

Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Halichondriidae

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ABSTRACT

Fifteen species in six genera of the family Halichondriidae, including two new species, *Halichondria* (*Halichondria*) *carotenoidea* sp. nov. and *Halichondria* (*Halichondria*) *microbiana* sp. nov., are recorded for northern Australia as part of a revision of the order Halichondrida (Porifera: Demospongiae) in this region. Descriptions and discussion of those species are presented here. Eight new combinations within the family Halichondriidae are here established, i.e. *Amorphinopsis fenestrata* (Ridley, 1884, as *Leucophloeus*), *Amorphinopsis maculosa* (Pulitzer-Finali, 1996, as *Topsentia*), *Axinyssa bergquistae* (Hooper *et al.*, 1997, as *Halichondria*), *Axinyssa mertonii* (Hentschel, 1912, as *Ciocalypa*), *Axinyssa gracilis* (Hentschel, 1912, as *Ciocalypa rutila gracilis*), *Axinyssa terpnis* (De Laubenfels, 1954, as *Phycopsis*), *Ciocalypa vansoesti* (Hooper *et al.*, 1997, as *Halichondria*) and *Topsentia ridleyi* (Hooper *et al.*, 1997 as *Halichondria*) and one species is relocated into the family Dictyonellidae, i.e. *Stylissa vernonensis* (Hooper *et al.*, 1997, as *Hymeniacidon*). A lectotype is designated for *Ciocalypa stalagmites* Hentschel, 1912.

KEYWORDS: sponge, Porifera, Halichondrida, Halichondriidae, northern Australia, new species, taxonomy.

INTRODUCTION

The family Halichondriidae was revised by Erpenbeck & Van Soest (2002). Its definition is based entirely on a few skeletal characters, i.e. presence of an ectosome with specialised skeleton, a disorganised choanosomal skeleton, dimensions of oxae and styles, absence of microscleres. Other morphological characters (e.g. general shape of megascleres, presence or size categories among the megascleres, spicule density and its relation to consistency, orientation of spicules at the ectosomal level) are used in combination with the diagnostic characters to separate species and genera within this family. All these characteristics are very simplistic, and often displayed as a gradient of variation which makes separation of species very subjective as reflected by the large number of synonyms (see Van Soest *et al.* 2008).

The family includes 14 genera and at least 296 valid species (Van Soest *et al.* 2008); however, the status and generic allocation of many of the species listed on this database on the Internet needs to be revised and validated against the current concept of the genera.

The Australian Faunal Directory (Hooper 2005) currently lists a total of 42 species of Halichondriidae. Twenty species were reported and described for the Beagle Gulf (northern Australia) by Hooper *et al.* (1997). No

other revision of species of Halichondriidae in Australia or adjacent areas is presently available.

The present paper represents the third part of a revision of the order Halichondrida in the northern Australian region and includes the family Halichondriidae. Alvarez & Hooper (2009, 2010) provided details and presented an introduction to the revision of the order and the families Axinellidae and Dictyonellidae.

MATERIALS AND METHODS

This revision includes material of the family Halichondriidae recorded for the tropical northern Australian waters of the Northern Territory and Queensland coast (from Admiralty Gulf in the west to Torres Strait in the east, approx. between the 125° E and 142° E).

Complete locality and collection data for non-type voucher material deposited at the Queensland Museum and the Museum and Art Gallery of the Northern Territory are available in Appendix 1.

The distribution of species is given according to the marine provinces defined by Spalding *et al.* (2007). Spicule measurements are in micrometres and are based on 25 spicules (unless indicated in square brackets) and denoted as range (and mean \pm 1 S.E.) of spicule length and width. All other methods as discussed in Alvarez & Hooper (2009, 2010).

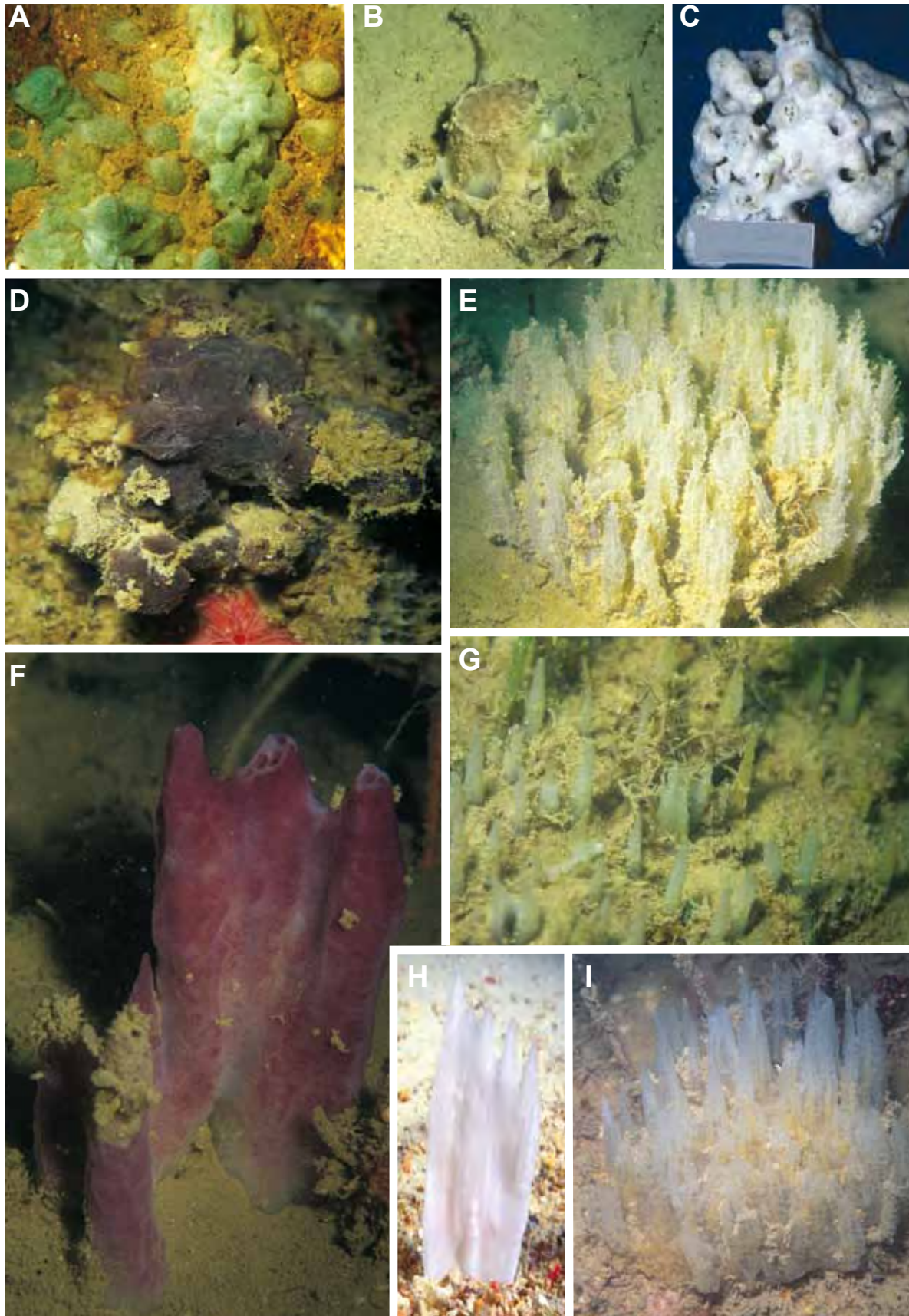


Fig. 1. **A**, *Amorphinopsis excavans*, specimen *in situ* at South Shell I., Darwin Harbour, N.T.; **B**, *Amorphinopsis fenestrata*, specimen *in situ* at Weed Reef, Darwin Harbour, N.T. **C**, *Amorphinopsis maculosa*: Specimen (QM G313577) dredged at Groote Eylandt, Gulf of Carpentaria, Queensland; **D**, *Axinyssa bergquistae*, specimen (NTM Z. 5976) *in situ* at Stevens Rock, Darwin Harbour, N.T.; **E**, *Axinyssa mertoni*, specimen *in situ* at South Shell I., Darwin Harbour, N.T.; **F**, *Ciocalypta heterostyla*, specimen *in situ* at Channel Rock, Darwin Harbour, N.T.; **G,H**, *C. stalagmites*, specimens with different colouration *in situ* at Channel Rock and Stevens Rock, respectively; **I**, *C. vansoesti*, specimen *in situ* at Channel Rock, Darwin, N.T. Photographs: A,B – M. Browne; D,G–I – H. Nguyen, H,E,F – B. Alvarez.

ABBREVIATIONS

Abbreviations used in the manuscript are: AIMS, Australian Institute of Marine Sciences, Townsville; BMNH, Natural History Museum, London (formerly British Museum (Natural History)); CRRF, Coral Reef Research Foundation, Palau; GBR, Great Barrier Reef, MAGNT, Museum and Art Gallery Northern Territory; MNHN, Musée National d'Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy; MAGNT/NTM, Museum and Art Gallery Northern Territory (formerly Northern Territory Museum), Darwin, Northern Territory, Australia; NHMB – Naturhistorisches Museum, Basel, Switzerland; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt; QLD, Queensland, Australia; QM, Queensland Museum, Brisbane; WA, Western Australia; ZMA, Zoologisch Museum, University of Amsterdam, ZMB, Museum für Naturkunde und der Universität Humboldt zu Berlin, Berlin, Germany.

Numbers prefixed with Q666C, 0CDN, 0M9H are the cross-reference sample number collected for the United States National Cancer Institute, under the 'Collection of shallow-water organisms' programme, by the Australian Institute of Marine Sciences, CRRF and MAGNT (subcontracted through CRRF) respectively.

TAXONOMY

Family Halichondriidae Gray, 1867**Genus *Amorphinopsis* Carter, 1887**

Gender feminine. Type species, by monotypy, *Amorphinopsis excavans* Carter, 1887. Recent, Indian Ocean.

***Amorphinopsis excavans* Carter, 1887**

(Figs 1A, 2)

Amorphinopsis excavans Carter, 1887: 77; Hooper & Wiedenmayer 1994: 205; Hooper *et al.* 1997: 25; Erpenbeck & Van Soest 2002: 791; Lim, de Voogd & Tan 2008: 115.

Amorphinopsis sacciformis. – Hooper *et al.* 1997: 27.

Material examined. Darwin Harbour: NTM Z.2215, Z.4093, Z.4125 (0CDN-8016-W), Z.5213 (0M9H2184-Q); Z.5222 (0M9H2251-O), Z.5736. Vernon Is: G303658.

Description

Shape (Fig. 1A). Thinly to thickly encrusting (up to 50 mm thick), massive to lobate, or developing short projections and small lumps, generally growing in patches and following substrate, semi-buried in substrate.

Colour. Olive green, yellow inside.

Oscula. Round to ovate, inconspicuous, 10 mm diameter.

Surface. Hispid, bumpy.

Skeleton. Ectosomal skeleton (Fig. 2A) thin, detachable tangential layer, composed by a disorganised criss-cross reticulation of paucispicular-multispicular tracts of oxeas,

up to 100 µm thick, with small styles tangentially to paratangentially oriented, sometimes in disorganised tufts. Choanosomal skeleton (Fig. 2B) halichondroid, with large oxeas oriented in all directions, sometimes grouped in directionless multispicular tracts; slightly cavernous at subectosomal area with short multispicular tracts supporting the ectosomal skeleton.

Spicules (Fig 2C). Oxeas, hastate, in a large range of sizes, 213.4–945.3 µm (598±221) x 5.9–25.1 µm (16.3±5.5). Smaller ectosomal styles 140.8–264.9 µm (193.8±41.3) x 4.1–7.5 µm (5.5±0.9).

Remarks. The material examined here agrees with the description of the syntype by Erpenbeck & Van Soest (2002: 790).

The specimen described under *Amorphinopsis sacciformis* by Hooper *et al.* (1997) is better allocated to *A. excavans*. It does not agree with the syntype of *Ciocalypta sacciformis* Thiele which, as mentioned below (see under remarks of *A. carpentariensis*), should be interpreted as *Halichondria*. The material described by Hooper *et al.* (1997) is a thin crust covering a bivalve shell with skeleton similar to the rest of the material assigned here to *A. excavans*.

Species considered synonyms of *Amorphinopsis excavans* by Hooper & Wiedenmayer 1994, following Burton (1959), were excluded by Hooper *et al.* (1997) and Erpenbeck & Van Soest (2002).

Distribution. The species was recorded originally from the Mergui Archipelago (Andaman province). Records from Singapore and northern Australia extend the distribution of the species to the Sunda and Sahul Shelf provinces. The northern Australian and Singaporean populations seem to be common at the intertidal region associated with piers and wharfs. The species is found also subtidally between 9 and 16 m.

***Amorphinopsis fenestrata* (Ridley, 1884) comb. nov.**

(Figs 1B, 3)

Leucophloeus fenestratus Ridley, 1884: 464; Dendy 1922: 124; Burton 1928: 127.

Leucophloeus fenestratus unnamed variety. – Ridley 1884: 464.

Suberites oculatus Kieschnick, 1896: 534.

Hymeniacidon fenestratus. – Lindgren 1897: 483; Lindgren 1898: 312 [?].

Ciocalypta oculata. – Thiele 1900: 75.

Ciocalypta oculata maxima Hentschel, 1912: 428.

Axinyssa fenestratus. – Van Soest, Díaz & Pomponi 1990: 27; Hooper & Bergquist 1992: 102.

Ciocalypta confossa Hooper *et al.*, 1997: 23.

Ciocalypta fenestrata. – Hooper *et al.* 1997: 17.

Ciocalypta oscitans Hooper *et al.*, 1997: 20.

Amorphinopsis foetida. – Hooper *et al.* 1997: 28.

Material examined. TYPE MATERIAL – *Leucophloeus fenestratus*, HOLOTYPE, BMNH 1882.2.23.255, Darwin Harbour, N.T., 16–24 m depth, October 1881, HMS *Alert*. *Leucophloeus fenestratus* unnamed variety, BMNH

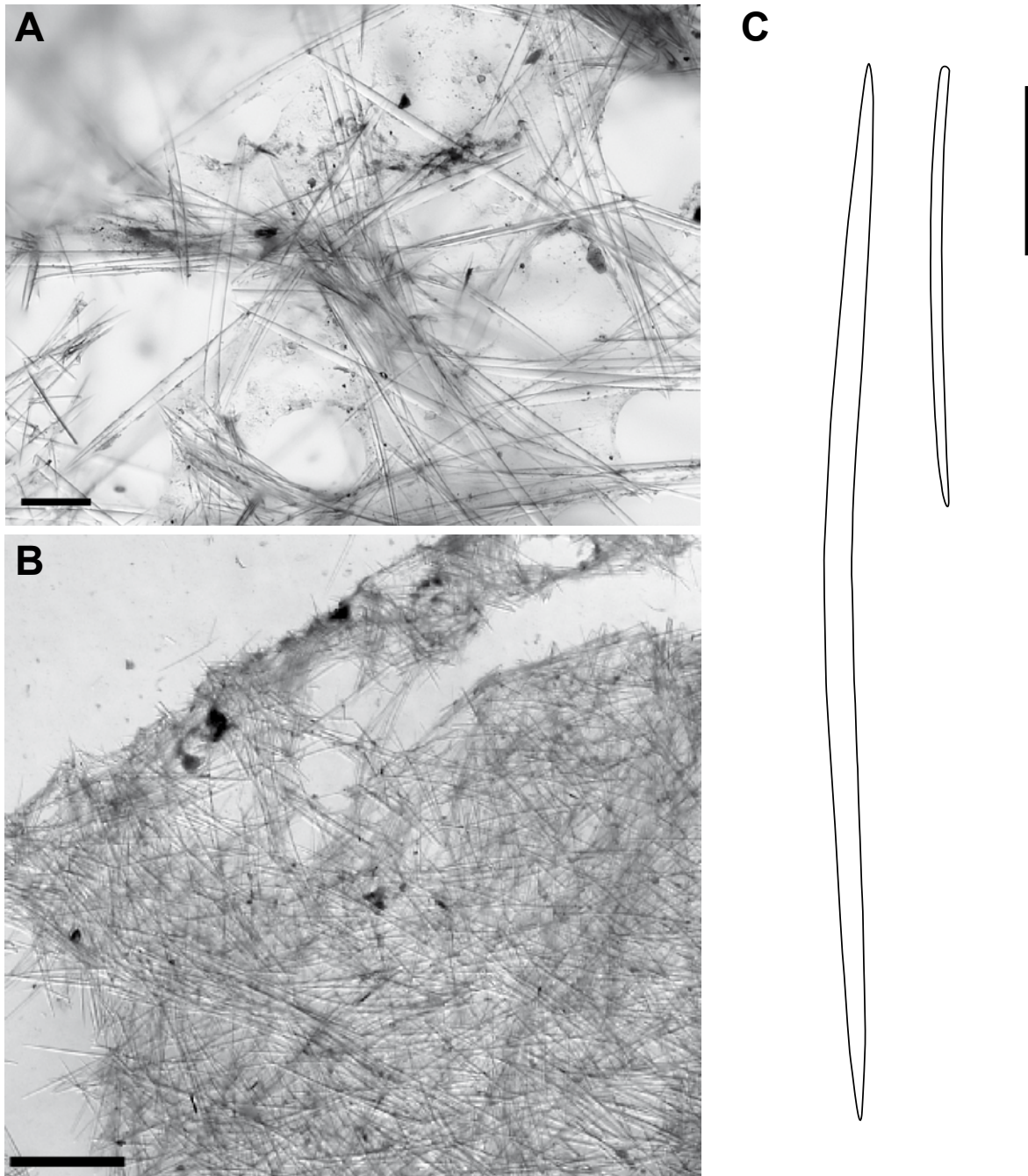


Fig. 2. *Amorphinopsis excavans* (NTM Z.5213): **A**, light microphotograph of tangential section of ectosomal skeleton, showing oxeas organised in bundles and small styles, paratangentially oriented in disorganised brushes; **B**, light microphotograph of section perpendicular to surface, showing choanosomal skeleton; **C**, diagram of spicules. Scale bars: A,C, 100 μ m; B, 500 μ m.

1882.2.23.195, Arafura Sea, 64–72 m depth, 18 October 1881, coll. HMS *Alert*. *Suberites oculatus*, syntype SMF 680, Ternate, Maluku Sea, coll. Kükenthal, W, 1894. *Ciocalypa oculata maxima*, SMF 971, Aru Is, between Meriri and Leer, 6–10 m depth, 31 March 1908, coll. Merton, H. *Ciocalypa oscitans*, HOLOTYPE, QM G303560, Bynoe Harbour, E Fish Reef, N.T., 12°24.1334' S, 130°28.16' E, 17 m depth, 6 October 1993, coll. CCNT Ocean Rescue 2000 Program, dredge. *Ciocalypa confossa*, NTM Z.3106, Parry Shoals, Arafura Sea, N.T., 11°12.5167' S, 129°42.07' E., 20 m depth, 15 August 1987, coll. Mussig, AM and NCI team. ADDITIONAL SPECIMENS – Melville Is: QM G313543.

Shoal Bay, Vernon Is, Cape Hotham: QM G303558, G303677, G303541. Bynoe Harbour: NTM Z.5207 (0M9H2319-N), Z.5208 (0M9H2543-H). Darwin Harbour: QM G303287, G310170; NTM, Z.2018, Z.4085, Z.4122, Z.4123, Z.5215 (0M9H2137-P), Z.5206 (0M9H2192-Y). Cobourg Peninsula, NTM Z.1391. Gulf of Carpentaria: QM G314246, G314247, G315205.

