’S, 38°41’W), Private Terminal, Salvador Capital (12°58’S, 38°30’W), Magnetic Measurement Station, Itaparica Is. (12°52’S, 38°41’W), Bom Jesus dos Passos Is. (12°45'S, 38°38'W), decommissioned oil platform, Paraguaçu estuary (12°51’S, 38°50’W); Sampaio *et al*. 2012 (TSB); Miranda *et al*. 2016a (TSB); Rio de Janeiro State (Ferreira 2003, de Paula & Creed 2004); São Paulo State (Mantelatto *et al*. 2011), Santa Catarina State (Capel 2012), Espírito Santo State (Costa *et al*. 2014), Sergipe State (Creed *et al*. 2017), Ceará State (Soares *et al*. 2018). Northwestern Atlantic Ocean: Curaçao, Aruba (Boschma 1953), Jamaica, Cuba (Zlatarski 1982), Gulf of Mexico (Fenner 2001). Northeastern Atlantic: Cape Verde, Gulf of Guinea (Cairns 2000). Indo-Pacific Ocean: China Sea, South Korea (Cairns 1994), Japan, Philippines, Indonesia (Cairns & Zibrowius 1997), Taiwan, Hong Kong (Lam *et al*. 2008), Australia (Cairns 2004), Mexico (Gulf of California) (Paz-García *et al*. 2007).

*Ecology*: *Tubastraea coccinea* is the sun coral with the widest geographic distribution – one of the first *Tubastraea* species to disperse from the Pacific to the Atlantic Ocean under anthropic influence (Cairns 2000). This species shows highly variable growth patterns – irregular to regular massive forms, including encrusting colonies, usually growing negatively and/or vertically over dendroid sun corals (competitive interaction between congeners was observed *in situ*), and other benthic organisms in the biofouling, such as mussels and barnacles.

*Remarks*: Despite the morphological variation, its status, as a valid species, has been ensured in taxonomical studies (Cairns 1991, 1994, 2000, Cairns & Zibrowius 1997). Indeed, *T. coccinea* is promptly distinguishable from other plocoid congeners (*T. aurea*, *T. faulkneri*, *T. megalostoma* sp. nov, *T. grandidentata* sp. nov.) because of the short cylindrical corallites closely spaced. It differs from *T. megalostoma* sp. nov. due to smaller columella and a fewer number of septa, and from *T. grandidentata* by the regular, non-dentate, theca margins. Variation in the corallite height of *T. coccinea* may occur in distinct geographic scales - according to Cairns (1991, 1994), corallites range from 10.0 mm to 12.0 mm in the Pacific Ocean, whereas its height variation was wider in the TSB populations, from 1.8 to 15.2 mm. Moreover, data on reproduction and early development are available to the species. Planulation is a conservative mechanism in the species' reproduction from the Pacific and Atlantic as well (Glynn *et al*. 2008, de Paula *et al*. 2014). According to de Paula *et al*. (2014), this sun coral undergoes multiple oogenesis but has only two reproductive peaks at higher latitudes (22º-23ºS).

***Tubastraea aurea*** (Quoy & Gaimard, 1833) (Fig. 3e-h; Fig. 5d-f)

*Australopsammia aurea* – Rowlett 2020

*Lobophyllia aurea* – Quoy & Gaimard 1833

*Tubastraea coccinea* – Sampaio *et al*. 2012: Fig. 2B.

*Material examined* (length x height): UFBA 973a, 55.1 x 32.8 mm, 15 corallites; UFBA 973b, 45.6 x 36.3, 12 corallites; UFBA 999, 85.9 x 31.0 mm, 32 corallites; UFBA 996, 45.7 x 23.7 mm, 20 corallites; UFBA 998, 58.3 x 24.6 mm, 22 corallites.

