

Revision and redescription of the species previously included in the genus *Amphilaphis* Studer and Wright in Studer, 1887 (Octocorallia: Primnoidae)

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SUMMARY: The taxonomy of the primnoid genus *Amphilaphis* Studer and Wright in Studer, 1887 has been in a confused state for a long time and a revision of the species included in that genus has become a necessity. We have revised and redescribed the species previously included in the genus using up-to-date technology, such as polyp and sclerite images obtained with scanning electron microscopy (SEM). As a result of this study, because the type species of *Amphilaphis* is actually a *Thouarella* species, we consider the genus *Amphilaphis* to be no longer valid. One of the species previously considered in *Amphilaphis* has a set of morphological characters that are not recognizable in any of the current primnoid genera. *Primnocapsa* n. gen. has a dichotomous branching pattern, polyps placed singly, in spirals around the branchlets, 8 opercular scales with the inner surface keeled and with 2 mounds basally and 8 marginal scales offset from the operculars. The new genus is described and illustrated. Moreover, one of the re-examined species has been included in a new subgenus, *Faxiella* n. subgen. of *Plumarella* Gray, 1870 because it has polyps placed in pairs. Finally, the remaining re-examined species have been included in the genus *Thouarella* Gray, 1870, one of the most speciose primnoid genera.

Keywords: Cnidaria, new genus, new subgenus, *Faxiella*, *Primnocapsa*, *Thouarella*.

RESUMEN: REVISIÓN Y REDESCRIPCIÓN DE LAS ESPECIES INCLUIDAS PREVIAMENTE EN EL GÉNERO *AMPHILAPHIS* STUDER Y WRIGHT EN STUDER, 1887 (OCTOCORALLIA: PRIMNOIDAE). – Durante mucho tiempo, el género de primnoido *Amphilaphis* Studer y Wright en Studer, 1887, ha sido un cajón de sastre y la revisión de las especies incluidas en este género se ha convertido en algo indispensable. Mediante el uso de la tecnología más actual, como es la microscopía electrónica de barrido (SEM), para la obtención de imágenes de pólipos y escleritos, hemos revisado y redescrito todas las especies previamente incluidas en el género. Como resultado de este estudio, y dado que la especie tipo de *Amphilaphis* es de hecho una especie perteneciente al género *Thouarella*, concluimos que el género *Amphilaphis* no debería considerarse válido. Una de las especies previamente consideradas en este género presenta un conjunto de caracteres morfológicos no reconocibles en ningún género de primnoido. *Primnocapsa* n. gen. se caracteriza por tener un patrón de ramificación dicotómico, pólipos aislados dispuestos en espiral alrededor de las ramas, ocho escamas operculares con quilla y con dos protuberancias basales y ocho escamas marginales dispuestas de forma alterna con las operculares. El nuevo género es descrito e ilustrado. Además, una de las especies re-examinadas ha sido incluida en un nuevo subgénero, *Faxiella* n. subgen. de *Plumarella* Gray, 1870 por poseer pólipos dispuestos en pares. Por último, las restantes especies re-examinadas han sido incluidas en el género *Thouarella* Gray, 1870, uno de los géneros de primnoidos con más especies.

Palabras clave: Cnidaria, nuevo género, nuevo subgénero, *Faxiella*, *Primnocapsa*, *Thouarella*.

INTRODUCTION

Primnoidae is one of the richest gorgonian families in terms of the number of genera and species (Bayer 1980, 1981, 1988, 1998). This family is present in both polar waters, north and south, and in deep wa-

ters at temperate latitudes (Bayer 1996), dominating, together with the Isididae family, the high latitudes of the Southern Hemisphere (Alderslade 1998, Bayer 1998, López-González and Gili 2002). According to Cairns and Bayer (2009), 36 genera with 233 species are currently recognized for Primnoidae, although new

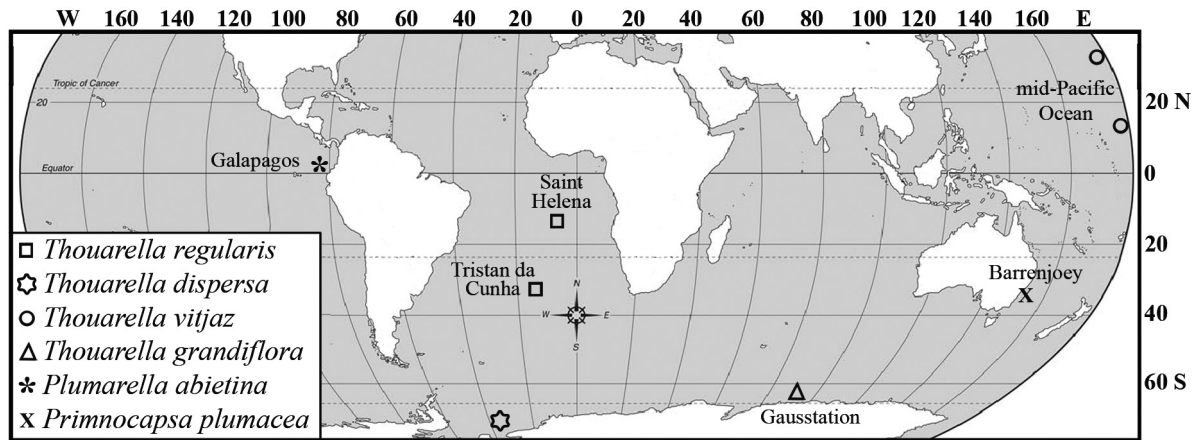


FIG. 1. – Known distribution of primnoid species studied in this paper: square, *Thouarella regularis*; star, *T. dispersa*, Antarctica, no specific location; circle, *T. vitjaz* n. sp.; triangle, *T. grandiflora*; asterisk, *Plumarella (Faxiella) abietina*; cross, *Primnocapsa plumacea*.

species and genera are constantly being proposed (see for example Zapata-Guardiola and López-González 2010a,b,c, and Cairns 2010).

The genus *Amphilaphis* Studer and Wright in Studer (1887) is one of the least cohesive primnoid genera. Since its original description it has been placed either inside or outside of the related genus *Thouarella* by different authors (Kükenthal 1912, 1915, Bayer 1981, Bayer and Stefani 1989). Furthermore, up to 8 species have been included in the genus by previous authors (Wright and Studer 1989, Nutting 1908, Thomson and Mackinnon 1911, Kükenthal 1915). In an initial attempt, Cairns and Bayer (2009) transferred 2 of them to the genus *Thouarella*, while the remaining species were tentatively maintained in *Amphilaphis*. Due to this ongoing uncertainty we considered it appropriate to revise the 6 species currently assigned to *Amphilaphis*.

An effort is made herein to redescribe the species assigned to *Amphilaphis* under the current descriptive formats, revising the true recognizable distribution and, when possible, establishing relationships with the closest congeners. The study of the type material of the 6 species currently included in *Amphilaphis*, one of which is the type species of the genus, has allowed us to propose a series of changes in the placement of this group of primnoids. These changes include the allocation of 4 of the species (one of them the type species) to the genus *Thouarella* (this act invalidates the genus *Amphilaphis*), the establishment of a new subgenus of *Plumarella* and a new primnoid genus to accommodate *Amphilaphis abietina* Studer, 1894 and *Amphilaphis plumacea* Thomson and Mackinnon, 1911, respectively.

MATERIALS AND METHODS

The material of the species here examined is deposited in different museums around the world: the Australian Museum (AM), Sydney; The Natural History Museum (NHMUK), London; the Museum für

Naturkunde (ZMB), Berlin; the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge; the Museum of Natural History (MNHW), Wrocław University, Poland; the National Museum of Natural History (NMNH), the Smithsonian Institution, Washington DC; the Zoological Museum of Amsterdam (ZMA), the Netherlands, and the P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences (IORAS), Russia. All of these institutions kindly sent us part of their specimens for scanning electron microscopy (SEM) examination of polyp and sclerite morphology. Fragments of the colonies were prepared for study by SEM employing the usual methodology previously described by several authors (e.g. Bayer and Stefani 1989, Alderslade 1998), and permanent mounts were made for light microscopy observation. In order to better observe the arrangement of the scales on the polyps using light microscopy, their outlines were usually highlighted by applying methylene blue. The colony and sclerite terminology herein mainly follows Bayer *et al.* (1983) and Cairns and Bayer (2009). Sclerite measurements are presented as the height range X the width range. The distribution of the species here studied is shown in Figure 1.

RESULTS

Family PRIMNOIDAE Gray, 1858
Genus *Thouarella* Gray, 1870

Diagnosis. Primnoidae commonly with a bottle-brush colony shape and simple or ramified branchlets, or fan-shaped. Polyps cylindrical to club-shaped with 8 rows of body scales that decrease near calyx base, angled upward or almost perpendicular to stem, straight or adaxially incurved, and arranged singly or in whorls. Opercular scales usually keeled, 8 in number, arranged in 2 alternate cycles. Marginal scales also 8 in number with a keel or multiple keels, alternating in 2 cycles, and folding over the operculars in an indented way. Adaxial body scales often reduced in size and number.



FIG. 2. – *Thouarella regularis* (Wright and Studer, 1889), lectotype (NHMUK 1889.5.27.60): A, whole colony; B, detail of branchlet.

Thouarella regularis (Wright and Studer, 1889)
(Figs. 2-6)

Amphilaphis regularis Wright and Studer 1889: 71-72; pl. 15, Figs. 1, 1a; pl. 21, fig. 7. Versluys 1906: 22. Thomson and Ritchie 1906: 854. Cairns and Bayer 2009: 28, 38; Fig. 10 j-q.

Thouarella regularis, Kükenthal 1912: 307.
Thouarella (Amphilaphis) regularis, Kükenthal 1915: 149.
Kükenthal 1919: 409-410. Kükenthal 1924: 289. Parrish and Baco 2007: 192.
not *Thouarella regularis* Kükenthal 1907: 206-207. [= *Thouarella laxa* Versluys, 1906]
not *Amphilaphis regularis*, Nutting 1908: 573-574. [= *Plumarella circumoperculum* Cairns, 2010]

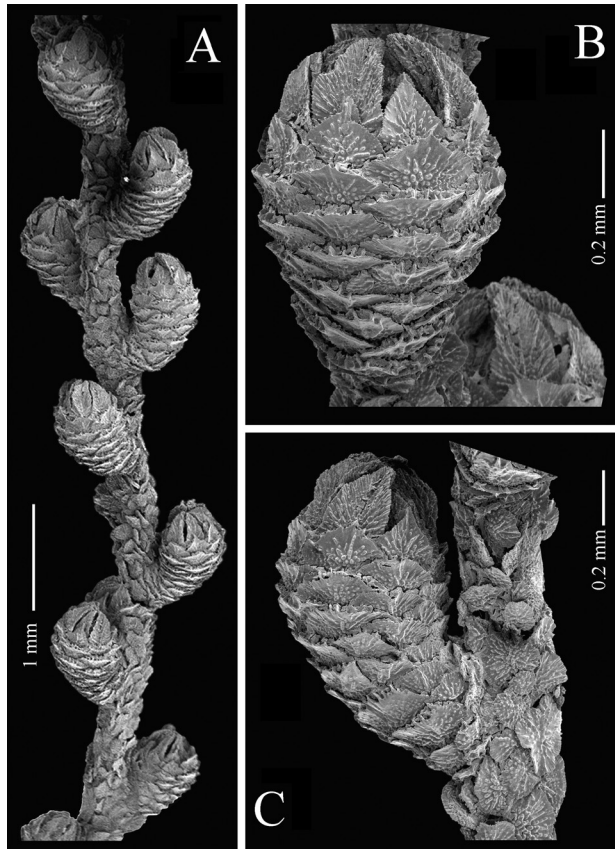


FIG. 3. – *Thouarella regularis* (Wright and Studer, 1889), lectotype (NHMUK 1889.5.27.60): A, detail of branchlet; B, polyp on abaxial view; C, polyp on lateral view.

Examined material. Lectotype (here designated): NHMUK 1889.5.27.60, on label: “Challenger Expedition, stn 135a, 37°16.83'S 12°45.25'W, off Inaccessible Island, Tristan da Cunha, SubAntarctica, 137 m depth, 16 October 1873; stn 135c, 37°25.5'S 12°28.5'W, off Nightingale Island, Tristan da Cunha, SubAntarctica, 183-274 m depth, 17 October 1873”. (According to the information on the label and that in the archives of the NHMUK, 2 close localities are indicated for the lectotype material here designated (stns. 135a and 135c) (Emma Sherlock, pers. comm.). Paralectotypes (here designated): NHMUK 1932.12.8.7, Challenger Expedition, stn 135, 37°1.83'S 12°19.16'W, off Tristan da Cunha, SubAntarctica, 658 m depth, 15 October 1873, one colony fragmented in several pieces; NHMUK 1889.7.5.11.15 and 1889.7.5.17, Challenger Expedition, stn 135a, 37°16.83'S 12°45.25'W, off Inaccessible Island, Tristan da Cunha, SubAntarctica, 137 m depth, 16 October 1873, 5 colonies and more than 10 fragments; NHMUK 89.7.5.18 and 89.7.5.21, stn. 135b, 37°22.5'S 12°33'W, off Nightingale Island, Tristan da Cunha, SubAntarctica, 851 m depth, 17 October 1873, stn 135c, 37°25.5'S 12°28.5'W, off Nightingale Island, Tristan da Cunha, SubAntarctica, 201 m depth, 17 October 1873, stn 135d, 37°25'S 12°30.5'W, off Nightingale Island, Tristan da Cunha, SubAntarctica, 132 m depth, one colony each (according to the information on the label and that in the archives of the NHMUK, 3 close localities are indicated for both specimens). Additional material: ZMA COEL 04937, Scottish National Antarctic Expedition, Saint Helena, SubAntarctica, 1904.

