Zootaxa 3780 (3): 481–502
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3780.3.3
http://zoobank.org/urn:lsid:zoobank.org:pub:E8B88941-65A4-44F8-8D93-D2F7B541152D

First occurrence of the non-native bryozoan *Schizoporella japonica* Ortmann (1890) in Western Europe

JOHN S. RYLAND[1,6], ROHAN HOLT[2], JENNIFER LOXTON[3,4,5], MARY E. SPENCER JONES[4] & JOANNE S. PORTER[3,4]

[1]*Department of Biosciences, Wallace Building, Swansea University, Swansea SA2 8PP, Wales UK. E-mail: j.s.ryland@swansea.ac.uk*
[2]*Natural Resources Wales, Maes Y Ffynnon, Bangor LL57 2DW, Wales UK*
[3]*School of Life Sciences, Centre for Marine Biodiversity and Biotechnology, Heriot-Watt University, James Muir Building, Gait 1, Edinburgh EH14 4AS, Scotland UK*
[4]*Department of Zoology, Natural History Museum, Cromwell Road, London SW7 5BD, England UK*
[5]*University Marine Biological Station Millport, Isle of Cumbrae KA28 0EG, Scotland UK*
[6]*Corresponding author*

Abstract

Schizoporella japonica Ortmann was described from Japan but was subsequently introduced on Pacific oysters to the Pacific coast of North America, where it is now well established. In this paper we record it for the first time in European waters. The initial discovery was in a marina at Holyhead, North Wales, in July 2010 but *S. japonica* has since been observed abundantly in the Orkney Islands (from May 2011) and, subsequently, at other localities in northern Scotland. Introduction seems most likely to have been on an ocean-going vessel. The British material is here fully described and illustrated with SEMs and colour photographs; some unusual characters are discussed. Unlike other recently introduced bryozoans, *S. japonica* is a cold-water species and its breeding season in Britain extends through the winter. Extensive confusion between this and other species of *Schizoporella* on the west coast of Canada and the USA led us to make thorough morphometric comparisons between the species concerned (*Schizoporella unicornis* (Johnston in Wood), *Schizoporella errata* (Waters) and *Schizoporella pseudoerrata* Soule, Soule and Chaney). Zooid size in cheilostomate bryozoans is variable and often an unreliable character for species separation but shape (and therefore ratios between variables, which are independent of size) are often valuable: *S. japonica* zooids have a much greater length:width ratio than the other species. Density of frontal pseudopores provides a useful discriminatory character. *Schizoporella unicornis*, repeatedly reported in error from the Pacific coast of North America, does not occur there; it is a European species. Full comparisons are made between *S. japonica* and *S. unicornis* for European identification and between *S. japonica*, *S. errata* and *S. pseudoerrata* (which are also illustrated) for North American localities.

Key words: Bryozoa, Cheilostomatida, Japan, Pacific northwest, fouling, marina, pontoons, tidal turbine, boat hull, morphology, cheilostomate morphometrics

Introduction

In June 2008, when the aggressively invasive ascidian *Didemnum vexillum* Kott (2002) was discovered in Holyhead marina, it was perceived as a potential threat both to cultured molluscan shellfish in North Wales and to biodiversity in the Natura 2000 marine Special Area of Conservation (SAC) around Anglesey. Accordingly, during the 2009–2010 winter, an eradication programme was initiated. All floating and submerged structures in the marina were isolated by fitting waterproof barriers (bags and wraps of various sizes) and treated with lethal doses of calcium hypochlorite. Following this first attempt the submerged surfaces of the pontoons were monitored for the return of native and non-native species. By the end of 2010 recolonisation was evident and among the species was an unfamiliar, fast-growing, orange-red bryozoan, samples of which were given to JSR for identification at a meeting on non-native species held in February 2011. Despite being midwinter, the colonies were actively reproducing, suggesting that the bryozoan was not—unlike a majority of recent introductions—of warm-water

Accepted by D. Gordon: 29 Jan. 2014; published: 24 Mar. 2014

origin. By June 2011 most surfaces had returned to pre-eradication state with full, luxuriant growths of algae and sessile encrusting fauna including solitary and colonial ascidians, and encrusting and erect bryozoans. The unfamiliar encrusting bryozoan was noted to occur at particularly high densities, growing apparently very quickly just below the waterline on floating structures. In particular it was conspicuous on the white plastic fenders and mooring buoys that were left hanging semi-submerged from pontoons and boats (Fig. 2A, B). Colony sizes ranged from <1 cm to 20 cm across. Colonies were also found on the vertical walls of the pontoons, although these were less conspicuous amongst the turf-forming algae and fauna over the dark background.

The bryozoan was identified as *Schizoporella japonica* Ortmann (1890) on the basis of the most recent comprehensive redescription of material from Alaska and Japan (Dick *et al*. 2005; Grischenko *et al*. 2007). The original description by Ortmann (1890), as *S. unicornis* var. *japonica*, was of specimens from Sagami Bay, Honshu, from which Dick *et al*. (2005) provided SEMs of the type, as they did also for a specimen from Ketchikan, Alaska. What became apparent from their account was the extent of the confusion between, and misidentification of, somewhat similar species of *Schizoporella* in both Japan and, particularly, the Pacific coast of North America. It was clear, therefore, that not only was a full description of the European material required but comparisons would have to be made with those species involved in the confusion. Fortuitously, the type material of two of these, *Schizoporella unicornis* (Johnston *in* Wood 1844; see Johnston 1847) and *S. errata* (Waters 1878) had recently been redescribed and illustrated with SEMs (Tompsett *et al*. 2009). As it appeared that there were quantifiable, species-specific differences in the shape of both the zooids and of their orifices, metric analysis also seemed appropriate and likely of taxonomic value.

Since *Schizoporella japonica* was identified from Holyhead, it has been found in other British localities, as described later in the paper.

Material and methods

Schizoporella japonica forms extensive, incipiently foliose encrustations, which have been photographed *in situ* and collected by scraping and lifting with a knife. Collected material (from various sources) of all species has been either washed in fresh water, cleaned by short exposure to ultrasound (3kHz) and dried, or treated with dilute hypochlorite bleach (Domestos™) for 24–48 h to remove non-calcified tissue, and cleaned by ultrasound for optical (transmitted light) and scanning electron (SEM) microscopy. SEM was initially performed on an uncoated specimen from Holyhead at NHM, London, using a Leo 1455VP low-vacuum SEM. Specimens from other localities, which showed somewhat different characters, have later been scanned. Preparations of chitinous parts were made by dissolving calcification with acidified 50% ethanol, staining soft tissue with borax carmine, differentiating in acidified 70% ethanol, and staining opercula and avicularian mandibles with saturated picric acid in absolute ethanol (see Hayward & Ryland 1979, for further details). Photomicrographs were taken with an Olympus E420 digital camera. Linear and areal measurements were made using computer-based image analysis and MTV software (Updegraff 1990) with a Cohu video camera on a Wild Makroskop M420, at ×25 for zooids and ×45 for orifices; both balsam mounts of bleached zooids and cleaned, dried colonies (incident light) were used. Pseudopore counts were made manually on the computer screen within defined polygons marked over a selected area of frontal surface; young, clean zooids are required. Descriptive statistics and graphics were performed in Microsoft® Excel 2003 with XLstat 6.18 add-in (Fahmy & Aubry 2002) and further analysis in BIOMstat 3.3 (Rohlf & Slice 1995).

Morphometry. It is normal practice in bryozoan taxonomy to provide zooid (and, if appropriate, orifice) measurements (Figure 1), generally given as a range, as in the *Synopses of the British Fauna* (Hayward & Ryland 1999). Occasionally this can be useful as cheilostomate zooids vary in size from about 0.2 mm to >1.2 mm in length (data in Ryland & Warner 1986; Thorpe & Ryland 1987; Winston 1979). However, since the majority of cheilostomate zooids lie between 0.4 and 0.7 mm in length, ranges commonly overlap: e.g., 0.4–0.7 × 0.3–0.5 mm for both *Schizoporella errata* and *S. unicornis* (Hayward & Ryland 1999), yet a more precise measurement set reveals a useful shape difference between these two species (see later). Recent papers with more detailed descriptions (e.g. Dick *et al*. 2005; Grischenko *et al*. 2007) generally include means and standard deviations (but need also to include sample size), in addition to range, so that the data sets can be incorporated into any subsequent analysis (as in this paper). To conform with usual practice, we include ranges in Tables 1, 3 and 4.

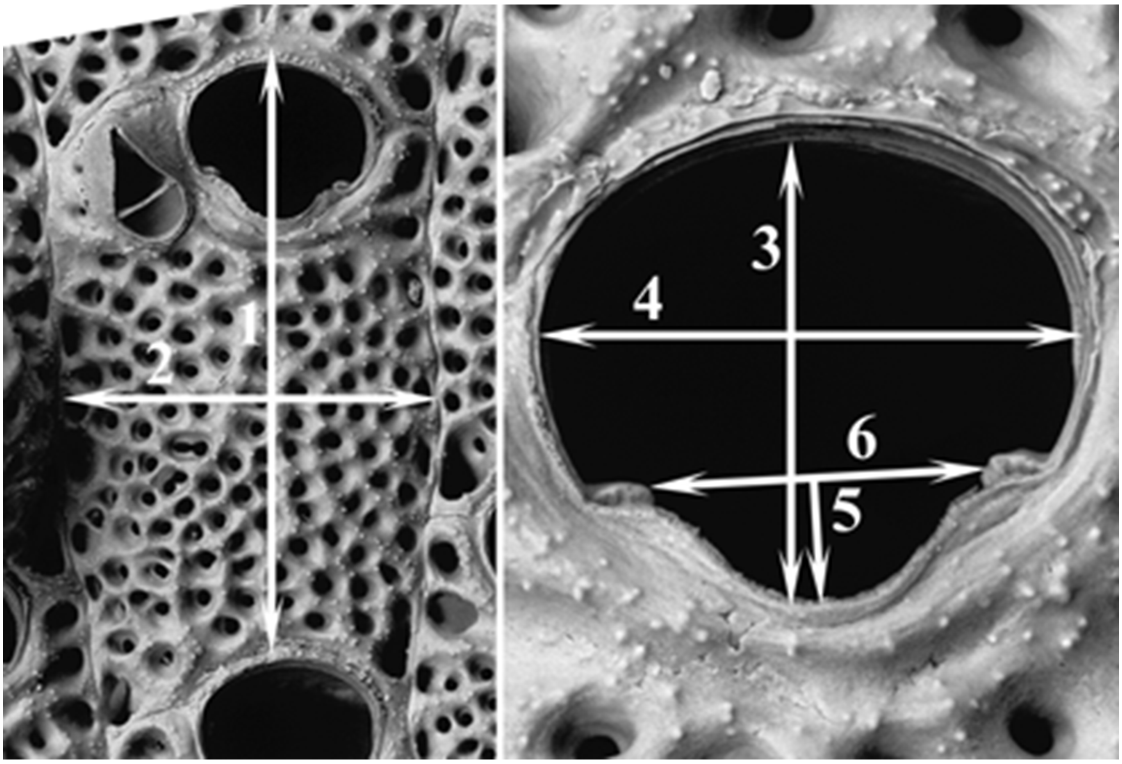

FIGURE 1. Measurements of *Schizoporella* used in this study. 1, zooid length; 2, zooid width; 3, orifice length; 4, orifice width; 5, sinus depth; 6, sinus width (inter-condyle distance).

