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Redescription and systematic status of the Antarctic genus Abietinella Levinsen, 1913 (Lafoeidae, Hydrozoa, Cnidaria)

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Redescription and systematic status of the Antarctic genus *Abietinella* Levinsen, 1913 (Lafoeidae, Hydrozoa, Cnidaria)

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Abstract
The Antarctic–Patagonian genus *Abietinella*, comprising two known species, *Abietinella operculata* (Jäderholm, 1903) and *Abietinella grandis* (Vanhöffen, 1910), is reviewed. The holotype of *Abietinella operculata* is fully redescribed, including morphometry and cnidome, unknown up to now. Its distinctive characters are the growth habit, hydrothecal shape and, most important, the presence of a dish-shaped operculum attached to the adcauline side of the hydrothecal aperture. We corroborate its conspecificity with *A. grandis* and, therefore, the monotypic condition of *Abietinella*.

Keywords: Abietinella, *Antarctic, Cnidaria, cnidome, Hydrozoa, morphometry*

Introduction

The genus *Abietinella* was proposed by Levinsen (1913, p 294) to accommodate the only two known species, originally described as *Zygophylax* but bearing an operculum, namely *Zygophylax operculata* Jäderholm, 1903 and *Zygophylax grandis* Vanhöffen, 1910. The presence of an operculum and a caecum at the abcauline side of the hydranth led Levinsen to consider the genus in the family Sertulariidae, although subsequent authors had another opinion (e.g. Blanco 1968, 1976; Vervoort 1972; Stepan'yants 1979; Rees and Vervoort 1987; El Beshbeeshy 1991; Peña and García-Carrascosa 1993; Blanco et al. 1994). Recent authors, concerned with the importance of the mixed features of the group, considered the genus as having ''intermediate characteristics between the families Lafoeidae and Sertulariidae'' (Peña and García-Carrascosa 1993, p 1009).

Besides the uncertainties of the taxonomic position of the genus, the validity of these two species is also unsettled. Although both are morphologically similar, their general dimensions are different, some authors considering them conspecific (Stepan'yants 1979;

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El Beshbeeshy 1991, p 92), and others not (Vervoort 1972, p 82; Rees and Vervoort 1987, p 46; Peña and García-Carrascosa 1993, p 1010, the latter regarded *A. grandis* as doubtful).

We redescribe the holotypes of *A. operculata* and *A. grandis*, carrying out comparisons with non-type material, which allowed us to assess the extent of the morphological variation exhibited in the genus.

Material and methods

The material studied belongs to the collections of the Museum für Naturkunde (ZMB), Berlin; Natural History Museum (BMNH), London, UK; Swedish Museum of Natural History (SMNH), Stockholm, Sweden; United States National Museum of Natural History—Smithsonian Institution (USNM), Washington, DC, USA; and to the private collection of A. L. Peña Cantero (ALPC, Valencia, Spain). The holotypes of *Zygophylax operculata* and *Zygophylax grandis* were examined, measured and photographed under compound microscope and stereoscope. Measurements of nematocysts were made on non-discharged capsules; cnidome terminology follows Weill (1934) and Mariscal (1974). Other study methods for Lafoeidae are from Peña and García-Carrascosa (1993) and Peña Cantero et al. (1998).

Genus *Abietinella* Levinsen, 1913

Abietinella Levinsen 1913, p 294, Plate 4 Figures 21, 22a; Totton 1930, p 166; Vervoort 1972, p 82; Stepan'yants 1979, p 58; Rees and Vervoort 1987, p 45–46.

Type species: *Zygophylax operculata* Jäderholm, 1903, by subsequent designation by Totton (1930, p 166).

Diagnosis

Colonies erect, polysiphonic, arising from a creeping hydrorhiza. Hydrothecae campanulate and sinuous adcaudally, pedicellate; pedicel resting on cauline apophysis, each demarcated from pedicel basally by an annular perisarcal thickening; dish-shaped operculum attached to adcauline side of hydrothecal aperture. One nematotheca on each side of hydrothecal apophysis; nematothecae scattered on polysiphonic tubes of stem.

Gonophores fixed sporosacs. Gonothecae arranged in coppinia, placed on stem and main branches.

Remarks

The type species of the genus was subsequently selected by Totton (1930, p 166) as *Z. operculata* (and not by monotypy as considered by Rees and Vervoort 1987, p 45).

Although Rees and Vervoort (1987, p 46) assert that in the genus *Abietinella* the hydrocladia and hydrothecae are "rigorously in one plane", in *A. operculata* some hydrocladia are slightly rotated in relation to the plane of stem. This slight rotation should be considered, however, a plastic condition of the species, characteristic of deep waters.