*Diagnosis*: Massive colonies, hemispherical growth, flattened basis, subdendroid corallites, extracalicinal budding, non-costate coenosteum; coenosarc and polyps orange to bright red, yellow tentacles; corallite large, distinctly conical and high (up to 21.7 mm height), circular calice, corallites closely spaced basally and spaced distally; synapticulotheca porous, moderately thick, medium size pores (168.0-272.0 µm), along coastae and intercostal grooves; septa arranged hexamerally (35-51 septa), four cycles non-exsert (S1≥S2>S3>S4); S1-S3 complete, S4 conspicuous, S1-S3 slightly thicker, S4 slender; septal face heavily ornamented, with small, more pointed granules, S1-S3 septal margins with dentate projections (eventually bifurcated) close to columella; columella small (0.9-6.8 mm), spongy, with irregular mesh of septa distal dentition, fossa columellar moderately deep (5.5-10.1 mm).

*Description*: Massive adult colonies, hemispherical growth pattern, wide and flattened base, subdendroid corallites (Fig. 3e-f); extracalicinal budding, with new individuals emerging from the polyp base, adjacent to a porous, non-costate coenosteum. Coenosarc and polyp orange to bright red, polyps with yellow tentacles (Fig. 3e). Corallum and corallites porous, corallite large, distinctly conical, and high (12.1-21.7 mm height) with circular calice (LCD: 8.4-9.8 mm, GCD: 12.5-15.1 mm), corallites closely spaced basally and spaced distally (Fig. 3f). Synapticulotheca porous, moderately thick, and granular. Costae regularly thick with deep intercostal grooves. Medium size pores (168.0-272.0 µm), distributed along the coastae and intercostal grooves (Table S.I) (Fig. 5d). Septa arranged hexamerally, number of septa varying from 35 to 51, organized in five cycles non-exsert (S1≥S2>S3>S4>S5) (Table S.II), S1-S3 complete, S4 conspicuous, S5 incomplete and rudimentary (Fig. 3g), S1-S3 slightly thicker, S4 slender, occasionally with free axial margins. Septal face heavily ornamented, with small, more pointed granules (Fig. 3h; Fig. 5e-f), S1-S3 septal margins with dentate projections (eventually bifurcated) close to the columella, and moderately smooth towards the distal calicular edge (Fig. 3g; Fig. 5e). Columella small (LCD: 0.9-2.0 mm; GCD: 4.4-6.8 mm) with a distinct spongy appearance, formed by an irregular mesh of the septa distal dentition, not projecting upwards (Fig. 3g), fossa columellar moderately deep (5.5 mm to 10.1 mm).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State – Localities: Marina de Itaparica, Itaparica Is. (12°53’S, 38°41’W), Magnetic Measurement Station, Itaparica Is. (12°52’S, 38°41’W), Bom Jesus dos Passos Is. (12°45'S, 38°38'W); Rio de Janeiro State (Bastos *et al*. 2022); Puerto Rico (Larson 1987); Pacific Ocean: Indonesia (Boschma 1953); Japan (Fusetani *et al*. 1986).

*Ecology*: Colonies of *T. aurea* were observed growing negatively and/or vertically on columns and deck piers, harbors, and shipyards, selecting biogenic substrates, such as mollusk and barnacle shells.

*Remarks*: Originally described as *Lobophyllia aurea* by Quoy & Gaimard (1833), *T. aurea* shares the main diagnostic characteristics of the corals from the