Description of the lectotype. Colony fan-shaped, pinnately branched in one plane (Fig. 2A) 25 cm in high and 13 cm wide. Simple or pinnately ramified branchlets up to second order and inclined upward, terminal branchlets up to 9 cm long. Axis yellowish brown, holdfast present and attached to hard substrate

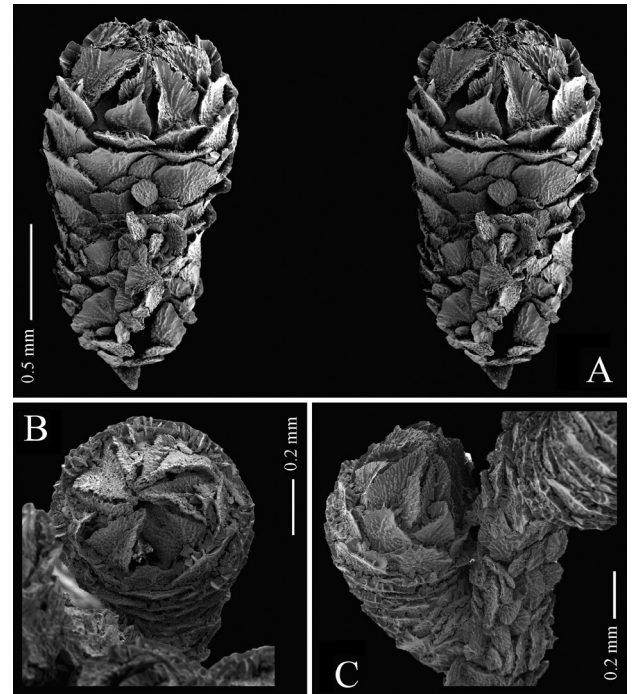


FIG. 4. – *Thouarella regularis* (Wright and Studer, 1889), lectotype (NHMUK 1889.5.27.60): A, polyp on adaxial view, stereo pair; B, polyp on oral view; C, polyp on latero-adaxial view.

(scleractinian coral), basal axis diameter of 4 mm. Polyps (Fig. 2B, 3A) inclined upward to branchlets, singly placed, present on main stem, branches and branchlets, and arranged in spirals or biserially, 11-14 polyps per cm. They are cylindrical to club-shaped (Fig. 3B, C), about 0.9-1.8 mm tall and 0.54-1.02 mm in greatest diameter, with body scales in 8 longitudinal rows. Each abaxial row has 7-9 scales (Fig. 3B) and there are 3-4 scales in each adaxial row that are slightly disorganized (Fig. 4A).

Eight opercular scales (Fig. 4B, 5A), 0.38-0.52×0.19-0.3 mm, pentagonal-shaped, slightly bilobed basally and with an acute apex. Proximal inner surface tuberculate covering up to half of the length. Prominent apical keel with multiple lateral ridges. Distal inner surface of scale with radial ridges. Outer surface radially granular from a basal nucleus. Basal margin with irregular processes, free margin finely serrated.

Eight marginal scales (Fig. 5B) 0.32-0.41×0.27-0.34 mm, pentagonal-shaped, with an acute apex. Inner surface tuberculate, covering at least the proximal half and up to about 80% of the length. Prominent apical keel with multiple lateral ridges, lateral inner distal surface almost smooth. Outer surface radially granular from a basal nucleus. Basal margin with irregular tuberculate processes, free margin finely serrated.

Body scales (Fig. 6A) 0.23-0.31×0.29-0.49 mm and fan-shaped. Inner surface almost completely tuberculate, short ridges in the middle of the distal margin decreasing in number and size from distal to basal scales; outer surface radially granular, basal margin

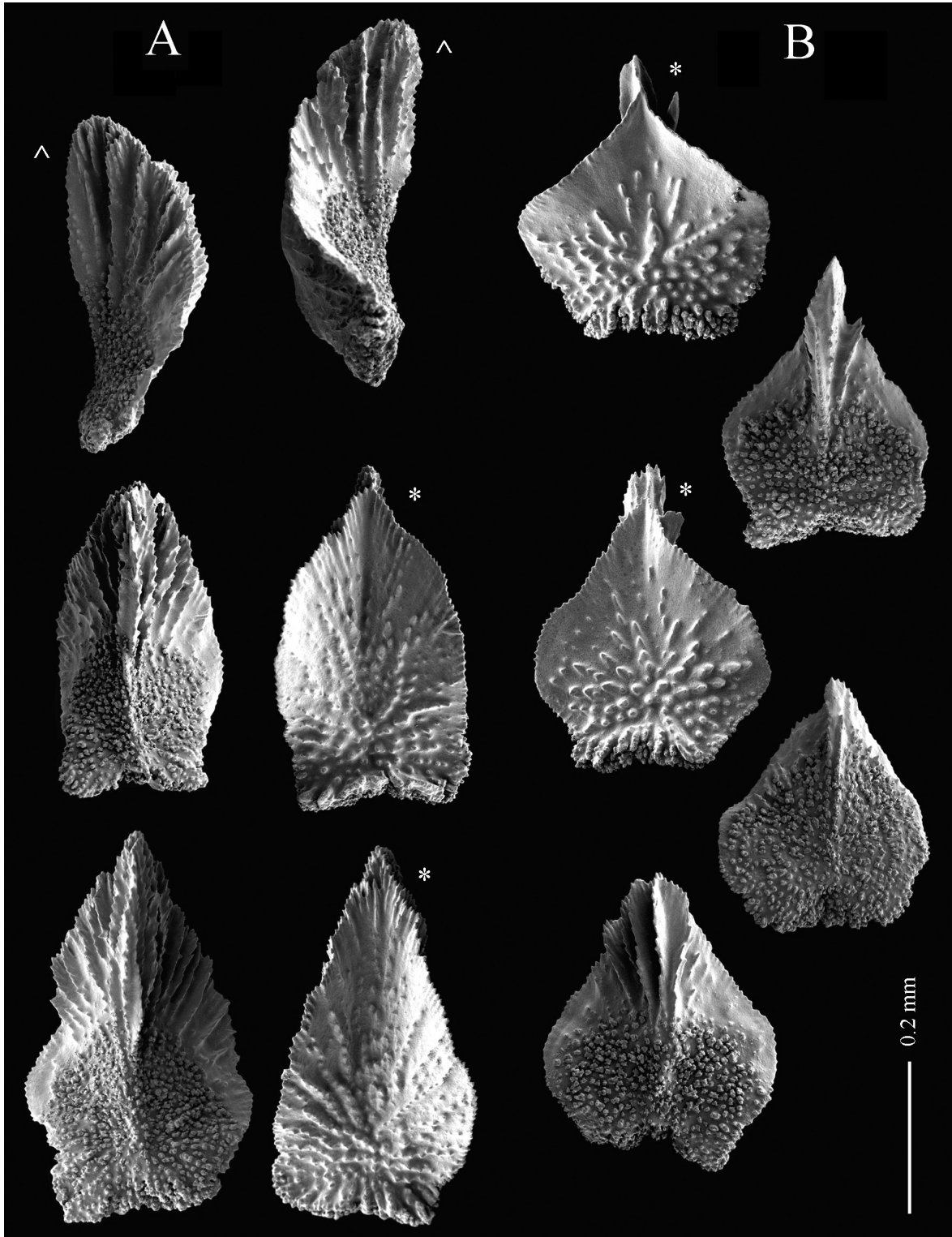


FIG. 5. – *Thouarella regularis* (Wright and Studer, 1889), lectotype (NHMUK 1889.5.27.60): A, opercular scales; B, marginal scales. [*outer surface view; ^ lateral view].

with irregular tuberculate processes, free margin finely serrated. Adaxials with tendency to be reduced in size.

Coenenchymal sclerites (Fig. 6B) in 2 layers: outer layer of round to oval-shaped, 0.07-0.3 mm maximum

length. Inner surface completely tuberculate, outer surface with granules sometimes forming ridges. Margin similar to that of body scales. Inner layer consisting of tuberculate, irregular sclerites.

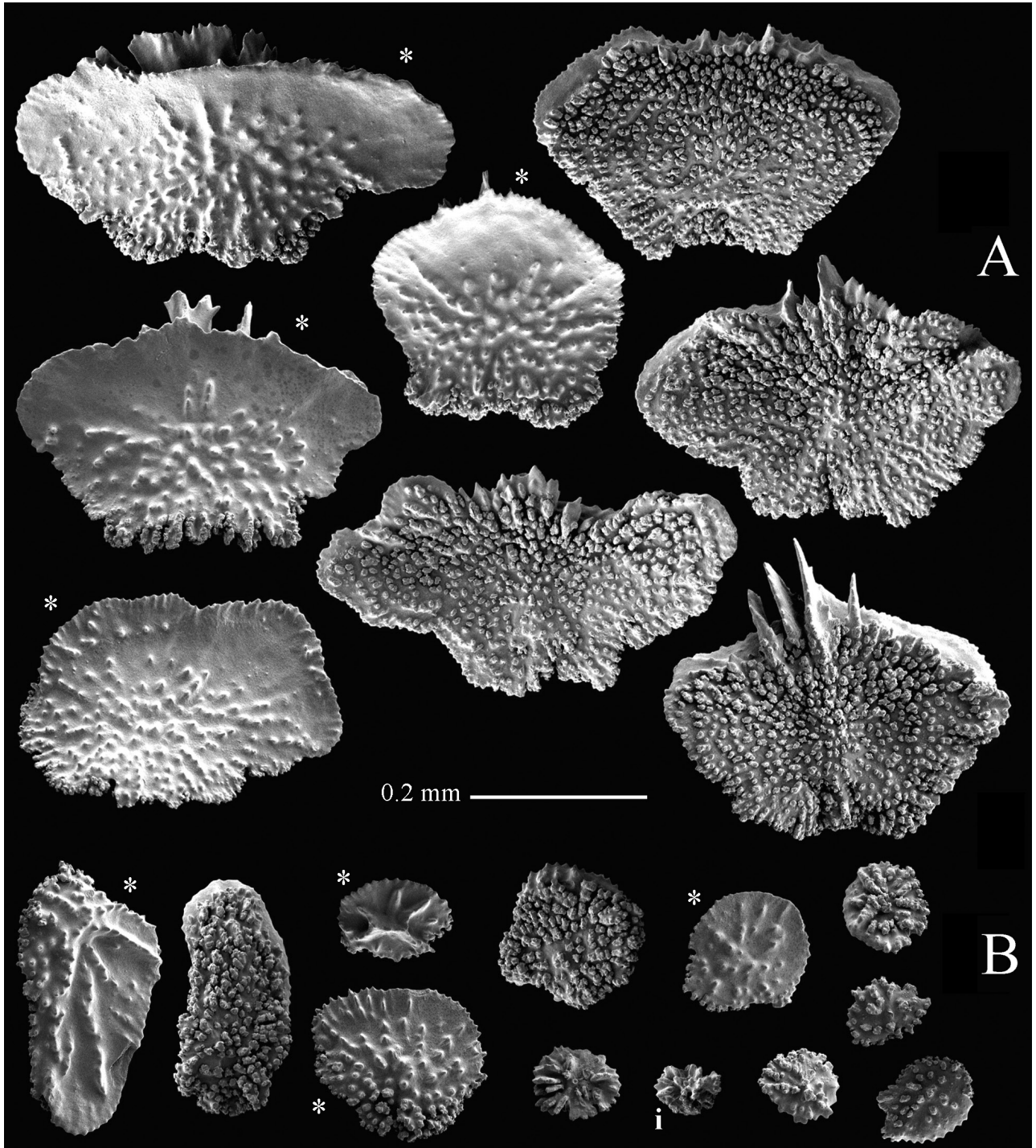


FIG. 6. – *Thouarella regularis* (Wright and Studer, 1889), lectotype (NHMUK 1889.5.27.60): A, body scales; B, coenenchymal sclerites. [* outer surface view; i sclerite from inner layer].

Variability. The paralectotypes and additional material are pinnate colonies branched in one plane, branchlets ramified up to the second order and up to 9 cm long. The maximum height and width of the colonies is 25 cm and 13 cm, both measurements belonging to the lectotype. The number of polyps per centimetre can vary from 7 to 14. The polyps' shape, their arrangement

and the shape of the sclerites are similar to those in the lectotype.

Geographical and bathymetrical distribution. *Thouarella regularis* is known from Inaccessible and Nightingale Island from the archipelago of Tristan da Cunha, and from Saint Helena, SubAntarctica, between 137 and 658 m in depth.

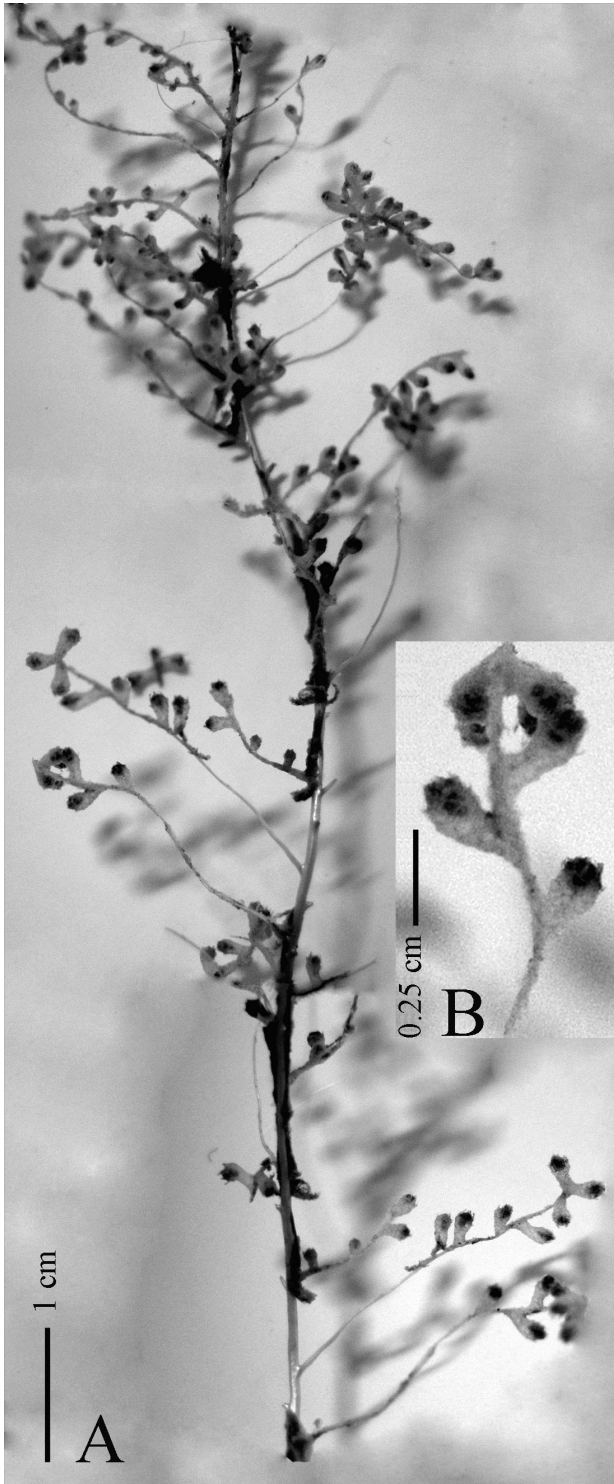


FIG. 7. – *Thouarella dispersa* Kükenthal, 1912, holotype (ZMB Cni 5468): A, whole colony; B, detail of branchlet. [Photo: Carsten Lueter, ZMB, Berlin].

