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Article

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

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Abstract

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

Key words: bryozoans, lectotype, redescription, taxonomy, *Scrupocellaria*, new species

Introduction

Scrupocellaria reptans (Bryozoa) was introduced, without illustration, by Carl Linnaeus (1758). The sole geographic/habitat information accompanying the species description (basonym *Sertularia reptans*) was “in Oceano” but it has been recorded from numerous localities around the British coast (e.g. Ellis & Solander 1786; Johnston 1847; Busk 1852; Hincks 1880; Hayward 1971; Hayward & Ryland 1998), in the North Sea (e.g. Smitt 1867; Marcus 1940; de Blauwe 2009), off Madeira (Norman 1909) and in the Mediterranean (e.g. Waters 1879; Prenant & Bobin 1966; Zabala 1986; Zabala & Maluquer 1988). The species 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 *S. reptans*, the type specimen described by Linnaeus (1758) has apparently never been described or figured.

Some species of *Scrupocellaria* have been treated as widespread in tropical to subtropical waters (Tilbrook 2006; Tilbrook & Vieira 2012). Recent studies, however, on widespread bryozoan species using SEM techniques, have helped to clarify their taxonomic status as well as redefine the characters for species differentiation (Berning & Kuklinski 2008). In addition, studies on geographic and morphological variation in cheilostome bryozoans have revealed a higher diversity than previously recorded by earlier authors (Berning *et al.* 2008; Vieira *et al.* 2010, 2012). In the present study we give a complete redescription of Linnaeus’s material of *S. reptans* to clarify and stabilize its identity; we also describe a new and closely related species, *Scrupocellaria ellisi* n. sp.

Material and Methods

The syntype specimens described by Linnaeus and letters relating to his collections are held at the Linnean Society of London (LSL). The specimens examined here were photographed under a Zeiss Discovery V20 stereomicroscope with AxioCam HRc at the Natural History Museum, London (NHMUK). Additional comparative material has been 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®. Historic distributions of taxa listed in synonymies are cited as the authors stated them, i.e. 'Oceano', 'European Sea', etc.

Linnaeus's herbarium specimens

The type material of *Scrupocellaria reptans* comprises two herbarium sheets in the Linnean Collection (LSL n.1248.31 and LSL n.1248.32). These sheets were labelled '*S. reptans*' [= *Sertularia reptans*] by Linnaeus, comprising 26 syntype specimens. We have introduced a letter code for each colony on sheet no.1248.31, selecting specimen "I" as the lectotype and the other specimens as paralectotypes (Figure 1); the three specimens found on herbarium sheet no. 1248.32 are badly preserved.

The colony selected as lectotype (LSL n.1248.31.I, Figure 1) is large and well preserved, with many zooids; two fragments from the same colony are also present, with the frontal and basal surfaces visible. The lectotype has zooids with ovicells and these have 8–11 medium-sized rounded pores on the surface and pinkish embryos preserved inside the ooecial cavity; the radicles (rootlets) are have retroussé hooks. Details on the condition and major attributes of the paralectotype specimens from sheet no. 1248.31 are given in Table 1.

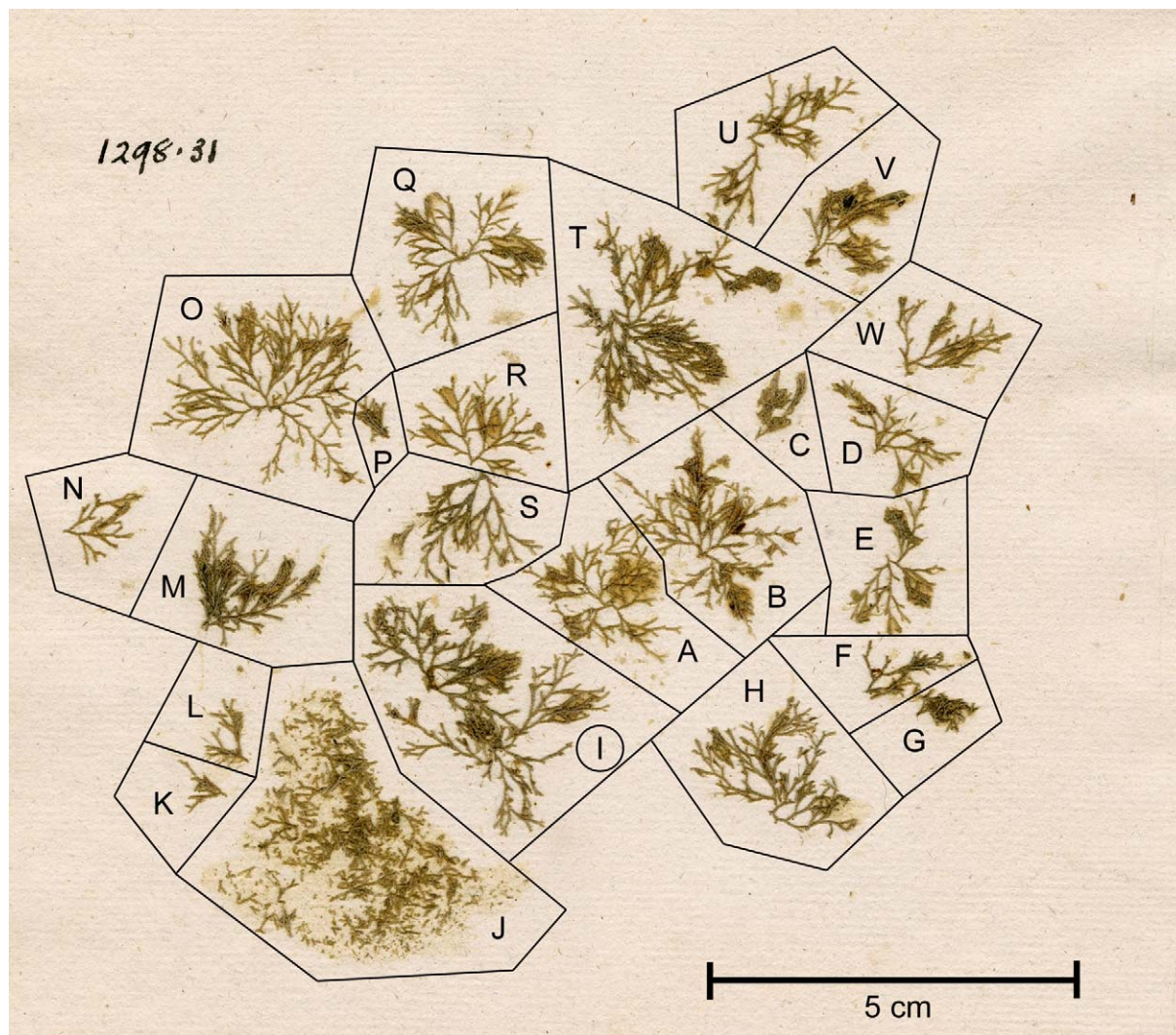


FIGURE 1. Linnaeus herbarium sheet no. 1248.31. The colonies were codified by different letters (A–W), with specimen "I" (circled) selected as lectotype.

