A NEW *CLATHRIA* (PORIFERA: DEMOSPONGIAE: MICROCIONIDAE) FROM THE WESTERN INDIAN OCEAN

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A new species of microcionid marine sponge *Clathria (Microciona) richmondi* sp. nov. is described from Zanzibar, Tanzania, and is highly unusual in having extremely large accolada toxas that form dragmata and skeletal tracts within the choanosomal and ectosomal skeletons, rudimentary spination on echinating acanthostyles, a live blue colouration and a prominent sub-surface aquiferous system with radiate arrangement around oscules. The new species is compared with the other 64 species of *Clathria* described from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces, and other species known to have toxodragmata. ❐ *Porifera, Demospongiae, Poecilosclerida, Microcionidae, new species, taxonomy, Zanzibar, Western Indian Ocean.*

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The extensive literature on sponges of the Western Indian Ocean is evidence of a rich and diverse fauna (Table 1). Even though this inventory already contains ‘several hundred’ species (Kelly, 1997), it is undoubtedly far from complete. For example, Van Soest (1994b) collected 240 species from the Seychelles and Amirante islands whereas only 167 species were known previously from the region.

Within the Western Indian Ocean (i.e. extending along the continental shelf from Natal to Somalia and including the islands from Madagascar to the Seychelles; Richmond, 1997), Southeast African regions (Natal to the Cape) and Arabian Gulf-Red Sea provinces 74 species of Microcionidae have been reported (Hooper, 1996a), of which 64 belong to *Clathria*, 10 still unnamed (Table 2). Of these, 44 (or 69%) have not yet been found outside the region. This number of ‘apparent endemics’ may decrease over time as the region’s biodiversity becomes better known, but it still represents an extra ordinarily high level of endemism compared to other sponge genera and other phyla. For example, Van Soest (1994b) found about 24% of all sponges collected from the Seychelles and Amirante islands were endemic to the W Indian Ocean fauna, and Richmond (1997) suggested that only about 15% of all the regional marine biota may be endemic to the W Indian Ocean region.

Biogeographic affinities of the sponge fauna are thought to be essentially Tethyan (Van Soest, 1994a), with southern incursions of species of Gondwanan origin (Hooper & Lévi, 1994; Hooper, 1996a). This fauna is thought to be most similar to the central Indian Ocean and Indo-Malaya regions (Van Soest & Hajdu, 1997), and in this regard follows the general pattern seen in other marine invertebrate phyla (e.g. scleractinarian corals; Veron, 1986; Veron, 1993). Richmond (1997) suggested that about 35% of the West Indian Ocean marine biota was widely distributed, extending into the Red Sea and perhaps as far as the Indo-Malay region, 35% ranged across the whole Indo-Pacific region, and 15% extended into the warm temperate regions of the Atlantic Ocean. To date only one microcionid, *Clathria (Thalysias) vulpina* (Lamarck), appears to be truly Indo-Pacific ‘cosmopolitan’, with a confirmed distribution extending from Tonga to the Red Sea (i.e. with conspecificity confirmed through morphological comparisons between recent collections of living populations; Hooper, 1996a). However, even this finding has yet to be confirmed through genetic analysis to determine whether slight morphological differences between regional populations represent intraspecific variability or indicate the existence of a series of possible allopatric sibling species.

Van Soest (1994b) also noted a high level of regional heterogeneity between sponge faunas of the Seychelles and Amirante Island groups, with only 17% of species common to both regional faunas. This supports a similar finding from

TABLE 1. Literature on the sponges of the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces.

Province	Locality	Sponge literature
Coastal East Africa	Zanzibar	Lendenfeld, 1897; Baer, 1905; Jenkin, 1908; Burton, 1959; Thomas, 1976a, 1979b; Pulitzer-Finali, 1993; Kelly, 1997; Magnino & Gaino, 1998
	Tanzania	Jenkin, 1908; Thomas, 1976a; Pulitzer-Finali, 1993; Magnino & Gaino, 1998
	Mozambique	Lévi, 1964; Thomas, 1979a, 1979c, 1980a, 1980b; Laghi et al., 1984; Schmidt et al., 1997
	Kenya	Marsden, 1975; Bruce, 1976; Thomas, 1981a; Vacelet et al., 1991; Pulitzer-Finali, 1993
	Somalia	McCabe et al., 1982; Finamore et al., 1983; Hooper, 1996a
	South Africa	Ehlers, 1870; Carter, 1871; Gray, 1873; Vosmaer, 1880; Kirkpatrick, 1900, 1901, 1902a, 1902b, 1903, 1904, 1908, 1913; Sollas, 1908; Stephens, 1915; Burton, 1926, 1929, 1931, 1933a, 1933b, 1936, 1958; Lévi, 1963, 1967; Borojevic, 1967; Day, 1981; Schleyer, 1991; Pettit et al., 1993b; Rudi et al., 1993, 1994a, 1994b, 1995; Barkai et al., 1996; Hooper et al., 1996; Samaai, 1997; Beukes et al., 1998; Koren Goldshlager et al., 1998; McPhail et al., 1998
Offshore East Africa	Madagascar	Bosraug, 1913; Decary, 1946; Lévi, 1956; Vacelet & Vasseur, 1965, 1966, 1971, 1977; Vacelet, 1967a, 1967b, 1977; Vacelet et al., 1976; Ivanova et al., 1993; Hooper, 1996b
	Aldabra	Lévi, 1961
	Comoros	Sarà et al., 1993b; Pettit et al, 1993a, 1994a, 1994b
	Réunion	Lévi, 1986; Aknin et al., 1996
	Mauritius	Thomson, 1868; Duncan, 1880; Topsent, 1890; Dendy, 1922; Van Soest, 1993
	Saya de Malha	Dendy, 1922; Kolbasov, 1992
	Seychelles	Wright, 1881; Ridley & Dendy, 1887; Topsent, 1893a; Dendy, 1922; Lévi, 1961; Thomas, 1973, 1979c, 1981b; Hooper & Krasochin, 1989; Ngoc Ho, 1990; James et al., 1991; Venkateswarlu et al., 1991; Van Soest, 1994b; Van Soest et al., 1994; Trimurtulu & Faulkner, 1994; Hooper, 1996a; Pettit et al., 1997
	Amirante	Carter, 1880; Ridley, 1884; Ridley & Dendy, 1887; Dendy, 1922; Van Soest et al., 1994; Braekman et al., 1998
Northwest Indian Ocean	Red Sea	Keller, 1889, 1891; Topsent, 1892; Row, 1911; Lévi, 1958, 1965; Burton, 1959; Delseth et al., 1979; Sarà et al., 1979; Kashman et al., 1982, 1989; Mergner, 1982; Sokoloff et al., 1982; Mebs, 1985; Carmely & Kashman, 1986; Vine, 1986; Gebreyesus et al., 1988; Ilan & Loya, 1988, 1990; Carmely et al., 1990; Kolbasov, 1990; Isaacs & Kashman, 1992; Rinkevich et al., 1993; Rudi & Kashman, 1993; Kelly-Borges & Vacelet, 1995; Guo et al., 1996, 1997a, 1997b; Ramadan, 1997; Beer & Ilan, 1998; Wörheide, 1998
	Ethiopia	Isaacs et al., 1991
	Eritrea	Hooper, 1996a
	Arabian Sea	Carter, 1869; Topsent, 1893b; Dendy, 1913, 1915, 1916a, 1916b, 1916c, 1922; Kumar, 1924a, 1924b, 1924c, 1925; Burton & Rao, 1932; Burton, 1959; Thomas, 1975, 1976b, 1979b, 1988, 1989; Rahim, 1979; Kamat et al., 1981; Patel et al., 1985; Kondracki & Guyot, 1987; James et al., 1989; Parameswaran et al., 1989, 1992a, 1992b, 1994, 1997; Kobayashi et al., 1992a, 1992b; Pettibone, 1993; Sarà & Bavestrello, 1995; Bavestrello et al., 1996; Thomas et al., 1997
	Oman	Sarà & Bavestrello, 1995; Bavestrello et al., 1996

