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ORIGINAL PAPER

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On two new species of *Oswaldella* Stechow, 1919 (Cnidaria, Hydrozoa) from Bransfield Strait (Antarctica)

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Abstract Two species of the genus *Oswaldella* Stechow, 1919 new to science (*Oswaldella crassa* sp. nov. and *O. curiosa* sp. nov.) were studied. Both species are described and figured; their systematic position amongst the remaining species of the genus is discussed. The material originates from the Bransfield Strait area (Antarctica) and was collected during the United States Antarctic Research Program with R.V. *Eltanin*. A comparative table listing the main features of the known species of *Oswaldella* is presented. Finally, a general survey of geographical and bathymetrical distribution of the known species of *Oswaldella* is given.

Introduction

During the last few years the list of known species of the genus *Oswaldella* Stechow, 1919 has increased considerably, making this genus one of the hydroid genera best represented in the antarctic benthic ecosystem. Before El Beshbeeshy's paper of 1991, which added three new species, only four species were known. Over the last 3 years, however, the study of the material collected during several French, German and Spanish antarctic expeditions, and the revision of old material, resulted in the discovery of 12 species new to science (cf. Peña Cantero et al. 1995; Peña Cantero and Vervoort 1996, 1997; Peña Cantero et al. 1997).

In this paper we present the first results of the study of the huge hydroid material of the U.S.A.R.P. (United States Antarctic Research Program), collected over many years by several American antarctic expeditions, upon which study has recently been started. Amongst the many species present, we found two species of the genus *Oswaldella* Stechow, 1919 that we consider new to science and that are described below as *Oswaldella crassa* sp. nov. and *Oswaldella curiosa* sp. nov.

Materials and methods

The material examined comes from the Bransfield Strait area (Antarctica) and was collected during U.S.A.R.P. with R.V. *Eltanin* in the austral summer of 1962/1963.

Andriashev (1964) and Picken (1985) are followed in considering the northern limit of the pack ice as the most valid limit for the antarctic benthic ecosystem.

The type series specimens have been deposited in the collections of the Nationaal Natuurhistorisch Museum (National Museum of Natural History), Leiden, The Netherlands (registration numbers indicated by RMNH Coel. and a number) and in the collections of the National Museum of Natural History (Smithsonian Institution), Washington, DC (with registration numbers as USNM and a number).

Results and discussion

Description of the species

Oswaldella crassa sp. nov. (Fig. 1)

Material examined. ELTANIN 006-428, 5 January 1963, 62°41′–62°39′S, 57°51′–57°46′W, 662–1120 m, three stem fragments, 32, 25 and 15 mm high (the last two belonging to the same stem), with immature gonothecae (holotype, USNH no. 97230; paratype, RMNH-coel. 27851; slide 4031).

The work was done in the National Museum of Natural History of Leiden, The Netherlands

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Description. Three feather-like stem fragments; none belonging to basal part of colony. Colony rigid, due to strong development of perisarc. Normally stem not divided into internodes; nodes only occasionally present. Stem and hydrocladia brown, stem darker.

Stem with two longitudinal series of apophyses, alternately arranged in one plane and directed upwards at ca 45° (Fig. 1c). Apophyses giving rise to hydrocladia; node between cauline apophyses and hydrocladia absent (Fig. 1a–c).

Hydrocladia usually bifurcated; basal internode of primary hydrocladium giving rise to two secondary hydrocladia (Fig. 1b). Frequently, however, first internode of one second-order hydrocladium supporting third-order hydrocladium (Fig. 1a). Hydrocladia short, with up to ten hydrothecae.

Each cauline apophysis normally with three nematophores (Fig. 1b,c): two emerging through perisarc holes placed at axil between apophysis and stem; third nematophore emerging through a raised, perforated part of perisarc (''mamelon'') situated at one side of upper dorsal part (Fig. 1b).

Hydrocladia divided into hydrothecate internodes; occasionally without separation between two or more internodes (Fig. 1a,b). Each internode usually with one hydrotheca and two naked nematophores (Fig. 1d–h): one mesial superior emerging through a circular hole placed behind free part of adcauline hydrothecal wall and one mesial inferior nematophore emerging through a perisarc hole situated at strong elevation of internode and deprived of nematotheca.

Forked hydrocladial internodes with one hydrotheca at axil of bifurcation and three naked nematophores (Fig. 1a,b): one mesial inferior and two superior, placed one on each prong behind free part of adcauline hydrothecal wall. However, forked internode of primary hydrocladium deprived of mesial inferior nematophore (Fig. 1b).