Thouarella dispersa Kükenthal, 1912
(Figs. 7-9)

Thouarella dispersa Kükenthal, 1912: 307-309; pl. 20, fig. 4; text Figs. 13-16.

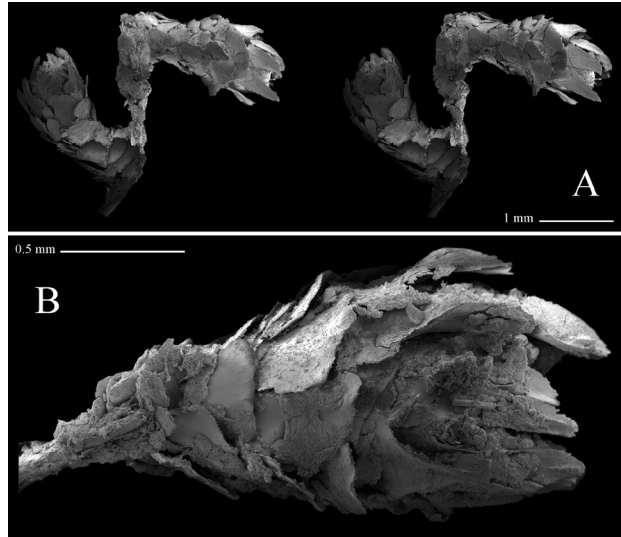


FIG. 8. – *Thouarella dispersa* Kükenthal, 1912, holotype (ZMB Cni 5468): A, polyps on lateral view, stereo pair; B, polyp on latero-axial view.

Thouarella (*Amphilaphis*) *dispersa*, Kükenthal, 1915: 149. Kükenthal 1919: 411-412; pl. 31, Fig. 11. Kükenthal 1924: 290-291.

Amphilaphis dispersa, Cairns and Bayer, 2009: 28.

Examined material. Holotype: ZMB Cni 5468, Deutsche Südpolar-Expedition, Antarctica, 2450 m depth, 1 March 1903.

Description of the holotype. Slender bottlebrush colony (Fig. 7A), 18 cm in high and 5.3 cm wide. Simple slender branchlets, up to 3.5 cm long, sparsely arranged, 4 branchlets per centimetre, in acute angles upward to stem. Axis pearl in colour, slender and graceful, without holdfast. Basal axis diameter 1.6 mm.

Polyps (Fig. 7B) inclined upward to branchlet, singly placed and occasionally biserial, present also on main stem, 6 polyps per cm arranged on 2 sides. Polyps (Fig. 8) relatively elongated, funnel-shaped, up to 1.9 mm tall and 0.8-1 mm maximum diameter, with a conical operculum. Polyp body with 8 rows of scales, 5 in each abaxial row, and 3-4 smaller scales in each adaxial row (Fig. 8B).

Eight opercular scales (Fig. 9A), 0.64-0.99×0.22-0.40 mm, long tongue-shaped wider basally, rounded apex and bilobed base. Proximal inner surface tuberculate covering up to half of the length; sclerites convex, with longitudinal ridges forming an incipient distal keel. Outer surface smooth or radially granular. Free margin finely serrated.

Eight marginal scales (Fig. 9B), 0.63-0.85×0.32-0.52 mm, pentagonal-shaped with acute apex. Proximal inner surface tuberculate covering about half of the length, multi keeled distally. Outer surface almost radially granular. Basal margin with irregular processes, free margin finely serrated.

Body scales (Fig. 9C) roughly round in shape, 0.21-0.53 mm maximum length. Inner surface almost completely tuberculate, outer surface almost smooth with some granules. Basal margin with tuberculate processes, free margin finely serrated.

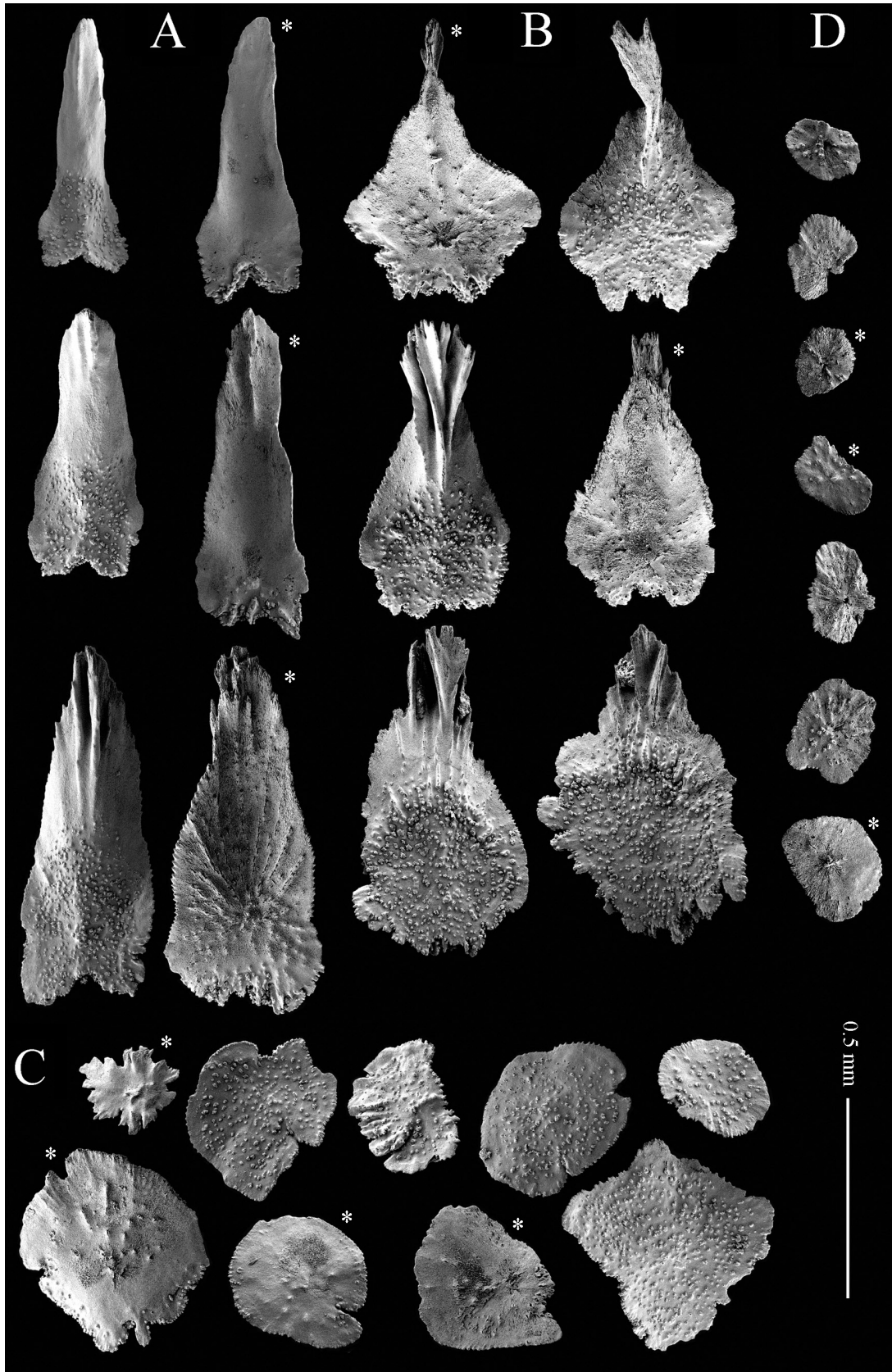


FIG. 9. – *Thouarella dispersa* Kükenthal, 1912, holotype (ZMB Cni 5468): A, opercular scales; B, marginal scales; C, body scales; D, coenenchymal sclerites. [* outer surface view].

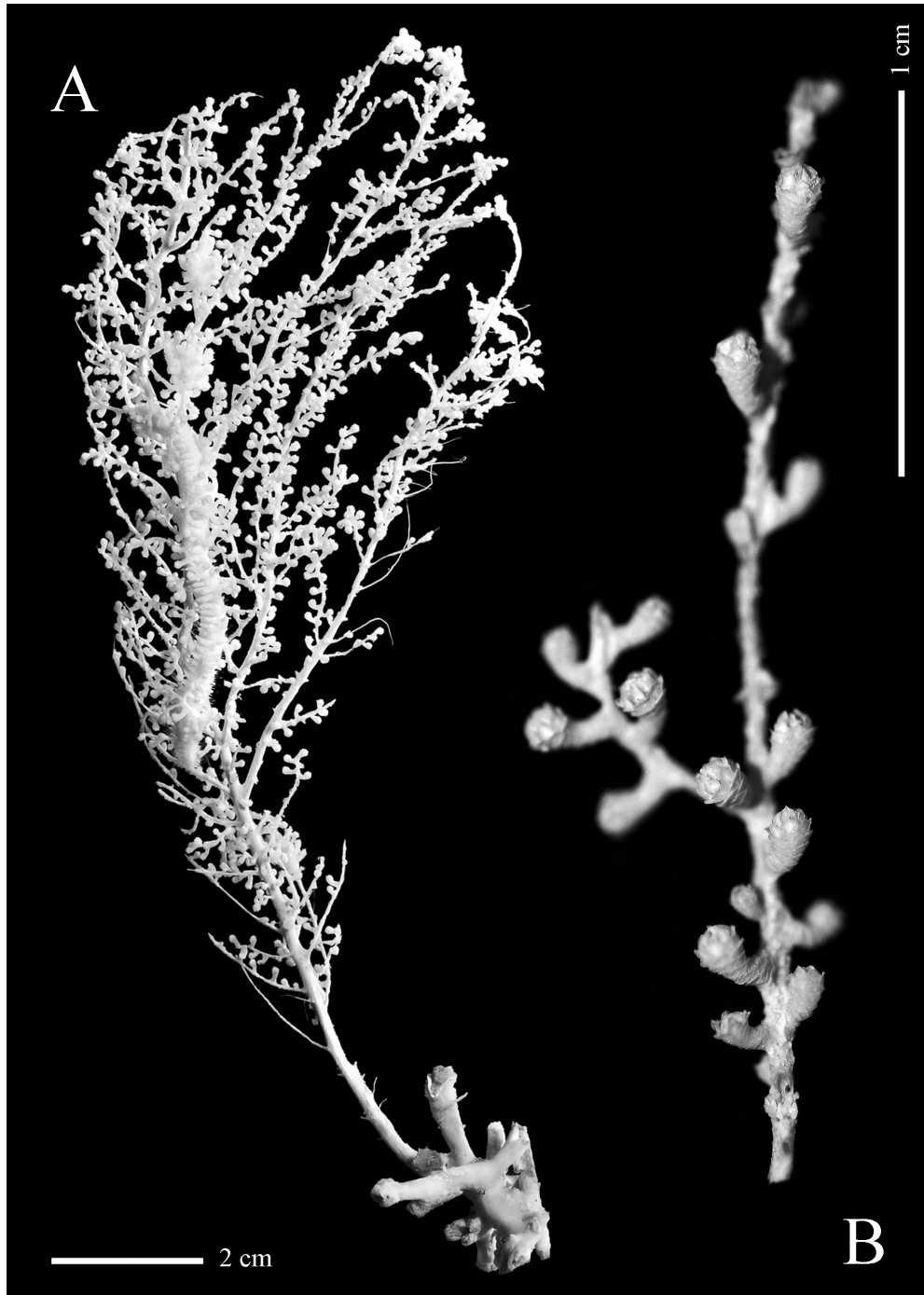


FIG. 10. – *Thouarella grandiflora* Kükenthal, 1912: A, holotype (ZMB Cni 5469), whole colony, [photo: Carola Radken, ZMB, Berlin]; B, paralectotype (MPUW 44), detail of branchlet.

Coenenchymal sclerites (Fig. 9D) round in shape, 0.12–0.28 mm maximum length. Inner surface with scattered tubercles, outer surface slightly smooth with some granules, margin finely serrated.

Geographical and bathymetrical distribution. *Thouarella dispersa* is only known from the type locality, Antarctica, at a depth of 2450 m.

***Thouarella grandiflora* Kükenthal, 1912**
(Figs. 10–14)

Thouarella grandiflora Kükenthal, 1912: 309–310; pl. 21, Fig. 6; text Figs. 17–20.

Thouarella (Amphilaphis) grandiflora, Kükenthal, 1915: 149. Kükenthal 1919: 413; text Fig. 180. Kükenthal 1924: 291.

Amphilaphis grandiflora, Cairns and Bayer, 2009: 28.



FIG. 11. – *Thouarella grandiflora* Kükenthal, 1912, holotype (MPUW 44): A, detail of branchlet, stereo pair; B, polyp on oral view, stereo pair.

Examined material. Holotype: ZMB Cni 5469 and MPUW 44, Deutsche Südpolar-Expedition, Gauss Station, Antarctica, 385 m. depth, 7 February 1903.

Description of the holotype. Bottlebrush colony (Fig. 10A), 18 cm high and 7.6 cm wide. Colony ramified up to the second order with branchlets up to 3.7 cm long. Axis ochre, holdfast present and attached to a hard substrate, basal axis diameter 2.4 mm. Polyps almost perpendicular but slightly curved upward to stem and branchlets (Fig. 10B, 11A), singly placed, arranged in spirals, spaced about 8 polyps per cm. Polyps club-shaped (Fig. 11, 12), about 1.5–2.4 mm tall and 0.4–1.2 mm greatest diameter, with body scales in 8 longitudinal rows, adaxial scales reduced in size and number; 6–8 in each abaxial row (Fig. 12B) but 4 smaller scales in each adaxial row (Fig. 12C).

