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New sciaphilic plakinids (Porifera, Homoscleromorpha) from the Central-Western Pacific

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Abstract

The sponge class Homoscleromorpha is a key model for the evolutionary biology of the Metazoa but its diversity remains poorly known. Here we describe six new species of the homoscleromorph family Plakinidae found in shaded habitats (submarine caves, tunnels and overhangs) of New Caledonia and Marquesas Islands, Central-Western Pacific. The new species belong to four genera: *Corticium* (*Corticium vaceleti* **sp. nov.**), *Plakina* (*Plakina finispinata* **sp. nov.**), *Plakinastrella (Plakinastrella osculifera* **sp. nov.**, *Plakinastrella nicoleae* **sp. nov.** and *Plakinastrella pseudolopha* **sp. nov.**), and *Plakortis* (*Plakortis ruetzleri* **sp. nov.**). *Plakinastrella pseudolopha* **sp. nov.** has a novel spicule type called here 'pseudolophose spicules'. The diversity of Homoscleromorpha is raised to 50 species in the Pacific Ocean and 120 spp. worldwide.

Key words: Homosclerophorida, morphology, new species, taxonomy, submarine caves, Pacific Ocean

Introduction

The class Homoscleromorpha is an intriguing group of Porifera which shares several characters with higher Metazoa that are absent in other sponges, such as a basement membrane made of type IV collagen and asynchronous spermatogenesis within spermatocysts (Boute *et al.* 1996; Ereskovsky 2010). The presence of acrosome in spermatozoa is shared with higher Metazoa but also with only few other sponges, which have a different ultrastructure (Bacetti *et al.* 1986; Riesgo & Maldonado 2009). These unique traits within the Porifera led to propose the Homoscleromorpha as a key model for studying the evolution of the Metazoa (Ereskovsky *et al.* 2009a; Nielsen 2008). Despite the relevance of this sponge class for evolutionary biology, its diversity is still poorly known. With only 114 species currently valid, the Homoscleromorpha is the smallest of the four classes of Porifera (van Soest *et al.* 2018). This low number possibly reflects the paucity of taxonomic studies and the difficulty of spotting and collecting them in their favourite cryptic habitats (submarine caves, overhangs, and the undersides of boulders and corals; e.g., Muricy *et al.* 1998; Muricy & Díaz 2002; Ereskovsky *et al.* 2009b; Gerovasileiou & Voultsiadou 2012; Ruiz *et al.* 2015; Lage *et al.* 2018). A large effort recently deployed to explore such habitats has allowed a significant improvement in our knowledge of Homoscleromorpha diversity. For instance, 16 new species and two new genera were described from 2013 to 2018 only in the Tropical Western Atlantic, what represents approximately 14% of the total known diversity of the Class (Domingos *et al.* 2016; Vicente *et al.* 2016; Ruiz *et al.* 2017; Pérez & Ruiz 2018).

The diversity and distribution of Homoscleromorpha species were recently revised in the Mediterranean (25 species; Ereskovsky *et al.* 2009b; Lage *et al.* 2018) and in the Tropical Western Atlantic (33 species; Ereskovsky *et al.* 2014; Domingos *et al.* 2016; Vicente *et al.* 2016; Ruiz *et al.* 2017; Pérez & Ruiz 2018). The Pacific Ocean is the largest of the world's oceans and includes several biogeographical provinces, different ecoregions (Spalding *et al.* 2007), and innumerable remote islands, but it has been comparatively less studied than the Mediterranean and the Caribbean. To date, 44 species of Homoscleromorpha were reported from the Pacific Ocean (e.g. Desqueyroux-

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Faúndez & van Soest 1997; Bergquist & Kelly 2004; Muricy & Pearse 2004; Cruz-Barraza & Carballo 2005; Lehnert *et al.* 2005; Ereskovsky 2006; Ereskovsky *et al.* 2009c; van Soest *et al.* 2011, 2012; Cruz-Barraza *et al.* 2014; Ruiz *et al.* 2015; Ereskovsky *et al.* 2017). *Plakina* is the most diverse genus in the Pacific with 13 species, followed by *Plakortis* with 12 species (e.g. de Laubenfels 1951, 1954a, 1954b; Díaz & van Soest 1994; Cruz-Barraza & Carballo 2005; Lehnert *et al.* 2005; Muricy 2011; van Soest *et al.* 2011, 2012; Cruz-Barraza *et al.* 2014). The Tropical Western Pacific harbours the highest diversity of Homoscleromorpha in the Pacific, especially the Philippines with 10 species, Northeast Australia and Indonesia with nine species each, and Papua New Guinea with seven species (e.g., Lendenfeld 1907; Lévi & Lévi 1989; Diaz & van Soest 1994; Muricy 2011; Yong *et al.* 2011).

Here we describe six new species of Plakinidae collected in underwater caves, tunnels and overhangs in New Caledonia and the Marquesas Islands, in the Central-Western Pacific Ocean. One of these species has a novel spicule type that widens the known morphological diversity of the class Homoscleromorpha.

Material and methods

Collections were made by SCUBA diving in January 2012 in the Marquesas Archipelago during the Pakaihi Ite Moana cruise, and in February 2013 in New Caledonia during a field trip organized by the Nouméa IRD Centre (Fig. 1). All sponges were collected in semi-dark or dark habitats, such as tunnels in the reef or underwater caves. Specimens were photographed *in situ* prior to collection and then preserved in ethanol 90%. Thick transversal sections were made with scalpel from specimens embedded in paraffin after dehydration in ethanol 90–100% and clearing in butanol 100% and xylene (2X each). Tangential sections of dried specimens of *Plakortis* and *Plakinastrella* were made with scalpels. Spicule were dissociated in boiling nitric acid and mounted in slides with Entellan for light microscopy. For each spicule type, we measured 30 spicules per specimen, except when noted otherwise. Spicule measurements are expressed as min–med–max length / min–med–max width in micrometres. Dissociated spicules were also coated with gold or gold-palladium and observed in a JEOL JSM 6390 and a Hitachi S-570 scanning electron microscopes. Museum acronyms (Porifera Collections): BMNH, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro; UFRJPOR, Instituto de Biologia, Universidade Federal do Rio de Janeiro.

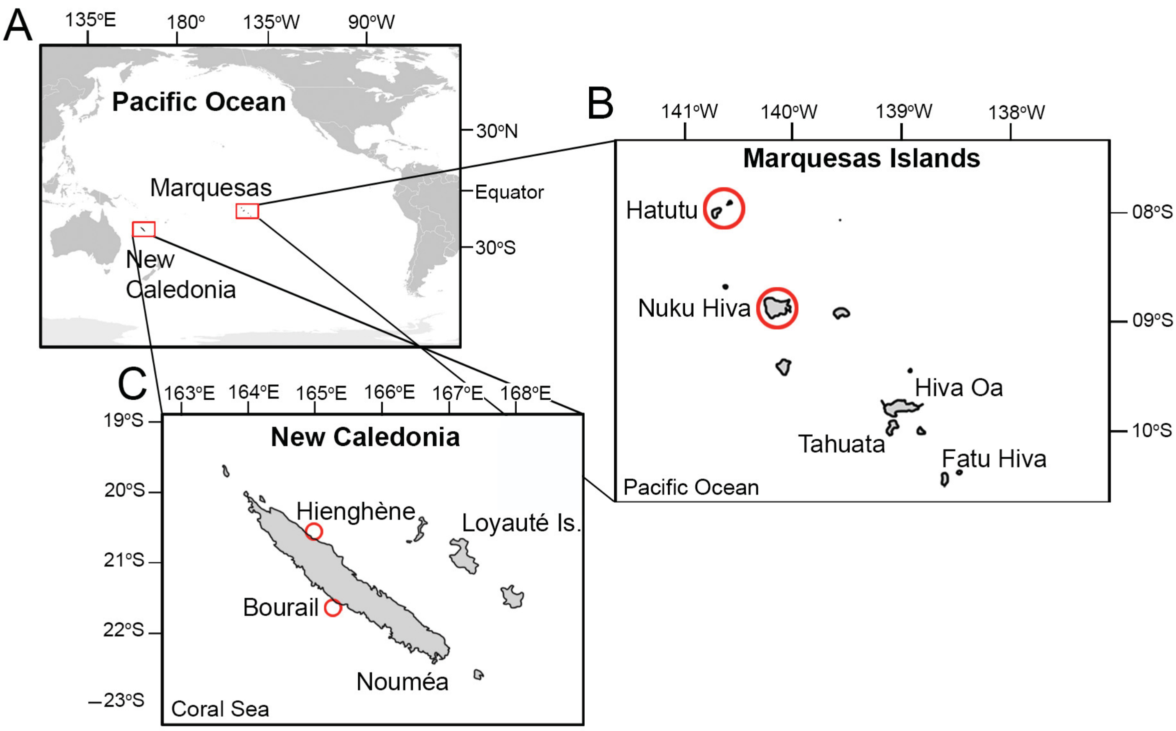

FIGURE 1. Location of collection sites. A, Pacific Ocean showing New Caledonia and Marquesas Islands. B, Marquesas Islands showing Nuku Hiva and Hatutu Island (red circles). C, New Caledonia showing Bourail and Hienghène (red circles)

Systematics

Class Homoscleromorpha Bergquist, 1978

Order Homosclerophorida Dendy, 1905

Family Plakinidae Schulze, 1880

Definition. Homosclerophorida with siliceous spicules, when present, represented by diods, triods and/or calthrops; spicules are lacking in two species. Aquiferous system sylleibid-like or leuconoid, made up by eurypylous or aphodal choanocyte chambers (Lage *et al.* 2018).

Genus *Corticium* Schmidt, 1862

Definition. Thin encrusting to massive plakinids, with spicules always including candelabra. Smooth or spined diods, triods and calthrops, and lophose calthrops can also be present (amended from Muricy & Díaz 2002).

Type species. *Corticium candelabrum* Schmidt, 1862.

Corticium vaceleti sp. nov.

(Fig. 2, Table 1)

Definition. Encrusting, cream to beige *Corticium* with spicules exclusively candelabra, concentrated in the ectosome and canal borders. Oscules membraneous, located on a translucent marginal canal. Ectosomal cavities absent, basal cavities small.

Type Material. Holotype: MNRJ 18050 (130207-NC4-04), collected in Bourail, New Caledonia (21°41.303'S, 165°27.811'E), in a narrow and dark underwater cave (20–25 m depth), dug into the outer slope of the coral reef. Coll. Thierry Pérez, February 07, 2013. Paratype: MNRJ 18051 (130207-NC4-03), same data of holotype.

Material examined for comparison: *Corticium simplex* Lendenfeld, 1907: Syntype BMNH 1908.9.24.101, Dampier Island, NW Australia. *Corticium bargibanti* Lévi & Lévi, 1983: Holotype MNHN.LBIM.D.CL. 2967, New Caledonia.

Description. Thick encrusting sponge, with irregular outline, up to 17 cm wide by 0.5–0.8 cm thick. Colour *in vivo* varies from uniformly cream in some specimens to a gradient from cream to light brown in others (Fig. 2A–B). Surface uneven, smooth or striated, perforated by numerous small inhalant openings aligned or irregularly dispersed. Borders rounded, slightly elevated from the substrate, surrounded by a thin, translucent marginal canal. Oscules 1–2 mm in diameter, circular or elongate, membraneous, located at the marginal canal or dispersed sparsely at the sponge surface. Consistency relatively firm, cartilaginous.

Anatomy. The skeleton is composed of candelabra in low density, concentrated in the ectosome, the base and around canals and rare to absent in the choanosome (Fig. 2C–D). Ectosomal lacunae absent; basal cavities relatively small, ovoid in section (Fig. 2D). Long, straight aquiferous canals run perpendicular to the surface.

Spicules (Fig. 2E–F). The spicules are exclusively heterolophose calthrops (candelabra) with basal actines smooth or with few irregular spines and usually ramified medio-distally in 2–3 conical rays with blunt or acerate tips. The apical actine ramifies in 4–7 spined, conical rays with acerate, blunt or terminally spined endings. Spines are large, acerate, sometimes with bifurcated tips, and curved towards the centre of the spicule. The spined rays form a circle that may contain a central ray (Fig. 2E, left). In a few spicules, interpreted here as growth forms, the rays of the apical actine are smooth (Fig. 2F, left). Full spicule size 21–$\underline{31}$–38 µm (Table 1).

Reproduction. Cinctoblastula larvae 400–475 µm in diameter are abundant in the whole choanosome of both specimens (Fig. 2D).

Ecology. *Corticium vaceleti* **sp. nov.** is a sciaphilic species that dwells in dark cavities, caves and tunnels dug into the coral reef. A relatively dense population was found between 20 and 25 m depth, growing on rocks, close to the recently described *Plakina kanaky* Ruiz & Pérez in Ruiz *et al.*, 2015. No sign of epibiosis or predation were observed.

Distribution. New Caledonia (Figs. 1, 3).

Etymology. The species name *vaceleti* is given in honour of Dr. Jean Vacelet, for the inestimable source of inspiration he represents and for his immense contribution to the knowledge of sponges from dark and shaded habitats, especially submarine caves and the deep sea.

