Redescription of Oswaldella antarctica (Jäderholm, 1904) (Cnidaria Hydrozoa) with notes on related species (Notes on Antarctic hydroids, I)

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Key-words: Cnidaria; Hydrozoa; hydroids; Antarctic; redescription of *Oswaldella antarctica*, new species. Jäderholm's type of *Schizotricha antarctica*, collected by the Swedish Antarctic Expedition 1901-1903, is redescribed from a syntype in the collections of the Swedish National Museum, Stockholm. The type lot of that species proved to be composite, the material best resembling Jäderholm's (1904, 1905) descriptions and figures has been designated as the syntype. There are two more species in the type lot, that have also been described, but are too poorly represented to be either recognized as one of the described species of *Oswaldella* or to merit a new specific name; they have been indicated as *Oswaldella* spec. 1 and spec. 2.

Resumen: Se ha revisado y redescrito el material tipo de *Schizotricha antarctica* Jäderholm, 1904, recogido durante la Swedish Antarctic Expedition 1901-1903 y depositado en el Swedish Museum of Natural History de Stockholm. Dicho material ha resultado estar compuesto por tres especies. Se ha elegido como sintipo de *Oswaldella antarctica* la especie más próxima a la descripción y figuras de Jäderholm (1904, 1905). Las otras dos especies están tan pobremente representadas que no es posible adscribirlas a ninguna especie conocida de *Oswaldella* ni asignarles un nuevo nombre específico, con lo que se denominan *Oswaldella* spec. 1 y spec.2.

Introduction

Through the kind cooperation of Dr Lennart Sandberg and Dr Karin Sindemark, Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden, we were able to study the type lot of *Schizotricha antarctica* Jäderholm, 1904, collected by the Swedish Antarctic Expedition 1901-1903. This type lot consists of material preserved in three tubes, the re-examination of which, surprisingly, showed the presence of three different species. We have indicated below one of these colonies as the syntype of *Schizotricha antarctica* Jäderholm, 1904 [now *Oswaldella antarctica* (Jäderholm, 1904)]; this is the only complete colony in this lot, the one figured by Jäderholm (1905, pl. 14 fig. 6) and it is the nearest to Jäderholm's original description. The remaining two species, though clearly different from the species of *Oswaldella* that we have studied so far, are represented in the type lot by a fragment of hydrocaulus and some hydrocladia only; they have momentarily been described and indicated as *Oswaldella* spec. 1 and spec. 2, awaiting the discovery of a more abundant material to complete the present descriptions. The differences of the present colonies from other well described species of *Oswaldella* are also indicated.

Descriptions

Oswaldella antarctica (Jäderholm, 1904) (fig. 1)

Schizotricha antarctica p.p. Jäderholm, 1904: 12; 1905: 35, pl.14 figs 6-8.

? Schizotricha antarctica; Vanhöffen, 1910: 336, fig. 48.

Oswaldella antarctica; Stechow, 1919: 853; Stechow, 1920: 40(32).

? Polyplumaria antarctica; Jäderholm, 1926: 16.

- ? Oswaldella antarctica; Totton, 1930: 209; Peña Cantero, 1991: 168, pls 31, 56, pl. 68 fig. a.; Peña Cantero and García Carrascosa, 1994: 125-126, fig. 8a-c.
- Not Polyplumaria antarctica; Billard, 1914: 28, fig. 17 (= Oswaldella billardi Briggs, 1938);
- Not Oswaldella antarctica; Blanco, 1984: 41, pl. 38 figs 86-88 (= Oswaldella blanconae El Beshbeeshy, 1991); Broch, 1948: 13-16, fig. 4a; Stepan'yants, 1979: 112, pl. 21 figs 5A-B (= Oswaldella stepanjant-sae El Beshbeeshy, 1991); Naumov & Stepan'yants, 1972: 52, figs 14a-b (= partly Oswaldella stepanjantsae El Beshbeeshy, 1991), partly another species of Oswaldella).

