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REVISION OF MICROCIONIDAE (PORIFERA: POECILOSCLERIDA: DEMOSPONGIAE), WITH DESCRIPTION OF AUSTRALIAN SPECIES.

JOHN N.A. HOOPER


A phylogenetic revision of the poecilosclerid Microcionidae is based on type material, the worldwide literature, and comprehensive Australian collections. Of 73 available generic names 7 genera and 12 subgenera are recognised here. Of 561 available species names 459 are considered valid (10 virtually unrecognisable), including 52 new species. The Australian fauna, including Australian Antarctic Territory, contains 148 species (31 new), many new records, most are new combinations, and many illustrated for the first time. A synonymy of world species is provided. Valid taxa include: Clathria (with 7 subgenera: C. (Clathria) (with 31 Australian species, 82 other species worldwide, with new species murphyi, noarlunga, bicolathura, borealis, burtoni, sarai, sarapisiniferu), C. (Wilsonella) (6, 8, abrothosensis, eniae, liungreni spp. nov.), C. (Microciona) (5, 91, illawarrae, lizardei, sinuae, broadstedi, campecheae, claudii, hentschelli, leighensis, stephensae, tunisiae, urizeae, vacelettia spp. nov.), C. (Dendrocia) (7 species endemic to Australia), C. (Asociella) (6, 6, patula, fromontiae, georgianensis spp. nov.), C. (Isoeicaria) (4, 1, selachia, skia spp. nov.), and C. (Thalyssia) (36, 53, aphylla, cruspeda, darwinensis, fasterna, hallmanni, hesperia, lematolae, phorbasiformis, styloprothesis, tingens, weeselensis, amiranteiensis, heechi spp. nov.; Anthe (with 3 subgenera: A. (Anthe) (12, 10), A. (Phocaenidia) (2, 17) and A. (Isoeicaria) (3, 1, punicea, saintvincenti spp. nov.; Echinoclathria (14, 15, marguetiae, levii, notialis, parkeri, riddéli spp. nov.; Holossomma (9 species endemic to Australia), 1 indeterminate species; Echinoclathria (with 2 subgenera: E. (Echinoclathria) (10, 2, felisi sp. nov.), E. (Protophithiopsis) (8 species endemic to Australia and New Caladonia, collata, favulosa, isauici, tuberosa spp. nov.); Artemistria (4, 10); and Pandaros (incertae sedis) (3, 0), 2. Generic keys are provided. Morphometric characters of primary importance include the origin, geometry and distribution of structural megascleres within the skeleton, modification of megascleres to monactinal or diactinal forms, the presence or absence of a specialised ectosomal skeleton, presence of detritus incorporated into spongin fibres, and overall skeletal structure (including compression of the axial skeleton and differentiation of axial and extra-axial regions). Brief zoogeographical comparisons are made between continental Australian and adjacent Indo-west Pacific faunas. Australian species comprise about 32% of the world's microcionid diversity; about 75% of species are endemic for the Australian region, and temperate species (81%) have higher levels of endemism than tropical species (59%).

Polifera, Demospongiae, Poecilosclerida, Microcionidae, family revision, new species, taxonomy, biogeography, Australia.

John N.A. Hooper, Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101. Australia; received 1 December 1995.

INTRODUCTION

Microcionidae is one of the largest families of Demospongiae, comprising about 8% of all described (extant) Porifera species (Hooper & Levi, 1993a). The family has contained at one time or another about 70 genera and 550 species, although fewer than these are now recognised as valid. The family has a worldwide distribution and it is found from the intertidal zone to depths exceeding 2000m. It is clearly one of the more important, ecologically successful groups of Porifera.

Within the Indo-Australian region microcionids are particularly abundant, with some species being dominant components of the shallow water macrobenthos. Previous works describing this fauna (and other literature containing extra-limital records of Australian species) include: Lamarck (1814, 1815, 1816), Gray (1858, 1867, 1869, 1870), Bowerbank (1864, 1875, 1877), Barnard (1879), Kent (1871), Ridley (1884a), Ridley & Dendy (1886, 1887), Lendenfeld (1888, 1889a), Kieschnick (1896, 1900), Thiele (1898, 1899, 1900, 1903), Kirkpatrick (1900a, b), Whitelegge (1901, 1902), Hentschel (1909, 1911, 1912),

Prior to the present study more than 200 species of Microcionidae had been described in the Australian fauna (including its territorial waters), but many of these were found to be either composite (consisting of several sibling species), or synonymy of other species. This study 1) describes 148 species (31 new), many new locality records for Australia and new taxonomic combinations; 2) provides an annotated synonymy for 311 other species worldwide (including 21 new species); 3) revises the morphometric characters used for classification and population variability for particular species; and 4) determines levels of endemism amongst provincial faunas.

MATERIALS AND METHODS

COLLECTION AND HISTOLOGICAL TECHNIQUES. Material examined in this study was predominantly collected using SCUBA (0-40m depth) or dredging and trawls (30-360m depth). Seasonal sampling for reproductive periodicity was conducted over two years in the Darwin and Cobourg Peninsula regions, NT. Immediately after collection specimens were either fixed in 80-100% methylated ethanol or frozen (which to some extent fixes the pigments), and later preserved in 70% alcohol. Reproductive products were searched for in fresh or frozen tissue.

Nitric acid spicule preparations, thick-sections and thin-section mounts were routinely made as follows. Fragments of each sponge, including ectosomal and choanosomal regions, were heated directly on a glass microscope slide in several drops of nitric acid (the solution was evaporated rather than boiled, using low heat), and mounted in Canada balsam once completely dry, and cooled. Thick, hand-cut sections were made perpendicular to the surface, soaked in a saturated solution of phenol and xylene (for approximately 24 hours), and mounted in Durcupan (ACM Fluka Products) using glass slides or card to raise the coverslip level. Phenol-xylene precluded the necessity for dehydration through an alcohol series. Some microtome sections cut at 30-35μm were made for each species. Fragments were passed through a dehydration series, cleared in toluene or Histosol, and wax embedded for at least 2 hours. Sections were cut from trimmed wax blocks (cutting from the centre of the block to the exterior so as to include both the outer surface and inner skeleton relatively intact), placed in clearing agent for an adequate period to dissolve wax and/or dewaxing on a hot plate, then soaked in ethanol until perfectly clear, floated onto albumen-coated slides, orientated and flattened, stained with basic fuchsin and mounted. Fragments of dry specimens (e.g., type material) were reconstituted in 5% buffered formalin for 12 hours, which produced rehydration of the mesohyl and enabled cleaner histological sections to be made.

MORPHOMETRIC ANALYSES. Spicules were measured with a stage micrometer, either directly through a microscope or computer digitiser. Twenty five spicules, of each spicule category, in all specimens were measured. Acanthostyle width measurements were taken immediately below the base. Toxa lengths refer to chord length; isochelae are measured from apex of alae; length measurements of other spicules refer to maximum width.

Spicule dimensions were sorted and statistically compared for various parameters (e.g., season, locality, depth), including one- and two-way ANOVs with replication, two-way ANOV with unequal replication, means differentiated using two-tailed tests. Line-drawings were made using a calibrated camera lucida, and microphotographs were taken with an Olympus microphoto system. Taxonomic keys were constructed using ordered multistate, disordered multistate, morphometric and binary characters, utilising the DELTA system (Dallwitz & Paine, 1986).

SCANNING ELECTRON MICROSCOPY. Sections were prepared as follows:

1) Cut at 1-1.5mm thick, ensuring that both the ectosome and choanosome were represented.

2) Placed in a cavity block and covered with several drops of sodium hypochlorite to etch the mesohyl matrix from the skeleton. The etching process was monitored through a dissecting microscope in order to prevent the skeleton falling apart. Delicate structures (plumose, halichondroid, hymedesmoid skeletons) only required a few seconds treatment with bleach; robust skeletons (reticulate, fibrous, articulated
skeletons) required several minutes; but generally 30 seconds was adequate.

3) Bleach was pipetted off at the appropriate time and 70% ethanol immediately added. Sections were left to stand for several minutes to ensure bleach was completely neutralised.

4) Steps 2-3 were repeated, without removing section from cavity block, substituting concentrated hydrogen peroxide in place of sodium hypochlorite, finally rinsing in ethanol. The hydrogen peroxide step was omitted for very delicate sections.

5) Sections were placed on clean microscope slides and let dry completely.

6) Sections mounted on SEM stubs using double-sided tape, copper dag, or 'Supa Glue' (Supa Glue, Selleys Chemical Company, Padstow). An alternative method used to fix samples to stubs was to cover stub with 'Aquadhere' wood glue (Aquadhere, Selleys Chemical Company, Padstow), let dry completely (usually several days), then prior to use exposed dry glue to vigorous steam (which softened the set glue), and placed the section on top of the stub (it would sink in a short way but was bonded reasonably well to the stub, and had the advantage of producing a perfectly smooth background).

7) The stub was sputter-coated well to ensure that all fibres were well coated to reduce 'charging'. In some cases uncoated sections could be viewed successfully under low accelerator voltage, but better results were generally obtained on coated specimens at higher voltage. Typical viewing conditions used were 25kV, at close working distance to provide best depth of field and focus, and at low magnifications.

Spicule were prepared as follows:

1) Thinly cut sections including both ectosome and choanosome were placed in a durham tube (micro-test tube), to which drops of concentrated nitric acid are added, using drop-by-drop addition so as to control the oxidation reaction and production of by-product oxides.

2) Upon completion of acid digestion the durham tube was half filled with acid and gently heated over an alcohol flame, ensuring that only small bubbles form (low heat, no boiling), for 1-2 minutes.

3) Solution was let stand to cool, then centrifuged (approximately 4000rpm for 30 seconds).

4) Nitric acid was pipetted off leaving a spicule mass at the bottom of the tube, undisturbed.

5) Spicules were resuspended in fresh nitric acid and gently stirred using clean, fine, glass rod.

6) These steps were repeated if any collagen remained.

7) Spicules were resuspended firstly in demineralised water, 70% ethanol, then two series of 100% ethanol solutions, centrifuging and decanting the supernatant between each change of solution, finally ending with suspended spicules in a solution of absolute ethanol.

8) A micro-cover glass was adhered to an SEM stub using double-sided tap or copper dag, several drops of suspended spicules placed onto the cover glass, the alcohol-spicule solution ignited and spread across the glass with a glass rod or forceps until all ethanol was vapourised. Spicules bond to glass relatively firmly, but excess spicules could be blown off glass using compressed air, or spread out over the glass by adding further ethanol and igniting. The distribution of spicules on the cover glass was monitored under compound or dissecting microscope (magnification depending on spicule size). More drops of spicule solution added and this step repeated if too few spicules were present, ensuring not to overcrowd field of view for SEM photographic purposes.

9) An alternative method was used to produce a perfectly smooth background, using an "Aquadhere" glue-coated stub, dried for several days then softened with steam, and spicules placed directly onto soft glue (in this case ethanol was not burnt but evaporated). Single spicules would sink into glue too far if it was too soft (i.e., left in steam too long).

10) Spicule coated stubs were sputter coated briefly and viewed at 25kV, minimum working distance and smallest aperture for best resolution.

**ABBREVIATIONS**

AAT, Australian Antarctic Territories; ABIP, Centro de Estudios Avanzados de Blanes, Instituto de Investigaciones Pesqueras Barcelona, Aquarium de Blanes, Gerona; ABRS, Australian Biological Resources Survey, Canberra; AFZ, Australian Fishing Zone; AHF, Alan Hancock Foundation, University of Southern California, Los Angeles; AIMS, Australian Institute of Marine Science, Townsville; AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; BPBM, Bernie P. Bishop Museum, Honolulu; CP, Cobourg Peninsula, NT; CPMPN, Cobourg Peninsula Marine National Park, NT; CSIRO, Commonwealth Scientific and Industrial Research Of-
organisation, Marine Laboratories, Hobart, Cleveland and Perth; DAR, Darwin region, NT; DELTA, Description Language for Taxonomy computer software (Dallwitz & Paine, 1986); EIS, Environmental Impact Study; CSIROEMG, CSIRO Food Research Laboratory, Division of Food Processing, North Ryde, Sydney. EMU, Ensign (formerly Environmental Management Unit), Water Board (Sydney, Illawarra, Blue Mountains), Sydney; EPA, Environment Protection Authority, Sydney; EPALR, East Point Aquatic Life Reserve, Dudley Point, Darwin Harbour, NT; FNO, far northern Queensland (Cooktown to Torres Straits); FUB, Freie Universität Berlin; GBR, Great Barrier Reef, Queensland; HNUK, Natural History Museum, Ham Nam University, South Korea; ICBUC, Instituto Central de Biología, Universidad de Concepción, Chile; ICZN, International Code of Zoological Nomenclature (see Anonymous, 1985); IM, Indian Museum (Zoological Survey of India), Calcutta; IMZUB, Istituto e Museo di Zoolgia ed Anatomia Comparata della Università di Bari, Bari; IMZUN, Instituto e Museo di Zoolgia dell’Università di Napoli, Naples; INM, National Museum of Ireland, Dublin; IZUG, Musen Civico di Storia Naturale di Genova, Genova; JCU, James Cook University of North Queensland, Townsville; KFAU, Zoologischen Sammlung der Universität Erlangen-Nürnberg, Erlangen; LFM, Merseyside County Museums (formerly Liverpool Free Museum), Liverpool; LMJG, Abteilung für Zoologie am Landesmuseum Joanneum (Landes Museum Jubiläum Graz), Graz; MABA, Museo Argentino de Ciencas Naturales “Bernardino Rivadavia”, Buenos Aires; MCNP, Div. Invest. del Museo de Ciencias Naturales de la Plata, Argentina; MCZN, Museum of Comparative Zoology, Harvard University, Cambridge (Mass.); MEQ, mid eastern Queensland (Gladstone to Bowen); MHNG, Museum d’Histoire Naturelle de Genève, Genève; MLUM, Marine Laboratory of the University of Miami, Miami; MMBS, Mukaishima Marine Biological Station, Faculty of Science, Hiroshima University, Onomichi; MNHN, Muséum National d’Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Paris (DT, Topsent collections; DCL, Lévi collections; DJV, Vacelet collections; DNBE, Boury-Esnault collections); MOM, Musée Océanographique de Monaco, Monaco; MRAC, Koninklijk Museum voor Midden-Afrika, Tervuren; MRHN, Musée Royal d’Histoire Naturelle de Belgique, Bruxelles; NTQ, Queensland Museum, Museum of Tropical Queensland, Townsville; NCICQ66C-, United States National Cancer Institute, Australian Institute of Marine Science shallow water collection contract (1984-91), Townsville (primary voucher samples now lodged in QM, others in NTM and USNM); NCIOCDN-, United States National Cancer Institute, Coral Reef Research Foundation shallow water collection contract, Chuuk State (voucher samples lodged in QM and USNM); NEQ, northeast Queensland (Bowen to Cooktown); NM, Natal Museum, Pietermaritzburg; NMB, Naturhistorisches Museums zu Basel, Basel; NMICIC, National Museum of Natural Sciences, National Museums of Canada, Ottawa; NMNZ, National Museum of New Zealand (formerly Dominion Museum), Wellington; NMV, Museum of Victoria (formerly National Museum of Victoria), Melbourne; NSM, National Science Museum, Tokyo; NSW, New South Wales; NT, Northern Territory; NTM, Northern Territory Museum of Arts and Sciences, Darwin; NTU, Northern Territory University, Darwin; NWS, Northwest Shelf region, Western Australia; PAUP, Phylogenetic Analysis Using Parsimony (see Swoford, 1991); PIBOC, Pacific Institute of Bio-organic Chemistry, Far East Scientific Centre, Academy of Sciences of the USSR, Vladivostok; PMJ, Phyletisches Museum, Jena; PNG, Papua New Guinea; QFS, Queensland Fisheries Service, Department of Primary Industries, Brisbane and Cairns; QLD, Queensland; QM, Queensland Museum, Brisbane; QVML, Queen Victoria Museum and Art Gallery, Launceston; RMBS, Roscoff Marine Biological Station, Roscoff, France; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; RRIMP, Roche Research Institute of Marine Pharmacology, Sydney (discontinued; sponge collections now held in AM); RSME, Royal Scottish Museum, Edinburgh; SA, South Australia; SAM, South Australian Museum, Adelaide; SEQ, southeast Queensland (Tweed River to Gladstone); SM, Musée Zoologique, Strasbourg; SME, Station Marine d’Endoume, Marseille; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt; TAS, Tasmania; TM, Museo e Istituto di Zoologia Sistematica dell’Universita di Torino, Turin; TMAG, Tasmanian Museum and Art Gallery, Hobart; UAZD, University of Auckland, Zoology Department, Auckland; UB, Übersee-Museum, Bremen; UCT, South African Museum of Natural History, Cape Town; UQ, University of Queensland, Brisbane; USC, University of Southern California,
Los Angeles; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC; UZM, Zoologisk Museum, Universitetsparken, Copenhagen; VIC, Victoria; WA, Western Australia; WAM, Western Australian Museum, Perth; YPM, Peabody Museum of Natural History, Yale University, New Haven (Conn.); ZIL, Zoological Institute of Leningrad, Academy of Sciences Museum of Zoology, St Petersburg; ZMA, Zoologisches Museum, Universität van Amsterdam, Amsterdam; ZMB, Museum für Naturkunde an der Humboldt-Universität zu Berlin, Berlin; ZMC, Zoologisk Museum, Copenhagen; ZMH, Zoologisches Institute und Zoologisches Museum der Universität Hamburg, Hamburg; ZMUU, Uppsala Universitets Zoologiska Museet, Zoologiska Institutionen, Uppsala; ZSN, Aquarium e Museo della Stazione Zoologica di Napoli, Naples; ZRS, Zoologiska Riksmuseum, Stockholm.

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DEFINITION OF CHARACTERS

MINERAL SKELETON. The form, composition and division of the skeleton remains the most important factor for classification of Demospongiae. Recent attempts at higher systematics of Demospongiae based on non-skeletal characters (e.g., Simpson, 1968a; Bergquist & Hartman, 1969; Bergquist, 1980a; Lee & Gilchrist, 1985; Hooper et al., 1992) have had only limited success because in many instances they are unable to corroborate all skeletal and non-skeletal evidence into a single systematics. In some cases amongst Demospongiae (e.g., Verongida), non-skeletal evidence has been decisive and to some extent well correlated with other characters. In other cases (e.g., Axinellida) that evidence has merely highlighted inadequacies in systematics based solely on skeletal morphology (Simpson, 1968a; Bergquist & Hartman, 1969; Bergquist, 1980a; Vacelet, 1985; Hooper et al., 1992).

COMPOSITION OF THE SKELETON. All microcionids are siliceous with discrete, free spicules. So far no desma-bearing species or hypercalcified ‘relic’ species are known. Many species undergo secondary acquisition, loss or reduction of spicule mineralisation, particularly when displaced by arecanaceous particles (e.g., Holopsumma). C. (Wilsonella) is partly defined by this feature, with various degrees of arecanaceous development among species; this trend is widespread throughout the Poecilosclerida.

ORGANISATION OF THE SKELETON. Gross organic and inorganic skeletal architecture, structural differentiation of the inorganic skeleton, and distribution of mineral components in that structure are primary diagnostics (Levi, 1960a, 1973; Bergquist, 1978a; Hartman, 1982). However, when used alone skeletal architecture is not necessarily a reliable indicator of relationships. Hooper (1991, herein) noted that the so-called typical, compressed, axinellid-like skeleton of many Raspailiidae (Raspailia punatilida; Hooper, 1991: Fig.2b) also occurred in C. (Axociella) (Figs 7G, 119A). It is also probable that skeletal structure is influenced to some extent by environmental conditions, and there is some evidence to suggest that flexible, compressed axial skeletons are produced in response to high energy environments (e.g., Palumbi, 1984). Similarly, skeletal characters such as those found in encrusting species have obviously evolved independently in many (otherwise unrelated) taxa. Review of microcionid skeletal structures showed that species which were similar in spicule geometry had different skeletal architectures (Hooper, 1988).

Architectural types amongst the Microcionidae include: 1, hymedesmoid (with thin layer of basal spongin lying on the substrate containing erect megascleres (Fig. 7l); 2, microcionid (with a compressed basal spongin, producing ascending fibre nodes and plumose spicular columns) (Fig. 100F); 3, renieroid reticulate (consisting of a rectangular basal reticulation of uni- or pauciispicular tracts fully enclosed within spongin fibres or cemented at their nodes by loose collagen) (Fig. 7C); 4, isotropic reticulation (a disorientated, random uni-, pauci- or multispiricular reticulation in erect or massive forms, in which there is no distinction between primary or secondary tracts (not figured; seen only in nominal genus Qasimella); 5, isodictylreticulation (reticulation with triangular meshes formed by uni- or paucispicular tracts of spicules, cemented at their nodes by collagen or fully enclosed within spongin fibres) (Fig. 131A); 6, regularly or irregularly reticulate (with large multispiricular tracts and/or fibres forming irregular oval or rectangular meshes (Fig. 7A-B); 7, plumo-reticulate (producing ascending and consecutively diverging tracts and fibres, forming pauci- or multispiricular primary lines, and interconnected by transverse uni- or paucispicular tracts and fibres) (Fig. 7D); 8, dendro-reticulate (similar to the preceding, but where ascending tracts are sinuous and more obviously diverging and branching than the less conspicuous transverse elements) (Fig. 231C); 9, plumose (with ascending and diverging primary lines that are not connected by transverse elements) (Fig. 7E); 10, axially or basally compressed (having a skeleton clearly divided into a compressed central or basal core of fibres and/or
spicules, forming tight anastomosing meshes, and from which arise plumose or plumoreticulate extra-axial (subectosomal) fibres and/or spicules) (Fig. 7G). Some species have combinations of these skeletal structures with different structural types found in different parts of the skeleton (e.g., axis and periphery).

Structural Regions of the Skeleton. The skeleton may be divided into three main structures or regions (Fig. 1): 1, ectosomal (outer perforated epithelium comprised of single elongate flattened pinacocytes, including an ectosomal skeleton, where present, arising from the mesohyl directly below the exopinacoderm); 2, choanosomal or axial core (central or basal region containing choanocyte chambers, fibres and spicule tracts and the mesohyl ground substance, in addition to the diverse and mobile cell types); 3, subectosomal or cortical zone (strictly part of the choanosome since it lies within the bounds of the external epithelial barrier, but is immediately subdermal, and the delimitation of this region from the choanosome proper is based on the development of an extra-fibre in some species structurally differentiated from the deeper choanosomal or superficial ectosomal skeletons).

This system is used in conjunction with spicule nomenclature (Hallmann, 1912), based on origin of types: 1, principal spicules (Fig. 2A), robust, straight or slightly curved primary styles, subtylostyles, tylostyles or quasi-monactinal forms generally (but not invariably) confined within fibres; 2, auxiliary spicules (Fig. 2B), more slender, curved, sinuous or straight styles, subtylostyles, tylostyles or quasi-diactinal forms most commonly located outside fibres in the ectosomal or subectosomal skeletons, or dispersed throughout the mesohyl; 3, accessory spicules (Fig. 4), styles, acanthostyles or modified quasi-diactinal forms generally echinating fibres. Thus, most species have principal spicules coring fibres (=choanosomal principals), some (e.g., Echinochalina) have coring spicules derived from auxiliaries (=choanosomal auxiliaries), and some (e.g., Clathria (Dendrocia)) lack principal spicules altogether.

Ectosomal Skeleton. Within Microcionidae the ectosomal skeleton has been attributed greater importance (Van Soest, 1984b) than over elements such as choanosomal architecture and growth form (e.g., Lévi, 1960a; Berquist & Fmmon, 1988), microsclere diversity (e.g., de Laubenfels, 1936a), or megascleres echinating fibres and choanosomal spicules (e.g., Hallmann, 1912, 1920). Within the family ectosomal development ranges from membraneous, without an ectosomal skeleton (Fig. 94F); membraneous, with a specialised tangential, reticulate fibre skeleton (Fig. 255C); with an ectosomal tangential reticulation of detritus (Fig. 92A); with subectosomal spicules erect, paratangential or tangential to surface (Fig. 65F), or forming discrete bundles (Fig. 59E); with special ectosomal spicules erect or paratangential to surface, forming a continuous palisade (Fig. 155G) or discrete bundles (Fig. 151F).

Subectosomal Skeleton. The region between choanosomal and ectosomal layers may or may not be differentiated into a subectosomal (subdermal or extra-axial) structure. This region may occupy a small proportion of the peripheral mesohyl (e.g., Holoparmassa; Fig. 269D), or it may comprise the majority of sponge diameter

(e.g., C. (Axociella); Fig. 118F). When present, subectosomal extra-fibre development may be completely disorganised or it may be well organised into radial non-plumose bundles of spicules (Fig. 127B). The composition and geometry of spicules within the subectosomal skeleton varies from species lacking any form of subectosomal spicules (e.g., C. (Microciona); Fig. 102F), those with a single form of auxiliary spicule throughout the skeleton (e.g., C. (Dendrocia); Fig. 112D), those with two categories of structural megascleres, one in the ectsosome and one in spongin fibres (e.g., C. (Clathria); Fig. 73F), to those with three forms of structural megascleres, all of which occur to some extent in the subdermal region (e.g., C. (Thalysias); Fig. 197G), and spicules may be monactinal (for most microcionid species; e.g., Fig. 28A-B), or quasi-diactinal (Fig. 298A-B), or truly diactinal (Fig. 307A-B) as seen in E. (Protophtiaspongia).

Choanosomal Skeleton. In Microcionidae skeletal structures are diverse (listed above), and traditionally important in classification. In terms of differentiated regions within the choanosomal skeleton there are species with simple reticulate fibres without any axial or extra-axial differentiation (Fig. 7C), those with marked axial and extra-axial differentiation of the choanosomal and subectosomal skeletons, which are structurally distinct from the peripheral skeleton (Fig. 7G), and those in which the choanosome is simply reduced to a basal layer of spongin lying on the substrate (Fig. 7H). Similarly, choanosomal skeletal tracts may be diversified into more than one element, including those with no obvious division of primary or secondary skeletal lines (Fig. 159F), those with more-or-less well differen-
tiated primary (usually ascending) and secondary (usually transverse) lines of skeletal fibres or tracts (Fig. 45E), and those in which secondary (choanosomal) connecting tracts may be absent, leaving only radial primary lines (Fig. 227C).

**DISTRIBUTION OF SPICULES WITHIN THE SKELETON.** Coring spicules. (Fig. 2) Spicules coring spongion fibres or forming tracts within the skeleton (bound by loose collagen) range from principal megascleres (e.g., C. (Clathria); Figs 2A, 28A), auxiliary monads (e.g., C. (Wilsonella); Figs 2B, 83A), auxiliary diads or quasi-diads (e.g., E. (Echinolachina); Figs 2B, 280B), haste oxeas (e.g., E. (Protophilaspongia); Figs 2B, 296A), secondarily incorporated echinating spicules (e.g., C. (Thalysias) phorbasiformis; Fig. 183G), acantho principal styles, strongyles or rhabdostyles ‘plumatiform’ species; e.g., A. (Plocamia) ridleyi; Fig. 218C), coring spicules partially or completely absent replaced by foreign particles (detritus, algal filaments) (C. (Wilsonella); Fig. 91F; Holop孒amma; Fig. 257D), primary fibres cored by principal styles, whereas secondary (connecting) fibres contain auxiliary megascleres (e.g., C. (Thalysias) mutabilis; not figured), primary fibres contain auxiliary spicules whereas secondary fibres mostly devoid of any spicules (e.g., C. (Clathria) norulungue sp. nov.; Fig. 55F), axial fibres cored by auxiliary megascleres whereas peripheral fibres heavily arenaceous (e.g., C. (Clathria) echinonematous; not figured).

**Echinating spicules.** (Fig. 4) The presence, absence, distribution, geometry and secondary modification (including ornamentation) of echinating spicules (accessory spicules in the terminology of Hallmann, 1912) have been used as relatively important taxonomic characters by some authors (e.g., de Laubenfels, 1936a), whereas their importance in the supra-specific classification of the microcionids has been recently questioned (Simpson, 1968a; Van Soest, 1984b). The presence of echinating megascleres in the two families Microcionidae and Raspailiidae indicate the retention of an ancestral character by both families, interpreted as a synaplesiomorphy (Hooper, 1991).

In Microcionidae echinating spicules may be absent (e.g., C. (Axociella), Fig. 124F; C. (Isociella), Fig. 134D; presumably to be a secondary loss), echinated sparsely by acanthostyles or styles (e.g., C. (Clathria) nexus; Fig. 53E), heavily echinated by acanthostyles or smooth styles (e.g., C. (Thalysias) procera; Fig. 187G), echinated by a second category of (acanthose) principal spicule (e.g., A. (Antho) tuberosa; Fig. 214F), or with both acanthose principal spicules and true echinating spicules present on fibres (e.g., A. (Plocamia) ridleyi; Fig. 218H).

Similarly, echinating spicules may be confined to the exterior surface of fibres (most microcionids), or clumped on basal spongion only and absent from ascending skeletal lines (e.g., C. (Thalysias) tingens sp. nov.; Fig. 201G), concentrated in tufts at fibre nodes or fibre junctions (C. (Thalysias) spinifera; Fig. 197G), concentrated on exterior edges of fibres, or exclusively on primary fibres, and/or in the peripheral skeleton only (e.g., C. (Thalysias) abietina; Fig. 138F), or secondarily incorporated into fibres (e.g., C. (Dendrocia) myxilloides; Fig. 112D).

**Extra-fibre spicules.** (Fig. 2) The distribution of structural megascleres within the choanosomal skeleton is certainly a feature relied upon by earlier authors (e.g., Carter, 1885 et seq.; Hallmann, 1912), but its value to the supra-specific classification has been recently questioned (Van Soest, 1984b). In most species these megascleres are confined within choanosomal fibres, lying parallel to fibres (e.g., C. (Clathria) raphana; Fig. 67D), or in the case of encrusting species, embedded in basal spongion (e.g., C. (Microciona) illawarrae sp. nov.; Fig. 100F). In other species they may core choanosomal fibres but also occur as plumose brushes on fibre endings (e.g., C. (Thalysias) spinifera; Fig. 197G). Choanosomal spicules may also poke out of fibres, much like echinating spicules (termed ‘spicate’), forming plumose tracts near the surface (e.g., C. (Thalysias) major; Fig. 181A), or they may be absent from the fibre core, standing perpendicular to the nodes or fibre junctions (e.g., C. (Clathria) biclathra; Fig. 30G), strew in loosely aggregated, halichondroid, extra-fibre tracts (e.g., E. (Echinolachina) anomala; Fig. 277A), form a renieroid structure, without a fibre component, but merely bound at the nodes by loose collagen (e.g., C. (Clathria) anguifera; Fig. 26F).

**SPICULE GEOMETRY.** Spicule geometry is an important, sometimes ultimate (e.g., de Laubenfels, 1936a), feature of existing sponge classifications, based largely on the great diversity of megascleres and microscleres throughout the Porifera. This theoretical basis of sponge systematics using the mineral skeleton rests heavily on the assumption that morphogenesis of megascleres and microscleres is a function of the genotype (e.g., Reid, 1963). Whilst there is no
evidence to reject this hypothesis there is certainly some experimental data to show that spicule geometry and morphogenesis is at least partly influenced by environmental perturbations (e.g., Hartman, 1981; Jones, 1991), including examples from the Microcionidae (e.g., influence of seasonality (Simpson, 1978) and geographical distribution (Hooper et al., 1990) on spicule size and geometry). But the extent to which these phenotypic modifications occur within natural populations has not yet been examined rigorously. In general, however, these features appear to be relatively stable across wide geographical ranges as shown by studies on raspaillidiids (Hooper, 1991) and microcionids (Hooper & Lévi, 1993a) from east and west coasts of Australia and the western Pacific. Hartman (1981) and Simpson (1990) outline the various theories on the functional significance, process of silification and evolution of demosponge spicules.

**Structural Megascleres. Spicule axes.** Microcionidae have exclusively monaxonic spicule axes. Megascleres are usually monaxial, although some may have modified secondary axes (i.e., anisoxeotic diactinal modifications to styles), and a few appear to have true diactinal forms (E. (Protophithuscspongia)). Unlike Trikentrition and Cyasimon in the allied Raspaillidiidae (Hooper, 1991) there are no tetraxonic spicule modifications in this family (triactinal, tetractinal or polyaclinal forms). Furthermore, the Microcionidae have a comparatively small range of structural megascletere types in the skeleton, whereas some raspaillidiids have many. Major types of structural megascleeres are illustrated in Figs 2-4. These range from hastate styles or tylostyles (Fig. 87A), fusiform styles or tylostyles (Fig. 77A), asymmetrical styloid, rounded, quasi-diactinal or strongylote spicules (Fig. 280B), and oxote megascleeres (Fig. 296A).

**Spicule ornamentation.** Spines on megascleeres are of dubious importance to supraspecific classification (e.g., Simpson, 1968a), although they have been used frequently in the past to define genera (e.g., de Laubenfels, 1936a). Microcionid structural spicules frequently have basal microspines (Fig. 2C-D), occasionally with spines on shafts (Fig. 180B) or points of spicules (Fig. 3D). Spicule ornamentation ranges from entirely smooth (Fig. 28A), smooth shafts with acanthos e bases (Fig. 30A), vestigial spination on the proximal portions of shafts only (Fig. 153A), acanthose on both bases and points (Fig. 83A), or entirely acanthose (Fig. 98A).

**ECHINATING MEGASCLERES.** There is a diverse range of echnating spicule geometries in Microcionidae, although not as great as in Raspaillidiidae. Major types (Fig. 4) include: evenly spined (granular), claviform or stump-like acanthostyles; acanthose styles with aspinose bases; acanthose styles with aspinoce points; acanthose styles with aspinoce 'necks' (i.e., area proximal to the basal swelling); acanthostrongyles; entirely smooth styles identical in geometry to principal megascleeres; derived oxotees; or entirely smooth styloles of different geometry than principal spicules.

**Microscleeres.** The geometry, ornamentation and modification of microscleeres is an important character for classification (Dendy, 1921), although it has probably been overemphasised by some authors (de Laubenfels, 1936a) and its primary importance has been questioned (Van Soest, 1984b). Within Microcionidae there are two forms of diactinal microscleeres: meniscoid forms (chelae) and toxas. Other poeciloscleere microscleeres (microxeas, raphides and meniscoid forms such as true sigmas) are not present. Microcionids show many modifications to both chelae and toxas, the latter sometimes resembling microxeas, and frequently microscleeres are lost altogether.

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CHELAE. These are autapomorphic for Poecilosclerida, although Hajdu et al. (1994b) suggested that the *Isodictya* might belong to Haplosclerida (with chelae retained as an ancestral feature), although it is more likely that its niphatid-like isodictyal skeleton is merely convergent on the haplosclerid condition. There are many geometric modifications possible to chelae (Fig. 5) which Hajdu et al. (1994a) proposed could be accommodated into three main lines: palmate, arcuate and anchorate (the latter two also termed bidentate- or tridentate-derived). These authors hypothesised further that chelae geometry might be an absolute indicator of phylogeny for the Poecilosclerida based on the assumption that they might be less susceptible to phenotypic modifications than structural spicules, following the arguments of Dendy (1921, 1922). This interpretation is based on parsimony and to some extent is corroborated by
other evidence (such as congruence of structural features). There are, however, some anomalous examples of chelae that fall between these three categories (see Discussion).

Palmate. (Fig. 5A-B) This is the simplest form with 'typical' morphology consisting of straight shaft, front alae completely free and well developed, and lateral alae more-or-less completely fused to the shaft along its longest dimension. Most micriscionids have unmodified 'typical' palmate isochelae. Modifications to this 'typical' palmate form include: partial reduction of alae (Fig. 5B), nearly vestigial alae producing a sigmoid spicule (Fig. 5C), partial fusion of alae along lateral margins producing spatulæ (Fig. 5E), partial fusion (Fig. 5G) or complete fusion along medial margins in which both the front alae meet and/or fuse at the centre producing cleistochelae (Fig. 7G), sculpturing on fluting on alae (Fig. 5J), contortion of the shaft such that alae are at 90° to each other at each end of the shaft (Fig. 5F), expansions of the lateral alae fused with the shaft producing wing-like process on the shaft (Fig. 5H), 'crocaë' or j-shaped sigmoid forms where the alae are vestigial and asymmetrical, producing a simple hook-like spicule (Fig. 17F), and deep curvature of shaft and reduction of alae to tooth-like structures (termed unquiferous; Fig. 5R-T).

Arcuate. (Fig. 50) Here the lateral alae are more fully developed than in palmate forms and become almost completely detached from the shaft, and the shaft is usually prominently curved and thickened. However, there is no clear transition between the palmate and arcuate forms, whereby an increase in curvature and thickening of the shaft (Fig. 5D-E) and partial detachment of lateral alae (Fig. 5J-K) extend along a continuum from true palmate to true arcuate (compare Fig. 5D-G, J-L, N-Q, T). Somewhere along this continuum chelae are deemed to be arcuate (Fig. 5O-P).

Anchorate. (Fig. 5U) Further along the continuum are anchorate chelae, in which all three alae are fully formed, the lateral ones completely detached from the shaft, and there are also lateral ridges on the shaft. In this study I use the terms 'arcuate-like' or 'anchorate-like' for modified chelae although it is equivocal whether these spicules are truly arcuates or anchorates.

TOXAS. Toxas are found in only a few families of poecilosclerids but also known from Haplosclerida. There is also some evidence to suggest that they may be particularly common in young or larval tissue (e.g., Simpson, 1968b). Eight major morphotypes are delineated here (Fig. 6), although intermediates are also possible: 1. Oxhorn toxas (wide central curve, reflected arms and greatly recurved points; usually thick) (Fig. 6A); 2. Wing-shaped toxas (sharply curved at centre, with recurved alae and reflexed points; usually thick) (Fig. 6B); 3. U-shaped toxas (with wide central curvature but lacking reflexed arms) (Fig. 6C); 4. V-shaped toxas (pinched hairpin-like central curvature, straight arms running more-or-less vertical, and slightly reflexed points; usually thick) (Fig. 6C); 5. Oxeote toxas (virtually straight and points) (Fig. 6D); 6. Accolada toxas (wide or slightly pinched central curvature, straight arms running more-or-less horizontal, and straight points; usually thin) (Fig. 6E); 7. Raphidiform toxas (sharply angular central curvature, straight arms and straight points; very thin, hair-like) (Fig. 6F); and 8. Sinuous toxas (asymmetrical, sinuous, raphidiform; very thin, hair-like) (Fig. 6F). The presence or absence of microspines on toxas was at one time considered to be an important supraspecific character (e.g., de Laubenfels, 1936a), but these have since been found in many genera and may not be important above the species level.

SIZE OF SPICULES. Variation of spicule size has also been an important diagnostic criterion, but this has been applied mainly at the species level of classification. Numerous (possibly a majority) of taxa have been erected solely on the basis of megasclere and microsclere dimensions, but only a few studies have investigated the statistical variability of spicule size or commented on the effects of physico-chemical factors on that variability (e.g., Hartman, 1958, 1981; Jones, 1984). There is some evidence to show that intraspecific variability can be significant for a given taxon, and spicule size-ranges can span across several closely related taxa which were otherwise erected solely on that basis. Hooper et al. (1990) demonstrated that two sibling species of Clathria (Thalysias) could not be reliably distinguished by their absolute spicule sizes, and only statistical comparisons between these species were of any value in this regard. Thus spicule dimensions used as diagnostic characteristics are of most significance at the species level of classification, and consequently their application is generally comparative rather than absolute.

ORGANIC SKELETON. The development of the organic skeleton, the amount of spongin it contains, its architecture and foreign inclusions contained within it, are diagnostic features for the Demospongiae in general. The organic skeleton
can be differentiated into two components: a fibre system and a collagenous mesohyl.

**Spongin fibres.** These may be well developed, present but relatively lightly developed, secondarily lost, with or without spicule tracts, or even replaced partially or entirely by algal filaments (e.g., *Anomocathria* (Fig. 9A-B)). Simpson (1984) elucidates two morphological types of spongin fibres (= type A spongion of Bergquist, 1978a): those that are cored by siliceous spicules and those that incorporate foreign particles.

Detrital-entrapping fibres are most prevalent in the ‘keratose’ sponges (*Dicyoceratida, Dendrocetida, Verongida*), Haplosclerida (*Arenosclera*), and Poecilosclerida of the Desmacididae (*Psammosclera, Desmazia*), as well as several species of Microcionidae (i.e., *C. (Wilsonella*) and *Holoptisoma*). In these species fibres may be totally void of true megascleres (e.g., *Holoptisoma laminaeovosa*), or they may have a combination of both foreign particles and indigenous megascleres (e.g., *C. (Wilsonella*) *tuberosa*). The independent occurrence of detrital-entrapping fibres throughout the various orders of Demospongiae indicates that it is a character of ecological importance rather than of any phylogenetic significance.

Spiculose fibres are typical for microcionids, and the form, size, orientation and origin of megascleres coring the organic skeleton, and the structural complexities of the fibres themselves are important diagnostic characters for this family. In encrusting species that have a basal layer of spongin anchoring themselves to the substrate this spongion is continuous with the spiculated fibres, and as such both actually lie outside the living organism (Weissenfels, 1978). **Mesohyl.** The development of collagen in the mesohyl matrix, also termed ‘interstitial’ spongion, extra-fibre spongion, type B spongion (Bergquist, 1978), or ground substance, and including collagenous fibrils, has not been given much value as a systematic character for the Microcionidae, whereas in the ‘keratose’ orders

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these features have more significance, and in
\textit{Aiptos} (Hadromerida) it has been used to dif-
ferentiate species through deposition patterns
(Kelly-Borges & Bergquist, 1995). However,
within the Microcionidae there is evidence to
show that the development of collagen
throughout the mesohyl varies intra-specifically,
especially between specimens in different
reproductive condition or as a consequence of
overwintering behaviour (e.g., \textit{Pandaros acan-
thifolium}; Wiedenmayer, 1977; Van Soest,
1984b; \textit{Microciona prolifera}; Simpson, 1963,
1968b; Knight & Fell, 1987). Simpson (1968a)
tried to define species and genera of
Microcionidae on the basis of the organic
skeleton and cytological characteristics but to a
large extent his results did not corroborate with
a classification based on the mineral skeleton, and
in some cases evidence was directly conflicting.

Growth Form. The use of external morphology
as an important or even crucial diagnostic char-
acteristic has diminished since early systematics
(e.g., Lamarck, 1814). Bowerbank (1864), in
developing Grant’s (1861) scheme for the
Porifera, de-emphasised sponge habit in his sys-
tematics although he recognised that growth form
was related to ‘anatomical peculiarities’. That
external morphology is often closely linked to the
internal architecture and composition of the
skeleton has been well documented (e.g., Lévi,
1973; Bergquist, 1978). Although there are some
groups which are immediately recognisable by
their growth form and skeletal architecture (e.g.,
the honeycomb reticulate structure of \textit{Holop-
samma}), other groups show a higher degree of in-
specific variability in their morphology (e.g.,
most \textit{Clathria}), ranging from encrusting to mas-
sive forms. Moreover, there is now evidence to
suggest that gross morphology is highly plastic,
greatly influenced by prevailing environmental
conditions (temperature, depth, turbidity, cur-
cents, substrate etc.) (e.g., Hartman, 1958;
Simpson, 1968a; Fry, 1971; Palumbi, 1984). It is
not entirely clear to what extent abiotic factors
influence growth form, or the degree to which
genotype dictates possible shapes attainable by
particular species, but it is becoming more ap-
parent that the sponge ‘species’ is not as im-
mutable as previously suspected. Palumbi (1984)
proposed that sponges have evolved to be capable
of producing a quick and decisive response to
environmental adversities (unpredictable, high
energy environments), and those responses are
most readily seen as changes to both growth form
and skeletal structure (e.g., the degree to which
the skeletal becomes compressed). It also is not
clearly understood why some species seem to be
highly plastic (e.g., \textit{C. (Thalysias) lendenfeldi})
(Hooper et al., 1990), whereas others with com-
parable depth and geographical distributions are
much more conservative (e.g., \textit{C. (Thalysias)
abietina}). Growth forms, as characters used in a
classification, can be defined as determinate (e.g.,
\textit{Holopamma}, \textit{C. (Microciona)}) or indeterminate
(e.g., most other \textit{Clathria}, \textit{Antho}).

Consistency. Sponge texture is a highly sub-
jective characteristic, which is difficult to quantify,
but one which may provide clues as to the com-
position of the skeleton, the amount of spongin
present, whether or not detritus is incorporated
into the sponge, and silification of the skeleton
(Bergquist, 1978). A description of sponge con-
sistency is usually an integral part of any species
description, but its application in systematics has
been mostly comparative rather than absolute.
More recently de Weerdt (1985) used consistency
as an objective feature in the systematics of
Haplosclerida. She noted that it was not only
useful in characterising particular species but that
in broad terms, texture was able to be used at the
family level of classification. For the
Microcionidae this character does not vary great-
ly, with most species being firm, compressible,
flexible (e.g., \textit{Clathria (Thalysias)}) or soft, com-
pressible, spongy (e.g., \textit{Holopamma}).

Macroscopic Features of the Surface. Surface
sculpturing. Macroscopic features of the
sponge surface are important for some sponge
groups (e.g., Haplosclerida), and surface or-
namentation, such as tangential webs of spicules
or fibres, perpendicular brushes of spicules, or
elevated oscules may be diagnostic for particular
genera. Within the Pocillopsclerida however, in-
cluding the Microcionidae, these features are less
consistent, and they are usually only reliable in
characterising particular species or occasionally
genera (Simpson, 1968a). Encrusting species fre-
cently exhibit intricate drainage canals radiating
away from oscules, or highly hirsute (furry) sur-
faces (e.g., \textit{C. (Thalysias) texifera}), whereas
more massive or digitate species may have sur-
facer papillae or conules (e.g., \textit{C. (Thalysias)
abietina}), or a surface which is composed of
reticulate ecosomal fibres (e.g., \textit{Holopamma}
globosa).

Oscules. The distribution of oscules on the sur-
face may vary considerably between related
species, ranging from being confined to distinct
pore areas, such as sieve-plates of *Echinochalinia tubulosa*, or restricted to certain regions, such as lateral sides of branches, the tops of digits, or the exterior surface of vases, or scattered indiscriminantly over the surface. Oscules may also be conspicuous, discrete, with a membranous lip, slightly raised or flush with the surface (e.g., *C. (Thalysias) reinwardtii*), or terminal, raised on the apex of surface papillae or stoloniferous tubes (e.g., *C. (Isosciella) eccentrica*), or scattered, conspicuous, producing a porous reticulate surface (e.g., *Holopsumma arborea*), or minute and not easily visible optically (e.g., *C. (Thalysias) coppingeri*).

**Colouration.** Sponge pigments are not generally diagnostic (Bergquist, 1978). Some species may show high intra-specific variation in live pigmentation, and this variability may be related directly to microhabitat and depth distribution. The nature of these pigments, their distribution within the mesohyl and their specific cellular association is still poorly known, but it is well established that carotenoids are predominant (Simpson, 1984). Isolation and identification of these pigments is more difficult, as is the determination of whether they are produced or modified by the host, or obtained directly from symbiotic associations (e.g., Litchfield & Liaaen-Jensen, 1980). The major proportion of sponge carotenoids are metabolised by the sponge (i.e., primary metabolites) and are intracellular (Simpson, 1984), whereas it is suspected that some sponges have a variable proportion (up to 20%) of pigments synthesised by symbiotic algae (e.g., Litchfield & Liaaen-Jensen, 1980; Liaaen-Jensen et al., 1982). Litchfield & Liaaen-Jensen (1980) studying *C. (Microciona) prolifera* suggested that the sponge could modify (aromatise) a large proportion of algal carotenoids, and Liaaen-Jensen et al. (1982) divide the classes of carotenoids into a phytoplankton-type, zooplankton-type, bacterial and/or fungal origin, and sponge metabolised (oxidative) groups. These authors found that phytoplankton derived and sponge metabolised carotenoids comprised the major proportion of carotenes in Demospongiae. The Poecilosclerida and Axinellida were found to exhibit the highest capacity for carotenoid accumulation and transformation, explaining their diverse and often brightly coloured pigmentation, and furthermore they possessed a similar carotenoid diversity.

Evidence suggests that carotenoid pigments may be photoprotective, in which case it would be expected that intertidal species contain a higher proportion of these pigments than deeper-water species. But it is not clear why some sympatric species have consistent pigmentation (e.g *C. (Wilsonella) tuberosa*), whereas in others pigmentation is highly variable even in specimens growing side-by-side (e.g., *C. (Thalysias) abietina*; Plate 4D). Colour consistency is not generally used as a reliable diagnostic character, but it is also true that only very few authors have investigated the intraspecific colour variability of any species. It is therefore advantageous to determine whether live colouration is stable and specific to a species, or has very narrow limits in variation (e.g., *C. (Isosciella) eccentrica*). Alternatively, pigmentation may be highly unstable, not specific and without an accurately definable ‘typical’ colouration (e.g., *C. (Thalysias) abietina*).

**Reproductive Products and Reproductive Cycles.** Reproductive products and modes of reproduction, as diagnostic characters, have been used predominantly at higher levels of classification (e.g., Bergquist, 1980a), whereas breeding seasons and spawning cycles are most useful for detecting sibling species (e.g., Fromont, 1989). As far as known, within the Microcionidae larvae are viviparous parenchymella with bare posterior poles. The apparent form of sexuality varies from gonochoristic to contemporaneous hermaphroditism (Fell, 1984; 1990; Simpson, 1984). Breeding seasons and/or spawning cycles may be continuous or periodical.

**Cytology.** Simpson (1984) provided a definitive treatment of sponge cell biology, including a description of diverse cell types and their functional morphology. He suggested that descriptions of characters such as cells with inclusions and the morphology of choanocyte chambers will probably provide further information directly relevant to demosponge systematics. For the Microcionidae, Simpson (1968a) showed that seemingly morphologically convergent genera could be readily differentiated by the presence and morphology of special cell types (gray cells), and that their higher systematic relationships could be defined in terms of cytological characters. However, there were many incongruities between systematics based on skeletal characteristics and those indicated by cytological data. Specific examples of these differences are discussed below in the synopsis of genera, but some general comments are appropriate.

Taxonomic groupings indicated by Simpson's microcionid cytological data suggested that many skeletal characters used previously by authors
had little importance in differentiating genera. These included the presence or absence of palse
tate isochelae, the presence of acanthoceph versus
smooth echinating megascleres, quantity of spongi
in the skeleton, plumose versus anastomosing fibres, megascleres with basal spination or
smooth bases, the presence of surface conules and
distinct oscules, the production of upright branches, and the presence or absence of an ec-
tosomal skeleton. With the exception of the last
feature these conclusions are supported in the con-
temporary classification of Microcionidae (e.g., Van Soest, 1984b). However, other
cytological evidence presented by Simpson (1968a) is more difficult to reconcile with
microcionid skeletal data. For example, encrust-
ing species (i.e., the nominal genera Microciona
and Ophitiaspiongia) were cytologically relatively-
ly homogeneous and distinct from ramose forms
(Clathria). The cytological characteristics of
these encrusting species were more similar to
renieroid microcionids (nominal genus Plocamil-
la) than they were to the ramose forms (nominal
genera Rhabdophillus and Thalysias) which
otherwise had the most similar spicule and sur-
ficial characteristics.

Simpson concluded that generic definitions
based primarily on spicule types did not lead to
natural classifications, and he proposed that these
definitions should include skeletal, cytological
and histological evidence. He suggested that the
numerous classification systems that were based
solely on various combinations of skeletal char-
acters, such as those of Vosmaer (1933, 1935a-b),
de Laubenfels (1936a) and Lévi (1960a), could
be defended with equal justification. Although
some cytological features have been incorp-
ated into existing systematics (e.g., morphol-
ogy and arrangement of choanoctyes), much of
Simpson’s (1968a) important work cannot be
used in classification based primarily on skeletal
characters.

SYSTEMATICS

Class Demospongiae Sollas, 1885

Order Poecilosclerida Topsent, 1928

Suborder Microcionina Hajdu, Van Soest &
Hooper, 1994

Poecilosclerida Topsent, 1928a: 64, 309.

REMARKS. This order is the largest and most
diverse of Demospongiae (Bergquist 1978). It is
characterised by a skeleton of both spicule and
spongian elements, usually well developed, some-
times vestigial, in which megascleres are monac-
tinal, diactinal or both, and spongin development
varies from well developed horny fibres enclos-
ing spicules to an interspicular collagen cement
(Bergquist, 1978; Hartman, 1982). Simpson
(1984) suggested that the order is characterised
by at least two distinctly localised types of
megascleres (with or without distinctive
geometry). Those megascleres are chaonosomai
principal spicules embedded in spongin fibres,
and subectosomal auxiliary megascleres which
are free in the mesohyl or protrude from spongin
fibres in which they are embedded. This defini-
tion is consistent with the inclusion of
Raspaillidae in the Poecilosclerida as proposed
by Hooper (1991). Poecilosclerids usually have
an abundantly collagenous mesohyl matrix, and
microscleres may include chela (apomorphic
for the order), although not all taxa have them.
Sexual reproduction is predominantly
viviparous, oviparous in two families, and in
those species inciting larvae they are
parenchymella with uniform flagellum size and
bare posterior poles.

The suborder Microcionina was established to
include four families of Poecilosclerida
(Microcionidae, Raspaillidae, lophonidae and
Rhabdermiidae), which have terminally spined
ectosomal monactinal megascleres (occasionally
modified to quasidactinal forms), isochelae of
palmate origin, diverse forms of toxas, up to five
categories of megascleres and lacking sigmas.
The other suborders (Myxillina and Mycalina)
were also defined by their chela morphology
(bidentate-derived and sigmancistra-derived
cheles, respectively), and absence of toxas and
presence of sigmas, respectively (Hajdu et al.,
1994), but assignment of particular genera to
these suborders is still contentious.

The number of families recognised in the order
varies according to different authors (e.g., Lévi,
1973; Wiedenmayer, 1977; Bergquist, 1978;
Hartman, 1982; Van Soest, 1984b; Bergquist &
Fromont, 1988). Recently Hooper & Wieden-
Desmacellidae, Cladorhizidae, Guitarridae). Latrunculiidae, included in the order by Lévi (1973) and Van Soest (1984b) has also been assigned to Hadromerida (Reid, 1968; Bergquist, 1978; Hartman, 1982), but is now considered to be polyphyletic (Kelly-Borges & Vacelet, 1995) with Latrunculidae having affinities with Iophonidae and Diacaruns, Sigmoseptrella, Negombata more closely related to the Mycalidae.

Family Microcionidae Carter, 1875

Ophitiaspongiidae de Laubenfels, 1936a; Thomas, 1968; Hoshino, 1981.

Growth form encrusting, lobate, arboreaceous or flabellate; skeleton differentiated into choanosomal (axial), subectosomal (extra-axial) and ectosomal regions; axial skeleton formed by uniserial or multiserial tracts of choanosomal (principal) megascleres, typically coring spongin fibres or sometimes simply bound together by collagen; fibres echninated by (acantho-) styles (accessory spicules); skeletal structures include isodictyal, renieroid, reticulate, plume-reticulate, plumose or hymedesmoid, but never radial; extra-axial skeleton formed by tracts of subectosomal (auxiliary) spicules, usually dispersed outside of fibres, rarely well organised but usually with some degree of difference between axial and extra-axial regions; ectosomal skeleton ranges from membraneous, or with protruding subectosomal (auxiliary) spicules, or with a special category of ectosomal (auxiliary) spicules; principal megascleres monaxial, rarely quadriaxial, smooth shaft and basal spines, more slender than choanosomal spicules; echinating styles or subiyloydons smooth, partially or completely spined; microscleres include toxas of several morphologies (including raphidiform and microxoecotes), and isochela primarily of palmate origin (but occasionally with partial 'arculus' and 'anchorate' modifications); larvae viviparous.

REMARKS. There has been disagreement as to which of Microcionidae Carter and Clathriidae Hentschel should be used. Wiedenmayer (1977: 139) argued that Microcionidae was established in 1875, whereas Clathriidae did not appear until 1884. He noted that under Article 40 of the International Code of Zoological Nomenclature (Anonymous, 1984), it was irrelevant whether or not Clathria Schmidt (1862) had priority over Microciona Bowerbank (1862; apparently published 1863). Conversely, Van Soest (1984b: 89) argued that the priority of Clathria over Microciona did have bearing on the choice of the family name. Although 'Clathriidae' is in current usage by most contemporary workers, its preferred use is in direct contravention with the Code and to long term stability of the group and Microcionidae is used here following Hooper & Wiedenmayer (1994).

The definition given above restricts Microcionidae to genera which possess predominantly smooth monaxial ectosomal and choanosomal spicules. It excludes certain microcionid-like genera which have true tyloids or strongyloids as their ectosomal spicules (e.g., Acaruns, Megaciella). These taxa are now referred to Iophonidae, as defined by their ectosomal features (Hajdu et al., 1994). However, the definition barely distinguishes species with modified or reduced quasidactinal (styloid) auxiliary megascleres (e.g., several Echinoclathria, Holopsaumaria and Echinogalina species), or quasimonomaxial (amphistrongyloid or tomouth-like) auxiliary megascleres (e.g., E. (Protophitiaspongia)). These modified auxiliary spicules are usually asymmetrical and are interpreted here as convergent upon true dactinal spicules. These anomalous microcionids share certain characteristics of both Microcionidae and Desmacididae, and the importance of these characters at higher levels of systematics must therefore be questioned, or a certain level of homoplasy must be accommodated in the phylogeny of the order.

Similarly, the definition given above cannot always clearly distinguish some Microcionidae and Raspailiidae, but this is a problem of semantics rather than a biological one. As a general rule most species of Raspailiidae have well compressed axial skeletons, and well differentiated axial and extra-axial skeletons. In contrast, most Microcionidae lack these features or they are only poorly developed and probably convergent, perhaps related to growth form (e.g., Clathria (Axiocellia)). Nevertheless, there are examples in both families where the boundaries between taxa blur, such as the microcionid-like Raspailia (Clathriodendron) arborea (see Hooper 1991: Figs 19-
20), and the raspailiid-like Clathria (Axociella) canaliculata (Figs 118-119)). These families are consistently differentiated by their euctomal features and microscleres, which appear to be more important characters than skeletal structure.

Hajdu et al. (1994) restricted Microcionina (and hence Microcionidae) to taxa with only palmate isochele, tacitly excluding several microcionid-like genera specifically created for species with bidentate-derived (arcuate or anchorate) chelae. Theoretically this is a viable system for the suprafamily classification of Microcionidae but in practical terms it is not always possible to distinguish between true bidentate-derived chela and palmate chela with ‘arcuate-’ or ‘anchorate-like’ modifications. These cases are discussed individually below.

REVIEW. There are several problems in the taxonomy of Microcionidae that need to be addressed in order to clearly recognise and define valid genera and produce a phylogenetically valid systematics for the family.

1) The family is large, containing about 540 described species and many other as yet undescribed species known from various collections. 79 nominal genera have been previously included, of which 69 are currently recognised as residing here although fewer than this number are valid. Some of these genera have been merged in others by previous authors (e.g., Lévi, 1960a; Simpson, 1968a; Van Soest, 1984b; Bergquist & Fromont, 1988; Hooper, 1990a), but in some cases these synonymies are now deemed wrong and have produced further nomenclatural complexities. Several contemporary studies have attempted partial revisions of Microcionidae (Van Soest, 1984; Bergquist & Fromont, 1988; Hooper, 1990a), but these have mainly focused on smaller regional faunas without consideration of all the higher taxa. In the present work each of these genera is redefined and illustrated from its type species (i.e., strict definition).

2) The literature on Microcionidae is vast, scattered, mostly antiquated (pre-1900), descriptions are far too brief for modern purposes and many taxa have never been illustrated. The present work deals primarily with museum material and living populations of species, and decisions are less reliant on the literature than previous studies.

3) There are many characters in sponges whose expressions (character states) change subtly within populations of supposedly single species and across the whole range of species, usually without clear boundaries between related taxa. Some of these characters have been used as important diagnostic criteria in earlier works. This study has examined large numbers of specimens and species, and documents the range of intraspecific and inter-specific character states in an effort to clearly define taxa and understand relationships between them. Inclusion of non-skeletal evidence into the systematics can further support or refute opinions based solely on skeletal characters and gross morphology (to decide whether one character is more important than another, whether morphological characters are homologous, and whether the observed high levels of homoplasies within most Porifera classifications are in fact real or acceptable). The previous studies of Hooper et al. (1990) and Hooper (1990a) are preliminary to this study.

4) There are nearly as many subjective interpretations between different authors, as to the phylogenetic importance of one character over another in the systematics, as there are taxa. This has arisen partly as a consequence of over reliance on definitions of type species (and hence nominal genera) from the literature (especially the work of de Laubenfels, 1936a), given that many type species are poorly described, misdescribed or barely differentiated from their congers. The present study uses a phylogenetic framework to produce an objective and consistent taxonomy for the family. Two previous studies (Van Soest, 1984b; Hooper, 1990a) partially resolved infrafamily relationships within Microcionidae, both are preliminary to this work.

GENERIC NAMES INCLUDED IN MICROCIOnIDAE

Preoccupied generic names are shown in square brackets. The synonymy lists provided in this section refer to works in which the name is used and in the case of genera considered valid do not include the numerous synonyms. The diagnoses provided in this list are based solely on the type material of the type species unless otherwise stated.

[Abila] Gray, 1867. (Fig. 8A-B)

Abila Gray, 1867: 539.
Not Abila Gray, 1867: 522.

TYPE SPECIES Microciona laevia Bowerbank, 1866: 124 (by monotypy) (holotype BMNH1877.5.21.1543).

Encrusting growth form. Surface hispid, even. Choanosomal skeleton composed of short
plumose spongion fibre nodes, cored by very long smooth or basally spined choanosomal principal styles, with only slightly swollen bases, and with bases embedded in spongion fibres on substrate and points protruding through ectosome. Echinating acanthostyles erect on substrate. Sub-ectosomal skeleton of a single category of very long, curved, sinuous or straight subectosomal auxiliary subtylostyle, with smooth or microspined bases, forming irregular brushes on ectosome. Special ectosomal spicules absent. Microscleres thick wing-shaped toxas. Isochelae absent.

REMARKS. Gray (1867) used the generic name Abila on two occasions, for two separate taxa. The senior name (Gray, 1867: 522) refers to a species originally described in Raspailia (viz. R. freyerii Schmidt), which Strand (1928: 52) unnecessarily proposed a replacement name Abilana Strand and which is a junior synonym of Raspailia Nardo (Strand should have replaced the junior name). The junior name (Gray, 1867: 539) was used for a microcionid, M. laevis Bowerbank, related to Microciona in skeletal structure, and related to Thalysia erythraea de Laubenfels in lacking isochelae and having an encrusting growth form. De Laubenfels (1936a: 112) merged Abila with Hymantho Burton (see below), and Van Soest (1984b: 90) subsequently reduced Hymantho into synonymy with Clathria. Re-examination of the type species shows that the genus belongs with Clathria (Microciona).

Alloca Hallmann, 1920
(Fig. 8C-E)


TYPE SPECIES. Spaniolioplax chelliferum Hentschel, 1911: 362 (by original designation) (holotype ZMB4440, paratype SMF1571).

Arborescent, foliose, planar growth form. Surface hispid, uneven. Choanosomal skeleton reticulate, with multispecific ascending primary fibres and paucispicular transverse connecting fibres. Spongion fibres heavy, cored by styles and tyloites (also scattered throughout mesohyl), echinated by acanthostyles with spine shafts and bases, apinose 'necks', and large recurved spines. Subectosomal region with ascending primary fibres cored by choanosomal principal styles, latter protruding through surface. Ectosomal skeleton with both tangential and paratangential layers of auxiliary spicules, latter protruding from peripheral fibres and also lying tangential to surface. Megascleres completely smooth principal styles of a single size category, smooth subectosomal auxiliary stylole spicules, with asymmetrical rounded and microspined ends, and acanthostyles. Microscleres palmate isochelae of two sizes. Toxas absent.

REMARKS. Hentschel (1911, 1912) expressed doubts concerning the initial generic assignment of S. chelliferum suggesting it showed certain affinities with Ectodoryx Lundbeck. Hallmann (1920) created Alloca to receive the species, including it in Microcionidae because of its 'typical' microcionid microscleres, echinating and coring megascleres. For similar reasons Dendy (1922: 70) merged the type species with Clathria. Based on its described ectosomal characteristics, supposedly consisting of true tylole spicules, the genus would be assigned to Ilophonidae (see discussion for Acarnus), but re-examination of the type material found that these spicules were asymmetrical, modified styles very similar to those found in Clathria (Thalysia) major.

Alloca is monotypic and belongs in Clathria (Clathria). The type species is known from the north and southwest coasts of Australia (Arnhem Sea and Perth region), Amirante (Indian Ocean), and New Zealand (Bergquist & Fromont, 1988).

Anaata de Laubenfels, 1932
(Fig. 8F-H)

Not Anaata Semenov, 1906.
Anaata de Laubenfels, 1930: 27.

TYPE SPECIES. Anaata spongigartina de Laubenfels, 1930: 27 (by original designation) (holotype USNM21428).

Encrusting growth form. Surface hispid, even. Choanosomal skeleton hymedesmoid, with bases of both echinating acanthostyles and choanosomal principal subtylostyles embedded in basal fibres. Ectosome with dense erect palisade of subectosomal auxiliary subtylostyles overlaying choanosomal megascleres, both protruding through surface. Megascleres principal choanosomal styles with prominently acanthose bases and partially acanthose shafts, echinating acanthostyles with apinose points, and auxiliary subtylostyles of a single size category, being completely smooth. Microscleres two size categories of palmate isochelae with arcuate modifications (strong curvature, partially detached lateral alae, slightly pointed unguiferous teeth). Toxas absent.
REMARKS. De Laubenfels (1932: 90) suggested that *Anaata* was characterised in part by lacking echinating acanthostyles, although he noted that two size categories of choanosomal megascleres may be present. However, in the holotype the smaller category of spined spicule standing perpendicular to spongins fibres are true echinating acanthostyles, as found in most other microcionids. These smaller spicules are predominantly spined, whereas larger choanosomal spicules are only partially spined and are principals.

*Anaata* was originally assigned to Hymedesmiidae Topsent, compared with genera such as *Leptosiosis* Topsent (1927: 13) and *Leptosara* Topsent (1904a: 194) (both of which have choanosomal tomotes with polytylote or anisotomote modifications, and aniscoelae). All three genera have hymedesmoid architecture, which is persistent in Hymedesmiidae but also seen in many encrusting Microcionidae. Van Soest (1984b) mentioned that *Anaata* differed from other thinly encrusting microcionids, such as *Clathria* (*Microciona*) having arcuate isochelae replacing (or in addition to) palmate isochelae. It is questionable, however, whether these chelae are truly arcuate (as defined by Hajdu et al., 1994), given that their lateral alae are fused to the spicule shaft more than half way along their length. The smaller chelae are more-or-less evenly curved, slightly unguiferous (with reduced, slightly pointed alae), and lateral alae are fused to the shaft for about three-quarters their length. The larger spicules have more pronounced central curvature, they are more unguiferous (alae are reduced, sharper), and lateral alae are fused to the shaft for only about half their length. *Anaata* is considered here to be a *Clathria* (*Microciona*) with hymedesmoid architecture and chelae with slight 'arcuate' modifications.

**Anomoclathria** Topsent, 1929
(Figs 81, 9A-B)

**Anomoclathria** Topsent, 1929: 26.

**TYPE SPECIES.** *Alcyonium opuntioides* Lamarek, 1815: 164 (by original designation) (lectotype MNHNLBIMDT564).

Erect, arborescent or flabellate-digitate growth form. Surface smooth, not hispid. Choanosomal skeleton divisible into two components. Ascending primary skeleton plumose, with spongins fibres cored by paucispiracular tracts of choanosomal principal styles and also incorporate algal filaments. Secondary basal skeleton renicroid reticulate, with spongins fibres fibres cored by large acanthostyles also grouped into plumose bundles on surface and secondarily incorporated into ascending primary fibres. Echinating spicules absent. Ectosome with sparse tangential skeleton of subectosomal auxiliary subtylostyles. Megascleres smooth choanosomal principal styles, acanthostyles with large spines in renieroid skeleton, with same morphology as principal spicules, and smooth subectosomal auxiliary subtylostyles. Microscleres palinate isochelae, wing-shaped and accolada toxas.

REMARKS. This diagnosis on the lectotype differs slightly from Topsent's (1929, 1932) redescriptions of the species, particularly in the emphasis on the secondary renieroid skeleton overlaying the ascending plumoreticulate primary skeleton. This is a prominent diagnostic feature of *Antho*. In *A. (Antho)* the secondary renieroid skeleton is composed of acanthostyles, as described above for *A. opuntioides*, whereas in another species originally referred to *Anomoclathria*, *Spongia fromidifera* Lamarek, 1814: 445 (lectotype MNHNLBIMDT565), the spicules forming the renieroid skeleton are acanthostyles (diagnostic for *A. (Plocanaria)*). Topsent (1932: 103) considered that *S. fromidifera* a junior synonym of *A. opuntioides*, whereas Lamarek's type material shows that their differences in a number of characters, including spicule geometry, is sufficient to warrant species level separation.

*Anomoclathria* was erected on the basis of 'styloproolithese' (Topsent, 1929), whereby algal filaments are incorporated into spongins fibres, partially or completely replacing the coring choanosomal spicules. But this symbiosis has subsequently been shown to be relatively common in marine sponges (Scott et al., 1984), occurring in many families (e.g., Bowerbank, 1862a; Carter, 1878; Lendenfeld, 1886b; Topsent, 1929, 1932, 1933; Weber-van Bosse, 1910, 1921; Sciscioli, 1966; Scott et al., 1984; Price et al., 1984), and is an ecological rather than phylogenetic phenomenon. Although there is some evidence to suggest that particular species of algae are specific to particular sponge species, or at least restricted to a narrow range of taxa (Price et al., 1984), it is unlikely that this symbiosis can be used as a diagnostic character at the supraspecific level. Nevertheless, it is intriguing to consider that a sponge can shed most or all of its diagnostic characters (spicules), replacing them with organic symbionts (e.g., see *Clathria*...
(Thalysias) abietina) or inorganic foreign particles (e.g., see Clathriopsamma, Wilsonella).

Antherochalina Lendenfeld, 1887
(Fig. 9C-E)

Antherochalina Lendenfeld, 1887b: 741, 786; Burton, 1934a: 558; de Laubenfels, 1936a: 112.

TYPE SPECIES. Antherochalina crassa Lendenfeld, 1887b: 787 (by subsequent designation; Burton, 1934a: 558) (holotype BMNH 1886.8.27.450).

Erect, thin lamellate growth form. Surface smooth, not hispid. Choanosomal skeleton with differentiated axial (compressed, renieroid reticulate) and extra-axial (loose plumose) skeletons, although no regional differences in spiculation. Spongulin fibres heavy, cored by choanosomal principal subtylостyles, echinateg by small acanthostyles. Ectosomal skeleton with sparse tangential subectosomal auxiliary subtylостyles. Megascleres include robust, entirely smooth choanosomal principal subtylостyles, lightly spined acanthostyles, and auxiliary subtylостyles with basal spines. Microscleres palmate isocheleae and wing-shaped toxas.

REMARKS. Burton (1934a) designated A. crassa as type species of Antherochalina, in preference to Lendenfeld’s (1887b) first-named species, Veluspa polymorpha var. infundibuliformis Maclay which was unrecognisable. He noted that A. crassa was a synnym of Clathria s.s. Furthermore, of the eight species placed in the genus by Lendenfeld, only the type species now belongs here, whereas the other species are either unrecognisable or have affinities with Rasposia (Syringella), Phakellia, Ophtiaspongia, Cympodicta (A. concentrica; Hooper & Bergquist, 1992) or Ectoplasia (A. frondosa; Hooper, 1991). Antherochalina also resembles some Desmacellidae (such as Sigmaxinella) and some Axinellidae (such as Axinella) in skeletal structure, having a slightly compressed renieroid axial and plumose extra-axial skeletons.

Antho Gray, 1867
(Fig. 10A-C)


TYPE SPECIES. Myxilla involvens Schmidt, 1864: 37 (by monotypy) (schizotype BMNH 1867.3.11.92).

Thinly encrusting (s.s.) or erect, arboreescent, lamellate or vassiform growth forms. Surface rugose, hispid. Choanosomal skeleton renieroid reticulate with acanthostyles-strongyles coring spongulin fibres, or simply united at nodes by variable quantities of spongulin, producing triangular and rectangular skeletal meshes. Junctions of skeletal meshes with principal choanosomal styles echinating fibre nodes, standing erect or at oblique angles, in tufts or singly. True echinating megascleres absent (i.e., undifferentiated from choanosomal principal styles). Ectosome contains tangential or paratangential multispiracular brushes of subectosomal auxiliary styles protruding through surface. Megascleres acantho principal styles/strongyles of renieroid basal skeleton, smooth or acantho principal styles/subtylostyles of the choanosomal skeleton, and smooth subectosomal auxiliary styles, often with basal spines. Microscleres palmate isocheleae, wing-shaped and accolada toxas.

REMARKS. This diagnosis is based on the type species and primarily on the type material, given the existing confusion about the true identity of A. involvens (cf. its alleged synonym A. inconspans; Ackers, Moss & Picton, 1992). Antho appears to be the earliest available name for a group of myxillid-like plocamiform sponges (sensa de Laubenfels, 1936a) which have microscleres spiculation typical of other Microcionidae. These taxa have an axial or basal skeleton composed of mostly acanthostyles or strongyles, producing a more-or-less regular renieroid reticulation. For this reason Bergquist & Finali (1988) referred Antho to the Myxillidae, but the genus has monactinal rather than specialised tyloite ectosomal spicules and does not fit the concept of Myxillidae (Van Soest, 1984b).

The potential generic synonymy of Antho is large. Burton (1930a: 501), de Laubenfels (1936a: 77), Lévi (1960a: 57) and Van Soest (1984b) combined species of Dictyoclostulia Topsent in Antho (see below), and that genus has largely disappeared from current usage. Burton’s (1959a: 252) merger of Myxichela de Laubenfels (1935: 331, 1936a: 85) (type species Lissodendoryx tawiansis Wilson (1925: 432)) into Antho is not upheld here, because it has a true myxillid ectosomal skeleton (diactinal (tylote) ectosomal spicules).

Renieroid reticulate skeletal architecture is not restricted to Myxillidae, known to occur in other families of sponges (e.g., Chalimidae (Haplosclerida), Iophonidae (Acarnus), Raspaillidae (Amphinomina Hooper, Plocamione Topsent, Lithoplocamia Dendy) and Axinellidae (Pitalia
Laubenfels), although it is certainly most common in the Myxillidae. The importance of a renicroid skeleton is interpreted differently by different authors, some giving it primary emphasis (e.g., Bergquist & Fromont, 1988) and others relegating it lesser importance (e.g., Van Soest, 1984b). Several species-groups have been created to accommodate microcionid-like species, with spiculation typical of the family, supplemented by a renicoid (myxillid-like) basal choanosomal skeleton composed of acanthostyles or strongyles. Vosmaer (1935a: 653) called this group Microciona prolifera tropus renieroides and de Laubenfels (1936a) recognized it at the family level (i.e., Plocamididae sensu de Laubenfels (a junior homonym of Plocamiidae Topsent, 1928a)). However, only three genera appear to be sufficiently different to encompass all these microcionids: 1) Plocamia Schmidt (including Plocamilla Topsent, Dirrhopalum Ridley, and Holoplocamia de Laubenfels), which has predominantly (acantho)strongyles forming the renicoid skeleton (less commonly styles), and echinating acanthostyles overlap the main skeleton; 2) Antho Gray (including Anthoarcuata Bakus, Dictyoctathria Topsent, Isociona Hallmann and Jia de Laubenfels), which has predominantly (acantho)styles forming the renicoid skeleton (less commonly strongyles), and echinating acanthostyles are absent; and 3) Isopenecrta Hallmann, which has an axially compressed and extra-axially renicoid reticulate skeleton composed of two forms of choanosomal spicules inside spongin fibres, overlaid by a second extra-axial plumose skeleton. Several authors (Lévi, 1960a; Simpson, 1968a; Pulitzer-Finali, 1973) were unable to reach a consensus of whether or not Plocamilla and Antho were identical, since they only really differed by the presence or absence of echinating spicules, and the extent to which basal spicules of the renicoid skeleton are styles or strongyles (i.e., intermediates occur). Most authors tentatively retain these two genera; Simpson (1968a) and Van Soest & Stone (1986) suggest edhat any decision on these genera, which differ from Clathria in having a renicoid skeletal architecture, would require thorough re-examination of all type species. This has now been done and the conclusion reached here is that differences between all three species-groups (Antho, Plocamia and Isopenecrta) are not as great as the similarities (as conferred by the possession of renicoid skeletal structure), and these differences are emphasized only at subgenus.

Anthoarcuata Bakus, 1966
(Fig. 9F-I).


TYPE SPECIES, Anthoarcuata gracieae Bakus, 1966:431 (by original designation) (holotype USNM36284 (161848)).

Thickly encrusting, massive, cylindrical growth form. Surface even, microscopically hispid. Choanosomal skeleton with basal renicoid reticulation composed of uni- or paucispeciular tracts (occasionally multispeciular) of acanthostyles joined at nodes by light collagen. Peripheral ascending spicule tracts terminate in brushes of smooth principal styles, originating in choano(some and protruding through surface. Ec(tonosal skeleton has a dense, mostly tangential crust of smooth subectosomal auxiliary styles (of a single size category). Megascles include smooth ectosomal auxiliary styles-subtylostyles, sometimes with mucronate bases and telescoped points, and principal acanthostyles with even spination forming basal skeleton. True echinating megascles absent. Microscles palmate isochelae with slight arcuate modifications (curvature, partial detachment of lateral alae from shaft, slightly pointed teeth). Toxas absent.

REMARKS. The type species was originally identified as Burtonancora lacunosa (Lamb, 1892) by de Laubenfels (1961: 195), but Bakus (1966) noted that B. lacunosa (sensu de Laubenfels) was neither conspecific with Lamb's species nor referable to Burtonanchochora (which in any case seems to be a synonym of Myxilla). Anthoarcuata gracieae has the same spicle geometry and is structurally identical to Antho, differing only in the supposed possession of arcuate rather than palmate isochelae. However, in the type material chelaes are not truly arcuate but are predominantly palmate with some "arcuate" modifications including curvature and thickening of the shaft, partial detachment of lateral alae from the shaft (but for less than 20% of alar length), and reduced, slightly pointed, slightly unguiferous alae. They may be classed as palmate on the basis that lateral alae are only partially formed and are fused to the shaft for most of their length.

Artemisina Vosmaer, 1885
(Fig. 10D-E)

Artemisina Vosmaer, 1885b: 25; Ridley & Dendy, 1887: 112; Topsent, 1894: 12; Lundbeck, 1905: 110; Burton, 1930a: 501, 528-531; de Laubenfels.
Artemisina: Burton, 1934b: 54 [lapsus].

**TYPE SPECIES.** Artemisina suberitoides Vosmaer, 1885: 25 (by monotypy) (holotype ZMAPOR443); junior synonym of Suberites arciiger Schmidt, 1870: 37 (Burton, 1930a: 528) (schizotype BMNH1870.5.3.90).

Massive, subspherical, growth form. Surface skin-like, microscopically hispid, with few raised oscules; texture distinctly stringy. Choanosomal fibres indefinite or absent, overall architecture plumo-recticate, nearly halichondroid in places, composed of multispectral ascending and paucispectral transverse tracts of choanosomal principal styles, bound together within spongion. Echinating megascleres absent. Ectosomal skeleton plumose, composed of single category of subectosomal auxiliary styles forming discontinuous palisade of discrete brushes. Megascleres smooth choanosomal principal substyles and smooth fusiform subectosomal auxiliary styles or subyllostyles. Microscleres palmate isochelae, and wing-shaped toxas with spinous extremities.

**REMARKS.** Defining Artemisina in phylogenetic terms is problematic. The taxon has no real distinctive features, although it differs from other Microcionidae in lacking a distinctive choanosomal skeleton or dense spongin fibres (also found in Qasimella Thomas), lacking echinating spicules, and having a nearly radial ectosomal skeleton reminiscent of some Ceratopora (Raspailiidae; Hooper, 1991). These characteristics, two of which might be interpreted as reductions or secondary losses and the third as a convergence, are the only definable morphological apomorphies. Moreover, ectosomal structure varies between several species, ranging from the typical condition composed of erect brushes (e.g., A. arciger) to a tangential layer of spicules in criss-cross fashion (e.g., A. melanu Van Soest). This variability is equivalent to (or analogues of) the Mycale subgenera Carmia and Aegagropilla, respectively (e.g., Topsent, 1924b). At least one species lacks a specialised ectosomal skeleton completely (e.g., A. transiens Topsent).

Some species of Artemisina (e.g., A. foliata (Bowerbank)) have honeycombed reticate growth forms, approaching the characteristic Holopora morphology, but there is no consistency or pattern of gross morphologies amongst Artemisina, and in any case it is unlikely that the genus can be solely defined by its growth form. De Laubenfels (1936a) and Ristau (1978b) suggested that the Artemisina was defined by the absence of echinating acanthostyles and by the presence of spinous extremities on toxas. Neither character has much systematic value at the generic level. In the present interpretation echinating acanthostyles represent the retention of an ancestral character, in which case their presence or absence does not constitute a valid reason to define a phylogenetic grouping, and in any event they occur and disappear throughout numerous microcionid and raspailiid taxa. Similarly, toxas with spinous extremities are also known to occur in many Microcionidae, including the type species of Clathria, C. compressa Schmidt, Microciona spinarhca Carter & Hope, M. coccinea Bergquist, M. rubens Bergquist M. spinatoxa Hoshino, Eurypon acanthota Strehl, and Oph militiae thiefler Burton. They also occur in genera which have an ectosomal structure consistent with the Myxillidae (e.g., Melonchela clathrata Kolun). Several species of Artemisina have smooth toxas (e.g., A. melanu), and one (A. archegonu Ristau) has oxoeto toxas similar to Paratenaciella Vacelet and Vasseur.

Thus, in the broad sense Artemisina contains a heterogenous assemblage of species, which prompted Burton (1930a) to divide the group into three sections based on the number of megasclere categories present. The simplest forms have only one category of spicule (choanosomal principal megascleres; e.g., A. transiens Topsent); the typical form has two categories of megascleres (larger choanosomal principal styles and smaller subectosomal auxiliary styles; e.g., A. arciger); and the third form has an incompletely differentiated series of three megasclere types (two choanosomal spicules and one subectosomal spicule; A. plumosa Hentschel). In all these forms species are only really united in their lax choanosomal skeletal structure. The majority of species have been described from Antarctic and Arctic regions.

**[Aulen] sensu Lendenfeld, 1888**

[Aulen]; Lendenfeld, 1888: 228, 1889a: 90; Topsent, 1894a: 19; de Laubenfels, 1936a: 16; Wiedenmayer, 1989: 58.

Not Aulen Lendenfeld, 1885c: 309.

**TYPE SPECIES.** Aurelia villosa Lendenfeld, 1885c: 309 (by subsequent designation; de Laubenfels, 1936a: 16) (syntypes AMZ130, G8901).

Bulbous, subspherical growth form, consisting of fused digitate projections. Surface highly papillose but not hispid. Choanosomal skeleton
regularly reticulate, with heavy spongin fibres cored by sparsely scattered sand grains mostly at nodes of fibres, and with a secondary fibre network between main skeleton. Ectosome lacks sand cortex or any other mineral skeleton. Megascleres and microscleres absent.

REMARKS. Hallmann (1912:275) merged Aulena and Echinochalinia Carter, whereas Wiedenmayer (1989) noted that in the strict sense (i.e., Lendenfeld, 1885c) it belongs to the Dictyoceratida (possibly related to Coscinodermata). Conversely, most other species referred to Aulena by Lendenfeld (1888) (A. laxa (Lendenfeld), A. gigantea (Lendenfeld), A. crassa (Carter)) belong to Holopsamma.

Aulena Burton & Rao, 1932
(Fig. 10F-G)


TYPE SPECIES. Aulena foraminifera Burton & Rao, 1932: 345 (by original designation and monotypy) (holotype IMP1167/1).

Flabellate-digitate growth form, with subspherical, closely reticulate, honeycomb branching pattern. Surface uneven, not hispid. Choanosomal skeleton irregularly reticulate, with spongin fibres more-or-less fully cored by foreign particles and fewer choanosomal principal subtylos- tyles. Echinating acanthostyles abundant. Ectosome with single size category of subectosomal auxiliary subtylosstyles forming paratangential tracts to substrate and extending non-anastomosing fibre nodes, each node containing plumose short-unbranched tracts of choanosomal principal subtylosstyles, standing perpendicular to substrate with only bases embedded in spongin fibres. Echinating subtylosstyles erect on basal spongin and also echinating erect plumose brushes of choanosomal megascleres. Ectosomal skeleton with single category of subectosomal auxiliary subtylosstyles forming paratangential tracts at surface and plumose brushes extending from ends of choanosomal megascleres. Megascleres smooth or minutely basally spined choanosomal principal subtylosstyles, echinating subtylosstyles with only bases spined, subectosomal auxiliary subtylosstyles mostly smooth, occasionally basally spined, of a single size category. Microscleres palmate isochelae and small wing-shaped toxas.

REMARKS. The ‘honeycombed’ reticulate growth form of Aulena is reminiscent of Holopsamma and some E. (Echinochalinia). The incorporation of foreign particles into the skeleton is also seen in species of Holopsamma, Aulena of authors, Clathriopsamma, Fisherispongia, Wilsoniola and Anomoclinia. It also occurs in other Poecilosclerida Raspailia (Clathriodendron) (Raspailiidae), and many species of Phoriospongiidae and many Dictyoceratida, and is considered here to be a successful ecological adaptation independently acquired by several groups. Thus, Aulena is not defined by any unique features, and furthermore the holotype of A. foraminifera has spiculation identical to Clathria (s.s.), lacking only toxas microscleres. Vacelet et al. (1976:75) correctly synonymised Aulena and Clathriopsamma, both of which now belong to C. (Wilsoniola) (Van Soest, 1984b; Wiedenmayer, 1989; Hooper & Levit, 1993a).

Axocielia de Laubenfels, 1936
(Fig. 10H-I)


TYPE SPECIES. Microciona similis Stephens, 1915: 441 (by original designation) (holotype RSMB-1921.143.1447). Thicksly encrusting growth form. Surface even, and hispid. Choanosomal skeleton hymedemoid, with spongin fibres forming basal layer on substrate and ascending non-anastomosing fibre nodes, each node containing plumose short-unbranched tracts of choanosomal principal subtylosstyles, standing perpendicular to substrate with only bases embedded in spongin fibres. Echinating subtylosstyles erect on basal spongin and the shape of plumose brushes of choanosomal megascleres. Ectosomal skeleton with single category of subectosomal auxiliary subtylosstyles forming paratangential tracts at surface, and plumose brushes extending from ends of choanosomal megascleres. Megascleres smooth or minutely basally spined choanosomal principal subtylosstyles, echinating subtylosstyles with only bases spined, subectosomal auxiliary subtylosstyles mostly smooth, occasionally basally spined, of a single size category. Microscleres palmate isochelae and small wing-shaped toxas.

REMARKS. De Laubenfels (1936a) created Axocielia for thinly encrusting sponges resembling Axociella (i.e., lacking spined echinating megascleres). However, this is incorrect, based on misconceptions of both the type species (i.e., the published characters of Microciona similis do not agree with those seen in the holotype), and Axociella by de Laubenfels’ (1936a). In the holotype of M. similis, diagnosed above, there is only a single category of auxiliary spicule, whereas Axociella s.s. has two distinct categories of auxiliary spicules in the peripheral skeleton. Thus, on the basis of its ectosomal features Axociella is strictly a Thalysia, whereas Axociella has an unspecialised ectosomal spiculation typical of Clathria. In having plumose unbranched fibres forming a microcind skeleton Hechtel (1965: 43) referred Axociella to Microcina. He supported this
decision on the basis that \( M. \) \textit{similis} has both spined and smooth styles, which he considered to be diagnostic for \textit{Microciona} (although considered in the strict sense that feature is diagnostic for \textit{Anaasta}). \textit{Axociella} is referred here to \textit{Clathria} (\textit{Microciona}).

\textbf{Axociella Hallmann, 1920}

(Fig. 11A-B)


\textbf{TYPE SPECIES.} \textit{Experiospis cylindrica} Ridley & Dendy, 1886: 340 (by original designation) (holotype BMNH1887.5.2.96).

Arborescent, dichotomously branched, stalked growth form. Surface even, membranous, transparent, hispid. Choanosomal fibre skeleton compressed at centre of stalk, with heavy spongion fibres forming reticulate axis, with longitudinal primary fibres cored by multispicular tracts and secondary connecting fibres aspicular or paucispicular tracts of choanosomal principal styles. Echinating megascleres absent. Subectosomal extra-axial skeleton plumose or plumo-re ticulate, well-differentiated from axial core, with light spongion fibres cored by multi- or paucispicular larger subectosomal auxiliary styles and few aspicular transverse fibres. Ectosomal skeleton composed of specialised category of smaller ectosomal auxiliary styles forming continuous palisade or individual brushes of spicules. Megascleres entirely smooth principal choanosomal styles-subtylostyles, and two categories of entirely smooth auxiliary styles-subtylostyles. Microscleres palmate isochelae and oxhorn toxas.

\textbf{REMARKS.} \textit{Axociella} has been misinterpreted by all authors since it was first reviewed by de Laubenfels (1936a). It is similar to \textit{Tenaciella} Hallmann in lacking echinating megascleres but it has a distinctive, compressed reticulate axis and plumose or plumo-reticulate subectosomal (extra-axial) skeleton, reminiscent of the distinctive extra-axial skeletal architecture seen in Raspailiidae. The structure of the ectosomal skeleton in the type species of \textit{Axociella} (i.e., the possession of two categories of auxiliary megascleres) is the same as seen in \textit{Thalysias}, and Van Soest (1984b) merged the two genera on this basis. However, unlike typical species of \textit{Thalysias} or \textit{Clathria}, those of \textit{Axociella} have a distinctive skeletal structure (compressed axis and a radial extra-axial skeleton), which is more-or-less homogeneous amongst the several known species, and this structure is interpreted here as indicative of supraspecific relationships. This interpretation is consistent with the treatment of similar structures in Raspailiidae (Hooper, 1991). In fact, \textit{Axociella} could be justifiably included in Raspailiidae (Hooper, 1991; Hooper et al., 1992), apart from having isochelae and toxan microscleres and lacking the unique raspaidiid ectosomal specialisation (large protruding auxiliary or principal spicules surrounded by bundles of smaller auxiliary spicules). True examples of these ectosomal spicules are not seen in the Microcionidae, although two species have analogues of this ectosomal condition: \textit{Experiospis canaliculata} Whitelegge, \textit{Ophlitaspongia thetidis} Hallmann — both belonging to \textit{Clathria (Axociella)}.

\textit{Axociella} is convergent upon Raspailiidae in skeletal structure, best developed in three Australian species, \textit{Experiospis cylindrica}, \textit{E. canaliculata} and \textit{Ophlitaspongia thetidis}, all of which also have a \textit{Thalysias} ectosomal skeleton. Another species from the NW Pacific, \textit{Microciona lambei} Koltun, has a mix of both Raspailiidae and Microcionidae skeletons, being convergent on \textit{Endectyton} in structure (with a markedly compressed axis, brushes of acanthostyles surrounding the bases of protruding choanosomal principal styles) but it also has palmate isochelae and a tangential layer of auxiliary styles lying tangential to the surface (i.e., the \textit{Clathria} condition). \textit{Axociella} is recognised here as a subgenus of \textit{Clathria} based on its specialised compressed skeletal structure.

\textbf{Axosuberites Topsent, 1893}

(Fig. 11C-D)

\textit{Axosuberites Topsent, 1893: 179; de Laubenfels, 1936a: 118.}

\textbf{TYPE SPECIES.} \textit{Axosuberites fauroni} Topsent, 1893a: 179 (by monotypy) (portion of holotype MNHN-LBIMDT1859).

Flabellate, flattened digitate growth form. Surface hispid, conulose. Choanosome with compressed reticulate axis and plumose extra-axial skeleton, with only light spongion fibres. Axial fibres produce close-meshed reticulation of multispicular tracts cored by choanosomal principal subtylostyles forming criss-cross reticulation, tracts plumose near periphery. Echinating megascleres absent. Subectosomal extra-axial skeleton well differentiated from axial region, with ascending plumose columns of larger subectosomal auxiliary subtylostyles arising from
peripheral choanosomal skeleton. Ectosome with brushes of smaller auxiliary subtylostyles overlaying larger subectosomal spicules. Megascleres entirely smooth choanosomal principal subtylostyles-tylostyles, and two size classes of auxiliary subtylostyles-tylostyles, both with smooth bases. Microscleres absent.

REMARKS. Redescription of the type species above is based on examination of a slide preparation in the MNHN collection and Topsent's (1893a) description; the corresponding specimen has not yet been seen. Topsent (1893a) initially compared Axosuberites with Caudosphongia Kent and Pseudosuberites Topsent in Suberitidae (Hadromerida), noting that it showed a certain level of morphological similarity in choanosomal fibres and geometry of tylostyle megascleres. However, in skeletal structure and spiculation Axosuberites appears to be a microcionid, most similar to Axociella, both genera showing similarities in their ectosomal specialisation, axial and extra-axial differentiation, and absence of echinating megascleres. Van Soest (1984b) also suggested that the genus was probably an Axociella without microscleres, and under his scheme it was therefore referable to Thalysias, but in both genera axial and extra-axial skeletal structures are well developed and closely comparable, and it is suggested here that they both should be included in the same subgenus (i.e., Clathria (Thalysias)).

Bipocilotopsis Koltun, 1964
(Fig. 11E-G)

Bipocilotopsis Koltun, 1964a: 79.

TYPE SPECIES. Bipocilotopsis nexus Koltun, 1964a: 80 (by monotypy) (holotype ZIL10644, paratype BMNH1963.7.29.56).

Erect, arborescent growth form with cylindrical reticulated branches. Surface hispid, raised into irregular sharp conules. Choanosomal skeleton subrenieroid reticulate, with ascending spongulin fibres cored by multispecific plumose tracts and interconnected by paucispecific transverse tracts of choanosomal principal subtylostyles, and echinated by acanthostyles. Subectosomal region with heavy paratangential bundles of subectosomal auxiliary styles protruding through surface and also scattered between fibres. Ectosomal skeleton without specialised spiculation but with bundles of subectosomal auxiliary styles surrounding protruding choanosomal spicules, and also lying paratangential to ectosome.

Megascleres choanosomal principal subtylostyles invariably with basal spines and sometimes with spines on shaft, echinating acanthostyles of similar morphology to principal megascleres but shorter and more extensively spined, and single category of entirely smooth subectosomal auxiliary style. Microscleres isochelae, strongly sigmoid, unguiferous with very reduced pointed alae, possibly anchorate. Toxas absent.

REMARKS. Bipocilotopsis resembles Damoseni in lacking ectosomal specialisation and having modified sigmoid isochelae, but differs in growth form (arborescent versus encrusting) and subectosomal skeletal architecture (thickly paratangential versus tangential). The genus is monotypic and may be included in Clathria (Clathria) by its skeletal structure, whereas Damoseni has hydromedusan skeletal structure typical of Clathria (Microciona). Chelae morphology has been described as tridentate sigmoid, allegedly related to the arcuate form, but this is very difficult to tell with certainty given that alae are nearly vestigial. There is no doubt that these chelae are more highly modified than most other microcionids. They are very small, strongly unguiferous (sigmoid curved with small pointed teeth), and lateral alae are completely free of the shaft and undifferentiated from the front ala, suggesting they may be of anchorate origin. However, there is no lateral ridge on the shaft of chelae to indicate an anchorate condition. The derivation of these chelae is indeterminable. Under the scheme of Hajdu et al. (1994) this genus could be included in Myxillina in possessing tridentate-derived isochelae, whereas all other features (skeletal structure, principal and auxiliary megascleres and ectosomal skeleton) indicate relationships with the Microcionidae, in which it is retained here tentatively. This decision is supported by the case of Damoseni, discussed below, which have chelae of identical form to Bipocilotopsis with the addition of oxhorn toxas (which are not found in Myxillina).

Cionanchora de Laubenfels, 1936
(Fig. 12E-G)

Cionanchora de Laubenfels, 1936a: 108.

TYPE SPECIES. Hymerathia tuberoscapitata Topsent, 1890b: 68 (by original designation) (fragment of holotype MNHNLB1M1DT939).

Encrusting growth form. Surface smooth, even, microscopically hispid. Choanosomal skeleton hydromedusan. Spongulin fibres reduced to basal
layer lying on substrate, with choanosomal principal subtylostyles erect and forming unispicular ascending columns protruding through euctosome, and echinating acanthostyles standing parallel to these. Ectosome tangential skeleton of subectosomal auxiliary subtylostyles, of a single category, forming brushes surrounding protruding choanosomal principal spicules. Megasclesers choanosomal principal subtylostyles with tuberculate bases, echinating acanthostyles with large spines evenly dispersed over entire spicule except for bare point, and subectosomal auxiliary subtylostyles completely smooth. Microsclesers anchorate-like isochelae. Toxas absent.

REMARKS. The diagnosis is based on a slide of the holotype and Topsent’s (1890b) description; the corresponding specimen has not been seen. Cionanchora was erected for thinly encrusting sponges with hymedesmoid skeletal construction, similar to Anaata, but with anchorate-like instead of arcuate-like modifications to isochelae (de Laubenfels, 1936a). Both those genera were merged with Clathria (s.l.) by Van Soest (1984b) on the basis that modified microsclesers were a homoplaspy throughout the Pocilosclerida, and are interspecific discriminators only. Anchorate-like modifications are also found in Folitissa (both of which were included in Clathria by Hooper, 1990a). Microciona dubia from Christmas Island (Kirkpatrick, 1900a: 136), was referred to Cionanchora by de Laubenfels (1936a: 108) supposedly in having anchorate-like chelae but these are of palmate origin. Both species have skeletal architecture typical of Microciona where they are referred.

**Clathria** Schmidt, 1862

(Fig. 12A-B)


Clathria Schmidt, plus Rhaphidophilius Ehlers; Ridley & Dendy, 1887: 146,151; Topsent, 1894a: 14-15,18.

Clathria: Kumar, 1925: 221 [lapsus].

TYPE SPECIES. Clathria compressa Schmidt, 1862: 58 (by subsequent designaion (Schmidt, 1884: 35)) (holotype LMG15509).

Erect, arborescent, thinly lamellate, branching growth form. Surface even, not hispid. Choanosomal skeleton regularly reticulate, with well developed spongin fibres forming regular or irregular anastomoses of differentiated primary and secondary spongin fibres. Fibres cored by choanosomal principal subtylostyles in multispicular ascending tracts and uni- or bispicular transverse connecting tracts, and echinated by acanthostyles perpendicula to or at acute angles to spongion fibres. Ectosomal skeleton with tangential layer of subectosomal auxiliary subtylostyles, of a single size category. Megasclesers basally spun choanosomal principal subtylostyles, entirely smooth subectosomal auxiliary subtylostyles, and echinating acanthostyles with even spination. Microsclesers palmate isochelae and forceps-shaped or accolada toxas with spinose extremities.

REMARKS. Strictly defining Clathria is essential in assigning a vast number of microcionids included in the genus by numerous authors. For example, C. compressa has toxas with spinose extremities, which therefore becomes a character 'typical' of Clathria, whereas earlier authors considered that this feature was diagnostic for Artemisia Vosmaer (de Laubenfels, 1936a). Clathria-like (viz. Labaceae de Laubenfels) and Artemisia-like genera (viz. Ligrota de Laubenfels) also have spinous toxas, indicating that this character is homoplasious and probably not important above the species level of classification. In general, the original definition of Clathria (s.s.) is upheld here, as re-examination of Schmidt’s syntype confirmed that all published characters cited in the species description (Schmidt, 1862: 58; Topsent, 1925: 647) are present in type material.

Topsent (1925: 648) noted that C. compressa has variable spicule dimensions, skeletal architecture, and live colouration. He correlated this variability with the diverse growth forms shown by the species: thinly encrusting examples had a hymedesmoid skeletal architecture, thickly encrusting forms had a plumeose skeleton, and erect ramose forms had anastomosing fibres (i.e., encompassing the nominal genera Leptoclathria, Microciona and Clathria). He also found correlation between the size of megasclesers and growth form variability, although he could find no obvious trends. Topsent’s observations are invaluable in deciding whether to maintain nominal
encrusting genera and more massive sponges as distinct genera, and whether to differentiate taxa with hymedesmoid, plumose or plumo- reticulate skeletal structure.

*Clathria compressa* is known only from the north Atlantic and Mediterranean regions, but judging by its extensive synonymy it appears to be (or have been) moderately common within those regions.

**Clathriella** Burton, 1935

(Fig. 11H-I)


TYPE SPECIES. *Clathriella primitiva* Burton, 1935c: 73 (by original designation) (holotype BMNH1938.7.4.93).

Crumpled, irregular, massive growth form. Surface porous, uneven, hispid, with meandering ridges covered by thin transparent dermal membrane. Choanosomal skeleton renieroid reticulate, with spongin fibres forming regularly triangular meshes cored by multispiracular tracts of smaller principal rhabdostyles (confined to renieroid network) and larger principal styles (later producing secondary plumose, subisodictyal skeleton of bi- or pauci-spiracular ascending tracts). Echinating spicules absent. Ectosomal skeleton radially arranged tracts of subectosomal auxiliary styles, of a single size category. Extra-fibre skeleton (apparently) has centrally curved (arcuate) oxoete megascleres scattered throughout mesohyl. Megascleres two categories of choanosomal principal styles, larger smooth with rounded bases, smaller spined with rhabdose bases, and smooth or basally spined subectosomal auxiliary styles-subtylostyles. Microscleres absent.

REMARKS. *Clathriella primitiva* is obviously closely related to *Clathria chartacea* Whitelegge in its skeletal structure and spiculation, conforming to the definition of *Isopenectya* (see below). *Clathriella* also shows similarities to *Isociella* in having an isodictyal reticulate skeleton and in lacking echinating spicules, although in *Isociella* all megascleres are smooth and chelae and toxo microscleres are present. The presence of smaller spined rhabdostyles and an isodictyal component of the choanosomal skeleton are reminiscent of *Rhabdemicidae*, although the absence of thraustosigmata, thraustotexa and other rhabdemicid microscleres in *C. primitiva* suggest that these similarities are convergent.

Burton (1935c) considered that *Clathriella* was a primitive member of the Microcionidae, in which styles and acanthostyles had not yet become differentiated or segregated into coring and echinating megascleres. He suggested further that the toxiform oxases, recorded by both Burton (1935c) and Koltun (1959), were derived from acanthostyles, and that both forms were remnants of a primitive condition. There is no empirical evidence to support either argument, and the present study takes the alternative point of view, that species like *Clathriella primitiva* are derived or modified microcionids. Koltun (1959) also suggested that arcuate oxases of *C. primitiva* were microoxae, and in that respect the genus should be compared with *Paratenaciella*. However, in *Clathriella* these spicules are supposedly large (200x7 µm), indicating that they are true megascleres, whereas in *Paratenaciella* microoxae are very small (40-75 x 0.7-3µm). In any case, re-examination of the holotype of *C. primitiva* (above) and more recent material from the Sakhalin Is, NW Pacific collected by PIBOC (QMG300052), did not find any toxiform oxases although several examples of smaller auxiliary styles were sinuous, and it may be these the authors were referring to. The genus is referred here into synonymy with *Antho* (*Isopenectya*).

**Clathriopsamma** Lendenfeld, 1888

(Fig. 12C-D)


Erect, anastomosing, arborescent growth form. Surface uneven, arenenaceous, microscopically hispid. Choanosomal skeleton irregularly reticulate. Spongin fibres without well developed primary or secondary differentiation, cored by choanosomal principal subtylostyles and abundant foreign debris. In subectosomal skeleton principal subtylostyles also form plumose brushes, protruding through ectosome. Fibres heavily echinated by acanthostyles also associated with ectosomal spicule brushes. Ectosome with paratangential tracts of subectosomal auxiliary subtylostyles, of a single category, usually forming discrete brushes of spicules at surface. Megascleres basally spined, fusiform choanosomal principal subtylostyles, smooth and basally spined subectosomal
auxiliary subtylostyles, and echinating acanthostyles with large spines evenly dispersed. Microscleres palmate isochelae of two size categories, including contort forms, and sinuous-rhiphidiform or accolada toxas.

REMARKS. In Clathriopsanuna the ectosome is structurally close to the Thalysias condition, but there is only one category of auxiliary spicule producing surface bundles. The genus is distinguished from most other microcionid genera in having foreign particles incorporated into the skeleton (Hallmann, 1920) (see remarks for Aulenella). Detrital entrapment is also known to occur in other Microcionidae (e.g., some Holopsammas), other Poecilosclerida (e.g., Phniospongidae), and it certainly also occurs commonly in other sponge orders (Dysideidae, Thorectidae and Ircinidae in the Dictyoearitida, and many Haplosclerida). This evidence indicates that this feature has arisen independently several times within the Porifera, probably indicative of ecological specialisation, and obviously arisen independently in several groups. However, species of Microcionidae that do incorporate sand appear to be relatively homogeneous in most of their other characters (i.e., there are no other conflicting characters such as presence/absence of ectosomal specialisation, or modifications to chelae), and consequently this specialisation is recognised here at the subgenus level. Vacelet et al. (1976) synonymised Clathriopsanuna with Aulenella, and Van Soest (1984b) merged Clathriopsanuna with Clathria, whereas in this work it is shown that the earliest available name for these species is Wilsonella (see below).

**Collocithria** Dendy, 1922  
(Fig. 12H-I)

Collocithria Dendy, 1922: 74.

**TYPE SPECIES.** Collocithria ramosa Dendy, 1922: 74 (by monotypy) (holotype BMNH 1921.11.7.64).

Cylindrical, arboreal, digitate growth form. Surface even, hispid, Choanosomal skeleton reticulate, with slightly compressed axis and slightly more cavernous extra-axial skeleton. Spongion fibres cored by large principal choanosomal styles, forming multipuncular ascending tracts interconnected by multisepcular transverse tracts. Echinating acanthostyles distributed irregularly over fibres. Subectosomal skeleton reduced to immediate outer edge of skeleton, with plumose tracts of larger subectosomal auxiliary subtylostyles extending through ectosome. Larger auxiliary megasclelere also scattered between fibres and sometimes coring fibres. Ectosomal skeleton with smaller ectosomal auxiliary subtylostyle forming discrete brushes overlying subectosomal spicules. Megasclelere smooth principal choanosomal styles, echinating acanthostyles with spined bases and points (bare ‘necks’), and two sizes of auxiliary subtylostyles, usually with basal spines. Microscleres palmate isochelae, cleistocheelae and accolada toxas.

REMARKS. Collocithria has a specialised ecosomal identical to Thalysias with two categories of auxiliary spicules forming surface spicule bundles, and on that basis Van Soest (1984b: 115) suggested the two genera should be merged: it is included here in synonymy with Clathria (Thalysias). The possession of cleistocheelae in *C. ramosa* is not unique to Microcionidae also found in Plocamiospis, Quizictona and several species of Clathria (e.g., *C. Clathria toxipraedita*).

**Damoseni de Laubenfels, 1936**  
(Fig. 13A-C)

Damoseni de Laubenfels, 1936a: 110.

**TYPE SPECIES.** Hymeraphia michaelseni Hentschel, 1911:351 (by original designation) (fragment of holotype SMF969T).

Encrusting growth form. Surface sparsely hispid, even. Choanosomal skeleton hyinedesmoid, with spongion fibres reduced to basal layer of spongion lying on substrate, with bases of choanosomal principal subtylostyles and acanthostyles embedded in spongion, standing perpendicular to substrate, spicules protruding through ectosome. Ectosomal skeleton with paratangential, slightly plumose tracts of both larger and smaller auxiliary subtylostyles. Megascleres large principal choanosomal subtylostyles with spined bases, echinating acanthostyles with spined bases and shafts (bare ‘necks’), and two size classes of subectosomal auxiliary subtylostyles with either smooth or spined bases. Microscleres strongly unguiferous, sigmoid isochelae with vestigial alae, arcuate- or anchorate-like but of uncertain affinity, and large wing-shaped (oxhorn derived) toxas.

REMARKS. Hentschel’s (1911) description of Hymeraphia michaelseni does not mention the presence of toxas microscleres, nor that principal spicules protrude a long distance through the surface. The modified unguiferous isochelae (of
possible anchorate or arcuate derivation) are identical to those of *Bipocillopsis*, and the combination of toxas and uguiferous isochelae of possible tridentate-derivation supports the inclusion of such taxa in Microcionidae contrary to Hajdu et al.'s (1994) proposal. *Damoseni* is similar to other encrusting genera with hymedesmoid architecture and it could be included in *Clathria* (*Microciona*) on this basis. However, the specialised ectosomal skeleton composed of smaller ectosomal and larger subectosomal auxiliary spicules indicates affinities to *Clathria* (*Thalysias*).

**Dendrocia** Hallmann, 1920

*(Fig. 13D-E)*


**TYPE SPECIES.** *Clathria pyrumida* Lendenfeld, 1888: 222 (by original designation) (holotype AMG99047).

Massive, lobate-digitate growth form. Surface conulose, with subdermal sculpturing, oscules slightly raised above surface with membraneous lip. Choanosomal skeleton dendritic, slightly plumo-reticulate near axis, without any obvious division of primary or secondary fibres, but with clear structural differences between choanosomal, subectosomal and ectosomal regions. Spongian fibres heavy, meandering, bored by auxiliary styles distinguishable from those in ectosomal skeleton, and heavily echinating by acanthostyles (sometimes also secondarily incorporated into fibres). Subectosomal skeleton plumose or radial, with spicule tracts composed of auxiliary styles diverging from ends of peripheral choanosomal fibres and supporting overlying ectosomal skeleton. Ectosomal skeleton with continuous, heavy palisade of erect auxiliary styles. Principal spicules absent, and megascleres include only echinating acanthostyles with spined bases and necks but smooth points, and single category of structural spicule (auxiliary styles-subylostyles), entirely smooth with hastate points and sometimes secondarily pointed bases. Micro scleres modified palmate isochelae with curved, thickened shaft and reduced alae. Toxas absent.

**REMARKS.** This strict diagnosis based on the type species should be widened to include the presence of modifications to isochelae, ranging from typical palmate forms (with straight shaft, completely fused lateral alae, as in *Clathria* (*Dendrocia*) *abrolhensis* sp. nov.), modified palmate isochelae (with greatly curved, thickened shaft, partially detached lateral alae, as in *C. (D.) dura*), to anchorate-like forms (in which lateral alae are detached from shaft, shaft is curved, thickened and has a lateral ridge, as in *C. (D.) myxilloides*). One species also has oxtorn toxas (*C. (D.) scabida*) supporting the hypothesis that *Dendrocia* has affinities with Microcionidae.

*Dendrocia*, like *Wilsonella*, differs from other microcionids in having auxiliary styles both coring fibres and forming the ectosomal skeleton. However, whereas *Wilsonella* has two categories of auxiliary spicules and detritus is incorporated into the skeleton, *Dendrocia* has only one category of structural spicule throughout the skeleton. *Dendrocia* also has a characteristic dendritic or plumo-reticulate skeletal architecture, whereas *Wilsonella* is invariably reticulate.

In ectosomal skeletal structure (with a continuous ectosomal palisade of spicules) *Dendrocia* resembles the *Thalysias* condition, but it has only one geometric form of auxiliary spicule producing the extra-fibre skeleton (i.e., subectosomal and ectosomal regions) more similar to *Clathria*. For this reason *Dendrocia* is enigmatic, and Hooper (1990a) maintained it as a separate taxon, whereas earlier Van Soest (1984b) had indicated that it was probably a synonym of *Clathria*. In this work it is referred to *Clathria* (*Dendrocia*).

Two Australian species were initially included in *Dendrocia* by Hallmann (1920), the type species and *C. alata* Dendy (holotype NMV G2280). Both are undoubtedly synonyms. They apparently differ only in their spicule dimensions (styles: 175-230x2-μm versus 240-250x4-μm; acanthostyles: 63-95x3-1μm versus 79-154x8-1μm; arcuate isochelae: 23-2μm versus 20-2μm, respectively). In contrast, *D. antyaja* Burton & Rao, from the Indian Ocean, should be removed from *Dendrocia* because it has regularly reticulate choanosomal architecture, lacks an ectosomal skeleton, and has palmate isochelae indicating affinities to *Clathria*. Several other Australian species previously referred to *Clathria* s.s. should also be referred to *Dendrocia* on the basis of their skeletal architecture and spiculation.

**Dictyociona** Topsen, 1913

*(Fig. 13F-G)*


**TYPE SPECIES.** *Microciona discreta* Thiele, 1905: 447 (by monotypy) (holotype ZMB3302).
Thickly encrusting, lobate growth form. Surface composed of interconnected micropapillae. Choanosomal skeleton plumose, becoming plu mo-rectilcate in thicker sections. Spongian fibres divided into primary and secondary elements, heavier in axis, lighter in subectosomal region where dermal spicules implanted at nodes of peripheral fibres. Fibres cored by multispheric tracts of choanosomal principal sublylostyles, and heavily echinated by acanthostyles projecting from fibres at all angles. Ectosomal skeleton composed of paratangential tracts of subectosomal auxiliary sublylostyles, of a single size category, arising from peripheral fibres and piercing surface. Megascleres choanosomal principal sublylostyles with acanthose bases and acanthose shafts near basal end, echinating acanthostyles with spined bases and points (bare 'necks'), and subectosomal auxiliary sublylostyles with microspined bases. Microscleres palmate isochelae and thin toxas intermediate between wing-shaped and oxhorn forms.

REMARKS. *Dictyociona* resembles *Microciona* in its plumose skeletal structure but has partially acanthose choanosomal megascleres similar to those found in *Anaata* and *Antho*. These spicules are also present in several Raspilliidae (e.g., *Hymeraphia*, *Eurypon*), and they are considered here to be of minor diagnostic importance above the species level following Simpson (1968a). Lévi (1960a: 60) merged *Dictyociona* with *Clathria*, although the species could as easily be placed in *Microciona*. It is included here within *Clathria* (*Clathria*). Apart from the type species, other taxa referred to *Dictyociona* at one time or another include: *Microciona clathrata* Whitelegge, *M. heterotoxa* Hentschel, *M. pyramidalis* Bronsted, *Hymeraphia oxneri* Topsent, *Eurypon asodes* de Laubenfels, *E. acanthotoxa* Stephens, *E. ditoxa* Stephens, *E. microchela* Stephens, *E. tenussima* Stephens, *Clathria terranovae* Dendy, *D. contorta* Bergquist & Fromont and *D. atoxa* Bergquist & Fromont.

*Dictyoclista* Topsent, 1920

(Fig. 13H-I)


*Dictioclathria* [lapsus]; Ferrer Hernández, 1921: 172.

TYPE SPECIES. *Clathria morisca* Schmidt, 1868: 9 (by original designation) (schizontype BMNH-1868.3.2.21); junior synonym of *Antha involvens* (Schmidt, 1864) (Lévi, 1960a: 57) (schizontype BMNH1867.3.11.92).

Arborescent growth form. Surface hispid, uneven. Choanosomal skeleton renieroid reticulate composed of spined acanthostyles forming triangular or rectangular meshes, enclosed within fibres (axis) or bound together at nodes by collagen (near periphery). Echinating megascleres absent. Subectosomal (extra-axial) skeleton plumose, with smooth principal styles standing perpendicular to fibre nodes, individually or in bundles, protruding through surface. Ectosomal skeleton with dense plumose or paratangential bundles of subectosomal auxiliary sublylostyles, sometimes surrounding protruding principal styles. Megascleres shorter highly spined acanthostyles (renieroid skeleton) and longer completely smooth principal styles (extra-axial skeleton), and smaller subectosomal auxiliary sublylostyles with spined bases. Microscleres palmate isochelae and toxas intermediate between wing-shaped and oxhorn forms.

REMARKS. *Dictyoclistharia* is an objective synonym of *Antha*, since the type species of both genera are conspecific (Lévi, 1960a). The type specimen of *Dictyoclistharia* is remarkable in having a nearly raspaliid ectosomal condition with bundles of ectosomal spicules appearing to surround the protruding extra-axial spicules, but this is not as perfectly developed as in many *Raspahtia*.

**Dirrhopalum** Ridley, in Ridley & Duncan, 1881

*Plocamia* Schmidt, 1870: 62.

*Dirrhopalum* Ridley in Ridley & Duncan, 1881: 477. See *Plocamia*.

*Echinochalina* Thiele, 1903

(Fig. 14A-B)


TYPE SPECIES. *Ophilitaspongia australiennis* Ridley, 1884a: 442 (by subsequent designation (Hallmann, 1912: 288)) (holotype BMNH1881.10.21.299).

Massive-digitate, reticulate growth form. Surface with low ridges and interconnected lamellae, producing angular cells with thin dermal membrane stretched between. Choanosomal skeleton irregularly reticulate, with heavy primary spongian fibres cored by paucissipicular tracts of auxiliary spicules (tomatoes), and heavy secondary spongian fibres cored by uni-
bispicular tracts of auxiliary spicules. Fibres lightly echinuated by principal subtylostyles. Ectosomal skeleton with undulating fibres and loose paratangential tracts of auxiliary spicules (also distributed throughout mesohyl). Megascleres include quasidiactinal auxiliary tornotes with asymmetrical or symmetrical ends (coring fibres and on ectosome), and completely smooth principal subtylostyles-styles (echinating fibres), sometimes modified to oxetes (asymmetrical with two pointed ends). Microscleres wing-shaped toxas. Isochelae absent.

REMARKS. In the type species coring spicules are tornotes, whereas in other species of *Echinochalinia* they range from true styles to oxetes. Re-examination of the holotype of *O. australiensis*, and Thiele's (1903a) specimen from Ternate, Indonesia (SMFI855) also found that echinating principal styles can sometimes be modified to oxote spicules, providing support for the otherwise tenuous placement of *Protophilitaspongia* with this group of microcionids.

Hallmann (1912: 288) noted that *Echinochalinia* differs from the allied *Echinoclathria* of authors (= *Holopsamma* as defined here) in having fibres cored by auxiliary spicules (tylostyles or strongyles), which may be modified to quasi-monactinal forms (tylostrongyles, tommostylostyles), and echinated by smooth styles or subtylostyles. By comparison, *Echinoclathria* in the strict sense (or *Ophtilataspongia* of authors) has principal choanosomal styles (or modified monaxonial megascleres) which both core and echinate fibres, as well as a second category protruding through the surface; *Holopsamma* has only a single category of coring and echinating principal spicule. As such, Van Soest (1984b: 129) suggested that *Echinochalinia* possibly did not belong with the Microcionidae, and might be more appropriately placed elsewhere within the Poecilosclerida (e.g., Phoriospongiidae). However, examination of a suite of species included here in *Holopsamma* found that this group also undergoes a reduction in coring spicules (e.g., *H. pluritoxa* (Pulitzer-Finali)), whilst retaining other characteristics common to the genus, and it is possible that *Echinochalinia, sensu* Hallmann, undergoes similar reduction.

Probably of greater importance in determining the appropriate placement of *Echinochalinia* is its lack of any special ectosomal skeleton, and in this respect it is similar to *Dendroclathria* (both with only one form of structural (auxiliary) spicule). Whereas *Echinoclathria* (s.s.) possesses monaxonial auxiliary spicules in the peripheral skeleton (sometimes reduced to quasi-diactinal forms), *Echinochalinia* has spicules which are closer to true diactinals (although sometimes modified to quasi-monaxonial forms). Both genera lack definite ectosomal specialisation. Some *Echinochalinia* appear to have affinities with certain species of *Echinodictyum* (Raspaillidae) and with the Desmacididae, and both Thiele (1903a) and Topsent (1904a) have already noted this resemblance, suggesting that they differ mainly in the geometry, ornamentation and derivation of the echinating megascleres. By comparison, Hallmann (1912) considered that these differences, and the presence of long subectosomal styles in many *Echinodictyum* species, are sufficient to maintain the two genera as distinct taxa (see Hooper, 1991d).

Although *Echinochalinia* usually has smooth echinating megascleres, linking it to *Echinoclathria* and *Holopsamma*, there are two species which were previously referred to *Echinodictyum* (E. ridleyi Dendy and *E. spongiosum* Dendy), which have acanthose echinating megascleres but otherwise conform to *Echinochalinia* in their spicule geometries and skeletal architectures. Hooper (1991) transferred these species to *Echinochalinia*.

*Tablis* de Laubenfels is an obvious synonym of *Echinochalinia*. The two genera differ only by the absence of microscleres and the presence of a reticulate architecture in *Tablis*.

**Echinoclathria** Carter, 1884
(Fig. 14C-E)


**TYPE** SPECIES, *Echinocloathsia tenuis* Carter, 1885f: 355 (by subsequent designation; Burton, 1934a: 562) (holotype BMNH1886.12.15.147); junior synonym of *Spongia leporina* Lamarck, 1814: 444 (Topsent, 1932: 101) (holotype MNHNLBIMDMT567).

Thinly flabellate, flattened palmate, stalked growth form. Surface membranous, microscopically hispid. Choanosomal skeleton renieroid reticulate, slightly compressed with well developed spongin fibres in axis, more openly reticulate, less compressed and with lighter spongin towards periphery. Axial fibres cored by pauci- or multispecific tracts of smaller principal styles producing rounded or irregularly shaped meshes, and echinated by same spicules.
Subectosomal (extra-axial) skeleton radial, unifo
or paucispicular, with larger principal spicules er
cating on terminal fibres and usually protruding
through surface. Ectosomal specialisation absent,
with bundles of subectosomal auxiliary subtylo
styles embedded perpendicularly and forming
paratangential brushes surrounding larger prin
cipal spicules. Megascleres include smaller,
robust, entirely smooth principal subtylostyles
(coring and echinating fibres), larger principal
subtylostyles of similar geometry (projecting from
peripheral fibres and protruding through surface),
and smooth subectosomal auxiliary subtylo
styles, straight or flexuous. Microscleres absent.

REMARKS. There is substantial confusion con
cerning the precise definition of Echinocladuria,
and its relationship with other nominal genera
such as Holopsamma, Halme, Aulena and Op
litaspongia. Consequently the above diagnosis is
strict, pertaining only to the type species, and a
detailed explanation is justified below.

Most authors follow Hallmann's (1912: 275)
interpretation of Echinocladuria in which the
genus is essentially characterised by "a honycomb mass of anastomosing flattened
trabeclae", a reticate skeleton of heavy spon
gin fibres cored and echinated by smooth monact
principal megascleres of the same geometry,
and with monactinal subectosomal auxiliary
styles distributed throughout the mesohyl (and in
some species also forming a radial subectosomal
skeleton). Hallmann also noted that in some
species he assigned to Echinocladuria there are
both chelae and toxo microscleres, with quasi
monactinal auxiliary megascleres, or they may
have their coring megascleres replaced partially
or completely by detritus (e.g., Holopsamma
laminaeofavaea). Hallmann suggested further that
Echinocladuria and Ophlitaspongia essentially
differed only in growth form, a view perpetuated
by Wiedenmayer (1989). This interpretation is
emended here.

Most species included in Echinocladuria prior
to the present study do have the characteristics
outlined by Hallmann (1912), and most are rela
tively homogeneous and easily recognisable in
the field by their characteristic "honeycomb reticulate" growth form. It is therefore unfor
tunate that Burton (1934a) subsequently des
ignated E. tenuis (a junior synonym of Spon
gia leporina) as the type species of Echinocladuria,
because this species has a flabellate growth form
(very dissimilar to 'honeycombed reticulate'
species), skeletal architecture consisting of a dif
ferentiated axis, extra-axis, a renieroid skeleton,
and a second category of principal spicules protrud
ing through the ektosome. Echinocladuria leporina
is typical of most Ophlitaspongia (of authors)
(e.g., O. axinelloides Dendy).

Confusing the generic boundaries even further,
Spongia leporina closely resembles Antho
(Isopenectya) in growth form and gross skeletal
construction, but differentiated by their skeletal
structures, spicule ornamentation and localisa
tion of particular spicules to certain regions of the
skeleton. Nevertheless, it could be argued that
Isopenectya could be included in Echinocladuria
as equally as in Antho. The former option is
tentatively rejected here based on the unequivo
cal possession of spined (versus smooth) styles
composing the renieroid skeleton, and possession
of a secondary, longitudinal, subicosidedral sec
ondary skeleton in Isopenectya. Similarities in
renieroid skeletal construction may link both
these genera into a clade based on secondary
reduction or loss. The difficulty in positively ass
signing Isopenectya is discussed further below.

Wiedenmayer (1977: 144) suggested that
Echinocladuria should be restricted to Indo
Pacific species, although there were similarities
in skeletal architecture with Pandaros from the
West Indies (which lacks microscleres). He noted
further that Echinocladuria had mostly smooth
chaoonosomal spicules, except for occasional ves
tigial spines on the bases of some auxiliary
spicules, whereas Pandaros had acanthose
ehcinating spicules. Simpson (1968a) has already
demonstrated that the loss of spination on
ehcinating spicules is common amongst
microcionids and not correlated with any
cytological differences (i.e., of low taxonomic
value). Wiedenmayer (1977, 1989) concluded that
although two genera intergraded they could
not be consistently differentiated, and Pandaros
is not included in this group.

Thus, on the basis of evidence presented by
Hallmann (1912: 275), Burton (1959a: 246) and
Wiedenmayer (1989: 58), and re-examination of
all nominal species belonging to these groups, it
is clear that we are dealing with two distinct,
homogenous groups. One, agreeing with the
definition of Spongia leporina above, includes
the genera Echinocladuria (in the strict sense
only, and not of authors), and Ophlitaspongia (of
authors, and not in the strict sense).
Echinocladuria is the earliest available name for
this group, and its characteristics should be taken
as those traditionally associated with the concept
of Ophlitaspongia (of authors). This genus is
most closely related to Antho in its renieroid main skeletal structure, differing in having smooth choanosomal spicules and a single skeletal structure (i.e., Antho has 2 skeletal structures: a renieroid skeleton composed of spined spicules and a plumose or subsidicalyct skeleton composed of smooth spicules).

The second group contains honeycombed reticulate species traditionally associated with Echinoclathria (of authors, not in the strict sense), together with Holopsamma, Holme, Plectispa and Anuma (of authors, not in the strict sense). The earliest available name for this group is Holopsamma Carter (1880f). There is no doubt that this honeycombed reticulate group of microcionids warrants inclusion in a separate taxon, although its level of divergence is arguable (cf. Wiedenmayer, 1977, 1989; Hooper, 1991). Its peculiar growth form is consistent for all 12 Australian species (all from southern Australia (Gondwanan) faunas), and 4 non-Australian species (2 from South America (Gondwanan) and 2 from the Indo-west Pacific (Tethyan) faunas). This growth form is correlated with a reticulate skeletal architecture, forming a homogeneous group which is recognised here at the generic level.

A honeycombed reticulate growth form is also known for Acamasa de Laubenfels (1936a: 117) in Mycalidae (Van Soest, 1984b) and Pandaros (see below), both known only from the West Indies.

**Echinonema** Carter, 1875
(Fig. 14F-G)

*Echinonema* Carter, 1875: 194 (nomen nudum); Carter, 1881a: 378; Ridley, 1884a: 615; Topsent, 1894a: 19; Dendy, 1896: 32; Whitelegge, 1901: 80; Topsent, 1928a: 61, 1932: 89, 98; de Laubenfels, 1936a: 112; Lévi, 1960a: 56.

**TYPE SPECIES.** *Echinonema typicum* Carter, 1881a: 377 (by taphonomy) (lectotype BMNH1877.5.21.149); junior synonym of *Spongia cactiformis* Lamarck, 1814: 440 (lectotype MHNHLBIMDTS80).

Arborescent, shrubby, lamellate growth form. Surface even, hispid, subectosomal striations. Choanosomal skeleton reticulate, with open rectangular or elongate open meshes although slightly compressed in axis. Primary spongion fibres ascending, heavy, cored by multiparticular tracts of choanosomal principal styles, interconnected by pauci- or aspicular secondary spongion fibres. Fibres echinated by acanthostyles heaviest in peripheral skeleton. Subectosomal skeleton plumose, with brushes of larger subectosomal auxiliary stylostyles erect on peripheral choanosomal fibres. Ectosomal skeleton dense, with smaller ectosomal auxiliary stylostyles forming a dense palisade on surface. Megascleres include smooth choanosomal principal styles, larger subectosomal auxiliary stylostyles with smooth or microspined bases, smaller ectosomal auxiliary stylostyles with smooth or microspined bases, and short thick echinating acanthostyles with spined base and point but bare neck. Microscleres palmate isochelae of two sizes, including contort forms, and thin accolada and asymmetrical toxas.

**REMARKS.** It is confirmed here that Carter's (1881a) *Echinonema typicum* is identical to Lamarck's (1814) *Spongia cactiformis*, and consequently the name *cactiformis* has seniority over the better known junior synonym *Clathria typica*, widely used in the literature. Lendenfeld (1888), Whitelegge (1901) and Hallmann (1912) created many new subspecific names (as varieties) for this species, and Hooper & Wiedenmayer (1994) assigned Lamarck's (1814) specimen to *Clathria* (*Thalysias*) *cactiformis* *cactiformis*, and Carter's (1881) specimen to *C. (T.) cactiformis* *typica*. Examination of type material of all these subspecies (var. *typica* (SMF1589); var. *porrecta* (SMF1653); var. *brevispinus* (AMZ931); var. *favosus* (AMZ944); var. *gender* (AMZ928); var. *obesus* (AMZ937); var. *proximus* (AMZ930); var. *stelligera* (AME648); and three unnamed varieties of Hallmann (1912) (AMZ1158; AMZ1430; G9135; Z938; and AMZ41), showed that they were conspecific with the homotypic variety (based on spicule size, spicule geometry and skeletal structure), whereas growth forms and surface features varied substantially between each taxon. The recognition of these subspecies, a preoccupation of many earlier authors, does at least demonstrate a high degree of external morphological variability for the species, but is not of particular nomenclatural importance because there are no other morphological characters that correlate with these differences in external morphology. It may be eventually determined from biochemical or genetic data, that this polymorphism is indicative of sibling species relationships, but no studies of this sort have yet been undertaken.

De Laubenfels (1936a: 112) suggested that *Echinonema* was identical to *Thalysias* (*sensu de Laubenfels*), whereas Van Soest (1984b) and others placed both genera into synonymy with *Rhaphidophlus* (see below). The genus is in-
cluded here in *Clathria* (*Thalysias*) on the basis of its ectosomal specialisation.

**Fisherispongia** de Laubenfels, 1936  
(Fig. 15A-C)

*Fisherispongia* de Laubenfels, 1936b: 460.

**TYPE SPECIES.** *Fisherispongia ferrea* de Laubenfels, 1936b: 460 (by original designation) (holotype USNM22239).

Encrusting growth form. Surface tuberculate, arenaceous, hispid, choanosomal skeleton hymedesmoid, with basal layer of spongion fibre incorporating detritus and bases of larger choanosomal principal subtylostyles and smaller echinating styles, standing perpendicular to substrate, in groups or individually, ascending to but not protruding through ectosome. Ectosomal skeleton plumose, with subectosomal auxiliary polytylostyles, of a single category, arising from ends of choanosomal microsceleres in multi-spicular bundles protruding through surface. Microsceleres large choanosomal principal subtylostyles with smooth bases, smaller smooth echinating styles with smooth or micropinned bases, and polytyloite auxiliary tylostyles with smooth or micropinned bases. Microsceleres palmate isochelae, including contorted forms, and thick wing-shaped toxas.

**REMARKS.** De Laubenfels (1936b) distinguished *Fisherispongia* from other microcionids by the polytyloite bases on their subectosomal auxiliary styles. In all other respects, however, the type species resembles other encrusting species with hymedesmoid architecture (e.g., *Leptocelathtria*). Polytyloite ectosomal megascleres are known in several other species of Microcionidae (e.g., *Clathria aceratoobtusa*, *Paratenaciella microcea*, as well as in other Poecilosclerida (e.g., *Campitiscoccia* Topsent and *Phelloderma* Ridley & Dendy; Coelosphaeridae). The incorporation of detritus into the choanosome and fibres is well known for several microcionids and other sponges (see remarks for *Aulenella*) and on this basis the species is included in *Clathria* (*Wilsonella*). Re-examination of the holotype found a marked contrast in size between the smaller and larger (so-called principal) spicules, with no intermediate sizes, and these smaller spicules are interpreted here as being smooth echinating styles. By its toxo morphology *Fisherispongia ferrea* (from the Atlantic coast of Panama) is very similar to *Clathria aceratoobtusa* (from the Indo-west Pacific).

**Folitispa** de Laubenfels, 1936  
(Fig. 15D-F)

*Folitispa* de Laubenfels, 1936a: 119.

**TYPE SPECIES.** *Hymedesmia laevissima* Dendy, 1922-81 (by original designation) (holotype BMNH1921.11.7.69).

Thickly encrusting growth form. Surface even, slightly hispid. Choanosomal skeleton hymedesmoid, with spongion fibres lying on substrate and bases of choanosomal principal subtylostyles embedded, standing perpendicular to substrate individually or forming short multi-spicular plumose columns protruding through surface. Echinating megascleres absent. Subectosomal skeleton irregularly plumose, with loosely aggregated bundles of subectosomal auxiliary subtylostyles erect on surface or lying tangential to it. Megascleres include smooth choanosomal principal subtylostyles, and smooth subectosomal auxiliary subtylostyles with mucronate or telescoped points. Microsceleres palmate isochelae with anchorate-like modifications (curvature, partially detached alae, continuous ridge on shaft). Toxas absent.

**REMARKS.** The type species of *Folitispa* differs from other encrusting microcionids with hymedesmoid skeletal architecture (e.g., *Leptocelathtria*) in lacking echinating acanthostyles (cf. *Asoiectella*) and having chelae with anchorate-like modifications instead of typical palmate isochelae (cf. *Cionanchora*). These chelae are strongly curved, with lateral alae partially detached from the shaft and a continuous lateral ridge running the length of the shaft. However, these lateral alae are not fully formed (being about two-thirds the size of the front alae), nor are they completely detached from the shaft (attached for approximately 50% of their length), and consequently they cannot be considered true anchorate chelae but perhaps palmate isochelae with substantial anchorate modifications. The genus is included here in *Clathria* (*Microciona*) based on its skeletal structure.

[Halme] Lendenfeld, 1885  
(Fig. 14H-I)

Not *Halme* Pascoe, 1869.

**TYPE SPECIES.** *Holopisamma laminaefavosa* Carter, 1885b: 212 (by subsequent designation; de Laubenfels, 1936a: 17) (holotype BMNH1886.12.15.312).
Massive, globular, lobate-digitate honeycombed reticulate growth form. Surface composed of small branches ("lacunae") interconnected to form regular network. Choanosomal skeleton irregularly reticulate, with heavy spongin fibres fully cored by both sand particles and other detritus, and with fewer choanosomal principal subtylostyles both coring and echinating fibres. Subectosomal skeleton with peripheral fibres cored and echinated by principal megascleres, slightly heavier, more plumose at periphery than at core, and with subectosomal auxiliary strongyles forming irregular paratangential tracts near surface. Ectosome with external fibre reticulation reinforced by sand. Megascleres vary from common to relatively scarce (or spicules reportedly absent entirely in some specimens), including short entirely smooth choanosomal principal subtylostyles, and smooth sinuous or straight subectosomal auxiliary strongyles or quasidiactinal styles. Microscleres absent.

REMARKS. Halmé (sensu Lendenfeld, 1889b) is virtually identical to Aulena (of authors, e.g., Lendenfeld, 1888, but not Lendenfeld, 1885c), in skeletal construction, growth form and the presence of detritus within the fibre skeleton. In contrast, Halmé (of Lendenfeld, 1885c) differs from Aulena (of authors) by the virtual absence (or inconsistent presence) of proper, heavily mineralised spicules. However, examination of relevant type material, recent material from southern and eastern Australian waters (see below) and the literature (e.g., Wiedenmayer, 1989) shows that *H. laminaefavosa* is relatively polymorphic in its growth form, surface structure, spongin fibre construction, amount of detritus incorporated into the skeleton and the number and presence or absence of megascleres. Despite this variability, the species is clearly a synonym of *Holopsamma*, closely related to other honeycombed reticulate species. Of the numerous species referred to Halmé by Lendenfeld (1885c, 1888) many are Dictyoceratids (Bergquist, 1980b), whereas the type species is undoubtedly a microcionid. Unfortunately the name Halmé Carter, 1885b is preoccupied by Halme Pascoe, 1869 (Wiedenmayer, 1989), and Holopsamma Carter is the senior-most available name for this group of honeycomb reticulate microcionid sponges.

**Heterocladhria** Topsent, 1904
(Fig. 16A-B)

**Heterocladhria** Topsent, 1904b; 93; Burton, 1935a: 403.

**TYPE SPECIES.** *Heterocladhria hallesi* Topsent, 1904b: 94 (by original designation and monotypy) (schizotype MNHNLMBDMT1884).

Erect, digitate growth form. Surface even, microscopically hispid. Choanosomal skeleton regularly renieroid reticulate, with heavy spongin fibres well differentiated into primary ascending multiscleresh, cored by choanosomal principal tylostyles, and secondary transverse unisarticulated fibres cored by amphistrongyles. Subectosomal skeleton plumose or paratangential, with subectosomal auxiliary subtylostyles forming poorly developed brushes arising from peripheral primary fibres, and also forming clusters around margins of oscules. Echinating acaulostyles absent, but choanosomal principal styles sometimes echinate primary fibres. Megascleres choanosomal principal tylostyles with microspined bases, large strongyles (dumbbell spicules) of renieroid skeleton with spined bases, and subectosomal auxiliary subtylostyles with microspined bases. Microscleres paltmate isocheilae and thin wing-shaped toxas.

REMARKS. *Heterocladhria* is unusual to the plocamiform group of sponges (de Laubenfels, 1936a), such as *Antho* and *Plocamilla*, in having a differentiated primary and secondary fibre network cored by monactinal and diactinal megascleres, respectively. The type species is only known from the holotype which unfortunately lacks collection data. Burton (1935a: 403) referred two other species to the genus, *Plocamilla karykino* de Laubenfels (1927: 262) and *P. manaarensis* (sensu Lambe, 1895: 124; holotype USNM6331; not Carter, 1880a: 34), which he renamed *H. lambei* Burton, and which Bakus (1966: 512) also renamed *Plocamilla zim- meri*. De Laubenfels (1936a: 78) suggested that *Heterocladhria* was a synonym of *Plocamia*, and this is confirmed here from re-examination of both *H. lambei* and *H. hallesi*. *Heterocladhria* is referred here to *Antho* (*Plocamia*) in having (acantho)-strongyles in the renieroid skeleton, although true echinating spicules are absent.

Another species which shows some similarities to *Heterocladhria* in skeletal structure is *Stylotellina cornuta* Topsent (1897b: 464), from the Andaman Sea off Malaysia, for which Burton & Rao (1932: 343) created *Acanthostylotella*. That species lacks the characteristic 'dumbbell spicules' but has
a renieroid skeleton of primary ascending multispicular fibres interconnected by unispecific tracts of smooth styles. It lacks an ecosomal skeleton and lacks microscleres, and it possibly best placed in lophonidae.

**Holoplocamia** de Laubenfels, 1936

(Fig. 15G-I)

*Holoplocamia* de Laubenfels, 1936a: 75; Lévi, 1960a: 80; Little, 1963: 47.

**TYPE SPECIES.** *Holoplocamia penneyi* de Laubenfels, 1936a: 75 (by original designation) (holotype USNM22460).

Thinly encrusting growth form. Surface rugose, microscopically hispid. Chaoosomal skeleton hymedesmoid, with basal layer of spongin fibre, principal chaoosomal styles embedded in fibre nodes, standing perpendicular to and protruding through surface, and with basal mass of acanthostrongyles forming an irregular renieroid secondary reticulation of spicules around principal spicules, interconnected by sparse collagen at nodes. Smaller acanthostyles also present echinating fibre nodes. Mesohyl incorporates large quantities of detritus and auxiliary spicules. Ectosomal skeleton with tangential or paratangential tracts of subectosomal auxiliary styllostyles. Megascleres principal chaoosomal styles-substylolostyles with either smooth or micropinned bases, acanthostrongyles or acanthostyles of basal skeleton more heavily spined at ends than middle, echinating acanthostyles evenly spined, and subectosomal auxiliary styllostyles with micropinned bases. Microscleres palmate isochelae, including contorted forms, and wing-shaped toxas.

**REMARKS.** *Holoplocamia* was erected for sponges similar to *Plocamia* Schmidt, but having spiny rather than smooth principal spicules. Lévi (1960a) suggested that the genus was a synonym of *Plocamilla*, whereas Topsent (1928a) and Little (1963) argued that *Plocamilla* was different from both *Plocamia* and *Holoplocamia* in lacking any differentiation between primary and secondary skeletal tracts. This opinion is not upheld here. de Laubenfels (1936a: 75) referred several 'plocamiform' species to *Holoplocamia*, and it is now generally accepted that *Holoplocamia* and *Plocamilla* are synonymous (Bakus, 1966; Simpson, 1968a; Lévi & Lévi, 1983a; Pulitzer-Finali, 1983; Van Soest, 1984b). Most of the 'plocamiform' species discussed by de Laubenfels (1936a) were subsequently found to belong to *Plocamione* Topsent (Raspailiidae; Hooper, 1991), whereas the poecilosclerids (including *Holoplocamia*) are considered here to belong to *Antho* (*Plocamia*) (the latter a senior name for *Plocamilla*).

**Holopsamma** Carter, 1885

(Fig. 16C-D)

*Holopsamma* Carter, 1885c: 211.


Subspherical, digitate, regularly 'honeycomb' reticulate growth form. Surface arenaceous, porous, with tympanic membrane-like ecosomal crust stretched across adjacent subdermal cavities. Chaoosomal skeleton reticulate, with well developed spongin fibres not well differentiated into primary or secondary elements, although many ascending fibres have core of small quantities of detritus (mostly spicule fragments), whereas other fibres clear of detritus completely. Coring and echinating spicules absent from chaoosomal skeleton. Ectosomal skeleton heavily arenaceous, with crust of sand and scattered reticulate (or plumose or paratangential in places) bundles of subectosomal auxiliary strongyles lying tangential on surface crust. Mesohyl matrix relatively heavy between fibres. Megascleres only smooth subectosomal auxiliary strongyles. Microscleres absent.

**REMARKS.** De Laubenfels (1936a: 97) noted that *Holopsamma* differs from other 'sandy sponges' (i.e., the polyphyletic 'family Psammascidae' de Laubenfels) in lacking microscleres and having both monactinal and diaactinal megascleres. It is unfortunate that he designated *H. crassa* as the type species because in some of the 5 'valid' syntypes the monactinal (principal) styles may be lost completely, and the diaactinal (auxiliary) strongyles are vestigial, leaving only heavy spongin fibres (the major ones with a core of detritus), and a heavy ecosomal sand cortex.

The status and affinities of this genus are still confused, despite the comprehensive redescription and discussion of the type species by Wiedenmayer (1989). This confusion is due to the fact that no-one had previously nominated a lectotype amongst the 31 syntypes of the type species, which are composite and represent at
least 6 different species: only 5 of these actually
conformed to Carter's (1885c) original description
of Holopsamma crassa.

Furthermore, the lectotype (BMNH-886.12.15.313) designated by Hooper & Wiedenmayer (1994) and figured by Wiedenmayer (1989: pl.6, fig.7) is identical to Halme
globosa Lendenfeld, and there is some conjecture
as to which name is the most valid. Wiedenmayer
(1989: 63) chose to use the name H. globosa over
H. crassa, although he admitted that crassa was
more senior (apparently by only several months),
and therefore under the rules of the ICZN it must
take precedence. His arguments in choosing
globosa over crassa were that type material of
globosa was firmly established whereas the type
series of crassa was an unresolvable mess, but
this is irrelevant with the subsequent designation
of a lectotype for H. crassa by Hooper & Wieden-
mayer (1994).

Wiedenmayer (1989: 63) provided many fur-
ther details concerning these species synonymsies
and the affinities of 'sandy sponges' belonging to
the Microcionidae. But more important than the
nomenclatural problems associated with the type
species (and the genera Halme and Holopsam-
ma), there are some biological questions un-
answered by Wiedenmayer's (1989) work. Hol-
opsamma crassa is very similar to Holopsam-
na laminaevavosa, the type species of Halme
Lendenfeld, 1885 (not Halme Pascoe, 1869), and
it is possible that in fact the two species are
synonymous (given that they are both allegedly
very polymorphic). A comparison of type
material shows that the only substantial differ-
ces are that in H. crassa spongin fibres contain
virtually no sand and principal spicules have been
lost, whereas in H. laminaevavosa primary fibres
are virtually fully cored with sand, and both prin-
cipal and auxiliary spicules are retained. In deal-
ing with preserved material (i.e., without
accompanying field characters), these definitions
should be adhered to strictly. Conversely, follow-
ing Wiedenmayer's (1989) definition, diagnostic
characters in each species overlap substantially
providing reasonable cause to synonymise the
species (and genera Holopsamma and Halme).

In the present work Holopsamma is the senior
name for the group of honeycomb reticulate
sponges traditionally known as Echinocolathria
(of authors).

**Hymanto** Burton, 1930
(Fig. 16F-G)

**Hymanto** Burton, 1930a: 503.

**TYPE SPECIES.** Hymanto normani Burton, 1930a:
503 (by original designation) (holotypeBMNH
1910.1.1.791).

Thiny encrusting growth form. Surface even,
hispid. Choanosomal skeleton hymedmoid, with
basal layer of spongin on substrate and bases of
choanosomal principal subtylostyles and
echinating acanthostyles embedded and standing
perpendicularly to substrate. Ectosomal skeleton
with paratangential bundles of subectosomal
auxiliary subtylostyles of single size category.
Mesohyl matrix with some debris incorporated.
Megascleres choanosomal principal subtylo-
styles with acanthose bases, echinating acanthos-
tyles with spined bases and shafts but aspinose
points, and smooth auxiliary subtylostyles or
polytylostyles. Microscleres palmate isochelae
and thick forceps-shaped or v-shaped toxas.

**REMARKS.** Hymanto normani was originally
described with only toxo microscleres but re-
examination of the holotype discovered that large
palmate isochelae (18-22μm), with large alae, are
also present. Hymanto was erected by Burton
(1930a), being similar to Leptoclathria Topsent
in its hymedmoid skeletal architecture, but sup-
pessedly lacking chelae microscleres (Levi,
1960a: 60). In this latter respect the genus was
also be compared with Pseudanchnacine and Querc-
ciclon, which Van Soest (1984b) considered to
be junior synonyms of Clathria (s.l.), but in any
case the discovery of isochelae in the type species
negates the concept of the genus. Alander (1942)
and Van Soest & Stone (1986) also suggested that
the secondary loss of isochelae and the presence
of a leptoclathrid skeleton have little generic
value in the Microcionidae. The genus is referred
to synonym with Clathria (Microciona).

**Isociella** Hallmann, 1920
(Fig. 16H-I)


**TYPE SPECIES.** Phakellia flabellata, in part (sensu
Ridley & Dendy, 1886: 478) (by monotypy) (not P.
flabellata Carter, 1885f: 363); = Phakellia jacksoniana
Dendy (replacement name; Dendy, 1897: 236)
(holotype BMNH1887.5.2.9), both junior synonyms of
Clathria macropora, in part, Lendenfeld, 1888: 221
(holotype AMZ466) (this work).

Erect, stipitate, flabelliform growth forms. Sur-
face hispid, relatively smooth, with ridges and
lamellae. Choanosomal skeleton relatively
homogeneous, renieroid, composed of primary,
multispicular, plumose, ascending tracts of

**Hymantho** Burton, 1930
(Fig. 16F-G)
choanosomal principal styles, interconnected by secondary, uni- or paucispicular, transverse tracts of same spicules, together forming regular renieroid or sub-renieroid (triangular) meshes; principal spicules bonded together at nodes by collagen or enclosed in relatively poorly developed spongion fibres. Echinating acaenthes absent. Subectosomal auxiliary styles of a single category, arranged tangentially, paratangentially or in plumeous brushes on surface, with some principal styles also protruding through peripheral skeleton singly or in sparse plumeous brushes. Megascleres robust smooth choanosomal principal styles, and small smooth or basally spined subectosomal auxiliary styles-sublagnostyles. Microscleres palmate isochelae with 'fluted' alae, no toxas (in type species).

REMARKS. Isociella contained 3 species prior to the present study (Clathria macropora Lendenfeld, Ophitaspangia ecentrica Burton (1934a: 560), and I. incrustans Bergquist (196a: 42)), although Hallmann (1920: 784) suggested that there were some other species included in his concept of Ophitaspangia (=Echinoclaithria as defined in this study) which could also be referred here. The definition above is widened below to include species with toxas and different forms of palmate isochelae.

Dendy (1897) renamed the type species jacksoniana because Phakellia flabellata Ridley & Dendy (1886) was preoccupied by Phakellia flabellata Carter (1885f) from Port Phillip Bay, but Hallmann (1920) considered that the 2 species belonged to different genera, and the replacement name flabellata was unnecessary. However, P. flabellata Ridley & Dendy is a junior homonym of P. flabellata Carter, and Dendy's (1897) replacement name P. jacksoniana is a valid emendment. Neither species belongs to Phakellia. In any case C. macropora Lendenfeld is identical to, and the senior available name for, P. jacksoniana.

Isociella is distinguished from other microcionids by its relatively homogeneous, wide-meshed, sub-renieroid reticulation of a single category of smooth choanosomal styles, lacking echinating spicules, and without any differentiation between axial and extra-axial regions (although choanosomal spicules may diverge slightly towards periphery, sometimes becoming plumeous on surface). It differs from the two other groups of microcionids that have renieroid skeletal structure. Anthe (including Isociona, Plocania, Plocamilla, Plocaniopsis, and Isopenecrya), has two categories of choanosomal megascleres, one acaenthes forming a basal renieroid skeleton, and one smooth forming ascending plumeous extra-fibre tracts of the true choanosomal skeleton. Some Echinoclaithria species (as defined in the present study, including Ophitaspangia in the sense of most authors), have a renieroid main skeleton of smaller, smooth choanosomal styles and the same spicules echinating fibres, a radial peripheral skeleton in which larger, smooth choanosomal styles are embedded in the subectosomal skeleton and protrude a long way through the surface, and a very well developed spongion fibre reticulation seen in most species, often with some axial compression (reflecting a digitate or flabellate growth form).

The most abundant Australian species, Isociella ecentrica, has a choanosomal skeleton reminiscent of Calyxongia (Haplosclerida) and an open, reticulate ectosomal skeleton, and all 3 known Australian species have closest affinities with certain Clathria species (e.g., C. (Clathria) connectens, C. (Thalysia) hirsuta). Thus, the definition of the type species is expanded below to include forms which are predominantly semi-encrusting, branching, with rugose reticulate surface sculpturing, well developed spongion fibres (as opposed to only having collagen binding principal spicules together); poorly differentiated primary and secondary skeletal tracts, and to allow for the presence of toxas microscleres. Isociella is included here as a subgenus of Clathria.

Isociona Hallmann, 1920
(Fig. 17A-B).

Isociona Hallmann, 1920: 768; de Laubenfels, 1936a: 111.

TYPE SPECIES. Lissodendoryx tuberosa Hentschel, 1911: 326 (by monotypy) (holotype ZMB4417).

Thickly encrusting, bulbous growth form. Surface irregularly microconulose, hispid. Choanosomal skeleton with differentiated primary and secondary skeletons. Secondary skeleton renieroid or subrenieroid reticulate, with acaenthes styles forming uni-, pauci-, or less frequently multispirical tracts, bound together by very light fibres or collagen at spicule nodes. Primary skeleton plumeous, with choanosomal principal styles forming larger primary ascending tracts irregularly connected by smaller secondary transverse tracts. Subectosomal skeleton plumeous, with principal styles protruding through
ectosome overlayed by erect bundles of subectosomal auxiliary subtylostyles. Echinating megascleres absent. Megascleres large smooth chaoanosomal principal styles, basally spined or entirely lightly spined styles-subtylostyles of renieroid skeleton, and smooth auxiliary subectosomal subtylostyles. Microscleres palmate isochelae and thick wing-shaped toxas.

REMARKS. Isociona tuberosa and Isosciella ecencnitra appear very similar from published descriptions whereas examination of type material shows that they are different. Isosciella ecencnitra has a wide meshed renieroid reticulate skeleton composed of smooth principal spicles, whereas I. tuberosa has a close-meshed renieroid secondary skeleton of spined monactinal spicles, overlayed by a plumeose primary skeleton of smooth principal spicles. Van Soest (1984b) merged Isociona with Antho, although this relationship is not straightforward given that Antho is usually reserved for forms with diactinal megascleres (in the renieroid basal skeleton). Nevertheless, the two taxa have similar skeletal architecture and Isociona is maintained as a synonym of Antho herein.

Isopenectya Hallmann, 1920
(Fig. 17C-D)


TYPE SPECIES, Clathria (?) chartacea Whitelegge, 1907: 497 (by monotypy) (holotype AMZ436).

Thiny flagellate-lamellate growth form. Surface smooth, even. Chaoanosomal skeleton renieroid reticulate, with differentiated axial and extra-axial regions of skeleton. Axial skeleton with compressed spongin fibres running through centre of lamellae, cored by smooth chaoanosomal principal styles (marginally smaller than those in surface bundles) forming subisodictyal tracts, overlain by renieroid skeleton of small spined styles. Extra-axial skeleton with more open-meshed, regularly reticulate spongin fibres, cored by uni- or bispicular renieroid tracts of small acanthose styles, and plumeose, subisodictyal tracts of longer smooth styles standing perpendicularly to axis, both fully enclosed in spongin fibres. Echinating megascleres absent. Subectosomal skeleton plumeose, with bundles of smooth chaoanosomal principal styles protruding through surface and tangential or paratangential tracts of subectosomal auxiliary styles. Ectosome lacks specialised spiculation. Megascleres lightly acanthose styles-subtylostyles forming renieroid skeleton, short and long smooth chaoanosomal principal styles, and subectosomal auxiliary styles with spined bases. Microscleres absent.

REMARKS. Isopenectya is similar to other renieroid 'plocamiform' genera (sensu de Laubenfels, 1936a), Antho, Plocamilla, Plocamioptis, Isociona, Labueca, Pandaros, Isosciella and Echinolathria, in having a primarily renieroid reticulate skeleton. Unlike these other genera, however, Isopenectya has 2 forms of chaoanosomal megascleres enclosed within spongine fibres. The smaller acanthose styles forming the renieroid structure, whereas smooth styles form the subisodicytal, mostly longitudinal skeleton. These latter spicles also produce the extra-axial plumeose tracts that ascend to the surface, and larger, smooth chaoanosomal styles produce brushes on the ectosome. Although the fibre skeleton is compressed in the axis the renieroid skeleton is barely different between axial and extra-axial regions.

Isopenectya chartacea is remarkable in that it closely resembles the type species of Echinolathria (E. leporina) in growth form, gross skeletal architecture and fibre characteristics. Whereas E. leporina has one category of relatively homogeneous smooth principal styles throughout the choanosomal skeleton, I. chartacea has 2 differentiated structures within the choanosome (renieroid and plumeose or subisodicytal skeletons) and 2 geometrically different categories of megascleres forming these skeletal structures. Skeletal architecture is also more regularly renieroid and renieroid fibres/tracts are relatively homogeneous than in most Echinolathria species, but this is a matter of degree. Echinolathria has a radial skeleton of larger, smooth principal styles embedded in peripheral fibres, poking through the surface, and it could be argued that this is a vestigial subisodicytal skeleton like that in Isopenectya. But this similarity is inferred and any relationship is equivocal, with emphasis placed here on the possession of spined spicles of the renieroid skeleton and clearly differentiated renieroid and subisodicytal skeletal structures in deciding on affinities of Isopenectya. Nevertheless, these 2 species are certainly remarkably similar and potentially may be confused.

Van Soest (1984b) suggested that Isopenectya may be valid, but 'plocamiform' microcionid type shows that it is a close relative of this group. of Antho in particular, differing from it only in
having a unique subsidiectyal skeleton of smooth spicules overlaying the renieroid basal skeleton. It is recognised here as a subgenus of Antho.

Jia de Laubenfels, 1930 (Fig. 17E-F)


TYPE SPECIES. Jia jia de Laubenfels, 1930: 28 (by original designation) (holotype USNM21510).

Encrusting growth form. Surface uneven, hispid. Choanosomal skeleton confused renieroid reticulate, composed of smaller smooth or acanthosstyles forming basal more-or-less rectangular network, overlayed by larger smooth principal styles standing erect, forming ascending bundles or single spicules projecting through surface. Subectosomal auxiliary subtylostyles paratangential to surface. Ectosome without special spicules. Megascleres larger smooth choanosomal principal styles, smaller smooth or acanthosstyles-subtylostyles of basal skeleton, and subectosomal auxiliary subtylostyles with basal spines. Microscleres palmate isochelae, modified J-shaped chelae resembling signas (= 'crocae'), and wing-shaped toxas with spinous extremities.