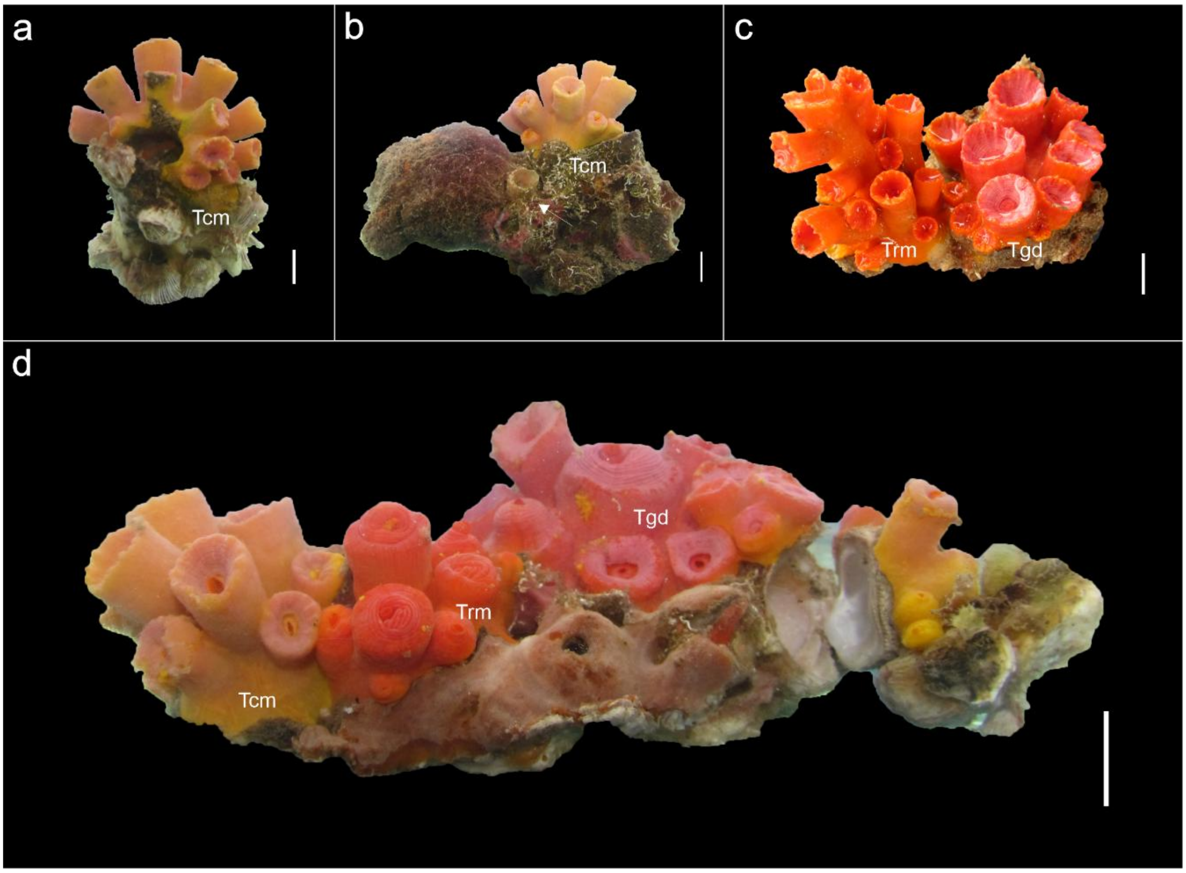


**Fig. 6** Sun coral colonies settled on other organisms from the biofouling. **a**: colony of *Tubastraea columnata* sp. nov. growing over a barnacle dead shell, **b**: *Tubastraea columnata* sp. nov. on a *Eualetes* sp. vermetiid shell (white arrow) and in contact with a tunicate, **c**: competitive interaction between *Tubastraea ramosa* sp. nov. and *Tubastraea grandidentata* sp. nov., **d**: *Tubastraea columnata, Tubastraea ramosa* and *Tubastraea grandidentata* sp. nov. growing on bivalves and barnacles and in contact with a sponge (Tcm: *Tubastraea columnata* sp. nov., Trm: *Tubastraea ramosa* sp. nov., Tgd: *Tubastraea grandidentata* sp. nov.) (scale bar: 1 cm)

genus *Tubastraea*. Its position within *Australopsammia*, as it was suggested by Rowlett (2020), is not supported by morphology nor by molecular data. Here, we also support the validity of the species status due to the colonial growth, corallite development, and aspects related to the radial structures. The conical and well-developed subdendroid corallites facilitate its differentiation from all other sun coral species. These features can be occasionally shared with some colonies of *T. megalostoma* sp. nov., but the new species has a well-developed columella and, occasionally, five septa cycles, whereas *T. aurea* has a discreet columella and rarely five septal cycles. Moreover, *T. aurea* has a dentate projection on the septal margins and septal faces ornamented with pointed granules, while *T. megalostoma* sp. nov. has a smooth septal margin with rounded granules on septal faces.

***Tubastraea faulkneri*** Wells, 1982 (Fig. 3i-l; Fig. 5g-i)

*Dendrophyllia aurea* – van der Horst 1926: 46, pl. 2, fig. 1

*Tubastraea aurea* – Boschma 1953: 112, pl. 9, figs. 5, 6 Nemezo 1971: 182, pl. 12, fig. 3

*Material examined* (length x height): UFBA 1325, 103.8 x 90.0 mm, 165 corallites; UFBA 1355, 57.1 x 47.2 mm, 49 corallites; UFBA 1356, 48.0 x 24.4 mm, 31 corallites; UFBA 1359, 59.7 x 25.6 mm, 37 corallites; UFBA 1362, 75.5 x 43.0 mm, 55 corallites.