Eight opercular scales (Fig. 11B, 13A), 0.42–0.58×0.15–0.29 mm, arrow-head-shaped with an acute apex and a bilobed base. Proximal inner surface sparsely tuberculate up to half of scale length; distal part with strong-ridged keel. Outer surface radially granular forming ridges, concave surface deeper distally. Free margin finely serrated, basal margin with tuberculate processes.

Eight marginal scales (Fig. 13B), pentagonal-shaped, 0.44–0.54×0.31–0.46 mm. Inner surface

sparsely tuberculate covering up to 75% of the scale, with middle longitudinal prominent multi-keels distally. Outer surface radially granular, forming ridges. Free margin finely serrated, basal margin with irregular processes.

Body wall scales (Fig. 14A) fan-shaped, 0.26–0.48×0.26–0.56 mm. Inner surface almost completely sparsely tuberculate with or without crests centrally placed on the distal border. Outer surface granular. Free margin finely serrated, basal margin with irregular processes. Coenenchymal sclerites (Fig. 14B) round or oval-shaped, 0.18–0.47 mm maximum length. Inner surface completely tuberculate, outer surface with few granules, free margin finely serrated, proximal border with tubercles.

Geographical and bathymetrical distribution. *Thouarella grandiflora* is only known from the holotype locality of Gauss Station, Antarctica at a depth of 385 m.

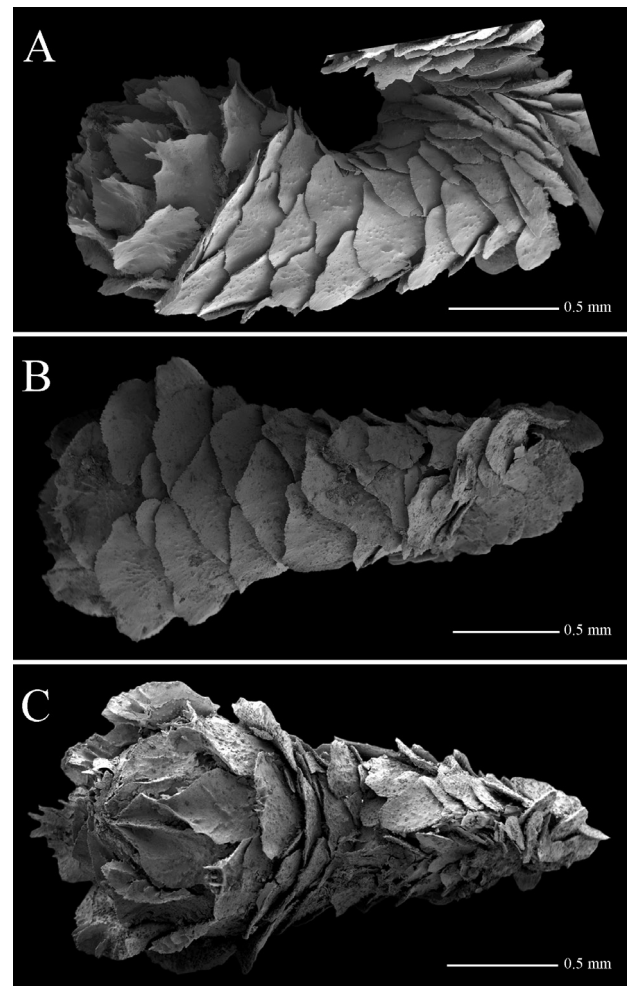


FIG. 12. – *Thouarella grandiflora* Kükenthal, 1912: A, holotype (ZMB Cni 5469), polyp on lateral view; B, paralectotype (MPUW 44), polyp on abaxial view; C, paralectotype (MPUW 44), polyp on adaxial view.

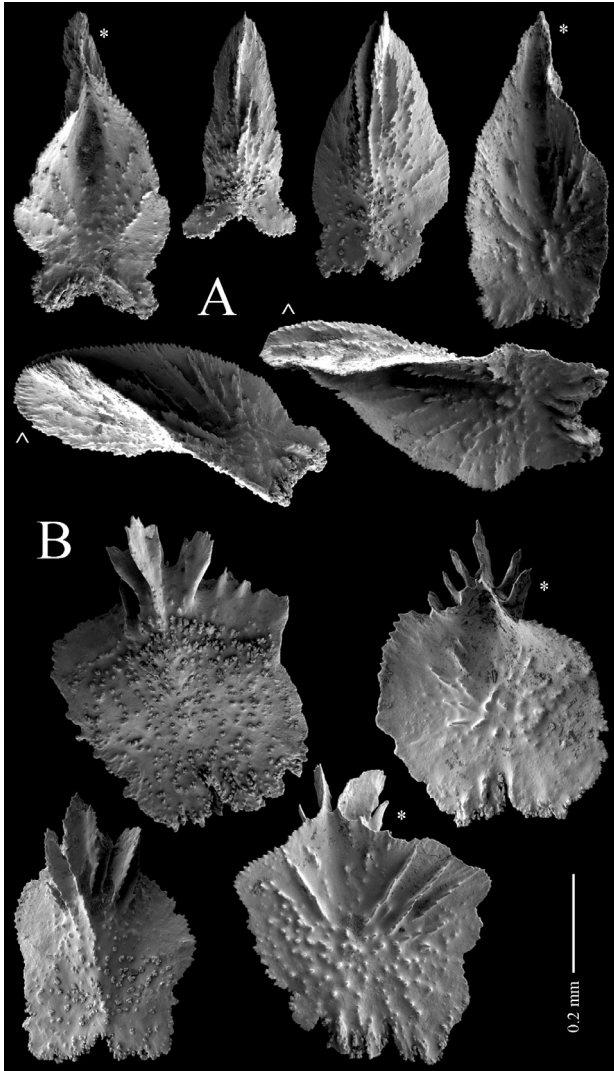


FIG. 13. – *Thouarella grandiflora* Kükenthal, 1912, holotype (MPUW 44): A, opercular scales; B, marginal scales. [* outer surface view; ^ lateral view].

***Thouarella vitjaz* n. sp.**
(Figs. 15-17)

Thouarella abietina, Pasternak, 1981: 49-50.

Examined material. Holotype: IORAS IV-9-Alc-010-002, *RV Vitjaz*, cruise 48, stn 6275, 12°12'N 179°49'E, 6400 m depth, 2 branchlets. Paratype: IORAS IV-9-Alc-010-001, *RV Vitjaz*, cruise 48, stn 6265, 26°56.1'N 178°38'E, 3200 m depth, 23 May 1970, 2 fragments.

Description of the holotype. Two small, delicate dry branchlets, 1.3 and 1.4 cm long (Fig. 15A). Polyps small, curved upward to branchlets at 45° (Fig. 15B), placed in pairs about 0.5 mm apart, 7 pairs per cm. They are trumpet-shaped (Fig. 16), about 0.74-1.1 mm tall and 0.39-0.57 mm greatest diameter with a low operculum and body scales in 8 longitudinal rows. Each abaxial row has 5-6 scales (Fig. 16A) and 3 in each adaxial row (Fig. 16B).

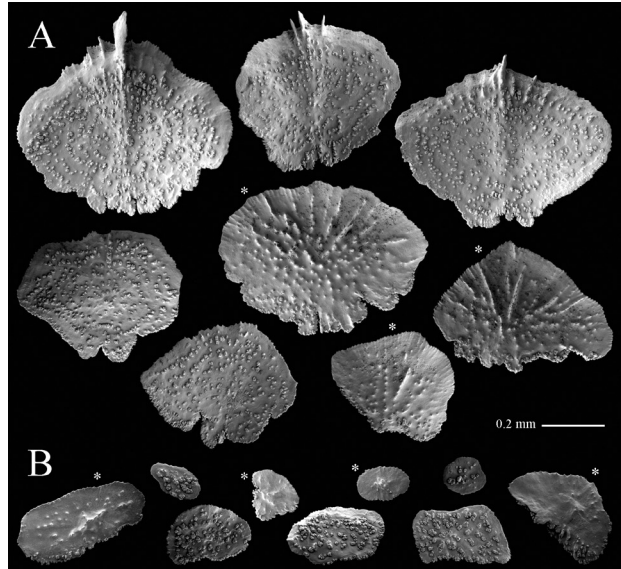


FIG. 14. – *Thouarella grandiflora* Kükenthal, 1912, holotype (MPUW 44): A, body scales; B, coenenchymal sclerites. [* outer surface view].

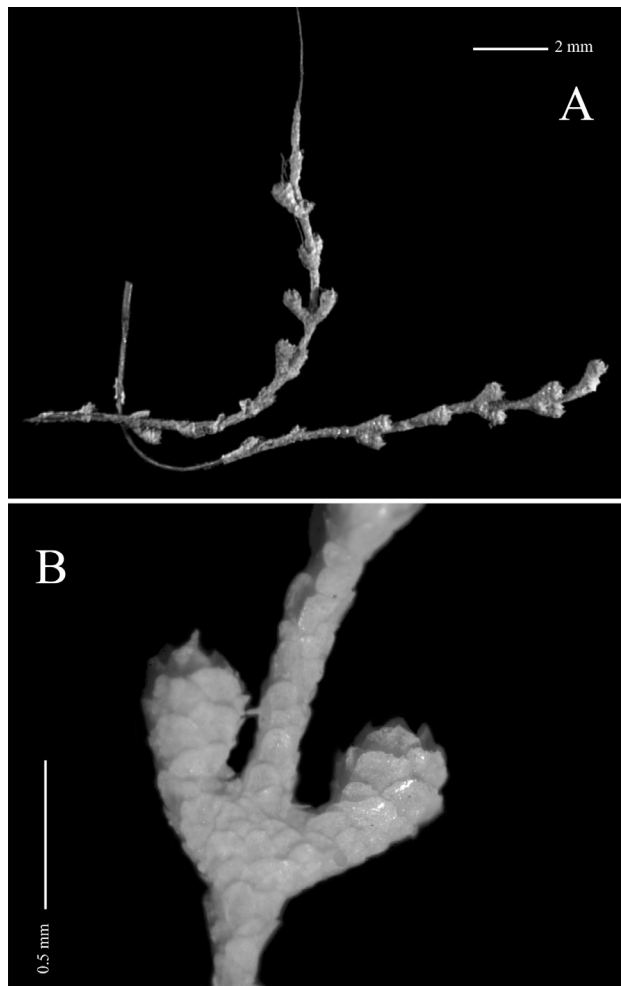


FIG. 15. – *Thouarella vitjaz* n. sp., holotype (IORAS IV-9-Alc-010-002): A, detail of branchlet; B, detail of a whorl of two polyps.

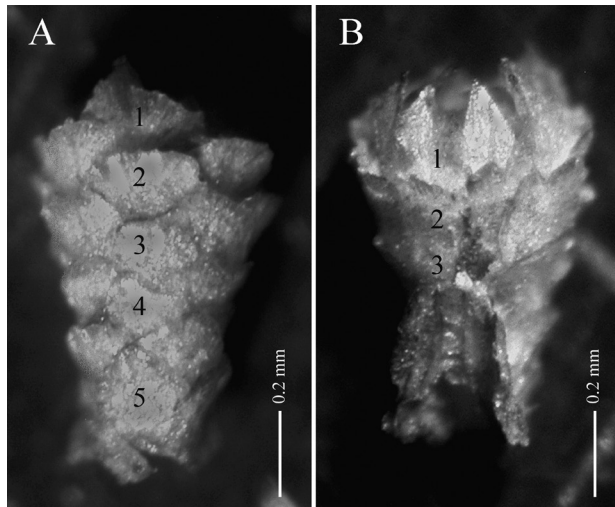


FIG. 16. — *Thouarella vitjaz* n. sp., holotype (IORAS IV-9-Alc-010-002): A, polyp on abaxial view; B, polyp on adaxial view.

Eight opercular scales (Fig. 17A), 0.14–0.21×0.06–0.11 mm, tongue-shaped. Proximal inner surface tuberculate covering up to a third of the length, distal surface with several longitudinal ridges. Outer surface granular, free margin finely serrated.

Eight marginal scales (Fig. 17B), 0.23–0.27 mm tall and 0.12–0.16 mm wide, lancet-shaped with an acute apex; adaxials reduced. Inner proximal surface tuberculate, covering less than a half of their length, distal portion from smooth to ridged, with a modest medial keel. Outer surface granular. Basal margin with small granular processes, free margin finely serrated.

Upper cycle of body scales, or submarginals, (Fig. 17C: sms), roughly triangular-shaped, 0.25–0.30 mm tall and 0.18–0.24 mm wide. Inner proximal surface tuberculate, covering up to half of the length, long ridges distally and a modest medial keel. Remaining body scales (Fig. 17C), round to fan-shaped, 0.11–0.24 mm tall and 0.16–0.28 mm wide. Inner surface tuberculate covering at least 75% of the scale, with long radial ridges distally decreasing in size in the more basal scales. Outer surface granular. Basal margin with small granular processes, free margin finely serrated.

Coenenchymal scales (Fig. 17D) round to oval-shaped, 0.07–0.20 mm maximum length. Inner surface tuberculate, outer surface granular. Basal margin with small granular processes, free margin finely serrated.

Variability. The paratype consists of 2 small dry fragments, of which the largest is 1.8 cm long. The shortest is a branchlet of 1.2 cm. The polyps' shape and arrangement and the shape of the sclerites are similar to those in the holotype.

Geographical and bathymetrical distribution. *Thouarella vitjaz* n. sp. is only known from the middle of the northern Pacific Ocean, between the Marshall Islands and Johnston Atoll and from the south west of

Green Island, the Midway Islands, the Hawaiian archipelago, Pacific Ocean, at 3200 and 6400 m depth.

Etymology. The species name, *vitjaz*, refers to the Soviet Union's research vessel "Витязь" (=knight), from which the new species was collected. The name is treated as a noun in apposition.

Remarks on the species transferred to the genus *Thouarella*

The genus *Amphilaphis* was originally erected by Wright and Studer (1889: 71), for *Amphilaphis regularis*, the type species. Subsequently, Kükenthal (1912: 307) included this species in the genus *Thouarella*, giving as reasons the shape of the polyps, the number of scales in each longitudinal abaxial row, and mainly the biserial arrangement of the branchlets which he had found in other *Thouarella* species he described (e.g. *Thouarella flabellata* Kükenthal, 1907), although the colony shape was considered by Wright and Studer as a generic character to differentiate *Thouarella* (bottlebrush) from *Amphilaphis* (fan-shaped). However, a few years later, Kükenthal considered *Amphilaphis* to be a subgenus of *Thouarella* (Kükenthal, 1915) because it has 8 well-organized rows of scales from the distal to the basal part of the polyp, and because of the long and slender appearance of the branchlets. The last revisionary contribution concerning the family Primnoidae (Cairns and Bayer 2009) treated *Amphilaphis* at the generic level, distinguishing it from other primnoid genera because of the equal size of the 8 rows of body scales and the pinnate branching pattern, but they did not illustrate the adaxial side of the polyps, thus attributing an equal size of body scales by mistake.