REMARKS. De Laubenfels (1932) description of the type is incomplete. The essential specific characteristics include the modified (J-shaped) isochelae (crocae of Van Soest & Stone, 1986), and a renieroid albit ill-defined reticulation. Those characters are contrasted with the Antho- like nature of closely related A. (Jia) brattegardi Van Soest & Stone, which has acanthos styles monac- tinal and diactinal spicules in the main skeleton, whereas Jia (s.s.) has predominantly smooth spicules. Despite these differences, Van Soest & Stone (1986) justifiably merged Jia and Antho because many other Antho-like species without crocae also have predominantly smooth styles and poorly defined skeletal construction (e.g., A. dichotoma (Esper)). Jia is referred to Antho (Antho).

Crocae are not unique to Jia; other taxa with similarly modified chelae are Dendoryx luciensis Topsent (Myxillidae) and Zygerhera hyaloderna de Laubenfels (Hamacanthidae) (de Laubenfels, 1932; Bakus, 1966; Van Soest & Stone, 1986.

Labacea de Laubenfels, 1936 (Fig. 17G-H)

Labacea de Laubenfels, 1936a: 125.

TYPE SPECIES. Clathria juncea sensu Burton, 1931a: 343 (by original designation) (type fragment BMNH1926.2.19.2).

Erect digitate, arborescent growth form. Surface even, minutely hispid. Choanosomal skeleton reticulate, with well differentiated primary ascending and secondary transverse skeletal tracts. Primary skeleton with well developed thick sponge fibres, ascending to surface, cored by multipspicular tracts of choanosomal principal styles, interconnected by thin transverse secondary fibres cored by pauci- or unispicular tracts of same spicules. Echinating acanuhostyles moderately common in axial skeleton, very heavy in peripheral skeleton, forming plumose brushes at surface. Subectosomal skeleton tangential with subectosomal auxiliary subtylostyles lying on surface. Ectosome without specialised spiculation, but with many foreign spicule fragments embedded in outer layer of skeleton. Mesohyl with abundant detritus and auxiliary spicules dispersed between fibres. Megascleres include both smooth and completely lightly spined fusiform choanosomal principal styles, evenly spined echinating acanuhostyles, and smooth auxiliary subectosomal subtylostyles. Microscleres large palmate isochelae and accolada toxas with microspined points.

REMARKS. Clathria juncea is attributed to Burton (1931a), and a lectotype designated from the syntypes (BMNH1933.7.4.4-7). However, Burton and de Laubenfels (1936a) suggested that Clathria juncea sensu Burton may be synonymous with Alcyonium junceum Lamarck, 1816. Topsent (1933: 26) merged Lamarck's species as a variety of Anomoclostria opuntioiides, but noted that the type was missing from the MNHN. It is still missing, and must now be presumed destroyed. If Lamarck's species is identical with A. opuntioiides then C. juncea sensu Burton is quite different (see remarks for Anomoclostria).

Burton's (1931a) description, and de Laubenfels' (1936a) interpretation of the type species are both erroneous. Burton's described material exhibits several characters not noted by either of these authors, so that Labacea is incor- rectly diagnosed. The skeletal architecture of C. juncea is reticulate, not renieroid as supposed by de Laubenfels, and echinating acanuhostyles (a prominent feature of the peripheral skeleton in particular) and palmate isochelae were over- looked. I assign it to Clathria (Clathria).

De Laubenfels (1936a) assigned Clathria azeifera Ferrer Hernandez to this genus; it sup-
posedly differed from the type species in having echinating acanthostyles (as distinct from acanthostyles of choanosomal principal megascleres (Lévi, 1960a: 84)) but as noted above these spicules are typical for the genus, and de Laubenfels' observation is redundant.

**Leptocladthria** Topsent, 1928
(Figs 171, 18A)

*Leptocladthria* Topsent, 1928a: 298.

**TYPE SPECIES.** *Leptocladthria haplotaxa* Topsent, 1928: 298 (by monotypy) (holotype MNHNLBIMDT-1101).

Encrusting growth form. Surface irregular, hispid. Choanosomal skeleton heteroporous, with spongilla fibres reduced to basal layer of spongilla, having bases of choanosomal principal subtylostyles and abundant smaller acanthostyles standing perpendicular to substrate. Subectosomal skeleton with light tangential tracts of subectosomal auxiliary subtylostyles occurring in bundles or individually, forming irregular dermal brushes surrounding protruding choanosomal megascleres. Ectosomal skeleton without specialised spiculation. Megascleres include entirely acanthose choanosomal principal subtylostyles, even spined echinating acanthostyles, and subectosomal auxiliary subtylostyles with spined bases and telescoped or mucronate points, sometimes quasidiactal. Microscleres palmate isochelae and toxas intermediate between wing-shaped and v-shaped.

**REMARKS.** The type species is simply a thinly encrusting *Microciona*-like species with a heteroporous skeletal architecture, but which differs from *Microciona* (s.s.) in having entirely acanthose principal styles (similar to *Dictyociona*, *Hymeraphia* and *Anura*). Lévi (1960a) proposed that *Leptocladthria* should be merged with *Microciona*, and this is certainly true for the type species (referred here to *C. (Microciona)*), but there are some species which have a clearly differentiated ectosomal and subectosomal auxiliary spicules (e.g., *L. lambda* Lévi), and these species are more appropriately included in *C. (Thalysias)*.

Topsent (1928a) overlooked the spined basal toxas and telescoped (or mucronate) points on subectosomal auxiliary subtylostyles which are prominent in the holotype. Furthermore, and of greater taxonomic significance, there are at least a small proportion of auxiliary megascleres with tylote (quasidiactal) geometry, including basal microspination, which is reminiscent of the specialised diactal ectosomal megascleres characteristic of *Myxillidae* and *Lophonidae*. Only a few other microcionids have this feature, *C. (Clathria)* *chelisera*, *C. (Wilsonella)* *australensis* and *C. (Thalysias)* *major* (see also Hooper et al., 1990). These quasi-diactal spicules are analogous to (but not homologous with) ectosomal tylostyles found in *Myxillidae* for example (see remarks for *Acarnus* below).

**Ligrota** de Laubenfels, 1936
(Fig. 18B-C)

*Ligrota* de Laubenfels, 1936a: 125.

**TYPE SPECIES.** *Clathria lobata* Vosmaer, 1880: 151 (by original designation) (holotype RMNH276).

Arborescent growth form with flattened branches. Surface even, microscopically hispid. Choanosomal skeleton regularly reticulate, with poorly developed spongilla fibres forming differentiated primary and secondary tracts. Primary fibres ascend to surface, cored by plumose masticophores of choanosomal principal styles, secondary fibres transverse, paucispicular, cored by main spicules. Subectosomal skeleton plumose, with bundles of choanosomal principal megascleres extending into ectosome and protruding through surface. Echinating acanthostyles most abundant in periphery, below surface spicule brushes. Some detritus incorporated into mesohyl, scattered between spicle tracts. Ectosome radially arranged, erect brushes of subectosomal auxiliary subtylostyles of a single size class. Megascleres robust choanosomal principal styles-subtylostyles with smooth bases, echinating acanthostyles with large spines and axismose points, and subectosomal auxiliary subtylostyles with basal spines. Microscleres palmate isochelae and wing-shaped toxas with spined points.

**REMARKS.** This definition from the holotype differs from descriptions provided by Vosmaer (1880), Ridley & Dendy (1887), and Lévi (1963), but corresponds with Stephens's (1915) concept of the species. In particular, the species has a regularly reticulate skeleton with radial architecture, but it lacks a well differentiated axial and extra-axial region as suggested by these authors. *Ligrota* has spiculation virtually identical to that of *Clathria* (s.s.), including spines on the points of toxas. It is not a *Thalysias*, as supposed by Ridley & Dendy (1887), because it has only a
single, undifferentiated category of auxiliary sub-
tylostyle and is referred here to Clathria
(Clathria). Similarly, de Laubenfels' (1936a)
diagnosis of Ligrola is incorrect. Clathria lobata
of Stephens (1915) does not have diactinal
megascleres or sigmas. Those attributes were
described by Vosmaer (1880) for the type
specimen, but were discounted by Ridley &
Dendy (1887) as being probable contaminants;
nor were they observed in type material.

Lissoplocamia Brandstedt, 1924
(Fig. 18D-E)

Lissoplocamia Brandstedt, 1924: 470.

TYPE SPECIES. Lissoplocamia prima Brandstedt,
1924: 470 (by original designation) (holotype in ZMC,
not seen; MNHNLBIMDCL637 from South Africa).

Digitate, arborescent, flattened or cylindrical
branches. Surface prominently hispid, velvety.
Choanosomal skeleton renieroid reticulate, with
differentiated axial and extra-axial regions. Axial
skeleton slightly compressed, with well
developed spongin fibres cored by uni-
or paucispicular tracts of tylostyles forming renieroid
reticulation, overlaid by plumose (or plumoreticulate)
extra-axial skeleton composed of diverging single or multiple choanosomal
principal styles, echinating (protruding from) spongin
fibres and ascending to surface. Spongin fibres in
extra-axial skeleton lighter, more-widely spaced.
Subectosomal skeleton plumose, with bundles of
subectosomal auxiliary styles perched on ends of
principal megascleres. Ectosome without special
category of megascleres, but isochelae micro-
scleres predominant in peripheral skeleton.
Megascleres tylostyles ('dumbbell-shaped' spicules)
of renieroid skeleton with swollen microspined bases,
choanosomal principal styles-subtylostyles,
with smooth or faintly microspined bases,
and smooth subectosomal auxiliary styles.
Microscleres palmate isochelae and wing-shaped toxas.

REMARKS. This definition is based on a recent
redescription of the holotype from New Zealand
(Bergquist & Fromont, 1988: 122) and Lévi's
(1963) specimen from South Africa. Lévi's
material is more complete, with an intact ecto-
somal skeleton and containing palmate
isochelae, whereas Brandstedt's (1924) holotype
is poorly preserved, lacking an ectosomal
skeleton in which the isochelae are predominant-
ly found (Bergquist & Fromont, 1988).

Lissoplocamia belongs to de Laubenfels'
(1936a) 'plocamiform' group of sponges in
having diactinal, quasi-diactinal or monactinal
'dumbbell-shaped' spicules forming a renieroid
basal skeleton (it should be noted that this char-
acter is different from (analogous to) similar
'sausage-shaped' diactinal spicules found in the
ectosomal skeletons of some genera in families
such as Coelosphaeridae and Petrosiidae). Some
of these 'plocamiform' genera belong to
Raspailliidae (Hooper, 1991: 1319), whereas
others are closely related to Microcionidae and
are referred to Antho (Plocamia), Bergquist &
Fromont (1988: 122) mentioned several of these
genera (Lissoplocamia, Holoplocamia, Ploc-
amilla, Heteroclothis, and Plocamia), and to
this group should also be added Antho and Dia.
Axoplocamia, included by them with the
microcionids, was shown to be a raspailliid
including only 2 New Zealand species in
Plocamia, Dirthropalum novizelanidum Ridley
and L. prima, both of which are referred here to
Antho. Lissoplocamia differs from most other
'plocamiform' microcionids, such as Antho (Antho)
in having predominantly smooth 'dumb-
bell-shaped' spicules, similar to the type
species of Plocamia, P. gymnazusa, but this char-
acter is considered insignificant at the generic
level given its large variability within the family.

Litasporgia de Laubenfels, 1954
(Fig. 18F-G)

Litasporgia de Laubenfels, 1954: 162.

TYPE SPECIES. Ophthiasporgia arbuscula Row,
1911: 347 (by original designation) (holotype
BMNH1912.2.1.63).

Convolute arborescent growth form. Surface
irregularly conulose, arenaceous, minutely
hispid. Choanosomal skeleton regularly reticu-
late, with heavy spongin fibres cored by uni-
or paucispicular tracts of choanosomal principal
subtylostyles (sometimes fibres aspiculoose).
Echinating acanthostyles sparse. Subectosomal
skeleton plumose, with dense bundles of prin-
cipal styles (identical to coring spicules) diverging
from ends of peripheral fibres and forming
discrete brushes on surface. Ectosomal skeleton
with sparse subectosomal auxiliary subtylostyles
tangential to surface and also dispersed
throughout mesohyl. Megascleres thin smooth
choanosomal principal subtylostyles, smooth
quasi-diactinal subectosomal auxiliary subtylo-
styes (usually resembling asymmetrical strongyles),
and evenly spined echinating acanthostyles. Micro-
scleres wing-shaped toxas. Isochelae absent.
REMARKS. De Laubenfels (1954) stated that *Litaspangia* was established for sponges like *Echinoclathria* (as defined here) in having monactinal megascleres, toxa microscleres and arborescent growth form. The holotype also has echinating acanthostyles, previously overlooked by Row (1911). The resemblance between *O. arbuscula* and *Echinoclathria* is here considered superficial, based on the fact that principal spicules in *O. arbuscula* are thin, attaining only the thickness typical of auxiliary spicules found in most other *Clathria* species; auxiliary spicules are quasidiactinal in *O. arbuscula*, resembling diactinal ectosomal spicules in some species of *Echinoclathria* (e.g., *E. chalinoides*) and *Holop- samma* (e.g., *H. ramosa*); and spongin fibres are regularly reticulate, well developed, and tend to dominate skeletal structure over spicule components. But unlike *Holopsamma* and *Echinoclathria* which have undifferentiated coring and echinating spicules, *Litaspangia* has different principal spicules coring fibres from those echinating fibres. I consider it a reduced *Clathria* (*Clathria*).

De Laubenfels (1954: 162) synonymised *O. arbuscula* and *O. horrida* Row (1911: 349), and re-examination of both holotypes (the latter BMNH1912.2.1.65) supports this decision. He added *Echinoclathria nodosa* (which he merged with *E. subjispida*) to *Litaspangia*, but both are species of *Echinoclathria*. Pulitzer-Finali (1982: 105) referred *O. arbuscula* and *O. horrida* to *Kerasemna* (*Desmacellidae*) (Hooper, 1984b), but neither have sigma microscleres and this placement was unjustified.

**Marleyia** Burton, 1931
(Fig. 18H-I)


**TYPE SPECIES.** *Marleyia irregularis* Burton, 1931a: 346 (by original designation) (holotype NM1279).

Digitate growth form, flattened branches. Surface uneven, porous, with specialised reticulate external fibrous skeleton. Choanosomal skeleton reticulate, with subsoid actinal reticulation of well-developed primary and secondary spongin fibres. Primary fibres ascending, cored by multispecific tracts of both choanosomal principal subtylostyles and subectosomal auxiliary subtylostyles. Fibres heavily echinated by short acanthostyles. Secondary fibres transverse, aspicular, but of similar diameter and density of echinating spicules as primary fibres. Abundant detritus scattered through mesohyl, but not incorporated into fibres. Ectosome with tangential reticulation of spongin fibres, more closely reticulate and slightly thinner than choanosomal fibres, lightly cored by both subectosomal and choanosomal subtylostyles and echinated by abundant acanthostyles. Megascleres smooth robust choanosomal principal subtylostyles, smooth straight or sinuous subectosomal auxiliary subtylostyles, and robust echinating acanthostyles with bare neck. Microscleres absent.

REMARKS. The holotype is dry and lacks a well-preserved ectosomal skeleton. Burton suggested that *Marleyia* differs from all other *Microcionidae* genera in having a special ectosomal skeleton formed by a tangential reticulation of spongin fibres, which are thinner and more closely compacted than choanosomal fibres. This feature was not as remarkable as we are led to believe from the original description (although the holotype is not well preserved), nor is it unique in the *Microcionidae* (also seen in *Echinochalinida* (*Protophlitaspangia*) *laborata* Hooper & Lévi) or other families (e.g., *Callyspongiidae* (*Haplosclerida*).

In gross morphology and fibre characteristics, *Marleyia* is similar to several *Holopsamma* species, but it has different spicules coring and echinating spicules (whereas *Holopsamma* has only one category of principal spicule performing these functions). Burton (1931a) made further casual comparisons between *Marleyia* and certain Dictyococatidae, based on fibre characteristics and a greatly reduced skeleton. De Laubenfels (1936a: 109) suggested that *Marleyia* may have affinities with *Acanthurellus*, representing a more mature form of the genus, but he noted that *Marleyia* had a remarkable external resemblance to 'keratose' sponges. On the basis of its unusual ectosomal fibre characteristics Van Soest (1948b) suggested that *Marleyia* might be a valid genus of *Microcionidae*, but re-examination of type material indicates that it clearly belongs to *Clathria* (*Clathria*). *Marleyia* is monotypic, and known only from the Durban region, Natal coast, South Africa.

**Microciona** Bowerbank, 1862
(Fig. 19F-G)

Encrusting growth form. Surface hispid, uneven. Choanosomal skeleton hymedesmoid, with spongins fibres reduced to basal layer lying on substrate, bearing erect, non-anastomosing, rarely branching, scattered fibre nodes perpendicular to substrate ('microcionid' fibres), each cored by plumose ascending columns of choanosomal principal subtylostyles, wholly or partly embedded in fibres, with points of spicules usually projecting through ectosome. Echinating acaenthostyles also erect on fibre nodes. Subectosomal skeleton with tangential layer of subectosomal auxiliary subtylostyles, singly or in bundles on surface. Ectosomal skeleton without specialised spiculation, but choanosomal and subectosomal spicules protrude through surface. Meganuclei choanosomal principal subtylostyles with smooth or microspined bases, evenly spined echinating acanthonstYLES, and smooth or basally spined subectosomal auxiliary subtylostyles. Meganuclei palmate isochelae and wing-shaped toxas.

REMARKS. In many publications, Clathria Schmidt and Microciona Bowerbank have the date 1862. In merging the two genera, Wiedenmayer (1977, 1989) and Van Soest (1984b) note that the former has priority, because Bowerbank's work was not officially published until 1863.

This definition of Microciona is compiled from description of the type species (Bowerbank, 1862b, 1864, 1866) and histological prepararion of the holotype and paratypes (BMNH1910.-1.168, 1930.7.3.226). Microciona (s.s.) differs from Clathria (s.s.) in its encrusting growth form, a reduced hymedesmoid skeleton with erect fibre nodes cored by plumose tracts of principal and echinating spicules standing erect on the substrate (= 'microcionid' architecture of Lévi, 1960a), and smooth toxas. The critical difference between these genera, therefore, is the possession of the plumose, non-anastomosing fibre nodes, whereas cofamilial encrusting genera have hymedesmoid skeletal construction (Lep)toclathria, Anaeta, Cionanchora, Hymanto) or a basal renieroid reticulation (e.g., some Antho, Plocamilla). By comparison, erect or massive Microcionidae commonly have reticulate or plumo-reticulate skeletons (Clathria, Holopsam...
the ontogeny of the sponge individual (Simpson, 1968a). They argued from a phylogenetic basis that the recognition of this character as being a primary one confers exceptionally high levels of homoplasy within the classification, cutting across lines of apparent evolutionary decent based on a combination of other characters (such as the origin and disposition of structural megascleres within the skeleton, spicule geometry). For example, there are many thinly encrusting species with hymedesmoid architecture and plume spongin fibre nodes referable to Microciona (e.g., M. maunaloa de Laubenfels, M. micerechela Hechtel), but also having two differentiated categories of auxiliary spicules (i.e., a specialised ectosomal skeleton), which is characteristic of Thalysias species. Which genus do these species then belong to, Microciona or Thalysias, or do we recognise a third genus because they have both characters? This third alternative was adopted by Bergquist & Fromont (1988), largely following de Laubenfels' (1936a), who recognised Aoxiella for microcionids with Microciona-like fibre skeletons and Thalysias-like ecyctosomal skeletons (although, like de Laubenfels (1936a), they misinterpreted Aoxiella which is neither encrusting nor hymedesmoid). This is a 'convenient classification' for managing species, but it is also responsible for most of the 70 or so microcionid genera that exist today (i.e., approximately 1 genus per 6 species).

Few authors agree on the level of taxonomic divergence, or the phylogenetic interpretation of character polarity: is encrusting growth form and hymedesmoid architecture a primitive or derived strategy? Is a 'microcionid' architecture (hymedesmoid with ascending plume fibres nodes) a subsequent developmental stage of hymedesmoid architecture (spongin fibres flat against the substrate)? Is it anticipated that evidence from biochemical or genetic sources will eventually contribute towards the resolution of these conflicts. A resolution is provided here based on phylogenetic interpretation of morphology. We follow Lévi's (1960a) arguments in considering three alternatives.

1) One generic taxon may be used to encompass all the skeletal types from leptoelathroid (hymedesmoid), 'microcionid', to reticulate. This option was used by Vosmaer (1933, 1935a-b), who suggested that varying grades of skeletal construction (from hymedesmoid, plume to reticulated) could be seen within populations of particular species and was apparently largely related to ontogenetic development. Van Soest (1984b), Hooper & Lévi (1993a) and others used this ontogenetic argument to merge Microciona and Clathria (as well as Thalysias and Clathria), and Hooper et al. (1992) presented some empirical data to show that there was no homogeneity in biochemical profiles to support the retention of distinct taxa for encrusting versus erect species.

2) Two separate taxa can be recognised for species with hymedesmoid plumose (Microciona) and reticulate (Clathria) architectures. This was the argument accepted by Lévi (1960a), Bergquist & Fromont (1988), and others, on the basis that these skeletal structures were consistent for populations of particular species, and therefore represented fixed genetic differences. Simpson (1968a) suggested further that this option had some empirical support from cytological evidence, although (unfortunately) the cytological characters themselves are at the moment not particularly useful taxonomic characters. A more pragmatic argument for the retention of the name Microciona is that it is in current widespread use by sponge biochemists, ecologists and experimental biologists, and retaining this name provides some sort of nomenclatural stability consistent with the previous literature. This argument, unfortunately, has a pragmatic rather than biological basis.

3) The name Clathria could be used for an adult terminal phase of skeletal architecture, related directly to the ontogeny of the sponge, whereas Microciona could be used for the juvenile phase of the same species. Dictyociona is an example of a Clathria with an intermediate Microciona-like skeleton, and Pseudanchinoe is an example of a Microciona verging on a reticulate Clathria-like skeleton. This argument presupposes that plumose skeletons are always precursors of, and juvenile to, reticulate skeletons. But there are several thinly encrusting species which do have reticulate skeletons (e.g., Sara & Melone, 1966), even though most plumose species are also persistently encrusting.

In recognising Microciona at the subgeneric level, Van Soest (1984b) implicitly also recognised a phylogenetic basis for the 'microcionid' skeletal specialisation, even though there were no other corroboratory characters, such as unique spicule geometries. The phylogenetic interpretation of this skeletal specialisation taken in the present study is that Microciona is a persistently encrusting sponge which consistently has non-anastomosing basal spongin fibres cored by non-anastomosing plumose spicule tracts or single
spicules, also lacking any ecosomal specialisation; it is an incompletely differentiated sister taxon of *Clathria* and recognised here at the subgenus level (*Clathria* (Microciona)). The *Lep- toclathria* (flat, hymedesmoid) and *Microciona* (ascending 'microcionid' fibre nodes) conditions are not differentiated, these being interpreted as being more likely to be related to the thickness of encrusting growth forms than anything else.

**Ophlitaspongia** Bowerbank, 1866  
*(Fig. 20A-B)*

*Seriatula* Gray, 1867: 515; de Laubenfels, 1936a: 122.  

**TYPE SPECIES.** *Ophlitaspongia papilla* Bowerbank, 1866: 378 (by original designation) (holotype BMNH1910.1.1.395); = *Spongia seriata* Grant, 1826: 116 (Simpson, 1968a:37) (holotype BMNH1847. 9.7.14).

Encrusting bulbous growth form. Surface microconulose, microscopically hispid. Choanosomal skeleton isodictyal reticulate, with compressed layer of spongin fibre lying on substrate and regularly reticulate spongin fibres arising from base, producing regular isodictyal fibre network divided into primary ascending and secondary transverse fibre elements. Primary fibres cored by plumose tracts of choanosomal principal styles, which also protrude from fibres at acute angles resembling quasi-echinating spicules. Secondary transverse fibres uncored or with unispicular tracts of usually smaller choanosomal principal styles. Subectosomal skeleton paratangential, with scattered subectosomal auxiliary styles lying on or near surface and also dispersed throughout mesohyl. Ectosome without specialised spiculation, but plumose tracts of choanosomal principal megascleres protrude through surface. Megascleres large and small, entirely smooth choanosomal principal styles-subtylostyles, and thin smooth subectosomal auxiliary styles. Microscleres u-shaped toxas. Chelae absent.

**REMARKS.** This definition is based on type material and Simpson's (1968a) description of live populations. *Ophlitaspongia papilla*, was shown by Simpson (1968a: 95) to be a synonym of the type species of *Microciona* (*M. atrasanguinea*). A broader concept of *Ophlitaspongia* (Wiedenmayer, 1989), (not *O. seriata* (Grant)), is identical to *Echinoclathria* (s.s.) (see remarks for *Echinoclathria*). Wiedenmayer (1989) provided further explanation of these relationships, although his nomenclatural decisions are not entirely correct.

*Seriatula* was erected for *Spongia seriata* Grant (Gray, 1867) which is conspecific with *O. papilla* Bowerbank (e.g., Simpson, 1968a), and therefore *Seriatula* becomes an objective synonym of *Ophlitaspongia*.

**Pandaros** Duchassaing & Michelotti, 1864  
*(Fig. 20C-E)*

*Pandaros* Duchassaing & Michelotti, 1864: 88;  
Schmidt, 1870: 59; de Laubenfels, 1936a: 123;  

**TYPE SPECIES.** *Pandaros acanthifolium* Duchassaing & Michelotti, 1864: 90 (by subsequent designation of de Laubenfels, 1936a: 123) (lectotype TMPOR57).  

Bushy arborescent growth form. Surface highly conulose, with flattened or lobate lamellae. Choanosomal skeleton reticulate, with well-developed flattened spongin fibres (trabeceulae) cored by choanosomal principal subtylostyles lying in all directions within fibres (from isodictyal reticulate to echinating) and with sparse acanthostyles echinating or also incorporated into fibres. Subectosomal skeleton radial, reduced to single long subectosomal auxiliary subtylostyles protruding through surface and also scattered throughout mesohyl. Ectosome without special spicules. Megascleres smooth choanosomal principal subtylostyles-tylostyles, often with slightly rhabdose bases and terminal or subterminal basal swellings, long curved or straight subectosomal auxiliary subtylostyles, and lightly acanthose or rarely smooth styles 'echinating' fibres. Microscleres absent.

**REMARKS.** This definition is based on the type and a fragment of the type MNHNLBIMDNB1 1309, specimen BMNH1884.7.11.2 and description of live populations by Van Soest (1984b). Important features are: 1) the prominently flattened fibres cored by smooth slightly rhabdose principal subtylostyles-tylostyles (more reminiscent of *Rhabderemiiidae* than of *Microcionidae*); 2) the sparse, lightly spined styles which more closely resemble a second category of principal spicules than than they do echinating (accessory) spicules typical of other *Microcionidae*; furthermore, these spicules are only rarely seen echinating fibres, but more commonly they are incorporated into them together with the principal megascleres; and 3) the long subectosomal auxiliary subtylostyles protruding through the
surface (more similar to a reduced Raspailiidae, such as *Echinodictyum* or *Ceratopson*, than to typical Microcionidae).

*Pandaros* could be legitimately included in either Raspailiidae or Microcionidae. Van Soest (1984b) noted that only the rare echinating acanthostyles in *P. acanthifolium* gives any cause to link it to the Microcionidae at all. He speculated that it might be necessary to erect a separate family for the species, or even remove it from the Poecilosclerida altogether, as it also shows affinities with axinellids such as *Ptilocaulis*. There are no microscleres to give any further clues as to its affinities. *Pandaros* is maintained as a separate genus and tentatively included in Microcionidae. Of 12 species referred to *Pandaros*, only the type clearly belongs here. *Raspailia kasumiensis* Tanita (MMBS SIS-052) was assigned to *Pandaros* (Hooper, 1990a).

Wiedenmayer (1977) merged *Thalyseurypion* with *Pandaros*, because he considered that its type species had architecture closely comparable to *P. acanthifolium* (Hechel, 1965), but this is not upheld here. The only features these genera have in common is lacking microscleres. Wiedenmayer (1977) also speculated that the genus had a close relationship with *Echinoclathria* (= *Holopsammina* as defined here), based on alleged similarities in skeletal architecture, and he suggested that the two genera probably intergrade in habit and spiculation, but these suggested affinities are not evident in relevant specimens.

**Paradoryx** Hallmann, 1920

(Fig. 20F-G)


**TYPE SPECIES.** *Clathria dura* Whitelegge, 1901: 83 (by original designation) (holotype AMG 3046).

Arborescent, flabellate growth form with compressed branches. Surface even, smooth. Choanosomal skeleton reticulate, with heavy spongine fibres forming irregular anastomoses in axis becoming more regular and rectangular towards periphery. Spongine fibres differentiated into primary ascending and secondary connecting components, cored by auxiliary styles and heavily echinated by acanthostyles. Subectosomal skeleton plumose, with bundles of auxiliary styles forming plumose brushes on peripheral fibres. Ectosome fibrous, without specialised skeleton, and peripheral fibres form more-or-less reticulate structure through which choanosomal spicules protrude. Megascleres entirely smooth, hastate or quasidiactinal auxiliary styles or subtylostyles, and echinating acanthostyles with large and even spination. Microscleres palmate isochelae resembling arcuate forms with lateral alae fused to shaft for about 1/2 alae length, and shaft greatly curved, thickened. Toxas absent.

**REMARKS.** Ectosomal fibres of *Paradoryx* are unspecialised, identical to choanosomal fibres in size and form, unlike the *Callyspongia*-like ectosome of *Marleyia*. Hallmann (1920) erected *Paradoryx* for *Wilsonella* species (with auxiliary megascleres coring fibres) which had arcuate chelae instead of palmate isochelae. Loss or replacement of principal megascleres varies considerably between otherwise allied microcionid taxa and this feature is considered to be of lesser significance at the generic level than assumed by Hallmann (Hooper, 1990a; Hooper et al., 1990). Similarly, isochelae described by Hallmann (1920) as arcuate in the type species are modified (curved, thickened) palmate forms.

Apart from the type species, Hallmann (1920) included: *Dictyocelis pintornis* Carter and *W. oxyphila* (both of which belong to *Clathria* (*Clathria*)), and *Clathria elegans* Ridley & Dendy and *Wilsonella curvicilia* Hallmann (which are referred here to *Clathria* (*Dendrocia*)).

**Paratenaciella** Vacelet & Vasseur, 1971

(Fig. 20H-I)


**TYPE SPECIES.** *Paratenaciella microsca* Vacelet & Vasseur, 1971: 103 (by original designation) (holotype MNHN B1 MJDV 27).

Encrusting growth form. Surface uneven, hispid. Choanosomal skeleton hymedemoid, with spongine fibres reduced to basal layer on substrate and with ascending fibre nodes enclosing bases of choanosomal principal subtylostyles standing perpendicular to substrate. In thicker sections up to 3-4 spicules form ascending plumose tracts, protruding through surface. Echinating megascleres absent. Subectosomal skeleton plumose or paratangential composed of bundles of subectosomal auxiliary subtylostyles often forming brushes around protruding principal spicules and protruding through ectosome. Megascleres entirely smooth choanosomal principal subtylostyles, and subectosomal auxiliary subtylostyles with microspined bases and polytylole shafts. Microscleres palmate
isochelae, including contort forms, and oxoete toxas.

REMARKS. *Paratenaciella* has a Microciona-like choanosomal fibre skeleton composed of non-anastomosing, plumose fibre nodes, but lacks acanthostyles (similar to *Axociella, Axociellita, Tenaciellita*), has polytylete modifications to auxiliary spicules (similar to *Fishertspongia ferrea* de Laubenfels and *Microciona acerautoobsusa* Carter), and has modified (oxoete) toxas, like those in *Artemisina urcegona* Ristau (although type material shows that they do resemble true microxeas). This latter feature appears to be the only unique character for the type species, and as far as is known it is also unique amongst the Microcionidae. *Paratenaciella* shows some similarities to *Esperipopsis canceliculata* Whitelegge (which is referred here to *Axociella*) in its spiculation, although *P. microxeas* has a microcionid architecture, microxeote microsclees and undifferentiated ec- tosomal-subectosomal megasclees. The genus is monotypic and is synonymised with *Clathria* (Microciona).

**Plectispa** Lendenfeld, 1888
(Fig. 21C-D)


**TYPE SPECIES.** *Plectispa macropora*, in part, Lendenfeld, 1888: 226 (by subsequent designation of Hallmann, 1912: 204) (holotype AMG9159).

Lobodigigate growth form. Surface 'honeycomb' reticulate. Choanosomal skeleton reticulate, with well developed spongion fibres forming more-or-less regular oval or elliptical meshes, sparsely cored and abundantly echinated by principal sub- tylostyles, and fewer auxiliary styles-tornotes also in fibres. Echininating megasclees less predominant in periphery than in axis. Some detritus also incorporated into choanosomal fibres. Subectosomal skeleton plumose, with brushes of principal subtylostyles from ascending fibres of peripheral skeleton protruding through surface, surrounded by paratangential loose bundles or individual auxiliary spicules. Megasclees smooth principal subtylostyles, and long curved, setaceous or sinuous auxiliary styles or quasi-diactnal tornotes, both with blackened axial canals. Microsclees palmate isochelae, including contort forms. Toxas absent.

REMARKS. This genus is poorly defined due to the dubious status of all of Lendenfeld's syntypes, inaccuracies in Lendenfeld's (1888) original description, and misinterpretation of the species (e.g., *Clathria macropora*, Whitelegge (1901: 91) is different from *C. macropora* Lendenfeld (1888)). Hallmann (1912: 165) attempted to sort out these problems but was only partially successful. He rejected Whitelegge's proposed merger of *P. macropora* with *Echinonema levis* Lendenfeld (1888), but instead he synonymised the latter with *C. macropora* (sensu Whitelegge), as *Clarella* *in- crustans* Carter, var. *levis* Lendenfeld. However, Hallmann's (1912) remarks and assumptions concerning the genus are not entirely correct (see remarks below for *Clathria macropora* and *Holopsamma macropora*), and there is no evidence that he actually re-examined relevant type material. His nomenclatural decisions are erroneous and not supported here.

There are 4 type specimens and one other specimen in the AM and BMNH which bear the name 'macropora'. 1) AMZ959 (with the label 'dry, cotype') from Port Stephens, NSW, is the so-called 'type' of *Clathria macropora* (sensu Whitelegge), and is a species of *Clarella*. It is probably a syntype of Lendenfeld's (1888) *Echinonema levis*, but that assumption is difficult to corroborate due to the loss of Lendenfeld's 'key-list' from the Australian Museum (E. Pope & F. Rowe, pers. comm.). 2) AMZ466 (with label stating 'spirit preserved, ?type') from Port Stephens, NSW is the lectotype of Lendenfeld's (1888: 221) *Clathria macropora*, later referred to *Wilsonella* by Hallmann (1912: 240). It is neither a *Wilsonella*, nor closely related to such species as *W. australiensis* Carter, but is a *Clathria* lacking echinating megasclees and having an axially compressed skeleton (e.g., *Clathria (Axociella)*). 3) AMG9159 (with the label stating 'dry, type'), probably from Port Jackson, NSW (i.e., there is a discrepancy between the published locality of Torres Strait, Qld. and the museum specimen label and register), is the holotype of *Plectispa macropora*. 4) BMNH1925.1.1.555 (with label stating 'Plectispa macropora, dry, Dendy collar') from Manly Beach, NSW, is identical to *Clathria multipes* Hallmann. 5) Another specimen (BMNH1957.8.30.2, with label stating 'Plectispa macropora, dry') belongs to *Clathria lendenfeldi*. Consequently, only a single syntype is valid becoming the holotype of *P. macropora*, and the diagnosis of *Plectispa* is based on this specimen.

Hallmann (1912: 205) referred the type species (and genus *Plectispa*) to *Wilsonella*, but then returned it to *Clathria* (Hallmann, 1920: 768). The species has a 'honeycombed reticulate'
growth form and smooth echinating spicules (not acanthose as supposed by Lendenfeld (1888) and Hallmann (1912)). It also has long, setaceous, quasi-diaxial auxiliary megascelers, which also core fibres, scattered throughout the mesohyl and associated with spicule brushes on the surface. These characters indicate that Plectispa belongs to Holopsammina, and the species shows some resemblance to H. ramosa (Hallmann, 1912) and H. laminaefavosa Carter, 1885b (sensu Wiedenmayer, 1989).

Plocamia Schmidt, 1870
(Fig. 21A-B)

Plocamia Schmidt, 1870: 62.
Dirrhopalum Ridley in Ridley & Duncan, 1881: 477.

TYPE SPECIES. Plocamia gymnazaSchmidt, 1870: 62 (by subsequent designation (Burton, 1935a: 401)) (holotype possibly LMJG, schizotype MNHNLB1MDCL1105L).

DIAGNOSIS. Encrusting growth form. Surface even, microscopically hispid. Chondosal skeleton renieroid, with tyloles forming basal reticulation, interconnected at nodes by light spogin fibres, and with plumose columns of choanosomal principal styles and echinating styles embedded in basal renieroid skeleton, individually or in bundles, largest protruding through surface. Subectosomal skeleton with paratangential and erect tracts of subectosomal auxiliary styles. Megascelers robust slightly curved choanosomal principal styles with microspined or smooth bases, robust tyloles with swollen microspined bases, long subectosomal auxiliary styles with smooth or microspined bases, smaller echinating styles with microspined bases. Microscelers palmate isochelae and wing-shaped toxas.

REMARKS. Ridley (in Ridley & Duncan, 1881) suggested that Plocamia Schmidt was preoccupied by Plocamium Lamouroux, 1828, a seaweed, and consequently proposed the replacement name Dirrhopalum Ridley. However, under Article 56b of the ICZN (Anonymous, 1985) this is an unjustified emendation and Plocamia stands. Bergquist & Fromont (1988) also used Plocamia over Dirrhopalum.

This definition is based on slides of the holotype and published descriptions (Schmidt, 1870; Ridley in Ridley & Duncan, 1881). The type species is essentially the same as Plocamilla in structure and spicule geometry, but spines on both the basal tylole spicules and echinating spicules are much better developed in Plocamilla. Plocamia is the earliest available name for a group of Antho-like ('plocamiform') microcystids having basal tyloles and echinating spicules (see remarks for Holoplocamia, Lis-soplocamia).

Plocamilla Topsent, 1928
(Fig. 21E-F)


TYPE SPECIES. Isodictya coriacea Bowerbank, 1874: 136 (by original designation of Topsent, 1928a: 63) (holotype BMNH1910:1.1.251).

DIAGNOSIS. Encrusting growth form. Surface uneven, porous, microscopically hispid. Chondosal skeleton renieroid, with regular basal reticulation of acanthose strongyles in uni- or paucispicular tracts, overlaid by plumose brushes of larger choanosomal principal styles and echinating acanthostyles projecting perpendicularly from nodes of renieroid spicule skeleton. Ectosomal skeleton contains plumose or paratangential brushes of subectosomal auxiliary styles and projecting echinating acanthostyles from peripheral nodes of choanosomal renieroid skeleton. Megascelers acanthose strongyles or tyloles with spines mostly on basal ends, larger choanosomal principal styles-subtylostyles with spined bases, subectosomal auxiliary styles-subtylostyles with smooth or microspined bases, and small echinating acanthostyles with few spines concentrated mainly on basal end. Microscelers palmate isochelae, smaller wing-shaped toxas, and larger accolada toxas with spined points.

REMARKS. This definition is based on the holotype and descriptions of the type species (Topsent, 1928a; Lévi, 1960a). Plocamilla has spiculation similar to Plocamia Schmidt, but it has an encrusting growth form and therefore its skeleton is not clearly differentiated into primary or secondary lines (Topsent, 1928a: 63; Lévi, 1960a: 80). This skeletal development is probably related to growth form and not an important generic character. The genus was not formally diagnosed until Burton (1935a: 402) differentiated a number of 'plocamiform' genera, all of which had acanthostrongyles or acanthostyles forming the basal renieroid skeleton. Burton emphasised the diagnostic value of choanosomal.
acanthostrongyles ("dumbbell spicules") which united those genera, but be differentiated them by their skeletal architecture and the presence or absence of various spicule types.

_Holoplocamia_ is a synonym of _Plocamilla_ (Lévi, 1960a: 80), although Little (1963: 47) argued to the contrary. Lévi (1960a) also noted that the skeleton of _P. coriacea_ was very close to _Antho_ and _Dictyocanthia_ (both of which are objective synonyms), lacking special echinating spicules and having acanthostyles instead of acanthostrongyles in the basal renierid skeleton. Lévi (1960a) and Pulitzer-Finali (1973: 40) were cautious in interpreting whether _Plocamilla_ was distinct from _Antho_, because the spined acanthostyles and smooth principal styles could not be consistently differentiated in all taxa. For example, _P. elegans_ (Ridley & Dendy) does not show any clear separation between the smaller category of smooth principal styles and the more sparsely spined acanthostyles (Pulitzer-Finali, 1973). On that basis, Pulitzer-Finali suggested that future studies may show that _P. elegans_ should be referred to _Antho_, whereas _P. coriacea_ has clearly differentiated coring and echinating megascleres, and should remain in _Plocamilla_. Lévi (1960a), Simpson (1968a), Pulitzer-Finali (1973) and Van Soest (1984b) maintained _Plocamilla_ and _Antho_ as separate genera, the former having echinating acanthostyles and predominantly (acantho)strongyles in the renierid skeleton. However, all these authors admitted that the two genera may be too similar to maintain sufficient generic separation. Van Soest & Stone (1986) noted that the genus should probably be merged with _Antho_, together with other plocamiform genera containing renierid skeleton of acantho megascleres, and this suggestion is supported here (i.e., _Antho (Plocamilla)_).

Simpson (1968a: 95) found that although _Plocamilla_ and _Microciona_ were easily differentiated by their skeletal construction and spicule geometries, they were remarkably similar in their cytological characteristics. These findings contradict the more obvious similarities between microcionid genera, based on spicule geometry and skeleton construction. _Microciona, Clathria_ and _Thalysia_ are a relatively homogenous group in skeletal construction, compared to any inferred relationship between _Plocamilla_ and _Microciona_ for example. Probably Simpson’s (1968a) cytological characters have not been incorporated into the classification, nor have the the implications of his findings to phylogeny of demosponges been widely discussed.

**Plocamiopsis Topsent, 1904**

(Figs 21G-H, 22A)


TYPE SPECIES. _Plocamiopsis signata_ Topsent, 1904a: 155 (by monotypy) (holotype MNHN-LBIMD7947).

DIAGNOSIS. Encrusting growth form. Surface even, hispid. Choanosomal skeleton irregularly renierid, with basal reticulation of acanthostrongyles in uni- or bispicular tracts lying on substrate. Choanosomal principal subtylostyles, smaller acanthostyles and spicules intermediate to both embedded individually in basal skeleton, standing perpendicular to substrate. Subectosomal skeleton plumose, with ascending brushes of subectosomal auxiliary subtylostyles surrounding principal megascleres. Ectosome without specialised spiculation, but with both tangential and plumose tracts of subectosomal auxiliary spicules protruding through surface. Megascleres choanosomal principal subtylostyles with spines on bases and proximal region of shaft, smaller acanthostyles with aspinose points, and subectosomal auxiliary subtylostyles with spined bases. Microscleres cleistochelae and smooth wing-shaped toxas.

REMARKS. _Plocamiopsis_ is a member of _de Laubenfels'_ (1936a) plocamiform group of sponges having a basal renieroid skeleton of acanthostrongyles. It differs from others in this group (_Dirrhpalum, Heterocladia, Holoplocamia, Lissoplacania, Plocamilla_) having cleistochelae, which are also seen in _Collocladia_ and _Quizziona_. Cleistochelae are hypersilicified palamate isochelae with the front alae fused (Fig. 22A) but probably have little phylogenetic significance given the complete transitional series from palmate to cleistochelate (Fig. 76G). _Plocamiopsis_ is referred to _Antho (Plocamia)_.

**Protophilitaspongia Burton, 1934**

(Fig. 22B-C)

_Protophilitaspongia_ Burton, 1934a: 562.

TYPE SPECIES. _Siphonochalina bispiculata_ Dendy, 1895: 246 (by original designation) (lectotype NMVG2319).

Lamellar, tubulo-digitate growth form, with osculum on apex of each tube. Surface uneven, microscopically hispid. Choanosomal skeleton subsidiary reticulate, with more-or-less regularly anastomosing heavy spongine fibres
form primary ascending and secondary transverse lines. Primary fibres cored by multispecular tracts of longer auxiliary oxeas; secondary fibres usually aspiculose occasionally with only single coring auxiliary oxeas. Fibres sparsely echinated by smaller, smooth hastate oxeas (presumed to be homologous with principal spicules). Ectosome lacks specialised spiculation, but has plumose erect brushes of oxeas from peripheral skeleton protruding through surface. Megascleles modified diactinal, including longer smooth hastate auxiliary oxeas, and smaller smooth hastate principal oxeas. Microscleles absent.


The genus has a characteristic three-dimenionalectosomal architecture reminiscent of *Hemigellius* and *Amphimedon* (Haplosclerida: Niphatidae), with only oxeas as megascleles. However, smooth hastate oxeas echinating fibres, with a similar geometry but smaller size than coring spicules, gives some clues as to probable phylogenetic relationships (i.e., Microcionidae, some lophoniidae, and Raspalidiidae). This pattern of spiculation is seen in *Echinoclathria*, and to a lesser extent *Echinoclyathria* as defined here. It is particularly well developed in *E. axinelloides*, and for this reason Burton (1934a: 562) tentatively referred *Protophlatispanga* to the Microcionidae. Conversely, de Laubenfels (1936a: 54, 1954: 96) suggested that the genus was closer to *Guitarra* (although lacking their peculiar microscleles), or *Liosina*, and he referred *Protophlatispanga* to the Desmacdonidae, but he was probably referring mainly to his two Micronesia species in doing this. Pulitzer-Finali (1986: 138) followed similar reasoning, placing the genus in Esperiopsidae, but none of these species belong to *Protophlatispanga* in any case.

Further clues as to the most appropriate placement of this genus can be seen from other characteristics: the palmate isochelae in *E. (P.) bargibanti*, the accocola toxas in *E. (P.) oxeata*, and the plumose ectosomal skeleton, composed of auxiliary spicule brushes (typical of Microcionidae, Axinellidae and Raspaliidae) in all species. The present interpretation of *Protophlatispanga* suggests affinities with *Echinoclathria* and *Holopsamma* microcionids and the reticulate Raspaliidae, and in the distribution of its megascleles (i.e., auxiliary spicules in fibres and peripheral skeleton, principal spicules echinating fibres) it is assigned to *Echinocalathia*.

**Pseudanchinoe** Burton, 1929

(Fig. 22D-E)


**TYPE SPECIES.** *Stylostichon toxiferum* Topsent, 1913a: 621 (by original designation and monotypy) (holotype MNHNLBIMDT1612).

Massive subspherical growth form. Surface uneven, apical surface conules. Chaoansomal skeleton plumoreticulate, with spongion fibres forming primary plumose ascending columns, partially interconnected by transverse secondary fibres, both cored by multispecular tracts of choanosomal principal subtylostyles and heavily echinating by acanthostyles. Subectosomal skeleton plumose, non-anastomosing, composed of multispecular plumose tracts of choanosomal principal spicules from peripheral fibres surrounded by plumose bundles of subectosomal auxiliary subtylostyles. Ectosomal skeleton with second tier of subectosomal auxiliary subtylostyles forming dense palisade on surface. Megascleles choanosomal principal subtylostyles with or without basal spines, subectosomal auxiliary subtylostyles with microspinned bases, and echinating acanthostyles varying from smaller forms with even spination to larger forms with aspinose points. Microscleles oxhorn and accocola toxas. Chelae absent.

REMARKS. Burton (1929a) recorded palmate isochelae in the type species but none were found in the holotype nor did Topsent (1913a) record any in his original description. In fact the absence of isochelae and the possession of plumoreticular skeletal architecture are virtually the only two diagnostic features that distinguish *Pseudanchinoe* from other *Clathria* (s.s.). Similarly, Topsent (1913a) stated that there were
microspines on the points of toxas, but these were not seen in the holotype.

The type species of *Pseu<alpha>anchinoe* is intermediate between *Clathria* and *Th<alpha>ysias*, having the e<alpha>ctosomal structure of the latter (i.e., with a thick continuous palisade of erect spicules overl<alpha>ying a similar subectosomal skeleton), but with spicule composition of the former (single category of auxiliary styles), further supporting the decision to merge these two genera in a single taxon (*Clathria* s.l.). In skeletal structure and diversity of megascleres the genus could be placed in the series: *Dendro<alpha>*(single category of structural spicule in the entire skeleton), *Clathria* (one category of auxiliary spicule and one category of principal spicule), *Pseu<alpha>anchinoe* (one category of auxiliary spicule forming a continuous e<alpha>ctosomal palisade), *Th<alpha>ysias* (two categories of auxiliary spicules the smaller forming a continuous e<alpha>ctosomal palisade, and one category of principal spicule), and *Anuho* (some of which have two categories of auxiliary spicules and two categories of principal spicules).

Burton (1929a) remarked on the apparent similarities between *Pseu<alpha>anchinoe* and *An<alpha>hinoe* Gray (= *Phorbas* Duchassaing & Michelotti; An<alpha>hinoidae). The latter genus has plumose columns of intermingled acanthostyles and ton<alpha>tes (or oxeas), which are echinated by acanthostyles, but these similarities are superficial. An<alpha>hinoidae have tangential e<alpha>ctosomal d<alpha>cnial megascleres and plumose columns of choanosomal megascleres in which acanthostyles predominate (e.g., *Van Soest, 1984b: 86*). Of the numerous species assigned to *Pseu<alpha>anchinoe* (e.g., *de Laubenfels, 1936a: 109*) most are interpreted here as belonging to *Clathria*, having secondarily lost their isochelae. Australian examples are *C. (C.) caelata* Hallmann, *C. (C.) costifer<alpha>* Hallmann, *C. (C.) inanchorata* Ridley & Dendy, and *C. (C.) partita* Hallmann. Two other species belong to *Clathria* (*Th<alpha>ysias*) (*C. dentata* Topsent and *C. fascicularis* Topsent, which are synonymous) (Van Soest, 1984b). Of contemporary authors only K<alpha>ltun (1976) recognises this genus whereas *Van Soest* (1984b) and (Wiedenmayer, 1989) merged it with *Clathria*. It is included here in *Clathria* (*Clathria*).

**Qasimella** Thomas, 1974

*Qasimella* Thomas, 1974: 311.

**TYPE SPECIES.** *Qasimella indica* Thomas, 1974: 311 (by original designation)(holotype CMFRICT84/1 not seen).

Specialised tubular growth form, with apical oscules and central cavity running longitudinally through body. Surface smooth, even. Choanosomal fibres apparently absent, and skeletal structure poorly defined with more-or-less longitudinal tracts of choanosomal principal stylosomes bound together at nodes by collagen. E<alpha>chinating acanthostyles absent. Subectosomal skeleton rudimentary, composed of subectosomal auxiliary stylosomes lying just below surface, not protruding through it. E<alpha>ctosomal skeleton absent. Megascleres choanosomal principal stylosomes with spined bases, and slender smooth subectosomal auxiliary stylosomes. Microscleres described as 'arcuate' isochelae and wing-shaped toxas.

**REMARKS.** The holotype and paratypes (CMFRICT84/2) of *Q. indica* are housed at the Central Marine Fisheries Research Institute, Mandapam Camp, Cochin, India. A slide of the holotype is housed at the IM (A.K. Mandal, pers. comm.).

The genus is monotypic and known only from its original description (Thomas, 1974). It is an unusual, very thin-walled hollow tubular sponge with pseudo-syconoid construction, and attached to the substrate by short peduncles reminiscent of *Aulospongus* Norman (Raspailiidae). Apart from spicule diversity and geometry, which place the type species in Microcionidae, we know of few other characters that give clues as to its affinities with other microcionids. From its skeletal structure, or lack of it, *Qasimella* shows similarities to *Artemisina*: It is also possible that *Q. indica* is a larval sponge, but until type material is seen its published description suggests that it has affinities to *Artemisina*: The chelae have been described as 'arcuate', but this cannot be confirmed and must be regarded as suspect (e.g., they may be merely modified, curved, palmate ones).

**Qui<alpha>ziona** de Laubenfels, 1936

(Fig. 22F-G)

*Qui<alpha>ziona* de Laubenfels, 1936a: 111.


Encrusted growth form. Surface hispid, uneven. Choanosomal skeleton differentiated into two components: renieroid basal layer composed of spongin fibres lying on substrate cored by bispicular tracts of acanthostyles forming triangular meshes; basal fibres ascending non-anas-
tomosing fibre nodes echinated by multipsicular plumose tracts of both choanosomal principal subtylostyles and echinating acanthostyles (of same morphology as basal renieroid skeleton spicules) embedded and erect on substrate. Ectosomal skeleton parataxial, composed of two size classes of subectosomal auxiliary subtylostyles, forming occasional brushes and scattered in mesohyl matrix near periphery. Megascleses longer choanosomal principal subtylostyles with heavily microspined bases, shorter acanthostyles with aspinose points (forming both renieroid basal skeleton and echinating fibre nodes), and two size classes of auxiliary subtylostyles with smooth or spined bases. Microscleres palmate isochelae, cleistocheleae and small accolada toxas.

REMARKS. The original description differs slightly from the definition above. In particular, the very small, thin toxas were overlooked, as was a renieroid basal skeleton typical of de Laubenfels’ (1936a) plocamiform sponges. Brondsted’s (1924) description of Quizcione suggests that it is close to Microciona with a hymedesmoid basal skeleton and plumose ascending fibre nodes but having cleistocheleae in addition to palmate isochelae. The type material shows the species more closely related to Antho with a renieroid basal skeleton. Smaller acanthostyles and larger principal styles echinating basal fibres is similar to Plocamilla, whereas acanthostyles rather than acanthostrangyles coring the basal fibres is similar to Antho, and this mix of characters illustrates the difficulty in separating these two taxa.

Cleistocheleae have been recorded in several microcionids (Microciona cleistochelea Topsent, M. clathrata Whitelegge, M. chelifera Lévi, Clathria simpsoni Van Soest, C. toxipraedita Topsent and Collocathria ramosa Dendy). Alander (1942) and Van Soest (1984b) suggested that cleistocheleae are modified palmate isochelae (with fused chelate teeth) which have arisen several times independently within the Microcionidae, and consequently they do not have primary taxonomic significance. Interestingly, Brondsted (1924) also remarked on the similarities between cleistocheleae of Microcionidae and clavidiscs of the hypercalcified sponge Merlia Kirkpatrick, supporting current theories on the origin and affinities of the ‘sclerosponges’ with the demosponges (e.g., Vacelet, 1985).

Bergquist & Fromont (1988) merged M. heterospiculata with Clathria mortenseni and suggested that Quizcione should be abandoned on the basis that they did not find cleistocheleae in their material, contrary to de Laubenfels’ (1936a) description. This synonymy is not upheld here, although Bergquist’s (1961a: 39) record of M. heterospiculata from northern New Zealand may be Clathria mortenseni. I interpret Quizcione, based strictly on the type specimen, as a synonym of Antho (Antho).

**Ramoses** de Laubenfels, 1936

(Fig. 22H-I)


**Type Species.** Clathria pauper Brondsted, 1927: 3 (by original designation) (fragment of type BMNH1930.11.5.2).

Arborescent, tubulo-digitate growth form. Surface shaggy, uneven, microscopically hispid. Choanosomal skeleton irregularly plumo-reticulate, with vaguely ascending multipsicular primary tracts interconnected by transverse paucispicular secondary tracts cored by both smooth and partially spined choanosomal principal styles and echinated by plumose bundles of smaller acanthostyles. Spongin fibres not seen but spicules united by moderate quantities of collagen. Subectosomal skeleton plumose, with bundles of subectosomal auxiliary subtylostyles protruding through surface. No special ectosomal skeleton. Megascleses longer entirely smooth choanosomal principal styles, slightly shorter principal subtylostyles with spines on bases and distal end of shaft, small slender echinating acanthostyles with even spination, and subectosomal auxiliary subtylostyles with spined bases. Microscleres accolada toxas, some with contort centres. Chelae absent.

REMARKS. The holotype of *C. pauper* has not yet been discovered in the Brondsted collection at UHM (O. Tendal, pers. comm.), but a fragment of it is held at the BMNH. A fragment of *C. pauper* (with second label stating ‘Protocathria antarctica, 29.1.19?? [illegible], 340 fathoms, M Burton’) is in Sydney (AMZ2239). It is possible that this material is also a fragment of the holotype, but its status and origin are not certain. Brondsted’s (1927) original description conforms closely to the type material, although he appears to have overlooked the thin accolada toxas microscleres (some with asymmetrical contort central curvature).
Ramoses is similar to Pseudanchniae in lacking chelae microscleres, and Koltun (1976: 155) synonymised the type species of Ramoses with P. toxiferum Topsent, the type species of Pseudanchniae (both species are from the Ross Sea, Antarctica). This synonymy is confirmed here from type specimens and both species are lipochealous Clathria (Clathria). Koltun (1976) suggested that C. pauper was a synonym of Microciona toxifera (Topsent), also from the Antarctic, but this synonymy is rejected. Comparison of relevant type specimens shows that the two species differ substantially in their skeletal structure, spicule size and spination on megascleres.

**Rhaphidophalus Ehlers, 1870**

(Fig. 23A-C)


**TYPE SPECIES. Spongia ceratina** Esper, 1797: 195 (by original designation) (fragment of type ZMB4577).

Arborescent growth form. Surface microscopically hispid, conulose. Choanosomal skeleton irregularly reticulate, with heavy spongine fibres cored by multispicular tracts of choanosomal principal subtylostyles which terminate in plumose tracts on peripheral fibres. Plumose multispicular tracts of echinating acanthostyles clumped around fibre nodes and also protruding from fibres at regular intervals. Subectosomal skeleton plumose, with well-developed multispicular columns of subectosomal auxiliary subtylostyles arising from ends of principal spicule brushes in peripheral skeleton. Ectosome with bundles of erect ectosomal auxiliary subtylostyles overlaying subectosomal plumose brushes of spicules. Megascleres entirely smooth hastate choanosomal principal subtylostyles, larger smooth subectosomal auxiliary subtylostyles, shorter thinner smooth ectosomal auxiliary subtylostyles, and echinating acanthostyles with aspinose necks. Microscleres palmate isochelae of two size categories, and two forms of toxins (small wing-shaped and larger asymmetrical sinuous toxins).

**REMARKS.** The type species is from the Indo-west Pacific region where most species occur.

The primary and only consistent morphological feature that distinguishes Rhaphidophalus from other Clathria-like taxa is the specialised ectosomal skeleton, consisting of two differentiated categories of auxiliary subtylostyles which form brushes on the surface (either as discrete brushes (s.s.) or in a continuous palisade). This is identical to the condition described for Thalysia (which has seniority).

Hallmann (1912), followed most recently by Van Soest (1984b), suggested that the two sizes of auxiliary megascleres may represent age differences in spicules, in which case the genus has a distinct localisation of adult and juvenile megascleres. This assertion, however, does not yet have any empirical (experimental) support. This difference in size/age of auxiliary spicules is crucial to the definition of Rhaphidophalus, because some species of Clathria, Microciona and Dendrocia have a dermal skeleton of similar structure but containing only one sort of auxiliary spicule (C. imperfecta, C. striata, C. pyramida). Similarly, some species of Antho (e.g., A. ridleyi) also have relatively dense ectosomal brushes, but these consist of a single undifferentiated category of subectosomal megasclere. Hallmann (1912) debated the value of ectosomal specialisation as a generic character, concluding that although the distinction between the two genera may eventually breakdown, they can be consistently differentiated on composition of peripheral skeleton rather than its development or density. These conclusions are supported here.

Another character predominant in Thalysia (including Rhaphidophalus) is the presence of more than one size category of isochelae, of which one or more may be contort (Fig. 5F). This feature is not consistent among species, nor is it exclusive to the genus. Contort chelae are common in Clathria (Thalysia) (e.g., Spongia abietina Lamarck, Spongia caetiformis Lamarck, Rhaphidophalus cervicornis Thiele, R. spiculosus Dendy, R. topsenti Thiele, Clathria fasciculatus Wilson and C. spiculosus var. macilenta Hentschel), Clathria (Clathria) and Clathria (Microciona) (e.g., Dictyociona adioristica de Laubenfels, Clathria mixta Hentschel, C. bulbosa Van Soest, Fisherispongia ferrea de Laubenfels, Esperiopsis obliqua George & Wilson, Wilsonello connectens Hallmann, and M. prolifera (sensu Wilson)), Clathria (Wilsonella) (e.g., Microciona tuberosa Bowerbank, Clathriopsonoma reticulata Lendenfeld),
Clathria (Axociella) (e.g., Esperopsis caraholiculata Whitelegge), Anho (Anho) (e.g., Holoplocamia penneyi de Laubenfels) and Holopsammia (e.g., Plectispa macropora Lendenfeld). It is also known to occur in Cornulium Carter (Iophonidae) (e.g., C. johnsoni (de Laubenfels)) and consequently it cannot be given much diagnostic value above the species level.

There are several other characters used by authors to define genera present in many species of Thalysias (including Rhaphidophalus), but are not apomorphies occurring throughout related groups in all combinations (e.g., encrusting growth form and hymedesmoid architecture (e.g., Leptoclasthria lambela Lévi); absence of echinatizing megascleres (e.g., Axociella arteria de Laubenfels), absence of microscleres (e.g., Clathria fascicularis Topsent), and modified isochelae (e.g., Colloclasthria ramosa Dendy)). A systematics based on these features conflicts with one based on ectosomal specialisation and dispersal of structural megascleres within the skeleton.

By comparison, Dendy (1905), Wilson (1925), de Laubenfels (1936a), Hartman (1955), Wells et al. (1960), Bergquist (1965), Hooper (1990a), Hooper et al. (1990, 1992) and Hooper & Lévi (1993a) amalgamated Thalysias (including Rhaphidophalus) and Clathria (including Microciona) on the basis that dermal specialisation can vary intraspecifically, especially in relation to growth form and age of an individual. These authors suggest that this feature is probably not a sound base on which to separate genera. In contrast, Simpson (1968a), Wiedenmayer (1977) and Bergquist & Fromont (1988) maintain these genera separately, although they do state that dermal specialisation may not be important at the generic level (i.e., they offer a convenient classification rather than one based on phylogeny).

Simpson (1968a) showed that despite very close morphological similarities between Clathria and Rhaphidophalus, there were cytological differences between the taxa which he considered were sufficient to separate them at the generic level of classification. Thus, Simpson’s (1968a) cytological data supports the conclusion above based on morphological evidence that the only morphological character of consistent diagnostic importance, and which correlates to some extent with supposed biological differences between those genera, is the possession of ectosomal specialisation. This conclusion is upheld in this study and used at the subgeneric level.

There are several nomenclatural complexities that still exist for Rhaphidophalus; and these require further discussion.

1) Van Soest (1984b: 91) argued that Thalysias should be abandoned in favour of Rhaphidophalus, following Lévi (1960a: 52). His argument was based on the premise that Carter (1876: 311) designated the ‘representative’ of Thalysias as Thalysias subtriangularis (Duchassaing, 1850), and he suggested that although Carter (1876) did not actually use the words ‘type’ or ‘type species’, there was no doubt of his intentions (T. subtriangularis is a species of Xestospongia; Wiedenmayer, 1977: 255; Van Soest et al., 1983: 199).

Van Soest (1984b) also suggested that the use of Rhaphidophalus over Thalysias was a pragmatic solution since the name was in current usage by the majority of contemporary authors. Conversely, Wiedenmayer (1977: 140), Hooper (1990a), Hooper et al. (1990, 1992) and Hooper & Lévi (1993a) note that Carter (1876) merely compared three small specimens from the North Atlantic with Thalysias, but left them unnamed. Wiedenmayer (1977) states that although Carter did cite Duchassaing’s (1850: pl. 17, fig. 1) figure of Thalysias subtriangularis, Carter’s action cannot be construed as a subsequent designation of a type species under Articles 67c and 69a of the ICZN (Anonymous, 1985). Therefore, de Laubenfels’ (1936a: 104) subsequent designation of Thalysias virgulosa (Lamarck, 1814) as type species of Rhaphidophalus is valid, and the genus is a junior synonym of Thalysias.

2) Simpson (1968a: 98) suggested that arguments supporting or refuting the choice of one genus name over another were irrelevant because Rhaphidophalus, Thalysias and Axociella showed different cytological features, apparently justifying their recognition at the generic level. There are no arguments based on skeletal evidence which can contend with Simpson’s hypothesis since his cytological data do not correlate with any skeletal features. However, Simpson’s (1968a) conclusions are based on only three species, one in each genus, and it could be interpreted that the differences he observed may be applicable only at the species level.

Simpson (1968a) found that Thalysias was distinct from both Microciona (cf. Hartman, 1955: Wells et al., 1960). Rhaphidophalus and Clathria (cf. Lévi, 1960a). Thalysias was related to Rhaphidophalus, but cytologically distinct, which he stated was also apparently reflected in ectosomal cytological and morphological differences between the two genera. Rhaphidophalus
(sensu Simpson) had a specialised and extensive region containing a secondary fibre system and a continuous ectosomal skeleton, whereas Thalysia had fibre cell tracts organised into dermal columns which produce tufts of ectosomal styles. However, no similar correlations were observed in any other species examined (Van Soest, 1984b; Hooper, 1990a). Simpson's (1968a) system is intrinsically unworkable as it presently stands, given that the existing systematics is based on skeletal attributes, and essentially Thalysia and Rhaphidophlus differ only in their nomenclature.

3) Simpson (1968a) suggested that Axocielita was distinct from, but most closely related to Thalysia, but this conclusion is not supported by their morphology. Axocielita similis (Stephens) has a hymedesmoid skeleton with plumose fibre nodes, each node cored by plumose spicule tracts, echinating acanthostyles are absent and only one size class of auxiliary spicule is present, suggesting that the species is more closely related to Microciona than Thalysia (Hooper, 1990a). Simpson (1968a: 113) also agreed that echinating acanthostyles are of minor diagnostic importance. The implication of these data is that Axocielita hartmani Simpson and A. similis (Stephens) are either not congeneric, which is not indicated by their morphological characters, or that morphological systematics is not corroborated by cell biology, and this is the main obstacle in using Simpson's results.

4) Simpson (1968a) also suggested that Clathria was more closely related to Rhaphidophlus and Thalysia in its cytological characteristics, than it was to the morphologically more-similar Microciona. This result conflicted with the system proposed by Lévi (1960a), and developed further by Van Soest (1984b), which distinguished microcionid genera on the basis of their skeletal architecture and ectosomal characteristics, respectively. Nevertheless, it suggests that thinly encrusting microcionid sponges may have different cytological characteristics than ramose or massive forms, and this poses questions concerning environmental influences on cellular behaviour.

5) Hallmann (1920: 769) preferred Tenacia Schmidt (1870) to Rhaphidophlus Ehlers (1870) because Tenacia had been firmly established by the redescription of T. clathrata Schmidt (Wilson, 1902: 397), whereas Rhaphidophlus was imperfectly known only from Ehlers' (1870: 18, 31) inadequate redescription of Spongia crattitia Esper. The argument is irrelevant, since S. crattitia is recognisable, and Thiele (1903a: 957) has already redescribed portions of the type material (ZMB4577, 4578), even though the whereabouts of the actual type specimen is presently unknown. Hallmann (1920) also suggested that Tenacia should be preferred to Rhaphidophlus because Schmidt's publication was abstracted in the Zoological Record for 1870, whereas Ehlers work was abstracted in 1872. There is no doubt that the genera are synonymous (Hartman, 1955: 176; Lévi, 1960a: 56; Wiedenmayer, 1977: 140; Van Soest, 1984b: 91) but Rhaphidophlus has seniority over Tenacia, and Thalysia has seniority over both. It is included in Clathria (Thalysia).

**Seriatula Gray, 1867**

*Seriatula Gray, 1867: 515; de Laubenfels, 1936a: 122. (Refer to Ophlitaspongia).*

**Sophax Gray, 1867**

*(Fig. 23D-E)*

*Sophax Gray, 1867: 521; de Laubenfels, 1936a: 112.*

**Typespecies.** *Microciona fallax* Bowerbank, 1866: 128 (by monotypy) (lectotype BMNH1910.1.1.71; paralectotype BMNH1930.7.3.198; fragment of lectotype USNM5047).

Encrusting growth form. Surface uneven, microscopically hispid. Choanosomal skeleton plumose (slightly plumocorticulate), with spongins reduced to basal layer of spongins on substrate with ascending spongins fibre nodes cored by multispecular columns of choanosomal principal subtylostyles, and echinated by acanthostyles. Ascending fibres interconnected by sparse transverse spongins fibres, aspiculose or with few coring principal spicules. Ectosomal skeleton with tangential, paratangential or poorly developed brushes of subectosomal auxiliary subtylostyles. Megascleres long choanosomal principal subtylostyles with heavily microspined bases, entirely smooth, flexuous, sinuous or straight subectosomal auxiliary subtylostyles, and echinating acanthostyles of variable size and evenly distributed spines. Microscleres absent.

**Remarks.** Gray (1867) erected Sophax for *M. fallax*, without further comment or comparison with other Microciona species. The type species has a Microciona-like hymedesmoid skeleton with erect spongins fibre nodes (similar to other nominal genera such as Abila, Axosuberites, Stylotellopsis, and Thalyseurypon), but unlike this it also has some transverse fibres intercon-
necting multipilcular tracts, producing a slightly plumoreticulate architecture. *Sophax* is referred here to *Clathria* (*Microciona*).

**Stylotellosps** Thiele, 1905  
(Fig. 23F-G)

*Stylotellosps* Thiele, 1905: 456; de Laubenfels, 1936a: 112.

**Type Species.** *Stylotellosps amabilis* Thiele, 1905: 456 (by monotypy) (holotype ZMB13309).

Thickly encrusting growth form. Surface hispid, uneven. Choanosomal skeleton hymedesmoid, with basal layer of spongine fibres lying on substrate and plumose non-anastomosing fibre nodes. Spongine fibre nodes cored by large echinating acanthostyles standing perpendicular to substrate, forming multipilcular plumose tufts on basal skeleton. Subectosomal skeleton plumose, with multipilcular columns of subectosomal auxiliary subtylostyles arising from ends of echinating spicule brushes, producing dendritic whisk tracts especially near periphery. Ectosomal skeleton without special spiculation but erect subectosomal auxiliary styles form nearly continuous palisade on surface. Mesohyl has heavy deposits of loose spongine. Megascleres single category of smooth subectosomal auxiliary styles with tapering bases and hastate points, and large echinating acanthostyles with swollen bases, large spines, and aspinose points. Principal spicules undifferentiated from auxiliary spicules. Microscleres absent.

**Remarks.** From published descriptions (Thiele, 1905; Topsent, 1928a; Koltun, 1964a) *Stylotellosps* appears to be similar to *Thalyssias* in having differentiated subectosomal and ectosomal auxiliary spicules (i.e., a specialised ectosomal skeleton), and Van Soest (1984b) synonymised the two genera on this basis. Re-examination of type material found that auxiliary spicules range greatly in their length, and principal spicules are very similar to auxiliary spicules scattered throughout the skeleton. The genus has a ‘microcionid’ choanosomal skeletal structure (i.e., hymedesmoid with plumose fibre nodes), and an unusual subectosomal skeleton composed of dendritic or sinuous auxiliary spicule tracts. It also lacks microscleres (although several arcuate isochelae were seen in histological preparations of the holotype, but these are probably foreign). *Stylotellosps* is interpreted here as being an encrusting (hymedesmoid) species of *Clathria* (*Thalyssias*). De Laubenfels (1936a) included the genus with *Eurypon* (*Raspallidae*), but this is not upheld here: similarities between *Stylotellosps* and *Thalyssias* in their peripheral skeletal structure and the geometry of auxiliary spicules are closer than with the rapsailiids (see Hooper, 1991).

**Tablis** de Laubenfels, 1936  
(Fig. 23H-I)

*Tablis* de Laubenfels, 1936a: 76.

**Type Species.** *Echinochalinus anomala* Hallmann, 1912: 292 (by original designation) (holotype AMG10548).


**Remarks.** *Tablis* was erected for Whitelegge’s (1907) specimen of *Echinochalinus glabra* from Woolongong, NSW, a junior homonym of Ridley & Dendy’s (1887) species renamed by Hallmann (1912) to *E. anomala*. This species has also been recorded from the Great Barrier Reef (Burton, 1934a). Three other species were referred to *Tablis* by de Laubenfels (1936a): *Echinochalinus glabra* Ridley & Dendy (a synonym of *Spongilla barba* Lamarck), *E. reticulata* Whitelegge, both from SW Australia, and *Spongilla clavosa* Lamarck. The last mentioned species is unknown: it was not mentioned in Topsent’s (1933) revision of Lamarck’s species nor found in the Lamarck collections (MNHN). These other 2 species differ from *E. anomala* in having microscleres but lacking an Holopsamma-like ‘honeycombed reticulate’ growth form. *Tablis* is returned here to *Echinochalinus* (*Echinochalinus*),
Tenacia Schmidt, 1870
(Fig. 24A-C)


TYPE SPECIES. Tenacia clathrata Schmidt, 1870: 56 (by monotypy) (fragment of type BMNH1870-5,3,156); = Spongia virgulosa Lamare, 1814: 444 (fragment of type MNHNLBIMDNE1344, 1338).

Erect, arborescent, reticulate branching growth form. Surface highly conulose, uneven, microscopically hispid. Choanosomal skeleton irregularly reticulate, with well developed spongin fibres differentiated into ascending primary and transverse secondary fibres. Principal spicules confined to axis of primary fibres, but absent completely from secondary connecting fibres, and all fibres cored by paucispicular tracts of subectosomal auxiliary subtylosstyles, and heavily echinated by small acanthostyles. Subectosomal skeleton plumose, with tracts of subectosomal auxiliary subtylosstyles originating from deeper regions of choanosomal skeleton; subectosomal auxiliary subtylosstyles also scattered throughout between mesohyl fibre meshes. Ectosome plumose, with brushes of smaller ectosomal auxiliary subtylosstyles arising from ends of subdermal spicule brushes. Megascles smooth choanosomal principal styles, smooth subectosomal auxiliary subtylosstyles, smooth ectosomal auxiliary subtylosstyles, and short thick echinating acanthostyles with aspino points and necks. Microscleres palmate isochelae of two sizes, and wing-shaped, acolada and sinuous asymmetrical toxas.

REMARKS. Tenacia and Rhaphidophlus are synonyms (Hallmann, 1920; Topsent, 1932; Lévi, 1960a), and use of one name over another is merely a nomenclatural decision (see remarks for Rhaphidophlus). Topsent’s (1932: 97) synonymy of T. clathrata and Spongia juniperina Lamare is not upheld here; the former is considered here to be a synonym of T. virgulosa and restricted to Caribbean and NE. Atlantic populations, whereas T. juniperina (including T. clathrata of Hallmann, 1912) is known only from the Indian Ocean. The genus is synomynised with Clathria (Thalysias).

Tenaciella Hallmann, 1920
(Fig. 24D-E)


TYPE SPECIES. Esperiopsis canaliculata Whitelegge, 1906: 471 (by monotypy) (lectotype AMG4325).

Erect, branching, digitate growth form. Surface even, hispid, with oscules dispersed over lateral margins of branches. Choanosomal skeleton irregularly reticulate, nearly radial, with compressed axial and plumose extra-axial skeletons. In axis heavy spongins fibres cored by multispecific tracts of choanosomal principal styles, and in extra-axial skeleton principal styles protrude from peripheral fibres forming radial or plumose tracts, lying immediately below and supporting subectosomal skeleton. Echinating megascles absent. Subectosomal skeleton plumose, with multispecific ascending tracts of subectosomal auxiliary styles at ends of peripheral choanosomal fibres. Ectosomal skeleton with thick continuous palisade of smaller ectosomal auxiliary styles standing perpendicular to surface. Megascles smooth fusiform choanosomal principal styles, subectosomal auxiliary styles-subtylosstyles with smooth or micropined bases, and ectosomal auxiliary styles-subtylosstyles with micropined bases. Microscleres palmate isochelae of two sizes, including contorted forms, and ooxhorn and wing-shaped toxas.

REMARKS. Hallmann (1920) erected Tenaciella for species like Tenacia (= Thalysias), but lacking echinating megascles, Wells et al. (1960) also referred Esperiopsis obliqua George & Wilson to Tenaciella, but this species lacks dermal specialisation and is more closely allied with Asocelitia (= Clathria). Ristau (1978) suggested that Artemisina archehoga Ristau (USNM 24528) was similar to the type species of Tenaciella in having prominent subectosomal (extra-axial) spicule columns, and he suggested that the two species differed only in growth form, shape of the toxas microscleres and the appreciably more organised skeletal architecture in T. canaliculata. However, differences observed in types of these species are more noticeable than their similarities (e.g., ectosomal skeleton, fibre reticulation, degree of axial and extra-axial differentiation), and their supposed affinities (Ristau, 1978), are superficial.

In its skeletal structure, differentiation of axial and extra-axial skeletons, fibre characteristics, the possession of similar extra-axial radial bundles of megascles, and having a continuous ectosomal palisade of spicules the type species shows close similarities to Ceratopsis axifera (Hentschel) (Raspailiidae) from the Arafura Sea.
(Hooper, 1991). In fact the resemblance between these two species is remarkable (although *Esperiopsis canaliculata* obviously belongs to Microcionidae, having isochelae and toxas, whereas *Ceratopion* belongs to Raspailliidae in having long extra-axial spicules surrounded by bundles of ectosomal spicules and lacking chela or tox microscleres). These structural similarities suggest a closer relationship between the two families, as proposed by Hooper (1991) in returning Raspailliidae to the Poecilosclerida, and subsequently supported by chemotaxonomic evidence (Hooper et al., 1992).

In skeletal architecture *E. canaliculata* is identical to *E. cylindrica*, the type species of *Axociella*. Consequently, both *Tenaciella* and *Axociella* are synonymised here (the latter being the most senior available name), both having a compressed reticulate axis and plumose or plumo-reticulate extra-axial (subectosomal) skeletons, isochelae and tox microscleres, lacking echinating spicules, and referred to *Clathria* (*Axociella*).

**Thalassodendron** Lendenfeld, 1888

*Thalassodendron* Lendenfeld, 1888: 222; de Laubenfels, 1936a: 112.

**TYPE SPECIES.** *Thalassodendron typica* Lendenfeld, 1888: 223 (by indication) (holotype unknown).

Flabellate, cup-shaped growth form. Surface striated longitudinally. Chaoanosomal skeleton reticulate, with differentiated primary ascending and secondary transverse connecting spongion fibres; primary fibres cored by multispecific tracts of chaoanosomal principal styles, lightly echinated by acantho-styles (often secondarily incorporated into fibres), whereas secondary fibres aspiculose. Subectosomal and ectosomal skeletons unknown. Megascleres include smooth chaoanosomal principal styles, and short stout echinating acantho-styles. Microscleres unknown.

**REMARKS.** This diagnosis is based on Lendenfeld’s (1888) description of the type species which is virtually unrecognisable (de Laubenfels, 1936a). It is suspected that *Thalassodendron typica* Lendenfeld is a synonym of *Echinoneuma typicum* Carter, given Lendenfeld’s propensity for describing other authors’ species as his own ‘new species’. However, it is not possible to associate any type material with the name *Thalassodendron typicum* and this synonymy remains doubtful. *Echinoneuma typicum* is also a synonym of *Spongia cactiformis* Lamarck, in which case *Thalassodendron* would belong to *Clathria* (*Thalysias*). *Thalassodendron typica* of Whitegege (1901: 86; holotype AMZ958) is not the same as Lendenfeld’s species, being a synonym of *Echinodictyon mesenterinum* (Lamarck) (*Raspailliidae*) (Hooper, 1991: 1379).

**Thalysia** Duchassaing & Michelotti, 1864

(Figs 24A-C, 25A-B, 176-177)


TYPE SPECIES. 1) Interpretation by Wiedenmayer (1977), (i.e., Thaliaysia s.s.): Spongia virgulosa Lamarck, 1814 (by subsequent designation; de Laubenfels, 1936a: 104) (holotype BMNH1954.2.20.67; junior synonym of Spongia juniperina Lamarck, 1814 (lectotype MNHN.BUM.IDT70) (de Laubenfels, 1936a: 104). 2) Interpretation by Van Soest (1984b), i.e., Thaliaysia of authors: Thaliaysia subtriangularis Duchassaing, 1850 (by subsequent designation; Carter, 1876: 311): = Xestospongia subtriangularis (Wiedenmayer, 1977: 255).

DEFINITION OF TYPE SPECIES. As for Tenacia.

REMARKS. The nomenclatural complexities of Thaliaysia have been discussed above (see Rhaphidophalus and Tenacia). According to Van Soest (1984b), Carter's (1876) statement that T. subtriangularis was 'representative' of the genus means that Thaliaysia sensu Carter is a haplolsclerid, but this is not a valid subsequent designation. Wiedenmayer (1977) stated that de Laubenfels' (1936a) subsequent designation of T. virgulosa is the type, which makes Thaliaysia (established 1864) a senior synonym of Rhaphidophalus (established 1870). Moreover, Tenacia is an objective synonym of Thaliaysia by synonymy of their respective type species.

This has been confirmed by type material (although the holotype of Spongia virgulosa is only represented by a fragment in the BMNH). Thaliaysia is used here as the earliest available subspecific name for Clathria with differentiated ectosomal and subectosomal spiculation (i.e., specialised ectosomal skeleton).

Wetmoreus de Laubenfels, 1936
Wetmoreus de Laubenfels, 1936a: 112.

TYPE SPECIES. Microciona novaezelandica Brondsted, 1924: 463 (by original designation) (holotype UZM not found).

Encrusting growth form. Surface shaggy, hispid. Choanosomal skeleton hymedesmoid, with spornin fibres reduced to basal layer of spongion on substrate with plumose non-anastomosing fibre nodes. Fibre nodes cored by erect multispiracular bundles of choanosomal principal subtylostyles forming ascending plumose skeletal columns, and echinating acanthostyles at oblique angles to skeletal columns, usually forming brushes. Subectosomal skeleton paratangential or plumose, with single category of subectosomal auxiliary subtylostyles forming light dermal brushes erect on surface, or scattered individually on surface and throughout mesohyl. Megascleres choanosomal principal subtylostyles with prominent basal spines, smooth subectosomal auxiliary subtylostyles-styles, and small evenly spined echinating acanthostyles. Microscleres allegedly include both palmate and arcuate forms. Toxas absent.

REMARKS. This definition is from Brondsted's (1924) description of the type. The holotype is possibly extant in Brondsted's collection at the UZM, but has not been located (O. Tendal, pers. comm.). Wetmoreus differs from Microciona (s.s.) in allegedly having both palmate and arcuate isochelae, and lacking toxas (see remarks for Paradoryx), but this cannot be verified. It is possible that both forms of isochelae are merely modified (curved, thickened) palmate forms. Wetmoreus is included here in Microciona based on the possession of a hymedesmoid basal skeleton with plumose fibre nodes.

Wilsonella Carter, 1885
(Fig. 24H-I)


TYPE SPECIES. Wilsonella australiensis Carter, 1885f: 366 (by monotypy) (holotype BMNH1886.12.15.43).

Erect, massive or flabelliform growth forms. Surface prominently conulose at apex of sponge, with conspicuously raised oscules. Choanosomal skeleton reticulate, with moderately light spongion fibres forming irregular meshes with distinct primary ascending and secondary transverse lines. Primary fibres cored by paucispicular tracts of robust auxiliary subtylostyles and abundant detritus, and heavily echinating by acanthostyles particularly at fibre nodes. Secondary connecting fibres with paucispicular tracts, little detritus and lightly echinated. Ectosomal skeleton lightly arenaceous, mostly with spicule fragments, lacking specialised spiculation but with light tangential or paratangential tracts of more slender subectosomal auxiliary subtylostyles. Megascleres fusiform robust auxiliary subtylostyles with smooth bases and hastate or telescoped points (inside fibres), more slender auxiliary subtylostyles with spines on both bases and points (outside fibres), and echinating acanthostyles with even spination. Microscleres palmate isochelae and wing-shaped toxas.

REMARKS. Wilsonella is characterised by auxiliary megascleres coring fibres (i.e., without
true choanosomal principal spicules), incorporation of sand and foreign spicule detritus into the skeleton, and lacking any differentiation between ectosomal and subectosomal skeletons. Wilsonella australiensis is unusual amongst "sandy" microcionid sponges in that subectosomal auxiliary styles outside fibres (e.g., in the ectosomal skeleton) are geometrically very similar to those coring fibres differing only in having spines on both their bases and points. These spicules are characteristic of the type species (although they are also known in several other microcionids, such as Clathria (C.) chelifera and Clathria (T.) major). Even though spicules coring the fibres cannot be construed as being true principal megascleres, it must be concluded that this species has two distinct categories of auxiliary spicules. In this respect it is contrasted with Clathria (Dendroclia), which has a completely plumose skeletal architecture, including ectosomal and subectosomal differentiation, but only a single undifferentiated category of structural megascleres throughout the skeleton.

Species referred to Paradorayx by Hallmann (1920) are similar to Wilsonella in having only auxiliary megascleres in the skeleton, but these have arcuate-like chelae instead of palmate isochelae, more than one category of structural megasclere (i.e., Clathria (Clathria)), or only 1 category of auxiliary spicules and a plumose architecture (i.e., Clathria (Dendroclia)). In contrast, the type species of Wilsonella incorporates detritus into spongin fibres, and this character is interpreted as probably being phylogenetic rather than merely ecological despite being homoplous throughout Porifera (known also in Phorospongidae, Raspailiidae, Ircinidae, Dysideidae, etc.), because it is correlated with distribution of megascleres within skeletal regions as described above. Contemporary authors (e.g., Lévi, 1967b) have included Wilsonella as a synonym of Clathria, whereas in the present work the type species of Wilsonella is synonymised with Clathriopsamma (both with detritus in the skeleton), the former being the senior name, and used as at the subgenus level, Clathria (Wilsonella).

**GENERAE EXCLUDED FROM MICROCIONIDAE**

**Acarnus** Gray, 1867


**TYPE SPECIES.** *Acarnus innominatus* Gray, 1867: 544 (by monotypy) (holotype BMNH not found).

Thickly encrusting, massive, flabellate or vaseiform growth forms. Surface smooth or minutely hispid, uneven, often sculptured with subdermal canals in encrusting forms. Choanosomal skeleton with short plumose tracts connected by renieroid reticulation of spongion fibres, reduced to plumo-reticulate skeletal tracts, or further reduced to plumo-halichondroid skeleton in encrusting forms. Skeletal tracts composed of uni- or paucispicular tracts of smooth choanosomal principal styles or subtylostyles, sometimes with spined bases. Fibres usually heavily invested with spongin, with granular collagenous around nodes of skeletal tracts, and fibres echinate by smooth and/or spined cladotylotes of one or two size categories, with or without additional, smaller echinating acanthostyles. Ectosomal skeleton with a tangential or paratangential layer of basally spined tyloths. Microscleres, palmate isochelae and up to three distinct forms of toxas: oxhom, wing-shaped and accolada toxas.

**REMARKS.** The type species concept follows Van Soest (1984b: 61) based on material from the Caribbean given that the holotype is missing from the BMNH. The type has two categories of cladotylote megascleres, a larger smooth and smaller spined variety, whereas other species are known to have various combinations of those spicules (Van Soest et al., 1991), together with acanthostyles in some species (A. (Acanthacarnus) Lévi).

Although the genus has now been exhaustively discussed (Hooper, 1987; Hiemstra & Hooper, 1991; Van Soest et al., 1991), its family placement is still debatable. In its microsclere complement (palmate isochelae, diverse toxas), differentiated principal and auxiliary spicules, echinating acanthostyles in some species (as well as having a highly modified second category of echinating spicules (cladotylotes) which are unique to the genus, derived from either acanthostyles (Hooper, 1987) or ectosomal tyloths (Hiemstra & Hooper, 1991)), the genus appears to have affinities with the Microcionidae (e.g., Burton, 1959; Lévi, 1960a; Vacelet et al., 1976). Other authors (de Laubenfels, 1936a; Tantia, 1963; Hechtel, 1965; Bakus, 1966; Thomas, 1970a, 1973; Hoshino, 1981; Van Soest, 1984b; Hooper, 1987; Hiemstra & Hooper, 1991; Van Soest et al.,
1991; Hooper & Lévi, 1993a) suggest that true diactinal ecosomal spicules (tylostyles with terminal spines and swollen tips) and a renieroid reticulation indicate relationship to Myxillidae (in the sense of Hartman, 1982). Hajdu et al. (1994) resurrected lophonidae for Acanthus, Megaciella, Melonchela and others with microcionid-like spiculation (terminally spined megascleres of diverse categories, palmate isochelae, toxas) as well as ecosomal tylostyles (previously considered diagnostic for the Myxillidae; Van Soest, 1984b). This revised interpretation de-emphasises the primary importance placed on skeletal structure (Bergquist & Fromont, 1988) for example, and allows for the inclusion of renieroid reticulate skeletons in several families (Lophonidae, Microcionidae, Raspailiidae, Phoriospongoidae, Cornulfidae, etc.). Skeletal structure would, therefore, be a highly homoplasic character but this interpretation does allow a consistent differentiation between Microcionidae and lophonidae based on monaxial versus diactinal-derived ecosomal spicules, whilst also acknowledging their affinities based on their possession of similar microscleres through their inclusion similar microscleres through their inclusion together in Microcionidae.

**Amphilectus** Vosmaer, 1880

*Amphilectus* Vosmaer, 1880: 109; Ridley & Dendy, 1887: 123; Burton, 1929a: 428; Lévi, 1960a: 55.

**Type species.** Isodictya gracilis Bowerbank, 1866: 149 (by subsequent designation of Burton, 1929a: 428) (holotype BMNH1877.5.21.754).


**Remarks.** Vosmaer (1880: 109) established *Amphilectus* for a heterogeneous assemblage of 42 poecilosclerid species, most of which were related to Mycale, Esperiopsis (Mycalidae), Desmacidon (Phoriospongoidae) or Myxilla (Myxillidae). Ridley & Dendy (1887) restricted the genus to taxa with smooth styles and palmate isochelae, but even so, they remarked that the taxon was undoubtedly artificial. Burton (1929a) designated Vosmaer's first-named species as genotype, and suggested that in the strict sense (i.e., the above diagnosis) the genus had affinities with Esperiopsis. Lévi (1960a) decided to abandon Amphilectus because, in the sense of Vosmaer (1880), it was too vague and served only as a catch-all taxon. In the broad sense Amphilectus contains some microcionid species (e.g., Microciona armata Bowerbank) whereas in the strict sense it fits with the concept of Myxillidae (Bergquist & Fromont, 1988; Hajdu et al., 1994).

**Caulospongia** Kent, 1871

*Caulospongia* Kent, 1871: 616; Burton, 1930c: 673; de Laubenfels, 1936a: 118.

**Type species.** Caulospongia verticillata Kent, 1871: 616 (by subsequent designation of Hallmann, 1914a: 306) (holotype BMNH1895.7.16.1); =Spongilla perfoliata Lamarck, 1814: 439 (Topsent, 1932: 85) (lectotype MNHNLBIM5758).

Distinctive foliose growth form with lamellae arranged in whorls, or in plates, around an erect stalk. Surface even, minutely hispid. Chaoosomal skeleton plumoreticulate, with well developed spongion fibres cored by pauci- or multispiracular tracts of choanosomal principal tylostyles; longitudinal primary fibres form dandritic branches through axis, and ascending or oblique secondary fibres produce a nearly regular secondary reticulation. Subectosomal skeleton plumose, with erect brushes of choanosomal megascleres protruding through ectosome. Ectosome with tangential or paratangential crust of smaller tylostyles. Megascleres tylostyles of two sizes but with same geometry. Microscleres absent.

**Remarks.** Caulospongia has been included in Suberitidae (Hadromerida) by most authors since Burton (1930c). The type species is distinctive in growth form, and although it is common in NW Australian coastal waters it has been recorded in the literature only infrequently (Lamarck, 1814; Kent, 1871; Topsent, 1932; Hooper, 1984a). De Laubenfels (1936a: 118) defined Caulospongia in Ophioglossidae presumably based on similarities to ophioglossids (most now included in Microcionidae) in skeletal architecture (differentiated axial and extra-axial regions), localisation of spicules to different parts of the skeleton, and growth form (erect, whereas 'typical' suberitids are massive). However, these similarities are convergent. The presence of true tylostyles in Caulospongia (which are charac-
teristic of suberitids, as opposed to subtylole styles seen in many microcionids), and the absence of microscleres (which often provide useful clues on phylogenetic affinities) suggest that the genus should be retained in Suberitidae.

*Plectrodendron* (type species *Plectrodendron elegans* Lendenfeld, 1888: 66, by monotypy) was also referred to *Caidospongia* by Hallmann (1914a: 306).

**Megaciella** Hallmann, 1920
(Fig. 19A-B)


**TYPE SPECIES.** *Amphilectus pilosus* Ridley & Dendy, 1886: 350 (by original designation) (lectotype BMNH1887.2.125).

Lobate flabellate growth form. Surface shaggy, ridged, hispid. Choanosomal skeleton reticulate, with ascending multi- or paucispicular tracts of choanosomal principal styles, interconnected by secondary uni- or bispicular tracts within light spongin, producing irregular wide meshes. Echinating spicules absent. Subectosomal skeleton radial or plumose, with erect choanosomal principal styles protruding from peripheral fibres through surface. Ectosome with tangential or paratangential layer of tylotes, often in bundles. Megascleres very large smooth choanosomal principal styles, and ectosomal tylole, often curved or sinuous, with slightly swollen microspined bases. Microscleres minute palmate isochelae and two sizes of toxas (very large accolada and wing-shaped).

**REMARKS.** This diagnosis is based on the lec
totype which differs slightly from the original description of Ridley & Dendy (1886, 1887). Specifically, the so-called ‘long thin centrally curved oxcas’ are very large accolada toxas with slight central curvature and slightly reflexed hastate points, some of which exceed 100 μm long (i.e., larger than the principal styles). Similarly, these toxas are not associated with the ectosomal skeleton but are scattered throughout the mesohyl, whereas bundles of ‘oxcas’ described by Ridley & Dendy (1887) are actually bundles of ectosomal tylole. A second morph of toxas is
also present, being large and wing-shaped, and these too have hastate points.

Hallmann (1920) suggested that a lax skeletal construction and supposedly comparable spiculation indicated affinities between *Megaciiella* and *Artemisia*. He noted that *Megaciiella* differed from that genus in lacking ornamentation on toxas, which he considered was a significant diagnostic character at the generic level. However, in regard to this latter character, it has been found that a number of microcionid species have distally spined toxas (see remarks for *Clathria*), and in any case, both genera have quite different ectosomal skeletons. On the basis of its ectosomal characteristics (consisting of basally spined diactinal tylole spicules), Van Soest (1984b) referred *Megaciiella* to the *Myxillidae*, whereas *Artemisia* (with a monactinal ectosomal skeleton) was retained in Microcionidae. Under the revised scheme proposed by Hajdu et al. (1994) *Megaciiella* is included in lophonidae, with palmate isochelae and toxas which being the only real synapomorphy between *Megaciiella* and the *Microcionidae* (i.e., *Microcionina*).

**Melonchela** Koltun, 1955
(Fig. 19C-L)


**TYPE SPECIES.** *Melonchela clathrata* Koltun, 1955a: 17 (by original designation) (paratype BMNH 1963.7.29.7).

Arborescent, reticulate planar, branching growth form. Surface even, microscopically hispid. Choanosomal skeleton plumose, with bundles of independent ascending fibres cored by large and small choanosomal principal styles. Ascending fibres not interconnected. Echinating acanthostyles absent. Subectosomal skeleton plumose, with principal styles projecting through surface. Ectosome with tylole forming tangential layer or erect brushes on surface. Megascleres large and small choanosomal principal styles, with smooth or microspined bases, and diactinal ectosomal tylole (swollen bases) and strongyles (rounded bases) with microspined bases. Microscleres abundant, palmate cleistocheles, palmate isochelae, small wing-shaped toxas, and exohem toxas with spines, mucronate points, or telescoped points, or simply with subterminal ridge.

**REMARKS.** This species is remarkable in several features: its erect planar reticulate growth form (superficially resembling the microcionid *Clathria coppingeri* and the raspaiiitid *Echinodiscum cancellatum*); extremely large size range of principal spicules, the largest protruding a long way through fibre bundles, reminiscent of Raspaiiitidae; the apparent lack of connecting fibres between the ascending plumose spicule tracts; a ridge-like subterminal ornamentation on toxas; and extremely abundant tracts of chela microscleres throughout the mesohyl.

Diacital ectosomal spicules (tylole, strongyles and intermediates, varying in the degree of swelling of their bases), palmate isochelae and toxas indicates that the species has affinities to *Acarnus* and *Megaciiella* in the lophonidae.

**Naviculina** Gray, 1867
(Fig. 19H-I)


**TYPE SPECIES.** *Naviculina cliffordii* Gray, 1867: 538 (by monotypy); for *Hydatelmia sp. nov.* of Bowerbank, 1864: 252 (fragment of type BMNH 1877.5.21.270).

Growth form and surface details unknown. Ectosomal features unknown. Choanosomal skeleton evenly reticulate, wide meshed, composed of tracts of subtylostyles bound together with nodal spongin, with multiplicitic tracts several spicules wide interconnected by uni- or paucispicular tracts only one spicule wide, both producing even triangular meshes. Megascleres single category of subtylostyles. Microscleres cleistochele anisocheles, dispersed throughout mesohyl particularly between fibre anastomoses.

**REMARKS.** *Naviculina* is monotypic, and the type species, from Fremantle is characterised by cleistocheles ('naviculoid spiculum' of Bowerbank, 1864), but nothing else was known about the species. de Laubenfels (1936a) considered *Naviculina* dubious, with alleged affinities to *Plocamiosis* (having cleistocheles), although several other nominal genera are also known to have cleistochele microscleres, interpreted as modified palmate isochelae (*Colloclathria*, *Plocamiosis* and *Quizirionia* of the Microcionidae; and *Melonchela* of the Lophonidae). The holotype no longer exists. The holotype slide (Bowerbank, 1864; Gray, 1867) contains a small section of the skeleton (Fig. 19H-I), but enough detail to indicate the Mycalidae, probably *Arenochalina*.

**Paracornulum** Hallmann, 1920

**Paracornulum** Hallmann, 1920: 772.
TYPE SPECIES, *Cornulium dubium* Hentschel, 1912: 346 (by original designation) (holotype SMF964).

Encrusting growth form. Surface smooth, even. Choanosomal skeleton hymedesmoid, with spongin fibres lying on substrate and bases of acanthostyles embedded and spicles standing perpendicular to surface. Subectosomal skeleton radial or plumose, with ascending tracts of erect tonotes. Acanthostyles also scattered throughout mesohyl. Ectosome with tangential tracts of tonotes. Megascleres radial tonotes (with finely rugose bases) and principal acanthostyles (with some oxente or strongylote modifications). Microscleres palmate isochelae and oxthorn toxas.

REMARKS. *Paracornulum* does not appear to be as closely related to microcionids as inferred by Hallmann (1920), showing similarities in possession of echinating acanthostyles, hymedesmoid basal spongin fibres, palmate isochelae and toxas. Two other species referred by Hallmann to this genus (*Cliona purpurea* Hancock and *Subertes fuliginosus* Carter) are very poorly known and further comment on these taxa must await redescription of relevant type material. Based on its ectosomal characteristics and megascle spiculation *Paracornulum* was subsequently referred to Cornulidae (Lévi & Lévi, 1983a: 966). The type species appears close to *Cornulium* Carter, *Iophon* Gray and *Zyzya* de Laubenfels because the ectosomal tonotes are reduced tylothes with rugose (i.e., vestigially microspined) bases. These genera are referred to lophonidae (Hujdu et al., 1994).

*Paresperia* Burton, 1930

*Paresperia* Burton, 1930a: 501.


Irregularly massive, low growth form. Surface even, smooth. Choanosomal skeleton reticulate, with loose, unispicular, irregular reticulation of light spongin fibres cored by auxiliary subtylo- styles, of same geometry as those in subectosomal and ectosomal skeletons. Echinating acanthostyles absent. Subectosomal and ectosomal skeletons lack specialised spiculation, but have loose tangential reticulation of subectosomal auxiliary megascles. Megascleres only auxiliary subtylostyles, entirely acanthose or only basally spined. Microscleres palmate isochelae. Toxas absent.

REMARKS. Burton (1930a) assigned *Paresperia* to the Microcionidae based on supposed affinities to *Artemisina* (*sensu* Burton), having an irregular, confused skeletal architecture composed of undifferentiated choanosomal and ectosomal megascles. The genus differed from *Artemisina* (s.s.) in having lightly and evenly spined auxiliary megascles and lacking toxas. Burton also noted that *Paresperia* had affinities with the Mycalidae, whereas Van Soest & Stone (1986) suggested that the presence of a unispicular choanosomal reticulation of acanthostyles and palmate isochelae placed the genus closer to *Esperiopsis* (placement still controversial in either Mycalidae or Esperiosidae) than to other microcionids.

*Quercictona* de Laubenfels, 1936

*Quercictona* de Laubenfels, 1936: 49.

TYPE SPECIES. *Anthrochalina quercifolia* Keller, 1889: 383 (by original designation) (holotype ZMB429).

Erect, arborescent, flabellate growth form. Surface even, hispid, regularly porous with oscules. Choanosomal skeleton reticulate, with heavy spongin fibres producing tight and irregular meshes, fibres cored by choanosomal principal styles which form primary ascending multisicular (eventually plumose) tracts, and secondary transverse uni- or paucisicular tracts, together producing a subsidictylal reticulation. Axial skeleton slightly different from extra-axial region: near axis skeletal architecture isodictyal, whereas towards periphery skeleton plumose. Echinating megascles absent. Subectosomal skeleton plumose, with brushes of choanosomal principal styles protruding through surface. Ec- tosomal skeleton with brushes of smaller choanosomal styles surrounding one or few larger subectosomal styles. Megascles small smooth choanosomal principal styles, and long smooth subectosomal auxiliary styles. Microscleres absent.

REMARKS. *Quercictona* seems to be a case where inadequate primary taxonomy has been badly misinterpreted. The genus is restricted here to include only *A. quercifolia*, and its association with the Microcionidae rests solely upon the original placement of the type species in *Anthrochalina* (whereby many of the species originally described for the genus by Lendenfeld (1888) are true microcionids). By comparison, de Laubenfels (1936a) originally intended *Quer-
cielona to include Haliclona-like species (Haplosclerida), but this is only true for a second species, Arenochalina arabica Keller (which was subsequently transferred to Arenosclera Pulitzer-Finali (1982), but is probably an arenaceous Callypostra). Conversely, the type species belongs to the Axinellidae.

Antherochalina quercifolia is structurally close to Isosciella (s.s.) and Phakellia of authors. It has an almost regular isodictyal choanosomal reticulation of spongin fibres cored by primary and secondary skeletal lines, without any pronounced compression of the axial skeleton but with some differentiation of the axial and extra-axial skeletons, and it also lacks a specialised ectsosomal skeleton. Details of the holotype (re-examined and redescribed above) bear close resemblance to Keller’s (1889) original description, and it is concluded that Querciclona is most appropriately referred to Phakellia (Axinellidae) (Hooper & Lévi, 1993b). A specimen label in M. Burton’s handwriting accompanying a fragment of the holotype in the BMNH (BMNH 1908.9.24.179) suggests further that A. quercifolia is a synonym of Phakellia donnani (Bowerbank), but this synonymy is far so unsubstantiated.

Scopalina Schmidt, 1862

Scopalina Schmidt, 1862: 78; Gray, 1867: 535.

TYPE SPECIES. Scopalina lophyropoda Schmidt, 1862: 79 (by monotypy) (holotype LMUG15117/154).

Thickly encrusting growth form. Surface prominently conulose. Choanosomal skeleton hymedesmoid, with heavy spongin fibres forming basal layer of spong inon substrate, with ascending non-anastomosing fibre nodes cored by plumose brushes of auxiliary styles. Echinating microscleres absent. Ectsosome lacks specialised spiculation, although brushes of auxiliary styles protrude through surface. Mesohyl matrix heavy. Microscleres only a single category of long auxiliary style. Microscleres absent.

REMARKS. Gray (1867) and de Laubenfels (1936a) suggested that Scopalina was Microciona-like with plumose skeletal architecture and greatly reduced spiculation. Although skeletal architecture is hymedesmoid containing non-anastomosing ('microcionid') fibre nodes, and the possession of only a single category of auxiliary spicules could be construed as reduction of the typical Microciona condition (analogous to Dendrocia (Microcionidae) or Amphilectus s.l. (Myxillidae)), no other characters support its inclusion in the Microcionidae. Boury-Esnault (1971) and Uriz (1982) include it in the Halichondrida, and suggested close affinities with Stylinos.

KEY TO GENERA

1(0). Choanosomal skeleton more-or-less undifferentiated, unstructured

2. Choanosomal skeleton well structured, hymedesmoid to reticulate, but lacking any differentiated components

3. Choanosomal fibres or skeletal tracts cored by one or more category of principal spicules

4. Choanosomal skeleton with noticeably compressed axis and well differentiated axial and extra-axial (radial, plumose or plumoreticulate) regions

5. Choanosomal fibres or skeletal tracts cored by auxiliary spicules identical to those in ectsosomal and subectosomal skeletons

6. Choanosomal fibres or skeletal tracts cored by auxiliary spicules different from those in peripheral skeleton

7. Choanosomal fibres or skeletal tracts cored by auxiliary spicules different from those in ectsosomal and subectosomal skeletons

8. Choanosomal skeleton without any marked axial compression or differentiated axial and extra-axial regions

9. Choanosomal skeleton with noticeably compressed axis and well differentiated axial and extra-axial (radial, plumose or plumoreticulate) regions

10. With single category of (subectosomal) auxiliary spicule on surface forming tangential, paratangential or plumose tracts

11. With two categories of auxiliary spicules, smaller ectsosomal spicules generally overlying larger subectosomal spicules forming discrete bundles or continuous palisade on surface

12. Special category of (acantho)styles present echinating fibres, differentiated from principal spicules
Echinating spicules styles or acanthostyles undifferentiated from principal spicules coring spongin fibres

Holopsammia

6(2). Special category of (acantho)styles present echinating fibres, differentiated from principal spicules.

Clathria (Dendrocia)

Echinating spicules styles or acanthostyles representing principal spicules, but different from those coring fibres

Echinochalinia (Echinochalinia)

Echinating spicules oxeas or anisoxeas representing principal spicules, but different from those coring fibres

Echinochalinia (Protophilataspanga)

7(1). Primary skeleton renieroid cored by axially or basally compressed tracts of acanthostyles, secondary skeleton cored by smooth principal styles in plumose, subsidodictyal or plumoreticular tracts

Antha (Antha)

Primary skeleton renieroid cored by axially or basally compressed tracts of acanthostyles, secondary skeleton cored by smooth principal styles in plumose, subsidodictyal or plumoreticular tracts

Antha (Plocamia)

Primary skeleton axially compressed spongion fibres cored by renieroid tracts of sparsely spined principal styles intermingled with plumose or plumoreticular tracts of smooth principal styles, overlaid by secondary extra-axial plumose skeleton cored by larger smooth principal styles

Antha (Isopeneectya)

Primary renieroid reticulate skeleton cored by smooth principal styles and echinated by identical spicules, with secondary radial extra-axial skeleton on exterior edge of skeleton only cored by larger smooth principal styles

Echinothelia

DESCRIPTION OF AUSTRALIAN SPECIES

Clathria Schmidt, 1862

Refer to subgenera for synonymy.

TYPE SPECIES. Clathria compressa Schmidt, 1862: 58 (designated Schmidt, 1864: 35).

DEFINITION. Monactinal auxiliary spicules in 1 or 2 categories forming ecososomal skeletons ranging from sparse, mostly membraneous (C. (Microciona)), sparse, tangential (C. (Clathria)) to relatively dense, erect (C. (Thalysias)). Echosomal skeletal tracts usually enclosed within spongion fibres, sometimes simply with nodal spongion; fibres cored by smooth, basally spined or partially spined principal monactinal megascleres, usually geometrically different from auxiliary megascleres, sometimes secondarily lost and cored by single category of auxiliary subtylostyle (C. (Dendrocia)), or sometimes replaced partially or fully by detritus in fibres (C. (Wilsonella)). Echinating megascleres partially or entirely acanthose, occasionally smooth or vestigial spination, sometimes secondarily lost (C. (Axociella), C. (Iscioiella)). Echosomal structure ranges from leptoclathrid to microcionid plumose (C. (Microciona)), renieroid (C. (Iscioiella)), plumoreticulate or reticulate, with (C. (Axociella)) or without compressed axis and radial extra-axial regions. Mierascleres include palmate isochelae and modified forms, and toxas with smooth or spined points, occasionally absent.

REMARKS. This definition is necessarily broad to encompass the 7 subgenera included in Clathria, showing a wide spectrum of character states, most of which are interpreted as secondary losses rather than unique apomorphies, and many characters show intermediate states making it virtually impossible to maintain generic boundaries recognised by earlier authors.

Clathria (Clathria) Schmidt, 1862

Clathria Schmidt, 1862: 57.

Allocia Hallmann, 1920: 768.

Antherocholina Lendenfeld, 1887b: 741.

Bipocilopsis Kolton, 1964a: 79.

Dictyociona Topsent, 1913a: 579.

Labacea de Laubenfels, 1936a: 125.

Ligrota de Laubenfels, 1936a: 125.

Litospongia de Laubenfels, 1954: 162.

Marleya Burton, 1931a: 346.


Thalyssepyon de Laubenfels, 1936a: 107.

TYPE SPECIES. Clathria compressa Schmidt, 1862: 58 (by subsequent designation of Schmidt, 1864).

DEFINITION. Ectosomal skeleton composed of a single undifferentiated category of auxiliary megasclere; echinosomal skeletal structure plumoreticulate or reticulate, usually without marked difference between axial and extra-axial regions; spongion fibres cored by completely smooth, basally spined or partially spined principal megascleres, geometrically differentiated from auxiliary megascleres, but sometimes secondarily lost; echinating megascleres entirely or partially acanthose, occasionally smooth, sometimes secondarily lost. Mierascleres include palmate isochelae and modified forms, and toxas with smooth or spined points.
TABLE 1. Comparison between present and published records of Clathria (Clathria) angulifera Dendy. Measurements in μm, denoted as range (and mean) of spicule length × spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (NMV2286) (Victoria)</th>
<th>Specimens (N=2) (SEQ, Queensland)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>144-(172.4)-211 x 3-(4.3)-6</td>
<td>128-(141.3)-150 x 3-(3.8)-5</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>168-(175.0)-216 x 2.5-(3.6)-4.5</td>
<td>181-(195.8)-223 x 2-(2.3)-5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>58-(64.2)-72 x 3.5-(4.1)-4.5</td>
<td>58-(61.8)-72 x 2-(3.3)-5</td>
</tr>
<tr>
<td>Chelae</td>
<td>5.5-(7.1)-8.5</td>
<td>5-(6.7)-9</td>
</tr>
<tr>
<td>Toxic</td>
<td>18-(67.4)-101 x 0.5-(1.7)-3.3</td>
<td>absent</td>
</tr>
</tbody>
</table>

REMARKS. Of the 154 named species described in, or subsequently referred to Clathria, or one of its synonyms listed above, 112 are retained in this subgenus. There are 31 (2 new) species known from Australian waters.

Clathria (Clathria) angulifera Dendy, 1896 (Figs 26-27, Plate 1A, Table 1)


HABITAT DISTRIBUTION. Submerged rock reef; 10-30m depth; Bass Strait (Vic), N. Stradbroke 1 and Noosa Heads (SEQ) (Fig. 26C).

DESCRIPTION. Shape. Thickly lamellate, approximately 9 cm long, 30mm wide, 50mm high, with numerous bulbous lobate digits up to 15mm long.

Colour. Bright yellow-orange alive (Munsell 2.5Y 8/10), grey-brown in ethanol.

Oscules. Occasional large oscules, 1.5-3mm diameter, on edges and between lobes.

Texture and surface characteristics. Firm, compressible; glabrous skin-like surface.

Ecotome and subectosome. Ecotomal skeleton membraneous, with loose, irregular, tangential, occasionally paratangential or erect tracts of subectosomal auxiliary subtylote styles; rarely protruding above surface. Subectosomal portion of peripheral skeleton slightly plumose, with sparse diverging brushes of auxiliary megascleres which arise from ascending choanosomal tracts.

Choanosome. Choanosomal skeleton regularly reticulate, cavernous, vaguely renieroid; fibre anastomoses produce wide oval, rectangular or sometimes slightly triangular meshes; spongin fibres thin, only lightly invested with spongin, barely differentiated from mesohyl matrix; spongin fibres cored by uni- or paucispicular tracts of choanosomal principal megascleres; echinating acanthostyles sparsely dispersed on fibres; mesohyl matrix heavy, lightly pigmented, containing few straight or sinuous subectosomal auxiliary megascleres and abundant spherical incubated larvae (275-345μm diameter) with well differentiated cellular development.

Megascleres (Table 1). Choanosomal principal styles short, thin, fusiform, straight or slightly curved towards basal end, with rounded or only slightly subtylote, smooth bases.

Subectosomal auxiliary subtylote styles straight, thin, relatively long, almost bastate, with smooth and only slightly subtylote bases.

Acanthostyles small, thin, prominently subtylote, with rudimentary granular spinulation and small aspinose 'neck' near basal constriction.

Microscleres (Table 1). Palmate isochelae very small, weakly silicified, unmodified.

Toxas not common, relatively large, v-shaped, with sharply angular central curvature and straight arms.

REMARKS. The thickly lamellate, lobate growth form, glabrous surface, relatively open, slightly renieroid, paucispicular skeletal structure (cf. Dendy, 1896), and aspects of spiculation in C. (C.) angulifera are quite distinctive and unusual amongst microcionoids (cf. Hallmann, 1912). Many of these features are similar to those in C. (T.) aphylla sp. nov. from the Houtman Abrolhos, WA, although the latter has a specialised ecotosomal skeleton and hence is included in C. (Thalysias) rather than C. (Clathria). These species together with C. (C.) hispidula are sister species belonging to a species group termed here 'angulifera' group. They are compared in detail in discussion on C. (T.) aphylla.

This species is also slightly reminiscent of C. (C.) connectens, differing in that megascleres coring fibres are true principal spicules rather than just undifferentiated auxiliary spicules (albeit these differences are not as well marked in C. (C.) angulifera as in many other species of Clathria). This reduction in coring spicules was interpreted by Hallmann (1912) to be chara-
teristic of C. (Wilsonella) (although this is shown here to be an erroneous interpretation of Wil-sonella). De Laubenfels (1936a) also transferred C. (C.) angularis to Thalysia; but this was completely unjustified.

Although known only from 2 widely separated localities it is probable that it is more widely distributed within shallow coastal waters in southeastern Australia.

Clathria (Clathria) arcuophora Whitelegge, 1907 (Figs 28-29)

Clathria arcuophora Whitelegge, 1907: 491, 500-501. pi.45, fig.29; Hallmann, 1912: 211, 229, 234-237, 260, 263, text-fig. 49-49a; Hooper & Wiedenmayer, 1994: 258.

Thalysia arcuophora, de Laubenfels, 1936a: 105.

Microciona arcuophora; Vosmaer, 1935a: 611, 649, 665.

MATERIAL. LECTOTYPE: AMG 4346: Off Barra-njoey, S. coast of NSW, 33°35’S, 151°20’E, 50-60m depth, coll. FIV ‘Thetis’ (dredge). PARALEC-

TYPTE: AMZ 1209: Off Botany Bay, NSW, 34°00’S, 151°11’E, 40-46m depth, coll. FIV ‘Thetis’ (dredge).

HABITAT DISTRIBUTION. Depth range 30-90m; substrate unknown; central and S. coast of NSW (Fig.

DESCRIPTION. Shape. Thinly flabelliform, 170mm long, 120mm maximum breadth, up to 4mm thick, with long cylindrical stalk, 90mm long, 13mm diameter, and rounded or slightly lobate margins. Colour. Grey-brown in dry state.

Oscules. Surface covered with evenly distributed minute oscules, up to 1.5mm diameter.

Texture and surface characteristics. Harsh in dry state; surface optically smooth.

Ectosome and subectosome. Ectosome microscopically bispic, with regularly distributed choanosomal principal styles forming erect plumose brushes, and protruding from peripheral fibre endings; tangential layer of subectosomal auxiliary spicules lying on or just below surface, at base of principal styles. Subectosome with only slightly plumose tracts of choanosomal megascleres, virtually undifferentiated from choanosomal skeleton.

Choanosome. Choanosomal skeleton more-or-less regularly reticulate, sub-renieroid; axial skeleton slightly compressed, peripheral skeleton slightly plumo-reticulate; branching between moderately heavy spongion fibres produces ovoid to square meshes, and fibres differentiated into primary ascending and secondary transverse components; primary fibres with pauci- to multispicular core of choanosomal principal styles; secondary fibres with uni- or bipincurar tracts of principal spicules; echinating acanthostyles sparse, slightly more abundant on peripheral fibres; mesohyl matrix light, with only few subectosomal auxiliary megascleres dispersed between fibres.

Megascleres. Choanosomal principal styles thick, slightly curved, slightly fusiform, with rounded smooth bases. Length 176-(258.4)-

444µm, width 12-(22.2)-27µm.

Subectosomal auxiliary stylostyles small, thin, straight, with smooth or microspined bases, bases slightly subtyloite, points fusiform. Length 192-(231.1)-276µm, width 3.5-(4.8)-6µm.

Acanthostyles small, slightly subtyloite, with relatively even granular spination. Length 68-(93.2)-104µm, width 6.5-(7.5)-10µm.


Toxas intermediate between oxeote and oy-horn, thick, gently curved at centre, with straight arms or slightly reflexed points. Length 28-(104.0)-132µm, width 1.5-(4.8)-6µm.

REMARKS. This species is distinctive by its renieroid choanosomal skeleton, plumo-reticulate subectosomal skeleton, distinctive spongion fibres which contain only few but very thick coring spicules, and an ectosomal region which is dominated by plumose brushes of principal spicules. The renieroid skeletal construction is superficially similar to Antho (Isopecena) and Clathria (Isoscella), and several other (otherwise unrelated) groups (some Raspailiidae (e.g., Ectyplasia), Axinellidae (e.g., Axinella arnensis (Hentschel, 1912)), lophophorididae (e.g., Acans) and Myxillidae (Lissodendoryx) (see also remarks for C. (C.) crassa). Clathria (C.) arcuophora is most reminiscent of Ectoplasiadronso (Lendenfeld) (Raspailiidae; see Hooper, 1991: figs 47-48), which was originally described in the Microcionidae, having closely comparable architecture, fibre characteristics and geometry of some spicules. Within the Microcionidae, C. (C.) arcuophora is also similar to C. (C.) bicalathara in spicule geometry and fibre characteristics, although there are substantial differences between them in skeletal construction. The species should also be compared to C. (C.) striata, which differs mainly in the morphology of its toxo.
Clathria (Clathria) bieclathrata sp. nov.  
(Figs 30-31, Table 2)  


*Clathria clathrata*; Hallmann, 1912: 209.  

*Dictyociona clathrata*; de Laubenfels, 1936a: 110.  

*Thalysia clathrata*; de Laubenfels, 1953: 527.  

Not *Tenacia clathrata* Schmidt, 1870: 56,80.  

Not *Clathria clathrata*; Vosmaer, 1880: 153; Ridley & Dendy, 1887: 147; Wilson, 1902: 397-398; Alcoado, 1976: 5.
TABLE 2. Comparison between present and published records of Clathria (Clathria) biclathrata, sp. nov. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMG4355)</th>
<th>Paralectotype (AMG10530)</th>
<th>Specimen (N=1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>253-(372.3)-446 x 18- (22.8)-33</td>
<td>226-(337.5)-423 x 17- (22.6)-28</td>
<td>233-(319.8)-418 x 14- (17.8)-24</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>132-(214.0)-293 x 2-(4.9)-7</td>
<td>125-(165.4)-243 x 3-(5.5)-7</td>
<td>144-(197.0)-253 x 3-(4.6)-7</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>73-(158.4)-231 x 4.5-(14.7)-19</td>
<td>114-(161.1)-193 x 11-(13.6)-18</td>
<td>113-(150.2)-193 x 8-(12.4)-16</td>
</tr>
<tr>
<td>Chelae</td>
<td>7-(10.4)-14</td>
<td>6-(8.6)-11</td>
<td>4-(7.8)-12</td>
</tr>
<tr>
<td>Toxas I</td>
<td>28-(93.0)-149 x 0.8-(2.4)-3.5</td>
<td>43-(102.8)-141 x 1.8-(2.8)-3.5</td>
<td>38-(66.6)-104 x 1-(2.7)-4</td>
</tr>
<tr>
<td>Toxas II</td>
<td>4-(10.2)-18 x 0.8-(1.7)-2.0</td>
<td>6-(18.0)-36 x 0.8-(1.9)-2.5</td>
<td>3-(12.4)-24 x 0.5-(1.4)-2.0</td>
</tr>
</tbody>
</table>


HABITAT DISTRIBUTION. Up to 112m depth, substrate unknown; S. coast of NSW (Fig. 30H).

DESCRIPTION. Shape. Clavulate to subspherical, bushy, honeycombed mass, 85-105mm high, 30-55mm wide, up to 40mm maximum thickness, composed of numerous thin, cylindrical, tightly anastomosing branches; small cylindrical stalk, 8-15mm long, up to 8mm diameter.

Colour. Live colouration unknown, grey-brown to dark brown in dry state.

Oscules. Small oscules, 1-2.5mm diameter, on edges of surface microconules.

Texture and surface characteristics. Surface very hispid, minutely porous, with numerous slightly elevated microconules; texture unusually tough. Ectosome and subectosome. Ectosomal skeleton a tangential layer of subectosomal auxiliary styles in multispiricular tracts, with numerous choanosomal principal spicules protruding and extending a long way through surface; subdermal skeleton, if present, totally obscured by dense mass of erect choanosomal megascleres.

Choanosome. Choanosomal skeletal architecture irregularly reticulate, slightly reniform, with heavy spongin fibres forming tight meshes, and some compression of axial fibres; spongin fibres not clearly divisible into primary or secondary components, but merely ascend and diverge towards surface; fibres mostly aspicular, sometimes with one or few choanosomal principal subtylostyles in core, heavily echinated by both acanthostyles and choanosomal principal subtylostyles (the latter 'spicate' in arrangement), and some intermediate spicules with rudimentary spines on shaft; echinating megascleres most abundant on peripheral fibres; mesohyl matrix heavy, with few subectosomal auxiliary subtylostyles between meshes.

Megascleres (Table 2). Choanosomal principal subtylostyles slightly curved or straight, fusiform, slightly constricted at base, heavily spined bases (smaller examples may also have scattered spines on shafts).

Subectosomal auxiliary subtylostyles short, fusiform, straight, with slightly subtylole microspined bases.

Acanthostyles relatively long, thick, slightly curved, with prominent subtylole bases, with evenly distributed large spines over entire spicule or with an aspincous region proximal to base.

Microscleres (Table 2). Palmate isocheleae, some twisted.

Toxas include larger thick wing-shaped forms with large central curvature, slightly reflexed arms and microspined points, and smaller oxhorn forms, the smallest with abbreviated arms.

REMARKS. This species is characterised by its compressed skeletal architecture, fibre and ectosomal features, and is unlikely to be confused with other members of Hallmann’s (1912) spicata group of microcionid species (cf. Hooper et al., 1990) which have principal spicules protruding through fibres and surface skeletons but few within fibres themselves. A feature overlooked by previous authors is the presence of spinous extremities on toxas, which are virtually identical to those of type species of Clathria, C. (C.) compressa, also occurring in C. (C.) juncea, C. (C.) lobata, and Artemisina suberoides. The geometry of spicles in C. (C.) biclathrata is similar to those in C. (C.) arcuophora, although these species differ quite substantially in their skeletal architecture.

Clathria (Clathria) caelata Hallmann, 1912
(Figs 32-33, Table 3)

Clathria caelata Hallmann, 1912: 139, 177, 206, 211-216, pl.33, fig.4, text-fig.43; Hooper & Wiedenmayer, 1994: 258.

Clathria caelata; Burton & Rao, 1932: 336 [lapses].

Pseudanchniae caelata; de Laubenfels, 1936a: 109.

Not *Clathria inanchorata* Ridley & Dendy, 1886: 475; Ridley & Dendy, 1887: 150, pl.28, fig.4, pl.29, figs 13,13a.


MATERIAL. LECTOTYPE: AMZ778: (wet) 64km W. of Kingston, SA, 36°50’S, 139°05’E, 60m depth, coll. FIV ‘Endeavour’ (dredge; label ‘4th consignment’). PARALECTOTYPES: AME53: (dry) same locality. AMZ952-953: unspecified locality, W. coast Tas. (ref. G255’). OTHER MATERIAL: TAS-AME2273.

HABITAT DISTRIBUTION. Depth 53-106m; substrate unknown; Kingston (SA), Bass Strait (Vic), Cape Barren, W coast (Tas) (Hallmann, 1912).

DESCRIPTION. Shape. Planar or multiplanar, digitate fans, 110-150mm high, 70-90mm wide, with short cylindrical stalk, 8-17mm long, 5-
10mm diameter, rounded lobate, or digitate margins.

**Colour.** Light to dark brown preserved.

**Oscules.** Small pores on margins of lobes, up to 1.5mm diameter.

**Texture and surface characteristics.** Surface highly rugose, with numerous close-set microconules, subdermal canals and grooves, between which extends a skin-like dermal membrane; texture firm, compressible.

**Ectosome and subectosome.** Ectosome microscopically hispid, with plumose brushes of choanosomal principal styles protruding through surface, and with thin layer of subectosomal auxiliary styles tangential to surface; subdermal region not markedly differentiated from choanosome containing bundles of diverging principal styles embedded in peripheral fibres; peripheral fibres heavily echinated on their exterior surfaces; acanthostyles may extend into ectosomal skeleton.

**Choanosome.** Choanosomal skeletal architecture irregularly reticulate, with well developed spongine fibres forming ovoid to elongate meshes; fibre anastomoses relatively cavernous in axis, although smaller in peripheral skeleton; fibres clearly differentiated into primary ascending and secondary transverse components, although fibre diameter is consistent throughout skeleton: primary fibres contain pauci- or multispiral tracts of choanosomal principal subtylostyles, forming a radial architecture; secondary fibres uni- or aspicular; spongine fibres echinated on external surfaces only, with a variable density of echinating acanthostyles, mostly relatively light except at the periphery; choanosomal styles also echinate fibres, particularly at fibre nodes; mesohyl matrix moderately heavy, granular, pigmented; extra-fibre mesogloea (subectosomal subtylostyles) usually abundant.

**Megascleres** (Table 3). Choanosomal principal subtylostyles thick, straight or slightly curved, fusiform, with slightly subtylote smooth bases, although some examples are obvious intermediates to echinating acanthostyles, bearing rudimentary spines on the shaft.

Subectosomal auxiliary subtylostyles straight or slightly curved, fusiform, relatively thin, evenly rounded or slightly subtylote bases, and smooth or micropinned bases.

Echinating acanthostyles variable in length, subtylote, with evenly spined shafts on smaller forms, or with aspinose necks on larger forms.

**Microscleres** (refer to Table 3 for dimensions). Isochelae absent.

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMEZ778)</th>
<th>Paraleotype (AMEZ53)</th>
<th>Specimen (N=1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>148(215.4)-176 x 8(12.2)-16</td>
<td>154(222.2)-262 x 9(11.8)-14</td>
<td>186(254.5)-353 x 6(9.4)-10</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>128(216.4)-294 x 2(3.2)-5</td>
<td>134(234.8)-324 x 3(4.6)-7</td>
<td>166(267.9)-355 x 2(3.5)-7</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>45(71.9)-122 x 2(5.1)-8</td>
<td>64(89.4)-131 x 4(6.4)-8</td>
<td>23(64.4)-120 x 2(4.8)-18</td>
</tr>
<tr>
<td>Chelae</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Toxas I</td>
<td>122(151.7)-190 x 0.5(1.1)-1.5</td>
<td>72(101.8)-165 x 0.8(1.4)-2</td>
<td>86(121.1)-165 x 0.5(1.1)-2</td>
</tr>
<tr>
<td>Toxas II</td>
<td>21(55.9)-83 x 1(2.3)-4</td>
<td>24(48.2)-92 x 1(2.1)-3.5</td>
<td>13(38.8)-75 x 1(2.2)-4</td>
</tr>
</tbody>
</table>

Toxas separated into two morphs: I - long, thin accolada toxas, with straight points and slight central curvature; II - relatively thick oxhorn toxas, ranging from almost straight with only slight and angular central curvature, to widely curved at the centre with reflected points.

**REMARKS.** Not all of the specimens described by Hallmann (1912) belong to this species: AME771, B772 and E773 are species belonging to Axinellidae - Reniochalina (2 specimens) and Acanthella, respectively. All three specimens look very similar in external morphology to C. (C.) caelata, but differences are immediately obvious upon examination of the skeleton.

Among the few known specimens of this species there is relatively high variability in choanosomal skeletal construction although this is difficult to define concisely. The development of spongine fibres, the degree to which the skeletal meshes are compressed or elongated, and the density and pigmentation of the mesohyl matrix may vary between specimens. Growth form and spicule geometry appear to be closely comparable between all specimens, but some (e.g., AME2273) have predominantly long thin toxas, whereas others (e.g., AMZ952) have mostly short and thick toxas. All specimens have both choanosomal styles and acanthostyles echinating fibres, and in this respect the species belongs to Hallmann's (1912) 'spicata' group, together with Clathria (C.) biclathrata, C. (C.) inanchorata, C. (Thylasiacia) costifera, C. (T.) coppingeri, C. (T.) lendenfeldi and others (Hooper et al., 1990).
Clathria (Clathria) calopora Whitelegge, 1907

Clathria calopora Whitelegge, 1907: 499-500, pl.46, fig.34; Hallmann, 1912: 211; Hooper & Wiedenmayer, 1994: 259.

Thalysias calopora; de Laubenfels, 1936a: 105.

MATERIAL. HOLOTYPE: AM (presently missing): Shoalhaven Bight, NSW, 34°49'S, 151°04'E, 30-90m depth, 1.vii.1911, coll. FIV 'Endeavour' (trawl).

HABITAT DISTRIBUTION. Depth 27-32m, substrate unknown; S. coast of NSW.

DESCRIPTION. Shape. Branching, 195mm high, with thin, bifurcate, cylindrical, mostly non-anastomosing digits, 3-8mm diameter, with tapering points, short cylindrical stalk.

Colour. Live colouration unknown, greyish-yellow preserved.

Oscules. Small oscules, about 1mm diameter, scattered over surface.

Texture and surface characteristics. Surface uneven, minutely hispid, honeycomb-like, with prominent bulbous conulose processes scattered over surface; texture hard, incompressible in dry state.

Ectosome and subectosome. Ectosome microscopically rugose, close-meshed reticulation of peripheral spongin fibres covered by a thin membrane; ectosomal skeleton with a thin tangential layer of subectosomal auxiliary subtylestyles, also forming plumose tufts on surface, through which choanosomal principal styles from peripheral fibres protrude, individually or in plumose brushes; subdermal auxiliary megascleres run parallel with peripheral fibres, but not forming organised extra-fibre tracts.

Choanoosome. Choanosomal skeleton irregularly reticulate, with some axial and extra-axial differentiation; spongin fibres relatively heavy, clearly divided into primary ascending and secondary transverse components; primary fibres sinuous, forming radial architecture, with a paucispicular core of choanosomal principal styles; primary fibres more compressed at axis than at periphery; secondary fibres less common, with uni- or paucispicular core of megascleres; branching of spongin fibres produces elongate meshes in axis and round or rectangular meshes in periphery; spongin fibres very heavily echinated, particularly in peripheral regions; numerous sinuous toxodragmata dispersed in mesohyl between fibres.

Megascleres. Choanosomal principal styles thick, slightly curved, fusiform, with rounded smooth bases. Length 300-500μm, width 15-22μm.

Subectosomal auxiliary subtylestyles thin, straight or slightly curved, with smooth slightly subtyle bases. Length 150-200μm, width 2-4μm.

Acanthstyles short, stout, evenly spined, spines large. Length 30-80μm, width up to 12μm.

Microscleres. Palmate isochelae. Length 8-10μm.

Toxa morphology unknown, apparently long, slender, with large central curvature. Length ? 200-300μm, width ? up to 2μm.

REMARKS. This species is known only from Whitelegge's (1907) poor description. It is not possible to determine whether dimensions of echinating acanthostyle (cited as 0.3-0.8mm long by Whitelegge) is merely a typographical error. Whitelegge gave no indication of whether C. (C.) calopora has a special ectosomal skeleton, but described the species as having a tangential or paratangential layer of subdermal (auxiliary) megascleres, through which protrude choanosomal (principal) styles. Consequently, there was no justification for de Laubenfels (1936a) referring the species to Thalysias.

Clathria (Clathria) chelifera (Hentschel, 1911) (Figs 34-35, Table 4)


Allocia chelifera; Hallmann, 1920: 768; Bergquist & Fromont, 1988: 96, fig. 8e, pls 45e-f, 46a-c, table 73; Dawson, 1993: 44 (note).

Clathria chelifera; Dendy, 1922: 70-71, pl.14, fig. 3a-c; Hooper & Wiedenmayer, 1994: 259.

Not Microciona chelifera Lévi,1960a: 70, fig.12.


HABITAT DISTRIBUTION. 10-100m depth; rock or gravel substrates; Arafura Sea (NT) and Perth region (S. WA) (Fig. 34F). Also Indian Ocean (Amirante), New Zealand (Three Kings Is) and South China Sea (Hon Trung Lon, Vinh Loi coast, S. Vietnam).

DESCRIPTION. Shape. Arborescent, foliose, planar growth form, up to 50mm high made up of fused porous-reticulate lamellae 10-15mm thick.
TABLE 4. Comparison between present and published records of Clathria (Clathria) chelifera (Hentschel).
All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Chaanoosomal principal styles</td>
<td>140(190.1)-161 x 4(6.1)-7</td>
<td>270(404)-550 x 15(18)-20</td>
<td>192(164.6)-174 x 4(6.4)-10</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>173(193.4)-203 x 2(3.9)-5</td>
<td>280(334)-375 x 4(5)-6.5</td>
<td>192(204.6)-212 x 4(6.4-7)</td>
</tr>
<tr>
<td>Clathinating acanthostyles</td>
<td>84(93.2)-100 x 7(7.8)-9</td>
<td>162(207)-290 x 12.5(14)-19</td>
<td>192(165.5)-132 x 4(6.4)-10</td>
</tr>
<tr>
<td>Celia I</td>
<td>13(14.6)-1</td>
<td>20(21)-23</td>
<td>15(17.6)-20</td>
</tr>
<tr>
<td>Celia II</td>
<td>7(8.7)-10</td>
<td>absent</td>
<td>9(10.3)-12</td>
</tr>
</tbody>
</table>

- **Colour.** Red alive (10R 5/8), beige or yellow brown in ethanol.

- **Oscules.** Not seen.

**Texture and surface characteristics.** Surface hispid, uneven, irregularly conulose, with transparent ectosomal membrane stretched between adjacent conules; texture firm, compressible.

**Ectosome and subectosome.** Ectosomal skeleton with a tangential layer of auxiliary tylostyles and numerous isochelae scattered between adjacent conules; texture firm, compressible.

**Chaanoosomal and subectosomal.** Chaanoosomal skeleton with a tangential layer of auxiliary tylostyles and numerous isochelae scattered between adjacent conules; texture firm, compressible.

**Ectosomal and subectosomal.** Ectosomal skeleton with a tangential layer of auxiliary tylostyles and numerous isochelae scattered between adjacent conules; texture firm, compressible.

**Ectosome and subectosome.** Ectosomal skeleton with a tangential layer of auxiliary tylostyles and numerous isochelae scattered between adjacent conules; texture firm, compressible.

**Megascleres** (Table 4). Principal styles slender, slightly curved near basal end, with abrupt hastate points, and completely smooth.

Subectosomal auxiliary spicules tylostyles or quasitylotes, asymmetrical (and therefore probably modified styles), usually with microspined bases and points or sometimes completely smooth at both ends.

Echinating acanthostyles with spinose shaft, base and point but spinose 'neck'; spines large, recurved.

**Microscleres** (Table 4). Palmate isochelae of two sizes, both with thickened and elongate alae.

Toxas are absent.

**REMARKS.** Dimensions of some spicules were found to differ in type material (Table 4) from those published by Hentschel (1911). Similarly, two size classes of isochelae were found in the WA population, not one as described by Hentschel (1911). In both respects this population is the same as the one described from Amirante (Dendy, 1922) and the material described above from Vietnam, whereas the specimen described by Bergquist & Fromont (1988) from New Zealand has substantially larger spicule dimensions than either of the Indian Ocean populations, including only one size class of isochela. In spicule geometry, chaanoosomal skeletal structure and ectsosomal characteristics (including the distribution of isochela in the ectsosomal membrane), these 4 disjunct populations are relatively homogeneous and I follow Bergquist & Fromont (1988) in recognising only a single species. No intermediate populations of *C. (C.) chelifera* are known, and the species is relatively rare with only few known specimens in the Indo-West Pacific.

This species is unusual to most *C. (Clathria)* in possessing modified auxiliary spicules with spines on both ends, considered by some authors to be true tylostyles typical of the Myxillidae (Hallmann, 1920; Bergquist & Fromont, 1988) or Iophonidae (Hajdu et al., 1994). But these spicules are clearly asymmetrical (quasitylotes), not true diactinal megascleres, and Dendy (1922) correctly assigned this species (and thus the genus *Allocia* to *Clathria*). These modified quasidiactinal auxiliary spicules are infrequent but known in several other microcionids (e.g., *C. (C.) bulbosa*, *C. (Thalysias) major*, *C. (Dendroclathria) pyramidica*, *A. (Wilsonella) australiensis*, most *Echinochalinia*, some *Holopzxanna*, and some *Echinoclathria* species).

*Clathria* (Clathria) *conectens* (Hallmann, 1912) (Figs 36-37, Plate 1B. Table 5)

Wilsonella *connexens* Hallmann, 1912: 245-247, pl.32, fig.2, text-fig.50.

*Clathria* *connexens*; Hallmann, 1920: 768; Hooper & Wedemayer, 1994: 259.

**MATERIAL.** LECTOTYPE: AMZ220: (dry) 16km E of Fraser J., Qld, 25°22'S, 153°07'E, 48-52m depth,
coll. FIV ‘Endeavour’ (dredge). PARALECTOTYPE: AME1533 (dry; presently missing): same locality. OTHER MATERIAL: QUEENSLAND - QMG-300455, QMGL714 (fragment NTMZ1537), QMGL2757 (fragment NTMZ1564), QMGL2770 (fragment NTMZ1581), QMG301037, QMG303190, QMG303217, QMG304980, QMG304985, QMG305135, QMG304005, QMG304016. NEW SOUTH WALES - QMG301387.

HABITAT DISTRIBUTION. Acropora coral reef, fringing rock reef, boulders, algal turf, wharf pylons; inshore waters, 4-80m depth; Green L., S. Direction L., Innisfail (FNQ), Fraser I., Mudjimba I., Moreton I., N. Stradbroke I., Moreton Bay (SEQ), and Byron Bay (N. NSW) (16-28S) (Fig. 36G).

DESCRIPTION. Shape. Massive, subcylindrical mass 40-65mm high, 85-120mm broad, composed of irregularly reticulate, lamellate bulbous branches, up to 15mm diameter, standing erect on substrate.

Colour. Live colouration bright orange-yellow to bright orange-red (Munsell 2.5YR 7/10-10R 6/10), brown in ethanol.

Oscules. Small oscules, up to 1.5mm diameter, on edges and tips surface bulbs.

Texture and surface characteristics. Surface uneven, porous, optically smooth.

Ectosome and subectosome. Ectosome with tangential or paratangential layer of thin subectosomal auxiliary stylolytostyles, on or just below a membraneous dermal layer; subectosomal auxiliary styles confined entirely to peripheral skeleton; subectosomal skeleton virtually non-existent, with only few erect, plumeose choanosalional principal styles, arising from peripheral choanosalional spong fibre, projecting into tangential ectosomal layer.

Choanosome. Choanosomal skeleton irregularly reticulate, with regular circular, oval or elongate meshes enclosing small oval choanocyte chambers; spong fibre relatively heavy, without size differentiation of primary or secondary components, although ascending (primary) skeletal fibres cored by paucispicular or multispiicular tracts of choanosalional styles, whereas connecting, transverse (secondary) fibres uni-, pauci- or entirely aspicular; echninating acanthostyles sparse, scattered evenly throughout skeleton, occasionally incorporated into fibres; mesohyl matrix very light, some choanosalional styles scattered between fibres; some specimens also incorporating detritus into mesohyl, but not into fibres. Megascleres (Table 5). Choanosalional principal styles thin, fusiform, occasionally stylloid, slight-ly curved, with rounded or very slightly subtylote, smooth bases.

Subectosomal auxiliary stylolytostyles slightly curved, sometimes sinuous, exceedingly thin, hastate, almost vestigial, with very slightly subtylote, smooth bases.

Acanthostyles subtylote, with more-or-less evenly distributed vestigial (granular) spination. Microscleres (Table 5). Palmate isochelae small, unmodified.

Toxas accolada rare, thin, with sharply angular central curvature and straight arms.

REMARKS. Specimen AMZ220 is designated lectotype (labelled ‘cotype of Wilsonella conectens, duplicate of E1533’) as the latter specimen is presently missing from AM collections. Despite Hallmann’s (1912) remarks to the contrary C. (C.) conectens is clearly different from C. (C.) angulifera (see above), although both species do fit into his (erroneous) concept of Wilsonella. Moreover, in C. (C.) conectens the megascleres which core fibres (choanosalional styles) are differentiated from those occurring in the dermal skeleton (subectosomal styles), and although their geometry is very similar, they have very different morphology (see Fig. 36) and thickness (see Table 5). Each category of spicule is localised in the choanosalional and ectosomal regions, respectively, and they are not intermingled as supposed by Hallmann (1912). The entire spiculation of this species is reduced, and for that reason it is easily recognisable. This species is a common member of the Solanderian-Peronian biogeographical overlap zone centred around Moreton Bay, Queensland.

### TABLE 5. Comparison between present and published records of Clathria (Clathria) conectens (Hallmann).

<table>
<thead>
<tr>
<th>Spicule</th>
<th>Lectotype (AMZ220)</th>
<th>Specimens (N=7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>94(168.4)-268 x 2.5(4.1)-5</td>
<td>110-(171.4)-218 x 3(4.3)-6</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>92(171.3)-219 x 1.5(2.9)-4</td>
<td>174-(230.6)-295 x 1.5(2.4)-3.5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>48(58.3)-65 x 3(3.7)-5</td>
<td>36(64.2)-78 x 2(3.9)-5</td>
</tr>
<tr>
<td>Chelae</td>
<td>6(7.2)-8</td>
<td>4.5(6.7)-9</td>
</tr>
<tr>
<td>Toxas</td>
<td>22(69.8)-111 x 0.5(0.9)-1.5</td>
<td>51(102.6)-164 x 0.5(0.7)-1.0</td>
</tr>
</tbody>
</table>

**Clathria (Clathria) crassa** (Lendenfeld, 1887) *(Figs 38-39)*

Antherochalina crassa Lendenfeld, 1887: 787, pl.22, fig.41.  
Clathria crassa; Burton, 1934a: 558; Hooper & Wiedenmayer, 1994: 259.  
Microciona or Thalysias crassa; de Laubenfels, 1936a: 112.  
Not Reniera crassa Carter, 1876: 312.  
Not Aulena crassa; Lendenfeld, 1889a: 101.

**MATERIAL.** HOLOTYPE: BMNH1886.8.27.450 (fragments AMG3460, AMZ1991): Port Jackson, NSW, 33°51'S, 151°16'E, other details unknown.

**HABITAT DISTRIBUTION.** Ecology unknown; central coast NSW.

**DESCRIPTION.** Shape. Thin fan, 230mm high, 190mm maximum width, up to 8mm thick, with short stalk, 25mm long, digitate margins.

Colour. Live colouration unknown, grey-brown in ethanol.

Oscules. Small pores seen on both faces of fan, 1-2mm diameter, with subdermal drainage canals surrounding oscules.

Texture and surface characteristics. Surface smooth, not optically hispid, with stellate sculpturing on both faces of fan (associated with aquiferous system); texture firm, flexible.
**Ectosome and subectosome.** Ectosome microscopically hirsute, with points of large choanosomal principal styles from peripheral fibres protruding through surface in plumose brushes; thin tangential layer of subectosomal auxiliary subtlystles lying on or just below surface, at base of protruding choanosomal megscleres.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with slightly renieroid axis and plumoreticulate extra-axis; spongin fibres in axis flattened, very heavy, running longitudinally through lamellae; axial fibres clearly divisible into primary (longitudinal) and secondary (ascending, connecting) components; primary fibres cored by paucispicular tracts of principal choanosomal styles; secondary fibres unispicular; extra-axial skeleton diverges from axis at an oblique angle, with moderately heavy fibres, divided into primary (multispicular, ascending) and secondary (unispicular, transverse) elements; choanosomal principal styles project from primary fibres in plumose tracts; secondary fibres connect ascending primary lines, producing renieroid reticulation, except at periphery where architecture is distinctly plumose; echinating acanthostyles moderately common, evenly distributed throughout skeleton; mesobyal matrix abundant, containing few microscleres but few loose megscleres.

**Megascleres.** Choanosomal principal styles thick, fusiform, slightly curved, with rounded or slightly subtlyote, smooth bases. Length 184-292.3-463 \( \mu \)m, width 9(17.5)-22 \( \mu \)m.

Subectosomal auxiliary subtlystles thick, straight, fusiform, with microspined subtlyote bases. Length 118-226.7-316 \( \mu \)m, width 3(4.8)-6 \( \mu \)m.

Acanthostyles short, thick, subtlyote or rounded, with evenly dispersed vestigial (granular) spination. Length 51-(66.3)-82 \( \mu \)m, width 5(6.5)-9 \( \mu \)m.

**Microscleres.** Palmate isochelae large, unmodified. Length 17(19.5)-23 \( \mu \)m.

Toxas oxhorn, thick, with rounded central curvature, slightly reflexed points although the smaller ones may lack reflexed points and are intermediate between oxhorn and u-shaped forms. Length 28(68.0)-112 \( \mu \)m, width 0.8(2.6)-4.5 \( \mu \)m.

**Remarks.** Burton (1934a) designated *A. crassa* type species of *Anthitherechinula*, and subsequently declared that the genus was a synonym of *Clathria*. Lendenfeld’s (1887b) brief description of *A. crassa* is vague and not very useful in distinguishing it from other *Clathria*, but type material is still extant and recognisable. However, there is little agreement between characters in the type material and as described by Lendenfeld, *C. (C.) crassa* is very closely related to *C. (C.) arcuophora*, with similar skeletal architecture (with 2 components, renieroid and plumoreticulate), spicule geometry, spicule sizes, similar fibre characteristics and comparable growth forms. It is possible that the two species are synonyms, but their formal merger is not warranted on the basis of the existing relatively poor material. Similarly *C. (C.) crassa* shows some similarities with *C. (Isocella)*, particularly to *C. (I.) eccentrica*. This resemblance is mostly due to the renieroid axial skeletal architecture and geometry of both principal and auxiliary styles.

**Clathria (Clathria) decumbens** Ridley, 1884

(Figs 40-41)

*Clathria decumbens* Ridley, 1884a: 612, pl.53, fig.1; pl.54, fig.g-g'; Ridley & Dendy, 1887: 148; Burton, 1938a: 29, pl.3, fig.23; Hooper & Wiedenmayer, 1994: 259.

*Wilsonella decumbens*; Hallmann, 1912: 239.

**Material.** Holotype: BMNH1882.10.17.51: Boudouze and Etoile Is, Amirante Is Group, Indian Ocean, 6°S, 53°10'E, coll. HMS ‘Alert’ (dredge).

Paratypes: BMNH1882.10.17.71, 1882.10.17.76: same locality. OTHER MATERIAL: QUEENSLAND-BMNH1887.5.2.139.

**Habitat and Distribution.** 6-26m depth; on sand and coral rubble substrate; Cape York, Torres Strait (FNQ) (Fig. 40F) (Ridley, 1884a). W. Indian Ocean (Ridley & Dendy, 1887), Madras (Burton, 1938a).

**Description.** Shape. Small, subcylindrical, irregularly lobate, 32-50mm long, 15-40mm wide, up to 25mm thick.

**Colour.** Brown to red-brown in ethanol.

**Oscules.** Numerous small oscules, 1-2mm in diameter, dispersed between surface conules. 

**Texture and Surface Characteristics.** Surface rugose, irregularly conulose, with canals, grooves and ridges meandering over the surface.

**Ectosome and Subectosome.** Ectosome membranous between ridges and surface projections, with spongin fibres from choanosome producing a dermal reticulation; dermal region lacks a mineral skeleton entirely; spongin fibres in subectosomal region closely reticulate, with relatively small mesh sizes.

**Choanosome.** Choanosomal skeletal architecture regularly to irregularly reticulate; spongin fibres
Clathria (Clathria) echi nonematissima  
(Carter, 1881)

Wilsonella echi nonematissima Carter, 1881a: 366;  

Clathria echi nonematissima; Dendy, 1896: 33, 34;  

MATERIAL. HOLOTYPE: BMNH not found (slide  
containing only a desilicified section is the only type  
material known to exist); Westernport Bay, 38°26' S,  
145°08' E, or Port Phillip, Vic, 38°09' S, 144°52' E, coll.  
J.B. Wilson (dredge).

HABITAT DISTRIBUTION. Ecology unknown;  
Victoria.

DESCRIPTION. Shape. Massive.

Colour. Unknown.

Oscules. Unknown.

Texture and surface characteristics. Unknown.

Ectosome and subectosome. Ectosomal skeletal  
tracts heavily cored with detritus, megascleres  
excluded.

Choanosome. Choanosomal skeleton irregularly  
reticulate, with relatively heavy spongine fibres;  
fibres of peripheral skeleton are solely  
arenaceous, whereas within choanosome fibres  
cored by subectosomal auxiliary styles; echinat-  
ing acanthostyles dispersed throughout skeleton.

Megascleres. Choanosomal principal megascleres  
apparently absent.

Subectosomal auxiliary subtylostyles with  
smooth bases. Length 210μm, width 4μm.

Acanthostyles apparently divided into two size  
categories. Length from 145μm, width 8.3μm.


Toxas absent.

REMARKS. This species is barely recognisable as  
Clathria from Carter’s (1881) description, and  
it is only poorly differentiated from other  
microcionid species. One category of auxiliary  
spicule and the absence of choanosomal principal  
spicules places it in Wilsonella (sensu Hallmann,  
1912). It also was described with arcuate  
ischelae, similar to species grouped by  
Hallmann (1920) in Paradoryx, but this is incom-  
coroborated. Clathria echi nonematissima is a  
species inquirendum as it is only known from a  
slide preparation, now desilicified, allegedly  
made from the missing holotype.

Clathria (Clathria) hispidula (Ridley, 1884)  
(Figs 42-43)

Amphilectus hispidulus Ridley, 1884a: 429-430, pl.40,  
fig.c, pl.41, fig.y.

moderately heavy, undifferentiated into primary  
or secondary lines, lightly cored by paucisepicular  
tracts of both choanosomal principal styles and  
subectosomal auxiliary styles; heavily echinated  
by acanthostyles; coring spicules in peripheral  
fibres ascend to surface, piercing surface process-  
es in light brushes; subectosomal auxiliary sub-  
tylostyles also sparsely scattered within mesohyl;  
spicules in choanosomal skeleton cavernous;  
mesohyl matrix abundant, lightly pigmented.

Megascleres. Choanosomal principal styles  
straight or slightly curved near base, hastate  
points, with evenly rounded bases, smooth or  
with microspines on both points and bases.  
Length 128-(156)-176μm, width 4-(4.9)-6μm.

Subectosomal auxiliary subtylostyles straight,  
with hastate points, slightly subtylole bases,  
bases smooth or occasionally microspined.  
Length 159-(1177.8)-193μm, width 2-(3.7)-  
6μm.

Acanthostyles subtylole, with strongly formed,  
recurved spines over apical end, shaft and base  
but bare neck. Length 62-(63.2)-104μm, width  
4-(6.2)-8μm.

Microscleres. Palmate isochelae unmodified, two  
discrete size classes, the smaller showing varia-  
tion in fusion of alae. I: Length 14-(20.4)-28μm,  
II: length 5-(7.4)-10μm.

Toxas absent.

REMARKS. Hallmann (1912) referred this  
species to Wilsonella, presumably because Ridley  
(1884a) did not differentiate between choanosomal (principal) and  
subectosomal (auxiliary) megascleres. Subsequently, Burton  
(1938a) described additional specimens from Madras which had differentiated principal  
and auxiliary spicules (but were otherwise identical  
with Ridley’s (1884) description). In type  
material there were consistent morphological  
differences between principal and auxiliary  
spicules, confirming that the species should be  
retained in Clathria (Clathria).

Although C. (C.) decumbens has been described  
from three widely separated localities, it remains  
poorly known, being only poorly differentiated  
from other low growing, lobate Clathria species.  
The species is similar to C. (Thyalysia) major  
(with spines on both the bases and points of some  
of its megascleres), while at the same time being  
similar to species in the ‘juniperina’ species com-  
plex (i.e., Clathria in which the geometry of  
choanosomal principal and subectosomal  
 auxiliary spicules is barely different), but the  
species has little else of distinction.
Axociella hispidula; de Laubenfels, 1936a: 114.
Esperiopsis hispidula var. ramosa; Hentschel, 1911: 313.
Not Hymeraphia hispidula Topsent, 1904a: 164-165, pl.14, fig.2.

MATERIAL. LECTOTYPE: BMNH1881.10.21.261: Thursday I., Torres Strait, N. Qld, 10°35'S, 142°13'E, 6-10m depth. 01.vi.1881, coll. HMS 'Alert' (dredge).

HABITAT DISTRIBUTION. Encrusting on bivalves, hydroids, and gorgonians and algae; 6-11m depth; Torres Strait (FNQ), and Shark Bay (WA) (Fig. 42G).

DESCRIPTION. Shape. Erect, irregular branching reticulate mass of clathrous digits, up to 60mm long, 55mm diameter.
Colour. Live colour unknown, light brown in ethanol.
Oscules. Small oscules, <2mm diameter in preserved material, scattered over lateral margin. Texture and surface characteristics. Harsh, compressible, slightly elastic; surface with meandering irregular ridges and microconules scattered over branches, and tips of fibres from primary skeleton protruding.
Ectosome and subectosome. Sparse paratangential skeleton of subectosomal auxiliary subtylos-

styles forming bundles or lying more-or-less erect on the surface, particularly on ends of surface conules; tips of conules with choanosomal principal styles also protruding only short distance through surface; choanosomal fibres immediately below surface skeleton with poorly developed subectosomal region.

Choanosome. Skeleton regularly reticulate, slightly renieroid, with thin but well developed spongin fibres forming oval or rectangular, relatively wide meshes, 150-350 μm diameter, generally more cavernous in axis than in peripheral region; spongin fibres 20-70 μm diameter, imperfectly divided into primary, ascending, multispecular tracts of 4-10 spicules per tract, interconnected by uni-, pauci- or aspicular secondary transverse tracts; fibres cored by choanosomal principal styles not occupying en-
tire fibre diameter, and sparsely echinated by slender acanthostyles; mesohyl matrix light containing scattered microscleres and some auxiliary megascleres.

**Megascleres.** Choanosomal principal styles slender, straight or slightly curved midway along shaft, with evenly rounded smooth bases and fusiform points. Length 88-(162.7)-219 μm, width 4-(4.8)-6 μm.

Subectosomal auxiliary subectostyles similar in geometry to principal spicules, but more slender and with subtylolate bases; thinner (younger) principal spicules frequently sinuous. Length 94-(143.0)-175 μm, width 2-(3.4)-5 μm.

Echinating acanthostyles club-shaped, slender, slightly subtylolate, evenly spines or with bare 'neck' below base, fusiform or rounded points, granular spination. Length 52-(59.4)-63 μm, width 2-(4.1)-5 μm.

**Microscleres.** Palmate isochelae very abundant, small, unmodified, with lateral alae completely fused to shaft and front ala entire; lateral and front alae of approximately equal length. Length 9-(11.6)-13 μm.

Toxas uncommon, small, thick, wing-shaped, with rounded central curve and slightly reflexed arms. Length 17-(56.8)-104 μm, width 1.5-(2.1)-3 μm.

**REMARKS.** This species has not yet been rediscovered from either of the known locations of early collections, and it remains relatively poorly known from museum specimens. Surprisingly, both Ridley (1884a) and Hentschel (1911) failed to describe several spicule types present in their respective material, particularly echinating acanthostyles which are uncommon but certainly present, as well as auxiliary subectostyles and less common toxas microscleres. Furthermore, Hentschel’s material essentially differs from Ridley’s only in the specific dimensions of spicules and growth form (being more elongate, branching), and it is not considered to be necessary to recognize the subspecific taxon proposed by Hentschel (1911) for the WA population.