Abietinella operculata (Jäderholm, 1903)

(Figure 1 A–H; Table I)

Zygophylax operculata Jäderholm 1903, p 262, 276–278, Plate 12 Figures 7, 8; 1905, p 4, 22, 38; Billard 1905, p 98; 1906, p 181; Clarke 1907, p 16, 17; Vanhöffen 1910, p 315, 317; Totton 1930, p 166.

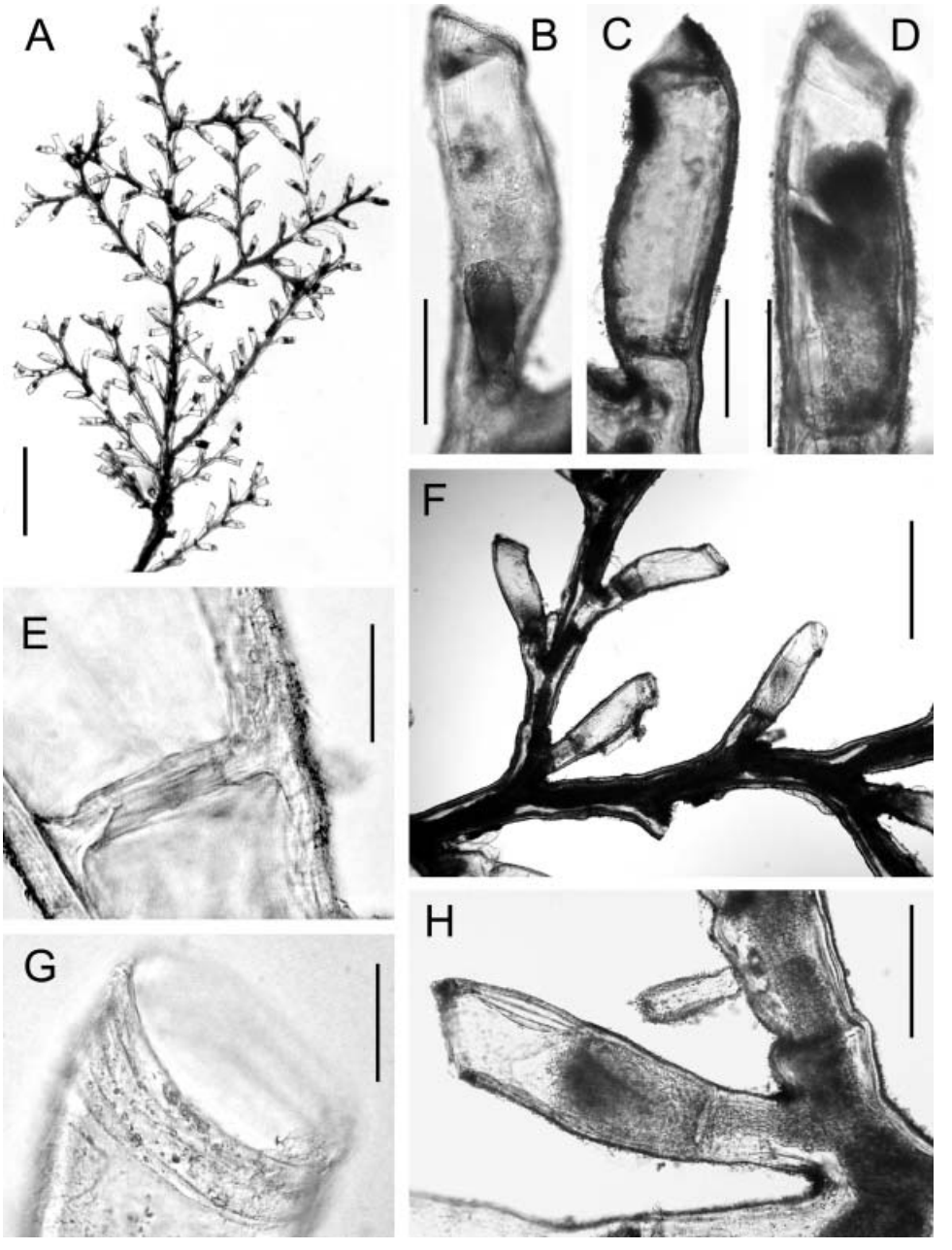

Figure 1. *Abietinella operculata* (Jäderholm, 1903), holotype SMNH 5708. (A) Apical portion of colony; (B) hydrotheca with dish-shaped operculum and basal lateral nematothecae; (C) lateral view of hydrotheca and apophysis; (D) hydrotheca and hydranth with abcauline triangular caecum; (E) hydrothecal diaphragm; (F) origin of lateral branch; (G) hydrothecal rim renovation; (H) basal hydrotheca without nematothecae. Scale bars: 2 mm (A); 200 μm (B–D, H); 50 μm (E, G); 400 μm (F).

