Leandro Manzoni Vieira

Revisão taxonômica do gênero *Scrupocellaria* van Beneden (Bryozoa, Candidae)

São Paulo

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Taxonomic revision of the genus *Scrupocellaria* van Beneden (Bryozoa, Candidae)

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências Biológicas, na Área de Zoologia.

Orientador: Alvaro Esteves Migotto
Co-Orientadora: Judith Ellen Winston

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Esta dissertação não constitui publicação no sentido do artigo 9 do ICZN e portanto quaisquer atos nomenclaturais nela contidos tornam-se sem efeito para princípios de prioridades e de homonímia.

This dissertation should not be considered as a publication in the sense of the article 9 of the ICZN, therefore, any nomenclatural acts herein proposed are considered void for the principles of priority and homonymy.

Aos meus pais, William e Célia,
por todo carinho, apoio e incentivo

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Índice

INTRODUÇÃO GERAL

O gênero *Scrupocellaria* foi primeiramente proposto por VAN BENEDEN (1845) para acomodar *Sertularia scruposa* Linnaeus, 1758. Durante anos o gênero tem agrupado espécies com colônias eretas, bisseriais, articuladas, com campo de abertura oval ocupando grande parte da parede frontal, presença de aviculário lateral e vibraculário basal (HARMER, 1923). Ao menos três gêneros foram sinonimizados com *Scrupocellaria*—*Cellarina* van Beneden (1848), *Crisina* van Beneden (1850) e *Licornia* van Beneden (1850) (HARMER, 1926)—e várias espécies anteriormente descritas no gênero foram realocadas em outros gêneros, tais como *Amastigia* Busk, 1852 e *Notoplites* Harmer, 1923 (HARMER, 1923, 1926; HASTINGS, 1943).

Segundo BOCK (2012), *Scrupocellaria* compreende atualmente *c.* 92 espécies, 20 das quais fósseis. Muitas delas são morfologicamente semelhantes, o que levanta a suspeita de que ao menos algumas sejam coespecíficas ou que uma espécie nominal corresponda a mais de uma espécie morfológica (FRANSEN, 1986).

Várias espécies de *Scrupocellaria* foram relatadas para águas rasas no Atlântico. No Atlântico Norte, destacam-se os relatos para a costa e mares da Europa (NORMAN, 1868; BUSK, 1852; HARMER, 1926; HASTINGS, 1943; HAYWARD & RYLAND, 1998), e para a costa ocidental americana e Caribe (SMITT, 1872; MARCUS 1937, 1955; HASTINGS, 1943; LAGAAIJ, 1963; OSBURN, 1912, 1914, 1940, 1947; FRANSEN, 1986; WINSTON, 1977, 1982, 2005; MCCANN *et al*., 2007). No Atlântico Sul, os estudos são escassos, com apenas uma espécie, *Scrupocellaria scrupea*, relatada para a costa ocidental africana (COOK, 1985), além de outras 11 para o litoral brasileiro, das quais uma nova espécie, até o momento não descrita, foi relatada por VIEIRA *et al.* (2007) e outras 10 espécies foram listadas por VIEIRA *et al.* (2008). Apenas três revisões das espécies de *Scrupocellaria* foram realizadas, todas tratando de espécies do Indo-Pacífico (MENON, 1972; LIU, 1984; TILBROOK & VIEIRA, *no prelo*); entre estes, apenas TILBROOK & VIEIRA (*no prelo*) utilizaram imagens de microscopia eletrônica de varredura para o estudo de caracteres ultraestruturais da colônia, sendo, até o momento, o único levantamento de espécies de *Scrupocellaria* que incluiu comparações entre espécimes-tipo depositados em diferentes coleções científicas.

Morfologia

HARMER (1923) distinguiu vários grupos de briozoários eretos a partir do padrão de bifurcação da colônia, incluindo as disposições dos zooides que participam na formação dos novos ramos.

A notação utilizada para classificar os zooides na bifurcação foi baseada em colônias bisseriais: zooides “A” e “B”, para os dois zooides mais proximais que formam a bifurcação; zooides “C” e “D”, aqueles situados nas margens externas da bifurcação e originados dos zooides “A” e “B”, respectivamente; zooide “E”, ou zooide axial, derivado de “A” e em contato com lado interno de “C”; zooides “F” e “G”, posicionados no lado interno após a bifurcação e adjacente aos zooides “D” e “C”, respectivamente; zooides “J” e “K”, formados pelos zooides “D” e “C”, respectivamente (Figura 1; HARMER, 1923). Entre os táxons caracterizados, *Scrupocellaria* distingue-se pela presença de colônias bisseriais, com articulações passando através dos zooides CG e DF, e através do opésio dos zooides externos (bifurcação do tipo 8, acc. HARMER, 1923).

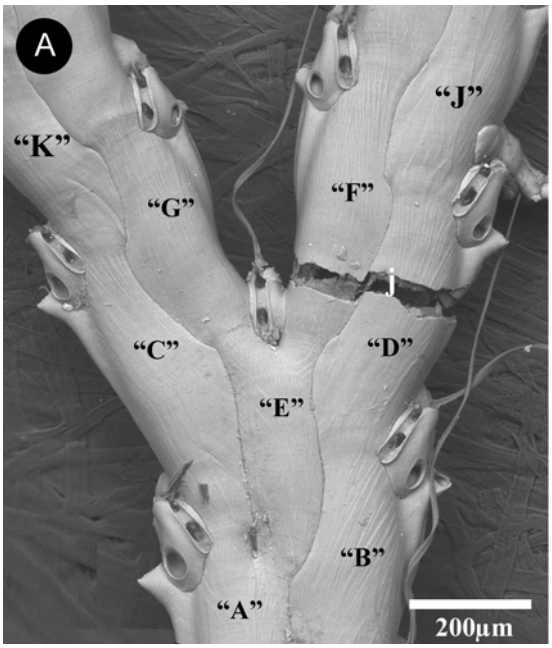

Figura 1. Notação utilizada para diferenciar os zooides formadores da bifurcação em nas espécies de Candidae; note em j a articulação da colônia

Apesar da notação proposta por HARMER (1923) para caracterizar espécies do gênero *Scrupocellaria*, também denominada bifurcação do tipo 8, o gênero apresenta uma ampla variação na posição das articulações (ver HARMER, 1923, 1926; OSBURN, 1950; TILBROOK & VIEIRA, *no prelo*). As articulações, que são importantes na distinção de espécies (HARMER 1923, 1926), podem ocorrer em três posições distintas: (i) no

ponto mediano do comprimento do opésio dos zooides externos, (ii) na parte proximal do opésio, e (iii) no gimnocisto, como ocorre nas espécies do gênero *Tricellaria* Fleming, 1828.

Ao contrário de outras espécies da família, as espécies do gênero *Scrupocellaria* tendem a perder estruturas morfológicas importantes para identificação, tais como escudo, espinhos orais, aviculários frontais e laterais (Figura 2A). Quando presente, tais estruturas apresentam uma grande variedade morfológica (Figura 2B–L), sem um padrão característico como descrito para outros gêneros, como *Caberea* ou *Canda* (OSBURN, 1950; GORDON, 1984).

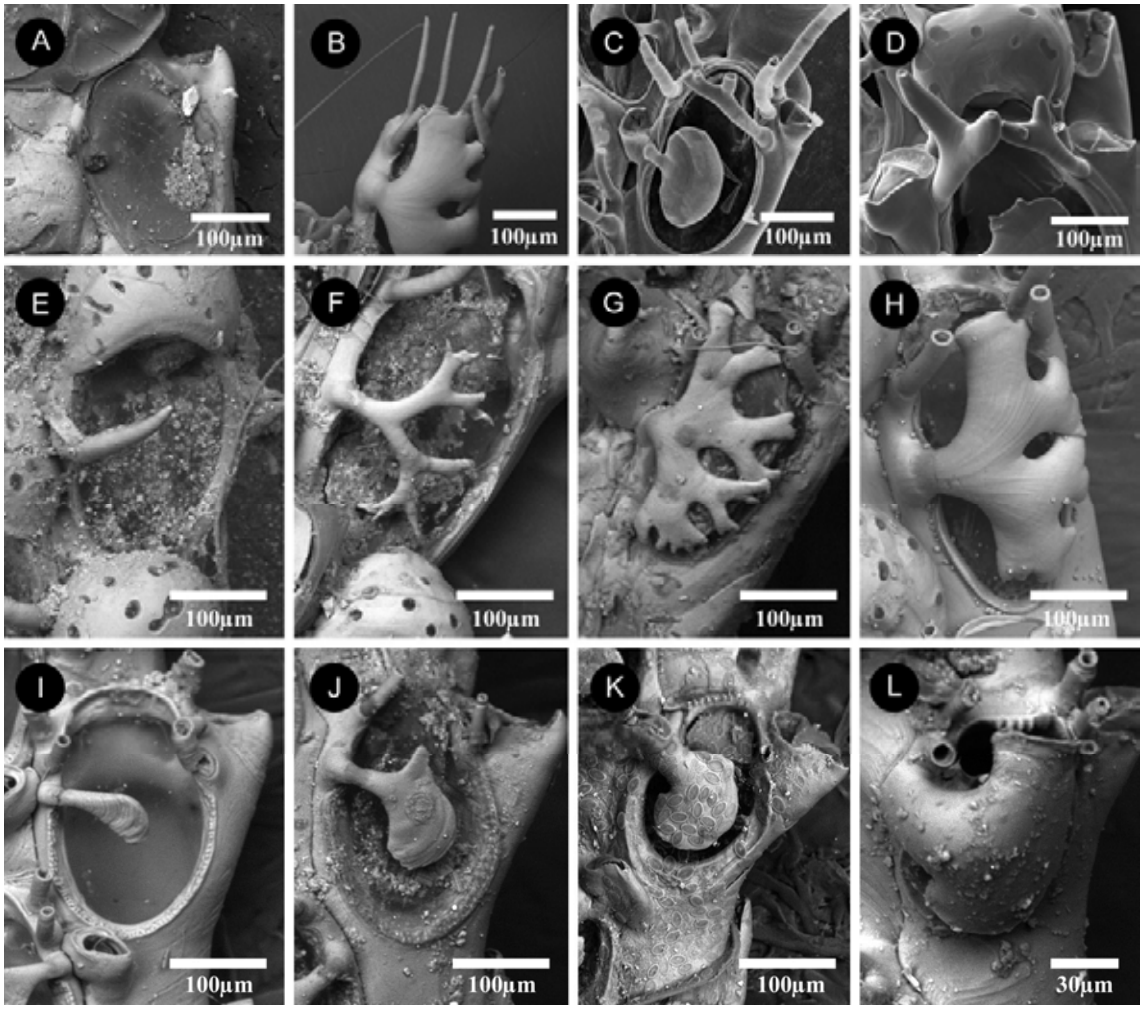

Figura 2. Variedade morfológica encontrada em espécies de *Scrupocellaria*. Veja em **A** uma espécie sem escudo e espinhos orais. Diferentes formas de espinhos orais podem ser vistas em **B**, **C** e **D**. A forma do escudo é totalmente variável entre as espécies, assim como seu local de origem, inseridos na margem mediana externa do opésio (**E–H**) ou situados no terço distal, próximo ao espinho oral interno proximal (**I–L**).

Algumas espécies de Candidae apresentam aviculários basais, *i.e.* zooides modificados sem polipídio funcional e com opérculo modificado (mandíbula) (RYLAND, 1970, WINSTON, 1984, CARTER *et al.*, 2010). Dois tipos de aviculários basais podem ocorrer: (a) aviculários adventícios, com mandíbula aguda e um poro na parede da câmara do aviculário, e (b) vibraculários, com mandibular setiforme (seta) e orifício tubular (CARTER *et al.*, 2010). Apesar da ausência de algumas estruturas zoeciais em *Scrupocellaria*, vibraculários abfrontais são geralmente presentes, ocorrendo regularmente em cada zoécio do ramo (Figura 3C,E–I).

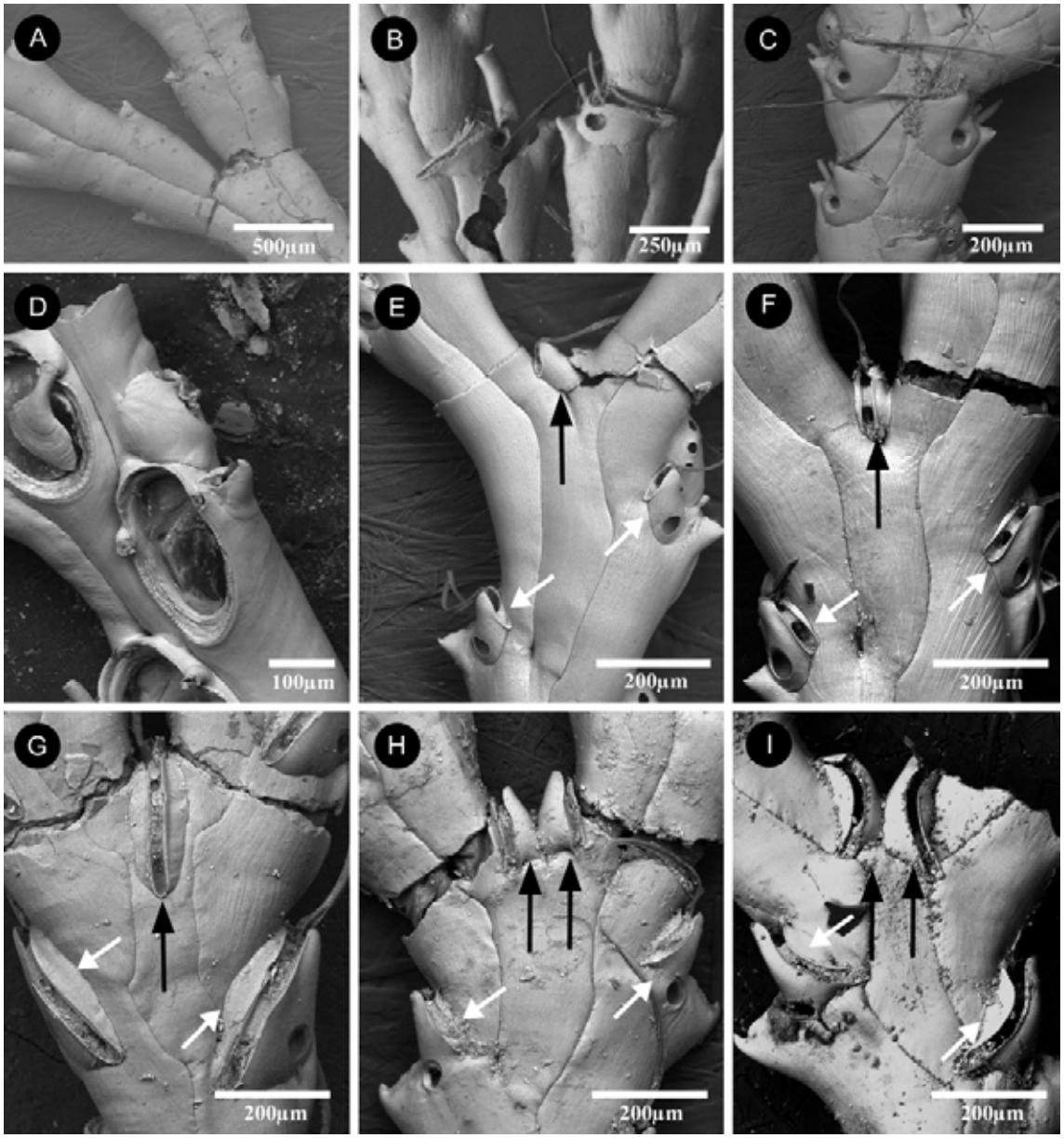

Figura 3. Diferentes tipos de câmaras aviculárias abfrontais encontrados em *Scrupocellaria*. Compare **A**, uma espécie sem aviculários, **B**, uma espécie com aviculário adventício, e **C,E–I**, diferentes formas de vibraculários (setas brancas), com

distinção no número nos zooides axiais (setas pretas), **D**, uma espécie com câmara do rizoide, porém sem aviculário.

Espécies de *Scrupocellaria* apresentam estruturas globulares para o desenvolvimento dos embriões, denominados ovicelos (Figura 4). Tais estruturas apresentam duas paredes calcárias, uma interna (endooécio) e outra externa (ectooécio). Entretanto, a parede externa apresenta calcificação variada, com um poro irregular simples (Figura 4A), bem como uma grande abertura frontal, o que torna o endooécio visível (Figura 4B). Em outras espécies, a superfície do ectooécio pode apresentar vários poros regulares em toda a superfície (Figura 4C). Um pequeno aviculário pode ser encontrado na parede distal do ectooécio (Figura 4A), mas em muitas espécies tal aviculário é ausente.

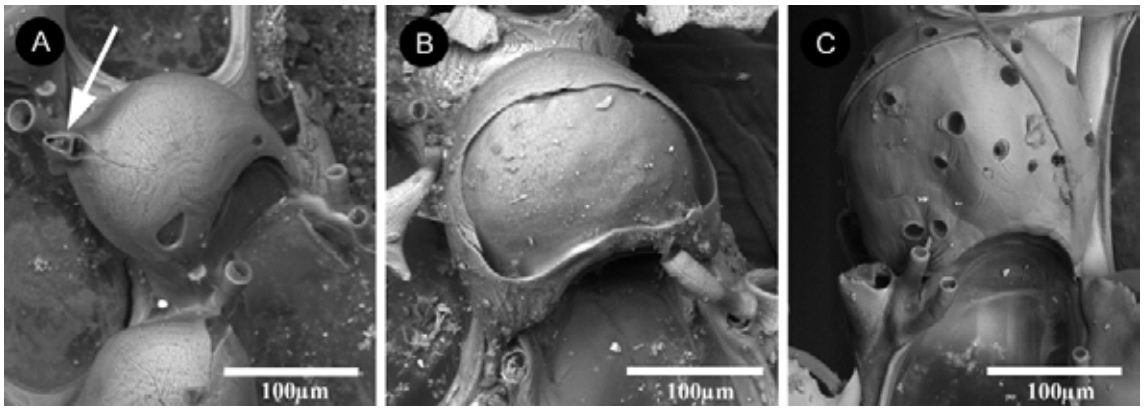

Figura 4. Três diferentes tipos de ovicelos encontrados em *Scrupocellaria*. **A**, ovicelo com um poro irregular na margem proximal; observe o pequeno aviculário na parede distal; **B**, ectooecio incompleto, deixando exposto o endooécio; **C**, ectooécio perfurado por vários poros redondos.

A grande variação morfológica encontrada no gênero *Scrupocellaria*, a ausência de estudos utilizando técnicas adequadas para a caracterização morfológica (*e.g.* observação em microscópio eletrônica de varredura), o número relativamente pequeno de espécies, e a existência de coleções zoológicas representativas da diversidade do gênero são alguns dos aspectos que possibilitam, dentro do prazo limitado disponível, a realização de um estudo sistemático de revisão, o que motivou a escolha desse táxon para a consecução do presente estudo.

Objetivos gerais

Este estudo tem como objetivo realizar o levantamento das espécies de *Scrupocellaria* descritas e investigar a sua distribuição, delimitando a variação intraespecífica dos táxons através de dados morfológicos, e fornecer a morfologia comparada de *Scrupocellaria* com uma hipótese de relações filogenéticas entre as espécies do gênero. Nesse sentido, a presente Tese é apresentada em quatro capítulos.

O **Capítulo 1**, intitulado "The identity of *Sertularia reptans* Linnaeus, 1758 (Bryozoa, Candidae)", refere-se à redescrição de *Scrupocellaria reptans* (Linnaeus, 1758) baseado nos espécimes estudados por LINNAEUS (1758). O histórico sobre a origem dos espécimes descritos por Linnaeus é discutido. No capítulo é citada a importância da utilização de alguns caracteres morfológicos na distinção de outras espécies do gênero, incluindo uma nova espécie, *Scrupocellaria* n. sp.1, amplamente relatada no Mar do Norte sob o nome de *S. reptans*.

O **Capítulo 2**, intitulado "Redescription of *Achamarchis jolloisii*, a new nonindigenous bryozoan species in Atlantic waters, and the resurrection of the genus *Licornia* van Beneden, 1850", refere-se à redescrição de *Scrupocellaria jolloisii* (Audouin, 1826) a partir da escolha do neótipo, incluindo o primeiro registro da espécie no Atlântico Ocidental (Flórida, EUA e Brasil). O estudo também inclui informações taxonômicas sobre o subgênero *Retiscrupocellaria* d'Hondt, 1988, considerado sinônimo júnior de *Licornia* van Beneden, 1850, criado para acomodar *Achamarchis jolloisii*. Além de *Licornia jolloisii*, nove espécies anteriormente tratadas como *Scrupocellaria* são incluídas no gênero *Licornia*: *Licornia annectens* (MacGillivray, 1887) n. comb., *Licornia cervicornis* (Busk, 1852) n. comb., *Licornia cyclostoma* (Busk, 1852) n. comb., *Licornia diadema* (Busk, 1852) n, comb., *Licornia ferox* (Busk, 1852) n. comb., *Licornia gaspari* (Thornely, 1907) n. comb., *Licornia longispinosa* (Harmer, 1926) n. comb., *Licornia macropora* (Osburn, 1950) n. comb. e *Licornia prolata* (Tilbrook & Vieira, *no prelo*). A distribuição de cada uma das espécies de *Licornia* é discutida.

O **Capítulo 3**, intitulado "A new bryozoan genus for *Scrupocellaria bertholletii* (Audouin) (Cheilostomata, Candidae): taxonomy, biodiversity and distribution", refere-se à descrição de um gênero novo, ereto para acomodar *Scrupocellaria bertholletii* (Audouin, 1826), espécie-tipo do gênero, e outras 26 espécies, 18 das quais descritas como novas. Oito espécies previamente tratadas como *Scrupocellaria* são incluídas no novo gênero: *Scrupocellaria curacaoensis* Fransen, 1986, *Scrupocellaria hirsuta* Jullien & Calvet, 1903, *Scrupocellaria macrorhyncha* Gautier, 1962, *Scrupocellaria*

nanshaensis Liu, 1991, *Scrupocellaria reptans* (Linnaeus, 1758), *Scrupocellaria serrata* Waters, 1909, *Scrupocellaria tenuirostris* Osburn, 1950 e *Scrupocellaria* n.sp.1 Vieira & Spencer Jones. O capítulo apresenta uma chave dicotômica para as espécies do gênero e a discussão da distribuição das espécies.

O **Capítulo 4**, intitulado "Evidence of polyphyly of the genus *Scrupocellaria* (Bryozoa, Candidae) based on a phylogenetic analysis of morphological characters", inclui um estudo filogenético baseado em 35 caracteres morfológicos de 84 espécies de Candidae. O gênero *Scrupocellaria* é redefinido e outros 5 novos gêneros são propostos para acomodar espécies anteriormente classificadas como *Scrupocellaria*.

Para a consecução do trabalho, foram realizadas coletas de espécimes em vários pontos da costa brasileira, mas grande parte do material examinado compreende espécimes depositados em coleções científicas nacionais e internacionais. Dez instituições foram visitadas durante o estudo: American Museum of Natural History (AMNH, EUA), Musée océanographique de Monaco (MOM, Monaco), Museum of Comparative Zoology, Harvard University (MCZ, EUA), Muséum national d'Histoire naturelle (MNHN, França), Museu de Zoologia da Universidade Federal da Bahia (MZUFBA, Brasil), Museu de Zoologia da Universidade de São Paulo (MZUSP, Brasil), Natural History Museum of London (NHMUK, Reino Unido), Nederlands Centrum voor Biodiversiteit (Naturalis, Holanda), Smithsonian Institution National Museum of Natural History (NMNH, EUA), Virginia Museum of Natural History (VMNH, EUA). Espécimens identificados por OSBURN (1947, 1950), depositados na coleção de Bryozoa do Santa Barbara Museum of Natural History (SBMNH, EUA), foram enviados como empréstimo durante a visita no VMNH.

As colônias foram examinadas preliminarmente sob estereomicroscópio. Alguns espécimes (incluindo tipos) foram selecionados para observação em Microscópio Eletrônico de Varredura (MEV). Os espécimes fotografados no NHMUK e NMNH foram observados em microscopia eletrônica de varredura (MEV) de baixo vácuo, enquanto espécimes depositados no VMNH e MZUSP foram metalizados para a aquisição das imagens em MEV de alto vácuo. Vários espécimes coletados por outros pesquisadores foram enviados para comparação e, quando possível, depositados no NHMUK e no MZUSP.

Como anexo (Anexo 1) é apresentado um catálogo das espécies (exceto fósseis) relatadas como *Scrupocellaria*, incluindo dados dos espécimes-tipo. Na análise preliminar dos exemplares-tipo das espécies de *Scrupocellaria* (82 espécies, incluindo 10 tratadas anteriormente como sinônimos de espécies válidas), foram

encontrados holótipos de 34 espécies, sintipos de 24 espécies, e lectótipo de 1 espécie (Anexo 1). Para 11 espécies, os espécimes-tipo são considerados perdidos, enquanto os de outras 12 não foram localizados.

Pelo menos três subespécies e uma variação foram consideradas como espécies distintas: *Scrupocellaria bertholleti tenuirostris* Osburn, 1950 [=*Scrupocellaria tenuirostris* stat. nov.], *Scrupocellaria elongata congesta* Norman, 1903 [=*Scrupocellaria congesta* stat. nov.], *Scrupocellaria scabra paenulata* Norman, 1903 [=*Scrupocellaria paenulata* stat. nov.] e *Scrupocellaria scabra paenulata* var. *orientalis* Norman, 1903 [=*Scrupocellaria orientalis* stat. nov.]. Entre os táxons anteriormente sinonimizados por HARMER (1926) com *Scrupocellaria diadema* Busk, 1852 e *Scrupocellaria maderensis* Busk, 1860, ao menos cinco espécies são morfologicamente distintas: *Scrupocellaria annectens* MacGillivray, 1887, *Scrupocellaria cervicornis* Busk, 1852, *Scrupocellaria gaspari* Thornely, 1907, *Scrupocellaria dongolensis* Waters, 1909 e *Scrupocellaria gilbertensis* Maplestone, 1909.

Ao menos três espécies classificadas como *Scrupocellaria* pertencem a gêneros diferentes: *Scrupocellaria arctica* (Busk, 1855) [=*Tricellaria* Fleming, 1828], *Scrupocellaria elegantissima* David & Pouyet, 1986 [=*Notoplites* Harmer, 1923], *Scrupocellaria muricata* (Lamouroux, 1816) [=*Tricellaria* Fleming, 1828]. A comparação entre os tipos examinados revelou que ao menos três espécies podem ser tratadas como sinônimos: *Scrupocellaria grimaldii* Jullien & Calvet, 1903 [=*Scrupocellaria inermis* Norman, 1867], *Scrupocellaria mansueta* Waters, 1909 [=*Scrupocellaria jolloisii* (Audouin, 1826)] e *Scrupocellaria ulrichi* Canu & Bassler, 1929 [=*Scrupocellaria curvata* Harmer, 1926]. Duas espécies, *Scrupocellaria brevisetis* Hincks, 1882 e *Scrupocellaria spatulata* (d'Orbigny, 1851), são aqui consideradas *nomina dubia* pela ausência de material tipo e descrição/figuras insuficientes para caracterização do material.

Após a análise dos tipos, foi observada a necessidade de uma revisão em nível mundial das espécies do gênero *Scrupocellaria*, devido à grande plasticidade morfológica e ampla distribuição relatada para vários dos táxons reportados no Atlântico. A abordagem global visa contribuir na compreensão da sistemática de *Scrupocellaria*, bem como comparar a morfologia e conhecer a diversidade do gênero até então sem estudos taxonômicos para o grupo.

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CAPÍTULO 1

THE IDENTITY OF *SERTULARIA REPTANS* LINNAEUS, 1758 (BRYOZOA, CANDIDAE)

O capítulo corresponde ao manuscrito de autoria de Leandro M. Vieira e Mary E. Spencer Jones, submetido no periódico *Zootaxa*.

The identity of the *Sertularia reptans* Linnaeus, 1758 (Bryozoa, Candidae)

ABSTRACT

This paper includes the reassessment of *Scrupocellaria reptans* (Linnaeus, 1758) based on Linnaeus's *Sertularia reptans*, whose lectotype is selected and figured from among the herbarium sheet specimens held at the Linnean Society of London. Material previously assigned to *S. reptans* was examined and provided morphological characteristics to distinguish a newly described species *Scrupocellaria* n.sp.1. *Scrupocellaria reptans* has a geographically limited distribution in the United Kingdom, while *Scrupocellaria* n.sp.1 is more widespread in the North Sea, Northeast Atlantic, Adriatic and Tasmania.

INTRODUCTION

The species *Sertularia reptans* was introduced by Carl LINNAEUS (1758), from "Oceano" and has been recorded from several localities around the British coast (*e.g.* ELLIS & SOLANDER, 1786; JOHNSTON, 1847; BUSK, 1852; HINCKS, 1880; HAYWARD, 1971; HAYWARD & RYLAND, 1998), North Sea (*e.g.* SMITT, 1867; MARCUS, 1940; DE BLAUWE, 2009), Madeira (NORMAN, 1909) and in the Mediterranean (*e.g.* WATERS, 1879; PRENANT & BOBIN, 1966; ZABALA, 1986; ZABALA & MALUQUER, 1988). *Scrupocellaria reptans* has been considered common and well-known around Britain, although some morphological variations have been described in different populations (*e.g.* GAUTIER, 1962; PRENANT & BOBIN, 1966; ZABALA & MALUQUER, 1988; HAYWARD & RYLAND, 1998). At the same time, ZABALA & MALUQUER (1988) noted that at least one different species was previously misidentified as *S. reptans* in Mediterranean waters. Despite some recent descriptions and illustrations of this species, the type specimen described by LINNAEUS (1758) has apparently never been described or figured.

Some species of *Scrupocellaria* had been treated as widespread in tropical to subtropical waters (TILBROOK, 2006; TILBROOK & VIEIRA, *in press*). Recent studies, however, on widespread bryozoans species using SEM techniques have helped to clarify the taxonomic status of species, as well as redefine the characters for differentiation of species (BERNING & KUKLINSKI, 2008). In addition, studies on geographic and morphological variation have revealed a higher diversity than previously recorded by earlier authors (BERNING *et al.*, 2008; VIEIRA *et al.*, 2010). In the

present study we give a complete redescription of Linnaeus's *Sertularia reptans*, to clarify the identity of this species and describe a new and closely related species.

MATERIAL AND METHODS

The syntypes specimens described by Linnaeus and letters included herein are held at the Linnean Society of London (LSL). The type specimens were photographed under a Zeiss Discovery V20 stereomicroscope with AxioCam HRc at the Natural History Museum, London (NHMUK). Additional comparative material is deposited at the NHMUK and Muséum national d'Histoire naturelle, Paris (MNHN). Colonies were examined under a stereomicroscope and selected specimens were scanned using a LEO 1455-VP scanning electron microscope (SEM) with an environmental chamber. Measurements were made from digital SEM images directly, using the analysing software ImageJ®.

LINNAEUS'S HERBARIUM SPECIMENS

The type material of *Scrupocellaria reptans* comprise two herbarium sheets in the Linnean Collection deposited at the Linnean Society of London (LSL n.1248.31 and LSL n.1248.32). These sheets were labelled '*S. reptans*' [=*Sertularia reptans*] by Linnaeus and consistes of 26 syntype specimens. We have associated a letter for each colony on sheet no. 1248.31, selecting specimen "I" as the lectotype, and the other specimens as paralectotypes (Figure 1.1); the three specimens found on herbarium sheet no. 1248.32 are badly preserved colonies.

The colony selected as lectotype (LSL n.1248.31.I, Figure 1.1) is a very large and well preserved colony with several zooids: two fragments of the same colony are present, with the frontal and basal surface visible. In the lectotype specimen, ovicells are present and have 8–11 medium rounded pores on surface and with pinkish embryos preserved inside of the ooecial cavity; the radicles are characterized by a surface with many retroussé hooks. We characterised the paralectotype specimens from sheet no. 1248.31 in Table 1.1.

All Linnaeus's type specimens are characterised by the presence of joints that pass across the distal gymnocyst, below and never on the opesia, branched scuta, large frontal avicularia, almost trapezoid-shaped basal vibracula, and rhizoids with retroussé hooks. The last characteristic was also given by ELLIS (1755), and described as "*…to be full of Hooks, the better to secure the Coraline…*"; a characteristic easily recognized from the illustration (ELLIS, 1755, pl. 20B). The presence of a vibracular

chamber at the basal surface of the colony varies in different specimens, but one or more vibracular chambers are often present per internode.

PROVENANCE OF LINNAEUS'S SPECIMENS

The name *Sertularia reptans* was introduced by Carl LINNAEUS (1758), without illustration. The protologue has a descriptive phrase name '*denticulus alternis bidentibus, ramis dichotomis*', with an uninformative locality '*Habitat in Oceano*'. Among the elements involved in the protologue of *Sertularia reptans,* there are two synonyms from earlier authors, '*Ellis. corall. 37. n. 3. t. 20. f. B.*' and '*Raj. Suppl. 15.*'. The first synonym is from ELLIS (1755, p. 37, pl. XX, Figs. b, B), with a description and figures. ELLIS's (1755) "*An essay towards a natural history of the corallines…*" comprises descriptions and drawings of some bryozoan specimens collected from the British coast and Ireland. Some of these were used by LINNAEUS (1758) to introduce names of species in the 10th edition of *Systema Naturae*. Fortunately, the high quality of Ellis's plates has proved useful in solving the identity of some bryozoan species described by Linnaeus (PORTER *et al.*, 2008). The second synonym '*Raj. Suppl. 15.*' refers to *Historia plantarum vol. 3, Supplementum* (RAY, 1704), which provides a very brief description quoting an authority, is without drawings, and makes reference to an earlier author.

Ellis's '*Corallina cellifera minor repens ramofa, tubulis laevibus: interdum hamofis fparfim difpofitis, fucis teftisque alligata*' was characterized as very common among the 'celliferous Corallines', collected on diverse substrata, such as *Fucus* and shells, and distinct from other species by the presence of tubular roots. He noted the presence of several hooks on these tubes, conspicuous under the microscope and probably used to secure the colonies on soft substrata. In addition, ELLIS & SOLANDER (1786) cited that *S. reptans* was a common species along British coasts on shells and algae, quite distinct from other species by the presence of hooks along the stems to anchor the colonies.

Ray's description '*Mufcus coralloides pumilus ramofu Ejufdem. Fucus variis adhaeret. M. mar. capillaries brevior aliis adhaerens albus & niger Morif. Hift. P. 3*.' was short and gave no locality or collector. The '*Ejufdem*' referred to Doody, who was mentioned in a previous description. Samuel Doody (1656–1706) was a London apothecary and was considered an authority on mosses, fungi, and other non-flowering plants (JACKSON, 2010). Though he only published one medical paper, his observations and specimens were sent to many of his close botanical acquaintances, such as John

Ray (1627–1705), Leonard Plukenet (1641–1706), James Petiver (1663–1718) and Sir Hans Sloane (1660–1753). Johann Jakob Dillen *Dillenius* (1684–1747) also made use of his notes when preparing the third edition of *Synopses*.

There are two specimens in the Sloane collection at the NHMUK, which are referable to the description given in Ray's '*Historia plantarum vol. 3, Supplementum 15'.* Both specimens are *Scrupocellaria* species but neither have rhizoids with retroussé hooks. Ray's synonym '*Morif. Hift. P. 3'* refers to the third part of Robert Morison's *Plantarum Historiae Universalis Oxoniensis,* which was completed by Jacob Bobart (the Younger) in 1699. Morison's collection is housed in the Oxford University Herbarium, but no relevant material has currently been located.

Typification was not a concept that Linnaeus or his contemporaries used, and in 1983 it was estimated that only a small percentage of Linnaean taxa had been typified (CANNON *et al*., 1983). Over the years, several authors have expressed the opinion that Linnaeus used Ellis's "*Corallines*" as the foundation for his Zoophyta text in *Systema Naturae (1758).* Correspondence between the two men seems to have started around 1756–7 after the publication of Ellis's book. In a letter dated 21st July 1758, Ellis wrote "*I am obliged to you for methodizing the corallines mentioned in my book.*" In the same paragraph, Ellis expresses his disappointment at the lack of figures in *Systema Naturae*, a fact which has irritated many taxonomists for over 250 years, and he says " *I suppose the books that are coming for the bookseller have the plates, which will greatly illustrate them*.". The sought after plates would never appear.

Only the specific name *S. reptans* appears on the two Linnean herbarium sheets. John Ellis and Carl Linnaeus are known to have exchanged some specimens (SAVAGE, 1945), as well as letters, drawings and descriptions; however, there appears to be no record of *S. reptans* specimens being sent to Uppsala. There are also no marks or indications on the sheets that the material could have been collected and sent to Sweden by Linnaeus' disciples, Pehr Kalm (1716–1779) and Daniel Solander (1733–1782), who both visited England in 1747 and 1760 respectively. English herbarium material is known to have reached Linnaeus from various sources, such as the British botanist William Hudson (1730–1793) (JARVIS, 2007), and the Rev. John Burgess (1725–1795), a lichenologist at Kirkmichael in Dumfries and Galloway, Scotland (JACKSON, 1922), but at the present time the provenance of the Linnean *Sertularia reptans* herbarium sheets remains uncertain.

SCRUPOCELLARIA REPTANS: A WIDESPREAD OR COMPLEX SPECIES?

Scrupocellaria reptans has been reported from different localities of Northeast Atlantic, North Sea and Mediterranean (ZABALA & MALUQUER, 1988; HAYWARD & RYLAND, 1998), despite the morphological differences (*e.g.* shape of rhizoids and frontal scuta) of specimens from different areas.

HINCKS (1880, p. 52, pl. 7, figs. 1–7) described two kinds of rhizoids (smooth and hooked) among British specimens of *Scrupocellaria reptans*. The "toothed" rhizoids (HINCKS 1880, pl. 7, fig 6) are similar to those figured by ELLIS (1755, 1756a, 1756b, 1767), as well as those observed in Linnaeus's specimens (Figure 1.12) and other specimens from European waters (Figures 1.3, 1.17, 1.18). The hooked rhizoids were also reported in specimens from Cornwall, U.K. (COUCH, 1844, pl. 23, fig. 3). The second kind of rhizoids were characterized as "*…simple, and giving off at the extremity a number of anastomosing fibrils forming a netted disk*", and were figured by HINCKS (1880, pl. 7, fig. 5). These rhizoids, of simple tubes, were described as early as 1847 by JOHNSTON (1847, p. 337, pl. LVIII, figs. 3, 4), with the distal end of each tube branching into two or three small knob-like processes. In both Johnston's and Hincks's specimens from the British coast (NHMUK 1842.12.19.2; NHMUK 1899.5.1.3; NHMUK 1899.5.1.359) the rhizoids are smooth with a branched distal adherent end. HINCKS (1880) suggested that these two forms of rhizoids are an ecological adaptation of this species. The colonies with smooth fibres forming circular reticulate disks distally are attached to the hard surfaces, like rocks or algae, while hooked rhizoids are plunged into soft substrates like sponges. This variation in hook shape was also observed by PEACH (1878), who described smooth rhizoids in colonies found on *Flustra foliacea*.

PEACH (1878) refers to Busk's *Scrupocellaria macandrei* from Spain and *Scrupocellaria ferox* from Bass Strait, which were characterized by presence of rhizoids with hooks. WATERS (1909, 1913) also used the hook shape to distinguish some *Scrupocellaria* taxa. On the other hand, PRENANT & BOBIN (1966) cited the presence of both hooked and smooth rhizoids in some species (*viz. Scrupocellaria reptans*, *Scrupocellaria diadema*, *Scrupocellaria maderensis*, *Scrupocellaria delilii*). We analysed more than 50 specimens deposited at the Natural History Museum, London and identified as *S. reptans*, but we found only a few lots with hooked rhizoids. These specimens have hooks with a consistent shape and position along the rhizoid tubes. We found the same type of hooked rhizoids in Linnaeus's specimens (Figures 1.7 and 1.11), and in a specimen found in herbarium material identified by Alfred Norman (NHMUK 1915.4.2.13), four specimens from the west coast of Britain (NHMUK

1849.2.12.51, NHMUK 1963.3.6.35, NHMUK 1994.3.4.5–6 and NHMUK 1995.9.25.26) and two colonies from the Thanet coast, southern England (NHMUK 1884.12.12.9). Careful examination of colonies from Thanet revealed that two different morphotypes occur together, but they are distinguished by the shape of rhizoids and frontal scuta. Due to the presence of these two phenotypic varieties in different colonies on the same shell, we suggest that these varieties are not conspecific. At the same time, the hooked rhizoids have not been found in several colonies from western Britain, or in colonies from the east coast of Britain and North European waters, which suggests a more restricted distribution of the morphotype with hooked rhizoids.

Among some *Scrupocellaria* seen in the NHMUK bryozoan collection, the presence and shape of hooked rhizoids are uniform in colonies of the same species, which suggests it to be a character to define species rather than representing an environmental adaptation of the same species. In addition, we observed at least three kinds of rhizoidal surfaces in the Candidae—hooked (Figures 1.2–1.3), smooth (Figure 1.4) and ringed (Figure 1.5)—, morphologically distinct in different species.

Under light microscopy the morphology of zooids of the two phenotypes previously identified under name *S. reptans* (with and without hooks) looks similar, but detailed study using scanning electron microscopy shows differences between them—see Figures 1.2, 1.12–1.17, 1.24, 1.26 (morphotype with hooked rhizoids, *Scrupocellaria reptans* sensu stricto) and Figures 1.3, 1.18–1.23, 1.25, 1.27 (morphotype with smooth rhizoids, herein assigned as a distinct species). In later ontogeny both species are distinct in the shape of scuta (Figures 1.4 and 1.21). Despite having the same proportion between opesia and scuta length, *Scrupocellaria reptans* sensu stricto (Linnaeus's specimens, NHMUK 1849.2.12.51, NHMUK 1884.12.12.9, NHMUK 1915.4.2.13, NHMUK 1963.3.6.35, NHMUK 1994.3.4.5–6 and NHMUK 1995.9.25.26) have a slender and less branched scutum when compared with specimens without smooth rhizoids. In Linnaeus's specimens, the scutum is branched twice (sometimes shortly branched at distal tip), with a large gap between each slender branch (Figure 1.9). In early ontogeny, however, the frontal scuta are quite similar in both species (Figures 1.26–1.27), but the scuta become highly branched in colonies without hooks (Figures 1.20–1.21). Variation in the shape of frontal avicularia makes it hard for comparisons between young colonies of both morphotypes. Both morphotypes have frontal avicularia in the same position and direction, but in early ontogeny the rostrum of the avicularium is slender and taller in *S. reptans* (Figures 1.24–1.27). In Linnaeus's type material, the basal vibracular chamber is often absent, while in the

morphotype with smooth rhizoids the vibracular chamber is usually present. In addition, colonies from the British coast with smooth rhizoids are characterized by robust scuta, more branched than those found in Linnaeus's type specimens.

TAXONOMIC ACCOUNT

Class Gymnolaemata Allman, 1856

Order Cheilostomata Busk, 1852

Suborder Neocheilostomina d'Hondt, 1985

Infraorder Flustrina Smitt, 1868

Family Candidae d'Orbigny, 1851

Genus *Scrupocellaria* van Beneden, 1845

***Scrupocellaria reptans* (Linnaeus, 1758)**

(Figures 1.1, 1.2, 1.6–1.17, 1.24, 1.26)

'Mufcus coralloides pumilus ramofus' Ray, 1704, p. 15 [British coast]

'Creeping coralline' Ellis, 1755, p. 37, pl. 20, figs. b, B. [British coast]

Sertularia reptans Linnaeus, 1758, p. 815; 1767, p. 1315. [Ocean]

Cellaria reptans: Ellis & Solander, 1786, p. 23. [British coast]

Cellularia reptans: Couch, 1844, p. 127, pl. 23, fig. 3. [British coast]

Scrupocellaria reptans: Hincks, 1880, p. 52 (part), pl. 7, fig. 6. [British coast]

Scrupocellaria reptans: Prenant & Bobin, 1966 (part), fig. 134.vi. [not Mediterranean specimens]

Scrupocellaria reptans: Hayward & Ryland, 1998, p. 270 (part). [British coast]

Material examined. Lectotype (chosen here): LSL n. 1248.31.I, no locality, but supposedly U.K. Paralectotype (chosen here): LSL n. 1248.31.A–H, J–W; LSL n. 1248.32, no locality, but supposedly U.K. Additional material: NHMUK 1849.2.12.51 (part), *Scrupocellaria reptans* (Linn.), on shells (dry), W.P. Cocks collection, Falmouth, Cornwall, U.K.; NHMUK 1884.12.12.9 (part), *Scrupocellaria reptans* (Linn.), O. Ridley *det*., Thanet coast; NHMUK 1915.4.2.13, *Scrupocellaria reptans* (Linn.), A.M. Norman collection, George Barlee coll. on algae; NHMUK 1963.3.6.35, *Scrupocellaria reptans* (Linn.), C.H. O'Donoghue *det.*, Arisaig, Scotland, U.K.; NHMUK 1995.9.25.26, *Scrupocellaria reptans* (Linn.), J.R. Ryland *leg*. et *det*., Porth Mellick, Scilly Isles, 11th June 1972; NHMUK 1994.3.4.5–6, *Scrupocellaria reptans* (Linn.), P. Hayward *det*., J. Ellis *leg.*, East side of Dun, St. Kilda, July 1993.

Comparative material. *Scrupocellaria n.sp.1* [Figures 1.4, 1.18–1.23, 1.25, 1.27]: (see next entry). *Scrupocellaria* sp.1 [Figure 1.28]: NHMUK 2010.12.6.1, *Scrupocellaria reptans* (part), C.H. O'Donoghue collection, Arisaig, Scotland. *Scrupocellaria* sp.2 [Figure 1,29]: NHMUK 1963.8.2.16, *Scrupocellaria reptans*, C.H. O'Donoghue collection, Alexandria 1937, Stn. 7, 66,

17–20 fms. *Scrupocellaria* sp.3 [Figure 1.30]: NHMUK 1911.10.1.355, *Scrupocellaria reptans*, A.M. Norman collection, Madeira. *Scrupocellaria* sp.4 [Figure 1.31]: NHMUK 2010.12.6.21–22, *Scrupocellaria reptans* (part), C.H. O'Donoghue collection, Gairloch, Scotland.

Redescription. Colony erect, branched, with branches comprising 4–10 zooids. Lateral edge of internodes almost straight to slightly curved; chitinous joints pass across the gymnocyst and bellow opesia in both outer zooids at the bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (zooids F and G). Autozooids almost elongate, narrowed proximally, 0.350–0.500 mm long and 0.165–0.205 mm wide, with smooth proximal gymnocyst. Oval opesia occupying about distal half of the zooid, cryptocyst very narrow and inconspicuous. Scutum inserted at midline of inner edge of opesia, branched, occupying most of opesia; scutum slender, flattened, branched two or three times, with 6–9 distal stout projections; scutum angled at 100–120 degrees, with first branches about 0.035–0.045 mm wide, and secondary branches about 0.025–0.035 mm. Distal spines single and long; three outer spines, one or two inner spines; most proximal outer and inner spines directed frontally; axial zooid with five distal spines. One disto-lateral avicularium sometimes present in each zooid, disto-laterally directed and obscured by outer distal spines; rostrum triangular, with slightly serrated lateral edge, mandible triangular. A very large avicularium present on gymnocyst of some zooids, almost aquiline, with a raised tubular base, rostrum serrated laterally, slightly curved and directed forwards; mandible triangular with hooked tip. A basal vibracular chamber often present, proximally on basal surface of each zooid, 0.126–0.155 mm long and 0.085–0.115 mm wide, inconspicuous in frontal view; setal groove directed transversally, straight, with smooth setae longer than one zooid length. Single axial vibraculum. A rhizoidal foramen on proximal outer corner of vibracular chamber, absent in axial vibracula. Rhizoids with several closed spaced reverse hooks in most of its length. Ovicells hyperstomial, hemispherical, with 8–13 medium rounded pores; two outer and one or two inner distal spines in ovicelled zooids.

Distribution. United Kingdom.

Scrupocellaria n.sp.1

(Figures 1.4, 1.18–1.23, 1.25, 1.27)

Cellularia reptans: Pallas, 1766, p. 73 [European sea]

Not *Sertularia reptans* Linnaeus, 1758, p. 815; 1767, p. 1315. [Oceano]

? *Sertularia reptans*: Fabricius, 1780, p. 445 [Greenland]

? *Sertularia reptans*: Olivi, 1792, p. 290 [Adriatic]

? *Sertularia reptans*: Turton, 1807, p. 217 [British coast]
? *Canda reptans*: Gosse, 1856, p. 11, fig. 12 [British coast]
Crisia reptans: Lamouroux, 1816, p. 140 [European sea]
Cellaria reptans: Lamarck, 1816, p. 141 [European sea]
Cellaria reptans: Bertoloni, 1819, p. 272 [Italy]
Crisia reptans: Lamouroux, 1824a, p. 60 [European sea]
Crisia reptans: Lamouroux, 1824b, p. 225 [European sea]
? *Crisia reptans*: Risso, 1826, p.3185 [European sea]
? *Cellularia reptans*: Fleming, 1828, p. 540 [British coast]
? *Cellularia reptans*: Bosc, 1830, p. 132 [European sea]
Cellaria reptans: Lamarck, 1836, p. 191 [European sea]
Cellularia reptans: Johnston, 1838a, p. 291, pl. 38, figs. 3–4 [British coast]
Cellaria reptans: Johnston, 1838b, p. 262 [British coast]
? *Cellularia reptans*: Hassall, 1840, p. 72 [Ireland]
? *Cellularia reptans*: Reid, 1845, p. 385, pl. 12, figs. 1–5 [Scotland]
Cellularia reptans: Dalyell, 1847, p. 235, pl. 45, figs. 1–4 [Scotland]
Cellularia reptans: Johnston, 1847, p. 336, pl. 38, figs. 3–4 [British coast]
Scrupocellaria reptans: Gray, 1848, p. 112 [British coast]
? *Cellularia reptans*: d'Orbigny, 1851, p. 50 [France, Fossil]
Canda reptans: Busk, 1852, p. 26, pl. 21, figs. 3–4 [British coast]
? *Cellularia reptans*: Landsborough, 1852, p. 339 [British coast]
? *Cellularia reptans*: Gosse, 1853, p. 435 [British coast]
Cellularia reptans: Alder, 1856, p. 148 [British coast]
Cellularia reptans: Smitt, 1867, p. 318, pl. 17, figs. 37–4 [Scandinavia]
Canda reptans: Heller, 1867, p. 87 [Adriatic]
Scrupocellaria reptans: Hincks, 1880, p. 52 (part), pl. 7, fig. 1–6, 7. [British coast]
Scrupocellaria reptans: Pennington, 1885, p. 223, pl. 17, fig. 5 [British coast]
? *Scrupocellaria reptans*: Carus, 1889, p. 5 [Mediterranean]
Scrupocellaria reptans: Levinsen, 1894, p. 44, pl. 1, figs. 26–31 [Denmark]
Scrupocellaria reptans: Nordgaard, 1900, p. 5 [Norway]
Scrupocellaria reptans: Nichols, 1907, p. 82 [Ireland]
? *Scrupocellaria reptans*: Calvet, 1907, p. 374 [European sea]
? *Scrupocellaria reptans*: Canu & Bassler, 1928, p. 19 [Tunisia]
? *Scrupocellaria reptans*: Marcus 1940, p. 173, fig. 91 [Denmark]
? *Scrupocellaria reptans*: Eggleston, 1963, p. 50 [Isle of Man]
Scrupocellaria reptans: Ryland, 1965, p. 57, figs. 28a–c [European sea]
Scrupocellaria reptans: Ryland & Hayward, 1977, p. 135, fig. 64 [British coast]
Scrupocellaria reptans: Ryland, 1986, p. 29, fig. 20A–B [British coast]
Scrupocellaria reptans: Hayward, 1987, p. 92, fig. XI, 27 [British coast]

Scrupocellaria reptans: Hayward & Ryland, 1998, p. 270 (part), Fig. 90A–B [British coast]
Scrupocellaria reptans: De Blauwe, p. 240, figs. 245–246 [Belgium and Netherlands]

Examined material. Holotype: NHMUK 1911.10.1.353, *Scrupocellaria reptans*, A.M. Norman collection, Shetland, U.K. Additional specimens: NHMUK 1812.12.21.386, *Scrupocellaria reptans*, A.M. Norman collection, Isle of Wight, Mr. Waddington; NHMUK 1812.12.21.388, *Scrupocellaria reptans*, A.M. Norman collection, Birterbury Bay, Ireland 1874; NHMUK 1812.12.21.389, *Scrupocellaria reptans*, A.M. Norman collection, Strangford Lough, Ireland; NHMUK 1812.12.27.840A, *Canda reptans*, A.M. Norman collection, Norway 1878; NHMUK 1842.12.19.2, *Scrupocellaria reptans*, G. Johnston collection, British coast; NHMUK 1849.1.30.67, *Scrupocellaria reptans*, W.P. Cocks collection, Falmouth, UK; NHMUK 1867.5.7.24, *Scrupocellaria reptans*, G.D. Westendorp herbarium, Belgium; NHMUK 1868.3.13.2, *Canda reptans*, Prof. Sven Loven, Skar, Bohuslank, Sweden; NHMUK 1882.2.28.9, *Scrupocellaria reptans*, [no locality]; NHMUK 1882.7.7.94, *Scrupocellaria reptans*, Director Kew, England; NHMUK 1884.12.12.9 (part), *Scrupocellaria reptans* (part), O. Ridley *det*., Thanet coast; NHMUK 1885.12.5.22, *Scrupocellaria reptans*, E.F. Nolte herbarium, Dithmarschen, Germany; NHMUK 1885.12.5.37, *Scrupocellaria reptans*, E.F. Nolte herbarium, Föhr, Germany; NHMUK 1885.8.24.1, *Scrupocellaria reptans*, W. Saville Kent collection, Jersey; NHMUK 1886.1.9.4, *Scrupocellaria reptans*, [no locality]; NHMUK 1889.9.17.3, *Scrupocellaria reptans*, [no locality]; NHMUK 1890.8.27.2, *Scrupocellaria reptans*, [no locality]; NHMUK 1890.8.29.2, *Canda reptans*, G. Busk collection (Kirchenpauer), Helgoland, Germany; NHMUK 1892.2.13.6, *Scrupocellaria reptans*, John Murray, Between Plockton and Loch Arisaig, 8–24fms; NHMUK 1897.5.1.214–216, *Scrupocellaria reptans*, [no locality]; NHMUK 1899.5.1.359, *Canda reptans*, T. Hincks collection, [no locality]; NHMUK 1899.5.1.359, *Canda reptans*, T. Hincks, collection, Great Britain; NHMUK 1899.7.1.4450, 4551, 4556, 4557, *Scrupocellaria reptans*, G. Busk collection, [no locality]; NHMUK 1899.7.1.5781, 5783, 1585, *Canda reptans*, G. Busk collection, Weymouth, U.K.; NHMUK 1911.10.1.351, *Scrupocellaria reptans*, A.M. Norman collection, G. Barlee *leg*.; NHMUK 1911.10.1.352, *Scrupocellaria reptans*, A.M. Norman collection, Bergen Fjord 1878; NHMUK 1911.10.1.354, *Canda reptans*, A.M. Norman collection, Adriatic (Prof. Heller); NHMUK 1911.10.1.356, *Scrupocellaria reptans*, A.M. Norman collection, Guernsey, UK; NHMUK 1961.8.14.1, *Scrupocellaria reptans*, [no locality]; NHMUK 1963.3.6.30, *Scrupocellaria reptans*, C.H. O'Donoghue collection, Lochranza, Isle of Arran, U.K.; NHMUK 2010.12.6.24, *Scrupocellaria reptans* (part), C.H. O'Donoghue collection, Arisaig, Scotland, U.K.; NHMUK 1963.3.6.37, *Scrupocellaria reptans*, C.H. O'Donoghue collection, Lochranza, Isle of Arran, UK 1933; NHMUK 1963.3.6.7a, *Scrupocellaria reptans* (part), C.H. O'Donoghue collection, Gairloch, Scotland; NHMUK 1975.7.18.13, R. Lagaaij *leg.* et *det.*, [no locality]; NHMUK 1994.3.4.5–6, *Scrupocellaria reptans*, P. Hayward *det*., J. Ellis *leg.*, East side of Dun, St. Kilda, July 1993; NHMUK 1994.8.25.3, 8, *Scrupocellaria reptans*, J.R. Lewis *leg*. et *det.*, Loch Sween, Argyll, U.K.; NHMUK 2003.6.3.1, *Scrupocellaria*

reptans, K.J. Tilbrook *leg*. et *det.*, Strandline, Portmeirion, Wales, 10th March 1996; NHMUK 2005.1.14.8, *Scrupocellaria reptans*, S.M. Turk *det*., St. Ives, Cornwall, 18th August 1974, P. Renwick *leg*.; NHMUK 2010.12.6.23, *Scrupocellaria reptans*, D. Turner herbarium, Scotland; NHMUK 2010.12.6.29–30. *Scrupocellaria reptans*, Tasmania.

Description. Colony erect, branched, with branches comprising 5–12 zooids. Lateral edge of internodes almost straight to slightly curved; chitinous joints pass across the gymnocyst and below or slightly overlapping the opesia in both outer zooids at the bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (zooids F and G). Autozooids almost elongate, slightly narrower proximally, 0.400–0.615 mm long and 0.190–0.220 mm wide, with smooth proximal gymnocyst. Oval opesia occupying about the distal half of the zooid, cryptocyst very narrow and inconspicuous. Scutum inserted at midline of inner edge of opesia, branched, occupying almost opesia area; scutum slender, flattened, branched two or three times, with 8–13 stout projections at distal tips; scutum angled at 115–155 degrees, with first branches about 0.045–0.060 mm width, and secondary branches about 0.035–0.045 mm. Distal spines single and long; three outer spines, one or two inner spines; most proximal outer and inner spines directed frontally; axial zooid with five distal spines. One distolateral avicularium sometimes present in each zooid, disto-laterally directed and obscured by outer distal spines; rostrum triangular, with slightly serrated lateral edge, mandible triangular. A large avicularium present on gymnocyst of some zooids, sometimes robust, rostrum serrated laterally, slightly curved and directed forwards; triangular mandible with hooked tip. A basal vibracular chamber often present, proximally on basal surface of each zooid, 0.130–0.140 mm long and 0.100–0.135 mm wide, rarely conspicuous in frontal view; setal groove directed transversally, straight, with smooth setae longer than one zooid length. Single axial vibraculum. A rhizoidal foramen on proximal outer corner of vibracular chamber, absent in axial vibracula. Rhizoids smooth, disc-like, with some projections at its distal end. Ovicells hyperstomial, hemispherical, with 12–18 small rounded pores; two outer and two inner distal spines in ovicelled zooids.

Remarks. This species was previously recorded by numerous authors under the name *S. reptans*. *Scrupocellaria n.sp.1*, is, however, distinctive due to the presence of smooth rhizoids, robust and more branched scuta, and ovicells with small rounded pores.

Distribution. Widespread in North Sea, British Channel, Irish Sea, Celtic Sea; Adriatic and Tasmania.

DISCUSSION

The examination of specimens previously assigned to *Scrupocellaria reptans* and deposited in NHMUK revealed that they comprise at least four different species, distinguished by the number of distal spines, and the shape of zooids, frontal avicularia and frontal scuta (Figures 1.28–1.31), as well as some misidentified specimens. ZABALA & MALUQUER (1988) noted that some species were misidentified as *Scrupocellaria reptans* in Mediterranean waters, and herein we suggest that *S. reptans* is geographically restricted to the western British coast. The specimens from the North Sea are morphologically similar to *S. reptans*, but the differences in the shape of scuta, pores in ovicells and smooth rhizoids indicate that this phenotype represents a distinct species, herein described as *Scrupocellaria n.sp.1*. The colonies from North Europe, Adriatic and Tasmania identified as *Scrupocellaria n.sp.1* are characterized by a scutum branched two to four times, with 8–13 stout projections at distal tips; the scutum forms a wider angle when compared with *S. reptans* (120–155 degrees in *Scrupocellaria n.sp.1* versus 100–120 degrees in *S. reptans*) and the first branches are wider, about 0.045–0.060 mm wide.

GAUTIER (1962) described a species from Mediterranean waters with branched and robust scuta, named *Scrupocellaria macrorhyncha*, but distinct due to the presence of six distal spines and very large frontal avicularia. Six oral spines and a robust frontal scutum are also found in some specimens from Mediterranean waters (e.g. Figure 1.29), but, until a redescription of Gautier's specimens is undertaken, we consider the identity of these specimens uncertain. In addition, SAVIGNY (1817) figured a similar colony from Egypt, described by AUDOUIN (1826) under the name *Acamarchis geoffroyi* and which was later synonymized with *S. reptans*. Unfortunately, few characters of frontal avicularia and vibracula can be seen in Savigny's plates. The type specimen of *A. geoffroyi* is lost and the presence of similar species in Mediterranean and Red Sea will make it difficult to resolve the identity of Savigny's species.

At least four more species of *Scrupocellaria* with branched scuta have previously been described, *viz. Scrupocellaria bertholletii* (Audouin, 1826), *Scrupocellaria curacaoensis* Fransen, 1986, *Scrupocellaria micheli* Marcus, 1955 and *Scrupocellaria tenuirostris* Osburn, 1950; these species are herein refered to as the *Scrupocellaria reptans-bertholletii* complex, characterized by branched scutum and an almost trapezoid vibracular chamber, and distinct by characteristics of the scuta, distal spines and frontal avicularia. Neither redescription of type specimens nor recent studies using SEM were done to try resolving the taxonomic problems of these or

related taxa. In addition, some hitherto well-known species were reported worldwide (*e.g. Scrupocellaria reptans* and *Scrupocellaria bertholletii*), but the lack of comparative studies between different populations makes it hard to distinguish morphospecies, probably resulting in additional new species being overlooked. Furthermore, this reveals that the widespread distribution of bryozoans could indicate taxonomic problems, which can involve endemic species with restricted distributions (BERNING & KUKLINSKI, 2008; BERNING *et al.*, 2008; VIEIRA *et al.*, 2010). This was also observed with the examination of NHMUK's *Scrupocellaria reptans* and *Scrupocellaria bertholletii*, which indicated that more than ten different species, some of those with restricted distributions included under these two names (L.M. Vieira, unpublished data).