Taxonomic remarks. The genus *Corticium* currently includes seven valid species (van Soest *et al.* 2018): *C. acanthastrum* Thomas, 1968, *C. bargibanti* Lévi & Lévi, 1983, *C. candelabrum*, *C. diamantense* Ereskovsky *et al.*, 2014; *C. niger* Pulitzer-Finali, 1996, *C. quadripartitum* Topsent, 1923, and *C. simplex* Lendenfeld, 1907. Most of these species have calthrops and/or lophose calthrops in addition to the typical candelabra of the genus. The only exceptions are the new species and *Corticium simplex*, in which the spicules are exclusively candelabra distributed mostly at the surface and the canal borders. *Corticium simplex* however greatly differs from *C. vaceleti* **sp. nov.** by a combination of six characters: shape massive lobate with a small base, red-brown external colour with yellowish interior in ethanol, absence of marginal canal, presence of ectosomal cavities, peculiar apical clusters of oscules, and especially by the thick cartilaginous tissue without choanocyte chambers at the centre of the sponge body and surrounding the oscule clusters (Lendenfeld 1907). *Corticium diamantense* from the Caribbean shares with the new species the encrusting shape with irregular outline, the uneven surface perforated by inhalant orifices, and the translucent marginal canal around the borders, but it clearly differs by the uniform light brown colour, abundance of spicules in the choanosome, and especially by the smooth calthrops and tetralophose calthrops, absent in the new species. Furthermore, in *C. diamantense* the apical actine of the candelabra is microspined, while in the new species it has large spines that are curved inwards.

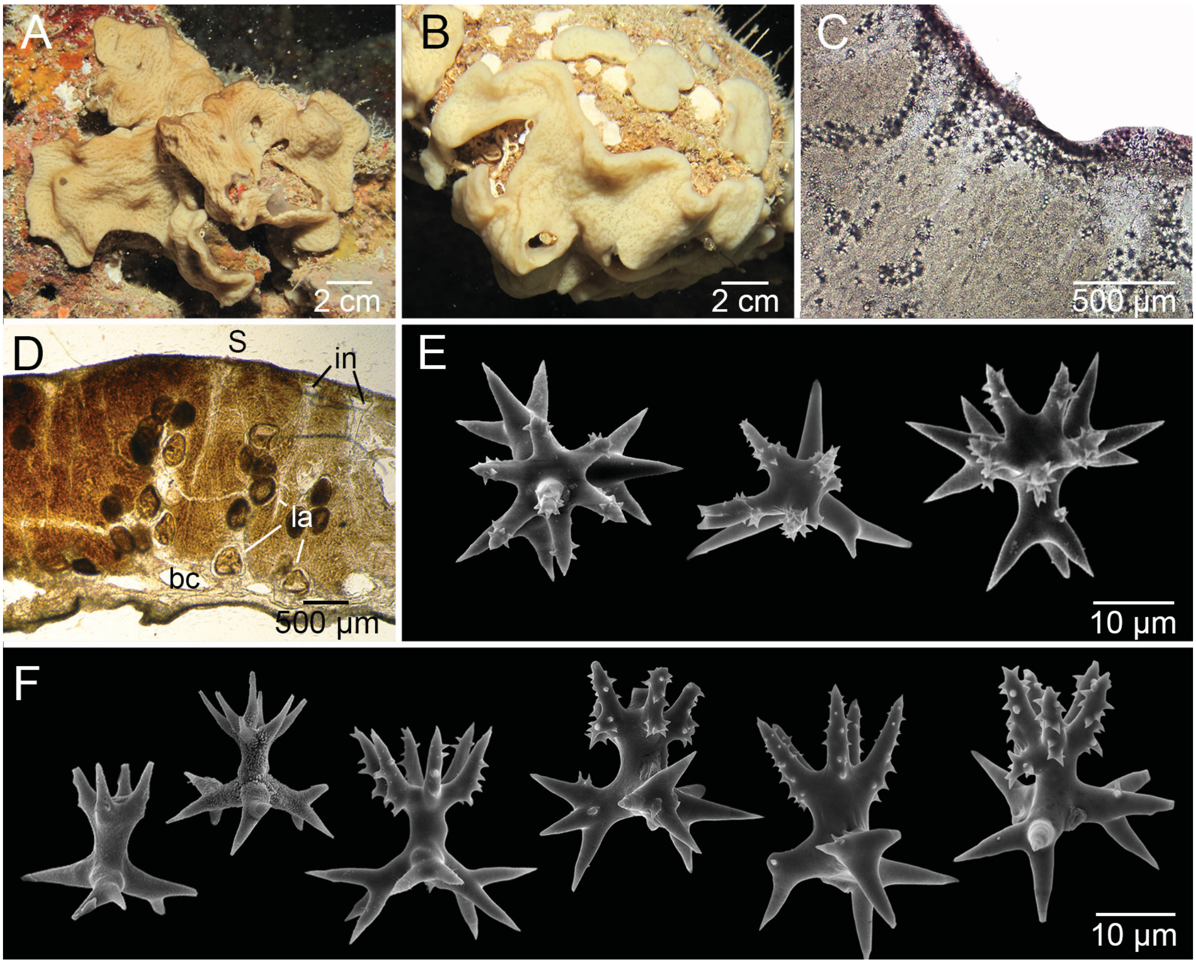

FIGURE 2. *Corticium vaceleti* **sp. nov.** A, holotype MNRJ 18050 *in vivo.* B, paratype MNRJ 18051 *in vivo*. C, ectosome and part of choanosome in transversal section. D, transversal section through the whole sponge, showing the system of basal cavities, straight transversal inhalant canals, and cinctoblastula larvae. E, candelabra in upper view. F, candelabra in side view (E–F, SEM).
Key: bc, basal cavities; in, inhalant canals; la, cinctoblastula larvae; s, surface

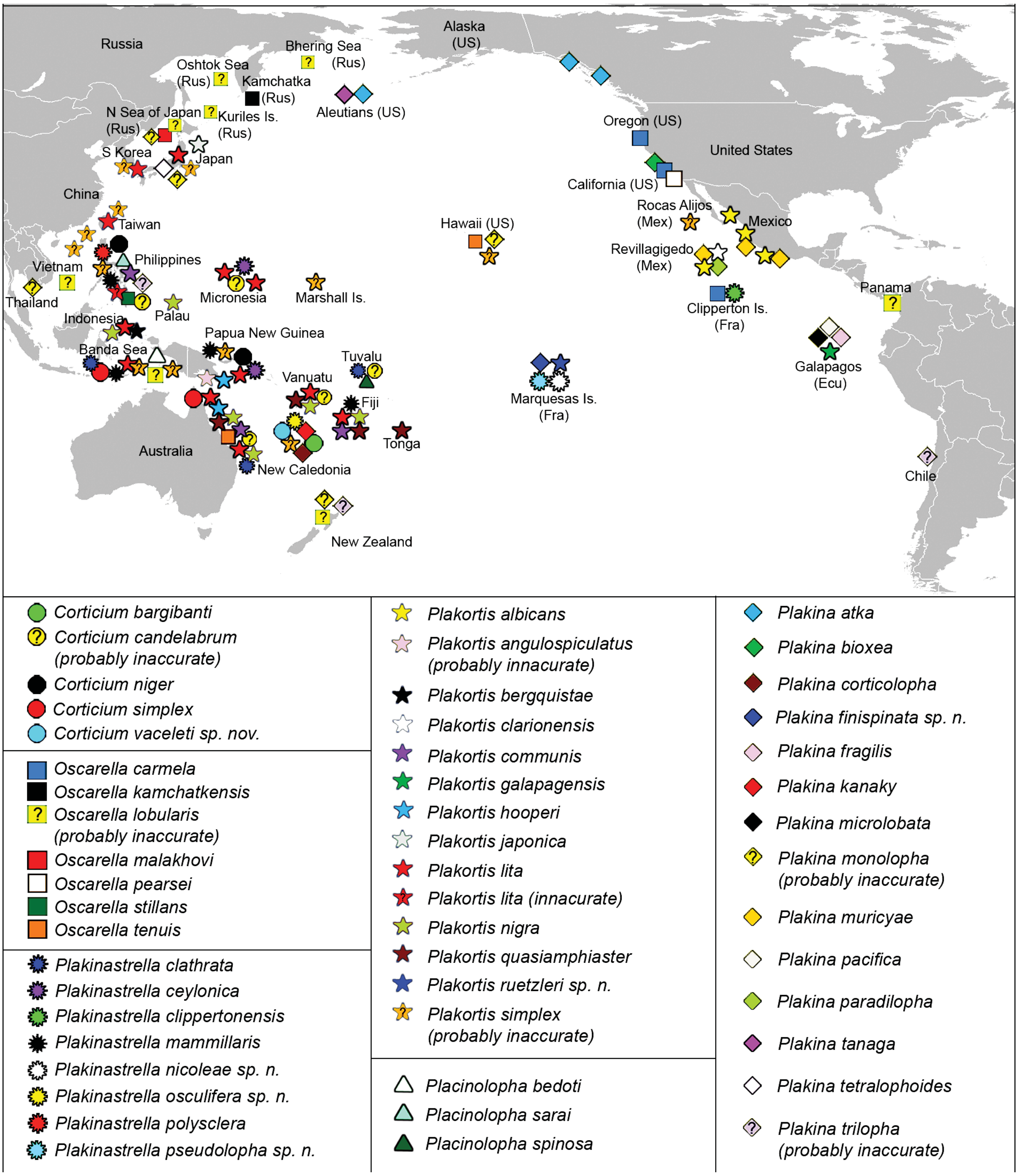

FIGURE 3. Distribution of Homoscleromorpha species in the Pacific Ocean. Records identified only to genus level (as sp., *cf.*, or *aff.*) and from Antarctica were not included. See Table 4 for locality names and references

The only species of *Corticium* previously reported from New Caledonia is *C. bargibanti*, which is easily distinguishable from the new species by the presence of calthrops with large proximal spines (acanthocalthrops *sensu* Lévi & Lévi 1983).

Genus *Plakina* Schulze, 1880

Definition. Encrusting Plakinidae usually with diods, triods, calthrops (all may be absent), and always with at least one type of homolophose calthrops, which may have one to four lophate actines and different ramification patterns. Irregular spicules are common and intraspecific variation in spicule shape may be high. One species has papillae and a microcavity-filling habit, and in another species the skeleton is absent (Lage *et al.* 2018).

Type species. *Plakina monolopha* Schulze, 1880.

TABLE 1. Main morphological characters of *Corticium vaceleti* **sp. nov.** and *Corticium simplex*

Species	Colour	Shape	Surface	Oscules	Candelabra (full size)
C. vaceleti **sp. nov.**					
MNRJ 18050 (Holotype)	Cream with brown patches	Encrusting	Uneven, perforated	Membranous, dispersed	23–<u>33</u>–40 (38)
MNRJ 18051 (Paratype)	Cream	Encrusting	Uneven, perforated	Membranous, dispersed	23–<u>32</u>–45 (39)
C. simplex Lendenfeld, 1907	Red-brown*	Massive lobate	Smooth	Clustered, apical	25–<u>37</u>–43

Measurements are min–<u>med</u>–max full spicule size in micrometres. Number of measurements in parenthesis. *, colour after fixation in ethanol.

***Plakina finispinata* sp. nov.**
(Figs. 4–5, Table 2)

Definition. *Plakina* with diods, triods, calthrops, abundant trilophose calthrops, rare mono- and dilophose triods, and rare mono-, di-, and tetralophose calthrops. Lophose spicules have simple ramification pattern (1m, ts) and all actines usually have terminal spines.

Type Material. Holotype: MNRJ 18470 (120112-MQ2GR-TP31), collected in Nuku Hiva island, Marquesas Islands, French Polynesia (8°56.231'S, 140°07.240'W), in a large underwater cave belonging to a system of four caves ("les quatre grottes"), the entrance being at 19 m depth. January 12, 2012, coll. Thierry Pérez. Paratype: MNRJ 21832, same data of holotype.

Material examined for comparison. *Plakina trilopha* Schulze, 1880: UFRJPOR 4335, Marseille, France (Muricy *et al.* 1998).

Description. Encrusting sponge, 13 mm wide by 1–3 mm thick (Fig. 4A–B). Borders rounded, slightly elevated from the substrate, bearing a translucent marginal canal. Colour white *in vivo*, becoming light brown after fixation (Fig. 4A–B). Surface smooth, densely punctuated by small inhalant openings. Oscules 1–2 mm in diameter, slightly tubular, associated to the marginal canal. Consistency relatively firm, cartilaginous.

Anatomy. The skeleton is a dense, disorganized reticulation of diods, triods and simple calthrops, with lophose calthrops concentrated at the base, at the surface and around canals (Fig. 4C). The ectosome is differentiated from the choanosome by a thin dense layer of lophose spicules with the lophose actines mostly pointing outwards (Fig. 4C). Aquiferous system sylleibid-like, with vertical inhalant and exhalant canals, small ectosomal lacunae 40–50 µm wide and large basal cavities 100–130 µm high leading to the marginal canal at the sponge border. Choanocyte chambers rounded to irregular, eurypylous, 29–50 µm in diameter (Fig. 4D).

Spicules (Table 2). Diods abundant, straight or curved, smooth, acerate, with a central irregularity varying from very slightly to markedly s-bent or centrotylote-like (Fig. 5A): Full size: 56–<u>83</u>–104 / 2.7–<u>4.0</u>–7.6 µm. Some diods have one actine reduced.