Table I. Morphometric data of the type specimen of *Abietinella operculata* (Jäderholm, 1903) (measurements in mm).

Characters	Mean ± SD (range) (*n*)
Diameter of stem (base)	0.93
Diameter of stem (apex)	0.33
Diameter of primary branches	0.16 ± 0.02 (0.15–0.20) (12)
Distance between successive branches (same side)	2.03 ± 0.09 (1.92–2.25) (14)
Length of abcauline side of pedicel	0.18 ± 0.07 (0.11–0.32) (10)
Length of adcauline side of pedicel	0.10 ± 0.05 (0.05–0.22) (10)
Length of nematotheca	0.22 ± 0.01 (0.20–0.23) (8)
Diameter of nematothecal aperture	0.05 ± 0.01 (0.04–0.06) (8)
Length of hydrotheca	0.48 ± 0.05 (0.36–0.55) (10)
Diameter at diaphragm	0.14 ± 0.02 (0.12–0.19) (10)
Maximum diameter of hydrotheca	0.19 ± 0.01 (0.18–0.22) (10)
Diameter at aperture	0.16 ± 0.01 (0.15–0.17) (10)
Number of tentacles	06–10

Zygophylax grandis Vanhöffen 1910, p 273, 315–317, 327, 339, Figure 33a–e; Totton 1930, p 166; Stepan'yants 1979, p 59; Rees and Vervoort 1987, p 71.

Abietinella grandis: Levinsen 1913, p 295; Vervoort 1972, p 82; Rees and Vervoort 1987, p 46, 71.

Abietinella operculata: Levinsen 1913, p 294, Plate 4 Figures 21, 22a; Kudelin 1914, p 361. Figure 127; Naumov and Stepan'yants 1962, p 78–80, Figure 4; Blanco 1968, p 198–200, Plate 1 Figures 8–10; 1976, p 33–35, Plate 2 Figures 4–8, Plate 3 Figures 1–3; Vervoort 1972, p 79–82, Figure 24a, b; Stepan'yants 1979, p 59, Plate 10 Figure 2, Plate 25 Figure 4; Rees and Vervoort 1987, p 46, 69; El Beshbeeshy 1991, p 90–93, Figure 21; Peña (Cantero) and García-Carrascosa 1993, p 1003–1011, Figures 1–3; Peña Cantero and García Carrascosa 1994, p 119, Figure 2a–c; 1995, p 16–19, Figure 3A–E; Blanco et al. 1994, p 1–7, Figures 1–3.

Cryptolaria operculata: Salvini-Plawen 1972, p 391.

Material examined

Antarctic region: (ALPC) Sta. ANT 133, South Georgia, 54°59.60′S, 35°34.80′W, 10 December 1986, 229–240 m, leg. "Antártida 8611" expedition (two small fragments 10 mm high, no coppinia); (ALPC) Sta. ANT 408, Elephant Island, 61°30.10′S, 55°16.70′W, 10 January 1987, 438–471 m, leg. "Antártida 8611" expedition (two polysiphonic stems up to 50 mm high, one with coppinia); (ALPC) Sta. ANT 470, King George Island, 61°50.90′S, 58°36.00′W, 24 January 1987, 150–154 m, leg. "Antártida 8611" expedition (small monosiphonic stems, no coppinia); (ALPC) Sta. ANT 491, Robert Island, 62°14.80′S, 59°47.80′W, 27 January 1987, 63 m, leg. "Antártida 8611" expedition (detached polysiphonic stem up to 280 mm high, with coppinia); (ALPC) Sta. ANT 550, Robert Island, 61°47.60′S, 58°46.30′W, 4 February 1987, 270–272 m, leg. "Antártida 8611" expedition (two detached polysiphonic stems up to 60 mm high, one with coppinia); (ALPC) Sta. ANT 556, King George Island, 61°51.20′S, 57°39.00′W, 4 February 1987, 150–202 m, leg. "Antártida 8611" expedition (single colony composed of four hydrothecae, no coppinia); (ALPC) Sta. N.A. 173, Elephant Island, 60°53′S, 55°46′W, 12 January 1987,