Hydrotheca large and deep, placed in middle of internode (Fig. 1d–h). Hydrothecal length slightly increasing along hydrocladia; for example, length of abcauline hydrothecal wall may be 260 μm in first unforked internode and 286 μm in fifth. Abcauline wall straight or slightly convex. Adcauline wall mainly adnate and slightly shorter than abcauline wall; hydrothecal aperture slightly tilted adcaudally.

Immature, inverted cone-shaped gonothecae present (Fig. 1i), inserted on hydrocladial internodes just under mesial inferior nematophore.

Remarks. *Oswaldella crassa* sp. nov. is clearly different from the remaining species of the genus (cf. Table 2), although it has features in common with several species. Thus, by the absence of the infrathecal scale-shaped nematotheca on the hydrocladial internodes, *O. crassa* sp. nov. is allied to *O. bifurca* (Hartlaub, 1904), *O. shetlandica* Stepan'yants, 1979, *O. blanconae* El Beshbeeshy, 1991, *O. elongata* Peña Cantero, García Carrascosa and Vervoort, 1995 and *O. garciacarrascosai* Peña Cantero, Svoboda and Vervoort, 1997 (cf. Table 2). Nevertheless, the species have important differences:

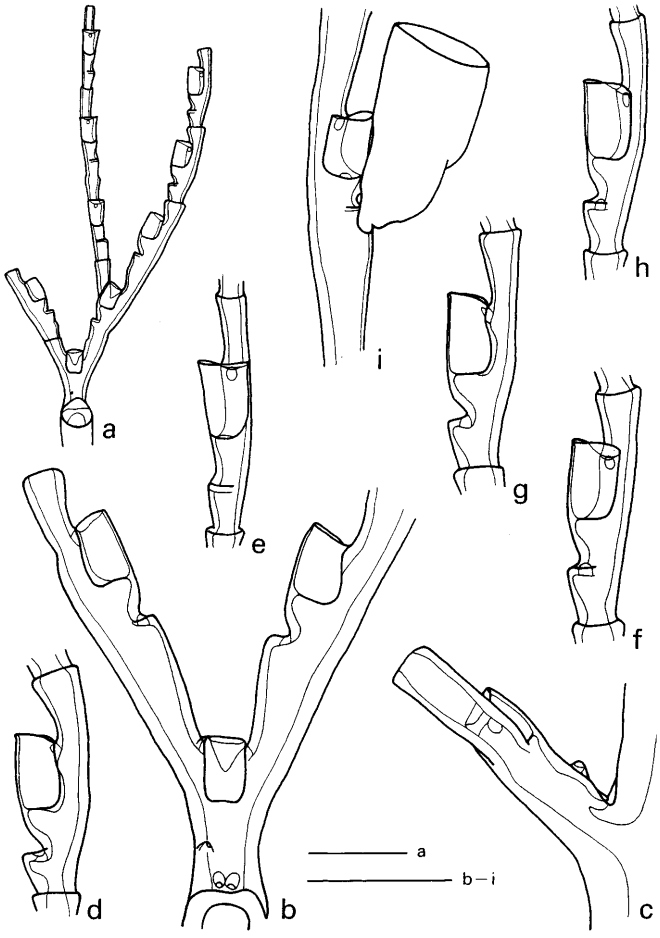


Fig. 1a–i *Oswaldella crassa* sp. nov. **a** Branch showing hydrocladial branching and hydrothecal disposition; **b** cauline apophysis with two axillary nematophores and a "mamelon", and basal part of hydrocladia (frontal view); **c** cauline apophysis showing one axillary nematophore and a "mamelon" (lateral view); **d–h** hydrocladial internodes with hydrotheca and both mesial superior and mesial inferior nematophores; **i** hydrocladial internode with gonotheca. Scale bars: **a** 1 mm; **b–i** 500 μm

Oswaldella bifurca, though it also shares with *O. crassa* sp. nov. the absence of a node between cauline apophyses and hydrocladia, mainly differs from *O. crassa* sp. nov. because the hydrothecal shape is completely different (the hydrotheca is low and its aperture is frontally depressed); there is a single axillary nematophore emerging through a perisarc hole in the cauline apophyses; the hydrothecae are situated on the basal third of the hydrocladial internodes; the angle formed between the cauline apophyses and the stem is larger (ca 70°) and the stem is divided into internodes.

