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CYMBASTELA, A NEW GENUS OF LAMELLATE CORAL REEF SPONGES

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Seven species of lamellate, stalked sponges from Australasian waters are referred to a new genus, *Cymbastela* gen.nov. Six species from tropical, predominantly coral reef habitats: *C. stipitata* (Bergquist & Tizard) (type species) and *C. vespertina* sp.nov., both from NW Australia, *C. concentrica* (Lendenfeld) and *C. coralliophila* sp.nov. both from the Great Barrier Reef, Queensland, *C. marshae* sp.nov. from the Houtman-Abrolhos Is, Western Australia, and *C. cantharella* (Lévi) from New Caledonia). Another species is recorded from temperate South Australian waters (*C. notiaina* sp.nov. from the Gulf of St Vincent). All the species conformed to the existing interpretation of *Pseudaxinyssa* Burton, but they are referred here to *Cymbastela* since all are substantially different from the type species of *Pseudaxinyssa, A. tethyoides* Kirkpatrick. *Pseudaxinyssa* is synonymized with *Axinyssa* Lendenfeld. The seven species of *Cymbastela* are primarily differentiated by their spicule length and geometry, axial and extra-axial skeletal development, growth form, lamella thickness and live colouration. Four species are sympatric over part of their range in tropical Australia, whereas three species have more restricted, allopatric distributions in temperate Australia and the western Pacific Ocean.

☐ *Pseudaxinyssa, Axinyssa, Cymbastela, new genus, new species, Porifera, Axinellidae, taxonomy, biogeography, Australasia.*

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No formal revision of the complete order Axinellida has yet been published, even though for many years it has been recognized these marine sponges were polyphyletic (Bergquist & Hartman, 1969). Recent work on several families within the Axinellida, using a phylogenetic framework, has gone some way towards redistributing some of these taxa amongst other existing orders. Families considered so far (with their affinities as suggested by particular authors), are Axinellidae (Halichondrida; Van Soest et al., 1990), Desmacellidae (Poecilosclerida; Van Soest, 1984), Hemiasterellidae (Hadromerida; Hooper, 1986; Voultsiadou-Koukoura & Van Soest, 1991), Rhabderemiidae (Poecilosclerida; Hooper, 1990), and Raspailiidae (Poecilosclerida; Hooper, 1991). However, it is not yet clear whether the concept of an order Axinellida should be abandoned completely, or retained and restricted to one or few families. Additional, non-morphological data is required to confirm or refute these ideas (discussion in Hooper et al., 1992), and until such is available none of the above assignments can be completely endorsed.

Axinellidae is undoubtedly the most difficult of all the families of Axinellida to interpret. The original conception of the family, basically corresponding to the old subfamily Axinellinae of Lendenfeld (1889), with major additions by Hallmann (1916) and de Laubenfels (1936), included genera with an 'axinellid skeletal plan' consisting of a condensed axial core with diverging plumose or plumo-reticulate extra-axial branches. This definition stands today (e.g. Hartman, 1982), even though nearly half of the 50 nominal genera included in the family have skeletal structures other than axinellid (e.g. evenly reticulate - *Reniochalina*; sinuous - *Rhaphoxya*; dendritic - *Acanthella*; thickly encrusting/leptoclathrid - *Fasubera*). In such cases, genera with atypical skeletal structures were included in Axinellidae because their spicule geometries were similar to those with axinellid skeletons. However, recent biochemical evidence indicates that the family contains several distinctly heterogenous groups of genera (Bergquist & Hartman, 1969; Hooper et al., 1992).

A recent revision of halichondriids by Van Soest et al. (1990), based primarily on morphological characters, suggested that genera of Axinellidae could be redistributed into three existing families (Axinellidae, Desmoxyidae and Halichondriidae) and a new family (Dictyonellidae). Van Soest et al. (1990) referred these four families to the order Halichondrida, and although we do not presently support or refute this ordinal placement, we agree that for the Axinellidae at least, there is a pressing need for a re-evaluation of the major morphological characters used to distinguish taxa within the Axinellidae, including the relative importance of these characters as reliable indicators of phylogenetic affinity.

It is difficult in many cases to assign species of Axinellidae to genera with complete assurance, as there are few morphological characters with clear importance at the supraspecific level. Unlike most groups within Poecilosclerida, for example, Axinellidae lack any unique or diverse spicule geometries, and lack microscleres which could provide clues on affinities between genera. Thus, the major problem preventing resolution of the supraspecific taxonomy of Axinellidae is the difficulty or inability to define autapomorphies and, furthermore, there is disagreement in the interpretation of the relative importance of the few existing morphological characters that do occur in the group - in particular spicule shape and skeletal organization. Biochemical evidence may provide more objective information on the affinities of the numerous genera presently included in the family, but the few data available are not entirely clear (Hooper et al. 1992): there are, in many cases, no obvious morphometric characters that correlate consistently with generic groupings based on chemotaxonomic data (see Hooper et al., 1992). The 'axinellids' are one group of Porifera that require rigorous genetic study.

The existing subdivision within Axinellidae, resting solely on morphological features, concerns the skeletal architecture, presence or absence of a specialised ectosomal skeleton, and morphology and diversity of structural megascleres. The curvature and geometry of megascleres, however, is thought to vary considerably within a particular species groups, and confuse the interpretation of interrelationships between species even further. This problem was first identified by Dendy (1905), who noted that oxeas may become strongyles or even styles, and curved or sinuous strongyles, once considered apomorphic for genera such as *Acanthella*, reappear throughout the family.

Consequently, it is not surprising that there are many genera of Axinellidae that presently contain heterogenous assemblages of species, particularly the large groups of *Phakellia*, *Acanthella*, *Axinella*, to each of which numerous species have been assigned. A similar situation exists for *Pseudaxinyssa*, and although it contains only eight nominal species - prior to the present work - some of these are obviously quite different from the type species. Lévi (1983) first stated that *Pseudaxinyssa* was probably polyphyletic, and this was recently reiterated by Van Soest et al. (1990). The present paper re-evaluates *Pseudaxinyssa*, returns its type species and several other described species to *Axinyssa*, and creates a new genus to receive several described species and a number of new species mainly from tropical Australian coral reef habitats.

METHODS

Preparation of material for light microscopy and scanning electron microscopy (SEM) is described elsewhere (Hooper, 1991). Abbreviations used in the text are as follows: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; CMNZ, Canterbury Museum, Marine Invertebrate collection, Christchurch; MNHN LBIM, Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Paris; NCI Q66C-, US National Cancer Institute shallow water collection program (Australian Institute of Marine Science, Townsville, contract) - primary material in USNM, duplicates/fragments in NTM and QM; NTM, Northern Territory Museum, Darwin; ORSTOM, Institute Français de Recherche Scientifique pour le Developpement en Cooperation, Noumea; PIBOC, Pacific Institute of Bio-organic Chemistry, Far Eastern Scientific Centre, Academy of Sciences of the USSR, Vladivostok; QM, Queensland Museum, Brisbane; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington; ZMB, Zoologisches Museum für Naturkunde an der Humboldt-Universität, Berlin.

SYSTEMATICS

Family AXINELLIDAE Ridley & Dendy

Axinyssa Lendenfeld, 1897

Axinyssa Lendenfeld, 1897:116; Burton, 1931:349; Van Soest et al., 1990:25.

Axinomimus de Laubenfels, 1936:163; Van Soest et al., 1990:27 (type species *Axinella paradoxa* Ridley & Dendy, 1886:482 [by monotypy]; holotype BMNH 1887.5.2.68).

Pseudaxinyssa Burton, 1931:350; Van Soest et al., 1990:27 (type species *Axinyssa tethyoides* Kirkpatrick, 1903:245 [by original designation]; holotype BMNH 1902.11.16.25, schizotype MNHN LBIM DCL298).

Not *Pseudaxinyssa*, sensu Bergquist & Tizard, 1967: 190; Lévi, 1983:719.

TYPE SPECIES

Axinyssa topsenti Lendenfeld, 1897:116 (by monotypy) (holotype ZMB 2971, schizotype BMNH 1908.9.24.145).

DIAGNOSIS (emended)

Massive, frequently subspherical, sometimes lobate or lobate-digitate growth forms, often with an apical cloacal cavity or fistulose surface conules; surface with prominent, regularly spaced conules; choanosomal axial skeleton open plumose, dendritic or vaguely radiating tracts of larger oxeas, without axial compression, with poorly developed spongin fibres; fibres cored by larger oxeote megascleres; subectosomal extra-axial skeleton plumose, plumo-reticulate, ascending to surface, without obvious spongin fibre component; mesohyl usually with abundant collagenous spongin; specialised ectosomal skeleton may be present in the type species, or absent, consisting of tufts of smaller oxeas perched on peripheral choanosomal skeleton, protruding through surface, forming surface conules; megascleres oxeas or modified oxeas, one or two sizes.

REMARKS

Lendenfeld (1897:116) created the genus *Axinyssa* for a single species, *A. topsenti* Lendenfeld, which had a vaguely plumose, ascending choanosomal skeleton composed of multispicular tracts of large oxeas, with smaller stylote oxeote spicules in brushes on the surface. These choanosomal spicule tracts and smaller ectosomal brushes protrude through the surface for a short distance, producing characteristic microconules. There is no distinctive, compressed core in the skeleton (termed 'axial condensation'), although there is differentiation between the axial and extra-axial regions. Several other species were subsequently described and included in *Axinyssa* (Kirkpatrick, 1903; Topsent, 1906; Wilson, 1925).

Burton (1931) created *Pseudaxinyssa* for two species previously assigned to *Axinyssa* - the type species *A. tethyoides* Kirkpatrick (1903), and *A. gravieri* Topsent (1906). He also included a previously undescribed species, *P. tenuispicula* Burton (1931) from Natal. All three species differed from *Axinyssa* sensu stricto in lacking a specialised ectosomal skeleton of smaller styloid oxeas. They were closer to *Axinella* in their skeletal structure, but had only oxeas as megascleres (*Axinella* usually has styles and oxeas, or only styles, although at least one anomolous oxea-bearing species is also known [see below]). Van Soest et al. (1990) noted that a specialised ectosomal skeleton, such as that seen in *A. topsenti*, commonly occurs within many axinellids and, as such, it may not be a reliable or even valid taxonomic character when used above the species level. We provide further evidence to support this conclusion in the present work, (i.e. *Cymbastela coralliophila* sp.nov. having a specialised ectosomal skeleton), supporting the proposal that *Axinyssa* and *Pseudaxinyssa* (s.s.) should be merged.

Pseudaxinyssa, as defined by Burton (1931), were massive sponges, without strong differentiation between the axial and extra-axial skeletons, and without any evidence of axial condensation. The type species *Axinyssa tethyoides* (Kirkpatrick) is subspherical, with fistulose, usually blind surface papillae, with large oxeas between 530-790µm long scattered between skeletal tracts and forming a branching reticulate, non-compressed, undifferentiated skeletal architecture (i.e. no distinct axial and extra-axial components). However, the subsequent addition of two stalked, cup-shaped sponges from the Indo-west Pacific, *Pseudaxinyssa stipitata* Berquist & Tizard (1967) and *P. cantharella* Lévi (1983), did not fit at all with the original conception of the genus. These two species had compressed-reticulate axial skeletons, with diverging plumose (or plumo-reticulate) extra-axial skeletons, and spongin fibres were reasonably well developed. Both groups of species were similar to *A. tethyoides* only in having diverging tracts of oxeas near the periphery of the skeleton, whereas in other features they were quite different. Therefore, it is proposed here to include these anomolous stalked, predominantly cup shaped species in a new genus.

Following from Van Soest et al.'s (1990) revision of *Axinyssa* and our own observations on various museum specimens, 13 species may be referred to the genus, most from the tropical oceans (also indicating known geographic distributions, and material we have examined):

A. aculeata Wilson (1925:445) (Philippines; none).

A. ambrosia (de Laubenfels, 1934:14) (Puerto Rico; none).

A. aplysinoides (Dendy, 1922:39) (Cargados Carajos, Amirante, Seychelles; none).

A. digitata (Cabioch, 1968:229) (Roscoff; none).

A. fenestratus (Ridley, 1884:464) (Arafura Sea; holotype BMNH 1882.2.23.255).

A. gravieri Topsent (1906:563) (Red Sea; specimen of Lévi (1965:15), MNHN LBIM DCL327L).

A. paradoxa (Ridley & Dendy, 1886:482) (Tristan de Cunha Is; none).

A. pitys (de Laubenfels, 1954:178) (Palau Islands; holotype USNM 23103).

A. radiata (Lévi & Lévi, 1983:968) (New Caledonia; paratype MNHN LBIM DCL 2955).

A. tenuispicula (Burton, 1931:350) (Natal; none).

A. tethyoides Kirkpatrick (Natal; holotype BMNH 1902.11.16.25).

A. topsenti Lendenfeld (Adriatic; holotype ZMB 2971).

A. valida (Thiele, 1899:12) (Moluccas; ? paratype SMF 1821).

Another species exists in the MNHN collections, identified as a new species of *Pseudaxinyssa* by Claude Lévi (pers.comm.) ('holotype' MNHN LBIM DCL1497) from Anborombe, Africa (M. A. Crosnier stn CRO 69), and it too should be included in *Axinyssa*. The affinities of the remaining species which have been included in *Pseudaxinyssa* at one time or another are as follows:

P. cantharella Lévi (1983:719) (New Caledonia) belongs to the new genus described below.

P. stipitata Bergquist and Tizard (1967:189) (northern Australia) also belongs to the new genus described below.

P. tricalyciformis (Bergquist, 1970:15) (holotype CMNZ Mar. Inv. 3/63), a replacement name for *Axinella lamellata* Bergquist (1961:188) (preoccupied), from the Chatham Islands, was referred to *Pseudaxinyssa* by Bergquist & Tizard (1967:190). It has oxeas, some with styloid modifications, forming a condensed axial skeleton and plumose extra-axial skeleton, and is returned to *Axinella*. Discrepancies in dates of referral and description of that species are a consequence of delayed publication of the 1970 paper, which was completed in 1966 (Bergquist, 1970:4).

Following Van Soest et al.'s (1990) revision of the 'halichondrid' axinellids *Axinyssa* was referred to the family Halichondriidae Vosmaer, as emended by them, in having vague, ill-defined spicule tracts, with a high ratio of spicules to spongin. By comparison, 'true' members of the Axinellidae have ordered, axially condensed, extra-axially plumo-reticulate skeletons. The type species of *Pseudaxinyssa*, *A. tethyoides* fits well with the emended definition of Halichondriidae (see Figs 1-2), and a redescription of *A. tethyoides* is provided here for comparative purposes with the new genus described below.

Axinyssa tethyoides Kirkpatrick
(Figs 1-2)

Axinyssa tethyoides Kirkpatrick, 1903: 245-6, pl. 5, fig.12, pl.6, fig.8a,b.; Van Soest et al., 1990:27, fig.18.
Pseudaxinyssa tethyoides; Burton, 1931:350.

MATERIAL EXAMINED
HOLOTYPE: BMNH 1902.11.16.25: Cone Point, Natal, South Africa, 68m depth. SCHIZOTYPE: MNHN LBIM DCL298.

SUBSTRATE AND DEPTH RANGE
Broken shell substrate.

GEOGRAPHICAL DISTRIBUTION
Known only from the type locality.

DESCRIPTION
Shape: Subspherical, massive growth form, 64mm diameter, with slightly flattened basal region (point of attachment) (Fig. 1A).

Surface features: Detachable, relatively fragile skin, covered with numerous small papillae, 2-5mm long, 1-2.5mm diameter, most erect, fistulose, but few open at the apex. When open, diameter of oscule approximately 1mm.

Colour: Live colouration unknown, mottled black and dark brown in ethanol.

Texture: Firm, barely compressible consistency, easily crumbled.

Ectosome: Membraneous, without specialised skeleton, with moderate quantities of detritus within heavy organic matrix, occasionally with spicules from peripheral choanosomal skeleton protruding through surface, corresponding to surface papillae (Fig. 2B).

Choanosome: Skeleton branching reticulate, open-meshed (mesh diameter 140-320μm), without trace of axial condensation or differentiation between axial or extra-axial regions. Skeletal tracts pauci- or multispicular, 80-170μm wide, composed of tightly bound oxeas, without spongin fibres, bound together within heavy collagenous mesohyl (Fig. 1B). Near periphery skeletal tracts diverge to surface, protruding through ectosome slightly or not at all.

Spicules: Oxeas of single size class, long, robust, symmetrical, slightly curved at centre,

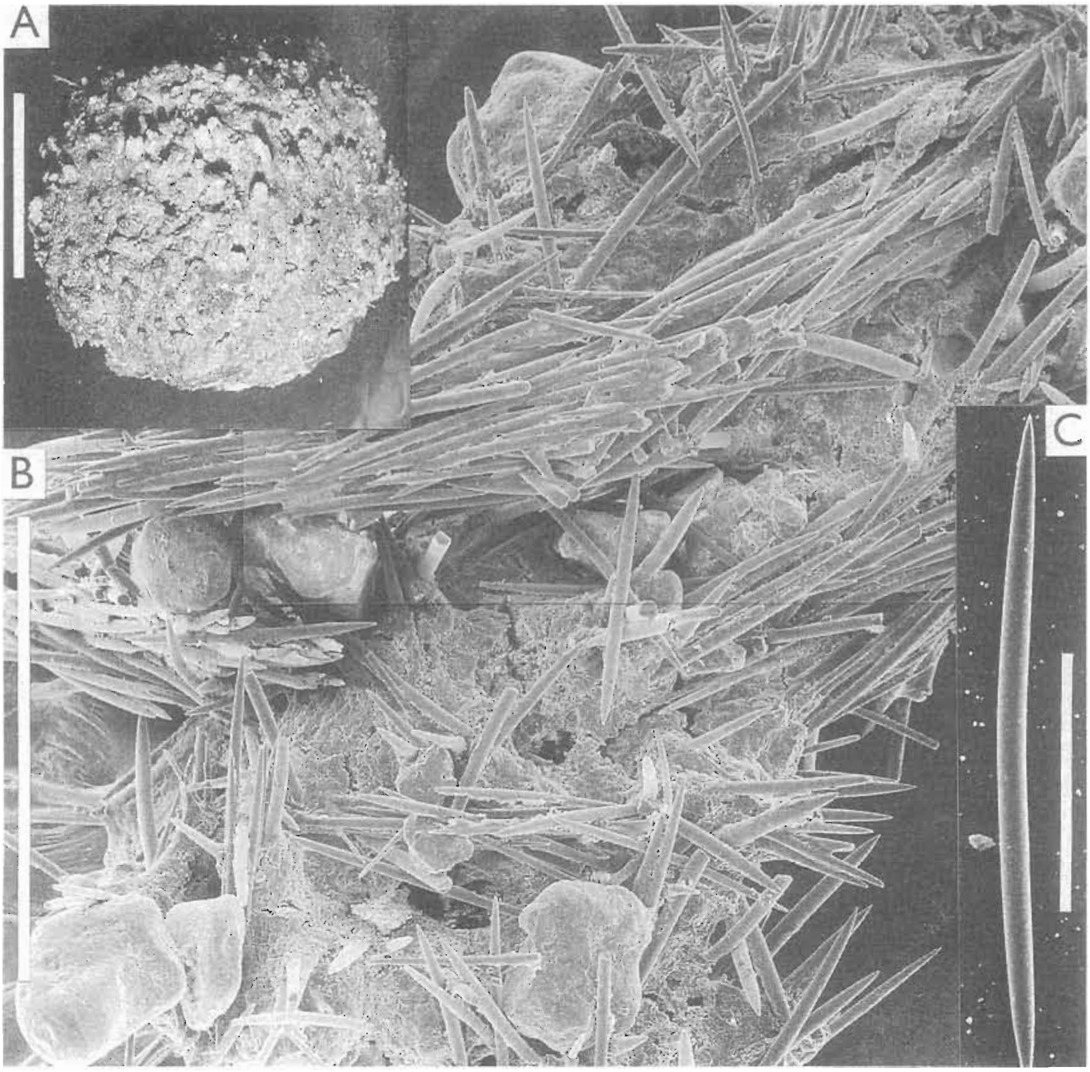


FIG. 1. *Axinyssa tethyoides*, holotype (BMNH 1902.11.16.25). A,whole specimen (scale=30mm). B,SEM of skeleton (scale=1mm). C,spicule (scale=250µm).

tapering to sharp points (Fig. 2A) (length 533-<u>648.4</u>-789µm, width 18-<u>29.6</u>-43µm).

