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The identity of the invasive fouling bryozoan *Watersipora subtorquata* (d'Orbigny) and some other congeneric species

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Abstract

Watersipora subtorquata (d'Orbigny, 1852) has been widely reported as a fouling species from tropical to temperate waters. The continued confusion over the correct name for this species led us to provide a redescription of d'Orbigny's type of *Cellepora subtorquata*, and to make comparisons with other species of *Watersipora*. We show that the majority of specimens assigned to *W. subovoidea* (d'Orbigny, 1852) are morphologically distinct from the recently erected neotype of *W. subovoidea*; these specimens are here reidentified as *Watersipora subtorquata*. Other specimens previously assigned to *W. subtorquata* belong to *W. subatra* (Ortmann, 1890), described originally from Japan. Owing these inconsistences, we suggest setting aside the neotype of *Watersipora subovoidea*, which is based on Busk's *Lepralia cucullata* and is not from the same locality as d'Orbigny's type. *Watersipora cucullata* is redescribed and figured using Busk's specimens; the species is known from the Mediterranean, including the Adriatic. Three other species—*Watersipora atrofusca* (Busk, 1856), *Watersipora aterrima* (Ortmann, 1890) and *Watersipora nigra* (Canu & Bassler, 1930)—are also refigured. *Watersipora edmondsoni* Soule & Soule, 1975 is synonymised with *W. subtorquata* (d'Orbigny). Two new species are described, *Watersipora mawatarii* n. sp. from Japan and *Watersipora souleorum* n. sp. from the Azores, Cape Verde, Naples and Indian Ocean. A key is given to the Recent species of *Watersipora*.

Key words: Bryozoa, Cheilostomata, Watersiporidae, fouling species, invasive species, new species, taxonomy, type specimens

Introduction

Watersipora subtorquata (d'Orbigny, 1852) and *Watersipora subovoidea* (d'Orbigny, 1852) have been widely reported as fouling species in harbour areas, from tropical to temperate waters (Harmer 1957; Ryland 1974; Soule & Soule 1975; Ryland *et al.* 2009; Mackie *et al.* 2012). Ryland *et al.* (2009) noted that these species are frequently confused owing to the absence of a modern taxonomic account comparing *W. subtorquata* with *W. subovoidea*. D'Orbigny (1842) first reported *Escharina torquata* (Lamouroux, 1825) from Rio de Janeiro, Brazil, later renaming the species *Cellepora subtorquata* d'Orbigny, 1852 because of homonymy (d'Orbigny 1852). Marcus (1937) described similarities between specimens from Santos and Rio de Janeiro that had been described by d'Orbigny, but adopted the name *Watersipora cucullata* (Busk, 1854), commonly used by contemporary taxonomists, for this Brazilian material. This name was still being used for specimens from São Paulo and Espírito Santo, Brazil (Marcus 1938, 1955) until Vieira *et al.* (2008) followed Taylor & Gordon (2002) in using the name *W. subtorquata* for the Brazilian specimens. Recently, Ramalho *et al.* (2011) compared the Rio de Janeiro specimens with recent descriptions given by Ryland *et al.* (2009) and applied the name *W. subovoidea* to Brazilian material, even though this species was originally introduced by d'Orbigny (1852) for material (Savigny 1817, pl. 8, fig. 1) from Egypt. These authors suggested that the specimens of Marcus (1937, 1938, 1955) required revision.

Molecular studies investigating introduced populations of *Watersipora* (Mackie *et al.* 2006, 2012; Geller *et al.* 2008) have suggested that a common haplotype of *W. subtorquata* is found in southern Australia, New Zealand and

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California, whereas *W. subovoidea* is found in the Western Atlantic (Florida and Brazil) and Australia. Despite the type locality of *W. subtorquata* being Rio de Janeiro, neither recent taxonomic nor molecular studies have reported the occurrence of this species along the Brazilian coast (Mackie *et al.* 2006, 2012; Geller *et al.* 2008; Ryland *et al.* 2009; Ramalho *et al.* 2011). Ryland *et al*. (2009) designated a neotype for *W. subovoidea* to recognize its conspecificity with *W. cucullata*, but no redescription of d'Orbigny's type of *Cellepora subtorquata* was given. Previously, Taylor & Gordon (2002) had reproduced d'Orbigny's original plates (d'Orbigny 1842, pl. 4, figs 2 and 3), along with a scanning electron micrograph of the putative type specimen found in the d'Orbigny Collection, but did not redescribe this important invasive fouling species.

The current paper provides a redescription of the type specimen of *Watersipora subtorquata* and makes comparisons with a range of congeneric species based on new SEM studies. This taxonomic revision clarifies the complex taxonomy of *Watersipora* and leads to the introduction of two new species. All Recent species of *Watersipora* are included in a key that aims to simplify identification of the species belonging to this invasive fouling bryozoan.

Material and methods

Specimens used in this study are deposited at the Musée Océanographique de Monaco, Monaco (MOM), Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP), Natural History Museum, London (NHMUK), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), and Santa Barbara Museum of Natural History, Santa Barbara (SBMNH). D'Orbigny's type of *Watersipora subtorquata* is deposited in the palaeontological collections at the Muséum national d'Histoire naturelle, Paris (MNHN). The type specimens of *Watersipora aterrima* (Ortmann, 1890) and *Watersipora subatra* (Ortmann, 1890) are deposited in the collection of the Musée zoologique de la Ville de Strasbourg (MZS). Material was photographed using a Zeiss Discovery V20 stereomicroscope with AxioCam HRc. Selected specimens were imaged at the NHMUK using a LEO 1455-VP scanning electron microscope (SEM) equipped with a low-vacuum chamber and back-scattered electron detector.

Measurements were made directly from digital SEM images using ImageJ analysing software (http://rsbweb.nih.gov/ij/). Abbreviations used for measurements are as follows: ZL, zooid length; ZW, zooid width; ZA, zooid area, calculated as a rectangle (ZL x ZW); OL, orifice length; OW, orifice width; OA, orifice area, calculated as an ellipse (ð · OL/2 · OW/2); SinL, sinus length; SinW, sinus width; PorD, pore diameter.

Results and discussion

Identity of *Watersipora subtorquata* (d'Orbigny, 1852)

Critical to understanding the correct name of the common fouling species of *Watersipora* is establishing the identity of *W. subtorquata* (d'Orbigny, 1852). Specimens of a bryozoan from Rio de Janeiro described by d'Orbigny (1842) as *Escharina torquata* (Lamouroux, 1825) were later renamed by him (d'Orbigny 1852, p. 399) as *Cellepora subtorquata*, presumably to avoid homonymy with another species he referred to as *Cellepora torquata* (Quoy & Gaimard, 1827) (see d'Orbigny 1852, p. 403). Waters (1879) synonymised d'Orbigny's *Cellepora subtorquata* with *Lepralia cucullata* Busk, 1854 but inexplicably applied the name of the junior synonym *L. cucullata* for his specimens from Naples. The first revision of d'Orbigny's type was undertaken subsequently by Waters (1905) who studied d'Orbigny's material deposited at the MNHN. He noted the high quality of d'Orbigny's original figures but remarked that, in the original specimens, the projecting lateral wings on each side of the sinus were more developed than those depicted by d'Orbigny (1842). Taylor & Gordon (2002) reviewed the bryozoan work of Alcide d'Orbigny (1802–1857), publishing a scanning electron micrograph of d'Orbigny's type specimen (Taylor & Gordon 2002, fig. 1C) in which it is possible to recognize some of the diagnostic features (orifice shape and frontal pseudopores) depicted in the original figures of this species. The type specimen of d'Orbigny (MNHN, d'Orbigny Collection 13637) (Figs 1–5) comprises a large colony with some intact opercula (Figs 1–2); the projecting proximolateral wings are well developed in most zooids (Fig. 4), as observed by Waters (1905), but with increasing calcification can become obscured, shallow and inconspicuous in

frontal views of the orifice (Figs 3, 5). The subcircular orifice (Fig. 5) was well figured in d'Orbigny's plates; the orifice is slightly wider than long, with a U-shaped sinus demarcated by triangular condyles that project distomedially.

Comparisons of d'Orbigny's type specimen and the specimens identified by Marcus (1937, 1938) from Brazil under the name *Watersipora cucullata* (NHMUK 1948.2.16.18, and uncatalogued specimens deposited at MZUSP) indicate that they represent the same species, as has been suggested by Gordon (1989) and Ryland *et al.* (2009). Marcus (1937, pl. 24, fig. 63A, B) showed the orifice to have well-developed proximolateral wings in Brazilian colonies. In addition, the operculum in the Brazilian specimens is characterized by a parallel-sided dark band of two proximal lucidae adjacent to the condyles (Marcus 1937, pl. 24, fig. 63A, B). The same operculum shape and lucidae were observed in Rio de Janeiro specimens figured by Ramalho *et al.* (2009, fig. 3D) in material they named *Watersipora subovoidea*. Ramalho *et al*. (2011) followed Ryland *et al.* (2009) in using the name *W. subovoidea* for specimens with "triangular, tooth-like condyles, located distomedially [*sic*], and a strongly pigmented operculum with a parallel-sided dark central band". All characteristics described for *W. subovoidea* by Ryland *et al.* (2009) suggest that their specimens actually belong to *W. subtorquata*, and restudy of the material they analyzed (NHMUK 2007.12.14.2–8) confirms this supposition. However, neither figures nor descriptions of Busk's type specimen of *Lepralia cucullata* (NHMUK 1854.11.15.189), designated by Ryland *et al.* (2009: 54) as the neotype of *Watersipora subovoidea*, were given by Ryland *et al.* (2009), a situation which we rectify below.

Identity of *Watersipora cucullata* (Busk, 1854)

Busk (1854) described *Lepralia cucullata* from the Aegean Sea and noted that, owing to the absence of ovicells, it was not possible to assign his specimens to Savigny's species (Savigny 1817, pl. 8, fig. 6), which had been named *Cellepora mangnevillana* Lamouroux, 1816 by Audouin (1826). The species was characterized by a black colouration and a granular surface (Busk 1854), and Waters (1879) described frontal pseudopores in Busk's specimens as well as his own colonies from Naples. Hincks (1886) used the name *Schizoporella atrofusca* Busk, 1856 for the specimens reported by Waters (1879) and included the form *labiosa* from the Arabian Sea, but gave no additional accounts of Busk's types of *L. cucullata* or *S. atrofusca*. Waters (1909) and Hastings (1927, 1930) also included *S. atrofusca* under *L. cucullata*, but their description encompassed more than one species (see also Soule & Soule 1975). Harmer (1957) synonymised three species—*Cellepora subtorquata*, *Lepralia cucullata* and *Schizoporella atrofusca*—under *Watersipora subovoidea* (as *Dakaria subovoidea*), which contrasts with the statement of Hastings (1930), who suggested the existence of more than one species under the name *Watersipora cucullata*; nevertheless, Hastings did not introduce new names for specimens with distinct opercular shapes. Mawatari (1952), however, introduced the variety *watersi* for specimens reported by Waters (1909) and Hastings (1930), which may represent at least two distinct species (see below).

Following examination of the type specimens of Busk's *L. cucullata*—i.e. *Watersipora cucullata*, NHMUK 1854.11.15.189, lectotype (Figs 6–9), chosen by Soule & Soule (1975), plus NHMUK 2012.6.30.1, paralectotype (Figs 25–29)—and *S. atrofusca*—i.e. *Watersipora atrofusca*, NHMUK 1892.9.6.4 (Fig. 10)—we conclude that these should be considered as distinct species, as was suggested by Soule & Soule (1975). Orifice size in the two species differs, being larger in *W. cucullata* than in *W. atrofusca*. Two small latero-oral multiporous septula in the frontal shield (equivalent to the 'intrazoidal septula' of Banta 1970, p. 39), one on each side of the orificial sinus, are present in *W. cucullata* (Figures 8, 29) but are lacking in *W. atrofusca*. *Watersipora subtorquata* is distinguished from Busk's *W. cucullata* by the shape of the orifice, the shape and size of the condyles, and the size of the frontal pseudopores. Ryland *et al.* (2009) considered the identity of Busk's *W. cucullata* "clear", following the descriptions of Hastings (1930), but Hastings mentioned a distinct variety among her specimens, as noted in her description and plates (Hastings 1930, p. 730, pls 102–104).

Ryland *et al.* (2009, p. 53) attempted to solve nomenclatural problems concerning *W. subovoidea* and to stabilise d'Orbigny's species name by designating Busk's type of *W. cucullata* as the neotype of d'Orbigny's *W. subovoidea*, thereby making *Watersipora subovoidea* the senior synonym of *Watersipora cucullata*. Unfortunately, the descriptions and figures of *W. subovoidea* in Ryland *et al.* (2009) are actually of *W. subtorquata* (see above). Furthermore, the selection of a neotype for *W. subovoidea* from a site (Aegean Sea) distant from the type locality (Egyptian Red Sea) is contentious. According to the ICZN (1999, Article 75.3.6) evidence should be provided that

the neotype came as nearly as practicable from the original type locality, which was not provided in the Ryland *et al*. (2009) paper. Thus, *Cellepora subovoidea* d'Orbigny, 1852 is here considered a *nomen dubium*.

Below we provide redescriptions of d'Orbigny's species *W. subtorquata* and *W. cucullata* and reassign the species erroneously identified as *Watersipora subtorquata* by Ryland *et al*. (2009) to a third species previously described by Ortmann (1890) under the name *Schizoporella aterrima* var. *subatra* (=*Watersipora subatra*, see below). We also describe two new species: *Watersipora mawatarii* **n. sp.** from Japan, and *Watersipora souleorum* **n. sp.** for specimens from Cape Verde and Naples previously assigned to *Watersipora cucullata*.

Taxonomic account

Family Watersiporidae Vigneaux, 1949

Genus *Watersipora* Neviani, 1896

Watersipora Neviani, 1896: 120; Osburn 1952: 471; Gordon 1989: 40.
Dakaria Jullien *in* Jullien & Calvet, 1903: 90; Harmer 1926: 1921 (part).
Pachycleithonia Canu & Bassler, 1930: 25.

Type species. *Lepralia cucullata* Busk, 1854, by original designation.

Diagnosis. Colony encrusting, multiserial, uni- to multilamellar, or erect, foliaceous and bilamellar. Colony coloured reddish to black in life owing to pigmented epitheca. Autozooids subrectangular to hexagonal, separated by raised walls. Cryptocystidean frontal shield with numerous rounded pseudopores; latero-oral intrazooidal septula sometimes present proximolateral to orifice; intrazooidal septula sometimes present at proximal corners of frontal shield. Orifice subcircular to oval; poster sometimes with well-defined proximal sinus; condyles present. Operculum reddish-brown to black in colour, often with central band demarcated by sclerites; lucidae often present. Spines absent. Avicularia absent. Ooecia absent; embryos brooded internally in maternal zooid. Multiporous mural pore plates in distolateral and transverse distal walls. Ancestrula schizoporelloid, single, smaller than autozooids, often obscured in later astogeny.

Remarks. *Watersipora* was introduced monotypically for "*Smittia cucullata* Busk, 1854" (=*Lepralia cucullata* Busk, 1854) by Neviani (1896) who stated that his fossil specimens were morphologically distinct from *Lepralia cucullata*. As a consequence, Harmer (1957) suggested using *Dakaria* Jullien *in* Jullien & Calvet, 1903 (type species: *Dakaria chevreuxi* Jullien *in* Jullien & Calvet, 1903, now *Watersipora subtorquata*; see below) rather than *Watersipora* for Busk's species. Despite Neviani's misidentification of his fossil specimens as *Smittia* (*Watersipora*) *cucullata* (Neviani 1896, p. 120; Gordon 1989, p. 40), *Lepralia cucullata sensu* Busk, 1854 is best used as the type species of *Watersipora* for the purpose of stability (see ICZN 1999, Article 70.3).

Pachycleithonia Canu & Bassler, 1930 was introduced monotypically for *Pachycleithonia nigra* Canu & Bassler, 1930, from the Galapagos. The genus has been characterized as having ovicells (Cook 1985), but the ovicellate specimens are distinct from Canu & Bassler's *P. nigra*, and Tilbrook (2006) subsequently reassigned them to *Nigropercula* Tilbrook, 2006. Osburn (1952) synonymised *Pachycleithonia* with *Watersipora*, but included *Pachycleithonia nigra* under the name *Watersipora cucullata*. We have examined the type material of *Pachycleithonia nigra* (USNM 8495; Fig. 11) and additional material from the Galapagos (NHMUK 1975.5.12.1); this species resembles *W. cucullata* in colony shape and in having a thick-rimmed orifice and triangular condyles. However, whereas *Pachycleithonia nigra* has a sinusoid orifice with a convex proximal edge, *W. cucullata* has a straight or slightly concave proximal edge, as found in the majority of species assigned to *Watersipora*, and paired intrazooidal (frontal) septula, which are lacking in *Pachycleithonia nigra*. These two characters in *Pachycleithonia nigra* also occur, however, in other *Watersipora* species, e.g. *Watersipora subtorquata*, which lacks paired intrazooidal septula, and *Watersipora arcuata* Banta, 1969a, which has an orifice with a convex proximal edge. Following Soule (1961), we recognize the combination *Watersipora nigra* (Canu & Bassler, 1930).

