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Taxonomy of the fouling cheilostome bryozoans *Schizoporella unicornis* (Johnston) and *Schizoporella errata* (Waters)

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The cheilostomes *Schizoporella unicornis* (Johnston, 1847) and *Schizoporella errata* (Waters, 1878) have been used as model species in several ecological and taxonomic studies. However, these species have been consistently misidentified in a large percentage of such works. Here full taxonomic descriptions of both species, based largely on scanning electron micrographs of type specimens, are presented. A lectotype is chosen for *S. errata* and it is shown that the species described as “*Lepralia unicornis?* Johnson MS” from the Pliocene Coralline Crag by Wood (1844) is not conspecific with Johnson’s *L. unicornis* introduced for Recent material three years later. This work has implications for the application of seemingly cosmopolitan species to the study of anthropogenic disturbance and identifies the need for molecular characterization of cryptic species complexes.

Keywords: Bryozoa; Cheilostomata; taxonomy; fouling

Introduction

The cheilostome bryozoan *Schizoporella* is found throughout the world’s oceans and in all climatic zones from polar to tropical regions (Marcus 1940; Hayward and Ryland 1995). More than 50 Recent species have been placed in *Schizoporella* (Bock 2009), including nine recorded European species (Zabala and Maluquer 1988; Hayward and Ryland, 1999). A further 52 fossil species from the Paleocene to the Pleistocene have been attributed to *Schizoporella*.

The importance of the genus *Schizoporella* is emphasized by the fact that, as noted by Hayward and McKinney (2002), *Schizoporella unicornis* and *Schizoporella errata* have been used as model species in studies of: larval settlement behaviour (Hurlbut 1991; McKinney and McKinney 2002), competition for substrate space (Sutherland 1978; Buss 1981; Turner and Todd 1994; Tzioumis 1994), chemical-mediated hyperplasia (Powell et al. 1970), induction of row bifurcations (Banta 1972), environmentally mediated colony morphology (Cocito et al. 2000), epifaunal associations (Maluquer 1985; Morgado and Tanaka 2001), skeletal carbonate composition (Rucker and Carver 1969) and skeletal ultrastructure (Tavener-Smith and Williams 1970). Of particular ecological interest has been the role of *Schizoporella* as an invasive fouling organism in ports and on ships and harbour structures (Ryland 1965; Powell 1970; Gordon and Mawatari 1992; Relini et al. 1998; Kocak 2007). The ability of *S. errata* to survive transportation by shipping has led to the inference of a

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recent anthropogenic displacement from the Mediterranean to Australia (Wyatt et al. 2005), New Zealand (Gordon and Mawatari 1992) and the Californian coast (Zabin et al. forthcoming). Finally, *Schizoporella* has also been used as a model organism in studies of the relationships between genetic population structuring and morphometric characters (Schopf and Gooch 1971; Watts and Thorpe 2006).

Schizoporella is readily identified by its sinuate primary orifice, single or paired adventitious avicularia lateral to the orifice, lepralioid frontal shield with areolae and pseudopores and prominent ovicells. However, differences between species can be subtle and very few of the species have been adequately described by modern standards. This has led to a common assumption that certain species have cosmopolitan ranges, encompassing either entire or multiple ocean basins. In common with some other cheilostome genera (e.g. *Microporella*, see Taylor and Mawatari 2005) this is no doubt partly because earlier descriptions were based solely on optical microscopy, which may fail to resolve all of the important morphological features. Adding to these taxonomic problems have been doubts about the identity and authorship of the type species of the genus, *Lepralia unicornis*. Berning (2006) suggested that the identity of *S. unicornis* is confused because its primary description can be interpreted either as a Pliocene fossil from the Coralline Crag (Wood 1844) or a Recent specimen from the British Isles (Johnston 1847). In addition, *S. unicornis* has also been mistaken for *S. errata* (Waters, 1878). Although this problem was partially clarified in a scanning electron microscopy (SEM) study of the lectotype specimen of *S. unicornis* by Soule et al. (1995), no comparison was made with the type material of *S. errata*. Following the work of these authors, the identity of species from the west coast of the USA has been further called into question by the comprehensive redescription of the invasive Pacific species *S. japonica* (Ortmann, 1890) by Dick et al. (2005).

A well-founded taxonomy of *S. unicornis* and *S. errata* is, therefore, of great importance. This is particularly so as we enter an era where concerns over climate change and ocean acidification stimulate comparative studies using model species over wide geographical ranges. Although recent works (Dick et al. 2005; Winston 2005) have gone some way towards clarifying the status of these two species, a thorough study of the type specimens of *S. unicornis* and *S. errata* has not been previously undertaken using SEM. Furthermore, redescription of the type material of *S. errata* is necessary because of the still outstanding question of whether this is a single species or a species complex (Winston 2005).

The aims of the current paper are to (1) give detailed descriptions of *S. unicornis* and *S. errata* based on SEM analysis of type and other material, and (2) review the ecological literature to assess the true identity of supposed examples of these two species used in these studies. This information will serve to inform ongoing molecular investigations of the genus *Schizoporella*.

Material and methods

Studied specimens of *S. unicornis* are from the Johnston Collection at the Natural History Museum, London (NHM), whereas specimens of *S. errata* come from the Waters Collection in the Manchester Museum (MM). As material from the MM could not be bleached for analysis of skeletal morphology, additional topotypical material from Naples was collected and lodged in the NHM. Fossil specimens of putative *S. unicornis* from the palaeontological collections of the NHM were also studied.

