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Cradoscrupocellaria, a new bryozoan genus for *Scrupocellaria bertholletii* (Audouin) and related species (Cheilostomata, Candidae): taxonomy, biodiversity and distribution

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Abstract

A new genus, *Cradoscrupocellaria* **n. gen.**, is erected for *Scrupocellaria bertholletii* (Audouin, 1826), reported as widespread in tropical and subtropical waters. Here we select a neotype of this species in order to establish its identity and distinguish it from morphologically similar species. We include redescriptions and figures of additional species now assigned to this new genus: *Cradoscrupocellaria curacaoensis* (Fransen, 1986) **n. comb.**, *Cradoscrupocellaria hirsuta* (Jullien & Calvet, 1903) **n. comb.**, and *Cradoscrupocellaria macrorhyncha* (Gautier, 1962) **n. comb.** Five additional species are assigned to the genus: *Cradoscrupocellaria ellisi* (Vieira & Spencer Jones, 2012) **n. comb.**, *Cradoscrupocellaria nanshaensis* (Liu, 1991) **n. comb.**, *Cradoscrupocellaria reptans* (Linnaeus, 1758) **n. comb.**, *Cradoscrupocellaria serrata* (Waters, 1909) **n. comb.**, and *Cradoscrupocellaria tenuirostris* (Osburn, 1950) **n. comb.** Eighteen new species are described: *Cradoscrupocellaria aegyptiana* **n. sp.**, *Cradoscrupocellaria arisaigensis* **n. sp.**, *Cradoscrupocellaria atlantica* **n. sp.**, *Cradoscrupocellaria calypso* **n. sp.**, *Cradoscrupocellaria floridana* **n. sp.**, *Cradoscrupocellaria galapagensis* **n. sp.**, *Cradoscrupocellaria gautieri* **n. sp.**, *Cradoscrupocellaria gorgonensis* **n. sp.**, *Cradoscrupocellaria hastingsae* **n. sp.**, *Cradoscrupocellaria insularis* **n. sp.**, *Cradoscrupocellaria jamaicensis* **n. sp.**, *Cradoscrupocellaria lagaaiji* **n. sp**., *Cradoscrupocellaria macrorhynchoides* **n. sp**., *Cradoscrupocellaria makua* **n. sp.**, *Cradoscrupocellaria marcusorum* **n. sp.**, *Cradoscrupocellaria normani* **n. sp.**, *Cradoscrupocellaria odonoghuei* **n. sp**., and *Cradoscrupocellaria osburni* **n. sp.**

Key words: Bryozoa, Buguloidea, new species, taxonomic review, taxonomic key

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). Dumont (1981) noted that, whereas Audouin's species were based on specimens figured from the Red Sea and Mediterranean, no specific localities were given for 40 of them, including *Acamarchis bertholletii*. Thus, the type locality of *Scrupocellaria bertholletii* within that region remains uncertain. The species was indeed subsequently reported in the 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 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). Hincks (1886) was the first to use the combination *Scrupocellaria bertholetii*, based on material from the Adriatic. He characterized the specimens by presence of bifurcated to highly branched spines overarching the frontal membrane (scutum). As was noted by Hincks (1886), however, the highly branched scutum of Adriatic specimens is distinct from the single forked scutum illustrated by Savigny (1817), suggesting that 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, 1927; 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, re-examination of the type material of other supposedly widespread species of *Scrupocellaria* van Beneden, 1845 and related genera has revealed the presence of species complexes in some putative well-established taxa (Tilbrook & Vieira 2012; Vieira & Spencer Jones 2012; Vieira *et al.* in press). Vieira *et al.* (in press) also used morphological features to characterize the genus *Licornia* van Beneden, 1850, a senior synonym of *Retiscrupocellaria* d'Hondt, 1988, and to suggest that *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, *Cradoscrupocellaria* n. gen. to accommodate it and morphologically similar species. We suggest that at least nine 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 American Museum of Natural History (USA)
MCZ Museum of Comparative Zoology (USA)
MNHN Muséum national d'Histoire naturelle (France)
MOM Musée océanographique de Monaco (Monaco)
MZUSP Museu de Zoologia da Universidade de São Paulo (Brazil)
NHMUK Natural History Museum, London (United Kingdom)
RMNH Nationaal Natuurhistorich Museum, Leiden (Netherlands) (Nederlands Centrum voor Biodiversiteit Naturalis)
SBMNH Santa Barbara Museum of Natural History (USA)
UFAL Setor de Comunidades Bentônicas da Universidade Federal de Alagoas (Brazil)
USNM National Museum of Natural History, Smithsonian Institution, Washington DC (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 VMNH and at the Zeiss LEO 440 at MZUSP for coated specimens and SEM with an environmental chamber, a LEO 1455-VP at NHMUK and Philips XL-30 at USNM for uncoated specimens. Some slide specimens were photographed under a stereomicroscope with AxioCam. Measurements were made from digital SEM images using the analyzing software ImageJ®: zooid length (Lz), zooid width (Wz), opesia length (Lo), scutum length (Lsc), scutum width (Wsc), vibracular chamber length (Lvib), vibracular chamber width (Wvib), ovicell length (Lov) and ovicell width (Wov).

Systematic account

Family Candidae d'Orbigny, 1851

Genus *Cradoscrupocellaria* 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, 1850, *nomen protectum*)

Etymology. Greek *krados*, branch, alluding to the characteristic branched scutum of some species previously assigned to *Scrupocellaria* van Beneden, 1845.

Diagnosis. Biserial member of the family Candidae with articulated unbranched distal spines, branched scutum inserted at midline of inner edge of opesia, rounded to trapezoidal vibracular chamber, single axial vibraculum and ooecium perforated by ectooecial pores.

Description. Candidae with almost-straight branches, with chitinous joints passing across opesia or below it in zooids C and D at bifurcation; zooids with articulated 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 highly branched with truncate or acute tips, inserted at midline of inner edge of opesia and overarching frontal membrane; scutum occasionally absent. Distolateral avicularium often present at outer distal corner of zooid, placed laterally or behind spines. Vibracular chamber subrounded to trapezoidal, setal groove transverse to internode axis, with smooth seta. Axial vibraculum single, without rhizoidal foramen. Ooecium perforated by rounded ectooecial pores.

Remarks. Insofar as *Scrupocellaria* van Beneden, 1845 comprised species with a mixture of characters, Vieira *et al*. (in press) resurrected and redefined *Licornia* van Beneden, 1850 to accommodate some of them.

The perforated ooecium, branched scutum and rounded to trapezoidal vibracular chamber with its setal groove transverse to the internode axis distinguish *Cradoscrupocellaria* n. gen. from the characters observed in the type of *Scrupocellaria*, *Scrupocellaria scruposa* (Linnaeus, 1758). The shape of scutum, regularly branched, and shape of the vibracular chamber, with a transverse setal groove are also distinct from the equivalent characters in *Licornia* (see Vieira *et al.* in press). These morphological characteristics, clearly observed in *Scrupocellaria bertholletii* and reported in *Scrupocellaria reptans* (see Vieira & Spencer Jones 2012), lead us to erect a new genus to include nine species previously assigned to *Scrupocellaria*: *Cradoscrupocellaria bertholletii* (Audouin, 1826) n. comb.,

Cradoscrupocellaria curacaoensis (Fransen, 1986) n. comb., *Cradoscrupocellaria ellisi* (Vieira & Spencer Jones, 2012) n. comb., *Cradoscrupocellaria hirsuta* (Jullien & Calvet, 1903) n. comb., *Cradoscrupocellaria macrorhyncha* (Gautier, 1962) n. comb., *Cradoscrupocellaria nanshaensis* (Liu, 1991) n. comb., *Cradoscrupocellaria reptans* (Linnaeus, 1758) n. comb., *Cradoscrupocellaria serrata* (Waters, 1909) n. comb. and *Cradoscrupocellaria tenuirostris* (Osburn, 1950) n. comb. Another 18 new species are described in this paper.

Scrupocellaria bellula Osburn, 1947 is also characterized by ovicells with ectooecial pores, trapezoidal vibracular chamber and branched scutum; this species is not reassigned to *Cradoscrupocellaria*, however, because of its distinctive growth pattern—colonies are apparently unbranched, but rarely have a chitinous joint crossing the gymnocyst of a single zooid at the new branch—and because of the presence of branched distal spines, absent in *Cradoscrupocellaria* species. The scutum of *S. bellula* is also distinct in having 12–30 acute tips and covering almost the entire frontal membrane (Fig. 1).

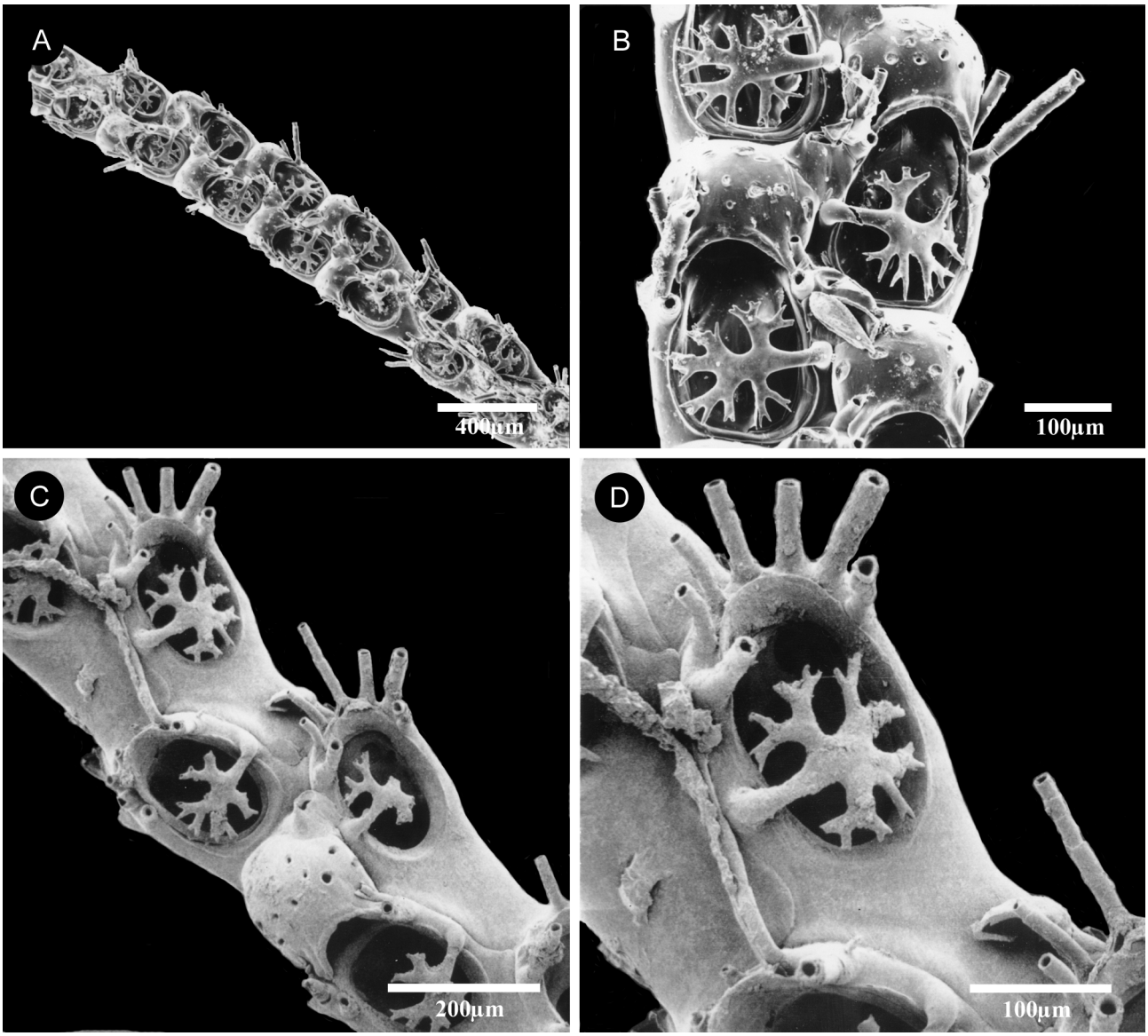

FIGURE 1. *Scrupocellaria bellula* Osburn, 1947. A–D, Uncatalogued specimen (part of AMNH 1518.1), Jamaica. A, Frontal surface of branch with ovicelled zooids. B, Close-up of two ovicelled zooids; note the branched frontal scutum and small frontal avicularium on zooids. C, Frontal surface of branch; note the presence of seven distal spines. D, Close-up of frontal surface of autozooid.

Licornia resembles *Cradoscrupocellaria* in having porous ovicells but is distinguished by its branched oral spines, unbranched scuta and the shape of its basal vibracular chambers with the setal groove oblique to the internode axis. Some other species of *Scrupocellaria* also have porous ovicells, e.g. *Scrupocellaria frondis*

Kirkpatrick, 1890 and *Scrupocellaria sinuosa* Canu & Bassler, 1927 (see Tilbrook & Vieira 2012), but they are distinguished from *Cradoscrupocellaria* in having broad paddle-shaped scuta and monomorphic frontal avicularia.

Van Beneden (1850) erected the genus *Crisina* for *Crisie rampante* (=*Sertularia reptans* Linnaeus) and *Acamarchis bertholetii* (sic) Audouin. This name has not been used in the literature since Harmer (1926), who included *Crisina* van Beneden as junior synonym of *Scrupocellaria* van Beneden, 1845; thus, *Crisina* van Beneden is a lapsed name. On the other hand, the homonym *Crisina* d'Orbigny, 1850 has been used for some fossil cyclostomes in the last two centuries (e.g. d'Orbigny 1853; Beissel 1865; Gabb & Horn 1862; Stoliczka 1865; Hamm 1881; Smitt 1872; Jullien 1882; Waters 1884; Marsson 1887; MacGillivray 1895; Gregory 1899; Neviani 1900; Harmer 1915; Canu 1920; Borg 1941; Brood 1972, 1976).

Crisina d'Orbigny was published in 1850 in the "*Prodome de Paléontologie*"; though dated 1849, it was possibly published in January 1850 (Dennis P. Gordon & Paul D. Taylor, pers. comm.), whereas *Nomenclator Zoologicus* has November 1850 (Neave 2012). *Crisina* van Beneden was also published in a work dated 1849 that was also published in 1850, but no exact date is known for the issue. To promote the stability and according to ICZN Article 23.2, we consider the unused homonym *Crisina* van Beneden, 1850 as a *nomen oblitum* and the homonym *Crisina* d'Orbigny, 1850 is declared a *nomen protectum*.

Species with slender scutum and acute tips

Cradoscrupocellaria bertholletii (Audouin, 1826) n. comb.

(Figs 2–3, Table 1)

Acamarchis Bertholletii Audouin, 1826: 241; Savigny 1817: pl. 11, figs 3.1–3.5. [Egypt]
? *Scrupocellaria capreolus* Heller, 1867: 11, pl. 1, fig. 1. [Adriatic]
Scrupocellaria Bertholletii (Audouin): Hincks 1886: 258, pl. 9, figs 1–2. [Adriatic]
? *Scrupocellaria bertholletii* (Audouin): Waters 1909: 133. [Suez Canal]
? *Scrupocellaria bertholletii* (Audouin): Waters 1918: 5 (in part). [Mediterranean and Suez Canal]
Scrupocellaria bertholletii (Audouin): Hastings 1927: 335. [Suez Canal]
Scrupocellaria bertholletii (Audouin): Calvet 1927: 7. [Monaco]
Scrupocellaria bertholletii (Audouin): Marcus 1938: 24 (in part), pl. 5, figs 11A–B. [Brazil: São Paulo]
? *Scrupocellaria bertholletii* (Audouin): Gautier 1962: 85. [Mediterranean]
? *Scrupocellaria bertholletii* (Audouin): Prenant & Bobin 1966: 418 (not figs 136–137). [Mediterranean]
? *Scrupocellaria bertholletii* (Audouin): Zabala i Limosin 1986: 315 (non fig. 86). [Mediterranean]
? *Scrupocellaria bertholletii* (Audouin): Zabala & Maluquer 1988: 97, figs 157–158. [Mediterranean]
Scrupocellaria bertholletii (Audouin): d'Hondt 1988: 198. [Israel]
Scrupocellaria bertholletii (Audouin): Ramalho 2006: 127, fig. 28. [Brazil: Rio de Janeiro]
Scrupocellaria sp. Gordon *et al.* 2008: 44, 46, figs 4.1–4.3. [New Zealand]
Not *Scrupocellaria reptans* var. *bertholletii* (Audouin): Water 1897: 6, pl. 1, figs 18–19. [Italy]
Not *Scrupocellaria bertholletii* (Audouin): Norman 1909: 283, pl. 36, figs 1–2. [Madeira]
Not *Scrupocellaria bertholletii* (Audouin): Waters 1918: 5. [Cape Verde]
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 1926.9.6.58 (Fig. 2A–C), *Scrupocellaria bertholletii*, A.B. Hastings det., Suez Canal Expedition, coll. H.M. Fox, 15 December1924, Suez Canal P.3, 46B.

Additional material examined. NHMUK 1885.8.12.1, *Menipea jeffreysii*, S.O. Ridley det., S.O. Ridley Collection, 9 August 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 1899.7.1.736 (Fig. 2D–F), *Scrupocellaria bertholletii*, Mediterranean. 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 1926.9.6.60, *Scrupocellaria*

bertholletii, A.B. Hastings det., Suez Canal Expedition, coll. H.M. Fox, 26 October 1924, Suez Canal, barge 690, Port Taufiq. NHMUK 1926.9.6.66–7, *Scrupocellaria bertholletii*, A.B. Hastings det., Suez Canal Expedition, coll. H.M. Fox, 15 December 1924, Suez Canal P.3. NHMUK 1926.9.6.68, *Scrupocellaria bertholletii*, A.B. Hastings det., 26 October 1924, Suez Canal, Port Taufig, Barga 690. NHMUK 1926.9.6.69, *Scrupocellaria bertholletii*, A.B. Hastings det., Suez Canal Expedition, coll. H.M. Fox, Suez Canal, Dredger N.8. NHMUK 1963.1.26.2, *Scrupocellaria bertholletii*, J.S. Ryland det., 30 December 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 February 1962, A.P. Austin leg., Malta, Mediterranean. USNM 9083, Mediterranean. NHMUK 2012.7.1.11 (Fig. 3C–F), Station Cru82.043, 14 August 1982, Charles H.J.M. Fransen leg., Curaçao, Piscadera Inner Bay, Candelichi, 0–0.5 meters, on *Rhizophora* roots. MOM 421467, *Scrupocellaria bertholletii*, L. Calvet det., Monaco, 652i, slide 84. MOM 42529, *Scrupocellaria bertholletii*, Calvet det., Port of Monaco, 1903, slide 85. MOM 421681 (part of specimens in NHMUK 2012.7.1.4, Fig. 3A–B), L. Calvet det., 30 January 1908, Sur le Coffre du Port Monaco. UFAL 548, coll. M.D. Correia, November 1987, Station #A, Paranaguá Bay, Paraná, Brazil, colony found on acrylic panels. USNM 9678, *Scrupocellaria bertholletii*, A.B. Hastings det., Suez Canal Expedition, coll. H.M. Fox, 26 December 1924, Port Taufig, Barga 690. Cambridge Expedition. USNM 9083, *Scrupocellaria scruposa*, Mediterranean.

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

Redescription. Colony erect, branched, with internodes comprising 5–9 zooids. Internodes almost straight, with acute bifurcating pattern; chitinous joints passing across proximal end of opesia in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to three fifths of zooidal length, with two lateral folds where lateral spines are inserted; cryptocyst proximal very narrow, inconspicuous, deep and smooth. Scutum sometimes present, inserted at midline of inner opesial edge, small, forked, angled at 70–90°, overarching to 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 aquiline avicularium, 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 transverse to axis of internode, 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 *C. bertholletii* in the literature (e.g. Prenant & Bobin 1966: 418) led us to examine specimens collected at 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 on specimens illustrated by Savigny (1817), presumably lost (d'Hondt 2006). Two diagnostic characteristics are observed, however, in Savigny's plates, viz the bifurcated frontal scutum and the shape of the basal vibraculum. These characteristics are also observed in some specimens from the Suez Canal and Mediterranean, as well as in a small specimen from Madeira (NHMUK 1911.10.1.357) identified by Alfred M. Norman (1831–1918) under an unpublished name (*Scrupocellaria bertholletii* var. *aperta*). Thus, the neotype of *C. bertholletii* is here selected from the Suez Canal (NHMUK 1926.9.6.58) in order to establish the identity of this species. The majority of specimens deposited at AMNH, NHMUK and USNM assigned to *C. bertholletii* have scuta with distinct branching patterns and belong to distinct species. Some of those species are reassigned to new species (see below). Unfortunately, we have no access to specimens assigned to *C. bertholletii* by Gautier (1962), Prenant and Bobin (1966) and Zabala i Limosin (1986), hence their identities remain uncertain.

Cradoscrupocellaria bertholletii has been reported in tropical and subtropical waters worldwide. Hastings (1930) noted distinct differences in morphology among specimens of *C. bertholletii* from different localities in the

Pacific and Egypt, but, notwithstanding, used the same name for three morphologically distinct specimens from Pacific waters. Likewise, morphological differences were described by other authors (e.g. Waters 1897, 1918; Norman 1909; Marcus 1938; Osburn 1940, 1950). Osburn (1950) first described one distinct form of *C. bertholletii* from California, named *Scrupocellaria bertholletii* var. *tenuirostris*, characterized by the elongate shape of the frontal avicularia and the branching pattern of the scutum, now assigned as a distinct species (see below). Later, Fransen (1986) also used morphological characteristics of the scutum and absence of lateral avicularia to distinguish the Caribbean species *C. curacaoensis* (see below). Among the specimens identified by Marcus (1938) as *Scrupocellaria bertholletii*, a colony without lateral avicularia was observed; this specimen is assigned to a distinct species (see below), while the specimens with lateral avicularia belong to *C. bertholletii*.

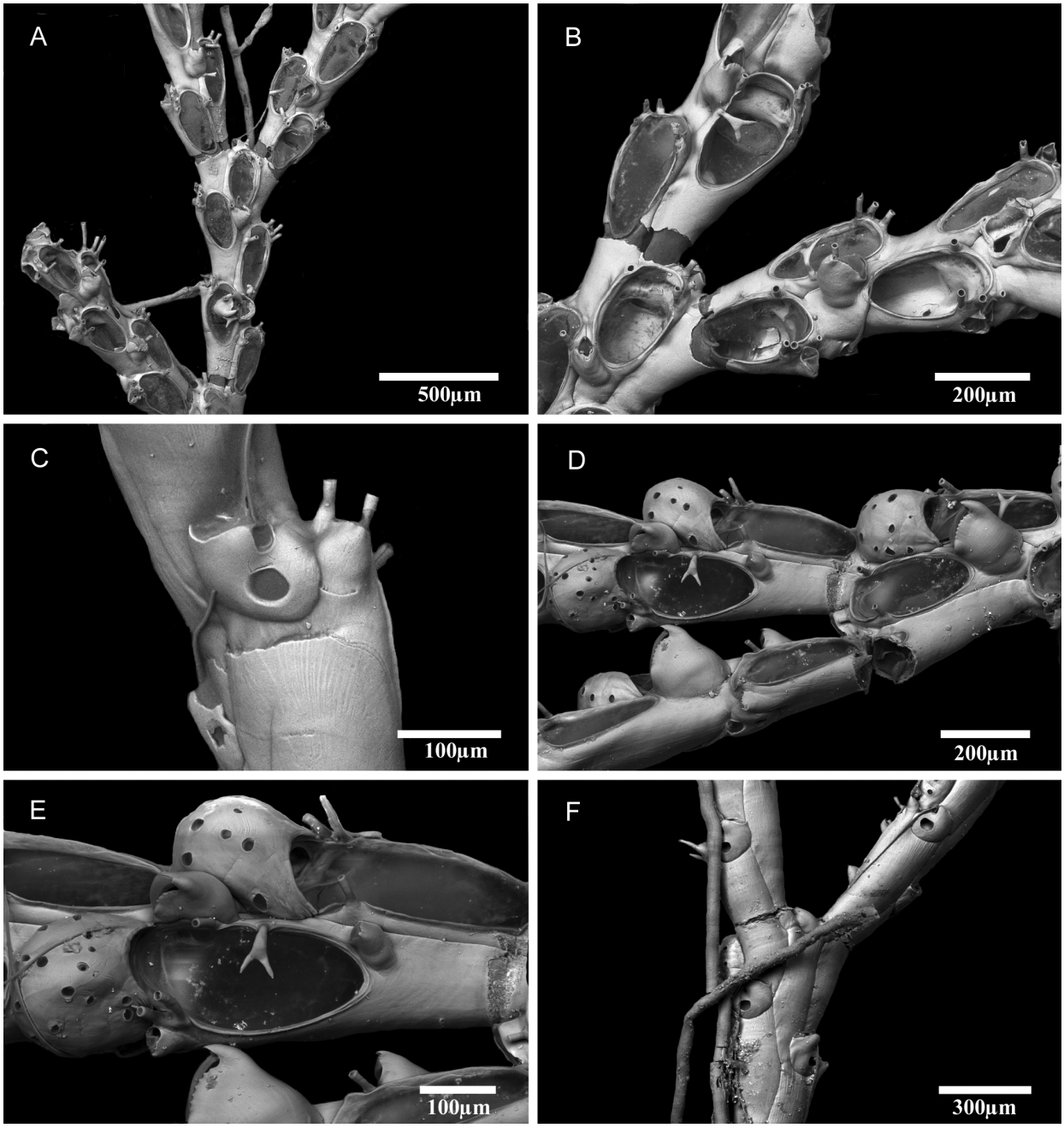

FIGURE 2. *Cradoscrupocellaria bertholletii* (Audouin, 1826) **n. comb.** A–C, NHMUK 1926.9.6.58, neotype, Suez Canal; D–F, NHMUK 1899.7.1.736, Mediterranean. A, Frontal surface of branches and two bifurcations. B, Frontal surface of a branch; note zooids with and without scuta. C, Close-up of an abfrontal vibraculum. D, Frontal surface of a branch bifurcation; note the presence of dimorphic frontal avicularia (gigantic on axial zooid) and two zooids with scutum. E, Close-up of an ovicelled zooid with scutum; note the small lateral avicularium. F, Abfrontal surface of branch; note the smooth surface of rhizoids.

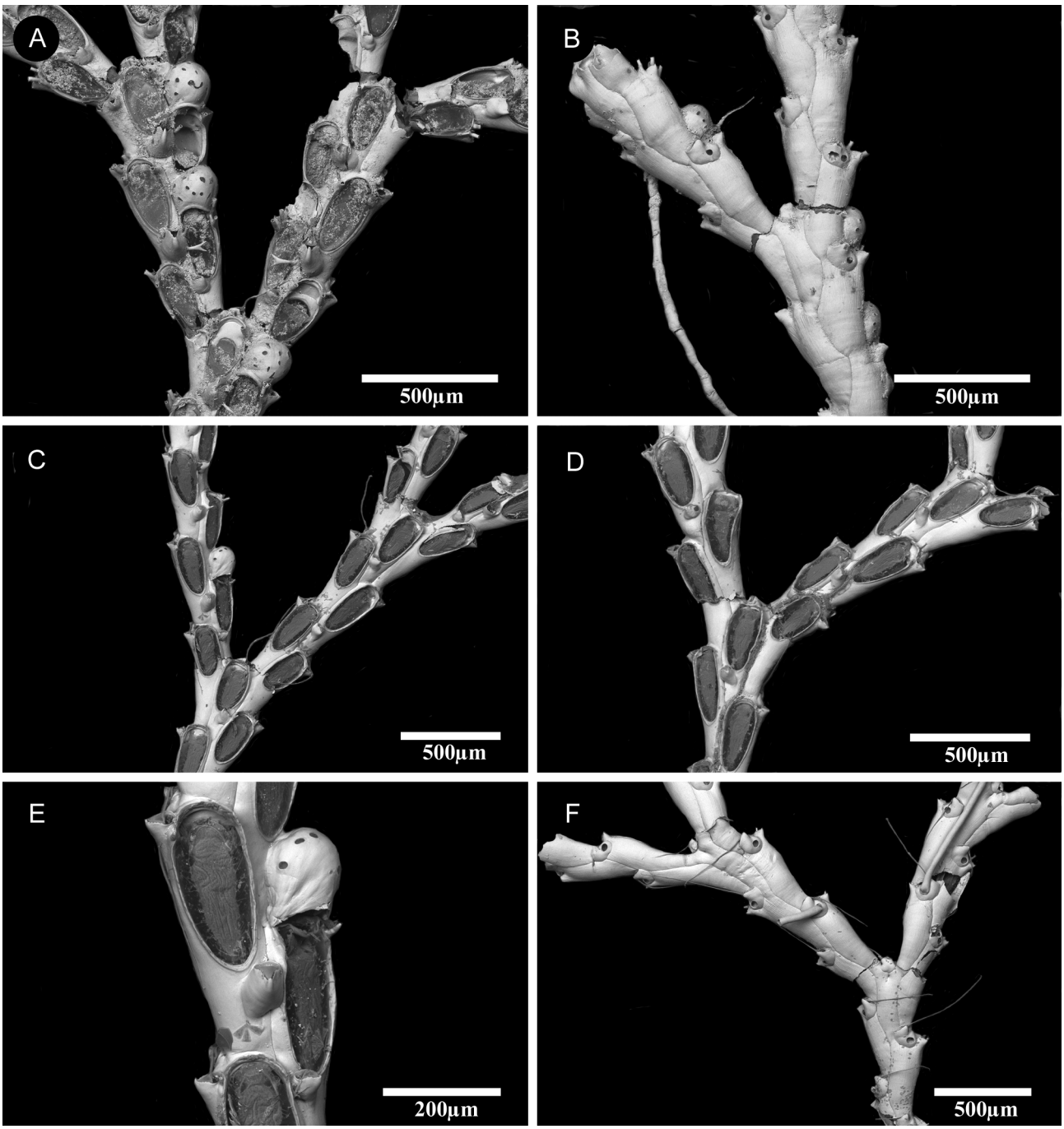

FIGURE 3. *Cradoscrupocellaria bertholletii* (Audouin, 1826) **n. comb.** A–B, NHMUK 2012.7.1.4, Monaco; C–F, NHMUK 2012.7.1.11, Curaçao. A, Frontal surface of branches and bifurcation. B, Abfrontal surface of branch. C, Frontal surface of branches; note the absence of scuta in the entire colony. D, Frontal surface of bifurcation. E, Close-up of two zooids, one with ovicell; note the absence of scuta in ovicelled and non-ovicelled zooids. F, Abfrontal surface of colony.

Six other species with branched scuta previously assigned to *Scrupocellaria* are known so far—*Scrupocellaria bellula*, *Scrupocellaria ellisi*, *Scrupocellaria macrorhyncha*, *Scrupocellaria micheli* (Marcus, 1955), *Scrupocellaria nanshaensis,* and *Scrupocellaria reptans*. *Scrupocellaria micheli* differs from *Cradoscrupocellaria* by the presence of large lateral avicularia and a basal vibracular chamber with the setal groove oblique to the internode axis; *Scrupocellaria bellula* (Fig. 1) is distinguished from *Cradoscrupocellaria* by its branching pattern, the presence of branched distal spines and its elaborately forked scutum. The other four species are herein assigned to *Cradoscrupocellaria*—*Cradoscrupocellaria ellisi*, *C. macrochyncha*, *C. nanshaensis,* and *C. reptans*.