REMARKS

The large size of spicules, undifferentiated axial and extra-axial skeletons, lack of a condensed axial skeleton, absence of spongin fibres, presence of heavy collagen in the mesohyl, and a spherical fistulose growth form distinguish this species from all the Australian '*Pseudaxinyssa*' species. For reasons discussed above we consider that this distinction is at the generic level.

Cymbastela gen.nov.

Pseudaxinyssa, in part, Bergquist & Tizard, 1967: 190; Lévi, 1983:719.

TYPE SPECIES

Pseudaxinyssa stipitata Bergquist & Tizard, 1967:189 (holotype AM Z3101).

DIAGNOSIS

Typically stalked, cup-shaped, thinly lamellate growth form. Ectosome with or without

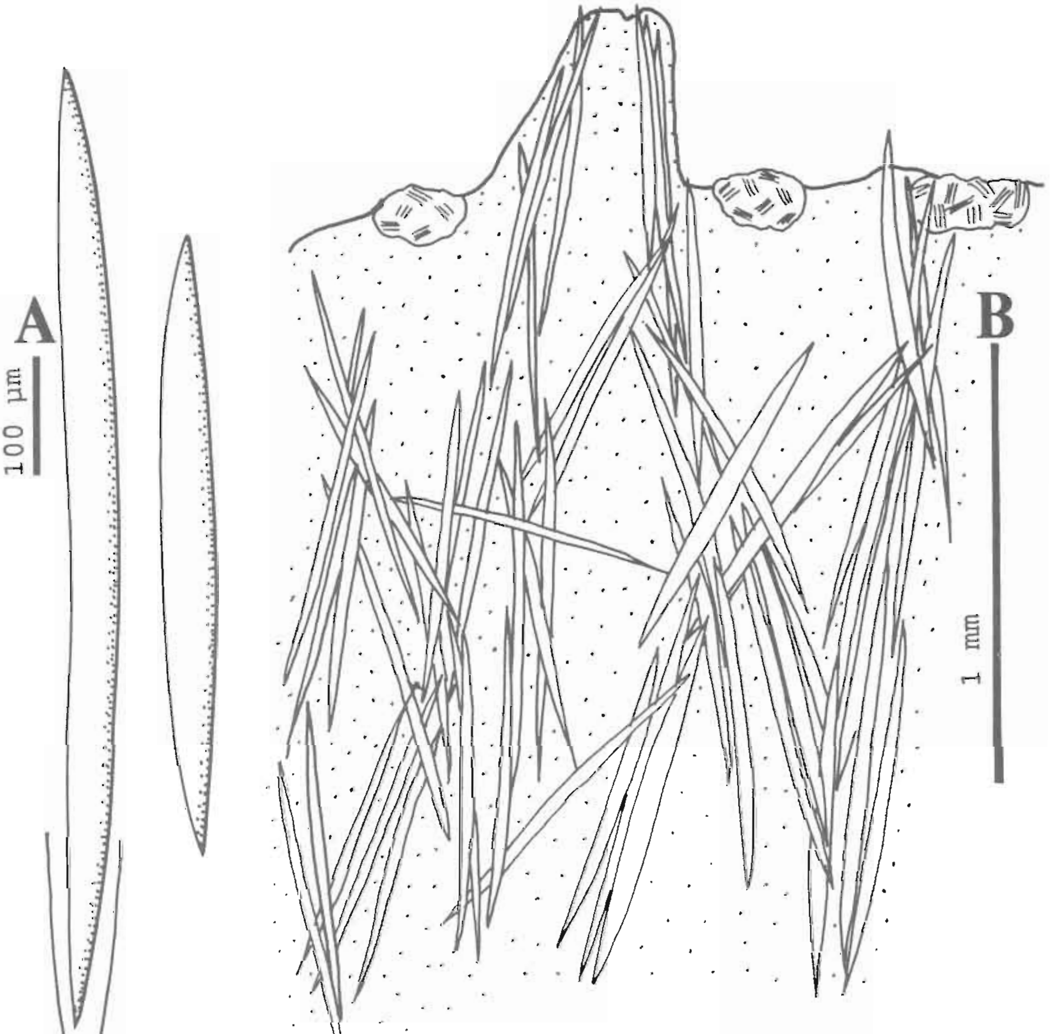


FIG. 2. *Axinyssa tethyoides*, holotype. A, spicules. B, section through peripheral skeleton.

specialised skeleton of smaller oxeas. Choanosomal skeleton with compressed reticulate axial region, in which major tracts run longitudinally through lamellae, and with gradually ascending, diverging, radial, plumose or plumo-reticulate extra-axial region, in which tracts become plumose and project through surface. Spongin fibres well developed, cored by oxeas, frequently with telescoped points. Predominantly autotrophic, most species containing symbiotic cyanobacteria. Oviparous.

ETYMOLOGY

Latin, *cymba* - cup, *stela* - column (f.); *Cymbastela*, for the predominantly stalked, cup-shape growth forms.

REMARKS

Cymbastela is an unusual axinellid in its growth form, although this morphology is also repeated in several Haplosclerida, such as some *Haliclona* and *Amphimedon*. Typically the genus has a reticulated, compressed axial skeleton and a plumose extra-axial skeleton, both composed of

TABLE 1. Comparison in spicule dimensions between described species of *Cymbastela*. All measurements given in micrometres, and expressed as minimum - mean - maximum range of measurement. N=number of specimens examined.

SPECIES	OXEAS	
	Length	Width
C. cantharella (N=3)		
Holotype	187-215.5-232	4.0-8.1-10
Other specimens	143-220.1-245	2.5-8.7-12
C. concentrica (N=5)		
Type material	172-239.6-305	2.5-9.5-16
Other specimens	79-152.6-189	1.6-5.9-11
C. coralliophila (N=8)		
Holotype I	263-318.8-357	6.5-14.4-21.7
II	135-166.8-255	1.1-3.2-5.6
Other specimens I	190-293.1-356	6.1-12.5-18.6
II	119-162.5-279	1.1-3.2-7.2
C. marshae (N=3)		
Holotype	124-156.8-192	2.0-5.4-9.0
Other specimens	119-150.7-180	1.6-6.4-11.3
C. notiaina (N=1)		
Holotype	49-77.1-98	1.5-3.2-4.5
C. stipitata (N=38)		
Holotype	155-259.1-344	2.7-8.6-16.0
Other specimens	133-267.4-361	2.0-11.4-19.5
C. vespertina (N=8)		
Holotype	167-252.2-270	5.2-11.9-15.0
Other specimens	152-238.8-283	3.6-10.7-16.2

well formed spongin fibres. In the extra-axial region there are always fewer paucispicular, reticulate fibres interconnecting the multispicular, radial or plumose, ascending fibres. This structure shows some similarities to the skeletons found in *Axinella* Schmidt (i.e. *A. polypoides* Schmidt, sensu Vosmaer, 1912), in which there is a condensed, reticulate axis and plumose-branching and reticulated extra-axis, and *Phakellia* Bowerbank (i.e. *P. ventilabra* Linnaeus, sensu Vosmaer, 1912), in which there is a condensed, reticulate axis, and a plumose, radial, non-branching or poorly-branching extra-axial skeleton. Both *Axinella* and *Phakellia* have spicules consisting of styles, strongyles and oxeas, in all combinations, whereas in *Cymbastela* spicules are only oxeas, usually with telescoped ends. *Cymbastela* is superficially most similar to *Phakellia* (sensu Vosmaer), due to the emphasis of the extra-axial skeleton over other structures, but it is probably most closely related to *Axinella* in all other features.

It is difficult to define any particular character which may serve as a synapomorphy for *Cymbastela*, clearly differentiating it from its sister group *Axinella*, in particular. Virtually no single feature is unique; levels of homoplasy are comparatively high within the Axinellidae. The lamellate growth form is characteristic and consistent, but not unique to *Cymbastela*: two species of *Axinella*, *A. vaceletia* (Pansini) and *A. shoemakeri* de Laubenfels, are also lamellate. Similarly, *Axinella polycapella* de Laubenfels has a reduced spicule complement, with mostly only oxea megascleres, although in *Cymbastela* many of the oxeas have telescoped ends, and it is probably this feature that is most important in defining the genus. Therefore, all three characters in combination - growth form, spiculation and skeletal architecture - are considered to be valid discriminatory characters defining the new genus.

Seven species are referred here to *Cymbastela*, only three of which have been previously described. The genus is most common in the tropical Australian - western Pacific region, although one temperate species is also known.

KEY TO THE SPECIES OF *CYMBASTELA*

Characters found in both preserved material [and live specimens] are indicated.

1. Oxeas mostly with telescoped ends .... 3.

Oxeas mostly with tapering ends .... 2.

2. Thicker lamellate, cup-shaped growth form, often with external buttresses, concentric lamellae, and lateral projections [typically pigmented olive-green and mauve]) .... *C. stipitata* (Bergquist & Tizard).

Thinly lamellate, usually simple, concentric or asymmetrical cup-shaped growth forms, without exterior projections [dark maroon-brown, evenly pigmented] .... *C. vespertina* sp.nov.

3. Oxeas well silicified .... 4.

Oxeas poorly silicified, vestigial, thin, with strongyloid-rounded telescoped ends [small symmetrical vase-shaped, thin lamellae, even surface, live colouration unknown] ....*C. notiaina* sp.nov.

4. Specialised ectosomal skeleton of smaller oxeas present, overlaying projecting subdermal skeleton of larger oxeas [wide cups or thickly lamellate lobes attached directly to substrate, usually with convoluted external surface, mot-

tled olive-green and olive-brown colouration] .... *C. coralliophila* sp.nov.

Without specialised ectosomal skeleton .... 5.

5. Axial skeleton not compressed, predominantly plumo-reticulate, extra-axial skeleton radial, not plumose, ectosomal skeleton with plumose projecting spicules [concentric cups, usually buttressed or with other sorts of external projections, thin lamellae, convoluted margins, with obvious differences between interior (porous, inhalant) and exterior (smooth, exhalant) surfaces, pale orange] .... *C. cantharella* (Lévi).

Axial skeleton compressed, predominantly reticulate, extra-axial skeleton predominantly reticulate, ectosomal skeleton with plumose projecting spicules [concentric or convoluted cups, thin lamellae, evenly pigmented dark brown or olive-brown] .... *C. concentrica* (Lendenfeld).

Axial skeleton compressed, predominantly plumose or longitudinal, less obviously reticulate, extra-axial skeleton predominantly plumose, ectosomal skeleton plumose [irregular cups, thin lamellae, no basal stalk, smooth surface on both interior and exterior faces, evenly pigmented olive-green/maroon] .... *C. marshae* sp.nov.

Cymbastela stipitata (Bergquist and Tizard)
(Figs 3-5, Table 1)

Pseudaxinyssa stipitata Bergquist and Tizard, 1967:189-191, text-figs 3-4, pl.5, fig.3.

MATERIAL EXAMINED

HOLOTYPE: AM Z3101: East Point Reef, Darwin, NT, 12°25.0'S, 130°49.1'E, intertidal, 13.x.1965, coll. E. Pope and R.S. Williams.

OTHER MATERIAL: (All material collected by the author unless otherwise indicated). DARWIN REGION, NT: NTM Z163-165: East Point Aquatic Life Reserve, 12°25.0'S, 130°49.1'E, 0.5m depth, 13.xi.1981 (stn EP6). NTM Z261 (4 specimens): same locality, 17.ix.1981 (stn EP3). NTM Z294: same locality, 1m depth, 18.viii.1981 (stn EP4). NTM Z309: same locality, 0.5m depth, 20.ix.1981 (stn EP5). NTM Z2145: same locality, 27.ix.1984 (stn EP17). NTM Z2207: same locality, 23.xi.1984 (stn EP18). NTM Z2225: same locality, 22.i.1985 (stn EP20). NTM Z2240: same locality, 8.iii.1985 (stn EP21). NTM Z2250: same locality, 12.iv.1985 (stn EP22). NTM Z2412: same locality, 7.x.1975 (stn Don.196, coll. A.J. Dartnall). NTM Z2422: same locality, 3m depth, 14.viii.1985 (stn EP24). NTM Z2542: same locality, 0.5m depth, 4.x.1985 (stn EP25). NTM Z2547: same locality, 15.xi.1985 (stn EP26; coll. A.M. Mussig). NTM Z2552: same locality, 12.xii.1985 (stn EP27; coll. A.M. Mussig and C. Hood). NTM Z2250: same locality, 12°24.5'S, 130°48.0'E, 10m depth, 12.iv.1985, coll. C. Hood and J.R. Hanley (stn EP22). QM G300001 (fragment NTM Z2392): same locality, 8m depth, 29.vii.1985 (stn EP23). NTM Z3179: same locality, 12°29.5'S, 130°48.0'E, 0.5m depth, 10.ix.1987, coll. N. Smit, by hand (stn JH-87-017). NTM Z401: Vestey's Beach, 12°26.2'S, 130°49.9'E, intertidal, 11.xii.1981 (stn MB4). NTM Z479: Fannie Bay beach, 12°25.0'S, 130°50.0'E, intertidal, 9.ii.1982 (stn EP7). NTM Z2009

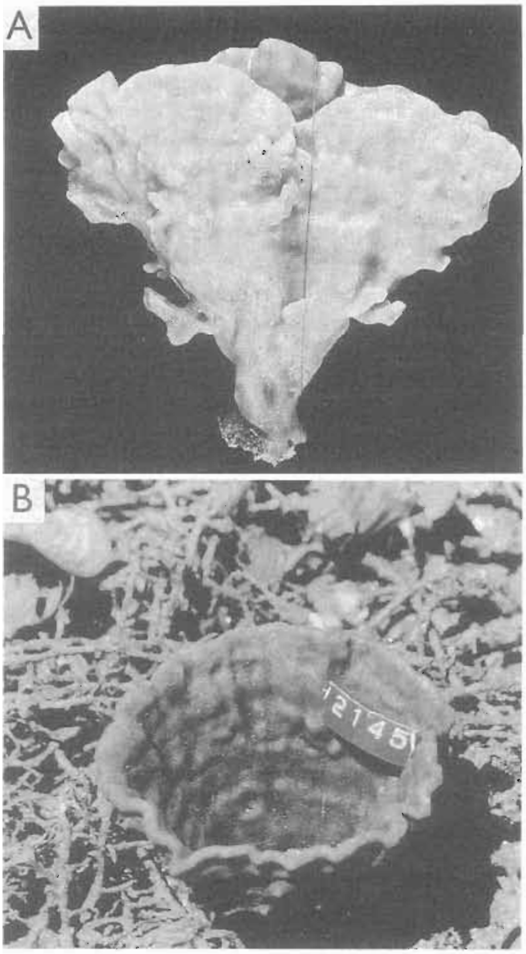


FIG. 3. *Cymbastela stipitata*. A, typical growth form (specimen NTM Z2009). B, in situ (specimen NTM Z2145).

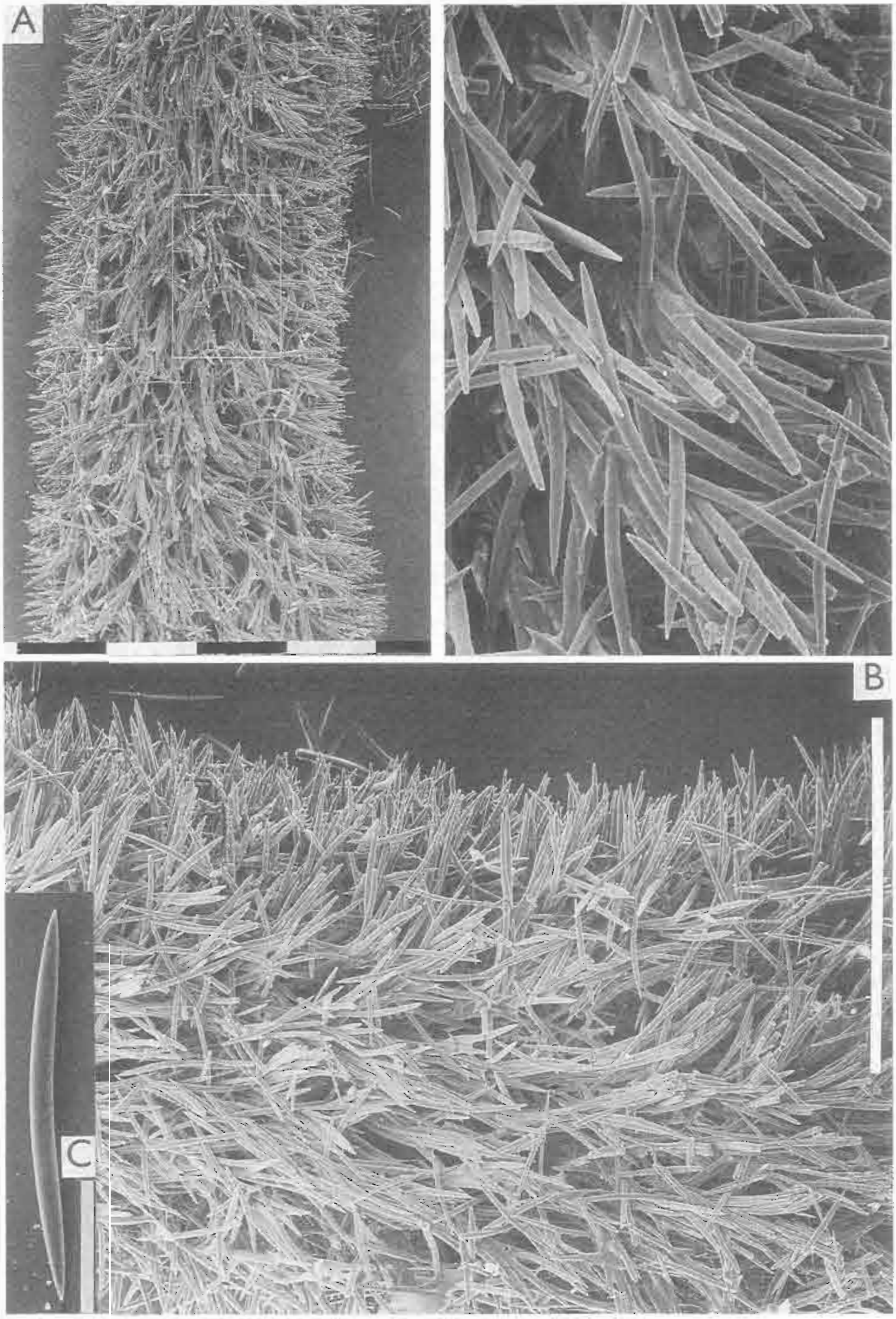


FIG. 4. *Cymbastela stipitata*. A, SEM of skeleton (specimen NTM Z2009) (scale=500µm; left magnified 40.8 times, right magnified 320 times). B, peripheral skeletal architecture (scale=1mm). C, oxea (scale=100µm).

