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Diversity of Indo-Australian *Plakortis* (Demospongiae: Plakinidae), with description of four new species

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A collection of 32 specimens of the genus Plakortis *(Demospongiae: Plakinidae) from Australia and the Indo-Pacific is here examined. Six species are described, four of which are new to science.* Plakortis lita *has microrhabds, an irregular tangential ectosomal reticulation, a confused choanosomal skeleton and irregular diods and triods.* Plakortis quasiamphiaster *has quasiamphiasters (spined diods and triods), spheres and a skeleton with a distinct subectosomal region.* Plakortis communis *sp. nov. has diods and a tangential ectosomal reticulation with circular meshes; triods and spheres may be present or absent.* Plakortis bergquistae *sp. nov. has diods in two size-classes, the larger one up to 330–356 μm long, and large triods (actines up to 75–121 μm long).* Plakortis fromontae *sp. nov. has large diods (up to 220 μm long), rare triods and a double ectosomal reticulation.* Plakortis hooperi *sp. nov. has diods, triods, microrhabds and spheres, with a confused ectosomal skeleton, a thinly encrusting shape and cream colour. Detailed descriptions of external morphology, skeletal arrangement of the ectosome and spicules in SEM are essential for the taxonomy of* Plakortis. *The number of valid species in the genus is raised from 15 to 19. A key to Indo-Australian species of* Plakortis *is given.*

Keywords: taxonomy, Porifera, Homosclerophorida, *Plakortis*, Australia, Indo-Pacific

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INTRODUCTION

The small sponge order Homoscleromorpha, with a single family Plakinidae, seven genera and approximately 60 species, has recently become the subject of an increasing interest by biologists. This is due to the discovery that its species share characters with other metazoan phyla that are absent in other sponges: the presence of an acrosome in spermatozoa (Baccetti *et al.*, 1986) and a basal lamina underlining choanocytes and pinacocytes both in adults and in the larvae (Boute *et al.*, 1996; Boury-Esnault *et al.*, 2003). In addition, phylogenetic analyses of 18S rRNA, LSU rDNA and COI sequences suggest that the Homoscleromorpha may not form a monophyletic group with other Demospongiae, appearing instead more closely related to the Calcarea (Borchiellini *et al.*, 2004; Nichols, 2005; Boury-Esnault, 2006).

Our understanding of the phylogenetic relationships of the Homoscleromorpha is partly hampered by the limited knowledge on its diversity. The low number of species currently known largely reflects insufficient sampling due to small size, rarity and cryptic habits of many species, together with the existence of several unresolved complexes of allegedly cosmopolitan species (e.g. *Oscarella lobularis*, *Plakina monolopha*, *Plakina trilopha* and *Plakortis simplex*), rather than a really low diversity. Also, sponges of the cosmopolitan plakinid genus *Plakortis* Schulze, 1880 are known to produce several interesting natural products and bioactive compounds such as cyclic peroxides (e.g. plakorstatins), pyrroloacridine alkaloids (e.g. plakinidines and amphiasterins) and polyketides (e.g. plakortides), which display antibacterial, antifungal, cytotoxic, antineoplastic and antineuroinflammatory activities (e.g. Higgs & Faulkner, 1978; Davidson, 1991; Yao & Steliou, 2002; Pettit *et al.*, 2004; Rahm *et al.*, 2004; Laroche *et al.*, 2007; Ralifo *et al.*, 2007; Mayer *et al.*, 2008). This chemical diversity makes the genus *Plakortis* an interesting target group for pharmacological studies.

Despite its importance and wide distribution, the genus *Plakortis* has many unsolved taxonomic problems, such as cryptic speciation and alleged but unlikely cosmopolitanism of some species (e.g. *P. angulospiculatus* (Carter, 1879) and *Plakortis simplex* Schulze, 1880). The spiculation of *Plakortis* is simple, composed almost exclusively of irregular diods and triods, making the distinction of closely related species very difficult (Diaz & van Soest, 1994; Muricy & Diaz, 2002). Only in a few *Plakortis* species there are other spicules such as microrhabds and quasiamphiasters to help in identification (*P. lita* de Laubenfels, 1954, *P. microrhabdifera* Moraes & Muricy, 2003 and *P. quasiamphiaster* Diaz & van Soest, 1994). The architecture of the aquiferous system and of both choanosomal and tangential ectosomal skeletons provides useful taxonomic characters (cf. Lévi, 1952; Moraes & Muricy, 2003), but it has been rarely described in detail. Furthermore, as few descriptions have been documented with underwater photographs, there is little information available on external morphological characters observed *in situ*,

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which could also provide useful information for species discrimination (e.g. Zea, 1987; Bakus & Nishiyama, 2000; Moraes & Muricy, 2003; Cruz-Barraza & Carballo, 2005). In this paper, particular attention is given to the architecture of the tangential ectosomal skeleton and, when possible, to the morphology of living specimens.

So far, 15 valid species of *Plakortis* have been described worldwide: *P. albicans* Cruz-Barraza & Carballo, 2005; *P. angulospiculatus* (Carter, 1879), *P. copiosa* Pulitzer-Finali, 1993, *P. erythraena* Lévi, 1958, *P. galapagensis* van Soest & Desqueyroux-Faúndez, 1997, *P. insularis* Moraes & Muricy, 2003, *P. japonica* (Hoshino, 1977), *P. kenyensis* Pulitzer-Finali, 1993, *P. lita* de Laubenfels, 1954, *P. halichondrioides* (Wilson, 1902), *P. microrhabdifera* Moraes & Muricy, 2003, *P. nigra* Lévi, 1953, *P. quasiamphiaster* Diaz & van Soest, 1994, *P. simplex* Schulze, 1880 and *P. zyggompha* (de Laubenfels, 1934). Most of these species have restricted distributions, with the exception of *P. simplex*, *P. angulospiculatus* and, to a lesser extent, *P. nigra*.

After its description from the Mediterranean (Schulze, 1880), the type species *P. simplex* has been recorded from distant regions such as the Mediterranean Sea, north-east Atlantic, east Atlantic, south-west Atlantic, Caribbean Sea, Indo-Pacific, north-west Pacific, central Pacific and west Indian Ocean (e.g. Schulze, 1880; Topsent, 1897, 1901, 1928, 1934; Hentschel, 1912; Burton, 1930; de Laubenfels, 1950; Lévi, 1952; Boury-Esnault, 1973; Thomas, 1973; Vacelet *et al.*, 1976; Cruz & Bacallado, 1981; Hoshino, 1981; Pulitzer-Finali, 1986). However, in view of the low dispersal abilities of sponge larvae, the apparent co-specificity of distant, disjunct populations probably only reflects the difficulty of taxonomists to discriminate between closely related species due to the simple and non-diagnostic nature of their spiculation and external morphology (Lévi, 1953; Diaz & van Soest, 1994; Muricy & Diaz, 2002), similarly to other allegedly cosmopolitan species such as *Chondrilla nucula, Clathrina clathrus*, *Oscarella lobularis* and *Plakina trilopha* (Solé-Cava *et al.*, 1991; Muricy *et al.*, 1996a, b, 1998; Klautau *et al.*, 1999). Therefore, *Plakortis simplex sensu lato* most probably defines a complex of sibling species rather than a single biological species and will be treated here accordingly. Here I will use the expression 'species complex' for such groups composed of sibling species that are currently not discriminated by morphological methods, and 'species group' for groups of similar but clearly distinct species (see Discussion).

As described by Schulze (1880) and Muricy & Diaz (2002), *Plakortis simplex sensu stricto* is a thin encrustation (maximum 5 mm thick), light-coloured (light brown, tan, yellow or white), with smooth surface, few small oscules (1 mm in diameter) and a compressible consistency. The aquiferous system has both ectosomal inhalant cavities and basal exhalant cavities; the skeleton is confused in both the choanosome and ectosome. The spicules are diods 60–150 μm long and triods with actines 20–50 μm long. In contrast, the *Plakortis simplex* species complex (or *P. simplex sensu lato*) in the Pacific and Indian Oceans is a heterogeneous group that includes dull olive brown, dull grey, pale yellow brown, greenish, bluish black externally and white internally, and dark blue sponges, 0.2–4.0 cm thick, with surface smooth or tuberculated, and with oscules up to 5 mm in diameter. The skeleton is usually described as confused and the aquiferous system has not been described at all. The spicules are diods in one size-class (varying from 40–250 μm) or in two size-classes (25–40 μm and 80–140 μm), alone or accompanied by triods with actines measuring 10–100 μm long (Topsent, 1897, 1928; Hentschel, 1912; de Laubenfels, 1950; Thomas, 1973; Vacelet *et al.*, 1976; Desqueyroux-Faúndez, 1981; Lévi & Lévi, 1983). Due to this high heterogeneity and to insufficient descriptions, comparisons to *P. simplex* will be based here on the original and subsequent descriptions from the type locality (Naples, Italy) and nearby areas (viz., Adriatic and Mediterranean Seas), here referred to as *Plakortis simplex sensu stricto*.

The sponge fauna of Australia and the Indo-Pacific is relatively well known (e.g. van Soest, 1989; Hooper, 2005), but to date only four species of *Plakortis* were described from this region: the species complex *P. simplex* from Indonesia (Aru Island and Amboine), Papua New Guinea and New Caledonia, *Plakortis* aff. *angulospiculatus* from Indonesia and Papua New Guinea, *P. lita* from the Caroline Islands, Indonesia, Papua New Guinea and Philippines, and *P. quasiamphiaster* from Vanuatu and Fiji (Topsent, 1897; Hentschel, 1912; de Laubenfels, 1954; Desqueyroux-Faúndez, 1981; Lévi & Lévi, 1983; Diaz & van Soest, 1994; Pulitzer-Finali, 1996; Bakus & Nishiyama, 2000; Longakit *et al.*, 2005). Several other records of *P. angulospiculatus*, *P. simplex*, *P. lita*, *P. nigra*, *P.* cf. *nigra* and *Plakortis* sp. were reported without description, mostly in checklists, ecological, chemical and pharmacological studies (e.g. van Soest, 1989, 1990; West *et al.*, 1990; Hooper *et al.*, 2000; Pettit *et al.*, 2004, Hooper & Ekins, 2004; Pangan *et al.*, 2007). Here I describe a collection of six species of *Plakortis* from Australia and the Indo-Pacific, four of which are new to science, and discuss the usefulness of different morphological characters for the taxonomy of *Plakortis*. A key to Indo-Australian species of *Plakortis* is provided.