Description

Shape (Fig. 1B). Massive to subspherical, with tapering, hollow, rudimentary, subconical or volcano-shaped fistules, up to 18 mm long and 30 mm diameter; basal portion buried beneath sediment and fistules protruding through substrate.

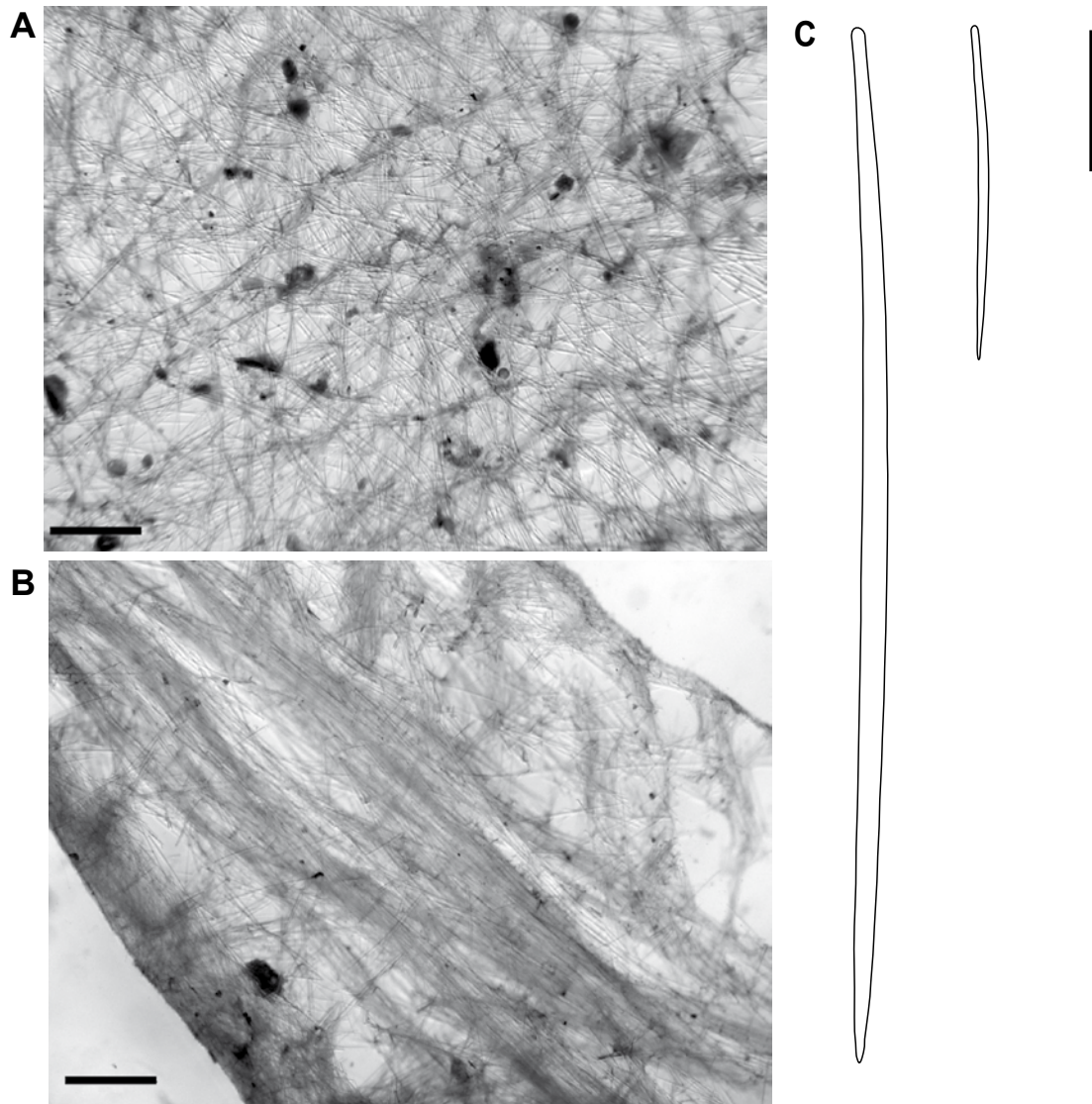


Fig. 3. *Amorphinopsis fenestrata*: **A**, light microphotograph of tangential section of ectosomal skeleton (NTM Z.5206), showing spicule tracts criss-crossing and forming a reticulation of polygonal meshes; **B**, light microphotograph of section perpendicular to surface (NTM Z.5215) showing choanosomal skeleton; **C**, diagram of spicules. Scale bars: A-B, 500 μ m; C, 100 μ m.

Colour. Yellow, brown or pale mauve, alive.

Oscula. Large, up to 10 mm in diameter or, grouped on a terminal sieve-plate, on apex of fistules.

Texture and consistency. Compressible, harsh, easily torn.

Surface. Irregular, rugose, translucent, hispid, marked in some specimens with longitudinal channels.

Skeleton. Ectosomal skeleton (Fig. 3A) detachable, supported by subectosomal multispicular tracts. Formed by multispicular tracts of larger choanosomal styles, up to 3 spicules abreast, lying tangential to surface, directionless or criss-crossing, forming a nearly regular reticulation of polygonal meshes; and, irregular bundles of smaller ectosomal styles arranged mostly paratangential to surface as plumose brushes or tufts. Choanosomal skeleton disorganised, halichondroid criss-cross of both unispicular and multispicular tracts, containing 5–20 spicules abreast, with larger choanosomal styles mainly confined to central region; becoming more wide-meshed, paratangentially

oriented and cavernous at subectosomal region. In fistules choanosomal tracts more compressed in central region (Fig. 3B), cavernous towards periphery. Single spicules, including smaller styles scattered through choanosome.

Spicules (Fig. 3C, Table 1). Choanosomal styles and styloids (thicker in apical third and with basal ends narrower than the centre), slender, straight or slightly curved at centre, fusiform, in a great size range (163–895 \times 3.3–17.4 μ m). Smaller styles can be transitional to subtylostyles. Relative proportions of styles, styloids and subtylostyles vary among populations.

Remarks. The species was originally described by Ridley (1884) under *Leucophloeus*, a junior synonym of *Ciocalypa* (Van Soest *et al.* 1990; Erpenbeck & Van Soest 2002) and related to species of *Ciocalypa* by Hooper *et al.* (1997) based on the characteristics of the ectosomal skeleton, and the presence of styles. As described above, the growth form of *Amorphinopsis fenestrata* is characterised by the presence of fistule-like projections of several shapes

Table 1. Comparison of spicule dimensions among specimens of *Amorphinopsis fenestrata*.

Specimen	Locality	Styles
BMNH 1882.2.23.255 (Holotype)	Darwin Harbour	193.6–611.8µm (390.4±136.4) x 5.3–12.7µm (8.6±2)
BMNH 1882.2.23.195 (Ridley's unnamed variety specimen)	Arafura Sea	252.9–895.3µm (617.7±217.3) x 5.9–15.4µm (9.6±2.6)
SMF 680 (Syntype of <i>Suberites oculatus</i>)	Ternate, Indonesia	210.2–761.6µm (431.1±160) x 4.7–17.4µm (8.1±2.8)
SMF 971 (Syntype of <i>Ciocalypta oculata maxima</i>)	Aru Is, Indonesia	306.4–892.8µm (563.3±176) x 3.3–11.6µm (6.6±1.8)
NTM Z.3106 (Holotype of <i>Ciocalypta confossa</i>)	Parry Shoals	217.8–649µm (448.9±149.7) x 6.4–12.6µm (9.2±1.9)
QM G303560 (Holotype of <i>Ciocalypta oscitans</i>)	Bynoe Harbour	175.1–690.4µm (502.7±155.8) x 5.2–13.3µm (8.7±2.2)
NTM Z.5215	Darwin Harbour	178.5–891.1µm (427.1±199.8) x 4–12.3µm (7.7±2.3)
NTM Z.5207	Bynoe Harbour	163.5–833.1µm (432.4±214.6) x 3.7–13.7µm (7.3±2.3)
QM G314247	Gulf of Carpentaria	218.8–599.3µm (412.2±120.3) x 4.3–11.1µm (7.2±2.2)

(e.g. pointy, hollow, pyramidal or volcano-shaped), some with a system of exhalant channels. They project from a semi-buried massive base and protrude through the substrate/sand. The skeletal architecture in these fistulose projections, although similar, is considered here not to be homologous to the one observed in *Ciocalypta* species, which is characterised by a central spicular axis and extra-axial secondary tracts supporting the ectosomal skeleton (see below under *Ciocalypta*). Instead, the skeleton of the fistulose projections of this species is formed by multiple axes, oriented longitudinally and radiating towards the surface. Based on these arguments, we suggest that the species is better allocated to the genus *Amorphinopsis*. It needs to be noted however, that the skeleton of the present species is composed totally by styles with a great size range and lacks of 'true' oxeas, a diagnostic characteristic of this genus. In the majority of specimens examined, including the holotype, a great proportion of the styles are 'subacerate' (styloids) similar to those observed in *Aptos* (Hadromerida: Suberitidae) where the thickest part of the spicule occurs in the apical third and the basal end is substantially narrow. The relative proportion of styloids varies among the populations examined. Subtylostyle modifications, especially in the smaller styles are also common. We are unable to confirm whether this type of styles might be considered a derived form of oxea (as stated in the current definition of the genus) and therefore we propose to expand slightly the definition of *Amorphinopsis* to accept species with spicules differentiated into oxeas and/or styles in a large size range, with smaller ones concentrated at the surface.

The examination of additional specimens allowed us to understand the concept of this species better and to conclude that the material from Beagle Gulf described by Hooper *et al.* (1997) under *Ciocalypta oscitans*, *C. confossa* and *Amorphinopsis foetida*, and the Indonesian species *Suberites oculatus* Kieschnick and *Ciocalypta oculata maxima* Hentschel are all conspecific with *A. fenestrata*.

Amorphinopsis subacrata (Ridley & Dendy, 1886) from the Philippine Islands is very similar to *A. fenestrata* and as stated by those authors they share many characteristics including the type of styles but differ in external form and in having larger and thicker styles. Study of local populations and examination of the type material is required to establish whether the two species are conspecific.

Distribution. *Amorphinopsis fenestrata* is common throughout the Northern Territory coast (Sahul Province), from Parry Shoals (NW of Darwin Harbour) to the Gulf of Carpentaria. The records of Lindgren (1897, 1898) from Vietnam and China, of Dendy (1922) from the Indian Ocean and of Burton (1928) from the Malay Archipelago need to be verified.

***Amorphinopsis maculosa* (Pulitzer-Finali, 1996)
comb. nov.
(Figs 1C, 4)**

Topsentia maculosa Pulitzer-Finali, 1996: 114.

Axinyssa aplysinoides. – Hooper *et al.* 1997: 4. Not *Axinyssa aplysinoides* Dendy, 1922: 39.

Material examined. HOLOTYPE – MSNG 48701, Laing Is., 4° 09' S, 144° 52' E, Papua New Guinea, 6 m depth, 23 August 1986. ADDITIONAL SPECIMENS – Gulf of Carpentaria: QM G300854, G301034, G313577, G314255, G314267, G315207, G320819, G320904. Shoal Bay: QM G303561.

Description

Shape. Thickly encrusting, following substrate with convoluted ridges and short projections.

Colour. Light grey or yellow alive; yellow inside beige in ethanol.

Oscula. Inconspicuous, of different diameter, flushed and irregularly distributed or aggregated in top of the short projections (Fig. 1C).

Surface. Smooth, lumpy, with dermal skin of reticulated appearance.

Consistency and texture. Firm but crumbly.

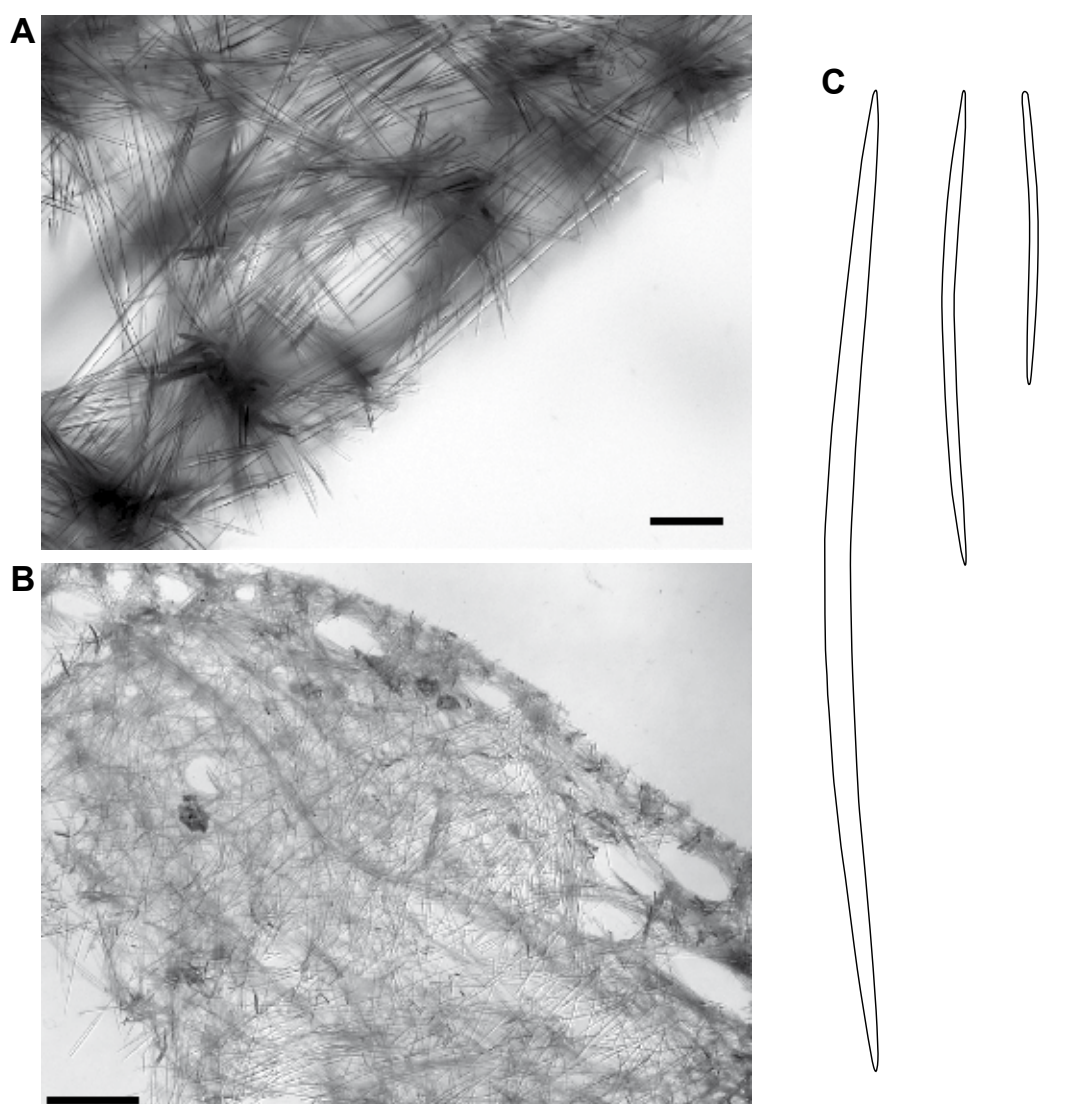


Fig. 4. *Amorphinopsis maculosa* (QM G313577): **A**, light microphotograph of tangential section of ectosomal skeleton showing brushes of small styles with ends projecting through surface; **B**, light microphotograph of section perpendicular to surface showing choanosomal skeleton; **C**, diagram of spicules. Scale bars: A, 100 μm ; B, 500 μm ; C, 100 μm .

Skeleton. Ectosomal skeleton (Fig. 4A) consisting of tangential to paratangential crust, approx. 200–300 μm thick, supported by choanosomal tracts of spicules and with disorganised brushes of small styles with ends projecting through surface, forming a discontinuous palisade spaced roughly at regular distances. Choanosomal skeleton (Fig. 4B) halichondroid, forming oval to round lacunae, 300–1000 μm in diameter, becoming compact towards surface, with very little collagen and abundant spicule content. Spicule tracts long and multispicular, running either towards surface or parallel to surface at the subectosomal area.

Spicules (Fig. 4C, Table 2). Oxeas and much less frequent styles in a large size variation, 207–994 \times 5–38 μm ; small ectosomal styles (and transitional to oxeas), 139–274 \times 3–8 μm .

Remarks. The holotype of *Topsentia maculosa* Pulitzer-Finali was examined and is comparable in external morphology and skeletal characteristics to material collected in the Gulf of Carpentaria and Shoal Bay. The species is redescribed using this material and assigned to the genus *Amorphinopsis*.

Table 2. Comparison of spicule dimensions among specimens of *Amorphinopsis maculosa*.

Specimen	Locality	Oxeas	Styles
MSNG 48701 (Holotype of <i>Topsentia maculosa</i>)	Papua New Guinea	240.2–994.6 μm (633.7 ± 255.1) \times 7.4–37.6 μm (21.7 ± 9.9)	138.5–259.2 μm (211 ± 35.5) [16] \times 3–9.7 μm (6.6 ± 1.8) [16]
QM G313577	Gulf of Carpentaria	369.1–863.5 μm (675.8 ± 124.6) \times 7.9–20.3 μm (15.2 ± 3.2)	143.7–273.8 μm (187.7 ± 35.2) \times 3.2–7 μm (4.8 ± 1)
QM G314255	Gulf of Carpentaria	207.9–819.5 μm (560.1 ± 166.3) \times 4.5–22.1 μm (12.6 ± 4)	147.5–240.4 μm (174.2 ± 20.9) \times 3–7.8 μm (5.6 ± 1)

Amorphinopsis maculosa is very similar in habit and skeletal organisation to *A. fenestrata* (Ridley, 1884) but that species has only styles as megascleres and lacks the oxeas of variable sizes present in this species (see above). Fistulous projections, as observed in *A. fenestrata*, are not present in the examined material of *A. maculosa*.

The specimen assigned to *Axinyssa aplysinoides* (Dendy) by Hooper *et al.* (1997) was re-examined and has characteristics (i.e. habit, ectosomal skeleton, oxeas and smaller styloids) that agree with *Amorphinopsis maculosa*.

Amorphinopsis maculosa was also compared to other species of *Amorphinopsis* recorded for northern Australia and adjacent biogeographical regions – *Amorphinopsis excavans* (Dendy, 1889) from the Indian Ocean, *A. foetida* (Dendy, 1889) from the Gulf of Manaar, *A. maza* (De Laubenfels, 1954), *A. oculata* (Kieschnick, 1896), and *A. sacciformis* from Indonesia. *Amorphinopsis excavans* has similar habit, skeletal structure and spicule composition, but differs in the organisation of the ectosomal skeleton; in *A. excavans* it consists of a tangential layer of thick intercrossing tracts of large oxeas, and loose oxeas of all sizes with small styles filling up the spaces (Erpenbeck & Van Soest 2002). The material of *A. excavans* from northern Australia described above also has a clearly tangential and detachable ectosomal skeleton of large oxeas grouped in bundles and small styles tangentially to paratangentially oriented, sometimes in disorganised tufts. Other characteristics that differentiate *A. maculosa* from *A. excavans* are the predominance of small styles in the ectosome (instead oxeas and styles as reported in most populations of *A. excavans*) and the lacunar appearance of the choanosomal skeleton.