Oswaldella shetlandica also shares with *O. crassa* sp. nov. the absence of a node between cauline apophyses and hydrocladia, the angle formed between cauline apophyses and stem, and the high hydrotheca, but they differ mainly in the hydrothecal shape, the hydrotheca in *O. shetlandica* having a strongly convex abcauline wall

Table 1 Measurements of the species (in μm)

	O. crassa sp. nov.	*O. curiosa* sp. nov.
Hydrothecae		
Length of abcauline wall	228–286	169–195
Length of free part of adcauline wall	–	98–137
Diameter at rim (lateral view)	143–163	65–91
Diameter at rim (frontal view)	163–189	150–163
Hydrocladial internodes		
Length	804–853	–
Diameter under hydrotheca	180–246	–
Diameter under nematophore	131–230	–
Diameter of the stem	ca 410	ca 280
Gonothecae		
Length	541–689	ca 440
Maximal diameter	344–377	ca 330
Nematocysts (microbasic mastigophores)		
Larger size group	13.3–14.7 × 3.5–4.9	14.7–17.5 × 5.6–7
Smaller size group	7–7.7 × 2.1	7–7.7 × 2.1–2.5

and a kidney-shaped aperture that is strongly directed adcaudally. Moreover, in *O. shetlandica* the stem is divided into internodes and there are, together with the two axillary nematophores in the cauline apophyses, two more nematophores emerging through ''mamelons''.

Oswaldella blanconae also shares with *O. crassa* sp. nov. the size of the angle between the cauline apophyses and the stem. Nevertheless, in *O. blanconae* the hydrotheca is low and situated at the basal third of the internode; the stem is divided into internodes; a node is present separating the cauline apophyses and the hydrocladia; only secondary hydrocladia have been reported, and there are two nematophores on the cauline apophyses, one emerging through a ''mamelon'' and the second a single axillary nematophore emerging through a simple perisarc hole.

Oswaldella elongata also shares with *O. crassa* sp. nov. the shape of the angle between cauline apophyses and stem. However, in *O. elongata* the stem is divided into internodes; there is a node between cauline apophyses and hydrocladia; there are only secondary hydrocladia; the hydrothecae are much longer and there are, together with the two axillary nematophores emerging through perisarc holes, two more nematophores emerging through ''mamelons'' on the cauline apophyses.

Oswaldella garciacarrascosai also shares with *O. crassa* sp. nov. the size of the angle between cauline apophysis and stem, the presence of three nematophores in the cauline apophyses, two emerging through perisarc holes and another through a ''mamelon'', the high hydrotheca, and the position of the hydrotheca on the internode. However, in *O. garciacarrascosai* the stem is divided into internodes; there is a node between the cauline apophyses and the hydrocladia; there are only secondary hydrocladia; the perisarc is much less developed, and the hydrothecal shape is different, with the hydrothecal aperture even.

In having three nematophores in the cauline apophyses (two axillary nematophores emerging through perisarc holes and another emerging through a ''mamelon''), *Oswaldella crassa* sp. nov. is also allied with *O. antarctica* (Jäderholm, 1904) and *O. obscura* Peña Cantero, Svoboda and Vervoort, 1997 (cf. Table 2). However, distinct differences are apparent. Both *O. antarctica* and *O. obscura* have an infrathecal, scale-shaped nematotheca on the hydrocladial internodes, a node between the cauline apophyses and the hydrocladia and a different hydrothecal shape. *Oswaldella obscura*, moreover, has polysiphonic, branched stems.

The differences from the remaining species of the genus are even greater (cf. Table 2).

Ecology and distribution. *Oswaldella crassa* sp. nov. seems to be a deep-water, probably bathyal, species, having been collected from 662 to 1120 m depth. The fertile material was collected in January. *Oswaldella crassa* sp. nov. originates from the Bransfield Strait area (62°41′–62°39′S; 57°51′–57°46′W).

Etymology. The specific name, *crassa*, has been taken from the latin adjective ''crassus'' meaning thick and refers to the thick, strongly developed perisarc of the colony.

Oswaldella curiosa sp. nov. (Fig. 2)

Material examined. ELTANIN 006-428, 5 January 1963, 62°41′–62°39′S, 57°51′–57°46′W, 662–1120 m, three stems up to 35 mm high (holotype, USNM no. 97230; paratype, RMNH-coel. 2785; slide 4032).

Description. Monosiphonic, feather-like stems, divided into internodes; occasionally nodes obscure because of strong development of perisarc. All stems deprived of basal part. Stems and hydrocladia brown, stems darker.

Cauline internodes normally with one or two apophyses, occasionally with three or four. Cauline apophyses alternately arranged in one plane and directed upwards at ca 45° (Fig. 2b).