TABLE 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 |

All of Linnaeus's type specimens are characterized by the presence of joints that pass across the distal gymnocyst (below, never across, the opesia), branched scuta, large frontal avicularia, subtrapezoidal basal vibracula, and rhizoids with retroussé hooks. This last characteristic was also noted by Ellis (1755), who wrote "... full of Hooks, the better to secure the Coraline..." and plainly illustrated them (Ellis 1755, pl. 20B). The presence of vibracular chambers on the basal surface of the colony varies in different specimens, but one or more are often present per internode.

Provenance of Linnaeus's specimens

Linnaeus's (1758, p. 815) 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 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 and cnidarian 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). It provides a very brief description quoting an authority and is without drawings.

Ellis's '*Corallina cellifera minor reptans ramofa, tubulis laevibus: interdum hamofis sparfim 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) noted that *S. reptans* was a common species on the English coast on shells and algae, readily distinguished from other species by the presence of hooks along the rootlets 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 who was considered an authority on fungi, mosses and other non-flowering plants (Jackson 2010). Though he published only one medical paper, his observations and specimens were shared with 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 Ray's *Synopses* (Ray 1724).

There are two specimens in the Sloane collection at NHMUK that pertain to the description given in Ray's '*Historia plantarum vol. 3, Supplementum 15*'. Both specimens are *Scrupocellaria* species but neither has 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 1756–57 after the publication of Ellis's book. In a letter dated 21 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 that 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.

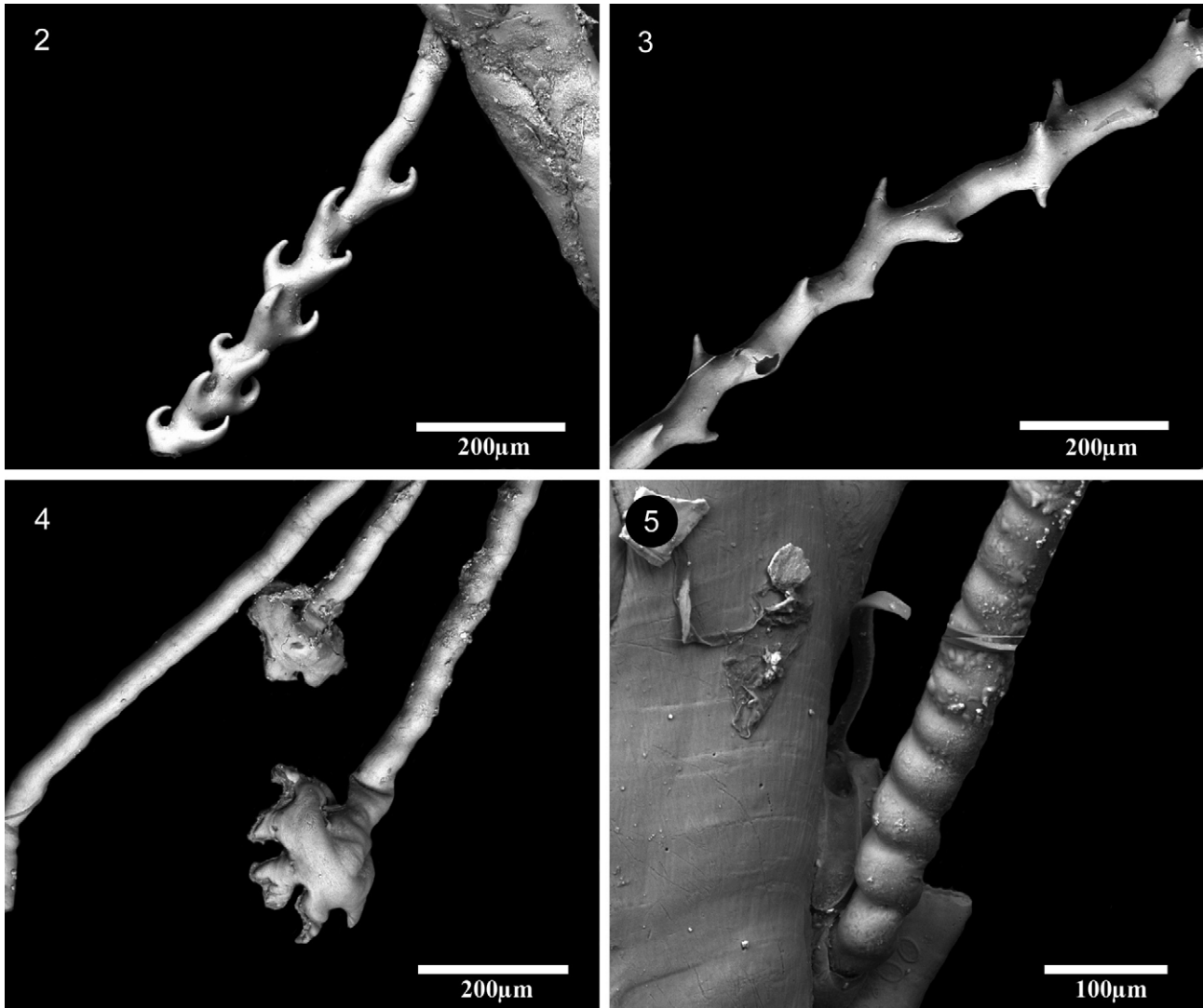
Only the epithet *S. reptans* appears on the two Linnean herbarium sheets. John Ellis and Carl Linnaeus are known to have exchanged some specimens (Savage 1945), as well as letters, drawings and descriptions; however, there appears to be no record of *S. reptans* specimens being sent to Uppsala. There 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 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). 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 in the Northeast Atlantic, North Sea and Mediterranean (Zabala & Maluquer 1988; Hayward & Ryland 1998), despite the morphological differences (e.g. shape of rhizoids and frontal scuta) among 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 11) and other specimens from European waters (Figs 2, 16, 17). The hooked rhizoids were also reported in specimens from Cornwall, U.K. (Couch 1844, pl. 23, fig. 3). The second type of rhizoid was characterized by Hincks (1880) as "...simple, and giving off at the extremity a number of anastomosing fibrils forming a netted disk" and figured by him in Plate 7, fig. 5. These rhizoids, of simple tubes, had been described earlier 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 rhizoid are an ecological adaptation in this species. Colonies with smooth rhizoids that form circular reticulate disks distally are attached to firm surfaces like rocks or algae, while hooked rhizoids are found deeper in soft substrata like sponges. Hooks were observed by Peach (1878), who also described smooth rhizoids in colonies found on *Flustra foliacea*.