Cradoscrupocellaria bertholletii is characterized by a forked scutum (often absent, see Figs 2A–B, D–E, 3A, C–E), the presence of small distolateral avicularia and an almost rounded basal vibraculum chamber. An

unidentified specimen from New Zealand (see Gordon *et al.* 2008, pp. 44, 46, figs. 4.1–4.3) is characterized by the lack of a scutum; this specimen belongs to *C. bertholletii.* The specimen figured and described by Heller (1867) as *Scrupocellaria capreolus* from the Adriatic Sea differs from *C. bertholletii* by the presence of bi- to trifurcate scuta (Heller 1867, pl. 1, fig. 1); this species, however, requires further examination.

TABLE 1. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. bertholletii			*C. curacaoensis*	
	Mediterranean[1]	Monaco[2]	Curaçao[3]	Curaçao[4]	Bermuda[5]
Lz	7	7	10	10	5
Mean (SD)	0.471 (0.036)	0.411 (0.038)	0.460 (0.031)	0.369 (0.035)	0.413 (0.021)
Range	0.441–0.530	0.366–0.481	0.418–0.528	0.314–0.439	0.375–0.428
Wz	7	7	10	10	5
Mean (SD)	0.161 (0.014)	0.154 (0.011)	0.144 (0.005)	0.133 (0.011)	0.135 (0.005)
Range	0.142–0.186	0.132–0.162	0.132–0.151	0.110–0.149	0.129–0.139
Lo	7	7	10	10	5
Mean (SD)	0.296 (0.022)	0.286 (0.024)	0.310 (0.023)	0.216 (0.007)	0.210 (0.010)
Range	0.280–0.345	0.256–0.316	0.253–0.321	0.204–0.224	0.189–0.212
Lo/Lz	7	7	10	10	5
Mean (SD)	0.64 (0.04)	0.60 (0.06)	0.67 (0.06)	0.58 (0.05)	0.50 (0.07)
Range	0.58–0.67	0.57–0.73	0.50–0.70	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	7	5	3
Mean (SD)	0.125 (0.008)	0.103 (0.011)	0.122 (0.007)	0.096 (0.007)	0.097 (0.016)
Range	0.108–0.133	0.093–0.118	0.112–0.133	0.084–0.103	0.088–0.120
Wvib	7	5	7	5	3
Mean (SD)	0.106 (0.007)	0.098 (0.007)	0.096 (0.006)	0.070 (0.003)	0.086 (0.010)
Range	0.105–0.123	0.085–0.101	0.090–0.110	0.067–0.076	0.073–0.093
Lov	5	6	1	7	-
Mean (SD)	0.187 (0.003)	0.174 (0.022)	0.152	0.159 (0.006)	-
Range	0.183–0.192	0.162–0.223	-	0.151–0.167	-
Wov	5	6	1	7	-
Mean (SD)	0.189 (0.004)	0.172 (0.012)	0.150	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 2012.7.1.11, Curaçao. [4]NHMUK 2012.7.1.12, Curaçao. [5]USNM 559182, Bermuda.

The specimens reported by Waters (1897) from Italy are distinguished from *C. bertholletii* by more-branched scuta; their identities, however, remain uncertain. Specimens identified by Waters (1918) from Cape Verde belong

to a distinct species (see below), while the identity of his specimens from the Mediterranean and Suez Canal remain uncertain. The figures of *C. bertholletii* given by Zabala and Maluquer (1986) are characterized by bifurcate scuta, but no specimens were examined by us to confirm their identification. In the MNHN collections, dozens of specimens from the Mediterranean and Red Sea were previously assigned to *C. bertholletii*; they also require re-examination.

Distribution. New Zealand; Suez Canal; Mediterranean; Adriatic; Madeira; Curaçao; Brazil; shallow waters.

***Cradoscrupocellaria curacaoensis* (Fransen, 1986) n. comb.**
(Figs 4–5, Table 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 curacaoensis 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 August 1982, Curaçao, Fuikbaai, eastern part, 1.5–3 m. *Paratypes*. NHMUK 2012.7.1.12 (Fig. 4A–C), dry (part of specimen RMNH 02975, in alcohol), same data as holotype. RMNH 03034, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.081, 17 September 1982, Curaçao, Spaanse water, entrance, Spaanse Lagoen, 0–0.5 m. RMNH 03035, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.066, 10 September 1982, Curaçao, Fuikbaai, eastern part, 0–1 m. RMNH 03036, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Cur82.066, 10 September 1982, Curaçao, Fuikbaai, eastern part, 0–3 m. RMNH 03037, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1620, 14 October 1967, Curaçao, Piscadera Baai, Carmabi pier, 0–1 m. RMNH 03038, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1037A, 21 April 1949, Curaçao, Spaanse water, Spaans Lacoen, south side, 0–1.5 m. RMNH 03040, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1218, 3 March 1955, Curaçao, Schottegat on Venezuelan destroyer, 0–2 m. RMNH 03041, wet, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station PWH.1049C, 13 September 1948, Klein Bonaire, sandy reef, 1–3 m. RMNH 03064, wet and slide, *Scrupocellaria curacaoensis*, Charles H.J.M. Fransen det., Station Car.1629, 17 November 1968, Curaçao, Spaanse water, inner bay, Jan Sofat, islet, 0–1 m. *Additional material*. MCZ 112, wet; USNM 559180, balsam slide; USNM 559181, balsam slide, *Scrupocellaria bertholletii*, Osburn & Hutchins det. 1942, US Coast Survey Steamer *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 m (36 fms). USNM 559182 (Fig. 4D–F), *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-4-A-4303, Bermuda. USNM 559183 (Fig. 5A–B), balsam slide, *Scrupocellaria bertholleti*, Allan Hancock Foundation, Sta. 2381, off Guanica Harbor, Porto Rico, about 9 m. USNM 559184, balsam slide, *Scrupocellaria bertholletii*, R.C. Osburn & & L.W. Hutchins det., Station 2381, Porto Rico. USNM 559185, balsam slide, *Scrupocellaria bertholleti*, Bermuda, H. Pratt coll. USNM 559186, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-12-A-4333, Bermuda. USNM 559187, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-10-B-4321, Bermuda. USNM 559188, *Scrupocellaria bertholletii*, Roger Cuffey det., Bermud-10-B-4331, Bermuda. USNM 559189, *Scrupocellaria regularis*, Roger Cuffey det., Bermud-4-9-A-4304, Bermuda. SBMNH 96400 (Fig. 5C–D), balsam slide, *Scrupocellaria bertholletii*, Allan Hancock Foundation, R.C. Osburn Collection, ‘Velero III’, Station A18-39, 10 April 1939, San Nicholas Bay, Aruba Island, 12°21'28" N, 70°4'45" W. USNM 16934 (found with *Scrupocellaria regularis*), dry, Continental Shelf Associatioes, 18 July 1981, Station 01, Expedition SW Florida Shelf Cr. II, Gulf of Mexico, off Florida, 26°45’46” N, 82°43’07” W, 24 m.

Diagnosis. Chitinous joints passing across proximal end of opesia in zooids C and D at 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.

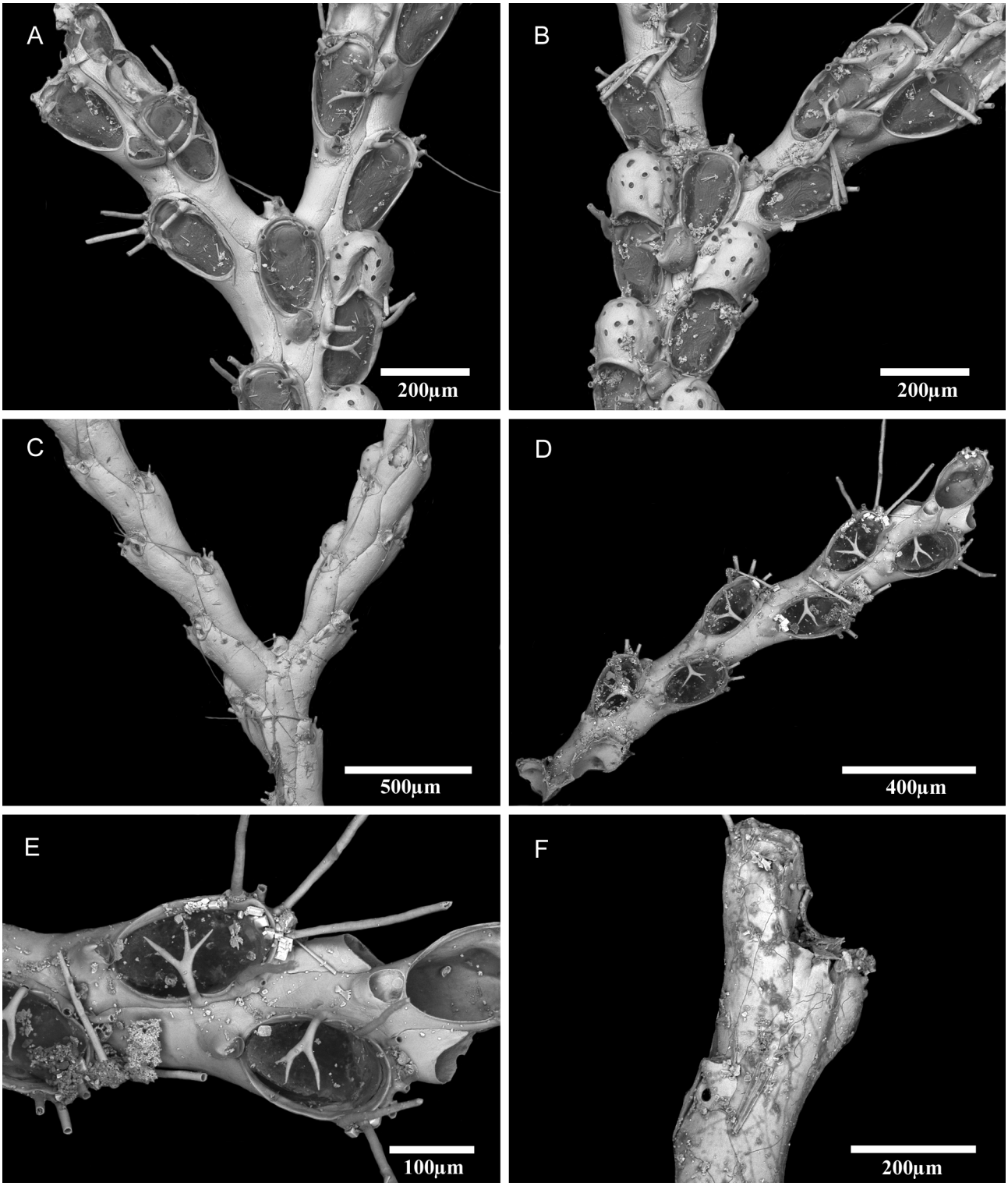

FIGURE 4. *Cradoscrupocellaria curacaoensis* (Fransen, 1986) **n. comb.** A–C, NHMUK 2012.7.1.12, paratype, Curaçao. D–F, USNM 559182, Bermuda. A, Frontal surface of branch; note the forked scutum in some zooids. B, Frontal surface of branch bifurcation; note ovicelled zooids. C, Abfrontal surface of branch. D, Frontal surface of branch; note the bi- and trifurcated scuta. E, Close-up of two zooids; note the trifurcated scutum. F, Abfrontal surface of branch; note the vibracular chamber with transverse setal groove.

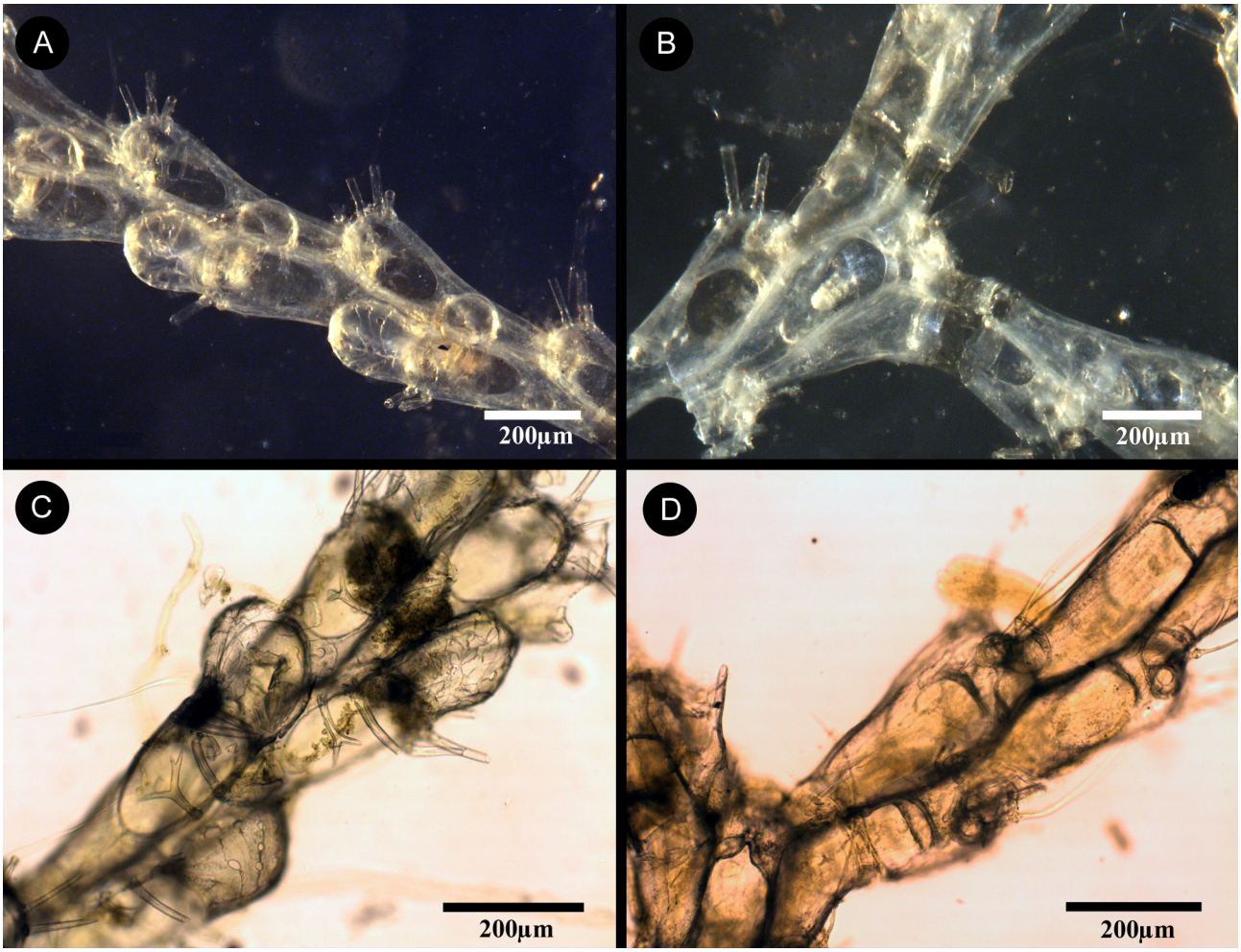

FIGURE 5. *Cradoscrupocellaria curacaoensis* (Fransen, 1986) **n. comb.** A–B, USNM 559183, Porto Rico. C–D, SBMNH 96400, Aruba Island. A, Frontal surface of branch with two ovicells. B, Abfrontal surface of branch bifurcation. C, Frontal surface of branch; note one zooid with trifurcated scutum and two zooids with forked scutum. D, Abfrontal surface of branch; note the joints passing across the opesia in outer zooids at the bifurcation.

Redescription. Colony erect, branched, with branches comprising 3–11 zooids. Internodes slightly curved; chitinous joints pass across proximal end of opesia in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, tapering proximally and slightly curved laterally. Oval opesia occupying distal half of zooidal length; cryptocyst inconspicuous around opesial rim. Scutum often present, inserted at midline of inner edge of opesia, bifurcated 60–120 degrees, often trifurcated, reaching beyond midline of opesia. 5–7 distal spines, long and unbranched; proximalmost inner spines often directed toward 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, 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 transverse to internode axis, 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*. Examination of specimens identified as *Scrupocellaria bertholletii* from the Caribbean (Osburn 1940, 1947) revealed two distinct species in Caribbean waters: *Cradoscrupocellaria curacaoensis* (Figs 4–5) and

C. floridana **n. sp.** (Fig. 9), distinguished by the shape of the scutum and the frontal avicularia. Examination of specimens deposited at AMNH identified as *Scrupocellaria bertholletii* from Jamaica also revealed a species resembling *C. curacaoensis* and *C. floridana* in the absence of lateral avicularia; these specimens are here described as *C. jamaicensis* **n. sp.** (Fig. 14). They are distinguished by zooid size and the shape of avicularia and ovicells.

Cradoscrupocellaria curacaoensis is morphologically similar to *C. bertholletii* in the shape of the vibracular chamber, but differs from it in the branching pattern of the scutum, absence of distolateral avicularia, and in having elongate frontal avicularia and ooecia with tubular pores.

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

Cradoscrupocellaria nanshaensis (Liu, 1991) n. comb.

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

Remarks. Liu (1991) characterized *C. 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. Frontal avicularia are also absent from *C. serrata* from Red Sea, but neither lateral avicularia nor basal vibracula are found in this species. The presence of a granular cryptocyst and segmented rhizoids in *C. nanshaensis* distinguish it from congeners.

Distribution. China (Nansha Island).

Cradoscrupocellaria serrata (Waters, 1909) n. comb.

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

Remarks. 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.

Cradoscrupocellaria serrata is distinguished by the absence of lateral avicularia in non-ovicelled zooids, in having ovicelled zooids with large bi- to trifurcated avicularia, and no basal vibracula. The shape of the large lateral avicularia has been described in 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, fig. 1a–b). Both *S. obtecta* and *S. unguiculata* are distinguished from the present species by their rounded scuta. *Scrupocellaria talonis* specimens are distinguished by 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 the opesia has a rare, vestigial spine-like scutum; no ovicells were found in the specimens described by Osburn (1950). The scutum and gigantic lateral avicularia of *S. varians* resemble those described for *C. serrata*, but *S. varians* is distinguished by its small lateral avicularia, basal vibracula and ovicells with a single pore in the ectooecium.

Distribution. Red Sea.

Cradoscrupocellaria tenuirostris (Osburn, 1950) n. comb.

(Fig. 6, Table 2)

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

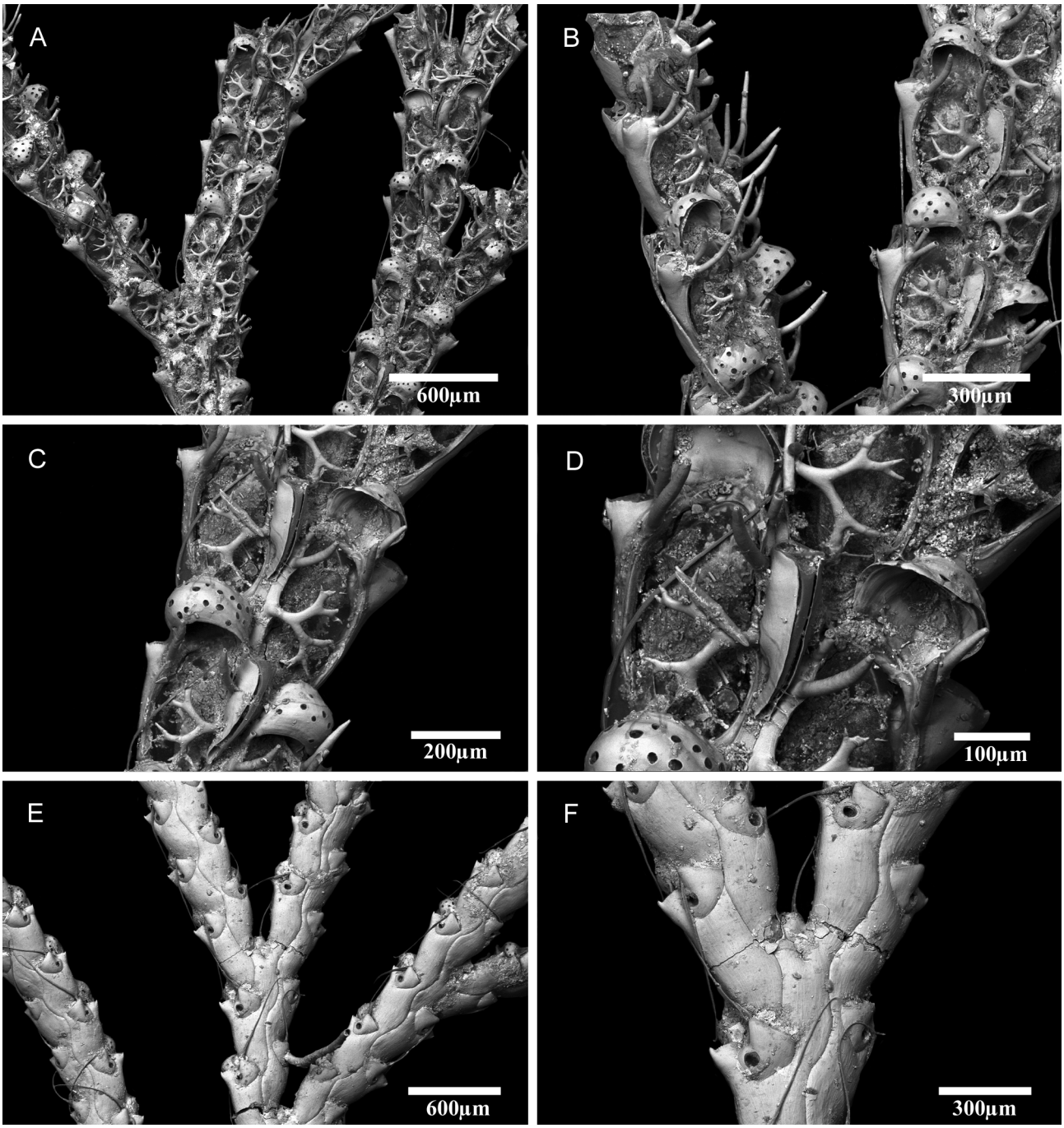

FIGURE 6. *Cradoscrupocellaria tenuirostris* (Osburn, 1950) **n. comb.** A–F, NHMUK 2010.10.5.1, California. A, Frontal surface of colony. B, Frontal surface of branches; note the ovicelled zooid and lanceolate frontal avicularia in right branch. C, Frontal surface of branch; note two ovicelled zooid 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.

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 February 1936. *Additional material*. AMNH 1506.1, Santa Clara Point, Missin Bay, California, 18 February 1991. NHMUK 2010.10.5.1 (Fig. 6), L.M. Vieira det., B. Okamura & P. Taylor leg., August 2010, San Diego, California. USNM 10344, Gulf Lower California, Angelus Bay, Mexico. USNM 10350, Gulf Lower California, San Francisquito Bay, Mexico. USNM 559191, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, University of Southern California, Corona del Mar, California, 30 December 1944, low tide. USNM 559192, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn

Collection, University of Southern California, Allan Hancock Pacific Expedition Station 253-34. USNM 559193, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, Allan Hancock Pacific Expedition, Station 775-38. USNM 559194, balsam slide, *Scrupocellaria bertholleti* var. *tenuirostris*, R.C. Osburn Collection, Newport Harbor, California. USNM 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.

TABLE 2. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. tenuirostris	*C. atlantica*		*C. calypso*	*C. floridana*
	California[1]	Brazil[2]	USA[3]	Brazil[4]	Tortugas[5]
Lz	10	8	8	8	10
Mean (SD)	0.437 (0.020)	0.405 (0.045)	0.428 (0.027)	0.381 (0.020)	0.384 (0.039)
Range	0.420–0.473	0.343–0.473	0.402–0.483	0.358–0.415	0.325–0.443
Wz	10	8	8	8	10
Mean (SD)	0.221 (0.014)	0.174 (0.016)	0.201 (0.019)	0.152 (0.008)	0.156 (0.010)
Range	0.192–0.229	0.147–0.200	0.153–0.206	0.140–0.165	0.144–0.181
Lo	10	8	8	8	10
Mean (SD)	0.354 (0.020)	0.308 (0.018)	0.308 (0.020)	0.238 (0.015)	0.242 (0.021)
Range	0.327–0.387	0.279–0.343	0.296–0.350	0.219–0.264	0.223–0.277
Lo/Lz	10	8	8	8	10
Mean (SD)	0.78 (0.05)	0.78 (0.05)	0.74 (0.005)	0.63 (0.04)	0.65 (0.05)
Range	0.70–0.85	0.65–0.83	0.65–0.79	0.54–0.67	0.55–0.69
Lsc	10	8	8	8	10
Mean (SD)	0.146 (0.014)	0.132 (0.012)	0.133 (0.019)	0.105 (0.007)	0.099 (0.011)
Range	0.130–0.170	0.108–0.140	0.096–0.152	0.097–0.117	0.0740.113
Wsc	10	8	8	8	10
Mean (SD)	0.225 (0.009)	0.148 (0.017)	0.153 (0.020)	0.105 (0.009)	0.085 (0.019)
Range	0.218–0.241	0.133–0.186	0.122–0.189	0.090–0.115	0.053–0.100
Wsc/Lo	10	8	8	8	10
Mean (SD)	0.67 (0.03)	0.49 (0.05)	0.50 (0.05)	0.44 (0.005)	0.34 (0.06)
Range	0.58–0.68	0.43–0.59	0.40–0.54	0.34–0.52	0.24–0.41
Lvib	8	10	8	10	7
Mean (SD)	0152 (0.016)	0.134 (0.011)	0.133 (0.008)	0.120 (0.005)	0.117 (0.007)
Range	0.140–0.187	0.120–0.154	0.121–0.143	0.114–0.128	0.107–0.129
Wvib	8	10	8	10	7
Mean (SD)	0.126 (0.0.17)	0.100 (0.007)	0.109 (0.010)	0.092 (0.007)	0.106 (0.007)
Range	0.115–0.156	0.090–0.110	0.097–0.123	0.085–0.108	0.097–0.119
Lov	10	10	8	8	10
Mean (SD)	0.134 (0.020)	0.145 (0.014)	0.134 (0.016)	0.157 (0.012)	0.150 (0.014)
Range	0.110–0.177	0.129–0.174	0.124–0.176	0.135–0.173	0.127–0.173
Wov	10	10	8	8	10
Mean (SD)	0.176 (0.011)	0.166 (0.007)	0.180 (0.007)	0.156 (0.005)	0.162 (0.013)
Range	0.159–0.193	0.158–0.179	0.171–0.197	0.151–0.165	0.146–0.189

[1] NHMUK 2010.10.6.1, California, USA. [2] MZUSP 532, São Paulo, Brazil. [3] VMNH 10403.0000, Florida, USA.
[4] MNHN 15979, Recife, Brazil. [5] NHMUK 2010.12.6.2, Tortugas, USA.

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

Redescription. Colony erect, highly branched, branches comprising 5–9 zooids. Internodes almost straight, acute bifurcating pattern with new branches directed slightly inward; chitinous joints passing across proximal end of opesia in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, subrectangular, slightly narrower proximally than distally. Oval opesia occupying more than three-fifths of zooidal length; smooth cryptocyst reduced to very narrow strip around opesia. Slender scutum inserted at midline of inner opesial border, branched 3–4 times, with 8–16 (often 10) acute tips and covering most of 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 serrated lateral edge and slightly hooked tip. Frontal avicularia dimorphic: a small frontal avicularium with triangular rostrum; large frontal avicularium with elongate rostrum, 0.213–0.286 mm long, raised and compressed laterally, with deep curved groove directed downward at axis of internode, between adjacent series of autozooids; mandible very long and narrow, lanceolate and curved laterally. 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 transverse to internodal axis, with smooth seta 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. *Cradoscrupocellaria tenuirostris* is distinguished from congeners by its unique frontal avicularia having an elongate rostrum with a lanceolate mandible directed downward along the axis. Osburn's (1950) original description and illustration of this species differ slightly from the specimens described and figured here, including those in the R.C. Osburn Collection at USNM and SBMNH, in having wider vibracular chambers than figured by Osburn (1950, plate 21, fig. 6).

Distribution. Eastern Pacific Ocean: California to Costa Rica.

Descriptions of new taxa

Cradoscrupocellaria atlantica n. sp.

(Fig. 7, Table 2)

Material Examined. *Holotype*: MZUSP 532, L.M. Vieira coll., Araçá, São Sebastião, São Paulo, Brazil, 7 July 2009, 0–1 m (Fig. 7A–D). *Paratypes*: MZUSP 533–535, same data as holotype; MZUSP 536, L.M. Vieira coll., Araçá, São Sebastião, São Paulo, Brazil, 04 November 2009, 0–1 m; MZUSP 537, Praia Grande, São Sebastião, São Paulo, Brazil, 19 April 2010, 0–2 m. *Additional material*. MZUSP 538, L.M. Vieira & K.H. Fehlauer-Ale coll., 25°34'26" S, 48°19'07" W, Encantadas, Ilha do Mel, Paraná, Brazil, 16 November 2009, 0–1 m; MZUSP 539–540, L.M. Vieira & K.H. Fehlauer-Ale coll., 25°33'51" S, 48°19'00" W, Pontinha, Ilha do Mel, Paraná, Brazil, 14–15 November 2009, 0–1 m; VMNH 10403.0000 (Fig. 7E–F), *Scrupocellaria bertholleti*, J.E. Winston coll., 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 coll., Coon Island, North Beach, Fort Pierce, St Lucie County, Florida, USA, 3 July 1998; VMNH 11036.0000, *Scrupocellaria bertholleti*, J.E. Winston coll., Walton Rocks, South Hutchinson Island, St Lucie County, Florida, USA, 19 February 1999, intertidal; VMNH 11058.0000, *Scrupocellaria bertholleti*, J.E. Winston coll., 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 coll., 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 coll., Johnson Seagrass bed, HBO1, Fort Pierce, St Lucie County, Florida, USA, 7 April 1999; VMNH 11952.0000, *Scrupocellaria bertholleti*, J.E. Winston & N. Tuross coll., E. side of North Beach bridge, Route A1A, Indian River, Fort Pierce, St Lucie County, Florida, USA, 10 April 2000; VMNH 12717.0000, *Scrupocellaria bertholleti*,

J.E. Winston coll., 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 coll., North Beach, south side of inlet, Fort Pierce, St Lucie County, Florida, USA, 30 June 2001, intertidal; VMNH 13143.0001, *Scrupocellaria bertholleti*, J.E. Winston coll., off South Beach, *Mellita* site #1, Fort Pierce, St Lucie County, Florida, USA, 31 July 2002, 6 m, dredge; VMNH 13303.0000, *Scrupocellaria bertholleti*, J.E. Winston coll., 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 coll., Fort Pierce Inlet, S. side beach near Historical Museum, beach drift, 14 July 2003, on drift plastic.