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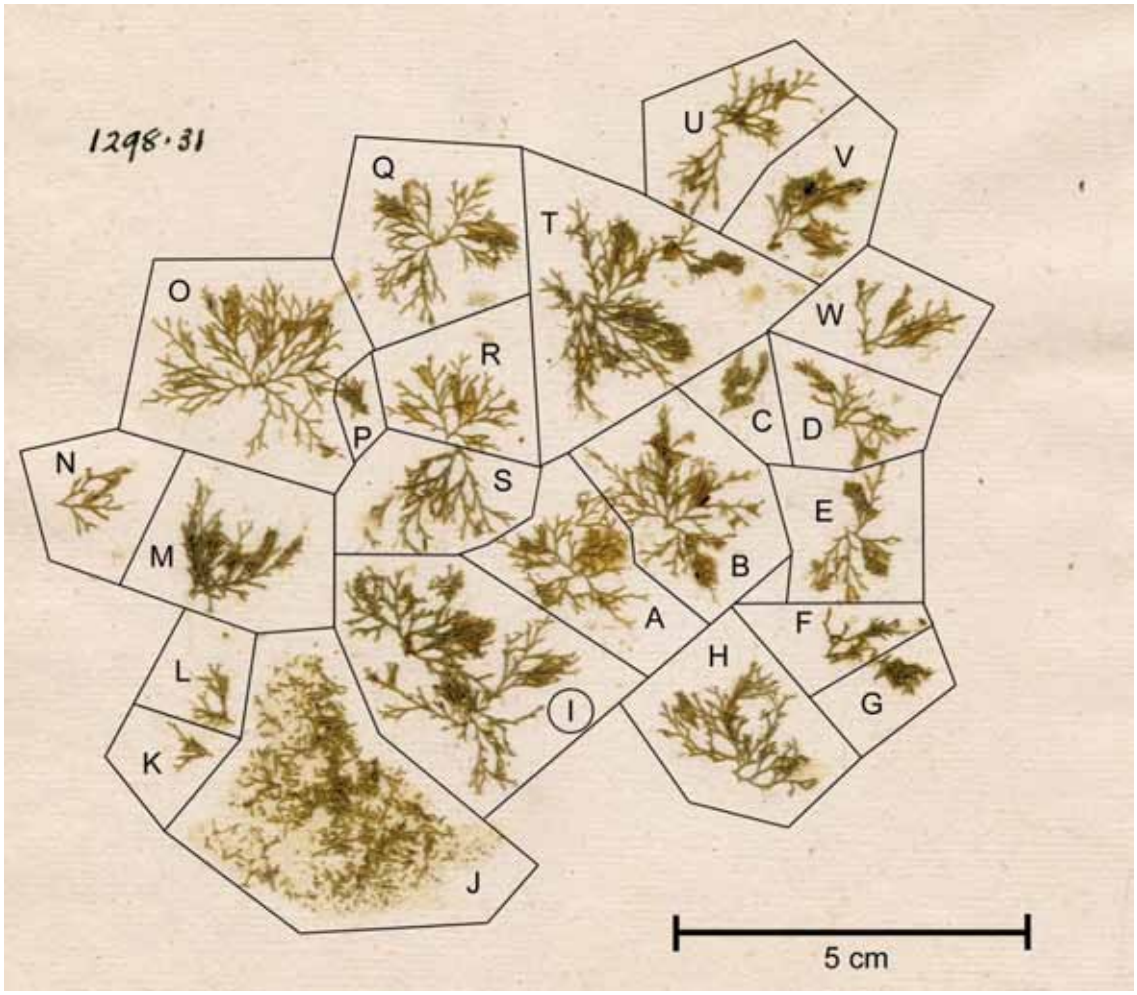
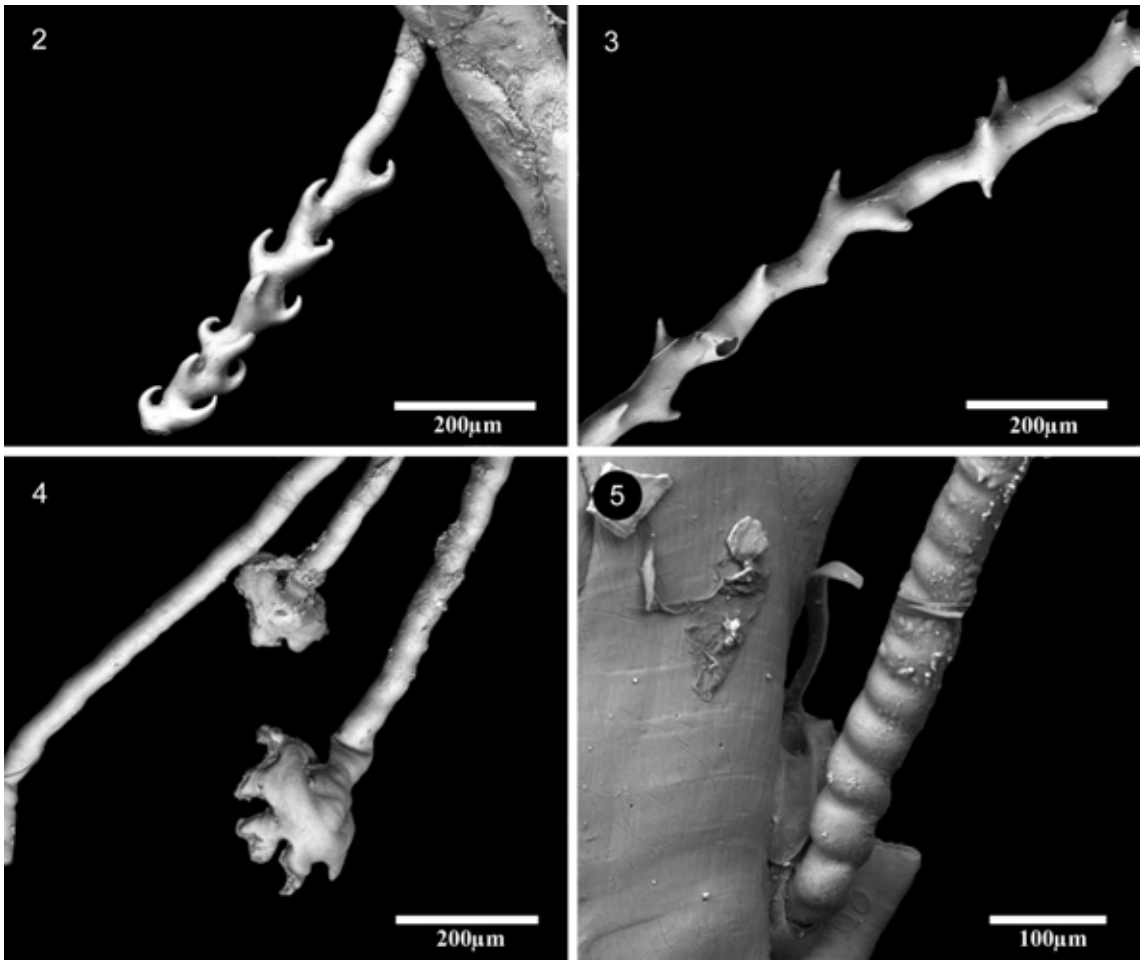
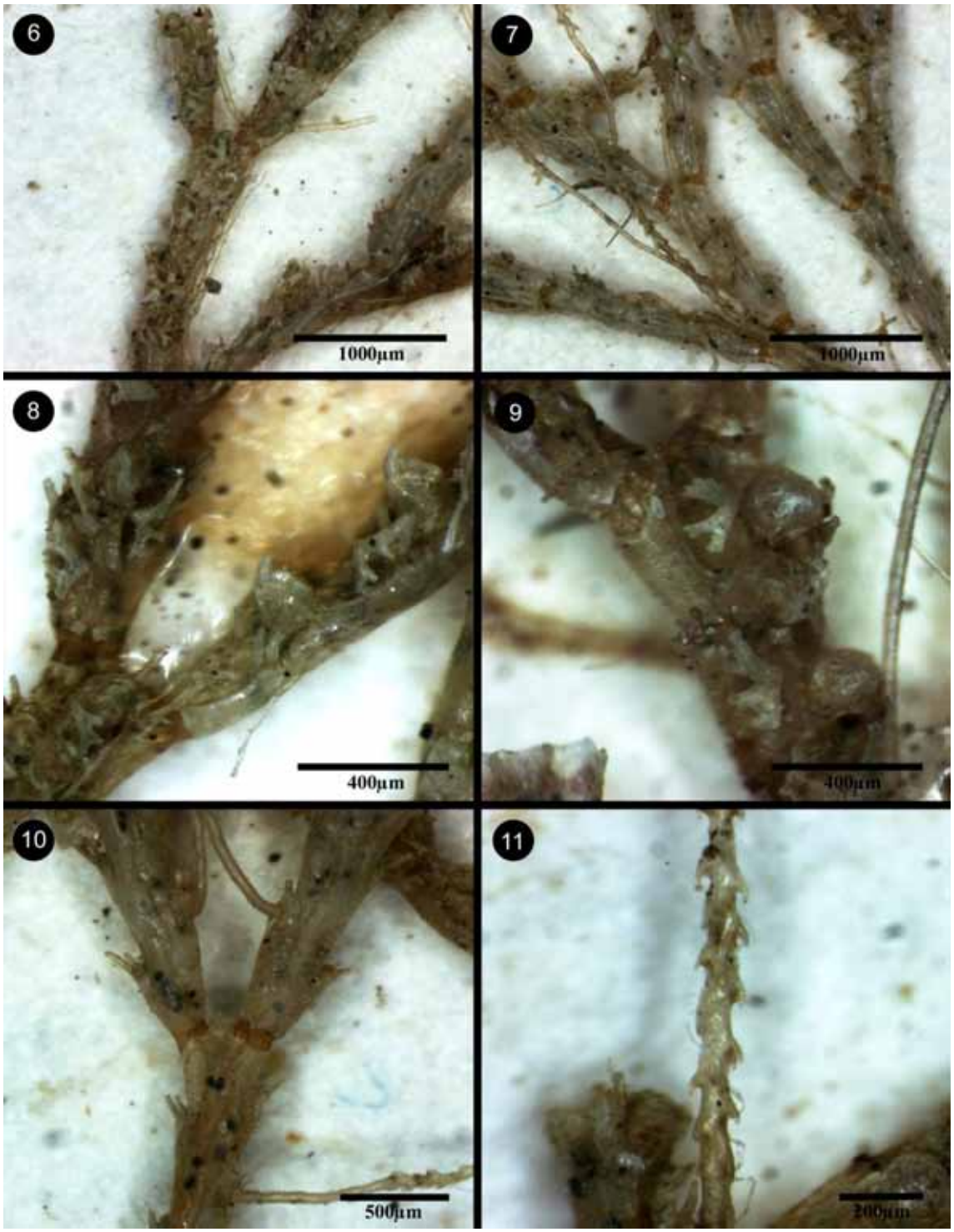


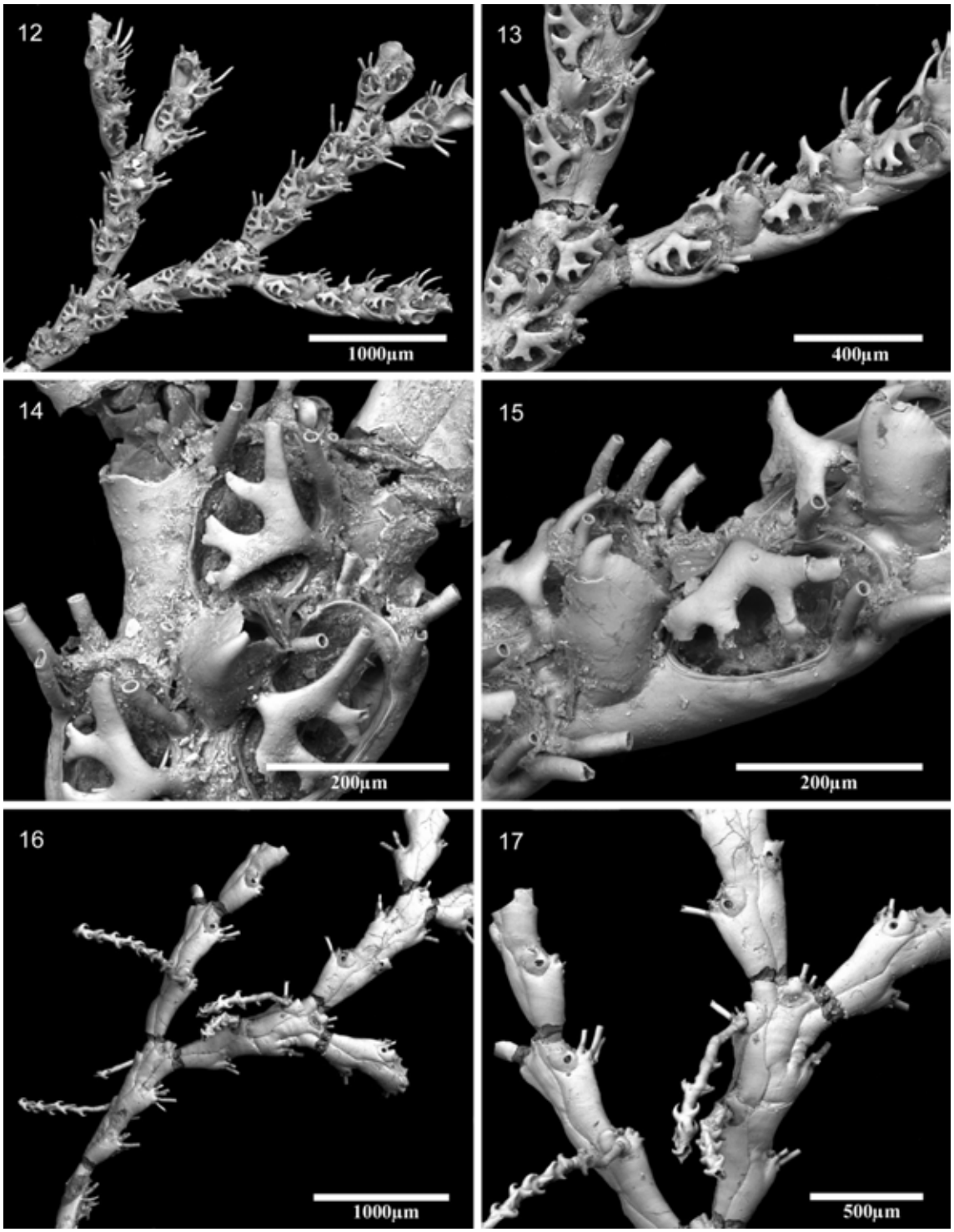
Figure 1.1. Linnaeus herbarium sheet no. 1248.31. The colonies were associated with different letters (A–W), with specimen “I” (circled) selected as lectotype.



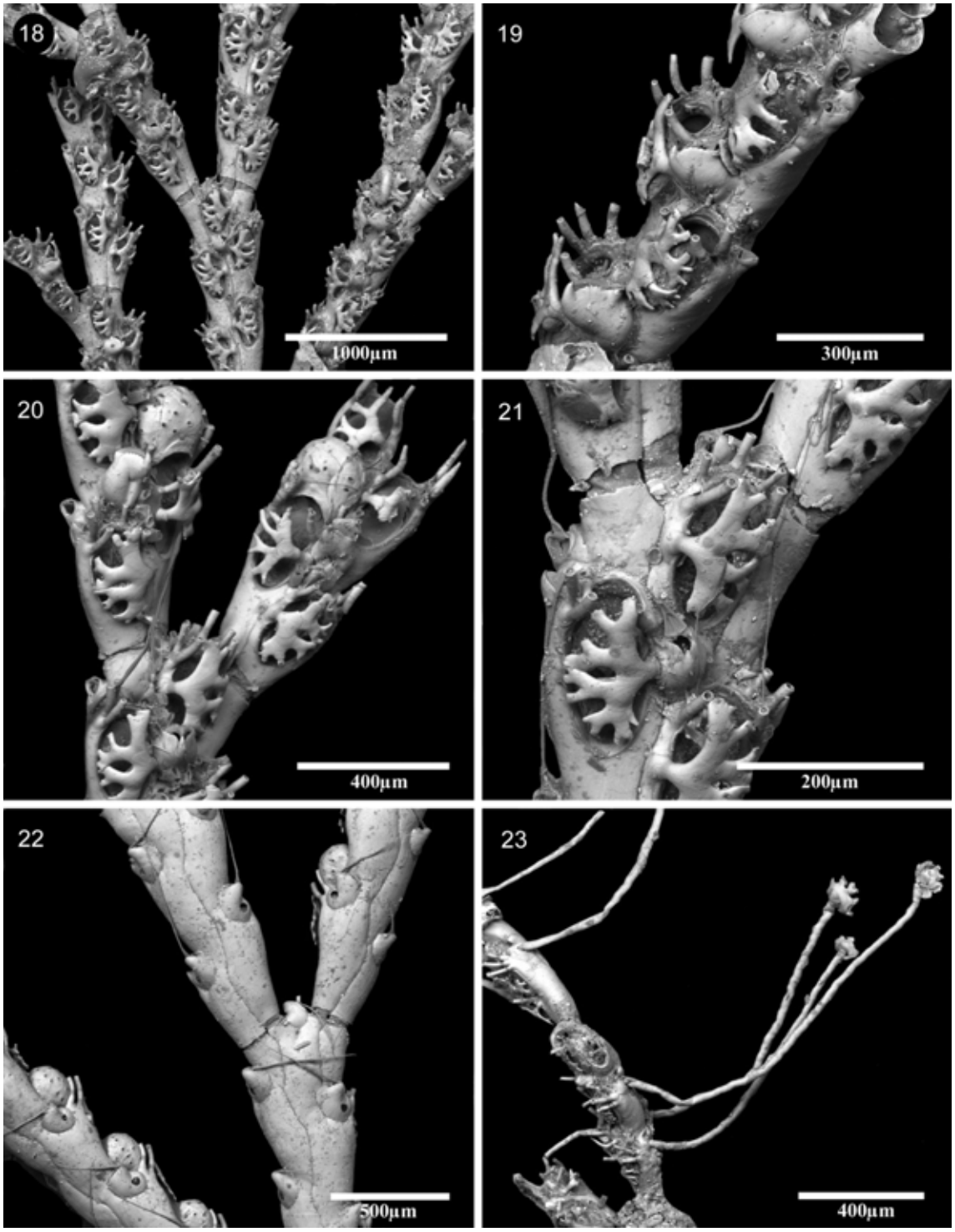
Figures 1.2–1.5. Different shape of rhizoids found in *Scrupocellaria*. **1.2**, Several closed-spaced hooks in rhizoids of *Scrupocellaria reptans* (Linnaeus, 1758) from British coast (NHMUK 1963.3.6.35). **1.3**, Some well-spaced hooks in rhizoids of *Scrupocellaria* sp. from Red Sea (NHMUK 1928.3.6.177). **1.4**, Smooth surface in rhizoids of *Scrupocellaria* n.sp.1 from Scotland (NHMUK 1963.3.6.7a part). **1.5**, Rigged surface of rhizoids of *Scrupocellaria cyclostoma* Busk, 1852 from Australia (NHMUK 1899.6.1.240).



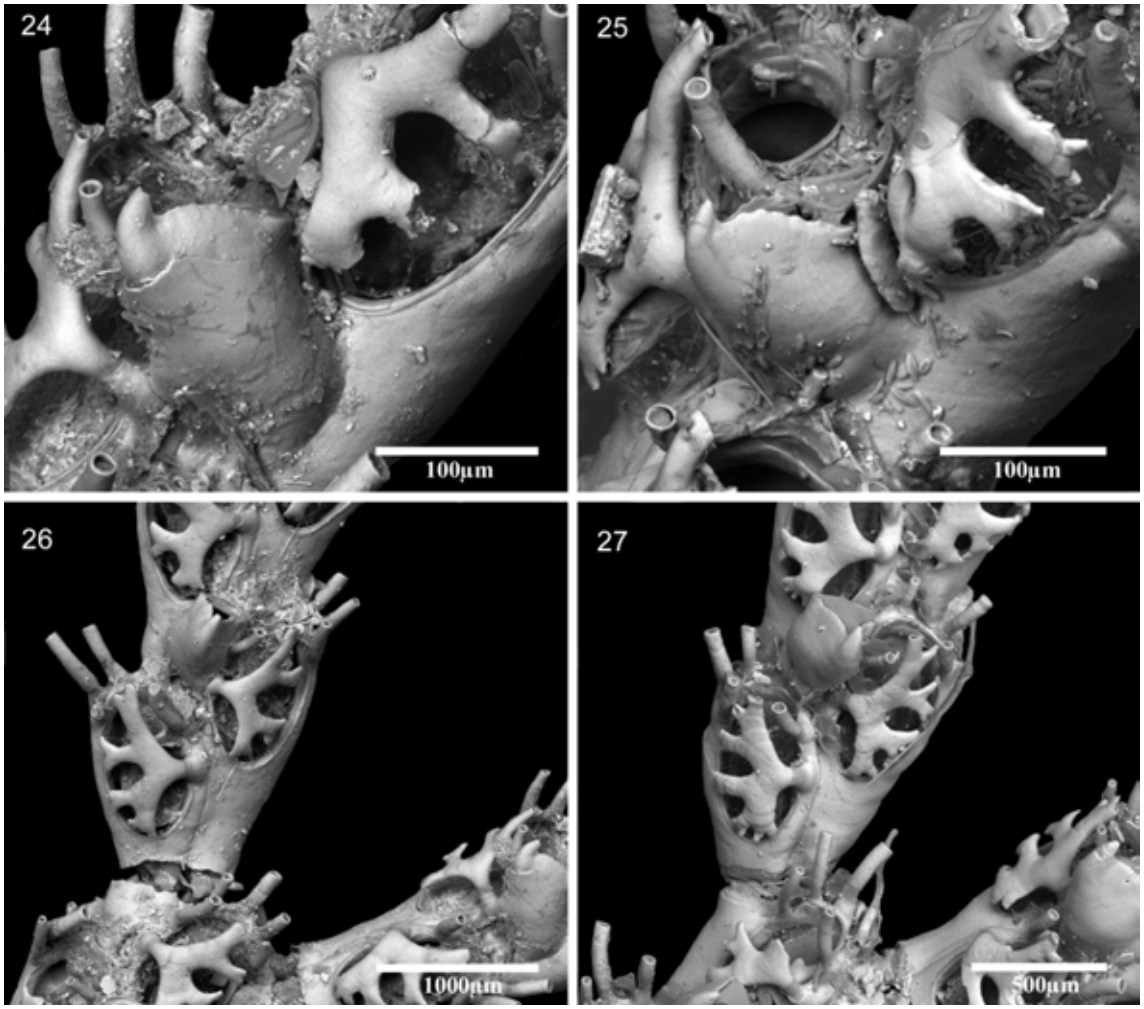
Figures 1.6–1.11. *Scrupocellaria reptans* (Linnaeus, 1758), type specimens on Linnaeus herbarium sheet n. 1248.31. **1.6–1.8**. Lectotype specimen, LSL no. 1248.31.I; **1.6**, frontal view of a branch; **1.7**, basal view of a branch, note the hooked rhizoids; **1.8**, close-up of axial zooid with two branches, note the large frontal avicularia. **1.9–1.11**, Paralectotypes; **1.9**, close-up of one axial zooid and two ovicelled zooids in paralectotype n. 1248.32.T; **1.10**, close-up of basal surface of paralectotype no. 1248.32.D; **1.11**, close-up of rhizoids with regularly spaced hooks in paralectotype no. 1248.32.H.



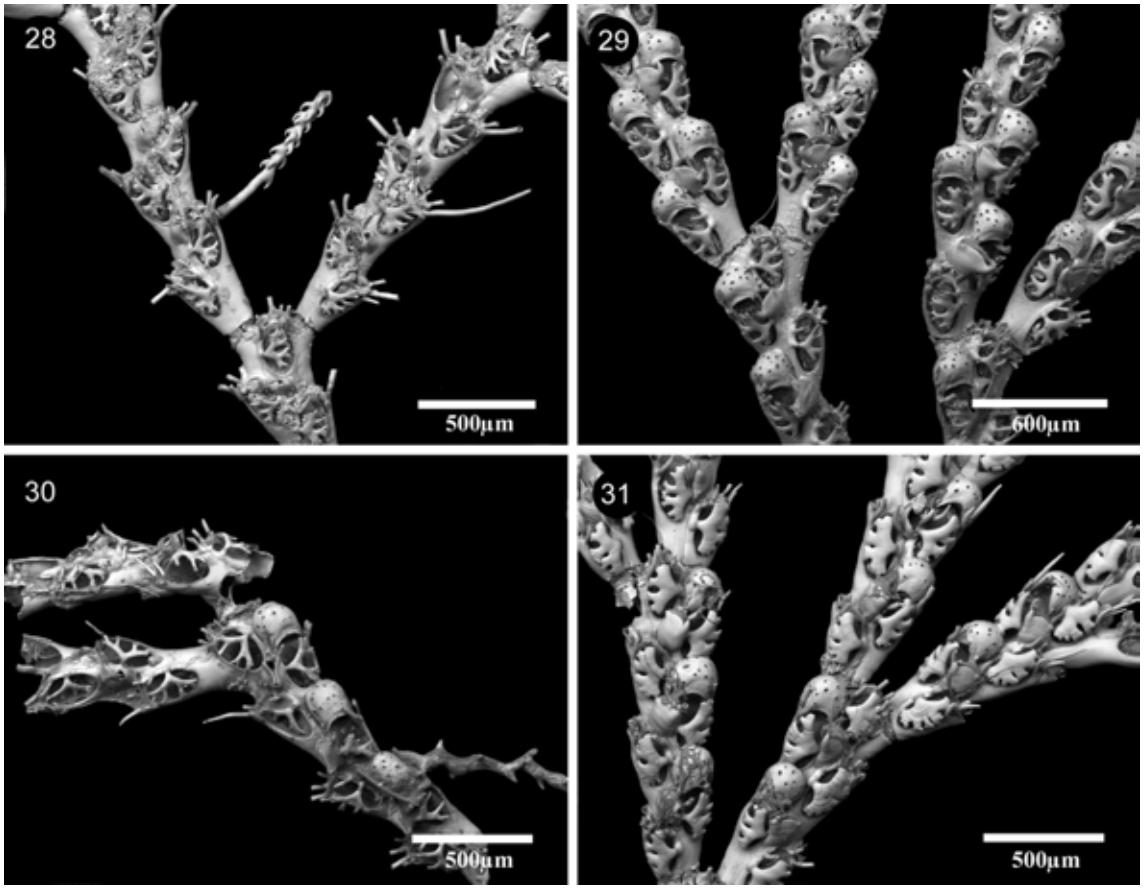
Figures 1.12–1.17. SEM of *Scrupocellaria reptans* (Linnaeus, 1758), NHMUK 1963.3.6.35. **1.12–1.15**, Frontal surface; **1.12**, colony; **1.13**, close-up of branch, with some frontal avicularia; **14**, close-up of axial zooid with frontal avicularium; **1.15**, frontal avicularia in lateral view. **1.16–1.17**, Basal surface; **1.16**, colony; **1.17**, close-up of branch, showing the hooked rhizoids.



Figures 1.18–1.23. SEM of *Scrupocellaria n.sp.1*. **1.18–1.22**, NHMUK 1911.10.1.353, from Shetland, UK; **1.18**, colony; **1.19**, close-up of branch, with some frontal avicularia in lateral view; **1.20**, close-up of branch, note the two ovicelled zooids; **1.21**, close-up of axial zooid with frontal avicularium; **1.22**, basal surface. **1.23**, Colony from Scotland (NHMUK 1963.3.6.7a), showing the rhizoids with smooth surface and distal disc.



Figures 1.24–1.27. Comparison between *Scrupocellaria reptans* (Linnaeus, 1758) (NHMUK 1963.3.6.35) and *Scrupocellaria n.sp.1* (NHMUK 1963.3.6.7a). **1.24–1.25**, Close-up of frontal avicularia, with similar size in young colonies, but with taller base in *S. reptans* (24) than found in *Scrupocellaria* aff. *reptans* (**1.26**). **1.26–1.27**, Frontal surface of colonies, note the scutum slightly more slender and angled in *S. reptans* (**1.26**) than found in most proximal zooids of *Scrupocellaria* aff. *reptans* (**1.27**); note the differences in size of frontal avicularia and number of distal projections in both specimens.



Figures 1.28–1.31. Four different species found in NHMUK's collection previously misidentified as *Scrupocellaria reptans*. **1.28**, Specimen from Arisaig, Scotland (NHMUK 2010.12.6.1); despite presence of hooks in rhizoids, this species has a differently shaped frontal scutum, frontal avicularia and number of distal spines. **1.29**, Specimen from Alexandria, Egypt (NHMUK 1963.8.2.16); note the distinct size of the zooid, frontal avicularia and number of distal spines. **1.30**, Specimen from Madeira (NHMUK 1911.10.1.355); note the distinct shape of ovicell, slender scuta, shape of frontal avicularia and rhizoids with large and well-spaced rhizoids. **1.31**, Specimen from Scotland (NHMUK 2010.12.6.22); note the robust scuta and very large frontal avicularia.

Table 1.1. Characterization of paralectotypes of *Scrupocellaria reptans* (Linnaeus, 1858).

Paralectotype	Condition of colony	Colony surface view	Ovicells	Rhizoids
LSL n.1248.31.A	well preserved colony	frontal	absent	present, with hooks
LSL n.1248.31.B	well preserved colony	frontal	absent	present, with hooks
LSL n.1248.31.C	badly preserved fragments	basal	?	present, with hooks
LSL n.1248.31.D	well preserved colony	frontal and basal	present	present, with hooks
LSL n.1248.31.E	well preserved colony	basal	?	present, with hooks
LSL n.1248.31.F	well preserved fragment	frontal and basal	present	present, with hooks
LSL n.1248.31.G	badly preserved fragment	frontal	present	Absent
LSL n.1248.31.H	well preserved colony	frontal and basal	present	present, with hooks
LSL n.1248.31.J	badly preserved fragments	frontal and basal	absent	Absent
LSL n.1248.31.K	badly preserved fragments	frontal and basal	absent	Absent
LSL n.1248.31.L	badly preserved fragments	frontal and basal	absent	Absent
LSL n.1248.31.M	well preserved colony	frontal and basal	absent	present, with hooks
LSL n.1248.31.N	well preserved colony	frontal	absent	two small fragments
LSL n.1248.31.O	well preserved colony	frontal and basal	present	present, with hooks
LSL n.1248.31.P	badly preserved fragments	basal	?	present, with hooks
LSL n.1248.31.Q	well preserved colony	frontal and basal	absent	present, with hooks
LSL n.1248.31.R	well preserved colony	frontal and basal	absent	present, with hooks
LSL n.1248.31.S	well preserved colony	frontal and basal	present	present, with hooks
LSL n.1248.31.T	well preserved colony	frontal and basal	present	present, with hooks
LSL n.1248.31.U	well preserved colony	frontal and basal	absent	present, with hooks
LSL n.1248.31.V	well preserved colony	frontal and basal	absent	present, with hooks
LSL n.1248.31.W	well preserved colony	frontal and basal	present	present, with hooks

CAPÍTULO 2

REDESCRIPTION OF *ACHAMARCHIS JOLLOISII*, A NEW NONINDIGENOUS BRYOZOAN SPECIES IN ATLANTIC WATERS, AND THE RESURRECTION OF THE GENUS *LICORNIA* VAN BENEDEN, 1850

O capítulo corresponde ao manuscrito de autoria de Leandro M. Vieira, Mary E. Spencer Jones e Judith E. Winston, submetido no periódico *Journal of the Marine Biological Association of the United Kingdom*.

Redescription of *Scrupocellaria* (*Retiscrupocellaria*) *jolloisii*, a new nonindigenous bryozoan species in Atlantic waters, and the resurrection of the genus *Licornia*

ABSTRACT

Recent study of the genus *Scrupocellaria* has shown a greater degree of taxonomically informative morphological variation in zooids, opesia, and polymorphic structures than previously recognized. Only one subgenus has been named within the genus, *Retiscrupocellaria* d'Hondt, 1988, erected for *Scrupocellaria jolloisii*. In this work we further analyze S. jolloisii and its related species, resurrecting an earlier genus name, *Licornia* van Beneden, 1850 for *Licornia jolloisii*, and nine relatives, *L. annectens*, *L. cervicornis*, *L. cyclostoma*, *L. diadema*, *L. ferox*, *L. gaspari*, *L. longispiosa*, *L. macropora*, and *L. prolata*. *Licornia jolloisii* was originally described from the Red Sea, and most species of the genus occur in the Indo-Pacific region. The species, however, has now been found in the Western Atlantic, in the Florida Keys, US, and in Bahia de Todos Santos, Brazil.

INTRODUCTION

The genus *Scrupocellaria* van Beneden, 1845 comprises about 80 extant species of Candidae (BOCK, 2012) characterized by bifurcation type 8 (acc. HARMER, 1923) and zooids with a basal vibracular chamber. Despite the morphological variations found among species assigned to *Scrupocellaria* (*e.g.* shape of zooids, opesia and polymorph structures; see HARMER, 1926), only one species has been reassigned to a distinct subgenus. The subgenus *Retiscrupocellaria* d'Hondt, 1988, erected for *Acamarchis jolloisii* Audouin, 1826, is distinguished by branches joined by transversal tubes and basal vibracular chambers with an oblique groove. Neither additional records nor taxonomic information have been published on this subgenus since its description, and a thorough search of the bryozoan taxonomic literature revealed that VAN BENEDEN (1850) had already introduced a new genus *Licornia* for *Acamarchis jolloisii,* giving that name priority.

Acamarchis jolloisii was described from Egypt (AUDOUIN, 1826), and later recorded in the same locality (Red Sea) by WATERS (1909) under two different names, *Scrupocellaria jolloisii*, for specimens with spines, and a new species *Scrupocellaria mansueta* Waters, characterized by unarmed zooids. Both were synonymized by

D'HONDT (1988) under *S. jolloisi* (incorrect subsequent spelling). WATERS (1909) noted the absence of *Scrupocellaria jolloisii* in the Suez Canal, but HASTINGS (1927) later reported its occurrence from the Suez Canal (Port Said area, Egypt). D'HONDT (1988) reported the species from the Mediterranean coast of Israel.

The present study includes a redescription of the genus *Licornia* and the type species, *Licornia jolloisii*. Additional information on the genus *Licornia* is provided, and new combinations for nine species previously assigned to *Scrupocellaria* are established. We also report *Licornia jolloisii* for the first time outside the Red Sea and Mediterranean waters; newly invasive for the southeastern Atlantic coast of United States of America and the northeastern coast of Brazil.

MATERIALS AND METHODS

Western Atlantic material of *Licornia jolloisii* was obtained from 1–2 m of water under overhangs in the limestone walls of a man-made canal at Big Torch Key, one of the Florida Keys. It was collected in December, 2005 by Don De Maria of Sea Samples, Summerland Key, Florida. Northeastern Brazilian specimens were obtained from 1 m depth on artificial substratum at Itaparica, Todos os Santos Bay, Bahia state. It was collected in January, 2011 by Laura Pioli Kremer and in February, 2012 by Rosana Moreira Rocha from fouling panel samples. Voucher specimens were deposited at the Virginia Museum of Natural History (VMNH, U.S.A.) and Museu de Zoologia da Universidade de São Paulo (MZUSP, Brazil). Comparative specimens listed are deposited at the Natural History Museum, London (NHMUK, U.K.), Museum Victoria (NMV, Australia), Santa Barbara Museum of Natural History (SBMNH, U.S.A.) and the Smithsonian Institution, National Museum of Natural History (NMNH, U.S.A.). In addition to the comparative material, type and non-type specimens of *Scrupocellaria* deposited in different collections, including those of American Museum of Natural History (AMNH, U.S.A.), Museum of Comparative Zoology (MCZ, U.S.A.) and Muséum national d'Histoire naturelle (MNHN, France) were also examined.

All colonies were examined under a stereomicroscope and selected specimens were mounted for examination in a scanning electron microscope (SEM), a Zeiss EVO-60 at the Virginia Museum of Natural History for coated specimens and an SEM with an environmental chamber, a LEO 1455-VP at the Natural History Museum for uncoated specimens. Measurements were made from digital SEM images using the analyzing software ImageJ®.

TAXONOMIC ACCOUNT

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852
Suborder Neocheilostomina d'Hondt, 1985
Infraorder Flustrina Smitt, 1868
Family Candidae d'Orbigny, 1851
Genus *Licornia* van Beneden, 1850

Type species. *Acamarchis jolloisii* Audouin, 1826 by original designation.

Synonym. *Retiscrupocellaria* d'Hondt, 1988 [Type species: *Acamarchis jolloisi* Audouin, 1826 (incorrect subsequent spelling) by original designation, see D'HONDT, 1988: p. 198]

Diagnosis. Candidae with branches sometimes joined by anastomosing transversal tubes; almost rectangular zooids with broadly oval opesia occupying most of the frontal surface. Joints crossing the proximal opesia of outer zooids and below the opesia of the inner zooids at the bifurcation. Cryptocyst vestigial or absent. Frontal scuta sometimes present, spine-like to broader in shape, inserted at inner margin of the opesia. Frontal avicularia often dimorphic. Vibracular chamber almost triangular, small, with a proximal rhizoidal foramen; setal groove directed obliquely; single axial vibraculum. Ooecia with porous ectooecium.

Remarks. Bryozoan taxonomists have long considered *Scrupocellaria* van Beneden, 1845 to be a well-defined genus. Mixtures of characters, however, are observed among the many species assigned to this genus: *viz.* ovicells with single fenestra or with many pores, variable shape and size of opesia, basal vibracular chamber, frontal and lateral avicularia. D'Hondt (1988) also recognized the presence of shared characteristics between *Scrupocellaria jolloisii* and some other species of both *Scrupocellaria* and *Canda*, and designated a new subgenus, *Retiscrupocellaria*. This subgenus was characterized by the presence of anastomosing tubes connecting the colony branches (as in *Canda* Lamouroux, 1816) and a vibracular chamber at the proximal end of basal zooidal surface (as in *Scrupocellaria*). We consider *Retiscrupocellaria* discrete from other *Scrupocellaria* on the basis of the quite distinct characteristics observed in zooids of the type-species of *Scrupocellaria*, *Scrupocellaria scruposa* (Linnaeus, 1758) (*e.g.* shape of zooids, shape of basal vibracula and porous ooecia), and *Acamarchis jolloisii*. According to the principle of priority of ICZN (Art. 23),

however, *Retiscrupocellaria* d'Hondt, 1988 must be considered a junior synonym of *Licornia* van Beneden, 1850, which was also established for *Acamarchis jolloisii*.

Licornia jolloisii **(Audouin, 1826)**

(Figure 2.1A–F; Table 2.1)

Acamarchis jolloisii Audouin, 1826 [figured by Savigny, 1817].

Scrupocellaria jolloisii: Waters, 1909; Hastings, 1927.

Scrupocellaria mansueta Waters, 1909.

Scrupocellaria (Retiscrupocellaria) jolloisi (sic): d'Hondt, 1988.

Type material. *Neotype* (choosen here). Red Sea [NHMUK 1926.9.6.84, Figure 2.1A,C,E].

Additional material examined. *Licornia jolloisii* (Audouin, 1826): *Scrupocellaria jolloisii*, A.B. Hastings det., Red Sea [NHMUK 1926.9.6.85–94]; OM9G-0366-5, 24°25'18.80"S 81°15'23.50"W, Florida, Big Torch Key, #2, collected on 11 December 2005 by Don De Maria, 1–2 m, on limestone [acc. no.2009-015, VMNH 13708.0000, Figure 2.1B,D,F]; 12°53'21"S 38°41'03"W, Itaparica, Baía de Todos os Santos, Bahia, Brazil, collected on January 2011 by Laura P. Kremer, 1 m, on panels [MZUSP, uncatalogued specimen]. *Licornia annectens* (MacGillivray, 1887) n. comb.: *Syntypes*. *Scrupocellaria annectens* MacGillivray, MacGillivray det., 3 microslides, Gaspar Strait, Indonesia, Indian Ocean [NMV F.45606.1–3, Figured specimens on home page of Museum Victoria – http://collections.museumvictoria.com.au]. *Licornia cervicornis* (Busk, 1852) n. comb.: *Holotype*. *Scrupocellaria cervicornis* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS '*Rattlesnake*', off Cumberland Island, 45.7 m (25 fms) [NMHUK 1854.11.15.81]. *Paratypes*: *Scrupocellaria cervicornis* Busk, G. Busk det., Voyage of HMS '*Rattlesnake*', Australia [NMHUK 1899.7.1.4552–3]. *Additional specimens. Scrupocellaria diadema* Busk, S. Harmer det., *Siboga* Expedition, St. 163, specimen 501.G[4], Malay Archipelago, Seget, N. end of New Guinea, 29 m [NHMUK 1928.3.6.180, Figure 2A,B]. *Licornia cyclostoma* (Busk, 1852) n. comb.: *Holotype*. *Scrupocellaria cyclostoma* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS '*Rattlesnake*', Bass Straits, Australia, 82.3 m (45 fms) [NHMUK 1854.11.15.77]. *Additional specimen*. *Scrupocellaria annectens* MacGillivray, T. Hincks det., Port Phillip Heads, Victoria, Australia (*Scrupocellaria cyclostoma* Busk, S. Harmer det., 12.7.1922) [NHMUK 1899.6.1.340, Figure 2.2C,D]. *Licornia diadema* (Busk, 1852) n. comb.: *Holotype*. *Scrupocellaria diadema* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS '*Rattlesnake*', Moreton Bay [NHMUK 1854.11.15.80, Figure 2.2E,F]. *Additional specimens*. *Scrupocellaria diadema* Busk, Canu & Bassler det., U.S. Fish Commission Steamer '*Albatross*', St. 5478, off Tacbuc Point, East Leyte, Philippines, 104 m (57 fms) [NMNH 7894]; *Scrupocellaria diadema* Busk, Great Barrier Reef Expedition, St. 12, collected on 24 February 1929 [NMNH 9565]. *Licornia gaspari* (Thornely, 1907) n. comb.: *Syntypes*. *Scrupocellaria gaspari* Thornely, L.

Thornely det., Gaspar Strait, Indonesia [NHMUK 1936.12.30.146, Figure 2.3A,B; 1907.8.24.1pt]; *Scrupocellaria gaspari* Thornely, L. Thornely det., Andaman Islands, Indian [NHMUK 1936.12.30.126; NHMUK 1936.12.30.136]. *Licornia ferox* (Busk, 1952) n. comb.: *Holotype. Scrupocellaria ferox* Busk, G. Busk det., British Museum Catalogue Collection, Voyage of HMS '*Rattlesnake*', Louisiade Archipelago [NHMUK 1854.11.15.76]; balsam slide with part of holotype (schizoholotype), mounted by S. Harmer, 28.vi.1922 [NHMUK 1899.7.1.6540]. *Additional specimen*. *Scrupocellaria ferox* Busk, S. Harmer det., *Siboga* Expedition, St. 7, specimen 2.A[2], Batjulmati, Java, coral reef [NHMUK 1928.3.6.156, Figure 2.3C,D]. *Licornia longispinosa* (Harmer, 1926) n. comb.: *Holotype*. *Scrupocellaria longispinosa* Harmer, S. Harmer det., *Siboga* Expedition, St. 144, specimen 108.Ai, Maluku Islands, Indonesia, anchorage N of Solamakiëe, 07.viii.1899, 45m [ZMA 01063au, schizoholotype; RMNH 00054, schizoholotype, NHMUK 1928.3.6.189–90, schizoholotypes, Figure 2.3E,F; NMNH 9389, schizoholotype]. *Licornia macropora* (Osburn, 1950) n. comb.: *Paratypes*. *Scrupocellaria macroposa* Osburn, R. Osburn det., AHF 33, Allan Hancock Pacific Expedition, '*Velero III*', St. 1162-40, 33°33'5"N 118°9'45"W, California, Orange County, 11 miles of South of Seal Beach, collected on 23 July 1940 [SBMNH 96151]; *Scrupocellaria macroposa* Osburn, R. Osburn det., Allan Hancock Pacific Expedition, St. 1263-41, 1.5 miles off north end of Cedros Island, Mexico, Lower California, 82–100 m (45–55 fms) [NMNH, uncatalogued specimen]. *Additional specimen*. U.S. Fish Commision Steamer '*Albatross*', station 2886, off Oregon Coast [NMNH, uncatalogued specimen, Figure 2.4A,B]. *Licornia* spp.: *Comparative material*. *Scrupocellaria diadema* Harmer, S. Harmer det., Siboga Expedition, St. 99, specimen 68.B[2], N. Ubian, Sulu Archipelago, 16–23m [NHMUK 1928.3.6.178, Figures 2.4C,D]; *Scrupocellaria diadema* Harmer, P. Hayward det., Coral Reef Research Foundation, OCDN2370-L, KB CHAN, 07°19.24'N, 134°31.28'E, Palau, Channel between Koror and Babeldaod, 14.v.1994, 20m [NHMUK 2005.7.27.12, Figures 2.4E,F].

Redescription. Colony erect, branched, with branches comprising 5–17 zooids, sometimes joined by anastomosing transversal tubes, pale reddish brown in color in life. Internode almost straight, with chitinous joints passing across the proximal opesia in both outer zooids at the branch bifurcation. Autozooids elongate, almost tubular, slightly wider distal than proximally, with curved distal edges. Oval opesia occupying almost all the zooidal length, broader distally. Cryptocyst absent. Scutum sometimes present, inserted at midline or slightly distal of inner edge of the opesia, spine-like, stout, obliquely directed forward and over frontal membrane. One outer and one inner oral spine, vestigial, often absent. Axial zooid without oral spines or, rarely with 1–2 vestigial oral spines. A lateral avicularium present near distal outer edge in each zooid, small, laterally directed; rostrum triangular with hooked mandible. Frontal avicularia (sometimes absent) at inner proximal margin of opesia, monomorphic; rostrum triangular, serrated, directed obliquely downwards, triangular mandible hooked distally.

A vibracular chamber present on basal surface of each zooid, sometimes inconspicuous in frontal view, almost triangular, small, with oblique setal groove and one proximal rhizoidal foramen; vibracular setae smooth as long as two zooids. Single axial vibraculum, with proximal rhizoidal foramen. Rhizoids tubular with some retroussé hooks. Ovicells almost globular, with ectooecium perforated by funnel-shaped elongate to circular pores.

Remarks. *Acamarchis jolloisii* was described by AUDOUIN (1826) based on Egyptian specimens figured by SAVIGNY (1817). No type material exists for *Acamarchis jolloisii.* We, therefore, designate a neotype from the Red Sea (NHMUK 1926.9.6.84) that is consistent with Savigny's original figures and with the most recent redescription of the species given by D'HONDT (1988).

Notwithstanding the similar appearance of zooids in Red Sea colonies of *Licornia jolloisii*, WATERS (1909) described a new species from the same locality, *Scrupocellaria mansueta*, distinct from *L. jolloisii* only by absence of scuta and oral spines in many zooids. In all examined specimens from Red Sea, Suez Canal, Florida and Brazil, however, the presence or absence of oral spines, as well the stout spiny scuta, change randomly along the branches of *L. jolloisii* (Figure 2.1A–B), and *S. mansueta* is here considered to be a junior subjective synonym of *Licornia jolloisii*.

ADDITIONAL SPECIES OF *LICORNIA*

We examined in detail a huge range of material of *Scrupocellaria* deposited in different scientific collections and found some specimens that share the following characters with *Licornia jolloisii*: zooids almost rectangular with opesia occupying almost all of frontal area; joints passing across the proximal opesia in both outer zooids at the bifurcation; cryptocyst vestigial or absent; frontal scuta sometimes absent; small, almost triangular vibracular chamber with oblique setal groove; single axial vibraculum; and ooecium with many ectooecial pores. These characteristics are also observed in *Scrupocellaria diadema* (see HARMER, 1926; TILBROOK & VIEIRA, *in press*), and this species should be reassigned to *Licornia*.

HARMER (1926) noted that many specimens previously assigned to *L. diadema* showed variation in the size of the vibracular chamber, the shape of scuta and the number of oral spines. Despite the differences in material from Indo-Pacific waters, HARMER (1926) synonymized three species under Busk's *S. diadema*: *Scrupocellaria cervicornis* Busk, 1852, *Scrupocellaria annectens* MacGillivray, 1887, *Scrupocellaria gaspari* Thornely, 1907. Our study shows that the type specimens of these three

species are morphologically distinct from each other in autozooid shape, presence and shape of frontal scuta and the number of oral spines (i.e. Figure 2.2A–B: *S. cervicornis*; Figure 2.3A–B: *S. gaspari*), as well as being distinct from Busk's *S. diadema* (Figure 2.2E–F).

TILBROOK (2006) noted differences between Busk's *S. diadema* and some specimens from Indonesian and Malaysian regions, which led TILBROOK & VIEIRA (*in press*) to describe a new species from the Queensland coast, *Scrupocellaria prolata*. The specimen recorded under the name *Scrupocellaria diadema* from the Solomon Islands (SBMNH 365098–99; see TILBROOK, 2006: 58, pl. 9, figs. A–C) also belongs to a distinct undescribed species (TILBROOK & VIEIRA, *in press*).

OSBURN (1950) recorded 18 *Scrupocellaria* species from the Eastern Pacific, seven of them described as new to science. The examination of the Osburn's *Scrupocellaria* specimens deposited at the SBMNH and NMNH revealed one species, *Scrupocellaria macropora* Osburn, 1950 (Figure 2.4A–B), which shares with *Licornia jolloisii* and *Licornia diadema* the characteristics of shape of zooids, position of the joints, frontal avicularia, ovicells and basal vibracula.

The characteristics of *L. jolloisii*—i.e. opesia occupying almost all of the frontal area, joints passing across the proximal opesia in both outer zooids at the bifurcation, the vibracular chamber almost triangular with an oblique setal groove, a single axial vibraculum, and ooecium with many ectooecial pores—are also seen in Busk's *Scrupocellaria cyclostoma* (Figure 2.2C – D) and *Scrupocellaria ferox* (Figure 2.3C–D), as well as the Indo-Pacific specimens of *Scrupocellaria longispinosa* Harmer, 1926 (Figure 2.3E–F).

Thus, at least nine additional species previously assigned to *Scrupocellaria*, including most of those described by BUSK (1852), are herein reassigned to the genus *Licornia* van Beneden, 1850: *Licornia annectens* (MacGillivray, 1887) n. comb., *Licornia cervicornis* (Busk, 1852) n. comb., *Licornia cyclostoma* (Busk, 1852) n. comb., *Licornia diadema* (Busk, 1852) n. comb., *Licornia ferox* (Busk, 1852) n. comb., *Licornia gaspari* (Thornely, 1907), *Licornia longispinosa* (Harmer, 1926) n. comb., *Licornia macropora* (Osburn, 1950) n. comb., and *Licornia prolata* (Tilbrook & Vieira, *in press*).

Among the taxa herein assigned to *Licornia*, two species, *L. annectens* and *L. ferox*, are characterized by the absence of frontal scuta, while in *L. cyclostoma* the scuta are present only in ovicelled zooids. In type specimens of *Licornia diadema* the scutum is often present and dimorphic in ovicelled zooids, but its presence varies in

non-ovicelled zooids, as in *L. prolata*. *Licornia jolloisii* is distinguished from other species of *Licornia* by the presence of a spine-like stout scutum with a sharp point.

DISCUSSION

The redescription of *L. jolloisii* allows us to reassign nine additional species to this genus: *L. annectens* n. comb., *L. cervicornis* n. comb., *L. cyclostoma* n. comb., *L. diadema* n. comb., *L. ferox* n. comb., *L. gaspari* n. comb., *L. longispinosa* n. comb., *L. macropora* n. comb and *L. prolata* n. comb. The genus *Licornia*, formerly a monomorphic subgenus, now comprises nine species, characterized by (i) fan-shaped colonies with joints crossing the proximal opesial area of outer zooids at the bifurcation, (ii) rectangular to sub-rectangular zooids with broad opesia, (iii) presence of frontal dimorphic avicularia (rarely monomorphic), (iv) small, almost triangular basal vibracular chambers, longer than wider, with oblique setal grooves, (v) single axial vibracula and (vi) ovicells with many ectooecial pores.

The jointed transversal tubes on the branches, described for *L. jolloisii* (Figure 2.1A), were also observed in some colonies of *L. gaspari* and *L. diadema*. The majority of species have rhizoids with hooks, but *L. cyclostoma* has distinctly annulated rhizoids. HINCKS (1880) noted smooth and hooked rhizoids in different colonies of *Scrupocellaria reptans* from British waters, while WATERS (1909) used these characteristics to distinguish different species of *Scrupocellaria*. No variation in the surface of rhizoids was observed in different species of *Licornia*, which suggests that the different morphology in distinct specimens (hooked, smooth or annulated) is not an ecological response and may be useful to distinguish different taxa. Further observation using SEM will be important to distinguish additional characteristics (*e.g.* shape of frontal scuta, shape and position of frontal avicularia) necessary for detection of species complexes (*e.g. Licornia diadema*, see HARMER, 1926), such as have been observed for other bryozoan taxa (BERNING *et al.*, 2008; WINSTON & WOOLLACOTT, 2008; VIEIRA *et al.*, 2010; VIEIRA *et al.*, 2012).

The genus *Licornia* is widely distributed in Indian and Pacific waters and more species may exist, but the group does not seem to be as diverse in the Atlantic. Crossland's specimen from Cape Verde Island of *Scrupocellaria cervicornis* Busk was redescribed as *Scrupocellaria tridentata* Waters, 1918, but due to the presence of very large basal vibracula and distinct trifoliate frontal avicularia this species is not reassigned to *Licornia*. Specimens of *L. diadema* were previously reported by G. Busk from Cape Verde Island (under the name *Scrupocellaria ciliata* Audouin, 1826; see

BUSK, 1884: 23). Recently *Licornia diadema* has been recorded from the Western Atlantic from Rio de Janeiro, Brazil, by RAMALHO *et al.* (2005), making the Florida Key and Brazilian specimens of *Licornia jolloisii* the second record for the genus in Atlantic waters (Figure 2.5). Due to the presence of similar species in Australian waters (TILBROOK & VIEIRA, *in press*) and the possibility of cryptic species among colonies from Korea (LEE *et al.*, 2011), however, we suggest detailed morphological studies on specimens reported by RAMALHO *et al.* (2005) as *Scrupocellaria diadema* to confirm the identity of Brazilian specimens.

MCCANN *et al.* (2007) reported 35 species on plates in six different localities of the Southern United States, four of those classified as non-native. Among species classified as cryptogenic (unknown origin), only one member of the family Candidae, *Scrupocellaria bertholletii* Audouin, 1826, was recorded, but examination of the specimens at the VMNH showed that two supposedly endemic species are involved, one of them belonging to *Scrupocellaria curacaoensis* Fransen, 1986. Recently, JOHNSON *et al*. (2012) reported the first invasive Candidae species on the Northeastern Atlantic coast, *Tricellaria inopinata* d'Hondt & Occhipinti-Ambrogi, 1985. Therefore, *Licornia jolloisii* is the second non-native Candidae species reported from the Atlantic coast of United States, the first on the southeast coast.

Licornia jolloisii was first reported on an artificial substratum (buoy) by WATERS (1909) from Suez Bay, while ROBERTSON (1921) noted that this species was very common in the vicinity of the Bay of Bengal, between 70–90 m depth. The species was first reported as invasive in six different points along the Suez Canal, including Port Said which is at the Mediterranean entrance of the Suez Canal (HASTINGS, 1927). The last record for *L. jolloisii* was from the Mediterranean (Israel) by D'HONDT (1988), who found colonies on sandstones and banks of bivalves, an invasion supposedly carried from the North Suez Canal to the coast of Israel, but with an unknown dispersal vector (GALIL, 2007). The location of the Florida Keys specimens (Figure 2.6) in a manmade canal near a major recreational boat route to and from Key West, as well as the volume of commercial shipping traffic through the Straits of Florida, makes it likely that it represents a recent invasion of the area. More collections in this region are needed to determine whether or not the species has persisted or spread since 2005. More recently, some specimens of *L. jolloisii* were also found on artificial panels in Itaparica, Baía de Todos os Santos, NW Brazilian coast. This place is characterized by intense commercial shipping traffic due to the presence of small boat marinas, the Harbor of Aratu and one oil refinery, with piers for the oil cargo ships and a large shipyard.

Further efforts towards extending the understanding of local invasive marine species dynamics are in progress in this area (L.P. Kramer & R.M. Rocha, pers. comm.).

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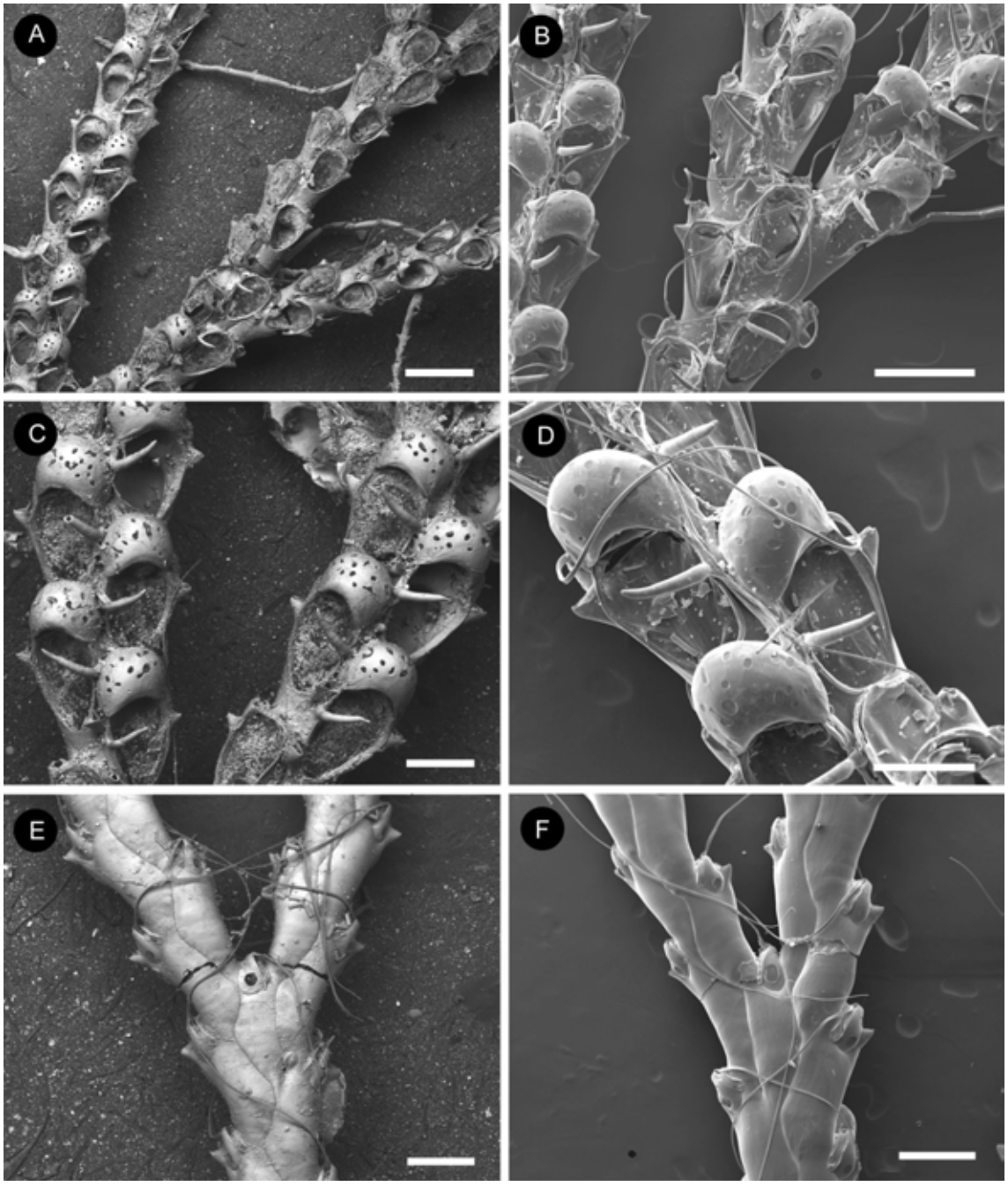

Figure 2.1. *Licornia jolloisii* (Audouin, 1826). **A,C,E**, NHMUK 1926.9.6.84, Neotype, Red Sea. **B,D,F**, VMNH 13708.0000, Florida, U.S.A. Scale bars: A,B, 0.4 mm; C,D,E, 0.2 mm; F, 0.3 mm.

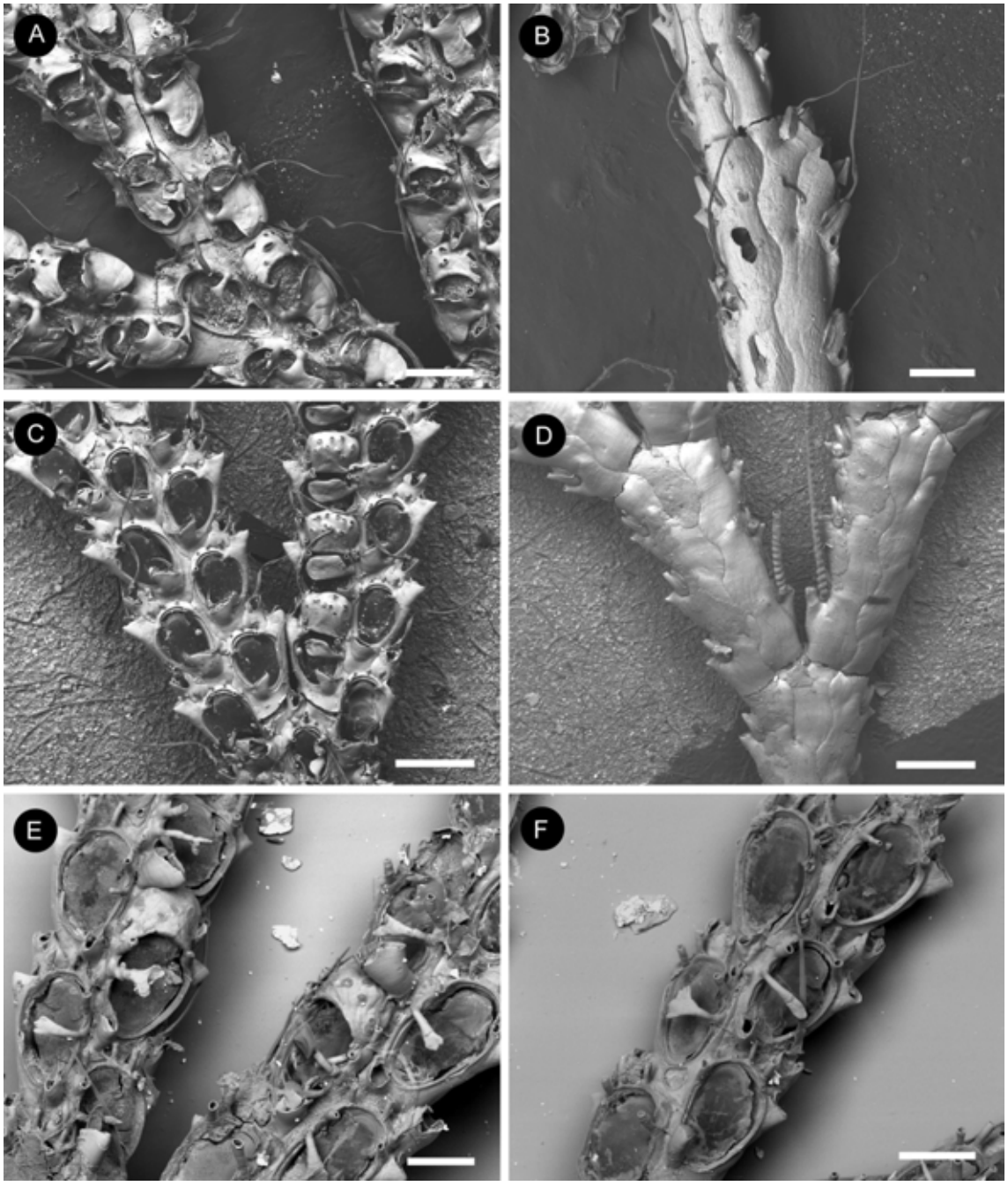

Figure 2.2. Species of *Scrupocellaria* herein reassigned to *Licornia*. **A–B**, *Licornia cervicornis* (Busk, 1852) n. comb., NHMUK 1928.3.6.180, North of New Guinea. **C–D**, *Licornia cyclostoma* (Busk, 1852) n. comb., NHMUK 1899.6.1.340, Port Phillip Heads, Australia. **E–F**, *Licornia diadema* (Busk, 1852) n. comb., NHMUK 1854.11.15.80, Holotype, Moreton Bay, Australia. Scale bars: A,B,E,F, 0.2 mm; C,D, 0.4 mm.

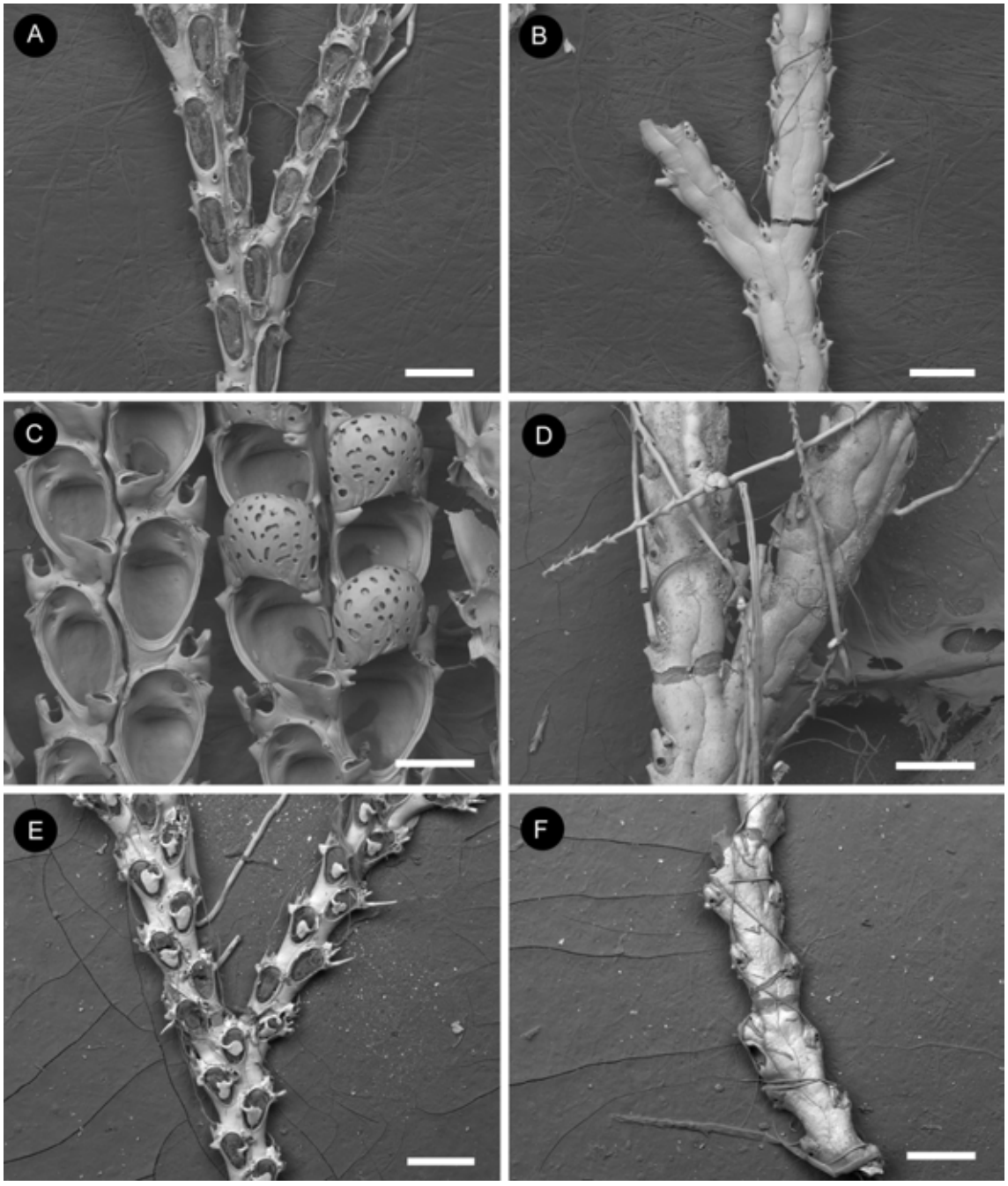

Figure 2.3. Species of *Scrupocellaria* herein reassigned to *Licornia*. **A–B**, *Licornia gaspari* (Thornely, 1907) n. comb., NHMUK 1936.12.30.146, Syntype, Gaspar Strait, Indonesia. **C–D**, *Licornia ferox* (Busk, 1852) n. comb., NHMUK 1928.3.6.156, Java. **E–F**, *Licornia longispinosa* (Harmer, 1926) n. comb., Schizoholotype, NHMUK 1928.3.6.189, Maluku Islands, Indonesia. Scale bars: A,B,D,E,F, 0.4 mm; C, 0.2 mm.

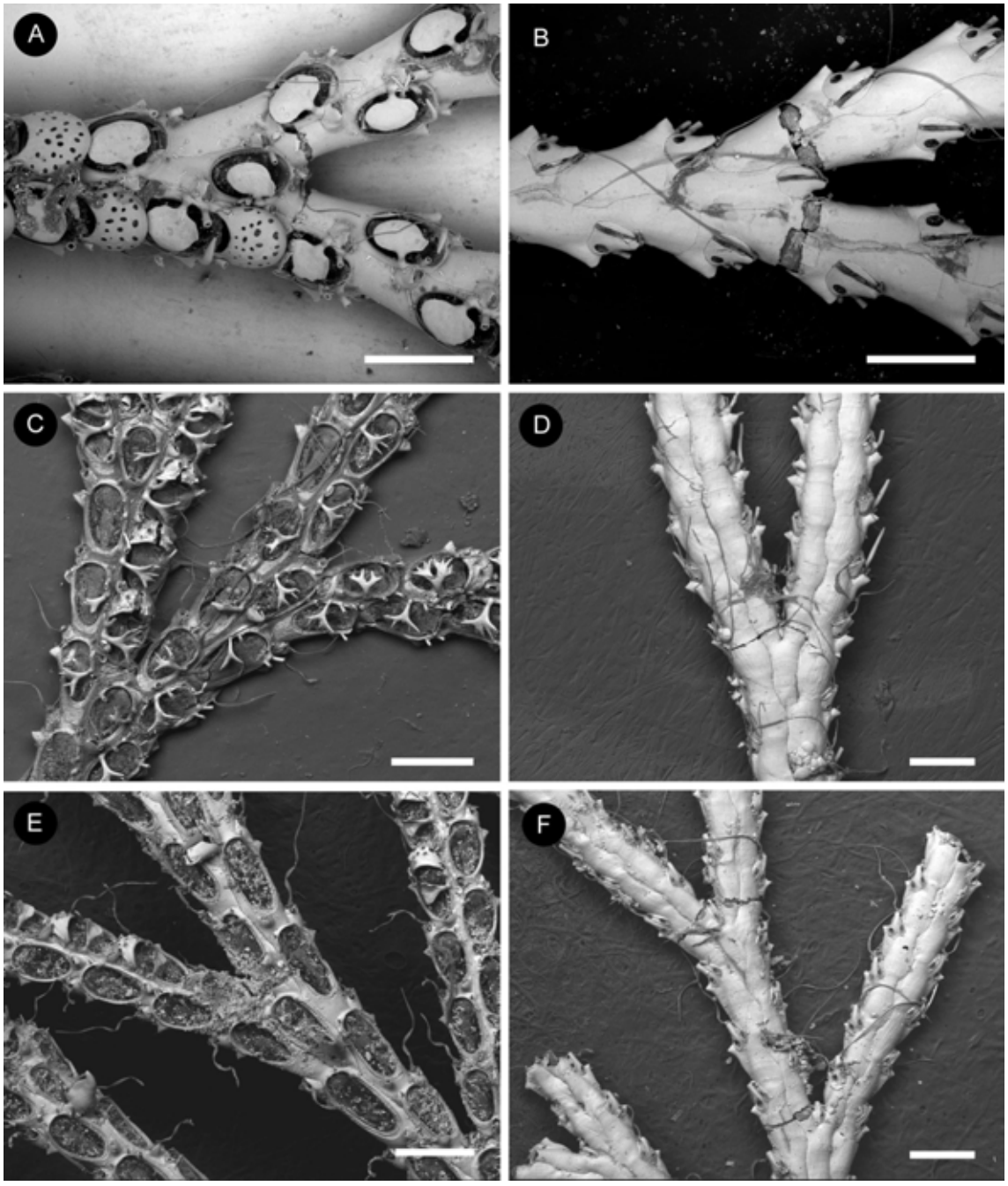

Figure 2.4. A–B, *Licornia macropora* (Osburn, 1950) n. comb., NMNH no number, off Oregon, U.S.A. **C–F**, Two different species of *Licornia*, previously assigned to *Scrupocellaria diadema* Busk, 1852. **C–D**, NHMUK 1928.3.6.178, Malay Archipelago. **E–F**, NHMUK 2005.7.27.12, Palau. Scale bars: A–F, 0.4 mm.