FIGURES 2–5. Different shapes of rhizoids found in *Scrupocellaria*. **2**, closely spaced hooks in rhizoids of *Scrupocellaria reptans* (Linnaeus, 1758) from Great Britain (NHMUK 1963.3.6.35); **3**, well-spaced hooks in rhizoids of *Scrupocellaria* sp. from Red Sea (NHMUK 1928.3.6.177); **4**, smooth-surfaced rhizoids of *Scrupocellaria ellisi* n. sp. from Scotland (NHMUK 1963.3.6.7a part); **5**, annulated surface of rhizoid in *Scrupocellaria cyclostoma* Busk, 1852 from Australia (NHMUK 1899.6.1.240).

Peach (1878) mentioned Busk's *Scrupocellaria macandrei* from Spain and *S. ferox* from Bass Strait, which were characterized by rhizoids with hooks. Waters (1909, 1913) also used 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*, *S. diadema*, *S. maderensis*, *S. delilii*). We analysed more than 50 specimens deposited at NHMUK that had been identified as *S. reptans*, but 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 (Figs 7, 11), in a specimen found in herbarium material identified by Alfred Norman (NHMUK 1915.4.2.13), in 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 in two colonies from the Thanet coast, southern

England (NHMUK 1884.12.12.9). Careful examination of the Thanet colonies revealed that two different morphotypes occur together, but they are distinguished by the shape of their rhizoids and frontal scuta. The presence of these two phenotypes on the same shell suggested that they may not be conspecific. At the same time, 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.

Examination of *Scrupocellaria* at NHMUK showed that the occurrence and shape of hooked rhizoids are uniform in colonies of the same species, indicating a species-specific character rather than an environmental adaptation. In addition, we observed at least three kinds of rhizoidal surfaces in the Candidae —hooked (Figs 2–3), smooth (Fig. 4) and ringed (Fig. 5), morphologically distinct in different species.

By light microscopy, the morphology of zooids of the two phenotypes previously identified as *S. reptans* (with and without hooks) appears similar, but detailed study using SEM shows differences between them (Figs 2, 12–17, 24, 26—morphotype with hooked rhizoids, =*Scrupocellaria reptans* sensu stricto; and Figs 4, 18–23, 25, 27—morphotype with smooth rhizoids, herein recognized as a distinct species). In later ontogeny both species are distinguished by scutum shape (Figs 14, 21). Despite having the same proportions of opesia and scutum length, *S. reptans* sensu stricto has a slender, less-branched scutum compared to specimens with smooth rhizoids. In Linnaeus's specimens, the scutum is branched twice (sometimes shortly branched at the distal tip), with a large gap between each slender branch (Fig. 9). In early ontogeny, however, the frontal scuta are quite similar in both species (Figs 26–27) but become highly branched in colonies without hooks (Figs 20–21). Variation in the shape of frontal avicularia makes it difficult to compare young colonies of both morphotypes; both have frontal avicularia with the same position and orientation, but in early ontogeny the rostrum of the avicularium is slender and taller in *S. reptans* (Figs 24–27). In Linnaeus's type material, the basal vibracular chamber is often absent, while in the morphotype with smooth rhizoids it is usually present.

Systematic 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)

(Figs 1, 2, 6–17, 24, 26)

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

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

Sertularia reptans Linnaeus, 1758: 815; 1767: 1315. [Oceano]

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

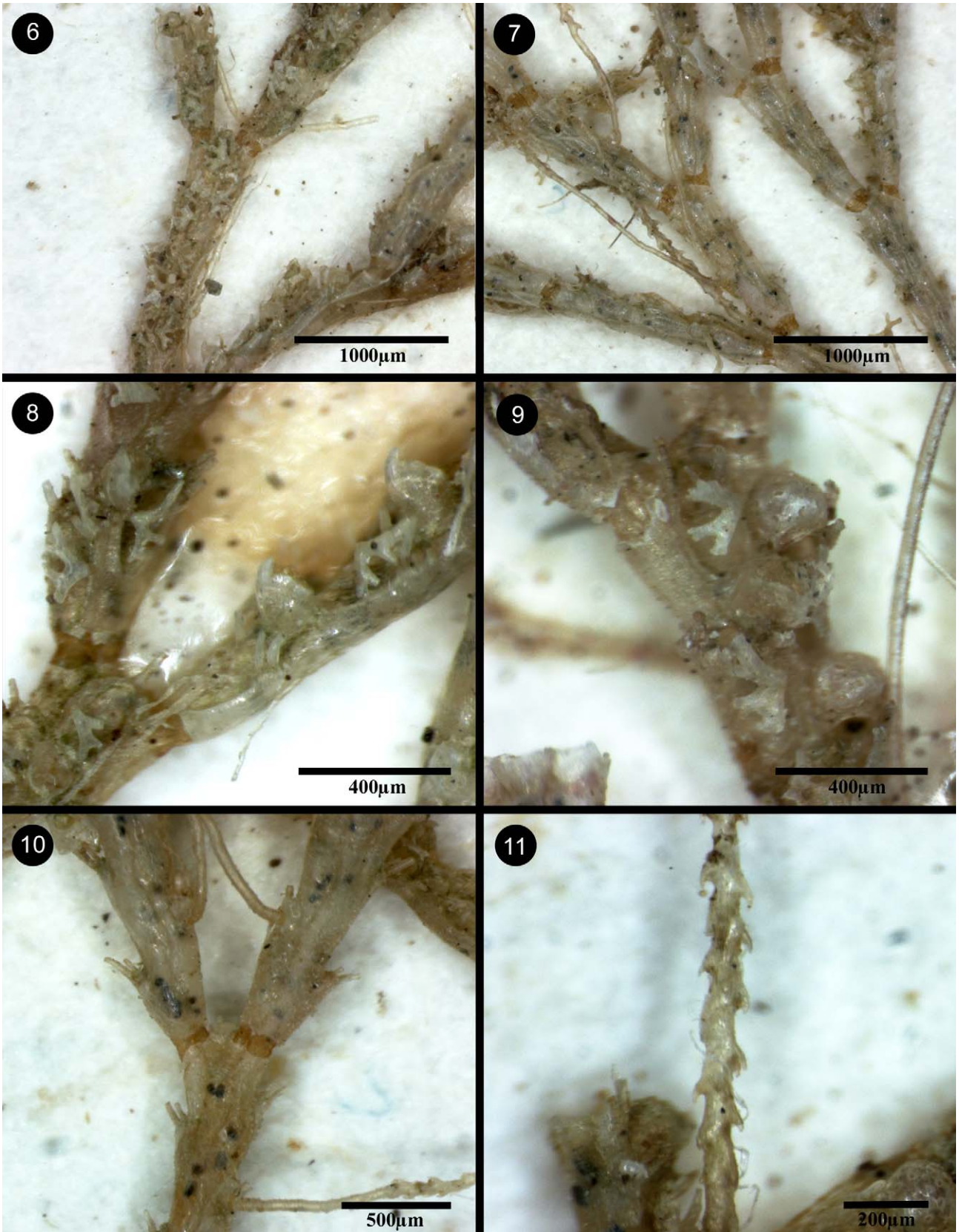
Cellularia reptans: Couch 1844: 127, pl. 23, fig. 3. [British coast]