Although the identity of this species has never been clearly established from either published record, it is obviously a *Clathria* with relatively cavernous skeletal architecture and standard spiculation. It is similar to *C. (C.) angulifera* (Dendy) from Victoria and southern Queensland, and *C. (T.) aphylia* from the Houtman Abrolhos, in having a cavernous, slightly renieroid skeletal structure (‘angulifera’ species group), differing in the protruding fibrous ectosomal skeleton, spicule geometries (e.g., toxas, acanthostyles), a more-or-less branching growth form (cf. lobate lamellate and folioid lamellate, respectively), and spicule sizes.

**Clathria (Clathria) inanchorata** Ridley & Dendy, 1886 (Figs 44-45, Table 6)


**MATERIAL.** HOLOTYPE: BMNH1887.5.2.99: Bass Strait, Tas, 36°59'S, 150°20'9, 14.iv.1874, coll. HMS ‘Challenger’ (trawl). OTHER MATERIAL: NSW - AMG5675, AMZ131; AMZ145; AMZ141.

**HABITAT DISTRIBUTION.** Depth 110-300 m, substrate mud; Bass Strait (Tas) (Ridley & Dendy, 1886), S. coast (NSW) (Whitelegge, 1907). Ternate, Molucas, Indonesia (Kieschnick, 1896).

**DESCRIPTION.** Shape. Erect, irregularly cylindrical digits, 38-120 mm high, 8-12 mm diameter, encrusting on organic debris or standing free in substrate.

- **Colour.** Grey- or yellow-brown preserved.

- **Oscules.** Numerous oscules, up to 2.5 mm diameter, scattered over branches.

- **Texture and surface characteristics.** Surface rugose, reticulate, minutely hispid; texture firm, flexible.

**Ectosome and subectosome.** Ectosomal skeleton prominently hispid, with choanosomal principal megascleres from peripheral fibres protruding a long way through surface, and with a sparse tangential layer of subectosomal auxiliary megascleres dispersed between erect principal spicule brushes; subectosomal skeleton plumose, undifferentiated from choanosomal fibres which are immediately subdermal.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with relatively heavy spongion fibres incompletely divided into primary ascending and secondary transverse components; secondary fibres uncoined, lightly echinated by small acanthostyles; primary fibres contain sparse tracts of subectosomal auxiliary subectostyles, identical to those occurring in the ectosomal skeleton, enclosed completely within spongion fibres, together with plumose brushes of choanosomal.
TABLE 6. Comparison between present and published records of *Clathria (Clathria) inanchorata* Ridley & Dendy. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype</th>
<th>Specimens (N=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaenosomal principal styles</td>
<td>292-(417.5)-535 x 8- (18.4)-28</td>
<td>273-(384.5)-540 x 12-(17.8)-25</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>252-(328.6)-432 x 3- (8.2)-11</td>
<td>290-(341.8)-410 x 3- (8.5)-12</td>
</tr>
<tr>
<td>Echinating acanthostyles I</td>
<td>58-(66.4)-78 x 3- (5.2)-7</td>
<td>58-(75.2)-88 x 4- (5.4)-7</td>
</tr>
<tr>
<td>Echinating acanthostyles II</td>
<td>118-(150.2)-175 x 4- (7.4)-11</td>
<td>119-(169.3)-228 x 6- (8.8)-12</td>
</tr>
<tr>
<td>Chela</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Toxas I</td>
<td>35-(73.8)-121 x 1.5- (2.0)-3</td>
<td>22-(66.2)-105 x 1.5- (3.4)-5</td>
</tr>
<tr>
<td>Toxas II</td>
<td>118-(349.2)-478 x 1.5-(2.1)-2.5</td>
<td>304-(408.3)-545 x 1.5-(2.1)-3</td>
</tr>
</tbody>
</table>

Principal styles usually poking out of fibres; chaenosomal principal styles, protruding through spongin fibres, together form multissacular ascending plumose tracts, also lightly echinated by acanthostyles; fibre anastomoses form circular to oval, cavernous meshes; mesohyl matrix, very light, with few megascleres dispersed between fibres.

*Megascleres* (Table 6). Chaenosomal principal styles long, thick, fusiform, slightly curved, with rounded or slightly subtylote, smooth or minutely micropinned bases.

Subectosomal auxiliary subtylotes straight, relatively thick, robust, almost hastate, with slightly subtylote micropinned bases.

Acanthostyles very variable in size, with slightly subtylote bases, incompletely separated into two size classes with some intermediate examples. Smaller morph usually straight, often with aspinose necks, whereas larger morphs slightly curved, with evenly distributed large spines.

*Microscleres*. (Table 6). Isochelae absent.

Toxas clearly separated into two morphs - I: most common form are oxeform toxas, small, relatively thick, with large, rounded or slightly angular curvature at centre, and reflexed points. II: Less frequent are accolada toxas, long, thin, sharply angular at centre, unreflexed arms.

**REMARKS.** This species has a distinctive growth form, spicule geometry, and spongin fibre characteristics, but otherwise it is similar to other species included in Hallmann's (1912) 'spicata' group, particularly *C. (T.) costifera* and *C. (C.) caelia*. There is no doubt that Whitelegge's (1907) specimens from Wollongong are conspecific although this claim was disputed by Hallmann (1912: 206). Kiescknick's (1896) record of this species from Indonesia is dubious, since his material was not described and could possibly be any one of these 'spicata'-like sponges, Thiele (1903a) compared Kiescknick’s specimen with *C. (T.) coralliophila* from the same region, but that comparison is misleading: both taxa have quite different spiculation and spongin fibre characteristics.

*Clathria (Clathria) kylista* Hooper & Lévi, 1993 (Figs 46-47, Plate 1C, Table 7)

**MATERIAL.** **HOLOTYPE:** QMG300035: Inner Gneering Shoals, off Moooloolaba, Qld., 26°38.5’S, 153°09.5’E, 10m depth, 10.xii.1991, coll. J.N.A. Hooper & S.D. Cook (SCUBA). **PARATYPE:** QMG300090 (ORSTOM R1338; fragment NTMZ3876): N. entrance, Récif des Cinq Milles, SW, New Caledonia Island, 22°29.3’S, 166°44.4’E, 8m depth, 30.iv.1976, coll. G. Bargibant (SCUBA). **OTHER MATERIAL:** QUEENSLAND – QMG-303166.

**HABITAT DISTRIBUTION.** 8-20m depth; on rock pinnacles, in caves and coral rubble substrates; Moooloolaba and Moreton I. (SEQ) (Fig. 46F). New Caledonia (Hooper & Lévi, 1993a).

**DESCRIPTION.** (See Hooper & Lévi, 1993a).

**DIAGNOSIS.** (refer to Table 7 for spicule dimensions) Simple digitate, tubular or bulbous, erect, branching growth form; dark orange to pale orange alive; terminal osculum on single tubes and oscules scattered over the apical regions of more complex lobate digitate growth forms; oscules surrounded by membranous lip; prominently conulose surface with large, bulbous tubercles; ectosome membrane, with sparse, tangential layer of subectosomal auxiliary styles and erect brushes of auxiliary spicules scattered throughout both peripheral and subectosomal regions; chaenosomal skeleton plumoseciliated with differentiated primary and secondary fibres; primary fibres ascending, paucispicular occupying only small proportion of fibre diameter, cored by principal spicules with fewer auxiliary megascleres interdispersed; secondary fibres transverse, uni- or aspicular; echinating styles
FIG. 47. *Clathria (Clathria) kylista* Hooper & Lévi (paratype QMG300690); A, Choanosomal skeleton. B, Fibre characteristics in peripheral skeleton. C-D, Echinating acanthostyles. E, Acanthostyle vestigial spines. F, Subtylote base of auxiliary subtylostyles.
TABLE 7. Comparison in spicule dimensions between types and specimen of Clathria (Clathria) kylist Hooper & Lévi. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (QMG300035) (SE.Qd)</th>
<th>Paratype (QMG300060) (New Cal.)</th>
<th>Specimen (QMG303156) (SE.Qd)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>64-(84.7)-112 x 2.5-(2.9)-4.0</td>
<td>61-(81.6)-97 x 1.6-(2.7)-3.6</td>
<td>55-(78.2)-104 x 2.0-(3.1)-4.5</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>143-(168.9)-181 x 1.0-(2.4)-4.1</td>
<td>138-(159.4)-183 x 0.4-(2.1)-3.5</td>
<td>110-(142.3)-166 x 1.0-(1.8)-3.5</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>26-(32.8)-40 x 1.0-(2.6)-4.0</td>
<td>32-(35.5)-39 x 1.1-(3.1)-5.0</td>
<td>18-(27.3)-35 x 1.0-(2.4)-3.5</td>
</tr>
<tr>
<td>Toxas</td>
<td>65-(129.6)-231 x 0.5-(1.3)-2.5</td>
<td>65-(135.6)-266 x 0.2-(1.1)-1.6</td>
<td>35-(146.5)-222 x 0.5-(1.0)-2.0</td>
</tr>
<tr>
<td>Chelae</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

moderately common on primary ascending fibres, sparse on secondary connecting fibres; choanosomal principal styles slender, straight, relatively short, with hastate points and smooth, slightly swollen, subtyloyte bases; subectosomal auxiliary styles long, slender, straight, with hastate points and smooth, elongated, swollen subtyloyte bases; echinating styles entirely smooth, short, slender, sharply pointed, with prominent basal constriction ('neck'), subtyloyte base and widest just below basal constriction; isochelae absent; accolada toxas abundant, moderately long, ranging from slender to raphidiform, with straight arms and prominent central curve.

REMARKS. This species was assigned to Clathria (Clathria) by Hooper & Lévi (1993a), even though echinating spicules are smooth (cf. Echinoclathia), because coring (principal) and echinating megascleres have different geometries (see also C. (M.) aceratoobtusa). Clathria (C.) kylist is similar to C. (C.) angulifera and C. (C.) noarlanuae in skeletal structure, having sparsely cored ascending primary fibres and uncorred secondary connecting fibres, although both these other species have acanthose echinating spicules and palmate isochelae, and C. (C.) noarlanuae also has slightly curved toxas. The unusual geometry of the echinating styles in C. (C.) kylist is the strongest apomorphy for the species, not seen elsewhere in the genus.

Clathria (Clathria) lipoche] Burton, 1932 (Fig. 48)


MATERIAL. HOLOTYPE: BMNH1928.2.15.352: Edystone Rock, Falkland Is, 105-115m depth, coll. HMS "Discovery" (trawl).

HABITAT DISTRIBUTION. 22-115m depth; on sand and hard substrates; King George Land (Australian Antarctic Territory), Antarctica (Koltun, 1964a) (Fig. 48F). South Georgia (Koltun, 1964a), Falkland Is (Burton, 1932a), Caleta Santa Marta, Chile (Desqueyroux, 1972), Mar del Plata, Argentina (Burton, 1940), Kerguelen Is (Koltun, 1964a), Magellan Straits (Burton, 1940), Cape Sebastian, Punta Arenas, Rio Grande, Cape Domingo, Cape Viamonte, Tierra del Fuego (Sarà, 1978).

DESCRIPTION. Shape. Stalked, irregularly flabellate; digitate margins of fan.

Colour. Unknown.

Oscules. Not seen.

Texture and surface characteristics. Firm, compressible; uneven, pitted, porous surface.

Ectosome and subectosome. Surface skeleton with sparse paratangential or erect brushes of subectosomal auxiliary styles, mainly at ends of ascending primary spicule tracts; choanosomal principal styles protrude through surface in places; detritus scattered over surface but not embedded in ectosome.

Choanosome. Skeletal architecture regularly reticulate with ascending primary multispecular fibres and transverse uni-, pauci- or occasionally aspicular fibres, interconnecting at more-or-less regular intervals producing rectangular or elongate meshes, up to 450μm diameter; fibres cored by choanosomal principal styles and moderately heavily echinated by acanthostyles evenly scattered over fibres in both axial and peripheral regions of skeleton; spongine fibres well developed; few spicules scattered between fibres; mesohyl matrix light, smooth, virtually unpigmented.

Megascleres. Choanosomal principal styles short, relatively slender, fusiform, rounded and smooth bases, straight or only slightly curved near basal end. Length 153-(206.7)-254μm, width 7-(11.0)-14μm.

Subectosomal auxiliary styles long, slender, slightly hastate pointed, slightly subtyloyte or
rounded bases, microspined or smooth bases. Length 164-(179.4)-198μm, width 3-(3.9)-5μm.

Echinating acanthonostyles relatively long, slender, straight, with subtylostyles, fusiform points, spines concentrated in basal and apical regions and bare 'necks'. Length 79-(93.1)-111μm, width 6-(8.7)-12μm.

**Microsceleres.** Palmate isochelae small, unmodified, relatively abundant. Length 7-(8.5)-11μm.

Toxas absent.

**REMARKS.** Burton (1932a) named this species for the apparent absence of chela, but these were found to be common in sections of the holotype. Burton's (1932a) comparison with *Raspatilia phakellina* Topsent (Hooper, 1991:1199), is misleading as they do not resemble each other in skeletal structure or spicule geometry. *Clathria* (C.) *lipochela* resembles C. (*T.*) *vulpina* (Lamarck) in geometry of principal and echinating spicules and skeletal architecture to some extent, although they differ in many other features.

**Clathria (Clathria) multipes** Hallmann, 1912
(Figs 49-50, Table 8)

**Clathria (Plectispa) arborea**, in part, Whitelegge, 1901; 88, pl.11, fig.15.


**Clathria (Plectispa) multipes** Hallmann, 1912: 204, 211.

**Clathria multipes**; Hooper & Wiedenmayer, 1994: 280.

**MATERIAL.** LECTOTYPE; AMG9038 (dry): Tuggerah Beach, Illawarra region, NSW, 34°32’S, 150°50’E (beach debris, label 'Clathria arborea Lendenfeld; ms name = Clathria plicatella'). PARALEC- TOTYPES: AMG9162 (dry): Maroubra Bay, NSW, 33°45’S, 151°20’E (label 'Plectispa arborea Lend. = Clathria arborea'). BMNH1887.4,27.9 (fragment AMG3590): Port Jackson, NSW, 33°51’S, 151°16’E (label 'Thalassodendron reticulata RvL, MS'). Other type fragments ZMB2264, 6894. SYNTYPE of *P. macropora*: BMNH1925.11.1.555: Manly Beach, NSW, 33°50’S, 151°17’E, other details unknown.

**HABITAT DISTRIBUTION.** Ecology unknown; central and S coast (NSW) (Fig. 49F).

**DESCRIPTION.** Shape. Branching, reticulate branches, planar, 85-140mm long, 62-73mm wide, with compressed, cylindrical and regularly anastomosing branches, 4-8mm diameter, and several small basal stalks (multiple points of attachment).

**TABLE 8.** Comparison between present and published records of *Clathria (Clathria) multipes* Hallmann. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype AMG9038</th>
<th>Paralecotype AMG9162</th>
<th>Paralecotype BMNH1887.4,27.9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>142-(136.6)-174 x 4-(5.9)-7</td>
<td>145-(157.6)-178 x 6-(8.2)-10</td>
<td>112-(147.8)-262 x 7-(9.3)-12</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>162-(194.6)-239 x 1.5-(2.8)-4</td>
<td>132-(167.0)-222 x 2-(3.1)-4</td>
<td>143-(189.5)-262 x 2-(3.2)-4.5</td>
</tr>
<tr>
<td>Echinating anastomosings</td>
<td>52-(62.8)-91 x 4-(5.6)-8</td>
<td>71-(85.8)-98 x 5-(6.4)-8</td>
<td>64-(78.5)-93 x 4-(6.6)-9</td>
</tr>
<tr>
<td>Chela</td>
<td>4-(6.1)-8</td>
<td>5-(4.8)-8</td>
<td>3(5.7)-8</td>
</tr>
<tr>
<td>Toxas</td>
<td>16-(112.2)-147 x 1-(4.3)-6</td>
<td>19-(101.4)-141 x 1-(3.9)-5</td>
<td>130-(124.8)-178 x 2-(4.4)-5</td>
</tr>
</tbody>
</table>

**Colour.** Live colouration brick red, grey-brown dry.

**Oscules.** Numerous large oscules, up to 3mm diameter, distributed over all surfaces.

**Texture and surface characteristics.** Surface irregularly rugose, with small elevated conules scattered mainly on lateral sides of branches.

**Ectosome and subectosome.** Ectosome, rarely intact in dry type material, consists of three dimensional fibre reticulation, with fibre endings forming small surface conules, and choanosomal principal styles protruding through peripheral fibres in light brushes or singly; subectosomal auxiliary subtylostyles dispersed in a tangential layer around projecting dermal fibres.

**Choanosome.** Choanosomal skeletal architecture irregularly reticulate, consisting of relatively heavy spongin fibres forming incompletely differentiated primary (vaguely ascending, multipersistic) and secondary fibres (transverse uni-, pauci- or aspicular), and producing relatively tight oval to elongate meshes; fibres echinated by small, sparsely distributed acanthonostyles; mesohyl matrix light, with moderate quantities of subectosomal subtylostyles and microsceleres dispersed.

**Megascleres** (Table 8). Choanosomal principal styles hastate or stepped, relatively thick, slightly curved, with tapering or slightly subtyloide and smooth bases.

**Subectosomal auxiliary subtylostyles** long, thin, fusiform, straight, curved or sinusous, with slightly subtyloide, smooth bases.

**Acanthonostyles** subtyloide, with vestigial spination and an aspinose neck.

**Microsceleres** (refer to Table 8 for dimensions). Palmate isochelae minute.

Toxas u-shaped, relatively thick, oxeote, with hastate points, typically curved at right angles at the centre, with straight and unreflexed points.

REMARKS. All known specimens are in poor condition, and it is not possible to accurately determine ectosomal characteristics. The species is most closely related to Clathria (Clathria) rather than Clathria (Thalysias). Whitelegge (1901) remarked that the species was frequently washed up onto coastal beaches of S NSW after storms, inferring that it was a relatively prominent component of the benthos, and therefore it is surprising that it has not been collected since that time despite intensive trawling. The growth form of C. (C.) multipes (reminiscent of

C. (T.) coppingeri and Echinodictyum cancellatum (Raspailiidae), the small size of isochelae, the peculiar angular shapes of toxas, and the vestigial acanthostyles differentiates this species from other Clathria.

Clathria (Clathria) murphyi sp. nov. (Figs 51-52, Plate 1D)

MATERIAL. HOLOTYPE: QMG300656 (NCIQ66C-2904-N, fragment NTMZ3754): Old jetty, E. end of Princess Royal Drive, Albany, WA, 35°02.3'S, 117°54.2'E, 9m depth, 27.ii.1989, coll. NCI (SCUBA).

HABITAT DISTRIBUTION. Wood jetty piles; 9m depth; SW WA (Fig. 51G).

DESCRIPTION. Shape. Thickly encrusting, bulbous digitate lumps, up to 80mm diameter, resembling the tropical Higginsia massalis (Desmoxyidae).

Colour. Orange-red alive (Munsell 10R 6/10), pale brown preserved.
Oscules. Large oscules, more than 5mm diameter, on ends of bulbs.

Texture and surface characteristics: Surface porous, microvillose, uneven, with epi- and zoophytes; texture soft, compressible, easily torn off wooden piles.

Ectosome and subectosome. Ectosome membranous, with heavy, brown collagen and brushes of choanosomal principal styles poking through surface in plumose bundles, mainly on ends of microconules; subectosomal auxiliary styles in irregular, paratangential bundles below surface, at base of principal style brushes, not protruding through surface.

Choanosome. Choanosomal skeleton renieroid reticulate, cavernous, without visible spongine fibres, with differentiated primary and secondary spicule tracts; primary skeletal tracts ascending, multipricular, 20-40μm diameter, composed of plumose brushes of choanosomal principal styles, 3-10 spicules abreast; secondary tracts uni- or bi- or paucipricular, transverse, 8-20μm diameter, connecting primary tracts; echinating acanthostyles relatively sparsely dispersed throughout choanosome; mesohyl matrix heavy, granular, darkly pigmented, surrounding large oval, paired choanoocyte chambers, up to 320μm diameter, with abundant toxa and isochelae microscleres dispersed throughout.

Megascleres. Choanosomal principal subtylosstyles short, stout, straight, fusiform points, tapering smooth bases, terminally subtylole, with slightly swollen subterminal region. Length 87-116.5-149μm, width 5.7-9μm.

Subectosomal auxiliary subtylosstyles short, slender, fusiform, slightly subtylole, smooth bases. Length 114-138.4-165μm, width 1.5-2.6-3.5μm.

Echinating acanthostyles short, slender, slightly subtylole bases, spines recurved, evenly spined except for bare neck. Length 42-55.7-68μm, width 3.5-4.2-5.5μm.

Microscleres. Paltme isochelae, small, poorly silicified, about 10% with twisted shafts. Length 5-8.4-14μm.

Toxas accoladora form, long, very slender hair-like, with straight, unreflexed arms and angular central curvature. Length 72-115.6-164μm, width 0.5-0.7-0.8μm.

ETYMOLOGY. For Dr Peter Murphy, Australian Institute of Marine Science, Townsville.

REMARKS. This species is separated from other Clathria (Clathria) by its distinctive spicule geometries (principal styles with marked basal constrictions and swollen 'necks'), relatively small, poorly silicified spicules of all categories, renieroid choanosomal skeletal structure (with multipricular ascending tracts and uni- or paucipricular plumose transverse connecting spicule tracts, both sparsely echinated by acanthostyles), bulbous-digitate growth form, orange-red colouration, microvillose surface with plumose brushes of choanosomal styles protruding through the ectosome especially on the tips of microconules. Clathria (C.) murphyi has a skeletal architecture reminiscent of C. (C.) arcuiphora and C. (C.) erossa (both of which have much larger spicules of different geometry), and in this respect the species is included in the 'striata' group (see remarks for C. (C.) striata).

Clathria (Clathria) nexus (Koltun, 1964) (Figs 53-54)


Clathria nexus; Hooper & Wiedenmayer, 1994: 260

MATERIAL. HOLOTYPE: ZIL 10644 (not seen): Clarie Coast or Wilhelm Land, Australian Antarctic Territory, 65°48'S, 89°49'E, 310-400m depth (dredge).

PARATYPES: BMNH1963.7.29.56, ZIL 11525: same locality.

HABITAT DISTRIBUTION. 310-400m depth; substrate unknown; Australian Antarctica Territory (Fig. 53P).

DESCRIPTION. Shape. Erect arborescent growth form, 88-100mm high, 32-55mm wide, with tightly anastomosing cylindrical branches, up to 4mm diameter; tips of branches bifurcate, relatively sharply pointed.

Colour. Grey-brown preserved.

Oscules. Numerous small oscules, 1-2mm diameter, scattered over lateral margins of all branches.

Texture and surface characteristics. Surface hispid, raised into irregularly distributed, sharply pointed microconules.

Ectosome and subectosome. Ectosomal skeleton with choanosomal principal styles erect on surface, and bundles of subectosomal auxiliary spicules surrounding protruding principal spicules, or lying paratangential to surface.

Choanosome. Choanosomal skeleton subrenieroid-reticulate, without clearly defined spongine fibres, but with heavy collagen enclosing principal subtylosstyles and sparse acanthostyles echinating; mesohyl matrix heavy, with numerous isochelae, few auxiliary styles and some detritus dispersed throughout.

**Megascleres.** Choanosomal principal styles long, robust, straight or slightly curved towards the distal end, tapering to sharp points, with slightly swollen subtylote bases, liberally microspined; basal spines may partially extend up shaft near basal end. Length 518-(567.3)-620μm, width 18-(22.4)-25μm.

Subectosomal auxiliary styles long, straight, abruptly pointed, with only slight basal swelling and pointed-hastate bases. Length 366-(394)-415μm, width 3-(5.6)-7μm.

Echinating acanthostyles relatively long, robust, subtylote, sharply pointed, with heavy recurved spines and heaviest concentrations of spines on basal end. Length 214-(241.3)-278μm, width 9-(13.8)-17μm.

**Microscleres.** Isochelae, strongly curved sigmoid, unguiferous with vestigial teeth, of anchorate or arcuate modification. Length 14-(16.6)-19μm.

Toxas absent.

**REMARKS.** This species is similar to *C. (T.) michaelensi* in having bidentate sigmoid isochelae, but differing in skeletal architecture and in most other features. These unguiferous, sigmoid-like chelae with vestigial, pointed alae, are not unique to these austral species, also known in W. Indian Ocean *C. (C.) spongodes* Dendy (including its synonym *C. madrepora* Dendy). In *C. (C.) spongodes* these reduced chelae were initially thought to be sigmas (Dendy, 1922; Burton, 1959a; Vacelet et al.,...
1976), but the type material showed that these are in fact reduced unguiferous isochelae with vestigial teeth.

Clathria (C.) nexus is also unusual in Microcionidae in having auxiliary styles obviously associated with (surrounding) protruding principal spicules, reminiscent (or analogous to) Raspailiidae. Unlike raspailiids, however, auxiliary spicules are also dispersed within the peripheral skeleton, paratangential to the surface. The other alternative, that the species belongs to Raspailiidae, is rejected due to the chelae microscleres. The bidentate-derived chelae is unusual to the Microcionidae and grounds to exclude the species from it under the phylogeny of Poecilosclerida hypothesised by Hajdu et al. (1994), but in all other respects the species fits in this group supporting the present classification.

Clathria (Clathria) noarlunga sp. nov.
(Figs 55-56, Plate 1E, Table 9)


HABITAT DISTRIBUTION. 5-30m depth, from rock reef substrate; Port Noarlunga and Kingston, SE S.Aust.

DESCRIPTION. Shape. Branching, 58-190mm long, cylindrical digitate, bulbous-lolate branches, 15-33mm diameter, with bulbous lobes on tips of digits, single or bifurcate tips.

Colour. Orange alive (Munsell 10R 6/10), grey-brown preserved (7.5YR 5/4).

Oscules. Large oscules, 3-5mm diameter, in line on lateral sides of branches and on apex of terminal bulbs.

Texture and surface characteristics. Texture rubbery, compressible, fibrous, difficult to tear; surface optically smooth, with few low rounded bulbous projections; detachable skin-like dermis, which is microscopically evenly porous, without projecting spicules.

Ectosome and subectosome. Ectosomal skeleton consisting of relatively even, light series of plumose brushes of ectosomal auxiliary subylostyles, standing perpendicular or paratangential to surface, usually surrounding inhalant pores and forming a spiculo-fibrous reticulation on surface; ectosomal skeleton thin, 75-149μm wide, perched on ends of peripheral, ascending choanosomal fibres; subectosomal skeleton not differentiated from dermal skeleton, and ectosomal spicule brushes composed of a single category of auxiliary megascleres only; megascleres coring peripheral fibres sometimes project into, but not through ectosomal skeleton, but this is exceptional.

Choanosome. Choanosomal skeletal architecture arborescent, cavernous, consisting of well differentiated primary ascending and secondary transverse components; primary spongin fibres multispicular, 35-98μm diameter, relatively heavily invested with spongin, forming dendritic, arborescent, radial, relatively even structure; coring spicules in primary fibres occupy only a small proportion of sponge diameter in axial skeleton, becoming more heavily cored and increasingly plumose towards peripheral skeleton; spongin fibres cored by larger subectosomal auxiliary styles, and echinating acanthostyles occur only sparsely throughout entire skeleton; secondary spongin fibres entirely free of coring megascleres, 12-57μm diameter, forming a plumo-reticulate structure; meshes formed by primary and secondary spongin fibre branching are ovoid-elongate to rectangular in shape, relatively even, and markedly cavernous (155-560μm maximum diameter); choanocyte chambers paired, 90-311μm maximum diameter, becoming larger towards periphery; mesohyl matrix slightly granular; with toxas dispersed singly or in dragmata; thin, raphidiform, vestigial auxiliary megascleres also dispersed between fibres, difficult to distinguish from toxas.

Megascleres (refer to Table 9 for dimensions). Choanosomal principal megasclere absent, or completely undifferentiated from subectosomal auxiliary spicules.

Subectosomal auxiliary styles, coring fibres, thin, mostly straight, varying from hastate to almost fusiform, with smooth tapering, rounded or very slightly subtyloete bases.

Ectosomal auxiliary styles geometrically similar to larger auxiliary styles, with slightly more pronounced, smooth, subtyloete basal constrictions.

Acanthostyles vestigial, with subtyloete bases, fusiform points, rudimentary spination, aspinose points and necks.

Vestigial auxiliary megascleres dispersed within mesohyl are stylloid or quasidiactinal, often sinuous, with tapering or rounded bases, long fusiform points.

Megascleres (refer to Table 9 for dimensions). Palmate isochelae minute, abundant, frequently twisted (80% of samples), two size classes observed.
Toxas accolada, rhaphidiform, common, occurring individually or in dragmata, exceedingly thin, rhaphidiform with very slight rounded central curvature and straight points, or less often with more angular central curvature and slightly reflexed arms.

ETYMOLOGY. Named for type locality.

REMARKS. There are some minor differences in spicule dimensions between the two known specimens of C. (C.) noarlungae (Table 9), although there is no doubt that they are conspecific. In having sparsely cored ascending primary fibres and uncored secondary connecting fibres this species is similar to C. (C.) kylistus and C. (C.) angulifera although spicule geometry and dimensions differs between all three. This species is also similar to C. (T.) cactiformis (Lamarck) in growth form and skeletal structure but they differ in geometry and size of spicules, number of spicule categories and structure of euctosomal and subectosomal skeletons.

This species is enigmatic in its higher systematic placement. On the one hand C. (C.) noarlungae has a classical, albeit thin euctosomal skeleton typical of Thalysias species, consisting of erect plumose brushes of smaller euctosomal auxiliary spicules. This feature is structurally discrete from the primary dendritic, and secondary plumo-reticulate choanosomal skeleton. Conversely, there is only a single category of auxiliary style which forms these euctosomal brushes, whereas the larger (subectosomal) auxiliary spicules are confined to inside the choanosomal fibres. Consequently this species technically belongs to C. (Clathria) (in having an undifferentiated euctosomal-subectosomal skeletal composition). Clathria (C.) noarlungae may be confused with C. (Dendroclathra) curviclhel and C. (D.) elegantula due to superficial similarities in spiculation and fibre characteristics, but it differs from these (and other Dendroclathra) in having two different auxiliary spicule geometries, with palmate isochelae instead of arcuate-like isochelae, and different skeletal construction.

This species differs from all other known Clathria (and other Microcionidae) in several features: orange colouration; bulbous-lobate digitate growth form; rounded bulbous surface projections; absence of choanosomal principal styles, where dendritic multispecific primary spongins fibres are cored by subectosomal auxiliary styles, and the secondary fibre system is aspicular, plumo-reticulate, and sparsely echinated by vestigial acanthostyles; and specific spicule geometries.

Clathria (Clathria) oxyphila (Hallmann, 1912) (Figs 57-58, Table 10)


MATERIAL. HOLOTYPE: AMZS1 (dry, fragment AME817); Off Marsden Point, Kangaroo L., SA, 35°30'S, 137°45'E, 344m depth, 19 viii. 1909, coll. FlV 'Endeavour' (dredge; label 'Wilsonella oxyphila (curviclhel) Hallmann, type'). PARATYPE: AME495 (dry): Oyster Bay, Tas, 42°40'S, 148°03'E, 60-80m depth, coll. FlV 'Endeavour', dredge; (specimen label 'Wilsonella oxyphila, Type'; AM register MS name 'Parclathria oxyphila sp. nov'.)

HABITAT DISTRIBUTION, 34-80m depth; substrate unknown; E. coast (Tas.) and Kangaroo L. (S. Aust.) (Fig. 57G).

DESCRIPTION. Shape. Fan, 150 mm high, 155 mm wide, planar or multplanar, with a small compressed, cylindrical basal stalk, 22 mm long, 18 mm diameter, thickly lobate, rounded, even margins. Colour. Grey-brown preserved. Oesces. Oscules dispersed on margins of branches. Texture and surface characteristics. Surface relatively even, with radiating longitudinal subdermal grooves and pitted and porous euctosome. Ectosome and subectosome. Ectosome membraneous with relatively heavy mesohyl matrix below surface, sparsely arenaceous, with very few choanosomal principal megascleres protruding through surface, and with sparse euctosomal skeleton of subectosomal auxiliary megascleres lying paratangential to surface, sometimes in light brushes around fibre endings. Choanosome. Choanosomal fibres immediately subdermal, becoming slightly plumose near periphery; choanosomal skeleton sometimes dendritic in places, usually plumo-reticulate. Spongins fibres well developed, clearly divided into primary (ascending, sinuous, multispecific) and connecting (transverse, aspicular) elements; coring megascleres vestigial principal styles, barely differentiated from subectosomal auxiliary styles; spongins fibres heavily echinated.
by acanthostyles, evenly dispersed over fibres; mesohyl matrix heavy, with few scattered subectosomal megascleres.

**Megascleres** (Table 10). Choanosomal principal styles slightly shorter and thicker, but otherwise with similar geometry to those occurring in peripheral skeleton; straight, hastate, with tapering or quasidiactinal, smooth bases.

Subectosomal auxiliary styles long, thin, slightly curved or sinuous, often with blackened axial canals; geometrically similar to principal megascleres.

Acanthostyles slightly sublylole, evenly spined, including oxeote modifications.

**Microscleres** (Table 10). Palmate isochelaic sigmoid with reduced alae or vestigial teeth resembling true sigmas; isochelaic predominant on membraneous ectosome.

Toxas intermediate between wing-shaped and u-shaped, uncommon, with low, rounded central curves, slightly reflexed points.

**Larvae.** Incubated parenchymella larvae oval-elongate, 120 x 210μm, with moderately light mesohyl.

**REMARKS.** This species was included in *Wilsonella* by Hallmann (1912, 1920) and other authors on the basis that principal and auxiliary styles were allegedly undifferentiated, but re-examination of type material found them to be similar but not identical in geometry (both relatively vestigial and modified quasidiactinal form). In this respect the species is similar to C.
TABLE 9. Comparison between present and published records of *Clathria (Clathria) noartengae* sp. nov. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (SAMTS4047)</th>
<th>Specimen (NCI0662468X)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chanoosomal principal styles</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>167-(204.4)-236 x 2.5-(4.8)-7.8</td>
<td>232-(250.2)-278 x 3- (4.3)-5</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>87.5-(112.8)-156 x 1.8-(3.4)-4.6</td>
<td>117-(146.0)-175 x 2- (2.7)-3.5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>36-(46.6)-54 x 3.8- (5.2)-6.5</td>
<td>48-(55.6)-61 x 4.5- (5.2)-6</td>
</tr>
<tr>
<td>Vestigial auxiliary styles</td>
<td>133-(186.2)-202 x 1.5-(2.1)-2.6</td>
<td>118-(170.1)-186 x 1.0-(1.6)-2.0</td>
</tr>
<tr>
<td>Chela I</td>
<td>3-(6.3)-8.5</td>
<td>5-(7.3)-10</td>
</tr>
<tr>
<td>Chela II</td>
<td>12-(13.5)-16.5</td>
<td>13-(15.7)-19</td>
</tr>
<tr>
<td>Toxas</td>
<td>36-(159.5)-216 x 0.4-(0.8)-1.1</td>
<td>19-(145.3)-265 x 0.5-(0.9)-1.5</td>
</tr>
</tbody>
</table>

(C.) *piniformis*, C. (C.) *raphanus* and C. (Dendrocia) *elegantula*, all referred here to an artificial species-group termed the 'oxyphila' group, loosely corresponding to Hallmann's (1912, 1920) concept of *Wilsonella* (which is also possibly artificial). The present species differs from these by its sigmoid microscelers (virtually intermediate between palmate and arcuate-like geometry). Hallmann (1912) suggested that these chelae were arcuate, and thus he considered that the species had affinities with C. (Dendrocia) *curvichela*, but they actually appear to be no more than slightly modified, vestigial palmate forms. Similarly, Hallmann (1912) did not record toxas in his description, which are definitely present in type material. The modification of echinating acanthostyles to acanthoxeote megascelers in this species is reminiscent of *Crellidae* but this modification is superficial. *Clathria (C.) oxyphila* was transferred to *Paradoryx* on the basis of its alleged arcuate chela, but in all other respects the species is clearly a *Clathria* (Clathria).

*Clathria (Clathria) partita* Hallmann, 1912 (Figs 59-60)

*Clathria partita* Hallmann, 1912: 223, pl.32, fig.3, text-fig.46; Hooper & Wiedenmayer, 1994: 260.

*Clathria (Clathria) cf. partita*; Rudman & Avern, 1989: 335.


**MATERIAL.** HOLOTYPE: AME1024(dry); Unknown locality, South Australian coast, 60m depth, 12.vii.1909, coll. FIV 'Endeavour' (dredge); (label 'Pseud anchinoae partita, type').

**HABITAT DISTRIBUTION.** 60m depth; substrate unknown; SA (Hallmann, 1912), and possibly S WA (Rudman & Avern, 1989) (Fig. 59F).

**DESCRIPTION.** Shape. Arborescent branching. 340mm long, 160mm wide, with a long cylindrical stalk, 55mm long, 14mm diameter, planar, bifurcate and occasionally anastomosing flattened branches, 12-25mm wide, approximately 8mm thick.

*Colour.* Orange alive (Rudman & Avern, 1989), brown, with a slightly whitish ecbosomal crust.

*Oscules.* Small oscules, up to 2mm diameter, on lateral sides of branches.

*Texture and surface characteristics.* Surface rugose, laterally striated, resembling *Ectyoplasia tabula* (Rapsaliidae; Hooper, 1991: Fig. 50), and margins of branches slightly wider and more spartuliforous than basil portions.

*Echosomal and subectosomal.* Ecbosomal skeleton almost halichondroid, well differentiated from choanosomal region, consisting of paraskeletal multispiriculature of subectosomal auxiliary styles, forming criss-cross tracts on surface.

*Choanosome.* Choanosomal architecture basically isodictyal, consisting of differentiated axial and extra-axial sections of skeleton; axial region composed of very heavy and sinuous spongin fibres, forming relatively tight, oval or elongated triangular meshes; axial fibres divided into larger primary and smaller secondary elements, both containing paucispicular core of choanosomal principal styles; extra-axial skeletal architecture an irregular isodictyal reticulation of sinuous spongin fibres of approximately same diameter as axial secondary elements, relatively lightly invested with spongin, containing uni-, bi-, or more
rarely paucispicular tracts of choanosomal styles; extra-axial fibres incompletely divided into primary (ascending) and secondary (vaguely transverse) components, differentiated mainly by number of coring spicules; echinating acanthostyles sparse, evenly distributed throughout skeleton, rarely incorporated into fibres (cf. Hallmann, 1912); some choanosomal principal styles may protrude through (echinate) fibres, particularly in extra-axial skeleton; mesohyl matrix very light containing few subectosomal auxiliary megascleres.

**Megascleres.** Choanosomal principal styles short, slightly curved or straight, almost hasteate, with smooth rounded or very slightly subtylote bases. Length 112-(172.6)-239µm, width 5-(8.7)-12µm.

Subectosomal auxiliary styles long, slightly curved or straight, fusiform, with rounded or slightly subtylote bases. Length 222-(267.7)-315µm, width 3.5-(5.1)-7µm.

Acanthostyles slightly subtylote, with vestigial spines and an aspiny basal region. Length 56-(60.4)-88µm, width 3-(5.0)-6µm.

**Microscleres.** Isochelae absent.

Toxas sinuous raphidiiform, usually symmetrical with slight angular central curvature and straight points, but asymmetrical and reflexed examples also occur. Length 72-(115.6)-212µm, width 0.5-(0.7)-1.2µm.

**REMARKS.** This species was referred to *Pseudarchimnoe* by de Laubenfels (1936a) because it lacked chelae microscleres, but that feature has since been shown to be of little systematic value (e.g., Burton, 1940: 111). As noted by Hallmann (1912), *C. (C.) partita* is known only from a single dry specimen, and it is possible that isochelae may be eventually discovered in other better preserved specimens should additional material become available.

**Clathria (C.) partita** has an unusual skeletal construction, combining features of myxillid-like microcionids (e.g. a basically isodictyal extra-axial skeleton closely resembling *C. (Isosciella) eccentrica*) and raspalliid-like microcionids (e.g. compressed axis of *C. (Axosciella) canaliculata*), and features of the compressed axial skeleton are also reminiscent of the skeletal plan seen in certain Axinellidae such as *Cymbastela*. On the basis of these characteristics *C. (C.) partita* is similar to *C. (C.) rubens* (Lendenfeld).

The record of *C. (C.) partita* from WA (Rudman & Avern, 1989), is based on a photograph without accompanying sample. The photograph was taken of a nudibranch (*Rostanga calumnus* Rudman & Avern) feeding on an orange sponge from Esperance Bay (33°51'S, 121°57'E).

**Clathria (Clathria) paucispicula** (Burton, 1932) (Fig. 61)

**Rhaphidoplus paucispiculatus** Burton, 1932a: 320, pl.56, fig.1, text-fig.30; Burton, 1940: 111; Desqueyroux, 1975: 68; Koltun, 1964a: 75; Desqueyroux-Faundez & Moyano, 1987: 49.

**Clathria paucispicula**; Hooper & Wiedenmayer, 1994: 260

**MATERIAL.** HOLOTYPE: BMNH1928.2.15.243a: Near Shag Rocks, South Georgia, 53°43.4'S, 40°57.0'W, 171m depth, coll. R.R.S. 'Discovery' (dredge).

**HABITAT DISTRIBUTION.** 74-198m depth; on mud, sand and rock substrates; Australian Antarctic Territory: Queen Mary Land (Koltun, 1964a) (Fig. 61D); Also Falkland Is, South Georgia and S. Shetland Is (Burton, 1932a), Mar del Plata, Argentina (Burton, 1940), Low Is, Chilean Antarctic Territory (Desqueyroux, 1975), Tierra del Fuego (Desqueyroux-Faundez & Moyano, 1987).

**DESCRIPTION.** Shape. Massive, flabellate-digitate with irregular ridges and convoluted branches.

**Colour.** Live colouration unknown, light brown preserved.

**Oscules.** Large oscules 3-5mm diameter sparsely scattered on apex of ridges.

**Ectosome and subectosome.** Surface skeleton tangential confused crust of smaller ectosomal auxiliary styles, choanosomal principal styles and foreign spicule fragments together forming a dense crust 0.5-1.0mm thick; immediately below tangential ectosomal skeleton are erect bundles of both auxiliary styles (producing an irregular radial palisade of spicules), and principal styles (more sparsely dispersed).

**Choanosome.** Skeletal architecture reticulate, slightly plumo-reticulate near periphery, less organised towards axis; spongion fibres moderately well developed cored by pauci- or multispicular ascending tracts and interconnected by uni- or paucispicular tracts of choanosomal principal styles, producing rectangular or triangular meshes up to 250µm diameter; echinating megascleres absent; mesohyl matrix light, smooth, unpigmented.
**Megasclices.** Choanosomal principal styles long, thick, slightly hastate pointed or occasionally slightly telescoped pointed, curved at centre, with smooth rounded or slightly subtylote bases. Length 535-(663.4)-754 μm, width 18-(23.3)-31 μm.

**Subectosomal auxiliary styles** relatively long, thick, straight or slightly curved near basal end with evenly rounded smooth bases and tapering fusiform points. Length 255-(318.6)-402 μm, width 6-(10.4)-14 μm.

Echinating spicules absent.

**Microsclices.** Absent.

REMARKS. This species resembles a Suberitidae (Hadromerida) in skeletal structure, with the main clue as to its affinities with Microcionidae being the possession of megascleres that are not truly tylote in geometry, two distinct categories of principal and auxiliary megascleres, and slight compression of the skeleton in the axial region not generally seen in suberitids. Certain allocation of this species is difficult given that spicule diversity and skeletal structure are the main diagnostic characters for microcionids, and the species is aptly named for the reduction in these characters. It is well known and possibly widely distributed in Antarctic waters.

Clathria (Clathria) pauper Brandsted, 1926 (Figs 62-63).

Clathria pauper Brandsted, 1926: 3, text-fig. 3; Burton, 1929a: 398; Burton, 1940: 109; Koltun, 1964a: 69, pl.12, figs 4-6; Sánchez, 1978: 66-67, text-fig.40; Desqueyroux-Fauzeau & Moyano, 1987: 50.

Ramoses pauper; de Laubenfels, 1936a: 109.

MATERIAL. HOLOTYPE: NRHM (fragments BMNH 1930.11.5.2, AMZ2239): N. of Discovery Inlet, Victoria Land, Antarctica, 640m depth, 10.i.1924, coll. Sten Warren (dredge).

HABITAT DISTRIBUTION. 10-640m depth; hard and soft substrates; Australian Antarctic Territory: Victoria Land, Banzare Coast, Wilkes Land (Brandsted, 1926; Koltun, 1964a) (FIG. 62G). Also SW. Maldonado, Mar del Plata, Argentina, S. Brazil (Burton, 1940), Cape Sebastião, Cape Domingo, Rio Grande, Tierra del Fuego (Sánchez, 1978).

DESCRIPTION. Shape. Erect branching digitate sponge, up to 80mm high.

Colour. Grey-brown preserved.

Oscules. Unknown.

Texture and surface characteristics. Texture firm, compressible, elastic; surface conulose with irregularly digitate processes, up to 20mm long and 4mm thick, and with convoluted distinct ectosomal membrane visible between conules.

Ectosome and subectosome. With irregular plumose brushes of subectosomal auxiliary styles protruding from end of choanosomal primary skeletal columns.

Choanosome. Skeletal architecture plumose-reticulate, with differentiated primary and secondary fibre systems; primary fibres ascending, multispiracular, diverging near surface, cored by erect choanosomal principal styles with points of spicules directed upwards and outwards; skeletal columns dominated by spicules with poor spon-

**Clathria (Clathria) perforata** (Lendenfeld, 1887) (Fig. 64)

*Anthrochalina perforata*, in part, Lendenfeld, 1887b: 788; in part, Lendenfeld, 1888: 89-90. (Not Lendenfeld, 1887b: pl.22, fig.44.)


**MATERIAL.LECTOTYPE:** AMMG9010: Port Phillip. Vic, 38°09'S, 144°52'E, other details unknown (specimen label reads *'Anthrochalina perforata*
forata could also be assigned to Pandaros or Echinoclathria, whereas the few vestigial acanthostyles seen in the lectotype suggest that Clathria (Clathria) is more appropriate.

**Clathria (Clathria) piniformis** (Carter, 1885) (Figs 65-66, Table 11)

*Dictycocylindrus piniformis* Carter, 1885f: 354.  
*Wilsonella piniformis*; Hallmann, 1912: 241.  
*Paradoryx piniformis*; Hallmann, 1920: 768.

OTHER MATERIAL: VIC - NMVRN412-508.

**HABITAT DISTRIBUTION.** 38-40m depth; substrata unknown; Port Phillip Bay (Fig. 65G).

**DESCRIPTION.** Shape. Massive, subspherical lobate or lobo-digitate growth form, 110-130mm long, 55-65mm wide, with thick cylindrical stalk, 45mm long, 18-22mm diameter.  
Colour. Bright orange-brown alive, olive-brown preserved.  
Oscules. Large oscules, 2-4mm diameter dispersed over both faces of digitate lobes.  
Texture and surface characteristics. Surface rugose, with irregularly distributed conules, and a skin-like dermis.  
Ectosome and subectosome. Ectosome membraneous, with tangential and paratangential bundles of subectosomal auxiliary styles, sometimes forming quite thick, simous tracts.  
Choanosome. Choanosomal skeleton reticulate; spongion fibres well developed, thin, forming simous tracts, branching and splitting, and producing oval or elongate meshes; spongion fibres without clear differentiation between primary or secondary elements, although thicker fibres, usually ascending and cored by principal styles, whereas connecting fibres usually aspiculose; spongion fibres cored with paucispicular tracts of vestigial choanosomal principal styles, and echnimated by small acanthostyles in heavy concentrations and relatively evenly dispersed; mesohyl matrix heavy, with numerous extra-fibre spicules, especially acanthostyles and auxitary styles in the peripheral skeleton.

**Megascaleres** (Table 11). Choanosomal principal subystyles very thin, vestigial, with blackened axial canals, fusiform, usually straight, some-
times slightly curved, with rounded, tapering or more frequently quasidiactinal, smooth bases.

Subectosomal auxiliary styles almost identical to principal styles, longer, thin, slightly curved or sinuous, fusiform, with basal endings similar to principal megascleres.

Acanthostyles slightly subtylote with vestigial, evenly dispersed spines, include quasidiactinal modifications to base. Microscleres (Table 11). Palmate isochelae rare, unmodified.

Toxas raphidiform, uncommon, with slight central curvature and reflected points, sometimes sinuous.

REMARKS. In vestigial spicule geometry and generally reduced skeletal structures C. (C.) piniformis is most similar to C. (C.) oxyphila, both of which have most of their megascleres modified to quasidiactinal forms (see remarks for C. oxyphila), but the present species has quite different microsclere geometry, skeletal construction and growth form.

Clathria (Clathria) raphanus (Lamarck, 1813) (Figs 67-68)

*Spongia raphanus* Lamarck, 1813: 444; 1814: 373.

Clathria raphanus: Topsent, 1932: 100, pl.4, fig.9; Hooper & Wiedenmayer, 1994: 261.


Thalyseurypon raphanus; de Laubenfels, 1936a: 107.


MATERIAL. HOLOTYPE: MNHNTDS572 (dry): Australian seas, Peron & Lesueur collection, no other details known.

HABITAT DISTRIBUTION. Ecology unknown; Australia.

DESCRIPTION. Shape. Arborescent fan, 90mm high, 95mm wide, with flattened multilinar branches 48-80mm long, 5-10mm thick, which anastomose tightly to form several lobes.

Colour. Grey-brown dry.

Oscules. Large oscules, up to 3.5mm diameter, scattered over both faces of flattened branches.

Texture and surface characteristics. Surface microconulose with tapering processes; texture harsh in dry state.

Ectosome and subectosome. Ectosomal skeleton a sparse tangential or paratangential layer of subectosomal auxiliary styles.

Choanosome. Choanosomal skeleton almost regularly reticulate, with heavy spongin fibres forming oval or elongate meshes, without differentiation of primary or secondary elements; spongin fibres almost totally uncured, and where present, choanosomal principal styles form uniform paraspicular tracts within axis of fibres; spongin fibres sparsely echinated by acanthostyles; mesohyl light (dried material).

Megascleres. Choanosomal principal subystylodes fusiform, slightly curved, with rounded or slightly subtylote, smooth bases. Length 108-148.6-230μm, width 3.5-5.6-9μm.

Subectosomal auxiliary subystylodes straight or slightly curved, thin, fusiform, with subtylote, smooth bases. Length 168-(225.7)-315μm, width 1.5-(2.6)-4μm.

Acanthostyles curved, slightly subtylote, with vestigial, granular, evenly dispersed spines. Length 47-(65.2)-82μm, width 2.5-(4.1)-5μm.

Microscleres. Absent.

REMARKS. This species is known only from an antiquated dried specimen collected from 'somewhere in the vicinity of Australia' (Topsent, 1932). It was made the type species of Thalyseurypon de Laubenfels and has since been the subject of lengthy discussions by de Laubenfels (1936a), Hechtel (1965), Wiedenmayer (1977), van Soest (1984b) and Fromont & Bergquist (1990). These discussions have centred mostly on the value of the loss of meniscolloid (chelae) microscleres used as a valid taxonomic character. These arguments have been addressed in the synopsis of Thalyseurypon (see Included Genera, above). Clathria raphanus bears little resemblance to Pandaros as supposed by Wiedenmayer (1977) which has flattened fibres, or Echinoclathria (as interpreted by Wiedenmayer, 1989) which has smooth echinating megascleres. This species is most appropriately placed in Clathria (Clathria) based on the distribution and geometry of its megascleres.
Clathria (C.) raphanus is depauperate in morphological features, with a reduced spicule diversity and vestigial spicule development, and a relatively heavy evenly reticulate fibre skeleton, and in this respect the species is associated with a species-group (the 'oxyphila' group; also containing C. (C.) piniformis, C. (C.) oxyphila and C. (Dendrocl) elegansula.

Clathria (Clathria) rubens (Lendenfeld, 1888) (Figs 69-70, Table 12)

*Thallassodendron rubens* Lendenfeld, 1888: 223.
Not *Thallassodendron rubens* var. *lamel/ia*, in part, Lendenfeld, 1888: 224, pl.7.

Clathria rubens, in part; Whitelegge, 1901: 85-86, pl.11, fig.13.
Clathria rubens; Hallmann, 1912: 218-223, pl.32, fig.1, text-fig.45; Burton, 1934a: 558; Burton, 1936b: 29a; Shaw, 1927: 425-426; Guiller, 1950: 7; Hooper & Wiedenmayer, 1994: 261.

Clathria *tenuiflora* Whitelegge, 1901: 82-83, pl.11, fig.10; Whitelegge, 1902b: 274, 279, 287, 287; Hallmann, 1912: 211.

*Thalassias tenuiflora* de Laubenfels, 1936a: 105.
Lischeclamina pedunculata var. mollis in part; Lendenfeld, 1888: 91-92; Whitelegge, 1902b: 274.

Not Microciona rubens Bergquist, 1961a: 38.

MATERIAL. LECTOTYPE: AMG9119 (dry); Port Jackson, NSW, 33°51'S, 151°16'E, no other details known (label 'Thalassodendron rubens RvL, type'). PARALECTOTYPES: AMZ455 (slide AMG3585: same locality (dry, label 'Clathria rubens, type or cotyple, Lendenfeld's duplicate A50'). AMZ634: same locality; (dry, label 'Thalassodendron rubens RvL, type or cotyple, Lendenfeld's no.240'). BMNH1887.1.24.35 (fragment AMG3586: same locality, Ramsay collection (listed as 'var. intermedia MS name'). HOLONOTYPE OF *C. tenuiflora*: AMG3045(dry): Lake Illawarra region, NSW, 34°32'S, 150°50'E (label 'Thalassias tenuiflora Whitelegge, type'). OTHER MATERIAL: NSW - QMG300452.

HABITAT DISTRIBUTION. Shallower than 56m depth; on shell, gravel and Halimeda substrates; Port Jackson (Lendenfeld, 1888), Broken Bay, Lake Illawarra, and Woolongong (NSW) (Whitelegge, 1901; Hallmann, 1912); Direction and Eagle Is, Great Barrier Reef (FNO) (Burton, 1934a); Maria I. (Tas) (Shaw, 1927; Guiller, 1950); St Vincent Gulf (SA) (Hallmann, 1912) (Fig. 69G).

DESCRIPTION. Shape. Arboresecent digitate sponge, 100-190mm high, 60-110mm wide, with numerous anastomosing, repeatedly bifurcate, stoloniferous branches, 30-75mm long, up to 19mm diameter, without definite basal stalk; branches subcylindrical, slightly flattened at ends.

Colour. Grey-brown in ethanol.

Oscules. Large oscules, 2-4mm diameter, scattered over surface of branches, often raised on a small lip.

Texture and surface characteristics. Surface even, optically smooth, but with prominent subdermal grooves and stellate drainage canals radiating from a central osculum (not seen in dry material).

Ectosome and subectosome. Ectosome region membranous, with a sparse tangential layer of subectosomal auxiliary styles, through which protrude sparse brushes of choanosomal principal styles; subectosomal skeleton has auxiliary styles dispersed paratangentially, and peripheral choanosomal fibres diverging slightly just below surface.

Choanosome. Choanosomal skeletal architecture subsidicystal, with triangular or irregular meshes and thin spongine fibres, cored by uni-, bi- or paucispicular tracts of choanosomal principal styles; spongine fibres imperfectly divided into axial and extra-axial components, differing only in fibre diameter; axial fibres comparatively thick, paucispicular, forming cavernous and irregular ovaloid meshes; extra-axial skeletal meshes more obviously triangular, subsidicystal, with thin, paucispicular ascending primary spongine fibres interconnected by uni- or bipspicular secondary fibres; echinating acanthostyles lightly and evenly dispersed over fibres; mesohyl matrix heavier in peripheral skeleton than at core, containing few principal and auxiliary styles and microscleles.

Megascleres (Table 12). Choanosomal principal styles thick, mostly straight, hastate-fusiform, with rounded, tapering or subtylote bases, usually smooth, occasionally microspined.

Subectosomal auxiliary stylostyles longer than principal styles, thin, straight, fusiform, with slightly subtylote, microspined bases.

Acanthostyles subtylote, with mostly granular, evenly dispersed spines, sometimes with aspinose necks, and some clearly intermediate forms of choanosomal styles.

Microscleles (refer to Table 12 for dimensions). Palmate isochelae rare, small, unmodified.

Toxas accolada, thin, long, usually with very large, angular, sometimes coiled, central curves, slightly reflexed points, or they may be nearly straight with coiled central flexion.

REMARKS. Clathria (C.) rubens is very similar to C. (C.) partita in skeletal architecture and fibre characteristics. Both species have a more-or-less differentiated axial and extra-axial choanosomal skeleton. Whereas the present species has an irregularly subisodictyal reticulate skeleton with ovoid meshes and heavy fibres, C. (C.) partita has a nearly regular Isociella-like isodictyal skeleton. These two species are also similar in the extent to which axial and extra-axial skeletons are separated (with more marked separation in C. (C.) partita), geometry of choanosomal styles and toxas (Figs 59, 69), and having similar growth forms (although branches are cylindrical in C. (C.) rubens but flattened in C. (C.) partita). Nevertheless, spicule geometries, fibre characteristics and spicule dimensions indicate that they are probably separate sibling species.

There are 3 other AM specimens which have been associated with C. (C.) rubens. One, AMZ4810 from Port Jackson (with label ‘Thalassodendron rubens, donated by A. Dendy’), is probably a fragment of the BMNH paralectotype, but this has not been verified. AMZ2241 from Tasmania (apparently identified by M. Burton, with an old label ‘Rhaphidophalus typicus, dried up in 1917-18’), and AMZ2246 (locality unknown, also identified by M. Burton, with an old label which reads ‘CRELLA incrustans’), were both obtained from the Antarctic Publications Committee (donated by Prof. Haswell). All three are in too poor condition to identify reliably, but they appear related to C. (Thalysias) cactiformis. The origin of the QM specimen, obviously of great antiquity, is not known (L. Cannon, pers. comm.), but it may have been an exchange specimen from the AM during Whitelegge’s era. That specimen certainly belongs to C. (C.) rubens.

The holotype of C. tenuifibra is also in poor condition, and irrespective of skeletal reconstitution following rehydration during sectioning only few features were discernible. What little can be seen of the skeletal structure is identical to C. (C.) rubens, particularly the fibre characteristics and spiculation, and on this basis the two species are merged here.

Clathria (Clathria) squalorum Wiedenmayer in Hooper & Wiedenmayer, 1994 (Figs 71-72)

Not Clathria dura Whitelegge, 1901: 83.
Not Clathria mollis Kirkpatrick, 1903: 249.


HABITAT DISTRIBUTION. 3.5-11 m depth; on sand, stone, mud and algal bed substrates; Bunbury-Shark Bay region (WA) (Fig. 71G).
TABLE 12. Comparison between present and published records of Clathria (Clathria) rubens (Lendenfeld). All measurements are given in µm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMG9119)</th>
<th>Paraleptotypes (N=3)</th>
<th>Holotype of C. tenuiflora (AMG9045)</th>
<th>Specimen (N=1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal</td>
<td>96-(135.3)-162</td>
<td>128-(135.6)-147</td>
<td>112-(139.2)-159</td>
<td>118-(140.6)-155</td>
</tr>
<tr>
<td>principal styles</td>
<td>x 5-(9.0)-11</td>
<td>x 5.5-(7.1)-9</td>
<td>x 3-(9.4)-11</td>
<td>x 6-(7.8)-10</td>
</tr>
<tr>
<td>Subectosomal</td>
<td>106-(157.2)-212</td>
<td>132-(146.2)-168</td>
<td>112-(153.7)-185</td>
<td>105-(139.2)-165</td>
</tr>
<tr>
<td>auxiliary styles</td>
<td>x 1.5-(2.9)-4</td>
<td>x 2.5-(2.9)-4</td>
<td>x 2.5-(3.7)-4.5</td>
<td>x 2.5-(3.3)-4.5</td>
</tr>
<tr>
<td>Echinating</td>
<td>55-(71.6)-111 x 3</td>
<td>58-(77.3)-112 x 4</td>
<td>51-(68.6)-118 x 3</td>
<td>48-(69.4)-108</td>
</tr>
<tr>
<td>acanthostyles</td>
<td>4.5-(5.6)-6.5</td>
<td>5.6-(6.9)-8.5</td>
<td>4.45-(8.5)-7.5</td>
<td></td>
</tr>
<tr>
<td>Chelae</td>
<td>6-(9.6)-13</td>
<td>7-(9.8)-13</td>
<td>8-(9.7)-11</td>
<td>6-(9.0)-12</td>
</tr>
<tr>
<td>Toxas</td>
<td>101-(153.4)-215</td>
<td>115-(161.6)-208</td>
<td>94-(126.3)-153</td>
<td>114-(138.6)-194</td>
</tr>
<tr>
<td></td>
<td>x 0.8-(1.3)-1.3</td>
<td>x 1-(1.4)-2</td>
<td>x 1.1-(1.2)-1.5</td>
<td>x 1-(1.4)-2</td>
</tr>
</tbody>
</table>

DESCRIPTION. Shape. Variable growth form, ranging from thickly encrusting with small stoloniferous digits, to digitate planar arborescent with anastomosing branches.

Colour. Live colouration unknown, beige preserved.

Oscules. Large oscules on apex and lateral margins of stoloniferous branches.

Texture and surface characteristics. Surface microconulose.

Ectosome and subectosome. Ectosomal skeleton hispid, with points of choanosomal principal styles protruding through surface individually or in small bundles, piercing a sparse paratangential layer of subectosomal auxiliary subtyloslyles.

Choanosome. Choanosomal skeletal architecture wide-meshed nearly rhenieretic reticulate, more regular in peripheral skeleton than in axis, with differentiated primary (ascending, multispiracular) and secondary (transverse, pauci- or unispiracular) spongin fibres; fibre diameter generally small (primaries 30-50µm; secondaries 10-22µm), fibre anastomoses rectangular, and fibres cored by choanosomal principal styles; coring spicules in axial region heavier, more plumose (protruding through fibres) than in peripheral skeleton; echinating acanthostyles relatively sparse, evenly distributed throughout skeleton; mesohyl matrix light, usually containing choanosomal and/or subectosomal megascleres dispersed between fibres.

Megascleres. Choanosomal principal subtyloslyles slightly curved, fusiform, entirely smooth, very slightly subtylote. Length 124-(152.4)-165µm, width 4-(8.8)-12µm.

Subectosomal auxiliary subtyloslyles straight, thin, fusiform, with smooth slightly subtylote bases. Length 85-(148.5)-184µm, width 2-(2.8)-4µm.

Acanthostyles slightly subtylote, with evenly dispersed relatively large spines, slightly less spines below basal region. Length 48-(62.3)-74µm, width 2-(4.2)-6µm.

Microscleres. Palmate isochelae unmodified. Length 4-(8.6)-12µm long.

Accolada toxas very thin, straight arms, sharply angular central curvature, occasionally raphidiform. Length 105-220µm, width 1-(2.2)-3µm.

REMARKS. Hallmann (1912) noted that C. dura var. mollis Hentschel was distinctly different from C. dura Whitelegge and he considered that Hentschel’s (1911) species required a new name. The subspecific name ’mollis’ is preoccupied by C. mollis Kirkpatrick, 1903, and so a new name C. squalorum was proposed by Wiedenmayer (in Hooper & Wiedenmayer, 1994). Some of the characters and measurements of the lectotype differ from those published by Hentschel (1911). His description was presumably based on a series of syntypes, but these have not been located or re-examined.

Comparison between the type material of C. (C.) squalorum and C. (Dendrocia) dura show that both species are different in several significant respects: (1) differences in the geometry of structural spicules where C. (C.) squalorum has differentiated principal and auxiliary spicules (and hence is referable to C. (Clathria)), and C. (D.) dura has completely undifferentiated structural megascleres (and hence is referable to C. (Dendrocia)); (2) palmate isochelae versus arcuate-like isochelae; (3) long thick accolada toxas versus no toxas; (4) nearly rhenieretic reticulation of thin fibres versus a regularly reticulate skeleton with heavy fibres, respectively. In having a slightly rhenieretic skeletal architecture C. (C.) squalorum is reminiscent of C. (Isosciella) ecentrica, although spicule geometry and spicule dimensions are otherwise different.

Clathria (Clathria) striata Whitelegge, 1907 (Figs 73-74, Plate 1F, Table 13)

Clathria striata Whitelegge, 1907: 495-496, pl.45, fig.27; Hooper & Wiedenmayer, 1994: 261.
Thalysias striata: de Laubenfels, 1936a: 105.
Rhaphidophius tenebratus: Whitelegge, 1907: 501–503, pl.45, fig.19.

MATERIAL, LECTOTYPE: AMG4344 (in part): Near Coogee, Sydney, NSW, 34°05’S, 151°10’E, coll. FIV ‘Thetis’ (dredge; label ‘Clathria striata; type’).
PARALECTOTYPES: AMG4344 (in part), Z823 (in part): Off Botany Bay, NSW, 34°00’S, 151°11’E, 40–46m depth, coll. FIV ‘Thetis’ (dredge; dry, two specimens, label ‘Thalysias striata; cotyless’).

HABITAT DISTRIBUTION. 40–50m depth; on rock substrate; central and S. coasts (NSW) (Fig. 73G).

DESCRIPTION. Shape. Flabellate, digitate or a combination of both, 170–285mm long, 30–110mm wide, with short, tapering, cylindrical stalk, 35–55mm long, 6–13mm diameter, cylindrical or flattened branches and even, slightly undulating, ragged margins.

Colour. Live colouration unknown, dark grey-brown preserved.

Oscules. Not observed on flabellate specimens, but small oscules, up to 2mm diameter, seen on lateral margins of branches for digitate specimens.

Texture and surface characteristics. Surface optically smooth, with prominent longitudinally radiating subdermal grooves and low ridges.

Ectosome and subectosome. Ectosome strongly hispid, with discrete, plumose, or paratangential tufts of subectosomal auxiliary spicules surrounding protruding choanosomal principal styles; principal styles in peripheral skeleton usually larger than principal spicules within fibres; ectosomal skeleton relatively dense in places, merely paratangential or sometimes tangential to the surface in other places; thick tracts of palmate isochelae mostly confined to dermal and subdermal regions; subectosomal region plumose, with diverging tracts of choanosomal principal styles intermingled with extra-fibre tracts of auxiliary styles, together producing relatively dense peripheral skeleton.

Choanosome. Choanosomal skeleton predominantly renieroid but with differentiated plumose and renieroid-reticulate components, and clearly differentiated axial and extra-axial regions but no well-marked separation of primary or secondary fibre elements (cf. Whitelegge, 1907); axial skeleton with very heavy, thick spongin fibres forming relatively tight ovoid meshes, with paucispicular core of choanosomal styles forming vaguely ascending skeletal tracts; extra-axial region with much heavier, rectangular, almost renieroid spicule skeleton, with a cross-cross of longitudinal and transversely orientated spicules, and spongin fibres lighter than in axis; longitudinal spongin fibres in periphery cored by paucispicular tracts of principal styles; transverse/ascending tracts with multispecific tracts of spicules, many protruding through fibres and forming plumose brushes at right angles to surface; tendency for some larger principal styles to form ascending tracts, and small styles to occur mainly in longitudinal tracts; ultimate choanosomal spicule tracts diverge into subectosomal region; echinatising acanthostyles relatively sparse in axis, only marginally more abundant in peripheral skeleton; mesohyl matrix heavy, granular, with few megascleres between fibres.

Megascleres (Table 13). Choanosomal principal styles thick, curved, relatively variable in length, fusiform, mostly sharply-pointed, less frequently with rounded points, with smooth rounded, or occasionally very slightly subtylote bases.

Subectosomal auxiliary subtylostyles thin, fusiform, straight or slightly curved, occasionally sinuous, usually with smooth, sometimes microspined, slightly subtylote bases, occasionally polytylote bases.

Acanthostyles subtylote, with small and evenly distributed spines.

Microscleres (Table 13). Palmate isochelae abundant, unmodified.

Toxas accolada, long, moderately thick, with sharply angular or slightly angular central curvature, straight unreflexed points.

REMARKS. Rhaphidophius tenebratus is a synonym of Clathria striata, both species having identical skeletal architecture, fibre characteristics and spicule geometry, although there is some variation in spicule dimensions between these two nominal species (Table 13). They differ only in growth form (C. striata being flabellate, R. tenebratus being digitate, with flattened and anastomosing branches; Fig. 73I). In his original description Whitelegge (1907) omitted to mention toxas, abundant in the preserved specimens but relatively rare in the dry holotype, and also, that echinatising acanthostyles were 0.6–0.8mm long (typographical error for 0.06–0.08mm).
Clathria (C.) striata is similar to C. (C.) sartaginula (Lamarck) in shape, slightly renieroid skeletal architecture, and to some extent spiculation. However, fibre characteristics differ markedly between the two species, particularly the density of coring and echinating spicules on fibres, the degree to which peripheral fibres radiate from the skeletal axis, and the very small but thick, stumpy choanosomal styles in C. (C.) sartaginula. This species is also compared with C. (C.) arcuophora and C. (C.) biclathrata in spicule geometry, spicule dimensions, and to
some extent fibre characteristics. *Clathria (C.) striata* also has a similar skeletal architecture as *C. (C.) arcuophora*, differing substantially only in toxa geometry. All these species (*C. (C.) striata*, *C. (C.) arcuophora*, *C. (C.) sartaginula*, *C. (C.) crassa* and *C. (C.) biclathrata*), are characterised by their slightly renieroid or sub-renieroid choanosomal skeletons and spongine fibres cored by few, thick principal spicules. They are grouped together here in the 'striata' species
TABLE 13. Comparison between present and published records of *Clathria* (*Clathria* striata Whitelegge. All measurements are given in µm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMG3434)</th>
<th>Paralexotype (N=2)</th>
<th>Holotype of <em>R. tenerrima</em> (AMG3436)</th>
<th>QMG303755</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal</td>
<td>x12(17.9)-28</td>
<td>x14(19.2)-24</td>
<td>184(285.2)-246</td>
<td>15(19.1)-23</td>
</tr>
<tr>
<td>principal styles</td>
<td>158(268.3)-523</td>
<td>184(285.2)-246</td>
<td>193(282.2)-254</td>
<td>209(299.7)-462</td>
</tr>
<tr>
<td>Subectosomal</td>
<td>x3-(4.1)-6</td>
<td>x3(4.2)-6</td>
<td>175(274.4)-387</td>
<td>x2(2.9)-5</td>
</tr>
<tr>
<td>auxiliary styles</td>
<td>142(245.6)-363</td>
<td>153(229.2)-294</td>
<td>175(274.4)-387</td>
<td>x2(2.9)-5</td>
</tr>
<tr>
<td>Chelae</td>
<td>14(16.5)-21</td>
<td>14(16.4)-19</td>
<td>64(97.8)-112</td>
<td>6(92.2)-11</td>
</tr>
<tr>
<td>Toxas</td>
<td>153(223.4)-265</td>
<td>110(241.2)-255</td>
<td>108(202.4)-305</td>
<td>14(16.4)-20</td>
</tr>
</tbody>
</table>

group, *Clathria* (*C.*) *striata* differs from other 'striata' species in growth form, spicule geometry and spicule dimensions.

De Laubenfels (1936a) referred *C. striata* to *Thalysia* but his decision is not supported. Although there are relatively dense plumeous ectosomal brushes composed of auxiliary megascleres (structurally similar to *Clathria* (*Thalysia*)) there is only one undifferentiated size category (142-387 µm long) (composition of *Clathria* (*Clathria*)).

*Clathria* (*Clathria*) *toxipraedita* Topsent, 1913 (Figs 75-76)

*Clathria toxipraedita* Topsent, 1913a: 620-621, pl.5, fig.4, pl.6, fig.12; Burton, 1932a: 319; Burton, 1934b: 32, pl.4, figs 2-3, text-fig.3; Koltun, 1964a: 68-69, pl.12, figs 15-24; Koltun, 1976: 187; Hooper & Wiedenmayer, 1994: 262.


**MATERIAL.** HOLOTYPE: RSME1921.143.1400: Burwood Bank, off Tierra del Fuego, S. Atlantic, 54°25'S, 57°32'W, 112 m depth, 1.xii.1903, coll. R.R.V. 'Scotia' (dredge).

**HABITAT DISTRIBUTION.** 93-540 m depth; on mud, sand and hard substrates; Australian Antarctic Territory; MacRobertson Land (Koltun, 1976) (Fig. 75H). Also Tierra del Fuego (Topsent, 1913a), South Georgia, Shag Rock (Burton, 1932a, 1934b), South Sandwich Is, Falkland Is (Koltun, 1964a), Palmer Archipelago, Antarctica (Burton, 1932a).

**DESCRIPTION.** Shape. Massive encrusting, subspherical, 70 mm long, 60 mm wide, up to 25 mm thick, composed of fused irregular fibre bundles superficially resembling a *Pseudaxinella* (Axinellidae).

**Colour.** Pale yellow-brown preserved.

**Oscules.** Not seen.

**Texture and surface characteristics.** Texture harsh, compressible; surface prominently conulose, hispid.

**Ectosome and subectosome.** Surface skeleton with protruding single principal styles embedded in peripheral skeleton and forming a plumose hispid surface; thick bundles of both subectosomal auxiliary styles and toxa microscleres surrounding protruding principal spicules, and also scattered paratangentially across surface.

**Choanosome.** Skeletal architecture plumo-reticulate, with slightly differentiated axial and extra-axial regions; in peripheral region skeleton more plumose than reticulate, with skeletal columns diverging but without connecting elements; skeletal columns composed of erect multispherical bundles of light spongin fibres fully cored by choanosomal principal styles; spicules mostly contained within fibres but also slightly protruding through fibres producing the plumose ('spicate') arrangement; towards base skeleton more disorganised, predominantly reticulate, and spicules more-or-less completely contained within fibres; echinating acanthostyles moderately abundant; mesohyl matrix heavy, smooth, containing abundant microscleres.

**Megascleres.** Choanosomal principal styles long, robust, straight or slightly curved near base, with fusiform points and rounded or slightly subtylolate smooth bases. Length 518-(616.2)-894 µm, width 19-(27.7)-33 µm.

Subectosomal auxiliary subtylostyles short, very slender, straight, hastate pointed, subtylole, with pointed (mucronate) or minutely spined bases. Length 278-(310.2)-343 µm, width 4-(4.8)-6 µm.

Echinating acanthostyles small, straight, long tapering fusiform pointed, subtylole or tylote bases, with small spines and aspinoe bases and points. Length 102-(99.2)-154 µm, width 4-(7.8)-11 µm.

**Microscleres.** Palmate isochelae in two size categories, both modified. Smaller chelae with relatively small alae and a small plate/ridge on central inner margin of shaft protruding between
the alae. Length 12-(15.7)-18µm. Larger chelae often cleistochelate, with teeth partially or completely fused and a large central plate/ridge on inner margin of shaft between alae. Length 20-(22.3)-24µm.

Two categories of toxas. Longer toxas accolada, very long, thick, with sharply angular but only slight central curvature, straight arms and smooth fusiform points. Length 635-(1022.6)-1470µm, width 4-(5.2)-6µm. Smaller toxas wing-shaped, more widely curved at centre, occasionally looped/twisted at centre, with slightly reflexed arms and points. Length 56-(85.3)-132µm, width 0.5-(1.1)-2.0µm.

REMARKS. Clathria (C.) toxipraedita has peculiar, large palmate cleistochelae resembling sigmacistras (in some Mycalidae), with alae varying from partially to completely fused, and with the addition of a well formed central plate-like ridge protruding between the alae (Fig. 76G). Smaller chelae have smaller diffuse alae and a smaller central plate-like ridge, indicating that they are ontogenetic stages of the larger forms. Cleistochelae are known in a number of other poecilosclerids including a several microcionids (e.g. C. (Microciona) cleistochela Topsent, C. (T.) ramosa (Dendy), Antho (Plocamia) signata (Topsent)), whereas the central plate-like ridge appears to be unique to the family and only previously recorded from Mycalidae (E. Hajdu, pers.comm.). Clathria toxipraedita is unusual amongst the aboral species in having a great diversity of spicule geometries; generally microcionids from Antarctic waters appear to have reduced spicule diversity in comparison to the tropical fauna.

**Clathria** (Clathria) transiens Hallmann, 1912
(Figs 77-78, Plate 2A, Table 14)

Clathria transiens Hallmann, 1912: 205, 226-234, 253, 254, pl.33, figs. 1-3, pl.34, fig.2, text-figs 47-48; Shaw, 1927: 426; Burton, 1934a: 599; Guiler, 1950: 7; Burton, 1959a: 244; Wiedenmayer, 1989: 57, pl.5, fig.8, pl.23, fig.6, text-fig.38; Hooper & Wiedenmayer, 1994: 262; Thalysias transiens; de Laubenfels, 1936a: 105. cf. Microciona prolifera, tropus styloa and tropus senta, Vosmaer, 1935a: 611, 649-650, 666.

**MATERIAL.LECTOTYPE:** AME302: off Devonport, N. coast Tas., 41°11'S, 146°21'E, coll. FIV 'Endeavour' (dredge) (label 'Clathria transiens; typical form a'). PARALECTOTYPES: AMZ49 + EB19: 64km W. of Kingston, SA, 36°50'S, 139°05'E, 60m depth, coll. FIV 'Endeavour' (dredge) (specimen cut in half, form b). AME779: same locality; (form c).


**HABITAT DISTRIBUTION.** Shallow subtidal-60m depth; on rock substrates; Port Phillip (Vic) (Hallmann, 1912; present study), Farnmex Is and Devonport (Tas) (Shaw, 1927; Guiler, 1950; Wiedenmayer, 1989; present study), Kingston (SA) (Hallmann, 1912), Qld. (Burton, 1934a) (Fig. 77G). Burton (1959a) recorded the species from the Red Sea but his material was not described, and his record is questionable.

**DESCRIPTION.** Shape. Usually arborescent with short, bulbous branches, 75-185mm long, 40-160mm wide; stipitate with short cylindrical stalk, 25-55mm long, 8-22mm diameter; branches simply bifurcate, or repeatedly bifurcate and arborescent, flabell-digitate, or they may anastomose to form thickly clathrous, bushy lobes.

**Colour.** Live colouration vermilion red (Munsell 5R 3/10), beige-brown or dark brown preserved.

**Oscules.** Small oscules, up to 3mm diameter, in ridges and grooves of branches.

**Texture and surface characteristics.** Surface markedly conulose, with conules actually being rounded vestigial branches; with or without irregular ridges striating surface; surface covered by distinct membraneous skin-like ectosome.

**Ectosome and subectosome.** Ectosome minutely hispid, with the points of larger choano somal principal styles protruding through membraneous surface, with a paucisicular, usually tangential layer of subectosomal auxiliary styllostyles, lying on or just below surface; occasionally auxiliary styles form plumose brushes, surrounding 1 or more principal style; subectosomal skeletal structure vaguely plumose, formed by diverging peripheral spongin fibres and spicule tracts of smaller choano somal principal styles.

**Choanosome.** Choano somal skeletal architecture almost regular, radial-renieroid, with poorly differentiated axial and extra-axial skeletons; axis formed by evenly anastomosing spongin fibres, forming relatively cavernous, rectangular or circular meshes; spongin fibres bored by pauci- or multispecific tracts of smaller choano somal principal styles; primary and secondary skeletal tracts in axis vaguely differentiated, but not pronounced, and spongin fibre elements only dif-
ferentiated by density of coring spicules; extraaxial skeletal architecture regularly renieroid, with ascending plumo-reticulate primary and secondary fibre elements which diverge increasingly towards surface; fibre anastomoses much closer towards periphery than at core; primary ascending fibres heavily multispectular, secondary transverse fibres more irregular, pauci- or multispectular; all fibres relatively heavily invested with spongin; echinating acanthostyles abundant on all fibres, only slightly more dense at fibre nodes; mesohyl matrix light, containing numerous subectosomal styles and microscleres scattered between fibres.

**Megascleres** (Table 14). Choanosomal principal styles divided into 2 (overlapping) size classes: larger found in brushes protruding from surface; smaller coring choanosomal spongic fibres; both similar in geometry, fusiform, straight or slightly curved, with smooth, rounded or very slightly subtylote bases.

Subectosomal auxiliary subtylostyles straight, thin, fusiform, with smooth subtylole bases, variable length but only 1 size class.

Acanthostyles slightly subtylote, very sharply pointed, with granular, vestigial, evenly dispersed spines, sometimes completely smooth.
**Microscleres** (Table 14). Palmate isochelae large, unmodified, rare in some material.

Toxas oxhorn, relatively thick, with rounded, large or small central curvature, slightly reflexed or straight arms.

**Larvae.** Larvae viviparous, ovoid or elongate parenchymella, up to 210μm diameter, with larval megascleres dispersed throughout axis.

**REMARKS.** The status of specimen AMZ743 (from Port Phillip Bay) is not completely certain. The label states that it is a ‘dry, type’, but the four type specimens described by Hallman (1912) are accounted for by other AM register numbers (cited above). It is possible that the specimen is a fragment of the paratype (AMZ744), as both come from the same locality.

**Clathria (C.) transiens** is relatively well known from SE Australian waters (e.g. Wiedenmayer, 1989). The species appears to be the temperate water equivalent of the widely distributed tropical species C. (Thalysias) lendenfeldi (see Hooper et al., 1990). Both species have a large range of growth forms and comparable surface features, although this resemblance is superficial, in the field, and the two species differ markedly in most other features. The ectosomal features of **C. (C.) transiens** (with protruding chaenosomal styles), and fibre characteristics (almost a subrenieroid peripheral skeleton), are also reminiscent of **C. (T.) vulipina**, although growth form and spicule diversity differ significantly between these two species. **Clathria (T.) darwiniensis** sp. nov. from northwest Australia is similar to **C. (F.) transiens** in ectosomal features, vaguely subrenieroid skeletal architecture, and toxa morphology, but differs in acahanostyle geometry, possession of 2 size classes of auxiliary styles, gross morphology and spicule dimensions.

**TABLE 14.** Comparison between present and published records of **Clathria (Clathria) transiens** Hallmann. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lechoptype (AMZ 302)</th>
<th>Paralectotypes (N=4)</th>
<th>Specimens (N=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large chaenosomal principal styles</td>
<td>273-(339.4)-409 x 12-(16.8)-19</td>
<td>264-(359.7)-528 x 13-(16.1)-19</td>
<td>269-(408.2)-632 x 9-(13.8)-19</td>
</tr>
<tr>
<td>Small chaenosomal principal styles</td>
<td>133-(188.4)-24 x 3-8-(13.2)-18</td>
<td>113-(170.3)-247 x 6-(9.5)-13</td>
<td>132-(191.8)-275 x 8-(11.2)-13</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>162-(272.4)-357 x 2.5-(4.8)-6.5</td>
<td>96-(249.2)-416 x 1.5-(3.6)-6</td>
<td>142-(277.0)-402 x 1.5-(4.2)-6</td>
</tr>
<tr>
<td>Echinating acahanostyles</td>
<td>58-(70.7)-88 x 3-(4.9)-6.5</td>
<td>42-(71.1)-98 x 2-(4.9)-7.5</td>
<td>63-(76.2)-92 x 3.5-(5.1)-7</td>
</tr>
<tr>
<td>Chelae</td>
<td>15-(17.8)-20</td>
<td>14-(18.4)-22</td>
<td>14-(19.2)-22</td>
</tr>
<tr>
<td>Toxas</td>
<td>17-(84.6)-131 x 0.8-(1.5)-3</td>
<td>18-(109.1)-192 x 0.8-(1.8)-3</td>
<td>71-(108.4)-134 x 0.8-(1.1)-1.8</td>
</tr>
</tbody>
</table>

present in **C. (C.) transiens** and it technically belongs to **Clathria (Clathria)**.

**Clathria (Clathria) wilsoni** Wiedenmayer, 1989
(Figs 79-80)

**Clathria wilsoni** Wiedenmayer, 1989: 57-58, pl.5, fig.9, pl.24, fig.1, text-fig.39; Hooper & Wiedenmayer, 1994: 262.


**HABITAT DISTRIBUTION.** 10m depth; on algal covered boulders; Bass Strait and E. coast (Tas) (Fig. 79H).

**DESCRIPTION.** **Shape.** Small sponge, thickly encrusting with irregular low-formed branches, 5mm high, up to 20mm diameter.

**Colour.** Live colouration dull vermilion, beige preserved.

**Oscules.** Oscules small, up to 2mm diameter, scattered on base and sides of branches.

**Texture and surface characteristics.** Surface uneven, microconulose, hispid, particularly on points of branches. Texture easily compressible, spongy.

**Ectosome and subectosome.** Ectosome skeleton a layer of subectosomal auxiliary styles, in small

bundles, erect on surface, with acanthostyles echinating peripheral fibres also contributing to ectosomal skeleton; choanosomal principal styles, embedded in peripheral fibres, form plumose brushes, which approach but usually do not pierce surface.
**Choanosome.** Choanosomal skeleton irregularly reticulate, consisting of moderately light, slender spiong fibres, up to 35μm diameter, forming irregular rectangular or polygonal meshes; spiong fibres cored by multisicular tracts of choanosomal styles, in rows of 2–10 spicules abreast, echinated by regularly dispersed acanthostyles; mesohyl matrix light, many vestibul and fully formed subectosomal styles, and numerous rhaphidiform toxu microscleres.

**Megascleres.** Choanosomal principal styles slightly curved, with evenly rounded or slightly subtylote, smooth or rarely micropined bases. Length 164–(191.8)–290μm, width 2.4–(5.1)–7.4μm.

Subectosomal auxiliary subtylostyles straight, occasionally slightly curved, with tapering or rounded, smooth bases. Length 83–(153.6)–282μm, width 1–(2.3)–3.5μm.

Acanthostyles short, thick, subtylote, with relatively evenly dispersed spines. Length 31.6–(62.6)–71μm, width 2.6–(6.6)–10μm.

**Microscleres.** Palmate isochelae very rare, small, poorly silicified. Length 4–(5.5)–9μm.

**Toxas accolada,** straight, very thin rhaphidiform, occasionally with roughened points; some smaller examples slightly curved, with reflected arms. Length 71–(121.6)–168μm, width 0.4–(0.7)–2μm.

**Remarks.** This species is transitional between the ectosomal structures of *Clathria* and *Thalysias,* and it is not surprising that Carpay (1987) referred it to the latter. However, although there is a large size range of auxiliary styles, ectosomal spicule brushes are composed only of a single size of spicule, and the species is technically correctly included in *Clathria* (*Clathria*). Nevertheless, this example further illustrates the inappropriateness of recognising a strict (phylogenetic) boundary between these two genera.

*Clathria* (*C.*) *wilsoni* is peculiar in having almost straight raphide-like toxas, which are known to occur in only a few microcionids (e.g. *C. (Thalysias)* costifera and *C. (Wilsonella)* reticulata, both from Australia, *C. (T.) juniperina* from the Caribbean, *C. (C.) microxea* from Madagascar, and *Artemisia archeagona* from the Pacific coast of America). Wiedenmayer (1989) notes some similarities between *C. (C.) wilsoni* and other species of Hallmann’s (1912) ‘spicata’ group, but this is not upheld here.

OTHER SPECIES OF **CLATHRIA**

**Clathria (Clathria) acanthostylia** (Hoshino, 1981)

*Thalysias acanthostylia* Hoshino, 1981: 156-157, text-fig.68, pl.7, fig.2 [Uchinoura, Japan].

**Material.** Holotype: MMBSSAT-020. Japan.

**Clathria (Clathria) acanthotaxa** (Stephens, 1916)


**Microciona acanthotaxa**; Stephens, 1921: 50, pl.5, fig.1; Alander, 1942: 62 [Sweden]; Burton, 1959b: 43 [Iceland]; Lévi, 1960a: 75 [Isle of Man, W. Ireland].


Not *Microciona acanthotaxa* Lévi & Lévi, 1989: 81, fig. 49 [see C. claudeli, nom. nov.].

**Material.** Holotype: INMSR253.8.1916. NE. Atlantic, North Sea.

**Clathria (Clathria) anchorata** (Carter, 1874)

*Dictyocylindrus anchoratus* Carter, 1874: 251 [Gulf of Manas, Ceylon].


*Microciona anchorata*; Alander, 1942: 62 [Sweden].

*Echinonema anchoratrum*; Dendy, 1889a: 44; *Wilsanella anchoratrum*; Hallmann, 1912: 152, 185, 189, 210, 211, 243, 296, 298, 299.

*Cliona anchorata*; de Laubenfels, 1936a: 108 [note].

Not *Echinonema anchoratrum* Carter, 1881a: 362, 379, 380 [S. coast of Australia].

Not *Echinonema anchoratrum* var.; Lendenfeld, 1888: 219–220 [Port Jackson, New South Wales].

Not *Echinonema anchoratrum* var. *ramosa*; Whitelegge, 1903: 171.

*Clathria typica,* in part; Dendy, 1896: 32; Kirkpatrick, 1903: 248–249.


**Material.** Holotype: LFM destroyed, fragments BMNH1953.11.11.63–69. NE. Atlantic, Mediterranean, Gulf of Mansar.

**Clathria (Clathria) anytaya** (Burton & Rao, 1932)

*Ophitaspangia anytaya* Burton & Rao, 1932: 348–350, pl.28, fig.12, text-figs 13–14 [Indian Ocean].

**Material.** Holotype: IMP791/1. Indian Ocean.

**Clathria (Clathria) anthoides** Lévi, 1994

*Clathria anhaides* Lévi, 1994: 36–37, fig. 21A, pl.7, fig.5 [Norfolk Rise, 610m depth].

**Material.** Holotype: MNHNDC13637. SW. Pacific.

**Clathria (Clathria) arbuscula** (Row, 1911)

*Ophitaspangia arbuscula* Row, 1911: 347–349, pl.39, fig.22, pl.40, fig.25, text-fig.22 [Red Sea].

*Ophitaspangia harida* Row, 1911: 349–351, pl.40, fig.26, text-fig.23 [Red Sea].
Liásaspis arbuscula; de Laubenfels, 1954: 162 [note].
Kerasemma arbuscula; Pulitzer-Finali, 1982: 105.
Kerasemma horrida; Pulitzer-Finali, 1982: 105.

Material. Holotype: BMNH1912.2.1.63 (O. arbuscula), BMNH1912.2.1.65 (O. horrida). Red Sea.

Clathria (Clathria) asodes (de Laubenfels, 1930)
Eurypon asodes de Laubenfels, 1930: 27; de Laubenfels, 1932: 92-93, text-fig.54 [Carmel, California]; Lee & Gilchrist, 1985: 24-32 [biochemistry].
Dicyrtciona asodes, de Laubenfels, 1936a: 110 [note].
Clathria asodes; Van Soest, 1984b: 7 [generic synonymy].
Leptoclathria asodes; Siim & Bakus, 1986: 10 [California]; Bakus & Green, 1987: 72 [California].


Clathria (Clathria) atoxa (Bergquist & Fromont, 1988)


Clathria (Clathria) axoconia Lévi, 1963
Clathria axoconia Lévi, 1963: 49, text-fig.56, pl.8A [Cape of Good Hope, South Africa]; Uriz, 1988a: 83-84, pls 20-21a, text-fig. 59 [Namibia].


Clathria (Clathria) barleei (Bowerbank, 1866)
Isodictya barleei Bowerbank, 1866: 333; Bowerbank, 1874: pl.57.
Tragosia barleei; Topsent, 1894a: 25.
Astinella barleei; Arndt, 1935: 85, fig.186.
Clathria barleei; Van Soest & Stone, 1986: 45-46, fig.4 [Norway]; Ackers, Moss & Picton, 1992: 138 [Ireland].
Halichondria foliata Bowerbank, 1874: 198, pl.73, figs 1-5; Carter, 1876: 310, pl.12, fig.10, pl.29, fig.29; Bowerbank, 1882: 106.
Esperia foliata; Fristedt, 1885: 41.
Homoedictya foliata; Topsent, 1894a: 12.
Artemisina foliata; Burton, 1930a: 501, 529, pl.2, figs 1-2 [Norway]; Burton, 1959b: 42-43 [Iceland].
Amphilectus foliatus; Vosmaer, 1880: 118.
Antho foliata; Aländer, 1942: 63 [Sweden; defined in Espereciopidae].

? Halichondria muula Bowerbank, 1874: 209, pl.74, figs 4-8; Bowerbank, 1882: 96 [as H. mutulus].
? Amphilectus mutulus; Vosmaer, 1880: 118.
Isodictya laciniosa Bowerbank & Norman, 1869: 333.
Amphilectus laciniosus; Vosmaer, 1880: 116.
Clathria laciniosa; Arndt, 1935: 81, fig.167; Burton, 1959b: 42 [Iceland].
Artemisina laciniosa; Burton, 1950: 891 [revision].


Clathria (Clathria) basiliana Lévi, 1961
Clathria basiliana Lévi, 1961b: 520, fig.11 [Zambounga, Philippines]; Van Soest, 1989: 1-2, fig.6 [Lesser Sumba Is, Indonesia].


Clathria (Clathria) borealis sp. nov.
Clathria robusta Kolton, 1959: 186, pl.25, fig.5, text-fig. 147 [Arctic, USSR]; Van Soest & Stone, 1986: 47 [note].
Not Microciona strepisida var. robusta Dendy, 1922: 60.

Material. Holotype: ZIL, no fragment in BMNH.
Note: C. (C.) robusta (Dendy, 1922) has priority. Arctic.

Clathria (Clathria) bulbosa Hooper & Lévi, 1993
Clathria (Clathria) bulbosa Hooper & Lévi, 1993a: 1268-1270, figs 23-24 [Chesterfield Is, Coral Sea].


Clathria (Clathria) burtoni sp. nov.
Clathria prolifera Burton, 1940: 109, pl.4, figs 3-4, text-fig.2 [Argentina].
Not Spongia prolifera Ellis & Solander, 1786: 189.


Clathria (Clathria) caespes (Ehlers, 1797), unrecognizable.
Spongia tubulosa, in part, Esper, 1797: 196, pl.44 [Cape of Good Hope, South Africa].
Scopalinca caespes; Ehlers, 1870: 19-20, 31.


Clathria (Clathria) calypso Boury-Esnault, 1973
Clathria calypso Boury-Esnault, 1973: 286, text-fig.47 [Brazilian Basin].


Clathria (Clathria) cantabrica (Orucuta, 1901)
Rhaphidophalus filifer var. cantabrica Orenua, 1901: 331-335, pls.3-4 [Bay of Biscay].
Tenacilla filifer var. cantabrica; Hallmann, 1920: 771.
Clathria cantabrica; Lévi, 1940a: 55-56, 63


Clathria (Clathria) compressa Schmidt, 1862

**Clathria (Clathria) conica** Lévi, 1963

Clathria conica Lévi, 1963: 50-51, text-fig.57, pl.8E [Cape of Good Hope].

**Clathria (Clathria) contorta** (Bergquist & Fromont, 1988)

Dicyoclostomum contorta Bergquist & Fromont, 1988: 105, pl.48, figs.6-7 [Manitou]; Dawson, 1993: 38 [note].

**Clathria (Clathria) coralloides** (Olivieri, 1792)

Spongia coralloides Olivieri, 1792: 264; Bertoloni, 1819: 228; Blainville, 1819: 125; Lamouroux, 1824: 369; Martens, 1824: 535.

**Clathria (Clathria) compressa** (Clare, 1894a: 1869: 50, pl.12 [Westermost Bay, Victoria].

**Clathria (Clathria) depressa** Sarà & Melone, 1966


**Clathria (Clathria) discoidea** Zaucha, 1885: 53-54 [Cape of Good Hope].

**Clathria (Clathria) diversa** (Reuss, 1855: 57-58, pl.41 [Olivetta, Portofino, Levante coast, Italy]; Pulitzer-Finali, 1963: 610.

**Clathria (Clathria) disjuncta** (Thiele, 1905)

Microciona disjuncta Thiele, 1905: 447-449, 494, pl.31, fig.65a-e [Cabo, Chile].

Dicyoclostomum disjuncta, Topsent, 1913a: 580, 583, 614, 618-620, 642, pl.3, fig.3 [Gough Is., S. Atlantic Ocean]; Burton, 1932: 324, pl.56, figs.3-4 [Falkland Is]; Burton, 1940: 112; fig.4, figs.1-2, pl.6; fig.2 [Argentina and Chile]; de Laubenfels, 1953a: 527; Desqueyroux, 1972: 29-30, figs.95-102, 136-137 [Chile]; Desqueyroux & Moyana, 1987: 49 [Chile, Tierra del Fuego, Argentina, Falkland Is, Kerguelen Is.]

cf. Microciona proliferá; Vosmaer, 1935a: 608, 646.

**Clathria (Clathria) elastica** Lévi, 1963

Clathria elastica Lévi, 1963: 52, text-fig.59, pl.8C [Cape of Good Hope].

**Clathria (Clathria) elegans** Vosmaer, 1880

Clathria elegans Vosmaer, 1880: 152 [North America]; Vosmaer, 1884b: 492.


Not Antherochalinia elegans Lendenfeld, 1887: 787.


**Clathria (Clathria) foliacea** Tropsen, 1889


Thalysia foliacea; de Laubenfels, 1936a: 107-108 [Florida].

Pandoros foliaceus; Wiedenmayer, 1977: 144 [note].


Thalysia forsteri; de Laubenfels, 1936a: 107.

Pandoros forsteri; Wiedenmayer, 1977: 144 [note].


Thalysia forsteri; de Laubenfels, 1936a: 107.

Pandoros forsteri; Wiedenmayer, 1977: 144 [note].


Clathria foliacea (Vacelet & Vatsev, 1977: 114; figs 5-6) (Tulear, Madagascar); Vacelet & Vatsev, 1977: 114; Vacelet et al., 1976: 71 [Tulear, Madagascar]

MATERIAL. HOLOTYPE: MNHN-DV30, W. Indian Ocean.

Clathria (Clathria) frondiculata (Schmidt, 1864)

Renierea (?) frondiculata Schmidt, 1864: 39, 40, 45, pl.4, fig.10 [Adriatic].

Pitulia frondiculata; Gray, 1867: 524.


Clathria (Clathria) gorgonoides (Dendy, 1864)


Clathria (Clathria) hexagonopora Lévi, 1963

Clathria hexagonopora Lévi, 1963: 53-54, text-fig.60, pl.8D [Cape of Good Hope].

MATERIAL. HOLOTYPE: MNHN-DCL260, S. Africa.

Clathria (Clathria) indica Dendy, 1889

Clathria indica Dendy, 1889b: 73, 84, pl.4, fig.10 [Gulf of Manaar, Ceylon]; Burton & Rao, 1952: 336-337, pl.18, figs 8-9 [Tucitcion, India]; Thomas, 1979a: 58, pl.3, fig.10 [Mozambique].

Wilsonella indica; Dendy, 1905: 171 [Ceylon]; Hallmann, 1912: 242; Burton, 1931a: 346 [Natal Coast].


Clathria (Clathria) inhacensis Thomas, 1979

Clathria inacensis Thomas, 1979: 27-28, pl.2, fig.2 [Inhaca 1, Mozambique].

MATERIAL. HOLOTYPE: MRAC511. E. Africa.

Clathria (Clathria) intermedia Kirk, 1911

Clathria intermedia Kirk, 1911: 579, text-fig.5 [Kermadec Is]; Fell, 1950: 11, text-fig.2; Berquist & Fromont, 1988: 109-110; Dawson, 1993: 37 [note].

Thalysias intermedia; de Laubenfeld, 1936a: 105.


Clathria (Clathria) irregularis (Burton, 1931)

Marleavia irregularis Burton, 1931a: 346, pl.23, fig.6, text-fig.5 [Durban, Natal]; de Laubenfeld, 1936a: 109 [note]; Van Soest, 1984b: 130 [note].

MATERIAL. HOLOTYPE: NMNZ1279; paratype: BMNH 1934.10.1.17, S. Africa.

Clathria (Clathria) juncea Burton, 1931

Clathria juncea Burton, 1931a: 343, pl.23, fig.5, text-fig.3 [Natal coast]; Lévi, 1960a: 83; Lévi, 1963: 66 [note].

Labecera juncea; de Laubenfeld, 1936a: 66 [note].

cf. Alcyonium junceum Lamarc, 1816: 77.

cf. Anomocladia opuntioides var., Topsent, 1933: 26 [note].

MATERIAL. HOLOTYPE: MNHN missing (fragment BMNH 1954.2.20.85, unconfirmed); *representative specimen*: BMNH 1926.2.9.12. Note: Burton's species is probably the same as Lamerk's but this cannot be verified and the species is taken in the sense of Burton (1931a). South Africa.

Clathria (Clathria) labyrinthica (Schmidt, 1864)

Renierea labyrinthica Schmidt, 1864: 39, pl.4, fig.9 [Adriatic].

Clathria labyrinthica; Burton, 1930a: 514 [imperfectly known].

MATERIAL. HOLOTYPE: LMIG, Mediterranean.

Clathria (Clathria) laevigata Lambe, 1893

Clathria laevigata Lambe, 1893: 31-32, pl.2, figs 9-9' [Pacific coast, Canada]; Lambe, 1900: 160, Koytun, 1959: 185, text-fig.146 [Kurile Is].

Thalysias laevigata; de Laubenfeld, 1936a: 105


MATERIAL. HOLOTYPE: NMCIC1900-2892. NW. and NE. Pacific.

Clathria (Clathria) lissosclera Bergquist & Fromont, 1983


MATERIAL. HOLOTYPE: MNZPSP112. New Zealand.

Clathria (Clathria) lobata Vosmaer, 1880

Clathria lobata Vosmaer, 1880: 151 [Cape of Good Hope]; Vosmaer, 1882: 45; Carter & Hope, 1889: 101, 105; Stephens, 1915: 444-445 [Cape of Good Hope]; Lévi, 1963: 54, text-fig.61, pl.8P [Cape of Good Hope].

Rhaphidoplus lobatus, var. horrida; Ridley & Dendy, 1887: 153-155, pl.28, fig.1, pl.29, fig.4a-c [Simon's Bay, Cape of Good Hope].

Ligrota lobata; de Laubenfeld, 1936a: 125.

Artemisina lobata; Van Soest, 1984b: 130 [generic synonymy for Ligrota].


MATERIAL. HOLOTYPE: unknown, fragments: RMNH276-277, BMNH1887.5.2.100. S Africa.

Clathria (Clathria) macroisocheila Lévi, 1994

Clathria (Clathria) macroisocheila Lévi, 1994: 37, fig.21b, pl.7, figs 7-9 [Norfolk Rise, 680m depth].


Clathria (Clathria) maenandrina Ridley, 1884

Clathria maenandrina Ridley, 1884a: 588, 614, pl.53, fig.1, pl.54, fig.4H [Amirante Is]; Burton, 1930a: 668 [Gulf of Manaar]; Burton, 1959: 244 [Red Sea].


Clathria (Clathria) marissuperi Pulitzer-Finali, 1983

Clathria marissuperi Pulitzer-Finali, 1983: 569-571, text-fig.67 [Italy].


Clathria (Clathria) menoui Hooper & Lévi, 1993
Clathria (Clathria) menou Hooper & Lévi, 1993a: 1270-1273, figs 25-26 [New Caledonia].

MATERIAL. HOLOTYPE: QM301267. SW. Pacific.

Clathria (Clathria) meyeri (Bowerbank, 1877)

Ophiopertis meyeri Bowerbank, 1877: 456 [Selat Jepan, Irian Jaya, E. Indonesia].

Clathria meyeri; Vosmaer, 1980: 154.


Clathria (Clathria) microchela (Stephens, 1916)


Dictyococia microchela; de Laubenfels, 1936a: 110 [note]; de Laubenfels, 1953: 528.

Clathria microchela; Van Soest, 1984b: 7 [generic synonymy].


MATERIAL. HOLOTYPE: INMSR353; 10.1916. NE. Atlantic.

Clathria (Clathria) microxa Desqueyroux, 1972

Clathria microxa Desqueyroux, 1972: 27-28, text-figs 76-80,134 [Gulf of Corcovado, Chile].

MATERIAL. HOLOTYPE: ICBU. SE Pacific.

Clathria (Clathria) mortensenii Brandsted, 1923


Microciona mortensenii; de Laubenfels, 1936a: 111; Burton, 1940: 111 [Argentina].

Microciona heteroperculata; Bergquist, 1961a: 39 [N of New Zealand].

Not Microciona heteroperculata Brandsted, 1924: 465, text-fig.20.

MATERIAL. HOLOTYPE: UZM, fragment: BMNH1930.8.11.10. SW. Atlantic, Subantarctic, New Zealand.

Clathria (Clathria) mosulpia Sim & Bakus, 1989

Clathria mosulpia Sim & Byeon, 1989: 38-39, pl.3, figs 1-5 [South Korea].

MATERIAL. HOLOTYPE: HNUKPor9. S. China Sea.

Clathria (Clathria) obliqua (George & Wilson, 1919)

Esperioplis obliqua George & Wilson, 1919: 148-150, pl.60, figs 20-23, pl.66, fig.58 [North Carolina].


Haliotina oculata; Pearse & Williams, 1951 [North Carolina].

Cholina arborescula; Coues & Yarrow, 1879: 312; Verrill & Smith, 1873: 743 [North Carolina].

Tenaciella obliqua; Wells et al., 1960: 218-219, text-figs 16,25 [North Carolina].

Not Tenaciella obliqua; Alcolado, 1976: 5, Clathria obliqua; Van Soest, 1984b: 104,105, table 4 [affinity with Clathria prolifera].


MATERIAL. HOLOTYPE: USNM23612, paratype-USNM23613. NW. Atlantic-Caribbean.

Clathria (Clathria) oculata Burton, 1933

Clathria oculata Burton, 1933: 250-251, text-fig.2 [Natal].

Thalysias oculata; de Laubenfels, 1936a: 105.

MATERIAL. HOLOTYPE: BMNH1933.7.4.65. S. Africa.

Clathria (Clathria) oxneri (Topsent, 1928)

Hymedesmia oxneri Topsent, 1928a: 256 [Azores].

Dictyoeciona oxneri; de Laubenfels, 1936a: 110 [note]; de Laubenfels, 1953a: 528.

Clathria oxneri; Van Soest, 1984b: 7 [generic synonymy for Dictyoeciona].


Clathria (Clathria) pachystyla Lévi, 1963

Clathria pachystyla Lévi, 1963: 56, text-fig.63, pl.8G [Cape of Good Hope].

MATERIAL. HOLOTYPE: MNHNDC609. S. Africa.

Clathria (Clathria) papillosa Thiele, 1905

Clathria papillosa Thiele, 1905: 449-450, text-fig.66 [Calbuco, Chile]; Burton, 1932a: 319 [Falkland Is]; Desqueyroux-Fauvez & Moyana, 1987: 49 [Chile, Argentina, Falkland Is, Kerguelen Is].

Pseudonchinoe papillosa; de Laubenfels, 1936a: 109; Burton, 1940: 115, pl.5, fig.1-7 [Argentina].


Clathria (Clathria) pellicula Whitelegge, 1897

Clathria pellicula Whitelegge, 1897: 327-328 [Funaufuti (Ellice Is)].


MATERIAL. HOLOTYPE: AMG1660. SW. central Pacific.

Clathria (Clathria) pluriytila Pulitzer-Finali, 1983

Clathria pluriytila Pulitzer-Finali, 1983: 571-572, 610, text-fig.68 [Italy].


Clathria (Clathria) productitoxa (Hoshino, 1981)

Thalysias productitoxa Hoshino, 1981: 157-159, text-fig.69, pl.7, fig.3 [Uchinoura].


Clathria (Clathria) prolifera (Ellis & Solander, 1786)

Spongina prolifera Ellis & Solander, 1786: 189-190, pl.58, fig.5; Linnaeus, 1791: 3822; Esper, 1794: 178, 281; Bosc, 1802: 143; Lamarck, 1814: 372; Lamouroux, 1816: 81-82;
Not *Rhiphodophthus* sifter var. *spinifera* Lindgren, 1897: 483.
Not *Rhiphodophthus spinifer* Thiele, 1903a: 958; pl.28, fig. 23; Hallmann, 1912: 177.
MATERIAL. HOLOTYPE: IZUG147, fragment: MNHNDC2755. SW. Atlantic. Note: *C. spinifera* (Lindgren, 1897) has seniority.

**Clathria (Clathria) sartaginula** (Lamarck, 1814)
*Spongia sartaginula* Lamarck, 1814: 383,362 [locality unknown].
*Pseudanchnoe sartaginula*: de Laubenfels, 1936a: 109 [note].
*Clathria sartaginula*: Topsent, 1930: 45, pl.4, fig.1.
MATERIAL. HOLOTYPE: MNHNDC2757. Unknown.

**Clathria (Clathria) shirahama** Tanita, 1977
*Clathria shirahama* Tanita, 1977: 38, pl.2, fig.9, text-fig.6 [Kii-Shirahama]; Hoshino, 1981: 161.
MATERIAL. HOLOTYPE: MMBS. Japan.

**Clathria (Clathria) spinispicula** Tanita, 1968
*Clathria spinispicula* Tanita, 1968: 48-49, pl.1, fig.6, text-fig.8 [Ariake Sea]; Rho et al., 1972: 5, pl.4, figs 9-10 [South Korea]; Hoshino, 1981: 161 [Ariake Sea]; Sim & Bakus, 1988: 25 [Korea]; Sim & Byeon, 1989: 38 [Korea].
MATERIAL. HOLOTYPE: MMBS. Japan. S. China Sea.

**Clathria (Clathria) spongodes** Dendy, 1922
*Clathria spongodes* Dendy, 1922: 69, pl.6, fig.1, pl.14, fig.2 [Amirante]; Vacelet et al., 1976: 70-71, text-fig.48, pl.3, fig.6 [Madagascar].
*Damoseni spongodes*: de Laubenfels, 1936a: 110 [note].
*Clathria madreporea* Dendy, 1922: 68-69, pl.5, fig.3, pl.14, fig.1 [Seychelles]; Sim & Kim, 1988: 25, pl.2, figs 1-2 [Korea]; Sim & Byeon, 1989: 38 [Korea; possible misidentification].
*Thalysias madreporea*: de Laubenfels, 1936a: 105.
*Clathria spongiosa* Burton, 1959a: 245, text-fig.26 [Red Sea]; Vacelet et al., 1976: 70 [with question].
MATERIAL. HOLOTYPE: BMNH1921.11.7.58. W. Indian Ocean, S. China Sea.

**Clathria (Clathria) surfosula** (Esper, 1797)
*Spongia surfosula* Esper, 1797: 39, pl.65 A3 ['East Indies'].

**Clathria (Clathria) terranovae** Dendy, 1924
*Clathria terranae-navae* Dendy, 1924a: 353-354, pl.12, fig.5, pl.14, figs 9-13 [North Cape, New Zealand]; Dawson, 1993: 37 [note].
*Clathria terranovae*: Koltun, 1976: 188. Rho & Sim, 1976: 74, pl.6, figs 3-4 [Seogwipo, South Korea; possible misidentification]; Boury-Esnault & van Beveren, 1982: 107-108, pl.18, fig.69, text-fig.31 [Kerguelen Is.]; Bergquist & Fromont, 1988: 109, pl.50, figs d-f, pl.51, fig.a [N. New Zealand]; Sim & Byeon, 1989: 38 [Korea].
MATERIAL. HOLOTYPE: BMNH1923.11.1.132, para-type BMNH1923.11.1.133. 134. Antarctica, Subantarctic, New Zealand, SW Atlantic.

**Clathria (Clathria) textile** (Carter, 1876)
*Corumbal textile* Carter, 1876: 309.
*Clathria textile*: Vosmaer, 1880: 154 [Shetland Is; imperfectly known].
MATERIAL. HOLOTYPE: BMNH1882.7.28.75. SW Atlantic.

**Clathria (Clathria) tortuosa** Uriz, 1988
*Clathria tortuosa* Uriz, 1988a: 86-87, pls 22a, 42a-b, text-fig.62 [Namibia].
MATERIAL. HOLOTYPE: AIBPB-11d. SW Africa.

**Clathria (Clathria) toxistrica** Topsent, 1925

**Clathria (Clathria) toxistyla** (Sarà, 1959)
*Microciona toxistyla* Sarà, 1959: 17, text-fig.6 [Naples]; Siribelli, 1960: 9-10, text-fig.38 [Naples]; Sarà, 1961: 47 [Adriatic Sea]; Cimino et al., 1979: 3619-3622 [biochemistry].
MATERIAL. HOLOTYPE: ZSN1000. Mediterranean.

**Clathria (Clathria) toxivarixia** (Sarà, 1959)
*Microciona toxivarixia* Sarà, 1959: 14, pl.1C, text-fig.5 [Naples]; Siribelli, 1960: 8, text-fig.3A [Naples].
*Clathria toxivarixia*

**Clathria (Clathria) toxotes** (Schmidt, 1868)
*Scopolina toxotes* Schmidt, 1868: 12, 26, 39, 40, 44, pl.5, fig.5 [Canal de Zara, Adriatic]; Schmidt, 1870: 2, 56; Pagenstecher, 1872-43; Hyatt, 1877-500; Schmidt, 1880: 81; Vosmaer, 1880: 118-119; Fristedt, 1885: 37; Vosmaer, 1885b: 353; Carter & Hope, 1889: 101; Schulze & Lenzenfeld, 1889: 9; Heider, 1895: 281; Kieschnek, 1896: 533; Thiele, 1903a: 959; Sánchez-Vizur, 1905: 342; Livi, 1960a: 55.
*Microciona toxotes*: de Laubenfels, 1936a: 111 [imperfectly known].
MATERIAL. HOLOTYPE: unknown, possibly LMG. Mediterranean.
Clathria (Clathria) typica Kirkpatrick, 1904
*Clathria typica* Kirkpatrick, 1904: 148 [Natal]; Hallmann, 1912: 208 [anomalous species].
MATERIAL. HOLOTYPE: BMNH1902.11.16.31. Note: imperfectly known; listed in BMNH register as *C. typica* Carter, S Africa.

Clathria (Clathria) ulmus Vosmaer, 1880
*Clathria ulmus* Vosmaer, 1880: 154 [locality unknown]; Riedel, 1993: fig.4 [Plumohaltera].
*Thalysta ulmus*: de Laubenfels, 1936a: 105 [note].
MATERIAL. HOLOTYPE: possibly RNHL. Unknown locality.

Clathria (Clathria) unica Cuatras, 1993
*Clathria unica* Cuatras, 1993: 112 [Argentina].
MATERIAL. HOLOTYPE: Division Invertebrados del Museo de Ciencias Naturales de La Plata, Argentina. SW Atlantic.

Clathria (Clathria) vasiformis (de Laubenfels, 1953)
*Thalysya vasiformis* de Laubenfels, 1953a: 525, text-fig.4 [Gulf of Mexico]; Little, 1963: 50 [note].
*Panodos vasiformis*, Wiedenmayer, 1977: 144 [note].
MATERIAL. HOLOTYPE: USNM23403, paratype PLUMMLA-232, E Pacific.

Clathria (Clathria) zoanthifera Lévi, 1963
*Clathria zoanthifera* Lévi, 1963: 58, text-fig.66, pl.9D [Cape of Good Hope].
MATERIAL. HOLOTYPE. UCT (fragment MNNHDC607). S Africa.

Transfers

List of other species described in *Clathria* (*Clathria*), or one of its synonyms, but now transferred to another genus.

*Clathria australis* Lendenfeld, 1888: 222 [Port Phillip, Victoria].
*Wilsonella australis*: Hallmann, 1912: 239.
Not *Clathria australis* Whitelegge, 1901: 90.
Not *Plumolahicordina australis* Whitelegge, 1901: 90, pl.11, fig.14.

*Plumolahicordina australis* Whitelegge, 1901: 90-92, pl.11, fig.14a,b, [New South Wales coast]; Whitelegge, 1907: 492 [New South Wales coast].
MATERIAL. HOLOTYPE: AMG9042. Note: referred Crelidae, synonym of *Crelia incrustans* (Hallmann, 1912: 160).

*Eodictya beanii* Bowerbank, 1866: 274, 334, 335 [Britain]; Gray, 1868: 164; Schmidt, 1870: 77; Bowerbank, 1874: 147, pl.58, figs 1-6.
*Amphilectus beanii*: Vosmaer, 1880: 115.
*Clathria beanii*: Ridley, 1881: 485, 486; Bowerbank, 1882: 13, 23, 150; Topsent, 1890c: 203.


*Echinonema caespitosa* Carter, 1885f: 352 [Port Phillip, Victoria].

*Antherocalina concentrica* Lendenfeld, 1887b: 788, pl.22, fig.42 [Port Moller (Airlie Beach), Qld.].
MATERIAL. HOLOTYPE: AMZ1993 (lectotype), fragment: BMNH1886.8.27.451, 460 (paralactotypes). Note: referred to Axinellidae, *Cymbastela*.

*Clathria coronarhizoides* Fristedt, 1887: 460, pl.25, figs 73-77, pl.29, fig.23.

*Antherocalina elegans* Lendenfeld, 1887b: 787, pl.22, fig.40.
*Syringella elegans*: Burton, 1934a: 558.
MATERIAL. HOLOTYPE: BMNH1886.8.27.452. Note: referred to Raspaliidae, *Raspailia*.

*Echinonema incrustans* Carter, 1885f: 353 [Port Phillip, Victoria].
*Plumolahicordina incrustans*: Dendy, 1896: 42.
*Plumolahicordina mammillata*: Carter, 1885f: 355; Ridley & Dendy, 1887: 156, pl.30, fig.4, pl.47, fig.4.
*Crelia incrassata*: Hallmann, 1912: 152-156, pl.23, figs 2-3, pl.24, text-figs 28-34.
MATERIAL. HOLOTYPE: BMNH1886.12.15.123, paratypes 1886.12.15.249, AME651, AMZ957. Note: referred to Crelidae, *Crelia*.

*Coralicum johnsoni* de Laubenfels, 1934: 15.
*Clathria johnsoni*: Van Soest, 1948b: 104 [possible synonym of *Clathria*].
MATERIAL. HOLOTYPE: USNM Note: referred to Coelosphaeridae, possibly *Coralum* (imperfectly known).

*Echinonema levis* Lendenfeld, 1888: 220 [Port Jackson, New South Wales].
*Plumolahicordina australis*, in part; Whitelegge, 1901: 65, 91, 92; Whitelegge, 1902a: 212.
*Crelia incrassata var. levis*: Hallmann, 1912: 164-167, text-figs 33-34.
MATERIAL. LECTOTYPE: AMG959, paraltotype AMG9708. Note: referred to Crelidae, synonym of *Crelia incrustans* (Hallmann, 1912: 164).

*Clathria loveni* Fristedt, 1887: 458, pl.25, figs 70-72, pl.30, fig.24 [Cape Jakon, Siberian Arctic Ocean]; Lambe, 1900: 160.
[?] *Esperella loveni*: Lambe, 1895: 123, pl.4, fig.1 (W coast, North America).

*Esperella loveni*: de Laubenfels, 1936a: 120 [note].
**Plumohalichondria microcionoides** Carter, 1876: 236, pl.12, fig.11, pl.15, fig.30 [between Scotland and Faroe Is.].

**Clathria microcinoides**; Vosmaer, 1880: 154.

**Plocamium microcionoides**; Alander, 1942: 53 [Sweden].

**Not Hyperamphipha microcionoides** Carter, 1876: 390.

**Not Plocamia microcionoides**; Topsent, 1891a: 529, 544-545.

**MATERIAL.** **HOLOTYPE:** BMNH1993.4.3.173. Note: referred to Anchioaoidae, Plocamionidae.

**Clathria mollis** Kirkpatrick, 1903: 249-250, pl.5, fig.15, pl.6, fig.16 [East London Coast, Natal].


**Not Clathria dura var. mollis**; Hentschel, 1911: 370.

**MATERIAL.** **HOLOTYPE:** BMNH1902.11.6.32. Note: referred to Anchoaoidae, Pronaxidae.

**Clathria morisca** Schmidt, 1868: 9, 41, 43, pl.2, fig.7 [Algeria, Mediterranean]; Vosmaer, 1880: 150-151 [Algeria]; Topsent, 1902: 329; Topsent, 1938: 11; Desqueyroux-Faunde & Stone, 1992: 10, 35.

**Dictyocladha morisca**; Topsent, 1920a: 18-21 [re-examination of holotype]; Topsent, 1925: 660-661, pl.8, fig.1 [Gulf of Naples]; Topsent, 1928a: 301-302, pl.3, fig.3 [Porto Santo, Azores]; Lévi, 1959: 134, text-fig.27, pl.5, fig.1 [Río de Oro, Gulf of Guinea]; Lévi, 1960b: 761-762, text-fig.15 [var. aisanotyla; SW Cape of Nize, W Africa]; Sarà, 1960a: 462 [Ischia, Mediterranean].

**Artemisina mediterranea** Babcic, 1921: 87 [Adriatic]; Babcic, 1922: 258, text-fig.3; Burton, 1930a: 528.


cf. **Clathria coralloides** and **C. compressa**; Vosmaer, 1935a: 626 [intermediate form].

**MATERIAL.** **HOLOTYPE:** MNHN DT2170, fragment BMNH 1868.3.2.21. Note: **Synonym of Antho involvens** (Lévi, 1960a: 57).

**Clathria oroides** Schmidt, 1864: 35, pl.4, figs 1-2 [Quarnero, Adriatic]; Carter, 1875: 195; Vosmaer, 1880: 155; Dendy, 1889a: 41; Desqueyroux-Faunde & Stone, 1992: 10, 35, 103.

? **Oroide aadriae**; Gray, 1867: 520.

**Chalinopsis oroides**, Schmidt, 1870: 60.

**Ophioplaspongea oroides**; Bowerbank, 1874: 10.


**MATERIAL.** **HOLOTYPE:** BMNH 1868.3.2.22. Note: referred to Agelasidae, Aegialas.

**Artemisina paradoxa** Babcic, 1921: 87; Babcic, 1922: 258-261, pl.8, fig.6, text-fig.c [Adriatic]; Lévi, 1960a: 85-86 [Adriatic; with question].

**Clathria paradoxa**; Burton, 1930a: 528.

**Dictyocladha morisca**; Topsent, 1925: 660; Ristau, 1978: 585-586 [note on affinities].

**MATERIAL.** **HOLOTYPE:** unknown. Note: **synonym** of **Antho involvens** (Topsent, 1925: 660).

**Clathria pelligera** Schmidt, 1864: 34, pl.3, fig.13 [Lézina, Adriatic]; Desqueyroux-Faunde & Stone, 1992: 10, 36, 103.

**Rhaphistyla pelligera**; Burton, 1935b: 652; Sarà, 1958: 246-247, fig.15 [Gulf of Naples].

**Stylolella pelligera**; Topsent, 1925: 638; Boury-Esnault, 1971: 328 [Banyuls].

**Dicynonella pelligera**; Pulitzer-Finali, 1983: 545.

**MATERIAL.** **HOLOTYPE:** BMNH 1867.3.11.29. Note: referred to Dicyonellidae, Dicyonella.

**Clathria procumbens** Bröndsted, 1923; Bröndsted, 1926: 329 [probably a typographic error for **Clathria** (Calcarea), and possibly synonym of **Ascetella procumbens** Lendenfeld, 1885].

**An throchalinia quercifolia** Keller, 1889: 383-384, pl.23, fig.34 [Red Sea].

**Querclionia quercifolia**; de Laubenfels, 1936a: 46 [note].

**MATERIAL.** **HOLOTYPE:** ZMB429, fragment BMNH1908.9.24.179. Note: referred to Axinellidae, Phakellia.


**An throchalinia renieroides** Lendenfeld, 1887b: 788, pl.28, figs 18, 23 [New Zealand].

**MATERIAL.** **HOLOTYPE:** BMNH1886.8.27.440. Referred to Axinellidae, synonym of **Phakellia flabellata** (Carter) (see Hooper, 1991).

**Holymphophia tuberoscapitata** Topsent, 1892b: 68 [Azores, Atlantic]; Topsent, 1925a: 113, pl.11, fig.6 [Atlantic].

**Cionanchora tuberoscapitata**; de Laubenfels, 1936a: 108 [note].

**Clathria tuberoscapitata**; Van Soest, 1984b: 7 [generic synonymy for **Cionanchora**].


**MATERIAL.** **HOLOTYPE:** MOM040323, fragment MNHN1998. referred to Hymedesmidae, Discorhabdella.

**Clathria (Wilsonella)** Carter, 1885

**Hooper & Wiedenmayer, 1994**

**Wilsonella Carter, 1885f: 366** (not Hallmann, 1912: 242), **Clathriopsamma Lendenfeld, 1888:** 227.

**Aulencella Burton & Rao, 1932:** 345.

**TYPE SPECIES.** **Wilsonella australiensis** Carter, 1885f: 366 (by monotypy).

**DEFINITION.** Sand grains and foreign spicules partially or completely replacing coring spicules inside fibres; coring spicules same or very similar geometry to auxiliary spicules located outside fibres; skeletal architecture reticulate.

**REMARKS.** Microcionoids with sand and foreign debris incorporated into fibres ('arenaceous sponges') are a predominant feature of Australian waters. Of the 17 species in Wilsonella or a synonym, 14 are valid and 6 are known to live in this region including 2 new species.

This group of arenaceous microcionoids is well known as **Clathriopsamma** (Hooper, 1991a; Hooper & Lévi, 1993a). However, the inclusion of **C. (W.) australiensis** in this group means that **Wilsonella** (1885) takes precedence over **Clathriopsamma** (1888).
Clathria (Wilsonella) abrolhosensis sp. nov.  
(Figs 81-82, Plate 2C)

MATERIAL. HOLOTYPE: NTM3218 (fragment QMG300584), N. edge of Pelsart Is, Houman Abrolhos, WA, 28°47.2’S, 113°58.5’E, 10.vii.1987, 22m depth, coll. J.N.A. Hooper (SCUBA).

HABITAT DISTRIBUTION. 22m depth; on an Acropora reef; Houman Abrolhos, WA (Fig. 81F).

DESCRIPTION. Shape. Fistulose, with multiple fistules composed of erect, bulbous-cylindrical digits, single or fused together with adjacent digits, each tapering at base and apex, thickest in apical portion, attached directly to substrate without stalk; each digit between 75-140mm long, up to 45mm maximum diameter.

Colour. Pale beige-yellow alive (Munsell 2.5Y 8/4), dark brown in ethanol.

Oscules. Single, large, apical oscule on apex of each digit, 10-15mm diameter in life, with slightly raised membrane-like lip surrounding oscule; oscules nearly completely contractile upon preservation; pores not observed in life or preserved.

Texture and surface characteristics. Compresible, spongy, relatively easily torn; surface glabrous, even, without any ornamentation.

Ectosome and subectosome. Discrete, erect bundles of auxiliary styles, relatively closely packed together, arising from ends of peripheral fibres, with tangential layer of auxiliary styles connecting adjacent bundles; erect spicules protrude only a short distance through surface; mesohyl matrix light in ectosomal region; subectosomal region slightly cavernous, reticulate.

Choanosome. Almost regular, ovoid reticulation of fibres and spicle tracts forming ovoid, square or rectangular meshes, 220-360μm diameter; spongin fibres moderately light, relatively homogenous in size, 40-70μm diameter, but with differentiated primary and secondary tracts; primary ascending fibres cored by multispicular tracts of auxiliary styles, interconnected by secondary, pauci- or multispicular transverse tracts of auxiliary styles; fibres relatively heavily echinated by acanthostyles; sparse core of detritus in primary ascending fibres only, mostly foreign spicules; mesohyl matrix moderately heavy, lightly pigmented; choanocyte chambers small, oval, 40-90μm diameter, usually lined by isochelae.

Megascleres. Principal spicules absent.

Auxiliary spicules coring fibres and forming dermal skeleton moderately thin, straight or slightly curved near base, with slightly subtylole bases, hasteate or slightly telescoped points, and apical and basal spination on most spicules. Length 124-(151.7)-162μm, width 3-(4.1)-6μm.

Echinating acanthostyles short, thin, claviform, sharply pointed, slightly subtylole bases, lightly and evenly spined, with relatively large recurved spines. Length 71-(76.3)-86μm, width 3-(4.7)-7μm.

Microscleres. Isochelae of ‘typical’ palmate form, with straight shaft, lateral alae completely fused to shaft, very long, broad front ala. Length 14-(15.7)-18μm.

Toxas wing-shaped, slender, with pronounced central curvature, slightly reflexed arms. Length 48-(88.4)-112μm, width 0.8-(1.6)-2.0μm.

ETYMOLOGY. For Houman Abrolhos.

REMARKS. This species is a sibling species of C. (Wilsonella) australiensis having basal and apical spines on auxiliary styles. It was first assigned to the Western Australian subspecies C. australiensis spinulata Hentschel (1911) but subsequent re-examination of Hentschel’s (1911) syntype (ZMB4446) found that he omitted several crucial characters from his description (and that his species was not substantially different from typical C. australiensis). Conversely, C. (W) abrolhosensis differs from that species in several respects, warranting its recognition as a distinct taxon. Growth form in C. (W) abrolhosensis is endolithic, consisting of discrete bulbous-cylindrical digits arising from a partially burrowing, encrusting massive base, and with large terminal oscules (superficially resembling syconoid calcarean growth forms) (wheras C. (W) australiensis has lobate or clavulate morphologies); there is only one class of auxiliary spicule (as compared with two); fibre reticulation is small, close-set, nearly regular, and predominantly ovoid (wheras in C. australiensis meshes are elongate and cavernous); spongin fibres are poorly developed (compared with well developed fibres); there is very little detritus in fibres, and these are completely confined to primary ascending fibres and more-or-less restricted to foreign spicules without sand (C. (W) australiensis has abundant detritus in all fibres, including sand grains, and this is a prominent feature of the skeleton); and spicule dimensions differ between both species. Further comparisons are given below under remarks for C. (W) australiensis.

This species strictly belongs to Clathria (Dendroclia) in having only a single undifferentiated category of structural megasclere within
fibres, it is included here in *Clathria* (*Wilsonella*) having detritus in fibres and spined terminations on auxiliary spicules similar to *C. (W.) australiensis*. This further illustrates the unclear generic boundary between many nominal genera of Microcionidae, and supports the recognition of a wide definition for *Clathria*.

**Clathria (Wilsonella) australiensis** (Carter, 1885) (Figs 83-84, Plate 2B, Table 15)

<table>
<thead>
<tr>
<th>Spicule</th>
<th>Lectotype (BMNH1886.12.15.43)</th>
<th>Paralectotype (BMNH1886.12.15.284)</th>
<th>Holotype of <em>C. lobosa</em> (AMG9053)</th>
<th>Holotype of <em>T. ramsayi</em> (AMG8820)</th>
<th>Paratype of var. <em>spinulata</em> (ZMB4446)</th>
<th>Specimen (Abrolhos Is) (NClQ66C4266C)</th>
<th>Specimen (N=1) (NTMZ1526)</th>
<th>Specimen (Lévi, 1967) (New Caledonia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaorosomal auxiliary styles</td>
<td>92-(119.8)-152 x 2.5-(3.6)-4</td>
<td>105-(125.6)-152 x 2.5-(3.2)-4</td>
<td>92-(122.6)-146 x 1.5-(2.7)-4</td>
<td>106-(127.4)-173 x 2.5-(3.7)-5</td>
<td>112-(118.8)-135 x 2.5-(3.7)-5</td>
<td>121-(149.0)-163 x 2.5-(3.7)-5</td>
<td>89-(111.4)-175 x 2.5-(4.1)-8</td>
<td>125-180 x 4</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>92-(122.6)-148 x 2-(2.9)-4</td>
<td>101-(118.3)-155 x 1.5-(2.9)-4</td>
<td>94-(119.6)-141 x 2-(2.7)-4</td>
<td>98-(117.2)-139 x 2-(2.8)-4</td>
<td>108-(120.1)-134 x 2.5-(3.7)-6</td>
<td>118-(154.8)-172 x 3-(4.1)-4</td>
<td>95-(123.1)-1 64 x 2-(2.8)-5</td>
<td>-</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>49-(59.8)-68 x 2-(3.6)-4</td>
<td>45-(64.0)-77 x 2-(3.8)-4</td>
<td>54-(62.6)-78 x 2-(3.5)-4</td>
<td>46-(58.4)-70 x 2.5-(3.4)-4.5</td>
<td>46-(57.7)-66 x 4-(6.1)-9</td>
<td>59-(67.6)-74 x 3-(3.9)-6</td>
<td>51-(60.4)-81 x 2.5-(3.7)-5</td>
<td>65-80 x 4</td>
</tr>
<tr>
<td>Texas</td>
<td>35-(61.2)-89 x 0.5-(0.7)-1</td>
<td>28-(33.4)-75 x 0.5-(0.8)-1</td>
<td>32-(53.2)-74 x 0.5-(0.8)-1</td>
<td>24-(45.4)-75 x 0.5-(0.8)-1</td>
<td>72-(89.4)-105 x 1-(1.1)-2.5</td>
<td>28-(39.4)-59 x 0.5-(0.6)-1</td>
<td>43-(35.6)-88 x 0.5-(0.8)-1</td>
<td>40-75 x 1-2</td>
</tr>
</tbody>
</table>


**HABITAT DISTRIBUTION.** Subtidal to 160m depth; on rock, sand and algal bed substrates; known only from Australia; throughout temperate Australian waters — from Houtman Abrolhos, Perth, Bunbury (WA) (Hentschel, 1911; present study), Nuyts Archipelago, St Vincent Gulf (SA) (present study), Port Phillip (Carter, 1885f; present study), Bega, Jervis Bay, Port Hacking, Port Jackson, Botany Bay, N. Sydney, Tweed River region (NSW) (Lendenfeld, 1888 Whitelegge, 1901; present study), and extending into the tropics as far as Low Isles, GBR, Qld. (Burton, 1934a) (Fig. 83G).

**DESCRIPTION.** Shape. Lobate, lobate-digitate, club-shaped, thickly lamellate, or thickly encrusting-bulbous growth forms, up to 140mm high, 110mm wide, with subspherical, tubular, bulbous or flabellate digits, up to 75mm high, 45mm wide, 25mm thick.

**Colour.** Pale orange alive (Munsell 7.5 YR 8/6), pale pink, brown or yellow preserved.

**Oscules.** Large oscules, up to 4mm diameter, on apical or lateral margins of surface digits/lobes. **Texture and surface characteristics.** Surface optically even, microscopically rugose, with a whitish arenaceous, slightly hispid dermal membrane.
**Ectosome and subectosome.** Ectosome membranous, without specialised dermal megasclere, varying from densely arenaceous, with most or all dermal megascleres obscured by large sand grains and spicule fragments, or with light palisade of erect brushes of subectosomal auxiliary subtylostyles, arising from ascending primary choanosomal fibres; sand grains at surface slightly larger than those in choanosome.
**Memoirs of the Queensland Museum**

*Choanosome*. Choanosomal skeleton irregularly reticulate, with clearly differentiated primary and secondary spongin fibres, forming a vaguely longitudinal reticulation with cavernous meshes; spongin fibres well developed; primary ascending fibres marginally thicker, producing ascending lines abundantly cored by detritus, lightly cored by auxiliary styles, heavily echinated by acanthostyles, particularly at fibre nodes; smaller secondary spongin fibres mainly transverse, connecting with primary elements, with no or little detritus, paucisclerotic tracts of auxiliary styles and lightly echinated by acanthostyles; auxiliary megascleres coring fibres occupy only a small proportion of fibre diameter; detritus in fibres consists of scattered sand grains and spicule fragments; mesohyl matrix heavy; choanocyte chambers oval to elliptical, some appear to be paired, and chambers lined by microscleres.

*Megascleres* (Table 15). Choanosomal auxiliary styles coring fibres differ from subectosomal auxiliary styles only in being slightly thicker and lacking characteristic apical microspines of the latter. Coring spicules relatively thin, straight, smooth, mostly hastate, with slightly subtylote and occasionally micropinned bases.

Subectosomal auxiliary styles, dispersed between fibres and in dermal skeleton, straight, usually hastate, subtylote bases with microspines on both points and bases.

Echinating acanthostyles small, evenly spinose or with granular, vestigial spines, slightly subtylote bases, fusiform points.

*Microscleres* (Table 15). Palmate isochelae relatively large, unmodified.

Toxas oxhorn, uncommon, rare in some specimens, often forming thichodragmata, usually with wide, angular, central curves and slightly reflexed points.

Larvae. Ovoid, incubated parenchymella larvae, up to 350μm diameter seen in some material.

*Associations*. Commensal polychaetes common in many specimens; Abrolhos specimen with epizoic zoanthids on surface.

**Remarks.** Clathria (W.) australiensis is the only species retained by Hallmann (1920) in Wilsonella; other species were transferred to either Clathria or Paradoxyx, depending on whether they had palmate or arcuate-like isochelae microscleres. Some of these, however, are further allocated here to Clathria (Dendrocia) or Clathria (Thalysias), depending on their ectosomal skeletons, choanosomal skeletal structure and spicule diversity (i.e., there are differences in interpretation of character importance between the present study and that of Hallmann (1920) (see also Hooper, 1990a).

Unlike Clathria (Dendrocia), in which there is only a single category of coring and extra-fibre megasclere, most Clathria (Wilsonella) have more than one form of auxiliary style, one coring the fibres (choanosomal megascleres) and one outside of fibres (subectosomal megascleres). In some cases (e.g., C. (W.) australiensis, C. (W.) ensae sp. nov.), these spicules are only slightly different in geometry, although showing clear differences in patterns of spination; in others (e.g., C. (W.) reticulata, C. (W.) mixta) these spicules have different geometry; whereas in one (C. (W.) abrolhosensis) there are no apparent differences which is interpreted as a convergence or subsequent loss of a spicule category. Clathria (Dendrocia) and Clathria (Wilsonella) can also be distinguished by their skeletal architecture—being predominantly plumose in the former and reticulate in the latter.

In material listed above most of the larger auxiliary styles without spines on points appeared to be located within spongin fibres (i.e., choanosomal spicules), whereas most of the auxiliary styles with spines on both bases and points were found predominantly outside fibres, strewn within the mesohyl, and in the dermal skeleton (i.e., subectosomal spicules). However, this observation is difficult to verify in all cases because of the dense core of sand particles in fibres. In this species both sorts of spicules are classed as auxiliary styles due to their very similar geometry: true principal styles are absent (i.e., Wilsonella s.s.).

The principal diagnostic characteristics of C. (W.) australiensis and its affinities with other species are discussed elsewhere (see Table 19 and remarks for C. (W.) tuberosa). This species differs from most Australasian Clathria (Wilsonella) in having spinose extremities on both the bases and points of quasidiactmal auxiliary subtylostyles. In this regard it is similar to its sibling species, C. (W.) abrolhosensis from the Houtman Abrolhos, WA (which is sympatric with C. australiensis) and the allopatric species C. (W.) rugosa, from New Caledonia (Hooper & Lévi, 1993a; Table 19). Spicule geometry (megascleres and toxas) are useful in distinguishing these species of Clathria (Wilsonella) (Table 19).

Lévi’s (1967b) material from New Caledonia, described as C. australiensis, was referred to C. (W.) rugosa (Hooper & Lévi, 1993a), based on differences in spicule geometry (especially shape...
and spination of auxiliary spicules), and the latter having flabellate-digitate growth forms. The quasidiactional (strongyloides) modifications of some of the subectosomal auxiliary spicules in both species, with weakly spined points and bases, is a unique trait within the Wilsonella group, but is also known in a few other species of Microcionidae (C. (Dendrocia) pyramida, C. (Thalysias) major, C. (Clathria) chelifera). These quasidiactional spicules are convergent in geometry with true tornotes and strongyles found in other groups such as Iophonidae (see remarks for Megaciella and Acarnus in the introductory section above).

Hentschel (1911) created a subspecies spinulata for material from WA, indicating that it differed substantially from typical forms of the species in spicule dimensions (particularly isochelae), and supposedly lacked toxas. However, Hentschel's type has toxas and isochelae dimensions are within the size range of other S Australian populations, and all other aspects (growth form, fibre characteristics, amount and form of detritus in fibres) are identical between populations. Hentschel (1911) suggested that spinulata differed from other populations in having spines on both the points and bases of auxiliary spicules, but this feature occurs in all other populations, and the WA population is conspecific with C. (W.) australiensis.

Clathria (W.) australiensis is widely distributed throughout temperate Australia, from the Houtman Abrolhos on the W coast (30°S), around S Australia to the Tweed River (28°S). Burton (1934a) recorded this species from Low Isles, (16°S), but his voucher material has not been examined, and his description is not detailed enough to differentiate between C. (W.) australiensis and C. (W.) rugosa from New Caledonia. Recent collections from this region do not include the species. Examination of many other specimens (cited above), from many locations throughout Australia, showed that C. (W.) australiensis is a heterogeneous species. Most regional populations differ from each other slightly in spicule geometry or spicule size, but there is not enough available material of any of these populations to determine whether these differences are consistent within populations, nor are there any features in any of these regional populations worthy of distinguishing separate taxa (cf. Hentschel, 1911). Widespread sampling of regional populations, collection of samples for biochemical and genetic studies, and determination whether or not observed morphological differences correlate with any fixed genetic differences is a worthwhile study for the future.

**Clathria (Wilsonella) claviformis** Hentschel, 1912
(Figs 85-86, Table 16, Plate 2D)

**Clathria claviformis** Hentschel, 1912: 366-367, pl.19, fig.29.


**HABITAT DISTRIBUTION.** 18-23m depth; sand, rock and dead coral substrate; Timor Seas (Fig. 85G). Also Arafura, SE. Indonesia.

**DESCRIPTION.** Shape. Claviform, 160-220mm high, 60-150mm wide, with small cylindrical base and stalk, and one or more lobate, club-shaped, or bulbous digits, up to 80mm long, 65mm diameter.

**Colour.** Pale 'dusty' beige and red-brown mottled colour alive (Munsell 2.5Y 8/6 and 5R 8/4), yellow-grey preserved.

**Oscules.** Large oscules, up to 5mm diameter, on ends of bulbous digits, occasionally in crevices between digits.

**Texture and surface characteristics.** Surface even, with distinct, partially arenaceous, skin-like covering, and with several longitudinal ridges on sides of digits and between bulbous digits; texture rubbery, compressible, sandy.

**Ectosome and subectosome.** Ectosome lightly and evenly arenaceous, hispid, with plumose tufts of subectosomal auxiliary subtylostyles protruding through surface, sometimes in dense brushes; subectosomal cavernous, with sparsely cored, arenaceous, ascending primary spongion fibres forming large meshes in periphery.

**Choanosome.** Choanosomal skeleton irregularly reticulate, cavernous, with light spongion fibres and spicule tracts; spongion fibres divisible into primary and secondary components; primary fibres relatively large, with very little fibre spongion content, cored by both large and small sand grains, Foraminifera and pseudococci of cavernous principal styles, becoming sinuous during towards periphery; secondary fibres consist of uni- or pseudococci spicile tracts bound together by collarogenous spongion and debris; primary fibres moderately echinatated, slightly heavier towards periphery; secondary fibres with
no or few echinating canthostyles; mesohyl matrix heavy, granular, with abundant microscleres and detritus scattered throughout, usually lining small oval choanoocyte chambers. 

Megascleres (Table 16). Choanosomal principal styles thin, slightly curved, fusiform, with rounded or slightly subtolyte, lightly microsponged bases. Subectosomal auxiliary subtyloslotes hastate, thin, mostly straight, with slightly subtolyte bases, usually microsponged. 

Echinating acanthostyles slightly subtolyte, with few, dispersed, large spines on base and apex, usually with aspinose neck; spines located on point usually more recurved than those on base. 

Microscleres (Table 16). Palmate isochelae large, abundant, with some twisted examples. 

Toxas thin, with slight angular central curvature and straight, unreflexed points. 

REMARKS. C. (W.) claviformis is relatively easily differentiated from other arenaceous species by its skeletal architecture, fibre characteristics and spiculation (see remarks for C. (W.) tuberosa below, and compare spicule dimensions between species in Table 19). Hentschel’s (1912) mention of similar isochelae geometry in C. (W.) claviformis and other microcionid species such as C. (Dendrocia) pyramidata is misleading, since the latter species has arcuate-like chelae whereas those of C. (W.) claviformis are simply palmate. The nearest relative of C. (W.) claviformis is probably C. (W.) tuberosa, especially in specific features of its arenaceous ectosome.

Clathria (Wilsonella) ensiae sp. nov. 
(Figs 87-88, Table 17, Plate 2E)

MATERIAL. HOLOTYPE: NTM33561 (NCIQ66C-2384-I) (fragment QMG05004); Marion Reef, off Edithburg, S. Yorke Peninsula, SA, 35°09.5'S, 137°48.0'E, 10.ii.1989, 6m depth, coll. NCI (SCUBA). PARATYPE: NTM33821 (NCIQ66C-3744-L) (fragment QMG300270); Trap Reef, Bicheno, Tas., 41°51.7'S, 148°18.6'E, 30m depth, 26.ii.1990, coll. NCI (SCUBA).

HABITAT DISTRIBUTION. 6-30m depth; on sand covered rock substrate, with algae and seagrasses on patch reef; Yorke Peninsula (SA), E coast (Tas) (Fig. 87F).

DESCRIPTION. Shape. Erect, digitate, flabellate growth form, 205-350mm high, 70-150mm wide, with multiple branches usually aligned in one plane, composed of long, slender, flattened or cylindrical, bifurcate digits, 70-190mm long, up to 18mm diameter, frequently fused near their basals ends, attached to a common base or on a short cylindrical stalk. 

Colour. Red-brown alive (Munsell 2.5R 8/8), darkening in air (2.5R 6/10), brown preserved. 

Oscules. Large oscules, up to 4mm diameter, scattered evenly over all surfaces of digits, in life slightly raised above the surface with a membranous lip.

Texture and surface characteristics. Surface even, optically smooth, broken only by raised oscules; texture firm, compressible, rubbery. 

Ectosome and subectosome. Ectosome heavily arenaceous, with peripheral spongin fibres fully packed with mostly sand particles and some large spicule fragments (holotype; vice versa in paratype), and with sparse plumose tracts of subectosomal auxiliary styles, confined completely below surface; spongin fibres in subectosomal region ascend to surface, plumose, fully arenaceous, with plumose brushes of subectosomal auxiliary spicules.

Choanosome. Choanosomal skeleton irregularly reticulate in axis, plumo-reticulate near periphery, clearly divided into primary, ascending fibres, 60-130μm diameter, and secondary, connecting, transverse spongin fibres, 30-70μm diameter; primary fibres fully arenaceous, incorporating both sand and foreign spicule fragments, and a sparse core of choanosomal auxiliary styles amongst the debris; secondary fibres without sand particles, with some foreign spicules, and also with a light core of choanosomal auxiliary spicules; echinating acanthostyles not abundant on fibres, usually echinating fibres at acute angles, directed towards surface; mesohyl matrix moderately heavy, with few foreign spicules and few foreign particles.

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (QMG05004)</th>
<th>Specimens (N=25)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>258-(208.6)-364 x 6- (9.6)-13</td>
<td>235-(287.2)-338 x 7- (8.4)-10</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>164-(292.0)-371 x 3- (5.1)-8</td>
<td>169-(289.2)-375 x 3- (5.2)-7</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>79-(88.8)-103 x 4- (6.4)-8</td>
<td>64-(74.0)-82 x 4- (6.4)-8</td>
</tr>
<tr>
<td>Chelae</td>
<td>16-(18.4)-22</td>
<td>14-(16.8)-20</td>
</tr>
<tr>
<td>Toxas</td>
<td>28-(140.8)-266 x 0.6-(1.1)-1.5</td>
<td>44-(133.6)-218 x 0.8-(0.9)-1.2</td>
</tr>
</tbody>
</table>
TABLE 17. Comparison between present and published records of <i>Clathria (Wilsonella) ensiae</i> sp.nov. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>Spicule</th>
<th>Holotype (NCI6G6C384D)</th>
<th>Paratype (NCI6G6C3744L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chonoosomal principal styles</td>
<td>69-(111.4)-132 x 3.5-(4.2)-6</td>
<td>87-(108.6)-120 x 4-(4.4)-5.5</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>106-(130.7)-147 x 1.5-(2.6)-3.5</td>
<td>97-(132.0)-154 x 2-(2.4)-3.5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>28-(40.7)-54 x 2.5-(3.1)-4</td>
<td>48-(61.1)-70 x 3.5-(4.3)-5.5</td>
</tr>
<tr>
<td>Chelae</td>
<td>11-(14.2)-16</td>
<td>13-(14.4)-16</td>
</tr>
<tr>
<td>Toxic</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

very little sand; choanocyte chambers large, 180-480 μm diameter, oval or elliptical.

<i>Megascleres</i> (Table 17). Chonoosomal auxiliary megascleres straight or slightly curved towards base, slightly subtylote bases, hastate, abruptly pointed; very similar geometry to subectosomal auxiliary styles but shorter, slightly thicker.

Subectosomal auxiliary styles short, slender, straight or rarely slightly curved at centre, slightly subtylote bases, hastate, stepped points.

Echinating acanthostyles short, slender, straight or slightly subtylote bases, fusiform points, spined all over but spines slightly heavier on base and point.

<i>Microscleres</i> (Table 17). Palmate isochelae relatively long, slender, unmodified.

Toxas absent.

**ETYMOLOGY.** Phonetac acronym in the National Cancer Institute (NCI), in appreciation of the AIMS group who provided the author with unrestricted access to all their sponge collections.

**REMARKS.** There are some differences between the two specimens of <i>C. (W.) ensiae</i> in the size of acanthostyles (Table 17). Similarly, primary spongins fibres of the holotype are predominantly cored with sand particles, whereas in the paratype foreign spicules are more abundant than sand, but in all other respects both these specimens are identical, and these observed differences are considered to be relatively minor.

<i>C. (W.) ensiae</i> differs from other species of the Wilsonella group primarily in its flattened-flabeliform, erect, bifurcate, branching growth form and in having auxiliary styles with peculiar hastate, telescoped points. Other features such as skeletal structure and spicule dimensions can also be used to distinguish allied species (Table 19). Like <i>C. (W.) australiensis</i>, the present species could also be included in <i>C. (Dendrocia)</i> due to close resemblance between choanosomal and subectosomal styles, both classed here as auxiliary spicules (i.e., Wilsonella s.s.). However, like <i>C. (W.) australiensis</i>, those styles coring fibres differ subtly in their terminations from those styles outside of fibres.

**Clathria (Wilsonella) reticulata** (Lendenfeld, 1888)

(Figs 89-90, Table 18)

<i>Clathriopsamma reticulata</i> Lendenfeld, 1888: 227;

<i>Clathria reticulata</i>; Hooper & Wiedenmayer, 1994: 275.

Not <i>Echinolchalinia reticulata</i>; Whitelegge, 1907: 506, pl.45, fig.25; Hallmann, 1912: 287, pl.30, fig.2, text-fig.66.

Not <i>Dictyocylindrus reticulatus</i> Carter, 1881a: 377.

Not <i>Rhaphidophius reticulatus</i>; Hallmann, 1912: 177.


**HABITAT.** Ecology unknown; central E coast (NSW) (Fig. 89G).

**DESCRIPTION.** Shape. Subspherical, reticulate-branched growth form, 80-150mm high, 55-95mm wide, composed of lobate, bifurcating, sometimes anastomosing tubular digits with rounded margins, 30-50mm long, up to 18mm diameter.

**Colour.** Dark brown in ethanol.

**Oscules.** Not seen (available material dry and surface contracted).

**Texture and surface characteristics.** Surface shaggy, reticulate; texture brittle in dry state.

**Ectosome and subectosome.** Ectosomal skeleton lightly arenaceous, with plumose brushes or individual choanosomal principal styles protruding, together with a paratangential layer of subectosomal auxiliary stylostyles, lying near bases of principals, and echinating acanthostyles projecting into these.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with moderately heavy, large spongins fibres forming relatively wide ovoid meshes, lined by very large, typically curved oxoete toxas; spongins fibres not easily divisible into primary or secondary components based on fibre diameter, although primary, ascending fibres contain plumose, paucispicular tracts of both principal...
and auxiliary megascleres; secondary, transverse, connecting fibres without coring spicules; both sorts of spongin fibres contain a light core of detritus, especially small sand grains; echinating acanthostyles very abundant, including peripheral fibres; mesohyl matrix heavy, darkly pigmented, with abundant microsclerites, especially bundles of whispy, sinuous toxas (toxodragmata); extra-fibre auxiliary megascleres organised into ascending subdermal tracts, with few loose spicules scattered between fibres.

Megascleres (Table 18). Choanoasomal principal subiostyles well differentiated from auxiliary spicules, mostly straight, fusiform, with profusely microspined, slightly subiylote bases. Subectosomal auxiliary subiostyles thin, fusiform, straight, slightly curved, sometimes sinuous, with minutely microspined, subiylote bases.

Echinating acanthostyles with rounded bases, relatively even spination, although basal and distal portions slightly more heavily spined than points. Microscleres (Table 18). Palmate isochelaie differentiated into 2 size classes, smaller with approximately 75% of contact forms. Toxas extremely abundant, long, thin, sinuous, characteristically oxeote, with only very slight or no central curvature and straight tapering points.

REMARKS. This species is poorly known from 3 specimens but differentiated from other species in the Wilsonella group having only a very light core of detritus in fibres, usually composed of small sand and spicule particles, differentiated primary and secondary fibres, and prominent bundles of sinuous toxas lining aquefierous chambers (Fig. 90). Affinities with other species (Table 19) are discussed elsewhere (remarirs under C. (W.) tuberosa and C. (W.) australiensis). In some respects (growth form, geometry of some spicules, presence of two sizes of isochelaie with contort forms) the species is closest to C. (W.) tuberosa, but toxas geometry is quite different between these two species.

Clathria (Wilsonella) tuberosa (Bowerbank, 1875) (Figs 91-93, Table 19, Plate 2F)


Clathria tuberosa; Ridley, 1881: 121; Ridley, 1884a: 444-445, pl.42, fig.g; Hentschel, 1912: 365-366; Hooper & Wiedenmayer, 1994: 275.


| TABLE 18. Comparison between present and published records of Clathria (Wilsonella) reticulata (Lendenfeld). All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25). |
|-----------------|-----------------|-----------------|
| **SPICULE**     | **Lectotype**   | **Paralectotype** | **Paralectotype** |
|                 | (AMG9135)       | (AMZ2457)        | (BMNH 1925.11.1.576) |
| Choanoasomal    | 173(-209.4) -   | 182(-240.2) -    | 227(-251.5) -       |
| principal       | 258 x 7(-9.1)  | 289 x 8(-9.3)   | 296 x 9(-9.4)       |
| styles          | 11             | 11              | 11                 |
| Subectosomal    | 163(-236.8) -  | 187(-259.0) -    | 198(-243.4) -       |
| auxiliary       | 324 x 3(-4.0)  | 322 x 3(-4.2)   | 309 x 3(-4.6)       |
| styles          | 6             | 5               | 7                 |
| Echinating      | 52(-61.7) - 7  | 54(-63.6) - 75  | 65(-67.8) - 72     |
| acanthostyles  | 71 x 3(-6.5)  | 4(-7.2) - 9     | 6(-7.3) - 9        |
| Chelia I        | 5(-6.6) - 9    | 4(-5.8) - 7     | 6(-6.1) - 9        |
| Chelia II       | 12(-14.4) - 17 | 13(-14.8) - 17  | 14(-15.2) - 17     |
| Toxas           | 238(-402.7) -  | 45(-231.3) - 3  | 302(-247.7) - 5    |
|                 | 684 x 0.8(2.4) | 433 x 0.5(1.9) | 593 x 1(-2.2) - 4  |

HABITAT DISTRIBUTION. Semi-encrusting on rock, dead or live coral heads, epizoic on other sponges and gorgonians; usually associated with shallow coral reef habitats; 2-19m depth range; prevalent in the tropical, Australian and Indo-Malay shallow water macrobenthic community, extending as far south as 13°S latitude: Torres Strait (FNIQ) (Ridley, 1884a), Bynoe Harbour, Darwin Harbour, Coral Bay, Port Bremer, Wessel Is (NT). Also Straits of Malacca (Bowerbank, 1875; Ridley, 1881) and Aru Is, Indonesia (Hentschel, 1912).

DESCRIPTION. Shape. Subspherical, predominantly bulbous growth form, 60-135mm diameter, less often club-shaped with apical lobate digits, or pseudo-vasiform on low stalk with convoluted, apical, lobate digits; surface projections (or branches) rounded lobate, relatively close-set, attached to common centre, which in turn is usually attached to substrate by a small peduncle; lobate digits usually bifurcate with rounded margins. In life lobes prominently bulbous, evenly rounded; after preservation lobes become slightly flattened and angular.

Colour. Live pigmentation dusty pale pink-red (Munsell 2.5R 6/10) to pink (SRP 8/6), with a darker choanoosome (SRP 7/8); lighter ectosomal colouration due to arenaceous nature of ectosome; dessicated colouration darkens to brown (2.5Y 8/2), red-brown (5Y 8/4), or red-purple (SRP 3/6), as paler ectosome collapses. In situ, subdental ridges and canals red-pink in life, showing darker choanoosomal pigmentation.