As a result of our research, we consider it more appropriate to include the species *Amphilaphis regularis* in the genus *Thouarella* for the following reasons: 1) its adaxial body scales are reduced (Fig. 4A); 2) its marginal scales fold over the operculars in an indented way (Fig. 4); 3) its pinnate branching pattern is included among the current variations of colony form for that genus; and 4) its biserial polyp arrangement is also found in other *Thouarella* species. However, that transfer of *Amphilaphis regularis* to *Thouarella* produces a junior secondary homonym of *T. regularis* Kükenthal, 1907 that must be treated as invalid as both species are considered congeneric and thus replaced by a substitute name (International Commission on Zoological Nomenclature 1999). In the revision of the genus *Thouarella* by M. Taylor *et al.* (submitted, pers. comm.), *T. regularis* Kükenthal, 1907 would be synonymized with *T. laxa* Versluys, 1906. Furthermore, *T. regularis* should be included in the subgenus *Epithouarella* due to the lack of a thorn in the marginal scales (Kükenthal 1915, Cairns and Bayer 2009). As a consequence of the removal of the type species from genus *Amphilaphis*, the genus should no longer be considered valid.

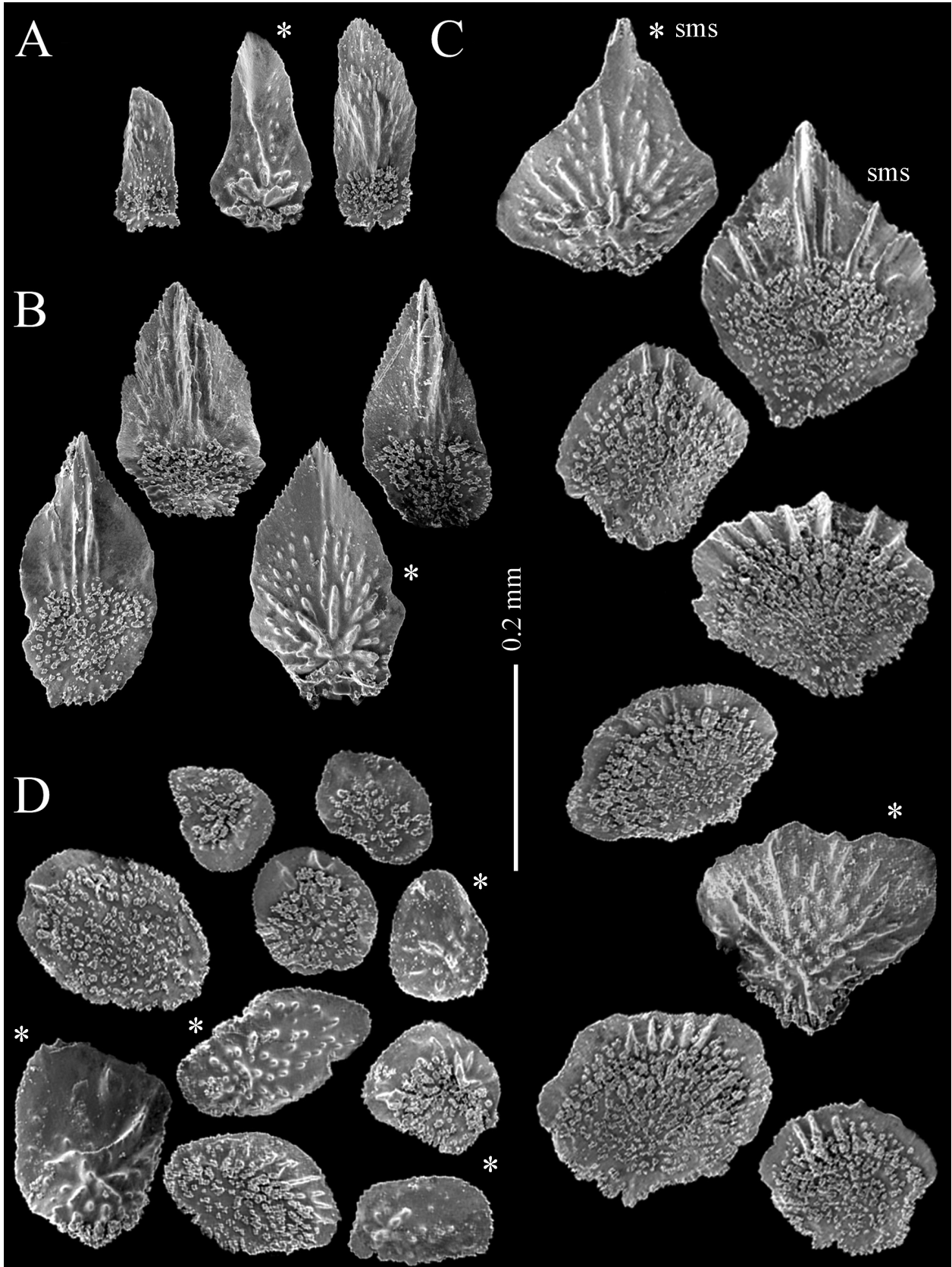


FIG. 17. – *Thouarella vitjaz* n. sp., holotype (IORAS IV-9-Alc-010-002): A, opercular scales; B, marginal scales; C, body scales; D, coenenchymal sclerites. [*outer surface view; sms=submarginal scales].

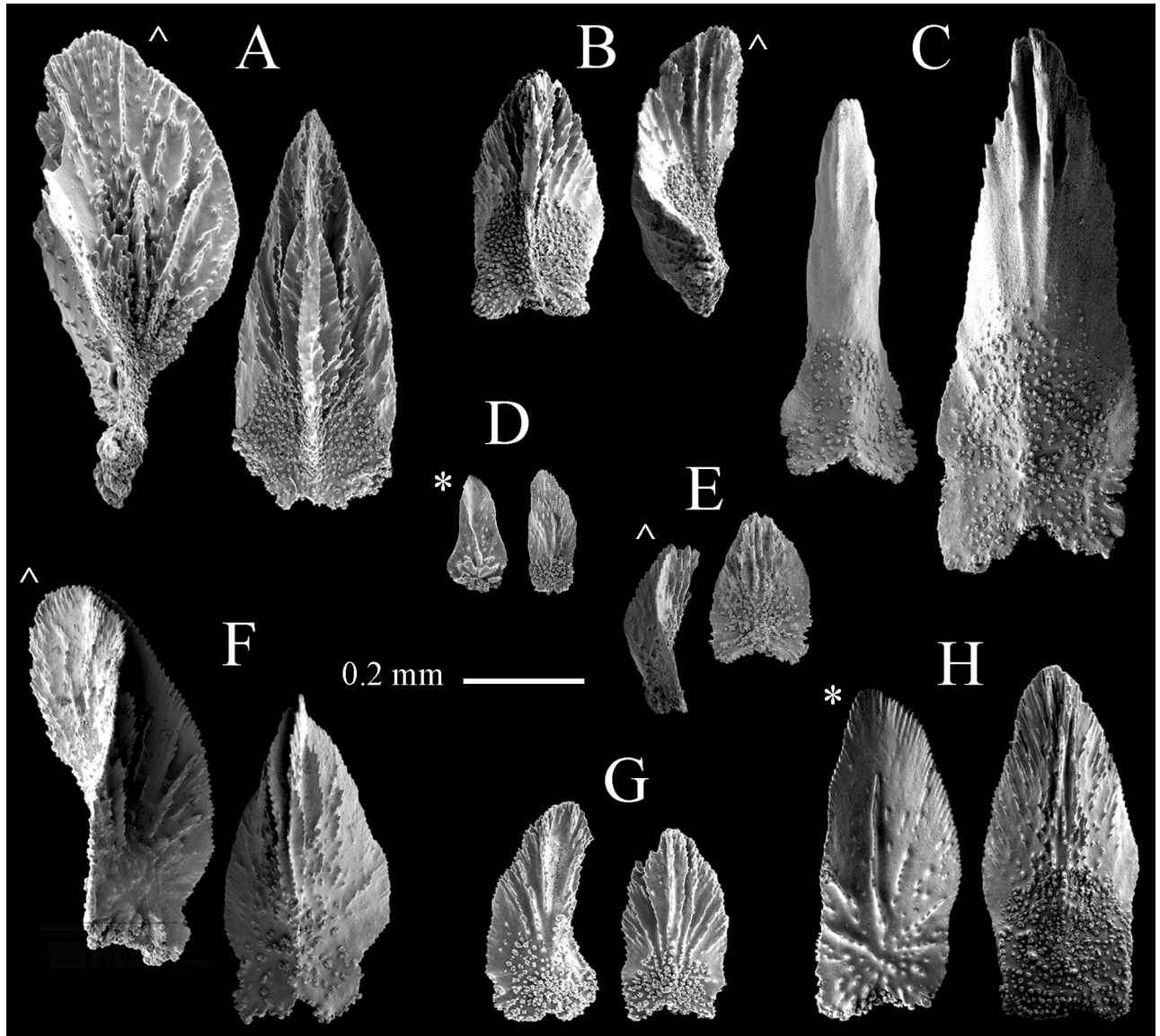


FIG. 18. – Comparison of opercular scales from species included in subgenus *Epithouarella*: A, *Thouarella viridis* Zapata-Guardiola and López-González, 2010, holotype (ZIZMH C11744); B, *T. regularis* (Wright and Studer, 1889), lectotype (BMNH 1889.5.27.60); C, *T. dispersa* Kükenthal, 1912, holotype (ZMB Cni 5468); D, *T. vitjaz* sp.nov., type IORAS IV-9-Alc-010-002); E, *T. crenelata* Kükenthal, 1907, syntype (ZMB Cni 6081); F, *T. grandiflora* Kükenthal, 1912, holotype (MPUW 44); G, *T. chilensis* Kükenthal, 1908, type fragment (ZMB Cni 6079); H, *T. affinis* Wright and Studer, 1889, holotype (BMNH 1889.5.27.44). [*outer surface view; ^ lateral view].

As a consequence, the most plausible proposal now is to assign the species *Thouarella dispersa* and *T. grandiflora*, which were originally described by Kükenthal in 1912 but later transferred by him to *Amphilaphis* (as a subgenus of *Thouarella*) in 1915, to the genus *Thouarella*. The reduction in size and number of the adaxial body scales (Fig. 12C, 16B), and the presence of 8 keeled marginal scales (Figs. 9B, 13B, 17B) aligned with the operculars and folding over them (Figs. 8B, 11B), are characters supporting the inclusion of both *Thouarella dispersa*, *T. grandiflora* (Kükenthal 1912: 307) and *T. vitjaz* n. sp. in the genus *Thouarella*. Furthermore, the lack of a well-developed thorn on the marginal scales allows us to include these species in the subgenus *Epithouarella*.

Although there are currently 4 species included in the subgenus *Epithouarella*: *Thouarella affinis* Wright and Studer, 1889, *T. crenelata* Kükenthal, 1907, *T. chilensis* Kükenthal, 1908 and *T. viridis* Zapata-Guardiola and López-González, 2010, the species here re-described are clearly distinguishable.

Considering the few data provided by Pasternak (1981), *Thouarella vitjaz* n. sp. seems to be ramified in one plane. In the subgenus *Epithouarella*, only *T. regularis* and *T. vitjaz* n. sp. have colonies in one plane, while the other species in the subgenus have bottle-brush colonies. However, the polyps of *T. regularis* are placed alternately in the branchlets, while they are in pairs in the new species. Other differences can also be

found in the structure of the sclerites (see Figs. 18B, D and 19B, D in this paper), and the development of the keel on the opercular and marginals is especially noticeable.

Thouarella dispersa has 5 scales in each longitudinal abaxial row, while the other *Epithouarella* species have between 6 and 10 scales. Furthermore, *T. dispersa* has a low density of polyps per cm, which is similar only to *T. affinis*, but the opercular and marginal scales of the two species are completely different. In *T. dispersa* the operculars are larger, their inner distal surface is quite smooth and the proximal warts are distant (Fig. 18C), while in *T. affinis* the operculars are smaller, their distal inner surface is covered by prickly granules and the proximal warts are closer (Fig. 18H). The marginal scales of *T. dispersa* are triangular-shaped with a strong multi-keel

on the inner surface (Fig. 19C), while in *T. affinis* the marginals are rhomboidal-shaped with a thin projection like a small thorn (Fig. 19H).