*Diagnosis*: Massive, hemispherical to spherical colonies, large pedunculated base; plocoid corallites; extracalicinal budding, costate coenosteum, corallites well-spaced; coenosarc and polyps orange to reddish, yellow-orange tentacles; corallite cylindrical and short (up to 11.3 mm height), circular calice, corallites widely spaced, base slightly wider; synapticulotheca slightly thick, medium size pores (150.0-353.0 µm) along intercostal grooves; septa arranged hexamerally (19-43 septa), four cycles

(S1≥S2>S3>S4), S1-S3 complete, S1 slightly exsert in some corallites, S4 rudimentary, poorly developed, or absent; septal faces ornamented with a few and small rounded granules, septal margins poorly ornamented; columella small (0.3-4.9 mm), spongy, fossa columellar shallow (1.2-6.1 mm).

*Description*: Massive adult colonies, hemispherical to spherical growth pattern, with a large pedunculated basis, plocoid corallites (Fig. 3i-j); extracalicinal budding, with new individuals emerging from polyp basis, adjacent to porous and costate coenosteum, corallites well-spaced. Coenosarc and polyps from orange to reddish, polyps with yellow-orange tentacles. Corallum and corallite porous, corallite cylindrical and short (3.0 to 11.3 mm height) with circular calice (LCD: 5.6-6.7 mm; GCD: 8.4-9.4 mm), corallites widely spaced, base slightly wider (fig. 3j). Synapticulotheca porous, slightly thick, and granular. Costae moderately thick, and well-defined, with deep and regular intercostal grooves. Medium-sized pores (150.0-353.0 µm) distributed along depressions inside intercostal grooves (Table S.I) (Fig. 5g). Septa arranged hexamerally, number of septa varying from 19 to 43, organized in four cycles (S1≥S2>S3>S4) (Table S.II), S1-S3 complete, S4 rudimentary (Fig. 3k), S1 and S2 similar in size, S1 slightly exsert in some corallites, S3 rudimentary and rarely reaching the columella, S4 incomplete, poorly developed, or absent. Septal faces ornamented with few small rounded granules, apparently arranged in parallel lines towards septal margins (Fig. 5h-i), septal margins poorly ornamented, S1 and S2 smoother than S3 (Fig. 5h-i). Columella small (LCD: 0.3-2.6 mm; GCD: 2.8-4.9 mm), spongy (Fig. 3k), fossa columellar shallow (1.2 mm to 6.1 mm deep).

*Distribution*: Southwestern Atlantic Ocean: Brazil: Todos-os-Santos Bay, Bahia State – Localities: Private Terminal, Salvador Capital (12°58’S, 38°30’W), decommissioned oil platform, Paraguaçu estuary (12°51’S, 38°50’W); Papagaio Is., Angra dos Reis, Rio de Janeiro State (23°04'S, 44°23'W); Pacific Ocean: Ecuador (Isabela Is., Galapagos Arch.), Indonesia, Philippines (Wells 1982, Cairns 1991); Palau (Cairns 1991); Korea; Taiwan and Hong Kong (Choi & Song 2017).

*Ecology*: A large colony of *T. faulkneri* encrusted in the hull of a decommissioned platform was analyzed. However, in the biofouling communities monitored in this study, only a few small colonies, about 31-49 corallites, from a Private Terminal (Salvador Capital) were identified as *T. faulkneri*. This is the rarest sun coral species in the TSB, and it has been probably identified as *T. coccinea* so far.

*Remarks*: According to Wells (1982), *T. faulkneri* has spaced calices (5.0-15.0 mm), which are slightly sunken in the coenosteum. In the TSB, the colonies have the same characteristics, with corallites ranging from moderate to highly spaced (2.0- 20.0 mm), the coenosteum stands out compared to other sun coral species. The coenosteum is costate, and the corallite area is demarcated in a ceroid-like pattern. Although the corallites do not present the ‘sunken’ aspect pointed out by Wells (*op. cit.*), they have a robust and prominent basis, in a typical plocoid development. As mentioned by Wells (*op. cit.*) and Cairns (1991), the primary septa are also slightly exserted in some corallites, with 12 to 24 septa reaching the columella. Samples of adult colonies were collected from the pillars and the floating structures of a decommissioned oil platform.