Two other genera have been assigned to the family Watersiporidae. *Veleroa* Osburn, 1952 is distinct in having numerous communication pores covering the surface of the lateral and distal walls (see Osburn 1952: pl. 57, fig. 7), and *Uscia* Banta, 1969b has dimorphic ovicellate zooids (see Banta 1969b, figs 2–4).

***Watersipora subtorquata* (d'Orbigny, 1852)**
(Figs 1–5, 12–16, 18–24, 67, 70; Table 1)

Escharina torquata: d'Orbigny, 1842: pl. 4, fig. 3; 1847: 11 [Brazil].
Cellepora subtorquata d'Orbigny, 1852: 399 [Brazil]. ?Non *Cellepora subovoidea* d'Orbigny, 1852: 402 [Red Sea; *nomen dubium*].
Schizoporella atrofusca: Hincks 1886: 269 (part; f. *labiosa*), pl. 10, fig. 5 (non fig. 4) [Arabian Sea]. Non *Schizoporella atrofusca* Busk, 1856: 178 [Mexico].
Dakaria chevreuxi Jullien *in* Jullien & Calvet, 1903: 90, pl. 10, fig. 6 [Senegal].
Lepralia? *cucullata*: Waters 1909: 150 (part), pl. 15, fig. 1 [Suez]. Non *Lepralia cucullata* Busk, 1854: 81, pl. 96, figs 4–5 [Aegean Sea].
Watersipora cucullata: Hastings 1930: 729 (part), pl. 15, figs 102 [Suez].
Watersipora cucullata: Marcus 1937: 118, pl. 24, fig. 63A, B [Brazil].
Watersipora cucullata: Marcus 1938: 46 [Brazil].
Watersipora cucullata: Osburn 1952: 472 (part), pl. 56, fig. 4 [Colombia].
Dakaria subovoidea: Harmer 1957: 1022 (part).
Watersipora edmondsoni Soule & Soule, 1968: 215, pl. 2, fig. 3 [Hawaii].
Watersipora subovoidea: Ryland 1974: 345, fig. 3A [SE Australia].
Watersipora subtorquata: Soule & Soule 1975: 302, pl. 3, fig. 3 [Brazil]; 304, pl. 2, fig. 3 [Virgin Islands]; pl. 2, fig. 5 [Bermuda].
Watersipora subovoidea fide Harmer: Soule & Soule 1975: 302 (part), pl. 3, fig. 4 [Alexandria].
Watersipora subovoidea: Winston 1982: 139, fig. 66 [Florida].
Watersipora subtorquata: d'Hondt 1988: 199, figs. 6.1–2 [Israel].
Watersipora subtorquata: Seo 1999: 222 (?part), fig. 1 [Korea].
Watersipora subtorquata: Taylor & Gordon 2002: 4 (text), fig. 1A–C [Brazil].
Watersipora subtorquata: Florence *et al*. 2007: 39, fig. 14I, J [South Africa].
Watersipora subtorquata: Abdel Salam & Ramadan 2008: 9, fig. 3 [Alexandria].
Watersipora subovoidea: Ryland *et al.* 2009: 54, figs. 4C, D, G, H [Australia and Italy].
Watersipora subovoidea: Ramalho *et al.* 2011: 772, fig. 3 [Brazil].

Material examined. *Holotype:* MNHN, d'Orbigny Collection 13637, Rio de Janeiro, Brazil. *Other material:* MZUSP 0257, *Watersipora subtorquata*, Araçá, São Sebastião, São Paulo, Brazil, 7 July 2009. NHMUK 1863.8.2.41, dry, *Watersipora cucullata*, Alexandria, Egypt, Station 34a, Eastern Harbour, O'Donoghue coll. NHMUK 1879.4.25.23, dry slide, *Schizoporella atrofusca*, Naples, Italy, A.W. Waters coll. NHMUK 1884.4.21.2, dry, *Watersipora cucullata*, South Chinese Seas. NHMUK 1885.1.26.6–7, dry, *Watersipora subovoidea*, Red Sea, A. Carpenter Esq. NHMUK 1888.11.14.110, dry slide, *Schizoporella* sp., Port Phillip Heads, Australia, January 1887, K. Bracebridge Wilson coll. NHMUK 1888.11.14.111, dry slide, *Schizoporella cucullata*, Port Phillip Heads, Australia, January 1887, J. Bracebride Wilson coll. NHMUK 1888.11.14.358, dry slide, *Lepralia cucullata*, Port Phillip Heads, Australia, January 1887, J. Bracebride Wilson coll. NHMUK 1899.5.1.974 [one dry slide and one balsam slide], *Schizoporella atrofusca* form. *labiosa*, Type, Arabian Sea, T. Hincks coll. NHMUK 1899.7.1.139, dry slide, *Lepralia cucullata*, John Adams Bank, H.M.S. *Herald*, G. Busk coll. NHMUK 1899.7.1.5061, dry slide, *Phylactella* sp., Pensian Gulf?, G. Busk coll. NHMUK 1899.7.1.5214, dry slide, *Lepralia cucullata*, Tangiers, Morocco, 35 fm [62.18 m], HMS *Shearwater*, G. Busk coll. NHMUK 1913.6.4.11, dry slide, *Leraplia cucullata*, Muscat, Oman, 8–10 fm [14.6–18.3 m], Major S.G. Knox. NHMUK 1926.9.6.164, dry slide, *Lepralia cucullata*, Suez Canal, K13, 4 November 1924, A. Hastings. NHMUK 1926.9.6.165, dry slide, *Lepralia cucullata*, Suez Canal, K13, 4 November 1924, A. Hastings. NHMUK 1926.9.6.166, balsam slide, *Lepralia cucullata*, Suez Canal, K13, 4 November 1924, A. Hastings. NHMUK 1929.8.31.1, balsam slide, *Watersipora cucullata*, Shema Creek, Malta, Mediterranean. NHMUK 1948.2.16.28, wet, *Watersipora cucullata*, Santos, Brazil, E. Marcus coll. NHMUK 1968.1.16.77, dry, *Watersipora cucullata*, St James, South Africa, 15 February 1933, F78, O'Donoghue coll. NHMUK 1963.8.2.41pt, dry, *Watersipora subovoidea*, J. Soule & D. Soule det., Alexandria, Egypt, Station 34a, Eastern Harbour, O'Donoghue coll. NHMUK 1973.1.10.3, dry, Accra, Ghana, No. 13B, 14 February 1949, Bassindale coll. NHMUK 1973.1.10.4pt, dry slide, *Watersipora cucullata*, Pram Pram 0.25 m, Gold coast [Ghana], 6 February 1950, Bassindale coll. NHMUK 1980.1.12.3, dry slide, *Watersipora subovoidea*, Townsville harbour, Queensland, Australia, D. Hall. NHMUK 1981.4.1.2, dry slide, *Schizoporella cucullata*, Hurghada, Red Sea, Yellow 935. NHMUK 1986.8.14.3, dry slide, *Watersipora subovoidea*, Hutchinson Island, Florida, 14 November 1974, JWD coll. NHMUK 1996.9.4.1, dry, *Watersipora subtorquata*, ?Site 4, Punta Mochila, Venezuela, October

1971, J.S. Ryland. NHMUK 1996.9.4.2, dry, *Watersipora subtorquata*, Site 1, West of Punto Arrecifes, West of Caracas, Venezuela, 8 October 1971, J.S. Ryland. NHMUK 1997.3.12.7, dry, *Watersipora subtorquata*, Mochina Bay, nr. Naiguatá, coast of Caracas, Venezuela, Loc. 2a, West shore of Gay, 11 October 1971, J.S. Ryland. NHMUK 1997.3.12.3, dry, *Watersipora subtorquata*, Site 5, Playa Caribe, Juan Griego, Venezuela, 12 October 1971, J.S. Ryland. NHMUK 1998.8.5.2, dry, *Watersipora subtorquata*, Mughsay', near Salalah, Southern Oman, 10 October 1983, J.D. Taylor coll. NHMUK 2012.6.30.3, dry slide A/B [part of NHMUK 1998.8.5.2], *Watersipora subtorquata*, Mughsay', near Salalah, Southern Oman, 10 October 1983, J.D. Taylor coll. NHMUK 1999.3.30.11, dry slide, *Watersipora* sp., New Caledonia, Beach of Ile du Phare (Lighthouse), Noumea, A. Willey. NHMUK 2007.12.14.2, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Naples, Italy, 20 October 1960. NHMUK 2007.12.14.3, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Arrawarra, New South Wales, Australia, January 1972. NHMUK 2007.12.14.4, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Arrawarra, New South Wales, Australia, January 1972. NHMUK 2007.12.14.5, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Arrawarra, New South Wales, Australia, January 1972, J.S. Ryland coll. NHMUK 2007.12.14.6, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Genoa Harbour, Italy, 12 November 2007, M. Faimali coll. NHMUK 2007.12.14.7, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Genoa Harbour, Italy, 12 November 2007, M. Faimali coll. NHMUK 2007.12.14.8, balsam slide, *Watersipora subovoidea*, J.S. Ryland det., Genoa Harbour, Italy, 12 November 2007, M. Faimali coll. NHMUK 2012.6.30.15, dry, *Watersipora subovoidea*, Shaab Baraja, Sudan, Red Sea, Large lump covered in soft coral, 23m, 15 September 1978, Dumont coll. NHMUK 2012.6.30.16, dry, *Watersipora subovoidea*, Shaab Baraja, Sudan, Red Sea, 25°52'N, 37°24'W, coral rock, 20 m, 22 September 1978, Dumont coll. NHMUK 1926.9.6.167, balsam slide, *Lepralia cucullata*, Suez Canal, K2, 17 October 1924, A. Hastings. NHMUK 2012.6.30.2, dry slide [part of NHMUK 1973.1.10.3], *Watersipora subovoidea*, Accra, Ghana, No. 13B, 14 February 1949, Bassindale coll. NHMUK 2012.6.30.4, dry slide [part of 1970.6.1.23], *Watersipora subovoidea*, Mikhmoret, Israel, 16 October 1967, G. Eitan.

Description. Colony encrusting, multiserial, primarily unilamellar on flat substrata, becoming multilamellar on irregular substrata, sometimes erect, foliaceous and bilamellar; orange (Figs 20–21) to brownish-purple or black in life, dried colonies becoming dark-orange to grey. Zooids subrectangular to hexagonal, about twice as long as wide, separated by slightly raised lateral walls. Frontal shield flat to slightly convex, sometimes raised more distally than proximally, with numerous round pseudopores about 25 µm in diameter; latero-oral and disto-oral pseudopores sometimes smaller than frontal pseudopores. Latero-oral intrazooidal septula absent. Frontal shield obscured by transparent cuticle in unbleached material. Orifice large, subcircular to oval, slightly wider than long, with well-defined proximal sinus; orificial rim often with raised subtriangular projections on each side of sinus; condyles triangular, projecting distomedially, tooth-like, sometimes inconspicuous and obscured by proximal raised projections. Operculum with broad, parallel-sided dark central band demarcated by sclerites; two lucidae proximally, adjacent to condyles. Avicularia absent. Ooecia absent; orange-red embryos brooded internally, filling most of coelom of maternal zooid. Polypides bright red-orange, lophophore with 20–22 tentacles.

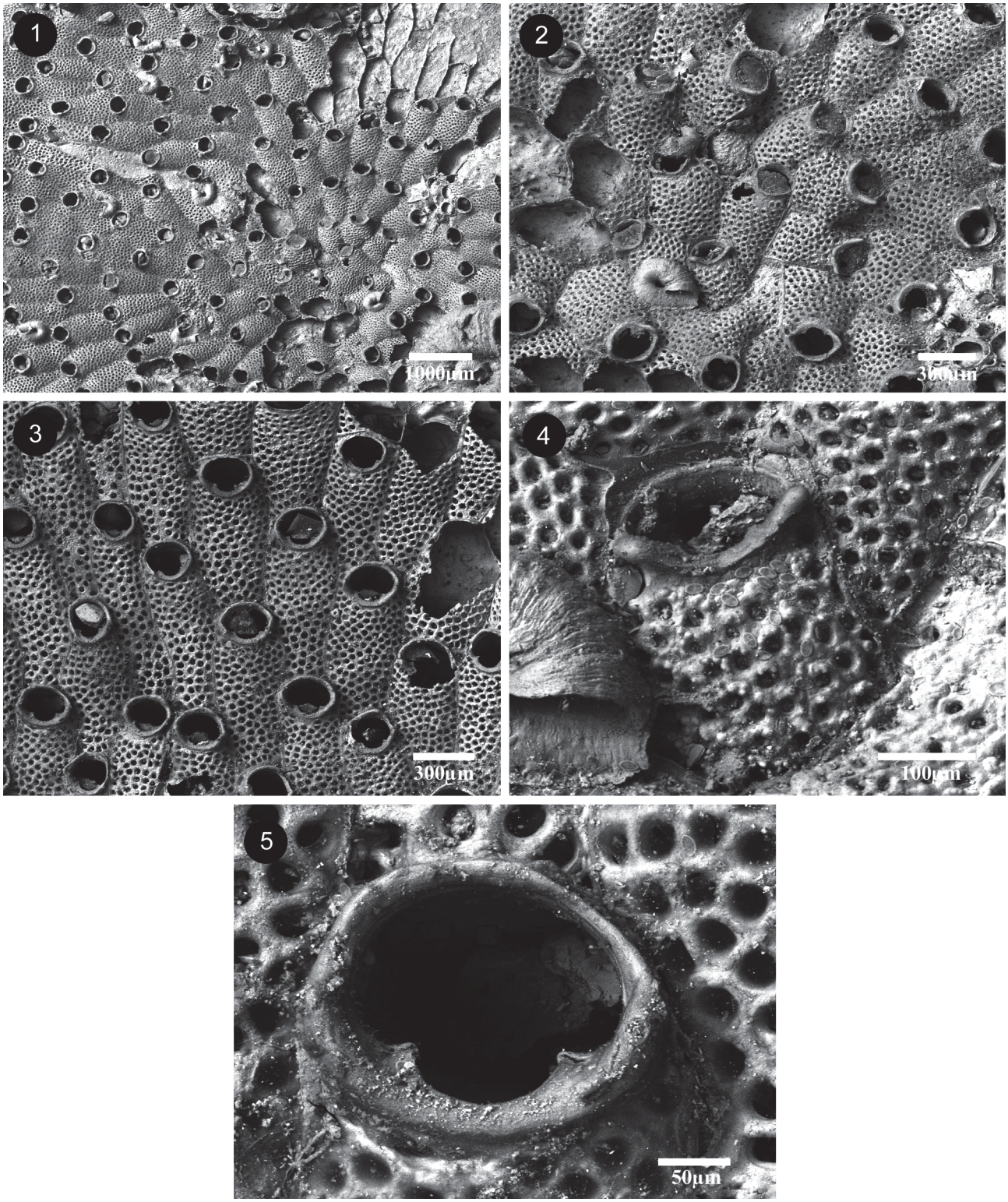
Remarks. We figure scanning electron micrographs of specimens from Mediterranean Israel (NHMUK 1970.6.1.23, Figs 12, 18), the Indian Ocean [Oman (NHMUK 1998.8.5.2, Fig. 13)] and the Atlantic [Ghana (NHMUK 1973.1.10.3, Figs 14–16), as well as from Brazil (MZUSP 0257; Fig. 19)] to show their similarity with the holotype of *W. subtorquata* (Figs 1–5). Ryland *et al.* (2009), followed by Ramalho *et al.* (2011), used the name *W. subovoidea* in error for this species. *Watersipora subtorquata* is characterized by a suborbicular orifice with a sinus demarcated by triangular condyles and an operculum with a parallel-sided dark band and two well-defined lucidae adjacent to the condyles. Ryland *et al.* (2009) suggested that *Lepralia cucullata* of Waters (1909) comprised two species. Based on the figured specimens we suggest that the Suez specimens belong to *W. subtorquata* and the Naples specimens (Waters 1909, pl. 15, figs 2–4) to an undescribed species. We also found a species from Naples in the NHMUK collection (NHMUK 1912.12.21.1019, Fig. 17) that differs from *W. subtorquata* in the operculum and in having a wider orifice compared with the Brazilian specimens; this specimen resembles Waters's specimens from Naples, which are here reassigned to *Watersipora souleorum* **n. sp.** (see below). Mawatari (1952) erected the 'variety' *watersi* for specimens of *Lepralia cucullata* reported by Waters (1909), but this name is preoccupied by a fossil, *Microporella watersi* de Stefani, 1884, which is supposedly a species of *Watersipora* (see Waters 1909). Japanese specimens assigned to *W. cucullata* var. *watersi* by Mawatari (1952, fig. 1G) lack the triangular condyles and lucidae in the operculum and probably belong to *Watersipora subatra* (see below).

TABLE 1. Measurements (in µm) for *Watersipora subtorquata* (d'Orbigny, 1852). The holotype specimen is in the first column. [A] = Holotype specimen of *Watersipora edmondsoni* Soule & Soule, 1969 (=*W. subtorquata*).