Thouarella grandiflora is comparable with *T. viridis* because the two species share some characters, such as the number of scales in the abaxial row, the strong keel present on the inner surface of the opercular scales and the similar polyp size. However, the two species are distinguished by the size of the opercular scales, larger in *T. viridis* than in *T. grandiflora*; by the density of polyps on the branchlets, 14–15 polyps per cm in *T. viridis* and only 8 per cm in *T. grandiflora*; and by the ornamentation on the inner surface of the scales (in *T. viridis* the proximal warts are more crowded (Fig. 18A) than in *T. grandiflora* (Fig. 18F)). In addition, the ornamentation on their marginal scales is also different, those of *T. viridis* having a small blunt

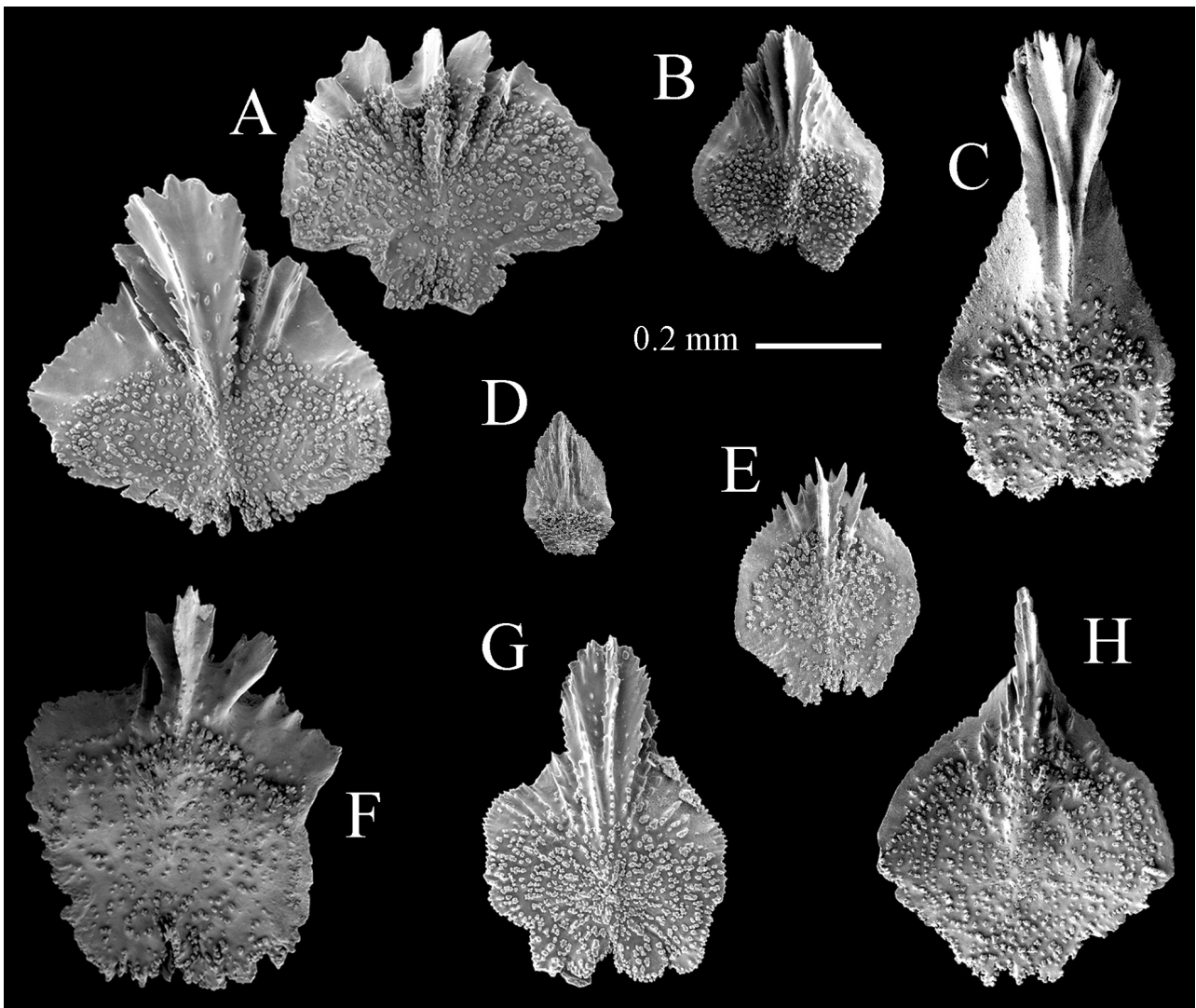


Fig. 19. – Comparison of marginal scales, inner surface view, from species included in subgenus *Epithouarella*: A, *Thouarella viridis* Zapata-Guardiola and López-González, 2010, holotype (ZIZMH C11744); B, *T. regularis* (Wright and Studer, 1889), lectotype (BMNH 1889.5.27.60); C, *T. dispersa* Kükenthal, 1912, holotype (ZMB Cni 5468); D, *T. vitjaz* sp.nov., type (IORAS IV-9-Alc-010-002); E, *T. crenelata* Kükenthal, 1907, syntype (ZMB Cni 6081); F, *T. grandiflora* Kükenthal, 1912, holotype (MPUW 44); G, *T. chilensis* Kükenthal, 1908, type fragment (ZMB Cni 6079); H, *T. affinis* Wright and Studer, 1889, holotype (BMNH 1889.5.27.44). [*outer surface view].

spine or short medial ridges (Fig. 19A) and those of *T. grandiflora* having a multi-keel (Fig. 19F).

Thouarella regularis should be compared with *T. crenelata* and *T. chilensis* as they have 8 scales in the abaxial row and an incipient keel consisting of numerous longitudinal ridges (Fig. 18B,E,G) on the inner surface of the opercular scales. However, the operculars are larger in *T. regularis* than in the other 2 species. Furthermore, the marginal scales in *T. chilensis* are strongly ornamented and larger than in *T. crenelata* and *T. regularis* (Fig. 19B,E,G); the tendency in *T. crenelata* is to have fine longitudinal apical crests, whereas in *T. regularis* it is to have a prominent distal keel with lateral ridges. In addition, in *T. crenelata* the polyps are more perpendicular to the branchlets than in *T. regularis*, where they are inclined upward to the branchlets (compare Kükenthal 1919: Fig. 70 and Fig. 3A, present work).

However, in the revision of genus *Thouarella* by M. Taylor *et al.* (submitted, pers. comm.) the different subgenera will surely be reconsidered.

Thouarella biserialis (Nutting, 1908) was originally described in the genus *Amphilaphis* but immediately afterwards it was included in the genus *Thouarella* by Kinoshita (1908a). In the recent generic revision of Primnoidae by Cairns and Bayer (2009), it was again placed in the genus *Amphilaphis*. However, Cairns placed it back in the genus *Thouarella* in 2010. During this present work we also had the opportunity to examine the type of *Thouarella biserialis* (Nutting, 1908), which consists of just one small and poorly preserved branch fragment, and this led us to agree with Kinoshita (1908a) and Cairns (2010) in the re-assignment of this species to the genus *Thouarella* because of the reduction of its adaxial body scales and the presence of a keel on marginal scales that fold over the operculars. *Thouarella biserialis* seems to have a dichotomous branching pattern, which in combination with the arrangement of polyps in pairs places the species in the subgenus *Diplocalyptra* Kinoshita, 1908, as suggested by Cairns (2010). Kinoshita (1908b: 60) already noticed the similarities of *Thouarella biserialis* with those attributable to *Diplocalyptra* species and thus including it in this subgenus. He pointed out that *Thouarella coronata* (Kinoshita, 1908b) and *T. parva* (Kinoshita, 1908b) are clearly differentiated from *T. biserialis* by the arrangement and orientation of the polyps (in whorls of 3 or 4 and perpendicular in *T. coronata*, but in pairs and curved upward in *T. biserialis*) and by the total number of longitudinal body row scales (these being 8 in *T. parva* and 4 in *T. biserialis*). Moreover, the density of whorls or pairs per centimetre is also different in the two species, being 7 in *T. coronata*, and 5 in *T. biserialis*.

Because of the unknown location of the type material of *Thouarella parva*, we can only compare it with *T. biserialis* through the original description. Kinoshita (1908b) distinguished the two species by the lower

number of longitudinal rows of body wall scales in *T. biserialis*. In the original description of *T. biserialis* (Nutting, 1908) we can read “*The calyx walls are covered with... and usually 4 longitudinal rows*”. However, a study of the type material reveals the presence of 8 longitudinal rows of scales. This contradiction can be explained by the fact that Nutting only counted the abaxial rows and did not include the 2 inner-laterals and the 2 adaxial rows. Furthermore, after comparing the description of *T. parva* with the type of *T. biserialis* we have not been able to find any useful character to distinguish between the species. Since no additional material attributable to *T. parva* was available we prefer not to propose any synonymy.

Genus *Plumarella* Gray, 1870

Diagnosis. Primnoidae, usually with a uniplanar colony shape and alternately pinnate branching, may also be dichotomously branched and bottlebrush in shape. Polyps placed in an alternate biserial arrangement, in pairs or without order on all sides of branchlets. Polyps completely covered by 8 longitudinal rows of body scales, adaxials may be reduced in number and size. Eight opercular aligned with the 8 marginal scales without folding over them. Marginals variable in shape, their distal edges being spinose, pointed, or straight; inner surface of marginals may be smooth, ridged, or spiny but never keeled.

Subgenus *Faxiella* n. subgen.

Diagnosis. *Plumarella* with a planar colony shape and pinnate branching. Cylindrical-shaped, elongate polyps placed in pairs and curved upward toward the stem and branchlets. Opercular and marginal scales with longitudinal distal ridges. Adaxials smaller and slightly disorganized but always present.

Etymology. The subgeneric name comes from *fax*, the Latin word for torch, in reference to the shape of the polyps. Gender: feminine.

Type species. *Amphilaphis abietina* Studer, 1894, here designated.

Plumarella (Faxiella) abietina (Studer, 1894) n. comb. (Figs. 20-22)

Amphilaphis abietina Studer, 1894: 65. Meneking 1905: 255-260; pl. 8, Fig. 7-8; pl. 9, Fig. 17-20. Versluys 1906: 22. Cairns and Bayer 2009: 28.

Thouarella (Amphilaphis) abietina, Kükenthal, 1915: 149. Kükenthal 1919: 410-411. Kükenthal 1924: 290. not *Thouarella abietina*, Pasternak, 1981: 49-50. [= *Thouarella vitjaz* n. sp.]

Examined material. Holotype: MCZ 4802, Albatross Expedition, stn Alb-3399, 1°7'N 81°4'W, west coast of central America to the Galapagos, 3181 m depth, 1891.

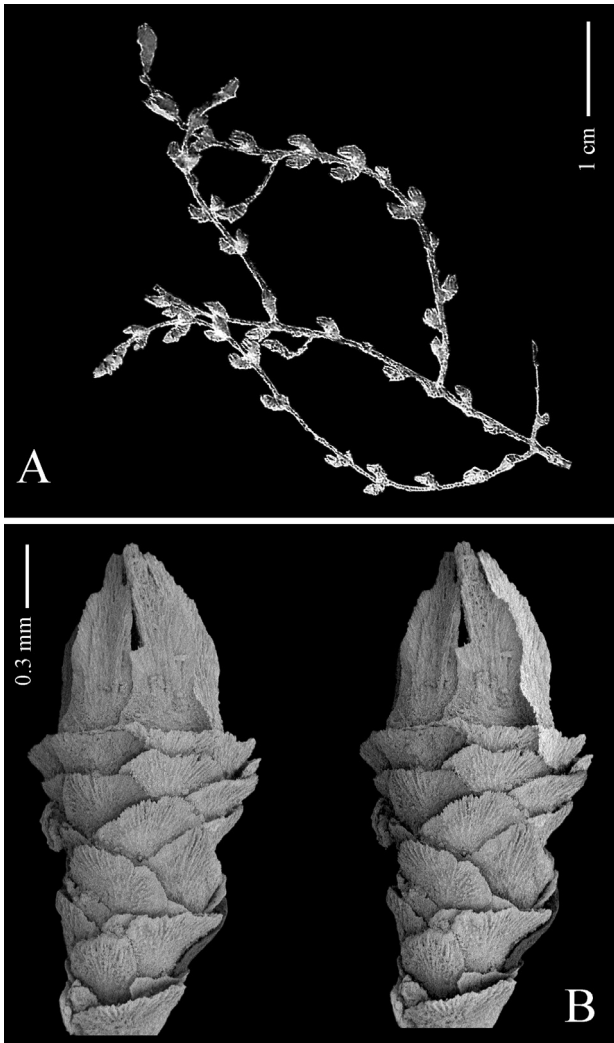


FIG. 20. – *Plumarella (Faxiella) abietina* (Studer, 1894) n. comb., holotype (MCZ 4802): A, fragment of colony from Menneking, 1905: pl. 8, Fig. 7; B, polyp on abaxial view, stereo pair. [Photo: Stephen D. Cairns, NMNH, Washington].

Description of the holotype. Fragment of colony ramified in one plane (Fig. 20A) 6 cm in high and 3 cm wide; ramified up to the third order, with slender branchlets up to 5 cm long. Axis without holdfast, with a basal diameter of 1 mm. The polyps are curved upward to the stem and branchlets, placed in pairs and sparsely arranged with 2-3 mm between them; 2 pairs of polyps per cm. They are relatively elongate (Fig. 20B, 21A), cylindrical, up to 2.6 mm tall and 1.0-1.2 mm in diameter, with a high conical, well-developed operculum. Polyp body with 8 rows of scales, 6 in each abaxial row (Fig. 20B) and 5-6 smaller and slightly disorganized scales in each adaxial row (Fig. 21A).

Eight opercular scales (Fig. 21B, 22A), 0.74-1.22×0.24-0.46 mm, shaped like elongated isosceles triangles. Proximal inner surface tuberculate covering up to half of the length; distal part with numerous longitudinal ridges. Outer surface granular and forming ridges distally. Free margin finely serrated.

Marginal and body scales (Fig. 22B) roughly square to oval-shaped, 0.31-0.64 mm maximum length. Inner surface almost completely tuberculate, outer surface granular, with distal longitudinal ridges. Free margin finely serrated. Scales decreasing in size from abaxial to adaxial side. Eight marginal scales aligned with opercular scales without folding over them; slightly disorganized on the adaxial side.

Geographical and bathymetrical distribution. *Plumarella (Faxiella) abietina* is only known from the west coast of central America to the Galapagos, at a depth of 3181 m.

Remarks. According to the treatment of Cairns and Bayer (2009), a number of characters would place the new species closer to *Acanthoprinnia* Cairns and Bayer, 2004 and *Plumarella* Gray, 1870: the pinnately colony branching pattern, the disposition of the polyps not being adnate to the coenenchyme, the arrangement of the body scales being complete rows on all sides of the polyps, the marginal scales not folding over the bases of opercular scales, the number of marginal scales and their alignment with the operculars.