MATERIALS AND METHODS

The specimens studied were housed in the sponge collections of the Western Australian Museum, Perth, Australia (WAM) and in the Queensland Museum, Brisbane, Australia (QM) and were kindly sent on loan by their curators, Dr Jane Fromont from WAM and Drs Steve Cook and Merrick Ekins from QM. Type specimens of *Plakortis quasiamphiaster* and *P. lita* were loaned from the Porifera collections of the Zoological Museum of Amsterdam, The Netherlands (ZMAPOR) and The Smithsonian Institution (USNM), Washington DC, USA, by Dr Rob van Soest and Dr Klaus Rützler, respectively. Specimens were collected from October 1990 to July 1999 by different researchers (see 'Specimens examined' sections). Collections were made through SCUBA and free diving from 7–42 m depth in Australia (western and eastern coasts), Vanuatu, Fiji, Tonga, Indonesia, Philippines, Palau, and Papua New Guinea. Specimens collected were preserved in ethanol 70%. Spicule slides were prepared by dissociation of a small fragment of the sponge in boiling nitric acid. Hand-made, thick sections of the skeleton were observed under light microscope; transversal sections were made in paraffin-embedded specimens, and tangential sections of the ectosome were made in wet or dry specimens. Two to 20 spicules of each kind, depending on their abundance, were measured per individual. Spicule measurements are expressed as minimum–medium–maximum length/minimum–maximum width in μm (number of

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measurements). Other abbreviations used: MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; MNHN, Muséum National d'Histoire Naturelle, Paris, France; UFRJPOR, Porifera collection of the Universidade Federal do Rio de Janeiro, Brazil; USNM, United States National Museum, Smithsonian Institution, Washington DC. Scanning electron microscopy (SEM) of spicules was made in Jeol JSM-5310 and Jeol JSM-6390 electron microscopes after metallization with gold.

SYSTEMATICS

Order HOMOSCLEROPHORIDA Dendy, 1905
Family PLAKINIDAE Schulze, 1880
Genus *Plakortis* Schulze, 1880

DEFINITION

Plakinidae with a skeleton formed by diods and triods in varying abundance. Diactine-derived microscleres (microrhabds) spheres and spined diods (amphiaster-like spicules) may be present in some species (emended from Muricy & Diaz, 2002).

Plakortis lita de Laubenfels, 1954

(Figures 1 & 2; Table 1)

Plakortis lita de Laubenfels, 1954: 247; Diaz & van Soest, 1994: 104. Non-*Plakortis lita sensu* Bakus & Nishiyama, 2000: 1164; Longakit *et al.*, 2005: 58.

DIAGNOSIS

Brown or black, cushion-shaped *Plakortis* with microrhabds, an irregular tangential ectosomal reticulation, a confused choanosomal skeleton and thin, irregular, acerate diods and triods.

SPECIMENS EXAMINED

Holotype: USNM 23069 (by original designation; cf. de Laubenfels, 1954: 247), Micronesia: Caroline Islands: Truk Atoll: Moen Islet, 7°28′0.84″N–151°50′33.04″E, 10 August 1949, 3 m depth.

ADDITIONAL SPECIMENS

Australia: Queensland: GQM-305093, mid east-side lagoon, Osprey Reef, Coral Sea, 13°53.3′S–146°39.1′E, J.N.A. Hooper coll., 24 February 1995, 26 m depth; GQM-315928, Lagoon entrance, Osprey Reef, Coral Sea, 13°53′47.10″S–146°38′50.30″E. J.A. Kennedy and D.W. Edson coll., 13 December 1999, 20 m depth; GQM-305715, Bacci Cay, Riversong Cays, Swain Reefs, 21°38.4′S–152°23.1′E, J.N.A. Hooper, S.D. Cook, J.A. Kennedy, P.A. Tompkins coll., 29 July 1995, 28 m depth; GQM-314186, Fitzroy Reefs, Bunker Group, 23°37.88′S–152°07.84′E, J.N.A. Hooper, S.D. Cook, J.A. Kennedy, A. Carrol coll.; 26 February 1998, 7.7 m depth; GQM-314454, Davies Reefs, 18°49.555′S–147°37.561′E, S.D. Cook, J.A. Kennedy, C.I. Adams, G. Wörheide coll., 24 January 1998, 24 m depth; GQM-314532, GQM-314534, Stanley Reef, 19°18.83′S–148°02.56′E, S.D. Cook, J.A. Kennedy, C.I. Adams, G. Wörheide coll., 25 January 1999, 30 m depth; GQM-315094, Inner Gneerings, Sunshine Coast, 26°39.19′S–153°10.996′E, S.D. Cook, J.A. Kennedy, J.N.A. Hooper, G. Wörheide coll., 14 October 1998, 19 m depth; GQM-315240, Hook Reef Lagoon, 19°45.229′S–149°10.753′E; S.D. Cook, J.A. Kennedy, C.I. Adams, G. Wörheide, D. Edson coll., 5 June 1999, 9.4 m depth; GQM-315311, Edgell Reef, 20°08.879′S–149°55.152′E, S.D. Cook, J.A. Kennedy, C.I. Adams, G. Wörheide, D. Edson coll., 6 July 1999, 18 m depth. Vanuatu: Mota Lava Island: GQM-315558, Banks Territory, 13°43.130′S–167°37.423′E, J.A. Kennedy, G. Wörheide coll., 15 July 1999, 27 m depth. Fiji: Viti Levu: GQM-315197, north side of Òné Island, off Rakiraki, 17°16′48.40″S–178°12′55.77″E, J.N.A. Hooper, A. Carrol, A. Wright coll., 5 March 1999, 19.8 m depth.

DESCRIPTION (FIGURE 1A–C)

Sponge thickly encrusting, irregular. Size up to 18 cm wide and 1–2 cm thick. Size of collected fragments up to 6.0 × 5.0 cm wide by 2 cm thick. External colour *in vivo* black, dark brown or grey-brown; internal colour brown or grey-brown. Preserved specimens are reddish to dark greyish brown. Surface smooth, slimy or sticky, sometimes with large tubes with small terminal oscules, which are contracted in preserved specimens. Consistency soft, liver-like, easily torn.

SKELETON (FIGURE 1D, E)

Ectosomal skeleton dense, forming an irregular reticulation with round or elliptical meshes, 110–165 μm in diameter (Figure 1D). Subectosomal lacunae often higher than wide, 80–200/100–700 μm, separated by spicule columns 50–150 μm thick. Choanosomal skeleton is a confused, low-density mass of diods dispersed between choanocyte chambers and canals (Figure 1E). Choanosome with large canals, 200–600 μm in diameter, and spherical to ovoid choanocyte chambers, 30–60 μm in diameter.

SPICULES (FIGURE 1F–H; TABLE 1)

Diods abundant, slightly curved, smooth or irregular, with a well-marked centre; the central irregularity varies from a barely detectable thickening to a series of 1–4 short bends which look like bumps or thicker rings (Figure 1F). Endings acerate; styloid modifications are rare: 23–87–145/0.5–8.0 μm (N = 188).

Triods relatively rare, absent in one specimen, irregular, with high variation in angles between actines and in size of actines in the same spicule, usually with acerate endings (Figure 1G): actines 1–20–66/0.5–2.5 μm (N = 60).

Microrhabds irregular, strongyloid (Figure 1H), sometimes vaguely triactinal: 1–25 × 0.5–2.0 μm (N = 60).

REPRODUCTION

Ovoid or spherical larvae 140–1000 μm in diameter were found in specimens collected in January, February and August.

HABITAT

Coral reefs: fore-reef, back-reef, boomies and sand, gulleys, spur and groove, patch reef in lagoon, pinnacles, *Acropora* thickets, vertical walls, sheer slope, and terraces, 3–30 m depth.

DISTRIBUTION

Indo-West Pacific: Caroline Islands, Micronesia (Truk Atoll and Ponape; de Laubenfels, 1954), Indonesia, Papua New Guinea (Diaz & van Soest, 1994), Vanuatu, Fiji and Eastern Australia (Great Barrier Reef, Queensland) (present study; Figure 2).

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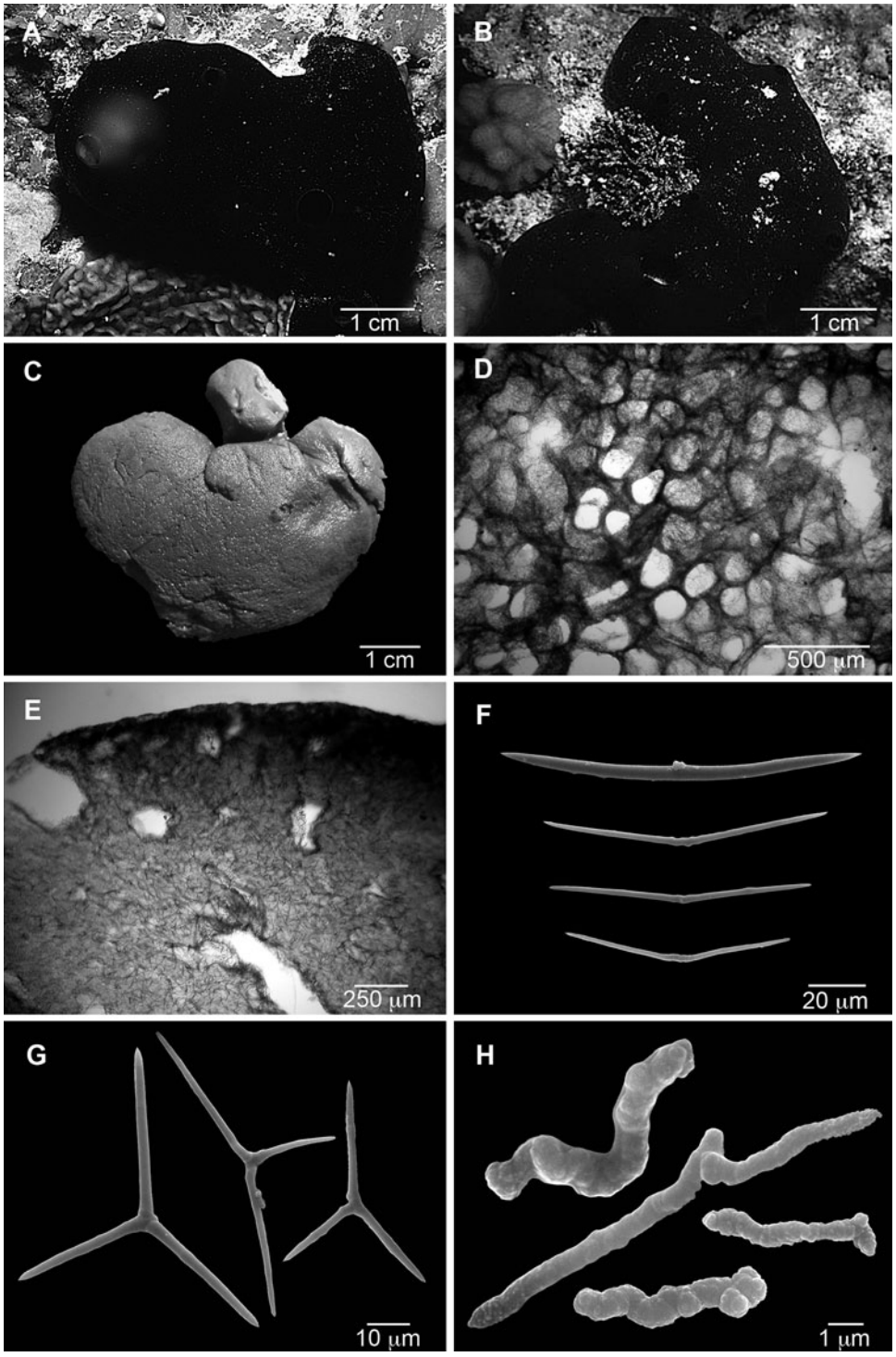