However metric data (basically zooid length and zooid width, with derivatives such as area) are presented, problems remain. The first is that, within the range for a given species, zooid size is inversely proportional to ambient temperature during ontogeny, so that colonies growing in colder water (e.g. at higher latitudes) will have larger zooids than those where it is warmer, and zooids produced in winter will be larger than those developing in summer (Menon 1972; O'Dea & Okamura 1999). The second is related to the shape of (encrusting) colonies: growth of an expanding circle or arc of a circle (as in Fig. 4F), involves division of radial zooid series such that zooids prior to a bifurcation are wider than average while those immediately succeeding it are narrower. Thus in *S. japonica* (as *S. unicornis* in the paper) from Friday Harbor, Thorpe & Ryland (1987) found that the average length:width ratio was 1:0.55 (SD ±0.12) but ranged from 1:0.88 below division of the series to 1:0.32 above it (see Fig. 3A, E; 4F); however, narrower zooids tended to be longer so that area remained fairly stable at 0.25 mm^2. It is, therefore, desirable to make use of derived values or ratios that can be independent of linear measurements though, of course, these may not necessarily eliminate the confounding effect of temperature on size. An example in which this was achieved was the separation of two *Watersipora* species, *W. subovoidea* (d'Orbigny) and *W. subtorquata* (d'Orbigny) in which there was a large range of zooid sizes, by the ratio of orifice area : zooid area, where the (size-dependent) slopes were virtually identical but the intercepts highly different (Ryland *et al*. 2009).

As in the above example, species comparisons frequently make use of bivariate graphs: e.g. of length *vs* width, but these introduce a third problem. In scatter plots with *x*, *y* coordinates, *x* should be an independent variable (e.g. time, temperature) but for length:width graphs there is no independent variable: the allocation as *x* or *y* is arbitrary. The question of obtaining a valid line to express the length:width relationship is easily resolved by using Ricker's (1975) geometric mean regression, but there is no wholly satisfactory method for comparing the two populations (Sokal & Rohlf 1995). The use of ANCOVA, designed for use when there is a proper, independent covariate, is inevitable but its theoretical limitations must be borne in mind; the result depends upon which variable is designated as covariate.

In view of the extensive past confusion between the here-included *Schizoporella* species, we have conducted metric analysis of zooid and orifice features to try to find additional, reliable distinctions between species. The basic measurements for *S. japonica*, pertaining to the following species description, are given in Table 1.

TABLE 1. Measurement summary (mean ± SD and range, µm) for *Schizoporella japonica*. Sinus width is distance between condyles; $n = 20$ unless stated otherwise. For further details see Figs 6–8 and Appendix 1.

Source	Zooid length	Zooid width	Orifice length	Orifice width	Sinus depth	Sinus width
Drakes Bay, California	623 (±46) 526–734	368 (±46) 261–476	133 (±9) 118–149	143 (±7) 133–153	34 (±3) 29–42	91 (±6) 79–106
San Francisco Bay (NHMUK 1978.1.4.2)	680 (±63) 613–860	311 (±42) 230–394	138 (±11) 119–156	169 (±7) 158–183	30 (±5) 23–39	101 (±7) 88–112
Morro Bay, California	656 (±56) 572–825	335 (±55) 224–438	141 (±10) 125–157	163 (±11) 134–178	29 (±5) 20–39	100 (±6) 81–106
Oshoro Bay, Sea of Japan, Hokkaido	631 (±46) 551–704	383 (±55) 279–468	143 (±11) 123–157	157 (±11) 130–179	36 (±5) 24–47	101 (±8) 85–111
Zenibako Beach, Sea of Japan, Hokkaido	672 (±82) 523–865	333 (±64) 244–488	144 (±8) 131–157	171 (±10) 153–194	32 (±5) 23–43	110 (±6) 97–121
Akkeshi Bay, Pacific Ocean, Hokkaido	566 (±52) 492–656	355 (±46) 255–427	135 (±10) 120–153	152 (±13) 126–173	36 (±5) 25–44	87 (±7) 75–99
Holyhead marina, North Wales	609 (±45) 504–673	348 (±10) 257–417	142 (±5) 132–152	164 (±5) 158–175	32 (±3) 26–36	103 (±5) 97–111
Kirkwall, Orkney Is. (boat hull)	678 (±55) 574–763	274 (±34) 233–368	136 (±14) 112–165	165 (±8) 148–176	32 (±7) 19–46	99 (±11) 77–118

Taxonomy

Order Cheilostomatida Busk, 1852

Family Schizoporellidae Jullien, 1883

Genus *Schizoporella* Hincks, 1877

Type species. *Lepralia unicornis* Johnston in Wood, 1844.

Diagnosis. Colony encrusting, unilaminar to multilaminar, sheet-like or mammillate, or developing partially erect plates and mounds. Autozooids with an evenly perforated cryptocystidean frontal shield. Orifice with clearly differentiated anter and poster, the latter more or less narrowed to form a sinus; condyles well defined. Avicularia adventitious, occasionally dimorphic, typically adjacent to the autozooid orifice. Oral spines impermanent or absent. Ovicell recumbent on distally succeeding autozooid, prominent, spherical or subglobular, perforate, ribbed or umbonate. Vertical walls with uniporous or multiporous septula (Hayward & Ryland 1999).

Remarks. The species of *Schizoporella* fall into two fairly distinct groups, based on the shape of the sinus. In the first, the sinus is broadly and shallowly U-shaped, wider than deep; in the second, the sinus is narrow, as deep—or deeper—than its greatest width. All the species to be discussed in this paper (*S. errata, S. japonica, S. pseudoerrata* and *S. unicornis*) belong in the first group. The main characters traditionally used for species separation in this group are: size, budding pattern, and layering of the colony; the shape of the orifice (including that of the sinus); the appearance of the porous frontal wall; and the morphology of the ovicell, especially ribbing and distribution of pores.

Despite being reasonably distinct, the above species have often been confused with each other, especially when found in fouling communities, usually as a result of ignoring well-described characteristics. Known British species (also including *S. errata*, which has not yet been recorded from Britain) have been described by Hayward & Ryland (1995, 1999), while SEM-illustrated redescriptions of the type specimens of two of these (*S. errata* and *S. unicornis*) have been recently published (Tompsett *et al*. 2009). Details of the specimens we have studied are given in Appendix 1.

Schizoporella japonica Ortmann, 1890
(Figures 2–5)

Schizoporella unicornis var. *japonica* Ortmann, 1890: 49, pl. 3, fig. 35.
Schizoporella unicornis: Okada 1929: 20, fig. 7; Powell 1970: 1849, figs 2–3; Ross & McCain 1976: 164, figs 1–6; Kubota & Mawatari 1985: 201, fig. 3A–E; Thorpe & Ryland 1987: 281 (Friday Harbor, in part); Osburn 1952: 317, pl. 37, figs 1–2 (part; some = *S. pseudoerrata*); Soule *et al*. 1995: 204, pl. 75A–F.
Schizoporella japonica: Dick *et al*. 2005: 3742, figs 15–16; Grischenko et al. 2007: 1115.

Material examined. See Appendix 1. *Holotype*. Strasbourg Museum, MZS Bry001 as *S. unicornis* var. *japonica*; type Locality Sagami Bay, Japan, collected Dr L. Döderlein, 1880–1881. A photograph of the supporting stone and holotype colony is shown in Fig. 4E.

Description of British material. Colonies at first more or less circular (Fig. 4F), rapidly becoming extensive, pale whitish-pink to vivid orange-red (Figs 2, 4; British material between Munsell 2.5YR6/14 and 10.0R6/10 (see Kelly & Judd 1955)); mainly unilaminar but frequently with raised edges or displaying slightly elevated lobes (Fig. 2B, C). Zooids generally in obviously linear series, quincuncial away from bifurcations; rectangular; conspicuously longer (often twice as long) than broad (0.5–0.7 × 0.25–0.35 mm; Table 1); length:width proportions (1.7–2.5:1) varying according to distance from a bifurcation (Figs 2D–E, 3A, E); the dividing line between series distinct, slightly depressed; frontal shield with marginal areolae and regularly distributed pseudopores, except sometimes (in Holyhead material) for an incipient suboral umbo; the distolateral pair of areolae somewhat larger. Frontal pseudopores very numerous (c. 600 mm^{-2}, range ~400−800 mm^{-2}). Orifice shallower than wide (0.8–0.9:1), though variable within a colony (110–140 × 150–175 µm); the sinus shallow and broad (0.3–0.4:1; 20–35 × 80–120 µm), with sinuous margins, delimited by horizontal, obtusely pointed condyles (Figs 2F, 3D); distal margin of orifice and lip of sinus with minute tubercles. Operculum matching the orifice, with no additional sclerites (Fig. 2F). Some Scottish specimens with occasional orifices closed by perforated calcification (Fig. 5H). Holyhead specimens most commonly with a single avicularium lateral to the orifice but frequently none; distolaterally directed, inner end of hinge-line level with the condyles; mandibles triangular, their height scarcely exceeding the hinge width (Fig. 3A, B, D, E). The Scottish material has 0–5 avicularia per autozooid, with most colonies typically featuring 1–3; there may also be frontal avicularia, of the same basic form but slightly larger and with an elevated chamber (Fig. 5B, C). Ovicells prominent, subglobular, with numerous pores except near the mid-proximal margin; with slender sinuous ridges ascending from the distal zooid, between the pores, and converging in a mid-proximal direction (Fig. 3B, C); sometimes >1 (up to 5 in Scottish material) per autozooid (Fig. 5F–G, and discussion below). Polypide with c. 19 tentacles (Friday Harbor). Embryos reddish, apparently increasing in size during development; half-sized embryos present at Holyhead even in midwinter (February). Ancestrula with D-shaped orifice and 8 marginal spines; a central, patterned circular area on the frontal calcification (Fig. 4A–C); approximately 350–400 × ~300 µm overall (settlement panel, Stromness).

Additional descriptions. Colonies collected from different parts of the world may vary, may offer reproductive stages not seen elsewhere, or be described in a slightly different manner. Full descriptions accompanied by SEM illustrations have recently been provided for each of the main geographic areas from which *S. japonica* is known—Alaska and the Pacific coast of North America (Dick *et al*. 2005) and Japan (Grischenko *et al*. 2007). Salient features have been selected.

Alaska. Colony encrusting, unilaminar but sometimes bilayered as a result of overgrowth; colour ranging from whitish to red. Zooids distinct, separated by suture lines and shallow grooves. Frontal surface slightly to moderately convex, with marginal areolae and frontal pseudopores; pseudopores becoming infundibular with age and thickening calcification, the frontal shield becoming reticulate. Orifice medial or offset, with an avicularium beside it; usually broader than long, anter semi-circular, separated by paired blunt stout condyles, directed medially; operculum light golden brown, transparent. Avicularia paired, single or absent on any given zooid; additionally, occasional zooids bearing a somewhat larger frontal avicularium with raised rostrum and chamber. With increasing secondary calcification, the ovicells—similar to those from Holyhead—become increasingly rugose (Dick *et al*. 2005).