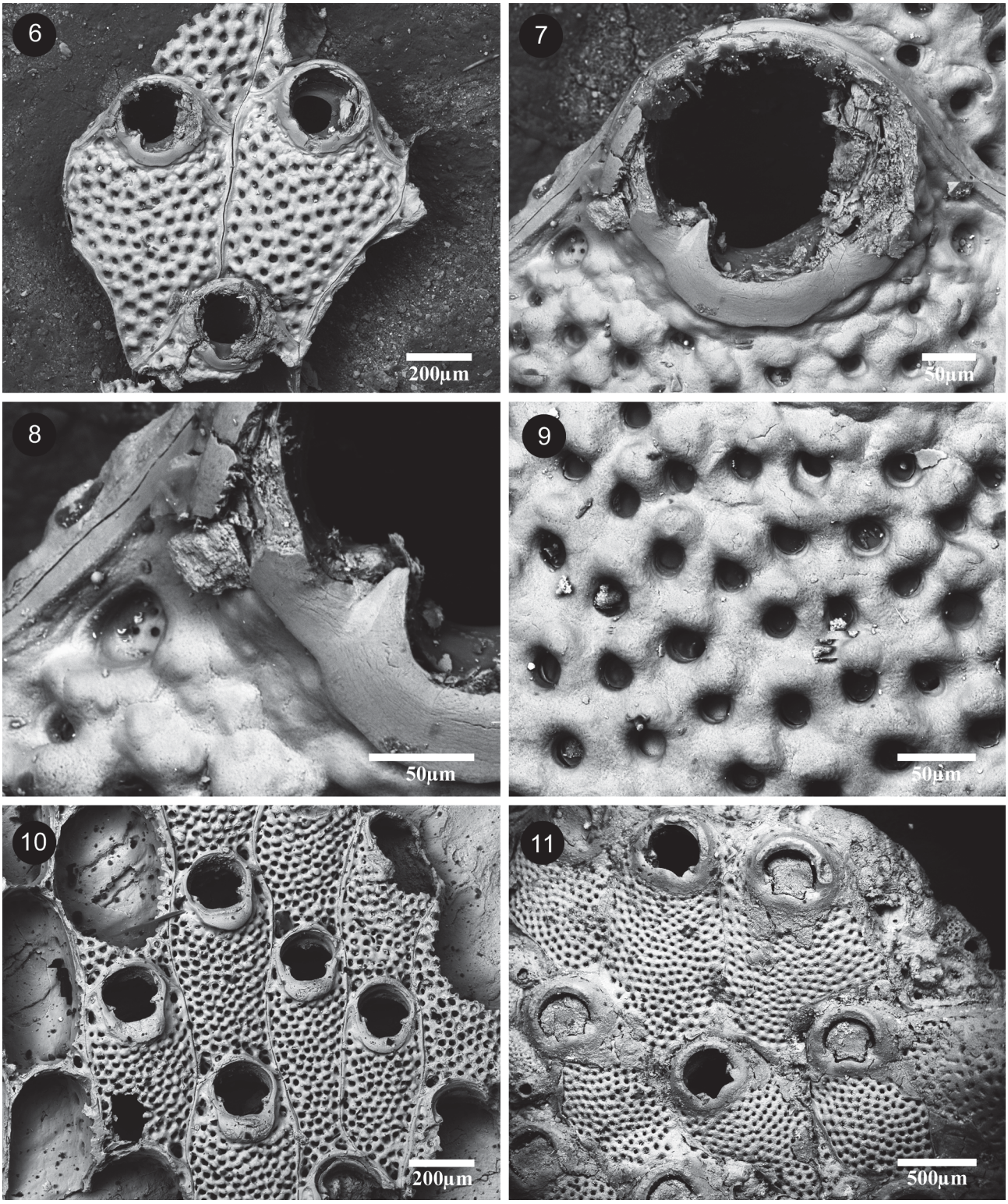
	MNHN	SBMNH	NHMUK	NHMUK	NHMUK
	13637	96310[A]	1970.6.1.23	1973.1.10.3	1998.8.5.2
	Brazil (n=10)	Hawaii (n=10)	Israel (n=5)	Ghana (n=10)	Oman (n=10)
ZL					
Min–Max	728–1029	670–1005	792–962	660–878	636–1184
Mean (SD)	863 (91)	818 (108)	870 (70)	775 (75)	864 (158)
ZW					
Min–Max	226–398	319–426	342–406	295–436	242–396
Mean (SD)	329 (50)	356 (36)	372 (32)	354 (44)	299 (56)
ZL x ZW [x10^3]					
Min–Max	222–327	255–344	229–346	222–346	185–323
Mean (SD)	282 (42)	296 (23)	322 (21)	272 (41)	254 (40)
OL					
Min–Max	161–180	168–195	178–191	162–187	181–198
Mean (SD)	171 (6)	182 (11)	186 (6)	174 (10)	189 (5)
OW					
Min–Max	190–230	212–242	193–219	185–218	191–228
Mean (SD)	213 (15)	227 (8)	202 (12)	205 (9)	214 (12)
OA [x10^3]					
Min–Max	25.7–31.8	28.8–36.6	27.1–32.8	23.5–32.0	27.1–34.2
Mean (SD)	28.7 (2.6)	32.5 (2.5)	29.6 (2.6)	28.0 (2.5)	31.7 (2.2)
ZL / OL					
Min–Max	4.5–5.8	3.5–5.8	4.1–5.2	3.7–5.4	3.4–6.1
Mean (SD)	5.0 (0.5)	4.5 (0.7)	4.7 (0.5)	4.4 (0.5)	4.6 (0.8)
OL / OW					
Min–Max	0.75–0.93	0.72–0.89	0.87–0.95	0.79–0.93	0.80–0.99
Mean (SD)	0.81 (0.06)	0.80 (0.05)	0.92 (0.03)	0.85 (0.04)	0.88 (0.06)
ZA / OA					
Min–Max	7.7–12.3	8.1–11.9	10.1–12.0	8.3–11.9	6.8–9.9
Mean (SD)	9.9 (1.3)	9.1 (1.2)	10.9 (0.7)	9.8 (1.1)	8.0 (0.9)
SinL					
Min–Max	33–46	33–48	38–46	26–41	32–45
Mean (SD)	37.6 (3.7)	40.7 (5.1)	41.5 (3.4)	34.9 (5.9)	40 (4.7)
SinW					
Min–Max	86–123	97–128	105–116	101–122	96–116
Mean (SD)	107 (12)	113 (9)	110 (6)	110 (7)	106 (8)
PorD					
Min–Max	21–32	36–37	20–27	22–29	24–36
Mean (SD)	28 (3)	31 (4)	24 (3)	25 (3)	29 (4)

Ryland *et al.* (2009) noted that the rim of the orifice in *W. subtorquata* (as *W. subovoidea*) may be elevated on either side of the sinus, a character easily recognizable in colonies on algae from Israel and Brazil (Figs 18–19). Gordon (1989) showed a range of orificial morphologies in New Zealand specimens identified as *W. subovoidea*,

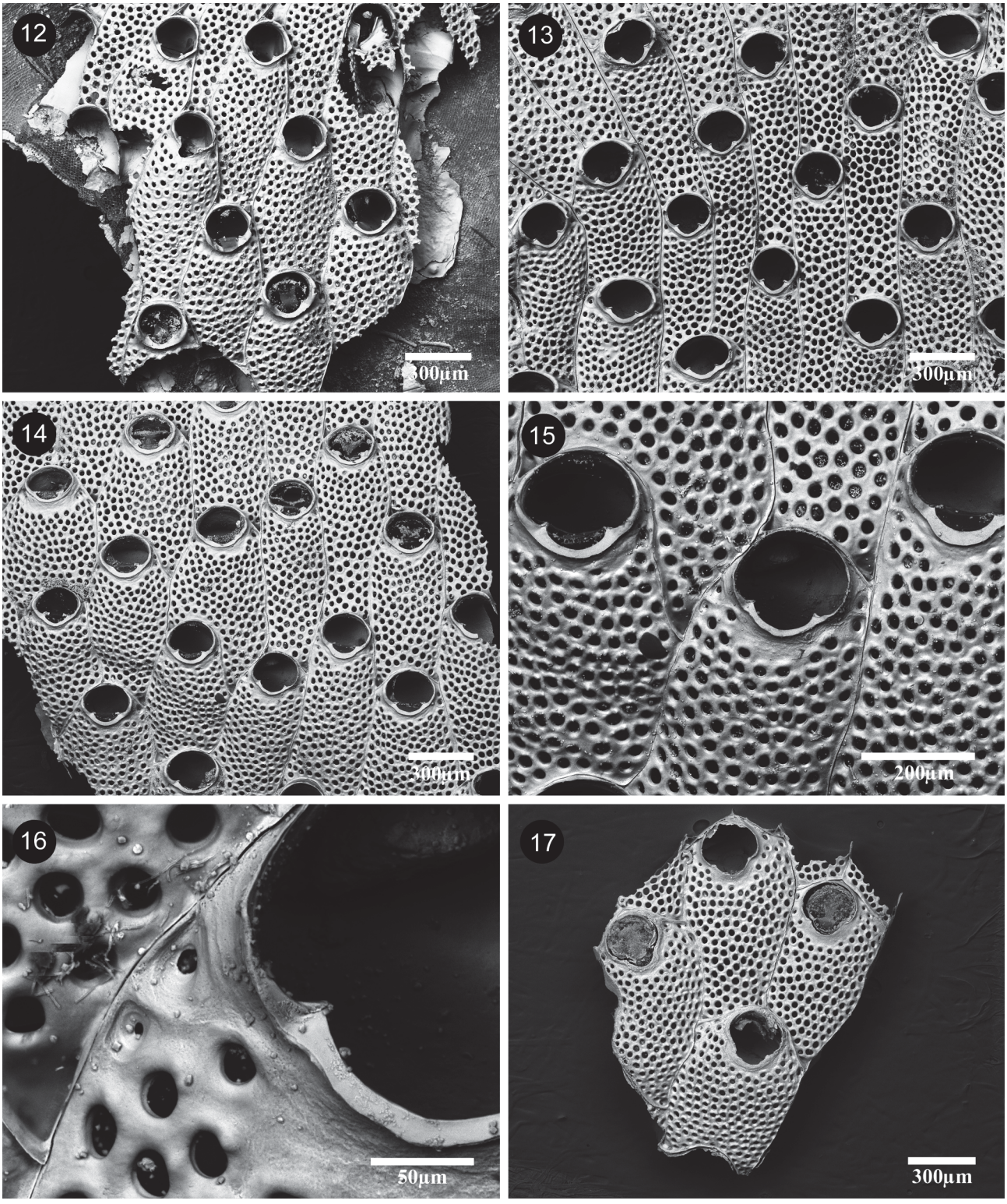
which all seem to represent one species (D.P. Gordon pers. comm. to LMV, 2013). He described two latero-oral intrazooidal septula in his specimens (Gordon 1989, p. 40), a character we also saw in specimens from New Zealand deposited at the NHMUK (Fig. 47). Thus, the New Zealand specimens are here reassigned to *Watersipora subatra*.



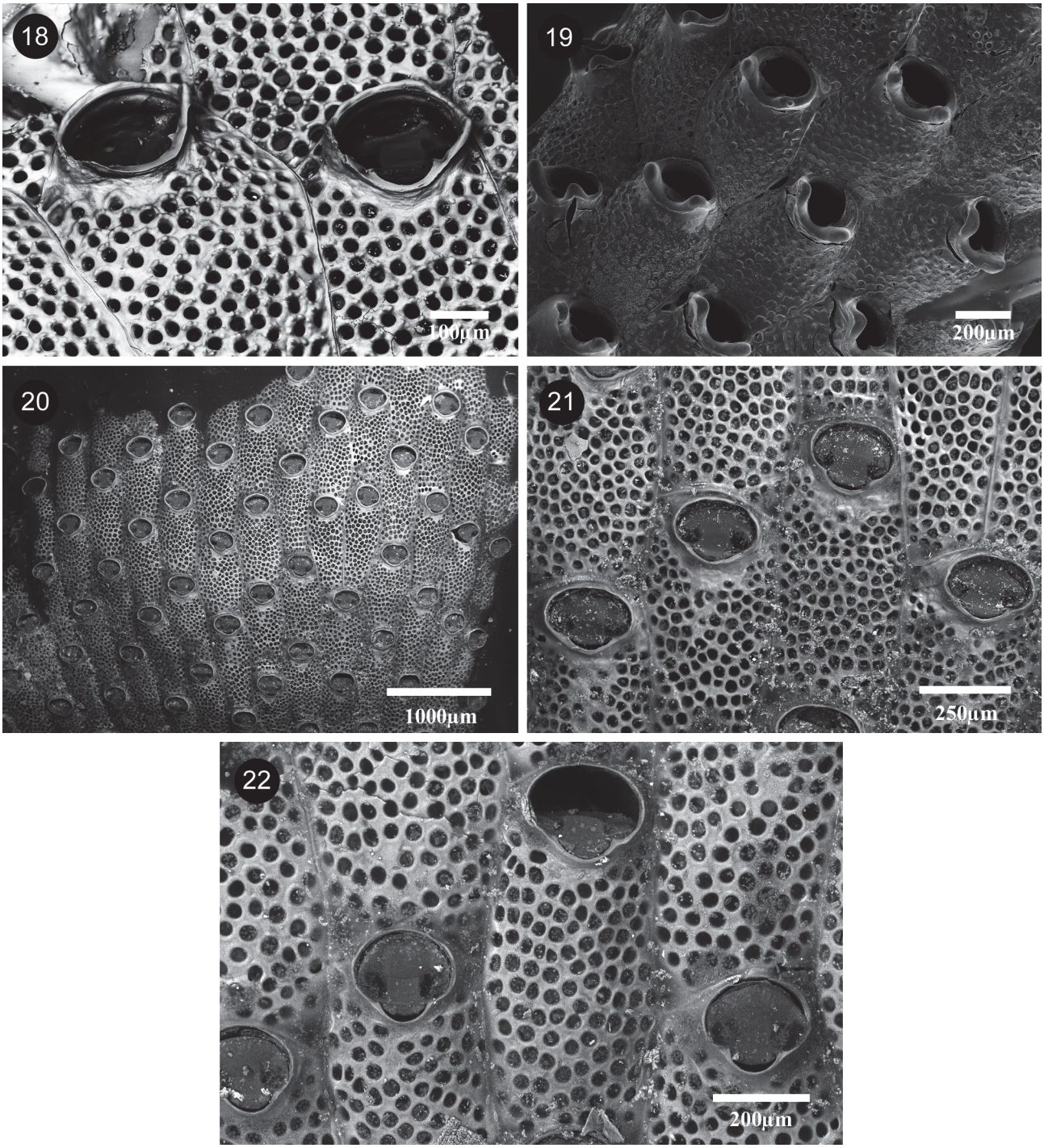
FIGURES 1–5. *Watersipora subtorquata* (d'Orbigny, 1852), MNHN, d'Orbigny Collection 13637, holotype, Rio de Janeiro, Brazil. **1**, general view of the colony; **2**, autozooidal arrangement around the ancestrular area; **3**, autozooids; **4**, close-up of the ancestrula, showing the orifice with projecting proximo-lateral wings; **5**, close-up of orifice with wide sinus and condyles.



FIGURES 6–11. 6–9, *Watersipora cucullata* (Busk, 1854), NHMUK 1854.11.15.189, lectotype, Aegean Sea. **6**, specimen with two autozooids; **7**, close-up of an orifice; **8**, close-up of the lateral edge of the orifice, showing the condyle and the latero-oral intrazooidal septulum; **9**, close-up of the frontal shield. **10**, *Watersipora atrofusca* (Busk, 1856), NHMUK 1892.9.6.4pt, lectotype, Mazatlan, Mexico; autozooidal arrangement. **11**, *Watersipora nigra* (Canu & Bassler, 1930), USNM 8495, holotype, Galapagos; autozooidal arrangement.