Fig. 1. *Plakortis lita*. (A, B) Specimens *in situ*: (A) GQM-315197 from Fiji; (B) GQM-315928 from Osprey Reef, Coral Sea, north-eastern Australia (photographs by the collectors); (C) preserved specimen (GQM-305093); (D) ectosome (tangential section); (E) choanosome and ectosome (transverse section); (F) diods; (G) triods; (H) microrhabds.

REMARKS

In the original description, de Laubenfels (1954) reported the absence of triods in all his specimens, but close observation showed that they are present both in the holotype and in most specimens examined here. Although rare, triods were also observed by Diaz & van Soest (1994). *Plakortis lita* is easily recognizable by the presence of microrhabds, which are so far only shared in the genus with *P. microrhabdifera* from the central Western Atlantic (Atol das Rocas, north-east Brazil; Moraes & Muricy, 2003) (see the description of *P. hooperi* sp. nov. below). *Plakortis lita* and *P. microrhabdifera* strongly differ in colour (black, dark reddish or greyish brown in *P. lita*, light brown in *P. microrhabdifera*), ectosomal skeleton (with irregular, mostly elliptical meshes in a single size category in *P. lita* and with regular, rounded meshes in two size-classes in *P. microrhabdifera*), and in diod shape

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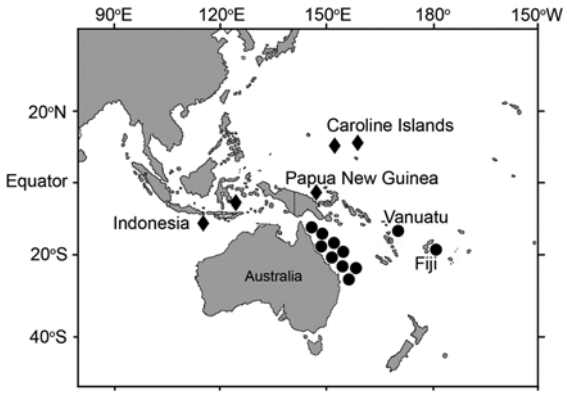

Fig. 2. Distribution of *Plakortis lita*. White circles, previous records; black circles, new records.

(with acerate endings in *P. lita*, often strongyloid in *P. microrhabdifera*). So far, triods have not been found in *P. microrhabdifera* (Moraes & Muricy, 2003; Muricy *et al.*, 2008).

Plakortis lita sensu Bakus & Nishiyama (2000) and Longakit *et al.* (2005) from Cebu Island, Philippines, differs from *Plakortis lita sensu* de Laubenfels, 1954 in the firm consistency, more regular diods, and absence of microrhabds; it therefore must be assigned to a different species. It is similar to *P. nigra* in its dark colour, thick encrusting habit and firm consistency; however, its colour is dark brown versus black in *P. nigra*, its oscules are smaller and more numerous than in *P. nigra* (which has a single apical oscule, 3 mm in diameter) and its spicules are larger than those of *P. nigra* (90–148 versus 20–90 μm). The dark brown *Plakortis* from Cebu is therefore provisionally included in the *Plakortis simplex* species complex, but it is probably a new species.

Plakortis quasiamphiaster Diaz & van Soest, 1994
(Figures 3 & 4; Table 2)

Plakortis quasiamphiaster Diaz & van Soest, 1994: 107.

DIAGNOSIS

Plakortis with quasiamphiasters and a skeleton with a distinct subectosomal region.

Table 1. Intraspecific variation of spicule measurements of *Plakortis lita* (length minimum–medium–maximum in μm). h, holotype.

Specimens	Diods	Triod actines	Microrhabds
USNM 23069 (h)	62–74–90	20–22–25	4–15
GQM-315311	31–78–113	27–37–49	4–8
GQM-314186	23–57–93	17–27–30	4–11
GQM-314454	66–84–101	7–17–28	4–17
GQM-315928	99–114–129	24–27–29	3–12
GQM-315094	57–91–121	10–25–53	3–10
GQM-314532	60–117–145	–	6–20
GQM-315197	25–81–119	20–27–37	5–9
GQM-305093	53–70–101	29–34–39	2–14
GQM-315558	48–115–144	2–40–66	4–8
GQM-314534	63–92–117	1–15–30	2–10
GQM-305715	33–60–91	2–13–38	5–25
GQM-315240	49–88–110	8–26–45	1–12

SPECIMENS EXAMINED

Holotype: ZMAPOR 7777, Vanuatu, P. Crews coll., 20 m depth.

ADDITIONAL SPECIMENS

Vanuatu: Espiritu Santo: GQM-306848, Malvioror Reef, Hog Harbour, 15°08′S–167°06′E, J.N.A. Hooper coll., 28 June 1996, 42 m depth. Malicolo: GQM-306864, GQM-306907, outer Reef, Benehour Point, South-West Bay, 16°30′S–167°24′E, J.N.A. Hooper coll., 4 July 1996, 32 m depth. Emae: GQM-306925, 17°03′S–168°21′E, ORSTOM Nouméa coll., 9 July 1996, 20 m depth. Malekula Island: GQM-312976, 21 May 1997, 21.7 m depth; GQM-313029, 22 May 1997, 35.5 m depth; both from Dixon Reef, 16°21′S–167°21′E, J.N.A. Hooper coll. Fiji: Motua Levu: GQM-312813, Goldea Wall, 16°41′S–179°38′E, J.N.A. Hooper coll., 30 October 1996, 34.2 m depth. Tonga: GQM-313236, Hunga Lagoon, 18°42′S–174°07′W, J.N.A. Hooper coll., 9 November 1997, depth unknown; GQM-313281, Fotula, rock just off west coast of Vava'u Island, 18°38′S–174°04′W, J.N.A. Hooper coll., 13 November 1997, 32 m depth.

DESCRIPTION (FIGURE 3A)

Sponge thickly encrusting to massive, columnar or lobate. Size up to 5 cm wide by 12 cm high. Colour *in vivo* usually reddish-brown, sometimes paler internally, but one specimen was deep blue. Preserved specimens are light or dark reddish-brown, and often produce a dark red-brown exudate. The sponge is firmly attached to the substrate through a large base. Surface uniform, smooth or microhispid, often striated or with superficial canals converging to the oscules. Oscules rounded, up to 5 mm in diameter, surrounded by a membrane, contracted in 70% ethanol. Consistency compressible but resistant in spirit; dry specimens are brittle.

SKELETON (FIGURE 3B, C)

Ectosome distinct, 100–1012 μm thick, with parallel, ascending multispicular tracts 19–98 μm in diameter and 5–200 μm apart, slightly protruding through the surface (Figure 3B). The ectosome has a tangential reticulation of spicule tracts forming rounded meshes (Figure 3C). In most specimens there is a well-marked subectosomal region, 250–1265 μm thick, composed of an irregular reticulation of multispicular tracts 20–80 μm thick, forming rounded or irregular meshes 49–200 μm in diameter (Figure 3B). Within the subectosomal region and between it and the ectosome, there are elongated or elliptical aquiferous cavities, 50–1012 μm long. Inner choanosome with a dense, confused reticulation of diods (Figure 3B).

SPICULES (FIGURE 3D–H; TABLE 2)

Abundant diods, robust, straight or curved, smooth, relatively uniform, with a lightly marked centre, just slightly thickened or with 1–3 very short, almost imperceptible bends; endings acerate: 28.7–94.8–179.6/0.8–7 μm (N = 166; Figure 3D).

Triods relatively abundant, smooth, with variable angles between actines and size of actines in the same spicule, usually with acerate endings: actines 10.5–34.3–78.4/1–5 μm (N = 121; Figure 3E).

Diactinal quasiamphiasters relatively abundant to rare, straight or curved, with thick, irregular centre and acerate endings (Figure 3F). Each spicule has 2–15 spines, 1–45 μm