Material examined.— Swedish Southpolar Expedition 1901-03, Stn nº 5, 64°20'S 56°38'W, SE Seymour Island, Graham Land, 150 m, 16.i.1902 (Swedish Museum of Natural History, Coel. no. 431), one stem up to 45 mm high; no gonothecae (syntype). Fragment (schizosyntype) as RMNH Coel. nº 27295, slide nº 3143.

Description.— Colony composed of single erect, monosiphonic stem with pinnately arranged hydrocladia, height c. 45 mm, emerging from a stolon and broken up into internodes. The first internode is c. 5 mm long and gives rise to two hydrorhizal stolons, running downwards and detaching themselves from the axis, both stolons branching. Second internode also c. 5 mm long; remaining internodes shorter. Apophyses are found from the fifth internode onwards, this fifth internode has four apophyses without hydrocladia, these, or their remains are present from the sixth internode onwards.

The apophyses are alternately arranged in two longitudinal series in one plane and are directed upwards under an angle of c. 45°. Number of apophyses one to four per internode, though two is the normal number. Apophyses with three nematophores on the upper surface, two as simple holes in the perisarc of the axil between apophysis and stem, the third in the form of a "mamelon" and always situated at the same locality of the dorsal part of the apophysis (fig. 1b-d).

Hydrocladia inserting on the apophyses, always separated by a distinct node. Ramification of hydrocladia varied, the majority forked, giving rise to two hydrocladia of the second order, the bifurcation taking place at the first internode (fig. 1d). A single hydrocladium of the third order is fairly frequent (fig. 1a); the presence of two tertiary hydrocladia was observed once. One hydrocladium has three secondary hydrocladia, all springing from the first hydrocladial internode. In another hydrocladium a tertiary hydrocladium gives rise to one of the fourth order. Unbranched hydrocladia are also present.

Hydrocladia divided into homomerous internodes each bearing one hydrotheca and two nematophores: one mesial superior, as a simple hole in the perisarc and placed behind the free part of the hydrothecal adcauline wall, and one mesial inferior, provided with a small, much reduced nematotheca and placed on a slightly



Fig. 1. Oswaldella antarctica Jäderholm, 1904. a, branch showing hydrocladial ramification and disposition of hydrothecae; b, cauline apophysis with two axillary nematophores and one mamelon, frontal view; c, idem, lateral view: d, first hydrocladial internodes; e-i, typical hydrocladial internodes, showing hydrothecae and nematophores, with the inconspicuous mesial inferior nematotheca. Scale bars: a, 1 mm; d-i, 500 μm; b-c, 250 μm.

raised part of the internode. Hydrotheca inserting on middle of internode. Abcauline wall of hydrotheca straight; adcauline wall almost completely adnate with only a minor distal part free. Hydrothecal rim smooth and almost circular, slightly inclined towards internode (fig. 1d-i). Hydrothecae moderately deep, but length increasing along the hydrocladia. For instance, the length of the abcauline hydrothecal wall may be 208 μ m in the first internode and 267 μ m in the seventh. Forked internodes with hydrotheca placed in axil between the two prongs and with three nematophores: one mesial inferior and provided with a rudimentary nematotheca and two mesial superior, shaped as simple holes in the perisarc of each prong and placed behind the adcauline hydrothecal wall.

Hydrothecae		
length abcauline wall	208-299	(258.6 ± 24.3)
length free part of adcauline wall	19.5	
diameter at rim	156-195	(174 ± 9.9)
Nematotheca, length	13-19.5	(17.9 ± 3.3)
Internode		
length	738-934.8	(837.4 ± 60.7)
diameter under hydrothecae	156-214.5	(184.3 ± 16.6)
diameter under nematophore	123.5-182	(149.9 ± 14.3)
Diameter of the hydrocaulus	196.8-459.2	
Length of apophyses	195-227.5	
Nematocysts (microbasic mastigophores)	11.9-14 × 4.2-5.6	

Measurements (in µm, with mean and standard deviation).