sponge surveys of NW and NE Australian reefs (Hooper, 1994; Hooper et al., 1999), with the implication that taxonomic inventories of regional sponge faunas are largely incomplete, with possibly many new taxa remaining to be discovered within these highly heterogeneous and 'apparent endemic' regional populations. The present study describes one such species discovered during routine surveys of Zanzibar undertaken by MK as part of a project to produce an inventory of the marine fauna and flora and popular field guide to the region (Richmond, 1997).

Methods for preparation and examination of material are described by Hooper (1996a). Spicule measurements refer to (minimum-(mean)-maximum) dimensions of lengths and widths taken from 25 random samples of each spicule category and are given in micrometres unless otherwise stated. Abbreviations: BMNH, The Natural History Museum, London; QM, Queensland Museum, Brisbane. MK is grateful to Dr Matthew Richmond for facilitating her participation in the East Africa marine surveys.

SYSTEMATICS

PORIFERA Grant
DEMOSPONGIAE Sollas
POECILOSCLERIDA Topsent
MICROCIONINA Hajdu, Van Soest & Hooper
MICROCIONIDAE Carter

Clathria Schmidt, 1862

Clathria (Microciona) Bowerbank, 1862
Refer to synonymy in Hooper (1996a)

Clathria (Microciona) richmondi sp. nov.
(Figs 1-4)

ETYMOLOGY. For Dr Matthew D. Richmond, Institute of Marine Sciences, Zanzibar, in recognition of his substantial contribution towards documenting the marine flora and fauna of the E African coastline (Richmond, 1997).

MATERIAL. HOLOTYPE. QMG306785 (fragment BMNH 1995.6.29.96). E side of Pange Sandbank Reef, Zanzibar Town, Unguja I., Tanzania, 6°10.0'S, 39°9.3'E, 10m depth, 7.viii.1995. coll. M. Kelly, SCUBA.

DISTRIBUTION. Known only from the fringing reefs off Zanzibar Town, Unguja Island, encrusting dead coral substrate on a shallow fringing reef.

DESCRIPTION. *Shape*. Very thinly encrusting (0.2-0.7mm thick) in small patches (10-20cm diameter) or completely enveloping coral rubble.

Colour. Royal blue with a violet tinge alive, brownish-orange in ethanol.

Oscules. Large (up to 5mm diameter), raised on membraneous lip (approximately 4mm high), scattered over entire surface and with prominent, vein-like, radial subsurface drainage canals radiating towards each oscule; oscules and drainage canals collapsed upon preservation.

Texture and Surface Characteristics. Slimy, very smooth, fleshy surface.

Ectosome. No special category of ectosomal spicules present, although choanosomal principal styles arising from the underlying skeleton, standing perpendicular to the substrate, may protrude a long way through the surface. Bundles of toxodragmata occasionally lie on the surface, although most of these appear to be confined below the peripheral skeleton.

Subectosome. Below the surface are plumose bundles of auxiliary subtylostyles, mostly running perpendicular and paratangential to, or occasionally protruding through, the surface. These subectosomal skeletal bundles form stellate brushes associated with (or parallel to) the larger protruding choanosomal principal styles. Toxodragmata form thick bundles below the peripheral skeleton, resembling megasclere spicule tracts, lying tangential to the surface and scattered between the erect choanosomal principal styles.

Choanosome. Microcionid skeletal structure, with thin hymedesmioid basal layer of spongin fibre, approximately 50 thick, highly collagenous, granular, dark brown pigmented, with calcitic detritus embedded beneath; basal spongin with sparsely dispersed echinating acanthostyles embedded and standing perpendicular to substrate, and bulbous spongin fibre nodes up to 150 thick found only in thicker sections of the encrustation; each bulbous fibre node discrete, erect, without any anastomoses between adjacent nodes, and each with 1-5 choanosomal principal styles embedded and perpendicular to substrate, with spicules diverging slightly, becoming plumose towards surface and protruding up to 350 through ectosome; smaller echinating acanthostyles confined mostly to hymedesmioid basal spongin fibre, rarely seen on bulbous fibre nodes; conversely, principal styles only seen on bulbous fibre nodes and not on hymedesmioid basal fibres. Dense horizontal bands of accolada toxodragmata (up to 70 thick) occur about midway through the choanosomal skeleton cross-section, and also in the ectosomal region, lying on or below the surface; few single toxas observed in the mesohyl mostly comprising wing-shaped forms, whereas most toxas forming dragmata. Palmate isochelae moderately abundant within mesohyl; collagen within mesohyl dense, relatively smooth, moderately heavily pigmented orange-brown; choanocyte chambers elongate-oval, up to 40x12.