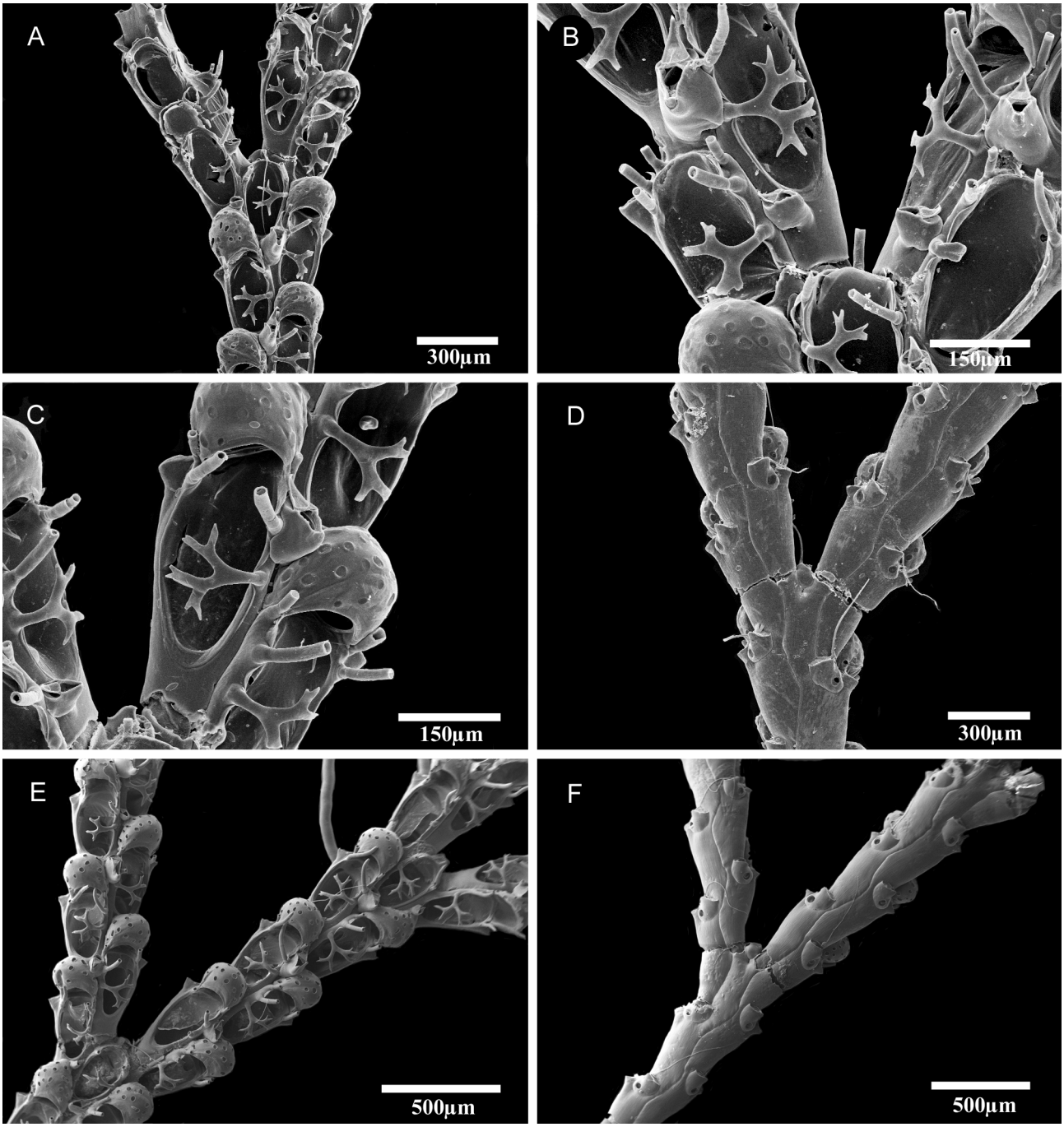

FIGURE 7. *Cradoscrupocellaria atlantica* **n. sp.** A–D, MZUSP (uncatalogued specimen), part of holotype, São Paulo, Brazil. E–F, VMNH 10403.0000, Florida. A, Frontal surface of branch bifurcation. B, Close-up of branch bifurcation; note the presence of three distal spines in the axial zooid. C, Close-up of ovicelled zooid; note the small lateral and frontal avicularia. D, Abfrontal surface of branch bifurcation. E, Frontal surface of colony; note ovicelled zooids and the variation in size of the frontal avicularia. F, Abfrontal surface of colony.

Type locality. São Paulo, Brazil.

Etymology. The specific name *atlantica* refers to the occurrence of this species on the Western Atlantic coast.

Diagnosis. Chitinous joints passing across opesia in outer zooids at bifurcation (zooids C and D); opesia covering almost entire frontal surface; 2 inner and 2–3 outer distal spines, only 3 distal spines in axial zooid; scutum flattened, regularly branched 3 times, occupying two thirds of frontal membrane; small distolateral avicularium on each zooid; ooecium with regularly spaced rounded pseudopores.

Description. Colony erect, branches with 5–9 zooids. Lateral edge of internodes almost straight; chitinous joints passing across opesia in outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids almost elongate, slightly tapering proximally, with smooth proximal gymnocyst. Oval opesia occupying almost entire zooidal length, cryptocyst narrower laterally than proximally, sometimes inconspicuous. Scutum branched 3 times, with 5–8 acute tips, inserted at midline of inner opesial border and occupying two thirds of entire 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. Vibracular chamber proximally on basal surface of each zooid, inconspicuous in frontal view; setal groove transverse to internode axis, straight, with smooth seta 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 colony. Ovicell hemispherical, with 15–22 rounded and regularly spaced pseudopores; ovicelled zooids with 2 outer and 2 inner distal spines.

Remarks. Ramalho (2006) noted differences between British *Cradoscrupocellaria reptans* and Rio de Janeiro specimens assigned to *Scrupocellaria* aff. *reptans* in the the position of the lateral avicularia, directed laterally in specimens from Brazil and distolaterally directed and often obscured by outer oral spines, in *C. reptans*. These specimens, as well other colonies collected in Brazil, here reassigned to *Cradoscrupocellaria atlantica* **n. sp.**, are also distinguished by the branching pattern of the scuta and the presence of smooth rhizoids. *Cradoscrupocellaria atlantica* is commonly found on algae and drift plastic in south–southeastern Brazil. The specimens from Florida previously identified as *Scrupocellaria bertholletii* (Fig. 7E–F; J.E. Winston, unpubl. data) are similar to those here described as *C. atlantica* in the number of oral spines, shape of scuta, and position and size of basal vibracula. The gigantic avicularia in Floridan specimens are, however, often present on zooids at the internode, while they are present on axial zooids in Brazilian colonies. Despite small differences in the position of the gigantic frontal avicularia between USA and Brazilian specimens, we assign specimens from Florida and Brazil to *C. atlantica* because of the chitinous joints passing across the opesia in outer zooids at the bifurcation, 4–5 distal spines in each zooid (except axial zooids, characterized by 3 distal spines), shape of scutum, a distolateral avicularium and the shape of the frontal avicularia.

Cradoscrupocellaria atlantica **n. sp.** is similar to two Pacific species, *C. gorgonensis* **n. sp.** and *C. osburni* **n. sp.**, in the position of the joints at the bifurcation, the shape of the frontal scutum and the presence of a distolateral avicularium on each zooid. *Cradoscrupocellaria atlantica* **n. sp.** is distinguished by its 5 distal spines, smaller basal vibraculum compared to *C. gorgonensis* **n. sp.** and *C. osburni* **n. sp.** and the shape and position of the frontal avicularia.

Distribution. Atlantic Ocean: USA (Florida) and Brazil (Rio de Janeiro, São Paulo and Paraná states); 0–7 m.

Cradoscrupocellaria calypso n. sp.

(Fig. 8, Table 2)

Material examined. *Holotype*. MNHN 15979 (Fig. 8), *Scrupocellaria* sp., RV *Calypso*, Station 29, Recife, Brazil, 8°28’ S, 34°55’ W, 21 November 1961, 22–30 m. *Paratypes*. NHMUK 2013.4.10.1, RV ‘Calypso’, Station 29, Recife, Brazil, 8°28’S, 34°55’W, 21 November 1961, 22–30 m. *Additional material*. USNM 559195. United States Exploring Expedition, Rio de Janeiro, Brazil.

Type locality. Recife, Pernambuco, Brazil.

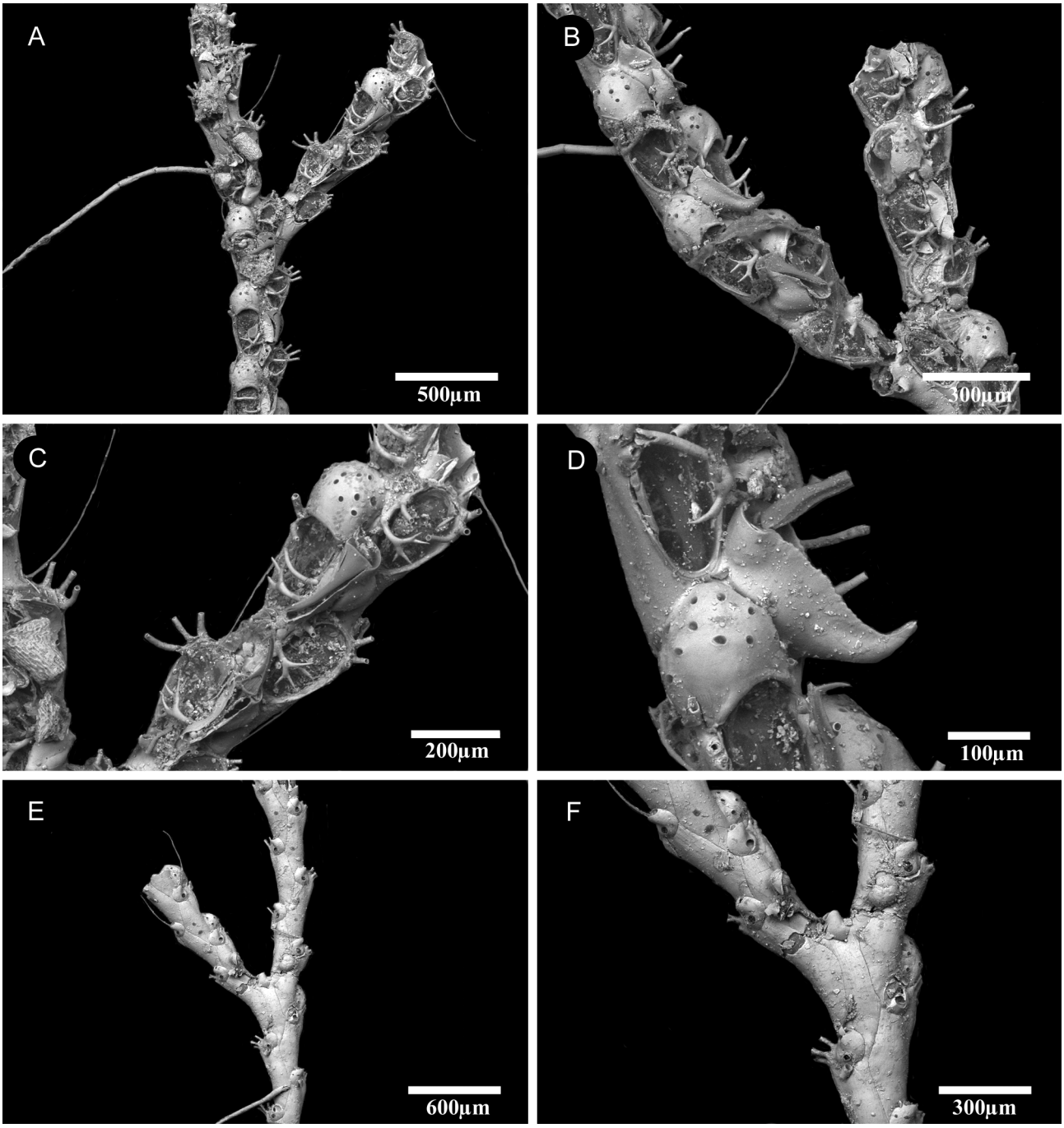

FIGURE 8. *Cradoscrupocellaria calypso* **n. sp.** A–F, MNHN 15979, holotype, Recife, Brazil. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the dimorphic frontal avicularia. C, Close-up of branches; note the absence of lateral avicularia, the gigantic frontal avicularia 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.

Etymology. Noun in apposition based on RV *Calypso*.

Diagnosis. Chitinous joints passing across proximal end of opesia in outer zooids at 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 zooidal length; scutum slender, regularly branched twice, occupying half length of opesial membrane; distolateral avicularia absent; frontal avicularia dimorphic; very large and elongate avicularia often present, lanceolate, with curved, serrated rostrum.

Description. Colony erect, with branches of 5–11 zooids. Internodes slightly curved, with acutely bifurcating pattern; chitinous joints passing across proximal end of opesia of outer zooids at bifurcation (zooids C and D) and

across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to two thirds of zooidal length; cryptocyst minimal and deep around opesia. Scutum inserted at midline of inner opesial border, regularly branched twice at 50–80°, with acute tips, extending past midline of frontal membrane. Distal spines delicate, long, unbranched; 2 inner and 3 outer, 1 median distal spine rarely present; proximalmost 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, with curved tip; mandible long, curved, its tip hooked. 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 transverse to internode axis, straight, with smooth seta 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. *Cradoscrupocellaria calypso* **n. sp.** is similar to four Atlantic species, *C. curacaoensis*, *C. floridana* **n. sp.**, *C. jamaicensis* **n. sp.** and *C. normani* **n. sp.**, in the position of the joints, the slender scutum and the absence of distolateral avicularia. *Cradoscrupocellaria calypso* is distinguished by the presence of the very long dimorphic frontal avicularium and the regular twice- bifurcated, acute-tipped scutum.

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

Cradoscrupocellaria floridana n. sp.

(Fig. 9, Table 2)

Scrupocellaria bertholletii Audouin: Osburn 1940: 386 (in part). [Tortugas]
Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material examined. *Holotype*: NHMUK 2010.12.6.2 (Fig. 9), *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 (~4 m), Tortugas, Florida, USA.

Type locality. Tortugas, Florida, USA.

Etymology. Alluding to the type locality (Florida).

Diagnosis. Chitinous joints passing across proximal end of opesia in outer zooids at bifurcation (zooids C and D); 2 inner and 2–3 outer distal spines; scutum forked, rarely trifurcated, often bifurcating at its tip, tines very acute; distolateral avicularia absent; vibracular chamber small, rounded; rhizoid with retroussé hooks; ooecium with rounded pseudopores with raised edges.

Description. Colony erect, with branches of 3–11 zooids. Internodes slightly curved, with acute bifurcating pattern; chitinous joints passing across proximal end of opesia in outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, tapering proximally and slightly curved laterally. Oval opesia occupying distal half of zooidal length; inconspicuous cryptocyst around opesia. Scutum bifurcating at 60–90°, rarely trifurcated, extending beyond midline of frontal membrane, often bifurcating at its tips, inserted at midline of inner opesial border. Distal spines short, unbranched; 2 inner and 2–3 outer, rarely 1 median distal spine; proximalmost 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. 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 transverse to internode axis, straight, with smooth seta 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. *Cradoscrupocellaria floridana* resembles *C. calypso* **n. sp.**, *C. curacaoensis*, *C. jamaicensis* **n. sp.**

and *C. normani* **n. sp.** in having zooids without distolateral avicularia, but differs in possessing a bifurcated scutum with forked distal tips, robust dimorphic avicularium and ovicells with rounded pseudopores with raised edges.

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

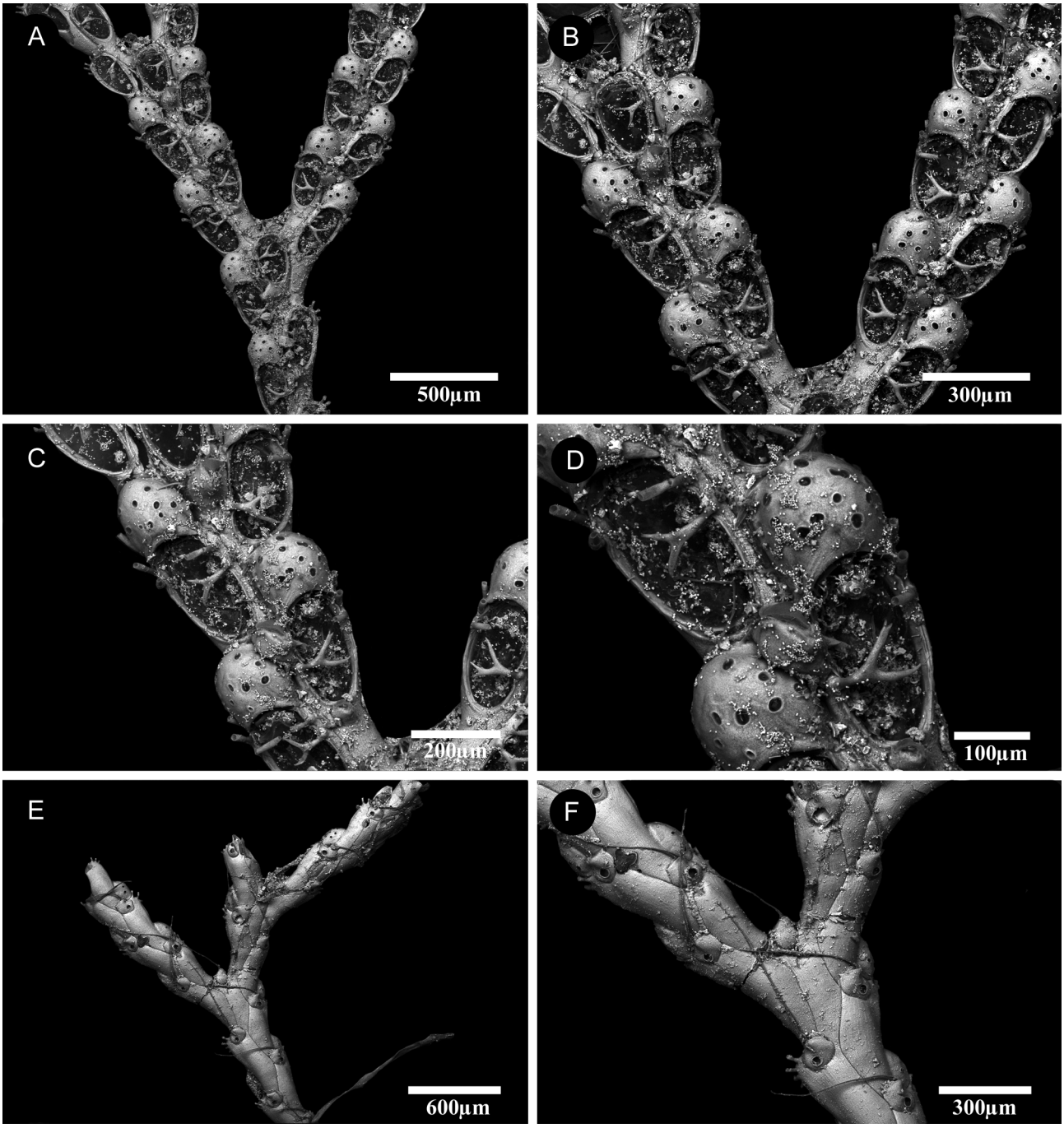

FIGURE 9. *Cradoscrupocellaria floridana* **n. sp.** A–F, NHMUK 2010.12.6.2, holotype, Florida. A, Frontal surface of colony. B, Frontal surface of branches with ovicelled zooids. C, Close-up of a branch; note the dimorphic frontal avicularia and the ooecia with pores having raised edges. D, Close-up of ovicelled zooid and one frontal avicularium; note the forked scutum with forked, acute tips. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Cradoscrupocellaria galapagensis n. sp.

(Fig. 10, Table 3)

Scrupocellaria bertholletii (Audouin): Hastings 1930: 703 (in part), pl. 1, fig. 3 (non figs 1, 2, 4, 5). [Galapagos Islands]
Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

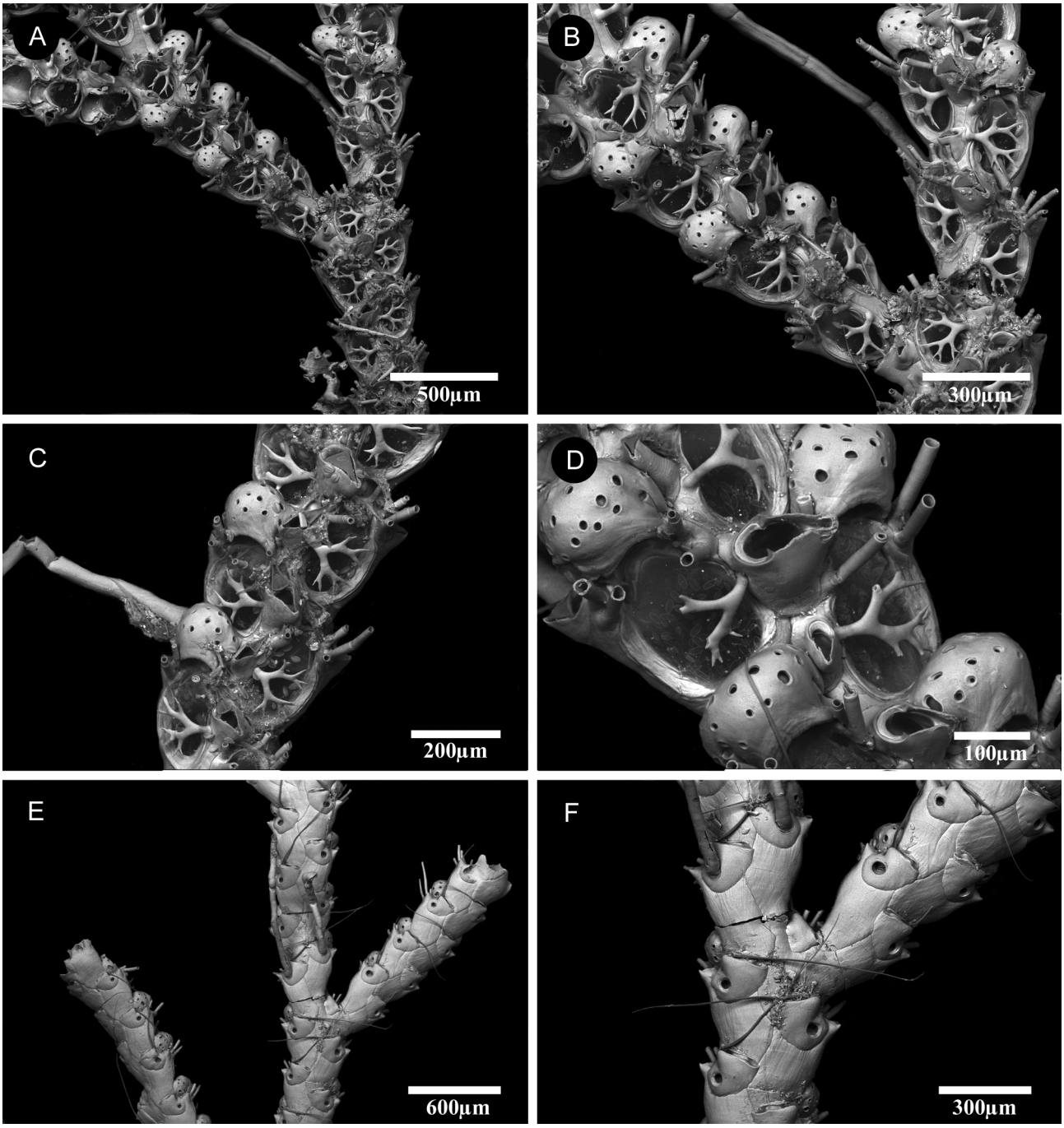

FIGURE 10. *Cradoscrupocellaria galapagensis* **n. sp.** A–F, NHMUK 2010.12.6.3, holotype, Galapagos. A, Frontal surface of colony. B, Frontal surface of branch bifurcation with ovicelled zooids. C, Close-up of a branch; note two ovicelled zooids at left. D, Close-up of ovicelled zooids; note the wide periopesial cryptocyst and dimorphic frontal avicularia. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Material examined. *Holotype*. NHMUK 2010.12.6.3 (Fig. 10), *Scrupocellaria bertholletii*, A.B. Hastings det., 25 July1924, 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 (22 m).

Type locality. Galapagos Islands.

Etymology. Alluding to the type locality.

TABLE 3. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. galapagensis Galapagos[1]	*C. gorgonensis* Gorgona[2]	*C. hastingsae* Galapagos[3]	*C. insularis* Cape Verde[4]	*C. jamaicensis* Jamaica[5]
Lz	10	10	10	10	10
Mean (SD)	0.316 (0.016)	0.354 (0.023)	0.420 (0.030)	0.368 (0.026)	0.421 (0.039)
Range	0.283–0.337	0.328–0.400	0.374–0.453	0.338–0.425	0.369–0.494
Wz	10	10	10	10	10
Mean (SD)	0.190 (0.016)	0.156 (0.012)	0.206 (0.014)	0.155 (0.012)	0.166 (0.012)
Range	0.168–0.215	0.141–0.173	0.180–0.228	0.143–0.180	0.144–0.178
Lo	10	10	10	10	10
Mean (SD)	0.253 (0.013)	0.243 (0.022)	0.307 (0.020)	0.247 (0.018)	0.253 (0.015)
Range	0.230–0.273	0.223–0.286	0.272–0.344	0.208–0.276	0.222–0.268
Lo/Lz	10	10	10	10	10
Mean (SD)	0.81 (0.04)	0.69 (0.04)	0.75 (0.04)	0.66 (0.04)	0.55 (0.04)
Range	0.73–0.86	0.63–0.74	0.69–0.80	0.61–0.74	0.53–0.66
Lsc	10	10	-	10	-
Mean (SD)	0.138 (0.009)	0.107 (0.011)	-	0.97 (0.004)	-
Range	0.128–0.158	0.086–0.126	-	0.90–0.105	-
Wsc	10	10	-	10	-
Mean (SD)	0.162 (0.011)	0.109 (0.023)	-	0.074 (0.016)	-
Range	0.148–0.183	0.085–0.152	-	0.061–0.105	-
Wsc/Lo	10	10	-	10	-
Mean (SD)	0.64 (0.004)	0.47 (0.07)	-	0.32 (0.07)	-
Range	0.58–0.72	0.35–0.57	-	0.24–0.45	-
Lvib	10	10	8	10	7
Mean (SD)	0.160 (0.014)	0.144 (0.007)	0.145 (0.009)	0.134 (0.015)	0.126 (0.014)
Range	0.128–0.174	0.129–0.152	0.136–0.162	0.110–0.163	0.101–0.144
Wvib	10	10	8	10	7
Mean (SD)	0.149 (0.012)	0.118 (0.010)	0.120 (0.013)	0.111 (0.011)	0.101 (0.012)
Range	0.130–0.169	0.105–0.134	0.096–0.134	0.100–0.130	0.087–0.118
Lov	6	10	10	7	10
Mean (SD)	0.145 (0.011)	0.140 (0.015)	0.183 (0.012)	0.152 (0.007)	0.183 (0.015)
Range	0.131–0.164	0.131–0.177	0.163–0.201	0.145–0.168	0.166–0.217
Lov	6	10	10	7	10
Mean (SD)	0.155 (0.013)	0.162 (0.015)	0.198 (0.013)	0.159 (0.013)	0.161 (0.009)
Range	0.138–0.172	0.142–0.184	0.170–0.206	0.153–0.189	0.140–0.173

[1] NHMUK 2010.12.6.3, Galapagos.[2] NHMUK 2010.12.6.4, Gorgona, Colombia.[3] NHMUK 1929.4.26.25, Galapagos.[4] NHMUK 2010.12.6.16, Cape Verde.[5] AMNH (Unregistered specimens), same data as holotype, Jamaica.

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

Description. Colony erect, highly branched, with branches of 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 passing across proximal end of opesia and cryptocyst in outer zooids at bifurcation

(zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, subrectangular, slightly narrower proximally than distally. Oval opesia occupying almost entire zooid length; cryptocyst smooth, deep, forming a wide and conspicuous strip around opesia. Scutum slender, inserted at midline of inner opesial border, branched 3–4 times with 8–15 (often 8–10) acute points, covering almost entire 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, oblique to axis. A vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; vibraculum trapezoidal, occupying a third of basal surface, with rhizoidal foramen on its proximal outer corner; setal groove transverse to internode axis, with smooth seta twice 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 the Pacific (Gorgona Island and Galapagos) and noted variable morphology among the specimens. Despite the differences noted by her—scuta, frontal avicularia and zooid shape—the Pacific specimens have shared characteristics, such as the shape and size of the basal vibraculum, lateral avicularium and ovicells. Among Hastings's specimens deposited at NHMUK were three distinct species: specimens with highly branched scuta (specimen 36D, from Galapagos, see Hastings 1930, p. 703) are described as *Cradoscrupocellaria galapagensis* **n. sp.** (Fig. 10), while specimens with slender zooids and less-branched scuta, from Gorgona and Galapagos, comprise two distinct species, *Cradoscrupocellaria gorgonensis* **n. sp.** (see below, Fig. 11), with the scutum bifurcated twice, and *Cradoscrupocellaria hastingsae* **n. sp.** (see below, Fig. 12), with forked scutum (sometimes absent) and robust dimorphic avicularia.

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

Cradoscrupocellaria gorgonensis n. sp.

(Fig. 11, Table 3)

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 (Fig. 11), *Scrupocellaria bertholletii*, A.B. Hastings det., St. George Collection, Gorgona 3, Specimen 15D. *Paratypes*. NHMUK 1929.4.26.19, same data as holotype. NHMUK 2010.12.6.5, same data as holotype. NHMUK 2010.12.6.6, same data as holotype. NHMUK 2010.12.6.7, same data as holotype. *Additional specimens*. NHMUK 1929.4.26.18, same data as holotype. NHMUK 1929.4.26.18pt, same data as holotype. USNM 559196, *Scrupocellaria bertholletii*, Panama, (Lot 124 Museum of Comparative Zoology).

Type locality. Gorgona, Colombia.

Etymology. Alluding to the type locality.

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

Description. Colony erect, highly branched, branches of 5–9 zooids. Internodes with alternating zooids, slightly back to back, pattern acutely bifurcating; chitinous joints passing across opesia in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, subrectangular, slightly tapering proximally. Oval opesia occupying distal two thirds of zooid length; crytptocyst smooth, deep, forming strip around opesia. Scutum slender, inserted at midline of inner opesial border, branched twice and with acute tips, covering less than half 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 outer spines and ovicells; rostrum triangular, with serrated lateral edge and slightly hooked tip.

Variably sized frontal avicularium present in outer zooids along internodes, with triangular curved rostrum and mandible, directed obliquely forward and downward. Vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, occupying one quarter of basal surface, with rhizoidal foramen on its proximal outer corner; setal groove transverse to internode axis, with smooth seta twice autozooid length. Single, near-triangular axial vibraculum, without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells globular, with ectooecium perforated by several rounded pores linked by internal sutures; ovicelled zooids with 2 inner and 3 outer spines.