Triods abundant, irregular, Y- and T-shaped, smooth, acerate (Fig. 5B). Actines: 17–<u>31</u>–38 / 2.7–<u>3.7</u>–6.8 µm.

Calthrops abundant, irregular, smooth, with acerate or bifurcated ends (Fig. 5C). Actines: 17–<u>27</u>–35 / 2.0–<u>3.3</u>–5.4 µm.

Monolophose triods (Fig. 5D) rare, irregular, non-lophose actines with acerate tips or with terminal spines. Lophose actines ramify once in medial to distal position in 2–5 cylindrical, acerate or terminally spined rays. Full size: 35–<u>50</u>– 60 µm.

Dilophose triods uncommon, with two different shapes (Fig. 5E, F). In the most common type, non-lophose actines are conical, with acerate tips or with 2–3 small terminal spines. Lophose actines ramify once in medial position in 3–5 rays with 2–3 short terminal spines (Fig. 5E). More rarely, the lophose actines have one medial point of ramification and usually also a distal ramification in 2–3 very short rays with 3–5 large terminal spines (Fig. 5F). Both types have the same size range. Full spicule size: 17–24–35 µm.

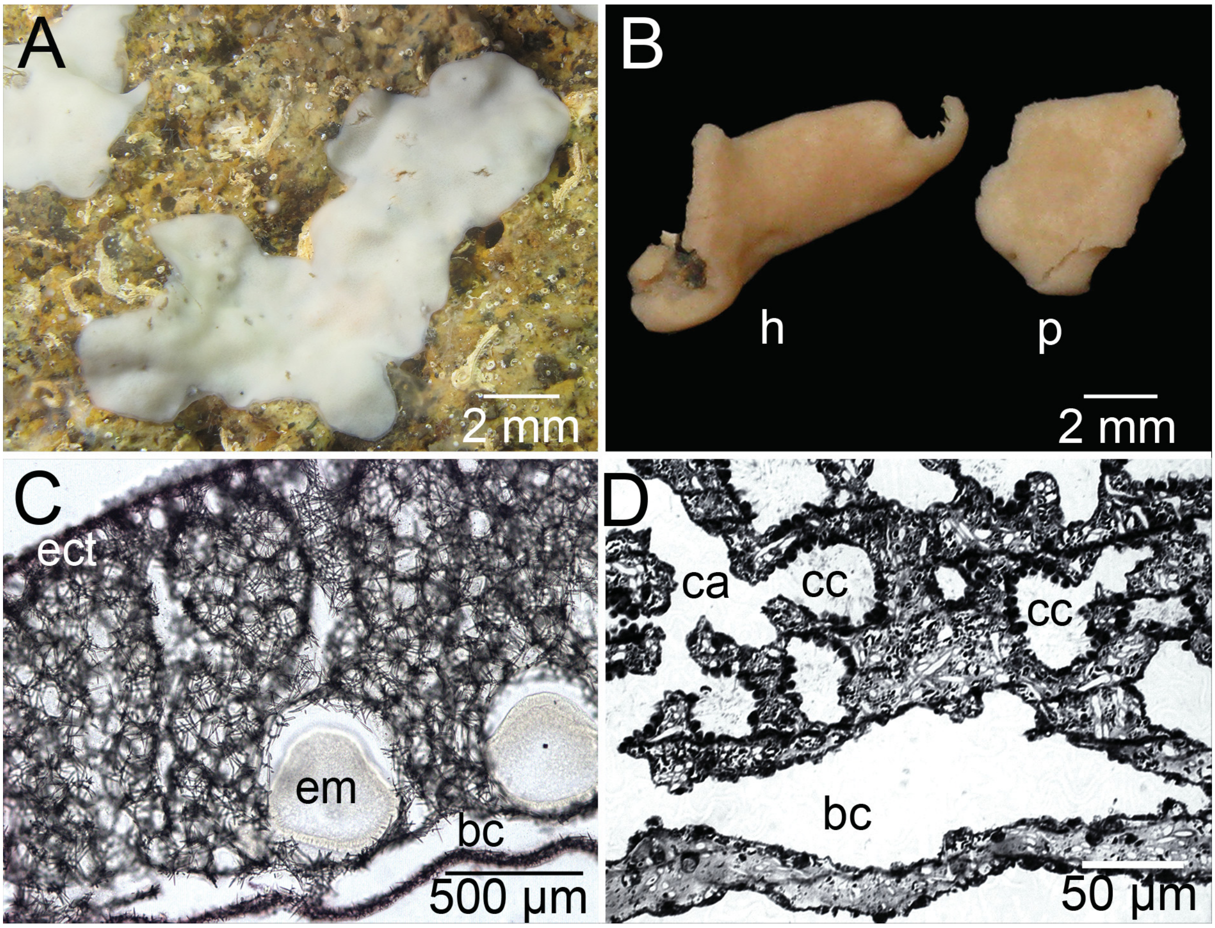

FIGURE 4. *Plakina finispinata* **sp. nov.** A, holotype MNRJ 18470 *in vivo*. B, specimens after fixation: h, holotype (MNRJ 18470); p, paratype (MNRJ 21832). C, Transverse section through the whole body showing the ectosome, embryos, and the system of basal cavities. D, Semithin section after desilification showing the basal cavity, canals, and eurypylous choanocyte chambers. Key: bc, basal cavities; ca, canals; cc, choanocyte chambers; ect, ectosome; em, embryos.

TABLE 2. Spicule measurements of *Plakina finispinata* **sp. nov.**

Specimens	Diods (full size)	Triods (actine size)	Calthrops (actine size)	Monolophose triods (full size)	Dilophose triods (full size)
MNRJ 18470 (Holotype)	65–86–104 / 3.0–4.0–5.0 (30)	25–32–38 / 3.0–3.4–4.0 (30)	17–29–35 / 2.0–3.3–5.4(30)	50–53–60 (3)	20–25–30 (14)
MNRJ 21832 (Paratype)	56–80–100 / 2.5–4.3–7.6 (33)	17–30–35 / 2.7–4.0–6.8 (32)	18–25–31 / 2.0–3.3–4.0 (32)	35–47–60 (2)	17–24–35 (13)

continued.

Specimens	Monolophose Calthrops (full size)	Dilophose Calthrops (full size)	Trilophose Calthrops (full size)	Tetralophose Calthrops (full size)
MNRJ 18470 (Holotype)	45–47–50 (2)	29–36–45 (3)	10–16–23 (30)	20 (2)
MNRJ 21832 (Paratype)	40 (1)	30 (1)	10–16–25 (31)	15–19–20 (4)

Measurements are min–med-max length or length / width in micrometres. Numbers of measurements in parentheses.

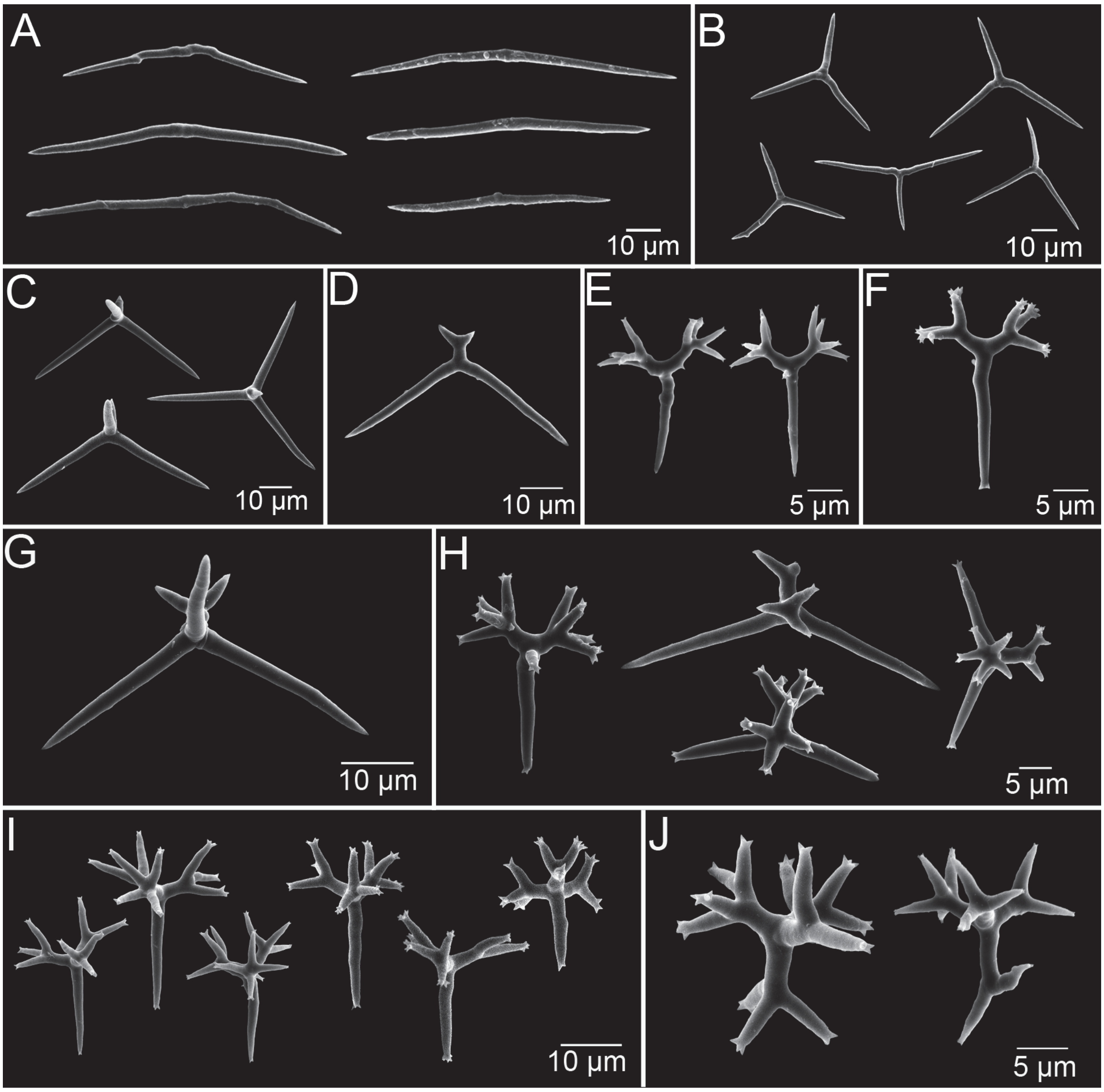

FIGURE 5. *Plakina finispinata* **sp. nov.** Spicules (SEM): A, diods. B, triods. C, calthrops. D, monolophose triod. E–F, dilophose triods. G, monolophose calthrops. H, dilophose calthrops. I, trilophose calthrops. J, tetralophose calthrops.

Monolophose calthrops very rare, irregular in shape. Non-lophose actines smooth, with terminally spined, acerate or blunt ends. Lophose actines ramify once medially in 2–4 conical rays with terminally spined, acerate or blunt extremities (Fig. 5G). Full size: 40–45–50 µm.

Dilophose calthrops very rare, irregular in shape, similar to dilophose triods. Non-lophose actines straight, acerate or terminally spined. Lophose actines ramify once in medial to distal position in 3–5 rays with acerate tips or, more often, with 2–5 terminal spines (Fig. 5H). Full size: 29–35–45 µm.

Trilophose calthrops abundant, very uniform in shape. All actines typically have 2–4 terminal spines. Lophose actines ramified medially in 2–4 rays that bear 2–5 terminal spines (ramification pattern 1m, ts; Fig. 5I). Full size: 10–16.3–25 µm.

Tetralophose calthrops very rare, irregular in shape, with actines ramifying medially in 2–5 conical or cylindrical, terminally spined rays. Terminal spines vary from almost imperceptible to relatively large and conspicuous (Fig. 5J). Full size: 15–19–21 µm.

Reproduction. Embryos 100–240 µm in diameter are incubated mainly near the base of the sponge, just above the basal cavities (Fig. 4C).

Ecology. *Plakina finispinata* **sp. nov.** is a sciaphilic species dwelling in dark caves. Several specimens were found at 20 m depth on the wall of the back of the cave where the community is dominated by encrusting sponges.

There, the sponge fauna is mostly unknown (Pérez *et al.* 2016). No sign of epibiosis or predation were observed on the new species.

Distribution. Nuku Hiva, Marquesas Islands (French Polynesia; Figs. 1, 3).

Etymology. The name *finispinata* refers to the consistent presence of terminal spines in most lophose spicules, and especially in all actines of the trilophose calthrops, which are the dominant lophose spicules in this species (from Latin *finis* = end, extremity, and *spinae* = spines).

