

A revision of the deep-sea genus *Axiokebuita* Pocklington and Fournier, 1987 (Annelida: Scalibregmatidae)

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Abstract

The deep-sea genus *Axiokebuita* (Annelida, Scalibregmatidae) has hitherto been considered to contain two species, *Axiokebuita minuta* (Hartman, 1967) and *Axiokebuita millsii* Pocklington and Fournier, 1987, each rarely recorded in the literature and both supposedly having bipolar distributions. From the study of some types, other museum collection material, plus newly collected specimens from the slope depths of the Bellingshausen Sea and off the Antarctic Peninsula (Antarctica), Iceland and Iberian Peninsula, as well as from hydrothermal vents of the southeastern Pacific Ocean, the taxonomic history of the genus is revisited. Based on the results of this study, the features traditionally used to distinguish between the two species are actually the same in both. Therefore, *A. millsii* is proposed to be synonymised with *A. minuta*, which is redescribed and considered the only valid species of the genus, leaving *Axiokebuita* monotypic. Two previously unnoticed body sensory structures, i.e. a ciliated neck organ and a prostomial depression, were observed under scanning electron microscopy.

Keywords: Polychaeta, *Scalibregmatidae* *Axiokebuita*, *A. minuta*, *A. millsii*, revision, molecular taxonomy, Antarctica, hydrothermal vents, deep sea.

Introduction

The genus *Axiokebuita* (Scalibregmatidae) was erected by Pocklington and Fournier (1987) for a new species collected from the slope depths off eastern Canada, *Axiokebuita millsii* Pocklington and Fournier, 1987. These authors also proposed the inclusion of *Kebuita minuta* Hartman, 1967, described from South Orkney Islands, in this new genus. They also indicated that some Antarctic specimens, previously identified as *Kebuita minuta* by Hartman (1978) and Blake (1981), were actually

Axiokebuïta millsii. As a result of this, *A. millsii* was considered to have a bipolar distribution and this fact was reflected in the etymology of the genus ('Axio' in Latin meaning 'the pole'). According to Pocklington and Fournier (1987), the two species are essentially distinguished by the presence of a globular notopodial cirrus in *A. millsii*, which was supposed to be absent in *A. minuta*. Recently, Persson and Pleijel (2005) collected additional specimens of *Axiokebuïta* from Norwegian waters. They studied the taxonomic affinities between both species and also assessed the phylogenetic relationships of the genus with other scalibregmatids using the nuclear genes 18S rDNA and 28S rDNA. They concluded that the Norwegian specimens could not be referred to either of the two known species due to delineation problems between the taxa and the poor condition of the holotype of *A. minuta*. They believe that 'without access to further specimens in good conditions from type locality of *A. minuta*, it is difficult to state if the separation between the two can be corroborated by other features'.

In the present study, new material of *Axiokebuïta* mainly collected in the Bellingshausen Sea (BS) and Weddell Sea (WS) and west coast of the Antarctic Peninsula (BENTART-06 and ANDEEP II cruises) was studied. These specimens were compared with type specimens of both species, other material from southwest Iceland (BIOICE project) and northwestern Iberian Peninsula (DIVA-Artabria II project) continental slope, hydrothermal vents of the southeast Pacific Ocean, as well as relevant museum specimens. As a result of this, *Axiokebuïta millsii* is proposed as a junior synonym of *A. minuta* and a redescription of the species is presented.

Materials and methods

The present work is largely based on Antarctic specimens collected during the BENTART project (2006 cruise) aboard the R/V *Hesperides* (2 January to 17 February 2006). A total of 13 stations located in the Bellingshausen Sea and Antarctic Peninsula were sampled using a modified version (Cartes et al. 1994) of the Macer-GIROQ suprabenthic sled (Brunel et al. 1978 ; Dauvin & Lorgere 1989). Description of sampling methodology can be found in San Vicente et al. (2007) and Corbera et al. (2009). Data concerning sampling positions, dates and water depth are reported in Table I. Sorting of samples was carried out onboard and specimens were fixed in 4% formalin and then transferred in 70% ethanol. Specimens used for scanning electron microscopy (SEM) were dehydrated via a graded ethanol series, critical-point dried using CO₂, covered with gold in a sputter coater and examined and photographed under a JEOL JSM-6400 scanning electron microscope at the SAIN (Servicio de Apoio á Investigación), Universidade da Coruña, Spain (UDC). This material was augmented by one specimen from hydrothermal vents of the southeastern Pacific Ocean and the loan of two specimens from the BIOICE and DIVA-Artabria II projects in Iceland and the Iberian Peninsula, respectively. Comparative material included several ANDEEP II specimens from the Weddell Sea and South Sandwich Islands (Antarctica) and material from Museum collections, including Hartman's and Pocklington and Fournier's type material.

Genomic DNA was extracted from a single specimen collected in the southeast Pacific and ethanol-preserved, using a Qiagen DNeasy tissue kit (Valencia, CA). Just over 1000 base pairs of the small subunit ribosomal DNA (*18S*) and approximately 650 base pairs of the mitochondrial *COI* gene were amplified using primers and protocols as outlined in (Osborn & Rouse 2011). All sequencing was carried out by Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) at the University of Hawaii at Manoa using Applied Biosystems BigDye terminator chemistry and an ABI 3730XL sequencer.

Table I. Coordinates and depth (referred to the start of the tow) of locations where new material of *Axiokebuta* was sampled. (*) *Alvin* dive number

	Location	Cruise	Ship	Station	Date	Latitude	Longitude	Depth (m)	Specimens
North Atlantic	Southwest Iceland	BIOICE	<i>Bjarni Sæmundsson</i>	2410	20 July 1993	62.86000 N	-21.735000 W	1074	1
	Northwest Spain	DIVA-Artabria II	<i>Sarmiento de Gamboa</i>	27	05 October 2009	42°42.8406'N	11°49.7939'W	764.9	1
Southeast Pacific	Easter Island		<i>Alvin</i>	4097*	02 April 2005	23°49.396'S	115°27.348'W	2649	1
Antarctica	Weddell Sea	ANDEEP II	<i>Polarstern</i>	131-3	05 March 2002	65°19.83'S	51°31.62'W	3049	3
	South Sandwich Islands			143-1	25 March 2002	58°44.69'S	25°10.27'W	774	3
	Bellingshausen Sea	BENTART-06	<i>Hesperides</i>	30	26 January 2006	69°58.404'S	87°26.892'W	1799	35
	Bellingshausen Sea			31	28 January 2006	69°57.760'S	86°22.134'W	1395	18
	Bellingshausen Sea			34	01 February 2006	70°06.026'S	84°52.617'W	620	3
	Bellingshausen Sea			35	31 January 2006	69°55.617'S	85°09.209'W	1136	5
	Bellingshausen Sea			38	04 February 2006	69°15.184'S	80°12.184'W	1339	3
	Antarctic Peninsula			42	10 February 2006	65°09.969'S	68°56.012'W	1272	1

Specimens were deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN), Scripps Institution of Oceanography (SIO-BIC) and Stazione Zoologica Anton Dohrn, Napoli (SZN). For comparative purposes, additional material from the German ANDEEP II expeditions to the Antarctica (Brandt & Hilbig 2004) and the coast of Norway (Persson & Pleijel 2005) was loaned by the Deutsches Zentrum für Marine Biodiversitätsforschung-Senckenberg Forschungsinstitut und Naturmuseum (DZMB) and the Naturhistoriska Riksmuseet-Stockholm (SMNH), respectively.

Results

Family Scalibregmatidae Malmgren, 1867

Genus *Axiokebuitta* Pocklington and Fournier, 1987.

Axiokebuitta minuta (Hartman, 1967)

Kebuitta minuta. Hartman 1967: 131–132; Hartman 1978: 179, fig. 27a,b; Blake 1981: 1153–1154, fig. 11a,b.

Axiokebuitta millsii. Pocklington and Fournier 1987: 108, figs. 1, 2. Blake & Hilbig 1995: 242, fig. 13a–c.

Axiokebuitta. sp. Persson and Pleijel 2005 : 8, figs. 1, 2.

Material examined

This study is based on 74 specimens mostly collected in the Antarctic Seas during Spanish and German cruises but also in the Atlantic Ocean (southwest Iceland, northwest Spain) and the eastern Pacific Ocean (near Easter Island) (Table I, Figure 1). In addition, for comparison purposes, type specimens of both species and nine Norwegian non-type specimens from museum collection were also examined.