Japan. Colonies as from Alaska but red to bright orange. Zooids with frontal shield uniformly porous except suborally, with 7–9 larger areolae along each margin; usually with a small suboral umbo. Oral avicularia most

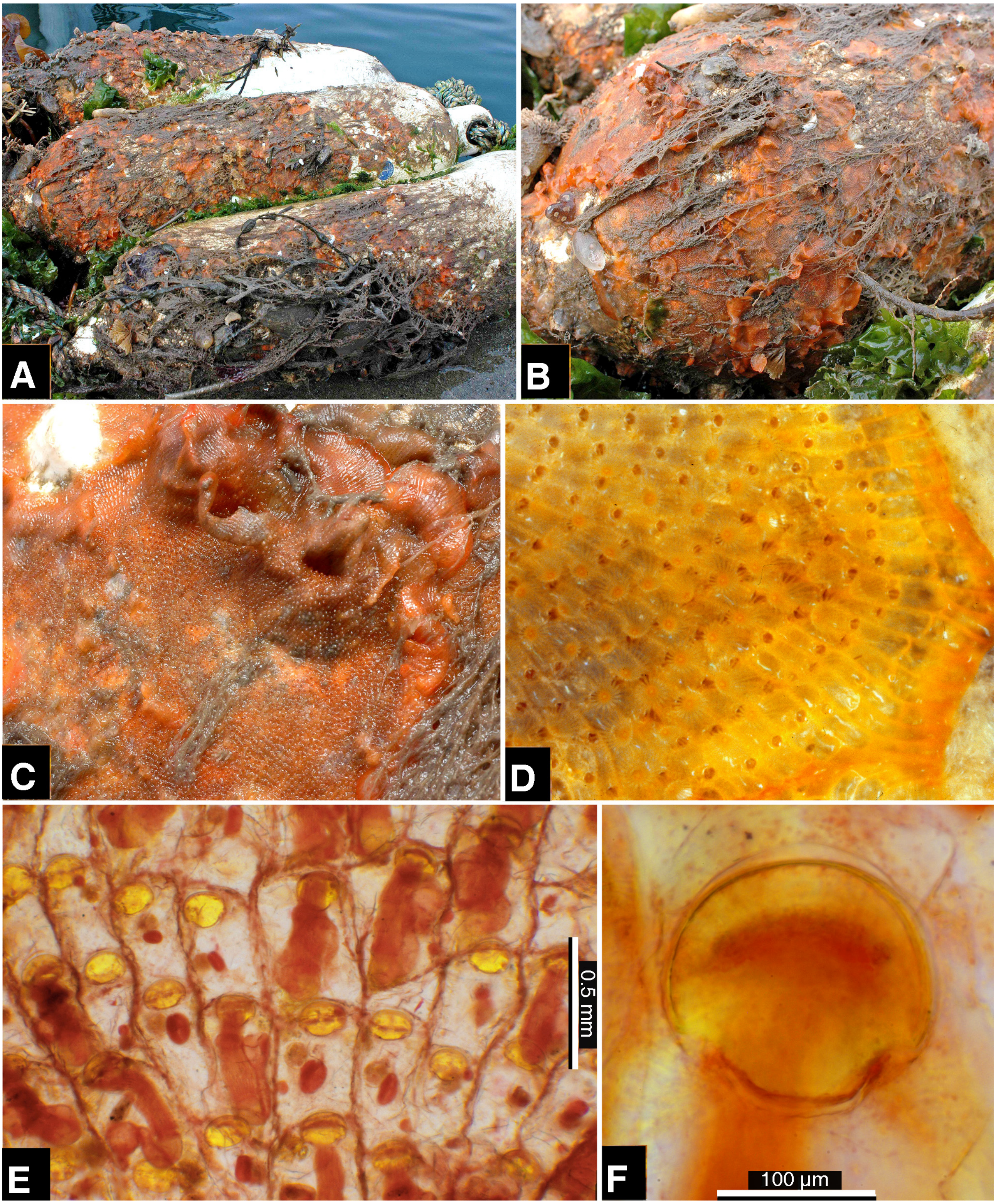

FIGURE 2. *Schizoporella japonica*. **A,** Colonies on fenders, Holyhead marina, June 2011; **B,** closer view of encrustations on the centre fender in A; **C,** Close-up of same encrustation (photos A–C, RH); **D,** macro-photograph of expanded zooids on flat substratum, Friday Harbor, WA, July 1986; **E,** balsam preparation of decalcified material stained with borax carmine and picric acid to show opercula, Holyhead marina, February 2011; **F,** enlarged view of operculum in E (photos D-F, JSR).

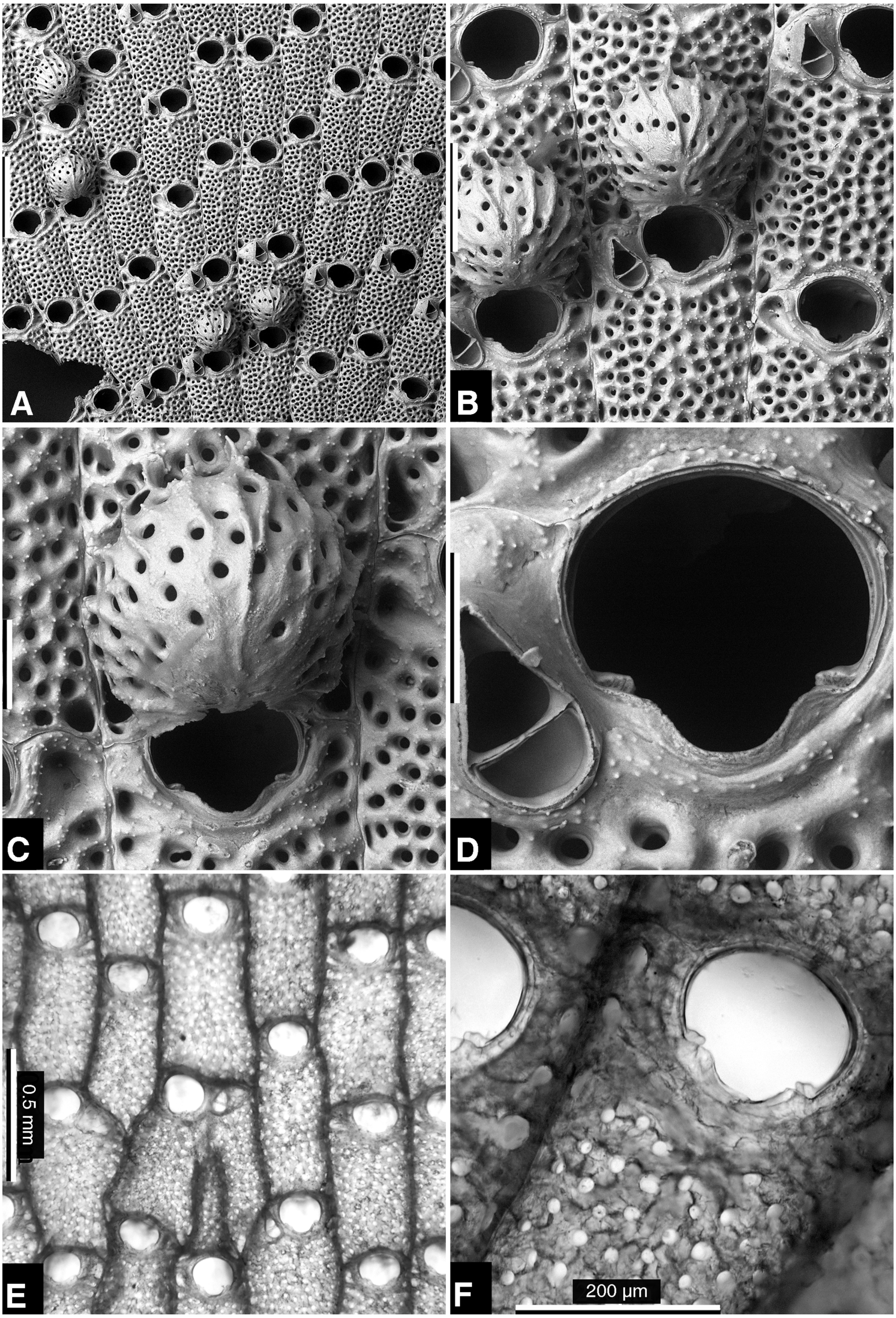

FIGURE 3. *Schizoporella japonica*. **A,** SEM of part of cleaned colony, Holyhead marina, February 2011; **B,** SEM at higher magnification; **C,** close-up of ovicell; **D,** close-up of non-ovicellate orifice, condyles and avicularium lateral to orifice. (A–D, SEMs at NHMUK by P. D. Taylor); **E,** balsam mount seen with transmitted light from same material showing variation in zooid width caused by row division; **F,** orifice from E at high magnification to show details of condyles (photos E–F, JSR). Scalebars: A, 500 µm; B, 200 µm; C, 100 µm; D, 50 µm.

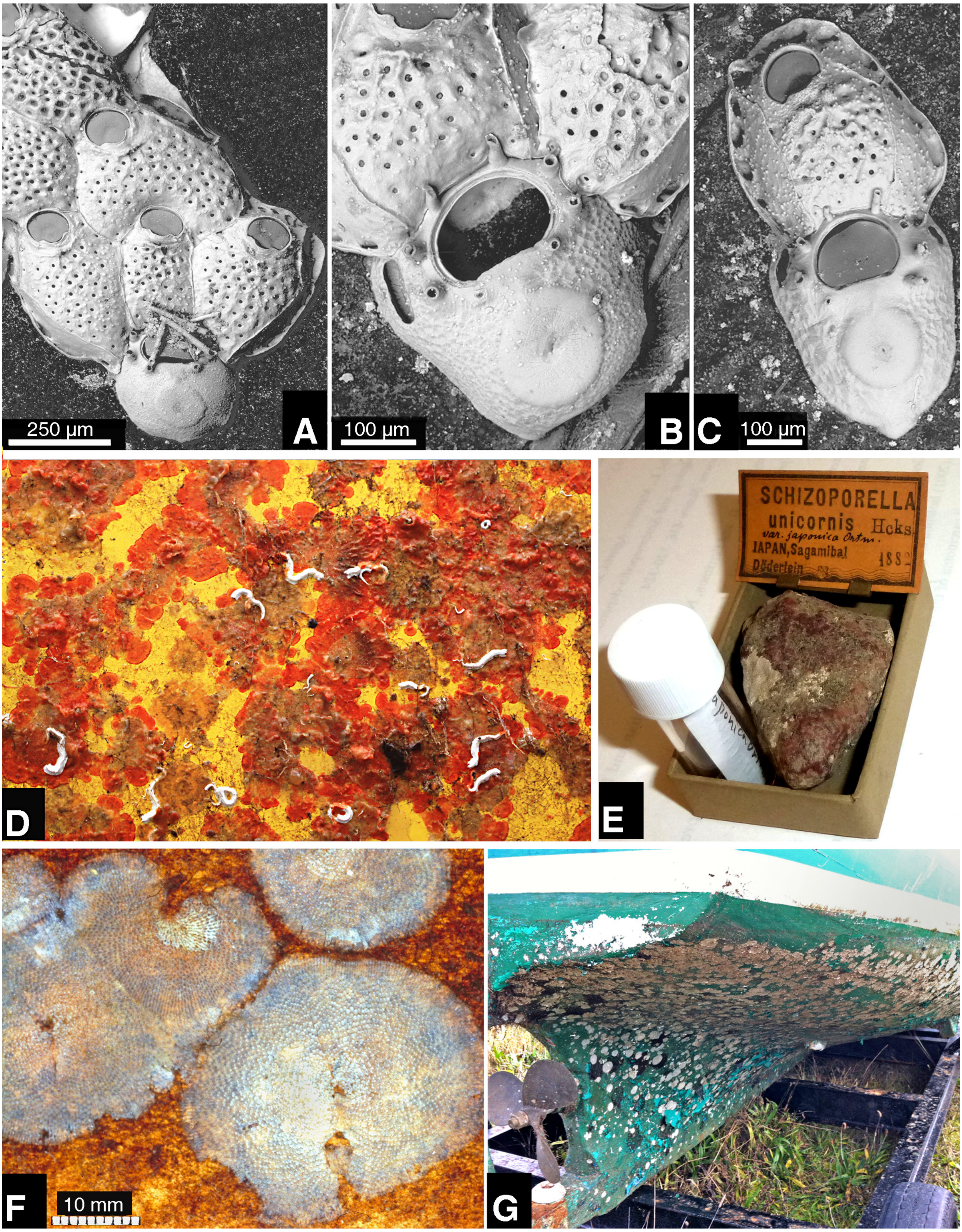

FIGURE 4. *Schizoporella japonica*. **A,** Ancestrula and early astogeny (one distal and symmetrical distolateral zooids); **B, C,** ancestrulae; (A–C from young colonies on a settlement plate immersed at 0.5 m in Stromness marina, Orkney Islands, December 2012); **D,** established colonies on a prototype tidal turbine following a two-year sea trial in the Orkney Islands (photo Andrew Want, EMEC,) January 2013; **E,** type specimen of *S. japonica* (MZS Bry001 in the Strasbourg Museum; photo Marie Meister); **F,** young colonies, Jakle's Lagoon, San Juan Island WA, collected by the late C. G. Reed and photographed by JSR in July 1986 (at the present time this lagoon is cut off from the sea by a shingle barrier); **G,** heavy settlement on hull of beached vessel, Orkney Islands (photo JSP).