*Worldwide key of <u>Tubastraea</u> species* (adapted from Yiu and Kiu, 2022):

1. Branching colony … 2
   Not branching colony … 3

2. Dark green, brown to black polyps … *T. micranthus* (Ehrenberg, 1834)
   Orange polyps, with yellow tentacles … *T. dendroida* Yiu & Qiu, 2022

3. Plocoid corallum … 4
   Non-plocoid corallum … 8

4. Moderate to widely spaced corallites … 5
   Closely spaced corallites … 6

5. Four septa cycles, small columella with shallow fossa … *T. faulkneri* Wells, 1982
   Five septa cycles, big columella, moderately deep fossa … ***T. megalostoma* sp. Nov.**

6. Thecal margin strongly dentate … ***T. grandidentata* sp. nov.**
   Thecal margin non-dentate … 7

7. Circular calice, very porous and fragile theca ... *T. diaphana* (Dana, 1846)
   Circular to elliptical calice, porous and thicker theca … *T. coccinea* Lesson, 1830

8. Ceratoid corallum … *T. stimpsonii* (Verrill, 1866)
   Non-ceratoid corallum … 9

9. Subdendroid corallum … 10
Dendroid corallum … 12

10. Three septa cycles … *T. floreana* Wells, 1982
Four septa cycles … 11

11. Conical corallites… *T. aurea* (Quoy & Gaimard, 1833)
Cylindrical corallites … *T. tagusensis* Wells, 1982

12. Septa arranged in Pourtlès plan … 13
Septa regularly arranged … 14

13. Violet to purple polyps, septal formula S1=S2>S3>S5>S4 … *T. violacea* Yiu & Qiu, 2022
Orange to red polyps, septal formula S1=S2>S3>S4=S5… *T. megacorallita* Yiu, Chung & Qiu, 2021

14. Corallites with anastomosis … ***T. ramosa*** **sp. nov.**
Corallites without anastomosis … 15

15. Olive green polyps, 34-40 septa … *T. chloromura* Yiu & Qiu, 2022
Yellow to light orange polyps, 23-48 septa … ***T. columnata*** **sp. nov.**

*Brazilian key of* *Tubastraea* *species:*

1. Plocoid corallum … 2
Non-plocoid corallum … 5

2. Thecal margin strongly dentate, S1-S2 thicker … ***T. grandidentata*** **sp. nov.**
Thecal margin non-dentate … 3

3. Corallites widely spaced … *T. faulkneri* Wells, 1982
Corallites closely to moderately spaced … 4

4. Four septal cycles, small columella … *T. coccinea* Lesson, 1830
Five septal cycles, big columella … ***T. megalostoma*** **sp. nov.**

5. Conical corallites … *T. aurea* (Quoy & Gaimard, 1833)
Cylindrical corallites … 6

6. Corallites with anastomosis; extracalicinal budding along the polyp column … ***T. ramosa*** **sp. nov.**
Corallites without anastomosis, extracalicinal budding from the polyp base … ***T. columnata*** **sp. nov.**

**Discussion**

This study reveals a great diversity of Atlantic 'sun corals', a group of exotic dendrophylliids whose biodiversity has been underestimated in the Tropical Southwestern Atlantic. 'Atlantic' *Tubastraea* is challenging taxonomists, mainly because the aspects related to the corallite (plocoid *vs*. dendroid) and colonial development (branching *vs.* non-branching) have prevailed over other major diagnostic characters. Indeed, clades of plocoid and dendroid species are phylogenetically related, but this attribute must be considered with other corallite traits usually adopted in Scleractinia taxonomy (Bastos *et al.* 2022). Scleractinian corals usually form species complexes, with close congeners sharing morphologies, and because of the overlapping of the macrostructures, microstructures must be evaluated carefully (Budd & Stolarski 2009, Budd *et al*. 2012).