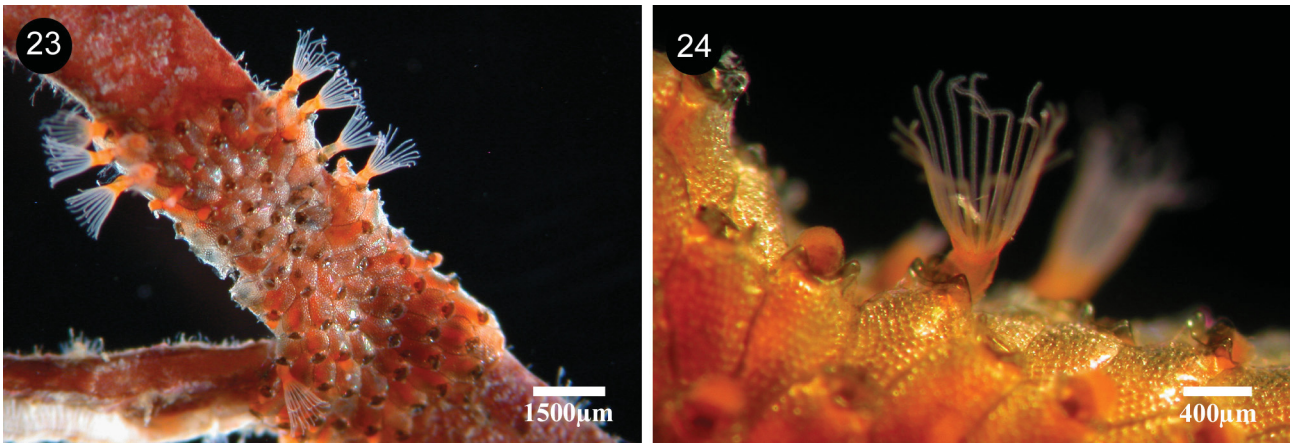


FIGURES 12–16. 12–15, *Watersipora subtorquata* (d'Orbigny, 1852); **12**, colony from Israel (NHMUK 1970.6.1.23); **13**, colony from Oman (NHMUK 1998.8.5.2); **14–16**, colony from Ghana (NHMUK 1973.1.10.3); **14**, autozooidal arrangement; **15**, close-up of autozooids; **16**, close-up of an orifice showing a condyle and the absence of a latero-oral intrazooidal septulum. **17**, *Watersipora souleorum* **n. sp.**, NHMUK 1912.12.21.1019, Naples, Italy; specimen previously misidentified as *W. subtorquata*; the zooids are wider than those of *W. subtorquata*.



FIGURES 18–22. *Watersipora subtorquata* (d'Orbigny, 1852); **18, 19**, orifices with projecting proximolateral wings; **18**, colony from Israel (NHMUK 1970.6.1.23); **19**, colony from São Sebastião, Brazil (MZUSP 0257); **20–22**, SBMNH 96310, AHF 149 (holotype of *Watersipora edmondsoni* Soule & Soule, 1969), Hawaii; **20**, colony; **21, 22**, close-up of zooids.

Hincks (1886) and Calvet (*in* Jullien & Calvet 1903) both independently introduced '*labiosa*': as *Schizoporella atrofusca* f. *labiosa* Hincks, 1886 (p. 269, pl. 10, fig. 5), from the Arabian Sea; and *Schizoporella cucullata* var. *labiosa* Calvet *in* Jullien & Calvet, 1903 (p. 141, pl. 16, fig 7), from Cape Verde. The specimens identified as form *labiosa* by Hincks (1886) are conspecific with other specimens examined from the Arabian Sea (Fig. 13) and belong to *W. subtorquata*. The specimens previously identified as var. *labiosa* from the Azores by Calvet (*in* Jullien & Calvet 1903) (MOM 420379) are distinct in having a deep sinus and an operculum with a narrow, biconcave dark central band; these specimens are badly preserved, but they may be conspecific with *W. souleorum* **n. sp.** (see below).



FIGURES 23, 24. Living colonies of *Watersipora subtorquata* (d'Orbigny, 1852) from São Sebastião, Brazil.

Seo (1999, 2005) figured specimens of putative *Watersipora subtorquata* from Korea, with reddish-brown to black colonies (Seo 2005: pls 154–156). The size of the orifice in her specimens (Seo 2005: pl. 156B) resembles *W. subtorquata* but the condyles are sometimes minute and obscured by the proximal peristome.

Material reported as *W. subtorquata* by Ryland *et al.* (2009) has shallow, bar-shaped condyles and an operculum with a proximal biconcave band, quite distinct from *W. subtorquata* and *W. cucullata*; these specimens are here identified as *Watersipora subatra* (see below).

Examination of the holotype material of *Watersipora edmondsoni* Soule & Soule, 1968 (SBMNH 96310, AHF 149; Fig. 20–22) revealed it to be *W. subtorquata*. We believe, however, that the additional specimens examined by Soule & Soule (1968, 1975) probably include one or more additional species from the same locality [e.g. the specimen reported as *W. edmondsoni* (Soule & Soule 1975, pl. 1, fig. 7)]. Specimens recently reported as *Watersipora subovoidea sensu* Harmer by Dick *et al.* (2006) belong to an undescribed species that may be conspecific with *W. edmondsoni sensu* Soule & Soule, 1975 (*non* Soule & Soule, 1968).

Distribution. Atlantic (Brazil, Caribbean, Virgin Islands, Florida, Cape Verde, Senegal, Ghana and South Africa), Mediterranean (Italy, Alexandria), Red Sea, Arabian Sea and Pacific (China Sea, Korea, Hawaii and Australia).

Watersipora cucullata (Busk, 1854)

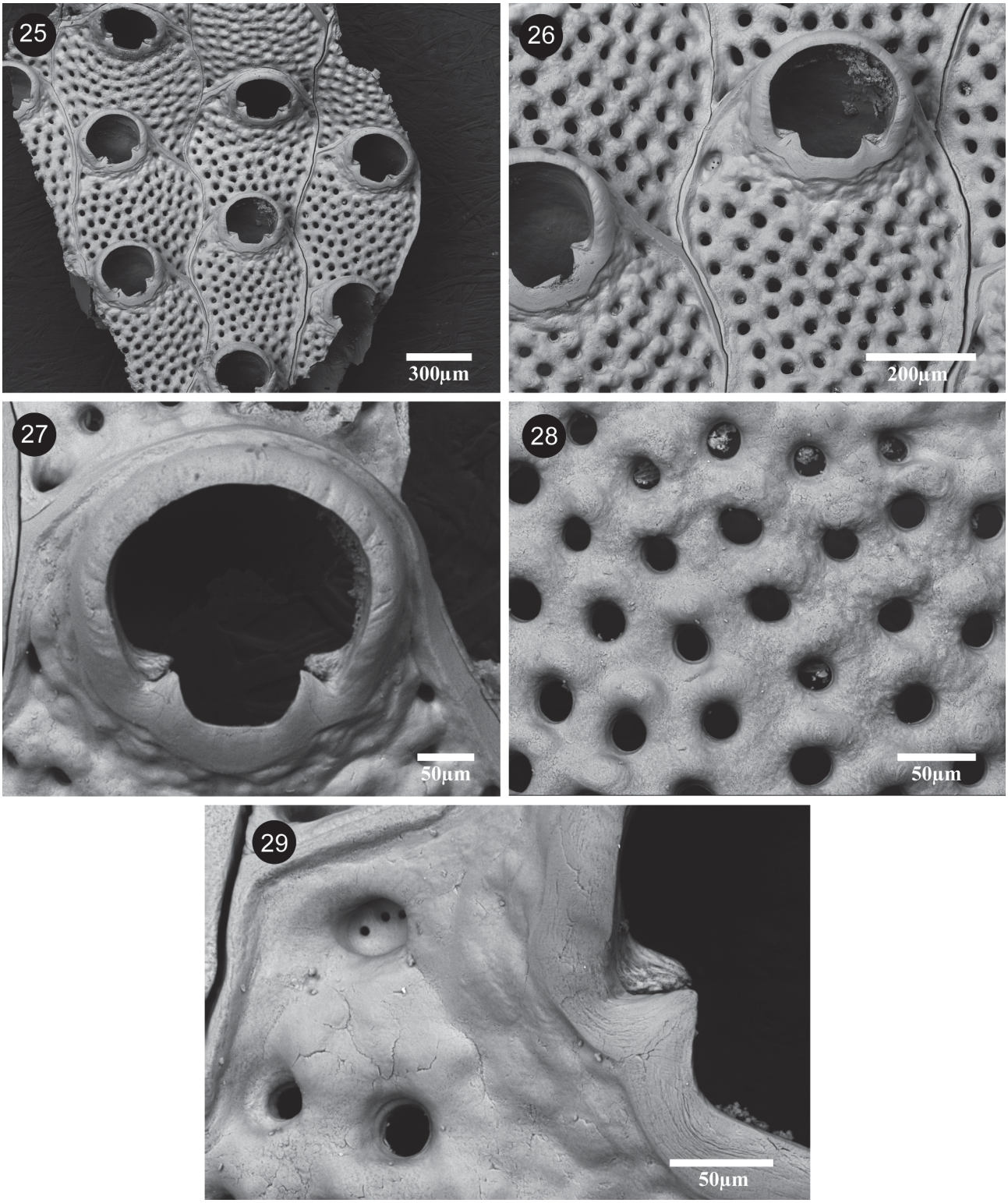
(Figs 6–9, 25–34, 65; Table 2)

?*Cellepora subovoidea* d'Orbigny, 1852: 402 [Red Sea; *nomen dubium*].
Lepralia cucullata Busk, 1854: 81, pl. 96, figs 4–5 [Aegean Sea].
Schizoporella atrofusca: Hincks 1886: 269 (part), pl. 10, fig. 4 (non fig. 5) [Adriatic]. Non *Schizoporella atrofusca* Busk, 1856: 178 [Mexico].
Dakaria subovoidea: Harmer 1957: 1022 (part) [Aegean Sea].
Watersipora cucullata: Soule & Soule,1975: 302, pl. 2, fig. 2; pl. 3, fig. 1; pl. 4, fig. 3 [Aegean Sea; Naples].
Watersipora subovoidea: Hayward & McKinney 2002: 63, fig. 29A–B [Adriatic]. Non *Watersipora subovoidea*: Ryland *et al.* 2009: 54, fig. 4C, D, G, H [=*Watersipora subtorquata*].

Material examined. *Lectotype* (chosen by Soule & Soule 1975): NHMUK 1854.11.15.189 (specimen mounted on one dry slide and two balsam slides), *Lepralia cucullata*, 1854, G. Busk det., Aegean Sea, E. Forbes. *Paralectotypes*: NHMUK 1899.7.1.1398, dry, same data as for lectotype; NHMUK 2012.6.30.1, dry slide, same data as for lectotype. *Other material:* NHMUK 1899.5.1.456, *Schizoporella atrofusca*, dry slide, T. Hincks det., Adriatic, Pieper coll. NHMUK 1899.5.1.975, dry slide, *Schizoporella atrofusca*, T. Hincks det., Adriatic. NHMUK 1965.8.14.10, dry slide, *Watersipora cucullata*, Balearic Islands, Mediterranean, Cox coll.

Description. Colony encrusting, multiserial, unilamellar; blackish in colour. Zooids subrectangular to hexagonal, separated by slightly raised grooves. Frontal shield slightly more convex distally than proximally, with small tubercles and uniformly perforated by round pseudopores about 20 µm diameter; two latero-oral intrazooidal

septula, small, near the lateral zooidal margin proximolateral to the orifice; each with 2–4 small pores; frontal shield obscured by thick, black epitheca. Orifice large, slightly wider than long, with a well-defined, broad, shallow, U-shaped sinus demarcated by triangular projections; orificial rim robust and thickened around whole orifice, sometimes better developed proximally than distally; condyles upturned, large and conspicuous. Operculum with broad, parallel-sided dark central band and slightly thinner lateral area. Avicularia absent. Ooecia absent.



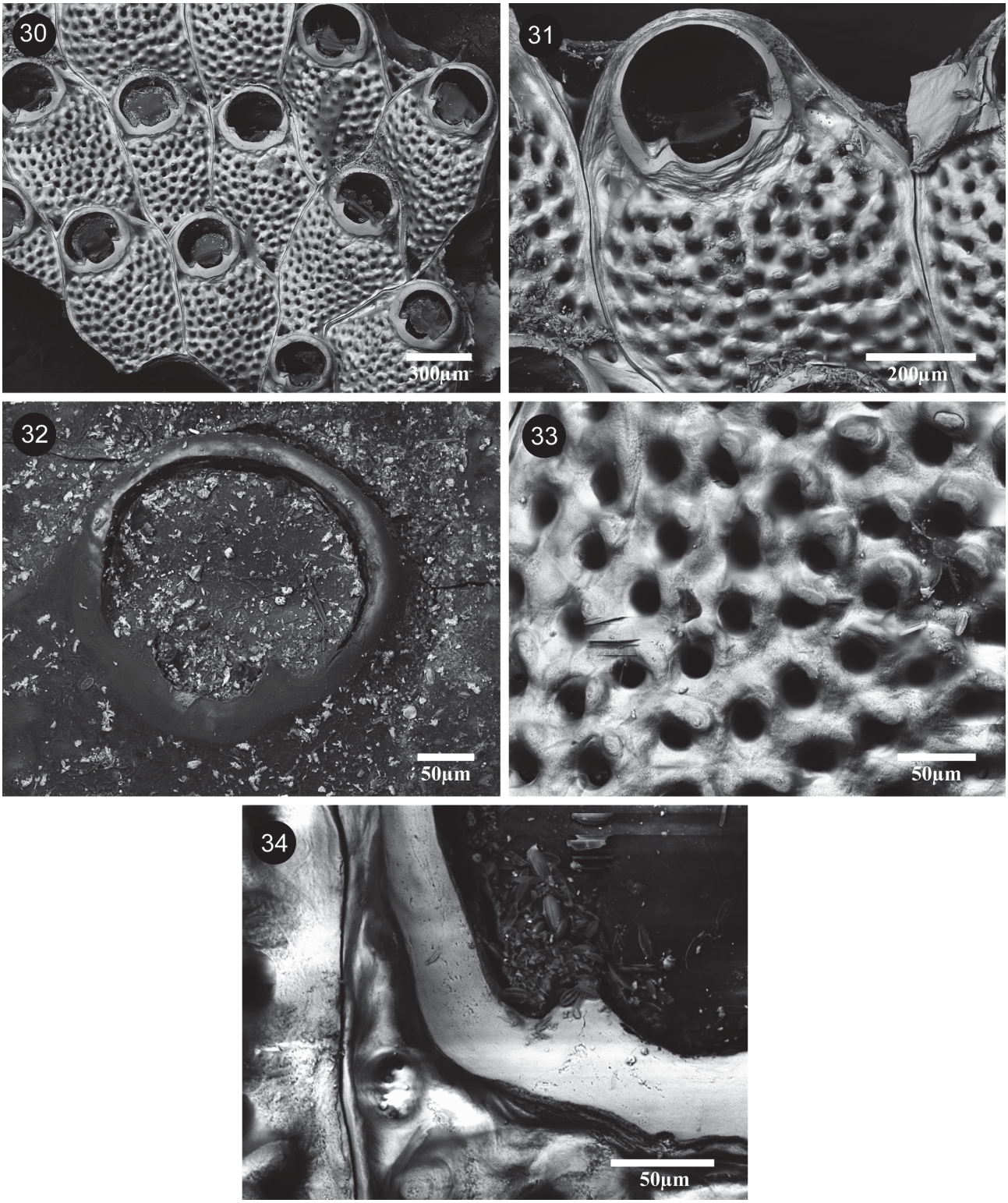
FIGURES 25–29. *Watersipora cucullata* (Busk, 1854), NHMUK 2012.6.30.1, paralectotype, Aegean Sea. **25**, autozooidal arrangement; **26**, autozooid; **27**, close-up of an orifice; **28**, close-up of the frontal shield; **29**, close-up of the lateral edge of the orifice, showing a condyle and the latero-oral intrazooidal septulum.

TABLE 2. Measurements (in µm) for *Watersipora cucullata* (Busk, 1854), *W. atrofusca* (Busk, 1856) and *W. nigra* (Canu & Bassler, 1930). Type specimens are marked with asterisks.