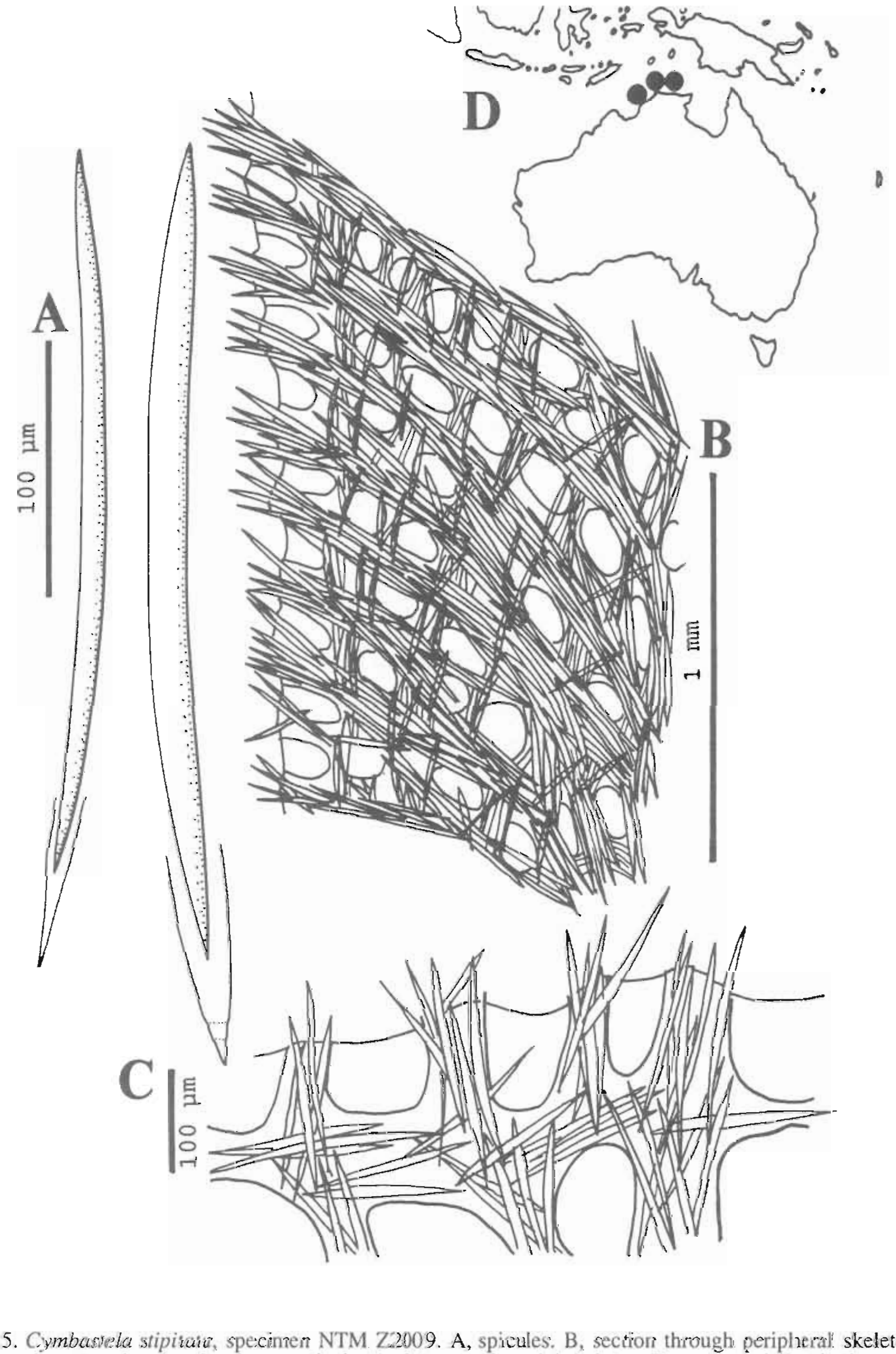


FIG. 5. *Cymbastela stipitata*, specimen NTM Z2009. A, spicules. B, section through peripheral skeleton. C, enlarged portion showing the close-meshed reticulate near the axial skeleton. D, confirmed distribution.

(fragment QM G300006): W side of Weed Reef, 12°29.2'S, 130°47.1'E, 19m depth, 11.v.1984 (stn WR2). NTM Z2190: 'Bommies', Weed Reef, 12°29.2'S, 130°37.6'E, 6-10m depth, 16.xi.1984 (stn WR6). SAM TS4023 (fragment NTM Z1655): Old Man Rock, Nightcliff, 12°21'S, 130°51'E, intertidal, 16.vi.1962 (coll. R.N. Southcott and A.E. Adams, stn A573). NTM Z424: Lee Point, 12°19.2'S, 130°53.1'E, intertidal, 13.xii.1981 (stn LP2). NTM Z779: W side of Channel I., Middle Arm, 12°33.4'S, 130°52.5'E, 2m depth, 7.vii.1982 (stn CI2). NTM Z796: S side of Channel I., Middle Arm, 12°32.3'S, 130°51.3'E, 11m depth, 16.vii.1982, coll. S. Chidgey. NTM Z2105: N side of Fish Reef, Bynoe Harbour 12°26.2'S, 130°26.2'E, 9-10m, 5.ix.1984 (stn FR2). COBOURG PENINSULA REGION, NT - NTM Z2491: Coral Bay (now known as Seven Spirit Bay), Port Essington, 11°09.4'S, 132°04'E, 4-7m depth, 13.ix.1986 (stn CP71). NTM Z3301, 3302: Inside outer barrier to Coral Bay, S side of Bay, Port Essington, 11°09.4'S, 132°04.0'E, 2-7m depth, 12.ix.1986, SCUBA (stn JH-85-020). NTM Z3244: SW side of cliff face, Table Head, Port Essington, 11°13.5'S, 132°10.5'E, 2-5m depth, 11.ix.1986, SCUBA (stn JH-85-019). NTM Z119: Sandy I. No. 2, Arafura Sea, 11°05.5'S, 132°17'E, 7m depth, 20.x.1981 (stn CP26). NTM Z536: E of Point Edwards, Port Bremer, CPMNP, 11°08.5'S, 132°18.8'E, 6-7m depth, 1.v.1982 (stn CP33).

SUBSTRATE AND DEPTH RANGE

Restricted to shallow coastal waters, ranging from intertidal to 19m depth. Substrate predominantly rock or coral rubble, and the sponge is most abundant in areas where there are relatively light loads of sediment.

GEOGRAPHICAL DISTRIBUTION

Northwestern Australian waters (Fig. 5D). Lévi (1983) suggested that *C. stipitata* also occurs in the lagoon off Noumea, New Caledonia, but it is possible that he was referring to the new species described below from the Great Barrier Reef, *Cymbastela coralliophila* sp.nov.

DESCRIPTION

Shape: Stalked, cup-shaped growth form, usually with thick, uneven, crenellated margins, smooth interior surface, mostly smooth exterior surface of vase, but often with lateral growths and projections on exterior surface. Growth variants common, sometimes with 2-4 concentric, successively smaller cups growing inside each other, with or without buttressed exterior projections near base. Margins and stalk typically relatively thick, up to 14mm and 32mm maximum widths, respectively. Although growth variants may occur within metres of each other, specimens tend to be thinner, more elongate (more vasiform), and less convoluted with increasing depth (Figs 3A,B).

Surface features: Oscules not visible optically, although small, evenly distributed pores (0.8-1.8mm diameter) seen under higher magnification, usually situated on points of surface conules. In some cases distribution of pores coincides with distribution of parasitic barnacles (*Acasta* sp.), whereas other openings appear to be true inhalant or exhalant pores.

Colour: Live colouration clearly dependent on well-being of resident algal symbionts - variations in pigmentation related to degree of shading, water depth and water clarity. Typical live colouration of intertidal specimens olive-green on margins (Munsell 2.5GY 5/4), olive-green with maroon-brown tinge on inside of vase (5GY 4/4-2.5R 4/2), maroon-brown on exterior of vase and stalk (2.5R 4/4). Subtidal specimens typically evenly pigmented olive-brown or olive-maroon (2.5-10R 3/2). Heavily shaded, damaged specimens or material from waters with exceptionally high turbidity may be completely beige (i.e. without pigments).

Texture: Consistency always stiff, firm, but flexible, with roughened, sand-paper texture produced by spicules protruding slightly from dermal skeleton. Surface always optically smooth, microscopically hispid and microconulose, frequently raised into regular or irregular ridges or rounded digitate projections.

Ectosome: No specialized skeleton on surface, but with prominent, relatively closely meshed, diverging plumose brushes of choanosomal oxeas protruding through ectosome for short distances (up to 150μm maximum), producing microscopic surface conules. Subdermal skeleton more-or-less plumose, with more closely meshed multispicular skeletal tracts than on ectosome. Tracts may or may not be interconnected by paucispicular transverse fibres, but usually hidden by diverging spicules (Figs 4, 5B-C).

Choanosome: Axial skeleton compressed, composed of very close-meshed plumose or vaguely plumo-reticulate multispicular fibres, mostly running longitudinally along core of lamellae, occupying majority of lamella diameter. Only few interconnecting uni- or paucispicular tracts observed at core, but these mostly obscured by close-meshed reticulation. Disjunction between longitudinally orientated axial skeleton and vertically disposed extra-axial skeleton only noticeable very close to periphery. Choanosomal fibres lightly invested with spongin, with few extra-fibre megascleres. Mesohyl matrix lightly reinforced with collagen, with abundant microalgae scattered throughout.

Spicules (refer to Table 1 for dimensions): Megascleres unmodified oxeas, symmetrical, thick, curved centrally, with mostly fusiform sharply pointed ends, sometimes with very slightly telescoped points but this feature never as well developed as in other species. Structural megascleres coring fibres slightly larger than those scattered between fibres (Fig. 5A).

ASSOCIATIONS

With the exception of a few specimens from very turbid waters, which may have shed their algal symbionts, most specimens of *C. stipitata* contained cyanobacteria (blue-green algae), dispersed evenly throughout the sponge mesohyl. Only rarely were these symbionts seen inside spongin fibres. The olive-green, olive-brown sponge pigmentation, characteristic of this species, may be a photosynthetic by-product of these symbionts: the several shallow water specimens tested were chlorophyll positive (as demonstrated by acetone extracts of tissues). Parasitic barnacles of the genus *Acasta* are also common within this sponge.

REMARKS

This species is immediately differentiated from other tropical Australasian *Cymbastela* species by the emphasis of its plumose skeletal architecture over other skeletal components. In other species the reticulate connections within the skeleton are more obvious, and overall skeletal architecture is predominantly plumo-reticulate, but in *C. stipitata* the reticulate component of the skeleton is masked slightly by the dense plumose tracts. In this regard the species is most similar to *C. marshae* sp.nov. from the Houtman-Abrolhos Is, WA, which has much smaller spicules (Table 1). In some respects it also resembles the northwestern Australian *C. vespertina*, which is found in deeper, less turbid waters. The latter species, however, has much thinner lamellae and is usually evenly pigmented maroon-brown to purple-grey alive. *Cymbastela stipitata* is contrasted further with other species below.

Cymbastela vespertina sp.nov.

(Figs 6-8, Table 1)

Pseudaxinyssa n.sp.; Hooper et al., 1992: Table 1, Fig 3b.

MATERIAL EXAMINED

HOLOTYPE: NTM Z3939 (fragment QM G300010): N side of Cumberland Strait, Wessel Is, NT, 11°27.6'S, 136°28.7'E, 32m depth, 15.xi.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-028). PARATYPES: NTM Z2615: East Point Aquatic Life Reserve, Darwin, NT, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986, coll. J.N.A. Hooper, SCUBA (stn EP28). QM G300002 (fragment NTM Z3948): S of W headland, Rimbija I., Cape Wessel, Wessel Is, NT, 11°0.5'S, 136°43.8'E, 15m depth, 16.xi.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-030).

OTHER MATERIAL: (All material collected by the author unless otherwise indicated). NORTHWEST SHELF REGION, WA: NCI Q66C-1323-F (fragment NTM Z3470): Offshore from Norcape Lodge, Learmonth, Exmouth Gulf 21°56.6'S, 114°09.1'E, 6m depth, 17.viii.1988, coll. NCI, SCUBA. DARWIN REGION, NT: NTM Z2696: East Point Aquatic Life Reserve, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986, coll. J.N.A. Hooper, SCUBA (stn EP28). NTM Z2699: East Point Aquatic Life Reserve, 12°24.5'S, 130°48.0'E, 9-12m depth, 3.iv.1986 (stn EP28). ARAFURA SEA, NT: NTM Z3069, NCI-Q66-0519-F: Parry Shoals, 11°11.72'S, 129°43.26'E, 16m depth, 12.viii.1987, coll. A.M. Mussig, SCUBA (stn AM 87-2). WESSEL ISLANDS, NT: NCI Q66C-4828-O: S of W headland, Rimbija I., Cape Wessel, 11°0.5'S, 136°43.8'E, 15m depth, 16.xi.1990, coll. NCI, SCUBA (stn JH-90-030).

SUBSTRATE AND DEPTH RANGE

Patch rock reef, fringing coral reef, or rock heads, sandy bottom over hard corals, gorgonians, sponges and algae, in areas of strong current; 6-32m depth range.

GEOGRAPHICAL DISTRIBUTION

Northwest coast of Australia, from Exmouth Gulf to Wessel Islands (Fig. 8C).

ETYMOLOGY

Latin, *vespertinus*, western, or of the evening; for the west Australian coastal distribution of this species.

DESCRIPTION

Shape: Thin-walled, lamellate, cup shaped sponges, 95-190mm high, 70-170mm maximum diameter, lamellae 2-4.5mm thick. Lamellae typically do not rejoin completely, usually producing asymmetrical cups. Apical margins of lamellae usually even, but larger specimens may consist of 2-4 concentric cups, with lamellae forming spiral walls. Sponges attached to substrate by large, flat basal plates, up to 55mm maximum diameter, with

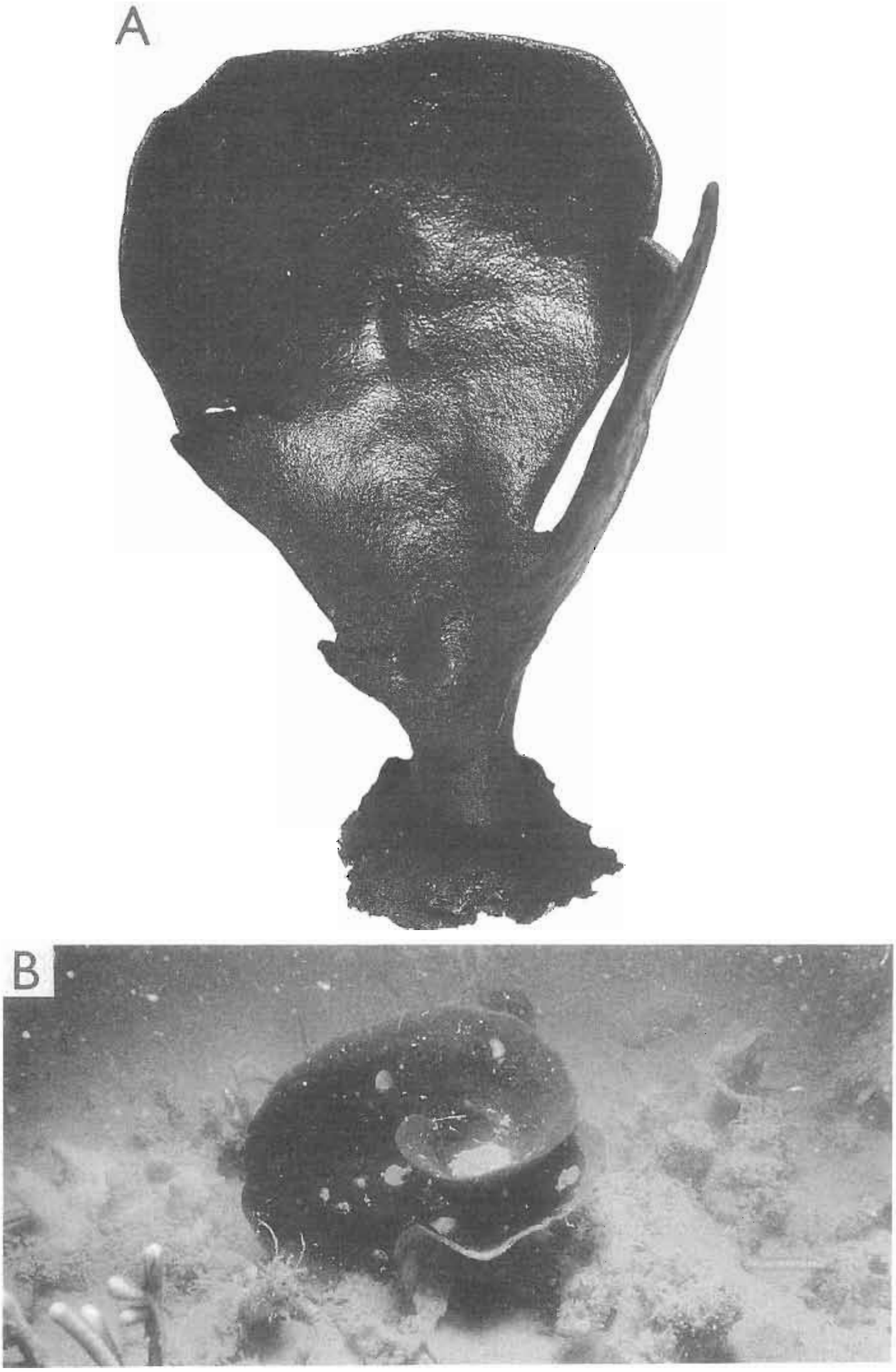
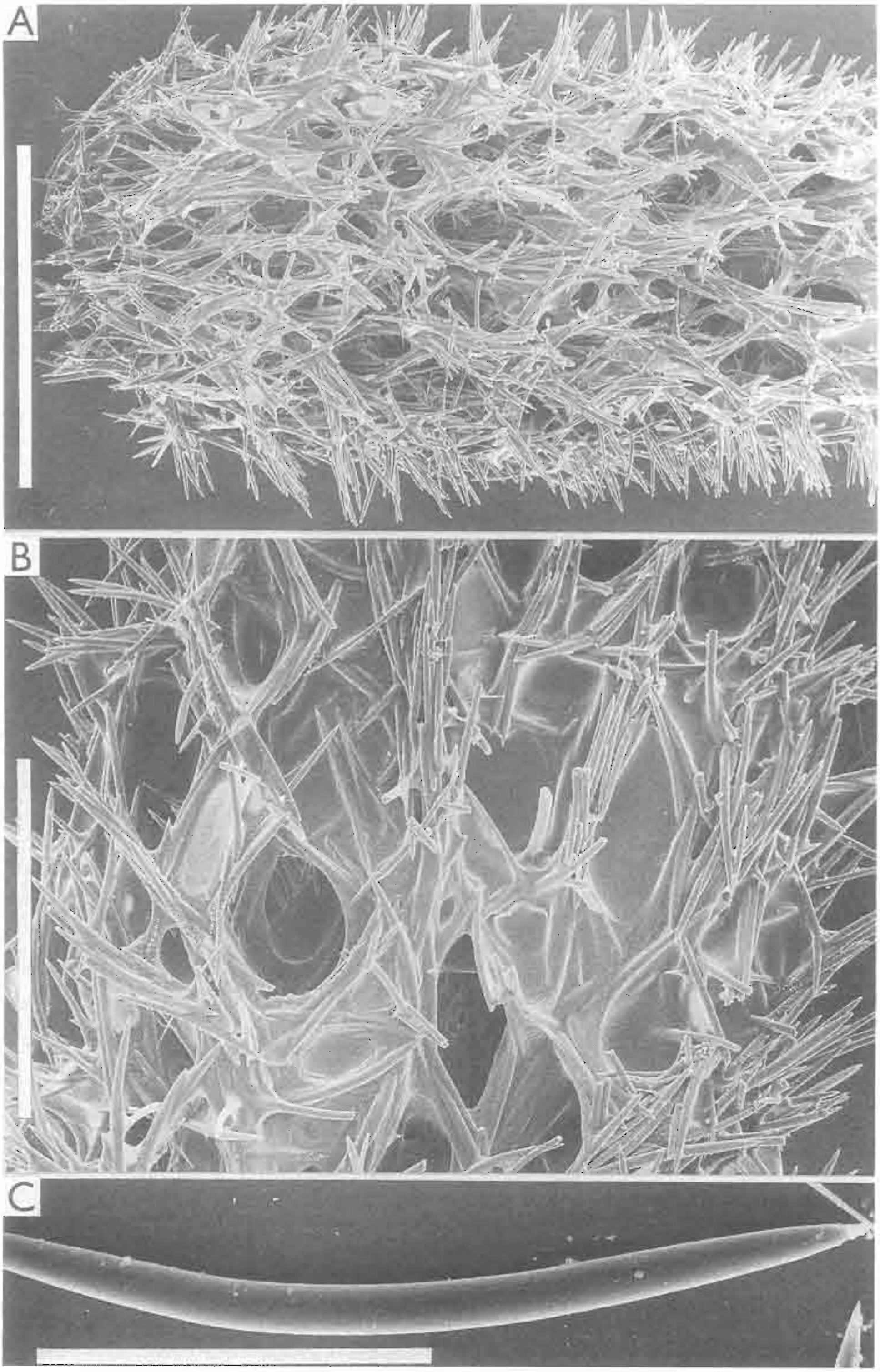


FIG. 6. *Cymbastela vespertina* sp.nov. A, holotype (NTM Z3939). B, paratype (NTM Z2615), in situ.