Amorphinopsis foetida (type specimen BMNH 1889.1.21.55, examined) is also a massive and slightly lobose species but with a skeletal architecture and spicule geometry different to *A. maculosa*. The ectosomal skeleton of *A. foetida* is formed by a halichondroid dermal crust, tangential-paratangentially oriented, 500–900 µm thick, with a mixture of oxeas and small styles projecting through the surface, and with vague tracts and small rounded meshes approx. 100–300 µm. The choanosomal skeleton is halichondroid, cavernous, with large rounded lacunae, 500–700 µm approx., and ill-formed multispicular tracts and fibres irregularly oriented through the skeleton; less compact than the ectosome and bounded by little collagen. The spicules are mixture of oxeas of different thickness and sizes, characteristically curved or sinuous (165.4–720.6 µm x 3.3–16.6 µm). The smaller styles are curved, and some are transitional to oxeas (154–281.7 µm x 2.7–7.9 µm).

Amorphinopsis maza was re-examined by Erpenbeck & Van Soest (2002) and differs from *A. maculosa* in habit, skeletal organisation and spicule composition.

Suberites oculatus Kieschnick, 1896, accepted as *Amorphinopsis oculata* (Van Soest *et al.* 2008) is a synonym of *Amorphinopsis fenestrata* (see above).

Ciocalypta sacciformis Thiele, 1900 (syntypes, SMF 685, 1818, Ternate Maluku Sea, 1894, coll. Kükenthal

W., examined) was transferred from its original genus to *Ciocalapata* by De Laubenfels (1936) and related it to species-like *Ciocalypta* including oxeas and styles. The species was interpreted as *Amorphinopsis* by Hooper *et al.* (1997). The revision of the type material indicates that the specimens described by Thiele agree better with the current concept of *Halichondria* but not with *Ciocalypta*, *Ciocalapata* or *Amorphinopsis* as suggested by previous authors. The syntypes examined are small fragments with a pouch-like shape as described by Thiele. The ectosomal skeleton is a thick tangential to paratangential layer up to 500–800 µm, with single spicules and short tracts criss-crossing in a disorganised manner. The choanosomal skeleton is disorganised with bundles of spicules irregularly spaced and running towards the surface where they merge with the ectosomal skeleton. The skeleton is formed entirely by oxeas in a great size range 195–706 µm. The skeleton of SMF 1818 includes styles in low frequency 463–525 µm (491.2±17.4) x 6–16 µm. As admitted by Thiele, the styles might be modifications of oxeas.

Distribution. Papua New Guinea (Eastern Coral Triangle Province), Gulf of Carpentaria and outer region of Shoal Bay (Sahul Shelf province) between 6–28 m depth. It is also found in Torres Strait (Northeastern Australian Province) (Alvarez & Hooper unpublished data).

Remarks on *Amorphinopsis*. *Amorphinopsis* includes approx. 13 valid species (Van Soest *et al.* 2008) distributed mainly throughout the Indian Ocean but with species also recorded from the Atlantic and Mediterranean oceans.

The genus is represented in northern Australia (Sahul Shelf Province) by three species – *Amorphinopsis excavans*, *A. fenestrata* comb. nov. and *A. maculosa* comb. nov.

Amorphinopsis foetida was recorded by Hooper *et al.* (1997) from the Beagle Gulf but it is concluded here that the specimen is better allocated to *A. fenestrata*.

The species originally described as *Leucophloeus fenestratus* Ridley, 1884 is common in the study area. Its habitat and skeletal characteristics have been interpreted as typical from the genus *Ciocalypta* but as discussed above, these similarities are considered not homologous and we propose to include the species in *Amorphinopsis*. The choanosomal skeleton of *A. fenestrata* is formed entirely by styloids and lacks ‘true’ oxeas as seen in other species of *Amorphinopsis* and other genera of Halichondriidae. We propose to expand the definition of *Amorphinopsis* slightly to include species with spicules differentiated into oxeas and/or styles.

Genus *Axinyssa* Lendenfeld, 1897

Gender feminine. Type species, by original designation, *Axinyssa topsenti* Lendenfeld, 1897: 116. Recent, western Indian Ocean.

Axinyssa bergquistae (Hooper *et al.*, 1997) com. nov.

(Figs 1D, 5)

Halichondria bergquistae Hooper *et al.*, 1997: 45.

Material examined. HOLOTYPE – QM G303351, East Point Bommies, Darwin Harbour, Northern Territory, Australia, 12°24.083' S, 130°48.14' E, 10 m depth, 23 September 1993, coll. Hooper, JNA & Hobbs, LJ. ADDITIONAL SPECIMENS – Cartier Island: QM G301059. Bynoe Harbour: Z.5224 (0M9H2375-X); Z. 5901. Darwin Harbour: Z.5976. Gulf of Carpentaria: QM 313572.

Description

Shape (Fig 1D). Massive-lobate, bulbous-digitate; with erect columns or irregular coalescent plates. Individuals approx. 70–100 mm high, 45–200 mm thick.

Colour. Purple-mauve, grey-brown; some individuals with lighter tinges.

Oscula. Variable in size (3–7 mm diameter), conspicuous, discrete, with raised white and opaque membranous lips (Fig. 1D), irregularly distributed.

Surface. Smooth to microconulose at base with shallow and meandering channels covered by a translucent

membrane; becoming distinctively conulose at erect columns or digits. Conules up to 2 mm long organised in longitudinal rows along erect columns and digits, with brushes of larger choanosomal spicules protruding through surface.

Texture and consistency. Hispid due to projection of spicules through surface, firm and incompressible.

Skeleton (Fig. 5A,B). Ectosome without specialised skeleton, with lightly coloured collagenous skin. Choanosomal skeleton halichondroid, with high spicule density in deeper regions; becoming more organised at subectosomal region, with multispicular spicule tracts, 50–200 μm running longitudinally and ascending towards surface, becoming more radial and plumose near periphery; ending in disorganised brushes that project through ectosome.

Spicules (Table 3, Fig. 5C). Mixture of oxeas of variable thickness and length (354–948 \times 4–27.8 μm), slightly bent

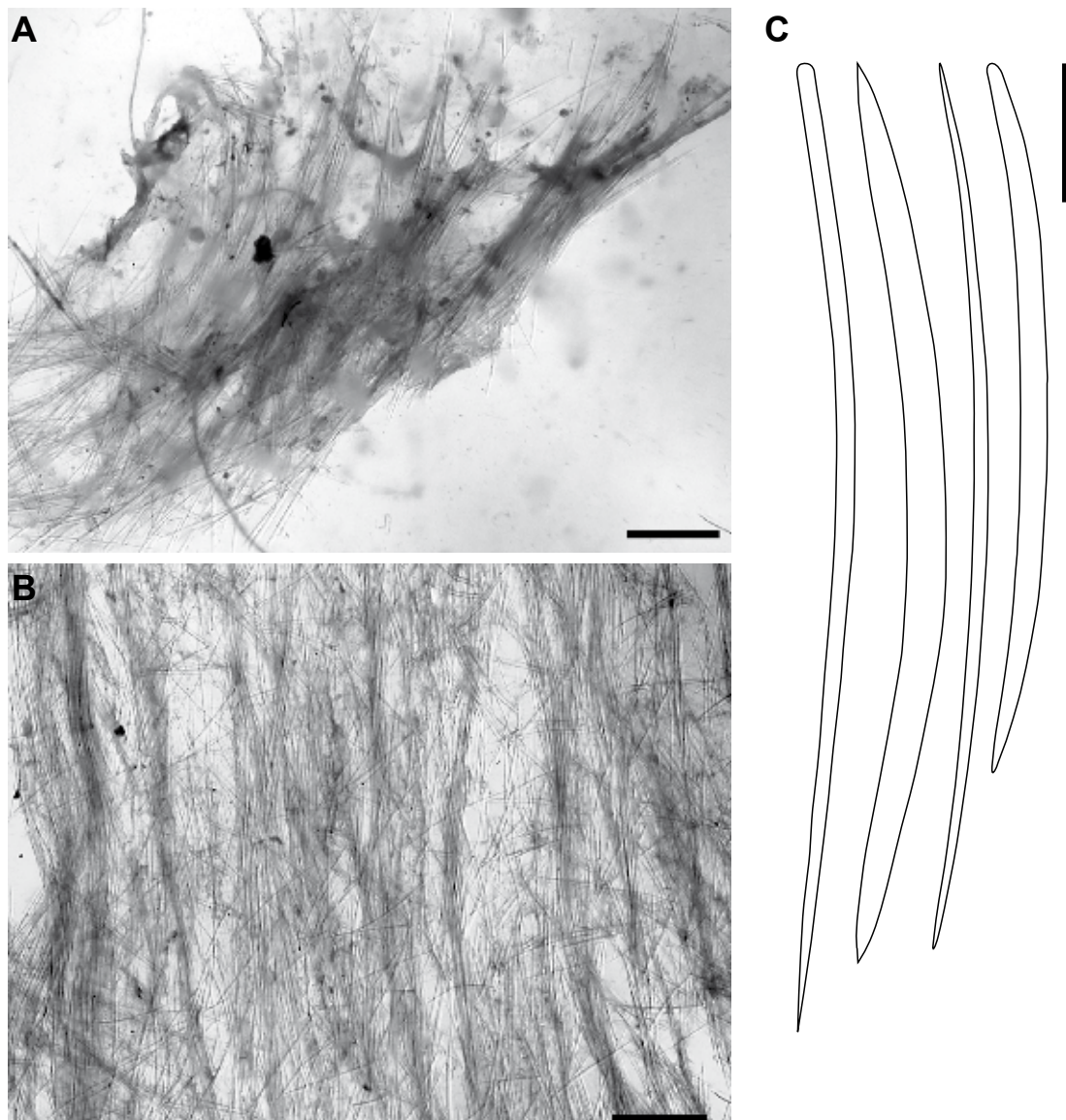


Fig. 5. *Axinyssa bergquistae*: **A**, light microphotograph of perpendicular section (NTM Z. 5976) showing choanosomal spicule tracts projecting through surface; **B**, light microphotograph of perpendicular section through surface (NTM Z.5224), showing choanosomal skeleton with longitudinal plumose tracts; **C**, diagram of spicules. Scale bars: A-B, 500 μm ; C, 100 μm .

and sometimes slightly sinuous. Styloid modifications common.

Remarks. The species was initially described under *Halichondria*. Examination of additional material considered conspecific with the specimen described by Hooper *et al.* (1997) allowed us to conclude that the species is better allocated in *Axinyssa*. The plumose conules observed in some areas of the surface of *A. bergquistae* resembles *Axinyssa merton* (described below), but that species has a more lax skeleton with less spicular density and more collagen. It differs also in general shape, colour and the oscula morphology.

Axinyssa bergquistae is comparable to *A. valida* (Thiele, 1899: 12) [holotype NHMB 13, examined] in external morphology, skeletal organisation and size of spicules [(290.3–859.3 μm (599 \pm 201.8) \times 9.7–34.8 μm (20.6 \pm 8.3)] and could possibly be conspecific. But both the skeleton and the size of spicules of most *Axinyssa* species are very similar and the separation of species is difficult and subjective (see below under remarks on the genus). The examination of more material from Indonesia (Alvarez & De Voogd in progress) will help to determine whether the northern Australian populations belong to the same species.

Distribution. Darwin Harbour and Bynoe Harbour (Sahul Shelf Province). Probably present also in the Northeast Australian Shelf Province (Alvarez & Hooper unpublished data).

Table 3. Comparison of spicule dimensions among specimens of *Axinyssa bergquistae*.

Specimen	Locality	Oxeas
QM G303351 (Holotype of <i>Halichondria</i> <i>bergquistae</i>)	Darwin Harbour	407.3–793.8 μm (619.7 \pm 82.8) \times 10.3–27.8 μm (15.5 \pm 4.3)
NTM Z.5224	Bynoe Harbour	366.3–948.1 μm (749.2 \pm 135.7) \times 4.5–33.2 μm (21.3 \pm 7)
QM G313572	Gulf of Carpentaria	353.6–747.3 μm (618.3 \pm 77.5) \times 4–20.9 μm (14.7 \pm 4.2)

***Axinyssa merton* (Hentschel, 1912) com. nov.**

(Figs 1E, 6)

Ciocalypta merton Hentschel, 1912: 424; Burton 1934: 564.

Halichondria tyleri. – Hooper & Wiedenmayer 1994: 209.

Halichondria merton. – Hooper *et al.* 1997: 52.

Pseudaxinyssa pitys De Laubenfels, 1954: 178; Bergquist 1965: 175 [?].

Axinyssa pitys. – Hooper & Bergquist 1992: 102.

Material examined. TYPE MATERIAL – *Ciocalypta merton*, holotype, SMF 1608, Aru Is, North of Penambulai; station 10, 8 m depth, 2 April 1908, coll. Merton exp. 1908. *Pseudaxinyssa pitys*, holotype, USNM 23103, Caroline Islands, Palau Is, Koror I., Iwayama Bay, 2 m depth, 1 September 1949, coll. De Laubenfels, M.W. ADDITIONAL SPECIMENS – Darwin Harbour: NTM Z.5221 (0M9H2189-V).

Description

Shape (Fig. 1E, 6A). Massive with conspicuous fistules up to 50 mm long, 1–2 mm thick, projecting from semi-buried basal portion up to 100 mm diameter.

Colour. Grey alive.

Oscula. On top of fistules, flushed, less than 5 mm diameter.

Surface. Regularly conulose with translucent membrane stretching over conules; marked with choanosomal axes.

Skeleton (Fig. 6B). Ectosomal skeleton absent. Choanosomal skeleton plumose to halichondroid with multispicular axes of spicules running longitudinally, nearly parallel and close to each other, anastomosing and diverging towards surface and becoming dendritic, bounded with collagen and ending in disorganised plumose brushes that project through surface. Spongin fibres ill-defined and short, direction-less, embedding spicule tracts.

Spicules (Fig. 6C, Table 4). Oxeas, hastate, slightly bent, straight or crooked, 476–1470.2 \times 11.2–29.7 μm . Style and strongylote modifications also present.

Remarks. *Ciocalypta merton* is conspecific with *Pseudaxinyssa pitys* and is better allocated to the genus

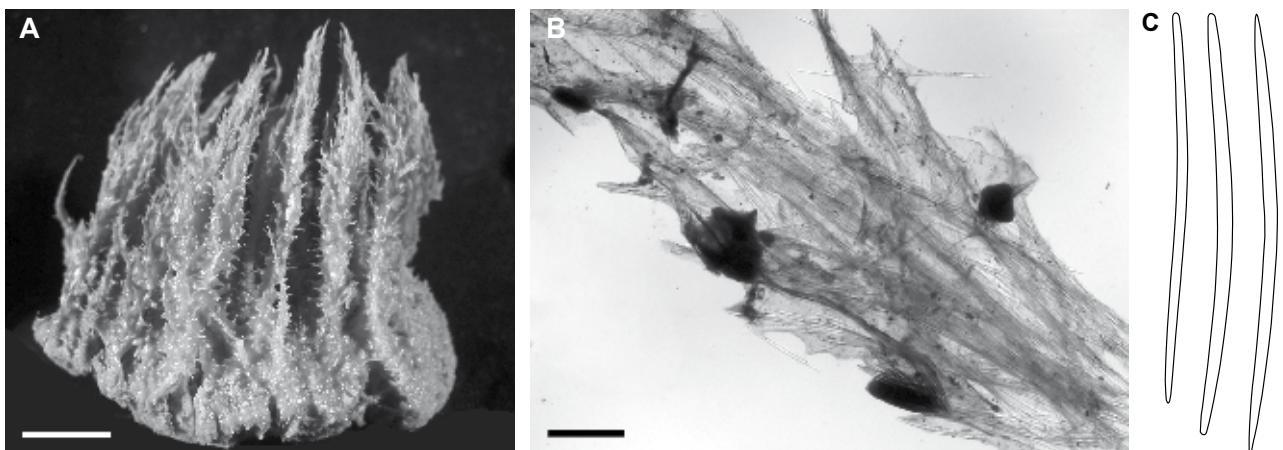


Fig. 6. *Axinyssa merton*: **A**, preserved specimen (NTM Z.5221); **B**, light microphotograph of perpendicular section through surface showing choanosomal skeleton with longitudinal tracts projecting through surface (Holotype, SMF 1608); **C**, diagram of spicules. Scale bars: A, B, 500 μm ; C, 100 μm .

Axinyssa. The type material of both species were examined here, and they are identical in all their characteristics. *Ciocalypta mertoni* was considered a junior synonym of *Halichondria tyleri* by Hooper & Wiedenmayer (1994) (following Burton 1959), but this synonym was later rejected by Hooper *et al.* (1997) who considered it a valid species of *Halichondria*, but admitted that the lack of an ectosomal skeleton was atypical of that genus. The species agrees well with the concept of *Axinyssa*, as it lacks an ectosomal skeleton and has a halichondroid to vaguely plumose choanosomal skeleton bounded by relatively high amounts of collagen and formed by oxeads of variable size and common styles and strongyles. The growth form of this species however, is not reported for other species of *Axinyssa*, thus a slight expansion in the diagnosis of the genus is necessary to accommodate species with fistulose projections.

A single specimen found in Darwin Harbour is assigned to this species. It differs from the type material examined only on spicule dimensions. The oxeads of the Darwin specimen are in average longer and thicker, but this might correspond to intraspecific variation within the species.

Distribution. *Axinyssa mertoni* is rare within the study area with only one specimen recorded here. The distribution of the species is extended to the Sahul Shelf and the Tropical Northwestern Pacific provinces. The record of Bergquist (1965) from Palau needs to be verified as there are several sympatric species of *Axinyssa* occurring in the area (Lori Bell Colin pers. comm.).

Remarks on *Axinyssa*. *Axinyssa* is represented in the area of the Indo-Pacific by several species: *A. aculeata* Wilson, 1925 (Philippines); *A. aplysinoidea* (Dendy, 1922) (Seychelles); *A. oinops* (De Laubenfels, 1954) (central West Pacific); *A. topsenti* Lendenfeld, 1897 (Tanzania); *A. variabilis* Lindgren, 1897 (Malaysia); and *A. valida* (Thiele, 1899) (Indonesia). The new combinations established in this revision extend the list by two additional species – *A. mertoni* (Sahul Shelf and Tropical Northwest Pacific provinces) and *A. bergquistae* (Sahul Shelf and probably Northeast Australian Shelf). Two additional species from the central Indo-Pacific region are also referred to *Axinyssa* after examination of type material – *Ciocalypta rutila gracilis* Hentschel, 1912 (SMF 1566, Aru Is, examined; see under remarks of *Ciocalypta*), and *Phycopsis terpnis* De Laubenfels, 1954 (Caroline Is, Central Pacific, USNM 23061, examined).

We were not able to revise all the type material of the Indo-Pacific species of *Axinyssa* thoroughly, therefore it remains inconclusive whether *A. mertoni* and *A. bergquistae* might be conspecific with other species recorded from the region. As mentioned above, the skeletal organisation and the size of spicules among *Axinyssa* species is very similar and separation of species is subjective. The external morphological characteristics seem to be more discrete, but study of individual populations is necessary to determine the actual range of variability present within these species.