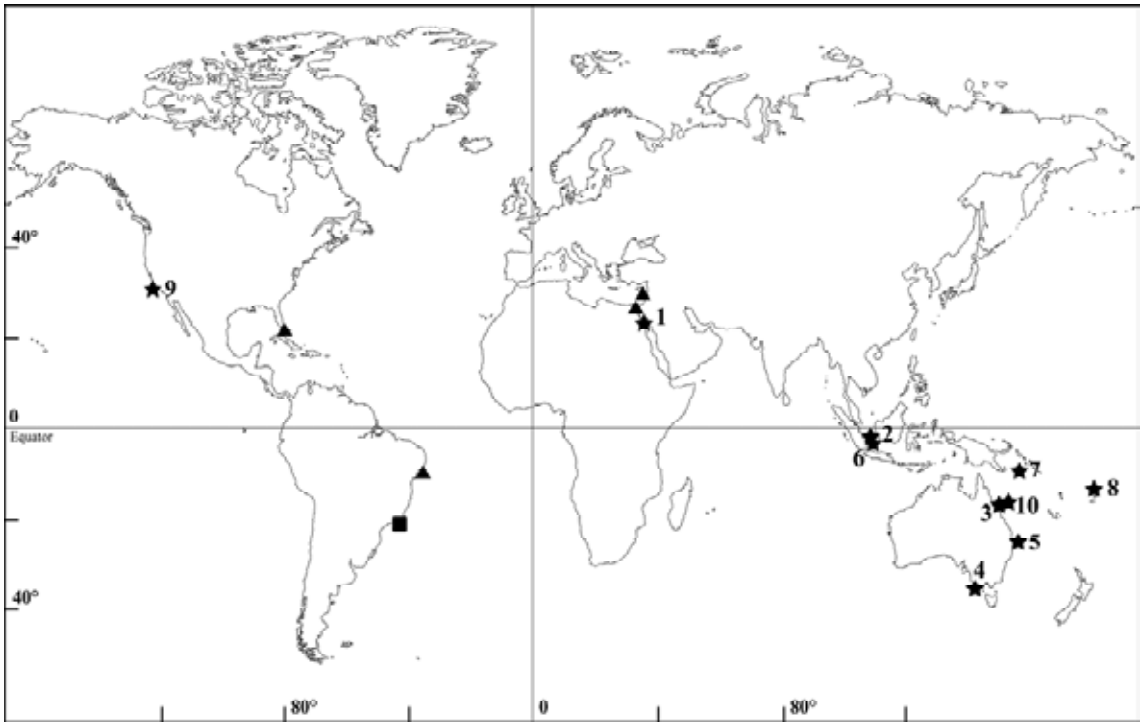

Figure 2.5. Type locality of *Licornia* species worldwide [stars] and new locality records: 1, *Licornia jolloisii* (Audouin, 1826); 2, *Licornia annectens* (MacGillivray, 1887); 3, *Licornia cervicornis* (Busk, 1852), 4, *Licornia cyclostoma* (Busk, 1852), 5, *Licornia diadema* (Busk, 1852), 6, *Licornia gaspari* (Thornely, 1907); 7, *Licornia ferox* (Busk, 1952) n. comb.; 8, *Licornia longispinosa* (Harmer, 1926), 9, *Licornia macropora* (Osburn, 1950) n. comb.; 10, *Licornia prolata* (Tilbrook & Vieira, *in press*). Additional records of *Licornia jolloisii* [triangle] and *Licornia diadema* [square] in Atlantic and Mediterranean.

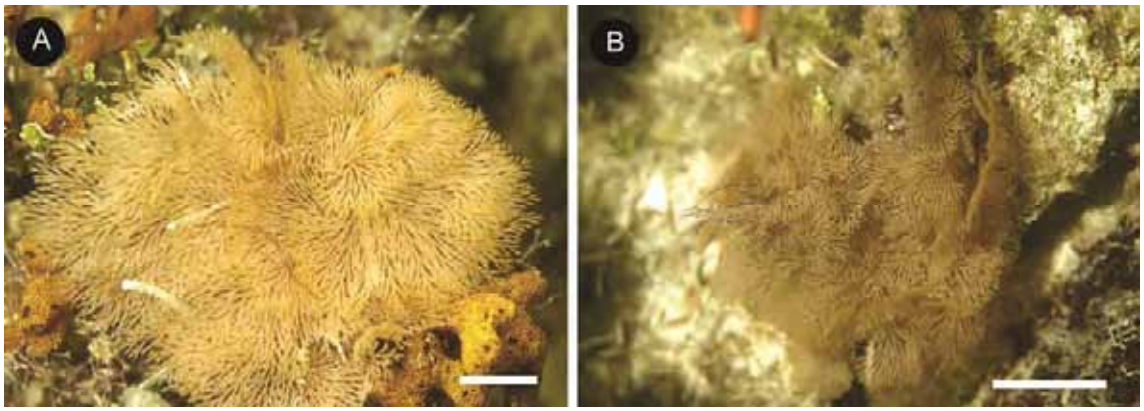

Figure 2.6. A–B, Colonies of *Licornia jolloisii* (Audouin, 1826) on natural substrata found in Florida Keys, U.S.A. Scale bars: 2 cm. Photographs by Don De Maria, Sea Samples, Summerland Key, Florida.

Table 2.1. Measurements (in mm) of Neotype of *Licornia jolloisii* (Audouin, 1826) from Red Sea (NHMUK 1926.9.6.84).

Structures	N	Min	Max	Mean	±SE
Zooid length	15	0.345	0.497	0.438	0.048
Zooid width	15	0.162	0.225	0.193	0.019
Opesia length	15	0.255	0.342	0.288	0.029
Opesia / autozooid	15	0.56	0.76	0.71	0.08
Scuta length	15	0.115	0.173	0.126	0.022
Frontal avicularia length	15	0.055	0.070	0.060	0.005
Vibracular chamber legth	15	0.118	0.136	0.129	0.006
Ooecia length	15	0.145	0.204	0.171	0.016
Ooecia width	15	0.199	0.218	0.208	0.007

Min, minimum; Max, maximum; N, number; SE, standard Error

CAPÍTULO 3

A NEW BRYOZOAN GENUS FOR *SCRUPOCELLARIA BERTHOLLETII* (AUDOUIN) (CHEILOSTOMATA, CANDIDAE): TAXONOMY, BIODIVERSITY AND DISTRIBUTION

O capítulo corresponde ao manuscrito de autoria de Leandro M. Vieira, Mary E. Spencer Jones e Judith E. Winston, a ser submetido no periódico *Zootaxa*.

A new bryozoan genus for *Scrupocellaria bertholletii* (Audouin) (Cheilostomata, Candidae): taxonomy, biodiversity and distribution

ABSTRACT

A new genus, *N.gen.1*, is erected for *Scrupocellaria betholletii* (Audouin, 1826), a species that has been reported as widespread in tropical and subtropical waters. Here we select a neotype of this species to establish its identity and distinguish it from other morphologically similar species. We include the redescription and figures of additional species, now assigned to this new genus: *N.gen.1 curacaoensis* (Fransen, 1986) n. comb., *N.gen.1 hirsuta* (Jullien & Calvet, 1903) n. comb., and *N.gen.1 macrorhyncha* (Gautier, 1962) n. comb. Five additional species are assigned to the genus: *N.gen.1 n.sp.1* (Vieira & Spencer Jones) n. comb., *N.gen.1 nanshaensis* (Liu, 1991) n. comb., *N.gen.1 reptans* (Linnaeus, 1758) n. comb., *N.gen.1 serrata* (Waters, 1909) n. comb., and *N.gen.1 tenuirostris* (Osburn, 1950) n. comb. Eighteen new species are described: *N.gen.1 n.sp.2*, *N.gen.1 n.sp.3*, *N.gen.1 n.sp.4*, *N.gen.1 n.sp.5*, *N.gen.1 n.sp.6*, *N.gen.1 n.sp.7*, *N.gen.1 n.sp.8*, *N.gen.1 n.sp.9*, *N.gen.1 n.sp.10*, *N.gen.1 n.sp.11*, *N.gen.1 n.sp.12*, *N.gen.1 n.sp.13*, *N.gen.1 n.sp.14*, *N.gen.1 n.sp.15*, *N.gen.1 n.sp.16*, *N.gen.1 n.sp.17*, *N.gen.1 n.sp.18*, and *N.gen.1 n.sp.19*.

INTRODUCTION

Acamarchis bertholletii was introduced by AUDOUIN (1826) in reference to the figured specimens from Egypt given by SAVIGNY (1817: pl. 11, figs. 3.1–3.5). DUMOND (1981) noted Audouin's species comprise specimens from Red Sea and Mediterranean, but no localities were given for 40 of Audouin's species, including *Acamarchis bertholletii*. Thus, the type locality of *Scrupocellaria bertholletii* remains uncertain, although likely Mediterranean or Red Sea. The species has been reported in Mediterranean (WATERS, 1897; BARROSO, 1923; GAUTIER, 1962; D'HONDT, 1988), Suez Canal (HASTINGS, 1927) and Red Sea (WATERS, 1909; HASTINGS, 1927; BALAVOINE, 1959). In the Red Sea, the species has been previously reported on the Northern coast—despite of the absence of that species in recent collections (see OSTROVSKY *et al.*, 2011)—, whereas there is no record for the Southern coast (*e.g.* WATERS, 1909; POWELL, 1969; REDIER, 1970; DUMONT, 1981; AMUI & KASELOWSKY, 2006). After the original description, the species was reported by HINCKS (1886) from the Adriatic under the name *Scrupocellaria bertholletii*. Hincks characterized the specimens by presence of bifurcated to higthly

branched spines overarching the frontal membrane (scutum). As was noted by HINCKS (1886), however, the highly branched scutum of Adriatic specimen is distinct from the single forked scutum illustrateded by SAVIGNY (1817), suggesting more than one species is included under the name *S. bertholletii*.

Scrupocellaria bertholletii has been reported as widespread in tropical and subtropical waters worldwide (WATERS, 1897, 1909, 1918; CALVET, 1906; NORMAN, 1909; KLUGE, 1914; BARROSO, 1923; HASTINGS, 1927, 1930; MARCUS, 1938; OSBURN, 1950; BALAVOINE, 1959; GAUTIER, 1962; PRENANT & BOBIN, 1966; WINSTON, 1986; D'HONDT, 1988), but with a high degree of morphogical plasticity shown in specimens from different localities (*e.g.* KLUGE, 1914; HASTINGS, 1930; OSBURN, 1950; PRENANT & BOBIN, 1966). Recently, the re-examination of the type material of other supposedly widespread species of *Scrupocellaria* van Beneden, 1845 has revealed the presence of species complexes in some putative well-established taxa (TILBROOK & VIEIRA, *in press*; VIEIRA & SPENCER JONES, unpublished data, see Chapter 1; VIEIRA *et al.*, unpublished data, see Chapter 2). VIEIRA *et al.* (unpublished data; Chapter 2) also used morphological features to characterize the genus *Licornia* van Beneden, 1850, a junior synonym of *Retiscrupocellaria* d'Hondt, 1988, and to suggest *Scrupocellaria sensu lato* includes several morphologically distinct genera and unexpectedly high diversity. In the present study we designate a neotype for Audouin's *Acamarchis bertholletii*, and erect a new genus, *N.gen.1*, to accommodate morphologically similar species. We suggest that at least 9 species previously assigned to *Scrupocellaria* belong in this genus, and we describe 18 new species of the genus

MATERIAL AND METHODS

Type and non-type specimens included in this study are deposited in the following institutions:

AMNH, the American Museum of Natural History (USA)
MOM, Musée Océanographique de Monaco (Monaco)
MCZ, Museum of Comparative Zoology (USA)
MNHN, Muséum national d'Histoire naturelle (France)
MOM, Musée océanographique de Monaco (Monaco)
MZUFBA, Museu de Zoologia da Universidade Federal da Bahia (Brazil)
MZUSP, Museu de Zoologia da Universidade de São Paulo (Brazil)
NMV, Museum Victoria (Australia)
NHMUK, Natural History Museum of London (United Kingdom)

NCB, Naturalis, Nederlands Centrum voor Biodiversiteit Naturalis (formerly Nationaal Natuurhistorich Museum, Leiden; Netherlands)
SBMNH, Santa Barbara Museum of Natural History (USA)
NMNH, Smithsonian Institution, National Museum of Natural History (USA)
VMNH, Virginia Museum of Natural History (USA)

All colonies were examined under a stereomicroscope and selected specimens were mounted for examination in a scanning electron microscope (SEM), a Zeiss EVO-60 at the VMNH and at the Zeiss LEO 440 at the MZUSP for coated specimens and SEM with an environmental chamber, a LEO 1455-VP at the NHMUK and Philips XL-30 at the NMNH for uncoated specimens. Some slide specimens were photographed under a Zeiss Discovery V20 stereomicroscope with AxioCam HRc at the NHMUK, a petrographic compound microscope with camera at the VMNH. Measurements were made from digital SEM images using the analyzing software ImageJ®.

TAXONOMIC ACCOUNT

Family Candidae d'Orbigny, 1851
Genus *N.gen.1* Vieira, Spencer Jones & Winston n. gen.

Type species. *Acamarchis bertholletii* Audouin, 1826, by original designation.

Synonym. *Crisina* van Beneden, 1850, *nomen oblitum* (not *Crisina* d'Orbigny, 1853, *nomen protectum*)

Diagnosis. Biserial candidae with articulate distal spines, branched scutum inserted at midline of the inner edge of the opesia, trapezoidal vibracular chamber, single axial vibracula and ooecium perforated by some ectooecial pores.

Description. Candidae with almost straight branches, with chitinous joints passing across the opesia or below it in zooids C and D at the bifurcation; zooids with some articulate distal spines, unbranched. Frontal avicularia often present and dimorphic, aquiline to elongate, with serrated rostrum and hooked mandible. Frontal scutum delicate or stout, forked to hightly branched with truncate or sharped tips, inserted at the midline of the inner edge of the opesia and overarching the frontal membrane; scutum occasionally absent. Distolateral avicularium often present at the outer distal corner of zooid, laterally to the spines or behind it. Vibracular chamber almost rounded to trapezoidal, setal groove transversal with smooth setae. Axial

vibracula single and without rhizoidal foramen. Ooecium perforated by some ectooecial rounded pores.

Remarks. VIEIRA *et al.* (unpublished data, Chapter 2) used the fact that the present genus *Scrupocellaria* van Beneden, 1845 comprises some species with a mixture of characters to resurrect and to define *Licornia* van Beneden, 1850.

The presence of perforated ooecium, branched scutum and rounded to trapezoidal vibracular chamber with transversal setal groove are distinct from characters observed in the type of *Scrupocellaria*, *Scrupocellaria scruposa* (Linnaeus, 1758). The shape of scutum, the unbranched spines and shape of vibracular chamber are also distinct from those of *Licornia* (VIEIRA *et al.*, unpublished data). These morphological characteristics, clearly observed in *Scrupocellaria betholletii* and *Scrupocellaria reptans*, led us to erect a new genus, *N.gen.1*, to include 7 species previously assigned to *Scrupocellaria*: *N.gen.1 bertholletii* (Audouin, 1826) n. comb., *N.gen.1 curacaoensis* (Fransen, 1986) n. comb., *N.gen.1 hirsuta* (Jullien & Calvet, 1903) n. comb., *N.gen.1 macrorhyncha* (Gautier, 1962) n. comb., *N.gen.1 tenuirostris* (Osburn, 1950) n. comb., *N.gen.1 nanshaensis* (Liu, 1991) n. comb. and *N.gen.1 serrata* (Waters, 1909) n. comb. Other 18 species are here described for the genus.

The species of *N.gen.1* are distinct from other *Scrupocellaria* species by the presence of porous ovicells, branched scutum and trapezoidal vibracular chamber with transversal setal groove. *Licornia* resembles *N.gen.1* by the presence of porous ovicells, but is quite distinct int the shape of its basal vibracular chambers, with oblique setal groove, and unbranched scuta. Some other species of *Scrupocellaria* also have porous ovicells, *e.g. Scrupocellaria frondis* Kirkpatrick, 1890 and *Scrupocellaria sinuosa* Canu & Bassler, 1927 (see TILBROOK & VIEIRA, *in press*) but they are quite distinct from *N.gen.1* in the shape of frontal scuta and absence of dimorphic frontal avicularia.

VAN BENEDEN (1850) erected the genus *Crisina* for *Crisie rampante* (=*Sertularia reptans* Linnaeus) and *Acamarchis bertholetii* (sic) Audouin. This name was not used in literature since HARMER (1926), who included *Crisina* van Beneden as junior synonym of *Scrupocellaria* van Beneden, 1845. On the other hand, the junior homonym *Crisina* d'Orbigny, 1853 had been used for some fossil cyclostomes in the last century (*e.g.* NEVIANI, 1900; HARMER, 1915; BORG, 1941; BROOD, 1976). To promote the stability and according to ICZN Article 23.2, we consider the unused senior homonym *Crisina* van Beneden, 1850 as a *nomen oblitum* and the junior homonym *Crisina* d'Orbigny, 1853 is declare a *nomen protectum* (Vieira & Winston, unpublished data).

***N.gen.1 bertholletii* (Audouin, 1826) n. comb.**

(Figures 3.1–3.2, Table 3.1)

Acamarchis Bertholletii Audouin, 1826: 241; Savigny, 1817: pl. 11, figs. 3.1–3.5. [Egypt]

Scrupocellaria Bertholletii Audouin: Hincks, 1886: 258, pl. 9, figs. 1–2. [Adriatic]

Scrupocellaria bertholletii Audouin: Hastings, 1927: 335. [Suez Canal]

Not *Scrupocellaria bertholletii* Audouin: Norman, 1909: 283, pl. 36, figs. 1–2. [Madeira]

Not *Scrupocellaria bertholletii* Audouin: Waters, 1918: 5 (part). [Cape Verde Island]

Not *Scrupocellaria bertholletii* Audouin: Hastings, 1930: 703, pl. 1, figs. 1–5. [Galapagos and Gorgona Island]

Not *Scrupocellaria bertholletii* Audouin: Marcus, 1938: 24, pl. 5, figs. 11A–B. [Brazil: São Paulo]

Not *Scrupocellaria bertholletii* Audouin: Osburn, 1940: 386. [Bermuda, Puerto Rico and Tortugas]

Not *Scrupocellaria bertholletii* Audouin: Osburn, 1947: 20. [N Colombia and Aruba Island]

Not *Scrupocellaria bertholetii* (sic) Audouin: Osburn, 1950: 133, pl. 18, figs. 7–8, pl. 21, fig. 8. [Pacific]

Not *Scrupocellaria bertholletii* Audouin: Banta & Carson, 1977: 389, fig. 3 [Costa Rica]

Neotype (chosen here). NHMUK 1899.7.1.736 (Figure 3.1A–F), *Scrupocellaria bertholletii*, Mediterranean.

Additional material examined. NHMUK 1885.8.12.1, *Menipea jeffreysii*, S.O. Ridley det., S.O. Ridley Collection, 9.viii.1922, Viareggio, Mediterranean. NHMUK 1899.5.1.264, with *Scrupocellaria scruposa*, T. Hincks Collection, Adriatic. NHMUK 1899.5.1.341–2, *Scrupocellaria bertholletii*, T. Hincks det., T. Hincks Collection, Adriatic. NHMUK 1899.5.1.421, *Scrupocellaria bertholletii*, T. Hincks det., T. Hincks Collection, Adriatic. NHMUK 1911.10.1.357, *Scrupocellaria bertholletii* var. *aperta*, A.M. Norman det., Madeira, 1897. NHMUK 1911.10.1.358, *Scrupocellaria bertholletii*, Prof. Heller det., A.M. Norman Collection, Adriatic. NHMUK 1926.9.6.66–7, *Scrupocellaria bertholletii*, A.B. Hastings det., 15.xii.1924, Suez Canal P.3. NHMUK 1926.9.6.68, *Scrupocellaria bertholletii*, A.B. Hastings det., 26.x.1924, Suez Canal, Barga 690 P.T. NHMUK 1926.9.6.69, *Scrupocellaria bertholletii*, A.B. Hastings det., Suez Canal, Dredger N.8. NHMUK 1963.1.26.2, *Scrupocellaria bertholletii*, J.S. Ryland det., 30.xii.1960, Porto d'Ischia, Italy. NHMUK 1964.3.12.6, *Scrupocellaria reptans*, Malta, Mediterranean. NHMUK 2007.11.9.42–3, *Scrupocellaria bertholletii*, J.S. Ryland det., 26.ii.1962, A.P. Austin leg., Malta, Mediterranean. NMNH 9083, Mediterranean. NHMUK 2012.7.1.11 (Figure 3.2C–F), Station Cru82.043, 14.viii.1982, Charles H.J.M. Fransen leg., Curaçao, Piscadera Inner Bay, Candelichi, 0–0.5 meters, on rhizophora-roots. MOM 421681 (part of specimens in NHMUK 2012.7.1.4, Figure 3.2A–B), Calvet det., 30.I.1908, Sur le Coffre du Port Monaco.

Diagnosis. Colony with chitinous joints passing across the proximal end of opesia in zooids C and D at the bifurcation; zooids with 1 inner and 1–2 outer spines, 1 distal spine rarely present; forked scutum sometimes present at the inner margin of opesia, overarched to the midline of membranous area; small distolateral avicularium present in each zooid; vibracular chamber almost rounded and small.

Redescription. Colony erect, branched, with internodes comprising 5–9 zooids. Internodes almost straight, with acute bifurcating pattern; chitinous joints pass across the proximal end of the opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of the inner zooids (zooids F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to three fifths of the zooidal length, with two lateral folds where the lateral spines are inserted; cryptocyst proximal very narrow, inconspicuous, deep and smooth. Scutum sometimes present, inserted at the midline of inner opesial edge, small, forked, angled at 70–90 degrees, overarched to the midline of frontal membrane. Distal spines short, unbranched; 1 inner, 1–2 outer spines, rarely 1 distal spine; most proximal outer and inner spines directed forward; axial zooid with 3–4 spines. One distolateral avicularium present in each zooid, small, laterally directed; rostrum triangular, 0.044–0.062 mm long, with serrated lateral edge and slightly curved tip. Frontal avicularia often present, dimorphic: small frontal avicularium with raised tubular base, 0.040–0.065 mm long, rostrum slightly serrated, triangular, directed forward; large frontal avicularium aquiline, 0.115–155 mm long, rostrum serrated and slightly curved, directed forward, with triangular curved mandible with hooked tip. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost circular, with large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, slightly enlarged distally, with ectooecium perforated by 12–16 medium sized rounded pores; ovicelled zooids with 1 inner and 2 outer spines.

Remarks. The morphological variation reported for *N.gen.1 bertholletii* in the literature (*e.g.* PRENANT & BOBIN, 1966: 418) led us to examine specimens collected in different localities worldwide. *Acamarchis bertholletii* was introduced by AUDOUIN (1826), based on colonies from Egypt, but their exact locality is unknown; they could have been collected in either the Red Sea or Mediterranean coast. Audouin's description was based in specimens drawn by SAVIGNY (1817), which were supposedly lost (D'HONDT, 2006). However, two diagnostic characteristics are observed in

Savigny's plates: (I) the bifurcated frontal scutum and (II) the shape of basal vibracula. These characteristics are also observed in some specimens from Suez Canal and Mediterranean, as well a small specimen from Madeira Island (NHMUK 1911.10.1.357) identified by Alfred M. Norman (1831–1918) under an unpublished name *Scrupocellaria bertholletii* var. *aperta*. Thus, the neotype of *N.gen.1 bertholletii* is here selected from Mediterranean specimen (NHMUK 1899.7.1.736) in order to establish the identity of this species. The majority of specimens deposited at the NHMUK, NMNH and AMNH assigned to *N.gen.1 bertholletii* have scutum with distinct branching patterns and belong to other distinct species. Some of those species are reassigned below to nine new species: *N.gen.1 n.sp.6*, *N.gen.1 n.sp.7*, *N.gen.1 n.sp.9*, *N.gen.1 n.sp.10*, *N.gen.1 n.sp.11*, *N.gen.1 n.sp.12*, *N.gen.1 n.sp.13*, *N.gen.1 n.sp.15*, and *N.gen.1 n.sp.16*.

N.gen.1 bertholletii has been reported in tropical and subtropical waters worldwide. HASTINGS (1930) noted distinct differences in morphology among specimens of *N.gen.1 bertholletii* from different localities of Pacific and Egypt, but notwithstanding used the same name for three morphologically distinct specimens from Pacific waters. Likewise, morphological differences were also described by other authors (*e.g.* NORMAN, 1909; WATERS, 1918; MARCUS, 1938; OSBURN, 1940, 1950). OSBURN (1950) first described one distinct form of *N.gen.1 bertholletii* from California, named *Scrupocellaria bertholletii* var. *tenuirostris*, characterized by elongate shape of frontal avicularia and branching pattern of scutum, now assigned as a distinct species (Figure 3.11). Later, FRANSEN (1986) also used morphological characteristics of scutum and absence of avicularia to distinguish the Caribbean species *N.gen.1 curacaoensis*. Other six species with branched scuta previously assigned to *Scrupocellaria* are so far known: *Scrupocellaria bellula*, *Scrupocellaria n.sp.1*, *Scrupocellaria macrorhyncha*, *Scrupocellaria micheli* (Marcus, 1955), *Scrupocellaria nanshaensis,* and *Scrupocellaria reptans*. *Scrupocellaria bellula* has a highly branched scutum (Figure 3.3) and oral spines branched three or more times, distinct from other species of *N.gen.1*. *Scrupocellaria micheli* differs from *N.gen.1* species by the presence of large lateral avicularia and a basal vibracular chamber with oblique setal groove (MARCUS, 1955). The others four species are herein reassign to *N.gen.1*—i.e. *N.gen.1 n.sp.1*, *N.gen.1 macrochyncha*, *N.gen.1 nanshaensis,* and *N.gen.1 reptans*— and they are distinct by the presence of a stout scutum, occupying almost the frontal membrane.

N.gen.1 bertholletii is characterized by zooids with oval opesia and reduced cryptocyst, forked scutum (often absent, see Figures 3.1B–D, 3.2A,C–E), presence of

small distolateral avicularia and an almost rounded basal vibraculum chamber. The specimen figured and described by HELLER (1867) as *Scrupocellaria capreolus* from Adriatic Sea differs from *N.gen.1 bertholletii* by the presence of bi- to trifurcate scuta; this species requires further examination to confirm its identity.

Distribution. Suez Canal; Mediterranean; Adriatic; Madeira Island; Curaçao; shallow waters.

***N.gen.1 curacaoensis* (Fransen, 1986) n. comb.**

(Figures 3.4–3.5, Table 3.1)

Scrupocellaria bertholletii Audouin: Osburn, 1940: 386 (in part). [Bermuda and Puerto Rico]

Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Scrupocellaria bertholletii Audouin: Osburn, 1947: 20. [N Colombia and Aruba Island]

Scrupocellaria coracaoensis Fransen, 1986: 45, figs. 15a–d. [Bonaire and Curaçao]

Material Examined. *Holotype*. RMNH 02975, balsam slide (figured by Fransen 1986), *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.033, 9.viii.1982, Curaçao, Fuikbaai, eastern part, 1.5–3 meters. *Paratypes*. NHMUK 2012.7.1.12 (Figure 3.4A–C), dry (part of specimen RMNH 02975, in alchool), same data as holotype. RMNH 03034, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.081, 17.ix.1982, Curaçao, Spaanse water, entrance, Spaanse Lagoen, 0–0.5 meters. RMNH 03035, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.066, 10.ix.1982, Curaçao, Fuikbaai, eastern part, 0–1 meters. RMNH 03036, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.066, 10.ix.1982, Curaçao, Fuikbaai, eastern part, 0–3 meters. RMNH 03037, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1620, 14.x.1967, Curaçao, Piscadera Baai, Carmabi pier, 0–1 meters. RMNH 03038, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1037A, 21.iv.1949, Curaçao, Spaanse water, Spaans Lacoen, south side, 0–1.5 meters. RMNH 03040, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1218, 3.iii.1955, Curaçao, Schottegat on Venezuelan destroyer, 0–2 meters. RMNH 03041, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1049C, 13.ix.1948, Klein Bonaire, sandy reef, 1–3 meters. RMNH 03064, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Car.1629, 17.xi.1968, Curaçao, Spaanse water, inner bay, Jan Sofat, islet, 0–1 meters. *Additional material*. MCZ 112, wet; NMNH Hutchins-9, balsam slide NMNH Hutchins-13, balsam slide, *Scrupocellaria bertholletii*, Osburn & Hutchins det. 1942, *US Coast Survey Stemer Blake*, Station 12, 1877–78, C.P. Patterson, Gulf Stream and Gulf of Mexico Exploration, Alexander Agassiz leg., 24°34'N 83°16'W, 65.8 meters (36 fms). NMNH SEM-3 (Figure 3.4D–F), *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-4-A-4303, Bermuda. NMNH Osburn-04 (Figure 3.5A–B), balsam slide, *Scrupocellaria bertholleti*,

Allan Hancock Foundation, Sta. 2381, off Guanica Harbor, Porto Rico, about 9 meters. NMNH Osburn-10, balsam slide, *Scrupocellaria bertholleti*, Bermuda, H. Pratt coll. NMNH BR-5, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-12-A-4333, Bermuda. NMNH BR-4, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-10-B-4321, Bermuda. NMNH BR-3, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-10-B-4331, Bermuda. NMNH BR-2, *Scrupocellaria regularis*, Roger Cuffey det., Bermud-4-9-A-4304, Bermuda. SBMNH 96400 (Figure 5C–D), balsam slide, *Scrupocellaria bertholletii*, Allan Hancock Foundation, R.C. Osburn Collection, 'Velero III', Station A18-39, 10.iv.1939, San Nicholas Bay, Aruba Island, 12°21'28"N, 70°4'45"W. NMNH Hutchins-8, balsam slide, *Scrupocellaria bertholletii*, Osburn det., Station 2381, Porto Rico. NMNH 16934 (found with *Scrupocellaria regularis*), dry, Continental Shelf Associatioes, 18.vii.1981, Station 01, Expedition SW Florida Shelf Cr. II, Gulf of Mexico, off Florida, 26°45'46"N 82°43'07"W, 24 meters.

Diagnosis. Chitinous joints passing across the proximal end of opesia in zooids C and D at the bifurcation; Zooids with 1–2 inner and 3 outer distal spines, an additional distal spine often present; scutum often present, bi- or trifurcated, sometimes bifurcated and branched again; distolateral avicularium absent; vibracular chamber almost rounded and small; rhizoid with retroussé hooks; ooecium with pores linked by internal sutures.

Redescription. Colony erect, branched, with branches comprising 3–11 zooids. Internodes slightly curved; chitinous joints pass across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, tapering proximally and slightly curved laterally. Oval opesia occupying distal half of the zooidal length; cryptocyst inconspicuous around opesia rim. Scutum often present, inserted at midline of inner edge of opesia, bifurcated 60–120 degrees, often trifurcated, reaching beyond midline of opesia. Five to seven distal spines, long and unbranched; most proximal inner spines often directed on the opercular area; axial zooid with 6 spines. No distolateral avicularium. Frontal avicularia dimorphic: small frontal avicularium with triangular mandible; large frontal avicularium with triangular curved rostrum proximally directed and with hooked tip; mandible slightly curved and hooked distally. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibracula almost circular, with large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, straight, with smooth setae longer than one autozooid length. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some retroussé hooks. Ovicells hyperstomial, globular; ectooecium perforated by

7–15 tubular rounded pores linked by internal sutures; two inner and three outer orificial spines in ovicelled zooids.

Remarks. OSBURN (1940) first observed the absence of lateral avicularia in Caribbean specimens of *Scrupocellaria bertholletii*. FRANSEN (1986) used the absence of lateral avicularia, as well the branching pattern of frontal scuta (sometimes trifurcated) and the shape of frontal avicularia to describe a new species, *Scrupocellaria curacaoensis*. The examination of specimens identified as *Scrupocellaria bertholletii* from the Caribbean (OSBURN, 1940, 1947) revealed two distinct species in Caribbean waters: *N.gen.1 curacaoensis* and *N.gen.1 n.sp.6*, distinct by the shape of scutum and the frontal avicularia. The examination of specimens deposited at the AMNH identified as *Scrupocellaria bertholletii* from Jamaica also revealed a species similar to *N.gen.1 curacaoensis* and *N.gen.1 n.sp.6* by absence of lateral avicularia; these specimens are here described as *N.gen.1 n.sp.12*, distinct in zooid size and in shape of avicularia and ovicells.

N.gen.1 curacaoensis is morphologically similar to *N.gen.1 bertholletii* in the shape of the vibracular chamber, but is distinct from it in branching pattern of scutum, absence of distolateral avicularia, and in the presence of elongate frontal avicularia and ooecia with tubular pores.

Distribution. Caribbean Sea: Gulf of Mexico, Aruba Island, Bermuda, Bonaire, Colombia, Curaçao and Puerto Rico; from 0–66 meters depth.

***N.gen.1 n.sp.1* (Vieira & Spencer Jones) n. comb.**

(Figure 3.6, Table 3.2)

Scrupocellaria n.sp.1 Vieira & Spencer Jones, unpublished (see Chapter 1).

Remarks. *N.gen.1 n.sp.1* has been misidentified as *Scrupocellaria reptans* by some authors, but VIEIRA & SPENCER JONES (unpublished data) distinguished *N.gen.1 n.sp.1* by the presence of smooth rhizoids, stouter scuta and by the size of oecial pores, smaller in *N.gen.1 n.sp.1* than those of *N.gen.1 reptans*.

Distribution. Widespread in Northeast Atlantic to North Sea; Adriatic; Tasmania.

***N.gen.1 hirsuta* (Jullien & Calvet, 1903) n. comb.**

(Figures 3.7–3.8, Table 2)

Acamarchis hirsuta Jullien & Calvet, 1903: 35, pl. 1, figs. 3a–c. [Azores Archipelago]

Scrupocellaria hirsuta Jullien & Calvet: Norman, 1909: 284. [Madeira Island]

Material Examined. *Lectotype*. MOM 420323 (Figure 7A–B), dry, *Scrupocellaria hirsuta*, Jullien & Calvet det., Campagnes Scientifiques du Principe de Monaco, *Hirondelle*, Station 226, 1888, Fosse de Fayal, Pico of Fayal (Azores), 130 meters. *Paralectotypes*. MOM 420323, dry (2 colonies), same data as lectotype. *Additional specimens*. NHMUK 2012.7.1.1 (Figure 7C–F), dry, *Scrupocellaria hirsuta*, L.M. Vieira det., Campagnes Scientifiques du Principe de Monaco, *Hirondelle*, Station 569, 1895, Azores, 27 meters. NHMUK 1911.10.1.386 (Figure 8), *Scrupocellaria hirsuta*, A.M. Norman det., A.M. Norman Collection, Madeira Island. NMNH Osburn-19, balsam slide, *Scrupocellaria hirsuta*, R.C. Osburn det., 1936, Castle Island, Bermuda, 20 feet (6 meters).

Diagnosis. Chitinous joints passing across the gymnocyst in outer zooids at the bifurcation (zooids C and D); 7 regularly spaced and very long distal spines; scutum absent; small distolateral avicularium present in each zooid, obscured by outer oral spines, directed latero-distally; dimorphic frontal avicularium aquiline, directed forward; vibraculum with trapezoidal chamber on basal surface of each zooids; ooecium with some large rounded pores.

Description. Colony erect, branched, with branches comprising 5–9 alternated zooids. Internodes slender, slightly curved, angled at the axis, with an acutely bifurcating pattern; chitinous joints pass across the gymnocyst in both outer (zooids C and D) and inner zooids (zooids F and G) at the bifurcation. Autozooids cylindrical, tapering proximally. Oval opesia occupying three quarters of the zooidal length; cryptocyst reduced to a very narrow and often inconspicuous rim around the opesia. Distal spines very long, unbranched; 7 regularly spaced distal spines, with most proximal spines directed forward; rarely 1–2 distal spines absent. Scutum absent. Very small distolateral avicularium obscured by outer oral spines. Frontal avicularia dimorphic: a small aquiline avicularium directed forwards or rarely obliquely to the axis of the autozooid, close to inner proximal margin of the opesia; large frontal avicularium anquiline, rostrum serrated, about 0.140 mm long, directed forward or slightly downward, mandible triangular and hooked distally. Large vibracular chamber on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a rhizoidal foramen at its outer proximal corner; setal groove directed transversely, straight, with smooth setae longer than two autozooids. Single

axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with some large rounded pores; ovicelled zooids with 1–2 inner and 3 outer spines.

Remarks. *N.gen.1 hirsuta* is quite distinct from other *N.gen.1* species by the absence of scuta, the presence of zooids with seven long and well-spaced distal spines, a very small distolateral avicularium obscured by outer oral spines and joints which pass across the midpoint of the gymnocyst in outer zooids at the branch bifurcation. JULLIEN & CALVET (1903) described 4 distal spines in this species, but the type specimens have 7 distal spines (rarely 5–6 spines) in non-ovicelled zooids, with 4–5 spines in ovicelled zooids. This species was reported by NORMAN (1909) from Madeira. A single specimen from Bermuda was found in the NMNH collection; this specimen was identified as *Scrupocellaria hirsuta* by Osburn (unpublished data) and has the same morphological characteristics as those of the Madeira and Azores specimens.

Distribution. Atlantic Ocean: Bermuda, Azores and Madeira Islands; from 6–130 meters depth.

***N.gen.1 macrorhyncha* (Gautier, 1962) n. comb.**

(Figure 3.9, Table 3.2)

Cellularia reptans Linnaeus: Waters, 1879: 117. [Naples]

Not *Sertularia reptans* Linnaeus, 1758, p. 815. [?United Kingdom]

Scrupocellaria macrorhyncha Gautier, 1962: 90, fig. 12. [Mediterranean]

Scrupocellaria macrorhynchus Prenant & Bobin, 1966: 412 (part), fig. 135.I (not figs. 135.II–VI). [Mediterranean]

Material Examined. *Lectotype* (chosen here). NHMUK 1965.9.2.4 (Figure 3.9), *Scrupocellaria macrorhyncha*, Y.V. Gautier Collection, Mediterranean, Station 258. *Additional specimens*. NHMUK 1874.4.25.34, *Cellaria reptans*, A.W. Waters det., A.W. Waters Collection, 40 fath. (73 meters), Naples (Secca), Italy, Mediterranean. NHMUK 1975.1.12.434, *Scrupocellaria macrorhyncha*, P.J. Hawyard det., Chios, Aegean Sea, Station 57.

Diagnosis. Chitinous joints passing across the proximal end of opesia in zooids C and D at the bifurcation; zooids alternated, with adjacent zooids slightly back-to-back, forming an angle at the axis of the branches; 2 inner and 2–3 outer distal spines; large stout scutum, highly branched at its tip, fully developed and completely covering the whole opesia; small distolateral avicularium obscured by outer oral spines;

dimorphic frontal avicularia elongate with hooked tip; vibracular chamber on basal surface of zooids, almost lateral; ooecium with small rounded pores.

Redescription. Colony erect, branched, with branches comprising 9–21 alternated zooids. Internodes slender, almost straight, angled at the axis, with acute bifurcating pattern; chitinous joints pass across the proximal opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids cylindrical with straight sides. Oval opesia occupying three quarters of the zooidal length; cryptocyst reduced to a narrow rim around the opesia. Large scutum inserted at the midline of inner edge of opesia, stout, highly branched at its tip, fully developed and completely covering the whole opesia. Distal spines short, unbranched; 2 inner and 3–4 outer spines, with outer distal spines closer to the scutum; axial zooid with 5 spines. Very small distolateral avicularium rarely present and obscured by outer oral spines. Frontal avicularia dimorphic: a very small avicularium with triangular mandible often present in inner zooids of each internode, close to the inner proximal opesial margin; large frontal avicularia with elongate mandible often present in outer zooids of each internode; elongate rostrum, 0.264–0.290 mm long, with fringed edge, proximally directed and with strongly hooked tip; mandible long and hooked distally. Vibracular chamber laterally placed on the basal surface of each zooid, conspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a proximal rhizoidal foramen; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with slightly raised and straight proximal rim; ectooecium perforated by 12–19 small rounded pores; ovicelled zooids with 2 inner and 2 outer spines.

Remarks. GAUTIER (1962) noted morphological similarities between *N.gen.1 macrorhyncha* and *N.gen.1 reptans*, but distinguished them by number of zooids per internode (shorter in *N.gen.1 reptans*), colony shape (erect in *N.gen.1 macrorhyncha*), number of oral spines (six spines in *N.gen.1 macrorhyncha* versus four or five in *N.gen.1 reptans*), shape of frontal avicularia (longer and proximally directed in *N.gen.1 macrorhyncha*), position of vibracular chamber and surface of ooecium. The specimen of Gautier (GAUTIER, 1962: fig. 12; see Figure 3.9) deposited at the Natural History Museum, London (NHMUK 1965.9.2.4) is here designated lectotype. The specimen named *Scrupocellaria macrorhyncha* by PRENANT & BOBIN (1966: figs. 135.II–VI) has the same number of oral spines, but is quite distinct in the shape of frontal avicularia

and in its wider branches; this specimen requires reexamination and probably belongs to a different species.

Two other specimens deposited at the NHMUK are here assigned to *N.gen.1 macrorhyncha*: a specimen identified by HAYWARD (1974) under name *Scrupocellaria macrorhyncha* from Chios (Aegean Sea) (NHMUK 1975.1.12.434) and the specimen misidentified as *Cellularia reptans* (NHMUK 1874.4.25.34; labeled as *Cellaria reptans*) from Naples by WATERS (1879).

Distribution. Mediterranean (Naples, Golf of Marseille, Scilly and Tunisia) and Aegean Sea; from 1–80 meters depth.

***N.gen.1 reptans* (Linnaeus, 1758) n. comb.**

(Figure 3.10, Table 3.2)

Sertularia reptans Linnaeus, 1758: 815; 1767: 1315. [No Locality, but possibly United Kingdom]

Scrupocellaria reptans Linnaeus: Vieira & Spencer Jones.

Remarks. VIEIRA & SPENCER JONES (unpublished data) gave a complete redescription of this species, with additional remarks on the differences between *N.gen.1 reptans* and the widespread *N.gen.1 n.sp.1*. *N.gen.1 reptans* is quite distinct by virtue of a more slender scutum than those of *N.gen.1 n.sp.1* and the presence of hooked rhizoids.

Distribution. North Atlantic: United Kingdom.

***N.gen.1 tenuirostris* (Osburn, 1950) n. comb.**

(Figure 3.11, Table 3.3)

Scrupocellaria bertholetii var. *tenuirostris* Osburn, 1950: 134, pl. 18, fig. 8, pl. 21, fig. 6. [California and Costa Rica]

Material examined. *Paratype*. SBMNH 96148, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, Allan Hancock Foundation n. 32.2, R.C. Osburn Collection, Allan Hancock Pacific Expedition Station 255, 520-35, 25°31’0” N, 111°1’45” W, Gulf of California, 27.ii.1936. *Additional material*. AMNH 1506.1, Santa Clara Point, Missin Bay, California, 18.ii.1991. NHMUK 2010.10.5.1 (Figure 3.11), L.M. Vieira det., B. Okamura & P. Taylor leg., viii.2010, San Diego, California. NMNH 10344, Gulf Lower California, Angelus Bay, Mexico. NMNH 10350, Gulf Lower California, San Francisquito Bay, Mexico. NMNH Osburn-08, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, University of Southern California, Corona del Mar, California, 30.xii.1944, low tide. NMNH Osburn-09, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, University of Southern California, Allan Hancock Pacific Expedition Station 253-34. NMNH Osburn-56, balsam slide, *Scrupocellaria*

bertholleti var. *tenuirostris*, R.C. Osburn Collection, Allan Hancock Pacific Expedition, Station 775-38. NMNH Osburn-57, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, Newport Harbor, California. NMNH 10343, *Scrupocellaria* sp., Gulf Lower California, Angelus Bay, Mexico. VMNH 13105, *Scrupocellaria tenuirostris*, Judith E. Winston det., SERC 07750, San Diego, California, 2000, L. McCann col., intertidal.

Diagnosis. Chitinous joints passing across the proximal opesia in zooids C and D at the bifurcation; zooids with 2 inner and 2–3 outer distal spines; scutum slender, branched 3–4 times, with 8–16 sharp tips; large distolateral avicularium in each zooid; dimorphic frontal avicularia with lanceolate mandibles; ooecium wider than long, with several rounded pores.

Redescription. Colony erect, highly branched, with branches comprising 5–9 zooids. Internodes almost straight, acute bifurcating pattern with new branches directed slightly inward; chitinous joints pass across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, subrectangular, slightly narrower proximally than distally. Oval opesia occupying more than three-fifths of the zooidal length; smooth cryptocyst reduced to a very narrow strip around the opesia border. Slender scutum inserted at the midline of inner opesial border, branched 3–4 times, with 8–16 (often 10) sharp tips, and covering most of the frontal membrane. Distal spines slightly curved and long, unbranched; 2 inner and 2–3 outer spines, often 1 median spine; axial zooid with 5–6 distal spines. Conspicuous distolateral avicularium present in each zooid, directed laterally; rostrum triangular, 0.051–0.070 mm long, with a serrated lateral edge and slightly hooked tip. Frontal avicularia dimorphic: a small frontal avicularium with a triangular rostrum; large frontal avicularium with an elongate rostrum, 0.213–0.286 mm long, raised and compressed laterally, with a deep curved groove directed downward at axis of internode, between the adjacent series of autozooids; mandible very long and narrow, lanceolate and curved laterally. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, with rhizoidal foramen on its proximal outer corner; setal groove directed transversally, with smooth setae longer than one autozooid length. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some retroussé hooks. Ovicells subglobose with abruptly deep edge, with ectooecium perforated by 15–22 medium sized rounded pores; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. *N.gen.1 tenuirostris* is quite distinct from other known *N.gen.1* in the presence of unique frontal avicularia having an elongate rostrum with a lanceolate

mandible directed downward along the axis. The original description and illustration of this species given by OSBURN (1950) differ slightly from specimens here described and figured, including the specimens of the R.C. Osburn Collection deposited at the NMNH and SBMNH, in having wider vibracular chambers than those figured by OSBURN (1950, plate 21, fig. 6).

Distribution. Eastern Pacific Ocean: California to Costa Rica.

Remarks on other known species

***N.gen.1 nanshaensis* (Liu, 1991) n. comb.**

Scrupocellaria nanshaensis Liu, 1991: 70, figs. 5A–B. [China: Nansha Island]

Remarks. Liu (1991) characterized *N.gen.1 nanshaensis* as having autozooids with a curved outline, narrower proximally than distally, opesia with a granular cryptocyst, 5–6 oral spines (2 inner, 2–3 outer and 1 median distal spine), robust scuta bifurcated 3–5 times (without internal cavities), the presence of a small distolateral avicularium on each zooid, no frontal avicularia and segmented rhizoids. The frontal avicularia are also absent in *N.gen.1 serrata* from Red Sea, but neither lateral avicularia nor basal vibracula are found in this species. The presence of granular cryptocyst and segmented rhizoids in *N.gen.1 nanshaensis* are quite distinct from other known species of *N.gen.1*.

Distribution. China (Nansha Island).

***N.gen.1 serrata* (Waters, 1909) n. comb.**

Scrupocellaria serrata Waters, 1909: 133, pl. 10, figs. 11–14. [Red Sea]

Remarks. WATERS (1909) described and figured a new species, *Scrupocellaria serrata,* from the Red Sea. This species is characterized by zooids with 1 inner and 2 outer distal spines, spine-like, sometimes branched scuta, no basal vibracula, serrated rhizoids, and neither frontal nor lateral avicularia, except in ovicelled zooids where distolateral avicularia with large bi- or trifurcated rostra are present.

N.gen.1 serrata is distinct in the absence of lateral avicularia in non-ovicelled zooids, ovicelled zooids with large bi- to trifurcated avicularia, and the absence of basal vibracula. The shape of large lateral avicularia have been described for four *Scrupocellaria* species: *Scrupocellaria obtecta* Haswell, 1880 (see MACGILLIVRAY, 1886: pl. 126, fig. 5), *Scrupocellaria talonis* Osburn, 1950 (see OSBURN, 1950: pl. 17,

fig. 3), *Scrupocellaria unguiculata* Osburn, 1950 (see OSBURN, 1950: pl. 17, figs. 1–2), and *Scrupocellaria varians* (Hincks, 1882) (see HINCKS, 1882: pl. 19, figs. 1a–b). Both *S. obtecta* and *S. unguiculata* are distinct from the present species by their rounded scuta. *Scrupocellaria talonis* specimens are distinct through their smooth rhizoids, zooids with dimorphic lateral avicularia, the usual presence of 1 inner and 1 outer orificial spines (sometimes these spines are absent) and the inner edge of opesia rarely with a vestigial spine-like scutum; no ovicells were found in specimens described by OSBURN (1950). The scutum and gigantic lateral avicularia of *S. varians* resemble those described for *N.gen.1 serrata*, but *S. varians* is quite distinct in having small lateral avicularia, basal vibracula and ovicells with single fenestrate ectooecium.

Distribution. Red Sea.

Description of new taxa

N.gen.1 n.sp.2

(Figure 3.12, Table 3.3)

Material Examined. *Holotype*. NHMUK 1963.8.2.16 (Figure 3.12), *Scrupocellaria reptans*, C.H. O'Donoghue det., C.H. O'Donoghue Collection, 17–20 fms (31–37 meters), Alexandria, Egypt, Stan. 7, 66.

Type locality. Alexandria, Egypt.

Diagnosis. Chitinous joints passing across the gymnocyst and below the opesia in zooids C and D at the bifurcation; zooids with 2 inner and 3–4 outer distal spines; scutum stout and flattened, branched 3 times, overarching almost of the frontal membrane; no distolateral avicularia; frontal avicularia monomorphic, large, with rostrum directed forward and to midline of the branches; ovicells with some rounded pores linked by internal sutures.

Description. Colony erect, branched, fan-shaped, with branches comprising 5–13 zooids. Internodes almost straight, with adjacent zooids positioned slightly back to back in alternate series; chitinous joints pass across the gymnocyst and below opesia of outer zooids at the bifurcation (zooids C and D), and across the proximal end of inner zooids (zooids F and G). Autozooids almost cylindrical, slightly narrower proximally than distally, with a slightly curved outline in basal view. Oval opesia occupying three fifths of the zooidal length; cryptocyst, smooth, very narrow, forming a deep strip around the opesia. Scutum large, stout, flattened, branched three times, inserted at midline of inner edge of the opesia, and occupying almost the whole frontal

membrane. Distal spines short, un-branched; 2 inner and 3–4 outer distal spines; most distal outer and inner spines smaller than proximal ones; most proximal spines directed forward; axial zooid with 6 spines. Lateral avicularia absent. Frontal avicularia monomorphic, very large, 0.152–0.185 mm long, with acute mandible, serrated laterally with hooked tip, with one side slightly down-curved; mandible long, hooked distally, directed forward to the inner side of the internode and forming a right angle with the adjacent zooid of the branch. Vibracular chamber slightly lateral on basal surface of each zooid, sometimes conspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a large proximal rhizoidal foramen; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells subglobular; ectooecium perforated by 12–22 rounded pores linked by radial sutures; ovicelled zooids with 2 inner and 2–3 outer spines.

Remarks. Among the specimens deposited at the NHMUK assigned to *Scrupocellaria reptans* we examined a robust and fan-shaped colony from Alexandria identified by C.H. O'Donoghue, here assign to *N.gen.1 n.sp.2*. This colony resembles *N.gen.1 reptans* and *N.gen.1 n.sp.1* by the shape of zooids and frontal scuta, but *N.gen.1 n.sp.2* is distinct by absence of lateral avicularia, presence of monomorphic frontal avicularia with longer rostrum and zooids often having 4 outer distal spines.

Distribution. Mediterranean: Egypt (Alexandria); between 31–40 meters depth.

N.gen.1 n.sp.3

(Figure 3.13, Table 3.3)

Material Examined. *Holotype*. NHMUK 2010.12.6.1 (Figure 3.13), *Scrupocellaria reptans*, O'Donoghue det., C.H. O'Donoghue Collection, Arisaig, Scotland, United Kingdom.

Type locality. Arisaig, Scotland.

Diagnosis. Chitinous joints passing across the gymnocyst in zooids C and D at the bifurcation; zooids with 6 distal spines; the most distal spine slender and shorter than the outer and inner ones; scutum stout and flattened, branched 3–4 times, occupying almost the whole frontal membrane; no distolateral avicularia; frontal avicularia monomorphic, variable in size and with rostrum directed proximo-medially; rhizoids with short-spaced retrousée hooks.

Description. Colony erect, branched, with branches comprising 5–9 zooids. Internodes with alternated zooids, slightly curved; chitinous joints pass across the

gymnocyst in both outer (zooids C and D) and inner zooids (zooids F and G) at the bifurcation. Autozooids almost cylindrical, tapering proximally and with slightly curved outline in basal view. Oval opesia occupying half to three fifths of the zooidal length; cryptocyst very narrow and inconspicuous, forming a double band of calcification around the opesia. Large, stout, flattened scutum, branched 3–4 four times, inserted at the midline of inner opesial border and occupying almost the whole frontal membrane. Distal spines long, unbranched; 6 equally spaced distal spines, with second outer spine longer and stouter than other ones; the most distal spine shorter than outer and inner spines; the most proximal spines directed slightly forward; axial zooid with 6 spines. Lateral avicularium absent. Frontal avicularia monomorphic with an acute and slightly curved rostrum of variable size, serrated laterally and with a hooked tip; mandible triangular, hooked distally and directed forward. Vibracular chamber slightly lateral on basal surface of each zooid, sometimes conspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a proximal rhizoidal foramen; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with several short-spaced retroussé hooks. Ovicells not observed.

Remarks. *N.gen.1 n.sp.3* resembles *N.gen.1 reptans* in the shape of scutum and the presence of rhizoids with retrousée hooks, but differs in the presence of longer spines, stouter frontal scuta, absence of distolateral avicularia and the smaller distance between hooks on rhizoids. *N.gen.1 n.sp.2* is also characterized by absence of lateral avicularia, but differs from *N.gen.1 n.sp.3* by shape of frontal avicularia.

Distribution. United Kingdom: west coast of Scotland (Arisaig).

N.gen.1 n.sp.4

(Figure 3.14, Table 3.3)

Material Examined. *Holotype*: MZUSP no number, São Paulo, Brazil (Figure 3.14A–D). *Additional material*. VMNH 10403.0000 (Figure 3.14E–F), *Scrupocellaria bertholleti*, J.E. Winston col., pilings of dock, A1A, Little Jim Island Fish Camp, Indian River Lagoon channel, North Beach, Fort Pierce, St. Lucie County, Florida, USA, 18 February 1993, 0–1 m; VMNH 10861.0000, *Scrupocellaria* sp., J.E. Winston col., Coon Island, North Beach, Fort Pierce, St. Lucie County, Florida, USA, 3 July 1998; VMNH 11036.0000, *Scrupocellaria bertholleti*, J.E. Winston col., Walton Rocks, South Hutchinson Island, St. Lucie County, Florida, USA, 19 February 1999, intertidal; VMNH 11058.0000, *Scrupocellaria bertholleti*, J.E. Winston col., Sebastian Beach, N. Side of Wabasso Causeway (Rte 510), Indian River Lagoon, Florida, USA,

21 February 1999; VMNH 11093.0000, *Scrupocellaria bertholleti*, J.E. Winston col., N. Beach Causeway, E. side of 1st bridge, Indian River, Fort Pierce, St. Lucie County, Florida, USA, 8 April 1999; VMNH 11103.0000, *Scrupocellaria bertholleti*, J.E. Winston col., Johnson Seagrass bed, HBO1, Fort Pierce, St. Lucie County, Florida, USA, 7 April 1999; VMNH 11952.0000, *Scrupocellaria bertholleti*, J.E. Winston & N. Tuross col., E. side of North Beach bridge, Route A1A, Indian River, Fort Pierce, St. Lucie County, Florida, USA, 20 April 2000; VMNH 12717.0000, *Scrupocellaria bertholleti*, J.E. Winston col., South Beach, south side of inlet, Fort Pierce Inlet, St. Lucie County, Florida, USA, 21 July 1999, intertidal; VMNH 12784.0000, *Scrupocellaria bertholleti*, J.E. Winston col., North Beach, south side of inlet, Fort Pierce, St. Lucie County, Florida, USA, 31 June 2001, intertidal; VMNH 13143.0001, *Scrupocellaria bertholleti*, J.E. Winston col., off South Beach, *Mellita* site #1, Fort Pierce, St. Lucie County, Florida, USA, 31 July 2002, 6 meters, dredge; VMNH 13303.0000, *Scrupocellaria bertholleti*, J.E. Winston col., East side of S. A1A Causeway, South Beach, Fort Pierce, St. Lucie County, Florida, USA, 02 July 2002, intertidal; VMNH 13471.0000, *Scrupocellaria bertholleti*, J.E. Winston col., Fort Pierce Inlet, S. Side beach near Historical Museum, beach drift, 14 July 2003, on drift plastic.

Type locality. São Paulo, Brazil.

Diagnosis. Chitinous joints passing across the opesia in outer zooids at the bifurcation (zooids C and D); opesia occupying almost the whole frontal surface; 2 inner and 2–3 outer distal spines, but just 3 distal spines in axial zooid; scutum flattened, regularly branched 3 times, occupying two third of the frontal membrane; small distolateral avicularium present in each zooid; ooecium with some regularly spaced rounded pores.

Description. Colony erect, branched, with branches comprising 5–9 zooids. Lateral edge of internodes almost straight; chitinous joints pass across the opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids almost elongate, slightly tapering proximally, with smooth proximal gymnocyst. Oval opesia occupying almost the whole zooidal length, cryptocyst narrower laterally than proximally, sometimes inconspicuous. Scutum branched 3 times, with 5–8 sharp tips, inserted at the midline of inner opesial border and occupying two third of the whole frontal membrane. Distal spines unbranched; 2–3 outer and 2 inner spines; axial zooid with 3 distal spines. One distolateral avicularium present on each zooid, conspicuous, 0.046–0.070 mm long, directed laterally, rostrum triangular with slightly serrated lateral edge, mandible triangular. Frontal avicularia often small, 0.046–0.070 mm long, triangular, obliquely directed forward. A very large avicularium present on gymnocyst of some zooids, often present on axial zooid, aquiline with raised tubular base, rostrum serrated laterally,

slightly curved and directed forward and downward; mandible triangular with hooked tip. A basal vibracular chamber found proximally on basal surface of each zooid, inconspicuous in frontal view; setal groove directed transversally, straight, with smooth setae longer than one autozooid. Single axial vibraculum. A rhizoidal foramen on proximal outer corner of vibracular chamber, absent in axial vibracula. Rhizoids smooth, present in proximal portion of the colony. Ovicell hemispherical, with 15–22 rounded and regularly spaced pores; ovicelled zooids with 2 outer and 2 inner distal spines.

Remarks. This species is commonly found on algae and drift plastics in South-Southeast Brazil. The specimens from Florida previously identified as *Scrupocellaria bertholletii* (Figure 3.14E–F; J.E. Winston, unpublished data) are similar from those here described as *N.gen.1 n.sp.4* by number of oral spines, shape of scuta, position and size of basal vibracula. However, the gigantic avicularia in Florida specimens is often present on zooids at the internode, while it is present on axial zooids in Brazilian colonies. Despite the small differences in position of the gigantic frontal avicularia between USA and Brazilian specimens, we assigned specimens from Florida and Brazil to *N.gen.1 n.sp.4* due presence of chitinous joints passing across the opesia in outer zooids at the bifurcation, 4–5 distal spines in each zooids (except by axial zooids, characterized by 3 distal spines), shape of scutum, presence of distolateral avicularium and shape of frontal avicularia.

N.gen.1 n.sp.4 is similar to two Pacific species, *N.gen.1 n.sp.9* and *N.gen.1 n.sp.19*, in the position of joints at the bifurcation, shape of the frontal scutum and presence of a distolateral avicularium on each zooid. *N.gen.1 n.sp.4* is quite distinct by presence of 5 distal spines, smaller basal vibraculum and shape and position of frontal avicularia.

Distribution. Atlantic Ocean: USA (Florida) and Brazil (Rio de Janeiro, São Paulo and Paraná states); from intertidal to 7 meters depth.

N.gen.1 n.sp.5

(Figure 3.15, Table 3.4)

Material Examined. *Holotype*. MNHN 15979 (Figure 3.15), *Scrupocellaria* sp., RV 'Calypso', Station 29, Recife, Brazil, 8°28'S, 34°55'W, 21 November 1961, 22–30 meters. *Paratypes*. NHMUK no number, RV 'Calypso', Station 29, Recife, Brazil, 8°28'S, 34°55'W, 21 November 1961, 22–30 meters. *Additional material*. NMHN no number. United States Exploring Expedition, Rio de Janeiro, Brazil.

Type locality. Recife, Pernambuco, Brazil.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); 2 inner and 3 outer distal spines (rarely 1 additional medial spine), but 5–6 spines in axial zooid; opesia occupying two thirds of the zooidal length; scutum slender, regularly branched 2 times, occupying half of the opesial membrane length; distolateral avicularia absent; frontal avicularia dimorphic; very large and elongate avicularia often present, lanceolate, with curved and serrated rostrum.

Description. Colony erect, branched, with branches comprising 5–11 zooids. Internodes slight curved, with an acutely bifurcating pattern; chitinous joints pass across the proximal end of the opesia of outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to two thirds of the zooidal length; cryptocyst minimal and deep around the opesia. Scutum inserted at the midline of inner opesial border, regularly branched two times at 50–80 degrees, with sharp tips and reaching more than midline of the frontal membrane. Distal spines delicate, long, unbranched; 2 inner and 3 outer distal spines, 1 median distal spine rarely present; most proximal outer spines directed forward; axial zooid with 5–6 spines. Distolateral avicularium absent. Frontal avicularia dimorphic: small frontal avicularium with triangular mandible; large frontal avicularium, 0.209–0.274 mm long, with lanceolate, curved and serrated rostrum proximally directed and with a curved tip; mandible long, curved and hooked at its tip. A vibracular chamber present on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost circular, with large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, straight, with smooth setae as long as one autozooid length. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some short spaced retroussé hooks. Ovicells subglobular, with ectooecium perforated by 9–18 rounded pores with raised edges; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. *N.gen.1 n.sp.5* is similar to four Atlantic species, *N.gen.1 curacaoensis*, *N.gen.1 n.sp.6*, *N.gen.1 n.sp.12* and *N.gen.1 n.sp.17*, in the position of the joints, slender scutum and absence of distolateral avicularia. *N.gen.1 n.sp.5* is quite distinct through the presence of the very long dimorphic frontal avicularium and the twice regularly bifurcated, sharp tipped scutum.

Distribution. Atlantic Ocean: Brazil (Pernambuco and Rio de Janeiro state); from 22–30 meters depth.

N.gen.1 n.sp.6

(Figure 3.16, Table 3.4)

Scrupocellaria bertholletii Audouin: Osburn, 1940: 386 (in part). [Tortugas]

Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*: NHMUK 2010.12.6.2 (Figure 3.16), *Scrupocellaria bertholletii*, Colman & Tendy Collection, Dry Tortugas, Florida, USA. *Paratypes*: NHMUK 1931.12.19.3–4, *Scrupocellaria bertholletii*, Colman & Tendy Collection, Dry Tortugas, Florida, USA. NHMUK 1931.12.19.4pt, *Scrupocellaria bertholletii*, Colman & Tendy Collection, Dry Tortugas, Florida, USA. NHMUK 1935.11.26.1, *Scrupocellaria bertholletii*, R.C. Osburn det., 2 fms (about 4 meters), Tortugas, Florida, USA.

Type locality. Tortugas, Florida, USA.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); two inner and two or three outer distal spines; scutum forked, rarely trifurcated, often bifurcating at its tip with very sharp ends; distolateral avicularia absent; vibracular chamber rounded and small; rhizoid with retroussé hooks; ooecium with rounded pores with raised edges.

Description. Colony erect, branched, with branches comprising 3–11 zooids. Internodes slightly curved, with acute bifurcating pattern; chitinous joints pass across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of the inner zooids (zooids F and G). Autozooids elongate, tapering proximally and slightly curved laterally. Oval opesia occupying distal half of the zooidal length; inconspicuous cryptocyst around the opesia. Scutum bifurcated at a 60–90 degree angle, rarely trifurcated, reaching more than the midline of the frontal membrane, often bifurcating at its tips, inserted at the midline of the inner opesial border. Distal spines short, unbranched; 2 inner and 2–3 outer distal spines, rarely 1 median distal spine; most proximal outer spines directed toward opercular area; axial zooid with 5–6 distal spines. Distolateral avicularium absent. Frontal avicularia dimorphic: small frontal avicularium with triangular mandible; large frontal avicularium with triangular curved rostrum proximally directed and with hooked tip, mandible slightly curved and hooked distally. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost circular, with large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some retroussé hooks.

Ovicells globular, with ectooecium perforated by 10–17 rounded pores with raised edges; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. *N.gen.1 n.sp.6* resembles *N.gen.1 n.sp.5*, *N.gen.1 curacaoensis*, *N.gen.1 n.sp.12* and *N.gen.1 n.sp.17* in having zooids without distolateral avicularia, but differs in possessing a bifurcated scutum with forked distal tips, robust dimorphic avicularium and ovicells with rounded pores with raised edges.

Distribution. Atlantic Ocean: USA (Florida: Tortugas); from shallow waters.

N.gen.1 n.sp.7

(Figure 3.17, Table 3.4)

Scrupocellaria bertholletii Audouin: Hastings, 1930: 703 (in part), pl. 1, fig. 3 (non figs. 1, 2, 4, 5). [Galapagos Island]

Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*. NHMUK 2010.12.6.3 (Figure 3.17), *Scrupocellaria bertholletii*, A.B. Hastings det., 25.vii.1924, St. George Collection, Galapagos 1, Specimen 42S, James Island, James Bay, Galapagos. *Paratypes*. NHMUK 1924.4.26.243, *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Galapagos 8, Specimen 3H. NHMUK 1924.4.26.17, same data as the holotype. NHMUK 1924.4.26.286, same data as the holotype. NHMUK 1924.4.26.20, *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Galapagos 11, Specimen 36D[1] (figured by Hastings 1930: pl. 1, fig. 3) and Specimen 36D[2], Tagus Cove, 12 fms.

Type locality. Galapagos Island.

Diagnosis. Chitinous joints passing across the proximal end of opesia in both outer zooids at the bifurcation (zooids C and D); zooids with 3 inner and 4 outer distal spines; scutum slender, branched 3 times and with 8–15 sharp points; large distolateral avicularium in each zooid; dimorphic frontal avicularium with triangular mandible, obliquely directed along the axis of the internode; ooecium globular, with deep proximal border and several rounded pores.

Description. Colony erect, highly branched, with branches comprising 7–11 zooids. Internodes robust with curved outlines, zooids alternating slightly back to back; acute bifurcating pattern with new branches directed slightly inwards; chitinous joints pass across the proximal end of opesia and on cryptocyst in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, subrectangular, slightly more narrowed proximally than distally. Oval opesia occupying almost the whole zooidal length;

cryptocyst smooth, deep, forming a wide and conspicuous strip around the opesia. Scutum slender, inserted at the midline of inner opesial border, branched 3–4 times with 8–15 (often 8–10) sharp points, covering almost the whole frontal membrane. Distal spines straight and long, unbranched; 3 inner and 4 outer distal spines; axial zooid with 7 spines. One conspicuous distolateral avicularium present in each zooid, laterally directed, rostrum triangular, 0.060–0.077 mm long, with serrated lateral edge and slightly hooked tip. Frontal avicularia dimorphic: a small frontal avicularium with triangular rostrum; a large frontal avicularium with triangular serrated rostrum, obliquely directed to the axis. A vibracular chamber present on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, occupying a third of the basal surface, with rhizoidal foramen on its proximal outer corner; setal groove directed transversely, with smooth setae twice of autozooidal length. Single axial vibraculum, almost triangular, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, deeper proximally than distally, with ectooecium perforated by several rounded pores; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. HASTINGS (1930) reported *Scrupocellaria bertholletii* from Pacific (Gorgona Island and Galapagos) and noted variable morphology among these specimens. Despite the differences noted by her—scuta, frontal avicularia and shape of the zooid—the Pacific specimens have shared characteristics, such as the shape and size of basal vibraculum, lateral avicularium and ovicells. Among Hastings's specimens studied deposited at the NHMUK we found three distinct species: specimens with highly branched scuta (specimen 36D, from Galapagos, see HASTINGS 1930, p. 703) are described as *N.gen.1 n.sp.7*, while the specimens with slender zooids and less branched scuta, from Gorgona and Galapagos, comprise two distinct species, *N.gen.1 n.sp.9*, with scutum bifurcated twice, and *N.gen.1 n.sp.10*, with forked scutum (sometimes absent) and robust dimorphic avicularia.

Distribution. Pacific Ocean: James Island and Tagus Cove, Galapagos Island.