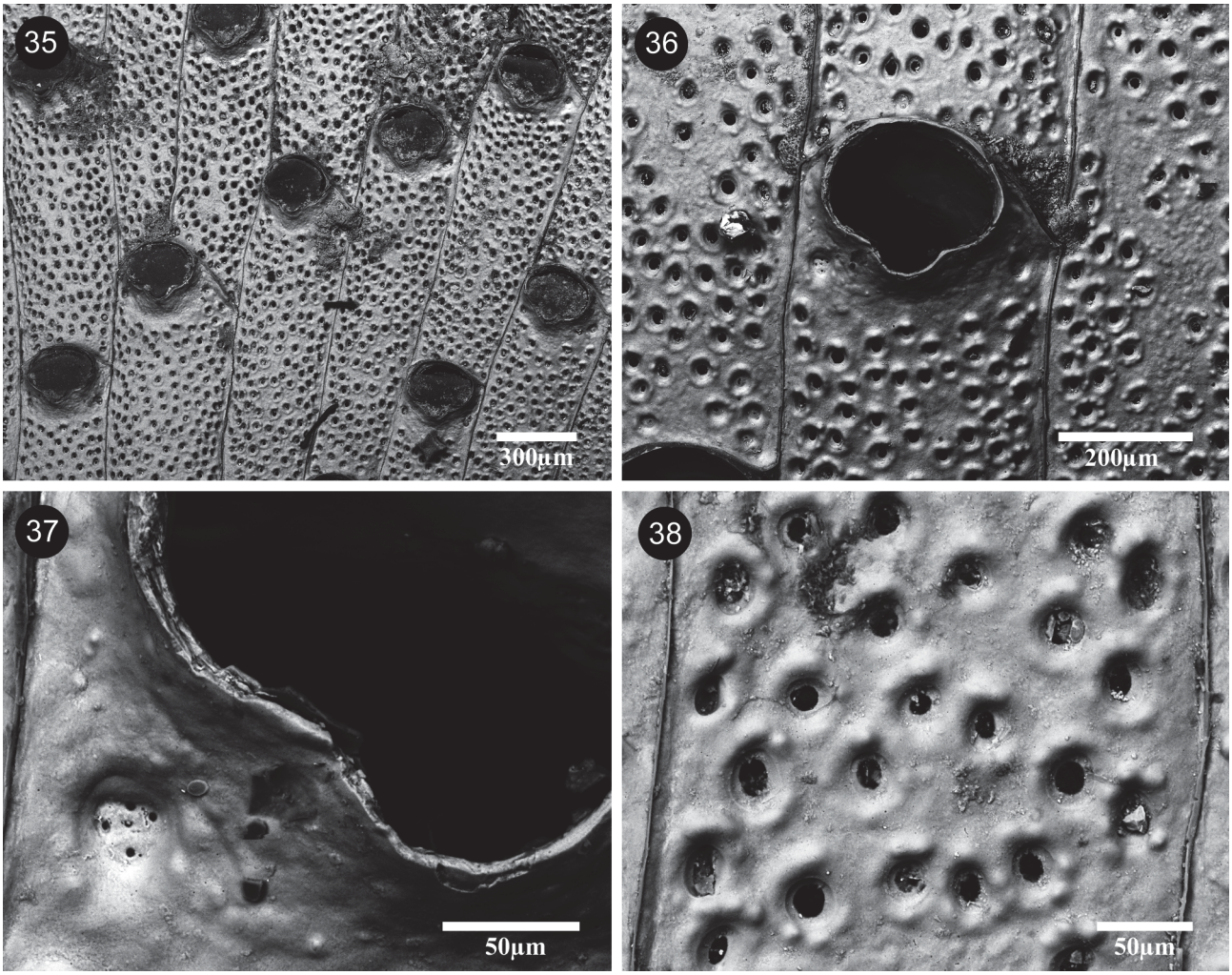
	W. atrofusca	*W. cucullata*		*W. nigra*
	NHMUK 1892.9.6.4*	NHMUK 2012.6.30.1	NHMUK 1899.5.1.975	NHMUK 1975.5.12.1
	Japan (n=6)	Aegean Sea (n=6)	Adriatic (n=10)	Galapagos (n=10)
ZL				
Min–Max	567–801	697–902	673–911	972–1102
Mean (SD)	646 (96)	789 (80)	805 (80)	1038 (47)
ZW				
Min–Max	252–359	480–570	422–650	663–861
Mean (SD)	304 (47)	524 (30)	534 (68)	740 (76)
ZL x ZW [x10^3]				
Min–Max	162–214	362–457	284–518	673–926
Mean (SD)	194 (20)	413 (46)	431 (77)	769 (93)
OL				
Min–Max	158–175	202–228	200–226	224–236
Mean (SD)	168 (6)	216 (9)	218 (8)	230 (5)
OW				
Min–Max	160–185	227–245	223–258	317–333
Mean (SD)	175 (10)	233 (7)	240 (11)	325 (7)
OA [x10^3]				
Min–Max	21.0–25.4	35.9–41.5	35.0–44.6	58.3–59.5
Mean (SD)	23.2 (1.9)	39.2 (1.9)	41.1 (3.2)	58.7 (0.4)
ZL / OL				
Min–Max	3.3–5.1	3.3–4.2	3.1–4.0	4.3–4.7
Mean (SD)	3.8 (0.7)	3.7 (0.3)	3.6 (0.3)	4.5 (0.1)
OL / OW				
Min–Max	0.92–1.06	0.86–0.98	0.85–0.94	0.67–0.75
Mean (SD)	0.96 (0.05)	0.93 (0.05)	0.90 (0.03)	0.71 (0.03)
ZA / OA				
Min–Max	7.6–9.6	9.1–11.9	7.0–13.5	11.47–15.56
Mean (SD)	8.4 (0.8)	10.5 (1.2)	10.3 (2.0)	13.1 (1.5)
SinL				
Min–Max	39–52	40–56	39–50	51–58
Mean (SD)	44 (6)	48 (5)	44 (4)	55 (3)
SinW				
Min–Max	112–131	109–130	100–134	213–233
Mean (SD)	122 (8)	115 (7)	122 (11)	219 (7)
PorD				
Min–Max	17–23	20–27	21–29	27–43
Mean (SD)	20 (2)	24 (2)	25 (3)	30 (6)

Remarks. *Watersipora subovoidea* has been reported in subtropical and tropical waters, i.e. Brazil, Florida and Australia (Mackie *et al.* 2006; Geller *et al.* 2008; Ryland *et al.* 2009), but the great majority of these records belong to *W. subtorquata* (see above). D'Orbigny (1852) did not give any description or figures for *Cellepora subovoidea*,

and according to the ICZN Article 75.3.6 “evidence that the neotype came as nearly as practicable from the same original type locality” should be provided, which is not apparent in the Ryland *et al.* (2009) paper. Thus, we suggest setting aside the neotype selection of *Cellepora subovoidea* (NHMUK 1854.11.15.189) made by Ryland *et al*. (2009).



FIGURES 30–34. *Watersipora cucullata* (Busk, 1854), NHMUK 1899.5.1.975, T. Hincks Collection, Adriatic. **30**, general view of the colony; **31**, autozooid; **32**, close-up of an orifice with operculum; **33**, close-up of the frontal shield; **34**, close-up of the lateral edge of the orifice, showing the condyle and a latero-oral intrazooidal septulum.



FIGURES 35–38. *Watersipora aterrima* (Ortmann, 1890), MZS BRY 003, syntype, Japan. **35**, autozooidal arrangement; **36**, close-up of an orifice; **37**, close-up of the lateral edge of the orifice, showing the latero-oral intrazooidal septulum; **38**, close-up of the frontal shield.

Watersipora cucullata is characterized by a suborbicular orifice with a shallow, wide sinus demarcated by triangular projections (Figs 8, 27, 29, 31, 32, 34), large, conspicuous condyles (Figs 8, 27, 29, 31), and a small latero-oral intrazooidal septula on each side of the zooid (Fig 8, 29, 34). Latero-oral intrazooidal septula are also present in *Watersipora aterrima* and *W. subatra*, but these species are distinguished by the shape of the orifice and condyles (see below). *Watersipora cucullata* differs from *W. nigra* in having smaller zooids and orificial area (see Canu & Bassler, 1930, p. 26; Fig. 11; Table 2) and paired intrazooidal septula, near the lateral zooidal margin, proximolateral to the orifice.

Watersipora atrofusca (Busk, 1856) (Fig. 10; Table 2), known from Mazatlan (Mexico), resembles *W. cucullata* in colony shape but differs in having a smaller, almost circular orifice and in lacking intrazooidal septula.

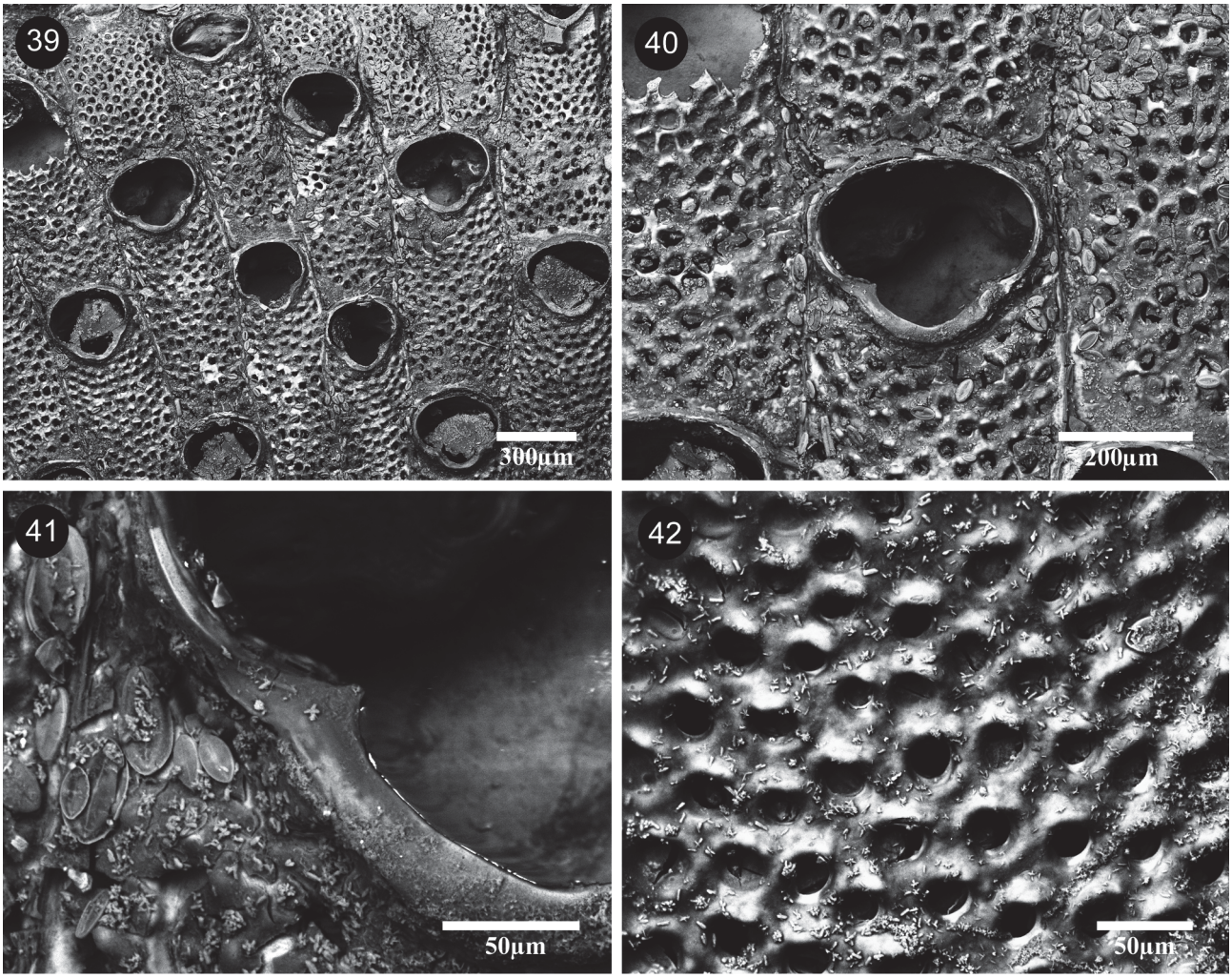
Distribution. Mediterranean (including the Adriatic and Aegean seas).

Watersipora subatra **(Ortmann, 1890) n. stat.**

(Figs 39–53, 66, 69; Table 3)

Schizoporella aterrima var. *subatra* Ortmann, 1890: 49 [Japan].
?*Watersipora cucullata* var. *watersi* Mawatari, 1952: 12 (part), fig. 1G [Japan].
Dakaria subovoidea: Harmer 1957: p. 1022 (part), pl. 49, figs 11–12, 14 [Indonesia].
?*Cellepora subovoidea* d'Orbigny, 1852: 402 [Red Sea; *nomen dubium*].
Watersipora subtorquata: Ryland 1974: 345, fig. 3C [Low Island]. Non *Cellepora subtorquata* d'Orbigny, 1852: 399 [Brazil].

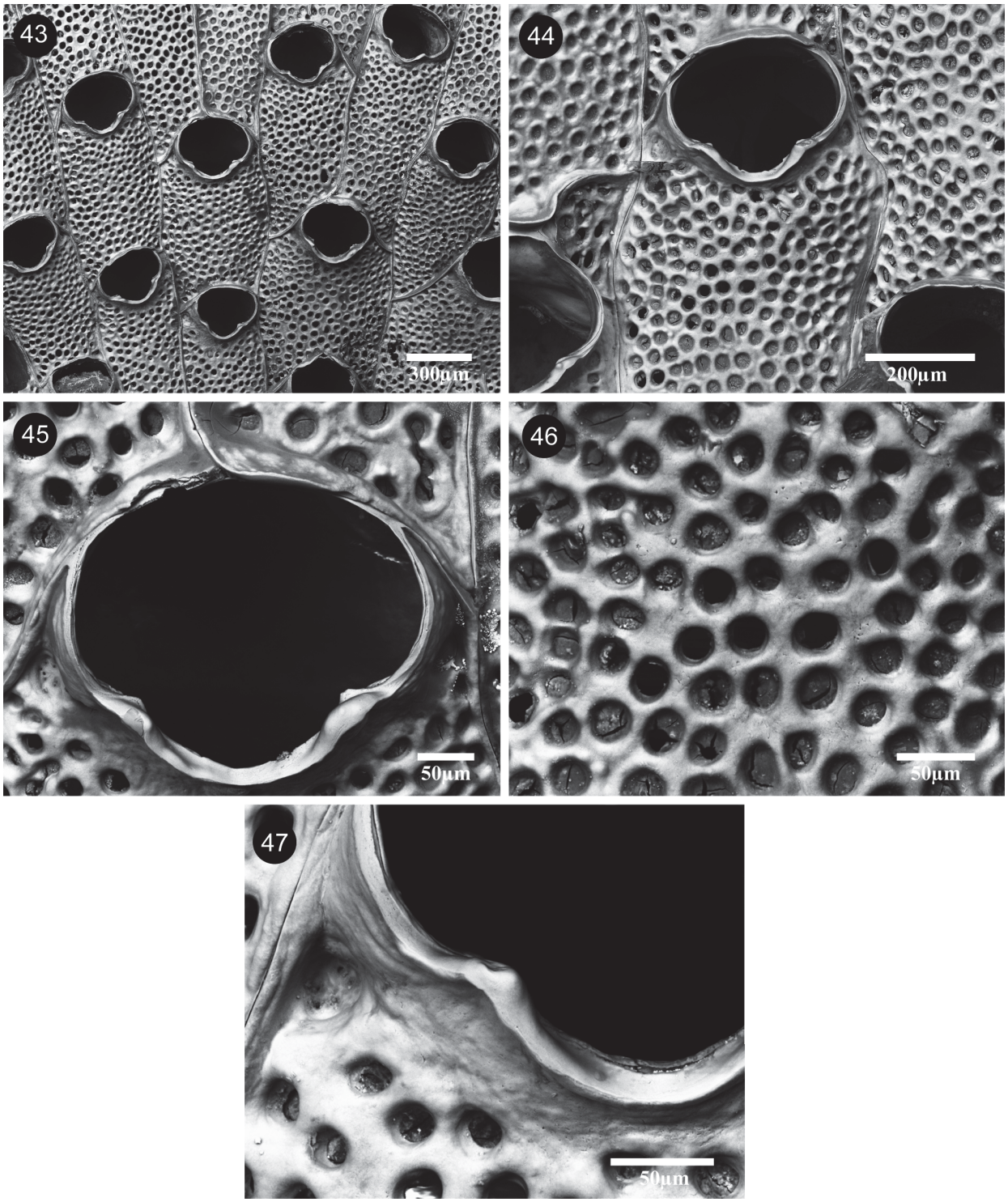
"*Watersipora subovoidea*" fide Harmer: Soule & Soule 1975: 308 (part), pl. 3, fig. 6 [Australia].
"*Watersipora subovoidea*" fide Harmer: Winston & Heimberg, 1986: 15, figs 35–37 [Komodo].
Watersipora subtorquata: Gordon 1989: 40, pl. 20, B–H [New Zealand].
Watersipora subtorquata: Gordon & Mawatari, 1992: 30 [New Zealand].
Watersipora subtorquata: Ryland *et al.* 2009: 55, figs 3, 4A, C, E, F [Australia, Bay of Biscay and English Channel].
Watersipora subtorquata: Kelso & Wyse-Jackson 2012: 2010, fig. 1 [Ireland].
Watersipora subtorquata: Kuhlenkamp & Kind 2013: 3, figs 1B, C, 2A–F [North Sea: Helgoland].



FIGURES 39–42. *Watersipora subatra* (Ortmann, 1890), MZS BRY 002, holotype, Sagami Bay, Japan. **39**, autozooidal arrangement; **40**, close-up of an orifice; **41**, close-up of the lateral edge of the orifice, showing the very small condyle; **42**, close-up of the frontal shield.