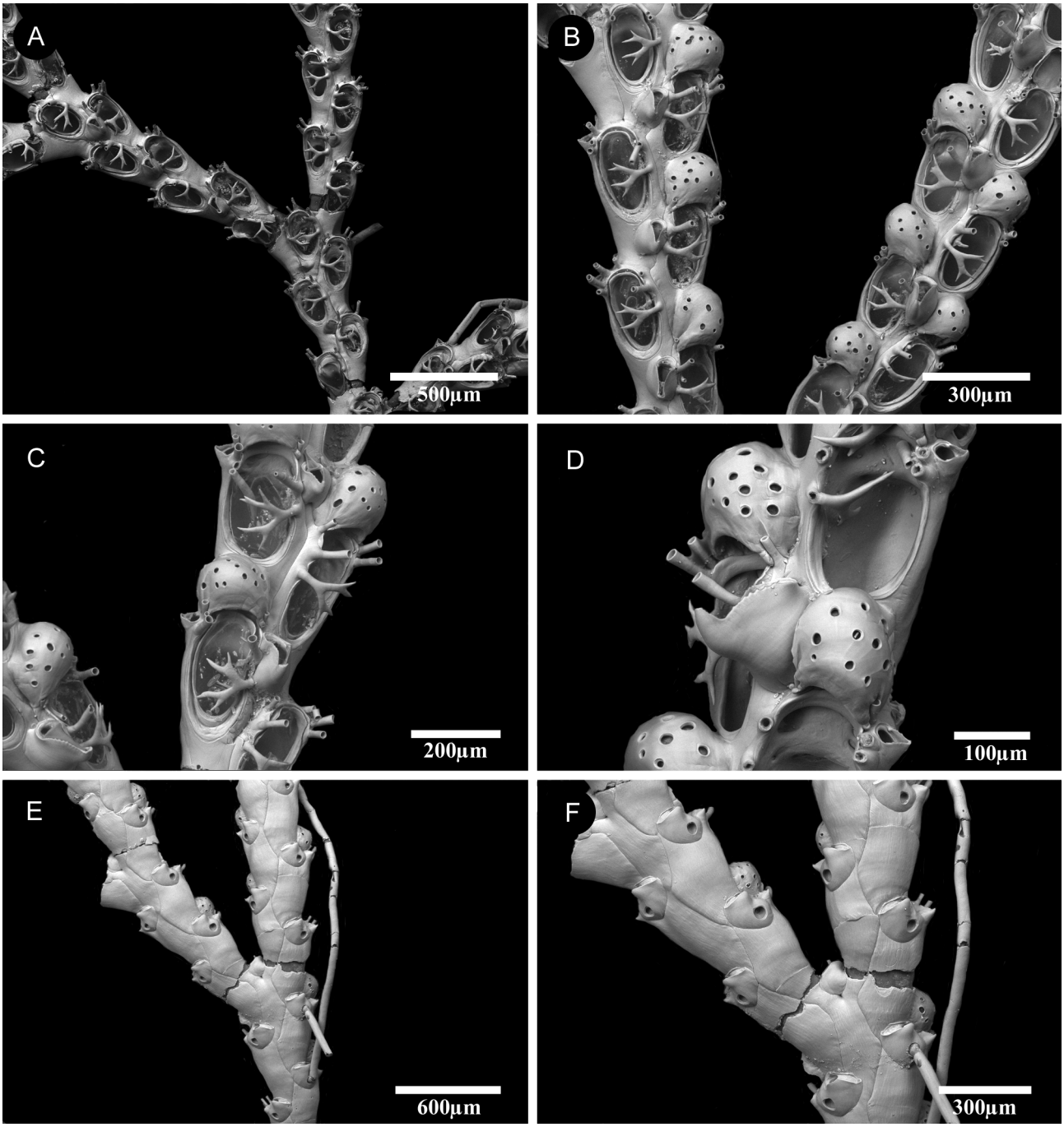

FIGURE 11. *Cradoscrupocellaria gorgonensis* **n. sp.** A–F, NHMUK 2010.12.6.4, holotype, Gorgona. A, Frontal surface of colony. B, Frontal surface of two branches with ovicelled zooids. C, Close-up of a branch; note the frontal avicularium with curved rostrum. D, Close-up of frontal avicularium; note the serrated rostrum, hooked distally. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Remarks. Part of Hasting's (1930) specimens are identified here as *Cradoscrupocellaria gorgonensis* **n. sp.**, which resembles *C. hastingsae* **n. sp.** in its overall appearance, but differs in the shape of the frontal scutum—twice-bifurcating in *C. gorgonensis* (Fig. 11C) and forked in *C. hastingsae* (Fig. 12C)—and the shape and size of the frontal and distolateral avicularia.

Distribution. Pacific Ocean: Gorgona Island, Colombia.

Cradoscrupocellaria hastingsae n. sp.

(Fig. 12, Table 3)

Scrupocellaria bertholletii Audouin: Hastings 1930: 703 (in part), pl. 1, figs 1, 2, 4, 5 (non pl. 1, fig. 3). [Galapagos Islands]
Not *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

Material examined. *Holotype*. NHMUK 2010.12.6.8 (Fig. 12), *Scrupocellaria bertholletii*, A.B. Hastings det., St George Collection, Galapagos 9, Specimen 31F, Tagus Cove, Albemarle Island, Galapagos. *Paratypes*: NHMUK 1929.4.26.244, data as for holotype, but Specimen 8E (figured by Hastings 1930: pl. 1, figs 2, 4, 5). NHMUK 1929.4.26.25, same data as holotype, but Specimen $31F^{1}$. NHMUK 2010.12.6.9–12, same data as holotype. NHMUK 2010.12.6.13, same data as holotype, but Specimen $31F^{1}$. NHMUK 2010.12.6.14, same data as holotype, but Specimen $31F^{2}$. NHMUK 2010.12.6.15, same data as 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 Islands.

Etymology. Honorific for the late British bryozoologist Anna Birchall Hastings (1902–1977).

Diagnosis. Chitinous joints passing across opesia in outer zooids at 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 aquiline frontal avicularium with elongate base, triangular mandible directed forward; ooecium globular, with several rounded pseudopores.

Description. Colony erect, branches comprising 5–11 zooids. Internodes with alternating zooids, slightly back to back; acute bifurcating pattern; chitinous joints passing across opesia in outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, almost rectangular, slightly tapering proximally. Oval opesia occupying three quarters of zooid length; cryptocyst smooth, wide and deep around opesia. Slender scutum sometimes present, inserted at midline or slightly distally at inner opesial border, bifurcated (rarely trifurcated), with acute 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. Vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, occupying a quarter of basal surface, with a large rhizoidal foramen on its proximal outer corner; setal groove transverse to internode axis, with smooth seta as long as an autozooid. Single axial vibraculum almost trapezoidal, without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells globular, more 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. A portion of the specimens from the Galapagos Islands identified as *Scrupocellaria bertholletii* by Hastings (1930) are here assigned to *C. hastingsae* **n. sp.** The second species from Galapagos, *C. galapagensis* **n. sp.**, is distinguished from *C. hastingsae* **n. sp.** by its highly branched scutum, a wider basal vibraculum and the shape and position of the frontal avicularia.

Distribution. Pacific Ocean: Tagus Cove, Galapagos Islands.

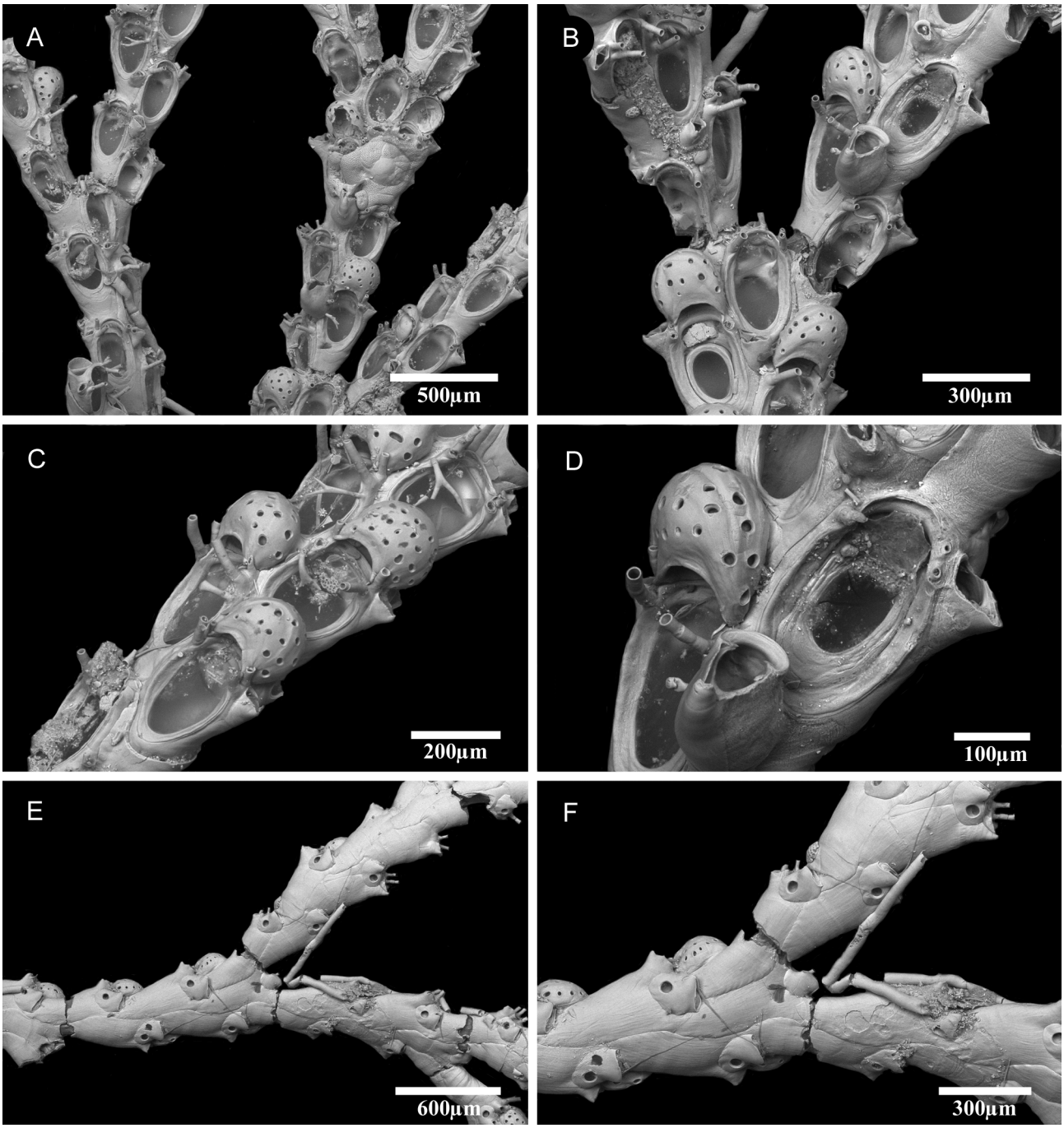

FIGURE 12. *Cradoscrupocellaria hastingsae* **n. sp.** A–F, NHMUK 2010.12.6.8, holotype, Galapagos. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the joints passing across opesia in outer zooids at bifurcation. C, Close-up of a branch; note one zooid without scutum and three distalmost zooids with forked scutum. D, Close-up of zooid; note the absence of a scutum and the gigantic frontal avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Cradoscrupocellaria insularis **n. sp.**

(Fig. 13, Table 3)

Scrupocellaria bertholletii Audouin: Kluge 1914: 616, text-fig. 6. [Cape Verde]
Scrupocellaria bertholletii Audouin: Waters 1918: 5. [Cape Verde]
Non *Acamarchis Bertholletii* Audouin, 1826: 241. [Egypt]

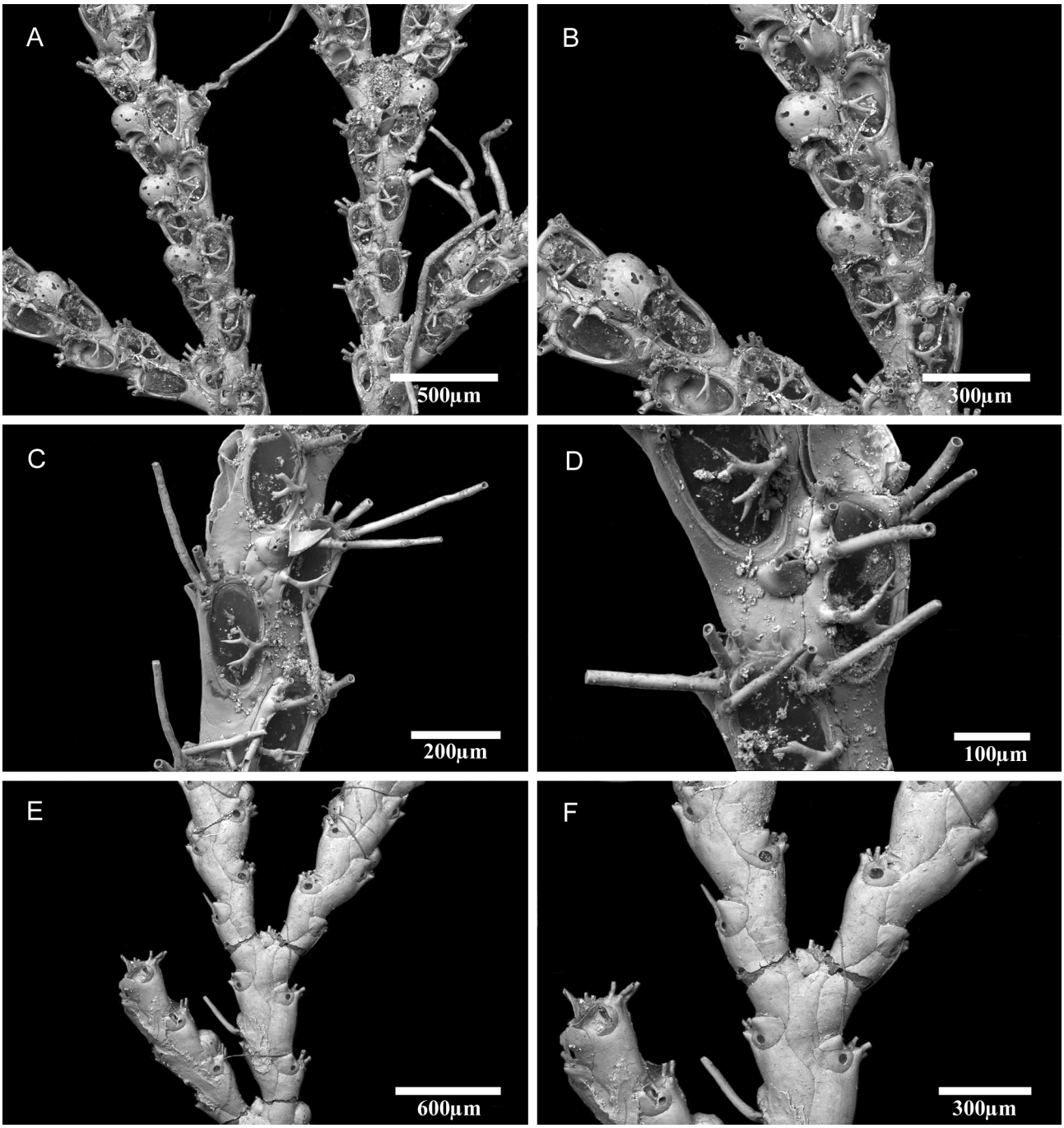

FIGURE 13. *Cradoscrupocellaria insularis* **n. sp.** A–B, E–F, NHMUK 2010.12.6.16, holotype, Cape Verde. C–D, NHMUK 1899.7.1.837, paratype, Cape Verde. A, Frontal surface of colony. B, Frontal surface of branch with ovicelled zooids. C, Close-up of a branch; note the small distolateral avicularium and the scutum occupying less than half the opesial length. D, Close-up of small frontal avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Material examined. *Holotype*. NHMUK 2010.12.6.16 (Fig. 13A–B, E–F), *Scrupocellaria bertholletii*, C. Crossland Collection, St Vicente, Cape Verde. *Paratypes*. NHMUK 1899.7.1.837 (Fig. 13C–D), *Canda bertholletii*, G. Busk det., G. Busk Collection, St Vicente, Cape Verde. NHMUK 2010.10.1.7, same data as holotype. NHMUK 2010.10.1.8, *Scrupocellaria bertholletii*, St Vicente, Cape Verde. *Additional specimens*. NHMUK 1899.7.1.821, *Scrupocellaria bertholletii*, G. Busk det., G. Busk Collection, 1857, Madeira.

Type locality. Cape Verde Island.

Etymology. Latin *insularis*, "of islands", alluding to the occurrence of this species around two Atlantic oceanic island groups.

Diagnosis. Chitinous joints passing across opesia in outer zooids at bifurcation (zooids C and D); zooids with 7 long and regularly spaced distal spines; scutum slender, branched twice (rarely bifurcating at tip), with 4–7 acute 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 pseudopores.

Description. Colony erect, branched, with branches comprising 5–9 (often 7) zooids. Internodes with biserial alternating zooids with curved outlines; chitinous joints passing across the opesia in outer zooids at the bifurcation (zooids C and D) and across the proximal gymnocyst of inner zooids (F and G). Autozooids elongate, subrectangular, slightly narrower proximally than distally. Oval opesia occupying two thirds of zooidal length; cryptocyst smooth, forming a conspicuous strip around opesia, often better developed proximally than laterally. Scutum slender, inserted at midline of inner opesial border, branched twice with acute points, rarely bifurcated at its tips, overarching to midline of opesia. Distal spines straight and long, unbranched; 7 regularly spaced distal spines; axial zooid with 7 spines; proximalmost 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 serrated lateral edge. Frontal avicularia dimorphic: a small frontal avicularium with triangular rostrum and mandible, obliquely directed downward; a large frontal avicularium with aquiline rostrum, directed forward and slightly downward, mandible triangular, slightly curved. Vibracular chamber present on 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 transverse to internode axis, with smooth seta as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells globular, with ectooecium perforated by 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 collected by Cyril Crossland and specimens from the Mediterranean. These island specimens, here described as *C. insularis* **n. sp.**, are characterized by zooids with 7 long and regularly spaced distal spines, the distinctive shape of the branched scutum and the size and position of the distolateral avicularia. The specimens reported from Cape Verde by Kluge (1914) also belong to *C. insularis*.

Distribution. Atlantic Ocean: Madeira and Cape Verde.

***Cradoscrupocellaria jamaicensis* n. sp.**
(Fig. 14, Table 3)

Material examined. *Holotype*. AMNH 1522.1, *Scrupocellaria* sp., J.E. Winston det., Rio Bueno, Jamaica, 10 m, 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.

Etymology. Alluding to the type locality.

Diagnosis. Chitinous joints passing across proximal end of opesia in outer zooids at 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, covering a small part of frontal membrane; distolateral avicularium absent; dimorphic frontal avicularium elongate, longer than wide, almost lanceolate; vibracular chamber almost rounded, small; ooecium longer than wide, with raised pseudopores.

Description. Colony erect, branches comprising 5–11 zooids. Internodes with biserial zooids in alternating series; chitinous joints passing across proximal end of opesia (rarely below it) in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate with tapering proximal gymnocyst. Oval opesia occupying distal half of zooid length; cryptocyst very narrow, inconspicuous around opesia. Scutum often present, bifurcated or rarely trifurcated, inserted at midline of inner opesial border and extending beyond midline of frontal membrane. Distal spines long, unbranched, delicate; 1–2 inner and 2–3 outer distal spines, rarely 1 median distal spine; proximalmost inner and outer spines directed forward; axial zooid with 5 spines. Distolateral avicularium absent. Frontal avicularia dimorphic: a small frontal avicularium with triangular

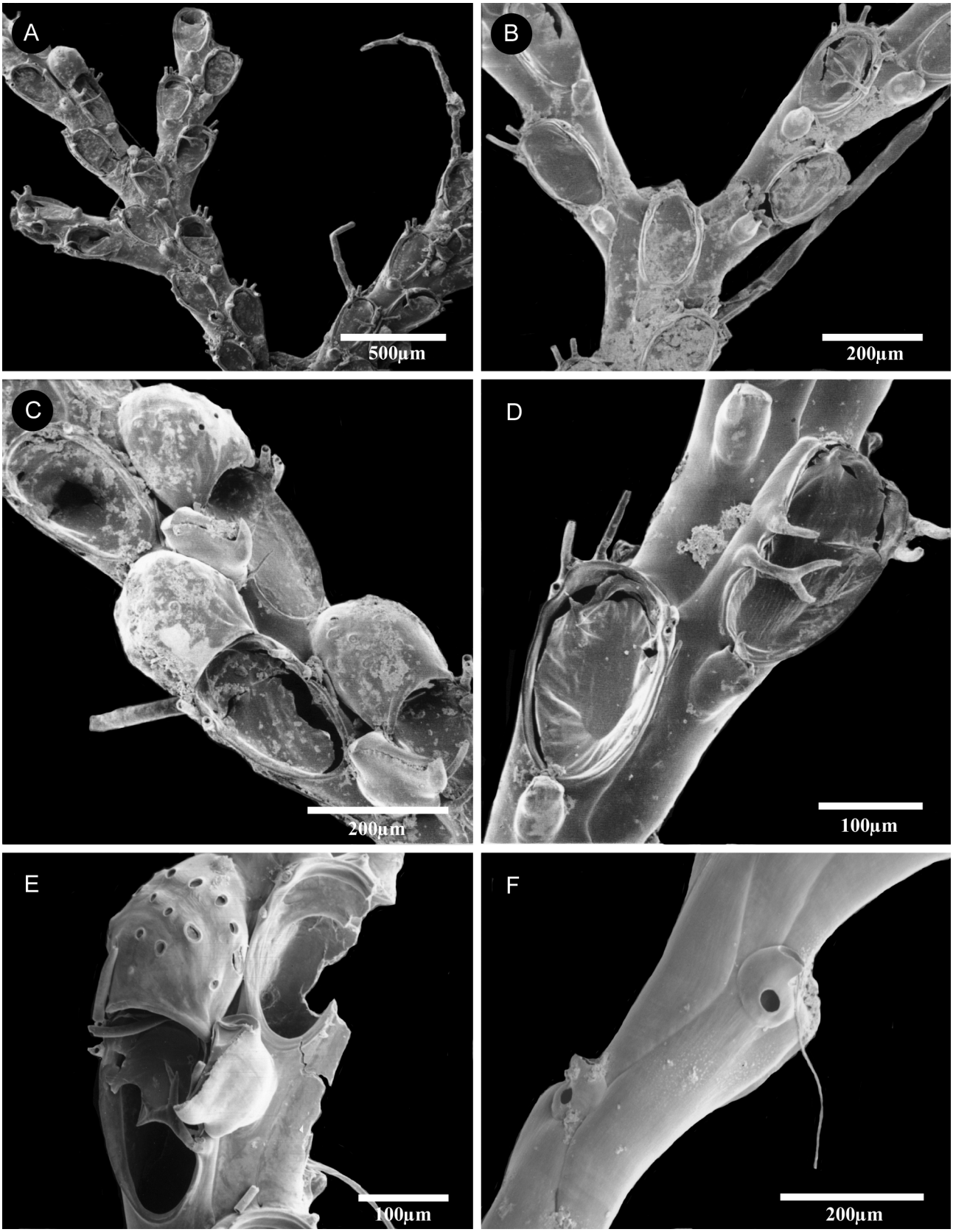

FIGURE 14. *Cradoscrupocellaria jamaicensis* **n. sp.** A–F, Uncatalogued specimen from Rio Bueno, Jamaica (type locality). A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note a zooid with trifurcated scutum at upper right. C, Close-up of a branch with ovicelled zooids. D, Close-up of two zooids; note the presence of a forked scutum in the zooid at right of the branch. E, Close-up of ovicelled zooid and one gigantic frontal avicularium. F, Abfrontal surface of branch.

mandible, directed forward; large frontal avicularium sometimes present, 0.155–0.190 mm long, with elongate downward-directed rostrum close to adjacent zooid, its edge serrated, mandible lanceolate, hooked distally. Vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber almost circular, occupying a small part of basal area, with large rhizoidal foramen on its proximal outer corner; setal groove short, transverse to internode axis, straight, with smooth seta as long as one autozooid. Single axial vibraculum without rhizoid foramen. Rhizoids tubular, with some well-spaced retroussé hooks. Ovicells longer than wide, with raised and striate transverse bands of raised pseudopores; 2 inner and 3 outer distal spines in ovicelled zooids.

Remarks. *Cradoscrupocellaria jamaicensis* **n. sp.** resembles *C. calypso* **n. sp.**, *C. curacaoensis* and *C. floridana* **n. sp.** in lacking distolateral avicularia but differs in the shape of the dimorphic frontal avicularium and scutum.

Distribution. Caribbean: Jamaica.

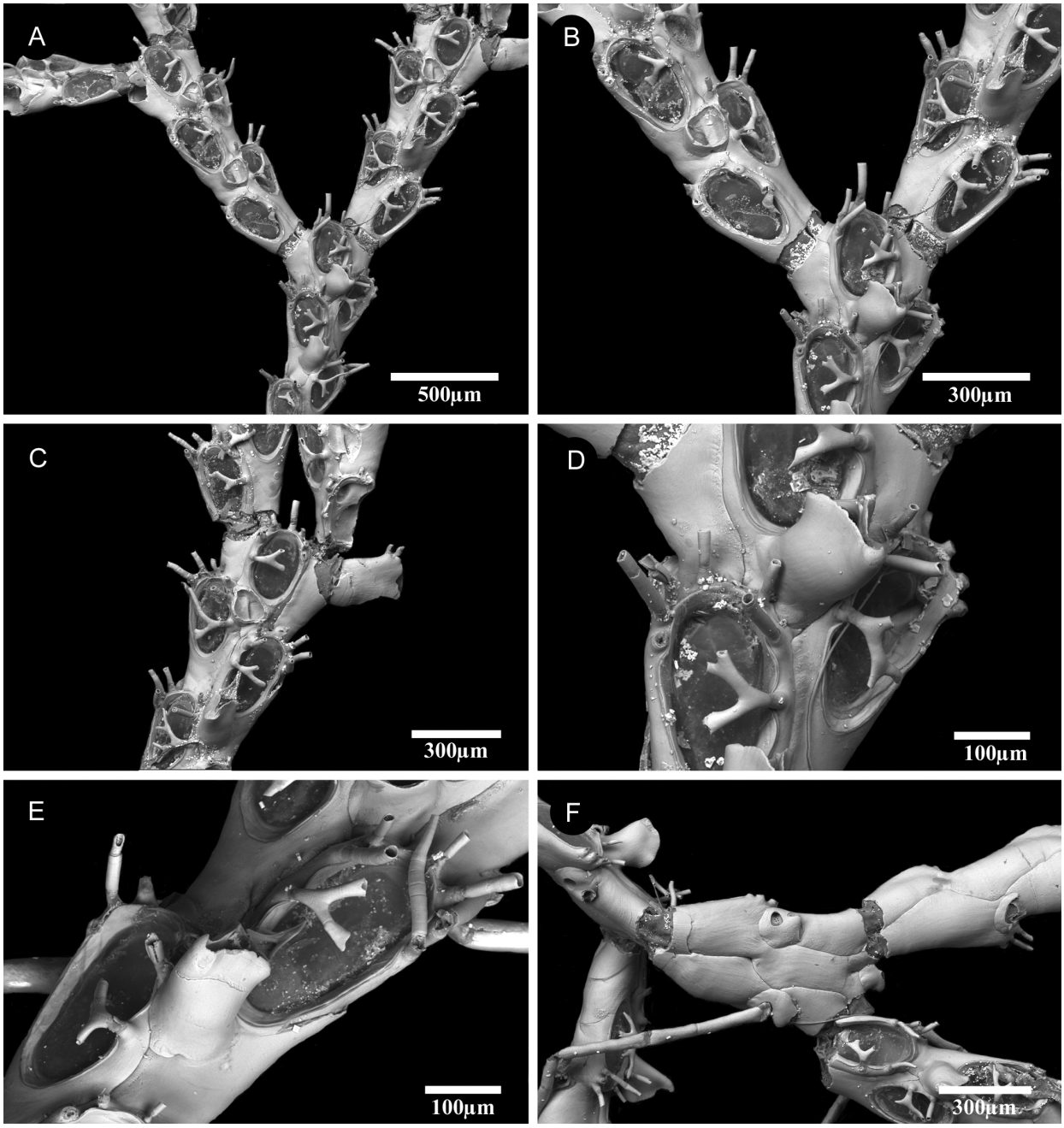

FIGURE 15. *Cradoscrupocellaria lagaaiji* **n. sp.** A–F, NHMUK 1975.7.18.31, holotype, France, Mediterranean. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the gigantic frontal avicularium on the axial zooid. C, Close-up of a branch bifurcation; note the absence of a lateral avicularium. D, Close-up of a gigantic frontal avicularium. E, Close-up of a zooid; note the gigantic frontal avicularium and presence of six distal spines. F, Abfrontal surface of branch.

***Cradoscrupocellaria lagaaiji* n. sp.**
(Fig. 15, Table 4)

Material examined. *Holotype*. NHMUK 1975.7.18.31 (Fig. 15), *Scrupocellaria bertholletii*, R. Lagaaij det., 04 April 1970, St Raphael, Boulouris, France, Mediterranean.

Type locality. Boulouris, France.

TABLE 4. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. lagaaiji	*C. makua*	*C. marcusorum*	*C. normani*	*C. osburni*
	Mediterranean[1]	Mozambique[2]	Brazil[3]	Madeira[4]	Panama[5]
Lz	8	10	8	9	7
Mean (SD)	0.446 (0.032)	0.428 (0.012)	0.425 (0.023)	0.436 (0.045)	0.389 (0.035)
Range	0.385–0.488	0.407–0.454	0.377–0.437	0.400–0.523	0.359–0.454
Wz	8	10	8	9	7
Mean (SD)	0.182 (0.013)	0.184 (0.012)	0.160 (0.11)	0.175 (0.017)	0.174 (0.011)
Range	0.164–0.196	0.167–0.204	0.142–0.172	0.150–0.209	0.161–0.194
Lo	8	10	8	9	7
Mean (SD)	0.278 (0.016)	0.260 (0.017)	0.249 (0.017)	0.254 (0.014)	0.296 (0.016)
Range	0.256–0.303	0.248–0.301	0.219–0.277	0.240–0.282	0.271–0.309
Lo/Lz	8	10	8	9	7
Mean (SD)	0.63 (0.03)	0.62 (0.04)	0.60 (0.03)	0.60 (0.006)	0.75 (0.08)
Range	0.57–0.66	0.57–0.67	0.57–0.64	0.47–0.65	0.61–0.85
Lsc	-	10	8	9	7
Mean (SD)	-	0.101 (0.008)	0.091 (0.010)	0.132 (0.017)	0.110 (0.010)
Range	-	0.095–0.120	0.086–0.111	0.106–0.152	0.096–0.120
Wsc	-	10	8	9	7
Mean (SD)	-	0.131 (0.022)	0.093 (0.014)	0.212 (0.017)	0.130 (0.012)
Range	-	0.096–0.158	0.072–0.111	0.172–0.221	0.127–0.160
Wsc/Lo	-	10	8	9	7
Mean (SD)	-	0.49 (0.06)	0.38 (0.06)	0.82 (0.06)	0.46 (0.04)
Range	-	0.35–0.56	0.26–0.46	0.71–0.90	0.42–0.54
Lvib	3	6	6	5	7
Mean (SD)	0.158 (0.020)	0.156 (0.007)	0.100 (0.010)	0.161 (0.008)	0.137 (0.008)
Range	0.143–0.172	0.144–0.162	0.091–0.117	0.156–0.176	0.120–0.146
Wvib	3	6	6	5	7
Mean (SD)	0.130 (0.002)	0.123 (0.012)	0.075 (0.003)	0.106 (0.005)	0.117 (0.011)
Range	0.128–0.132	0.113–0.147	0.071–0.081	0.101–0.114	0.107–0.139
Lov	-	8	1	7	-
Mean (SD)	-	0.186 (0.005)	-	0.188 (0.011)	-
Range	-	0.177–0.192	0.177	0.179–0.211	-
Lov	-	8	1	7	-
Mean (SD)	-	0.182 (0.016)	-	0.171 (0.013)	-
Range	-	0.162–0.209	0.180	0.146–0.188	-

[1] NHMUK 1975.7.18.31, Mediterranean. [2] NHMUK 1938.5.2.4, Mozambique.[3] NHMUK 2010.12.6.28, Santos, Brazil. [4] NHMUK 1911.10.1.355, Madeira Island. [5] NHMUK 2010.6.14.3, Panama.