In the case of lectotypes, cleaning was limited to gently removing loose debris using an air gun. Other specimens were soaked in a 10% solution of domestic bleach (Domestos Thick Bleach, Lever Fabergé Ltd, Wirral, UK) containing 4.9% sodium hypochlorite and non-ionic surfactants. Specimens were treated overnight, or until coelomic material and chitinous parts had been fully removed. They were then thoroughly washed in water to remove residual bleach and dried at room temperature.

Uncoated specimens were imaged using a LEO 1455VP low-vacuum scanning electron microscope at the NHM. All images were standardized based on a working distance of 12 mm at an accelerating voltage of 20 kV and a chamber pressure of 15 Pa. Topotype specimens were sputter coated with platinum palladium and then imaged in a Hitachi S-4700 FEG at Aberystwyth University (AU) using the same standardization. From the images obtained measurements were taken using IMAGE J software (rsbweb.nih.gov: IMAGE-J).

Systematics

Infraorder **LEPRALIOMORPHA** Gordon, 1989
 Superfamily **SCHIZOPORELLOIDEA** Jullien, 1883
 Family **SCHIZOPORELLIDAE** Jullien, 1883
 Genus *Schizoporella* Hincks, 1877

Type species

Lepralia unicornis Johnston, 1847, Recent, British Isles. By original designation.

Remarks

Canu (1908) considered *S. unicornis* to be a junior subjective synonym of *Multiporina ostracites* d'Orbigny, 1852, an Oligocene fossil that is the type species of *Multiporina* d'Orbigny, 1852 by monotypy, making *Schizoporella* Hincks, 1877 a junior synonym of *Multiporina*. This synonymy was supported by Bassler (1935) who noted that although *Multiporina* is the senior synonym, because of the common use of *Schizoporella* in later studies the latter genus should be maintained. The issue was revisited by Buge (1975) who figured d'Orbigny's holotype of *M. ostracites* and confirmed the synonymy of *Multiporina* and *Schizoporella*. Gordon and Taylor (2005) noted that *Multiporina* should be treated as *nomen oblitum* because it has not been used for over 50 years.

Figures of the holotype of *M. ostracites* in Buge (1975) show that it is indeed a species of *Schizoporella* but is not conspecific with *S. unicornis* as described below from the lectotype. In particular, the avicularia of *M. ostracites* are situated further distally on the frontal shield, are more distally directed and the rostrum is convex in shape.

The genus *Schizopodrella* was erected by Canu and Bassler (1917) and assigned the type species *L. unicornis* Johnston, 1847. *Schizopodrella* was used to describe species in which the orifice of the ovicell is closed by a membrane, whereas *Schizoporella* was preserved as a means of categorizing all of those species "imperfectly studied". The decision of Canu and Bassler (1917) to select *L. unicornis* as type species is based

on their assertion that Hincks did not designate a type species for his genus *Schizoporella*. However, this is not the case as Hincks (1877) clearly stated that *L. unicornis* (Johnston) is the type species. It is likely that Canu and Bassler (1917) referred to Hincks (1880) in which the genus *Schizoporella* is redescribed without any indication of the type species. *Schizopodrella* is therefore an objective junior synonym of *Schizoporella* as the two genera share the same type species. This was noted by Bassler (1935) who placed *Schizopodrella* in synonymy with *Schizoporella*.

***Schizoporella unicornis* (Johnston, 1847)**

(Figures 1E,F; 2A–F)

?*Lepralia coccinea* (Abildgaard, 1806): Johnston, 1838, p. 278, pl. 34, figs 1–3.

Lepralia unicornis Johnston, 1847, p. 321, pl. 57, fig. 1.

Lepralia spinifera (var.) Busk, 1854, p. 69, pl. 81, figs 6–7.

Schizoporella unicornis (Johnston): Hincks, 1880, p. 288, pl. 35, figs 1, 2, 4, 5; Lagaaij, 1952, p. 65, pl. 5, fig. 7; Ryland, 1965, p. 65, fig. 32a,b; Hayward and Ryland, 1999, p. 221, fig. 91a,b,c.

Schizoporella unicornis (Johnston, in Wood, 1844): Soule et al., 1995, p. 204, pl. 75, figures A–F.

Material

Lectotype. Designated by Lagaaij (1952), NHM 1847.16.174, Britain, Johnston Collection, figured by Johnston (1847, pl. 57, fig. 1) and Figure 2(A,B) herein, an unbleached, unilaminar encrusting colony on the surface of a broken stone. NHM 1847.16.174(a) is a fragment of the lectotype bleached for SEM analysis (Figures 1E,F, 2C–F herein).

Description

Colony encrusting, multiserial, unilamellar or multilamellar, generally less than 5 cm in diameter. Colour normally pink or whitish pink.

Autozooids large but variable in size, length 387–715 μm (mean 529 μm , SD 84.38 μm , $n = 35$), width 273–537 μm (mean 383 μm , SD 59.14 μm , $n = 35$), on average about 1.4 \times longer than wide, broadening before row bifurcations, generally rectangular in shape with wide, squared distal end accommodating single or paired adventitious avicularia. Frontal shield convex, covered with numerous irregularly arranged pseudopores and deep marginal areolar pores. Umbo stout, congruent with boundary between pseudoporous and non-pseudoporous frontal shield. Pseudopores have small openings not changing in size or shape during secondary calcification. Primary orifice broader than long, length (including sinus) 115–145 μm (mean 131 μm , SD 8.32 μm , $n = 25$), width 143–186 μm (mean 163.5 μm , SD 10 μm , $n = 25$), anter forming a wide D-shape, sinus (poster) a broad U-shape. When the operculum is removed, orifice edge adjacent to condyles runs proximally from sinus to proximolateral corners (i.e. slopes downwards). Condyles prominent, fully visible above proximal edge of primary orifice, tips rounded and directed distally; viewed from within, condyles are clearly constructed from calcified oral rim.