Taxonomic remarks. Among the 34 species of *Plakina* currently accepted, *P. finispinata* **sp. nov.** is most similar to *P. trilopha* and *P. anisoactina* (Schulze 1880; Muricy *et al.* 1998; Lage *et al.* 2018). The new species shares with *P. trilopha* the encrusting shape, smooth surface, white colour, and presence of trilophose calthrops. However, *P. trilopha* have neither a marginal canal nor mono- and dilophose triods, and its trilophose calthrops ramify medio-distally in rays that may bear terminal spines but are usually acerate (Schulze 1880; Muricy *et al.* 1998), whereas in *P. finispinata* **sp. nov.** all actines of lophose spicules are very often terminally spined and only exceptionally acerate. *Plakina anisoactina* shares with *Plakina finispinata* **sp. nov.** the presence of a marginal canal, of mono- and dilophose triods, and of mono-, di- and trilophose calthrops. In *P. anisoactina* however the spicules are typically anisoactinal (with both acerate and terminally spined extremities in the same spicule), trilophose calthrops are rare and mono- and dilophose triods are common, contrarily to the new species. *Plakina finispinata* **sp. nov.** differs from all other species of *Plakina* by its lophose calthrops being predominantly trilophose and with all actines terminally spined.

Genus *Plakinastrella* Schulze, 1880

Definition. Plakinidae with skeleton composed by diods, triods and non-lophose calthrops. Spicules often show wide size variation, and sometimes can be separated in up to three size classes. Microrhabds are present in one species (from Domingos *et al.* 2013).

Type species. *Plakinastrella copiosa* Schulze, 1880.

Plakinastrella nicoleae sp. nov.

(Fig. 6, Table 3)

Definition. Light greyish-brown, massive to drop-shaped *Plakinastrella* with short tubular oscules, uneven surface, and generally small spicules: diods 27–125 µm long, triods actines 12–59 µm, calthrops actines 10–30 µm. Microrhabds absent.

Type Material. Holotype: MNRJ 19726 (MQ32GR-TP10-b1), collected in Hatutu island, Marquesas Islands, French Polynesia (7°54.387'S, 140°07.240'W), in a large overhang which continues into a dark underwater cave, at 10 m depth. January 27, 2012, coll. Thierry Pérez.

Description. Shape irregular, with an encrusting basis and thin irregular or drop-shaped lobes hanging from the ceiling of a cave, 3.8 cm long by 0.1–1.2 cm wide and 0.5–1.0 cm thick (Fig. 6A). Colour light greyish-brown with light beige tinges, both *in vivo* and after fixation (Figs. 6A–B). Surface smooth but uneven. Sparse oscules, small, 0.5–1.0 mm in diameter, circular, with an elevated membrane up to 1.3 mm high. Consistency relatively firm but compressible.

Anatomy. The skeleton is composed of diods, triods and calthrops forming a dense alveolar reticulation in the choanosome (Fig. 6C) and a palisade of small diods in the surface (Fig. 6D). The tangential ectosomal skeleton is a double reticulation of multispicular tracts forming small rounded meshes 12–49 µm in diameter inside larger meshes 49–148 µm in diameter (Fig. 6E). Aquiferous system leuconoid. Both ectosomal and basal cavities absent.

Spicules (Table 3). Diods common, irregular, almost straight, smooth, acerate, with central irregularity inconspicuous, often only slightly centrotylote-like; highly variable in size and thickness (Fig. 6F): Full size 27–<u>81</u>–125 / 2.5–<u>6.1</u>–7.5 µm.

Triods abundant, regular, smooth, with acerate ends, usually Y-shaped (Fig. 6G): Actines 12–<u>25</u>–59 / 2.5–<u>6.1</u>–7.5 µm.

Calthrops abundant, regular, smooth, with acerate ends (Fig. 6H): Actines 10–<u>19</u>–30 / 2.5–<u>5.3</u>–7.5 µm.

TABLE 3. Spicule measurements of the new species of *Plakinastrella* and *Plakortis* from the Marquesas Island and New Caledonia

Species / Specimens	Diods I (full size)	Diods II (full size)	Triods I (actine)	Triods II (actine)	Calthrops I (actine)	Calthrops II (actine)	Pseudolophose spicules (full size)
***Plakinastrella nicoleae* sp. nov.**							
MNRJ 19726 (Holotype)	37–85–125 / 2.5–6.1–7.5 (40)	–	20–27–35 / 2.5–6.1–7.5 (40)	–	12.5–21–30 / 2.5–5.3–7.5 (40)	–	–
***Plakinastrella osculifera* sp. nov.**							
MNRJ 18459 (Holotype)	14–75–122 / 1.7–4.1–8.0 (40)	277 / 8 (1)	20–35–50 / 2.5–6.3–7.5 (30)	87–116–135 / 15–18–21 (5)	2.5–27–40 / 0.5–4.3–7.5 (36)	75–96–125 / 12.5–16.0–22.5 (24)	–
MNRJ 21831 (Paratype)	20–83–150 / 2.5–6.0–10 (40)	210 / 7 (1)	20–36–62 / 2.5–5.6–10 (40)	87–113–147 / 12–17.5–22 (5)	12–25–37 / 2.5–5.4–7.5 (40)	57–88–135 / 10–13.9–22 (30)	–
***Plakinastrella pseudolopha* sp. nov.**							
MNRJ 18463 (Holotype)	30–43–60 / 1.0–1.5–2.0 (30)	60–82–120 / 3.0–4.0–5.0 (30)	10–17–20 / 1.0–1.3–2.0 (30)	20–29–36 / 3.0–3.7–5.0 (30)	9.0–15–22 / 1.0–2.3–4.0 (30)	–	10–16–25 (30)
***Plakortis ruetzleri* sp. nov.**							
MNRJ 21833 (Holotype)	30–107–127 / 2.5–5.6–7.5 (40)	–	12–36–50 / 2.5–4.3–5.0 (7)	–	–	–	–
MNRJ 18462 (Paratype)	45–114–150 / 2.5–5.7–7.5 (40)	–	12–39–52 / 2.5–3.8–5.0 (8)	–	–	–	–
MNRJ 21924	70–104–130 / 5–5–5 (40)	–	30–36–40 / 2–2–2 (4)	–	–	–	–
MNRJ 21925	70–105–140 / 5–5–5 (40)	–	30–32–40 / 2–2–2 (7)	–	–	–	–

–, absent. Measurements are min-med-max length or length / width in micrometres. Numbers of measurements in parentheses

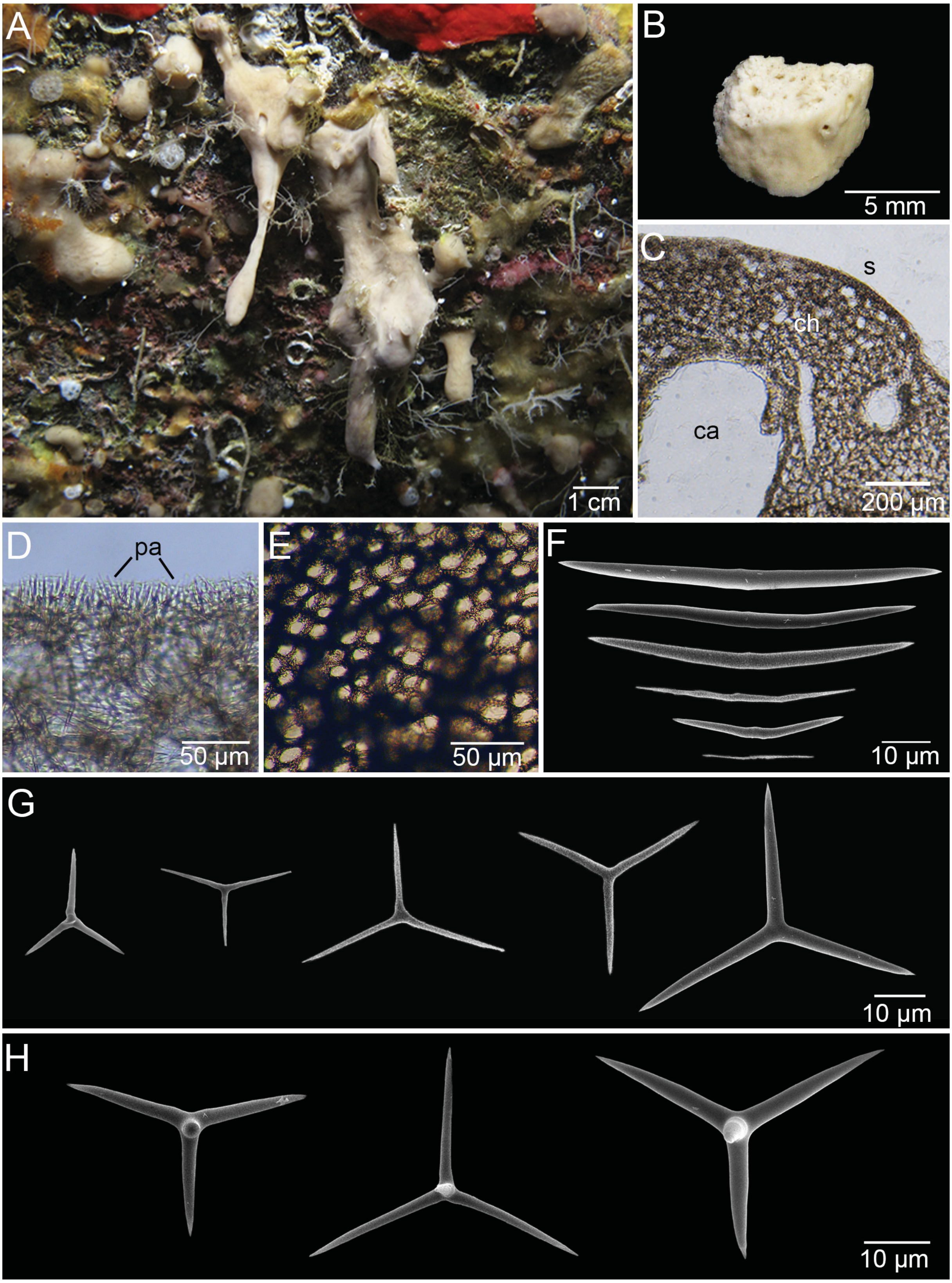

FIGURE 6. *Plakinastrella nicoleae* **sp. nov.** A, holotype MNRJ 19726 *in vivo*. B, fragment of the holotype after fixation. C, Transverse section showing the dense, alveolar choanosomal skeleton, the dense surface layer, and canals. D, transversal section of the ectosome showing the palisade of small diods. E, Tangential section showing ectosomal reticulation with rounded primary and secondary meshes. F, diods. G, triods. H, calthrops (F–H, SEM). Key: ca, canals; ch, choanosomal skeleton; pa, palisade; s, surface.

Reproduction. Cinctoblastula larvae approximately 500 µm in diameter were found near the basis of the sponge.

Ecology. *Plakinastrella nicoleae* **sp. nov.** colonizes semi-dark caves, and lives in syntopy with *Plakinastrella pseudolopha* **sp. nov.** and *Plakortis ruetzleri* **sp. nov.** This sponge was collected at 10 m depth on the roof of a large overhang dominated by black coral colonies (Pérez *et al.* 2016). No sign of epibiosis or predation were observed.

Distribution. Marquesas Islands, French Polynesia (Figs. 1, 3).

Etymology. The specific epithet *nicoleae* is given in honour of Dr. Nicole Boury-Esnault for her exceptional contribution to the systematics of the Homoscleromorpha and for her enthusiastic efforts for the development of sponge biology and the formation of new scientists.

Taxonomic remarks. *Plakinastrella* currently includes 14 species with uniform spiculation of diods, triods and calthrops (van Soest *et al.* 2018). Many species are poorly described, and the main morphological character used for species discrimination in *Plakinastrella* is spicule size. *Plakinastrella nicoleae* **sp. nov.** shares the small size of the spicules—all shorter than 150 µm—with *Plakinastrella copiosa*, *P. clippertonensis* van Soest *et al.*, 2011, *P. globularis* Domingos *et al.*, 2013, *P. osculifera* **sp. nov.**, *P. microspiculifera* Moraes & Muricy, 2003 and *P. mixta* Maldonado, 1992. However, *P. copiosa, P. clippertonensis,* and *P. mixta* differ by the small size (maximum 2 cm long) and external colours (white, yellow, or cream). *Plakinastrella globularis* differs by the massive shape, dark blue colour *in vivo*, and presence of microrhabds, absent in the new species. *Plakinastrella osculifera* **sp. nov.** differs from *Plakinastrella nicoleae* **sp. nov.** by the encrusting shape, chocolate-brown colour, conspicuous oscules, and larger calthrops. The species most similar to *Plakinastrella nicoleae* **sp. nov.** is *P. microspiculifera* from the Tropical Southwestern Atlantic, which shares the small spicule size, the massive drop-shaped habit, the ectosomal skeleton architecture, and the presence of ectosomal cavities. *Plakinastrella microspiculifera* differs by the dark grey to black colour, irregular surface, presence of ectosomal cavities, rarity of triods, and by the regular shape of its calthrops (Moraes & Muricy 2003). These differences are relatively small but are congruent, and together with the highly disjunct distributions they support the distinction of *Plakinastrella nicoleae* **sp. nov.** as a new taxon.

Plakinastrella osculifera sp. nov.
(Figs. 7–8, Table 3)

Definition. *Plakinastrella* encrusting, brown, with oscules conspicuous, abundant and regularly distributed. Tangential skeleton reticulated, with uniform, small circular meshes. Ectosomal cavities rounded, subectosomal lacunae large and irregular, basal cavities absent. Diods, triods and calthrops in two size classes each: diods 14–150 and 210–277 µm long, actines of triods 20–62 and 87–147 µm, actines of calthrops 2–40 and 57–135 µm. Microrhabds absent.