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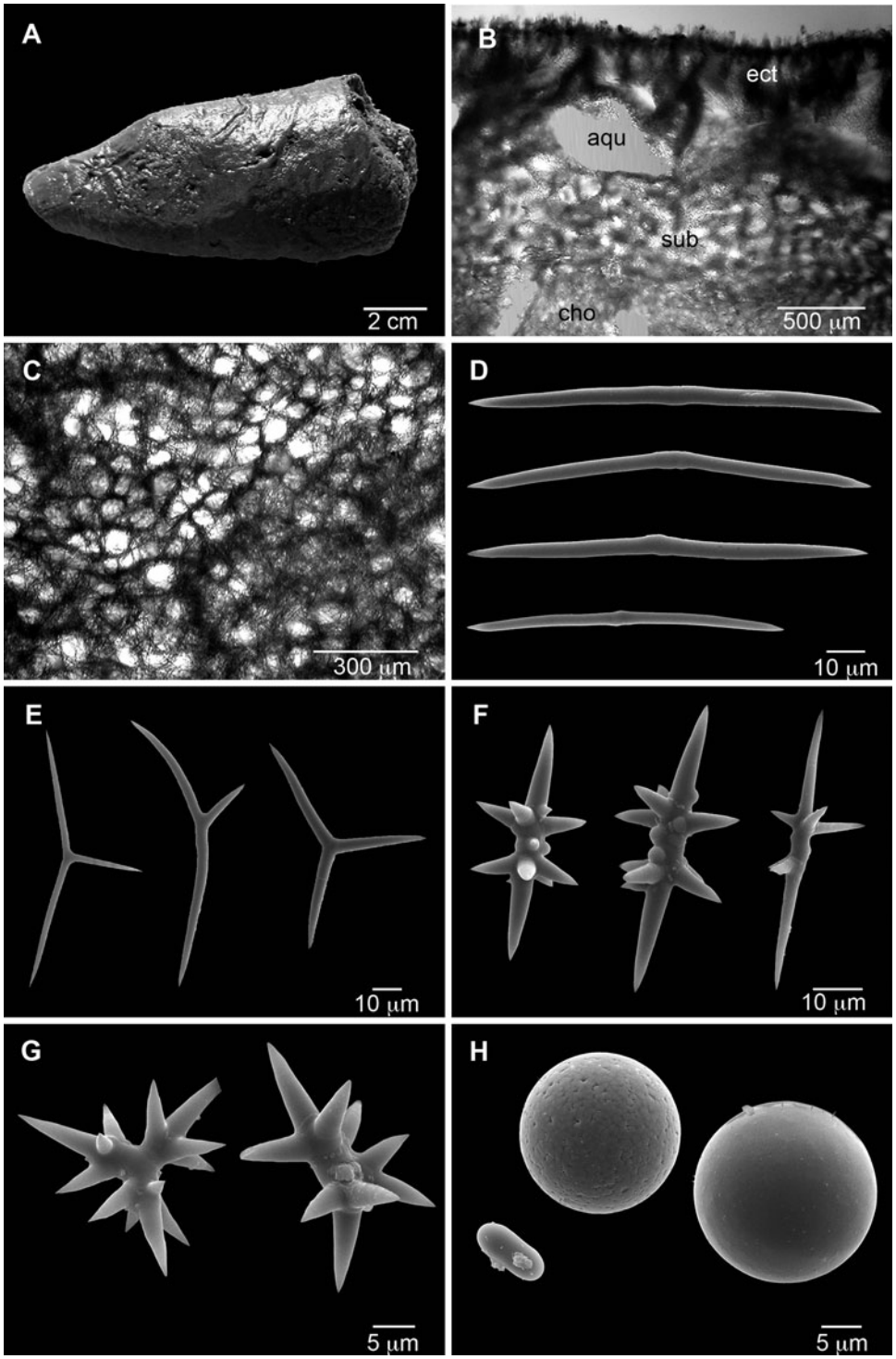

Fig. 3. *Plakortis quasiamphiaster*. (A) Preserved specimen (GQM-306925); (B) choanosome and ectosome (transverse section; ect, ectosome; sub, subectosomal region; aqu, aquiferous cavities; cho, inner choanosome); (C) ectosome (tangential section); (D) diods; (E) triods; (F) diactinal quasiamphiasters; (G) triactinal quasiamphiasters; (H) spheres and microstrongyle.

long, usually concentrated in two rows in opposite sides near the centre: 9.0–33.3–91.0/1.5–6.0 μm (N = 117).

Triactinal quasiamphiasters rare or absent in most specimens (Figure 3G): actines 7.8–11.3–16.0/1–4 μm, with spines 2–7 μm long (N = 9).

In all specimens studied there are smooth or irregular spheres, 2–15 μm in diameter, which are sometimes elongated to form short thick microstrongyles, 4–10/2–4 μm (Figure 3H).

REPRODUCTION

Ovoid larvae, 200–393 μm long, were found in a few specimens collected in July and October.

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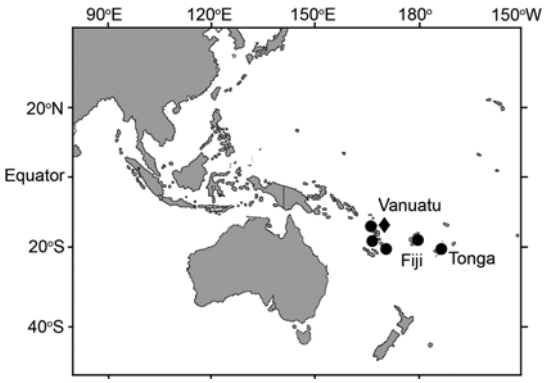

Fig. 4. Distribution of *Plakortis quasiamphiaster*. White circles, previous records; black circles, new records.

HABITAT

Coral reefs, 20–42 m depth.

DISTRIBUTION

Vanuatu (Diaz & van Soest, 1994); Fiji and Tonga are new records (Figure 4).

REMARKS

Plakortis quasiamphiaster is easily distinguishable from all other species of *Plakortis* by the peculiar amphiaster-like spicules called quasiamphiasters (spined diods and triods), and by the distinct subectosomal region with a reticulation of multispicular tracts. These traits are very unusual in the genus *Plakortis*, and could justify its placement in a separate, monotypic genus. This species could also be considered to belong to the closely related genus *Plakina* due to the resemblance between its triactinal quasiamphiasters and trilophose triods of, e.g. *Plakina weinbergi* Muricy *et al.*, 1998. However, the lophose calthrops diagnostic of *Plakina* are absent in *P. quasiamphiaster*. This species is left in the genus *Plakortis* until more information is available to solve its phylogenetic relationships.

The distinctive skeletal architecture and the spheres were not reported previously (Diaz & van Soest, 1994). The spheres may be an ecomorphological, variable trait depending on silicate levels of seawater (see Discussion section), but since they are present in all specimens examined including the holotype, it cannot be ruled out that they can be a genetically determined, constant part of the spiculation of the species.

Plakortis communis sp. nov.
(Figures 5 & 6; Table 3)

DIAGNOSIS

Plakortis greyish-brown to black externally and greyish or light brown internally, with a tangential ectosomal reticulation forming circular meshes approximately 50–100 μm in diameter. In transverse sections, the ectosome is differentiated, with columns and subectosomal lacunae. Choanosome confused or vaguely reticulated. Microrhabds absent.

SPECIMENS EXAMINED

Holotype: Australia: WESTERN AUSTRALIA: GQM-301057, Cartier Island, 12°32.2′S–123°31.9′E, J.N.A. Hooper coll., 4 May 1992, 12 m depth.

Paratypes: Australia: WESTERN AUSTRALIA: WAM Z-1272, 19 March 1997, 25 m depth, WAM Z-14, 20 March 1997, 18 m depth, both from Houtman Abrolhos, Beacon Island, Goss Passage, 28°29′S–113°46′E, J. Fromont coll. GQM-304653, Houtman Abrolhos, near to Rat Island, 28°40.0′S–113°50′E, C. Bryce coll., depth and date unknown. QUEENSLAND: GQM-314832, Alcyonarian Point, Hook Island, Whitsunday Group, 20°03.932′S–148°55.408′E, S.D. Cook, J.A. Kennedy, C.L. Adams, G. Wörheide, D. Edson coll., 3 June 1999, 15 m depth. Philippines: CEBU ISLAND: GQM-300346, south-west tip, 9°24′1.81″N–123°17′57.59″E, NCI, Australian Institute of Marine Science coll., 26 April 1991, 25 m depth. Fiji: TAVEUNI: GQM-312793, Robert's Reef, Nggamea Island, 16°42.9′S–179°48.2′E, J.N.A. Hooper coll., 29 October1990, 42 m depth.

ETYMOLOGY

This species is named after its apparent abundance and wide distribution in the Indo-Australian region.

DESCRIPTION (FIGURE 5A, B)

Sponge thickly encrusting to cushion-shaped, irregular, up to 6.5 × 4.5 cm wide by 3 cm thick. Colour *in vivo* dark or light brown, khaki-brown, greyish-brown, rusty-brown, fawn with purple eggs or black with whitish eggs; internal colour usually lighter (greyish or light brown); preserved specimens are beige to light brown. Surface smooth, regular. Oscules flush or elevated, contracted in preserved specimens. Consistency variable from firm to soft, liver-like; sponge rather easy to tear off.

Table 2. Intraspecific variation of spicule measurements of *Plakortis quasiamphiaster* (length minimum–medium–maximum, in μm). h, holotype.

Specimen	Diods	Triod actines	Spined diods	Spined triod actines	Sphere diameter
ZMA-7777 (h)	49–99–179	29–35–47	23–35–65	7–12–16	2–11
GQM-306848	52–93–136	16–35–78	23–32–42	–	4–15
GQM-306864	65–100–136	18–36–55	9–23–48	12–13–14	4–7
GQM-306907	57–104–136	12–38–60	15–29–42	12–13–14	2–10
GQM-306925	65–96–125	26–39–57	27–34–39	–	2–10
GQM-312813	39–91–149	18–30–50	16–30–50	8–11–13	4–11
GQM-312976	37–84–123	10–38–65	18–30–42	6–7–7	2–7
GQM-313029	29–80–115	13–26–55	16–32–44	12–12–12	4–7
GQM-313236	65–102–154	16–34–50	29–47–81	7–12–17	2–10
GQM-313281	63–104–136	18–31–47	31–41–47	–	2–5