Oscules. Exhalant pores variable in diameter, ranging from 1-3mm, each with prominent,
membranous, raised lip (collapses upon preservation); oscules confined to apex of lobate digits, with subdermal canals and grooves radiating away from pores in cruciform pattern.

**Textural and Surface Characteristics.** Surface optically smooth, even in situ, distinctly membranous; ectosomal membrane transparent or slightly opaque when intact, stretched across adjoining lobes, with darker subdermal pigmentation and fibre reticulation clearly visible below; subdermal grooves and minute subdermal canals produce a more-or-less microscopically reticulate surface; upon dessication ectosome collapses to become optically reticulate, distinctly arenaceous, with convoluted ridges and conules, and large amounts of clear mucous usually produced; texture stiffly compressible, arenaceous, harsh to touch, minutely hispid.

**Ectosome and Subectosome.** Ectosomal skeleton heavily arenaceous, with delicate traces of sand coring peripheral fibres, through which protrude sparse tufts of subectosomal auxiliary styles, usually raised on low surface conules; special ectosomal megascleres absent; subectosomal auxiliary subtylostyles also form tangential or paratangential tracts perpendicular to dermal crust. Intermingled with foreign particles auxiliary spicules variable in size, but no distinct localisation of smaller or larger forms; subectosomal region obscured by abundant sand grains coring peripheral subdermal fibres; individual extra-fibre auxiliary styles are intermingled amongst sand and fibres in subdermal region, sometimes forming dense paratangential plumose brushes, ascending to ectosome, but usually producing sparse tangential subdermal tracts; subdermal tracts clustered tightly around fibres and sand matrix, bound together with abundant collagen; on peripheral fibres, choanosomal principal spicules produce plumose brushes, sometimes protruding through surface, but usually only obvious in places where ectosome has collapsed and peripheral fibres are closest to surface.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with light spongin fibres fully cored by sand grains and fewer choanosomal principal megascleres, the latter in rows of 6-10 abreast in larger fibres; spicule fragments also common amongst detritus, particularly haplosclerid oxeas; spongin fibres heavily echinated by acanthostyles; fibre branching produces irregular oval meshes, 50-(334)-600μm diameter, with irregular eolithic choanoocyte chambers (38-121μm diameter), with light mesohyl matrix and abundant microscleres, without sand or any megascleres; spongin fibres not clearly divisible into primary or secondary elements, but thinner fibres (30-55μm diameter) have coring megascleres more visible (fewer detrital particles); larger spongin fibres 70-(104)-230μm diameter; megascleres core fibres in paucispicular tracts, slightly more heavily aggregated in thicker fibres but partially obscured by sand particles; mesohyl matrix in axis light, with little foreign debris or auxiliary megascleres. **Megascleres** (Table 19). Choanosomal principal subtylostyles slightly curved towards basal end, occasionally straight, with heavily microspined bases, tapering to sharp fusiform points.

Subectosomal auxiliary subtylostyles straight, variable in size, usually with microspined, prominently subtylolate bases, sharply tapering, fusiform points.

Acanthostyles very variable in length and width, straight, subtylolate, fusiform, evenly spinose with granular spines (thinner spicules) or heavy thorn-like spines (thicker spicules).

**Microscleres** (Table 19). Palmate isochelae typically very abundant, incompletely divided into two size classes, with some twisted smaller examples.

Toxas abundant, thin, usually long, without reflexed points, only slightly curved at centre, although smaller examples may have more angular central curvature; occurring individually or more often in toxodragmata within mesohyl matrix.

**Larvae.** Incubated parenchymella larvae were recorded in only 17% of specimens, collected from Darwin and Cobourg Peninsula regions, NT, during May, September, October and December, suggesting a possible breeding period during the wetter months (Fig. 93). Larvae orange-brown pigmented, oval - elongate, ranging from 165-280 x 110-160μm. All larvae contained juvenile megascleres scattered throughout central portion of mesohyl, usually with heavy collagen. In the few adult sponges seen incubating larvae, the

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FIG. 93. *Clathria (Wilsonella) tuberosa* (Bowerbank). Seasonal production of incubated larvae in populations from NW Australia.

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<table>
<thead>
<tr>
<th>SEASON</th>
<th>TOTAL SAMPLES</th>
<th>SAMPLES WITH LARVAE</th>
</tr>
</thead>
<tbody>
<tr>
<td>WET</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>PREDRY</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>DRY</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>PREWET</td>
<td>10</td>
<td>5</td>
</tr>
</tbody>
</table>
mesohyl was usually lightly orange in colour, whereas in non-fecund specimens the mesohyl matrix was invariably pigment light brown. 

**Associations.** Scyllid polychaete worms (Typosyllis spongicola) relatively common (31% of specimens examined).

**Morphological variation.** Gross morphology: characteristic, relatively consistent, varying only in elongation of basal stem and clump of digits on apex, ranging from low spherical bulbs (69%), club-shaped (16%), or convoluted, semivasiform growth forms (15%). Live colouration: consistent, only slight variation in pinkish hue. Exoskeletal structure: extends from densely arenaceous with few dermal spicules brushes (39%), arenaceous with abundant protruding plume subectosomal brushes (35%), to arenaceous with plume brushes of subec- tosomal spicules and single choanosomal styles erect on surface (26%). Subectosomal skeletal structure: varies from well-developed, plume ascending spicule tracts composed of subec- tosomal auxiliary styles (27%), few plume extra-fibre brushes with most extra-fibre spicules closely bound by collagen (31%), or with all extra-fibre spicules simply bound closely but external to spongins fibres (42%). Choanosomal skeletal structure: relatively consistent, ranging from simply regularly reticulate (54%) to regularly reticulate (46%), with oval meshes (88%) or less commonly longitudinally elongated meshes (12%). Mesohyl matrix: lightly pigmented (58%), moderately heavily pigmented (23%), or heavily pigmented collagen (19%). Echinating acanthostyles: forming dense (42%), moderately dense (50%), or only lightly echinat- ing fibres (8%). Megasclere geometry: consistent; majority of choanosomal subtylosstyles with microspined bases, 8% of specimens with smooth subtylote bases. Acanthostyles vary only in dimensions. Microsclere geometry: consistent although proportion of cortex versus unmodified

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**TABLE 19.** Comparison between morphological characteristics of some Australasian arenaeous Clathria (Wilsonella) species, based on present and published records. All measurements are given in μm.

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>MATERIAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Shape</td>
<td>massive subcircular tubular</td>
</tr>
<tr>
<td>Digits</td>
<td>lobate</td>
</tr>
<tr>
<td>Live colour</td>
<td>pale orange</td>
</tr>
<tr>
<td>Skeletal architecture</td>
<td>irreg. retic</td>
</tr>
<tr>
<td>Differentiated primary/seconda ry fibre system</td>
<td>yes</td>
</tr>
<tr>
<td>Choanosomal styles</td>
<td>89-175 x 2.5-8 smooth or spined base</td>
</tr>
<tr>
<td>Subectosomal styles</td>
<td>92-172 x 1.5-5 spined apex and base</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>49-83 x 2-6</td>
</tr>
<tr>
<td>Large chelae</td>
<td>11-19</td>
</tr>
<tr>
<td>Small chelae</td>
<td>absent</td>
</tr>
<tr>
<td>Toes</td>
<td>28-89 x 0-3-1.5 angular centre</td>
</tr>
</tbody>
</table>

Material:
1. W. australiensis (Carter) - present study.
2. C. lobata Lendenfeld (1888:149) = W. australiensis - holotype AMU G9053; Port Jackson,NSW.
3. W. claviformis (Hentschel) - present study.
4. W. ensisae, sp.nov. - present study.
5. W. ramosa (Lindgren, 1897:482) - schizotype BMNH 1929.11.26.48.
small isochelae varies from 0-20% of conort spicules (12%), 20-40% (19%), 40-60% (24%), 60-80 (35%), to 80-10% of spicules (12%). Spicule dimensions: Few specimens atypical but variation apparently random with no statistical significance between specimens irrespective of seasonal or geographical distribution of samples.

REMARKS. C. (W.) tuberosa is distinctive in the field: pink colour, bulbous growth form, soft texture. However, it is more difficult to differentiate descriptively. Pertinent differences are:

Choanosomal architecture and fibre characteristics of C. (W.) reticulata are identical to those of C. (W.) tuberosa; acanthostyles are as equally abundant in both species, but many acanthostyles have heavier spines on the distal part than on points; and there are two sizes of isochelae, 75% of the smaller being conort. Thus, the major features distinguishing the two taxa are the straight or sinuous oxeote toxas in C. (W.) reticulata, which are never present in C. (W.) tuberosa, and the light deposits of debris into fibres. Nevertheless, the two species are closely related.

Clathria (W.) australiensis has choanosomal fibres divided into ascending and radial primary elements, fully cored by detritus, with less heavily cored secondary transverse elements. Subectosomal auxiliary subystyles have spines on both bases and points, typically with a prominent terminal spine/point and also smaller spines occurring at least part of the way along the shaft. Choanosomal subystyles are also auxiliary spicules, with smooth or spined bases only. Acanthostyles are pointed and tapering; there is only one size of isochelae; and toxas have strongly curved (rounded or sharply angular) central curves.

Clathria (W.) rugosa is a sister species of C. (W.) australiensis; differing in having prominent subectosomal drainage canals ("astrorhiza"). Subectosomal auxiliary styles are also spined on both ends, but spines are perched only on the very extremity of the spicle point (not on the shaft); acanthostyles have bulbous points; there is only

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>MATERIAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shape</td>
<td>fae patracte- digitate</td>
</tr>
<tr>
<td>Digits</td>
<td>cylindrical</td>
</tr>
<tr>
<td>Live colour</td>
<td>bl.red-orange</td>
</tr>
<tr>
<td>Skeletal architecture</td>
<td>irrreg/retic.</td>
</tr>
<tr>
<td>Differentiated primary/secondary fibre system</td>
<td>yes</td>
</tr>
<tr>
<td>Choanosomal styles</td>
<td>13-159 x4.5-8 smooth base</td>
</tr>
<tr>
<td>Subectosomal styles</td>
<td>162-206 x2.5-4 spined apex and base</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>58-91 x4-7</td>
</tr>
<tr>
<td>Large chela</td>
<td>12-17</td>
</tr>
<tr>
<td>Small chela</td>
<td>absent</td>
</tr>
<tr>
<td>Toxas</td>
<td>24-122 x0.8-3 slight curve at centre</td>
</tr>
</tbody>
</table>

Material:
1. W. rugosa (Hooper & Lévi, 1993) - New Caledonian population (included for comparative purposes).
2. W. tuberosa (Bowerbank, 1875:28); holotype BMNH 1875.5.21.1312; Strath of Malacca (N=25).
3. W. tuberosa: Ridley, 1884:444; BMNH 1881.10.21, 325, 1882 2.23, 196, 253, 283, 334; Torres Strait (N=125).
5. W. tuberosa: present material - NW Australia (N=650).
6. W. reticulata (Lendenfeld) - present study.
a single small category of isochelae; and toxas are only slightly curved at their centre.

Clathria (W.) claviformis, C. (W.) ensiae, and C. (W.) ramosa are different from these other species in spicule geometry, spicule size, skeletal architecture and fibre characteristics. These Indo-Australasian species are relatively easy to distinguish from their gross morphology and field characteristics although their skeletal characters are usually at least partially obscured by the incorporation of sand into fibres.

With the exception of C. (W.) australiensis species of Clathria (Wilsonella) have relatively restricted, mostly allopatric distributions: C. (W.) tuberosa is from N Australia and SE Asia; C. (W.) claviformis from the Arafura and Timor Seas; C. (W.) mixta from 2 disjunct populations in the Arafura Sea and the S. Arabian coast; C. (W.) ramosa from the Java Sea; C. (W.) ensiae in S Australia and Tasmania; C. (W.) reticulata SE Australia. C. (W.) australiensis ranges from SW Australia to S Queensland, whereas its cryptic sibling C. (W.) rugosa is restricted to New Caledonia.

**OTHER SPECIES OF CLATHRIA (WILSONELLA)**

Clathria (Wilsonella) cecidochela (Vacelet & Vasseven, 1971)
Clathriopsamma cecidochela Vacelet & Vasseven, 1971: 104-105, text-fig.62, pl.3, fig.1 [Tulear, Madagascar].

Clathria (Wilsonella) ferrea (de Laubenfels, 1936)
Fisherispongia ferrea de Laubenfels, 1936b: 460, fig.44. [Atlantic coast of Panama].
Clathria (Microciona) ferrea: Van Soest, 1984b: 101-103, text-fig.40, table 4 [Curaçao].
Clathria ferrea; Zea, 1987: 172, text-fig.60 [Colombian Caribbean].
Microciona ferrea: Pulitzer-Finali, 1986: 149 [West Indies].
MATERIAL: HOLOTYPE: USNM22239, Caribbean.

Clathria (Wilsonella) foraminifera (Burton & Rao, 1932)
Aulenella foraminifera Burton & Rao, 1932: 345-346, pl.18, fig.11, text-fig.11 [Gaspar Straits, Java Sea].
MATERIAL: HOLOTYPE: IMP79/1. E Indonesia.

Clathria (Wilsonella) lindgreni sp. nov.
Clathria ramosa Lindgren, 1897: 482-483, Lindgren, 1898: 308-309, pl.17, fig.9, pl.18, fig.15, pl.19, fig.16 [Beliung 1, Java Sea]; Hentschel, 1912: 367. (Thalysia) ramosa; de Laubenfels, 1936a: 105.
Not Rhaphidophius ramosus Kieschnick, 1896: 533; Kieschnick, 1900: 53-54, pl.45, figs 47-50. Not Echinoclathria ramosa; Hallmann, 1912: 277, pl.30, fig.3.

Clathria (Microciona) Bowerbank, 1862

DEFINITION. Persistently encrusting growth form, with hymedesmoid skeletal architecture consisting of a basal layer of spongin, typically
with ascending, plumose, non-anastomosing, spongion fibre nodes, and megascleres embedded and erect on basal layer; ectosomal skeleton with only a single undifferentiated category of auxiliary megasclere.

**TYPE SPECIES.** *Microciona atrusangulata* Bowerbank, 1862b: 1109 (by subsequent designation of Bowerbank, 1864: 188).

**REMARKS.** Of 118 named species described in, or subsequently referred to *Microciona* or one of its synonyms, 103 appear to be valid, and 7 are recorded from Australasia, including 2 new species.

**Clathria (Microciona) aceratoobtusa**
(Carter, 1887)
(Figs 94-95, Table 20, Plate 3C)

*Microciona acerato-obtusa* Carter, 1887: 62, 67, 83, pl.5, figs 7-10; Dendy, 1896: 18; Hentschel, 1911: 348, text-fig. 32a-f.


**MATERIAL.** HOLOTYPE: LFM (confirmed destroyed during WWII); Kadan Kyun (King I.), Megui Archipelago, Andaman Sea, Burma. NEOTYPE: NTMZ3676: NW side of N. I., Ko Wao Yai Group, vicinity of Ko Samui, Gulf of Thailand, 9°46.7′N, 99°30.3′E, 12m depth, 6.v.1990, coll. J.N.A. Hooper (SCUBA). OTHER MATERIAL: NSW - NTMZ32835 (fragment QMG300543), NTMZ3125. QLD - QMG303089, QMGL713 (fragment NTMZ1536). SAHUL SHELF, WA - QMG301083, QMG301188. INDONESIA - BMNH1946.11.25.244.

**HABITAT DISTRIBUTION.** Coral rubble, rock and bivalve substrata; intertidal-14m depth; Shark Bay, Cartier I., Hibernia Reef, Saahul Sheilf (WA) (Hentschel, 1911, present study); Cairns and Shelleburne Bay (FNQ) (present study); Sydney and Illuka (NSW) (Rudman & Avern, 1989, present study) (Fig. 94G). Also Indo-Malay Archipelago - Andaman Sea (Burma) (Carter, 1887), Gulf of Thailand (present study).

**DESCRIPTION OF NEOTYPE.** Thinly encrusting on bivalves, up to 1mm thick; colour orange-red alive (Munsell 10R 6/12), firm texture; oscules not seen; surface microscopically hispid, with choanosomal principal styles protruding up to 100μm from ectosome; subectosomal auxiliary styles lie paratangential to surface, in bundles or individually; choanosomal skeleton lepiocladthriid, with principal styles and echinating acanthostyles embedded in and perpendicular to basal spongion fibres; principal styles form plumose brushes, and both sorts of spicules also scattered individually in skeleton; mesohyl matrix heavy, dark brown, granular, with incorporated detritus, numerous toxas and auxiliary styles dispersed; principal choanosomal styles long, fusiform, rounded or very slightly subtylole, with smooth or minutely spined bases (length 175-548μm, width 11-22μm); subectosomal auxiliary subtylostyles polytylole, with microspined swollen bases (length 264-387μm, width 1.5-4.5μm); echinating styles short, slightly curved, robust, with prominently swollen, usually microspined bases and smooth shafts (length 128-183μm, width 5-12μm); palmate isochelae small, relatively homogeneous in size, with many twisted forms (9-14μm long); toxas short, thickest at centre, tapering to sharp, slightly reflexed points (length 58-92μm, width 2-5.5μm).

**DESCRIPTION.** Shape. Thinly encrusting, contiguous or discrete mats on rock or coral substrata, covering up to 120mm², 0.4-2mm thick.

**Colour.** Bright orange-red alive (Munsell 10R 6/12-14), grey-brown in ethanol.

**Oscules.** Small exhalant apertures unevenly distributed over surface, up to 1.5mm diameter, slightly raised or flush with surface; small membraneous lip surrounding oscules at alive, collapsing in air. Minute inhalant pores irregularly dispersed, producing slightly reticulate appearance.

**Texture and surface characteristics.** Firm, mucusy alive, minutely hispid; surface with irregularly dispersed, bifurcate subdermal drainage canals meandering from oscules.

**Ectosome and subectosome.** Ectosomal skeleton hispid, with points of large choanosomal principal styles protruding up to 200μm from surface, occurring individually or in paucispicular plumose brushes of about 5 spicules; subectosomal auxiliary styles usually lie paratangential to surface, sometimes forming tangential tracts lying immediately subdermal; auxiliary styles arise from skeleton at oblique angles, rarely protruding through ectosome; tracts of auxiliary spicules originate in basal half of skeleton, with 8-12 spicules per tract.

**Choanosome.** Choanosomal skeletal architecture hydromesod in thin sections, microcionid in thicker regions, with a relatively thick layer of heavy spongion fibre lying on basal substrate, 22-43μm diameter; bases of principal and echinating styles embedded in basal spongion, perpendicular to substrate, individually or in plumose bundles;
in thick sections basal spongin fibres form small erect nodes, 22-35μm thick, up to 48μm high, enveloping bases and parts of spicule shafts; mesohyl matrix heavy, granular, darkly pigmented, incorporating irregularly dispersed sand grains and other foreign debris, numerous toxas occurring singly or in dragmata, more-or-less ascending tracts of subectosomal auxiliary megascleres, and fewer isochela; choanocyte chambers minute, ovoid but rarely seen, 12-18μm diameter, mostly obscured by heavy collagen; large subectosomal cavities, 110-145μm diameter, visible where inorganic substrate is fragmented and discontiguous.

*Megascleres* (Table 20). Choanosomal principal subtylostyles long, thick, fusiform, typically curved in basal third, with slightly subtylole mostly smooth, less often microspined bases.

Subectosomal auxiliary subtylostyles usually long, straight, thin, fusiform, with prominently swollen, smooth or microspined bases.

Echinating subtylostyles entirely smooth or occasionally with lightly microspined bases, small, thick, fusiform, slightly curved or straight. Intermediates between echinating and principal styles also occur.

*Microscleres* (Table 20). Palmate isochela small, with long lateral alae fused to shaft for most of its length; ischela relatively common, of a single size class, homogeneous in size and geometry, approximately 70% with contort shafts.

Toxas very abundant, othorn, with slightly rounded central curves, straight or slightly reflexed points; central part thickest whereas tips taper to fine points.

**TABLE 20.** Comparison between present and published records of *Clathria (Microciona) aceratoobrassa* (Carter). All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Neotype (NTMZ3376)</th>
<th>Hentschel (1911)</th>
<th>Specimens (N=6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>175(386.0)-548 x 11-(15.5)-22</td>
<td>up to 408 x 8</td>
<td>235(352.8)-492 x 12.5-(17.2)-22</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>264(324.3)-387 x 1.5-(3.8)-4.5</td>
<td>168 x 4</td>
<td>217(379.8)-443 x 3.5-(4.3)-6</td>
</tr>
<tr>
<td>Echinating styles</td>
<td>128(149.9)-183 x 5-(7.2)-12</td>
<td>from 64 x 5</td>
<td>97(150.8)-194 x 5.2-(6.8)-9</td>
</tr>
<tr>
<td>Chelae</td>
<td>9-(12.2)-14</td>
<td>9-12</td>
<td>10.5(13.5)-16</td>
</tr>
<tr>
<td>Toxas</td>
<td>58(71.5)-92 x 2-(3.1)-5.5</td>
<td>35-92 x 3.4</td>
<td>18(57.3)-84 x 0.8(2.2)-3.5</td>
</tr>
</tbody>
</table>

**Associations.** On the NSW coast this species has been found in association with pairs of nudibranchs grazing on the sponge, Rostanga arbutus (AMC151078, 154589) (W.B. Rudman, pers.comm.). These predators are identical in their live colouration to the sponge, presumably utilising the sponge’s carotenoid pigments.

**REMARKS.** This species was originally recorded from Mergui Archipelago and by Hentschel (1911) from Shark Bay, WA. The holotype was destroyed during WWII (its absence from the LFM collections has been checked by Shirley Stone, BMNH, pers.comm.); the neotype comes from an area in Thailand relatively close to the type locality. The first record of the species in the Pacific Ocean is also made here.

Previous published descriptions of this species are relatively poor and non-discriminatory; some attributes of the type material are still uncertain. Carter (1887) did not give any spicule dimensions, but his figures indicate that Mergui specimens are very similar to present material. There are some minor differences between my material and descriptions by Carter (1887) and Hentschel (1911). Hentschel’s specimens from Shark Bay were thickly encrusting with stoloniferous, mammiform surface processes. Choanosomal architecture varied from leptoclathrid, with a thin layer of spongin lying on the substrate, to microsclerid in thicker regions, with fibre nodes and single, non-anastomosing columns of spongin arising from the substrate. Principal styles were fusiform, prominently subtylole, often with microspined bases. Palmate isochela were frequently contort. By comparison, Carter (1887) reported the holotype had principal styles with hastate or styloid points, and their bases were completely smooth and only slightly subtylole. Similarly, there was no mention in Carter’s description whether isochela were modified (contort). Vosmaer (1935a) expressed doubts about the conspecificity between Carter’s and Hentschel’s material based on alleged differences between them in megasclere and microsclere geometries, but this criticism is unfounded. Both Carter and Hentschel reported that their specimens were thinly encrusting on living and dead serpulid worm tubes, bivalves and gastropods; color was brown to beige preserved; toxas geometry was distinctive and identical; and echinating megascleres were entirely smooth.

De Laubenfels (1936a) erected *Axocielita* for this species, having smooth echinating
TABLE 21. Spicule dimensions of *Clathria (Microciona) antarctica* (Topsent), giving comparisons between nominotypical material and other type material. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype of S. toxiferum (MHNDT1612)</th>
<th>Part of type of <em>M. basispinosus</em> (BMNH1933.3.17.39)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal</td>
<td>409-(519.9)-676 x 9- (13.8)-22</td>
<td>293-(498.3)-618 x 9- (12.6)-18</td>
</tr>
<tr>
<td>principal</td>
<td>213-(424.9)-899 x 4- (10.5)-16</td>
<td>252-(360.9)-303 x 4- (7.2)-10</td>
</tr>
<tr>
<td>styles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subectosomal</td>
<td>52-(110.8)-214 x 2.5-(6.8)-10</td>
<td>78-(130.1)-265 x 3- (8.7)-11</td>
</tr>
<tr>
<td>ancathostyles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Echinating</td>
<td></td>
<td></td>
</tr>
<tr>
<td>subectosomal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chelae</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Toxas</td>
<td>31-(46.1)-84 x 0.8- (1.3)-3.0</td>
<td>18-(27.8)-35 x 1.5- (2.3)-4.0</td>
</tr>
</tbody>
</table>

megascleres (i.e., like *Axociella*) but also with a *Microciona*-like encrusting growth form. This is surprising given that *Ophlitaspisanga seriata*, a north Atlantic species, also has an encrusting growth form, microcionid architecture and smooth echinating spicules (which Simpson (1968a) subsequently showed was a synonym of *Microciona* based on cytology and other characters). These arguments demonstrate that the apparent generic boundaries between microcionids based on growth form and spicule spination are tenuous at best.

QMGL713 from the Cairns region, encrusting on an ascidian, has skeletal architecture, fibre characteristics and spiculation closely comparable to other material of *C. (M.) aceratoobtusa* but lacks toxas completely. It is difficult to confirm the identity of this specimen (i.e., because the species is largely characterised by the geometry of its toxas), but given that all other characters are the same it is included here.

Although only known from few specimens it is likely that this species is widespread in the Indo-West Pacific shallow-water fauna.

**Clathria (Microciona) antarctica** (Topsent, 1917) (Figs 96-97, Table 21)

*Stylrotchichon toxiferum* Topsisent, 1913a: 621-622, pl.4, fig.7, pl.6, fig.14.

Not *Hymenaphisia toxifera* Hentschel, 1912: 382.

*Anchiote toxifera var. antarctica*; Topsisent, 1917: 43, pl.4, fig.5, pl.6, fig.5.


*Clathria toxiferum*; Van Soest, 1984b: 129.

*Pseudanchinoctoxiferum*: Kolton, 1976: 155, 188.

*Stylrotchichon tuberculata* Burton, 1934b: 35, pl.3, fig.2, text-figs 6-9; Kolton, 1976: 188.


*Clathria antarctica*; Hooper & Wiedenmayer, 1994: 266.


**HABITAT DISTRIBUTION.** Deeper water rock reefs; 1610m depth (Kolton, 1976); Antarctica - Discovery Inlet, Ross Sea, McMurdo Sound, Graham Land, Victoria Land, Enderby Land; Subantarctic - Macquarie I. (Fig. 96F). Also SW Atlantic; SW and SE Pacific - Tierra del Fuego, Falkland Is, Shag Rocks, South Georgia, Gough Is., Argentina, Chile, Kerguelen, New Zealand.

**DESCRIPTION.** Shape. Growth forms range from thickly encrusting to massive, sub spherical. Colour. Brown in ethanol. Oscules. Small, 2mm diameter, on apex of surface conules. Texture and surface characteristics. Compressible; smooth surface with scattered prominent conules, translucent surface. Ectosome and subectosome. Moderately dense plumose brushes of auxiliary subtylostyles, of a single size category, arising from ends of erect fibre nodes, protruding through surface and interdispersed with long principal spicules. Choanosome. Skeletal architecture microcioniid, with hymedesmoid basal layer of spongin lying on substrate echinated by erect acanthostyles of various sizes, and erect fibre nodes at 200-400μm intervals; fibre nodes non-anastomosing, forming discrete skeletal columns in choanosome; erect fibre columns, 40-100μm diameter, cored by long choanosomal subtylostyles, usually protruding through fibres in plumose bundles or individually, and also heavily echinated by smaller acanthostyles in their basal portion only; fibres form single, discrete columns of spongin and spicules for most of their length but diverge into 2 or more branches in subectosomal region, ultimately producing ectosomal spicule brushes at their ends; mesohyl matrix light, choanoocyte chambers 30-50μm diameter, numerous spherical cells, and dispersed auxiliary spicules outside.
fibres also form plumose columns; mesohyl collagenous.

Megascleres (Table 21). Choanosomal principal subtylostyles very long, slender, with fusiform points, slightly curved towards apical end, subtyloite or slightly subtylote bases, smooth or microspined bases.

Subectosomal auxiliary subtylostyles short, robust, straight or slightly curved near basal end, hastate points or at least less fusiform than principal spicules, with subtyloite microspined bases.

Echinating acanthostyles variable size range, the larger ones clearly intermediate between principal spicules and smaller spined spicules; spicules straight or slightly curved, moderately heavily spined, evenly spined, spination becoming vestigial on larger spicules, fusiform points, subtyloite bases.

Microscleres (Table 21). Chelae absent.

Toxas short, thick, wing-shaped, with wide central curvature, curved at slight angle, slightly reflexed arms.

REMARKS. Hentschel’s (1912) toxifera has seniority over Topsent’s (1913a) name, and hence the next available name antarctica (Topsent, 1917) is used for this species (Hooper & Wiedenmayer, 1994).

Koltun (1976) proposed that M. basispinosa Burton was conspecific with S. toxiferum Topsent, and this is now confirmed. Koltun’s (1976) proposed synonymy of this species and S. tuberculata Burton has not yet been corroborated (types not yet found). His proposal to include C. (Clathria) pauper Brøndsted, 1927, in this taxon is rejected, the latter species having a plumo-reticulate skeleton (as opposed to exclusively plumose skeleton), different pattern of spination on acanthostyles, two toxas morphologies (C. (M.) antarctica

having only one), and spicule sizes differing substantially between the two species (compare Table 21 and description of C. (C) pauper above).

**Clathria (Microciona) grisea** (Hentschel, 1911) (Figs 98-99, Table 22)


**MATERIAL.** **HOLOTYPE:** ZMB4435: NW. of Middle Bluff, Shark Bay, WA. 2548'S, 11326'E, 7-8m depth, 21.i.x.1905, coll. W. Michelsen & R. Hartmeyer (dredge). OTHER MATERIAL: WA- NTMZ2863 (fragments QMG300054, PIBOC 04-295).

**HABITAT DISTRIBUTION.** 7-25m depth; growing on bivalves and *Acropora cf. robusta*; Shark Bay and Pelsart Is, Houtman Abrolhos (WA) (Fig. 98F).

**DESCRIPTION.** Shape. Thinly encrusting, up to 3mm thick (holotype) or long cylindrical digitate sponge, 480mm long. 70mm maximum width, with few, slightly flattened, bifurcate, cylindrical branches, up to 40mm diameter, and short basal, half-detached attachment.

**Colour.** Red-brown alive (Munsell 10R 4/10), brownish-grey preserved.

**Oscules.** Large oscules, up to 4mm diameter, irregularly distributed on lateral sides of branches in ramose material.

**Texture and surface characteristics.** Surface smooth, unornamented, with distinct skin-like detachable covering; texture compressible, rubbery.

**Ectosome and subectosome.** Ectosome heavily collaginous, up to 180μm thick, including a light crust of arculate isochelae, and with tangential fibres running longitudinally along surface; subectosomal skeleton consists of plumose brushes of auxiliary subtylostyles, in bundles, standing erect or semi-erect but not protruding beyond surface; subectosomal spicules bundles arise from ends of principal spicules erect on the substrate (in holotype) or from peripheral fibres (in specimen).

**Choanosome.** Holotype – choanosomal skeleton hymedesmoid, with a basal layer of spongin fibre, acanthose bases of principal styles and smaller acanthostyles embedded in basal spongin, standing erect upon substrate. Specimen – choanosomal skeleton irregularly plumose, slightly reticulate, with sinuous, heavy spongin fibres, up to 220μm diameter, cored by both subectosomal auxiliary subtylostyles and principal styles, and echinated by plumose brushes of both choanosomal principal styles and echinating acanthostyles poking through fibres into mesohyl; mesohyl matrix light, choanocyte chambers elongate-oval, up to 150μm diameter, with abundant arculate isochelae dispersed throughout.

**Megascleles** (Table 22). Choanosomal principal styles thick, long, slightly curved at centre, subtylostyle, with heavily spined bases and sparsely microspined shafts.

Subectosomal auxiliary subtylostyles, in dermal skeleton within choanosomal fibres, long, thick, straight, with fusiform points and very slightly subtylostyle, smooth bases.

Echinating acanthostyles long or short, relatively slender, straight, slightly subtylostyle, heavily spined all over spicule except for aspinose point. **Microscleles** (Table 22). Aruncate-like isochelae divided into two size classes, without intermediates; larger cheliae with very thick, strongly curved shaft, small round or rounded lateral alae attached to shaft for most of its length, front ala completely free; smaller cheliae with slightly curved shaft, long lateral alae only partially attached to shaft.

**Toxas** absent.

**REMARKS.** There are some notable differences in skeletal structure and spicule sizes between the encrusting holotype and the branching specimen described above (Table 22), but the two specimens agree so closely in spicule diversity and geometry that they are obviously conspecific. These differences may be due to the holotype being immature, having smaller spicule dimensions and a hymedesmoid skeleton, whereas the larger branching specimen still retains the ascending plumose (non-anastomosing) fibre nodes, typical of the *Microciona* condition.

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**TABLE 22. Comparison between present and published records of Clathria (Microciona) grisea** (Hentschel). All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (ZMB4435)</th>
<th>Specimen (N=1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>135-198.2-212 x 6-10</td>
<td>241(268.5)-298 x 11(13.2)-16</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>195-218.9-242 x 4-6</td>
<td>246(264.4)-283 x 4-6</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>95-103.4-116 x 6-8</td>
<td>109(124.6)-138 x 8-9</td>
</tr>
<tr>
<td>Chelae I</td>
<td>15(16.8)-19</td>
<td>14(15.2)-17</td>
</tr>
<tr>
<td>Chelae II</td>
<td>20(22.9)-28</td>
<td>23(25.5)-28</td>
</tr>
<tr>
<td>Toxas</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>
The major distinguishing features in *C. (M.) grisea* are the arcuate isochelae and spined principal spicules. On this basis it is surprising that de Laubenfels (1936a) did not refer it to *Ataata* which he created specifically for this purpose (i.e., to include species with acanthose principal spicules, echinating acanthostyles, smooth sub-ectosomal styles and arcuate isochelae). The holotype of *Leptosia grisea* has a hymedesmoid choanosome, without plumose fibre nodes (and therefore strictly a member of *Leptocladithria*), and only a single category of auxiliary spicule. *Ataata, Leptocladithria* and *Microciona* are considered synonyms of *Clathria*.

*Clathria* (M.) *grisea* belongs to Hallmann’s (1912) *spicata* group of species (see comments for *C. *Thalysias* lendenfeldii), having a spicate arrangement of principal and echinulating spicules, which protrude through fibres in a plumose manner (Hooper et al., 1990).

*Clathria* (Microciona) *illaawarrae* sp. nov. (Figs 100-101, Plate 3D)


**HABITAT DISTRIBUTION.** Shallow subtidal; on rock reef, growing over bivalves and coralline algae; central E coast (NSW) (Fig. 100G).

**DESCRIPTION.** Shape. Thinly encrusting, 0.3-1.5 mm thick, following contours of substrate. Colour. Pale yellowish-orange alive (Munsell 2.5Y 8/10), beige in ethanol.

**Oscules.** Minute, less than 2 mm diameter, scattered over surface, with slightly raised surrounding membranous lip; pores very small covering entire surface.

**Texture and surface characteristics.** Soft, compressible, easily torn; porous, opaque, even, fleshy surface, without any sculpturing or other ornamentation.

**Ectosome and subectosome.** Single category or large subectosomal auxiliary subtylosclerostyles form paratangential plumose brushes, protruding only slightly through surface but extending well into mesohyl.

**Choanosome.** Skeleton microcionid, with thin basal layer of spongin lying on substrate, 30-40 µm thick, containing incorporated sand grains; erect spongin fibre nodes arise at approximately 200 µm intervals along basal spongin, 20-40 µm thick, 100-150 µm long, cored by erect choanosomal principal styles in uni- or multispicular tracts, up to 5 spicules per bundle, forming perfectly erect or slightly plumose brushes ascending to but not protruding through surface; fibre nodes discrete, not anastomosing with adjacent nodes, but some principal spicules from adjacent nodes cross within mesohyl; paratangential plumose brushes of auxiliary spicules located in several places within mesohyl, forming a tangential tract near basal spongin layer, forming stellate brushes midway along erect fibre nodes, and forming plumose paratangential brushes near surface; echinating acanthostyles relatively sparse on both basal spongin and erect fibre nodes; mesohyl matrix moderately heavy with microscleres dispersed throughout; choanocyte chambers not seen.

**Megascleres.** Choanosomal principal styles long, thin, slightly curved or whispy near point, often bent in distal third of spicule, with smooth tapering haste bases and fusiform points, occasionally slightly telescoped. Length 62-(129.4)-165 µm, width 3-(3.6)-4.5 µm.

Subectosomal auxiliary subtylosclerostyles long, thin, straight, with elongated smooth stylostyles bases and haste points. Length 176-(206.5)-228 µm, width 1.0-(2.3)-3.0 µm.

Echinulating acanthostyles short, relatively thick, cylin- drical, usually thickest above basal constriction, slightly spined, aspinose slightly constricted neck, slightly swollen base, rounded or fusiform point. Length 36-(53.2)-68 µm, width 2-(3.8)-6 µm.

**Microscleres.** Palmate isochelae very small, with greatly reduced lateral alae, often no more than ridge on shaft, and small front ala complete; sometimes asymmetrical ends. Length 4-(5.9)-7.5 µm.

**Toxas.** Small, thick, u-shaped or forceps shaped, with angular central curve and non-reflexed arms. Length 6-(8.1)-11 µm, width 0.5-(0.8)-1.0 µm.

**ETYMOLOGY.** For the type locality.

**REMARKS.** This species is one of the most thinly encrusting microcionids, with most sections no more than 300 µm thick. Its choanosomal skeleton is typical of *Microciona* (erect fibre nodes arising from a hymedesmoid basal skeleton), but subectosomal auxiliary spicules have an unusual distribution within the skeleton forming both stellate brushes around the fibre nodes and basal tangential tracts near the substrate. The species is also unusual amongst thinly encrusting microcionids in that there are no substratum drainage canals associated with the aquiferous system, whereas the surface is smooth, porous and fleshy. These live surface features, the
skeletal structure, spicule geometry, and spicule sizes differentiate this species from other Microciona in the Indo-west Pacific.

Clathria (Microciona) lizardensis sp. nov.
(Figs 102-103, Plate 3E)


HABITAT DISTRIBUTION. Coral reef, patch reef in lagoon, under coral overhangs, on ledges or exposed coral heads, growing on live coral, coral rubble at base of reef or on dead bivalves; 9-12m depth; Lizard I. (FNQ) (Fig. 102G).

DESCRIPTION. Shape. Thinly or thickly encrusting, bulbous in life, usually following contours of substrate, up to about 10mm thick, collapsing and less than 4mm thick when preserved. Colour. Pale red alive (Munsell 2.5R 6-5/10), light brown in ethanol. Oscules. Large, up to 4mm diameter alive, surrounded by raised membranous lip, usually situated on apex of bulbous (flaccid) surface, with drainage canals radiating towards pores; oscules and drainage canals not visible in preserved material.

Texture and surface characteristics. Soft, slimy, easily peeled from substrate; smooth, fleshy flaccid surface in life, with slightly sculptured subectosomal drainage canals visible in live sponge; in preserved material surface uneven, regularly papillose.

Ectosome and subectosome. Membraneous, collagenous, rarely intact in histological sections, with some detritus; tips of choanosomal principal
styles arising from fibre endings, and subectosomal auxiliary subtylostyles protrude through surface in preserved material, but probably do not when alive; no special ectosomal skeleton but plumose bundles of subectosomal subtylostyles clustered on intact parts of surface skeleton, usually lying just below the ectosome.

**Choanosome.** Microcionid skeletal structure, with very thick, relatively long spongin fibre nodes, 450–1900μm long, up to 420μm diameter, arising from hymedesmoid basal spongin fibre, 70–230μm diameter, lying directly on substrate; fibre nodes discrete, erect, without any anastomoses between adjacent nodes, 300–770μm
apart, unbranched except at apex of each node which bifurcates 1 or more times; fibres dark brown, with heavy spongion, cored by multi- or paucispiricular plumose tracts of choanosomal principal styles, with 1 or more principal styles protruding from apex of each fibre node; fibres moderately heavily echinated by acanthostyles dispersed evenly over each ascending fibre node and all basal fibres; exterior surface of most fibres often with small amount of collagen and plumose bundles of auxiliary spicules lying parantagential to surface (but this is probably an artifact of preservation, the mesohyl region collapsing around the fibres, whereas in life the arcs between fibres is likely to contain a more structured aquiferous system); mesohyl matrix granular, containing some detritus, abundant auxiliary spicules, and rare microscleres; choanoocyte chambers difficult to see in preserved material, small, oval, up to 40μm diameter. 

_Megascleres._ Choanosomal principal styles long or short, thick, straight, cylindrical or club-shaped, variable basal terminations from tapering hastate, evenly rounded or faintly subtylotic, fusiform points. Length 183-(272.5)-345μm, width 8-(12.3)-16μm.

_Subectosomal._ Very slender, usually straight, rarely curved, sometimes sinuous, with well developed smooth subtylote bases, fusiform points. Length 211-(306.2)-428μm, width 2-(3.8)-6μm.

_Echinating acanthostyles_ relatively long, thick, prominently subtylote, fusiform pointed, with more-or-less evenly dispersed very small spines, but abundant larger spines concentrated only on base and point, giving appearance of aspinose shaft. Length 81-(94.3)-112μm, width 4-(6.6)-11μm.

_Microscleres._ Isochelae palmate, unmodified, uncommon, moderately large, with long broad front ala, reduced lateral alae completely fused to shaft, front and lateral alae approximately the same size. Length 16-(22.4)-28μm.

_Toxas_ uncommon, acolada to U-shaped, long or short, very thin, with slight central curvature, straight alae or faintly reflexed arms. Length 22-(85.5)-112μm, width 1.0-(1.2)-1.5μm.

**ETYMOLOGY.** For the type locality.

**REMARKS.** This species has typical _'microcionid'_ skeletal structure, with long, discrete, virtually unbranched spongion fibre nodes arising from a hymedesmoid basal fibre skeleton. The species is also remarkable for the thickness and density of its spongion fibres, which are even heavier than those found in _C. (T.) corneolia_ from New Caledonia (which was named for this character). The external colouration and bulbous surface processes seen in _C. (M.) lizardeensis_ are also reminiscent of _C. (T.) corneolia_, although spicule geometry, spicule size and skeletal structure differ substantially between the two species (Hooper & _Lévi_, 1993a), and they do not appear to be otherwise closely related. In its live external appearance this species could also be mistaken for _C. (M.) aceratoobtusa_, but that species has entirely smooth echinating styles, curved principal styles, oxhorn toxas and abundant isocheleae. Comparisons with other Indo-west microcionids are discussed in the remarks for _C. (M.) aceratoobtusa_.

**OTHER SPECIES OF CLATHRIA (MICROCIONA)**

**Clathria (Microciona) adioristica** (de Laubenfels, 1953)

_Dictyocia adioristica_ de Laubenfels, 1953: 526-528, text-fig.5 [Gulf of Mexico]; Wells _et al._, 1960: 217-218, text-figs 21,24 [North Carolina].

_Clathria (Microciona) adioristica_; _Van Soest_, 1984b: 104, 108-109, table 4 [affinity with Clathria obliqua, possible synonym].

**MATERIAL.** HOLOTYPE: USNM23403, paratype MLUM-ML4-214. NW. Atlantic, Caribbean.

**Clathria (Microciona) affinis** (Carter, 1880)


_Not Microciona affinis;_ de Laubenfels, 1936a: 111.

_Not Hymeraphia affinis_ Topsent, 1889: 43, fig.8.

**MATERIAL.** HOLOTYPE: LFM destroyed, fragment BMNH1936.3.4.597. Gulf of Manaar, Arabian Gulf.

**Clathria (Microciona) africana** (_Lévi_, 1956)

_Microciona africana_ _Lévi_, 1956b: 402-403, text-fig.8 [Dakar, Senegal].

**MATERIAL.** HOLOTYPE: MNHNDC1276. NW. Africa.

**Clathria (Microciona) angularis** (Sarà & Siribelli, 1960)


**MATERIAL.** HOLOTYPE: IMZUN100.4. Mediterranean.

**Clathria (Microciona) anonyma** (Burton, 1959)

_Microciona anonyma_ Burton, 1959a: 250-251, fig.30 [Zanzibar area, Indian Ocean].
MATERIAL. HOLOTYPE. BMNH1936.3.4.575. Central E. Africa.

Clathria (Microciona) armata (Bowerbank, 1862).

Microciona armata Bowerbank, 1862a: 79, 1858, pl.24, figs. 26-28; Bowerbank, 1864: 41, pl.4, figs 96-98; Bowerbank, 1866a: 129, 131, 134 [Britain]; Gray, 1867: 535; Norman, 1869a: 330; Schmidt, 1870: 76; Bowerbank, 1874a: 60, pl.23, figs 17-24; Carter, 1874a: 405, pl.21, fig.27; Carter, 1874c: 456-457; Carter, 1876: 310; Carter, 1880a: 40-41, 151 [Gulf of Munster]; Koecher, 1886a: 62 [English Channel]; Topsent, 1888a: 117, 124, 125, 141, 156, 158, pl.6, fig.8; Topsent, 1891a: 528 [Roscoff]; Stephens, 1916: 234 [W coast Iceland]; Stephens, 1921; Vosmaer, 1935a: 6-7, 665; Alander, 1942: 62 [Sweden]; Lévi, 1956b: 399-400, text-fig.6 [Bukar, Senegal]; Kolton, 1959: 181-182, text-fig. 141 [White Sea]; Lévi, 1960a: 73, text-figs 16, 17 [Roscoff; Sidmouth]; Poggiorno, 1965: 3, 7, 11-14, text-fig.5, tables 1, 2 [Italy]; Pulitzer-Finali, 1983: 573-574, 610, text-fig. 69 [Mediterranean]; Winterrath-Kilian & Kilian, 1984: 134 [Colombia]; Ackers, Moss & Picton, 1992: 143 [Ireland].


Scopalinia armata Wright, 1868: 224. 

Expertia armata Frison, 1883: 36-38.

Not Microciona armata de Laubenfels, 1936a: 111.

Microciona scrobiculata de Laubenfels, 1936a: 111; Lévi, 1960a: 73. 

Clathria (Microciona) ascendenens (Cabiochi, 1968a).

Microciona ascendenens Cabiochi, 1968a: 239, text-fig.11 [Roscoff, France]; Rodriguez Solórzano et al., 1979a: 44, 59-60, text-fig.15 [Galicia, Spain]. 

MATERIAL. HOLOTYPE. RMBS. NE Atlantic.

Clathria (Microciona) assimilis Topsent, 1925.

Clathria assimilis Topsent, 1925: 649; Topsent & Olivier, 1943: 1 [no diagnosis; Adriatic].

Pseudachinone assimilis: De Laubenfels, 1936a: 109 [note].


Clathria (Microciona) basifixa (Topsent, 1913).


Clathria (Microciona) basifixa: Van Soest & Stone, 1986: 45 [Norway].

Clathria (Microciona) bitoxa (Burton, 1930)  
_Hymanto bitoxa_ Burton, 1930a: 503, text-fig.2 [Norway];  
Alander, 1942: 63 [Sweden].  
_Microciona_ leucia; Pistaert, 1887: 416.  
Clathria bitoxa; Van Soest, 1984b: 90 [generic synonymy];  
_Microciona bitoxa_ Rodríguez Solórzano & Rodríguez Babío, 1993: 62 [Iberian Peninsula].  
MATERIAL. HOLOTYPE: BMNH1910.1.1.787/VE, NE Atlantic.  

Clathria (Microciona) brepha (de Laubenfels, 1930)  
_Antara brepha_ de Laubenfels, 1930: 27 [California]  
_Antara brepha_; de Laubenfels, 1936a: 91, text-fig.53.  
Clathria brepha: Van Soest, 1984b: 7 [generic synonymy].  
MATERIAL. HOLOTYPE: USNM21427. PARATYPES  
BMNH1929.8.22.236, 57, NE Pacific.  

Clathria (Microciona) bromstedi sp. nov.  
_Hymenopodia bromstedi_ Bromsted, 1932: 12 [Faeroe Is].  
_Antara bromstedi_; de Laubenfels, 1936a: 109.  
_Microciona bromstedi_; Van Soest, 1984b: 7 [generic synonymy for _Antara_].  
Not _Desmacella pennaata_ Lambe, 1985: 129.  
MATERIAL. HOLOTYPE: UZM (not located). NE Atlantic.  
Clathria (Microciona) penna (Lambe, 1895) has seniority.  

Clathria (Microciona) bulboretorta (Carter, 1880)  
_Microciona bulboretorta_ Carter, 1880a: 41, 42, 151, 153, pl.4,  
fig.3a-e [Gulf of Manao, Ceylon]; Vosmaer, 1935a: 608.  
MATERIAL. HOLOTYPE: LFHM destroyed. Gulf of Manao.  

Clathria (Microciona) bulbotoxa Van Soest, 1984  
Clathria (Microciona) bulbotoxa; Van Soest, 1984b: 103-104,  
pl.7, figs 3-8, text-fig.41, table 4 [Curaçao, West Indies].  
_Microciona bulbotoxa_; Pulitzer-Finali, 1986: 149-150 [West Indies].  
MATERIAL. HOLOTYPE: ZMA204789. Caribbean.  

Clathria (Microciona) calla (de Laubenfels, 1934)  
_Axostilis cala_ de Laubenfels, 1934: 16 [Puerto Rico].  
_Axostilis cala_; de Laubenfels, 1954: 149 [note]; Sim &  
Byeon, 1989: 40, pl.5, figs 3-5 [Korea: probable misidentifi-  
cation].  
Clathria calla: Boury-Esnault, 1973: 286, text-fig.46  
[Brazilian Basin]; Zea, 1987: 170, text-fig.59, pl.2, fig. 3  
[Colombian Caribbean].  
Clathria (Microciona) calla; Van Soest, 1984b: 100-101, pl.7,  
fig.1, text-fig.39, table 4 [Curaçao, Florida: affinity with  
Clathria coralloides from Mediterranean].  
_Microciona calla_; Pulitzer-Finali, 1986: 150 [West Indies].  
_Microciona rarastrina_ Heinelt, 1965: 44-42, text-fig.8]Port  
Royal, Jamaica]; Winternanth-Kilian & Kilián, 1984: 135  
[Colombia].  
MATERIAL. HOLOTYPE: USNM. Caribbean, tropical SW Atlantic.  

Clathria (Microciona) campcheae nom. nov.  
_Hymenopodia affinis_ Topsent, 1893: 43, fig.8A [Banc de  
Campêche]; Topsent, 1904a: 162-3 [Azores].  

Clathria (Microciona) affinis; de Laubenfels, 1936a: 111.  
Clathria (Microciona) affinis; Van Soest, 1984b: 93-95, 108,  
text-fig.36, table 4 [Curaçao, West Indies].  
Clathria cf. affinis; Kobuk & Van Soest, 1989: 1216  
[Bonaire].  
Not _Microciona affinis_ Carter, 1880a: 41, pl.14, fig.15; Vos-  
maer, 1933: 608.  
MATERIAL. HOLOTYPE: MNHN1185. paratype  
MNHN1358. Caribbean, NE Atlantic.  

Clathria (Microciona) carnosa (Bowerbank, 1862)  
_Microciona carnosa_ Bowerbank, 1862a: 804, 1110 [Britain];  
Bowerbank, 1866: 133; Vosmaer, 1935a: 607  
? _Halichondria incrassata_ Schmidt, 1866a: 150.  
MATERIAL. HOLOTYPE: BMNH1930.7.3.203, fragment  
BMNH1910.1.1.666. NE Atlantic, tropical SW Atlantic.  

Clathria (Microciona) clavariata sp. nov.  
_Microciona clavariata_ Lévi & Lévi, 1989: 81, fig.49  
[Philippines].  
Clathria clavariata (Stephens) has seniority.  

Clathria (Microciona) cleistochela Topsent, 1925  
Clathria cleistochela Topsent, 1925: 650-651, fig.9 [Gulf of  
Naples].  
_Microciona cleistochela_; de Laubenfels, 1936a: 111 [note];  
Lévi, 1960a: 72, fig.14 [Naples,Banyuls]; Siribelli, 1960:  
12-14, fig.5B [Naples]; de Laubenfels, 1951b: 214 [Black  
Sea]; Pulitzer-Finali, 1983: 610; Boury-Esnault & Lopes,  
1985: 193-194, fig.42 [Azores].  
MATERIAL. HOLOTYPE: MOM, fragment MNHN1329.  
Mediterranean, NE Atlantic.  

Clathria (Microciona) cocinea (Bergquist, 1961)  
_Microciona cocinea_ Bergquist, 1961a: 38, fig.8Aa [N. New  
Zealand]; Bergquist & Sinclair, 1968: 427, 428, fig.14  
[morphology and larvae]; Bergquist & Sinclair, 1973: 43;  
195-196; Bergquist & Fromont, 1988: 102-103, pl.47,  
fig.f, pl.48, fig.e; Rudman & Averm, 1989: 335; Dawson,  
1993: 36 [note].  
Not _Thalasites cocinea_ Duchassaing & Michelotti, 1864: 84,  
pl.18, fig.5 [St.Thomas; Wiedemayer, 1978: 253, table 49.  
MATERIAL. HOLOTYPE: NMNZ unregistered. New  
Zealand.  

Clathria (Microciona) ctenichela (Alander, 1942)  
_Microciona ctenichela_ Alander, 1942: 61-62, pl.15, fig.20  
[Sweden].  
Clathria (Microciona) ctenichela; Van Soest & Stone, 1986:  
44-45 [Norway].  
MATERIAL. HOLOTYPE: ZMA. NE Atlantic.  

Clathria (Microciona) denvyi (Bergquist & Fromont, 1988)  
_Microciona denvyi_ Bergquist & Fromont, 1988: 100-102,  
pl.47, figs.d.e [Slipper Is]; Dawson, 1993: 37 [note].  
Clathria (Microciona) densa (Burton, 1959)
Microciona densa Burton, 1959a: 248, text-fig. 28 [S Arabian coast]
MATERIAL. HOLOTYPE: BMNH1936.3. 4.456: Arabian Gulf.

Clathria (Microciona) dianae (Schmidt, 1875)
Subcristes dianae Schmidt, 1875: 116, pl.11.fig.1 [Norway]; Czerniawsky, 1880: 70.
Microciona dianae: Thiele, 1903b: 394, 395, 398, pl.21, fig.28a-e; Vosmaer, 1935a: 608, 630; de Laubenfels, 1936a: 111 [note].
Not Artemizina dianae Topsent, 1907: 69; Vosmaer, 1935a: 630.
MATERIAL. HOLOTYPE: unknown. NE Atlantic.

Clathria (Microciona) ditoxa (Stephens, 1916)
Microciona ditoxa: Lévi, 1960a: 66 [W coast of Ireland].
Dictyoconia ditoxa: de Laubenfels, 1936a: 110 [note].
MATERIAL. HOLOTYPE: INMSR151.9.1916. NE Atlantic.

Clathria (Microciona) duplex Sarà, 1958
Clathria duplex Sarà, 1958: 262-264, fig.24 [Gulf of Naples].

Clathria (Microciona) echinata (Alcolado, 1984)
Axociella echinata Alcolado, 1984: 7 [Cuba].
Clathria (Microciona) tsimpoti Van Soest, 1984b: 97-99, pl.7, fig.2-4, text-fig.38, table 4 [Puerto Rico, Curaçao].
Pulitzer-Finali, 1986: 150 [West Indies].
Clathria simpsoni, Zea, 1987: 168, text-fig.58, pl.3, fig.1 [Colombian Caribbean].

Clathria (Microciona) ellipticella (Alander, 1942)
Microciona ellipticella Alander, 1942: 58-61 [Sweden].
Clathria ellipticella: Van Soest & Stove, 1960a: 45 [note].
MATERIAL. HOLOTYPE: ZMA. NE Atlantic.

Clathria (Microciona) fallax (Bowerbank, 1866)
Sophax fallax, Gray, 1867: 521.
MATERIAL. HOLOTYPE: BMNH1910.1.1.71. PARALEOTYPE: BMNH1930.7.3.198, fragment USNM5047. NE Atlantic.

Clathria (Microciona) fascispiculifera (Carter, 1880)
Microciona fascispiculifera Carter, 1880a: 44, 45, 151, 153, pl.4, fig.7a-g [Gulf of Manar]; Hallmann, 1916a: 637 [note]; [71] Vosmaer, 1935a: 608.
Damasemi fascispiculifera; de Laubenfels, 1936a: 110.
MATERIAL. HOLOTYPE: LPM destroyed, no extant fragment in BMNH. Gulf of Manar.

Clathria (Microciona) fraudata (Bowerbank, 1874)
MATERIAL. HOLOTYPE: BMNH1930.7.3. 205. NE Atlantic.

Clathria (Microciona) frogeti (Vacelet, 1969)
Microciona frogeti Vacelet, 1969: 208, text-fig.47 [Mediterranean].
Microciona frogeti [sic]; Pulitzer-Finali, 1983: 610 [list].
MATERIAL. HOLOTYPE: MNHN missing. W Mediterranean.

Clathria (Microciona) gradalis Topsent, 1925
Microciona gradalis var. inea; Topsent, 1928a: 299, pl.10, fig.14 [Boavista I., Senegal].
MATERIAL. HOLOTYPE: MOM, fragment MNHN'T328. Mediterranean. NE Atlantic, NW Africa.

Clathria (Microciona) haematodes (de Laubenfels, 1957)
Microciona haematodes de Laubenfels, 1957: 240, text-fig.6 [Oahu, Hawaii]; Bergquist, 1977: 67 [Hawaii].
MATERIAL. HOLOTYPE: USNM23533. Hawaii.

Clathria (Microciona) haploptoxa (Topsent, 1928)
MATERIAL. HOLOTYPE: MNHN'T1110. Mediterranean, NE Atlantic, NW Africa.

Clathria (Microciona) hentschelli sp. nov.
Hymertaphia lendenfeldii Hentschel, 1912: 378-379, pl.20, fig. 35 [Mumien Bay, Aru I., Arafura Sea].
Eurypontus lendenfeldii; de Laubenfels, 1936a: 110.
Not Clathria lendenfeldii Ridley & Denby, 1886: 474.
MATERIAL. HOLOTYPE: SPM, 17b. Indonesia, Clathria (Thalysia) lendenfeldii Ridley & Denby has priority.
Clathria (Microciona) heterotoxa  
(Hentschel, 1929)  
*Microciona heterotoxa* Hentschel, 1929: 891-892, 970, pl.14, fig.5 [White Sea]; Kolom. 1959: 182-183, text-fig.142 [Arctic, USSR].  
*Dictyociona heterotoxa* de Laubenfels, 1936a: 110 [note]; de Laubenfels, 1953a: 527.  
MATERIAL. HOLOTYPE: HM or ZMB (not located). Arctic.  

Clathria (Microciona) hymedesmioides Van Soest, 1984  
*Microciona hymedesmioides Van Soest, 1984b: 104-105, pl.7, figs 9-10, table 4 [Curaçao].*  
MATERIAL. HOLOTYPE: ZMAPOR4790. Caribbean.  

Clathria (Microciona) ixauda (Lévi, 1969)  
*Microciona ixauda* Lévi, 1969: 965, text-fig.7a [Vema Seamount].  

Clathria (Microciona) jecusculum (Bowerbank, 1866)  
*Hymeniacidon jecusculum* Bowerbank, 1866: 198 [Harris L., Hebrides].  
*Microciona jecusculum*; Bowerbank, 1874: 273-275, pl.83, figs 1-6; Carter, 1876: 237 [Cape St. Vincent; Faroe Is.]; Vosmaer, 1933: 607 [imperfectly known].  
MATERIAL. HOLOTYPE: unknown; fragments BMNH1934.3.176, 177, NE Atlantic.  

Clathria (Microciona) kentii (Bowerbank, 1874)  
MATERIAL. HOLOTYPE: BMNH1910.1.1.77, fragment USNM3044. NE Atlantic.  

Clathria (Microciona) laevis (Bowerbank, 1866)  
*Microciona laevis* Bowerbank, 1866: 124, 127-128 [Britain]; Stephens, 1917: 12, pl.1, fig.3 [N. of Boulus Head, Ireland]; Vosmaer, 1935a: 607; Burton, 1959b: 43 [Iceland].  
Not *Microciona laevis*; Fristedt, 1887: 415.  
*Abila laevis*; Gray, 1867: 539.  
*Hymantho laevis*; de Laubenfels, 1936a: 111; Atander, 1942: 63 [Sweden].  
MATERIAL. HOLOTYPE: BMNH1930.7.3. 215 NE Atlantic.  

Clathria (Microciona) laevissima (Dendy, 1922)  
*Hymanesmia laevissima* Dendy, 1922: 81-82, pl.15, fig.1 [Mauritius].  
*Fottipta laevissima*; de Laubenfels, 1936a: 119 [note].  
MATERIAL. HOLOTYPE: BMNH1921.11. 769. W Indian Ocean.  

Clathria (Microciona) lajorei (de Laubenfels, 1954)  
*Clathria lajorei*; Van Soest, 1984a: 129 [generic synonym].  
MATERIAL. HOLOTYPE: USNM22927. W central Pacific.  

Clathria (Microciona) leighensis sp. nov.  
*Microciona rubens* Bergquist, 1961a: 38, text-fig.9 [N New Zealand]; Bergquist & Green, 1977b: 289-302 [ontogeny]; Bergquist & Fromont, 1988: 103, pl.48, figs h-c [N New Zealand]; Dawson, 1993: 37 [note].  
Not *Thalassodendron rubens* Lendenfeld, 1888: 223.  
MATERIAL. HOLOTYPE: NMNZ unregistered. New Zealand. C (Clathria) rubens (Lendenfeld, 1888) has priority.  

Clathria (Microciona) levii (Sarà & Siribelli, 1960)  
*Microciona levii* Sarà & Siribelli, 1960: 71-73, text-fig.19 [Bay of Naples]; Siribelli, 1960: 6-8, text-fig.2 [Naples]; Poggioni, 1965: 3, table 1; Politzer-Finali, 1983: 610 [list].  

Clathria (Microciona) longispiculum (Carter, 1876)  
*Microciona longispiculum* Carter, 1876: 231, 237, 238, 470, pl.12, fig.1h, pl.15, fig.31a-c [N. Scotland]; Vosmaer, 1935a: 608 [insufficiently known].  
MATERIAL. HOLOTYPE: BMNH1887.10.29.3. NE Atlantic.  

Clathria (Microciona) longistyla (Burton, 1959)  
*Microciona longistyla* Burton, 1959a: 249-253, text-fig.29 [S. Arabian coast]; Sun & Kim, 1988: 26 [Korea]; Sim & Byeon, 1989: 40 [Korea; possible misidentifications].  
MATERIAL. HOLOTYPE: BMNH1936.3.4. 583. Arabian Gulf, 7 S China Sea.  

Clathria (Microciona) macrochela (Lévi, 1960)  
*Microciona macrochela* Lévi, 1960a: 70, text-fig.13 [Rosscoff].  
MATERIAL. HOLOTYPE: MNHNDC1940. NE Atlantic.  

Clathria (Microciona) microjoanna (de Laubenfels, 1930)  
*Microciona microjoanna* de Laubenfels, 1930: 27 [Carmel, California]; de Laubenfels, 1932: 93-95, text-fig.55 [California]; Bakus, 1966: 433-435, text-fig.4, table 4 [San Juan Arch., Washington State]; Lee & Gilchrist, 1985: 24-32 [biochemistry]; Bakus & Green, 1987: 72 [S. California].  
MATERIAL. HOLOTYPE: USNM21468. PARATYPE USNM21469, fragment BMNH1929.8.22.28. NE Pacific.  

Clathria (Microciona) micronesia (de Laubenfels, 1954)  
*Microciona micronesia* de Laubenfels, 1954: 145-146, text-fig.93 [Majuro Atoll].  
MATERIAL. HOLOTYPE: USNM22833. W central Pacific.  

Clathria (Microciona) microxea (Vacelet & Vasquez, 1971)  
*Paraeniacella microxea* Vacelet & Vasquez, 1971: 103, text-fig.61 [Tulear, Madagascar].  
MATERIAL. HOLOTYPE: MNHNDCJ27. W Indian Ocean.
Clathria (Microciona) mima (de Laubenfels, 1954)

**MATERIAL.** HOLOTYPE: USNM22839. NW central Pacific, Caribbean.

Clathria (Microciona) namibiensis (Uriz, 1984)

**MATERIAL.** HOLOTYPE: ABIPB-12. SW Africa.

Clathria (Microciona) normani (Burton, 1930)
Hymanthus normani Burton, 1930a: 503, text-fig.1 [Norway].


**MATERIAL.** HOLOTYPE: BMNH1910.1.1.791.iii. NE Atlantic.

Clathria (Microciona) novaeezealandiae (Brodstedt, 1924)

Wetmoreus novaeezealandiae; de Laubenfels, 1936a: 112.

**MATERIAL.** HOLOTYPE: UZM not located, no fragment in BMNH. New Zealand

Clathria (Microciona) osismica (Cabioch, 1968)
Microciona osismica Cabioch, 1968a: 240-244, text-fig.12 [Roscoff, France].

**MATERIAL.** HOLOTYPE: RMBS. NE Atlantic.

Clathria (Microciona) parthena (de Laubenfels, 1930)

**MATERIAL.** HOLOTYPE: USNM21383. PARATYPE BMNH1929.9.30.6. NE Pacific.

Clathria (Microciona) pennata (Lambe, 1895)
Desmocella pennata Lambe, 1895: 129, pl.4, figs 6a-d [Sooke, Vancouver I., Canada]; Ricketts & Calvin, 1948: 34 [Vancouver I., Canada].


Tyloidesma pennata; Koltun, 1959: 96 text-fig.51, 1-3 [S. Kuriles].

Bienna pennata; Koltun, 1958: 54.

Ophiliaspangia affinis basifixa; Burton, 1935c: 74 [Possiet Bay, Sea of Japan].

Microciona pennata; Simpson, 1968a: 40, pl.15 [Washington State].

Clathria (Ophiliaspangia) pennata; Rudman & Avern, 1989: 335 [associates; probable misidentification of sponge].


Not Hymedesmia pennata Brodstedt, 1932: 12 [see C. brodasteli sp. nov.].

**MATERIAL.** HOLOTYPE: USNM7488. PARATYPE NMCIC1900-2826. NE Pacific, NW. Pacific, Japan.

Clathria (Microciona) plana (Carter, 1876)
Microciona planum Carter, 1876: 238, 472 [Cape St. Vincent, Hebrides].

Microciona plana; Topsent, 1889: 41-42 [Banc de Campeche]; Norman, 1892: 9.

Amphiectus planus; Vosmaer, 1880: 121; Dendy, 1889: 18.

Clathria plana; Topsent, 1894b: 30; Van Soest, 1984b: 108 [unrecognisable].

cf. Microciona pliforma; Vosmaer, 1935a: 608.

**MATERIAL.** HOLOTYPE: BMNH1890.4.10.13. NE Atlantic.

Clathria (Microciona) plinthina (de Laubenfels, 1954)
Microciona plinthina de Laubenfels, 1954: 144-145, text-fig.92 [Ailing-lap-lap Atoll].

**MATERIAL.** HOLOTYPE: USNM22949. W central Pacific.

Clathria (Microciona) poecilosclera (Sara & Siribelli, 1960)

**MATERIAL.** HOLOTYPE: IMZUN350. Mediterranean.

Clathria (Microciona) polita (Ridley, 1881)
Hymedesmia polita Ridley, 1881: 121-122, pl.10, fig.9 [Sandy Point, Magellan Straits; supposed affinities with Clathria tuberosa (Bowerbank)].

Microciona polita; Topsent, 1900: 113 [English Channel; identified with doubt].

**MATERIAL.** HOLOTYPE: BMNH1879.12.27. 22. SW Atlantic, NE. Atlantic.

Clathria (Microciona) primitiva (Koltun, 1955)
Microciona primitiva Koltun, 1955a: 16-17, text-fig.6 [Behring Sea]; Burton, 1959: 43 [Iceland]; Koltun, 1959: 184, text-fig.144 [USSR].

Not Clathriella primitiva Burton, 1935c: 73.


Clathria (Microciona) proxima (Lundbeck, 1910)
Hymedesmia proxima Lundbeck, 1910: 81 [Denmark Strait].

Anoata proxima; de Laubenfels, 1936a: 109 [imperfectly known].

**MATERIAL.** HOLOTYPE: USNM22949. W central Pacific.
Clathria provinciae: Van Soest, 1984b: 7 [generic synonymy for Anaatala].

MATERIAL. HOLOTYPE: ZRS. NE Atlantic.

Clathria (Microciona) pugio (Lundbeck, 1910)

Hymedesmia pugio Lundbeck, 1910: 94 [Denmark Strait].
Anaatala pugio; de Laubenfels, 1936a: 109.

Clathria pugio; Van Soest, 1984b: 7 [generic synonymy for Anaatala].

MATERIAL. HOLOTYPE: ZRS. NE Atlantic.

Clathria (Microciona) postulosa (Carter, 1882)

Halichondria postulosa Carter, 1882a: 285, pl.11, fig.1 [vicinity of Pantagonia and Falkland Is].

Not Halichondria postulosa; Carter, 1886g: 450 [Port Phillip Bay, Victoria].

Anaatala postulosa; de Laubenfels, 1936a: 109.

MATERIAL. HOLOTYPE: BMNH not found. fragments: BMNH1954.9.3.233. SW Atlantic.

Clathria (Microciona) quadirradiata (Carter, 1880)

Microciona quadirradiata Carter, 1880a: 42, 43, 151, 153, pl.4, figs 4a-d [Gulf of Manaar]; [?] Vosmaer, 1935a: 608.

MATERIAL. HOLOTYPE: IFM destroyed; Gulf of Manaar.

Clathria (Microciona) rhopaloptora (Hentschel, 1912)

Hymeraphia rhopaloptora Hentschel, 1912: 380, pl.20, fig. 37 [Art l., Arafura Sea].

Microciona rhopaloptora; Burton, 1959a: 248 [Maldives];

Thomas, 1970b: 206, text-fig.7 [Cocos-Keeling Basin, Gulf of Manaar].

Euroyn rhopaloptora; de Laubenfels, 1936a: 111.


Clathria (Microciona) scotti Dendy, 1924

Clathria scotti Dendy, 1924a: 352, pl.10, fig.1, pl.14, figs 5-7 [E. of North Cape, New Zealand].

Pseudachome scotti; de Laubenfels, 1936a: 109 [note];


Clathria (Microciona) seriata (Grant, 1826)

Candler seriata; Grant, 1826: 116.

Halichondra seriata; Johnston, 1842: 74, 125, 197, 248, 258, pl.14, fig.2; Gray, 1848: 12,16.

Halichona seriata; Bowerbank, 1861: 235; Bowerbank, 1862a: 769, 824, pl.29, fig.10.

Chalinna seriata; Bowerbank, 1864: 24,2275, pl.17, fig.287; Bowerbank, 1866: 139, 294, 361, 376-378; Wright, 1868: 228; Norman, 1869: 298-299; Schmidt, 1870: 3;7; Carter, 1871b: 196.

Clathria seriata; Schmidt, 1866b: 10, 24, pl.1, fig.7; Vosmaer, 1935a: 619 [uncertain affinity];

Hantsch, 1889: 158; Hantsch, 1890: 205-207 [England];

Babic, 1921: 84 [Adriatic];

Babic, 1922: 244-245, text-fig. T [Adriatic].

Seriata seriata; Gray, 1867: 515.

Desmocedodes seriata; Schmidt, 1868: 12.

Clathria (Microciona) similis (Thiele, 1903)

Microciona similis Thiele, 1903: 85-88, figs 53-57, 67 [Mar del Plata, Argentina].

MATERIAL. HOLOTYPE: MCNPO04-81-43. SW Atlantic.

Clathria (Microciona) simae sp. nov.

Axochelia cylindrica; Sim & Byeon, 1989: 39-40, pl.5, figs 1-2 [S. Korea].

Not Esperiopos cylindrica Ridley & Dendy, 1886: 340; Ridley & Dendy, 1887: 79-80, pl.19, figs 2a-b.

Not Axoceliela cylindrica; Hallman, 1920: 780-783, pl.37, figs 2-4, text-fig.2.

Not Rhaphidaphus cylindricus Kieschnick, 1903: 53, pl.44, fig.10.

MATERIAL. HOLOTYPE: Department of Biology, Han Nam University, Korea 18/9/1987. S China Sea. C. (Axochelia) cylindrica (Ridley & Dendy, 1886) has priority.

ETYMOLOGY. Named for Dr C.J. Sim.

Clathria (Microciona) similis (Thiele, 1903)

Microciona similis Thiele, 1903a: 971, fig.22 [Ternate, Moluccas];

Hantschel, 1912: 377; [Art l., Arafura Sea].

Euroyn similis; de Laubenfels, 1936a: 111.

Clathria (Microciona) spinarcus (Carter & Hope, 1889)

Microciona armata, in part; Carter, 1874c: 457; Carter & Hope, 1889: 101-106.
Lagena spinarceae; de Laubenfels, 1936a: 126 [transferred with hesitation].


Clathria (Microciona) spinata (Hoshino, 1981)
Microciona spinata Hoshino, 1981: 155, text-fig.67, pl.7, fig.1 [Sasajima].


Clathria (Microciona) spinata (Hoshino, 1981)

Clathria (Microciona) spinosa (Wilson, 1902)
Microciona spinosa Wilson, 1902: 396-397 [St. Thomas, Puerto Rico]; Simpson, 1968a: 37, pls 9-10, text-fig.2 [Bahamas]; Simpson, 1968b: 26, pls 6-8, tables 5-7; Wiedenmeyer, 1977: 141-142, text-fig.145 [Bimini].


Clathria (Microciona) spinosa; Van Soest, 1984b: 95-96, table 4, text-fig.37 [Curaçao].

Clathria spinosa; Zea, 1987: 167, text-fig. 57 [Columbia Caribbean].

cf. Microciona prolifera; Vosmaer, 1935a: 608, 615.

MATERIAL. HOLOTYPE: USNM7680, Caribbean.

Clathria (Microciona) spongigartina (de Laubenfels, 1930)
Ataura spongigartina de Laubenfels, 1930: 27 [Carlisle, California].

Anacta spongigartina; de Laubenfels, 1932: 89-91, text-fig. 52; Sim & Baktus, 1986: 12 [California].

Clathria spongigartina; Van Soest, 1984b: 7 [generic synonymy].

MATERIAL. HOLOTYPE: USNM21428, fragment BMNH1929.9.122.13. NE Pacific.

Clathria (Microciona) stephensae sp. nov.
Microciona similes Stephens, 1915: 441, pl.40, fig.6 [Saldanha Bay]; Lévi, 1963: 58-59, text-fig.67, pl.9A [St. Helena Bay]; Hechtel, 1965: 43-44 [note].

Anactia similis; de Laubenfels, 1936a: 118.

Not Hymeryphila similis Thiele, 1903a: 957.

Clathria (Microciona) tetraestyla (Hentschel, 1912)

Hymeryphila tetraestyla Hentschel, 1912: 379-380, pl.20, fig.36 [Aru I., Arfaka Sea];

Clathria tetraestyla; de Laubenfels, 1936a: 111.

MATERIAL. HOLOTYPE: SMF94, Indonesia.

Clathria (Microciona) thielei (Hentschel, 1912)

Hymeryphila thielei Hentschel, 1912: 377-378 [Aru I., Arfaka Sea],

Not Ophitusangia thielei Burton, 1932a: 322, pl.55, fig.8; text-fig.32, Kolom, 1964a: 70.

MATERIAL. HOLOTYPE: SMF1708, Indonesia.

Clathria (Microciona) toximajor Topsent, 1925

Clathria toxim major Topsent, 1925: 653-655, text-fig.11 [Gulf of Naples]; Sarà, 1960a: 461 [Iscchia].

Clathria (Microciona) toxiecta (Sará &Siribelli, 1960)


Clathria (Microciona) toxieneus Topsent, 1925


Clathria (Microciona) tumolosa (Bowerbank, 1882)


MATERIAL. HOLOTYPE: BMNH1910.1.1.82. NE Atlantic.

Clathria (Microciona) tunisiae sp. nov.

Microciona chellifer Lévi, 1960a: 70, fig. 12 [Sicily-Tunisian Strait]; Pulsitzer-Finali, 1983: 610.

MATERIAL. HOLOTYPE: MNHN missing. W Mediterranean. Spanioplax (= Clathria) chelliferum Hentschel, 1911 has seniority.

Clathria (Microciona) urizae sp. nov.


Not Microciona similis Stephens, 1915: 441 [see C. (M) stephensae sp. nov.].

MATERIAL. SPECIMENS: ABIP78-58, 78-59, 7B-61. SW Africa, Note: E. similis of Uriz (1988a) is conspecific with neither Clathria (Microciona) similis (Thiele, 1903a), nor Microciona similis Stephens, 1915 (= C. (M) stephensae sp. nov.), and requires a new name.

ETYMOLOGY. Named for Dr. M.J. Uriz.

Clathria (Microciona) vacelettia nom. nov.

Microciona curvichela Vacelet & Vasseur, 1965: 106-108, pl. 9, fig. 31 [Madagascar].

Not Wilsonella curvichela Hallmann, 1912: 247.

MATERIAL. HOLOTYPE: MNHN missing. W Indian Ocean. C. (D) curvichela (Hallmann, 1912) has priority.

TRANSFERS

Other species described in Clathria (Microciona), or a synonym, but now transferred to other genera.

Microciona ambigua Bowerbank, 1862b: 1110; Bowerbank, 1864: 188; Bowerbank, 1866: 124, 136-138 [Britain]; Gray, 1867: 535; Norman, 1869: 330; Schmidt, 1870: 76; Bowerbank, 1874: 65, pl. 25, figs 1-3; Marenzeller, 1878: 2, 4, 5, 14-15, 370, pl. 1, fig. 3, pl. 2, figs 3-3a; Urban, 1880: 257; Bowerbank, 1882: 7, 18, 53; Topsent, 1891a: 528, 543, 554 [Roscoff, France]; Norman, 1892: 6, 11; Vosmaer, 1935a: 607.

Hasatus ambigua; Frissted, 1885: 31-32, pl. 3, fig. 1a-h; Frissted, 1887: 443, 465.

Plocamium ambigua; Topsent, 1894a: 8, 14, 21-22, 23, 26; Topsent, 1895: 214, 216; Topsent, 1896: 115, 127; Topsent, 1898: 226; Topsent, 1900: 112-113; Topsent, 1904a: 30, 24, 26, 154-155, 201 [et var. elegans; Azores]; Arnesen, 1903: 22-23, pl. 3, fig. 5 [Norway]; Thiele, 1903b: 389, 395, 397, pl. 21, fig. 21; Arndt, 1913: 119; Topsent, 1913b: 6, 7, 32, 63, pl. 5, fig. 15; Hentschel, 1914: 120; Burton, 1984a: 494 [Norway]; Hentschel, 1929: 895, 973 [White Sea].


Scopatina ambigua; Schmidt, 166a: 149; Schmidt, 166b: 15; Schmidt, 1868: 26, 40.

Amphilectus ambigua; Vosmaer, 1880: 116.

Stylactichon ambigua; Hanisch, 1894: 176, 195.

Hymedesmia indistincta Bowerbank, 1874: 303-306, pl. 87, figs 1-10.

Myxilla indistincta; Vosmaer, 1880: 129.

Hymeraphia indistincta; Hanisch, 1894: 181, 196.

Plocamia microcionoides; Carter, 1876: 390 [Cape St. Vincent]; Topsent, 1891a: 529, 544-545 [Roscoff]; Topsent, 1892a: 117.

MATERIAL. HOLOTYPE: BMNH1930.7.3.227, fragment BMNH1910.1.1.65. Referred to Anclhinoidea, Plocamionida.


Stylactichon bhamigera; Lilly et al., 1953 [Lough Ine, Ire.]. Pronax bhamigera; Van Soest & Weinberg, 1980: 10 [Lough Ine, Ireland].

MATERIAL. HOLOTYPE: unknown. Referred to Anclhinoidea, Pronax.

Microciona dives Topsent, 1891a: 529, 543-544, 554, pl. 22, figs 2-3 [Roscoff, France].


MATERIAL. HOLOTYPE: BMNH1910.1.1.498-9, Referred to Anclhinoidea, probably Planoahlichondia.


Hymedesmia fictilia; Alander, 1942: 36 [Sweden].

Anclhino fictilia; Stephens, 1916: 242 [W cost of Ireland].
Phorbas ficita; Lilly et al., 1953 [Lough Ne, Ireland]; Van Soest & Weinberg, 1980: 10 [Lough Ne, Ireland].

**MATERIAL.** **HOLOTYPE:** BMNH1930.7.3. 199, fragment USNM5043. Referred to Anchoziidae, *Phorbas*.

**Microciona intexta** Carter, 1876: 238-239, pl. 15, fig. 43a-c [Cape St. Vincent, Hebrides; Vosmaer, 1935a: 607].

**Rhabderemia intexta**; Topsent, 1892a: 116; Topsent, 1903a: 152 [transferred with hesitation]; Hooper, 1990: 72; Van Soest & Hooper, 1993: 337.


**MATERIAL.** **HOLOTYPE:** BMNH1890.4. 10.12, referred to Rhabderemiidae, *Rhabderemia*.

**Microciona minutula** Carter, 1876: 479, pl. 16, fig. 51 [affirmed emendation]; Carter, 1880a: 44; Vosmaer, 1935a: 608.

**Rhabderemia minutula**; Topsent, 1904a: 152-153, pl. 1, fig. 10, pl. 13, fig. 13 [Banyuls; Lévi, 1956b: 393, fig. 2; Boury-Esnault, 1971: 306 [Banyuls; Bibiloni & Gili, 1982: 231; Pulitzer-Finali, 1983: 533-534, text-fig. 51 (Mediterranean).]

**Microciona pusilla** Carter, 1876: 239, pl. 16, Carter, 1880c: 437; Topsent, 1889: 41, text-fig. 7.


**Rhabderemia indica**, in part; Sarrà, 1961: 44, text-fig. 8; Pulitzer-Finali, 1983: 534.

**MATERIAL.** **HOLOTYPE:** BMNH1902.11. 16.32, fragment BMNH1954.3.9.178. Referred to Rhabderemiidae, *Rhabderemia*.

**Axinella monticularis** Ridley & Dendy, 1886: 481; Ridley & Dendy, 1887: 185, pl. 38, fig. 5 [Cape Verde Is].


**Microciona monticularis**; Burton, 1956: 132 [Sao Vincente, W. Africa].

**Aulospongella monticularis**; Burton, 1956: 141.

**MATERIAL.** **HOLOTYPE:** BMNH1887.5.2.20, paratype BMNH1887.5.2.273. Referred to Raspailiidae, *Aulospongeus*.

**Spongia plumosa** Montagu, 1818: 118 [Devon, UK].

**Hymeniocodium plumosum**; Bowerbank, 1866: 195, figs 141-143.

**Porax plumosum**; Gray, 1867: 536.

**Microciona plumosa**; Bowerbank, 1874: 61-63, pl. 24, figs 7-13; Topsent, 1891b: 128 [France].

**Mytilia (?) plumosa**; Ridley & Dendy, 1887: 145-146 [Bahia, Brazil].

**Styllostichon plumosa**; Topsent, 1891a: 529; Lilly et al., 1953 [Lough Ne, Ireland].

**Plumosohelichondra plumosa**; Kervil, 1901: 175 [Normandy].

**Hymnedesmiia plumosa**; Vosmaer, 1935a: 607.

**Porax plumosum**; Van Soest & Weinberg, 1980: 10 [Lough Ne, Ireland].

**MATERIAL.** **HOLOTYPE:** unknown, fragments BMNH1930.7.3.216, 224. Referred to Anchoziidae, *Porax*.

**Microciona pusilla** Carter, 1876: 239, pl. 16, figs 51a-d [tropical]; Carter, 1880c: 437 [name emended to M. minutula]; Topsent, 1889: 41, text-fig. 7 [Banc de Campeche].


**MATERIAL.** **HOLOTYPE:** BMNH1902.11. 16.32, referred to Rhabderemiidae, synonym of *Rhabderemia minuta* (Dendy, 1905: 180).

**Microciona quinguerauicita** Carter, 1880a: 43, 153, pl. 4, figs 5a-c [Gulf of Mannai].

cf. **Microciona prolifera**; Vosmaer, 1935a: 608.

**MATERIAL.** **HOLOTYPE:** LFM destroyed, no fragment in BMNH. Referred to Raspaliidae, *Cyamum*.

**Microciona simplicissima** Norman, 1869: 330; Bowerbank, 1874: 198, 204-205, pl. 73, figs 16-19 [Shetland]; Vosmaer, 1935a: 607.

**Tetalia simplicissima**; Hanisch, 1890: 192.

**Bubaris simplicissima**; de Laubenfels, 1936a: 131.

**Not Leptosia simplicissima** Hentschel, 1911: 359-360, text-fig. 40 [Shark Bay, Western Australia].

**Not Protoaxinella simplicissima** Burton, 1932a: 321, pl. 56, fig. 2, text-fig. 31 [Falkland Is].

**MATERIAL.** **HOLOTYPE:** BMNH1930.7.3.213, referred to Axinelliidae, *Bubaris*.

**Microciona spinulenta** Bowerbank, 1866: 124, 132, 133 [Britain]; Gray, 1867: 534; Vosmaer, 1935a: 607.

**Pocillo spinulenta**; Topsent, 1893b: 34 [plus Isodictya implicita Bowerbank].

**MATERIAL.** **HOLOTYPE:** BMNH1930.7.3.213, referred to Myxillidae, *Iophon*.

**Microciona virgula** Sara & Siribelli, 1960: 77-79, text-fig. 27 [Bay of Naples]; Siribelli, 1960: 16-17, text-fig. 7A [Naples].

**MATERIAL.** **HOLOTYPE:** IMZUN237: 0.5, Synonym of Antho involventis (Sarrà, 1964: 228-229).

**Clathria (Dendrocia)** Hallmann, 1920

**Dendrocia Hallmann, 1920: 767.**

**Paradorina Hallmann, 1920: 767.**

**Wilsonella in part; sensu Hallmann, 1912: 242 (not Carter, 1885F: 366).**

**DEFINITION.** Single undifferentiated category of smooth auxiliary spicule (style, substylolytic or modified style) forming plumose or plumoreticulate choanosomal tracts, ectosomal brushes and dispersed between skeletal tracts; echinating acanthostyles usually heavily spined and distributed evenly over skeletal tracts; microscleres include isochelae ranging from typical palmate form (straight shaft, lateral alae fused to shaft), modified palmate forms (thickened, curved shaft, partially detached lateral alae) to anchorate-like forms (ala detached from shaft, shaft with lateral ridge); toxas if present include oxe horns.

**TYPE SPECIES.** **Clathria pyramidal** Lendenfeld, 1888: 222 (by original designation).

**REMARKS.** Seven species are included in **Clathria (Dendrocia)**, all of which are endemic to temperate Australian waters, with an hypothesised Gondwanan origin.
Clathria (Dendrocia) curvichela
(Hallmann, 1912)
(Figs 104-105)

Wilsonella curvichela Hallmann, 1912: 247-249, pl.34, fig.4, text-fig.51.
Paradoryx curvichela; Hallmann, 1920: 768.
Clathria curvichela; Hooper & Wiedenmayer, 1994: 263.

MATERIAL. HOLOTYPE: AMZ59 (part) + E926a (part): 21km S. of St. Francis L., SA, 32°44'S, 133°18'W, 60m depth, coll. FIV 'Endeavour' (dredge).

HABITAT DISTRIBUTION. 60m depth; substrate unknown; S Aust (Fig. 104E).

DESCRIPTION. Shape. Branching digitate, 130mm high, 35mm maximum width, with short, cylindrical, bifurcate, anastomosing, tapering branches up to 14mm diameter, and short subcylindrical stalk, 15mm long, 8mm diameter. Colour. Live colouration unknown, yellowish-brown in ethanol.

Oscules. Minute oscules, up to 1mm diameter, dispersed on lateral margins of branches. Texture and surface characteristics. Smooth, even, compressible.

Ectosome and subectosome. Ectosome not hispid, although peripheral spongins fibres produce small surface projections; subectosomal auxiliary subtylostyles tangential to surface, or protruding through ectosome only a short way.

Choanosome. Choanosomal skeletal architecture almost regularly reticulate, with heavy, thick spongins fibres incompletely divided into primary and secondary components, differentiated only by presence or absence of coring auxiliary megacleres, respectively; spicule tracts in primary fibres vaguely ascend to surface in multi-spicular bundles; secondary fibres pauci- or aspicular, usually running parallel to surface; all fibres very heavily echinated by acenthostyles, dispersed evenly over fibres; mesohyl matrix heavy but only lightly pigmented, with scattered microcleres.

Megacleres. Choanosomal principal styles absent or undifferentiated from auxiliary spicules.

Subectosomal auxiliary subtylostyles (coring fibres and scattered below membraneous ectosome) straight or slightly curved, hastate, with subtylote, slightly pointed, smooth bases. Length 132-(149.5)-186µm, width 1.5-(3.5)-4µm.

Acanthostyles subtylote, with large and even spination. Length 64-(74.1)-89µm, width 4-(6.8)-8µm.

Microcleres. Isochelae palmate, large, with greatly curved shaft; lateral alae fused with shaft about 3/4 way along alae; front alae ranges from well developed to vestigial; poorly silicified sigma-like forms also present. Length 22-(23.8)-32µm.

Toxas absent.

REMARKS. Hallmann (1912) originally assigned this species to Wilsonella because it had only one type of auxiliary spicule coring the fibres and scattered in the subectosomal skeleton. However, it lacks detritus in fibres, and principal spicules, and has modified palmate isochelae (curved, thickened with partially detached lateral alae) and heavily echinated fibres indicates that it belongs with Dendrocia. Hallmann (1920) erected Paradoryx for this and several other species (C. oxyphila, C. piniformis, C. dura and C. elegantula), of which the present species has the most heavily echinated fibres and the most regular fibre reticulation, although slightly plumose near the periphery. Other species of Dendrocia have predominantly plumose (or plumo-reticulate) choanosomal skeletons.

Clathria (Dendrocia) dura Whitelegge, 1901
(Figs 106-107, Table 23)

Clathria dura Whitelegge, 1901: 83, 84, 117, pl.11, fig.11; Hooper & Wiedenmayer, 1994: 263.
Wilsonella dura; Hallmann, 1912: 242, 244, 245, 298; Shaw, 1927: 426; Guiler, 1950: 9.
Paradoryx dura; Hallmann, 1920: 768.
Microciona prolifera; sensu Vosmaer, 1935a: 611, 644.

Not Antherochalina dura Lendenfeld, 1887b: 788.
Not Clathria dura var. mollis Hentschel, 1911: 370.

MATERIAL. LECTOTYPE: AMG3046; (dry) Tuggerah Beach, NSW, 33°18'S, 151°30'E, coll. NSW Fish Commission (trawl). PARALECTOTYPE: AMG3046a; (dry) same locality. OTHER MATERIAL: NSW-AMZ1052.

HABITAT DISTRIBUTION. Ecology unknown; Tuggerah Beach, Balmoral Beach and Port Jackson (NSW) (Whitelegge, 1901), Maria I. (Tas.) (Shaw, 1927; Guiler, 1950) (Fig. 106E).

DESCRIPTION. Shape. Flabellate or flabellate-digitate, lobate, planar or multiplanar growth form, 95-110mm high, 85-210mm wide, composed of fused anastomosing or free digits and flattened lobes, on small compressed basal stalk, 8-15mm diameter, and branches bifurcate and taper towards apex.

Colour. Sandy yellow preserved.
Oscules. Oscules mostly confined to lateral margins of branches.
Texture and surface characteristics. Firm, flexible; even, microscopically reticulate and porous.

Ectosome and subectosome. Ectosome with nearly continuous palisade of acanthostyles standing erect on peripheral fibres, with plumose brushes of subectosomal auxiliary styles projecting and forming bundles; spicule bundles correspond in position with ascending choanosomal primary spongin fibres; subdermal region also with scattered subectosomal megascleres lying tangential to surface, interdispersed with projecting acanthostyles.
TABLE 23. Comparison between present and published records of *Clathria* (Dendrocia) *dura* (Whitelegge). Measurements in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMC3046)</th>
<th>Paratype (AMC3046a)</th>
<th>Specimen (N=1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>58-(87.4)-105 x 2-(3.9)-6</td>
<td>78-(88.2)-102 x 3-(4.1)-5.5</td>
<td>82-(96.5)-115 x 3-(3.6)-5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>48-(57.0)-66 x 4-(5.5)-8</td>
<td>56-(64.6)-75 x 4-(5.6)-9</td>
<td>61-(66.3)-75 x 4-(5.1)-8.5</td>
</tr>
<tr>
<td>Chelae</td>
<td>17-(18.6)-22</td>
<td>14-(17.4)-19</td>
<td>16-(18.8)-22</td>
</tr>
<tr>
<td>Toxas</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

**Choanosome.** Choanosomal skeletal architecture irregularly reticulate, with sinuous, relatively thick spongin fibres; fibres incompletely divided into primary ascending, and secondary transverse components; primary fibres with a multipolar core of subectosomal auxiliary styles, identical to those in ectosomal skeleton, together with heavy tracts of acanthostyles secondarily incorporated into fibres; secondary fibres with multi- or paucispicular core of both subectosomal and acanthostyle megascleres; acanthostyles echinate fibres in moderate quantities, at right angles to skeleton, also lying inside the spicule tracts; mesohyl matrix heavy, darkly pigmented, granular with scattered megascleres and microscleres of all kinds.

**Megascleres** (Table 23). Choanosomal principal megascleres absent or undifferentiated from auxiliary spicules.

Subectosomal auxiliary styles quasidiactinal, curved or straight, hastate, with tapering, rounded, styloid, or pointed, smooth bascs.

Acanthostyles rounded or slightly subtylote, with large, evenly dispersed spines.

**Microscleres** (Table 23). Isochelae abundant, palmate, with lateral alae fused to shaft for only about 1/2 length of ala; shaft greatly curved, thickened (‘hunchback’), front ala well developed.

Toxas absent.

**Larvae.** Incubated parenchymella, up to 270μm in diameter, with heavy mesohyl matrix.

**REMARKS.** In possessing a single category of structural megasclere this species is assigned to *C. (Dendrocia).* Its quasidiactinal megascleres are reminiscent of those found in *C. (D.) pyramida*; the modified palmate isochelae (curved, thickened, partially detached lateral alae) are similar to those found in other species assigned to *Paradoryx* by Hallmann (1920) (e.g., *C. (D.) curvichela*); and skeletal architecture and spongin fibre characteristics are reminiscent of those in *C. (C.) sartagiunula.* The presence of acanthostyles incorporated into skeletal spicule tracts is now known to occur in several species, collectively termed here the ‘phorbasiformis’ group (including *C. (Thalysias) phorbasiformis*, *C. (T.) orientalis*, *C. (Dendrocia) dura*, *C. (D.) imperfecta*, *C. (D.) myxiloides* and *C. (Clathria) squarorum*), and this feature is analogous to (but not homologous with) that seen in the Crellidae. The presence of acanthostyles in the ectosomal skeleton is also seen in the Crellidae. Whereas species of *Crella* have a thick tangential ectosomal crust of acanthose megascleres, in *C. (D.) dura* these acanthostyles stand erect on peripheral skeletal fibres, pierced by plumose tracts of smooth subdermal (auxiliary) spicules.

The synonymy cited above for *C. (D.) dura* requires further comment. Lendenfeld (1887a) described *Anthrochalinia dura* from Port Jackson, but the species is unrecognisable from his brief description. Lendenfeld’s type material was not located in the AM collections, and only a slide of the holotype was found in the BMNH collections (BMNH1886.8.27.684). Apparently a dry specimen of the species was also deposited in the BMNH collections (BMNH1886.8.27.608, possibly the holotype), but this has not yet been rediscovered. Re-examination of the holotype slide confirms that *A. dura* is a synonym of *Phakellia flabellata*, as supposed by Burton (1934a).

**Clathria (Dendrocia) elegantula** Ridley & Dendy, 1886 (Figs 108-109)

*Clathria elegantula* Ridley & Dendy, 1886: 474; Ridley & Dendy, 1887: 149, pl.28, figs 3,3a, pl.29, figs 14a-b; Guiler, 1950: 7; Carpay, 1986: 26; Hooper & Wiedenmayer, 1994: 263.

*Clathria elegantula* var. *occidentalis* Hentschel, 1911: 372-374, text-fig.46.

*Wilsonella elegantula*; Hallmann, 1912: 241.

*Paradoryx elegantula*; Hallmann, 1920: 768.


**HABITAT DISTRIBUTION.** 6-76m depth; on sand and shell grit substrate; Bass Strait and E coast (Tas)
DESCRIPTION. Shape. Massive, lobate fan, 73 mm long, 75 mm wide, with erect, flattened, digitate lobes, 22-31 mm long, 8-20 mm wide, lobes with uneven margins, arising from sprawling encrusting base. 

Colour. Live colouration unknown, pale beige preserved.

Oscules. Differentiated inhalant and exhalant surfaces of lobes; ostia scattered, 1-2 mm diameter, oscules confined to sieve-plates.

Texture and surface characteristics. Harsh; uneven, prominently microconulose, translucent dermal membrane, covering reticulate fibrous surface, stretched between microconules.

Ectosome and subectosome. Fibrous, reticulate ectosomal skeleton, with sparse tangential subectosomal auxiliary stylostyles lying directly on surface; sinuous plumose tracts of these spicules below, ascending from choanosomal skeleton.

Choanosome. Choanosomal skeleton plumoreticulate, cavernous, with well-developed primary and secondary spongin fibres; primary ascending fibres sinuous, almost dendritic, core by several discrete multi- or paucispecific tracts of subectosomal auxiliary stylostyles, occupying only small portion of fibre diameter; primary fibres interconnected by reticulate secondary fibres, and terminating in plumose spicule bundles at periphery; secondary transverse fibres pauci- or aspicular, thin; echinating acanthostyles most abundant in axial region, sparse or absent in peripheral skeleton; mesohyl matrix light, with abundant scattered chelae.

Megascleres. Choanosomal principal megascleres absent or undifferentiated from auxiliary spicules.

Subectosomal auxiliary stylostyles straight, rarely slightly curved, quasidiactinal, hastate points, with tapering, rounded or slightly pointed, smooth bases. Holotype: Length 145-(160.6)-168 mm, width 1.5-(2.6)-4 mm. (Hentschel's specimen: 133-(142.3)-152 mm, width 2-(3.5)-4 mm).

Acanthostyles slender, evenly spun, with rounded or slightly subtylostyles bases, sharp points. Length 53-(64.1)-72 mm, width 2-(3.6)-5 mm. (Length 52-(68.2)-84 mm, width 3-(6.4)-8 mm).

Microscleres. Isochelae large, palmate, sigmoid curved, with lateral alae nearly completely fused to shaft, sometimes well developed, sometimes vestigial and reduced to small ridge on shaft; front ala usually reduced. Length 13-(15.4)-17 mm. (Length 13-(17.2)-20 mm).

Toxas absent.

REMARKS. The nearly dendritic, predominantly plumose skeletal architecture and the concentration of acanthostyles in the axial region are quite distinctive features for this species. These characters, together with the possession of a single category of structural spicule in both fibres and the ectosomal skeleton indicate that the species is best placed in C. (Dendrocia). In having quasidiactinal modified, vestigial structural megascleres with principal and auxiliary spicules having similar geometry, and vague similarities in skeletal structure, this species is included in the 'oxyphila' species group (also containing C. (C.) raphana, C. (C.) oxyphila and C. (C.) piniformis). Spongin fibres are also characteristic (whereby each fibre may have several discrete spicule tracts), but in most other respects this species is very similar to C. (D.) dura Whitelegge (both having sinuous spongin fibre systems and heavily echinated fibres). These two species differ in the size of their auxiliary styles (notably straight, longer, more slender, with subtylostyles in C. (D.) eleganlula, whereas in C. (D.) dura these spicules are curved, short, thick, with tapering haste (or sometimes pointed) bases), and the incorporation of acanthostyles into skeletal fibre tracts in C. (D.) dura.

There is a remarkably close concordance in these features between Bass Strait and Shark Bay populations, despite their widely separated geographical distribution. These samples differ only slightly in the more robust acanthostyles seen in Shark Bay material, but no other morphological differences were seen to justify subspecies separation (Hentschel, 1911).

Clathria (Dendrocia) imperfecta Dendy, 1896 (Figs 110-111)


HABITAT DISTRIBUTION. 36 m depth; substrate unknown; Port Phillip Bay (Vic) (Fig. 110E).

DESCRIPTION. Shape. Erect, bulbous-lobate, with small cylindrical lobate digits.

Colour. Colour in life recorded as dull brown-orange exterior, yellow interior.
Oscules. Minute, less than 2mm diameter, mainly on apex of lobes.

**Texture and surface characteristics.** Surface irregular, uneven, micropapilllose, with subdermal ridges and grooves. Texture is crumb-of-bread, easily torn.

**Ectosome and subectosome.** Microscopically hispid, with thick brushes of subectosomal auxiliary styles from peripheral skeleton protruding through dermal crust, composed of same megascleres, lying paratangential to or standing erect on surface; subectosomal architecture thickly plumose, arising from ultimate ascending choanosomal fibres.

**Choanosome.** Choanosomal skeleton irregularly plumo-reticulate, with prominent primary ascending spicule tracts interconnected by irregularly dispersed secondary tracts; fibres weakly developed in spongion but fully cored by subectosomal auxiliary styles and also acanthostyles secondarily incorporated into tracts; fibres moderately echinated; fibre anastomoses form irregular oval-elongate meshes; mesohyl matrix heavy but only lightly pigmented, with auxiliary styles and sparse detritus scattered throughout.

**Megascleres.** Choanosomal principal styles absent or undifferentiated from auxiliary megascleres.

Subectosomal auxiliary spicules fusiform, mostly straight, occasionally slightly curved towards bases, with tapering, or rounded, or slightly subtylole smooth bases. Length 189-213.3-234µm, width 1.5-4.4-7.5µm.

Acanthostyles long, rounded or faintly subtylole, with large and evenly distributed spines. Length 102-114.8-122µm, width 5-5.8-7µm. Microscleres absent.

**Larvae.** Oval-elongate parenchymella, 345-412x275-370µm, without larval spicules but with heavy mesohyl and differentiated cells clearly visible.

**Remarks.** This species was assigned to Wilsonella by Hallmann (1912) because it has only a single category of smooth megasclere, but was tacitly returned to Clathria by Hallmann (1920) when he restricted Wilsonella to the type. *Clathria (Dendrocia) imperfecta* is more appropriately placed in *Dendrocia* because it lacks detritus incorporated into fibres and has only one undifferentiated category of smooth auxiliary style, whereas Wilsonella (sensu Hallmann, 1912) and Paradoryx (sensu Hallmann, 1920) have two categories of auxiliary styles, one found in fibres and the other on the ectosomal skeleton.

All three nominal genera lack true principal megascleres. This species is similar to *C. (Thalaysia) orientalis*, *C. (T.) phorbasiformis*, *C. (D.) myxilloides* and *C. (D.) dura* in having acanthostyles incorporated into fibres, intermingled amongst the smooth coring megascleres (termed the 'phorbasiformis' species complex).

**Clathria (Dendrocia) myxilloides**

Dendy, 1896

(Figs 112-113, Plate 3A)


**Habitat distribution.** 18m depth; on rock substrate; Port Phillip Bay (Vic.), Kangaroo J. (SA) (Fig. 112E).

**Description.** Shape. Massive, subspherical, lobate digitate growth form. Colour. Orange-red alive (Munsell 5R 5/10), grey-brown in ethanol. Oscules. Small, less than 3mm diameter; scattered evenly over surface. Texture and surface characteristics. Hard, compressible; shaggy, uneven, microconulose, appearing pock-marked alive due to scattering of small oscules.

**Ectosome and subectosome.** Relatively dense discrete bundles of subectosomal auxiliary styles, identical to those coring the fibres, forming erect palisade on surface. Tracts of isochelae also found in peripheral skeleton, scattered throughout heavily pigmented peripheral spongion; subectosomal region relatively disorganised, paratangential, merging into peripheral choanosomal fibres lying almost immediately subectosomal.

**Choanosome.** Choanosomal skeletal architecture irregularly plumo-reticulate, without clearly differentiated primary or secondary components although fibre diameter varies considerably and fibres become sinuous towards surface; fibres composed of only light spongion, heavily cored by multispicular tracts of subectosomal auxiliary styles and heavily, irregularly echinated by acanthostyles lying parallel with, or at acute angles to spicule tracts but also secondarily incorporated into fibres; mesohyl matrix light, with smaller,
thinner auxiliary spicules, and numerous isochelae organised into tracts surrounding large choanocyte chambers.

Megascleres. Principal choanosomal megascleres absent, or undifferentiated from auxiliary spicules.

Subectosomal auxiliary styles differ slightly in size according to location within skeleton: those coring fibres and in ectosomal skeleton relatively homogenous, straight or slightly curved, hastate, with smooth, tapering or slightly subtylote bases, some appearing quasi-diactinal. Length 287-(311.4)-330μm, width 3.5-(4.9)-6μm; auxiliary styles also scattered between fibres probably younger forms of main structural megascleres, being thin, wispy, hastate, usually curved or

sinuous, with rounded or tapering bases. Length 212-(233.0)-284μm, width 2-(2.2)-3μm.

Acanthostyles long, slender, straight or slightly curved near basal end, evenly and heavily spined. Length 84-(112.6)-133μm, width 6-(7.4)-10μm. Microscleres. Isochelae relatively large, abundant, anchorate, with well formed lateral alae detached from shaft nearly completely, lateral ridge on shaft (possibly vestigial point of attachment of lateral alae); some modified unguiform forms with pointed alae, or sigmoid forms with greatly reduced alae also present. Length 21-(24.4)-29μm.

Toxas absent.

REMARKS. This species is similar to C. (D.) imperfecta in growth form and incorporation of some acanthostyles into fibres (see remarks for C. (Thalysia) phorbasiformis). It also shows similarities to C. (D.) pyramida in growth form and megasclere morphology, although all three species differ in isochelae geometry.

Clathria (Dendrocia) pyramida Lendenfeld, 1888
(Figs 114-115, Table 24, Plate 3B)


Wilsonella pyramida; Hallmann, 1912: 240, 244; Shaw, 1927: 426; Guiter, 1950-9.


Clathria alata Dendy, 1896: 34; Hentschel, 1911: 375-377, text-fig.48; Hentschel, 1923: 387, fig.356; Ayling et al., 1982: 100; Van Soest, 1984b: 120.


MATERIAL. LECTOTYPE: AMG9047; Port Jackson, NSW, 33°51'S, 151°16'E, no other details known. PARALECTOTYPE: BMNH1887.1, 24.62 (fragment AMG3579); same locality. LECTOTYPE of C. alata: NMVG2280 (fragment BMNH1902.10.18.330); Port Phillip Bay, Vic., 38°09'S, 144°52'E, coll. J.B. Wilson (dredge, RN 752). PARALECTOTYPES of C. alata: NMVG2281 (fragment AMG2686); same locality (RN 763). NMVG2282 (fragment BMNH1902.10.18.31); Sorrento Jetty, Port Phillip Bay, 38°33'S, 145°21'E (dredge, RN 792). NMVG2283 (fragment BMNH1902.10.18.49); same locality (RN 801). NMVG2284 (fragment BMNH1902.10.18.332); same locality (RN 842). NMVG2285 (fragment BMNH1902.10.18.333); same locality (RN 843).

OTHER MATERIAL: VIC- AME298, AMZ1145, AM unreg. (small vial, label 'donated by A Dendy'). AM unreg. (fragment BMNH1887.4.27.103) (small vial, label 'Clathria tethyops, donated by A Dendy, Lendenfeld or Burton MS name'). NSW- AMZ3216, NTM22667, QMG304507, QMG304522, QMG304574. S AUST- SAMTS4095 (fragment NTMZ1629), SAMTS6290, QMG30503 (NCIQ66C-2119-T) (fragment NTMZ3520), QMG301354, QMG301358, QMG301374, QMG301382, QMG304041, QMG304049, QMG304051, QMG304053, QMG304054, QMG304063, QMG304064, QMG304069, QMG304070. WA- QM G300604 (NCIQ66C-4271-J), QM G300191 (NCIQ66C-4651-V). (Not AM unreg. (label 'Clathria alba. Port Jackson, NSW'. = Lendenfeld or Burton MS name: = Clarella incrustans)).

HABITAT DISTRIBUTION. 0.8-25m depth; on sand, rock reef or muddy bottoms; associated with oysters and algal beds, Spondylius, Pinna and Chalamus asperimus bivalves, rock or wood jetty substrates; Illawarra, Port Jackson, N. Sydney, Port Hacking and Durras L (NSW); Mana L. (Tas); Port Phillip Bay (Vic); St. Vincent Gulf, Yorke Peninsula and Kangaroo I. (SA); Albany and Pelsart Is, Houtman Abrolhos (WA) (Fig. 114E).

DESCRIPTION. Shape. Massive, lobate, lobodigitate, irregular growth form with small lobate surface projections.

Colour. Dark brown or orange-brown live exterior (Munsell SYR 4/6-5/10), paler choanosome, brown in ethanol.

Oscules. Few, relatively large oscules (up to 8mm diameter) on apex of lobes, each with slightly raised membranous lip, and with membranous, divided exhalant canals visible inside oscule; oscules collapse on preservation.

Texture and surface characteristics. Firm, compressible; smooth, relatively even, bulbous, fleshy surface in live state; optically smooth, membranous surface in preserved state, with irregularly rugose microscopic conulose and lobate projections.

Ectosome and subectosome. Microscopically hirsut, with dense crust of subectosomal auxiliary styles forming continuous, erect, regular (straight) or irregular (stellate, paratangential), plumeose palisade.

Choanosome. Skeletal architecture irregularly plume-reaticulate, with sinuous spongin fibres ascending to surface in meandering tracts; fibres Anastomose more frequently at axis than in peripheral skeleton; peripheral fibres and skeletal tracts often diverge becoming plumeose in subectosomal region, or forming a paratangential layer immediately below erect ectosomal skeleton; fibres contain moderately light to very heavy spongin, cored by multispecific, sinuous tracts of subectosomal auxiliary styles; fibres not obviously divided into primary or secondary components,
although fibre diameter varies within same sections of skeleton; acanthostyles heavily echinating most fibres, occasionally rare or absent from some; mesohyl matrix very heavy but only lightly pigmented, with abundant isochelae and auxiliary megascleres; microalgae present in mesohyl of some specimens. 

Megascleres (Table 24). Choanosomal principal megascleres absent, or at least undifferentiated from auxiliary spicules. 

Subectosomal auxiliary styles are thin, hastate, straight or slightly curved towards basal end, usually with smooth, slightly subtyloite bases that taper towards end into a small point (partially mucronate), points hastate. 

Acanthostyles vary considerably in length, usually club-shaped, subtyloite, with large spines mostly confined on base and more-or-less aspinoce towards point; spines usually robust. 

Microscleres (Table 24). Isochelae large, very abundant, primarily palmate, heavily silicified, usually with thickened and slightly curved shaft, large lateral alae completely fused to shaft resembling 'wings', with front ala free, but sometimes with reduced alae and sigmoid curvature. 

Toxas absent. 

Larvae. Larvae oval-elongate parenchymella, up to 518x340μm, with larval raphidiform spicules scattered throughout the axis and forming stellate tufts at the posterior pole. 

REMARKS. Type material of Clathria pyramida and of C. alata are virtually identical in their growth form, surface features, spicule geometry, spicule distribution and fibre characteristics, differing only slightly in choanosomal skeletal construction (predominantly plumo-recticate versus predominantly plumo to slightly plumo-recticate), and ectosomal structure (either producing a continuous erect palisade (C. alata s.s.) or punctuated palisade resulting in stellate plumo brushes (C. pyramida s.s.), respectively). But there are no consistent or significant differences between these species in the spongion content of fibres, density of spicule tracts, presence or absence of connecting secondary fibres, or spicule dimensions (Table 24), as supposed by Hallmann (1912: 241). On this basis the two species are merged here. For all other specimens examined the main variability involves the degree to which fibres were compacted (mesh size), the spongion content of skeletal tracts ('fibre' diameter), and spicule dimensions between different geographic populations (Table 24). In this latter regard populations from NSW and WA had relatively larger, more robust acanthostyles than other populations (VIC, SA). In particular, spicules from a small population in the Gulf of St Vincent, SA, were noticeably more poorly silicified and less robust than 'typical' specimens found in all other localities. 

In spiculation and skeletal architecture C. (D.) pyramida is remarkably similar to Crella incrus- tans var. digitata ('cotype' AME503), although upon careful examination of both species there are obvious differences in skeletal structure (Crella with a tangential ectosomal layer), composition of the ectosomal skeleton (styles versus acanthostyles or acanthoxeas), and spicule geometry (quasi-diactinal auxiliary styles versus anisoxeas or quasi-monactinal megascleres, respectively). Nevertheless, these species demonstrate remarkably close convergences in several prominent features making them easily confused in the field and laboratory. 

Specimens from the south coast of NSW have peculiar biochemistry and significant biological activity against both gram positive and gram negative bacteria (Hooper et al., 1992). Unlike many other bioactive sponges, however, the activity in C. (D.) pyramida was found to be related to a unique, modified free sugar, 5-Thio-D-mannose (Capon & MacLeod, 1987). This discovery represents the only known occurrence to date of that class of thiosugar in nature, although the compound has a glucose-based synthesised analogue which has been known for several years. Thio sugars have considerable pharmaceutical and medical potential: they inhibit the release of insulin and transport of glucose, and are able to cause reversible inhibition of sperm-cell development without displaying acute toxicity (R. Capon, pers. comm.). The taxonomic significance of those compounds is not clear, but it is possible to speculate on the biological role of those chemicals. Recent evidence (A. Butler, pers.comm.) suggests that C. (D.) pyramida together with a few other species (e.g., Crella incrustans) occur in association with (are epizootic on) scallops (Chlamys asperrma) from South Australian waters. Chernoff (1987) found that the presence of those epizootics increased the survival of the scallop in both field and caging experiments and it is possible that the sponges provide some sort of chemical defence of the host: thio-mannose sugar may play some sort of role in that defence.

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TABLE 24. Comparison between published records and different populations of *Clathria (Dendrocia) pyramidata* Lendenfeld. All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25) (bracket = number of specimens per locality examined).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (AMG9047)</th>
<th>Lectotype of C. Alata (NMVG2280)</th>
<th>Specimens NSW (N=7)</th>
<th>Specimens VIC (N=10)</th>
<th>Specimens SA (N=16)</th>
<th>Specimens WA (N=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaoanosomal principal styles</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>208-(220.6)-231 x 4,6-6-8</td>
<td>211-(229.4)-243 x 3,4-4,8-7</td>
<td>190-(209.5)-225 x 4,5-5,1-7</td>
<td>202-(222.6)-247 x 4,5-5,9-9</td>
<td>195-(213.4)-228 x 4,4-4,9-7</td>
<td>214-(227.4)-242 x 4,5-5,3-7</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>87-(99.0)-135 x 8-(9.2)-11</td>
<td>75-(85.2)-118 x 7-(9.2)-11</td>
<td>82-(103.9)-145 x 5-(8.4)-12</td>
<td>68-(89.6)-125 x 4-(7.2)-12</td>
<td>64-(78.6)-90 x 4-(7.8)-11</td>
<td>82-(103.5)-155 x 6-(9.0)-11</td>
</tr>
<tr>
<td>Chelae</td>
<td>21-(23.8)-27</td>
<td>23-(24.5)-27</td>
<td>20-(23.6)-27</td>
<td>20-(22.5)-25</td>
<td>17-(22.1)-30</td>
<td>22-(24.3)-27</td>
</tr>
</tbody>
</table>

*Clathria (Dendrocia) scabida* (Carter, 1885) (Figs 116-117, Table 25)

*Halichondria scabida* Carter, 1885b: 112, pl.4, figs 4-5; Carter, 1886c: 449.


*Anacta scabita* (lapsus); de Laubenfels, 1936a: 109.

*Clathria scabida*; Hooper & Wiedenmayer, 1994: 264.

*Halichondria pustulosa*, in part; Carter, 1886c: 450.

Not *Halichondria pustulosa* Carter, 1882a: 285, pl. 11. fig. 1.

**MATERIAL.** HOLOTYPE BMNH1887.7.11.9 (fragment AMG2760); Port Phillip, Vic, 38°09'S, 144°52'E, coll. J.B. Wilson (dredge). OTHER MATERIAL: VIC - NMVRN143, NMVRN1025, NMVRN1038, BMNH1887.7.11.26 (slide AMG-2916).

**HABITAT DISTRIBUTION.** 30m depth; substrate unknown; Port Phillip and Westport Bays (Vic) (Fig. 116F).

**DESCRIPTION.** Shape. Low, globular, erect, arborescent, digitate sponge, 80-95mm high, 45-70mm wide, with subospherial, or lobate branches, 28-42mm long, 12-28mm diameter, on a short stalk, 22mm long, 12-15mm diameter.

**Colour.** Live colouration orange-brown, brown exterior and yellow-brown interior preserved.

**Oscules.** Large oscules, up to 5mm diameter, situated in groups (seive-plates) on all sides of branches; seive-plates sunken, resembling poroalyses of the Tethyidae.

**Texture and surface characteristics.** Surface uneven, fibrous, with numerous large pores; seive-plates and subdermal canals covered with prominent membraneous skin, raised into small papillae and ridges.

**Ectosome and subectosome.** Ectosome hispid, with subectosomal auxiliary subtylosystyles forming sparse but continuous dermal palisade of erect brushes, sometimes tangential, protruding from surface, piercing heavy crust of isochelae lying on ectosomal membrane; subectosomal region plumose, with sinuous tracts of subectosomal subtylosystyles diverging from ends of chaonoasomal fibres, and with numerous, relatively large subdermal cavities lined by isochelae.

**Chaanosome.** Chaanosomal skeleton irregularly plumo-reticulate, with sinuous, heavy, spongion fibres cored by subectosomal auxiliary styles and fewer larger acanthostyles, and echinated by two sizes of acanthostyles; smaller acanthostyles echinate fibres in relatively heavy, even concentrations, whereas larger acanthostyles must common at fibre nodes and echinate fibre terminations in radiating brushes; spongion fibres not divided into primary or secondary components, and fibre anastomoses occur irregularly throughout skeleton; mesohyl matrix very heavy, with abundant isochelae scattered and also congregated around fibres and choanoocyte chambers.

**Megascleres** (Table 25). Chaanosomal principal megascleres absent or at least completely undifferentiated from auxiliary spicules.

**Subectosomal auxiliary subtylosystyles, coring fibres and in dermal membrane, long, thin, mostly straight, hasteate, with elongated, subtylote, smooth bases.**

Larger acanthostyles subtylote, slightly curved, with sparse but large spines along shaft and base, and usually with an aspinose apex. Smaller acanthostyles subtylote, evenly and heavily spined.

**Microscles** (Table 25). Isochelae extremely abundant, anchorate-like, with curved shaft, lateral alae nearly completely detached from shaft, completely free front ala, and lateral ridge on shaft (possibly vestigial point of alae attach-
TABLE 25. Comparison between present and published records of Clathria (Dendrocia) scabida (Carter). Measurements in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (BMNH1887.7.11.9)</th>
<th>Specimens (N=3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>201-(237.2)-273 x 3-</td>
<td>195-(226.5)-278 x 2-</td>
</tr>
<tr>
<td></td>
<td>(4.4)-5.5</td>
<td>(3.7)-5</td>
</tr>
<tr>
<td>Echinating acanthostyles I</td>
<td>153-(191.6)-219 x 5.5-</td>
<td>193-(201.1)-221 x 6-</td>
</tr>
<tr>
<td></td>
<td>(7.1)-9</td>
<td>(7.3)-9</td>
</tr>
<tr>
<td>Echinating acanthostyles II</td>
<td>78-(90.4)-98 x 3-</td>
<td>82-(95.3)-105 x 5-</td>
</tr>
<tr>
<td></td>
<td>(6.8)-10</td>
<td>(6.4)-8</td>
</tr>
<tr>
<td>Chelae I (sigmoid)</td>
<td>16-(18.2)-21</td>
<td>19-(20.9)-24</td>
</tr>
<tr>
<td>Chelae II (arcuate-like)</td>
<td>24-(29.2)-33</td>
<td>28-(31.4)-34</td>
</tr>
<tr>
<td>Chelae III (bipocilla-like)</td>
<td>14-(16.2)-18</td>
<td>18-(19.3)-22</td>
</tr>
<tr>
<td>Toxas</td>
<td>35-(72.4)-120 x 1-(1.8)-3</td>
<td>70-(121.1)-156 x 1-(2.2)-3</td>
</tr>
<tr>
<td></td>
<td>uncommon</td>
<td>common</td>
</tr>
</tbody>
</table>

Remarks: reduced chelae also present, unguiculiform, with pointed alae.

Toxas oxhorn, with wide central curvature and slightly reflexed arms.

Remarks. Carter's (1885a) holotype (BMNH1887.7.11.9), and his (1886g) specimen of H. pustulosa, BMNH1887.7.11.26 are identical, as suspected from their respective descriptions, whereas H. pustulosa from the Falkland Is (Carter, 1882a) is different.

Clathria scabida has skeletal architecture, fibre structure, euctosomal characteristics and spicule geometry characteristic of Dendrocia, whereas the presence of a second, larger size class of acanthostyle (which may be incorporated into skeletal spicule tracts as well as echinating the fibre endings and fibre nodes) is unusual to the genus. Possession of hymedesmoid-plumose or plumose skeletal architecture links several microcionids termed the 'scabida' group (C. (D.) scabida, C. (Microciona) similis, C. (M.) hentschelii, C. (M.) tetraystyla, C. (M.) thielei, C. (Thalysias) tingens sp. nov. and C. (T.) distincta).

Earlier records of this species (Carter, 1885a, 1886g; Hallmann, 1912) differentiate isochelae microscleres into 3 or 4 morphs, but all isochela in both specimens are not as vastly different as supposed by Carter (1885a). They are not arcuate, as supposed by previous authors, but anchorate with completely detached lateral alae and ridges on the lateral sides of shaft. This is the only known species of Clathria (Dendrocia) with toxas microscleres.

Clathria (Axociella) Hallmann, 1920


Axosuberites Topsent, 1893a: 179.

Tenaciella Hallmann, 1920: 772.

Definition. Well differentiated axial and extra-axial skeletal architecture (reminiscent of Raspailiidae); axial skeleton markedly compressed, reticulate; extra-axial skeleton radial, plumose or plumo-reticulate composed of large subectosomal auxiliary styles-subtylostyles; specialised euctosomal skeleton present composed of smaller auxiliary spicules; echinating megascleres absent although principal spicules may protrude through fibres at acute angles.

Type Species. Esperiopsis cylindrica Ridley & Dendy, 1886: 340 (by original designation).

Remarks. Axociella is represented in Australasian waters by six species, one new, all of which have very well differentiated skeletal structures closely resembling the compressed skeletons common in Raspailiidae. The existence of microcionids with compressed axial skeletons and differentiated axial and extra-axial skeletons supports the proposal for a closer relationship between Raspailiidae and Microcionidae, as proposed by Hooper (1990a, 1991), and formalised further by Hajdu et al. (1994) in their subordinal classification of Poecilosclerida. Crucial characters differentiating the Axociella group from typical Raspailiidae are the possession of chelae and absence any true echinating spicules in the former, versus possession of a specialised euctosomal skeleton (composed of small styles or oxeas in brushes surrounding larger protruding spicules) in the latter (see Hooper, 1991).

Clathria parva Lévi (from S and SW Africa) and Axosuberites fauroti Topsent (from the Gulf of Aden), are also referred here to C. (Axociella) because they have well differentiated axial and extra-axial regions, whereas 3 NZ species (Bergquist & Fromont, 1988) are retained in this group only on a tentative basis since their skeletal structures are not typical of Axociella. Other species referred to Axociella e.g., de Laubenfels, 1936a) are simply encrusting and/or lack echinating acanthostyles (a secondary loss common amongst Microcionidae and Raspailiidae), and do not belong to Axociella as defined here.
Clathria (A xo c iell a) canaliculata
(Whitelegge, 1906)
(Figs 118-119)

Esperiopsis canaliculata Whitelegge, 1906: 471,
pl.43, fig.7
Tenaciella canaliculata; Hallmann, 1920: 773, pl.36,
figs 1-2, pl.37, fig.1, text-fig.1; Ristau, 1978: 585-
586.
Artemisina canaliculata; Ristau, 1978: 585-586.
Rhaphidophilus canaliculata; Van Soest, 1984b: 115.
Clathria canaliculata; Hooper & Wiedenmayer, 1994:
262.

MATERIAL. LECTOTYPE: AMG4325: Off Wata
Mooli, Bulgo, Woolongong, NSW, 34°30'S, 151°10'E, 104-126m depth, 01.iii.1900, coll. FIV
'Thetis' (dredge). PARALECTOTYPE: AMZ988: Off
Woolongong, NSW, 34°25'S, 151°10'E, 220-224m
depth, 01.iii.1900., coll. FIV 'Thetis' (dredge).
OTHER MATERIAL: QLD- QMG300460 (fragment
NTMZ1562).

HABITAT DISTRIBUTION. Growing in soft sediments, associated with gorgonian beds in deeper waters of
the continental shelf; 94-126m depth; Woolongong
(NSW), S. Stradbroke I. (SEQ) (Fig. 118G).

DESCRIPTION. Shape. Erect, whip-like, cilindrical branching digits, 150-190mm long,
with short cylindrical stalk 30-50mm long, 10-
15mm diameter, and few thick subcilindrical branches, mostly in 1 plane, bifurcating and occasionally
anastomosing.

Colour. Drab grey in ethanol.
Oscules. Small, less than 2mm diameter, dispersed over lateral margins of branches.

Texture and surface characteristics. Firm, flexible; surface smooth, fleshy, velvety, felt-
like, slightly porous, without obvious ornamentation.

Ectosome and subectosome. Thick, erect, plumose brushes of ectosomal auxiliary styloty-
styles form dense, continuous palisade on exterior
surface; discrete tracts of larger subectosomal auxiliary styles form thick, multispicular, ascending
or paratangential brushes supporting ectosomal skeleton.

Choanosome. Partially compressed, open-meshed reticulate axial skeleton and radial extra-
axial skeleton, becoming plumose in periphery;
skeleton composed of very heavy spongin fibres of
large diameter, up to 250µm diameter, forming
ovoid meshes, and clearly divided into primary ascending and secondary connecting elements, differing substantially in diameter; fibres cored by multispicular tracts of choanosomal principal styles occupying most of fibre diameter; spicule
content of fibres increases towards periphery; secondary fibres less heavily cored; echinating megascleres absent; mesohyl matrix moderately heavy with scattered microscleres, but megascleres largely confined within fibres except
at periphery.

Megascleres. Choanosomal principal styles thick, slightly curved or rarely straight, fusiform,
with smooth, rounded or very slightly subtylole bases. Length 130-(318.7)-465µm, width 4-
(21.2)-26µm.

Subectosomal auxiliary styles long, thick, straight, fusiform, with tapering rounded or very slightly subtylole bases, usually smooth, oc-
asionally microspined. Length 240-(465.0)-
590µm, width 10-(12.2)-16µm.

Ectosomal auxiliary subtylostyles straight or slightly curved, with microspined subtylole bases, fusiform points. Length 80-(114.6)-
165µm, width 5-(6.1)-8µm.

Microscleres. Palmate isochelae with long lateral alae completely fused to shaft and fused
front ala; chela clearly differentiated into two size classes, the smaller often twisted. Length I:
4-(4.6)-8µm; length II: 14-(17.5)-22µm.

Toxas accolada, usually long, thin, slight central curvature and straight or only slightly
reflexed points. Length 18-(220.8)-550µm, width 0.5-(1.9)-3.3µm.

REMARKS. Hallmann (1920) erected Tenaciella
for this species on the basis that it lacked echinating
spicules and had a Thalysias-like ectosomal skeleton. Simpson (1968a) found no correlation
between these 2 features and histological evidence to support recognition of this genus
distinct from Clathria. Spicule geometry and the
ectosomal skeleton in C. (A.) canaliculata indicate relationship with Thalysias, whereas skeletal
structure (particularly the radial choanosomal skeleton), is reminiscent of Raspailia nuda
(Hooper, 1991). The shared skeletal structure in
Axociella and Raspailiidae support the contention
that they are monophyletic, belonging to the sub-
order Microcionina (Hajdu et al., 1994).

The well developed felt-like ectosomal spicula-
ion and radial subectosomal spicule tracts in the
peripheral skeleton of C. (A.) canaliculata is vir-
tually at the opposite end of a continuum from
encrusting Microciona-like species (with
membraneous dermal skeletons). These differences
contrast so greatly with species such as C.
(M.) aceratoobtusa that it is tempting to maintain
generic separation between typical Microciona
and Thalysias-like species, but as demonstrated
elsewhere in this work there are too many other microcionid species with intermediate conditions making it impossible to clearly define a generic boundary within this continuum.

*Clathria* (Axociella) *canaliculata* is most closely related to *C. (A.) cylindrica*, with similar growth form, surface characteristics and skeletal structure. However, this species has slightly compressed open-reticulate axis, radial extra-axis, and continuous plumose ectosome, whereas *C. (A.) cylindrica* has a greatly compressed close-meshed axis, a radial extra-axis and a sparse, discontinuous, plumose ectosome. Toxa morphology and spicule size also differ substantially between these two species.

**Clathria (Axociella) cylindrica**

*(Ridley & Dendy, 1886)*

*(Fig. 120-121)*

*Esperiopsis cylindrica* Ridley & Dendy, 1886: 340; Ridley & Dendy, 1887: 79-80, pl.19, figs 2a-b.  
*Axociella cylindrica*; Hallmann, 1920: 780-783, pl.37, figs 2-4, text-fig.2.  
*Clathria cylindrica*; Hooper & Wiedenmayer, 1994: 262.  
Not *Rhaphidophlus cylindricus* Kieschnick, 1900: 53, pl.44, fig.10.

**MATERIAL. HOLOTYPE:** BMNH1887.5.2.96; Off Port Jackson, NSW, 33°51'S, 151°16'E, 60-70m depth, coll. HMS 'Challenger' (dredge). OTHER **MATERIAL:** NSW-AMZ1527.

**HABITAT DISTRIBUTION.** Soft sediments; 40-70m depth; Port Jackson, Botany Bay (NSW) (Fig. 120G).

**DESCRIPTION.** *Shape.* Thin, cylindrical digitate, branching, whip-like, 130-190mm long, 10-20mm diameter, with thin, dichotomously branched, cylindrical or slightly flattened, distally tapering branches, up to 130mm long, 16mm diameter, short stalk and expanded basal attachment.

*Colour.* Grey-brown in ethanol.

*Oscules.* Not seen.

**Texture and surface characteristics.** Firm, flexible, tough consistency; surface even, felt-like, unornamented, prominently hispid.

*Ectosome and subectosome.* Sparse, plumose brushes of small ectosomal auxiliary subtylos- 
tyles form discrete, discontinuous bundles on surface, arising from ends of radial skeletal columns, scattered around the larger, protruding subëctosomal auxiliary styles which project some distance through surface.

*Choansome.* Skeletal structure with clearly differentiated axial and extra-axial components, markedly compressed in axis and radial in extra-axis; compressed axial skeleton with longitudinal fibres cored by short choanosomal principal subtylostles, interconnected by thinner pauci- or aspicular fibres; axial spongin fibres heavy, and fibre anastomoses very close-meshed forming elongate reticulation; mesohyl matrix in axis light with abundant loose auxiliary styles dispersed between and congregated around fibres; echinating megascleres absent; radial extra-axial skeleton with large auxiliary styles perpendicular to axis, forming pauci- or multispecific radial (non-plumose) tracts associated with very light, ascending spongin fibres but very few transverse uni- or aspicular connecting fibres; mesohyl matrix in extra-axial region moderately heavy, with few scattered auxiliary megascleres.

*Megascleres.* Choanosomal principal subtylos- 
tyles coring axial fibres relatively short, slightly curved at centre, with smooth subylote or sometimes evenly rounded bases and fusiform points. Length 215-(311.2)-395μm, width 5-(10.4)-15μm.

Subectosomal auxiliary styles forming extra-axial bundles much longer and thicker than principal spicules, with smooth rounded or tapering (hastate) bases, and fusiform points. Length 424- 
(559.6)-725μm, width 15-(21.0)-29μm.

Ectosomal auxiliary subtylostles straight, variable length, with smooth rounded or slightly subtylote bases and fusiform points. Length 208- 
(361.8)-575μm, width 6-(8.2)-10μm.

*Microscleres.* Palmate isochelae unmodified, differentiated into two size classes, with long lateral alae entirely fused to shaft and completely fused front ala. Length I: 6-(9.3)-13μm; length II: 19- 
(22.3)-25μm.

Toxas oxhorn, thick, with wide central curvature and slightly reflexed points. Length 45- 
(86.2)-130μm, width 2.5-(4.3)-6μm.

**REMARKS.** The chclae and toxa microscleres show that this species belongs to the Microcionidae, whereas skeletal architecture is most closely related to the Raspailiidae (cf *Raspailia* (*Syringella*) and *Ectyoplasia*). Like *C. (A.) canaliculata*, this species lacks echinating megascleres, and this was the primary reason why Hallmann (1920) created *Axociella*. Despite contrary arguments by Van Soest (1984b), *Axociella* is considered sufficiently different from *Thalysias* in skeletal construction to be differentiated at the superspecific level (although not for

the reason that it lacks echinating acanthostyles; Simpson, 1968a). Supporting this interpretation is the fact that a specialised Thalysias ectosomal skeleton is absent in C. (A.) macropora and C. (A.) thetidis. AMZ1133 from the FIV 'Thetis' expedition, although not described by Hallmann (1912), is very close to C. (A.) cylindrica differing only in having echinating acanthostyles and long thin, almost straight rhaphidiform toxas. This material almost certainly represents a new species but its antiquated condition is too poor to serve as the holotype of a new taxon. Clathria (Axociella) cylindrica also shows some similarities to C. (Thalysias) procera in growth form and having well differentiated axial and extra-axial skeletons, but these species differ in most other respects.

Axociella cylindrica of Sim & Byeon (1989) from Korea does not compare to the Australian population, differing markedly in most features, and is referred here to Clathria (Microciona) sinae sp. nov.
Clathria (Axociella) nidificata
(Kirkpatrick, 1907)
(Figs 122-123

Ophitaspanga nidificata Kirkpatrick, 1907: 274;
Kirkpatrick, 1908a: 25, pl.22, fig.6, pl.24, fig.5;
Hallmann, 1912: 254; Burton, 1929a: 433; Burton,
1932a: 324; de Laubenfels, 1936a: 120; de Lauben-
fels, 1954: 162.

Axociella nidificata; Burton, 1940: 116; Koltun,
1964a: 70, pl.12,figs 7-11; Koltun, 1976: 155, 190;
Desqueyroux, 1975: 67-68, pl.4,figs 47-50;

Clathria (Axociella) nidificata; Hooper & Wieden-
mayer, 1994: 263; Mothes & Lerner, 1995: 159-160,
figs 22-27, 55.

Ophitaspanga flabellata Topsent, 1916: 167; Top-
sent, 1917: 41, pl.1, fig.4, pl.6, fig.2; Burton, 1929:
433; Burton, 1932: 325; Burton, 1934b: 34.

Axociella flabellata; Koltun, 1964a: 70-71, pl.12,
figs 12-14; Hoshino, 1977a: 45-46, table 1.

Axociella rameus Koltun,1964a: 71, text-fig.17;

MATERIAL. HOLOTYPE: BMNH1908.2.5. 131:
Coulman I., Victoria Land, Ross Dependency,
Antarctica. 73°30'S, 17°00'E, 200m depth, coll. HMS
‘Discovery’ (dredge).

HABITAT DISTRIBUTION. On hard substrates; 93-
540m depth; Antarctica; BANZARE coast; Budd
Coast, Wilkes Land; Kemp Land, Enderby Land;
Mawson Peninsula, Oates Land; Coulman I., Victoria
Land; Prydz Bay, MacKenzie Bay and Mawson Coast,
MacRobertson Land; King Edward Ice Shelf, Enderby
Land; Joinville and Elefante Is; Palmer Archipelago;
Graham Land; also South Georgia, S. Shetland Is (Fig.
122E).

DESCRIPTION. Shape. Erect, claviform-flabellate,
narrow stalk.

Colour. Yellow-brown in ethanol.

Oscules. Oscules on upper surface of club, 1-
2mm diameter.

Texture and surface characteristics. Texture
compressible, tough, harsh surface; surface
hispid, conulose, membraneous between conules.

Ecotomae and subectosome.

Ecotomal skeleton plumose, composed of discrete bundles of subec-
tosomal auxiliary subostyles perched on ends of
protruding principal spicules, corresponding to
surface conules.

Choanosome. Skeleton compressed in axis and
plumose in extra-axis; axial region slightly com-
pressed containing heavy spongy fibres cored by
plumo-reticulate pauci- or multispicular tracts of
choanosomal principal styles; skeletal tracts form
oval meshes, up to 250µm diameter; extra-axial
tracts plumose, diverging towards periphery, with
pauci- or multispicular tracts of choanosomal
principal styles coring heavy spongy fibres;
styles in peripheral regions of fibres often
protrude from fibres at acute angles, but these are
identical to principal megascleres and cannot be
considered as true echinating spicules; mesohyl
matrix moderately heavy, granular, containing
abundant toxas, often in bundles, and occasional
detritus.

Megascleres. Choanosomal principal styles long,
thick, entirely smooth, slightly curved towards
base, with slightly subtylostyle evenly rounded or
slightly constricted haste bases and fusiform
points. Length 595-(914.7)-1140µm, width 21-
(43.7)-61µm.

Subectosomal auxiliary subostyles short, slen-
der, straight, with slightly subtylostyle microspined bases, fusiform pointed. Length 331-(405.4)-447µm, width 6-(9.4)-12µm.

No echinating spicules.

Microscleres. Chelae absent.

Toxas accolada, thick, variable in length, with
prominent but narrow angular central curvature,
straight arms and straight or slightly reflected tips;
larger toxas with spined tips, small toxas entirely
smooth. Length 98-(286.2)-546µm, width 1.5-
(3.2)-5µm.

REMARKS. The synonymy given above follows
Koltun (1976). The species appears to vary in
growth form, from bushy, branching, reticulate,
digitate to flabellate, but skeletal architecture and
spicule geometry are relatively consistent.
Several echinating acanthostyles were seen in
spicule preparations made from the holotype
(evenly spined, club-shaped, 94-123x5-9µm),
but none were seen in section preparations and it
is presumed that these are contaminants, although
it is possible that they are present but rare.

The specialised ecosomal skeleton of discrete
auxiliary spicule brushes perched over larger
principal spicules, and compressed ‘axinellid’
skeletal construction, are reminiscent of
Raspailiidae (e.g., Aulospongus), and were it not
for the toxas in this species it could be included
in Raspailiidae. This species fits best in Clathria
(Axociella) although it lacks differentiated ec-
tosomal and subectosomal spicules (i.e., it has 1
size class of auxiliary styles). Its toxas and spin-
ination should be compared with C. (A.) georgiae-
sis sp. nov. (see below).

Clathria (Axociella) patula sp. nov.
(Figs 124-125)

MATERIAL. HOLOTYPE: NTM2Z9909: Between
North and East Wallabi Is, Houtman Abrolhos, WA,


HABITAT DISTRIBUTION. Broken limestone reef, usually in sand sediments; 39-85m depth; Carnarvon and Wallabi Is, Houtman Abrolhos (WA) (Fig. 124G).

DESCRIPTION. Shape. Thickly flabellate, palmate-digitate fan, 140-475mm long, 180-310mm
wide, 6-15mm thick, with even apical margin or long, erect flattened digits arising from apex of fan; digits single or planar branching, 40-70mm wide, bifurcated and tapering, with short, thick cylindrical stalk, 35-63mm long, 15-32mm diameter; lateral margins of fans prominently crenellated, apical margins range from slightly crenellated to prominently digitate.

**Colour.** Dark red, red-brown or orange-brown alive (Munsell 5R 5/10 - 10R 7/8), grey-brown in ethanol.

**Oscules.** Small oscules, less than 2mm diameter, scattered over surface.

**Texture and surface characteristics.** Firm, compressible, flexible; surface uneven, rippled, slightly conulose, with few large digitate projections arising at oblique angles from surface in fan specimens.

**Ectosome and subectosome.** Thick plumose or paratangential layer of erect auxiliary styles, usually in thick bundles, forming more-or-less continuous palisade on ectosomal skeleton; subectosomal skeleton with plumose brushes of both subectosomal auxiliary styles and choanosomal principal styles supporting ectosomal palisade, arising directly from choanosomal fibres in peripheral skeleton.

**Choanosome.** Skeletal structure wide-meshed heavily reticulate, slightly compressed axial region and differentiated axial and extra-axial skeletons; axial skeleton composed of heavy spongin fibres, 80-145μm diameter, thickest and bulbous at fibre nodes, 130-200μm diameter, forming relatively wide reticulation of oval or rectangular meshes, 180-360μm diameter; axial fibres cored by both principal styles and subectosomal styles in multispecific brushes of 2-5 spicules; principal spicules also protrude through fibres in plumose bundles, at acute angles, although these cannot be considered as echinating spicules; extra-axial skeleton with wider fibre meshes than axial region, with heavy spongin fibres, 60-120μm diameter, bulbous fibre nodes, 80-140μm diameter, forming elongate or rectangular meshes, 300-470μm diameter, cored by ascending multispecific tracts of intermingled choanosomal principal and subectosomal styles, up to 10 spicules per fibre, and thinner transverse fibres cored by only principal spicules in paucispicular tracts; spicules usually protrude through fibres in plumose bundles, particularly in peripheral skeleton, but true echinating spicules absent; mesohyl matrix heavy but only lightly pigmented, containing abundant microscleres; choanoocyte chambers large, oval, 50-130μm diameter.

**Megascleres.** Choanosomal principal styles variable in length, predominantly long, thick, slightly curved near basal end, evenly rounded smooth

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bases and fusiform points. Length 225-(383.6)-370μm, width 10-(13.2)-15μm.

Subectosomal auxiliary styles long, thinner than principal spicules, straight, with rounded microspined bases, slightly subtylate spined bases, or subtylate smooth bases, and fusiform points. Length 193-(265.2)-303μm, width 5-(7.1)-8μm.

Ectosomal auxiliary styles short, straight or slightly curved near base, relatively thick, with rounded smooth or microspined bases and fusiform points. Length 104-(147.2)-185μm, width 1.5-(3.8)-6μm.

Echinating spicules absent.

**Microscleres.** Palmate isochelae small, unmodified, with lateral and front alae of approximately equal length; lateral alae fused completely to shaft, front ala entire. Length 14-(15.8)-19μm.

**Texta** basically oxhorn, with some intermediate wing-shaped, short, moderately thick, rounded or slightly angular central curvature and slightly reflexed points 57-(69.6)-84μm, width 1-(1.9)-2.5μm.

**ETYMOLOGY.** Latin *patulus*, spread out; for the flat growth form.

**REMARKS.** This species could be included in *C. (Thalysias)*, having a thick tangential ectosomal skeleton composed of two discrete size classes of auxiliary styles, but it is most appropriately placed in *C. (Axociella)* given that it has differentiated axial and extra-axial skeletons and lacks any echinating spicules. *C. (Axociella) patula* has a flabellate, planar growth form similar to *C. (T.) cancellaria*, although these species differ substantially in their spicule geometry (the latter having echinating acanthostyles and accolada textas), different spicule sizes of most categories, and skeletal structures (the latter species with a heavy, evenly reticulate skeleton and abundant echinating acanthostyles).

**Clathria (Axociella) thetidis** (Hallmann, 1920) (Figs 126-127, Plate 4B)


*Clathria thetidis,* Hooper & Wiedenmayer, 1994: 263

*Esperiopsis cylindrica,* in part; Whitelegge, 1906: 470, pl.43,fig.6.

Not *Esperiopsis cylindrica* Ridley & Dendy, 1887: 79.

**MATERIAL.** **LECTOTYPE:** AMG9199: Off Woolongong, NSW, 34°30'S, 151°10'E, 104-142m depth, coll. FIV ‘Theitis’ (dredge). **PARALECOTYPE:** AMG9191: Off Wata Mooli, Bulgo, Woolongong, NSW, 34°30'S, 151°12'E, 98-138m depth, coll. FIV ‘Theitis’ (dredge).

**OUTHER MATERIAL:** NSW- QMG303752. S. AUST-AMZ4624.

**HABITAT DISTRIBUTION.** Deeper offshore reefs; 50-142m depth; Sydney and Woolongong (NSW), SW. Great Australian Bight (SA) (Fig. 126H).

**DESCRIPTION.** Shape. Erect, arborescent or digitate, whip-like growth forms, 190-480mm long, with long thin cylindrical stalk and thinly cylindrical branches, 15-25mm diameter; branching planar or in more than one plane, either irregularly bifurcate or pininate, with evenly dichotomous bifurcations arising from larger, laterally disposed branches; apical margins of digits taper to fine points.

**Colour.** Deep red alive (Munsell 2.5R 5/10), grey-brown when dry.

**Oscules.** Very small, less than 1.5mm diameter, scattered over lateral sides of branches.

**Texture and surface characteristics.** Firm, flexible; surface optically even, velvety, microscopically prominently furry, hispid.

**Ectosome and subectosome.** Ectosome very hispid, with discrete, multispiral plume brushes of larger (extra-axial) principal styles protruding through surface, with sparsely dispersed, tangential or paratangential tracts of subectosomal auxiliary styles in between principal spicules.

**Choanosome.** Skeletal architecture reticulate, with compressed axis and plume extra-axial regions; strong axial compression composed of irregularly reticulate, heavy, large spongin fibres producing oval to elongate meshes, 90-220μm diameter; axial fibres relatively heavy, thick, irregularly anastomosing, with bulbous fibre nodes, cored by comparatively small choanosome styles; axial fibres incompletely differentiated into primary, uni- or paucispiricular, ascending, long, radial fibres, 70-180μm diameter, and secondary, connecting, mostly unpiscular, sometimes bi- or aspicular, short fibres, 58-102μm diameter. Axial and extra-axial skeletons strongly differentiated (cf. Hallmann, 1920), with fibres becoming plume and fibre reticulation more regular towards periphery; extra-axial fibres form elongate-elliptical, wider meshes than axis, 155-510μm diameter; extra-axial fibres diminish in thickness towards peripheral skeleton, whereas coring spicules increase in size and density towards surface; principal styles in both primary and secondary fibres protrude through fibres at oblique angles, in both

the axial and extra-axial regions, but true echinat- ing spicules absent; mesohyl matrix heavy, relatively darkly pigmented; choanocyte chambers paired, oval-elongate, 60-155μm diameter; numerous microscleres and subectosomal auxiliary subtylostyles scattered between fibres. *Megascleres.* Choanosomal principal styles divided into two size categories, both fusiform, thick, long or short, slightly curved, with evenly rounded, smooth bases; smaller size found in axial skeleton (length 180-(246.5)-365μm, width 11-(14.2)-20μm), and larger in extra-axial skeleton (length 377-(608.0)-825μm, width 22-(26.4)-35μm.

Subectosomal auxiliary styles long, thin, fusiform, straight, slightly curved or flexuous, with subtylole, smooth or lightly microspined bases. Length 158-(379.1)-585μm, width 3-(5.8)-8μm.

*Microscleres.* Palmate isochelae abundant, with lateral alae completely attached to shaft and front ala entirely fused. Length 9-(13.4)-16μm.
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Toxas divided into two geometrically different forms: oxoete toxas common, usually found in dragmata dispersed between fibres, long, thin, symmetrical or asymmetrical-sinuous, with slight angular central curvature or completely straight, fusiform points. Length 175-(774.5)-1280µm, width 1.5-(2.4)-5µm; wing-shaped toxas common, thin, with large rounded central curvature, reflexed points. Length 22-(104.4)-168µm, width 1-(2.1)-3.5µm.

REMARKS. This species is not conspecific with Esperiopsis cylindrica Ridley & Dendy as supposed by Whitelegge (1906), having different ectosomal skeletal architecture, spicule geometries and spicule sizes; Hallmann (1920) recognised a new species for Whitelegge's material referring it to Ophitespongia (= Echinoclathria) on the basis that it lacked echinating megascleres; de Laubenfels (1936a) assigned it to Aoxeciella for the same reason. De Laubenfels was correct in this transfer, although not for his stated reason (that it lacked acanthostyles) but because of its compressed skeletal construction, spicule localisation and spicule geometry. Hallmann's tentative placement of C. (A.) thetidis in Echinoclathria was probably also based on comparisons with species such as E. nodosa (Carter) and to a lesser extent E. subhispida (Carter) which, unlike most species of Echinoclathria, have a slightly compressed axial skeleton and plumose, plmo-reticulate or radial extra-axial fibres. However, spiculation and spicule localisation within the skeleton of C. (A.) thetidis is different from all those species. Similarly, in C. (A.) thetidis there are two distinctive size categories of principal megascleres, restricted to either axial or extra-axial fibre skeletons, whereas Echinoclathria have homogeneous principal spicules dispersed throughout all skeletal tracts.

Clathria (Aoxeciella) georgiensis sp.nov. (Figs 128-129)

Ophitespongia thiellei Burton, 1932a: 322, pl.55, fig.8, text-fig.32; Koltun, 1964a: 70.
Aoxeciella thiellei de Laubenfels, 1936a: 113 [note].

HABITAT DISTRIBUTION. On rocks; 18-236m depth range; Wilkes Land, Australian Antarctic Territory (Fig. 128F); also South Georgia, SW. Atlantic.

Oscules. Up to 2mm diameter, scattered over surface, with slightly raised membranous lip. Texture and surface characteristics. Firm, compressible; surface conulose, with meandering ridges producing a clathrous, convoluted mass. Ecitosome and subecitosome. Erect plumose brushes of sparse choanosomal principal styles protruding from peripheral skeletal tracts, and paratangential bundles of subectosomal auxiliary subtylostyles in variable abundance, heavier on ends of surface conules, lighter between conules. Choanosome. Skeletal architecture reticulate, slightly plumo-reticulate near surface, vaguely renieroid reticulate at core; skeleton with differentiated primary ascending spongip fibres cored by multispiracular tracts of choanosomal principal styles, with 3-6 spicules per tract, and lighter transverse connecting fibres containing 1-2 spicules per tract, together producing a slightly renieroid skeleton; no marked differentiation between axial or extra-axial regions; fibre reticulation produces cavernous rectangular or triangular meshes, up to 550µm diameter; true echinating spicules absent although principal spicules protrude through fibres at obtuse angles; mesohyl matrix heavy, slightly granular, with abundant chelae and toxas.
Megascleres. Choanosomal principal styles moderately long, slender, straight or slightly curved at centre, rounded smooth bases, fusiform points. Length 390-(446.6)-518µm, width 14-(17.4)-22µm.
Subectosomal auxiliary subtylostyles short, slender, straight, slightly subtylostyles bases, heavily microspined with large spines, slightly hastate or rounded points. Length 216-(285.2)-348µm, width 5-(7.4)-10µm.
Echinating spicules absent.
Microscleres. Palmate isochelae abundant, relatively small, with lateral and front alae approximately same length, lateral alae fused to shaft, front alae nearly completely detached, virtually no curvature of shaft. Length 9-(13.2)-17µm.
Toxas wing-shaped, thick, variable in length, the thicker ones with wide angular central curvature, curved arms, slightly reflexed points, and terminal spines, thinner ones more sharply curved.

MATERIAL. HOLOTYPE: BMNH 1928.2.15. 219 (fragment AMZ2219); 6.3nm N 89°E to 4nm N 39°E off Jason Light, Cumberland Bay, South Georgia, S. Atlantic, 120-204m depth, RRS 'Discovery', 1928 (otter trawl).

at centre, sharply pointed. Length 28-(107.7)-258 µm, width 0.5-(1.7)-3.5 µm.

REMARKS. This species requires a new name since *C. (Microciona) thielei* (Hentschel, 1912) has seniority. Previous authors could not agree on its generic assignment: Burton (1932a, 1938b) compared *C. (A.) georgiaensis* with *Artemisina*, but the possession of a well-structured, slightly compressed choanosomal skeleton indicates that
placement in Clathria is more appropriate. Based on Burton’s (1932a) description this species was included in Echinoclathria by Hooper & Wiedenmayer (1994), but re-examination of the holotype showed that skeletal structure was not markedly renieroid, there was no difference between principal spicule sizes in the axis and those in the peripheral skeletons, and spicule sizes were magnitudes larger than those found in other Echinoclathria (but much closer to those seen in Axociella). De Laubenfels (1936a) also suggested this species should be included in Axociella although his reasons for doing so are different (i.e., lack of echinating spicules). Kolun (1964a) also made a general comparison between C. (A.) georgianaensis and Ophlitaspongia membranacea Thiele (the latter referred here to Clathria (Thalysias), but this comparison is simply based on similarities in toxa morphology, whereas C. (T.) membranacea has two size classes of auxiliary spicules and true echinating spicules (albiet smooth). Toxa measurements recorded by Burton (1932a) for this species differ substantially from those actually seen in the holotype, but in most other characters his description is an accurate representation of the species.

OTHER SPECIES OF CLATHRIA
(Axociella)

Clathria (Axociella) faurori (Topsent, 1893)
Axosuberites faurori Topsent, 1893a: 179-181, fig.3 [Tadjoura, Gulf of Aden]; de Laubenfels, 1936a: 118.
? Rhaphidophles faurori; Van Soest, 1948a: 130 (possible generic synonymy).

Clathria (Axociella) fromontae sp. nov.
Axosiella toxixenir Bergquist & Fromont, 1988, 117-118, pl.55, figs a-c; Dawson, 1993: 36 [index to fauna].
MATERIAL. HOLOTYPE: NMNZPOR120. New Zealand.
Note: C. toxixenir Topsent, 1925 has seniority.

Clathria (Axociella) lambei (Koltun, 1955)
Microciona lambei Koltun, 1955a: 49, 67, pl.4, fig.5 [Japan and Okhotsk Seas]; Koltun, 1958: 66-67, text-fig.22 [Kuriles]; Koltun, 1959: 183, pl.29, fig.2, text-fig.143 [USSR].
MATERIAL. HOLOTYPE: ZIL, fragment BMNH1932.11.7.67. NW. Pacific, Japan. Note: Koltun (1955a) attributes this species to Burton (1935c) but, it does not appear in that publication.

Clathria (Axociella) macrotoxa Bergquist & Fromont, 1988
Axociella macrotoxa Bergquist & Fromont, 1988: 117, pl.54, figs c-f; Dawson, 1993: 36 [index to fauna].

Clathria (Axociella) multitoxaformis
Bergquist & Fromont, 1988
Axociella multitoxaformis Bergquist & Fromont, 1988: 118-119, pl.55, figs d-f, pl.56. fig.a; Dawson, 1993: 36 [index to fauna].
MATERIAL. HOLOTYPE: NMNZPOR121. New Zealand.

Clathria (Axociella) parva (Levi, 1963)
Clathria parva Levi, 1963: 56-57, text-fig. 64, pl.10D [Cape of Good Hope, South Africa]; Uniz, 1988a: 84-85, pl.21b, text-fig.60 [Namibia].
Not Clathria parva; Sim & Byeon, 1989: 39, pl.4, figs 3-4 [Korea; dubious conspecificity].
MATERIAL. HOLOTYPE: UCT (fragment MNHN'DC612). S and SE Africa.

Clathria (Isociella) Hallmann, 1920

DEFINITION. Relatively homogeneous isodictyal (triangular meshes) and/or renieroid (rectangular meshes), wide-meshed, main skeleton with primary plumose ascending, multiparticulate tracts cored by smooth choanosomal styles, interconnected by secondary, uni- or paucispicular tracts cored by same spicules, and choanosomal spicules sometimes diverging and forming plumose brushes at surface; echinating megascleres absent; choanosomal skeleton with single category of auxiliary spicule, tangential, paratangential. Microscleres palmate-derived isochelae and toxas.

TYPE SPECIES. Clathria macropora, Lendenfeld, 1888: 221 (= Phakellia jacksoniana Dendy, 1897: 236) (by monotypy).

REMARKS. Four species of Isociella are known for the Australian fauna, three from tropical WA, NT and Qld., and one temperate species from NSW. Only one other species is known from New Zealand.

Clathria (Isociella) eccentrica (Burton, 1934)
(Figs 130-131, Table 26, Plate 4A)
Ophlitaspongia eccentrica Burton, 1934a: 560, pls 1,8,9, text-fig.12a.
TABLE 26. Comparison between present and published descriptions of *Clathria (Isociella) eccentrica*. Measurements in μm (N=25).