A
B
C

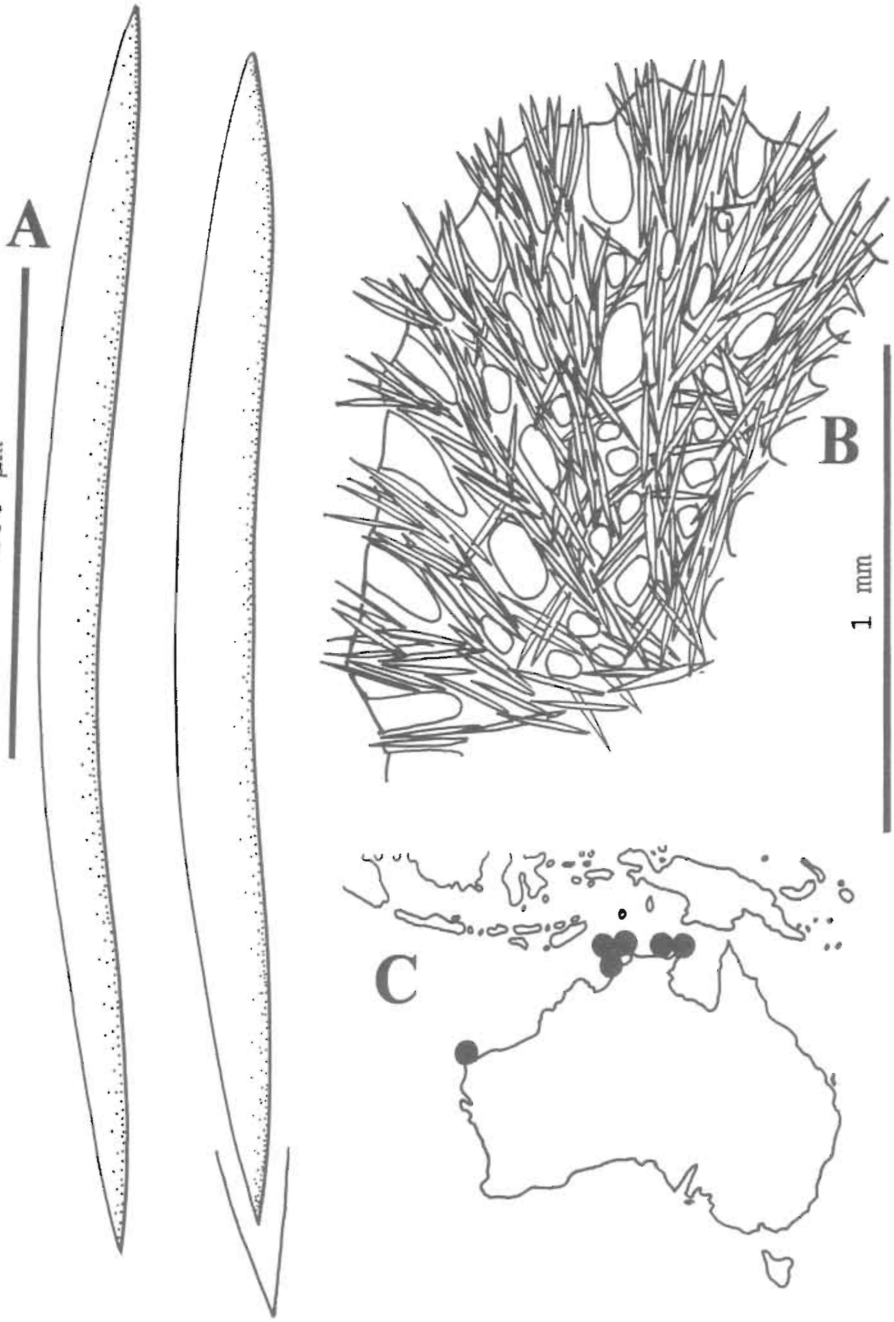


FIG. 8. *Cymbastela vespertina* sp.nov. (holotype NTM Z3939). A, spicules. B, section through peripheral skeleton. C, known distribution.

FIG. 7. *Cymbastela vespertina* sp.nov. (paratype QM G300002). SEMs of skeleton showing: A, section through lamella (scale=1mm); B, slightly compressed plumo-reticulate axial arrangement (scale=500µm); C, oxeas and terminations (scale=100µm).

short, thick stalk, 14-36mm long, 14-28mm diameter (Fig. 6A,B).

Surface features: Smooth, even, uninterrupted by any surface processes. Microscopically surface with minute conules. Oscules not seen, but small evenly distributed pores, up to 0.8mm diameter, scattered over surface of lamellae.

Colour: Live colouration dark maroon brown (Munsell 2.5R 4/4) to greyish purple (5R 5/2), always evenly pigmented, whereas in ethanol colour usually dark brown or dark grey.

Texture: Firm, slightly compressible texture, sandpaper-like to touch.

Ectosome: Membraneous, without specialised spiculation, but with regularly spaced plumose brushes, composed of 3-8 oxeas, from ascending extra-axial tracts, protruding through surface for short distances, up to 100μm from ectosome. Position of plumose spicule brushes on surface coincides with minute surface conules. Subectosomal region predominantly plumose, slightly plumo-reticulate, with ascending plumose portion of skeletal tracts greatly emphasised over uni- or paucispicular reticulate, transverse, connecting tracts. Spongin fibre mesh size in peripheral skeleton up to 140μm diameter, more open than in axial region (Figs 6,7).

Choanosome: Skeleton slightly axially compressed, plumo-reticulate, with plumose component emphasized only slightly over reticulate component of skeleton: former consisting of multispicular ascending tracts, latter with paucispicular, connecting tracts, both enclosed within spongin fibres (Fig. 8B). Spongin fibres light but well developed, with small mesh sizes, up to 90μm maximum diameter. Mesohyl with moderate quantities of brown-pigmented collagenous spongin, and only few spicules dispersed outside fibres. Choanocyte chambers oval, 28-90μm diameter.

Spicules (refer to Table 1 for dimensions): Megascleres oxeas without any modifications, relatively long, slender, slightly curved centrally, tapering to sharp fusiform points, with very few examples bearing telescoped points (Fig. 8A).

ASSOCIATIONS

This species is usually associated with symbiotic microalgae (cyanobacteria) in shallow water (i.e. is chlorophyll positive), and the symbionts are probably responsible for producing the characteristic dark purple-mauve live pigmentation, although one specimen (Z3939) was pale beige in situ and may have shed its algae. Parasitic barnacles are rare.

REMARKS

This species was originally thought to be merely a modified, deeper-water form of *C. stipitata*, as there are similarities in skeletal architecture and spicule dimensions. However, morphological differences described above, particularly the asymmetrical cup shape, the very thin lamellae and darker pigmentation, and differences in free amino acid profiles between *C. vespertina* and *C. stipitata* (Hooper et al., 1992), indicate that these two sympatric populations are heterogenous and sibling species.

Cymbastela concentrica (Lendenfeld) comb.nov. (Figs 9-11, Table 1)

Antherochalina concentrica Lendenfeld, 1887:788, pl.22, fig.42.

MATERIAL EXAMINED

LECTOTYPE (here designated): AM Z1993: Port Molle (now Airlee Beach), Qld, 20°13'S, 148°49'E, no other collection details known. (cf. published locality of St Vincent Gulf, South Australia). PARALECTOTYPES: BMNH 1886.8.27.451, 460: same locality.

OTHER MATERIAL. QUEENSLAND - NTM Z3169 (fragment QM G300009): Outer slope of reef front, Blue Lagoon, Lizard I., Great Barrier Reef, 14°40'S, 145°48'E, 10-20m depth, 1987, coll. A.W.D. Larkum (ref.no. PC 348T, PC 346). QM G300003: Inner Gneerings, Moreton Island, 26°38.5'S, 153°09.5'E, 14m depth, 01.v.1991, coll. Thorogood, JA, SCUBA (ref.JT-8).

SUBSTRATE AND DEPTH RANGE

Inshore fringing reefs and coral reef slope, up to 20m depth.

GEOGRAPHICAL DISTRIBUTION

Northern, central and southern Queensland (Fig. 11C).

DESCRIPTION

Shape: Cup- or vase-shaped growth forms, up to 150mm high, 125mm maximum width, consisting of relatively thin (approximately 2mm wide), convoluted, conical lamellae or symmetrical cups on short basal stalk. Stalk length up to 45mm long, 25mm diameter. Lamellae may produce concentric whorls inside cup, or merely contain a few irregular bumps; margins of lamellae slightly convoluted (Fig. 9A-C).

Surface features: Lamellae smooth, slightly irregular, with low conules and ridges on exterior surface, more even interior surface; no buttresses or external processes.

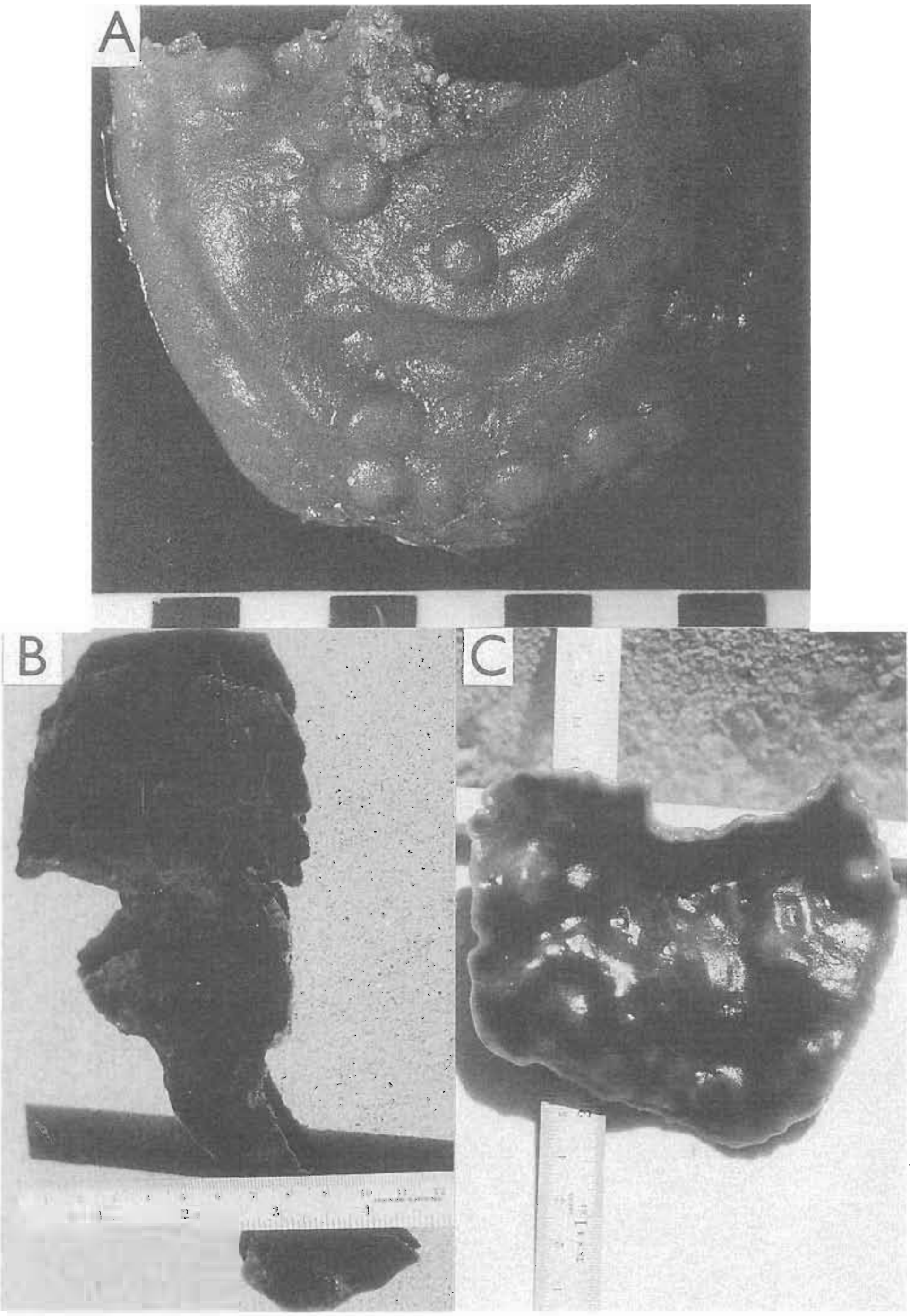


FIG. 9. *Cymbastela concentrica*. A, Paralectotype (BMNH 1886.8.27.451). B, specimen (NTM Z3169; photo A. Larkum). C, field number PC 346, unaccompanied by voucher specimen (photo A. Larkum).

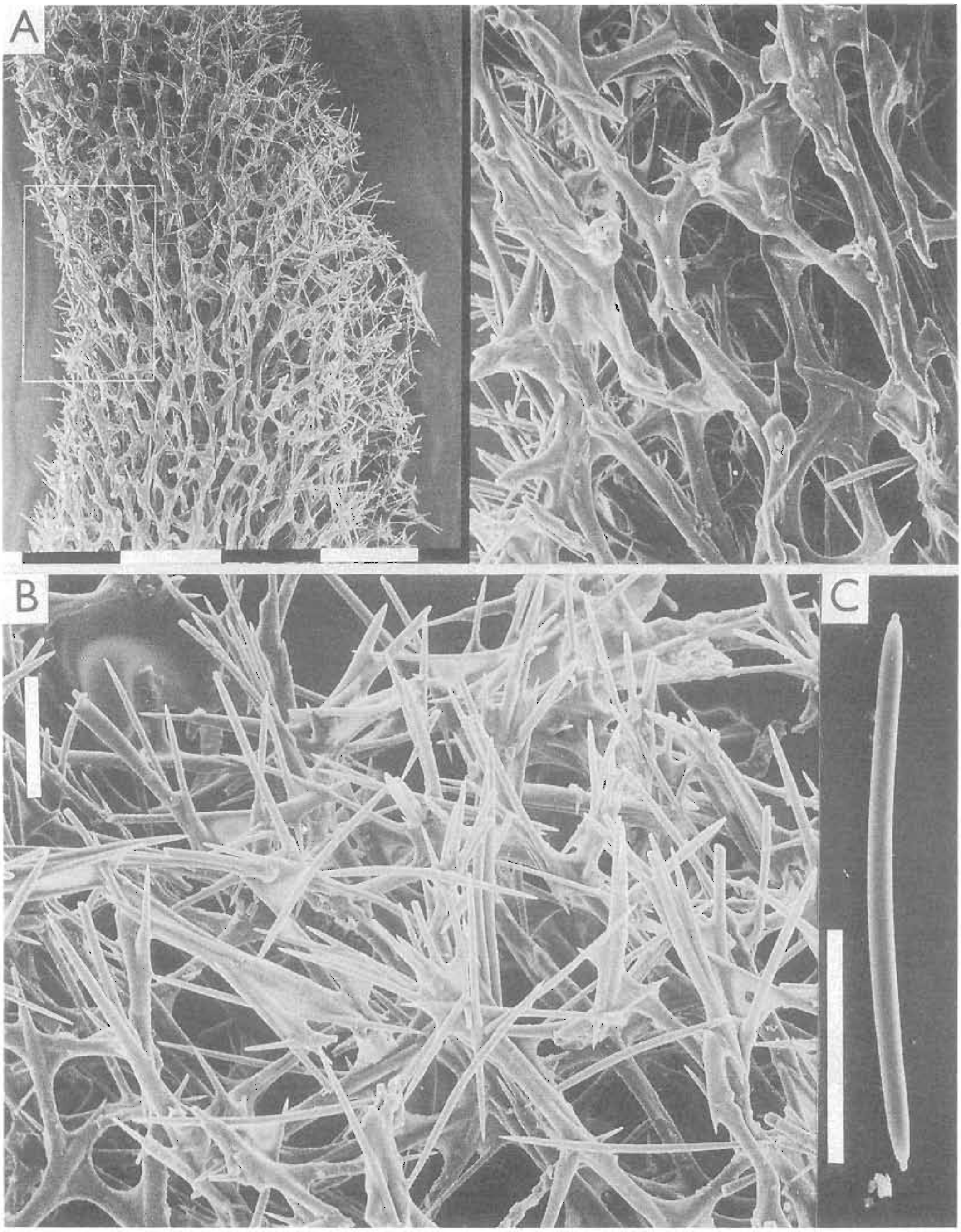


FIG. 10. *Cymbastela concentrica*. A, SEM of skeleton (specimen NTM Z3169) (scale=500µm; left magnified 21.2 times, right magnified 186 times). B, peripheral skeletal architecture (scale=100µm). C, spicule with telescoped ends (lectotype AM Z1993) (scale=50µm).