Material examined. *Holotype:* MZS 002, Ortmann Collection, Sagami Bay, Japan, 50–100 fm (15–30 m), 1882. *Other material:* NHMUK 1922.10.8.3, dry slide, *Schizoporella cucullata*, sea level, Misaki, Japan, No. 1, Insole coll. NHMUK 1929.12.31.1, dry slide, *Watersipora atrofusca*, Australia, MacGillivray coll. NHMUK 2005.5.26.19, dry, *Watersipora subtorquata*, scraped from hull of *Seasprite*, Leigh Wharf/Marina, North Island, New Zealand, 6 October 2004, K. Tilbrook coll. NHMUK 2007.12.14.9, balsam slide, *Watersipora subtorquata*, J.S. Ryland det., Low Islands, Great Barrier Reef, July 1974, J.S. Ryland coll. NHMUK 2007.12.14.10, balsam slide, *Watersipora subtorquata*, J.S. Ryland det., Low Islands, Great Barrier Reef, July 1974, J.S. Ryland coll. NHMUK 2007.12.14.12, balsam slide, *Watersipora subtorquata*, J.S. Ryland don., on shell, Bay of Arcachon, August 2003, Hans de Blauwe coll. NHMUK 2007.12.14.14, balsam slide, *Watersipora subtorquata*, J.S. Ryland don., St-Jacut-sur-la-Mer, April 2005, Hans de Blauwe coll. NHMUK 2007.12.14.15, balsam slide, *Watersipora subtorquata*, J.S. Ryland don., St-Jacut-sur-la-Mer, April 2005, Hans de Blauwe coll. NHMUK 2007.12.14.16, balsam slide, *Watersipora subtorquata*, J.S. Ryland don., Guersey, 2007, R. Lord coll. NHMUK 2007.12.14.17, balsam slide, *Watersipora subtorquata*, J.S. Ryland don., Guersey, 2007, R. Lord coll. NHMUK 2007.12.14.18,

balsam slide, *Watersipora subtorquata*, J.S. Ryland don., Guersey, 2007, R. Lord coll. NHMUK 2010.12.1.2, dry, *Watersipora* sp., Point Loma, Marina, San Diego, California, USA, September 2010. P.D. Taylor & B. Okamura coll. NHMUK 2010.6.30.7, dry and dry slide, Long Beach, Los Angeles, USA. NHMUK 2012.6.30.6, dry slide [part of NHMUK 2005.5.26.19], *Watersipora subtorquata*, scraped from hull of *Seasprite*, hauled out Leigh Wharf/Marina, North Island, New Zealand, 6 October 2004, K. Tilbrook coll.



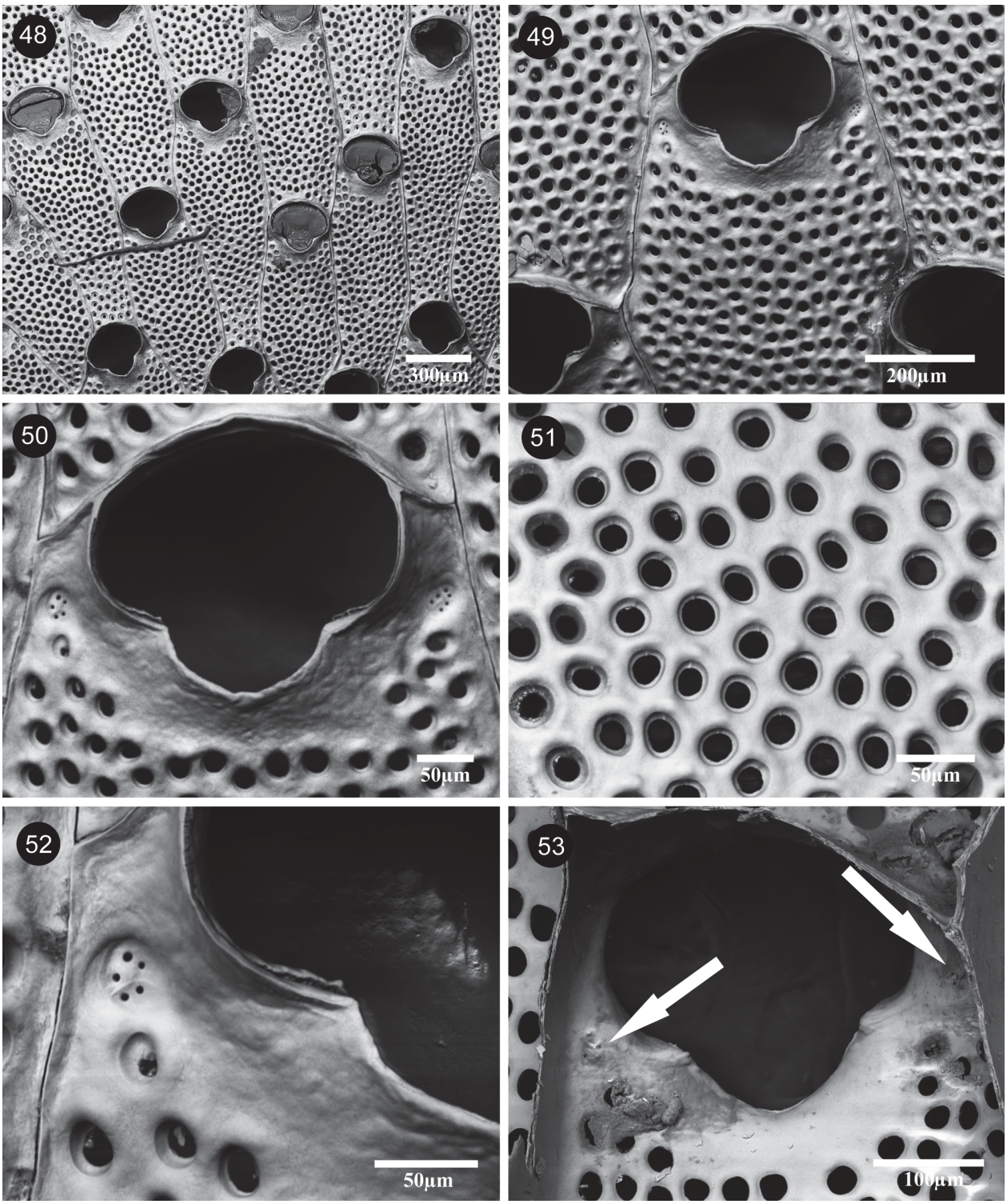
FIGURES 43–47. *Watersipora subatra* (Ortmann, 1890), NHMUK 2005.5.26.19, New Zealand. **43**, autozooidal arrangement; **44**, autozooid; **45**, close-up of an orifice; **46**, close-up of the frontal shield; **47**, close-up of the lateral edge of the orifice, showing the condyle and the latero-oral intrazooidal septulum.

TABLE 3. Measurements (in µm) for *Watersipora aterrima* (Ortmann, 1890) and *W. subatra* (Ortmann, 1890). Type specimens are marked with asterisks.

	W. aterrima	*W. subatra*		
	MZS BRY 003*	MZS BRY 002*	NHMUK 2005.5.26.19	NHMUK 2012.6.30.5
	Japan (n=5)	Japan (n=10)	New Zealand (n=10)	California (n=10)
ZL				
Min–Max	1155–1393	815–1000	685–1430	921–1259
Mean (SD)	1260 (101)	919 (60)	909 (213)	1062 (111)
ZW				
Min–Max	348–430	320–489	334–598	308–447
Mean (SD)	378 (32)	409 (62)	445 (76)	368 (38)
ZL x ZW [x10^3]				
Min–Max	447–508	299–437	286–633	304–504
Mean (SD)	474 (45)	374 (53)	400 (93)	392 (67)
OL				
Min–Max	215–229	245–283	220–289	210–242
Mean (SD)	220 (6)	263 (14)	257 (19)	228 (10)
OW				
Min–Max	230–249	263–348	280–329	255–271
Mean (SD)	238 (7)	309 (22)	303 (13)	261 (6)
OA [x10^3]				
Min–Max	39.5–44.7	52.8–77.3	48.3–72.3	43.7–50.9
Mean (SD)	41.3 (2.1)	63.9 (6.6)	61.4 (6.4)	46.9 (2.3)
LZ / OL				
Min–Max	5.3–6.2	2.9–3.9	2.9–5.1	3.4–5.5
Mean (SD)	5.7 (0.4)	3.5 (0.3)	3.5 (0.6)	4.6 (0.6)
OL / OW				
Min–Max	0.89–0.98	0.78–0.97	0.76–0.98	0.79–0.95
Mean (SD)	0.92 (0.03)	0.85 (0.06)	0.85 (0.05)	0.87 (0.04)
ZA / OA				
Min–Max	10.6–12.8	5.0–7.1	5.3–8.7	6.8–10.1
Mean (SD)	11.5 (0.9)	5.8 (0.7)	6.5 (1.0)	8.3 (1.3)
SinL				
Min–Max	38–48	61–74	52–71	47–65
Mean (SD)	43 (4)	67.3 (4.2)	61.1 (5.6)	55.4 (4.8)
SinW				
Min–Max	85–101	125–174	152–178	121–140
Mean (SD)	94 (6)	145 (16)	164 (9)	130 (6)
PorD				
Min–Max	16–20	22–38	23–32	18–27
Mean (SD)	17 (1)	29 (5)	27 (3)	22 (3)

Description. Colonies encrusting, multiserial, uni- to multilamellar; sometimes erect, foliaceous and bilamellar; colour in life variable, from orange to brownish-purple or greyish to black. Zooids subrectangular to hexagonal, about twice as long as wide, separated by slightly raised lateral walls. Frontal shield slightly convex, with numerous round pseudopores about 25 µm diameter; two large latero-oral intrazooidal septula near lateral

zooidal margin, proximolateral to orifice, each with 3–8 (often 5) small pores. Frontal shield obscured by translucent cuticle. Orifice large, subcircular to oval, slightly wider than long, with broad, well-defined proximal, U-shaped sinus; orificial rim thin, sometimes slightly raised; narrow bar-shaped condyles, sometimes inconspicuous. Operculum with broad, biconcave proximal band, without lucidae. Avicularia absent. Ooecia absent.



FIGURES 48–53. *Watersipora subatra* (Ortmann, 1890), NHMUK 2012.6.30.5, California. **48**, autozooidal arrangement; **49**, autozooid; **50**, close-up of an orifice; **51**, close-up of the frontal shield; **2**, close-up of the lateral edge of the orifice, showing the condyle and the latero-oral intrazooidal septulum; **53**, internal view of the orificial area; arrows show the latero-oral intrazooidal septula.

Remarks. Ortmann (1890) described and figured *Schizoporella aterrima* from Japan, including the new variety *subatra* without drawings or description. Ryland *et al.* (2009) noted that *Schizoporella aterrima* Ortmann, 1890 is unrecognizable and that the description given by Mawatari (1952) for *Watersipora cucullata* var. *watersi*, another species reported from Japan, may include at least two species. One of us (MSJ) has examined Ortmann's specimens deposited at the Musée zoologique de la Ville de Strasbourg, concluding that they represent two species, *Watersipora aterrima* (MZS 003; Figs 35–38; Table 3) and *Watersipora subatra* (MZS 002; Fig. 39–42; Table 3). *Watersipora aterrima* is distinguished from *W. subatra* by having a smaller orifice, narrower sinus and smaller frontal pseudopores.

Mawatari (1952) introduced variety *watersi* for specimens with distinctive opercula. His notes on this new variety are based on specimens from Japan, and two others recorded by Waters (1909) from Naples and by Hastings (1930) from Cape Verde. Unfortunately, Mawatari's specimens from Japan assigned to *W. cucullata* var. *watersi* could not be located, but part of his description and figures resembles *W. subatra* and may refer to this species. We have assigned the Cape Verde and Naples specimens to a different species, *Watersipora souleoroum* **n. sp.** (see below).

Comparisons between specimens from New Zealand (Figs 43–47), California (Fig 48–53) and Britain (some slides at NHMUK; see Ryland *et al.* 2009, fig. 3, as *W. subovoidea*) with the type specimens of *W. cucullata*, *W. subatra* and *W. subtorquata*, indicate that *W. subatra* was previously misidentified as *W. subtorquata* by some authors (e.g. Ryland 1974; Gordon 1989; Gordon & Mawatari 1992; Mackie *et al.* 2006, 2012; Geller *et al.* 2008; Ryland *et al.* 2009; Láruson *et al.* 2012; Cockrell & Sorte 2013; Needles & Wendt 2013; Sorte & White 2013; Davis & Marshall 2014). Since Ryland *et al.* (2009) found the COI haplotype in colonies from Guernsey and Brittany to be identical to the commonest haplotype identified in other areas, and the morphology of the genetically identified specimens to be the same (as *W. subtorquata*; Mackie *et al.* 2006), we believe that *W. subatra* is the commonest putatively invasive species of *Watersipora* in Britain, Australia, New Zealand and California, whereas *W. subtorquata* is the predominant species in subtropical and tropical waters of the Atlantic and Mediterranean. Colonies from California (Figs 48–53) often have a well-demarcated, U-shaped sinus and a smooth suborificial region (without pseudopores), as has been figured in specimens from Brittany (Ryland *et al.* 2009, fig. 3A, D, as *W. subtorquata*). All specimens assigned to *W. subatra* have an orifice with a U-shaped sinus and narrow, bar-shaped condyles, opercula with a broad, biconcave band proximally, frontal shields with pseudopores 18–30 µm in diameter, and two latero-oral intrazooidal septula.

Soule and Soule (1975) indicated that Harmer (1957) included at least two species under *Dakaria subovoidea*, which may be a mixture of *W. subtorquata* and *W. aterrima*. According to the list of specimens published by Harmer (1957), however, his description and remarks included at least four species: *W. subtorquata*, *W. cucullata*, *W. atrofusca* and *W. subatra* (specimens figured from *Siboga* Stns 181 and 184, see Harmer 1957, pl. 49, figs 11–12, 14). *Watersipora subatra* is distinguished from *W. subtorquata* by the shapes of the orifice and condyles, and the presence of latero-oral intrazooidal septula (Figs 47, 52, 53). Latero-oral intrazooidal septula are also found in *W. cucullata* (Figs 8, 29, 34), *W. aterrima* (Fig. 37) and *W. mawatarii* **n. sp.** (Fig. 58; see below), but these species have different shapes of orifice and condyles.

Despite the wide distribution of *W. subatra* in Pacific waters (see Ryland *et al.* 2009; Mackie *et al.* 2012; as *W. subtorquata*), its occurrence in some localities in the northwest Pacific, as well as the occurrence of *W. subtorquata*, are unconfirmed and require morphological and molecular investigation.

Distribution. NE Atlantic (Ireland and British Isles), Indo-West Pacific (Indonesia) and Pacific (New Zealand, Australia and California).

Watersipora mawatarii n. sp.

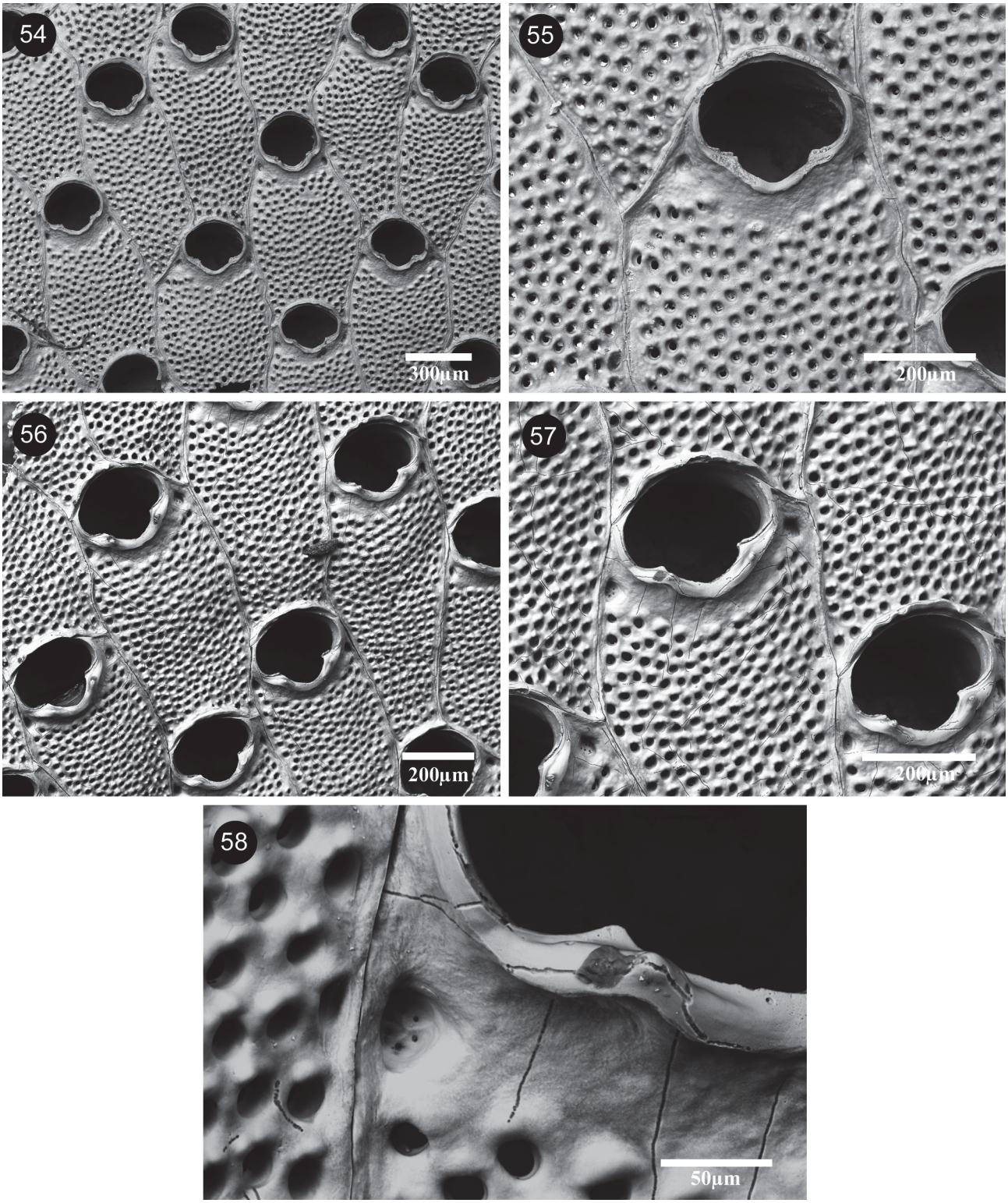
(Figs 54–58; Table 4)

?*Dakaria typica* Okada & Mawatari, 1937: 438, pl. 11, fig. 6; text-fig. 2 [Japan].
?*Dakaria subovoidea*: Kubota & Mawatari, 1985: 203, fig. 4 [Japan].