Table 4. Comparison of spicule dimensions among specimens of *Axinyssa mertoni*.

Specimen	Locality	Oxeads
SMF 1608	Aru Island, Indonesia	515.6–779.6µm (691.4±61) x 11.2–21.7µm (18±2.5)
USNM 23103 (holotype of <i>A. pitys</i>)	Caroline Is, Central West Pacific	514.3–871µm (788.2±74.9) x 8.6–18.5µm (15±2.5)
NTM Z.5221	Darwin Harbour, NT	476–1470.2µm (979.5±285.9) x 14.7–29.7µm (21.6±4.8)

Study of different populations of *Axinyssa* through Indonesia (Alvarez & De Voogd unpublished data) is currently in progress and will help to re-define the limits of *Axinyssa* species.

The diagnosis of *Axinyssa* is here expanded to include species like *Axinyssa mertoni* with fistulose projections. We note however, that the skeletal organisation of the fistules observed in *A. mertoni* is considered not to be homologous with the organisation observed in species of *Ciocalypta*. The fistulose projections of *Ciocalypta* spp. are transparent with the skeleton formed by a central axis of spicules and extra-axial tracts diverging towards the surface. The fistulose projections of *A. mertoni* are opaque, tough-cartilaginous, arising from a massive base, and without a central axis of spicules which is diagnostic for *Ciocalypta*.

Axinyssa mertoni shares with the Indian Ocean *Ciocalypta digitata* (Dendy, 1905) the lack of an ectosomal skeleton, and the presence of fistulose projections; however, the fistules of *C. digitata* are transparent with a spicular axis from which thick bundles of spicules diverge towards the surface ending in conules (Erpenbeck & Van Soest, 2002). In our view the expansion of the definition of *Axinyssa* to include species with fistular projections such as *A. mertoni* does not affect the current position of *C. digitata* or the definition of the *Ciocalypta*.

The current position of the genus *Axinyssa* within the family Halichondriidae is debatable as molecular data (Erpenbeck *et al.* 2005) indicate that some species currently allocated to this genus are related to other dictyonellid genera such as *Acanthella* and *Dictyonella*. From a morphological point of view, the lack of an ectosomal skeleton, the presence of abundant collagen in the skeleton and the common occurrence of styles, strongyles and transitional forms, also points to possible relationships with members of Dictyonellidae. These relationships should be further explored to confirm the placement of this genus within the family Halichondriidae. However, taxonomic verification of the species of *Axinyssa* used in the molecular analyses should also be taken in consideration, particularly given the paucity of morphometric characters in this group and our still rudimentary understanding of character homology.

Genus *Ciocalypta* Bowerbank, 1862.

Gender feminine. Type species, by monotypy, *Ciocalypta penicillus* Bowerbank, 1862. Recent, eastern Atlantic Ocean.

***Ciocalypa heterostyla* Hentschel, 1912**

(Figs 1F, 7)

Ciocalypa heterostyla Hentschel, 1912: 424; Hooper *et al.* 1997: 36.

Material examined. HOLOTYPE – SMF 1569, Aru Is, N Penanbuli, 8 m depth, 2 April 1908, coll. H. Merton. ADDITIONAL SPECIMENS – Darwin Harbour, NTM Z.5902.

Description

Shape (Fig. 1F). Fistulose, with semi-buried and massive base. Fistules pointed, projecting perpendicularly from base, 20–30 mm long, less than 10 mm diameter wide, slightly translucent especially at tips.

Colour. Light yellow.

Oscula. Apical on fistules.

Surface. Smooth, microconulose.

Ectosomal skeleton (Fig. 7A). Thin layer formed by tangentially oriented pauci- to multispicular tracts of spicules, crossing over and forming a reticulation of triangular meshes; supported by choanosomal tracts.

Choanosomal skeleton. Differentiated at fistules, with central column formed by thick multispicular tracts oriented longitudinally and expanding into thick brush at tip of fistule (Fig. 7B). Secondary tracts, 20–100 μ m thick, slightly plumose, diverging nearly perpendicularly from central column toward surface, regularly spaced and connected irregularly by unispicular-paucispicular tracts of spicules; becoming thicker and ending in fan-like brushes at the subectosomal area, generally with smaller spicules oriented with their ends towards surface. Skeleton at base

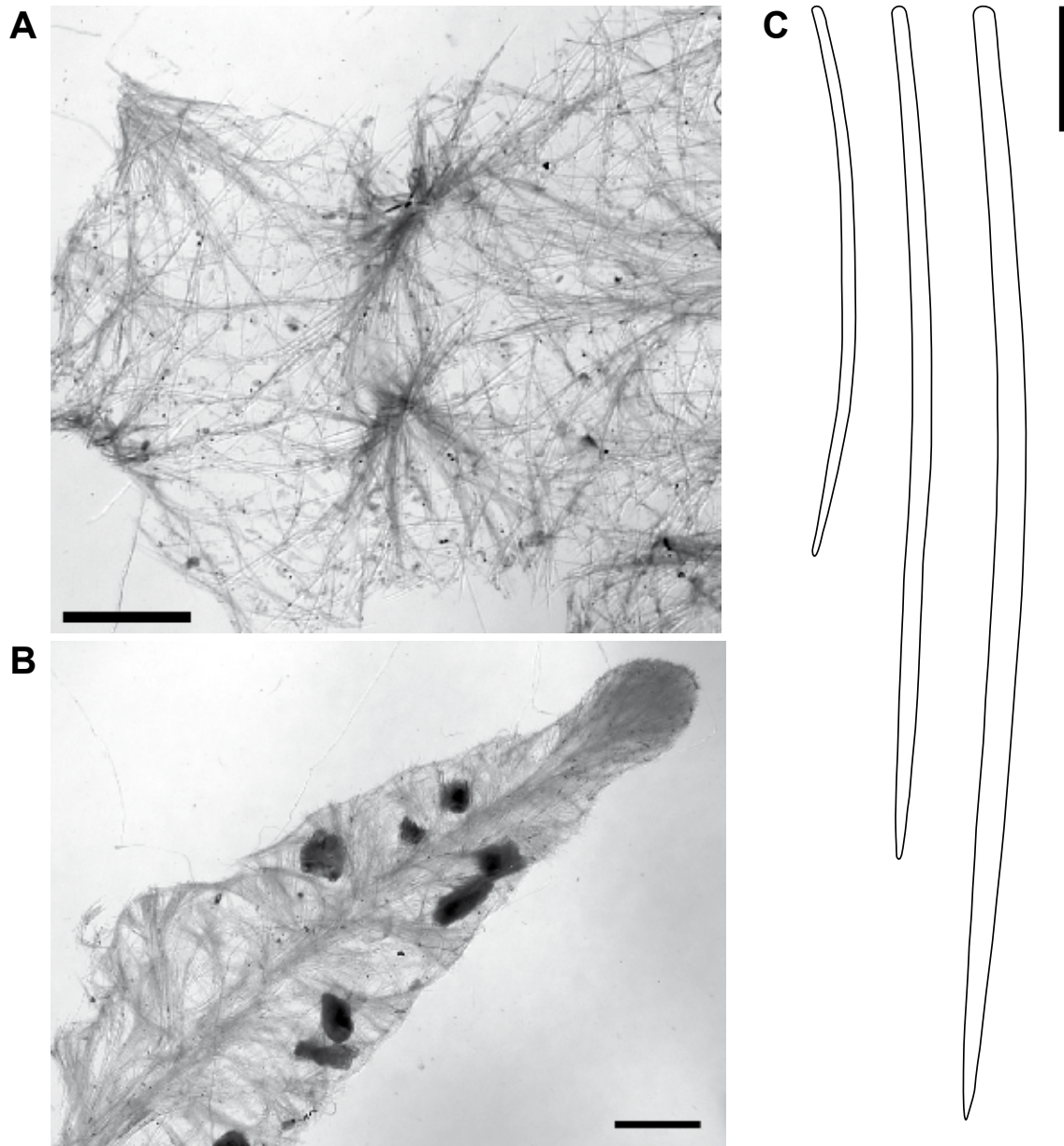


Fig. 7. *Ciocalypa heterostyla* (Holotype SMF 1569): **A**, light microphotograph of tangential section of ectosomal skeleton, showing tracts of spicules, forming a reticulation of triangular meshes; **B**, light microphotograph showing choanosomal skeleton at a fistule. **C**, diagram of spicules. Scale bars: A-B, 500 μ m; C, 100 μ m.

halichondroid, with directionless multispicular tracts and single spicules in confused reticulation.

Spicules (Fig. 7C, Table 5). Mixture of styles in a large range of sizes, straight to slightly curved, some sinuous, some with rounded ends, $184\text{--}809 \times 4\text{--}19 \mu\text{m}$.

Remarks. *Ciocalypta heterostyla* was originally described from the Aru Is (Indonesia) and it has not been re-described or recorded until this present study. The material from Darwin Harbour agrees closely with the type. Only the spicule dimensions are on average slightly larger in the specimen from Darwin. The species is not very conspicuous due to its cryptic habit. It is apparently rare in the study area with only one specimen collected so far.

Hooper & Wiedenmayer (1994) followed Burton (1959) and considered this species a synonym of *Ciocalypta tyleri* Bowerbank. The two species are certainly similar in external morphology and skeletal organisation, however the skeleton of *C. heterostyla* is formed exclusively by styles instead of oxeas, and the skeleton within the fistules is much more organised with a regular reticulation. Because of these characters we considered that *C. heterostyla* is not only a valid species but also it can be easily differentiated from its South African relative.

Distribution. Known only from the type locality (Aru Is, Indonesia) and from Darwin Harbour (Sahul Shelf province). It is found between 8–12 m depth.

Table 5. Comparison of spicule dimensions between specimens of *Ciocalypta heterostyla*.

Specimen	Locality	Styles
SMF 1569	Aru Is, Indonesia	$199.9\text{--}584.1 \mu\text{m}$ (387.3 ± 137) $\times 3.5\text{--}14.8 \mu\text{m}$ (8.3 ± 3.2)
NTM Z.5902	Darwin Harbour	$184\text{--}809.2 \mu\text{m}$ (466.5 ± 229.1) $\times 3.9\text{--}18.6 \mu\text{m}$ (9.4 ± 5.5)

Ciocalypta stalagmites Hentschel, 1912

(Figs 1G–H, 8)

Ciocalypta stalagmites Hentschel, 1912: 426.

Halichondria tyleri. – Hooper *et al.* 1997.

Material examined. LECTOTYPE – SMF 1567 (here designated, a representative specimen of the species, chosen from six examined specimens deposited at SMF and registered as syntypes with a single accession number), Aru Is, Mimien I., Indonesia, 15 m depth, 9 April 1908, coll. Meron, H. PARALECTOTYPES – SMF 1537, Aru Is, Sungi Manumbai (Kapala Sungi), Indonesia, station 17, Merton Expedition Aru and Kei Is 1907–1908, 20 m depth, 5 May 1908, coll. Merton, H. SMF 1574, Aru I., SW Lola I, Indonesia, station 9, Merton Expedition Aru and Kei Is 1907–1908, 8–10 m depth, 1 April 1908, coll. Merton, H. SMF 1595, Aru Is, Bambu I., Indonesia, station 11, Merton Expedition Aru and Kei Is 1907–1908, 10 m depth, 3 April 1908, coll. Merton, H. SMF 1623, Aru Is, SW Mariri and Leer Is, Indonesia, Merton Expedition Aru and Kei Is 1907–1908, 6–10 m depth, 31 March 1908, coll. Merton, H. SMF 1627, Aru Is, N Penambulai I., Indonesia, Merton Expedition Aru and Kei Is 1907–1908, 8 m depth, 2 April 1908, coll. Merton, H. ADDITIONAL SPECIMENS – Parry Shoals, NT, NTM Z.3133. Charles Point, NT, NTM Z.5230 (0M9H2574-P). Bynoe Harbour: NTM Z.5226 (0M9H2511-V). Darwin Harbour: NTM Z.941, Z.5210 (0M9H2571-M), Z.5229 (0M9H2299-Q), Z.5977. Cobourg Peninsula: NTM Z.592, Z.1358, Z.1395, Z.3286. Wessel Is: Z.3920, Z.5218 (0M9H2666-P).

Description

Shape (Figs 1G–H, 8A). Flat cushion-shaped or massive base, buried or semi-buried, strongly attached to substrate, up to 35 mm thick, 4–100 mm diameter, with fistules projecting perpendicularly above surface. Fistules

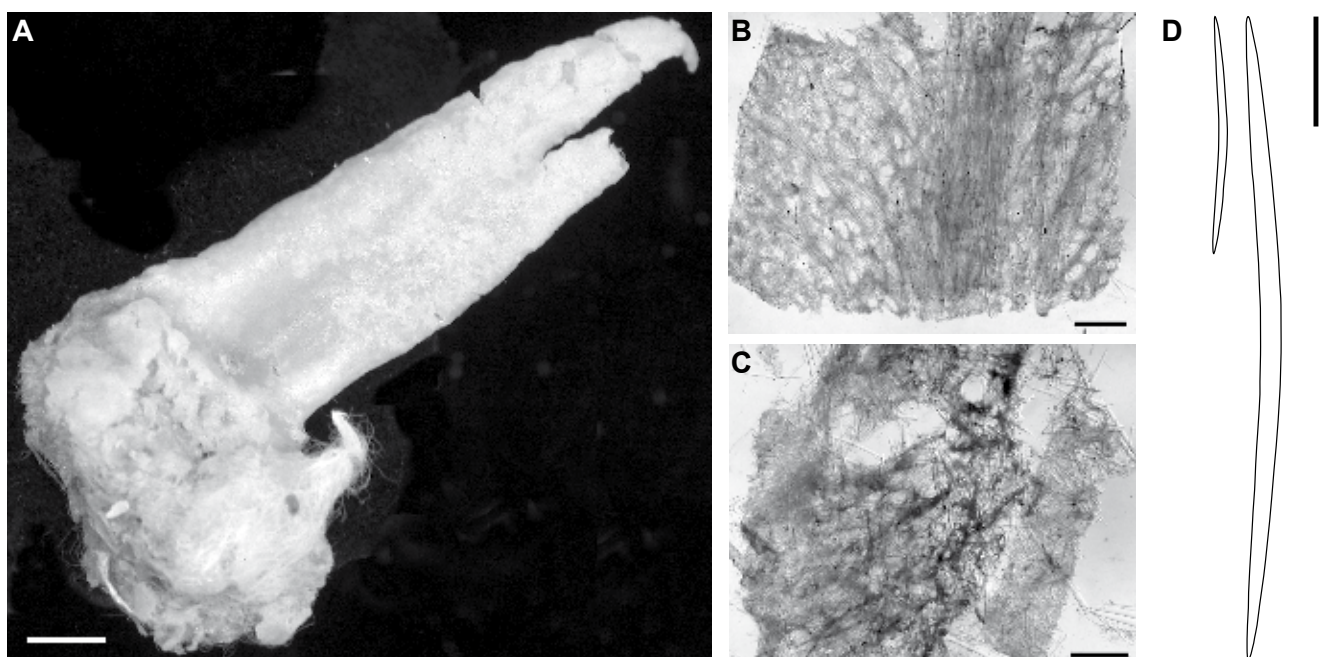


Fig. 8. *Ciocalypta stalagmites* (Lectotype, SMF 1567): **A**, Preserved lectotype; **B**, light microphotograph showing choanosomal skeleton at fistule; **C**, light microphotograph showing choanosomal skeleton at base; **D**, diagram of spicules. Scale bars: A, 2 cm; B–C, 500 μm ; D, 100 μm .

sharply pointed, globular or flattened, mammiform, tubular, rounded, 5–125 mm long, laterally fused sometimes or branching at tips.

Colour. Base generally pale-beige. Fistules, transparent, mauve-brown-purple, greenish-yellow. Internally, beige.

Oscula. Generally at apex of fistules or tubes but also observed irregularly distributed along fistules, with membranous rims.

Consistency and Texture. Compressible-spongy, easily torn.

Surface. At fistules, smooth to slightly conulose, marked with longitudinal rows of minute conules. Choanosomal tracts of spicules, visible through the ectosome of translucent specimens. At base smooth, opaque, rough, spiculous.

Skeleton. Ectosomal skeleton, tangential layer of variable thickness (5–300 μm) easily peeled in some specimens, formed by a dense mass of smaller oxeas and supported by choanosomal skeleton. Choanosomal skeleton (Fig. 8C) at base, halichondroid, densely spiculous, with mixture of large and smaller oxeas and no distinct tracts of spicules. In fistules (Fig. 8B), becoming distinctive and organised, with central column of large spicules oriented longitudinally and smaller spicules criss-crossing. Multispicular tracts generally formed by medium-size spicules radiating from central column towards surface, connected by shorter tracts and single spicules, forming a regular reticulation. Large subectosomal spaces (up to 5 mm diameter) in some areas.

Spicules (Fig. 8D, Table 6). Two size classes of oxeas: I, smaller, thinner, fusiform, straight or slightly flexuous (147–321 \times 4–10 μm); II, large, thick and slightly curved, fusiform, occasionally crooked-sinuous (378–886 \times 11–40 μm), and styles in equivalent size categories are common.

Remarks. The growth form of *Ciocalypta stalagmites* is remarkably variable. Fortunately this variation is also well represented in the type material. The external colouration is also variable and is possibly related to the presence of different cyanobacterial associations. The skeletal organisation, composition and size of spicules, however, are consistent and very similar among specimens with different habits and colouration. A very consistent characteristic through all the populations we examined is that the oxeas are differentiated in size categories not only by their length but also by their thickness. Proper statistic and morphometric analyses could be employed to demonstrate whether this is

diagnostic to separate *C. stalagmites* from other *Ciocalypta* species.

Ciocalypta stalagmites is very similar to *C. tyleri* Bowerbank, 1873 from South Africa, and it was interpreted as such by Hooper *et al.* (1997) but allocated to the genus *Halichondria* (following Van Soest *et al.* 1990; Van Soest 1991). Both species are now referred to *Ciocalypta* under the revised concept of Halichondriidae (Erpenbeck & Van Soest 2002). The two species are similar in external morphology and skeletal organisation, however, the skeleton of *C. stalagmites* seems to be less organised. Despite similarities between these two species, it is unlikely that the Indonesian and northern Australian populations are conspecific with their South African relatives, thus we propose to reserve *C. stalagmites* for those populations inhabiting the Sahul Province and adjacent areas. Future independent evidence might demonstrate whether *C. tyleri* and *C. stalagmites* belong to a complex of cryptic species that cannot be easily separated using traditional morphological characters, or are instead conspecific and genuinely a widely distributed species.

Ciocalypta stalagmites is also very similar to *C. vansoesti* (Hooper *et al.*, 1997). comb. nov. The two species have similar growth form and skeletal characteristics, but they can be differentiated from each other by some distinctive characteristics (see below).

Distribution. *Ciocalypta stalagmites* is very common throughout the northern Australian localities of the Sahul Shelf province and its distribution extends to adjacent provinces including the Northeast Australian Shelf, Papua New Guinea (Alvarez & Hooper unpublished), and Indonesia (Alvarez & De Voogd unpublished). It is found from the intertidal zone to 40 m.

***Ciocalypta vansoesti* (Hooper *et al.*, 1997) comb. nov.**
(Figs 11, 9)

Halichondria vansoesti Hooper *et al.*, 1997: 37.