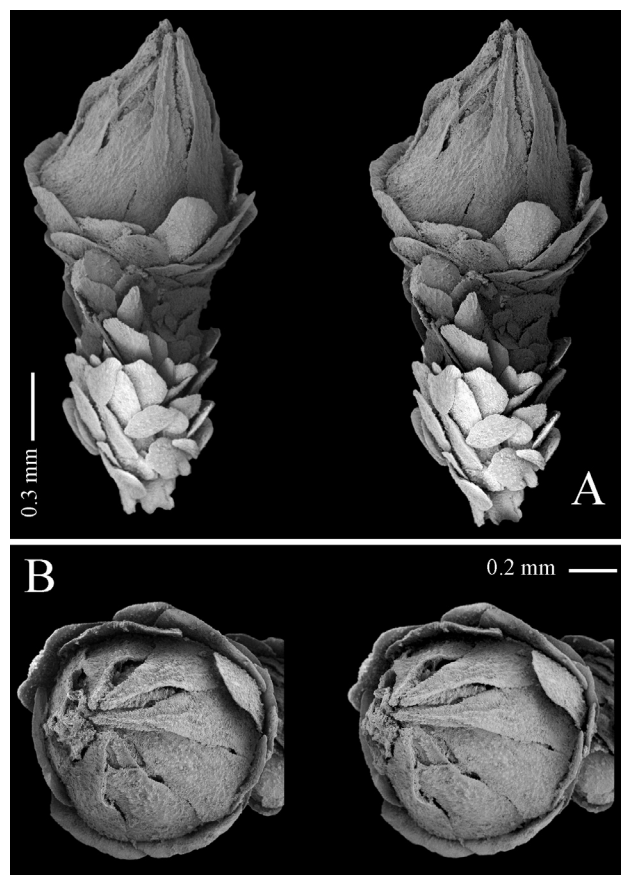


FIG. 21. – *Plumarella (Faxiella) abietina* (Studer, 1894) n. comb., holotype (MCZ 4802): A, polyp on adaxial view, stereo pair; B, polyp on oral view, stereo pair. [Photo: Stephen D. Cairns, NMNH, Washington].

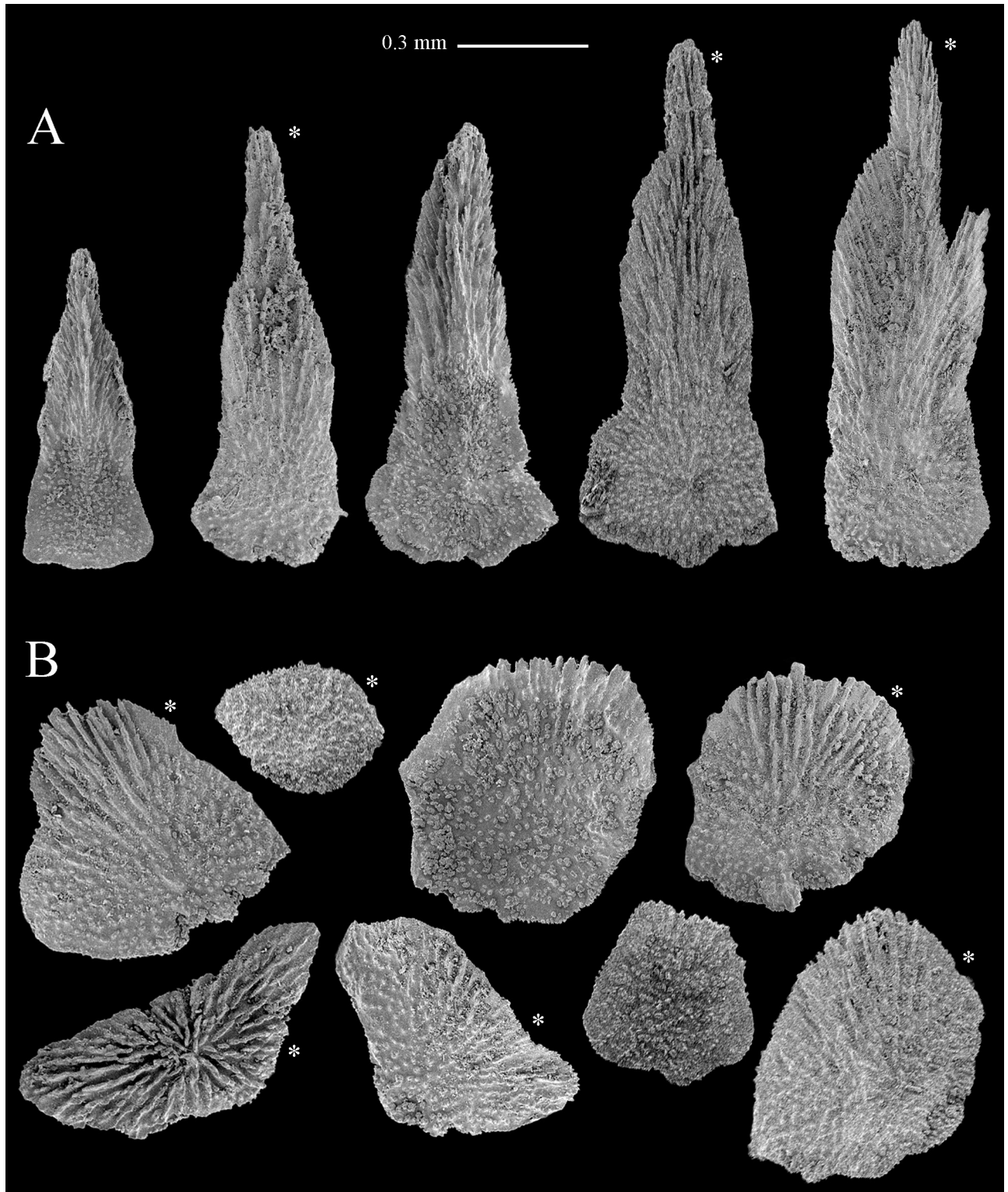


FIG. 22. – *Plumarella (Faxiella) abietina* (Studer, 1894) n. comb., holotype (MCZ 4802): A, opercular scales; B, marginal and body scales. [*outer surface view; photo: Stephen D. Cairns, NMNH, Washington].

However, the main character of genus *Acanthoprinnia* and thus to distinguish from the new subgenus, sclerites with a smooth inner surface and pectinate margins are absent in *Faxiella* n. subgen.

Although there is a set of characters supporting the inclusion of the new species in the genus *Plumarella*, we have had to enlarge the limits of the genus to include the arrangement of polyps in pairs. Subsequently,

following Cairns (2011), who splits *Plumarella* into 2 subgenera depending on the arrangement of polyps, we propose *Faxiella* as a new subgenus to accommodate species with paired polyps.

Genus *Primnocapsa* n. gen.

Diagnosis. Primnoidae with a planar colony shape and dichotomously branched. Short polyps club-shaped, slightly curved upward to stem and branchlets, singly placed and arranged in spirals. Eight opercular scales with the inner surface keeled and with 2 irregular basal mounds. Eight marginal scales with strong radial ridges on the distal inner surface, offset from the opercular scales. Polyps completely covered by 8 longitudinal rows of body scales reduced in number

and size from distal to basal part. Body scales reduced adaxially but always present. Coenenchyme with a single layer of round shaped scales with a central bulk on the inner surface.

Etymology. The generic name combines *primno-* a common prefix in reference to the gorgonian family, and *-capsa*, a Latin word meaning box, in reference to the perfect closed operculum like the capsule fruits of some herbaceous plant groups. Gender: feminine.

Type species. *Amphilaphis plumacea* Thomson and Mackinnon, 1911, here designated.

Remarks. The type material was initially described by Thomson and Mackinnon (1911) as a new species

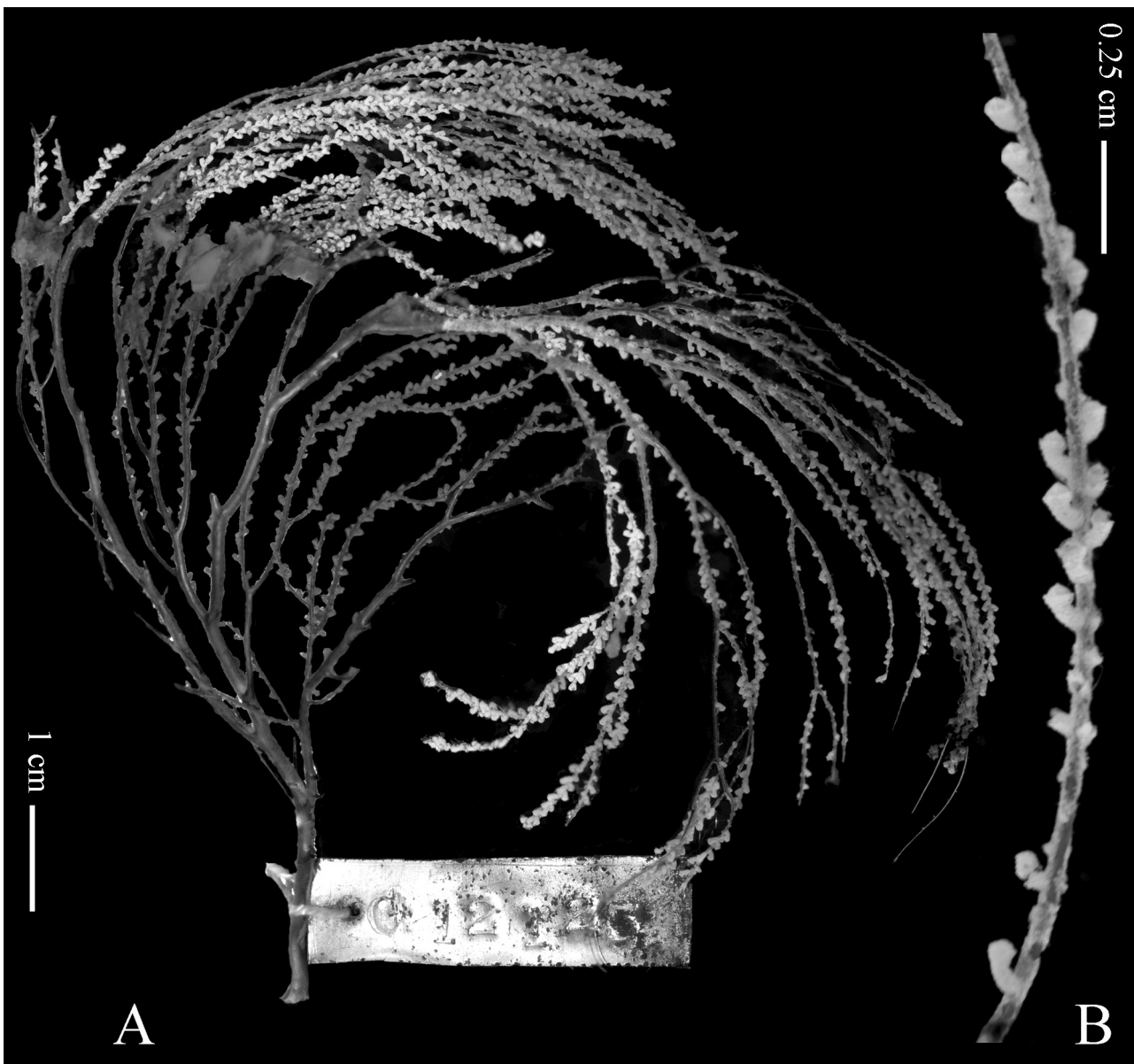


FIG. 23. – *Primnocapsa plumacea* (Thomson and Mackinnon, 1911) n. comb., holotype (AM G12123): A, whole colony; B, detail of branchlet.

of the genus *Amphilaphis*. These authors showed the differences between *Amphilaphis plumacea* and the species already included in that genus (Thomson and Mackinnon 1911: 681). However, they did not explain why the new species should be included in the genus *Amphilaphis*. Taking into account that the name *Amphilaphis* is not available (see remarks on *Thouarella regularis* in this work) and the characters observed in the re-examined type material, the species cannot be placed in any of the currently described primnoid genera, so a new genus, *Prinnocapsa* n. gen., is hereby proposed for it.

Although we include some of the previous *Amphilaphis* species in the genus *Thouarella*, *Prinnocapsa plumacea* n. comb. cannot be included for the following reasons: The opercular scales are not arranged in 2 alternate cycles, marginal scales are offset from the operculars and do not fold over them.

The presence of dichotomously branched colonies, polyps not adnate to the coenecyme, 8 longitudinal rows of sclerites in the polyp, and marginal scales not folding over the operculars, allies the new primnoid genus *Prinnocapsa* n. gen. with the genera *Plumarella* Gray, 1870, and *Acanthoprinnia* Cairns and Bayer, 2004. *Prinnocapsa* n. gen. differs from *Plumarella* and *Acanthoprinnia*, however, because of the presence of a keel on the inner surface of the opercular scales and the different arrangement of polyps on the branchlets, these being in spirals in *Prinnocapsa* n. gen. Other differences between *Prinnocapsa* n. gen., *Plumarella* and *Acanthoprinnia* can be found in the inner proximal structure and the general inner and outer ornamentation of the opercular sclerites (see Fig. 25 in this paper, and Cairns and Bayer 2009: Fig. 11).

As in the genus *Parastenella* Versluys, 1906, the genus *Prinnocapsa* n. gen. has a dichotomous branching pattern and its 8 opercular scales have a strong keel on their inner surface and are offset from the marginal scales (Versluys 1906: 39, Cairns 2007: 518). However, both genera differ in the orientation of the polyps on the branchlets [perpendicular or downward in *Parastenella* (see Cairns 2007: 518) and upward in *Prinnocapsa* n. gen. (Fig. 23B)], the shape of the marginal scales [flute-shaped apically in the former (Cairns 2007: 518) and fan-shaped in the latter (Fig. 25B)], and the distinct basal structure of the opercular scales [which have 2 irregular mounds in *Prinnocapsa* n. gen. (Fig. 25A)]. The presence of these irregular mounds on the opercular scales makes it necessary to compare the *Prinnocapsa* n. gen. with the genus *Pseudoplumarella* Kükenthal, 1915, which was, until now, the only known primnoid genus with this unique opercular locking mechanism (Cairns and Bayer 2009: 48). However, in *Prinnocapsa* n. gen., the branching pattern is dichotomous and the polyps are inclined to the branchlets and not adnate (Fig. 23), the number of marginal scales is 8, the number of rows of scales on the abaxial side is 3 (Fig. 24A), and adaxial body scales are present (Fig. 24C). In contrast for *Pseudoplumarel-*

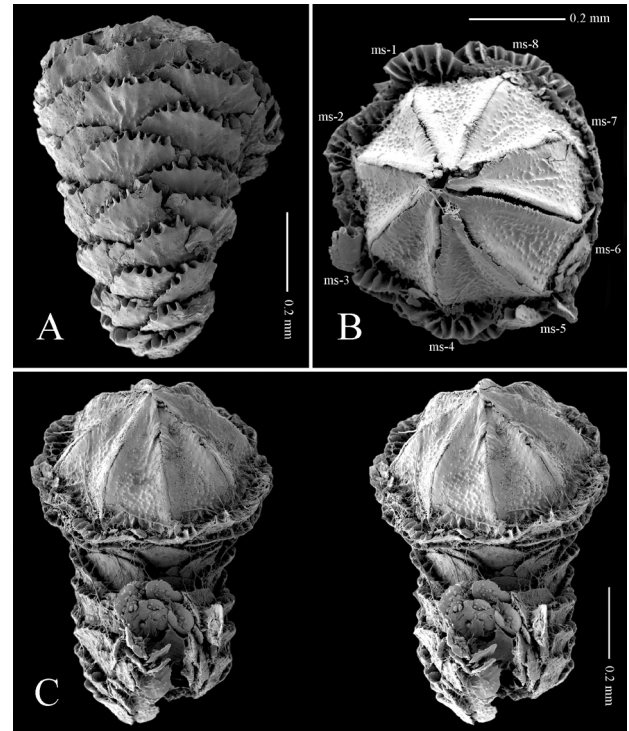


FIG. 24. – *Prinnocapsa plumacea* (Thomson and Mackinnon, 1911) n. comb., holotype (AM G12123): A, polyp on abaxial view; B, polyp on oral view; C, polyp on adaxial view, stereo pair. [ms= marginal scales].

la, the branching pattern is pinnate (see pl. 76-79 in Thomson and Mackinnon 1911, Bayer 1981: 622, Fig. 1, Cairns and Bayer 2009: 48), polyps are adnate to the branchlets (see Fig. 29b in Cairns and Bayer 2009), the number of marginal scales is 5, the polyps only have one longitudinal row on the abaxial side, and the adaxial body scales below the marginals are absent (Cairns and Bayer 2009: 48).