Megascleres. Choanosomal principal styles and subtylostyles very long, slender, slightly curved near basal end, long tapering fusiform points, base either slightly constricted or non-tylote, smooth or very occasionally with anisoxeote terminations. Length 178-(403.7)-622, width 6-(10.2)-12.

Subectosomal auxiliary subtylostyles very long, very slender, straight, fusiform points, with well developed, entirely smooth subtylote bases. Length 198-(351.5)-428, width 2-(3.8)-5.

Echinating acanthostyles relatively uncommon, short, slender, straight or very slightly curved at centre, fusiform-pointed, with moderately well-developed basal constriction; shaft and base with vestigial granular spines confined mainly to basal half of spicule. Length 58-(89.6)-134, width 3-(5.4)-8.

Microscleres. Palmate isochelae moderately common, well-silicified, with thick, well-developed alae comprising over 70% of spicule length. Length 14-(15.2)-17.

Toxas in two forms: Accolada toxas extremely abundant, exceptionally long and very slender, with slight central curvature and straight

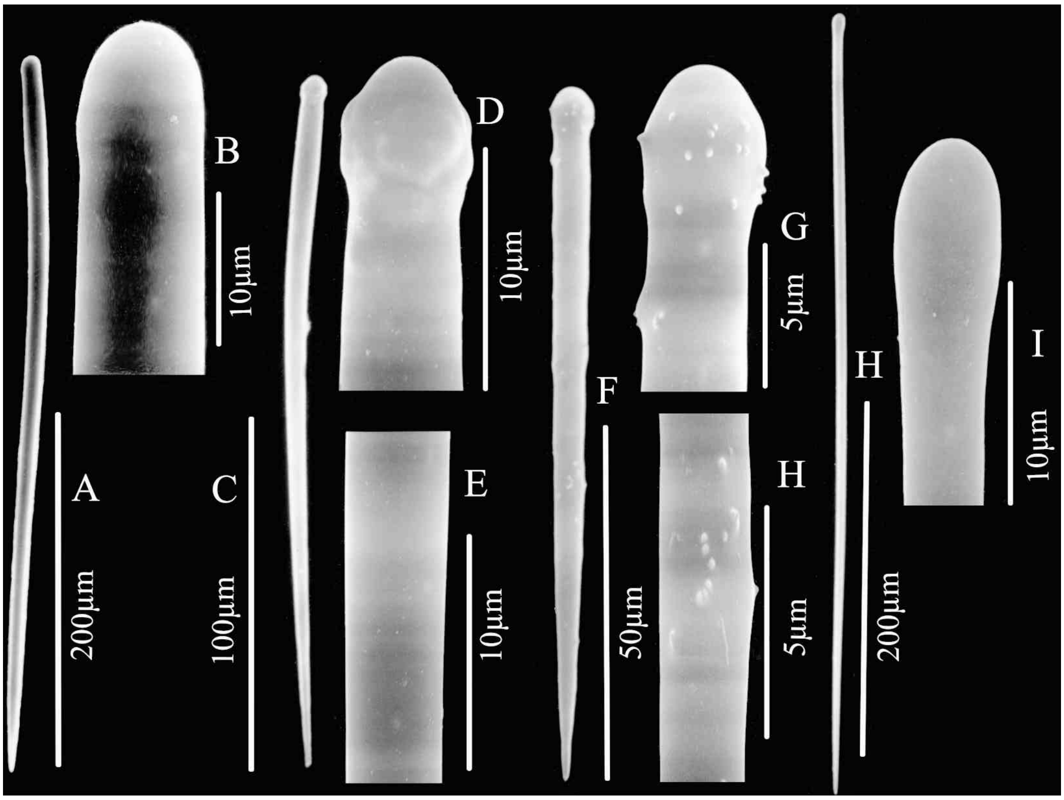

FIG. 1. Megascleres from *Clathria (Microciona) richmondi* sp. nov. (holotype QMG306785). A-B, Choanosomal principal style and subtylote base. C-E, Larger echinating acanthostyle, base and shaft, illustrating mostly smooth, tuberculate ornamentation. F-H, Smaller echinating acanthostyle, base and shaft with rudimentary small spines. I-J, Subectosomal auxiliary subtylostyle and smooth base.

(non-reflexed) arms, invariably forming toxodragmata. Length 262-(501.3)-975, width 1.5-(1.9)-2.0. Shorter toxas present but uncommon, intermediate between wing-shaped and accolada in morphology, with slight to moderate central curvature, slightly reflexed arms; found in toxodragmata together with accolada toxas and also occasionally singly within the mesohyl. Length 84-(114.8)-154, width 0.8-(1.04)-1.5.

REMARKS. *Clathria (Microciona) richmondi* sp. nov. is unusual in having 1) huge accolada toxas in dragmata, forming dense bands both within the mesohyl and lying tangential to the surface; 2) a second, less common and much smaller form of toxas, intermediate between wing-shaped and accolada morphology, scattered singly within the mesohyl; 3) a skeleton composed of hymedesmioid basal spongin fibres in thinner sections and microcionid bulbous spongin fibre nodes in thicker parts of the skeleton, each node with one or few choanosomal principal styles perpendicular to the surface; 4) relatively uncommon echinating acanthostyles, with rudimentary spination, apparently confined to the hymedesmioid basal skeleton; and 5) distinctive field characteristics including a royal blue colour, large oscules with a prominent raised 'lip' and prominent subsurface drainage canals radiating towards each oscule. Although individually these distinctive characters are not unique amongst known species of *Clathria*, in combination they clearly differentiate the Zanzibar species from others.