Etymology. Honorific for the late Dutch paleontologist and bryozoan taxonomist Robert Lagaaij (1924–1975).

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

Description. Colony erect, branches comprising 5–9 zooids. Internodes with alternating zooids, slightly curved; chitinous joints passing across gymnocyst and below opesia in outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids subcylindrical, tapering proximally. Oval opesia occupying half to three fifths of zooidal length; cryptocyst narrow, deep and smooth, more strongly developed proximally than laterally. Scutum slender, slightly flattened, branched twice, inserted at midline of inner opesial border and covering most of frontal membrane. Distal spines long, unbranched; 3 outer and 2 inner distal, an additional median distal spine sometimes present; proximalmost 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 branch, shape almost aquiline, with raised base, placed on proximal edge of opesia, rostrum directed forward, mandible triangular, hooked distally. Vibracular chamber on basal surface of each zooid, inconspicuous in frontal view; chamber almost trapezoidal, with proximal rhizoid foramen; short setal groove transverse to internode axis, straight, with smooth seta longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells not observed.

Remarks. *Cradoscrupocellaria lagaaiji* **n. sp.** is distinguished from the other species described herein by the shape of the frontal avicularium, characterized by a raised base and covering the proximal part of the opesia, and in having a scutum regularly branched twice. This species resembles *C. makua* **n. sp.**, from Mozambique, in the absence of distolateral avicularia and the overall appearance of zooids, but differs in the shape of the frontal avicularia, scutal size and wider cryptocyst.

Distribution. Mediterranean: South of France.

Cradoscrupocellaria makua n. sp.

(Fig. 16, Table 4)

Material examined. *Holotype*. NHMUK 2010.12.6.17 (Fig. 16), *Scrupocellaria bertholletii*, Dr Y.J. Hinde Collection, Mozambique. *Paratypes*. NHMUK 1938.5.2.4, same data as for holotype. NHMUK 2010.12.6.18, same data as for holotype.

Type locality. Mozambique.

Etymology. The specific name *makua* is a noun in apposition refers to a human ethnic group living in Mozambique.

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

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

Remarks. *Cradoscrupocellaria makua* **n. sp.** resembles *C. lagaaiji* **n. sp.** in the shape of the autozooids, position of joints and number of distal spines, but differs in the shape of the frontal avicularia and size of the scutum.

Distribution. Indian Ocean: Mozambique.

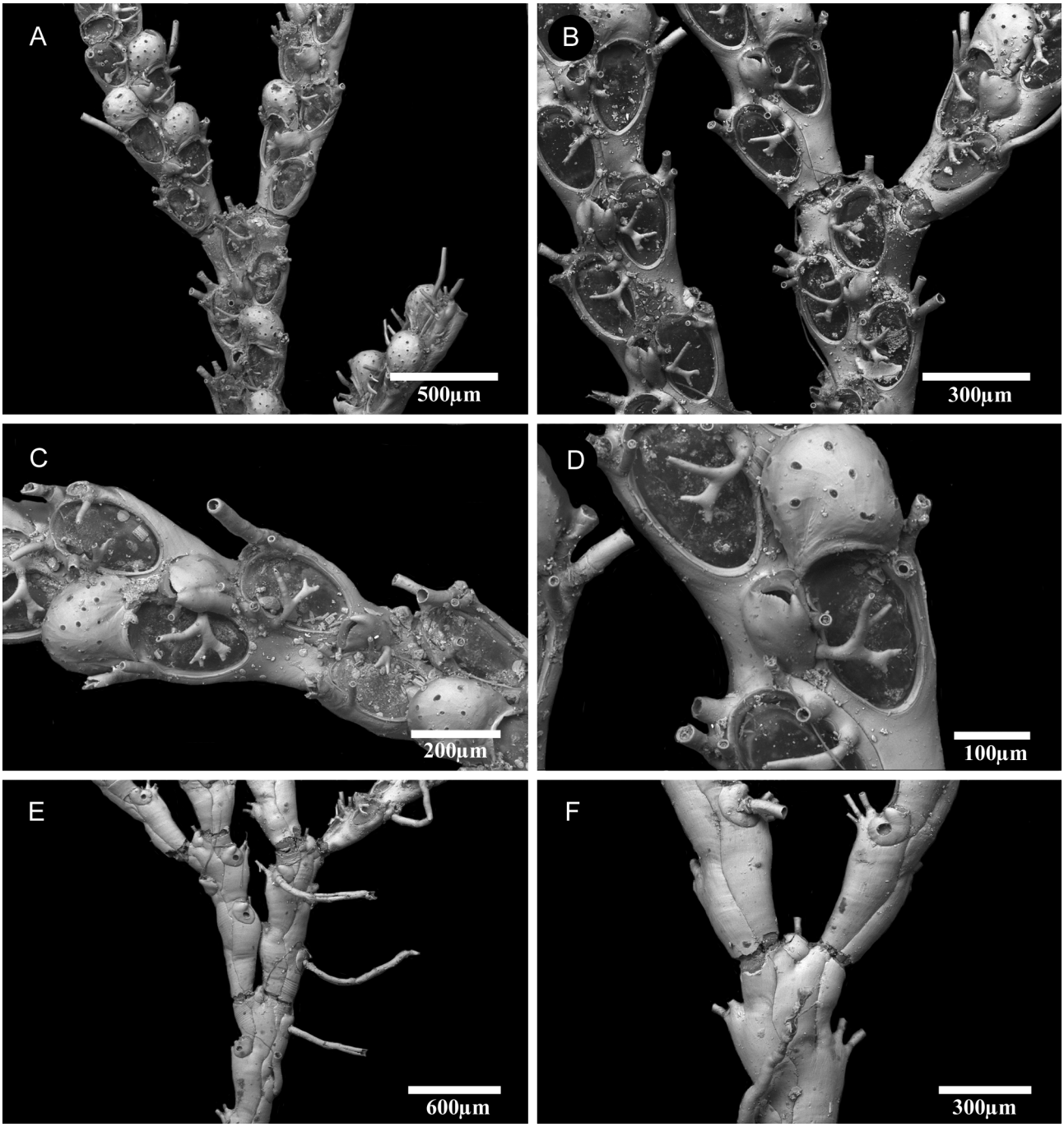

FIGURE 16. *Cradoscrupocellaria makua* **n. sp.** A–F, NHMUK 2010.12.6.17, holotype, Mozambique. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the joints passing across the gymnocyst of outer zooids at the bifurcation. C, Close-up of a branch bifurcation; note ovicelled and non-ovicelled zooids. D, Close-up of ovicelled zooid and frontal avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation; note the absence of a vibracular chamber in some zooids.

***Cradoscrupocellaria marcusorum* n. sp.**
(Fig. 17, Table 4)

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 (Fig. 17), *Scrupocellaria bertholletii*, E. Marcus det., Santos, São Paulo, Brazil. *Paratype*. NHMUK 1948.2.16.46, same data as for holotype.

Type locality. São Paulo, Brazil.

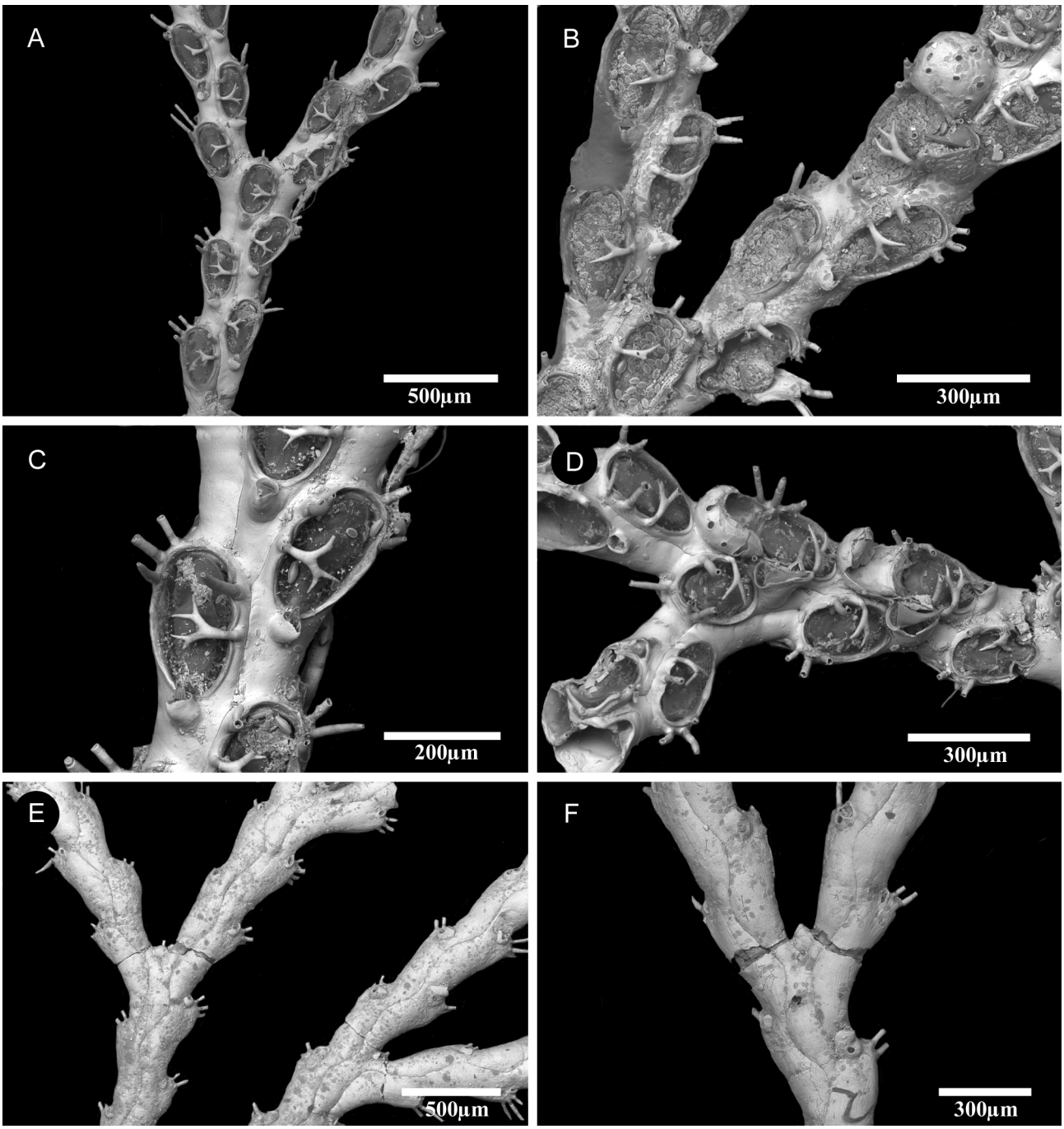

FIGURE 17. *Cradoscrupocellaria marcusorum* **n. sp.** A–F, NHMUK 2010.12.6.28, holotype, Santos, Brazil. A, Frontal surface of colony; note the absence of lateral avicularia. B, Frontal surface of branch bifurcation; joints pass across the proximal opesia of outer zooids at the bifurcation; note the gigantic frontal avicularium at upper right. C, Close-up of a branch bifurcation; note the presence of a small scutum and four distal spines (three outer and one inner). D, Frontal view of avicularia; note the slightly curved rostrum. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation; note the small vibracular chambers.

Etymology. Named after Ernst Gustav Gotthelf Marcus (1893–1968) and Eveline du Bois Reymond Marcus (1901–1990) for their work on the taxonomy and biology of bryozoans.

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

Description. Colony erect, branches comprising 5–9 zooids. Internodes slight curved, with acute bifurcating pattern; chitinous joints passing across proximal end of opesia of outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying distal half to two thirds of frontal wall; cryptocyst minimal around opesia. Scutum regularly branched twice at acute angles, with acute tips, reaching beyond midline of frontal membrane, inserted at midline of inner opesial border. Distal spines delicate, long, unbranched; 1 inner and 3 outer distal spines; proximalmost 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 curved rostrum directed forward and slightly downward, with a curved tip; mandible long, curved and hooked at tip. A small vibracular chamber present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost circular, with small rhizoidal foramen on proximal outer corner; setal groove transverse to internode axis, straight, with smooth seta 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. Marcus (1938) figured specimens from Santos (São Paulo, Brazil) as *Scrupocellaria bertholletii*, characterized by zooids with bifurcating frontal scuta and distolateral avicularia (see Marcus 1938, pl. 5, figs 11A, B). In his description, however, he mentioned variations 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 Marcus's specimens at NHMUK (NHMUK 1948.2.16.46, 2010.12.6.28).

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

***Cradoscrupocellaria normani* n. sp.**
(Fig. 18, Table 4)

Scrupocellaria reptans Linnaeus: Norman 1909: 283. [Madeira]
Not *Sertularia reptans* Linnaeus, 1758, p. 815. [?British Isles]

Material examined. *Holotype*. NHMUK 1911.10.1.355 (Fig. 18), *Scrupocellaria reptans*, A.M. Norman det., A.M. Norman Collection, 1897, Madeira.

Type locality. Madeira.

Etymology. Honorific for the late British naturalist Alfred Merle Norman (1831–1918).

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

Description. Colony erect, branches comprising 5–11 zooids. Internodes straight, with acute bifurcating pattern; chitinous joints passing across proximal end of opesia in outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids elongate, slightly tapering proximally. Oval opesia occupying half to three fifths of zooid length; inconspicuous vestigial cryptocyst around opesia. Scutum present, regularly branching three times, covering entire frontal membrane, inserted at midline of inner opesial border and overarching frontal membrane. Distal spines long, unbranched; 6–7 distal spines, proximalmost outer and inner spines directed forward; axial zooid with 5 spines. Distolateral avicularium absent. Dimorphic frontal avicularia present: small frontal avicularium with triangular mandible; large frontal avicularium with elongate

curved rostrum, 0.177–0.203 mm long, directed downward and forward, with curved tip, mandible long, curved and hooked distally. Vibracular chamber on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, with large rhizoidal foramen on proximal outer corner; setal groove transverse to the internode axis, straight, with smooth seta as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular with some retroussé hooks. Ovicell long than wide, with ectooecium perforated by rounded pores linked by internal sutures; ovicelled zooids with 2 inner and 3 outer spines.

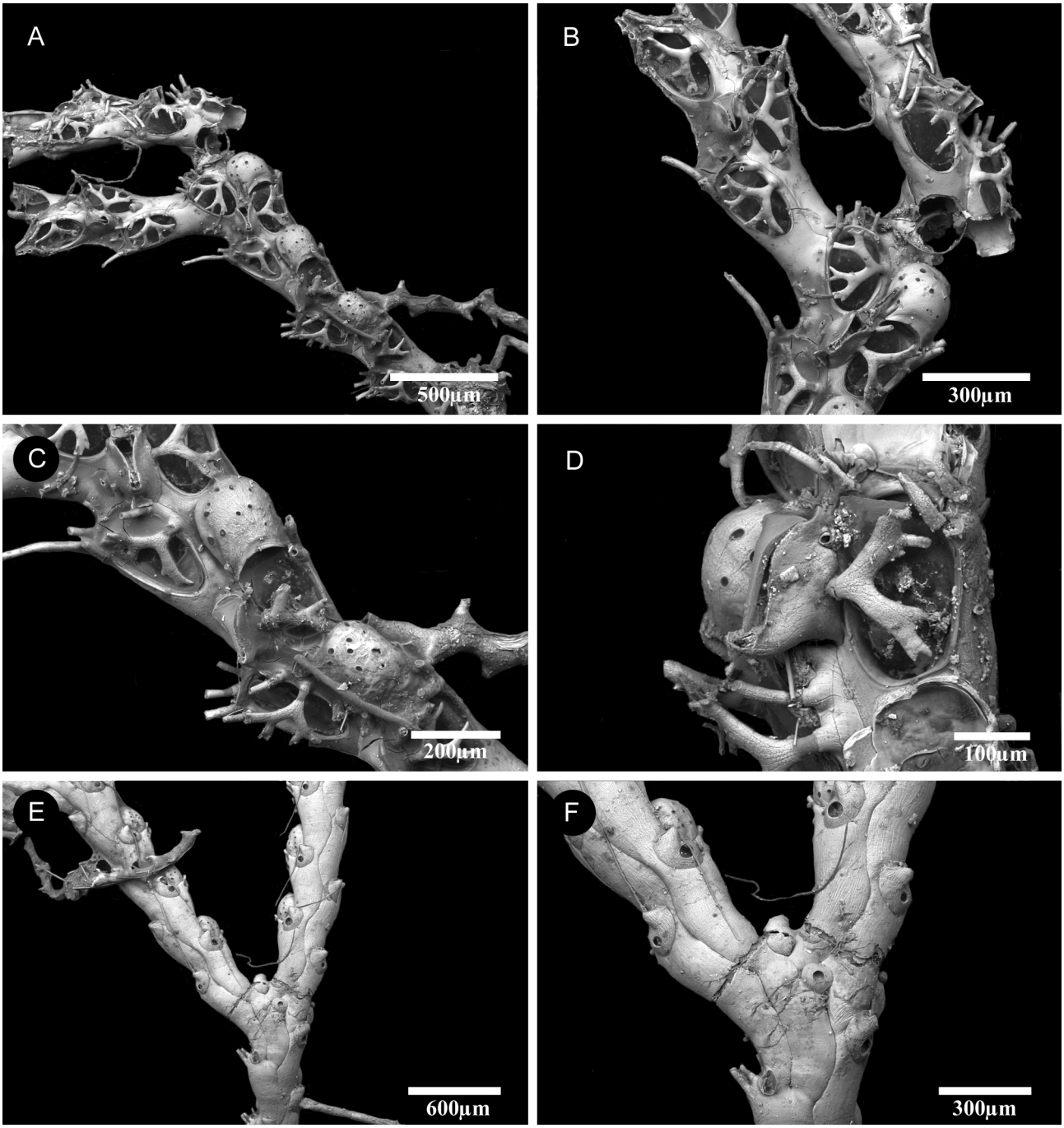

FIGURE 18. *Cradoscrupocellaria normani* **n. sp.** A–F, NHMUK 1911.10.1.355, holotype, Madeira. A, Frontal surface of colony; note a rhizoid with some well-developed hooks at bottom right. B, Frontal surface of branch bifurcation; note the regularly branched scutum. C, Close-up of a branch bifurcation; 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.

Remarks. Norman (1909) reported *S. reptans* from Madeira based on part of a colony from Funchal. Comparison of this NHMUK specimen and *S. reptans*, however, revealed morphological differences—absence of lateral avicularia, shape of frontal avicularia and scuta—which led us to segregate the Madeira specimens as *C.*

normani **n. sp.** It is distinguished from other species in the *C. bertholletii-reptans* complex by virtue of the shape of its frontal avicularia and scutum.

Distribution. Atlantic Ocean: Madeira.

***Cradoscrupocellaria osburni* n. sp.**
(Fig. 19, Table 4)

Material examined. *Holotype*. NHMUK 2010.6.14.3 (Fig. 19), Panama.

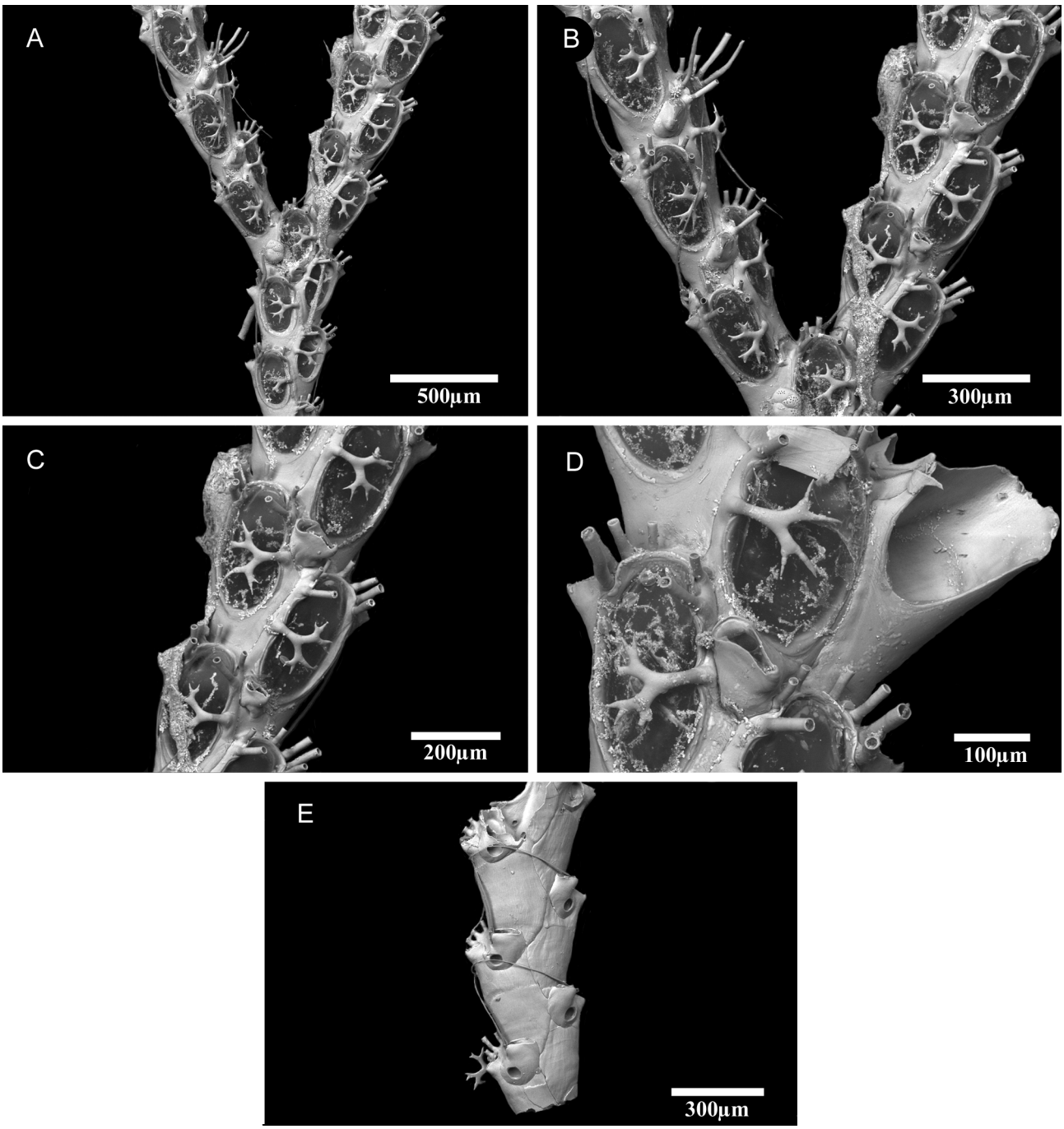

FIGURE 19. *Cradoscrupocellaria osburni* **n. sp.** A–F, NHMUK 2010.6.14.3, holotype, Panama. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note joints passing across the proximal end of the opesia in outer zooids at the bifurcation. C, Close-up of a branch bifurcation; note two diferent sizes of frontal avicularia. D, Close-up of axial zooid; note the presence of six and seven distal spines in proximal zooids. E, Abfrontal surface of colony.

Type locality. Panama.

Etymology. Honorific for the late American bryozoologist Raymond Carroll Osburn (1872–1955).

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

Description. Colony erect, branches comprising 5–7 zooids. Internodes with alternating zooids, slightly back to back; acute bifurcating pattern; chitinous joints passing across proximal end of opesia in both outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner 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 opesia. Scutum slender, branching three times, with acute tips, inserted at midline of inner opesial border and overarching part of frontal membrane. Distal spines straight to slightly curved, 1ong, delicate, unbranched; 2–3 inner and 4 outer distal spines; axial zooid with 6 spines. One conspicuous distolateral avicularium on each zooid, directed laterally; rostrum triangular, with serrated lateral edges and slightly hooked tip. Frontal avicularia variable in size, present in outer zooids along internodes, with triangular curved rostrum, serrated, with short hooked tip, directed obliquely forward and downward. Vibraculum on basal surface of each zooid, inconspicuous in frontal view; chamber trapezoidal, occupying a quarter of basal surface, with a rhizoidal foramen in its proximal outer corner; setal groove transverse to internode axis of internode, with smooth seta as long as one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells not observed.

Remarks. *Cradoscrupocellaria osburni* **n. sp.** resembes *C. atlantica* in the position of the joints that pass across the opesiae of the outer zooids at the bifurcation, the shape of the frontal scutum and in having a distolateral avicularium; this species, however, differs in the number of distal spines (6–7 in non-ovicelled zooids) and the shape and position of the frontal avicularia. *Cradoscrupocellaria gorgonensis* is distinguished from *C. osburni* by its very large frontal avicularia and wide cryptocyst around the opesia.

Distribution. Pacific Ocean: Panama.

Species having stout scutum with truncate tips

Cradoscrupocellaria ellisi **(Vieira & Spencer Jones, 2012) n. comb.**
(Fig. 20, Table 5)

?*Scrupocellaria reptans* (Linnaeus): Zabala i Limosin 1986: 321, fig. 90. [Mediterranean]
Scrupocellaria ellisi Vieira & Spencer Jones, 2012: 34, fig. 4, 18–23, 25, 27 (cum syn.).

Diagnosis. Chitinous joints passing across gymnocyst in outer zooids at bifurcation (zooids C and D); 1 long distal spine, 3 outer spines and 1–2 inner spines; axial zooid with 5 distal spines; scutum more branched than in *C. reptans*, occupying almost entire opesial area, flattened, branched 2–3 times, with 8–13 stout projections at distal tips; scutum angled at 115–155°, with first branches about 0.046–0.060 mm wide, secondary branches about 0.035–0.045 mm; small distolateral avicularum sometimes present, obscured by outer oral spine; rhizoids smooth; ooecium with 12–18 small rounded pseudopores.

Remarks. *Cradoscrupocellaria ellisi* was previously misidentified as *Scrupocellaria reptans*, but Vieira and Spencer Jones (2012) distinguished *C. ellisi* by the presence of smooth rhizoids, stouter scuta and the size of oecial pseudopores, smaller in C. ellisi than in C. reptans.

The misidentifications of specimens assigned to *C. macrorhyncha* (Gautier, 1962) and *C. reptans* suggest that Gautier's species has never been redescribed or figured since its original description (see Zabala & Maluquer 1988). In the present paper we redescribe Gautier's specimens to distinguish it from *C. ellisi* and *C. reptans*. *Cradoscrupocellaria macrorhyncha* is distinguished by the shape of frontal avicularia and the number of distal spines (see below). The specimens from the Mediterranean reported as *Scrupocellaria reptans* by Zabala i Limosin (1986), may belong to *C. ellisi*.

Distribution. Widespread in Northeast Atlantic to the North Sea; Adriatic; western Mediterranean?; Tasmania.

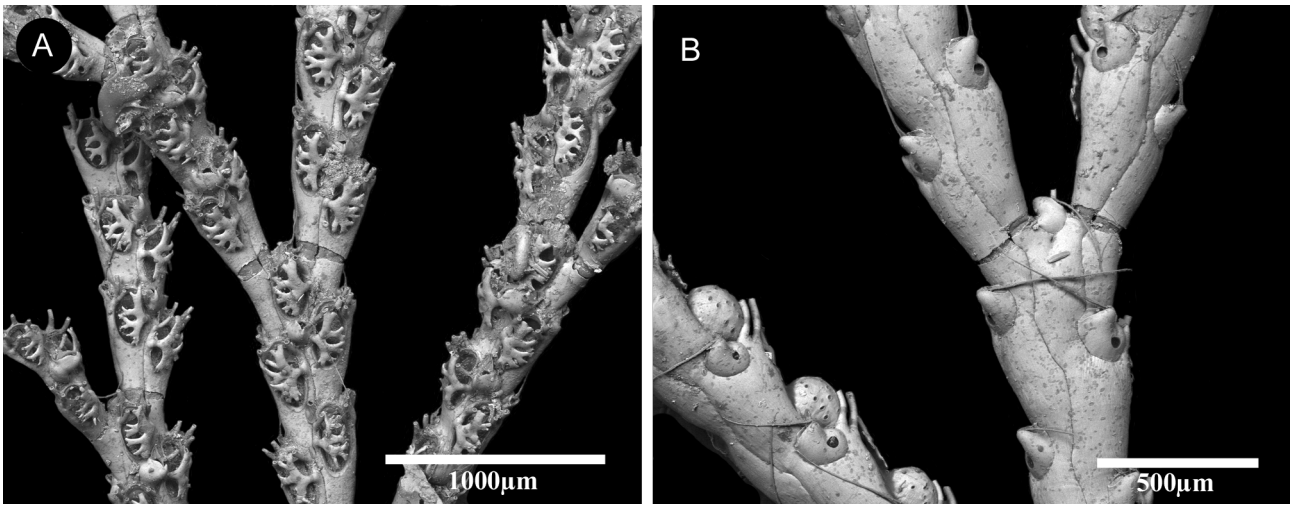

FIGURE 20. *Cradoscrupocellaria ellisi* (Vieira & Spencer Jones, 2012) **n. comb.** A–B, NHMUK 1911.10.1.353, holotype, U.K. A, Frontal surface of branch. B, Abfrontal surface of branch bifurcation.

Cradoscrupocellaria macrorhyncha (Gautier, 1962) n. comb.

(Fig. 21, Table 5)

Cellularia reptans (Linnaeus): Waters 1879: 117. [Naples]
Not *Sertularia reptans* Linnaeus, 1758, p. 815. [No Locality, but possibly British Isles]
Scrupocellaria macrorhyncha Gautier, 1962: 90, fig. 12. [Mediterranean]
?*Scrupocellaria macrorhynchus* Gautier: Prenant & Bobin 1966: 412 (part), fig. 135.I (not figs 135.II–VI). [Mediterranean]
Scrupocellaria macrochyncha Gautier: Hayward 1974: 370, 399. [Aegean Sea]
Not *Scrupocellaria macrorhyncha* Gautier: Zabala i Limosin 1986: 318, fig. 88, pls 3A, B, D, [Mediterranean]

Material examined. *Lectotype* (chosen here). NHMUK 1965.9.2.4 (Fig. 21), *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 m), Naples (Secca), Italy, Mediterranean. NHMUK 1975.7.1.29, *Scrupocellaria macrorhyncha*, P.J. Hayward det., Chios, Cape Mastika. NHMUK 1975.1.12.434, *Scrupocellaria macrorhyncha*, P.J. Hayward det., Chios, Aegean Sea, Station 57.