In Brazil, *Tubastraea* was for the first time cited by Castro & Pires (2001). Later, two species, *T. coccinea* and *T. tagusensis*, were identified by de Paula & Creed (2004) at a higher latitude on the Southeastern Coast (23ºS). This early work has supported all monitoring and ecological studies developed so far, including the first report of *T. tagusensis* to the Mexico Gulf in 2019 (Figueroa *et al*. 2019).

Based on a phylogenetic approach, Bastos *et al*. (2022) refused the identity of *T. tagusensis* for the dendroid colonies from Northern Rio de Janeiro (22ºS). Indeed, dendroid corallites with anastomosis are a trend in the *Atlantia* genus, but there is not a single concise model for *Tubastraea*, in which colonies may range from subplocoid and plocoid, to subdendroid and dendroid.

Highly diverse morphological groups of scleractinian corals have been studied in Brazil – and intraspecific analyses and comparisons among closely related congeners have been developed for some native genera, such as *Mussismilia* Ortmann, 1890, *Madracis* Milne Edwards & Haime, 1849 and *Siderastrea* Blainville, 1830 (Souza & Amaral 2002, Neves *et al*. 2009, Neves *et al*. 2010, Menezes *et al*. 2013, Menezes *et al*. 2014). Morphological variation is expected to occur among all natural groups that reproduce sexually. Dendrophylliidae may be a Pandora's box with species exhibiting unexpected morphological variation. However, primary morphological analysis has supported all integrative approaches. Surprisingly, four new species of *Tubastraea* were reported to the China Sea between 2021 and 2022 – *T. megacorallita*, *T. dendroida*, *T. chloromura*, and *T. violacea* (Yiu *et al*. 2021, Yiu & Qiu 2022). According to the authors, although *T. megacorallita* is more closely related to *T. coccinea* and *T. micranthus* in molecular phylogenetic analysis, they differ substantially in corallite morphology. Colonies of *T. micanthus* have corallites that form long tree-like branches, a unique characteristic of the species (Cairns & Zibrowius 1997). This species may have been misidentified as *T. coccinea* by Scott (1984) in previous records of ahermatypic corals in Hong Kong. More recently, *Balanophyllia stimpsonii* has been moved into the genus *Tubastraea* (Mehrotra *et al*. 2023). The change from one genus to another occurred after the description of *T. megacorallita* – the septa arrangement of the species from China Sea follows the Pourtalès plan, supporting *Tubastraea stimpsonii* (Yiu *et al*. 2021, Mehrotra *et al*. 2023). It is worth noting that, despite the molecular analysis, no publication has refuted the morphological diagnoses of the *Tubastraea* species described in the last years. On the contrary, new diagnoses are supporting the repositioning of species within the genus *Tubastraea.*

The incredible diversity of sun corals in the TSB shows that the protocol hitherto adopted for the *Tubastraea* species identifications in Brazil is inappropriate for defining the interspecific limits. It has been based on a narrow dichotomic concept (plocoid *vs*. dendroid). Indeed, the sun corals are a group on apparent geographical expansion, and in occupation of new niches along coastal environments. Furthermore, identifying sun coral species based on this concept alone can lead to a chain reaction of misidentifications that hamper the progress of scientific investigation.

Therefore, in addition to adding four new species of *Tubastraea* to the world*: T. ramosa* sp. nov., *T. columnata* sp. nov., *T. grandidentata* sp. nov., and *T. megalostoma* sp. nov., a new occurrence was reported from the Southwestern Atlantic, *T. faulkneri* – originally from the Pacific (Galapagos Is.), the Wells' species (1982), configures an important geographic expansion of an exotic dendrophylliid to Brazil. It is imperative to accurately identify the species present in each region, especially since it is known that the wide distribution and the notable diversity of these corals in the Southwest Atlantic may be a consequence of multiple introduction events, over more than forty years (Fenner 2001, Capel et al. 2019).