Material examined. As listed by Hooper *et al.* (1997). ADDITIONAL SPECIMENS – Darwin Harbour: Z.5904, Z.5217 (0M9H2568-J), Z.5903, Z.5978. Bynoe Harbour: Z.5212 (0M9H2498-I). Gulf of Carpentaria: QM G303524.

Remarks. This species was well described by Hooper *et al.* (1997), but allocated to the genus *Halichondria* (following Van Soest *et al.* 1990; Van Soest 1991). It is

Table 6. Comparison of spicule dimensions between specimens of *Ciocalypta stalagmites*.

Specimen	Locality	Oxea type I	Oxea type II
SMF 1567 (Lectotype)	Aru Is, Indonesia	167.8–240.2 μm (200.8 \pm 17.4) \times 4.4–10 μm (7.9 \pm 1.3)	377.7–837 μm (626.2 \pm 102.8) \times 12.3–37.1 μm (18.7 \pm 4.7)
NTM Z.5212	Bynoe Harbour	165.3–320.6 μm (238.2 \pm 34) \times 5.5–10.3 μm (7.6 \pm 1.2)	411.4–659.5 μm (524.9 \pm 56.8) \times 11.1–26.3 μm (18.9 \pm 4.1)
NTM Z.5210	Darwin Harbour	188.3–258.7 μm (214 \pm 19.1) \times 5.6–9.2 μm (7.4 \pm 0.9)	440.1–662.8 μm (601.8 \pm 53.9) \times 11.3–38.5 μm (21.9 \pm 7.7)
NTM Z.5218	Wessel Is	147.2–202.7 μm (169.1 \pm 12.8) \times 5.3–9.4 μm (6.7 \pm 0.9)	437.7–886.5 μm (588.1 \pm 135.1) \times 8.7–39.5 μm (21.7 \pm 7.9)

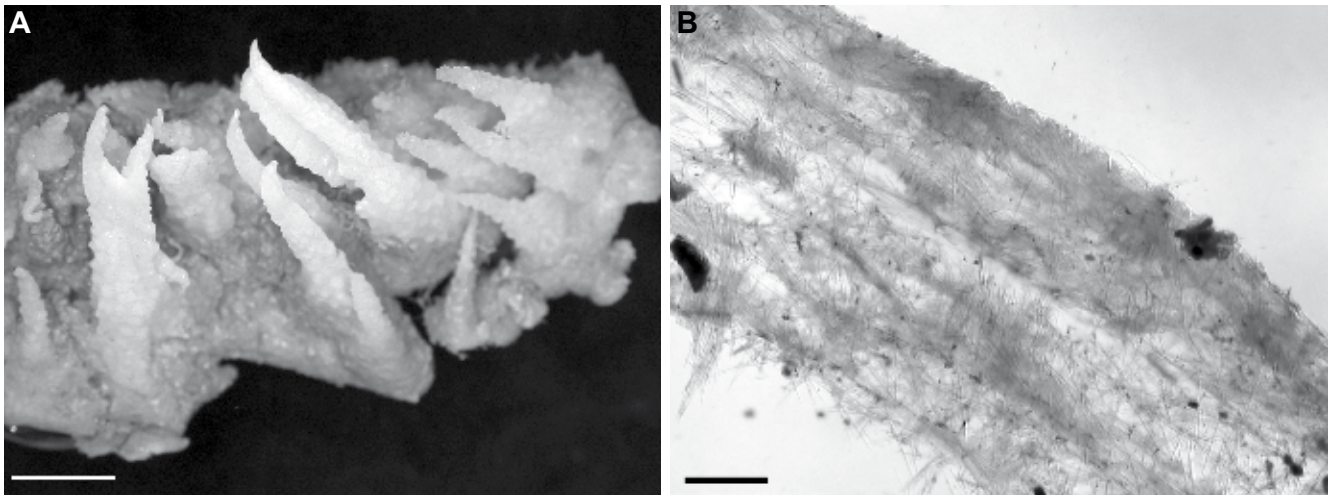


Fig. 9. *Ciocalypta vansoesti*: **A**, preserved paratype specimen (QM G303450); **B**, light microphotograph showing choanosomal skeleton at fistule. Scale bars: **A**, 20 mm; **B**, 500 μm .

now referred to *Ciocalypta* under the revised concept of Halichondriidae (Erpenbeck & Van Soest 2002).

As mentioned by Hooper *et al.* (1997) and above, *Ciocalypta vansoesti* is closely related to *C. stalagmites*, both with similar growth form, skeletal organisation and type of spicules. Both species have fistules projecting from a buried-semiburied mass, but in the case of *C. vansoesti* the fistules are translucent-white with the surface regularly conulose and subectosomal tracts and central column visible beneath (Figs 11, 9A). However, the skeleton in the fistules, when compared to *C. stalagmites*, is denser and slightly disorganised; the central column is not as condensed and the extra axial reticulation is vague (Fig. 9B, Hooper *et al.* 1997, figs. 22a, 23a). The dimensions of the oxeas are similar and overlap with those of *C. stalagmites*, but in *C. vansoesti* there is not a clear difference in size categories, with the two classes of spicules overlapping both in length and in width (Table 7).

Ciocalypta vansoesti is also similar in some of the field characteristics to *Axinyssa mertoni*, indicating once again that fistule-like growth forms are common among halichondriids and so are not useful to differentiate species unless they are used in combination with other skeletal characters.

Distribution. *Ciocalypta vansoesti* is common in Darwin Harbour and Bynoe Harbour. It is also recorded from Cobourg Peninsula and the Gulf of Carpentaria. It is found intertidally and subtidally to 40 m depth.

Remarks on *Ciocalypta*. Burton (1959) considered many species of halichondriid genera with a fistulose

habit conspecific with *Ciocalypta penicillus* (type species of *Ciocalypta*). These synonyms were not properly substantiated and some of them have been rejected by Hooper *et al.* (1997) and the present revision, i.e. *Ciocalypta heterostyla*, *C. stalagmites*, *C. tyleri*, *C. oculata maxima* (referred here to *Amorphinopsis fenestrata*), and *C. mertoni* (referred here to *Axinyssa mertoni*).

Additional species of *Ciocalypta* recorded from the Sahul Shelf Province and adjacent areas besides the three revised here (i.e. *C. heterostyla*, *C. stalagmites* and *C. vansoesti*) are *C. rutila gracilis* Hentschel, 1912 (see below), *C. digitata* (Dendy, 1905, as *Collocalypta*), *C. melichlora* Sollas, 1902, *C. rutila* Sollas, 1902, and *C. simplex* Thiele, 1900: 76.

One of the syntypes of *Ciocalypta rutila gracilis* Hentschel, 1912 (SMF 1566, examined) belongs in *Axinyssa*. Both the external morphology (based on Hentschel's description) and the arrangement of skeleton agree with the concept of that genus. The skeleton of the material examined is formed by two classes of oxeas: straight $480.8\text{--}706.4\text{ }\mu\text{m}$ (601.6 ± 76.7) \times $9\text{--}24\text{ }\mu\text{m}$ (17 ± 3.1) and vermicular, crooked sinuous, relatively thinner, and often bent up to a 90 degree angle, $193\text{--}600.7\text{ }\mu\text{m}$ (406.7 ± 110.6) \times $5.3\text{--}16\text{ }\mu\text{m}$ (10.6 ± 3) [18]; less often styles are also present. Specimens recorded for Northeast Australian Shelf and Indonesia correspond with the type examined (Alvarez & Hooper unpublished data; Alvarez & De Voogd unpublished data) and will be redescribed under the name of *Axinyssa gracilis* in forthcoming publications.

Ciocalypta digitata (Dendy, 1905) resembles *Ciocalypta stalagmites* and *C. vansoesti* in habit but differs in skeletal

Table 7. Comparison of spicule dimensions between specimens of *Ciocalypta vansoesti*.

Specimen	Locality	Oxea type I	Oxea type II
NTM Z.2648	Darwin Harbour, East Point	185.3–459.7 μm (320 ± 60.9) \times 6.4–9.5 μm (8 ± 0.9)	475.2–616.4 μm (546.2 ± 38.3) \times 14–21.6 μm (17.9 ± 2.3)
QM G303450	Bynoe Harbour	194.1–361.7 μm (275.3 ± 45.6) \times 2.1–9.8 μm (6.8 ± 1.8)	382–662.1 μm (536.1 ± 78.2) \times 6.8–30.8 μm (16.8 ± 6)
QM G303524	Gulf of Carpentaria	237.5–429.2 μm (314.9 ± 56.5) \times 6.4–11.9 μm (8.4 ± 1.3)	432.8–677.3 μm (541.2 ± 58.7) \times 8.2–31.9 μm (17.5 ± 4.8)

organisation and composition and size of spicules. This species lacks an ectosomal skeleton, but the fistular processes have spicular axis and extra-axial tracts as in other species of *Ciocalypa*.

Genus *Halichondria* Fleming, 1828

Gender feminine. Type species, by subsequent designation (of Bowerbank 1862), *Spongia panicea* Pallas, 1766. Recent, East England.

Subgenus *Halichondria* (*Halichondria*) Fleming, 1828

***Halichondria* (*Halichondria*) *carotenoidea* sp. nov.**

(Figs 10A,B, 11)

Halichondria stalagmites. – Hooper *et al.* 1997: 43 [in part, not Z.131, Z.1097, Z.1991 = *Halichondria* (*Halichondria*) *microbiana* sp. nov.]

Phakellia sp. 614. – Hooper *et al.* 1992.

Axinella sp. 244. – Hooper *et al.* 1992.

Material examined. HOLOTYPE – NTM Z.5909, off Dudley Point, Fannie Bay, Darwin Harbour, N.T., 12°24.96' S, 130°48.83' E, 4–7 m depth, 4 June 2002, coll. Alvarez, B and party. PARATYPES. – NTM Z.4451 (0M9H2036-G), Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, N.T., 12°29.103' S, 130°47.111' E, 8–14 m depth, 7 May 2002, coll. Alvarez, B and party. NTM Z.5225 (0M9H2462-S), Spencer Point, Indian I., Bynoe Harbour, N.T., 12°35.351' S, 130°31.454' E, 6–8 m depth, 11 June 2003, coll. Alvarez, B and party. ADDITIONAL SPECIMENS – N Adele I., Collier Bay, NW Shelf: Z.712. Parry Shoals, NT: NTM Z.3147. Darwin Harbour NT: NTM Z.194, Z.919, Z.934, Z.986, Z.1979, Z.2086, Z.2245, Z.2651, Z.2697.

Description

Shape (Figs 10 A,B). Fan shaped, digito-palmate, multiplanar, arborescent, erect, stalked, bifurcated at base, with complex branching; branches or digits flattened generally with pointed tips but round tips also common; specimens reaching up to 350 mm high, 300 mm wide.

Colour. Orange. Blue-grey, or beige in alcohol

Consistency and texture. Soft, easily torn, rubbery.

Oscula. Regularly distributed along lateral side of branches (Fig 10B) less than 5 mm in diameter, generally in rows, with membranous rims slightly elevated. Some specimens with subectosomal thin canals ending in oscula.

Surface. Smooth, wrinkled, evenly covered with microconules when exposed to air. Marked with subectosomal drainage canals in some specimens.

Skeleton (Fig 11 A, B). Ectosomal skeleton formed by 100–200 µm thick continuous layer, supported by choanosomal skeleton and packed mainly with smaller category of oxeas, in short, ill-defined and criss-crossing bundles, oriented tangentially- paratangentially, protruding occasionally through surface in disorganised manner (Fig. 11A). Choanosomal skeleton, halichondroid to plumose, formed by ill-defined bundles of larger spicules, criss-crossing in all directions in the inner region of choanosome. Skeleton becomes more organised at

subectosomal region, with a vague reticulation of ascending tracts connected by short bundles and single spicules. Near surface, spicule tracts become more defined and even slightly plumose, supporting ectosomal skeleton and occasionally protruding through surface (Fig. 11B).

Skeleton of some specimens is obscured by granular pigments and cyanobacteria when examined under light microscope.

Spicules (Fig. 11C, Table 8). Mixture of oxeas not separable into size categories 112–389 x 2–12 µm, hastate, pointed, straight or occasionally slightly bent in middle.

Remarks. *Halichondria carotenoidea* is diagnosed by a unique combination of features (i.e. growth form, organisation of the skeleton, and the size and composition of spicules) not found in other species of *Halichondria* revised here or reported for adjacent areas (see Table 9).

The skeleton and spicule composition of all the material examined is almost identical to *Halichondria* (*H.*) *microbiana* sp. nov. (see below). Both species are sympatric and include a high density of cyanobacteria in the choanosome. The two species clearly differ in shape, which is branching to arborescent in *H.* (*H.*) *carotenoidea* and massive to cushion shape in *H.* (*H.*) *microbiana*. Both species can be further distinguished by the size of the oxeas, which are separated into class categories in *H.* (*H.*) *microbiana* but not in *H.* (*H.*) *carotenoidea*.

The material described by Hooper *et al.* (1997) as *Halichondria stalagmites* (Hentschel) is a composite of *H.* (*H.*) *carotenoidea* (specimens NTM Z.2651 and Z.3147) and *H.* (*H.*) *microbiana* (specimens NTM Z. 131, Z.1097, Z. 1991), and it does not agree with the concept of the species described by Hentschel (1912) as *Ciocalypa stalagmites* (see above).

Distribution. *Halichondria carotenoidea* is common in Darwin and Bynoe Harbours, and it was also observed at Wessel Is (Raragala I.).

Etymology. Named after carotenoid, a pigment which might give the red-orange colour to the species. It is intended as a noun in apposition.

Table 8. Comparison of spicule dimensions between specimens of *Halichondria* (*Halichondria*) *carotenoidea*.

Specimen	Locality	Oxeas
NTM Z.5909	Darwin Harbour, Dudley Point	113.2–388.9µm (263.2±87.1) x 2.3–12.3µm (7.3±3)
NTM Z.5225	Bynoe Harbour	111.7–379.5µm (245.3±80.2) x 2.3–10.7µm (6.2±2.4)

***Halichondria* (*Halichondria*) *darwinensis* Hooper *et al.*, 1997**

(Fig. 10C)

Halichondria darwinensis Hooper *et al.*, 1997: 49.

Material examined. Specimens as listed in Hooper *et al.* (1997). ADDITIONAL SPECIMENS – Darwin Harbour, NTM Z.5211.

Remarks. *Halichondria darwinensis* was described by Hooper *et al.* (1997). Additional material, an *in situ*

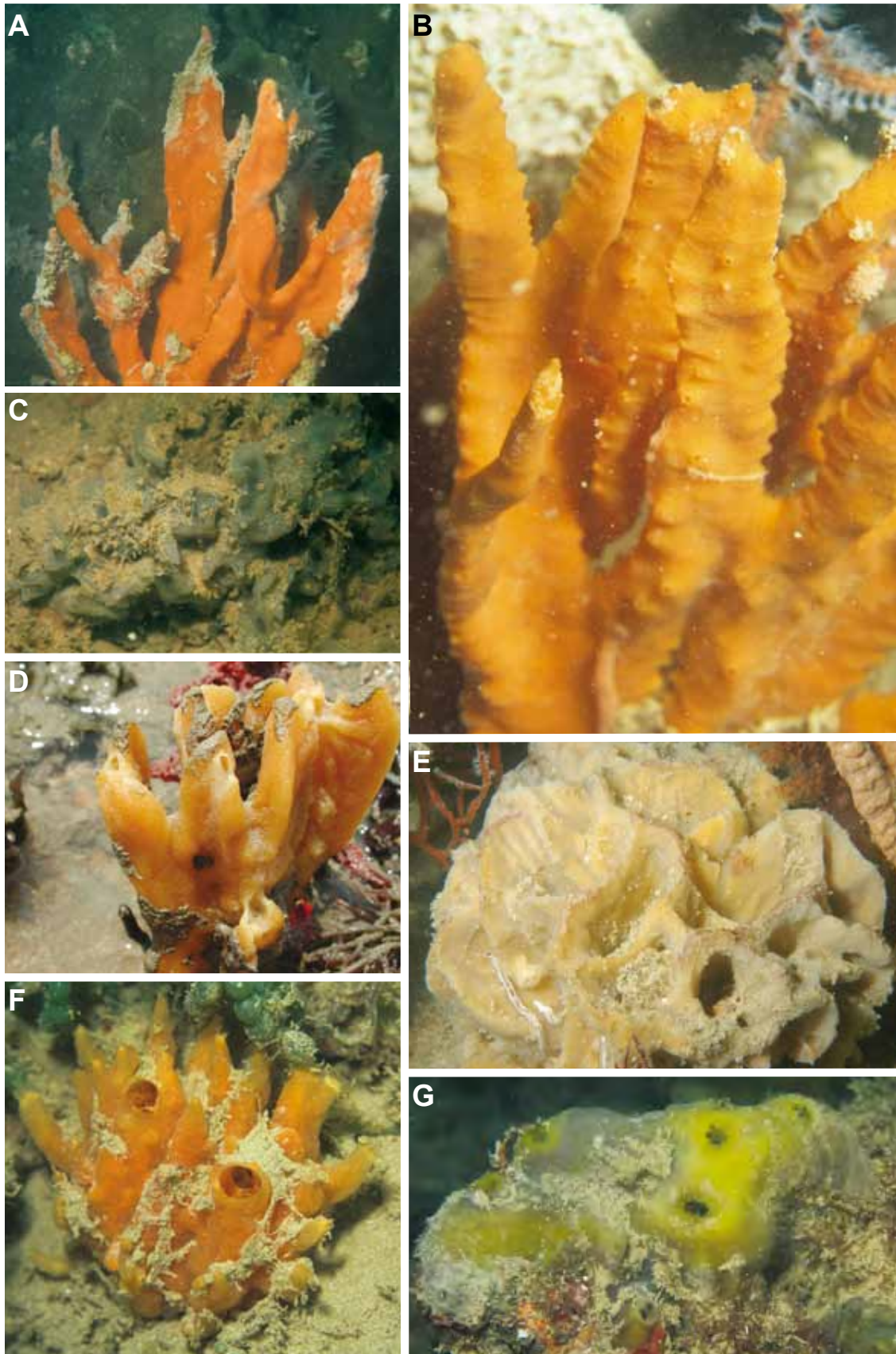


Fig. 10. *Halichondria* (*Halichondria*) *carotenenoidea* sp. nov.: **A**, specimen *in situ* at Dudley Point, Darwin Harbour, N.T.; **B**, specimen *in situ* at Spencer Point, Bynoe Harbour, N.T., showing oscula distributed along lateral side of branches. **C**, *Halichondria* (*H.*) *darwinensis*, specimen *in situ* at Weed Reef, Darwin Harbour, N.T. *Halichondria* (*H.*) *phakellioides*: **D**, specimen *in situ* exposed at the reef flat of East Arm, Darwin Harbour during the low tide of 18 October 2001; **E**, specimen *in situ* at Raragala I. Wessel Is, 20 m depth. **F**, *Halichondria* (*H.*) *microbiana* sp. nov., specimen *in situ* at Lee Point, Darwin Harbour, N.T. **G**, *Topsentia dura*, specimen *in situ* at Nightcliff bommies, Darwin Harbour, N.T. Photographs: A,D,G – B. Alvarez; B – M. Browne; C,F – H. Nguyen; E – P. Colin.

Table 9. *Halichondria* (*Halichondria*) species from the Central Indo-Pacific (after Van Soest *et al.* 2008), with remarks on current taxonomic allocation, type material and description.