Type Material. Holotype: MNRJ 18459 (130205-NC10-01) collected off Hienghène, New Caledonia (20°36.756'S, 164°56.958'E), in a network of tunnels crossing an islet, at 22–23 m depth. February 05, 2013, coll. Thierry Pérez. Paratype: MNRJ 21831, same data of holotype.

Description. Thin to thickly encrusting sponge, very large (up to 45 cm long by 40 cm wide), with irregular outline. External colour brown with light brown patches *in vivo* (Fig. 7A) and homogeneously brown after fixation; the interior is lighter than the surface. Surface smooth but uneven. Oscules abundant, conspicuous, 0.5–3.0 mm in diameter, circular, slightly elevated, regularly distributed on the surface. Consistency relatively firm.

Anatomy. Aquiferous system leuconoid. Ectosomal cavities small, rounded, 30–108–310 µm, located over large, irregular subectosomal lacunae (Fig. 7B–C). Basal cavities absent. In transverse sections, the skeleton is a dense, disorganized reticulation of diods, triods, and calthrops, slightly denser between the ectosomal cavities and at canal borders (Figs. 7B–D). The base of the sponge is lined by a palisade and a tangential layer of small spicules, mainly diods (Fig. 7B). Large diods, triods and calthrops are dispersed throughout the choanosome (Fig. 7D). In tangential sections, the ectosomal skeleton is a simple and uniform reticulation of multispicular spicule tracts forming circular meshes 48–82–105 µm in diameter (Fig. 7E).

Spicules (Table 3). Diods of two size categories, similar in shape: straight or slightly curved, smooth, acerate, with central irregularity varying from strongly S-bent to slightly thickened, with large size variation: Full size: Diods I (Fig. 8A) abundant, 14–79.1–150 / 1.7–5.0–10 µm. Diods II (Fig. 8B) very rare to absent, 210–243–277 / 7–7.5–8 µm.

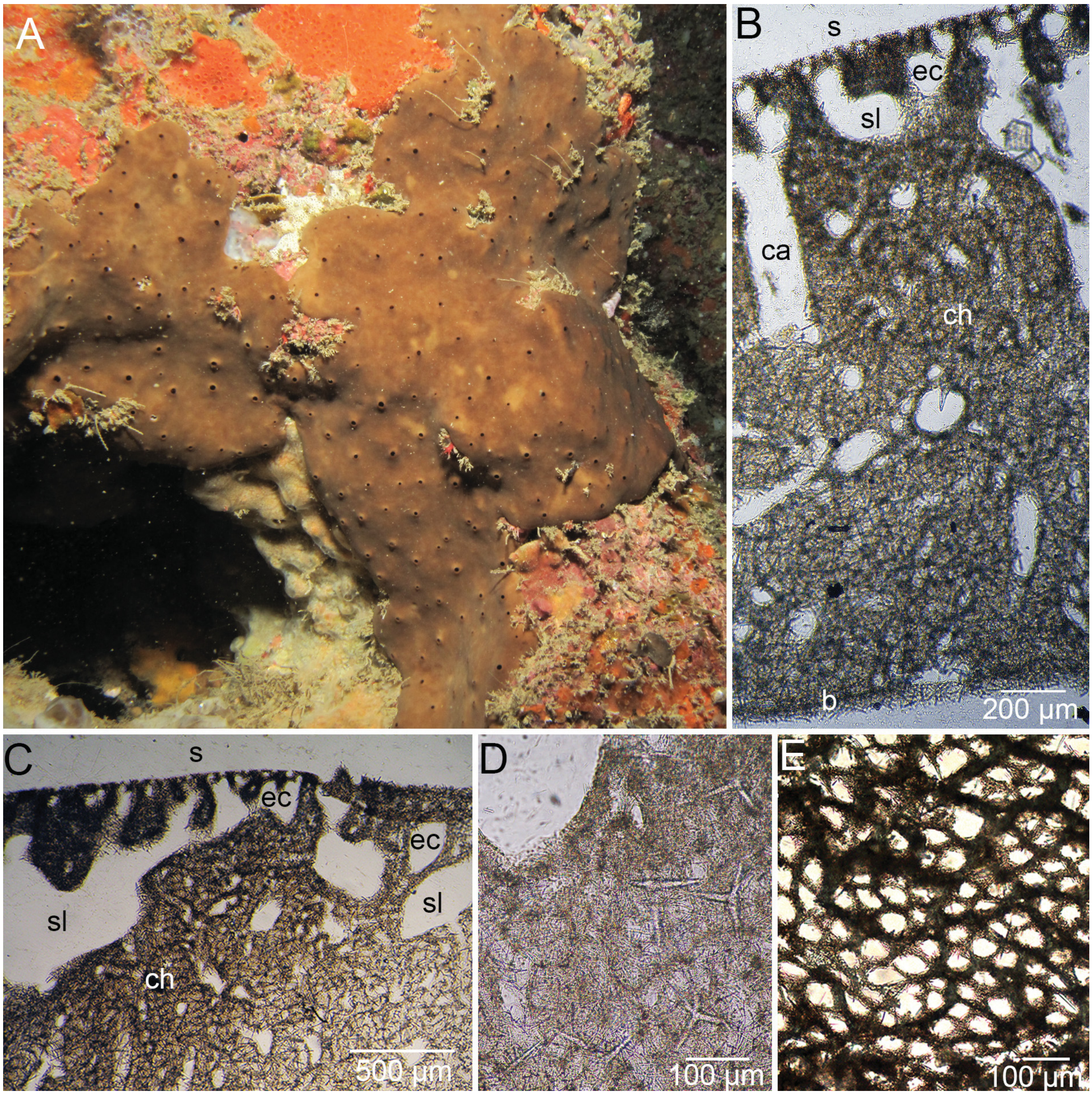

FIGURE 7. *Plakinastrella osculifera* **sp. nov.** A, holotype MNRJ 18459 *in vivo*. B, Transverse section through the whole sponge body. C, transverse section of ectosome and upper choanosome with small rounded ectosomal cavities, large subectosomal lacunae, and disorganized choanosomal skeleton. D, disorganized choanosomal skeleton with large triods and calthrops dispersed. E, tangential section of the ectosomal reticulation with simple rounded meshes. Key: b, basal layer; ca, canals; ch, choanosomal skeleton; ec, ectosomal cavities; s, surface; sl, subectosomal lacunae.

Triods of two size categories. Triods I common, slender, smooth, irregular, Y- or T-shaped, acerate (Fig. 8C). Actines 20–35.6–62,5/ 2.5–5.9–10 µm. Triods II rare, stout, smooth, regular, Y- or T- shaped, acerate (Fig. 8D). Actines 87.5–114–147 / 12.5–17–22.5 µm.

Calthrops also of two size categories. Calthrops I abundant, slender, smooth, regular, with acerate ends (Fig. 8E). Actines 2.5–26.3–40 / 2.5–5.3–7.5 µm. Calthrops II common, stout, smooth, regular, with acerate ends (Fig. 8F). Actines 57.5–92–135 / 10–14.9–22.5 µm.

Reproduction. Reproductive elements were not found.

Ecology. *Plakinastrella osculifera* **sp. nov.** dwells in a semi-dark habitat. This sponge was collected at 22–23 m depth in muddy little ledges on the side of the tunnel, shaded from the light by very turbid water, large sea-fans, and black corals colonizing the access to the cave. This new species is syntopic of the recently described *P. kanaky* (Ruiz *et al.* 2015). No signs of epibiosis or predation were observed on its surface.

Distribution. New Caledonia (Figs. 1, 3).

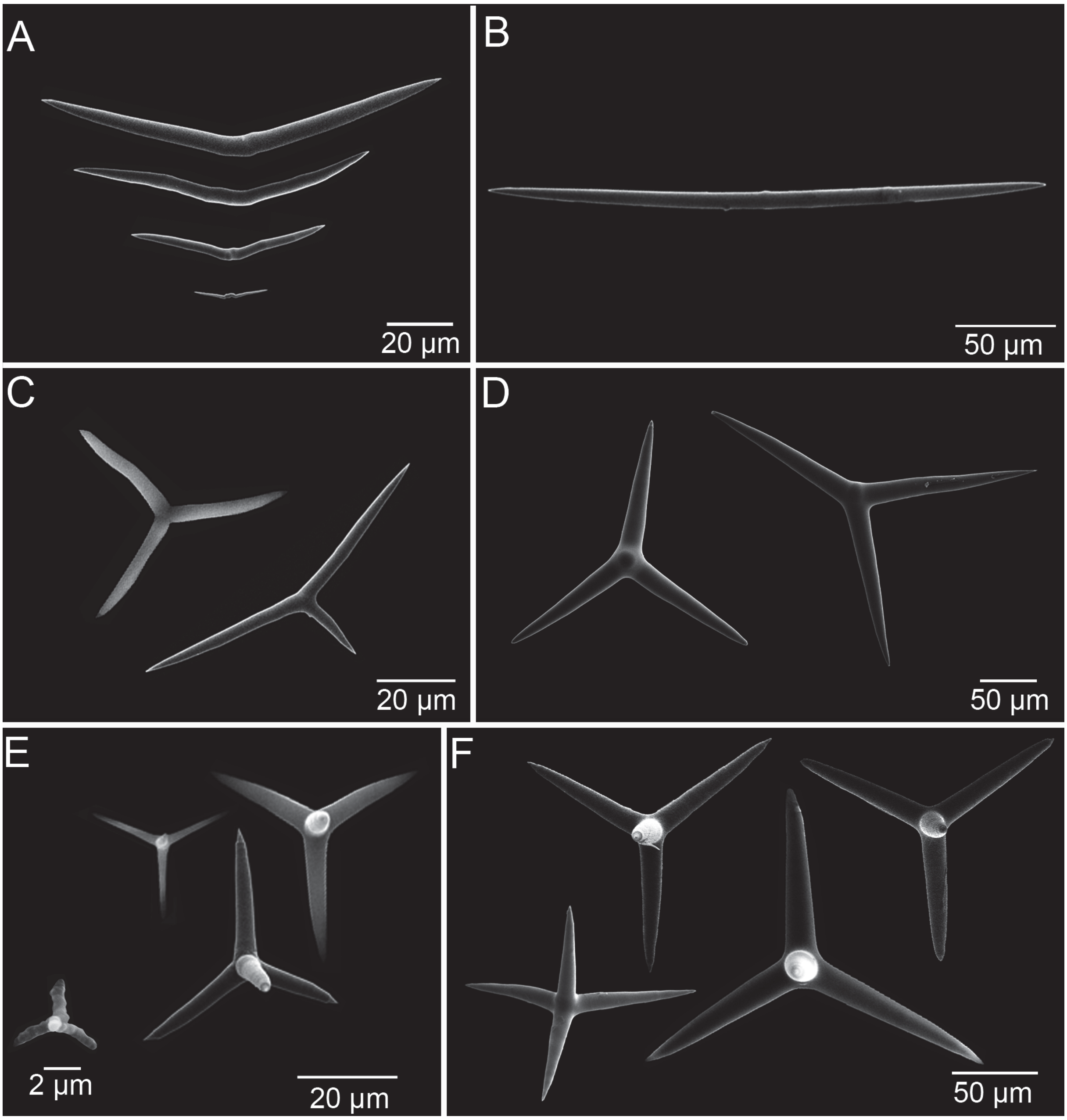

FIGURE 8. *Plakinastrella osculifera* **sp. nov.** Spicules (SEM). A, diods I. B, diods II. C, triods I. D, triods II. E, calthrops I. F, calthrops II.

Etymology. The species name *osculifera* derives from the abundance and regular distribution of the conspicuous oscules of this sponge.

Taxonomic remarks. The new species is distinguished from its congeners mainly by spicule size. It has two size categories of diods, triods, and calthrops, with the largest diods attaining 277 µm and the actines of triods and calthrops up to 147 µm and 135 µm, respectively. In seven species of *Plakinastrella,* all spicules are shorter than approximately 150 µm: *Plakinastrella clathrata* Lendenfeld, 1900, *P. clippertonensis, P. copiosa*, *P. globularis*, *P. microspiculifera*, *P. nicoleae* **sp. nov.**, and *P. mixta*. In other six species, the diods are approximately 200 µm or more but the actines of the triods and/or the calthrops are much shorter than 150 µm: *P. ceylonica* (Dendy, 1905), *P. mammillaris* Lendenfeld, 1907, *P. minor* (Dendy, 1916), *P. onkodes* Uliczka, 1929, *P. stinapa* van Soest *et al.*, 2014, and *P. trunculifera* Topsent, 1927. *Plakinastrella oxeata* Topsent, 1904 and *P. polysclera* Lévi & Lévi, 1989 have much larger spicules, with diods over 1000 µm and actines of triods and calthrops over 400 µm long. *Plakinastrella osculifera* **sp. nov.** is well characterized within the genus by the combination of large encrusting shape, abundant and conspicuous oscules, and by the size of its spicules.

***Plakinastrella pseudolopha* sp. nov.**
(Figs. 9–10, Table 3)

Definition. *Plakinastrella* with a small columnar shape and with diods, triods, calthrops, and unique spicules with 2–4 actines that ramify in 2–8 conical, fused rays (pseudolophose spicules).