Remarks.— The 45 mm high stem bearing the hydrocladia originates from another hydrocaulus, 28 mm high. It has a hydrorhiza composed of a few thick stolonial fibres and is broken up into internodes bearing apophyses that, as in the axis described above, are alternately arranged in two longitudinal series placed in one plane. Normally there are two apophyses per internode; occasionally there is only one. The axis begins with a short, 0.25 mm long internode without apophyses. These occur from the second internode onwards. This second internode is 7 mm long and has a single apophysis in its distal part. A regular series of internodes bearing apophyses follows, though occasionally interrupted by the presence of up to three short internodes without apophyses. Eventually the older stem becomes a stolonial structure giving rise to the axis bearing hydrocladia described earlier.

Jäderholm (1904, 1905), as *Schizotricha antarctica*, described a new species of hydroid from the collections of the Swedish Antarctic Expedition 1901-1903. He characterized this species by the condition of the hydrocauli that are broken up into internodes, by the forked hydrocladia, by the presence of a rudimentary mesial inferior nematotheca, and by the almost cylindrical hydrothecae, being approximately twice deeper than wide and with the distal part of the adcauline hydrothecal margin free. As mentioned above the type lot of *Schizotricha antarctica* is composite and a detailed study of this material allows us to distinguish in it three different species. We indicate the only more or less complete colony in this material, 45 mm high and provided over the greater part of its length with hydrocladia, as the syntype of *Schizotricha*

antarctica Jäderholm, 1904, this is apparently the material figured by Jäderholm, 1905; it agrees best with his descriptions. The hydrothecae, though, are not as deep as those figured by Jäderholm (1905, pl. 14 figs 7-8), being only slightly longer than wide. *Oswaldella antarctica* (Jäderholm, 1904) in our present conception is also characterized by the presence of three nematophores on the upper surface of the apophyses - two axillary as simple perisarcal holes and one "mamelon" -, by its inconspicuous mesial inferior nematotheca and by the dimensions of the hydrotheca.

Oswaldella antarctica differs considerably from the other known species of the genus. From Oswaldella bifurca (Hartlaub, 1904) it differs mainly in size and shape of the hydrothecae: in that species the hydrotheca is smaller and cup-shaped, the mesial inferior nematotheca is fully absent, and the cauline apophyses have a single nematophore in the shape of a simple, circular perisarcal hole.

Oswaldella billardi Briggs, 1938, chiefly differs by size and shape of hydrothecae that are longer and thicker, with a strongly convex abcauline wall. There are two nematophores on the cauline apophyses, shaped as circular holes. The stem shows no internodes.

Oswaldella herwigi El Beshbeeshy, 1991, differs by the absence of a rudimentary mesial inferior nematotheca. Also the hydrothecae are here smaller, cup-shaped and placed on the distal third of the internode. Moreover O. herwigi is the only species in Oswaldella where thecate and athecate internodes alternate in the hydrocladia. In the cauline apophyses there are only two nematophores, one a simple perisarcal hole in the axil, the other a "mamelon".

Oswaldella blanconae El Beshbeeshy, 1991, is different because of the absence of a rudimentary mesial inferior nematotheca, the hydrothecae are smaller and placed on the basal third of the internode. There is also difference in the degree of ramification because forked hydrocladia have only occasionally been observed in this species. The cauline apophyses, finally, have only a single nematophore shaped as a "mamelon".

Oswaldella stepanjantsae El Beshbeeshy, 1991, shares with O. antarctica the presence of an inconspicuous mesial inferior nematotheca and has similar hydrothecal morphology, though the hydrothecae are bigger. There is difference in hydrocladial structure, as these normally begin with some short, athecate internodes. The caudal apophyses have four axillary nematophores shaped as perisarcal holes and two "mamelons" (unpublished data).

In connection with Oswaldella nova (Jarvis, 1922), removed to Oswaldella by Millard, 1975, mention should be made of its epibiotic mode of life and its totally different colony structure, as it has no main axis but only hydrocladia, rising direct from the creeping stolon. Also O. nova has a fully different mode of hydrocladial ramification as the secondary hydrocladia do not originate from the first thecate hydrocladial internode. Another important difference is the presence of a nematotheca in the apophysis carrying the hydrocladium; this has never been described in any species of Oswaldella. It might therefore be necessary to place Oswaldella nova (Jarvis, 1922) in a separate genus.