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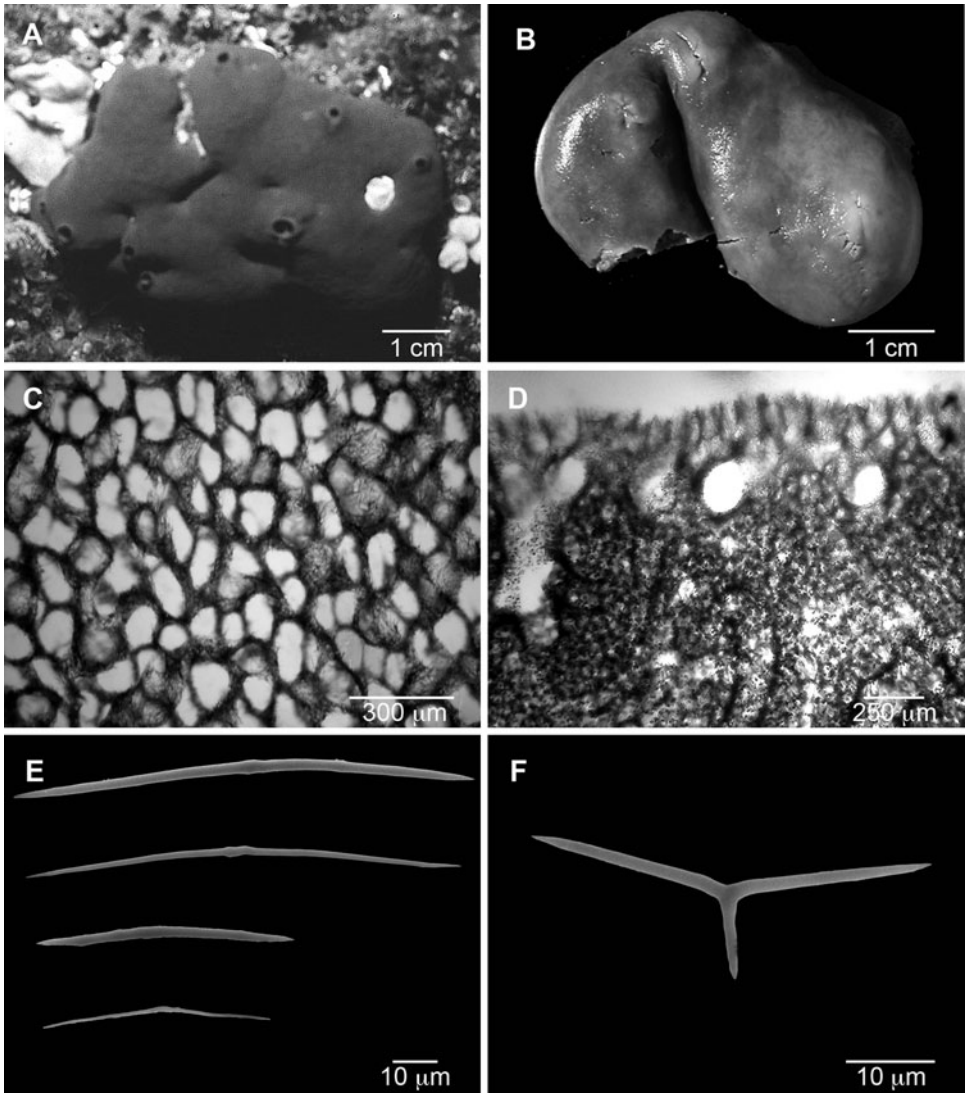

Fig. 5. *Plakortis communis* sp. nov. (A) Specimen *in situ* (GQM-300346) (photograph by the collectors); (B) preserved specimen (WAM Z-14); (C) ectosome (tangential section); (D) choanosome and ectosome (transverse section); (E) diods; (F) triod.

SKELETON (FIGURE 5C, D)

Ectosomal skeleton with a tangential reticulation, with pauci- to multispicular tracts forming irregularly elliptical meshes around 40–100 µm in diameter (Figure 5C). In one of the specimens studied, uni- to paucispicular tracts may form, inside the main reticulation, smaller, irregular meshes, with approximately 30 µm in diameter. The ectosome is usually well differentiated from the choanosome, most often showing, in transverse sections, ascending multispicular tracts (columns) and irregular subectosomal lacunae (Figure 5D). Choanosomal skeleton confused or vaguely reticulate, with irregular meshes. Choanosome usually with large canals. One specimen (WAM Z-14) has abundant spherulous cells dispersed in the choanosome.

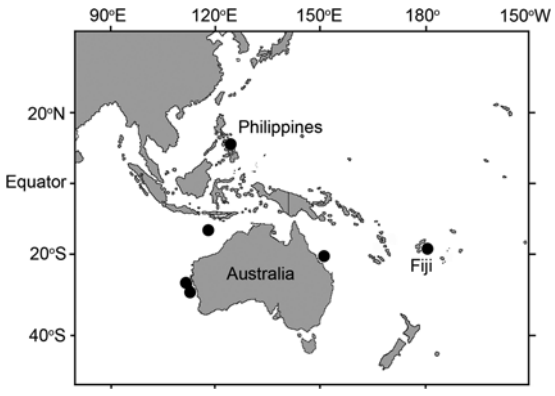

Fig. 6. Distribution of *Plakortis communis* sp. nov.

Table 3. Intraspecific variation of spicule measurements of *Plakortis communis* sp. nov. (length minimum–medium–maximum in µm). h, holotype.

Specimens	Diods	Triod actines	Sphere diameter
GQM-301057 (h)	84–104–125	22–32–39	3–7
WAM Z-1272	62–106–143	30–42–54	1–6
WAM Z-14	72–107–136	24–40–49	3–12
GQM-300346	77–111–141	34–40–50	–
GQM-304653	50–98–132	27–37–49	–
GQM-312793	27–92–142	20–33–44	–
GQM-314832	88–121–137	27–44–60	–

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SPICULES (FIGURE 5E, F; TABLE 3)

Diods abundant, slightly curved or straight, thin, regular; centre slightly thickened or with 1–3 short irregular, barely visible bends; endings acerate (Figure 5E): 27–105–143/1–6 μm (N = 90).

Triods irregular, often sagittal, rare or absent (Figure 5F): actines 30–47–60/1–5 μm (N = 22).

Some specimens have smooth or irregular spheres, 1–12 μm in diameter (not shown).

REPRODUCTION

Spherical or ovoid larvae, 450–800 μm in diameter, were found in specimens collected in March and April.

HABITAT

Outer patch reef, fringing coral reef, spurs and grooves, caves, overhangs, tunnels near shore, euryhaline lake surrounded by limestone cliffs, sometimes encrusting on coral branches, from 5–42 m depth.

DISTRIBUTION

Cartier and Houtman Abrolhos Islands (Western Australia), Great Barrier Reef, Queensland (Eastern Australia), Cebu and Fiji (Figure 6).

REMARKS

Plakortis communis sp. nov. is part of the *P. simplex* species group, which is characterized by the absence of any clearly distinctive traits such as microrhabds, quasiamphiasters, or large spicules; the group includes 10 species (*P. albicans*, *P. communis* sp. nov., *P. copiosa*, *P. erythraena*, *P. galapagensis*, *P. insularis*, *P. japonica*, *P. nigra*, *P. simplex* and *P. zyggompha*; see Discussion). The new species could have been included in the *P. simplex* complex, but Mediterranean specimens of *Plakortis simplex sensu stricto* (cf. Schulze, 1880) differ from *P. communis* sp. nov. in external characters such as a thinly encrusting shape and light colours (white, yellow and light brown) versus a thickly encrusting to cushion shape usually with dark colours in the new species. Furthermore, the ectosomal skeleton of the new species has a tangential reticulation of pauci- to multispicular tracts forming irregularly elliptical meshes, whereas *P. simplex sensu stricto* seems to have no ectosomal specialization (Schulze, 1880; Diaz & van Soest, 1994; Muricy & Diaz, 2002). The other species of this group also differ from *Plakortis communis* sp. nov. by few, rather subtle characters: *Plakortis zyggompha*, *P. galapagensis* and *P. erythraena* are thinly encrusting; furthermore, *P. galapagensis* has diods in two size-categories and *P. erythraena* has smaller diods (maximum 90 μm; Lévi, 1958; van Soest & Desqueyroux-Faúndez, 1997). *Plakortis albicans* and *P. japonica* are thinly encrusting and respectively white or pinkish-white externally (Hoshino, 1977). *Plakortis copiosa* from Kenya was poorly described, without information on skeletal architecture, but its diods are smaller than those of *P. communis* sp. nov. (maximum size 110 μm) and its triods are regularly symmetrical and very abundant (Pulitzer-Finali, 1993). *Plakortis insularis* from north-east Brazil differs from the new species by its softer consistency and absence of ectosomal reticulation (Moraes & Muricy, 2003). Finally, *P. nigra* from the Red Sea differs from *P. communis* sp. nov. in the bluish black colour both externally and internally, single large apical oscules with tangential exhalant canals, and in the massive, lobate shape (Lévi, 1953). Also, its diods are thinner and smaller (<20–50–90 μm versus 27–105–143 μm), and triods are completely absent.

Unfortunately, several characters vary within the new species, including shape, colour, oscules, consistency and presence of spheres. Some characters co-vary, allowing the distinction of two groups: (1) dark brown, thick encrusting to massive sponges, with rounded borders (GQM-301057 (holotype), GQM-300346, GQM-304653, WAM Z-14); and (2) light brown sponges with shiny smooth surface (GQM-312793, WAM Z-1272, GQM-314832). These groups might deserve status of distinct species, but I consider that the differences between them are not conspicuous enough to allow unequivocal distinction of individuals at the species level and are based in a small number of characters. Most other characters appear to vary randomly respective to each other and are within the range of variation of *Plakortis simplex sensu lato*. I have preferred to group all these specimens under the single name *Plakortis communis* sp. nov. to avoid the enlargement of the *Plakortis simplex* species complex or excessive splitting without good characters to distinguish the species. The problem of determining the limits between intra- and interspecific variation in *Plakortis simplex sensu lato* and in the new species can be solved only by careful underwater examination of living populations together with histological, cytological or molecular analyses.

Plakortis bergquistae sp. nov.
(Figures 7 & 8)

DIAGNOSIS

Plakortis with diods in two size-classes, the larger one up to 330–356 μm long, and large triods (actines up to 75–121 μm long).

SPECIMENS EXAMINED

Holotype: GQM-312579, Indonesia: N. SULAWESI: Bitung, 1°28′N–125°13′E, L. & D. Tackett coll., 16 August 1995, 38 m depth.

Paratypes: GQM-301163 (2 specimens): Australia: WESTERN AUSTRALIA: Hibernia Reef, 11°58.2′S–123°21.8′E, J.N.A. Hooper coll., 12 March 1992, 24 m depth.

ETYMOLOGY

This species is named in honour of Dame Professor Patricia Bergquist, a remarkable taxonomist and biologist of sponges, unfortunately deceased in September 2009.

DESCRIPTION (FIGURE 7A)

Sponge thickly encrusting, up to 6 × 5 cm wide by 2 cm thick. Colour *in vivo* unknown; preserved specimens are light brown to orange brown. Surface smooth but irregular, sometimes with pore-fields or star-shaped canals converging to contracted oscules. Consistency firm, cartilaginous.