semi-pelagic, leg. "Antártida 8611" expedition (five detached polysiphonic stems up to 140 mm high, no coppinia); (USNM) Sta. 32/2128, Cape Adare, Victoria Land, 71°12′S, 171°24′E, 13 February 1968, 1610 m, RV *Eltanin* (several stems up to 70 mm high, no coppinia); (USNM) Sta. 575/052, Islas Orcadas, 57°39.4′S, 26°26.7′W (Saunders Island, South Sandwich Islands, Scotia Sea), 26 May 1975, 415–612 m; (ZMB Cni 958* holotype of *Zygophylax grandis* Vanhöffen, 1910) "Deutsche Südpolar-Expedition 1901–1903" Gauss Station, 65°21′S, 86°06′E, 8 February 1903, 385 m, leg. Deutsche Südsee Expedition. Sub-Antarctic region: (SMNH type-5708 holotype of *Zygophylax operculata* Jäderholm, 1903; part of holotype as BMNH 1960.8.29.41) "Nordenskjölds Expedition till Eldslandet och Patagonien 1895–96" Sta. 1026, Magellan Sound, Cape Valentin, 274 m, on shell debris, 12 March.1896, leg. Nordenskjölds Expedition till Eldslandet och Patagonien; (USNM) Sta. 715/875, Staten Island, Tierra del Fuego, 54°55′–54°54′S, 64°00–63°53′W, 27 October 1971, 771–903 m, RV *Hero* (seven stem fragments up to 50 mm long, no coppinia).

Type specimen

Fragments of holotype: *Zygophylax operculata* Jäderholm, 1903; in two parts, SMNH 5708 (stem ca 45 mm high, fragmented into four pieces, plus a few detached secondary branches), and BMNH 1960.8.29.41 (four fragments, namely a top part of the colony 9 mm long, a stem fragment with three hydrocladia 6 mm high, and two branched hydrocladia 8 and 9 mm long; the condition of these fragments is fair; Rees and Vervoort 1987, 46; personal observation).

Type locality

"Nordenskjölds Expedition till Eldslandet och Patagonien 1895–96" Sta. 1026, Magellan Sound, Cape Valentyn, 274 m, on shell debris.

Description of holotype

Stem erect, ca 45 mm high (SNHM: basal fragment 9 mm, medium 20 mm, medium-apical 9 mm, apical 7 mm; BMNH: basal fragment of stem 6 mm long with three hydrocladia, distal 9 mm long, and two branched hydrocladia 8 and 9 mm long), pinnate, polysiphonic, composed of main tube, divided into internodes, and a few secondary tubes involving main tube up to its distal part; branches arising from main stem tube; basal polysiphonic part of stem ca 0.93 mm, distal part 0.33 mm in diameter. No hydrorhiza present. Stem with branches up to third order; pedicels arising from main cauline tube and branches of first, second and third orders. First-order branches (ca 30) up to 30 mm long, 0.15–0.20 mm (0.16 ± 0.02, $n=12$) in diameter, monosiphonic, occasionally the largest polysiphonic, planar, alternate; branches of same side arising 1.92–2.25 mm (2.03 ± 0.09, $n=14$) apart from each other. Secondary and third-order branches, and hydrothecae, in the same plane as primary branches.

Main cauline tube divided into internodes bearing apophyses (visible only at distal part of stem); cauline apophyses generally bearing alternately arranged branches and hydrothecae, although median-distal region sometimes with series of up to five hydrothecae in a row; distal stem bearing only hydrothecae. Stem apparently without nematothecae. Accessory tubes of polysiphonic part not divided into internodes

and without apophyses, but with irregularly distributed nematothecae. Lateral branches arising at angles of 45–60° in relation to long axis of stem, with an axillary pedicellated hydrotheca without nematothecae at origin. Apophysis separated from branch by a well-marked septum. Branches not divided into internodes, with apophyses bearing lower-order branches or pedicels. Pedicels short, continuous to apophyses, 0.11–0.32 mm (0.18 ± 0.07, $n=10$) long at abcauline side, 0.05–0.22 mm (0.10 ± 0.05, $n=10$) long at adcauline side, ending at diaphragm of hydrothecae. One pair of nematothecae at adcauline side of apophyses, one on each side of hydrotheca, rod-shaped with circular distal aperture, 0.20–0.23 mm (0.22 ± 0.01, $n=8$) long, 0.04–0.06 mm (0.05 ± 0.01, $n=8$) in diameter at aperture.

Hydrotheca tubular, adcauline wall sinuous, convex basally and concave distally; abcauline wall straight, but occasionally curved as well. Hydrothecae 0.36–0.55 mm (0.48 ± 0.05, $n=10$) long (from diaphragm to margin at the abcauline side), with fine transversal striation on outer surface. Base of hydrotheca 0.12–0.19 mm (0.14 ± 0.02, $n=10$) in diameter at diaphragm level; maximal diameter of 0.18–0.22 mm (0.19 ± 0.01, $n=10$); diameter at aperture 0.15–0.17 mm (0.16 ± 0.01, $n=10$). Hydrothecal wall thickened basally. Diaphragm thick, circular, generally transverse though few oblique in relation to hydrothecal long axis. Hydrothecal aperture circular, oblique in relation to hydrothecal long axis but almost perpendicular to branch long axis, rim even and slightly flared, eventually with up to five renovations. Hydrotheca closed by thick disc-shaped operculum, attached to adcauline wall and projecting into the hydrotheca at 30–45°. Operculum frequently lost. Hydranths tubular, basal region constricted by diaphragm, median region often with well-developed abcauline triangular caecum, apical region with one whorl of ca 6–10 tentacles, hypostome conical.