Species	Remarks
<i>Halichondria</i> (<i>Halichondria</i>) <i>armata</i> Lindgren, 1897	Unrecognisable from the description; no type material available.
<i>Halichondria</i> (<i>Halichondria</i>) <i>bergquistae</i> Hooper, Cook, Hobbs & Kennedy, 1997	Referred here to <i>Axinyssa</i> (see Remarks of <i>Axinyssa</i> this revision).
<i>Halichondria</i> (<i>Halichondria</i>) <i>cartilaginea</i> (Esper, 1794)	Valid, common species through Indo-Pacific. Always associated to symbiotic green algae (Lim <i>et al.</i> 2008).
<i>Halichondria</i> (<i>Halichondria</i>) <i>darwinensis</i> Hooper, Cook, Hobbs & Kennedy, 1997	Valid (see under genus <i>Halichondria</i> , this revision).
<i>Halichondria</i> (<i>Halichondria</i>) <i>fragilis</i> Kieschnick, 1896	Unrecognisable from the description; no type material available.
<i>Halichondria</i> (<i>Halichondria</i>) <i>incrustans</i> Kieschnick, 1896	Unrecognisable from the description; no type material available.
<i>Halichondria</i> (<i>Halichondria</i>) <i>pelliculata</i> Ridley & Dendy, 1886	Valid, recognisable from the description. Type material not examined. Distinctive shape and surface characteristics, not comparable to the new species recorded here.
<i>Halichondria</i> (<i>Halichondria</i>) <i>ridleyi</i> Hooper, Cook, Hobbs & Kennedy, 1997	Referred in this revision to <i>Topsentia</i> (see Remarks of <i>Topsentia</i> this revision)
<i>Halichondria</i> (<i>Halichondria</i>) <i>stalagmites</i> (Hentschel, 1912)	Referred here to <i>Ciocalypa</i> (see remarks of <i>Ciocalypa</i> this revision)
<i>Halichondria</i> (<i>Halichondria</i>) <i>syringea</i> Pulitzer-Finali, 1996	Valid. Type material examined (MSNG 48700). Coalescent fistules on a buried base [?]. Detachable ectosome differentiated into a thick layer, with spicules oriented paratangentially, disorganised. Choanosome halichondroid with some ill defined, multispicular, ascending to surface and supporting ectosome. Oxeas several sizes, 256.4–706.7µm (539.3±137) x 5.2–19µm (13±3.7); few styles.
<i>Halichondria</i> (<i>Halichondria</i>) <i>vansoesti</i> Hooper, Cook, Hobbs & Kennedy, 1997	Referred here to <i>Ciocalypa</i> (see under genus <i>Ciocalypa</i> , this revision)

photograph (Fig 10C), and spicule measurements (Table 10) are provided here to complement the original description.

Halichondria darwinensis is very inconspicuous and represented so far by only three individuals (including the holotype and the paratype). Its encrusting habit with small and insubstantial digits makes it inconspicuous and hard to find. The re-examination of the available material and additional measurements of spicules, indicate that the differences in the thickness of the spicules reported by Hooper *et al.* (1997) as a distinctive character for the species, no longer appear to be significant (see Table 10). Both the length and the thickness of the oxeas are variable, but not divisible into size classes.

The species seems to have affinities with the genus *Axinyssa*. The skeleton is poorly developed, with very little

spongin and relatively less spicule density when compared to other *Halichondria* species; the ectosomal skeleton is quite undifferentiated and the spicules are similar in shape and dimensions to other *Axinyssa* species. Therefore, the assignment of this species to the genus *Halichondria* is inconclusive.

Distribution. *Halichondria darwinensis* is presently known only from Darwin Harbour. It occurs intertidally and subtidally to 10 m.

***Halichondria* (*Halichondria*) *phakellioides* Dendy & Frederick, 1924**

(Figs 10 D, E, 12)

Halichondria phakellioides Dendy & Frederick, 1924: 498; Burton 1934: 600; Hooper *et al.* 1997.

Material examined. Specimens as listed in Hooper *et al.* (1997). ADDITIONAL SPECIMENS – Bynoe Harbour, NT: Z.241, Z.5223 (0M9H2321-P). Darwin Harbour, NT: Z.2026, Z.4100, (0CDN-8022-F), Z.5219 (0M9H2057-C), Z.5905, Z.5906, Z.5915, Z.5923, Z.5925, Z.5928, Z.5948, Z.5949, Z.5950, Z.5965, Z.5970. Parry Shoals, N.T., QM G310137. Boucat Bay, E of Maningrida, Arnhem Land, N.T.: Z.5623. Wessel Is: Z.5228 (0M9H2655-C).

Remarks. *Halichondria phakellioides* was described by Hooper *et al.* (1997). Additional material, illustrations (Figs 10D, E, 12), and spicule measurements (Table 11) are provided here to complement the original description.

Table 10. Comparison of spicule dimensions among specimens of *Halichondria* (*Halichondria*) *darwinensis*.

Specimen	Locality	Oxeas
NTM Z.3205 (Holotype)	Darwin Harbour, East Point	272.3–659.6µm (467.2±112) x 3.7–13.2µm (8.5±2.5)
QM G303252 (Paratype)	Darwin Harbour, East Arm	307–627.5µm (538.8±90.6) x 4.3–16µm (10.2±3.2)
NTM Z.5211	Darwin Harbour, Weed Reef	386.2–663.7µm (524±68) x 7–14.9µm (11.8±1.9)

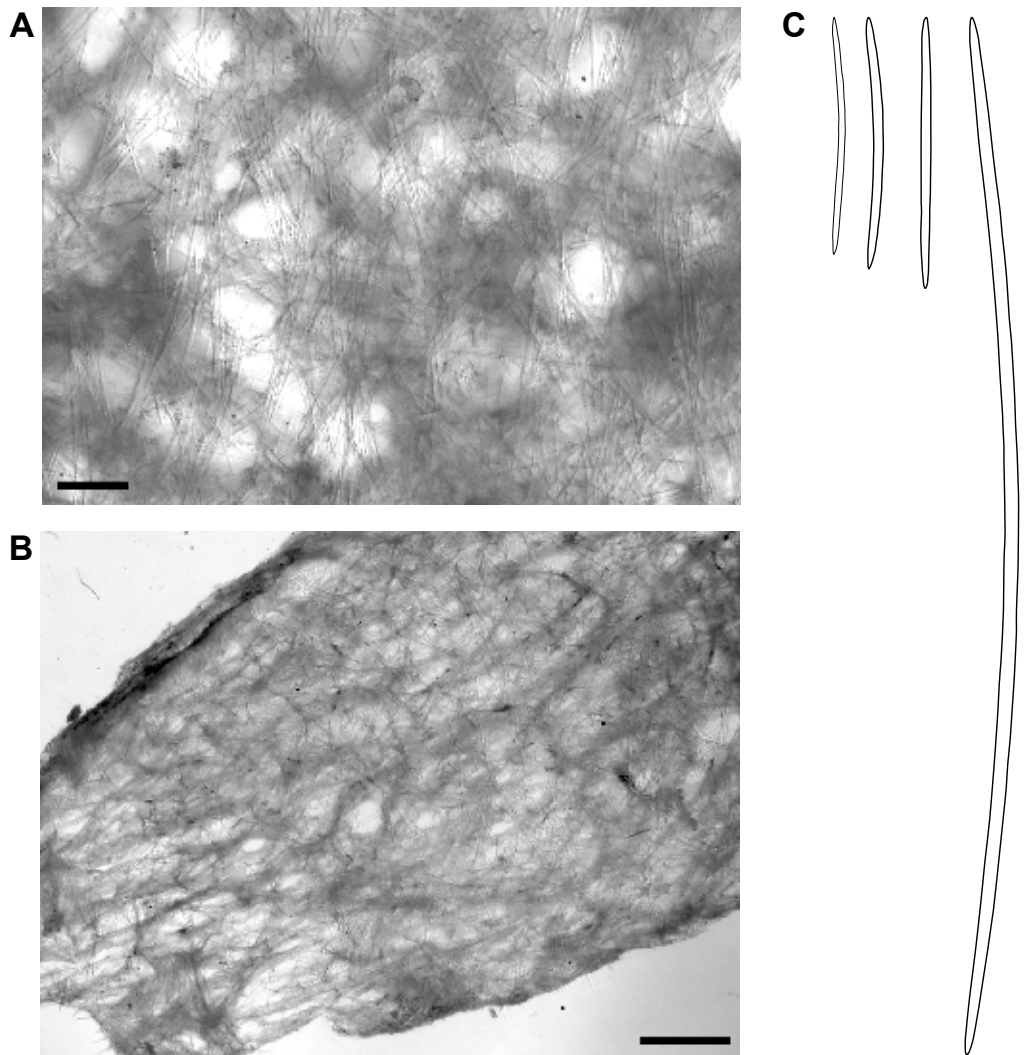


Fig. 11. *Halichondria (Halichondria) carotenenoidea* sp. nov. (NTM Z.5909): **A**, light microphotograph of tangential section of ectosomal skeleton showing ill-defined and criss-crossing bundles of spicules; **B**, light microphotograph of perpendicular section through surface showing organisation of choanosomal skeleton and part of ectosomal skeleton layer (left upper corner of section); **C**, diagram of spicules. Scale bars: A, 100 µm; B, 500 µm; C, 50 µm.

Distribution. *Halichondria phakellioides* is widely distributed through the Northwest Australian Shelf and Sahul Shelf provinces. It is found from the intertidal to 20 m depth.

***Halichondria (Halichondria) microbiana* sp. nov.**
(Figs 10F, 13)

Halichondria stalagmites.—Hooper *et al.* 1997: 43 [in part; not Z.2651 and Z.3147 = *H. (H.) carotenenoidea*].

Material examined. HOLOTYPE. —NTM Z.5907, Lee Point, Darwin, N.T., 12°20.538' S, 130°52.184' E, 9–12 m

depth, 7 August 2003, coll. Nguyen, H. PARATYPES.—NTM Z.1097, Dudley Point Reef, East Point, Darwin, N.T., 12°25.0001' S, 130°48.01' E, 6–7 m depth, 22 December 1982, coll. Hooper, JNA. NTM Z.5908, Moira Reef, Bynoe Harbour, N.T., 12°30.799' S, 130°30.527' E, 5–8 m depth, 25 June 2003, coll. Nguyen, H. ADDITIONAL SPECIMENS.—Darwin Harbour NT: NTM, Z.1991. Cobourg Peninsula, N.T.: NTM Z.131.

Description

Shape (Fig.10F). Cushion-shaped with globular, subspherical or massive base, sometimes semi-buried

Table 11. Comparison of spicule dimensions among specimens of *Halichondria (Halichondria) phakellioides*.

Specimen	Locality	Oxea type I	Oxea type II
NTM Z.5223	Bynoe Harbour	170.1–308.4µm (232±30.7) x 4.1–10.3µm (8±1.5)	363.2–524.6µm (440.6±40.8) x 11.5–24.4µm (17.9±3.7)
NTM Z.5219	Darwin Harbour	154.2–293.2µm (228.6±34.5) x 5–10.3µm (7.3±1.4)	356.7–499.6µm (425.5±38.7) x 10.5–20.2µm (16.3±3)
NTM Z.5228	Wessel Is	162.1–313.9µm (242.4±48.6) x 3.7–7.5µm (5.6±0.9)	326.5–519.3µm (440.5±45.5) x 10.6–21.1µm (15.6±3)

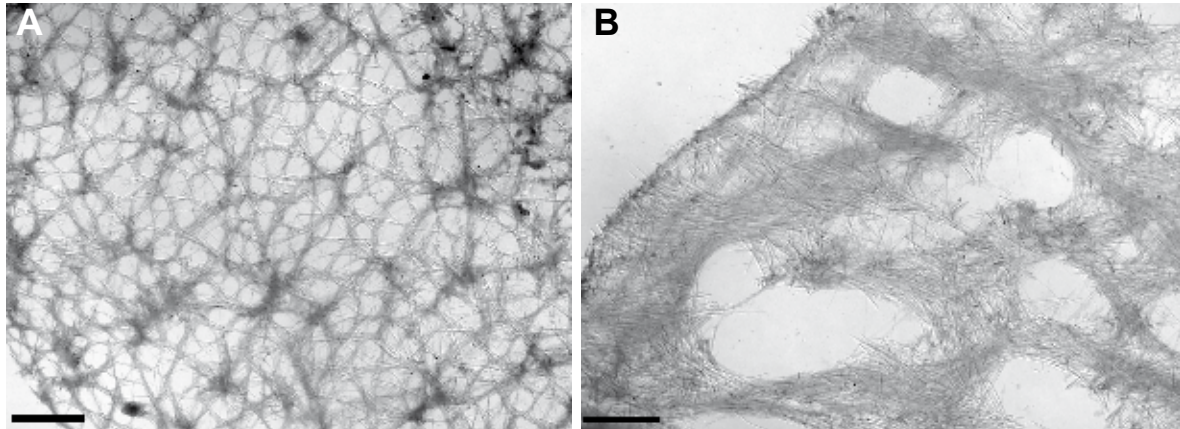


Fig. 12. *Halichondria* (*Halichondria*) *phakellioides* (NTM Z.5228): **A**, light microphotograph of tangential section showing organisation of ectosomal skeleton; **B**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton. Scale bars: A-B, 500 µm.

in substrate, and small tapering erect projections (from 10 mm long and less than 5 mm diameter) at apex. Erect projections vary in shape, i.e. fistulose-like, convoluted, bifurcating and lobate; generally small 30–70 mm diameter, 10–20 mm thick.

Colour. Orange. Blue-grey, in alcohol.

Consistency and texture. Soft, easily torn, rubbery.

Oscula. Apical and conspicuous on small digits, with membranous rims.

Surface. Semitransparent at apex of digits in some specimens.

Skeleton (Fig. 13A,B). Ectosomal skeleton, halichondroid, formed by a thin (less than 50 µm), wavy, loose membranous layer, with oxeas tangentially oriented and supported by choanosomal tracts (Fig. 13A). Choanosomal skeleton, halichondroid, formed by ill-defined bundles of larger spicules, criss-crossing and without any particular orientation connected by short bundles and single spicules. In subectosomal region, skeleton becoming cavernous with large lacunae, 100–600 µm diameter (Fig. 13B) and vague reticulation of pauci-multispicular, ill-defined tracts, diverging towards surface or condensed and running nearly parallel to it, supporting ectosomal skeleton. High densities of filamentous cyanobacteria present in both ectosome and choanosome, especially near surface. Spongin or collagen scarce.

Spicules (Fig. 13C; Table 12). Oxeas, hastate, straight, possibly in two size categories, larger and thicker (249–587 x 5–14 µm) and smaller and thinner (88–217 x 3–7 µm). Style modifications slightly common within larger category.

Remarks. We compared *Halichondria microbiana* with the valid species recorded for the Central West

Pacific (Table 7) and those reported in this revision. It is diagnosed by a unique combination of features (i.e growth form, organisation of the skeleton, size and composition of spicules and presence of cyanobacteria in the ectosome and the choanosome) not found in those species.

All the specimens examined here have a high density of filamentous cyanobacteria in the choanosome, generally concentrated at the subectosomal region, a character shared with *H. (H.) carotenoidea*. As mentioned above, this new species is also very similar in skeletal characteristics to *H. (H.) carotenoidea* sp. nov., but it differs in habit and size of spicules, which are larger and separated in size categories in *H. (H.) microbiana*.

Hooper *et al.* (1997) interpreted this species as *Halichondria stalagmites*. However, a thorough re-examination of the type material of that species indicates that it is not conspecific with *H. (H.) microbiana* (see description of *C. stalagmites* above).

Distribution. *Halichondria microbiana* is relatively common at Darwin and Bynoe Harbours, and it was also observed at Wessel Is (Raragala I.) and recorded from the Northeastern Australian Shelf (Alvarez and Hooper, unpublished data). It occurs between 6–12 m depth.

Etymology. Named after the symbiotic microorganisms hosted by the species. The specific name is intended as a noun in apposition.

Remarks on *Halichondria* (*Halichondria*). The subgenus *Halichondria* is large with approx. 95 valid species (Van Soest *et al.* 2008). Table 7 lists species distributed within the Central Indo-Pacific Realm (following Spalding *et al.* 2007) which includes the study area and adjacent areas. Some of those species, in particular the

Table 12. Comparison of spicule dimensions between specimens of *Halichondria* (*Halichondria*) *microbiana*.

Specimen	Locality	Oxea type I	Oxea type II
NTM Z.5907	Darwin Harbour, NT	87.9–203µm (126.5±24.8) x 3.3–7.1µm (5±0.9)	249.2–587µm (482.9±75.1) x 6.3–14.2µm (8.9±1.8)
NTM Z.5908	Bynoe Harbour, NT	91.3–217µm (137.8±32) x 2.9–7.2µm (5.1±1)	282.5–572.1µm (446.6±93.5) x 5.2–13.2µm (8.8±2)

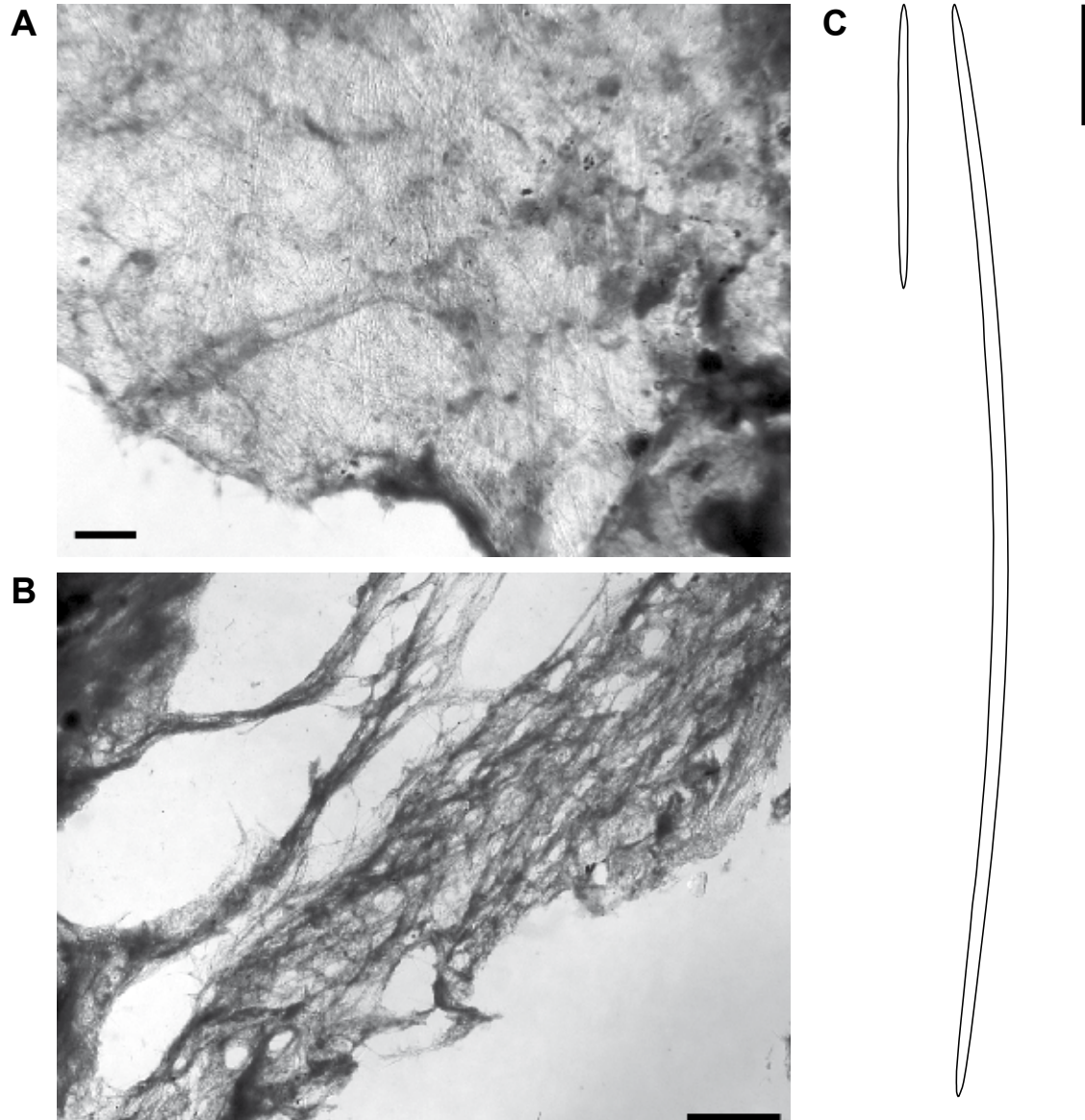


Fig. 13. *Halichondria (Halichondria) microbiana* sp. nov. (NTM Z.5908): **A**, light microphotograph of tangential section of ectosomal skeleton, showing oxaeas on membranous thin layer; **B**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton and large lacuna at subectosomal level (left upper corner of section); **C**, diagram of spicules. Scale bars: A, 200 µm; B, 500 µm; C, 50 µm.

ones described by Kieschnick (1896) and Lindgren (1897), are unrecognisable and their type material has never been relocated. Other species reported for the area have been allocated to other genera as result of this revision, thus *Halichondria (Halichondria)* is represented within this realm by nine species including the two new species described above.