Regarding *T. coccinea* and *T. aurea,* both corals were previously encountered in Brazil (de Paula & Creed 2004, Bastos *et al*. 2022). *Tubastraea aurea* was synonymized by Bastos *et al*. (2022) as *T. coccinea*, because of genetic similarity, although a small genetic distance may occur among close scleractinian congeners, as reported by Neves *et al*. (2008) for *Siderastrea*. In contrast, this species was transferred into a new genus, *Australopsammia*, based exclusively on the type locality without any further robust analysis (Rowlett 2020 *apud* Yiu & Qiu 2022). *Tubastraea aurea* differs morphologically from *T. coccinea* due to the size and development of the corallites. It is also important to emphasize that *Tubastraea aurea* has been considered a valid species in phylogenetic studies developed by Arrigoni *et al*. (2014), Yiu & Qiu (2022), and Mehrotra *et al*. (2023). Moreover, Yiu & Qiu (2022) positioned *T. aurea* as the sister group of *T. diaphana*.

The importance of the analysis of micromorphology using SEM images has been pointed out by several authors in taxonomic and systematic studies (Budd & Stolarski 2009, 2011, Budd *et al*. 2012, Benzoni *et al*. 2012, Arrigoni *et al*. 2014, Capel *et al*. 2019, Bastos *et al*. 2022). Macro and micromorphology data are a powerful diagnostic tool for Scleractinia taxonomy, and useful in studies of species complexes, in which a high degree of morphological variation, and the overlapping of diagnostic characteristics among morphotypes, are expected to hinder the identifications.

Mechanisms of larval dispersion by currents, including rafting transport on marine debris, the extensive anthropic activities in the coastal zone, and the development of biofouling communities on artificial substrates are likely to be involved with sun corals overspread across the Atlantic Ocean, extending the distribution range of the Indo-Pacific species (Mantelatto *et al*. 2020). Therefore, a broader evaluation is needed, considering the risk analysis of exotic organisms with a strong dispersive behavior for local benthic communities. Finally, our results support the relevance of taxonomic studies for the consolidation of public policies for the management of sun corals in protected marine areas - still inconspicuous in the face of very basic questions, such as the identity of the species currently established along the Brazilian Coast.

**Ethical statement**

Collection of biological samples were conducted following all applicable ethical regulations regarding collection of biological samples and experimentation with animals. Investigation was performed under permit Sisbio Nº 15161-1, issued by Chico Mendes Institute for Biodiversity Conservation (ICMBio).

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# Four new species of Tubastraea (Scleractinia, Dendrophylliidae) from the Brazilian Coast, Southwestern Atlantic

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## Supplementary material

**Table SI.** Comparison of the morphological characters (corallum and corallite) among ‘sun coral’ species in the Todos-os-Santos Bay (Bahia State), Brazil (adapted from Yiu & Qiu, 2022). LCD, lesser calicular diameter; GCD, greater calicular diameter.

| | corallum | | | corallite | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **growth pattern** | **tissue color** | **intercorallite distance** | **development** | **corallite shape** | **calice shape** | **height (mm)** | **LCD x GCD calice (mm)** | **synapticulotheca** | **pores** |
| ***Tubastraea ramosa* sp. nov.** | branching, irregular monopodial, arborescent | yellow to intense orange, yellow to orange tentacles | closely spaced at the basis and spaced distally | dendroid | cylindrical | circular to elliptical | 10.4-39.1 | 6.0-7.8 x 9.5-12.4 | moderately thick, shallow intercostal grooves | 130.0-450.0 µm, along costae and intercostal grooves |
| ***T. columnata* sp. nov.** | massive, bushy with flattened basis | yellow to light orange, yellow tentacles | closely spaced at the basis and widely apart distally | dendroid | cylindrical | circular to elliptical | 11.1-25.4 | 6.1-6.7 x 9.0-10.8 | thick, shallow intercostal grooves | 80.0-138.0 µm, along intercostal grooves |
| ***T. grandidentata* sp. nov.** | massive, hemispherical to encrusting | yellow-orange at the basis, pink to orangish-pink in the polyps, yellow tentacles | closer at the basis and spaced distally | plocoid | cylindrical | circular to elliptical | 5.5-15.0 | 6.9-9.2 x 10.0-12.8 | basis thick and top fragile, shallow to moderately deep intercostal grooves, deeply dentate margin | 80.0-300.0 µm, along costae and intercostal grooves |
| ***T. megalostoma*** | massive to | dark pink to | closely to moderately | plocoid | slightly | circular to | 4.5-15.3 | 8.0-11.6 x 11.6-16.2 | moderately thick, | 138.0-275.0 |