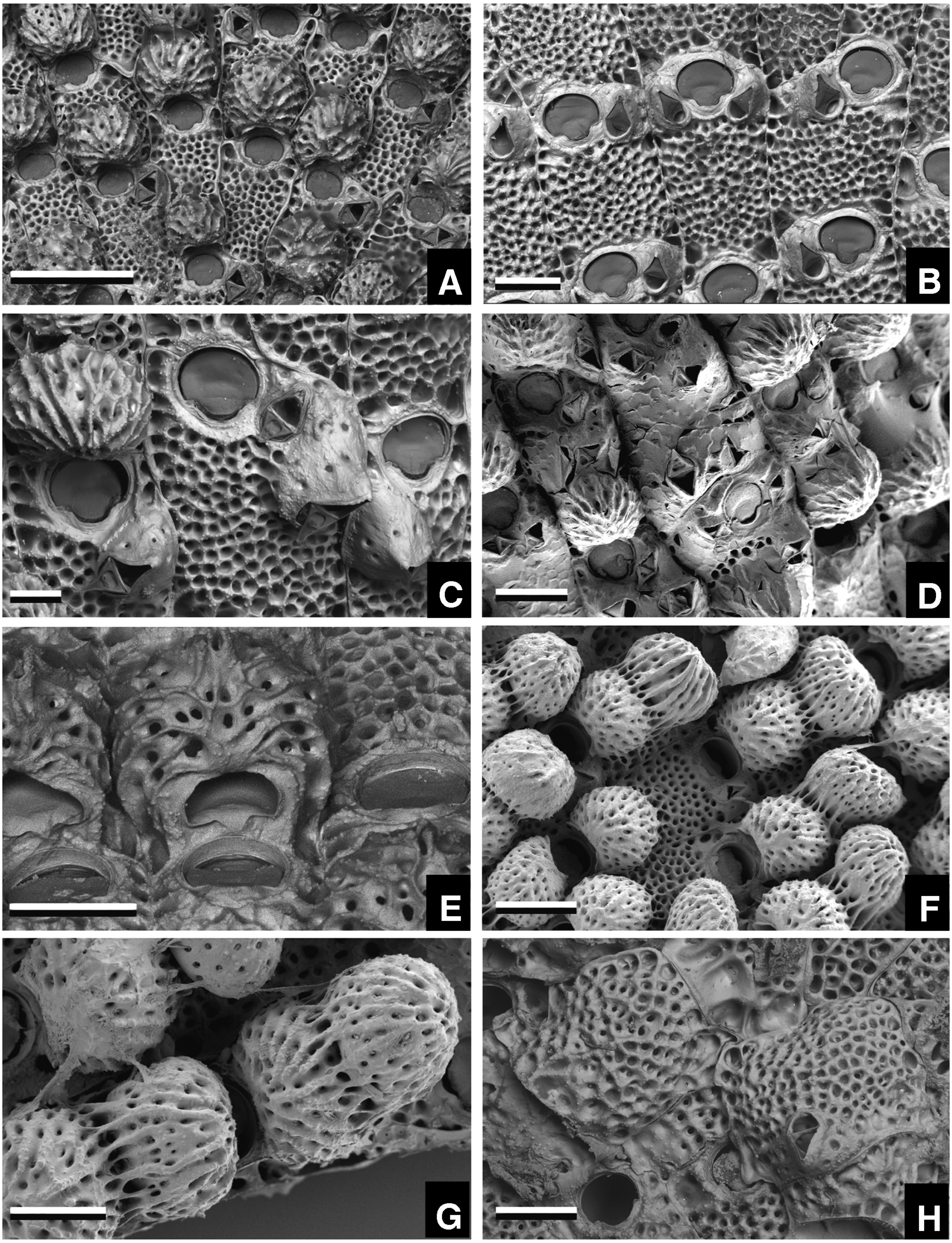

FIGURE 5. *Schizoporella japonica.* Samples from Stromness marina, Orkney, bleached (A–C, E, H) and lightly bleached (F, G), and sample from Portavadie marina, Scotland, unbleached (D). **A,** Array of ovicellate zooids; **B,** array of zooids featuring single and paired oral avicularia; **C,** zooids (left and right) with a single large frontal avicularium and autozooid (centre) with both oral avicularium and a large frontal avicularium; **D,** array of zooids with multiple mixed avicularia, up to four per zooid; **E,** angled zooid (centre) showing perforate ovicell and ovicell opening; **F,** array of ovicellate zooids showing single and double ovicells; **G,** close-up of multi-ovicellate zooid (centre) showing secondary ovicell on frontal shield facing primary ovicell and third ovicell stacked on primary ovicell; **H,** zooids (left and right) with perforate closure plates covering orifice. Scale bars: A, 500 µm; F, 300 µm; B, D, E, G, H, 200 µm; C, 100 µm.

commonly single but frequently absent or paired; situated lateral or proximolateral to orifice; mandible elongate-triangular, its tip acute, with distal to distolateral orientation; crossbar complete; chamber comparatively small, with 1–3 minute pores laterally around the base; sometimes, in older parts of the colony and associated with complete ovicells, one avicularium is larger, with raised chamber. Zooidal communication via 3–5 distal and 6 lateral basal pore-chambers. Ovicells prominent, hemispherical, partially overhanging the orifice, evenly porous, with larger slit-like pores around the base; sparsely distributed or in a reproductive band within the colony. Ancestrula oval, imperforate, 0.33 × 0.28 mm; orifice D-shaped, 0.13 × 0.15 mm, with 8 marginal spines; 3 zooids budded distally (Grischenko *et al*. 2007).

Remarks. *Variations and discussion.* Some striking variations that appear characteristic of *S. japonica* have been reported earlier and observed by us. A remarkable feature is the occurrence in Scottish material of multiple ovicells, arranged serially one behind another, and occasionally stacked (Fig. 5F–G). Powell (1970) and Powell *et al*. (1970) earlier described and illustrated a similar aberration in specimens from British Columbia and Washington State, and in a colony found on a scallop shell transplanted with oysters (*Crassostrea gigas*) from Onagawa Bay, on the Pacific coast of Honshu, Japan. Powell *et al*. (1970), using transplant experiments in Willapa Bay, Washington, attributed this occurrence of multiple ovicells to creosote-treated wood and the presence of petroleum derivatives in the water of harbours and marinas. It is not clear whether the occurrence of this phenomenon in Scotland is attributable to pollution; however, multiple ovicells were observed at sites all around the Scottish coastline. Powell et al. (1970) also noted that *S. japonica* (as *S. unicornis*) occurred in hyposaline water, down to salinities of 15.

All of the British occurrences have been in marinas, suggesting that—unlike the Pacific coast of North America (see later)—small, ocean-going vessels must have been the vectors (Fig. 4F shows colonies on a boat hull). We have no evidence to suggest whether Japan or North America was the source.

Distinction from Schizoporella unicornis. On the Atlantic coasts of Western Europe, including the British Isles, confusion of *S. japonica* is likely only with *S. unicornis*, although the usual habitats of the two species are quite different. *Schizoporella japonica* is so far known only from harbours and marinas, and is a typical fouling species; *S. unicornis* occurs in non-fouling situations, on stones, rocks, shells and kelp holdfasts on the lower shore and sublittorally. Comprehensive descriptions, variously illustrated, are available (Hayward & Ryland 1979; 1999; Ryland 1990; 1995; Tompsett *et al*. 2009) but, to facilitate ready comparison the morphological differences are summarized in Table 2.

TABLE 2. The characters of two *Schizoporella* species occurring on coasts in western Europe. Note that mandible lengths are foreshortened when seen from above using a high-powered stereoscope; since they project upwards at very roughly 30°, the true length is about 15% greater than that given in the table. (N = number of colonies; n = number of zooids).

Feature	*S. japonica*	*S. unicornis*
Colony form	Mainly unilaminar; sometimes with over-growing layer and flaky. A fouling species.	Unilaminar. Found on rock and algal substrata on open coasts.
Colour	Whitish-grey, pinkish or bright orange-red	Whitish-grey or pinkish-red
Zooid shape	On average about twice as long as broad	On average about 1.5 times as long as broad
Frontal wall	Densely covered with slightly sunken pseudopores: 615 (420–770) mm^{-2} (N = 4; n = 40)	Covered with rather small pseudopores: 525 (350–780) mm^{-2} (N = 5; n = 52)
Orifice	Width slightly >length (0.9:1.0); inter-condyle distance 100 µm	Width slightly >length (0.9:1.0); inter-condyle distance 80 µm
Condyles	Shoulders with subacute angles close to rounded angles of shallow sinus	Variably projecting shoulders almost reaching rounded angles of sinus
Ovicell	With radial ridges and numerous pores; sometimes >1 distal to an autozooid	With radial ridges; pores absent or few
Avicularia	Usually 0–1 (rarely >1); proximolateral to orifice, hinge-line about level with condyles; occasionally frontal and enlarged; mandible 75–95 µm, orientation variable but <45° from medial axis	Usually 1–2; proximolateral to orifice, hinge-line level or proximal to condyles; mandible length 65–85 µm, orientation variable but ~45° from medial axis

Results—morphometric analysis

Measurements (Figs 6–8) have been made (generally $n = 20$) for four species of *Schizoporella*: *S. errata* (eight: #1–8), *S. japonica* (12: #10–21), *S. pseudoerrata* (one only: #22) and *S. unicornis* (ten: #23–32) (Tables 3 and 4). Provenance of colonies is given in Appendix 1. Specimens were selected, as far as possible, from a wide geographical range, to avoid replicates from any one locality, but there was a surprising paucity of material in NHMUK; some has been freshly collected and much was sent by colleagues from overseas. When measuring zooids, it is a limitation that colonies must be fairly flat to ensure accuracy (avoiding foreshortening of oblique zooids), and frontally budded zooids—as found in multilaminar *S. errata*—are difficult to measure and tend to be differently shaped from those in the primary layer. Zooid measurements, such of those of type specimens (#1, 22, 23), have been taken from other sources, when necessary statistical variables had been included (see data in Appendix 1), or are shown without 95% confidence limits (#11, 20) in Figs 6 and 9. Even a cursory look at these shows that *S. japonica* zooids are different from those of *S. errata* and *S. japonica*. ANCOVA for all three species (Fig. 6; with length as covariate (x) and width as variate (y) shows no difference in slopes or means but, with width as covariate, there is still no difference in slopes ($P = 0.07$) but a huge difference between mean lengths ($P = 6.1 \times 10^{-7}$. That is an important result. The mean lengths of *S. errata* (521.4 (SD±41.9) µm) and *S. unicornis* (548.7 (±39.9) µm) do not differ (t-test, $P = 0.18$) but that of *S. japonica* (640.2 (±41.9) µm) is hugely different from both of the others (t-test, from *errata*, $P = 1.25 \times 10^{-6}$; from *unicornis*, $P = 2.5 \times 10^{-5}$; Tables 1, 3 and 4).