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

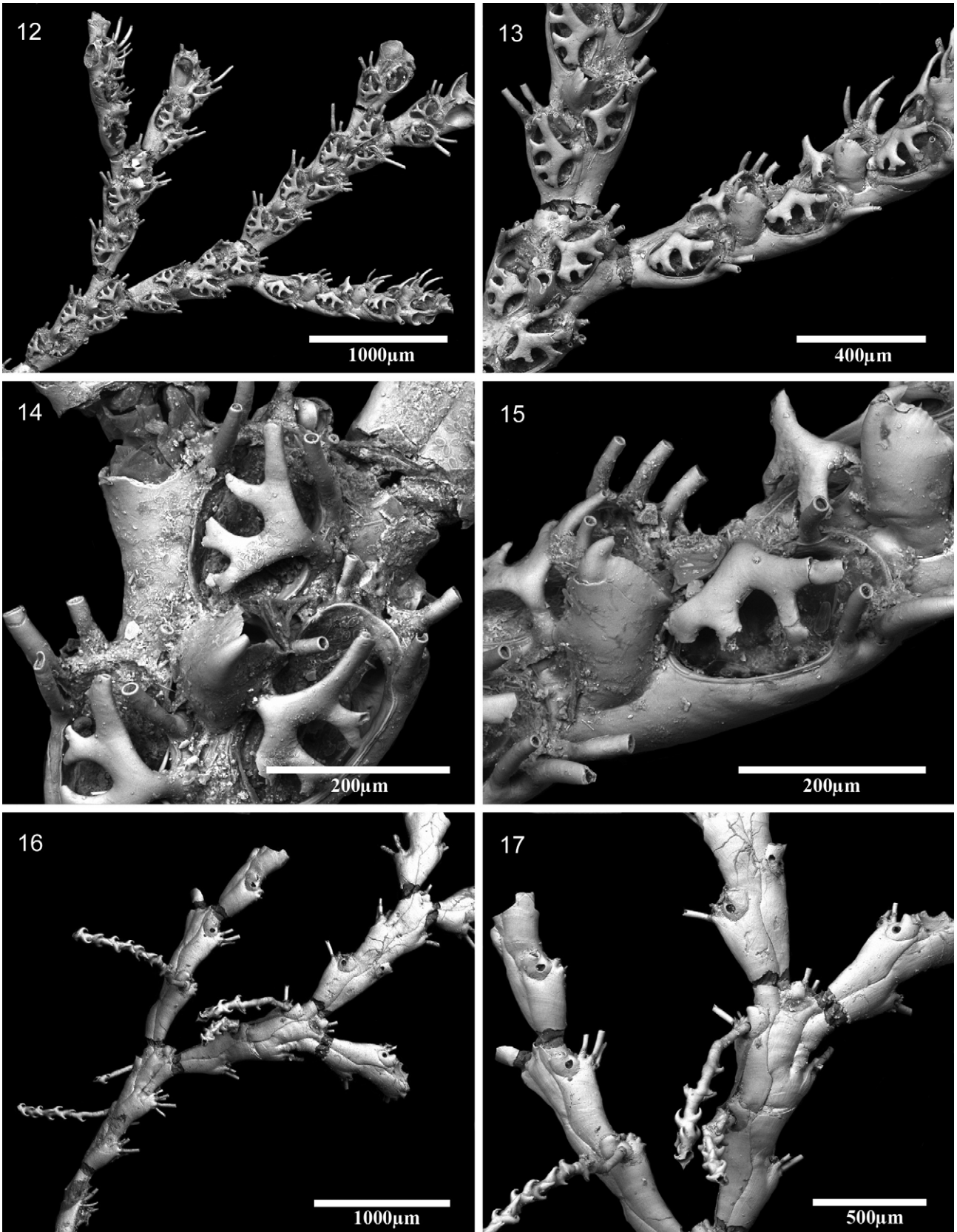
Scrupocellaria reptans: Prenant & Bobin 1966 (part): fig. 134.vi. [not Mediterranean specimens]

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

Material examined. *Lectotype* (chosen here): LSL n. 1248.31.I, no locality, but supposedly British Isles. *Paralectotype* (chosen here): LSL n. 1248.31.A–H, J–W; LSL n. 1248.32, no locality, but supposedly British Isles. 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, British Isles; NHMUK 1995.9.25.26, *Scrupocellaria reptans* (Linn.), J.S. Ryland *leg. et det.*, Porth Hellick, 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.



FIGURES 6–11. *Scrupocellaria reptans* (Linnaeus, 1758), type specimens on Linnaeus herbarium sheet n. 1248.31. **6–8**, lectotype specimen, LSL no. 1248.31.I: **6**, frontal view of branches; **7**, basal view of branches, with hooked rhizoids; **8**, close-up of an axial zooid at a bifurcation, a large frontal avicularium on the right-hand branch. **9–11**, paralectotypes: **9**, close-up of one axial zooid and two ovicelled zooids in paralectotype n. 1248.32.T; **10**, close-up of basal surface of paralectotype no. 1248.32.D; **11**, close-up of rhizoid with regularly spaced hooks in paralectotype no. 1248.32.H.