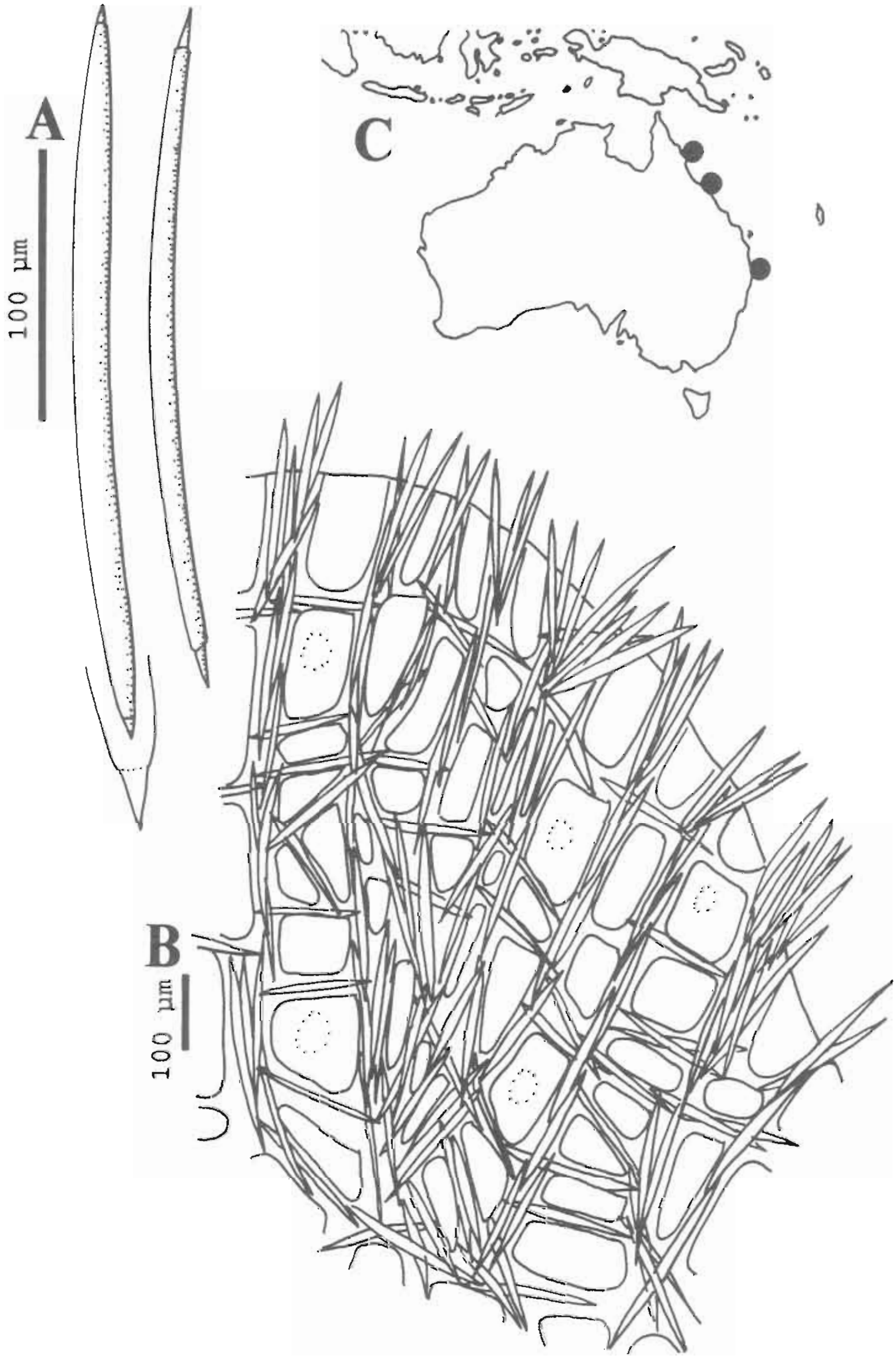


FIG. 11. *Cymbastela concentrica*, lectotype (AM Z1993). A, spicules. B, section through peripheral skeleton. C, known distribution.

Colour: In life, dark brown (interior) (Munsell 5YR 3/2) or olive brown (exterior) (2.5YR 4/4). Chlorophyll pigments abundant (seen in acetone extracts of freshly preserved material), due to presence of large population of cyanobacteria (microalgal) symbionts.

Texture: Smooth, stiff and flexible consistency, with a slightly velvet surface texture.

Ectosome: Optically smooth, lacking specialized skeleton, but microscopically villose, with substantial portions of spicule from peripheral skeleton protruding through surface and forming plumose brushes. Spicules protrude up to 230µm from surface, and brushes may contain up to 8 spicules (Figs 10, 11B). Microalgae, seen in fresh material, appear to be concentrated near periphery of skeleton.

Choanosome: Skeletal architecture plumo-reticulate, with poorly differentiated axial and extra-axial skeletal regions - reticulate skeleton emphasised over plumose portion (Figs 10, 11B). Central region of choanosomal skeleton only slightly axially condensed, predominantly reticulate, with plumose paucispicular ascending tracts curving gradually towards surface, interconnected by uni- or paucispicular transverse tracts, whereas peripheral skeleton more clearly diverges into plumose ascending multi- or paucispicular tracts, interconnected by uni- or paucispicular transverse tracts. Spongin fibres and spicule tracts, 40-60µm wide in axis, become less heavily cored and more widely spaced towards periphery, 20-40µm wide, ultimately forming distinctive plumose dermal brushes. Spongin fibres (22-60µm wide) lightly developed, nearly fully cored by megascleres, producing ovoid to eliptical meshes (42-77µm, 60-185µm wide in axial and extra-axial regions respectively). Collagen abundant in mesohyl but very lightly pigmented. Choanocyte chambers oval to elliptical, 45-150µm diameter.

Spicules (refer to Table 1 for dimensions): Variable length, relatively, slender, fusiform oxeas, moderately curved at centre, usually with very faintly telescoped points (Fig. 11A).

ASSOCIATIONS

Cyanobacteria were only seen in freshly preserved material, not in the type material, and appears to be concentrated mainly in the peripheral skeleton.

REMARKS

Lendenfeld (1887) states that *C. concentrica* was originally collected from St Vincent Gulf, South Australia, whereas both the AM and BMNH registers, and the specimen labels with the type material, indicate that the collection locality was Port Molle, Queensland. Although the exact type locality of this species will always be doubtful, the new record of the Queensland material described here from Lizard and Moreton Is suggests that the Museum register notations may be correct. According to Burton (1934:558), and notes in the BMNH register (in M. Burton's handwriting), this species has some similarities with *Phakellia flabellata* (Carter) from southern Australia. However, the skeletal architecture and spiculation of *C. concentrica* is quite different from that of *Phakellia*, and the two species are regarded as convergent in these two superficially prominent features.

The redescription presented above differs slightly from the description given by Lendenfeld (1887), who recorded oxea dimensions of 130x5µm. In this regard his description conforms more closely to the new specimens described above than to the type material (Table 1). Apart from their smaller spicule dimensions these two specimens are identical to the type material in growth form, including lamellae thickness and surface features, skeletal architecture, spicule-spongin fibre structure and spicule geometry, and it is suggested here that all five specimens of *C. concentrica* described above are conspecific. However, the existence of these two anomalous specimens casts some doubt over the accuracy of absolute spicule dimensions as a useful diagnostic character within this genus (see Fig. 24), suggesting that spicule size may vary with latitudinal distribution.

Cymbastela concentrica is similar to most of the other lamellate Australasian *Cymbastela* species in a number of features. Many species contain symbiotic algae (i.e. are chlorophyll positive), they all have a thin, lamellar, plate-like, cup- or vase-shaped growth form, with well developed spongin fibres, and a more-or-less slightly condensed plumo-reticulate axial skeleton, plumose or plumo-reticulate extra-axial skeleton, and if present, a plumose ectosomal skeleton. Species appear to differ substantially only in spicule dimensions, spicule geometry (presence or absence of telescoped points, and possession of hastate or fusiform points), and the degree to which the skeleton is organized into axial and extra-axial sections. For example, *C. stipitata* (from inshore waters of northern Australia) has larger megascleres, spicules are only rarely terminated by telescoped points, and there is a more obvious differentiation between the axial and extra-axial regions of the skeleton, including a more condensed axial core, and an emphasis on the plumose portion of the skeleton. *Cymbastela cantharella* from the outer reefs of New Caledonia also has a stalked lamellar growth form, slightly differentiated axial and extra-axial skeletons, but it has distinctive orange, yellow-orange live colouration, and relatively slender oxeas. In contrast, *Cymbastela concentrica* has a relatively poorly differentiated axial and extra-axial skeleton, only slightly condensed choanosomal axis with emphasis on the reticulate extra-axial portion of the skeleton. This takes the form of a plumo-reticulate extra-axial skeleton, a plumose ectosome, and oxeas which are similar in size to those of *C. cantharella*.

Cymbastela cantharella (Lévi)
(Figs 12-14, Table 1)

Pseudaxinyssa cantharella Lévi, 1983:719-722, fig.1, pl.1.

MATERIAL EXAMINED

HOLOTYPE: MNHN LBIM DCL3141: Outer reef, SW coast New Caledonia, 40m depth, no other details known.

OTHER MATERIAL: NTM Z3869: Precise locality unknown, Noumea lagoon, SW coast, New Caledonia, 22°20'S, 166°13'E, 25m depth, coll. ORSTOM, SCUBA (ref. R1261). NTM Z3872 (fragment QM G300004): Exterior of Grand Recif Mbere, off Noumea, New Caledonia, 22°20'S, 166°13'E, 30m depth, 21.ix.1990, coll. J.N.A. Hooper, SCUBA (stn JH-90-018).

SUBSTRATE AND DEPTH RANGE

Slope and ledges near base of barrier reef, dead coral and silt substrates, 15- 75m depth.

GEOGRAPHICAL DISTRIBUTION

Known only from the New Caledonia region (Fig. 14C).

DESCRIPTION

Shape: Short, erect cup-shaped or semi-vasiform lamellae, 80-150mm high, up to 170mm maximum diameter, on short stalk, 30-40mm long, 10-17mm diameter, with thin lamellate walls, 3-6mm diameter, usually with convoluted margins, occasionally with secondary cups or lamellae growing inside primary cup, often with buttresses and secondary projections (Fig. 12A).

Surface features: Surface of lamellae predominantly smooth, although distinct differences between interior (inhalant) and exterior faces of cups exist. Exterior of lamellae microscopically smooth, optically uneven, interior of cup with numerous small oscules, 0.5-2mm diameter, each surrounded by slightly raised membraneous lip (Fig. 12B). Oscules approximately 2mm apart, throughout interior surface of lamellae producing concentric striations within interior of cup.

Colour: Pale orange alive (Munsell 2.5-7.5 YR 8/10), beige in ethanol.

Texture: Firm, flexible, slightly compressible; exterior of lamellae with sandpaper like texture, interior more compressible.

Ectosome: Membraneous, without specialised skeleton, with heavy layer of slightly darker collagen, up to 80µm wide, through which choanosomal oxeas protrude for about half their length. Projecting oxeas occur individually or in paucispicular plumose bundles, regularly dispersed across surface, arising from ascending radial tracts in peripheral skeleton (Figs 13, 14B).

Choanosome: Choanosomal skeleton plumo-reticulate, without axial compression or any noticeable differentiation between axial and extra-axial regions, apart from plumose ectosomal spicules (Fig. 14B). Two components of skeleton predominant: first, radial spongin fibres, cored by multispicular tracts of oxeas, run longitudinally through lamellae, and gradually ascend to surface, becoming plumose and diverging near periphery; second, radial fibres interconnected by uni- or paucispicular tracts of oxeas, only weakly organised as a reticulum. The skeleton in places is almost halichondroid (Fig. 13). Spongin fibres only lightly invested in spongin, up to 75µm diameter, forming elongate or rectangular meshes, up to 125µm diameter, with small oval choanocyte chambers, 25-40µm diameter. Mesohyl heavily reinforced with collagen and containing scattered small (possibly juvenile) spicules.

Spicules (refer to Table 1 for dimensions): Oxeas relatively short, slender, slightly curved at centre, occasionally asymmetrical, tapering, fusiform, sharply pointed but usually with very slightly telescoped points at absolute apex of spicule (Fig. 14A).

ASSOCIATIONS

No symbiotic cyanobacteria were seen in any of the three specimens examined.

REMARKS

Cymbastela cantharella is apparently unlike all other species of the genus in that it contains a number of biologically active metabolites (Lévi, 1983, and pers.comm.), although the nature of this chemical activity is not yet published. It also differs from other tropical species in lacking any evidence of symbiotic microalgae, and in this respect it is similar to the two temperate species described here. *Cymbastela cantharella* has other features typical of the genus, especially growth form - being thinly flabellate with irregular, buttressed surface processes similar to those seen on *C. stipitata*, and the geometry of the oxeas is also similar in these two species. However, the New Caledonian species differs from other *Cymbastela* in external colouration (orange alive, possibly due to the lack of photosynthetic pigments found in other tropical species), prominent surface sculpturing on the oscular face of cups, skeletal architecture (having a dense radial-plumose skeleton, with a secondary paucispicular secondary reticulate skeleton, with an overall nearly-halichondroid appearance, and radial-plumose ectosomal skeleton), and specific dimensions of oxeas (Table 1).

Cymbastela coralliophila sp.nov.
(Figs 15-17, Table 1)

Pseudaxinyssa sp.; Wilkinson, 1983:411.

Pseudaxinyssa n.sp.; Bergquist et al., 1980:424, Table 1; Lévi, 1983:720.

MATERIAL EXAMINED

HOLOTYPE: NTM Z4038: S side of Blanchard Reef, Qld, 13°23.4'S, 143°44.4'E, 14m depth, 12-xii-1990, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-90-054).

OTHER MATERIAL: GREAT BARRIER REEF, QLD - FAR NORTHERN SECTION: NTM Z4039: S side of Blanchard Reef, 13°23.4'S, 143°44.4'E, 14m depth, 12-xii-1990, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-90-054). NCI Q66B-2242-Y: W side Canoe I., 10°20.6'S, 142°06.4'E, 4m depth, 6.v.1987, coll. NCI, SCUBA. - CAIRNS SECTION: NTM Z3165, 3166, 3167, 3168 (fragments): Outer slope, reef front, Blue Lagoon, Lizard I., 14°40'S, 145°28'E, 10-20m

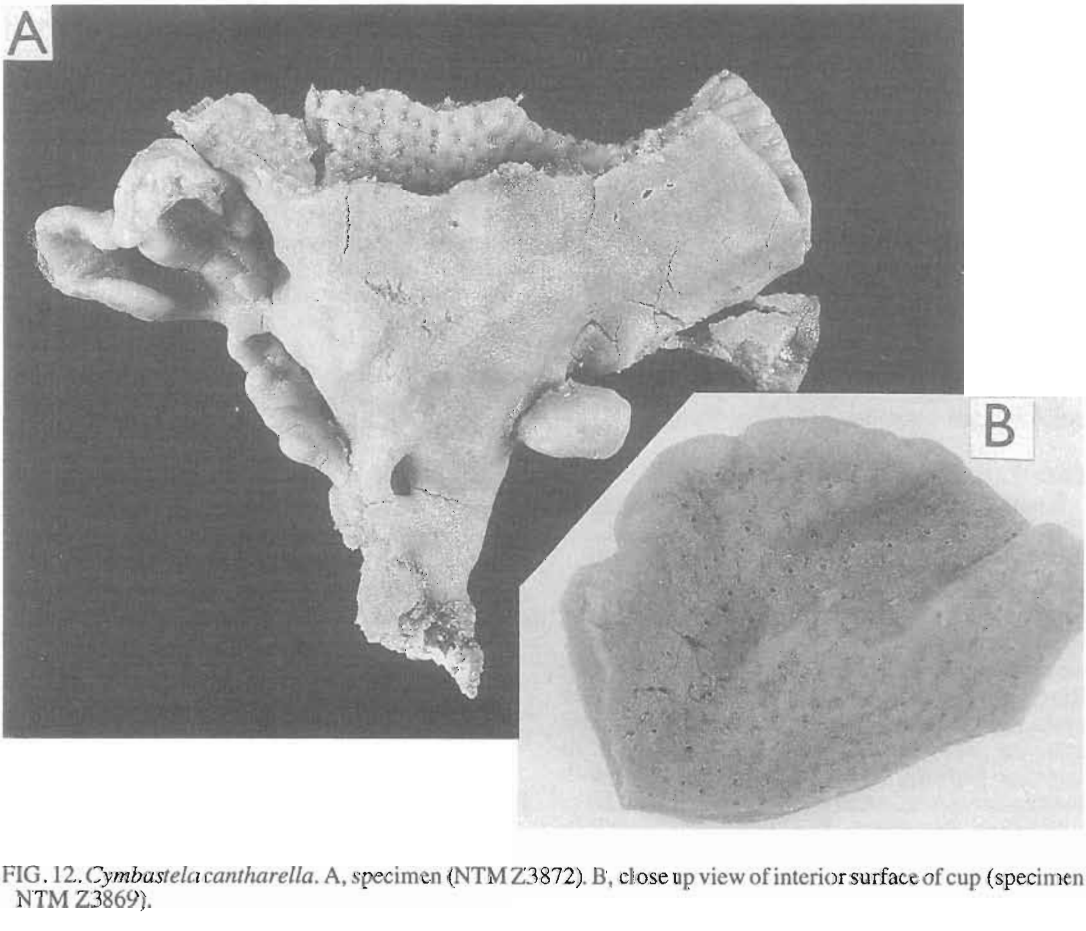


FIG. 12. *Cymbastela cantharella*. A, specimen (NTM Z3872). B, close up view of interior surface of cup (specimen NTM Z3869).

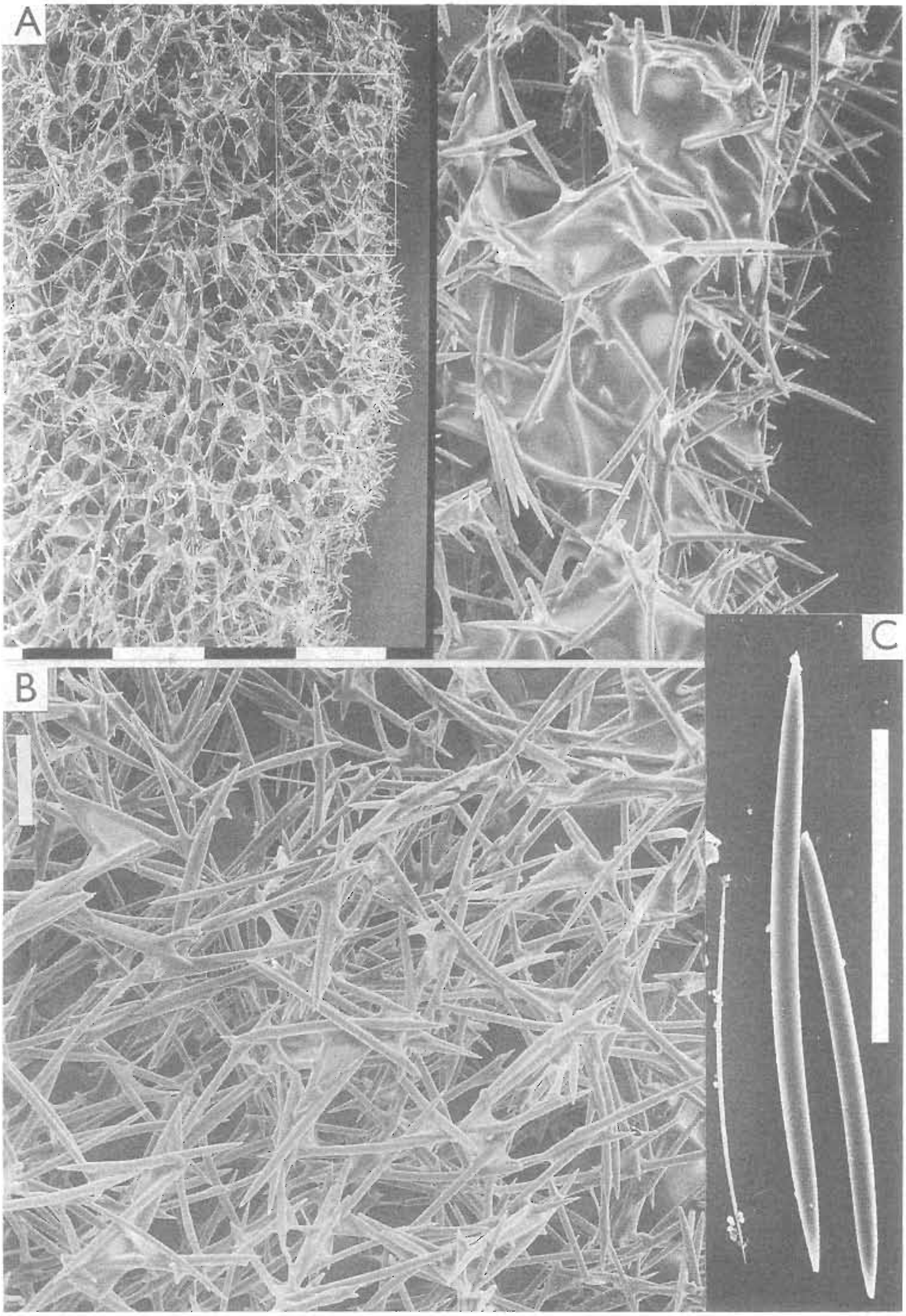


FIG. 13. *Cymbastela cantharella*. A, SEM of skeleton (specimen NTM Z3872) (scale=500μm; left magnified 106 times, right magnified 566 times). B, peripheral skeletal architecture (scale=100μm). C, oxeas, including juvenile form (specimen ORSTOM RA1279) (scale=100μm).