N.gen.1 n.sp.8

(Figure 3.18, Table 3.4)

?*Scrupocellaria macrorhyncha*: Zabala i Limosin, 1986: 318, fig. 88, pl. 3, figs. A, B, D. [Mediterranean]

Not *Scrupocellaria macrorhyncha* Gautier, 1962: 89, fig. 12. [Mediterranean]

Material Examined. *Holotype*. NHMUK 1882.5.24.9 (Figure 3.18), *Scrupocellaria reptans*, R. Kirkpatrick det., P.H. Carpenter leg., Porcupine Expedition, 30–120 fms (54–220 meters), Skensi Banki, Algeria. *Paratypes*. NHMUK 1882.5.24.8–12, same data as the holotype.

Type locality. Algeria.

Diagnosis. Chitinous joints passing across the proximal end of opesia in both outer zooids at the bifurcation (zooids C and D); zooids tubular, with 6 well-spaced distal spines; scutum large and stout, highly branched at its tip, fully developed and completely covering the frontal membrane; small distolateral avicularium obscured by outer oral spines often present; dimorphic frontal avicularium elongate with hooked tip; basal vibraculum larger than those of *N.gen.1 macrorhyncha*.

Description. Colony erect, branched, with branches comprising 5–9 zooids. Internodes stout, almost straight, with acute bifurcating pattern; chitinous joints pass across the proximal opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids cylindrical with parallel sides. Oval opesia occupying three quarters of the zooidal length; cryptocyst reduced to a narrow strip around opesia. Large scutum, robust and branched at its tip, fully developed, inserted at the midline of inner opesial border and covering the whole frontal membrane. Six regularly spaced distal spines, unbranched: 2 inner and 3–4 outer spines. Very small distolateral avicularium rarely present and obscured by outer distal spines. Dimorphic frontal avicularia present: a small avicularium with a triangular mandible present in inner zooids of each internode, close to the inner proximal border of the opesia; a large frontal avicularium with an elongate mandible present in outer zooids of each internode, rostrum longer than wide, 0.206–0.244 mm long, serrated, directed proximally and with strongly hooked tip, mandible long and hooked distally. Vibracular chamber placed on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, large, with a proximal rhizoidal foramen; setal groove directed transversely, straight, with smooth setae long as one autozooid length. Single axial vibraculum small, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells not observed.

Remarks. *N.gen.1 n.sp.8* is similar to *N.gen.1 macrorhyncha* in the shape of scuta, frontal avicularia and distolateral avicularia, but differs from it in the number of the zooids in each internode (shorter in *N.gen.1 n.sp.8* than *N.gen.1 macrorhyncha*), the presence of 6 regularly spaced distal spines and larger basal vibracula than those of *N.gen.1 macrorhyncha*. *N.gen.1 n.sp.14*, from Australia, is distinct from *N.gen.1 n.sp.8* in the zooid size, and in having dimorphic frontal avicularia and more slender

scuta. *N.gen.1 n.sp.18* resembles *N.gen.1 n.sp.8* in the shape of frontal scuta, but differs by the presence of large frontal avicularia.

Distribution. Mediterranean: Algeria; from 54–220 meters depth.

N.gen.1 n.sp.9

(Figure 3.19, Table 3.4)

Scrupocellaria bertholletii Audouin: Hastings, 1930: 703 (in part), (non pl. 1, figs. 1–5). [Gorgona Island]

Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*. NHMUK 2010.12.6.4 (Figure 3.19), *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Gorgona 3, Specimen 15D. *Paratypes*. NHMUK 1929.4.26.19, same data as the holotype. NHMUK 2010.12.6.5, same data as the holotype. NHMUK 2010.12.6.6, same data as the holotype. NHMUK 2010.12.6.7, same data as the holotype. *Additional specimens*. NHMUK 1929.4.26.18, same data as the holotype. NHMUK 1929.4.26.18pt, same data as the holotype.

Type locality. Gorgona, Panama.

Diagnosis. Chitinous joints passing across the opesia in outer zooids at the bifurcation (zooids C and D); zooids with 2 inner and 3–4 outer distal spines; one median distal spine sometimes present; scutum slender, branched two times; small distolateral avicularium present in each zooid; dimorphic frontal avicularium with triangular curved mandible, directed forward and slightly downward; ooecium globular, with several rounded pores linked by internal sutures.

Description. Colony erect, highly branched, with branches comprising 5–9 zooids. Internodes with alternated zooids, slightly back to back, pattern acutely bifurcating; chitinous joints pass across the opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, subrectangular, slightly tapering proximally. Oval opesia occupying distal two thirds of the zooidal length; crytptocyst smooth, deep, forming a strip around the opesia. Scutum slender, inserted at the midline of inner opesial border, branched two times and with sharp tips, covering less than half the area of frontal membrane. Distal spines straight and long, often broken, unbranched; 2 inner and 3–4 outer distal spines, a median distal spine often present; axial zooid with 5 spines. One inconspicuous distolateral avicularium present in each zooid, 0.033–0.051 mm long, laterally directed, obscured by the outer spines and ovicells; rostrum triangular, with serrated lateral edge and slightly hooked tip. Variably sized frontal avicularium present

in outer zooids along the internodes, with triangular curved rostrum and mandible, directed obliquely forward and downward. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, occupying one quarter of basal surface, with rhizoidal foramen on its proximal outer corner; setal groove directed transversely, with smooth setae twice autozooidal length. Single axial vibraculum almost triangular, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with ectooecium perforated by several rounded pores linked by internal sutures; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. Part of HASTING's (1930) specimens are identified here as *N.gen.1 n.sp.9*; this species resembles *N.gen.1 n.sp.10* in its overall appearance, but differs by the shape of the frontal scutum—bifurcated two times in *N.gen.1 n.sp.9* and forked in *N.gen.1 n.sp.10*—and the shape and size of frontal and distolateral avicularia.

Distribution. Pacific Ocean: Panamá (Gorgona Island).

N.gen.1 n.sp.10

(Figure 3.20, Table 3.5)

Scrupocellaria bertholletii Audouin: Hastings, 1930: 703 (in part), pl. 1, figs. 1, 2, 4, 5. (non pl. 1, fig. 3). [Galapagos Island]

Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*. NHMUK 2010.12.6.8 (Figure 3.20), *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Galapagos 9, Specimen 31F, Tagus Cove, Albemarle Island, Galapagos. *Paratypes*: NHMUK 1929.4.26.244, same data as the holotype, but Specimen 8E (figured by Hastings 1930: pl. 1, fig. 2, 4, 5). NHMUK 1929.4.26.25, same data as the holotype, but Specimen 31F[1]. NHMUK 2010.12.6.9–12, same data as the holotype. NHMUK 2010.12.6.13, same data as the holotype, but Specimen 31F[1]. NHMUK 2010.12.6.14, same data as the holotype, but Specimen 31F[2]. NHMUK 2010.12.6.15, same data as the holotype, but Specimen 1G (figured by Hastings 1930: pl. 1, fig. 1). *Additional specimens*. NHMUK 1929.4.26.228pt, *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Galapagos 10, Specimen 43C[1–2], Tagus Cove, Galapagos. NHMUK 1929.4.26.24pt, same data as the holotype, but Specimen 7E[1–2].

Type locality. Galapagos Island.

Diagnosis. Chitinous joints passing across the opesia in outer zooids at the bifurcation (zooids C and D); zooids with 1–2 inner and 2–3 outer distal spines; 5 distal spines in axial zooid; scutum sometimes present, slender, bifurcated (rarely trifurcated); large distolateral avicularium present in each zooid; dimorphic frontal

avicularium aquiline with elongate base, triangular mandible directed forward; ooecium globular, with several rounded pores.

Description. Colony erect, branched, with branches comprising 5–11 zooids. Internodes with alternated zooids, slightly back to back; acute bifurcating pattern; chitinous joints pass across the opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, almost rectangular, slightly tapering proximally. Oval opesia occupying three quarter of the zooidal length; cryptocyst smooth, wide and deep around the opesia. Slender scutum sometimes present, inserted at the midline or slightly distal at the inner opesial border, bifurcated (rarely trifurcated), with sharp points and slightly directed downwards, overarching part of the frontal membrane. Distal spines often broken, unbranched; 1–2 inner and 2–3 outer distal spines; axial zooid with 5 distal spines. One conspicuous avicularium present in outer distal corner of each zooid, 0.061–0.092 mm long, directed laterally; rostrum triangular with serrated lateral edge and slightly hooked tip. Frontal avicularia dimorphic: small avicularia triangular with slightly serrated edges, obliquely directed downward and positioned below the opesia; large aquiline avicularium, occupying majority of gymnocyst, directed forward, mandible triangular and hooked. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, occupying a quarter of basal surface, with a large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, with smooth setae as long as an autozooid. Single axial vibraculum almost trapezoidal, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, flattened proximally than distally, with ectooecium perforated by several funnel-shaped pores linked by internal sutures; ovicelled zooids with 1–2 inner and 2 outer spines.

Remarks. Part of the specimens from the Galapagos Islands identified as *Scrupocellaria bertholletii* by HASTINGS (1930) are here assigned to *N.gen.1 n.sp.10*. The second species from Galapagos, *N.gen.1 n.sp.7*, is quite distinct from *N.gen.1 n.sp.10* in having a highly branched scutum, a wider basal vibraculum, and by the shape and position of frontal avicularia.

Distribution. Pacific Ocean: Tagus Cove, Galapagos Islands.

N.gen.1 n.sp.11

(Figure 3.21, Table 3.5)

Scrupocellaria bertholletii Audouin: Kluge, 1914: 616, text-fig. 6. [Cape Verde Island]

Scrupocellaria bertholletii Audouin: Waters, 1918: 5. [Cape Verde Island]
Non *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*. NHMUK 2010.12.6.16 (Figure 3.21A–B,E–F), *Scrupocellaria bertholletii*, C. Crossland Collection, S. Vicent, Cape Verde Island. *Paratypes*. NHMUK 1899.7.1.837 (Figure 3.21C–D), *Canda bertholletii*, G. Busk det., G. Busk Collection, St. Vicent, Cape Verde Island. NHMUK 2010.10.1.7, same data as the holotype. NHMUK 2010.10.1.8, *Scrupocellaria bertholletii*, St. Vicente, Cape Verde Island. *Additional specimens*. NHMUK 1899.7.1.821, *Scrupocellaria bertholletii*, G. Busk det., G. Busk Collection, 1857, Madeira Island.

Type locality. Cape Verde Island.

Diagnosis. Chitinous joints passing across the opesia in outer zooids at the bifurcation (zooids C and D); zooids with 7 long and regularly spaced distal spines; scutum slender, branched two times (rarely bifurcated at its tip), with 4–7 sharp tips; a small distolateral avicularium often present in each zooid, obliquely directed and obscured by outer spines; dimorphic frontal avicularium aquiline, obliquely directed forward and slightly downward; ooecium globular with some rounded pores.

Description. Colony erect, branched, with branches comprising 5–9 (often 7) zooids. Internodes with biserial alternate zooids with curved outlines; chitinous joints pass across the opesia in outer zooids at the bifurcation (zooids C and D) and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, subrectangular, slightly narrower proximally than distally. Oval opesia occupying two thirds of the zooidal length; cryptocyst smooth, forming a conspicuous strip around the opesia, often better developed proximally than laterally. Scutum slender, inserted at the midline of inner opesial border, branched two times with sharp points, rarely bifurcated at its tips, ovearching up to the midline of the opesia. Distal spines straight and long, unbranched; 7 regularly spaced distal spines; axial zooid with 7 spines; the most proximal inner and outer spines directed forward. One small and inconspicuous distolateral avicularium often present on each zooid, directed laterally and slightly upward, often obscured by outer distal spines; rostrum triangular, with a serrated lateral edge. Frontal avicularia dimorphic: a small frontal avicularium with triangular rostrum and mandible, obliquely directed downward; a large frontal avicularium with an aquiline rostrum, directed forward and slightly downward, mandible triangular, slightly curved. A vibracular chamber present on the basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, occupying a third of basal surface, with a large rhizoidal foramen on its proximal outer corner; setal groove directed transversely, with smooth

setae as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with ectooecium perforated by some rounded pores; ovicelled zooids with 3 inner and 3 outer spines.

Remarks. WATERS (1918) noted the difference in size of avicularia between *Scrupocellaria bertholletii* specimens from Cape Verde Island collected by Cyril Crossland and specimens from Mediterranean. These island specimens, here described as *N.gen.1 n.sp.11*, are characterized in having zooids with 7 long and regularly spaced distal spines, in the shape of branched scutum, and in the size and position of distolateral avicularia. The specimens reported from Cape Verde by KLUGE (1914) also belong to *N.gen.1 n.sp.11*.

Distribution. Atlantic Ocean: Madeira and Cape Verde Islands.

N.gen.1 n.sp.12

(Figure 3.22, Table 3.5)

Material Examined. *Holotype*. AMNH 1522.1, *Scrupocellaria* sp., J.E. Winston det., Rio Bueno, Jamaica, 10 meters, J.B.C. Jackson coll., 1978. *Paratypes*. AMNH 1524.1, Jamaica; AMNH 1529.1, *Scrupocellaria bertholletii*, J.E. Winston det., Drunkenmans Cay, Jamaica, J.B.C. Jackson coll., 1978. *Additional specimens*. AMNH 1521B.1, *Scrupocellaria bertholletii*, J.E. Winston det., Discovery Bay, Jamaica, J.B.C. Jackson coll., 1978.

Type locality. Rio Bueno, Jamaica.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); zooids with 1–2 inner and 2–3 outer distal spines, an additional median distal spine often present; scutum bi- or trifurcated, occupying a small part of the frontal membrane; distolateral avicularium absent; dimorphic frontal avicularium elongate, longer than wide, almost lanceolate; vibracular chamber almost rounded and small; ooecium longer than wide, with some raised pores.

Redescription. Colony erect, branched, with branches comprising 5–11 zooids. Internodes with biserial zooids in alternated series; chitinous joints pass across the proximal end of opesia (rarely below it) in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate with a tapering proximal gymnocyst. Oval opesia occupying distal half of the zooidal length; cryptocyst very narrow, inconspicuous around the opesia. Scutum often present, bifurcated or rarely trifurcated, inserted at the midline of inner opesial border and reaching more than midline of the frontal membrane. Distal spines long,

unbranched, delicate; 1–2 inner and 2–3 outer distal spines, rarely 1 median distal spine; most proximal inner and outer spines directed forward; axial zooid with 5 spines. Distolateral avicularium absent. Frontal avicularia dimorphic: a small frontal avicularium with triangular mandible, directed forward; large frontal avicularium sometimes present, 0.155–0.190 mm long, with an elongate downward directed rostrum close to adjacent zooid, its edge serrated and with a lanceolate mandible, hooked distally. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost circular, occupying a small part of the basal area, with large rhizoidal foramen on its proximal outer corner; setal groove short, directed transversely, straight, with smooth setae as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some well-spaced retroussé hooks. Ovicells longer than wide, with raised and striate transversal bands of raised pores; 2 inner and 3 outer distal spines in ovicelled zooids.

Remarks. *N.gen.1 n.sp.12* resembles *N.gen.1 n.sp.5*, *N.gen.1 curacaoensis* and *N.gen.1 n.sp.6* by absence of distolateral avicularia, but differs by shape of dimorphic frontal avicularium and scutum.

Distribution. Caribbean: Jamaica.

N.gen.1 n.sp.13

(Figure 3.23, Table 3.5)

Material Examined. *Holotype*. NHMUK 1975.7.18.31 (Figure 3.23), *Scrupocellaria bertholletii*, R. Lagaaij det., 04.iv.1970, St. Raphael, Boulouris, France, Mediterranean.

Type locality. Boulouris, France.

Diagnosis. Chitinous joints passing across the gymnocyst and below the opesia in outer zooids at the bifurcation (zooids C and D); zooids with 5–6 distal spines; scutum slender, slightly flattened, branched two times, occupying most of the frontal membrane; distolateral avicularia absent; frontal avicularia monomorphic, with an elongate base, rostrum directed forwards and covering the proximal part of the opesia of some zooids.

Description. Colony erect, branched, with branches comprising 5–9 zooids. Internodes with alternated zooids, slightly curved; chitinous joints pass across the gymnocyst and below the opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids almost cylindrical, tapering proximally. Oval opesia occupying half to three fifths of the zooidal length; cryptocyst narrow, deep and smooth, more strongly developed

proximally than laterally. Scutum slender, slightly flattened, branched two times, inserted at the midline of inner opesial border and occupying most of the frontal membrane. Distal spines long, unbranched; 3 outer and 2 inner distal, an additional median distal spine sometimes present; most proximal spines directed slightly forward; axial zooid with 6 regularly spaced spines. Lateral avicularium absent. Frontal avicularia monomorphic, but of variable size, present on surface of third and axial zooid of the branch, shape almost aquiline with a raised base, placed on proximal edge of the opesia, rostrum directed forward, mandible triangular, hooked distally. One vibracular chamber on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a proximal rhizoidal foramen; short setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells not observed.

Remarks. *N.gen.1 n.sp.13* is quite distinct from other species here described and figured in the shape of the frontal avicularium, characterized by a raised base and covering proximal part of the opesia, and in having a scutum regularly branched two times. This species resembles *N.gen.1 n.sp.15*, from Mozambique, in absence of distolateral avicularia and overall appearance of zooids, but differs in the shape of frontal avicularia, size of the scutum and in its wider cryptocyst.

Distribution. Mediterranean: South of France.

N.gen.1 n.sp.14

(Figure 3.24, Table 3.5)

Material Examined. *Holotype*. NHMUK 2010.12.6.19 (Figure 3.24), Brisbane, Queensland, Australia. *Paratype*. NHMUK 2010.12.6.20, same data as the holotype.

Type locality. Queensland, Australia.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); 2 inner and 2–3 outer distal spines; scutum stout, large, highly branched at its tip, fully developed and completely covering the frontal membrane; small distolateral avicularium sometimes present, obscured by the outer oral spines; dimorphic frontal avicularium elongate with hooked tip, shorter than those in *N.gen.1 macrorhyncha*; vibracular chamber almost basal rather than lateral as in *N.gen.1 macrorhyncha*; ooecium with small rounded pores.

Description. Colony erect, branched, with branches comprising 5–11 alternated zooids, with zooidal surfaces in the same plane. Internodes slender, almost

straight, with an acutely bifurcating pattern; chitinous joints pass across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids cylindrical, with straight sides. Oval opesia occupying three quarters of the zooidal length; cryptocyst reduced to a narrow often inconspicuous rim around the opesia. Scutum large, stout, flattened, highly branched at its tip, fully developed, inserted at midline of inner opesial border and overarching the whole frontal membrane. Distal spines short, unbranched and curved; 2 inner and 3 outer spines; 1 additional median distal spine often present; axial zooid with 5 spines. Very small distolateral avicularium rarely present, obscured by outer distal spines. Dimorphic frontal avicularia present: a very small avicularium with triangular mandible often present in inner zooids of the internode close to the proximal margin of opesia, obliquely directed below to the midline of the zooids; a large frontal avicularium, 0.165–0.220 mm long, with an elongate mandible often present in outer zooids of each internode, rostrum longer than wide with a fringed edge, directed proximally and with strongly hooked tip, mandible long and hooked distally. One vibracular chamber on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a rhizoidal foramen at its outer proximal corner; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum, small, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with proximal slightly raised straight rim, ectooecium perforated by 14–22 small rounded pores; ovicelled zooids with 1 inner and 2 outer spines.

Remarks. *N.gen.1 n.sp.14* resembles *N.gen.1 macrorhyncha* by its overall appearance, but differs in size of the branches, position of zooids along the branches (slightly angled in *N.gen.1 macrhoryncha*), position of basal vibraculum (basal and inconspicuous on frontal view in *N.gen.1 n.sp.14*) and size of dimorphic frontal avicularium (smaller in *N.gen.1 n.sp.14* than *N.gen.1 macrorhyncha*).

Distribution. Pacific Ocean: Queensland, Australia.

N.gen.1 n.sp.15

(Figure 3.25, Table 3.6)

Material Examined. *Holotype*. NHMUK 2010.12.6.17 (Figure 3.25), *Scrupocellaria bertholletii*, Dr. Y.J. Hinde Collection, Mozambique. *Paratypes*. NHMUK 1938.5.2.4, same data as the holotype. NHMUK 2010.12.6.18, same data as the holotype.

Type locality. Mozambique.

Diagnosis. Chitinous joints passing across the gymnocyst and below opesia in outer zooids at the bifurcation (zooids C and D); zooids with 3 outer and 1–2 inner distal spines; scutum slender and flattened, branched two times, sometimes forked at its tips, occupying half to two thirds of the zooidal length; distolateral avicularia absent; frontal avicularia variable in size, aquiline; ovicell with some small pores linked by internal sutures.

Description. Colony erect, branched, with branches comprising 5–11 zooids. Internodes with alternated zooids, slightly curved, with new branches directed inward. Chitinous joints pass across the gymnocyst in both outer (zooids C and D) and inner zooids (zooids F and G) at the bifurcation. Autozooids almost cylindrical, tapering proximally. Oval opesia occupying half to three fifths of the zooidal length; cryptocyst deep and smooth, forming a very narrow strip around opesia. Scutum slender, flattened, branched two times and sometimes forked at its tips, inserted at the midline of inner opesial border and occupying half to one third of the frontal membrane. Distal spines unbranched; 3 outer and 1–2 inner distal; most proximal spines directed slightly forward; axial zooid with 5 spines: 2 lateral pairs and 1 median distal. Distolateral avicularium absent. Frontal avicularia monomorphic, of variable size, aquiline with slightly curved rostrum directed forward; mandible triangular and curved, hooked distally. Vibracular chamber sometimes present on the basal surface of the zooid, inconspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a rhizoidal foramen at its outer proximal corner; setal groove directed transversely, straight, with smooth setae longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells almost globular, with some regularly spaced pores linked by internal sutures; ovicelled zooids with 2 outer and 1 inner distal spines.

Remarks. *N.gen.1 n.sp.15* resembles *N.gen.1 n.sp.13* in shape of autozooids, position of joints, and number of distal spines, but differs in the shape of frontal avicularia and the size of frontal scutum.

Distribution. Indian Ocean: Mozambique.

N.gen.1 n.sp.16

(Figure 3.26, Table 3.6)

Scrupocellaria bertholletii Audouin: Marcus, 1938: 24 (in part; non pl. 5, figs. 11A–B). [Brazil: São Paulo]

Non *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material Examined. *Holotype*. NHMUK 2010.12.6.28 (Figure 26), *Scrupocellaria bertholletii*, E. Marcus det., Santos, São Paulo, Brazil. *Paratype*. NHMUK 1948.2.16.46, same data as the holotype.

Type locality. São Paulo, Brazil.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); 1 inner and 3 outer distal spines; 3–4 four spines in axial zooid; opesia occupying two third of zooidal length; scutum slender, regularly branched two times, occupying half of frontal membrane length; distolateral avicularia absent; frontal avicularia dimorphic; very large and elongate avicularia often present, triangular in shape, with curved smooth edged rostrum.

Description. Colony erect, branched, with branches comprising 5–9 zooids. Internodes slight curved, with acute bifurcating pattern; chitinous joints pass across the proximal end of opesia of outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to two thirds of the frontal wall; cryptocyst minimal around the opesia. Scutum regularly branched two times at acute angles, with sharp tips, reaching more than the midline of the frontal membrane, inserted at the midline of inner opesial border. Distal spines delicate, long, unbranched; 1 inner and 3 outer distal spines; most proximal outer and inner spines directed forward; axial zooid with 3–4 spines. Distolateral avicularium absent. Dimorphic frontal avicularia present: small frontal avicularium with triangular mandible, rostrum directed forward; large frontal avicularium with high base, triangular and curved rostrum directed forward and slightly downward, with a curved tip; mandible long, curved and hooked at its tip. A small vibracular chamber present on the basal surface of each zooid, inconspicuous in frontal view; the chamber of vibraculum almost circular, with a small rhizoidal foramen on its proximal outer corner; setal groove directed transversely, straight, with smooth setae the length of one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with some short spaced retroussé hooks. Ovicells subglobular, with ectooecium perforated by 9–18 rounded pores with raised edges; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. Under the name *Scrupocellaria bertholletii* MARCUS (1938) figured specimens from Santos (São Paulo, Brazil), characterized by zooids with bifurcated frontal scuta and by the presence of distolateral avicularia (see MARCUS, 1938: pl. 5, figs. 11A–B). In description of his specimens, however, he mentioned a variation in the shape of the scutum (sometimes trifurcate) and the presence of a very large frontal avicularium with a high base in some zooids; these characteristics were observed in

specimens deposited at bryozoan collection in NHMUK (NHMUK 1948.2.16.46 and NHMUK 2010.12.6.28). However, these specimens are also distinct from figured specimens from Santos by the absence of distolateral avicularia.

Distribution. Atlantic Ocean: Brazil (São Paulo); about 20 meters depth.

N.gen.1 n.sp.17

(Figure 3.27, Table 3.6)

Scrupocellaria reptans Linnaeus: Norman, 1909: 283. [Madeira Island]

Not *Sertularia reptans* Linnaeus, 1758, p. 815. [?United Kingdom]

Material Examined. *Holotype*. NHMUK 1911.10.1.355 (Figure 3.27), *Scrupocellaria reptans*, A.M. Norman det., A.M. Norman Collection, 1897, Madeira Island.

Type locality. Madeira Island.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); 6–7 distal spines, but 5 spines in axial zooid; scutum slender, flattened, regularly branched three times, occupying entire frontal membrane; distolateral avicularium absent; frontal avicularia dimorphic, with a small avicularium directed upwards and forwards and a large avicularium, longer than wide, directed obliquely forward and downward; ovicells longer than wide, with some pores linked by internal sutures.

Description. Colony erect, branched, with branches comprising 5–11 zooids. Internodes straight, with acute bifurcating pattern; chitinous joints pass across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying half to three fifths of the zooidal length; vestigial and inconspicuous cryptocyst around the opesia. Scutum present, regularly branched three times and occupying whole frontal membrane, inserted at the midline of the inner opesial border and overarching the frontal membrane. Distal spines long, unbranched; 6–7 distal spines, the most proximal outer and inner spines directed forward; axial zooid with 5 spines. Distolateral avicularium absent. Dimorphic frontal avicularia present: a small frontal avicularium with a triangular mandible; a large frontal avicularium with an elongate and curved rostrum, 0.177–0.203 mm long, directed downward and forward, with curved tip, mandible long, curved and hooked distally. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, with large rhizoidal foramen on its proximal outer corner; setal groove directed transversally, straight, with smooth setae as longer

as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular with some spaced retroussé hooks. Ovicells long than wide, with ectooecium perforated by some rounded pores linked by internal sutures; ovicelled zooids with 2 inner and 3 outer spines.

Remarks. NORMAN (1909) reported *S. reptans* from Madeira Island based on a part of colony from Funchal. However, comparison between this specimen deposited at the NHMUK and *S. reptans* revealed morphological differences—absence of lateral avicularia, shape of frontal avicularia and scuta—which led us to assign the Madeira specimens to a new undescribed species, *N.gen.1 n.sp.17*. *N.gen.1 n.sp.17* is quite distinct from other species of *N.gen.1 bertholletii-reptans* complex by virtue of the shape of its frontal avicularia and scutum.

Distribution. Atlantic Ocean: Madeira Island.

N.gen.1 n.sp.18

(Figure 3.28, Table 3.6)

Material Examined. *Holotype*. NHMUK 2010.12.6.21 (Figure 3.28), *Scrupocellaria reptans*, C.H. O'Donoghue det., C.H. O'Donoghue Collection, Gairloch, Scotland, United Kingdom. *Paratype*. NHMUK 2010.12.6.22, same data as the holotype.

Type locality. Gairloch, Scotland.

Diagnosis. Chitinous joints passing across the gymnocyst in outer zooids at the bifurcation (zooids C and D); zooids almost tubular, slightly tapering proximally, with 3 outer and 2 inner distal spines; scutum large, stout, highly branched and curving at its tip, fully developed and completely covering the opesia; distolateral avicularium present in each zooid, placed behind the outer oral spines; monomorphic aquiline frontal avicularia; basal vibraculum sometimes present; ovicells with some frontal pores linked by internal sutures.

Description. Colony erect, branched, fan-shaped, with branches comprising 5 (rarely 7) zooids. Internodes stout, almost straight, with acutely bifurcating pattern; chitinous joints pass across the gymnocyst in both outer (zooids C and D) and inner zooids (zooids F and G) at the bifurcation. Autozooids cylindrical, tapering proximally. Oval opesia occupying half to three fifths of the zooidal length; cryptocyst forming a very narrow rim around the opesia. Scutum large, robust and stout, branched and curved at its tip, fully developed, inserted at midline of inner opesial border and overarching whole frontal membrane. Five distal spines, unbranched and curved; 2 inner and 3 outer spines, with most proximal outer and inner spines directed forward. A

small distolateral avicularium present in each zooid, obscured by outer oral spines. A large aquiline frontal avicularium often present on gymnocyst of the outer zooids of internodes, rostrum with serrated edge, directed forward, with a triangular and hooked mandible. Vibracular chamber often present, placed on the basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, large, with a proximal rhizoidal foramen; setal groove directed transversely, straight, with smooth setae long as one autozooid. Single axial vibraculum small, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with some rounded pores linked by internal sutures.

Remarks. *N.gen.1 n.sp.18* resembles *N.gen.1 n.sp.8*, *N.gen.1 macrorhyncha* and *N.gen.1 n.sp.14* in its stout and branched frontal scutum, but differs by presence of an aquiline rather than elongate frontal avicularium.

Distribution. United Kingdom: Scotland.

N.gen.1 n.sp.19

(Figure 3.29, Table 3.1)

Material Examined. *Holotype*. NHMUK 2010.6.14.3 (Figure 29), Panama.

Type locality. Panama.

Diagnosis. Chitinous joints passing across the proximal end of opesia in outer zooids at the bifurcation (zooids C and D); zooids with 6–7 distal spines; scutum slender, branched three times and with sharp tips; small distolateral avicularium present in each zooid; frontal avicularia variable in size, with triangular mandible, obliquely directed downward.

Description. Colony erect, branched, with branches comprising 5–7 zooids. Internodes with alternated zooids, slightly back to back; acutely bifurcating pattern; chitinous joints pass across the proximal end of opesia in both outer zooids at the bifurcation (zooids C and D), and across the proximal gymnocyst of inner zooids (zooids F and G). Autozooids elongate, subrectangular, slightly tapering proximally. Oval opesia occupying three quarters of frontal surface; cryptocyst smooth and deep, forming a narrow strip around the opesia. Scutum slender, branched three times and with very sharp points, inserted at the midline of inner opesial border and overarching part of the frontal membrane. Distal spines straight to slightly curved, long, delicate, unbranched; 2–3 inner and 4 outer distal spines; axial zooid with 6 spines. One conspicuous distolateral avicularium present in each zooid, directed laterally; rostrum

triangular, with serrated lateral edges and a slightly hooked tip. Frontal avicularia variable in size, present in outer zooids along the internodes, with a triangular curved rostrum, serrated, with short hooked tip, directed obliquely forward and downward. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, occupying a quarter of basal surface, with a rhizoidal foramen on its proximal outer corner; setal groove directed transversally, with smooth setae as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells not observed.

Remarks. *N.gen.1 n.sp.19* resembes *N.gen.1 n.sp.4* by position of joints at the bifurcation, that pass across the the opesia in outer zooids, shape of frontal scutum and presence of distolateral avicularium; however, this species differs by number of distal spines (6–7 in non-ovicelled zooids) shape and position of frontal avicularia. *N.gen.1 n.sp.9* is distinct from *N.gen.1 n.sp.19* in its very large frontal avicularia and wide cryptocyst around the opesia.

Distribution. Pacific Ocean: Panama.

KEY TO SPECIES OF *N.GEN.1*

1 Scutum absent in whole colony; distal spines as long as an autozooid ..…….. *N.gen.1 hirsuta*
- Scutum present, at least in ovicelled zooids; distal spines shorter than an autozooid ……..… 2

2 Frontal avicularia absent 3
- Frontal avicularia present 4

3 Lateral avicularia absent; scutum single o branched 1–2 times; rhizoids with hooks ..... *N.gen.1 serrata*
- Lateral avicularia present; scutum branched more than 3 times; rhizoids segmented ..... *N.gen.1 nanshaensis*

4 Lateral avicularia absent 5
- Lateral avicularia present in few or all zooids ……..... 15

5 Scutum absent in few zooids; when present, scutum forked or trifurcated 6
- Scutum present in all zooids, forked with bifurcated tips to hightly branched 7

6 Dimorphic frontal avicularia with aquiline rostrum, large ones two times larger than small ones; most proximal outer spines overarching opercular area ..... *N.gen.1 curacaoensis*
- Dimorphic frontal avicularia with elongate rostrum, three times larger or more than single ones; most proximal outer spines directed forwards *N.gen.1 n.sp.12*

7 Scutum forked, with branched distal tips *N.gen.1 n.sp.6*
- Scutum branched three times or more 8

8 Dimorphic frontal avicularia with elongate rostrum 9
- Dimorphic frontal avicularia aquiline 10

9 Scutum branched 2 times, with sharp tips; scutum occupying about half opesial area; 5–6 distal spines *N.gen.1 n.sp.5*
- Scutum branched 3 times, with truncate tips; scutum occupying whole opesial area; 6–7 distal spines *N.gen.1 n.sp.17*

10 Joints passing across opesia in outer zooids at the bifurcation; 3–4 distal spines *N.gen.1 n.sp.16*
- Joints passing across gymnocyst in outer zooids at the bifurcation; 4 or more distal spines 11

11 Rhizoids with some shortly spaced retroousé hooks *N.gen.1 n.sp.3*
- Rhizoids with smooth surfarce 12

12 Scutum wide, occupying more than 2/3 of whole frontal membrane *N.gen.1 n.sp.2*
- Scutum slend, occupying 2/3 or less than whole frontal membrane 13

13 Frontal avicularia with raised base *N.gen.1 n.sp.13*
- Frontal avicularia with stout base *N.gen.1 n.sp.15*

14 Lateral avicularia laterally directed 14
- Lateral avicularia directed obliquely upward 21

15 Rhizoids with some retrouseé hooks; dimorphic frontal avicularia elongate, with lanceolate mandible and directed downwards ..... *N.gen.1 tenuirostris*
- Rhizoids with smooth surface; dimorphic frontal avicularia aquiline, with triangular mandible 16

16 Scutum sometimes present in some zooids of the colony; scutum forked 17
- Scutum present in all zooids; scutum branched 2 or more times 18

17 Scutum short, occupying half of opesial width; ooecium with rounded pores; cryptocyst vestigial, often inconspicuous at the proximal edge of the opesia ..... *N.gen.1 bertholletii*
- Scutum long, reaching the lateral outer margin of the opesia; ooecium with funel-shaped pores; cryptocyst well developed around opesia *N.gen.1 n.sp.10*

18 Scutum occupying more than two third of opesial area *N.gen.1 n.sp.7*
- Scutum occupying less than half of the opesial area 19

19 Cryptocyst well developed around the opesia *N.gen.1 n.sp.9*
- Cryptocyst narrow proximally, sometimes inconspicuous 20

20 Axial zooid with 3 distal spines; other zooids with 5 distal spines …….. *N.gen.1 n.sp.4*
- Axial zooid with 5 distal spines; others zooids with 6–7 distal spines *N.gen.1 n.sp.19*

21 Scutum hightly branched, with flat frontal surface 22
- Scutum stout, branched at its tips 24

22 Joints passing across opesia in outer zooids at the bifurcation *N.gen.1 n.sp.11*
- Joints passing across gymnocyst in outer zooids at the bifurcation 23

23 Rhizoids with some retroussé hooks ..... *N.gen.1 reptans*
- Rhizoids with smooth surface *N.gen.1 n.sp.1*

24 Joints passing across gymnocyst in outer zooids at the bifurcation; dimorphic aquiline frontal avicularia *N.gen.1 n.sp.18*
- Joints passing across gymnocyst in outer zooids at the bifurcation; dimorphic elongate frontal avicularia 25

25 Internodes very long, with 9–21 autozooids; frontal surfaces of adjacent zooids not in the same plane, with angle between them ..... *N.gen.1 macrorhyncha*
- Internodes short, with less than 9 autozooids; frontal surface of adjacent zooids in the same plane 26

26 Internodes stout, with zooids 0.193–0.221 mm wide *N.gen.1 n.sp.8*
- Internodes flat frontally, 0.148–0.191 mm wide *N.gen.1 n.sp.14*

DISCUSSION

Shared morphological features among some species previously assigned to *Scrupocellaria*, i.e. unbranched otal spines, trapezoidal vibracular chamber, presence of single axial vibracula, porous ectooecium and branched scutum, led us to erect the new genus *N.gen.1*. Besides the difference in shape of scutum, which is characteristically branched in *N.gen.1*, all species of this genus have porous ectooecium as those described for *Licornia* van Beneden, 1850 (VIEIRA *et al.*, unpublished data) and other species assigned to the genus *Scrupocellaria*, *e.g. Scrupocellaria curvata* Harmer, 1926, *Scrupocellaria frondis* Kirkpatrick, 1890, *Scrupocellaria sinuosa* Canu & Bassler, 1927 and *Scrupocellaria hamata* Tilbrook & Vieira, *in press* (see TILBROOK & VIEIRA, *in press*). The genus *Licornia* is distinct by the shape of the basal vibracula, with oblique setal groove, such as those found in *S. curvata*, *S. sinuosa* and *S. hamata*. *Scrupocellaria frondis* is also characterized by basal trapezoidal vibracula, but this species differs from *N.gen.1* by the presence of paddle-shaped to oval scutum and absence of dimorphic frontal avicularia.

To clarify the taxonomic status and establish the identity of the Egyptian species described by AUDOUIN (1826), we have selected a Mediterranean specimen deposited at the NHMUK as neotype of *N.gen.1 bertholletii*. The main diagnostic feature of this species is the shape of the scutum, i.e. short and forked (when present), as for those figured by SAVIGNY (1817) and which is distinct from the other species of the genus. Eigth species previously assigned to *Scrupocellaria* are reassigned to the new genus *N.gen.1*—i.e. *N.gen.1 curacaoensis*, *N.gen.1 n.sp.1* (see Chapter 1), *N.gen.1 hirsuta*, *N.gen.1 macrorhyncha*, *N.gen.1 nanshaensis*, *N.gen.1 reptans*, *N.gen.1 serrata* and *N.gen.1 tenuirostris*—and 18 species are newly described.

The main morphological features distinguishing among the species of *N.gen.1* were found in the position of the joints at the bifurcation, shape of scuta, shape and position of dimorphic frontal avicularia, presence and position of sessile lateral avicularia, and size of basal vibracular chamber. Among the species included here, in 11 species the lateral avicularia are absent: *N.gen.1 n.sp.2*, *N.gen.1 n.sp.3*, *N.gen.1 n.sp.5*, *N.gen.1 curacaoensis*, *N.gen.1 n.sp.6*, *N.gen.1 n.sp.12*, *N.gen.1 n.sp.13*, *N.gen.1 n.sp.15*, *N.gen.1 n.sp.16*, *N.gen.1 n.sp.17* and *N.gen.1 serrata*. In eigth species, the lateral avicularia are sometimes absent in the zooids: *N.gen.1 n.sp.1*, *N.gen.1 n.sp.8*, *N.gen.1 hirsuta*, *N.gen.1 n.sp.11, N.gen.1 macrorhyncha*, *N.gen.1 n.sp.14*, *N.gen.1 n.sp.18* and *N.gen.1 reptans*; when present, the avicularium has rostrum directed latero-distally and it is obscured by outer lateral spines or ooecia.

The utilization of SEM and comparison of specimens deposited in different museums aided in redefining these morphological features to distinguish species previously assigned to *Scrupocellaria*. The main diagnostic characteristics among species include the position of the joints at the bifurcation, the number of distal spines, the branching pattern of the scutum, the presence and position of lateral avicularia and the shape of frontal avicularia. Morphologically, it is possible to distinguish two groups of *N.gen.1* species based on the shape of frontal scuta: (i) species with stout scutum and truncate tips, which include 8 species found on the British coast, the North Sea, the Mediterranean and Eastern Australia (*N.gen.1 macrorhyncha*, *N.gen.1 n.sp.1*, *N.gen.1 n.sp.2*, *N.gen.1 n.sp.3*, *N.gen.1 n.sp.8*, *N.gen.1 n.sp.14*, *N.gen.1 n.sp.18* and *N.gen.1 reptans*) and (ii) species with slender scutum with sharp tips, which includes the majority of species.

The majority of *N.gen.1* species are known from tropical to subtropical waters, with four species known for temperate waters of northeast Atlantic and North Sea (Figure 3.30). Sometimes several species co-exist in the same area. Twenty three species of *N.gen.1* are reported in tropical and subtropical areas: five species are recorded in eastern Pacific waters; eight species are reported only in the Atlantic; four species are reported in the Mediterranean; four species are reported in the Indo-West Pacific; and one species is reported as widespread in the Suez Canal, the Mediterranean and the Atlantic. Some species which until now have been reported as widespread, i.e. *N.gen.1 reptans*, actually have a more restricted distribution.

The high number of new species described here and the very restricted distribution of some of the them, sometimes being known from a unique locality, suggest that much remains to be discovered about the geographic distribution of these taxa and indicates that some new species of *N.gen.1* may be expected in poorly sampled areas of the world.

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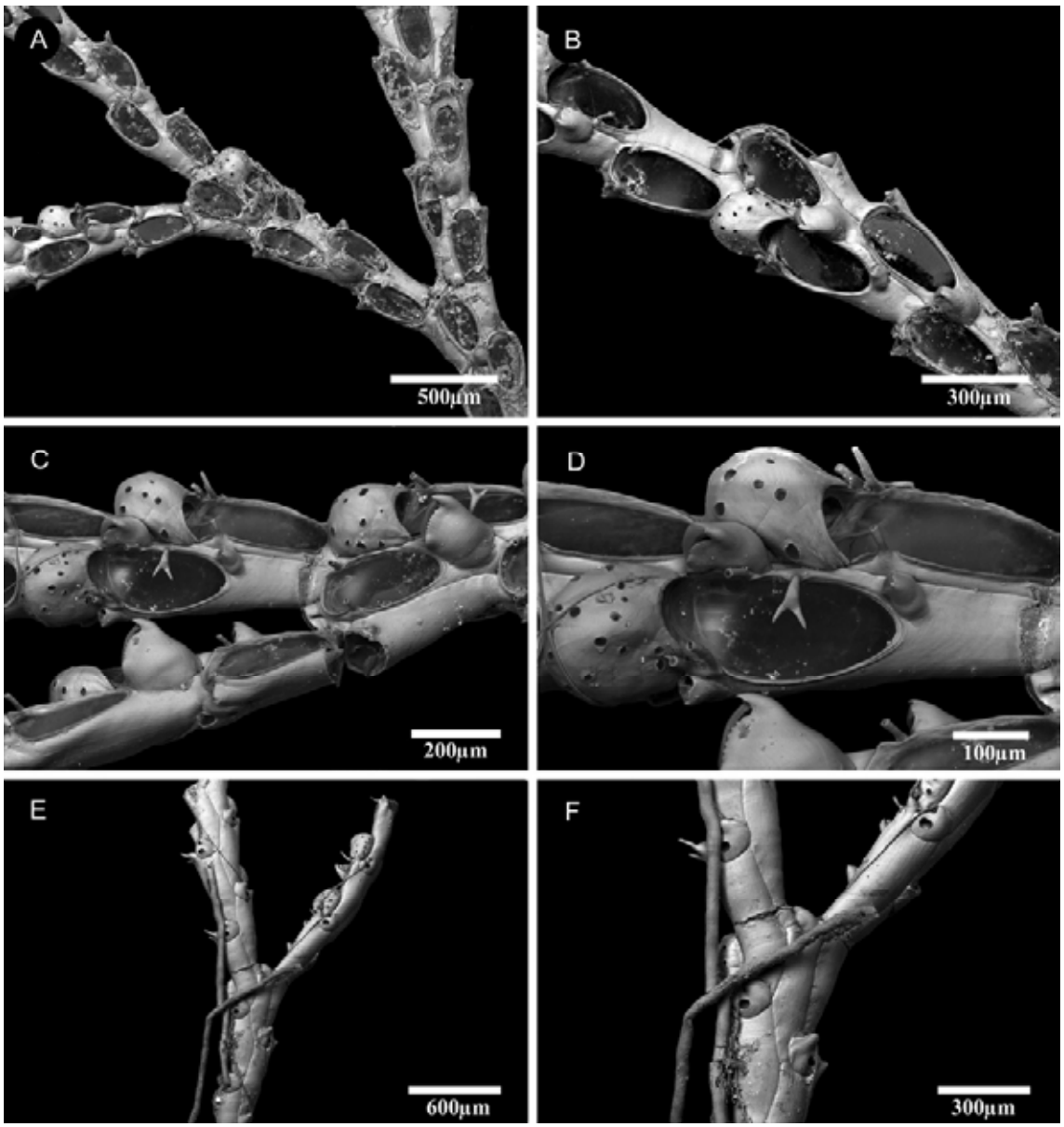

Figure 3.1. *N.gen.1 bertholletii* (Audouin, 1826) n. comb. **A–F**, NHMUK 1899.7.1.736, neotype, Mediterranean. **A**, Frontal surface of branches and two bifurcations. **B**, Frontal surface a branche; note a ovicelled zooid and absence of scuta. **C**, Frontal surface of a branch bifurcation; note the presence of dimorphic frontal avicularia (gigantic on axial zooid) and two zooids with scutum. **D**, Close-up of an ovicelled zooid with scutum; note the small lateral avicularium. **E–F**, Abfrontal surface of branch; note the smooth surface of rhizoids.

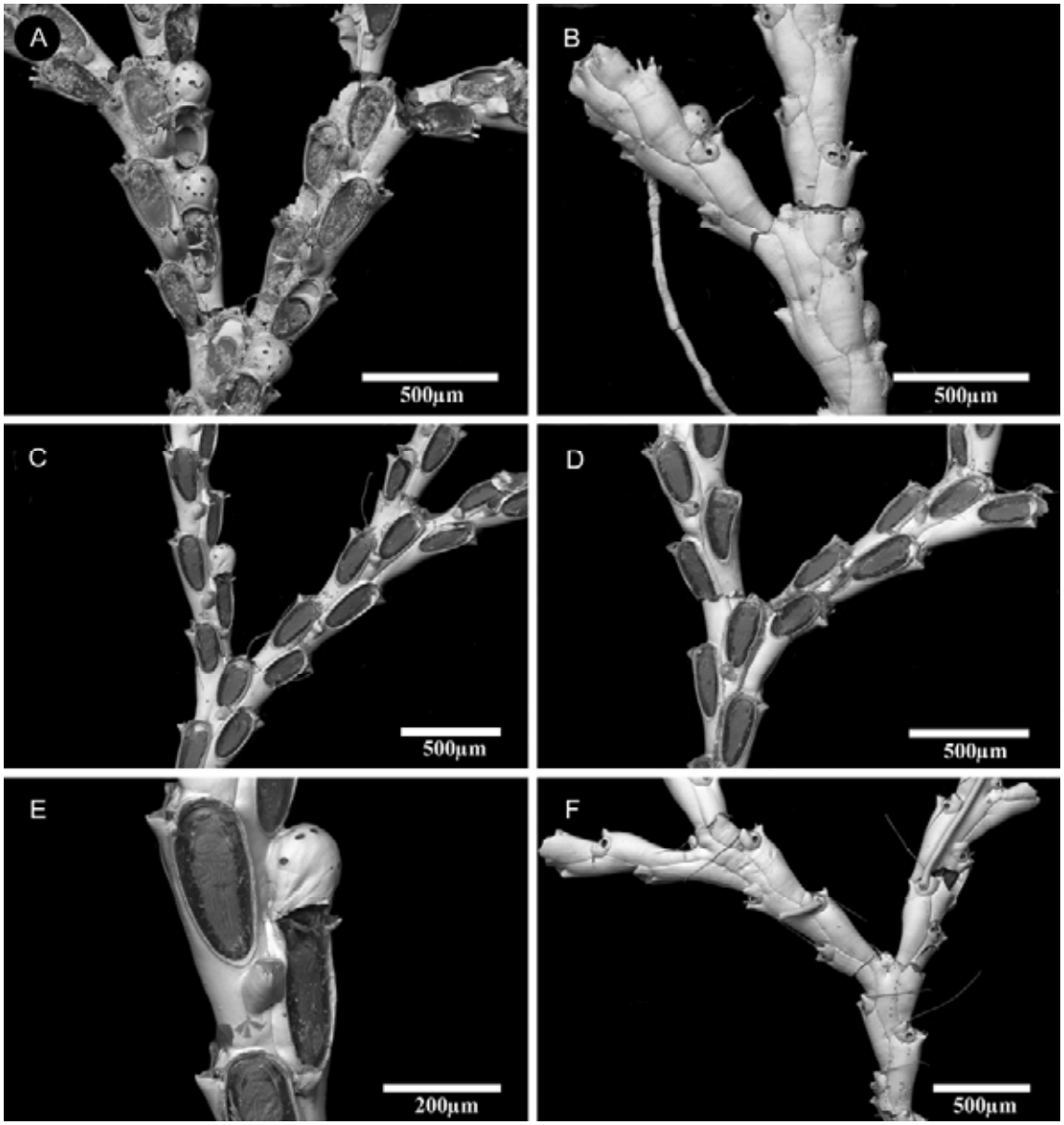

Figure 3.2. *N.gen.1 bertholletii* (Audouin, 1826) n. comb. **A–B**, NHMUK 2012.7.1.4, Monaco; **C–F**, NHMUK 2012.7.1.11, Curaçao. **A**, Frontal surface of branches and bifurcation. **B**, Abfrontal surface of branch. **C**, Frontal surface of branches; note the absence of scutum in whole colony. **D**, Frontal surface of bifurcation. **E**, Close-up of two zooid, one with ovicell; note the absence of scuta in ovicelled and non-ovicelled zooid. **F**, Abfrontal surface of colony.

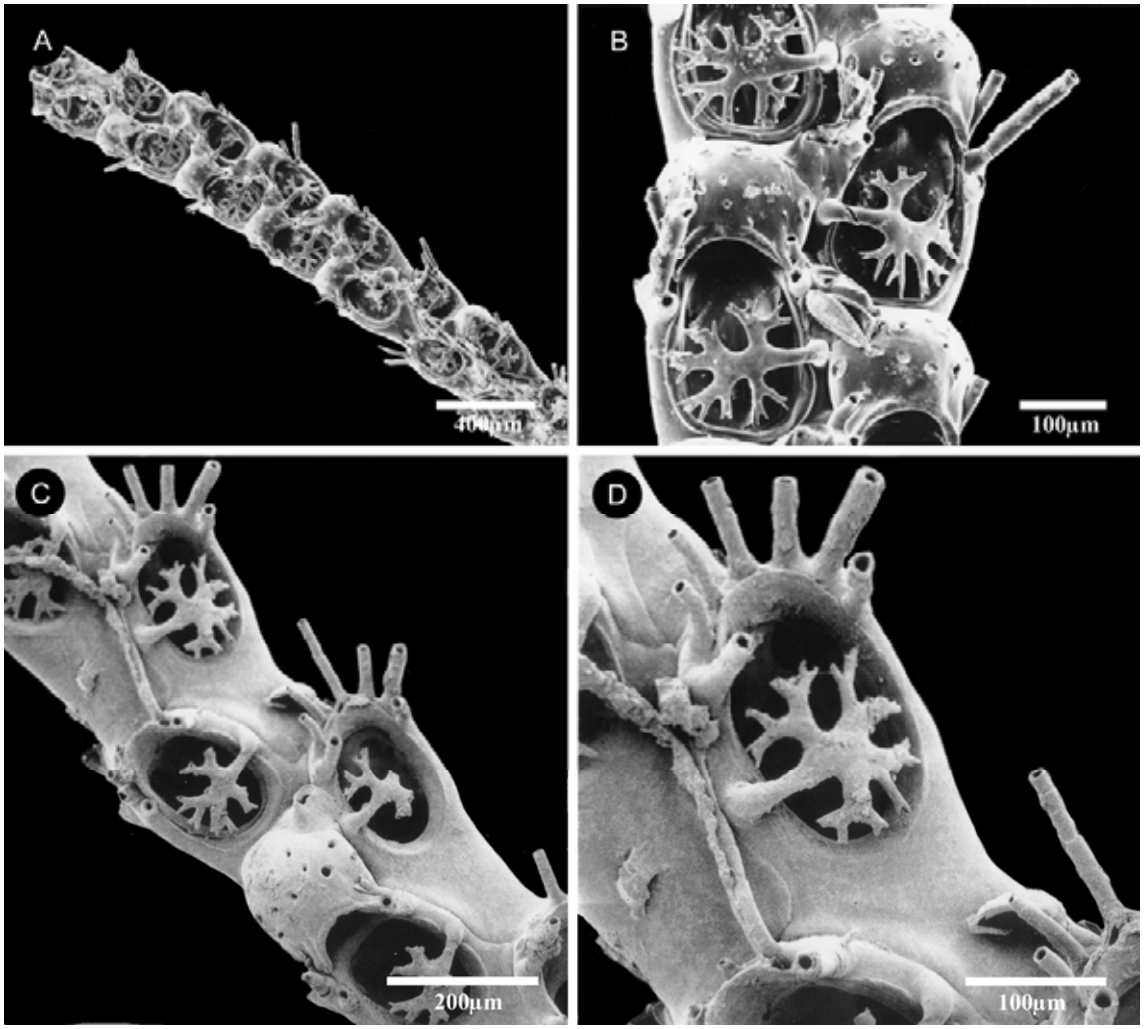

Figure 3.3. *Scrupocellaria bellula* Osburn, 1947. **A–D**, Jamaica (uncatalogued specimen, part of AMNH 1518.1). **A**, Frontal surface of branch with some ovicelled zooids. **B**, Close-up of two ovicelled zooids; note the branched frontal scutum and small frontal avicularium on zooids. **C**, Frontal surface of branch; note the presence of 7 distal spines broken at its tips (see OSBURN, 1947 to see the branched spines). **D**, Close-up of fronta surface of autozooid.

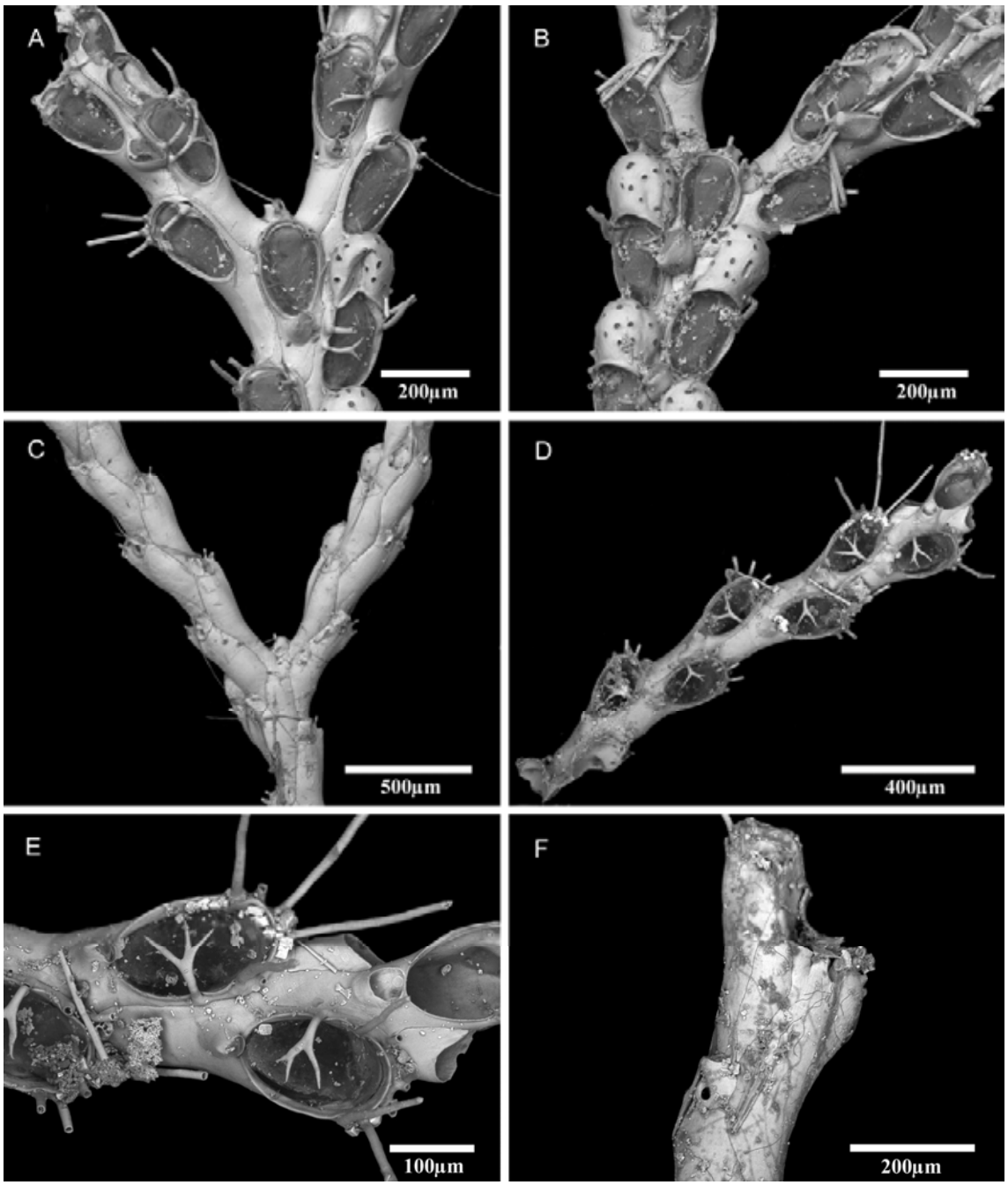

Figure 3.4. *N.gen.1 curacaoensis* (Fransen, 1986) n. comb. **A–C**, NHMUK 2012.7.1.12, Curaçao. **D–F**, NMNH (uncatalogued specimen, SEM-3), Bermuda. **A**, Frontal surface of branch; note the forked scutum in some zooids. **B**, Frontal surface of branch bifurcation; note some ovicelled zooids. **C**, Abfrontal surface of branch. **D**, Frontal surface of branch; note the bi and trifurcated scutum. **E**, Close-up of two zooids; note the trifurcated scutum. **F**, Abfrontal surface of branch; note the vibracular chamber with transversal setal groove.

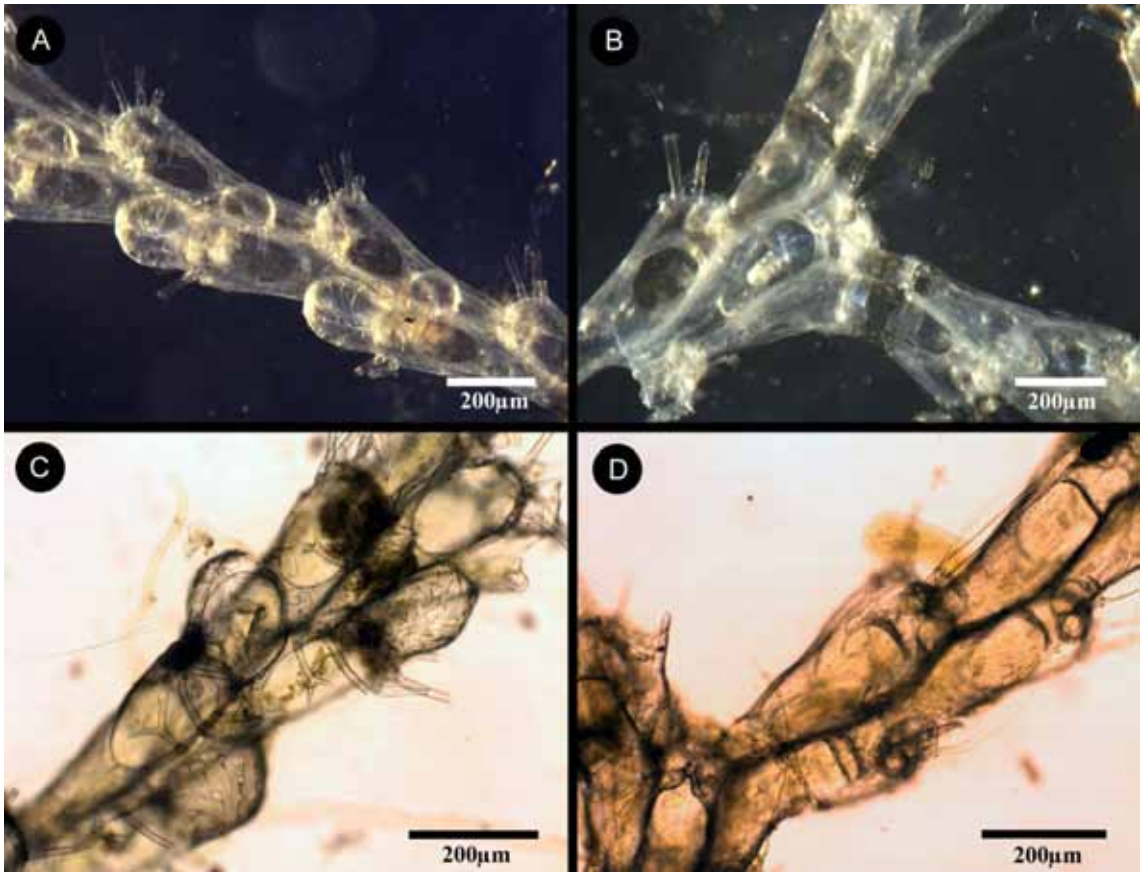

Figure 3.5. *N.gen.1 curacaoensis* (Fransen, 1986) n. comb. **A–B**, NMNH (uncatalogued specimen, Osburn-04), Porto Rico. **C–D**, SBMNH 96400, Aruba Island. **A**, Frontal surface of branch with two ovicells. **B**, Abfrontal surface of branch bifurcation. C, Frantal surface of branch; note one zooid with tirfurcated scutum and two zooids with forked scutum. **D**, Abfrontal surface of branch; note the joints passing across the opesia in outer zooids at the bifurcation.

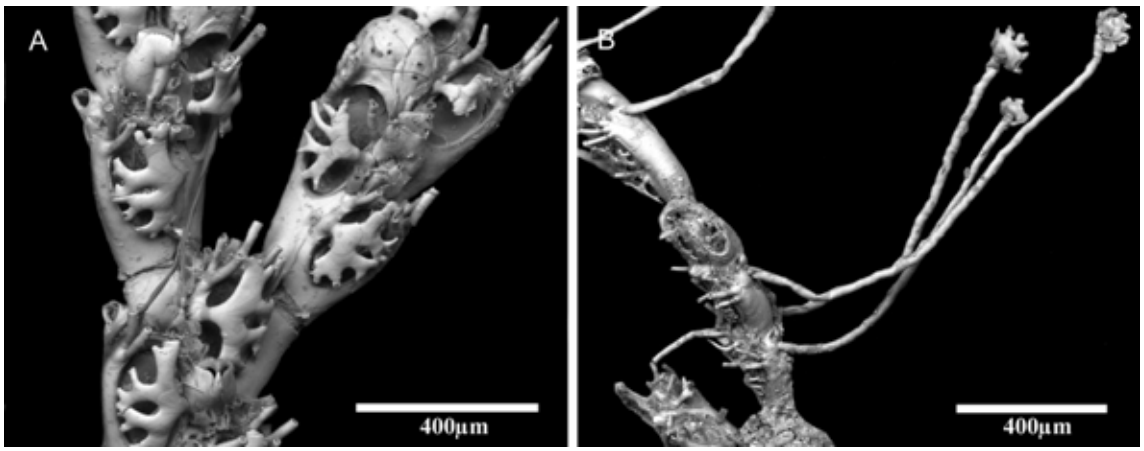

Figure 3.6. *N.gen.1 n.sp.1* (Vieira & Spencer) n. comb. **A–B**, NHMUK 1911.10.1.353, holotype, British coast. **A**, Frontal surface of branch. **B**, Rhizoids with smooth surface.

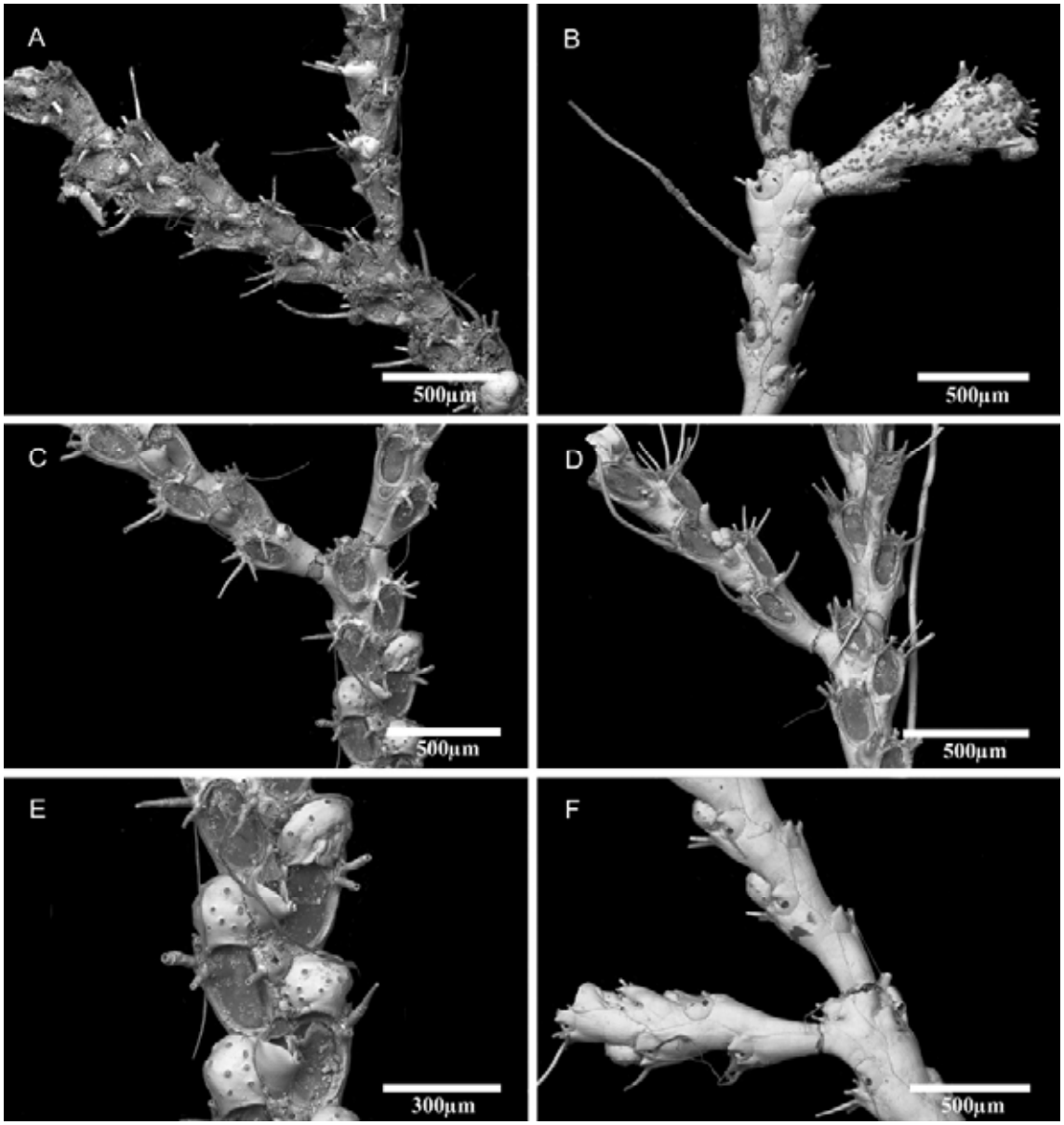

Figure 3.7. *N.gen.1 hirsuta* (Jullien & Calvet, 1903) n. comb. **A–B**, MOM 420323, lectotype, Azores. **C–F**, NHMUK 2012.7.1.1, Azores. **A**, Frontal surface of branch; note the presence of dimorphic frontal avicularium and absence of scutum. **B**, Abfrontal surface of branch. **C**, Frontal surface of branch bifurcation; note the dimorphic frontal avicularia and three ovicelled zooids at proximal region of the colony. **D**, Frontal surface of branch; note the presence of 7 long oral spines in each zooid and the absence of scutum. **E**, Close-up of four ovicelled zooids and the dimorphic frontal avicularia. **F**, Abfrontal surface of branch.