FIGURES 12–17. SEM of *Scrupocellaria reptans* (Linnaeus, 1758), NHMUK 1963.3.6.35. **12–15**, frontal surface: **12**, part of colony; **13**, close-up of branch bifurcation, with several frontal avicularia; **14**, close-up of axial zooid with frontal avicularium; **15**, frontal avicularium in lateral view. **16–17**, basal surface: **16**, part of colony; **17**, branches with hooked rhizoids.

Comparative material. *Scrupocellaria ellisi* [Figs 4, 18–23, 25, 27]: (see next entry). *Scrupocellaria* sp. 1 [Fig. 28]: NHMUK 2010.12.6.1, *Scrupocellaria reptans* (part), C.H. O’Donoghue collection, Arisaig, Scotland. *Scrupocellaria* sp. 2 [Fig. 29]: NHMUK 1963.8.2.16, *Scrupocellaria reptans*, C.H. O’Donoghue collection, Alexandria, 1937, Stn 7, 66, 17–20 fms. *Scrupocellaria* sp. 3 [Fig. 30]: NHMUK 1911.10.1.355, *Scrupocellaria reptans*, A.M. Norman collection, Madeira. *Scrupocellaria* sp. 4 [Fig. 31]: NHMUK 2010.12.6.21–22, *Scrupocellaria reptans* (part), C.H. O’Donoghue collection, Gairloch, Scotland.

Redescription. Colony erect, branched, internodes comprising 4–10 zooids. Lateral edge of internode almost straight to slightly curved; chitinous joint passing across gymnocyst and below opesia in both outer zooids (C and D) of bifurcation, and across proximal gymnocyst of inner zooids (F and G). Autozoid subelongate, narrowed proximally, 0.350–0.460 mm long, 0.165–0.205 mm wide, with smooth proximal gymnocyst. Opesia oval, occupying distal half (almost) of zooid, cryptocyst very narrow, inconspicuous. Scutum inserted at midline of inner edge of opesia, branched, occupying most of opesia; slender, flattened, branched 2–3 times, with 6–9 distal stout projections; angled at 100–120°, with first branches about 0.035–0.045 mm wide, and secondary branches about 0.025–0.035 mm. Zooid spines as follows: 1 long distal spine, 3 outer spines, 1–2 inner spines; most proximal outer and inner spines directed frontally; axial zooid with 5 distal spines. One distolateral avicularium sometimes present on each zooid, distolaterally 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 vibraculum chamber often present proximally on basal surface of each zooid, 0.126–0.155 mm long, 0.085–0.115 mm wide, inconspicuous in frontal view; setal groove directed transversely, straight, with smooth seta longer than one zooid length. Single axial vibraculum. A rhizoidal foramen on proximal outer corner of vibraculum chamber, absent in axial vibracula. Rhizoids with several close-spaced reverse hooks for most of their length. Ovicell hyperstomial, hemispherical, with 8–13 medium-sized rounded pores; 2 outer and 1–2 inner distal spines in ovicelled zooids.

Distribution. Western Britain.

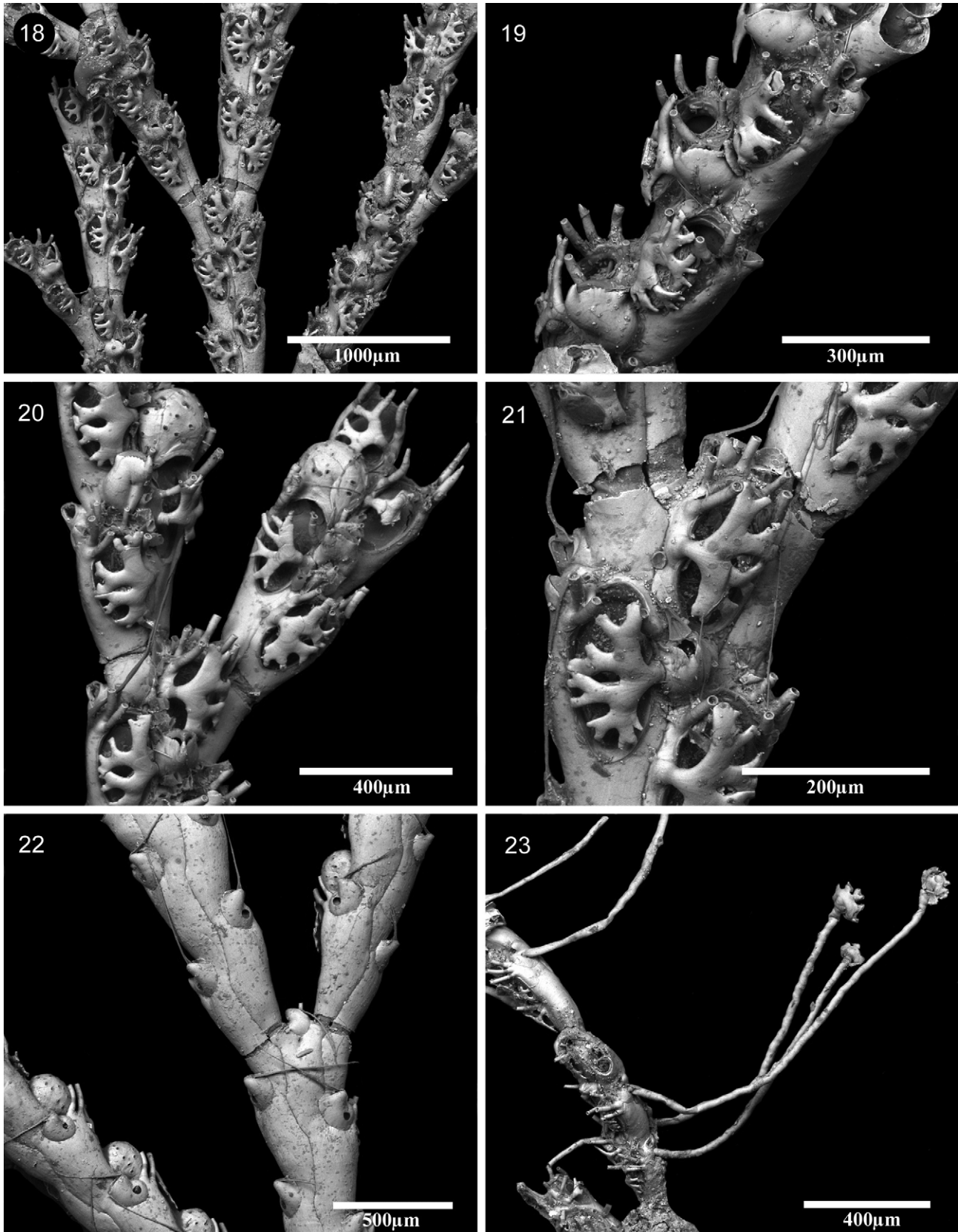
Scrupocellaria ellisi n. sp.