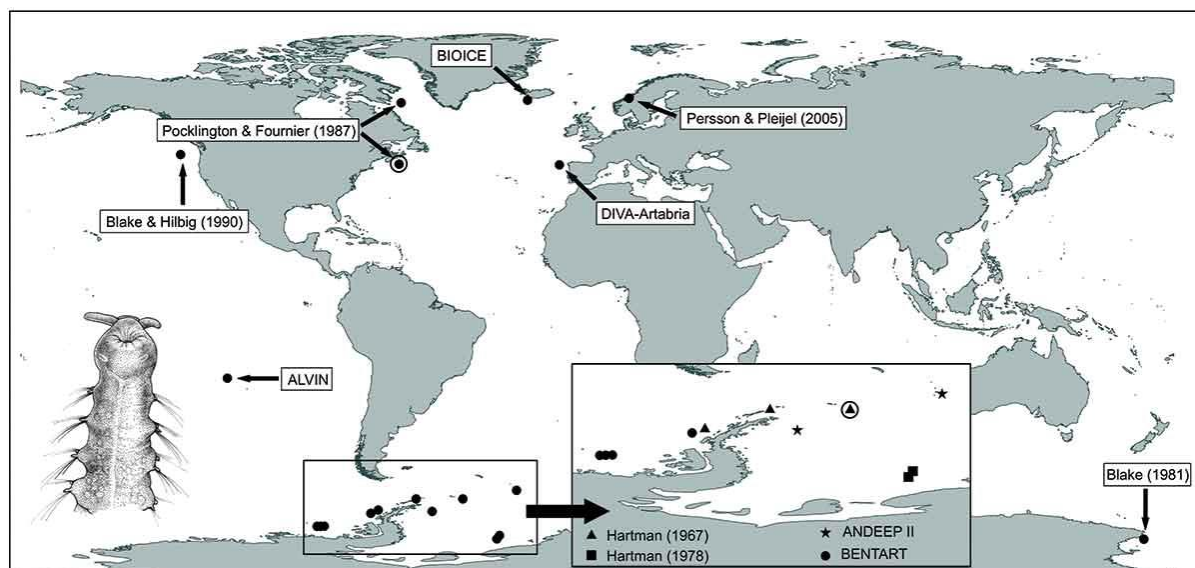


Figure 1. Positions of all the worldwide records of *Axiokebuitta* extracted from the literature, and newly collected material from Iceland (BIOICE cruise), Spain (DIVA–Artabria II cruise), SE Pacific (ALVIN dive) and Antarctica (BENTART–06 cruise). The boxed area is represented at a larger scale showing in detail the positions in the northwest Antarctic littoral. Encircled dot and triangle show positions of the type localities of *A. millsii* and *A. minuta*, respectively.

Axiokebuita minuta ICELAND: Southwest coast (BIOICE project, 1 specimen; MNCN 16.01/13603), IBERIAN PENINSULA: northwest coast (DIVA-Artabria II, corals with sand, 1 specimen used for DNA extraction). SOUTH-EAST PACIFIC (DSV *Alvin*; around 700 km northwest of Easter Island, rock fissures and mussel clumps near active venting areas, 1 specimen; middle part used for DNA sequencing, the anterior and posterior MNCN 16.01/13602). ANTARCTICA: Scotia Sea (USNM 56625, 62°25'S, 56°30'–56°32'W, 300 m deep, coll. USNS *Eltanin*, 13 March 1964; 1 paratype including 2 slides with parapodia). Weddell Sea (ANDEEP II cruise): DZMB 79-0077 and 79-0081(stat. 131-3, 2 specimens); MNCN 16.01/13601 (DZMB 79-0079; 1 specimen in SEM stub).

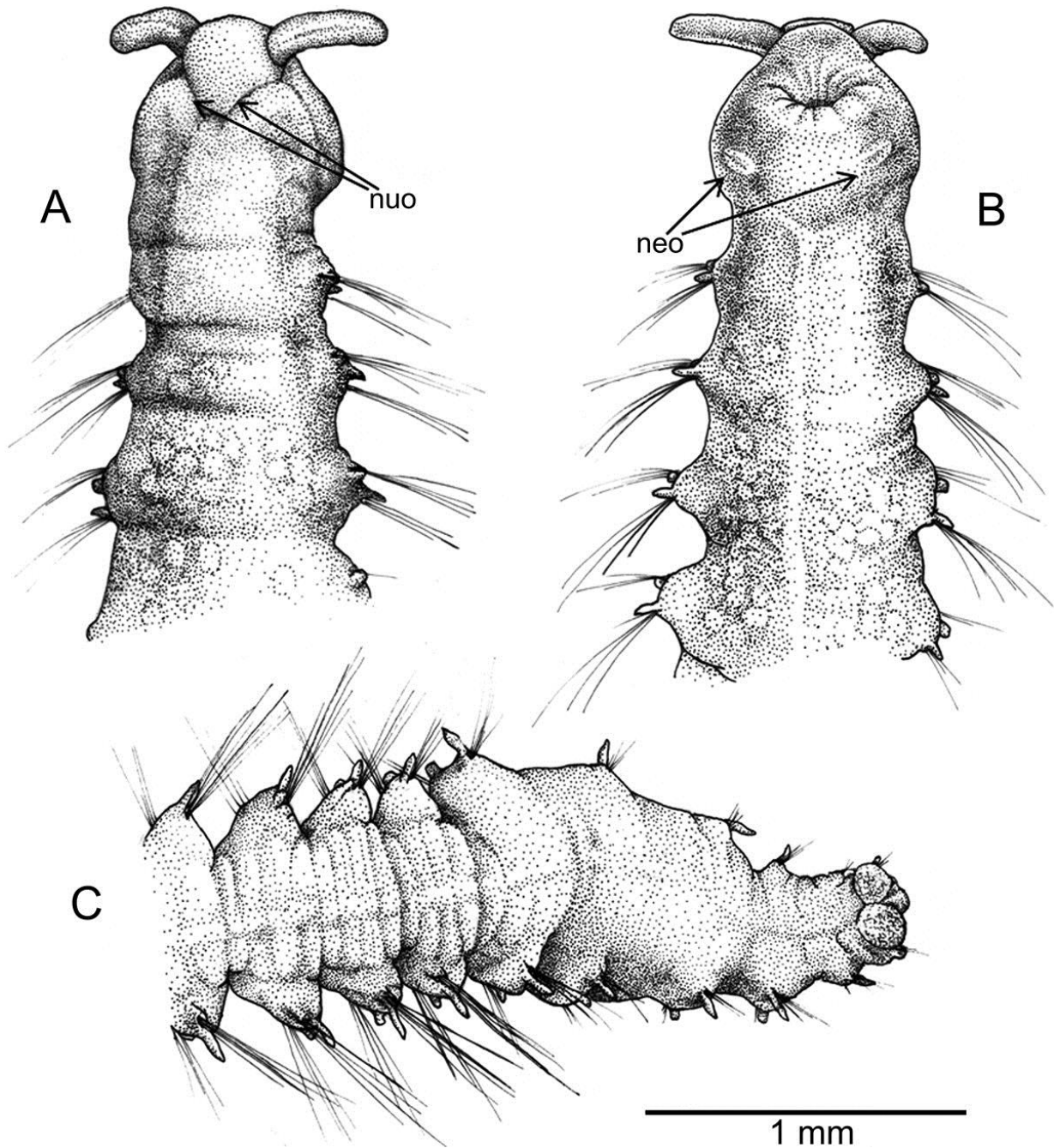


Figure 2. *Axiokebuita minuta*, Antarctic (Bellingshausen Sea) specimens from BENTART-06 cruise. MNCN 16.01/13600, (A) anterior end in dorsal view, (B) anterior end in ventral view, (C) posterior end in ventral view. nuo, nuchal organ; neo, neck organ. Oocytes could be seen through the body wall.

Bellingshausen Sea and West Antarctic peninsula (BENTART-06 cruise): MNCN 16.01/13596 (stat. MB30, 30 specimens). MNCN 16.01/13600 (stat. MB30, 5 specimens in 3 SEM stubs). MNCN 16.01/13597 (stat. MB31, 17 specimens). MNCN 16.01/13598 (stat. MB35, 5 specimens). MNCN 16.01/13599 (stat. PA42, 1 specimen). SZN 013 (stat. MB31, 1 specimen for TEM analysis; stat. MB 34, 3 specimens; MB38, 3 specimens).