| | corallum | | | corallite | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **growth pattern** | **tissue color** | **intercorallite distance** | **development** | **corallite shape** | **calice shape** | **height (mm)** | **LCD x GCD calice (mm)** | **synapticulotheca** | **pores** |
| **sp. nov.** | encrusting | reddish, yellow-orange tentacles | spaced at the basis and rather apart distally | | conical to cylindrical | elliptical | | | strongly granular, shallow intercostal grooves | µm, along intercostal grooves |
| ***T. coccinea*** | massive to encrusting, broad and flat basis | light orange to intense red, yellow-orange tentacles | closely spaced | plocoid | cylindrical | circular to elliptical | 1.8-15.2 | 6.3-8.0 x 8.9-10.7 | irregularly thick, moderately deep intercostal grooves | 116.0-280.0 µm, along intercostal grooves |
| ***T. aurea*** | massive, hemispherical, wide and flattened basis | orange to bright red, yellow tentacles | closely spaced at the basis and spaced distally | subdendroid | conical | circular | 12.1-21.7 | 8.4-9.8 x 12.5-15.1 | moderately thick, deep intercostal grooves | 168.0-272.0 µm, along costae and intercostal grooves |
| ***T. faulkneri*** | massive, hemispherical to spherical, pedunculated basis | orange to reddish, yellow-orange tentacles | widely spaced | plocoid | cylindrical | circular | 3.0-11.3 | 5.6-6.7 x 8.4-9.4 | slightly thick, deep and regular intercostal grooves | 150.0-353.0 µm, along intercostal grooves |

**Table SII.** Comparison of the morphological characters (septa and columella) among 'sun coral' species in the Todos-os-Santos Bay (Bahia State), Brazil (adapted from Yiu & Qiu, 2022). S, septa; LCD, lesser calicular diameter; GCD, greater calicular diameter

| | **septa** | | | | | **columella** | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **number** | **cycles** | **formula** | **face ornamentation** | **margin** | **aspect** | **LCD x GCD (mm)** | **fossa depth (mm)** |
| ***Tubastraea ramosa* sp. nov.** | 21-51 | 4 | S1>S2>S3>S4 | rounded and slightly pointed granules | S1 and S2 regular and smooth, S3 irregular, with laciniate projections | spongy | 1.1-2.6 x 5.0-7.1 | 4.9-12.9 |
| ***T. columnata* sp. nov.** | 23-48 | 4 | S1≥S2>S3≥S4 | small slightly pointed granules | S1 and S2 small dentate projections near to columella, S3 irregularly dentate | spongy | 0.8-2.3 x 3.6-5.7 | 4.4-14.7 |
| ***T. grandidentata* sp. nov.** | 25-44 | 4 | S1>S2>S3>S4 | strongly ornamented with small and rounded granules | axial margins poorly ornamented | solid to spongy | 1.2-2.5 x 3.1-6.1 | 3.5-8.4 |
| ***T. megalostoma* sp. nov.** | 32-65 | 5 | S1=S2≥S3>S4>S5 | heavily ornamented with small, closely spaced rounded granules | S1-S3 regular and poorly ornamented, S4 smooth axial margin, with depressions towards the theca | spongy | 1.2-4.2 x 4.8-10.1 | 4.4-11.1 |
| ***T. coccinea*** | 13-55 | 4 | S1>S2>S3>S4 | small and slightly pointed granules | S1 smooth, S2-S4 dentate projections | solid to spongy | 1.2-3.0 x 3.4-8.0 | 3.1-8.2 |
| ***T. aurea*** | 35-51 | 5 | S1≥S2>S3>S4>S5 | small more pointed granules | S1-S3 axial margin with dentate projections, eventually bifurcated | spongy, irregular mesh of septa distal dentition | 0.9-2.0 x 4.4-6.8 | 5.5-10.1 |
| ***T. faulkneri*** | 19-43 | 4 | S1≥S2>S3>S4 | few and small rounded granules | S1 and S2 smooth, S3 irregular | spongy | 0.3-2.6 x 2.8-4.9 | 1.2-6.1 |