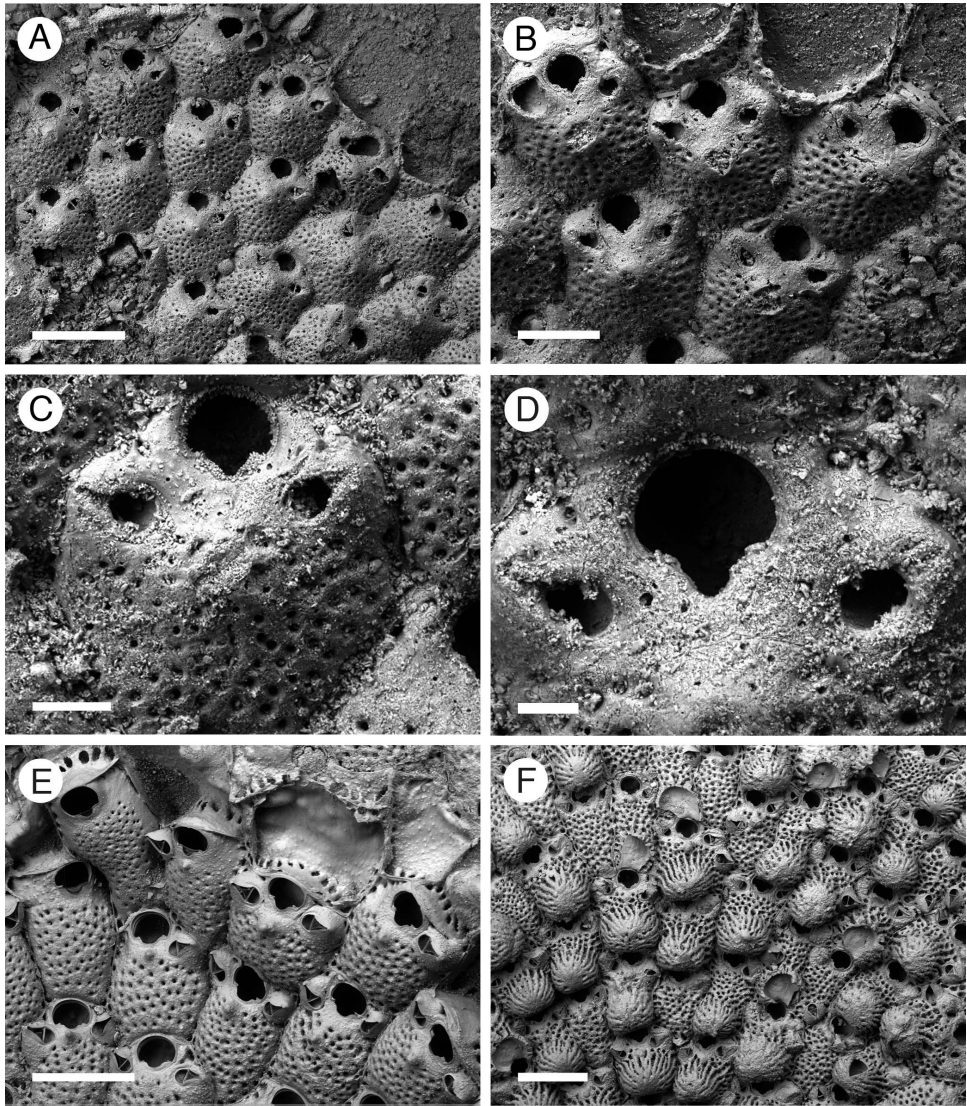


Figure 1. (A–D) Images of Wood's Pliocene specimen from the Coralline Crag, Suffolk (NHM B1675) described in Busk (1859). (A) Group of autozooids at growing edge of colony within small bivalve shell. (B) Autozooids exhibiting deep V-shaped sinus. (C) Frontal shield with paired avicularia and deep V-shaped sinus. (D) Detail of primary orifice and sinus. (E, F) Lectotype of *Schizoporella unicornis* [NHM 1847.16.174 (a)] bleached portion. (E) Group of autozooids at the distal edge of colony with adventitious avicularia, paired, single or absent. (F) Ovicellate autozooids showing radially aligned scalloped grooves. Scale bars: 500 μm (A); 250 μm (B); 100 μm (C, E); 50 μm (D, F).

Adventitious avicularia either single or paired, directed distolaterally from centre-line. Occasional additional adventitious avicularia developed on frontal shield proximal to primary orifice. In early ontogeny avicularia appear raised but are subsumed into frontal shield during secondary calcification. Rostrum acute with concave