Axiokebuita millsii ANTARCTICA: Ross Sea (USNM 60574, 73°59'S, 170°41'E-73°58'E, 170°58'S, 608 m deep, coll. USNS *Eltanin*, 13 January 1968; 1 paratype of *A. millsii*). South Sandwich Islands (ANDEEP II cruise): DZMB 79-0126, 79-0127 and 79-0128 (stat. 143-1, 3 specimens).

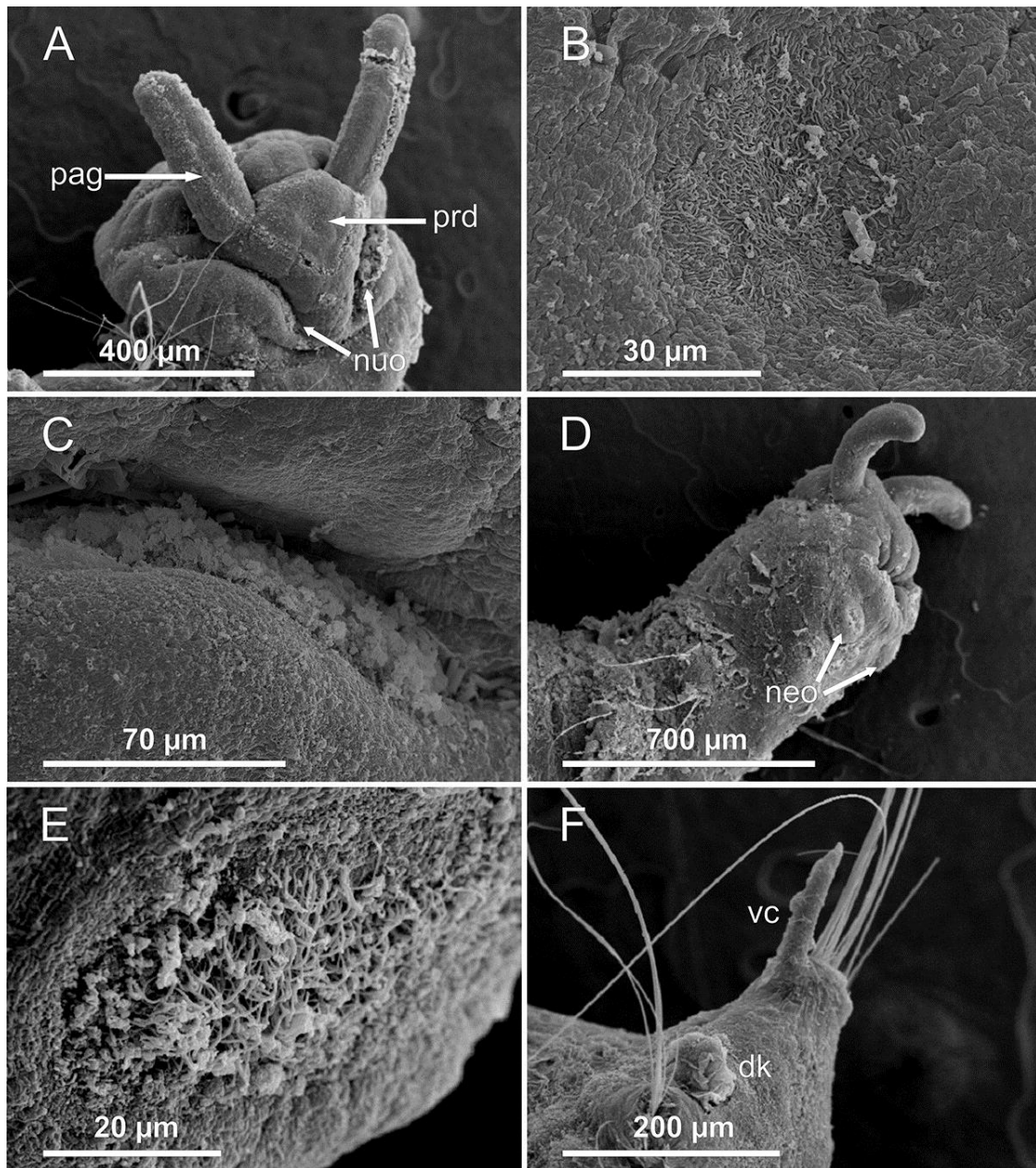


Figure 3. *Axiokebuita minuta*, Antarctic (Bellingshausen Sea) specimens from BENTART-06 cruise. MNCN 16.01/13600, (A) prostomium in dorsal view, (B) detail of prostomial depression, (C) detail of nuchal organ, (D) anterior end, ventro-lateral view, (E) detail of neck organ ciliation, (F) chaetiger 7. neo, neck organ; dk, dorsal knob; nuo, nuchal organ; prd, prostomial depression; pag, palp groove; vc, ventral cirrus.

Axiokebuita spec. NORWAY: Trondheim's fjord: SMNH 75817 (Rødberg, 63°28.36'N, 10°00.04'E, 180–250 m, *Lophelia* reef, triangular dredge, coll. F. Pleijel, 21 Feb 2003, 2 specimens). SMNH 75819 and 75820 (same locality data, 26 Feb 2003, 6 – one in SEM stub – and 1 specimens, respectively).