Cauline apophyses supporting hydrocladia without any distinct separation between them (Fig. 2a,b). Each apophysis with a single naked nematophore emerging through a perisarc hole placed at axil between apophysis and stem (Fig. 2a,b).

Table 2 Major features of the known species of *Oswaldella* Stechow, 1919. (*) indicates that the situation may occasionally be contrary

	Polysiphony	Branched stem	Divided stem	Angle between cauline apophyses and stem	Mesial inferior nematotheca	Number of axillary nemato-phores	Number of mamelons	Maximal order of hydrocladia	Hydrotheca	Hydro-thecal aperture	Node between apophyses and hydrocladia	Position of hydrotheca on internode
O. antarctica (Jäderholm, 1904)	No	No	Yes	45°	Yes	2	1	4th	High	Even	Yes	On the middle
O. bifurca (Hartlaub, 1904)	No	No(*)	Yes	70°	No	1	0	4th	Low	Frontally depressed	No	Basal third
O. billardi Briggs, 1938	No	No	Yes	45°	Yes	2	0	2nd	High	Adcaudally directed	Yes	Distal half
O. blanconae El Beshbeeshy, 1991	No	No	Yes	45°	No	1	1	2nd	Low	Even	Yes	Basal third
O. delicata Peña Cantero et al., 1997	No	No	Yes	45°	Yes	1	0	2nd	High	Even	Yes	On the middle
O. elongata Peña Cantero et al., 1995	No	No	Yes	45°	No	2	2	2nd	High	Even	Yes	On the middle
O. encarnae Peña Cantero et al., 1997	No	No	Yes	45°	Yes	2	0	1st	Low	Even	Yes	On the middle
O. erratum Peña Cantero and Vervoort, 1997	Yes	No	No	70–80°	Yes	2	0	4th	High	Adcaudally directed	No	On the middle
O. garciacarrascosai Peña Cantero et al., 1997	No	No	Yes	45°	No	2	1	2nd	High	Even	Yes	On the middle
O. gracilis Peña Cantero et al., 1997	No	No	Yes	45°	Yes	1	0	1st	Low	Laterally depressed	Yes	On the middle
O. grandis Peña Cantero et al., 1997	Yes	No	Yes(*)	45°	Yes	2	2	3rd	Low	Even	Yes	Distal half
O. herwigi El Beshbeeshy, 1991	No	Yes	Yes	45°	Yes	1	1	2nd	Low	Even	Yes	Distal third
O. incognita Peña Cantero et al., 1997	No	No	Yes	45°	Yes	2	0	2nd	High	Even	No	On the middle
O. obscura Peña Cantero et al., 1997	Yes	Yes	Yes(*)	45°	Yes	2	1	2nd	High	Even	Yes	On the middle
O. rigida Peña Cantero et al., 1997	No	Yes	Yes(*)	70–90°	Yes	2	0	3rd	High	Adcauline elevation	No	On the middle
O. shetlandica Stepan'yants, 1979	Yes	Yes	Yes	45°	No	2	2	4th	High	Adcaudally directed	No	On the middle
O. stepanjantsae El Beshbeeshy, 1991	Yes	Yes	Yes	45°	Yes	4–2	2–0	3rd	High	Even	Yes	On the middle

Table 2 (continued)

	Polysiphony	Branched stem	Divided stem	Angle between cauline apophyses and stem	Mesial inferior nematotheca	Number of axillary nemato-phores	Number of mamelons	Maximal order of hydrocladia	Hydrotheca	Hydro-thecal aperture	Node between apophyses and hydrocladia	Position of hydrotheca on internode
O. terranovae Peña Cantero and Vervoort, 1996	No	Yes	Yes	45°	Yes	2	2	3rd	High	Even	Yes	On the middle
O. tottoni Peña Cantero and Vervoort, 1996	No	No	Yes(*)	45°	Yes	2	0	2nd	Low	Even	Yes	Distal half
O. crassa sp. nov.	?	?	No	45°	No	2	1	3rd	High	Adcaudally directed	No	On the middle
O. curiosa sp. nov.	No	?	Yes	45°	No	1	0	3rd	High	Abcaudally directed	No	On the middle

Hydrocladia short, scarcely developed (Fig. 2a), with up to five hydrothecae. Branching of hydrocladia asymmetrical (Fig. 2a); first hydrocladial internode forked, giving rise to two secondary hydrocladia. One of these much more developed and supporting up to three tertiary hydrocladia, the other second-order hydrocladium giving rise to a single third-order hydrocladium. Last hydrocladial internodes with a sharp tip (Fig. 2a,c–f).