SKELETON (FIGURE 7B, C)

Ectosomal skeleton reticulate, with multispicular tracts forming circular or irregular meshes, 100–300 μm in diameter (Figure 7B). The ectosome is poorly differentiated, slightly denser than the choanosome, without subectosomal lacunae (Figure 7C, transverse section). Choanosomal

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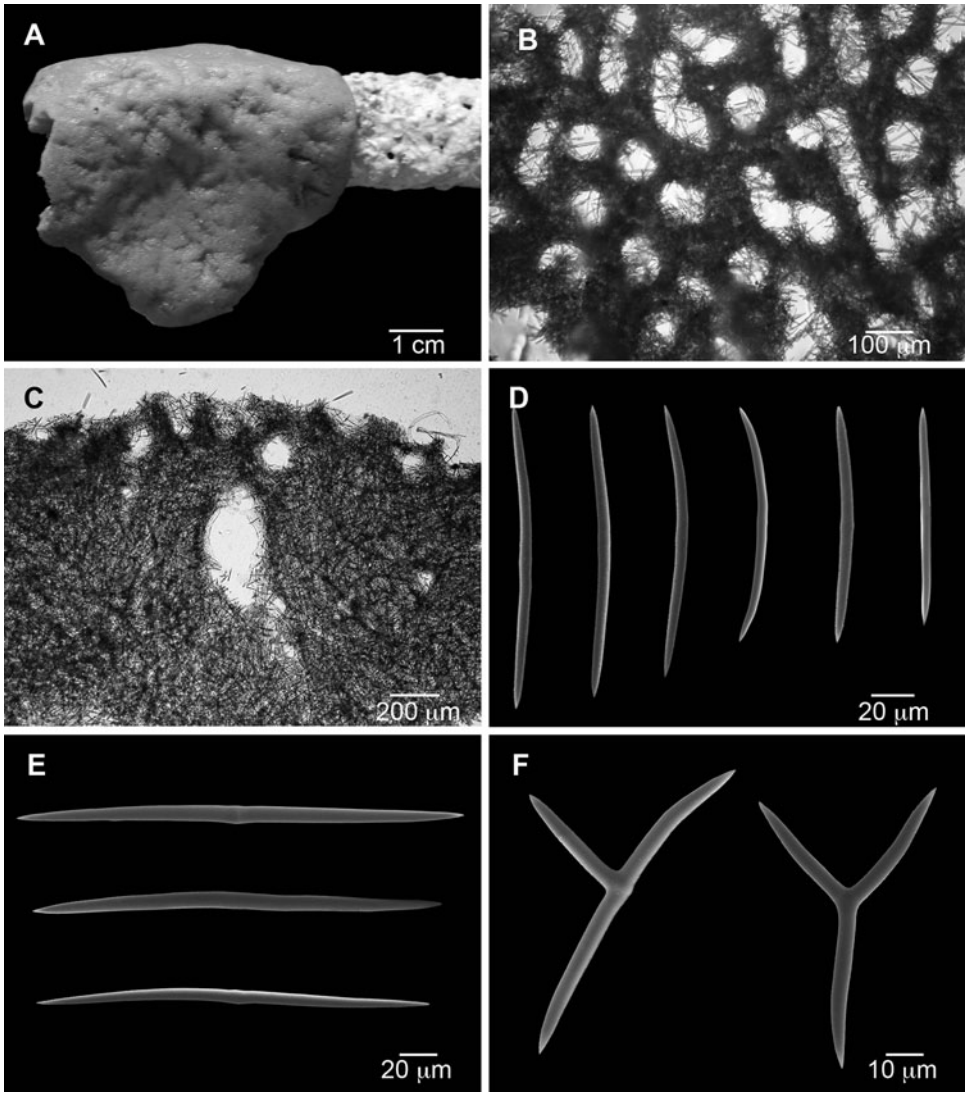

Fig. 7. *Plakortis bergquistae* sp. nov. (A) Preserved specimen (GQM-301163); (B) ectosome (tangential section); (C) choanosome and ectosome (transverse section); (D) small diods; (E) large diods; (F) triods.

skeleton confused to vaguely reticulate. Choanosome with large canals.

SPICULES (FIGURE 7D–F)

Diods abundant, straight or slightly curved, smooth, regular, with slightly thickened centre, and in two size-classes: the smaller measures 91–133–163/2–5–6 µm (N = 30) (Figure 7D) and the larger 202–280–356/5–9–11 µm (N = 28) (Figure 7E).

Triods large, mainly sagittal, smooth, regular; actines 30–72–122/5–11–20 µm (Figure 7F) (N = 8).

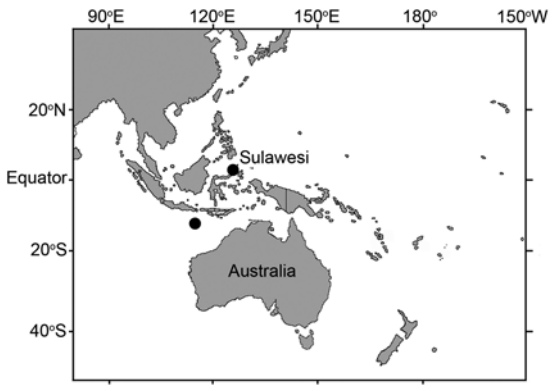

Fig. 8. Distribution of *Plakortis bergquistae* sp. nov.

REPRODUCTION

The specimens examined, collected in May and August, have ovoid to spherical larvae.

HABITAT

Patch reef, inner reef slope, from 24–38 m depth.

DISTRIBUTION

Hibernia Reef (Western Australia) and North Sulawesi (Indonesia) (Figure 8).

REMARKS

In the specimens from Hibernia Reef, the ectosomal reticulation forms larger meshes (approximately 300 µm diameter) than in the specimen from Sulawesi, with meshes 100–150 µm in diameter. In transverse sections, the distinction

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between ectosomal and choanosomal skeletons is clearer in the Sulawesi specimen than in Hibernia Reef specimens. Such differences were here considered intraspecific in view of the similarity of the three specimens in the large size of diods, with two size-classes, the larger one up to 350 μm long. This character is exclusive of this species and allows easy distinction of *Plakortis bergquistae* sp. nov. from all other species of *Plakortis*. The lack of calthrops distinguishes it from species of *Plakinastrella*, which have diods in a similar size-range.

Plakortis fromontae sp. nov.
(Figures 9 & 10)

DIAGNOSIS

Plakortis with curved diods in a wide size-range (20–220 μm long), rare triods, and a double ectosomal reticulation with circular meshes 30 and 120 μm in diameter.

SPECIMENS EXAMINED

Holotype: WAM Z-1280, Australia: WESTERN AUSTRALIA: Rat Island, Houtman Abrolhos, 28°43′S–113°46′E, J. Fromont coll., 4 December 1996, 14 m depth.

ETYMOLOGY

This species is named in honour of Dr Jane Fromont, from the Western Australian Museum, who collected the holotype and who first drew my attention to the great diversity of Australian *Plakortis*.

DESCRIPTION (FIGURE 9A)

Sponge thickly encrusting to cushion-shaped, up to 7.5 × 4 × 2 cm. Colour *in vivo* black with cream interior. Preserved specimens are light orange-brown. Surface smooth, regular. Oscules contracted, sometimes elevated, 1–2 mm in diameter. Consistency firm, cartilaginous, or compressible.

SKELETON (FIGURE 9B, C)

Ectosomal skeleton with a double reticulation. Pauci- to multispicular tracts form larger circular meshes, 120–400 μm in diameter, inside which uni- to paucispicular tracts form smaller meshes, circular to irregular, 30–100 μm in diameter (Figure 9B). In transverse sections, the ectosomal skeleton appears differentiated, with columnar spicule tracts. Subectosomal lacunae relatively abundant, spherical or irregular, 150–500 μm in diameter. Choanosome with a confused to

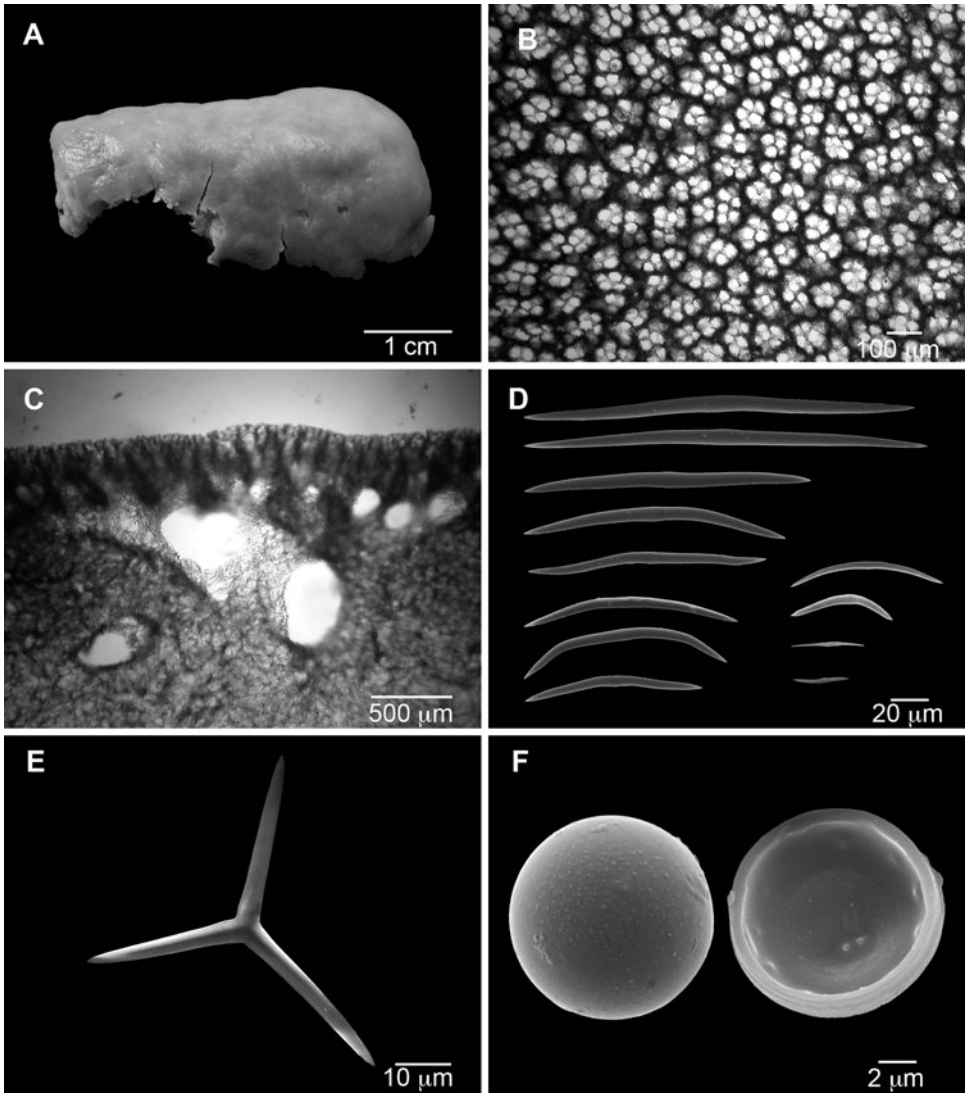

Fig. 9. *Plakortis fromontae* sp. nov. (A) Preserved holotype (WAM Z-1280); (B) ectosome (tangential section); (C) choanosome and ectosome (transverse section); (D) diods; (E) triod; (F) spheres.