(Figs 4, 18–23, 25, 27)

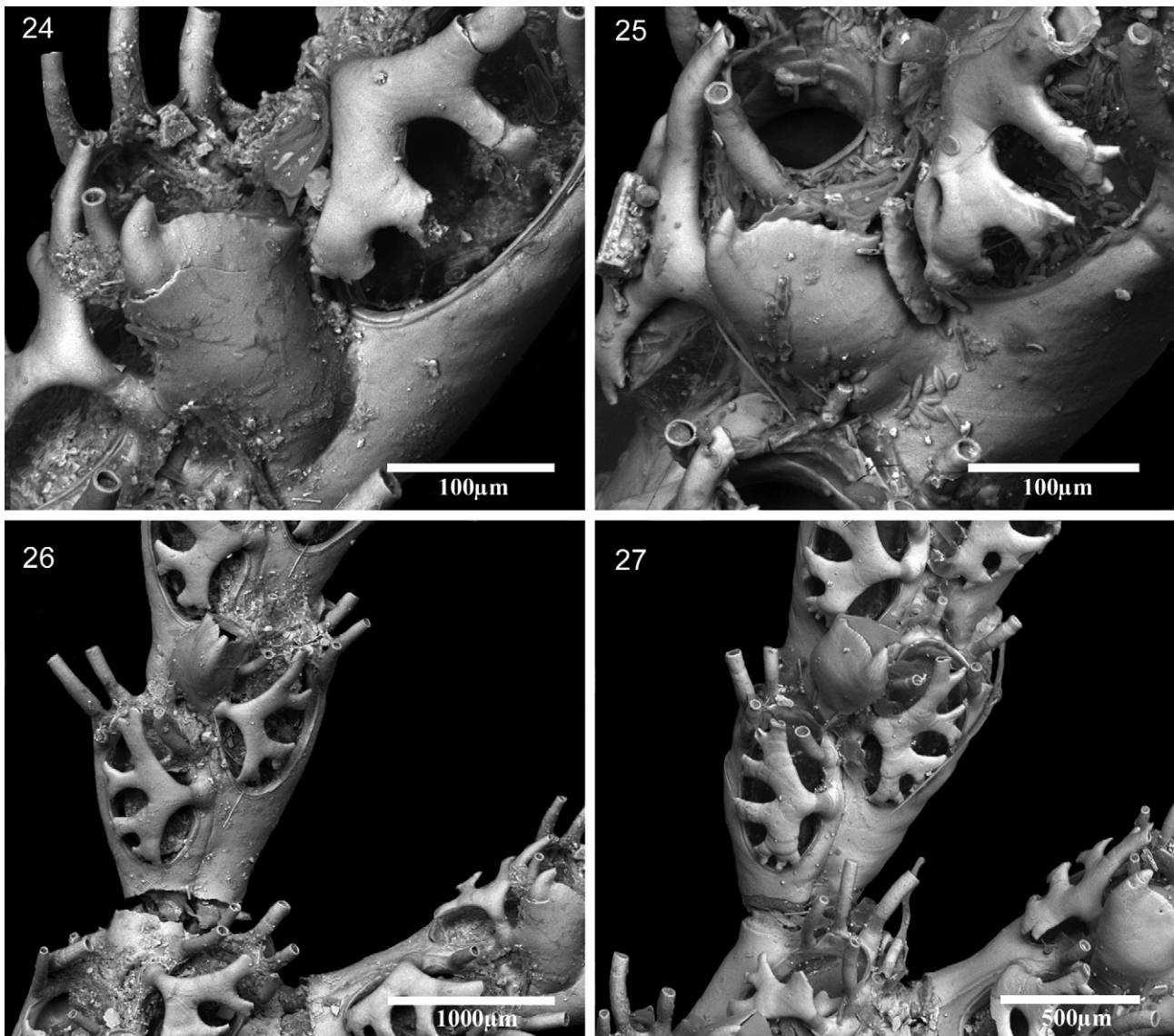
- Cellularia reptans*: Pallas 1766: 73. [European sea]
Not *Sertularia reptans* Linnaeus, 1758: 815; 1767: 1315. [Oceano]
? *Sertularia reptans*: Fabricius 1780: 445. [Greenland]
? *Sertularia reptans*: Olivi 1792: 290. [Adriatic]
? *Sertularia reptans*: Turton 1807: 217. [British coast]
? *Canda reptans*: Gosse 1856: 11, fig. 12. [British coast]
Crisia reptans: Lamouroux 1816: 140. [European sea]
Cellularia reptans: Lamarck 1816: 141. [European sea]
Cellularia reptans: Bertoloni 1819: 272. [Italy]
Crisia reptans: Lamouroux 1824a: 60. [European sea]
Crisia reptans: Lamouroux 1824b: 225. [European sea]
? *Crisia reptans*: Risso 1826: 3185. [European sea]
? *Cellularia reptans*: Fleming 1828: 540. [British coast]
? *Cellularia reptans*: Bosc 1830: 132. [European sea]
Cellularia reptans: Lamarck 1836: 191. [European sea]
Cellularia reptans: Johnston 1838a: 291, pl. 38, fig. 3–4. [British coast]
Cellularia reptans: Johnston 1838b: 262. [British coast]
? *Cellularia reptans*: Hassall 1840: 72. [Ireland]
? *Cellularia reptans*: Reid 1845: 385, pl. 12, figs 1–5. [Scotland]
Cellularia reptans: Dalyell 1847: 235, pl. 45, figs 1–4. [Scotland]
Cellularia reptans: Johnston 1847: 336, pl. 38, figs 3–4. [British coast]
Scrupocellaria reptans: Gray 1848: 112. [British coast]
? *Cellularia reptans*: d’Orbigny 1851: 50. [France, Fossil]
Canda reptans: Busk 1852: 26, pl. 21, figs 3–4. [British coast]
? *Cellularia reptans*: Landsborough 1852: 339. [British coast]
? *Cellularia reptans*: Gosse 1853: 435. [British coast]