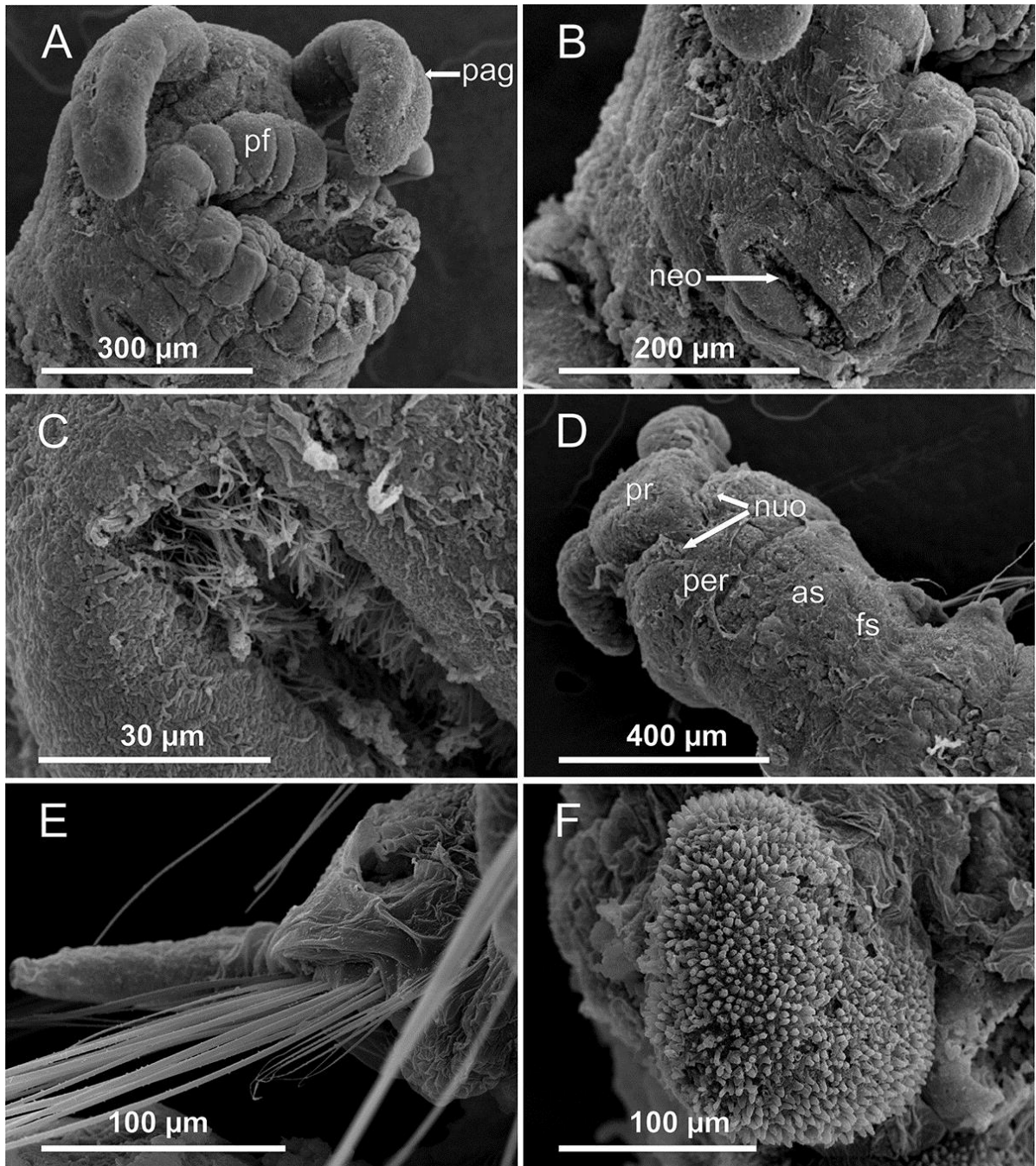


Figure 4. *Axiokebuita minuta*, Antarctic (Bellingshausen Sea) specimens from BENTART–06 cruise. MNCN 16.01/13600, (A) anterior end, antero-ventral view, (B) ventral neck organ, (C) detail of neck organ ciliation, (D) anterior end, dorsal view, (E) neurochaetae and ventral cirrus from chaetiger 14, (F) right pygidial lobe. as, achaetigerous segment; fs, first chaetiger; neo, neck organ; nuo, nuchal organ; pag, palp groove; per, peristomium; pf, proboscideal folds; pr, prostomium.

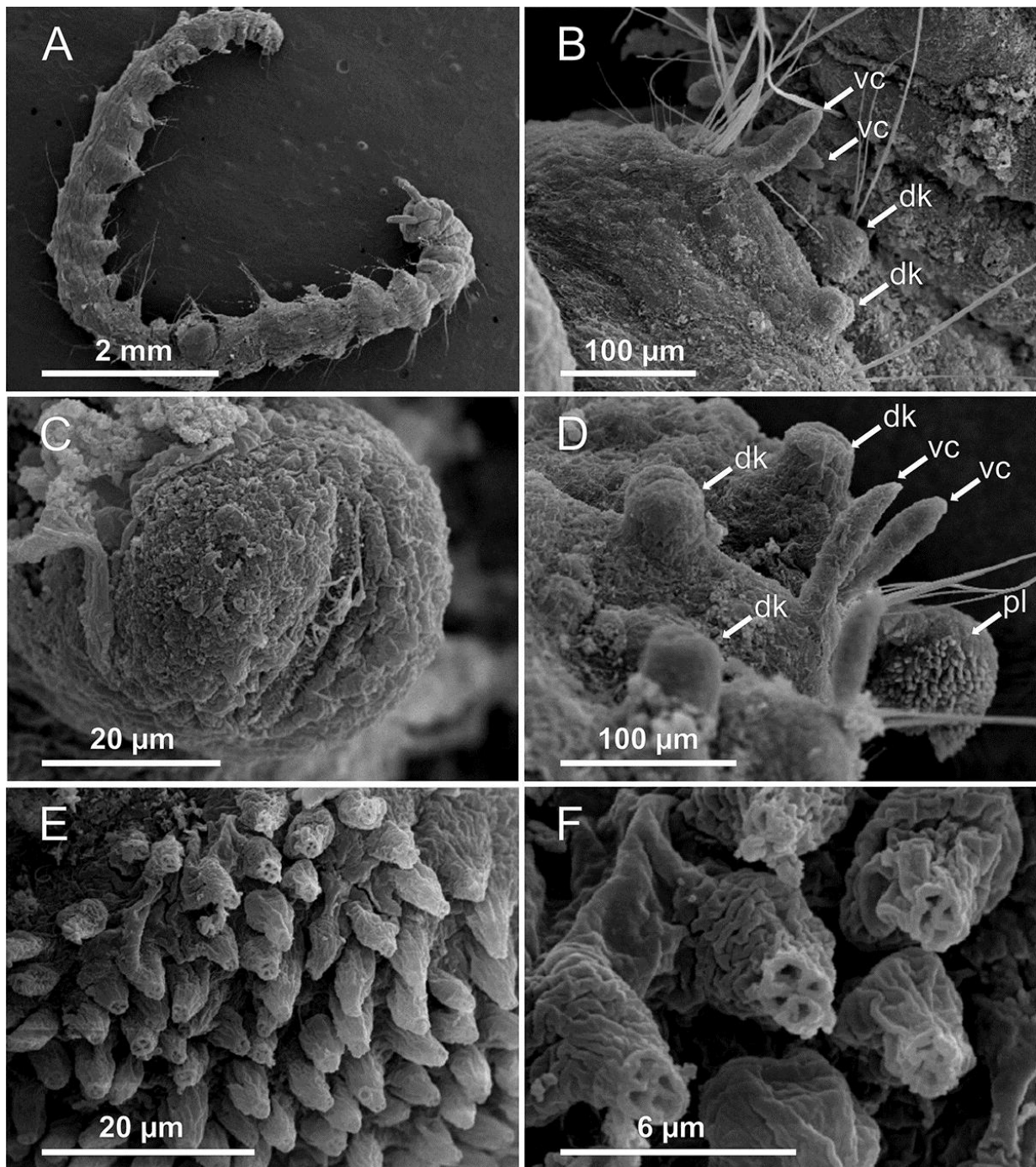


Figure 5. *Axiokebutia minuta*, Antarctic (Bellingshausen Sea) specimens from BENTART-06 cruise. MNCN 16.01/13600, (A) general view of the animal, (B) chaetiger 3, (C) chaetiger 20 notopodial knob with ciliation, (D) chaetigers 21–23 and pygidial lobe, (E,F) detail of pygidial adhesive papillae. dk, dorsal knob; pl, pygidial lobe; vc, ventral cirrus.