Hydrocladia irregularly divided into hydrothecate internodes (Fig. 2a). "Normal", unforked internodes with one hydrotheca and two naked nematophores (Fig. 2c–f): one mesial superior emerging through a circular perisarc hole placed behind free part of adcauline hydrothecal wall; second mesial inferior, emerging through a perisarc hole situated on strongly elevated part of internode and deprived of nematotheca. Other unforked hydrocladial internodes with a varied number of hydrothecae and with two naked nematophores associated with each hydrotheca and with a disposition identical to that in "normal", unforked hydrocladial internodes (Fig. 2c–e).

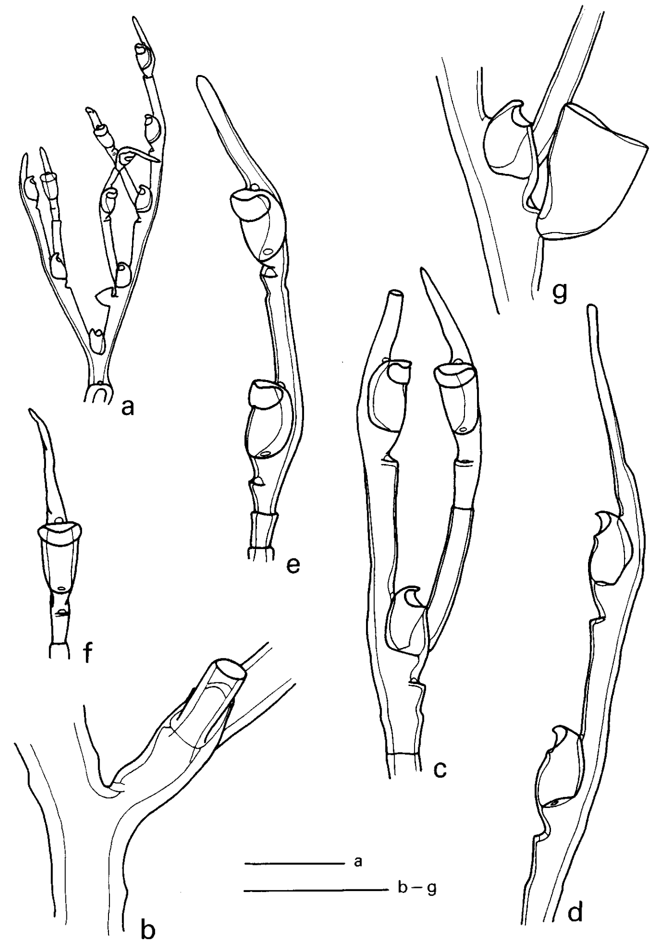


Fig. 2a–g *Oswaldella curiosa* sp. nov. **a** Branch showing hydrocladial branching and hydrothecal disposition; **b** cauline apophysis with axillary nematophore; **c–f** hydrocladial internodes with hydrotheca and mesial superior and mesial inferior nematophores; **g** hydrocladial internode with gonotheca. Scale bars: **a** 1 mm; **b–g** 500 μm

Hydrotheca of a peculiar shape (Fig. 2c–g). Abcauline wall convex; adcauline wall with large, convex free part. Hydrothecal aperture strongly laterally depressed and directed abcaudally, being perpendicular to longitudinal axis of hydrotheca.

Immature, inverted cone-shaped gonothecae present (Fig. 2g), inserted on hydrocladial internodes, just under mesial inferior nematophore.

Remarks. *Oswaldella curiosa* sp. nov. is unique and remarkable by the shape of the hydrotheca. It is the only known species of the genus that has the hydrothecal aperture completely directed abcaudally, perpendicular to the longitudinal axis of the hydrotheca, and strongly laterally depressed. This gives the species a distinctive appearance. *Oswaldella curiosa* sp. nov. is also distinctive in its asymmetrical hydrocladial branching pattern, with one secondary hydrocladium much more developed than the another. In this last character *O. curiosa* sp. nov. is allied to *O. herwigi* El Beshbeeshy, 1991, since in the latter the primary hydrocladium gives rise to several secondary hydrocladia that do not branch. However, they are clearly different because in *O. herwigi* there is an alternate series of ahydrothecate and hydrothecate hydrocladial internodes.