1) Microsclere morphology, including toxas, appears to be a relatively consistent and useful character to differentiate between similar species (Hooper, 1996a). Six species of *Clathria* have been recorded with accolada toxas forming toxodragmata (*C. (Thalysias) cactiformis* (Lamarck), *C. (Microciona) densa* (Burton),

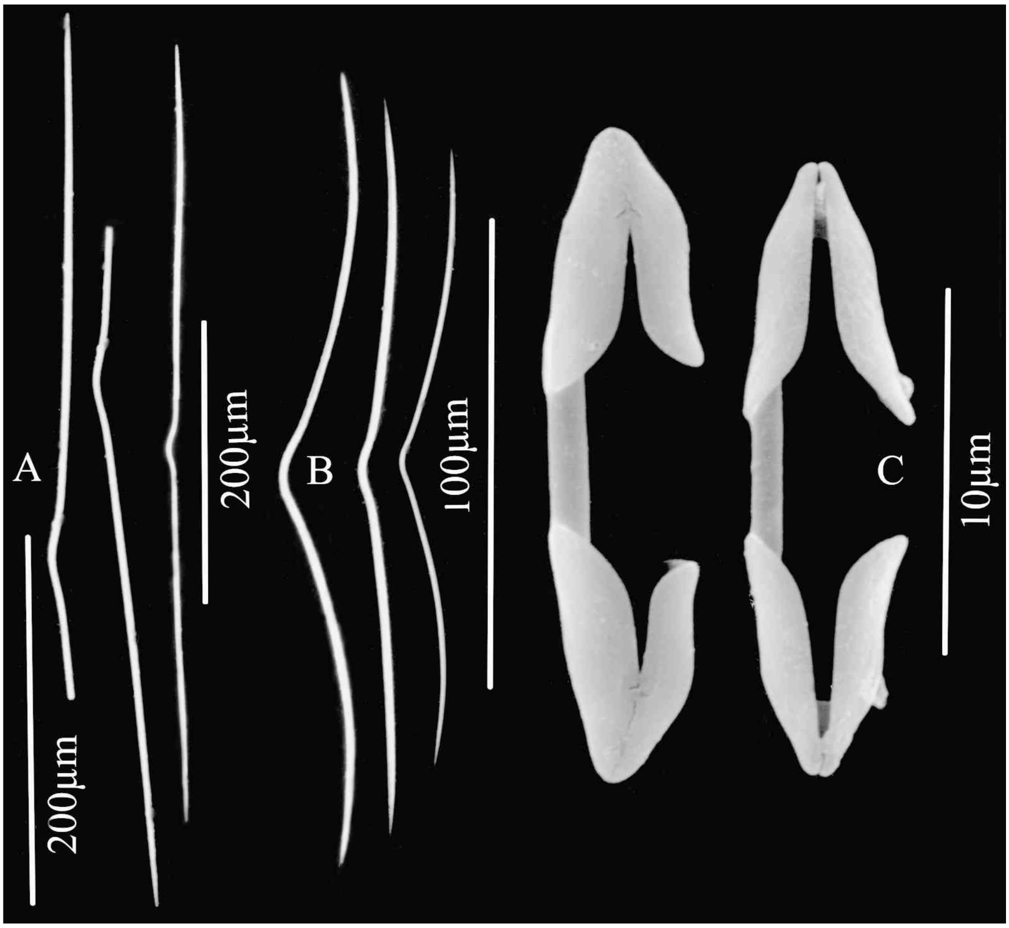

FIG. 2. Microscleres from *Clathria (Microciona) richmondi* sp. nov. (holotype QMG306785). A, Longer accolada toxas. B, Smaller toxas, intermediate between wing-shaped and accolada forms. C, Palmate isochelae.

C. (T.) lendenfeldi Ridley & Dendy, *C. (T.) oxitoxa* Lévi, *C. (Axociella) thetidis* (Hallmann) and *C. (T.) vulpina* (Lamarck) (Hooper, 1996a)); refer to Table 2 for known distributions. In *C. richmondi* the accolada toxas are exceptionally large compared to most species of *Clathria* (262-975 long), and also form very prominent bands within the skeleton. By comparison, those of *C. (T.) cactiformis* are 8-355 long, *C. (M.) densa* (205-305), *C. (T.) lendenfeldi* (7-361) and *C. (T.) vulpina* (8-200), and are scattered throughout the skeleton in loose bundles not forming skeletal tracts. In contrast, accolada toxas of *C. (A.) thetidis* and *C. (T.) oxitoxa* are much larger than those of *C. (M.) richmondi* (175-1280 and 170-3000 long, respectively), and moreover those of *C. (T.) oxitoxa* also form skeletal tracts within the skeleton (Lévi, 1963). In this regard *C. oxitoxa* is most similar to *C. richmondi*, although all three taxa differ in virtually every other respect (see redescription of *C. oxitoxa* below and *C. thetidis* in Hooper (1996a)).

2) Many species of *Clathria* have two toxa morphologies, and this feature is probably of little diagnostic importance above the species level. Of the species mentioned above only *C. densa* and *C. vulpina* lack both morphologies of toxas.

3) Hymedesmioid – microcionid skeletal structure has been used in the past as a primary diagnostic character for several nominal microcionid genera (e.g. *Axocielita* de Laubenfels, *Hymantho* Burton, *Leptoclathria* Topsent), although this view is no longer widely held (Van

Soest, 1984; Hooper, 1996a). Within *Clathria* these species are now placed in either the subgenera *Microciona* or *Thalysias*, depending on whether ectosomal specialisation is absent or present, respectively. Worldwide there are hundreds of encrusting microcionid species with hymedesmioid and/or microcionid spongin fibre skeletons and a mineral skeleton composed of perpendicular and/or plumose spicule tracts, of which 22 occur in this region (Table 2; species annotated (2)).