Type Material. Holotype: MNRJ 18463 (MQ32GR-TP10-b2), collected in Hatutu island, Marquesas Islands, French Polynesia (7°54.387'S, 140°07.240'W), in a large overhang which continues in a dark underwater cave at 10 m depth. January 27, 2012, coll. Thierry Pérez.

Description. Small columnar sponge with rounded top, 1.5 cm high by 0.5 cm in diameter, hanging upside down from the cave ceiling (Fig. 9A). Colour *in vivo* cream, becoming light brown after fixation (Figs. 9A–B). Surface smooth, with thin sub-surface canals. Oscules circular, elevated, 0.5–1 mm in diameter and up to 1 mm high, contracted after fixation. Consistency relatively firm, cartilaginous.

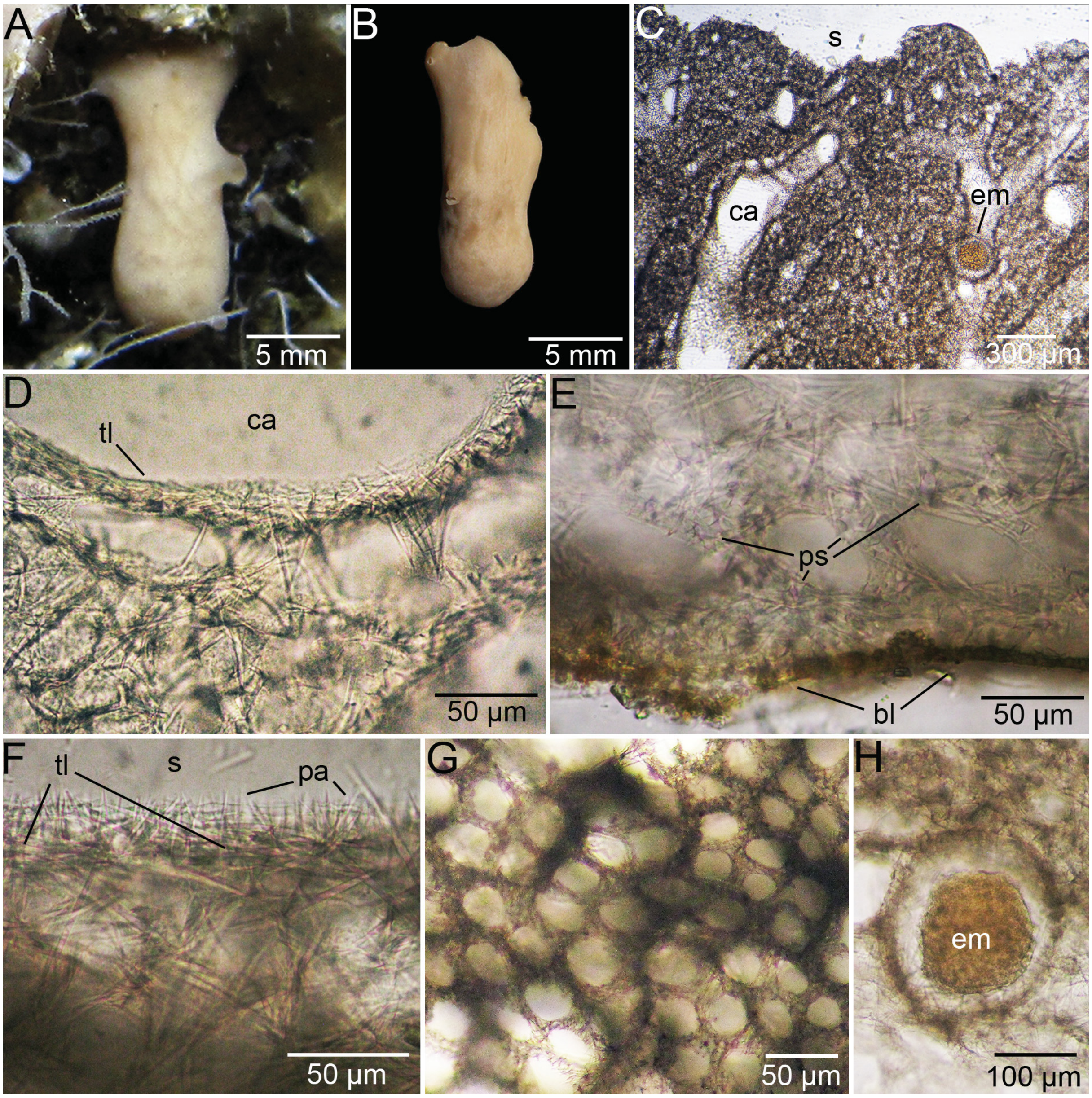

FIGURE 9. *Plakinastrella pseudolopha* **sp. nov.** A, holotype MNRJ 18463 *in vivo*. B, holotype after fixation. C, transversal section showing the dense choanosomal reticulation, canals and an embryo. D, tangential layer of spicules around a canal. E, basal layer of tangential spicules and part of the choanosome with pseudolophose spicules. F, ectosome with a palisade of small diods over a tangential layer of diverse spicule types. G, tangential ectosomal reticulation with simple, uniform, rounded meshes. H, embryo. Key: bl, basal layer; ca, canal; em, embryo; pa, palisade; ps, pseudolophose spicules; s, surface; tl, tangential layer.

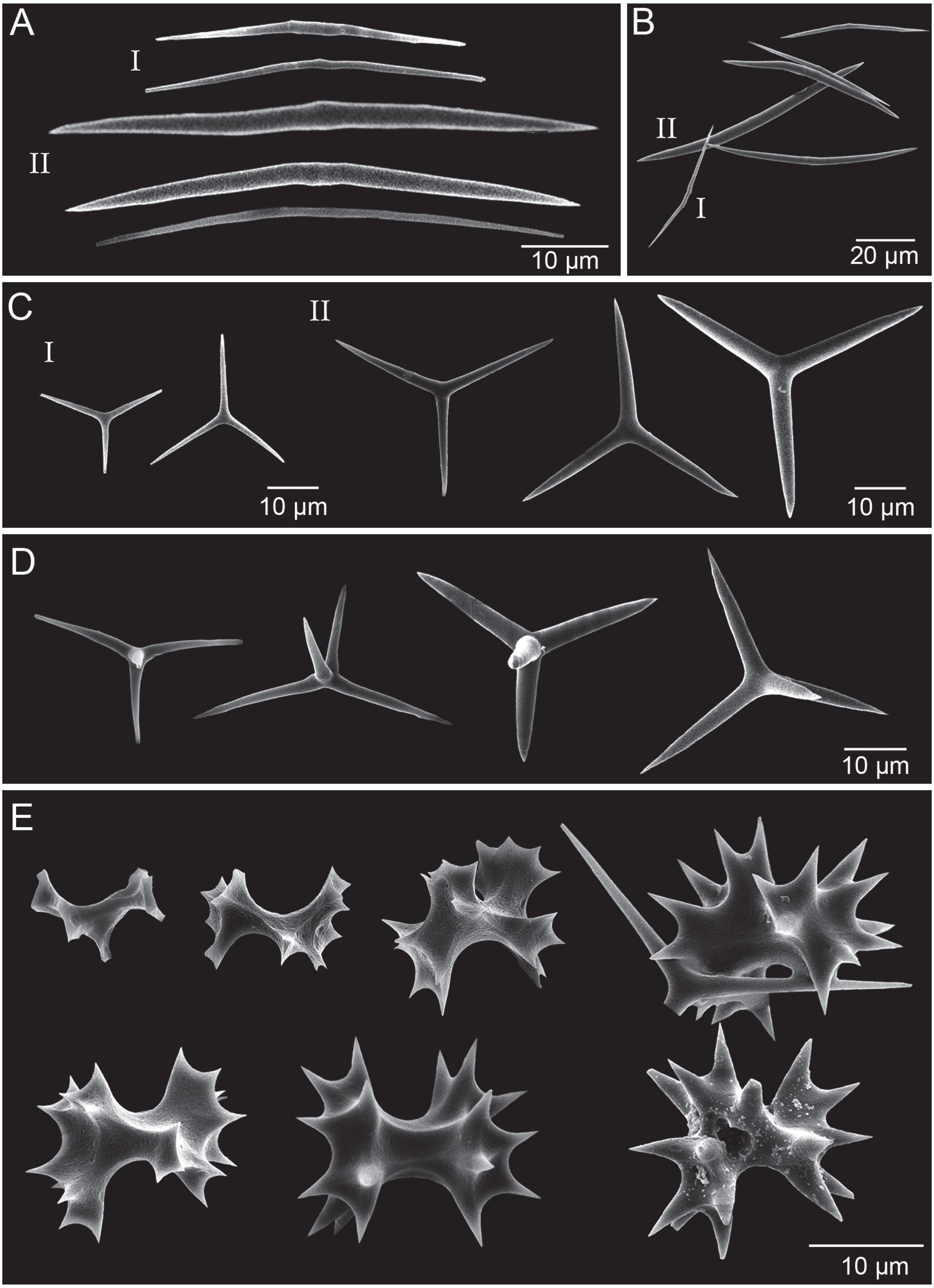

FIGURE 10. *Plakinastrella pseudolopha* **sp. nov.** Spicules (SEM). A–B, diods. C, triods. D, calthrops. E, pseudolophose spicules.

Anatomy. The choanosomal skeleton is a disorganized alveolar reticulation surrounding choanocyte chambers, with a dense tangential layer at the margins of aquiferous canals and at the basal surface of the sponge (Figs. 9C–E). Pseudolophose spicules are dispersed throughout the choanosome but are slightly more abundant near the base (Fig. 9E). Subectosomal lacunae and basal cavities absent, but the choanosome is pierced by large cylindrical canals, 100–650 µm in diameter (Fig. 9C). In transverse sections, the ectosomal skeleton is a palisade of small diods over a thin layer of tangential spicules (Fig. 9F). In tangential sections, the ectosomal skeleton is a reticulation of multispicular tracts forming uniform, rounded meshes 20–40 µm in diameter (Fig. 9G).

Spicules (Figure 10, Table 3). Diods of two size categories, but not clearly separated (Figs. 10A–B). Diods I thin, smooth, slightly S-bent at the centre, extremities blunt or terminally microspined. Full size 30–43–60 µm / 1.0–1.5–2.0 µm. Diods II abundant, robust, straight or curved and slightly S-bent at the centre, with acerate or blunt ends. Full size 60–82–120 / 3.0–4.0–5.0 µm.

Triods of two size categories, but not easily separated (Fig. 10C). Triods I small, thin, regular, Y- or T-shaped, with smooth actines and blunt or terminally microspined tips. Actines 10–17–20 / 1.0–1.5–2.0 µm. Triods II abundant, regular, most often Y-shaped, smooth, with acerate endings. Actines 20–29–36 / 3.0–3.7–5.0 µm.

Calthrops relatively uncommon, small, regular, smooth, with acerate endings (Fig. 10D). Actines 9.0–15–22 / 1.0–2.3–4.0 µm.

Pseudolophose spicules (Fig. 10E) common, with 2–4 irregular, often slightly spiralled actines that ramify medially in 2–8 short, partly fused, conical rays with acerate endings: Full spicule size 10–16–25 µm.

Reproduction. Embryos 150–300 µm in diameter were found throughout the choanosome of the only specimen, collected in January. All embryos were in morula stage and were brooded in roughly spherical chambers surrounded by a tangential layer of spicules (Figs. 9C, H).

Ecology. *Plakinastrella pseudolopha* **sp. nov.** lives in semi-dark caves in syntopy with *Plakinastrella nicoleae* **sp. nov.** and *Plakortis ruetzleri* **sp. nov.** (see below). This sponge was collected at 10 m depth on the ceiling of a large overhang dominated by large black coral colonies (Pérez *et al.* 2016). No sign of epibiosis or predation were observed.

Distribution. Marquesas Islands, French Polynesia (Figs. 1, 3).

Etymology. The name *pseudolopha* refers to the unique spicule type named here 'pseudolophose spicules'.

Taxonomic remarks. *Plakinastrella pseudolopha* **sp. nov.** differs from all other plakinids by the presence of unique spicules with ramified actines and fused conical rays named here ‘pseudolophose spicules’. The symmetry of these spicules is variable and the spicules may have two, three or four actines (Fig. 10E). The actines ramify in fused, conical rays in a pattern that is sometimes similar to the smooth actines of the candelabra of *Corticium* (Figs. 2E–F), and of the lophose calthrops of some *Plakina* species such as *P. weinbergi* Muricy, Bézac, Boury-Esnault and Vacelet, 1998 and *P. anomala* Lage, Gerovasileiou, Voultsiadou and Muricy, 2018. However, the absence of true candelabra precludes its allocation in *Corticium*, and a possible homology between truly lophose and the pseudolophose spicules is difficult to determine. Although their shape is slightly similar, the distribution of pseudolophose spicules throughout the choanosome of the new species contrasts with the concentration of lophose spicules in the ectosome and around canals in *Plakina* species. On the other hand, the new species shares with *Plakinastrella* the ectosomal palisade of small diods, the tangential reticulation with rounded meshes, and the presence of two size categories of diods and triods. One species of *Plakinastrella*, *P. globularis* Domingos, Moraes and Muricy, 2013 has microrhabds, which could be related to the diactinal pseudolophose spicules. A close relationship of the new species with *Plakinastrella* was also supported by preliminary *cox-1* gene sequence data (not shown). The classification of this species, however, should be verified through molecular and morphological phylogenetic analyses of the whole family Plakinidae, which are out of the scope of this contribution.