One type of nematocyst observed: heterotrichous ?microbasic mastigophores (not seen discharged), $15–18 \times 2–3\ \mu$m ($16.60 \pm 0.97 \times 2.6 \pm 0.46$, $n=10$), elongated oval, common. Nematocysts on tentacles and nematophores neither identified nor measured.

Gonothecae not seen.

Additional data

Peña and García-Carrascosa (1993, p 1005) inferred the ontogeny of the fasciculation of *A. operculata* as: "Main stem and lower-order branches are polysiphonic. However, *A. operculata* begins to grow by forming an erect, monosiphonic stem that emerges from a stolonal hydrorhiza, and carries hydrothecae set in the same plane. As the colonies develop, the stem is covered by secondary tubes that finally conceal the whole stem and its hydrothecae, in the basal area of the colony. The covered area decreases to the distal portion until it disappears close to the apex of the colony, where the stem is visible". The authors indicated the presence of nematothecae also on the hydrorhizal stolons. Finally, the description of the gonosome by Peña and García-Carrascosa (1993, p 1009) can be synthesized as: coppiniae set along stem and main branches, fusiform, 9–17 mm long, 3–4 mm in maximum diameter, gonothecae closely aggregated around stem, elongate, flask-shaped gradually increasing in diameter from base to two-thirds of height, then hood-like apically with large lateral opening, height 1.08–1.12 mm, maximum diameter 0.40–0.43 mm; surface view of gonothecae with wider parts fused though keeping their individual perisarc delimitation, distal parts free with no preferential orientation for aperture; protective tubes with nematothecae arising amongst gonothecae of coppinia.

Remarks

There is a general lack of information in the literature concerning the cnidome of lafoeids (or Leptothecata in general), although it is known as a rule that the cnidome of Leptothecata is less diversified than that of Anthoathecata, for instance (see Bouillon 1985). The cnidome of *A. operculata* has not previously been studied, even though comparisons with the nematocysts of other leptothecates would be highly desirable. The nematocysts of the holotype of *Abietinella operculata* are of the same type (microbasic mastigophores), morphology (elongated oval) and equivalent dimensions (22×3 μm cf. Boero 1980, Figure 7) as those of the cnidome of the Lafoeidae Hebellinae *Hebella parasitica* (Ciamician, 1880) (Boero 1980, 136, Figure 7), though Itô and Inoue (1962, p 449, Figures 78, 79) reported quite different dimensions for the same species (6.0–6.4×1.9–2.1 μm). However, we also studied nematocysts from a better preserved non-type specimen of *A. operculata* (USNM, Sta. 575/052, from Saunders Island) and the holotype of *Abietinella grandis* (ZMB Cni 958*, from Eastern Antarctic), and found three different size classes of nematocysts (Tables II, III; see description below), apparently belonging to two different types: large and medium ?macrobasic mastigophores and small microbasic euryteles. Nematocysts of the type specimen of *A. operculata* are intermediate in size between the large and medium-sized nematocysts of the specimens from Saunders Islands and Eastern Antarctic and, once all determinations are dubious, it is very plausible they are correspondent. We possibly overlooked two size-classes of nematocysts in the type because it is not well preserved. Therefore, we conclude that the cnidome of *Abietinella* is variable concerning nematocyst dimensions, and different from that of known lafoeids Hebellinae.

Table II. Cnidome data of a non-type specimen of *Abietinella operculata* (USNM, 575/052, from Saunders Island) (measurements in μm).

Nematocyst	Mean $\pm$ SD (range) (*n*)
Large ?macrobasic mastigophores	23–26×6.5–7 ($23.85 \pm 0.88 \times 6.70 \pm 0.26$) (10)
Medium ?macrobasic mastigophores	10–11.5×3–4 ($10.50 \pm 0.58 \times 3.75 \pm 0.35$) (10)
Small microbasic mastigophores	7–7.5×2–2.5 ($7.33 \pm 0.29 \times 2.17 \pm 0.29$) (3)

Table III. Morphometric data of the type specimen of *Abietinella grandis* (Vanhöffen, 1910) (measurements in mm; nematocysts measure in μm).