Material examined. *Holotype:* NHMUK 2012.6.30.8, Oshoro Marine Station, near Otaru, Hokkaido, Japan, intertidal, 16 April 1996, M.J.Weedon coll. *Paratypes:* NHMUK 2012.6.30.9–11, same data as holotype; NHMUK 2012.6.30.12–13, 17, Otaru chiko, Japan, on dead barnacles near shore, 12 December 1996, T. Kato coll. NHMUK

2012.6.30.18, dry, Amakusa Marine Biological Laboratory, Kyushu, Japan, 40–50m, dredged, 22 October 1996, T. Kato coll.

Etymology. Named for Japanese bryozoologist Prof. Shunsuke F. Mawatari.



FIGURES 54–58. *Watersipora mawatarii* **n. sp.**, from Japan. **54–55**, NHMUK 2012.6.30.8, holotype, Hokkaido; **54**, autozooidal arrangement; **55**, distal of an autozooid. **56–58**, NHMUK 2012.6.30.13, paratype, Otaru; **56**, autozooids; **57**, close-up of an orifice and the two latero-oral intrazooidal septula; **58**, close-up of the lateral edge of the orifice, showing a condyle and a latero-oral intrazooidal septulum.

TABLE 4. Measurements (in μm) of *Watersipora souleorum* **n. sp.** and *W. mawatarii* **n. sp**. Holotype specimens are marked with asterisks.

	W. souleorum **n. sp.**		*W. mawatarii* **n. sp.**	
	NHMUK 2014.07.29.1*	NHMUK 1912.12.21.1019	NHMUK 2012.6.30.8*	NHMUK 2012.6.30.13
	Cape Verde (n=10)	Naples (n=7)	Hokkaido (n=10)	Otaru (n=3)
ZL				
Min–Max	807–930	815–869	850–999	818–971
Mean (SD)	872 (39)	848 (29)	909 (53)	-
ZW				
Min–Max	316–493	339–496	408–510	395–433
Mean (SD)	402 (70)	459 (53)	463 (45)	-
ZL x ZW [x10^3]				
Min–Max	282–424	325–431	370–461	354–383
Mean (SD)	350 (55)	391 (57)	420 (27)	-
OL				
Min–Max	228–250	237–247	200–230	187–220
Mean (SD)	239 (8)	240 (6)	211 (10)	-
OW				
Min–Max	226–260	234–251	238–265	239–270
Mean (SD)	244 (10)	242 (8)	252 (8)	-
OA [x10^3]				
Min–Max	40.5–48.4	43.7–48.7	37.9–45.6	35.1–46.6
Mean (SD)	45.7 (2.3)	45.8 (2.5)	41.0 (2.6)	-
ZL / OL				
Min–Max	3.3–3.9	3.3–3.6	3.7–4.7	3.7–4.7
Mean (SD)	3.7 (0.2)	3.5 (0.1)	4.3 (0.3)	-
OL / OW				
Min–Max	0.91–1.05	0.98–1.01	0.77–0.92	0.78–0.82
Mean (SD)	0.98 (0.04)	0.99 (0.02)	0.84 (0.04)	-
ZA/OA				
Min–Max	6.3–9.1	7.2–9.5	8.7–11.4	7,6–9.6
Mean (SD)	7.6 (1.0)	8.5 (1.1)	10.0 (0.9)	-
SinL				
Min–Max	60–70	57–65	40–48	48–59
Mean (SD)	64.9 (3.3)	59.7 (4.6)	43.8 (2.7)	-
SinW				
Min–Max	110–130	133–148	117–137	126–150
Mean (SD)	117 (8)	138 (8)	126 (6)	-
PorD				
Min–Max	23–29	25–32	9–15	10–14
Mean (SD)	27 (2)	29 (3)	12 (2)	-

Description. Colonies encrusting, multiserial, uni- to multilamellar; sometimes erect, foliaceous and bilamellar; colour greyish to black in dead colonies. Zooids elongate-elliptical to rectangular, widest below the orificial area, about twice as long as wide, separated by slightly raised lateral walls; zooids arranged in quincuncial

series. Frontal shield thick, granulated, slightly convex, with numerous small (10–15 µm diameter), round pseudopores covering entire surface except for suborificial region; two latero-oral intrazooidal septula, near lateral zooidal margin, proximolateral to orifice, each with 3–6 small pores. Frontal shield obscured by opaque, dark cuticle. Orifice large, transversely elliptical, usually conspicuoualy wider than long, with well-defined proximal broad sinus; orificial rim often thick and raised, but some zooids with thin, slightly raised rim; narrow bar-shaped condyles occupying entire proximal edge of orifice, sometimes projecting medially as triangular projection. Operculum black, mushroom-shaped; lucidae present. Avicularia absent. Ovicells absent.

Remarks. The overall zooidal morphology of specimens here figured and described resemble some Japanese specimens—viz. *Dakaria typica* Okada & Mawatari, 1937 (=*Watersipora typica*) from Miyagi, and *Dakaria subovoidea* from Hokkaido (Kubota & Mawatari 1985)—but they are distinguished by having fewer pseudopores in the frontal shield than *Watersipora mawatarii* **n. sp**. The thinner circular area in the distal half of the operculum, characteristic of *W. typica*, is also absent in *W. mawatarii* **n. sp.**

Watersipora mawatarii **n. sp.** resembles *W. edmondsoni sensu* Soule & Soule (1975) from Hawaii (the holotype of *Watersipora edmondsoni* belongs to *Watersipora subtorquata*, see above), characterized by its long zooids (about 0.80–1.20 mm long and 0.40–0.60 mm wide) and dark-brown mushroom-shaped opercular pigmentation, with a curved lower portion that fits into the sinus area. Soule & Soule (1975) also reported frontal shields with very small pseudopores like those of *W. mawatarii* **n. sp**. The shape of the zooids (widest below the orificial area) and the absence of pseudopores in the suborificial region were also described for some specimens from different Indo-West Pacific sites—Bali (Winston & Heimberg 1986; as *Watersipora edmondsoni*), Vanuatu (Tilbrook *et al.* 2001; as *Watersipora subovoidea* sensu Harmer) and Hawaii (Dick *et al.* 2006; as *Watersipora subovoidea* sensu Harmer)—which we believe belong to an undescribed species; these specimens differ from *W. mawatarii* **n. sp.** in having a narrower sinus and smaller orifice: 0.189–230 mm long and 0.238–0.270 mm wide in *W. mawatarii* **n. sp.** versus 0.162–0.216 mm long and 0.198–0.234 mm wide in species from Bali (Winston & Heimberg 1986), and 0.15–0.18 mm long and 0.20–0.25 mm wide in specimens from Hawaii (Dick *et al.* 2006).

Watersipora mawatarii **n. sp.** resembles *W. subatra* in having a U-shaped sinus, bar-shaped condyles, and two latero-oral intrazooidal septula. The two species differ, however, in the size of the pseudopores (smaller in *W. mawatarii* **n. sp.**) and condyles (more conspicuous in *W. mawatarii* **n. sp.**) and in the absence of pseudopores in the suborificial region (characteristic of *W. mawatarii* **n. sp.**).

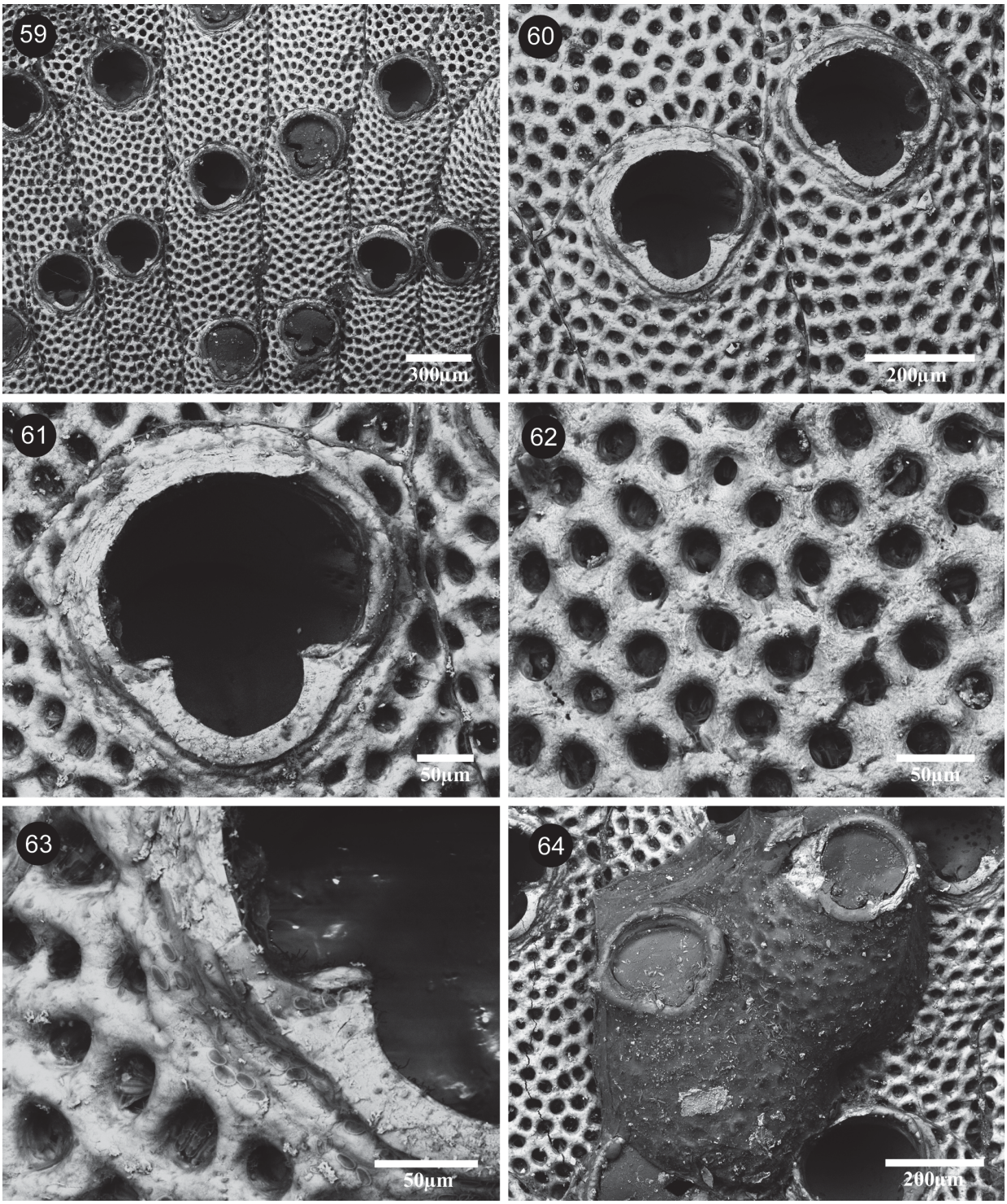
Distribution. Japan.

***Watersipora souleorum* n. sp.**
(Figs 17, 59–64, 68, 71; Table 4)

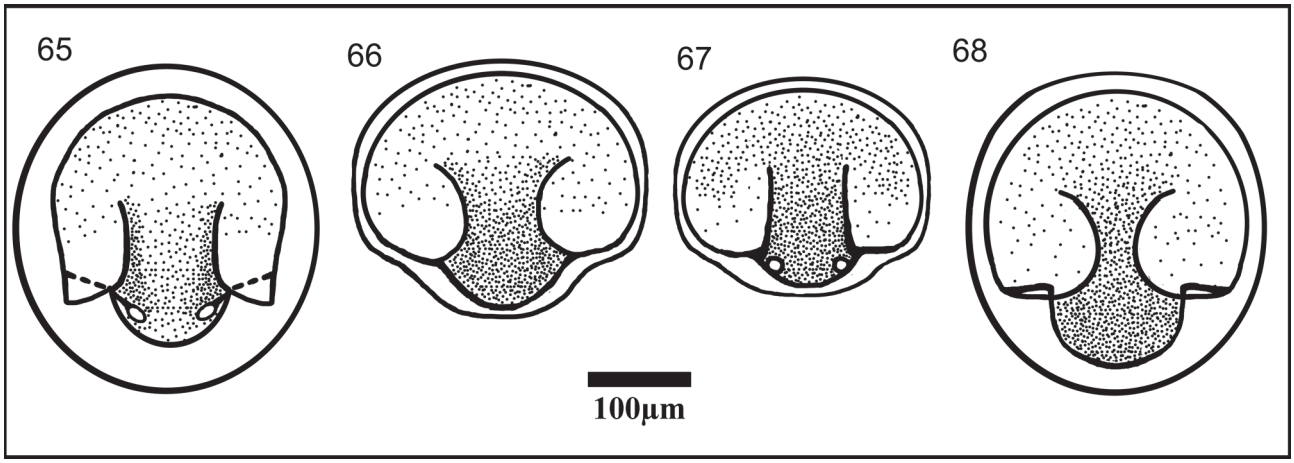
?*Cellepora subovoidea* d'Orbigny, 1852: 402 [Red Sea; *nomen dubium*].
Lepralia cucullata: Thornely 1905: 120 [Sri Lanka]. Non *Lepralia cucullata* Busk, 1854: 81, pl. 96, figs 4–5 [Aegean Sea].
Schizoporella cucullata var. *labiosa* Calvet *in* Jullien & Calvet, 1903: 141, pl. 16, fig. 7a–c [Azores].
Lepralia? cucullata: Waters 1909: 150 (part), pl. 15, figs 2–5 [Naples and ?Cape Verde].
Watersipora cucullata: Hastings 1930: 729 (part), pl. 15, fig. 104 [Cape Verde].
Watersipora cucullata var. *watersi* Mawatari, 1952: 12 (part) [Cape Verde].
"*Watersipora subovoidea*" fide Harmer: Soule & Soule 1975: 308 (part), pl. 3, fig. 5 [Sri Lanka].

Material examined. *Holotype:* NHMUK 2014.07.29.1, dry slide, Porto Grande, St. Vicent, Cape Verde Islands, on coral, 10 fm [18.3 m], Vallentin coll. *Paratype:* NHMUK 1935.3.6.367, same data as for holotype. *Other material:* MOM 420379, *Schizoporella cucullata* var. *labiosa*, L. Calvet 1903, *l'Hirondelle*, Stn 236, Azores, 20 August 1888. NHMUK 1872.2.3.147, dry, *Watersipora cucullata* var. *atrofusca*, west coast of Spain, S. Kent coll., on shells. NHMUK 1873.7.21.7, dry and dry slide, *Watersipora cucullata*, Ceylon [Sri Lanka], E.W.H. Holdsworth. NHMUK 1882.10.18.3.4–41pt., *Watersipora* sp., Seychelles Island, on coral, 12 fm [22 m], Voyage of H.M.S. *Alert*, pres. Lords of the Admiralty. NHMUK 1882.10.18.3.100–104., *Schizoporella* sp., Seychelles Island, coral, 12 fm [22 m], Voyage of H.M.S. *Alert*, pres. Lords of the Admiralty. NHMUK 1899.5.1.976 [3 slides], *Watersipora atrofusca*, Trincomalee, Sri Lanka, T. Hincks coll. NHMUK 1899.7.1.1396, dry slide, *Lepralia cucullata*, Persian Gulf, on pearl oyster, G. Busk coll. NHMUK 1899.7.1.1893, dry slide [part in balam slide], *Lepralia cucullata*, Cape Verde Island, Mrs Gatty, G. Busk coll. NHMUK 1890.1.31.13, dry, *Watersipora subovoidea*, Madras [Chennai], India. NHMUK 1912.12.21.1019, *Watersipora cucullata*, Naples, Italy, A.M. Norman. NHMUK

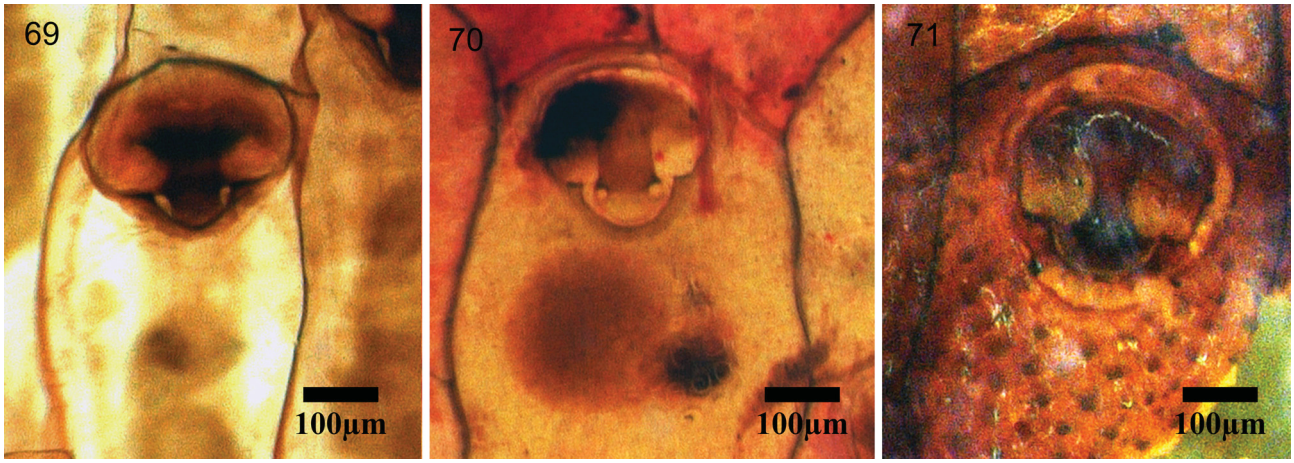
1921.5.24.18C, dry, *Watersipora subovoidea*, Cape Verde, Voyage of the *Herald*, Lords of the Admiralty. NHMUK 1936.12.30.35, *Lepralia cucullata*, Ceylon [Sri Lanka], L.R. Thornely. NHMUK 1936.12.30.116, *Lepralia cucullata*, India, No. 116, 1906, Yellow 2247, L.R. Thornely. NHMUK 1969.1.16.3, dry, *Watersipora subvoidea*, Point de Fomone, M'Bour, Senegal, 10 m, M-Marchad II. NHMUK 1973.1.10.2, dry slide, *Watersipora subvoidea*, No. 32, Point de Fomone, M'Bour, Senegal, 10 m, 13 April 1954, M-Marchad II. NHMUK 1981.4.1.3pt, dry and balsam slide, *Watersipora subovoidea*, Ceylon [Sri Lanka], L.R. Thornely, Rep. Pearl Oyster Fish., 26, p120. NHMUK 2012.6.30.1 [part of NHMUK 1912.12.21.1019], *Watersipora cucullata*, Naples, Italy, A.M. Norman.