TABLE 3. Measurement summary (mean ± SD and range, µm) for *Schizoporella errata* and *S. pseudoerrata.* Sinus width is distance between condyles; $n = 20$ unless stated otherwise. [1]From Tompsett *et al*. (2009); [2]this is a multilaminar colony and the measured zooids had no consistent shape or orientation; [3]Hayward & McKinney (2002), data from two colonies; [4]Winston & Hayward (2012), which might refer to *S. variabilis*; [5]measured from SEMs. For further details see Figs 6–8 and Appendix 1.

Source	Zooid length	Zooid width	Orifice length	Orifice width	Sinus depth	Sinus width
S. errata						
Bay of Naples, 1879 (Type)[1]	494 (±43) 381–558	371 (±71) 263–508	154 (±15) 125–181	147 (±11) 125–172		
Bay of Naples, 2009[2]	589 (±73) 480–721	391 (±64) 271–582	131 (±10) 111–145	145 (±8) 125–156	31 (±4) 22–39	93 (±8) 82–104
Rovinj, 1950s (YV Gautier)	598 (±73) 404–693	315 (±54) 286-490	138 (±14) 112–171	146 (±13) 121–165	38 (±10) 23–54	88 (±9) 62–100
Rovinj, 1987-97[3]	570 (±48) 495–676	384 (±78) 288–518	124 (±18) 103–151	128 (±10) 112–146	29 (±4) 22–36	64 (±5) 53–72
Pearl Harbor, 1996	488 (±42) 396–565	378 (±67) 289–511	121 (±7) 107–132	132 (±10) 104–152	27 (±4) 20–34	72 (±7) 60–87
Pearl Harbor, 2011	500 (±58) 366–671	309 (±48) 200–401	143 (±9) 130–154	133 (±7) 124–148	25 (±6) 18–39	71 (±12) 55–101
San Francisco Bay, CA	470 (±81) 340–699	312 (±63) 198–444	126 (±9) 108–140	132 (±8) 112–149	29 (±4) 22–36	74 (±7) 59–88
Mystic Seaport, CT[4]	542 (±56) 439–670	370 (±58) 228–477	133 (±8) 115–143	137 (±8) 123–151	32 (±6) 24–47	75 (±10) 58–94
Bodega Harbour, CA	667 (±61) 527–822	289 (±30) 245–332	136 (±9) 118–158	157 (±9) 141–169	31 (±5) 23–39	107 (±7) 94–118
S. pseudoerrata						
Elkhorn Slough Type[5] ($n = 40$)	600 (±79) 504–927	318 (±78) 199–565	152 (±15) 113–182	161 (±14) 130–200		

TABLE 4. Measurement summary (mean ± SD and range, µm) for *Schizoporella unicornis*. Sinus width is distance between condyles; $n = 20$ unless stated otherwise. For further details see Figs 6–8 and Appendix 1. [1]From Tompsett *et al.* 2009; [2]from Hayward & McKinney 2002, two colonies.

Source	Zoid length	Zooid width	Orifice length	Orifice width	Sinus depth	Sinus width
Northeast England (Type) ($n = 35$)[1]	494 (±43) 381–558	371 (±71) 263–508	154 (±15) 125–181	147 (±11) 125–172		
Shetland ($n = 40$ for zooids)	604 (±45) 485–722	381 (±46) 287–481	130 (±9) 114–152	150 (±6) 136–159	31 (±4) 23–38	78 (±5) 69–87
"Great Britain" Hincks ($n = 30$ for zooids)	578 (±50) 485–729	390 (±60) 303–548	133 (±9) 118–149	143 (±7) 133–153	34 (±3) 29–42	91 (±6) 79–106
Stromness, Orkney	579 (±51) 507–727	367 (±43) 315–466	143 (±7) 133–156	157 (±11) 129–173	37 (±5) 29–47	85 (±7) 73–99
Strangford Lough, Northern Ireland	583 (±50) 525–721	371 (±60) 278–524	143 (±8) 122–153	164 (±10) 143–181	39 (±6) 23–49	97 (±6) 86–110
Great Castle Head, Pembrokeshire	526 (±37) 419–589	352 (±35) 294–415	129 (±6) 118–140	148 (±10) 135–168	35 (±7) 23–47	81 (±7) 69–96
Ría de Ferrol, Galicia (1)	528 (±61) 433–672	435 (±37) 371–502	118 (±5) 108–128	142 (±9) 127–157	27 (±4) 21–37	76 (±6) 65–86
Ría de Ferrol, Galicia (2)	499 (±47) 415–583	377 (±51) 284–492	117 (±8) 100–130	143 (±7) 133–154	25 (±7) 10–37	71 (±7) 61–84
Rovinj, Croatia[2]	488 (±36) 421–550	327 (±59) 244–428	102 (±9) 85–119	104 (±6) 98–111	27 (±6) 17–38	49 (±7) 33–62

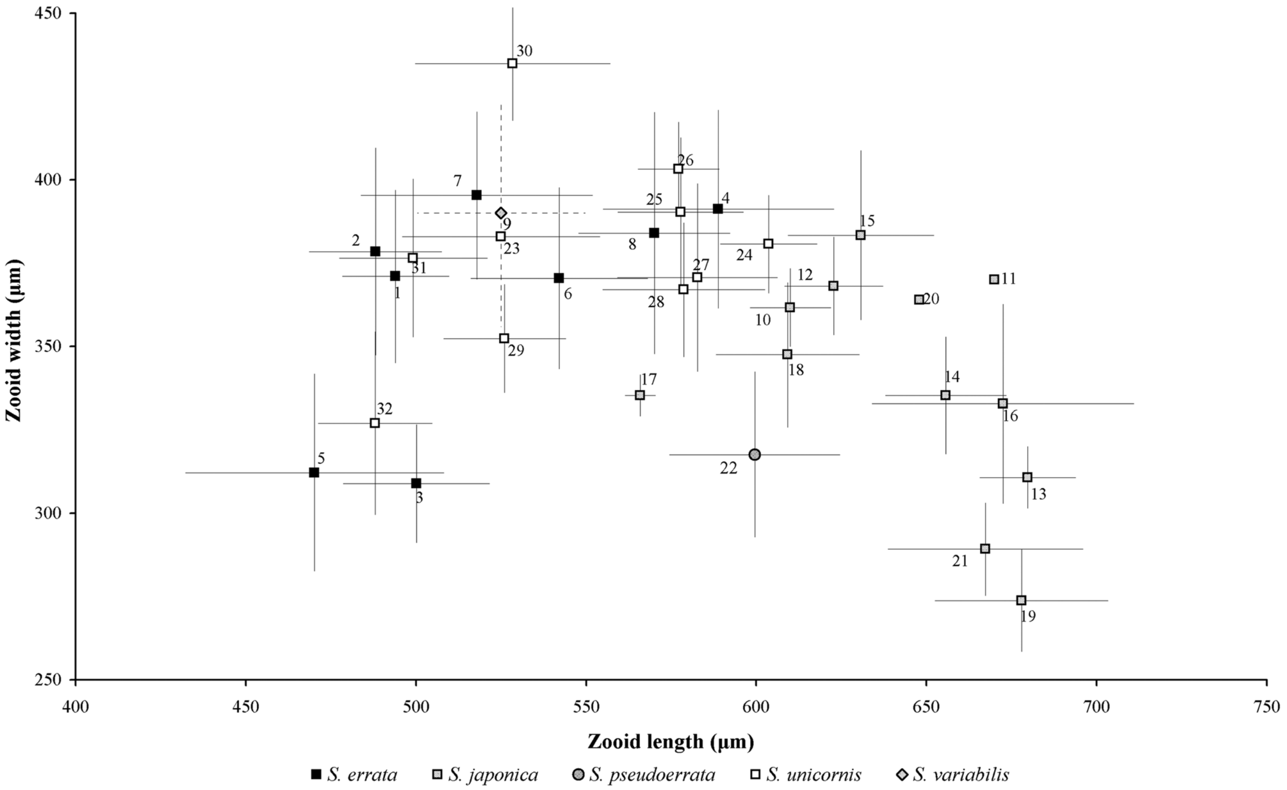

FIGURE 6. Zooid measurements (length and width) for five species of *Schizoporella*. Error bars are 95% confidence limits of the mean, labels identify particular specimens (refer to Appendix A); $n = 20$ in most cases. Only one specimen of *S. pseudoerrata* was available and this species, though shown in the graph, has been excluded from the analyses. The New England material of "*S. errata*" is regarded as a different species, *S. variabilis*, by Winston & Hayward (2012).