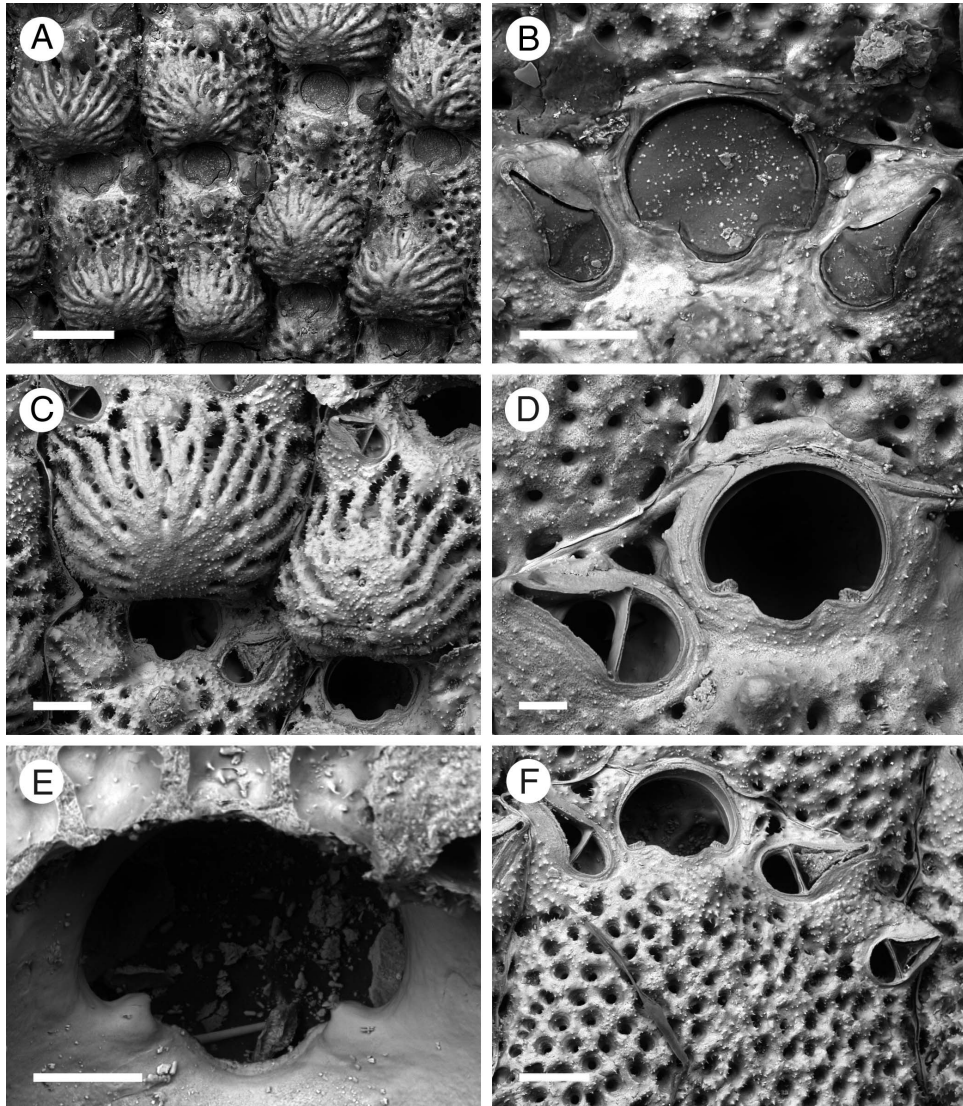


Figure 2. (A, B) Lectotype of *Schizoporella unicornis* (NHM 1847.16.174) unbleached portion. (A) Group of ovicellate autozooids. (B) Primary orifice with operculum and paired adventitious avicularia. (C–F) Lectotype of *Schizoporella unicornis* [NHM 1847.16.174 (a)] bleached portion. (C) Autozooids with detail of ovicell structure. (D) Detail of primary orifice and adventitious avicularium. Note the wide U-shaped sinus and prominent condyles. (E) View of primary orifice from the interior of the autozooid, showing condyles formed from frontal shield calcification. (F) Autozooid with additional adventitious avicularium. Scale bars: 250 μ m (A, C, F); 100 μ m (B); 50 μ m (D, E).

sides and upturned tip. Opesia rounded, D-shaped; crossbar without columella. Mandible with an acutely pointed distal tip curved upwards, Rostrum length 102–181 μ m (mean 131 μ m, SD 17 μ m, $n = 26$), width of crossbar 56–83 μ m (mean 68 μ m, SD 7.5 μ m, $n = 26$).

Ovicells found in localized clusters or more widely distributed, prominent, round and globular, recumbent on frontal shield of distal zooid, large, 247–356 μm (mean 292 μm , SD 29 μm , $n = 26$) long by 318–452 μm (mean 372 μm , SD 32 μm , $n = 26$) wide. Ooecial surface cryptocystal, bearing radially aligned, scalloped grooves around edges; pores few in number, present only at the periphery, centre imperforate.

Remarks

The type species of *Schizoporella* is commonly cited in taxonomic works as *L. unicornis* Johnston in Wood (1844). Wood's paper described fossil bryozoans from the Pliocene Coralline Crag Formation of Suffolk, UK. However, the type material of *S. unicornis* is generally regarded as Recent (e.g. Lagaaij 1952; Soule et al. 1995), an anomaly pointed out by Berning (2006). The description by Wood (1844: 278) of the species, from the Coralline Crag locality of Sutton, is brief and lacks a figure:

“The aperture of this has vestiges of spines. The ovarian capsule above the aperture, observable in many specimens of this genus, will occasionally alter the shape of the aperture, and is itself sometimes worn into an opening.”

Tellingly, the species name is cited as “*Lepralia unicornis?* Johnston MS.”, suggesting that (1) Wood was uncertain of the identity of his material, and (2) he based his tentative determination on Johnston's manuscript for the second edition of *A History of the British Zoophytes* (Johnston 1847). The fact that a Recent specimen of *L. unicornis* was described comprehensively in Johnston's later work, and is well figured, supports the interpretation of *L. unicornis* based on Recent rather than fossil material. Indeed, Lagaaij (1952) concluded that “The lectotype must be chosen from the specimens upon which Johnston originally based his identification” (p. 66), and went on to select a Recent specimen (NHM 1847.9.16.174) as lectotype. However, Lagaaij still placed *L. unicornis* (Wood ex Johnston, 1844) in synonymy with the Recent *L. unicornis sensu* Johnston. This synonymy is doubtful based on an SEM study of Wood's Coralline Crag material (Figure 1A–D). Wood's specimen, although poorly preserved, has a distinctly narrower and deeper sinus than the Recent lectotype of *S. unicornis*.