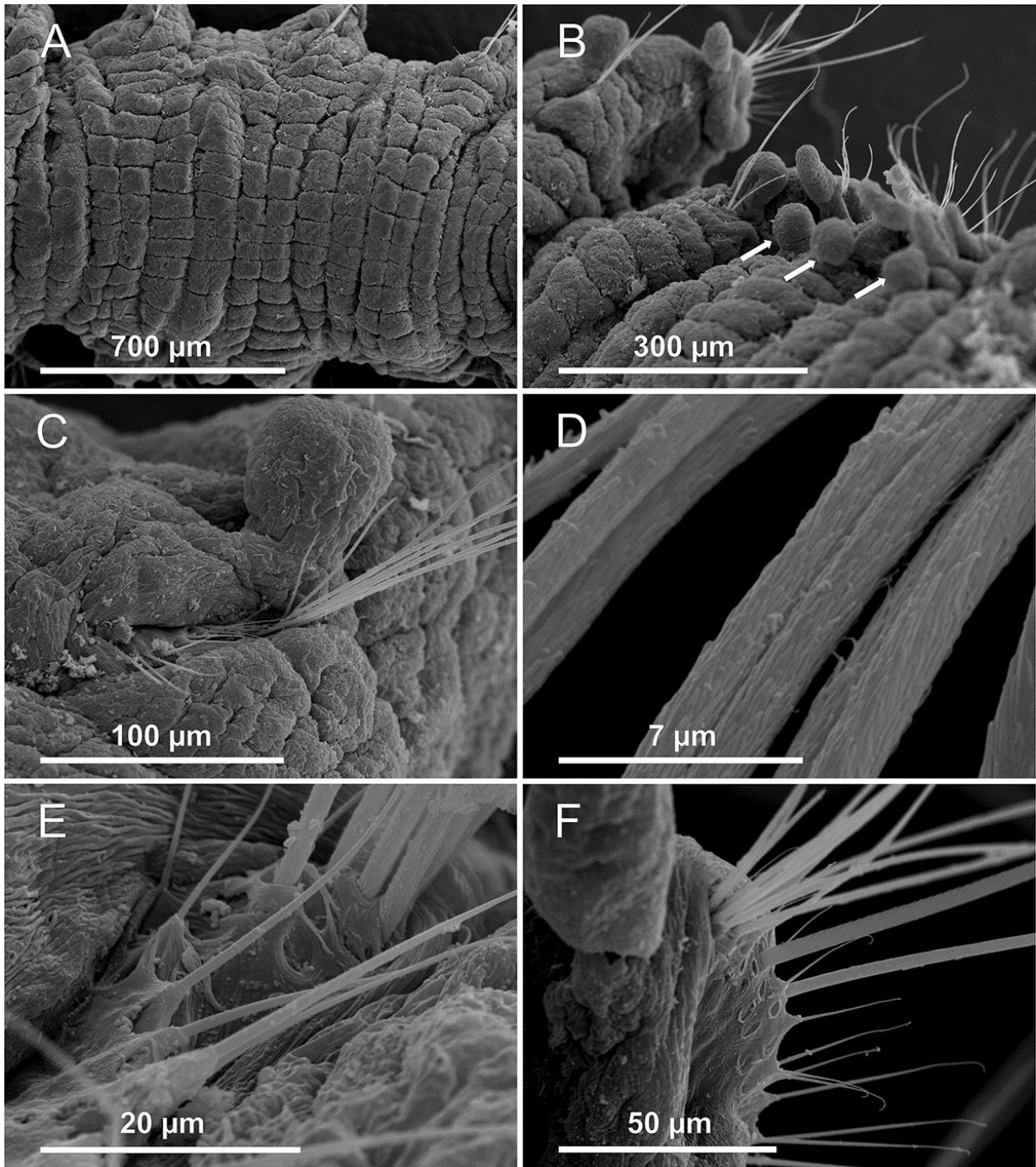


Figure 6. *Axiokebutia minuta*, Antarctic (Bellingshausen Sea) specimens from BENTART-06 cruise. MNCN 16.01/13600, (A) mid-body segments, dorsal view, (B) five posterior end segments, dorsal view, arrows marking three posterior achaetous notopodial rami, (C) detail of notochaetae from posterior chaetiger, (D) detail of scale covering of long notochaetae, (E) detail of short notochaetae, (F) neurochaetae from same chaetiger.

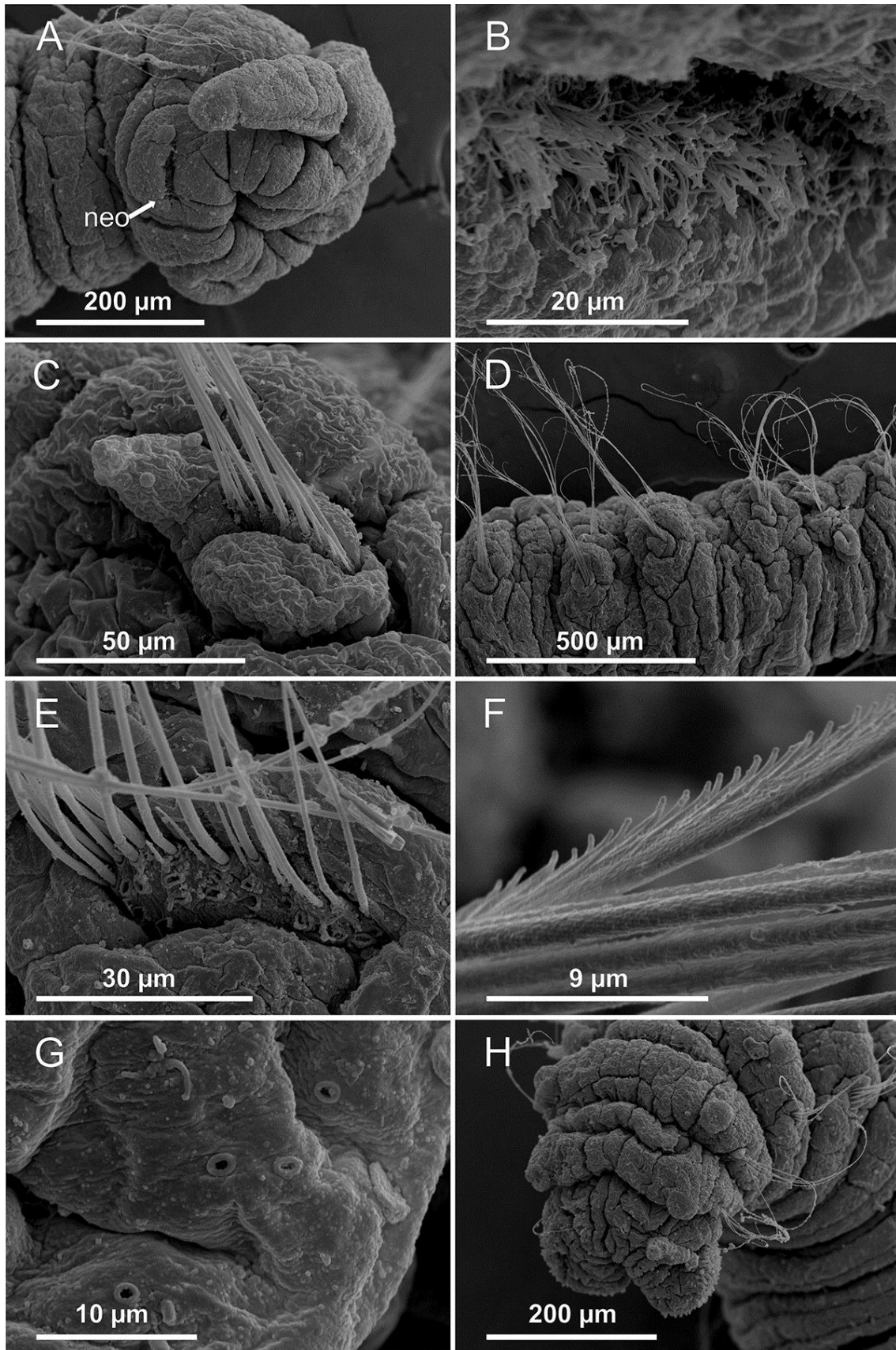


Figure 7. *Axiokebuitta* spec. sensu Persson and Pleijel (2005), Norwegian specimen. SMNH 75819, (A) anterior end, ventro-lateral view, (B) detail of neck organ, (C) neuropod of chaetiger 4, (D) neuropodia of chaetigers 5–10, (E) chaetiger 14 neurochaetae, (F) detail of neurochaetal serration, (G) detail of cuticle porous, (H) posterior end, latero-dorsal view. neo, neck organ.

Description of Bellingshausen specimens (BENTART-06) Body elongated, slightly tapered at both ends, swollen in middle (Figures 2, 5A). Specimens 8–13 mm long and 1.0–1.8 mm wide at widest part for 22–24 chaetigers. Prostomium pentagonal, with straight frontal margin bearing two distinct laterally directed and well delineated projections (palps) (Figures 2A, 3A); eyes lacking. Mid-dorsal prostomial depression observed with the SEM (Figure 3A,B). Nuchal organs bordering posterior part of prostomium (Figures 2A, 3A,C). Basal part of everted proboscis with longitudinal folds (Figures 2B, 4A). Peristomium complete ring, dorsally incised giving a biannulate appearance slightly larger than following segments (Figure 4D). Segment 1 achaetigerous; similar to following segments (Figure 4D). A pair of ciliated slits located ventrally on peristomium behind buccal opening (Figures 2B, 3D,E, 4B,C). Each segment with four annuli (Figure 6A). Parapodia similar throughout the body. Notopodia and neuropodia jointed on a vertically orientated parapodial extension; all chaetigers bearing notopodia provided with a small knob located ventrally to chaetal bundle (Hartman's ‘interramal cirri’ and Blake's ‘postchaetal lamella’; see Discussion) and neuropodia provided with digitate, distally pointed cirrus located dorsally to chaetal bundle (Figures 3F, 5B–D). A ciliated band visible with the SEM in the dorsal part of the notochaetal knob (Figure 5C). Notochaetae less numerous than neurochaetae; notochaetae disappear in the last three body chaetigers (Figure 6B). Two types of chaetae in both parapodial rami: long, slender capillaries in ventral part of notopodium and dorsal part of neuropodium and shorter and thinner capillaries in dorsal part of notopodium and ventral part of neuropodium (Figures 4E, 6C–F). Pygidium with two pad-shaped lobes (Figure 1C), densely covered with conical papillae (Figure 4F); each papilla terminating in four pores (Figure 5E,F).