We suspect that the material recorded by Vanhöffen (1910, as *Schizotricha antarctica*), Jäderholm (1926, as *Polyplumaria antarctica*), Totton (1930, as *Oswaldella antarctica*), and Peña Cantero (1991, as *O. antarctica*) does not belong here and represents other species.

Oswaldella spec. 1 (fig. 2)

Schizotricha antarctica p.p. Jäderholm, 1904: 12; 1905: 35, pl.14, figs 6-8.

Material examined.— Swedish Southpolar Expedition 1901-1093, Stn n° 8, 64°03′S 56°37′W, Graham Land, 360 m, 11.ii.1902 (Swedish Museum of Natural History, Coel. no. 434), one single stem up to 31 mm; no gonothecae. Fragment on slide as RMHH Coel. n° 27296, slide n° 3144.

Description.— This species is represented by a branched and monosiphonic stem with pinnately arranged hydrocladia, height 31 mm, basally and distally fragmented. Perisarc of hydrocaulus dark brown. Axis, after a node, forked in two hydrocauli of approximately same diameter. Only four unbranched hydrocladia are present (fig. 2a). Axis broken up into internodes of varied length, bearing alternately arranged apophyses in two longitudinal series in one plane, directed upwards under an angle of 45°. Number of apophyses per internode varying between one and seven; first internode without apophyses. Each apophysis provided with a single axillary nematophore in the shape of a circular perisarcal hole (fig. 2b, c).

Hydrocladia inserting on apophyses, first internode thecate and sharply separated from apophysis. Hydrocladia unbranched, homomerously segmented, each internode with one hydrotheca and two nematophores: one mesial superior as a simple hole in the perisarc behind the free part of the adcauline hydrothecal wall, and a mesial inferior, provided with a rudimentary nematotheca and placed on a slightly raised part of the internode. Hydrotheca large and deep, with straight abcauline wall; adcauline wall nearly completely adnate. Hydrothecal rim smooth, circular and perpendicular to hydrocladial longitudinal axis (fig. 2d-g).

Hydrothecae		
length abcauline wall	325-364	(337.6 ± 15.2)
length free part of adcauline wall	32.5	
diameter at rim	150-189	(172.4 ± 10.6)
Nematotheca, length	26-45.5	(37.3 ± 5.2)
Internode		
length	967.6-1279.2	(1137.8 ± 99.5)
diameter under hydrothecae	169-214.5	(194.6 ± 12.5)
diameter under nematophore	136.5-169	(151 ± 10.7)
Diameter of the hydrocaulus	246-279	
Length of apophyses	162.5	
Nematocysts (microbasic mastigophores)	11.9-12.6 × 3.2-3.5	

Measurements (in µm, with mean and standard deviation).

Remarks.— Oswaldella spec. 1 agrees with the original description of O. antarctica in all features with the exception of the hydrocladia, that are unbranched. However, a closer inspections shows that it has important differences with that species as it is understood now. It differs in the number and disposition of the nematophores on the cauline apophyses: in O. antarctica there are two nematophores shaped as simple perisarcal holes and one "mamelon" while in Oswaldella spec. 1 only one single nemato-

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Fig. 2. Oswaldella spec. 1. a, fragment of stem, showing hydrocladial and hydrothecal disposition; b, cauline apophysis showing axillary nematophore; c, cauline apophysis and first hydrocladial internode, showing disposition of nematophores and mesial inferior nematotheca; d-g, typical hydrocladial internodes, with hydrothecae and nematophores. Scale bars: a, 1 mm; c-g, 500 µm; b, 250 µm.

phore in the form of a circular perisarcal hole has been observed. The hydrothecae in *O. antarctica* are much smaller. The mesial inferior nematotheca is quite inconspicuous in *O. antarctica*; in *Oswaldella* spec. 1 it is bigger and much more prominent. In *O. antarctica* the hydrocladia are ramified, ramifications of the third order having been observed; in *Oswaldella* spec. 1 the hydrocladia are unbranched, though only a few hydrocladia are present.