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Chao nosomal styles</td>
<td>318-464 x 8-22</td>
<td>288-440 x 9.1-18</td>
<td>232-(361.7)-540 x 7-(17.4)-30</td>
<td>276-(343.1)-450 x 11-(19.2)-29</td>
</tr>
<tr>
<td>Subectosomal styles I</td>
<td>298-457 x 3-9.5</td>
<td>300-470 x 5-8</td>
<td>257-(335.6)-440 x 3-(6.8)-13</td>
<td>284-(373.3)-455 x 4-(6.3)-9</td>
</tr>
<tr>
<td>Subectosomal styles II</td>
<td>85-286 x 1.5-5.2</td>
<td>208-220 x 4.0</td>
<td>85-(185.0)-255 x 1-(3.5)-7</td>
<td>141-(191.8)-255 x 2-(3.7)-6</td>
</tr>
<tr>
<td>Chelae</td>
<td>15-19</td>
<td>16-17.5</td>
<td>8-(17.4)-23</td>
<td>13-(17.2)-21</td>
</tr>
<tr>
<td>Toxas</td>
<td>10-334 x 1.5-10</td>
<td>76-270 x 2.5-6.5</td>
<td>16-(148.0)-283 x 1-(5.4)-11</td>
<td>64-(161.2)-292 x 2-(6.0)-11</td>
</tr>
</tbody>
</table>

**HABITAT DISTRIBUTION.** Usually on dead or partially dead favid coral heads, coral rubble, sand and *Halimeda* substrates; most specimens partially sheltered under coral rubble or in crevices; shallow sublittoral distribution; 0-18m depth range; Lizard I. (FNQ), Darwin Harbour, Bynoe Harbour, Trengganu Bay, Port Essington, Cobourg Peninsula (NT) (Fig. 1306); also SE. Indonesia (unpublished data).

**DESCRIPTION.** Shape. Bulbous-digitate, massive or semi-encrusting, with irregularly anastomosing, erect or stoloniferous branches; branches irregularly cylindrical, flattened or bulbous; specimens range from thick encrustations 45mm high, 20-30mm diameter, with few bulbous branches on surface, to massive branching growth forms up to 130mm high, 300mm wide, with branch diameter between 15-40mm.

**Colour.** Dark red (Munsell 5R 3/8), orange-red (5R 6/10), or less commonly bright orange (10R 6/10); pigmentation water miscible, associated with mucous, confined to the ectosomal and subectosomal regions; pigment washed from sponge; subectosomal colouration light brown or beige; grey-brown in ethanol.

**Oscules.** Large, 4-15mm in diameter, on apex of bulbous digits, usually at extremities of branches; oscules with slightly raised membranous lips, collapsing upon dessication and preservation; numerous inhalant pores, 0.5-1.0mm diameter, scattered over entire surface.

**Texture and surface characteristics.** Rubbery, easily compressible, mucous, but tough, difficult to tear; surface porous, membranous, minutely microconulose with protruding fibre nodes from peripheral skeleton, with small ridges and depressions connecting adjacent conules; surface usually silt covered.

**Ectosome and subectosome.** Ectosomal skeleton microscopically hispid, with chao nosomal principal styles protruding up to 300μm from surface, at regular intervals 150-400μm apart, singly or in paucispicular bundles of 2-4 spicules, with peripheral spongin fibres forming projections and enclosing at least basal portion of protruding spicules; subectosomal auxiliary styles form tangential or paratangential tracts at base of peripheral skeleton, interdispersed between choanosomal principal styles of subrenieroid skeleton; auxiliary spicules sparsely dispersed, rarely protruding through surface, composed of 2 sizes of auxiliary styles without regional localisation; peripheral skeleton undifferentiated from choanosomal skeleton, and choanosomal fibres immediately subdermal.

**Choanosome.** Irregular subsidocytic, or in places more regular isodictyal, sometimes renieroid reticulation of moderately light spongin fibres, 30-110μm diameter, without any obvious or consistent differentiation between primary or secondary elements; fibres cored by 1-10 rows of choanosomal principal styles entirely enclosed within fibres, occupying entire fibre diameter; spicules diverge only slightly towards periphery whereas at core of skeleton spicules more evenly dispersed within fibres; echinating megascleres absent; fibre anastomoses form irregular, elongate-oval, triangular or sometimes regularly rectangular meshes, 250-850μm diameter; mesohyl matrix light, granular, with abundant microscleres and auxiliary spicules; collagen heaviest at fibre nodes but sparse elsewhere; choanoocyte chambers oval or elongate, 60-150μm diameter.

**Megascleres** (Table 26). Choanosomal principal styles straight or slightly curved near base, with smooth rounded or very slightly subtyloate bases, fusiform points.

Subectosomal auxiliary subtylostyles thin, usually straight, either with slightly subtyloate or
rounded bases, and microspined or smooth bases in approximately equal proportions, and with fusiform points; 2 size categories recognised, although undifferentiated in distribution.

Echinating spicules absent. Microscleres (Table 26). Palmae isochelae abundant, relatively large, unmodified, with long lateral alae completely fused to shaft and entirely fused front ala.

Wing-shaped toxas variable length, relatively thick, with moderate, rounded central curvature, slightly reflexed or straight points; some oxoate toxas also present but rare; toxas frequently occur in dragmatata within mesohyl.

Associations. Sometimes smothering live favid coral heads, produced localised bleaching and necrosis of coral tissues at the point of contact with sponge; probable that this species involved in chemical bioerosion of coralline substrate; most specimens (81%) contained scyllid polychaete worms.

Morphological variation. In growth form, live colouration, surface features, skeletal construction and spiculate geometry this species shows very little apparent variation. Some variation observed for: Detritus incorporated into ectsomal skeleton: abundant (33%), lightly dispersed particles (24%), entirely clear of detritus (43% of specimens). Ectosomal skeleton: strictly tangential (43%), disorganised paratangential (33%), or with both structures on different parts of the surface (24% of specimens). Choanosomal skeleton: characteristically subsidical (82%), regularly isodictyal (9%), or regular renieroid construction (9% of specimens). Fibre meshes: cavernous (86%), or close-meshed skeletal reticulation (14% of specimens). Mesohyl matrix: relatively heavy, darkly pigmented (19%), heavy, lightly pigmented (57%), or very light, unpigmented (24% of specimens). Detritus incorporated into mesohyl: seen in only 14% of specimens. Abundance of microscleres: very abundant in tracts or irregularly dispersed throughout the mesohyl (67%), or uncommon (33% of specimens). Auxiliary styles dispersed between fibres within mesohyl: numerous (43%), moderate (19%) or sparse extra-fibre tracts (38% of specimens). Spicule dimensions: spicule dimensions varied considerably between specimens, but this variation was not explained by either geographic distribution or seasonality of collections.

REMARKS. This species is a distinctive component of the tropical Australian intertidal fauna, although it is only known from two disjunct locali-

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Phakellia flabellata Ridley & Dendy, 1886: 478; Ridley & Dendy, 1887: 171, pl.34, figs 2-3, pl.40, fig.6 [preocc.]

Not Phakellia flabellata Carner, 1885f: 363.

Clathria macropora, in part, Lendenfeld, 1888: 221;

Hallmann, 1920: 768; Bergquist & Fromont, 1988:


Not Pleistias macropora Lendenfeld, 1888: 226;


Not Clathria macropora; Whitelegge, 1901;

Not Wilsonella macropora; Hallmann, 1912: 203, 240, 242, 205.

Not Plumohalichondria australis Whitelegge, 1901;

Isoscleria flabellata; Hallmann, 1920: 784-789, pl.39,

figs 1-2, pl.40, fig.1, text-fig.3.

Phakellia jacksoniana Dendy, 1897: 236; Whitelegge, 1907: 507.


MATERIAL. HOLOTYPE: AMZ466: Port Stephens, NSW, 32°42'S, 152°06'E, no other details known (label 'Clathria macropora Lend.; type'). LECTOTYPE of P. jacksoniana: BMNH1887.5.2.9: Port Jackson, NSW, 33°51'S, 151°16'E, 54-90m depth, coll. HMS 'Challenger' (dredge). PARALECTOTYPE of
P. jacksoniana: BMNH 1887.5.2.8: same locality. OTHER MATERIAL: VIC - AMZ771.

HABITAT DISTRIBUTION. Subtidal rock reef to deeper offshore reefs, in soft sediments; 12-90m depth; known only from Australia: Port Stephens, Port Jackson (NSW), Port Phillip (Vic) (Fig. 132E).

DESCRIPTION. Shape. Irregularly flabellate-digitate or flabellate, planar, 85-170mm long, 55-105mm maximum breadth, with short cylindrical stalk 15-25mm long, 7-15mm diameter, one or more thinly lobate, bifurcated branches, up to 8mm thick, either free or fused to adjacent branches, with rounded, digitate, uneven or shaggy margins.

Colour. Yellow-grey or brown in ethanol. Oscules. Oscules small, 1-3mm diameter, in special areas (seive-plates) scattered over surface of branches, with series of stellate subdernal drainage canals surrounding each osculum.

Texture and surface characteristics. Firm, flexible; branches with separate inhalant and exhalant faces; one surface porous, rugose, with irregular longitudinal ridges, microconules or irregular striations; other surface relatively smooth, membranous.

Ectosome and subectosome. Ectosome membranous, hispid, with points of choanosomal principal styles protruding through surface, individually or in multispiculate plumeous bundles; surface skeleton with relatively sparse tangential, paratangential or sometimes plumeous erect skeleton of small subectosomal auxiliary styles projecting between principal spicules, sometimes surrounding (in proximity to) principal spicules reminiscent of Raspailiidae.

Choanosome. Choanosomal skeleton with very slightly compressed axis and plumeous sub-isodictyal, sometimes renieroid extra-axis. Axial region with moderately heavy spongic fibres, forming tight irregularly reticulate meshes cored by paucispicular tracts of choanosomal principal styles; axis (corresponding to central lamelleae and basal stalk) has few ascending, primary tracts, forming multispicular, halichondroid structures, 250-400μm diameter, producing few multispicular, dendritic tracts running from basal stalk to periphery, 50-150μm diameter; extra-axial skeleton sub-isodictyal with plumeose-spicule tracts bound by collagen (without fibre component), ascending to surface, cored by uni-, pauci- or less frequently multispicular tracts of choanosomal principal styles; primary ascending extra-axial spicule tracts (up to 5 spicules side-by-side) arise perpendicular to axis, interconnected by more-or-less transversely orientated, smaller secondary uni- or paucispicular tracts producing predominantly subisodictyal structure; peripheral spicule tracts more plumeous than deeper choanosomal tracts; meshes produced by spicule-fibre anastomoses in extra-axial region triangular or rectangular in shape, 280-560μm diameter; echinating acanthostyles absent; mesohyl matrix contains abundant relatively heavily pigmented spongion, with moderate quantities of auxiliary spicules, and choanocyte chambers oval, 50-198μm diameter.

Megascleres (Table 27). Choanosomal principal styles long or short, thick, slightly curved at centre, less often straight, with rounded or slightly tapering, smooth bases, varying from fusiform to hastate points.

Subectosomal auxiliary styles variable in length, thin, straight or very slightly curved, with basal terminations varying from evenly rounded, tapering hastate, quasi-diactinal micrurate or slightly subtyloate, and with hastate points.

Echinating spicules absent.

Microscleres (Table 27). Palmate isochelae with highly modified, relatively small alae bearing wing-shaped fluted processes; lateral alae entirely fused to shaft; front ala complete or bifurcated with medial tooth; chelae frequently twisted or occasionally anisochelate.

Toxas absent.

REMARKS. The synonymy of C. macropora and P. jacksoniana is obvious on type material, but virtually impossible to tell from published descriptions, so the synonymy was overlooked by Hooper & Wiedenmayer (1994). In nearly all
features type material of both species is identical although auxiliary spicules in *macropora* are relatively larger.

The name *macropora* is the senior name. Ridley & Dendy’s (1886) *flabellata* is a junior homonym of Carter’s (1885) species, and Dendy’s (1897) replacement *jacksoniana* now considered to be redundant. Unfortunately *macropora* requires further clarification given that it has been misused and misinterpreted. My interpretation of *macropora* is based solely on the holotype because despite Hallmann’s (1912: 166) arguments in defense of Lendenfeld’s systematics, there is no doubt that Lendenfeld was dealing mainly with specimens which did not belong to the Microcionidae. *Clathria macropora* is nothing like *Plectispa macropora* (sensu Lendenfeld, 1888; holotype AMG9159), which has smooth echinulating spicules, identical to those coring fibres, and is referred here to *Holopsamma*. *Clathria macropora* Lendenfeld (1888) (AMZ959) from Port Jackson, NSW and *C. macropora* from Port Chalmers, Qld (BMNH 1950.2.12.60) are specimens of *Crella incrustans* (Ceriidae). Three other specimens in the AM collections bearing the name ‘*macropora*’: one specimen from Nelson Bay, New Zealand collected by Arthur Dendy (AM unreg.) is a *Crella* with an ectosomal crust similar to *C. levis var. digitata* (AMZ454) (= *C. incrustans*); another (AMZ4035) collected from Dee Why, Sydney (RRMPFN1338) and the third (AMZ4187 (RRMPFN1428)) from ‘Tumbledown’, Jibbon Head, NSW, both from the Roche Collection, are haplosclerid sponges with three dimensional ectosomal skeletons, probably related to *Amphimedon* (Niphatidae).

This taxon was not among several hundreds of specimens from subtidal and deeper water in Port Jackson, Port Stephens and the adjacent coastline (collected by the NSW Environmental Protection Authority and Sydney Water Board benthic monitoring surveys). It is also doubtful that it occurs in New Zealand, as Bergquist & Fromont (1988) questioned Lendenfeld’s (1888) record given that it was not subsequently rediscovered during their substantial contemporary collections of the NZ fauna. This is confirmed here from re-examination of Lendenfeld’s voucher specimen from Nelson Bay, NZ (mentioned above), which belongs to *Crella*.

*Clathria (Isociella) macropora* has distinctive fluting on the teeth isochelae. This feature is barely visible under light microscopy, and therefore it is possible that it may also occur in other species of *Clathria*, which have not yet been studied using SEM, but apparently it is unique to the family. The species also has a slightly compressed axial skeleton partially offset from the diverging plumose, subisodictyal reticulate extra-axial skeleton, showing vague structural similarities to *Ceratopanion* and *Raspailia* (*Syringella*) (*Raspailiidae*). This skeletal structure could also justify its inclusion in *C. (Axociella)*, but it is considered here that the subsidiotyal reticulation dominates the skeleton and is more characteristic of *Isociella* than *Axociella*.

*Clathria (Isociella) selachia* sp. nov. (Figs 134-135, Plate 3F)

**MATERIAL.** HOLOTYPE: NTMZ2946; E. side of Steep Point Lighthouse, South Passage, Dirk Hartog I., Shark Bay, WA, 26°08.5’S, 113°10.3’E, 13.vii.1987, 7m depth, coll. J.N.A. Hooper (SCUBA). PARATYPE: QMG300562: same data.

**HABITAT DISTRIBUTION.** Encrusting on excavated limestone plates, in surge zone; 7m depth; central W coast (WA) (Fig. 134E).

**DESCRIPTION.** Shape. Massively encrusting, bulbous lobate-digitate, holotype 155mm wide, 105mm high, paratype 65mm wide, 60mm high, with thickly flabellate, slightly flattened lobes, up to 55mm thick, 110mm long, mostly fused to adjacent lobes, together forming a bulbous mass. *Colour*. Bright red-orange alive (Munsell 10R 6/10), grey-brown in ethanol. *Oscules*. Large, up to 8mm diameter, clustered on tops of bulbous lobes or on margins of flattened lobes, slightly raised above surface with membranous lip. *Texture and surface characteristics*. Firm, compressible, moderately difficult to tear; surface fleshy, bulbous, slightly microconulose, membranous *in situ*, with membrane collapsing upon preservation producing fibrous, reticulate, porous, prominently conulose, shaggy surface. *Ectosome and subectosome*. Ectosome membranous, slightly hispid from protruding choanosomal spicule tracts, with relatively thick paratangential or tangential skeleton of subectosomal auxiliary subtylostyles in multispecific tracts; ectosomal skeleton thickest at apex of surface microconules, perched on ends of ascending choanosomal skeletal tracts.

*Choanosome*. Choanosomal skeleton plumo-reticulate, subisodictyal and subrenieroid, with differentiated primary ascending and secondary transverse spongin fibres and spicule tracts; primary ascending fibres well developed, 65-

120μm diameter, cored by multispicular tracts of larger choanosomal principal subtylostyles, 3-15 spicules per tracts; spicules not occupying entire fibre diameter; primary fibres bifurcate repeatedly, but anastomose only occasionally, producing prominent plumose structure most noticeable at periphery; principal subtylostyles mainly form axial core of spicules but sometimes they protrude through primary fibres producing plumose brushes; primary fibres interconnected at more-or-less regular intervals by well developed uni- or paucispicular spongin fibres, 20-45μm diameter, cored by principal subtylostyles, forming triangular, rectangular or oval meshes, 90-180μm diameter; skeleton slightly more cavernous near periphery, more plumose in structure; fibres heaviest in axis, more subsodicidal in structure; echinating megascleres absent; mesohyl matrix light, nearly unpigmented, with many smaller auxiliary subtylostyles and isochelae dispersed between fibres; generally spicules dispersed between fibres more slender,

Microscleres. Isochelae anchorate-like, with slightly to greatly curved shaft, variable alae development from vestigial, tooth-like producing ungiffurous chelae, to spatulate, fused forming lobate alae; lateral alae detached from shaft; front alae incompletely fused to adjacent alae; distal portions of shaft with lateral ridge. Length 26-(31.2)-34μm. Toxas absent.

ETYMOLOGY. Greek selachos, shark, for Shark Bay, WA.

REMARKS. This species belongs to Clathria, based on its spiculation, choanosomal skeletal structure, ectosomal skeleton and fibre characteristics. It is assigned here to C. (Isociella) given its prominent subisodictyal skeleton, most obvious in the axial region, and lack of echinating spicules. It differs from other Isociella in having a predominantly plumo-reticulate skeleton in the peripheral region (although subisodictyal in the axis) and in its spicule dimensions.

When this species was first examined it was considered that the anchorate-like isochelae described above might be contaminants from another sponge or from the substrate upon which it grew. But numerous histological preparations made from the holotype, from various regions within the sponge, repeatedly turned up these chelae. Furthermore, examination of chelae in situ found them to be scattered both within the surface skeleton, intermingled with the paratangential bundles of auxiliary spicules, and also surrounding choanocyte chambers within the choanosomal mesohyl. They are native to this species, although this is at odds with the current hypothesis concerning the derivation and evolutionary significance of these spicules (Hajdu et al., 1994).

The holotype and paratype were found growing side by side and are probably clones of the same individual.
Revised of Microcionidae

Clathria (Isociella) skia sp. nov.

(Figs 136-137, Table 28)


Habitat Distribution. Attached to shell fragments or coral rubble, in soft sediments; 33-40m depth; Cairns region (NEQ), Gladstone region (MEQ) (Fig. 136F).

Description. Shape. Erect, bulbous-lobate digitate, clathrous sponge, 45-95mm long, 18-35mm diameter, with irregularly and closely anastomosing digits, rounded and irregular margins, branches 8-18mm diameter.

Colour. Live colouration unknown, dark brown in ethanol.

Oscules. Not observed.

Texture and Surface Characteristics. Firm, compressible; surface macroscopically even, microscopically conulose, hispid, with subectosomal striations.

Ectosome and Subectosome. Ectosome with specialised skeleton composed of smaller auxiliary subtylostyles, forming sparse multispicular bundles on surface, arising directly from heavy, darkly pigmented peripheral fibres; tips of primary spongins fibres in peripheral region protrude through surface, producing surface microconules up to 300μm long; majority of peripheral fibres nearly tangential, forming irregular reticulate meshes, cored by multispicular tracts of larger auxiliary spicules (6-10 spicules per tract).

Choanosome. Skeletal architecture is irregularly isodictyal and renicroid reticulate, with clearly differentiated primary, ascending fibres, 60-125μm diameter, cored by pauci- or multispicular fibres of larger auxiliary subtylostyes, up to 8 spicules abreast, interconnected by secondary, transverse, regular or irregular, uni- or pauci- spicular fibres (22-48μm diameter). Spongins fibres heavy; echinating spicules absent, although coring megascleres may protrude through fibres at oblique angles, becoming more plumose towards periphery; fibre anastomoses produce triangular, rectangular or oval meshes, 190-425μm in diameter, becoming more regular near periphery; mesohyl matrix heavy, darkly pigmented, and many scattered auxiliary subtylostyes dispersed between fibres; choanoocyte chambers small, oval, 40-85μm diameter.

Megascleres (Table 28). Principal spicules absent.

Auxiliary subtylostyes (coring fibres) long, slender, invariably straight, with prominent, smooth subtylole bases and fusiform points.
Ectosomal auxiliary subtylostyles significantly smaller than coring spicules but otherwise of identical geometry.

Echinating spicules absent. 

**Microscleres** (Table 28). Palmate isosciella uncommon, unmodified, with long lateral alae entirely fused to shaft and front ala completely fused, slightly spatulate.

Toxas raphidiform, extremely thin, slightly curved at centre, sometimes nearly straight or bow shaped, rarely asymmetrical.

**ETYMOLOGY.** Greek *skias*, dark, dim.

**REMARKS.** This species is a greatly reduced *Clathria*, lacking true principal spicules, echinating spicules and having containing relatively sparse microscleres. Conversely its spongion fibre system is well developed and fibres are heavy. It is assigned to the *Isosciella* group on the basis that its skeletal structure is essentially subsidictyal, and it lacks echinating spicules, but it is admitted that its reduced characteristics make its true affinities speculative.

The sparsely developed ectosomal skeleton, composed of plumose bundles of smaller auxiliary styles, also indicates affinities to the *Thalysias* group, but in most respects (spicule geometry, skeletal structure, fibre development and growth form) it differs from all other species of either *Isosciella* and *Thalysias*. *Clathria (Isosciella) skia* was initially thought to be *Amphilectus hispidulus* Ridley, from Torres Strait (FNQ). From both published descriptions of *A. hispidulus* (Ridley, 1884a; Hentschel, 1911) it apparently lacked echinating megascleres, lacked principal spicules and had well developed subsidictyal skeletal structure, but re-examination of the holotype showed that it does have echinating acanthostyles, and differentiated principal and auxiliary megascleres (thus more appropriately included in *Clathria* (*Clathria*); see above), and it also has substantially different fibre characteristics from *C. (L.) skia* indicating that they are not conspecific.

**OTHER SPECIES OF CLATHRIA (ISOCIELLA)**

**Clathria (Isosciella) incrustans** (Bergquist, 1961)


**MATERIAL.** **HOLOTYPE:** NMNZ unregistered. NZ.

**TABLE 28.** Comparison between of *Clathria (Isisciella) skia* sp.nov. Measurements in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (QMG300449)</th>
<th>Paratype (AMG5043)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Auxiliary (coring) styles</td>
<td>162-(248.4)-368 x 2.5-(4.5)-8</td>
<td>154-(242.1)-318 x 2-(4.1)-6</td>
</tr>
<tr>
<td>Auxiliary (ectosomal) styles</td>
<td>97-(111.9)-129 x 1.5-(2.4)-4</td>
<td>87-(110.2)-132 x 1.5-(2.4)-4</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Chelae</td>
<td>9-(15.3)-18</td>
<td>14-(16.3)-19</td>
</tr>
<tr>
<td>Toxas</td>
<td>72-(104.4)-145 x 0.2-(0.4)-0.8</td>
<td>65-(81.1)-108 x 0.2-(0.5)-0.8</td>
</tr>
</tbody>
</table>

**Clathria (Thalysias)** Duchassaing & Michelotti, 1864

*Thalysias* Duchassaing & Michelotti, 1864: 82. 
*Rhaphidophillus* Ehlers, 1870: 19. 
*Tenacia* Schmidt, 1870: 56. 
*Echinonema* Carter, 1881a: 378. 
*Stylo telopsis* Thiele, 1905: 456; de Laubenfels, 1936a: 112. 
*Colloclathria* Dendy, 1922: 74. 
*Damosent* de Laubenfels, 1936a: 110.

**DEFINITION.** Specialised ectosomal skeleton composed of two size classes of auxiliary (subtylo)styles, with smaller ectosomal spicules usually overlaying larger subectosomal ones forming a continuous palisade, or discrete bundles, mainly erect, sometimes paratangential, or rarely tangential to surface; choanosomal skeleton without any marked differentiation between axial and extra-axial regions; echinating acanthostyles usually present.

**TYPE SPECIES.** *Spongia juniperina* Lamarck, 1814: 444 (by synonymy).

**REMARKS.** Of 137 named species described in, or referred to *Thalysias* or one of its synonyms, 93 are thought to be valid of which 37 are recorded here from Australian waters including 10 new species.

**Clathria (Thalysias) abietina** (Lamarck, 1814) (Figs 138-141, Tables 29-30, Plate 4C-D)

*Spongia abietina* Lamarck, 1814: 450, 377. 
**Clathria aculeata** Ridley, 1884a: 443-444, pl.40, fig.1, pl.42, fig.k; Ridley & Dendy, 1887: 147, 246, 254; Topson, 1897b: 447; Burton, 1934a: 558; Burton, 1959a: 243; Lévi & Lévi, 1989: 80-81, pl.7, fig.3.

**Rhaphidophlus aculeatus** Topson, 1932: 115, pl.4, fig.10; Vacelet & Vasseau, 1977: 114; Vacelet et al., 1976: 73-74.


**Microciona prolifera**; Vosmaer, 1935a: 610, 633, 664.

**MATERIAL.** LECTOTYPE: MNHN D634; preess locality unknown (suspected to be 'Australia'; Topson (1932: 115)). PARALECTOTYPES: MNHN D334; same details.

**HOLOTYPE of** C. aculeata: BMNH 1882.2.23. 2358. Torres Strait, Qld, 9°41'S, 1°2-17'E, 6-8m depth, coll. HMS 'Alert' (dredge). OTHER MATERIAL. MICRONESIA - USNM 22808, USNM 23090. QLD - BMNH 1887.5.2.110, QMG 300791.

**HABITAT DISTRIBUTION.** Shallow-water 0-25m depth, predominantly on sides and tops of rock and dead coral heads, invariably exposed to currents. Deeper-water specimens (26-86m depth) mostly associated with exposed rock substrates in gravel, silt or shell-grit substrates; central SW Pacific Ocean (Low Isles, Great Barrier Reef (Burton, 1934a); Torres Strait (Ridley, 1884a; Ridley & Dendy, 1887)); E Indian Ocean (Arafura Sea, Timor Sea, mid-WA coast (present study)); also tropical Indo-west Pacific; central NW Pacific Ocean (Marshall and Caroline Is (de Laubenfels, 1954), Philippines (Lévi & Lévi, 1989)); W Indian Ocean (Madagascar (Vacelet et al., 1976, 1977), Red Sea (Burton, 1959a)). Within Australian waters this species extends across the N and NW coasts, from the Cairns region, Torres Strait and Gulf of Carpentaria, Qld, to the Exmouth Gulf region, WA (Fig. 138J). It is only rarely encountered on the E Qld. coast and must be considered a predominantly Indian Ocean species.

**DESCRIPTION.** Shape. Arborose; thickly cylindrical digitate branches on long or short, thick stalk (3-21mm basal diameter) with expanded basal attachment, never rhizomous; branches rarely anastomosing, branching mostly irregular, bushy, occasionally regular growing in 1 plane, sometimes flagelliform, occasionally expanded, club-shaped; total length and branch diameter variable (50-460mm; 2-22mm, respectively).

**Colour.** Live colouration highly variable, ranging from maroon, red, orange, yellow, brown to grey; colour in ethanol ranges from black, brown to grey (Munsell values given below); pigments oxidise in air; maroon colouration is highly alcohol soluble; yellow pigmentation more stable in ethanol but easily scratched from surface of living sponge, leaving a maroon or mauve pigmentation beneath; pigmentation extends into periphery of chonosomal mesohyl.

**Oscules.** Exhalent pores usually very small, 0.6-2.0mm diameter, barely visible opically, dispersed on distal ends of branches surrounded by surface conules; occasionally scattered along entire lateral margins of branches.

**Texture and surface characteristics.** Firm, barely compressible; branches rubbery whereas stalk more rigid; surface dense, entirely opaque in life, with characteristic regularly scattered surface conules; conules tapering, distally rounded or blunt, usually absent from basal and distal extremities of branches, 2-6mm maximum basal diameter.

**Ectosome and subectosome.** Very dense, continuous palisade of small ectosomal auxiliary subtylosyles forming discrete brushes overlay-
ing thickly plumose tracts of larger subectosomal auxiliary subtylostyles in peripheral skeleton (the latter often obscuring ectosomal brushes); subectosomal spicule tracts arise from ultimate choanosomal fibres, intermingled with tufts of principal choanosomal subtylostyles echinating peripheral fibres; principal spicules not extending into ectosomal skeleton; mesohyl matrix heavy and pigmented in both ectosomal and subectosomal regions.

**Choanosome.** Skeleton irregularly reticulate; heavy sponglin fibres, 50-125 \( \mu \)m diameter, heavily anastomosing, not divided into primary or secondary elements but forming irregular, close-meshed reticulation; fibre meshes oval to elliptical, 100-350 \( \mu \)m diameter; fibres cored by multispecific tracts of larger auxiliary subtylostyles occupying 60-80% of fibre diameter; choanosomal principal subtylostyle uncommon within fibres, mainly found at fibre nodes protruding through fibres individually or in bundles; fibres also echinated by acanthostyles especially on peripheral fibres; mesohyl matrix heavy but only lightly pigmented, slightly granular; choanocyte chambers oval or elliptical,
TABLE 29. Comparison in range of spicule dimensions between present and published records of Clathria (Thalysias) abietina. All measurements are given in μm and denoted as length x width (N=25).

<table>
<thead>
<tr>
<th>CLASS</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>principal styles</td>
<td>165-258 x 9-16</td>
<td>230</td>
<td>172-254 x 12.7</td>
<td>172-254</td>
<td>270-320 x 6-15</td>
</tr>
<tr>
<td>subectosomal styles</td>
<td>157-343 x 5-10</td>
<td>350 x 8.5</td>
<td>149-276 x 2-5</td>
<td>120-250 x 2-3</td>
<td>127-387 x 1-20</td>
</tr>
<tr>
<td>ectosomal styles</td>
<td>62-132 x 2-5</td>
<td>81-117 x 2-4</td>
<td>45-230 x 1-10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>61-94 x 4-10</td>
<td>90 x 7.9</td>
<td>53-74 x 4-6</td>
<td>50-70 x 7-8</td>
<td>41-109 x 1-19</td>
</tr>
<tr>
<td>Chelae I</td>
<td>11-15</td>
<td>12.7</td>
<td>10-14</td>
<td>10-15</td>
<td>8-20</td>
</tr>
<tr>
<td>Chelae II</td>
<td>4-6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1-10</td>
</tr>
<tr>
<td>toxas</td>
<td>13-180</td>
<td>63</td>
<td>91-210</td>
<td>45-55</td>
<td>3-345</td>
</tr>
</tbody>
</table>

Material:
1. Spongia abietina - holotype MNHN DT634.
2. Clathria aculeata - Ridley (1884a: 443).
5. Present material (N=25).

40-170μm diameter; larger auxiliary styles also dispersed between fibres in disorganised tracts. Megascleres. Choanosomal principal styles—subtylostyles usually uncommon, short, stout, slightly curved at centre or near base, occasionally straight, with slightly subtylo bases or evenly rounded bases; spicules usually completely smooth, exceptionally with minutely microspined bases, tapering to abruptly (hastate) sharp points. Length 121-(202.7)-300.5μm, width 5-(14.4)-24μm (lectotype 165-(215.5)-258μm x 9.5-(14.3)-15.5μm).

Subectosomal auxiliary subtylostyles straight or slightly curved near base, with prominent subtylo, usually microspined bases, tapering to fusiform points. Length 127-(258.4)-386.9μm, width 1.1-(8.2)-20.1μm (lectotype 157-(274.4)-343μm x 5-(6.7)-10μm).

Ectosomal auxiliary subtylostyles short, thin, invariably straight, with prominently subtylo, typically microspined bases, tapering to fusiform points. Length 44.8-(114.6)-230μm, width 1.1-(3.8)-10.1μm (lectotype 62-(85.5)-132 x 2-(3.4)-5μm).

Echinating acahanthostyles moderately long, thick, straight, with prominently subtylo, spinous base, virtually aspinose 'neck' (proximal to base), and lightly spined shaft; spines relatively large. Length 40.6-(82.4)-109μm, width 1.1-(7.5)-19μm (lectotype 61-(74.4)-94 x 4-(6.5)-10μm).

Microscleres. Palmate isochelae with long lateral alae completely fused to shaft, shorter entire front alae; two size categories present, both relatively abundant, both with examples of contort shafts (more abundant in smaller form). Length I: 7.9-(12.1)-19.9μm (lectotype 11-(12.5)-14.5μm), length II: 0.5-((5.8)-10μm (lectotype 4-(5)-6μm).

Toxas relatively uncommon with 2 geometric forms; (i) wing-shaped, short, thin, generally curved at central with reflected points; (ii) accolada toxas long, thin almost straight with small angular central curvature and straight points. Length I: 5-(24.9)-75μm, width 1.8-(2.4)-4.1μm (lectotype 3.5).---

Larvae. Parenchymella larvae observed in peripheral choanosomal skeleton of about 20 specimens, predominantly during the tropical wet season (February-April) and less so during the pre-dry season (May-July). Larval incubation was distinctly seasonal and occurred more or less evenly throughout the population (i.e., irrespective of depth of collection; Fig. 141). Larvae were 600-950μm diameter, elongate-oval in shape and many contained larval megascleres; cilia were not observed (preserved material).

Associations. 3% of specimens had filamentous algal coring fibres in addition to longer auxiliary megascleres.

Variation. Highly variable in live colouration, non-fibre skeletal development, megasclere size, relatively consistent in growth form, surface features, fibre skeleton, spicule geometry. Gross morphology: stalked, bushy, branching in more than 1 plane, branches bifurcate, occasionally anastomosing (46%), planar branching (33%), dendritic planar branching (fans) (14%), or single digits with no or few bifurcations (7% of specimens). Atypical growth forms (few surface conules, few branches, thin branching) found predominantly in deeper offshore coastal waters (40m depth). Live colouration: highly variable, no particular pigment considered to be typical, ranging from (i) maroon, evenly pigmentation (Munsell 5R4/10-2.5R4/8-10), (ii) red-maroon, even (5R5/8-10), (iii) bright red-orange, even

(5R5/12), (iv) bright orange, even (10R5/12-10R6/10-12-10R7/10), (v) orange-brown, even (10R4/8-10), (vi) orange-yellow, even (7.5YR7/12), (vii) pale brown-pink, even (10R7/4), (viii) light brown, with pink conules (10R7/4, 5R8/4), (ix) light brown, with dark grey-brown conules (2.5YR7/4-5YR7/2-6, 2.5YR6/6-5YR3-5/2), (x) pale brown, even (5YR6/6-5YR7/4-6-5YR8/4), (xi) muddy grey, even (7.5YR7/2-8/2) (xii) yellowish grey, even (2.5Y8/6), (xiii) yellow, even (2.5Y7/8), (xiv) yellow, with pink conules (2.5Y8/6, 10R7/6), (xv) lime-yellow, with dark brown conules (2.5Y7/10, 2.5Y5/2), (xvi) yellow-green mottle (5Y8/12). No obvious relationship between live colouration and depth or substrate type from present data; moreover, specimens with widely different pigmentation observed growing side-by-side (Plate 4D). Subectosomal skeletal development: correlation between branch diameter and extent of development of peripheral skeleton, with 8% of specimens (all thinly
TABLE 30. Summary of results from one-way ANOVA's (Model I), testing for variability in spicule lengths and widths between locality, bathymetric and seasonal distributions of *Clathria (Thalysias) abietina*.

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>LOCALITY</th>
<th>DEPTH²</th>
<th>SEASON¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N)</td>
<td>F</td>
<td>Prob.</td>
</tr>
<tr>
<td>Choaonosomal styles L</td>
<td>(1950)</td>
<td>3.31</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>W</td>
<td>(1950)</td>
<td>0.54</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Subectosomal styles L</td>
<td>(1950)</td>
<td>6.21</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>W</td>
<td>(1950)</td>
<td>1.89</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Ectosomal styles L</td>
<td>(1950)</td>
<td>0.85</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>W</td>
<td>(1950)</td>
<td>0.77</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Acanthostyles L</td>
<td>(1950)</td>
<td>4.74</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>W</td>
<td>(1950)</td>
<td>3.17</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>Chelae I L</td>
<td>(1925)</td>
<td>0.48</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Chelae II L</td>
<td>(1925)</td>
<td>0.14</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Toxas L</td>
<td>(1925)</td>
<td>0.39</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>W</td>
<td>(1925)</td>
<td>0.42</td>
<td>P&gt;0.05</td>
</tr>
</tbody>
</table>

Number of groups:
1. 3 locality groups (NWS, DAR, CP localities).
2. 4 depth groups (0-4m, 4-10m, 10-40m, 40m depth).
3. 4 seasonal groups (Darwin region only: wet (FMA), pre-dry (MJJ), dry (ASO), pre-wet (NDJ)).

branching) having peripheral choaonosomal fibres lying immediately below ectsosomal crust, thin paratangential subectosomal region, and acanthostyles echinating peripheral fibres piercing ectsosomal skeleton. Development of extra-fibre skeleton: 4% with very abundant juvenile auxiliary subtylostyles distributed throughout mesohyl, 90% with at least some interstitial auxiliary spicules, and 6% of specimens without any interstitial auxiliary spicules dispersed between fibres. Megasclere geometry: Principal spicules range from relatively common (21%), uncommon (61%), or very rare (18% of specimens). Bases of all principal spicules smooth (79%), or up to one-quarter of principal spicules with microspined bases (21% of specimens). Larger auxiliary spicules predominantly subtylote with minutely microspined bases, but 0-74% of spicules may be smooth in any particular specimen. Acanthostyle geometry relatively consistent, although in 5% of specimens two size categories were recognised (although smaller category probably juvenile form of larger and subsequently lumped together in analyses), in 4% they were significantly thinner, and 1% had significantly shorter and stouter acanthostyles than typical forms. Acanthostyle spination slightly variable, from scattered robust, recurved spines (65%), spines arranged in regular longitudinal rows (5%), or minutely microspined (12% of specimens). Microsclere geometry: Proportion of costot to normal morphs of palmtate isochelae varied from 0-44% for smaller category, 0-20% for larger. Chelae typically abundant, 7% of specimens isochelae of both classes very rare, 3% smaller category rare but larger abundant, 4% larger category rare but smaller, 1% of specimens isochelae absent entirely. Toxas of both categories very abundant (12%), uncommon (70%), rare (17%), or absent entirely (1% of specimens).

**Variability in spicule dimensions:** Some spicules (choaonosomal principal styles, larger auxiliary subtylostyles, acanthostyles) showed significant variations in dimensions between samples collected from different localities (Tables 29-30), although statistical significance was never high, and no obvious patterns were apparent when groups of specimens from the same localities were compared with other groups. Some spicule categories varied between samples collected from different depths, in some cases with high levels of statistical significance (P<0.001) (e.g., larger auxiliary subtylostyles), but no obvious trends apparent. It is probable that effects of differential geographical and bathymetric distributions of specimens are linked due to the preponderance of deeper water samples from the Northwest Shelf region and shallow water samples from the Darwin region, making it im-
possible to separate the influences of either factors on this observed variability. Variability of spicule size between samples collected during different seasons were analysed for Darwin samples only (Table 30), with significant differences observed for length of ectosomal auxiliary subtylostyles and larger isochelae, and widths of acanthostyles. Data also indicate a higher level of variability in sizes of larger isochelae during the wet season (February-April) than during other seasons, although this result is of uncertain biological significance.

**Remarks.** Notwithstanding its considerable morphological variability *C. (T.) abietina* is easily recognised in the field with distinctive stalked digitate growth form and prominent surface corules. The most similar species in growth form is *C. (T.) cervicornis* but this has a much thinner, stoloniferous branching morphology, lacks principal megascleres completely, fibres have less spongion, toxas are different in morphology and size, and spicule dimensions are different. Skeletal structure is unusual where larger auxiliary subtylostyles are found in three locations in the skeleton: 1) subectosomal skeletal tracts forming organised plumose tracts supporting the ectosomal skeleton; 2) dispersed between fibres in disorganised tracts; 3) and coring all spongion fibres to the virtual exclusion of principal spicules. Principal styles mainly form plumose brushes protruding from fibres in plumose bundles, functionally representing a second category of echinating spicule.

There are some minor differences between type material and other specimens examined, including a higher proportion of choanosomal principal spicules found echinating fibres, the absence of contort isochelae, and specific details in some spicule dimensions (Table 29). But given the large range of variation in some characters, the relatively large sample sizes from widely dispersed populations, and the antiquity of the dried holotype this variability is insignificant. Re-examination of Ridley's (1884a) holotype of *C. aculeata* confirmed that it is a synonym of *C. (T.) abietina*, with shape, texture, colour in spirit, spiculation and skeletal architecture virtually identical. Conversely, *C. (T.) coralliophila* (see below) has different spicule geometry and skeletal architecture, and Burton's (1959a: 243) proposed merger of *C. coralliophila* into *C. aculeata* is rejected.

Specimens described by de Laubenfels (1954) from the central west Pacific differ from Australian populations in that they have a more restricted size range of isochelae (i.e., one size category), relatively small acanthostyles (Table 29), and an ectosomal (peripheral) skeleton almost completely covered by subectosomal spicule brushes (as opposed to ectosomal spicule brushes). In fact de Laubenfels (1954) completely overlooked the presence of ectosomal megascleres, not differentiating between spicules coring fibres from those forming the peripheral skeleton.

**Clathria (Thalysias) aphylla** sp. nov. (Figs 142-143, Plate 5D)


**Habitat Distribution.** Staghorn and plate coral fringing reef; 20m depth; known only from the type locality, Houtman Abrolhos (WA) (Fig. 142H).

**Description.** Shape. Thin, leaf-like, foliaceous, convoluted, basically frondose bundles of lamellae covering coral substrate; individual fronds attached directly to substrate, sometimes completely enveloping staghorn corals, or attached via small basal stalk, up to 24mm long, 5mm diameter, or attached to adjacent lamellae; individual lamellae usually flat, elongate, oval or elliptical, up to 65mm long, 2mm thick, with rounded or sinuous, convoluted margins, superficially resembling a *Padina* algae, or palmate-digitate margins, or sometimes curled in vasiiform growth forms.

**Colour.** Dull yellow alive (Munsell 2.5Y 8/8), pale brown in ethanol.

**Oscules.** Small, on upper surface, less than 2mm diameter, flush with surface.

<table>
<thead>
<tr>
<th>SEASON</th>
<th>TOTAL SAMPLES</th>
<th>SAMPLES WITH LARVAE</th>
</tr>
</thead>
<tbody>
<tr>
<td>WET</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>PREDRY</td>
<td>17</td>
<td>3</td>
</tr>
<tr>
<td>DRY</td>
<td>19</td>
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<td>PREWET</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>DEPTH</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-4m</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>4-10m</td>
<td>30</td>
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<td>10-40m</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>&gt;40m</td>
<td>11</td>
<td>0</td>
</tr>
</tbody>
</table>

**Fig. 141. Clathria (Thalysias) abietina** (Lamark) Incidence of incubated larvae within sampled populations from NW Australia.
Texture and surface characteristics. Soft, compressible but difficult to tear; upper osculariferous surface slightly concave, smooth, usually even, occasionally concentrically striated, or producing short fronds of folds on surface; lower porous surface slightly convex, even or slightly striated, with parasitic zoanthids covering parts of surface.

Ectosome and subectosome. Erect or paratangential brushes of ectosomal auxiliary styles forming thin surface layer, with choanosomal principal styles protruding through ectosome perpendicular to surface, singly or several together, extending up to 150μm through surface; choanosomal fibres immediately below ectosome, with reduced subectosomal skeleton; subectosomal auxiliary styles tangential or paratangential, lying immediately below surface underlying ectosomal spicule brushes; mesohyl matrix in peripheral skeleton heavy, darkly pigmented.

Choanosome. Regularly reticulate, slightly renieroid skeleton; without compression or major differences between peripheral skeleton and core; spongin fibres heavy, 20-70μm diameter, not obviously differentiated into primary or secondary elements, cored by multisicular (up to 15 spicules abreast) or paucisicular (2 or more spicules abreast) tracts of principal choanosomal styles; at core of skeleton principal styles confined entirely within fibres whereas in peripheral fibres, principal spicules erect, perpendicular to fibres, protruding through surface in plumose bundles; fibres moderately lightly echinated by acanthostyles, mainly at fibre nodes; fibre meshes mainly rectangular (fibres oval), 90-170μm diameter, with some triangular meshes, relatively even throughout skeleton; mesohyl matrix light, with few scattered megascleres; choanoocyte chambers oval to elliptical, 25-40μm diameter, lined by abundant, minute isochelae.

Megascleres. Choanosomal principal styles long, thick, straight or slightly curved towards basal end, rounded or slightly tapering bases, invariably smooth bases, fusiform points. Length 152-(205.1)-252μm, width 4.5-(8.4)-11μm.

Subectosomal auxiliary styles long, slender, straight, with rounded or faintly subtylote smooth bases, fusiform points. Length 208-(258.1)-297μm, width 2-(2.7)-4.5μm.

Ectosomal auxiliary styles short, slender, straight, rounded or slightly subtylote bases, smooth or microspined (or mucronate) bases, fusiform points. Length 162-(178.2)-204μm, width 1-(1.6)-2.5μm.

Echinating acanthostyles relatively long, slender, subtylote, sharply pointed, evenly spined although fewer spines in 'neck' region proximal to base (but not aspinose); spines small, sharp, recurved. Length 45-(86.3)-102μm, width 3-(5.5)-8μm.

Megascleres. Palmate isochelae very abundant, minute, with lateral alae completely fused to shaft and partially fused to front ala. Length 4-(5.1)-6μm.

Toxas not abundant, predominantly v-shaped, variable in size, with angular central curvature and arms bent at approximately right angles to each other, non-reflexed arms, occasionally toxas forceps shaped with pinched central curve and nearly parallel arms. Length 34-(62.3)-106μm, width 0.8-(1.3)-2.5μm.

ETYMOLOGY. Greek phyllon, leaf; for the growth form.

REMARKS. This species is a sister of C. (C.) anguifera (Vic. and S Qld), having similar live colour, slightly renieroid skeletal structure (mainly rectangular meshes), similar toxa morphology and chela size. In particular both species have large v-shaped toxas, and a skeletal architecture that verges on isodictyal (some triangular meshes). However, they are clearly different species showing both obvious and subtle differences in a number of characters. Clathria (T.) aphylla has a very thin, leaf-like growth form (whereas C. (C.) anguifera is thickly lamellate, lobate); very thick, well developed, evenly spaced fibres cored by multisicular tracts of large principal styles (versus widely spaced, vestigial fibres with light spongion, cored by much smaller principal spicules in uni- or paucisicular tracts); a specialised ectosomal skeleton composed of two size classes of auxiliary spicules forming brushes and principal spicules protruding through the surface forming plumose brushes and piercing the ectosome (versus a single category of auxiliary spicule forming a tangential or occasionally paratangential ectosomal skeleton, without participation of principal spicules in the ectosomal skeleton); clearly differentiated principal and auxiliary spicule geometry (versus more subtle differences, mainly in thickness and basal termination); rounded bases of principal and auxiliary megascleres with the smaller microspined (versus subtylote and completely smooth); and substantially larger dimensions for most megascleres. Another species with a similar, slightly renieroid skeleton reminiscent of C. (T.) aphylla is C. (C.) hispidula

(from Torres Strait and Shark Bay), which has only one category of auxiliary spicule and different ectosomal structure, wing-shaped toxas, different acanthostyle geometry and specific differences in spicule sizes. All three species probably have sister species relationship based on skeletal architecture, here referred to the ‘angulifera’ group.

A few other *Clathria* species also have V-shaped toxas (*C. (T.) juniperina*) and vaguely isodictyal skeletal structure (e.g., *C. (T.) hirsuta*), but these differ from *C. (T.) aphylla* in most other respects and are not considered here to be closely related.

*Clathria (Thalysias) arborescens* (Ridley, 1884) (Figs 144-145)

*Rhaphidophlus arborescens* Ridley, 1884a: 450-451, pl.40, fig.L, pl.42, figs n-n'; Thiele, 1903a: 958.
Clathria arborescens; Hooper & Wiedenmayer, 1994: 268.
cf. Microciona prolifera; Vosmaer, 1935a: 610, 634.

MATERIAL. HOLOTYPE - BMNH1881.10.21.272: Friday 1., Torres Strait, Qld, 10°36'S, 142°10'E, 1.v.1881, coll. HMS 'Alert' (dredge).

HABITAT DISTRIBUTION. Ecology unknown; Torres Strait, Qld (Fig. 144H).

DESCRIPTION. Shape. Branching, arborescent, 125mm long, 60mm maximum width of branching, with short stalk, 18mm long, 8mm diameter; no basal attachment (presumed not collected), proliferous bushy, slightly flattened cylindrical branches, up to 12mm diameter, with individual branches up to 55mm long, mostly anastomosing with adjacent branches; branching mostly planar. Colour. Live colouration unknown, grey-brown in dry state.

Oscules. Not observed.

texture and surface characteristics. Texture harsh in dry state; surface peel thick, darker than choanosomal skeleton, lightly hispid, with numerous irregular subectosomal striations, irregular conules and low ridges.

Ecotosome and subectosome. Ectosomal skeleton with very thick crust of discrete spicule brushes composed of ectosomal auxiliary subtylostyles, occasionally paratangential or tangential to surface; supported below by thick, vaguely plumose, slightly disorganised bundles of larger subectosomal auxiliary subtylostyles arising from terminal choanosomal fibres; subectosomal skeleton lacking any spongine fibres and only light mesohyl matrix; together ectosomal and subectosomal bundles extend up to 800µm from peripheral fibre skeleton, and comprise up to 25% of branch diameter.

Choanosome. Choanosomal skeleton irregularly close-meshed reticulate. Spongine fibres very large, heavy dark yellow-brown, 110-170µm diameter, forming tight oval or elongate meshes, 130-350µm diameter; fibre reticulation without any clear distinction between primary or secondary components, although ascending fibres marginally more abundantly echinated than transverse connecting fibres, and some smaller fibres between major meshes with uni- or paucispicular core; fibres generally all cored by multispicular tracts of choanosomal principal subtylostyles together with subectosomal auxiliary subtylostyles, forming a dense axial core within fibre but occupying only about 50% of fibre diameter; fibres abundantly echinated by relatively large acanthostyles, more-or-less evenly dispersed throughout skeleton (not con- gregated in periphery as reported by Ridley); choanoocyte chambers not observed (dry material).

Megascleres. Choanosomal principal subbylos- tyles with similar geometry to larger auxiliary spicules, long, straight, usually with subtylole, smooth or micropinned bases, rarely rounded bases, with tapering fusiform points. Length 205-(225.3)-262µm, width 8-(9.7)-12µm.

Subectosomal auxiliary subtylostyles more slender but longer than principal spicules, straight or slightly curved towards base, with smooth, slightly constricted bases, fusiform points. Length 210-(251.4)-282µm, width 4-(5.4)-7µm.

Ectosomal auxiliary subtylostyles relatively long, straight or slightly curved towards base, prominently subtylole, with smooth or micropinned bases, fusiform points. Length 82-(132.7)-147µm, width 2-(3.3)-4µm.

Echinating acanthostyles long, robust, subtylole, large conical (not recurved) spines, scattered mainly over base and midsection of shaft, frequently with bare point and 'neck'. Length 68-(76.3)-88µm, width 6-(8.2)-11µm.

Microscleres. Palmate isochelae small, frequently contort, single size category, with long lateral alae completely fused to shaft and entire front ala of equal length. Length 6-(10.8)-14µm.

Toxas short, robust, wing-shaped, with generous angular central curvature, recurved and slightly reflexed points Length 27-(41.8)-58µm, width 1.5-(1.8)-2.0µm.

REMARKS. This species is relatively poorly known, recorded so far only from the holotype. But several important characters were seen in the holotype using SEM (Fig. 145), not described by Ridley (1884a). These include: presence of differentiated principal and auxiliary spicules, presence of toxas, spination pattern on acanthostyles, and his spicule dimensions were inaccurate. These characters now provide better clues as to its affinities.

Ridley (1884a) considered this species similar to C. (T.) caeciformis in growth form and skeletal structure. They also both have principal and auxiliary megascleres very similar in geometry (i.e., on first appearances fibres seem to be cored only by auxiliary spicules), but they have many morphological differences. Clathria (T.) arbores- cens has a substantially better developed ec- toosomal peel occupying a significant proportion of branch diameter, a close-meshed reticulate
choanosomal skeleton, very thick fibres all cored by megascleres (C. (T.) cactiformis has a relatively thin ectosomal skeleton, cavernous subectosomal region, wide-meshed choanosomal reticulation, substantially thinner fibres with only primary ones cored). Also, echinating acanthostyles are much larger than those of cactiformis, they have erect conical spines rather than hook-like recurved ones, and acanthostyles are found throughout the skeleton rather than mainly on peripheral fibres (although both species have spines absent from both "necks" and points of acanthostyles). Toxa morphology differs markedly between the two, with arborescens having only thicker, wing-shaped toxas, and cactiformis with mainly very thin, raphidiform, sinuous or accolada toxas but occasionally also with small wing-shaped forms. Spicule dimensions also differ considerably between the two species. Both species belong to the 'juniperina' species complex (refer to discussion below under C. (T.) cactiformis and C. (T.) hirsuta).

Dendy (1922), Burton & Rao (1932) and Burton (1938a) merged C. arborescens with C. (T.) procer on the basis that choanosomal principal megascleres were supposedly excluded from the axis of fibres, but this is not entirely correct (in any case the character is also known to occur in
Clathria (Thalysia) cactiformis (Lamarck, 1814) (Figs 146-148, Table 31, Plate 4-E-F)

Spongia cactiformis Lamarck, 1814: 440-370
Wilsonella appendiculata; Topsent, 1930: 46, pl.12, fig.3; Topsent, 1933: 22.
Not Thalassodendron typica; Whitelegge, 1901: 86.
Not Clathria typica var. porrecta Hentschel, 1912: 298, 359-360.
Not Clathria typica; Kirkpatrick, 1903: 248-249; Kirkpatrick, 1904: 148; Vacelet & Vasseur, 1971: 94-95, pl.3, fig.5, text-fig. 48.
Not Tenacia typica var. porrecta Hallmann, 1920: 711.
Echinonema anchoratum var. dura Whitelegge, 1901: 81.
Echinonema anchoratum var. lamellosa; Lendenfeld, 1888: 219-220.
Rhaphidophalus anchoratum; Bergquist & Fronont, 1988: 112; Dawson, 1933: 39.
Wilsonella anchoratum var. lamellosa; Hallmann, 1912: 211 [imperfectly known].
Not Echinonema anchorata var. lamellosa; Whitelegge, 1901: 82.
Echinonema flabelliformis Carter, 1885f: 352.
Echinonema pectiniformis Carter, 1885f: 353.
Phakella ventilabra var. australiensis Carter, 1886g: 379.

Thalassodendron brevispina Lendenfeld, 1888: 225; Whitelegge, 1901: 87.
Clathria favosa Whitelegge, 1907: 498-499.
Clathria indurata Hallmann, 1912: 299.
Clathria acanthis Hentschel, 1911: 367-270, text-fig.44; Hentschel, 1923: 380, fig.349.
Rhaphidophalus acanthis; Hallmann, 1912: 177.
Rhaphidophalus sp. 2; Vacelet & Vasseur, 1971: 97-98, text-fig. 52.
Not Microciona prolifera; Vosmaer, 1935a: 609, 628-629, 647, 667.


HABITAT DISTRIBUTION. Colonises a wide variety of substrates, including rock reefs, coral-rubble, soft sand, mud sediments, algal beds; shallow subtidal to 100m depth; widely distributed in temperate waters of eastern and western Australian coasts, with incursions into subtropical waters extending to the Port Hedland region on the west coast and Byron Bay on the east coast (Fig. 146H). This species is not yet recorded from the Indonesian archipelago, contrary to Hentschel (1912) — his records being misidentifications (see below) — but it does appear to range across the Indian Ocean, with confirmed records from Madagascar (Vacelet et al., 1971, 1976, 1977), East Africa and Seychelles (present study).

DESCRIPTION. Shape. Typically flabellate, planar, stalked, with long bifurcate, occasionally anastomosing digitate processes on margin of fan; gross morphology variable, with or without basal stalk and expanded basal attachment, varying from globular, cylindrical planar digitate, globular digitate, planar flabellate, lamellate branching in more than one plane, or thinly lamellate.

Colour. Live colouration pale orange-brown (Munsell SYR8/4) to bright red (5R5/10); beige,
TABLE 31. Comparison between present and published records of Clathria (Thalysias) cactiforis (Lamarck). All measurements are given in μm, denoted as range, or as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype</th>
<th>Lectotype of S. appendiculatus</th>
<th>Specimens (N=66)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>134 (191.2-232 x 5-7.6-11</td>
<td>157-181 x 4.5-6</td>
<td>103.6 (199.2-314 x 3.2-4.5)</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>204 (229.8-268 x 4-5.4-6</td>
<td>191-297 x 4-5.5</td>
<td>115.7 (235.7-356.6 x 1.6-2.5)</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>101 (124.3-148 x 1.5-2.5-3</td>
<td>85-104 x 2.5-3.5</td>
<td>73.8 (114.7-162.1 x 1.6-2.5)</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>68 (74.4-79 x 5.5-8.8-11</td>
<td>46-57 x 3.4-4.5</td>
<td>38.2 (61.3-93.1 x 1.7-3.5)</td>
</tr>
<tr>
<td>Chelea 1</td>
<td>12 (14.7-18</td>
<td>7-8</td>
<td>8.5 (13.9-22.2)</td>
</tr>
<tr>
<td>Chelea 2</td>
<td>6 (8.8-10</td>
<td>15-17</td>
<td>2.5 (7.1-11)</td>
</tr>
<tr>
<td>Toxas</td>
<td>113 (201.7-296 x 0.8-1.2-2</td>
<td>82-146 x 0.5-1.0</td>
<td>8 (127.8-355 x 0.8-1.3-2.5)</td>
</tr>
</tbody>
</table>

skeletal components; fibre anastomoses produce widely spaced rectangular meshes formed by ascending primary fibres, containing pauci- or multisipicular bundles of choanosomal principal styles which occupy only the central portion of fibres, and uncored secondary fibres; occasionally secondary fibres uni- or paucisipicular, usually with an optically diffuse pith reminiscent of dicystoceratid sponges, spongion fibres characteristically thin, without marked differences between primary and secondary fibre diameter, with pigmentation ranging from extremely light, yellow (specimens from Port Phillip, Vic) to extremely heavy and dark brown (material from Port Hedland, WA); echinating acanthostyles very heavy, especially on peripheral fibres immediately below subectosomal skeleton; larger auxiliary subtylostyles usually abundant between fibres, strain without order within mesohyl, mesohyl matrix relatively light, choanoocyte chambers large, oval or elongate, up to 120μm diameter.

Megascleres (Table 31). Choanosomal principal styles morphologically similar to larger auxiliary subtylostyles but relatively shorter, thicker, slightly curved near base, usually with tapering, evenly rounded smooth bases but sometimes slightly subtyloite, and fusiform points.

Subectosomal auxiliary subtylostyles nearly completely straight, occasionally slightly curved or sinuous, usually with slightly subtyloite smooth bases, less frequently with micropined bases, tapering to fusiform points.

Ectosomal auxiliary subtylostyles more prominently subtyloite, slightly curved at centre, with micropined or smooth bases and fusiform points.

Echinating acanthostyles relatively short, stout, prominently subtyloite, with large spines mainly dispersed on base and midsection, leaving a bare ‘neck’ (below basal swelling) and bare point.

Microscleres (Table 31). Larger palmate isochelae variable in abundance, with lateral alae completely fused to shaft, wide gap between lateral and front alae, and fused front ala; usually non-contort. Smaller isochelae common, frequently contort.

Toxas differentiated into two main morphs, larger often found in toxodragma; accolada toxas most common, long, very thin, slight angular central curvature, straight arms, sometimes sinusous asymmetrical. Small toxas less abundant, relatively thick, widely curved at centre, slightly reflexed points.
**Larvae.** Reproductive products observed in only four specimens. Incubated parenchymella larvae large, oval to elliptical in shape, 220-420μm diameter, containing well developed centrally aggregated larval styles.

**Associations.** Heavy infestations of zoophytic organisms observed on surfaces of several specimens (both compound ascidians and zooanthid polyps); numerous microalgal cells seen in sponge mesohyl of few samples; sponge apparently serves as a food source to *Rostanga* sp. nudibranchs (W. Rudman, pers. comm.).

**Variation.** Extremely variable in some features (e.g., gross morphology, spicule size) but not in others (e.g., surface features, spicule geometry, skeletal structure). Gross morphology: Victorian, Queensland and Indonesian morphs showed greatest differences in growth form, but all specimens retained most other characteristics common to other populations. Ectosomal skeletal structure: typically heavy, erect plumose brushes, well differentiated from subectosomal plumose tracts (52%), moderately developed (34%), or thick tangential ectosomal peel reminiscent of *Crelia* (*Crelildae*) (14% of specimens). Subectosomal skeletal structure: very cavernous, well differentiated ascending plumose (extra-fibre) skeletal tracts (36%), paratangential, immediately subdermal tracts (21%), or intermediate of these conditions (43% of specimens). Choanosomal skeletal structure: irregularly reticulate (64%), regular fibre anastomoses (22%), or predominantly radial to plumose primary fibre architecture (14% of specimens). Fibre meshes: wide, rectangular, with uncored secondary elements (67%), with central pith component (7%), close-meshed, irregularly oval to elliptical fibre reticulation with uncored secondary fibres (7%), or with both cored primary and secondary fibre elements (19% of specimens). Spongins fibres: very light (7%), moderately heavy, yellow (48%), very heavy, yellow (43%), or extremely heavy, dark brown in colour (2% of specimens). Echinating acanthostyles: concentrated on peripheral fibres, more sparsely dispersed on axial fibres (69%), evenly distributed throughout fibres (17%), rare (14% of specimens). Extra-fibre spicules: typically abundant, dispersed without order within mesohyl (74%), very light or absent entirely (24%), or organised into ascending extra-fibre tracts (2% of specimens). Megasclere geometry: Choanosomal principal styles: predominantly fusiform (76%), distinctly hastate (abruptly pointed) points (7%), or mixture of both types of terminations (17% of specimens); bases of spicules predominantly smooth (90%), with both smooth and spined bases (8%), or only microspined bases on choanosomal styles (2% of specimens); bases of spicules tapering, non-tylote (46%), rounded, slightly subtylote (52%), or with both conditions (2% of specimens); megascleres slightly curved (83%), exclusively straight (7%), or both conditions (10% of specimens). Subectosomal auxiliary subtylote styles: tapering, rounded or very slightly subtylote bases (69%), or distinctly subtylote (31% of specimens); exclusively straight (69%), predominantly curved (7%), or both conditions (24% of samples). Ectosomal auxiliary subtylote styles: subtylote (76%), tapering nontylote (10%) or both conditions (14% of specimens); bases predominantly microspined (71%), exclusively smooth (3%), or with both conditions (26% of specimens); ectosomal spicules slightly curved near base (54%), completely straight (29%), or with examples of both (17% of specimens); most megascleres with fusiform points (95%), or also including few hastate spicules (5% of specimens). Echinating acanthostyles: typically short, fusiform (69%), significantly smaller, stouter (19%), or longer, thinner (12% of specimens); bases subtylote (81%), or distinctly nontylote (19% of specimens); spines characteristically long, thick, recurved (74%), or reduced, granular spination (26% of specimens). Microsclere geometry: Larger isochelae: common (70%), uncommon (26%), rare (2%), or common but poorly silicified (2% of specimens); cortort larger isochelae present but uncommon (10%), present, common (2%), or absent (86% of specimens). Smaller isochelae: abundant (7%), common (62%), uncommon (21%), rare (3%) or absent entirely (7% of specimens); 0-10% of smaller chelae were cortort (2%), 10-30% cortort (5%), 30-50% cortort (12%), 50-70% cortort (24%), 70-90% cortort (43%), or 100% cortort (7% of specimens). Toxas: typically very abundant (82%), common (3%), uncommon (5%), rare (3%), or absent entirely (7% of specimens); only symmetrical toxas present, with large central curvature and relatively straight points (52%), with both symmetrical and asymmetrical, sinusous toxas (41%), or with both these and wing-shaped toxas (7% of specimens).

**Variability in spicule dimensions:** With few exceptions, and despite apparent morphological incongruence in many other features, spicule dimensions were surprisingly closely comparable between specimens despite that they were col-
lected from widely separated geographic localities. Results were not analysed statistically because bathymetric, habitat and season data were not available for the majority of material. However, scatterplot comparisons between samples found that for each spicule category there were only few anomalous specimens which consistently differed from typical forms of the species. These anomalies are discussed further below.

REMARKS. Clathria (Thalysias) cactiformis is predominantly temperate. It is characterised by its typically flabellate or flabello-digitate growth form, a smooth surface with a detachable thick ectosomal peel which is usually paler than the choanosome, relatively thin spongins fibres heavily echinaten but poorly cored, and especially its short, thick, squat acanthostyles. Due to its presence, bare points and large recurved spines over the remainder of the spicule. There is considerable morphological variability between regional populations (see Variation, above), to some extent vindicating Hallmann’s (1912) subdivision of the species into ‘varieties’ (subspecies), based mainly on differences in growth form. In fact some specimens examined were assigned to this species with hesitation given their diverse external morphologies, but no other consistent skeletal or other characters were found to correlate with these morphotypes. Nevertheless, this taxon is probably composed of several cryptic sibling species (morphospecies) which might only be reliably differentiated using biochemical, genetic and other non-skeletal data.

N MVTRN0436 and RN0551 from Port Phillip Bay, Vic. have acanthostyles which are long, evenly spined, spines are sparse and small; echinating spicules occur in heavy concentrations and are evenly dispersed throughout the choanosome, not predominant in the peripheral skeleton; ectosomal skeleton is very well developed and well differentiated from subectosomal plume tracts; the subectosomal region is noticeably more cavernous than in most typical forms; the choanosome is distinctly pluromaticulate; mesohyl matrix is very heavy and fibres are heavily invested with spongins; the smaller category of isochelae and toxas are absent. In some respects these features correspond to Spongia appendiculata, perhaps justifying the retention of that species separately form cactiformis, but other general morphological features indicate that these specimens cannot be otherwise reliably separated.

WAM133-82 from the Northwest Shelf of WA has consistently basally spined choanosomal styles, and isochelae are completely unmodified. The ectosome and subectosomal regions are poorly developed and incompletely differentiated, but the specimen is otherwise comparable with typical forms.

Some further comment is necessary on the synonymy above. Spongia appendiculata is included here as a new synonym of C. (T.) cactiformis (cf. Hooper & Wiedenmayer, 1994) with virtually identical growth form, spicule geometry and skeletal structure as typical forms of this species. However, there are some notable differences between these nominal species, especially in the markedly smaller dimensions of most spicules in appendiculata, acanthostyles have a vestigial granular spination, and they are also almost entirely incorporated into the fibres themselves (i.e., enveloped by collagen). These differences are not presently considered sufficient to recognise it as a distinct taxon. Incorporation of echinating acanthostyles into spongins fibres is also known for several other species of Clathria (termed here the ‘phorbasiformis’ species complex, including C. (T.) phorbasiformis, C. (D.) dura, C. (D.) myxilloides, and others). However, in Spongia appendiculata acanthostyles are inserted perpendicular to fibres, much like typical echinating megascleres, but they have ‘sunk’ into them, whereas in these other species acanthostyles run parallel to fibres and replace or supplement the usual coring spicules.

Clathria acanthodes is considered a synonym of C. (T.) cactiformis, despite having slightly different acanthostyle morphology (‘neck’ often spined). The characters used by Hentschel (1911) to differentiate C. acanthodes from other species (i.e., similar geometry between principal and auxiliary spicules, presence or absence of microspines on bases of principal and auxiliary spicules, presence of two size classes of palmate isochelae, and possession of rhaphidiform toxas), are found in most other populations of C. (T.) cactiformis and are not considered to be of primary importance in differentiating species. Clathria typica var. porrecta, also described by Hentschel (1912) from Indonesia, is a synonym of Clathria (T.) reinwardti not of C. (T.) cactiformis (this synonym was overlooked by Hooper & Wiedenmayer, 1994). The type material of Clathria indurata and Echinonema anchoratum var. dura from WA have a uni- or paucispicular core of choanosomal styles in secondary fibres, whereas typical populations of C. (T.) cactiformis
generally have an aspicular secondary fibre system, but otherwise spiculation and architecture is similar between these morphs and they are obvious synonyms.

The species is included in the juniperina complex (see discussion of C. (T) hirsuta) all of which have reduced skeletal and fibre characteristics. This group includes 12 species (with about 20 synonyms): C. (T) arborescens, C. (T) caeciformis, C. (T) cervicornis, C. (T) clathrata, C. (T) cornelia, C. (T) crassipes sp. nov., C. (C) decumbens, C. (T) fuscens sp. nov., C. (T) hirsuta, C. (T) juniperina, C. (T) rubra and C. (T) placenta. Many of these species barely differ in their gross morphologically, and Hallmann (1912) suggested they should be combined into one or few species, but this contention cannot be resolved without access to live populations of all species, to determine accurately their field characteristics, nor on the basis of preserved material.

Clathria (Thalysias) cancellaria (Lamarck, 1814) (Figs 149-150, Plate 5A)

Spongia cancellaria Lamarck, 1814: 382, 361.
Rhipidophillus cancellarius, Topsent, 1930: 43, pl.2, fig.6.
Clathria cancellaria; Hooper & Wiedenmayer, 1994: 270.


HABITAT DISTRIBUTION. Rock substrate, on or under ledges, or exposed on isolated rock in sand substrate; 12-40m depth; known only from Australia: Northwest Shelf, Wallaby Is and Houtman Abrolhos (WA) (Fig. 149H).

DESCRIPTION. Shape. Lamellate, massive, mostly planar growth form, with or without basal attachment, consisting of more-or-less fused erect thin digit forming a continuous lamella, 370mm maximum span, with some free or barely anastomosing sections; lamellae are 116-135mm high, 4.5-7mm thick, forming irregular meshes between branch anastomoses, 3-14mm diameter. Colour. Salmon-pink (Munsell SRP 8/2) to orange-red alive (5 YR 6/10), light grey-brown in ethanol.

Oscules. Small, 2-3mm diameter, mainly between ridges; pores minute, 0.5-1mm diameter, scattered over entire surface.

Texture and surface characteristics. Firm, compressible, difficult to tear. Lamellae prominently striated with longitudinal ridges, grooves and discontinuous conules; margins of lamellae digitate, microconulose.

Ectosome and subectosome. Relatively thin, dense ectosomal crust, 60-95μm thick, composed of erect ectosomal auxiliary subtylosyles forming continuous erect dermal palisade; immediately below ectosome, protruding through palisade, are mostly paratangential subectosomal auxiliary subtylosyles; in thicker, more elongated sections larger auxiliary subtylosyles form plumeose ascending tracts supporting ectosomal skeleton, but in most sections they lie paratangential to surface, arising from ends of peripheral choanosomal fibres; subectosomal region relatively cavernous; in growing points of sections in peripheral skeleton elongate conulose protrusions extend from surface for up to 0.5mm, fully cored by dense tracts of subectosomal subtylosyles.

Choanosome. Skeletal architecture irregularly reticulate, without axial or extra-axial differentiation; spongin fibres relatively heavy, imperfectly separated into primary and secondary elements, forming ovoid or elongate, relatively cavernous meshes, 140-680μm diameter; primary fibres, 92-165μm diameter, predominantly ascending, cored by multispecific tracts of choanosomal principal styles occupying about 75% of fibre diameter; secondary fibres unio- to paucispicular, 26-71μm diameter, predominantly transverse; all fibres heavily echinated by acanthostyles protrude at various obtuse angles from fibres; mesohyl matrix heavy but only lightly pigmented, slightly granular, with abundant larger auxiliary megascles throughout, sometimes completely obscuring skeletal architecture; choanoocyte chambers, small, oval, 42-68μm diameter.

Megascles. Choanosomal principal styles short, thick, slightly curved towards basal end, with rounded or very slightly subtylosyle smooth bases, fusiform points. Length 166-(185.5)-218μm, width 7.5-(12.6)-16μm (holotype 161-(198.1)-224 x 6-(12.1)-16μm).

Subectosomal auxiliary subtylosyles long, thick, straight or very slightly curved, with slightly subtylosyle or rounded bases, usually microspined, fusiform points. Length 134.6-(218.8)-286μm, width 3.5-(6.5)-8.6μm (holotype 148-(229.7)-265 x 3.5-(5.9)-8μm).

Ectosomal auxiliary subtylosyles short, thin, straight, with prominent subtylosyle bases, invariably microspined, fusiform points. Length 86-(97.6)-114.5μm, width 2.5-(3.3)-4.5μm (holotype 85-(93.4)-102 x 2-(3.7)-5μm).
Acanthostyles long, thick, with slightly sub-tylote rounded bases, large spines dispersed over apical and basal extremities, usually with aspinose neck, occasionally evenly spinose; spines conical, barely recurved. Length 67-(79.8)-92.5\(\mu\)m, width 3.8-(8.6)-11.6\(\mu\)m (holotype 62-(80.2)-88 x 3-(8.1)-10\(\mu\)m).

**Microscleres.** Palmate isochelae divided into two size classes, largely usually unmodified, smaller often contorted; long lateral alae completely fused to shaft; front alae complete. Length I: 9-(10.9)-16\(\mu\)m (holotype 9-(12.3)-16\(\mu\)m), length II: 3-(4.4)-8\(\mu\)m (holotype 3-(4.8)-6\(\mu\)m).

**Tetras** thin, rhaphidiform, acclada to sinus, varying from small forms with slightly curved centres and slightly reflexed points, to long forms with only very slightly rounded central curvature and straight or slightly reflexed points. Length 11-(121.1)-166\(\mu\)m, width 0.4-(0.8)-1.2\(\mu\)m (holotype 17-(102.3)-186 x 0.5-(1.1)-1.3\(\mu\)m).

**REMARKS.** *Clathria* (Thalysias) cancellaria is most closely related to the New Caledonian C. (T.) flabellifera, both with similar skeletal architecture, spicule geometry and spicule size, and also (vaguely) growth form, surface features and live colouration (Hooper & Lévi, 1993a). The two populations differ in several cryptic characters, which Hooper & Lévi (1993a) suggested were indicative of sibling species relationships rather than population variability. *Clathria* (T.) cancellaria has only a single category of toxo microsclere, resembling neither of the two found in C. (T.) flabellifera; it has two size categories of isochelae microsclere (whereas the latter species has only one); acanthostyle spines are much larger, the spicules more robust, and spines are more evenly dispersed over the spicule (whereas those on the latter species are small and found mainly towards the extremities of the spicule); basal spines are present on most of the smaller and larger auxiliary spicules (whereas most auxiliary spicules are completely smooth in the latter species); and spicules of most categories are substantially thicker in the WA population.

*Clathria* (Thalysias) cancellaria also superficially resembles *C. (T.) raphana* and irregular growth morphs of *C. (T.) coppingeri*, with lamellate, planar growth form, although fibre characteristics, spicule geometry and spicule sizes are otherwise different between all these species. The species has a dense crust of erect ecosomal spicules, very unlike the paucispicular dermal skeleton of *C. (T.) coppingeri*, although both species conform to the *Thalysias* condition in having differentiated ecosomal and subecosomal megascleres.

**Clathria** (Thalysias) cervicornis (Thiele, 1903) (Figs 151-152, Table 32, Plate 5B)

*Rhaphidophulus* cervicornis Thiele, 1903a: 959, 968, pl.28, fig.24a-e; Hallmann, 1912: 177; Brondsted, 1934: 22-23, fig.23; Simpson, 1968a: 70, pl.15. Not *Rhaphidophorus cervicornis*; Vacelet & Vasseur, 1971: 96-97, text-fig.50, pl.4, fig.3. *Thalysias cervicornis*; de Laubenfels, 1954: 135-137, text-fig.86.


**MATERIAL.** HOLOTYPE: SMF679 (fragments ZMB3141, MNHNCL2312) Ternate, Moluccas, Indonesia, 0°48'N, 127°23'E, 1894, coll. W. Kükenthal (dredge). OTHER MATERIAL: QLD - QMGS00707 (fragment NTMZ4045), CAROLINE IS., CENTRAL W PACIFIC - USNM22892, USNM22905, QMG304828 (NCI ODCN-0488-O).

**HABITAT DISTRIBUTION.** Usually at base of coral reef slope, on coral rubble, rock or seagrass beds, forming tangled thickets; intertidal - 45m depth; Howick Is (FNQ), (Fig. 151G). Aru Is, Aratua Sea, Moluccas Sea, Marshall Is, Palau Is, Truk Atoll (Chuuk), Ponape.

**DESCRIPTION.** Shape. Stoloniferous, thin, cylindrical branches, 10-25mm diameter forming single digits, erect or creeping over substrate, to dense tangled thickets with numerous, thin, stoloniferous, anastomosing, cylindrical branches, and either small, central, single basal stalk, or multiple points of attachment to substrate via branches.

**Colour.** Pale orange or orange-red exterior (Munsell 7.5YR 7/10-2.5YR 7/8), bright vermilion or brown interior in life (2.5R 4/2-4/8); grey-brown in ethanol.

**Oscules.** Large, up to 8mm diameter in life, with large membranous lip, collapsing when preserved, dispersed mainly on lateral surface of branches in regular rows.

**Texture and surface characteristics.** Firm, flexible, compressible surface, wavy axis difficult to tear, surface usually optically smooth, even, with subectosomal ridges and drainage canals radiating away from raised oscules, occasionally sparsely conulose, microscopically hispid in life in thicker branches; surface even, glabrous, unornamented when preserved.

**Ectosome and subectosome.** Ectosomal skeleton a dense palisade of discrete, erect spicule brushes composed of smaller ecosomal auxiliary subtylostyles, supported by underlying, ascending,
plumose tracts of larger subectosomal auxiliary subtyloses, identical to those coring fibres which also protrude through surface; no fibre component in peripheral skeleton but plumose tracts in subectosomal region arise directly from terminations of ascending primary fibres; together ectosomal and subectosomal skeletons occupy up to 30% of branch diameter.

*Choanosome.* Skeleton regularly reticulate, with even, rectangular or ovoid, relatively cavernous meshes, 180-270μm diameter; spongine fibres very heavy, 90-125μm diameter, thicker at nodes, up to 200μm diameter, cored by multispecular tracts of subectosomal auxiliary subtyloses which occupy only 60% of fibre diameter; echninating acanthostyles moderate to lightly dispersed over fibres, predominantly clustered around fibre nodes, sometimes rare or absent completely in some specimens; mesohyl matrix moderately light, with numerous subectosomal auxiliary megascleres scattered between fibres; choanocyte chambers small, oval, 35-55μm diameter.

**Megascleres** (Table 32). Choanosomal principal megascleres absent or completely undifferentiated from subectosomal spicules.

Subectosomal auxiliary subtyloses long, slender or robust, straight or slightly curved near point, with prominently subtyloe, polytyloe, slightly subtyloe, or rarely rounded bases, smooth or minutely spined, fusiform points.

Echinating acanthostyles moderately short, robust or slender, subtyloe, with smooth point and 'neck' below basal swelling; spines moderately large, recurved.

**Microscleres** (Table 32). Palmate isochelae occur in two size classes, with some smaller contour forms; lateral alae long, completely attached to shaft, front ala entirely fused. Toxas wing-shaped, long or short, thin, with large central curvature, slightly reflexed points.

**REMARKS.** This widely distributed Indo-west Pacific species is easily recognisable in the field by its growth form, resembling prolific tangles of thinly branching thickets. In the western Pacific and Indonesian archipelago this species is a prominent member of the fringing coral reef community, commonly found at the base of reef slopes in the rubble and sediment, whereas on the Great Barrier Reef it has been found only in the far northern sector where it is rare and occurs as isolated thin single branches.

The species has consistent skeletal architecture, probably dictated by its persistent cylindrical growth form, and similar spicule dimensions (Table 32), notwithstanding its relatively widespread Indo-west Pacific distribution, although there is some variability in spicule geometries. Specimens from Chuuk lack microscleres and often have very thin megascleres, whereas those in the Great Barrier Reef specimen there is only sparsely echninating acanthostyles. Brondsted's (1934) material is reported to have differentiated principal and auxiliary megascleres — the former with rounded smooth bases coring fibres and the latter with slightly subtyloe smooth bases and found exclusively in the ectsosomal skeleton or scattered between fibres. Similarly, acanthostyles in

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (SMF679)</th>
<th>(N=1) (GBR)</th>
<th>(N=3) (Micronesia)</th>
<th>(N=1) (Brondsted, 1934)</th>
<th>(N=1) (Laubenfels, 1954)</th>
<th>(N=1) (Bell, 1968a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Principal megascleres</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Subectosomal subtylosyles</td>
<td>180-258.9</td>
<td>232-274.9</td>
<td>205-236.7</td>
<td>165-315</td>
<td>265 x 4</td>
<td>135-325 x 2.4-7.6</td>
</tr>
<tr>
<td>Ectosomal subtylosyles</td>
<td>112-128.3</td>
<td>85-117.4</td>
<td>105-118.3</td>
<td>160-180</td>
<td>194 x 7</td>
<td>95-132 x 3.4-5</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>48-62.0</td>
<td>52-53.6</td>
<td>47-56.2</td>
<td>60-82</td>
<td>63-86 x 6</td>
<td>50-73 x 4.6-5</td>
</tr>
<tr>
<td>Chelae I</td>
<td>10-12.4</td>
<td>10-11.6</td>
<td>absent</td>
<td>12</td>
<td>10</td>
<td>8-13.6</td>
</tr>
<tr>
<td>Chelae II</td>
<td>3-6.3</td>
<td>3-4.4</td>
<td>absent</td>
<td>Not recorded</td>
<td>Not recorded</td>
<td>Not recorded</td>
</tr>
<tr>
<td>Toxas</td>
<td>12-35.3</td>
<td>16-54.5</td>
<td>40-90</td>
<td>40-90</td>
<td>34-56</td>
<td></td>
</tr>
</tbody>
</table>
Brondsted’s material are evenly spinoise, whereas in the holotype these have aspino ‘necks’ and points. It is possible that Brondsted’s material represents a different species, or it has simply been misdescribed, but no formal diagnosis can be made until his specimens are found and these differences confirmed or refuted.

The presence of a second, smaller category of isochela, and frequent contortion of isochelae have not been recorded previously for this species, although these features were commonly seen in most material examined, including the holotype, and appear to have been overlooked by Thiele (1903a) and subsequently authors. Consequently, there is no justification in separating Moluccan populations from others described by Bergquist, Brondsted, de Laubenfels and Simpson, whereas material described by Vacelet & Vasser (1971) as Rhaphidophus cervicornis belong to C. (T.) abietina.

Clathria (Thalysias) cervicornis is closely related to C. (T.) cornelia Hoover & Levi (from New Caledonia), C. (T.) craspeda sp. nov. (from the Tweed River region) and C. (T.) fasterna sp. nov. (from the Gulf of Carpentaria), all having similarities in their skeletal structure and diversity of spicule types, but with major differences in their growth forms, live colouration and live surface features, some also in their spicule geometries (the latter three species with differentiated principal and auxiliary megascles), and spicule dimensions. These are discussed further below for the respective species (and see also Hoover & Levi, 1993a).

Clathria (Thalysias) copingperi Ridley, 1884
(Figs 153-154, Tables 33-34, Plate 6A)

Spongia juniperina, in part (variety beta only); Lamarck, 1814: 444.
Not Spongia juniperina (variety alpha); Lamarck, 1814: 444.


Thalysias copingperi: de Laubenfels, 1936a: 105.
Clathria tendenfeldi; Brondsted, 1934: 19-20, text-fig.9.
Not Clathria copingperi var. aculeata; Hentschel, 1912: 363.

MATERIA LF. LECTOTYPE: BMNH1881.10. 21.246 (dry); Albany L., N. Qld, 10°44'S, 142°37'E, 6-8m depth, coll. HMS ‘Alert’ (dredge). PARALEC-

TOTYPE: BMNH1881.10. 21.330 (spirit); same locality. SYNTYPES of var. thuyaefromis: MNHNDS571, DT3553; precise locality unknown, Indian Ocean, Turgot collection, no other details known (dry). OTHER MATERIAL: QMG4731 (fragment NTMZ1557), WA - NMV unregistered (fragment NTMZ1493). WA - NTMZ670, NTM3152, NTMZ1173, NTMZ1155, NTMZ1221, NTMZ2269, NTMZ2283, NTMZ3031, NTMZ3231, NTMZ3216, NTMZ3217, NTMZ 2363, NTMZ2463, NTMZ2040. INDONESIA - SMF1702 (fragment MHNDCL2325), SMF1265 (fragment MHNDCL2251).

HABITAT DISTRIBUTION. Deep offshore rock reefs, dead coral, coral heads, probably restricted to harder substrates (as indicated by presence of smooth encrusting basal attachment (peduncle); growth form consistently planar and likely that orientation of fan is towards direction of predominant currents; 15-94m depth; Port Headland region, Bedout I., Lægeede Is, Amphipinome Shoals, Barracouta Shoals, Northwest Shelf; Ashmore Reef, Sahul Shelf (WA); off Moreton Bay (SEQ) (Ridley, 1884a; Hoover, 1984a; present study) (Fig. 153H); also Aru and Kai Is, Indonesia (Hentschel, 1912; Brondsted, 1934).

DESCRIPTION. Shape. Growth form invariably thin, planar reticulate flabellate, 150-460mm long, 185-290mm maximum span, with short thick, cylindrical stalk (22-54mm long, 12-30mm diameter) and small peduncle; branching planar-dendritic reticulate, with ascending radial primary branches and interconnecting secondary branches; branches form tight meshes (4-9mm diameter); primary branch diameter 12-16mm, 6.5-9.5mm midway, 1.5-4mm near apex of fan; connecting branches 1.5-3mm diameter.

Colour. Consistent, unpigmented, light beige-brown in both life and ethanol (Munsell 2.5Y 8/2-5Y 8/4).

Oscules. Not observed in live or preserved material.

Texture and surface characteristics. Firm, barely compressible, particularly on woody basal stalk; surface optically smooth, without conules or other visible processes, little flesh; microscopically hirsut, irregular, consisting of tight reticulation of compacted fibres and protruding megascles.

Ectosome and subectosome. Poorly developed ectosomal skeleton, without obvious spicule brushes but with sparse paratangential smaller ectosomal auxiliary stylostyles scattered over surface; ascending plumose choanosomal principal styles usually protrude through ectosomal skeleton with bases embedded in peripheral spongin fibres; especially at fibre junctions and on fibre endings; detritus also often present on sur-
face, sometimes replacing dermal skeleton entirely; subectosomal peripheral skeleton not sharply delineated from deeper choanosomal regions with choanosomal fibres usually immediately subdermal; meshes formed by fibre anastomoses often wider in peripheral skeleton. 

**Choanosome.** Skeletal architecture irregularly reticulate, without differentiation between axial or extra-axial regions; spongib fibres heavy, 40-110 μm diameter, without any clear division between primary or secondary elements; fibres form oval or rectangular meshes, 100-220 μm diameter in axis, 280-405 μm diameter near periphery; fibres uncored, usually heavily echinated by both acanthostyles and principal spicules especially at fibre junctions; very few fibres have unispecific core of subectosomal auxiliary megascleres; extra-fibre spicle development minimal, where present consisting of plumose ascending tracts of subectosomal auxiliary subtylostyles; mesohyl matrix light and collagen found mostly around fibre nodes, with few microscleres and sometimes detritus scattered throughout.

**Megascleres** (Table 33). Principal choanosomal subtylostyles long, thick, slightly curved near the basal end, with slightly subtylote microspinose bases, fusiform points; occasionally completely smooth styles, sometimes both lightly spined shafts and bases intermediate between choanosomal spicules and acanthostyles (both echinating fibres).

Subectosomal auxiliary subtylostyles straight, thin, slightly subtylote microspined bases, occasionally smooth, fusiform points.

- Ectosomal auxiliary subtylostyles smaller, thinner than subectosomal, invariably with microspined bases. 
- Acanthostyles variable in size, characteristically curved at centre, lightly spined, spines small, recurved more-or-less evenly dispersed, bases slightly subtylote, points hesitate or rounded. 

**Microscleres** (Table 33). Palmate isochela commonly, relatively small, never contort, with lateral and front alae of equal size, lateral alae completely fused to shaft, front ala entire, sometimes alae vestigial reduced to a ridge on shaft.

Toxas accolada, very common in some specimens, rare in others, mostly thin, rhabidiform, long, with slight central curvature, tapering arms, little apical reflexion, less often short and curved.

**Associations.** Scyllidae polychaete worms (*Typosyllis spongicola*) abundant in 60% of specimens examined, identical to commensals seen in *C. (T.) reinwardtii* and *C. (T.) lendenfeldi*. 

**Variation.** Growth form and colour relatively consistent. Growth form: consistently planar, stalked, with more-or-less tightly anastomosing branches, although two morphs recognised; typical morph (64% of specimens, including type material) with thicker ascending almost dendritic (primary) branches radiating outwards to produce an arborescent appearance; second morph (36% of specimens, including type material of *S. juniperina*) have even branching, even branch sizes and mesh sizes closely resemble *Echinodictyum cancellatum* (*Raspailiidae*). Foreign detritus in skeleton: abundant in choanosomal mesohyl of deeper water specimens (70 m depth),
rare in samples from shallower habitats (38-46 m depth). Ectosomal skeleton: occasionally well developed, thick, typical of *Thalysias* condition (but also including principal spicules protruding through ectosome) (13% of specimens), more sparsely developed (20%), variable ectosomal development (well formed in some regions, such as surface irregularities, completely absent from other regions) (7%), or consistently poorly developed (60%). Subectosomal skeleton: poorly developed with peripheral choanosomal fibres lying immediately below the surface and thin paratangential spicule tracts (87% of specimens), or well formed (wide) plumose extra-fibre skeleton (13%). Choanosomal skeleton: fibres heavy (67% of specimens), or much lighter in construction (33%). Coring spicules: irregularly reticulate thick spongion fibres largely uncored (81% of specimens), more regularly renieroid-reticulate with thicker fibres cored by paucispicular tracts of choanosomal styles (12%), or fibres mostly cored by choanosomal styles (7%). Fibre diameter: even, consistent throughout skeleton (81% of specimens), with distinct primary (ascending) and secondary (transverse) fibre elements (12%), or noticeably heavier fibres in the axis than in the peripheral skeleton (7%). Echinating spicules: moderately heavy acanthostyles and choanosomal styles forming dense plumose tufts at fibre nodes, producing ascending extra-fibre tracts extending into peripheral skeleton (80% of specimens), or with more poorly developed echinating spicules seemingly dispersed at random throughout skeleton (20%). Mesohyl matrix: light with collagen found mainly around fibre nodes (93% of specimens), or heavy, granular (7%). Megasclere geometry: Principal spicules predominantly hasily spined, but with variable proportion of entirely smooth spicules in specimens, ranging from 0-10% of spicules sampled (67% of specimens), 16-30% (27%), up to 56% of spicules (6% of specimens). Larger auxiliary subtlyostyles usually with microspined bases, and only 0-10% of spicules sampled (73% of specimens) were smooth, 12-20% with higher proportion basaly spined (20%), up to 32% of spicules (7% of specimens). Smaller auxiliary spicules mostly common in histological preparations, although exceptionally producing well-formed dermal structures (93% of specimens), or scarce in both sections and spicule preparations. Microscleres: Isochelae abundant (26% of specimens), common (33%), rare (21%), or absent entirely (20%).

Toxas: abundant (26% of specimens), common (20%), rare (47%) or absent (6%).

Variability in spicule dimensions: Discounting the anomalous southern Queensland specimen (QMG4731) discussed further below, spicule dimensions were relatively consistent throughout the species' geographical distribution (Table 33). For all categories of megascleres, spicule length was on average higher for the Queensland specimen than samples from the northwest and west coast, whereas the mean width of most megascleres, and the length of isochelae were relatively more homogeneous between all samples. Toxas were also significantly shorter in the southern Queensland specimen. Analysed by locality, variation in spicule lengths and widths did not conform to any obvious latitudinal gradient in sample distribution (the three major sampling localities for this species were 19°, 16° and 12°S latitudes) for the west coast material (P<0.05), for all spicule types, although the inclusion of Queensland material (27°S) in analyses did reveal significant differences (commonly at P<0.005) in all spicule categories except isochelae (Table 34). Excluding Queensland material (collected at 94 m depth), there were no significant differences in mean spicule lengths or widths between specimens collected from 38-46m or 70-90m depth ranges (P>0.05) for all spicule categories except acanthostyles.

REMARKS. This species has a characteristic planar, flabellate growth form similar to *C. (C.) loveni* Fristedt (1887: 459) (from North America) and *C. (C.) ulmas* Vosmaer (1880: 151; 1935a: 633) (from an unknown locality). Previous descriptions omitted to mention thin, raphidiform toxas or presence of two size categories of auxiliary megascleres (Table 33). These were seen in all type and recent material, and possession of two size categories of auxiliary spicules places the species in the *Clathria* (*Thalysias* group although it is atypical of most other species in having only rudimentary ectosomal structure, with sparse spicule brushes.

This species belongs to the *spicata* complex (Hallmann, 1912; Hooper et al., 1990) based on skeletal architecture (virtual absence of coring megascleres in fibres, inclusion of choanosomal principal spicules echinating fibres, imperfect differentiation of principal and auxiliary megascleres, the semi-plumose or spiculate arrangement of choanosomal megascleres protruding through fibres, and dense echination of peripheral fibres). Included in this group are: *C. (T.) lenden-
TABLE 34. Summary of results of one-way ANOV’s (Model I), testing for variability in spicule lengths and widths between locality and bathymetric distribution of Clathria (Thalysias) cuppingeri.

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>LOCALITY</th>
<th>DEPTH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N)</td>
<td>F</td>
</tr>
<tr>
<td>CHOANOSOMAL STYLES L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>12.56</td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>2.89</td>
</tr>
<tr>
<td>SUBECTOSOMAL STYLES L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>8.18</td>
</tr>
<tr>
<td>ECTOSOMAL STYLES L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>0.29</td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>8.87</td>
</tr>
<tr>
<td>AcanthoStyles L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>(350)</td>
<td>9.95</td>
</tr>
<tr>
<td>Chelae L</td>
<td>(275)</td>
<td>0.37</td>
</tr>
<tr>
<td>toxas L</td>
<td>(325)</td>
<td>11.48</td>
</tr>
<tr>
<td>W</td>
<td>(325)</td>
<td>0.78</td>
</tr>
</tbody>
</table>

Number of groups: 1. 4 locality groups (27, 19, 16, 12°S latitude) 2. 2 depth groups (38-46m, 70-90m depth)

feli, C. (T.) major, C. (C.) caelata, C. (C.) inanchorata, C. (T.) clathrata, C. (T.) costifera (including the nominate species Clathria spicata, C. bispinosa, C. whiteleggei and Ophtisaspengia membranacea, which have since been shown to be conspecific with other species of the spicata group; Hooper et al., 1990). This assemblage of species does not appear to constitute a natural taxon because it cuts across a classification based on other (possibly more important) characters (viz. Clathria and Thalysias). Nevertheless, all species are very close in fibre construction and spicule geometry, and in fact C. (T.) cuppingeri and C. (T.) lendenfeldi can only be easily differentiated on the basis of their respective growth forms, which is very characteristic for the former, but relatively variable in the latter species (see Hooper et al., 1990).

The single known specimen from southern Queensland differs in many respects from other populations, accounting for most of the variability documented above. In shape it is close to Lamarck’s (1814) variety thuyaethformis (Topsent, 1932: pl.5, fig.1), whereas most samples examined resemble type material (Fig. 1531-J). This specimen also has a well developed ectosomal skeleton (consisting mainly of larger subectosomal megascleres which surround the bases of protruding choanosomal styles); true (smaller) ectosomal auxiliary spicules have haste points (whereas in typical material they are fusiform); ectosomal spicules occur in light paratangential bundles near the surface (versus not forming brushes); fibres are lightly cored by paucispicular tracts of choanosomal styles, which produce an irregular reticulation (whereas most specimens have aspicular fibres); acanthostyles are only sparsely spined, and together with choanosomal styles, always form ascending extra-fibre tracts within the skeleton. This specimen was initially assigned to C. (T.) cuppingeri with some hesitation, but there is no doubt that it belongs to this species and probably represents the southernmost extent of its geographical range.

There is a nomenclatural complexity that requires brief comment. Wiedenmayer (1989) suggested that the senior ‘variety’ name of S. juniperina (viz. thuyaethformis) had priority over Ridley’s (1884a) subsequent species name, but this is not accepted here. Lamarck (1814) described several distinct ‘varieties’ of S. juniperina, for which he used Greek symbols but not a trinomen. It was Topsent (1932) who subsequently elevated Lamarck’s ‘variety B’ to a subspecific rank by using it in a trinomen (ICZN Article 45fii), using the name thuyaethformis as a noun whereas it was previously used as an adjective by Lamarck. This subsequent designation is therefore considered to be infraspecific, not subspecific (ICZN, Article 45f), and does not take precedence over Ridley’s (1884a) species designation. Further support of this opinion is that S. juniperina thuyaethformis is a composite taxon as some of Lamarck’s syntypes belong to different species. Thus the choice of the name cuppingeri over thuyaethformis is also supported by ICZN Article 57g, and the pragmatic argument that Ridley’s (1884a) name has now become well known for this species.
Claithria (Thalysias) coralliphila (Thiele, 1903) (Figs 155-156, Table 35, Plate 5C)

Rhaphidophalus coralliphilus: Thiele, 1903a: 959, 968, pl.28, fig.25a-d.
Rhaphidophalus coralliphilus: Hallmann, 1912: 177.
Tomina coralliphila: Burton, 1934a: 560.


cf. Microciona prolifera; Voight, 1935a: 611, 645.

MATERIAL. LECTOTYPE: SMF1784 (fragment ZMB3145); Ternate, Moluccas, Indonesia, 0°48'N, 127°23'E, 1894, coll. W. Kükenthal (dredge).

HABITAT DISTRIBUTION. Growing on on Serioura coral, bivalves and dead coral substrates; shallow intertidal to 8m depth; Low I (NEQ) (Fig. 155H); also Moluccas, Indonesia; Motupore I., S. PNG.

DESCRIPTION. Shape. Thin, thick, or massively encrusting, covering up to 80mm surface.

Colour. Red, dark orange or pale pinkish alive (Munsell 5R 8/2 - 10R 6/10), grey in ethanol.

Oscules. Large, up to 4mm diameter, scattered over surface, slightly raised above surface with membranous lip.

Texture and surface characteristics. Firm, compressible; surface even, smooth, fleshy, without obvious sculpturing, microscopically hispid.

Ectosome and subectosome. Well developed, dense, continuous palisade of ectosomal auxiliary spicule brushes in 1 or more plume layers (several consecutive brushes of spicules overlaying one another); ectosomal skeleton supported by well developed series of discrete subectosomal plume layers, the latter not protruding through ectosome; subectosomal region cavernous with numerous plume brushes of larger auxiliary subtylostyles.

Choanosome. Skeletal structure ranges from thin basal layer of spongion on substrate (hydmedesmoid), to large, erect, non-anastomosing, single fibre nodes arising from encrusting basal layer of spongion (microcionid); basal (hydmedesmoid) fibres very heavily echinated by erect choanosomal principal styles and acanthostyles; digitate (microcionid) fibre nodes cored by erect multispiracular tracts of choanosomal principal spicules, congregated especially on ends of fibre nodes, forming plume brushes and producing a series of ascending plume or occasionally anastomosing tracts; subectosomal tracts mostly perpendicular, less commonly longitudinal in thinner sections, always plumose; echinating acanthostyles concentrated primarily in basal part of skeleton, rarely near surface, forming very dense erect layers on basal (hydmedesmoid) fibres; mesohyl matrix moderately heavy, granular, abundant subectosomal auxiliary styles dispersed between choanosomal spicules; choanoocytes chambers small, oval or elongate, 120-250μm diameter.

Megascleres (Table 35). Choanosomal principal styles long or short, slightly curved, with rounded or only slightly subtylolette, smooth bases, tapering to sharp fusiform points; rarely differentiated from subectosomal auxiliary spicules, being only marginally thicker and more curved and with predominantly smooth bases.

Subectosomal auxiliary subtylostyles relatively long, straight, thin, sharply pointed, with mostly microspinted subtylolette bases.

Ectosomal auxiliary subtylostyles short, relatively thick, slightly curved, usually with subtylole mockmicrospined bases.

Acanthostyles relatively long, thin, subtylolette with aspionine necks, spines slender, long, slightly recurved.

Microsclees (Table 35). Palmate isochelae very abundant, in two size classes, the smaller often contort; larger with lateral alae marginally smaller than front ala, with lateral alae not completely fused to shaft, and front ala widely separated from lateral alae.

Toxas very abundant, short, thin, mostly wing-shaped with slightly curved centre and slightly unreflexed points, sometimes u-shaped with nearly straight arms and slight central curvature. Larvae. Incubated larvae large, spherical parenchymella, up to 425μm diameter, with light matrix and no larval spicules.

REMARKS. The presence of two size classes of isochelae microsclees, some with geometric modifications, was not previously described for this species, but in other spicule measurements Thiele's (1903a) and Burton's (1934a) specimens agree closely. The two type specimens differ slightly in their gross morphology, and this provides some evidence to illustrate the effect of growth form directly determining skeletal development. Whereas the lectotype is thinly encrusting and hydmedesmoid in architecture, the paralectotype is thick and has a very well developed microcionid choanosomal structure, with ascending fibre nodes closely resembling C. (Microciona) seriata (sensu Simpson, 1968a).
Were it not for the presence of a specialised euctosomal skeleton this specimen would be included in the Microciona group, illustrating the difficulty in recognising generic concepts solely on the basis of skeletal architecture: leptoclathriid, hymedesmoid or microcionid (e.g., the concepts of Leptoclathria, Microciona, Clathria).

Specimens from the Great Barrier Reef and Papua New Guinea also differ from the Indonesian population in having some larger spicules (notably toxas, principal styles and acanthostyles; Table 35), but generally spicule size and spicule geometry are comparable between all specimens, and there is no doubt that these populations are conspecific.

This species is related to the New Caledonian C. (T.) araios, differing in the distribution of spines on acanthostyles and auxiliary spicules, and specific dimensions of megasccleres (which are generally smaller in C. (T.) araios, and Hooper & Lévi (1993a) suggested that these similarities in skeletal architecture and spicule geometry may be indicative of a sibling species relationship.

**Clathria (Thalysias) costifera** Hallmann, 1912 (Figs 157-158)


**MATERIAL. HOLOTYPE:** AME650: E. coast of Flinders Is, Bass Strait, Tas, 40°01’S, 148°02’E, coll. FIV ‘Endeavour’ (dredge). OTHER MATERIAL: S. AUST. – AME1035 (dry), VIC – QMG300666 (NC1Q66C3633-P) (fragment NTMZ3798).

**HABITAT DISTRIBUTION:** Rock reef; 15-60m depth; Bass Strait (Tas), Furneaux Is (Vic), Kingston (SA) (Fig. 157G).

**DESCRIPTION. Shape.** Large, thinly flabellate, planar, 170-220mm high, 120-270mm wide, with small cylindrical basal stalk, 24-55mm long, 18-38mm diameter, corrugated apical margins.

**TABLE 35. Comparison between present and published records of Clathria (Thalysias) corallipila (Thiele).** All measurements are given in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Lectotype (SMF1784)</th>
<th>Paralectype (SMF787)</th>
<th>GBR (BMNH 1908.13.107)</th>
<th>PNG (NC1Q66C4518A)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaoanosomal principal styles</td>
<td>145-(252.8)-406x 7-(10.5)-13</td>
<td>164-(279.8)-349x 10-(11.5)-14</td>
<td>285-(347.5)-408x 12-(13.8)-15</td>
<td>224-(345.2)-452x 10-(12.4)-15</td>
</tr>
<tr>
<td>Subeuctosomal auxiliary styles</td>
<td>321-(355.4)-390x 5-(7.3)-11</td>
<td>233-(302.7)-350x 6-(7.2)-9</td>
<td>312-(390.4)-488x 5-(7.9)-10</td>
<td>223-(347.2)-430x 5-(7.2)-9</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>104-(150.1)-208x 2-(3.1)-4</td>
<td>102-(115.8)-134x 2-(3.2)-4</td>
<td>118-(140.9)-174x 2-(3.1)-4</td>
<td>109-(121.5)-138x 2-(3.5)-5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>48-(56.3)-71x 4-(5.2)-6</td>
<td>52-(66.6)-78x 3-(5.2)-8</td>
<td>84-(95.0)-105x 4-(6.5)-8</td>
<td>76-(85.8)-95x 5-(6.6)-8</td>
</tr>
<tr>
<td>Chela I</td>
<td>2-(4.6)-8</td>
<td>3-(5.3)-8</td>
<td>2-(4.4)-8</td>
<td>3-(5.1)-8</td>
</tr>
<tr>
<td>Chela II</td>
<td>11-(13.1)-16</td>
<td>11-(12.8)-15</td>
<td>11-(13.5)-17</td>
<td>10-(12.1)-15</td>
</tr>
<tr>
<td>Toxas</td>
<td>18-(76.6)-118x 0.5-(0.9)-1.2</td>
<td>6-(35.2)-84x 0.5-(0.7)-1.0</td>
<td>69-(140.3)-244x 0.5-(1.4)-2</td>
<td>32-(125.3)-211x 0.5-(1.2)-2</td>
</tr>
</tbody>
</table>

**Colour.** Dark red alive (Munsell 2.5R4/10); grey-brown in ethanol.

**Oscules.** Small, up to 2.5mm diameter, scattered over entire surface, not apparently confined to any particular region.

**Texture and surface characteristics.** Harsh, firm, compressible, flexible; surface rugose with prominent striations, raised ridges and euctosomal grooves running longitudinally and radially.

**Ectosome and subeuctosome.** Dense euctosomal skeleton consisting of erect plumose brushes of smaller euctosomal auxiliary subtylostyles forming a continuous palisade on surface; subeuctosomal skeleton plumose with erect brushes of larger auxiliary subtylostyles arising and diverging from ends of choanosomal spicules in peripheral fibre skeleton; subeuctosomal megasceralcs protrude into and partially intermixed with smaller euctosomal spicules although both spicule categories with distinctly localised distribution.

**Choanosome.** Chaoanosomal skeletal architecture irregularly reticulate, with heavy fibres and ascending primary and transverse secondary fibre components; primary fibres have paucispecular core of both choanosomal principal and subeuctosomal auxiliary megasceralcs, and choanosomal styles also protrude through fibres to form ascending, plumose brushes near periphery; secondary fibres entirely aspcicular; echinating acanthostyles relatively sparse at core, slightly more numerous towards peripheral skeleton; mesohyl matrix moderately light, with few megasceralcs scattered between fibres.
Megascleres. Choanosomal principal styles long or short, moderately slender, straight or only slightly curved at centre, with rounded or slightly subtytule smooth bases, fusiform points. Length 110(189.6)-305\,\mu m, 4-(5.8)-7\,\mu m width (holotype 129-315 x 6-9\,\mu m).

Subectosomal auxiliary subtytlose styles slender, straight or very slightly curved near basal end, with smooth well developed subtytule bases, fusiform points. Length 296-(321.3)-342\,\mu m, width 3-(3.8)-5\,\mu m (holotype 198-336 x 3-7\,\mu m).

Ectosomal auxiliary subtytlose styles, straight or slightly curved at centre, with prominently subtytule smooth bases, fusiform points. Length 117-(152.2)-175\,\mu m, width 2-(2.6)-4\,\mu m (holotype 112-158 x 2-3.5\,\mu m).

Echinating acanthostyles slender, usually slightly curved at centre, with subtytule bases, fusiform points, rudimentary spination, small spines, aspinous 'neck' region proximal to base. Length 76-(85.4)-95\,\mu m, width 4-(4.3)-5\,\mu m (holotype 56-92 x 4-7\,\mu m).

Microscleres. Isochelae absent.

Toxas accolata, abundant, long, thin or rhaphidiform, with slightly angular central curvature, straight arms, unreflexed points, sometimes completely straight. Length 176-(215.2)-264\,\mu m, width 0.5-(0.8)-1.0\,\mu m (holotype 110-315 x 0.5-1.2\,\mu m).

REMARKS. Vosmaer's (1935a) remark that C. (T.) costifera was a synonym of C. (C.) caelata is not supported here, although both species do belong to Hallmann's (1912) 'spicata' group (with spicules protruding from fibres in plumose brushes). They differ in tox a geometry (rhaphidiform accolata versus thicker accolata plus oxhorn, respectively), and C. (C.) caelata has only a single size category of auxiliary spicule (whereas C. (T.) costifera obviously belongs to C. (Thalysias) in having two categories).

Although apparently initially identified only by superficial comparison with the holotype (according to its specimen label), another specimen found in general collections of the AM(E1035) also belongs to this species. The more recent material described above from the Furneaux Islands is surprisingly only the third known record for this large, conspicuous, brightly coloured species. It differs only slightly from the holotype in having abundant, very small sand grains scattered throughout the mesohyl, and accolata toxas that are nearly straight (oxeote) or have only very slight, angular, central curvature (whereas in the holotype they are more generously curved).

Clathria (Thalysias) craspedia sp. nov.
(Figs 159-160, Plate 5E-F)


HABITAT DISTRIBUTION. In sand, coral rubble, coral substrata at base of granite boulders; 15-22m depth; Tweed River region (NSW) (Fig. 159G).

DESCRIPTION. Shape. Growth form erect, lamellate, digitate or bulbous-lobate, 120-230mm long, 8-50mm diameter, partially buried into soft sediments with rhizomous root-like attachments found just below the surface; digits slightly flattened, irregularly shaped, usually branching, typically anastomosing with or entirely fused to adjacent digits forming contiguous lamellae, occasionally isolated, single, completely attached or only partially attached to substrate, with tapering and frequently bifurcate apex.

Colour. Yellow-orange (Munsell 7.5YR 7/10) to red-brown alive (10R 6/10), grey-brown in ethanol.

Oscules. Large, 2-5mm diameter, slightly raised above surface, with membranous lip, scattered over lateral margins of digits or on apex of digits. Texture and surface characteristics. Firm, compressible, flexible; surface fleshy, mostly smooth, relatively even in cylindrical specimens, or with crenellated margins in erect bulbous specimens.

Ectosome and subectosome. Ectosomal skeleton composed of relatively dense but discrete bundles of smaller ectosomal auxiliary styles, supported beneath by parangential, occasionally plumose brushes of larger subectosomal auxiliary subtytlostyles arising from terminal choanosomal spongion fibres; mesohyl matrix light in choanosome but more darkly pigmented in peripheral skeleton.

Choanosome. Regularly reticulate, widely meshed, with heavy spongion fibres differentiated into primary and secondary elements, but no axial compression or differentiation between axial and extra-axial regions of skeleton; fibre diameter relatively homogeneous throughout skeleton, with fibres distinguished mainly by numbers of coring spicules, whereas fibre nodes prominently bulbous, up to 160\,\mu m diameter; primary ascending fibres, 45-90\,\mu m diameter, cored by 4-8
spicules abreast; secondary mainly transverse, connecting fibres, 40-65μm diameter, with 1-3 spicules abreast; fibre reticulation forms cavernous, triangular or oval meshes, 180-360μm diameter; echinating acanthostyles absent; mesohyl matrix heavy but only lightly pigmented
thoughout choanosome, with numerous auxiliary spicules scattered between fibres; choanoocyte chambers oval, 30-45μm diameter.

**Megascleres.** Choanosomal principal styles long or short, slender, straight, with evenly rounded smooth bases, telescoped points. Length 103-(221.4)-305μm, width 3-(4.1)-6μm.

Subectosomal auxiliary subtylosstyles long, slender, straight, with smooth subtylostyle bases, fusiform points. Length 255-(316.6)-361μm, width 2.5-(3.8)-4.5μm.

Ectosomal auxiliary styles short, slender, straight, with smooth subtylostyle or evenly rounded bases, fusiform points. Length 107-(135.4)-174μm, width 1.5-(2.3)-3μm.

Echinating megascleres absent.

**Microscleres.** Palmate isochelae in single size class but variable length, with front ala slightly longer than lateral alae, lateral alae fused completely to shaft, front ala entire, and apex of spicule characteristically constricted, pointed. Length 5-(10.7)-14μm.

Textas moderately short, thick, wing-shaped, with rounded or slightly angular central curvature, non-reflexed arms. Length 16-(42.7)-76μm, width 0.8-(1.9)-2.5μm.

**ETYMOLOGY.** Greek kraspedon, edge or border; occurring in the transition zone between the Solanderian and Peronian biogeographic provinces.

**REMARKS.** This is a sibling species of C. (T.) cervicornis, initially referred to that species based on skeletal structure and spicule types; it is separate by its different growth forms, surface features, live colouration and several subtle but important skeletal characters (i.e., C. (T.) craspedia lacks echinating megascleres, the bases of all megascleres have different terminations such as telescoped points, smooth subtylostyle swellings, principal and auxiliary megascleres are differentiated within fibres, and isochelae have a terminal tooth-like constriction). These differences in skeletal characters might be intraspecific variability, and the 4 populations (i.e., including C. (T.) fusterna sp. nov. and C. (T.) corneolata) may represent a single, widely dispersed species. I consider major differences in growth forms, surface features and live colouration are consistently correlated to skeletal differences, supporting distinct taxa for the Tweed River and Gulf of Carpentaria populations (C. (T.) fusterna below and Hooper & Lévi, 1993a).

Whereas C. (T.) cervicornis is habitually long, thin, cylindrical, digitate, attached to the substrate at one or few points, and characteristically forms extensive tangles or thickets.

**Clathria (Thalysias) darwinensis** sp. nov. (Figs 161-162, Plate 6B)


**HABITAT DISTRIBUTION.** Coral pinnacle near mouth of estuary, high sediment, turbid water; 19m depth; Darwin Harbour (NT) (Fig. 161H).

**DESCRIPTION.** Shape. Arborescent, very thinly branching, reminiscent of an *Arxina* (Axinellidae), 290mm high, 340mm maximum breadth of branches, with short basal stalk and point of attachment, 85mm long, 35mm diameter; main branches long, subcylindrical, up to 22mm diameter, slightly flattened, producing numerous smaller branches, up to 14mm diameter, con-voluted, bulbous branch nodes, and branches repeatedly bifurcate, decreasing in size, towards tapering, pointed branch tips.

**Colour.** Pale cream alive (Munsell 5YR 8/2), darker yellow-brown in air, pale brown in ethanol.

**Oscules.** Small, on lateral sides of branches, up to 3mm diameter, surrounded by slightly raised membraneous lip.

**Texture and surface characteristics.** Soft, compressible, flexible branches, more harsh in ethanol; surface optically hispid, fleshy alive, even, bulbous, turgid, non-porous, but contract- ing greatly in ethanol producing porous, microconulose, uneven, irregular surface with scattered sharp conules.

**Ecosome and subectosome.** Ecosome dominated by long, single, erect principal styles at regular intervals on surface, 400-500μm apart, extending 300-450μm from surface, surrounded at base by paratangential tracts of both larger and smaller auxiliary subtylosstyles, sometimes in plumose brushes surrounding base of principal spicule, more often in tangential or paratangential tracts; echinating acanthostyles also erect peripheral fibres, protruding through surface; subectosomal skeleton usually reduced with peripheral choanosomal fibres immediately below ectosome, whereas on surface conules auxiliary spicules produce more-or-less erect bundles associated with protruding principal spicules; no obvious localisation of smaller (ectosomal) or larger (subectosomal) auxiliary spicules, both appearing to be intermingled in
surface brushes; mesohyl matrix moderately heavy in ectsosomal skeleton.

**Choanosomal**. Choanosomal skeleton irregularly reticulate, more regular (subrenieroid) in peripheral region, slightly compressed at axis; sponglin fibres heavier in axis (110-160μm diameter) than at periphery (60-90μm diameter), producing wide-meshed reticulation and slight axial compression; fibres imperfectly divided into primary and secondary elements; primary fibres ascend to surface with little or no bifurcation and relatively few transverse connecting fibres, producing a nearly subrenieroid peripheral skeleton; primary fibres cored by 2-5 principal spicules, confined entirely to centre of each fibre, not protruding through fibres except at surface; secondary fibres short, more-or-less transverse, cored by 1-3 principal spicules abreast, interconnecting primary fibres mainly in axial region of skeleton, producing oval or elongate fibre meshes, generally smaller at core (120-190μm diameter) than periphery (170-240μm diameter); fibres moderately heavily echinatcd by acanthostyles, evenly distributed over fibres although possibly more abundant on exterior surface of fibres, especially in peripheral skeleton; mesohyl matrix moderately light, including some auxiliary spicules scattered between fibres; choanosome chambers small, oval, 12-24μm diameter.

**Megascleres**. Choanosomal principal styles long, robust, slightly curved near base, entirely smooth, evenly rounded bases without any tylote swelling, long, tapering, fusiform points. Length 188-(301.8)-492μm, width 4-(12.5)-21μm.

Subectosomal auxiliary stylolysttes long, slender, straight, slightly subtylotylote microspined bases, fusiform points. Length 210-(282.2)-365μm, width 3-(4.3)-6μm.

Ectosomal auxiliary stylolysttes short, slender, straight, slightly subtylotylote microspined bases, fusiform points. Length 115-(135.3)-153μm, width 1.5-(2.1)-2.5μm.

Echinatcd acanthostyles long, slender, straight or slightly curved at centre, slightly subtylotylote bases, evenly spined except for aspinose 'neck' proximal to base; spines large, recurved, sharp, points sharp or slightly rounded, spinose. Length 96-(104.8)-116μm, width 3-(5.6)-11μm.

**Microscleres**. Palminate isochelae abundant, single size class, unmodified, with lateral and front alae approximately same length, long, lateral alae entirely fused to shaft, front ala detached along lateral margin. Length 15-(16.8)-18μm.

Toxas abundant, wing-shaped, thick, variable in length, with wide central curvature, slightly reflexed arms. Length I: 73-(111.2)-124μm, width 2-(3.8)-8μm; length II: 17-(26.2)-36μm, width 0.5-(1.7)-2.0μm.

**ETYMOLOGY.** For the type locality.

**REMARKS.** Clathria (T.) darwinensis is similar to C. (T.) lendenfeldi, C. (C.) inanchorata and C. (T.) coppingeri of the spicata group having choanosomal principal spicules protruding through peripheral sponglin fibres forming a hispid surface. It differs from these species, and to some extent the concept of the spicata group, having smooth principal styles enclosed within sponglin fibres, only protruding through fibres at the surface, and with all fibres more-or-less fully cored by principal spicules. This species is also similar to C. (C.) transiens in ectsosomal structure (with prominent, individually protruding, smooth principal spicules), and also in having a vaguely sub-renieroid skeletal architecture, and toxa morphology, but the two differ in their acanthostyle geometry (in C. (T.) darwinensis these are long, slender, unevenly spined, with large, recurved spines, whereas in C. (C.) transiens they are short, unspined, or even lightly spined with vestigial spines), possession of 2 size classes of auxiliary styles (versus one size class), thinly branching gross morphology (versus bulbous branches), and spicule dimensions.

**Clathria (Thalysias) dubia** (Kirkpatrick, 1900) (Figs 163-164)

**Microciona dubia** Kirkpatrick, 1900a: 128, 136, 141, pl.12, figs.3,3a, pl.13, fig.2a-f.

**Cionanchora dubia**; de Laubenfels, 1936a: 108.

**Clathria dubia**; Hooper & Wiedenmayer, 1994: 270.

**Microciona prolifera**; Vosmaer, 1935a: 608, 643.

**MATERIAL.** HOLOTYPE: BMNH1898.12. 20.37; Flying Fish Cove, Christmas I., Indian Ocean, 10°25.5'S, 105°40'W, coll. Mr Andrews (dredge).

**HABITAT DISTRIBUTION.** Coral rubble; probably intertidal; Christmas I. (Indian Ocean) (Fig. 163H).

**DESCRIPTION.** Shape. Thickly encrusting lamella, 12mm diameter, on eroded bivalve shell. Colour. Yellow preserved.

**Oscules.** Not seen.

**Texture and surface characteristics.** Compressible; optically smooth surface.

**Ectosome and subectosome.** Ectosome microscopically hispid, with bundles of ectsosomal auxiliary megascleres protruding through surface, forming a relatively thick dermal palisade, arising from subdermal brushes of subectosomal
spicules; subectosomal skeletal architecture plumose, with subectosomal auxiliary subtylostyles arising from ends of choanosomal megascleres.

**Choanosome.** Choanosomal skeletal hymedesmoid, with a thin layer of spongin lying on substrate, in which bases of erect choanosomal principal subtylostyles and acanthostyles are em-bedded; small amounts of detritus scattered within skeleton; mesohyl matrix relatively heavy. **Megascleres.** Choanosomal principal subtylostyles long or short, slightly curved, usually with prominently microspined bases, occasionally smooth, bases subtyloate, points fusiform. Length 132-(195.6)-292μm, width 7-(10.6)-16μm.

Subectosomal auxiliary subtylostyles long, straight, with prominent subtyloate, microspined
bases, fusiform points. Length 218-(280)-314μm, width 4.5-(5.9)-7μm.

Ectosomal auxiliary subtylostyles straight, with well formed tylole, microspined bases, fusiform points. Length 86-(110.2)-153μm, width 3-(3.9)-5μm.

Acanthostyles short, thick, tapering club-shaped, with large recurved spines on basal portion of shaft, aspinose point; spines on basal swelling often bifurcate, greatly recurved. Length 35-(46.4)-54μm, width 5-(8.2)-11μm.

Microsceres. Isochelae modified palmate, very small, often anisochelate, with lateral alae completely fused to shaft, front ala often bifurcate or trifurcate, producing multiple, partially fused teeth. Length 2-(4.8)-8μm.

Toxas divided into two morphs - I: very short, ? oxhorn, relatively thick, slightly curved at centre, with slightly reflexed points. Length 4-(6.6)-9μm, width 0.5-(1.1)-1.5μm. II: Accolada, long, thin, with gently rounded or angular curvature, with straight points. Length 112-(195.2)-295μm, width 0.5-(1.4)-2μm.

REMARKS. De Laubenfels (1936a) assigned this species to Cionanchora because it supposedly had anchorate (rather than palmate) isocheleae, although differing in no other respect from typical species of Clathria (Thalysias). Scanning electron micrographs show that these cheleae have modified lateral alae completely fused to the shaft and front alae often split into several 'teeth', producing an anchorate-like appearance, but they are obviously palmate in origin. The species is well characterised by its megascere and microscere geometry, although the species is so far known only from a single specimen from Christmas Island.

Clathria (Thalysias) erecta (Thiele, 1899)
(Figs 165-166, Table 36)

cf. Microciona prolifera; Vosmaer, 1935a: 611.

MATERIAL. LECTOTYPE: NMB19 (fragment BMNH1908.9.24.163); Kema, Minahassa, Celebes (Sulawesi), Indonesia, 2°S, 120°30'E, coll. P. & F. Sarasin (dredge). PARALECTOTYPE: NMB18 (fragment BMNH1930.7.1.7); same data. OTHER MATERIAL: NT - NTM23113 (fragment QMG-300579), NTMZ3146 (fragment QMG300219). INDONESIA - SMF1788.

HABITAT DISTRIBUTION. Coral reef and coral rubble; 16-20m depth; known Australian distribution: Parry Shoals, Timor Sea (Fig. 165H); also Moluccas and Sulawesi, Indonesia (Thiele, 1899, 1903a), Vietnam (Lévi, 1961a).

DESCRIPTION. Shape. Elongate, arborescent, 90-240mm high, with a short cylindrical stem, 25-75mm long, 15-25mm diameter, bifurcate and relatively thick cylindrical branches, up to 35μm diameter, or lamellate, fused, erect digitate branching pattern.

Colour. Orange to dull brown alive (Munsell 5 YR 7/10 - 7.5 YR 7/6), beige in ethanol.

Oscules. Numerous, small, up to 2mm diameter, scattered over all sides of branches, below surface conules.

Texture and surface characteristics. Firm, flexible, compressible; highly conulose, rugose surface, pocked with holes and drainage canals.

Ectosome and subectosome. Thin but prominent discrete brushes of small auxiliary subtylostyles standing more-or-less perpendicular to surface; subectosomal region cavernous, with plumose tracts of larger subectosomal auxiliary, and choanosomal principal megasceres supporting ectosomal skeleton and protruding through surface.

Choanosome. Very irregularly reticulate, cavernous, with very large primary fibres running longitudinally through branches, up to 140μm diameter, interconnected by smaller tanged secondary fibres, up to 70μm diameter, producing vaguely triangular skeletal meshes, up to 450μm diameter; both primary and secondary fibres heavy, fully cored by multispicular tracts of choanosomal principal styles, and lightly echinated by acanthostyles, the latter slightly more abundant at fibre nodes; mesohyl matrix moderately heavy, with auxiliary megasceres dispersed between fibres.

Megasceres (Table 36). Choanosomal principal styles characteristically curved near basal end, hasteate pointed, with rounded or faintly subtylole, smooth bases.

Subectosomal auxiliary subtylostyles long, thick, straight, fusiform pointed, faintly subtylole smooth bases, or minutely microspined bases.

Ectosomal auxiliary subtylostyles small, slender, prominently subtylole, with microspined bases.

Acanthostyles long, thick, with subtylole bases, fusiform points, heavily spined on base and point but unspined neck; spines characteristically large, recurved, heavily concentrated at point of spicule.

Microsceres (Table 36). Palmate isocheleae in two size classes, the smaller sometimes contort.
TABLE 36. Comparison between present and published records of Clathria (Thalysia) erecta (Thiele). Measurements in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (NMB19)</th>
<th>(Lévi, 1961) Vietnam</th>
<th>Specimens (2) (Timor Sea)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chanoosomal principal styles</td>
<td>174(224.6-292) x 9(13.7-19)</td>
<td>190-300 x 10-22</td>
<td>142(197)-259 x 6(10.9-14)</td>
</tr>
<tr>
<td>Subechosomal auxiliary styles</td>
<td>194(241-2-285 x 4(6.3-8)</td>
<td>255-310 x 6-7</td>
<td>165(226.9-262 x 4(6.6-9)</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>92(138.5-198 x 3(4.2-5)</td>
<td>100-200 x 3-5</td>
<td>85(102.7-134 x 4(4.2-6)</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>64(72.6-78 x 6(6.8-8)</td>
<td>80-95 x 9-10</td>
<td>61(68.5-75 x 5(6.7-8)</td>
</tr>
<tr>
<td>Chela I</td>
<td>4(6.1-8)</td>
<td>?</td>
<td>4(6.3-7)</td>
</tr>
<tr>
<td>Chela II</td>
<td>12(13.4-15)</td>
<td>10-17</td>
<td>10(12.2-14)</td>
</tr>
<tr>
<td>Toxas</td>
<td>12(197.0-265 x 0.8(1.1-1.5)</td>
<td>120-160 x ?</td>
<td>25(138.5-204 x 0.5(1.2-1.5)</td>
</tr>
</tbody>
</table>

Toxas accolada, relatively long, thin, with small, angular central curvature, or rounded centrally, straight arms and reflexed points; juvenile forms resemble oxhorn toxas.

Larvae. Incubated parenchymella larvae small, spherical, 140-190μm diameter. with light mesohyl matrix and larval toxas dispersed within axis.

REMARKS. This species is a sibling of C. (T.) reinwarditi based on similarities in skeletal structure (even-meshed, cavernous primary and secondary tracts), geometry of some spicules (smooth, curved principal styles; robust subechosomal auxiliary subtylostyles; slender accolada toxas with slightly angular central curvature; 2 sizes of isochelae), and live colouration (orange-brown). They differ significantly in growth form (C. erecta is arborescent, thickly branching; C. reinwarditi has only thin or slightly thick cylindrical branches), surface features (prominent surface conules versus completely smooth or irregularly rugose surface), and acanthostyle geometry (tapering, sharply pointed and subtylo bases versus rounded 'points' and only slightly subtylo or rounded bases). Spicule dimensions are also comparable (Tables 36, 39). These differences are consistent for the six known specimens of C. (T.) erecta and for the present these species are maintained as distinct.

Another species, C. (T.) fasciculata Wilson, from Indonesia and the central west Pacific (Wilson, 1925; de Laubenfels, 1954), is also very similar to both C. (T.) erecta and C. (T.) reinwarditi in the diversity and geometry of its spicules, but it differs again in growth form (being bushy, flattened branching), skeletal structure (more irregularly reticulate) and toxo morphology (includes asymmetrical sinuous forms). It is possible that all three species are extreme morphological variants of a single species, in which case reinwarditi would have priority, but all these morphological differences are consistent within each growth form type (morphospecies) and probably represent fixed genetic differences.

Clathria (Thalysia) erecta is also vaguely similar to C. (T.) vulpina in the overall structure of spongin fibre skeleton and spicule skeleton, both species having a characteristic, more-or-less triangular skeletal network of fibre meshes fully cored by principal styles, although this fibre reticulation is much more regular in the latter species. This structural feature is prominent and their inferred similarities are immediately obvious upon casual observation, but the two species differ from each other in most other respects.

The presence of two size classes of isochelae, including contort forms, has not been recorded previously for C. (T.) erecta but are consistently present in all specimens including the type material, Thiele's (1899, 1903a) Indonesian specimens are identical to the Timor Sea specimens in most respects (see Table 36), whereas Lévi's (1961a) material from Vietnam differs slightly in growth form (compare Lévi's (1961a) Plate 1 with Fig. 165-J of the present study), and spicule dimensions are relatively larger.

Clathria (Thalysia) fusterna sp. nov. (Figs 167-168)


HABITAT DISTRIBUTION. Soft sediments, mud, shell grit; 21-58m depth; Shelburne Bay, Torres Strait and Gulf of Carpentaria (FNQ), Gove Peninsula (NT) (Fig. 167H); also Eritrea, Red Sea (present study).

DESCRIPTION. Shape. Erect, club-shaped growth form 190-280mm long, with long thin, cylindrical stalk, 80-150mm long, up to 12mm
diameter, bifurcating several times towards base becoming filamentous, rhizomous (for embedding in soft sediments); rhizomous roots encrusted with sand and shell fragments; apex of club usually large, 50-100mm diameter, 60-110mm long, composed of fused, tightly anastomosing digits; adjacent digits fused with dense fleshy surface; apex of digits tapering slightly pointed.

**Colour.** Grey-brown on-deck (Munsell 2.5 Y 8/2), grey in ethanol.

**Oscules.** Few small pores, 0.5mm diameter, possibly oscules, scattered near apex of digits (seen in preserved material only).

**Texture and surface characteristics.** Stalk tough, wiry, flexible, apex of club softer, more compressible but with firm axis; slightly convoluted surface with sparse conules, up to 3mm high, low ridges or occasional folds on anastomosing digits. **Ectosome and subectosome.** Dense ectosomal skeleton composed of discrete bundles of smaller ectosomal auxiliary subtylostyles supported below by paratangential or plumose brushes of subectosomal auxiliary subtylostyles; mesohyl matrix moderately lightly pigmented in ectosomal skeleton; ectosomal and subectosomal spicule skeletons very dense but together comprise only 10-20% of branch diameter.
**Choanosome.** Heavily reticulate architecture; spongin fibres short, thick, 90-200μm diameter, heavily collagenous, forming tight oval or rectangular meshes, 150-400μm diameter; fibres not obviously differentiated into primary or secondary elements, but meshes slightly more cavernous in peripheral skeleton than in axis; fibres virtually fully cored by multispecific tracts of both subectosomal auxiliary subtylostyles and choanosomal principal styles, together occupying 80-90% fibre diameter, interconnected by very large, bulbous fibre nodes, 160-400μm diameter; fibre nodes contain larger bundles of spicules than in connecting fibres, indicating that fibres ascending through branches are heavier than fibres running from axis to peripheral skeleton; echinating acanthostyles abundant, concentrated mainly on fibre nodes; mesohyl
matrix heavy, with few auxiliary spicules scattered between fibres but abundant microscleres lining small oval choanocyte chambers, 20-45 μm diameter.

**Megascleres.** Choanosomal principal styles robust short or long, thickest towards middle of spicule, straight or slightly curved towards pointed end, with slightly constricted bases, smooth or faintly microspined, fusiform points. Length 185-(264.3)-355 μm, width 5-(13.9)-25 μm.

Subectosomal auxiliary subtylostyles long, thick or thin, mostly straight, with subtylolate microspined bases, only occasionally smooth bases, and fusiform points. Length 211-(369.2)-385 μm, width 4-(9.5)-12 μm.

Ectosomal auxiliary subtylostyles short, straight or slightly curved near basal end, subtylolate microspined bases, fusiform points. Length 99-(127.7)-163 μm, width 2-(3.2)-4 μm.

Echinulating acanthostyles thick, robust, relatively short, heavily spined but with bare neck and point; spines moderately large, conical erect (not recurved). Length 73-(82.8)-96 μm, width 3-(7.4)-12 μm.

**Microscleres.** Palmate isochelae abundant, small, single size class, some contort, with lateral and front alae approximately equal length, lateral alae completely fused to shaft, front ala entire, slight constriction at apex of chela. Length 5-(11.8)-14 μm.

Toxas wing-shaped, relatively thick, with slightly angular central curve, arms at wide angles from centre, straight or slightly reflexed points. Length 18-(41.4)-63 μm, width 1.5-(1.9)-2.5 μm.

**ETYMOLOGY.** Latin *fusta* , club or knotty part of a tree.

**REMARKS.** This species is possibly a very atypical, highly specialised population of *C. (T.) cervicornis* with a specialised, peculiar growth form adapted to living in soft sediments (long stalk, rhizomous roots, club-shaped apex). Its live colouration, gross skeletal structure and spicule diversity are closely comparable with typical populations of *C. (T.) cervicornis*. However, there are subtle differences in skeletal characteristics that consistently differentiate the two populations: possession of differentiated principal and auxiliary spicules (whereas *cervicornis* has undifferentiated structural megascleres), acanthostyly spines are erect, conical (not recurved), a single size class of palmate isochelae (not two), and slightly subtylolate bases on principal and auxiliary spicules (not prominently subtylolate as in most *C. cervicornis*). These subtle differences correlate with the major differences in growth forms and are consequently considered here to justify the recognition of the Gulf of Carpentaria population as a distinct species in a species complex of four: the cylindrical *C. (T.) cervicornis* from the Indo-Malay-western Pacific region; the lamellate *C. (T.) craspedia* sp. nov. from the southern Solanderian province of Australia, and the New Caledonian species *C. (T.) corneolata* (see Hooper & Lévi, 1993a). This species is discussed further in the remarks under *C. (T.) craspedia*.

**Clathria (Thalysias) hallmanni** sp. nov. (Figs 169-170, Plate 6C)


**HABITAT DISTRIBUTION.** Encrusting under beach rock and coral rubble; intertidal pools; NT (Fig. 169H).

**DESCRIPTION.** Shape. Thinly encrusting, up to 1.5 mm thick, extending approximately 7 cm across rock and dead coral substrata.

**Colour.** Dark grey-brown orange-brown in life (Munsell 2.5R 5/4); pale grey in ethanol.

**Oscules.** Minute, less than 1 mm diameter, scattered evenly over surface.

**Texture and surface characteristics.** Spongy, easily torn from substrate; surface has a dull slimy appearance due to production of small amounts of clear mucous upon exposure to air; surface optically smooth, even, without conules, ridges or canals, and encrustation conforms exactly with contours of substrate.

**Ectosome and subectosome.** Opaque in life, slightly pellucid, subdermal canals or cavities not visible; ectosomal skeleton with extensive plumose brushes of small auxiliary subtylostyles, through which protrude ascending, plumose tracts of larger subectosomal auxiliary subtylostyles; moderate quantities of detritus in ectosomal skeleton; subectosomal region extensive, occupying 70% of sponge thickness, composed of mostly paratangential tracts of larger auxiliary subtylostyles gradually ascending and diverge at surface.

**Choanosome.** Skeletal architecture hymedesmoid in choanosomal (basal) region, but distinctly plumose towards peripheral skeleton; spongian fibres consist of a basal layer of spongian lying against substrate, 18-35 μm thick, with bases of choanosomal principal subtylostyles and acan-
thostyles embedded in spongin and standing perpendicular to substrate; choanosomal principal subtylostyles morphologically close to subectosomal auxiliary subtylostyles, and so difficult to determine exactly where basal mineral skeleton ends and where subectosomal skeleton begins, but extra-fibre multispicular tracts appear to begin close to basal layer; moderately common acanthostyles echinate basal spongin, whereas principal megascleres less common; choanoocyte chambers 35-48µm diameter; mesohyl matrix heavy, granular, with small amounts of detritus Megascleres. Choanosomal principal subtylostyles long, fusiform, with slightly constricted bases or subterminal bases, entirely smooth or with low apical conules (? vestigial spines), and typically slightly curved towards basal end. Length 312-(385.5)-419.5µm, width 8-(9.3)-11µm.

Subectosomal auxiliary subtylostyles long, thin, fusiform, straight, almost indistinguishable from choanosomal megascleres but with prominent spined subtylostyle bases. Length 284.5-(362.2)-450µm, width 2-(3.2)-4.5µm. Ectosomal auxiliary subtylostyles short, thin, fusiform, with microspined subtylostyle bases. Length 94-(121.2)-151µm, width 0.8-(1.4)-2.5µm.

Acanthostyles subtylostyle, fusiform, relatively evenly spined although spines less heavily concentrated in ‘neck’ region, proximal to basin, heavier on apical and distal extremities; spines relatively small, weakly formed. Length 52-(59.5)-72µm, width 3-(4.5)-6.5µm. Microscleres. Palmate isochelae relatively common, variable in size but not easily differentiated into two size classes, unmodified, with lateral alae entirely fused to shaft, approximately equal in length to front ala, and entirely free from front ala except in juvenile forms. Length 5-(10.8)-17µm.

Toxas accolada, moderately common, long, thin, almost straight, with only slight angular central curvature, straight (unreflexed) points. Chord length 174-(208.0)-481µm, width 0.4-(0.8)-2.0µm. Associations. Single known specimen growing next to encrusting sponges (Renteria, Halicelona, Mycale), polychaete worm tubes (Pomateleos kraussii) and simple ascidians.

ETYMOLOGY. For E.R. Hallmann in recognition of his contributions to Australasian micrionids.

REMARKS. It is difficult to define C. (T.) hallmanni in any single unique character apart from the close resemblance between choanosomal principal and subectosomal auxiliary subtylostyles. As far as can be ascertained from personal knowledge of the Australasian sponge fauna and Indo-west Pacific literature its field characteristics are unique. It is acknowledged that many older published descriptions of encrusting microcionids, especially those from the Indo-Malay archipelago, rarely include details on live colouration or surface details. But none of these species match the present one in spicule geometry either. Consequently, C. (T.) hallmanni can be differentiated from other encrusting (hymedesmoid) Clathria (Thalysias) species in: grey-brown live colour; even (unornamented) surface, i.e., lacking subectosomal drainage canals commonly found in thinly encrusting species; plumose ectosomal and subectosomal skeletal structure as well as extensive paratangential tracts composed of both sorts of auxiliary spicules in the periphery; entirely smooth, relatively short and thin choanosomal subtylostyles, barely different from the subectosomal auxiliary subtylostyles except for pattern of spinination; evenly spinous acanthostyles, unmodified palmate isochelae, and thin, nearly straight toxas with unreflexed arms. None of these features are unique or particularly distinctive by themselves but their combination is unique for this new taxon.

Clathria (Thalysias) hesperia sp. nov.
(Figs 171-172, Plate 6D-E)


HABITAT DISTRIBUTION. Coral rubble and deeper rock reefs exposed amongst gravel and shell grit substrates; 17-50m depth; NW. coast (WA) (Fig. 171G).

DESCRIPTION. Shape. Thickly flabellate, simple planar fans resembling a Phakellia, or slightly cup-shaped with convoluted, concentric, smaller lamellae inside larger lamellae, resembling species of Cymbastela (Axinellidae); margins pointed digitate (paratype) or convoluted folded (holotype); lamellae up to 380mm wide, 235mm high, 15mm thick; holotype probably lying on, or parallel to, substrate, with con-
volute, concentric ridges or small digitate processes arising from upper surface; paratype erect, perpendicular to substrate, with folded ridged running longitudinally; both specimens with differentiated osculiferous (upper) and porous surfaces, latter relatively even, smooth. Colour Pale orange-red alive (Munsell SR 8/4), khaki-brown in ethanol.

Oscules. Small, up to 3mm diameter alive, smaller in preserved specimen, slightly raised above surface, with membraneous lip, only found on 1 surface of lamellae.

Texture and surface characteristics. Firm, harsh, flexible, slightly compressible, difficult to tear; lower surface smooth, even, upper surface more conulose (with terminal oscules), longitudinal folds, ridges or convoluted folds and small digits.

Ectosome and subectosome. Discrete surface brushes produce specialised ectosomal skeleton; brushes composed of ectosomal auxiliary subtylostyles on outer surface forming thick, erect bundles but not continuous palisade, with 1 or several choanosomal principal styles also protruding through surface associated with ectosomal brushes; subectosomal auxiliary subtylostyles intermingled with ectosomal spicules but originating slightly lower in peripheral skeleton; subectosomal region greatly reduced with peripheral choanosomal fibres lying immediately below ectosome; mesohyl matrix moderately heavy in peripheral region.

Choanosome. Choanosomal skeleton almost regularly renieroid reticulate although renieroid pattern severely disrupted by heavy concentrations of echinating spicules (both principal styles and acanthostyles); spongine fibres very well developed, dark brown, imperfectly divided into primary (90-140μm diameter) and secondary (25-45 diameter), and very large fibre nodes (up to 220μm diameter); primary ascending fibres cored by multispecific tracts of principal styles, 2-5 spicules abreast, with spicules protruding slightly through fibres, particularly at fibre meshes, producing nearly plumesome tracts; secondary more-or-less transverse fibres relatively short, interconnecting primary elements, cored by 1-3 spicules abreast; spicules occupy only 40-70% of fibre diameter for secondary and primary fibres, respectively; near peripheral skeleton principal styles distinctly plumesome, with those on ultimate fibres contributing to ectosomal structure, whereas at core skeleton more renieroid reticulate; echinating acanthostyles very abundant, particularly at fibre nodes, also contributing to ectosomal spicule brushes, with only small portion of base of acanthostyle embedded in spongine fibres and consequently protruding a long way into choanosomal mesohyl; fibre meshes oval or squarish, more cavernous in periphery (45-115μm diameter) than at core (170-250μm diameter); choanocyte chambers oval, 35-55μm diameter, often lined by isochelae; mesohyl matrix moderately heavy but only lightly pigmented. Megascleres. Choanosomal principal styles straight or slightly curved near centre, with rounded or very slightly subtylote bases, bases usually smooth, occasionally microspined, long tapering fusiform points. Length 162-(187.3)-213μm, width 8-(11.1)-14μm.

Subectosomal auxiliary subtylostyles straight or very slightly curved near basal end, slightly subtylote bases lightly microspined, fusiform points. Length 121-(138.1)-168μm, width 4-(4.6)-5.5μm.

Ectosomal auxiliary subtylostyles only slightly shorter than subectosomal spicules but consistently thinner, with smooth subtylote bases, fusiform points. Length 97-(121.1)-147μm, width 2-(2.9)-4.5μm.

Echinating acanthostyles long, slender, mostly straight, sometimes slightly curved near point, with subtylote bases, fusiform points, heavily spined on bases, shaft and points, aspinoine on 'neck' proximal to base; spines short, sharp, recurved. Length 97-(103.6)-112μm, width 4-(5.3)-6μm.

Microscleres. Palmate isochelae very abundant, poorly silicified, sigmoid, with short, sharp, vesigial unguiferous alae. Length 11-(13.7)-15μm.

Toxas absent.

ETYMOLOGY. Latin hesperius, western; from WA.

REMARKS. This species is borderline between Clathria and Thalysias given that the ectosomal skeleton consists of spicule brushes composed of auxiliary spicules of relatively homogenous lengths (i.e., not clearly differentiated into smaller auxiliary spicules supported by larger auxiliary spicules, characteristic of other Thalysias). Nevertheless, ectosomal and subectosomal spicules can be consistently differentiated by their thickness as well as the absence or presence of microspines on their base, respectively, even though there is no marked difference in length between the two categories.

Clathria (T.) hesperia has a distinctive lamellate growth form with differentiated osculiferous and porous faces. Its skeleton is a mixture of plumose tracts (reminiscent of C. (M.) coccinea, particularly its plumose fibre nodes, or the

'scabida' species group with principal spicules protruding through the peripheral skeleton), with an underlying renieroid reticulate skeleton. Palmate isochelae are vestigial, unguiferous, sigmoid reminiscent of *C. (T.) michaelseni* (which is an encrusting, hymedesmoid species, has toxa, and differs from this species in virtually every other respect).

*Clathria* (*Thalysias*) *hirsuta* Hooper & Lévi, 1993 (Figs 173-175, Table 37, Plate 6F, 7A)


MATERIAL. HOLOTYPE: QMG2746 (fragment NTMZ1551): Cairns region, Qld, 16°56'S, 146°00'E, 1982, coll. A. Kay (trawl). PARATYPES: QMG2750
MEMOIRS OF THE QUEENSLAND MUSEUM

(Fragment _NTMZ1555_), QMGL2754 (fragment _NTMZ1560_): Cairns region, Qld, 16°56'S, 146°00'E, coll. A. Kay (trawl). OTHER MATERIAL: QLD - QMG300528 (NCIQ66C-1893-X; fragment _NTMZ3513_), QMG303040, QMG304767, QMG300081, QMG303971, NSW - QMG300771 (NCIQ66C-1185-F). NEW CALEDONIA - QMG301274, QMG301325, QMG301340.

HABITAT DISTRIBUTION. Rock, dead coral and coral rubble substrates, usually on broken substrates, sides of bommies, or in gullies; 7-30m depth; Shetland Bay, Howick Is (FNQ), Whitsunday Is (NEQ), Noosa Heads, Stradbroke Is. (SEQ), Solitary Is. (N. NSW) (Fig. 173O). Also New Caledonia Jagoon (Hooper & Lévi, 1993a).

DESCRIPTION. (See Hooper & Lévi, 1993a).

DIAGNOSIS (Table 37). Tubular, lobed-digitate, reticulate-honeycombed, excavated growth forms superficially resembling _Phakellia cavernosa_; bright red (or orange-red) conules, paler pink or white between conules, prominent subdermal drainage canals; large oscules scattered between surface projections; texture firm, compressible, slightly arenaceous; surface prominently conulose, conules pointed (or rounded, fleshy); ectosome with irregular, tangential or paratangential layer of intermixed ec- tosomal and subectosomal subtylostyles (or with light palisade of smaller auxiliary styles forming erect brushes arising from ends of larger auxiliary spicules); thick choanosomal fibres immediately below ectosome (or subectosome cavernous); choanosomal skeleton irregularly reticulate (or regularly renieriod reticulate), with fibre skeleton dominant over spicule skeleton; primary fibres multisircular, running longitudinally through branches, ascending to surface, interconnected by shorter uni- or paucisicular secondary fibres, cored by both shorter choanosomal principal styles and longer subectosomal auxiliary styles; acanthostyles dispersed evenly over fibres; choanosomal principal styles straight, with smooth, rounded or slightly subtylote bases and fusiform points; subectosomal auxiliary subtylostyles long, slender, straight, fusiform, with rounded or subtylote, smooth or micropinned bases (or with simply rounded, smooth bases); ectosomal auxiliary subtylostyles short, straight, very slender, subtylote smooth or micropinned bases (or with simply rounded, smooth bases); acanthostyles small, subtylote, light or vestigial spines, aspinose 'neck' proximal to base; palmate isocheiae small, unmodified, imperfectly divided into two size categories; lateral alae completely fused to shaft, completely detached from front ala for whole of length, longer than front ala; toxas acclada and wing-shaped morphs, very thin, sometimes slightly sinuous, rarely raphidiform, only slightly curved at centre, with straight non-reflexed arms or only slightly reflexed points (or exclusively raphidiform with small angular central curve and straight arms).

REMARKS. _Clathria (T.) hirsuta_ was originally described and illustrated from both New Caledonian and Queensland populations (Hooper & Lévi, 1993a), in which it was reported that the New Caledonian population possessed ectosomal auxiliary subtylostyles (i.e., belonging to _Thalysia_) whereas Queensland specimens did not (i.e., belonged to _Clathria_). Since this publication several more samples have been collected along the Queensland coast and Great Barrier Reef (Fig. 173O) in which specialised ectosomal spicules were discovered. Conversely, isocheiae were originally reported only from the Queensland populations but absent in New Caledonian samples, but these have now also been observed in a recent sample collected from Noumea (albeit rare). Other differences between these two populations are discussed in Hooper & Lévi (1993a). Two 'atypical' specimens from SE. Australia (QMG300328, G300771) (which are included in the diagnosis above, in brackets) further illustrate the considerable variability of this species (toxas are only raphidiform, auxiliary spicules lack tylole bases, and a structured ectosomal skeleton is present (Figs 174-175)). These specimens are reminiscent of the 'reduced' New Caledonian population.

At first glance this species lacks any remarkable or unique feature that stands it apart from other _Clathria (Thalysia)_ but it possesses an unusual combination of characters not seen in any other species. It is superficially similar to _C. (T.) vulpina_ in growth form, but spiculation and fibre characteristics are quite different between the two species. Its skeletal architecture and spiculation is also very similar to _C. (T.) schoena_ (i.e., USNM22404; which may be different again from _Rhaphidophorus schoenius_ of authors; e.g., Simpson, 1968a; Alcolado, 1980; Van Soest, 1984b), but these species differ significantly in their growth form, spongin fibre architecture and ectosomal characteristics. _Clathria (T.) hirsuta_ has very lightly spined acanthostyles, comparable with those of _C. (T.) transiens_, and it is also closely related to that species in its fibre characteristics and spiculation, although they
TABLE 37. Comparison between Australian and New Caledonian populations of Clathria (Thalysias) hirsuta Hooper & Lévi. measurements in μm, denoted as range (and mean) of spicule length x spicule width (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (QMGL2746) (Cairns region)</th>
<th>Specimens (N=6) (Queensland)</th>
<th>Specimens (N=3) (New Caledonia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal principal styles</td>
<td>163-(178.3)-194 x 4-(7.8)-12</td>
<td>132-(155.2)-195 x 3-(5.8)-12</td>
<td>96-(141.4)-168 x 2-(4.8)-8</td>
</tr>
<tr>
<td>Subectosomal auxiliary styles</td>
<td>179-(241)-284 x 1.5-(3.4)-5</td>
<td>141-(216.9)-293 x 1.5-(3.1)-5</td>
<td>163-(204.3)-248 x 1.5-(3.1)-4</td>
</tr>
<tr>
<td>Ectosomal auxiliary styles</td>
<td>absent</td>
<td>74-(100.1)-115 x 1.5-(2.1)-3</td>
<td>72-(92.0)-111 x 0.8-(1.9)-2.5</td>
</tr>
<tr>
<td>Echinating acanthostyles</td>
<td>37-(57.8)-73 x 2-(4.4)-7</td>
<td>41-(60.4)-79 x 2.5-(4.4)-8</td>
<td>34-(51.9)-72 x 2.5-(3.5)-5</td>
</tr>
<tr>
<td>Chelae I</td>
<td>3-(4.8)-6</td>
<td>3-(4.3)-6</td>
<td>6-9, rare</td>
</tr>
<tr>
<td>Chelae II</td>
<td>9-(10.8)-12</td>
<td>9-(11.5)-14</td>
<td>10-12, rare</td>
</tr>
</tbody>
</table>

Learning differences considerably in growth form and geometry of choanosomal styles.

Clathria (T.) hirsuta belongs to the juniperina group. These species have choanosomal (coring) megascleres which are only slightly differentiated from the subectosomal auxiliary spicules, an irregular heavy fibre skeleton, and rhaphidiform toxas, but each species differs in one or more other significant features. More detailed comparisons by species C. (T.) hirsuta and other members of the juniperina group, are given by Hooper & Lévi (1993a).

Most specimens of Clathria (T.) hirsuta have a nearly vestigial ectosomal skeleton, unlike most of the other juniperina species, with ectosomal and subectosomal spicules intermingled in paratangential tracts on the surface, and consequently their placement in either Thalysias or Clathria is equivocal. However, the two atypical specimens from SE Australia mentioned above have much better structured ectosomal skeletons than most other known samples (Fig. 175), more reminiscent of the usual Thalysias condition. Moreover, the possession of two categories of auxiliary spicules in most specimens indicates that it belongs with C. (Thalysias), whereas those without specialised ectosomal spicules could be included in Clathria (Clathria). This is further evidence to question the distinction between these taxa at the generic level.

**Clathria (Thalysias) juniperina**

(Lamarck, 1814)

(Figs 176-177)

*Spongia juniperina* Lamarck, 1814: 444; Lamarck, 1816: 373.

*Clathria juniperina*; Hooper & Wiedenmayer, 1994: 270.

Not *Pandaros juniperina*; Duchassaing & Michelotti, 1864: 90, pl.19, fig.3.

Not *Thalysias juniperina*; de Laubenfels, 1936a: 105-107 (see synonymy for *T. virgiliosa* below).

*Rhaphidophalus clathratus*; Hallmann, 1912: 209; Top- sent, 1920b: 17-18; Topsent, 1932: 97, pl.5, fig.5, text-fig.3.

Not *Tenacilla clathrata* Schmidt, 1870: 56, 80.

**MATERIAL. LECTOTYPE: MNHN DT3750:** SW coast of Australia, Peron & Lesueur collection. **PARALECOTYPE:** MNHN DT3354: same details.

**HABITAT DISTRIBUTION.** Dead coral and rock substrates; shallow subtidal to 10m depth; SW coast WA (Fig. 176).

**DESCRIPTION.** Shape. Growth form ranging from thickly encrusting to frondose, lamellate, clathrous, with or without free or anastomosing branches.

**Colour.** Bright red to deep red alive, brown dry.

**Oscules.** Not observed.

**Texture and surface characteristics.** Harsh, firm in dry state; surface characteristics range from relatively smooth, even, with white subdermal canals in encrusting forms, to irregularly microconulose or clathrous in more massive forms.

**Ectosome and subectosome.** Ectosomal skeleton crust-like, easily detachable, relatively thin but dense palisade of erect or paratangential brushes supported by paratangential tracts of larger subectosomal auxiliary megascleres immediately below surface; peripheral fibres immediately subectosomal with vaguely ascending multiplicative subectosomal tracts arising to surface.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with very heavy spongin fibres forming oval meshes; fibres usually with paucispicular core of subectosomal auxiliary styles occupying only a small proportion of fibre diameter, and fewer choanosomal principal styles which are entirely enclosed in, or project from fibres; in some cases fibres completely uncored, whereas others contain abundant, disorganised auxiliary megascleres; fibres typically heavily echinated, some enveloping echinating megascleres entirely, some fibres without echinating megascleres; mesohyl matrix light,

with numerous choanosomal styles dispersed between fibres.

*Megascleres.* Choanosomal principal styles straight or slightly curved near basal end, with smooth, rounded or very slightly subtylote bases. Length 170-(244.4)-280 μm, width 9-(10.1)-12. Known only from Australia; m.

Subectosomal auxiliary subtylostyles straight or curved, sometimes with multiple curves (sinuous), with smooth subtylote bases. Length 169-(253.5)-310 μm, width 4-(5.4)-6.5 μm.

Ectosomal auxiliary subtylostyles with prominent subtylote, smooth bases. Length 93-(102.3)-110 μm, width 2-(3.7)-4.5 μm.

Acanthostyles small, stubby, with rounded or only slightly subtylote bases, with few spines and extensive aspinose regions on necks and points;
spines large, bulbous, erect. Length 45-(57.0)-65μm, width 5-(6.1)-8μm.

**Microscleres.** Palmate isochelae unmodified, incompletely differentiated into two size classes; lateral alae entirely fused to shaft, approximately same length as front ala and completely detached from front ala. Length I: 6-(7.1)-9μm, length II: 12-(13.8)-16.5μm.

Toxas very variable in length, mostly thin, ranging from accolada forms with large central curvature and slightly reflected points, large curvature and simply u-shaped, to asymmetrical sinuous forms. Length 55-(122.4)-180μm, width 0.8-(1.1)-1.5μm.

**REMARKS.** *C. (T.) juniperina* differs from that of Hartman (1955), Simpson (1968a), Wiedenmayer (1977) and Van Soest (1984b), who included *Spongia juniperina, Spongia virgulosa,* *Clathria copiosa,* *Microciona plana* and *Clathria clathrata* in synonymy. That 'species' concept was based on Caribbean populations, with only a single record from the E. Indian Ocean (i.e., nomenotypical population of *Spongia juniperina* inferring a widely disjunct geographical distribution. Three explanations are possible: 1) W. Indian Ocean and Caribbean populations are not conspecific but represent two cryptic sibling species populations with similar morphology; 2) the published province of the original material ('Indian Ocean, possibly Australia'; Topsent, 1932) is erroneous; 3) the species is widely distributed 'cosmopolitan' and these disjunct populations are conspecific. The latter two hypotheses are rejected (specimen labels record one of the types from SW Australia), so the first is considered to be the most probable explanation.