4) The presence or absence of echinating spicules, the degree to which they are smooth or spined, and the morphology of spines have been used as generic characters within Microcionidae at one time or another (e.g. *Anaata* de Laubenfels, *Axociella* Hallmann, *Folitispa* de Laubenfels, *Isociella* Hallmann, *Ophlitaspongia* Bowerbank, *Paratenaciella* Vacelet & Vasseur, *Tenaciella* Hallmann). The absence of echinating megascleres remains a valid diagnostic character (at the subgeneric level) for some taxa (e.g. *Isociella*, *Axociella*, *Ophlitaspongia*), by virtue of the consistent combination of this feature and the possession of unusual skeletal structures characterising each of the taxa (Hooper, 1996a; Howson & Chambers, 1999). Within *Clathria* s.s. there are also several species that have lost echinating spicules (e.g. *C.* (*C.*) *paucispicula* (Burton), *C.* (*T.*) *craspedia* Hooper). By comparison, the absence (loss), rudimentary development and shape of spines on echinating spicules vary widely amongst the many hundreds of species of *Clathria*, although these features appear to be consistent at the species level (e.g. *C.* (*M.*) *aceratoobtusa* (Carter) with virtually smooth spicules, *C.* (*C.*) *kylista* Hooper & Lévi with rudimentary spination, *C.* (*T.*) *dubia* (Kirkpatrick) with large, heavy spines). Within this continuum *C. richmondi* is most similar to the *C. kylista* condition.

5) As far as can be ascertained from the literature and from personal experience with the Microcionidae of the Indo-Pacific no other species

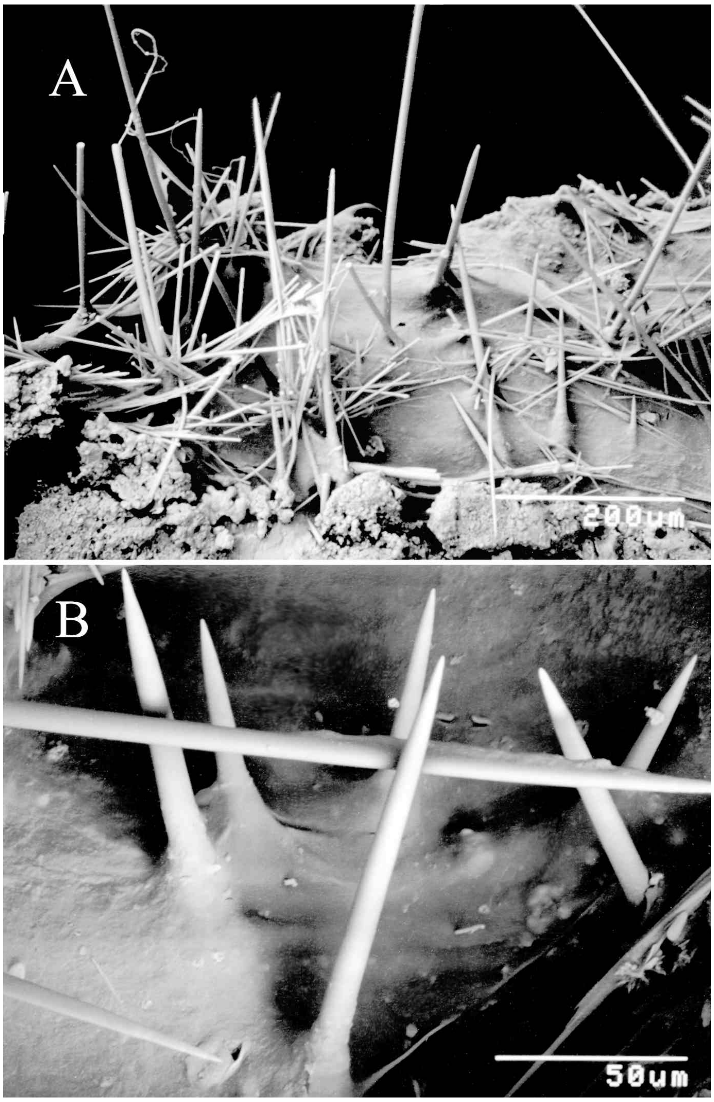

FIG. 3. Skeletal structure of *Clathria (Microciona) richmondi* sp. nov. (holotype QMG306785). A, Hymedesmioid-microcionid basal skeleton with tracts of auxiliary subtylostyles lying in multispicular bands within the choanosome. B, Erect echinating acanthostyles (mostly smooth) perpendicular to the hymedesmioid basal skeleton.

has a deep royal blue colour in life, but the importance of this character is limited by the lack of good knowledge of their living characters, most taxa known only from preserved specimens. Prominent raised oscules and a subsurface water canal system (radiating towards the oscules and producing a stellate surface pattern) are features common to many encrusting sponges (in which the aquiferous system is marginalised onto the external surface by virtue of the reduced choanosomal thickness), whereas in many microcionids this drainage system often has a different pigmentation from the adjacent ectosome.

Of the 64 species of *Clathria* recorded from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces 19 have accolada toxas (Table 2; species annotated (1)). Most of these species differ substantially from *C. richmondi* in major features such as growth form, skeletal structure, spicule geometries, spicule sizes, possession of specialised ectosomal skeleton (i.e. *Thalysias* condition) etc., whereas in 5 species these differences are more subtle.

Clathria (*T.*) *oxitoxa* Lévi (1963) is erect, bushy, flattened lamellate branches, yellow alive; skeleton plumo-reticulate with fibres irregularly cored by very large principal styles and bundles (dragmata) of large oxeote toxas scattered throughout the sponge skeleton; ectosomal skeleton with plumose brushes of both ectosomal and subectosomal styles; principal styles regularly curved, with smooth non-tylote bases (450-800x35-40); subectosomal auxiliary subtylostyles with microspined bases (350-500x9); ectosomal auxiliary subtylostyles similar (100-150x4); echinating acanthostyles entirely spined with large spines (75-90x10); palmate isochelae in 2 size classes (6 and 13-14); accolada toxas nearly oxeote, ranging from hair-like and faintly curved arms (170-250x0.5-1), thickly oxeote with straight arms (750-1300x4-7) and extremely long oxeotes with straight arms and only slight central curvature (2400-3000x 10-11); smaller wing-shaped toxas with large central curvature (35-40x0.5). This species is most similar to *C. (M.) richmondi* in having exceptionally large accolada toxas in dragmata forming skeletal bands, but differs significantly in its live colouration, growth form, skeletal structure and the geometry and size of all spicules (in particular the huge upper size range of accolada toxas).