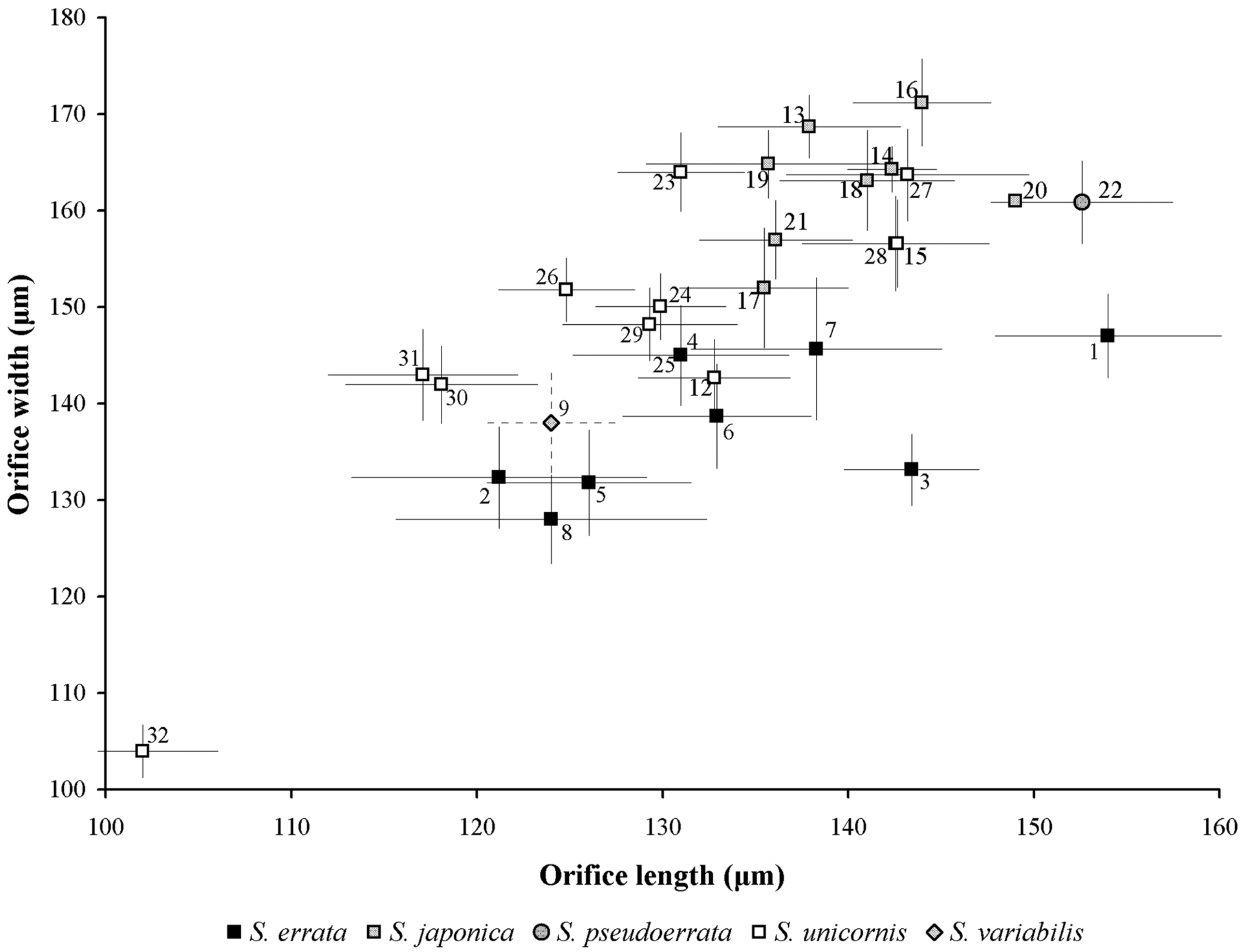

FIGURE 7. Orifice measurements (length and width) for five species of *Schizoporella*. Error bars are 95% confidence limits of the mean, labels identify particular specimens (refer to Appendix A); n = 20 in most cases. Only one specimen of *S. pseudoerrata* was available and this species, though shown in the graph, has been excluded from the analyses. The New England material of "*S. errata*" is regarded as a different species, *S. variabilis*, by Winston & Hayward (2012).

In the plot of orifice width *vs* orifice length (Fig. 7) one point (#32, *S. unicornis* from near Rovinj, Adriatic Sea) is clearly aberrant, but this site is geographically far removed from the remainder. ANCOVA has been performed with and without this point. In both cases there are no significant differences between slopes, but the adjusted means are highly so (P = 0.0008 with #32 included, 1.59×10^{-5} without it). The results show that the three species differ in orifice shape. Fortunately, when using t-tests the inclusion or exclusion of #32 has virtually no effect. Comparison of mean orifice widths in *S. errata* and *S. unicornis* shows no significant difference but the differences in mean width between *S. japonica* (160.49 ±8.9 µm) and the other two species are highly significant (*S. errata* 137.74 ±6.9 µm, $P = 1.63 \times 10^{-5}$; *S. unicornis* (with and without #32 respectively) 127.08 ±12.4 or 129.87 ±9.2 µm, $P = 3.79 \times 10^{-6}$ or 2.27×10^{-6}); little but the variance changes.

Differences in sinus shape are a little less marked. ANCOVA with width as covariate shows no differences between the three species (P = 0.35) but there are significant differences with length as covariate ($P \approx 0.001$). The mean width (inter-condyle distance) of *S. errata* (76.74 (±10.2) µm) and *S. unicornis* (78.36 (±14.6) µm) are very similar (Fig. 8) but that of *S. japonica* (98.90 (±7.1) µm) is markedly different from both of the others (t-test, from *errata*, P = 0.0003; from *unicornis*, P = 0.003).

To better establish which variables provide useful means for distinguishing species, a further series of t-tests was performed (Table 5) using the following ratios: zooid length:width, orifice length:width, and sinus depth:width. Each of these provided two highly significant results, with *S. japonica* being distinguishable from the other species by all characters, except from *S. unicornis* on the basis of sinus shape; using these characters *S. errata* was indistinguishable from *S. unicornis* except by the shape of the orifice (Table 5).

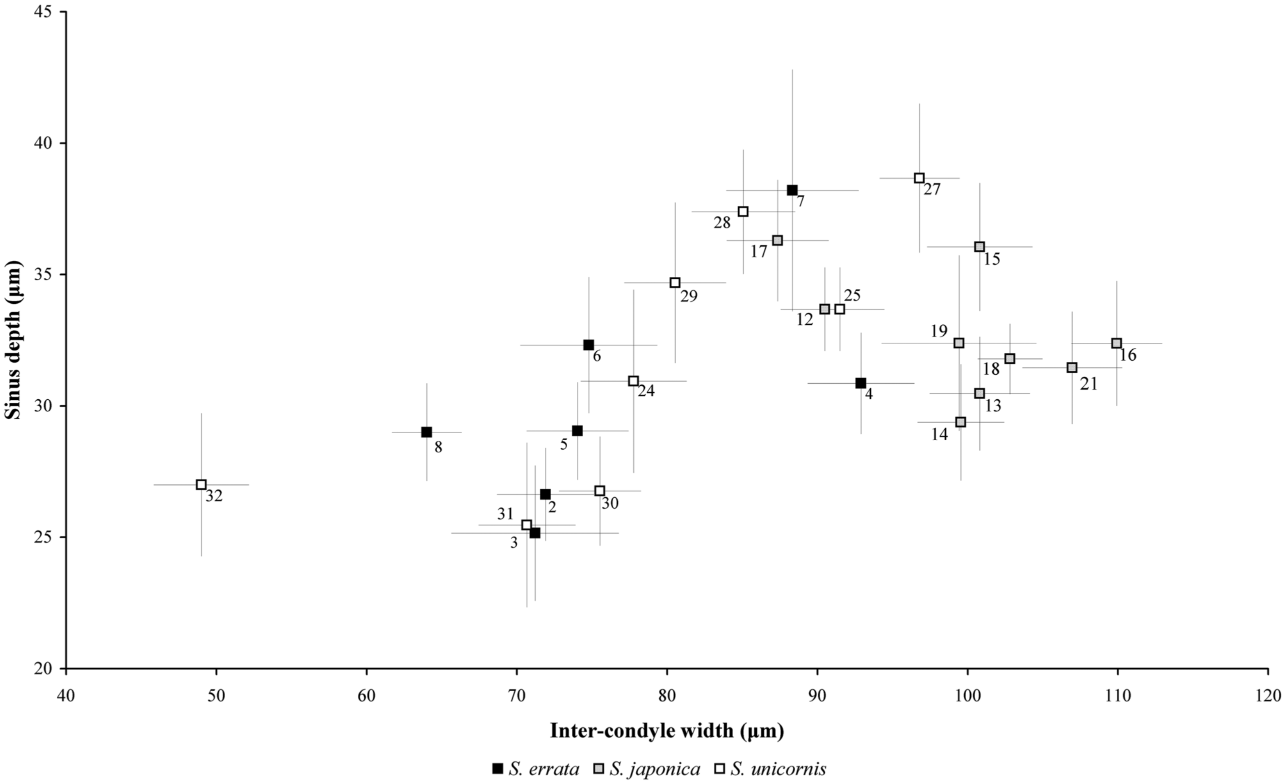

FIGURE 8. Measurements of the orificial sinus (length and width) for three species of *Schizoporella*. Error bars are 95% confidence limits of the mean, labels identify particular specimens (refer to Appendix A); $n = 20$ in most cases.

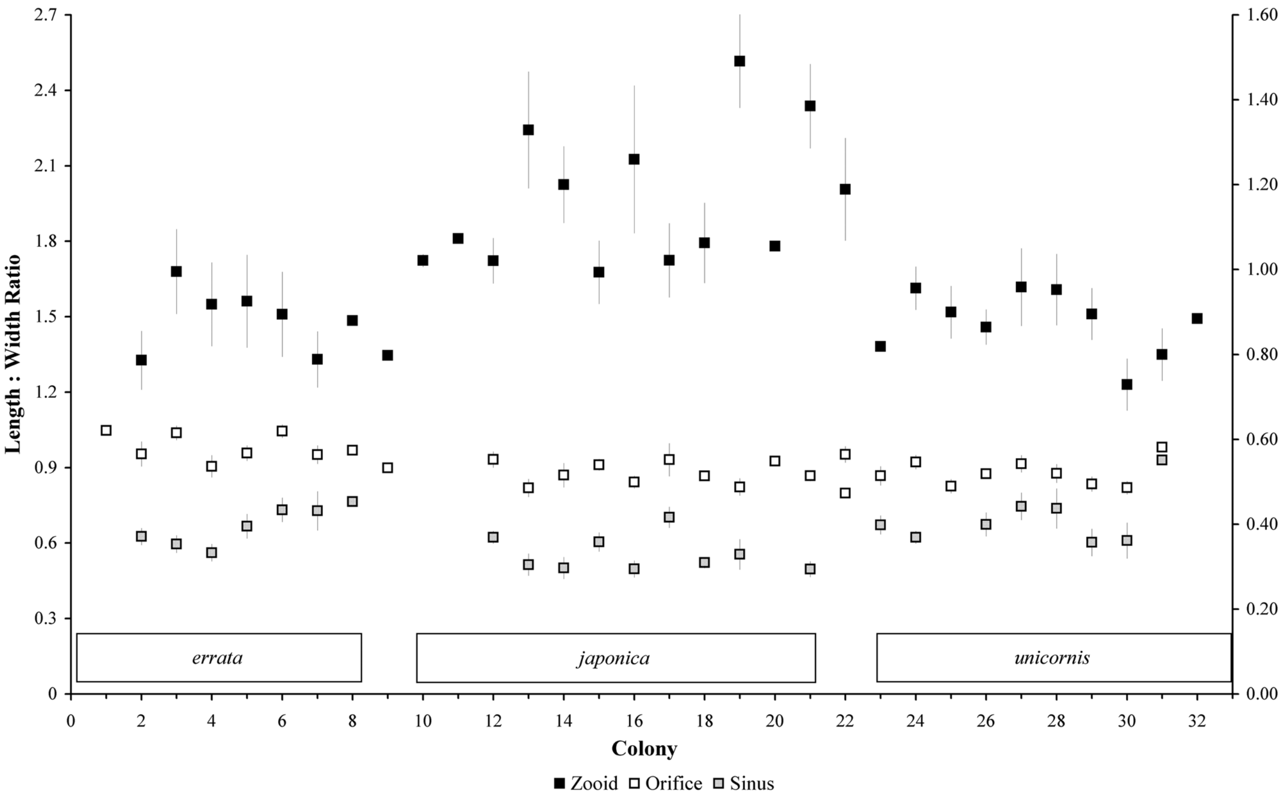

FIGURE 9. Variation between colonies of the length:width ratio of zooids (left ordinate), orifices (left ordinate) and sinuses (right ordinate) in three *Schizoporella* species. Error bars are 95% confidence limits of the mean. Colony numbers (abscissa) identify particular specimens (refer to Appendix A). All features display high inter-colony variation and the most reliable character appears to be the high length:width ratio in *S. japonica.*

TABLE 5. Significance levels for *t*-tests for four variables (zooid length, zooid length:width ratio, orifice length:width ratio, and sinus depth:width ratio) between three species of *Schizoporella*: *S. errata, S. japonica, S. unicornis*. Data tested are the means (n = 20) for the number of sets available (between seven and 11 according to species and variable being tested).