The present interpretation is that *C. (T.) juniperina* is restricted to the Indo-west Pacific (and the synonymy given above), whereas the the most senior name for the Caribbean population is *C. (T.) virgulosa* (including several other nominal species in synonymy; see *C. (T.) virgulosa* below). This conclusion conflicts with Topsent's (1932) revision of the relevant (preserved) type material, but this present action is more preferable than the unlikely alternative that such widely disjunct populations are conspecific.

*Clathria (T.) juniperina* is similar to *C. (T.) caeciformis* and several other species included here in a 'juniperina' species complex (spanning the groups *Clathria and Thalysias*; see comments for *C. (T.) caeciformis*), which has a depaupeaker skeleton (fibres shed some or all of their coring spicules) and principal and auxiliary spicules are similar in geometry.

**Clathria (Thalysias) kieschnicki** Hooper, in Hooper & Wiedenmayer, 1994

*Rhaphepolus cylindricus* Kieschnick, 1900: 569, pl.44, fig.10.


*Clathria (Thalysias) kieschnicki* Hooper, in Hooper & Wiedenmayer, 1994: 271.

**MATERIAL.** None. Holotype PMJ missing; (F. Wiedenmayer, pers. comm.).

**HABITAT DISTRIBUTION.** Ecology unknown; Thursday I., Torres Strait (FNQ).

**DESCRIPTION.** Shape. Bifurcate digitate, with short cylindrical stem, up to 40mm long, branches tapering towards apex, up to 80mm long.

**Colour.** Live colouration unknown, ash-grey in ethanol.

**Oscules.** Small, scattered between surface conules.

**Texture and surface characteristics.** Fragile; surface with prominent, irregularly distributed conules, and detachable skin-like crust.

**Ectosome and subectosome.** Ectosome relatively thick, with discrete plumose bundles of ectosomal auxiliary subtylostyles, forming a continuous palisade, below which plumose tracts of subectosomal auxiliary subtylostyles protrude through ectosome.

**Choanosome.** Choanosomal skeletal architecture irregularly reticulate, with heavy, lamellated spongine fibres, 60-160μm diameter, not obviously divisible into primary or secondary elements, forming ovoid meshes, 90-150μm diameter; fibres cored by irregular multispecific tracts of choanosomal principal styles and also fewer subectosomal auxiliary subtylostyles; echinating acanthostyles abundant, evenly distributed.

**Megascleres.** Choanosomal principal styles straight or slightly curved, with smooth bases. Length 90-180μm, width 9-15μm.

**Subectosomal auxiliary subtylostyles** straight, with microspined bases. Length up to 270μm, width up to 18μm.

**Ectosomal auxiliary subtylostyles** are fusiform, straight or slightly curved, with microspined bases. Length 135-230μm, width 4-8μm.

**Acanthostyles** subtyloste, with bare necks. Length up to 135μm, width up to 18μm.

**Microscleres.** Palmate isochelae. Length 15μm.
Toxas thin (but of unknown geometry), occurring in trichodragnata or singly. Length 70-100 μm.

REMARKS. This species is poorly characterised because Kieschnick's (1900) description is brief and does not differentiate it from other arborescent, branching Clathria (Thalysias). From his description spicule geometries (which were never figured), and growth form are similar to C. (T.) abietina, but its true affinities remain a mystery given that the holotype is missing from PMJ collections. Maurice Burton (note on BMNH1887.5.2.104 specimen label) suggested that it was similar to C. (T.) filifera, but any relationship is unsubstantiated. The specific name cylindrica is preoccupied by C. (Axociella) cylindrica (Ridley & Dendy, 1886).

Clathria (Thalysias) koltuni Hooper, in Hooper & Wiedenmayer, 1994

*Stylotelopsis antarcticus* Koltun, 1964a: 66, text-fig.16.

Not *Anchnoa toxifera antarctica* Topsent, 1917: 43, pl.4, fig.5, pl.6, fig.5.

*Clathria (Thalysias) koltuni* Hooper, in Hooper & Wiedenmayer, 1994: 271.

MATERIAL. None: 'Syntypes' (ZIL 10637, 11437) (not seen).

HABITAT DISTRIBUTION. Substrate unknown; 610–860 m depth; Budd Coast, Wilkes Land, Antarctica.

DESCRIPTION. Shape. Thinly encrusting, up to only 1 mm thick.

Colour: Red alive.

Oscules. Not seen.

Texture and surface characteristics. Even surface.

Ectosome and subectosome. Erect choanosomal principal subtylote styles protruding through surface with bundles of smaller auxiliary subtylote styles dispersed around principal spicules.

Choanosome. Hymedesmoid, with choanosomal principal and subectosomal auxiliary subtylote styles erect on basal spongion; bundles of echinating acanthostyles clumped around erect structural megascleres.

Megascleres. Choanosomal principal subtylote styles long, straight, fusiform, with subtylote bases and evenly microspined in basal third of spicule. Length 400–750 μm, width 26–36 μm.

Ectosomal and subectosomal auxiliary styles very long, slender, straight, fusiform, with microspined subtylote bases. Length 430–630 μm, width 8–12 μm.

Echinating acanthostyles short, club-shaped, fusiform, with prominent subtylote base and evenly spined over entire length of spicule. Length 100–260 μm, width 10–14 μm.

Microscleres. Absent.

REMARKS. This species is a lipochelous *Clathria*, but it is uncertain from Koltun's (1964a) brief description what subgenus it belongs to. It is retained in *Thalysias* (following Hooper & Wiedenmayer, 1994). It differs from other hymedesmoid species (especially those previously referred to *Pseudanchnoia*), in spicule dimensions and spicule ornamentation, but has few other noteworthy features. *antarcticus* is preoccupied by C. (M.) antarctica (Topsent, 1917).

Clathria (Thalysias) lendenfeldi

Ridley & Dendy, 1886

(Figs 178–179, Plate 7B–E)

*Clathria lendenfeldi* Ridley & Dendy, 1886: 474; Ridley & Dendy, 1887: 148, pl.28, fig.5, pl.29, fig.6, pl.47, fig.5, Whitelegge, 1889: 186; Whitelegge, 1901: 86; Whitelegge, 1907: 492–494; Burton & Rao, 1932: 334; Rudman & Averm, 1989: 335; Hooper et al., 1990: 126–133, figs 1, 2, 4, 6; Hooper & Wiedenmayer, 1994: 271.

Not *Clathria lendenfeldi*; Brondsted, 1934: 19–20, text-fig.19.

*Thalysias lendenfeldi*; de Laubenfels, 1936a: 105.

*Microciona lendenfeldi*; Dawson, 1993: 37.

*Spongia abietina*; in part, Lamark, 1814: 450.

*Echinomena anchoratum var. lamellosa*; Whitelegge, 1901: 82.


*Clathria spicata* Hallmann, 1912: 210; Dendy, 1922: 65–66, pl.5, fig.2, pl.13, fig.4a–f, Burton, 1959a: 244.

*Clathria diechinita* Hallmann, 1912: 211; 1914a: 268 (nomen nudum).

*Thalysias spicata*; de Laubenfels, 1936a: 105.


*Thalysias whiteleggi*; de Laubenfels, 1936a: 105.

*Clathria coppingeri* var. *aculeata* Hentschel, 1912: 363.


*Clathria bispinosa*; Hallmann, 1912: 177, 211.


MATERIAL. HOLOTYPE: BMNH1887.5.2.107; off Port Jackson, NSW, 33°40'S, 151°40'E, HMS


HABITAT DISTRIBUTION. Rock reefs and dead coral heads; intertidal to 108m depth; widespread Indo-Pacific; Port Jackson, Botany Bay (NSW); Shelburne Bay, Howick Is, Direction Is, Gulf of Carpentaria (FNPQ); Cairns, East Frankland Is, Pandora Bay (NEQ); Darwin Harbour, Bynoe Harbour, Melville I., Beagle Gulf, Port Essington, Cobourg Peninsula, Cootanundra Shoals, Wessel Is (NT); Broome, Port Hedland, Bedout I., Dampier Archipelago, Monte Bello Is, Exmouth Gulf, Northwest Cape, Amphinome Shoals, Northwest Shelf (WA); Bicheno (Tas)(Fig. 178G); also Gulf of Manaar (Burton & Rao, 1932), Aru Is, Indonesia (Hentschel, 1912), Cargados Carajos (Dendy, 1922), Gulf of Aden (Burton, 1959a), Arabian coast (Burton, 1959a), Andaman Sea (present study).
Red Sea and Somalia (present study), Saya de Malha (Dendy, 1922) to the Natal coast (Burton, 1931a).

DESCRIPTION. (See Hooper et al., 1990).

DIAGNOSIS. Variable growth form ranging from bushy clathros reticulate-branching to bushy lamellate planar digitate fans, usually with woody basal stalk and cylindrical branches; vivid red to pale red-brown alive in shallow waters to slightly turquoise or unpigmented in deeper waters; oscules small, congregated into special pore areas on points of digits or scattered between surface processes; surface usually microconulose; ectosome ranging from sparsely scattered smaller auxiliary spicules to dense, erect, continuous crust; choanosomal principal subtylostyles also protrude through surface; subectosomal skeleton poorly developed, paratangential, composed of larger auxiliary subtylostyles; choanosomal skeleton irregularly reticulate, heavy spongin fibres divided into primary (ascending) and secondary (transverse) components, producing regular or irregular meshes; fibre-meshes heavier in axis; fibres generally uncored, some with uni- or paucispicular tracts of principal spicules, and abundantly echinated by both acanthostyles and principal subtylostyles especially at fibre junctions ("spicate"); choanosomal principal subtylostyles long, curved or straight, sharply pointed, usually with heavily spined bases (119-(229.6)-492μm x 1.8-(12.9)-35μm); subectosomal auxiliary subtylostyles long, straight, fusiform, slightly subtylo, microspined bases (136-(241.5)-404μm x 2-(4.6)-15μm); ectosomal auxiliary subtylostyles short, thin, straight, fusiform, with microspined subtylo style bases (62-(123.4)-198μm x 2-(3.0)-10μm); acanthostyles slender, long or short, fusiform, slightly subtylo, evenly and lightly spined, spines small, recurved (49-(88.1)-151μm x 2-(6.4)-14μm); palemate isochelae small, rarely modified, narrow lateral alae completely fused to shaft, approximately same length as front ala; lateral alae completely and widely separated from front ala (6-(12.5)-25μm long); toxas accolada to wing-shaped, very thin (hair like); larger toxas usually accolada, straight, with slight but sharp angular central curvature and unreflexed arms; smaller toxas usually wing-shaped, with large central curvature and slightly reflexed arms; toxas found singly and in bundles (dragmata) (7-(136.4)-361μm x 0.4-(1.3)-3.6μm).

REMARKS. Variation has been comprehensively investigated from many living specimens and type material (Hooper et al., 1990). The synonymy above also includes several new synonyms added to the species since that earlier paper. This species is a cryptic sibling species of C.(T.) major, differing only substantially by its hair-like toxas, sharply pointed auxiliary megascleres, statistical differences in spicule dimensions and various biochemical features (Hooper et al., 1990), and both are members of Hallmann's (1912) "spicata" group.

Clathria (Thalysias) major Hentschel, 1912 (Figs 180-181)

Clathria fromdifiera var. major Hentschel, 1912: 361. 
Clathria (Thalysias) major; Hooper et al., 1990: 133-135, figs 1, 3, 5, 6; Hooper & Wiedenmayer, 1994: 272.


HABITAT DISTRIBUTION. Rock reefs and dead coral heads; intertidal to 82m depth; Bedout I., Port Hedland, Mary Anne I., Direction Is, Exmouth Gulf (WA); Bynoe Harbour, Darwin Harbour, Port Eslington (NT) (Fig. 180H); also Aru Is, Indonesia (Hentschel, 1912).

DESCRIPTION. (See Hooper et al., 1990).

DIAGNOSIS. Variable growth forms ranging from low, foliose, bushy, subspherical, clathrous digitate, to flabellate or digitate fans, usually with long basal stalk and flattened or irregularly cylindrical branches; bright red to orange-red alive; oscules small, congregated into special pore areas on lateral sides of branches or between surface conules; flabellate specimens may have Phakellia-like pores grouped into stellate pore-areas; surface irregularly microconulose with close-set subdermal ridges and striations; ectosomal skeleton ranges from very few tangentially placed ectosomal auxiliary subtylostyles to dense, erect or paratangential brushes of ectosomal spicules; subectosomal skeleton plumose, paratangential tracts of larger auxiliary subtylostyles; both larger auxiliary and principal spicules protrude through surface singly or in plumose bundles; choanosomal skeleton irregularly reticulate; fibre characteristics, skeletal structure and distribution of megascleres and microscleres identical to C. (T.) lendenfeldi;
choanosomal principal styles thick, slightly curved, fusiform, rounded or subtylote, usually with microspined bases, sometimes smooth (187-(250.5)-38μm x 5-(15.1)-36μm); subectosomal auxiliary subtylostyles long, straight, fusiform pointed, usually subtylote, microspined bases, or commonly with rounded apex (quasi-tornotes) also bearing microspines (156-(287.8)-439μm x 2-(5.7)-14μm); ectosomal auxiliary subtylostyles short, straight, subtylote microspined bases, usually with rounded apex (quasi-tornotes) and terminal spines (84-(136.8)-193μm x 2-(3.8)-9μm); acanthostyles relatively slender, long or short, fusiform, subtylote, with large spines on base and apex but nearly aspinose 'neck' (77-(112.7)-144μm x 3-(7.8)-15μm); palmate isochelae small, unmodified, wide lateral alae completely fused to shaft, approximately same
length as front ala; lateral alae completely separated but close to front ala (6-(10.4)-16μm long); toxas accolada or wing-shaped, the former long, very thick, with large rounded central curvature, straight or reflexed arms, the latter short, thin, widely curved at centre with reflexed arms (27-(108.9)-390μm x 0.6-(2.3)-5μm).

REMARKS. The species is a cryptic sibling of C. (T.) lendenfeldi with a sympatric but more restricted distribution. In gross morphology, sur-
face features, live colouration and in many of its skeletal characters C. (T.) major is indistinguishable from its sibling. However, they can be reliably differentiated by spines on the points of many of the auxiliary spicules (especially most of the smaller ones), marginally thicker and longer toxas, and statistically (but not absolute) larger size of most other megascleres in C. (T.) major. The importance of these apparently ‘relatively minor’ morphological differences is indicated by clear differences between the two species in their biochemical fingerprints (Hooper et al., 1990).

In a recent survey of several Western Australian species, C. (T.) major was found to contain significant quantities of the chemical 2,6-dibromophenol of potential commercial importance as an 'iodiform' or ‘fresh sea' flavour used in the production and marketing of commercial prawns (F. Whitfield, CSIRO, pers.comm.).

Clathria (Thalysias) Michaelseni (Hentschel, 1911) (Fig. 182).

Hymeraphia michaelseni Hentschel, 1911: 351-352, text-fig.34; Hentschel, 1912: 385.
Damoseni michaelseni; de Laubenfels, 1936a: 110.


HABITAT DISTRIBUTION. Bivalve and worm tubes, sand, coral and Halimeda bed substrata; 3-14m depth; central W coast (WA) (Hentschel, 1911); also Arafura Sea (Hentschel, 1912) (Fig. 182H).

DESCRIPTION. Shape. Thinly encrusting.

Colour. Live colouration unknown, brown in ethanol.

Oscules. Unknown.

Texture and surface characteristics. Firm; smooth unornamented surface.

Ectosomal and subectosomal. Star-shaped plumose brushes of intermingled ectosomal and subectosomal auxiliary stylostyles on surface; most auxiliary spicules perpendicular to surface, with choanosomal principal megascleres protruding through.

Choanosome. Hymedesmoid skeletal structure, with choanosomal principal stylostyles and smaller echinating acanthostyles embedded in and perpendicular to basal spongion; mesohyl matrix moderately heavy, without detritus.

Megascleres. Choanosomal principal stylostyles long, fusiform, slightly curved, subtylostyle, with microspined bases. Length 188-(381.6)-646μm, width 10-(14.6)-19μm.

Subectosomal auxiliary stylostyles long, thin, fusiform, prominently subtylostyle, lightly microspined, occasionally with smooth bases. Length 307-(403.6)-482μm, width 3-(4.4)-6μm.

Ectosomal auxiliary stylostyles, short, thin, strongly, prominently subtylostyle, smooth bases, usually poltylostate shafts. Length 141-(162.4)-197μm, width 2-(2.9)-4μm.

Acanthostyles long, thin, slightly subtylostyle, with lightly microspined base and central portions, aspinose points and neck regions. Length 96-(108.8)-125μm, width 3-(6.6)-8μm.

Microscleres. Isochelae sigmoid (bidentate) anchorate, with small alae attached only at their bases. Length 15-(17.2)-19μm long.

Toxas oxhorn or u-shaped, variable in size, relatively thick, gently curved at centre and with reflexed points or only slightly reflexed points. Length 38-(122.6)-239μm, width 1-(3.5)-6μm.

REMARKS. Hentschel (1911) initially overlooked the presence of toxas in this species, although later described by him in specimens from Aru Is, Indonesia (Hentschel, 1912), but these were also seen in the holotype redescribed above. Hentschel (1911, 1912) also overlooked the presence of two categories of auxiliary spicules indicating its assignment in C. (Thalysias) rather than C. (Clathria). Spicule dimensions seen in type material also vary slightly from those published by Hentschel (1911).

This species is well differentiated from other thinly encrusting (hymedesmoid) microcionids in having bidentate sigmoid isochelae, for which de Laubenfels (1936a) created Damoseni. The recognition of de Laubenfels' genus is not upheld since this feature is homoplasic, also known to occur in other microcionids (e.g., C. (C.) nexus Koltun, with an erect ramose growth form), and other poecilosclerids (e.g., Strongylacion stel-liderma Carter).

Clathria (Thalysias) phorbasiformis sp. nov. (Figs 183-184, Plate 7F-G).


Material, 8.i.1985, QMG300149 (fragment NTMZ2223), QMG300150 (fragment NTMZ2237).

HABITAT DISTRIBUTION. Encrusting on laterite rock, dead coral, exposed at ELWS tides, under dead coral boulders or in crevices and pools; intertidal; Darwin Harbour (NT) (Fig. 183H).

DESCRIPTION. Shape. Thickly encrusting, 0.7-1.3 cm thick, producing thin cylindrical...
stoloniferous digitate non-anastomosing stoloniferous processes, up to 6mm in diameter, which may or may not re-attach to substrate.

**Colour.** Orange-brown to brick-orange alive (Munsell 2.5 YR 7/6-8); grey-brown in ethanol.

**Oscules.** No oscules visible optically alive or preserved, but numerous minute pores, 0.1-0.25mm diameter, scattered over surface seen at higher magnification.

**Texture and surface characteristics.** Texture firm, compressible; abundant clear mucus produced upon exposure to air; surface optically smooth, microscopically hispid, even, or small ridges and low conules following contours of substrate; digitate surface processes may have more prominent sculpturing superficially resembling C. (T.) reinwardti.

**Ectosome and subectosome.** Usually dense ectosomal skeleton, only slightly opaque or pellucid between surface conules, with subectosomal cavities and canals barely visible below surface (alive); ectosome microscopically hispid, with points of choanosomal principal styles protruding, singly or in plumose brushes, with thickest brushes in areas where ultimate choanomasal fibres in peripheral region closest to surface; specialised ectosomal skeleton well developed, with discrete brushes of smaller ectosomal auxiliary subtylostyles forming continuous palisade; relatively thick but variable layer of spongin and detritus also on ectosome; clear regional and structural differentiation between ectosomal and subectosomal skeletons; subectosomal region variable in thickness dependent on proximity of peripheral fibres to surface, containing plumose columns of larger auxiliary subectosomal subtylostyles, not associated with fibres, but often bound together by collagen; subectosomal skeletal columns originate from ends of choanosomal principal megascleres, which in turn echinate fibres of peripheral skeleton in plumose tufts or singly.

**Choanosome.** Thick growth forms – Skeletal architecture vaguely plumo-reticulate; spongin fibres relatively light, irregularly anastomosing, fully cored by acanthostyles, lying in rows of 3-5 megascleres abreast (i.e., entirely incorporated into spongin fibres lying in parallel spicule tracts); principal subtylostyles only rarely seen coring fibres, and acanthostyles only rarely echinate fibres (i.e., lie at right angles to fibres); spongin fibres predominantly echinated by principal subtylostyles, in plumose tufts or singly, particularly abundant at fibre nodes; fibre anastomoses form oval or clongate meshes, 250-800μm diameter; fibres thicker in deeper areas of choanosome (70-100μm diameter) than in periphery (55-80μm diameter); major portion of branch diameter consists of extra-fibre plumose tracts of subectosomal auxiliary megascleres with choanosomal reticulate skeletal comprising less than half of branch diameter; extra-fibre plumose spicule tracts originate approximately half-way along length of perpendicular choanosomal styles, or in thicker sections they originate at ends of principal megascleres; extra-fibre plumose spicule tracts ascend to, diverge, and pierce ectosomal skeleton; mesohyl matrix only lightly pigmented, variable in density, usually heavier near periphery; extra-fibre spicules mostly occur in well defined tracts with few scattered randomly throughout mesohyl.

Thiny encrusting growth forms – hymedesmoid skeletal construction with basal layer spong in lying on substrate, uncored but very heavily echinated by both acanthostyles and choanosomal subtylostyles standing perpendicular to substrate; subectosomal spicule tracts arise from distal half of erect choanosomal megascleres, diverging and ascending to surface in plumose brushes, surmounted by plumose brushes of ectosomal auxiliary spicules at periphery.

**Megascleres.** Choanosomal principal subtylostyles fusiform, tapering to long points, slightly curved near the basal end or occasionally straight, with subtylote, mostly smooth bases, occasionally roughened subapically or slightly tubercular. Length 245.2-(425.8)-583.1μm, width 10.2-(19.5)-33.8μm.

Subectosomal auxiliary subtylostyles long, fusiform, mostly straight, with subtylote micropinned or occasionally smooth bases. Length 275-(386.2)-485.3μm, width 4.0-(9.6)-18.8μm.

Ectosomal auxiliary subtylostyles relatively short, straight or whispy, slender, with subtylote, relatively heavy basal micropinination. Length 70.0-(140.5)-261.2μm, width 1.2-(4.0)-6.9μm.

Acanthostyles fusiform, straight or slightly curved near base, slightly subtylote, evenly spined but characteristically free of spines at points; spines large, recurved. Length 95.4-(115.4)-132.4μm, width 4.6-(8.4)-12.7μm.

**Microscleres.** Palmate isochelae abundant, subdivided into 2 size categories, smaller ones sometimes contort; lateral alae completely attached to shaft, approximately same length as front ala but completely detached from it. Length I: 10-(14.9)-21.9μm, length II: 2.5-(5.6)-9.2μm.
Toxas moderately abundant, vaguely separated into 2 forms although intermediates occur: smaller wing-shaped toxas relatively thick, generously curved at centre with slightly reflexed, abruptly pointed ends; accolada toxas long, nearly straight, with slight central curvature and slight or no apical reflexion. Length 30-(95.1)-222.9μm, width 0.5-(1.4)-2.5μm.

**Associations.** Growing in dense clumps amongst algae (*Gellidium*), with stoloniferous branches intertwined, occasionally attached to algae itself; some specimens growing over, or next to other encrusting sponges (*Placospongia, Mycale, Antho (Plocamia)*), compound ascidians, and coralline algae.

**ETYMOLOGY.** Like *Phorbas* (Anchinoidea).

**REMARKS.** This species incorporates most echinating acanthostyles into sponging fibres, either together with one or few principal subtylostyles enveloped by spongin, or excluding principal megascleres completely. This feature is consistent except for one thinly encrusting specimen that lacks a reticulate fibre skeleton, in which case acanthostyles stand perpendicular to substrate. Principal spicules are mostly outside fibres, perpendicular to (echinating) fibres and fibre nodes, and protruding through the surface. This is reminiscent of Hallmann's *spicata* group (see *C. (T.) coppingeri*).

Incorporation of echinating acanthostyles secondarily into fibres has been observed in some specimens of *C. (Dendrocia) dura*, *C. (D.) imperfecta*, and to a lesser degree *C. (D.) myxilloides*, but these instances are infrequent, inconsistent (i.e., seen in some sections of the skeleton but not in others), and probably aberrant. A similar phenomenon has been described for *C. (T.) orientalis* by Brondsted (1934) but this too is atypical for the species (whereby the larger auxiliary subtylostyles usually core fibres). Analogous structures are described in other poeciloselaidids, particularly for the families Anchinoidea and Crellidae, but in these species acanthostyles also comprise the 'principal' structural spicules.

*Clathria* (*Thalysias*) *phorbasiformis* differs from other species in the 'phorbasiformis' complex in gross morphology and spicule geometry. In live surface features and colouration it some resemblance to thickly encrusting *C. (T.) reinwardtii*, although spicule geometry, spicule size, skeletal architecture and fibre characteristics are clearly different between them.

**Clathria (Thalysias) placenta**

(Lamarck, 1814)

(Figs 185-186)


**MATERIAL.** **HOLOTYPE:** MNHNDT552: King L. Bass Strait, Tas, 39°50'S, 144°00'E, Peron & Lesueur collection.

**HABITAT/DISTRIBUTION.** Ecology unknown; Bass Strait, Tasmania (Fig. 185G).

**DESCRIPTION.** **Shape.** Thick, flabellate growth form, 180mm high, 170mm wide, up to 10mm thick, with even margin; probably originally with basal stalk but now detached.

**Colour.** Grey-brown dry.

**Oscules.** Not seen.

**Texture and surface characteristics.** Harsh, flexible, brittle in dry state; surface relatively even, with longitudinal annular striations running from basal stalk to margin of fan, and raised fibre reticulations forming polygonal pattern.

**Ectosome and subectosome.** Ectosome almost completely detached from dry type specimen, but where present appears to be sparse, plumose, erect or paratangential palisade of ectosomal styles arising from ascending subectosomal spicule tracts, the latter embedded in peripheral skeleton; choanosomal fibres immediately subectosomal.

**Choanosome.** Choanosomal skeleton irregularly reticulate with primary (ascending) and secondary (transverse) fibres; primary fibres (105-175μm diameter) corded by multispecific tracts of subectosomal auxiliary styles, occupying up to 60% fibre diameter, tracts becoming plumose peripherally; secondary fibres (35-88μm diameter) without coring spicules; all fibres heavily echinated by small acanthostyles sometimes nearly enveloped in spongin; fibre anastomoses form irregular oval and rectangular meshes (145-510μm diameter); mesohyl matrix light, with few loose megascleres dispersed between fibres.

**Megascleres.** Choanosomal principal megascleres absent or completely undifferentiated from subectosomal spicules.

Subectosomal auxiliary styles thin, straight, slightly curved or slightly sinuous, with smooth rounded bases and sharp fusiform points. Length 175-(237.5)-285μm, width 5-(6.6)-8μm.

Ectosomal auxiliary styles straight or slightly curved near apical end, with rounded microspined bases, fusiform points. Length 115-(138.1)-156\(\mu\)m, width 2-(2.6)-4\(\mu\)m.

Acanthostyles short, slender, subtyloate, fusiform pointed, spined only on base and near apical end, with smooth regions at "neck" (proximal to base) and point. Length 52-(54.4)-58\(\mu\)m, width 3.5-(4.2)-6\(\mu\)m.
Microscleres. Palmate isochelae small, with some contort forms, small alae less than 30% of shaft length, lateral alae completely fused to shaft, front alae completely detached. Length 8-10.7-14μm.

Toxas accolada, moderately long, thick, with only very slight central curvature and straight points. Length 105-(19.5)-148μm, width 1.0-(1.4)-2.0μm.

REMARKS. Lamarck's (1814) holotype from Bass Strait and de Laubenfels' (1954) sample USNM22908 from Truk, Caroline Is are not conspecific; the latter becomes C. (T.) lemaitoue sp. nov. The Truk sample is only similar to C. placenta in having fibres cored by subectosomal auxiliary spicules instead of principal spicules (i.e., the principal and larger auxiliary spicules are undifferentiated in their geometry). In most other details the two species can be readily distinguished (the Chuuk sample has an encrusting growth form, an extremely smooth surface, skeletal structure is hymedesmoid indicating possession of a very extensive subectosomal skeleton, occupying almost half of the sponge diameter, acanthostyles are about twice the size of those in C. placenta with much more robust spination, toxas are slightly accolada but moreso wing-shaped, megascleres are mostly subylolate, and dimensions of most spicules differ).

Topsent (1930) implied that C. (T.) placenta was similar to C. (Wilsonella) australiensis (Carter), but this is certainly not true (the two having very different skeletal structures, spine geometries and absence of foreign detritus in the skeleton of C. (T.) placenta). Clathria (T.) placenta is a member of the 'juniperina' complex having a reduced spine skeleton (whereby fibres shed some or all their spicules, in this case only from the secondary fibres), and principal and auxiliary spine of similar geometry (refer to discussion under C. (T.) cactiformis).

Clathria (Thalysia) procera (Ridley, 1884) (Figs 187-188, Table 38)

Rhaphidophulus procera Ridley, 1884a:451-452, pl.39, fig.k, pl.42, fig.o; Burton, 1931a:343, pl.23, fig.2.


Tenacia procera; Burton & Rao, 1932:340; Burton, 1934a:559; Burton, 1934b:28.

Rhaphidophulus spiculasus Dendy, 1889b:75, 86, 87, 99, pl.4, fig.4 [Gulf of Manaar, Ceylon]; Dendy, 1922:64.

Clathria spiculasus; Dendy, 1905:171-173, pl.8, fig.2 [Gulf of Manaar, Ceylon]; Hentschel, 1912:363-364; Hallmann, 1912:17; Dendy, 1916a:46, 95, 128-129 [Okhamandal, Kattiar].

Clathria spiculasus vari. ramosa; Hentschel, 1912:363-364.

Not Clathria spiculasus var. macilenta; Hentschel, 1912:364 [Arul Is, Arafura Sea].

Echinomena gracilis Ridley, 1884a:617, pl.34, fig.1; Dendy, 1922:64.

Rhaphidophulus gracilis; Ridley & Dendy, 1887:152, 242, 252, Topsent, 1892b:24.

Clathria gracilis; Dendy, 1905:171; Vosmaer, 1935a:634.

Not Rhaphidophulus arborescens Ridley, 1884a:450-451, pl.40, fig.L, pl.42, fig.n; Burton & Rao, 1932:340.


MATERIAL. HOLOTYPE: BMNH1882.2.23; 313. Off East Point, Port Darwin, NT, 12°24.5'S, 130°48.0'E, 14-22m depth, coll. HMS 'Alert' (dredge). PARA.TYPE: BMNH1882.2.23,311; same locality. HOLOTYPE of R. spiculasus; BMNH1889.1.21.5 (fragment BMNH1954.2.23.101); Gulf of Manaar, Sri Lanka, 8°N, 78°E. PARA.TYPE of R. spiculasus; BMNH1887, 8.4.31; same locality. HOLOTYPE of E. gracilis: BMNH1882.10.17.111; Providence Island, Seychelles Is, Indian Ocean, 9°14'S, 51°02'E, 48m depth (dredge). HOLOTYPE of C. spiculasus vari. ramosa: SMF1698 (fragment MNHNDCL 2304); Straits of Dobo, Aru Is, Arafura Sea, Indonesia, 6°S, 134°50'E, 20.iiii.1908, 40m depth coll. H. Merton (dredge). OTHER MATERIAL: QLD- NTMZ3983, QMG 301032, QMG303514-QMG304392, QMG304771. NT- NTMZ2604, QMG303582. WA- NTMZ1308. INDIAN OCEAN - BMNH1907.2.1.63., BMNH 1954.2.23.113, BMNH1954.2.23.114.

HABITAT DISTRIBUTION. On loose, soft substrates (sand, mud, gravel, shell grit) associated with shallow-water or deeper offshore reefs; 11-78m depth; widespread throughout the Indian Ocean and Indo-west Pacific; Gulf of Carpentaria, Low Is, Direction Is, Snake Reef, Turtle Is (FNQ); Bynoe Harbour, Darwin Harbour, Cape Wessel, Arafura Sea (NT); Port Hedland (WA)(Fig. 187H); also Scottburgh, Natal (Burton, 1931a; Lévi, 1963), Cargados Carajos, Seychelles Is, Amirante, Red Sea and Arabian Sea (Ridley, 1884a; Ridley & Dendy, 1887; Dendy, 1922; Burton & Rao, 1932; Burton, 1959a; Thomas, 1973b); Tuticorin, Cape Comorin, Palk Straits, and Madras Straits, Gulf of Manaar (Burton & Rao, 1932; Burton, 1938a), Aru Is, Indonesia (Hentschel, 1912), Hawaii (Bergquist, 1967; 1977).

DESCRIPTION. Shape. Long, single or bifurcate cylindrical digits, whip-like, very slightly flattened laterally, 230-640mm long; stalk tapers in both directions from thick central region 4-14mm diameter, to woody base 4-6mm diameter, and rounded points 6-13mm diameter; apex with single or no bifurcation is single; point of attachment to substrate expanded, rhizomous; gross morphology superficially resembles *Junceella* gorgonian whip-coral.
TABLE 38. Comparison between present and published records of spicule dimensions for Clathria (Thalysias) procera (Ridley). Measurements in μm (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Holotype (BMNH)</th>
<th>Specimens (N=8)</th>
<th>Clathria spiculosus var. ramosa (SMF1698)</th>
<th>Specimen (N=1) (Burton, 1938)</th>
<th>Specimen (N=1) (Thompson, 1973b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chonosomal styles</td>
<td>322-(334.2)-348 x 11-(13.2)-16 (common)</td>
<td>248-(283.2)-309 x 16-(18.2)-22 (uncommon)</td>
<td>263-288 x 15-18 (rare)</td>
<td>220-360 x 13</td>
<td>201-310 x 4-12</td>
</tr>
<tr>
<td>Subectosomal styles</td>
<td>318-(334.2)-358 x 8-(9.2)-11</td>
<td>342-(367.1)-393 x 8-(11.3)-14</td>
<td>276-345.5 x 9.2-12.5</td>
<td>250 x 8</td>
<td>210-294 x 4-8</td>
</tr>
<tr>
<td>Ectosomal styles</td>
<td>172-(258.4)-295 x 3-(5.6)-7</td>
<td>124-(178.2)-290 x 2-(3.8)-5</td>
<td>112.3-235.6 x 2.2-5.8</td>
<td>180-200 x 6</td>
<td>100</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>91-(99.2)-110 x 8-(11.0)-13</td>
<td>89-(104.1)-114 x 7-(11.6)-16</td>
<td>72-98.9 x 9.2-12.1</td>
<td>present</td>
<td>58-75 x 4-9</td>
</tr>
<tr>
<td>Chelae I</td>
<td>12-(15.3)-18</td>
<td>13-(15.6)-19</td>
<td>14.5-19.2</td>
<td>16</td>
<td>12-16</td>
</tr>
<tr>
<td>Chelae II</td>
<td>4-(6.6)-10</td>
<td>6-(8.3)-10</td>
<td>6-10.5</td>
<td>9</td>
<td>-</td>
</tr>
<tr>
<td>Texas</td>
<td>18-(60.5)-122 x 0.8-(1.3)-1.5</td>
<td>31-(101.2)-145 x 0.9-(1.2)-1.8</td>
<td>62-142 x 1.2-2</td>
<td>45-56</td>
<td>&lt;147</td>
</tr>
</tbody>
</table>

Colour: Pale orange alive (Munsell 5YR 8/6), pale grey in ethanol.

Oscules. Not visible in either live or preserved specimens.

Texture and surface characteristics. Firm, only very slightly compressible but flexible, with obvious stiff axis; basal region woody, more rigid than central or apical regions; surface optically smooth, without conules or other surface processes, microscopically hispid with minute subdermal canals and grooves.

Ectosome and subectosome. Well developed series of erect spicule brushes forming a continuous palisade, composed of ectosomal auxiliary subtylostyles; ectosomal brushes embedded on ultimate fibres, with echinating acanthostyles and chonosomal principal styles protruding through bases of each spicule brush; subectosomal auxiliary subtylostyles form tangential or paratangential tracts below ectosomal skeleton; chonosomal principal styles embedded in peripheral fibres form diverging brushes contributing to subectosomal skeleton; mesohyl of peripheral skeleton heavier and more darkly pigmented than deeper regions of choanosome; subectosomal region relatively cavernous, occupying up to 50% of sponge diameter (less in basal stalk region).

Choanosome. Skeletal architecture distinctly axially compressed, with moderately heavy, yellow spongin fibres forming tight anastomoses near core, becoming more plumeous (or merely concentrated on peripheral fibres and at fibre nodes; chonosomal principal megascleres uncommon or even rare in some regions of skeleton, absent entirely from the fibre core, mostly found in peripheral skeleton echinating fibres and supporting ectosomal skeleton; mesohyl matrix relatively light in axial region with many loose subectosomal auxiliary megascleres scattered between fibres.

Megascleres (Table 38). Chonosomal principal subtylostyles straight or slightly curved at centre, with smooth slightly subtylote or rounded bases, fusiform points; principal subtylostyles differ from auxiliary subtylostyles in relatively thicker diameter with thickest part at centre of spicule, less pronounced basal constrictions, and smooth bases.

Subectosomal auxiliary subtylostyles fusiform, relatively long, straight or only slightly curved, tapering to sharp points, with distinct basal constrictions and prominent subtylote swelling; bases predominantly microspined, microspines long.

Ectosomal auxiliary subtylostyles similar to larger auxiliary megascleres but relatively short, thin, prominently subtylote, invariably microspined.

Echinating acanthostyles large, subtylote, heavily spined bases and central regions, aspinose at points and 'necks' proximal to base; spines large, robust, recurved.
**Microscleres** (Table 38). Palmate isochelae incompletely divided into 2 size categories, both abundant, larger unmodified, smaller often contorted (58-72% of spicules); lateral alae completely fused to shaft; front ala shorter and completely detached from lateral alae.

Toxas wing-shaped and u-shaped, thin, variable in length, with pronounced central curvature, slightly reflexed or straight points.

**REMARKS.** In live colour, surface characteristics, texture, gross morphology, spiculation and skeletal architecture this species is quite distinctive. In particular it has sparse choanosomal principal styles found only outside (echinating) peripheral fibres; subectosomal auxiliary megascleres coring fibres; axial compression of central fibres and the diverging, wide-meshed reticulation in the peripheral skeleton; and echinating megascleres are concentrated on peripheral fibres and spongion fibre nodes. This latter feature is also found in *C. (T.) cactiformis* although the 2 species are not conspecific as supposed by Burton & Rao (1932), where *C. (T.) cactiformis* has an aspicular secondary fibre skeleton and lacks any axial compression. The principal megascleres echinating fibres and absence of principal spicules from within the fibre core indicates it belongs to Hallmann's (1912) *spicata* group.

Records of *C. procera* subsequent to Ridley (1884a) make no mention of choanosomal principal spicules echinating peripheral fibres, although this feature is characteristic for the species. Conversely, authors following Dendy (1922) note that there are two classes of auxiliary megascleres, both of similar length but different thickness, the thicker ones coring fibres and the thinner ones scattered in the mesohyl, but this distinction was not corroborated from re-examination of any material.

Hallmann (1912), Dendy (1922), Burton & Rao (1932), Burton (1938a) and subsequent authors included a number of other species as synonyms of *C. (T.) procera*, but most of these synonymies are not supported here. *Clathria spiculosa* var. *macilenta* is certainly different from *C. (T.) procera* and is clearly a synonym of *C. (T.) reinwardti*. In contrast, *Clathria spiculosa* var. *ramosa* Hentschel (SMF1698) is conspecific with *C. procera*, having closely comparable skeletal structure, spicule geometry and spicule size (Table 38), although growth form differs slightly from typical morphs (being arborescent, with a woody cylindrical stalk and numerous, thin, evenly cylindrical branches bifurcating but not anastomosing, and bifurcate branch tips superficially resembling *Seriotopora* coral). There is some doubt about the conspecificity of some other specimens identified as *C. (T.) spiculosa* by Dendy (1889b, 1905, 1922) and *C. (T.) procera* by Burton (1931a, 1938a) and Thomas (1973b), in particular the clathrous and lamellate morphs. These specimens all differ from typical forms in their skeletal architecture, although their spicule geometries are all fairly similar and for this reason they are retained here in synonymy for the time being.

Contrary to Burton & Rao (1932) and Vosmaer (1935a) *C. (T.) arborescens* is a distinct species from *C. (T.) procera*, both species differing substantially in their spicule geometry, spicule sizes and skeletal architecture. *Clathria reinwardti* var. *palmata* Ridley is conspecific with *C. frontifera (= *C. (T.) vulpina*), as suggested by Bergquist & Tizard (1967), and not with *C. (T.) procera*, as supposed by Burton & Rao (1932). *Clathria (Thalysias) tomenti* is similar in many respects to *C. (T.) procera*, but shows virtually no axial compression of the choanosomal skeleton, spicule geometry is clearly different, and the two species are not considered to be synonyms.

**Clathria (Thalysias) ramosa**
(Kieschnick, 1896)
(Figs 189)

*Rhipidophyllum ramosum* Kieschnick, 1896:533;
Kieschnick, 1900:569-570, pl.45, figs 47-50.
Not *Clathria ramosa* Lindgren, 1897:482-483;
Lindgren, 1898:308-309, pl.17, fig.9, pl.18, fig.15, pl.19, fig.16; Hentschel, 1912:367.
Not *Thalysias ramosa*; de Laubenfels, 1936a:105.
Not *Cololecithria ramosa* Dendy, 1922:74-76.

**MATERIAL. HOLOTYPE:** PMJ Porif.92: Thursday 1, Torres Strait, Qld, 10°35'S, 142°13'E, no other details known (presently missing from collections; Wiedenmayer, pers. comm.)

**HABITAT DISTRIBUTION.** Ecology unknown; known only from Torres Strait, Qld.

**DESCRIPTION.** Shape. Arborescent, bushy, with small stalk and small lobate, conical branches, between which stretches a transparent dermal membrane.

**Colour.** Yellow-brown in preserved state.

**Oscules.** Unknown.

**Texture and surface characteristics.** Harsh; rugose.
**REVISION OF MICROCIDONIDAE**

![Diagram of Clathria](image)


**Ectosome and subectosome.** Ectosomal skeleton composed of discrete brushes of small auxiliary subtylostyles.

**Choanosome.** Choanosomal skeleton irregularly reticulate, with heavy spongin fibres divided into primary and secondary components differing significantly in diameter; fibres only lightly cored by choanosomal principal subtylostyles within axis of skeleton, occasionally absent; fibres usually more heavily cored towards periphery; echinating acanthostyles abundant; character of soft parts unknown.

**Megascleres.** Choanosomal principal subtylostyles prominently subtylole, straight or slightly curved, with basal spination. Length 150-480µm, width 13-24µm.

Subectosomal auxiliary subtylostyles long, thin, prominently subtylole with microspined bases. Dimensions unknown.

Ectosomal auxiliary subtylostyles identical in geometry to larger auxiliary spicules. Dimensions unknown.

Acanthostyles cylindrical, club-shaped, evenly spined, subtylole. Length up to 150µm, width 9-13µm.

**Microscleres.** Palamate isochelae in 2 size classes. Length up to 13µm.

Toxas thin, sinuous, raphidiform. Dimensions unknown.

**REMARKS.** This species is barely recognisable other than belonging to Clathria and having a specialised ectosomal skeleton (i.e., C. (Thalysias)) which is both implied in Kieschnick's (1900) description and his tacit inclusion of the species in Rhaphidophitus. Until the presently missing holotype is re-examined, the affinities of this species remain uncertain.

**Clathria (Thalysias) reinwardti** Vosmaer, 1880

(Figs 190-192, Table 39, Plate 8A-B)


Clathria reinwardti var. subcylinrica Ridley, 1884a:446-448.

Rhaphidophius reinwardti; Kelly Borges & Bergquist, 1968:141-143, figs 3-4, pl.3F.

Clathria typica var. porrecta Hentschel, 1912:298, 359-360.

Tenacia typica var. porrecta Hallman, 1920:771.

Clathria spiculosa var. mucilenta Hentschel, 1912:364.

Not Clathria reinwardti var. palmata Ridley, 1884a:447.


HABITAT DISTRIBUTION. Predominantly found on coral rubble and dead coral substrata, fringing coral reefs or lagoon faunas, occasionally growing on live coral on the reef crest; mostly found in turbid, shallow subtidal-intertidal waters between 0-10m depth, occasionally deeper. Speculated that association with dead coral substrates indicates some role in reef bioerosion; widely distributed throughout Indo-west Pacific; Darwin Harbour, Parry Shoals, Timor Sea, Port Essington, Oro Bates Reef, Trepang Bay, Cobourg Peninsula, Wessel Is (NT); Hibernia Reef, Carter I., Sahul Shelf, Direction I. (WA); Gulf of Carpentaria, Cockburn Is., Cape York, Shelburne Bay, Blanchard Reef, Adolphus I. (PNG) (Fig. 190H); also Cebu, Negros Oriental, Philippines (present study), Chau, Caroline Islands (present study), Hon Rai I., Vietnam (present study), Solomon Is (Bergquist et al., 1971), Motupore I., PNG (Kelly Borges & Bergquist, 1988; present study), Aru Is, Sulawesi, Lesser Sumba Is, Indonesia (Vosmaer, 1936a; Van Soest, 1989, present study).

DESCRIPTION. Shape. Typically simple digitate, stoloniferous, cylindrical or occasionally laterally compressed branches (7-25mm diameter), forming meandering digits with multiple points of attachment to substrate; no differentiation between branches and stalk, with branches attaching directly to substrate; branches frequently anastomose with adjacent branches sometimes forming complex intertwined digits; free branches mostly simple, rarely bifurcate; several thickly encrusting, bulbous specimens also collected, presumably immature growth stages.

Colour. Very light orange (Munsell 5YR 8/4), orange-brown (7.5YR 8/2-4), orange-red-brown (2.5YR 7/8), light brown (10R 7/4), to grey-white (2.5Y 8/2) pigmentation alive, orange-brown (5YR 8/4) to grey-white (2.5Y 8/2) in ethanol; ectosomal membrane varies from colourless (opaque), to grey (2.5Y 8/2); subectosomal and choanosomal regions generally darker than peripheral, usually clearly visible through ectosomal membrane when alive.

Oscules. Abundant, relatively large (560-2760μm diameter), predominant on lateral sides of branches; oscules slightly raised with prominent membraneous lip (often orange pigmented) surrounding aperture; generally thicker specimens have larger oscules raised further above surface and more prominent subectosomal sculpturing; oscules collapse in situ.

Texture and surface characteristics. Soft, compressible, flexible, moderately easy to tear; surface smooth, pellucid, semi-translucent in life, with prominent stellate subectosomal channels radiating towards oscules, particularly in thicker specimens, more even surface ornamentation in thinner specimens; ectosomal membrane collapses upon dessication and preservation, becoming roughened and pocked with ridges and cavities.

Ectosomal and subectosome. Thin layer of smaller ectosomal auxiliary subtylostyles form discrete brushes erect on surface, in a continuous palisade, supported by long or short subectosomal plumose tracts from peripheral fibre skeleton; ectosomal region generally poorly collagenous but variable in thicker specimens; subectosomal region cavernous with lacunae (120-660μm diameter) supported paucispicular plumose tracts of subectosomal auxiliary subtylostyles, no fibres, but moderate quantities of collagen between spicule tracts; plumose tracts of choanosomal principal styles also near periphery in some cases protruding through ectosomal skeleton.

Choanosome. Skeletal architecture irregularly or semi-regularly reticulate, with anastomosing spongion fibres (40-120μm diameter) forming curved oval, straight triangular or rectangular meshes (50-470μm diameter) in choanosome;

Fibre meshes generally more irregular near core than periphery; no clear distinction between primary and secondary fibres; fibres light, always fully cored by choanosomal principal styles, with dense echinating acanthostyles on surface; abundant auxiliary spicules scattered between fibres; mesohyl matrix light, poorly pigmented, surrounding ovoid to elliptical choanocyte chambers (130-250μm diameter); specimens from turbid, muddy intertidal habitats incorporate moderate amounts of inorganic detritus into mesohyl but not into fibres. 

Megascleres (refer to Table 39 for dimensions). Choanosomal principal styles slightly curved at centre, short, thick, invariably with smooth rounded bases, hastate or occasionally strongylote points.
TABLE 39. Comparison between spicule dimensions (in μm) between type specimens and other material of Clathria (Thalysia) reinwardti Vosmaer from different localities (N=25).

<table>
<thead>
<tr>
<th>SPECULE</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal styles</td>
<td>155-345 (stout)</td>
<td>223-305 x 5-16</td>
<td>135-215 x 6-10</td>
<td>111-(195.1)-280 x 5-(115.8)-21</td>
<td>131-(201.6)-273 x 6-(124.9)-18</td>
<td>146-(192.9)-236 x 7-(111.1)-16</td>
<td>110-(190.3)-259 x 7-(114.8)-21</td>
<td>116-(195.6)-279 x 8-(131.3)-21</td>
<td>148-(200.5)-264 x 9-(159.9)-21</td>
</tr>
<tr>
<td>Subectosomal styles</td>
<td>135-305 (spined)</td>
<td>155-323 x 3-12</td>
<td>170-211 x 3-9</td>
<td>113-(235.5)-337 x 3-(68.6)-16</td>
<td>141-(246.1)-326 x 3-(16.9)-11</td>
<td>141-(219.7)-301 x 3-(5.9)-11</td>
<td>113-(226.1)-337 x 4-(6.7)-14</td>
<td>146-(233.0)-317 x 5-(7.6)-13</td>
<td>137-(238.6)-317 x 5-(7.6)-13</td>
</tr>
<tr>
<td>Ectosomal styles</td>
<td>120-130 (slender)</td>
<td>97-181 x 3-7</td>
<td>84-102 x 3-6</td>
<td>66-(102.3)-170 x 2-(3.9)-8</td>
<td>85-(106.5)-162 x 2-(4.1)-7</td>
<td>82-(104.1)-157 x 2-(3.6)-7</td>
<td>66-(100.7)-166 x 2-(3.9)-7</td>
<td>69-(102.7)-170 x 4-(5.1)-8</td>
<td>73-(92.8)-139 x 4-(3.9)-8</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>50-70 x 6.3</td>
<td>54-82 x 3-10</td>
<td>59-74 x 4-11</td>
<td>31-(59.1)-79 x 3-(7.4)-13</td>
<td>45-(64.7)-78 x 3-(7.4)-12</td>
<td>42-(60.1)-72 x 3-(6.6)-10</td>
<td>39-(57.9)-79 x 3-(7.5)-13</td>
<td>31-(58.2)-77 x 5-(7.9)-13</td>
<td>35-(60.3)-76 x 8-(8.7)-12</td>
</tr>
<tr>
<td>Chelae II</td>
<td>-</td>
<td>4-8</td>
<td>4-8</td>
<td>2-(6.1)-9</td>
<td>2-(4.5)-9</td>
<td>2-(4.6)-9</td>
<td>2-(5.8)-9</td>
<td>4-(6.6)-9</td>
<td>4-(6.4)-9</td>
</tr>
<tr>
<td>Toxas</td>
<td>22-174 x 0.5-2</td>
<td>52-246 x 0.5-2</td>
<td>8-(121.2)-237 x 0.5-(12.2)-3.1</td>
<td>12-(119.5)-186 x 0.5-(12.2)-2.5</td>
<td>9-(102.5)-173 x 0.5-(12.2)-2.5</td>
<td>16-(125.8)-236 x 0.5-(12.2)-3.0</td>
<td>12-(124.1)-228 x 0.5-(12.2)-2.5</td>
<td>24-(115.6)-186 x 0.5-(12.2)-2.0</td>
<td></td>
</tr>
</tbody>
</table>


Subectosomal auxiliary styles straight or sometimes slightly curved near basal end, relatively thick, with fusiform, sharp points, sometimes telescoped or mucronate, and rounded or slightly subtylote, usually faintly microspined bases.

Ectosomal auxiliary styles morphologically similar to subectosomal spicules, but markedly shorter, thinner, fusiform, sharply pointed or mucronate, straight, with slight subtylote basal swellings and profusely microspined bases.

Echinating acanthostyles short, stout, with rounded, blunted points, slightly subtylote bases, unevenly spined with aspine 'neck' proximal to base; spines heaviest on base and points, spines broad at base, sharp, recurved. Microseleres (refer to Table 39 for dimensions). Palmate isochelae in 2 size classes, both abundant, scattered throughout mesohyl and lining choanocyte chambers; long lateral alae completely fused to shaft, completely detached from front ala; front ala entire; some smaller forms with contort shaft; some larger forms with median spikes on interior of shaft.

Toxas basically accolada although juvenile forms resemble oxhoms; extremely thin, hairlike, long, slight central curvature, slightly reflexed or with straight points; distributed singly or in trichodragmata throughout mesohyl.

Larvae. 28% of specimens examined contained incubated parenchymella larvae in varying stages of development; larvae oval to cleftical, 180-825μm long, 80-400μm wide; smaller larvae identical in colouration to adult mesohyl, larger larve relatively darkly pigmented with larval styles and toxas, mostly at periphery, and mature larvae well differentiated in cellular structure with a layer of cells surrounding periphery; cilia not observed (preserved material). No obvious reproductive period for C. (T.) reinwardti because sexual reproductive products present in samples from May to January (i.e., all seasons except wet season) from Darwin and Cobourg Peninsula regions (Fig. 192); larval size not correlated with seasonality with larvae in various stages of maturity encountered throughout year; apparent absence of reproductive products during wet season probably only due to low number of samples collected during February-April, and possible that this species produces viviparous larvae all year.

Associates. Virtually every specimen examined (94% of material) harboured Scyllilae polychaete worms (Typosyllis spongicola), lying between fibre meshes longitudinally within branches. The relationship between C. (T.) reinwardti and T. spongicola is probably widespread and facultative because specimens from all localities and material collected in 1965 (Bergquist & Tizard, 1967) and 1974 (AMZ4311) also contained infestations of this polychaete.
Variation. Shape: characteristic, consistent although some variability in number of branch bifurcations, thickness of branches, degree of lateral flattening; 3 morphs recognised: thin and evenly cylindrical; laterally flattened; or thickly cylindrical with knobbed and uneven surface; no correlation found between variability in skeletal architecture or spiculation and growth form; see Kelly-Borges & Bergquist (1988) for further details on variability in growth form and colouration. Colour: relatively consistent range from grey, orange-brown to red-brown; density of pigmentation may be related to exposure and water clarity where deeper and more turbid water populations are generally less heavily pigmented and shallow populations are brighter coloured.

Skeletal structure: Ectosomal skeleton typically dense, continuous, discrete spicule brushes, occasionally thin, paratangential ectosomal crust. Subectosomal skeleton cavernous with long plumose, non-echinatated spicule tracts (51%) or with choanosomal fibres close to surface (49%). Choanosomal skeleton typically irregularly reticulate, heavy and compact, with fully cored fibres forming rectangular meshes; but 4% of specimens with curved fibres forming oval-cylindrical meshes; 2% with cavernous skeletons throughout and very few thin fibres and spicule tracts; 4% regularly reticulate with ladder-like fibre anastomoses. Spicule skeleton lying outside fibres dense (48%) with abundant loose spicules strewn throughout mesohyl, moderate (32%), or very light (20%) with few extra-fibre spicules. Mesohyl matrix typically light (47% of specimens), moderate (25%), heavy but only lightly pigmented (18%), or heavy, dark brown pigmented (10%).

Microscleres: Subectosomal auxiliary subtylostyles typically with microspined bases although most specimens had at least some smooth ones (0-4% of microscleres were entirely smooth in 4% of specimens), 5-10% (15%), 11-20% (34%), 21-30% (15%), 31-40% (15%), up to 64% (17%). Choanosomal principal styles and smaller auxiliary ectosomal subtylostyles invariably with smooth and microspined bases, respectively. Echinatated acanthostyles dense, very heavily echinating fibres (17%), moderate (43%), light (17%) or very lightly echinating (23%).

Remarks. Vosmaer (1880) erected C. (Thalysias) reinwardtii for a specimen from the Moluccas incorrectly identified as Spongia cannabina Esper, but his original diagnosis was incorrect. Ridley (1884a) subsequently described two specimens (as var. subcylindrica) from Torres Strait where they were reportedly abundant. Vosmaer (1935a) redescribed the spiculation of the holotype which agreed closely with Ridley's diagnosis, and hence emended the definition of this species. From present data and published results of Kelly-Borges & Bergquist (1988) it is shown that C. (T.) reinwardtii is a dominant species of the intertidal and shallow subtidal fringing reef communities throughout the tropical Indo-west Pacific, particularly prevalent in more turbid waters.

Aside from Kelly-Borges & Bergquist (1988) the species has been described as lacking any ectosomal specialisation (viz. Clathria condition), whereas careful histological sectioning shows that it has a classical ectosomal skeleton of two distinct size categories of auxiliary megascleres, localised in the ectosomal and subectosomal regions respectively (viz. Thalysia condition). Bergquist & Tizard (1967) suggested that toxas were not previously recorded because they are very slender and tend to be associated with larvae. However, all specimens examined in this study contained toxas, irrespective of
very shallow subectosomal drainage canals radiating from large pores. Irregular and corrugated surface features were observed only in a small proportion of live samples, although these surface features are common in dessicated material soon after collection.

This species may be confused with *C. (T.) erecta*, differing only slightly in gross morphology and surface ornamentation, and having a similar skeletal structure, whereas comparison of spicule geometry and spicule sizes can distinguish the two species. Its spicule geometry is similar to *C. (T.) fasciculata*, but this has a bushy clathrous growth form and different skeletal structure (e.g., pronounced fascicular columns comprising the main skeletal tracts). In its nearly regular reticulate, rectangular skeletal structure *C. (T.) reinwardti* resembles to some extent *C. (T.) vulpina* (which has an open reticulate tubular and lamellate growth form (and to which Bergquist & Tizard (1967) referred the variety *C. reinwardti var. palmata*). *Clathria reinwardti* can be differentiated from all these species by its characteristic acanthostyle morphology, growth form, size and geometry of toxas, and ectosomal-subectosomal features. The species also differs from *C. (T.) proceras* and *C. (T.) spiculosa* with similar growth form in choanosomal architecture, spicule geometry and fibre characteristics.

*Clathria (Thalysias) ridleyi* (Lindgren, 1897) (Fig. 193)

*Rhaphidophlus* sp; Ridley, 1884a:452-453.
*Rhaphidophlus ridleyi* Lindgren, 1897:483; Dendy, 1896:44; Lindgren, 1898:283, 310, 311, pl.17, fig.8, pl.18, fig.14, pl.19, fig.17; Hallmann, 1912:187; Van Soest, 1984b:115.
Tenacia ridleyi; Lévi, 1961b:522-524, text-fig.14.
Clathria ridleyi; Hooper & Wiedenmayer, 1994: 273
of Clathria ramosa; Vosmaer, 1935a:611, 642, 669.

MATERIAL. HOLOTYPE: NHM (fragment BMNH1929.11 26.20); near Mambalong, SW. of Belitung I., Java Sea, Indonesia, 3°09'S, 107°38'E, coll. C. Aurielius (beach debris).

HABITAT DISTRIBUTION. Depth 10-14 m; on dead or live coral substraite; Torres Strait (FNQ) (Ridley, 1884a); also Java Sea (Lindgren, 1897), and Taganak I., Philippines (Lévi, 1961b).

DESCRIPTION. Shape. Ramose, with thin cylindrical bifurcating and anastomosing branches, short stalk.

Colour. Red alve.

Oscules. Unknown.

Texture and surface characteristics. Harsh; surface highly ornamented and hisdip, bearing ridges and conules.

Ectosome and subectosome. Ectosome relatively thin, with single layer of plurisomic siculo brushes, composed of intermingled ectosomal and subectosomal auxiliary substyles.

Choanosome. Choanosomal skeleton irregularly reticulate, with light spongion fbrres forming rectangular meshes and with both primary and secondary components; primary vaguely ascending fibres have multispecific core of 8-10 rows of choanosomal principal styles, whereas secondary elements less heavily cored; acanthostyles dispersed evenly over fibres.

Megasccleres. Choanosomal principal styles, slightly curved, with rounded, smooth non-tubule bases. Length 150-300μm, width 8-15μm.

Subectosomal auxiliary substyles straight, usually with microspined bases. Length up to 300μm, width up to 12.5μm.

Ectosomal auxiliary substyles identical in morphology to subectosomal spicles. Length up to 120μm, width up to 4μm.

Acanthostyles subylote, with blunt or rounded, profusely microspined points, with aspimone 'necks' proximal to base. Length 68-75μm, width 5-9.5μm.

Microscelere. Palmate isochelae unmodified, single size category. Length 9-18μm.

Texas not recorded in Ridley's or Lindgren's material, but described as raphidiform by Lévi, with slight central curvature and no apical flexion. Length 80-110μm.

REMARKS. Lindgren (1897, 1898) erected this species for Ridley's (1884a) unnamed specimen from Torres Strait, differentiating it from other ramose Clathria (Thalysias) in skeletal architecture, fibre characteristics, and Ectyoplasia-like acanthostyles (with recurved spines on the apex of spicules). However, the species is barely recognisable other than belonging to Clathria (Thalysias). Only a slide preparation of a skeletal section was located in the BMNH (Fig. 193), showing few distinctive characteristics. Acanthostyles with apical spines have also been recorded for C. (T.) mutabilis and C. (T.) topsenti, and it is possible that this species is related to, or synonymous with one of these. Lévi (1961b) recorded C. (T.) ridleyi from the Philippines, noting some similarities in growth form and surface characteristics with C. (T.) erecta, although spicle geometry and skeletal arrangement differ between the two species.

Clathria (Thalysias) rubra
(Lendcncld, 1888) (Figs 194-195)

Echinonema rubra Lendcnfeld, 1888:221.
Whitelegge, 1902a:212.


Rhaphidophythus paucispius; Hallmann, 1912:176-188, 195, 202, 203, 300, pl.25, figs 1-2, pl.26. fig.1, text-fig.36; Guiller, 1950:8.

Tenacia paucispina; Hallmann, 1920:770.
Not Tenacia paucispina; Burton, 1934a:559.

Thalassodendron rubens var. dura, in part; Lendcnfeld, 1888:224; Whitelegge, 1901:87.

Thalassodendron rubens var. lamella, in part; Lendcnfeld, 1888:224, pl.7; Whitelegge, 1901:87.

Not Thalassodendron rubens Lendcnfeld, 1888:223.
Clathria multipora Whitelegge, 1907:496, pl.45, fig.23.


MATERIAL. HOLOTYPE: AMG9048 (presently missing); Port Jackson, NSW, 33°51'S, 151°16'E. PARATYPE of E. rubra; AMG9049: unknown locality (label 'Clathria pumila var. rubra Lend, type '). LECTOTYPE of T. paucispina: AMG9121a; Port Jackson, NSW, 33°51'S, 151°16'E (dry, label 'Thalysias paucispina; type'). PARALECTOTYPES of T. paucispina: AMG9121b; same locality (dry, label 'cotype'). BMNH1887.1.27.1, 1954.2.10.71, 1954.2.12.54 (fragments AMG3557); same locality. AMZ961 (dry; presently missing); same locality. LECTOTYPE of T. rubens var. lamella: AMZ499; Port Jackson, NSW, 33°51'S, 151°16'E (wet). PARALECTOTYPES of T. rubens var. lamella: AMZ461; same locality (wet, fragment from figured specimen). BMNH1887.4.27.124 (1954.2.10.70); same locality (dry). BMNH1887.1.24.28 (fragment ZMB1147); same locality (wet). HOLOTYPE of T. rubens var. dura: AMG9123; same locality (dry). PARATYPES

HABITAT DISTRIBUTION. On rock reef, shell-grit or gravel substrates; 20-90m depth; Port Jackson, Botany Bay, Shoalhaven Bight (NSW); Maria l. (Tas) (Fig. 194H).

DESCRIPTION. Shape. Thick, flabellate-lamelate or branching growth forms up to 250mm long, 100mm wide, 30mm thick, usually with short basal stalk up to 60mm long, 25mm diameter; lamellate-flabellate morphs growing in 1 or more planes, even margins; ramosé forms with cylindrical tapering digits or with closely anastomosing branches; intermediate flabellate-digitate growth forms with uneven palmate digitate margins.

Colour. Live colouration unknown, preserved material dark-brown or grey-brown, usually with paler grey surface crust.

Oscules. Moderately large, up to 4mm diameter, confined to areas on lateral or apical margins of branches.

Texture and surface characteristics. Harsh, compressible, flexible when preserved; surface smooth, with or without small conules, often with well developed subectosomal ridges and oscular areas.

Ectosome and subectosome. Surface with distinct crust or peel; ectosomal skeleton ranges from very dense, well developed continuous palisade of erect plumose brushes, to sparse, with covering of erect discrete brushes dispersed over surface, sometimes on same specimen; subectosomal skeleton interdispersed with ectosomal brushes, consisting of plumose tracts of larger subectosomal auxiliary subtylostylyes arising from ends of peripheral choanosomal fibres, protrude through and/or lying paratangential to ectosomal layer.

Choanosome. Skeletal architecture more-or-less regularly reticulate, very heavy spongin fibres forming wide elongate-oval meshes (200-550µm diameter), imperfectly differentiated into primary (pauci- or multispecific) fibres (up to 160µm diameter) and secondary (uni- or paucispicular) fibres (up to 110µm diameter); fibres substantially heavier and more regularly reticulate at core, more radial and plumo-recticate towards periphery; peripheral fibres terminate in plumose tufts of choanosomal and subectosomal megascleres, supporting ectosomal skeleton; fibres cored by choanosomal principal styles occupying only 10-40% of fibre diameter; mesohyl matrix heavy but only lightly pigmented, containing few loose subectosomal and choanosomal megascleres dispersed between fibres; echinating acanthostyles sparse, confined mostly to larger fibres; choanocyte chambers oval, 50-80µm diameter.

Megascleres. Choanosomal principal styles relatively robust, usually slightly curved at centre or near basal end, with rounded or very slightly subtylate, smooth bases, and fusiform points. Length 168-(204.4)-295µm, width 9-(10.9)-14µm.

Subectosomal auxiliary subtylostylyes long, slender, straight, with slightly subtylate, smooth or micropinned bases, and fusiform points. Length 202-(227.1)-281µm, width 5-(6.6)-8µm.

Ectosomal auxiliary subtylostylyes short, slender, straight or slightly curved near basal end, with subtylene spined bases and slightly hastate points. Length 105-(125.4)-154µm, width 3-(4.4)-5µm.

Acanthostyles subtylate, tapering cylindrical, fusiform, with evenly distributed spines or fewer spines at 'neck' proximal to base, spines small, straight, erect. Length 75-(84.3)-98µm, width 4-(6.8)-8µm.

Microscleres. Palmate isochelae of a single size class, large, unmodified, with lateral alae longer than front ala; lateral alae completely attached to shaft but detached from front ala along lateral margin. Length 17-(20.1)-24µm.

Toxas u-shaped, thick, with only slight central curvature and tapering, non-reflexed points. Length 45-(54.7)-82µm, width 1.5-(2.1)-3µm.

REMARKS. This species is very similar to *C. (T.) cactiformis* in having a similar range of variability of growth forms and surface features, and on this basis Vosmaer (1935a) suggested they may be synonymous. However, *C. (T.) rubra* is substantially different from *C. (T.) cactiformis* in spicule geometries (particularly principal styles, acanthostyle spination, toxa morphology), spicule sizes, fibre characteristics (where all fibres are cored in this species but only the primary ascending fibres are cored in *C. (T.) cactiformis*), and the presence of plumose tufts of choanosomal principal styles, projecting through and echinating peripheral spongin fibres in *C. (T.)
Clathria (Thalysias) cf. rubra (Lendenfeld, 1888) (Figs 196)

cf. Echinonema rubra Lendenfeld, 1888:221.
Tenacina paucispina; Burton, 1934a:559.


HABITAT DISTRIBUTION. On rock and shell gravel; 20-31m depth; known Australian distribution: Cairns region (FNQ) (Fig. 196H).

DESCRIPTION. Shape. Arborecent, cylindrical branches 3-5mm diameter, branches bifurcate and anastomose producing a tangled mass.
Colour. Live colouration unknown, brown in ethanol.
Oscules. Unknown.
Texture and surface characteristics. Firm, compressible; slightly conulose surface.
Ectosome and subectosome. Erect, discrete brushes of ectosomal auxiliary subbyllostyes forming thin, discontinuous palisade on surface, with sparse, paratangential subbyllostosomal skeleton composed of larger auxiliary byllostyles and long principal byllostyles protruding from peripheral fibres supporting ectosomal skeleton; principal byllostyles also occasionally protruding through surface; terminal spongine fibres branch immediately below surface; mesohyl matrix heavy in peripheral skeleton.

Chaosomal. Skeletal architecture irregularly reticulate; very heavy spongine fibres forming wide, oval or elongate reticulate meshes (150-350μm diameter), more cavernous in periphery than at core; spongine fibres imperfectly divided into primary, mostly ascending, multispirical fibres (60-80μm diameter) and secondary, mostly transverse, paupsircical fibres (25-60μm diameter); echinating acanthostyles relatively sparse in deeper choanosome, more-or-less concentrated on exterior side of fibres and at fibre nodes; mesohyl matrix heavy, granular, with numerous microscleres and auxiliary spicules scattered throughout mesohyl between fibres; choanocyte chambers oval, up to 80μm diameter.
Megascleres. Chaonosomal principal byllostyles slender, straight or slightly curved near base, slightly subbylote smooth or faintly micrpsoned bases, fusiform sharply pointed or occasionally telescoped points. Length 174-(266.7)-346μm, width 5-(7.7)-10μm.

Subectosomal auxiliary subbyllostyles straight, slender, subbylote micrpsoned or smooth bases, fusiform points. Length 219-(262.0)-358μm, width 3-(4.5)-6μm.

Ectosomal auxiliary subbyllostyles very slender, straight, subbylote smooth or micrpsoned bases, fusiform points. Length 121-(152.8)-181μm, width 2-(3.3)-4μm.

Acanthostyles long, slender, subbylote, evenly spined except for partially aspinose area at 'neck' proximal to base, spines small, recurved. Length 73-(82.3)-93μm, width 4-(4.8)-7μm.

Toxas intermediate between wing-shaped and u-shaped, relatively thick, with gently rounded central curvature and reflected points. Length 18-(43.6)-106μm, width 0.8-(1.8)-4.0μm.

REMARKS. Burton’s (1934a) Tenacina paucispina from the Great Barrier Reef is similar to C. (T.) rubra but there is some doubt about its conspecificity. Burton (1934a) indicated that it was most similar to Clathria multipora Whitelegge, subsequently demoted to a variety (or subspecies) of C. (T.) rubra by Hallmann (1912), but comparison between Burton’s specimen and type material (see C. (T.) rubra; Figs 194-195) shows differences in the geometry of particular spicules (toxas, acanthostyles, bases of principal styles) and in some spicule sizes. Burton (1934) did not describe his specimen, and simply noted that his
specimen consisted of a 'tangled, anastomosing mass of angular ... nodulose branches, each 3-5 mm diameter'. Even with a fragment of Burton's specimen it is uncertain whether it is _rubra_ or a new taxon.

**Clathria (Thalysia) spinifera**
(Lindgren, 1897)
(Figs 197-198, Table 40)

_Rhaphidophulus filifer_ var. _spinifera_ Lindgren, 1897:483; Lindgren, 1898:311, pl.17, fig.7, pl.19, fig.18.

_Rhaphidophlus spinifer_, Thiele, 1903a:958, pl.28, fig. 23; Hallmann, 1912:177.

_Clathria spinifera_; Hooper & Wiedenmayer, 1994: 274.


**MATERIAL. LECTOTYPE:** ZMUU (not seen) (fragments BMNH1929.11.26.6, NHNDC1 2427): specific locality unknown, Java Sea, Indonesia, no other details known. **PARALECTOTYPES:** ZMUU (not seen); Off Phan Thiet, Vietnam, South China Sea, 11°05'N, 108°50'E, 45m depth, coll. Capt. Svensson (dredge). **OTHER MATERIAL: INDONESIA - SMF1815** (fragment MNHNDCL2378). WA - NTMZ1750 (fragment QMG300493).

**HABITAT DISTRIBUTION.** Rocky reef and associated sand, shell-grit and gravel beds; 45-84 m depth; Port Hedland (WA) (Fig. 197H); S China Sea and Java Sea (Lindgren, 1897), Moluccas (Thiele, 1903a).

**DESCRIPTION.** **Shape.** Arborescent, digitate, stalked sponge, 225 mm long, 230 mm wide, with slightly flattened cylindrical branches, 5-12 mm diameter (although junctions of anastomoses usually thicker), usually fused and anastomosing except at distal end; basal stalk cylindrical, woody, 55 mm, 15 mm diameter.

**Colour.** Light red-brown to grey-brown alive (Munsell 5YR 7/4) with olive-brown mottle (2.5YR 7/4), and flecks of black and copper-green on surface (possibly due to oxidation of pigments after collection); dark chocolate brown in ethanol.

**Oscules.** Infrequently seen, scattered, not localised to any particular region, flush with surface, 0.5-2 mm diameter.

**Texture and surface characteristics.** Basal stalk firm, almost rigid, branches firm, compressible, highly flexible; surface minutely rugose with distinct, shiny surface crust with numerous irregularly distributed microconules, dissected by minute ridges and canals.

**Ectosome and subectosome.** Moderately well developed ectosomal skeleton, with more-or-less continuous palisade of discrete spicule brushes composed of smaller ectosomal auxiliary subtylostles; some detritus on ectosomal skeleton and collagen heavier and more darkly pigmented in periphery than in core; subectosomal skeleton mostly erect, plumose, occasionally tangential or paratangential to surface crust, with individual megascleres arising from subectosomal brushes invariably protruding through surface, composed of larger auxiliary megascleres arising from plumose brushes of principal styles on ultimate choanosomal fibres; ectosome and subectosomal regions together comprise only small proportion of total branch diameter; principal styles and acanthostyles echinating peripheral fibres extend close to ectosomal crust but rarely protrude beyond ectosome.

**Choanosome.** Skeletal architecture contains both plumo-reticulate spongins fibres and plumose spicule tracts outside fibres; no differentiation of axial and extra-axial regions of choanosome although peripheral skeleton predominantly plumose; spongin fibres moderately heavy, 58-110 μm diameter (heavier in Indonesian specimen); fibres form oval to elongate meshes, 95-460 μm diameter, and fibre skeleton becomes increasingly plumose towards periphery; fibres indistinctively divisible into primary and secondary systems, both approximately equal diameter demarkated only by coring spicules; neither category of fibre cored by spicules for more than 60% of fibre diameter; primary ascending fibres multispicular with 2-6 principal styles per tract, many protruding through fibres at acute angles (pseudo-echinating) for less than half their length, forming plumose structures; secondary connecting fibres often transverse, rarely with more than 2 spicules per tract contained entirely within fibres; echinating acanthostyles heavy (lighter in Indonesian specimen), particularly abundant on fibre nodes (together with protruding principal styles) forming characteristic stellate-plumose echinations; towards periphery plumose brushes of principal styles protrude through fibres completely, forming multispicular tracts, and from midway along these brushes or at their points arise ascending tracts of subectosomal auxiliary megascleres; mesohyl matrix heavy, moderately lightly pigmented, containing few loose auxiliary megascleres.

**Megascleres** (refer to Table 40 for dimensions). Choanosomal principal styles robust, short, thick, usually curved at centre, slightly hastate (abrupt-
TABLE 40. Comparison between spicule dimensions for type and other material of Clathria (Thalysias) spinifera (Lindgren). Measurements in μm, and cited as range (and mean) (N=25).

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>Fragment of holotype (BMNH 1929.11.26.6)</th>
<th>Specimen (N=1)(Thiele, 1903a) (Indonesia)</th>
<th>NTMZ2.1750 (NW Australia)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choanosomal styles</td>
<td>153-(196.9)-242 x 8-(11.4)-14</td>
<td>183-(206.0)-242 x 12-(16.1)-18</td>
<td>155-(187.2)-200 x 8-(16.2)-20</td>
</tr>
<tr>
<td>Subectosomal styles</td>
<td>203-(233.8)-256 x 5-(6.8)-8</td>
<td>168-(258.2)-291 x 3-(6.9)-9</td>
<td>172-(196.4)-210 x 4-(6.4)-8.5</td>
</tr>
<tr>
<td>Ectosomal styles</td>
<td>97-(132.0)-171 x 3-(3.8)-5</td>
<td>92-(115.5)-151 x 3-(4.9)-6</td>
<td>96-(132.2)-158 x 2-(4.5)-6</td>
</tr>
<tr>
<td>Acanthostyles</td>
<td>75-(84.8)-93 x 6-(7.6)-9</td>
<td>69-(72.3)-77 x 7-(9.1)-11</td>
<td>102-(108.6)-114 x 5-(8.6)-9</td>
</tr>
<tr>
<td>Chelae</td>
<td>14-(18.7)-16</td>
<td>13-(15.2)-17</td>
<td>11-(13.9)-16</td>
</tr>
<tr>
<td>Toxas</td>
<td>26-(79.7)-124 x 0.5-(0.9)-1.5</td>
<td>50-(149.0)-194 x 0.8-(1.2)-1.5</td>
<td>32-(84.2)-119 x 0.5-(0.8)-1.2</td>
</tr>
</tbody>
</table>

Clathria (Thalysias) spinifera has unusual fibre characteristics with only basalcs of principal styles enclosed in primary sponge fibres (forming multiparical ascending plumose tracts), and fully enclosed in secondary fibres (forming paucispicular transverse connecting tracts). Together these fibres produce an irregular renieroid-reticulation. Points of principal styles, especially in ascending spicule tracts, usually protrude through spiculin fibres emphasising a plumose skeletal structure. This feature is more prominent in the Australian specimen than in Indonesian material and is reminiscent of Hallmann’s (1912) ‘spicata’ group (see remarks for C. (T.) lendenfeldi), and the ‘coccined’ group (e.g., M. coccinea Bergquist (1961a:38), M. rubens Bergquist (1961a:38), M. scottii Dendy (1924a:352), and M. parthena de Laubenfels (1930:27)). Both the ‘spicata’ and ‘coccined’ groups of species have extra-fibre tracts composed of choanosomal principal megascleres. In the ‘spicata’ group those tracts occur exclusively outside fibres, and usually ascend to the ectosomal region, whereas in the ‘coccined’ group tufts of principal styles congregate around fibre nodules, and they do not usually protrude beyond that region: C. (T.) spinifera shows a condition intermediate to both groups.

Clathria (Thalysias) styloprothesis sp. nov.
(Figs 199-200)


MEMOIRS OF THE QUEENSLAND MUSEUM

HABITAT DISTRIBUTION. Rock, sand and coralline substrates; 22-50 m depth; Houtman Abrolhos and SW coast (WA) (Fig. 199G).

DESCRIPTION. Shape. Flabellate, irregularly vasiorm, with relatively long lamellae, up to 130 mm high, 125 mm maximum breadth, and cylindrical basal stalk, 18 mm long, 6 mm diameter; lamellae moderately thin, up to 5 mm maximum thickness, with rounded or uneven, bifurcate margins.

Colour. Live colouration unknown, yellow-brown in ethanol.

Oscules. Sparse, scattered over external surface, up to 2 mm diameter; exhalant pores minute, dispersed over entire surface, giving ectosome slightly reticulate appearance.

Texture and surface characteristics. Texture rubbery, compressible; surface optically smooth, slightly uneven, with subdermal striations and grooves visible only near margins of lamellae. Ectosome and subectosome. Thin, disorganised ectosomal crust composed of acanthostyles erect on peripheral fibres, intermingled with paratangential or erect plumose brushes of auxiliary styles of 2 sizes (larger ones less common than smaller ones), together forming nearly continuous palisade of erect spicule brushes on surface; subectosomal skeleton absent entirely; choanosomal skeleton immediately subdermal.

Choanosome. Skeleton structure irregularly reticulate, with very thick 'fibres' formed almost exclusively by Codiophyllum algal filaments, 70-156 μm diameter, with only a superficial layer of spongocovering surface of algal filaments; coring spicules excluded entirely from within 'fibres', although some auxiliary stylostyles lie on surface of 'fibre' and many echinating acanthostyles embedded within surface and erect on 'fibre'; 'fibre' (algal filament) meshes usually form large nodes, and in peripheral skeleton nodes usually have tangential layer of subectosomal stylostyles lying on surface; 'fibres' sinuous, extending into peripheral skeleton, with ectosomal crust perched over 'fibre' ends; mesohyl matrix very light, with few microscleres scattered between meshes, and small oval choanocyte chambers, 49-86 μm diameter.

Megasceleres. Choanosomal principal styles absent.

Subectosomal auxiliary stylostyles relatively uncommon, straight, relatively thick, fusiform, with slightly constricted, smooth bases. Length 211-253.8-292 μm, width 3-5.2-8 μm.

Ectosomal auxiliary stylostyles most common, straight or slightly curved at centre, thick, fusiform, with smooth subtylotyle bases. Length 92-(128.5)-148 μm, width 4-(6.2)-7.5 μm.

Acanthostyles extremely abundant, short, thick, with slightly swollen subtylotyle bases, evenly spaced except for aspinose points; some modified to acanthostylytes; spines large, slightly recurved at point. Length 48-(56.4)-63 μm, width 3.5-(7.2)-9 μm.

Microscleres. Isochelae abundant, palmate, unmodified, of a single size category; lateral alae entirely fused to shaft, often reduced to small 'wings', front ala completely detached from lateral alae. Length 10.5-(13.2)-16 μm.

Toxas wing-shaped, short, relatively thick, slight angular central curves, slightly reflexed arms. Length 8-43.5-96 μm, width 1.0-(1.8)-2.5 μm.

Associates. Probable obligatory symbiotic relationship with red algae (Halymeniaceae), possibly Codiophyllum (identified from a superficial comparision with published descriptions and figures in Scott et al., 1984); algal filaments replace spongin fibres entirely, or alternatively, sponge parasitic on algae, penetrating into deepest layers of cortex of blades; association well documented (Scott et al., 1984), with similar associations known for some other microcionids (Antho opuntioidei (Lamarck) and A. frondifera (Lam.); Topsent, 1929).

ETYMOLOGY. Greek protheco- from Topsent's (1929) term 'styloprothése' referring to the incorporation of algal filaments into the skeleton, displacing spongin fibres.

REMARKS. This species is similar to C. (T.) cactiformis in acanthostyle geometry, and in fact a specimen of this species mentioned by Carter (1878) from the 'west coast of Australia' was originally named Echinonema typicum (a junior synonym of C. (T.) cactiformis). Carter's material has not been found in BMNH collections, but his description mentions the sponge-algae relationship as being a 'pseudomorph' of the free living sponge. Carter's (1878) original report of Echinonema typicum is not valid (nomen nudum), and his subsequent description of the species (Carter, 1881a) is based on different material from his 1878 notice of the species. Hence the name 'typicum' is not available for this species.

The external morphology of Clathria (Thalysias) styloprothesis appears to be identical to the red algae Codiophyllum flabelliforme (Sonder), redescribed and figured in detail by Scott et al. (1984) from the WA coast (lat. 28°-35°S, 5-21 m depth), particularly in the thickness

HABITAT DISTRIBUTION. Intertidal laterite rock, dead coral reef flats, in rock pools, encrusting on underside of dead faviid coral boulders, and on coral reef slopes in deeper waters, sheltered on the sides of faviid coral boulders or Acropora thickets; 0-32m depth; known only from Australia: Darwin Harbour, Port Essington, Cobourg Peninsula (NT); Hibernia Reef, Sahul Shelf (WA); Raine Island (FNQ), Hook Reef (MEQ) (Fig. 201H).

DESCRIPTION. Shape. Thickly encrusting, 5-30mm thick, gelatinous lobate, following contours of substrate with prominent surface folding and ridge-like sculpturing.

Colour. Ectosome pale pink and white mottle to pale red-orange alive (Munsell 5RP 8/4-2.5R 8/4); pigmentation below surface dark or bright red-brown (Munsell 2.5R 5/6-5/8); superficial pigmentation easily abraded from surface leaving a sponge resembling a bleeding wound; even grey-brown in ethanol.

Oscules. Pores not visible in either live or preserved specimens.

Texture and surface characteristics. Compressible, gelatinous, slimy in situ, producing abundant clear mucus upon exposure to air; surface optically smooth, lobate, with occasional folds and minute subectosomal canals and ridges, although striations not prominent; mottled or speckled external appearance superficially resembles a compound ascidian.

Ectosome and subectosome. Minute hispid, light, poorly differentiated series of ectosomal and subectosomal auxiliary spicule brushes pierce surface; choanosomal principal megascleres protrude through ectosome in thin encrustations but not in thicker sections; both ectosomal and subectosomal spicule brushes form plumose or stellate bouquets below peripheral skeleton but development variable, ranging from a dense continuous palisade in thicker regions to sparse, irregular paratangential bundles of spicules in thinner sections; thinly encrusting paratype (NTMZ2530) with simple tangential ectosomal skeleton composed of both sizes of auxiliary spicules; subectosomal skeleton with larger auxiliary subtylosistyles forming extensive, plumose, and discrete paratangential tracts originating close to substrate, ultimately diverging and piercing ectosomal skeleton; individual subectosomal auxiliary subtylosistyles also scattered throughout mesohyl; mesohyl matrix in peripheral skeleton heavy, granular, containing numerous pigmented spherulous cells with granular inclusions concentrated in periphery, together with occasional calcareous and siliceous foreign particles.

Choanosome. Skeletal architecture hymedesmoid, with spongins reduced to a basal layer, up to 30μm thick, lying on coralline substratum, with bases of choanosomal principal styles and acanthostyls embedded and perpendicularly to substrate; no folding of basal spongins or fibre nodes observed; choanosomal skeleton occupies only small percentage of sponge thickness with major portion being extensive plumose subectosomal and ectosomal skeletons in periphery of sections; mesohyl substantially lighter in deeper choanosomal skeleton, closer to substrate, than in peripheral skeleton; choanosomal chambers 52-65μm diameter.
Megascleres. Choanosomal principal megascleres long, thick subtylostyles, with distinctive curvature towards basal end, prominent tylole bases abundantly microspined, tapering towards fusiform point. Length 198.5-(374.3)-524.0 µm, width 8-(12.9)-19.1 µm.

Subectosomal auxiliary subtylostyles long, relatively thin, mostly straight, fusiform pointed, prominent tylole bases usually microspined but also with variable proportion of smooth or partly tylole bases (4-16% of spicules). Length 259.3-(377.4)-502.5 µm, width 4.5-(7.2)-10.5 µm.

Ectosomal auxiliary subtylostyles short, slender, straight, fusiform, with less prominent tylole bases, usually microspined occasionally smooth. Length 117.9-(170.0)-208.6 µm, width 2.3-(3.8)-5.6 µm.

Acanthostyles long, slender, straight, subtylole, fusiform pointed, evenly spined, spines small, sharp, slightly recurved. Length 79.9-(108.3)-150.9 µm, width 4.6-(8.0)-12.6 µm.

MICROSCLÆRES. Palmate isochelae abundant, unmodified, with lateral and front alae approximately smae length, front ala completely detached along lateral margin, lateral alae fused to shaft. Length 9.7-(15.3)-20.7 µm.

Toxas common or abundant, accolada, short or long, invariably thin, with very slight to moderate central curvature and straight or very slightly reflexed points. Length 37.4-(183.4)-341.7 µm, width 0.8-(1.9)-3.2 µm.

ASSOCIATIONS. Growing next to, or covering other encrusting sponges (Heterosclœa, Placosphœnia, Usosia, Mycale), compound and simple ascidians, and coralline algae.

ETYMOLOGY. Latin tingens, referring to its superficially tinted pink live colouration.

REMARKS. Clathria (Thalysias) tingens is similar to C. (T.) toxifera in spicule geometry and spicule dimensions, but differs in the geometry of its acanthosclæae (evenly spined), choanosomal principal styles (markedly curved basal region, bearing spination on the base and ‘neck’ region proximal to the base), and toxæ morphology (possession of accolada toxas). In addition, live colour, differential pigmentation between ectosomal and choanosomal regions, and surface sculpturing are also diagnostic for this species. In having an easily abraded dermal pigment, the present species is reminiscent of the pink C. (Wilsonella) tuberosa, and yellow morphs of C. (T.) abietina, both from NW Australia, and the yellow C. (T.) venosa from the West Indies. Clathria (Thalysias) tingens should also be compared with C. (Microciona) hymedesmoides Van Soest from Curacao in secondary colouration, hymedesmoid skeletal architecture (seen in thinly encrusting portions of C. (T.) tingens), and similarities in the morphology of some of their spicule categories. De Laubenfels (1954:135) recorded a specimen of C. (T.) cervicornis from the Marshall Is, which also had differentiated ectosomal (pale orange-brown) and choanosomal pigmentation (brilliant vermilion), although these two species differ in most other respects (e.g., growth form, skeletal architecture and spicule geometry). There are some geometric differences in spicules between Indian Ocean and Pacific Ocean specimens (Figs 202-203), but these are minor.

Clathria (Thalysias) toxifera (Hentschel) (Figs 204-205, Plate 8E)


MATERIAL. HOLOTYPE: SMP967T: Bei Mimen, Aru Is., Arafura Sea, Indonesia, 6°S, 134°50'E, 15 m depth, 8.iv.1908, coll. H. Merton (dredge). OTHER MATERIAL: NT-NTMZ2136, NTMZ2198, NTMZ2204, NTMZ2213, NTMZ2219 (fragment QMG300506), NTMZ2222, NTMZ2233 (fragment QMG300149), NTMZ2421, NTMZ2544, NTMZ2555, QMG303296, NTMZ2217, NTMZ2074b, NTMZ2173, NTMZ2504, NTMZ1348, NTMZ3909. WA- QMG301186, THAILAND - NTMZ3681.

HABITAT DISTRIBUTION. Intertidal laterite rock; dead coral reef flats, in rock pools, on sublittoral faviid coral heads, usually exposed at ELWS tides; usually encrusting under dead faviid coral boulders, in cavities, or on metal debris (aluminium and steel) scattered over coral reefs; 0-20 m depth; common intertidal encrusting sponge throughout Indo-Pacific; Darwin Harbour, Port Essington, Cobourg Peninsula, Wessel Is (NT); Hibernia Reef, Sahul Shelf (WA) (Fig. 204H); also Aru Is., Indonesia (Hentschel, 1912), Ko Samui, Gulf of Thailand (present study), Madras (Burton, 1938a).

DESCRIPTION. Shape. Thinly encrusting, 1-5 mm thick, often covering substantial areas of substrata.

Colour. Pale orange-brown to darker red-brown alive (Munsell 5YR 7/6-2.5R 4/10), with whitish stellate subdermal drainage canals running over surface; colourations darkens upon exposure to air, brown to beige-grey in ethanol.
Oscules. Oscules minute, 150-450μm diameter, scattered over surface, raised slightly above surface (on ends of conulose) or flush with surface (at nodes of drainage canals).

Texture and surface characteristics. Firm, hispid, compressible in thicker regions; surface uneven, roughened, usually following contours of substrate, with raised projections, meandering ridges and cavities in thicker growths, or more even and with only slightly sculptured surface in thinner growths; surface with prominent subectosomal drainage canals radiating towards oscules, but these collapse, and stellate surface sculpturing disappears upon preservation; sponges produce slight clear mucous when exposed to air.

Ectosome and subectosome. Ectosome slightly translucent or opaque in life, minutely hispid; spicule brushes paratangential or erect, composed of 2 layers: outer layer with smaller ectosomal subtylostyles, inner layer of larger subectosomal auxiliary subtylostyles; both layers appear intermingled but closer examination shows brushes of larger spicules originate deeper within mesohyl, whereas layer of smaller brushes occur only near periphery; points of choanosomal principal subtylostyles also protrude through surface brushes, up to 300μm in thin sections,
whereas in thicker sections principal megascleres barely pierce surface, surrounded at their points by ectosomal spicule brushes in classical Thalysias architecture; development of ectosomal skeleton variable, ranging from continuous dense palisade of spicule brushes in thicker growths, to sparse, irregularly paratangential, discrete brushes in thinner sections; foreign debris sometimes incorporated into ectosomal skeleton with particles by spicule brushes. In subectosomal region are also thin longitudinal bands, forming dense tracts, composed of subectosomal auxiliary subtylostyles usually congregated around erect principal spicules, running tangential or paratangential to ectosome; subectosomal tracts diverge near periphery to form plumose subectosomal brushes underlying ectosomal skeleton; in thin sections plumose tracts originate approximately halfway along length of principal spicules whereas in thicker sections subectosomal brushes do not diverge until peripheral skeleton; subectosomal region 0.5-3mm thick containing abundant, moderately heavily pigmented.

Choanosome. Choanosomal skeletal hymedesmoid in thinner sections with single megascleres embedded in basal sponge lying flat on substratum, or microcionid in thicker regions with basal sponge slightly raised nodes (="fibres"); peripheral skeletal architecture distinctly plumose; choanosomal principal megascleres and echinating acanthostyles perpendicular to substrate with bases embedded in basal sponge or in erect fibre nodes where present; basal sponge moderately heavy, yellow-brown, lying directly on calcareous substrate, 8-20μm thick in hymedesmoid sections, up to 45μm in microcionid sections; few choanoocyte chambers observed only in thicker sections, 13-55μm diameter, usually lined by toxas and/or isochelae. Megascleres. Choanosomal principal subtylostyles range greatly in length, thickest near base, usually slightly curved at centre, all with prominently swollen bases, most heavily microspined or granular, rarely completely smooth (0-16% of spicules in individual specimens), all with fusiform tapering points. Length 194.0-(368.7)-685.1μm, width 5.1-(14.1)-25.5μm.

Subectosomal auxiliary subtylostyles long, thin, fusiform, straight, with distinctly swollen tylole bases, usually lightly microspined, less frequently smooth (0(10% of spicules in individual specimens). Length 228.2-(354.3)-494.3μm, width 2.0-(6.5)-12.9μm.

Ectosomal auxiliary subtylostyles short, straight, fusiform, less markedly tylole than larger auxiliary subtylostyles, with smooth or basal spines. Length 123.3-(171.1)-229.6μm, width 1.5-(3.6)-6.6μm.

Acanthostyles thick, slightly curved towards basal end, with subtylole bases, long tapering points, mostly evenly, lightly spined except for bare 'neck' proximal to base, spines large, recurved, sharply pointed. Length 121.9-(154.5)-208.0μm, width 3.0-(7.9)-14.0μm.

Microscleres. Palmate isochelae usually abundant (uncommon in 14% of samples), moderately large, of a single size, unmodified (although more heavily silicified in 15% of specimens), with front ala detached from and generally shorter than lateral alae, lateral alae completely fused to shaft. Length 10-(22.6)-30μm.

Toxas verging on oxhorn, very abundant, relatively thick but variable in length, with wide central curvature and straight or only slightly reflexed points. Length 16-(89.8)-241μm, width 0.8-(2.9)-5μm.

Associations. Growing over or in proximity to other encrusting sponges (Desmanthus, Mycale, Ulosa, Haliclona, Petroisia, and other microcionids), compound ascidians, coralline algae, Platgyra and favid corals, barnacles (Chthamalus), and metal debris (aluminium cans) on the reef flat (with some evidence of etching on the metal substrate). It is probable that the species plays an active role in coral bioerosion.

REMARKS. This species is perfectly recognizable from Hentschel's (1912) original description and material described here from Northern Territory, Western Australia and Thai waters do not differ markedly from the Indonesian population. Conversely, we do not know any details of Burton's (1938a) specimen from Madras since he merely repeated verbatim the original description, spicule measurements and figures from Hentschel (1912).

Live colour, surface features, spicule size and spicule ornamentation differentiate C. (T.) toxifera from other encrusting Clathria (Thalysias) but there are no unique structural differences. The older literature mostly concerns preserved material, only rarely describing species' in situ characters, and most encrusting microcionids have few unique morphological features. Consequently, differentiation between encrusting microcionids relies mainly on details
of the mineral skeleton, particularly spicule geometries.

The possession of stellate subectosomal surface sculpturing (i.e., subectosomal drainage canals radiating towards oscules) is known for C. (TT) venosus, and to a lesser extent C. (TT) virgultosa (sensu Wiedenmayer, 1977:143), both from the Caribbean. But this feature cannot be given too much taxonomic importance given that it represents an ecological adaptation: viz. in thickly encrusting sponges subectosomal canals represent the primary means of water circulation whereas in thicker specimens the primary aequiferous system is predominantly internal. In any case C. (TT) toxifer a differs from the Caribbean species in spicule geometry and ornamentation and spicule sizes.

Clathria (Thalysias) toxifer a should also be compared with other encrusting microcionids from the Indo-Malay and Indo-Pacific region which have hymedesmoid architecture. These include numerous species from the Arafura Sea: C. (TT) aruensis (Hentschel, 1912:381), C. (TT) calochela (Hentschel, 1912), C. (TT) distincta (Thiele, 1903a), C. (TT) longitoxa (Hentschel, 1912), C. (Microciona) rhopalophora (Hentschel, 1912), C. (M.) hentscheli nom. nov., C. (M.) similis (Thiele, 1903a), C. (M.) tetra styla (Hentschel, 1912) and C. (M.) thielei (Hentschel, 1912) (all of which lack isochelae). Species from other localities are: C. (T.) michaelseni (Hentschel, 1911) from Shark Bay, WA (with sigmoid anchorate-like (bidentate) isochelae); C. (M.) aceratoobtusa (Carter, 1886g) from the Mergui Archipelago, Burma, and from Shark Bay, WA (Hentschel, 1911) (with smooth echinating megascleres); C. (M.) affinis (Carter, 1880a), C. (M.) bulboretorta (Carter, 1880a), C. (M.) fascispiculifera (Carter, 1880a) (with sigmoid palmate isochelae), and C. (M.) quadriradiata (Carter, 1880a) all from the Gulf of Manaar, Sri Lanka; C. (T.) dubia (Kirkpatrick, 1900a) from Christmas Is, Indian Ocean (with anchorate-like isochelae); C. (C.) pellicula Whitelegge (1897) from the Ellice Is, Pacific Ocean; C. (T.) euryphi (de Laubenfels, 1954) from Palau Is, and Suva, Fiji (Tendal, 1969:40) (with 2 categories of isochelae). All those taxa differ from the present species in various details of spicule size, spicule diversity, geometry and ornamentation. Some of these species are redescribed in the present work whereas others will be redescribed in a forthcoming monograph on the Indo-Malay microcionids (Hooper et al., in prep.). From re-examination of the relevant type material of each of these species, and from a detailed précis of the literature, it is clear that there are many encrusting species still undescribed, and that many of those already described are in urgent need of revision.

Clathria (Thalysias) vulpina (Lamarck, 1814) (Figs 206-209, Tables 41-42, Plate 8F)

Spongilla vulpina Lamarck, 1814:449; Lamarck, 1814:376
Rhaphidophius vulpinus; Ridley, 1884a:615.
Rhaphidophius vulpinus; Topsent, 1932:110, pl.5, fig.3.
Halichondria frondifera Bowierbank, 1875:288-289
Amphilectus frondifer; Vosmaer, 1880:115.
Clathria frondifera var. seta-tubulosa; Wilson, 1925:439.
Clathria frondifera var. dichela; Hentschel, 1912:360-361.
Tenacia frondifera var. dichela; Hallmann, 1920:771.
Rhaphidophius frondifera; Thiele, 1903a:958, text-fig.23.
Thalysias frondifera; de Laubenfels, 1954:138-139, text-fig.88.
Clathria dichela; Vacelet et al., 1976:71, pl.3, fig.b; Vacelet & Vasseur, 1977:114.
Rhaphidophius dichela; Vosmaer, 1884b:115.
Clathria corallina fida Dent, 1889:85, pl.2, fig.2; Burton, 1916b:128; Dendy, 1922:65.
Rhaphidophius seriatus Thiele, 1899:14, pl.1, fig.6, pl.5, fig.7.
Clathria reinwardtii var. palmata; Ridley, 1884a:447; Bergquist & Tizard, 1967:186.
Clathria typica; Vacelet & Vasseur, 1971:94.
Not Rhaphidophius fujii var. spinifer; Lindgren, 1898:311-312, pl.17, fig.7, pl.19, fig.18; Thiele, 1903a:958.
Not Clathria nuda; Hentschel, 1912:298, 359, 364-365, pl.19, fig.28.
Not Clathria frondifera var. major; Hentschel, 1912:361.
Clathria frondifera var. major; Hentschel, 1912:361.


FIG. 209. Clathria (Thalysias) vulgaris (Lamarck). Incidence of larval production in NT populations.

PIB034-457 (fragment QMG300053). QLD- QMG303522, QMG300861, QMG303038, QMG304758, QMG304409, QMG304370, QMG303898. NSW - QMG301376, QMG301385, QMG301405.

HABITAT DISTRIBUTION. Mostly on rock or dead coral reefs, exposed to currents or sheltered between coral heads; 0.5-10m depth; widely distributed throughout Indo-west Pacific; Bynoe Harbour, Darwin Harbour, Orontes reef, Melville Is, Wessel Is (NT); Shark Bay, Carnarvon, Barrow Isl, Exmouth Gulf, Port Hedland, Monte Bello Is, Amphinome Shoals (WA); Gulf of Carpentaria, Thursday Isl, Bird Isl, Home Is, Green Isl, Frankland Is, Low Is, Cook Reef, Shellburne Bay, Howick Is, Lizard I (FNQ); Hook Reef (MEQ); Byron Bay (N. NSW) (Fig. 206H); also Mozambique (Thomas, 1979a), Madagascar (Vacelet et al., 1971, 1976, 1977; present study), Amirante Is (Ridley & Dendy, 1887), Seychelles Is (Ridley & Dendy, 1887; Thomas, 1979a), Aldabra Is (Levi, 1961c), Red Sea (Topsent, 1892b; Burton, 1959a), Kattiarwar W. coast of India, Madras, Gulf of Mannar and Sri Lanka (Dendy, 1889b, 1916b; Lindgren, 1897; Burton, 1938a; Thomas, 1970b), Mergui Archipelago and Andaman Is (Burton & Rao, 1932), Straits of Malacca, Malaysia and Gaspar Straits (Bowerbank, 1875), Aru Is, Arafura Sea, Java Sea and Sulawesi, Indonesia (Thiele, 1889; Lindgren, 1898; Hentschel, 1912; present study), Hon K'ai L, Vietnam (present study), Negros Oriental, Bohol Sea, Mindinao, and S. Philippines (Wilson, 1925; Levi, 1961b; present study), Guam, Micronesia (de Laubenfels, 1954), S. Japan (Hoshino, 1981), New Caledonia (Hooper & Levi, 1993a), Madang, Papua New Guinea (present study).

DESCRIPTION. Shape. Tubulo-digitate, variable in size ranging from small single digits (80mm high) to massive multiple digitate lobes attached on a common base (450mm high); digits cavernous, insubstantial, composed of tight or loosely anastomosing sub-branches (trabeulae). Colour. Deep mauve-red (Munsell 2.5R 6/4) to pinkish red alive (2.5R 8/4) in shallow water specimens; pigmentation usually absent in deeper water specimens, beige brown alive (7.5YR 8/4). Oscules. Oscules scattered between surface contours, not confined to any particular region, 2-6mm diameter, raised slightly above surface with distinct membranous lip; ostia 0.4-2.2mm diameter flush with surface. Texture and surface characteristics. Soft, rubbery, compressible; surface usually with small tapering digitate or spiny processes arising from free branches; surface also ornamented by minute grooves and striations, irregularly folded and cavernous; when intact ectosomal membrane stretched across adjacent branches, through which subectosomal canals can be seen. Ectosome and subectosome. Conspicuous palisade of tangential, paratangential and erect spicule brushes composed of smaller auxiliary subtylostyles, with choanosomal principal megascleres protruding through surface, overlapping prominent plumose subectosomal spicule tracts; ectosomal skeletal density variable even within a single specimen. Choanosome. Choanosomal skeleton regular or subreniform reticulation of ascending, primary spongine fibres (60-135μm diameter) and transverse connecting fibres (25-39μm diameter); fibre Anastomoses form rectangular to square meshes lined by oval choanoocyte chambers (22.58μm); fibres heavy, slightly heavier in axis than towards periphery; primary fibres cored by multiserial tracts of both choanosomal principal and subectosomal auxiliary megascleres, and coring spicules occupy less than 66% of primary fibre diameter; secondary fibres paucispicular, and coring spicules comprise only 50% of fibre diameter; echinating acanthostyles usually abundant, and choanosomal principal styles also echinate fibre endings in peripheral skeleton, individually or forming plumose brushes, supporting plumose tracts of subectosomal auxiliary spicules and ultimately ectosomal brushes above; auxiliary megascleres also scattered between fibres. Megascleres. Choanosomal principal styles curved near base, thick, hastate or fusiform pointed, occasionally mucronate, with rounded, non-tylote, smooth bases. Length 113.3-(184.4)-253.0μm, width 3.6-(11.2)-19.4μm (holotype 156.5-(173.8)-193.3 x 10.1-(13.1)-15.9μm).
Subectosomal auxiliary subtylostyles mostly straight, less often slightly curved near base, only slightly subtyloite, frequently microsspin, less often smooth, fusiform pointed. Length 123.6- (221.4)-310.9 μm, width 1.0-(4.7)-10.4 μm (holotype 148.2-(196.8)-231.8 x 3.6-(6.1)-8.8 μm).

Ectosomal auxiliary subtylostyles styles straight, short, thin, subtyloite, invariably microsspin, fusiform pointed. Length 64.2-(99.1)-161.1 μm, width 1.0-(3.3)-6.9 μm (holotype 65.9-(87.8)-116.4 x 1.1-(3.4)-6.1 μm).

Acanthostyles subtyloite, fusiform sharply pointed, spined on base and midsection of shaft but aspinose on 'neck' proximal to base and point; spines large, recurved, sharp. Length 51.8-(73.1)-94.7 μm, width 1.1-(6.6)-11.6 μm (holotype 59.7-(74.3)-86.6 x 4.5-(7.8)-10.7 μm).

Microascleres. Palmar isochelae abundant, scattered throughout the mesohyl, in 2 size classes with very few intermediate sizes; contort forms extremely rare seen in few specimens; chelae relatively poorly silicified, lateral and front alae approximately same length; front ala completely detached from lateral alae, which are fused completely to shaft. Length I: 7.1-(12.4)-17.5 μm (holotype 9.1-(12.8)-17.1 μm), length II: 1.1-(3.8)-6.9 μm (holotype 1.1-(3.7)-6.1 μm).

Toxas common to uncommon, distributed singly or in toxodragmata throughout mesohyl, seen particularly surrounding choanocyte chambers; toxas commonly accolada (long, thin, rhaphidiform, with little or no central curvature or apical flexion), to less commonly wing-shaped (short, thin, widely curved centrally, without flexed points). Length 7.2-(97.9)-199.5 μm, width 0.5-(1.2)-3.2 μm (holotype 16.7-(55.8)-94.6 x 0.6-(1.7)-2.3 μm).

Larvae and reproductive periodicity. 28% of all specimens examined (including material reported by Hooper & Lévi, 1993a) contained incubated (viviparous) parenchymella larvae in various stages of development; young larvae spherical, more mature larvae oval-elongate, 170-420 μm diameter; cilia not observed (preserved material); undifferentiated forms (170-340 μm diameter) contain whiskly juvenile megascleres in axis, with mesohyl matrix similar in colouration to adult; more advanced larvae (230-420 μm diameter) contain juvenile styles and toxas at centre, isochelae towards periphery, and distinct ectosomal layer of differentiated cells. In Northern Territory populations sexual...
Table 42. Latitudinal gradients in spicule dimensions for populations of *Clathria (Thalysias)* vulpina. Measurements (in μm) are mean lengths (L) and widths (W) 1SE.

<table>
<thead>
<tr>
<th>SPICULE</th>
<th>LOCATION/LATITUDE</th>
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<tr>
<td></td>
<td>NCAL 23°S</td>
</tr>
<tr>
<td>(N)</td>
<td>(175)</td>
</tr>
<tr>
<td>Choanosomal styles L</td>
<td>156.8±9.2</td>
</tr>
<tr>
<td>W</td>
<td>6.2±0.9</td>
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<tr>
<td>Acanthostyles L</td>
<td>51.1±2.8</td>
</tr>
<tr>
<td>W</td>
<td>3.5±1.0</td>
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<tr>
<td>Chelae L</td>
<td>-</td>
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<tr>
<td>Texas L</td>
<td>79.3±17.2</td>
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<tr>
<td>W</td>
<td>0.6±0.2</td>
</tr>
</tbody>
</table>

Location: NCAL = New Caledonia; WNS = Northwest Shelf, WA; GBR = northern Great Barrier Reef, Qld; DAR = Darwin region, NT; CP = Cobourg Peninsula region, NT; INDO = Southeast Indonesia; PHIL = southern Philippines; MICRO = Marianas & Caroline Islands, Micronesia.

Reproduction was distinctly seasonal, with incubated larvae only seen in samples collected during September-October (dry season) (Fig. 209).

**Associations.** 24% of all specimens sampled had polychaete infestations by *Typosyllis spongicola* (with at least one worm in mesohyl); other epiphytic and epizootic associations not observed.

**Variation.** Two morphs differentiated - 83% with spinous (rounded or sharply pointed) surface processes, and 17% without surface processes superficially resembling *Hyatella intestinalis* (Lamarck) (Dictyoceratida) - but growth form apparently unrelated to water depth, season or geography of samples. Presence or absence of pigmentation directly related to water depth. Variable ectosomal development, with 52% of specimens having paratangential-tangential skeletons of intermingled ectosomal and subectosomal auxiliary spicules and choanosomal styles protruding through ectosome; 31% of specimens had tangential skeletons in some sections of ectosome and erect spicule brushes in other areas (e.g., on points of surface processes); 17% had a continuous, erect palisade of plumose spicule brushes (i.e., *true Thalysias* condition). 58% of specimens had thin paratangential subectosomal skeleton of larger auxiliary megascleres arising directly from ultimate choanosomal fibres; 28% had distinctly plumose tracts of subectosomal spicules, outside of fibres, supporting ectosomal skeleton; 14% had long plumose subectosomal spicule brushes and cavernous peripheral skeleton. 64% of specimens had regular choanosomal skeleton forming square (cninoc idol) or sometimes triangular (isodictyal) meshes at core, more irregular in periphery, whereas 36% were regularly (sub)renieroid-reticulate throughout skeleton, forming cavernous meshes. Fibre characteristics consistent; fibres heavy (59%) or moderately heavy (41% of specimens); primary fibres ascending (radial) (17%), transverse or longitudinal through branches (35%), or without any apparent pattern (48% of specimens); mesohyl matrix lightly pigmented (41%), abundant, moderately heavily pigmented (17%), or heaviy pigmented (28% of specimens). Choanosomal principal styles rare in 3% of specimens, largely replaced by subectosomal auxiliary spicules in fibres; proportion of subectosomal styles with smooth bases ranged from 0-4% of spicules sampled (7% of specimens), 5-10% (20%), 11-20% (24%), 21-30% (21%), 31-40% (14%), up to 76% of spicules (14% of specimens); acanthostyles heavy echinating (71%) or sparsely echinating (24% of specimens). Contort isochelae abundant (7%), common (90%) or rare (3% of specimens); larger contort chelae seen in only 10% of specimens (between 4-8% of spicules sampled); smaller contort chelae in 7% of specimens (2-10% of spicules); toxas very common (28%), common (45%), uncommon (24%) or rare (3% of specimens).

**Variability in spicule dimensions.** Intraspecific variability was relatively high for most spicule categories, but variability was not attributed to seasonal or bathymetric distributions of samples (for all northwest Australian populations combined) (i.e., variation was equally consistent within and between groups). Conversely, popula-
tions collected from various localities (Northwest Shelf, Darwin, Cobourg Peninsula, Great Barrier Reef, Indonesia, Philippines, Guam, New Caledonia) showed significant statistical differences in dimensions of some spicules (choanosomal styles, acahanostyles, larger isochela, toxas) (Table 42). Analysis of mean spicule size versus latitude (Table 41) showed certain trends in latitudinal gradients whereby spicule sizes diminish at higher latitudes. This is similar to the trend observed by Hooper & Bergquist (1992) for Cymbastela (Axinellidae).

REMARKS. Clathria (Thalysias) vulpina, better known under its junior synonym of Clathria frondifera, is a widely distributed, predominantly Indian Ocean species and a major component of the tropical maerobenthos. The cavernous, insubstantial tubulo-digite growth form, regularly rectangular skeletal construction and deep red colouration are characteristic for the species, although spicule geometry is unremarkable. The holotype is identical to NW, Australian material, and it is probable that original material collected by Perron & Lesueur was obtained from WA (although not specified by Lamarck, 1814). Neither Ridley (1884a), Wilson (1925) nor Topsent (1932) recorded toxas in the holotype, but these spicules are definitely present, relatively abundant albeit thin. Topsent (1932) compared the species with C. (T.) clathrata (Schmidt) and suggested that although spiculation was closely comparable, the two species could be differentiated by the presence of basal spination on both categories of auxiliary megascleres and the absence of toxas in C. (T.) vulpina. These characters are shown here to be of little systematic importance and erroneous, respectively, but these two species are otherwise differentiated by their skeletal construction and growth form.

Wilson (1925) also noted that C. (T.) vulpina showed considerable intraspecific variation in growth form (and size), but his statement over-emphasises this apparent variation. From the numerous published records of this species from Australasian and Indo-Malay regions in particular (most appearing under the name of C. frondifera), it is apparent that this species has a number of consistent and characteristic features including its cavernous growth form, regular (sub)renieroid choanosomal skeletal structure and individual spicule geometries, whereas ecosomal development is much more variable. To illustrate this variability, of the previously published material, Wilson's (1925) variety of C. setatubulosa from the Philippines and de Laubenfels' (1954) specimen of C. frondifera from Guam have well developed Thalysias special ecosomal skeletons (i.e., distinctly smaller auxiliary subytostyles producing an erect palisade). By comparison, Dendy's (1905) material from Sri Lanka lacks any specialised ecosomal structure, although there are two sizes of auxiliary spicules dispersed throughout the mesohyl and lying tangential to the surface. Using this species as a case-in-point, Wilson's (1925) presented pertinent arguments on the difficulty in clearly differentiating Clathria and Thalysias species based on this variability in ecosomal development, given that the formal definition of the two taxa rests on this feature, and these arguments are supported here in demoting Thalysias to subgenus status.

This species was briefly redescribed from New Caledonian specimens (Hooper & Lévi, 1993a), but no details on synonymy, population variability or living populations were given. The New Caledonian population is the most easterly recorded population and present material differs slightly from that described by Hooper & Lévi (1993a). The synonymy presented above is mostly new, corroborated by re-examination of the relevant type material, although Clathria coralloides Dendy (1889b) was already merged with C. frondifera by Dendy (1905), who also commented on the fact that ecosomal skeletal development varied substantially in the Gulf of Manaar population. Similarly, Clathria reinwardi var. palmata Ridley was synonymised with this species by Bergquist & Tizard (1967), and that decision is supported in the present study, Rhaphidophlus serius Thiele (1899) from Sulewasi has lighter spongin and more fully cored fibres than typical populations of C. (T.) vulpina, whereas the two species are identical in most other respects (spicule geometry, skeletal architecture, growth form), and there is no justification in maintaining the two species separately.

Conversely, Rhaphidophlus filifer var. spinifera Lindgren, proposed as a synonym of C. frondifera by Thiele (1903a), is rejected here given that they differ substantially in most characters and C. (T.) spinifera is maintained as a good species (see description above). Burton's (1938a) assertion that Hentschel's (1912) Clathria nuda from the Arafura Sea was also a synonym of this species is not upheld here. It has an almost regular radial (extra-axial) construction, nearly completely lacks echinating acan-
thostyles, has only a single size of isocheleae, and has substantially thicker toxas with different geometry than those seen in \textit{C. (T.) vulpina}.

\textbf{Clathria (Thalysias) wesselenensis} sp. nov.  
(Figs 210-211, Plate 9A)


\textbf{HABITAT DISTRIBUTION.} Fringing coral reefs, gentle slope, coral rubble, rich sponge beds, high sedimentation and turbidity; 13-15m depth; known only from Australia; Wessel Is (NT) (Fig. 210H).

\textbf{DESCRIPTION. \textit{Shape.}} Massive, club-shaped, up to 145mm high, with or without short, cylindrical basal stalk, 35mm long, 25mm diameter, expanded at apex, up to 75mm diameter, slightly flattened on upper surface.

\textbf{Colour.} Pale red-orange alive (Munsell 5R 7/6), khaki brown in ethanol.

\textbf{Oscules.} Large, up to 12mm diameter in life but contracted in ethanol, on apex of upper surface conules, surrounded by large, orange, transparent, membranous lips up to 30mm high, collapsing in air.

\textbf{Texture and surface characteristics.} Compressible, fibrous, basal skeleton firm, flexible.

\textbf{Ectosome and subectosome.} Thick crust of ectosomal auxiliary subtylostyles erect on surface, in discrete plumose bundles, forming continuous palisade, incorporating some scattered sand grains, and abundant, granular, dark brown collagen in peripheral skeleton; subectosomal skeleton thick, plumose brushes of large subectosomal auxiliary subtylostyles supporting ectosomal brushes, arising from ends of peripheral choanoconal fibres; subectosomal region extensive; ectosomal and subectosomal skeletens detachable, up to 250μm thick.

\textbf{Choanosome.} Skeletal structure irregularly reticulate, slightly more compressed at cor than in periphery; spongine fibres moderately light, 65-130μm diameter, predominantly longitudinal in sections (radial in sponge), not clearly divisible into primary or secondary elements except in axial region; primary fibres in peripheral skeleton long, close-set and parallel towards core, widely spaced and diverging near surface, becoming plumose at periphery, infrequently anastomosing along length but frequently bifurcating, especially closer to surface; primary fibres in axial region of skeleton close-set, short, irregularly interconnected by short secondary fibres, 30-50μm diameter; all fibres cored by choanoconal principal subtylostyles (but barely different in morphology from auxiliary spicules); primary longitudinal fibres cored by multispiral tracts of principal spicules, up to 25 abreast, occupying less than 60% fibre diameter; secondary fibres cored by uni- or paucispicular tracts of principal spicules, occupying up to 40% of fibre diameter; all primary fibres heavily echinized by small acanthostyles but sparse on secondary fibres; mesohyl matrix heavy, granular, lightly pigmented, with abundant microscleres and some secondary megascleres scattered between fibres; choanocyte chambers large, oval, 50-75μm diameter, lined by isocheleae; some detritus incorporated into mesohyl but mainly in peripheral skeleton.

\textbf{Megascleres.} Choanoconal principal subtylostyles long, slender, straight, with subtylote bases, usually microspined, tapering fusiform points. Length 307-(358.3)-395μm, width 4-(5.4)-7μm.

Subectosomal auxiliary styles very similar in geometry but slightly shorter, more slender than principal spicules; long, slender, straight, subtylote smooth or microspined bases, fusiform points. Length 207-(248.8)-265μm, width 2-(2.7)-4μm.

Ectosomal auxiliary subtylostyles short, slender, straight, subtylote smooth or occasionally microspined bases, fusiform points. Length 151-(172.8)-186μm, width 1.5-(2.1)-3μm.

Echinating acanthostyles short, slender, straight or slightly curved near distal end, subtylote, sharply pointed or blunt, more-or-less evenly spined; spines long, slender, prominently recurved. Length 78-(84.4)-95μm, width 3-(3.9)-4.5μm.

\textbf{Microscleres.} Palmate isocheleac very abundant, moderately large, single size class, front and lateral alae approximately same length, lateral alae completely fusc to shaft, front ala detached along lateral margin. Length 14-(17.2)-20μm.

Toxas very abundant, very slender, longer acocola toxas with slight angular curvature at centre, straight arms Length I: 146-(306.8)-415μm, width 0.5-(1.2)-2.0μm; shorter wing-shaped toxas moderately rounded at centre, reflexed arms. Length II: 33-(52.9)-72μm, width 0.5-(0.8)-1.5μm.

\textbf{Reproductive products.} Numerous, small, elliptical embryos present in holotype, 150-185μm
long, with extensive cellular differentiation but no observable larval spicules.

REMARKS. This species is similar to others in the 'juniperina' species complex having principal spicules barely differentiated from auxiliary spicules (see remarks for C. (T.) cactiformis above). Clathria (T.) wesselensis sp. nov. differs from most of these species in having all its fibres cored. By comparison, C. (T.) juniperina has fibres cored mainly by subectosomal auxiliary spicules, largely (but not completely) replacing principals as the primary coring spicules. In other species of the 'juniperina' group this character is further developed whereby principal spicules are completely excluded from some or all fibres, such as in C. (T.) cervicornis in which principal spicules have been lost completely, or C. (T.) cactiformis and C. (T.) placenta where only primary fibres are cored by principal spicules and
secondary fibres are completely clear. In this respect the present species is most similar to C. (T.) arborescens, differing substantially in gross morphology, geometry of acanthostyles and toxas, most spicule dimensions, and having principal spicules longer than auxiliary spicules. Both these occupy the base of the 'juniperina' species group (i.e., principal spicules are present but reduced in primary fibres), whereas species such as C. (T.) cervicornis are most derived having lost their principal spicules completely.

OTHER SPECIES OF CLATHRIA

*Clathria* (Thalysias) amabilis (Thiele, 1905)

*Rhaphidophlus amabilis*; Van Soest, 1984b:129 [generic synonymy].

MATERIAL. HOLOTYPE: ZMB3309. SE. Pacific rim, SW. Atlantic, Antarctica.

*Clathria* (Thalysias) anomala (Burton, 1933)
*Rhaphidophlus anomala* Burton, 1933:252-253, fig.3 [Natal]; Lévi, 1963:67 [Natal].

MATERIAL. Holotype: NMNZP1014. South Africa.

*Clathria* (Thalysias) araiosa
Hooper & Lévi, 1993
*Clathria* (Thalysias) araiosa Hooper & Lévi, 1993a:1256-1259, figs 17-18, table 9 [New Caledonia].

MATERIAL. HOLOTYPE: QMG300694 (fragments NTMZ3886, ORSTOMR327). SW Pacific.

*Clathria* (Thalysias) arteria
(de Laubenfels, 1954)
*Asociella arteria* de Laubenfels, 1954:148-149, text-fig.96 [NW. Ponape].

MATERIAL. HOLOTYPE: USNM22876. central W. Pacific.

*Clathria* (Thalysias) aruensis
(Hentschel, 1912)
*Hymeraphia aruensis* Hentschel, 1912:381, pl.20, fig. 38 [Aru Is., Arafura Sea].
*Eurypon (Hymeraphia) aruensis*; Lévi, 1958:27.

MATERIAL. HOLOTYPE: SMF9535T. Indonesia.

*Clathria* (Thalysias) basiarenaecea (Boury-Esnault, 1973)
*Rhaphidophlus basiarenaecea* Boury-Esnault, 1973:287, fig.49 [San Antonio Bay, Brazil]

MATERIAL. HOLOTYPE: MNHNDB8972. SW Atlantic.

*Clathria* (Thalysias) bitoxifera (Koltun, 1970)
*Asociella bitoxifera* Koltun, 1970:202-204, text-fig.29, pl.8, figs 1-2 [Kurile-Kamchatka Trench, NW. Pacific].

MATERIAL. HOLOTYPE: ZIL. NW Pacific.

*Clathria* (Thalysias) calochela
(Hentschel, 1912)
*Hymeraphia calochela* Hentschel, 1912:383-385, pl.20, fig.41 [Aru L., Arafura Sea].

MATERIAL. HOLOTYPE: SMF1679. Indonesia.

*Clathria* (Thalysias) coriocrasus
(Bergquist & Fromont, 1988)
*Rhaphidophlus coriocrasus* Bergquist & Fromont, 1988:111-112, figs e-f, pl.52, figs a-b; Dawson, 1993:39 [index to fauna].

MATERIAL. HOLOTYPE: MNNZPOR113. New Zealand.

*Clathria* (Thalysias) cornelia
Hooper & Lévi, 1993
*Clathria* (Thalysias) cornelia Hooper & Lévi, 1993a:1253-1256, figs 15-16, table 8 [New Caledonia].

MATERIAL. HOLOTYPE: QMG300691 (fragments NTMZ3877, ORSTOMR327). SW Pacific.

*Clathria* (Thalysias) cratita (Esper, 1797)
*Spongia cratita* Esper, 1797:195, 196, 221, pl.53 ['East Indies'].


*Thalysias cratita*; de Laubenfels, 1954:137-138, text-fig 87 [NW. Ponape, Caroline Is].


MATERIAL. HOLOTYPE: Unknown. Indonesia, central W. Pacific.

*Clathria* (Thalysias) cullingworthii
Burton, 1931
*Clathria cullingworthii* Burton, 1931a:345, pl.23, figs 3-4, text-fig.4 [Natal coast]; Lévi, 1963:66.

*Thalysias cullingworthii*; de Laubenfels, 1936a:105.

MATERIAL. HOLOTYPE: NMNZP1014. SW Pacific.

*Clathria* (Thalysias) delaufenbelsi
(Lévi, 1963)
*Rhaphidophlus delaufenbelsi* Lévi, 1963:60-62, text-fig.70 [Cape of Good Hope].

MATERIAL. HOLOTYPE: MNN100161. South Africa.

*Clathria* (Thalysias) amictantiensis sp. nov.
*Collectocithra ramosa* Dendy, 1922:74-76, pl.7, fig.2, pl.14, fig.4 [Amirante, Coetivy and Seychelles, Indian Ocean].

Not *Clathria ramosa* Lindgren, 1897:482-483.

**MATERIAL.** HOLOTYPE: BMNH1921.11.7. 64. *Note: C. (T.) ramosa* (Kieschnick, 1896) has priority. NW. Indian Ocean.

**Clathria (Thalysia) distincta** (Thiele, 1903) *Hymeraphis distincta* Thiele, 1903a:956-957, fig. 21 [Termate, Moluccas]; Hentschel, 1912:378-379.

**MATERIAL.** Holotype: SMF789T. Indonesia.

**Clathria (Thalysia) encrusta** Kumar, 1925 *Clathria encrusta* Kumar, 1925:221, fig. 4 [India].

**Thalysia encrusta;** de Laubenfels, 1936a:105.

**MATERIAL.** HOLOTYPE: IMP196/1. India.

**Clathria (Thalysia) euypa** (de Laubenfels, 1954)

*Dictyociona euypa* de Laubenfels, 1954:143, fig.91 [Palau Is.].


**MATERIAL.** HOLOTYPE: USNM22922. Central SW and NW Pacific.

**Clathria (Thalysia) fascicularis** Topsent, 1889

*Clathria fascicularis* Topsent, 1889:35-37, fig.3 [Banc de Campeche].


*Clathria denata* Topsent, 1889:37-38, fig.4A [Banc de Campeche].


**Clathria (Thalysia) fasciculata** Wilson, 1925

*Clathria fasciculata* Wilson, 1925:442, pl.42, fig.6, pl.49, figs 7-8 [Sulawesi, Indonesia]; de Laubenfels, 1954:140-141, text-fig.89 [Truk, Caroline Is];


*Van Soest, 1989b:1-2, fig. 47.

*Thalysia fasciculata;* de Laubenfels, 1936a:105.

**MATERIAL.** HOLOTYPE: USNM21326. Indonesia, Philippines; central W Pacific; Japan.

**Clathria (Thalysia) filifera** (Ridley & Dendy, 1886)

*Rhaphidophlus filifer* Ridley & Dendy, 1886:475; Ridley & Dendy, 1887:152, 247, 255, pl.28, fig.2, pl.46, fig.9 [Masbate, Philippines]; Thiele, 1899:13-15;

*Kirkpatrick, 1900a:136; Thiele, 1903a:958; Dragnewitsch, 1905:3, 16-17; Dragnewitsch, 1906:441 [Singapore]; Whitelege, 1907:503; Wellner, 1910a:33; Ferrer Hernández, 1914:4, 42.

**Not Rhaphidophlus filifer;** Topsent, 1897b:425, 447;

*Desqueyroux-Faundez, 1981:758, table2;

*Not Rhaphidophlus filifer;* Lindgren, 1898:283, 311, 312, pl.17, fig 7, pl.19, fig.17a-c


*Not Rhaphidophlus filifer var. mutabilis*; Topsent, 1897b:447-448, pl.20, fig.24, pl.21, fig.33.

*Not Rhaphidophlus filifer var. canadica*; Oructa, 1901:331-335, text-figs 1-5, pls 3-4.


**MATERIAL.** HOLOTYPE: BMNH18875.2. 104. Philippines; Indo-Malaya region.

**Clathria (Thalysia) flabellata** (Burton, 1936)

*Rhaphidophlus flabellata* Burton, 1936:145, fig.4 [Oudekraal, South Africa]; Lévi, 1963:67 [note].


**Clathria (Thalysia) flabellifera** Hooper & Lévi, 1993

*Clathria (Thalysia) flabellifera* Hooper & Lévi, 1993a:1250-1253, figs 13-14, table 7 [New Caledonia].

**MATERIAL.** HOLOTYPE: QM830093 (fragments NTMZ884, ORSTOMK1416). SW Pacific.

**Clathria (Thalysia) hartmani** (Simson, 1966)


**MATERIAL.** HOLOTYPE: PMNH: NE Pacific.

**Clathria (Thalysia) hechelti** sp. nov.

*Microciona microchela* Hechelt, 1965:41-42, text-fig 7 [Port Royal, Jamaica]; Winterrman-Kilian & Kilian, 1984:134 [Colombia].

*Not Dictyociona microchela;* de Laubenfels, 1953a:528.


**Clathria (Thalysia) isodictyoides** (Van Soest, 1984)

*Rhaphidophlus isodictyoides* Van Soest, 1984b:118-120, pl.8, fig.6, text-fig.47, table 4 [Curaçao].

**MATERIAL.** HOLOTYPE: ZMAPOR4781. Caribbean.

**Clathria (Thalysia) jolicoeurii** (Topsent, 1892)

Clathria (Thalysias) kilanea
(de Laubenfels, 1951)

Axoviella kilanea de Laubenfels, 1951a:262-263, text-fig.9 [Coconut I., Hawaii].

Axoviella kilanea; Hechel, 1965:43-44 [note].

MATERIAL. HOLOTYPE: USNM22779.

Clathria (Thalysias) lambda (Lévi, 1958)

Leptoclathria lambda Lévi, 1958:38, text-fig.35 [Marin, Red Sea].

MATERIAL. HOLOTYPE: MNHN missing. Red Sea.

Clathria (Thalysias) lematolae sp. nov.

Microciona placenta: de Laubenfels, 1954:146-147, text-fig.94.

Not Spongia placenta Lanarck, 1814:374.

MATERIAL. HOLOTYPE: USNM22908. Central west Pacific. C. placenta (Lanarck, 1814) has synonymy.

ETYMOLOGY: For the type locality.

Clathria (Thalysias) linda
(de Laubenfels, 1954)

Axoviella linda de Laubenfels, 1954:156-158, text-fig.102 [Atling-lap-lap, Truk].

Axoviella linda; Hechel, 1965:43-44 [note].

MATERIAL. HOLOTYPE: USNM22860. NW central Pacific.

Clathria (Thalysias) lissoclada (Burton, 1934)

Rhaphidophalus lissoclada Burton, 1934b:32-33, 51-52, pl.4, fig.1, text-figs 4-5, 16 [Falkland Is]; Lévi, 1963:62, pl.9, figs HJ, text-fig.71 [Cape of Good Hope, South Africa].

MATERIAL. HOLOTYPE: ZSM5955 (fragment BMNH1933.3.17.17b), PARATYPES BMNH 1933.3.17 30, 31, 32, 38, 154, South Africa, SW Atlantic.

Clathria (Thalysias) longitoxa
(Hentschel, 1912)

Hymeraphidoxa longitoxa Hentschel, 1912:381, pl.20, fig.39 [Aru I., Aruflora Sea].

Microciona longitoxa: Burton, 1938a:30-31, pl.5, fig.29 [Madras, India]; Burton, 1959a:248 [Gulf of Aden].

MATERIAL. HOLOTYPE: SMF1683. NE Indian Ocean, Indonesia, Arabian Gulf.

Clathria (Thalysias) maunaloa
(de Laubenfels, 1951)


MATERIAL. HOLOTYPE: USNM22775. Central Pacific.

Clathria (Thalysias) membranacea
(Tiele, 1905)


MATERIAL. HOLOTYPE: ZMB3303 (paratypes ZMB3304, BMNH1930.11.28.21). SW Atlantic, SE Pacific.

Clathria (Thalysias) micropunctata
(Burton & Ran, 1932)

Tenacia micropunctata Burton & Rao, 1932:340-341, text-fig.9 [Tuticorin, India].

Thalysiaeuropyen micropunctata; de Laubenfels, 1936a:107 [note].


MATERIAL. HOLOTYPE: IM788/1. India.

Clathria (Thalysias) minuta (Van Soest, 1984)


MATERIAL. HOLOTYPE: ZMAP40179. Caribbean.

Clathria (Thalysias) mutabilis (Topsent, 1897)

Rhaphidophalus fiüfer var. mutabilis Topsent, 1897b:447, pl.20, fig.24, fig.21, fig.33 [Ambon, Banda Sea].


MATERIAL. HOLOTYPE: MNHNG12727 (fragment BMNH1934.2). Indonesia.

Clathria (Thalysias) naikaniensis
(Hoshino, 1981)

Eurypon naikaniensis Hoshino, 1981:153-155, pl.6, fig.8, text-fig.8 [Sasajima, Japan].

MATERIAL. HOLOTYPE: MMBSS1000-4-a, Japan.

Clathria (Thalysias) nervosa (Lévi, 1963)

Axoviella nervosa Lévi, 1963:65-66, pl.9E, text-fig.75 [South Africa].

Rhaphidophalus nervosus; Van Soest, 1984b:115 [generic synonymy].

MATERIAL. HOLOTYPE: MNHNDCL223. South Africa.

Clathria (Thalysias) nuda Hentschel, 1912

Clathria nuda Hentschel, 1912:298, 359, 364-365, pl.19, fig.28 [Aru I., Aruflora Sea].

Tenacia nuda; Hallmann, 1920:771.

Clathria (Thalysias) ongulensis
(Hoshino, 1977)
Axociella ongulensis Hoshino, 1977a:45, text-fig.3, pl.1, fig.3 [fossil demosponge; W. Ongul1, Lutzow-Holm Bay, Antarctica].

MATERIAL. HOLOTYPE: MMBS. Antarctica.

Clathria (Thalysias) orientalis
(Broendsted, 1934)
Rhaphidophus orientalis Broendsted, 1934:20-22, text-figs 20-22 [Aru L. Arafura Sea].


Clathria (Thalysias) originalis
(de Laubenfels, 1930)
Esperioopsis originalis de Laubenfels, 1930:27; de Laubenfels, 1932:70-72, text-fig.38 [California].

AXOCIELETA originalis; Lee & Gilchrist, 1985:24-32 [biochemistry]; Sim & Bakus, 1986:11 [California]; Bakus & Green, 1987:71 [S California].

MATERIAL. HOLOTYPE: USNM21441, paratype BMNH1929.8.22.54. NE Pacific.

Clathria (Thalysias) oxota (Van Soest, 1984)
Rhaphidophus oxota Van Soest, 1984b:120-122, text-fig.48, table 4 [Curacao].

MATERIAL. HOLOTYPE: ZMAPOR4880. Caribbean.

Clathria (Thalysias) oxitoxa Lévi, 1963
Clathria oxitoxa Lévi, 1963:54-56, text-fig.62 [Humansdorp, South Africa].

RHAPHIDOPHUS oxitoxa; Van Soest, 1984b:115, 122.

MATERIAL. HOLOTYPE: MNHNDC610. South Africa.

Clathria (Thalysias) pachyaxia (Lévi, 1960)
Axociella pachyaxia Lévi, 1960b:763-764, text-fig.16, [Senegal, W Africa].

MATERIAL. HOLOTYPE: MNHNDC787. NW Africa.

Clathria (Thalysias) robusta (Dendy, 1922)
Microciona strepsitoxa var. robusta Dendy, 1922:60-61 [Amirante I.].

Tenacia robusta; Burton & Rao, 1932:339-340 [Singapore].

Not Clathria robusta Koltun, 1959:186, pl.25, fig.5, text-fig.147; Van Soest & Stone, 1986:47.

MATERIAL. HOLOTYPE: BMNH1921.11.7.49. W Indian Ocean, Indo-Malay region.

Clathria (Thalysias) schoenus (de Laubenfels, 1936)
Clathria copiosa var. curacaoensis Arndt, 1927:148, pl.1, fig.3, text-fig.9 [Curacao].

Aulospongos schoenus de Laubenfels, 1936a:100, pl.13, fig.3 [Dry Tortugas, Florida].

Thalysias schoenus; Simpson, 1968a:56, pls 13-14, text-fig.5 [Florida]; Randall & Hartman, 1968:223 [West Indies]; Alcolado, 1980:4 [Cuba].

Rhaphidophus schoenu; Van Soest, 1984b:112-113, pl.8, figs 1-4, text-fig.44, table 4 [Curacao, Bonaire, Puerto Rico; Chen & Mok, 1993:278 [probable misidentification, Taiwan].

Not Microciona microchela Hechel, 1965:41, text-fig.7 [Curacao, Bonaire, Puerto Rico, Jamaica].

MATERIAL. HOLOTYPE: USNM22404. Caribbean.

Clathria (Thalysias) tener Carter, 1887
Thalysias tener Carter, 1887a:70 [Mergui Archipelago].

MATERIAL. HOLOTYPE: IFNM14 ('Renieta fibrosa') (fragment BMNH1887.6.1.9). Andaman Sea. Imperfectly known.

Clathria (Thalysias) topsenti (Thiele, 1899)

Not Rhaphidophus filifer Ridley & Dendy, 1886:475.

Rhaphidophus topsenti Thiele, 1899:15, pl.2, fig.3 [Sulawesi, Indonesia]; Whitelegge, 1907:503; Hallmann, 1912:177.


Clathria (Thalysias) tricurvatifera
(Carter, 1876)
Thalysias tricurvatifera Carter, 1876:311-312 [Cape St. Vincent, Hebrides].

MATERIAL. HOLOTYPE: unknown, (fragment BMNH1954.5.9.244). NE Atlantic. Imperfectly known.

Clathria (Thalysias) venosa (Alcolado, 1984)

Rhaphidophus venosus; Meesters et al., 1991:194-195 [Curacao, Bonaire].

Rhaphidophus raraechelae Van Soest, 1984b:116-118, pl.8, fig.5, text-fig.46, table 4 [Curacao]; Pullen-Finali, 1986:151 [West Indies].


Clathria (Thalysias) virgultosa
(Lamarck, 1814)
Spongia virgultosa Lamarck, 1814; Duchassaing & Michelotti, 1864:86, pl.23, fig.3.


Microciona plena Carter. 1876:238, 472.

Clathria copiosa Topsent, 1889:40-41, fig.6; Topsent, 1894b:30, 36; Henschel, 1912:367.

Thalysias copiosa; de Laubenfels, 1936a:106.

Clathria jugosa; Wilson, 1902:37.

Clathria clathrata; Vosmaer, 1880:153; Ridley & Dendy, 1887:147; Wilson, 1902:397; Alcolado, 1976:5.

Not Rhaphidophlus clathratus; Hallmann, 1912:209; Topsent, 1920b:17-18; Topsent, 1932:97, pl.5, fig.6, text-fig.3.

Pandaros juniperina; Duchassaing & Michelotti, 1864:90, pl.19, fig.3; de Laubenfels, 1936a:106.


Rhaphidophlus juniperinus; Van Soest, 1984b:109-111, pl.7, fig.11, text-fig.43, table 4; Meesters et al., 1991:195.

Not Spongia juniperina Lamarche, 1814:444; Lamarche, 1816:373.

Not Microciona clathrata Whitelegge, 1907:493 [see C. bicaudata].


TRANSFERS

List of other species described in Thalysias but now transferred to another genus.

Spongia carbonaria Lamarche, 1814:375; 1816:357.

Thalysias carbonaria; Duchassaing & Michelotti, 1864:83, pl.17, fig. pl.19, fig.2 [St.Thomas]; Carter, 1882a:282, pl.11, fig.11 [Antigua, West Indies]; Tortonesu, 1962:23.


Thalysias cocinea Duchassaing & Michelotti, 1864:84, pl.18, fig.5 [St.Thomas].

Spirastrella cocinea; Wiedenmayer, 1977:255, table 50; Van Soest et al., 1983:204.

MATERIAL. LECTOTYPE: BMNH1928.11.12.46. PARALECTOTYPE ZMAPOR2076. Referred to Hadromerida; Spirastrellidae.

Thalysias hians Duchassaing & Michelotti, 1864:86, pl.16, fig.1 [St. Thomas, Caribbean; originally designated as hyano, but corrected in erratum].


Thalysias ignis Duchassaing & Michelotti, 1864:83, pl.18, figs 1-2 [St.Thomas, Caribbean].

Tedania ignis; Wiedenmayer, 1977:255, table 50; Van Soest et al., 1983:204.

MATERIAL. LECTOTYPE: TM POR 72 (fragment BMNH1928.11.12.437), paralecotype ZMAPOR2373 (fragment MNHNDBE1341). Referred to Tedaniidae.

Thalysias massalis Carter, 1886a:50 [Port Phillip, Vic].

Reniera massalis; Dendy, 1895:236.

MATERIAL. HOLOTYPE: BMNH1886.12. 15.433. Referred to Haplosclerida, Chalinidae.

Thalysias proxima Duchassaing & Michelotti, 1864:84, pl.18, fig.3 [Antilles, Caribbean].

Neofibularia proxima; Wiedenmayer, 1977:255, table 50.

Xestospongia proxima; Van Soest et al., 1983:204.

MATERIAL. LECTOTYPE: TEMPOR74 (fragments BMNH1928.11.12.45, USNM31047, MNHNDBE1342). Referred to Haplosclerida, Petrosiidae.

Thalysias repens Duchassaing & Michelotti, 1864 [St. Thomas, Virgin Is]; Carter, 1882a:282, pl.11, text-fig.10 [Pitero Cabello and Antigua, West Indies].

Xestospongia subtriangularis; Wiedenmayer, 1977:257, table 51.

MATERIAL. SYNTYPES: BMNH (3 specimens, unregistered). Referred to Haplosclerida, Petrosiidae.

Thalysias rugosa Duchassaing & Michelotti, 1864:84, pl.18, fig.4 [St. Thomas, Virgin Is]; Wiedenmayer, 1977:251, 253, tables 48,49 [note].

Xestospongia subtriangularis; Van Soest et al., 1983:204.

MATERIAL. LECTOTYPE: ZMAPOR2372. Referred to Haplosclerida, Petrosiidae.

Thalysias [as Thalasias] saxicava Duchassaing & Michelota, 1864:87 [St. Thomas, Virgin Is, Caribbean].


Dictyocephalus sessilis Carter, 1880a:38, pl.4, fig.2 [Gulf of Manaar, Ceylon].

Autospongia sessilis; Dendy, 1905:176 [note].

Xestospongia subtriangularis; Wiedenmayer, 1977:255, table 50; Van Soest et al., 1983:199, 204.

MATERIAL. LECTOTYPE: BMNH1928.11.12.47. Lectotype of var. lyrophorans: ZMAPOR2375, paralecotype of
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var. lyriformis: ZMAPOR2376. Referred to Haplosclerida, Petrosiidae.

Haliphysa tubulatum Bowerbank, 1873c:29 [India].

Axinella tubulata; Norman, 1978:267; Dent, 1905:176, text-fig.5 [Ceylon]; Dent, 1922:61; Burton & Rao, 1932:347 [Tuticorin, India]; de Laubenfels, 1936a:101 [note].

AXINELLA
tubulata; Dent, 1889b:89, pl.5, fig.2.

MATERIAL. HOLOTYPE: BMNH not found (poorly preserved fragments BMNH1887.5.21. 1331, 1332). Uncertain placement; possible Raspaillidae.

Thalysias varianis Duchassaing & Michelotti, 1864:86, pl.13, fig.6 [St. Thomas, Caribbean].


MATERIAL. LECTOTYPE: TM 70 (fragments USNM31048, MNHNDNBE1343); paratypotype of var. varianis; ZMAPOR2377 (fragments BMNH1928.11.12.49); leciotype of var. encrustans: BMNH1928.11.12.28. Referred to Hadromerida, Spirastrellidae.

Echinonema vasiplicata Carter, 1882b:114 [Swan River, WA]; Dent, 1889a:44.

Echinodictyum mesenterinum; Ridley, 1884b:185.

Echinodictyum bitanellatum; Dent & Frederick, 1924:504.


Antho Gray, 1867

Refer to subgenera for synonymy.

TYPE SPECIES. Myxilla involvens Schmidt, 1864: 37 (by monotypy).

DEFINITION. Two distinct skeletal components: (1) primary (basal or axial) renieroid (rectangular) or isodictyal (triangular) choanosomal skeleton composed of acanthostyles and/or acanthostyrgles; (2) secondary (extra-axial, subectosomal) skeleton composed of smooth choanosomal styles forming dendritic, plumose, subisodictyal or plumoreticulate tracts, or simply echinating main spicule tracts; secondary skeleton usually arising from nodes of renieroid skeleton, or ascending upwards from basal spongin fibres, with or without axial compression; spongin fibres relatively poorly developed; additional category of echinating acanthostyles present or absent; ectosomal skeleton tangential, paratangential or plumose tracts of 1 or 2 categories of auxiliary styles; microscleres diverse forms of isochelae and toxas.

REMARKS. Under Van Soest & Stone's (1986) system all microcionids having a renieroid (and/or isodictyal) basal (or axial) skeleton composed of acanthose megascles are grouped in Antho. This system is supported here with subgenera recognised on structure and composition of the renieroid skeleton (1) A. (Antho) (with predominantly (acantho)styles forming the renieroid skeleton, less often acanthostyrgles, without echinating acanthostyles); (2) A. (Plocamia) (with predominantly (acantho)styles forming the renieroid skeleton, less often acanthostyles, and a special category of echinating acanthostyles overlap the main skeleton); (3) A. (Isopenectya) (with an axially compressed and extra-axially renieroid reticulate skeleton composed of 2 forms of choanosomal spicules inside spongin fibres, overlaid by a second extra-axial plumose skeleton. Isopenectya (s.s.) could also be included in Echinocloathria, given the close resemblance in growth form and renieroid skeletal structure with E. leporina, but in A. (Isopenectya) the renieroid skeleton is of sparsely spined principal styles (differentiated from the larger smooth styles of the extra-axial skeleton), with differentiated axial (compressed) and an extra-axial (renieroid) regions, overlaid by a second extra-axial (plumose) skeleton composed of larger, smooth principal styles. In Echinocloathria, megascles of the renieroid skeleton are exclusively smooth, and the larger, smooth principal styles which form a radial skeleton are only found on the surface, embedded in peripheral fibres. Antho and Echinocloathria, differ from other microcionids in having a renieroid skeleton and it is possible that Echinocloathria is a highly derived form of Antho (loss of spined principal spicules, loss of extra-fibre skeleton, loss of spined acanthostyles (geometrically different from principal spicules)).

Antho (Antho) Gray, 1867


Anomocloathria Topsent, 1929: 26 (not Topsent, 1932: 103).


Dictyocloathria Topsent, 1920b: 18.

Dycloathria Ferrer-Hernandez, 1921: 172 [lapsus].

Isociona Hallmann, 1920: 768.

Jia de Laubenfels, 1930: 28.

Plocamilla; in part, Burton, 1935a: 402; Pulitzer-


Quizcina de Laubenfels, 1936a: 111.

TYPE SPECIES. Myxilla involvens Schmidt, 1864: 37 (by monotypy).
DEFINITION. Primary basal renieroid (and/or isodictyral) choanosomal skeleton composed of acanthostyles and/or acanthostrongyles; secondary extra-axial (subectosomal) skeleton plumose, plumoreticulate, or simply composed of choanosomal styles echinating (project from) basal renieroid skeleton; spongin fibres poorly developed; special category of echinating acanthostyles absent; ectosomal skeleton with tangential, paratangential, or plumose tracts of 1 size of auxiliary styles or subtylostyles; microscleres include diverse forms of isochelae and toxas.

REMARKS. Twenty one species have been included in, or referred to, Antho (Antho), although only 11 are widely accepted, 2 of which are known from Australia.

**Antho (Antho) opuntioides** (Lamarck, 1815) (Figs 212-213)


Not Anomocliathria opuntioides var. frondifera; Topsent, 1929: 26-29, text-figs 10-14; Tossent, 1932: 103, pl.1, figs 6-7.


HABITAT DISTRIBUTION. Unknown; known only from type locality (Fig. 212G).

DESCRIPTION. Shape. Lobate, digitate growth form, up to 255mm high, 375mm wide, 230mm thick, bifurcating cylindrical or slightly flattened branches, up to 120mm long, 18mm maximum diameter, occasionally anastomosing, slightly bulbous branch nodes, tapering or rounded branch tips. Colour: Live colouration unknown, grey in dry state. Oscules: Small pores up to 2mm diameter, possibly oscules, scattered over sides of branches. Texture and surface characteristics. Harsh, brittle in dry state, even, unornamented surface. Ectosome and subectosome. No ectosomal membrane intact (dry material), although remnants of sparse, tangential and paratangential skeleton composed of subectosomal auxiliary subtylostyles scattered near periphery; points of choanosomal styles and acanthostyles in peripheral skeleton protrude through surface; entire peripheral skeleton dense, virtually undifferentiated from deeper choanosomal skeleton (although spicule tracts with more sparse spongin component in periphery than at core), clearly dominated by close-set renieroid reticulation of acanthostyles.

Choanosome. Skeleton with 2 distinct components: plumose extra-axial skeleton composed of multispecific or paucispecific continuous tracts of large choanosomal principal styles extending from centre of skeleton to ectosome; renieroid skeleton regular, tight meshed, rectangular and triangular meshes, 80-150μm diameter; even mesh size throughout skeleton; spongin fibres heavier, slightly more compressed at centre of skeleton than in periphery, with oval meshes 60-135μm diameter; echinating spicules absent; mesohyl matrix light, with scattered microscleres; choanocyte chambers not seen (dry specimens).

Megascleres. Smooth choanosomal principal styles of plumose skeleton robust, short, thick, slightly curved at centre, with rounded smooth or occasionally very faintly microspined bases, fusiform points. Length 84-192.7-108μm, width 4-11.2-14μm.

Acanthosomal choanosomal styles of renieroid skeleton straight or slightly curved at centre, evenly spinose except for aspinose points and sometimes aspinose base; spines large, recurved, sharply pointed. Length 93-104.5-112μm, width 8-13.3-16μm.

Subectosomal auxiliary subtylostyles long, slender, straight, smooth or microspined bases, fusiform or occasionally with telescoped points. Length 102-152μm, width 2-3.4-4.5μm.

Microscleres. Palmate isochelae large, unmodified, with lateral and front alae approximately equal length, lateral alae completely used to shaft, front ala detached along entire length. Length 16-21μm.

Toxas wing-shaped, generously curved at centre, with only slightly reflexed points. Length 36-148μm, width 1.5-3.0μm.

REMARKS. I initially thought this species conspecific with C. (T.) styloploetherlands (see above), based on Tossent’s (1929) description of 'styloplothèque', whereby spongin fibres are replaced by algal filaments, but the two species differ in spicule geometry and skeletal architecture (see also A. (P.) frondifera below). It differs from the allied A. (A.) tuberosa in growth form,
spicule geometry (particularly its acanthostyle morphology), and spicule sizes (refer to discussion in A. (A.) tuberosa).

**Antho (Antho) tuberosa** (Hentschel, 1911)  
(Figs 214-215, Plate 9B-C)

*Lissodendoryx tuberosa* Hentschel, 1911: 326-328, text-fig. 21.


*Clathria harrimeyeri* Hentschel, 1911: 379-381, text-fig. 50.

*Thaliyuas harrimeyeri*: de Laubenfels, 1936a: 105.  

**MATERIAL.** **HOLOTYPE:** HM (fragment ZMB4417): 4 km SW. of Denham, Shark Bay, WA, 25°36.5'S, 113°30.0'E, 3 m depth, 10.VI.1905, coll. W. Michaelson & R. Hartmeyer ( dredge).  
**OTHER MATERIAL:** WA: WAM645-81(1) (fragment NTMZ1722) QMG300203 (fragment NTMZ2958), NTMZ3214 (fragments PIBOC04-352, QMG300044), QMG300678 (NCIQ66C-4229-N), NTMZ1466. S AUSTRALIA: SAMTS4050 (fragment NTMZ1637).

**HABITAT DISTRIBUTION.** Encrusting on macrophytes, coralline algae, corals, or other sponges; 3-40m depth; Shark Bay, Stragglar Rocks, Houtman Abrolhos, Port Hedland (WA); Port Noarlunga (SA) (Fig. 214G); Gajam, Madras, India (Burton & Rao, 1932).

**DESCRIPTION.** **Shape:** Variable, thinly encrusting, up to 3mm thick, lobo-digitate, up to 25mm high, 42mm wide, 28mm thick, with rounded margins, or lobate, flabellate, with several flattened digits joined to a common base, and with curved, even or sinuous margins, without a basal stalk, 79mm high, 120mm maximum width, lobes between 18-32mm wide, up to 15mm thick.  
**Colour:** Bright red (Munsell 2.5R 5/10), dark red (5R 4/10) or slightly yellow-red alive (2.5YR 8/8); yellow-brown or light brown in ethanol.  
**Oscules:** Indetectable in thinly encrusting specimen, scattered on lateral and upper surfaces of lobate specimens, up to 2.5mm diameter; surface minutely porous on lobate-flabellate specimen, pores 0.5-1.2mm diameter.  
**Texture and surface characteristics.** Texture compressible; surface optically even (encrusting-lobate specimens) or striated and pitted, with ridges most prominent near margins (flabellate specimen).  
**Ectosome and subectosome.** Hispid, with tracts of smooth choanosomal styles from plumose skeleton protruding singly or in brushes; smaller subectosomal auxiliary stylostyles form tangential tracts (encrusting specimen), paratangential tracts (lobate specimen), or distinct plumose brushes on ectosome, surrounding protruding choanosomal styles (flabellate specimen); subectosomal region undifferentiated from choanosomal skeleton; smaller acanthos whose choanosomal styles of renieroid skeleton terminate in uni- or paucispidic brushes just below surface; mesohyl matrix in peripheral region light, unpigmented.

**Choanosome.** Two distinct skeletal components: renieroid skeleton regular (encrusting-lobate specimens) or irregular (flabelliform specimen), rectangular and triangular meshes, tight meshed with mesh size 42-125μm diameter; meshes more open in lobate specimens (92-197μm) and flabellate specimens (97-208μm maximum diameter); vaguely differentiated primary and secondary components of skeleton, best developed in flabellate specimens, with primary ascending (multipsicular) and secondary transverse (uni- or bispicular) tracts of smaller acanthos whose choanosomal megascleres; encrusting and lobate specimens mesh size decreases and skeleton more compact, with poorer differentiation of primary and secondary lines; plumose skeleton of larger, smooth, choanosomal principal styles forming pauci- or multipsicular tracts; plumose tracts continuous, originating from basal attachment extending to peripheral skeleton in encrusting-lobate material, but not obviously continuous in flabellate specimens, prominent only near periphery; true echinating acanthostyles absent; mesohyl matrix light, containing few loose extra-fibre spicules; spongin fibres 45-108μm diameter relatively light, only barely differentiated from mesohyl matrix in flabellate specimens (with only primary ascending elements and small interconnecting secondary fibre components obvious); spicule skeleton only minimally associated with fibre skeleton, each forming more or less independent support systems; choanocyte chambers relatively large, 155-652μm diameter, ovoid, often paired, lined by isochelae and rare toxas.

**Megascleres.** Smooth choanosomal principal stylostyles of plumose skeleton slightly curved, fusiform, with tapering, rounded or subtyloste smooth bases, occasionally slightly microspined; very variable in length. Length 164-213.0-337μm, width 6.5-(9.9)-14.0μm (holotype 126-295 x 6.5-9μm).

Acanthose choanosomal styles of renieroid skeleton slightly curved or straight, subtyloste,
fusiform, with evenly distributed small spines; acanthose choanosomal spicules include intermediates between larger smooth megalascers of plumose skeleton and entirely spined spicules of renieroid skeleton. Length 86-(114.9)-136μm, width 3.5-(6.3)-10.0μm (holotype 63-128 x 2.5-6μm).

Subectosomal auxiliary subtylostyles of peripheral skeleton straight or slightly curved, single size category, thin, fusiform, with rounded or subtylole bases, usually microspined. Length 100-(177.4)-274μm, width 1.8-(3.1)-4.5μm (holotype 129-214 x 2.5-4μm).

Microscleres. Palmate isochelae common, unmodified, variable in size between specimens; lateral and front alae approximately equal length, lateral alae entirely fused to shaft, front ala only partially detached from lateral alae. Length 6-(13.5)-18μm (holotype 10-15μm).

Toxas wing-shaped, relatively common, ranging from small thin forms to long relatively thick forms, all with evenly rounded, wide central curvature, and straight or very slightly reflected points. Length 37-(94.5)-232μm, width 0.8-(1.8)-3.6μm (holotype 6-58 x 0.8-1.8μm).

Larvae. Larger flabellate-lobate specimen (WAM645-81(1)) contained ovoid-elongate, incubated embryos, 210-240μm diameter, with some cellular differentiation and few larval megalascers.

Associations. Several specimens had parasitic zooanthids on surface.