The subgenus *Eumastia* Schmidt, 1870 is not represented in the study area at all and it is reserved for *Halichondria*-like species from high latitudes (Erpenbeck & Van Soest 2002).

Genus *Hymeniacidon* Bowerbank, 1858

Gender: feminine. Type species, by subsequent designation of Bowerbank (1864), *Hymeniacidon caruncula* Bowerbank, 1958. Recent, Tenby, Wales.

Hymeniacidon gracilis (Henstschel, 1912)

(Fig. 14)

Stylotella digitata gracilis Henschel, 1912: 356.

Hymeniacidon gracilis. – Hooper *et al.* 1997.

Material examined. As listed by Hooper *et al.* (1997).

Remarks. The species was well described by Hooper *et al.* (1997) and elevated to full species rank in the genus *Hymeniacidon*. We provide a new illustration of the type material (Fig. 14) and additional spicule measurements (Table 13) to complement the description given by Hooper *et al.* (1997).

Only three specimens are recorded for the study area; no new material was located in recent collections.

Distribution. As recorded by Hooper *et al.* (1997).

Remarks on the genus *Hymeniacidon*. *Hymeniacidon gracilis* is the only valid species of the genus from the study area. Other species of *Hymeniacidon* recorded for the

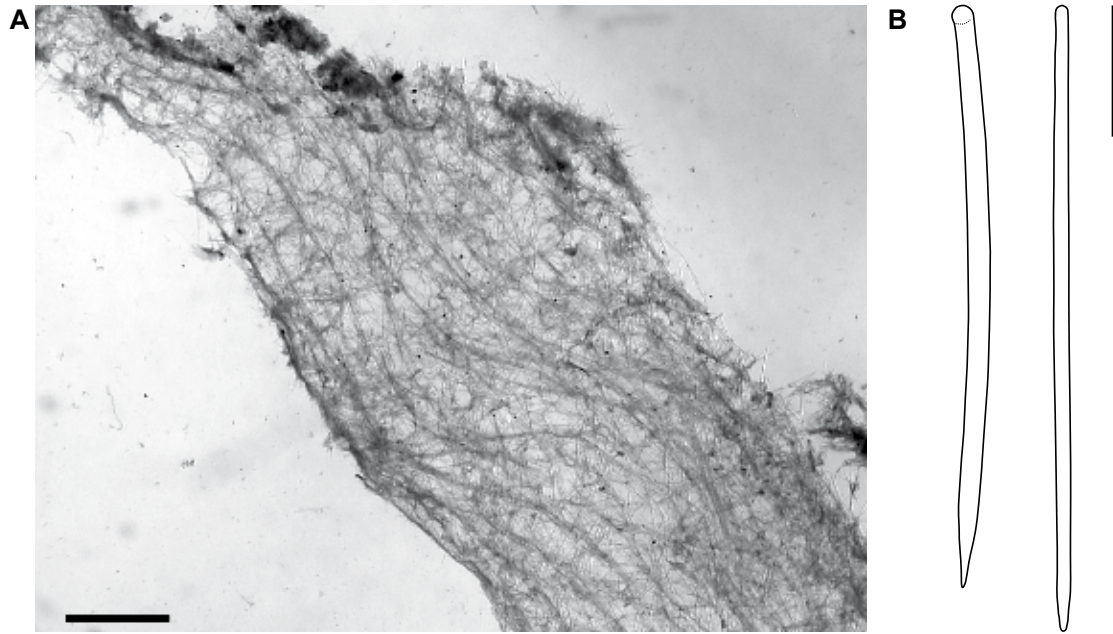


Fig. 14. *Hymeniacidon gracilis* (Synype SMF 970). **A**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton; **B**, diagram of spicules. Scale bars: A, 500 µm; B, 50 µm.

Sahul Shelf Province and adjacent areas are *H. vernonensis* Hooper *et al.*, 1997 and *H. flaccida* Pulitzer-Finali, 1996. The material described under *H. vernonensis* by Hooper *et al.* (1997) was revised and it does not agree with the current concept of the genus. The species is formally transferred here to the dictyonellid genus *Stylissa*. As admitted by Hooper *et al.* (1997), is very similar to *Stylissa flabelliformis* but *S. vernonensis* includes distinctive styles, curved at the centre, sinuous or rhabdose and frequent anisoxeas with one telescoped point. It should be noted however, that these spicule modifications are common among species of *Stylissa* and therefore they are not reliable for the delimitation of species. Both species are similar in growth form, surface characteristics and skeletal organisation. The choanosomal skeleton of *S. vernonensis* however, is nearly halichondroid with only vague tracts of spicules and with a much higher spicule density and no spongin fibres (whereas in *S. flabelliformis* is vaguely plumo-reticulated and with well developed spongin fibres).

The type specimen of *Hymeniacidon flaccida* (MSNG 48703) from Laing Is., Papua New Guinea, was re-examined and it does not correspond to the genus *Hymeniacidon*. The species belongs also to the dictyonellid genus *Stylissa* and is likely to be conspecific with *Stylissa massa* (Carter, 1887). The specimen examined however, includes distinctive subtylostyles transitional to strongyles with tylote modifications. As is the case with *S. vernonensis*,

these style modifications are common among the genus. Population genetics and additional morphometric analyses might reveal whether these style modifications of *Stylissa* are reliable characters for the separation of species.

Genus *Topsentia*

Gender feminine. Type species, by original designation, *Anisoxya glabra* Topsent, 1898. Recent, Azores Is.

Topsentia dura (Lindgren, 1897)

(Figs 10G, 15)

Halichondria dura Lindgren, 1897 : 480.

Topsentia dura.— Hooper *et al.* 1997: 14.

Material examined. As listed by Hooper *et al.* (1997). **ADDITIONAL MATERIAL.**— Darwin Harbour, N.T.: Z.5209, Z.5233. Wessel Is: Z.5234.

Remarks. Hooper *et al.* (1997) assigned material from the Beagle Gulf to this species under the genus *Topsentia*. Additional specimens from recent collections agree also with this material and are assigned to this species. Further illustrations (Figs 10G, 15) and spicule measurements (Table 14) are provided here to complement that description. The description agrees with the current concept of *Topsentia*, however it remains inconclusive whether the material from the Beagle Gulf is conspecific with Lindgren's species from Indonesia as the type was not examined. Examination of additional specimens from Indonesia (Alvarez & De Voogd unpublished data) and a re-description of the type might provide additional evidence to confirm if these populations belong in the same species.

Distribution. Indonesia [?], Darwin Harbour and Wessel Is. *Topsentia dura* occurs in the intertidal zone to 25 m depth.

Remarks on *Topsentia*. Hooper *et al.* (1997) described material under the Red Sea species *Topsentia halichondrioides* (Dendy, 1905) that seems very similar

Table 13. Comparison of spicule dimensions between specimens of *Hymeniacidon gracilis*.

Specimen	Locality	Styles
SMF 970	Indonesia	220.5–261.1 µm (238.4±9.6) x 3.3–8.9 µm (6.1±1.5) [25]
NTM Z.883	Darwin Harbour	243.1–279.1 µm (265.6±11.1) x 3–7.4 µm (5.1±1.1)

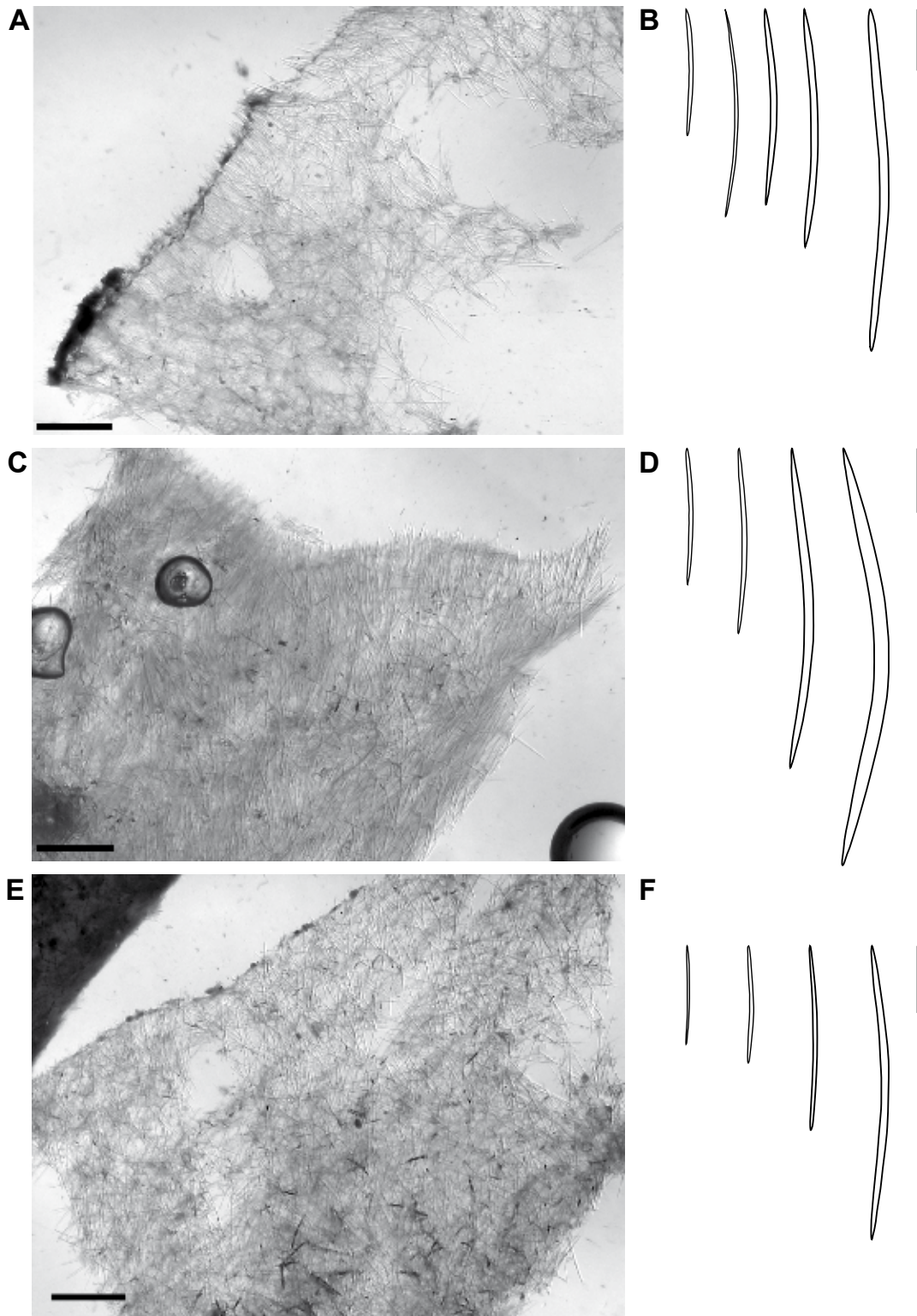


Fig. 15. *Topsentia dura* (NTM Z.5209): **A**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton and palisade of erect oxeas at surface; **B**, diagram of spicules. *Topsentia halichondrioides* (QM G303442): **C**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton and oxeas oriented perpendicularly at surface level; **D**, diagram of spicules. *Topsentia ridleyi* (QM G303309, Holotype): **E**, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton; **F**, diagram of spicules. Scale bars: A,C,E, 500 μ m; B,D,F, 100 μ m.

to *T. dura* (Fig. 15B,C). These species are massive, of hard consistency with skeletons made of a confused mass of oxeas of similar dimensions, not clearly differentiated into size classes (see Table 14) and differing only in colouration and shape of oscules (i.e. volcano-shaped in

T. halichondrioides, and sunken and small in *T. dura*). *Halichondria ridleyi* Hooper *et al.*, 1997 is referred here to the genus *Topsentia* (comb. nov.) and it is also very similar to *T. dura* (Fig. 15E,F). It differs from *T. dura* in having some surface fistules and processes.

Table 14. Comparison of spicule dimensions among specimens assigned to Central Pacific species of *Topsentia*.

Species	Specimen	Locality	Oxea type I	Oxea type II
<i>Topsentia ridleyi</i>	QM G303309	Darwin Harbour	142.3–273.5µm (207.7±39.4) x 3.3–7.6µm (5.4±1.2)	335.6–576.7µm (443.9±52.7) x 6.7–16.6µm (12±2.6)
<i>Topsentia ridleyi</i>	NTM Z.3262	Cobourg Peninsula		503–848.1µm (653.8±83.5) x 13.4–31.5µm (20.9±4.6)
<i>Topsentia halichondrioides</i>	G303442	Bynoe Harbour	160.6–331.2µm (257.4±50.3) x 4.2–12.3µm (8.2±2.3)	421.6–716.5µm (555.3±62.7) x 14–24.4µm (19.3±2.6)
<i>Topsentia halichondrioides</i>	NTM Z.5233	East Point	111.4–165.9µm (142.3±13.8) x 5.9–8.9µm (7.2±0.9)	487.6–914.9µm (711.2±99.1) x 13–30µm (18.9±4.4)
<i>Topsentia dura</i>	NTM Z.5234	Wessel Is	142.4–333.5µm (220.1±47.2) x 3.7–10.3µm (7.3±1.7)	348.6–568.1µm (448.9±57.8) x 11–23.7µm (16.8±3.2)
<i>Topsentia dura</i>	NTM Z.5209	Darwin Harbour	151.2–399.7µm (248.3±61.9) x 3–11.7µm (7.6±2.3)	373.9–656.5µm (477.9±79.2) x 10–23.9µm (15±3.2)
<i>Topsentia dura</i>	NTM Z.3178	Darwin Harbour	189.4–357.5µm (269.9±41.9) x 4.1–9.7µm (7.1±1.4)	352.5–525.1µm (441.4±46.2) x 9.9–18.5µm (13.7±2.4)
<i>Topsentia dura</i>	NTM Z.1442	Gunn Point	189.6–387.1µm (254.5±52.5) x 5.5–12.5µm (7.8±2)	341.2–611.2µm (482.6±69.2) x 8.3–22.7µm (15.6±3.4)
<i>Topsentia indica</i>	SMF 997	Aru Is, Indonesia		493.7–1078.1µm (734.4±125) x 11.1–39.4µm (21.7±5.5)

An additional species of *Topsentia* recorded from Aru Is, Indonesia, is *T. indica* Hentschel, 1912 (syntype SMF 995 and 997, examined).

The differentiation of these species using traditional morphological characters is extremely subjective. Molecular and morphometric studies of local populations might contribute to a better understanding of the concept of this species.

Other species of *Topsentia* recorded for the Sahul Province and adjacent areas that are better placed elsewhere include *Topsentia maculosa* Pulitzer-Finali, 1996 from Papua New Guinea (it belongs in *Amorphinopsis*, see above) and *Topsentia plurisclera* Pulitzer-Finali, 1996 (holotype, MSNG 48702, examined) is a species of *Petrosia*.

DISCUSSION

This revision of species of Halichondriidae from northern Australia recognises a total of 15 species belonging to the genera *Amorphinopsis*, *Axinyssa*, *Ciocalypta*, *Halichondria* (*Halichondria*), *Hymeniacidon* and *Topsentia*. Other genera of the family (i.e. *Epipolasis*, *Laminospongia*, *Vosmaeria*, *Ciocalapata* and *Spongisorites*) are not represented in the Sahul Shelf Province. *Epipolasis* and *Spongisorites* are however represented in the Northeast Australian Shelf (Alvarez and Hooper, unpublished data).

Of the species reported in this revision, *Axinyssa bergquistae*, *Ciocalypta vansoesti* and the two new species *Halichondria* (*Halichondria*) *carotenoidea* and *H. (H.) microbiana* are so far known only from northern Australian waters. The rest of the species have extralimital distributions through the Central Indo-Pacific realm. *Axinyssa mertoni* (Hentschel, 1912) in its new generic combination is recorded for northern Australia and it represents a new record for the study area.

As in other members of the order Halichondrida, particularly in Axinellidae and Dictyonellidae, species within and across all genera of Halichondriidae are extremely difficult to delimit. This problem is demonstrated by the large number of misidentifications in previous studies due to the lack of adequate generic definitions and also to the poor understanding of the importance, or indeed relevance, of some of the alleged pivotal characters that currently differentiate both species-groups and genera within the Halichondriidae. The additional information obtained from the collection of new material plus the revised generic definitions of the family (Erpenbeck & Van Soest 2002) allowed us to clarify the concept of halichondriid species of northern Australia and to allocate them to more appropriate genera.

Nevertheless, differentiating species within Halichondriidae continues to be ambiguous based solely on the present limited suite of accepted morphological characters, with a number of them shared among species and even genera. For example, *Ciocalypta heterostyla*, *C. vansoesti*, and *Axinyssa mertoni* are species with fistule-like growth form, nearly indistinguishable in the field (Fig 1). However, they all are easily diagnosed based on skeletal characteristics. This suggests that the growth form of these species in particular, might be an adaptation to the habit where they occur (i.e. soft and muddy sediments). *Amorphinopsis foetida* and *A. maculosa* are also very similar in habit and in their skeletal characteristics but they can be distinguished by the predominance of oxeas and styles. Separation of species based on the dominance of styles or oxeas however might be debatable, as this could possibly be related to intraspecific variation as seen in some species of Axinellidae (Alvarez *et al.* 1998; Alvarez & Hooper 2009).