Cellularia reptans: Alder 1856: 148. [British coast]
Cellularia reptans: Smitt 1867: 318, pl. 17, fig. 37-4. [Scandinavia]
Canda reptans: Heller 1867: 87. [Adriatic]
Scrupocellaria reptans: Hincks 1880: 52 (part), pl. 7, figs 1–6, 7. [British coast]
Scrupocellaria reptans: Pennington 1885: 223, pl. 17, fig. 5. [British coast]
? *Scrupocellaria reptans*: Carus 1889: 5. [Mediterranean]
Scrupocellaria reptans: Levinsen 1894: 44, pl. 1, figs 26–31. [Denmark]
Scrupocellaria reptans: Nordgaard 1900: 5. [Norway]
Scrupocellaria reptans: Nichols 1907: 82. [Ireland]
? *Scrupocellaria reptans*: Calvet 1907: 374. [European sea]
? *Scrupocellaria reptans*: Canu & Bassler 1928: 19. [Tunisia]
? *Scrupocellaria reptans*: Marcus 1940: 173, fig. 91. [Denmark]
? *Scrupocellaria reptans*: Eggleston 1963: 50. [Isle of Man]
Scrupocellaria reptans: Ryland 1965: 57, fig. 28a-c. [European sea]
Scrupocellaria reptans: Ryland & Hayward 1977: 135, fig. 64. [British coast]
Scrupocellaria reptans: Hayward 1987: 92, fig. XI.27. [British coast]
Scrupocellaria reptans: Hayward & Ryland 1990: 817, fig. 14.8. [British coast]
Scrupocellaria reptans: Hayward & Ryland 1998: 270 (part), fig. 90A-B. [British coast]
Scrupocellaria reptans: de Blauwe 2009: 240, figs 245–246. [Belgium and Netherlands]

Examined material. *Holotype*: NHMUK 1911.10.1.353, *Scrupocellaria reptans*, A.M. Norman collection, Shetland, British Isles. 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, Birterbuy 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, British Isles; NHMUK 1867.5.7.24, *Scrupocellaria reptans*, G.D. Westendorp herbarium, Belgium; NHMUK 1868.3.13.2, *Canda reptans*, Prof. Sven Loven, Skar, Bohuslän, 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, 8–24 fms; 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, British Isles; 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, Channel Islands; 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, Scotland; NHMUK 2010.12.6.24, *Scrupocellaria reptans* (part), C.H. O'Donoghue collection, Arisaig, Scotland, British Isles; NHMUK 1963.3.6.37, *Scrupocellaria reptans*, C.H. O'Donoghue collection, Lochranza, Isle of Arran, British Isles, 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, British Isles; NHMUK 2003.6.3.1, *Scrupocellaria reptans*, K.J. Tilbrook *leg. et det.*, Strandline, Portmeirion, Wales, 10 March 1996; NHMUK 2005.1.14.8, *Scrupocellaria reptans*, S.M. Turk *det.*, St. Ives, Cornwall, 18 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.



FIGURES 18–23. SEM of *Scrupocellaria ellisi* n. sp. **18–22**, NHMUK 1911.10.1.353, from Shetland, U.K.: **18**, part of colony; **19**, close-up of branch, with three frontal avicularia in lateral view; **20**, bifurcation and ovicelled zooids; **21**, close-up of axial zooid with frontal avicularium; **22**, basal surface at a bifurcation. **23**, colony from Scotland (NHMUK 1963.3.6.7a), showing smooth-surfaced rhizoids with distal attachment discs.



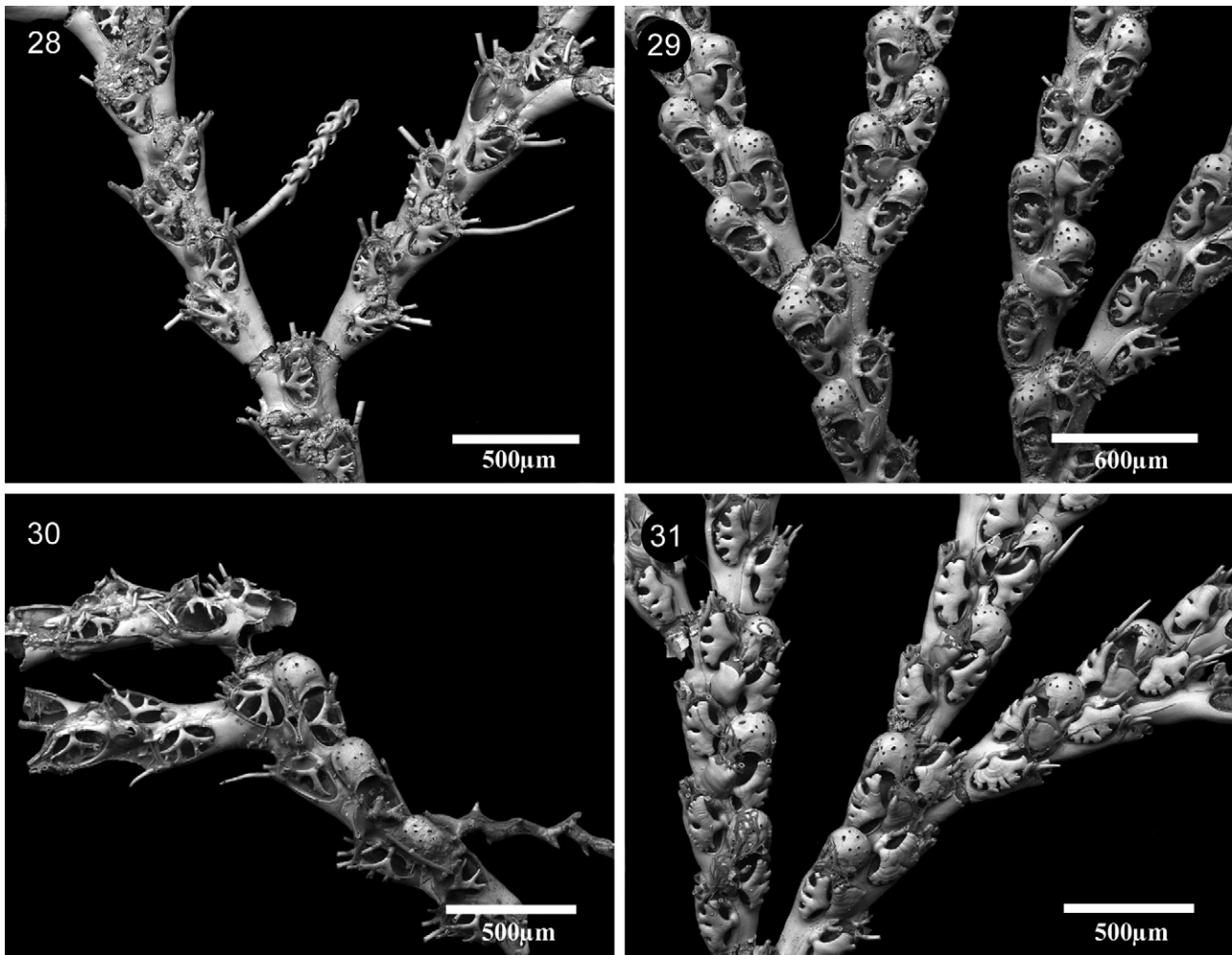
FIGURES 24–27. Comparison between *Scrupocellaria reptans* (Linnaeus, 1758) (NHMUK 1963.3.6.35) and *Scrupocellaria ellisi* n. sp. (NHMUK 1963.3.6.7a). **24–25**, Close-up of frontal avicularia, of similar size in young colonies of both species, but with a taller base in *S. reptans* (24) than found in *S. ellisi* (25); **26–27**, frontal surface of zooids, showing the slightly slenderer and more angled scutum in *S. reptans* (26) than in most proximal zooids of *S. ellisi* (27); note the differences in avicularium size and the number of distal tines in the scuta of both species.