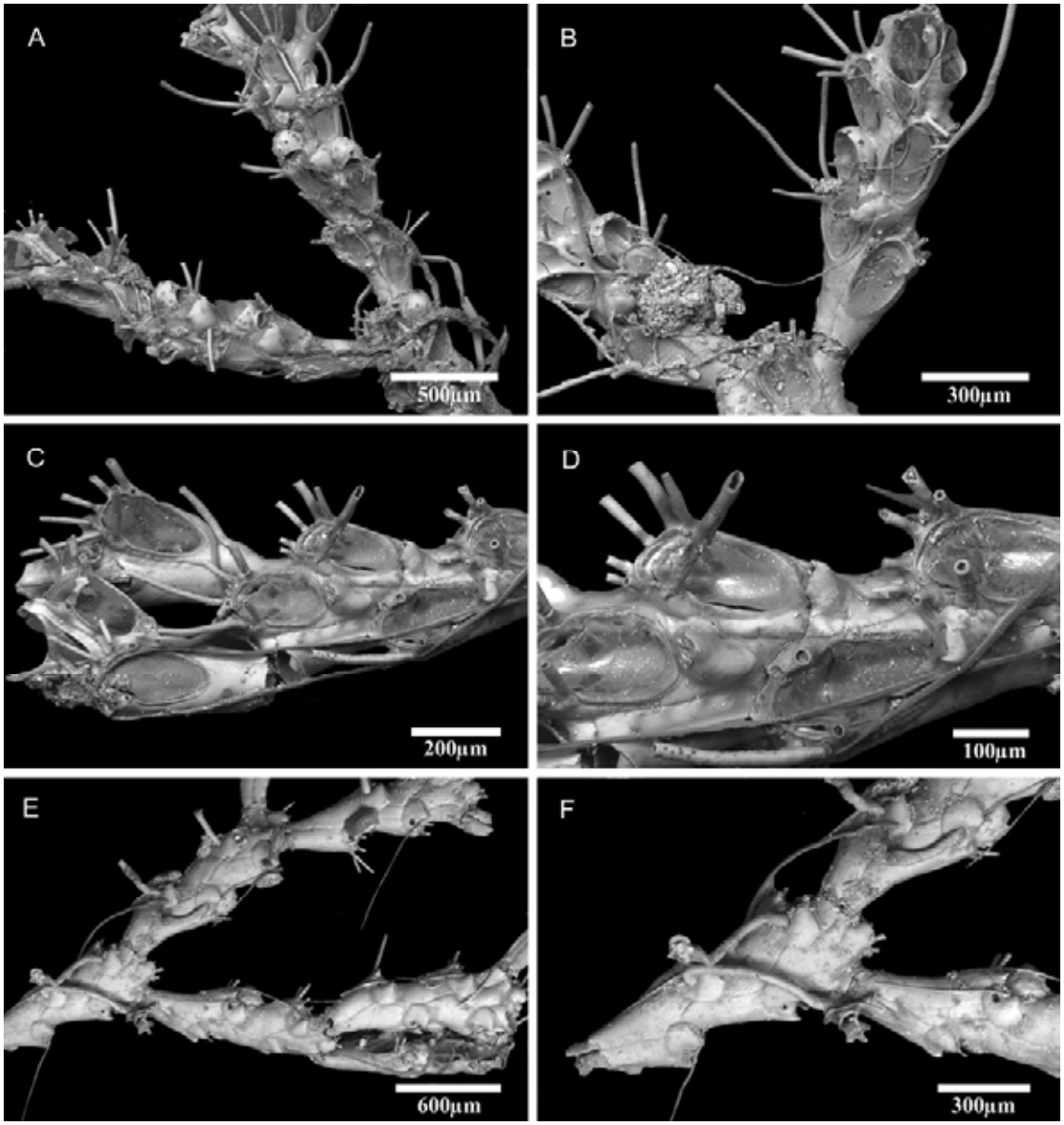

Figure 3.8. *N.gen.1 hirsuta* (Jullien & Calvet, 1903) n. comb. **A–F**, NHMUK 1911.10.1.386, Madeira. **A**, Frontal surface of colony. **B**, Frontal surface of branch; note the presence of latero-distal avicularia and the very long distal spines. **C**, Lateral view of branch bifurcation. **D**, Close-up of two autozooids; note the small aquiline frontal avicularia. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation; note the smooth rhizoids.

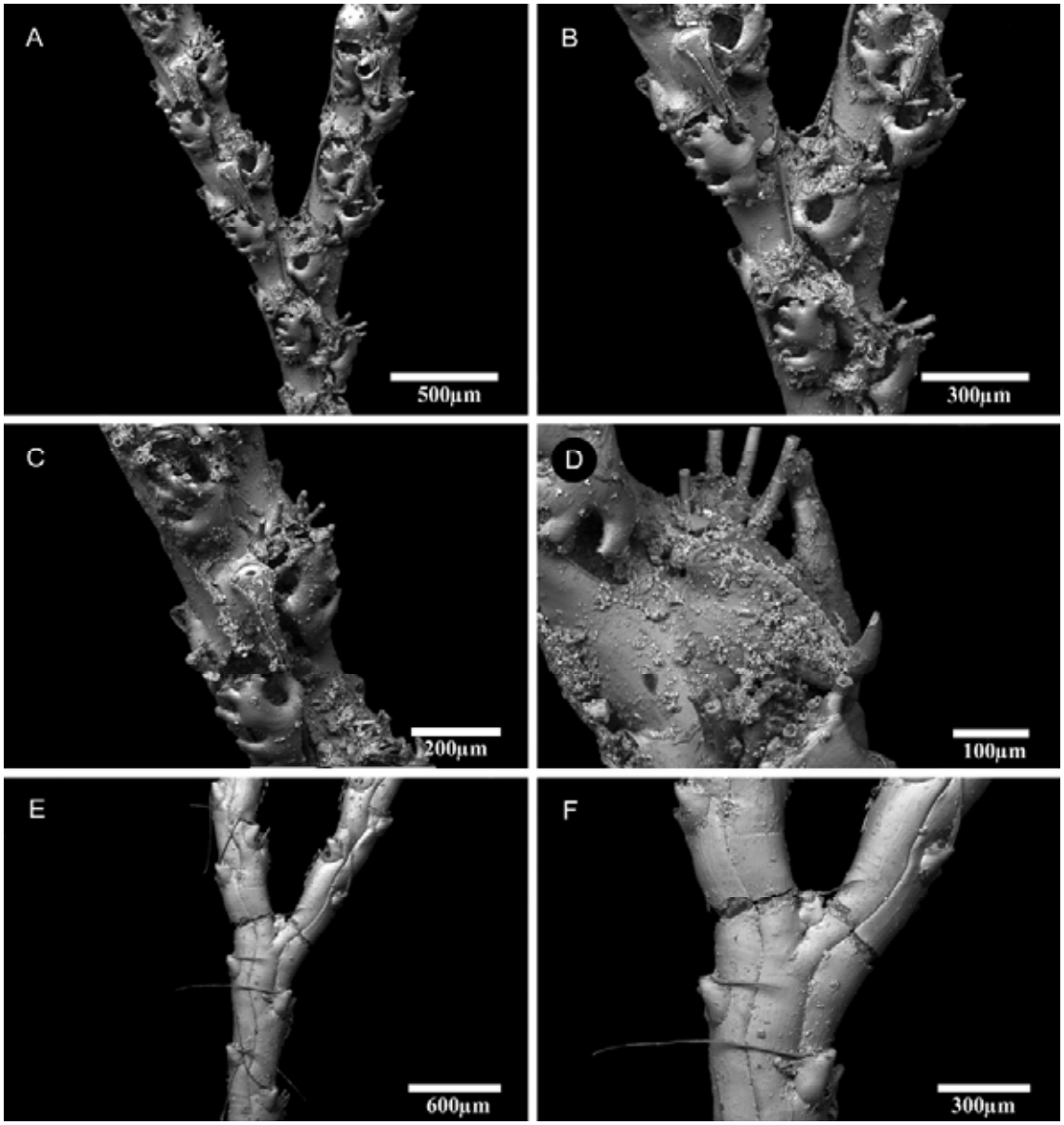

Figure 3.9. *N.gen.1 macrorhyncha* (Gautier, 1962) n. comb. **A–F**, NHMUK 1965.9.2.4, lectotype, Mediterranean. **A**, Frontal surface of branch; note the ovicelled zooid at the upper right. **B**, Frontal surface of branch bifurcation. **C**, Close-up of a zooid and gigantic frontal avicularium. **D**, Lateral view of gigantic frontal avicularium; note the fringed rostrum of avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

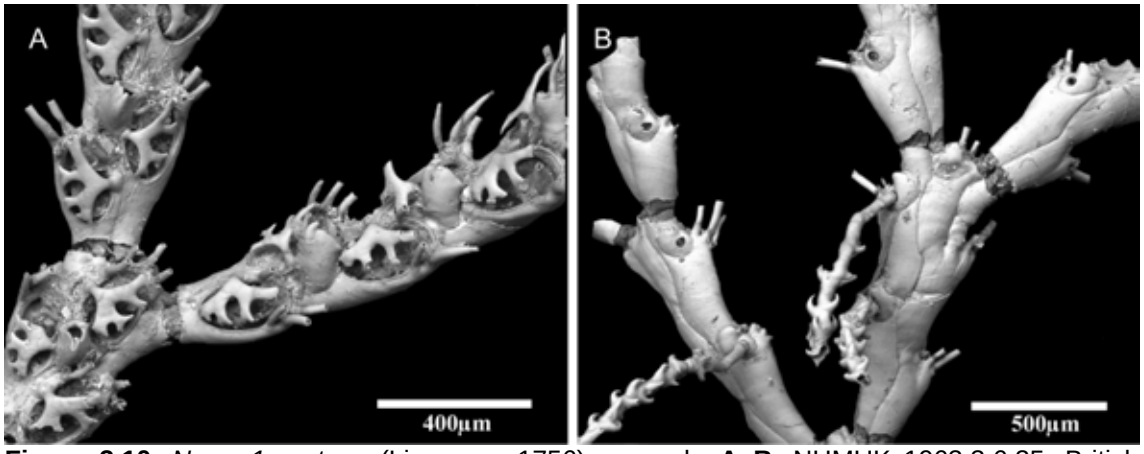

Figure 3.10. *N.gen.1 reptans* (Linnaeus, 1756) n. comb. **A–B**, NHMUK 1963.3.6.35, British coast. **A**, Frontal surface of branch. **B**, Abfrontal surface of branch bifurcation.

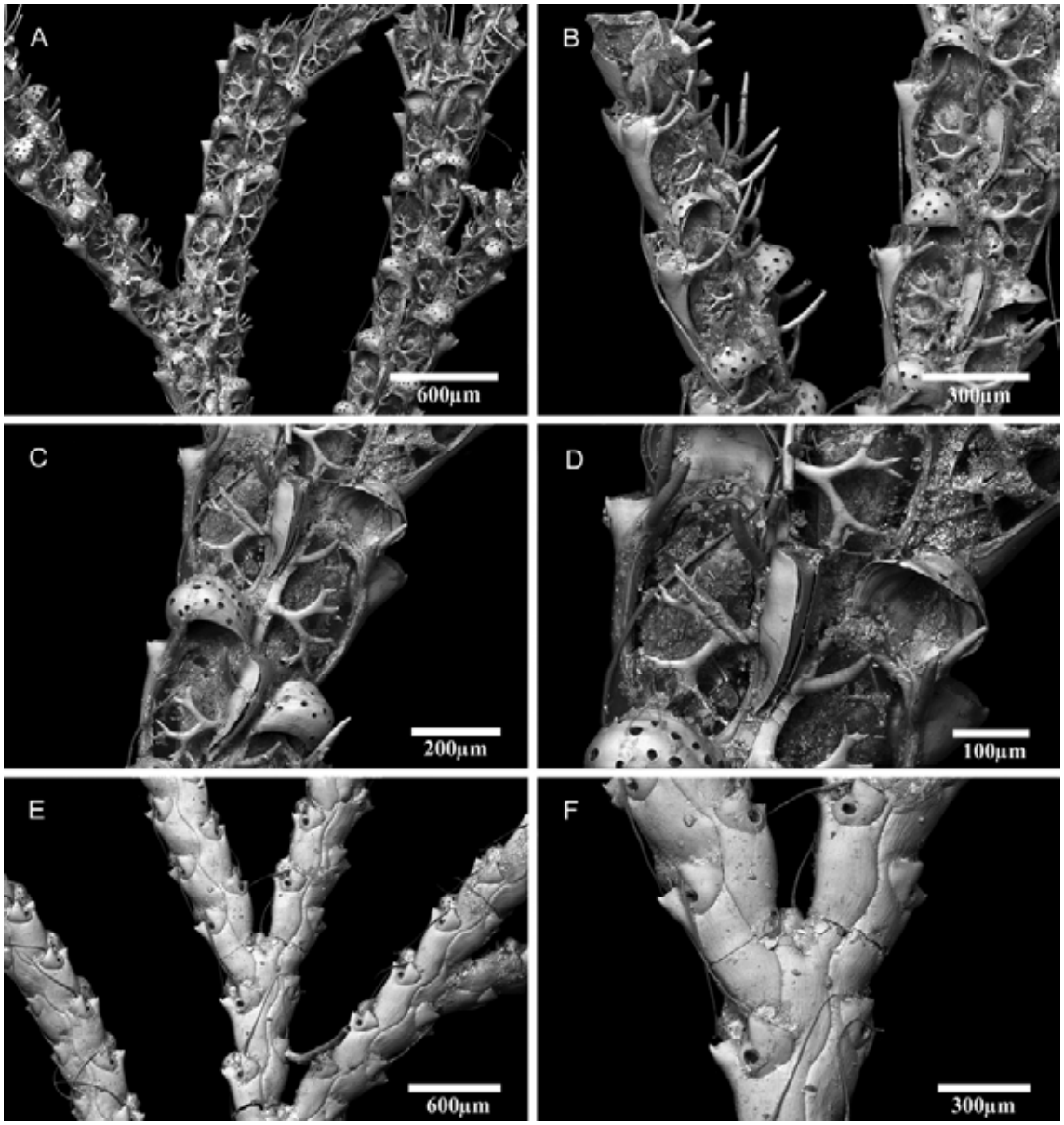

Figure 3.11. *N.gen.1 tenuirostris* (Osburn, 1950) n. comb. **A–F**, NHMUK 2010.10.5.1, California. **A**, Frontal surface of colony. **B**, Frontal surface of branches; note the ovicelled zooid and lanceolate frontal avicularia at right branch. **C**, Frontal surface of branch; note two ovicelled zooid and two lanceolate frontal avicularia, characteristic of this species. **D**, Close-up of lanceolate frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

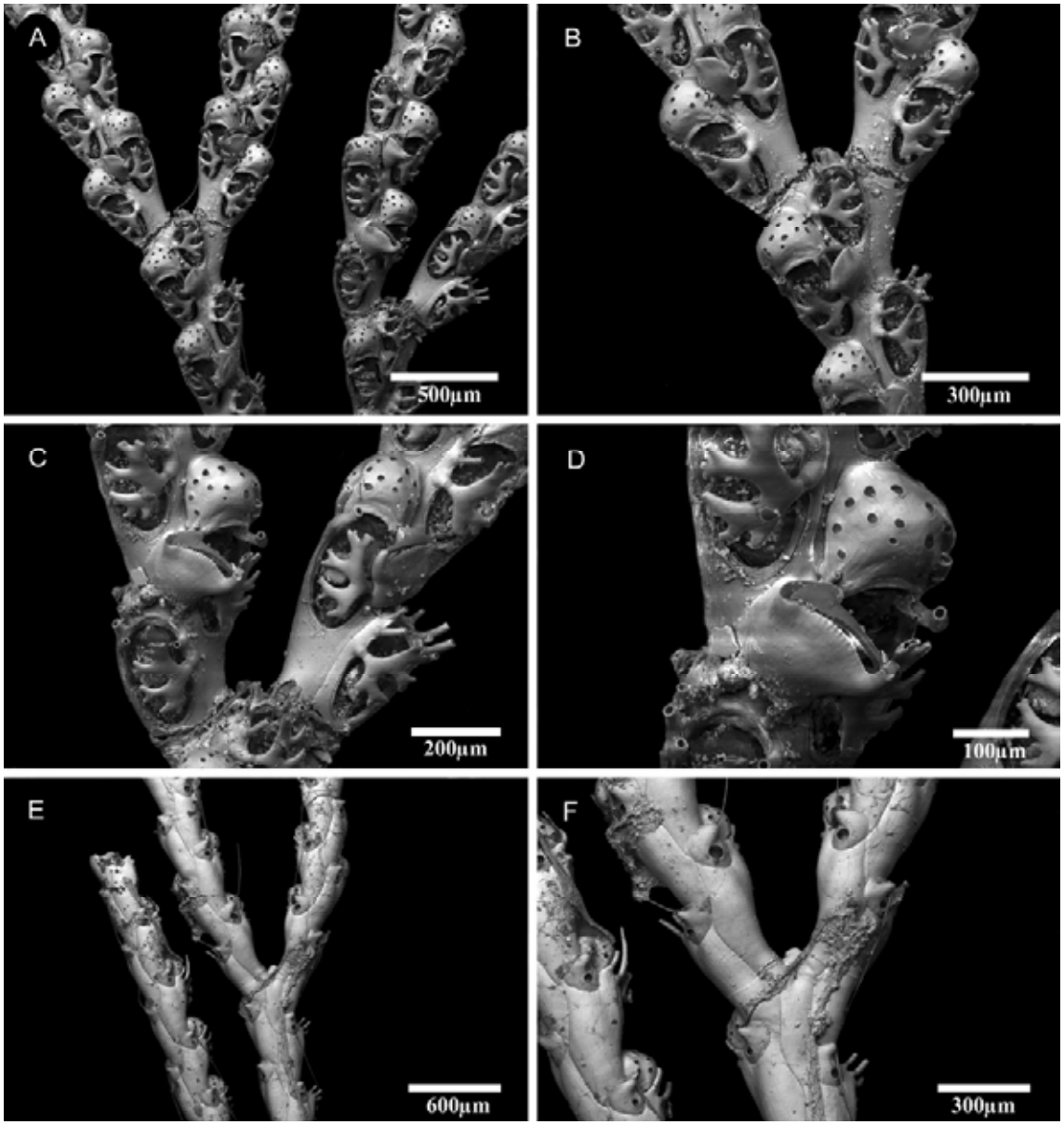

Figure 3.12. *N.gen.1 n.sp.2*. **A–F**, NHMUK 1963.8.2.16, holotype, Alexandria, Egypt. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the joints passing across gymnocyst in both outer zooids at bifurcation. **C**, Close-up of branches; note the gigantic frontal avicularia and two ovicelled zooids. **D**, Close-up of gigantic frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

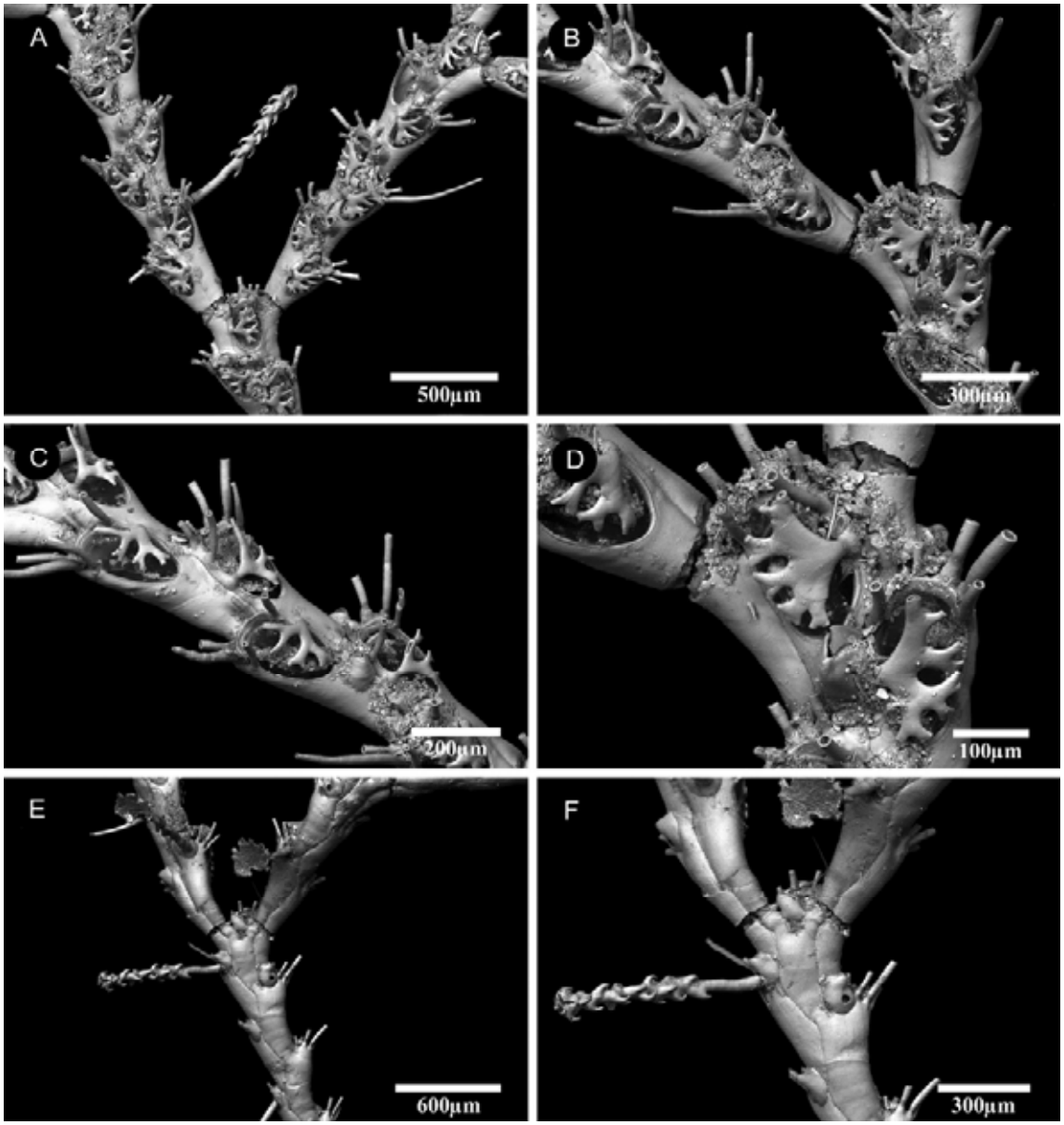

Figure 3.13. *N.gen.1 n.sp.3*. **A–F**, NHMUK 2010.12.6.1, holotype, Scotland. **A**, Frontal surface of colony; note the rhizoids with retrouseé hooks. B, Frontal surface of branch bifurcation; note the well-developed frontal scutum. **C**, Lateral view of branch; note the absence of lateral avicularium. **D**, Close-up of axial zooid; note the position of the joints at gymnocyst in inner and outer zooids at bifurcation. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation; note the rhizoids with several short-spaced retrouseé hooks.

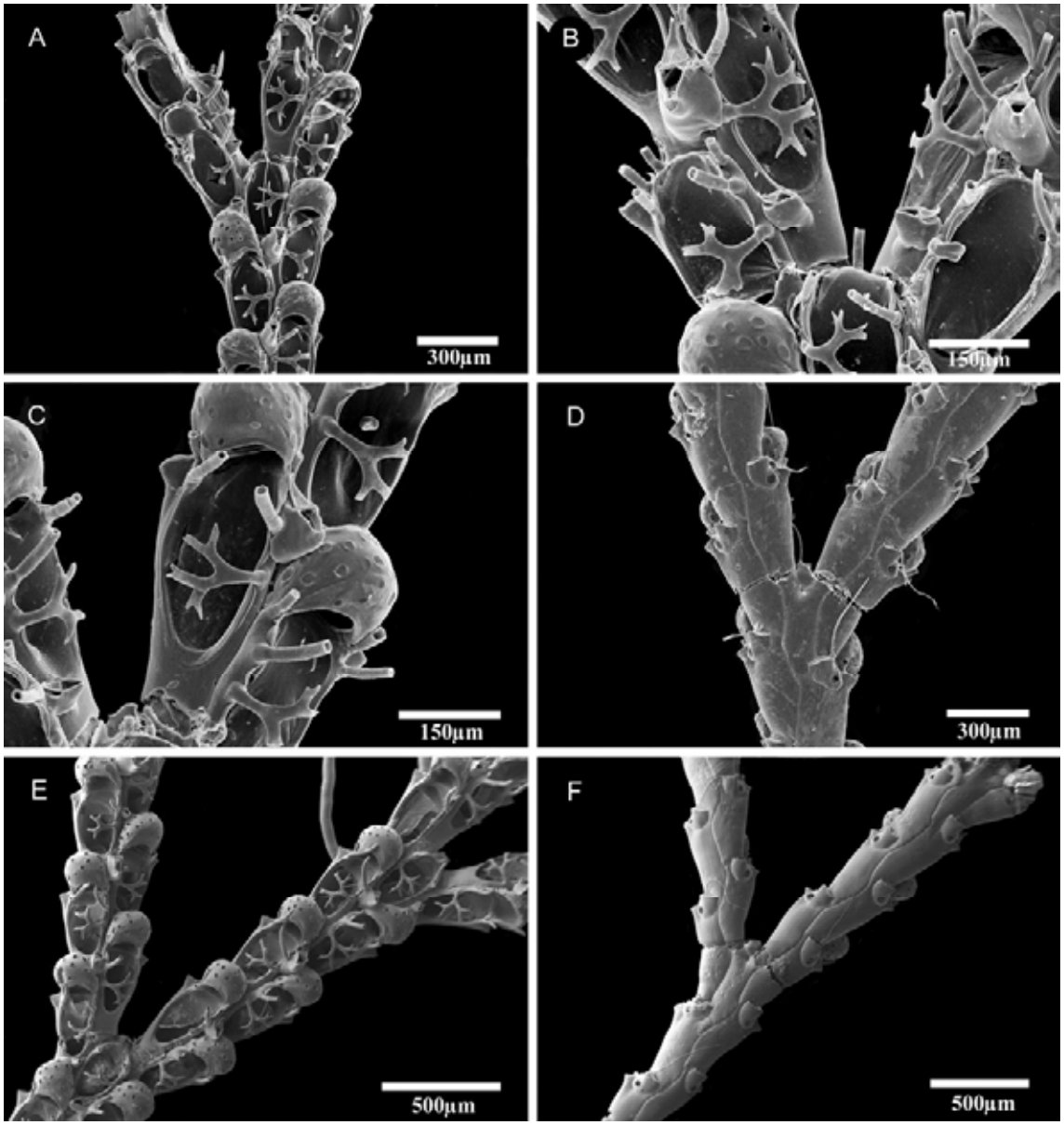

Figure 3.14. *N.gen.1 n.sp.4*. **A–D**, MZUSP (uncatalogued specimen), part of holotype, São Paulo, Brazil. **E–F**, VMNH 10403.0000, Florida. **A**, Frontal surface of branch bifurcation. **B**, Close-up of branch bifurcation; note the presence of 3 distal spines in axial zooid. **C**, Close-up of ovicelled zooid; note the small lateral and frontal avicularia. **D**, Abfrontal surface of branch bifurcation. **E**, Frontal surface of colony; note some ovicelled zooids and the variation of the size in the frontal avicularia. **F**, Abfrontal surface of colony.

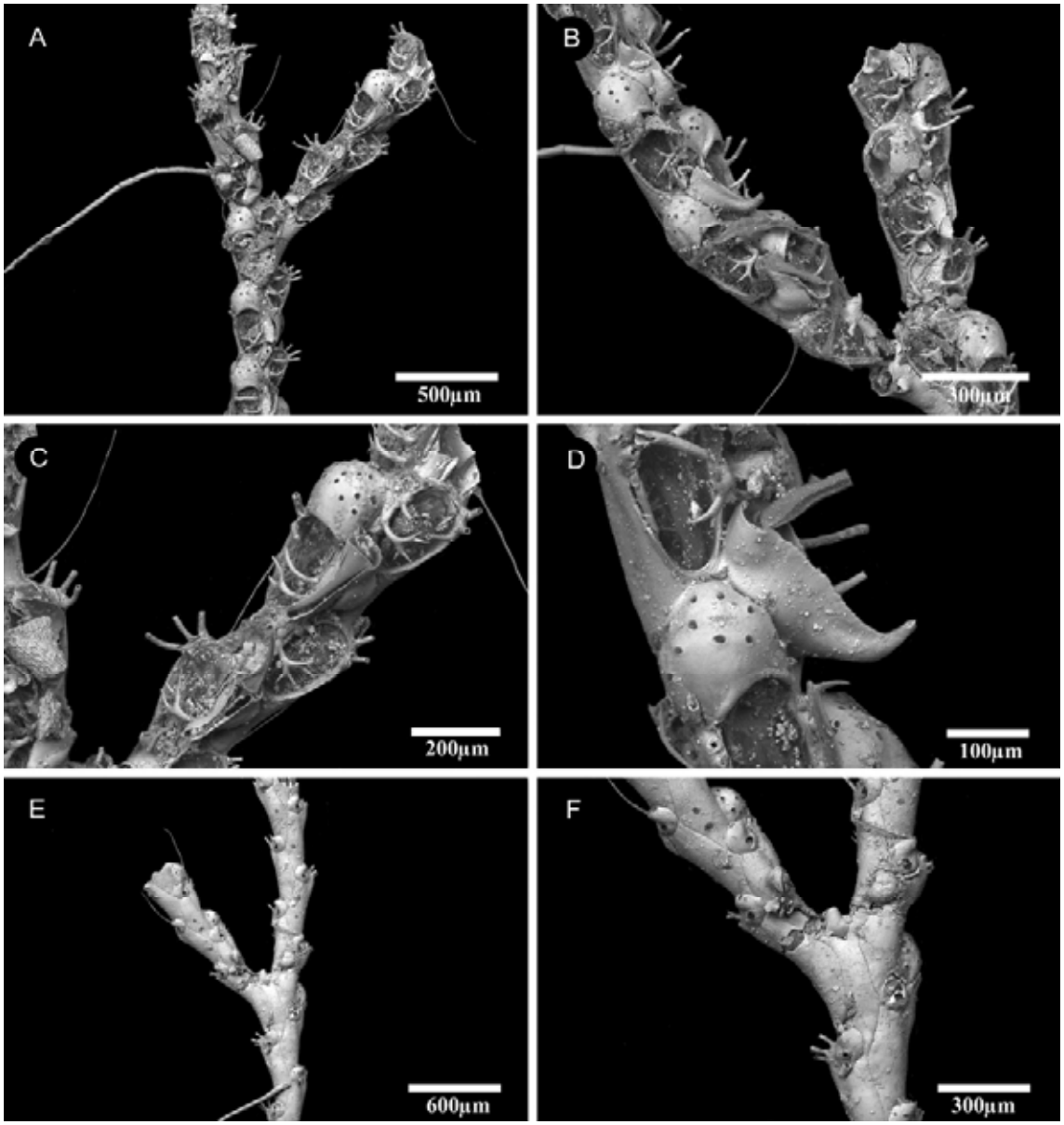

Figure 3.15. *N.gen.1 n.sp.5*. **A–F**, MNHN 15979, holotype, Recife, Brazil. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the dimorphic frontal avicularia. **C**, Close-up of branches; note the absence of lateral avicularia, the gigantic frontal avicularia and one ovicelled zooid. **D**, Close-up of gigantic frontal avicularium; note the curved rostrum. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

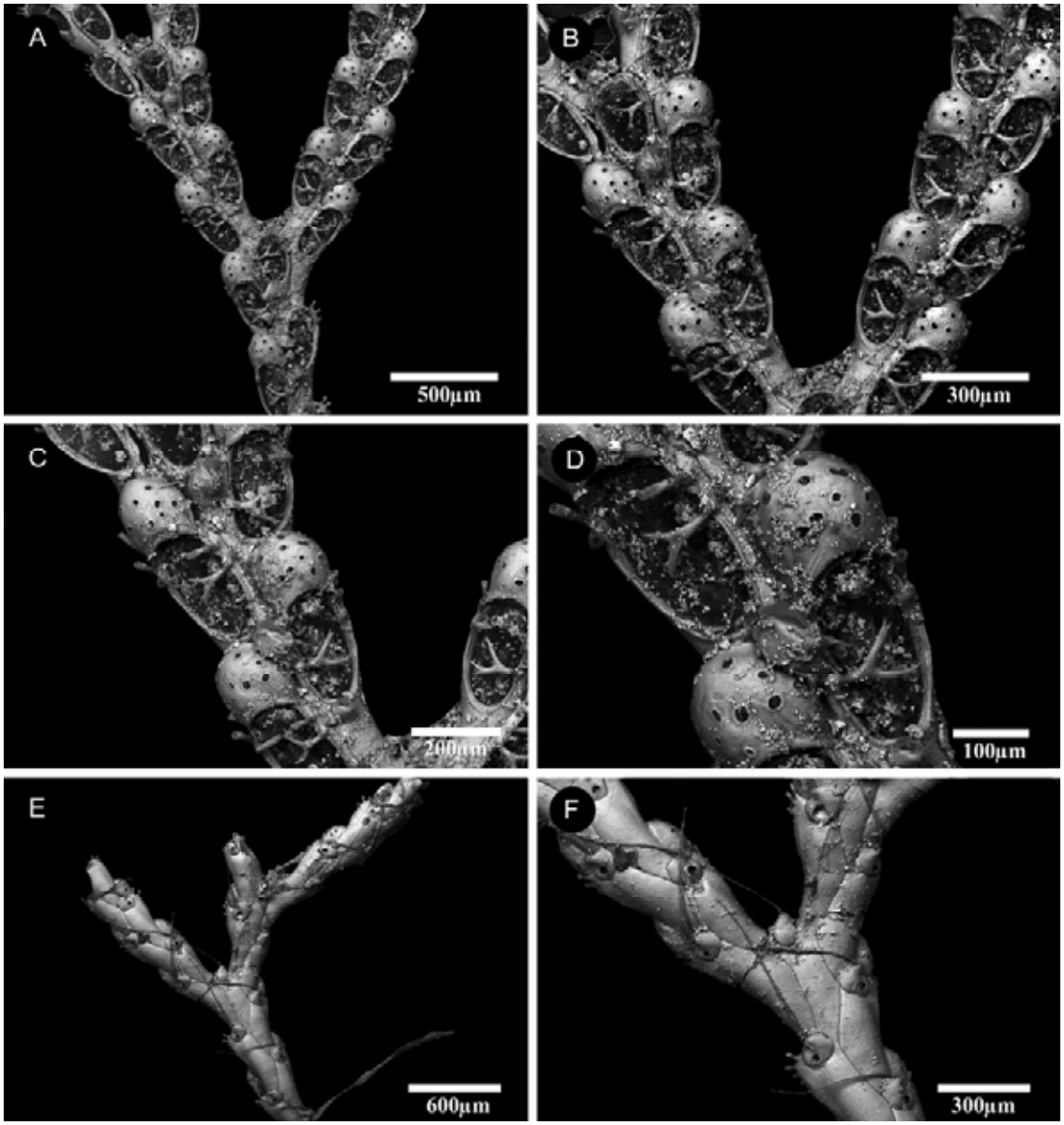

Figure 3.16. *N.gen.1 n.sp.6*. **A–F**, NHMUK 2010.12.6.2, holotype, Florida. **A**, Frontal surface of colony. **B**, Frontal surface of branches with ovicelled zooids. **C**, Close-up of a branch; note the dimorphic frontal avicularia and the ooecia some pores with raised edges. **D**, Close-up of ovicelled zooid and one frontal avicularium; note the forked scutum with forked and sharped tips. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

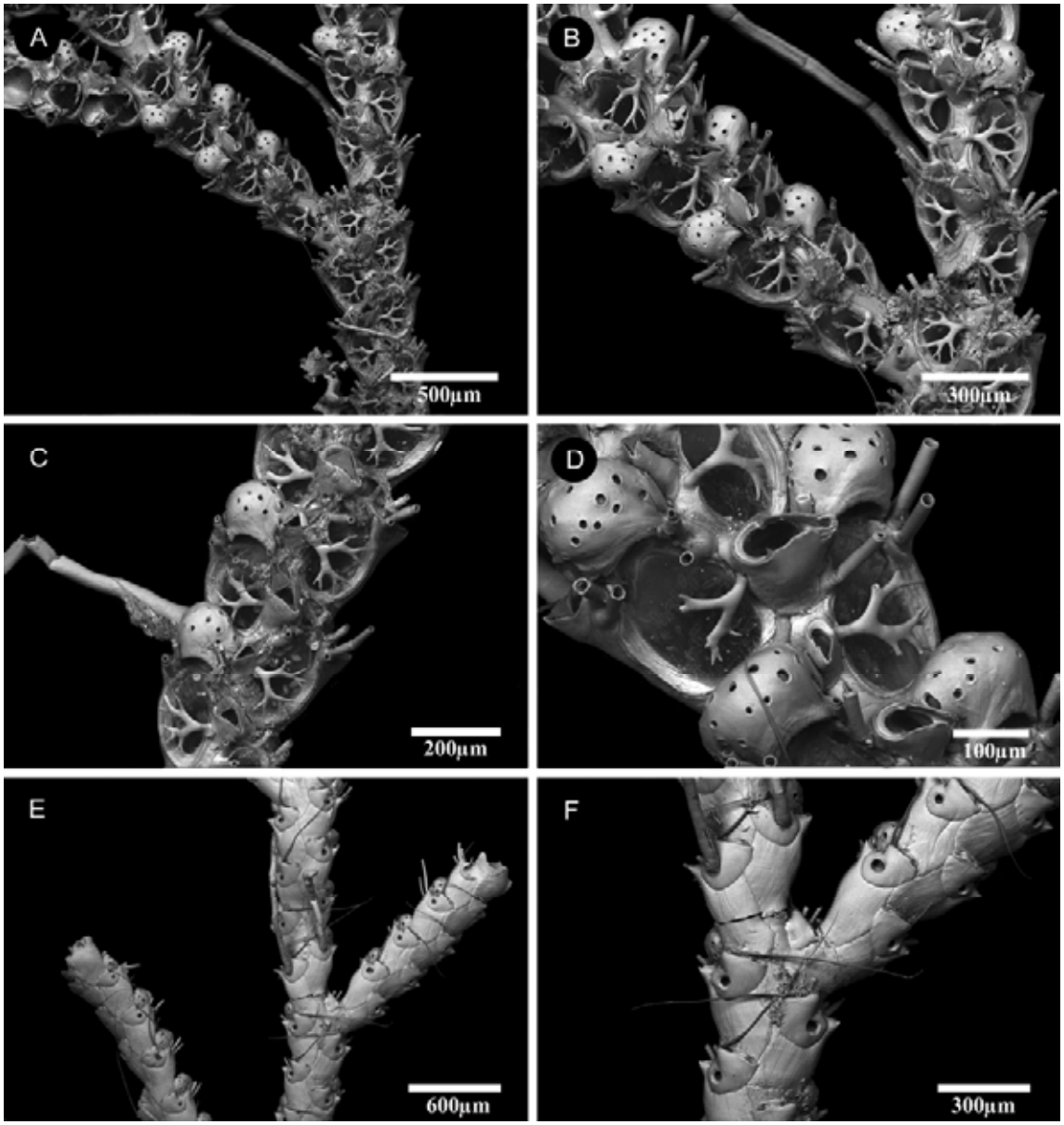

Figure 3.17. *N.gen.1 n.sp.7*. **A–F**, NHMUK 2010.12.6.3, holotype, Galapagos. **A**, Frontal surface of colony. B, Frontal surface of branch bifurcation with ovicelled zooids. **C**, Close-up of a branch; note two ovicelled zooids at left. **D**, Close-up of ovicelled zooids; note the wide cryptocyst around opesium and dimorphic frontal avicularia. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

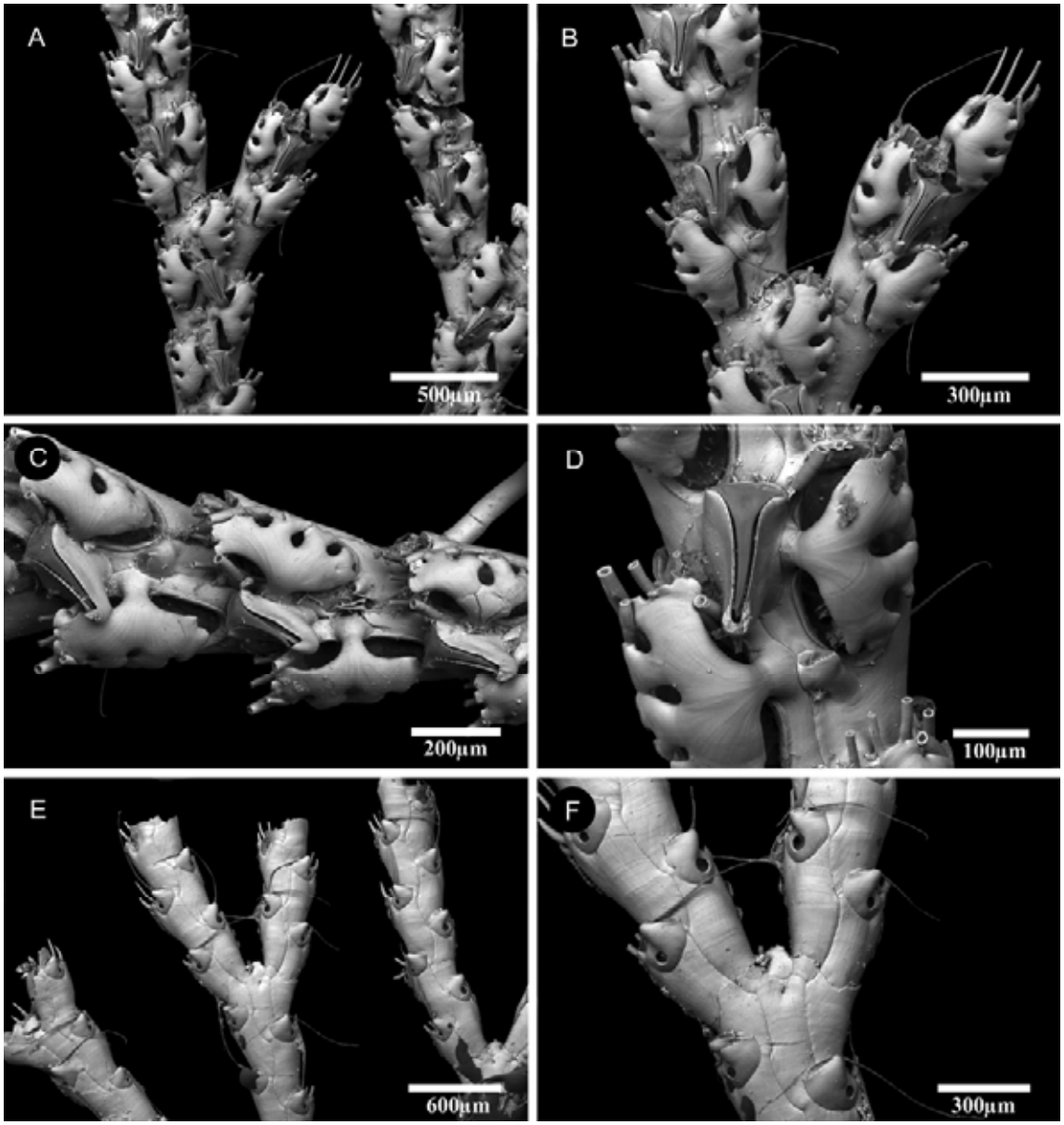

Figure 3.18. *N.gen.1 n.sp.8*. **A–F**, NHMUK 1882.5.24.9, holotype, Algeria. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the scutum covering whole opesium. **C**, Close-up of a branch; note the presence of a very small latero-distal avicularium of each zooid. **D**, Close-up frontal gigantic and small avicularia. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

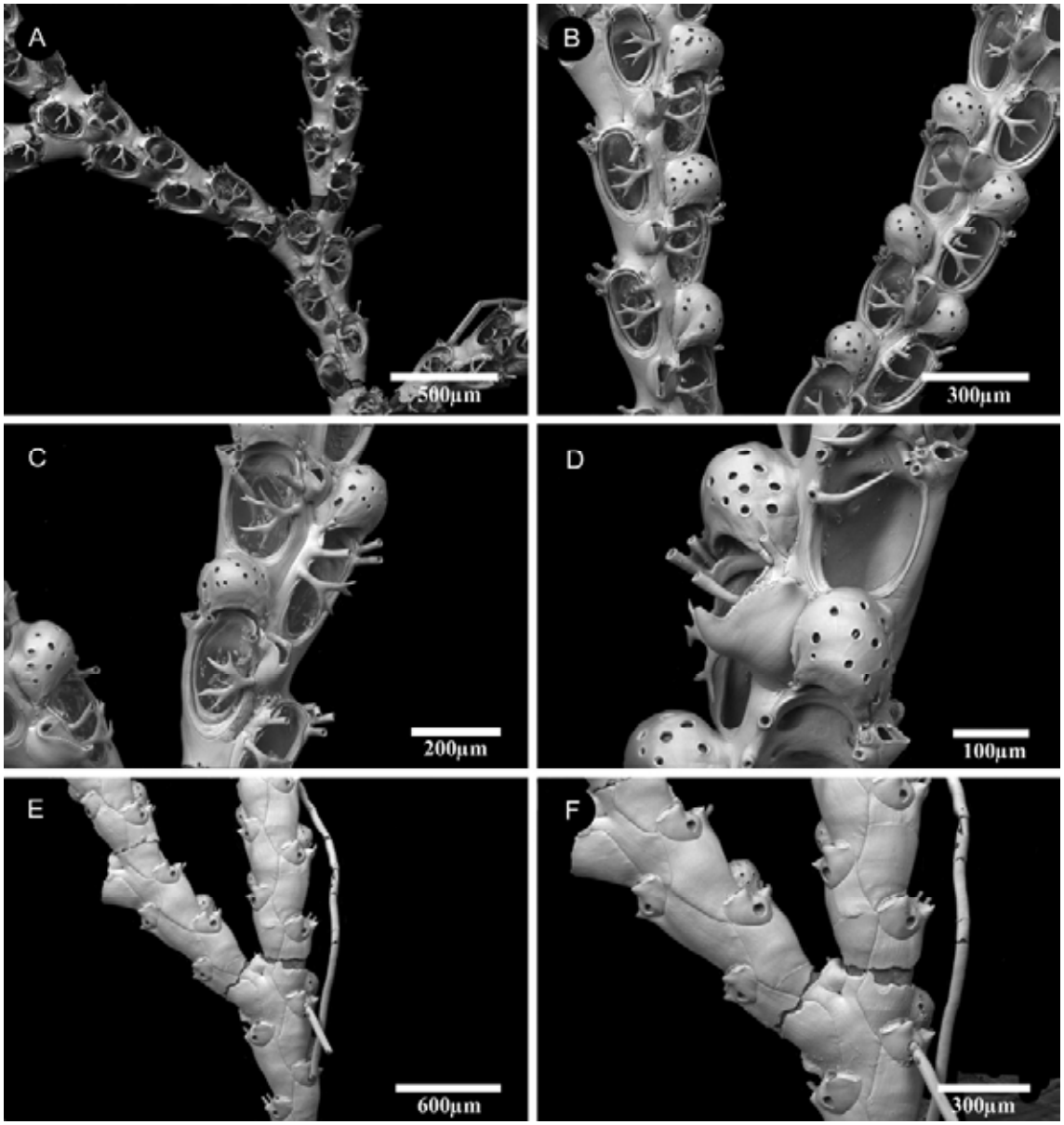

Figure 3.19. *N.gen.1 n.sp.9*. **A–F**, NHMUK 2010.12.6.4, holotype, Gorgona. **A**, Frontal surface of colony. **B**, Frontal surface of two branches with ovicelled zooids. **C**, Close-up of a branch; note the frontal avicularium with curved rostrum. **D**, Close-up of frontal avicularium; note the serrated rostrum, hooked distally. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

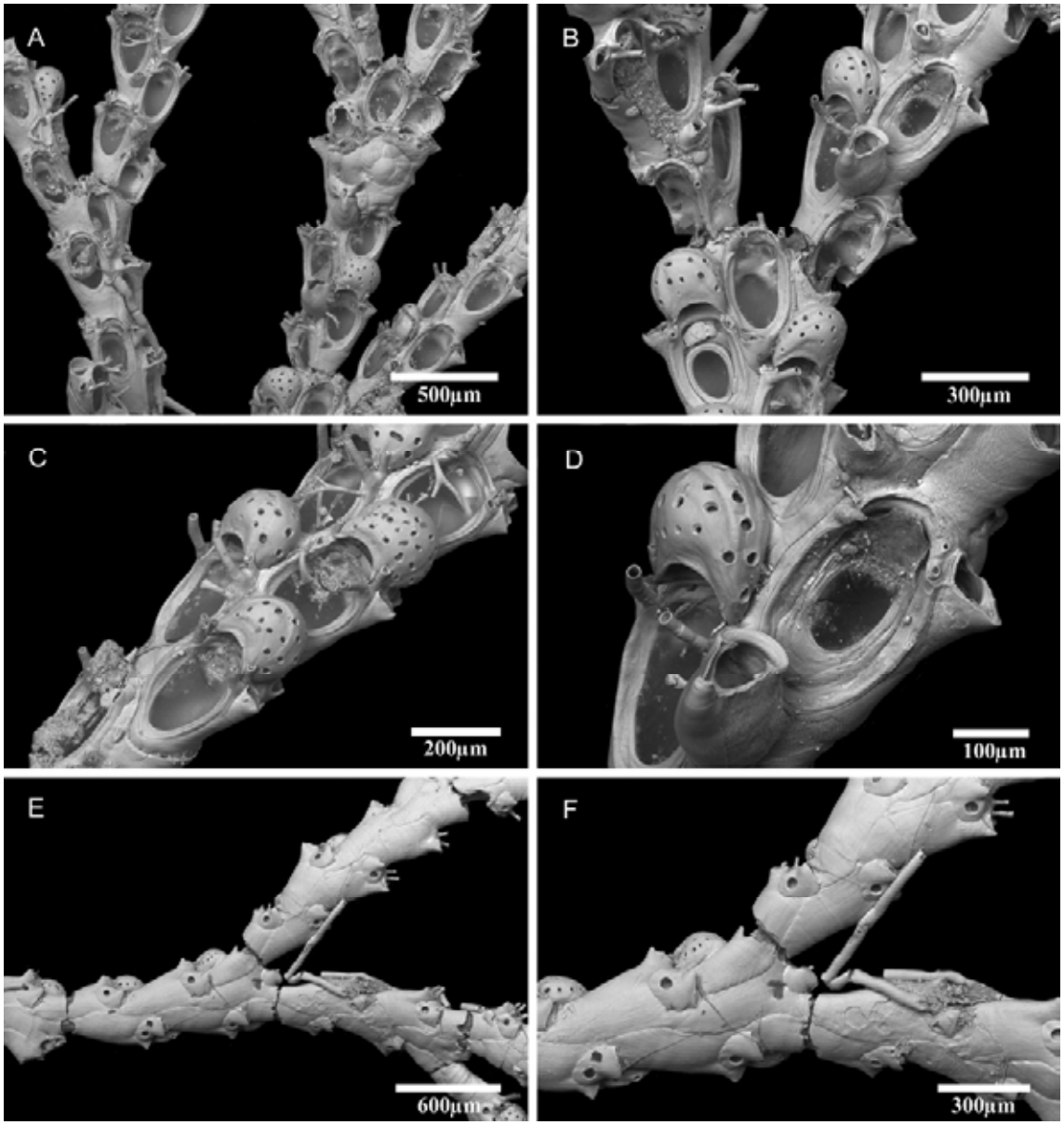

Figure 3.20. *N.gen.1 n.sp.10*. **A–F**, NHMUK 2010.12.6.8, holotype, Galapagos. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the joints passing across opesia in outer zooids at bifurcation. **C**, Close-up of a branch; note one zooid without scutum and three most distal zooids with forked scutum. **D**, Close-up of zooid; note the absence of scutum and the gigantic frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

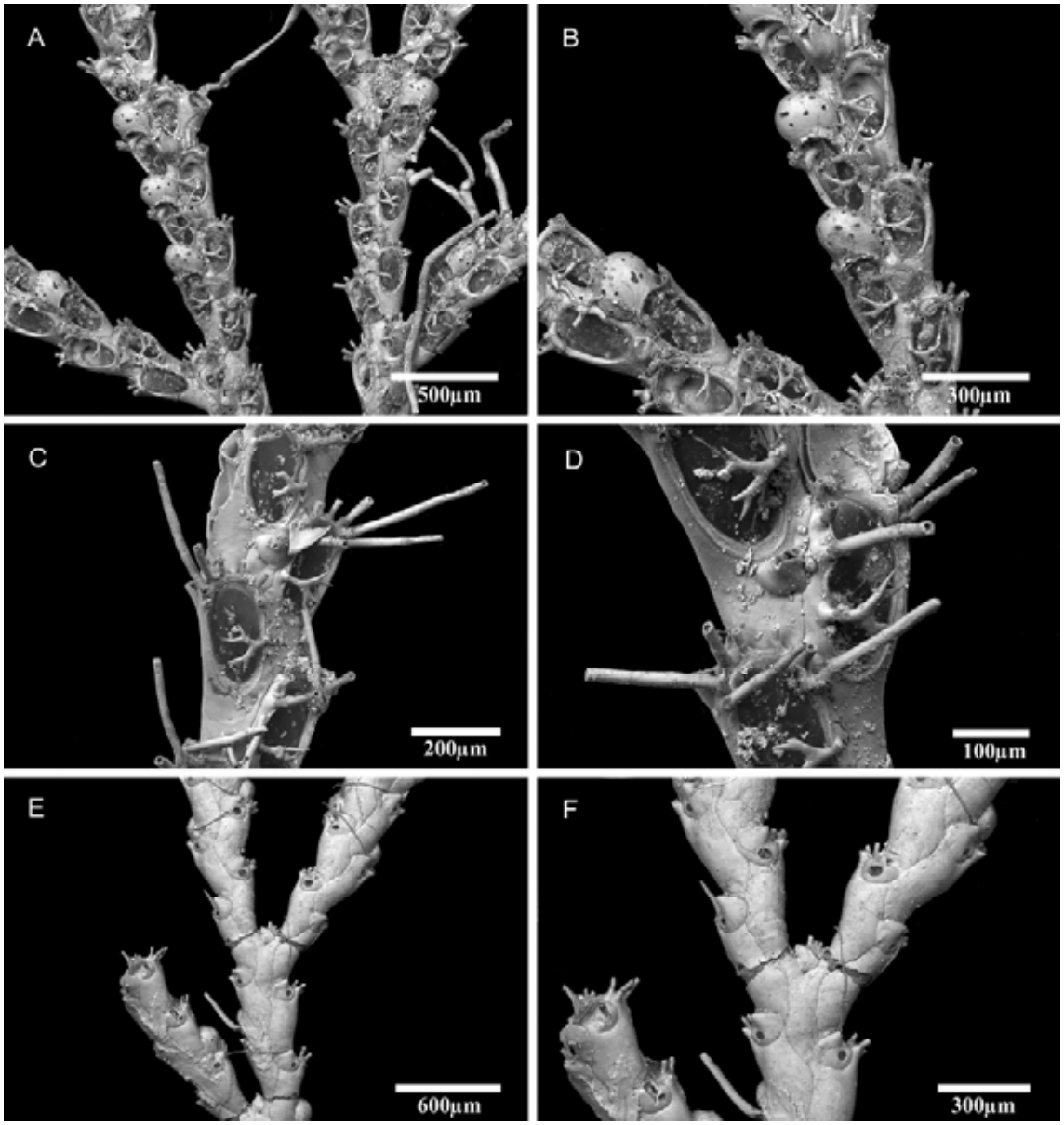

Figure 3.21. *N.gen.1 n.sp.11*. **A–B,E–F**, NHMUK 2010.12.6.16, holotype, Cape Verde**. C–D**, NHMUK 1899.7.1.837, paratype, Cape Verde. **A**, Frontal surface of colony. **B**, Frontal surface of branch with some ovicelled zooids. **C**, Close-up of a branch; note the small latero-distal avicularium and the scutum occupying less than half of opesial length. **D**, Close-up of small frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

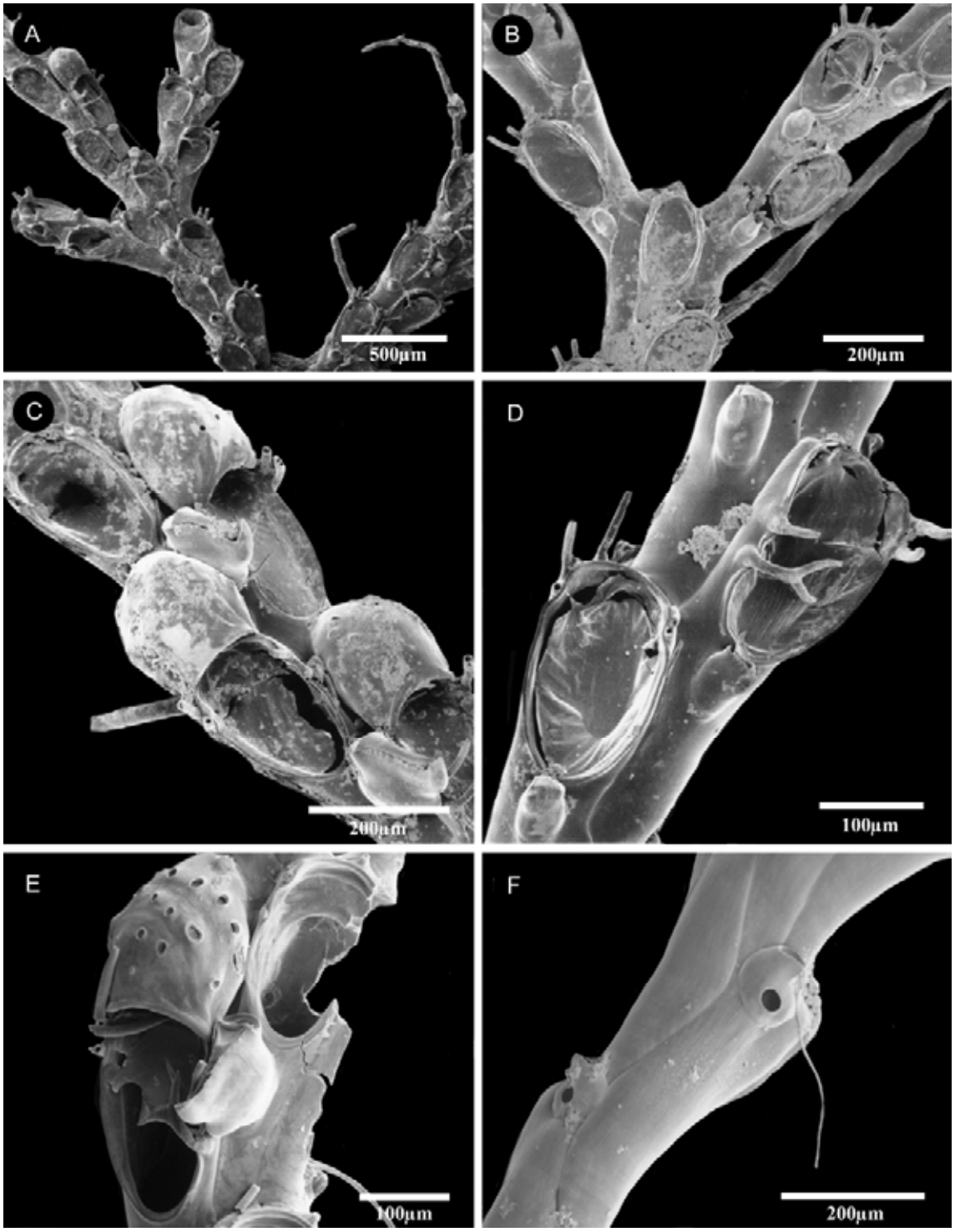

Figure 3.22. *N.gen.1 n.sp.12*. **A–F**, specimens from Rio Bueno, Jamaica (type locality). **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note a zooid with trifurcated scutum at upper right. **C**, Close-up of a branch with ovicelled zooids. **D**, Close-up of two zooids; note the presence of forked scutum in zooid at right of the branch. **E**, Close-up of ovicelled zooid and one gigantic frontal avicularium. **F**, Abfrontal surface of branch.

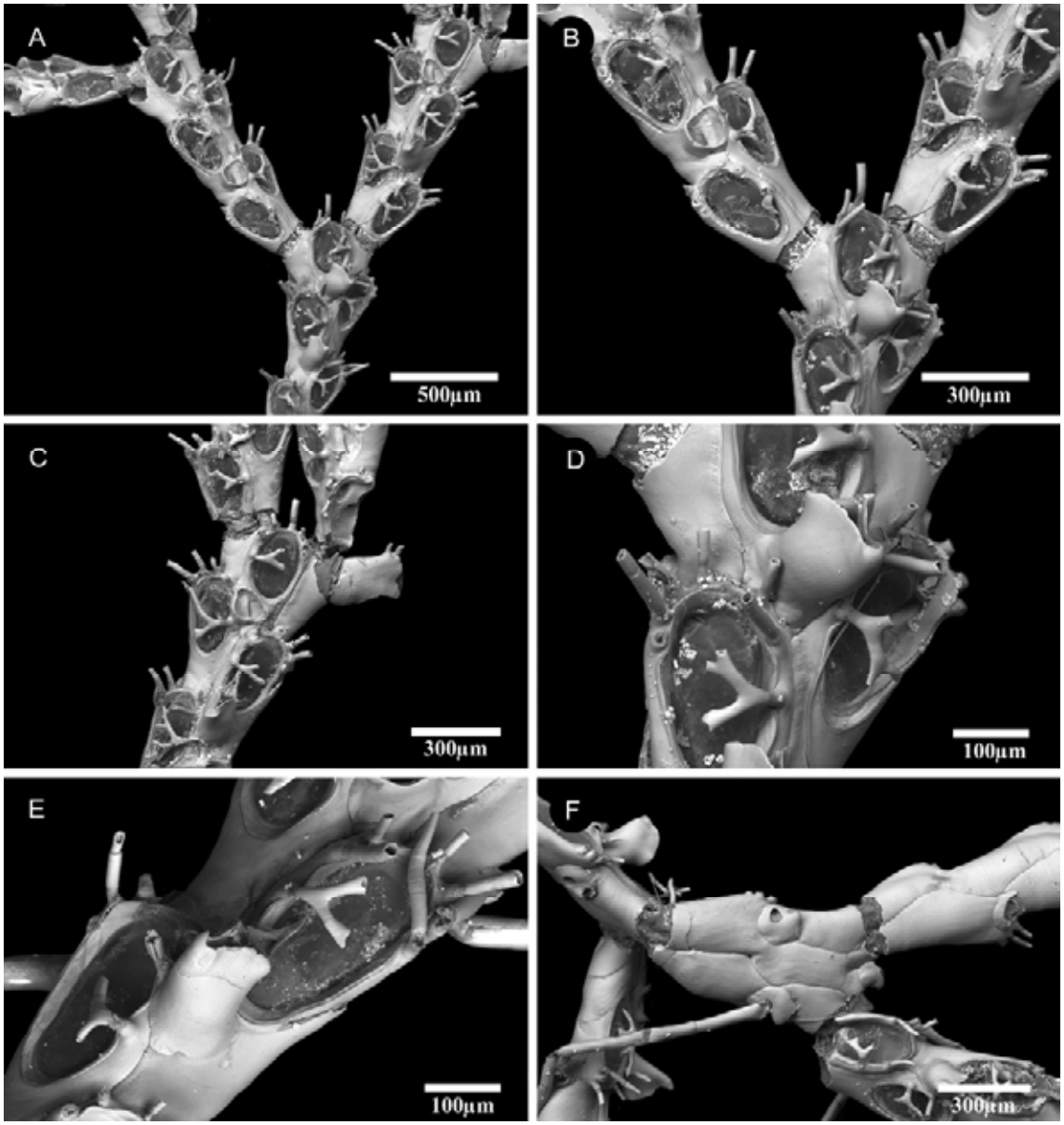

Figure 3.23. *N.gen.1 n.sp.13*. **A–F**, NHMUK 1975.7.18.31, holotype, France, Mediterranean. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the gigantic frontal avicularium on axial zooid. **C**, Close-up of a branch bifurcation; note the absence of lateral avicularium. **D**, Close-up of gigantic frontal avicularium. **E**, Close-up of a zooid; note the gigantic frontal avicularium and presence of 6 distal spines. **F**, Abfrontal surface of branch.

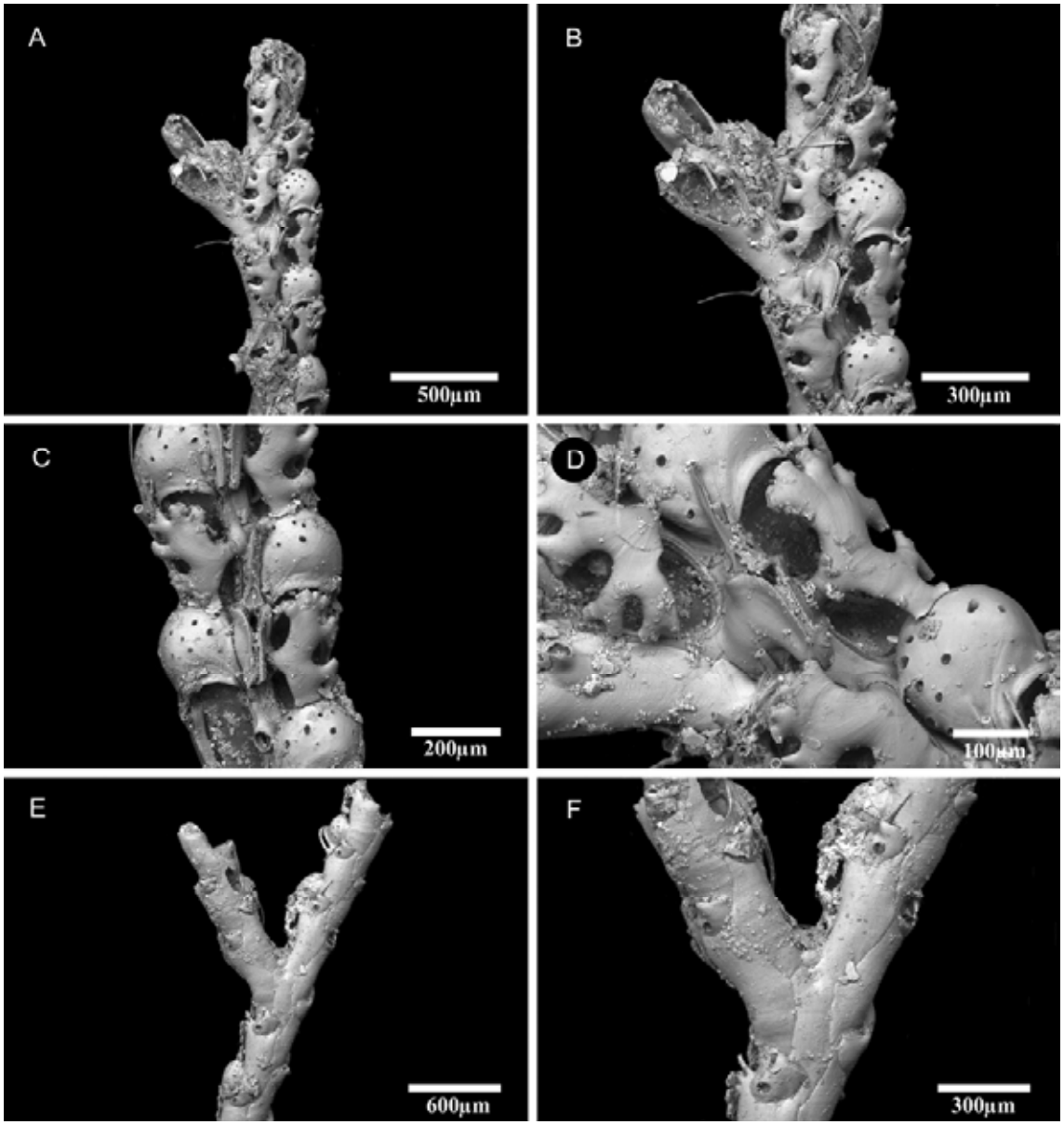

Figure 3.24. *N.gen.1 n.sp.14*. **A–F**, NHMUK 2010.12.6.19, holotype, Queensland, Australia. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the gigantic frontal avicularium on axial zooid. **C**, Close-up of a branch bifurcation; note the ovicelled zooids and the gigantic frontal avicularium. **D**, Close-up of gigantic frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation.