Genus *Plakortis* Schulze, 1880

Definition. Plakinidae always with diods, and with triods in variable abundance or absent. Calthrops are always absent. Microrhabds, spheres and spined diods (quasiamphiasters) may be present in some species (amended from Muricy 2011).

Type species: *Plakortis simplex* Schulze, 1880.

***Plakortis ruetzleri* sp. nov.**
(Fig. 11, Table 3)

Definition. Small, cushion-shaped *Plakortis* with diods and rare triods in a disorganized arrangement in both the ectosome and choanosome.

Type Material. Holotype: MNRJ 21833 (MQ32-GR-TP9), collected in Hatutu island, Marquesas Islands, French Polynesia (7°54.387'S, 140°07.240'W), in a large overhang which continues in a dark underwater cave at 10 m depth. January 27, 2012, coll. Thierry Pérez. Paratype: MNRJ 18462 (MQ32-GR-TP9), same data of holotype. Additional material: MNRJ 21924, MNRJ 21925, same data of type specimens.

Description. Sponge thinly encrusting to cushion-shaped, 0.5–2.0 cm wide by 3–5 mm thick, with slightly rounded borders. Colour *in vivo* and after fixation a gradient from light brown to a slightly darker reddish brown (Figs. 11A–C). Surface smooth. Oscules sparse, circular, with a translucent rim, 0.7–1.1 mm in diameter. Consistency relatively soft.

Anatomy. In transverse sections, the choanosomal skeleton is disorganized and relatively dense, with diods and triods dispersed throughout the choanosome (Fig. 11D). Ectosomal specialization absent. Tangential ectosomal skeleton disorganized, with rare vague tracts of diods forming an irregular reticulation around the ovoid pores, which measure 30–50 µm in diameter (Fig. 11E). Aquiferous system leuconoid. Both ectosomal and basal cavities absent.

Spicules (Table 3). Diods abundant (Fig. 11F), variable in size and shape. The smaller are slender, straight, smooth, with blunt ends and a conspicuous, usually s-bent central irregularity. The larger diods are stout, irregular, smooth, with acerate ends and central irregularity moderately developed, mainly centrotylote-like. Full size 30–<u>110.7</u>–150 / 2.5–<u>5.6</u>–7.5 µm.

Triods rare, uniform, Y- or T-shaped, smooth, with acerate ends (Fig. 11G). Actines 12–<u>40</u>–49 / 1.8–<u>2.5</u>–4.0 µm.

Reproduction. Roughly spherical embryos, 120–360 µm in diameter, are dispersed in the choanosome (Fig. 11D).

Ecology. *Plakortis ruetzleri* **sp. nov.** lives in semi-dark caves in syntopy with *Plakinastrella pseudolopha* **sp. nov.** and *Plakinastrella nicoleae* **sp. nov.** This sponge was collected at 10 m depth on the roof of a large overhang dominated by large black coral colonies (Pérez *et al.* 2016). No sign of epibiosis or predation were observed.

Distribution. Marquesas Islands, French Polynesia (Figs. 1, 3).

Etymology. The name *ruetzleri* is given in honour of Dr. Klaus Rützler, for his pioneering studies of sponges from submarine caves and for his outstanding long-term contribution to the development of sponge taxonomy.

Taxonomic remarks. The genus *Plakortis* has 29 valid species and few morphological characters for species discrimination. The main morphological characteristics of 27 species was recently tabulated (Ubare and Mohan 2016), and only two species were described thereafter (Vicente *et al.* 2016). Eight species are distinguished by the presence of microrhabds: *P. lita* de Laubenfels, 1954, *P. microrhabdifera* Moraes and Muricy, 2003, *P. hooperi* Muricy, 2011, *P. myrae* Ereskovsky, Lavrov and Willenz, 2014, *P. petrupaulensis* Domingos, Moraes and Muricy, 2013, *P. spinalis* Domingos, Moraes and Muricy, 2013, *P. potiguarensis* Domingos, Moraes and Muricy, 2013, and *P. badabaluensis* Ubare and Mohan, 2016. One species has quasiamphiasters (*P. quasiamphiaster* Díaz and van Soest, 1994). Triods are absent in *P. nigra* Lévi, 1953, *P. zyggompha* de Laubenfels, 1934, and *P. halichondrioides* Wilson, 1902. *Plakortis bergquistae* Muricy, 2011 has larger triods (30–122 *vs.* 12–49 µm in the new species) and diods (type I 91–163 µm, type II 202–365 µm *vs.* 54–126 µm in *P. ruetzleri* **sp. nov.**). Four species are distinguished by the large size of diods, up to 200 µm or more: *P. kenyensis* Pulitzer-Finali, 1993; *P. angulospiculatus* (Carter, 1879), *P. japonica* (Hoshino, 1977), and *P. fromontae* Muricy, 2011. The remaining 12 species have diods shorter than 180 µm and triods up to 65 µm (actine length) like the new species. Three of these however have diods in two size categories (*P. galapagensis* Desqueyroux-Faúndez and van Soest, 1997, *P. edwardsi* Ereskovsky, Lavrov and Willenz, 2014, and *P. dariae* Ereskovsky, Lavrov and Willenz, 2014). In *P. clarionensis* and *P. erythraena* Lévi, 1958 the diods are shorter than 90 µm. *Plakortis albicans* Cruz-Barraza and Carballo, 2005 is white to ivory, with thin surface canals. Two species, *P. deweerdtaephila* Vicente, Zea and Hill, 2016 and *P. symbiotica* Vicente, Zea and Hill, 2016 have obligatory associations with haplosclerid sponges.

Plakortis ruetzleri **sp. nov.** is most similar to the remaining four species of the *simplex* species group, with brown colour, diods, triods, and without microrhabds. *Plakortis simplex* Schulze, 1880 can be brown, white, yellow or tan, and has both ectosomal and basal cavities which are lacking in the new species. *Plakortis insularis* Moraes and Muricy, 2003 is chocolate to light brown, releases a dark exudate with strong terpenoid smell in ethanol, has a fragile consistency, ectosome with pigmented cells, and low spicule density. *Plakortis copiosa* Pulitzer-Finali, 1993 is grey or brown outside and cream inside, with hard or fragile consistency, and have particularly symmetrical triods. *Plakortis communis* Muricy, 2011 is greyish-brown to black, has a tangential ectosomal reticulation with circular meshes, and a partly alveolar choanosomal skeleton. The new species therefore differs from all other *Plakortis* species by a unique combination of characters: brown colour, disorganized skeleton, presence of diods and triods, asymmetrical shape of triods, and the absence of microrhabds, basal and ectosomal cavities, dark exudates, and of terpenoid smell.

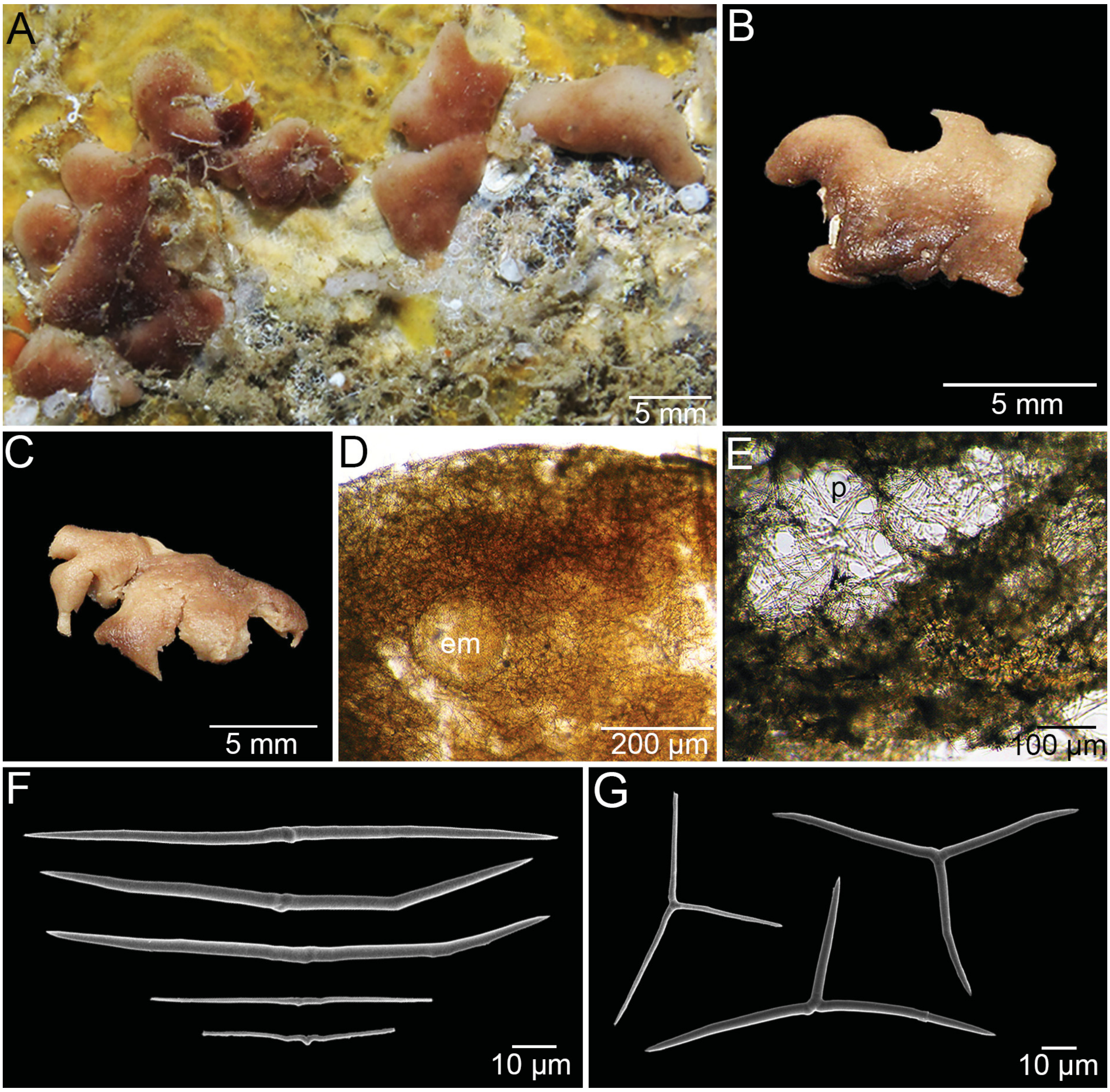

FIGURE 11. *Plakortis ruetzleri* **sp. nov.** A, specimens *in situ*. B, holotype MNRJ 21833 after fixation. C, paratype MNRJ 18462 after fixation. D, transversal section showing the disorganized choanosomal skeleton, the undifferentiated ectosomal skeleton and one embryo. E, tangential section showing the disorganized ectosomal skeleton and elliptical pores. F, diods. G, triods (F–G, SEM). Key: em, embryo; p, pores.

TABLE 4. Check-list of all records of Homoscleromorpha in the Pacific Ocean. Records identified only to genus level (as sp., *cf.*, or *aff.*) and those from the Antarctic were excluded.