The Wood specimen figured herein (Figure 1A–D) shares many characters with Recent *S. patula*, including a deep V-shaped primary orifice, paired distolaterally directed avicularia and umbo. However, Bishop and Hayward (1989) stated that many species of *Schizoporella* from the British, Dutch and Belgian Pliocene should be considered as *S. dunkeri*, which they figure from the Pliocene of Belgium (their fig. 67-9) with a columella. A columella is not visible on the Wood specimen but this may reflect its poor state of preservation. The only recent European species described to have a columella is *S. cornualis* (Hayward and Ryland 1995).

Schizoporella unicornis appears to have a geographical range in the northeast Atlantic, from northwest Africa and Spain to the Faeroes and Western Norway (Hayward and Ryland 1999). It is found commonly encrusting the undersides of stones, shells and kelp holdfasts at or slightly below low water spring tide.

The ancestrula is not visible in the lectotype of *S. unicornis*. However, according to Ryland (1965) and Hayward and Ryland (1999), this is tatiform in *S. unicornis*, with eight oral spines.

Schizoporella errata (Waters, 1878)
(Figures 3A–F, 4A–F)

Eschara spongites Pallas, 1766 (partim), p. 45.

Lepralia spinifera Busk, 1854 (partim), p. 69, pl. 91, figs 1,2.

Lepralia spinifera c) *L. serialis* Heller, 1867, p. 104.

Lepralia spinifera d) *L. spongites* Heller, 1867, p. 104.

Lepralia errata Waters, 1878, p. 11, pl. 1, fig. 9.

Lepralia errata, Stadium *Hemeschara* Waters, 1879, p. 39, pl. 10, fig. 5.

Schizoporella unicornis (Johnston): Waters, 1909 (partim), p. 143, pl. 12, figs 12, 13.

Schizoporella errata (Waters): Calvet, 1902, p. 23; Gautier, 1962, p. 149, fig. 151; Ryland, 1965, p. 64, fig. 31a,b; Hastings, 1967, p. 336; Hayward and Ryland, 1999, p. 212.

Schizoporella unicornis var. *errata* (Waters): Calvet, 1927, p. 16.

Schizopodrella violacea Canu and Bassler, 1930, p. 40, pl. 4, figs 1–14.

Schizopodrella errata (Waters): Canu and Bassler, 1930, p. 39; Barroso, 1935, p. 373, figs 1, 2.

Material

Lectotype (here chosen). MM H1186.3113, Bay of Naples, specimen labelled ‘Stadium *Hemeschara*, boiled in potash’, figured by Waters (1879, p. 39, pl. 10, fig. 5) (Figure 3A–F herein).

Other material (topotypic). NHM 2009.1.26.1, (Figure 4A). Bleached, Nisida Harbour, Naples, Italy and NHM 2009.1.26.2, (Figure 4B–F). Bleached, Nisida Harbour, Naples, Italy.

Description

Colony encrusting, multiserial, unilamellar or multilamellar as the result of frontal budding, sometimes tubular (“hemescharan”) growing around arborescent epibiota such as hydroids. Colour varying from white (at growth tips) to red and purple/brown in the older, multilamellar regions.

Basal autozooids longer than wide, 381–558 μm (mean 494 μm , SD 43 μm , $n = 31$) long by 263–508 μm (mean 371 μm , SD 71 μm , $n = 31$) wide, almost as wide as long at row bifurcations, surrounded by a distinct suture line; areolar pores deep. Frontally budded autozooids less consistent in shape, often more rounded. Frontal shield in basal zooids slightly convex, more so in frontally budded zooids. Pseudopores present everywhere apart from area distal of primary orifice, polygonal in early ontogeny (Fig. 4D), later reduced by secondary calcification, becoming occluded before frontal budding. Primary orifice broad, 125–172 μm (mean 147 μm , SD 11 μm ; $n = 25$) long by 125–181 μm (mean 154 μm , SD 15 μm ; $n = 26$) wide. Anter broad, D-shaped, sinus (poster) U-shaped, broader than deep. When the operculum is removed, the edge of primary orifice adjacent to the condyles runs slightly distally from sinus to proximolateral corners (i.e. slopes upwards). Condyles small with acute tips.