REMARKS. This species is relatively polymorphic in growth form, the extent to which the renieroid skeleton is compacted and size of isochelae, but more consistent in choanosomal and ectosomal skeletal architecture, spicule geometry, and to some extent spicule dimensions. However, there is no doubt that all specimens examined are conspecific, their similarities far more obvious than their apparent differences, especially in comparison to its sibling species A. (A.) opuntioides (from SW, Australia) and A. (A.) lithophoenix (from NW, Pacific). The lobate-encrusting specimen from SA shows the greatest departure from the holotype, particularly in spicule dimensions.

Hentschel (1911) described this species with a renieroid skeleton enclosed, to a greater or lesser extent, within spongin fibres, but the holotype does not substantiate this. In flabellate specimens fibres are more obviously associated with plumose skeletal tracts cored by smooth choanosomal styles, whereas the renieroid meshes appear independent of spongin fibres. Similarly, Hentschel did not describe toxas from the holotype but they are present being most abundant in SW WA flabellate-lobate specimens.

Burton & Rao (1932) suggested that A. (A.) tuberosa was probably conspecific with Clathria hartmeyeri, indicating that it differed only in the encrusting growth form, lighter mesohyl matrix and in supposedly lacking smooth subtylostyles. Although the latter assertion is incorrect the holotype of C. hartmeyeri has not yet been discovered in any museum and this synonymy cannot be corroborated. From Hentschel’s (1911) description of C. hartmeyeri it appears to be identical to the flabellate-lobate form of A. (A.) tuberosa and this synonymy is accepted.

Antho (A.) tuberosa is the type species of Isociona Hallmann’s (1920), which Van Soest (1984b) merged with Antho. In the strict sense (i.e., comparing A. (A.) tuberosa and A. (A.) involvens) the two genera are close in skeletal architecture, but A. (A.) tuberosa has entirely monactinal megalascers, whereas A. (A.) involvens has basal (renieroid) monactinal and/or diactinal spicules (acanthostyles, acanthostrangles). Also included in Isociona is Plocania lithophoenix de Laubenfels (1927) which is very similar to A. (A.) tuberosa in skeletal structure, spicule diversity and spicule geometry, differing only in the basal spines on choanosomal styles plumose skeleton and specific spicule dimensions (smooth choanosomal styles 152-238x11-15μm, acanthose choanosomal styles 129-166x8-14μm, subectosomal subtylostyles 133-293x3-6μm, palmate isochelae 18-26μm, and toxas 18-178x0.8-3μm). Both these and A. (A.) opuntioides are sibling species showing many skeletal and spicule similarities.

OTHER SPECIES OF ANTHO (ANTHO)

Antho (Antho) brattegardii Van Soest & Stone, 1986
Antho brattegardii Van Soest & Stone, 1986: 42-44, figs 1-3 [Norway]

MATERIAL. HOLOTYPE: ZMAPor5190. PARATYPE BMNH1982.9.6.1. NE Atlantic, species of Jude de Laubenfels.

Antho (Antho) brondstedi Bergquist & Fromont, 1988
Antho brondstedi Bergquist & Fromont, 1988: 97, pl 46d-f, 47a-c [New Zealand]; Dawson, 1993: 44 [index to fauna].

MATERIAL. HOLOTYPE: NMNZPor111. New Zealand.

Antho (Antho) dichotoma (Esper, 1794)
**Antho (Antho) graceae** (Bakus, 1966)

Not *Myxilla lacunosa* Lambe, 1892: 70-71.

*Anthocanthona graceae* Bakus, 1966: 431-432, text-fig.3 [San Juan Archipelago, Washington]; Ristau, 1978: 5737 [California]; Lee & Gilchrist, 1985: 24-32 [biochemistry].

**Antho (Antho) halzei** (Topsent, 1904)


*Plocamia halzei*: de Laubenfels, 1936a: 78.

**Antho (Antho) heterospiculata** (Brondsted, 1924)

*Microciantha heterospiculata* Brondsted, 1924: 465, text-fig.20 [Colville Channel, NZ].

*Quiziconathera heterospiculata*: de Laubenfels, 1936a: 111.

Not *Micraciana heterospiculata*: Bergquist, 1961a: 39 [probably = *Clathria mortensennii* Brondsted].


**Antho (Antho) involvens** (Schmidt, 1864)

*Myxilla involvens* Schmidt, 1864: 37, 45, pl.4, fig.6 [Adriatic]; Heller, 1864: 48.

*Hyemedemia involvens*: Schmidt, 1867: 16.


**Desmacodes involvens**: Vosmaer, 1880: 108; Vosmaer, 1885: 735.


*Clathria morisca* Schmidt, 1864: 37, 45 [Adriatic]; Schmidt, 1868: 9, 41, 43, pl.2, fig.7 [Mediterranean]; Vosmaer, 1880: 150-151 [Algiers]; Topsent, 1902: 329.

*Dictyoclasithra morisca*: Topsent, 1920b: 18-21; Topsent, 1928a: 301-302, pl.3, fig.3 [Porto Santos, Azores]; Lévi, 1959: 134, text-fig.27, pl.5, fig.1 [Rio de Oro, Gulf of Guinaca]; Lévi, 1960b: 761-762, text-fig.15 [var. *anisotyla*; SW. Cape of Naze, W. Africa]; Sarà, 1960a: 462 [Ishia, Mediterranean]; Desqueyroux-Faurend & Stone, 1992: 35 [index].

*Placocanthis involvens* Topsent, 1925: 661-664, text-fig.15 [Gulf of Naples]; Topsent, 1939: 6; Pulitzer-Finali, 1983: 610 [list].


*Holoplocamia involvens*: de Laubenfels, 1936a: 75.

*Antho involvens*: Ackers et al., 1992: 140 [Ireland].

*Isodictya beanii* Bowerbank, 1866: 274, 334, 335 [Britain]; Gray, 1868: 164; Schmidt, 1870: 77; Bowerbank, 1874: 147, pl.58, figs 1-6.


*Amphilectus beanii*: Vosmaer, 1880: 115.

*Clathria beanii*: Ridley, 1881: 485, 486; Bowcrbank, 1882: 13, 23, 150; Topsent, 1890c: 203.

*Myxilla beanii*: Topsent, 1892c: 23; Topsent, 1894a: 8, 9, 25; Hantsch, 1894: 179.

*Artemisina mediterranea* Babin, 1921: 87 [Adriatic]; Babin, 1922: 258-259, text-fig.8; Burton, 1930a: 528; Lévi, 1960a: 57, 76-80; Maldonado, 1992: 1154 [possible synonym of *A. (P.) navizelanica*].


? *Artemisina paradoxa* Babin, 1921: 87; Babin, 1922: 260-261, pl.8, fig.6, text-fig.e [Adriatic]; Topsent, 1925: 660; Lévi, 1960a: 85-86 [Adriatic]; Ristau, 1978: 585-586 [note on affinities].
Clathria paradoxa; Burton, 1930a: 528. 
Antho paradoxa; Pulitzer-Finali, 1983: 610. 
? Raspailia incrustans Svercakj, 1906: 52, pl.5, fig.6, pl.7, fig.1.

MATERIAL. HOLOTYPE: LMJG (fragment BMNH1867.3.11.92), fragments of holotype of C. morisco: MNHNDT2170, BMNH1868.3.2.21. NW. Atlantic, Mediterranean, NW Africa, South Africa. This is probably a species complex (Ackers et al., 1992) contesting the synonymy between involvens and inconstans.

Antho (Antho) oseifera(Ferrer-Hernandez, 1921) 
Labacea oseifera; de Laubenfels, 1936a: 125 [?]. 
Antho oseifera; Uriz & Maldonado, 1993: 359-362, figs 6-9 [W. Mediterranean].

MATERIAL. HOLOTYPE: Madrid. Mediterranean.

Antho (Antho) pancissipina Sarà & Siribelli, 1962 

MATERIAL. Holotype: IZUG. Mediterranean.

Antho (Plocamia) Schmidt, 1870 
Plocamia Schmidt, 1870: 62. 
Dibrhopalum Ridley, in Ridley & Duncan, 1881: 477. 
Plocamioepsis Topsent, 1904a: 155. 
Heterocladria Topsent, 1904b: 95. 
Lissiplocamia Bronsdte, 1924: 470. 
Anomocladria; in part, Topsent, 1932: 103 (not Topsent, 1929: 26).

Holoplocamia de Laubenfels, 1936a: 75.

TYPE SPECIES. Plocamia gymnozus Schmidt, 1870: 62.(by subsequent designation of Burton, 1935a: 401)).

DEFINITION. Regular basal or axial renieroid (and/or isodictyal) skeleton of acanthostyleny (less frequently acanthostyle), with or without spongion fibres; renieroid tracts may be echnated by acanthostyles at spongion fibre nodes; basal renieroid skeleton overlays lepocladthrid or microcionid main skeleton composed of echinating (acantho-)styles and/or chorosomal styles, standing perpendicular to base or axis, joining with echinating megaloscles to produce ascending plumose skeletal tracts; extra-axial (subecosomal) skeleton plumose, dendritic, or subisodictyal, composed of chorosomal styles, originating from substrate or simply confined to periphery, forming tangential, paratangential or plumose extra-axial tracts; ecosomal skeleton with or without specialised spiculation (1 or 2 categories of auxiliary styles); microscleres include diverse forms of isochelae and toxas.

REMARKS. Twenty one species have been referred to Plocamia or one of its synonyms; all are valid. However, A. (P) erecta is poorly known, and other species may eventually merge, particularly the 5 Indian Ocean species (Table 43). Only 2 species are known from Australasia.

Antho (Plocamia) frondifera (Lamarck, 1814) 
(Figs 216-217, Table 43) 
Spongia frondifera Lamarck, 1814: 445; Lamarck, 1816: 374. 
Anomocladria frondifera; de Laubenfels, 1936a: 108. 
Antho frondifera; Hooper & Wiedemayer, 1994: 256. 
Anomocladria opuntioidea var. frondifera; Topsent, 1929: 26-29, text-figs 10-14; Topsent, 1932: 103, pl.1, figs 6-7. 
Hymeniacidon cliftoni Bowerbank, 1862a: 773, pl.30, fig.9; Bowerbank, 1864: 276, figs 70, 291. 
Acarnia cliftoni, Gray, 1867: 515. 
Not Alcyonium opuntioidea Lamarck, 1815: 164.


HABITAT DISTRIBUTION. Ecology unknown; SW Australia (WA) (Fig. 216G).

DESCRIPTION. Shape. Lobate, thickly flabellate, digitate fans, 95-160mm long, up to 25mm thick, with uneven, digitate margins and irregular lobate surface ("macroconules") up to 6mm thick. No stalk remaining, if initially present.

Colour. Grey or grey-brown in dry state.

Oscules. Large, up to 4mm diameter, scattered evenly over surface and lateral margins of digits, with remnants of stellate drainage canals converging on each oscule.

Texture and surface characteristics. Harsh, brittle in dry state. Uneven, lumpy surface with distinct collagenous crust.

Ectosomal and subectosomal. Ectosomal skeleton membranous, heavily collagenous in places (although rarely intact in dry specimens), with some embedded detritus and sparse tangential and paratangential tracts or single auxiliary subtylosyles scattered near periphery, sometimes forming bundles protruding through ectosome; points of (smooth) chorosomal principal styles from ascending plumose tracts protrude only slightly
through collagenous surface membrane; subectosomal skeleton virtually undifferentiated from choanosome, although peripheral choanosomal styles of plumose skeleton slightly more dense, diverging, than tracts in skeletal core.

**Choanosome.** Skeleton with 2 distinct components: ascending plumose and basal/axial renieroid (in some places isodictyal) skeletons; plumose skeleton with pauci- or multispicular tracts of smooth choanosomal principal styles ascending to surface, rarely branching or anastomosing; tracts associated with, but not necessarily coring, heavy, dark brown, spongin-coated algal filaments (ostensibly *Ficus* (Topsent, 1932)), which dominates skeleton; filaments up to 250\(\mu\)m diameter, 300-400\(\mu\)m apart, branching, diverging from base of sponge through sponge surface; renieroid skeleton composed of 1 or 2 acanthostrongyles abreast forming square or triangular meshes up to 120\(\mu\)m diameter, even mesh size throughout skeleton, overlaying plumose skeleton; some detritus scattered between renieroid skeletal meshes, usually coated with spong; mesohyl not intact although some granular collagen containing microscleres scattered between spicule meshes; choanocytes not observed.

**Megascleres.** Choanosomal principal styles entirely smooth, short, robust, slightly curved at centre, with rounded or slightly subtyloste bases, fusiform points. Length 88-(103.4)-118\(\mu\)m, width 4-(8.1)-13\(\mu\)m.

Acanthostrongyles of the renieroid skeleton thick or thin, rounded or slightly subtyloste at both

TABLE 43. Comparison between species of Antho (Plocamia). Measurements in μm.

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>A(P.) ridleyi (Hentschel) Holotype (SMF1709)</th>
<th>A(P.) ridleyi (Hentschel) Specimens (N=13)</th>
<th>A(P.) frondifera (Lamarck) Holotype (MNHNDF 557)</th>
<th>A(P.) cirriacea (Bowerbank)1</th>
<th>A(P.) elegans (Ridley &amp; Dendy)2</th>
<th>A(P.) manuensis (Denby)3</th>
<th>A(P.) novialanuicus (Ridley)4</th>
<th>A(A.) circoniflexa (Lévi)5</th>
<th>A(P.) phasei (Lévi)6</th>
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<tr>
<td>Shape</td>
<td>encrusting</td>
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<td>flabellate</td>
<td>(encrusting)</td>
<td>digitate</td>
<td>digitate</td>
<td>digitate</td>
<td>encrusting</td>
<td>encrusting</td>
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<tr>
<td>Chorosomal</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>styles</td>
<td>212-388 x 14-20</td>
<td>183-562 x 7-25</td>
<td>89-118 x 4-13</td>
<td>120-660 x 11-16.4</td>
<td>160-550 x 8-2-15</td>
<td>475 x 20.6</td>
<td>500 x 25</td>
<td>150-450 x 10</td>
<td>100-350 x 7</td>
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<tr>
<td>Renieroid</td>
<td>spicules</td>
<td>92-104 x 6-6.5</td>
<td>99-142 x 4.5-15</td>
<td>85-103 x 3-14</td>
<td>70-120 x 3-10</td>
<td>234 x 19</td>
<td>177 x 15.8</td>
<td>130-170 x 10</td>
<td>75-100 x 7</td>
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<tr>
<td>Ectosomal</td>
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<td>129-209 x 1.8-4</td>
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<tr>
<td>Subectosomal</td>
<td>spicules</td>
<td>298-385 x 4-7</td>
<td>231-473 x 2.5-13</td>
<td>120-184 x 1-2.5</td>
<td>425-430 x 2.7</td>
<td>150-460 x 2.6</td>
<td>316.7 x 6.3</td>
<td>190-360 x 2-4</td>
<td>150-400</td>
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<tr>
<td>Echinat</td>
<td>spicules</td>
<td>170-202 x 8-15</td>
<td>107-248 x 5-15</td>
<td></td>
<td>75-158 x 7.9-12</td>
<td>140-180 x 5-11</td>
<td>114 x 9.5</td>
<td>272.4 x 17.4</td>
<td>80-120</td>
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<tr>
<td>Chelae</td>
<td>11-18</td>
<td>8-19</td>
<td>15-20</td>
<td></td>
<td>14-16</td>
<td>14-20</td>
<td>19</td>
<td>19</td>
<td>10-12</td>
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<tr>
<td>toxas I</td>
<td>24-46 x 0.8-1.2</td>
<td>21-86 x 1-4</td>
<td>40-116 x 1-2</td>
<td>20-30 x 1.3</td>
<td>44-200 x 7 (spined)</td>
<td>70 x 2.5</td>
<td>63.3 x 2.1</td>
<td>25-70 x 8</td>
<td>15-75 x 0.5</td>
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<tr>
<td>toxas II</td>
<td>82-211 x 2.4</td>
<td>63-354 x 2.11 (spined)</td>
<td></td>
<td>190-230 x 2.7-10 (spined)</td>
<td></td>
<td></td>
<td>85-130 x 2.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Sources:
1. Ridley & Duncan (1881: 481); Denby (1922: 76); Lévi (1960a: 81).
2. Ridley & Denby (1887: 158); Denby (1922: 77); Lévi (1960b: 760); Pulitzer-Finali (1973: 55).
5. Lévi (1960a: 81).

ends, heavily spined particularly at points, spines large, conical or slightly recurved, sharply pointed. Length 85-(95.2)-103μm, width 3-(7.8)-14μm.

Subectosomal auxiliary subtylostyles long, very slender, curved at centre or sinuous, subtylote usually microspined bases, fusiform or occasionally telescoped points. Length 120-(135.9)-184μm, width 1-(1.7)-2.5μm.

Microscleures. Palmate isochelae large, unmodified, with front and lateral alae approximately same length, lateral alae entirely fused to shaft, front ala detached along lateral margin. Length 15-(17.4)-20μm.

Toxas wing-shaped, short, moderately thick, with large central curvature and slightly reflexed points. Length 40-(67.6)-116μm, width 1-(1.3)-2μm.

REMARKS. Spongin fibres are excluded from the skeleton and replaced entirely by algal filaments ('stylrophytosis'; Topsent, 1929), although each filament contains a thin cover of collagen on its surface with embedded spicules. Of the 3 microcionid species demonstrating this symbiosis A. (A.) opuntioides, and A. (P.) frondifera are the major structural partners in the symbiotic relationship, whereas C. (T.) stylrophytosis is probably a cryptic, invasive sponge and the algal symbiont provides the growth form structure. Antho (P.) frondifera is most similar to A. (A.) opuntioides, differing in spicule geometry (acanthostyloge versus acanthostyles in the renieroid skeleton), and spicule dimensions (Table 43). Neither species has been subsequently recorded since the early 1800s.

**Antho (Plocamia) ridleyi** (Hentschel, 1912) (Figs 218-220, Table 43, Plate 9D-E)

**Plocamia ridleyi** Hentschel, 1912: 387-388, pl.20, fig.44.

**Holoplocamia ridleyi**; de Laubenfels, 1936a: 75.

**Antho ridleyi**; Hooper & Wiedenmayer, 1994: 256.

**MATERIAL.** HOLOTYPE: SMF1709 (fragment MNHNDFCL2183); Mimien Bay, Arm 1., Aru Fura Sea, Indonesia, 7°S, 134°50'E, 15m depth, 8.iv.1908, coll. H. Meriton (dredge). OTHER MATERIAL: NT-NTMZ0299, NTMZ2108, NTMZ2110, NTMZ2112, NTMZ2131, NTMZ2142, NTMZ2201, QMG300146 (fragment NTMZ2212), NTMZ2221, QMG300507 (fragment NTMZ2230), QMG303295, NTMZ2556, NTMZ2378. WA- QMG301185.
Habitat Distribution. Holotype collected from a sand substrate, encrusting on an *Oceania* species (Niphatidae; incorrectly identified as *Phloeodictyon fistulosum* (Bowerbank)); other specimens collected from subtidal laterite rock and coral reefs, associated with dead coral substrate, usually growing on the underside of coral rubble; restricted intertidal distribution to only 3m depth; known Australian distribution: Darwin Harbour (NT); Hibernia Reef, Sahul Shelf (WA) (Fig. 218); also Aru Is, Indonesia (Hentschel, 1912).

**DESCRIPTION.** Shape. Thinly, thickly or bulbous-encrusting, 2-14mm thick, forming extensive overgrowths on coral substrata.

**Colour.** Live colouration consistent, even bright red or blood red (Munsell 5R 5-3/10), turning grey or pinkish grey in ethanol (5R 8-2-4).

**Oscules.** Large oscules on exterior of bulbous lobes, 0.4-1.6mm diameter, with slightly raised membranous lip; minute pores, up to 150μm diameter scattered evenly over surface; pores and oscules contract upon dessication.

**Texture and surface characteristics.** Firm, barely compressible, easily crumbled alive; no mucous produced upon exposure to air; surface optically smooth, irregularly bulbous, mostly clear of silt in situ; surface lobes in thinly encrusting specimens collapse upon dessication or preservation, but thicker specimens retain shape.

**Ectosome and subectosome.** Surface microscopically hispid, with points of smooth choanosomal principal styles protruding and surrounded by plumose brushes of mostly smaller ectosomal auxiliary stylostyles (with fewer larger subectosomal megascleres contributing to ectosomal skeleton); subectosomal region structurally variable; thinly encrusting specimens with peripheral skeleton not clearly delineated from choanosomal skeleton, containing only thick tangential or paratangential tracts, up to 140μm diameter, composed of larger subectosomal auxiliary stylostyles; in thicker bulbous specimens subectosomal region cavernous, containing numerous plumose, stellate brushes composed of both of choanosomal and subectosomal megascleres, clearly distinguished from the renieroid component of choanosomal skeleton; subectosomal auxiliary megascleres also in deeper choanosomal skeleton, together with smooth choanosomal principal styles, together forming vaguely ascending, multispecular, extra-fibre tracts, 25-65μm diameter.

**Choanosome.** Skeletal structure with 3 distinct components: hymedesmoid skeleton, with basal layer of spongine fibre lying on substrate, 60-240μm thick, with smooth choanosomal principal styles and echninating acanthostyles perpendicular to substrate; renieroid skeleton forming regularly reticulation of acanthostyles, overlaying hymedesmoid basal skeleton, in pauci- or multispecular tracts (vaguely ascend-

<table>
<thead>
<tr>
<th>TABLE 43. (continued)</th>
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<tbody>
<tr>
<td><strong>CHARACTER</strong></td>
</tr>
<tr>
<td><strong>Shape</strong></td>
</tr>
<tr>
<td><strong>Choanosomal styles</strong></td>
</tr>
<tr>
<td><strong>Renieroid spicules</strong></td>
</tr>
<tr>
<td><strong>Ectosomal spicules</strong></td>
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<tr>
<td><strong>Subectosomal spicules</strong></td>
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<td><strong>Echinating spicules</strong></td>
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<tr>
<td><strong>Chelae</strong></td>
</tr>
<tr>
<td><strong>Toxas I</strong></td>
</tr>
<tr>
<td><strong>Toxas II</strong></td>
</tr>
</tbody>
</table>

**Sources:**
ing) and uni- or paucispicular (irregularly transverse) tracts, producing triangular (isodictyal) or rectangular (renieroid) meshes, 60-150μm diameter, without any obvious spongine fibre component; echinating acanthostyles, occurring singly or in plumose brushes, at major nodes of renieroid skeleton, sometimes also forming irregularly plumose, discontinuous, ascending tracts; subisodictyal extra-fibre skeleton well developed in thicker specimens but rudimentary (irregularly dispersed) in thinly encrusting specimens; subisodictyal skeleton composed of both smooth choanosomal principal styles and subectosomal auxiliary subtylostyles forming barely continuous subisodictyal tracts extending from leptochoanid basal skeleton to peripheral region, becoming more plumose or dendritic towards periphery; mesohyl matrix heavy but virtually unpigmented, surrounding renieroid meshes; choanocyte chambers circular to oval, 63-95μm diameter; mesohyl matrix in both basal and peripheral regions more heavily pigmented than in choanosomal region, and microscleres also more abundant near surface. **Megascleres.** Choanosomal principal styles long, thick, slightly curved, with rounded or slightly subtyloyte bases, smooth or with lightly microspined bases, fusiform points. Length 183-(317,9)-562μm, width 6.5-(14.8)-25μm (holotype 212-388 x 14-20μm).

Acanthostrongyles of renieroid skeleton short, thick, straight or slightly curved, with either symmetrical subtyloyte bases, or asymmetrical ends (subtyloyte bases, rounded or slightly subtyloyte points); usually evenly microspined, spines small, conical, sharply pointed. Length 98-(120.6)-142μm, width 4.5-(10.1)-15μm (holotype 92-104 x 6.5-10μm).

Subectosomal auxiliary subtyloyles long, thin, fusiform, straight, with prominent tyloyte, subtyloyte or polytyloyte bases, bases microspined or less commonly smooth. Length 231-(372.9)-473μm, width 2.5-(5.9)-12.5μm (holotype 298-388 x 4-7μm).

Ectosomal auxiliary subtyloyles identical in geometry but smaller than large auxiliary megascleres, with tyloyte or subtyloyte, smooth or microspined bases. Length 100-(192.7)-252μm, width 1.1-(3.3)-6.5μm (holotype 129-209 x 1.8-4μm).

Echinating acanthostyles long, thick, fusiform, slightly curved, with subtyloyte, lightly microspined bases, entirely smooth shafts or proximal half of shafts covered with small spines (these spicules possibly small morphs of principal styles). Length 107-(194.1)-248μm, width 5-(10.1)-15μm (holotype 170-202 x 8-13μm). **Microscleres.** Palmate isochelae abundant, single size category, unmodified, with front and lateral alae approximately same length, lateral alae completely fused to shaft, front ala detached from front alae along lateral margin. Length 8-(12.5)-19μm (holotype 11-18μm).

Toxas wing-shaped, incompletely differentiated into 2 size classes: smaller thin, extensive rounded central curvature, straight or slightly reflexed points; larger thick, sharply angular or slightly rounded central curvature, straight or very slightly reflexed arms characteristically bearing terminal bulbous swelling and a single apical spine surrounded by smaller spines. Length I: 21-(44.3)-86μm, width 1-(1.9)-4.1μm (holotype 24-46 x 0.8-1.2μm); length II: 62-(169.2)-355μm, width 2-(4.7)-10.6μm (holotype 82-211 x 2-4μm).

**Larvae.** Parenchymella larvae oval-elongate, 195-410μm long, 135-330μm wide, orange-brown alive, incompletely ciliated with a bare posterior pole. Younger larvae poorly differentiated in cellular construction, but containing clearly visible, longitudinally disposed, whiply sinuous monocinal megascleres. Older larvae have distinct, oval, cellular differentiation, radially disposed thin tyloyles, and small toxas and isochelae.

Incubated larvae were abundant in 33% of specimens, collected between January and May 1985 in the Darwin region, but absent from samples collected during latter part of year (Fig. 220). Probable reproductive period is wet-early dry seasons (January to June) but determination of complete reproductive period was not possible as samples could not be taken every month).

**Associations.** All NT specimens were encrusting dead faviid coral heads, growing next to, or over other sponges (e.g., Stelleita, Mycale, Placospongia, Ulosa, Clathria), coralline algae and ascidians.

**Variation.** Ectosomal structure variable, ranging from Clathria condition (with thin or thick tangential crust; 17%), Thalysias condition (with a stellate plumose ectosomal architecture; 50%), to merely paratangential (with elements of both structures; 33%). Subectosomal region cavernous (with plumose tracts of choanosomal and/or subectosomal megascleres; 67%), to merely tangential or paratangential (without subdermal cavities; 33%). Extra-axial (non-renieroid) skeleton ranges from subisodictyal, distinctly plumose, ascending, diverging towards periphery...
(58%), to irregularly disposed, mostly longitudinal extra-fibre tracts (48%). Echinating acanthostyles form plumose ascending structures (50%) or irregularly dispersed (50%). Spicule geometry consistent although spicule dimensions varied slightly for all specimens (holotype had smaller toxas and acanthostrongyles than NW Australian material).

REMARKS. This species is relatively common in cryptic habitats on shallow intertidal reefs in the Darwin region, and it is therefore surprising that it has not been found elsewhere in NW Australia despite extensive sampling in similar habitats along the N. coast. Dendy (1922) merged Plocamia ridleyi with Plocamina coriacea from the N. Atlantic and Mediterranean, but this
synonymy is clearly wrong. In their spicule diversity and growth form the two taxa are similar (Table 43), whereas comparisons between field observations on living populations of \( A. (P) \) ridleyi (present study) and \( A. (P) \) coriacea (Ackers, Moss & Picton, 1992: 141) show that the two species have quite different surface features, live colouration, and some differences in spicule dimensions (Table 43) indicating at most a possible sibling species relationship.

The separate category of echinating acanthostyles, a renieroid skeleton composed of diactinal or quasi-diactinal spicules, and a more-or-less plumose (non-renieroid), subdiscoidal skeleton of smooth choanosomal and subchoanosomal spicules are typical of Antho (Plocamia). However, Antho and Plocamia are barely differentiated on that basis and they are formally merged here. Some Plocamia have a mixture of both acanthostyles and echinatingstrongyles in the renieroid skeleton (Lévi, 1960a). Megascleres echinating fibre nodes may vary from true acanthostyles, with different geometry from other choanosomal spicules (\( A. (P) \) barbadensis (Van Soest, 1984b)), or smooth styles which are differentiated from choanosomal megascleres only by their marginally smaller size and light, irregular spination (most species including \( A. (P) \) ridleyi, \( A. (P) \) elegans (Ridley & Dendy, 1886) and \( A. (P) \) coriacea (Bowerbank, 1874)), or echinating megascleres may be entirely undifferentiated from choanosomal styles or absent (e.g., \( A. (P) \) novizelianicum (Ridley, in Ridley & Duncan, 1881), \( A. (P) \) penneyi (de Laubenfels, 1936a), \( A. (P) \) fronidifera (Lamarck)). Similarly, the extra-axial (non-renieroid) skeleton varies between specimens. Some thinly encrusting species, such as \( A. (P) \) ridleyi, \( A. (P) \) delaubenfelsi (Little, 1963) and \( A. (P) \) burtoni (Lévi, 1952) have choanosomal styles embedded in the basal spongin fibre and in the renieroid fibre nodes, ascending all the way to surface in more-or-less plumose tracts. Other species (e.g., \( A. (P) \) illgi (Bakus, 1966)) have plumose tracts of choanosomal styles mainly in the peripheral skeleton with the remainder of the skeleton being simply renieroid. Antho (Plocamia) ridleyi differs substantially from the other known Australian species \( A. (P) \) fronidifera in spicule geometry (particularly in having spined points on the larger toxas), spicule dimensions (Table 43), growth form and lacking algal filaments in the skeleton ("styloprothrosis").

**OTHER SPECIES OF ANTHO (PLOCAMIA).**

**Antho (Plocamia) barbadensis** (Van Soest, 1984)

\( Plocamilla barbadensis \) Van Soest, 1984b: 125-126, text-fig.50 [Barbados, West Indies].

**Antho barbadensis**; Van Soest & Stenfotel, 1988: 123 [Barbados].

**MATERIAL. HOLOTYPE: ZMAPO3R3832. Province: Caribbean.**

**Antho (Plocamia) burtoni** (Lévi, 1952)

\( Plocamilla burtoni \) Lévi, 1952: 53-54, text-fig.17 [Senegal, W. Africa]; Lévi, 1960b: 760 [note].

**MATERIAL. HOLOTYPE: MNHN missing. Province: NW. Africa.**

**Antho (Plocamia) circonflexa** (Lévi, 1960)


**MATERIAL. HOLOTYPE: MNHN missing. NE. Atlantic, Mediterranean.**

**Antho (Plocamia) coriacea** (Bowerbank, 1874)

\( Isodictya coriacea \) Bowerbank, 1874: 136, 228, pl.76, figs 7-12 [Britain].

**Dirrhopalum coriaceum**; Ridley, 1881: 481, pl.29, figs 3-7 [Ireland].

**Plocamia coriacea**; Hanitsch, 1894: 173 [Britain]; Dendy, 1922: 76-77 [Amirante, Indian Ocean].


**Holoplocamia copheae**; de Laubenfels, 1936a: 75.

**MATERIAL. HOLOTYPE: BMNH1877.5.21. 761/1910-1.1.251. NE. Atlantic, Mediterranean, E. Africa.**

**Antho (Plocamia) delaubenfelsi** (Little, 1963)

**Holoplocamia delaubenfelsi** Little, 1963: 45-48, text-fig.18 [Gulf of Mexico].

**TABLE 43.**

<table>
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<tr>
<th>SEASON</th>
<th>TOTAL SAMPLES</th>
<th>NO. SAMPLES WITH LARVAE</th>
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<tr>
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</tr>
<tr>
<td>PREWET</td>
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</tr>
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</table>

**FIG. 220.** Antho (Plocamia) ridleyi (Hentschel). Incidence of incubated parenchymella larvae in NT specimens.
**MATERIAL. HOLOTYPE: USNM23596. NE Pacific.**

**Antho (Plocamia) elegans** (Ridley & Dendy, 1886)

*Plocamia elegans* Ridley & Dendy, 1886: 475 [var.]; Ridley & Dendy, 1887: 158-159, pl.29, fig.9, pl.31, fig.1 [var. elegans; Azores]; Topsent, 1892a: 117, pl.7, fig.11 [var. elegans; Azores]; Topsent, 1904a: 155 [var. elegans; Azores].

*Plocamia elegans*: Dendy, 1922: 77-78 [Cargados Carajos, Indian Ocean]; Topsent, 1928a: 64.


*Plocamilla coriacea* var. *elegans*: Lévi, 1960b: 760-761, text-fig.13 [W. coast of Africa].

*Holoplocamella elegans*: de Laubenfels, 1936a: 75.

MATERIAL. HOLOTYPE: BMNH1887.5.2.109, NE Atlantic, E & W Africa.

**Antho (Plocamia) erecta** (Ferrer-Hernandez, 1923)

*Plocamia erecta* Ferrer-Hernández, 1923: 248, text-figs 1-3 [Spain].


*Holoplocamella erecta*: de Laubenfels, 1936a: 75 [San-tander, Atlantic].


MATERIAL. HOLOTYPE: Madrid. NE Atlantic.

**Antho (Plocamia) gymnauza** (Schmidt, 1870)

*Plocamia gymnauza* Schmidt, 1870: 62-63, pl.4, fig.17 [Florida]; Burton, 1935a: 401; de Laubenfels, 1936a: 76.

*Dirrhophalum gymnazon*: Ridley, 1881: 478-479, pl.29, figs 1-2.

MATERIAL. HOLOTYPE: BMNH1870.5.3.70 (fragment MNHNDC1.105L), Caribbean.

**Antho (Plocamia) ilgii** (Bakus, 1966)

*Plocamilla ilgii* Bakus, 1966: 440-443, pl.1A, figs 6a-j [San Juan Archipelago, Washington]; Simpson, 1968a: 43-47, 93, text-fig.3 [San Juan Is, Washington]; Lee & Gilchrist, 1985: 24-32 [biochemistry]; Bakus & Green, 1987: 73-74 [S. California].

MATERIAL. HOLOTYPE: USNM23737. NE Pacific.

**Antho (Plocamia) lambei** (Burton, 1935)

*Plocamia manoaensis*, in part; Lambe, 1895: 124 [California]; Lambe, 1900: 161.

Not *Dictyocyclinidus manoaensis* Carter, 1880a: 37.

*Heteroclathria lambei* Burton, 1935a: 403.

*Plocamilla zimmeri* Bakus, 1966: 512.

MATERIAL. HOLOTYPE: USNM66331. NE Pacific.

**Antho (Plocamia) lithophoenix** (de Laubenfels, 1927)

*Plocamia lithophoenix* de Laubenfels, 1927: 268.

*Isociona lithophoenix*: de Laubenfels, 1932: 99-100, text-fig.59 [California]; Burton, 1935a: 400 [note]; Dickinson, 1945: 23, pl.35, figs 69-70, pl.36, figs 71-72 [Pacific Grove, California].


MATERIAL. HOLOTYPE: USNM21460, para-type BMNH1929.8.2242. NE Pacific.

**Antho (Plocamia) manaarensts** (Carter, 1880)

*Dictyocyclindrus manaarensts* Carter, 1880a: 34, pl.4, fig.1 [Gulf of Manana, Ceylon].

*Dirrhophalum manaarensts*: Ridley, 1881: 482.

*Plocamia manaarensts*: Dendy, 1905: 179, pl.8, fig.1 [Gulf of Manaar, Ceylon]; Burton & Rao, 1932: 355 [Laccadive Sea, Mangalore and Karwar, India].

Not *Plocamia manaarensts*; Lambe, 1895: 124, pl.2, figs 11a-g [California].


MATERIAL. HOLOTYPE: LFM destroyed (fragment BMNH1986.2.49.1b). India, Arabian Sea.

**Antho (Plocamia) novizelanica** (Ridley, 1881)

*Dirrhophalum novizelanica* Ridley, 1881: 483-485, pl.29, figs 8-16 [Bay of Islands, New Zealand].


*Plocamilla novizelanica*: Lévi & Lévi, 1983a: 965-966, text-fig.27 [S. of New Caledonia]; [?] Utir; 1988a: 90-91, text-fig.65 [Namibia; ? affinity].

*Holoplocamella novizelanica*: de Laubenfels, 1936a: 75.

*Plocamilla novizelanica*: Bergquist & Fromont, 1988: 120-122, pl.56, fig.f, pl.57, figs a-b [New Zealand]; Dawson, 1993: 38 [index to fauna].

Not *Plocamilla* cf. *novizelanica*; Maldonado, 1992: 1154, fig.11-12, table 5 [Alboran Sea; ? affinity].

MATERIAL. HOLOTYPE: BMNH1964.1.1.1. SW Pacific (N.Z, New Caledonia); SW Africa, Mediterranean.

**Antho (Plocamia) ornata** (Dendy, 1924)

*Burbaris ornata* Dendy, 1924a: 351, pl.14, figs 25-27.

*Plocamia ornata*: Burton, 1928: 129.


MATERIAL. HOLOTYPE: BMNH missing (fragments BMNH1923.10.1.126, 322). W Indian Ocean.

**Antho (Plocamia) penneyi** (de Laubenfels, 1936)

*Holoplocamella penneyi* de Laubenfels, 1936a: 76 [Tortugas, Florida].

*Antho penneyi*: Van Soest & Stentoft, 1988: 126 [table].

MATERIAL. HOLOTYPE: USNM22460. Caribbean.

**Antho (Plocamia) plena** (Sollas, 1879)

*Plocamia plena* Sollas, 1879: 44, pl.6-7 [W Africa]; Topsent, 1894: 21.

*Holoplocamella plena*: de Laubenfels, 1936a: 75 [note].

*Clostria plena*: Vosmaer, 1880: 154 [Angola].

*Dirrhophalum plenum*: Ridley, 1881: 480-481.
REVISION OF MICROcionIDAE

MATERIAL. HOLOTYPE: Bristol (fragment BMNH1909.8.15.3), W Africa.

**Antho (Plocamia) prima** (Brondsted, 1924)

*Lissoplocamia prima* Brondsted, 1924: 470, fig. 24a-d [North Cape, New Zealand]; Topsent, 1928a: 63; Levi, 1963: 63, fig. 73 [S. Africa].

**Plocamia prima**; Bergquist & Fromont, 1988: 122, pl. 57e-c.

MATERIAL. HOLOTYPE: possibly UZC. South Africa, N.Z.

**Antho (Plocamia) signata** (Topsent, 1904)

*Plocamioptis signata* Topsent, 1904a: 155-157, pl. 14, fig. 1 [Azores]; Topsent, 1928a: 306-307, pl. 10, fig. 2 [et var. mitis; W. of Flores, Azores]; Burton, 1935a: 402 [note].

MATERIAL. HOLOTYPE: MOM (fragment BMNH1930.7.1.36), NE Atlantic.

**Antho (Isopenectya) Hallmann, 1920**


**TYPE SPECIES. Clathria chartacea** Whitelegge, 1907: 497 (by monotypy).

**DEFINITION.** Three skeletal components: (1) renieroid reticulation of acanthosyle styles, (2) overlayed by isodictyal or subisodictyal reticulation of smooth styles coring spong fibres, (3) surmounted by plumose or radial extra-axial skeleton of larger smooth styles, perpendicular to axis, in peripheral region; skeleton may be slightly compressed at core, spong fibres only moderately developed; echinating megascleres absent; ecosomal skeleton with single category of auxiliary subtylostyle forming tangential or paratangential tracts; microscleres absent.

**REMARKS.** *Isopenectya* contains 4 species, 3 from the SW Pacific and 1 from the NW Pacific. All lack microscleres but this is interpreted as secondary loss.

**Antho (Isopenectya) chartacea** (Whitelegge, 1907)

(Figs 221-222, Plate 9F)

*Clathria (?) chartacea* Whitelegge, 1907: 497.


*Anthrochalina perforata* Lendenfeld, 1887b: pl. 22, fig. 44.

Not *Anthrochalina perforata*, in part; Lendenfeld, 1887b: 788; Lendenfeld, 1888: 89-90.

MATERIAL. HOLOTYPE: AMZ436: Off Coogee, NSW, 33°45'S, 151°20'E, 98-100m depth, date of collection unknown, coll. FIV 'Theus' (trawl).

**HOLOTYPE of A. perforata:** BMNH1888.6.27.459; Broughton I., Port Stephens, NSW, 32°36'S, 152°19'E, other details unknown. OTHER MATERIAL. NSW: NTM 22831, AMZ3605, AMZ3604, AMZ3606, AMZ4216 (RRIMP FFN1339), AMZ4256 (RRIMP FFN1435), AMZ4255 (RRIMP FFN1434), AMZ3207, AMZ3162, AMZ4569 (RRIMP-59JP), QMG303711, QMG303713.

**HABITAT DISTRIBUTION.** 12-100m depth; rock platform, heads or outcrops on sand substrate; known only from Australia: Port Stephens, Botany Bay, Coogee, Long Reef, Dee Why, N. Sydney, Port Hacking, Cronulla, Manly (NSW) (Fig. 221E).

**DESCRIPTION.** Shape. Thinly flabellate, up to 80mm long, 55mm wide, with long, thickly cylindrical stalk, very thin lamellae, up to 8mm thick, with slightly digitate or evenly rounded margins.

**Colour.** Bright red-orange alive (Munsell 5R 5/10 - 10R 6/10), pale brown in ethanol.

**Oscules.** Not observed.

**Texture and surface characteristics.** Firm, barely compressible, flexible, slightly spiky; optically smooth, even surface.

**Ectosome and subectosome.** Ectosome prominently hispid, with pauci- or multispiracular plumose brushes of larger, smooth chaoanosomal principal styles protruding through surface, forming a vestigial radial extra-axial skeleton, arising from pauci- or multispiracular tracts of (marginally) smaller smooth principal styles in subectosomal region; subectosomal auxiliary subtylostyles tangential, paratangential, or rarely plumose, at base of protruding chaoanosomal spicule brushes; peripheral skeleton relatively cavernous in comparison to the central chaoanosomal skeleton, with moderately heavy mesohyl matrix.

**Choanosome.** Skeletal structure with 3 distinct components: (1) slightly compressed spong fibres forming close-meshed anastomoses at core of skeleton, more cavernous towards surface, (2) renieroid skeleton composed of acanthosyle styles, overlaying other structures; (3) longitudinal, ascending tracts of smooth principal styles, marginally smaller than those protruding through surface, forming subisodictyal tracts at core, more plumose in periphery, and usually (but not invariably) associated with larger spong fibres; spong fibres in axial skeleton heavy, 48-82μm diameter, producing irregularly oval or elongate meshes, 32-120μm diameter, cored by uni- or bipuscular tracts of smaller, smooth chaoanosomal principal styles; fibres closer to surface, 19-42μm
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diameter, regularly anastomosing, wide-meshed, 75-162 μm diameter, forming regular renieroid (triangular) spicule meshes and oval or elongate fibre meshes, cored by uni- or bispicular tracts of smaller acanthoskeletal styles; plumose extra-fibre skeleton composed of uni-, paeui- or multispicular ascending tracts of smooth choanosomal styles standing perpendicular to axis, becoming increasingly plumose, larger, and typically multispiracular towards periphery; echinating megascleres absent; mesohyl matrix lightly pigmented, with few auxiliary spicules scattered throughout; choanocyte chambers elongate-ovall, 36-75 μm diameter.

**Megascleres.** Smooth choanosomal principal styles long, thick, slightly curved or straight, with rounded or very slightly subylote bases, rarely with basal microspination, fusiform points. Length 117-(232.4)-312 μm, width 6-(11.8)-15 μm (holotype 168-274x13-17 μm).

Acanthochoanosomal styles of renieroid skeleton short, thick, fusiform, slightly curved or straight, with rounded or slightly subylote bases, lightly microspined bases and points, with fewer spines scattered on shaft, occasionally completely smooth shaft. Length 74-(86.1)-112 μm, width 4-(7.2)-8.5 μm (holotype 92-127x9-12.5 μm).

Subectosomal auxiliary subylote styles short, thin, usually straight, with prominent subylote, typically microspined bases, hastate points, abrupt points, or sometimes telescoped or bifid points. Length 134-(183.6)-203 μm, width 2.5-(2.9)-3.8 μm (holotype 163-243x2-4.5 μm).

Echinating megascleres absent.

**Microscleres.** Absent.

**Larvae.** Viviparous, parachymella larvae oval to elongate, 340-420x180-360 μm, with central core of juvenile styles, well differentiated cellular construction.

**Associations.** Obligatory (?) host for nudibranchnost Rostanga sp. (AMC150065) (W. Rudman, pers. comm.).

**REMARKS.** Hallmann (1920) erected Isopenec-tya for this species based on a renieroid skeleton, with two categories of choanosomal styles, without echinating acanthoskeletal styles, and without microscleres. The type species has affinities with Antho but differs from other 'plocamid' microcionids (with myxillid-like renieroid skeletons) (viz. Antho s.s., Dirrhopalum, Plocamilla, Plocamiopis, Labacea, Isociona, and Isoiciella) in having a compressed axis and more-or-less plumose extra-axial skeletons cored by smooth choanosomal (principal) styles, in one or more size categories, together with the usual renieroid structure overlaying the remainder of the skeleton composed of acanthose (or sometimes smooth) styles different from principal spicules.

This species superficially resembles Oph-litaspongia tenuis (Carter) (= Echinoclathria leporina (Lamarck)) mainly due to the emphasis of the compressed central skeleton and sub-renieroid skeletal structure in both species, whereas megascleres forming these skeletons are quite different. Choanosomal megascleres in A. (L.) chartacea are differentiated: small acanthose styles forming the renieroid skeleton (not echinating fibres), small smooth styles forming a secondary radial ascending skeleton, and larger smooth styles forming the peripheral perpendicular skeleton. By comparison, in E. leporina there is a smaller size class of smooth principal style both coring and echinating heavy spongin fibres, forming a renieroid skeletal structure, and a second, larger class of smooth principal style forming a sparse radial or plumose peripheral skeleton (embedded in peripheral fibres). This latter structure links the two groups. E. riddei sp. nov., is also similar in skeletal structure but lacks spined spicules in renieroid skeleton and has a vestigial extra-fibre skeleton perched on the outer surface. Antho (L.) chartacea should be contrasted with the renieroid Amphinomia (Raspailiidae), which also has acanthose structural spicules (Hooper, 1991).

**Antho (Isopenec-tya) punic-ea** sp. nov. (Figs 223-224, Plate 10A)

**MATERIAL.** HOLOTYPE: QMG304399: Mrs Watson's Bay, midway in bay, Lizard 1, Qld, 14°39.5'S, 145°26.7'E, 18 m depth, 10.iv.1994, coll. J.N.A. Hooper et al., SCUBA.

**HABITAT DISTRIBUTION.** Sand, coral rubble, Halimeda bed substrata, in depression in sand; 18 m depth; Lizard 1 (FNQ) (Fig. 223E).

**DESCRIPTION.** Shape. Bushy, subspherical, bulbous clump, 195 mm long, 142 mm maximum width, 138 mm maximum height, composed of individual, erect, digitate projections, each up to 16 mm diameter, 75 mm high, forming reticulated structure, attached to coral rubble and Halimeda on base.

**Colour.** Dull red alive (Munsell 5R 6/8), light brown in ethanol.

**Oscules.** Small, up to 2 mm diameter, mainly on lateral sides of digits, situated at junction of sur-
face aquiferous canals, surrounded by collapsible membranous lip.

Texture and surface characteristics. Firm, compressible, not easily torn; surface turgid in life, with distinctive choanosomal membrane, arteriolar-like longitudinal aquiferous canals obvious on external surface, branching and interconnecting, opening into common oscules, porous surface between canals; canals, ridges and oscules collapse in air, producing reticulate surface upon dessication; produces abundant red mucus upon exposure.

Ectosome and subectosome. Surface prominently hispid, with longer choanosomal principal styles embedded in peripheral fibres, arising from ascending primary, plumose spicule tracts, extending through surface for most of their length; subectosomal auxiliary stylostyles tangential, occasionally paratangential, confined to exterior collagenous layer below ectosome, occasionally protruding through surface in plumose brushes; mesohyl matrix heavy in peripheral region.

Choanosome. Skeleton without any compression or marked differentiation between core or subectosomal regions; 3 distinct skeletal components; (1) renieroid skeleton composed of both acanthothose styles and smaller smooth principal styles in uni-, bi- or paucispicular tracts, coring small, light spongion fibres up to 25 μm diameter, producing rectangular or triangular meshes up to 90 μm diameter; (2) plumose, diverging skeleton of smaller smooth choanosomal principal styles in multispecific ascending tracts, diverging towards periphery producing nearly radial skeletal tracts; (3) and with larger, smooth principal styles embedded in peripheral skeleton perpendicular to surface; echinating megascleres absent; mesohyl matrix light, without microscleres but few wispy (?) juvenile) auxiliary stylostyles scattered between fibre meshes; choanocyte chambers small, oval, 25-45 μm diameter.

Megascleres. Smooth choanosomal principal styles long or short, slender, slightly curved at centre, with rounded, predominantly smooth bases, occasionally microspined, telescoped points. Length 86-(155.6)-235 μm, width 2.5-(3.3)-4 μm.

Acanthothose styles of renieroid skeleton slender, slightly curved towards base; rounded, sparsely microspined bases, sparsely spined shaft, spines small, erect, conical; points of spicules fusiform. Length 88-(114.9)-153 μm, width 2-(3.6)-6 μm.

Subectosomal auxiliary stylostyles variable in length and thickness but only comprising a single category; bases subtylole, microspined, tuberculate (granular) or occasionally smooth, points fusiform or slightly telescoped; wispy juvenile forms present scattered throughout mesohyl. Length 78-(169.8)-296 μm, width 0.5-(1.6)-3 μm.

Echinating spicules absent.

Microscleres. Absent.

ETYMOLOGY. Latin punicea, reddish.

REMARKS. The bulbous growth form, red colour and production of abundant mucus is common to many other Indo-west Pacific microcionids (such as C. (Isosciellia) eccentrica, C. (Thalysias) vulpina, C. (T.) hirsuta, Echinoclathria axinelloides, and Echinochalinia (Protophlitaspongia) bargibanti), but this species belongs to Antho (Isopenectya) having a renieroid skeleton composed (mainly) of a special category of acanthothose styles (geometrically different from choanosomal spicules), a secondary, diverging, plumose skeleton of smaller, smooth choanosomal styles, and larger smooth choanosomal styles embedded in the peripheral skeleton. This latter character is reminiscent of Echinochalinia, and it could be argued for its inclusion in this genus on this basis, but the possession of 3 distinctive skeletal structures and acanthothose spicules forming the renieroid skeleton support its inclusion in Antho.

Antho (Isopenectya) saintvincenti sp. nov. (Figs 225-226)


HABITAT DISTRIBUTION. Substrate unknown; 7 m depth; St. Vincent Gulf (SA) (Fig. 225F).

DESCRIPTION. Shape. Erect, arborescent, lamellate-digate sponge, 235 mm long, 130 mm wide, with flattened or slightly cylindrical digits, up to 80 mm long, 11 mm diameter (cylindrical portions), or up to 20 mm diameter, 8 mm thick (lamellate portions of digits), repeatedly bifurcate, rarely anastomosing, expanding towards
spatula-like ends; short cylindrical basal stalk, 45mm long, 8mm diameter, and expanded basal attachment.

**Colour.** Beige-brown in ethanol.

**Oscules.** Small, probably contractile, 1-2mm diameter in preserved state, on edges of flattened digits.

**Texture and surface characteristics.** Firm, compressible, flexible; surface smooth, even, unornamented, finely porous in preserved state.

**Ectosome and subectosome.** Ectosome membranous, microscopically hispid, with larger, smooth principal styles protruding through surface individually or in sparse, erect, plumose brushes arising from terminal subsidictyal spicule tracts; subectosomal auxiliary stylolstes also protruding through surface in association with longer principal styles, in paratangential or plumose tracts; mesohyl matrix in peripheral skeleton light, poorly pigmented.

**Choanosome.** Skeleton regularly renieroid reticulate, slightly more compressed at core than periphery, with 3 components; (1) renieroid skeleton composed of differentiated axial and extra-axial regions; axial fibres heavy, homogeneous, without clearly differentiated primary or secondary elements, 40-60μm diameter, slightly more bulbous at fibre nodes, 70-90μm diameter; all axial fibres cored by uni- or paucispicular tracts of acanthose principal styles forming rectangular or less often triangular meshes, 70-100μm diameter; extra-axial fibres lighter, with differentiated primary, ascending fibres, 20-40μm diameter, cored by paucispicular tracts of both acanthose principal styles and smaller, smooth principal styles, becoming increasingly plumose towards surface, projecting from fibre nodes in particular as plumose brushes; primary fibres interconnected by uni- or paucispicular tracts of acanthose principal styles coring light spongin fibres, 15-30μm diameter; (2) plumose, diverging skeleton of smaller smooth choanosomal principal styles intermixed with acanthose spicules in primary ascending tracts, diverging towards periphery, together producing nearly radial skeletal tracts; (3) larger, smooth principal styles in plumose brushes protruding through surface, embedded in ascending primary fibres; echinating megascleres absent; mesohyl matrix heavy but only lightly pigmented, with both fully formed and raphidiform subectosomal auxiliary stylolstes scattered between fibre meshes; choanoocyte chambers small, oval, 40-50μm diameter.

*Megascleres.* Smooth choanosomal principal styles of plumose and radial surface skeleton long or short, thick or slender, slightly curved at centre, rounded or slightly subtylole, smooth bases, fusiform points, entirely smooth shaft. Length 78-(115.4)-156μm, width 4-(6.9)-10μm.

Acantho styles of renieroid skeleton short, thick, slightly curved at centre, subtylole microspined bases, fusiform pointed, evenly microspined shaft, spines small, granular. Length 76-(84.6)-98μm, width 4.5-(5.9)-8μm.

Subectosomal auxiliary stylolstes short or long, slender or raphidiform, straight or slightly curved at centre, prominently subtylole, smooth bases, fusiform points. Length 66-(115.7)-198μm, width 1-(1.7)-3μm.

*Microscleres.* Absent.

**ETYMOLOGY.** For the type locality.

**REMARKS.** This species resembles both *Antho* and *Echinoclathria*, having a renieroid architecture and larger, smooth principal styles protruding through the surface. Like *A. (I.) punicea* it is included in *Antho* because it has a special category of acanthose styles (geometrically different from choanosomal spicules) forming the renieroid skeleton, and a secondary, diverging, plumose skeleton of smaller, smooth choanosomal styles. *Antho (I.) saintviucenti* differs from *A. (I.) punicea* in its flattened or cylindrical-digitate, arborescent growth form, reminiscent of *Echinoclathria chalyboides*, although spiculoanl and skeletal architecture differ substantially.

**OTHER SPECIES OF ANTHO (ISOPENECTYA)**


MATERIAL. HOLOTYPE: BMNH1938.7.4.93 (fragment BMNH1932.11.17.89), NW Pacific.

**Echinoclathria** Carter, 1885

*Echinoclathria* Carter, 1885f: 355.

*Oppilitaspongia*; of authors; (not Bowerbank, 1866: 14).

**TYPE SPECIES.** *Echinoclathria tenuis* Carter, 1885f: 355 (by subsequent designation of Burton, 1934a: 562), =*Spongia leporina* Lamarek, 1814: 444.

**DEFINITION.** Two distinct skeletal components: (1) predominantly renieroid reticulate main skeleton cored by smaller, smooth principal
styles, echinated by identical spicules (occasionally absent), typically very well developed spongin fibres sometimes slightly compressed at axis, more openly reticulate towards periphery; and (2) a vestigial radial extra-axial skeleton perched on the external surface, barely extending into choanosome, consisting of larger, smooth principal spicules, with identical geometry to those at core, forming radial or plumose brushes on surface; ectosomal skeleton with single size class of auxiliary subptylostyle lying paratangential or embedded perpendicular to surface; microscleres include toxas and palmate isochelae.

REMARKS. Sixty nine species have been included in Echinoclathria (or one of its synonyms), but only 23 are appropriately referred here. Fourteen species are known from Australia, most restricted to temperate coasts; 5 are new.

Echinoclathria is similar to Antho (Isopenectya), as noted above, differing in having only 2 skeletal components: a relatively homogeneous renieroid choanosomal skeleton composed of smaller, smooth principal spicules, and vestigial radial extra-axial skeleton on the external surface. Isopenectya has in addition a renieroid skeleton of acanthospicules, and the smooth principal styles form longitudinal tracts extending all the way from the axis to the surface and beyond. Difficulties occur when trying to place species that have reduced structural characters: A. (F.) punicea sp. nov. with spined renieroid spicules; E. riddiei sp. nov. with smooth renieroid spicules; both species with a reduced extra-fibre skeleton.

Within Echinoclathria most of the variability centres around the development of the extra-fibre skeleton. In some species (e.g., E. leporina, E. confragosa) there are obvious size differences between principal styles coring fibres in the choanosome and those protruding through the surface, whereas in others (e.g., E. nodosa) there is no obvious size differences between principal styles at the core and those at the periphery, although structurally these are similar to the first condition. In others (e.g., E. egena, E. waldoschmidtii) there is further reduction whereby the extra-fibre skeletal is virtually absent and all spicules are vestigial, poorly silicified.

Groupings based on growth form (Hallmann, 1912) show little relationship to groupings made on skeletal characteristics. Thus previous classifications for Echinoclathria are rejected here.

Echinoclathria axinelloides (Dendy, 1896)
(Figs 227-228, Plate 10B)

Ophiactaspongia axinelloides Dendy, 1896: 39; Hallmann, 1912: 268-270, pl.36, fig.3, text-fig.58; Burton, 1934a: 599.


OTHER MATERIAL: VIC- AMZ802, AMZ1593. TAS- QMG300269 (NCIQ66C-3655-O) (fragment NTMZ3804).

HABITAT DISTRIBUTION. Rock reef; 20-36m depth; Port Phillip Bay (Vic); Furneaux Is (Tas) (Fig. 227D).

DESCRIPTION. Shape. Erect, club-shaped or arboreal, up to 115mm long, 75mm wide, with thick subcylindrical branches or slightly flattened lamellae, up to 34mm diameter, with rounded even margins, long thick basal stalk, 25-40mm long, 15mm diameter, slightly expanded basal attachment.

Colour. Colour deep red alive (Munsell 2.5R 4/10), pale brown in ethanol.

Oscules. Numerous, moderately small, 2-4mm diameter, mainly on lateral margins of lamellae or on 1 side of branches, slightly raised with membranous lip.

Texture and surface characteristics. Firm, compressible, rubbery in life; surface optically smooth, minutely reticulated, with distinct membranous covering.

Ecosome and subectosome. Membranous, with minutely reticulate, skin-like membrane stretched over surface, microscopically hispid from protruding choanosomal styles forming well developed, multispecific plumose brushes just below surface producing a more-or-less continuous palisade; surface spicule brushes heavier at surface than at core of skeleton; fewer subectosomal auxiliary styles paratangential to surface in association with oscules.

Choanosome. Skeleton more-or-less dendroreticulate, slightly sub-renieroid or irregularly reticulate in some parts, composed of heavy, well developed spongion fibre system incompletely separated into plumose primary and vestigial transverse secondary components; primary fibres (75-148μm diameter) multispecific, cored by distinctly plumose tracts of choanosomal principal styles, whereas secondary fibres (38-72μm diameter)

diameter) uni-, bi- or occasionally aspicular; echinating styles sparsely dispersed on fibres mainly confined to primary fibres; fibre anastomoses form oval, elongate or rectangular meshes, 38-195 μm diameter, more compact in peripheral skeleton, relatively cavernous towards axis (130-275 μm diameter), fibre nodes slightly enlarged, bulbous; choanosomal fibres and
spicule tracts become more regular and more compacted towards periphery; mesohyl matrix relatively heavy, granular, with oval to elliptical choanocyte chambers (56-216 μm diameter), with both choanosomal and subectosomal megascleres scattered between fibres. Megascleres. Choanosomal principal styles and subtylostyles, coring and echinating fibres short, thick, straight, with smooth, evenly rounded or very slightly tapering, constricted bases, slightly hastate points, and approximately 5-15% modified to diactinal or quasi-diactinal forms. Length 76-(109.8)-148 μm, width 4-(9.8)-14.5 μm.

Subectosomal auxiliary styles straight, slightly curved, or rarely sinuous, relatively thick, with smooth, rounded or very slightly subtylostyles bases, fusiform or slightly telescoped points. Length 96-(144.3)-187 μm, width 2.5-(4.1)-5 μm. Microscleres. Absent. Larvae. Viviparous, parenchymella larvae oval to elongate. 155-275 x 120-170 μm, without larval spicules.

REMARKS. This species differs from other Australasian Echinocladithra in its growth form and rubbery texture, having a well developed ectosomal membrane covering a thick ectosomal palisade of principal styles, a dendro-reticulate skeletal structure verging on subrenieroid, its fibre characteristics and spiculation. It is most similar to E. nodosa in spicule geometry and gross skeletal architecture although differs in most other respects. Hallmann (1912) suggested his specimen (AMZ802) differed from Dendy’s (1896) description having greater fibre diameter, less extensive spicule tract development, and a denser ectosomal skeleton, but comparison between both specimens showed them to be clearly conspecific (i.e., supposed discrepancies were a consequence of Dendy’s incomplete description). The collector of AMZ1593 is unknown; the AM register indicates Port Phillip, Vic. That specimen contained numerous small parenchymella larvae.

According to Burton (1934a) the Saville Kent collection contains this species, but this record is questionable as the specimens have not been discovered in the BMNH collections.

**Echinocladithra bergquistiae** sp. nov. (Figs 229-230, Plate 10C)

**MATERIAL. HOLOTYPE:** QMGL952 (fragment NTMZ1534): E. of Murdock 1., Howick Group, Great Barrier Reef, 14°36’S, 145°03’E, 14m depth, 18.ix.1979, coll. A. Kay (trawl).

**HABITAT DISTRIBUTION.** Coral reef, coral rubble; 14-28m depth; Howick Reefs (FNQ); Hook Reef (MEQ) (Fig. 229F).

**DESCRIPTION. Shape.** Erect or clumped, clathrous digitate mass, 90-110mm high, 65-150mm wide, attached directly to substrate without basal stalk, composed of fused lobate or vaguely cylindrical digits, up to 55mm long, 30mm wide.

**Colour.** Bright red alive (Munsell 2.5R 5/10), pale brown in ethanol.

**Oscules.** Small, up to 3mm diameter, with slightly raised membranous lip alive, scattered on exterior surface of lobate digits.

**Texture and surface characteristics.** Soft, compressible, fibrous, difficult to tear, produces slight, clear mucus alive (on deck), stains ethanol orange; surface highly clathrous with large, flattened lobate or pointed conules covering exterior surface of digits, 5-15mm long, up to 5mm wide; surface porous in preserved state, membranous alive.

**Ectosome and subectosome.** Surface prominently hispid with longer, smooth choanosomal principal styles embedded in peripheral fibres, extending nearly 70% of their full length through surface; near bases of protruding principal styles are relatively heavy multispicular tracts of subectosomal auxiliary subtylostyles, usually tangential to surface; mesohyl matrix in peripheral skeleton heavy but only lightly pigmented; choanosomal fibres extend directly to surface.

**Choanosome.** Skeleton irregularly renieroid reticulate, slightly compressed at axis, with renieroid structure partially obscured by both larger principal styles echinating and subectosomal auxiliary subtylostyles scattered throughout mesohyl; spongin fibres large, 40-60μm diameter, well developed but only lightly invested with spongin, without any marked differences between thickness of fibres at core or surface; ascending fibres approximately same thickness as transverse fibres but generally longer and containing more coring spicules; ascending fibres pauci- or multispicular, cored by smaller choanosomal principal styles, with 2-5 spicules per tract; transverse connecting fibres generally shorter, containing the same spicules, 1-3 spicules per tract, and both fibres sparsely echinated by same spicules; fibre anastomoses produce elongate-oval meshes; axial fibre

reticulation slightly more compressed than peripheral skeletal network, with meshes up to 90μm diameter in axis, 160μm diameter near surface; in addition to renieroid skeleton of smaller principal styles, larger principal styles also core ascending fibres and echinate fibre nodes especially closer to surface, forming sparse plumose bundles; mesohyl matrix heavy but only lightly pigmented, containing numerous toxas; choanocyte chambers oval, 35-55μm diameter.
**Megascleres.** Choanosomal principal styles (coring and echinating fibres) variable in length, straight or slightly curved at centre, with rounded bases, predominantly smooth but occasionally microspined, fusiform points. Length 71-(149.8)-309μm, width 2.5-(5.6)-12μm.

Subectosomal auxiliary subystyles long, slender, straight, subylote, smooth or less commonly microspined bases, fusiform points; numerous smaller and raphidiform styles also scattered through mesohyl presumably being younger forms. Length 203-(356.7)-480μm, width 2-(3.7)-6μm.

**Microscleres.** Palmate isochetae not common, relatively large, with short thin alae, lateral alae completely fused to shaft, front ala nearly completely detached from lateral alae, shaft straight. Length 18-(24.2)-32μm.

Toxas wing-shaped, relatively thick, with slightly rounded central raphidiform styles, slightly reflexed points. Length 32-(49.7)-68μm, width 0.5-(1.9)-3.0μm.

**ETYMOLOGY.** For Dame Professor Patricia Bergquist for her work on Indo-Pacific sponges.

**REMARKS.** Generic placement is not straightforward, with affinities to *Echinoclathria* and *Antho* (*Isopenectya*). The smaller, smooth choanosomal principal styles coring and echinating all spongin fibres, producing an irregularly renieroid reticulation, a vestigial radial skeleton of larger, smooth principal styles protruding through the surface, and a slightly compressed axial region are typical of *Echinoclathria*, and in this respect the species is similar to *E. leporina*. However, the larger principal styles coring the ascending spongin fibres, occasionally echinating fibre nodes, is reminiscent of *Antho* (*Isopenectya*). It is included in *Echinoclathria* because the ascending tracts of larger principal styles do not form a subsidocystal skeleton; rather, these spicules end abruptly at fibre nodes in sparse plumose brushes and usually do not form continuous tracts. This evidence it weak and illustrates the difficulty in separating some species in both genera.

This species is distinct from other *Echinoclathria* in toxas morphology and plumose brushes/tracts of larger principal styles within the choanosome.

**Echinoclathria chalinoides** (Carter, 1885)  
(Figs 231-232)

*Axinella chalinoides* Carter, 1885f: 358; Carter, 1886g: 377 (et var gluinosa, cribrosa).

*Axinella cladorhagellata* Carter, 1886g: 377.  
*Echinoclathria chalinoides*, de Laubenfels, 1936a: 119.

*Ophitaspangia chalinoides* Dendy, 1896: 36.  
*Echinoclathria chalinoides*; Hooper & Wiedenmayer, 1994: 279.

Not *Ophitaspangia chalinoides*; Hallmann, 1912: 270-272, text-fig.59.

**MATERIAL.** LECTOTYPE: BMNH1886.12.15.401 (dry): Port Phillip, Vic, 38°09'S, 144°52'E, coll. J.B. Wilson (dredge). PARALECTOTYPES: BMNH1886.12.15.402 (dry) (fragment AMG2900a); same locality. BMNH1886.12.15.403 (dry) (fragment AMG2900b); same locality. HOLOTYPE of *A. cladorhagellata*: BMNH1886.12.15.407; same locality as lectotype.

**HABITAT DISTRIBUTION.** Ecology unknown; Port Phillip (Vic) (Fig. 231D).

**DESCRIPTION.** Shape. Arborescent branching, up to 250mm long, 170mm maximum width, with small basal stalk up to 45mm long, 22mm diameter, long cylindrical branches up to 105mm long, 9mm diameter, slightly flattened, bifurcating repeatedly, rarely anastomosing.

**Colour.** "Dull brick-red" alive (Carter, 1885e), pale brown in ethanol and dry.

**Oscules.** Large, up to 4mm diameter, scattered mainly on lateral sides of branches, with series of radial subectosomal drainage canals radiating towards each oscule, and slightly raised membranous lip.

**Texture and surface characteristics.** Soft, compressible but difficult to tear, flexible branches, more rigid stalk; surface slightly microconulose, with fine surface network of radiating spicules associated with aquiferous system.

**Ectosome and subectosome.** Membranous, with points of larger principal styles protruding through surface, singly or in paucispicular brushes, for up to 30% of their length, and also with subectosomal auxiliary styles lying paratan-  
gential to surface; subectosomal region slightly cavernous, meshes up to 450μm diameter, substantially more wider-meshed than in axial region skeleton.

**Choanosome.** Skeletal architecture dendro-  
reticulate, vaguely subrenieroid and more regular towards periphery than axis, composed of heavy, well developed spongin fibres, 25-70μm diameter, thicker and slightly bulbous at fibre
nodes, without any marked differentiation between primary and secondary components but substantially compressed in axis and diverging near surface; ascending fibres slightly sinuous, larger than transverse fibres, containing pauci-or multispicular core of more-or-less plumose tracts of choanosomal styles; in periphery these tracts form radial bundles and composed predominantly of longer spicules whereas towards core of skeleton coring spicules generally smaller and contained mainly within fibres; transverse connecting fibres uni-, bi- or aspicular; echinating
megascleres not definitely present, although choanosomal principal styles protrude through fibres at oblique angles ("quasi-echinating"); fibre anastomoses form circular, polygonal or triangular meshes, 90-320 \( \mu \text{m} \) diameter in axis; mesohyl matrix heavy but only lightly pigmented, with ovoid choanocyte chambers (90-120 \( \mu \text{m} \) diameter), and numerous subectosomal auxiliary styles dispersed throughout.

*Megascleres.* Choanosomal principal styles, anisostyles or anisoxeas (asymmetrical), thin, slightly curved at centre, occasionally straight, entirely smooth, bases rounded or slightly tapering, sometimes subtylote or telescoped, with has-
tate or telescoped points, rarely completely modified to quasidiactinal forms (symmetrical ends). Length 176-(264.7)-325μm, width 8-(10.8)-13μm.

Subectosomal auxiliary styles, anisostyles or anisoxeas with similar geometry to principal spicules but generally longer, more slender, straight or occasionally slightly curved or sinuous, with smooth rounded bases, sometimes
telescoped, fusiform or telescoped points. Length 243-(315.5)-365μm, width 4-(5.3)-8μm.

*Micrascles.* Absent.

**REMARKS.** This species is restricted to the type material following re-examination of a number of other specimens assigned here (Hallmann, 1912) which were misidentifications. Hallmann's (1912: 270) concept and illustrations are rejected here. It is presumed that he based his descriptions on several older AM specimens from Port Phillip, allegedly donated to the Museum by Carter but their spiculation and skeletal structures are quite different from the types (see *E. subhisipida*).

*Echinochlastra chalinoides* has a markedly compressed axial skeleton composed of heavy fibres and close-meshed spicule tracts together forming a dendro-recticate skeleton; the skeleton becomes very wide-meshed near the surface, composed of poorly developed fibres and spicule tracts become more plumose; and coring/excating spicules are predominantly anisostyles. Dendy (1896) suggested that it was a synonym of *E. subhisipida* given their similarities in having a *Haliclona*-like branching growth form, distribution of oscules on lateral margins, soft compressible texture, and very heavy spongin fibres producing a compressed axial skeleton. However, there are major differences between these species in spicule geometries and skeletal architectures showing that they are not closely related.

*Echinochlastra confragosa* (Hallmann, 1912)  
(Figs 233-234)

*Ophitaspongia confragosa* Hallmann, 1912: 255-257, pl.35, fig.2, text-fig.53.

*Axociella confragosa*; de Laubenfels, 1936a: 113.


**MATERIAL. HOLOTYPE:** AMZ992 (dry): Shoalhaven Bight, NSW, 34°49'S, 151°04'E, 30-90m depth, 1.vii.1911, coll. FLV 'Endeavour' (trawl).

**HABITAT DISTRIBUTION.** Epizootic on Bryozoa; 30-90m depth; S. coast (NSW) (Fig. 233F).

**DESCRIPTION.** Shape. Irregularly digitate, lamellate branches, up to 50mm high, 5mm thick, arising from semi-encrusting base; branches vary from cylindrical to flattened lamellate, bifurcating and anastomosing, forming loose reticulate mass, with shaggy lobate surface projections on points of branches.

*Colour.* Grey-brown in dry state.

*Oscules.* Not seen.

*Texture and surface characteristics.* Firm, compressible, brittle, fibrous; surface porous, pitted, slightly arenaceous.

**Ectosome and subectosome.** Membranous ectosome, microscopically hispid, with principal subtylosyles erect on peripheral fibres, singly or in bundles of up to 3 spicules, protruding through surface for most of their length and forming a sparse, vestigial, radial extra-axial skeleton; subectosomal auxiliary styles form tangential and paratangential tracts on surface; thickness of ectosomal skeleton ranges from tangential (three spicules abreast) to paratangential (tracts of up to 20 spicules at obtuse angles to surface, forming low microconules).

**Choanosome.** Irregularly rhenieroid reticate skeleton, more-or-less homogenous throughout; spongion fibres thin, relatively light, 18-48μm diameter, without any obvious differentiation between primary or secondary components; fibres cored by uni- or paucispicular tracts of choanosomal principal styles, occasionally aspicular, echinated by choanosomal styles sparsely and irregularly dispersed over fibres; fibre meshes predominantly rectangular (=rhenieroid), less often oval or triangular (=isodietyal), 112-345μm diameter, slightly more cavernous at core and more compacted in peripheral regions of skeleton; mesohyl matrix heavy but only lightly pigmented, oval choanoeyte chambers 52110μm diameter; numerous microscles, subectosomal auxiliary styles, and also few choanosomal styles scattered between fibres.

*Megascleres.* Choanosomal principal subtylosyles (coring and excinating fibres) short, thick, straight, with smooth, slightly constricted subtylosyle bases, almost histate points, slightly rounded, telescoped or pointed. Length 142-(164.8)-197μm, width 5-(9.6)-12μm.

Subectosomal auxiliary styles long, thin or thick, straight, slightly curved or sinuous, with smooth, slightly subtylosolar or rounded bases, fusiform points, sometimes slightly telescoped. Length 136-(214.4)-291μm, width 3.5-(5.1)-6μm.

*Microscles.* Palmate isochelae abundant, small, poorly silicified, lateral alae completely fused to shaft, front alae detached from lateral alae for most of length, both alae sculptured with marginal ridges; shaft without any curvature. Length 8-(10.6)-14μm.

*Toxas oxhorn*, small, thick, with slight to moderate, evenly rounded central curvature, straight arms, slightly reflected points. Length 32-(58.2)-95μm, width 1-(2.2)-3.5μm.

REMARKS. Echinoclathria confragosa is only known only from a single specimen which differs notably from all other species in several important respects: encrusting lamellate-digitate growth form; more-or-less homogeneous renieroid (Haliclona-like) skeletal architecture (see also E. notialis sp. nov.); retaining only the vestiges of a radial extra-axial skeleton on the extreme outer edge of the ectosomal region; having a relatively thick tangential and paratangential ectosomal skeleton covering most of the surface; and distinctive oxhorn toxa morphology.
Echinocladthia digitata (Lendenfeld, 1888)  
(Figs 235-236, Plate 10D)

Thalassodendron digitata Lendenfeld, 1888: 223.  
Echinochalinina digitata; Thiele, 1903a: 962; Hooper &  

MATERIAL. HOLOTYPE: Missing from AM and  
BMNH collections. NEOTYPE: QMG304763: NW of  
Snake Reef, Howick Gp., Great Barrier Reef, Qld,  
14°28.6'S, 145°04.6'E, 21 m depth, 03. ix. 1994, coll.  
J.A. Kennedy (trawl).

HABITAT DISTRIBUTION. Soft substrata inter-reef  
region; 21 m depth; Torres Strait and Howick Reefs  
(FNQ) (Fig. 235E).

DESCRIPTION. Shape. Bushy, clathrateous mass  
of erect, bifurcate digits 54 mm high, 76 mm wide;  
digits short, stout, claviform, subcylindrical,  
bulbous, expanding and slightly flattened towards  
apical extremities, up to 32 mm long, 6 mm wide,  
bifurcating several times, occasionally anasto- 
mosing, with 1 or more blind branches; mass  
growing from a semi-encrusting common base.  
Colour. Bright red alive (Munsell 5R 4/10), grey- 
brown in ethanol.

Oscules. Small, up to 3 mm diameter, on apex of  
each digit.

Texture and surface characteristics. Firm, com- 
pressible, flexible, fibrous; surface bulbous,  
prominently microconulose, hispid.

Ectosome and subectosome. Membranous,  
granular collagenous heavier than in  
choanosomal mesohyl, with protruding primary  
fibres from ascending choanosomal skeleton and  
plumose bundles of principal subtylostyles erect  
on surface producing hispid ectosome; sparse  
tracts of thinner auxiliary styles tangential to  
surface.

Choanosome. Skeletal architecture more-or-less  
renieroid reticulate, with heavy spongion fibres  
producing wide-meshed rectangular reticulation;  
primary ascending fibres long, multispecific  
60-90 µm diameter, interconnected by numerous,  
shorter, secondary fibres, 30-55 µm diameter  
cored by 1 or few principal spicules; fibres  
sparely echinated by principal subtylostyles, iden- 
tical to but marginally thinner than those coring  
fibres, confined mostly to distal margins  
(periphery) of fibres; fibre anastomoses produce  
cavernous meshes, 80-320 µm diameter; mesohyl  
matrix sparse in choanosome, lightly pigmented,  
granular, containing numerous whispy auxiliary  
styles and fewer microscleres; choanocyte cha- 
mers elongate 20-30 µm diameter.

Megascleres. Principal subtylostyles coring and  
sparingly echinating fibres short, moderately  
shorter, straight or slightly curved at centre, entirely  
smooth, with slightly subtylote bases, blunted  
or slightly telescoped points. Length 186- 
(214.4)-238 µm, width 4-(4.6)-7 µm.

Auxiliary styles very similar in geometry to  
principal spicules except for being much thinner,  
whisper, and lacking subtylote bases; auxiliary  
styles straight or sinuous, rounded bases, pointed  
or telescoped points. Length 182-(204.2)- 
246 µm, width 1.5 -(1.9)-2.5 µm.

Microscleres. Palmate isochelae small,  
unmodified, long lateral alae approximately same  
length as front ala, entirely fused to shaft, front  
ala nearly completely detached. Length 10- 
(11.7)-13 µm.

REMARKS. Lendenfeld’s (1888) original  
material is not extant in the collections of either  
the AM or BMNH, but we know from his brief  
description that the species has a growth form  
reminiscent of Cioclypta (Halichondrida) and  
spiculation of Echinocladthia or Echinochalinina.  
The specimen described here from the Howick  
Islands group, close to the type locality of Torres  
Strait, agrees completely with Lendenfeld’s  
(1888) brief description and is nominated  
neotype of this species.

Echinocladthia digitata is similar to E. berguis- 
tae in its digitate growth form and having a  
cavernous, predominantly renieroid, reticulate  
skeletal architecture. It differs from E. berguis- 
tae in geometry and dimensions of all its spicules,  
lacking toxa microscleres, and having relatively  
homogeneous megascleres throughout the  
skeleton, coring and echinating tracts and  
scattered interstitially. In possessing relatively  
homogeneous megascleres E. digitata also  
resembles E. levi, although the latter has com- 
pletely different skeletal architecture, growth  
form and toxsa microscleres.

Echinocladthia egena Wiedenmayer, 1989  
(Figs 237-238, Plate 10E)

Echinocladthia egena Wiedenmayer, 1989: 64-66 pl. 6,  
fig 8, pl.24, fig.6, pl.25, figs 1-2, text-fig.44; Hooper  

MATERIAL. HOLOTYPE: NMVF51978: Winter  
Cove, E. side of Deal I., Kent Group, Bass Strait, Tas,  
39°29'S, 147°20'E, 26.iii.1981, 3-6 m depth. coll. F.  
Wiedenmayer et al. (SCUBA).OTHER MATERIAL:  
TAS: QMG300669 (NCIQ66C-3721-L) (fragment  
NTMZ3817).

HABITAT DISTRIBUTION. On granite boulders and rock reef in sand substrate; 3-6m depth; Kent Is, E. St Patrick’s Head (Tas) (Fig. 237D).

DESCRIPTION. Shape. Erect, digitate, ranging from young forms thickly encrusting basal mat, up to 5mm thick, with irregularly bifurcate and
occasionally anastomosing lobo-digitate branches, up to 38mm long, 5mm diameter, to arborescent branching, up to 220mm long, 115mm breadth, cylindrical branches up to 17mm diameter, with bulbous terminal and subterminal processes along branch length, and with short stalk, up to 50mm long, 21mm diameter, and enlarged basal attachment.

**Colour.** Dull orange-brown alive (Munsell 5 YR7-8/12), beige-brown in ethanol.

**Oscules.** Large oscules, up to 2mm diameter, mainly on lateral sides of branches, particularly on edges of lobate bulbs along branches, less common on basal mat; oscules usually raised on small conical projections with slight membranous lip.

**Texture and surface characteristics.** Compressible rubbery texture, difficult to tear; surface contorted, macroscopically even but microscopically reticulate.
Ectosome and subectosome. Fibrous, micropapilllose ectosome, with well developed surface fibres lying paratangential to surface, and with sparse subectosomal auxiliary megascleres lying on or just below surface, orientated tangential or paratangential to it; peripheral fibres swollen, bud-like, containing sparse core of plumose brushes of choanosomal principal styles, which rarely protrude beyond surface; subectosomal auxiliary megascleres not found directly in peripheral skeleton but some way below it.

Choanosome. Skeletal architecture regular, dendro- reticulate, slightly renieroid, with heavy spongine fibres divided into primary ascending
Peripheral skeleton become more compacted and oval (70-90μm diameter); fibres commonly stratified near periphery, with granular spongin; subectosomal auxiliary megascleres only sparsely dispersed within mesohyl; peripheral fibres also contain abundant microalgae.

**Megascleres.**

Choanosomal principal subtylostyles and styles (coring and quasi-echinating fibres) small, thin, straight, with smooth, tapering, slightly subtylote or rounded bases, fusiform or slightly telescoped points. Length 38-(47.7)-53μm, width 2.3-(2.5)-3.1μm.

Subectosomal auxiliary megascleres thin, straight, or rarely sinuous, strongylole styles (asymmetric, anisostyles), with evenly rounded points and slightly thicker bases. Length 88-(158.2)-178μm, width 1-(1.5)-2.4μm.

**Microscleres.** Absent.

**Larvae.** Viviparous parenchymella larvae, 150-195μm diameter, in various stages of development throughout mesohyl.

**REMARKS.** This species is placed with Burton's (1959a) group of flabellate, massive, ramose *Echinoclastra* sponges lacking microscleres (*axinelloides, chalinoides, inornata, leporina, nodosa*; none of which are synonyms contrary to Burton's (1959a: 247) opinion). It differs from these species in having much smaller, almost vestigial choanosomal styles and lacking true echinating spicules. It is close to *E. confragosa* in growth form, and *E. nodosa* in skeletal architecture and fibre characteristics, but differs from these species in spicule geometry and compression of peripheral spongin fibres. It should also be compared with *E.*
leporina which has heavily spiculose fibres and
ectosomal skeleton, whereas spiculation of E.
egena is very much reduced, virtually vestigial.

Echinoclathria inornata (Hallmann, 1912)
(Figs 239-240)

Ophitespora inornata Hallmann, 1912: 265-268,
pl.36, fig.2, text-fig.37; de Laubenfels, 1954: 163;
Coombe et al., 1987: 381; Chong et al., 1987: 85.

MATERIAL. HOLOTYPE: AM "ef. E826" (in same
specimen jar as O. tenuis); 24km S.of St. Francis Is,
Nuyts Archipelago, SA, 32°31'S, 133°18'E, 60m
depth, coll. FIV 'Endeavour' (dredge).OTHER
MATERIAL: WA - WAM622-81(1) (fragment
NTMZ1714), S AUST - SAMTS4055 (fragment
NTMZ1656), AME938, AME768.

HABITAT DISTRIBUTION, Rock reef; 31-60m
depth; Rottnest I. (WA); Nuyts Archipelago and Port
Noarlunga (SA) (Fig. 239E).

DESCRIPTION. Shape. Erect arborescent
digitate or club-shaped sponges, 55-270mm high,
25-65mm maximum width, with irregular
cylindrical or lobate branches, expanded
and bulbous at their ends, 7-25mm
diameter; long cylindrical basal stalk, 12-35mm
long, up to 15mm diameter, enlarged basal attach-
ment.

Colour. Live colouration unknown, pale brown or
yellowish grey in ethanol.

Oscules. Small, 1-2mm diameter, only seen on
upper portions of digits.

Texture and surface characteristics. Firm, com-
pressible, difficult to tear; surface membranous
in places, porous in poorly preserved material,
uneven, lumpy towards extremities of branches.
Ectosome and subectosome. Surface
membranous, microscopically hispid, with
longer choanosomal principal styles protruding
through surface, individually or in multispecific
brushes, arising from ends of ascending primary
spicule tracts within choanosome; subectosomal
auxiliary subtylostyles form tangential or
paratangential bundles lying just below ecto-
some, surrounding bases of protruding prin-
cipal spicules; choanosomal fibres immediately
subectosomal; mesohyl matrix in peripheral
skeleton heavy, granular.

Choanosome. Skeleton irregularly renieroid
reticulate, with slightly compressed axis and
plumo-reticulate extra-axial regions; spong
fibres in axial region relatively homogeneous,
small, 60-90μm diameter, bulbous, not clearly
divided into primary or secondary elements; axial
fibres contain only 1-2 smaller principal styles
per tract, producing nearly regular renieroid
skeleton, whereas fibres running longitudinally
through branches (seen in cross-section in skele-
tal preparations) are multispecific, partially
obscuring renieroid appearance of axial skeleton;
axial fibre anastomoses form tight oval meshes,
40-90μm diameter, and echinating acanthostyles
sparsely dispersed; extra-axial skeleton with
more poorly developed spongion fibres, clearly
divided into primary and secondary elements;
primary fibres ascending, 30-50μm diameter,
fibrurcating and anastomosing, cored by 1-3
smaller principal styles and very heavily
echinated by the same spicules, particularly near
surface; secondary connecting, transverse fibres
20-40μm diameter, 1-2 spicules per tract, occur-
cionally aspicular, also heavily echinated;
extra-axial fibre meshes not bulbous as in axial
region, forming large oval cavernous meshes up
to 250μm diameter; ascending primary fibres
also contain tracts of long, sinuous subectosomal
auxiliary subtylostyles secondarily incorporated
into fibres; spongion fibres closer to surface much
thinner than axial fibres but very heavily
echinated, eventually producing plumose
bundles of larger principal styles protruding
through surface; mesohyl matrix heavy, granular,
with few extra-fibre spicules; choanoocytes large,
oval, 55-90μm diameter.

Megascleres. Choanosomal principal styles
(coring and echinating fibres) long or short, rela-
tively thick, slightly curved towards basal end,
rounded or faintly subtylostyles bases, predominant-
ly smooth, rarely slightly micropinned bases,
lissiform points. Length 88-(124.2)-199μm,
width 3-(6.8)-10μm.

Subectosomal auxiliary subtylostyles long,
slender, straight, slightly curved or sinuous,
prominently subtylostyles, smooth or micropinned
bases, hastate points. Length 170-(205.6)-
235μm, width 0.5-(1.9)-3μm.

Microscleres. Raphidiiform toxas uncommon,
found in only 2 of 5 specimens (presumably as-
associated with larvae; impossible to retain intact
on SEM stubs); very long, hair-like, with slight
angular central curvature, straight arms, straight
points. Length 205-(225.4)-238μm, width up to
0.5μm.

Associations. Three of the five known specimens
of this species are covered with a zoanthid, al-
legedly a cornularid (Hallmann, 1912).

REMARKS. Hallmann (1912) erected this
species mainly by comparison with E. leporina
(as O. tenuis), remarking on their close
similarities. Hooper & Wiedenmayer (1994) used Hallmann's observations to suggest their synonymy, whereas the types and other material indicate that the Sw and SE populations are consistently different and are distinct species.

The skeleton of *E. inornata* is dominated by echinating principal spicules, particularly on peripheral fibres, more so than any other species. These echinating spicules tend to obscure the characteristic unispecular ascending and
transverse tracts, whereas in *E. leporina* tracts are consistently pauci- or multipspicular and echinat- ing spicules are sparse. *Echinoclathria inornata* also has a thick palmate-digitate or lobate- digitate growth form (whereas *E. leporina* is thin- ly flabellate), principal megascleres are generally larger, and some specimens of *E. inornata* have thin raphidiform toxas (although these are not
consistently present and might be associated with larvae).

**Echinolathria leporina** (Lamarck, 1814) (Figs 241-242)

*Spongia leporina* Lamarck, 1814: 444, 373.

**Echinolathria leporina**; Topsent, 1932: 101, pl.6, fig.1; de Laubenfels, 1936a: 119; de Laubenfels, 1954: 163; Wiedenmayer, 1989: 61-63, pl.6, fig.1, pl.24, figs 4-5, text-fig.42; Carpenter, 1986: 24; Hooper & Wiedenmayer, 1994: 279.

**Ophitaspongia leporina**; Burton, 1934a: 558, 562, 599.

**Echinolathria tenuis** Carter, 1885f: 355.

**Ophitaspongia tenuis**; Dendy, 1896: 37; Hallmann, 1912: 261-265, pl.35, fig.1, text-fig.56; Topsent, 1932: 101, pl.6, fig.1; Burton, 1934a: 558, 562, 599.

Not Clathria tenuis Hinshelw, 1911: 377-379, text-fig.49; Parish, Jakobsen, Coonbe & Bacic, 1991: 56-64.

**Phakellia papyracea** Carter, 1886g: 379.

**Antherochalina tenuspina** Lendenfeld, 1887b: 789.

Hallmann, 1912: 265; Burton, 1934a: 558.

**MATERIAL**.


**HABITAT DISTRIBUTION**: 5-42m depth in shallow coastal waters on rock reef substrate; known only from Australia: Coogee (NSW); Port Phillip, Westernport Bay (Vic); N. coast (Tas); Cape Martin (SA) (Fig. 241D).

**DESCRIPTION**.

**Shape**. Persistently very thin, flabellate digits, up to 330mm high, 190mm wide, 2-8mm thick, ranging from single elongate planar fans with evenly rounded margins, to bifurcate palmate digits growing in more than 1 plane, with uneven margins; usually with long or short cylindrical basal stalk, up to 65mm long, 18mm diameter.

**Colour**. Pale red or red-orange alive (Munsell 2.5R 5/8-5/10), light brown in ethanol.

**Oscules**. Relatively small, up to 2.5mm diameter, dispersed over margins of digits, without associated subectosomal drainage canals.

**Texture and surface characteristics**. Firm, flexible, moderately difficult to tear; surface even, without pronounced sculpturing; some with distinct radial growth lines on lamellae.

**Ectosome and subectosome**. Microscopically hispid, with larger sizes of principal style/subtylose style protruding through surface for up to 100μm, singly or in brushes, forming a vestigial plumose or radial extra-axial skeleton in peripheral region, and with a distinct tangential layer of subectosomal auxiliary subtyloses, in pauci- or multisporule tracts, underlying erect principal spicule brushes; mesohyl matrix moderately heavy, particularly near outer margin of peripheral skeleton.

**Choanosome**. Skeletal architecture with 3 components differentiated: (1) irregularly isodictyal, slightly compressed axis; (2) more open-reticulate renieroid or subrenieroid extra-axial region; and (vestigial) plumose or radial skeleton in the peripheral region; axial skeleton with single, thickened central core of heavy fibres, vaguely separated into primary ascending pauci- or multisporule fibres, 28-65μm diameter, and secondary, mostly transverse uni- or paucispicular fibres, 28-36μm diameter; primary fibres plumose, arborescent, producing radial tracts; secondary fibres regularly renieroid; fibres cored and sparsely echinated by smaller choanosomal principal styles/subtyloses in choanosomal skeleton (larger in peripheral skeleton); echinating principal spicules located predominantly on primary fibres; fibre anastomoses in axis form predominantly triangular meshes (=isodictyal), less often rectangular or oval meshes, 75-180μm diameter, obviously more compressed in axis than at periphery; peripheral fibres form more regular, rectangular meshes (=renieroid); primary spicule tracts mostly confined to within fibres in axial skeleton, becoming increasingly plumose, protruding through fibres, in peripheral skeleton; mesohyl matrix heavy but only lightly pigmented; choanoocyte chambers ovoid, 43-112μm diameter, with sparsely dispersed subectosomal auxiliary megascleres particularly in peripheral skeleton.

**Megascleres**. Choanosomal principal styles and subtyloses long or short (larger in peripheral region than in axis), thick, straight or slightly curved, with smooth, evenly rounded, or slightly tapering subtylose bases, sometimes quasi-oxeote, rarely microspined bases, usually with fusiform points. Length 62-(185.3)-305μm, width 4-(9.6)-14μm.
Subectosomal auxiliary subtylostyles long, thin, straight, slightly curved, or frequently sinuous, with predominantly smooth, occasionally microspined, subtylote bases, hastate points. Length 148-(265.8)-321μm, width 1.5-(3.1)-4.2μm.

Microscleres. Absent.

REMARKS. This species is better known under the junior names *Echinoclathria* or *Ophlitaspongia tenuis*. In growth form it is remarkably close to *A. (Isopenectya) chartacea*. This similarity, also noted by Hallmann (1912), is emphasised by their respective renieroid and isodictyal skeletal architecture, compression of the axial skeleton and fibre characteristics, whereas other characters indicate that similarities may be convergent and functionally related to flabellate growth form. Major features which differentiate the two species are the possession of 3 distinct skeletal structures (renieroid, plumose-isodictyal and peripheral skeletons) in *A. (I.) chartacea*, the

Presence of acanthose choanosomal styles forming the renieroid skeleton, and much larger smooth choanosomal styles protruding through the ectosome. Choanosomal styles in *E. leporina* are homogeneous, entirely smooth shafts, and the renieroid/isodictyal skeleton is cored and echinated by the same smooth principal spicules, with differentiated primary and secondary fibre
structures, there is less pronounced axial compression, larger, entirely smooth principal spicules are embedded only in the peripheral skeleton, barely extending into the choanosome, and there is no clear differentiation between renieroid/ isodictyal and plumose skeletons as in Antho. The two species may be confused and hence care has been taken in checking all available voucher specimens to ascertain conspecificity.

Echinoclathria leporina is probably widespread throughout temperate SE Australia although some published records (in the Zoological Record) are not corroborated by voucher samples and are not included in the present synonymy.

**Echinoclathria levii** sp. nov. (Figs 243-244, Plate 10F)

**MATERIAL.** _HOLOTYPE:_ QMG300675 (NCIQ66C-3764-I) (fragment NTMZ3832); Trap Reef, Bicheno, Tas., 41°51.7'S, 148°18.6'E, 30m depth, 26.ii.1990, coll. NCI (SCUBA).

**HABITAT DISTRIBUTION.** Large boulder reef; 30m depth; E. coast (Tas) (Fig. 243F).

**DESCRIPTION.** Shape. Erect, thickly flabellate fan in several planes, 155mm long, 155mm wide, each lamella 7-12mm thick, up to 80mm wide, margins irregularly digitate or palmate-digitate, with digits up to 30mm long, 5mm diameter; irregular digits and small lamellae ('buds') also arising from lateral sides of fan; stalk long, thickly cylindrical, 45mm long, 9mm diameter, with expanded basal attachment.

**Colour.** Dark red-orange alive (Munsell 5R 5/10), brown in ethanol.

**Oscules.** Large, up to 2.5mm diameter, scattered over 1 side of fan, without any obvious membranous lip, collapsing in air.

**Texture and surface characteristics.** Stalk stiff, lamella firm, flexible, slightly compressible; surface membranous, optically hispid, relatively even, slightly lumpy but without any conules or other ornamentation.

**Ectosome and subectosome.** Surface microscopically hispid, with longer principal styles protruding through surface in thick, bushy, erect brushes arising from ascending choanosomal fibres in peripheral skeleton; subectosomal auxiliary subtylostyles in sparse tangential brushes on surface; mesohyl matrix heavy but only lightly pigmented in peripheral skeleton.

**Choanosome.** Skeleton with 2 components: irregularly renieroid renieroid reticulate and plumo-tericulate, without any marked axial compression but clearly differentiated axial and extra-axial regions; (1) axial skeleton more-or-less renieroid, with heavy spongin fibres divided into primary and secondary elements; primary fibres ascending, 70-90μm diameter, cored by pasci- or multispicular tracts of generally smaller choanosomal principal styles; secondary fibres transverse, short, thinner 30-40μm diameter, interconnecting primary fibres, cored by unicellular tracts of smaller principal styles; fibre anastomoses in axial region produce cavernous oval or elongate meshes, 150-250μm diameter, fibre nodes heavy, slightly bulbous, containing multispicular tract ascending through longitudinal plane of lamellae; axial fibres sparsely echinated by smaller principal styles, mainly at fibre nodes; (2) extra-axial skeleton distinctly plumo-tericulate, with distinctly different primary and secondary spongin fibre systems; primary ascending fibres very thick, up to 130μm diameter, cored by multispicular tracts of smaller and larger choanosomal principal subtylostyles ascending to surface; spicule tracts become heavier, more plumose towards periphery; size of principal subtylostyles coring fibres generally increase towards surface; secondary, connecting fibres in extra-axial skeleton small, less than 30μm diameter, uni- or aspicular; echinating spicules in extra-axial region mostly obscured by ascending plumose spicule tracts; mesohyl matrix heavy, with numerous auxiliary megascleres (sometimes also incorporated into fibres) and numerous toxas scattered throughout; choanocyte chambers small, oval, 40-60μm diameter.

**Megascleres.** Choanosomal principal styles (coring and echinating fibres) long or short, moderately slender, slightly curved at centre, with smooth, rounded or slightly subtylolette bases, fusiform points. Length 172-(244.4)-341μm, width 5-(6.1)-7μm.

Subectosomal auxiliary styles relatively short, slender, slightly curved at centre, with slightly subtylolette, smooth bases, fusiform or hastate-rounded points. Length 154-(187.8)-205μm, width 2-(3.1)-4.5μm.

**Microscleres.** Palmate isochelae small, with lateral alae longer than front ala, completely fused to shaft, front ala wide, curved, nearly completely detached from lateral alae; shaft straight. Length 13-(14.8)-16μm.

Toxas oxhorn (although smaller wing-shaped forms also present), thick, with prominent, wide, even central curvature, slightly reflexed arms,

slightly reflexed points. Length 23-(91)-135\,\mu m, width 1-(1.4)-3\,\mu m.

**ETYMOLOGY.** For Professor Claude Lévi, MNHN Paris, for his contributions to Indo-Pacific sponges.
REMARKS. This species is an unusual Echinocladthria having well developed extra-axial plumo-reticulate skeleton in which the thick plumose spicule tracts completely dominate the thin unispiral connecting fibres, partially obscuring the renieroid skeleton (seen only clearly at the core of the skeleton). Although the thickness of the plumo-reticulate and renieroid portions of the skeleton varies from place to place within the sponge (the former dominant towards the edge of lamellae or surface digits (growing edges) and the latter predominant towards the basal stalk region), it is a prominent feature of skeletal structure. This species also differs from related flabellate species such as E. riddiei sp. nov. and E. leporina in having distinctive oxhorn toxas (cf. no toxas), megasclere dimensions (cf. substantially smaller, thinner megascleres), and a thickly flabellate, palmate-digitate growth form (cf. thinner flabellate lamellae).

**Echinocladthria nodosa** Carter, 1885
(Figs 245-246)


_Ophlitaspongia nodosa_; Dent, 1889: 37.

*Litaspongia nodosa*; de Laubenfels, 1954: 162.

**MATERIAL.** HOLOTYPE: BMNH1886:12.15.96 (fragment AMG2770): Port Phillip, Vic, 38°09'S, 144°52'E, 8m depth, coll. unknown (dredge). OTHER MATERIAL: VIC: NMVRN264, NMVRN628.

**HABITAT DISTRIBUTION.** Sand and shell grit, 8-38m depth; Port Phillip (Vic) (Fig. 245E).

**DESCRIPTION.** Shape. Bulbous-digicate, up to 55mm long, 30mm maximum width, 35mm breadth, small cylindrical basal stalk 5-15mm long, 10mm diameter; with bifurcate and occasionally anastomosing, irregularly cylindrical, slightly swollen branches, up to 22mm long, 8mm diameter.

**Colour.** Bright red to crimson alive, dark brown in ethanol.

**Oscules.** Numerous small oscules, up to 2mm diameter, scattered between surface conules.

**Texture and surface characteristics.** Soft, compressible, difficult to tear; surface nodulose, granular.

**Ectosome and subectosome.** Membranous, with protruding spongins fibres from ascending peripheral skeleton, and points of principal styles protruding beyond surface in sparse plumose brushes or individually, not forming continuous palisade; subectosomal auxiliary styles form sparse paratangential, tangential or occasionally erect layers below protruding skeleton of principal spicules.

**Choanosome.** Skeleton dendro-reticulate, more-or-less renieroid and homogenous throughout, without any axial compression and only slight differentiation between peripheral skeleton and core (the former with plumose primary tracts becoming increasingly dense towards periphery, the latter evenly renieroid with relatively sparse spicule skeleton); heavy spongins fibres dominate skeleton, clearly differentiated into primary and secondary components; primary fibres, 35-65μm diameter, ascending, multispicular with 3-8 spicules per fibre, spicules confined to within fibres at core but become plumose in subectosomal and peripheral regions; secondary fibres un- or paucispicular, 15-40μm diameter, predominantly transverse; fibre nodes usually bulbous, up to 80μm diameter; fibres cored by choanosomal principal styles and sparsely echinated by same spicules; echinating spicules confined mainly to core of skeleton, less common in periphery; fibre meshes triangular, rectangular or rhomboidal, 150-270μm diameter, slightly more cavernous in subectosomal region than at core; mesohyl matrix light, unpigmented, with few interstitial spicules; choanosome chambers small, oval, 15-25μm diameter.

**Megascleres.** Choanosomal principal styles short, thick, straight or very slightly curved at centre, smooth, evenly rounded bases, occasionally slightly subtylote, fusiform points; sometimes modified to quasi-oxote spicules. Length 109-(128.6)-164μm, width 6-(8.4)-13μm.

Subectosomal auxiliary styles long, slender, straight or very slightly curved at centre, smooth rounded bases or very slightly subtylote, long tapering fusiform points. Length 116-(161.1)-242μm, width 2-(3.6)-6μm.

**Microscleres.** Absent.

REMARKS. Similar to _E. thielei_ and _E. notialis_ sp. nov. this species lacks noticeable size differences between principal styles coring choanosomal fibres and those protruding through ectosome. It has bulbous branching growth form; bulbous fibre nodes in the skeleton are similar to _E. levii_ sp. nov. It is also reminiscent of _E. axinelloides_ in its spicule skeleton, which becomes increasingly dense and plumose towards the surface, but this resemblance is superficial, whereas characters such as growth form, bulbous fibres,
absence of microscleres, and the geometry and size of both categories of megascleres together differentiate it within the genus.

**Echinoclathria notialis** sp. nov.  
(Figs 247-248, Plate 11A)

MATERIAL. HOLOTYPE: QMG300614 (NCIQ66C-2243-F) (fragment NTMZ3541); American River, Kangaroo I., SA, 35°46.9'S, 137°46.5'E, 6m depth, 31.1.1989, coll. NCI (SCUBA).

HABITAT DISTRIBUTION. Rock reef, sand, mussel beds; 6m depth; Kangaroo I. (SA) (Fig. 247D).

DESCRIPTION. Shape. Erect, massive, club-shaped, bulbous-digitate, 75mm high, 85mm diameter; digits subcylindrical, bulbous, up to 45mm long, 38mm diameter, rounded margins,
fused to adjacent digits; attached directly to substrate, no stalk or basal 'holdfast'.

**Colour.** Pale red-brown alive (Munsell 5R 5/6), pale brown in ethanol.

**Oscules.** Large, 3-6mm diameter, on apex or subapex of digits, raised above surface with prominent membranous lip.

**Texture and surface characteristics.** Firm, compressible, relatively easily torn; surface with prominent surface conules when alive (mostly white and offset from darker ectosome), each conule bearing fine trace of radiating subectosomal auxiliary spicules which collapse upon exposure to air and preservation; in air surface membrane collapses, surface becomes highly porous (each pore up to 1mm diameter, scattered evenly over surface), superficially resembling a red-brown Acropora coral.

**Ectosome and subectosome.** Fibrous, with tips of ascending primary fibres protruding a long way through surface, with bundles of choanosomal spicules also protruding slightly from ends of

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primary fibres; moderately heavy tracts of subectosomal auxiliary styles lying tangential, paratangential or erect on surface; auxiliary spicules heaviest between protruding fibres, presumably surrounding surface pores and collapsing upon exposure to air and preservation.

*Choanosome.* Skeleton regularly renieroid reticulate, relatively homogenous skeletal tracts,
without any differentiation between axial and extra-axial regions; spongine fibres moderately well developed, 15-25 μm diameter; fibre meshes cavernous throughout, rectangular, square or occasionally triangular, 125-250 μm diameter; few obvious differences between ascending and transverse fibres; ascending fibres cored by 1 or few choanosomal principal styles, occasionally more near surface of sponge, with tracts becoming multispecific, plumose in ectosomal and protruding fibres; transverse fibres with similar spicule content; all fibres sparsely echinated by smooth principal styles, identical to those inside fibres; echinating spicules predominant at fibre nodes; mesohyl with abundant, mesohyl matrix only lightly pigmented, subectosomal auxiliary styles scattered throughout; choanoocyte chambers small, round or oval, 30-50 μm diameter.

Megascleres. Choanosomal principal styles (coring and echinating fibres) short, slender, straight, rounded smooth bases, fusiform or slightly telescoped points. Length 107-(123.6)-151 μm, width 1.5-(2.7)-4 μm.

Subectosomal auxiliary styles long, slender, straight, rounded smooth bases, fusiform or prominently telescoped points. Length 123-(163.2)-191 μm, width 1.0-(1.9)-2.5 μm.

Microscleres. Absent

ETYMOLOGY. Greek notos, south.

REMARKS. In growth form, texture, colouration, surface sculpturing and conules E. notialis is quite different from all other Echinoclathria, yet its skeletal structure, spicule geometry and distribution of spicules are more difficult to differentiate from other species. Skeletal differences are a matter of degree rather than absolute (which seems to be a feature of the genus), including regularity of the fenestroid skeletal reticulation (no axial compression; cf. E. confragosa), homogeneity of fibre meshes (without any marked differences between ascending and transverse tracts), and virtually unispicular spicule tracts throughout the skeleton (except at the surface where they become multispecific and slightly plumose; cf. E. inornata). The new species differs from all these others in most other respects. In fibre development, density of spicule tracts coring fibres, and possession of both fibres and terminal principal spicule brushes protruding through the surface this species is most similar to E. subhispira, differing substantially in spicule geometry, spicule size, skeletal architecture and field characteristics (see E. subhispira below).

It is not known if the live surface ornament (small white conules covered by a fine trace of radiating auxiliary spicules, overlaying surface pores) is unique to the genus as many named species are only known from preserved material.

Echinoclathria parkeri sp. nov. (Figs 249-250)


HABITAT DISTRIBUTION. Gravel, rock reef; 23-25 m depth; St. Vincent Gulf (SA) (Fig. 249E).

DESCRIPTION. Shape. Massive, subspherical-bushy or erect digitate growth forms, 75-130 mm high, 45-70 mm wide, with short, irregularly cylindrical, bulbous lamellae, up to 50 mm long, 20 mm diameter, expanded at apex, partially fused to adjacent branches, with small, irregularly cylindrical or subconical digits arising from apex of lamellae and basal mass, up to 15 mm long, 9 mm wide, tapering at apex.

Colour. Colour alive dark or bright red, dark brown in ethanol.

Oscules. Numerous small oscules, up to 3 mm diameter, apical or subapical on surface digits.

Texture and surface characteristics. Firm, compressible, not easily torn, harsh due to incorporation of detritus and bivalve shells into lamellae; surface rugose, porous on preserved state, with irregularly dispersed conules.

Ectosome and subectosome. Membranous, fibrous, with terminal fibres protruding slightly and larger principal styles protruding a long way through surface, in plumose brushes or singly; subectosomal auxiliary subtylostyles relatively dense, usually erect, forming plumose or paratangential tracts on surface; mesohyl in euctosomal region heavy, granular, darkly pigmented.

Choanosome. Skeleton irregularly fenestroid reticulate, slightly compressed in axis, slightly plumose at surface; spongine fibres very heavy, irregularly anastomosing, incompletely divided into primary and secondary fibre systems; axial skeleton with very heavy primary fibres, 90-120 μm diameter, running longitudinally (through longitudinal sections of surface digits), ascending to apex of digits, interconnected by heavy but shorter, thinner secondary fibres, 42-95 μm diameter, with slightly bulbous nodes at their junction, 155-195 μm diameter; fibre anas-
tomoses in axial skeleton close-meshed, 60-155 μm diameter; primary axial fibres cored by multispicular tracts of shorter length, secondarily choanosomal principal styles, secondary fibres unispicular, occasionally paucispicular; all fibres echinated by smaller principal styles; extra-axial skeleton more cavernous, fibre meshes 110-360 μm diameter, with more-or-less evenly reticulate fibres and irregularly renieroid reticulate spicule tracts; extra-axial primary fibres heavy, thick, 65-95 μm diameter, clearly ascending and arising perpendicularly from primary fibres in axis, multispicular, with spicule tracts composed of smaller and larger principal styles diverging increasingly towards periphery; secondary connecting fibres heavy, short, mainly transverse, 18-43 μm diameter, unispicular; echinating spicules moderately common in extra-axis; mesohyl matrix heavy, darkly pigmented, containing many scattered subectosomal auxiliary styles mostly near surface; choanocyte chambers oval, 30-50 μm diameter.

*Megascleres.* Choanosomal principal styles (coring and echinating fibres) long or short, relatively thick, slightly curved at centre, with smooth, rounded or slightly subtylote bases, fusiform points. Length 124-(196.6)-312 μm, width 5-(7.1)-10 μm.

Subectosomal auxiliary subtylote styles thin (occasionally raphidiform), straight, slightly curved or sinuous, smooth subtylote bases, fusiform points. Length 123-(238.4)-355 μm, width 1.5-(2.9)-4 μm.

*Microscleres.* Chelae absent.

Toxas accolada, moderately short, thin, with slightly rounded central curvature, straight arms, straight points. Length 63-(129.4)-175 μm, width 0.5-(1.6)-2.5 μm.

**ETYMOLOGY.** For the late Dr Shane Parker of the SA Museum, bryozoologist, sponge enthusiast, ornithologist and gentleman.

**REMARKS.** This species differs from other *Echinocladthria* in toxa geometry, growth form, skeletal structure and spicule dimensions. The massive, more-or-less bulbous-digitate growth form is similar to *E. notialis* sp. nov., although *E. parkeri* is irregularly digitate, lacks the specialised surface sculpturing and porous reticulation peculiar to the prominently bulbous *E. notialis*. Its skeletal architecture is also slightly similar to *E. subhispida*, both having heavy fibres, multispicular primary (ascending) tracts and greatly reduced secondary (transverse) tracts, but those of *E. parkeri* are consistently unispicular and renieroid in construction whereas in *E. subhispida* secondary fibres are aspicular. The two species differ in growth form, fibre thickness, spicule geometry and size. Only one other species (*E. inornata*) has toxas that approach the accolada geometry of *E. parkeri*. In *E. inornata* toxas are much longer, raphidiform, with slight angular central curvature whereas in *E. parkeri* they are short and have rounded central curvature (these two species also differ in most other respects). *Echinocladthria parkeri* has the heaviest spongin fibres of all species, and its skeletal architecture is also dominated by the longitudinal, multispicular fibres running through digits, with the renieroid component of the skeleton not as obvious as in most species of *Echinocladthria*.

**Echinocladthria riddlei** sp. nov. (Figs 251-252, Plate 11B)


**HABITAT DISTRIBUTION.** Rock reef, Ecklonia kelp and Sargassum beds; 15-30 m depth; Furneaux Is, Kent Is, Bass Strait, Bicheno (Tas) (Fig. 251D).

**DESCRIPTION.** Shape. Thiny flabellate, up to 190 mm long, 150 mm maximum width, with long or short, cylindrical basal stalk, 30-75 mm long, up to 18 mm diameter, and expanded basal attachment; fan very thin walled, 1-4 mm thick, flat, growing face-on to current, or convoluted growing in several planes; margins of fan digitate, palmate-digitate or heavily convoluted, never even.

**COLOUR.** Red or orange-brown alive (Munsell 2.5R 5/10-5YR 7/10), pale brown in ethanol.

**Oscules.** Minute, 0.5 mm diameter, scattered over interior face of convoluted fan (holotype), or on osculiferous face of flat fans.

**Texture and surface characteristics.** Soft, slightly compressible, flexible; surface smooth, perfectly even, without any sculpturing, or with only faint ridges on surface near margins of convoluted fan; surface porous in preserved state, collagenous alive.

**Ectosome and subectosome.** Ectosome microscopically hispid with protruding large
choanosomal principal subtylostyles embedded on outer edge of peripheral skeleton, extending up to 300 µm from surface, surrounded by irregular bundles of smaller thin subtylostyles lying tangential, paratangential or rarely forming brushes on ectosome; mesohyl matrix light in subectosomal region, ectosome membraneous.

Chooanosome. Skeletal architecture renieroid reticulate, without any division between axial or peripheral regions except for larger principal
spicules protruding through surface; spongian fibres light, imperfectly divided into primary and secondary elements; primary fibres ascending, 30-40 µm diameter, cored by pauci- or multispiracular tracts of smaller subectosomal auxiliary subtylostyles; secondary fibres connecting primary elements, mainly transverse, 10-20 µm diameter, cored by uni- or paucispiracular tracts of smaller principal spicules; primary and secondary fibre anastomoses form rectangular, irregular, or occasionally triangular meshes, 40-80 µm diameter; fibres echinated by smaller principal styles, mainly at core of skeleton, whereas in peripheral skeleton primary spicule tracts become plumose with principal spicules protruding through fibres at acute angles; mesohyl matrix light, unim[intended]pid光阴; choanocyte chambers small, oval, 15-45 µm diameter.

*Megascleres.* Choanosomal principal subtylostyles long or short (the longer ones confined to the ectsosomal skeleton), thick, slightly curved at centre, rarely straight, with smooth or microspined subtylote bases, entirely smooth shafts, fusiform points. Length 84-(146.4)-348 µm, width 4-(6.8)10 µm.

Subectosomal auxiliary styles long, straight, slender, with prominently subtylote bases, smooth or slightly microspined, points that are fusiform, hastate or slightly telescoped. Length 127-(191.9)-282 µm, width 1-(1.9)-3 µm.

*Microscleres.* Absent.

**ETYMOLOGY.** Named for Dr Martin Riddle for collecting this and many other undescribed sponge species throughout Australasia during the AIMS NCI contract 1984-1991, and providing the author with many opportunities to collect from remote sites throughout the Indo-west Pacific.

**REMARKS.** This species has a very thinly flabellate growth form and renieroid skeletal structure similar to *Antho (I.) chartacea*, with which it was initially confused. However, *A. chartacea* has 3 distinct skeletal components: the smaller, smooth choanosomal principal styles forming the renieroid skeleton in the compressed axis and ascending to the surface in longitudinal tracts, the larger, smooth principal styles embedded in terminal ascending tracts, and the entire spined styles forming extra-axial renieroid skeletal tract; principal styles are longer and thicker, with evenly rounded smooth bases, and tracts extend all the way into the choanosomal skeleton; auxiliary spicules are shorter, the skeletal meshes are more cavernous and the skeletal meshes comprising the renieroid skeleton are relatively homogenous. By comparison, *E. riddlei* sp. nov. has its principal styles with an entirely smooth shaft, bases arc smooth or microspined (and spines are morphologically quite different from those in *A. chartacea*), bases of principal spicules are subtylote, the longer principal styles are embedded only in external surface (i.e., there is no secondary, longitudinal subisodictyal skeleton), skeletal meshes are much closer, fibres are poorly developed and heterogeneous (differentiated into primary and secondary elements), and points of auxiliary spicules do not vary in their terminations as do those of *A. chartacea*. These two species may be confused in the field, and their convergent field characteristics further illustrates the difficulty in objectively defining a generic boundary between *Antho* and *Echinoclathria*.

**Echinoclathria subhisplda** Carter, 1885  
(Figs 253-254)


*Ophhitaia phoma* subhisplda*; Dendy, 1896: 36; Hallmann, 1912: 257-260, pl.36, fig.1, text-figs 54-55.

*Echinoclathria gracilis* Carter, 1885f: 356.


*Echinoclathria viminalis*; in part, Whitelegge, 1901: 87-88.


*Ceraclathina multiformis*; Whitelegge, 1902b: 287.

*Ophhitaia clathroides* in part, Hallmann, 1912: 270-272, text-fig.59.

*Not Axinella clathroides* Carter, 1885f: 358.

**MATERIAL.** LECTOTYPE: BMNH1886.12.15.70; Port Phillip, Vic, 38º09'S, 144º52'E, other details unknown. PARALLECTOTYPE: BMNH1886.12.15-73; same locality. LECTOTYPE of *E. gracilis*: BMNH1886.12.15.45 (fragment AMG2768); Port Phillip Heads, Vic, 38º17'S, 144º39'E, 40m depth, coll. J.B. Wilson (dredge). PARALLECTOTYPE of *E. gracilis*: BMNH1886.12.15.90 (fragment AMG2773); same locality. LECTOTYPE OF *T. viminalis*: AMZ948 (dry: Illawarra region, NSW, 34º32'S, 150º50'E, other details unknown) (label 'Distylinia viminalis (Thalassodendron); type'). PARALLECTOTYPE of *T. viminalis*: BMNH1887.4.24.116 (dry) (fragments AMG3589, ZMB7135); same locality. OTHER MATERIAL: VIC: AMZ922, AMZ797, AMZ1141, AMZ1142, AMZ1144, AMZ1763. S AUSTR-QMG300240 (NCI66C-2194-Z) (fragment NTMZ3554).
FIG. 251. *Echinocladria riddlei* sp.nov. (holotype QMG305005). A, Principal subtylostyles (coring and echinating fibres). B, Subectosomal auxiliary subtylostyles. C, Section through peripheral skeleton. D, Australian distribution. F, Holotype (at right) and unregistered specimen from same locality.

HABITAT DISTRIBUTION. Rock reef, sand, seagrass substrata; 38-440m depth; Port Phillip (Vic); Kangaroo I. (SA); Illawarra (NSW) (Fig. 253H).

DESCRIPTION. Shape. Erect, digitate, up to 220mm high, 90mm maximum width; digits long, whip-like, thinly cylindrical or slightly flattened, up to 120mm long, 12mm maximum thickness, repeatedly bifurcate, rarely anastomosing, with rounded, flattened, or bifid apical margins, occasionally palmate; short basal stalk, 15-65mm long, 18mm maximum diameter and expanded basal attachment.

Colour. Red to dark red alive; brown, dark red-brown to maroon in ethanol.

Oscules. Large oscules, up to 4mm diameter, scattered on lateral margins of branches, slightly raised on small conules, slightly stellate or irregular in shape.

Texture and surface characteristics. Digits compressible, rubbery, flexible; surface optically smooth, even except for microscopic conules

bearing apical oscules on lateral margins of digits.

Ectosome and subectosome. Surface membraneous, microscopically hispid, with points of longer choanosomal principal styles protruding slightly through surface, singly or in paucispicular plumose brushes, arising from terminal fibres, and fibres themselves also protrude through surface; few subectosomal auxiliary styles scattered tangential or paratangential to ectosome.

Choanosome. Skeleton regularly dendro-reticulate, composed of heavy spongin fibres more compressed in axial than extra-axial regions; axis irregularly reticulate, heavy fibres incompletely differentiated into primary and secondary elements, 46-182μm diameter, with markedly bulbous axial fibre nodes; extra-axial skeleton nearly
perfectly regular, dendro- reticulate, with clearly
differentiated primary ascending, radial,
paucispicular fibres branching at outer surface
(30-62µm diameter), interconnected at regular
intervals by thinner transverse, aspicular or rarely
unispicular secondary fibres (18-53µm
diameter); primary fibres both cored and
echinating by choanosomal principal styles,
slightly smaller than those at the surface; echinati-
ing spicules marginally more abundant on
peripheral fibres; fibre anastomoses form oval or
elongate meshes in axis (160-295µm diameter),
square, rectangular or oval meshes towards
periphery (125-290µm diameter); mesohyl
matrix heavy but only lightly pigmented, large
ovoid choanoocyte chambers 75-110µm diameter,
numerous loose choanosomal styles and fewer
subectosomal auxiliary megascleres scattered
between fibres.

Megascleres. Choanosomal principal styles
(coring and echinating fibres) moderately short,
short, slightly curved or straight, with smooth,
tapering, constricted and slightly subtylote bases,
fusiform points. Length 75-(131.3)-168µm,
width 4-(5.4)-7µm.

Subectosomal auxiliary subtylote styles long,
thin, straight or slightly curved at centre, with
smooth subtylote bases, fusiform points. Length
89-(183.1)-235µm, width 1-(2.2)-3µm.

Microscleres. Isochelae absent.

Toxas wing-shaped to oxeote, thin with slightly
rounded or slightly angular central curvature,
straight arms, straight or slightly reflexed points.
Length 30-(72.5)-95µm, width 0.8-(1.2)-1.5µm.

Larvae. Viviparous, spherical or elongate
parenchymella larvae, 180-280x150-210µm,
heavily pigmented, and with toxas and juvenile
styles dispersed.

REMARKS. AMZ948 of Whitelegge (1902b)
and Hallmann (1912), was labelled 'Cerro-
chalina multiforinis var. dura Lendenfeld (no.
332)', but is now labelled (in Hallmann's hand-
writing) 'Distylinia viminalis Lendenfeld, type
of Thalassodendron viminalis'. However, the
holotype of var. dura (with a surviving fragment
AMG3456) is different (cf. Lendenfeld, 1887b).
This variety was also described from Port
Chalmers, New Zealand (the only locality cited in the
original description), containing oxea
megascleres (cf. Whitelegge, 1902b). Thus,
AMZ948 is not a syntype contrary to
Lendenfeld's (1887b) descriptions. The specimen
Thalassodendron viminalis Lendenfeld, no.365
missing from AM (pers. obs.) was rejected as type
by Whitelegge (1902b), who made it the holotype
of his E. intermedia. Consequently, T. viminalis
is a junior synonym of Echinoclathria subhispida
var. viminalis. Further discussion on T. viminalis
and E. intermedia are given below under E. inter-
media. Some material (AMZ1141, 1142, 1144,
1763) described by Hallmann (1912) as E.
chalinoides also belong to E. subhispida, based
on different spiculation and skeletal architecture.

This species differs from most other
Echinoclathria in its renieroid fibre skeleton (i.e.,
rectangular meshes) rather than dendro-reticulate
spicule skeleton, but this is because the
transverse, connecting spicule tracts in secondary
fibres are either absent or vestigial, leaving only
the primary ascending spicule tracts (more-or-
less plumose, branching) dominating the mineral
skeleton. Size differences between principal
styles protruding through the surface and those
coring and echinating choanosomal fibres is only
marginal (the former slightly larger), whereas in
most Echinoclathria this feature is more
pronounced. Reductions of these characters in E.
subhispida are not good reasons to exclude it
from this genus. This species is similar to E.
notialis sp. nov. in microscopic surface features
(having spongin fibres and sparse spicule brushes
protruding through the surface), and in skeleton
dominated by spongin fibres (as opposed to well-
developed spicule tracts). However, E. notialis
has a bulbous-digitate growth form (cf. a digitate,
Haliclona-like habit in E. subhispida), lacks
toxas (cf. wing-shaped toxas), has substantially
smaller spicules, lacks any (or has very little)
compression of the axial skeleton (cf. well-dif-
ferentiated axial and extra-axial fibres), has
virtually no difference in size between principal
spicules coring fibres and those protruding
through the surface (cf. clear localisation of larger
spicules in the peripheral skeleton), and both
ascending and transverse fibres are cored by
greatly reduced, predominantly unispicular tracts
(cf. ascending fibres have well developed, multi-
spicular spicule tracts whereas transverse fibres
are often aspicular in E. subhispida).

OTHER SPECIES OF ECHINOCLATHRIA

Echinoclathria arborea (Tanita, 1968)
Litaspogonia arborea Tanita, 1968: 49-50, pl.1, fig.7,
text-fig.9 [Ariake Sea].
MATERIAL. HOLOTYPE: MMBS, Japan.

Echinoclathria arcifera (Schmidt, 1880)

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**REVISION OF MICROCIIONIDAE**

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Tenacia arcifera Schmidt, 1880: 81, pl.10 [Gulf of Mexico]; Hallmann, 1920: 771.

Ophiolithasia phakellia: Burton, 1959a: 247 [key to species].

Material: Holotype: LMJG. Caribbean.

Echinoclathria atlantica (Sarà, 1978)

Echinoclathria atlantica Sarà, 1978: 76-79, text-figs 49-51 [Cape Domingo, Tierra del Fuego]; Desqueyroux-Faundez & Moyano, 1987: 50 [Tierra del Fuego, Argentina].

Material: Holotype: IZUG124, fragment MNHNDC2750. SW. Atlantic.

Echinoclathria beringensis (Hentschel, 1929)

Phakellia papyracea, in part: Lambe, 1892: 76 [Alaska].

Phakellia beringensis Hentschel, 1929: 975.

Echinoclathria beringensis; de Laubenfels, 1954: 164 [note].

Echinoclathria schmitti de Laubenfels, 1942: 264 [Baffin Bay, Arctic].

Material: Holotype: USNM. Arctic.

Echinoclathria contexta Sarà, 1978


Material: Holotype: IZUG 170, fragment MNHNDC2749. SW. Atlantic.

Echinoclathria dichotoma (Lévi, 1963)

Ophiolithasia dichotoma Lévi, 1963: 59, pl.9G. text-fig.68 [South Africa].

Material: Holotype: MNHNDC615. South Africa.

Echinoclathria digitiformis (Row, 1911)

Ophiolithasia digitiformis Row, 1911: 351-353, pl.37, figs 14-15 [Shab-ul-Shuhuk, Red Sea].

Echinoclathria digitiformis; de Laubenfels, 1936a: 119 [note].


Echinoclathria hjorti Arnesen, 1920

Echinoclathria hjorti Arnesen, 1920: 21-22, pl.2, fig.5, pl.5, fig.3 [off Cape Bojador, Sahara, N. Atlantic].

Arxietella hjorti; de Laubenfels, 1936a: 119 [note].

Ophiolithasia hjorti; Burton, 1959b: 43-44 [Iceland].


Echinoclathria minor Burton, 1959)

Ophiolithasia minor Burton, 1959a: 246, text-fig.27 [Arabian Sea; key to species]; Sim & Kim, 1988: 24, pl.1, figs 1-2 [S. Korea, doubtful conspecificity].

Material: Holotype: BMNH1936.3.4. 669. Arabian Gulf.

Echinoclathria mutans (Sarà, 1978)


Material: Holotype: IZUG124, fragment MNHNDC2750. SW. Atlantic.

Echinoclathria noto (Tanita, 1963)

Ophiolithasia noto Tanita, 1963: 124-125, pl.4, fig.3, text-fig.3 [Sea of Japan]; Tanita, 1964: 17-18, 21, pl.1, fig.4 [Japan]; Tanita, 1965: 48 [Sea of Japan].

Sim & Kim, 1988: 24-25 [Korea]; Sim & Byeon, 1989: 37 [Korea].

Material: Holotype: MMBS. Japan, Korea.

Echinoclathria oxeata (Bergquist & Fromont, 1988)

Ophiolithasia oxeata Bergquist & Fromont, 1988: 115, pl.52, figs e-e [New Zealand]; Dawson, 1993: 38 [index to fauna].


Echinoclathria reticulata (Bergquist & Fromont, 1988)

Ophiolithasia reticulata Bergquist & Fromont, 1988: 113-114, pl.52, fig. f, pl.53, figs a-c [New Zealand]; Dawson, 1993: 38 [index to fauna].


Echinoclathria translatula (Pulitzer-Finali, 1977)


Echinoclathria waldoschmitti de Laubenfels, 1954


Material: Holotype: USNM23092. NW Pacific.

Transfers

Other species described in Echinoclathria but now transferred to other genera.

Ophiolithasia fucoides Bowerbank, 1876: 771, pl.80 [Shark Bay, WA].

Terpiosella fucoides; Burton, 1930b: 675.

Material: Holotype: BMNH1877.5.21.8. Note: referred to Suberitidae.

Holopsamma Carter, 1885

Holopsamma Carter, 1885c: 211

Plectispa Lendenfeld, 1888: 225.

Asplenoides in part, Lendenfeld, 1888: 228; (not Lendenfeld, 1885c: 309).

[Halme] Lendenfeld 1885c: 285 (preocc.).

Type Species. Holopsamma crassa Carter, 1885c: 211 (by subsequent designation of de Laubenfels, 1936a: 98).
DEFINITION. Honeycombed reticulate growth form of tightly anastomosing flattened fibre-branches (lacunae); choanosomal skeleton simply reticulate, without any axial compression or differentiation between axial and extra-axial skeletons; principal spicules core and echinate fibres, those inside fibres sometimes partially or completely replaced by detritus although those echinating fibres usually always present.

REMARKS. Holopsamma and Echinoclathria have been confused throughout the literature and Echinoclathria, Ophlitaspongia, Plectispa, Halme have been used interchangeably for all species. Holopsamma is separated from Echinoclathria by its honeycombed reticulate growth
form, homogeneous fibre reticulation, single size class of choanosomal spicule found both inside fibres and echinating fibres (i.e., lacking the larger, extra-axial styles found in the peripheral skeleton of most *Echinoclathria*): when type species are compared it is surprising why these genera have been confused. Twenty-four species have been referred to this genus, of which 10 are well established and live in Australian waters; they are probably part of the Gondwanan fauna.
Holopsamma arborea (Lendenfeld, 1888) (Figs 255-256, Plate 11C)

Plectispa arborea Lendenfeld, 1888: 226.
Echinoclathria arborea; Hallmann, 1912: 202, 280-282, pl.29, fig.2, text-Fig.63.
Not Clathria (Plectispa) arborea; Whitelegge, 1901: 65, 88, 89, pl.11, figs 15-15a; Hallmann, 1912: 211 [nomen nudum].
Not Lithaspanga arborea Tanita, 1968: 49.
Not Thalassodendron reticulata Lendenfeld, 1888: 227; Whitelegge, 1902a: 212.
Echinoclathria elegans; Whitelegge, 1901: 90.
Not Clathria multilinea Whitelegge, 1901: 88.

MATERIAL. HOLOTYPE: AMZ946/G9160 (dry); Ilawarra, NSW, 34°32'S, 150°50'E, other details unknown (old specimen label 'Halme arborea, type or cotype', new label 'Echinoclathria arborea Lendf. ? type'). OTHER MATERIAL: NSW- QMG303756, QMG303760, QMG303797, QMG303808, VIC- QMG311287 (NCIQ66C-3499-T) (fragment NTMZ23772), TAS- QMG311450 (NCIQ66C-3759-A) (fragment NTMZ23826), S AUST- QMG300239 (NCIQ66C-2148-Z) (fragment NTMZ3526), WA- QMG300192 (fragment NTMZ2907), NTMZ3368.

HABITAT DISTRIBUTION. Widely distributed in temperate coastal waters usually on rocky reefs; shallow subtidal-50m depth; Ilawarra, N. & S. Sydney (NSW); Westernport Bay ( Vic), Bicheno (Tas), Kangaroo I. (SA), Houtman Abrolhos, Barrow I. (WA) (Fig. 255D).

DESCRIPTION. Shape. Arborescent, cavernous-reticulate, tubulo-digitate sponge, up to 450mm long, with short basal stalk, up to 35mm long, 18mm diameter, and single or multiple, regularly or irregularly cylindrical branches which repeatedly bifurcate and occasionally anastomose; branches 120-330mm long, 15-38mm diameter, often tapering towards ends.

Colour. White or off-white alive, grey or grey-brown in ethanol.

Oscules. Large, up to 7mm diameter, recessed between honeycomb surface meshes, surrounded by membranous lip.

Texture and surface characteristics. Firm, compressible, flexible branches, slightly harsh surface; surface regularly or irregularly honeycomb reticulate, with fibre-branches (lacunae) forming close hexagonal meshes, 8-22mm diameter; lacunae ridge-like, projecting up to 10mm above surface, with thin membrane stretched between adjacent lacunae.

Ectosome and subectosome. Ectosome membraneous, collagenous, with few subectosomal auxiliary megascleres lying tangential or paratangential to surface, and single or paucispicular plumose brushes of principal styles protruding through surface; subectosomal skeleton undifferentiated from choanosomal skeleton, immediately below surface.

Choanosome. Skeletal architecture regularly reticulate, with relatively light, small spongins fibres differentiated into ascending primary, pauci- or multispicular (30-52μm diameter), and transverse bi-, uni- or rarely ascicular connecting elements (12-22μm diameter); fibre anastomoses form oval to elongate meshes, 60-140μm diameter; fibres cored and echinated by choanosomal principal styles, and echinating spicules most common on peripheral fibres, mesohyl matrix light, virtually unpigmented, with few scattered subectosomal auxiliary spicules between fibres; choanocyte chambers small, oval, 22-35μm diameter.

Megascleres. Choanosomal principal styles or subtylosyles short, thick, with tapering or slightly subtylole bases, typically smooth, sometimes vestigially microspinised bases, points tapering fusiform. Length 78-(104.8)-118μm, width 4-(5.6)-7.5μm.

Subectosomal auxiliary megascleres thin, straight or slightly curved at centre, rounded smooth bases and telescoped hastate-pointed or rounded strongylote points sometimes resembling anisostrongyles. Length 109-(133.2)-143μm, width 1.5-(2.2)-2.5μm.

Microscleres. Absent.

REMARKS. There is only a single type specimen in the AM collections, despite Hallmann's (1912: 282) remarks to the contrary, and I must assume that the double-registered AMZ946/G9160 is a holotype and not part of a type series (syntype). No other specimens with true affinities to H. arborea were found in the AM collections although there are several specimens labelled Clathria or Plectispa arborea that Hallmann may have been referring to, but these do not belong here (see remarks for C. multilinea).

This species is distinctive in the field in its nearly pure white colour, thinly cylindrical digitate branches (often bifurcate or arborescent in older specimens), and regular, close-meshed honeycomb reticulation (whereas in most other species the surface reticulation is generally wider and the lacunae thicker). This species is closest to H. ramosa and H. macropora, with comparable
spicule geometry and skeletal architecture, but differs in fibre diameter, spicule size and field characteristics.

**Holopsamma crassa** Carter, 1885
(Figs 257-258, Plate 11D)

**Holopsamma crassa** Carter, 1885c: 211; Hooper & Wiedenmayer, 1994: 281.

*Aulena crassa* Lendenfeld, 1889a: 101-102, pl.8, figs 1,2, 5, 6, 22, 23, pl.9, figs 5,9.

**Echinocotlia crassa**; Hallmann, 1912: 287.

*Not Antherochalina crassa* Lendenfeld, 1887b: 787.

**Halmie micropora** Lendenfeld, 1885e: 303; Lendenfeld, 1889a: 461, fig.12, pl.11, fig.4.

**Halmie globosa** Lendenfeld, 1885c: 303; Lendenfeld, 1889a: 456-457, pl.9, fig.11.

**Echinocotlia globosa**; Carpay, 1986: 24; Wiedenmayer, 1989: 63-64, pl.6, figs 2-5, 7, text-fig.43.

**MATERIAL. LECTOTYPE:** BMNH1886.12.15.313: Port Phillip, Vic, 38°00'S, 144°52'E, 38m depth, coll. J.B. Wilson (dredge). PARALECTOTYPES: BMNH1886.12.15.314, 316, 410, 485: same locality. LECTOTYPE of *H. globosa*: BMNH1886.8.27.71 (fragment AMG3753); Port Phillip, Vic, 38°09'S, 144°52'E, 38m depth, coll. J.B. Wilson (dredge) (only remaining syntype of two). LECTOTYPE of *H. micropora*: BMNH1886.8.27.89 (fragments BMNH1886.12.15.90, AMG3779); Illawarra, NSW, 34°33'S, 150°55'E, no other details known. PARALECTOTYPE of *H. micropora*: AMG8828 (dry): same locality. OTHER MATERIAL: QLD-QMG303235, S AUST- QMG301379, SAMTS4082 (fragment NTMZ1678), SAMTS4085 (fragments QMG300472, NTMZ1599), SAMTS4057 (fragment NTMZ1664), QMG310777 (NCI66C-2143-U) (fragment NTMZ3524), QMG310804 (NCI66C-2192-X) (fragment NTMZ3532).

**HABITAT DISTRIBUTION.** Rock reef, sand and kelp bed substrata; 2-38m depth; Stradbroke 1, Moreton Bay (SEQ); Byron Bay, Illawarra, (NSW); Port Phillip Bay, Westernport Bay (Vic); Bass Strait (Tas); Investigator Strait, St. Vincent Gulf, Kangaroo L., Port Norar- lunga, Great Australian Bight (SA) (Fig. 257E).

**DESCRIPTION.** Shape. Massive, subcylindrical, or lobate-digitate honeycomb reticulate sponge, 75-150mm diameter, with enlarged, flattened, slightly elongated basal attachment.

**Colour.** Yellow-brown to cream coloured alive (Munsell 2.5Y 8/6 or paler), brown in ethanol.

**Oscules.** Large, up to 6mm diameter, slightly recessed within reticulate meshes, surrounded by thin membranous lip in life.

**Texture and surface characteristics.** Texture varies according to amount of detritus in skeleton, ranging from flexible, soft, compressible, to distinctly brittle, arenaceous; surface reticulate, lacunose, consisting of irregularly meandering ridges forming large meshes producing characteristic honeycomb growth form, in life covered by moderately thin, translucent dermal membrane stretched between adjacent ridges.

**Ectosome and subectosome.** Ectosome heavily arenaceous, with a thick sandy external cortex covered by a fine membranous ectsosomal skeleton usually containing a tangential layer of auxiliary spicules, in tracts or scattered singly across surface, but easily detached when surface membrane collapses upon preservation (hence and not seen in some specimens); subectosomal region undifferentiated from choanosome, fibres immediately subectosomal.

**Choanosome.** Skeletal architecture irregularly reticulate, with heavy, relatively homogeneous spongine fibres, up to 200µm diameter, lamellated and virtually fully cored by sand grains, with or without a core of choanosomal principal styles; fibres usually always echinated by principal styles, sometimes echinating spicules reduced in heavily arenaceous specimens; mesohyl matrix heavy, darkly pigmented, granular, also containing foreign particles and some auxiliary megascleres scattered between fibres; mesohyl cavernous in places, with cavities up to 260µm diameter, and elongate choanoocyte chambers 80-120µm diameter usually obscured by detritus.

**Megascleres.** Choanosomal principal styles coring and echinating fibres short, thin, straight, with rounded or tapering smooth bases, fusiform, sharply pointed. Length 53-(67.4)-81µm, width 1.2-(4.1)-6µm.

Subectosomal auxiliary spicules long, slender, strongylote styles, straight or slightly curved or sinuous, with slightly subtylote bases, evenly rounded or bifid points. Length 188-(234.1)-261µm, width 1.5-(3.9)-6µm.

**Microscleres.** Palmate isochelae small, straight shaft, long, thick lateral alae fully fused to shaft, nearly completely detached from front ala, front ala shorter than lateral alae. Length 8-(11.6)-15µm.

*Toxas* absent.

**Larvae.** Viviparous parenchymella larvae spherical or subspherical, 320-410µm diameter, with vestigial quasidactinal megascleres scattered throughout mesohyl.

**REMARKS.** Under *Echinocotlia globosa* Wiedenmayer (1989) provided a detailed discussion of additional type specimens of each nominal species he examined (whereas only the specimens that have a direct bearing upon the
The polymorphic concept of this species was slightly overstated by Wiedenmayer (1989) and it does have a distinct identity. He also described only auxiliary spicules present in the species whereas all specimens examined have at least some echinating principal styles in the skeleton, even if most of the other spicules have been displaced by sand. In fact, most of the described variability in *H. crassa* is a conse-

sequence of the amount of sand incorporated into the skeleton, which appears to be directly related to the loss of spicules from within fibres and also reflected in the external 'honeycomb' reticulate appearance of the sponge. With the nomination of a lectotype of *H. crassa* by Hooper & Wieden-
mayer (1994) the senior name of Carter (1885c) now takes precedence over Lendenfeld’s (1885c) name *H. globosa* (which allegedly appeared several months later; Wiedenmayer, 1989). Wiedenmayer (1989) did not take this step due to the ambiguity of Carter’s original description, and the lack of a lectotype designation for *H. crassa* from a composite series of 31 syntypes (consisting of at least five different species belonging to three families).

*Holopsamma crassa* is well characterised by its external morphology (superficially resembling a favid coral), texture (close to *Xestospongia exigua*; Petrosiidae), and skeletal characteristics (superficially resembling the arenaceous ‘keratose’ sponges), but variability in these features can be illustrated by comparing 3 specimens from the St Vincent Gulf region. SAMTS4057 was almost entirely permeated by sand grains, obscuring most of the fibres and mesohyl matrix (with only echninating principal styles as obvious components of the sponge’s spiculation). SAMTS4085 had very heavy spongin fibres, heavily arenaceous fibre core, and a heavy, darkly pigmented mesohyl matrix superficially resembling a verongid sponge. Both these specimens had fine, sharp ridges forming the external honeycomb reticulation, with a bryozoan lace-like external reticulation in the preserved state. Both these specimens also had very few indigenous megacleres, and were initially confused with a dictyoceratid or verongid species (Fig. 258B). SAMTS4082 contained numerous subectosomal auxiliary megacleres scattered throughout the mesohyl, choanosomal styles echninating lightly arenaceous fibres in moderate quantities, and rounded edges on ridges forming the external reticulation producing a more robust, honeycomb reticulate structure.

*Holopsamma crassa* is most similar to *H. laminaefavosa*, and it is conceivable that they belong to a single species. They are retained here as distinct species in order to highlight their differences and not submerge them, although additional non-skeletal characters are needed to confirm or refute the validity of these taxa. *Holopsamma crassa* has a brownish live colouration; the lacunae forming its external honeycomb reticulate ridges are more robust, recessed more deeply, and meshes have only a light membraneous ectosomal covering between them; there is a more prominent sandy cortex; principal spicules are fusiform, sharply pointed; auxiliary strongylote styles have rounded or bifid points; and chelae are present. *H. laminaefavosa* is white alive; shallow meshes formed by the surface honeycomb reticulation are connected by a well formed tympanized membrane stretched between adjacent ridges; principal styles have telescoped points; auxiliary spicules have rounded or slightly hastate points; and chelae are absent. Wiedenmayer (1989) also suggested that the growth form of *H. crassa* was reminiscent of *Phoriospongia reticulum* Marshall, although the spiculation of the latter is quite different (strongyles, subtylotes and sigmas).

*Holopsamma elegans* (Lendenfeld, 1888) (Figs 259-260)


*Echinoclathria elegans*; Hallmann, 1912: 203.


Not *Echinoclathria elegans*; Whitelegg, 1901: 90.

Not *Antherochalinella elegans* Lendenfeld, 1887b: 787.

**MATERIAL.** **HOLOTYPE:** BMNH1887.4.27.98: Port Jackson, NSW, 33°51'S, 151°16'E, other details unknown.

**HABITAT DISTRIBUTION.** Ecology unknown; Port Jackson (NSW) (Fig. 259D).

**DESCRIPTION.** **Shape.** Honeycomb reticulate mass of irregularly cylindrical, thin digitate branches, up to 145mm long, 25mm diameter, with branches composed of tight-meshed fibre bundles up to 5mm wide.

**Colour.** Unknown live colouration, grey-brown dry.

**Oscules.** Large, up to 7mm diameter in dry state, within surface lacunae.

**Texture and surface characteristics.** Harsh, brittle in dry state; honeycomb reticulate surface, lacunae smooth.

**Ectosome and subectosome.** Membraneous, minutely hispid, with abundant subectosomal auxiliary subtyl邀styles erect on surface in plumose brushes; choanosomal fibres immediately subectosomal.

**Choanosome.** Irregularly reticulate skeletal structure, with differentiated multispecular primary, ascending fibres, up to 200μm diameter, and numerous transverse, pauci- or aspicular secondary fibres, up to 70μm diameter; echinating principal styles sparse, scattered only over ascending fibres; spongin fibres heavy; fibre meshes rounded, 30-150μm diameter; choanocyte chambers not seen (poor dry material).
Megascleres. Choanosomal principal styles long, robust, straight or very slightly curved at centre, evenly rounded, entirely smooth bases, fusiform or slightly telescoped points. Length 78-(90.3)-105 μm, width 4-(4.6)-6 μm.  
Subectosomal auxiliary subtylostyles long, slender, slightly curved near basal end, subtylole smooth bases, tapering rounded or quasi-stronglyelo Pluto points. Length 90-(141.2)-255 μm, width 1.0-(1.6)-2.5 μm.  
Microscleres. Absent.  

REMARKS. This species is known only from the poor, dry holotype from Port Jackson. It is possibly a synonym of *H. arboarea*, based on similarities in their spicule geometrics, although there are some differences in their respective skeletal structures. The species also shows similarities to *H. crassa*, *H. macropora*, *H. ramosa* and *H. rounda* in having stronglyelo points on auxiliary spicules, although all species differ in most other respects.

**Holophsamma favus** (Carter, 1885)  
(Figs 261-262)  

*Echinoclathria favus* Carter, 1885: 292; Ridley & Dendy, 1887: 160-161, pl.31, figs 4-5; Dendy, 1896: 40; Hallmann, 1912: 276-277, text-fig.61; Wiedenmayer, 1989: 59-60, fig.10, pl.24, fig.2, text-fig.40; Carpay, 1986: 23.  
*Axoicella favus*; de Laubenfels, 1954: 164.  

Not *Echinoclathria favus var. arenifera*; Carter, 1885f: 350.  
*Spongia cellulosa*; Ellis & Solander, in part; Lamarck, 1814: 373; Topsent, 1932: 20, pl.1, fig.3.  
Not *Spongia cellulosa* Esper,1797.  
*Echinoclathria carteri* Ridley & Dendy, 1886: 476; Ridley & Dendy, 1887: 162, pl.29, fig.12, pl.31, fig.3; Hallmann, 1912: 284-285, text-fig.65.  
*Axoicella carteri*; de Laubenfels, 1936a: 119.  
*Echinoclathria macropora*; Whitelegge, 1907: 504.  
Not *Echinoclathria macropora* Whitelegge, 1901: 89, 117.  

**MATERIAL.** HOLOTYPE: BMNH1887.5, 13.35: Port Phillip, Vic. 38°09'S, 144°52'E, other details unknown.  
HOLOTYPE of *E. carteri*: BMNH1887.5.2.751: Off Port Jackson, NSW, 33°51'S, 151°16'E, HMS 'Challenger' (dredge).  
PARATYPE of *E. carteri*: BMNH1887.5.2.44: same details.  

**OTHER MATERIAL:** TASMANIA - MNHNIT556 [specimen of *S. cellulosa sensu* Lamarck]. WESTERN AUSTRALIA - NTMZ3211, NTMZ3226, NTMZ3498.  

**HABITAT DISTRIBUTION.** Growing on bivalves, seagrass, rock reefs, vertical rock walls of cave, in sand and shell-grit substrata; 3-333 m depth; known only from Australia: Port Jackson, Shoalhaven Bight (NSW); Port Phillip Bay, Westernport Bay (Vic); King L., Bass Strait (Tas); Houtman Abrolhos, Monte Bello Is (WA) (Fig. 261E).  

**DESCRIPTION.** Shape. Elongate digitate, conical cylindrical or lobate-cylindrical honeycomb reticulate sponge, forming masses up to 380 mm high, 450 mm wide, composed of bifurcate, usually non-anastomosing branches, with individual branches up to 160 mm long, 20-45 mm diameter; branches formed by close-meshed fibre bundles (lacunae) producing a characteristic honeycomb surface; multiple points of attachment to substrate, without basal stalk or expanded point of attachment.  
**Colour.** External surface usually red-orange or orange-brown in life (Munsell 7.5YR 7/10-12), paler orange below surface, deeper water samples honey-brown, in ethanol specimens turn yellow-brown or dark brown.  
**Oscules.** Small, no more than 2 mm diameter, within meshes of surface reticulation.  
**Texture and surface characteristics.** Soft, compressible, rubbery, difficult to tear; regular, close-meshed honeycomb reticulate surface; meshes (alveoles) small, rounded or elongate formed by surface lacunae, up to 4 mm diameter, more-or-less regular, usually smaller than meshes within deeper regions of sponge.  
**Ectosome and subectosome.** Membranous, with thin transparent ectosomal membrane stretched across adjacent lacunae at surface of sponge; points of principal styles from ascending choanosomal skeleton protrude slightly producing hispid surface, and paucispicular bundles or single auxiliary subtylostyles lying par tangential to surface; peripheral lacunae rounded or bulbous, not flattened.  
**Choanosome.** Skeleton regularly or irregularly reticulate, cavernous; spongine fibres well developed, more-or-less differentiated into primary ascending and secondary transverse elements; primary fibres 35-60 μm diameter, cored by pauci- or multispecific, plumose or oblique tracts of principal styles and small quantities of foreign detritus; secondary fibres up to 20 μm diameter, unispicular or aspilucose; fibres sparsely echi natized by principal styles evenly dispersed throughout skeleton; fibre anastomoses form round to polygonal meshes, 20-100 μm diameter;
mesohyl matrix light, with abundant principal and auxiliary megascleres strewn between fibre meshes; auxiliary spicules predominantly in deeper regions of choanosomal mesohyl, less abundant in peripheral skeleton; choanocyte chambers large, elongate-oval, 35-55μm diameter.

**Megascleres.** Principal styles coring and echinating fibres straight or faintly curved at centre, relatively thick, entirely smooth, with rounded, tapering or occasionally anisoxeote bases, fusiform points. Length 69-(96.4)-132μm, width 2-(4.8)-7μm.

Subectosomal auxiliary subtylostyles long, thin, mostly straight, with slightly constricted bases, usually hastate, slightly rounded or slightly telescoped points, sometimes subtylostrongyloste with barely differentiated ends. Length 132-(120.7)-174μm, width 1.4-(1.9)-2.1μm.

**Microscleres.** Palmate isochelae sparse, small, with long lateral alae entirely fused to straight shaft, front ala shorter, often with expanded, spoon-shaped alae. Length 8-(11.9)-15μm.

Toxas absent.

**REMARKS.** *Holopsamma favus* has a red-orange external live colouration (most species of *Holopsamma* are pale or white), a cartilaginous, algae-like, contort lobate-digitate habit (most are globular or evenly cylindrical-digitate), palmate isochelae (most lacking chelae), skeletal architecture consisting of slightly differentiated as-

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descending and transverse fibres in reticulation (most have relatively homogeneous spongine fibres), and dominance of spicules over detritus within fibres (most are much more heavily arenaceous than *H. favus*). Comparing their respective type specimens it is obvious that *H. carteri* is a synonym of *H. favus*, given their identical growth forms, megasclere spicule geometry and spicule size, and dominance of spicule over detritus within fibres (although these similarities were overlooked by several recent authors; Carpay, 1986; Wiedenmayer, 1989; Hooper & Wiedenmayer, 1994). Wiedenmayer (1989) indicated that the pale red-orange live colouration was typical and consistent for this species, but this is only confirmed for shallow water specimens, whereas deeper water material is reportedly paler, honey-brown (e.g., Ridley &

Dendy, 1887; Hallmann, 1912). Similarly, some specimens were reported to shed their palmate isochelae microscleres (Wiedenmayer, 1989), making confident identification difficult. Never-
match fairly closely those of the type specimens to be confident of conspecificity.

This species is a common component of the benthic fauna in Bass Strait (Wiedenmayer, 1989), and the specimens from the Houtman Abrolhos and Monte Bello Islands indicate a more widespread distribution.

Holopsamma laminaefavosa Carter, 1885
(Figs 263-264, Plate 11E)


Echinolathria laminaefavosa: Wiedenmayer, 1989: 60-61, pl.5, fig.11, text-fig.41; Carpay, 1986: 24.

Halme nidus-vesparum Lendenfeld, 1885c: 288, pl. 26, figs 1-2, pl.27, fig.4-5, pl.28, figs 8-9, 11, pl.29, figs 12-13; Lendenfeld, 1888: 157; Lendenfeld, 1893a: 457, pl.11, figs 1, 7, 9-10, 15-18; Whitelegg, 1889-1894.

*Halme gigantea* Lendenfeld, 1886a: 847-9 [et var digita, macropora, micropora].

*Aulena gigantea*; Lendenfeld, 1888: 230-232 [et var intermedia, macropora, micropora].

*Lendenfeld, 1889a: 97, pl.8, figs 3.4, 7, 8, 18, 29, pl.9, figs 2-4; Whitelegg, 1889: 187; Whitelegg, 1901:93, 118; Whitelegg, 1907: 504; Hallmann, 1912: 268, 285-287; Burton, 1938a: 20; Guiler, 1950: 10.

Not *Halme micropora* Lendenfeld, 1885c: 303; Lendenfeld, 1889a: 461, pl.9, fig.12, pl.11, fig.4.

**Halme laxa** Lendenfeld, 1886a: 845-7 [et var digitata, minima].

*Aulena laxa*; Lendenfeld, 1888: 228-230; Lendenfeld, 1889a: 95-97, pl.8, figs 10-12, 15, 20-21, pl.9, fig.1; Whitelegg, 1889: 187; Hallmann, 1912: 287; Hallmann, 1914a: 268; Burton, 1938a: 20.


**Echinolathria laxa**; Hallmann, 1912: 287.

**Halme irregularis** Lendenfeld, 1889a: 49, 453-5, pl.9, fig.8, pl.11, fig.3 [et var micropora, lamellosa].

**Echinolathria favus var. arenifera** Carter, 1885f: 350.


**OTHER MATERIAL:** QLD- QMG303957. NSW- QMG301399, QMG301441, AMZ2225, VIC-NC1Q66C-3402-0 (fragment NTM3385).

**HABITAT DISTRIBUTION.** Rocky reefs, sand and shell grit substrata; 3-80m depth; Bass Strait, Maria L, Blackman’s Bay (Tas); Port Phillip Bay, Westernport Bay (Vic); Byron Bay, Jervis Bay, Port Jackson, Port Stephens, Morumba, Barranjeay, Illawarra, Broughton L, Sandon Bluffs (NSW); Noosa Heads, Tweed River (SEQ) (Fig. 263D). The reported localities of Torres Strait (FNQ) (Lendenfeld, 1888); and Palua Brani, Singapore (Drageweitsch, 1906) are suspect.

**DESCRIPTION.** Shape. Massive, lobate, cylindrical-digitate, honeycomb reticulate growth forms, up to 385mm long, 240mm wide at basal attachment, with individual digitis free at apical end, up to 210mm long, 75mm diameter, usually fused at base, forming globular lobate...
mass; attached directly to substrate, no expanded point of attachment.

Colour. White alive, brown, sandy brown or dark orange-brown in ethanol.

Oscules. Large, up to 7mm diameter, mostly on apex of digits but also in between some meshes of lacunae.

Texture and surface characteristics. Flexible digits, harsh, arenaceous, lacunae brittle; surface composed of regular, slightly raised ridges formed by honeycomb reticulation of lacunae;

meshes produced by reticulation of lacunae typically widely spaced, 4-13mm apart, cavities formed by meshes relatively shallow, covered by thick tympanised membrane stretched across adjacent ridges.

Ectosome and subectosome. Membranous, heavily arenaceous, without a well defined tangential spicule skeleton, but often with points of ascending principal styles protruding through surface in sparse bundles, below which are scattered individual auxiliary spicules; subectosomal
diameter, without any consistent size differences between meshes at core or periphery; primary fibres usually cored by detritus and sparse tracts of choanosomal principal styles, and echinated by pauci- or multispicular tracts of same principal styles; coring and echinating spicules together produce plumose or oblique, vaguely ascending tracts, usually heaviest on peripheral fibres; principal styles may be absent entirely from fibre core in heavily arenaceous specimens; secondary tracts arenaceous or entirely clear of detritus, in the latter case tracts of principal spicules clearly seen; mesohyl matrix usually darkly pigmented, usually with subectosomal auxiliary megascleres dispersed throughout; choanocyte chambers oval to elongate, 50-90μm diameter, often obscured by detritus.

*Megascleres.*
Choanosomal principal styles coring and echinating fibres short, straight, relatively thick, with tapering (hastate) or rounded smooth bases, telescoped or occasionally fusiform points. Length 52-(86.4)-115μm, width 2-(4.1)-7μm.

Subectosomal auxiliary megascleres strongly, styles, long, thin, straight or flexuous, with rounded or slightly subtylote bases, rounded, telescoped or sometimes hastate points. Length 128-(174.3)-195μm, width 1-(2.8)-4μm.

*Microscleres.* Absent.