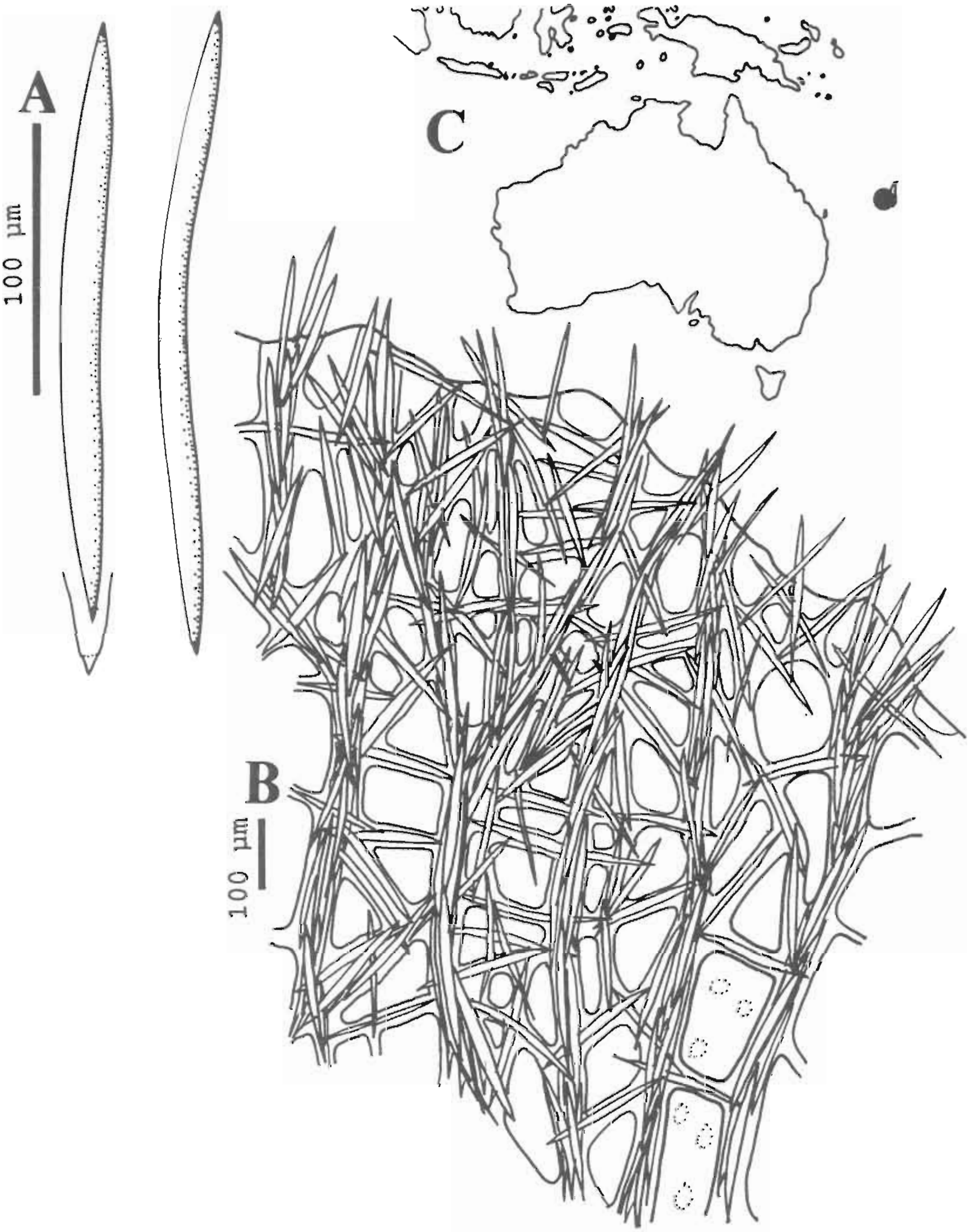


FIG. 14. *Cymbastela cantharella*, specimen (NTM Z3872). A, spicules. B, section through peripheral skeleton. C, known distribution.

depth, 1987, coll. A.W.D. Larkum et al. (ref. PC341T, PC342T, PC344T, PC345T, respectively). NCI Q66C-0260-W: N end Bowden Reef, off Townsville, 19°2.06'S, 147°55.89'E, 14m depth, 3.ii.1987, coll. NCI, SCUBA. - CENTRAL SECTION: AIMS RA3-PR (fragments NTM Z2735, QM G300012): Davies Reef, Townsville region, 18°50'S, 147°39'E, depth unknown, 17.viii.1982, coll. C.R. Wilkinson (stn Don.214). - CAPRICORN SECTION: NCI Q66C-1766-L (fragments NTM Z3509, QM G300008): 100m NW of small rocky point at embayment edge, NW Brampton Island, Whitsunday Islands Group, Mackay region, 20°48.0'S, 149°15.0'E, 12m depth, 07.xi.1988, coll. NCI, SCUBA (stn DON-0272). NCI Q66C-0816-A: W end Deloraine I., Whitsunday Is Group, Mackay region, 20°09'S, 149°04'E, 20m depth, 10.xi.1987, coll. NCI, SCUBA.

SUBSTRATE AND DEPTH RANGE

Coral reef substrates, including lagoon, sloping fringing reef, irregular coral boulders with muddy sand between, gorgonian beds, and also areas of high sedimentation. Depth range extends from subtidal to 20m.

GEOGRAPHICAL DISTRIBUTION

Northern, central and southern sections of the Great Barrier Reef, Queensland (Fig. 17C).

ETYMOLOGY

The species name refers to the restricted distibution of all material so far described, the sponge being found exclusively on coral reefs.

DESCRIPTION

Shape: Large vase-shaped, cup-shaped or simply lamellate growth forms, usually with large marginal opening, or sometimes nearly flattened completely against substrate, 80-170mm high, up to 350mm maximum marginal diameter. Usually attached to substrate by short stalk, up to 30mm high, 25mm diameter, sometimes lamellae are direct outgrowths of the basal attachment. Lamellae relatively thick, lobate, 8-15mm thick excluding lateral projections (Fig. 15).

Surface features: External, exhalant, surface optically smooth, relatively even, with or without bumps, ridges and lateral growths. Internal, inhalant, surface relatively uneven, often with concentric striations and ridges, or with irregular bumps, lobate growths and depressions on lamella walls, typically with small digitate or lobate projections at centre of cup. Occurrence and development of surface outgrowths, on both interior and exterior surfaces of lamellae is highly variable. Oscules small, 0.5-2mm diameter, dispersed on tips of microconules or ridges on interior surface of cups, subdermal canals visible below slightly translucent ectosome (Fig. 15C-D).

Colour: Live colouration typically mottled olive-brown (Munsell 7.5YR 5/4), olive-green (5Y 6/6) with maroon-brown tinge externally (5R 4/2), green (7.5GY 3/4) or olive-green internally (2.5GY 5/4). Colour in ethanol white or greenish-white.

Texture: Compressible, difficult to tear, rough exterior texture.

Ectosome: Ectosome microscopically hispid, with specialised skeleton. Subectosomal skeleton ascending, plumose, produced by pauci- or multispicular tracts of larger, choanosomal oxeas running at right angles to surface, overlain by specialised ectosomal skeleton of tangential, multispicular brushes made up of smaller ectosomal oxeas. Specialised dermal skeleton markedly plumose, mostly orientated tangentially or paratangentially to surface (Figs 16, 17B).

Choanosome: Choanosomal skeleton with only slight axial condensation, with axial and extra-axial components only slightly differentiated (Fig. 17B). Axial region predominantly radial-plumose, less markedly plumo-reticulate, with skeletal lines mostly directed longitudinally through lamellae, but gradually ascending towards peripheral skeleton; extra-axial skeleton more-or-less radial-plumose, with multispicular ascending spongin fibres interconnected by paucispicular transverse fibres (Fig. 16). Spongin fibres well formed but only very lightly invested with spongin, 75-110μm diameter. Fibre reticulation forms elongate oval to elliptical meshes, 85-350μm diameter, relatively similar in diameter between axial and extra-axial regions; choanocyte chambers relatively large, oval, 90-210μm diameter. Ascending fibres cored by multispicular tracts of larger choanosomal oxeas, whereas transverse fibres uncored or with uni- or paucispicular skeletal lines. Mesohyl matrix reinforced with moderate quantities of collagen. Very thin, smaller oxeas, similar in length to those on surface skeleton are dispersed throughout the mesohyl, possibly juvenile forms of larger choanosomal oxeas.

Spicules (refer to Table 1 for dimensions): Choanosomal oxeas thick, slightly curved at centre, typically symmetrical, occasionally anisoxeote, with hastate-rounded or slightly pointed, usually very faintly telescoped ends. Ectosomal oxeas thin, mostly straight, fusiform, with sharply pointed, rarely telescoped ends (Fig. 17A).

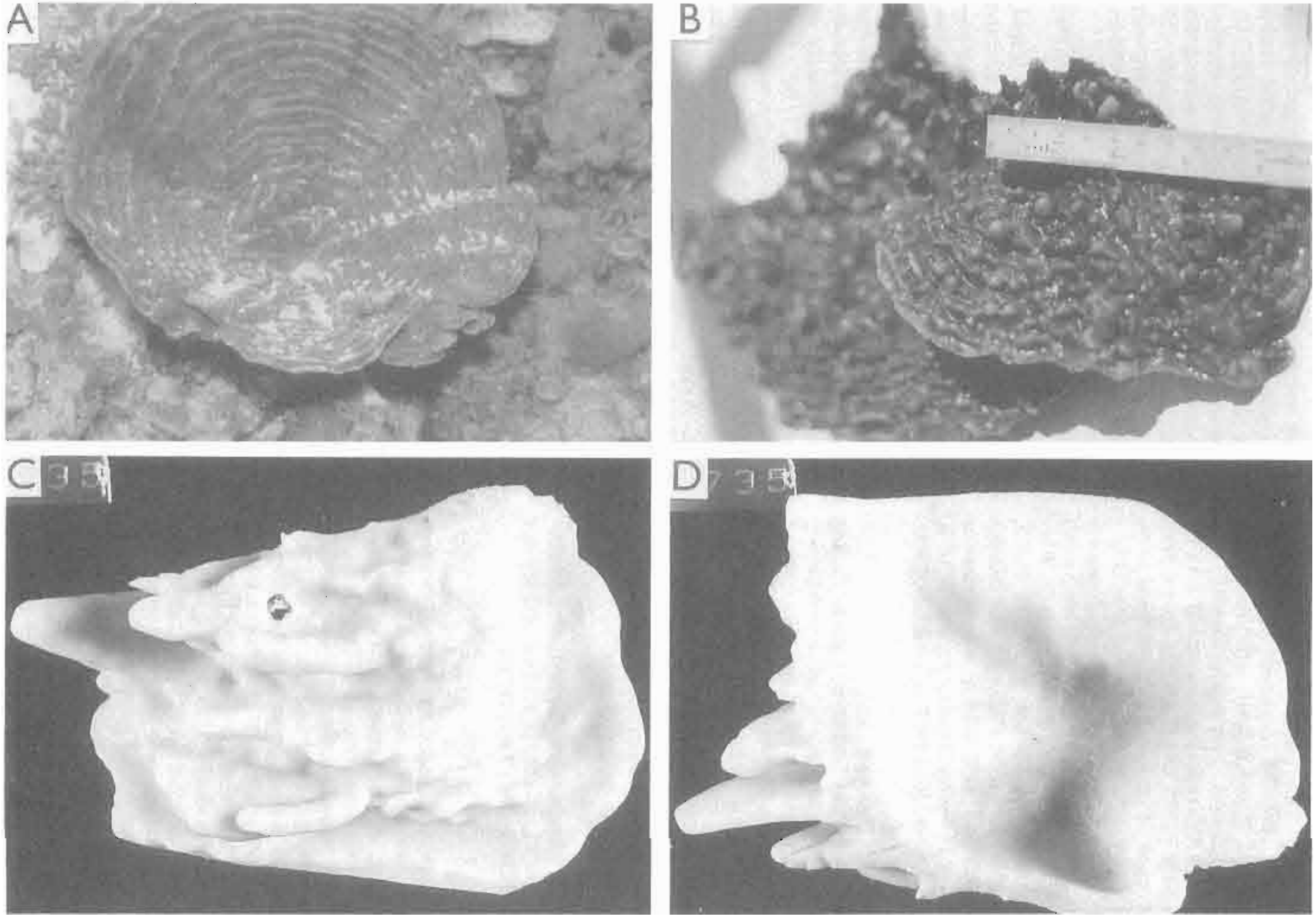


FIG. 15. *Cymbastela coralliophila* sp.nov. A, specimen in situ (NTM Z2735; photo C. Wilkinson). B, specimen (NTM Z3166), showing interior surface of lamellae in live state. C-D, specimen (NTM Z2735), showing close up view of exterior (C) and interior (D) surfaces of lamellae, in preserved state.

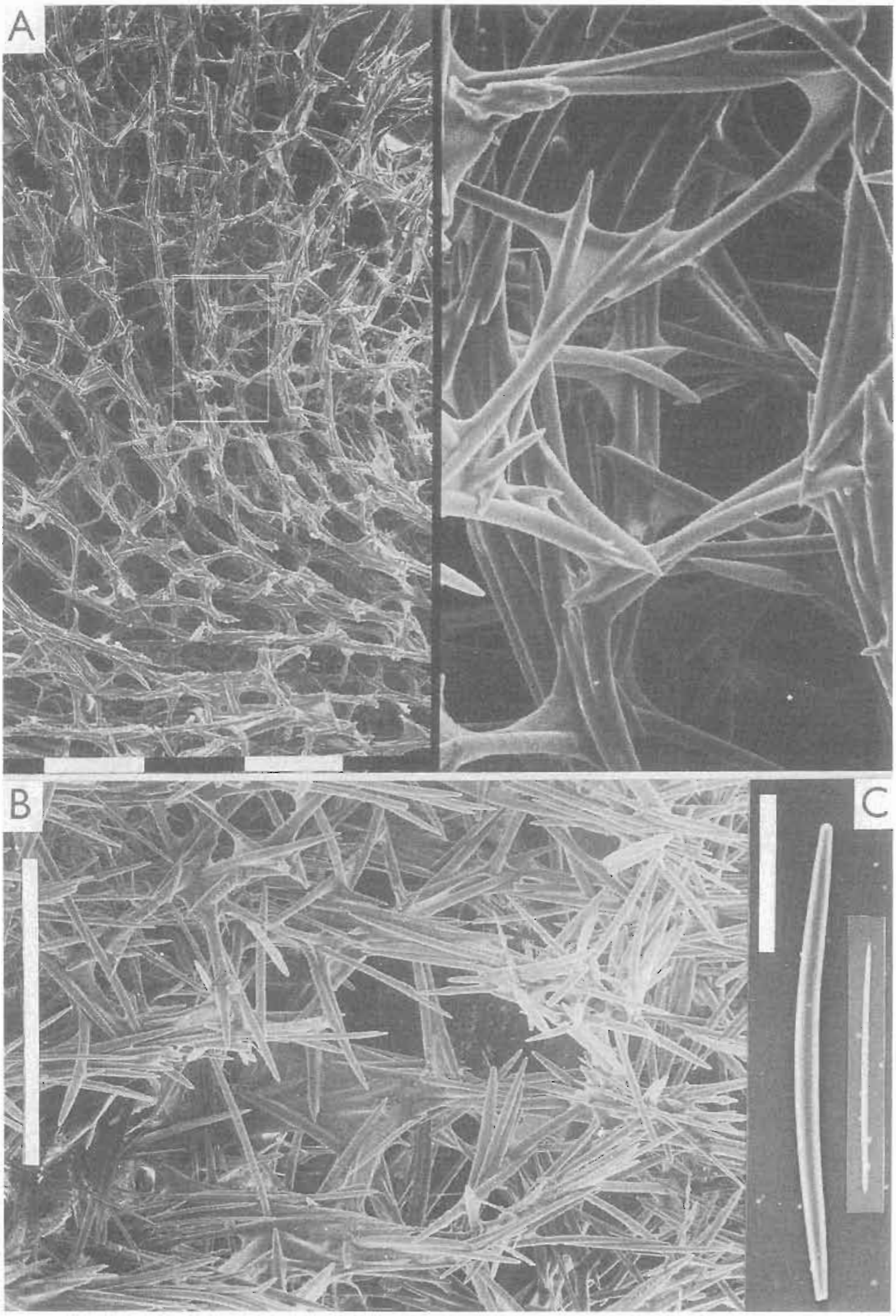


FIG. 16. *Cymbastela coralliophila* sp.nov. A, SEM of skeleton (specimen NTM Z2735) (scale=500μm; left magnified 19.5 times, right magnified 93 times). B, peripheral skeletal architecture (specimen NTM Z3509) (scale=500μm). C, two sizes of spicules (scale=100μm).