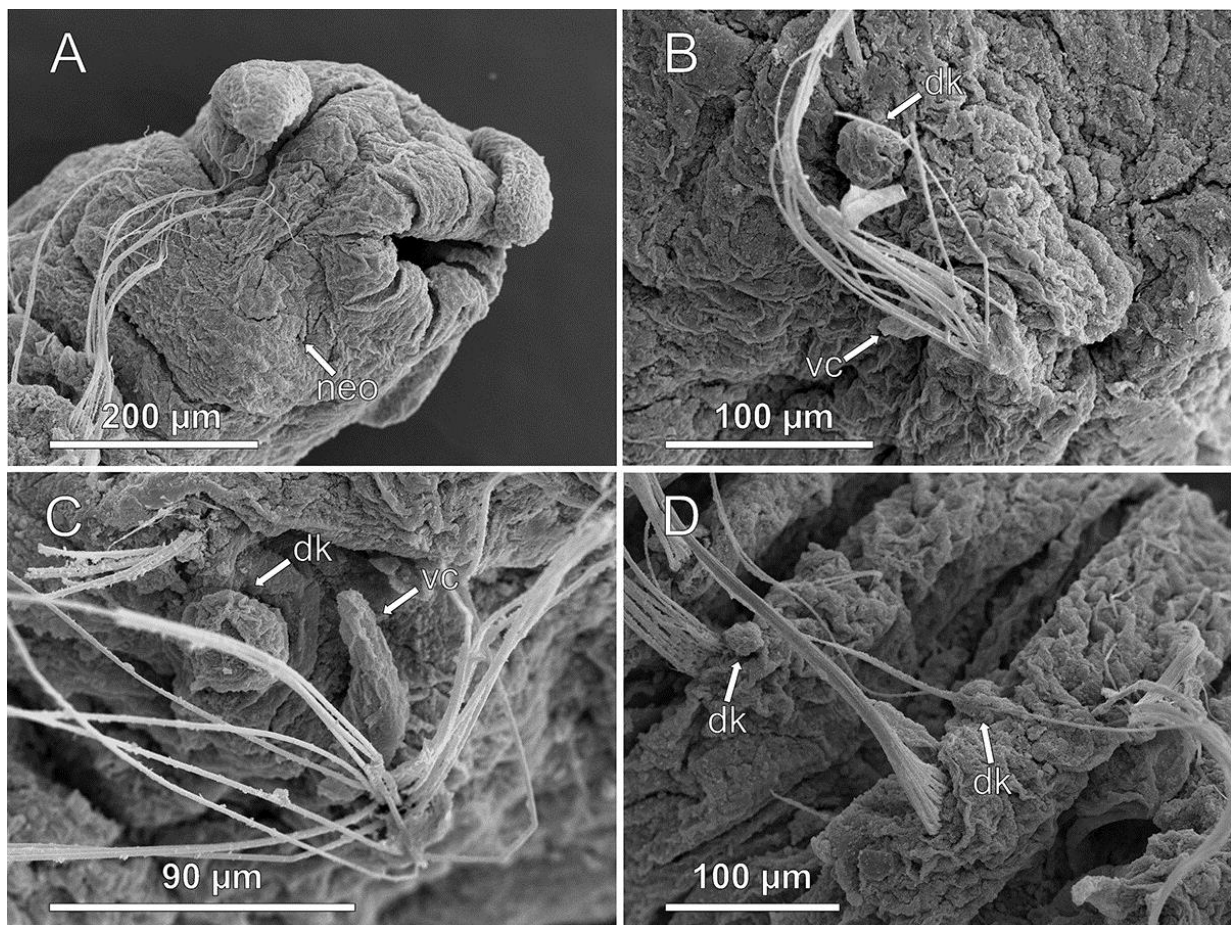


Figure 8. *Axiokebuita minuta sensu* Schüller and Ebbe (2007), Antarctic specimen from ANDEEP-II cruise. MNCN 16.01/13601, (A) anterior end, ventro-lateral view, (B,C) chaetigers 7 and 9, (D) chaetigers 18–19. neo, neck organ; dk, dorsal knob; vc, ventral cirrus.

The studied specimens from the Norwegian waters (Figure 7), Weddell Sea and South Sandwich Island waters (Figure 8) have the same body characteristics as those in the Bellingshausen Sea with the only exception of body size and chaetae. The European specimens are smaller (3–5 mm) than the BS specimens, but not that of the Weddell Sea (4–5 mm) and Ross Sea (6–7 mm) (see Pocklington & Fournier 1987 Pocklington, P and Fournier, JA. 1987. *Axiokebuita millsii*, new genus, new species, (Polychaeta: Scalibregmatidae) from eastern Canada. *Proceedings of the Biological Society of Washington*, 7: 108–113.), although in all cases the number of chaetigers is the same (22–25). In the North Atlantic specimens chaetae are longer than in Antarctic specimens (Figure 5A vs. 7D) and also the difference between long and short chaetae on each parapodial rami is much less pronounced (Figure 6F vs. 7C,E).

Re-examination of one paratype of *A. minuta* (USNM 56625) and one paratype of *A. millsii* (USNM 56625) did not reveal any difference among both species. The holotype of *A. minuta* (USNM 55553) was not examined but, as reported Persson and Pleijel (2005), the specimen is too poorly preserved to permit unequivocal assessment of any difference with *A. millsii* (e.g. presence or absence of notopodial lobes). *Axiokebuita minuta* paratype USNM 56625 is composed of two specimens: one is an *Axiokebuita* but the other is another scalibregmatid with furcate chaetae, from which the slide was made from (see Discussion). The *Axiokebuita* specimen is posteriorly incomplete, but the presence of globular notopodial cirri was confirmed. In *A. millsii* paratype USNM 60574 (slide and specimen) none of the supposed differences with *A. minuta* were apparent.

DNA sequence data

Unfortunately it was not possible to get adequate DNA extraction from any material except the specimen from the hydrothermal vents from the southeastern Pacific Ocean hydrothermal vent specimen. The specimen was divided into three fragments and the median fragment was used for molecular analysis. The anterior part, 4.0 mm long and 1.5 mm in its wider part, consists of prostomium, peristomium and 10 chaetigers. The posterior part was 2.0 mm long and 0.8 mm wide and 5 chaetigers. All prostomial, parapodial and pygidial features characteristic of *A. minuta* are present in this specimen. For this specimen, the partial 18S rDNA sequence (Genbank n. JN256053) showed 99% similarity with the 18s rDNA sequence for *Axiokebuita* sp. sequenced by Persson and Pleijel (2005), with only 6 bases different and 2 gaps. We also sequenced COI for the southeastern Pacific Ocean specimen and make this available on Genbank (n. JN256052) for future comparisons, but there are currently no other COI sequences available for *Axiokebuita*. DNA extractions for the specimen from the Iberian peninsula were attempted, but unfortunately failed to recover any usable DNA.

Reproduction

Pocklington and Fournier (1987) reported ovigerous females in specimens of *A. millsii* in July (North Atlantic) and January (Antarctica). Large eggs were observed through the tegument inside the body cavity in some of collected specimens in January 2006 in the BS. A single putative male specimen was used for TEM analysis (data not shown), but it did not reveal the occurrence of spermatids, or early or mature spermatozoa (M.C. Gambi, personal observation).

Ecology

The BS specimens were collected at various stations during the BENTART-06 cruise, exclusively with a suprabenthic sledge and occurred only on the lower net (located about 50 cm from the bottom). For the same stations where benthic material was collected with a box corer and Agassiz trawl many other

polychaetes were sampled, but not a single specimen of *Axiokebuita* occurred (Parapar et al. 2011a). Therefore the species probably thrives in the upper few centimetres of the sediment, and is so delicate that other tougher sampling gear destroyed the material. The species was collected in various stations located on the continental slope and deeper (from 620 to over 3000 m depth). The occurrence of *Axiokebuita* in deep hydrothermal vents habitat has previously been documented in the northeast Pacific for specimens identified as *A. millsii* by Blake and Hilbig (1990). These authors felt that *Axiokebuita* was unlikely to be a true vent taxon in terms of only being found at these habitats. The second record here of *Axiokebuita* from hydrothermal vents does not disprove this assertion until further material is acquired from various habitat and localities.

Distribution

On the basis of material collected and examined from museum collections, *A. minuta* appears to be present in all world oceans except the Indian Ocean, which may be due simply to the different sampling efforts. In terms of latitudinal distribution, the species seems to prefer high-latitude waters both boreal and austral, although again this may also be biased by lack of sampling. As presently known it is vertically distributed from 305 down to 3049 m depth.