Characters	Mean $\pm$ SD (range) (*n*)
Colony height	105
Diameter of stem (base)	1
Length of abcauline side of pedicel	0.07 ± 0.01 (0.06–0.08) (4)
Length of adcauline side of pedicel	0.09 ± 0.02 (0.08–0.12) (5)
Length of nematotheca	0.29 ± 0.06 (0.21–0.40) (10)
Diameter of nematothecal aperture	0.05 ± 0.004 (0.05–0.06) (10)
Proportion L/D of the nematotheca	4.3–7.1:1
Length of hydrotheca	0.68 ± 0.02 (0.66–0.72) (10)
Diameter at diaphragm	0.13 ± 0.01 (0.11–0.14) (10)
Maximum diameter of hydrotheca	0.23 ± 0.01 (0.22–0.25) (10)
Diameter at aperture	0.23 0.01 (0.21–0.25) (10)
Number of tentacles	*ca* 12
Large ?macrobasic mastigophores	$22.00 \pm 1.43 \times 6.50 \pm 0.47$ (20.0–23.5×6.0–7.5) (10)
Medium ?macrobasic mastigophores	$10.80 \pm 0.79 \times 3.55 \pm 0.28$ (10–12×3–4) (10)
Small microbasic mastigophores	No means (7.0–7.5×2.0–2.5)

The cnidome of *Abietinella* is also different in some aspects from that of the sertulariid genera used by Levinsen (1913) to justify the placement of *Abietinella* among the Sertulariidae. In general, the species of Sertulariidae do not have three size classes of nematocysts. *Diphasia tropica* Nutting, 1904 has microbasic mastigophores in two dimensions, 7.5–8.0 × 2.5–3.0 μm and 5.0–5.5 × 1.5–2.0 μm (see Migotto 1996). The cnidome of *Abietinaria*, on the other hand, is also constituted of microbasic mastigophores (e.g. 16.9–19.8 × 6.2–7.1 μm and 5.5–5.9 × 1.8–2.0 μm for *Abietinaria costata* Nutting, 1901) or by large holotrichous isorhiza [e.g. 20.5 × 10 μm for *Abietinaria abietina* (Linnaeus, 1758), personal observation of material from the Zoological Institute of Russian Academy of Sciences, ZIRAS, St Petersburg, nos 1/10051 and 3/10052.1]. In fact, the cnidome of species of Sertulariidae seems to be characterized by the presence of large and small microbasic mastigophores, although the larger are of diverse dimensions. A first group would have large microbasic mastigophores of equivalent length to those of *A. operculata*, although distinctly wider [e.g. *Dynamena crisioides* Lamouroux, 1824; *Dynamena dalmasi* (Versluys, 1899), *Dynamena disticha* (Bosc, 1802), *Dynamena quadridentata* (Ellis and Solander, 1786), *Idiellana pristis* (Lamouroux, 1816), *Symmetroscyphus intermedius* (Congdon, 1907), and *Thyroscyphus ramosus* Allman, 1877; see Calder 1991; Migotto 1996]. A second group would be constituted by the genus *Sertularia*, and would have smaller large microbasic mastigophore than those of *A. operculata* [e.g. *Sertularia distans* (Lamouroux, 1816), *Sertularia loculosa* Busk, 1852, *Sertularia marginata* Kirchenpauer, 1864, *Sertularia rugosissima* Thornely, 1904, *Sertularia turbinata* (Lamouroux, 1816); see Migotto 1996]. In any instance, the cnidome of *A. operculata* is somewhat different from both Lafoeidae (in this case Hebellinae) and Sertulariidae.

Zygophylax grandis (=*Abietinella grandis*) was described by Vanhöffen (1910) from material from the Gauss Station (65°21′S, 86°06′E, Davis Sea, Antarctica, 385 m, collected during the German South Polar Expedition), who considered the possibility that the five forms referred to *Zygophylax* at that time were conspecific. Vanhöffen (1910) did not report nematothecae on the main stem tube, and acknowledged hydrothecae and nematothecae are suppressed on the internal tubes. The differences remarked by Vanhöffen (1910) to justify his new species were the middle branches not lying on the same plane of the whole colony, general dimensions and proportions of hydrothecae and nematothecae. Although the holotype of *Z. grandis* was supposed to be lost (cf. Rees and Vervoort 1987) and the original description was apparently based on infertile material, the species was considered conspecific with *A. operculata* by Stepan'yants (1979; arguing that the size of hydrothecae may be, indeed, variable) and Vervoort (1972, p 82), Rees and Vervoort (1987, p 46) and El Beshbeeshy (1991, p 92) concurred.

We had the opportunity to study the holotype of *A. grandis* and may provide a re-description of the species, as follows.

Description of holotype of A. grandis

Stem erect, ca 105 mm high, basally and distally broken, pinnate, completely polysiphonic. Stem composed of main tube and a few accessory tubes involving main tube up to its distal end; branches arising from main stem tube; basal polysiphonic part of stem ca 1 mm in diameter, distal polysiphonic part ca 0.4 mm. Stem basally broken; no hydrorhiza present. Stem with branches up to second order. Monosiphonic branches up to 14 mm long. Only four primary branches, at 55, 75, 84, and 105 mm from stem base, giving rise to secondary branches; all forked primary branches, except the last one, polysiphonic and up to 15 mm

long. Polysiphonic, primary branches arising at a plane different from that formed by remaining first-order branches and hydrothecae; the first two at almost right angle.