		Zooid length			Orifice L:W		
	errata	*japonica*	*unicornis*	*errata*	*japonica*	*unicornis*	
errata		4.25E-06	NS		6.40E-04	5.32E-04	*errata*
japonica	4.64E-04		1.49E-04	0.0193		NS	*japonica*
unicornis	NS	1.49E-04		NS	0.0110		*unicornis*
	Zooid L:W			Sinus L:W			

TABLE 6. Pseudopore densities (count mm^{-2}) in the zooid frontal shield of *Schizoporella* species; n = 10 (11 in colonies 28 and 29); further locality details are given in Appendix 1. Colony 16 (*S. japonica*) is aberrant in its placement.

Mean pseudopore density (mm^{-2}) (±SD)	Range: density (mm^{-2})	Species of *Schizoporella*	Colony reference number	Location	Similar colonies ($P_{\text{difference}} > 0.05$)
264.7 ±19.7	241–296	*errata*	7	Rovinj, Croatia	4
299.5 ±64.9	209–363	*errata*	4	Naples, Italy	5,7
375.1 ±37.8	301–431	*errata*	5	San Francisco Bay	4,27
449.4 ±40.4	382–537	*unicornis*	27	Strangford Lough, Ireland	5,16,28,29
498.9 ±32.3	416–528	*japonica*	16	Zen Beach, Japan	27,28,29,30.31
503.6 ±106.5	357–780	*unicornis*	29	Pembrokeshire, Wales	16,18,27,28,29,30,31
510.5 ±49.1	348–661	*unicornis*	28	Orkney Islands	16,18,27,29,30,31
579.5 ±81.4	463–705	*unicornis*	30	Ría de Ferrol, Spain	14,16,18,28,29,31
585.0 ±107.5	424–785	*unicornis*	31	Ría de Ferrol, Spain	14,16,18,28,29,30
606.3 ±75.0	494–796	*japonica*	18	Holyhead, Wales	14,28,29,30,31
633.0 ±66.2	569–766	*japonica*	14	Morro Bay, CA, USA	18,21,30,31
721.5 ±40.4	637–772	*japonica*	21	Bodega Hbr, CA, USA	14,18,30,31

The density of pseudopores in the frontal shield provides a potentially useful but rarely employed character for the discrimination of similar species. Counts per unit area (expressed as number mm^{-2}; $n \approx 10$ zooids) were made on young, clean zooids from 12 colonies (*S. errata* 3, *S. japonica* 4, *S. unicornis* 5). The results are shown in Table 6. With the exception of one somewhat aberrant colony (*S. japonica* #16, from Japan) out of sequence, the colonies sort into separate groupings with *S. errata* having the fewest pseudopores (species mean 313 ±64, range 209−431 mm^{-2}), *S. unicornis* being intermediate (525 ±101, 348−785 mm^{-2}), and *S. japonica* having the most (615 ±97, 416−772 mm^{-2}). The overall differences among colonies are very great (ANOVA, $P = 4.8 \times 10^{-33}$), confirming the huge amount of variation, but differences between species are almost as great (ANOVA, $P = 1.75 \times 10^{-25}$) despite colony #16. Individual colony comparisons were obtained by multiple comparison of means and the results are shown in the final column of Table 6. We conclude that, despite the considerable variation that exists between conspecific colonies from different geographic locations, frontal pseudopore density provides a potent character for species separation, *S. errata* being very obviously distinguishable from the other two species by its large, relatively sparse pseudopores.

Schizoporella on the Pacific coast of North America

Schizoporella unicornis, a Recent bryozoan originally described in a work on the Coralline Crag by Johnston (*in* Wood 1844; see Tompsett *et al*. 2009 for details) is a well-known European species (Johnston 1847; Hincks 1880;

Ryland 1965; Hayward & Ryland 1995, 1999; but not Marcus 1940 (= *S. errata*, absent from northern Europe)) that is unknown on the Pacific coast of North America. Because of undue reliance on European literature, generally inappropriate for the Pacific coast (e.g. Ryland & Porter 2012), the characteristics of this species (Hayward & Ryland 1995, 1999; Tompsett *et al*. 2009), especially the marginally fluted but virtually non-porous ovicell, were missed by authors or deliberately ignored (e.g. Ross & McCain 1976) and the name *unicornis* has been incorrectly applied to at least two quite different species. Osburn (1952)—before *S. japonica* had been recognized in the northwest—included only one nominate species that would now be included in the genus *Schizoporella*, using the name *S. unicornis*, from various localities in California. Osburn's account is now known to have been based on a mixture of *S. japonica* and *S. errata* (Powell 1970) and *S. pseudoerrata* (described by Soule *et al*. 1995). The current distribution of *S. errata* is unclear since the species is not discussed by Soule *et al*. (1995, 2007), though it is certainly common in San Francisco Bay (Zabin *et al*. 2010). The differences between *S. unicornis* and *S. errata* are in fact numerous and considerable (this paper and Ryland 1965; Hastings 1968; Hayward & Ryland 1999; Hayward & McKinney 2002; Tompsett *et al*. 2009). Whether *S. errata* should be regarded as a single species, a complex, or several species is another issue (Winston & Hayward 2012), which cannot be resolved here.

While *Schizoporella errata*, being a well-known fouling species, seems likely to have been introduced to the Pacific coast well before its first recorded occurrences (as *S. unicornis*, by Osburn 1952), *S. japonica* is most certainly a recent alien. However, Powell (1970) established that it (as *S. unicornis*), as opposed to *S. errata*, was present in Newport Bay, Los Angeles, as long ago as 1938 (material collected by G. E. MacGinitie); he assumed that it had arrived with Pacific oysters, *Crassostrea gigas*, which had been imported from Japan (first to Morro Bay) since 1932. This is the earliest record for this species on the west coast of North America. Powell (1970) referred to additional material in USNM from Newport, collected 1943, and Morro Bay, collected 1968. Powell (1970) himself found it (still using the name *S. unicornis*) from the Strait of Georgia, Canada. It had not been found earlier by O'Donoghue & O'Donoghue (1923, 1925, 1926) but was found by Powell during 1966–69 from several stations in the San Juan Islands, on Vancouver Island, and from as far north as Pendrell Sound (50° N). As for California, he attributed its arrival to the extensive importation of Pacific oysters from Japan in the period 1926–1935. Its recorded range was extended to further localities in Washington State by Ross & McCain (1976), who conducted a thorough study of zooidal shape [the variability noted earlier that arises from the growth pattern of circular colonies, a topic also investigated in this species by Thorpe & Ryland (1987)]. It was also collected in San Francisco Bay during 1977 (NHMUK 1978.1.4.2). Whereas *S. errata*, as a warm-water species, is likely to be commonest south of San Francisco, the converse is true for *S. japonica*. It has spread northwards through Canada to southern Alaska (Dick *et al*. 2005) but, as already noted, it extends southwards beyond San Francisco to Morro Bay (#14) and (historically at least) to the Los Angeles area.

Thus it now appears that three distinct species of *Schizoporella* occur in central California (i.e. the Monterey Bay area), *S. errata, S. japonica*, and *S. pseudoerrata*, the first two, at least, being introductions. Sorte *et al*. (2010) listed an unidentified *Schizoporella* from Bodega Harbor, most likely *S. japonica* (see #21) but possibly *S. errata*, and Zabin *et al*. (2012) recorded unidentified *Schizoporella* from two sites at Santa Cruz. *Schizoporella pseudoerrata* at present has a very localized confirmed distribution (Soule *et al*. 1995) although it has been listed as present at two sites in the northern part of San Francisco Bay—Richmond Marina (Blum *et al*. 2007) and Tiburon (Crooks *et al*. 2011). It is possible that these records are based on misidentifications and might be either of the other two species. With all three species now recognized and described, it should be possible to correctly identify *Schizoporella* specimens from the Pacific coast. The characteristics of the three Californian species are summarised in Table 7 (particularly note the distinctive condyles, observation of which requires the preparation of specimens with a hypochlorite bleach such as Clorox: see Material and Methods above), which should be used in conjunction with Figures 2–4 and 10.

In addition to morphometric methods, genetic techniques have recently been applied in two non-native fouling bryozoan species-groups. In *Bugula neritina* (Linnaeus), three biological species were identified. One of these, haplotype S, was globally distributed (Fehlauer-Ale *et al*. 2013). In *Watersipora subtorquata*, three clades were identified by Mackie *et al*. (2012). These studies provide evidence for cryptic speciation in the fouling community. Genetic studies on *Schizoporella japonica* are currently underway to investigate the potential for cryptic species in this taxon.

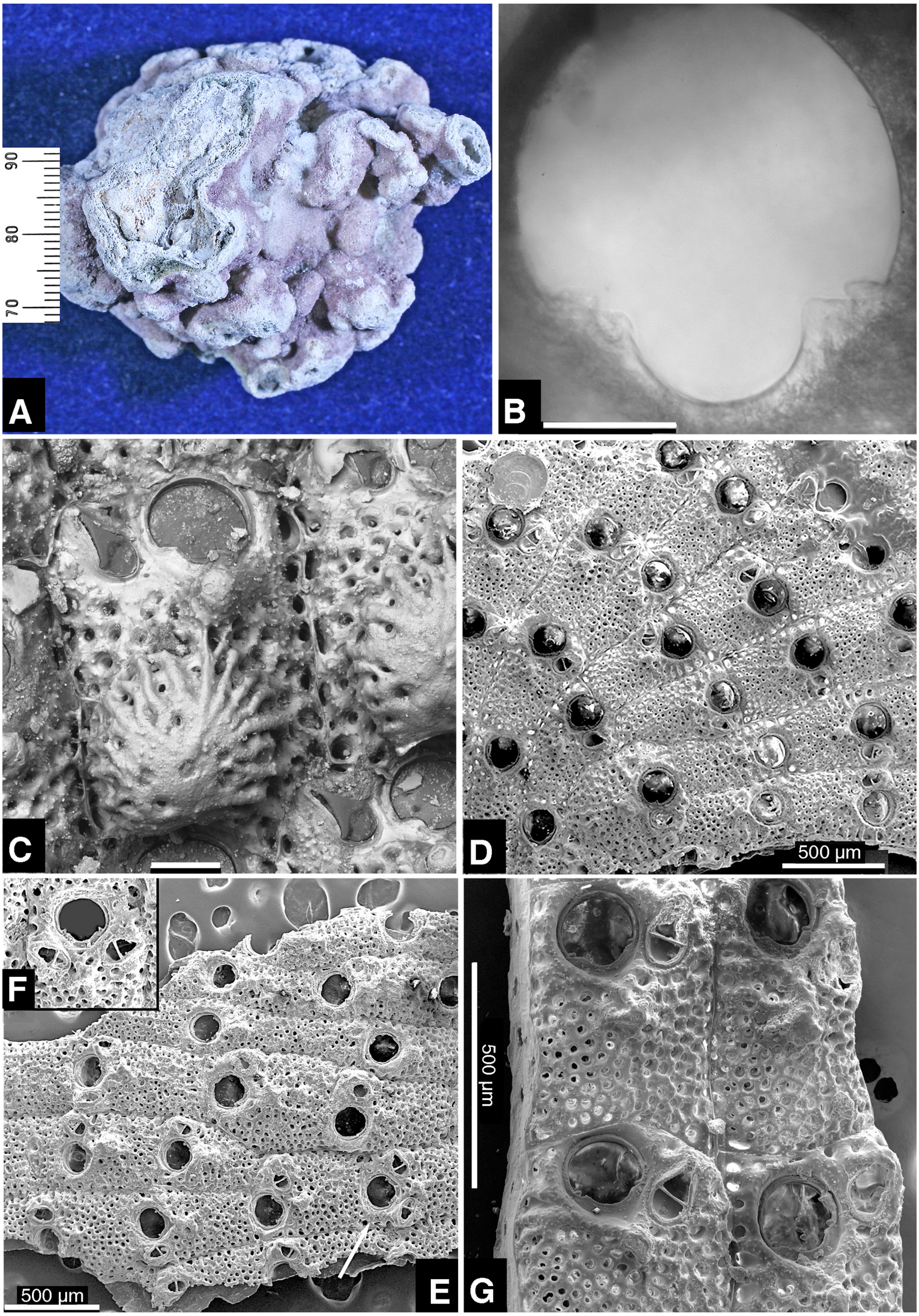

FIGURE 10. *Schizoporella errata* (A–C) and *S. pseudoerrata* (D–G). **A,** *S. errata* colony showing typically massive structure produced by repeated frontal budding (Coyote Point, San Francisco Bay, coll. J. T. Carlton, 11 October 2009); **B,** *S. errata*, orifice and condyles, transmitted light (Pearl Harbor, HI, coll. J. T. Carlton 7 June 2011), scale bar 50 µm; **C,** *S. errata*, SEM (photo MSJ), NHMUK 2009.1.26.2 (Nisida Harbour, Nisida Island, Naples, 1 m depth, coll. S Tompsett, 11/9/2008); D–E, *S. pseudoerrata*, SEM, parts of colonies (Elkhorn Slough, Monterey Bay, CA, coll. J. D. and D. F. Soule, 1995; SEMs H. Chaney), inset (F) shows orifice with paired suboral avicularia; G, *S. pseudoerrata*, SEM, detail (same provenance as D–E).