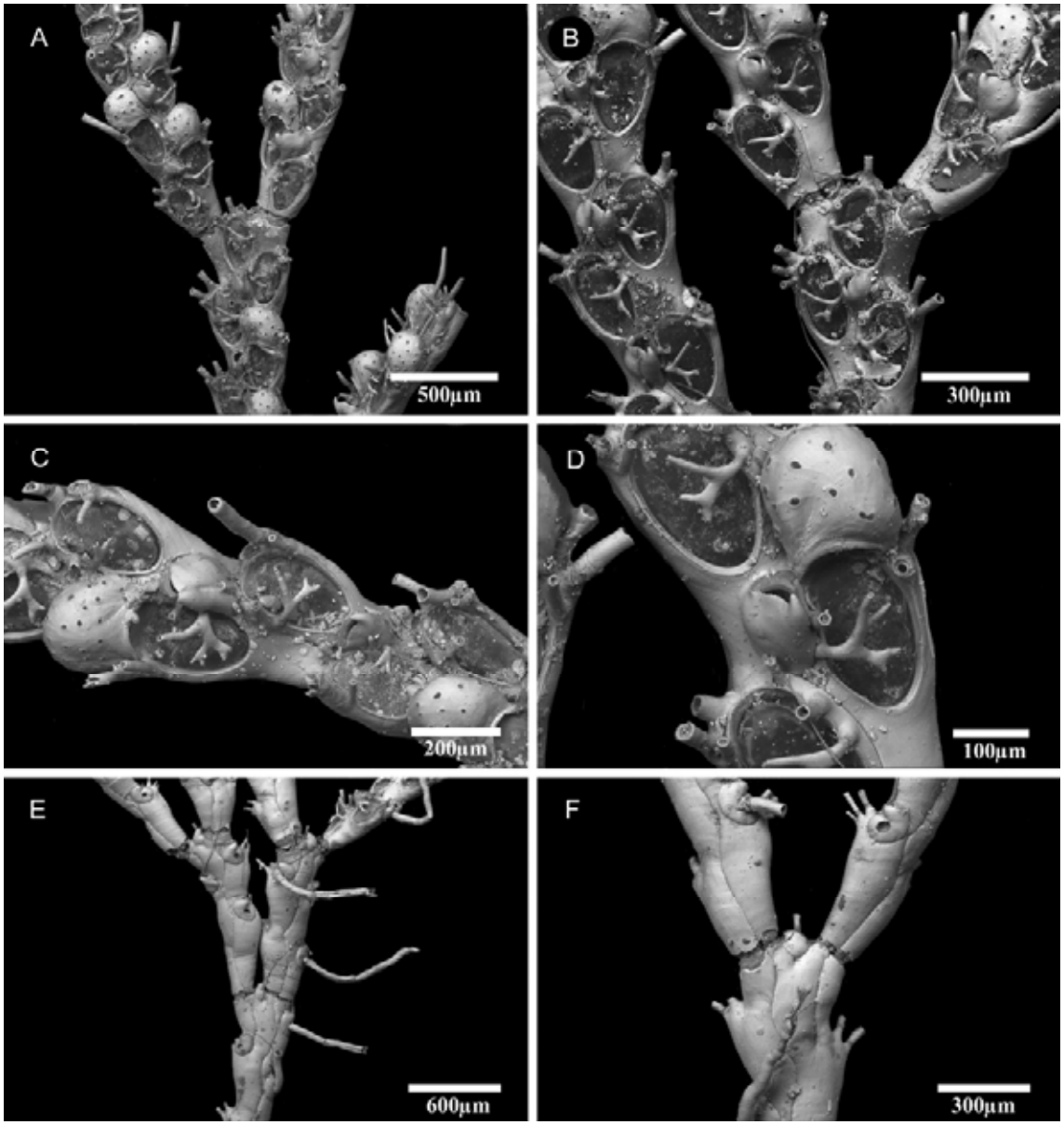

Figure 3.25. *N.gen.1 n.sp.15*. **A–F**, NHMUK 2010.12.6.17, holotype, Mozambique. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the joints passing across the gymnocyst of outers zooids at the bifurcation. **C**, Close-up of a branch bifurcation; note the ovicelled and non-ovicelled zooids. **D**, Close-up of ovicelled zooid and the frontal avicularium. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation; note the absence of vibracular chamber in some zooids.

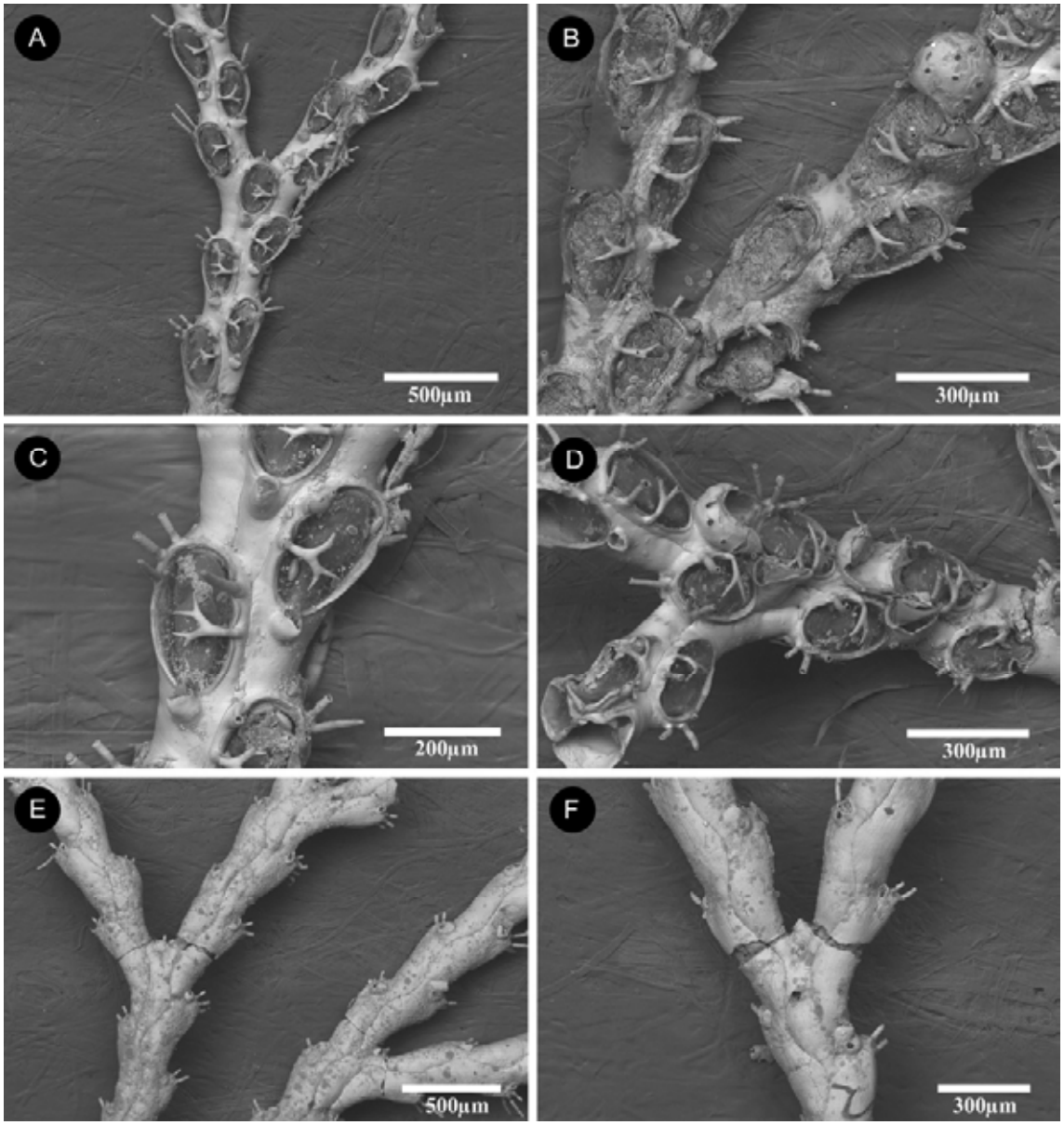

Figure 3.26. *N.gen.1 n.sp.16*. **A–F**, NHMUK 2010.12.6.28, holotype, Santos, Brazil. **A**, Frontal surface of colony; note the absence of lateral avicularia. **B**, Frontal surface of branch bifurcation; the joints passing across the proximal opesia of outer zooids at the bifurcation; note the gigantic frontal avicularium at upper right. **C**, Close-up of a branch bifurcation; note the presence of a small scutum and 4 distal spines (3 outer and 1 inner). **D**, Frontal view of to avicularia; note the slightly curved rostrum. **E**, Abfrontal surface of colony. **F**, Abfrontal surface of branch bifurcation; note the small vibracular chambers.

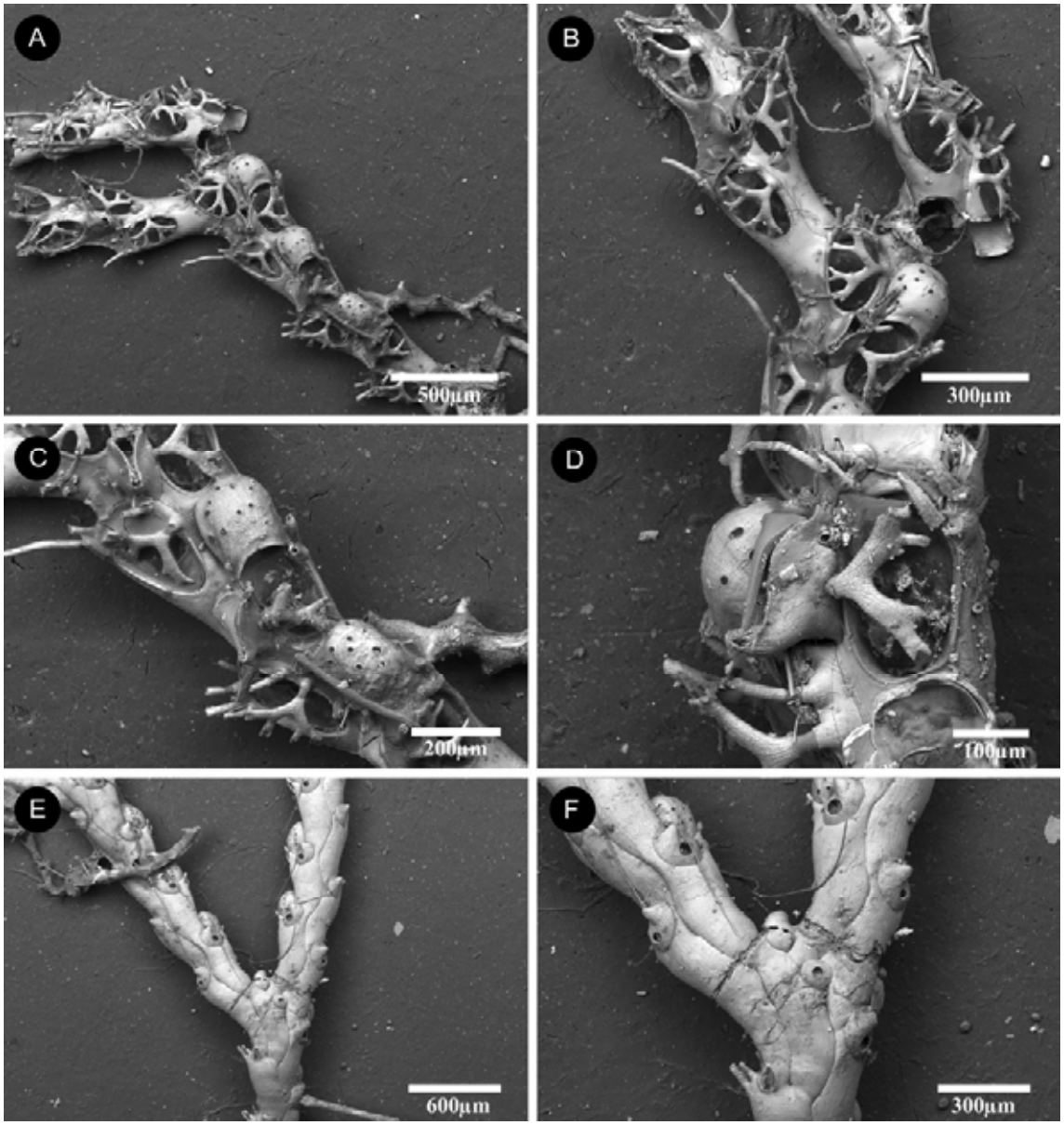

Figure 3.27. *N.gen.1 n.sp.17*. **A–F**, NHMUK 1911.10.1.355, holotype, Madeira. **A**, Frontal surface of colony; note a rhizoid with some well-developed hooks at bottom right. **B**, Frontal surface of branch bifurcation; note the regularly branched scutum. **C**, Close-up of a branch bifurcation; note the ovicelled zooids. **D**, Lateral view of gigantic frontal avicularium; note the rostrum with smooth edges. **E**, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

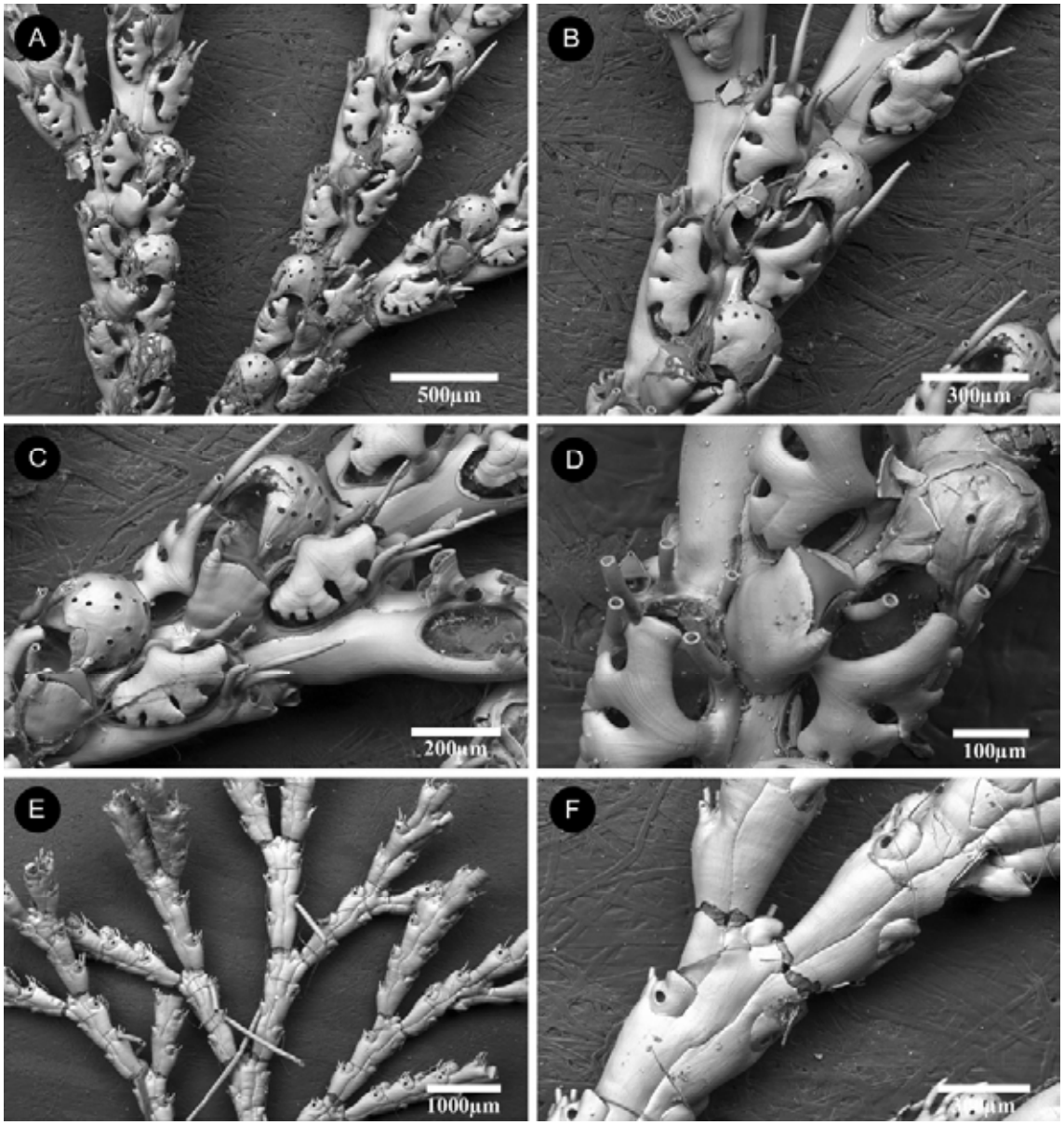

Figure 3.28. *N.gen.1 n.sp.18*. **A–F**, NHMUK 2010.12.6.21, holotype, Scotland. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the joints passing across gymnocyst of outer zooids at the bifurcation. **C**, Close-up of a branch bifurcation. **D**, Close-up of gigantic frontal avicularium. **E**, Abfrontal surface of colony; note the smooth rhizoids arising from proximal end of some vibracular chambers. **F**, Abfrontal surface of branch bifurcation.

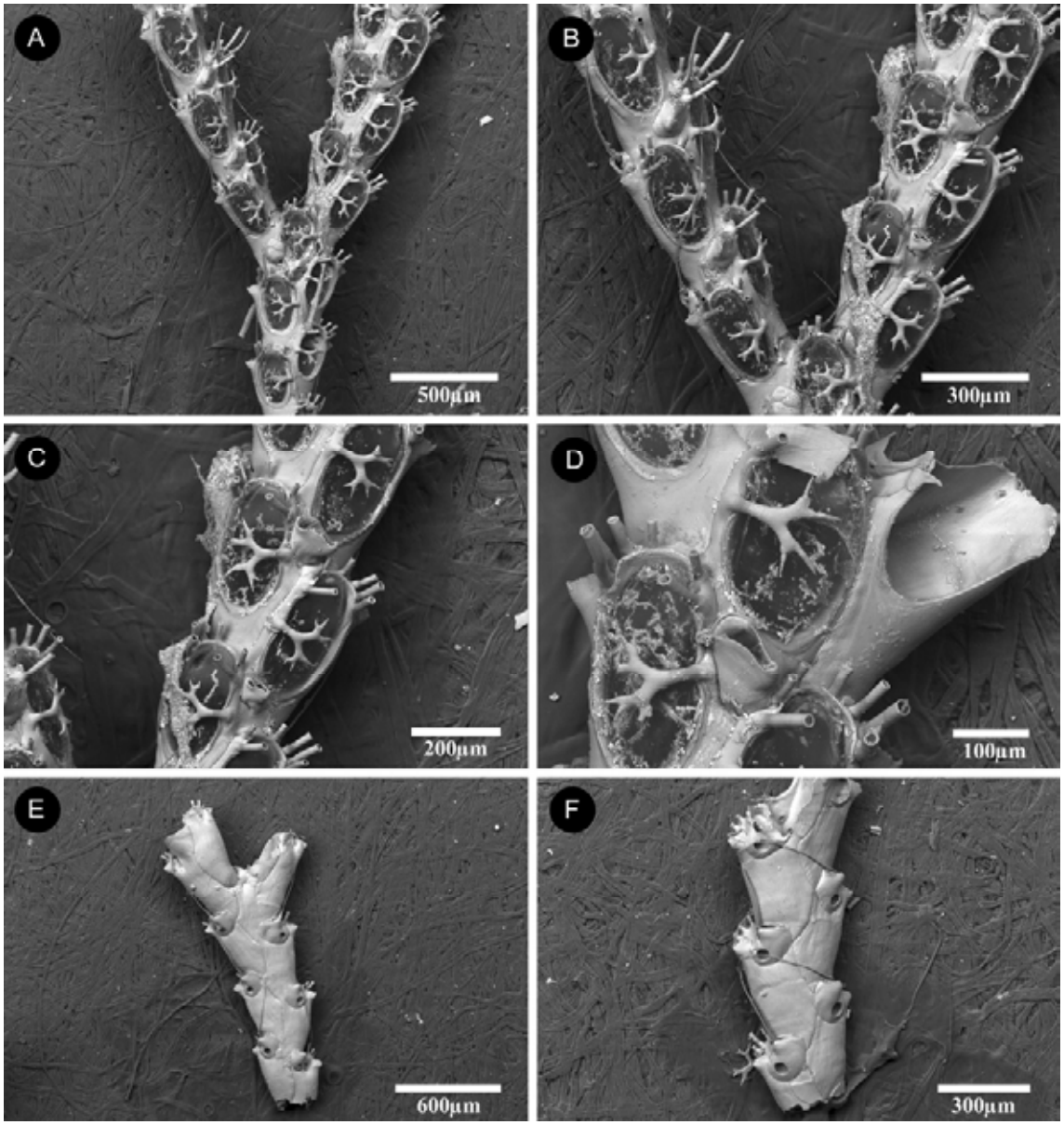

Figure 3.29. *N.gen.1 n.sp.19*. **A–F**, NHMUK 2010.6.14.3, holotype, Panama. **A**, Frontal surface of colony. **B**, Frontal surface of branch bifurcation; note the joints passing across proximal end of opesia in outer zooids at the bifurcation. **C**, Close-up of a branch bifurcation; note two diferente size of frontal avicularia. **D**, Close-up of axial zooid; note the presence of 6 and 7 distal spines in proximal zooids. **E–F**, Abfrontal surface of colony.

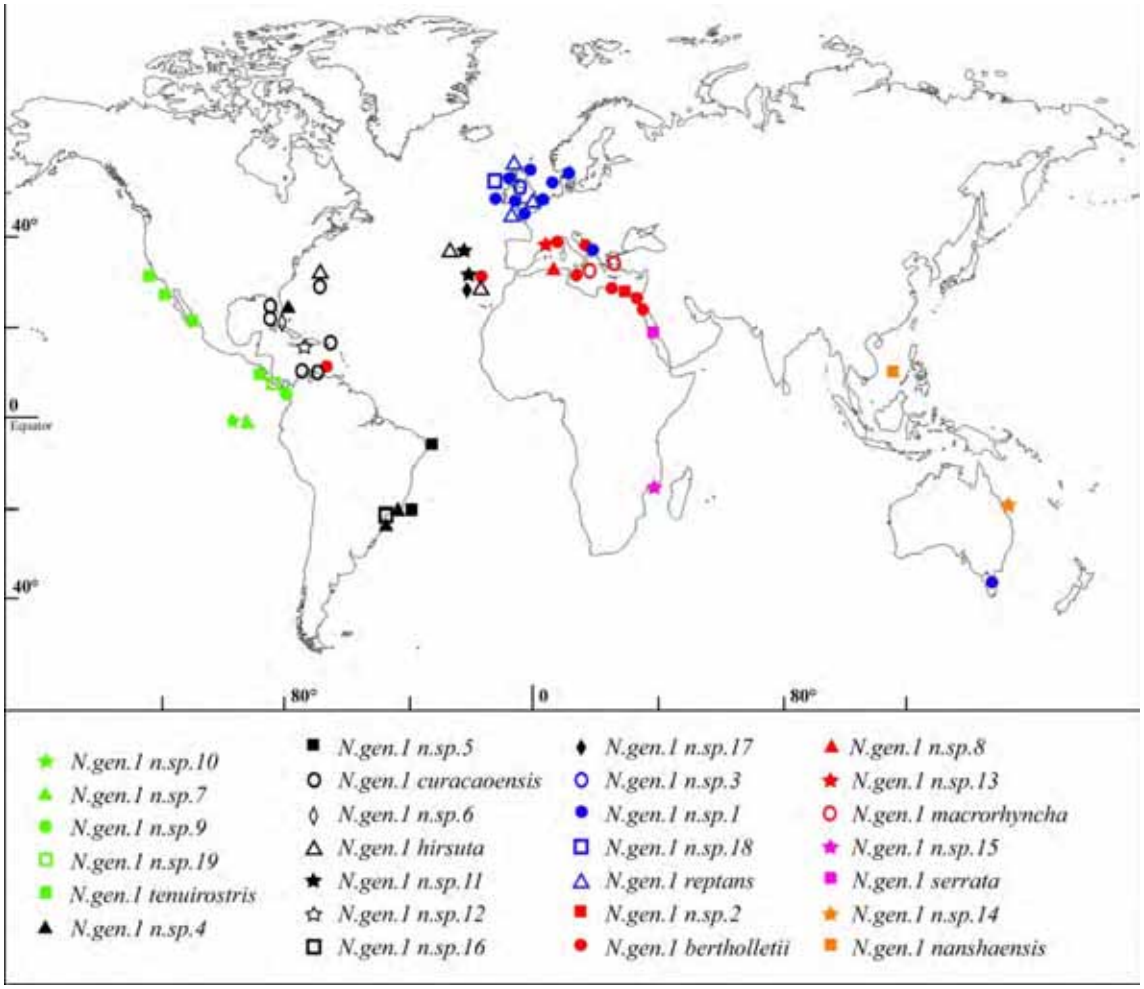

Figure 3.30. Distribution of *N.gen.1* species. Colours: Green, Eastern Pacific species; Black, Atlantic species; Blue, North Sea specimens; Red, Mediterranean species; Pink, Red-Sea and Indian species; Orange, Indo-Pacific species; Blue, Sounthern Australian species.

Table 3.1. Morphometric data for *N.gen.1* species studied (in mm).

		N.gen.1 bertholletii		*N.gen.1 curacaoensis*	
		Mediterranean[1]	Monaco[2]	Curaçao[3]	Bermuda[4]
Lz		7	7	10	5
	Mean (SD)	0.471 (0.036)	0.411 (0.038)	0.369 (0.035)	0.413 (0.021)
	Range	0.441–0.530	0.366–0.481	0.314–0.439	0.375–0.428
Wz		7	7	10	5
	Mean (SD)	0.161 (0.014)	0.154 (0.011)	0.133 (0.011)	0.135 (0.005)
	Range	0.142–0.186	0.132–0.162	0.110–0.149	0.129–0.139
Lo		7	7	10	5
	Mean (SD)	0.296 (0.022)	0.286 (0.024)	0.216 (0.007)	0.210 (0.010)
	Range	0.280–0.345	0.256–0.316	0.204–0.224	0.189–0.212
Lo/Lz		7	7	10	5
	Mean (SD)	0.64 (0.04)	0.60 (0.06)	0.58 (0.05)	0.50 (0.07)
	Range	0.58–0.67	0.57–0.73	0.48–0.66	0.49–0.51
Lsc		2	3	1	5
	Mean (SD)	0.079 (0.009)	0.087 (0.014)	0.090	0.095 (0.011)
	Range	0.073–0.086	0.071–0.099	-	0.080–0.106
Wsc		2	3	-	5
	Mean (SD)	0.044 (0.002)	0.044 (0.005)	-	0.080 (0.012)
	Range	0.043–0.046	0.038–0.047	-	0.067–0.098
Wsc/Lo		2	3	-	5
	Mean (SD)	0.12 (0.01)	0.15 (0.03)	-	0.40 (0.04)
	Range	0.10–0.013	0.12–0.18	-	0.34–0.46
Lvib		7	5	5	3
	Mean (SD)	0.125 (0.008)	0.103 (0.011)	0.096 (0.007)	0.097 (0.016)
	Range	0.108–0.133	0.093–0.118	0.084–0.103	0.088–0.120
Wvib		7	5	5	3
	Mean (SD)	0.106 (0.007)	0.098 (0.007)	0.070 (0.003)	0.086 (0.010)
	Range	0.105–0.123	0.085–0.101	0.067–0.076	0.073–0.093
Lov		5	6	7	-
	Mean (SD)	0.187 (0.003)	0.174 (0.022)	0.159 (0.006)	-
	Range	0.183–0.192	0.162–0.223	0.151–0.167	-
Wov		5	6	7	-
	Mean (SD)	0.189 (0.004)	0.172 (0.012)	0.155 (0.012)	-
	Range	0.181–0.193	0.163–0.193	0.130–0.163	-

[1] NHMUK 1899.7.1.736, Mediterranean.
[2] NHMUK 2012.7.1.4, Monaco.
[3] NHMUK 2012.7.1.12, Curaçao.
[4] NMNH (Bermud-4-A-4303), Bermuda.

Table 3.2. Morphometric data for *N.gen.1* species studied (in mm).

	N.gen.1 n.sp.1	*N.gen.1 hirsuta*		*N.gen.1 macrorhyncha*	*N.gen.1 reptans*
	UK[1]	Azores[2]	Madeira[3]	Mediterranean[4]	UK[5]
Lz	10	10	6	-	8
Mean (SD)	0.482 (0.059)	0.389 (0.050)	430 (0.060)	-	0.389 (0.033)
Range	0.405–0.612	0.311–0.485	0.337–0.504	0.620–0.680	0.356–0.451
Wz	10	10	6	-	8
Mean (SD)	0.200 (0.009)	0.150 (0.011)	0.151 (0.013)	-	0.186 (0.012)
Range	0.191–0.221	0.143–0.181	0.142–0.179	0.240–0.260	0.165–0.205
Lo	10	10	6	-	8
Mean (SD)	0.298 (0.026)	0.222 (0.014)	0.236 (0.015)	-	0.246 (0.016)
Range	0.270–0.332	0.203–0.247	0.228–0.263	0.300–0.350	0.209–0.267
Lo/Lz	10	10	6	-	8
Mean (SD)	0.67 (0.06)	0.60 (0.05)	0.58 (0.09)	-	0.64 (0.004)
Range	0.51–0.69	0.50–0.65	0.45–0.69	-	0.55–0.68
Lsc	10	-	-	-	8
Mean (SD)	0.155 (0.011)	-	-	-	0.131 (0.012)
Range	0.132–0.172	-	-	-	0.117–0.158
Wsc	10	-	-	-	8
Mean (SD)	0.265 (0.010)	-	-	-	0.205 (0.012)
Range	0.250–0.281	-	-	-	0.190–0.230
Wsc/Lo	10	-	-	-	8
Mean (SD)	0.88 (0.10)	-	-	-	0.83 (0.04)
Range	0.80–1.03	-	-	-	0.78–0.90
Lvib	8	10	7	4	5
Mean (SD)	0.135 (0.003)	0.129 (0.011)	0.137 (0.012)	0.174 (0.009)	141 (0.011)
Range	0.130–0.138	0.106–0.137	0.122–0.151	0.164–0.183	0.126–0.155
Wvib	8	10	7	4	5
Mean (SD)	0.116 (0.010)	0.111 (0.011)	0.116 (0.010)	0.131 (0.003)	0.101 (0.008)
Range	0.099–0.133	0.096–0.128	0.107–0.140	0.128–0.134	0.088–0.114
Lov	3	6	1	3	-
Mean (SD)	0.189 (0.008)	0.155 (0.011)	0.174	0.208 (0.011)	-
Range	0.186–0.202	0.146–0.173	-	0.207–0.227	-
Wov	3	6	1	3	-
Mean (SD)	0.194 (0.005)	0.164 (0.007)	0.154	0.204 (0.004)	-
Range	0.187–0.196	0.145–0.168	-	0.196–0.205	-

[1] NHMUK 1911.10.1.353, United Kingdom.
[2] MOM 420323, Azores.
[3] NHMUK 1911.10.1.386, Madeira.
[4] NHMUK 1965.9.2.4, Mediterranean; measurements of the autozooids and the opesia from Gautier (1962).
[5] NHMUK 1963.3.6.35, United Kingdom.

Table 3.3. Morphometric data for *N.gen.1* species studied (in mm).

	N.gen.1 tenuirostris California[1]	*N.gen.1 n.sp.2* Egypt[2]	*N.gen.1 n.sp.3* Scotland[3]	*N.gen.1 n.sp.4* Brazil[4]	*N.gen.1 n.sp.4* USA[5]
Lz	10	8	10	8	8
Mean (SD)	0.437 (0.020)	0.426 (0.025)	0.428 (0.030)	0.405 (0.045)	0.428 (0.027)
Range	0.420–0.473	0.390–0.453	0.401–0.489	0.343–0.473	0.402–0.483
Wz	10	8	10	8	8
Mean (SD)	0.221 (0.014)	0.172 (0.025)	0.166 (0.012)	0.174 (0.016)	0.201 (0.019)
Range	0.192–0.229	0.158–0.191	0.142–0.181	0.147–0.200	0.153–0.206
Lo	10	8	10	8	8
Mean (SD)	0.354 (0.020)	0.272 (0.010)	0.247 (0.008)	0.308 (0.018)	0.308 (0.020)
Range	0.327–0.387	0.257–0.281	0.229–0.254	0.279–0.343	0.296–0.350
Lo/Lz	10	8	10	8	8
Mean (SD)	0.78 (0.05)	0.64 (0.03)	0.57 (0.04)	0.78 (0.05)	0.74 (0.005)
Range	0.70–0.85	0.60–0.70	0.50–0.62	0.65–0.83	0.65–0.79
Lsc	10	8	10	8	8
Mean (SD)	0.146 (0.014)	0.140 (0.008)	0.118 (0.008)	0.132 (0.012)	0.133 (0.019)
Range	0.130–0.170	0.126–0.148	0.107–0.135	0.108–0.140	0.096–0.152
Wsc	10	8	10	8	8
Mean (SD)	0.225 (0.009)	0.193 (0.012)	0.185 (0.021)	0.148 (0.017)	0.153 (0.020)
Range	0.218–0.241	0.167–0.201	0.147–0.206	0.133–0.186	0.122–0.189
Wsc/Lo	10	8	10	8	8
Mean (SD)	0.67 (0.03)	0.68 (0.05)	0.75 (0.08)	0.49 (0.05)	0.50 (0.05)
Range	0.58–0.68	0.63–0.76	0.61–0.86	0.43–0.59	0.40–0.54
Lvib	8	10	4	10	8
Mean (SD)	0152 (0.016)	0.133 (0.010)	0.129 (0.005)	0.134 (0.011)	0.133 (0.008)
Range	0.140–0.187	0.127–0.159	0.122–0.134	0.120–0.154	0.121–0.143
Wvib	8	10	4	10	8
Mean (SD)	0.126 (0.0.17)	0.108 (0.004)	0.106 (0.007)	0.100 (0.007)	0.109 (0.010)
Range	0.115–0.156	0.103–0.115	0.099–0.113	0.090–0.110	0.097–0.123
Lov	10	10	-	10	8
Mean (SD)	0.134 (0.020)	0.145 (0.010)	-	0.145 (0.014)	0.134 (0.016)
Range	0.110–0.177	0.133–0.166	-	0.129–0.174	0.124–0.176
Wov	10	10	-	10	8
Mean (SD)	0.176 (0.011)	0.166 (0.008)	-	0.166 (0.007)	0.180 (0.007)
Range	0.159–0.193	0.160–0.187	-	0.158–0.179	0.171–0.197

[1] NHMUK 2010.10.6.1, California, USA.
[2] NHMUK 1963.8.2.16, Egypt.
[3] NHMUK 2010.12.6.1, Arisaig, Scotland.
[4] MZUSP no number, São Paulo, Brazil.
[5] VMNH 10403.0000, Florida, USA.

Table 3.4. Morphometric data for *N.gen.1* species studied (in mm).

	N.gen.1 n.sp.5 Brazil[1]	*N.gen.1 n.sp.6* Tortugas[2]	*N.gen.1 n.sp.7* Galapagos[3]	*N.gen.1 n.sp.8* Algeria[4]	*N.gen.1 n.sp.9* Gorgona[5]
Lz	8	10	10	10	10
Mean (SD)	0.381 (0.020)	0.384 (0.039)	0.316 (0.016)	0.467 (0.027)	0.354 (0.023)
Range	0.358–0.415	0.325–0.443	0.283–0.337	0.410–0.497	0.328–0.400
Wz	8	10	10	10	10
Mean (SD)	0.152 (0.008)	0.156 (0.010)	0.190 (0.016)	0.202 (0.009)	0.156 (0.012)
Range	0.140–0.165	0.144–0.181	0.168–0.215	0.193–0.221	0.141–0.173
Lo	8	10	10	10	10
Mean (SD)	0.238 (0.015)	0.242 (0.021)	0.253 (0.013)	0.301 (0.020)	0.243 (0.022)
Range	0.219–0.264	0.223–0.277	0.230–0.273	0.285–0.350	0.223–0.286
Lo/Lz	8	10	10	10	10
Mean (SD)	0.63 (0.04)	0.65 (0.05)	0.81 (0.04)	0.68 (0.05)	0.69 (0.04)
Range	0.54–0.67	0.55–0.69	0.73–0.86	0.60–0.73	0.63–0.74
Lsc	8	10	10	10	10
Mean (SD)	0.105 (0.007)	0.099 (0.011)	0.138 (0.009)	0.165 (0.011)	0.107 (0.011)
Range	0.097–0.117	0.0740.113	0.128–0.158	0.139–0.173	0.086–0.126
Wsc	8	10	10	10	10
Mean (SD)	0.105 (0.009)	0.085 (0.019)	0.162 (0.011)	0.298 (0.016)	0.109 (0.023)
Range	0.090–0.115	0.053–0.100	0.148–0.183	0.282–0.329	0.085–0.152
Wsc/Lo	8	10	10	10	10
Mean (SD)	0.44 (0.005)	0.34 (0.06)	0.64 (0.004)	0.96 (0.02)	0.47 (0.07)
Range	0.34–0.52	0.24–0.41	0.58–0.72	0.94–1.01	0.35–0.57
Lvib	10	7	10	10	10
Mean (SD)	0.120 (0.005)	0.117 (0.007)	0.160 (0.014)	0.185 (0.011)	0.144 (0.007)
Range	0.114–0.128	0.107–0.129	0.128–0.174	0.162–0.201	0.129–0.152
Wvib	10	7	10	10	10
Mean (SD)	0.092 (0.007)	0.106 (0.007)	0.149 (0.012)	0.152 (0.010)	0.118 (0.010)
Range	0.085–0.108	0.097–0.119	0.130–0.169	0.138–0.165	0.105–0.134
Lov	8	10	6	-	10
Mean (SD)	0.157 (0.012)	0.150 (0.014)	0.145 (0.011)	-	0.140 (0.015)
Range	0.135–0.173	0.127–0.173	0.131–0.164	-	0.131–0.177
Lov	8	10	6	-	10
Mean (SD)	0.156 (0.005)	0.162 (0.013)	0.155 (0.013)	-	0.162 (0.015)
Range	0.151–0.165	0.146–0.189	0.138–0.172	-	0.142–0.184

[1] MNHN 15979, California, USA.
[2] NHMUK 2010.12.6.2, Florida, USA.
[3] NHMUK 2010.12.6.3, Galapagos.
[4] NHMUK 1882.5.24.9, Algeria.
[5] NHMUK 2010.12.6.4, Gorgona, Colombia.

Table 3.5. Morphometric data for *N.gen.1* species studied (in mm).

	N.gen.1 n.sp.10 Galapagos[1]	*N.gen.1 n.sp.11* Cape Verde[2]	*N.gen.1 n.sp.12* Jamaica[3]	*N.gen.1 n.sp.13* Mediterranean[4]	*N.gen.1 n.sp.14* Queensland[5]
Lz	10	10	10	8	7
Mean (SD)	0.420 (0.030)	368 (0.026)	0.421 (0.039)	0.446 (0.032)	0.439 (0.029)
Range	0.374–0.453	0.338–0.425	0.369–0.494	0.385–0.488	0.406–0.499
Wz	10	10	10	8	7
Mean (SD)	0.206 (0.014)	0.155 (0.012)	0.166 (0.012)	0.182 (0.013)	0.167 (0.015)
Range	0.180–0.228	0.143–0.180	0.144–0.178	0.164–0.196	0.148–0.191
Lo	10	10	10	8	7
Mean (SD)	0.307 (0.020)	0.247 (0.018)	0.253 (0.015)	0.278 (0.016)	0.289 (0.011)
Range	0.272–0.344	0.208–0.276	0.222–0.268	0.256–0.303	0.271–0.300
Lo/Lz	10	10	10	8	7
Mean (SD)	0.75 (0.04)	0.66 (0.04)	0.55 (0.04)	0.63 (0.03)	0.66 (0.05)
Range	0.69–0.80	0.61–0.74	0.53–0.66	0.57–0.66	0.54–0.69
Lsc	-	10	-	-	7
Mean (SD)	-	0.97 (0.004)	-	-	0.146 (0.012)
Range	-	0.90–0.105	-	-	0.131–0.158
Wsc	-	10	-	-	7
Mean (SD)	-	0.074 (0.016)	-	-	0.262 (0.018)
Range	-	0.061–0.105	-	-	0.244–0.290
Wsc/Lo	-	10	-	-	7
Mean (SD)	-	0.32 (0.07)	-	-	0.92 (0.05)
Range	-	0.24–0.45	-	-	0.84–0.99
Lvib	8	10	7	3	5
Mean (SD)	0.145 (0.009)	0.134 (0.015)	0.126 (0.014)	0.158 (0.020)	0.144 (0.012)
Range	0.136–0.162	0.110–0.163	0.101–0.144	0.143–0.172	0.138–0.166
Wvib	8	10	7	3	5
Mean (SD)	0.120 (0.013)	0.111 (0.011)	0.101 (0.012)	0.130 (0.002)	0.134 (0.011)
Range	0.096–0.134	0.100–0.130	0.087–0.118	0.128–0.132	0.118–0.148
Lset	6	6	-	-	-
Mean (SD)	0.315 (0.010)	0.402 (0.045)	-	-	-
Range	0.304–0.325	0.373–0.480	-	-	-
Lov	10	7	10	-	7
Mean (SD)	0.183 (0.012)	0.152 (0.007)	0.183 (0.015)	-	0.185 (0.009)
Range	0.163–0.201	0.145–0.168	0.166–0.217	-	0.170–0.200
Lov	10	7	10	-	7
Mean (SD)	0.198 (0.013)	0.159 (0.013)	0.161 (0.009)	-	0.188 (0.009)
Range	0.170–0.206	0.153–0.189	0.140–0.173	-	0.175–0.200

[1] NHMUK 1929.4.26.25, Galapagos.
[2] NHMUK 2010.12.6.16, Cape Verde.
[3] Unregistered specimens, same data as holotype, Jamaica.
[4] NHMUK 1975.7.18.31, Mediterranean.
[5] NHMUK 2010.12.6.19, Queensland, Australia.

Table 3.6. Morphometric data for *N.gen.1* species studied (in mm).

	N.gen.1 n.sp.15 Mozambique[1]	*N.gen.1 n.sp.16* Brazil[2]	*N.gen.1 n.sp.17* Madeira[3]	*N.gen.1 n.sp.18* Scotland[4]	*N.gen.1 n.sp.19* Panama[5]
Lz	10	8	9	10	7
Mean (SD)	0.428 (0.012)	0.425 (0.023)	0.436 (0.045)	0.515 (0.039)	0.389 (0.035)
Range	0.407–0.454	0.377–0.437	0.400–0.523	0.454–0.605	0.359–0.454
Wz	10	8	9	10	7
Mean (SD)	0.184 (0.012)	0.160 (0.11)	0.175 (0.017)	0.209 (0.012)	0.174 (0.011)
Range	0.167–0.204	0.142–0.172	0.150–0.209	0.197–0.234	0.161–0.194
Lo	10	8	9	10	7
Mean (SD)	0.260 (0.017)	0.249 (0.017)	0.254 (0.014)	0.321 (0.018)	0.296 (0.016)
Range	0.248–0.301	0.219–0.277	0.240–0.282	0.283–0.353	0.271–0.309
Lo/Lz	10	8	9	10	7
Mean (SD)	0.62 (0.04)	0.60 (0.03)	0.60 (0.006)	0.64 (0.05)	0.75 (0.08)
Range	0.57–0.67	0.57–0.64	0.47–0.65	0.53–0.68	0.61–0.85
Lsc	10	8	9	10	7
Mean (SD)	0.101 (0.008)	0.091 (0.010)	0.132 (0.017)	0.163 (0.012)	0.110 (0.010)
Range	0.095–0.120	0.086–0.111	0.106–0.152	0.143–0.183	0.096–0.120
Wsc	10	8	9	10	7
Mean (SD)	0.131 (0.022)	0.093 (0.014)	0.212 (0.017)	0.283 (0.020)	0.130 (0.012)
Range	0.096–0.158	0.072–0.111	0.172–0.221	0.254–0.313	0.127–0.160
Wsc/Lo	10	8	9	10	7
Mean (SD)	0.49 (0.06)	0.38 (0.06)	0.82 (0.06)	0.87 (0.003)	0.46 (0.04)
Range	0.35–0.56	0.26–0.46	0.71–0.90	0.83–0.93	0.42–0.54
Lvib	6	6	5	8	7
Mean (SD)	0.156 (0.007)	0.100 (0.010)	0.161 (0.008)	0.178 (0.011)	0.137 (0.008)
Range	0.144–0.162	0.091–0.117	0.156–0.176	0.167–0.198	0.120–0.146
Wvib	6	6	5	8	7
Mean (SD)	0.123 (0.012)	0.075 (0.003)	0.106 (0.005)	0.144 (0.008)	0.117 (0.011)
Range	0.113–0.147	0.071–0.081	0.101–0.114	0.136–0.198	0.107–0.139
Lov	8	1	7	8	-
Mean (SD)	0.186 (0.005)	-	0.188 (0.011)	0.210 (0.009)	-
Range	0.177–0.192	0.177	0.179–0.211	0.195–0.221	-
Lov	8	1	7	8	-
Mean (SD)	0.182 (0.016)	-	0.171 (0.013)	0.208 (0.017)	-
Range	0.162–0.209	0.180	0.146–0.188	0.182–0.230	-

[1] NHMUK 1938.5.2.4, Mozambique.
[2] NHMUK 2010.12.6.28, Santos, Brazil.
[3] NHMUK 1911.10.1.355, Madeira Island.
[4] NHMUK 2010.12.6.21, Gairloch, Scotland.
[5] NHMUK 2010.6.14.3, Panama.

CAPÍTULO 4

EVIDENCE OF POLYPHYLY OF THE GENUS *SCRUPOCELLARIA* (BRYOZOA, CANDIDAE) BASED ON A PHYLOGENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS

O capítulo corresponde ao manuscrito de autoria de Leandro M. Vieira, Alvaro E. Migotto, Judith E. Winston & Antonio C. Marques, a ser submetido no periódico *Invertebrate Zoology*.

Evidence for polyphyly of the genus *Scrupocellaria* (Bryozoa, Candidae) based on a phylogenetic analysis of morphological characters

ABSTRACT

We proposed a hypothesis of the phylogenetic relationships among *Scrupocellaria* to serve as framework for a phylogenetic classification of the group using 35 morphological characters. Our results suggest that the genus *Scrupocellaria* is polyphyletic. *Scrupocellaria 'sensu stricto'* is redefined according to four morphological features: vibracular chamber with curved setal groove, ooecium with a single ectooecial fenestra, two axillary vibracula and membranous operculum with a distinct distal rim. Thus, the genus includes 10 species: *Scrupocellaria aegeensis*, *Scrupocellaria delilii*, *Scrupocellaria harmeri*, *Scrupocellaria incurvata*, *Scrupocellaria inermis*, *Scrupocellaria intermedia*, *Scrupocellaria jullieni*, *Scrupocellaria minuta*, *Scrupocellaria scrupea* and *Scrupocellaria scruposa*. The monophyly of *N.gen.1* is supported and five new genera are erected.

INTRODUCTION

The genus *Scrupocellaria* was erected to include *Sertularia scruposa* Linnaeus, 1758 (VAN BENEDEN, 1845). Later authors added additional species and described new characters (HARMER, 1923) – consequently, the bryozoan genus *Scrupocellaria* van Beneden, 1845 grew in size and morphological diversity over time. In its broad sense (*cf.* HARMER, 1926; HAYWARD & RYLAND, 1998) *Scrupocellaria* has been defined as having the following characteristics: erect, biserial, branching colonies anchored to the substratum by rhizoids, rhombic autozooids with partially membranous frontal wall, spines, including a modified lateral spine (the scutum), zooid polymorphs often including lateral and/or frontal avicularia, almost always baso-lateral vibracula, and subglobular hyperstomial ooecia (HAYWARD & RYLAND, 1998). At least three genera were synonymized under *Scrupocellaria*, *viz. Cellarina* van Beneden, 1848, *Crisina* van Beneden, 1850, and *Licornia* van Beneden, 1850 (HARMER, 1926). One of the previously synonymized genera, *Licornia*, has since been treated as a distinct taxon and its generic status restored (L.M. Vieira *et al*., unpublished data; see Chapter 2).

Neither a morphological nor a molecular phylogenetic hypothesis has been published for any taxa of Candidae. Thus, the goals of this study are (i) to assess and provide a comparative morphology of *Scrupocellaria*, finding overlooked homologies of

the character states in order to (ii) propose a hypothesis of the phylogenetic relationships among *Scrupocellaria* to (iii) serve as framework for a phylogenetic classification of the group and the validation of new nomenclatural decisions.

MATERIALS AND METHODS

Taxa sampling

We examined colonies of 84 species of Candidae deposited in the collections of the American Museum of Natural History (AMNH, USA), Linnean Society of London (LSL, UK), Musée océanographique de Monaco (MO, France), Museu de Zoologia da Universidade de São Paulo (MZUSP, Brazil), Muséum national d'Histoire naturelle (MNHN, France), Museum of Comparative Zoology of Harvard University (MCZ, USA), Museum Victoria (NMV, Australia), Museum of Tropical Queensland (MTQ, Australia), National Museum of Natural History (NMNH, USA), The Natural History Museum of London (NHMUK, UK), Nederlands Centrum voor Biodiversiteit, Naturalis (RMNH, The Netherlands), Santa Barbara Museum of Natural History (SBMNH, USA), Virginia Museum of Natural History (VMNH, USA) (Appendix 4.I.). Taxa whose identities were uncertain were not included in the analysis.

Because of the absence of any previous phylogenetic hypothesis related to the family Candidae, we selected 8 species from four genera to serve as outgroups for the analysis, *viz. Notoplites* Harmer, 1923, *Tricellaria* Fleming, 1828, *Canda* Lamouroux, 1816 and *Caberea* Lamouroux, 1816. Incorporating these taxa was also important in order to test the monophyly of *Scrupocellaria*. We chose *Notoplites marsupiatus* to root the unrooted cladogram of the analysis because of its distinct scutum shape (when compared with other Candidae species) and the presence of abfrontal avicularia rather than abfrontal vibracula [considered to be characteristic of *Scrupocellaria* species; see HARMER (1926), HASTINGS (1943), HAYWARD & RYLAND (1998); TILBROOK & VIEIRA (*in press*)].

Morphology and phylogenetic analysis

All specimens were examined under the stereomicroscope. Selected specimens were mounted for examination in a scanning electron microscope (SEM) (Zeiss EVO-60, Zeiss LEO 1455-VP and Zeiss DSM 940) for description and selection of the characters. We scored 35 characters for all terminal taxa; some of these characters show homoplasies among the family members (*e.g.* absence of scutum and rhizoids

with hooks). All characters were treated as unordered and equally weighted. Autapomorphies of terminal taxa, which do not provide evidence to support monophyly at supraspecific levels were excluded from the analysis. Unknown states were indicated as "?" in the data matrix, inapplicable states were in indicated as "-". Whenever necessary, polymorphisms were explicitly considered in the coding and are marked in the data matrix. The list and discussion of characters used are given in Appendix 4.II.

The character matrix (Appendix 4.III.) was edited using Mesquite v2.75 (MADDISON & MADDISON, 2011). Maximum parsimony analyses were carried out using TNT v1.1 (GOLOBOFF *et al.*, 2008), adopting "New Technology" search algorithms (sectorial search, ratchet, tree drifting and tree fusion) for 3,000 random addition sequences, 10 random seed, opting for collapsing trees after the search. The resulting forest of trees was summarized in a semi-strict consensus (BREMER, 1990) topology. The length of trees (L), consistency index (CI) and retention index (RI) for both tree and characters were calculated. Morphological characters were optimized in the semi-strict consensus tree (Figure 4.1), and the list of state optimizations was included in Appendix 4.IV.

RESULTS AND DISCUSSION

The TNT analysis yielded 30 most parsimonious trees (L= 125; CI= 0.412; RI= 0.810). The semi-strict consensus tree (L= 153; CI= 0.405; RI= 0.808) shows a polyphyly of the genus *Scrupocellaria* (Figure 4.1).

Tricellaria

The basal part of the tree of the Candidae has a low resolution, probably because of the high number of inapplicable characters present in those basal taxa causing unstable relationships. Taxonomically, we decided to consider two species of the basal polytomies part of the genus *Tricellaria* Fleming, 1828, *viz. Tricellaria arctica* n. comb. and *Tricellaria elongata* n. comb., instead of creating new generic names to accommodate these species. Our decision is based in some shared characters, such as (i) absence of abfrontal vibracula/avicularia, (ii) presence of a lateral rhizoidal chamber associated with the outer zooids of the bifurcation, (iii) a scutum arising from the distal third of the inner opesial rim and (iv) joints passing across the gymnocyst of outer zooids in the zooids C and D. *Tricellaria* is the sister group of *Scrupocellaria congesta* (genus *incertae sedis*) + Group A + Clade B.

Group A: taxa with basal avicularium

There is a polytomy of four species herein considered to be part of Group A and a large Clade B (with an unambiguous synapomorphy, presence of abfrontal vibracular chamber). The unresolved polytomy would allow a monophyletic Group A, to be tested in future analysis. Nomenclaturally, it is convenient to consider the species of Group A belonging to a unique genus. All species of Group A are endemic to Arctic and sub-Arctic waters, and may characterized by colonies with chitinous joints passing across the gymnocyst of outer zooids of the bifurcation, as those of *Tricellaria*, but with abfrontal avicularia. Thus, they are distinct from *Tricellaria* by absence of the lateral rhizoidal chamber associated to the outer zooids of the bifurcation, presence of abfrontal avicularia and scutum arising at the median region of the inner part of the opesia.

Clade B: taxa with abfrontal vibracula

The analysis supports the monophyly of the species of Candidae with an abfrontal vibracular chamber (Clade B). The switch from smooth lateral edge to serrated lateral edge of the rostrum of the lateral avicularium is another synapomorphy for this clade. This clade comprises four monophyletic groups (Clade C + Clade D + Clade E + Clade F). The topology of Clade B shows an interesting history concerning the development of setal groove of the vibracular chamber along the evolution of the species of Candidae. The possession of a vibracular chamber with transversal setal groove would be primitive (plesiomorphic, present in three Clade C, Clade D, and Clade E), and the change to oblique setal groove would be synapomorphic for the Clade F.

Clade C: the eastern Pacific clade

Clade C seems to be endemic to the Eastern Pacific. It has a basal phylogenetic position in Clade B and it is characterized by (i) abfrontal vibracular chamber with transversal setal groove, (ii) ooecium with large ectooecial fenestra, and (iii) single axial vibracula. Presence of abfrontal vibracula with a transverse setal groove is a character also present in Clade D and Clade E, but the two clades are distinguished by the presence of an ooecium with some ectooecial pores. The dimorphic lateral avicularia, characteristics of *N.gen.5 californica* n. comb. and *N.gen.5 varians* n. comb., are absent in *N.gen.5 inarmata* and *N.gen.5 talonis*. In the basalmost taxon, *N.gen.5 inarmata*, the scutum and oral spines are absent.

Clade D and Clade E

Members of Clade D and Clade E have a circumtropical distribution in shallow waters. Clade D has an unambiguous synapomorphy, the outer spines are branched three or more times (cervicorn); this clade also includes species with an oval scutum with internal channels (ornamentations), whereas the branched scutum with a planar frontal surface, present in *Scrupocellaria bellula* and in Clade E, may be considered a homoplasy.

The monophyly of the *N.gen.1* is supported (Clade E). Clade E, described as *N.gen.1*, is characterized by the presence of (i) articulate distal spines, (ii) branched scutum arising from midline of the inner edge of the opesia, (iii) trapezoidal vibracular chamber, 1 axial vibracula, and (iv) ooecium with some ectooecial pores (L.M. Vieira *et al*., unpublished data; see Chapter 3). Character 16 (the shape of scutum arising at the median region of opesia) is plesiomorphic for character state 1, found in majority of species, while character state 2 and 3 are apomorphic and they have an independent origin.

Clade F: taxa with vibracular chamber with oblique setal groove

Clade F has an unambiguous synapomorphy, a vibracular chamber with an oblique setal groove, derived from a primitive condition of short oblique setal groove to long oblique setal groove.

Despite of the low resolution of the semi-strict tree, we use part of the polytomous taxa of Clade G — characterized by presence of an avicularium at the outer wall of the ooecium — to redefine the genus *Scrupocellaria* '*sensu stricto*' according to four morphological features: (i) vibracular chamber with curved setal groove, (ii) ooecium with a single and small ectooecial fenestra, (iii) two axillary vibracula, and (iv) a membranous operculum with a distinct distal rim. Thus, the genus *Scrupocellaria* encompasses only eight species from the polytomy: *Scrupocellaria harmeri*, *Scrupocellaria minuta*, *Scrupocellaria delilii*, *Scrupocellaria incurvata*, *Scrupocellaria intermedia*, *Scrupocellaria scrupea*, *Scrupocellaria scruposa* and *Scrupocellaria aegeensis*. Although these species do not form a unique group, future studies may test the monophyly of the genus.

The monophyletic Clade H comprises four species distinct from *Scrupocellaria 'sensu stricto'* due to a (i) well chitinized operculum placed in an obliquely truncate distal area, and a (ii) scutum with a stout base arising at the distal third of opesia and with an enlarged portion developed proximally. Hence, Clade H has a mixture of the

morphological features of *Caberea* (*viz.* scutum with stout base and enlarged portion developed proximally, arising from the distal third of the inner opesial rim; distinct opercular area with strongly chitinous operculum) and *Scrupocellaria* (*viz*. vibracular chamber with obliquely curved setal groove). However, *Caberea* has been morphologically well defined due to the well-developed vibracular chamber with very long setal groove and barbate seta (HARMER, 1926; HASTINGS, 1943; GORDON, 1984) and, in present phylogeny, the monophyly of the genus *Caberea* is supported by these two unambiguous synapomorphies. The genus *Canda*, previously characterized by the presence of rhizoids forming cross connections between branches and zooids in two series with their frontal surfaces facing obliquely outwards from the axis (GORDON, 1984), has its monophyly supported by three unambiguous synapomorphies, *viz*. (i) joints passing across opesiae of the zooids J and K at the bifurcation, (ii) adjacent zooids abruptly inclined in relation to the axis, (iii) scutum arising at the median region of opesia and forming an asymmetrical plate, without internal channels.

The monophyly of *Licornia* is not supported by the analysis and the position of some *Licornia* species remains unresolved, most likely because of the elevated number of polymorphic characters included in the data matrix. At the same time, the diagnostic characteristics of the genus (L.M. Vieira *et al*., unpublished data; see Chapter 2) are insufficient to distinguish species of *Licornia* from six species previously assigned to *Scrupocellaria*. Thus, we herein transfer these taxa to the genus *Licornia*: *Licornia curvata* n. comb., *Licornia diegensis* n. comb., *Licornia drachi* n. comb., *Licornia regularis* n. comb., *Licornia securifera* n. comb. and *Licornia trindentata* n. comb. (despite the differences in the length of setal grooves, which are longer than those of *Licornia*, and the presence of barely chitinized setae in *Licornia*). According to the phylogeny, the taxonomic position of *Licornia macropora* remains uncertain.

The remaining species in the Clade F form a polytomy including one monophyletic clade (*N.gen.3 hamata* n. comb. + *N.gen.3 obtecta* n. comb. + *N.gen.3 sinuosa* n. comb.) defined by a dimorphic lateral avicularium with trifoliate rostrum, and two other species, *N.gen.3 limatula* n. comb. and *N.gen.3 pusilla* n. comb. The phylogeny suggests that the polytomy may comprise a distinct clade (Clade I) due to the (i) absence of bifurcated oral spines (characteristic of *Licornia* species), (ii) the presence of joints passing across the gymnocysts of outer zooids at the branch, and (iii) the presence of a shorter setal grove than those of *Licornia* species.

TAXONOMIC ACCOUNT

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852
Suborder Neocheilostomina d'Hondt, 1985
Infraorder Flustrina Smitt, 1868
Family Candidae d'Orbigny, 1851
Genus *Scrupocellaria* van Beneden, 1845

Type species. *Sertularia scruposa* Linnaeus, 1758 by original designation.

Diagnosis. Candidae with jointed branches, almost rectangular zooids, tapering proximally and with broadly oval opesia occupying most of the frontal surface. Joints crossing or slightly below the opesia of outer zooids and crossing the gymnocyst of the inner zooids at the bifurcation. Cryptocyst present or reduced. Oral spines often present, unbranched. Frontal scuta sometimes present, asymmetrical, arising from distal third of the inner margin of the opesia or slightly below it. Lateral avicularia present, aquiline, with a serrated rostrum and hooked tip. Frontal avicularia often present, small, monomorphic. Vibracular chamber almost triangular, with a rhizoidal foramen; setal groove curved and directed obliquely; 2 axillary vibracula. Ooecium with single ectooecial fenestra and a small avicularium at its outer border.

Remarks. Bryozoan taxonomists have long considered *Scrupocellaria* van Beneden, 1845 to be a well-defined genus, despite the mixtures of characters seen among the many species assigned to that genus (L.M. Vieira *et al*., unpublished data; see Chapter 2 and 3). According to the diagnostic features described above the genus is now redefined to accommodate 10 of the species previously assigned to it: *S. aegeensis* (Figure 4.2A,B), *S. delilli* (Figure 4.2C,D), *S. harmeri*, *S. incurvata* (Figure 4.2E,F), *S. inermis* (Figure 4.2G,H), *S. intermedia* (Figure 4.2I,J), *Scrupocellaria jullieni* Hayward, 1978 (see HAYWARD, 1978), *S. minuta* (Figure 4.2K,L), *S. scrupea* (Figure 4.3A,B) and *S. scruposa* (Figure 4.3C,D). The assignment of *Scrupocellaria macandrei* Busk, 1852 to the *Scrupocellaria 'sensu stricto'* was not confirmed because the morphological characteristics of the species cannot be recognized in the type specimen (NHMUK 1854.11.14.78).

The curved setal groove of the vibraculum of members of the genus *Scrupocellaria 'sensu stricto'* resembles those of *Canda* and Clade H (=*N.gen.2*, see below); the genus *Canda* is distinct in the shape of the internodes, position of the joints in relation to the bifurcation, the presence of interconnective rhizoids, and a well-

developed cryptocyst. The genus *N.gen.2* is distinct from *Scrupocellaria 'sensu stricto'* by the presence of a well-chitinized operculum placed at the distal truncate area of the zooid (Figure 4.3F,L).

Scrupocellaria inermis is distinct from the other species of the genus by absence of oral spines and scutum. The scutum is also absent in the type of the genus, *S. scruposa*. *Scrupocellaria aegeensis*, described from Mediterranean, has a scutum with a convex distal edge and cuspidate projections at the proximal and distal inner rim. *Scrupocellaria minuta* has a distinctly different scutum with a stout base three times wider than the distal spines and an enlarged portion more developed distally than proximally. Small differences are seen in scuta shape of *S. delilii*, *S. harmeri* and *S. scrupea*; they can be clearly distinguished by means of the position of the joints across the bifurcation, and the shape and size of abfrontal vibracula. *Scrupocellaria intermedia* and *Scrupocellaria jullieni* are unique among *Scrupocellaria* species in having a scutum arising from the median region of the inner part of the opesia; *S. intermedia* is also distinct in having dimorphic lateral avicularia with trifoliate rostra. Other species with trifoliate lateral avicularia are assigned to *N.gen.3* (below). *Scrupocellaria incurvata* has large scutum as wide as the opesia; this species is also characterized by the presence of dimorphic lateral avicularia with triangular laterally directed mandible.

Genus *N.gen.2* Vieira, Migotto, Winston & Marques n. gen.

Type species. *Scrupocellaria maderensis* Busk, 1860.

Diagnosis. Candidae with jointed branches, almost rectangular zooids, with broadly oval opesia occupying most of the frontal surface, and a truncate distal opercular area. Operculum well-chitinized. Joints crossing the gymnocyst of outer and inner zooids at the bifurcation. Cryptocyst present, well developed around the opesia. Oral spines present, unbranched. Frontal scuta asymmetrical, with a stout base, more developed proximally than distally, arising from the distal third of the inner margin of the opesia, below the proximal-most inner spine. Lateral avicularia present, aquiline, with a serrated rostrum and hooked tip. Frontal avicularia often present, small, monomorphic. Vibracular chamber almost triangular, with a rhizoidal foramen; setal groove curved and directed obliquely; 2 axillary vibracula. Ooecium with single and large ectooecial fenestra and a small avicularium at its outer border. Distal edge of ovicelled zooid with toothed rim.

Remarks. The presence of a well-chitinized operculum placed in an obliquely truncate distal area, a toothed rim on the distal edge of ovicelled zooids, and the presence of two axillary vibracula led us to include four species in a new genus, *N.gen.2* (*N.gen.2 dongolensis* n. comb., *N.gen.2 gilbertensis* n. comb., *N.gen.2 maderensis* n. comb. and *N. gen.2 ornithorhynchus* n. comb.).

N.gen.2 maderensis has been reported to be widespread in tropical and subtropical waters worldwide (HARMER, 1926; TILBROOK, 2006), but re-examination of some of the NHMUK specimens so identified revealed that this name represents a species complex (e.g. Figure 4.3K–L). At least two species were previously synonymized under *N.gen.2 maderensis* by HARMER (1926), *viz. N.gen.2 dongolensis* (Figure 4.3G–H) and *N.gen.2 gilbertensis* (Figure 4.3F); these species are distinct from *N.gen.2 maderensis* (Figure 4.3E) by virtue of the number of oral spines, shape of the scutum, shape of frontal avicularia, surface of the cryptocyst, and size of the autozooids. *N.gen.2 ornithorhynchus* also have well-chitinized operculum; this species differ from *N.gen.2 maderensis* in having a vibracular chamber with a shorter setal groove and by the shape of scutum.

Genus *N.gen.3* Vieira, Migotto, Winston & Marques n. gen.

Type species. *Scrupocellaria sinuosa* Canu & Bassler, 1927.

Diagnosis. Candidae with jointed branches, and almost rectangular zooids with short oval opesia occupying half the zooid length. Joints crossing the gymnocyst of outer and inner zooids at the bifurcation. Cryptocyst reduced around opesia. Oral spines present, unbranched. Frontal scuta symmetrical to asymmetrical, oval to subrectangular, arising at the median region (or slightly below) the inner part of the opesia. Lateral avicularia present, with a slightly serrated rostrum and straight tip; lateral avicularium sometimes replaced by an avicularium. Frontal avicularia often present, small, monomorphic. Vibracular chamber almost triangular, with a rhizoidal foramen; setal groove straight, obliquely directed and occupying half of the length of the vibracular chamber; the setal groove is placed distally to the rhizoidal pore; 1 axillary vibraculum with lateral setal groove. Ooecium with some ectooecial pores.

Remarks. Two major character differences, *viz.* presence of ooecia with ectooecial pores and 1 axillary vibraculum, can be use to reassign some species of *Scrupocellaria* to two separate genera, *Licornia* and *N.gen.1* (L.M. Vieira *et al*., unpublished data; see Chapter 2 and 3). The genus *N.gen.1* is quite distinct from

Licornia and *N.gen.3* in having a vibracular chamber with a transversal setal groove; this genus seems to be morphologically related to *N.gen.4*, but the two are distinct in the shape of frontal scutum, the presence of dimorphic frontal avicularia and the presence of branched distal spines. The genus *Licornia* resembles *N.gen.3* in the direction of the setal groove, but the two genera are distinct in the position of the joints in the outer zooids at the bifurcation (crossing the opesia in *Licornia* and the gymnocyst in *N.gen.3*), the presence of shorter opesia in *N.gen.3* than in *Licornia*, the presence of bifurcated distal spines in *Licornia*, and the length of setal groove, longer in *Licornia* than those of *N.gen.3*. The gigantic trifoliate lateral avicularia found in three species of *N.gen.3* seem to be absent in *Licornia*.