Taxonomic remarks

The genus *Kebuita* Chamberlin, 1919 (Scalibregmatidae) was erected for *Kebuita glabra* (Ehlers, 1887), from off Havana (Cuba). Hartman (1967) did the first description of *Kebuita minuta* based on specimens from the South Orkney Islands (type locality) and off the Antarctic Peninsula (Figure 1). Shortly after, and based on two specimens collected in the Weddell Sea, she presented a more detailed description along with the first drawings of the taxon (Hartman 1978) (Figure 9A,B); however, with no mention of any notopodial features. Blake (1981), in the context of a study on a large collection of scalibregmatids from western South America, Antarctica and sub-Antarctic regions, revised Hartman's material, presenting an improved description and illustration of the anterior body region. He described in detail the peristomium, as well as a developed ring overlapping the prostomium dorsally and with a mid-dorsal notch (Figure 9C). Hartman's 'interramal cirrus' (Figure 9B arrow) is named by Blake 'postchaetal lamella' (Figure 9D arrow), although still there was no reference to any structure in the notopodial lobe. The furcate chaetae reported by Hartman (1967 Hartman, O. 1967. Polychaetous annelids collected by the USNS 'Eltanin' and 'Staten Island' cruises, chiefly from Antarctic seas. *Allan Hancock Monographs on Marine Biology*, 2: 1–387. , 1978 Hartman, O. 1978. Polychaeta from the Weddell Sea Quadrant, Antarctica. *Antarctic Research Series, American Geophysical Union*, 26: 125–233.) were not confirmed by Blake (1981).

Pocklington and Fournier (1987) described the new genus *Axiokebuita* and the species *A. millsii* from slope depths off eastern Canada (Figure 1). They reported for the first time the 'globular notopodial postsetal lamellae' (Figure 9E,F arrow) in the parapodia, two types of neurochaetae (long and short) and confirm the lack of furcate chaetae in both *A. millsii* and *K. minuta*. The authors revised part of Hartman's (1978) and Blake's (1981) Antarctic specimens, previously identified as *K. minuta*, and found that they all should belong to *A. millsii* because of the presence of the globular notopodial lamellae. Nevertheless, because they did not revise all Antarctic material, they maintained both species as valid but now included *K. minuta* in the genus *Axiokebuita*. Following Hartman's (1967) original description of *Axiokebuita minuta*, the species was proposed by Pocklington and Fournier (1987) to differ from *A. millsii* in lacking the globular notopodial lamellae, in having the neuropodial postschaetal lamellae restricted to posterior chaetigers, and in having a simple pygidial ring, rather than a bilobed pygidium.

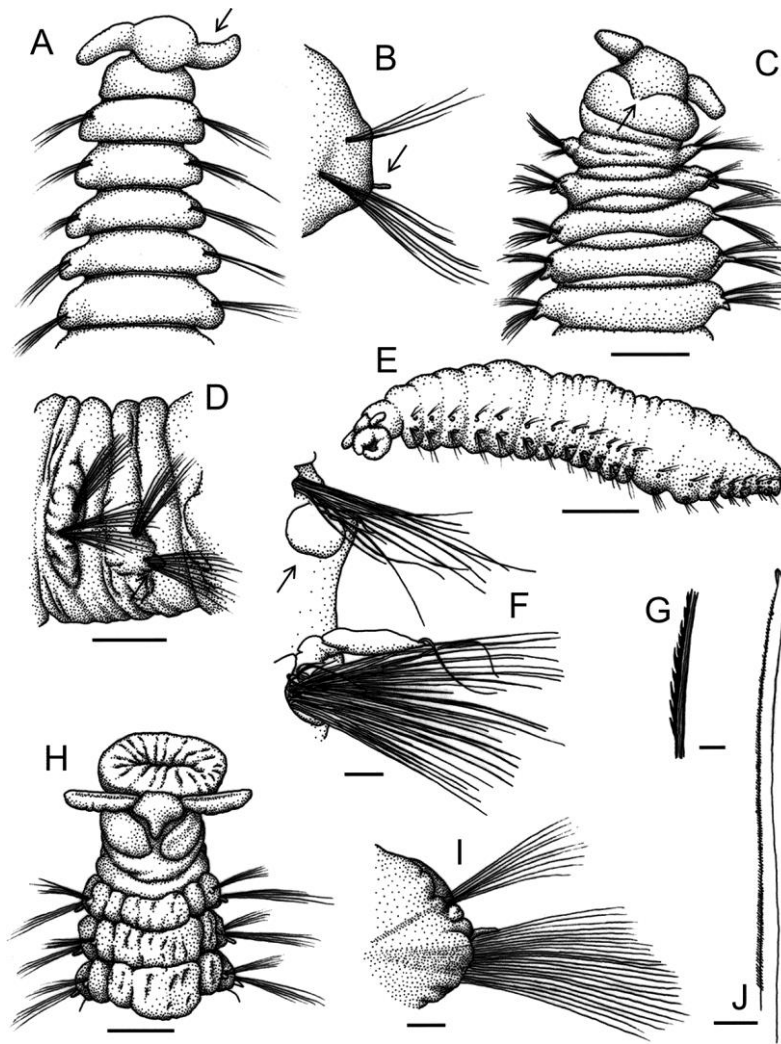


Figure 9. Line drawings of *Axiokebuita* from the earliest to the most recent illustrations in the literature, all redrawn from original, (A) anterior end in dorsal view, arrow showing Hartman's 'antennae' (now 'palps'), (B) postmedian parapodium, arrow showing Hartman's 'interramal cirrus' (from Hartman 1978 as *Kebuita minuta*), (C) anterior end in dorsal view, arrow showing Blake's 'peristomial mid-dorsal notch', (D) two anterior chaetigers in lateral view, arrow marking Blake's 'postsetal lamella' behind neurochaetae (from Blake 1981 as *Kebuita minuta*), (E) semi-diagrammatic latero-dorsal view of complete specimen (holotype), (F) parapodium, arrow showing 'globular notopodial postchaetal lamella', (G) detail of serrated chaetae (from Pocklington & Fournier 1987 as *Axiokebuita millsii*), (H) anterior end in dorsal view, (I) middle parapodium, (J) neurochaeta (from Blake & Hilbig 1990 as *Axiokebuita millsii*). [(A & B) From figure 27, Hartman, O., Polychaeta from the Weddel Sea quadrant, Antarctica. The biology of Antarctic seas. *Antarctic Research Series*, **26**:125–223, 1978. © 1978 American Geophysical Union. Reproduced by permission of American Geophysical Union; (C & D) from figure 11, Blake, J.A. 1981. The Scalibregmatidae (Annelida: Polychaeta) from South America and Antarctica collected chiefly during the cruises of the R/V Hero and USNS Eltanin. *Proceedings of the Biological Society of Washington*, **94**:1131–1162, 1981. © 1981 Biological Society of Washington. Reproduced by permission of Biological Society of Washington; (E, F & G) from figures 1 and 2, Pocklington, P. & Fournier, J.A. 1987. *Axiokebuita millsii*, new genus, new species, (Polychaeta : Scalibregmatidae) from eastern Canada. *Bulletin of the Biological Society of Washington*, **7**:108–113, 1987. Reproduced by permission of Biological Society of Washington; (H, I & J) from figure 13, Blake, J.A. & Hilbig, B., Polychaeta from the vicinity of deep-sea hydrothermal vents in the Eastern Pacific. II. New species and records from the Juan de Fuca and Explorer Ridge Systems. *Pacific Science* **44**:219–253, 1990. © 1990 University of Hawaii Press. Reproduced by permission of University of Hawaii Press.] Scale bars: (A) and (B) no scale; (C) = 300 μ m; (D) = 200 μ m; (E) = 1 mm; (F) = 30 μ m; (G) = 4 μ m; (H) = 1 mm; (I) = 200 μ m; (J) = 10 μ m.

According to the aforementioned criteria, Blake and Hilbig (1990) reported *A. millsii* from hydrothermal vents of the northeast Pacific (Figure 1) because of the presence of ‘globular postchaetal notopodial lamella’. The authors also present the most accurate drawing to date available for the species (Figure 9H,I), particularly regarding the prostomium/peristomium region, and reported neurochaetae with finely serrated shafts and slightly expanded bifid tips (Figure 9J).