By the presence of a single axillary nematophore emerging through a perisarc hole in the cauline apophyses and the stem being divided into internodes, *Oswaldella curiosa* sp. nov. is allied to *O. bifurca* (Hartlaub, 1904), *O. delicata* Peña Cantero, Svoboda and Vervoort, 1997 and *O. gracilis* Peña Cantero, Svoboda and Vervoort, 1997 (cf. Table 2). *Oswaldella bifurca* also shares with *O. curiosa* sp. nov. the absence of an infrathecal scale-shaped nematotheca on the hydrocladial internodes and the absence of a node between cauline apophyses and hydrocladia. In addition to hydrothecal shape, they also differ in that the hydrothecae of *O. bifurca* are placed on the basal third of the hydrocladial internodes and the angle between cauline apophyses and stem is ca 70°. The differences from the other two species are greater, since both have an in-

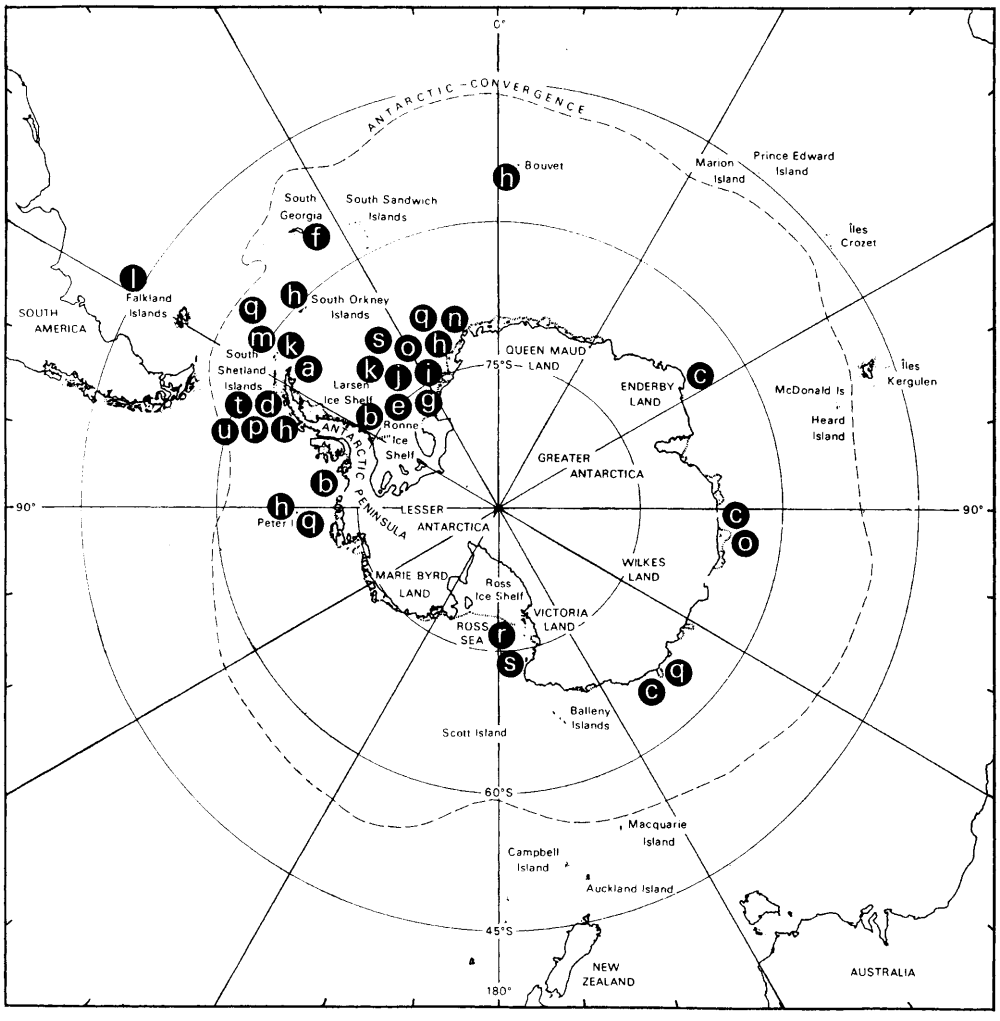
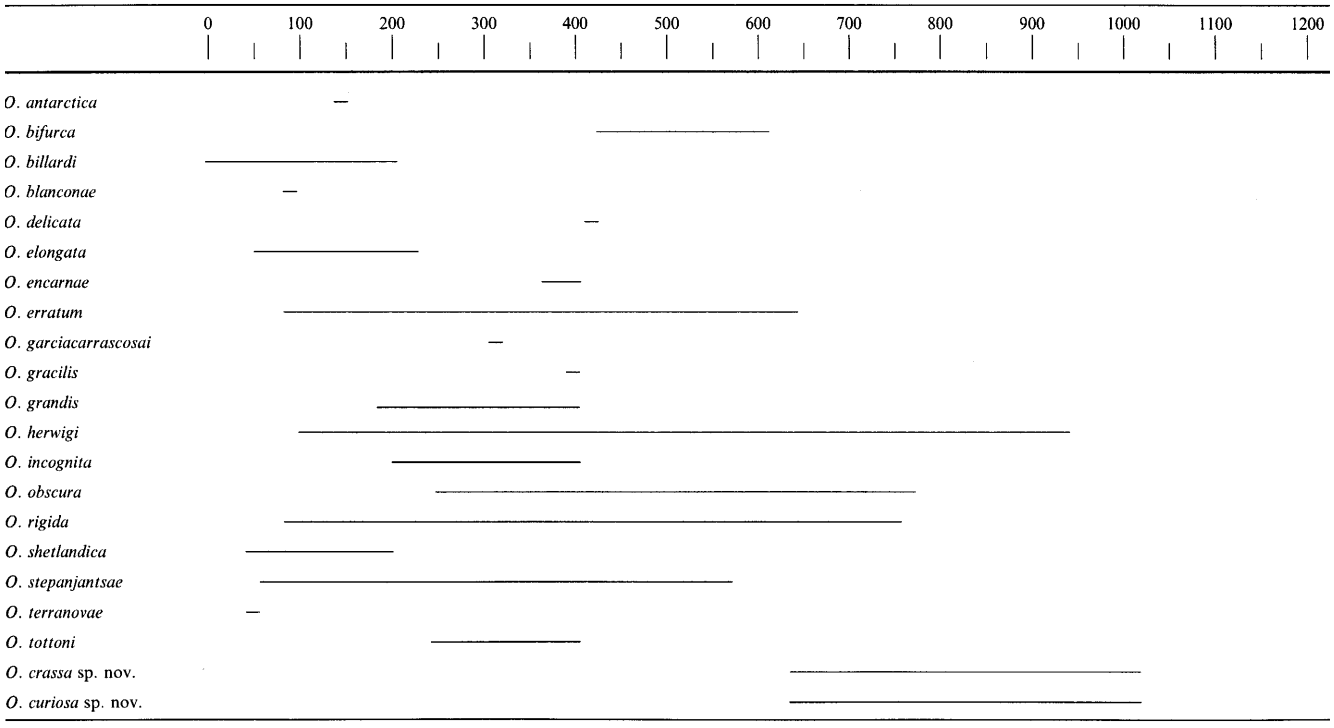