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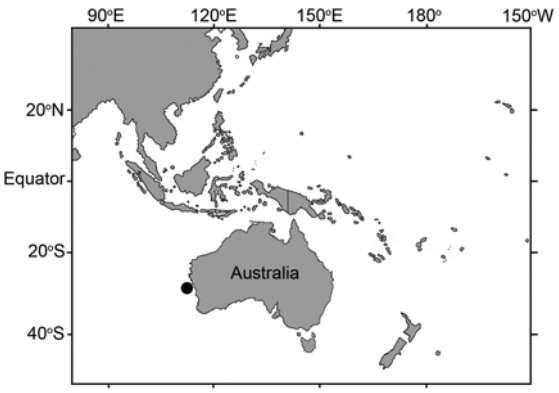

Fig. 10. Distribution of *Plakortis fromontae* sp. nov.

irregularly reticulate skeleton and large canals, 140–800 μm in diameter (Figure 9C).

SPICULES (FIGURE 9D–F)

Diods abundant, irregular, smooth, with centre only slightly thickened (not s-bent) and straight to strongly curved actines, acerate, with wide variation in size (Figure 9D): 25–124–223/2–6–10 μm (N = 40).

Triods rare, regular, mostly equiangular and equiradiate (Figure 9E): 6–24–44/0.5–1.6–5.0 μm (N = 10).

Spheres, relatively rare, hollow, never modified to microstrongyles (Figure 9F): 10–15 μm in diameter (N = 10).

REPRODUCTION

Ovoid larvae 350–600 μm in diameter were found in the single specimen, collected in December.

HABITAT

Cave and reef, 14–37 m depth.

DISTRIBUTION

Houtman Abrolhos (Western Australia) (Figure 10).

REMARKS

Plakortis fromontae sp. nov. is part of the *P. angulospiculatus* species group, characterized by a simple spiculation of diods and triods as in the *P. simplex* species-group, but with maximum diod size ranging between 190 and 300 μm long (see Discussion). Within this group, it shares a reticulate ectosomal skeleton only with *P. angulospiculatus* and *P. halichondrioides*. It differs in the external colour from *P. halichondrioides* (which is black) and from *P. angulospiculatus* in having a double tangential ectosomal reticulation versus a simple reticulation. The new species is similar to *Plakortis kenyensis* in shape and size, but they differ in consistency, colour and in spicule size (slightly larger in *P. kenyensis*). *Plakortis fromontae* sp. nov. differs from all other species of *Plakortis* by its irregularly curved diods, ranging in length from 25 to 223 μm. It is unclear whether the spheres are a constant part of the spiculation of this species or a variable trait depending on silicate levels of seawater (see Discussion).

Plakortis hooperi sp. nov.
(Figures 11 & 12)

DIAGNOSIS

Plakortis with diods, triods and microrhabds, with confused ectosomal skeleton. Shape thinly encrusting.

SPECIMENS EXAMINED

Holotype: GQM-312880, Papua New Guinea: Motupore Island: Round Hill Barrier Reef, south-east of Motupore Island, 9°57.1′S–147°28′9E, J.N.A. Hooper coll., 12 December 1996, 39 m depth.

ETYMOLOGY

This species is named in honour of Dr John N.A. Hooper, from the Queensland Museum, Brisbane, Australia, who collected the holotype and who has been greatly contributing to the progress of sponge taxonomy, especially of Australian and Indo-Western Pacific areas.

DESCRIPTION (FIGURE 11A)

Three fragments, with size up to 3 × 3 cm. Sponge thinly encrusting to cushion-shaped; studied fragments up to 5 mm thick. Colour *in vivo* brown-beige. Preserved specimens are cream to light brown externally and internally. Surface smooth, but irregular. Oscules large *in vivo*, contracted in alcohol. Consistency slightly compressible. The sponge releases abundant mucous and has a typical acetone smell.

Skeleton (Figure 11B, C): Ectosomal skeleton confused, without any trace of reticulation (Figure 11B). Ectosome undifferentiated, except for irregular, sparse subectosomal lacunae. Choanosomal skeleton confused (Figure 11C).

SPICULES (FIGURE 11D–F)

Diods abundant, relatively thick, centrotylote, regular, acerate (Figure 11D): 79–111.6–148/2–5 μm (N = 20).

Triods irregular, inequirradiate, relatively rare (Figure 11E): actines 17–29.9–61/2–3 μm (N = 10).

Microrhabds abundant, irregular, strongylote or deformed (Figure 11F): 2–5.5–8/0.5–1.0 μm (N = 17).

Spheres, relatively common, spherical or ovoid to irregular, sometimes elongated, forming microstrongyles (Figure 11F): 5–20 μm in diameter (N =20).

REPRODUCTION

Unknown.

HABITAT

Barrier Reef, 39 m depth.

DISTRIBUTION

Known only from Papua New Guinea.

REMARKS

Plakortis hooperi sp. nov. is related to *P. lita* and *P. microrhabdifera* by the presence of irregular microrhabds. It differs from both however in its confused ectosomal skeleton, whereas the other two species have a reticulated ectosome. The light beige colour in alcohol and the slightly compressible consistency are also distinctive traits of the new species. It differs from all other species of *Plakortis* in the presence of irregular microrhabds. The spheres and microstrongyles may be a constant part of the spiculation of this species or a variable trait depending on silicate levels of seawater (see Discussion).

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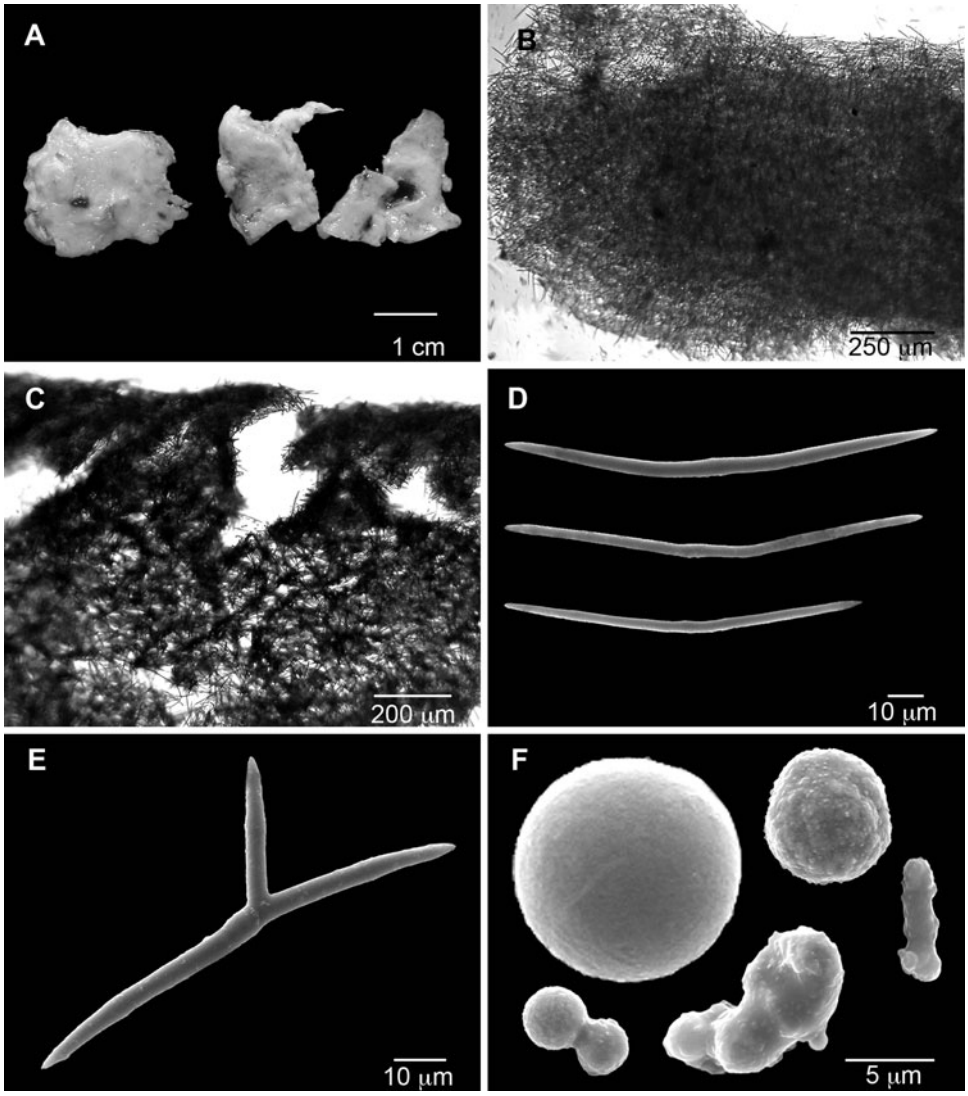

Fig. 11. *Plakortis hooperi* sp. nov. (A) Preserved holotype (GQM-312880); (B) ectosome (tangential section); (C) choanosome and ectosome (transverse section); (D) diods; (E) triod; (F) spheres and microrhabds.

DISCUSSION

The genus *Plakortis* is characterized by a simple spiculation, composed almost exclusively of very irregular diods and triods, and by high uniformity of external morphological characters, with several species with brown colour and encrusting shape. This morphological homogeneity makes the identification of species of *Plakortis* extremely hard (see also Diaz & van Soest, 1994; Muricy & Diaz, 2002). Furthermore, most descriptions of *Plakortis* species lack information on external morphology *in vivo* and on skeletal and aquiferous system architecture, and few studies show details of spicule shape in SEM micrographs. Such characters can be very useful for the distinction of species of *Plakortis* (Diaz & van Soest, 1994; Muricy & Diaz, 2002; Moraes & Muricy, 2003; Cruz-Barraza & Carballo, 2005) and must be included in future descriptions to allow better species discrimination. Revision of these characters is especially needed for *P. zyggompha*, *P. copiosa* and *P. kenyensis*, whose descriptions totally lack such information, and for several records of *P. simplex*, *P. nigra* and *P. angulospiculatus* worldwide, including the Indo-Australian region (e.g. Topsent, 1897; Hentschel, 1912; van Soest, 1989, 1990; Desqueyroux-Faúndez, 1981; Lévi & Lévi, 1983; Pulitzer-Finali, 1996; Hooper *et al.*, 2000; Hooper & Ekins, 2004; Pangan *et al.*, 2007). Designation of a neotype for the type species *Plakortis simplex* is also essential to achieve taxonomic stability in the genus.