FIGURES 59–64. *Watersipora souleorum* **n. sp.**, NHMUK 2014.07.29.1, holotype, Cape Verde. **59**, autozooidal arrangement; **60**, autozooids, with well-developed orificial rims; **61**, close-up of an orifice; **62**, close-up of the frontal wall; **63**, close-up of the lateral edge of the orifice, showing a condyle; **64**, colony with two zooids settled on the older colony.



FIGURES 65–68. Schematic drawings of opercula of *Watersipora*. **65**, *Watersipora cucullata* (Busk, 1852), Aegean Sea (redrawn from Hastings 1930, pl. 15, fig. 98); **66**, *Watersipora subatra* (Ortmann, 1890), New Zealand; **67**, *W. subtorquata* (d'Orbigny, 1982), Brazil; **68**, *Watersipora souleorum* **n. sp.**, Cape Verde (redrawn from Hastings 1930, pl. 15, fig. 104).



FIGURES 69–71. Opercula of some species of *Watersipora*. **69**, *Watersipora subatra* (Ortmann, 1890), NHMUK 2007.12.14.18, Guersey; **70**, *Watersipora subtorquata* (d'Orbigny, 1982), NHMUK 1926.9.6.165A, Suez Canal; **71**, *Watersipora souleorum* **n. sp.**, NHMUK 1899.7.1.1393, Cape Verde.

Description. Colonies encrusting, multiserial, uni- to multilamellar, sometimes erect, foliaceous and bilamellar; colour of dead colonies black. Zooids subrectangular, about twice as long as wide, separated by slightly raised lateral walls. Frontal shield slightly convex, with numerous (25–32 µm diameter), round pseudopores; latero-oral intrazooidal septula absent. Frontal shield obscured by dark cuticle. Orifice large, oval, with well-defined, broad, deeply U-shaped proximal sinus; slightly raised orificial rim sometimes present; bar-shaped condyles. Operculum with a narrow, biconcave dark central band, with lucidae. Avicularia absent. Ovicells absent.

Etymology. Named for John D. Soule (1920–2001) and Dorothy F. Soule (1923–2005), in recognition of their contributions to bryozoan taxonomy.

Remarks. The name *labiosa* was first introduced by Hincks (1886)—as *Schizoporella atrofusca* f. *labiosa*—but was synonymised under *W. subovoidea* by Ryland *et al.* (2009) (=*W. subtorquata*). Calvet (*in* Jullien & Calvet 1903) also introduced the name *labiosa* as *Schizoporella cucullata* var. *labiosa*—this name has never been considered valid since the original description and it was synonymised with *W. cucullata* by Hastings (1927)—for material from the Azores. Calvet's specimens (MOM 420379) are distinct from *W. subtorquata*, however, in having a deep sinus and an operculum with a biconcave dark central band. Hastings (1930, pl. 15, fig. 104, as *W. cucullata*) included an excellent drawing based on specimens from Cape Verde that corresponds with Calvet's variety. Waters (1909) used the name *L. cucullata* for species from Naples, Cape Verde and Suez, but the descriptions encompass at least two species. His specimens from Naples (Waters 1909, figs 2–5) have a wider sinus

and distinctive operculum when compared to those from Suez (=*W. subtorquata*); specimens from Naples resemble those reported by Calvet (*in* Jullien & Calvet 1903) and Hastings (1930) from the Azores and Cape Verde, respectively. Mawatari (1952) erected var. *watersi* for material with this distinctive type of operculum, but the name is preoccupied by the fossil *Microporella watersi* de Stefani, 1884, based on *Lepralia cucullata* of Manzoni (1875) which, to judge by Manzoni's figure (1875, pl. 4, fig. 47), is likely a species of *Watersipora* (see Waters 1909). We introduce the name *Watersipora souleorum* **n. sp.** for these specimens.

Watersipora souleorum **n. sp.** resembles *W. subtorquata* in lacking latero-oral intrazooidal septula. The new species differs, however, in having a larger orifice than *W. subtorquata*, a deep U-shaped sinus, bar-shaped condyles, and an operculum with a narrow dark central band.

Distribution. Atlantic (Azores, Cape Verde and Senegal), Mediterranean (Naples) and Indian Ocean (Sri Lanka and India).

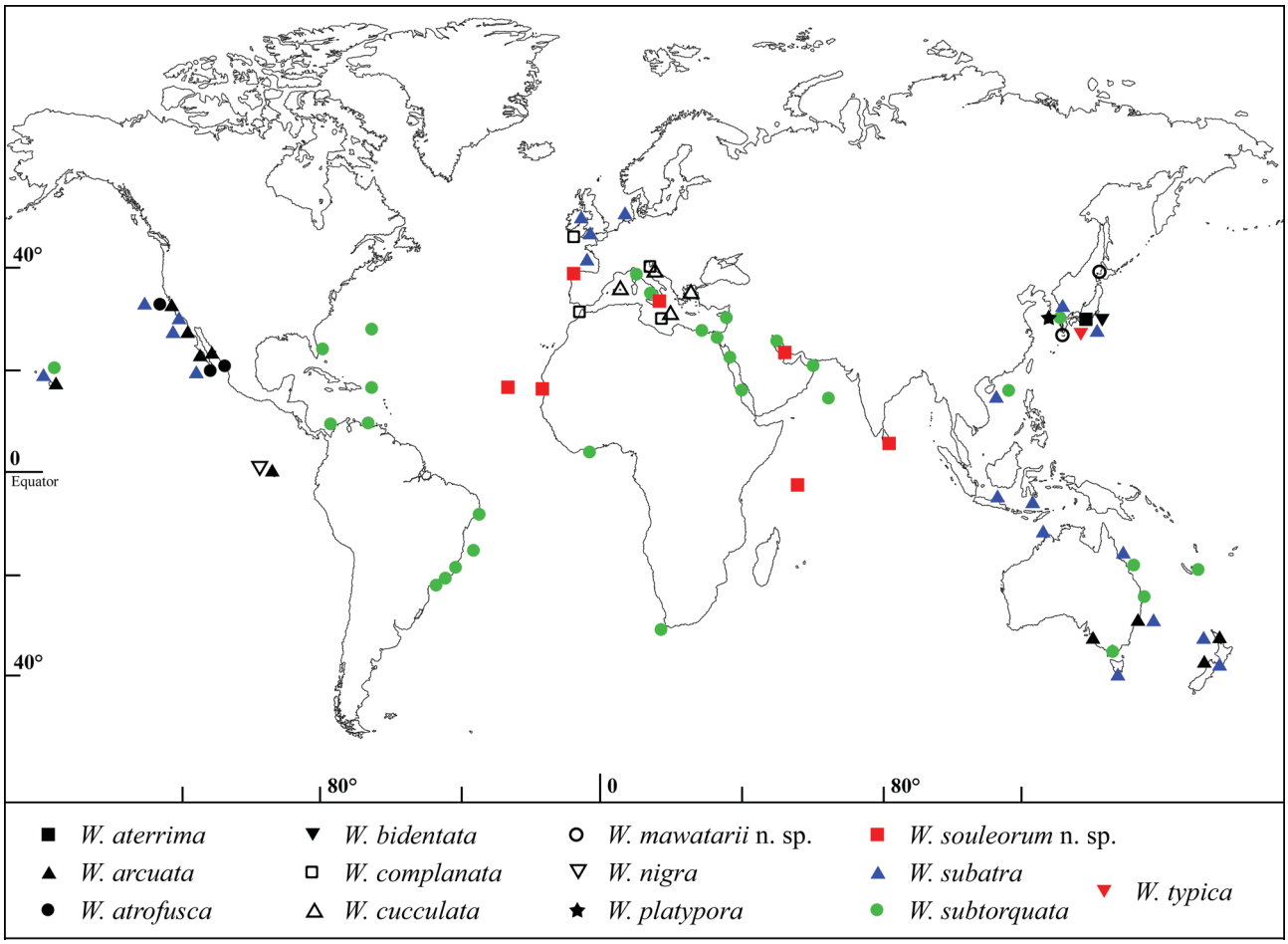


FIGURE 72. Distribution map (not exhaustive) of species of *Watersipora*.

Discussion

According to Bock (2010), nine species have been assigned to *Watersipora* Neviani, 1895: *Watersipora arcuata* Banta, 1969a, *Watersipora aterrima* (Ortmann, 1890), *Watersipora complanata* (Norman, 1864), *Watersipora edmondsoni* Soule & Soule, 1968, *Watersipora grandis* (Canu & Bassler, 1923), *Watersipora platypora* Seo, 1999, *W. subovoidea*, *W. subtorquata* and *Watersipora watersi* Mawatari, 1952. Some other nominal species have been synonymised under these names (Soule & Soule 1975; Abdel-Salam & Ramadan 2008; Ryland *et al.* 2009). Apart from *Watersipora grandis* (Canu & Bassler, 1923), which is a fossil from the Neogene of the southeastern USA, all of the species listed above are extant. Examination of type specimens has revealed that the holotype of *W. edmondsoni* is synonymous with *W. subtorquata*, and that two species previously synonymised under *W. subtorquata* and *W. subovoidea* belong to distinct species: *Watersipora atrofusca* (Busk, 1856) and *Watersipora*

subatra (Ortmann, 1890). Thus, *Watersipora* contains at least 13 valid Recent species: *W. aterrima*, *W. arcuata*, *W. atrofusca*, *W. bidentata* (Ortmann, 1890), *W. complanata*, *W. cucullata*, *W. mawatarii* **n. sp.**, *W. nigra* **n. comb.**, *W. platypora*, *W. souleorum* **n. sp.** (=*Watersipora watersi* Mawatari, 1952, non *Microporella watersi* de Stefani, 1884), *W. subatra*, *W. subtorquata* and *W. typica*. The taxonomic status of *Microporella watersi* de Stefani, 1884, a fossil species supposedly of *Watersipora* (see Waters 1909), requires reinvestigation.

The lack in *Watersipora* of diagnostic structures such as avicularia and ooecia that are often used in cheilostome taxonomy has led to the use of morphological and morphometric characters of the frontal shield, orifice and operculum to identify species in the genus (Soule & Soule 1975; Seo 1999; Ryland *et al.* 2009). Six species—*W. cucullata*, *W. arcuata*, *W. atrofusca*, *W. bidentata*, *W. nigra* and *W. platypora*—have an orifice with the sinus almost square or rectangular in shape (see Okada & Mawatari 1937; Banta 1969a; Seo 1999), while *W. complanata* is distinct in having an orifice with a straight proximal edge lacking a sinus (Hayward & McKinney 2002). The other six species—*W. aterrima*, *W. mawatarii* **n. sp.**, *W. souleorum* **n. sp.**, *W. subatra*, *W. subtorquata* and *W. typica*—have an orifice with a concave to almost straight proximal edge (V- or U-shaped sinus). The main distinguishing characteristics of these species are the morphometry of the zooids and orifices, shape of the orifice and operculum (used for some specimens, e.g. Figs 65–71), and morphology of the frontal shield, including pseudopores and the presence or absence of intrazooidal septula, which are difficult to observe except by using SEM. Early astogenetic characters, including the morphology of the ancestrula, deserve future investigation to evaluate their potential in discriminating species and subclades of *Watersipora*.

Ryland *et al.* (2009) suggested the need for more genetic studies on species of *Watersipora* because of cryptic speciation in *W. subatra* (as *W. subtorquata*) and a Californian lineage 15% divergent in COI nucleotide sequence from another widespread clade. Mackie *et al*. (2012) also showed two genetically shallow groups in *W. subatra* (as *W. subtorquata*): clade A in Europe and Australasia, and clade B in California. Since two species of the *Watersipora subatra* complex were considered not distinguishable using the zooid-area to orifice-area ratio (Ryland *et al.* 2009; as *W. subtorquata*), we suggest additional morphological studies based on the new descriptions presented here.

Resolution of the identity of Brazilian specimens, previously attributed to *Watersipora subovoidea*, as *W. subtorquata*, allows us to falsify the assertion of Mackie *et al.* (2012) that *W. subtorquata* has been displaced from its native locale of Brazil. The actual distribution of *W. subtorquata* and all congenerics are presented in Fig. 72. Populations of *Watersipora subtorquata* from Florida, Brazil and Australian are about 1% divergent in COI sequence, suggesting recent, widespread introductions of the species in tropical waters (Mackie *et al.* 2012, as *W. subovoidea*). Genetic studies should be conducted, however, to investigate the degree of genetic divergence along the Brazilian coast and to understand dispersal patterns in this important fouling species.

The continued confusion over the correct names for the two species commonly identified as *Watersipora subtorquata* and *Watersipora subovoidea* is particularly relevant in view of their importance as invasive fouling species. Their true identities are clarified by the new descriptions presented in this paper.

Key to Recent species of *Watersipora*

1	Orifice bell-shaped, without conspicuous sinus demarcated by condyles	*complanata*
	Orifice almost circular to skull-shaped, sinus demarcated by condyles	2
2	Sinus V- or U-shaped.	3
	Sinus approximately square or rectangular	8
3	Operculum with three small, thin circular areas	*typica*
	Operculum with distinct central band	4
4	Latero-oral intrazooidal septula absent	5
	Latero-oral intrazooidal septula present	6
5	Operculum with narrow, biconcave dark central band; bar-shaped condyles; orifice as long as wide, 0.225–0.250 mm long and 0.225–0.260 mm wide	*souleorum* **n. sp.**
	Operculum with a parallel-sided dark central band; tooth-like condyles, projecting distomedially; orifice wider than long, 0.160–0.200 mm long and 0.190–0.240 mm wide	*subtorquata*
6	Pseudopores smaller than 0.016 mm in diameter	*mawatarii* **n. sp.**
	Pseudopores larger than 0.016 mm in diameter	7
7	Condyles inconspicuous; sinus 0.085–0.101 mm long and 0.038–0.048 mm wide	*aterrima*
	Condyles bar-shaped; sinus 0.120–0.178 mm long and 0.048–0.074 mm wide	*subatra*

8	Poster with straight proximal border	9
	Poster with convex proximal border	11
9	Condyles bar-shaped; orifice wider than 0.270 mm	*bidentata*
	Condyles triangular; orifice narrower than 0.250 mm	10
10	Orifice up to 0.175 mm long and 0.185 mm wide; latero-oral intrazooidal septula absent	*atrofusca*
	Orifice more than 0.200 mm long and 0.220 mm wide; latero-oral intrazooidal septula present	*cucullata*
11	Sinus demarcated by triangular projections of the peristome and condyles	*nigra*
	Sinus only demarcated by condyles	12
12	Frontal wall with about 100 pseudopores; orifice more than 0.320 mm wide	*platypora*
	Frontal wall with about 150 pseudopores; orifice up to 0.225 mm wide	*arcuata*

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