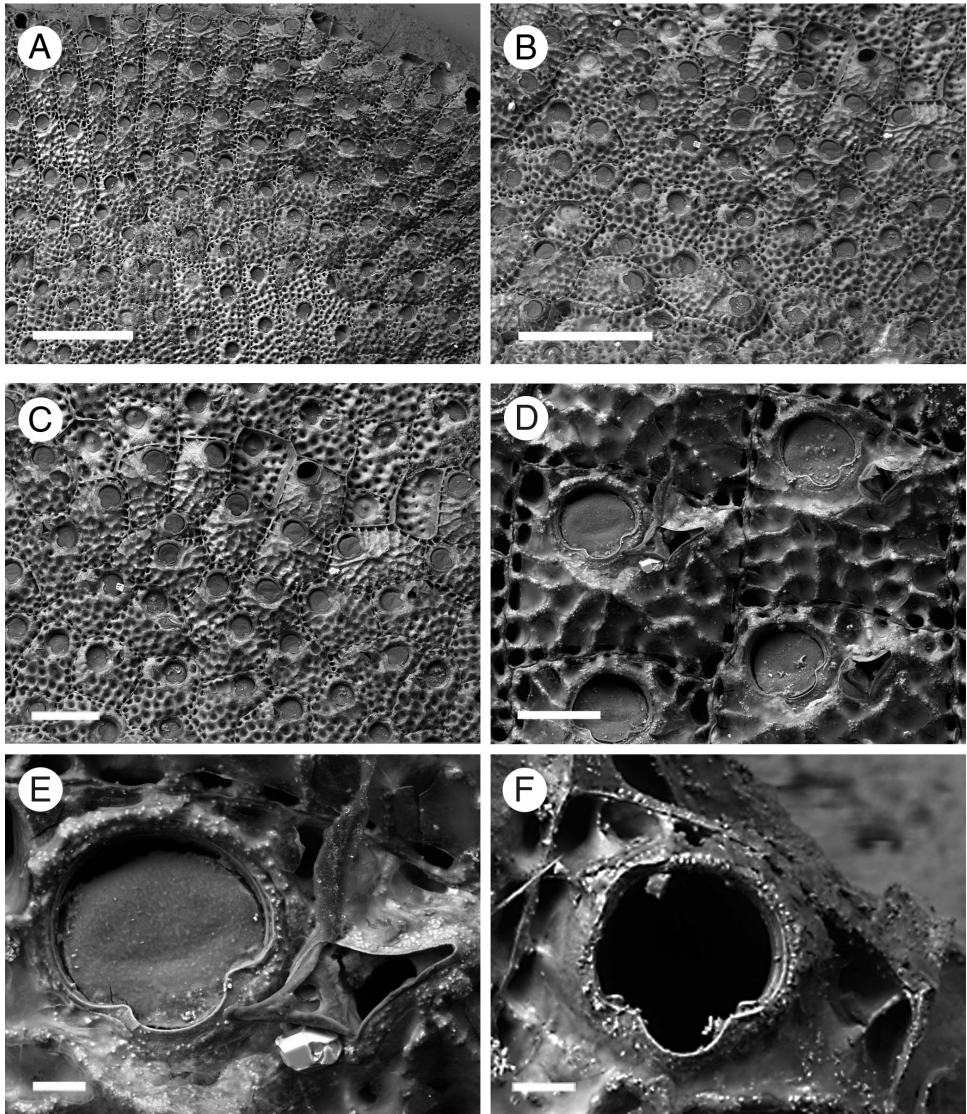


Figure 3. (A–F) Lectotype of *Schizoporella errata* (MM H1186.3113). (A) Growing edge of colony in primigenial unilamellar mode. (B) Portion of colony showing development of frontally budded zooids in initial phase of multilamellar growth. (C) Various stages of the development of the frontal shield of frontally budded autozooids. (D) Frontal shield of zooids in early astogeny with wide areolae and polygonal shaped border surrounding pseudopores. (E) Primary orifice and adventitious avicularia with operculum intact. The sinus is a wide U-shape with the proximal border of the orifice directed distally from the sinus. The avicularium bears an acutely pointed mandible with a hooked tip. (F) Primary orifice with operculum absent. Condyles small with acute tips. Scale bars: 1 mm (A, B); 500 μm (C); 250 μm (D); 50 μm (E, F).