Diagnosis. Chitinous joints passing across proximal end of opesia in zooids C and D at bifurcation; zooids alternatin, with adjacent zooids slightly back-to-back, forming an angle at axis of branches; 2 inner and 2–3 outer distal spines; large stout scutum, its tip highly branched, fully developed and completely covering whole opesia; small distolateral avicularium obscured by outer oral spines; dimorphic elongate frontal avicularia with hooked tip; vibracular chamber on basal surface of zooids, almost lateral; rhizoids smooth; ooecium with small rounded pseudopores.

Redescription. Colony erect, branched, with branches comprising 9–21 alternating zooids. Internodes slender, almost straight, angled at axis, with acute bifurcating pattern; chitinous joints passing across proximal opesia of outer zooids at bifurcation (zooids C and D), and across proximal gymnocyst of inner zooids (F and G). Autozooids cylindrical with straight sides. Oval opesia occupying three quarters of zooidal length; cryptocyst reduced to narrow rim around opesia. Large scutum inserted at midline of inner edge of opesia, stout, its tip highly branched, fully developed and completely covering entire opesia. Distal spines short, unbranched; 2 inner and 3–4 outer spines, with outer distal spines closer to 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 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, with strongly hooked tip; mandible long, hooked distally. Vibracular chamber laterally placed on basal surface of each zooid, conspicuous in frontal view; chamber of vibraculum almost trapezoidal, with a proximal rhizoidal foramen; setal groove transverse to internode axis,

straight, with smooth seta 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.

TABLE 5. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. ellisi	*C. macrorhyncha*	*C. reptans*	*C. aegyptiana*	*C. arisaigensis*
	UK[1]	Mediterranean[2]	UK[3]	Egypt[4]	Scotland[5]
Lz	10	-	8	8	10
Mean (SD)	0.482 (0.059)	-	0.389 (0.033)	0.426 (0.025)	0.428 (0.030)
Range	0.405–0.612	0.620–0.680	0.356–0.451	0.390–0.453	0.401–0.489
Wz	10	-	8	8	10
Mean (SD)	0.200 (0.009)	-	0.186 (0.012)	0.172 (0.025)	0.166 (0.012)
Range	0.191–0.221	0.240–0.260	0.165–0.205	0.158–0.191	0.142–0.181
Lo	10	-	8	8	10
Mean (SD)	0.298 (0.026)	-	0.246 (0.016)	0.272 (0.010)	0.247 (0.008)
Range	0.270–0.332	0.300–0.350	0.209–0.267	0.257–0.281	0.229–0.254
Lo/Lz	10	-	8	8	10
Mean (SD)	0.67 (0.06)	-	0.64 (0.004)	0.64 (0.03)	0.57 (0.04)
Range	0.51–0.69	-	0.55–0.68	0.60–0.70	0.50–0.62
Lsc	10	-	8	8	10
Mean (SD)	0.155 (0.011)	-	0.131 (0.012)	0.140 (0.008)	0.118 (0.008)
Range	0.132–0.172	-	0.117–0.158	0.126–0.148	0.107–0.135
Wsc	10	-	8	8	10
Mean (SD)	0.265 (0.010)	-	0.205 (0.012)	0.193 (0.012)	0.185 (0.021)
Range	0.250–0.281	-	0.190–0.230	0.167–0.201	0.147–0.206
Wsc/Lo	10	-	8	8	10
Mean (SD)	0.88 (0.10)	-	0.83 (0.04)	0.68 (0.05)	0.75 (0.08)
Range	0.80–1.03	-	0.78–0.90	0.63–0.76	0.61–0.86
Lvib	8	4	5	10	4
Mean (SD)	0.135 (0.003)	0.174 (0.009)	141 (0.011)	0.133 (0.010)	0.129 (0.005)
Range	0.130–0.138	0.164–0.183	0.126–0.155	0.127–0.159	0.122–0.134
Wvib	8	4	5	10	4
Mean (SD)	0.116 (0.010)	0.131 (0.003)	0.101 (0.008)	0.108 (0.004)	0.106 (0.007)
Range	0.099–0.133	0.128–0.134	0.088–0.114	0.103–0.115	0.099–0.113
Lov	3	3	-	10	-
Mean (SD)	0.189 (0.008)	0.208 (0.011)	-	0.145 (0.010)	-
Range	0.186–0.202	0.207–0.227	-	0.133–0.166	-
Wov	3	3	-	10	-
Mean (SD)	0.194 (0.005)	0.204 (0.004)	-	0.166 (0.008)	-
Range	0.187–0.196	0.196–0.205	-	0.160–0.187	-

[1] NHMUK 1911.10.1.353, British Isles. [2] NHMUK 1965.9.2.4, Mediterranean; measurements of autozooids and opesia from Gautier (1962). [3] NHMUK 1963.3.6.35, British Isles. [4] NHMUK 1963.8.2.16, Egypt. [5] NHMUK 2010.12.6.1, Arisaig, Scotland.

Remarks. Gautier (1962) noted morphological similarities between *Cradoscrupocellaria macrorhyncha* and *Cradoscrupocellaria reptans*, but distinguished them by the number of zooids per internode (shorter in *C. reptans*), colony shape (erect in *C. macrorhyncha*), number of oral spines (six in *C. macrorhyncha* vs four or five in *C.*

reptans), shape of frontal avicularia (longer and proximally directed in *C. macrorhyncha*), position of vibracular chamber and surface of ooecium. Gautier's specimen (Gautier 1962, fig. 12; NHMUK 1965.9.2.4, see Fig. 21) is here designated the lectotype. The specimen named *Scrupocellaria macrorhyncha* by Prenant and Bobin (1966, figs. 135.II–VI) has the same number of oral spines, but is readily distinguished by the shape of the frontal avicularia and its wider branches; this specimen requires re-examination and probably belongs to a different species.

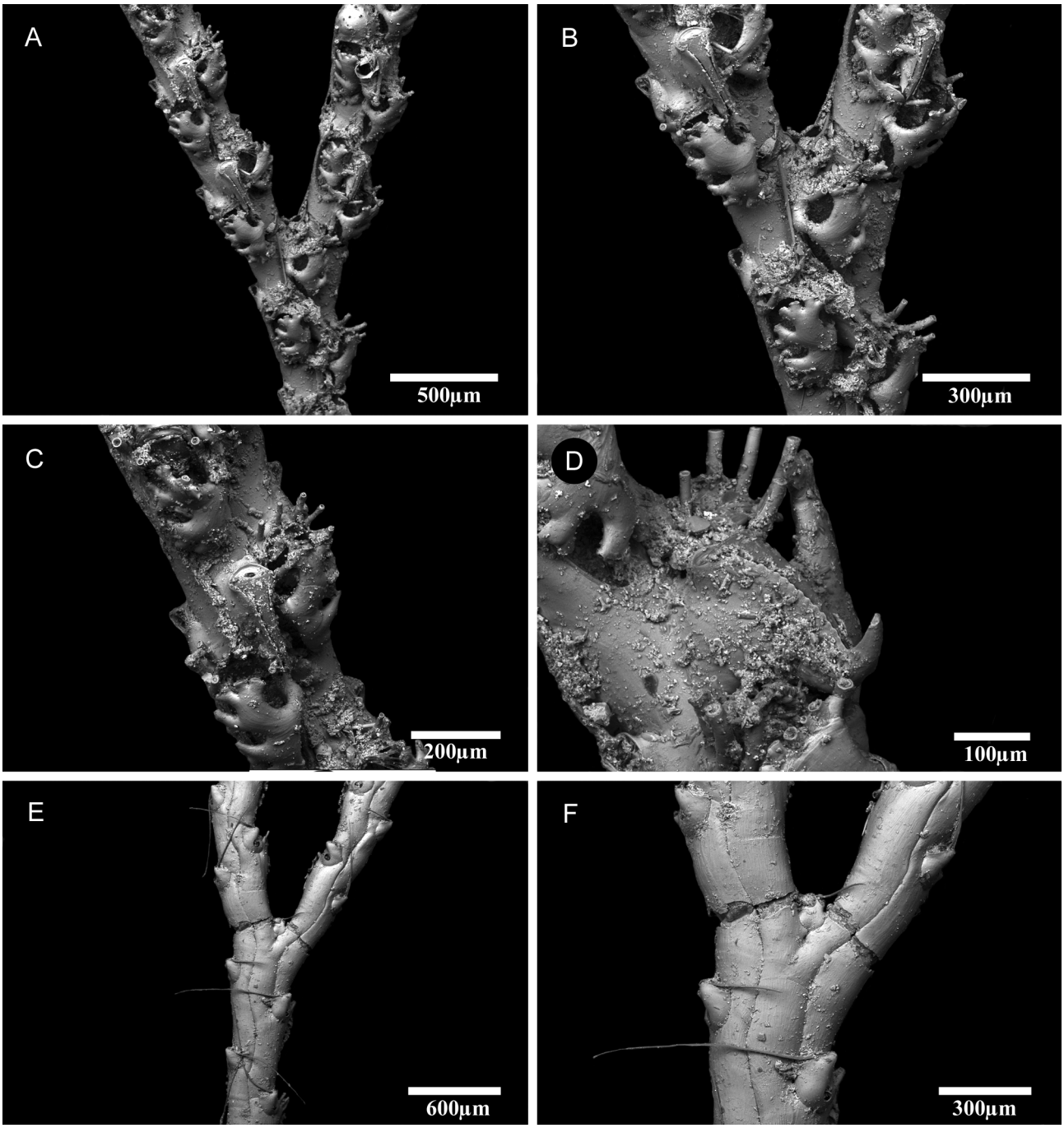

FIGURE 21. *Cradoscrupocellaria macrorhyncha* (Gautier, 1962) **n. comb.** A–F, NHMUK 1965.9.2.4, lectotype, Mediterranean. A, Frontal surface of branch; note the ovicelled zooid at upper right. B, Frontal surface of branch bifurcation. C, Close-up of a zooid and gigantic frontal avicularium. D, Lateral view of gigantic frontal avicularium; note the fringed rostrum of the avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

The Mediterranean specimens recorded as *Scrupocellaria macrorhyncha* by Zabala i Limosin (1986) were reassigned to *Scrupocellaria reptans* by Zabala and Maluquer (1988). They are distinct, however, from *C.*

macrorhyncha, *C. ellisi* and *C. reptans* in the shape of the scuta and frontal avicularia. These specimens may belong to a new undescribed species, conspecific with specimens assigned to *Scrupocellaria macrorhyncha* by Prenant and Bobin (1966).

Three other specimens deposited at NHMUK are here assigned to *C. macrorhyncha*: two specimens from Chios (Aegean Sea) labelled by Hayward (1974) as *Scrupocellaria macrorhyncha* (NHMUK 1975.1.12.434; NHMUK 1975.7.1.29) 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; 1–80 m.

Cradoscrupocellaria reptans (Linnaeus, 1758) n. comb.

(Fig. 22, Table 5)

Sertularia reptans Linnaeus, 1758: 815. [No Locality, but possibly British Isles]
Scrupocellaria reptans (Linnaeus): Vieira & Spencer Jones 2012: 31, figs 1, 2, 6–17, 24, 26. (cum syn.) [British Isles]

Diagnosis. Chitinous joints passing across gymnocyst in outer zooids at bifurcation (zooids C and D); 1 long distal spine, 3 outer spines and 1–2 inner spines; axial zooid with 5 distal spines; scutum slender, flattened, branched 2–3 times, with 6–9 distal stout projections; scutum angled at 100–120°, with first branches about 0.035–0.045 mm wide, secondary branches about 0.024–0.055 mm; small distolateral avicularum sometimes present, obscured by outer oral spine; rhizoids with several close-spaced reverse hooks for most of their length; ooecium with 8–13 medium-sized rounded pseudopores.

Remarks. Vieira and Spencer Jones (2012) gave a complete redescription of this species, with additional remarks on the differences between *C. reptans* and the widespread *C. ellisi*. *Cradoscrupocellaria reptans* is readily distinguished by its scutum (slenderer than in *C. ellisi* and *C. macrorhyncha*) and the presence of hooked rhizoids.

Distribution. North Atlantic: British Isles.

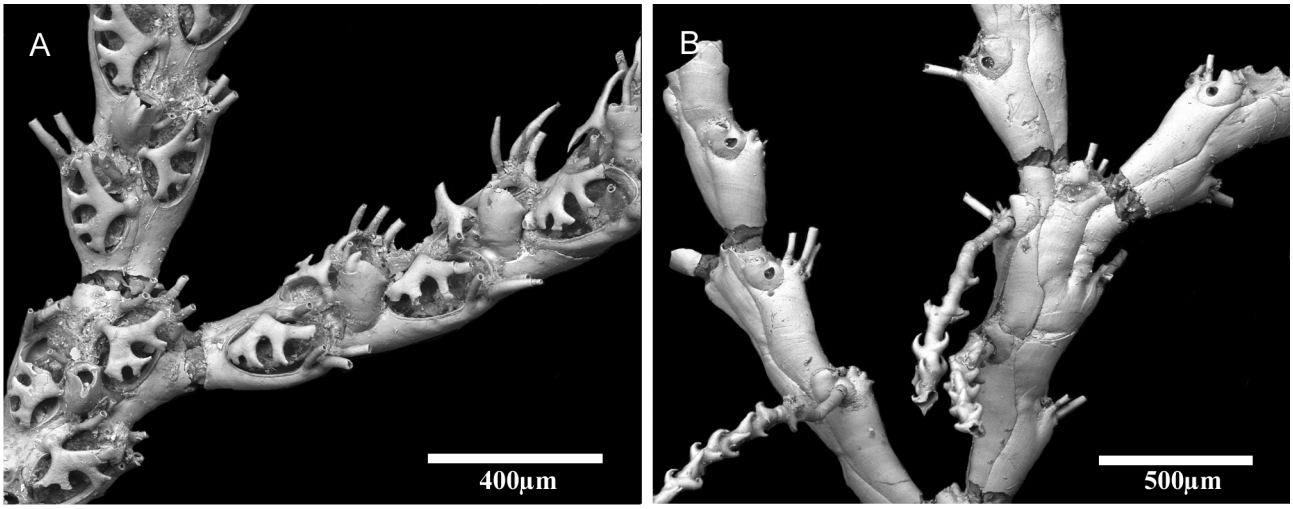

FIGURE 22. *Cradoscrupocellaria reptans* (Linnaeus, 1756) **n. comb.** A–B, NHMUK 1963.3.6.35, U.K. A, Frontal surface of branch. B, Abfrontal surface of branch bifurcation.

Descriptions of new taxa

Cradoscrupocellaria aegyptiana n. sp.

(Fig. 23, Table 5)

Scrupocellaria reptans (Linnaeus): O'Donoghue & de Watteville 1939: 17. [Egypt]
Not *Sertularia reptans* Linnaeus, 1758, p. 815. [No Locality, but possibly British Isles]

Material examined. *Holotype*. NHMUK 1963.8.2.16 (Fig. 23), *Scrupocellaria reptans*, C.H. O'Donoghue det., C.H. O'Donoghue Collection, 17–20 fms (31–37 m), Alexandria, Egypt, Stations 7, 66.

Type locality. Alexandria, Egypt.

Etymology. The specific name *aegyptiana* refers to the Latin name of the locality (Egypt).

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

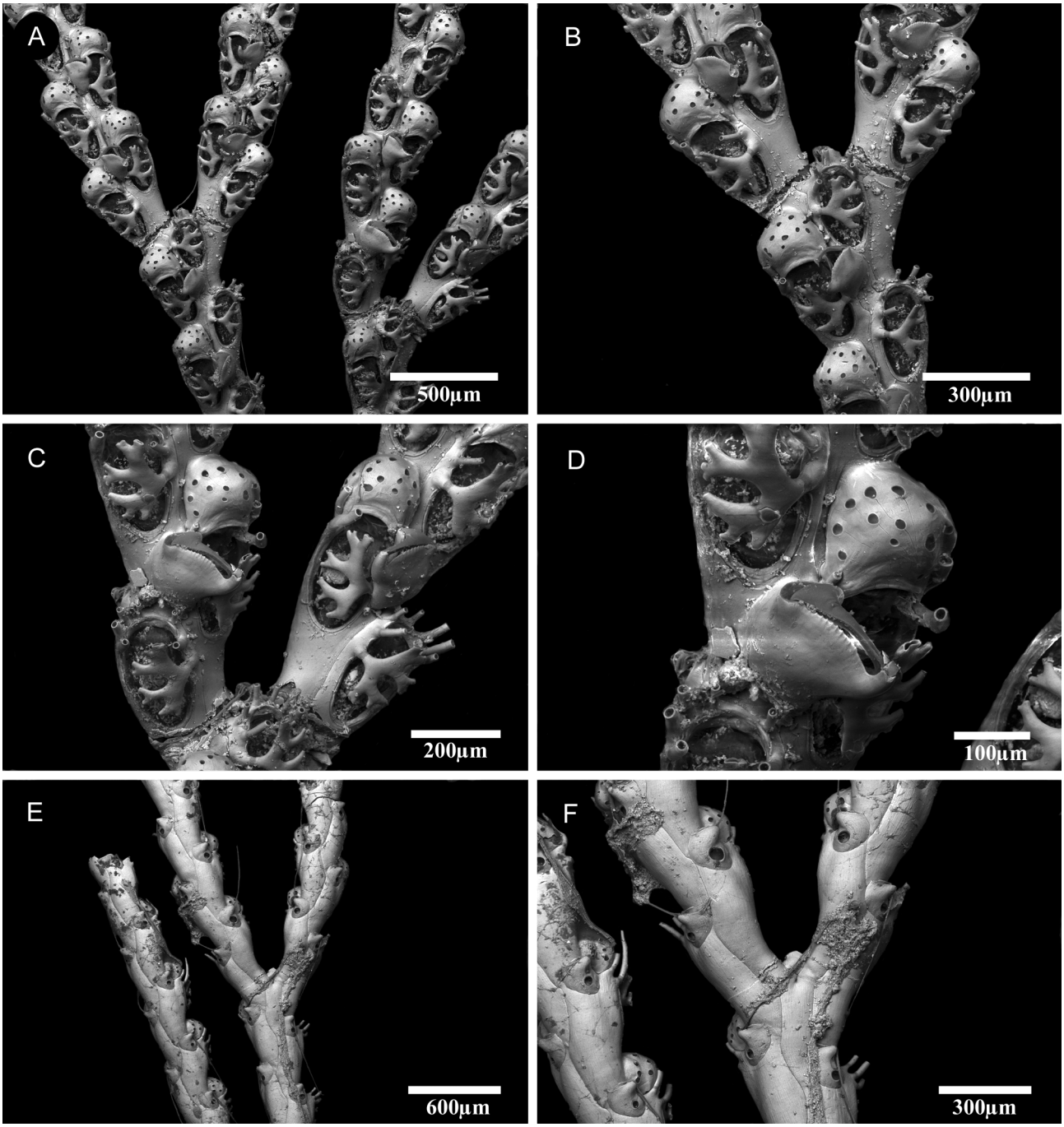

FIGURE 23. *Cradoscrupocellaria aegyptiana* **n. sp**. A–F, NHMUK 1963.8.2.16, holotype, Alexandria, Egypt. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the joints passing across the gymnocyst in both outer zooids at the bifurcation. C, Close-up of branches; note the gigantic frontal avicularia and two ovicelled zooids. D, Close-up of gigantic frontal avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Description. Colony erect, branched, fan-shaped, branches comprising 5–13 zooids. Internodes almost straight, with adjacent zooids positioned slightly back to back in alternating series; chitinous joints passing across gymnocyst and below opesia of outer zooids at bifurcation (zooids C and D), and across proximal end of inner zooids (F and G). Autozooids almost cylindrical, slightly narrower proximally than distally, with slightly curved outline in basal view. Oval opesia occupying three fifths of zooidal length; cryptocyst smooth, very narrow, forming a deep strip around opesia. Scutum large, stout, flattened, branched three times, inserted at midline of inner edge of opesia, almost entirely covering frontal membrane. Distal spines short, unbranched; 2 inner and 3–4 outer; distalmost outer and inner spines smaller than proximal ones; proximalmost 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 right angle with adjacent zooid of branch. Vibracular chamber slightly lateral on basal surface of each zooid, sometimes conspicuous in frontal view; chamber of vibraculum almost trapezoidal, with large proximal rhizoidal foramen; setal groove transverse to internode axis, straight, with smooth seta 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 NHMUK specimens assigned to *Scrupocellaria reptans* was a robust fan-shaped colony from Alexandria identified by O'Donoghue and de Watteville (1939), here assigned to *Cradoscrupocellaria aegyptiana* **n. sp.** This colony resembles *C. reptans* and *C. ellisi* in the shape of zooids and frontal scuta, but *C. aegyptiana* **n. sp.** is distinguished by the absence of lateral avicularia, the presence of monomorphic frontal avicularia with a longer rostrum and zooids often having four outer distal spines.

Distribution. Mediterranean: Egypt (Alexandria); 31–40 m.

Cradoscrupocellaria arisaigensis n. sp.

(Fig. 24, Table 5)

Material examined. *Holotype*. NHMUK 2010.12.6.1 (Fig. 24), *Scrupocellaria reptans*, O'Donoghue det., C.H. O'Donoghue Collection, Arisaig, Scotland, British Isles.

Type locality. Arisaig, Scotland.

Etymology. Pertaining to the locality (Arisaig).

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

Description. Colony erect, with branches of 5–9 zooids. Internodes with alternating zooids, slightly curved; chitinous joints passing across gymnocyst in both outer (zooids C and D) and inner zooids (F and G) at bifurcation. Autozooids almost cylindrical, tapering proximally, with slightly curved outline in basal view. Oval opesia occupying half to three fifths of zooidal length; cryptocyst very narrow and inconspicuous, forming a double band of calcification around opesia. Large, stout, flattened scutum, branched 3–4 four times, inserted at midline of inner opesial border and covering almost entire frontal membrane. Distal spines long, unbranched; 6 equally spaced distal spines, with second outer spine longer and stouter than others; distalmost spine shorter than outer and inner spines; proximalmost spines directed slightly forward; axial zooid with 6 spines. Lateral avicularium absent. Frontal avicularia monomorphic with acute and slightly curved rostrum of variable size, serrated laterally, 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 proximal rhizoidal foramen; setal groove transverse to internode axis, straight, with smooth seta longer than one autozooid. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, with several short-spaced retroussé hooks. Ovicells not observed.

Remarks. *Cradoscrupocellaria arisaigensis* **n. sp.** resembles *C. reptans* in the shape of scutum and the presence of rhizoids with retroussé hooks, but differs in having longer spines, stouter frontal scuta, no distolateral avicularia and a smaller distance between rhizoidal hooks. *Cradoscrupocellaria aegyptiana* **n. sp.** is also

characterized by absence of lateral avicularia, but differs from *C. arisaigensis* **n. sp.** in the shape of the frontal avicularia.

Distribution. British Isles: west coast of Scotland (Arisaig).

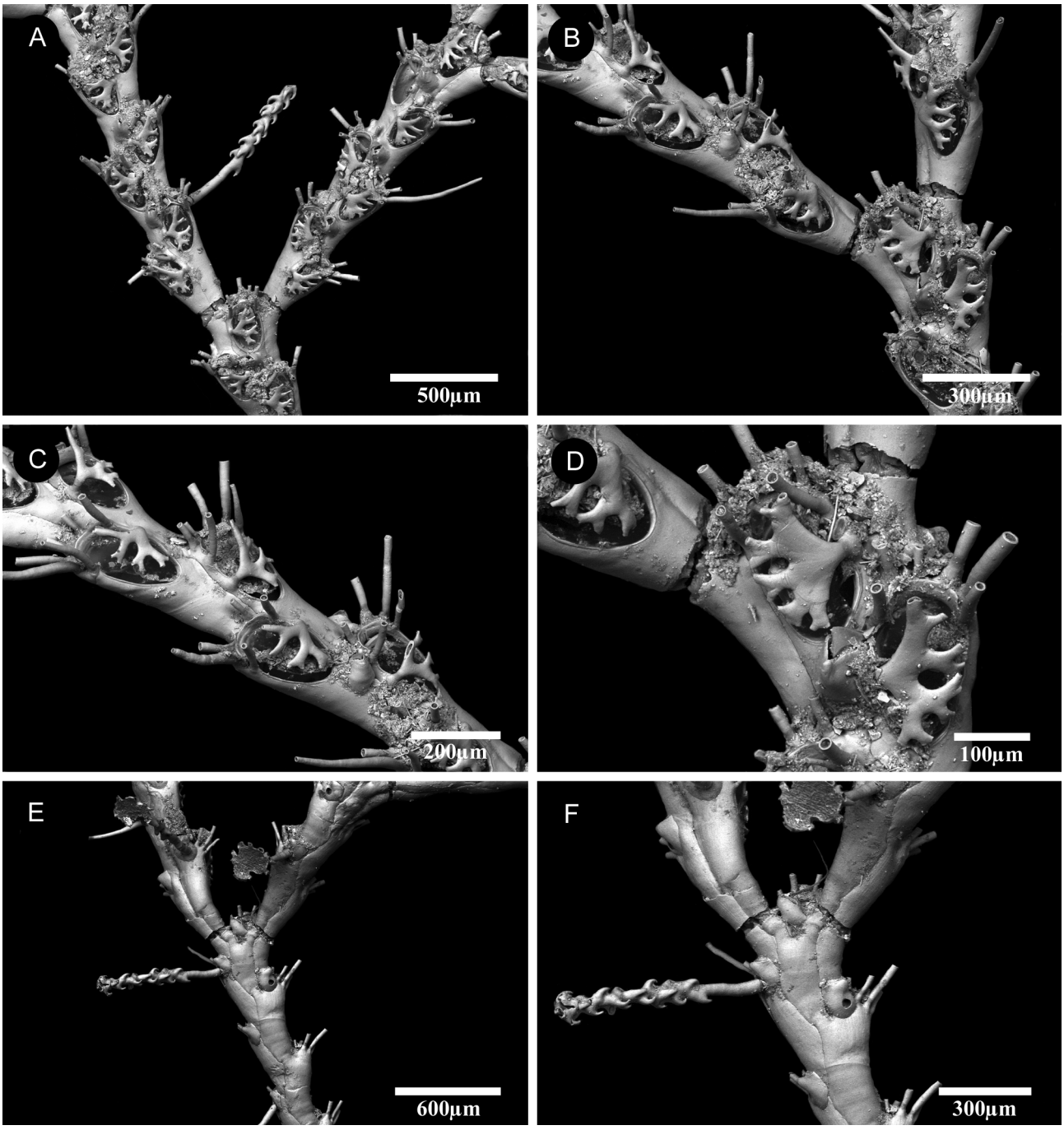

FIGURE 24. *Cradoscrupocellaria arisaigensis* **n. sp.** A–F, NHMUK 2010.12.6.1, holotype, Scotland. A, Frontal surface of colony; note the rhizoids with retroussé hooks. B, Frontal surface of branch bifurcation; note the well-developed frontal scutum. C, Lateral view of branch; note the absence of a lateral avicularium. D, Close-up of axial zooid; note the position of the joints in the gymnocyst of inner and outer zooids at the bifurcation. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation; note the rhizoids with several short-spaced retroussé hooks.

Cradoscrupocellaria gautieri n. sp.

(Fig. 25, Table 6)

Material examined. *Holotype*. NHMUK 1882.5.24.9 (Fig. 25), *Scrupocellaria reptans*, R. Kirkpatrick det., P.H.

Carpenter leg., Porcupine Expedition, 30–120 fms (54–220 m), Skensi Banki, Algeria. *Paratypes*. NHMUK 1882.5.24.8–12, same data as for holotype.

Type locality. Algeria.

Etymology. Honorific for the late French bryozoologist Yves-Victor Gautier (1930–1997).

Diagnosis. Chitinous joints passing across proximal end of opesia in both outer zooids at 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 frontal membrane; small distolateral avicularium often present, obscured by outer oral spines; dimorphic frontal avicularium elongate with hooked tip; basal vibraculum larger than those of *S. macrorhyncha*.

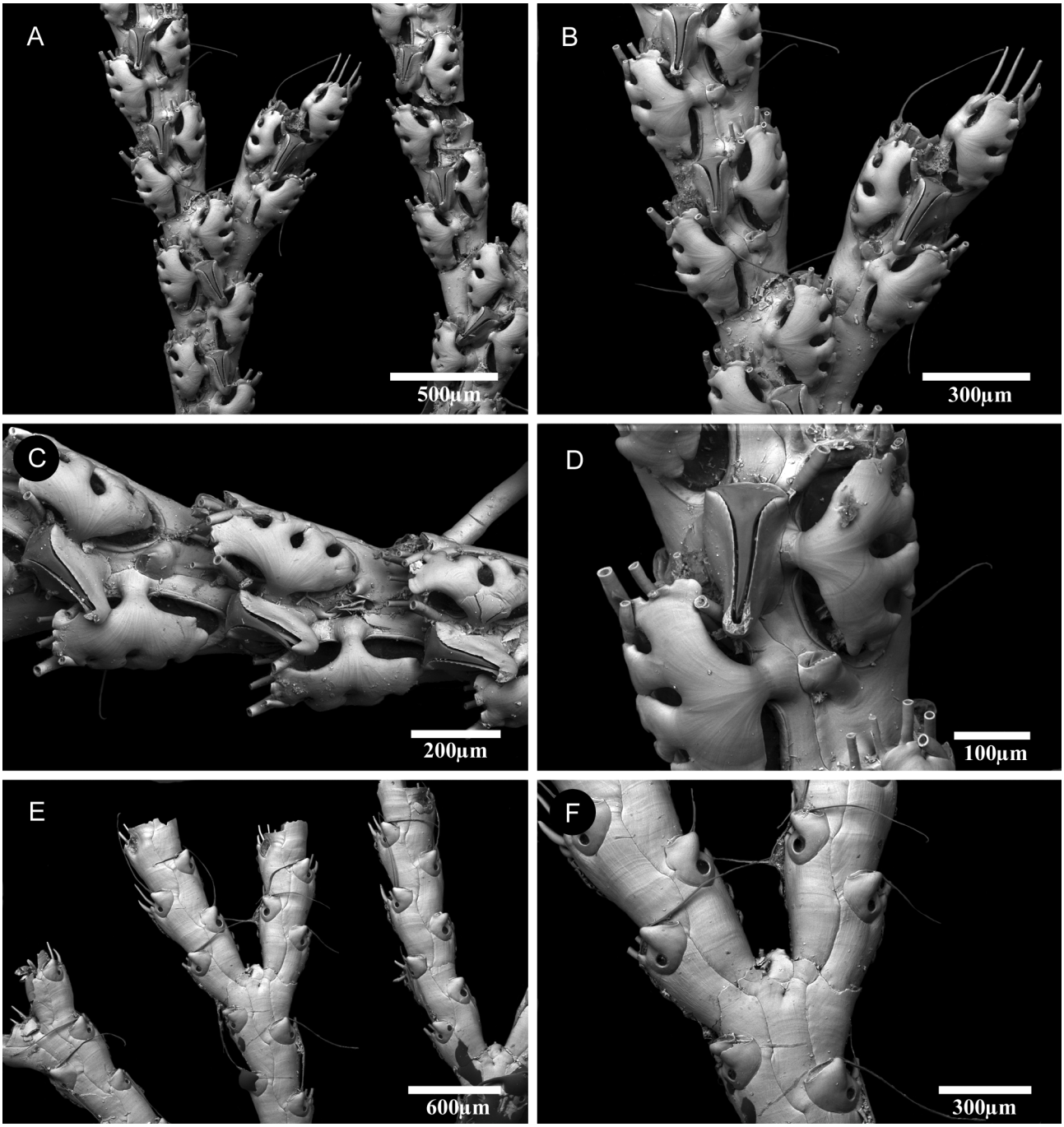

FIGURE 25. *Cradoscrupocellaria gautieri* **n. sp.** A–F, NHMUK 1882.5.24.9, holotype, Algeria. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the scutum covering whole opesia. C, Close-up of a branch; note the presence of a very small distolateral avicularium on each zooid. D, Close-up frontal gigantic and small avicularia. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

TABLE 6. Morphometric data for *Cradoscrupocellaria* species studied (in mm).