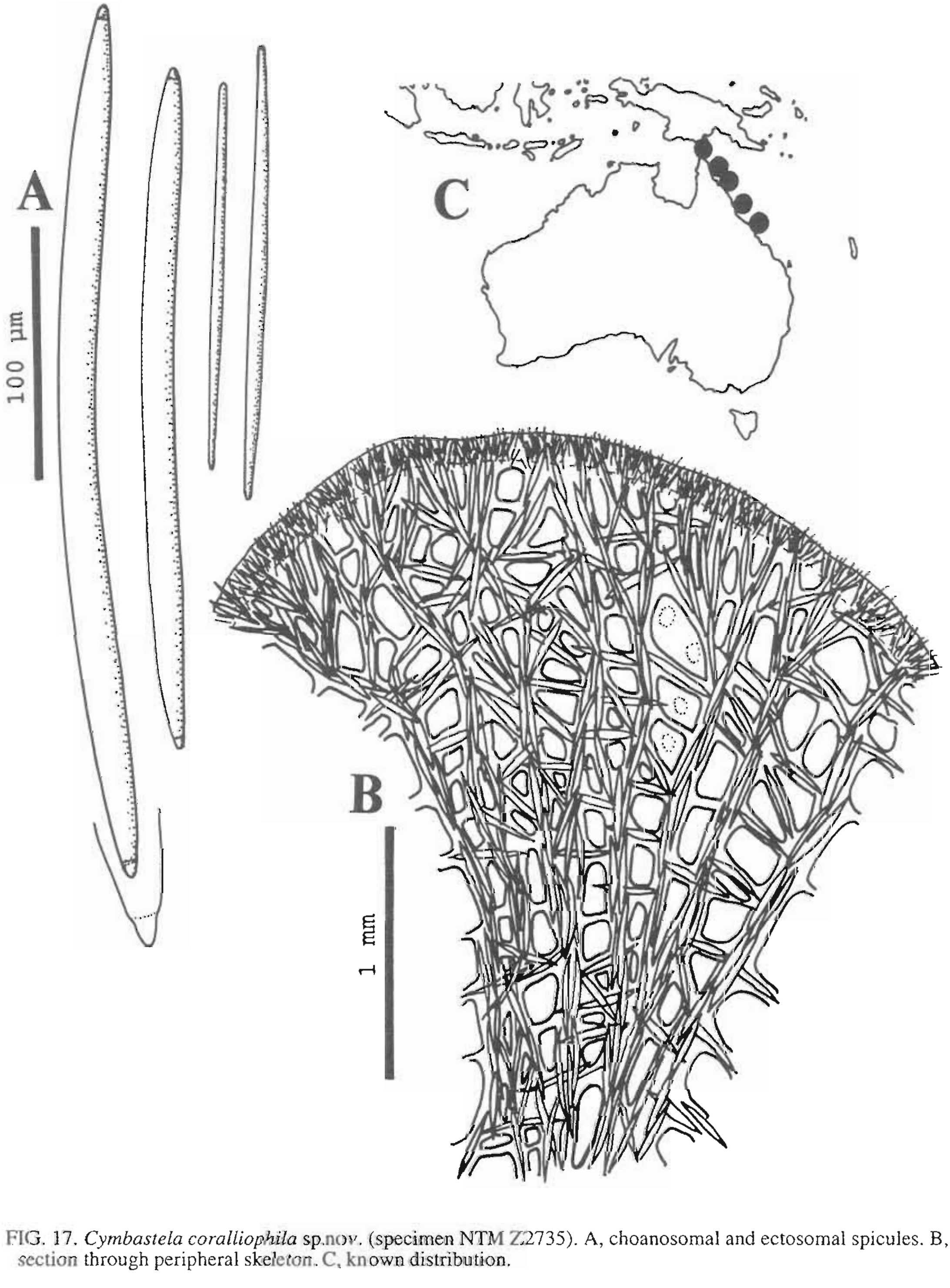


FIG. 17. *Cymbastela coralliophila* sp.nov. (specimen NTM Z2735). A, choanosomal and ectosomal spicules. B, section through peripheral skeleton. C, known distribution.

REPRODUCTION

Oviparous, with synchronous release of eggs and sperm (A. Ayling, pers. comm.).

ASSOCIATIONS

Sponges tested chlorophyll positive, and it is likely that the species' live pigmentation is partially or entirely produced by cyanobacterial symbionts. Several specimens also had numerous zoanthids on upper and lower surfaces, and barnacles (*Acasta* sp.) embedded within the mesohyl.

REMARKS

Cymbastela coralliophila has been recorded frequently from the Great Barrier Reef, but until now it has remained undescribed.

The species conforms with Burton's (1931) interpretation of the genus *Axinyssa*, as distinct from his nominal genus *Pseudaxinyssa*, in that it contains two distinct size classes of oxeas, the smaller found predominantly on the surface, the larger forming the structural skeleton. On the other hand, the very close similarities in growth form, skeletal architecture and spiculation that exist between this species and the other Australasian lamellate *Cymbastela* suggests that this feature is not important above the species level of classification. *Cymbastela coralliophila* also differs from other members of the genus, as construed here, in having an almost flattened, usually relatively large cup-shaped growth form, with flabellate lamellae. The skeletal structure is most similar to *C. cantharella*, with the radial-plumose skeletal tracts predominant over the reticulate component of the skeleton, and with only minor differences between the axial and extra-axial regions. The species are contrasted further in Table 1.

Cymbastela marshae sp.nov.
(Figs 18-20, Table 1)

MATERIAL EXAMINED

HOLOTYPE: NTM Z2876: Northern edge of Pelsar Islets, Houtman-Abrolhos Is, WA, 28° 47.6'S, 114° 00.7'E, 25m depth, 09.vii.1987, coll. J.N.A. Hooper, USSR RV 'Akademik Oparin', SCUBA (stn JH-87-001).

OTHER MATERIAL: HOUTMAN-ABROLHOS IS, WA - NTM Z2901 (fragment QM G300005): Pelsar Islets, 28°47.2'S, 113°58.5'E, 22m depth, 10.vii.1987, coll. J.N.A. Hooper, USSR RV 'Akademic Oparin', SCUBA (stn JH-87-002). NCI Q66C-4198-F: 1.5 km N of northern point, West Wallabi I., Wallabi Group, 28°25.7'S, 113°42.0'E, 8m depth, 12.ix.1990, coll. NCI, SCUBA.

SUBSTRATE AND DEPTH RANGE

Growing at base and on reef slope of *Acropora* and *Seriatopora* coral reef, in sand, silt or rock substrates, in *Turbinaria* zone, 8-25m depth.

GEOGRAPHICAL DISTRIBUTION

Known only from the Houtman-Abrolhos Islands, WA (Fig. 20C).

ETYMOLOGY

Named after Mrs Loisette Marsh, Curator of Marine Invertebrates, Western Australian Museum, Perth, in respect of her dedication to the study of the marine fauna of Western Australia.

DESCRIPTION

Shape: Thin, irregularly lamellate lobes forming asymmetrical vases, or symmetrical cup-shaped sponges, 125-255mm high, 120-235mm wide at apex of lamellae, with thin lamellae, 2-6mm maximum width, attached directly to substrate by a basal attachment, without a basal stalk (Fig. 18).

Surface features: Smooth, relatively even surface. Exterior surface with few low, irregular bumps, shallow depressions and concentric ridges, with or without horizontal lamellate projections growing on side of exterior surface. Interior, oscular surface of lamellae smooth, with concentric ridges, few low, irregular conules or depressions, sometimes with secondary lamellae or whole cups growing within interior surface. Very small oscules scattered over interior of cups, up to 1.5mm diameter.

Colour: Olive-green and maroon alive (Munsell 5Y 5/4 and 2.5R 4/8), evenly pigmented on exterior and interior surfaces, beige in ethanol.

Texture: Firm, flexible, slightly compressible texture, smooth to touch, difficult to tear.

Ectosome: Membraneous, without specialised skeleton, with plumose brushes of choanosomal oxeas protruding through surface for up to 170μm, consisting of 2-8 spicules per bundle. Ectosome with thin layer of darker pigmented granular collagen, 40-70μm wide, with heavy concentrations of microalgae, and also with a thin, disorganised paratangential layer of choanosomal oxeas scattered between erect, protruding ectosomal brushes. Subectosomal skeleton cavernous, predominantly plumose, slightly reticulate, with reticulate component decreasing closer to periphery (Figs 19, 20B).

Choanosome: Choanosomal skeleton plumo-reticulate, with axial skeleton dominated by longitudinal tracts running through lamellae, gradually ascending towards surface, becoming

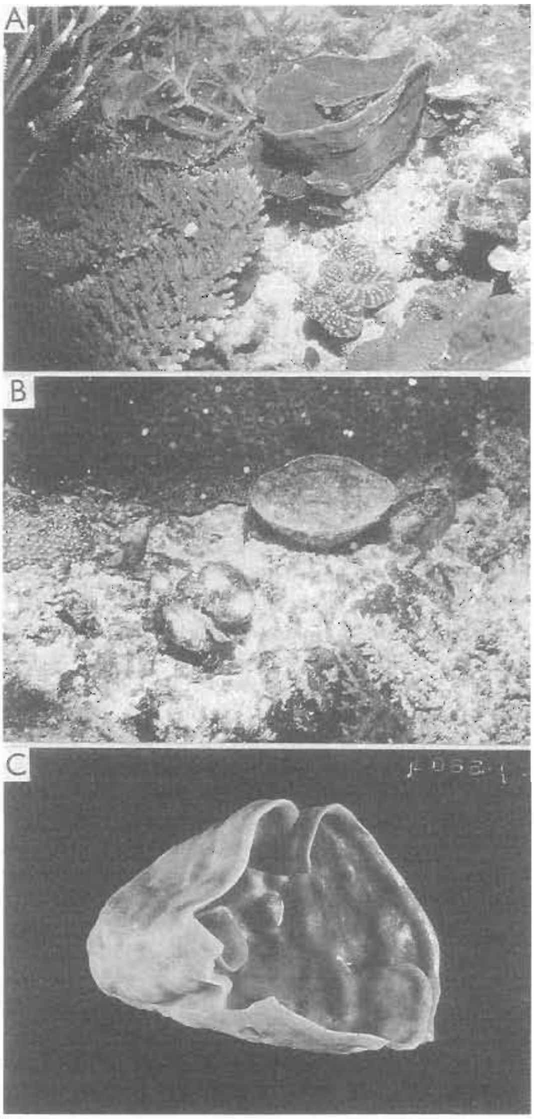


FIG. 18. *Cymbastela marshae* sp.nov. A, holotype (NTM Z2876), in situ. B-C, specimen (NTM Z2901) in situ (B) and preserved (C).

nearly plumose near peripheral skeleton (Fig. 20B). Axial skeleton slightly condensed at centre of lamella with reasonably well differentiated axial and extra-axial regions. Spongin fibres well developed, with obvious differentiation between multispicular primary (longitudinal and ascending) and uni- or paucispicular secondary (transverse, connecting) elements (Fig. 19). Primary fibres 30-80µm diameter, rarely fully cored with megascleres, secondary fibres much smaller, 15-25µm diameter, usually with greater silica to spongin ratio. Fibre meshes elongate oval or diamond-shaped in axis, 70-105µm maximum diameter, generally more cavernous in periphery, up to 150µm maximum diameter. Choanocyte chambers small, up to 45µm diameter. Mesohyl matrix only lightly invested with collagenous spongin, with abundant microalgae scattered throughout.

Spicules (refer to Table 1 for dimensions): Oxeas relatively short, slender, slightly curved at centre, with tapering, fusiform, usually telescoped points (Fig. 20A).

ASSOCIATIONS

Although not analysed chemically (acetone extracted), the olive-green and maroon pigments of this species are probably due to the presence of cyanobacteria scattered within the mesohyl. Each of the specimens examined was also found to have several barnacles boring within the lamella wall, near the base of the sponge.

REMARKS

This species is most closely related to *C. stipitata* in skeletal structure, as the plumose longitudinal and ascending primary tracts dominate the skeletal architecture. Both species have condensed axial regions and differentiated axial and extra-axial skeletons, with well developed plumose ectosomal skeletons. *Cymbastela marshae* also has a cavernous subdermal region, and spicules are about half the dimensions of those in *C. stipitata* (Table 1). The present species is close to *C. coralliophila* in growth form, lamella thickness and surface pigmentation.

Cymbastela notiaina sp.nov.

(Figs 21-23, Table 1)

MATERIAL EXAMINED

HOLOTYPE: SAM TS4025 (fragments NTM Z1623a, QM G300007): Precise locality unknown, Gulf of St Vincent, SA, 34°33-45'S, 137°57'-138°10'E, depth and date of collection unknown.

SUBSTRATE AND DEPTH RANGE

Unknown.

GEOGRAPHICAL DISTRIBUTION

South Australia (Fig. 23C).

ETYMOLOGY

Greek, *notos*, south; *notiaina* refers to the southern distribution of this species.

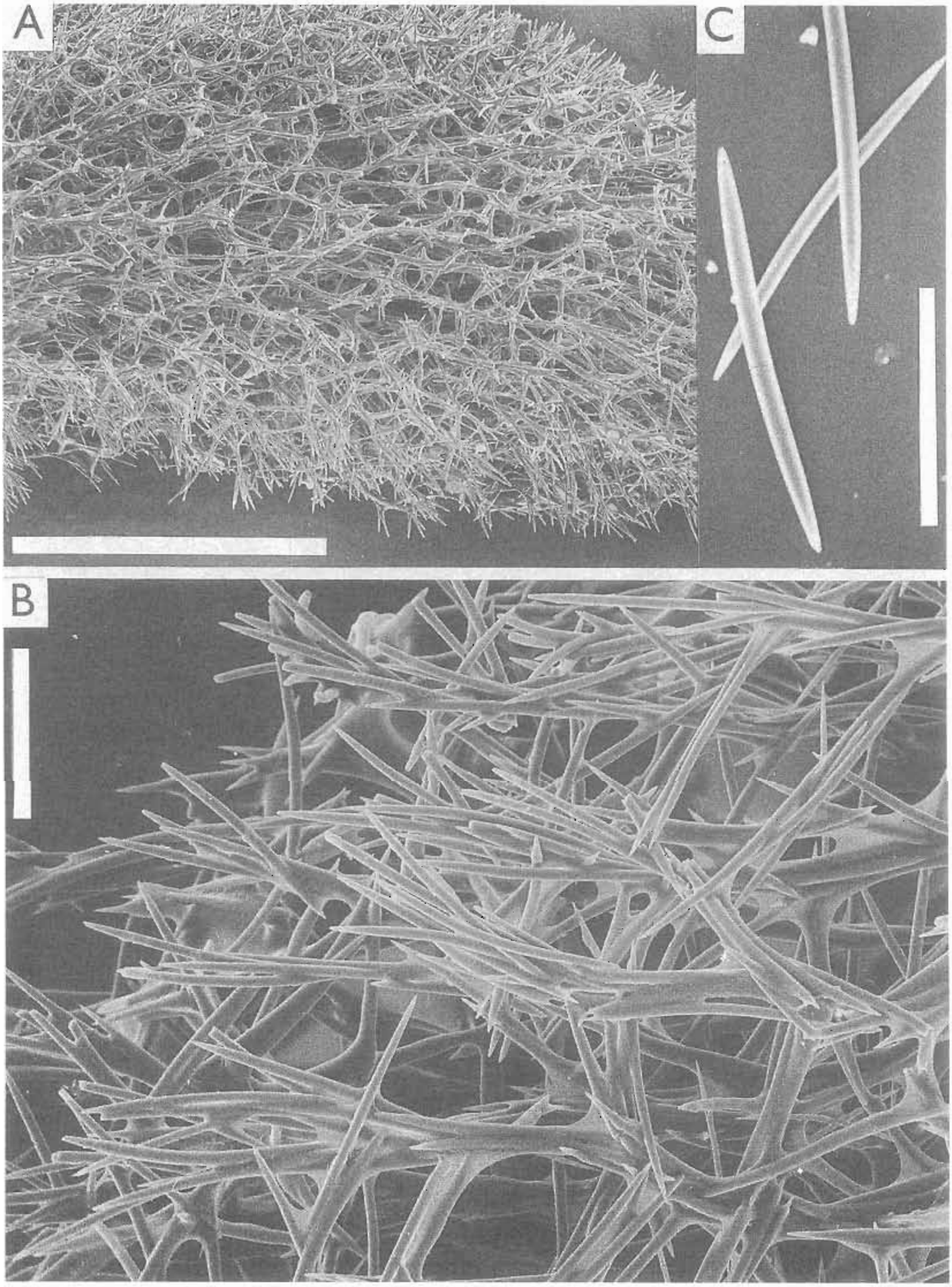


FIG. 19. *Cymbastela marshae* sp. nov. A, SEM of skeleton (specimen (NTM Z2901) (scale=1mm). B, peripheral skeletal architecture (scale=100µm). C, oxeas (scale=100µm).

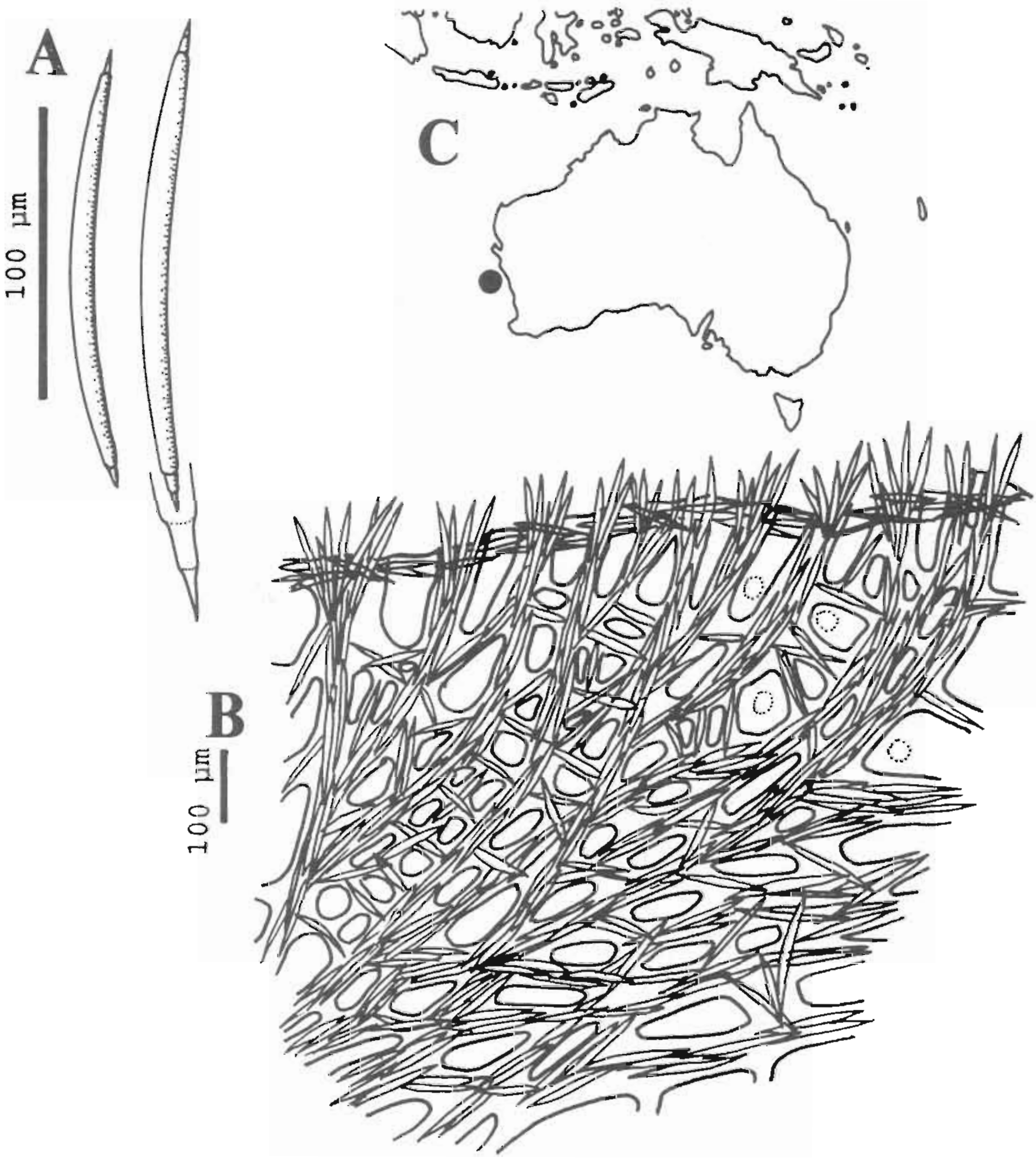


FIG. 20. *Cymbastela marshae* sp.nov. A, spicules. B, section through peripheral skeleton. C, known distribution.

DESCRIPTION

Shape: Small, symmetrical vasiform sponge, 96mm high, 125mm maximum diameter at apex of cup, on short thick stalk with expanded basal attachment, 12mm long, 35mm diameter, and thin lamellae, 3-5mm thick (Fig. 21).

Surface features: Interior and exterior surfaces optically even, without conules, buttresses or other lateral growth projections. Exterior surface has longitudinal, concentrically striated ridges. Oscules minute, less than 1mm diameter, dispersed over interior surface of cup.