Species	Localities	References
Corticium bargibanti Lévi & Lévi, 1983	Off Prony* (New Caledonia)	Lévi & Lévi 1983
Corticium candelabrum Schmidt, 1862**	GBR (NE Australia)	Burton 1934; Hooper & Wiedenmayer 1994; Hooper 2012
	Cebu (Philippines)	Schulze 1881; Lendenfeld 1903
	Pohnpei (as Ponapé, Micronesia)	Schulze 1881; Lendenfeld 1903
	Vanuatu	Hooper & Ekins 2004
	Funafuti Atoll* (Tuvalu)	Kirkpatrick 1900; Kelly-Borges & Valentine 1995
Corticium niger Pulitzer-Finali, 1996	Bismarck Sea* (Papua New Guinea)	Pulitzer-Finali 1996
	Boracay Island, Luzon Island (Philippines)	Ridley & Faulkner 2003; Sunassee *et al.* 2014
Corticium vaceleti sp. nov.	Bourail* (New Caledonia)	Present study
Corticium simplex Lendenfeld, 1907	N Australia	Hooper & Ekins 2004
	Flores Island (Indonesia)	Aoki *et al.* 2006, 2007a, b; Watanabe *et al*. 2007
Oscarella carmela Muricy & Pearse, 2004	California* (USA)	Muricy & Pearse 2004; Nichols *et al.* 2006; Goddard 2007
	Oregon (USA)	Goddard 2007
	Clipperton Island (French Polynesia)	van Soest *et al.* 2011
Oscarella kamchatkensis Ereskovsky *et al.*, 2009c	Kamchatka* (Russia)	Ereskovsky *et al.* 2009c; Sirenko 2013
Oscarella lobularis (Schmidt, 1862)**	New Zealand	Kelly *et al.* 2009
	SE Indonesia	Hooper *et al.* 2000
	N Sea of Japan, Sakhalin Island, Kurile Islands, Sea of Oshtok, Bering Sea (Russia)	Koltun 1962, 1966; Sirenko 2013
	Panama City (Panama)	de Laubenfels 1936
Oscarella malakhovi Ereskovsky, 2006	Vostok Bay* (Russia)	Ereskovsky 2006; Sirenko 2013
Oscarella pearsei Ereskovsky *et al*., 2017	California* (USA)	Ereskovsky *et al.* 2017
Oscarella stillans Bergquist & Kelly, 2004	Palawan: Fondeado Island*, Honda Bay (Philippines)	Bergquist & Kelly 2004; Kwon *et al.* 2017
Oscarella tenuis Hentschel, 1909	Hawaii (USA)	de Laubenfels 1954a, 1957; Bergquist 1977
	GBR (NE Australia)	Burton 1934; Hooper 2012
Placinolopha bedoti Topsent, 1897	Ambon* (Indonesia)	Topsent 1897; Lendenfeld 1903; Desqueyroux-Faúndez 1981; Hooper *et al.* 2000
Placinolopha sarai Lévi & Lévi, 1989	off Lubang Island* (Philippines)	Lévi & Lévi 1989
Placinolopha spinosa Kirkpatrick, 1900	Funafuti Atoll* (Tuvalu)	Kirkpatrick 1900; Kelly-Borges & Valentine 1995

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TABLE 4. (Continued)

Species	Localities	References
Plakina atka Lehnert *et al.*, 2005	Aleutian Islands*, SE Alaska, Gulf of Alaska (USA)	Lehnert *et al.* 2005; Stone *et al.* 2011; Lehnert & Stone 2016
	British Columbia (Canada)	Stone *et al.* 2011
Plakina bioxea Green & Bakus, 1994	California* (USA)	Green & Bakus 1994
Plakina corticolopha Lévi & Lévi, 1983	Off Prony* (New Caledonia)	Lévi & Lévi 1983
Plakina finispinata sp. nov.	Marquesas Islands* (French Polynesia)	Present study
Plakina fragilis Desqueyroux-Faúndez & van Soest, 1997	Galapagos* (Ecuador)	Desqueyroux-Faúndez & van Soest 1997; Chiriboga *et al.* 2012
Plakina kanaky Ruiz & Pérez, 2015	Bourail*, Hienghène (New Caledonia)	Ruiz *et al.* 2015
Plakina microlobata Desqueyroux-Faúndez & van Soest, 1997	Galapagos* (Ecuador)	Desqueyroux-Faúndez & van Soest 1997; Chiriboga *et al.* 2012
Plakina monolopha Schulze, 1880**	Rangitoto (New Zealand)	Bergquist 1961, 1968; Kelly *et al.* 2009
	Enoshima, Hakodate (Japan)	Thiele 1898; Lendenfeld 1903; Tanita & Hoshino 1989; Ise 2017
	Trat Province (Gulf of Thailand)	Putchakarn 2011
	Posyet Bay, Peter the Great Bay (N Sea of Japan, Russia)	Koltun 1971; Khodakovskaya 2005; Sirenko 2013
	Hawaii (USA)	de Laubenfels 1951; Bergquist 1977
Plakina muricyae Cruz-Barraza *et al.*, 2014	Revillagigedo, Nayarit*, Oaxaca (Mexico)	Cruz-Barraza *et al.* 2014
Plakina pacifica Desqueyroux-Faúndez & van Soest, 1997	Galapagos* (Ecuador)	Desqueyroux-Faúndez & van Soest 1997; Chiriboga *et al.* 2012
Plakina paradilopha Cruz-Barraza *et al.*, 2014	Revillagigedo* (Mexico)	Cruz-Barraza *et al.* 2014
Plakina tanaga Lehnert *et al.*, 2005	Aleutian Islands* (USA)	Lehnert *et al.* 2005; Stone *et al.* 2011
Plakina tetralophoides Muricy *et al.*, 1998	Sagami Bay* (Japan)	Tanita & Hoshino 1989 (as *P. tetralopha*); Muricy *et al.* 1998; Ise 2017
Plakina trilopha Schulze, 1880**	Rangitoto (New Zealand)	Bergquist 1961, 1968; Kelly *et al.* 2009
	Tingloy (Philippines)	Lévi & Lévi 1989
	Antofagasta (Chile)	Desqueyroux 1972; Desqueyroux & Moyano 1987
Plakinastrella clathrata Kirkpatrick, 1900	Funafuti Atoll* (Tuvalu)	Kirkpatrick 1900; Diaz & van Soest 1994; Kelly-Borges & Valentine 1995
	Mooloolaba (E Australia)	Yong *et al.* 2011; Hooper 2012
	Indonesia	Diaz & van Soest 1994
Plakinastrella ceylonica (Dendy, 1905)	Papua New Guinea	Kelly-Borges & Valentine 1995
	Chuuk (Micronesia)	Kelly-Borges & Valentine 1995

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TABLE 4. (Continued)

Species	Localities	References
Plakinastrella clippertonensis van Soest *et al.*, 2011	Clipperton Island* (French Polynesia)	van Soest *et al.* 2011; Cruz-Barraza *et al.* 2014
Plakinastrella mammillaris Lendenfeld, 1907	Fiji	Festa *et al.* 2012a, 2012b, 2013; di Micco *et al.* 2013
	Papua New Guinea	Kelly-Borges & Valentine 1995; Hooper & Ekins 2004
	Cebu (Philippines)	Hooper *et al.* 2000
	Komodo (Indonesia)	Diaz & van Soest 1994
Plakinastrella nicoleae sp. nov.	Marquesas Islands* (French Polynesia)	Present study
Plakinastrella osculifera sp. nov.	Hienghène* (New Caledonia)	Present study
Plakinastrella polysclera Lévi & Lévi, 1989	Off Lubang Island* (Philippines)	Lévi & Lévi 1989
Plakinastrella pseudolopha sp. nov.	Marquesas Islands* (French Polynesia)	Present study
Plakortis albicans Cruz-Barraza & Carballo, 2005	Sinaloa* (Mexico)	Cruz-Barraza & Carballo 2005
	Revillagigedo, Nayarit, Oaxaca (Mexico)	Cruz-Barraza *et al.* 2014
Plakortis angulospiculatus (Carter, 1879)**	Papua New Guinea	Hooper & Ekins 2004
Plakortis bergquistae Muricy, 2011	N Sulawesi* (Indonesia)	Muricy 2011; Gushiken *et al.* 2015
Plakortis clarionensis Cruz-Barraza *et al.*, 2014	Revillagigedo* (Mexico)	Cruz-Barraza *et al.* 2014
Plakortis communis Muricy, 2011	GBR (NE Australia)	Muricy 2011; Hooper 2012
	Cebu (Philippines)	Muricy 2011
	Taveuni (Fiji)	Muricy 2011
Plakortis galapagensis Desqueyroux-Faúndez & van Soest, 1997	Galapagos* (Ecuador)	Desqueyroux-Faúndez & van Soest 1997; Chiriboga *et al.* 2012
Plakortis hooperi Muricy, 2011	Motupore Island* (Papua New Guinea)	Muricy 2011
	GBR (NE Australia)	Hooper 2012
Plakortis japonica (Hoshino, 1977)	Hiwasa* (Japan)	Hoshino 1977, 1981 (as *P. simplex*); Yanai *et al.* 2003; Ise 2017
Plakortis lita de Laubenfels, 1954	Chuuk (as Truk Atoll)*, Ponhpei (as Ponapé) (Micronesia)	de Laubenfels 1954b; Diaz & van Soest 1994; Kelly-Borges & Valentine 1995; Muricy 2011
	Mota Lava (Vanuatu)	Longakit *et al.* 2005; Muricy 2011
	Viti Levu (Fiji)	Longakit *et al.* 2005; Muricy 2011
	Cebu (Philippines)**	Bakus & Nishyama 1999, 2000; Longakit *et al.* 2005
	Banda Sea, Sulawesi (Indonesia)	Diaz & van Soest 1994; Longakit *et al.* 2005; Calcinai *et al.* 2017
	Madang Bay, Bismark Sea (Papua New Guinea)	Diaz & van Soest 1994; Kelly-Borges & Valentine 1995; Harrison & Crews 1998

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TABLE 4. (Continued)

Species	Localities	References
	Coral Sea, GBR (NE Australia)	Muricy 2011; Hooper 2012
	S Korea	Sim 1990
	Taiwan	Lim *et al.* 2016
	Okinawa (Japan)	Takada *et al.* 2001; Ise 2017
Plakortis nigra Lévi, 1953	Sulawesi (Indonesia)	Hooper *et al.* 2000; Pettit *et al.* 2004
	Palau	Sandler *et al.* 2002
	GBR (NE Australia)	Hooper 1994; Hooper & Ekins 2004
	Vanuatu	Hooper & Ekins 2004
	Fiji	Hooper & Ekins 2004
Plakortis quasiamphiaster Díaz & van Soest, 1994	Espiritu Santu*, Efate, Malekula, Epi, Emae (Vanuatu)	Diaz & van Soest 1994; Kelly-Borges & Valentine 1995; Zampella *et al*. 2001; Hooper & Ekins 2004; Ralifo *et al.* 2007; Muricy 2011; Soapi *et al.* 2013
	Motua Levu, Viti Levu, Naukhatuvu (Fiji)	Muricy 2011; Bugni *et al.* 2008; Feussner *et al.* 2012
	Hunga Lagoon (Tonga)	Muricy 2011
	GBR (NE Australia)	Hooper 2012
Plakortis ruetzleri sp. nov.	Marquesas Islands* (French Polynesia)	Present study
Plakortis simplex Schulze, 1880**	Off Yaté (New Caledonia)	Lévi & Lévi 1983
	Bismarck Sea (Papua New Guinea)	Pulitzer-Finali 1996
	Aru (Indonesia)	Hentschel 1912
	Ambon (Indonesia)	Topsent 1897, 1901, 1928; Lendenfeld 1903; Desqueyroux-Faúndez 1981; Hooper *et al.* 2000
	Off Lubang Island (Philippines)	Lévi & Lévi 1989
	Vietnam	Hooper *et al.* 2000
	Cheju Island, Keomun Island, Chujado Island (S Korea)	Sim 1994; Lee & Sim 1999; Sim & Shim 2006; Oh *et al.* 2013
	Nan-Wan (Taiwan)	Shen *et al.* 2001
	Yongxing Island, Xisha Island (S China Sea)	Liu *et al.* 2011, 2012; Yu *et al.* 2012; Zhang *et al.* 2013; Chianese *et al.* 2014, 2015
	Japan	Hoshino 1987; Ise 2017
	Ailing-Lap-Lap Atoll (Marshall Islands)	de Laubenfels 1954b; Kelly-Borges & Valentine 1995
	Hawaii (USA)	de Laubenfels 1950, 1951, 1957; Bergquist 1977
	Rocas Alijos (Mexico)	Austin 1996

GBR, Great Barrier Reef. *, type localities. **, identification probably inaccurate, records needs revision.

Discussion

The description of six new species in this study increases the diversity of the class Homoscleromorpha to 120 species, 50 of which occur in the Pacific Ocean (41.6%; Fig. 3, Table 4). Two new species, *Corticium vaceleti* **sp. nov.** and *Plakinastrella osculifera* **sp. nov.**, are added to the fauna of New Caledonia, from where only four species were known before this study: *Corticium bargibanti*, *Plakina corticolopha* Lévi & Lévi, 1983, *P. kanaky,* and the *Plakortis simplex* complex (Lévi & Lévi 1983; Ruiz *et al.* 2015). The other four species described here, viz., *Plakina finispinata* **sp. nov.**, *Plakinastrella pseudolopha* **sp. nov.**, *Plakinastrella nicoleae* **sp. nov.**, and *Plakortis ruetzleri* **sp. nov.**, are the first records of Homoscleromorpha in the Marquesas Islands, where the sponge fauna remains very poorly known (Pérez *et al.* 2016). The new species are easily distinguishable from each other by spicule shape and size (Tables 1–3). They were all collected in dark or shaded habitats such as underwater caves and tunnels, which are the preferred environments of many homoscleromorph species (Ereskovsky *et al.* 2009b; Gerovasileiou & Voultsiadou 2012, 2016; Lage *et al.* 2018). The Homoscleromorpha fauna of the Pacific Ocean is probably much more diverse than currently estimated, and there is a high probability that explorations of further cryptic habitats in remote locations will shed light on a huge sponge diversity presently unknown.

The significance of the unique pseudolophose spicules found in *Plakinastrella pseudolopha* **sp. nov.** is puzzling. Three main features characterize these spicules: a slightly spiral shape, a ramification pattern with a single, medial round forming conical fused rays, and the presence of two to four irregular actines in each spicule. The number of actines is often difficult to determine due to the spiral shape of the spicule and the fusion of rays. The similarity with some lophose calthrops and candelabra suggests an affinity of this species with either *Corticium* or *Plakina*, but both the ectosomal skeleton with a palisade and a tangential reticulation, and the distinction of two size classes of both diods and triods, are more similar to *Plakinastrella*. Preliminary *cox-1* sequence data (authors' unpublished results) also support a close relationship with *Plakinastrella* species. A thorough phylogenetic analysis of the family Plakinidae using both molecular and morphological characters is needed to clarify the affinities of this species, and the discovery of pseudolophose spicules widens the known diversity of spicule morphologies within the Homoscleromorpha.

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