Clathria (M.) densa (Burton, 1959) is massive, dense choanosomal skeleton with semi-plumose ascending spongin fibres cored by principal styles, interconnected by few transverse fibres and spicule tracts; dense ectosomal skeleton of auxiliary subtylostyles; principal styles with subtylote spined bases (175-298x18-35); subectosomal auxiliary subtylostyles with thick spined bases (130-275x4-8), echinating acanthostyles thick, slightly curved, heavily spined with aspinose neck (118-156x9-16); palmate isochelae (9-13); hair-like accolada toxas, distinctly sinuous and raphidiform forming dragmata (205-305x 0.5-1.5). This species is a borderline case between the subgenera *Microciona* and *Clathria* given that its choanosomal skeleton is a well-developed microcionid architecture that is verging on reticulate given the existence of vestigial inteconnecting fibres and spicule tracts. It also differs from *C. (M.) richmondi* in spicule geometry, spicule sizes, and absence of smaller wing-shaped toxas: in fact the two species are only similar in possessing accolada toxas forming dragmata.

Clathria (*C.*) *inhacensis* Thomas (1979b) is thinly encrusting, surface conulose; ectosome reduced; choanosomal skeleton reticulate, with well developed ascending primary fibres cored by plumose tracts of principal styles, interconnected by thinner transverse fibres in which few spicules are found and fully embedded within fibres, and both echinated by acanthostyles; subtylostyles interstitial and in brushes arising from tips of main fibres; principal styles with smooth bases (121-172x4-5); subectosomal subtylostyles with smooth bases (124-181x 2-4); echinating acanthostyles with variably spined shaft and spined bases (41-58x3-5); palmate isochelae (8-10); accolada toxas hair-like (110-145x0.5-1.5). This species clearly sits within subgenus *Clathria* given its possession of a reticulate skeletal architecture. It also differs significantly from *C. (M.) richmondi* in spicule geometry, spicule size and absence of toxo dragmata.

Clathria (*T.*) *longitoxa* (Hentschel, 1912) ranges from thinly encrusting to massive growth form; hymedesmioid to closely reticulate skeleton of stout fibres, with larger and smaller principal styles coring fibres in plumose arrangement, echinated by acanthostyles; subectosomal auxiliary subtylostyles scattered; principal styles curved with smooth non-tylote bases (592-840x 22-26); smaller principal styles with subtylote granular bases (120-408x 8-20); subectosomal auxiliary subtylostyles with faintly microspined bases (430-584x4-9); ectosomal auxiliary subtylostyles similar (190-320x3-5); echinating acanthostyles evenly spined with spined points (64-80x 6-7); palmate isochelae (12-20); accolada toxas with central U-bend and straight arms (400-820x1-2). This species differs from *C. (M.) richmondi* in most respects, showing similarities only in growth form, skeletal structure and possession of accolada toxas.

Clathria (*C.*) *oculata* Burton (1933a) has an erect branching anastomosing growth form, drab colouration with tinges of occasional purple; skeletal architecture composed of a subisodictyal reticulation of spongin fibres fully cored by principal styles and evenly echinated by acanthostyles; principal styles with smooth non-tylote bases (140-7); subectosomal auxiliary subtylostyles with smooth bases (160x3); echinating acanthostyles evenly spined with small spines (65x4); accolada toxas slightly curved (160 long); palmate isochelae very small (6 long). This species is only similar to *C. (M.) richmondi* in possessing accolada toxas, differing in most other features.

In addition to these species there are three unnamed species described from Madagascar by Vacelet & Vasseur (1971) showing similarities to *C. richmondi* in the morphology of their accolada toxas, skeletal structure and growth form, although differing in most all other characters.

FIG. 4. Ectosomal skeleton of *Clathria (Microciona) richmondi* sp. nov. (holotype QMG306785). A, Bundles of subectosomal auxiliary subtylostyles paratangential to and protruding through the surface, loosely associated with erect principal styles. B, Toxodragmata (bundles of accolada toxa) lying on or close to the surface.

Clathria (T.) sp. 4 (Vacelet & Vasseur, 1971; see Table 2) is thinly encrusting, yellow alive; choanosomal skeleton microcionid with columns of fibres cored by principal styles and acanthostyles; ectosomal specialisation with some surface brushes but these are not thick; principal styles very slightly subtylote, smooth bases (130-440x6-12); subectosomal auxiliary subtylostyles with smooth bases (150-320x4); ectosomal auxiliary subtylostyles with microspined bases (110-200x3); echinating acanthostyles slightly subtylote, poorly developed spines (55-60x5); palmate isochelae in 2 size classes, the smaller contort (5 and 12.5 long); accolada toxas nearly

TABLE 2. List of *Clathria* species recorded from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces. Refer to Hooper (Hooper, 1996a) for full synonymy and taxonomic references. Annotation: 1 = species with accolada toxas; 2 = encrusting species with hymedesmioid-microcionid skeletal structure; 3 = identification has yet to be confirmed from examination of voucher specimen; 4 = identification unconfirmed, specimen voucher material missing; 5 = new combination; 6 = currently unrecognisable.