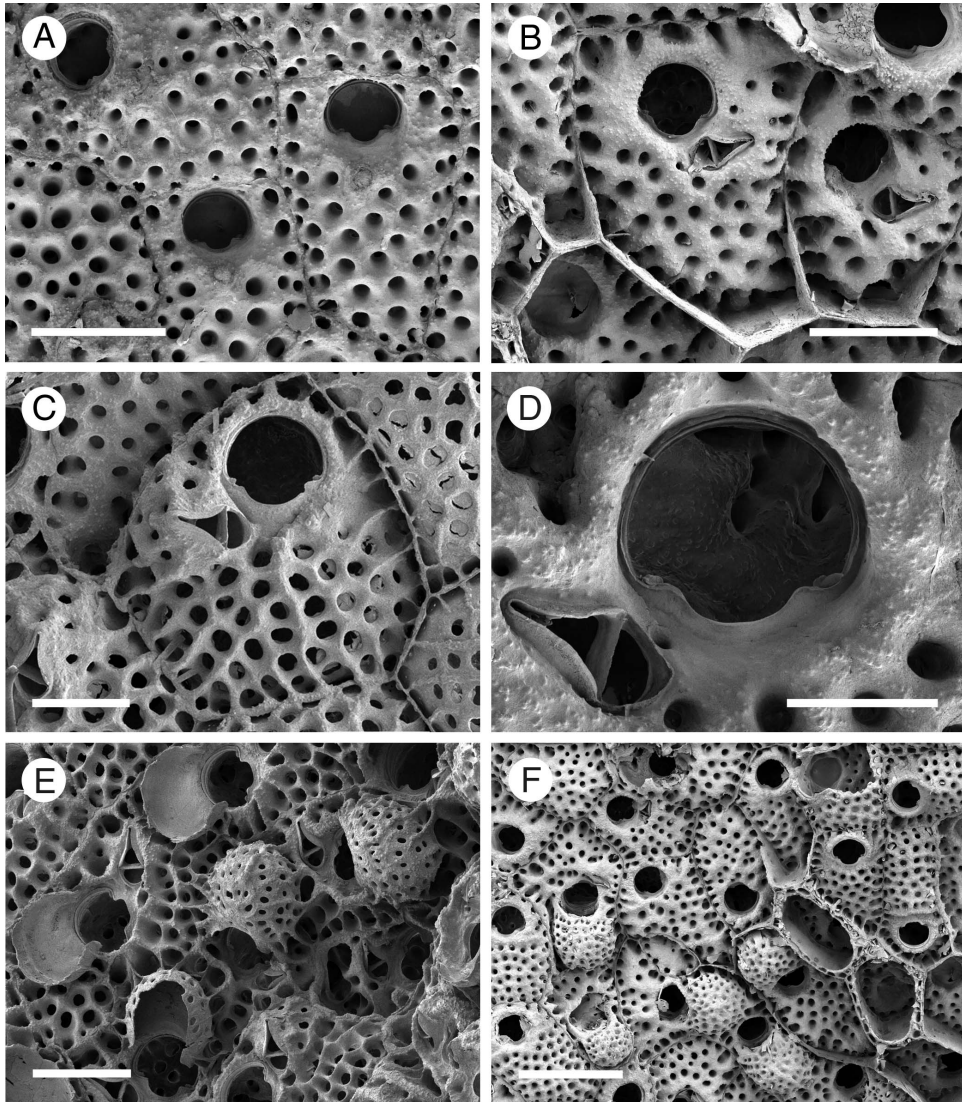


Figure 4. (A, B) Topotype of *Schizoporella errata* (NHM 2009.1.26.1). (A) Primogenial autozooids growing in unilamellar form. Later astogeny with secondary calcification of frontal shield. (B) Frontally budded autozooid in the process of budding a daughter zooid. Later astogeny with secondary calcification of the frontal shield. (C–F) Topotype (NHM 2009.1.26.2). (C) Frontally budded zooid in early astogeny with a polygonal shaped border around each pseudopore. (D) Detail of the primary orifice with its small condyles and the distolaterally directed adventitious avicularium. (E) Ovicells in various stages of development, with a completely porous surface. (F) A group of autozooids undergoing frontal budding. The frontal shield has been removed in some cases to reveal the occluded primary orifice of the basal zooid. Scale bars: 250 μm (A, B, E, F); 150 μm (C); 100 μm (D).

Adventitious avicularia generally single, developing proximolaterally to the primary orifice and orientated distolaterally from midline, small (mean 137 μm , SD 19 μm , $n = 10$). Rostrum pointed distally with concave sides and hooked tip. Opesia rounded, deeply D-shaped, no columella. Mandible with curved tip. Avicularia occasionally develop proximal to orifice and occupy a large proportion of frontal shield. Larger than regular adventitious avicularia but with similarly shaped rostrum and opesium. Mandible orientated proximally.

Ovicells not present in type specimen. In topotype material ovicells are globular, rounded, recumbent on the distal zooid, and have surfaces completely covered by pores but lacking radial ridges.

Remarks

Like *S. unicornis*, the introduction of *S. errata* is somewhat confused. Waters (1878) first mentioned the name in a study of cheilostome opercula. A more thorough and recognizable description was subsequently provided by Waters (1879), in which reference was made to a particular specimen described as “Stadium, *Hemeschara*” (i.e. with a tubular colony-form). It is very likely that Waters was referring to the same material in both publications. Hastings (1967) revised the synonymy of *S. errata* and attempted to designate a lectotype. However, she listed this putative lectotype under the Manchester Museum catalogue number HII86, a catalogue number prefix used for the entire Waters Collection at the museum. Fortunately, a specimen matching the descriptions of Waters (1879) and Hastings (1967) was found in the MM and has been examined by SEM.

The description by Waters (1879: 39) of this species reads:

“(A)n encrusting piece, measuring 9 × 10 mm. It consists of a regular layer of straight-sided zooecia over which two successive layers of superficial zooecia are spreading. The superficial zooecia are larger, irregular in shape and orientation and more rounded in outline . . .”

This description draws attention to the notable differences in zooidal morphology at different astogenetic and ontogenetic stages. This has no doubt been a cause of taxonomic confusion in past descriptions, which have often focused on zooids from any of the following three growth stages: (1) basal zooids of the unilaminar “primogenial” stage; (2) frontally budded zooids at early ontogenetic stages with minimal secondary calcification; or (3) frontally budded zooids at late ontogenetic stages with heavy secondary calcification of the frontal shield.

The true identities of *S. errata*-like specimens from places distant from the type locality remain open to question. The ability of *S. errata* to foul man-made structures, such as gas rigs (Relini et al. 1998) and ships (Ryland 1965; Gordon and Mawatari 1992) has no doubt mediated its transfer to ports around the world, where it has become highly invasive (Hayward and McKinney 2002). Furthermore, the opening of the Suez Canal in 1869 may have played a role in its transfer between the Mediterranean and the Red Seas (Eitan 1972). However, as highlighted by Winston (2005), it is possible that *S. errata* is part of a species complex that includes *S. pungens* (Canu and Bassler, 1928) and *S. isabelleana* (d’Orbigny, 1842). To complicate this issue further a subspecies called *S. unicornis floridana* (Osburn, 1914) has been

recognized in a number of works (Maturro 1957; Banta 1971, 1972; Soule et al. 1995). The origin of this species complex may have predated anthropogenic exchange, with species morphologically similar to *S. errata* being present in the Pliocene deposits of North Carolina and Jamaica (Taylor and Foster 1998). Redescription of the type material here should aid in deciding whether fossil material and that of *S. pungens* belongs to the same species. Fossil material of *S. errata* has not been found in any of the European deposits during the course of our investigation. Therefore, it may be the case that this species has been introduced anthropogenically or otherwise into the Mediterranean in recent times. However, because of high levels of intracolony morphological plasticity, it is likely that the true identity of the Recent *S. errata* complex will only be confirmed using molecular techniques.