Description. Colony erect, branched, internodes comprising 5–12 zooids. Lateral edge of internode almost straight to slightly curved; chitinous joint passing across gymnocyst and below or slightly overlapping opesia in both outer zooids (C and D) of bifurcation, and across proximal gymnocyst of inner zooids (F and G). Autozoid subelongate, slightly narrower proximally, 0.400–0.615 mm long, 0.190–0.220 mm wide, with smooth proximal gymnocyst. Opesia oval, occupying distal half (approximately) of zooid, cryptocyst very narrow, inconspicuous. Scutum inserted at midline of inner edge of opesia, branched, occupying almost entire opesial area, slender, flattened, branched 2–3 times, with 8–13 stout projections at distal tips; scutum angled at 115–155°, with first branches about 0.045–0.060 mm wide, secondary branches about 0.035–0.045 mm. Zooid spines as follows: 1 long distal spine, 3 outer spines, 1–2 inner spines; most proximal outer and inner spines directed frontally; axial zooid with 5 distal spines. One distolateral avicularium sometimes present on each zooid, distolaterally 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; mandible triangular with hooked tip. A basal vibracular chamber often present proximally on basal surface of each zooid, 0.130–0.140 mm long, 0.100–0.135 mm wide, rarely conspicuous in

frontal view; setal groove directed transversely, straight, with smooth seta longer than one zooid length. A single axial vibraculum. A rhizoidal foramen on proximal outer corner of each basal vibracular chamber, absent in axial vibracula. Rhizoids smooth, attachment disc-like, with some projections at distal end. Ovicell hyperstomial, hemispherical, with 12–18 small rounded pores; 2 outer and 2 inner distal spines in ovicelled zooids.

Remarks. This species was previously recorded by numerous authors as *S. reptans*. *Scrupocellaria ellisi* n. sp., named after the British naturalist John Ellis (1714–1776), is distinguished by smooth (not hooked) rhizoids, robust more-branched scuta and ovicells with small rounded pores.

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



FIGURES 28–31. Four different species found in the NHMUK collection previously misidentified as *Scrupocellaria reptans*. **28**, a specimen from Arisaig, Scotland (NHMUK 2010.12.6.1) with rhizoid hooks but different scutum, frontal avicularia and distal-spine number; **29**, a specimen from Alexandria, Egypt (NHMUK 1963.8.2.16), also with different frontal avicularia and distal-spine number; **30**, specimen from Madeira (NHMUK 1911.10.1.355), again with differences in ovicells, scuta and shape of frontal avicularia, plus rhizoids with well-spaced hooks; **31**, a specimen from Scotland (NHMUK 2010.12.6.22) with robust scuta and frontal avicularia.

Discussion

Examination of NHMUK specimens previously assigned to *Scrupocellaria reptans* revealed that they comprise at least four species (some simply misidentified) (Figs 28–31), distinguished by the number of distal spines and the shape of zooids, frontal avicularia and frontal scuta. This is not surprising; Zabala & Maluquer (1988) noted that some Mediterranean species had been misidentified as *Scrupocellaria reptans*, and we suggest herein that *S. reptans* is geographically restricted to western Britain. Specimens from the North Sea are morphologically similar

to *S. reptans*, but differences in scutal shape, ovicell pores and rhizoids (smooth) indicate that this phenotype represents a distinct species, herein described as *Scrupocellaria ellisi*. The scutum in *S. ellisi* from northern Europe, the Adriatic and Tasmania (presumably introduced) is branched two to four times with 8–13 stout projections at distal tips; it also forms a wider angle when compared with that of *S. reptans* (120–155° in *S. ellisi* vs 100–120° in *S. reptans*) and the first branches are wider, about 0.045–0.060 mm.

Gautier (1962) described a species from Mediterranean waters with robust, branched scuta, which he named *Scrupocellaria macrorhyncha*. It was distinguished six distal spines and very large frontal avicularia. Six such spines and a robust frontal scutum are also found in other specimens from Mediterranean waters (Fig. 29), but, until a redescription of Gautier's type is undertaken, we consider their identity to be uncertain. Savigny (1817) had figured a similar colony from Egypt, described by Audouin (1826) as *Acamarchis geoffroyi* and later synonymized with *S. reptans* (Busk 1852). Unfortunately, few frontal-avicularian and vibracular characters can be seen in Savigny's illustrations. The type specimen of *A. geoffroyi* is lost and the presence of other similar species in the Mediterranean and Red Seas will make it difficult to resolve the identity of Savigny's species.

At least four other similar species of *Scrupocellaria* with branched scuta have previously been described, viz. *S. bertholletii* (Audouin, 1826), *S. curacaoensis* Fransen, 1986, *S. micheli* Marcus, 1955 and *S. tenuirostris* Osburn, 1950; these are part of the *Scrupocellaria reptans-bertholletii* complex, all having a branched scutum and subtrapezoidal vibracular chamber and further distinguished by details of the scuta, distal spines and frontal avicularia. Detailed SEM studies of type material in this complex are underway to resolve the inherent taxonomic problems. Insofar as such well-known European species as *S. reptans* and *S. bertholletii* have been reported worldwide, detailed comparative studies are needful to determine their status. The lack of such studies means that additional morphospecies will have been overlooked. Recent inquiry into the putative widespread distribution of many bryozoan species has revealed the existence of endemic species with restricted distributions (e.g. Berning & Kuklinski 2008; Berning *et al.* 2008; Vieira *et al.* 2010). Such appears to be the case with respect to *S. reptans* and *S. bertholletii* based on the NHMUK material, indicating that more than ten different species, some with restricted distributions, are included under these two names (Vieira, unpubl.).

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