Six species previously assigned to *Scrupocellaria* are transferred here to *N.gen.3*: *N.gen.3 hamata* n. comb. (see TILBROOK & VIEIRA, *in press*), *N.gen.3 limatula* n. comb. (Figure 4.4A,B), *N.gen.3 obtecta* n. comb. (Figure 4.4C,D), *N.gen.3 pusilla* n. comb. (see WINSTON, 2005), *N.gen.3 sinuosa* n. comb. (see TILBROOK & VIEIRA, *in press*) and *N.gen.3 unguiculata* (Osburn, 1950) n. comb. *N.gen.3 unguiculata* has distinct dimorphic lateral avicularia with ligulate mandibles. However, the examination of specimens deposited at the NHMUK, AMNH and NMNH revealed that about a dozen new species of *N.gen.3* will also need to be described (Figure 4.4E–I).

Genus *N.gen.4* Vieira, Migotto, Winston & Marques n. gen.

Type species. *Scrupocellaria piscaderaensis* Fransen, 1986.

Diagnosis. Candidae with jointed branches, and almost rectangular zooids, with short oval opesia occupying half-length of the zooid. Joints crossing the gymnocyst of outer and inner zooids at the bifurcation, or at proximal end of the opesia of outer zooids. Cryptocyst variably developed around opesia. Oral spines often present, with proximal-most outer spines branched two or more times (cervicorn). Frontal scuta symmetrical, oval, arising at or slightly below the median region of the inner part of the opesia. Lateral avicularia often present, monomorphic, with a slightly serrated rostrum and straight tip. Frontal avicularia often present, small, monomorphic. Vibracular chamber trapezoidal, with a rhizoidal foramen; setal groove straight, directed transversely; the setal groove is placed distally to the rhizoidal pore; 1 axillary vibraculum with lateral setal groove present. Ooecium with some ectooecial pores.

Remarks. The vibracular chamber with transverse setal groove resembles those of *N.gen.1* and *N.gen.5*. *N.gen.4* is quite distinct from these two genera in having

the proximal-most spine cervicorn in shape. *N.gen.5* is distinct in the position of the scutum, arising from distal third of inner edge of the opesia, and in having an ooecium with a single frontal fenestra.

We assigned seven species to the *N.gen.4*: *N.gen.4 bellula* n. comb., *N.gen.4 carmabi* n. comb. (Figure 4.5A,B), *N.gen.4 cornigera* n. comb. (Figure 4.5C), *N.gen.4 frondis* n. comb. (see TILBROOK & VIEIRA, *in press*), *N.gen.4 hildae* n. comb. (Figure 4.5D,E), *N.gen.4 panamensis* (Osburn, 1950) n. comb (see OSBURN, 1950) and *N.gen.4 piscaderaensis* n. comb. (Figure 4.5F,G). Despite the lack of comparative specimens available for study, the Chinese species *Scrupocellaria unicornis* Liu, 1980 is assigned to *N.gen.4* due to the presence of proximal-most cervicorn spine, porous ooecium and vibraculum with transverse setal groove (LIU, 1980).

Three species of *N.gen.5* are characterized by absence of a lateral avicularium: *N.gen.4 frondis*, *N.gen.4 hildae,* and *N.gen.4 unicornis*; the three are distinguished from each other by the shape of the scutum, the shape and size of the frontal avicularium and the shape of ectooecial pores. *N.gen.4 carmabi* is distinct from *N.gen.4 piscaderaensis* by position of joints at the outer zooids at the bifurcation, and shape of frontal avicularium. *N.gen.4 cornigera* is characterized by a well-developed scutum with projections at its proximal and distal inner edge. The examination of some specimens of *N.gen.4* also revealed that some additional new species need to be described in this group also (Figure 4.5H–L).

Genus *N.gen.5* Vieira, Migotto, Winston & Marques n. gen.

Type species. *Scrupocellaria californica* Trask, 1857.

Diagnosis. Candidae with jointed branches, and almost rectangular zooids, with oval opesia occupying half-length of the zooid. Joints crossing the gymnocyst of outer and inner zooids at the bifurcation. Cryptocyst reduced around opesia. Oral spines often present, unbranched. Frontal scuta arising at the distal third of the inner part of the opesia. Lateral avicularia often present, dimorphic. Frontal avicularia often present, small, monomorphic. Vibracular chamber trapezoidal, with a rhizoidal foramen; setal groove straight, directed transversely; the setal groove is placed distally to the rhizoidal pore; 1 axillary vibraculum with lateral setal groove. Ooecium with single ectooecial fenestra.

Remarks. The *N.gen.5* is erected to include four Eastern Pacific species: *N.gen.5 californica* n. comb. (Figure 4.6A,B), *N.gen.5 inarmata* n. comb. (Figure

4.6C,D), *N.gen.5 talonis* n. comb. (Figure 4.6E,F) and *N.gen.5 varians* n. comb. (Figure 4.6G,H). The dimorphic lateral avicularium and distal spines are absent in *N.gen.5 inarmata*.

Genus *N.gen.6* Vieira, Migotto, Winston & Marques n. gen.

Type species. *Scrupocellaria americana* Packard, 1863.

Diagnosis. Candidae with jointed branches, and almost rectangular zooids, with oval opesia occupying about half of the length of the zooid. Joints crossing the gymnocyst of outer and inner zooids at the bifurcation. Cryptocyst reduced around opesia. Oral spines often present, unbranched. Frontal scuta symmetrical, oval, arising at the median region of the inner part of the opesia. Lateral avicularia often present, monomorphic. Frontal avicularia often present, small, monomorphic. Abfrontal avicularia often present, small, with a rhizoidal foramen; setal groove straight, directed transversely; the setal groove is placed distally to the rhizoidal pore. Ooecium with single ectooecial fenestra.

Remarks. This genus is distinct from *Tricellaria* by absence of the lateral rhizoidal chamber associated to the outer zooids of the bifurcation, presence of abfrontal avicularia and a scutum arising at the median region of the inner part of the opesia. The *N.gen.6* is erected to include five species reported in Arctic and sub-Arctic waters: *N.gen.6 americana* n. comb., *N.gen.6 aviculareae* (Yanagi & Okada 1918) n. comb, *N.gen.6 orientalis* n. comb. (Figure 4.6I–J), *N.gen.6 paenulata* n. comb. and *N.gen.6 scabra* n. comb. (Figure 4.6K–L).

Remarks on other species

Three species not included in this study probably belong to *Licornia* due to their having porous ooecia and similarly shaped abfrontal vibracula, *viz. Licornia mexicana* (Osburn, 1950) n. comb., *Licornia pugnax* (Osburn, 1950) n. comb. and *Licornia spinigera* (Osburn, 1950) n. comb. (see OSBURN, 1950). In *L. spinigera* the joints pass across distal end of the opesia of outer zooids at the bifurcation, but they pass more distally in *L. mexicana* and *L. pugnax*.

Three species are unassigned to any genus of Candidae, *Scrupocellaria profundis* Osburn, 1950, *Scrupocellaria micheli* Marcus, 1955 and *Scrupocellaria uniseriata* Liu, 1984. *Scrupocellaria profundis* is a deep water species (recorded from more than 1000 m deep), that is quite distinct by shape of zooids, which are twisted at

the axis of the maternal internode. The Brazilian species *Scrupocellaria micheli* Marcus, 1955 is a distinct genus in the irregular branching pattern of the colony and the presence large aquiline lateral avicularia (MARCUS 1955); the abfrontal vibracular chamber is morphological similar to those of *N.gen.3*. *Scrupocellaria uniseriata* Liu, 1984 has unique uniserial colonies (LIU, 1984), distinct from other genera of Candidae.

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Appendix 4.I

LIST OF SPECIMENS EXAMINED

For specimens of *N.gen.1* see Chapter 3. LMV, Leandro M. Vieira personal collection.

Caberea Lamouroux, 1816

Caberea boryi (Lamouroux, 1826). NHMUK no number. Additional morphological data given by TILBROOK (2006).
Caberea sp. LMV collection.

Canda Lamouroux, 1816
Canda retiformis Pourtalès, 1867. MCZ 167, syntypes. Additional morphological data given by WINSTON (2005).
Canda clypeata (Haswell, 1880). NHMUK 1910.6.16.1, paratype. Additional morphological data given by TILBROOK (2006).

Licornia van Beneden, 1850

Licornia annectens (MacGillivray, 1887). NMV F.45606.1–3, syntypes.
Licornia cervicornis (Busk, 1852). NHMUK 1899.7.1.4552–3, paratypes; NHMUK 1928.3.6.180, non-type. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Licornia cyclostoma (Busk, 1852). NHMUK 1854.11.15.77, holotype. NHMUK 1899.6.1.340, non-type.
Licornia diadema (Busk, 1852) NHMUK 1854.11.15.50, holotype. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Licornia ferox (Busk, 1852). NHMUK 1854.11.15.76, holotype; NHMUK 1928.3.6.156, non-type.
Licornia gaspari (Thornely, 1907). NHMUK 1936.12.30.126, 1936.12.30.136, 1936.12.30.146, syntypes.
Licornia jolloisii (Audouin, 1826) NHMUK 1926.9.6.84, neotype; NHMUK 1926.9.6.85–94, non-type.
Licornia longispinosa (Harmer, 1926). RMNH 00054, holotype; NHMUK 1928.3.6.189–90, part of holotype. NMNH 9389, part of holotype.
Licornia macropora (Osburn, 1950). NMNH no number, holotype; SBMNH 96151, paratype.
Licornia prolata (Tilbrook & Vieira, in press). MTQ G25341, holotype. Additional morphological data given by TILBROOK & VIEIRA (*in press*).

Notoplites Harmer, 1923

Notoplites marsupiatus (Jullien, 1882). MNHN 2817, lectotype. Additional morphological data given by SOUTO *et al.* (2011).
Notoplites clausus (Busk, 1884) NHMUK 1887.12.9.83, lectotype. Additional morphological data given by SOUTO *et al.* (2011).

Scrupocellaria van Beneden, 1828

Scrupocellaria aegeensis Harmelin, 1969. NHMUK 2010.12.7.3, 2010.12.7.4, syntypes.
Scrupocellaria americana Packard, 1863. MCZ 134, syntype.
Scrupocellaria arctica (Busk, 1855). NHMUK 1899.7.1.651–2, syntypes.
Scrupocellaria californica Trask, 1857. NHMUK 2010.12.8.1, non-type.
Scrupocellaria carmabi Fransen, 1986. RMNH 02977, holotype; RMNH 03042–52, paratypes.
Scrupocellaria congesta Norman, 1903. NHMUK 1911.10.1.385, holotype.
Scrupocellaria cornigera (Pourtàles, 1867). NHMUK 1911.10.1.368, non-type.
Scrupocellaria curvata Harmer, 1926. RMNH (ZMA 01063aq), holotype; NHMUK 1928.3.6.187, part of holotype. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Scrupocellaria diegensis Robertson, 1905. NHMUK 2010.12.9.3, non-type.
Scrupocellaria delilii (Audouin, 1826). NHMUK 2010.12.8.3, non-type.
Scrupocellaria dongolensis Waters, 1909. NHMUK 1928.9.13.98, syntype.
Scrupocellaria drachi Marcus, 1955, MZUSP no number.
Scrupocellaria elongata (Smitt, 1868). NHMUK 1911.10.1.379, 1911.10.1.384, non-types.
Scrupocellaria frondis Kirkpatrick, 1890. NHMUK 1888.4.16.20, holotype; NHMUK 1931.12.19.7, non-type. LMV collection, non-type. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Scrupocellaria gilbertensis Maplestone, 1909. MV 45061, holotype.
Scrupocellaria hamata Tilbrook & Vieira, *in press*. MTQ G25155, holotype. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Scrupocellaria harmeri Osburn, 1947. SBMNH 95952, holotype; SBMNH 95953, paratype.
Scrupocellaria hildae Fransen, 1986. RMNH 02980, holotype; RMNH 03065–70, paratypes.
Scrupocellaria inarmata O'Donoghue & O'Donoghue, 1926. NHMUK 1964.4.2.10, holotype.
Scrupocellaria incurvata Waters, 1897. NHMUK 1899.7.1.303, non-type.

Scrupocellaria inermis Norman, 1867. NHMUK 1911.10.1.367, 1912.12.21.834, 1912.12.21.8334, syntypes.
Scrupocellaria intermedia Norman, 1893. NHMUK 1910.10.1.369, 1912.12.21.835, syntypes.
Scrupocellaria limatula Hayward, 1988. NHMUK 1987.1.18.41, holotype.
Scrupocellaria maderensis Busk, 1860. NHMUK 1899.7.1.780, syntype; NHMUK 1911.10.1.388, 1922.9.6.1, non-types.
Scrupocellaria minuta (Kirkpatrick, 1888). NHMUK 1888.1.25.2A, lectotype.
Scrupocellaria obtecta Haswell, 1881. NHMUK 1928.9.13.103, syntype.
Scrupocellaria ornithorhynchus Thomson, 1858. NHMUK 1899.7.1.783, holotype.
Scrupocellaria orientalis Kluge, 1955. NHMUK no number, non-type.
Scrupocellaria paenulata Norman, 1903. MCZ 523, non-type.
Scrupocellaria piscaderaensis Fransen, 1986. RMNH 02979, holotype; RMNH 03053–62, paratypes.
Scrupocellaria pusilla (Smitt, 1872). MCZ 0100, syntypes. Additional morphological data given by WINSTON (2005).
Scrupocellaria regularis Osburn, 1940. MCZ 38, 40, 163, syntypes; NMNH 2347, syntype.
Scrupocellaria scabra van Beneden, 1848. NHMUK 1911.10.1.376, non-type.
Scrupocellaria scrupea Busk, 1852. NHMUK 1854.11.15.79, holotype; NHMUK 2010.12.8.5, non-type.
Scrupocellaria scruposa (Linnaeus, 1756). NHMUK 1888.12.21.57, 1966.1.10.9, non-types.
Scrupocellaria securifera Busk, 1884. NHMUK 1887.12.9.113–114, syntypes.
Scrupocellaria sinuosa Canu & Bassler, 1927. NMNH 8426, holotype. Additional morphological data given by TILBROOK & VIEIRA (*in press*).
Scrupocellaria tridentata Waters, 1918. MOM 420807 (syntype of *S. cervicornis spinosa* Calvet, 1931).
Scrupocellaria talonis Osburn, 1950. SBMNH 96168, holotype.
Scrupocellaria varians Hincks, 1882. NHMUK 1962.6.16.4, 1968.1.18.111, 2010.12.8.2, non-types.

Tricellaria Fleming, 1828

Tricellaria ternata (Ellis & Solander, 1786). NHMUK no number, non-type specimens from British coast; VMNH 11646.0000, 11647.0001, 11662.0003, 11663.0000, 11667.0001, 11669.002, 11673.000, non-types.
Tricellaria gracilis (van Beneden, 1848) NHMUK no number, non-type specimens from British coast; VMNH 11493.0000, 11570.0000, 11628.0000, 11629.0000, 11646.0000, 11661.0000, 12500.0001, 12501.0000, 12502.0000, 12617.0000, non-types.

Appendix 4.II

LIST AND DISCUSSION OF CHARACTERS

Rhizoids (Figure 4.7A–F)

[1] *Transverse tubes connecting adjacent branches.*
0. absent; 1. present (Figure 4.2A).
L= 2; CI=0.500 ; RI=0.833.
The presence of this character is typical of the species assigned to the genus *Canda* (HARMER, 1926) and some species of *Licornia* (Vieira *et al.*, unpublished data; see Chapter 2). The interconnective rhizoid (SILÉN, 1977; Figure 4.7A) arises from a proximal rhizoidal pore of the vibracular chamber and attaches to the pore of vibracular chamber in the adjacent branch or, rarely, to the abfrontal surface of the zooid in the adjacent branch. Such interconnective rhizoids are quite distinct in function from the holdfast rhizoids that attach to the substrate, that are often found in Candidae species (Figure 4.7B–D). In *Licornia*, smaller (presumably younger) colonies may not have the connecting tubes, but they are present in more developed colonies (L.M. Vieira, unpublished data).

[2] *Rhizoid surface.*
L= 10; CI=0.200; RI=0.579.
0. smooth (Figure 4.7B); 1. with retroussé hooks (Figure 4.7C); 2. ringed (Figure 4.7D).
Hooked rhizoids have been considered a phenotypical variation among *Scrupocellaria* species (HARMER, 1926). However, this character distinguishes species of *Scrupocellaria* and *Licornia* (See Chapter 1, 2 and 3).

[3] *Rhizoids adjacent to the abfrontal surface of the colony.*
L= 1; CI=1.00; RI=1.00.
0. absent (Figure 4.7E); 1. present (Figure 4.7F).
Character present in some species of Candidae (*Notoplites clausus* and *Notoplites marsupiatus*, see HARMER, 1926).

Branch (Figures 4.8A–B, 4.9A–C)

[4] *Position of the joints at bifurcation*.
L= 2; CI=0.500; RI=0.667.
0. passing across zooids FD and GC (Figure 4.8B); 1. passing across zooids FJ and GK (Figure 4.8A).
Chitinous joints between branches are often reported in Candidae species, maybe as a result of branch fragmentation (HARMER, 1926). The feature is conspicuous in some genera (*Licornia*, *Tricellaria, Notoplites*, and in most species of *Scrupocellaria*). In *Canda* spp., the joints are often seen in older branches; and in a few *Scrupocellaria* species (*viz.*, *Scrupocellaria curvata*, *Scrupocellaria diegensis*, *Scrupocellaria drachi*, *Scrupocellaria regularis,* and *Scrupocellaria securifera*) the joints are inconspicuous due to more calcification in all parts of the colonies of those species. The bifurcation pattern of the colony and position of the joints have been adopted to differentiate some genera of branching, erect bryozoans with membranous frontal walls (WATERS, 1897, 1913; HARMER, 1923). The notation system used here for the ordering of the zooecia at a branching event is based on the bifurcation of biserial colonies (Figures 4.8A–B): “A” and “B”, for the two most proximal zooids which form the bifurcation; “C” and “D”, those placed on the outer sides of the branches right before the bifurcation, budding off from “A” and “B” respectively; “E”, the axillary zooid, derived from “A” and lying on the inner side of “C”; “F” and “G”, on the inner side of the branches right after the bifurcation and adjacent to zooids “D” and “C” respectively; “J” and “K”, the zooids derived from “D” and “C”, respectively (HARMER, 1923). This character is not known for *Scrupocellaria bellula* because of the absence of bifurcation in the colonies studied; the joints are apparently rare, present in a single zooid at the base of the colony (see OSBURN, 1947).

[5] *Position of the joints in relation to zooids C and D*.
L= 5; CI=0.200; RI=0.889.
0. passing across the gymnocysts (Figure 4.9C); 1. passing across the opesiae (Figure 4.9B).

[6] *Position of the joints in relation to zooids J and K*.
L= 1; CI=1.000; RI=1.000.
0. passing across zooid gymnocysts; 1. passing across the zooid opesiae.

[7] *Position of adjacent zooids along the axis.*
L= 1; CI=1.000; RI=1.000.
0. placed side by side in the same plane or slightly inclined in relation to the axis (Figure 4.9B,C); 1. abruptly inclined, about 250 degrees or more in relation to the axis (Figure 4.9A).
Licornia diadema, *Scrupocellaria bertholletii*, *Scrupocellaria macrorhyncha,* and *Scrupocellaria reptans* have the frontal surface of adjacent zooids slightly inclined in relation to the axis in apical region of the colony, but placed side by side at the same plane in some branches at the basal region (coded with "0").

Zooid morphology (Figure 4.9B–F)
[8] *Aperture area*.
L= 3; CI=0.333; RI=0.714.
0. continuous and in the same plane as the frontal membrane (Figure 4.9B); 1. placed in an obliquely truncate distal area and separated from the frontal membranous area by two suborificial condyles (Figure 4.9C,E).
In *Scrupocellaria ornithorhynchus*, the truncate distal area is reduced and shorter than those of *S. dongolensis*, *S. gilbertensis,* and *S. maderensis*.

[9] *Distal edge of autozooid*.
L= 2; CI=1.000; RI=1.000.
0. smooth (Figure 4.9D); 1. toothed in ovicelled zooids (Figure 4.9E); 2. toothed in ovicelled and non-ovicelled zooids (Figure 4.9F).
A toothed distal edge in autozooids has not yet been described for Candidae species, because it can only be observed using scanning electron microscopy. The character is considered unknown ('?') for *Scrupocellaria harmeri*, whose type is a balsam slide.

[10] *Operculum.*
L= 3; CI=0.333; RI=0.714.
0. membranous, only rim distinctly chitinous (Figure 4.9B); 1. Whole operculum chitinous (Figure 4.9C).
The majority of Candidae species has a membranous operculum continuous with the frontal membrane, but distinguished from it by its inverted-U-shaped and slightly chitinous distal edge. The thick and entirely chitinous opercula of *Notoplites* spp., *S. dongolensis*, *S. gilbertensis*, *S. maderensis,* and *S. ornithorhynchus* are placed in the obliquely truncate distal area.

[11] *Cryptocyst*.
L= 12; CI=0.083; RI=0.389.
0. absent; 1. present, vestigial, as a very tiny rim around the opesia (Figure 4.9B); 2. present, forming a conspicuous stripe around the opesia (Figure 4.9C).

Spines (Figure 4.10A–H)
In Candidae the oral spine is characterized by the presence of a jointed base (sometimes with external calcification and distinct from the distal zooecial projections found in *Bugula* species – see VIEIRA *et al*., 2012). Candidae species have a variable number of oral spines (0–7 distal spines), some of those may be distinguished by their position at the distal margin of the opesia, *viz.* inner, outer and median spines. Both the presence of polymorphic data and the lack of topographic correspondence suggest that not all spines are homologous, but may be a product of serial homology. Hence, it is only possible to homologize the states between the spines of the same nature, as indicated by topographical correspondence. For example, the most proximal outer spines of different taxa are comparable with each other but not with the proximal inner spines of different taxa or even those in the same individual. Thus, we coded them as three separate characters [Characters 12 and 13 and 14], i.e. proximal-most outer, the proximal-most inner and distal-most oral spines.

[12] *proximal-most outer spine*.
L= 7; CI=0.429; RI=0.556.
0. absent (Figure 4.10A); 1. present, unbranched (Figure 4.10B); 2. present, branched in a bifid pattern (Figure 4.10D); 3. present, branched in a non-bifid pattern (cervicorn) (Figure 4.10C).

[13] *proximal-most inner spine*.
L= 7; CI=0.429; RI=0.200.
0. absent (Figure 4.10A); 1. present, unbranched (Figure 4.10B); 2. present, branched in a bifid pattern (Figure 4.10D); 3. present, branched in a non-bifid pattern (cervicorn).

[14] *distal-most spines*.
L= 8; CI=0.250; RI=0.625.
0. absent (Figure 4.10A); 1. present, unbranched (Figure 4.10B); 2. present, branched.

[15] *Scutal spine at the inner edge of opesia*.
L= 10; CI=0.200; RI=0.704.
0. absent (Figure 4.10A); 1. present, arising at the median region (or slightly below) of the inner part of the opesia (Figure 4.10C,E–H); 2. present, arising at distal third (Figure 10I–L).

[16] *Shape of scutum arising at the median region of opesia*.
L= 6; CI=0.833; RI=0.957.
0. spine-like and unbranched (Figure 4.10E); 1. forked to branched, branches homogeneous in width and with sharp tips (Figure 4.10F); 2. branched and flattened in cross section, branches heterogeneous in width, with a planar frontal surface and truncated tips (Figure 4.10G); 3. branched and cylindrical in cross section, branches heterogeneous in width, with a convex frontal surface and truncated tips (Figure 4.10H); 4. forming a single ovoid plate, but with internal channels (visible under light microscope because of their transparency) (Figure 4.10C); 5. forming an asymmetrical plate, without internal channels.
Licornia diadema has variable shape of scuta, varying from a simple paddle-shaped scutum to an incipient branched scutum bearing one or more slits at the outer margin (coded with “4”).

[17] *Shape of scutum arising at the distal third of opesia*.
L= 5; CI=0.800; RI=0.800.
0. slender base, *i.e.* as wide as distal spines, with unbranched asymmetrical enlarged portion in which the distal region is less developed than the proximal one (Figure 4.10I–J); 1. slender base, *i.e.* as wide as distal spines, with an irregularly branched enlarged portion; 2. stout base, *i.e.* two or more times wider than distal spines, enlarged portion developed proximally (Figure 4.10K); 3. stout base, i.e. two or more times wider than distal spines, enlarged portion more developed distally than proximally (Figure 4.10L); 4. stout base, *i.e.* two or more times wider than distal spines, enlarged portion continuous with edge of opesia and with some slits at the outer margin (Figure 4.10F).

[18] *Development of the unbranched asymmetrical portion of the scutum at the distal third of opesia*.
L= 2; CI=0.500; RI=0.800.
0. narrow paddle-shaped, curved towards the proximal region of opesia (Figure 4.10I); 1. enlarged shield-shaped, not curved towards the proximal region of opesia (Figure 4.10J).

Frontal and lateral avicularia (Figure 4.11A–F)
[19] *Sessile distolateral avicularium*.
L= 5; CI=0.200; RI=0.714.
0. absent (Figure 4.11A); 1. present (Figure 4.11B–H).

[20] *Direction of rostrum of sessile lateral avicularium*.
L= 3; CI=0.667; RI=0.889.
0. lateral (Figure 4.11C); 1. obliquely laterodistal (Figure 4.11B); 2. obliquely lateroproximal.
In species with a sessile laterodistally directed avicularium the avicularium is often obscured by the outer distal spines, therefore more difficult to see.

[21] *Rostrum of lateral avicularium*.
L= 4; CI=0.500; RI=0.900.
0. serrated lateral edge, straight to slightly curved at its tips (Figure 4.11D); 1. smooth lateral edge, with curved tips (Figure 4.11E); 2. serrated lateral edge, strongly hooked (Figure 4.11F).

[22] *Giant lateral avicularium.*
L= 4; CI=0.500; RI=0.667.
0. absent; 1. present, with triangular to elongate mandible (Figure 4.11G); 2. present, with trifoliate mandible (Figure 4.11H).

[23] *Dimorphic frontal avicularium.*
L= 12; CI=0.333; RI=0.750.
0. absent; 1. present, with triangular mandible (Figure 4.11I); 2. present, with lanceolate mandible; 2. present, with trifoliate mandible.

Ovicells (Figure 4.12A–C)
[24] *Surface of ectooecium*.
L= 5; CI=0.400; RI=0.900.
0. with a single proximal fenestra (Figure 4.12A); 1. with a single wide fenestra occupying the majority of the surface of the ooecium (Figure 4.12B); 2. porous (Figure 4.12C).
The single fenestra is reduced to a minute drop-shaped pore in *S. scruposa* (Figure 4.12A) and one minute pore in *S. aegeensis*. Smooth ooecia were described for *S. delilii* (HAYWARD & MCKINNEY, 2002), but an uncalcified proximal area, like those of *S. arctica*, is often seen in the proximal border of the ectooecium (L.M. Vieira, unpublished data; coded with “0”).

[25] *Sessile avicularium associated to ooecium*.
L= 1; CI=1.000; RI=1.000.
0. absent; 1. present (Figure 4.12A).

Abfrontal heterozooids (Figure 4.13A–I)
[26] *Heterozooids on abfrontal surface of the colony.*
L= 3; CI=0.667; RI=0.889.
0. absent (Figure 4.8A); 1. present, as vibracula (Figure 4.13C,E–I); 2. present, as avicularia (Figure 4.13B).
Some Candidae species have abfrontal avicularia, i.e. modified zooids that lack a functional polypide and with modified opercula (mandible) (RYLAND, 1970, WINSTON, 1984, CARTER *et al*,. 2009). Two distinct avicularia are found on the abfrontal surface of Candidae species: adventitious avicularia, with acute mandibles and one pore in the plane of the palate; and vibracula, with toothed setiform mandibles (seta) and with a tubular orifice at the base of seta (CARTER *et al.*, 2009).

[27] *Lateral rhizoidal (rootlets) chamber associated with outer zooids at the bifurcation*.
L= 1; CI=1.000; RI=1.000.
0. absent; 1. present (Figure 4.13D).
The relation between the joints and holdfast rhizoids is not altered during the development of the colony (HARMER, 1923). Species of *Tricellaria* produce holdfast rhizoids on the proximal sides of the joints, while *Notoplites* species produce holdfast rhizoids on the distal side of the joints (HARMER, 1923, 1926).

[28] *Palatal surface of setal groove in vibracular chamber*.
L= 4; CI=0.500; RI=0.931.
0. present, complete, without foramen (Figure 4.8C,E); 1. present, complete, with a foramen (Figure 4.13F); 2. absent (Figure 4.13I).
In some species the palatal surface is variable, entire complete to partially incomplete, near the tubular orifice (coded with “0”; Figure 4.13E).

[29] *Position of the setal groove on vibracular chamber in relation to the intermodal axis*.
L= 1; CI=1.000; RI=1.000.
0. transverse (Figure 4.13C); 1. oblique (Figure 4.13E–I).

[30] *Shape of oblique setal groove in vibracular chamber*.
L= 10; CI=0.500; RI=0.783.
0. curved, of medium length, occupying at maximum two thirds of the inner margin of the vibracular chamber length; setal groove developed up to half of the width of the zooid (Figure 4.13H); 1. curved, long, occupying entire inner margin of the vibracular chamber; setal groove developed up to the width of the zooid (Figure 4.13I); 2. straight, short, occupying half of the length of the vibracular chamber; setal groove placed distally to the rhizoidal pore (Figure 4.13E); 3. straight, medium, occupying two thirds of the length of the vibracular chamber; setal groove reaching the median part of the rhizoidal pore (Figure 4.13F); 4. straight, long, occupying the entire length of the vibracular chamber; setal groove passing through the lateral region of the rhizoidal pore but not reaching the line defined by the juxtaposed lateral walls of the zooids (Figure 4.13G); 5. straight, very long, greater than the length of the vibracular chamber and reaching the line defined by the juxtaposed lateral walls of the zooids.

[31] *Number of axial avicularia*.
L= 2; CI=0.500; RI=0.929.
0. one (Figure 4.13C,E–G); 1. two (Figure 4.13H–I).

[32] *Position of setal groove in a single axial vibraculum*.
L= 1; CI=1.000; RI=1.000.
0. lateral (Figure 4.13C,E); 1. longitudinal (Figure 4.13F,G).

[33] *Setal morphology*.
L= 7; CI=0.143; RI=0.333.
0. delicate, translucent white; 1. hard, chitinous, yellowish-gold.

[34] *Surface of seta*.
L= 1; CI=1.000; RI=1.000.
0. smooth; 1. barbate.

[35] *Length of seta*.
L= 2; CI=0.500; RI=0.929.
0. short, as long as internode width, shorter than zooid length (Figure 4.13H); 1. long, longer than internode width, longer than zooid length (Figure 4.13C).

Appendix 4.III

DATA MATRIX OF CHARACTERS

Data matrix of characters. Not applicable (–) and unknown state (?) were treated as missing in TNT. Polymorphic states are noted by: a (0&1); b (0&2); c (1&2).

Characters				1			2			3	
Taxa	**1 2 3 4**	**5 6 7 8 9**		**0 1 2 3 4**	**5 6 7 8 9**		**0 1 2 3 4**	**5 6 7 8 9**		**0 1 2 3 4 5**	
Notoplites marsupiatus	0 0 1 1	– 0 0 1 0		1 0 1 1 0	2 – 4 – 1		0 0 0 0 1	0 0 1 – –		– – – – – –	
Notoplites clausus	0 0 1 1	– 0 0 1 0		1 0 1 1 0	2 – 4 – 0		– – 0 0 1	0 2 1 – –		– – – – – –	
Tricellaria arctica	0 0 0 0	0 – 0 0 0		0 0 1 a 0	b – 0 0 a		0 1 0 0 1	0 0 1 – –		– – – – – –	
Tricellaria elongata	0 0 0 0	0 – 0 0 0		0 0 1 a 0	b – 0 0 1		0 1 0 0 1	0 0 1 – –		– – – – – –	
Tricellaria gracilis	0 0 0 0	0 – 0 0 0		0 0 1 a 1	2 – 0 1 1		0 1 0 0 1	0 0 1 – –		– – – – – –	
Tricellaria ternata	0 0 0 0	0 – 0 0 0		0 0 a 1 1	b – 0 0 a		0 1 0 0 1	0 0 1 – –		– – – – – –	
Scrupocellaria congesta	0 0 0 0	0 – 0 0 0		0 0 1 a 0	b – 0 0 1		0 1 0 0 2	0 0 1 – –		– – – – – –	
N.gen.6 americana	0 0 0 0	0 – 0 0 0		0 0 1 a 0	1 4 – – 1		0 1 0 0 2	0 2 0 – –		– – – – – –	
N.gen.6 orientalis	0 0 0 0	0 – 0 0 0		0 0 1 a 0	1 4 – – 1		0 1 0 0 2	0 2 0 – –		– – – – – –	
N.gen.6 paenulata	0 0 0 0	0 – 0 0 0		0 0 1 a 0	1 4 – – 1		0 1 0 0 2	0 2 0 – –		– – – – – –	
N.gen.6 scabra	0 0 0 0	0 – 0 0 0		0 0 1 a 0	1 4 – – 1		0 1 0 0 2	0 2 0 – –		– – – – – –	
N.gen.5 inarmata	0 0 0 0	0 – 0 0 0		0 0 0 0 0	0 – – – 1		0 0 0 0 2	0 1 0 0 0		– 0 0 0 0 1	
N.gen.5 talonis	0 0 0 0	0 – 0 0 0		0 0 a a 0	b – 0 0 1		0 0 1 0 2	0 1 0 0 0		– 0 0 0 0 1	
N.gen.5 californica	0 0 0 0	0 – 0 0 0		0 0 1 1 1	b – 0 0 1		0 0 1 0 2	0 a 0 0 0		– 0 0 0 0 1	
N.gen.5 varians	0 0 0 0	0 – 0 0 0		0 0 1 1 1	b – 1 – a		0 0 1 0 2	0 a 0 0 0		– 0 0 0 0 1	
N.gen.4 bellula	0 0 0 ?	? ? 0 0 0		0 0 3 3 2	1 2 – – 1		0 0 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.4 carmabi	0 0 0 0	0 – 0 0 0		0 0 3 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.4 cornigera	0 0 0 0	0 – 0 0 0		0 1 3 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.4 frondis	0 0 0 0	0 – 0 0 0		0 1 3 1 1	1 4 – – 0		– – 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.4 hildae	0 0 0 0	0 – 0 0 0		0 0 3 1 1	1 4 – – 0		– – 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.4 piscaderaensis	0 0 0 0	0 – 0 0 0		0 0 3 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 bertholletii	0 0 0 0	0 – 0 0 0		0 0 1 1 1	a 1 – – 1		0 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.4	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 1		0 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 tenuirostris	0 1 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 1		0 0 0 2 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.10	0 0 0 0	1 – 0 0 0		0 1 1 1 1	a 1 – – 1		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.7	0 0 0 0	1 – 0 0 0		0 1 1 1 1	1 1 – – 1		0 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.9	0 0 0 0	1 – 0 0 0		0 1 1 1 1	1 1 – – 1		0 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n. sp.11	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 1		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n. sp.19	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 1		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 macrorhyncha	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 3 – – a		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.8	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 3 – – a		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.14	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 3 – – a		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.18	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 3 – – a		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 sp.5	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 sp.6	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 sp.12	0 0 0 0	1 – 0 0 0		0 0 1 1 1	a 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 sp.16	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 curacaoensis	0 1 0 0	1 – 0 0 0		0 0 1 1 1	a 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.17	0 1 0 0	1 – 0 0 0		0 0 1 1 1	1 1 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 hirsuta	0 1 0 0	0 – 0 0 0		0 0 1 1 1	0 – – – a		1 0 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 reptans	0 1 0 0	0 – 0 0 0		0 0 1 1 1	0 2 – – a		1 0 0 1 3	0 a 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.3	0 1 0 0	0 – 0 0 0		0 0 1 1 1	0 2 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.2	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 2 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.1	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 2 – – a		1 0 0 1 3	0 a 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.13	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 2 – – 0		– – 0 1 3	0 1 0 0 0		– 0 0 0 0 1	
N.gen.1 n.sp.15	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 2 – – 0		– – 0 1 3	0 a 0 0 0		– 0 0 0 0 1	
N.gen.3 limatula	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 0 1		2 0 0 0 0 1	
N.gen.3 pusilla	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 0 1		2 0 0 0 0 1	
N.gen.3 hamata	0 1 0 0	0 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 2 0 3	0 1 0 0 1		2 0 0 0 0 1	
N.gen.3 obtecta	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 2 0 3	0 1 0 0 1		2 0 0 0 0 1	
N.gen.3 sinuosa	0 0 0 0	0 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 2 0 3	0 1 0 0 1		2 0 0 0 0 1	
Licornia macropora	0 0 0 0	1 – 0 0 0		0 0 1 1 1	1 4 – – 1		0 0 0 0 3	0 1 0 1 1		3 0 1 0 0 1	
Licornia cervicornis	0 1 0 0	1 – 0 0 0		0 0 2 2 1	1 4 – – 1		0 0 0 1 3	0 1 0 1 1		3 0 1 0 0 1	
Licornia prolata	0 0 0 0	1 – 0 0 0		0 0 c c 1	a 4 – – 1		0 0 0 1 3	0 1 0 1 1		3 0 1 0 0 1	
Licornia longispinosa	0 1 0 0	1 – 0 0 0		0 0 2 c 1	1 4 – – 1		0 0 0 3 3	0 1 0 1 1		3 0 1 0 0 1	

continued next page

Data matrix of characters. (continued)

Characters			1		2		3
Taxa	**1 2 3 4**	**5 6 7 8 9**	**0 1 2 3 4**	**5 6 7 8 9**	**0 1 2 3 4**	**5 6 7 8 9**	**0 1 2 3 4 5**
Licornia curvata	0 1 0 0	1 – 0 0 0	0 1 1 1 1	1 4 – – 1	0 0 0 4 3	0 1 0 1 1	4 0 1 1 0 1
Licornia diegensis	0 1 0 0	1 – 0 0 0	0 1 2 2 1	1 4 – – 1	0 0 0 1 3	0 1 0 1 1	4 0 1 1 0 1
Licornia drachi	0 1 0 0	1 – 0 0 0	0 1 1 1 1	0 – – – 1	2 0 0 0 3	0 1 0 2 1	4 0 1 1 0 1
Licornia tridentata	0 1 0 0	1 – 0 0 0	0 1 1 1 1	1 4 – – 1	0 0 0 4 3	0 1 0 1 1	4 0 1 1 0 1
Licornia regularis	0 0 0 0	1 – 0 0 0	0 1 c c 1	1 4 – – 1	0 0 0 0 3	0 1 0 1 1	4 0 1 1 0 1
Licornia securifera	0 0 0 0	1 – 0 0 0	0 1 2 2 1	1 4 – – 1	0 0 0 0 3	0 1 0 1 1	4 0 1 1 0 1
Licornia ferox	0 1 0 0	1 – 0 0 0	0 0 c c 1	0 – – – 1	0 0 0 1 3	0 1 0 1 1	3 0 1 0 0 1
Licornia annectens	1 ? 0 0	1 – 0 0 0	0 0 1 1 1	a 4 – – 1	0 0 0 1 3	0 1 0 1 1	3 0 1 0 0 1
Licornia cyclostoma	1 2 0 0	1 – 0 0 0	0 0 c c 1	a 4 – – 1	0 0 0 1 3	0 1 0 1 1	3 0 1 0 0 1
Licornia diadema	1 1 0 0	1 – 0 0 0	0 0 c c 1	a 4 – – 1	0 0 0 1 3	0 1 0 1 1	3 0 1 0 0 1
Licornia gaspari	1 1 0 0	1 – 0 0 0	0 0 1 1 1	0 – – – 1	0 0 0 1 3	0 1 0 1 1	3 0 1 0 0 1
Licornia jolloisii	1 1 0 0	1 – 0 0 0	0 0 a a 0	a 0 – – 1	0 0 0 0 3	0 1 0 1 1	3 0 1 0 0 1
S. incurvata	0 0 0 0	1 – 0 0 0	0 0 1 1 1	2 – 0 1 1	0 2 1 0 1	1 1 0 2 1	1 1 – 0 0 0
S. intermedia	0 0 0 0	? 0 0 0 0	0 0 1 1 1	1 4 – – 1	0 2 0 0 2	1 1 0 ? 1	1 1 – 0 0 0
Scrupocellaria harmeri	0 0 0 0	0 – 0 0 0	0 0 1 1 1	2 – 0 1 1	0 2 0 0 1	1 1 0 ? 1	0 1 – 0 0 0
Scrupocellaria minuta	0 0 0 0	0 – 0 0 2	0 0 1 1 1	2 – 3 – 1	0 2 2 0 1	1 1 0 2 1	0 1 – 0 0 0
Caberea boryi	0 0 0 0	1 – 0 1 0	1 1 1 0 0	2 – 2 – 1	0 0 0 1 1	1 1 0 2 1	5 0 1 1 1 1
Caberea sp.	0 0 0 0	1 – 0 1 0	1 1 1 0 0	2 – 2 – 1	0 0 0 0 1	1 1 0 2 1	5 0 1 1 1 1
Canda clypeata	1 0 0 1	– 1 1 0 0	0 1 1 1 a	1 5 – – 0	– – 0 1 2	1 1 0 2 1	1 1 – 1 0 0
Canda retiformis	1 0 0 1	– 1 1 0 0	0 1 1 1 0	1 5 – – 0	0 – – 0 2	? 1 0 2 1	1 1 – 1 0 0
N.gen.2 ornithorhynchus	0 0 0 0	0 – 0 1 1	1 1 1 1 1	2 – 0 1 1	0 2 0 0 1	1 1 0 1 1	1 1 – 0 0 0
N.gen.2 dongolensis	0 0 0 0	0 – 0 1 1	1 1 1 1 1	2 – 2 – 1	0 2 0 0 1	1 1 0 1 1	1 1 – 0 0 0
N.gen.2 gilbertensis	0 0 0 0	0 – 0 1 1	1 1 1 1 1	2 – 2 – 1	0 2 0 0 1	1 1 0 1 1	1 1 – 0 0 0
N.gen.2 maderensis	0 0 0 0	0 – 0 1 1	1 1 1 1 1	2 – 2 – 1	0 2 0 0 1	1 1 0 1 1	1 1 – 0 0 0
S. delilii	0 0 0 0	1 – 0 0 0	0 0 1 1 0	2 – 0 1 1	0 2 0 0 1	1 1 0 2 1	0 1 – 0 0 0
S. inermis	0 0 0 0	1 – 0 0 0	0 0 0 0 0	0 – – – 1	0 2 0 0 1	1 1 0 2 1	0 1 – 0 0 0
S. aegeensis	0 1 0 0	1 – 0 0 0	0 0 1 1 1	2 – 0 1 1	0 2 0 0 1	1 1 0 2 1	0 1 – 0 0 0
S. scrupea	0 1 0 0	1 – 0 0 0	0 0 1 1 1	2 – 0 1 1	0 2 0 0 1	1 1 0 2 1	0 1 – 0 0 0
S. scruposa	0 1 0 0	1 – 0 0 0	0 0 1 1 1	0 – – – 1	0 2 0 0 1	1 1 0 2 1	0 1 – 0 0 0

Appendix 4.IV

LIST OF CHARACTER STATE OPTIMISATIONS FOR SEMI-STRICT CONSENSUS TREE SHOWN IN FIGURE 1

Nodes 13, 16 and 22 have no synapomorphies.

Node 1. Character 3: 1→0; Character 4: 1→0; Character 8: 1→0; Character 10: 1→0; Character 17: 2→0; Character 21: 0→1.
Node 2. Character 14: 0→1.
Node 3. Character 24: 1→2.
Node 4. Character 15: 2→1; Character 26: 0→2; Character 27: 1→0.
Node 5. Character 21: 1→0; Character 26: 2→1.
Node 6. Character 15: 0→1.
Node 7. Character 12: 0→1.
Node 8. Character 14: 0→1.
Node 9. Character 14: 0→1; Character 24: 2→3.
Node 10. Character 10: 1→3.
Node 11. Character 16: 4→1; Character 23: 0→1.
Node 12. Character 5: 0→1.
Node 14. Character 11: 0→1.
Node 15. Character 20: 0→1.
Node 17. Character 16: 1→3.
Node 18. Character 19: 1→0.
Node 19. Character 2: 0→1.
Node 20. Character 16: 1→2.
Node 21. Character 5: 1→0.
Node 23. Character 29: 0→1
Node 24. Character 22: 0→2
Node 25. Character 5: 0→1; Character 28: 0→1; Character 30: 2→3; Character 32: 0→1
Node 26. Character 2: 0→1.
Node 27. Character 2: 1→0; Character 11: 0→1; Character 12: 1→2; Character 30: 3→4; Character 33: 0→1
Node 28. Character 15: 1→0; Character 23: 0→1
Node 29. Character 1: 0→1.
Node 30. Character 2: 1→0; Character 15: 1→2; Character 18: 0→1; Character 21: 0→2; Character 24: 3→1; Character 25: 0→1; Character 28: 1→2; Character 30: 3–1; Character 31: 0→1; Character 35: 1→0.
Node 31. Character 5: 1→0.; Character 30: 1→0.
Node 32. Character 8: 0→1; Character 10: 0→1; Character 11: 0→1; Character 13: 1→0; Character 14: 1→0; Character 17: 0→2; Character 21: 2→0; Character 30: 1→5; Character 31: 1→0; Character 33: 0→1; Character 34: 0→1; Character 35: 0→1.
Node 33. Character 1: 0→1; Character 4: 0→1; Character 6: 0→1; Character 7: 0→1; Character 11: 0→1; Character 14: 1→0; Character 15: 2→1; Character 16: 4→5; Character 19: 1→0; Character 1→2; Character 33: 0→1.
Node 34. Character 5: 1→0; Character 8: 0→1; Character 9: 0→1; Character 10: 0→1; Character 11: 0→1.
Node 35. Character 17: 0→2.
Node 36. Character 30: 1→0.
Node 37. Character 14: 1→0
Node 38: Character 2: 0→1.

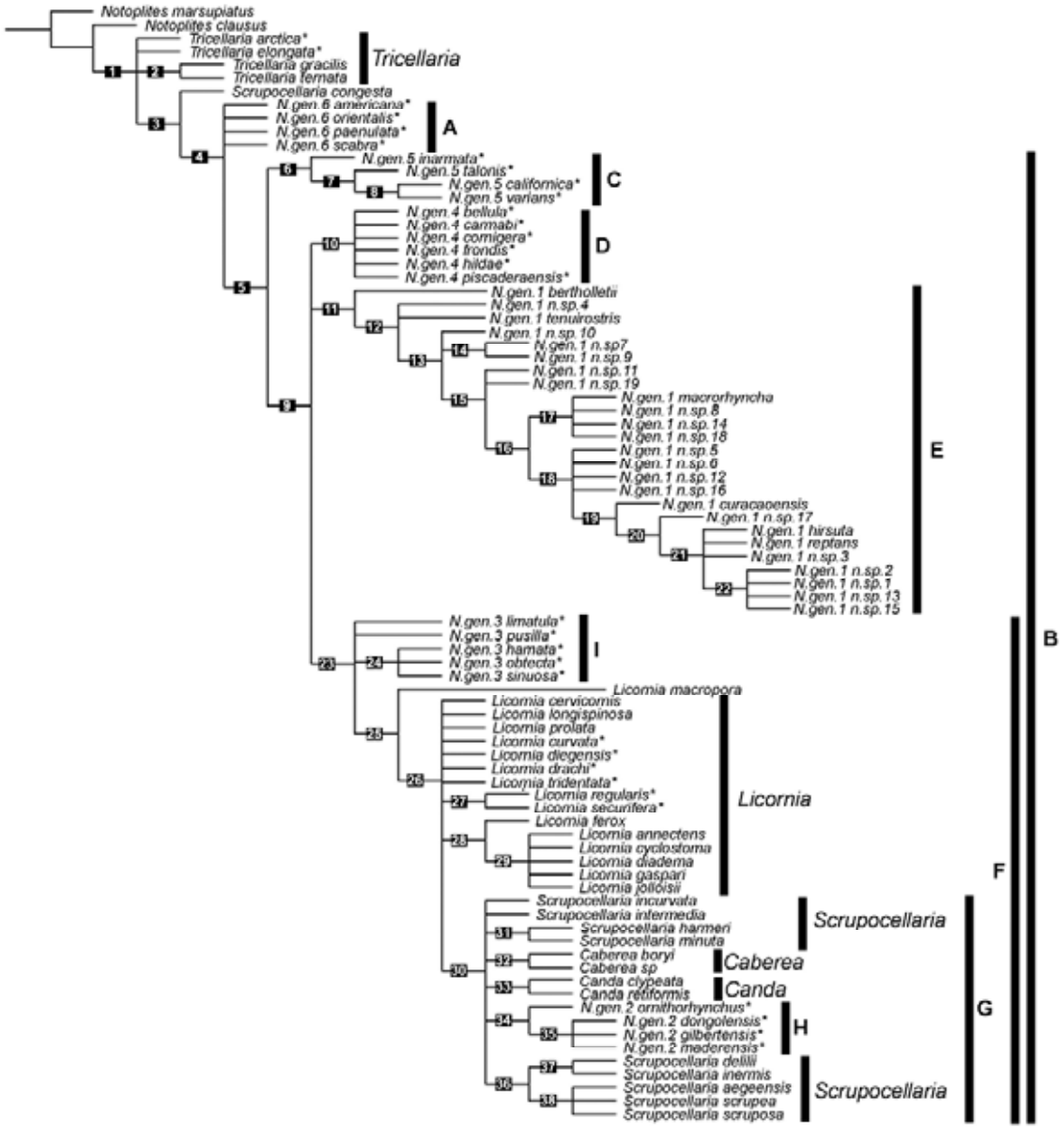

Figure 4.1. Semi-strict consensus tree based on *Notoplites* as outgroup. New combinations are marked with an asterisk (*).

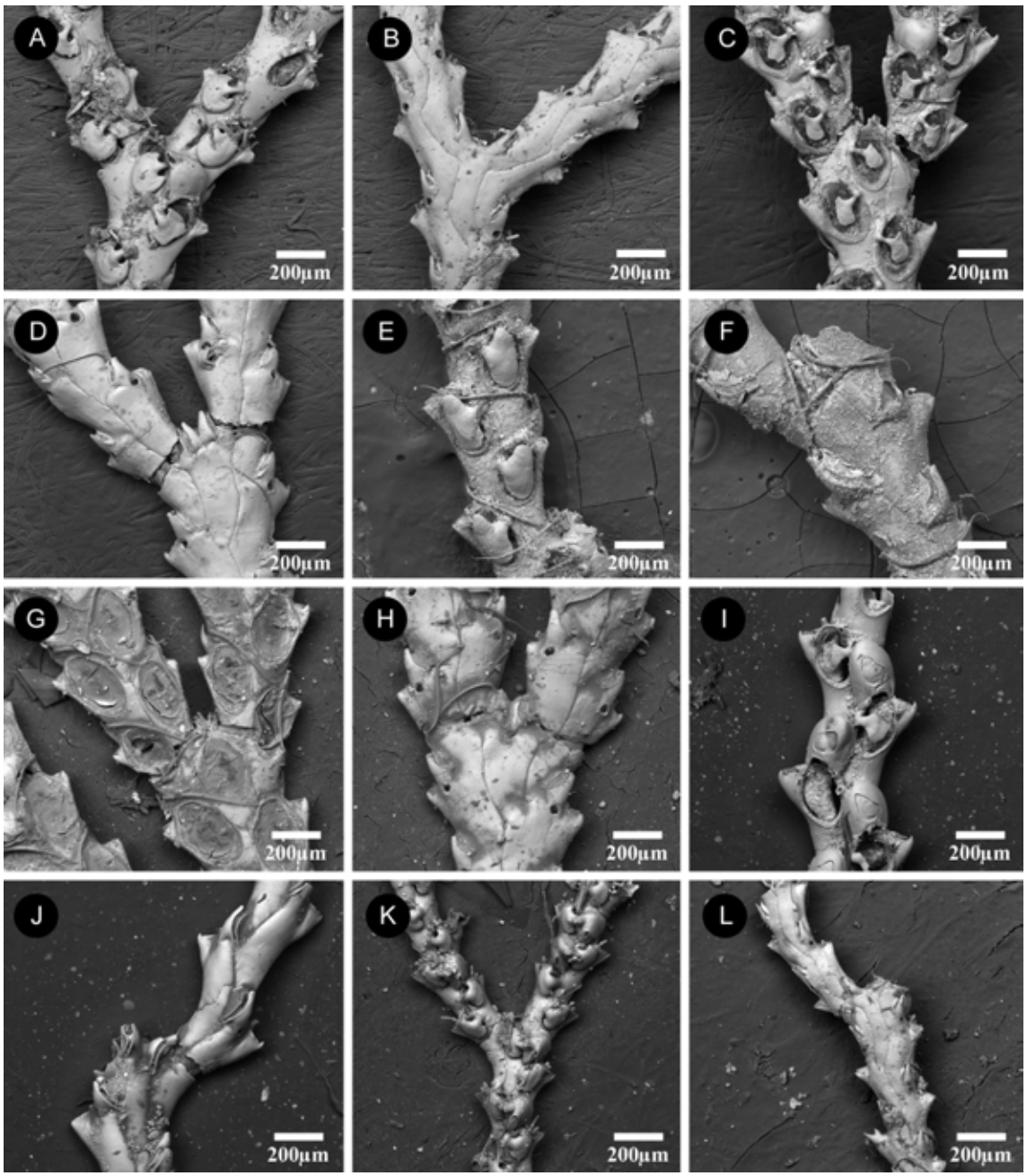

Figure 4.2. Species of *Scrupocellaria 'sensu stricto'*. **A–B**, *Scrupocellaria aegeensis*. **C–D**, *Scrupocellaria delilli*. **E–F**, *Scrupocellaria incurvata*. **G–H**, *Scrupocellaria inermis*. **I–J**, *Scrupocellaria intermedia*. **K–L**, *Scrupocellaria minuta*.

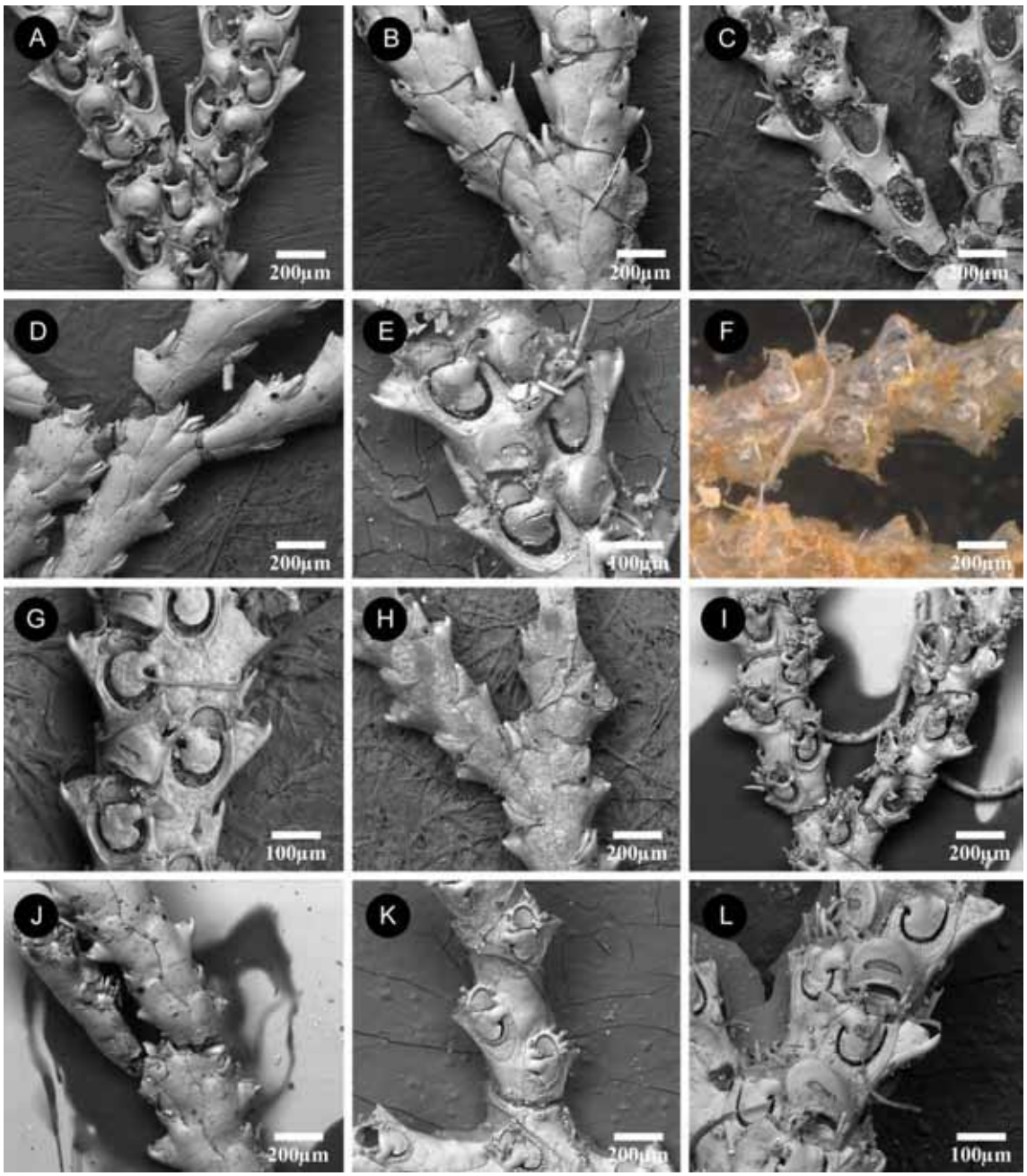

Figure 4.3. A–D. Species of *Scrupocellaria 'sensu stricto'*. **E–L**. Species assigned to *N.gen.2*. **A–B**, *Scrupocellaria scrupea*. **C–D**, *Scrupocellaria scruposa*. **E**, *N.gen.2*. *maderensis* n. comb. **F**, *N.gen.2*. *gilbertensis* n. comb. **G–H**, *N.gen.2*. *dongolensis* n. comb. **I–J**, *N.gen.2*. *ornithorhynchus* n. comb. **K–L**, Two undescribed species of *N.gen.2*. found in NHMUK collection.

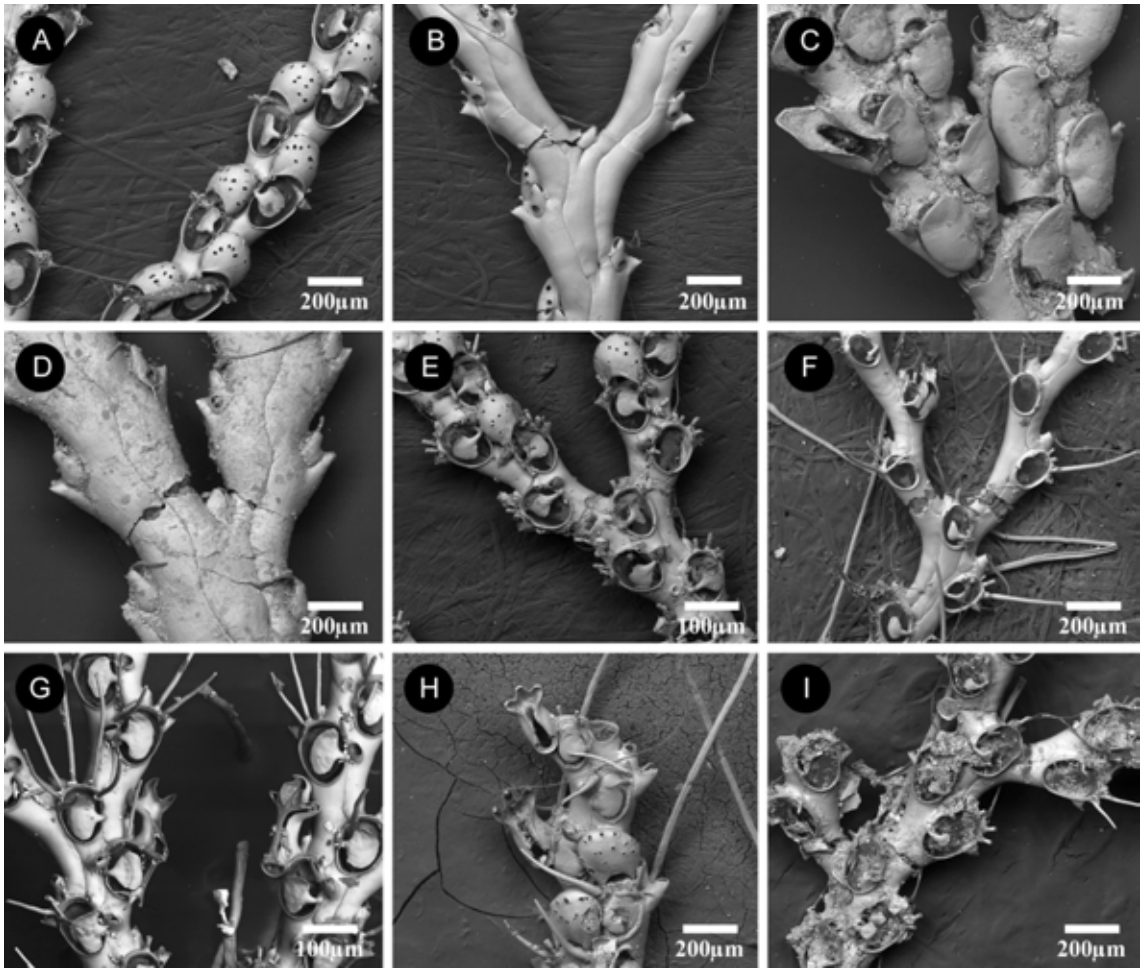

Figure 4.4. Species assigned to *N.gen.3*. **A–B**, *N.gen.3 limatula* n. comb. **C–D**, *N.gen.3 obtecta* n. comb. **E–I**, Five undescribed species of *N.gen.3* found in NHMUK collection.

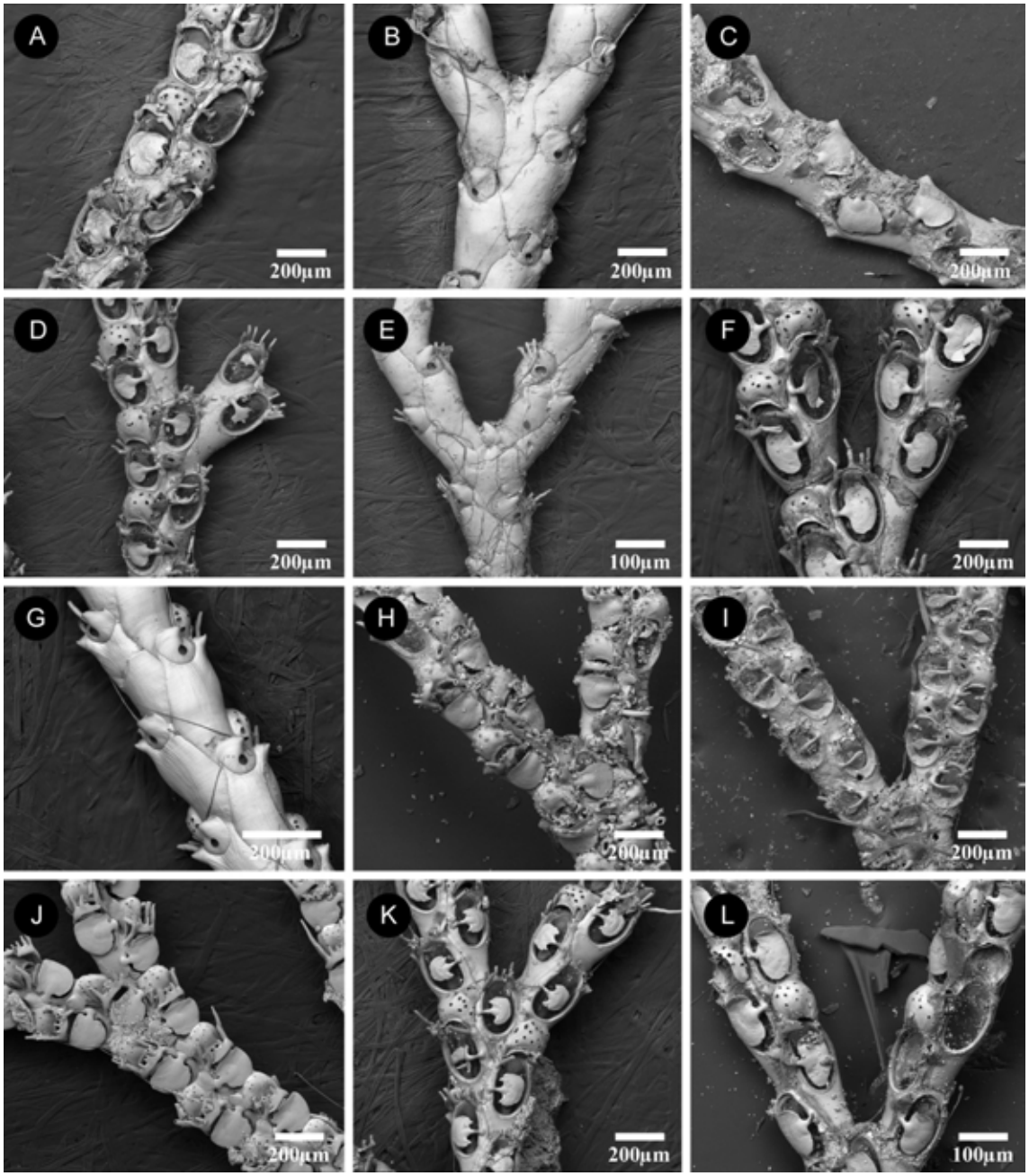

Figure 4.5. Species assigned to *N.gen.4*. **A–B**, *N.gen.4*. *carmabi* n. comb. **C**, *N.gen.4*. *cornigera* n. comb. **D–E**, *N.gen.4*. *hildae* n. comb. **F–G**, *N.gen.4*. *piscaderaensis* n. comb. **H–L**, Five undescribed species of *N.gen.4* found in NHMUK collection.

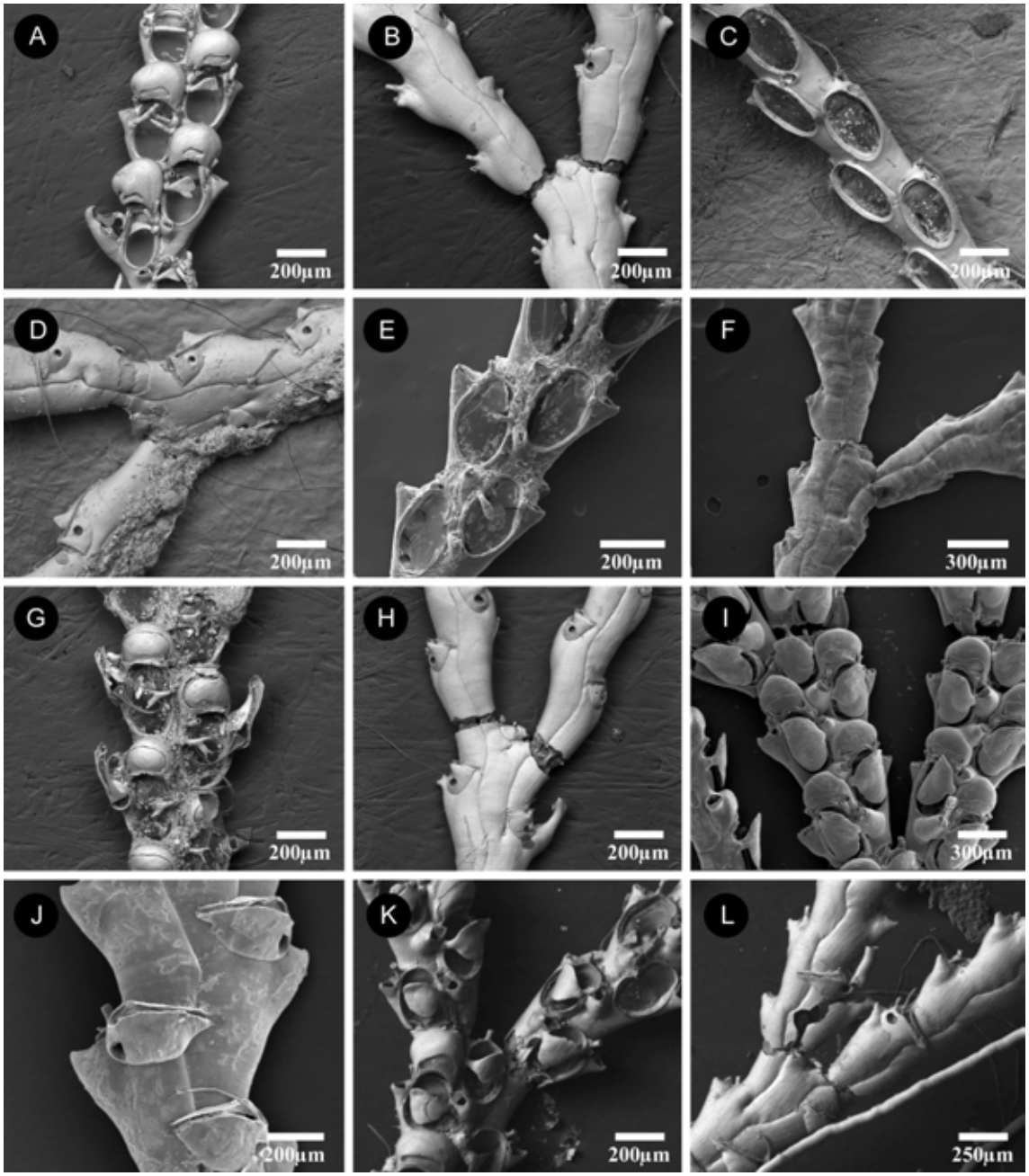

Figure 4.6. A–H, Species assigned to *N.gen.5*. **I–L**, Species assigned to *N.gen.6*. **A–B**, *N.gen.5 californica* n. comb. **C–D**, *N.gen.5 inarmata* n. comb. **E–F**, *N.gen.5 talonis* n. comb. **G–H**, *N.gen.5 varians* n. comb. **I–J**, *N.gen.6 orientalis* n. comb. **K–L**, *N.gen.6 scabra* n. comb.