Differences with the remaining species of *Oswaldella* are even bigger. *Oswaldella bifurca* (Hartlaub, 1904) shares with *Oswaldella* spec. 1 the presence of a single nematophore on the cauline apophyses, but it differs by shape and size of the hydrothecae, that are cup-shaped and much smaller; it also has no (rudimentary) mesial inferior nematotheca but a nematophore shaped as a circular hole.

Oswaldella billardi is mainly different by the shape of the hydrothecae, that have a thick perisarc and a strongly convex abcauline wall. There are two nematophores as simple holes in the perisarc of the cauline apophyses; there are no internodes in the stems.

Oswaldella herwigi El Beshbeeshy, 1991, differs by the absence of a rudimentary mesial inferior nematotheca, by size, shape and insertion of the hydrothecae and by the structure of the hydrocladia. The hydrothecae in *O. herwigi* are smaller, cupshaped and placed on the distal third of the internodes; the hydrocladia has athecate internodes alternating with the thecate internodes. It has two nematophores on the cauline apophyses: one "mamelon" and a simple, perisarcal hole.

Oswaldella blanconae El Beshbeeshy, 1991, is different because of the absence of a rudimentary mesial inferior nematotheca, by the smaller hydrothecae placed on the basal third of the internode and by the presence of a single nematophore on the cauline apophyses shaped as a "mamelon".

Oswaldella stepanjantsae El Beshbeeshy, 1991, though it has in common the presence of a rudimentary mesial inferior nematotheca, differs by the smaller hydrothecae with a wider aperture, and by the structure of the hydrocladia, that normally start with some short, athecate internodes. The cauline apophyses, in addition, have four axillary nematophores, all circular, perisarcal holes and two "mamelons".

> Oswaldella spec. 2 (fig. 3)

Schizotricha antarctica p.p. Jäderholm, 1904: 12; 1905: 35, pl.14, figs 6-8.

Material examined.— Swedish Southpolar Expedition 1901-03, n° 8, 64°3'S 56°37'W, Graham Land, 360 m, 11.ii.1902, (Swedish Museum of Natural History, Coel. no. 435), a single stem up to 30 mm high; no gonothecae. Fragment as RMNH Coel. n° 27297, slide n° 3145.

Description.— This species is represented by an erect, unbranched and monosiphonic stem 30 mm high with a small and dense rhizoidal hydrorhiza composed of a large number of thin hydrorhizal stolons. Axis broken up into internodes of varied length, bearing apophyses alternately arranged in two longitudinal series placed in one plane. Normally there are two apophyses to each internode, though occasionally there is only one while one of the internodes has three apophyses. The apophyses are quite short; there are two nematophores on the upper part: one shaped as a simple,



Fig. 3. Oswaldella spec. 2. a, fragment of stem, showing hydrocladial and hydrothecal disposition; b, cauline apophysis, showing axillary nematophore and mamelon; c-d, first hydrocladial internodes and cauline apophyses; e, forked hydrocladial internode; f-h, typical hydrocladial internodes with hydrothecae and mesial inferior nematothecae. Scale bars: a, 1 mm; c-h, 500 μ m; b, 250 μ m.

perisarcal hole in the axil with the stem, the second a "mamelon" and always placed on the same lateral part of the apophysis (fig. 3b-d). A change in orientation of this "mamelon" has been observed.

The specimen only has remains of three hydrocladia, one with three thecate internodes (fig. 3a), one with a single thecate internode and one with a forked internode (fig. 3e), so this species may have branched hydrocladia.