**REMARKS.** This species is similar to *H. crassa* in growth form, skeletal structure and more-or-less in spiculation, although both species may show considerable variation between regional...
populations in these features; they are also sympatric although they have not yet been found on the same reefs (present study). This polymorphism has been described in detail by Hallmann (1912; as *Echinoclathria gigantea*) and Wiedenmayer (1989; as *E. laminaefavosa*), and the numerous synonyms erected for this species by Lendenfeld (1885-1889) testify to the confusion that this variability can produce. Similarly, the range of variability within each species may overlap such that observable differences may be not be sufficient to consistently differentiate all populations, and it is conceivable that the two species may be synonyms. Nevertheless, *H. laminaefavosa* differs from *H. crassa* mainly in having a white colouration underwater; a shallow meshed surface honeycomb reticulation with a well formed tympanized membrane stretched between adjacent surface ridges; principal styles have telescoped points; and chelaæ are absent (see remarks for *H. crassa*). The species has been well illustrated by Lendenfeld (1885c; 1889a) under its numerous synonyms, and more recently by Wiedenmayer (1989). Wiedenmayer (1989) and others indicated that some specimens lack a spicule skeleton, with spicules being replaced by foreign detritus, but this cannot be corroborated from material examined in this study.

**Holopsammat macropora** (Lendenfeld, 1888) (Figs 265-266)


*Wilsonella macropora*; Hallmann, 1912: 240.

*Holopsammat macropora*; Hooper & Wiedenmayer, 1994: 283.


Not *Echinoclathria macropora* Whitelegge, 1901: 504.

Not *Clathria macropora*; Whitelegge, 1901: 91.

**MATERIAL.** **HOLOTYPE.** AM9159 (dry: Port Jackson, NSW, 33°51'S, 151°16'E (published locality of Torres Strait incorrect)).**

**OTHER MATERIAL.** *S. Aust.-SAMTS4094 (fragments QMG300476. NTMZ1622).*

**HABITAT DISTRIBUTION.** Rock reef; 15-25m depth; Port Jackson (NSW); St. Vincent Gulf (SA) (Fig. 265E).

**DESCRIPTION.** Shape. Small, lobate-digitate, honeycomb reticulate sponge, 80-100mm high, 85-140mm wide, with irregular, bulbous surface lobes up to 30mm high, 35mm diameter.

**Colour.** Live colouration unknown, light brown dry, dark brown in ethanol.

**Oscules.** Small, up to 3mm in preserved state, scattered within meshes of surface lacunae.

**Texture and surface characteristics.** Firm, compressible, flexible; surface honeycomb reticulation close-meshed, meshes 3-6mm diameter; surface fibre bundles (lacunae) with scattered microconules on exterior edges, relatively deep meshes.

**Ectosome and subectosome.** Surface microscopically hispid with points of principal styles protruding through surface, usually in plumose, multispicular brushes; subectosomal auxiliary spicules tangential to surface in sparse bundles or individually, associated with protruding spicule brushes; choanosomal fibres immediately subectosomal.

**Choanosome.** Skeletal architecture reticulate, increasingly plumose or plumo-reticulate near periphery, with a clearly differentiated primary and secondary fibre skeletons; primary ascending fibres very heavy, up to 120µm diameter, vaguely stratified, containing plumose uni-, pauci- or multispicular tracts of choanosomal principal styles, generally increasing in density towards periphery but overall sparsely cored; secondary transverse fibres relatively heavy, up to 55µm diameter, very short, interconnecting close-set ascending fibres, usually aspicular, rarely unispicular; some fibres also cored by auxiliary spicules; all fibres abundantly echninated by principal styles, particularly at core of skeleton; spicule tracts within fibres become increasingly plumose towards periphery; fibre anastomoses form small oval or elongate meshes, 25-126µm diameter; mesohyl matrix very lightly pigmented and auxiliary spicules scattered between fibres, particularly towards periphery; some detritus also incorporated into mesohyl but usually not into fibre skeleton; choanoocyte chambers oval, 20-65µm diameter.

**Megascleres.** Choanosomal principal styles or subtylostyles coring and echinating fibres straight, moderately thin, with slightly constricted, subtylole or rounded, smooth bases, tapering to fusiform points. Length 49-(68.4)-96µm, width 3-(3.9)-6µm.

Subectosomal auxiliary megascleres range from strongylote subtylostyles to tornotes; usually long, thin, straight or slightly curved with blackened axial canals, sometimes setaceous, sinuous, with rounded or hastate points. Length 123-(166.1)-184µm, width 1.5-(3.2)-4µm.**

**Microscleres.** Palmate isochelae uncommon, many smaller forms twisted, with very short alae.
straight shaft, lateral alae completely fused to shaft, front ala usually partially, or sometimes wholly fused to lateral alae. Length 4-(9.3)-12 μm.

Toxas absent.

**REMARKS.** The two specimens are the only validated records for the species. Other records quoted as 'macropora' by Lendenfeld and Whitelegge are spurious (see remarks for *Plectitispa*). From Lendenfeld (1888) and Whitelegge
(1901, 1902a, 1907) the species has been misinterpreted such that the holotype was referred (sight unseen) to Wilsonella by Hallmann (1912). This error is a direct result of Lendenfeld’s (1888) inaccurate description and probably also the confusion resulting from his continual usage of macropora for several supposedly unrelated species (see remarks for Clathria (Axociella) macropora).

The holotype belongs to Holopsamma, with the characteristic honeycombed reticulate growth form and smooth echinating spicules (not acantho- those as supposed by Lendenfeld (1888) and Hallmann (1912)), whereas all other alleged syntypes of Plectispa macropora belong to different species. In growth form H. macropora shows similarities to H. laminataefavosa, and to a lesser extent H. favus. In spiculation and skeletal construction it is reminiscent of specimens referred to H. laminataefavosa by Wiedenmayer (1989) and to a lesser extent H. ramosa (Hallmann, 1912) (i.e., those specimens with a diverging choanosomal skeleton which becomes increasingly dense towards the periphery). It is possible that H. macropora is simply a non-arenaceous morph of H. laminataefavosa although there are differences in spicule geometry and spicule dimensions to suggest that they are different species. In particular, the possession of long setaceous quasi-diaictal auxiliary megascleres (which also core fibres, are scattered throughout the mesohyl and associated with spicule brushes on the surface) do not appear in these other species; isochelae are also definitely present in H. macropora (albeit uncommon in both the holotype and SA specimen), although they were not recorded in the original description of the species by Lendenfeld (1888), whereas microscleres are definitely not present in H. laminataefavosa.

The type locality was given as Torres Strait by Lendenfeld (1888) but it is probably actually from Port Jackson, NSW (as noted on the AM register).

Holopsamma pluritoxa (Pulitzer-Finali, 1982) (Figs 267-268)

Holopsamma pluritoxa; Hooper & Wiedenmayer, 1994: 283.

MATERIAL: HOLOTYPE: MSNG 46938 (not seen); Heron I., Great Barrier Reef, Qld, 23°26’S, 151°55’E, 8.xii.1979, coll. A.J. Bruce (by hand).OTHER

MATERIAL: QLD- QMG6786 (fragments QMG300471, NTMZ1588).

HABITAT DISTRIBUTION. 3-8m depth, on sand, shell grit and coral rubble substrates; Moreton Bay, Heron I. (Fig. 267E).

DIAGNOSIS OF HOLOTYPE. Honeycombed reticulate growth form; irregularly reticulate skeleton with pale spongion fibres 20-100μm diameter, fibre meshes 300-500μm diameter, fibres sparsely cored by thin choanosomal principal substylolystyles (270-320x4-9μm); echinating spicules absent; strongylote subectosomal auxiliary substylolystyles scattered throughout mesohyl (230-250x2-3μm); abundant toxas wing-shaped or slightly oxhorn (10-188x1-4μm); palmate isochelae unmodified (13.5μm) (Pulitzer-Finali, 1982).

DESCRIPTION. Shape. Subspherical-lobate, shaggy and irregularly honeycombed reticulate construction, 55mm wide, 40mm long.  
Colour. Live colouration unknown, light grey-brown in ethanol.  
Oscules. Not seen.  
Texture and surface characteristics. Soft, compressible; surface reticulate fibre bundles in peripheral regions slightly flattened, with micropapilllose, shaggy points.

Ectosome and subectosome. Surface microscopically hispid, with plumose brushes of choanosomal principal styles protruding, inter- dispersed with subectosomal auxiliary megascleres lying tangential or paratangential to surface; subectosomal skeleton plumoreticulate.

Choanosome. Skeleton irregularly plumo-reticulate, with poorly developed spongion fibres, 20-155μm diameter, forming irregular ovoid to elongate meshes, 145-500μm diameter; fibres contain pauci- to multispecific tracts of choanosomal principal styles, without any division of primary or secondary fibre components, forming plumose ascending structures which coalesce and diverge to produce fibre anastomoses; fibres not echinated although choanosomal principal styles may protrude obliquely; mesohyl matrix relatively heavy, darkly pigmented, granular, with numerous toxas and scattered subectosomal auxiliary megascleres; choanocyte chambers large, oval, 40-90μm.  
Megascleres. Choanosomal principal styles straight or slightly curved, with smooth, rounded or slightly subylote bases, fusiform points. Length 167-(217,2)-289μm, width 4-(5,1)-7μm.

Subectosomal auxiliary megascleres straight, asymmetrical, varying from quasistrongyles with
smooth rounded extremities, to quasistylotes with subptyloyle micropinapted points. Length 195- 
(218.8)-262μm, width 2-(2.8)-4μm.

Microscleres. Isochrome absent.

Troxas wing-shaped, variable in size, thin or 
round, with rounded slight, or large central curva-
ture, straight or slightly reflexed points, arbitra-
arily divisible into two size classes. Length I: 
8-(26.7)-30μm, width 0.5-(0.8)-1μm; length II: 
65-(177.0)-250μm, width 1.5-(2.3)-4μm.

Remarks. This species is unusual in its fibre 
characteristics and skeletal architecture, lacking 
true echinating spicules, and having quasidiae-
tinal auxiliary megascleres. The specimen from 
Moreton Bay also differs in some respects from 
the holotype from Heron I. (known from the 
original diagnosis; type not seen). The skeletal 
architecture of the specimen is more obviously 
plumoreticulate than reticulate (reminiscent of 
Stylinos: Halichondriidae), ectosomal structure 
is distinctly plumose (reminiscent of Lissodendoryx; 
Myxillidae; ectosomal structure was not 
mentioned by Pulitzer-Finali, 1982), and 
tissue are absent (abundant in the holotype). 
In various respects the two specimens are obviously 
conspicuous having virtually identical spice 
geometries, growth forms and surface features 
although Pulitzer-Finali’s (1982) description is 
incomplete.

Holopsamma ramosa (Hallmann, 1912) 
(Figs 269-270)

Echinolathria ramosa Hallmann, 1912: 277-279, 
pl.30, fig.3, text-fig.62.

Holopsamma ramosa: Hooper & Wiedenmayer, 1994: 
283.

Echinolathria macropora; Whitelegge, 1901: 89, 
117.
Not Echinolathria macropora: Whitelegge, 1907: 
504.

Material. Lectotype: AMZ49 (dry): Swansea, 
off Lake Macquarie, NSW, 33°11’S, 151°59’E, 
depth unknown, coll. FIV ‘Tihets’ (trawl); PARALEC-
TOPYPE: AMZ40: 64km W. of Kingston, SA, 
36°50’S, 139°05’E, 60m depth, coll. FIV ‘Endeavour’ 
(trawl). OTHER MATERIAL: S AUST- SAMTS4105 
(fragments QMG300487, NTMZ1695).

Habitat Distribution. Reef reef and sandy 
substrate; 8-60m depth; Lake Macquarie (NSW), 
Kingston SE., Nuyts Archipelago (SA) (Fig. 269E).

Description. Shape. Profusely bushy, ar-
borescent branching, honeycomb reticulate 
sponge, up to 165mm high, 220mm wide, with 
small basal stalk and expanded point of attach-
ment; branches numerous, bifurcate, occasional-
ly anastomosing, relatively thin, cylindrical or 
slightly laterally compressed, up to 75mm long, 
32mm diameter.

Colour. Grey-brown to dark brown in ethanol.

Oscules. Moderately large, up to 5mm diameter, 
scattered between honeycomb lacunae.

Texture and surface characteristics. Harsh, 
slightly rubbery; fibre bundles form more-or-less 
regular hexagonal or elongated meshes, 1-5mm 
diameter.

Ectosome and subectosome. Membraneous, with 
points of sparse principal styles protruding 
through surface, but generally smooth, non-
hispid; sparse subectosomal auxiliary 
megascleres tangential to ectosome, never 
protruding through surface.

Choanosome. Skeletal architecture irregularly 
reticulate, with small, heavy, evenly compressed 
spongion fibres, 23-95μm diameter, divided into 
primary longitudinal and vaguely ascending, and 
secondary connecting components; primary 
fibres contain uni- or paucispicular tracts of 
choanosomal principal subptylostyles; secondary 
fibres mostly aspicular, rarely unispicular; fibre 
meshes close-set near core, 35-85μm diameter, 
more cavernous towards periphery, 112-220μm 
diameter; tendency for peripheral fibres to con-
tain spicle tracts of styles in more-or-less 
plumose brushes; fibres sparsely echinated by 
principal subptylostyles particularly on distal 
margin of peripheral fibres (cf. Hallmann, 1912); 
mesohyl matrix heavy, darkly pigmented, with 
scattered subectosomal auxiliary megascleres; 
choanocyte chambers small, oval, up to 50μm 
diameter.

Megascleres. Choanosomal principal styles 
straight, short, relatively thick, with tapering, 
constricted, smooth, slightly subptyloyle bases, 
slightly fusiform sharp points. Length 75-
(100.7)-144μm, width 4.5-(6.8)-8.5μm.

Subectosomal auxiliary subptylostyles or quasi-
strongyles (asymmetrical) straight or curved at 
centre, thin, with smooth, slightly subptyloyle bases 
and rounded points. Length 122-(139.8)-157μm, 
width 1.5-(2.7)-4μm.

Microscleres. Paltine isochrome small, poorly 
silicified, with approximately 30% contorn forms, 
small alac, lateral alae fused entirely to shaft, 
front ala completely detached, straight shaft. 
Length 7-(10.2)-12μm.
REMARKS. Hallmann (1912) suggested that spicule dimensions were highly variable in this species, particularly choanosomal styles, but in comparison with other Holopsamma species these are in fact relatively homogeneous. Similarly, palmate isochelae are probably native to this species because they were found in all material examined, although Hallmann did not describe them in the dry lectotype. Spicule geometry and certain aspects of skeletal architecture indicate that *H. ramosa* is allied to *H. macropora* and *H. arborea*, differing mainly in growth form, spicule dimensions and the presence of microscleres. Indeed Hallmann (1912) erected *H. ramosa* for Whitelegge’s (1901) specimen of *Echinoclathria macropora* (as distinct from *Plectispa macropora* Lendenfeld, 1888), but there has obviously been some confusion in the interpretation of the latter species. Any proposed merger of *H. macropora*, *H. arborea* and *H. ramosa* is not presently supported on the basis of existing material.

**Holopsamma rotunda** (Hallmann, 1912) (Figs 271-272)

*Echinoclathria rotunda* Hallmann, 1912: 282-284, pl.30, fig.1, text-fig.64.

Asociella rotunda; de Laubenfels, 1936a: 119 [note].

**Holopsamma rotunda**; Hooper & Wiedenmayer, 1994: 284.


**HABITAT DISTRIBUTION.** Substrate unknown; up to 330m depth; Lake Macquarie (NSW); off Fraser I. (SEQ); Portsea (Vic) (Fig. 271E).

**DESCRIPTION. Shape.** Massive, subspherical, globular, honeycomb reticulate sponge, up to 155mm high, 90mm maximum diameter, with short basal stalk and expanded point of attachment; sponge insubstantial, hollow internally.

**Colour.** Dark blue-grey alive (Munsell 2.5B 6/2), dark brown in ethanol.

**Oscules.** Large, up to 6mm diameter, scattered between lacunae.

**Texture and surface characteristics.** Firm, compressible alive, harsh in dry state; open, porous, tubular external construction; honeycombed surface fibre bundles produce very thin, flattened, erect lamellae with regular meshes, up to 4mm diameter.

**Ectosome and subectosome.** Membraneous, with points of principal subtylostyles protruding through surface in sparse plumose brushes, few subectosomal auxiliary subtylostyles tangential to and below surface.

**Choanosome.** Skeletal architecture distinctly plumo-reticulate, with ascending multi- or paucispicular primary fibres, interconnected by pauci- or aspicicular secondary fibres; fibres relatively light, 43-92µm primary fibre diameter, 18-56µm secondary fibre diameter, prominently flattened; fibre anastomoses form almost regular, circular or oval meshes, 38-96µm diameter, more compacted towards periphery than at core; fibres cored and echinated by single category of choanosomal principal subtylostyle; echinating megascleres predominant on (although not confined to; cf. Hallmann, 1912) distal edges of fibres; primary spicule tracts increasingly plumose towards periphery; mesohyl heavy in ectosomal region, relatively light in deeper choanosomal region, containing sparsely dispersed subectosomal auxiliary subtylostyles; choanoocyte chambers small, oval, up to 55µm diameter.

**Megascleres.** Choanosomal principal subtylostyles straight or slightly curved at centre, relatively long, thick, with tapering, constricted, smooth, subtyloble bases, fusiform pointed or slightly telescoped points. Length 85-(107.5)-138µm, width 4-(7.2)-9.5µm.

Subectosomal auxiliary subtylostyles thin, straight, slightly curved or sometimes sinuous, slightly subtyloble bases, varying from asymmetrical strongylote with rounded points or styloid with tapering points. Length 123-(152.3)-196µm, width 2.5-(2.9)-4µm.

**Microscleres.** Palmate isochelae abundant, unmodified, with long lateral alae completely attached to shaft, shorter front ala partially fused to lateral alae, straight shaft. Length 6-(10.7)-12µm.

REMARKS. *Holopsamma rotunda* has an insubstantial, hollow morphology, paper thin, lamellate fibre bundles (‘lacunae’), and regularly lamellate fibre reticulation with prominent flattened fibres, whereas in spicule geometry it could match most other species, particularly *H. crassa*, *H. elegans*, *H. macropora* and *H. ramosa* (i.e., with strongylote points on auxiliary spicules). So far the species is only known only from two type specimens, a poorly preserved deep water specimen from the E. continental shelf (represented only by a fragment), and a more recent
collection from Portsea, Victoria (unfortunately also now only represented by a fragment). The deeper water specimen differs from the others in having some detritus scattered throughout the mesohyl, and also lacking any clear division between ascending and transverse fibre elements, but otherwise it is clearly conspecific. Hallmann (1912) did not record a locality for the type but specimen labels and registers indicate Lake Macquarie, NSW.
Holopsamma simplex  
(Lendenfeld, 1885)  
(Figs 273-274)

_Halme simplex_ Lendenfeld, 1885c: 301-303, pl.26, fig.3, pl.27, fig.6.  
_Holopsamma simplex_ Hooper & Wiedenmayer, 1994: 284.

**MATERIAL.** LECTOTYPE: AMG8822 (dry): Torres Strait, Qld, 9°41'S, 142°17'E, no other details known. 
PARALECTOTYPE: BMNH1886.8.27.68 (dry) (fragment AMG3778): off Port Jackson, NSW.

**HABITAT DISTRIBUTION.** Substrate unknown, 10-20m depth; Torres Strait (FNQ); Port Jackson (NSW) (Fig. 273D).

**DESCRIPTION.** _Shape._ Thickly encrusting sponges, reportedly up to 20mm thick, with lobate margins and a maximum lateral spread of 100mm; surviving portion of lectotype is 30mm diameter and 10mm thick.

_Colour._ Live colouration apparently brown, beige-brown in dry state.

_Oscules._ Undifferentiated from honeycomb reticulate trabeculae.

_Texture and surface characteristics._ Surviving portion of lectotype brittle, partially crumbled when dry; surface minutely porous, partially arenaceous; close reticulation of rounded branches or 'lacunae' form interweaved ridges on encrusting base produced by irregularly honeycombed reticulate surface fibres. 

_Ectosome and subectosome._ Membraneous, with thick sand cortex; no specialised spicules or spongine fibres visible on surface; subectosome arenaceous.

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**Fig. 273. Holopsamma simplex** (Lendenfeld) (lectotype AMG8822). A, Principal styles (coring and echinating fibres). B, Subectosomal auxiliary stylostyles. C, Section through peripheral skeleton. D, Known Australian distribution. E, Lectotype.
**Choanosome.** Skeleton completely arenaceous, consisting of densely packed sand grains side-by-side, bonded together with abundant brown collagen; fibres absent; collagen covers surface of individual sand grains with smooth choanosomal principal styles embedded in and protruding from (?echinating) this basal layer, or sand grains may be free within mesohyl; subectosomal auxiliary subtylostyles scattered throughout mesohyl; choanocyte chambers not observed.

**Megascleres.** Choanosomal principal styles small, smooth, straight, with smooth, rounded or very slightly swollen bases, usually with telescoped points, sometimes slightly fusiform. Length 43-(50.8)-62μm, width 3-(4.1)-5μm.

Subectosomal auxiliary spicules thin subtylostyles, occasionally quasi-strongyles, straight,
slightly curved or sinuous, with asymmetrical ends. Length 68-(84.8)-99\(\mu\)m, width 2-(2.7)-3.5\(\mu\)m.

Microscleres. Absent.

REMARKS. This species is known only from two relatively poor type specimens. Lendenfeld's (1885c: 303) published geographical distribution for this species, supposedly including also Port Phillip Bay, Vic, NT waters, and Mauritius, is unsubstantiated by voucher material and not accepted here. This species is similar to E. (Protophilitaliaspongia) bispiculata in geometry of principal megascleres, and with several other arenaceous Holopsamma species (i.e., H. favus, H. crassa, H. laminaefavosa, H. felixi), although in H. simplex fibres cannot be differentiated from aggregated sand grains.

Holopsamma sp. indet. (Fig. 275, Plate 11F)

MATERIAL. QMG300620 (NCIQ66C-2389-N) (fragment MTMZ3563): Marion Reef, off Edinburgh, S. Yorke Peninsula, SA, 38°08.5'S, 137°48.0'E, 6m depth, 10.ii.1989, coll. NCI.

HABITAT DISTRIBUTION. 6m depth; on algae covered rock reef; SA (Fig. 275B).

DESCRIPTION. Shape. Groups of subspherical, bulbous lobes fused together, each composed of honeycombed reticulate lamellae producing a delicate Bryozoan-like lace.

Colour. Pale red-brown alive (Munsell 10R 7/8), brown in ethanol.

Oscules. Large, up to 6mm diameter, on apex of lobes; small ostia 1-2mm diameter scattered amongst surface lacunae.

Texture and surface characteristics. Harsh; surface membraneous, with distinct concentric ridges, slightly arenaceous layer on outer edge of ridges, fleshy between ridges.

Ectosome and subectosome. No ectosomal spicule skeleton; ectosome prominently arenaceous, fleshy below surface; ectosomal sand particles dispersed in association with primary ascending fibres.

Choanosome. Irregularly reticulate skeletal structure, with broad fibres up to 400\(\mu\)m diameter, partially or fully cored with detritus; mesohyl matrix very heavy; no native spicules; choanocyte chambers oval to elongate, 20-55\(\mu\)m diameter.

Megascleres. Absent.

Microscleres. Absent.

REMARKS. This single specimen is similar to several Holopsamma species (e.g., H. crassa, H. laminaefavosa) in being able to shed its spicules completely and replacing these with foreign detritus, particularly sand particles. Wiedenmayer (1989) discusses these arenaceous species in detail and the difficulty in assigning them to any particular taxon. On the basis of its growth form, fibre characteristics and skeletal architecture the specimen could be assigned to one of several species, and for the time being its specific identity is left indeterminate.

Echinochalina
Thiele, 1903

Refer to subgenera for synonymy.

TYPE SPECIES. Ophiolitaliaspongia australiensis Ridley, 1884a: 442 (by subsequent designation of Hallmann, 1912: 288).

DEFINITION. Monactinal, quasi-monactinal or thin diactinal auxiliary megascleres tangential or erect on ectosome; choanosomal skeleton irregularly reticulate; fibres cored by tracts of auxiliary megascleres, identical to those in ectosomal skeleton, and echinated by principal megascleres varying from true monactinal, quasi-diactinal to true diactinal forms, smooth or acanthose; microscleres may include palmate isochelae and toxas.

REMARKS. Twenty six species have been included in Echinochalina, of which 20 are valid, of which 16 live in Australian waters including 5 new species. All species are known from the Indo-west Pacific region (Hooper & Lévi, 1993a).

The genus contains 2 groups: one (Echinochalina (Echinochalina)) with true monactinal spicules, showing superficial affinities with Holopsamma (having honeycomb reticulate growth forms) and the Raspailiidae (fibre characteristics), and the other with quasi-diactinal or secondarily modified diactinal megascleres (Echinochalina (Protophilitaliaspongia)) superficially resembling Niphatidae (Haplosclerida). Both groups are linked by the common possession of auxiliary megascleres coring fibres and principal megascleres echinating fibres.

Echinochalina (Echinochalina)
Thiele, 1903

Echinochalina Thiele, 1903: 961; sensu Hallmann, 1912: 288.

Tablis de Laubenfels, 1936a: 76. [Echinoclathria]; Uriz, 1988: 89.

TYPE SPECIES. Ophiitaspongia australiensis Ridley, 1884a: 442.

DEFINITION. Monactinal, quasi-monactinal or secondarily derived true diactinal auxiliary megascleres core fibres, and monactinal principal spicules echinate fibres.

Echinochalina (Echinochalina) anomala
Hallmann, 1912
(Figs 276-277)


HABITAT DISTRIBUTION. 110-112m depth; substrate unknown; S. coast (NSW) (Fig. 276D).

DESCRIPTION. Shape. Massive, clathrous-honeycomb reticulate sponge, 125mm long, 75mm maximum width, composed of numerous, small, flattened fibre-branches, up to 12mm long, 4mm diameter, anastomosing and bifurcating.

forming tangled mass, attached directly to substrate.

*Colour.* Live colouration unknown, grey-brown in dry state.

*Oscules.* Not observed.

*Texture and surface characteristics.* Firm, harsh in dry state; surface fibres flattened, paper-like, porous reticulate with fibre-branches forming wide-meshed reticulation up to 3mm diameter.

*Ectosome and subectosome.* Membraneous, stretched across adjacent surface fibre-branches, with tangential auxiliary megascleres sparsely dispersed within ectosome, singly or less frequently in paucispicular bundles, and protruding echinating principal styles protruding through surface; choanosomal fibres immediately below ectosome.

*Choanosome.* Irregularly reticulate skeletal structure; primary spongin fibres large, heavy, 230-360μm diameter, irregularly interconnected by relatively thinner secondary fibres, 95-145μm diameter, forming cavernous meshes, 430-1090μm diameter; all fibres cored by multispecular tracts of auxiliary megascleres
occupied most of fibre diameter; fibres moderately heavily echinated by principal styles dispersed evenly over surface; mesohyl matrix light, containing numerous dispersed subeczosomal auxiliary spicules; choanocyte chambers not observed (dry material).

**Megascleres.** Principal styles echinating fibres relatively thick, straight or slightly sinuous, with smooth, slightly subtylote bases, fusiform points.

Length 160-(189.9)-236μm, width 7-(9.3)-11μm.

Auxiliary megascleres coring fibres and found interstitially long, thin, straight, entirely smooth, varying from nearly symmetrical quasi-strongyles to asymmetrical tornostyles with slightly subtylole bases and rounded points. Length 165-(215.4)-277μm, width 2-(4.3)-6.5μm.

*Microscleres.* Absent.

**REMARKS.** Burton (1934a) assigned a specimen from Eagle I. (Cairns section, Great Barrier Reef) to *E. (E.) anomala* but his material
was not found in the BMNH. Moreover, Burton’s figure does not resemble the holotype so that his record is dubious.

Skeletal fibre reticulation of *E. (E.) anomalata* is reminiscent of *Echinodictyum* (Raspailiidae), with very widely spaced fibre-meshes, and with fibres of large diameter which are heavily cored by megascleres. Unlike most *Echinodictyum* species, however, which have a greater emphasis on the mineral skeleton over the organic fibres, and which have true diactinal coring spicules, the fibres of *E. (E.) anomalata* are prominent and heavily cored by quasi-diactinal megascleres. The honeycomb reticulate growth form of *E. (E.) anomalata* is similar to *E. (E.) barba* (both reminiscent of *Holopsamma*) differing mainly in the geometry of its principal megascleres, differences in fibre construction and spicule dimensions.

**Echinochalina**
*(Echinochalina)*
*australiensis* (Ridley, 1884)
(Figs 278-279)

*Ophlitaspongia australiensis*
Ridley, 1884a: 442-443, pl.42, figs c.c*.

*Echinochalina australiensis*;
Thiele, 1903a: 961-962;


**MATERIAL.** HOLOTYPE: BMNH1881.10.21.299; Port Mole, Qld, 20°16’S, 148°42’E, l.v.1881, HMS ‘Alert’ (dredge). OTHER MATERIAL: SMF1855 (fragment MHNDCL2265).

**HABITAT DISTRIBUTION.** Rock and coral rubble substrata; 24m depth; Airlie region (NEQ)(Fig.278D); also Moluccas, Indonesia.

**DESCRIPTION.** Shape. Massive, branching, clathrous, honeycomb reticulate growth form, 55mm diameter, fibre-branches flattened, up to 12mm long, 5mm wide, with cavernous, angular meshes up to 10mm diameter.

*Colour.* Pale brown dry.

*Oscules.* Small, up to 4mm diameter, between adjacent fibre bundles.
Texture and surface characteristics. Firm, harsh dry; conulose surface produced by Anastomosing fibre bundles ("lacunae"), interconnected by translucent ectosomal membrane stretched between adjacent conules. *Ectosome and subectosome.* Membranous, with thinner choanosomal, undulating fibres lying immediately below ectosome, approximately 53 μm diameter, cored by paucispiracular tracts of auxiliary megascleres, and with irregular layer of auxiliary megascleres scattered tangential to surface.

*Choanosome.* Vaguely regularly reticulate skeleton, composed of primary, distinctively ascending, multispiracular fibres, 100-140 μm diameter, interconnected at irregular intervals by numerous transverse, paucispiracular, secondary fibres, approximately 70 μm diameter; fibre anastomoses form rounded or elongate, narrow meshes up to 270 μm diameter; fibres cored by auxiliary megascleres, sparsely echinated by principal subtylostyles; mesohyl matrix heavy but only lightly pigmented, with sparsely dispersed auxiliary megascleres between fibres; choanoocyte chambers ovoid, 20-25 μm diameter.

*Megascleres.* Principal subtylostyles (echinating fibres) straight, smooth, tapering, rounded or slightly subtyloide bases, fusiform or slightly telescoped points. Length 83-(111.2)-131 μm, width 6-7.2-9.5 μm.

Auxiliary megascleres (coring fibres and interstitial) straight, thin, subtylostyles, tornostyles or quasi-stongyles, with smooth, rounded, or very slightly subtyloide bases, tapering-rounded points. Length 147-178.2-192 μm, width 1.5-3.4-4.5 μm.

*Microscleres.* Absent.

REMARKS. Ridley (1884a) reported toxas (up to 42 μm long, 2 μm wide) but these were not found in either the holotype or in Thiele's (1903) material and they are probably contaminants. *E. (E.) australiensis,* like most members of the genus, has few diagnostic characteristics, superficially resembling *Echinodictyum cavernosum* (Raspailliidae) and *C. (Thalysias)* vulpina in growth form, with a heavy, well developed reticulate, *Clathria*-like, horny fibre skeleton cored by auxiliary spicules and echinated by principal spicules. It differs from other *Echinocochina* in spicule dimensions, well-developed skeletal structure and these fibre characteristics.

**Echinocochina** (*Echinocochina*) *barba* (Lamarck, 1814)  
(Figs 280-281, Plate 12A)

*Spongia barba* Lamarck, 1814: 372, 354; Topsent, 1930: 15-16, pl.4, fig.6.


*Spongia favosa* Lamarck, 1814: 373; Topsent, 1930: 19, pl.1, fig.5.

*Echinocochina glabra* Ridley & Dendy, 1886: 476; Ridley & Dendy, 1887: 163, pl.29, fig.11, pl.31, fig.2; Dendy, 1896: 40.

*Tabls glabra*; de Laubenfels, 1936a: 76.


Not *Echinocochina glabra*; Whitelegge, 1907: 504.


HABITAT DISTRIBUTION. Sandy, shell grit, rock or coral rubble substrata, kelp beds; 0-75 m depth; Montague I., Port Phillip Bay (Vic); King I., Deal I., Bass Strait (Tas); Kingston SE (SA); Flinders Is (FNS) (Fig. 281D). Thomas' (1977) reported locality of An-daman Sea is dubious from his description.

DESCRIPTION. Shape. Massive, subcylindrical, honeycomb reticulate sponge, up to 155 mm long, 75 mm wide, consisting of thin, flattened, irregularly anastomosing, reticulate fibre bundles; fibre anastomoses form meshes 3-5 mm diameter. Colour. Light grey-brown exterior, beige interior alive (Munsell 7.5Y8/6), yellowish brown in ethanol.

Oscules. Small, up to 3 mm diameter, recessed, dispersed between surface fibre bundles.

Texture and surface characteristics. Spongy, slightly rubbery, compressible, difficult to tear; surface of fibre bundles smooth, even, glabrous, porous and reticulate elsewhere, surface membrane stretched across adjacent fibre bundles.

*Ectosome and subectosome.* Thinly membranous, with irregularly dispersed
auxiliary megascleres lying tangential to surface and irregular, paucispicular, plumose brushes of principal spicules erect on peripheral fibres, barely protruding through ectosome; choanosomal fibres immediately subdermal.

*Choanosome.* Irregularly reticulate skeletal structure, with primary, vaguely ascending, distinctly meandering paucispicular fibres, 52-120 μm diameter, interconnected by aspicular or less frequently paucispicular, irregularly anastomosing, secondary fibres, 37-75 μm diameter; fibres cored by auxiliary megascleres, moderately echinated by principal subtylostyles especially on peripheral fibres; fibre anastomoses form nearly regular regular oval meshes, 165-370 μm diameter; mesohyl matrix heavy, moderately lightly pigmented, with numerous auxiliary megascleres dispersed between fibres; choanocyte chambers oval to elliptical, 38-145 μm diameter.

*Megascleres.* Principal subtylostyles (echinating fibres) short, thick, straight or very slightly curved, with smooth, tapering, distinctly subtylote bases, fusiform points. Length 62-(94.3)-115 μm, width 5-(7.1)-8.5 μm.

Auxiliary megascleres (coring fibres and interstitial) straight, quasi-diactinal subtylostragyles, rarely strongyles, with smooth, slightly subtylote bases and rounded points. Length 147-(189.2)-214 μm, width 1.5-(3.3)-4.5 μm.

*Microscleres.* Absent.

**Remarks.** *Echinoclinina barba* has a honeycombed reticulate construction similar to that of *E. (E.) anomal*a and reminiscent of *Holoponamma* species, but in which the surface is very smooth and flexible (superficially resembling an *Acanthella* (Axinellidae)). Both *E. anomal*a and *E. barba* also have asymmetrical (quasi-diactinal) auxiliary megascleres coring fibres, whereas in most other *Echinoclinina* these are more obviously monactinal. In *E. (E.) barba* fibre anastomoses are relatively closely compacted and principal styles (echinating fibres) are short, tapering, subtylote, whereas *E. (E.) anomal*a has a cavernous construction and long, more-or-less rounded principal megascleres.

**Echinoclinina (Echinoclinina) felixi** sp. nov. (Figs 282-283)

**Habitat Distribution.** Soft substrata inter-reef region; 19m depth; Turtle Is (FNQ) (Fig. 282F).

**Description.** *Shape.* Long, thinly cylindrical, fragile digit, 180 mm long, up to 60 mm diameter tapering towards base; embedded in soft substrata by small, cylindrical, basal root-like processes, up to 21 mm long, 3 mm diameter.

*Colour.* Beige-grey alive (Munsell 2.5Y 7/2), light brown in ethanol.

*Oscules.* Not observed.

**Texture and surface characteristics.** Firm, compressible; surface fibrous. macroscopically even, microscopically porous, honeycomb reticulate. *Ectosome and subectosome.* Fibrous, with peripheral spongin fibres tangential to surface, forming circular meshes up to 2.5 mm diameter, membranous ectosome stretched between adjacent fibres; outer surface of peripheral fibres with small blind fibre endings and protruding spicules, both visible under low magnification; auxiliary subtylostyles scattered on membranous ectosome, singly or in small bundles; subectosomal skeleton indistinguishable from choanosome.

*Choanosome.* Reticulate skeletal structure; fibres more-or-less homogeneous, 40-85 μm diameter cored by auxiliary subtylostyles in multispicular tract of up to 6 spicules abreast; fibres long, generally curved or sinuous, anastomosing, regularly bifurcate; shorter connecting fibres uni- or paucispicular; fibre meshes cavernous oval or elliptical, 170-490 μm diameter; fibres sparsely echinated by smaller principal subtylostyles; mesohyl matrix heavy, granular, cored by few microscleres and auxiliary megascleres; choanocyte chambers small, oval, 20-35 μm diameter.

*Megascleres.* Principal subtylostyles (echinating fibres) short, slender, straight, subtylote, smooth bases, tapering fusiform points. Length 207-(242.2)-278 μm, width 3-(3.3)-4.5 μm.

Auxiliary subtylostyles (coring fibres and dispersed in mesohyl) long, very slender, straight, slightly subtylote, smooth bases, tapering fusiform or sometimes blunted points. Length 285-(314.8)-345 μm, width 3.5-(4.3)-5 μm.

*Microscleres.* Palmate isochelae unmodified, front and lateral alae approximately equal length, lateral alae completely fused to shaft, front alae partially fused to lateral alae, straight shaft. Length 6-(10.1)-12 μm.

Toxas include both wing-shaped and slightly accolada forms, ranging from thin to raphidiform, often broken in preparations. Length 40-(65.8)-96 μm, width 0.8-(1.7)-2.5 μm.


ETYMOLOGY. For Dr Felix Wiedenmayer, Naturhistorisches Museum Basel, for his contributions to Australian sponges.

REMARKS. Echinochalina felixi is unusual having very thin megascleres and a cavernous reticulate construction, similar to E. digitata al-
though in that species fibres are both cored and echinated by principal styles, whereas in *E. felixi* auxiliary styles core fibres, growth form is cylindrical digitate, and toxas are present.
Echinochalina (Echinochalina) gabielli
(Dendy, 1896)
(Figs 284-285)

Echinochalina gabielli; de Laubenfels, 1936a: 119;

MATERIAL. HOLOTYPE: NMVG2359 (fragment
BMNH1902.10.18.341): Port Phillip Bay, Vic,
38°09'S, 144°52'E, 11-13m depth, coll. J.B. Wilson
dredge).

HABITAT DISTRIBUTION. Encrusting of shell fragments;
11-13m depth; Port Phillip (Vic) (Fig. 284F).

DESCRIPTION. Shape. Massive, lobate, semi-
encrusting on detritus, 130mm long, 65mm wide,
up to 45mm thick, with low bulbous lobes scattered
over surface.


Oscules. Single, large apical oscule, up to 3.5mm
diameter, on each surface lobe.

Texture and surface characteristics. Firm, com-
pressible, easily torn; surface lobate-bulbous, uneven,
microscopically rugose, reticulate, granular.

Ectosome and subectosome. Membranous, skin-
like ectosomal skeleton, minutely hispid with
points of auxiliary styles protruding through sur-
face in pauci- or multispecific plumose brushes,
some arising from ascending choanosomal skele-
tal tracts, others unattached to peripheral fibres
and free within mesohyl; sparse tangential tracts
of auxiliary styles below surface.

Choanosome. Irregularly reticulate skeleton,
with thin but well developed spongin fibres form-
ing primary, more-or-less ascending, and second-
ary connecting tracts; primary fibres, 40-70μm
diameter, cored by multi- or paucispecific tracts
of auxiliary styles in plumose or disorganised
arrangement; secondary connecting fibres, 15-
32μm diameter aspicular or unispicular, curved,
meandering throughout core of choanosomal
skeleton producing oval, elongate, cavernous
meshes, 180-310μm diameter, becoming more
regular, rectangular and cavernous towards
peripheral region of skeleton, with meshes 180-
360μm diameter; peripheral fibres slightly more
compacted; spicule tracts heavier in subec-
tosomal skeleton than at core; primary fibres
sparingly echinated by principal styles; mesohyl
matrix heavy, moderately heavily pigmented,
numerous principal styles dispersed between
fibres; choanocyte chambers elliptical, 62-
135μm diameter.

Megascleres. Principal styles echinating fibres
straight, short, relatively thick, with smooth,
rounded or slightly constricted, subtyloate bases
and nearly hastate points. Length 102-117.7-
138μm, width 3.8-(5.5)-6.5μm.

Auxiliary styles, coring fibres and interstitial,
straight or slightly curved, thin, relatively long,
fusiform, with smooth, rounded or very slightly
subtyloate bases. Length 142-(213.1)-264μm,
width 1.8-(2.7)-4.5μm.

Microscleres. Isochelae absent.

Toxas moderately uncommon, oxote, with slight
angular central curvature, straight points.
Length 90-(116.9)-135μm, width 1.5-(2.2)-
2.5μm.

Larvae. Viviparous, oval-elongate parenchymel-
la, 225-375x190-210μm, dark orange, heavily
collagenous, containing oxoete toxas and
juvenile styles.

REMARKS. De Laubenfels (1936a) referred this
species to Echinochalina (sensu Hallmann, 1912)
having fibres cored by megasceres geometrically
equivalent to auxiliary spicules, whereas styles
echinating fibres have a geometry equivalent to
principal megasceres of other Microcionidae.
Dendy's (1896) description differed in spicule
dimensions from my observations of the type.
Oxote toxas, much smaller than those described
by Dendy, are predominantly in association
with numerous larvae, and it is possible that
those spicules are merely juvenile quasidiactial
morphs of (auxiliary) coring megasceres. The
species differs from others in its spicule geometry
and size, in particular the toxas morphology,
and skeletal structure whereby spicule tracts increase
in density towards the peripheral skeleton.

Echinochalina (Echinochalina) intermedia
(Whitelegge, 1902)
(Figs 286-287, Table 44, Plate 12B)

? Echinochelaria viminalis; in part, Whitelegge, 1901:
87-88.

Not Thalassodendron viminalis Lendenfeld, 1888:
225.

Echinochelaria intermedia; in part, Whitelegge, 1902a:
214-215; Dendy, 1922: 71, pl.2, fig.8.

Echinochelaria intermedia; Hallmann, 1912: 294-295,
text-fig.69; Shaw, 1927: 427; Burton, 1934a: 563;
Hooper & Lévi, 1993a: 1273-1277, figs 27-28, table

MATERIAL. HOLOTYPE: AM: Lendenfeld's No.
365 (missing). NEOTYPE: QMGS300025: Inner
Gneerings, off Mooloolaba, 26°59'S, 153°10'E, 25m
depth, 10.xii.1991.

OTHER MATERIAL: (see Hooper & Lévi, 1993, for a list of additional material used in this study): QLD- QMG304757, QMG304293, QMG304388, QMG303863, QMG304025, QMG303984, QMG300834, QMG300865. INDONESIA - NCICDN-1306-F (fragment QMG303688).

HABITAT DISTRIBUTION. Sand, rock and coral rubble substrata; 8-50m depth; Lizard I., Day Reef.
and conules upon preservation; texture soft, compressible, mucous; pale orange-brown alive, brown in ethanol. Ectosome membranous, with tangential and paratangential tracts of auxiliary spicules scattered, barely protruding through surface; ectosome heavily collagenous, darker than choanosomal mesohyl; choanosomal skeleton irregularly reticulate, with long primary fibres, 90-130μm diameter, meandering through choanosome, becoming more plumo-reticulate near periphery, cored by multispicular tracts of whiskly auxiliary spicules, interconnected by short, aspicular or paucispicular secondary fibres, 40-70μm diameter, producing elongate or elliptical, cavernous meshes up to 450μm diameter; fibres sparsely echinated by principal spicules; mesohyl matrix heavy, with abundant auxiliary spicules scattered between fibres; choanocyte chambers large, oval, up to 60μm diameter. Principal styles short, thick, straight, smooth tapering or slightly subtylote bases, hastate or slightly telescoped points.

Direction Is, Howick Is, Snake Reef, Frankland Is, Sudbury Reef, Stanley Reef, Gulf of Carpentaria (FNQ); Hook Reef (NEQ); Mooloolaba, Moreton Bay (SEQ); Illawarra (NSW); E. coast (Tas); Dampier Archipelago, Northwest Shelf (WA) (Fig. 286F); also New Caledonia (Hooper & Lévi, 1993a), Cargados Carajos, Indian Ocean (Dendy 1922); Sulawesi, Indonesia (present study).

DESCRIPTION OF NEOTYPE. Massive, lobate, bulbous-digitate, 105mm high, 65mm maximum breadth; convoluted bulbous, cavernous surface in life, collapsing to form sharp ridges and conules upon preservation; texture soft, compressible, mucous; pale orange-brown alive, brown in ethanol. Ectosome membranous, with tangential and paratangential tracts of auxiliary spicules scattered, barely protruding through surface; ectosome heavily collagenous, darker than choanosomal mesohyl; choanosomal skeleton irregularly reticulate, with long primary fibres, 90-130μm diameter, meandering through choanosome, becoming more plumo-reticulate near periphery, cored by multispicular tracts of whiskly auxiliary spicules, interconnected by short, aspicular or paucispicular secondary fibres, 40-70μm diameter, producing elongate or elliptical, cavernous meshes up to 450μm diameter; fibres sparsely echinated by principal spicules; mesohyl matrix heavy, with abundant auxiliary spicules scattered between fibres; choanocyte chambers large, oval, up to 60μm diameter. Principal styles short, thick, straight, smooth tapering or slightly subtylote bases, hastate or slightly telescoped points.

Auxiliary spicules subtylostyles or tornostyles, long, slender, straight, slightly subtylote smooth bases, rounded points (178-206x2-3.5μm). Microscleres absent.

DESCRIPTION. (See Hooper & Lévi, 1993a).

DIAGNOSIS (Table 44 for spicule dimensions). Lobo-digitate with flattened branches and fibre bundles on surface, forming vaguely 'honeycombed' clathrous, reticulate growth form; pale orange-brown alive; large oscules mainly on apex of surface bulbs; surface conifuse with low ridges and grooves, paler translucent

TABLE 44. Comparison in spicule dimensions between populations of *Echinocyathus* (*Echinochalinia*) *intermedia* (Whitelegge). Measurements in μm (N=25). Comparative data from material examined here and Hooper & Lévi (1993a).

<table>
<thead>
<tr>
<th>Population (Latitude)</th>
<th>Auxiliary subbybystyles (core fibres)</th>
<th>Principal styles (echinating fibres)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neotype (QMG 300025) (26°S)</td>
<td>178-(190.7)-206 x 2-(2.6)-3.5</td>
<td>72-(85.1)-95 x 2.5-(3.1)-4.3</td>
</tr>
<tr>
<td>New Caledonia (22°S)</td>
<td>169-(175.3)-189 x 1.2-(1.9)-2.5</td>
<td>64-(87.1)-113 x 2.0-(2.8)-4.0</td>
</tr>
<tr>
<td>Great Barrier Reef (17-19°S)</td>
<td>184-(193.8)-205 x 2.0-(3.1)-5.0</td>
<td>85-(93.8)-110 x 4.0-(5.2)-6.0</td>
</tr>
<tr>
<td>Southern Qld (26°S)</td>
<td>184-(196.2)-208 x 1.5-(2.2)-3</td>
<td>72-(188.3)-101 x 2.5-(2.9)-4</td>
</tr>
<tr>
<td>NW Shelf WA (10°S)</td>
<td>89-(148.2)-180 x 1.5-(2.5)-4.0</td>
<td>92-(128.5)-149 x 4.0-(5.7)-7</td>
</tr>
<tr>
<td>Cargados Carajos (16°S)</td>
<td>200 x 3</td>
<td>110 x 7</td>
</tr>
<tr>
<td>Illawarra, NSW (34°S)</td>
<td>140-185 x 4</td>
<td>80-150 x 9</td>
</tr>
<tr>
<td>Sulawesi, Indonesia (1°N)</td>
<td>177-(183.2)-198 x 1.5-(4.9)-2.5</td>
<td>60-(82.7)-113 x 2.0-(3.2)-4</td>
</tr>
</tbody>
</table>

Source: 1. Dendy (1922); 2. Hallmann (1912).

**Remarks.** This species was redescribed mainly from New Caledonian material (Hooper & Lévi, 1993a). It is very characteristic in the field with a clathrous, 'honeycombed' reticulate growth form and pale orange-brown colour, and differs from other species in having an irregular plumo-reticulate skeletal architecture, poorly developed spongins fibres cored by a dense multispiracular axis of primary spicule tracts and light pauci-or aspicular tracts in secondary fibres, and hastate choanosomal (auxiliary) styles core fibres. Hooper & Lévi (1993a) note that the geometry of auxiliary spicules in this species varies between regional populations, ranging from exclusively styles in the original type material (now lost; Whitelegge, 1901, 1902a) and the Northwest Shelf of WA (Hooper & Lévi, 1993a), to virtually all strongyles in material from Mooloolabah including the neotype (present study) and Cargados Carajos (Dendy, 1922). New Caledonian population differs from others in having more abundant detritus and much more slender echinating styles, whereas growth form, skeletal architecture and spicule geometry are relatively homogeneous for the species.

_Echinochalinia intermedia_ is used in the sense of Hallmann (1912) and Dendy (1922), because the synonymy of this species is still confused, and the validity of type material of _Thalassosodendron viminalis_ and _Echinochalinia intermedia_ require further clarification. Lendenfeld (1888: 225) erected _T. viminalis_ for a specimen from Illawarra, NSW; whereas Whitelegge (1901: 87) found the original description incorrect based on a misidentified cylindrical branching specimen belonging to _Echinochalinia subhispida_. Whitelegge (1901) redescribed the species based on a clathrous specimen (No. 365, confirmed missing from AM collections), which he subsequently designated holotype of _intermedia_ (Whitelegge, 1902a: 214). However, he also redescribed a second specimen for the species (Lendenfeld's No. 332), which unfortunately belongs to _E. subhispida_. Both Lendenfeld's and Whitelegge's actions have created confusions, and, moreover, Lendenfeld's manuscript names and numbers on slides and specimens in the AM and BMNH do not completely correlate with the published descriptions (see remarks for _E. subhispida_). I accept _E. intermedia_ in the sense of Hallmann (1912), and designate a neotype for this species from the material described above, the most 'typical' being QMG300025 from Mooloolaba, SE. Qld.

skin-like membrane covering, darker below; ectosome membranous with tangential or occasionally paratangential sparse tracts of auxiliary spicules, lightly arenaceous, and sparse plumose brushes of auxiliary megascleres from ascending choanosomal fibres protruding short distance through surface predominantly on surface conules; choanosomal skeleton irregularly plumo-reticulate, spongins fibres well developed; primary fibres lightly cored by multispiracular tracts of auxiliary megascleres becoming increasingly plumose towards periphery; secondary connecting fibres un-, pauci- or aspicular; all fibres irregularly echinated by sparse principal styles, mainly on primary fibres; fibre anastomoses form irregular elongate, oval, elliptical or rarely rectangular meshes, meshes more cavernous in periphery than at core; mesohyl matrix heavy, numerous auxiliary spicules and detritus scattered between fibres; principal styles echinating fibres short, thick, straight, almost hastate, with smooth, rounded, tapering, or less frequently with very slightly subtylole bases; auxiliary megascleres cored fibres and dispersed within mesohyl long, thin, mostly straight, with rounded smooth bases, varying from styles, torosyles or less often strongyles, usually with blackened axial canals, with rounded or slightly hastate points; microscleres absent.
Echinocochalina (Echinocochalina) reticulata
Whitelegge, 1907
(Figs 288-289)

Echinocochalina reticulata Whitelegge, 1907: 506, pl.45, fig.25; Hallmann, 1912: 289-290, pl.30, fig.2, text-fig.66 (et var.); Hooper & Wiedenmayer, 1994: 278.

Tablis reticulata; de Laubenfels, 1936a: 76.


HABITAT DISTRIBUTION. Soft substrata; 110-112 m depth; Wollongong (NSW); Flinders I. (Tas) (Fig. 288D).

DESCRIPTION. Shape. Massive, rounded, globular, lobo-digitate to thickly flabellate, up to 240 mm long, 255 mm wide, 150 mm thick, with honeycomb reticulate construction produced by closely anastomosing, very thin membraneous, lamellate, apically pointed, fibre bundles. Colour. Brown to grey-brown in ethanol.

Oscules. Large, up to 5 mm diameter, scattered within lacunae of surface honeycomb reticulation.

Texture and surface characteristics. Firm, flexible, harsh in dry state; surface honeycomb reticulate, lamellae very thin, membraneous and uneven.

Ectosome and subectosome. Membranous, tangentially disposed auxiliary megascleres lying below surface, in pauci- or multispecific tracts, pierced by sparse plumose bundles of auxiliary spicules from ascending choanosomal tracts.

Choanosome. Irregularly reticulate skeletal structure, verging on subisodictyal, with differentiated primary and secondary spongion fibre systems; fibres relatively light, mostly flattened, meandering or sinuous; primary fibres, 65-112 µm diameter, pauci- or multispecific, running longitudinally through lamellae, intersected at regular intervals and obtuse angles by secondary fibres, 22-40 µm diameter, mostly uncored, occasionally unispecific; fibres anastomoses form cavernous elliptical meshes, 175-570 µm diameter; fibres cored by auxiliary megascleres, moderately heavily echinated by principal spicules; mesohyl matrix heavy but only lightly pigmented, with numerous auxiliary megascleres scattered between fibres; choanoocyte chambers large, oval, 45-75 µm diameter.

Megascleres. Principal styles echinating fibres straight, thick, with smooth, tapering, rounded or slightly subtylate bases, fusiform points. Length 108-(139.8)-196 µm, width 6-(8.9)-11 µm.

Auxiliary megascleres coring fibres straight, slightly curved or sinuous, thin, ranging from hastate subtylotyles to asymmetrical tonnostyles or sometimes strongyles, with rounded or slightly subtylate bases, rounded or telescoped points. Length 146-(252.0)-336 µm, width 2.5-(4.1)-5.5 µm.

Microscleres absent.

Larvae. Viviparous, small, oval parenchymella, 80-110 µm diameter, with heavy matrix.

REMARKS. In growth form, particularly its flattened spongion fibres, the holotype resembles the Caribbean Pandaros acanthifolium (Duchassaing & Michelotti), whereas Hallmann’s variety crassa is more reminiscent of honeycomb reticulate species of Holopsamma. However, in spiculation and skeletal architecture both morphs are identical and conspecific. Pandaros and Echinocochalina differ substantially in their spicular geometries, whereby Pandaros has smooth or acanthous principal styles coring and echinating fibres, equivalent to those of Holopsamma, E. reticulata has auxiliary styles coring fibres and principal styles echinating fibres, typical of the Echinocochalina condition. The species differs from other Echinocochalina in spicule geometry, particularly the endings of auxiliary subtylotyles, spicule size, possession of flattened fibres, and a nearly isodictyal skeletal architecture, whereas in growth form it is similar to E. (E.) barba.

Echinocochalina (Echinocochalina) ridleyi
(Dendy, 1896) (Figs 290-291)


? Clathrissa or Styloletopsis ridleyi; Hallmann, 1912: 151.


MATERIAL. LECTOTYPE: NMVG2409: Port Phillip Bay, Vic, 38°09'S, 144°52'E, 40 m depth, coll. J.B. Wilson (dredge). PARALECTOTYPES: NMVG2410: same locality, 38 m depth. BMNH1902.10.18.363; same locality, 38 m depth. BMNH1902.10.18.364, 57: same locality, 40 m depth.

HABITAT DISTRIBUTION. Substrate unknown; 38-40 m depth; Port Phillip (Vic) (Fig. 290D).

DESCRIPTION. Shape. Stalked, digitate, club-shaped, 85-165mm long, 50-80mm maximum width, with thick cylindrical stalk, 18-32mm long, 12-17mm diameter, bulbous digitate apex composed of more-or-less flattened, fused lamellae, up to 18mm wide, together producing bushy, flattened flabelliform or claviform growth.
**Colour.** Reportedly pale red-brown to red-orange in life, pale brown in ethanol.

**Oscules.** Not observed.

**Texture and surface characteristics.** Firm, compressible, flexible; surface optically smooth with distinct skin-like dermis.

**Ectosome and subectosome.** Membraneous, microscopically hispid with multispiracular, erect and paratangential tracts of auxiliary spicules, singly or in sparse plumeose brushes. Periphery of auxiliary megascleres, sparsely echinated by principal spicules; mesohyl matrix heavy but only lightly pigmented, with numerous auxiliary megascleres dispersed between fibres; choanocyte chambers large, oval to elongate, 90–120 μm diameter.

**Megascleres.** Principal acanthostyles echinating fibres small, straight, relatively thick, with tapering rounded bases, spined apical and basal extremities, fusiform points; spines small, conical, erect. Length 87–(104.1)–116 μm, width 5–(5.8)–7 μm.

Auxiliary spicules coring fibres long, thin, straight, slightly curved or sinuous, sometimes raphidiform, with variable terminations ranging from hastate oxeas, tomonts, quasi-monactinal tormostyles, or subtystalostyles. Length 184–(261.3)–314 μm, width 2–(4.1)–6.5 μm.

**Microscleres** Absent.

**REMARKS.** Dendy (1896) initially assigned this species to *Echinodictyum* (Raspallidae) having diactinal coring, monactinal echinating megascleres, extra-axial styles, and a more-or-less reticulate architecture. However, the spicules which actually core these fibres range from true diactinal to true monactinal forms, without obvious axial and extra-axial differentiation in their distribution. The skeletal architecture verges on plumeose, not prominently reticulate as is found in most *Echinodictyum* species, and fibres are much heavier than those normally found in species of that genus (see Hooper, 1991). Including this species in *Echinocelinala* requires broadening the generic definition to allow for the inclusion of spuned echinating styles, but these spicules appear to be true principal megascleres (as opposed to a special category of echinating acanthostyles such as those found in *Clathria*, for example). In any case, Simpson (1968a) and others have shown that acanthose verses smooth megascleres may be of minor consequence at higher systematic levels in Microcionidae, and in other respects the species fits well with the present concept of *Echinocelinala*. The species has closest affinities to *E. spongiosa*, also having acanthose principal spicules, though differing substantially in growth form, spicule geometry and spicule dimensions.

**Echinocelinala (Echinocelinala) spongiosa**

(Dendy, 1896)

(Figs 292–293).

**Echinodictyum spongiosum** Dendy, 1896: 45; Hallmann, 1912: 151.


**MATERIAL. LECTOTYPE:** NMV2452: Sorrento Jetty, Port Phillip Bay, Vic, 38°21′S, 144°42′E, 20 m depth, coll. J.B. Wilson (dredge). PARALETYPOE: BMNH1902.10.18.58, 365; same locality.

**HABITAT DISTRIBUTION.** Substrate unknown; 12m depth; Port Phillip (Vic) (Fig. 292D).

**DESCRIPTION.** Shape. Thickly encrusting, massive, subspherical sponge, 65 mm diameter, attached directly to substrate.

**Colour.** Reportedly grey in life, pale brown in ethanol.

**Oscules.** Not observed.

**Texture and surface characteristics.** Firm, compressible, spongy; surface shaggy, covered with large, mostly irregular, lobate papillae, low ridges and abundant striaions.

**Ectosome and subectosome.** Membraneous, lightly arenaceous ectosome, with irregular plumeose brushes of auxiliary megascleres barely protruding through surface arising from peripheral choanosomal fibres.

**Choanosome.** Plumo-reticulate skeletal structure, verging on plumeose-dendritic in periphery, without any obvious differentiation into primary or secondary fibres or tracts; fibres at core of skeleton light, whispy, multispiracular, sinuous, reticulate, 22–54 μm diameter, interconnected at irregular intervals by smaller multispiracular fibres,

8-18\(\mu\)m diameter, forming irregular ovoid, rectangular or elongate meshes, 65-118\(\mu\)m diameter; fibres increasingly plumose, more paucispicular towards periphery, terminating on or near surface as single spicules; skeletal tracts in periphery occupy most of fibre diameter, rang-

From 12-35 μm diameter, fibre meshes cavernous, elongate, 240-660 μm diameter; all fibres cored by auxiliary megascleres, sparsely echinated by principal spicules; mesohyl matrix very heavy, dark yellow-orange pigmented, with moderate numbers of auxiliary spicules scattered between fibres; choanocyte chambers small, oval, 15-54 μm diameter.

*Megascleres.* Principal styles echinating fibres straight, relatively thin, subtyloate, with light
spines concentrated mainly on base and near points, fusiform, bare points. Length 82-(92.3)-98μm, width 2.5-(4.4)-5.5μm.

Auxiliary spicules coring fibres thin, mostly straight, sometimes slightly curved or sometimes sinuous, varying from toornstyles, strongly or toornotes with rounded or subtylet exterimities. Length 166-(187.6)-214μm, width 1.5-(3.2)-4.2μm.

**Microscleres** absent.

**REMARKS.** *Echinochalina* (*E.*) *spongiosum* was originally assigned to *Echinodictyum*, like *E. (E.) ridleyi*, having diactinal coring and monactinal echinating spicules, but *E. (E.) spongiosum* was even more atypical of *Echinodictyum* in its skeletal architecture, having an almost completely plumeo skeleton, with only vestiges of reticulate construction. The species is easily assigned to *Echinochalina* even though it has acanthose (versus completely smooth) principal styles echinating fibres (see remarks for *E. (E.) ridleyi*), differing from *E. (E.) ridleyi* in growth form, spicule geometry and spicule dimensions.

**Echinochalina (Echinochalina) tubulosa**

(Hallmann, 1912)

(Figs 294-295, Plate 12C)

*Ophlitaspongia tubulosa* Hallmann, 1912: 272-275, pl.35, fig.3, text-fig.60.


*Echinoelathria tubulosa*; Wiedenmayer, 1989: 66, pl.6, fig.9, fig.25, figs 3-4, text-fig.45.


**HABITAT DISTRIBUTION.** Sand, rock and coral rubble substrata; 15-32m depth; Turtle ls, Agincourt Recfs (FNQ); Moreton I. (SEQ); Illawarra (NSW); Westemport Bay (Vic); Kent ls, Bass Strait (Tas); Kangaroo I. (SA) (Fig. 294D).

**DESCRIPTION.** Shape. Tubulo-digitate, massive, erect, up to 120mm high, attached directly to substrate, with erect, regularly cylindrical or irregular, stoloniferous, thin or thick, bulbous digits tapering towards their extremities, up to 45mm high, 22mm diameter.

**Colour.** Bright orange, yellow-orange, or vermilion-red alive (Munseil 10R 6/10 - 2.5R 5/10), pale brown in ethanol.

**Oscules.** Large, up to 10mm diameter, at apex or subapical on each digit.

**Texture and surface characteristics.** Firm, rubbery, compressible, flexible digits; surface even, porous, microscopically rugose fibre bundles.

**Ectosome and subectosome.** Membranous, with dense paratangential layer of auxiliary styles lying below, occasionally protruding through surface, in irregular plumose formations, with or without light arenaceous ectosomal layer; choanosomal fibres immediately below ectosome.

**Choanosome.** Regularly isodictyal to irregularly reticulate skeletal architecture, with poorly differentiated primary and secondary fibres; primary ascending fibres thin, 42-93μm diameter, heavy, paucispicular, sometimes uni- or aspicular, occasionally meandering, sinuous, often ascending directly to periphery, interconnected at irregular intervals by thin, more-or-less transverse, uni- or aspicular secondary fibres, 18-35μm diameter; secondary fibres branch and Anastomose amongst themselves, forming oval, retangular or triangular, relatively cavernous meshes, 124-650μm diameter; fibres cored by predominantly longer and thinner auxiliary megascleres, never forming more than paucispicular tracts, usually becoming plumeo towards periphery; fibres echinated by shorter, stouter principal spicules; mesohyl matrix heavy but only lightly pigmented, with numerous thin auxiliary spicules dispersed between fibres and occasionally also small quantities of inorganic debris; choanocyte chambers large, oval, 72-113μm diameter.

**Megascleres.** Principal styles echinating fibres styles straight, short, relatively thick, with smooth, evenly rounded bases or less frequently slightly subtylet bases, almost hasteate points. Length 74-(96.5)-128μm, width 4-(6.6)-8.5μm.

Auxiliary styles coring fibres and interstitial long, thin, straight or slightly curved hasteate styles, occasionally modified to asymmetrical styloids, toornotes or strongyles, rarely sinuous. Length 108-(226.1)-305μm, width 1-(2.2)-4.5μm.

**Microscleres** absent.
Larvae. Incubated parenchymella larvae in 1 specimen, oval, small 62-170μm diameter, containing abundant collagen but no larval spicules.

Associations. One specimen contained numerous algal filaments within fibres, almost completely obscuring spicules within fibre skeleton; Wieden-
mayer (1989) also noted microsymbionts in his material from Bass Strait.

**REMARKS.** This species shows some variability, particularly in organisation of skeletal structure (ranging from regularly isodictyal fibre network to irregularly reticulate), palmate isochelae were abundant in 1 specimen from SA (but presumed to be contaminants), and position of oscules (terminally or subterminally on digits), otherwise there is no doubt that all these specimens belong to *E. (E.) tubulosa*. The longer, thinner styles coring fibres and shorter, thicker styles echinating fibres indicate that it belongs to *Echinochalina*. Interpretation of these features is of primary importance in generic placement. This species has been included with *Ophlitaspongia (=Echinoclaethria) (Hallmann, 1912)*, or *Echinoclathria (=Holopsamma) (Wiedenmayer, 1989)*, based on misinterpretation of these genera and that megascleres coring and echinating fibres were geometrically identical. However, it is clear that longer, thinner auxiliary styles are most commonly found inside fibres, whereas shorter, thicker principal styles are most frequently found.

Echinochalina lacked Protophhtaspongia more-or-less infer 5mm supported isochelifera being with this pear monactinal several megascleres, Echinochalina Soest (Uriz, 1898) is modified megascleres (Protophhtaspongia) bispiculata, although spicule geometry is very different.

OTHER SPECIES OF ECHINOCHALINA

(ECHINOCHALINA)

Echinochalina (Echinochalina) isochelifera (Uriz, 1988)
Echinochalina isochelifera Uriz, 1988: 89-90, pl. 22b, 42c, 36b-d, text-fig. 64 [Namibia].
MATERIAL. HOLOTYPE: AB1P7B-6A, SW. Africa.

Echinochalina (Echinochalina) melana Van Soest & Stentoff, 1988
Echinochalina sp. Hartman in Lewis, 1965: in table. Echinochalina melana Van Soest & Stentoff, 1988: 123-125, pl. 12, fig. 1, text-fig. 60 [Barbados, West Indies].
MATERIAL. HOLOTYPE: ZMAPOR5509, Caribbean.

Echinochalina (Protophhtaspongia) bispiculata

Burton, 1934


TYPE SPECIES. Siphonochalina bispiculata Dendy, 1895: 246 (by original designation).

DEFINITION. Diactinal or quasi-monactinal auxiliary megascleres core fibres, with diactinal or quasi-monactinal principal spicules echinating fibres.

REMARKS. In this subgenus structural megascleres (coring and echinating fibres) appear to be diactinal, unlike all other microcionids, but they are interpreted here as being highly modified monactinal spicules allowing its inclusion in the Microcionidae. This interpretation is supported by the more-or-less plumeous ascending, primary spicule tracts, true echinating megascleres, isochelae and toxo microscleres in several species, and obvious (i.e., less modified) monactinal ectsosomal spicules in several species, indicating affinities with Echinochalina. The coring and echinating megascleres are equated here with auxiliary and principal spicules, respectively, of typical Echinochalina. Dendy (1896) included the type species in the Haplosclerida, but remarked on its unique spicule arrangement, particularly the ectsosomal structure and fibre echination. Burton (1934a) assigned the type to Microcionidae, for similar reasons as those outlined above, whereas de Laubenfels (1936a) referred it to the Desmacididae because, he suggested, the hastate diactinal megascleres resembled those of Guiterara and Liosina, although it lacked poecilosclerid microscleres. Echinochalina (P.) bispiculata is included in this subgenus since it has a paratangential ectsosomal skeleton composed of auxiliary megascleres, reticulate spongin fibres and echinating principal spicules, whereas other species described by de Laubenfels (1936a) (P. aca, P. aca and P. antiliana) are more appropriately placed in Desmacididae and Haplosclerida (see remarks for Protophhtaspongia under Genera Included).

Eight species are now included in this subgenus, 2 known exclusively from New Caledonia and the remainder from eastern Australia. (Table 46; Hooper & Lévi, 1993a: 1279).

Echinochalina (Protophhtaspongia) bispiculata

(Dendy, 1895)
(Figs 296-297, Table 45)


HABITAT DISTRIBUTION. Rock reef; 34-38m depth; Port Phillip (Vic) (Fig. 296D).

DESCRIPTION. Shape. Massive, subspherical, irregularly lobate, 90mm maximum diameter, with short bulbous surface lobes, or subcylindrical, flattened digitate spongy, 160mm long, 28mm wide, 15mm thick.

Colour. Pale yellow-brown in ethanol.

Oscules. Small, 2-3mm diameter, scattered over surface, particularly on apex of surface lobes.
Texture and surface characteristics. Soft, compressible, slightly rubbery; surface optically even, minutely reticulate.

Ectosome and subectosome. Microscopically hispid ectosome with scattered plumose brushes of long, thin auxiliary oxas, arising from the points of peripheral fibres and paratangential to surface; choanosomal fibres immediately below surface although spicule tracts more plumose in peripheral skeleton than at core.

Choanosome. Regularly reticulate to subisodictyal skeletal structure, with well developed fibres divided into primary and secondary elements; primary fibres ascending, multispicular, 60-95μm diameter, forming distinctly plumose tracts within core of fibre, interconnected at more-or-less regular intervals by slightly thinner secondary fibres, transverse, uni-, pauci- or aspicular fibres, 20-43μm diameter; fibres relatively light, cored by long, thin auxiliary oxas and echinated by short, stout principal oxas; fibre anastomoses form cavernous ovoid meshes, 180-540μm diameter; mesohyl matrix heavy but only lightly pigmented, with moderate quantities of auxiliary spicules dispersed between fibres; choanocyte chambers large, oval to elongate, 60-130μm diameter.

Megascleres (Table 45). Principal megascleres echinating fibres straight, short, thick, invariably smooth, hastate oxas, with abruptly pointed or telescoped ends.

Auxiliary megascleres coring fibres long, thin, straight, hastate or rarely fusiform oxas.

Microscleres absent.

Larvae. Incubated parenchymella larvae small spherical, with heavy mesohyl matrix, 210-240μm diameter, no larval megascleres.

REMARKS. Of all E. (Protolithaspongia) this species is the most reminiscent of Haplosclerida in skeletal characteristics (e.g., three dimensional ectosomal architecture like Hemigellius (Niphidiae); choanosomal fibre construction similar to Callyspongia (Callyspongiidae)). Echinochalina (P.) bispiculata is slightly similar to E. (P.) oxeata but that species lacks true geometric differentiation between coring and echinating spicules and has a different growth form (Table 46).
Echinochalinna (Protophilaspongia) collata sp. nov.

(Figs 298-299, Table 45, Plate 12D)

Echinochalinna (Protophilaspongia) collata sp. nov.

MATERIAL. HOLOTYPE: QMG304120: Blue Lagoon, Lizard I., Cairns section, Great Barrier Reef, Qld, 14°41.0'S, 145°27.5'E, 9m depth, 3 iv 1994, coll. J.N.A. Hooper & S. Cook (SCUBA).

HABITAT DISTRIBUTION. Coral pinnacles; 9m depth; Lizard I. (FNQ) (Fig. 298F).

DESCRIPTION. Shape. Thickly encrusting, up to 12mm thick, bulbous in places on surface following contours of substrate.

Colour. Dark red alive (Munsell 2.5R 4/10), light brown in ethanol.
**Oscules.** Very small, 1-2 mm diameter, on apex of larger surface bulbs, surrounded by radiating sub-ectosomal drainage canals.

**Texture and surface characteristics.** Harsh, firm, compressible; surface microconulose, minutely shaggy, conules close-set, less than 2 mm high, surface silty in situ with radiating drainage canals clear of silt.

**Ectosome and subectosome.** Slightly plumeose, multiserial brushes of auxiliary spicules from primary choanosomal tracts protrude through surface mainly on ends of conules; bundles of ectosomal auxiliary styles tangential to surface; abundant detritus and collagen in ectosomal layer.

**Choanosome.** Irregularly reticulate skeletal structure, very heavy spongy fibres relatively homogeneous throughout skeleton, 45-120 μm diameter, forming oval or elongate meshes, 120-440 μm diameter, without marked difference in mesh size between periphery and core of skeleton; ascending primary fibres cored by multiserial tracts of auxiliary spicules but occupying only about 50% of fibre diameter, interconnected by unibranchial secondary, transverse fibres; fibres sparsely echinated by thinner oxexes ('principal spicules') protruding at acute angles through fibres; mesohyl matrix heavy, with moderate numbers of auxiliary megascleres and toxas microscleres dispersed between fibres; choanoocyte chambers large, elongate, 30-60 μm diameter.

**Megascleres** (refer to Table 45 for dimensions). Principal (?) spicules echinating fibres short oxes, thin, straight or slightly curved at centre, with telescoped points.

Auxiliary spicules eoring fibres vary from true oxes to true styles, with many intermediates, long, thick, straight or slightly curved at centre, points usually telescoped.

Ectosomal auxiliary styles or anisosoxes long, thin, whipsy, straight or slightly curved, with rounded or spiked base and fusiform or telescoped points.

**Microscleres** (Table 45). Toxas intermediate between oxhorn and wing-shaped, thin, slightly curved at centre, slightly reflexed points.

**ETYMOLOGY** Latin collata (L.), extended, diffuse: for the growth form.

**REMARKS.** This species is unusual in its thickly encrusting growth form, conulose surface, multiserial tracts occupying only about 50% of fibre diameter, prevalence of telescoped points and asymmetrical spicules. It is most similar to, and probably a sibling species of, *E. (P.) tuberosa* in having a special category of ectosomal styles and oxhorn toxas, although spicule geometry and spicule sizes are substantially different between these species. Further comparisons between species of *E. (Protophyllatispongia)* are given in Table 46.

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<table>
<thead>
<tr>
<th>SPICULE</th>
<th><em>E. (P.) tuberosa</em> Hooper &amp; Lévi (QMG300068) (New Caledonia)</th>
<th><em>E. (P.) favalosia</em> Hooper &amp; Lévi (QMG301720) (New Caledonia)</th>
<th><em>E. (P.) favalosia</em> sp.nov. (QMG2166) (SE QLD)</th>
<th><em>E. (P.) favalosia</em> sp.nov. (QMG20050) (GBR, Qld)</th>
<th><em>E. (P.) favalosia</em> sp.nov. (QMG1930) (BMNH1930) (GRB, Qld)</th>
<th><em>E. (P.) favalosia</em> sp.nov. (QMG1930) (GRB, Qld)</th>
<th><em>E. (P.) favalosia</em> sp.nov. (QMG1930) (GRB, Qld)</th>
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</thead>
<tbody>
<tr>
<td><strong>Auxiliary (coring) oxes</strong></td>
<td>52(75.1)-108 x 1.8(2.9)-4.0</td>
<td>55(73.3)-98 x 0.8(1.9)-3.0</td>
<td>101(121.2)-166 x 3.5(6.1)-7.0</td>
<td>252(265.2)-287 x 3(3.5)-4.5</td>
<td>128(132)-164 x 3.5(4.2)-7.0</td>
<td>197(235.6)-326 x 6(8.7)-11</td>
<td>102(123.9)-158 x 3(4.6)-7</td>
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<tr>
<td><strong>Ectosomal auxiliary styles</strong></td>
<td>115(156.2)-194 x 1.0(1.7)-2.5</td>
<td>144(216.1)-278 x 1.0(2.4)-3.5</td>
<td>absent</td>
<td>212(234.0)-262 x 2(2.8)-3</td>
<td>absent</td>
<td>212(237.2)-264 x 1.5(2.2)-3</td>
<td>114(187.7)-215 x 1.5(2.2)-3</td>
</tr>
<tr>
<td><strong>Principal (echinating) oxes</strong></td>
<td>28(33.5)-42 x 2(2.5)-4.0</td>
<td>32(46.7)-58 x 1.0(2.0)-2.5</td>
<td>57(79.7)-122 x 4.5(6.2)-7.5</td>
<td>118(142.7)-162 x 2(3.4)-4</td>
<td>absent</td>
<td>94(148.0)-188 x 1.5(4.2)-6</td>
<td>54(71.2)-84 x 2(2.8)-4</td>
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<td><strong>Chelae</strong></td>
<td>absent</td>
<td>14(15.5)-21</td>
<td>9(10.7)-14</td>
<td>absent</td>
<td>absent</td>
<td>14(13.2)-118 x 1(1.6)-2</td>
<td>18(44.1)-64 x 0.5(0.9)-1.5</td>
</tr>
<tr>
<td><strong>Toxas</strong></td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>31(49.9)-62 x 0.5(1.1)-1.5</td>
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Echinochalina (ProtophHtaspongia) favulosa sp. nov.
(Figs 300-301, Table 45)


HABITAT DISTRIBUTION. Sand and shell grit substrata; 480m depth; Noosa region (SEQ) (Fig. 300E).

DESCRIPTION. Shape. Irregularly branching, cylindrical sponge, 195mm long, up to 33mm diameter, without apparent basal attachment; branches bifurcate few times.

Colour. Live colouration unknown, grey-brown ethanol.

Oscules. Large, up to 5mm diameter, on lateral margins and ends of branches.
Texture and surface characteristics. Soft, compressible; surface 'honeycomb' reticulate, highly porous, uneven, conulose.

Ectosome and subectosome. Membranous, minutely conulose surface with erect, paucispicular brushes of auxiliary megascleres arising from choanosomal spicule tracts protruding into surface conules but rarely through surface; some detritus scattered over surface; choanosomal fibres immediately below ectosomal skeleton.

Choanosome. Regularly reticulate, subisodictyal skeletal architecture composed of more-or-less ascending, multi- or paucispicular, primary fibres, 22-43 µm diameter, interconnected at irregular intervals by transverse, uni-, paucis- or aspicular fibres, 14-25 µm diameter; fibres cored by longer auxiliary megascleres and moderately echinated by shorter, principal spicules; fibre anastomoses form relatively wide, elongate or hexagonal meshes, 92-236 µm diameter; mesohyl matrix heavy, relatively darkly pigmented, granular, with auxiliary and principal megascleres dispersed between fibres; choanoocyte chambers small ovoid to elongate, 22-46 µm diameter.

Megascleres (Table 45). Principal megascleres echinating fibres relatively short, thick, straight, hastate oxeas, sometimes slightly telescoped, occasionally quasi-monactinal (asymmetrical ends), rarely styles, only marginally shorter than coring spicules.

Auxiliary spicules coring fibres long, slender, straight, hastate oxeas, often with telescoped points, occasionally modified to quasi-monactinal forms, rarely true styles, longer forms generally thinner.

Microscleres (Table 45). Palmate isochelae abundant, small, with approximately 15% twisted forms, lateral alae completely fused to shaft, front ala partially detached from lateral alae, shaft straight.

Toxas absent.

ETYMOLOGY. For its honeycomb reticulate growth form.

REMARKS. This species is unusual for its Holoparma-like honeycomb reticulate growth form, having palmate isochelae, both principal and auxiliary spicules ranging in geometry from (predominantly) oxeas to styles, with asymmetrical intermediate geometries, and coring and echinating spicules differing only marginally in their length and thickness. The possession of isochelae microscleres in the present species supports the inclusion of the genus in the Poecilosclerida, although it is still feasible that this species, and Protophllitaspanga, may be more appropriately assigned to the poecilosclerid Desmacididae (de Laubenfels 1936a) and followed by Pulitzer-Finali (1986), but little support for its inclusion in the haplosclerid Niphatidae as proposed for Isodictya by Hajdu et al., 1994b.

Echinochalintra (Protophllitaspanga) isaci sp. nov. (Figs 302-303, Table 45, Plate 12E)


HABITAT DISTRIBUTION. Fringing coral reefs, coral pinnacles, outer reef slopes, on dead coral, 20-33 m depth; Oyster Reef (FNQ); Swain Reefs (MEQ) (Fig. 302E).

DESCRIPTION. Shape. Arborescent, digitate, branching, up to 150 mm high, with conical cylindrical branches, up to 80 mm long, 15 mm diameter, bifurcate at tips and expanded towards apex of branches in life, collapses producing flattened branches in ethanol; basal stalk up to 25 mm long, 12 mm diameter, with expanded basal attachment.

Colour. Pale orange-brown alive (Munsell 5R 7/8), light brown in ethanol.

Oscules. Large, up to 15 mm diameter alive, on apex of each digit, surrounded by raised membranous lip, collapses completely in ethanol leaving no visible trace of oscule on external surface.

Texture and surface characteristics. Soft, spongy alive, firm, compressible, rubbery in ethanol; fleshy alive, with longitudinal striations and ridges running from terminal oscule along sides of digits, collapsing when preserved producing concave striations and pits on sides of digits.

Ectosome and subectosome. Well developed, discrete brushes of ectosomal auxiliary subtylosyles arising from ends of ascending choanosomal tracts; ectosome more heavily collagenous than choanosome, lightly pigmented; subectosomal skeleton slightly cavernous, with widely spaced peripheral fibres and skeletal tracts.
becoming progressively more plumose towards periphery.

*Choanosome.* Irregularly reticulate, wisemeshed fibre skeleton, cavernous choanosomal structure; fibres relatively homogeneous in size and distribution, 40-70\(\mu\)m diameter, without any marked differences between primary and secondary fibres; fibres light; fibre meshes wide, oval to clongate, up to 650\(\mu\)m diameter, slightly more cavernous in peripheral skeleton than at core;

ascending primary fibres cored by pauci- or multispecific tracts of auxiliary oxeas; smaller connecting secondary fibres, predominantly transverse through skeleton, cored by unispecific tracts of auxiliary oxeas, occasionally aspicular; fibres at core of skeleton sparsely echinated by principal oxeas; mesohyl matrix light, virtually unpigmented, with sparse auxiliary oxeas scattered between fibres; choanoocyte chambers large, oval, up to 60 µm diameter.

Megascleres (Table 45). Principal oxeas echinating fibres short, slender, straight, usually with telescoped points.

Auxiliary oxeas coring fibres long, slender, straight, usually with telescoped points.

Ectosomal auxiliary subtylostyles long, slender, straight, with slightly swollen bases, sometimes pointed at apex, with fusiform or slightly telescoped points.

Microscleres. Absent.

ETYMOLOGY. In memory of Isaac Cook, son of Stephen Cook, collector of many of the samples studied here.

REMARKS. This species has a cavernous, irregularly reticulate skeletal structure with relatively poorly developed fibre system and mostly dominated by more-or-less plumose tracts coring major fibres. The ectosomal skeleton is particularly well developed, moreso than other species of E. (Protophispongia), whereas the echinating spicule skeleton is very sparse, nearly vestigial. The species is most closely related to E. (P.) bargibanti in its growth form and aspects of its skeletal structure but they differ substantially in their respective live field characters, coring spicule skeleton, and spicule sizes. The species is compared further with other E. (Protophispongia) in Table 46.

Echinochalina (Protophispongia) oxeata
(Burton, 1934) (Fig. 304, Table 45)

Protophispongia oxeata Burton, 1934a: 562, text-fig. 128.


HABITAT DISTRIBUTION. On foraminifera and coral fragments, 40m depth; Cooktown (FNQ) (Fig. 304C).

DESCRIPTION. Shape. Branching, cylindrical sponge 3-5 mm diameter, now fragmented; branches bifurcate near ends.

Colour. Light brown in ethanol.

Oscules. Small, 1-2 mm diameter, on lateral sides of branches.

Texture and surface characteristics. Tough, elastic; surface smooth, even, porous.

Ectosome and subectosome. Membranous, with sparse, more-or-less erect bundles of auxiliary oxeas from ascending choanosomal tracts protruding through surface; choanosomal fibres immediately below ectosome.

Choanosome. Irregularly reticulate skeleton with differentiated primary and secondary spongins fibres; primary fibres ascending, pauci- or multispecific, 35-55 µm diameter, interconnected by transverse, uni- or aspicular secondary fibres, up to 22 µm diameter; fibre anastomoses produce large, cavernous, oval meshes in peripheral skeleton, up to 550 µm diameter, smaller, oval close-meshed reticulation at core of skeleton, up to 145 µm diameter; all spicule tracts occupy only small proportion of fibre diameter; differentiated echinating megascleres absent although auxiliary spicules may protrude through fibres at acute angles; mesohyl matrix heavy but only lightly pigmented, containing numerous auxiliary spicules scattered between fibres; choanoocyte chambers large, oval 45-95 µm diameter.

Megascleres (Table 45). Principal oxeas coring fibres short, slender, straight or slightly curved at centre, with hastate or slightly telescoped points, occasionally modified to styles.

Microscleres absent.

REMARKS. This species has reduced spiculation, lacking either echinating (principal) spicules or ectosomal styles. In spongion fibre structure, distribution of spicules within fibres, ectosomal spiculation, it is close to E. (P.) bispiculata. Hooper & Lévi's (1993a: 1279) E. (P.) oxaeta from Moreton Bay is not conspecific with the holotype of E. (P.) tuberosa, whereas E. (P.) oxeata is restricted to the type specimen.

Echinochalina (Protophispongia) tuberosa
sp. nov.
typical growth form
(Figs 305-306, Table 45 Plate 12F)


HABITAT DISTRIBUTION. Rock and coral reef, usually sheltered under ledges; 9-25m depth; Stradbroke I., Moreton Bay, Mooloolaba (SEQ) (Fig. 305F).

DESCRIPTION. Shape. Thickly encrusting with bulbous-digitate surface projections forming lobate-digitate or bulbous sponge, up to 120mm long, 70mm wide, 55mm thick.

Colour. Bright red to pale red alive (Munsell 2.5R 4-5/10), brown in ethanol.

Oscules. Small, up to 3mm diameter, scattered at base of surface bulbs, between adjacent bulbs, each with prominent membraneous lip.

Texture and surface characteristics. Firm, slightly hispid; surface uneven with prominent bulbous

protruberances, up to 9mm high, 5mm diameter, inflated at ends.

_Ectosome and subectosome._ Relatively thick paratangential brushes composed of ectosomal auxiliary subtylostyles perched on surface, overlying protruding principal oxeas from peripheral, ascending choanosomal skeletal tracts;
choanosomal fibres immediately below ectosome.

*Choanosome.* Regularly reticulate skeletal structure, without any marked compression at core, with nearly renieroid fibre skeleton and plumoreticulate spicule tracts diverging towards periphery; spongin fibres heavy, without noticeable size differences between primary or secondary fibres, 20-60μm diameter; all fibres cored by auxiliary oxeas and moderately heavily echinated by principal oxeas, particularly at fibre nodes; primary fibres with ascending multiprincipal tracts of auxiliary oxeas terminating in sparse bundles at surface; secondary fibres pauci- or unispicular in peripheral skeleton, uni- or bispicular at core of skeleton; fibre anastomoses produce square or round, relatively even meshes throughout skeleton, 70-150μm diameter; mesohyl matrix moderately heavy, with few auxiliary spicules scattered between fibres; choanoocyte chambers small, oval, 25-40μm diameter.

*Megascleres* (Table 45). Principal oxeas echinating fibres short, thick, straight, with fusiform or slightly teleoped points.

Auxiliary oxeas coring fibres, long, slender, straight or slightly curved at centre, with tapering fusiform or slightly teleoped points.

Ectosomal auxiliary subtylostyles long, very slender, whispy, usually curved at centre, base subtyloste, usually microspined, point hastate. Microscleres (refer to Table 45 for dimensions). Toxa oxhorns, short, thick, wide central curvature, points only slightly reflexed.

Digitate growth form (Figs 307-308, Table 45)


**DIAGNOSIS.** Shape. Arborescent, tubulodigicate growth form, 65mm high, 78mm wide, cylindrical or slightly flattened, repeatedly bifurcate, occasionally anastomosing branches, 3-5mm diameter, slightly swollen at extremities; sponge attached to substrate by expanded, short basal attachment.

*Colour.* Same as typical form.

Oscules. Small, up to 2mm diameter, on lateral sides of branches.

*Texture and surface characteristics.* Firm, compressible, slightly rubbery; surface of branches smooth, macroscopically even, microscopically slightly hispid.

**Ectosome and subectosome.** Thick, erect bundles of ectosomal auxiliary subtylostyles forming discrete plumose brushes on surface, usually at ends of ascending choanosomal spicule tracts, intermingled with protruding auxiliary coring oxeas; subectosomal region relatively thick, spiculose, with no fibre component.

*Choanosome.* Regularly reticulate skeletal structure without marked compression of axis.

**Megascleres** and **Microscleres.** As for typical form.

**ETYMOLOGY.** For the bulbous encrusting form.

**REMARKS.** There are several notable differences between the bulbous-encrusting, shallower water (typical) morph and the deeper water, digitate morph that warrant their separate description above (i.e., growth form, ectosomal development), but there is little doubt that they are conspecific given similarities in their skeletal structure, fibre characteristics, spicule geometry, spicule dimensions.

This species resembles *E. (P.) bispiculata* in growth form (both bulbous, massive), fibre characteristics (regularly reticulate), and geometry of coring and echinating megascleres. However, *E. (P.) tuberosa* has a special category of auxiliary style forming a thick ectosomal skeleton (whereas *E. (P.) bispiculata* simply has protruding auxiliary oxeas from the peripheral choanosomal fibre skeleton), toxo microscleres (versus no microscleres), and different spicule dimensions (see Table 46). The species is also related to *E. (P.) laboutei*, particularly the digitate morph, in having special auxiliary styles forming the ectosomal skeleton, and similar fibre characteristics with multiprincipal primary ascending fibres and un-, pauci- or aspicular secondary fibres, whereas *E. (P.) laboutei* lacks toxo microscleres, has a compressed central axial fibre skeleton and generally has aspicular fibres.

**OTHER SPECIES OF ECHINOCHALINA (PROTOPHLITASPONGIA)**

**ECHINOCHALINA (PROTOPHLITASPONGIA) BARGIBANTI** Hooper & Lévi, 1993

**ECHINOCHALINA (PROTOPHLITASPONGIA) BARGIBANTI** Hooper & Lévi, 1993a: 1280-1283, figs 31-32 [New Caledonia].

**MATERIAL.** HOLOTYPE: QMG301270. SW. Pacific.

**ECHINOCHALINA (PROTOPHLITASPONGIA) LABOUTEI** Hooper & Lévi, 1993

*Echinochalina (Protophlitaspongia) labourei* Hooper & Lévi, 1993a: 1277-1280, figs 29-30 [New Caledonia].

MATERIAL. HOLOTYPE: QMG300685. SW. Pacific.

**Artemisina** Vosmaer, 1885

*Artemisina* Vosmaer, 1885a: 25; Ridley & Dendy, 1887: 112; Topsent, 1894a: 12; Lundbeck, 1905: 110; Burton, 1930a: 501, 528-531; de Laubenfels,

Artenisina; Burton, 1934b: 54 [lapsus].
Qasimella Thomas, 1974: 311.

TYPE SPECIES. Artemisina suberitoides Vosmaer, 1885a: 25 (by monotypy) (junior synonym of Suberites arciger Schmidt, 1870: 47 (Burton, 1930a: 528)).
DEFINITION. Without choanosomal fibres or indefinite fibres, whereas skeletal architecture vaguely ascending longitudinal tracts of spicules bound by abundant collagen, cored by smooth choanosomal principal subtylostyles in a more-or-less confused halichondroid reticulation of vaguely multispecular ascending and scattered transverse megascleres; echinating megascleres absent; subectosomal peripheral skeleton more radially arranged; ectosome membrane, skin-like, with smooth styles of a single size category protruding through surface, forming paratangential or erect, discrete spicule bundles; microscleres palmate or arcuate isochelae and toxas with smooth or spinous points.

Artemisina apollinis (Ridley & Dendy, 1886) (Figs 309-310)

Amphilectus apollinis Ridley & Dendy, 1886: 350; Ridley & Dendy, 1887:125, pl.19, fig.10, pl.25,fig.2.

Artemisina apollinis; Lundbeck, 1905: 114-116, pl.13, fig.4; Kirkpatrick, 1908b: 34, pl.20, fig.4; Hentschel, 1914: 70; Topsent, 1917: 62, pl.4, fig.6, pl.6, fig.7; Burton, 1929a: 431; Hentschel, 1929: 876, 939; Burton, 1930a: 529; Burton, 1932a: 323; Koltun, 1964a: 73; Desqueyroux, 1975a: 66, pl.4, figs 42-46; Koltun, 1976: 188; Hooper & Wiedenmayer, 1994: 256.

Artemisina dianae Topsent, 1907:70-72; Topsent, 1908: 22, pl.3, fig.4, pl.5. fig.1; Vosmacr, 1935a: 630.

MATERIAL. HOLOTYPE: BMNH1887.5. 2.140; Royal Sound, Kerguelen, 40-120m depth. HOLOTYPE of A. dianae: MNHN DT1666.

HABITAT DISTRIBUTION. Rock reefs and soft substrata; 18-380m depth; widespread boreal and antarctic: Antarctica - MacRobertson Land, Australian Antarctic Territory (Koltun, 1976), Graham Land, William II Coast, Victoria Land (Desqueyroux-Faundez, 1975) (Fig. 309F), Gauss Station, Winter Quarters, South Georgia (Hentschel, 1914; Kirkpatrick, 1908b), Kerguelen Is (Ridley & Dendy, 1886, 1887; Koltun, 1976), Circum-polar (Koltun, 1964a). Arctic - East Greenland (Lundbeck, 1905), South Shetland Is (Topsent, 1907, 1908), Iceland, North Sea (Hentschel, 1929).

DESCRIPTION. Shape. Flattened, oval, cushion-shaped, up to 50mm long, 38mm wide, 19mm thick.


Texture and surface characteristics. Soft, compressible, friable; surface uneven, folded, shaggy, conulose, cavernous, with skin-like ectosomal membrane stretched across adjacent conules.

Ectosome and subectosome. Variably developed spicule brushes forming more-or-less continuous palisade on surface, sometimes also tangential or paratangential; plumose brushes of subectosomal auxiliary spicules with few choanosomal principal spicules protruding through surface from underlying skeleton.

Choanosome. Skeletal architecture irregularly reticulate or renieroid reticulate in places with rectangular and triangular meshes, up to 280μm diameter, made of uni- or paucispecular tracts of choanosomal principal styles; skeletal tracts not definitely differentiated into primary or secondary elements although ascending tracts contain 2-4 spicules abreast and connecting, usually transverse tracts contain 1-2 spicules per row; fibres absent and spicules bound by light collagen; mesohyl matrix heavy, with numerous microscleres dispersed.

Megascleres. Choanosomal principal styles long, slender, rounded smooth bases, occasionally slightly subtylote, with fusiform points, straight or slightly curved towards basal end. Length 352-(407.3)-458μm, width 11-(14.0)-17μm.

Subectosomal auxiliary styles long, slender, with slightly subtylote, lightly micropinched bases, occasionally smooth, tapering to fusiform points. Length 209-(244.6)-293μm, width 3-(4.4)-7μm.

Microscleres. Palmate isochelae small, well silicified, unmodified. Length 8-(12.3)-16μm.

Toxas wing-shaped, variable in length and thickness, with sharply angular, deep central curvature, long straight arms on larger spicules, or slightly recurved arms on smaller spicules; largest with micropinched points. Length 24-(123.2)-264μm, width 0.8-(2.3)-5μm.

REMARKS. Ridley & Dendy (1887) stated that this species had a halichondroid reticulate skeleton whereas the type shows the skeleton to be much more regular, renieroid-reticulate in places. Synonymy of A. dianae and A. apollinis, proposed by Koltun (1964a, 1976) is doubtful, as is the assumption that the species is bipolar (i.e., possible two or more sibling species). Their respective type specimens are similar, with only slight differences in spicule sizes, spicule geometries and skeletal structures, and consequently Koltun's proposed synonymy is maintained here.
**Artemisina jovis** Dendy, 1924
(Fig. 311)

*Artemisina jovis* Dendy, 1924a: 343, pl.12, fig.6; Burton, 1930a: 550; Koltun, 1964a: 74-75; Bergquist & Fromont, 1988: 119-120, pl.56, figs b-e; Dawson, 1993: 36; Hooper & Wiedenmayer, 1994: 257.

**MATERIAL.** HOLOTYPE: BMNH1923.10. 1.112: 5km east of North Cape, New Zealand, 138m depth.

PARATYPES: BMNH1923. 10.1.315, 316.

**HABITAT DISTRIBUTION.** Hard benthos; 45-138m depth; Antarctica - Wilkes Land, AAT (Koltun, 1964a) (Fig. 311E); also North Cape and Three Kings Is, New Zealand (Dendy, 1924a; Bergquist & Fromont, 1988).

**DESCRIPTION.** Shape. Flabellate, stalked, bifurcate digitate margins, 120-300mm high, 80-110mm wide, 8mm thick lamellae.

**Colour.** Greyish in ethanol.

**Oscules.** Oscules up to 6mm diameter, with slightly raised margins, clustered on osculiferous face of sponge.
Texture and surface characteristics. Firm, compressible; inhalant surface smooth, slightly undulating, with clearly visible porous ectosomal membrane stretched across pitted subectosomal region; exhalant surface osculiferous.

Ectosome and subectosome. Erect plumose brushes of subectosomal auxiliary styles producing continuous palisade at surface but markedly cavernous in subectosomal region.

Choanosome. Nearly regularly renieroid reticulate skeletal architecture composed of uni-, pauci- and multispicular tracts of choanosomal principal styles producing triangular meshes up to 350µm diameter, enclosed within moderately light collagen; fibres absent; spicule tracts relatively homogeneous, undifferentiated into primary or secondary elements; mesohyl matrix heavy, darkly pigmented, containing abundant microscleres.

Megascleres. Choanosomal principal styles large, robust, straight or slightly curved near basal end, fusiform pointed, with smooth rounded or very slightly subtylote bases. Length 361-(390.3)-448µm, width 12-(19.2)-26µm.
Subectosomal auxiliary styles slender, short, fusiform pointed, straight or slightly curved near basal end, with smooth round bases. Length 234-(290.6)-375μm, width 3-(7.1)-10μm.

Microscleres. Palmate isochelae unmodified, abundant, well silicified. Length 10-(12.5)-16μm.

Toxas intermediate accolada-wing shaped, long, slender, with slightly rounded central curvature, slightly reflexed arms, microspined points. Length 98-(155.2)-215μm, width 1.5-(2.4)-4μm.

REMARKS. The type material revealed some discrepancies from published descriptions of
both Dendy (1924a) and Bergquist & Fromont (1988), indicating variability between specimens. In particular skeletal meshes, described as being differentiated into ascending and transverse components, are virtually homogeneous in the holotype, and skeletal structure described by Bergquist & Fromont (1988) as plumose is regularly renieroid reticulate with no plumose component in the holotype. Spicule sizes also differ marginally from those described by Dendy (1924a). Artemisina jovis is very similar to A. apollinis in its skeletal structure, differing only substantially in growth form, toxo size and to a certain degree toxo geometry, and size and spination of other megascleres.

**Artemisina plumosa** Hentschel, 1914 *(Fig. 312)*

*Artemisina plumosa* Hentschel, 1914: 70-72, pl.4, fig.5, pl.6, fig.1 [et var. *lipochela*]; Burton, 1929a: 431 [Antarctica]; Burton, 1930a: 530; Koltun, 1964a: 73, pl.11, figs 1-8; Koltun, 1976: 190; Hooper & Wiedenmayer, 1994: 257.

**Artemisina strongylá** Hentschel, 1914: 72-73, pl.6, fig.2.

**MATERIAL.** HOLOTYPE: HM (fragments BMNH-1933.7.20.3, ZMB4762): Off Wilhelm II Coast, Antarctica.

**HABITAT DISTRIBUTION.** Soft substrata: 125-2269m depth: Antarctica - Enderby Land, Sabrina Coast, Princess Elizabeth Land, Wilhelm II Coast, Australian Antarctic Territory (Koltun, 1976) (Fig. 312F), also Falkland Is, Adelie Coast (Koltun, 1964a), Gauss Station (Hentschel, 1914; Burton, 1929a).

**DESCRIPTION.** Shape. Small, erect, bulbous, club-shaped, 28mm high, 25mm diameter.

**Colour.** Grey-brown in ethanol.

**Oscules.** Not observed.

**Texture and surface characteristics.** Firm, harsh texture; irregular reticulate conulose.

**Ectosome and subectosome.** Plumose bundles of choanosomal principal styles protruding, forming near continuous palisade on surface; subectosomal auxiliary styles tangential or paratangential to surface, sparse, dispersed between protruding bundles of choanosomal styles.

**Choanosome.** Exclusively plumose near peripheral skeleton, slightly more reticulate, less organised in deeper parts of choanosome, with multispecific ascending tracts of choanosomal styles, without spongion fibres, most obvious near peripheral region of skeleton; length and width of spicule tracts reduced at core with diminished skeletal organisation whereby only pauci- or small multispecific tracts form skeletal reticulation at core, with square or triangular meshes, up to 300μm diameter; mesohyl matrix heavy, lightly pigmented, smooth, containing very abundant microscleres throughout.

**Megascleres.** Choanosomal principal styles long, robust, fusiform pointed, smooth, with rounded bases and typically slightly curved near basal end. Length 305-(378.2)-472μm, width 11-(13.7)-18μm.

**Subectosomal auxiliary styles or tornostyles.** Short, thin, straight, with slightly subtylote bases, smooth or microspined bases, rounded, hastate or mucronate points often with small spines, or sometimes with single small terminal spine, or quasi-diactinal asymmetrical ends. Length 181-(196.7)-268μm, width 3-(6.1)-8μm.

**Microscleres.** Palmate isochelae very abundant, moderately large, well silicified, occasionally contorted. Length 8-(13.2)-16μm.

**Toxas** intermediate accolada-wing shaped, varying from minute to very large, typically with large angular central curvature, slightly reflexed arms, microspined points. Length 36-(140.1)-296μm, width 0.8-(2.5)-5μm.

**REMARKS.** Artemisina jovis differs from other species in having quasi-diactinal auxiliary megascleres, including some with basal spination. Its toxas are also much larger and more prominently spined than the other 3 Antarctic species described here, and skeletal architecture is highly reticulate at core and exclusively plumose near periphery.

Hentschel (1914) and Koltun (1964a) recorded a second category of large choanosomal style, with similar geometry to principal spicules but nearly twice their length (800-2160x21-44μm), but these were not seen in the fragment of the holotype examined.

**Artemisina tubulosa** Koltun, 1964 *(Figs 313-314)*

*Artemisina tubulosa* Koltun, 1964a: 74, text-fig.18; Hooper & Wiedenmayer, 1994: 257.

**MATERIAL.** HOLOTYPE: BMNH1963.7. 29.52, Mawson Coast, Australian Antarctic Territory, 100m depth.

**HABITAT DISTRIBUTION.** Hard benthos; 100m depth; Australian Antarctic Territory (Fig. 313F).

**DESCRIPTION.** Shape. Tubulo-digital, hollow, cylindrical, 100mm long, 30mm diameter.
**Colour**  Beige-brown in ethanol.

**Oscules.**  Not seen.

**Texture and surface characteristics.**  Firm, harsh; surface microconulose, goose-flesh, pitted.

**Ectosome and subectosome.**  Hispid, with plumose bundles of choanosomal principal styles protruding through surface in multispecular bundles; subectosomal auxiliary styles tangential or paratangential, scattered over surface, also with detritus embedded in surface.

**Choanosome.**  Reticulate skeletal architecture, with large multispecular tracts of choanosomal principal spicules ascending to surface, and ir-regular uni-, paucispecular or smaller, transverse multispecular tracts interconnecting main tracts, together producing a nearly myxillid-like triangular reticulation, with meshes up to 800μm diameter; spongion fibres absent, with spicule tracts bonded together by collagen; mesohyl matrix heavy but only lightly pigmented, with numerous microscleres scattered between fibres.

**Megascleres.**  Choanosomal principal styles thick, fusiform, rounded bases, smooth, slightly curved near basal end. Length 705-(778.8)-874μm, width 18-(30.2)-39μm.

Subectosomal auxiliary styles short, thin, mostly straight, with rounded or very slightly subtylothe or occasionally polytylothe bases, typi-
Artemisia tabulae is similar to A. plumosa in skeletal architecture and spicle geometry, and the two are probably at least sibling species. Whereas A. tubulosa has micropinse ed base on some of the auxiliary spicules it lacks diaclinal modifica tions to those spicules as found in A. plumosa. Similarly, skeletal structure is also prominently reticulate, with large spicle tracts clearly differentiated into primary and secondary elements, whereas those of A. plumosa are exclusively plumose in the peripheral skeleton.

OTHER SPECIES OF ARTEMISINA

Artemisia archegona Ristau, 1978
Artemisia archegona Ristau, 1978b; 585-587, text-figs 2F, 3F, 6C-D [Carmel, California].
Artemisia arciger Schmidt, 1870
Suberites arciger Schmidt, 1870: 47, pl.5, fig.6.
Artemisia suberiboides Vosmaer, 1885a: 25-26, pl.1, fig.6, pl.4, figs 11-14, pl.5, figs 51-55 [Arctic]; Ridley & Denny, 1887: 440; [off Nova Scotia]; Frosted, 1887: 112; [off Nova Scotia]; Fris tetti, 1887: 430, pl.24, figs 15-17; Whiteaves, 1901: 17; Lundbeck, 1905: 113.
Artemisia arciger; Lundbeck, 1905: 110-114, pl.1, figs 9-11, pl.13, fig.3; Arndt, 1913: 115; Topsent, 1913b: 47, pl.1, fig.6; Zonation, 1925: 197; [Arctic]; Topsent, 1930a: 84-84 [Arctic].
Artemisia arciger; Burton, 1905: 25; [Arctic]; Vosmaer, 1885a: 25-26, pl.1, fig.6.
Artemisia transiens Topsent, 1890
Artemisia transiens Topsent, 1890b: 164, figs 7-8, text-fig.49 [Curaçao]; Zolot, 1987: 585-587, text-fig.61, pl.11, figs 3-4 [Columbia].
MATERIAL. HOLOTYPE: ZMAPOR4881, paratype ZMAPOR4882. C. Atlantic.
Artemisia stipitata Koltun, 1958
Artemisia stipitata Koltun, 1958: 52-53, text-fig.10 [Kurile Strait].
MATERIAL. HOLOTYPE: BMNH1963.7. 29,39, NW. Pacific.
Artemisia vulci Leib, 1963
Artemisia vulci Leib, 1963: 64-65, pl.19F, text-fig.74 [South Africa].
MATERIAL. HOLOTYPE: BMNH1963.7. 29,39, NW. Pacific.

TRANSFERS

List of other species described in Artemisia but now transferred to another genus.

Artemisia erecta Topsent, 1904
Artemisia erecta Topsent, 1904a: 214-215, pl.5, fig.18, pl.15, fig.10 [Azores]; Burton, 1930a: 530. MATERIAL. HOLOTYPE: BMNH1923.10. 1.113. New Zealand, New Caledonia.
Artemisia hispanica Ferrer-Hernández, 1918
Artemisia indica (Thomas, 1974)
Qasimella indica Thomas, 1974: 311-312, text-fig.1 [Gulf of Manaar].
MATERIAL. HOLOTYPE: CMFRT84/1, paratype CMFRT84/2. N. central Indian Ocean.
Artemisia melana Van Soest, 1984
Artemisia melana Van Soest, 1984b: 122-124, pl.8, figs 7-8, text-fig.49 [Basa;]; Zolot, 1987: 173, text-fig.61, pl.11, figs 3-4 [Columbia].
Artemisia stipitata Koltun, 1958
Artemisia stipitata Koltun, 1958: 52-53, text-fig.10 [Kurile Strait].
MATERIAL. HOLOTYPE: BMNH1963.7. 29,39, NW. Pacific.
Artemisia transiens Topsent, 1890
Artemisia transiens Topsent, 1890b: 66 [non nudum]; Topsent, 1892a: 94, pl.2, fig.5, pl.4, fig.8, pl.9, fig.18 [Atlantic coast of France]; Ferrer-Hernández, 1914: 3; Burton, 1930a: 529-530; Leib, 1930a: 84-84 [Asturies, Mediterranean].
MATERIAL. HOLOTYPE: BMNH1963.7. 29,39, NW. Pacific.
Artemisia vulci Leib, 1963
Artemisia vulci Leib, 1963: 64-65, pl.19F, text-fig.74 [South Africa].
MATERIAL. HOLOTYPE: BMNH1963.7. 29,39, NW. Pacific.

Paresperia intermedia Burton, 1930a: 501 [Norway].
Artemisia intermedia; Van Soest, 1984b: 130 [possible generic synonymy].
Amphilectus pilosus Ridley & Denny, 1886: 350; Ridley & Denny, 1887: 126-127, pl.19, fig.5, pl.25, fig.3 [Kerguelen Is; Marion Is.].
Lissodendoryx pilosus; Topsent, 1901: 20.

*Artemisina pilosus*; Ristau, 1978: 585-586 [note on affinities].

MATERIAL. HOLOTYPE: BMNH1887.5.2. 124. Note: referred to lophonidae, *Megaciella*.

*Artemisina tylota* Boury-Esnault, 1973: 286-287, text-fig.48 [Brazilian Basin].

MATERIAL.  
HOLOTYPE:  
MNHNDNB 943.  Note: referred to  
lophonidae, Corallium incertae sedis

Pandaros Duchassaing & Michelotti, 1864

Pandaros Duchassaing & Michelotti,  
1864: 88; Schmidt, 1870: 59; de  

TYPE SPECIES. Pandaros acanthifolium Duchassaing & Michelotti, 1864: 90 (by subsequent designation of de Laubenfels, 1936a: 123).

DEFINITION. Well-developed choanosomal skeletal reticulation of spongin fibres woven into flattened anastomosing branches, or forming continuous sheets without any regular architecture; fibres cored by auxiliary styles, subtylosstyles to tylostyles, predominantly smooth, distributed within fibres in criss-cross fashion; fibres echinated by rare acanthostyles, rarely smooth styles; few anisotornotes, verging on oxeas, scattered throughout mesohyl; sparsely dispersed tangential subectosomal auxiliary spicules dispersed throughout peripheral skeleton; microscleres absent.

REMARKS. No Australian species.

SPECIES OF PANDAROS

Pandaros acanthifolium Duchassaing & Michelotti, 1864

Pandaros acanthifolium Duchassaing & Michelotti, 1864: 90, pl.20, fig.2  
[St. Thomas, Virgin Is]; de Laubenfels, 1936a: 123 [Florida]; Hechtel, 1965: 45; Wiedenmayer, 1977: 144,  
pl.30, figs 4-5, text-fig.148 [Bimini, Bermudas]; Schmitz et al., 1981: 853-865 [biochem.]; Van Soest, 1984b: 127-128, text-fig.51  
[Curaçao]; Pulitzer-Finali, 1986: 149, fig.68 [West Indies]; Zea, 1987: 175, pl.4, fig.4, text-fig.62  
[Columbian Caribbean].

FIG. 314. Artemisia tubulosa Koltun (holotype BMNH1963.7.27.52).  
Pandaros arbusculum, in part, Duchassaing & Michelotti, 1864: 88, pl.18, fig.6 [St. Thomas, Virgin Is].

Thalysyurus conulusa Hechtel, 1965: 44, pl.6, fig.1, text-fig.9 [Port Royal; Jamaica]; Alcolado, 1976: 5 [Cuba].

MATERIAL. LECTOTYPE: TMPOR57 (fragments USNM31020, MNHNDBE1309, BMNH1928.11.12.16), paralectotype: IZUGCE38.762 (fragment BMNH1928.11.12.15), holotype of T. conulusa: YPM5042, Caribbean.

Pandaros kasuniensis (Tanita, 1965), uncertain placement.


Thalysyurus kasuniensis; Hoshino, 1981: 159-161, text-fig.70 [Japan].


MATERIAL. HOLOTYPE: MMBSIS-052 NW Pacific.

**TRANSFERS**

List of other species described in Pandaros but now transferred to another genus.

Pandaros angulosa Duchassaing & Michelotti, 1864: 89, pl.19, fig.4 [St. Thomas, Virgin Is].

Mycale (Aegogopila) angulosa; Van Soest, 1984b: 16-19, pl.1, figs 5-6, text-fig.3 [plus synonymy]; Pulitzer-Finali, 1986: 130-133, figs 52-55.

Not Mycale angulosa; de Laubenfels, 1936a: 116.

Zygomycale parishii, in part; de Laubenfels, 1956: 3; Hechtel, 1965: 48, pl.5, fig.3; Alcolado, 1980: 4.

MATERIAL. LECTOTYPE: TMPOR54 (fragments USNM31021, MNHNDBE1310, BMNH1928.11.12.20), referred to Mycalidae, Mycale.

Pandaros arbusculum Duchassaing & Michelotti, 1864: 88, pl.18, fig.6 [St. Thomas, Virgin Is].

Ptilocaulis sp. aff. spiculifer (Lamarck, 1814); Wiedenmayer, 1977: 153, 251.


Pandaros arbusculum; Van Soest et al., 1983: 204.

MATERIAL. LECTOTYPE: ZMAPOR1728, paralectotype ZMAPOR1729, referred to Axinellidae, Ptilocaulis.

Pandaros lugubris Duchassaing & Michelotti, 1864: 89 [St. Thomas, Virgin Is].


MATERIAL. LECTOTYPE: TMPOR55 (fragments USNM31023, MNHNDBE1312, BMNH1928.11.12.21), referred to Raspailiidae.

Pandaros pennata Duchassaing & Michelotti, 1864: 88, pl.20, fig.3 [St. Thomas, Virgin Is].

Echinodictyum pennatum; Wiedenmayer, 1977: 251, 255.


Pandaros walpersii Duchassaing & Michelotti, 1864: 90, pl.20, fig.4, text-fig.2D [St. Thomas, Virgin Is].

Ptilocaulis walpersii; Wiedenmayer, 1977: 255.

Spongia spiculifera Lamarck, 1814: 449.

Ptilocaulis spiculifera; Pulitzer-Finali, 1986: 103-104 [West Indies].

MATERIAL. LECTOTYPE: TMPOR56 (fragments USNM31025, MNHNDBE1314, BMNH1928.11.12.17), paralectotype: IZUGCE38.763, referred to Axinellidae, Ptilocaulis.

**DISCUSSION**

Classification. Microcionidae contains 7 genera, 12 subgenera and 459 valid species of which 148 are recorded in the Australian fauna. The present work describes 31 new species from Australia, and 3 from other localities for misidentified taxa, 18 new names for preoccupied taxa, and 162 new taxonomic combinations. Many species are also new records for Australia and many are illustrated for the first time. Nevertheless, there are likely many more species still undescribed in this region; considering that the encrusting fauna has not yet been comprehensively sampled.

This revised classification is based on a re-evaluation of all characters, including an analysis of their consistency within populations of several species, and places primary importance on skeletal structure and localisation of spicule types to particular regions in the skeleton. This contrasts with previous schemes which gave priority to characters such as patterns of skeletal architecture (e.g., Lévi, 1960a), megasclere form and distribution within the skeleton (Hallmann, 1920), exoskeleton structure and composition (Van Soest, 1984a), microsclere geometry and diversity (e.g., de Laubenfels, 1936a), or combining all these characters into a consensus matrix with a consequent proliferation of genera (e.g., Bergquist & Fromont, 1988).

Re-examination of the type species of 73 nominal genera included in Microcionidae at one time or another found that many had been misdescribed, or important characters overlooked, with the consequence that previous interpretations of genera are mostly incorrect. Furthermore, many of these nominal genera are not valid in a phylogenetic sense given that their supposed apomorphic characters are unstable (inconsistent) within otherwise closely related species. These earlier classifications had extraordinary high levels of homoplasy (Hooper, 1990a), partly a consequence of relying on single morphological characters (which when used in isolation cut across a classification based on other single char-
characters). I use combinations of characters to develop a phylogeny.

At the species level several characters are prone to ecophenotypic variability (notably growth form, effect of water depth on colour, loss of microscleres, reduced silification and variability in spicule dimensions across broad geographical ranges), whereas most other skeletal characters are more consistent within populations of single species. It is proposed that small cryptic differences in skeletal characters are indicative of divergent, sibling species relationships, with some empirical support from biochemical and genetic data (Hooper et al., 1991).

Phylogenetic analysis. Hypothesised phylogenetic relationships based on coded, multistate (Table 47) data matrices were generated using PAUP 3.0 (Swofford, 1991), and CONTREE was used to obtain consensus information from these analyses as outlined by Hooper & Lévi (1994). Determinations of plesiomorphies were largely made through outgroup comparison (Raspalliidae), but these interpretations are complicated by the prevalence of analogous characters throughout Porifera (or misinterpretation of homology by authors). Consequently some information from the fossil record is considered below to assist in determining character polarity.

(1) Skeletal structure: Ordovician Succospongia had a clathrous, fibrous reticulate skeleton, cored by axially compressed and extra-axially plumose spicule tracts, with coring spicules also protruding through fibre endings in plumose bundles (Finks, 1967). A similar structure in some living poecilosclerids, such as Esperiopsis (Hooper & Lévi, 1989), which also have a ‘lithistid’ (desma-bearing) basal skeleton — a condition relatively widespread during the Ordovician (Finks, 1970) — imply that the axial compressed condition may be plesiomorphic for living Clathria (Asociella) and many Raspallia (Raspalliidae).

The use of Raspalliidae as an outgroup of Microcionidae is based on their proposed sister-group relationship (Hooper, 1991), sharing a similar range of skeletal structures (including hymedesmoid, microcionid, renieroid, reticulate and compressed architectural types), echinating acanthostyles and ecosomal specialisation. These structural similarities are considered to have a phylogenetic basis (with some empirical support from biochemical and genetic data; Hooper et al., 1992) rather than merely representing convergence of a few characters. Raspalliidae was previously included in order Axinellida based solely on possession of axial skeletal compression in some species (Bergquist, 1978), but this character is of dubious value when used alone occurring in many other poecilosclerids.

(2) Ecosomal skeleton: The ‘sclerosponge’ Calcifibrosponge has a tangential (isodictyal) ecosomal skeleton of strongyles lying on or just below the exopinacoderm (Hartman, 1979; Vacelet, 1985) and Van Soest (1978a) suggested that this feature links it with the Haplosclerida, particularly the Haliclonaide. This would infer that a tangential ecosomal skeleton is plesiomorphic for the haplosclerids. However, similar features in some Microcionidae represent parallel development (e.g., quasi-diactinal ecosomal spicules in some Holopsamma, quasi-diactinal structural spicules in Echinocochalinia). The tangential layer of amphitylotes in the Myxillidae is unique to the group (e.g., Lissodendoryx), upon which Van Soest (1984b) based his classification, but the myxillid (tangential amphitylote) ecosomal skeleton in Acarnus is enigmatic since its microscleres are typical of Microcionidae. Thus Hooper (1988, 1990a) considered that microscleres were more easily modified, acquired independently or lost in the Poecilosclerida than was the ecosomal skeleton, which in this case defined the Myxillidae. Hajdu et al. (1994) thought that microsclere geometry was far more conservative than that of megascleres (which might be more susceptible to phenotypic influences). Less obvious is the polarity of the sequence Clathria-Dendrocl-Thalysias, varying from a virtually aspicular ecosome to a dense, continuous palisade of erect megascleres. I suggest that the latter condition is more plesiomorphic based on the ‘raspallid ecosomal condition’ (i.e., smaller auxiliary spicules surrounding bases of protruding larger subecosomal spicules) being common to the outgroup Raspalliidae, and diminishment of ecosomal structure or loss of spicules representing a secondary derivation.

(3) Spicule axes: It could be argued that oxoeite (diactinal) megascleres represent the ancestral condition in this family because they appeared in the Cambrian (Rigby, 1986), whereas styloid (monactinal) spicules are not known earlier than the Ordovician. However, in Microcionidae oxoeites (in E. Protophthiaspongea) for example) represent recent derivations from styloid forms (much like the derived tetractinal styloid modifications in Acarnus (Myxillidae); Van Soest et al., 1991).
TABLE 46. Comparison between species of *Echinochalina* (*Protophilitaspongia*) in major morphological characters. Measurements in μm.

<table>
<thead>
<tr>
<th>CHARACTER</th>
<th>E. hiepiculata (Dendy)</th>
<th>E. oseata (Burton)</th>
<th>E. laboutei Hooper &amp; Lévi</th>
<th>E. bargibanti Hooper &amp; Lévi</th>
<th>E. favolata sp.nov.</th>
<th>E. tuberosa sp.nov.</th>
<th>E. isaaci sp.nov.</th>
<th>E. collata sp.nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fibre skeleton structure</td>
<td>irregularly reticulate, detritus cavernous in axis, more compact in periphery</td>
<td>irregularly reticulate, distinct primary and secondary fibres</td>
<td>heavily condensed axis, regularly reticulate throughout, cavernous meshes</td>
<td>irregularly reticulate, wide meshes, much detritus</td>
<td>regularly plumed reticulate, diverging near periphery, meshes even throughout</td>
<td>regularly reticulate, even meshes, fibres 2% corded</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Collagen in mesohyl</td>
<td>rich</td>
<td>rich</td>
<td>poor</td>
<td>poor</td>
<td>abundant</td>
<td>moderate</td>
<td>very light</td>
<td>abundant</td>
</tr>
<tr>
<td>Fibre mesh shape (and size)</td>
<td>elongate or oval (180-450)</td>
<td>cavernous oval (145-350)</td>
<td>elongate (50-250)</td>
<td>square or rounded (80-180)</td>
<td>elongate (100-300)</td>
<td>elongate (70-150)</td>
<td>elongate (370-650)</td>
<td>oval or elongate (120-440)</td>
</tr>
<tr>
<td>Fibre diameter</td>
<td>20-50</td>
<td>22-55</td>
<td>15-90</td>
<td>8-40</td>
<td>20-50</td>
<td>20-60</td>
<td>40-70</td>
<td>45-120</td>
</tr>
<tr>
<td>Spicules in skeletal tracts</td>
<td>abundant</td>
<td>mod. sparse</td>
<td>mod. sparse</td>
<td>very sparse</td>
<td>mod. abundant</td>
<td>mod. abundant</td>
<td>mod. abundant</td>
<td>abundant</td>
</tr>
<tr>
<td>Spicule silicification</td>
<td>well silicified</td>
<td>well silicified</td>
<td>poorly silicified</td>
<td>poorly silicified</td>
<td>well silicified</td>
<td>well silicified</td>
<td>well silicified</td>
<td>well silicified</td>
</tr>
<tr>
<td>Coring spicules in primary fibres</td>
<td>multipulicular</td>
<td>pauci- or multisulicular</td>
<td>bi- or paucispicular</td>
<td>uni- or paucispicular</td>
<td>pauci- or rarely multispicular</td>
<td>multispicular</td>
<td>pauci- or multisulicular</td>
<td>multispicular</td>
</tr>
<tr>
<td>Coring spicules in secondary fibres</td>
<td>uni- or aspicular</td>
<td>uni- or aspicular</td>
<td>aspicular</td>
<td>unispicular</td>
<td>uni- or paucispicular</td>
<td>unispicular</td>
<td>unispicular</td>
<td>uni- or paucispicular</td>
</tr>
<tr>
<td>Growth form</td>
<td>massive-lobate, tubular digits on surface</td>
<td>branching, cylindrical, digitate</td>
<td>cylindrical digitate, arborecent</td>
<td>clumped lobate-digitate</td>
<td>erect, cylindrical digitate,honey-combed surface</td>
<td>digitate, lobate-digitate, or encrusting digitate</td>
<td>erect, arborecent, cylindrical digitis</td>
<td>thickly encrusting, bulbous surface</td>
</tr>
</tbody>
</table>

(4) Spicule ornamentation: Hypercalcified sponges (‘sclerosponges’) were major contributors to reef building during the Palaeozoic and Mesozoic (Hartman & Goreau, 1975; Hartman, 1979), with extant species (in Mertiliida and Ceratoportellida) having entirely acanthose choanosomal megascleres (verticillate acanthostyles). Vacelet (1985) suggested that sclerosponges were polyphyletic having affinities with many demosponge groups, and if living species represent relict ancestral groups of Demospangiaceae, then there is argument to suggest that acanthochoanosal megascleres are ancestral. Conversely, smooth monaxons were predominant in Palaeozoic and Mesozoic sponges such as *Saccospongia* (Rigby, 1986), in which case the smooth condition may be more primitive. This is a subject of continual speculation, both hypotheses equally supported by tenable arguments (e.g., Van Soest, 1984a, 1987). Within Microcionidae it is considered that acanthochoanosal spicules are plesiomorphic, shared by most species, whereas smooth spicules represent a derived secondary loss of spination. This interpretation is consistent with similar determination for Raspailiidae (Hooper, 1991).

(5) Echinating spicules: Echinating spicules are known for 7 families of Poecilosclerida and may represent a synapomorphy for the suborders Microcionina and Myxillina (Hajdu et al., 1994) (i.e. absent from the base group Mycalina). Not all genera within these families have them and their absence is interpreted as a (derived) secondary loss (with the corollary that echinating spicules in Microcionidae is retention of an ancestral character). Similarly, smooth echinating or pseudo-echinating spicules, such as in *Echinoclathria* and *Echinochalina*, have prob-
ly lost their spination and are a derived condition because in most species they are spined.

(6) Chelae morphology: Hajdu et al. (1994a) subordinated classification of Poecilosclerida largely based on modifications to chelae (i.e., Microcionina with only palmate forms, Myxillina with modified bi- or tridentate modifications, Mycalina with signancistra derivatives). Palmate chelae were thought to be ancestral given their prevalence throughout Poecilosclerida and co-occurrence with other forms of chelae, whereas arcuate chelae were derived from archetypal palmate morphology. Similarly anchorate chelae were thought to have arisen from arcuate modifications to the primitive palmate archetypes. Lateral ridges on the shaft of anchorate chelae were interpreted by Hajdu et al. (1994a) as the beginning of two other (new) lateral alae (i.e., acquisition of new structures), which occasionally meet in the middle of the shaft to produce a continuous ridge along the length of the spicule. An alternative view is that these ridges may be the remnants of the point of attachment between the lateral alae and shaft (i.e., a reduction from the existing fused structure). If this latter interpretation is correct (and it is energetically more probable than the acquisition of a new structure), then anchorate chelae may

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**TABLE 47.** List of characters and character states used to judge apomorphy in the construction of the cladogram of relationships between genera of Microcionidae based on outgroup comparisons with members of the family Raspaliidae. States marked with an asterisk indicate plesiomorphic condition(s) and discussed in the Analysis of Morphometric Characters. Consistency Index (CI) is indicated for each character obtained from parsimony analysis (Swafford, 1991)
1. Growth form specialisation. (CI = 1.0) I. encrusting or bulbous-encrusting growth forms. 2. * massive, branching, lobate, flabellate, vaseform or tubular growth forms. 3. specialised honeycomb-reticulate growth forms composed of tightly anastomosing flattened fibre-branches (lacunae).

2. Ectosomal skeleton specialisation. (CI = 0.6) I. membranous, skin-like exterior, with single category of (subectosomal) auxiliary spicule extending from choanosomal skeleton protruding through surface forming discrete paratangential or erect brushes. 2. with single category of (subectosomal) auxiliary spicule on surface forming tangential, paratangential or plumose tracts. 3. with two categories of auxiliary spicules, smaller ectosomal spicules generally overlaying larger subectosomal spicules forming discrete bundles or continuous palisade on surface. 4. * with specialised ectosomal skeleton composed of smaller auxiliary spicules surrounding bases of protruding larger subectosomal spicules.

3. Subectosomal skeleton structure. (CI = 0.5) I. radial, with perpendicular bundles or single spicules supporting ectosome. 2. * plumose, plumoreticulate, or disorganised tracts of spicules in peripheral skeleton.

4. Differentiation within choanosomal skeleton. (CI = 0.667) I. choanosomal skeleton more-or-less undifferentiated, unstructured. 2. choanosomal skeleton well structured, hymedesmoid to reticulate, but lacking any differentiated components. 3. * choanosomal skeleton well structured, predominantly reticulate, differentiated into two distinct components.

5. Fibre development and skeletal architecture. (CI = 0.714) I. choanosomal skeleton without spongin fibres (or indefinite fibres), with spicules forming more-or-less disorganised halichondroid, vaguely ascending, longitudinal reticulate tracts. 2. choanosomal skeleton with poorly developed spongine fibres, primary (basal or axial) renieroid component derived by acanthostyles. 3. * choanosomal skeleton well structured, radial, and reticulate component derived by smooth principal spicules. 4. choanosomal skeleton with well developed spongine fibres, primary skeleton compressed, renieroid, cored smaller smooth principal styles, secondary skeleton vestigial or greatly reduced, consisting only of larger smooth principal styles embedded in peripheral fibres forming sparse radial tracts. 4. choanosomal skeleton with well developed spongine fibres forming more-or-less evenly reticulate or plumo-reticulate meshes throughout in massive forms, or thick basilar layer of spongine and hymedesmoid structure in encrusting forms. 5. choanosomal skeleton with well developed spongine fibres woven into flattened reticulate branches or forming continuous sheets without any regular architecture, cored by criss-cross of auxiliary styles. 6. * choanosomal skeleton with well developed spongine fibres forming compressed reticulate axis and well differentiated radial, plumose or plumo-reticulate extra-axis.

6. Compression of choanosomal skeleton. (CI = 0.8) I. choanosomal skeleton without any marked axial compression or differentiated axial and extra-axial regions. 2. choanosomal skeleton without marked axial compression but well differentiated axial and extra-axial (radial, plumose or plumo-reticulate) regions. 3. * choanosomal skeleton with noticeably compressed axis and well differentiated axial and extra-axial (radial, plumose or plumo-reticulate) regions. 4. choanosomal skeleton hymedesmoid or microcinion, with basal layer of spongine lying on substrate (with or without ascending, non-anastomosing fibre nodes), and bases of principal spicules standing perpendicular to substrate. 5. choanosomal skeleton evenly renieroid or isodictylar reticulate throughout with well developed spongine fibres cored by smooth principal styles.

7. Derivation of spicules coring fibres. (CI = 0.75) I. * choanosomal fibres or skeletal tracts cored by one or more category of principal spicules. 2. choanosomal fibres or skeletal tracts cored by auxiliary spicules but partially or wholly replaced by detritus. 3. choanosomal fibres or skeletal tracts cored by auxiliary spicules identical to those in ectosomal and subectosomal skeletons. 4. choanosomal fibres or skeletal tracts cored by auxiliary spicules different from those in peripheral skeleton.

8. Differentiation of primary and secondary skeletal components. (CI = 1.0) I. * primary and secondary skeletal components undifferentiated. 2. primary skeleton renieroid cored by axially or basally compressed tracts of acanthostyles, secondary skeleton cored by smooth principal styles in plumose, subscleritcal or plumoreticulate tracts. 3. primary skeleton renieroid cored by axially or basally compressed tracts of acanthostyles, secondary skeleton cored by smooth principal styles in plumose, subscleritcal or plumoreticulate tracts. 4. primary skeleton axially compressed spongine fibres cored by renieroid tracts of sparsely spined principal styles intermingled with plumose or plumo-reticulate tracts of smooth principal styles, overlaid by secondary extra-axial plumose skeleton cored by larger smooth principal styles. 5. primary renieroid reticulate skeleton cored by smooth principal styles and cored by identical spicules, with secondary radial extra-axial skeleton on exterior edge of skeleton only cored by larger smooth principal styles.

9. Derivation of echinating spicules. (CI = 0.444) I. echinatisng spicules absent. 2. * special category of (acanthostyles) present echinating fibres, differentiated from principal spicules. 3. echinating spicules styles or acanthostyles undifferentiated from principal spicules coring spongine fibres. 4. echinating spicules styles or acanthostyles representing principal spicules; but different from those coring fibres. 5. echinating spicules oxeas or anisoceae representing principal spicules, but different from those coring fibres.

10. Modifications to claeae microscleres. (CI = 0.5) I. claeae absent. 2. * isochelae palmate. 3. isochelae arcuate-like. 4. isochelae anchorite-like.

11. Ornamentation of toxa microscleres. (CI = 0.667) I. toxa absent. 2. * toxa with predominantly smooth points. 3. toxa with predominantly spined points.
Several Microcionidae genera have been established solely on the basis of bidentate- or tridentate-derived isochelae, including arcuate and bidentate sigmoid isochelae (Anaata, Anthoarcuata, Bipocillosis, Damoseni, Dendrocia, Paradox, Qasimella, Wetmoreus) and anchorate forms (Clionanchora, Infilis). However, most do not have true arcuate or anchorate chelae (as defined by Hajdu et al., 1994a), given that the lateral alae are not fully formed and still fused with the shaft for a greater proportion of their length, or the taxa do not belong in Microcionidae. Dendrocia, Bipocillosis and Damoseni are pivotal to the interpretation and are discussed further below.

Within Microcionidae several species have different chelae geometries but have homologous skeletal features (e.g., with megascere geometry and skeletal stucture that indicates close affinities to each other). The Australian endemic genus Clathria (Dendrocia) has a nearly complete series of chelae extending from 'typical' palmate isochelae in one species (with completely fused lateral alae and straight shaft), modified palmate chelae seen in most species (i.e., with thickened curved shaft and partially detached lateral alae, verging on 'arcuate') to anchorate-like chelae seen in two species (i.e. in which there are completely detached lateral alae and lateral ridges on the shaft). In other morphological characters species are very similar. The existence of this nearly complete transformation series within one genus raises the possibility that 'anchorateness' (or the detachment of lateral alae from the shaft of chelae) may have occurred more than once within the Poecilosclerida (an hypothesis discounted by Hajdu et al. (1994a), who suggested that anchorate and arcuate modifications to chelae were homologues within a single phylogeny containing bidentate-derived taxa). Interpretation of this transformation continuum in Clathria (Dendrocia) from 'typical' palmate to detached 'anchorate' chelae suggests that detachment of the lateral alae from the shaft of the spicule, leaving the residual 'scar' or lateral ridge along the shaft, may be a simple reduction process occurring more than once in the group, and that 'anchorateness' may not be homologous throughout the order. Other examples, such as the strongly unguiferous sigmoid chelae of Bipocillosis and Damoseni, of indeterminable arcuate or anchorate derivation, are less easily accountable and might validly be excluded from this family. However, the latter genus also has ooxhorn toxas which supports its present inclusion in Microcionidae.

De Laubenfels' (1936a) solution to this problem (in which species with modified isochelae have skeletons and spiculation otherwise structurally and geometrically identical to those containing palmate chelae), was to assign every occurrence of a modified chela to a new genus, with the consequence that there were nearly as many genera as species in some families. De Laubenfels' (1936a) classification had extraordinary high levels of homoplasy and the inferred relationships based on isochelae geometry cut across classifications based on both skeletal architecture (e.g., Hallmann, 1912, 1920) and ectosomal characteristics (e.g., Van Soest, 1984b). This proposal was rejected by most contemporary authors. Hooper (1990a) provided an alternative proposal that considered modified isochelae to be homoplasic, and a classification based primarily on this feature was both unparsimonious and incongruent with other structural and geometric features within the Poecilosclerida. Hajdu et al. (1994a) correctly noted that many cases of 'arcuateness' and 'anchorateness' in the literature of Poecilosclerida have not been subsequently substantiated by re-examination of original material using techniques other than routine light microscopy (e.g. many turned out to be merely modified palmate forms), and this is also true for most recorded instances within the Microcionidae. However, from evidence presented here it is likely that 'anchorateness' and 'arcuateness' may be a homoplasy for the Poecilosclerida, and consequently Hajdu et al. (1994a) major reorganisation of the Poecilosclerida requires further refinement, as to family composition.

(7) Toxa morphology: Van Soest et al. (1991) set a precedent for interpretation of toxa geometry in which ooxhorn-like toxas (including wing-shaped toxas) were considered to be an-
cestral because they are shared by outgroups such as Myxillidae, whereas accolada-like taxa (including raphidiform and oxoetype taxa) are more derived.

(8) Growth form: Micropcionids in areas of environmental extremes, or cryptic habitats where competition for space and other resources may be high, may show a trend in reduction of skeletal characters. In these cases it is common to find fibres reduced to a simple, heavy basal layer of spongin lying on the substrate (e.g., C. (Microciona)). Although some relict (possible ancestor) groups such as 'sclerosponges' have a similar growth form, particularly those species which lose their basal calcareous skeletons (e.g., deficient Merlia), it is considered here that in most cases an encrusting habit and a reduced basal skeleton is a derived condition and adaptive strategy, enabling colonization and survival in intertidal and cryptic habitats. Moreover, it is certain that this feature has arisen independently many times and in many different sponge groups. Within Micropcionidae there are several specialised growth forms, such as 'honeycomb' reticulate characteristic of Holoprossams, with may have some systematic value, whereas other growth forms occur throughout Porifera and are more difficult to interpret phylogenetically.

Phylogenetic analysis (Fig. 315) shows two fundamental groups of genera (A, B) differentiated primarily by their skeletal structure (character 6), composition or differentiation of the skeleton (character 4), and presence or absence, respectively, of a secondary renieroid reticulate skeleton overlaying the primary (reticulate, pluio-reticulate, plumose or hymedesmoid) skeleton (character 5). One group (B) containing Artemisina, Antho and Echinocclaria has suggested myxillid-like features, most possessing a secondary renieroid skeleton. The other group (A) containing Clathria, Echinochalinia, Holoprossama and Pandaros has suggested similarities to raspallids, including skeletal structure of typical genera (e.g., compare Clathria (Acanthella) and Raspallia) and atypical genera (e.g. compare Echinochalinia (Echinochalinia) and Echinochiton). It is suggested that the 'raspallid' group (A) retains more ancestral features common to the outgroup, whereas the 'myxillid' group (B) is more derived.

Within group (A) there are three taxa indicated as possibly polyphyletic (C. (Wilsonella), C. (Dendrocia), Pandaros). The first two may be simply more derived than other Clathria at the base of the tree, or they may represent full genera. The latter explanation is rejected given that the characters inferring polyphyly (partial substitution of coring megascleres by detritus in C. (Wilsonella), and loss of principal spicules completely in C. (Dendrocia)) are homoplasic representing convergences via functional acquisition or secondary loss of particular features rather than significant apomorphies, and their status is recognised only at the subgenus level. The third taxon, Pandaros, is incertae sedis. It is an anomalous, monotypic genus with greatly reduced fibre and spicular characteristics, not represented in the Indo-Pacific, and probably best considered a highly modified Clathria-like species stemming from the Clathria group.

The use of subgeneric taxa within this classification, following the precedent adopted for the Raspallidae (Hooper, 1991), is admittedly partially artificial given the existence of these homoplasies, but no alternative is presently available that allows both the construction of a sound phylogenetic hypothesis as well as the production of a useful, working classification for this large family of sponges (given especially the relatively poor character set that exists for sponges in general). Within Antho and Clathria the use of subgeneric taxa provides a convenient means to manage large groups of species within these genera, despite the possibility that some of the subgeneric criteria are of dubious phylogenetic value (e.g., possession of acanthose strongyles in place of acanthose styles in A. (Antho) and A. (Plocamia), respectively; presence of detritus within fibres in C. (Wilsonella); encrusting habit and plumose fibre nodes in C. (Microciona)). Conversely, other subgenera have a more sound phylogenetic basis and are more easily justified within the classification presented here (e.g., stylote versus oxoete structural megascleres in E. (Echinochalinia) and E. (Protophilaspongeia); presence or absence of ecosomal specialised in C. (Thalysias) and C. (Clathria)). Within Clathria, there are many species-groups that could be used to subdivide these taxa further (e.g., 'spicata', 'procera' 'phorbasisiformis' groups; see also Hooper et al., 1991; Hooper & Lévi, 1994). Many of these groups contain species that span across several subgenera and as such are of limited usefulness in phylogenetic reconstruction, but they are most useful in interpretation of sister-group relationships in a biogeographical context (Hooper & Lévi, 1994), and these species groups will be considered further in a more detailed study Indo-west Pacific micropcionids,
TABLE 48. List of species included in Microcionidae with their current taxonomic assignments.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>ORIGINAL GENUS</th>
<th>CURRENT ASSIGNMENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>obesiina Lamarck</td>
<td>Spongia</td>
<td>C. (Thalysias)</td>
</tr>
<tr>
<td>abrolhosensis sp.nov. Carter</td>
<td>-</td>
<td>C. (Wiltsanella)</td>
</tr>
<tr>
<td>abysstarum Carter</td>
<td>Dictyocylindrus</td>
<td>synonym of A. (Antho) dichotoma (Esper)</td>
</tr>
<tr>
<td>ocanthofolium Duchassaing &amp; Michelotti</td>
<td>Pandaros</td>
<td>Pandaros</td>
</tr>
<tr>
<td>acanthodes Hentschel</td>
<td>Clathria</td>
<td>synonym of C. (Thalysias) cactiformis (Lamarck)</td>
</tr>
<tr>
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| fascicularis Topsent  | Clathria       | C. (Thalysias) |
| fasciculata Wilson    | Clathria       | C. (Thalysias) |
| fasciculifera Carter  | Microciona     | C. (Microciona) |
| fauroti Topsent       | Axosuberites   | C. (Axociella) |
| favosa Whitelegge     | Clathria       | synonym of C. (Thalysias) cactiformis (Lamarck) |
| favosa Lamarck         | Spongia        | synonym of E. (Echinochalina) barba (Lamarck) |
| favulosa sp. nov.      | -              | E. (Protochlorispongia) |
| favus Carter          | Echinoclathria | Holopsamma |
| favus var. arenifera  | Echinoclathria | Holopsamma |
| Carter                | Microciona     | laminaeafavosa Carter |
| ferrera de Laubenfels | Fisherispongia | C. (Wilsonella) |
| ferrea                | Microciona     | Phorbas (Anchinoidea) |
| Bowerbank             | Microciona     | |
| filifer               | Rhaphidophlus  | C. (Thalysias) |
| filifer var. cantabrica| Orueta         | C. (Clathria) |
| Carter                | Rhaphidophlus  | C. (Thalysias) |
| filifer var. mutabilis| Topsent        | C. (Thalysias) |
| Lindgren              | Rhaphidophlus  | C. (Thalysias) |
| filifer var. spinifera| Lindgren       | C. (Thalysias) |
| flabellata Topsent    | Ophitiaspongia | synonym of C. (Axociella) nidificata (Kirkpatrick) |
| flabellata              | Phakellia      | synonym of C. (Axociella) macropora Lendenfeld |
| flabellata Burton      | Rhaphidophlus  | C. (Clathria) |
| flabellifera Hooper &amp; Lévi | Clathria (Thalysias) | C. (Thalysias) |
| flabelliformis Carter  | Echinonema     | synonym of C. (Thalysias) cactiformis (Lamarck) |
| foliacia Topsent      | Clathria       | C. (Clathria) |
| foliacens Vacelet &amp; Vaseur | Clathria  | C. (Clathria) |
| foraminifera Burton   | Aulenella      | C. (Wilsonella) |</p>
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| mina de Laubenfeld          | Ophlitaspongia          | C. (Microciona)                  |
| minor Burton                 | Ophlitaspongia          | Echinoclathria                   |
| minuta Van Soest Carter     | Rhophidophhus           | C. (Thalysias)                   |
| mixta Hentschel             | Clathria                | C. (Wilsonella)                  |
| mollis Kirkpatrick           | Clathria                | Pranax (Anchinidae)              |
| manticularis Ridley &amp; Dendy | Axinella                | synonym of A., Anopsammina involv. (Schmidt) |
| morisca Schmidt             | Clathria                |                                  |
| mortensii Brandsted         | Clathria                | C. (Clathria)                    |
| mutulpa Sim &amp; Byeon         | Clathria                | C. (Thalysias)                   |
| mutabilis Topsent           | Rhophidophhus           | C. (Thalysias)                   |
| multiformis Whitelegge      | Ceroochalina            | synonym of Echinoclathein lus. subc. Carter |
| multipes Hallmann           | Clathria                | C. (Clathria)                    |
| multipora Whitelegge        | Clathria                | C. (Clathria)                    |
| mutuliforusaxofarmis         | Asciella                | synonym of C. (Thalysias) rubra (Lendenfeld) |
| mutulo Bowerbank            | Halichondria            | C. (Dendrocia)                   |
| myxilloides Dendy           | Clathria                | C. (Dendrocia)                   |
| naikoensis Hoshino          | Eurypan                 | C. (Thalysias)                   |
| nimibieni Uriz              | Microciona              | C. (Microciona)                  |
| nervosa Lévi                | Asciella                | C. (Thalysias)                   |
| nexus Kolun                  | Bipocillopsis           | C. (Clathria)                    |
| nidificata Kirkpatrick      | Ophlitaspongia          | C. (Asciella)                    |
| nids-vespatorum Lendenfeld  | Halme                   | synonym of Halopsamma crassa Carter |
| nootangerae sp.nov.          |                        | C. (Clathria)                    |
| nadosa Carter               | Echinoclathein          | Echinoclathein                   |
| nanamno Burton              | Hynathia                | C. (Microciana)                  |
| natalis sp. nov.            |                        | Echinoclathein                   |
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<td>Cornuhum</td>
<td>C. (Clathria)</td>
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<td>Ophitiaspangia</td>
<td>C. (Axociella)</td>
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<tr>
<td>thieiei Burton [preced.]</td>
<td>Ophitiaspangia</td>
<td>see C. (Axociella) geographogenicis non.nov.</td>
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<tr>
<td>tiugens sp.nov.</td>
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<td>[for Microciona chelisfera Lévi]</td>
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<td>ulmus Vosmaer</td>
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<td>urceolata Desor</td>
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<tr>
<td>urge nom.nov.</td>
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<td>[for Microciona curvicauda Vacelet &amp; Vasseur]</td>
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<td>Pandaras</td>
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<td>wesselsensis sp.nov.</td>
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incorporating the Indonesian and Micronesian faunas (in prep.).

My phylogeny, based primarily on structural features of the skeleton, conflicts with that of Hajdu et al., 1994. Their hypothesis is based on the premise that microgeometry is less likely to be influenced by modification during the course of evolution than structural features. I emphasise skeletal structure and skeletal differentiation as primary characters in the evolution of Microcionidae. My classification allows inclusion of arcuate and anchorate modified chelae (which would otherwise be included in Myxillina). Identical structural features, primarily, and megascleere geometry, secondarily, in species with arcuate or anchorate chelae may indicate evolutionary similarity, whereas it is debatable whether or not observed modifications to chelae are homologous or merely convergent.

Biogeography. Many early attempts to analyse biogeographic patterns of marine sponges were unsuccessful because authors attempted too broad a taxonomic coverage without detailed taxonomic revisions and the belated recognition that many so-called 'widely distributed' species actually consist of allopatric, cryptic sibling species, thus masking potentially informative patterns on distribution and biasing proportions of regional endemism. By comparison, several contemporary biogeographic
analyses have had greater success based on relatively well-revised, restricted taxa (genera, families). (e.g., Van Soest et al., 1991; Hooper, 1991; Van Soest & Hooper, 1993; Hooper & Lévi, 1994; Bergquist & Kelly-Borges, 1995). Yet these studies too have not reached any consensus concerning general area statements for shallow water marine sponges, and they fail to distinguish between vicariant events or subsequent dispersals to explain species’ distributions (Hooper & Lévi, 1994).

Only one (Hooper & Lévi, 1994) included species of Microcionidae, providing a preliminary analysis of biogeographic patterns amongst Indo-west Pacific species, comparing levels of interpretation of data and to resolve a general area statement for the marine biome (Van Soest et al., 1991). It is inappropriate to undertake such a detailed areacladistic analyses in this present work restricted to the Australian fauna, whereas it will be much more useful to include a revised Indonesian and Micronesian microcionid fauna into analyses (in prep.). The present analysis follows the format used for Raspailiidae (Hooper, 1991).

From present data and the earlier analysis (Hooper & Lévi, 1994) there is little evidence for cosmopolitan microcionids. A possible exception is Clathria atrasanguinea which has contiguous species throughout world marine provinces, comparing regional faunas within the Indo-west Pacific region (targeting the New Caledonian fauna in particular), and contrasting these broad distribution patterns for Microcionidae with those of the families Raspailiidae and Axinellidae. These analyses are taken further in this study, focussing in particular on the Australian fauna, and incorporating additional data derived from the present revision. Hooper & Lévi (1994) also provided an areacladistic analysis of one species group (Clathria ‘procera’ group), comparing sibling species’ distributions and postulating historical biogeographic patterns and relationships throughout the world’s seas. Although it is clear from this study and others that historical biogeography can provide many more facets to the questions posed by biogeographers, who attempt to understand relationships between both provincial species and the provinces themselves, it is also clear that analysis of many species groups are required to gain a meaningful interpretation of data and to resolve a general area statement for the marine biome (Van Soest et al., 1991). It is inappropriate to undertake such a detailed areacladistic analyses in this present work restricted to the Australian fauna, whereas it will be much more useful to include a revised Indonesian and Micronesian microcionid fauna into analyses (in prep.). The present analysis follows the format used for Raspailiidae (Hooper, 1991).

From present data and the earlier analysis (Hooper & Lévi, 1994) there is little evidence for cosmopolitan microcionids. A possible exception is Clathria atrasanguinea which has contiguous
REVISION OF MICROCIONIDAE

populations (i.e. substantiated by comparison of voucher specimens) within the W and E Indian Ocean system, Mediterranean-E Atlantic system, and W Atlantic system (though not yet recorded from the Pacific). All other reported cases of cosmopolitan species consist of 2 or more sibling species. In contrast, 9 species of microcionids are widely distributed, usually with disjunct distributions (possibly explained by local extinctions within intermediate provinces; e.g., C. cactiformis). It is possible that some of these species also comprise more than one allopatric sibling species but it was not possible to detect any consistent differences between populations based solely on skeletal characters. Similarly, most species of Microcionidae are restricted to single ocean systems, and only about 5% of species range widely within any particular system (whereas most other species are much more restricted in their ranges). Worldwide 72% of species are restricted to a single biogeographic province although levels of regional endemism range from 30-80% of species (Fig. 316).

Microcionids are relatively diverse and prevalent, with most species found predominantly in shallow-waters but some ranging down to 2500m depth. They comprise between 7-16% of all species of demosponges within the various marine biogeographic regions of the world (8% average), with two major peaks of

FIG. 317. C-E. Biogeographic relationships between Australian microcionid species within Indo-west Pacific marine provinces, showing numbers of shared species between provinces (provincial endemic species circled).
diversity indicated: Indo-Australia region and NE Atlantic (Hooper & Levi 1994: fig.3). Within the Indo-west Pacific, extending from the Andaman Sea to islands of the W Pacific rim, there are 196 species of which 115 (or about 60%) are endemic to the region. This level of endemism is closely comparable to that in NE Atlantic species. The Indo-west Pacific species represent about 7% of the region’s demospponge fauna.

Australian continental marine provinces contain 148 species of microcionids, comprising about 11% of the entire demospponge fauna for the region, with 111 (or 75%) being endemic.

Although it is not possible to postulate detailed faunistic relationships using these crude analyses microcionid distribution data do support the concept of a differentiated southern Gondwanan fauna and northern Tethys fauna within coastal Australia (Hooper & Levi, 1994) based on a different data set. Temperate Australian marine provinces contain a higher diversity of microcionids (90 species) and greater endemism (81%) than tropical provinces (the latter with 74 species, 59% endemic) (Fig. 316). These levels of endemism are very similar to those observed for Raspailiidae (Hooper, 1991), although the temperate raspailiid fauna was less diverse but had greater endemism than did the tropical fauna.

This observation is further supported considering the Australian fauna in more detail (Fig. 317).

**Peronian** (Fig. 317A). Of all Australian continental provinces the SE Australian temperate (Peronian) province contains the greatest diversity of species (60) and also the highest proportion of regional endemism (28 species or 48%). Not surprisingly greatest similarities in species composition (i.e., numbers of shared species) are with the adjacent temperate provinces (Flindersian, Maugean) and adjacent tropical Solanderian province, with only few ‘widespread’ species common to all Indo-west Pacific provinces.

**Flindersian** (Fig. 317B). The southern and SW Australian temperate (Flindersian) province contains 46 species of which 22 (47%) are endemic, showing greatest similarities to the other two southern Australian temperate provinces (Peronian, Maugean), whereas few species are shared with the adjacent NW tropical (Dampierian) province (no doubt reflecting the relative importance of the Leeuwin current to the marine biogeography of the west coast (Pearce & Walker, 1991; Hooper, 1994)).

**Maugean** (Fig. 317C). The cool temperate Bass Strait-Tasmanian (Maugean) province contains 26 species of microcionids with only 5 (or 19%) endemic, showing greatest similarities to the other southern temperate provinces.

**Solanderian** (Fig. 317D). The NE Australian tropical (Solanderian) province contains 45 species (18 or 40% endemic), with similarities to the adjacent temperate Peronian, tropical Dampierian and SE Indonesian faunas.

**Dampierian** (Fig. 317E). A similar relationship is indicated for the tropical northwest Australian (Dampierian) province containing 42 species (17 species or 40% endemic).

From these comparisons between adjacent provincial faunas it is clear that the two tropical provinces (Dampierian and Solanderian) share the highest number of sympatric species and also share a large number of species with both Indonesia and the western Pacific rim islands. Nevertheless, nearly half the number of species in each of these provinces are unique. Similarly, the three southern Australian (continental, temperate) provinces share a large proportion of their species, especially Peronian and Maugean faunas, whereas there is very little mixing (less than 15% of species) between temperate and tropical Australian microcionid species. Only two species of microcionids have confirmed trans-Tasman Sea distributions (Bergquist & Fromont, 1988), and only four are found in both the Solanderian and New Caledonian provinces (Hooper & Levi, 1993a), with similar observations reported for Raspailiidae (Hooper, 1991) in which both New Zealand and New Caledonian faunas have exceptionally high numbers of endemic microcionid species (nearly 70% and 67% endemism, respectively).

The Antarctic and austral islands faunas have a low diversity of microcionids (18) and few endemic species (28%), sharing many species with adjacent provinces such as New Zealand, SW Atlantic, Subantarctic islands and SE Pacific. There are no austral temperate species found in the Australian continental faunas, as also observed for the Raspailiidae (Hooper, 1991).
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MEMOIRS OF THE QUEENSLAND MUSEUM


PLATE 2. A, Clathria (C.) transiens (QMG300268, Furneaux Is, Tas, 18m, photo NCI). B, Clathria (W.) australiensis (QMG301458, Cook I, NSW, 15m, photo author). C, Clathria (W.) abrolhosensis (NTMZ3218, Houtman Abrolhos, WA, 22m, photo author). D, Clathria (W.) claviformis (QMG300576, Parry Shoals, NT, 30m, photo NCI). E, Clathria (W.) ensiae (NTMZ3561, Marion Reef, SA, 6m, photo NCI). F, Clathria (W.) tuberosa (QMG303428, Mandorah, NT, 1m, photo author).
PLATE 4. A, Clathria (I.) eccentrica (NTMZ288, Darwin Harbour, NT, 1m, photo author). B, Clathria (A.) thetidis (QMG303752, North Head, NSW, 50m, photo D. Roberts). C, Clathria (T.) abietina (NTMZ2163, Darwin Harbour, NT, 10m, photo author). D, Clathria (T.) abietina (NTMZ2611, Darwin Harbour, NT, 12m, photo author). E, Clathria (T.) cactiformis (NTMZ3831, St. Patrick’s Head, Tas., 6m, photo NCI). F, Clathria (T.) cactiformis (QMG300736, Houtman Abrolhos, WA, 8m, photo NCI).
PLATE 6. A, Clathria (T.) coppingeri (NTMZ1152, Northwest Shelf, WA, 55m depth, photo author). B, Clathria (T.) darwinensis (QMG303375, Darwin Harbour, NT, 17m, photo author). C, Clathria (T.) hallmanni (NTMZ2218, Darwin Harbour, NT, 0m, photo author). D, Clathria (T.) hesperia (NTMZ3327, Exmouth Gulf, WA, 16m, photo NCI). E, Clathria (T.) hesperia (QMG300213, Amphinome Shoals, NW Shelf, WA, 50m, photo author). F, Clathria (T.) hirsuta (QMG300603, Whitsunday Is, GBR, 20m, photo NCI).
PLATE 8. A, Clathria (T.) reinwardti (NTMZ77, Port Essington, NT, 15m, photo author). B, Clathria (T.) reinwardti (NTMZ2206, Darwin Harbour, NT, 0m, photo author). C, Clathria (T.) tingens (NTMZ2231, Darwin Harbour, NT, 0m, photo author). D, Clathria (T.) tingens (QMG303826, Hook Reef, GBR, 31m, photo author). E, Clathria (T.) toxifera (NTMZ2222, Darwin Harbour, NT, 0m, photo author). F, Clathria (T.) vulpina (QMG301376, Byron Bay, NSW, 18m, photo author).
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