Accessory tubes of polysiphonic part not divided into internodes and without hydrothecae or branches, but with irregularly distributed nematothecae. Lateral branches arising at ca 45° in relation to long axis of stem, with an axillary pedicellated hydrotheca without nematothecae at origin (in one occasion first hydrotheca also with nematothecae). Apophysis separated from branch by a well-marked septum. Branches not divided into internodes, with apophyses bearing lower-order branches or hydrothecae. Hydrothecal pedicels short, continuous to apophyses, 0.064–0.08 mm (0.072 ± 0.009, $n=4$) long at abcauline side, 0.080–0.120 mm (0.093 ± 0.016, $n=5$) long at adcauline side, ending at diaphragm of hydrothecae. One pair of nematothecae at adcauline side of apophyses, one on each side of hydrotheca, rod-shaped with circular distal aperture, 0.208–0.400 mm (0.291 ± 0.065, $n=10$) long, 0.048–0.056 mm (0.053 ± 0.004, $n=10$) in diameter at aperture.

Hydrothecae alternately arranged in one plane, but sometimes in two planes making an obtuse angle. Hydrothecae arising at ca 45° in relation to longitudinal axis of branch. Hydrotheca tubular, adcauline wall sinuous, widely convex basally and concave at distal part; abcauline wall usually straight, but occasionally slightly curved as well. Hydrothecae 0.656–0.720 mm (0.683 ± 0.017, $n=10$) long (from diaphragm to margin at abcauline side), with fine striae on outer surface. Base of hydrotheca 0.112–0.144 mm (0.132 ± 0.01, $n=10$) in diameter at diaphragm level; maximal diameter of 0.224–0.248 mm (0.235 ± 0.009, $n=10$); diameter at aperture 0.208–0.248 mm (0.229 ± 0.012, $n=10$). Hydrothecal wall slightly thickened basally. Diaphragm thick, circular, usually slightly directed downwards in relation to hydrothecal long axis. Hydrothecal aperture circular, oblique in relation to hydrothecal long axis, rim even and slightly flared, and usually with a few short renovations. Hydrotheca closed by a disc-shaped operculum, attached to adcauline wall and projecting into the hydrotheca at 30–45°; operculum frequently lost. Hydranths tubular, basal region constricted by diaphragm, median region often with well-developed abcauline triangular caecum, apical region with one whorl of ca 12 tentacles, hypostome conical.

Three size classes of nematocysts observed (not seen discharged): large rice-shaped ?macrobasic mastigophores, $20–23.5 \times 6–7.5$ μm ($22.00 \pm 1.43 \times 6.5 \pm 0.47$, $n=10$), apparently restricted to nematophores, medium rice-shaped ?macrobasic mastigophores, $10–12 \times 3–4$ μm ($10.80 \pm 0.79 \times 3.6 \pm 0.28$, $n=10$), and tiny microbasic mastigophores, $7–7.5 \times 2–2.5$ μm, fusiform and common. Gonothecae not seen.

Because of the polysiphonic development it is not possible to determine whether or not the main cauline tube is divided into internodes. Apparently, the stem is old, being almost deprived of hydrothecae, except the distalmost 30 mm, where it is possible to see the hydrothecal and branch arrangement, alternate and in one plane. However, at distal part of the stem it is also possible to find a few hydrothecae arising from an accessory tube, probably because the original stem was broken. In fact, at the end of the stem there are two primary branches arising at the same level, apparently one from the original main tube and another from an accessory tube. One of them is unforked, but the other is branched and gives rise to two contiguous second-order branches alternately arranged in one plane. This forked, primary branch is not divided into internodes.

Peña and García-Carrascosa (1993, p 1010) also noted the resemblance of *A. operculata* and *A. grandis*, but admitted the existence of some differences: "in *A. grandis*, nematothecae are very long and narrow, with a small opening (ratio 6:1), while in *A. operculata* they are short and wide with a large opening (ratio 1.5–3:1)", the hydrothecae of *A. grandis* "are bigger, and the branches can emerge in more than one plane". However,

Table IV. Morphometric data of previous records of *Abietinella* spp. (all data in mm).