Colour: Live colouration unknown, olive-brown in ethanol.

Texture: Firm, flexible, compressible in preserved state, smooth to touch.

Ectosome: Ectosome optically smooth, membraneous, slightly hispid due to protruding spicule brushes, slightly microconulose, with microconules corresponding to surface brushes. Ectosomal skeleton distinctly plumose, with bundles of 2-15 choanosomal spicules protruding up to 90µm from surface, perched on ends of ascending extra-axial skeletal tracts (Figs 22, 23B).

Choanosome: Choanosomal skeleton with no axial condensation, and only slightly differentiated axial and extra-axial regions (Fig. 23B). Skeleton almost regularly reticulate at the core, with oval meshes, 70-120µm diameter, formed by multispicular spongin fibres, both longitudinal and connecting. Skeleton plumo-reticulate towards periphery, with ascending multispicular fibres predominant over uni- or paucispicular transverse connecting fibres. Spicules form plumose brushes close to, and protruding from, surface. Fibre meshes in peripheral skeleton elongate-rectangular, slightly larger than in axis, 100-140µm diameter (Fig. 22). Spongin fibres relatively large, 40-85µm diameter, partially but never fully occupied by spicules. Mesohyl matrix lightly reinforced with collagen, choanocyte chambers oval, 40-90µm diameter.

Spicules (refer to Table 1 for dimensions): Oxeas almost vestigial by comparison with other species, poorly silicified, very thin, small, only slightly curved at centre, with prominently telescoped ends and rounded tips (Fig. 23A).

ASSOCIATIONS

No symbiotic cyanobacteria were seen in the holotype.

REMARKS

This species is presently known only from the holotype described above, although a small fragment from a second specimen exists in the SAM collection (SAM TS4058 [section/fragments NTM Z1665, QM G300011], from Port Noarlunga, SA), may also belong to the species. *Cymbastela notiaina* is easily differentiated from other taxa by its regular, nearly completely reticulate choanosomal skeleton, the small size of megascleres (Table 1), and the telescoped, rounded (strongylote) points of oxeas, unlike any other species.

DISCUSSION

TAXONOMY

Small differences in field characteristics, such as live colouration, growth form, surface features, including outgrowths on the surface and lamellae thickness, as described above for each species, can serve as field identifiers for the seven known species of *Cymbastela.* However, morphological differences seen in preserved material, which correlate with these species boundaries are less obvious. Certainly, in terms of general skeletal structure and spicule geometry the genus is relatively homogenous, and it is only through small but significant differences in a small number of skeletal characters that species can be reliably differentiated. These characters, which are shown to be most important, include spicule length, spicule geometry, including the presence or absence of telescoped ends on spicules, and degree of silicification, and the relative, proportional development of the axial and extra-axial skeletons. On this basis it was possible to construct a key to species of *Cymbastela* (see above), with emphasis given to the morphology of preserved specimens. Thus, whereas the characters used to differentiate species in this key may seem trivial, these differences correspond with more obvious field characteristics, many of which are no longer visible in the preserved material.

It was also noted that, in general, species could be separated by their mean spicule dimensions. Generally, the relative size of oxea megascleres decreases with increasing latitude (Fig. 24A-B), such that species from low (tropical) latitudes (*C. stipitata*, *C. coralliophila*, *C. vespertina*) have larger oxeas than those species from higher latitudes (*C. cantharella*, *C. marshae*, *C. notiana*). *Cymbastela concentrica*, which has a wide latitudinal distribution (14-26°S; Fig. 24B), also has a relatively wide range of spicule dimensions (Fig. 24A, symbol 5).

BIOGEOGRAPHY

Although it is possible that more extensive sampling along the cool temperate Australasian coastline will reveal additional species, *Cymbastela* is presently known to be predominantly a shallow water, tropical or subtropical genus, usually associated with coral substrates. The genus appears to be endemic to the Indo-west Pacific, extending only as far as New Caledonia (longitude 166°E) to the east, and to the Houtman-Abrolhos Islands (113.5°E) to the west, and so far there are no confirmed records of the genus from either Indonesia (unpublished *Siboga* and *Snellius II* collections, R.W.M. Van Soest, pers.comm.) or New Zealand (personal observations). However, it is possible that misidentified specimens of *Cymbastela* exist in other museum collections. The genus is certainly not present in the published collections of Hentschel (1912), from the Aru and Kai Islands, southeast Indonesia (ZMB collections), in which close similarities with the northwest Australian sponge fauna can be seen (e.g. Hooper, 1991).

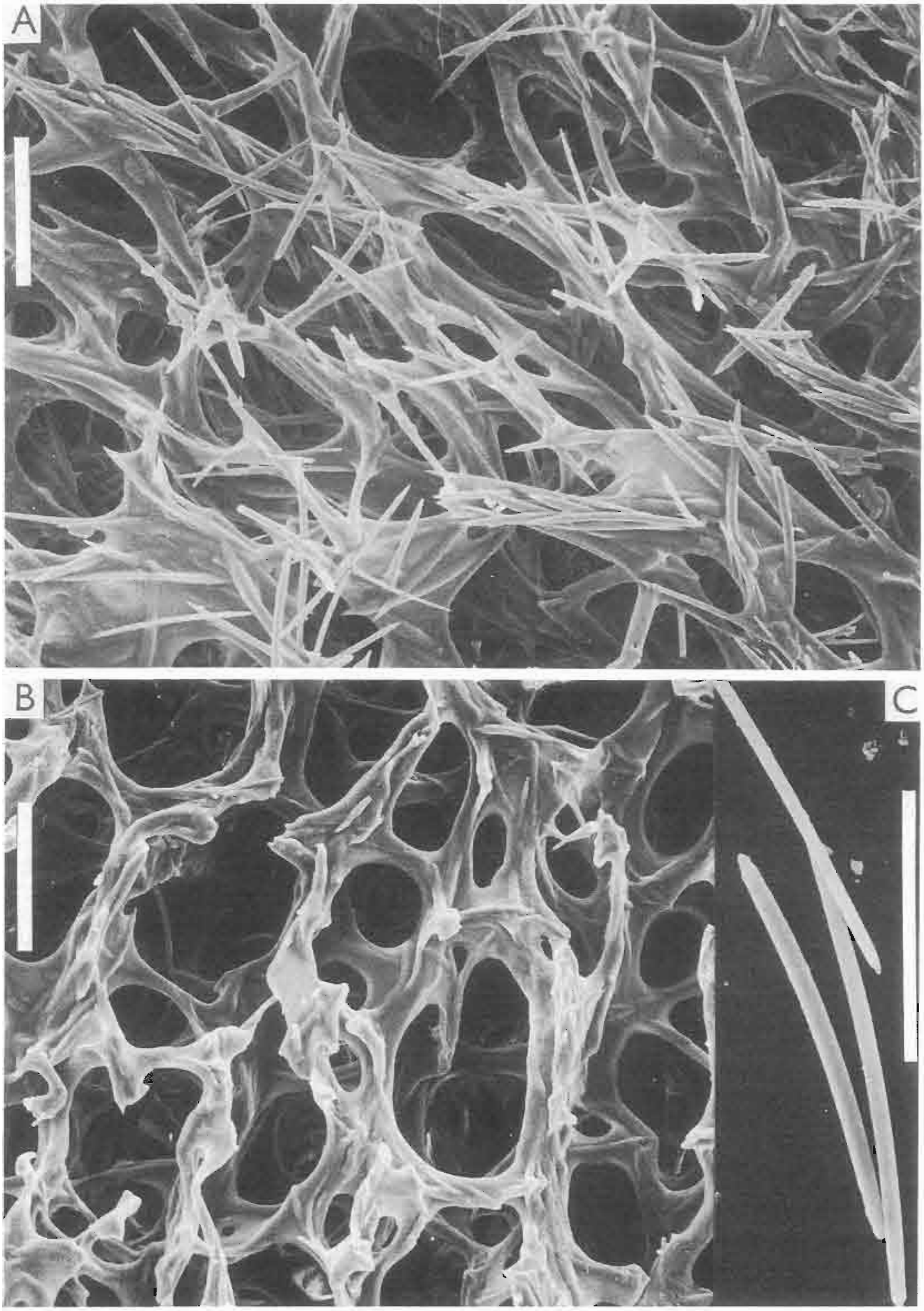
Three species of *Cymbastela* have restricted, allopatric distributions (*C. cantharella, C. marshae, C. notiaina*; Fig.25), whereas on the northwest and northeast coasts of Australia there are two groups of more-widely distributed, sympatric species. Within the northwestern area of sympatry (Fig. 25), there is some evidence of niche separation between the two populations, *C. stipitata* and *C. vespertina*. The former species has a predominantly shallow water distribution, found mostly in the intertidal region and only exceptionally down to 19m depth, whereas *C. vespertina* is found mostly in deeper water, only rarely above 8m depth. Population characteristics of the northeast Australian sympatric species, *C. coralliophila* and *C. concentrica*, have not yet been determined, and the latter species, in particular, is still poorly known.

PHYLOGENY

Under Van Soest et al.'s (1990) interpretation of the existing family Axinellidae *Cymbastela* would be placed with a group of genera having axially condensed and extra-axially plumo-reticulate skeletons, for example *Auletta, Axinella, Axinosia, Homaxinella, Phakellia, Pseudaxinella, Reniochalina* and *Teichaxinella*, which Van Soest et al. (1990) retained in a newly defined concept of family Axinellidae. Of these genera *Cymbastela* is most closely related to *Axinella*. Conversely, they placed the genus *Axinyssa*, previously considered to be a close relative of '*Pseudaxinyssa*' s.l. (= *Cymbastela*), in a redefined family Halichondriidae since it has poorly developed spicule tracts. This group would contain 'axinellid' genera such as *Axinyssa* and *Amorphinopsis*, several genera previously in-

FIG. 21. *Cymbastela notiaina* sp.nov. A, holotype (SAM TS4025).

FIG. 22. *Cymbastela notiaina* sp.nov. A, SEM of peripheral skeleton (holotype, SAM TS4025) (scale=100µm). B, axial skeleton (scale=100µm). C, spicules with telescoped ends (scale=50µm).


A
B
C

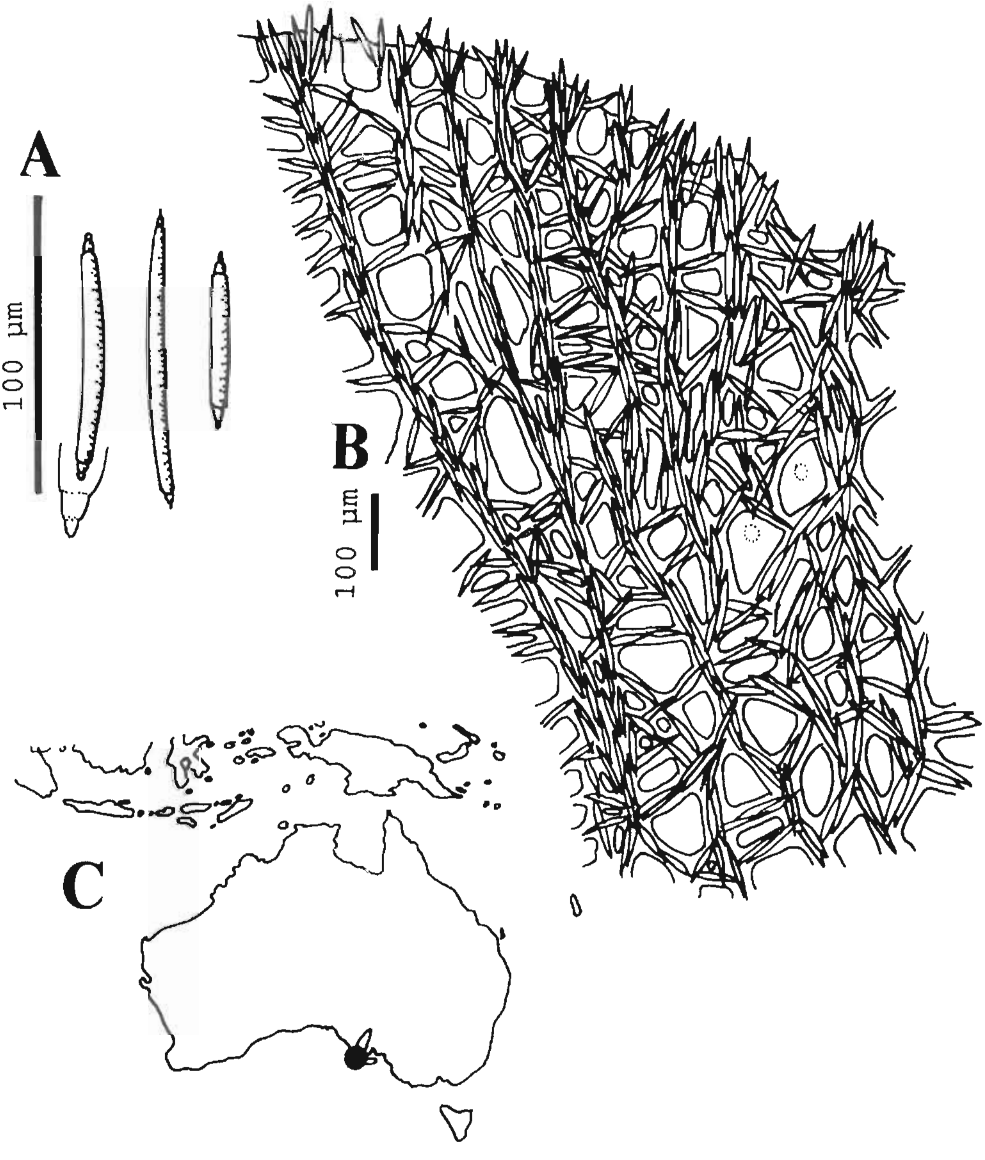


FIG. 23. *Cymbastela notiaina* sp.nov. A, spicules. B, section through peripheral skeleton. C, known distribution.

cluded in Desmoxyidae (e.g. *Myrmekioderma*), and other genera traditionally associated with the halichondrids and hymeniacidonids (e.g. *Ciocalypta*, *Hymeniacidon*). A third group of 'axinellids' with dendritic skeletons (e.g. *Acanthella*, *Dictyonella*, *Scopalina*), were removed to the new family Dictyonellidae. The fourth family, Desmoxyidae, was also previously aligned with the Axinellida, differing from other 'axinellids' in having a reticulate-fasciculate choanosomal skeleton and a fleshy corrugated surface (Van Soest et al., 1990:18). It contained several desmoxyid genera (e.g. *Higginsia*), but excluding *Myrmekioderma*, as well as some Axinellidae (e.g. *Ptilocaulis*). We consider that these new family divisions proposed by Van Soest et al.

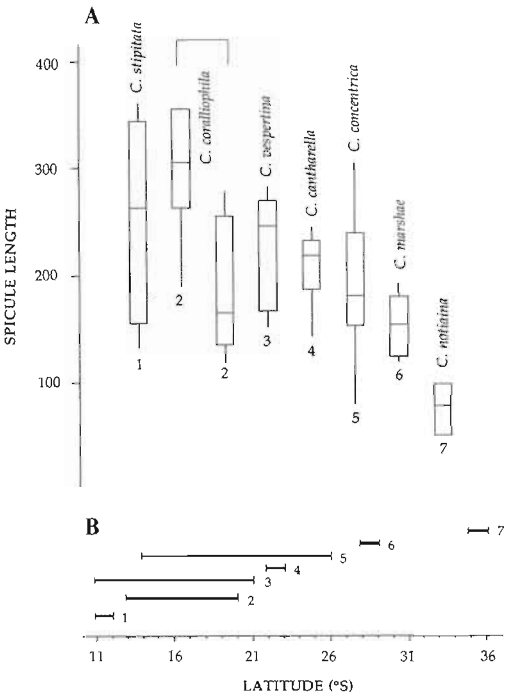


FIG. 24. A, Comparison in spicule lengths (μm) between seven species of *Cymbastela*, and B, latitudinal differences in distribution for each species. Box-and-whisker plots show the range of spicule dimensions (i.e. 'whiskers'), the median values (i.e. 50% of data values, between lower and upper quartiles - open boxes), and the average length of oxeas for each species (i.e. mid-range bars). Key to species codes: 1, *C. stipitata*; 2, *C. coralliophila* (large and small oxeas); 3, *C. vespertina*; 4, *C. cantharella*; 5, *C. concentrica*; 6, *C. marshae*; **7**, *C. notiaina*.

(1990) have some merit over the existing, confused system for Axinellidae - Halichondriidae - Hymeniacidonidae, but we are uncertain whether all these 'axinellids' and 'halichondrids' have a monophyletic origin, and we leave open the question of their ordinal classification for the time being. Further evidence from molecular and genetic nature may be useful in evaluating these relationships in an objective context.

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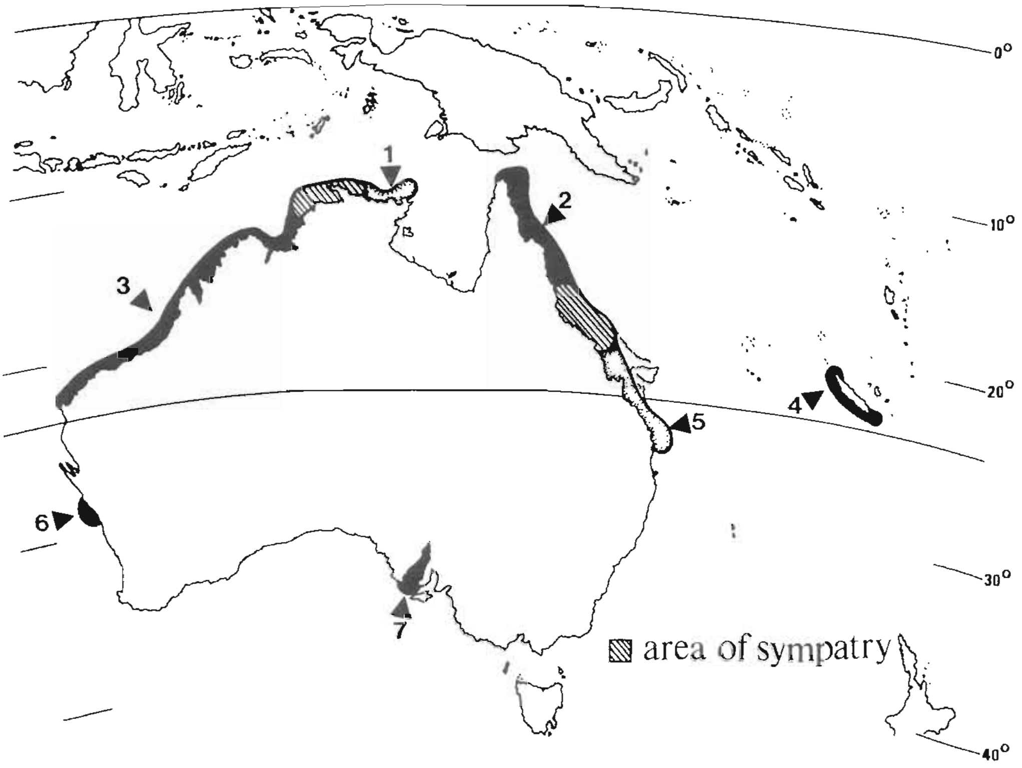

FIG. 25. Distribution of Australasian *Cymbastela* species, indicating three groups of allopatric species (numbers 4,6,7), and areas of overlap between four sympatric species (numbers 1,2,3,5) on the northeast and northwest coasts of Australia. 1, *C. stipitata*; 2, *C. coralliophila*; 3, *C. vespertina*; 4, *C. cantharella*; 5, *C. concentrica*; 6, *C. marshae*; 7, *C. notiaina*.

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