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
C. (Thalysias) abietina (Lamarck)	*C. aculeata* Ridley	Burton (1959), Vacelet et al. (1976, 1977)	Red Sea, S Arabian coast, Madagascar	Tropical Australia, central NW Pacific, Philippines
C. (Microciona) affinis (Carter) [2]	*M. affinis* Carter	Burton (1959)	S Arabian coast, Zanzibar	Gulf of Manaar
C. (Thalysias) amirantiensis Hooper [1]	*Colloclathria ramosa* Dendy (preocc.)	Dendy (1922), Hooper (1996)	Amirante, Coëtivy, Seychelles	-
C. (Thalysias) anomala (Burton) [1]	*R. anomala* Burton	Burton (1933)	S South Africa	-
C. (Thalysias) anonyma (Burton) [2,5]	*M. anonyma* Burton	Burton (1959)	Zanzibar	-
C. (Clathria) arbuscula (Row)	*Ophlitaspongia arbuscula* Row, *O. horrida* Row	Row (1911)	Red Sea	-
C. (Microciona) atrasanguinea (Bowerbank) [2]	*M. atrasanguinea* Bowerbank	Carter (1880), Dendy (1922), Burton & Rao (1932), Lévi (1965), Van Soest (1993)	Seychelles, Red Sea, Arabian Sea, Mauritius	Caribbean, NE Atlantic, Mediterranean, coast of India, Gulf of Manaar, Bay of Bengal, Andaman Sea
C. (Clathria) axociona Lévi	*C. axociona* Lévi	Lévi (1963)	S South Africa	Namibia
C. (Thalysias) cactiformis (Lamarck) [1]	*Rhaphidophlus typicus* (Carter), *C. (T.) cactiformis* (Lamarck), *Rhaphidophlus* sp. 2; Vacelet & Vasseur	Vacelet et al. (1971, 1976, 1977), Hooper (1996)	Madagascar, Somalia, E Africa, Seychelles, Red Sea	S, W & E coasts of Australia
? *C. (Clathria) caespes* (Ehlers) [6]	*Scopalina caespes* (Ehlers)	Hooper (1996)	S South Africa	-
C. (Wilsonella) cercidochela Vacelet & Vasseur	*Clathriopsamma cercidochela* Vacelet & Vasseur	Vacelet et al. (1971, 1977)	Madagascar	-
C. (Clathria) conica Lévi	*C. conica* Lévi	Lévi (1963)	S South Africa	-
C. (Thalysias) cullingworthi Burton	*C. cullingworthi* Burton	Burton (1931)	Natal	-
C. (Clathria) dayi Lévi	*C. dayi* Lévi	Lévi (1963)	S South Africa	(? Korea [3])
C. (Thalysias) delaubenfelsi (Lévi)	*Rhaphidophlus delaubenfelsi* Lévi	Lévi (1963)	S South Africa	-
C. (Microciona) densa (Burton) [1,2]	*M. densa* Burton	Burton (1959)	S Arabian coast	-
C. (Clathria) elastica Lévi	*C. elastica* Lévi	Lévi (1963)	S South Africa	-
C. (Axociella) fauroti (Topsent)	*Axosuberites fauroti* Topsent	Topsent (1893)	Gulf of Aden	-
C. (Thalysias) flabellata (Burton)	*Rhaphidophlus flabellata* Burton	Burton (1936)	S South Africa	-
C. (Clathria) foliascens Vacelet & Vasseur	*C. foliascens* Vacelet & Vasseur	Vacelet et al. (1971, 1976, 1977)	Madagascar	-
C. (Thalysias) fusterna Hooper	*C. fusterna* Hooper	Hooper (1996)	Eritrea	N & NE Australia
C. (Clathria) hexagonopora Lévi [1]	*C. hexagonopora* Lévi	Lévi (1963)	S South Africa	-
C. (Clathria) indica Dendy	*C. indica* Dendy	Burton (1931), Thomas (1979)	Natal, Mozambique	SE India, Gulf of Manaar
C. (Clathria) inhacensis Thomas [1]	*C. inhacensis* Thomas	Thomas (1979)	Mozambique	-
C. (Clathria) irregularis (Burton)	*Marleyia irregularis* Burton	Burton (1931)	Natal	-

TABLE 2. (*cont.*)

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
C. (Clathria) juncea Burton	*C. juncea* Burton	Burton (1931)	Natal	-
C. (Microciona) laevissima (Dendy) [2]	*H. laevissima* Dendy	Dendy (1922)	Mauritius	-
C. (Thalysias) lambda (Lévi)	*Leptoclathria lambda* Lévi	Lévi (1958)	Red Sea	-
C. (Thalysias) lendenfeldi Ridley & Dendy [1]	*C. spicata* Hallmann, *C. whiteleggii* Dendy	Dendy (1922), Burton (1931, 1959), Hooper (1996)	Red Sea, Gulf of Aden, S Arabian coast, Cargados Carajos, Saya de Malha, Somalia, Natal	SE, NE, N. & NW Australia, E Indonesia, Andaman Sea, Gulf of Manaar
C. (Thalysias) lissoclada (Burton)	*Rhaphidophlus lissocladus* Burton	Lévi (1963)	S South Africa	Falkland Is
C. (Clathria) lobata Vosmaer	*C. lobata* Vosmaer	Vosmaer (1880), Ridley & Dendy (1887), Stephens (1915), Lévi (1963)	S South Africa	-
C. (Thalysias) longistyla (Burton) [2,5]	*M. longistyla* Burton	Burton (1959)	S Arabian coast	(? Korea [3])
C. (Thalysias) longitoxa (Hentschel) [1,2]	*M. longitoxa* (Hentschel)	Burton (1959)	Gulf of Aden	E Indonesia, Madras
C. (Microciona) microxea (Vacelet & Vasseur) 2	*Paratenaciella microxea* Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
C. (Wilsonella) mixta Hentschel	*C. mixta* Hentschel	Burton (1959)	S Arabian coast	E Indonesia [3]
C. (Thalysias) nervosa (Lévi)	*Axociella nervosa* Lévi	Lévi (1963)	S South Africa	-
C. (Clathria) oculata Burton [1]	*C. oculata* Burton	Burton (1933, 1959)	Natal	-
C. (Thalysias) oxitoxa Lévi [1]	*C. oxitoxa* Lévi	Lévi (1963)	S South Africa	-
C. (Clathria) pachystyla Lévi	*C. pachystyla* Lévi	Lévi (1963)	S South Africa	-
C. (Axociella) parva Lévi	*C. parva* Lévi	Lévi (1963)	S South Africa	Namibia
C. (Thalysias) procera (Ridley)	*Rhaphidophlus procera* Ridley, *Echinonema gracilis* Ridley	Ridley (1884), Ridley & Dendy (1887), Dendy (1922), Burton & Rao (1932), Burton (1931, 1959), Lévi (1963), Thomas (1973)	Cargados Carajos, Seychelles, Amirante, Red Sea, Arabian coast, Natal	NE, N & NW Australia, E Indonesia, Gulf of Manaar, (? Hawaii [3])
C. (Clathria) rhaphidotoxa Stephens [1]	*C. rhaphidotoxa* Stephens	Stephens (1915), Lévi (1963)	S South Africa	-
C. (Microciona) rhopalophora (Hentschel) [2]	*M. rhopalophora* (Hentschel)	Burton (1959)	Maldives	E. Indonesia, Cocos-Keeling, Gulf of Manaar
C. (Thalysias) robusta (Dendy) [1,2]	*M. robusta* Dendy	Dendy (1922)	Amirante	Singapore
C. (Microciona) seriata (Grant) [2,4]	*Ophlitaspongia seriata* (Grant)	Lévi (1963)	S South Africa	NE. Atlantic, Mediterranean, New Zealand
C. (Clathria) spongodes Dendy	*C. spongodes* Dendy, *C. spongiosa* Burton, *C. madrepora* Dendy	Dendy (1922), Burton (1959), Vacelet et al. (1976)	Red Sea, Gulf of Aden, Amirante, Madagascar, Seychelles	(? Korea [3])
C. (Microciona) stephensae Hooper	*M. similis* Stephens (preocc.)	Stephens (1915)	S South Africa	-
C. (Microciona) tenuis (Stephens) [2]	*M. tenuis* Stephens	Stephens (1915)	S South Africa	-
C. (Clathria) transiens Hallmann [4]	*C. transiens* Hallmann	Burton (1959)	Red Sea	S Australian provinces