Fig. 3 Geographical distribution of the known antarctic and subantarctic species of *Oswaldella* Stechow, 1919. (*a O. antarctica*, *b O. bifurca*, *c O. billardi*, *d O. blanconae*, *e O. delicata*, *f O. elongata*, *g O. encarnae*, *h O. erratum*, *i O. garciacarrascosai*, *j O. gracilis*, *k O. grandis*, *l O. herwigi*, *m O. incognita*, *n O. obscura*, *o O. rigida*, *p O. shetlandica*, *q O. stepanjantsae*, *r O. terranovae*, *s O. tottoni*, *t O. crassa* sp. nov., *u O. curiosa* sp. nov.)

Table 3 Bathymetrical distribution of the known species of *Oswaldella* Stechow, 1919 (in meters)



frathecal scale-shaped nematotheca on the hydrocladial internodes and they have a distinct node separating the cauline apophyses from the hydrocladia. Moreover, only secondary hydrocladia have been reported in *O. delicata* and first-order hydrocladia in *O. gracilis*.

The differences with the remaining species of the genus are even larger (cf. Table 2).

Ecology and distribution. *Oswaldella curiosa* sp. nov. is a deep-water, probably bathyal, species collected from depths of 662 to 1120 m. The fertile colonies were obtained in January. *Oswaldella curiosa* sp. nov. comes from the Bransfield Strait area (62°41′–62°39′S, 57°51′–57°46′W).

Etymology. The specific name *curiosa* is taken from the latin adjective "curiosus" meaning strange, curious, and refers to the peculiar shape of the hydrotheca.

Geographical and bathymetrical remarks

With these remarks we emphasize the importance of the genus *Oswaldella* in the antarctic benthic ecosystem. Evidently, the present distribution of the species is based on fairly scarce data; we are certain that future surveys in poorly known areas of the Antarctic will extend the distribution of some species known at present.