The hydrocladia are borne by the apophyses and separated from those by a clear node. The first internode is thecate, the segmentation is homomerous and each internode has one hydrotheca and two nematophores: one mesial superior as a simple hole in the perisarc behind the free portion of the adcauline hydrothecal wall, and one mesial inferior, provided with a rudimentary nematotheca, located on an elevated part of the internode. The hydrothecae insert on the distal half of the internodes. They are shallow, sometimes wider than long, with a straight abcauline wall, tilted outwards; adcauline wall with conspicuous free distal portion. Hydrothecal rim smooth and circular (fig. 3c-h). Though only a few hydrothecae are present they seem to increase in length along the hydrocladia. In the hydrocladium with three hydrothecae the length of the abcauline wall is 221 μ m in the first and 254 μ m in the third hydrotheca.

The forked internode has a hydrotheca in the axil between both prongs; there are three nematophores: one mesial inferior provided with a rudimentary nematotheca and placed on a raised part of the internode under the hydrotheca, and two mesial superior shaped as circular holes in the perisarc, one on each prong and placed behind the free part of the adcauline hydrothecal wall.

Hydrothecae		
length abcauline wall	208-254	(224.9 ± 19.3)
length free part of adcauline wall	32.5-45.5	(40.6 ± 6.5)
diameter at rim	215-267	(231.4 ± 20.9)
Nematotheca, length	26-45.5	(35.1 ± 7.4)
Internode		
length	902-1066	$(1007 \pm 66-2)$
diameter under hydrothecae	214.5-273	(236.6 ± 30.3)
diameter under nematophore	162.5-195	(175.5 ± 15.2)
Diameter of the hydrocaulus	328-344.4	· ,
Length of apophyses	175.5-227.5	
Nematocysts (microbasic mastigophores)	12.6-14.7 × 3.5-3.9	

Measurements (in µm, with mean and standard deviation).

Remarks.— Oswaldella spec. 2 agrees with Jäderholm's original description of O. antarctica except for the hydrothecal morphology: the hydrothecae are only slightly longer than wide. There are, nevertheless, important differences with that species in our present conception. In O. antarctica three nematophores occur on the upper part of the cauline apophyses: two as simple perisarcal holes and one in the form of a "mamelon". There are bigger differences in shape, size and disposition of the hydrothecae, that in O. antarctica are slenderer and insert on the middle of the internode. There are also differences in the development of the reduced mesial inferior nema-

totheca: in *O. antarctica* it is present though quite inconspicuous, while in *Oswaldella* spec. 2 it is bigger and well visible.

The differences with *Oswaldella* spec. 1 are also distinct, this species having a single axillary nematophore as a perisarcal hole in the cauline apophyses. The hydrothecae are longer and slenderer, they occur in the middle of the internodes. Only unbranched hydrocladia have been observed.

The differences of *Oswaldella* spec. 2 with the remaining species of the genus may be summarized as follows:

Oswaldella bifurca (Hartlaub, 1904) principally differs by shape and size of the hydrothecae, that are cup-shaped and much smaller; the mesial inferior nematotheca is absent, while the cauline apophyses have a single nematophore shaped as a circular hole in the apophysial perisarc.

Oswaldella billardi Briggs, 1938, mainly differs by the longer hydrothecae with thick perisarc and highly convex abcauline wall. The number of nematophores on the apophyses is two, both being circular perisarcal holes. The stems are not divided into internodes.

Oswaldella herwigi El Beshbeeshy, 1991, differs by the absence of a rudimentary mesial nematotheca. The hydrothecae are smaller and cup-shaped. O. herwigi, moreover, is the only species of the genus where thecate and athecate internodes alternate in the hydrocladia. The number of nematophores on the apophyses is two: one a simple perisarcal hole, the second a "mamelon".

Oswaldella blanconae El Beshbeeshy, 1991, has no rudimentary mesial inferior nematotheca. The hydrothecae are smaller and placed on the basal third of the internode. There is a single nematophore on the apophyses, shaped as a "mamelon".

Lastly, Oswaldella stepanjantsae El Beshbeeshy, 1991, mainly differs in size, shape and disposition of the hydrothecae that are longer, slenderer and placed on the middle of the internode. The mesial, inferior nematotheca is small and quite inconspicuous. The hydrocladia normally first have some short, athecate internodes. There are six nematophores on the apophyses, four axillary represented by simple perisarcal holes and two "mamelons".

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