Compared to *S. unicornis*, *S. errata* differs in the shape of the primary orifice. In *S. unicornis* the edge of the primary orifice adjacent to condyles is directed proximally from the sinus towards the proximolateral corners of the orifice, whereas in *S. errata* it is directed slightly distally. In addition, the structure of the pseudopores differs, forming within shallow polygonal, almost octagonal, recesses in the early ontogeny of *S. errata* but not *S. unicornis*. Also diagnostic of *S. unicornis* are the scalloped ridges around the edges of the ovicells and imperforate central region. *Schizoporella unicornis* does not undergo frontal budding, unlike *S. errata*.

No ancestrulae were apparent in either the lectotype or associated material. However, according to Ryland (1965) and Hayward and Ryland (1999), these are tatiform and have eight oral spines.

Discussion

Although species of *Schizoporella* are commonly described in the literature, the species-level taxonomy of the genus is confused, causing problems for comparative ecological studies. Here we argue that the authorship of *S. unicornis* should be attributed to Johnston (1847) and not Wood (1844). Fossil material from the Coralline Crag Formation described by Wood (1844) as "*Lepralia unicornis?* Johnson MS" appears most similar to *S. patula* as it differs from *S. unicornis* Johnston, 1847 in the shape of the primary orifice.

The species names *S. unicornis* and *S. errata* have been wrongly applied on a number of occasions. In the case of *S. unicornis*, of 25 papers where the species is named, only four (16%) represent correct identifications. Only two of these studies (Ryland 1965; Hayward and Ryland 1999), give a full description of the species with figures, whereas the other two (Turner and Todd 1994; Watts and Thorpe 2006) are judged to represent correct identifications based on geographical provenance. Of the rest, 15 (62.5%) studies that identify *S. unicornis* are considered doubtful. In many cases geographical location alone is sufficient to raise doubts over the identifications. Specimens described as *S. unicornis* from Australia (Vail and Wass 1981; Tzioumis 1994) and the Pacific coast of North America (Soule DF and Soule JD 1967, 1968; Bullivant 1968; Powell 1970; Powell et al. 1970; Strathmann 1973; Ross and McCain 1976; Jokiel 1980) should be considered with caution. These may instead represent populations of *S. japonica* (see Dick et al. 2005) introduced on oyster seed. Evaluation of apparent *S. unicornis* from the eastern United States would benefit from SEM imaging. Mullineaux and Garland (1993) and Rogick and Croasdale (1949) each described *S. unicornis* from Woods Hole, Massachusetts. Although temperature and

salinity may be similar to that of the European occurrences of *S. unicornis*, the Woods Hole specimens named *S. unicornis* in the NHM are morphologically more similar to *S. errata*. The remaining six papers all describe species that are categorically not *S. unicornis*. Of these papers, Banta (1972) and Banta and Holden (1974) described the subspecies *S. unicornis floridana*, which is likely to be part of the complex of species similar or identical to *S. errata*. The species supposed by Rucker and Carver (1969) to be *S. unicornis* encompassed material from Massachusetts, Bermuda, Hawaii, California and Washington State and is accompanied by images that do not conclusively identify the species. A clarification of this apparent wide distribution is of great interest because the results of mineralogical analysis presented by Rucker and Carver are relevant to the effects of ocean acidification on bryozoan skeletal development as they show an increasing content of the vulnerable mineral aragonite in lower latitudes.

With regard to *S. errata*, seven out of 20 papers (35%) can be considered to represent correct identifications based on the published figures (Ryland 1965; Hastings 1967; Ferdeghini and Cocito 1999; Hayward and Ryland, 1999; Cocito et al. 2000; McKinney and McKinney 2002), or locality (Kocak, 2007). However, the rest (65%) must be considered doubtful. Of these putative *S. errata* from New Zealand (Gordon and Mawatari 1995) appears to have a more V-shaped sinus than the type material and an anter that is more constricted at the proximal end. Unfigured occurrences of *S. errata* from other New Zealand localities (Piola and Johnston 2006) may also be doubtful. Records of *S. errata* from Massachusetts (Buss 1981; Schopf 1974; Schopf and Dutton 1976) require further investigation, especially as these studies identify an important clinal temperature gradient in morphology and alleles. Further records of the species from Beaufort, North Carolina (Karlson 1980; Buss 1981; Karlson and Shenk 1983; Walter and Wethey 1996) and Brazil (Morgado and Tanaka 2001) could represent portions of a larger species complex on the eastern coast of North and South America that includes *S. pungens* (Winston 2005). Furthermore the true identity of fossil *S. errata* from the West Indies (Taylor and Foster 1998) needs to be investigated in relation to other Pleistocene material from the United States and Europe.

Schizoporella unicornis and *S. errata* both have long histories of being used as exemplar species. Large amounts of data have been gathered on the environmental responses of both species. However, the validity of such data as the basis for future studies can only be accepted in the light of a precise taxonomy. The morphological descriptions of the type material of *S. unicornis* and *S. errata* presented here clarify the true identities of these two fouling bryozoans. Molecular studies are still needed to ascertain the congruence between morphology and molecules. Only then will future research into climate change and ocean acidification using *Schizoporella* as a model organism be placed on a sound footing.

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