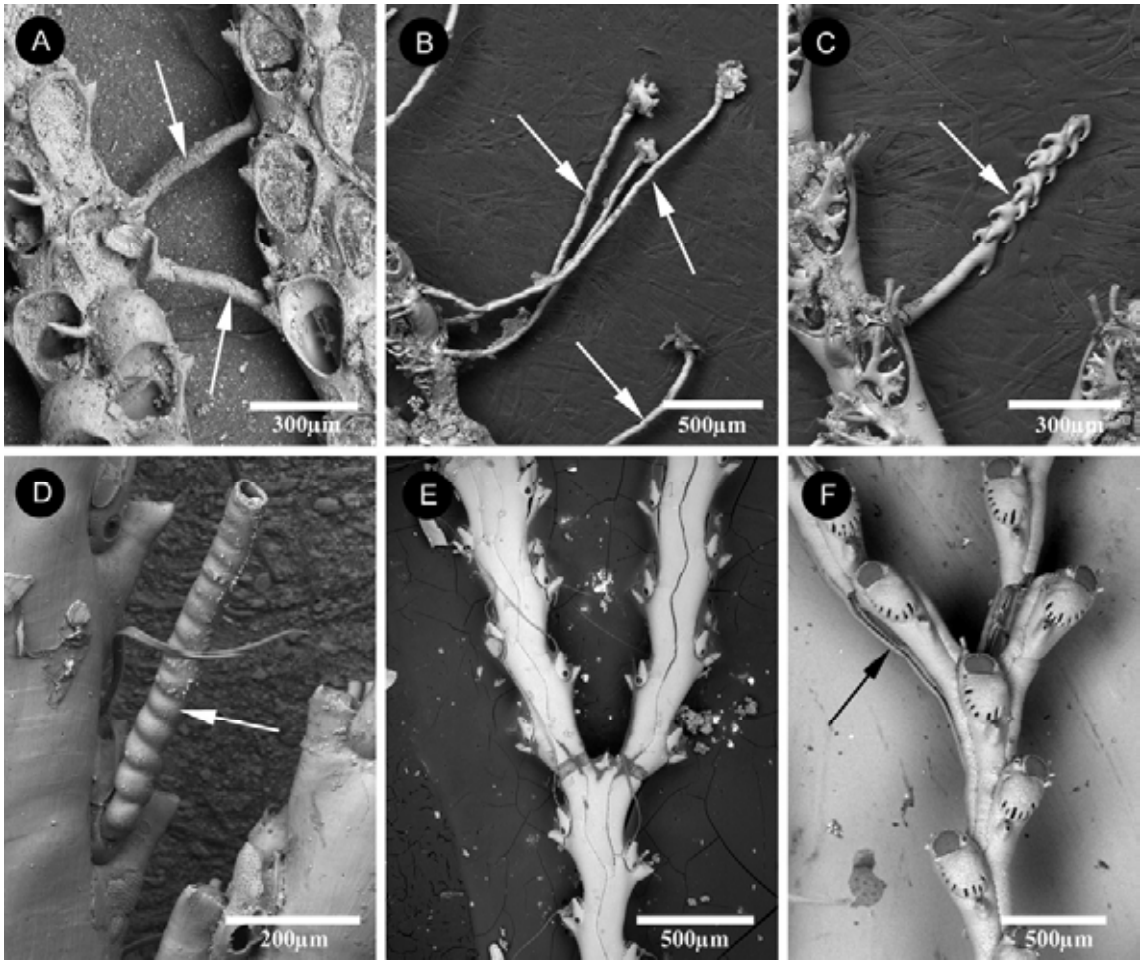

Figure 4.7. Rhizoids found in Candidae species (arrows). **A**, interconnective rhizoids (white arrow). **B–D**, Holdfast rhizoids (white arrows). **B**, Smooth rhizoids. **C**, Rhizoids with retroussé hooks. **D**, Ringed rhizoids. **E**, Colony without rhizoid. **F**, Colony with adjacent rhizoids on abfrontal surface (black arrow).

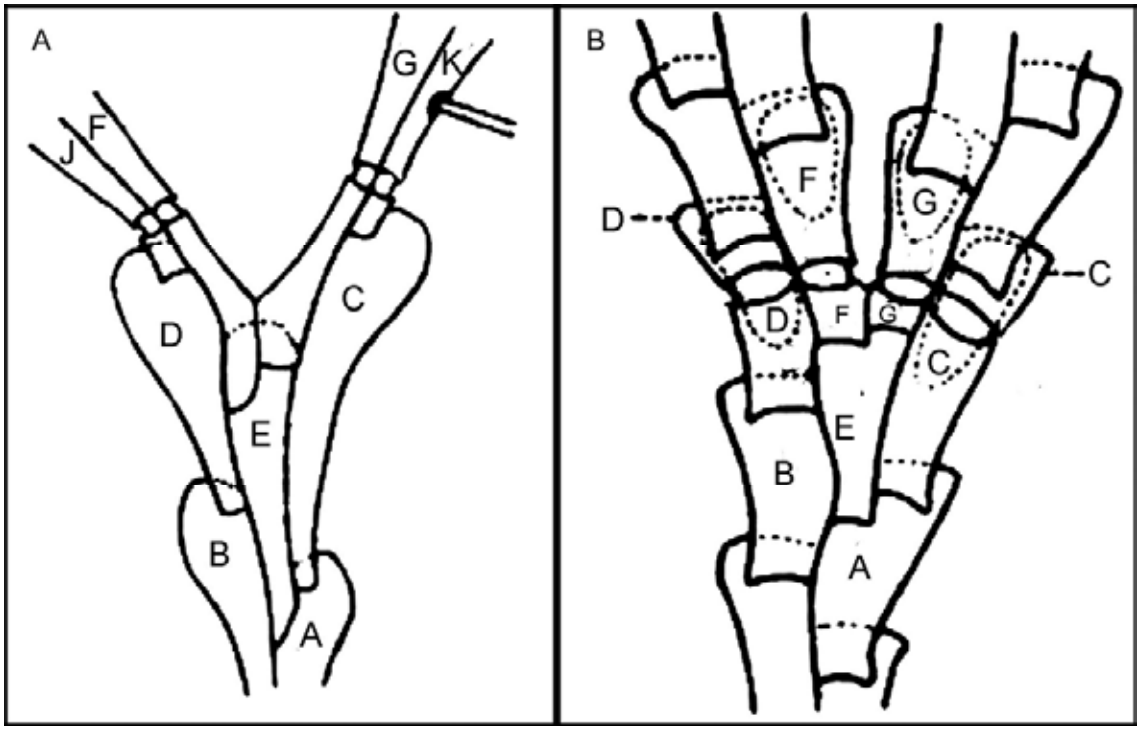

Figure 4.8. Abfrontal surface of colony showing the uniform notation for the order of zooids at branch bifurcations proposed by HARMER (1923) and the position of the joints (modified from HARMER, 1923). **A**, Joints passing across zooids FD and GC (type 15). **B**, Joints passing across zooids FJ and GK (type 8).

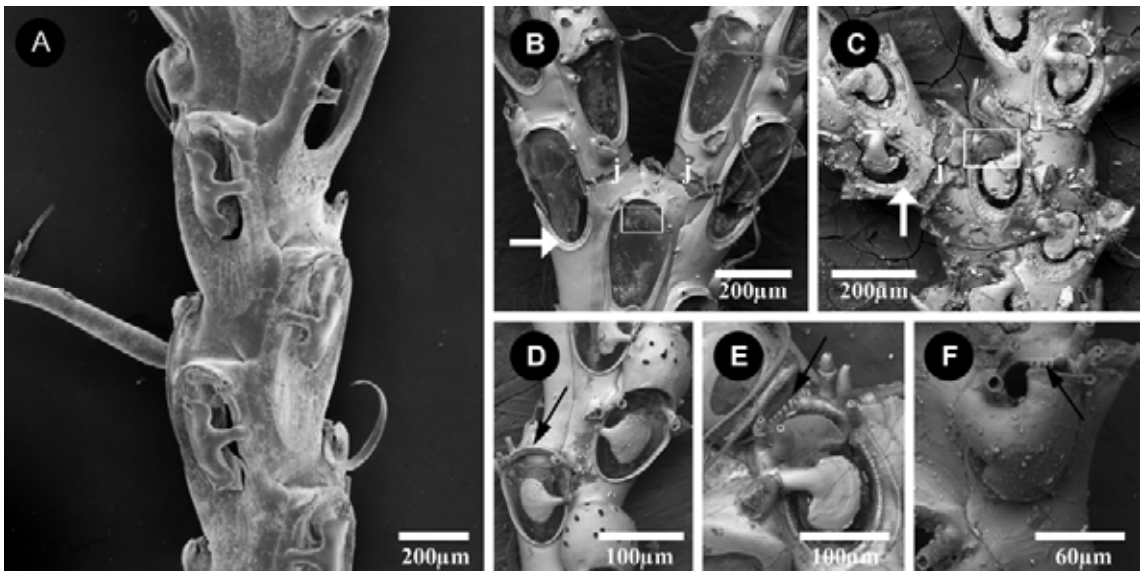

Figure 4.9. A, Adjacent zooids sharply inclined in relation to the axis, characteristic of *Canda*. **B–C**, Position of the joints in zooids C and D at bifurcation; note the development of cryptocyst (white arrows) and two distinct opercula (square). **B**, The joints pass across the opesiae in zooids C and D; note the membranous operculum with its distinctly chitinous distal rim. **C**, The joints are passing across the gymnocysts in C and D zooids; note the entirely chitinous operculum placed in an obliquely truncate distal area. **D–F**, Distal edge of autozooid (black arrow). **D**, Smooth distal edge. **E**, Corrugated distal edge in ovicelled zooids. **F**, Corrugated distal edge in non-ovicelled zooids.

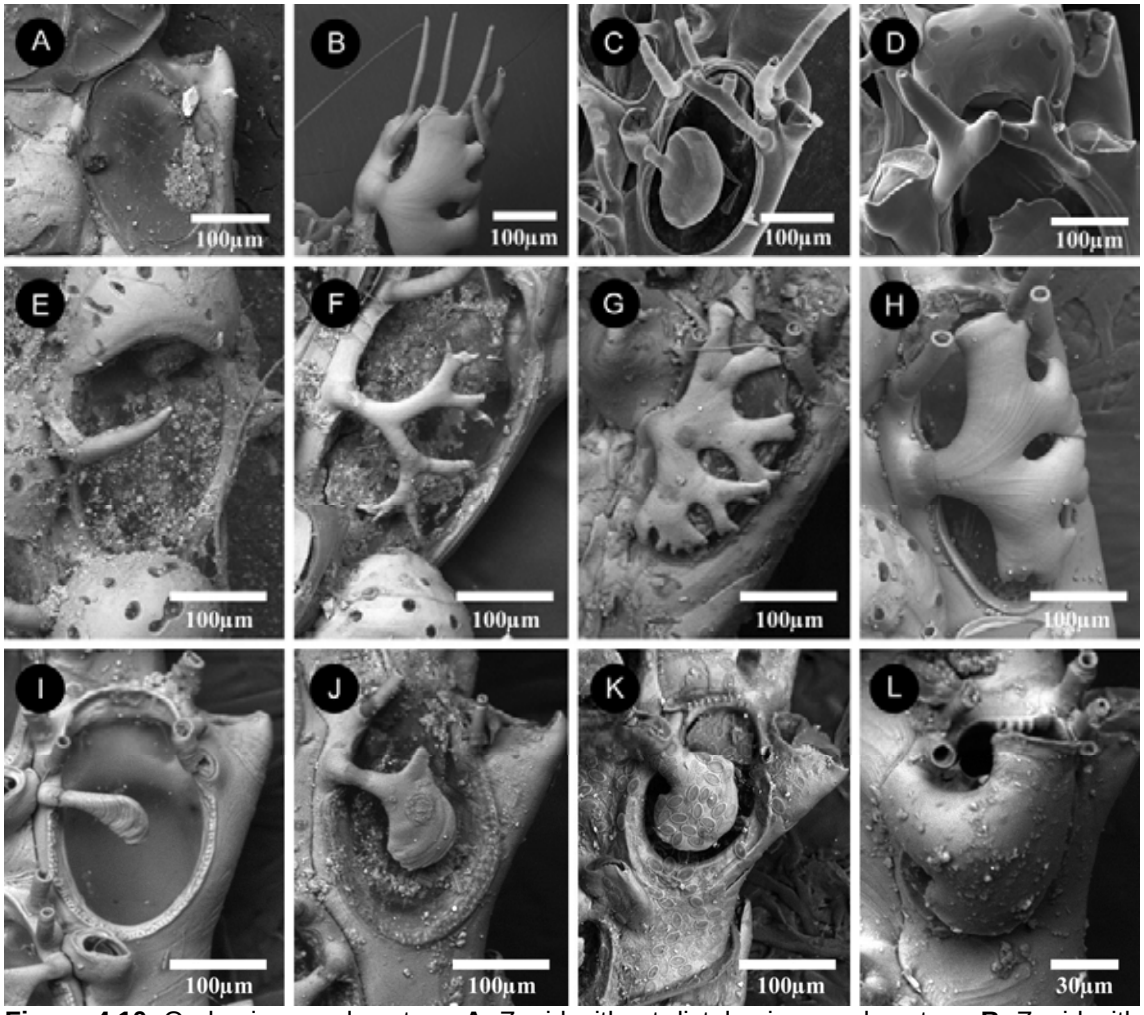

Figure 4.10. Oral spines and scutum. **A**, Zooid without distal spines and scutum. **B**, Zooid with unbranched oral spines. **C**, Zooid with proximal-most outer spine branched (cervicorn) and additional unbranched spines; note the single ovoid plate of scutum. **D**, Zooid with proximal-outer, outer and inner spines bifurcated, and distal unbranched spines. **E–L**, Distinct morphologies of scutum at the inner edge of opesia, arising at the median region of opesia (Character 16; **E**, state 0; **F**, state 1; **G**, state 2; **H**, state 3) or from its distal third (Character 17; **I–J**, state 0; **K**, state 2; **L**, state 3).

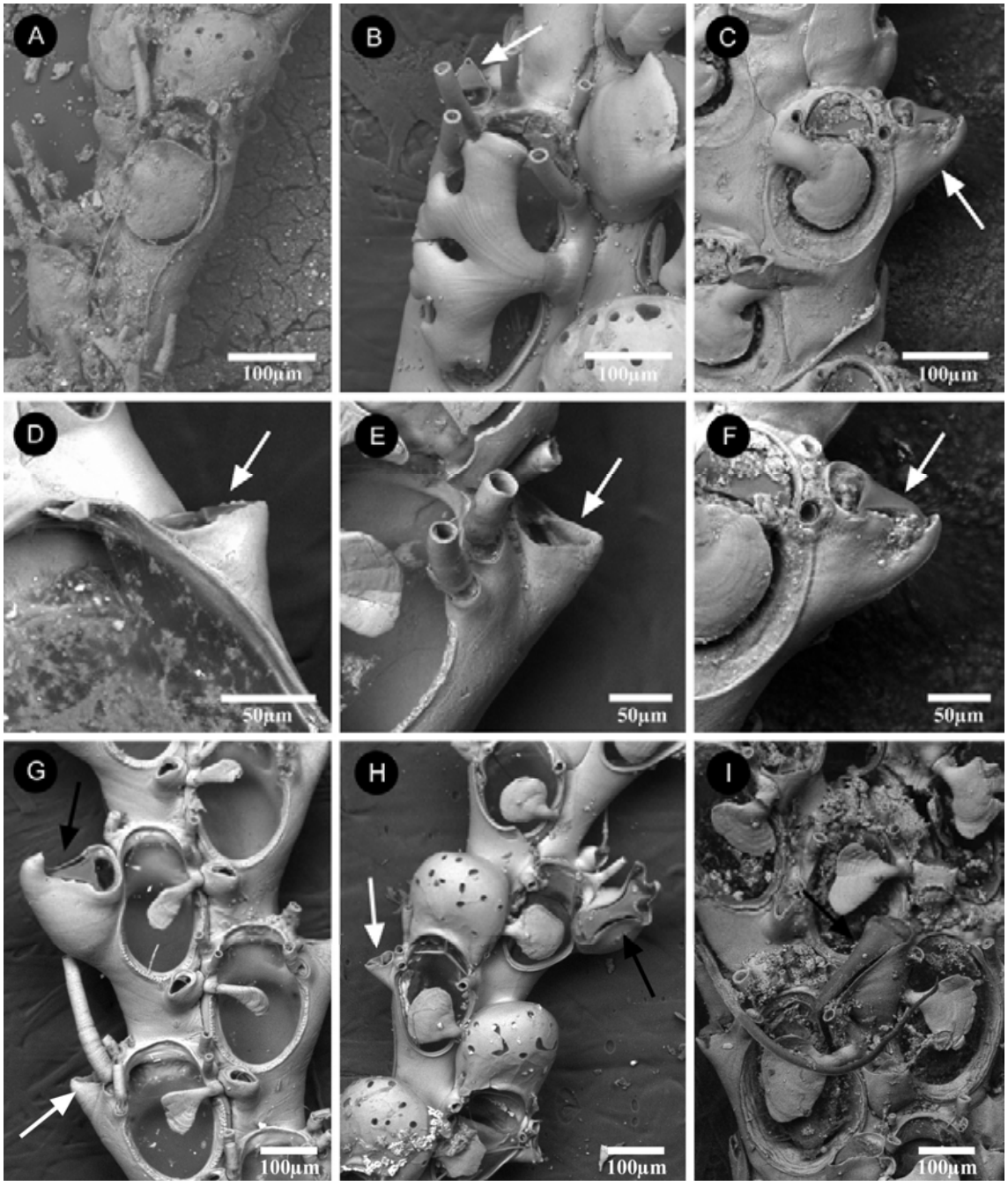

Figure 4.11. Frontal and lateral avicularia. **A**, Zooids without lateral avicularium. **B–H**, Zooids with sessile lateral avicularium (white and black arrows). **B**, Zooid with avicularium positioned at outer distal corner and directed obliquely distolaterally. **C**, Zooid with avicularium positioned lateral to the opercular area and directed laterally. **D–F**, Rostrum of lateral avicularium. **D**, Serrated lateral edge, straight at its tips. **E**, Smooth lateral edge, with curved tips. **F**, serrated lateral edge, strongly hooked. **G–I**, Dimorphic lateral and frontal avicularia (black arrows). **G**, Dimorphic lateral avicularium with triangular mandible. **H**, Dimorphic lateral avicularium with trifoliate mandible. **I**, Dimorphic frontal avicularium.

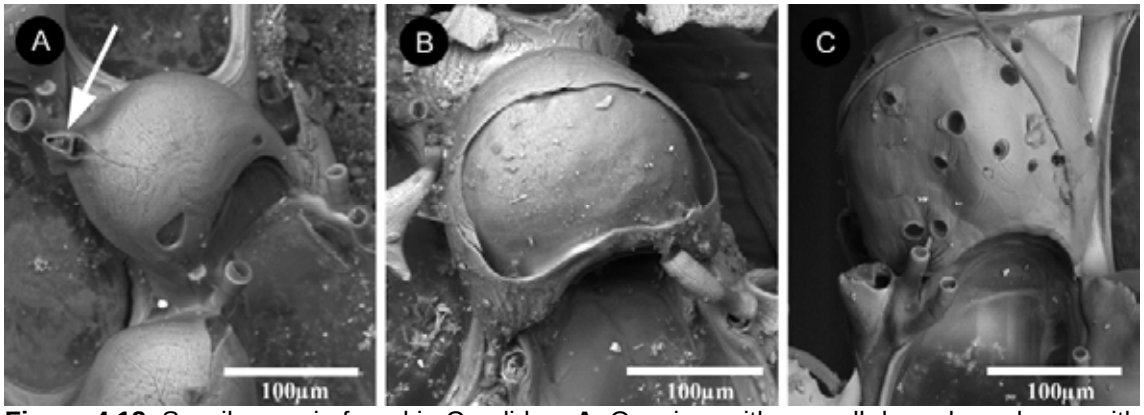

Figure 4.12. Sessile ooecia found in Candidae. **A**, Ooecium with a small drop-shaped pore with an distal avicularium (white arrow). **B**, Ooecium with single, large fenestra, without avicularium. **C**, Ooecium with porous ectooecium.

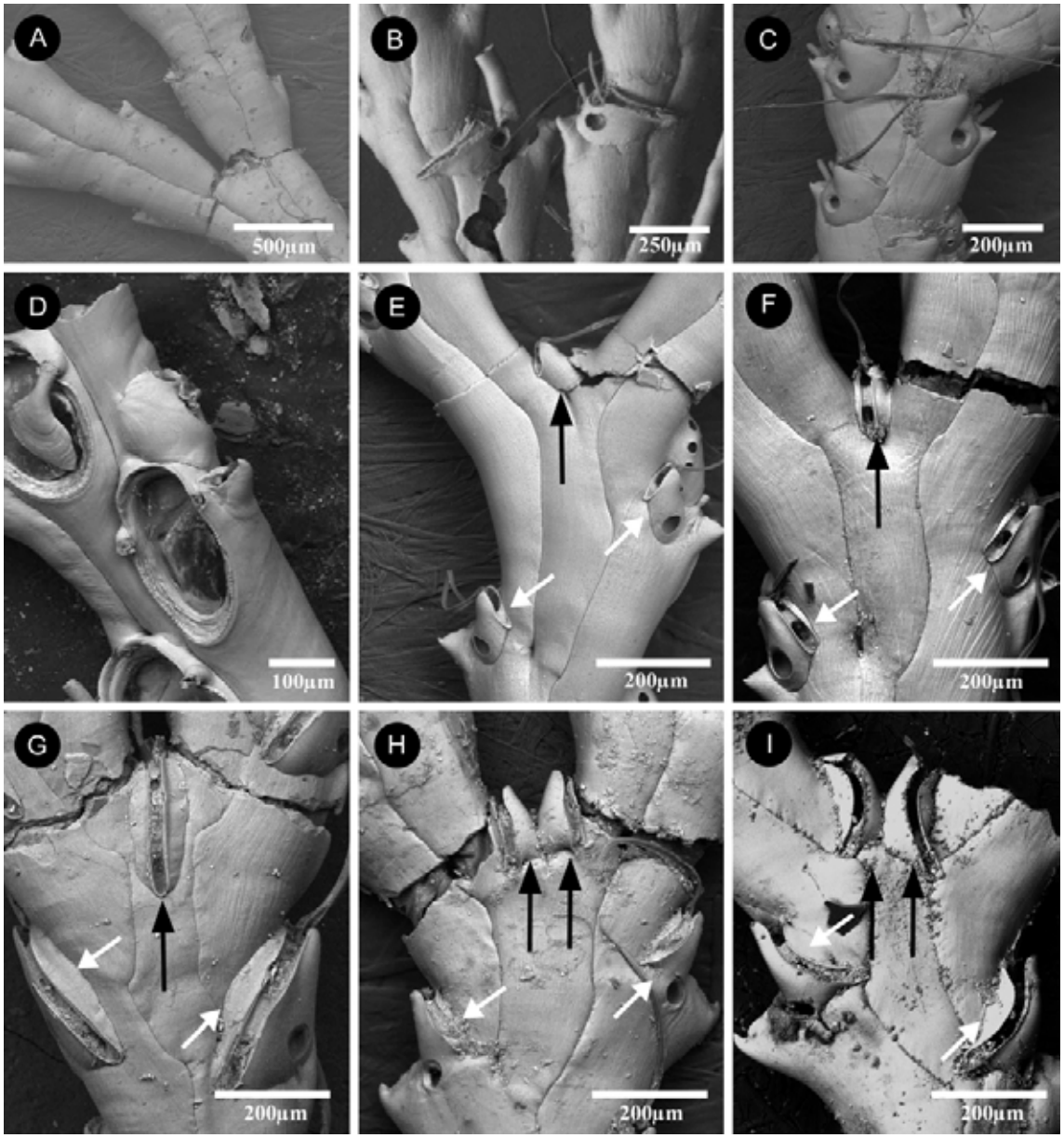

Figure 4.13. Heterozooids on abfrontal surface of the colony. **A**, Colony without abfrontal heterozooids. **B**, Abfrontal avicularia. **C**, Abfrontal vibracula, with transverse setal groove. **D**, Lateral rhizoidal chamber associated with outer zooids at the bifurcation; note the absence of abfrontal avicularia. **E–I**, Abfrontal vibracula with oblique setal groove (axial vibracula shown by black arrow and other vibracula shown by white arrow). **E**, Vibracula with straight setal groove occupying less than half the length of the vibracular chamber; the setal groove of the axial vibraculum is laterally placed. **F**, Vibracula with straight setal groove occupying two thirds of the length of the vibracular chamber; the palate is complete and with a small foramen. **G**, Vibracula with straight setal groove occupying the entire length of the vibracular chamber; note the presence of single axial vibraculum. **H**, Vibracula with curved setal groove occupying two thirds of the total length of the vibracular chamber; note the presence of two axial vibracula (black arrows). **I**, Vibracula with curved setal groove occupying the entire length of the vibracular chamber; note the presence of two axial vibracula (black arrows).

CONSIDERAÇÕES FINAIS

O presente estudo revela uma fauna e diversidade desconhecidas de briozoários (Candidae). Em relação ao gênero *Scrupocellaria*, estudos taxonômicos utilizando microscopia eletrônica de varredura são escassos (TILBROOK & VIEIRA, *no prelo*), o que redunda em pouco conhecimento na distribuição das espécies, que muitas vezes são tratadas como cosmopolitas ou de ampla variação morfológica (TILBROOK, 2006; BERNING & KUKLINSKI, 2008; VIEIRA *et al.*, 2010, 2012). Nossos resultados revelaram que a utilização de microscopia eletrônica de varredura e comparações morfométricas de estruturas coloniais são indispensáveis para distinção de espécies de *Scrupocellaria lato sensu*. Para as espécies estudadas, a plasticidade intraespecífica é menor que a relatada anteriormente por diversos autores (*e.g.* HARMER, 1923, 1926; GAUTIER, 1962; PRENANT & BOBIN, 1966).

O estudo taxonômico das espécies do gênero *Scrupocellaria*, com a análise filogenética de 84 espécies de Candidae utilizando 35 caracteres morfológicos mostrou que *Scrupocellaria* é um táxon polifilético, compreendendo espécies pertencentes a 7 grupos morfológicos distintos. Tais grupos morfológicos são caracterizados pela forma do vibraculário abfrontal, forma dos aviculários laterais, forma do ovicelo, forma e posição do escudo, e forma dos espinhos orais (ramificados ou não).

Apesar da ausência de suporte na análise filogenética morfológica, provavelmente resultante pelo número elevado de caracteres polimórficos, o gênero *Licornia* van Beneden, 1850 é redefinido para incluir espécies com oécios com vários poros, ramos conectados entre si através de tubos transversais, articulações atravessando os opésios dos zooides externos da bifurcação, câmara vibracular triangular com sulco do vibráculo obliquo e 1 vibráculo axial. A espécie *Licornia jolloisii* é relatada pela primeira vez para o Atlântico (Flórida, EUA e Brasil). A ocorrência de *Licornia diadema* na costa brasileira é questionada; a espécie é morfologicamente distinta dos espécimes da Austrália e necessita de comparações morfológicas adicionais (TILBROOK & VIEIRA, *no prelo*).

Um novo gênero (*N.gen.1*) é descrito para acomodar *Scrupocellaria bertholletii* e outras 8 espécies anteriormente tratadas no *Scrupocellaria*. Tais espécies são caracterizadas pelo escudo ramificado, espinhos orais não ramificados, câmara do vibraculário trapezoidal e ovicelos com vários poros frontais. Dezenove espécies novas são descritas para *N.gen.1*, muitas das quais relatadas em águas rasas sob o

nomes *Scrupocellaria bertholletii* e *Scrupocellaria reptans*. Espécies de *N.gen.1* são distintas entre si pela posição das articulações em relação à bifurcação, forma do escudo, forma e posição do aviculário dimórfico frontal, presença e posição dos aviculários laterais e tamanho da câmara do vibraculário. A maioria das espécies de *N.gen.1* são conhecidas para águas tropicais e subtropicais, com apenas 4 espécies relatadas para águas temperadas do Atlântico Norte e Mar do Norte. Uma espécie, *N.gen.1 bertholletii* tem uma ampla distribuição no Canal de Suez, Mediterrâneo e Atlântico, porém muitos dos registros da espécies para outras localidades representam táxons morfologicamente distintos. O elevado número de espécies novas de *N.gen.1* e a distribuição restrita dessas espécies sugerem que um maior esforço amostral pode revelar uma diversidade ainda maior para o gênero.

O gênero *Scrupocellaria*, anteriormente caracterizado pela presença de câmara vibracular basal e bifurcação do tipo 8 (HARMER, 1926), é redefinido para incluir 10 espécies caracterizadas por oécios com fenestra ectooecial simples e com um aviculário associado, opérculo colocado na membrana frontal sem côndilos proximais distintos, câmara vibracular com fenestra obliqua e zooide axial com dois vibraculários. Com base em dados morfológicos, outros cinco gêneros foram criados: *N.gen.2* (com 4 espécies), *N.gen.3* (com 6 espécies), *N.gen.4* (com 8 espécies) *N.gen.5* (com 4 espécies) e *N.gen.6* (com 5 espécies). A análise preliminar de espécimes depositados em coleções científicas revelou que uma diversidade maior para estes táxons está por ser descrita. Portanto, futuros estudos taxonômicos e filogenéticos, a partir de dados morfológicos e ferramentas moleculares, serão importantes para a melhor compreensão da diversidade, distribuição e relação filogenética entre as espécies de Candidae.

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RESUMO

O gênero *Scrupocellaria senso lato* (Família Candidae) compreende *ca*. 92 espécies, 20 fósseis e 72 recentes. Muitas dessas espécies são morfologicamente semelhantes ou tratadas como tendo grande plasticidade morfológica, as quais consequentemente têm ampla distribuição mundial. Embora o gênero tenha uma longa história taxonômica e seus representantes sejam abundantes e comuns desde as regiões entremares até mais de 1,000 metros de profundidade, estudos taxonômicos do gênero são escassos. Os objetivos desse estudo são: (i) realizar o levantamento das espécies de *Scrupocellaria*, (ii) delimitar a variação morfológica intraespecífica das espécies, (iii) analisar a morfologia comparada de *Scrupocellaria* visando propor uma hipótese de relações filogenéticas entre as espécies do gênero. O estudo inclui colônias coletadas em vários pontos da costa brasileira, bem como espécimes depositados em coleções científicas nacionais e internacionais. Alguns espécimes foram selecionados para observação em Microscópio Eletrônico de Varredura. Entre os espécimes estudados foram incluídos 32 holótipos, sintipos de 22 espécies e 1 lectótipo. Várias estruturas morfológicas foram utilizadas pela primeira vez na distinção dos táxons, *e.g.* forma da superfície dos rizoides, tamanho dos vibraculários basais, tamanho e forma dos aviculários frontais e laterais. O lectótipo de *Scrupocellaria reptans* foi escolhido para redefinir a identidade dos espécimes descritos por Carolus Linnaeus, distintos de uma nova espécie descrita para o Mar do Norte pela forma do escudo, tamanho dos zooides e rizoides cilíndricos sem ganchos em sua superfície. *Scrupocellaria jolloisii* é relatada pela primeira vez no Atlântico e classificada no gênero *Licornia,* nome que é ressuscitado para incluir outras 9 espécies: *Licornia annectens* n. comb., *Licornia cervicornis* n. comb., *Licornia cyclostoma* n. comb., *Licornia diadema* n. comb., *Licornia ferox* n. comb., *Licornia gaspari* n. comb., *Licornia longispinosa* n. comb., *Licornia macropora* n. comb. e *Licornia prolata* n. comb. Um novo gênero, *N.gen.1*, é criado para acomodar *Scrupocellaria bertholletii* (Audouin, 1826). Outras 26 espécies, 19 das quais descritas como novas, são classificadas em *N.gen.1*, e uma chave dicotômica para as espécies do gênero é apresentada. Um estudo filogenético, baseado em 35 caracteres morfológicos de 84 espécies de Candidae, indica que o gênero *Scrupocellaria* compreende um táxon polifilético e que o gênero *N.gen.1* é monofilético. *Scrupocellaria 'sensu stricto'* é redefinido utilizando quatro características morfológicas: câmara vibracular com sulco do vibráculo curvo e obliquo, ectooécio com fenestra frontal, 2 vibraculários axiais e opérculo membranoso com margem distal distinta. Assim, *Scrupocellaria 'sensu stricto'* inclui 10 espécies: *Scrupocellaria aegeensis*, *Scrupocellaria delilii*, *Scrupocellaria harmeri*, *Scrupocellaria incurvata*, *Scrupocellaria inermis*, *Scrupocellaria intermedia*, *Scrupocellaria jullieni*, *Scrupocellaria minuta*, *Scrupocellaria scrupea*, e *Scrupocellaria scruposa*. Cinco gêneros são criados para acomodar outras espécies classificadas anteriormente como *Scrupocellaria*, distintos pela forma do escudo e espinhos orais, forma do vibraculários e forma dos ovicelos. O presente estudo revelou uma diversidade ainda desconhecida para vários grupos de Candidae, e mostra a necessidade de mais estudos sobre a taxonomia e filogenia da família, para a melhor compreensão da distribuição, variação morfológica e relação filogenética entre os táxons.

ABSTRACT

The genus *Scrupocellaria sensu lato* (Family Candidae) comprises about 92 species, 20 fossil and 72 Recent. Many of the species are morphologically similar or have been treated taxonomically as having a high degree of morphological plasticity, with distributions of many of the species being reported to be “worldwide”. Despite the long taxonomic history of *Scrupocellaria* and its occurrence in habitats ranging from intertidal to deep water, taxonomic studies of the genus are scarce. Therefore the purpose of this study was: (i) to carry out a species survey of *Scrupocellaria*, (ii) to delimit the intraspecific morphological variations of species, (iii) to analyze the comparative morphology of *Scrupocellaria* in order to propose a hypothesis of phylogenetic relationships between species of the genus. This study included both colonies collected in various localities on Brazilian coast and material of non-Brazilian species deposited at scientific collections around the world. All specimens were studied by light microscopy. Some specimens were also chosen for study with the scanning electron microscope. Specimens studied included holotypes of 32 species, syntypes of 22 species and 1 lectotype. Some morphological characters were used for the first time to distinguish taxa, *e.g.* rhizoidal surface, size of abfrontal vibracula, and shape of lateral and frontal avicularia. The lectotype of *Scrupocellaria reptans* was selected to redescribe and define the identity of the type species of *Scrupocellaria* from specimens described by Carolus Linnaeus, and to show its distinction from a newly described species from North Sea by means of the shape of scuta, size of zooids and, occurence of rhizoids with retroussé hooks. *Scrupocellaria jolloisii* is reported by first time in the Atlantic Ocean and placed in the genus *Licornia*, a name resurrected to acommodate 9 species formerly placed in *Scrupocellaria*: *Licornia annectens* n. comb., *Licornia cervicornis* n. comb., *Licornia cyclostoma* n. comb., *Licornia diadema* n. comb., *Licornia ferox* n. comb., *Licornia gaspari* n. comb., *Licornia longispinosa* n. comb., *Licornia macropora* n. comb. e *Licornia prolata* n. comb. A new genus, *N.gen.1*, is described to include *Scrupocellaria bertholletii*. Twenty-six species, 19 of them described as new, are assigned to *N.gen.1*, and a taxonomic key for species of that genus is presented. A phylogenetic study using 35 morphological characters of 84 Candidae species suggests that the genus *Scrupocellaria* is a polyphyletic taxa and the genus *N.gen.1* is a monophyletic taxa. *Scrupocellaria ‘sensu stricto’* is redefined according to four morphological features: vibracular chamber with curved setal groove, ooecium with a single ectooecial fenestra, two axillary vibracula and a membranous operculum with a distinct distal rim. Thus *Scrupocellaria ‘sensu stricto’* includes 10 species: *Scrupocellaria aegeensis*, *Scrupocellaria delilii*, *Scrupocellaria harmeri*, *Scrupocellaria incurvata*, *Scrupocellaria inermis*, *Scrupocellaria intermedia*, *Scrupocellaria jullieni*, *Scrupocellaria minuta*, *Scrupocellaria scrupea*, and *Scrupocellaria scruposa*. Five genera are erected to include other species previously assigned to *Scrupocellaria*; they are distinct in the shape of scuta and oral spines, the shape of vibracular chamber and the surface of ovicells. The study revealed a high diversity in some groups of Candidae and the necessity of additional studies on taxonomy and phylogeny of the family to provide a better understanding of distributions, morphological variation, and phylogenetic relationships between the taxa.

ANEXO 1

Catalogue of the type specimens of Recent species of the genus *Scrupocellaria* (Bryozoa, Candidae)

1. *aegeensis* Harmelin, 1969
Type locality: Aegean Sea.
Syntypes: NHMUK 2010.12.7.3–2, dry, N.O. *Jean Charcot*, St. 20.MO.67, Strait of Scarpanto (Karpathos), Aegean Sea, 35°55.60' N, 27°29.01' E, 60–80m, 29.viii.1967.

2. *americana* Packard, 1863
Type locality: Labrador.
Syntype: MCZ 134, wet, *Scrupocellaria americana*, A.S. Packard det., no locality labeled.
Remarks: In the MCZ collection were localized other four jar of supposedly syntypes, but without *Scrupocellaria* specimens: MCZ 515, *Scrupocellaria* n. sp., A.S. Packard det., Labrador; MCZ 546, MCZ 569, *Scrupocellaria americana*, A.S. Packard det., no locality labeled; MCZ 640, *Scrupocellaria americana*, A.S. Packard det., Labrador.

3. *annectens* MacGillivray, 1887
Type locality: Straits of Gaspar.
Syntypes: MV 456061–3, slides, Straits of Gaspar, Malaysia.

4. *aquitanica* Jullien & Calvet, 1903
Type locality: Biscay Bay.
Syntypes: MOM 420193, two dry colonies (n.21 and n.84), *Hirondelle*, St. 58, Golfe de Gascogne, 134m, 7.viii.1886.

5. *arctica* (Busk, 1855)
Type locality: Greenland.
Syntypes: NHMUK 1899.7.1.651–2, dry, HMS *Sophia*, West Greenland, 73°20' N, 57°20' W, 11–36.6m (6–20fms).

6. *aviculareae* Yanagi & Okada, 1918
Type locality: Japan.
Type material: Not located.

7. *bellula* Osburn, 1947
Type locality: Aruba, Caríbe.
Holotype: SBMNH 95954, slide, AHF 4, St. A18039, At 505, Allan Hancock Expedition, R/V *Velero III*, St. A18-39, Atlantic, Aruba Island, San Nicholaas Bay, 12°21'28" N, 70°4'45" W, 42m (23fms), 10.iv.1939.
Paratype: SBMNH 95955, slide, same data as holotype.

8. *bertholletii* (Audouin, 1826)
Type locality: Egypt.
Type material: Presumably lost.

9. *bertholletii tenuirostris* Osburn, 1950
Type locality: California.
Holotype: SBMNH 96145, slide, California Orange County, Newport Harbour, 33°34'60" N, 117°52'0" W, 11.ii.1945.
Paratypes: SBMNH 96146, slide, Allan Hancock Expedition, R/V *Velero III*, St. 1053-40, Mexico, Isla Angel de la Guarda, Puerto Refugio, 29°32'47" N, 113°34'35" W, 28.i.1945; SBMNH 96147, slide, Allan Hancock Expedition, R/V *Velero III*, St. 1378-41, California, Los Angeles County, Channel Island, Santa Catalina Island, 33°24'20" N, 118°22'0" W, 4.viii.1941; SBMNH 96148, slide, AHF 32.2, Hancock 255, Allan Hancock Expedition, R/V *Velero III*, St. 520-36, Mexico,

Sur Bahia, Aqua Verde, 25°31’0” N, 111°1’45” W, 27.ii.1936; SBMNH 96149, slide, Allan Hancock Expedition, R/V *Velero III*, St. 459-35, Costa Rica, Playa Blanca, 10°56’45” N, 85°53’30” W, 8.ii.1935.

10. *brevisetis* Hincks, 1882
Type locality: Queen Charlotte Island, British Columbia.
Type material: presumably lost.

11. *bifurcata* Liu, 2001
Type locality: China.
Type material: Not located.
Remarks: *Scrupocellaria bifurcata* Liu, 2001 is junior homonym of *Scrupocellaria bifurcata* Kluge, 1914.

12. *californica* Trask, 1857
Type locality: Bay of San Francisco, California.
Type material: Presumably lost.

13. *carmabi* Fransen, 1986
Type locality: Curaçao.
Holotype: RMNH 02977, slide, St. Cur82.051, Netherlands Antilles, Curaçao, Spaanse water, Inner Bay, near Jan Sofat. 0–1m, 19.viii.1982.
Paratypes: RMNH 02977* (see remarks), wet, same data as holotype; RMNH 03042, wet, St. Cur82.057, Netherlands Antilles, Curaçao, Piscadera Inner Bay, entrance, on slope of canal (recently dug), 2–6m, 5.ix.1982; RMNH 03043, wet, St. Cur82.077, Netherlands Antilles, Curaçao, Spaanse water, entrance, east shore of Spaanse Lagoen, 0–1m, 17.ix.1982; RMNH 03044, wet, St. Cur82.029, Netherlands Antilles, Curaçao, Spaanse water, Inner Bay, Brakke Put, 0–1m, 9.viii.1982; RMNH 03045, wet, St. Cur82.078, Netherlands Antilles, Curaçao, Spaanse water, Inner Bay, near New Haven, 0–1m, 17.ix.1982; RMNH 0346, wet, St. Cur82.031, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 0–1m, 9.viii.1982; RMNH 0347, wet, St. Cur82.061, Netherlands Antilles, Curaçao, Fuikbaai, western part, 3–6m, 8.ix.1982; RMNH 0348, wet, St. Cur82.066, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 0–1m, 10.ix.1982; RMNH 0349, slide, St. PWH.1493, Netherlands Antilles, Curaçao, Piscadera Baai, Northern part, NW inlet of Piscadera Chikitu, 0–1m, 25.xi.1963; RMNH 0350, slide, St. PWH.1629, Netherlands Antilles, Curaçao, Spaanse water, inner bay, Jan Sofat, islet, 0–1m, 17.xi.1968; RMNH 0351, wet and slide, St. PWH.1039, Netherlands Antilles, Curaçao, Fuikbaai, W part, SE of Newport Bath, 0–1.5m, 20.xi.1948; RMNH 0352, wet and slide, St. PWH.1039, Netherlands Antilles, Curaçao, Fuikbaai, W part, SE of Newport Bath, 0–2m, 20.xi.1948.
Remarks. Few colonies stored in alcohol under number RMNH 03042 were also labeled as holotype. However, the holotype designed in original description is the figured specimens stored as balsam slide and the additional specimens in alcohol are paratypes.

14. *cervicornis* Busk, 1852
Type locality: Australia (Queensland).
Holotype: NHMUK 1854.11.15.81, slide, off Cumberland Island, Queensland, 46m (25fms).

15. *cervicornis spinosa* Calvet, 1931
Type locality: Cape Verde.
Syntypes: MOM 420807, slide, n.477, *Princesse Alice*, St. 1203, I. Boa Vista, Cape Verde, 91m, 1901; MOM 420807, dry, n.462 (see remarks), *Princesse Alice*, St. 1203, I. Boa Vista, Cape Verde, 91m, 1901.
Remarks: The dry specimens (n.462 by Calvet) belong to *Scrupocellaria maderensis* Busk, 1860.

16. *cornigera* (Pourtàles, 1867)
Type locality: Florida.
Type material: Presumably lost.

17. *curacaoensis* Fransen, 1986
Type locality: Curaçao.
Holotype: RMNH 02975, slide, Sta. Cur82.033, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 1.5–3m, 9.viii.1982.
Paratypes: RMNH 02975* (see remarks), wet, same data as holotype; RMNH 03034, wet, St. Cur82.081, Netherlands Antilles, Curaçao, Spaanse water, entrance, Spaanse Lagoen, 0–0.5m, 17.ix.1982; RMNH 03035, wet, St. Cur82.066, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 0–1m, 10.ix.1982; RMNH 03036, St. Cur82.066, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 0–3 m, 10.ix.1982; RMNH 03037, wet and slide, St. PWH.1620, Netherlands Antilles, Curaçao, Piscadera Baai, Carmabi pier, 0–1m, 14.x.1967; RMNH 03038, wet and slide, St. PWH.1037A, Netherlands Antilles, Curaçao, Spaanse water, Spaans Lacoen, S side, 0–1.5m, 21.iv.1949; RMNH 03040, wet, St. PWH.1218, Netherlands Antiles, Curaçao, Schottegat on Venezuelan destroyer, 0–2m, 3.iii.1955; RMNH 03041, wet, St. PWH.1049C, Netherlands Antilles, Klein Bonaire, sandy reef, 1–3m, 13.ix.1948; RMNH 03064, wet and slide, St. Car.1629, Netherlands Antilles, Curaçao, Spaanse water, inner bay, Jan Sofat, islet, 0–1m, 17.xi.1968.
Remarks: Few colonies stored in alcohol under number 02975 were also labeled as holotype. However, the holotype designed in original description is the figured specimens stored as balsam slide and the additional specimens in alcohol are paratypes.

18. *curvata* Harmer, 1926
Type locality: Aru Island.
Holotype: ZMA 01063aq, wet, Siboga Expeditie, St. 273, Indonesia, Irian Jaya, Aru Island (pearl banks), anchorage off Pulu Jedan, 13m, 23.12.1899. Schizoholotype: NHMUK 1928.3.6.187, slide, 299.D2.
Paratypes: ZMA 01063ao, wet, Siboga Expeditie, St. 60, Indonesia, Lesser Sunda Islands, Timor, Samau Island, Haingsisi, 23m, 27.iv.1899; ZMA 01063ap, Siboga Expeditie, St. 77, Indonesia, Borneo Bank, Kalimantan, 59m, 10.vi.1899; ZMA 01063ar, wet, Siboga Expeditie, St. 274, Indonesia, Irian Jaya, 57m, 26.xii.1899; ZMA 01063as, wet, Siboga Expeditie, St. 305, Indonesia, Lesser Sunda Islands, Solor Strait, Mid channel off Kampong Menanga, 113m, 08.ii.1900; ZMA 01063at; ZMA 01667, wet, Siboga Expeditie, St. 310, Indonesia, Lesser Sunda Islands, Sumbawa, 73m, 12.ii.1900; NHMUK 1928.3.6.186, dry, Siboga Expeditie, Indonesia; NHMUK 1928.9.13.105, dry, Siboga Expeditie, Singapore; NMNH 9388, dry, Siboga Expeditie, St. 310, 245B, Indonesia, Lesser Sunda Islands, Sumbawa, 73m, 12.ii.1900.

19. *cyclostoma* Busk, 1852
Type locality: Australia (Bass Straits).
Holotype: NHMUK 1854.11.15.77, slide (remounted by A.B. Hastings, 25.10.1927), Bass Straits, 82.3m (45fms).

20. *delilii* (Audouin, 1826)
Type locality: Egypt (Red Sea).
Type material: Presumably lost.

21. *diadema* Busk, 1852
Type locality: Australia (Queensland).
Holotype: NHMUK 1854.11.15.80, slide, Moreton Bay, Queensland.

22. *diegensis* Robertson, 1905
Type locality: California.
Type material: Presumably lost.

23. *drachi* Marcus, 1955
Type locality: Brazil (Espírito Santo).
Type material: Presumably lost.

24. *dongolensis* Waters, 1909
Type locality: Indian waters.
Syntypes: NHMUK 1928.9.13.98, dry, Thornely coll., Mannar, Ceylon (Sri Lanka), Rep. Pearl, Oyster Fisheries, XXVI, 1905, p. 109. Miss. L.R. Thornely, Reg. Apr. 25, 1906; NHMUK 1899.7.1.804–6, dry, G. Busk coll., Trincomalee, Sri Lanka, G. Johnston.

25. *elegantissima* David & Pouyet, 1986
Type locality: India.
Holotype: MNHN 13098, coated, Safari I, Station 19 (SIP12), 4283m [pl. 7, fig. 3, 4, 5].
Paratypes: MNHN 13131 (specimen lost), Safari I, St. 08 (SIP07), 4282m; MNHN 13132, Safari I, St. 03 (CP04), 4291m; MNHN 13133, wet, Safari I, St. 29 (CP19), 5040–5060m.
Remarks: This species is here assigned as *Notoplites elegantissima* David & Pouyet, 1986 **comb. nov.**, due presence of basal avicularia and branching pattern like those of *Notoplites* Harmer, 1923.

26. *elongata* (Smitt, 1868)
Type locality: Norway (Spitsbergen).
Type material: Not located, but supposedly deposited at the Naturhistoriska Riksmuseet (Stockholm).

27. *elongata congesta* Norman, 1903
Scrupocellaria elongata congesta: Ryland, 1963: 12, fig. 2.
Type locality: Norway (Finnmark).
Syntype: NHMUK 1911.10.1.385, dry, Arctic.

28. *ferox* Busk, 1852
Type locality: Louisiade Archipelago.
Holotype: NHMUK 1854.11.15.76, slide, Rattlesnake Expedition, Louisiade Archipelago.
Paratypes: NHMUK 1899.7.1.778, Rattlesnake Expedition, Australia; NHMUK 1899.7.1.179, 1899.7.1.6540, 1899.7.1.654, Rattlesnake Expedition, Louisiade Archipelago.

29. *frondis* Kirkpatrick, 1890
Type locality: Brazil (Pernambuco).
Holotype: NHMUK 1888.4.16.20, dry, Pernambuco, Brazil.

30. *gaspari* Thornely, 1907
Type locality: Gaspar Straits.
Syntypes: NHMUK 1936.12.30.126, dry; NHMUK 1936.12.30.136, slide; NHMUK 1936.12.30.146, dry; NHMUK 1907.8.24.1pt, slide, Gaspar Straits.

31. *gilbertensis* Maplestone, 1909
Type locality: Gilbert Island.
Holotype: MV 45061, slide, Gilbert Island.

32. *grimaldii* Jullien & Calvet, 1903
Type locality: Biscayne Bay.
Holotype: MNHN 6064, wet, Calvet coll. N.289, Campagnes Scientifiques du Principe de Monaco, *Hirondelle*, St. 42, Golf de Gascogne, 132m, 1886.
Remarks: This species is a junior synonym of *Scrupocellaria inermis* Norman, 1867.

33. *harmeri* Osburn, 1947
Type locality: Aruba Island.
Holotype: SBMNH 95952, slide, Allan Hancock Expedition, R/V *Velero III*, St. A18-39, Aruba Island, Nicholaas Bay, 12°21'28"N, 70°4'45"W, 10.iv.1939.
Paratype: SBMNH 95953, slide, same data as holotype.

34. *hildae* Fransen, 1986
Type locality: Curaçao.

Holotype: RMNH 02980, slide, St. Cur82.044, Netherlands Antilles, Curaçao, St Marta Bay entrance, 0.3–2m, 16.viii.1982.
Paratypes: RMNH 02980* (see remarks), wet, same data as holotype; RMNH 03039, wet and slides, St. Cur82.002, Netherlands Antilles, Curaçao, Piscadera Outer Bay, under Hilton pier, 3–6 m, 4.viii, 5.ix, and 11.ix.1982; RMNH 03065, wet, St. Cur82.027, Netherlands Antilles, Curçao, Spaanse water, entrance, near Punta Cabajero, 1.5–3m, 9.viii.1982; RMNH 03066, wet, St. Cur82.077, Netherlands Antilles, Curaçao, Spaanse water, entrance, east shore of Spaanse Lagoen, 0–1m, 17.ix.1982; RMNH 03067, wet, St. Cur82.033, Netherlands Antilles, Curaçao, Fuikbaai, eastern part, 1.5–3m, 9.viii.1982. RMNH 03068, wet, St. Cur82.024, Netherlands Antilles, Curaçao, St. Michiel Outer Bay, 2m, 7.viii.1982; RMNH 03069, slide, St. PWH.1039, Netherlands Antilles, Curaçao, Fuikbaai, W part, SE of Newport Bath, 0–1.5m, 20.xi.1948; RMNH 03070, slide, St PWH.1068a, Netherlands Antilles, Bonaire, Lac, entrance, Boca behind reef, 1–2m, x.1930.
Remarks: Few colonies stored in alcohol under number 02980 were also labeled as holotype. However, the holotype designed in original description is the figured specimens stored as balsam slide and the additional specimens in alcohol are paratypes.

35. *hirsuta* Jullien & Calvet, 1903
Type locality: Azores.
Syntypes: MOM 420323, dry (three colonies), Campagnes Scientifiques du Principe de Monaco, *Hirondelle*, Sta. 226, Fosse de Fayal, entre Pico of Fayal (Azores), 130m, 1888.

36. *inarmata* O'Donoghue & O'Donoghue, 1926
Type locality: British Columbia (Tricomali Channel).
Holotype: NHMUK 1964.4.2.10, dry, Pacific coast of N. America.

37. *incurvata* Waters, 1897
Type locality: Mediterranean (Naples).
Syntypes: Not located, but supposedly deposited at the MM.

38. *inermis* Norman, 1867
Type locality: United Kingdon (Scotland).
Syntypes: NHMUK 1911.10.1.367, dry, United Kingdom; NHMUK 1912.12.21.834, slide, United Kingdom; 1912.12.21.8334, wet, United Kingdom.

39. *intermedia* Norman, 1893
Type locality: Norway (Trodjhem Fjord).
Syntypes: NHMUK 1910.10.1.369, slide; NHMUK 1912.12.21.835, wet, Trodjhem Fjord, Norway.

40. *jolloisi* Audouin, 1826
Type locality: Egypt.
Type material: Presumably lost.

41. *jullieni* Hayward, 1978.
Type locality: Spain.
Holotype: MNHN 7916, wet, *Thalassa,* St. 39, Z438, 26.x.1973, 48°33.7'N, 10°25'W, 1400m.

42. *limatula* Hayward, 1988
Type locality: Mauritius.
Holotype: NHMUK 1987.1.18.41, wet, Tamarin, Mauritius, close to reef crest.

43. *longispinosa* Harmer, 1926
Type locality: Indonesia.
Holotype: ZMA 01063au, wet, Siboga Expeditie, St. 144, specimen 108.Ai, Indonesia, Maluku, anchorage N of Salomakiëe, 45m, 07.viii.1899. Schizoholotypes: ZMA 01558, slide, 108.Ai2; RMNH 00054, wet; NHMUK 1928.3.6.189–90, two slides, 108.Ai; NMNH 9389, dry, 108.Ai.
Paratypes: NHMUK 1928.3.6.191, NHMUK 1928.9.13.106.

44. *macandrei* Busk, 1852.
Type locality: Spain (Mediterranean).
Holotype: NHMUK 1854.11.14.78, slide, British Museum Catalogue Collection, Spain.
Remarks: Badly preserved specimens; the morphological characteristics of the type specimen is not recognized.

45. *macropora* Osburn, 1950
Type locality: Mexico (Pacific).
Holotype: SBMNH 96150, slide, *Velero III*, St. 1263-41, 1.5 miles of N end of Isla Cedros, Baja California, 28°22'18"N, 115°10'60"W, 28.ii.1941.
Paratypes: SBMNH 96151, slide, *Velero III*, St. 1162-40, California, 11 miles S. of Seal Beach, 33°33'5"N, 118°9'45"W, 23.vii.1940; SBMNH 96152, slide; NMNH (uncatalogued; Osburn-21), dry, same data as holotype.

46. *macrochyncha* Gautier, 1962
Type locality: Mediterranean.
Syntype: NHMUK 1965.9.2.4, dry, Mediterranean, St. 258.

47. *maderensis* Busk, 1860
Type locality: Madeira.
Holotype: NHMUK 1899.7.1.780, dry, Madeira.
Paratype: NHMUK 1899.7.1.796, dry, Madeira.
Remarks: The paratype specimens of *S. maderensis* (NHMUK 1899.7.1.796) belong to a distinct species.

48. *mansueta* Waters, 1909
Type locality: Suez.
Syntypes: Not located, but supposedly deposited at the MM.

49. *mexicana* Osburn, 1950
Type locality: Mexico (Pacific).
Holotype: SBMNH 96153, slide, AHF 34, off Acapulco, Mexico, 16°50'18"N, 99°52'38"W, Capt. Fred E. Lewis coll., 27.4m (15fms).
Paratypes: SBMNH 96154–5, slides, Allan Hancock Expedition, R/V *Velero III*, St. 1281-41, 3 miles E. of South Point, Santa Rosa Island, California, 33°53'30"N, 120°2'55"W, 42m (23fms), 10.iv.1941; SBMNH 96156, slide, Allan Hancock Expedition, R/V *Velero IV*, St. 1856-49, dredge, California, 34°13'32"N, 120°38'5"W, 587m (321fms), 14.vi.1949; SBMNH 96157, slide; NMNH (uncatalogued; Osburn-23), slide, AHF 270, Angel de la Guardia Island, Baja California, Mexico, 29°30'35"N, 113°27'20"W, 25.6m (14fms), 6.iii.1936.

50. *micheli* Marcus, 1955
Type locality: Brazil (Espírito Santo).
Type material: Presumably lost.

51. *minuta* Kirkpatrick, 1888
Type locality: Mauritian.
Lectotype: NHMUK 1888.1.25.2A, slide, Mauritius.
Remarks: The paralectotype specimen (NHMUK 1888.1.25.2B) is an undescribed species.

52. *muricata* (Lamouroux, 1816)
Type locality: Japan.
Syntype: NMHN19680, Lamouroux's herbarium, Japan.
Remarks: The examination of the type of *Crisia muricata* revealed that this species belongs to genus *Tricellaria* Fleming, 1828.

53. *nanshaensis* Liu, 1991.
Type locality: China.

Type material: Not located.

54. *obtecta* Haswell, 1881
Type locality: Australia (Queensland).
Syntype: NHMUK 1928.9.13.103, dry, W.A. Haswell, Port Denison, Queensland, Australian Museum, Reg. Oct. 23, 1899.

55. *ornithorhynchus* Thomson, 1858
Type locality: Australia (Bass Strait).
Holotype: NHMUK 1899.7.1.783, dry, G. Busk coll., Australia.

56. *panamensis* Osburn, 1950
Type locality: Panama.
Holotype: SBMNH 96158, slide, Las Perlas Island, Panama, 8°22'N, 79°1'60"W.
Paratypes: SBMNH 96159–60, slides, AHF 470, Charles Island, Galapagos, 0.5 mile north of Black Beach, 1°16'46"S, 90°29'56"W, 16.4m (9fms), 14.12.1934; NMNH (uncatalogued; Osburn-25), slide, AHF 850-38, off Cape San Francisco, Ecuador, 27.3m (15fms).

57. *piscaderaensis* Fransen, 1986
Type locality: Curaçao.
Holotype: RMNH 02979, slide, St. Cur82.043, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, Candelichi, 0–0.5m, 14.viii.1982.
Paratypes: RMNH 02979* (see remarks), wet, same data as holotype; RMNH 03053, wet and slide, St. Cur82.006, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, north of Marie Pampoen, 0–0.5m, 4.viii.1982; RMNH 03055, wet, St. Cur82.034a, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Punta Kibracos, 0.8–2m, 11.viii.1982; RMNH 03056, wet, St. Cur82.035, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Punta Kibracos, 0–0.8m, 11.viii.1982; RMNH 03057, wet, St. Cur82.046, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Candelchi, 0–0.5m, 17.viii.1982; RMNH 03058, wet and slide, St. Cur82.046a, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Candelchi, 0.4–0.8m, 17.viii.1982; RMNH 03059, wet, St. Cur82.047, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Candelchi, 0–1m, 17.viii.1982; RMNH 03060, wet and slide, St. Cur82.048, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, near Candelchi, 0–1m, 17.viii.1982; RMNH 03061, wet, St. Cur82.049, Netherlands Antilles, Curaçao, Piscadera Inner Bay, southern part, western shore, 0–0.08m, 18.viii.1982; RMNH 03062, wet and slide, St. Cur82.036, Netherlands Antilles, Curaçao, Piscadera Inner Bay, central part, near Punta Kibracos, 0–0.5m, 12.viii.1982.
Remarks: Few colonies stored in alcohol under number 02979 were also labeled as holotype. However, the holotype designed in original description is the figured specimens stored as balsam slide and the additional specimens in alcohol are paratypes.

58. *profundis* Osburn, 1950
Type locality: California.
Holotype: NMNH (uncatalogued; Osburn-26), dry, AHF 36, *Albatross*, St. 5681, Lower California, off San Lucas Bay, 22°48'20"N, 109°52'40"N, 898m (491fms), 1911.
Paratype: SBMNH 96161, same data as holotype.

59. *pugnax* Osburn, 1950
Type locality: Galapagos.
Holotype: SBMNH 96162, slide, AHF 541, Post Office Bay, Charles Island, Galapagos, 1°11'15"S, 90°31'10"W, 110m (60fms), 29.i.1934.
Paratype: SBMNH 96163, slide, same data as holotype.

60. *pusilla* (Smitt, 1872)
Type locality: off Tortugas.
Syntype: MCZ 0100, dry, Cast No. 13, Pourtàles, W off Tortugas, 124m (68fms).

61. *regularis* Osburn, 1940
Type locality: Caribbean.
Syntypes: MCZ 38 (Smitt collection), *Cellularia cervicornis*, off W. bank, Cape Fear River, 1868, 12.8 (7fms); MCZ 40 (Smitt collection), wet, *Cellularia cervicornis*, 1868; MCZ 163 (Smitt collection), *Cellularia cervicornis* (no data); NMNH 2347, dry, off mouth of Guanica Harbor, 54.9m (30fms); NMNH (uncatalogued; Osburn-33), slide, Osburn coll., Porto Rico; NMNH (uncatalogued; Osburn 34-35), slides, Osburn coll., Tortugas, 32.9m (18fms).

62. *reptans* (Linnaeus, 1767)
Type locality: Ocean (supposedly United Kingdom).
Syntypes: LSL 1248.31–32, Herbarium (no data, but supposedly United Kingdom).

63. *scabra* (van Beneden, 1848)
Type locality: North Sea.
Type material: Not located.

64. *scabra paenulata* Norman, 1903
Type locality: Norway (Finnmark).
Type material: Not located.

65. *orientalis* Kluge, 1955
Type locality: North Sea.
Type material: Not located.

66. *scrupea* Busk, 1852
Type locality: United Kingdon.
Holotype: NHMUK 1854.11.15.79, slide (mounted by A.B. Hastings in 24.x.1927), South West coast.

67. *scruposa* (Linnaeus, 1758)
Type locality: Ocean (supposedly United Kingdom).
Type material: Presumably lost.

68. *scruposa puelcha* (d'Orbigny, 1841)
Type locality: Argentina.
Syntype: MNHN F.R64248, dry, d'Orbigny Collection n.13612, Patagonia, Argentina.

69. *securifera* Busk, 1884
Type locality: Admiralty Island.
Syntypes: NHMUK 1887.12.9.113, dry; NHMUK 1887.12.9.114, dry (figured specimen), Admiralty Is, N. of New Guinea.

70. *serrata* Waters, 1909
Type locality: Suez.
Syntypes: Not located, but supposedly deposited at the MM.

71. *sinuosa* Canu & Bassler, 1927
Type locality: Hawaii.
Syntype: NMNH 8426, Pacific II.3999, Vicinity Kawai Island, Hawaii.

72. *spatulata* (d'Orbigny, 1851)
Type locality: Egypt.
Type material: Presumably lost.

73. *spatulatoidea* Liu, 1980
Type locality: China.
Type material: Not located.

74. *spinigera* Osburn, 1950.
Type locality: California.
Holotype: SBMNH 96164, AHF 38, Allan Hancock Expedition, R/V *Velero III*, St. 1340-41, II 38.2, San Diego, California, dredged, 32°40’60”N, 119°6’30”W, 69.5m (38fms), 10.vi.1941.
Paratypes: SBMNH 96165, slide, same data as holotype; SBMNH 96166, slide, Allan Hancock Expedition, R/V *Velero III*, St. 1150-40, off Avalon Bay, Santa Catalina Island, Southern California, 33°20’30”N, 118°17’10”W, 179.2–212.1 (98–116fms); SBMNH 96167, slide, Allan Hancock Expedition, R/V *Velero III*, St. 1247-41, off Cedros Island, Mexico, 28°30’46”N, 115°29’45”W, 140.8m (77 fms).

75. *talonis* Osburn, 1950
Type locality: Panama.
Holotype: SBMNH 96168, AHF 39 (ex. Osburn Collection), Perlas Island, Panama, 8°22’0”N, 79°1’60”W.

76. *tridentata* Waters, 1918
Type locality: Cape Verde Islands.
Syntypes: Not located, but supposedly deposited at the MM, Crossland leg., Boa Vista, Cape Verde Islands, 20fms.

77. *ulrichi* Canu & Bassler, 1929
Type locality: Phillipines.
Syntypes: NMNH 7889, dry, *Albatross*, St. 5147, off Sulade Island, Sulu Archipelago, Philippines, 5°41'40''N, 120°47'10''E, 38m (21 fms); NMNH 7890, dry, *Albatross*, St. 5478, off Tacbuc Point, E. Leyte, Philippines, 10°46'24''N, 125°16'30''E, 104m (57 fms); NHMUK 1932.9.16.22, *Albatross*, St. 5478, off Tacbuc Point, E. Leyte, Philippines, 10°46'24''N, 125°16'30''E, 104m (57 fms).

78. *unguiculata* Osburn, 1950
Type locality: Galapagos.
Holotype: SBMNH 96169, slide, Allan Hancock Expedition, R/V *Velero III*, St. 795-38, Sulivan Bay, James Island, Galapagos, 0°16’12”S, 90°34’50”W, 65.8–73.1m (36–40fms), 20.i.1938.
Paratypes: SBMNH 96170, slide, AHF 450, Albermale, Galapagos, 0°55’00”S, 90°30’00”W, 109.7m (60fms), 26.i.1934; SBMNH 96171, slide, AHF 451, Post Office Bay, Charles Island, Galapagos, 1°11’15”S, 90°31’10”W, 182.9m (100fms), 29.i.1934.

79. *unicornis* Liu, 1980
Type locality: China.
Type material: Not located.

80. *uniseriata* Liu, 1984
Type locality: China.
Type material: Not located.

81. *varians* Hincks, 1882
Type locality: Queen Charlotte Island, British Columbia.
Holotype: NHMUK 1886.3.6.12, slide (mounted by A.B. Hastings 25.10.1927), Queen Charlotte Island.

82. *wasinensis* Waters, 1913
Type locality: Wasini Island (Kenya).
Syntypes: Not located, but supposedly deposited at the MM.