TABLE 7. The characters of *Schizoporella* species occurring on the Pacific coast of North America. Note that mandible lengths are foreshortened, as seen from above using a high-powered stereoscope, since they project upwards at very roughly 30°; the true length is about 15% greater than that given in the table. (N = number of colonies; n = number of zooids).

Feature	*S. errata*	*S. japonica*	*S. pseudoerrata*
Colony form	Initially encrusting, becoming multilaminar and 3-dimensional; often with tubular extensions	Mainly unilaminar; sometimes with an overgrowing layer and flaky.	Initially encrusting, becoming multilaminar and 3-dimensional
Colour	Reddish-brown to dark violet	Whitish-grey, pinkish or orange-red	Not recorded
Zooid shape	On average about 1.5 times as long as broad	On average about twice as long as broad	About 1.5–2.0 times as long as broad
Frontal wall	Covered with relatively few large, sunken pseudopores: ~310 (200–430) mm^{-2} (N = 3; n = 30)	Densely covered with slightly sunken pseudopores: ~615 (420–770) mm^{-2} (N = 4; n = 40)	Irregularly covered with variably sized sunken pseudopores: ~630 (560–725) mm^{-2} (N = 1; n = 10)
Orifice	Width ≈ length; inter-condyle distance ~75 µm	Width >length (0.9:1.0); inter-condyle distance ~100 µm	Slightly wider than long (0.90–0.95:1); inter-condyle distance ~100 µm
Condyles	In the form of blunt teeth about their own width distant from the sharply obtuse angle of the sinus	Shoulders with subacute angles close to the rounded angles of the shallow sinus	Pointed teeth, distomedially directed, quite close to the gently curved transition to the sinus
Ovicell	Porous; radial ridges absent or few	Porous; with well developed radial ridges; >1, in series, may be present on one autozooid	Porous; sometimes with radial ridges
Avicularia	Usually 1, proximolateral to orifice, sometimes displaced; hinge-line often proximal to condyles; average mandible length ~90 µm but sometimes longer, biconcave, tapering, orientation variable but > 45° from medial axis	Usually 0 or 1 (rarely 2 or more); proximolateral to orifice, hinge-line about level with condyles; mandible 75–95 µm long, orientation variable but <45° from medial axis; occasionally frontal and enlarged	0, 1 or 2 proximolateral to orifice; hinge-line beside or proximal to condyles; mandible ~80 µm (from SEMs); orientation somewhat variable each side of 45°

Acknowledgements

We have been dependent on colleagues for the supply of specimens from outside Western Europe, especially to Matt Dick and Jim Carlton. Shetland sampling was facilitated by Georgia Conolly, Rachel Shucksmith, Richard Shucksmith and Bob Anderson. Orkney sampling was arranged by Lindsey Craddock at Orkney Marinas Ltd. Scottish West coast sampling assistance was provided by Sally Rouse. Hamish Mair provided fieldwork assistance for all Scottish East coast and Orkney marine surveys. Andrew Want provided photographs of *Schizoporella* on Orkney tidal turbines. Hank Chaney provided new SEMs of *S. pseudoerrata,* Paul Taylor made the original batch of SEMs of *S. japonica* from Holyhead, Marie Meister registered and took the photo of the type material of *S. japonica* in the Strasbourg Museum. All of our scanning electron microscopy has been performed in the EMMA unit at NHMUK. The views expressed in this paper should not be interpreted as those of the Environment Agency or Natural Resources Wales.

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APPENDIX. Index of *Schizoporella* sources and specimens used in the compilation of metric data.

	Species	Country and/or Ocean	Location	Date	Latitude	Longitude	Museum and/or Source	Collector	Specimen ID
1	*errata*	Italy, Mediterranean	Bay of Naples	before 1879	~14°40' N	~14°00' E	Tompsett *et al.* 2009	A.W. Waters	MM H1186.3113, TYPE
2	*errata*	Pacific USA	Pearl Harbor, Oahu, HI	01/08/1996	21°22' N	157°58' W	J.T. Carlton (JTC 03-A)	Ralph DeFelice	NHMUK 2013.12.18.1-3
3	*errata*	Pacific USA	Pearl Harbor, Oahu, HI	07/06/2011	21°22' N	157°58' W	J.T. Carlton	J.T. Carlton (JTC 04)	NHMUK 2013.12.18.4-7
4	*errata*	Italy, Mediterranean	Nisida Hbr, Bay of Naples	before 2009	40°47.9' N	14°10' E	Tompsett *et al.* 2009	S. Tompsett	NHMUK 2011.9.21.33
5	*errata*	Pacific USA	Coyote Pt, San Mateo County, San Francisco Bay, CA	11/10/2009	37°35' N	122°18.5' W	Zabin *et al.* 2010	J.T. Carlton (JTC 05)	NHMUK 2013.12.18.8
6	*errata*	Atlantic USA	Mystic Seaport, Mystic River Estuary CT	20/11/2009	41°21.7' N	71°58' W	JT Carlton	J.T. Carlton (JTC 07)	NHMUK 2013.12.18.9
7	*errata*	Croatia	Rovinj	1950s	45°4.7' N	13°38' E	NHMUK	Y.V. Gautier	NHMUK 1960.11.2.12
8	*errata*	Croatia	Rovinj &/or Limski Fjord (Lim Channel)	1987–1997	45°8' N	13°38' E	Hayward & McKinney 2002		
9	*variabilis*	Atlantic USA	East coast MA–NJ		40-42.5° N	70-74° W	Winston & Hayward 2012		
10	*japonica*	USA & Canada	Juan de Fuca Strait etc., Washington State & BC	1968–1975	46°14'-49° 10.5' N	~123°50' W	Ross & McCain 1976		
11	*japonica*	Pacific USA	Friday Harbor WA	Jul. 1986	48°32.2' N	123°1' W	Thorpe & Ryland 1987	JSR	
12	*japonica*	Pacific USA	Drakes Beach in Drakes Bay, Marin County, CA	09/10/2009	38°01.5' N	122°56' W	J.T. Carlton	J.T. Carlton (JTC 02)	NHMUK 2013.12.18.10
13	*japonica*	Pacific USA	Boatslip, St Francis Yacht Harbor, S Franciso Bay	03/10/1977	37°48.5' N	122°26.5' W	John Inase		NHMUK 1978.1.4.2
14	*japonica*	Pacific USA	Morro Bay, CA; east side of bay	25/09/1972	35°21.2' N	120°50.5' W	J.T. Carlton	J.T. Carlton (JTC 01)	NHMUK 2013.12.8.11-16
15	*japonica*	Japan; Sea of Japan	Oshoro Bay, Otaru, Hokkaido	Apr. 2004	43°12.3' N	140°49.2' E	Grischenko *et al.* 2010	M. Dick	NHMUK 2013.12.18.31
16	*japonica*	Japan; Sea of Japan	Zenibako Beach, Otaru, Hokkaido	29/06/2005	43°8.8' N	141°9.6' E	M. Dick	M. Dick	NHMUK 2013.12.18.17-19

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APPENDIX. (Continued)

	Species	Country and/or Ocean	Location	Date	Latitude	Longitude	Museum and/or Source	Collector	Specimen ID
17	*japonica*	Japan; Pacific	Akkeshi Bay, Hokkaido	04/06/2004	42°59.4' N	144°48' E	Grischenko *et al.* 2010		NHMUK 2013.12.18.20
18	*japonica*	Wales	Holyhead marina	15/02/2011	53°19.2' N	4°38.6' W		R. Holt	NHMUK 2013.12.18.21-25
19	*japonica*	Scotland, Orkney Is	Collected from under MV Challenge (which berths mainly at Kirkwall)	06/09/2011				J. Loxton	
20	*japonica*	Pacific USA	Alaska: East Tongass narrows, Ketchikan	12/09/2003	55°19.2' N	131°31.2' N	Dick *et al.* 2005		NHMUK 2013.12.18.26
21	*japonica*	Pacific USA	Bodega Harbor, Sonona County CA	Fall 1996	38°19.3' N	123°2.9' W	J.T. Carlton	J.T. Carlton	
22	*pseudoerrata*	Pacific USA	Elkhorn Slough, Monterey Bay CA	No date	36° 49.2' N	121°44.4' W	Soule *et al.* 1995		TYPE
23	*unicornis*	British Isles	Northeast England				Tompsett *et al.* 2009		TYPE
24	*unicornis*	British Isles	Shetland				NHMUK	A.M. Norman	NHMUK 1911.10.1.1053 (B)
25	*unicornis*	British Isles	“Great Britain”				NHMUK	T. Hincks	NHMUK 1899.5.1.62
26	*unicornis*	British Isles	Ballochmartin Bay, Great Cumbrae	24/05/1996	55° 46.9' N	4°53.8' W	JSR	JSR	Photo only
27	*unicornis*	Ireland	Strangford Narrows (Walter's Rock)	20/08/2012	54°23' N	5°33.3' W	JSR	JSR	NHMUK 2013.12.18.27
28	*unicornis*	Scotland, Orkney Is	Warbeth, Stromness, Orkney Mainland	08/06/2011	58°57.4' N	03°19.9’ W	J. Loxton	J. Loxton	SU50
29	*unicornis*	Wales	Great Castle Head, Dale, Pembrokeshire	19/09/2012	51°42.4’ N	5°11.3’ W	JSR	JSR	NHMUK 2013.12.18.28-30
30	*unicornis*	Spain	Punta Pitora, Ensenada del Baño, Ría de Ferrol, Galicia	03/07/2008	43º27.69' N	8º15.78' W	NHMUK	S. Tompsett, J. Souto	NHMUK 2011.9.21.22
31	*unicornis*	Spain	Punta Pitora, Ensenada del Baño, Ría de Ferrol, Galicia	03/07/2008	43º27.69' N	8º15.78' W	NHMUK	S. Tompsett, J. Souto	NHMUK 2011.9.21.30
32	*unicornis*	Croatia, Adriatic Sea	Punta Corrente, Rovinj	23/9/90 or 12/6/97	45°03.8' N	13°37.5' E	Hayward & McKinney 2002	F.K. McKinney	