	C. gautieri	*C. macrorhynchoides*	*C. odonoghuei*	*C. hirsuta*	
	Algeria[1]	Queensland[2]	Scotland[3]	Azores[4]	Madeira[5]
Lz	10	7	10	10	6
Mean (SD)	0.467 (0.027)	0.439 (0.029)	0.515 (0.039)	0.389 (0.050)	0.430 (0.060)
Range	0.410–0.497	0.406–0.499	0.454–0.605	0.311–0.485	0.337–0.504
Wz	10	7	10	10	6
Mean (SD)	0.202 (0.009)	0.167 (0.015)	0.209 (0.012)	0.150 (0.011)	0.151 (0.013)
Range	0.193–0.221	0.148–0.191	0.197–0.234	0.143–0.181	0.142–0.179
Lo	10	7	10	10	6
Mean (SD)	0.301 (0.020)	0.289 (0.011)	0.321 (0.018)	0.222 (0.014)	0.236 (0.015)
Range	0.285–0.350	0.271–0.300	0.283–0.353	0.203–0.247	0.228–0.263
Lo/Lz	10	7	10	10	6
Mean (SD)	0.68 (0.05)	0.66 (0.05)	0.64 (0.05)	0.60 (0.05)	0.58 (0.09)
Range	0.60–0.73	0.54–0.69	0.53–0.68	0.50–0.65	0.45–0.69
Lsc	10	7	10	-	-
Mean (SD)	0.165 (0.011)	0.146 (0.012)	0.163 (0.012)	-	-
Range	0.139–0.173	0.131–0.158	0.143–0.183	-	-
Wsc	10	7	10	-	-
Mean (SD)	0.298 (0.016)	0.262 (0.018)	0.283 (0.020)	-	-
Range	0.282–0.329	0.244–0.290	0.254–0.313	-	-
Wsc/Lo	10	7	10	-	-
Mean (SD)	0.96 (0.02)	0.92 (0.05)	0.87 (0.003)	-	-
Range	0.94–1.01	0.84–0.99	0.83–0.93	-	-
Lvib	10	5	8	10	7
Mean (SD)	0.185 (0.011)	0.144 (0.012)	0.178 (0.011)	0.129 (0.011)	0.137 (0.012)
Range	0.162–0.201	0.138–0.166	0.167–0.198	0.106–0.137	0.122–0.151
Wvib	10	5	8	10	7
Mean (SD)	0.152 (0.010)	0.134 (0.011)	0.144 (0.008)	0.111 (0.011)	0.116 (0.010)
Range	0.138–0.165	0.118–0.148	0.136–0.198	0.096–0.128	0.107–0.140
Lov	-	7	8	6	1
Mean (SD)	-	0.185 (0.009)	0.210 (0.009)	0.155 (0.011)	0.174
Range	-	0.170–0.200	0.195–0.221	0.146–0.173	-
Lov	-	7	8	6	1
Mean (SD)	-	0.188 (0.009)	0.208 (0.017)	0.164 (0.007)	0.154
Range	-	0.175–0.200	0.182–0.230	0.145–0.168	-

[1] NHMUK 1882.5.24.9, Algeria. [2] NHMUK 2010.12.6.19, Queensland, Australia. [3] NHMUK 2010.12.6.21, Gairloch, Scotland. [4] MOM 420323, Azores. [5] NHMUK 1911.10.1.386, Madeira.

Description. Colony erect, branches of 5–9 zooids. Internodes stout, almost straight, with acute bifurcating pattern; chitinous joints passing across proximal opesia in outer zooids at bifurcation (zooids C and D) and across proximal gymnocyst of inner zooids (F and G). Autozooids cylindrical with parallel sides. Oval opesia occupying three quarters of zooid length; cryptocyst reduced to narrow strip around opesia. Large scutum, robust and branched at its tip, fully developed, inserted at midline of inner opesial border and covering entire frontal membrane. Six regularly spaced distal spines, unbranched: 2 inner and 3–4 outer spines. Very small distolateral avicularium rarely present, obscured by outer distal spines. Dimorphic frontal avicularia present: a small

avicularium with triangular mandible present in inner zooids of each internode, close to inner proximal border of opesia; a large frontal avicularium with 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 basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, large, with a proximal rhizoidal foramen; setal groove transverse to internode axis, straight, with smooth seta long as one autozooid length. Single axial vibraculum small, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells not observed.

Remarks. *Cradoscrupocellaria gautieri* **n. sp.** is similar to *C. macrorhyncha* in the shape of its scuta, frontal avicularia and distolateral avicularia, but differs from it in the number of zooids in each internode (shorter in *C. gautieri* than *C. macrorhyncha*), the presence of 6 regularly spaced distal spines and larger basal vibracula than those of *C. macrorhyncha*. *Cradoscrupocellaria macrorhynchoides* **n. sp.** from Australia is distinguished from *C. gautieri* by zooid size, dimorphic frontal avicularia and more slender scuta. *Cradoscrupocellaria odonoghuei* **n. sp.** resembles *C. gautieri* in the shape of the scuta but differs in having large frontal avicularia.

Distribution. Mediterranean: Algeria; 54–220 m.

Cradoscrupocellaria macrorhynchoides n. sp.

(Fig. 26, Table 6)

Material examined. *Holotype*. NHMUK 2010.12.6.19 (Fig. 26), Brisbane, Queensland, Australia. *Paratype*. NHMUK 2010.12.6.20, same data as holotype.

Type locality. Queensland, Australia.

Etymology. The specific name *macrorhynchoides* refers to the similarity of this species to the Mediterranean species *Cradoscrupocellaria macrorhyncha* (Gautier, 1962).

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

Description. Colony erect, branches comprising 5–11 alternating 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 (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 to the axis of the internode, 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. *Cradoscrupocellaria macrorhynchoides* **n. sp.** resembles *C. macrorhyncha* in overall appearance but differs in the size of the branches, position of zooids along the branches (slightly angled in *C. macrorhyncha*), position of basal vibraculum (basal and inconspicuous in frontal view in *C. macrorhynchoides*) and size of the dimorphic frontal avicularium (smaller in *C. macrorhynchoides* than in *C. macrorhyncha*).

Distribution. Pacific Ocean: Queensland, Australia.

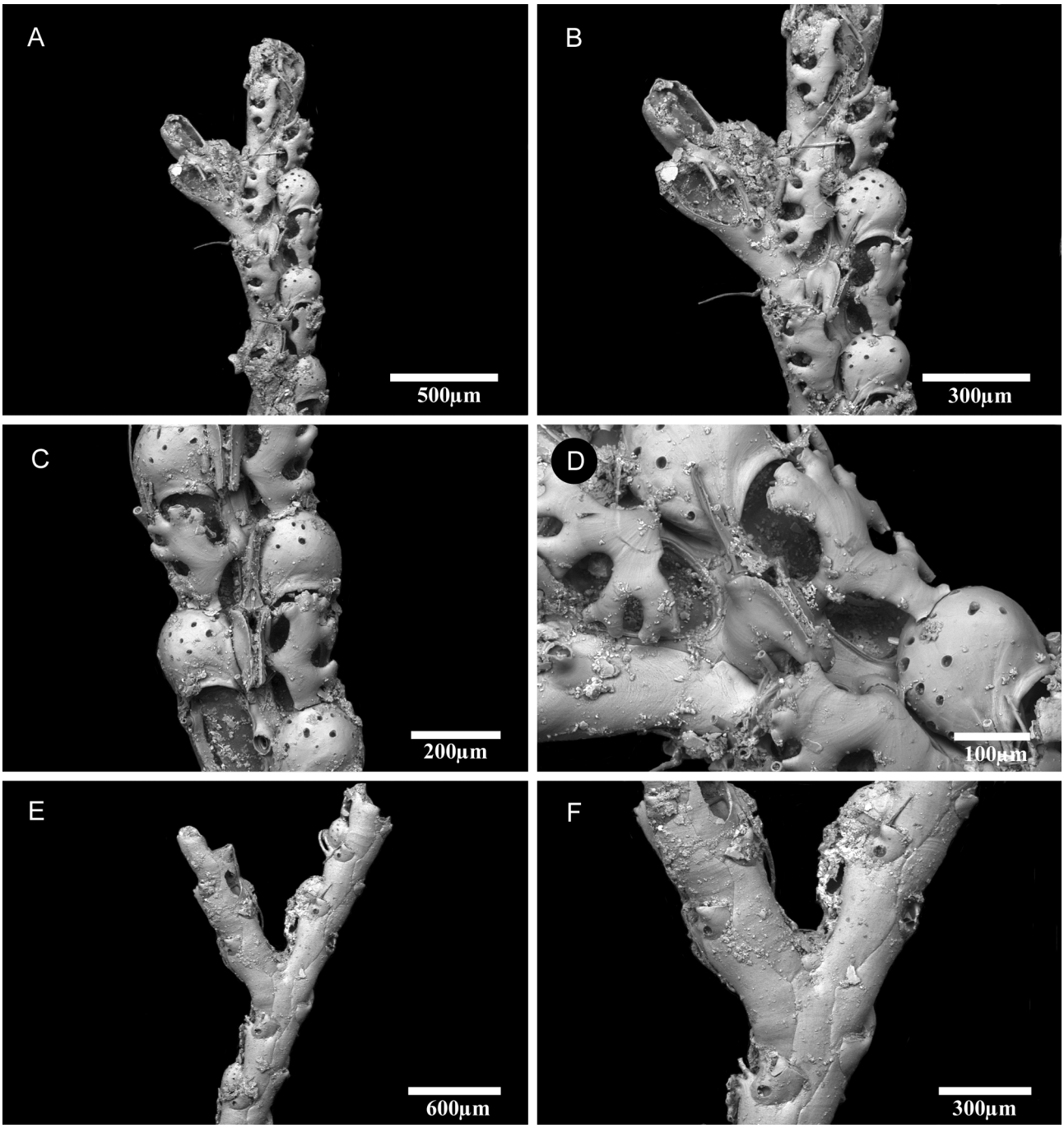

FIGURE 26. *Cradoscrupocellaria macrorhynchoides* **n. sp.** A–F, NHMUK 2010.12.6.19, holotype, Queensland, Australia. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the gigantic frontal avicularium on axial zooid. C, Close-up of a branch bifurcation; note the ovicelled zooids and the gigantic frontal avicularium. D, Close-up of gigantic frontal avicularium. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation.

Cradoscrupocellaria odonoghuei n. sp.

(Fig. 27, Table 6)

Material examined. *Holotype*. NHMUK 2010.12.6.21 (Fig. 27), as *Scrupocellaria reptans*, C.H. O'Donoghue det., C.H. O'Donoghue Collection, Gairloch, Scotland, British Isles. *Paratype*. NHMUK 2010.12.6.22, same data as for holotype.

Type locality. Gairloch, Scotland.

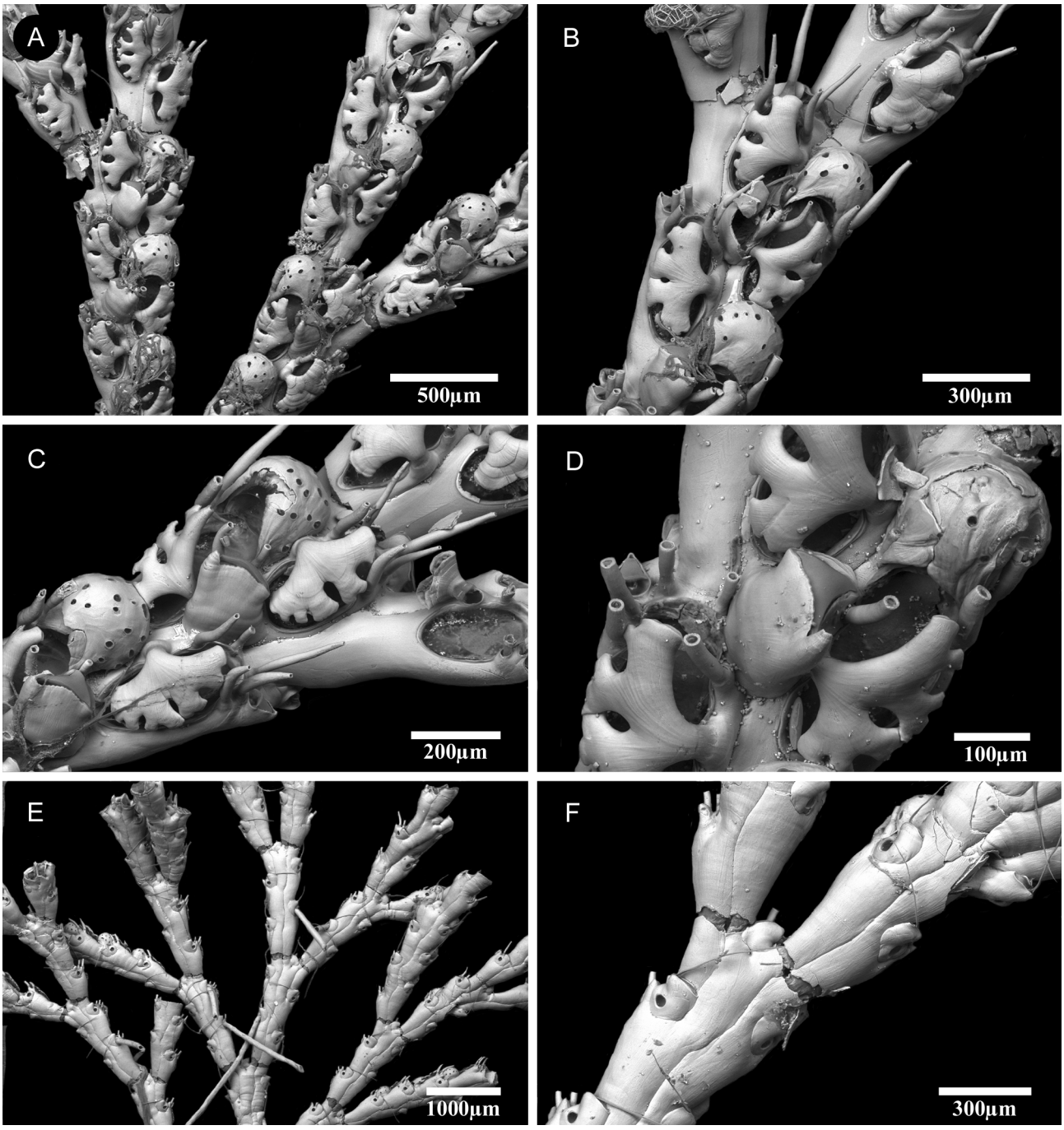

FIGURE 27. *Cradoscrupocellaria odonoghuei* **n. sp.** A–F, NHMUK 2010.12.6.21, holotype, Scotland. A, Frontal surface of colony. B, Frontal surface of branch bifurcation; note the joints passing across gymnocyst of outer zooids at the bifurcation. C, Close-up of a branch bifurcation. D, Close-up of 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.

Etymology. Honorific for the late British-born zoologist Charles Henry O'Donoghue (1885–1961).

Diagnosis. Chitinous joints passing across gymnocyst in outer zooids at 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 tip, fully developed and completely covering opesia; distolateral avicularium on each zooid, placed behind the outer oral spines; monomorphic aquiline frontal avicularium; basal vibraculum sometimes present; ovicells with frontal pseudopores linked by internal sutures.

Description. Colony erect, fan-shaped, branches comprising 5 (rarely 7) zooids. Internodes stout, almost straight, with acute bifurcating pattern; chitinous joints passing across gymnocyst in both outer (zooids C and D) and inner zooids (zooids F and G) at bifurcation. Autozooids cylindrical, tapering proximally. Oval opesia

occupying half to three fifths of zooid length; cryptocyst a very narrow rim around opesia. Scutum large, robust, stout, branched and curved at tip, fully developed, inserted at midline of inner opesial border and overarching entire frontal membrane. Five distal spines, unbranched and curved; 2 inner and 3 outer spines, with proximalmost outer and inner spines directed forward. Small distolateral avicularium on each zooid, obscured by outer oral spines. Large aquiline frontal avicularium often present on gymnocyst of outer zooids of internodes, rostrum with serrated edge, directed forward, with triangular hooked mandible. Vibracular chamber often present on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum trapezoidal, large, with proximal rhizoidal foramen; setal groove transverse to internode axis, straight, with smooth seta long as one autozooid. Single axial vibraculum small, without rhizoidal foramen. Rhizoids tubular and smooth. Ovicells globular, with rounded pseudopores linked by internal sutures.

Remarks. *Cradoscrupocellaria odonoghuei* **n. sp.** resembles *C. gautieri* **n. sp.**, *C. macrorhyncha* and *C. macrorhynchoides* **n. sp.** in its stout, branched frontal scutum, but differs in having an aquiline rather than elongate frontal avicularium and internodes with joints passing across gymnocyst in outer zooids at the bifurcation.

The Mediterranean specimens reported as *Scrupocellaria reptans* by Zabala and Maluquer (1988) (= *Scrupocellaria macrorhyncha* sensu Zabala i Limosin 1986, not Gautier 1962) resemble *C. adonoghuei* in having large, stout scuta completely covering the opesia, but they seem to be a distinct species in having smaller frontal avicularia, a more-branched scutum and the inconstant presence of lateral avicularia.

Distribution. British Isles: Scotland.

Species without scutum

***Cradoscrupocellaria hirsuta* (Jullien & Calvet, 1903) n. comb.**
(Figs 28–29, Table 6)

Acamarchis hirsuta Jullien & Calvet, 1903: 35, pl. 1, figs 3a–c. [Azores Archipelago]
Scrupocellaria hirsuta Jullien & Calvet: Norman 1909: 284. [Madeira]

Material examined. *Lectotype* (chosen here). MOM 420323 (Fig. 28A–B), dry, *Scrupocellaria hirsuta*, Jullien & Calvet det., Campagnes Scientifiques du Principauté de Monaco, *Hirondelle*, Station 226, 1888, Fosse de Fayal, Pico of Fayal (Azores), 130 m. *Paralectotypes*. MOM 420323, dry (2 colonies), same data as lectotype. *Additional specimens*. NHMUK 2012.7.1.1 (Fig. 28C–F), dry, *Scrupocellaria hirsuta*, L.M. Vieira det., Campagnes Scientifiques du Principauté de Monaco, *Hirondelle*, Station 569, 1895, Azores, 27 m. NHMUK 1911.10.1.386 (Fig. 29), *Scrupocellaria hirsuta*, A.M. Norman det., A.M. Norman Collection, Madeira. USNM 559190, balsam slide, *Scrupocellaria hirsuta*, R.C. Osburn det., 1936, Castle Island, Bermuda, 20 feet (6 m).

Diagnosis. Chitinous joints passing across gymnocyst in outer zooids at 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 laterodistally; dimorphic frontal avicularium aquiline, directed forward; vibraculum with trapezoidal chamber on basal surface of each zooids; rhizoids smooth; ooecium with large rounded pseudopores.

Description. Colony erect, branched, with branches of 5–9 alternating zooids. Internodes slender, slightly curved, angled at axis, with an acutely bifurcating pattern; chitinous joints passing across gymnocyst in both outer (zooids C and D) and inner zooids (F and G) at bifurcation. Autozooids cylindrical, tapering proximally. Oval opesia occupying three quarters of zooidal length; cryptocyst reduced to very narrow and often inconspicuous rim around 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 axis of autozooid, close to inner proximal margin of opesia; large aquiline frontal avicularium, rostrum serrated, about 0.140 mm long, directed forward or slightly downward, mandible triangular and hooked distally. Large vibracular chamber on basal surface of each zooid, inconspicuous in frontal view; chamber of vibraculum almost trapezoidal, with rhizoidal foramen at its outer proximal corner; setal groove transverse to internode axis, straight, with smooth setae longer than two autozooids. Single axial vibraculum without rhizoidal foramen. Rhizoids tubular, smooth. Ovicells globular, with large rounded pseudopores; ovicelled zooids with 1–2 inner and 3 outer spines.

Remarks. *Cradoscrupocellaria hirsuta* is distinguished by the absence of scuta, seven long and well-spaced distal spines, a very small distolateral avicularium obscured by outer oral spines and joints that pass across the midpoint of the gymnocyst in the outer zooids at a branch bifurcation. Jullien and 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 and 4–5 spines in ovicelled zooids. This species was reported by Norman (1909) from Madeira. A single specimen from Bermuda was found in the USNM 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; 6–130 m.

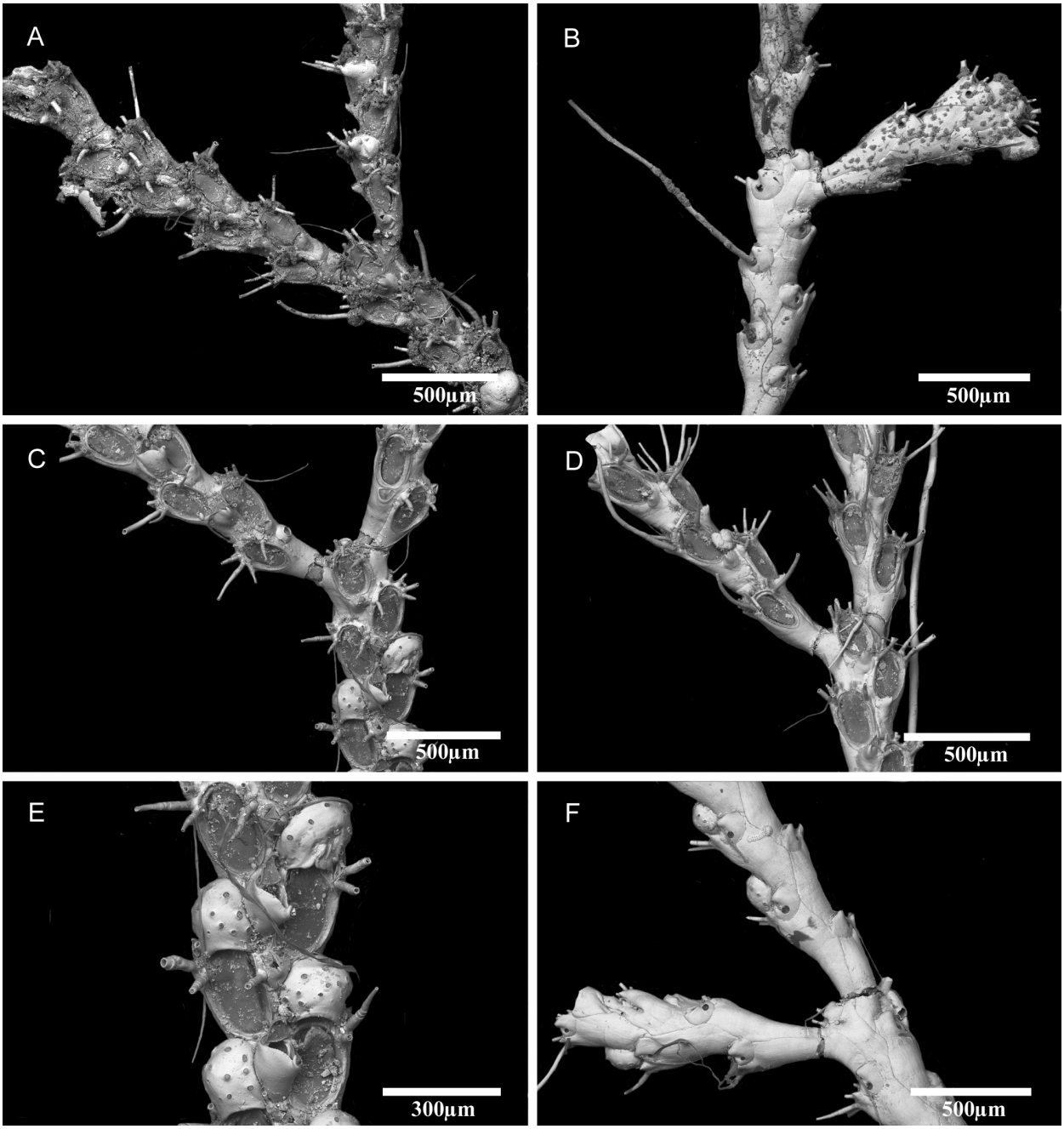

FIGURE 28. *Cradoscrupocellaria hirsuta* (Jullien & Calvet, 1903) **n. comb.** A–B, MOM 420323, lectotype, Azores. C–F, NHMUK 2012.7.1.1, Azores. A, Frontal surface of branch; note the presence of a dimorphic frontal avicularium and absence of scutum. B, Abfrontal surface of branch. C, Frontal surface of branch bifurcation; note the dimorphic frontal avicularia and three ovicelled zooids proximally in the colony. D, Frontal surface of branch; note the presence of seven long oral spines in each zooid and the absence of a scutum. E, Close-up of four ovicelled zooids and dimorphic frontal avicularia. F, Abfrontal surface of branch.

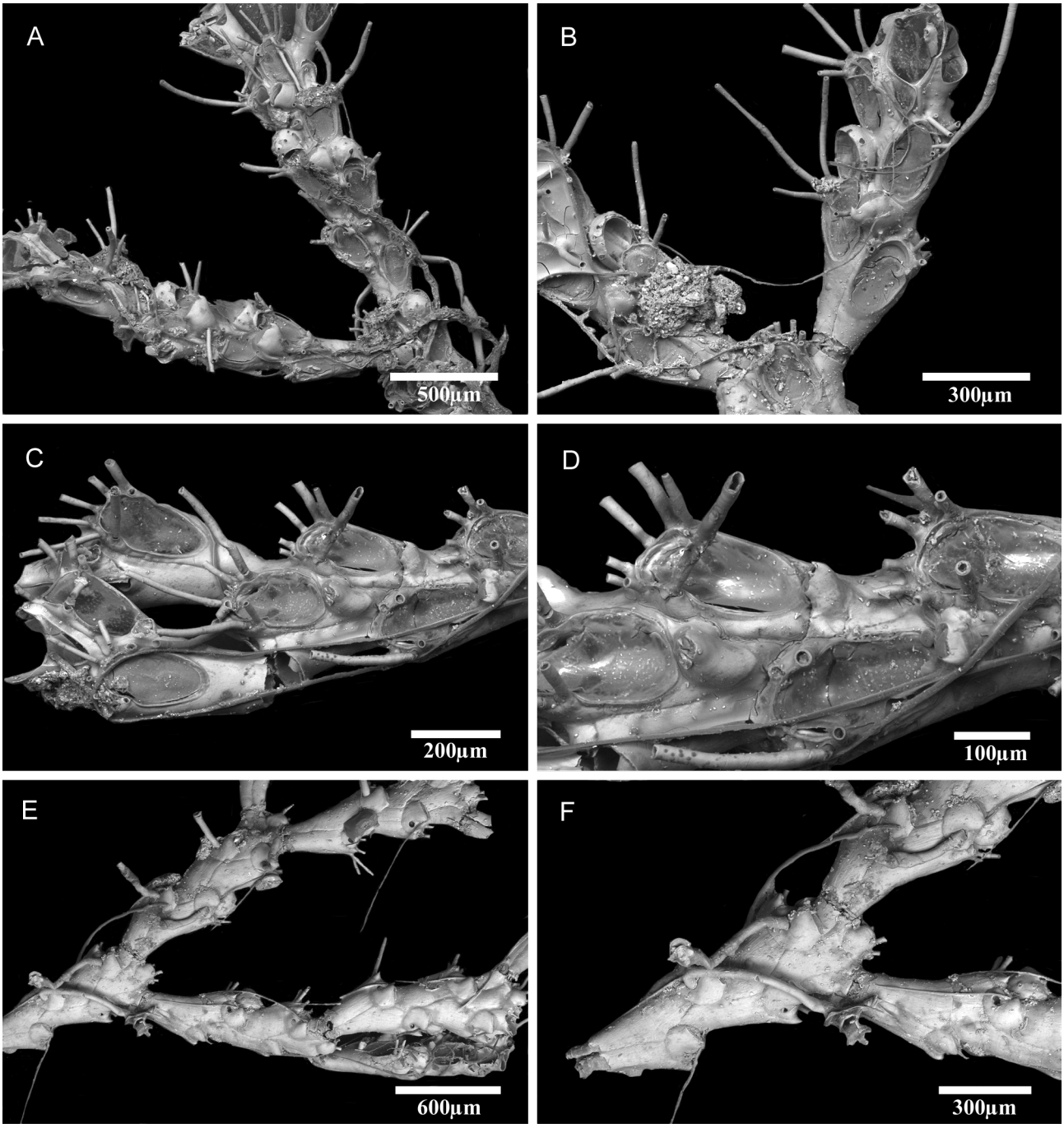

FIGURE 29. *Cradoscrupocellaria hirsuta* (Jullien & Calvet, 1903) **n. comb.** A–F, NHMUK 1911.10.1.386, Madeira. A, Frontal surface of colony. B, Frontal surface of branch; note the presence of distolateral avicularia and very long distal spines. C, Lateral view of branch bifurcation. D, Close-up of two autozooids; note the small aquiline frontal avicularia. E, Abfrontal surface of colony. F, Abfrontal surface of branch bifurcation; note the smooth rhizoids.

Key to species of *Cradoscrupocellaria* n. gen.