Spicule morphometrics (i.e. size variation of spicules) within Halichondriidae seems to be a useful tool for the

differentiation of species. *Ciocalypta stalagmites*, for example, is distinguished from the other species by the distinctive and nearly constant size of two categories of oxeas. Similarly, *Halichondria* (*H.*) *microbiana* can be distinguished from *H.* (*H.*) *carotenoidea* by the size of the larger category of oxeas. On the other hand, all the *Axinyssa* species we have studied have always a mixture of oxeas in a large size range, thus spicule sizes is not a useful character for the distinction of species within this genus.

These examples indicate that the characters currently used to separate genera and species within the family are extremely homoplastic and suggest that genera and species within Halichondriidae might be non-monophyletic. The study of local populations using both morphological and genetic methods will help to clarify whether these taxa are monophyletic.

This study represents the final contribution to the present taxonomic revision of the order Halichondrida of northern Australia, restricted to the marine province identified as the Sahul Shelf in the classification of Spalding *et al.* (2007). The result of this and previous studies (Alvarez & Hooper 2009, 2010) indicates that the group is represented in the study area mainly by the families Axinellidae (Alvarez & Hooper 2009), Dictyonellidae (Alvarez & Hooper 2010) and Halichondriidae (this revision).

One additional family, the Heteroxyidae (formerly Desmoxyidae see Van Soest & Hooper 2005), is represented in the area by two very common species: *Myrmekioderma granulatum* (Esper, 1830), which is documented and illustrated by Hooper *et al.* (1997); and *Higginsia mixta* (Hentschel, 1912). The type of *H. mixta* (SMF 968) was examined and it agrees with material deposited at the collections of QM and NTM and recorded for the area of study. The ectosomal skeleton of the specimens studied have a relatively thick tangential crust formed by a dense mass of spined microxeas and interrupted by disorganised brushes of thin raphidiform oxeas and extra long styles-strongyles (mostly broken in the preparations) projecting through surface. The similarities of this type of skeletal organisation with raspailiid genera such as *Ceratopsion* are remarkable and worth further investigation. Phylogenetic affinities based on molecular data (Erpenbeck *et al.* 2005) indicated that members of Heteroxyidae (i.e. *Didiscus* and *Myrmekioderma*) are closely related to the axinellid genera *Reniochalina* and *Ptilocaulis*. The position of these genera within Axinellidae (Halichondrida) and its relationships based on molecular data with other raspailiid genera such as *Axechina* has already been discussed (Alvarez 2009 and references within). Sequencing data of additional genera currently allocated to Heteroxyidae, and in particular of the species represented in the Sahul Shelf province will help to clarify these relationships and classification.

The family Bubaridae is the only family of Halichondrida not represented in the area of study.

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APPENDIX I

Collection and locality data of material examined in the collections of QM and NTM

QM material

G300854	Gulf of Carpentaria, northern central region, QLD, 9°36.0001' S, 136°6.01' E, 52 m, 23 Nov 1991, coll. Cook, SD. on CSIRO RV Southern Surveyor
G301034	SW Vrilya Point, SW, Gulf of Carpentaria, QLD, 11°29.0167' S, 142°55.09' E, 18 m, 1 Dec 1991, coll. Cook, SD. on CSIRO RV Southern Surveyor
G303252	South Shell I., reef N of boatramp, East Arm, Darwin Harbour, NT, 12°29.1334' S, 130°53.09' E, 0 m, 19 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303287	South Shell I., reef N of boatramp, East Arm, Darwin Harbour, NT, 12°29.1334' S, 130°53.09' E, 0 m, 19 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303309	Dudley Point Reef, East Point, Darwin, NT, 12°25.05' S, 130°49.01' E, 0 m, 20 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303351	East Point Bommies, Darwin Harbour, NT, 12°24.0834' S, 130°48.14' E, 10 m, 23 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303442	Fish Reef, west side, Bynoe Harbour, NT, 12°26.0167' S, 130°26.09' E, 11 m, 26 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303450	Fish Reef, west side, Bynoe Harbour, NT, 12°26.0167' S, 130°26.09' E, 11 m, 26 Sep 1993, coll. Hooper, JNA & Hobbs, L.J.
G303524	Duyfken Point, W Gulf of Carpentaria, QLD, 12°41.0501' S, 141°3.01' E, 42 m, 11 Nov 1993, coll. Cook, SD. & Kennedy, J. on CSIRO RV. Southern Surveyor
G303541	Vernon Is, W of South West Vernon I., NT, 12°6.15' S, 131°4.14' E, 13 m, 10 Oct 1993.
G303558	Cape Hotham, NW of cape, NT, 12°1.05' S, 131°13.16' E, 34 m, 9 Oct 1993.
G303560	Bynoe Harbour, 2 nmls E Fish Reef, NT, 12°24.1334' S, 130°28.16' E, 17 m, 6 Oct 1993, coll. CCNT Ocean Rescue 2000 Program
G303561	Shoal Bay, outer region of bay, NT, 12°6.15' S, 130°49.16' E, 18 m, 12 Oct 1993, coll. CCNT Ocean Rescue 2000 Program
G303595	Vernon Is, W of Knight Reef, NT, 12°1.0334' S, 131°3.16' E, 22 m, 11 Oct 1993.
G303658	Vernon Is, N marsh Shoal, NT, 12°07.0001' S, 130°56.1' E, 16 m, 11 Oct 1993, coll. CCNT stn. 138. Dredge
G303677	Shoal Bay, middle of bay, NT, 12°13.0167' S, 130°56' E, 17 m, 12 Oct 1993, coll. CCNT Ocean Rescue 2000 Program
G310137	Parry Shoals 35nm W Bathurst I., NT, 11°7.0321' S, 129°25.9' E, 16 m, 12 Aug 1987, coll. mussig, AM and NCI team
G310170	Darwin Harbour, NT, 12°15.1834' S., 130°29.11' E., 9 m depth, 17 August 1987, coll. mussig, AM and NCI team
G313543	N Bathurst I., Timor Sea, NT, 11°13.98' S, 130°34.21' E, 41.2 m, 5 Oct 1997, coll. Cook, SD. on RV Southern Surveyor
G313572	SW Groote Eylandt, NT, 14°25.0801' S, 135°58.51' E, 20.3 m, 13 Oct 1997, coll. Cook, SD. on RV Southern Surveyor
G313577	SW Groote Eylandt, NT, 14°20.22' S, 136°34.98' E, 19.6 m, 14 Oct 1997, coll. Cook, SD. on RV Southern Surveyor
G314246	N Groote Eylandt, Gulf of Carpentaria, NT, 13°32.2801' S, 136°18.13' E, 20 m, 27 Sep 1998, coll. Leys, SP. on RV Southern Surveyor
G314247	N Groote Eylandt, Gulf of Carpentaria, NT, 13°32.2801' S, 136°18.13' E, 21.7 m, 27 Sep 1998, coll. Leys, SP. on RV Southern Surveyor
G314255	W of Groote Eylandt, Gulf of Carpentaria, NT, 14°8' S, 136°8' E, 13 m, 6 Oct 1998, coll. Leys, SP. on RV Southern Surveyor
G314267	SW of Groote Eylandt, Gulf of Carpentaria, QLD, 14°20' S, 136°2' E, 22.1 m, 6 Oct 1998, coll. Leys, SP. on RV Southern Surveyor
G315205	W Groote Eylandt, Gulf of Carpentaria, NT, 14°8.5667' S, 136°16.51' E, 21.4 m, 13 Oct 1998, coll. Wassenberg T
G315207	SW of Groote Eylandt, Gulf of Carpentaria, NT, 14°22.5' S, 136°9.12' E, 22.2 m, 13 Oct 1998, coll. Wassenberg T
G320819	Gulf of Carpentaria, QLD, 15°20.037' S, 140°19.84' E, 28 m, 24 May 2003, coll. Bartlett C, Cook S on RV Southern Surveyor 2380403 CSIRO "Effects of Trawling"
G320904	Gulf of Carpentaria, QLD, 15°20.037' S, 140°19.84' E, 28 m, 11 Mar 2003, coll. Bartlett C, Cook S on RV Southern Surveyor 2380403 CSIRO "Effects of Trawling"

APPENDIX I (continued)

Collection and locality data of material examined in the collections of QM and NTM
NTM material

Z.84	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.5001'S, 132°2'E, 18 Oct 1981, coll. Hooper, JNA & Alderslade, PN
Z.131	Sandy I. No.2, Cobourg Peninsula, NT, 11°5.5001'S, 132°17'E, 10 m, 21 Oct 1981, coll. Hooper, JNA & Alderslade, PN
Z.194	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0–0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.241	Indian I., Bynoe Harbour, NT, 12°35'S, 130°33.01'E, 3 m, 18 Nov 1981, coll. Byers,P.,F.V. Skeleton
Z. 592	Table Head, Port Essington, Cobourg Peninsula, NT, 11°13.5'S., 132°10.51'E., 3 m depth, 4 May 1982, coll. Hooper, JNA
Z 712	N Adele I., Collier Bay, NW Shelf, WA 15°58.0167'S., 122°39.07'E., 59 m depth, 21 April 1982, coll. R.V.SPRIGHTLY, dredge.
Z.919	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10 m, 31 Aug 1982, coll. Hooper, JNA
Z.934	East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA
Z.941	East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA
Z.945	East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA
Z.986	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 26 Oct 1982, coll. Hooper, JNA
Z.987	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 26 Oct 1982, coll. Hooper, JNA
Z.1097	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, m, 22 Dec 1982, coll. Hooper, JNA
Z.1358	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S, 132°3.71'E, .5–6 m, 16 May 1983, coll. Hooper, JNA
Z.1391	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S, 132°3.71'E, 6 m, 17 May 1983, coll. Hooper, JNA
Z.1395	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°10.4'S, 132°2.8'E, 2 m, 19 May 1983, coll. Hooper, JNA
Z.1442	Blue Hole, Gunn Point, NT, 12°9.0001'S, 131°0'E, 25 m, 19 Aug 1983, coll. Alderslade, PN
Z.1979	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, m, 11 May 1984, coll. Hooper, JNA and party
Z.1991	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, m, 11 May 1984, coll. Hooper, JNA and party
Z.2018	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, m, 11 May 1984, coll. Hooper, JNA and party
Z.2026	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, 11 May 1984, coll. Hooper, JNA and party
Z.2086	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 20 Jul 1984, coll. Hooper, JNA
Z.2215	Vestey's Beach, Bullocky Point, Darwin, NT, 12°26.2'S, 130°49.89'E 21 Jan 1985, coll. Hooper, JNA
Z.2245	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 m, 12 Apr 1985, coll. Hood, C and party
Z.2648	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 3 Apr 1986, coll. Hooper, JNA and party
Z.2651	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2697	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.3106	Parry Shoals, Arafura Sea, NT, 11°12.5167'S, 129°42.07'E, 20 m, 15 Aug 1987, coll. Mussig, AM and NCI team
Z.3133	Parry Shoals, Arafura Sea, NT, 11°11.4'S., 129°43.01'E., 18 m depth, 13 August 1987, coll. Mussig, AM and NCI team
Z.3147	Parry Shoals, Arafura Sea, NT, 11°12.5167'S, 129°42.07'E, 16 m, 15 Aug 1987, coll. Mussig, AM and NCI team
Z.3178	East Point Reef, East Point, Darwin, NT, 12°29.5'S, 130°48.01'E, 0.5 m, 10 Sep 1987, coll. Smit, N
Z.3195	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 9 m, 16 Sep 1987, coll. Smit, N
Z.3205	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 25 Sep 1987, coll. Smit, N
Z.3262	Table Head, Port Essington, Cobourg Peninsula, NT, 11°13.5'S, 132°10.51'E, 11 Sep 1986, coll. Hooper, JNA & Johnson,C
Z.3920	Cumberland Strait, NE bay, Wessel Is, Gove Peninsula, NT, 11°26.8'S, 136°30.2'E, 13 m, 14 Nov 1990, coll. Hooper, JNA
Z.4085	Near Boat Ramp, East Arm Port, Darwin, NT, Australia, 12°29.8'S, 130°53.5'E, intertidal, 20 September 2001, coll. B. Glasby & party, by hand
Z.4093	Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 20 September 2001, coll. B. Glasby & party, by hand
Z.4100	Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 18 October 2001, coll. B. Glasby & party, by hand
Z.4122	Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 18 October 2001, coll. B. Glasby & party, by hand
Z.4123	Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 19 October 2001, coll. B. Glasby & party, by hand
Z.4125	Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 19 October 2001, coll. B. Glasby & party, by hand
Z.4451	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.103'S, 130°47.111'E, 8–14 m, 7 May 2002, coll. Alvarez, B and party

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Z.5206	South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 10–12 m, 21 Aug 2002, coll. Alvarez, B and party
Z.5207	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.238'S, 130°35.557'E, 5–10 m, 23 May 2003, coll. Alvarez, B and party
Z.5208	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 7–12 m, 24 Jul 2003, coll. Alvarez, B and party
Z.5209	Nightcliff bommies, off Nightcliff jetty, Darwin Harbour, NT, 12°22.751'S, 130°50.116'E, 5–8 m, 8 Aug 2003, coll. Alvarez, B and party
Z.5210	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.188'S, 130°47.110'E, 8–14 m, 22 Aug 2003, coll. Alvarez, B and party
Z.5211	Weed Reef, entrance to West Arm, Darwin Harbour, NT, 12°29.25'S, 130°47.54'E, 9–12 m, 6 Sep 2003, coll. Nguyen, H
Z.5212	off Herbert Point, Indian I., Bynoe Harbour, NT, 12°34.586'S, 130°31.419'E, 0–5 m, 24 Jun 2003, coll. Alvarez, B and party
Z.5213	South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 7–11. m, 19 Aug 2002, coll. Alvarez, B and party
Z.5215	West Arm, 2.5 km N of Stokes Point, Darwin Harbour, NT, 12°31.300'S, 130°48.500'E, 4–5 m, 3 Aug 2002, coll. Alvarez, B and party
Z.5216	Wickham Point, 2.5 km SW of East Arm Wharf, East Arm, Darwin Harbour, NT, 12°30.12'S, 130°52.39'E, 4–7 m, 15 Sep 2002, coll. Alvarez, B and party
Z.5217	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.188'S, 130°47.110'E, 8–14 m, 22 Aug 2003, coll. Alvarez, B
Z.5218	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5219	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.2001'S, 130°47.1'E, 5–19 m, 8 May 2002, coll. Alvarez, B and party
Z.5221	South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 7–14 m, 20 Aug 2002, coll. Alvarez, B and party
Z.5222	East Arm Wharf, East Arm, Darwin Harbour, NT, 12°29.19'S, 130°53.35'E, 0.6 m, 1 Mar 2002, coll. Alvarez, B and party
Z.5223	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.238'S, 130°35.557'E, 5–10 m, 23 May 2003, coll. Alvarez, B and party
Z.5224	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 3–7 m, 25 May 2003, coll. Alvarez, B and party
Z.5225	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.351'S, 130°31.454'E, 6–8 m, 11 Jun 2003, coll. Alvarez, B and party
Z.5226	Moira Reef, Bynoe Harbour, NT, 12°30.799'S, 130°30.527'E, 5–8 m, 25 Jun 2003, coll. Browne, M
Z.5228	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5229	Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 12–18 m, 16 Sep 2002, coll. Alvarez, B and party
Z.5230	Approx. 3 km NE Charles Point, Cox Peninsula, NT, 12°22.782'S, 130°38.371'E, 9–12 m, 23 Aug 2003, coll. Browne, M
Z.5233	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4–7 m, 4 Jun 2002, coll. Alvarez, B and party
Z.5234	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5736	Mandorah jetty, NW Cox Peninsula, Darwin Harbour, NT, 12°26.55'S, 130°46.05'E, 9–12 m, 5 Sep 2003, coll. Alvarez, B and party
Z.5901	Moira Reef, Bynoe Harbour, NT, 12°30.799'S, 130°30.527'E, 5–8 m, 25 Jun 2003, coll. Alvarez, B and party
Z.5902	Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 12–24 m, 3 Sep 2002, coll. Alvarez, B and party
Z.5903	Approx. 3 km NE Charles Point, Cox Peninsula, NT, 12°22.782'S, 130°38.371'E, 9–12 m, 23 Aug 2003, coll. Nguyen, H
Z.5904	West Arm, 2.5 km N of Stokes Point, Darwin Harbour, NT, 12°31.300'S, 130°48.500'E, 4–5 m, 3 Aug 2002, coll. Alvarez, B and party
Z.5905	Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, 12°33.09'S, 130°52.43'E, intertidal 0.02 m, 7 Nov 2006, coll. Alvarez, B
Z.5906	Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, 12°33.09'S, 130°52.43'E, intertidal 0.02 m, 7 Nov 2006, coll. Alvarez, B
Z.5907	Lee Point, Darwin, NT, 12°20.538'S, 130°52.184'E, 9–12 m, 7 Aug 2003, coll. Nguyen, H
Z.5908	Moira Reef, Bynoe Harbour, NT, 12°30.799'S, 130°30.527'E, 5–8 m, 25 Jun 2003, coll. Nguyen, H

Z.5909	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4–7 m, 4 Jun 2002, coll. Alvarez, B and party
Z.5915	Larrakeyah sewerage outfall, Darwin Harbour, NT, Australia, 12°28.04'S., 130°49.77'E., 20 m depth, 22 April 2009, coll. Sultana, S, SCUBA.
Z.5923	Larrakeyah sewerage outfall, Darwin Harbour, NT, Australia, 12°28.04'S., 130°49.77'E., 19.5 m depth, 22 April 2009, coll. Sultana, S, SCUBA.
Z. 5925	Larrakeyah sewerage outfall, Darwin Harbour, NT, Australia, 12°28.04'S., 130°49.77'E., 19.5 m depth, 22 April 2009, coll. Sultana, S, SCUBA.
Z.5928	Larrakeyah sewerage outfall, Darwin Harbour, NT, Australia, 12°28.04'S., 130°49.77'E., 19.5 m depth, 22 April 2009, coll. Sultana, S, SCUBA.
Z.5948	Stevens Rock, near Weed Reef, Darwin Harbour, NT, Australia, 12°29.17'S., 130°47.19'E., 10–16 m depth, 21 May 2009, coll. Alvarez, B and Sultana, S, SCUBA
Z.5949	Stevens Rock, near Weed Reef, Darwin Harbour, NT, Australia, 12°29.17'S., 130°47.19'E., 10–16 m depth, 21 May 2009, coll. Alvarez, B and Sultana, S, SCUBA
Z.5950	Stevens Rock, near Weed Reef, Darwin Harbour, NT, Australia, 12°29.17'S., 130°47.19'E., 10–16 m depth, 21 May 2009, coll. Alvarez, B and Sultana, S, SCUBA.
Z.5965	East Point, Fannie Bay, Darwin Harbour, NT, Australia, 12°25.01'S., 130°48.88'E., 6 m depth, 21 May 2009, coll. Alvarez, B and Sultana, S, SCUBA
Z.5970	East Point, Fannie Bay, Darwin Harbour, NT, Australia, 12°25.01'S., 130°48.88'E., 6 m depth, 21 May 2009, coll. Alvarez, B and Sultana, S, SCUBA
Z.5976	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.188'S, 130°47.110'E, 8–14 m, 22 Aug 2003, coll. Alvarez, B and party
Z.5977	Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 13–16 m, 5 Sep 2003, coll. Alvarez, B and party
Z.5978	Larrakeyah sewerage outfall, Darwin Harbour, NT, 12°28.04'S, 130°49.77'E, 5.8 m depth, 22 July 2010, coll. Sultana, S, SCUBA