Figure 3 illustrates the geographical records of the 21 known species of *Oswaldella*. Nearly all the species are endemics to the antarctic region, the majority being restricted to the continental antarctic region (high Antarctica and Scotia Ridge). Only one species (*Oswaldella herwigi*) has been reported outside the antarctic region, having a patagonian distribution. This species has been recorded from the area between 40°57′–50°06′S and 56°47′–65°36′W (cf. El Beshbeeshy 1991).

Of the 20 endemic antarctic species, only 3 (*Oswaldella rigida*, *O. stepanjantsae* and *O. tottoni*) are presumed to have a circumantarctic distribution (i.e. present both in east and west Antarctica). *Oswaldella rigida* has been reported both in the Davis Sea and in the Weddell Sea (cf. Peña Cantero et al. 1997); *O. stepanjantsae* has been found both in east Antarctica (off Adélie Coast), and in west Antarctica (Weddell Sea and off Elephant and Peter I Islands) (cf. Peña Cantero et al. 1997), and *O. tottoni* has been reported from both the Ross Sea and the Weddell Sea (cf. Peña Cantero et al. 1997).

Of the remaining 17 species, only 2 (*Oswaldella billardi* and *O. terranovae*) may be considered endemic in east Antarctica. *Oswaldella billardi* has been reported from the Davis Sea, off Queen Mary Coast and Enderby Land and from off the Adélie Coast (cf. Peña Cantero and Vervoort 1997); *O. terranovae* is, at least for the present, considered endemic in the Ross Sea, where it was found by Totton (1930) (cf. Peña Cantero and Vervoort 1996).

The remaining 15 species are endemic in west Antarctica. *Oswaldella erratum* has been recorded at the Antarctic Peninsula, off Peter I, Petermann and South Orkney Islands and in the Weddell Sea, but also off Bouvet Island at the limits of the antarctic region (cf. Peña Cantero and Vervoort 1997). *Oswaldella*

bifurca has been reported both from the Bellingshausen Sea (Hartlaub 1904) and from the Weddell Sea (Peña Cantero et al. 1997). *Oswaldella grandis* is known from both the Weddell Sea and the Elephant Island area (cf. Peña Cantero et al. 1997). Five species (*Oswaldella delicata*, *O. encarnae*, *O. garciacarrascosai*, *O. gracilis* and *O. obscura*) are only known from the Weddell Sea (cf. Peña Cantero et al. 1997). Six species (*Oswaldella antarctica*, *O. blanconae*, *O. incognita*, *O. shetlandica*, *O. crassa* sp. nov. and *O. curiosa* sp. nov.) have only been found in the area of the Antarctic Peninsula and the South Shetlands Islands: *O. antarctica* at Seymour Island (cf. Peña Cantero and Vervoort 1995); *O. blanconae* at Low Island (cf. El Beshbeeshy 1991); *O. incognita* at Elephant Island (cf. Peña Cantero et al. 1997); *O. shetlandica* at King George and Low Islands (South Shetland Islands) (cf. Peña Cantero et al. 1995); and *O. crassa* sp. nov and *O. curiosa* sp. nov. from Bransfield Strait (present material). Finally, the remaining species, *O. elongata*, is only known from off South Georgia (cf. Peña Cantero et al. 1995), which is usually considered a separate district of the continental antarctic region.

As shown in Fig. 3, there is a distinct asymmetrical distribution in the number of species both in east and west Antarctica. This undoubtedly reflects which of the two areas has been more intensively studied. However, it may also indicate that the speciation centre for the genus is located in the area of west Antarctica.

At present, *Oswaldella* appears to be essentially an antarctic genus, since only one known representative (*O. herwigi*) is found outside the antarctic region, having a patagonian distribution. The present distribution of the species makes it appear likely that *Oswaldella* is a genus originating in the antarctic region.

Nearly all antarctic species of *Oswaldella* seem to be shelf species (cf. Table 3). Though many have a wide bathymetrical range, their deepest records are either over, or at the limit of, the antarctic continental shelf-break, which occurs much deeper than in other oceanic regions (e.g. at 800-m depth in the Ross Sea). Only *O. crassa* sp. nov. and *O. curiosa* sp. nov. seem to be bathyal species (see above).

The species with a patagonian distribution, *Oswaldella herwigi*, is the only species that may be considered strictly eurybathic, being present both on the continental shelf and on bathyal bottoms, having been recorded from 90 to 1000 m depth (El Beshbeeshy 1991).

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