1	Scutum lacking in all zooids; distal spines as long as an autozooid	*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 or branched 1–2 times; rhizoids with hooks	*serrata*
-	Lateral avicularia present; scutum branched more than 3 times; rhizoids segmented	*nanshaensis*

4	Lateral avicularia absent	5
-	Lateral avicularia present in few or all zooids	14
5	Scutum lacking in some zooids; when present, 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 2 x larger than small ones; proximalmost outer spines overarching opercular area	*curacaoensis*
-	Dimorphic frontal avicularia with elongate rostrum, 3 x larger or more than single ones; proximalmost outer spines directed forwards.	*jamaicensis* **n. sp.**
7	Scutum forked, with branched distal tips	*floridana* **n. sp.**
-	Scutum branched three times or more.	8
8	Dimorphic frontal avicularia with elongate rostrum	9
-	Dimorphic frontal avicularia aquiline	10
9	Scutum branched 2 x, with acute tips, covering about half opesial area; 5–6 distal spines	*calypso* **n. sp.**
-	Scutum branched 3 x, with truncate tips, covering whole opesial area; 6–7 distal spines	*normani* **n. sp.**
10	Joints passing across opesia in outer zooids at bifurcation; 3–4 distal spines	*marcusorum* **n. sp.**
-	Joints passing across gymnocyst in outer zooids at bifurcation; 4 or more distal spines	11
11	Rhizoids with some shortly spaced retroussé hooks	*arisaigensis* **n. sp.**
-	Rhizoids with smooth surface	12
12	Scutum wide, covering more than 2/3 of entire frontal membrane.	*aegyptiana* **n. sp.**
-	Scutum slender, covering 2/3 or less of frontal membrane	13
13	Frontal avicularia with raised base	*lagaaiji* **n. sp.**
-	Frontal avicularia with stout base	*makua* **n. sp.**
14	Lateral avicularia laterally directed.	15
-	Lateral avicularia directed obliquely upward	21
15	Rhizoids with retroussé hooks; dimorphic frontal avicularia elongate, mandible lanceolate directed downwards	*tenuirostris*
-	Rhizoids with smooth surface; dimorphic aquiline frontal avicularia with triangular mandible	16
16	Scutum may be present in some zooids of colony, forked	17
-	Scutum present in all zooids; branched twice or more	18
17	Scutum short, covering half opesial width; ooecium with rounded pores; cryptocyst vestigial, often inconspicuous at proximal edge of opesia	*bertholletii*
-	Scutum long, reaching lateral outer margin of opesia; ooecium with funel-shaped pores; cryptocyst well developed around opesia.	*hastingsae* **n. sp.**
18	Scutum occupying more than two thirds of opesial area	*galapagensis* **n. sp.**
-	Scutum occupying less than half opesial area.	19
19	Cryptocyst well developed around opesia.	*gorgonensis* **n. sp.**
-	Cryptocyst narrow proximally, sometimes inconspicuous	20
20	Axial zooid with 3 distal spines; other zooids with 5 distal spines.	*atlantica* **n. sp.**
-	Axial zooid with 5 distal spines; others zooids with 6–7 distal spines	*osburni* **n. sp.**
21	Scutum highly branched, with flat frontal surface	22
-	Scutum stout, branched at tips.	24
22	Joints passing across opesia in outer zooids at bifurcation	*insularis* **n. sp.**
-	Joints passing across gymnocyst in outer zooids at bifurcation	23
23	Rhizoids with retroussé hooks	*reptans*
-	Rhizoids with smooth surface	*ellisi*
24	Joints passing across gymnocyst in outer zooids at bifurcation; dimorphic aquiline frontal avicularia.	*odonoghuei* **n. sp.**
-	Joints passing across opesia in outer zooids at bifurcation; dimorphic elongate frontal avicularia	25
25	Internodes very long, with 9–21 autozooids; frontal surfaces of adjacent zooids not in same plane, with angle between them	*macrorhyncha*
-	Internodes short, fewer than 9 autozooids; frontal surface of adjacent zooids in same plane	26
26	Internodes stout, zooids 0.193–0.221 mm wide	*gautieri* **n. sp.**
-	Internodes flat frontally, 0.148–0.191 mm wide	*macrorhynchoides* **n. sp.**

Discussion

The existence of several shared morphological features among some species previously assigned to *Scrupocellaria*, i.e. rounded to trapezoidal vibracular chamber, presence of single axial vibraculum, porous ectooecium and branched scutum, led us to erect the new genus *Cradoscrupocellaria* **n. gen.** Besides the difference in scutal shape, characteristically branched in *Cradoscrupocellaria*, all species of this genus have a porous ectooecium, a character found in *Licornia* (see Vieira *et al.* in press) and some species assigned to *Scrupocellaria*, e.g. *Scrupocellaria curvata* Harmer, 1926, *Scrupocellaria frondis* Kirkpatrick, 1890, *Scrupocellaria sinuosa* Canu & Bassler, 1927 and *Scrupocellaria hamata* Tilbrook & Vieira, 2012 (see Tilbrook & Vieira, 2012). The genus *Licornia* is distinguished

by the shape of the basal vibracula, which have a setal groove oblique to the internode axis, such as is found in *S. curvata*, *S. sinuosa* and *S. hamata* (these species are distinguished by having a longer setal groove than in *Licornia* and the joints cross below the opesia of the inner and outer zooids at the bifurcation). *Scrupocellaria frondis* is also characterized by basal trapezoidal vibracula, but differs from *Cradoscrupocellaria* in having paddle-shaped to oval scuta, branched oral spines and no dimorphic frontal avicularia. Further genetic and morphological studies are required to verify the identities and phylogenetic relationships of all of the species previously assigned to *Scrupocellaria*.

To clarify the taxonomic status and identity of the Egyptian species described by Audouin (1826), we have selected a specimen from the Suez Canal, deposited at NHMUK, as neotype of *Cradoscrupocellaria bertholletii*. The main diagnostic feature of this species is the shape of the scutum, i.e. short and forked (when present), as figured by Savigny (1817), a character distinct from the other species of the genus. Eight species previously assigned to *Scrupocellaria* are reassigned to *Cradoscrupocellaria*—i.e. *Cradoscrupocellaria curacaoensis*, *C. ellisi*, *C. hirsuta*, *C. macrorhyncha*, *C. nanshaensis*, *C. reptans*, *C. serrata* and *C. tenuirostris*—and 18 species are newly described: *C. aegyptiana* **n. sp.**, *C. arisaigensis* **n. sp.**, *C. atlantica* **n. sp.**, *C. calypso* **n. sp.**, *C. floridana* **n. sp.**, *C. galapagensis* **n. sp.**, *C. gautieri* **n. sp.**, *C. gorgonensis* **n. sp.**, *C. hastingsae* **n. sp.**, *C. insularis* **n. sp.**, *C. jamaicensis* **n. sp.**, *C. lagaaiji* **n. sp.**, *C. macrorhynchoides* **n. sp.**, *C. makua* **n. sp.**, *C. marcusorum* **n. sp.**, *C. normani* **n. sp.**, *C. odonoghuei* **n. sp.** and *C. osburni* **n. sp.**

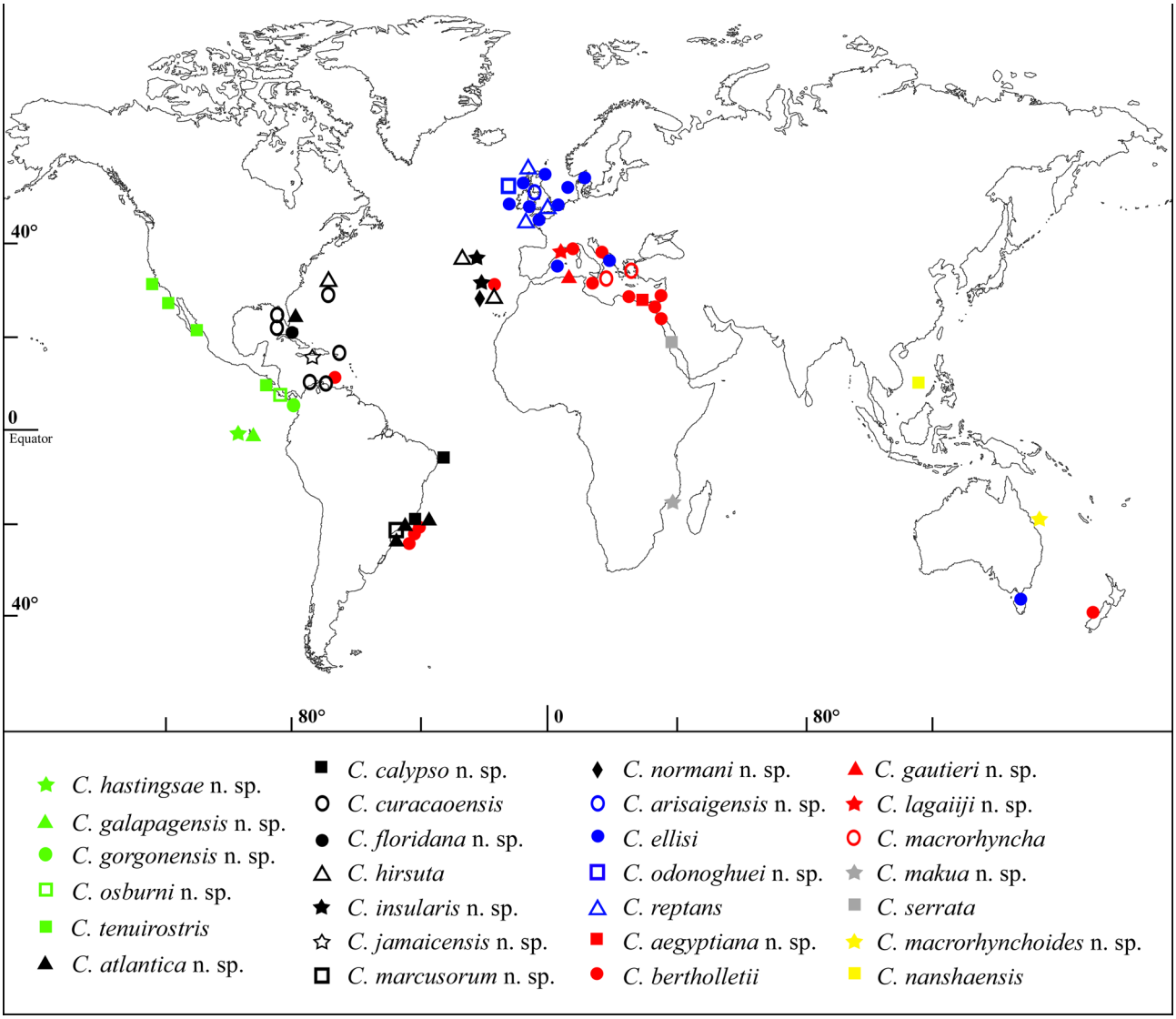

FIGURE 30. Distribution of *Cradoscrupocellaria* species. Colours: green, Eastern Pacific species; black, Atlantic species; blue, North Sea specimens; red, Mediterranean species; pink, Red Sea and Indian species; orange, Indo-Pacific species; blue, southern Australian species.

The main morphological characters distinguishing the species of *Cradoscrupocellaria* are the position of the joints at the bifurcation, the shape of scuta, the shape and position of dimorphic frontal avicularia, the presence and position of sessile lateral avicularia, and the size of basal the vibracular chamber (Tables 1–7). Among the species included here, lateral avicularia are absent in 11 species: *C. aegyptiana*, *C. arisaigensis*, *C. calypso*, *C. curacaoensis*, *C. floridana*, *C. jamaicensis*, *C. lagaaiji*, *C. makua*, *C. marcusorum*, *C. normani* and *C. serrata*. In eight species the lateral avicularia are sometimes absent in the zooids: *C. ellisi*, *C. gautieri*, *C. hirsuta*, *C. insularis* *C. macrorhyncha*, *C. macrorhynchoides*, *C. odonoghuei* and *C. reptans*; when present, the avicularium has the rostrum directed laterodistally and it is obscured by outer lateral spines or ooecia.

TABLE 7. Characteristics of *Cradoscrupocellaria* species. Present (+) and Absent (-).

Species	Joints	Scutum		Spines	Lateral avicularia	Rhizoids
		presence	shape			
C. aegyptiana	gymnocyst	+	branched; flattened in cross section	5–6	-	smooth
C. arisaigensis	gymnocyst	+	branched; flattened in cross section	6	-	hooked
C. atlantica	opesia	+	branched 3 times; sharp tips	5	+	smooth
C. bertholletii	opesia	+/-	bifurcate	2–5	+	smooth
C. calypso	opesia	+	branched 2 times; sharp tips	5–6	-	hooked
C. curacaoensis	opesia	+/-	bi-trifurcate	5–7	-	hooked
C. ellisi	gymnocyst	+	branched	4–5	+/-	smooth
C. floridana	opesia	+	bifurcate, with forked tips	4–6	-	hooked
C. galapagensis	opesia	+	branched 3–4 times; sharp tips	7	+	
C. gautieri	opesia	+	branched; cylindrical in cross section	5–6	+/-	smooth
C. gorgonensis	opesia	+	branched 2 times; sharp tips	5–7	+	smooth
C. hastingsae	opesia	+/-	bifurcate with forked tips	3–5	+	smooth
C. hirsuta	gymnocyst	-	-	5–7	+/-	smooth
C.insularis	opesia	+	branched 2–3 times; sharp tips	7	+/-	smooth
C. jamaicensis	opesia	+/-	bi-trifurcate	3–6	-	hooked
C. lagaaiji	gymnocyst	+	branched 2 times; sharp tips	5–6	-	smooth
C. macrorhyncha	opesia	+	branched; cylindrical in cross section	5–6	+/-	smooth
C. macrochynchoides	opesia	+	branched; cylindrical in cross section	5	+/-	smooth
C. makua	gymnocyst	+	branched 2–3 times; sharp tips	4–6	-	smooth
C. marcusorum	opesia	+	branched 2 times; sharp tips	4	-	hooked
C. nanshaensis	?	+	branched; flattened in cross section	5–6	+	segmented
C. normani	opesia	+	branched 3 times; sharp tips	6–7	-	hooked
C. odonoghuei	gymnocyst	+	branched; cylindrical in cross section	5	+/-	smooth
C. osburni	opesia	+	branched 2–3 times; sharp tips	6–7	+	smooth
C. reptans	gymnocyst	+	branched; flattened in cross section	4–5	+/-	hooked
C. serrata	opesia	+	single or bifurcate	3	-	hooked
C. tenuirostris	opesia	+	branched 3 times; sharp tips	4–6	+	hooked

The utilization of SEM and comparison between the specimens deposited in different museums aided in redefining these morphological features to distinguish a group of species previously assigned to *Scrupocellaria*. The main diagnostic features of these 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 the frontal avicularia. Morphologically, it is possible to distinguish two groups of *Cradoscrupocellaria* species based on the scutal shape: (i) scutum stout with truncate tips, comprising eight species from the British coast, the North Sea, the Mediterranean and eastern Australia (*C. aegyptiana*, *C. arisaigensis*, *C. ellisi*, *C. gautieri*, *C. macrorhyncha*, *C. macrorhynchoides*, *C. odonoghuei* and *C. reptans*) and (ii) scutum slender with acute tips, comprising the majority of species (see Table 7).

Most *Cradoscrupocellaria* species are known from tropical to subtropical waters, with four species known from the temperate waters of the northeast Atlantic and North Sea (Fig. 30). Sometimes several species co-exist in the same area. Twenty three species of *Cradoscrupocellaria* are reported from tropical and subtropical areas—five in the eastern Pacific, eight in the Atlantic, four in the Mediterranean, four in the Indo-West Pacific and one widespread in the Atlantic, Mediterranean and Suez Canal. Some species previously reported as widespread, e.g. *Cradoscrupocellaria reptans*, actually have a more restricted distribution. There is evidence of recent introductions for these two species, which are ecologically amenable to rafting on maritime vessels as reported for some other species of Candidae (Vieira *et al.* in press). Additional studies are required, however, to understand pathways of introduction.

The high number of new species described here and the very restricted distribution of some of them, sometimes from a unique locality, suggest that much remains to be discovered about the geographical distribution of these taxa, indicating that additional new species of *Cradoscrupocellaria* may be expected in poorly sampled areas of the world.

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References

Amui, A.-M. & Kaselowsky, J. (2006) Bryozoa from the Gulf of Aden and the Red Sea, Part I (Collections from the 5th expedition of the R.V. Meteor). *Fauna of Arabia*, 22, 1–16.

Audouin, J.V. (1826) Explication sommaire des planches de Polypes de l'Egypte et de la Syrie, publiées par Jules-César Savigny. *In*: Panckoucke, C.L.F. (org.), *Description de l'Egypte ou receuil des observations et des recherches qui ont été faites en Egyptes pendant l'Expedition de l'Armée française ... Histoire naturelle*. Tome 1(4). Imprimerie Impériale, Paris, pp. 225–244.

Balavoine, P. (1959) Bryozoaires. *In*: Philippe, R. & Dollfus, F. (eds), *Mission Robert Ph. Dolfus en Egypte (Décembre 1927 – Mars 1929). S.S. "Al Sayad". Résultats Scientifiques 3e partie,* 34, pp. 257–280.
Banta, W.C. & Carson, R.J.M. (1977) Bryozoa from Costa Rica. *Pacific Science*, 31(4), 381–424.
Barosso, M.G. (1923) Notas sobre Briozoos marinos españoles, 13, espécies de Mahón, Baleares. *Boletín de la Real Sociedad española de Historia natural*, 23, 249–251.
Beissel, I. (1865) Ueber die Bryozoen der Aachner Kreidebildung. *Natuurkundige Verhandelingen van der Hollandsche Maatschappij der Wetenschappen te Haarlem*, 22, 1–92.
Beneden, P.J. van (1845) Recherches sur l'anatomie, la physiologie, et de la développement des Bryozoaires qui habitent la côte d'Ostende. *Nouveaux Mémoires de l'Académie Royale des Sciences et des Belles-Lettres de Bruxelles*, 18, 1–44.
Beneden, P.J. van (1850) Recherches sur les Bryozoaires de la mer du Nord (suite), at projet d'une classification des animaux de ce groupe. *Bulletin de l'Académie Royale de Belgique, Classes des Sciences*, 16, 644–658.
Borg, F. (1941) On the structure and relationships of *Crisina* (Bryozoa, Stenolaemata). *Arkiv för Zoologi*, 33A, 1–44.
Brood, K. (1972) Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia. *Stockholm Contributions in Zoology*, 26, 1–464.
Brood, K. (1976) Cyclostomatous Bryozoa from the coastal waters of East Africa. *Zoologica Scripta*, 5, 277–300. http://dx.doi.org/10.1111/j.1463-6409.1976.tb00709.x
Calvet, L. (1906) Note préliminaire sur les Bryozoaires recueillis par les expéditions du Travailleur (1881–1882) et du Talisman (1883). *Bulletin du Muséum d'Histoire Naturelle*, 12, 154–166. http://dx.doi.org/10.5962/bhl.title.13677
Calvet, L. (1927) Bryozoaires de Monaco et environs. *Bulletin de l'Institut Océanographique, Monaco*, 24, 1–46.
Canu, F. (1920) Bryozoaires Crétacés des Pyrénées. *Bulletin de la Societé Géologique de France, sér. 4*, 19, 186–211.
Canu, F. & Bassler, R.S. (1927) Bryozoaires des Iles Hawai. *Bulletin de la Société des Seine-et-Oise*, 8(2), 1–23, suppl. [1928] 33–56.
Dumont, J.P.C. (1981) A report on the cheilostome Bryozoa of the Sudanese Red Sea. *Journal of Natural History*, 15, 623–637. http://dx.doi.org/10.1080/00222938100770441
Fransen C.H.J.M. (1986) Caribbean Bryozoa: Anasca and Ascophora Imperfecta of the inner bays of Curaçao and Bonaire. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 68, 1–119.
Gabb, W.M. & Horn, G.H. (1862) The fossil Polyzoa of the Secondary and Tertiary Formations of North America. *Journal of the Academy of Natural Sciences of Philadelphia*, 5, 111–179.
Gautier, Y.V. (1962). Recherches écologiques sur les Bryozoaires chilostomes en Mediterranée occidentale. *Recueil des Travaux de la Station marine d'Endoume*, 38(24), 1–434.
Gregory, J.W. (1899) *Catalogue of the Fossil Bryozoa in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa*. Trustees of the British Museum, London, 457 pp.
Gordon, D.P., Hosie, A.M. & Carter, M.C. (2008) Post-2000 detection of warm-water alien bryozoan species in New Zealand – the significance of recreational vessels. *In*: Hageman, S.J., Key, M.M.J. Jr & Winston, J.E. (eds), *Proceedings of the 14th International Bryozoology Association Conference, Boone, North Carolina, July 1-8, 2007, Virginia Museum of Natural History. Special Publication No. 15.* Virginia Museum of Natural History, Martinsville, Virginia, pp. 37–48.
Hamm, H. (1881) *Die Bryozoen des Maastrichter Ober-Senon. Theil. Die Cyclostomen Bryozoen*. Berlin, 47 pp.
Harmer, S.F. (1915) The Polyzoa of the Siboga Expedition. Part 1. Entoprocta, Ctenostomata and Cyclostomata. *Siboga Expeditie*, 28a, i–vi, 1–180, pls 1–12.
Harmer, S.F. (1926) The Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca. *Siboga Expeditie*, 28b, i–viii, 181–501, pls 13–34.
Hastings A.B. (1927). Zoological results of the Cambridge expedition to the Suez Canal, 1924, 20. Report on the Polyzoa. *Transactions of the Zoological Society of London*, 22, 331–353. http://dx.doi.org/10.1111/j.1096-3642.1927.tb00381.x
Hastings, A.B. (1930) Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. A. Crossland on the cruise of the S.Y. "St George". *Proceedings of the Zoological Society of London*, 99(4), 697–740. [1929 in cover] http://dx.doi.org/10.1111/j.1096-3642.1929.tb01453.x
Haswell W.A. (1880) On some Polyzoa from the Queensland coast. *Proceedings of the Linnean Society of New South Wales*, 5, 33–44.
Hayward, P.J. (1974) Studies on the cheilostome bryozoan fauna of the Aegean island of Chios. *Journal of Natural History*, 8, 369–402. http://dx.doi.org/10.1080/00222937400770321
Heller, C. (1867) Die Bryozoen des adriatischen Meeres. *Verhamdlungen der Zoologisch-botanischen Gesellschaft in Wien*, 17, 77–136.
Hincks T. (1882) Report of the Polyzoa on the Queen Charlotte Island. *Annals and Magazine of Natural History, series 5*, 10, 459–471. http://dx.doi.org/10.1080/00222938209459751
Hincks T. (1886) The Polyzoa of the Adriatic, I: a Supplement to Prof. Heller's 'Die Bryozoen des adriatischen Meeres,' 1867. *Annals and Magazine of Natural History, ser. 5*, 17, 254–271. http://dx.doi.org/10.1080/00222938609460142

Hondt, J.-L. d' (1988) Bryozoa from the coast of Israel. *Bolletino di Zoologia*, 55, 191–203. http://dx.doi.org/10.1080/11250008809386617

Hondt, J.-L. d' (2006) Bryozoaires. Nouvelle explications des planches de Polypes de la Description de l'Egypte (dessinées sous la direction de Jules-César Savigny, et commentées sommairement à l'origine par Victor Audouin). *Collection Nouvelle Description de l'Egypte*, 2, 1–86.

Jullien, J. (1882) Dragages du "Travailleur". Bryozoaires. Espéces draguées dans l'Océan Atlantique en 1881. *Bulletin de la Société Zoologique de France*, 7, 497–529. http://dx.doi.org/10.5962/bhl.title.4721

Jullien, J. & Calvet, L. (1903) Bryozoaires provenant des Campagnes de "l'Hirondelle" (1886–1888). *Résultats des Campagnes Scientifiques du Prince de Monaco*, 23, 1–188.

Kirkpatrick, R. (1890) On the zoology of Fernando de Noronha: Polyzoa. *Journal of the Linnean Society of London, Zoologia*, 20, 504–506.

Kluge, H. A. (1914) Die bryozoen der Deutschen Südpolar-Expedition 1901–1903, I. Die Familien Aetidae, Cellularidae, Bicellaridae, Farciminaridae, Flustridae, Membraniporidae und Cribrilinidae. *Deutsche Südpolar-Expedition 1901–1903, 15, Zoologie*, 7, 599–678.

Linnaeus, C. (1758) *Systema Naturae per Regna Triae Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th Edn. Laurentii Salvii, Holmiae, iv + 824 p.

Liu, X. (1991) A study on the anascan-cribrimorphan bryozoans from Nansha Islands of China. *Bulletin of the Marine Biology of Nansha Islands and Neighbouring Seas*, 5, 56–81. [In Chinese with English Summary]

MacGillivray, P.H. (1886) Polyzoa. *In*: McCoy, F. (Ed), *Prodomus of the Zoology of Victoria*. Government Printer, Melbourne, Decade XIII, pp. 99–111.

MacGillivray, P.H. (1895) A monograph of the Tertiary Polyzoa of Victoria. *Transactions of the Royal Society of Victoria*, 4, 1–166. http://dx.doi.org/10.5962/bhl.title.6076

Marcus, E. (1938) Bryozoarios marinhos brasileiros II. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia*, 2, 1–137.

Marcus, E. (1955) Notas sobre briozoos marinhos brasileiros. *Arquivos do Museu Nacional*, 42, 273–342.

Marsson, T.F. (1887) Die Bryozoen der weissen Schreibkreide der Insel Rügen. *Palaeontologische Abhandlungen*, 4, 1–122.

Neave, S.A. (2012) *Nomenclator Zoologicus*. The Zoological Society of London. Available from: http://uio.mbl.edu/NomenclatorZoologicus/ (Accessed 18 December 2012)

Neviani, A. (1900) *Monografia del Genere Idmonea (Bryozoa Ciclostomata). Pt. 2, Cap. 1º Stora del Genere*. Roma, pp. 53–66.

Norman, A. (1909) The Polyzoa of Madeira and neighbouring islands. *Journal of the Linnean Society of London, Zoology*, 30, 275–314.

O'Donoghue, C.H. & de Watteville, D. (1939) The fishery grounds near Alexandria: XX – Bryozoa. *Fouad i Institute of Hydrobiology & Fisheries*, Notes & Memoirs 34, 1–58.

Orbigny, A. d' (1850) *Prodrome de paléontologie stratigraphique universelle des Animaux mollusques et rayonnés faisant suite au 'Cours élémentaire de paléontologie et de géologie stratigraphiques'*. Victor Masson, Paris. [1850 (Tomes 1–2), 1852 (Tome 3)]

Orbigny, A. d' (1851–1854) *Paléontologie française. Description des Mollusques et Rayonnés fossiles. Terrains crétacés, V. Bryozoaires*. Victor Masson, Paris. [pp. 1–188 (1851); pp. 185 bis–472 (1852); pp. 473–984 (1853); pp. 985–1192 (1854); pls 600–800. Dates as given by Sherborn (1899).]

Osburn, R.C. (1940) Bryozoa of Porto Rico with a resume of West Indian bryozoan fauna. *Scientific Survey of Porto Rico and the Virgin Islands*, 16, 321–486.

Osburn, R.C. (1947) Bryozoa of the Allan Hancock Atlantic Expedition, 1939. *Report of the Allan Hancock Atlantic Expedition*, 5, 1–66.

Osburn R.C. (1950) Bryozoa of the Pacific coast of America, part 1, Cheilostomata–Anasca. *Report of the Allan Hancock Pacific Expeditions*, 14, 1–269.

Ostrovsky, A., Cáceres-Chamizo, J.P., Vávra, N. & Berning, B. (2011). Bryozoa of the Red Sea: history and current state of research. *In*: Wyse Jackson, P.N. & Spencer Jones, M.E. (eds), *Annals of Bryozoology 3: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin, pp. 67–97.

Powell, N.A. (1969) A checklist of Indo-Pacific Bryozoa in the Red Sea. *Israel Journal of Zoology*, 18, 357–362.

Prenant, M. & Bobin, G. (1966). Bryozoaires, deuxieme partie. Chilostomes Anasca. *Faune de France*, 68: 1–647.

Ramalho, L.V. (2006) Taxonomia, distribuição e introdução de espécies de briozoários marinhos (Ordens Cheilostomatida e Cyclostomata) do Estado do Rio de Janeiro. Thesis, UFRJ, Museu Nacional, Rio de Janeiro. xvii, 450 pp.

Redier, L. (1970) Resultats scientifiques des campagnes de la Calypso en Mer Rouge (1951–1952), 12, Bryozoaires. *Annales de l'Institut océanographique, Monaco*, 47 (9), 3–16.

Savigny, J.C. (1817) *Description de l'Égypte, ou receuil des observations et des recherches qui ont été faites en Égypte pendant l'Expedition de 'Armée française ... Histoire naturelle*. Vol. 2. Imprimerie Royale, Paris, 125 pls.

Sherborn, C.D. (1899) On the dates of the "Paléontologie Française" of d'Orbigny. *Geological Magazine*, series 4, 6, 223–225. http://dx.doi.org/10.1017/s0016756800143304

Smitt, F.A. (1872) Floridan Bryozoa, collected by Count L.F. de Pourtalès. Part I. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 10 (11), 1–20, pls 1–5.

Stoliczka, F. (1865) Fossile Bryozoen aus dem Tertiären Grünsandsteine der Orakei-Bay bei Auckland. *Reise der Österreichische Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. Geologischer Theil.*, 1(2), 89–158.

Tilbrook, K.J. & Vieira, L.M. (2012) *Scrupocellaria* (Bryozoa: Cheilostomata) from the Queensland coast, with the description of three new species. *Zootaxa*, 3528, 29–48.

Vieira, L.M. & Spencer Jones, M.E. (2012) The identity of *Sertularia reptans* Linnaeus, 1758 (Bryozoa, Candidae). *Zootaxa*, 3563, 26–42.

Vieira, L.M., Spencer Jones, M.E. & Winston, J.E. (in press) Resurrection of the genus *Licornia* for *Scrupocellaria jolloisii* (Bryozoa) and related species, with documentation of *L. jolloisii* as a non-indigenous species in the western Atlantic. *Journal of the Marine Biological Association of the United Kingdom.* [Published online by Cambridge University Press 23 March 2013]
http://dx.doi.org/10.1017/S0025315413000301

Waters, A.W. (1879) XI. On the Bryozoa (Polyzoa) of the Bay of Naples. *Annals and Magazine of Natural History, series 5*, 3: 114–126.
http://dx.doi.org/10.1080/00222937908682488

Waters, A.E. (1897) Notes on Bryozoa from Rapallo and other Mediterranean localities. *Journal of the Linnean Society of London, Zoology*, 26 (166), 1–21.
http://dx.doi.org/10.1111/j.1096-3642.1897.tb00241.x

Waters, A.W. (1884) Fossil cyclostomatous Bryozoa from Australia. *Quarterly Journal of the Geological Society (London)*, 40, 674–697.
http://dx.doi.org/10.1144/gsl.jgs.1884.40.01-04.55

Waters, A.W. (1909) Reports on the Marine Biology of the Sudanese Red Sea, from Collections made by Cyril Crossland, M.A., B.Sc., F.Z.S.; together with Collections made in the Red Sea by Dr. R. Hartmeyer. XII. The Bryozoa., Part I. Cheilostomata. *Journal of the Linnean Society of London, Zoology*, 31, 123–181.
http://dx.doi.org/10.1111/j.1096-3642.1909.tb00458.x

Waters, A.W. (1918) Some Collection of the littoral marine fauna of the Cape Verde Islands, made by Cyril Crossland, M.A., B.Sc., F.Z.S., in the Summer of 1904. Bryozoa. *Journal of Linnean Society of London, Zoology*, 34, 1–45.
http://dx.doi.org/10.1111/j.1096-3642.1918.tb01779.x

Winston, J.E. (1986) An annotated check-list of coral-associated bryozoans. *American Museum Novitates*, 2859, 1–39.

Zabala i Limosin, M. (1986) Fauna dels briozous dels Països Catalans. *Arxius de la Secció de Ciències*, 84, 1–836.

Zabala, M. & Maluquer, P. (1988) Illustrated keys for the classification of Mediterranean Bryozoa. *Treballs del Museu de Zoologia, Barcelona*, 4, 1–294.