	Holotype, Chilean Patagonia	Davis Sea (Vanhöffen 1910 as *A. grandis*, and our data)	Scotia Ridge Area (Peña and García-Carrascosa 1993)	Argentina (Blanco 1968, 1976)	Argentina (Vervoort 1972)	Argentine shelf (Stepan'yants 1979)	Patagonian shelf (El Beshbeeshy 1991)
Colony height	47	105	Up to 280				
Length of hydrothecae	**0.36**–0.55	0.64–**0.72**	0.60 ± 0.02[a]	0.41–0.56	0.48–0.49	0.44–0.62	0.46–0.53
Diameter at hydrothecal aperture	**0.15**–0.17	0.21–0.25	0.25 ± 0.01	0.16–**0.28**	0.16–0.17	0.16–0.22	0.16–0.17
Length of nematothecae	0.20–0.23	0.21–**0.40**	0.12 ± 0.01[a]	**0.05**–0.27	0.11–0.20	0.10–0.20	0.09–0.16
Diameter at nematothecal aperture	**0.04**–**0.06**	0.05–0.06	0.04 ± 0.006	0.05–0.06	0.04–0.06		0.05–0.06
Proportion L/D of nematothecae	3.8–5:1	4.3–7.1:1	3:1	1–4.5:1	2.8–3.3:1		1.8–2.7:1
Length of pedicel	0.11–**0.32**	**0.08**–0.14					
Maximum diameter of hydrothecae	**0.18**–0.22	0.22–**0.25**		0.18–0.23			0.18–0.20

In bold are marked the extreme values recorded for the species. [a]Measurements of the abcauline wall.

a comparison with the holotype and other material of *A. operculata* (namely Blanco 1968, 1976, Vervoort 1972; Stepan'yants 1979; El Beshbeeshy 1991; Peña and García Carrascosa 1993) indicates that *A. grandis* (Vanhöffen, 1910) falls within the size range of *Abietinella operculata*, except for the length of the hydrothecae and nematothecae. Correlation between morphometric data and the known distribution of the species, restricted to Antarctic and sub-Antarctic waters, may suggest that hydrothecae from high Antarctic areas are larger (0.72–0.75 mm in length and 0.22–0.24 mm in diameter at aperture for material from the Wedell Sea; see Peña Cantero et al. forthcoming). Therefore, we conclude that the hydrothecal and nematothecal lengths are variable and do not constitute enough evidence to support two different species.

Considering the previous descriptions of *A. operculata*, one can notice that the largest variation in the group concerns morphometry, but a gradual series of morphometric data can be observed (see above and Tables I, III, IV). The few morphological discrepancies amongst the different colonies of *A. operculata* were found in material recorded from several stations in the Patagonian region by El Beshbeeshy (1991, p 90), differing from the holotype in the abcauline attachment of the operculum and in the monosiphonic stem, though this last difference is possibly due to the less-developed or younger colonies.

The systematic position of *A. operculata* has been in dispute since its discovery. The species was primarily referred to the genus *Zygophylax* (Lafoeidae after Quelch, 1885, in his original description of the genus) by Jäderholm (1903), because of similarities concerning the morphology of the colony, hydrothecae, nematothecae, and abcauline blind sac; the same classification was followed by Billard (1905, 1906), Jäderholm (1905), Clarke (1907), and Vanhöffen (1910). Levinsen (1913) pondered on the existence of similarities (namely presence of operculum, hydrothecal and diaphragm shape) between *A. operculata* and the species of the genera *Abietinaria* Kirchenpauer, 1884 and *Diphasia* L. Agassiz, 1862, both considered to belong to the family Sertulariidae. This proposal of the sertulariid affinities of *Abietinella* was followed by Naumov and Stepan'yants (1962), disregarding the possibility of the existence of an operculum and caecum in any family but Sertulariidae. Agreement about the validity of the genus *Abietinella*, although placed among the Lafoeidae, was given by many authors (e.g. Blanco 1968, 1976; Vervoort 1972; Stepan'yants 1979; Rees and Vervoort 1987; El Beshbeeshy 1991; Peña and García-Carrascosa 1993; Blanco et al. 1994). On the contrary, Salvini-Plawen (1972), although regarding the species among the lafoeids, referred it to *Cryptolaria operculata*, a position neither justified nor followed by anybody else. Besides, the binomen *Cryptolaria operculata* had already used by Nutting (1905, p 947–948) to describe a hydroid from Hawaiian waters, presently named *Stegolaria operculata* (Nutting, 1905) (e.g. cf. Stechow 1913a, p 29; 1913b, p 137; Edwards 1973, p 594; Hirohito 1995, p 94).

The doubts concerning the taxonomic position of *Abietinella operculata* began to be clarified when Stepan'yants (1979) firstly observed specimens with coppinia, however not describing it in detail. Later, Rees and Vervoort (1987, p 46) also regarded the gonophores of the species as typical coppiniae, found on main stem and branches. However, a detailed account of the coppinia was only given by Peña and García-Carrascosa (1993). These data corroborated the position of *A. operculata* within the family Lafoeidae.

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