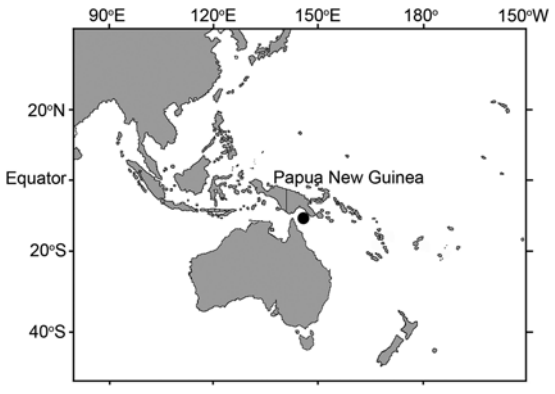

Fig. 12. Distribution of *Plakortis hooperi* sp. nov.

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The architecture of the tangential ectosomal skeleton is particularly useful for the taxonomy of Indo-Australian *Plakortis*, with three major types of arrangement: (1) reticulated, with multispicular tracts forming simple, rounded or elliptical meshes; (2) reticulated, with multispicular tracts forming rounded or elliptical meshes inside which paucispicular tracts form a secondary reticulation with smaller rounded meshes; and (3) confused, with no trace of reticulation. The same patterns were found in Brazilian and Mexican species (Moraes & Muricy, 2003; Cruz-Barraza & Carballo, 2005). However, most species of *Plakortis* are compressible and their oscules contract after fixation; some, such as *Plakortis lita*, can change shape and thickness remarkably after collection. Such changes might affect, to a limited extent, the ectosomal organization of these sponges, but as all descriptions and comparisons are based on preserved specimens, they do not reduce the usefulness of this character. Examination of living specimens *in situ* or in aquarium would be necessary to ascertain the degree of modification of the ectosomal skeleton after collection and fixation.

The finding of large diods (up to 350 μm long) and triods (actines up to 120 μm long) in *P. bergquistae* sp. nov. was unexpected. All other species of the genus have diods not longer than 260 μm, and usually shorter than 150 μm. Large diods and triods are found in the closely related genus *Plakinastrella* Schulze, 1880, but the two genera are distinguished by the presence of well-formed calthrops only in *Plakinastrella* (Diaz & van Soest, 1994; Muricy & Diaz, 2002; Moraes & Muricy, 2003). Although the distinction between *Plakortis* and *Plakinastrella* is probably artificial, it is followed here for the sake of stability of the classification until a phylogenetic analysis including the two genera is available.

The presence of spheres in four species of *Plakortis* (*P. quasiamphiaster, P. communis* sp. nov., *P. fromontae* sp. nov. and *P. hooperi* sp. nov.) was also surprising, although spheres were previously reported in a deep-sea species from New Caledonia identified as *Plakortis simplex* (Lévi & Lévi, 1983). Lévi (1953) also reported abundant ovoid or 8-shaped elements in *P. nigra*, without identifying them as spicules, cells or other structures. Beyond the genus *Plakortis*, smooth spheres have been found in species of the orders Astrophorida (*Isops apiarum* (Schmidt, 1870); *Caminus albus* Pulitzer-Finali, 1996; *C. chinensis* Lindgren, 1897; *Penares dendyi* (Hentschel, 1912)), Hadromerida (*Tethya ingalli* Bowerbank, 1858 (Lendenfeld, 1888 as *Tethya laevis*); *T. monstrosa* (Burton, 1924); *T. omanensis* Sarà & Bavestrello, 1995; Sarà & Sarà, 2004; van Soest & Beglinger, 2008), and Poecilosclerida (*Biemna megalosigma* Hentschel, 1912; *Guitarra flamenca* Carballo & Uriz, 1998). In the latter species, the perfectly spherical or lobate, smooth silica structures were considered as aberrant silica formations associated to silica-rich environments such as those off the coast of Namibia (Carballo & Uriz, 1998). This is a plausible explanation, since the occurrence of these spheres is rare and dispersed in few species from widely divergent taxonomic groups. Furthermore, several of these species also occur in Indo-Australian waters (e.g. *Caminus albus*, *Penares dendyi*, *Tethya laevis* and *T. monstrosa*). However, the relationship between silicate concentration and sphere production remains to be demonstrated experimentally. For the time being, these spheres are considered as a variable part of the spiculation of the species in which they occur, since it is likely that their presence varies depending on the locality.

Indo-Australian species of *Plakortis* seem to have no marked reproductive period, since embryos and larvae were found in most specimens, irrespectively of the period of collection. In contrast, most Mediterranean plakinids reproduce preferably during summer and autumn (Schulze, 1880; Muricy *et al.*, 1996a, 1998; Maldonado & Riesgo, 2008). This difference might be related to the low seasonal temperature variation in the tropics compared to temperate areas such as the Mediterranean Sea.

It is very difficult to evaluate the identity of previous Indo-Australian records of *P. nigra* and of the *Plakortis simplex* complex due to the lack of detailed descriptions of their external morphology *in vivo*, skeleton architecture and aquiferous system organization. In fact, the shortness of most descriptions is one of the main reasons for the very existence of the *P. simplex* species complex. The records of *P. nigra* from the Indo-Australian region cannot be objectively evaluated because there are no descriptions of the species from the area; the only descriptions of this species so far are from the Red Sea (Lévi, 1953, 1958; Diaz & van Soest, 1994). In his first description of *P. simplex* from Amboine (Indonesia), Topsent (1897) made no mention of its skeleton or spicules. In subsequent re-descriptions, the same specimen was described as having triods and microcalthrops (Topsent, 1901) and later as having diods in two size-classes (Topsent, 1928; Desqueyroux-Faúndez, 1981). In addition, the sponge is thickly encrusting and its colour is bluish-black externally and white internally (Topsent, 1897). It is thus clearly not co-specific with *P. simplex sensu stricto*, neither with any of the species described here. If it possesses true calthrops it should be transferred to *Plakinastrella* Schulze, 1880. In any case, it probably should receive a new species name, but more detailed examination of the specimen is needed before this can be done. *Plakortis simplex sensu* Vacelet *et al.* (1976), from Madagascar, differs from both *P. communis* sp. nov. and *P. simplex sensu stricto* in the massive shape, greenish colour, firm consistency and the large size of diods (40–250 μm long); it may either belong to *P. kenyensis* (cf. Pulitzer-Finali, 1993) or to an undescribed species. *Plakortis simplex sensu* Thomas (1973) from the Seychelles is close to *P. communis* sp. nov., from which it differs by a thinner shape (up to 10 mm thick), lighter colour and slightly smaller diods and triods. The record of *P. simplex* from Hawaii (de Laubenfels, 1950) is close to *P. simplex sensu stricto* in the thinly encrusting shape and light colours; however, its triods are much larger than those of both *P. communis* sp. nov. and *P. simplex sensu stricto* (actines average 100 μm long versus 30–60 and 25–50 μm, respectively). *Plakortis simplex* sensu Hentschel (1912) from Aru Island, Indonesia, and *sensu* Lévi & Lévi (1983) from New Caledonia have spicules in the same size-range of *P. communis* sp. nov. and *P. simplex sensu stricto*. Lévi & Lévi (1983) did not mention the colour of their specimens; de Laubenfels (1950) did not describe the size of diods; and no previous study has described the arrangement of the tangential ectosomal skeleton. In the lack of such information, these records are provisionally left in the *Plakortis simplex* species complex, although most of them probably deserve new species names. Due to these problems, it is currently impossible to estimate the actual diversity of *Plakortis* in the Indo-Australian region. Judging from the morphological heterogeneity of the *P. simplex* species complex and the large number of unnamed records (as *Plakortis* sp.) both in Australia (Hooper & Ekins, 2004) and Indonesia (Poppe &

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Poppe, 2010), it is clear that there are many species yet to be described in this area.

As the number of species and the information on their morphology increase, three groups of species can now be distinguished within the genus *Plakortis*, based on spicule types and size:

(1) *P. simplex* species group—includes the nominal species (which is itself a complex of sibling species) and all other species with spiculation composed of only diods and triods, and whose diods are smaller than 190 μm long (*P. albicans*, *P. communis* sp. nov., *P. copiosa*, *P. erythraena*, *P. galapagensis*, *P. insularis*, *P. japonica*, *P. nigra* and *P. zyggompha*);
(2) *P. angulospiculatus* species group—also with a nominal species complex and including species with only diods and triods, but the largest diods vary between 190 μm and 300 μm long (*P. angulospiculatus*, *P. fromontae* sp. nov., *P. halichondrioides* and *P. kenyensis*);
(3) *P. lita* species group—includes the species with microrhabds (*P. hooperi* sp. nov., *P. lita* and *P. microrhabdifera*).

Two species do not fit in any group: *P. bergquistae*, characterized by the presence of very large diods (up to more than 300 μm long) and triods (with actines up to more than 100 μm long); and *P. quasiamphiaster*, characterized by the presence of diactinal and triactinal quasiamphiasters. In the absence of a cladistic analysis, no phylogenetic value is assumed to these groups, neither are they proposed as subgenera, but they may be useful to help species identification in the genus. Within each group, species discrimination can be made by details of skeletal architecture, external morphology and spicule shape. As in other plakinid genera such as *Plakina* and *Oscarella* (Muricy *et al.*, 1996a, b, 1998), the taxonomy of *Plakortis* would greatly benefit from the inclusion of histological, cytological and molecular characters. With the data currently available, however, it is now clear that the morphological diversity within the genus, although lower than in most demosponges, is higher than previously thought.

IDENTIFICATION KEY FOR INDO-AUSTRALIAN SPECIES OF *PLAKORTIS*

1. Quasiamphiasters present . . . . . *P. quasiamphiaster*
   Quasiamphiasters absent 2
2. Microrhabds present 3
   Microrhabds absent 4
3. Colour dark brown or black; ectosomal reticulation simple, with irregularly elliptical meshes . . . . . *P. lita*
   Colour brown or light brown; ectosomal skeleton confused; sponge producing mucus. . . . . *P. hooperi* sp. nov.
4. Diods up to 350 μm long, triod actines up to 120 μm long . . . . . *P. bergquistae* sp. nov.
   Diods less than 300 μm long, triod actines less than 80 μm long 5
5. Largest diods 190 μm long or more; tangential ectosomal reticulation double-meshed . . . . . *P. fromontae* sp. nov.
6. Largest diods less than 190 μm long; tangential ectosomal reticulation single-meshed . . . . . *P. communis* sp. nov.

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