TABLE 2. (*cont.*)

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
C. (Clathria) typica Kirkpatrick (virtually unrecognisable)	*C. typica* Kirkpatrick	Kirkpatrick (1904)	Natal	-
C. (Microciona) vacelettia Hooper [2]	*M. curvichela* Vacelet & Vasseur (preocc.)	Vacelet & Vasseur (1965), Hooper (1996)	Madagascar	-
C. (Thalysias) vulpina (Lamarck) [1]	*C. frondifera* (Bowerbank), *C. dichela* (Hentschel)	Ridley (1884), Ridley & Dendy (1887), Topsent (1892), Row (1911), Burton (1959), Lévi (1961), Thomas (1973, 1979), Vacelet et al. (1971, 1976, 1977), Pulitzer-Finali (1993), Hooper (1996), Kelly (1997)	Madagascar, Amirante, Seychelles, Red Sea, Mozambique, Aldabra, Zanzibar	Tropical Australia, W & E coasts of India, Gulf of Manaar, Mergui Archipelago, Andaman Sea, Malaysia, E & W Indonesia, N Papua New Guinea, Vietnam, Philippines, Micronesia, S Japan, New Caledonia
C. (Clathria) zoanthifera Lévi	*C. zoanthifera* Lévi	Lévi (1963)	S South Africa	-
Clathria (Thalysias) sp.; Vacelet & Vasseur [1]	*Rhaphidophlus* sp. 1; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Thalysias) sp.; Vacelet & Vasseur	*Rhaphidophlus* sp. 3; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Thalysias) sp.; Vacelet & Vasseur [1,2]	*Rhaphidophlus* sp. 4; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Thalysias) sp.; Vacelet & Vasseur [1,2]	*Rhaphidophlus* sp. 5; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Thalysias) sp.; Vacelet & Vasseur [1,2]	*Rhaphidophlus* sp. 6; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Thalysias) sp.; Vacelet & Vasseur	*Rhaphidophlus* sp. 7; Vacelet & Vasseur	Vacelet et al. (1971, 1977)	Madagascar	-
Clathria (Microciona) sp.; Vacelet & Vasseur [2]	*Microciona* sp. 1; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Microciona) sp.; Vacelet & Vasseur [1,2]	*Microciona* sp. 2; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
Clathria (Microciona) sp.; Vacelet & Vasseur [2]	*Microciona* sp. 3; Vacelet & Vasseur	Vacelet et al. (1971, 1976)	Madagascar	-
Clathria (Microciona) sp.; Vacelet, Vasseur & Lévi [1,2]	*Microciona* sp. 4; Vacelet, Vasseur & Lévi	Vacelet et al. (1976)	Madagascar	-

oxeote, with slight to virtually no central curvature (85-820x0.5-2.5); U-shaped to wing-shaped toxas very small (5-7.5).

Clathria (*T.*) sp. 5 (Vacelet & Vasseur, 1971) is encrusting, orange alive; hymedesmioid skeleton of principal subtylostyles and acanthostyles erect on basal spongin fibres; subectosomal and ectosomal auxiliary subtylostyles differ only in size and both contribute to both subectosomal and ectosomal surface brushes; principal subtylostyles slender, moderately subtylote microspined bases (140-280x5-8); subectosomal auxiliary subtylostyles slightly subtylote, smooth bases (up to 360x3); ectosomal auxiliary subtylostyles similar (from 90x2); echinating acanthostyles slender, evenly spined (50-60x2-3); palmate isochelae in two size classes (4-5 and 12-12.5 long); accolada toxas nearly oxeote, with straight or only very slightly curved arms and slight angular central flexion (35-250 long).

Clathria (*M.*) sp. 2 (Vacelet & Vasseur, 1971) is encrusting, pinkish to red alive, with white subectosomal drainage canals clearly visible on the otherwise smooth surface; skeleton microcionid; principal subtylostyles with smooth or microspined bases (330-550x13-15); subectosomal auxiliary subtylostyles with smooth bases (120-550x2.5-5); echinating acanthostyles slender, entirely spined (100-120x5-7.5); palmate isochelae (7.5-20); accolada toxas with only slight curvature of arms and central flexion (130-320); small oxhorn toxas (7.5-20).

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