Prinnocapsa plumacea

(Thomson and Mackinnon, 1911) n. comb.
(Figs. 23-25)

Amphilaphis plumacea Thomson and Mackinnon, 1911: 680-681; pl. 65, Fig. 3; pl. 68, Fig. 3; pl. 74. Cairns and Bayer 2009: 28.
Thouarella (Amphilaphis) plumacea, Kükenthal, 1915: 149.
Kükenthal 1919: 414. Kükenthal 1924: 291-292; text Fig. 163.

Examined material. Holotype: AM G12123, Thetis Expedition, "11 miles E. by N. of Barrenjoey", 54.6-73.12 m depth.

Description of the holotype. Planar colony, dichotomously branched (Fig. 23A), 14 cm high and 5 cm wide, internodes about 7-21 mm long and terminal branchlets up to 29 mm. Axis dark brown, stiff, hold-fast present. Basal axis diameter 2 mm. Polyps slightly curved upward to stem and branchlets (Fig. 23B), singly placed, and arranged in spirals, 11-15 polyps per cm. They are relatively short (Fig. 24), club-shaped, up to 1.2 mm tall and 0.36-0.64 mm in diameter, with a conical operculum. Polyp body with 8 rows of

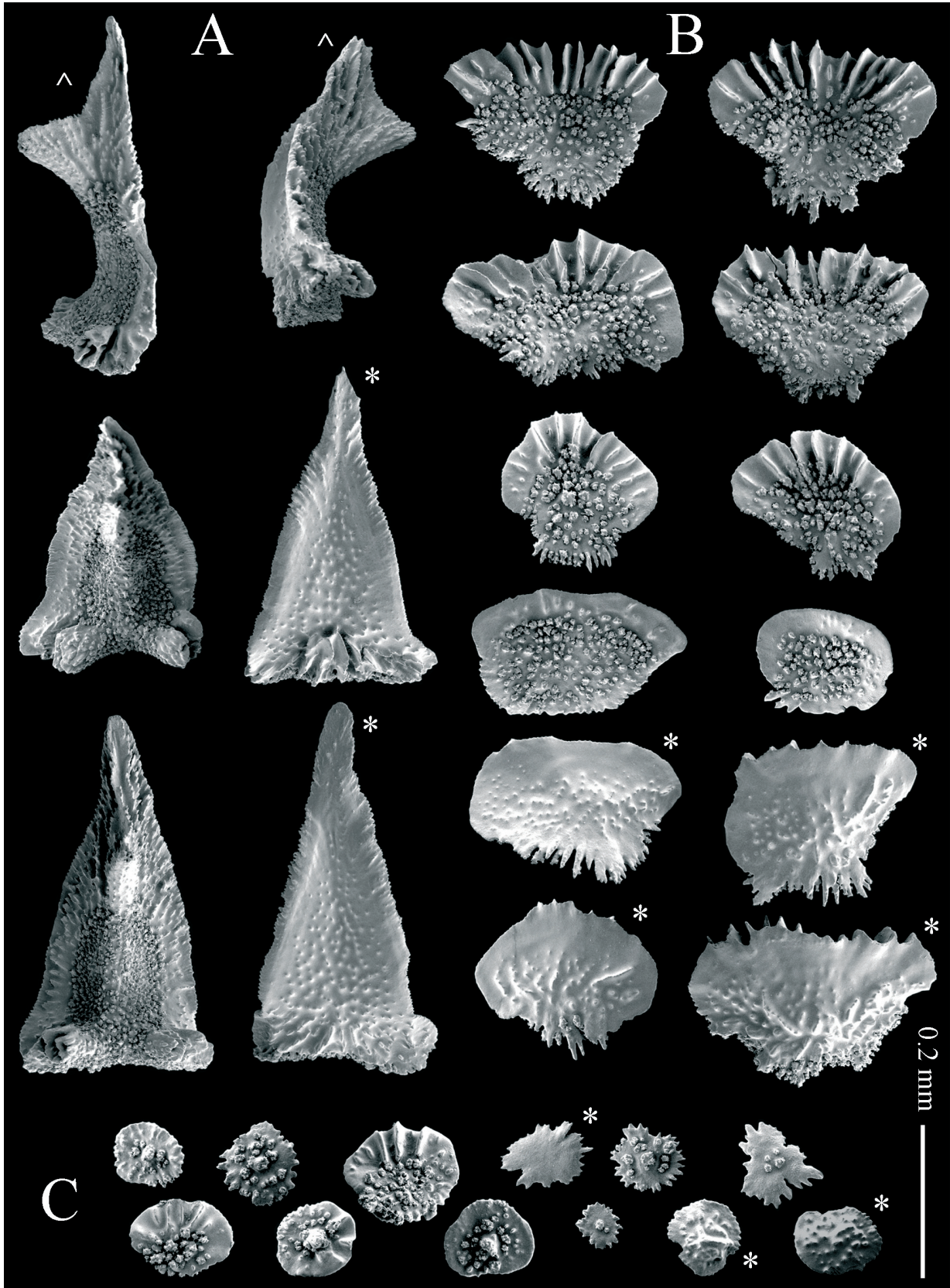


FIG. 25. – *Prinnocapsa plumacea* (Thomson and Mackinnon, 1911) n. comb., holotype (AM G12123): A, opercular scales; B, marginal and body scales; C, coenenchymal sclerites. [* outer surface view; ^ lateral view].

scales that are reduced in size and number adaxially. Each abaxial row has 8-12 scales (Fig. 24A) and each adaxial row has 2-3 scales (Fig. 24C). Marginal scales offset from opercular scales (Fig. 24B).

Eight opercular scales (Fig. 24B, 25A), 0.31-0.48×0.22-0.28 mm, isosceles triangle-shaped with an acute apex. Each vertex of the proximal inner surface has an irregular mound articulating with the corresponding mound of adjacent operculars; distal inner surface with a strong prominent keel. Inner surface of free lateral borders and the distal keel with granules forming ridges; remaining inner surface tuberculate. Outer surface of the lateral free borders grooved or smooth, remaining outer surface granular. Free margin finely serrated.

Abaxial marginals and body scales (Fig. 25B) fan-shaped, 0.11-0.25×0.14-0.33 mm with the proximal inner surface tuberculate covering at least 75% of the scale and strong, distal, radial ridges; adaxials without ridges. Outer surface granular. Free margin finely serrated, basal margin with digitate processes. Scales decrease in number and size from abaxial to adaxial side and from distal to basal portion. The 8 marginal scales offset from opercular scales.

Coenenchymal sclerites (Fig. 25C) round in shape, 0.06-0.15 mm in maximum diameter. Inner surface tuberculate with a central bulk, edge quite smooth or ridged, outer surface from quite smooth to granular. Margin quite smooth, or with digitate processes.

Geographical and bathymetrical distribution. *Prinnocapsa plumacea* is only known from the type locality off Barrenjoey, Australia (Fig. 1), between 54.6 and 73.12 m depth.

DISCUSSION

Taxonomic remarks

The family Primnoidae is one of the richest in genera and species (Bayer 1998, Cairns and Bayer 2009) and, with the results of the present contribution, currently includes 40 genera and more than 240 species. The first of these species was described in 1763 [*Prinnocapsa resedaeformis typica* (Günerus, 1763)] and since then the taxonomy of primnoids has increased considerably. Taxonomists are not only focused on describing new species, they are also constantly revising the more unclear genera (*Mirostenella* in Zapata-Guardiola and López-González submitted, *Thouarella* in Taylor *et al.* submitted). Thanks to these efforts the technology used to describe and identify species has improved, and because the level of precision is higher the assignment of the species to genera is being modified (Cairns and Bayer 2009, present work). The revision and the consequent reassignment of the species previously included in the genus *Amphilaphis* into an already existing genera (*Thouarella* and *Plumarella*) or into a new one (*Prinnocapsa*) make the current classification of

the family Primnoidae more understandable, although we need more comprehensive contributions to find a consensus regarding the characters used to cluster species and genera. Some taxonomic characters (e.g. the branching pattern of the colony or the arrangement of polyps on branchlets) have been commonly used to distinguish not only between genera such as *Plumarella* and *Parastenella* (Bayer 1981, Cairns and Bayer 2009), but also between species of the same genus as in the genus *Thouarella* (Kükenthal 1924, Cairns and Bayer 2009). Further morphological and molecular studies on species of the family could help to identify generic and specific morphological characters, as well as a number of possible homoplasies, their evolution through the family Primnoidae and the establishment of relationships among the different taxa.

Biogeography remarks. The 4 *Thouarella* species here reported are included in the subgenus *Epithouarella*. Recently, Cairns and Bayer (2009) established the geographical and bathymetrical distribution of *Epithouarella* species restricted to Antarctic and sub-Antarctic waters from 106 to 686 m depth. With the new inclusions, the distribution of *Epithouarella* is found to now involve the mid-Pacific Ocean with records up to 6400 m depth.

The different collection localities of the species of *Thouarella* studied confirm the presence of the genus in places like Gauss Station, where only one species, *T. longispinosa* Kükenthal, 1912 was previously reported, and Tristan da Cunha, where only *T. affinis* was previously recorded. Furthermore, the distribution of the species of *Thouarella* has also been extended, with *T. vitjaz* being the first record in the mid-Pacific Ocean (between Marshall and Johnston Atoll and Hawaiian archipelago). On a bathymetric scale, the maximum depth for a *Thouarella* species has been attributed to the holotype material of *T. flabellata* Kükenthal, 1907 with 1644 m (Kükenthal 1907: 208), but the new species *T. vitjaz* widely exceeds that finding, reaching 6400 m in depth. Additionally, the bathymetric range at some localities has been extended, as for Tristan da Cunha where *Thouarella* is currently known to occur from 130 to 660 m depth, and for Gauss Station, where the depth increases to 2450 m.

The new species *Thouarella vitjaz* enlarges the geographical and bathymetrical distribution of the family Primnoidae at 6400 m depth, being the deepest known primnoid and octocoral, exceeding the deepest pennatulacean *Umbellula* found at 6100 m depth (Williams 1995, 2011). Though the species here reported have been included in different genera, they had already been included in this family. The family Primnoidae, which includes 40 genera (15 of them monotypic) and 244 species, is found in all oceans, even the polar ones. Only 3 primnoid genera (*Narella* Gray, 1870, *Plumarella* and *Thouarella*) have a worldwide distribution (Atlantic, Pacific, Indian, Subarctic and Southern oceans), 2 of them being also the most speciose genera (*Thouarella* and *Narella*, with 40 and

38 species respectively). The biogeographical region with the greatest number of primnoid genera is the Southern Ocean, with 24 (60% of the total), 9 of them being monotypic, closely followed by the Pacific and Atlantic oceans with 23 and 14 genera respectively. Further to them we find the sub-Arctic with 8 genera and the Indian Ocean with only 5 genera recorded. However, the major number of species is found in the Pacific Ocean, with almost half of the primnoid species currently accepted (117), while in the Southern Ocean we only find a quarter of the total number of species. Despite this, the Southern Ocean is characterized by a great endemicity of primnoid genera (63%), doubling the percentage found in the Pacific Ocean (30%). In the other regions, endemicity is lower or does not exist, as in the sub-Arctic and Indian oceans.

To summarize, the family Primnoidae shows a high diversity in the Southern Ocean, with a greater grade of endemism in this region than in any other. This fact agrees with the patterns reported for other invertebrate groups (Arntz *et al.* 1997, Rodríguez *et al.* 2007). To explain this high diversity and level of endemism in Antarctic waters and surrounding areas, Clarke and Crame (1992) suggested that the climatic fluctuations during a long evolutionary history of the region have led to benthic fauna being concentrated at the poles, forming Antarctic ecosystems that are comparable with those in tropical and temperate regions. Moreover, there is evidence from mollusc fossil discoveries (Crame 1999) and phylogenetic variations in fishes (Bargelloni *et al.* 2000) of the dispersion and evolution of the Antarctic species being displaced outwards by gradations in diversity. These facts have caused Antarctica to be proposed as a marine centre of diversity (Briggs 2003). In this way, Antarctica will produce a regular pool of successful ancestral species capable of spreading to the nearest areas and becoming widely distributed outward in contrast to the derived species that will form the local populations (Briggs 2003). Strong similarities have been reported between South America and Antarctic regions for some invertebrate taxa (Rodríguez *et al.* 2007, Griffiths *et al.* 2009), but the direction of the linkage is uncertain. Antarctica has also been proposed as an immigrant receptor for opportunistic colonists, being able to combine both behaviours (drain and donor) at the same time (Briggs 2003, Griffiths *et al.* 2009). Primnoids are highly represented in the Southern Ocean and further biogeographical and population genetic analyses are required to confirm and define those connections, and to confirm Antarctica as a hotspot for primnoid biodiversity.

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