Persson and Pleijel (2005) collected new specimens from Norway (Figure 1), studying their affinities with both *A. minuta* (from Hartman's 1967 original material) and *A. millsii* (from Blake's 1981 material). The good condition of the Nordic specimens allowed a detailed description of the taxon *Axiokebuita* and the first SEM images. The main diagnostic characters of the genus were defined as follows: prostomium pentagonal with straight frontal margin bearing two palps; peristomium dorsally incised; each segment with four annuli; notopodia with a small knob ventral to chaetal bundle; neuropodia with digitate pointed cirrus dorsal to chaetal bundle; both noto- and neuro-chaetae capillary; two pad-shaped lobes on pygidium covered with papillae. Persson and Pleijel (2005) presented for the first time a detailed description of the pygidial lobes and reported the probable presence of nuchal organs as ciliated bands bordering the posterior part of the prostomium. From the examination of Hartman's type, Persson and Pleijel (2005) could not unambiguously refer the specimens from Norway to either *A. minuta* or *A. millsii* (but SEM pictures from Trondheim specimen in Figure 2 are named *A. minuta*) because the three differences proposed by Pocklington and Fournier (1987) to distinguish between the two taxa were not confirmed, largely due to poor preservation of the type specimens. Persson and Pleijel (2005) also proposed that the previously unnoticed bilobed pygidium with adhesive papillae may constitute an apomorphy of *Axiokebuita*.

In this work, the study of paratypes of *A. minuta* and *A. millsii* along with newly collected specimens from the BS and Antarctic Peninsula, from near the type locality of *A. minuta* (Figure 1), Norwegian specimens named as *Axiokebuita* sp. by Persson and Pleijel (2005), Antarctic specimens identified by Schüller and Ebbe (2007) and Schüller (2008a, 2008b) as *A. minuta* and *A. millsii*, one specimen from the Pacific Ocean (Easter Island) and two from NW Spain and SW Iceland, respectively, led us to confirm the constant presence of all relevant taxonomic characters (notopodial knob, neuropodial cirrus and pygidial lobes with papillae) in all specimens. Therefore, it is difficult to state any definite morphological difference between the two nominal species, except that Norwegian specimens are much smaller than those from the Antarctica (3–5 vs. 9–16 mm), but with a similar number of chaetigers (22–25 vs. 22–24). Specimens from South Orkney Islands identified as *A. millsii* by Schüller and Ebbe (2007) also have a notopodial knob, but this is less apparent than in specimens named as *A. minuta* by the same authors collected in the Central Weddell Sea.

Our examination of a relatively large number of specimens confirms the lack of furcate chaetae in *Axiokebuita*. Since Hartman (1967, 1978), no one else has reported the presence of this type of chaetae; subsequent authors who have examined Hartman's material also did not mention the presence of those chaetae in the types. We examined a microscope slide from USNM 56625 paratype that has some parapodia (available on the web: <http://collections.nmnh.si.edu/search/iz/>), supposedly corresponding to the type series of *Axiokebuita minuta* deposited in the Smithsonian National Museum of Natural History, Washington, DC. In that slide, furcate chaetae are clearly present, but this body fragment corresponds to a different scalibregmatid species which was incorrectly assigned to *A. minuta* and lies in the same vial.

Two new, previously unreported structures in the genus *Axiokebuita* were found in this study (both occurring in all studied specimens): a prostomial depression and a ciliated ‘neck organ’. The depression observed with the SEM in the dorsal part of the prostomium in BS specimens (Figure 3A,B) was

initially supposed to be an artefact, but this structure could also be observed in boreal specimens (see Figure 2A in Persson & Pleijel 2005); its location suggests a sensory role, but only a histological study would lead us to speculate about its function. Whereas nuchal organs are widely present in other scalibregmatids and many other polychaetes, the finding of the neck organ in this species reveals a probable new sensory structure in the family. Because of its location in the ventral part of the peristomium, its ciliated nature and the apparent possibility to modulate its degree of aperture (compare Figure 3D,E vs. Figure 4B,C), a chemosensory or mechanoreceptor role in the burrowing or food uptake could be suggested owing to that scalibregmatids are considered subsurface deposit-feeders (Schüller & Ebbe 2007).

Discussion

Axiokebuita was placed by Pocklington and Fournier (1987) in group II of scalibregmatids as defined by Kudenov and Blake (1978), and characterised by the maggot-like body and incised prostomium. This group included also *Polyphysia* Quatrefages, 1865 (with branchiae) and *Lipobranchus* Cunningham & Ramage, 1888 (without branchiae). The grouping of these genera by Kudenov and Blake (1978) was not based on a phylogenetic study, so that hypothetical relation requires further study based on additional knowledge of the morphology of the genus.

Axiokebuita, as noted above, can be diagnosed by five possibly apomorphic features: a pentagonal prostomium with strait frontal margin bearing two projections; notopodia each with a small knob ventral to chaetal bundle; neuropodia each with a digitate pointed cirrus dorsal to the chaetal bundle; both noto- and neuro-chaetae capillary; two pad-shaped lobes on pygidium covered with papillae. A sixth possible apomorphy, the ciliated organ located in the ventral peristomium here named the 'neck organs', and perhaps the prostomial depression, seem to be highly characteristic of *Axiokebuita*, as their presence has not been reported in any other scalibregmatid genus.

The position and shape of the notopodial knob resembles the interramal papillae or ciliated organs usually present in other scalibregmatids such as in *Sclerobregma* Hartman, 1965 and *Oligobregma* Kudenov and Blake, 1978 (see Blake 1981). Rouse and Pleijel (2001) proposed a possible homology of this structure with the lateral organs occurring in the same position in other taxa such as Opheliidae, Orbiniidae and Paraonidae within Scolecida and also in Canalipalpata (Spionidae and Pectinariidae) and Aciculata (Syllidae, Eunicidae and Amphinomidae) (Purschke 2005).

From the study of museum collections and newly collected material of both *A. minuta* and *A. millsii*, a clear separation between both taxa could not be established using classic morphological characters. Therefore, we propose to consider the two previous nominal species as a single 'species', and due to this to consider *Axiokebuita millsii* a junior synonym of *A. minuta*. Only the finding of new discriminating characters, either morphological or molecular, could in the future lead to the reconsideration of this conclusion.

The few records of this monotypic genus in the literature makes difficult to establish a definite pattern of geographic distribution. Although Schüller and Ebbe (2007) defined *Axiokebuita* as potentially cosmopolitan, in the light of currently available data, it may rather have a bipolar (or antitropical) distribution associated with the deep slope of boreal Atlantic and Pacific and west and east Antarctic. The findings of new specimens seem to confirm this pattern of distribution, although there are significant exceptions given the specimens from the hydrothermal vents of the southeast and northeast Pacific. The southeast Pacific specimen was located near the tropics 23°S, and therefore extends this

range to the deep bottoms of the Southern Pacific Ocean (Table I), while the northeast Pacific records are from south of 50°N (Blake & Hilbig 1990). This discontinuous pattern, with a possible connection, through the deep waters, in temperate latitudes, has also been observed in other deep-sea polychaetes such as the opheliids *Ammotrypanella* and *Ophelina* (e.g. Schüller 2008a; Parapar & Moreira 2008; Parapar et al. 2011b). Kirkegaard (1996) advocates the existence of a deep ocean current as described by Broecker and Denton (1989) as a possible explanation for the broad distribution of some deepwater species. Glasby (2005) suggests three reasons for this apparently disjunct distribution pattern: the result of long-distance dispersal, extinction events, or incorrect taxonomic assignments. As at the moment no discriminating morphological characters have been identified, while the molecular analysis is still limited to a few geographic locations, we cannot exclude the presence of sibling species which may have originated from this long distance dispersal and disjunct distribution. Therefore, the proposed synonymy and monotypic feature of the genus *Axiokebuita* should be further investigated and validated by additional analyses, especially at the molecular level.

In our case, however, a further reason could be proposed: the sampling effort and methodology. The sampling effort in deep ocean sediments is still much lower than in areas of continental shelf and slope (e.g. Parapar & Moreira 2009). In both BENTART and ANDEEP II cruises, specimens were collected with a suprabenthic sledge (Brenke 2005); other gears used (box corer, multibox corer and Agassiz trawl) in same areas and in different cruises did not collect *Axiokebuita* (Hilbig et al. 2006; Saiz et al. 2008, Parapar et al. 2011a). The high selectivity in the fauna collected by the suprabenthic sledge, primarily used to study of the suprabenthic community (mostly peracarid crustaceans; San Vicente et al. 2009), but also capable of collecting the first few centimeters of sediment, makes it very suitable for the capture of *Axiokebuita*. Suprabenthic sledges have so far not been very widely used, mainly in the European region (Mees & Hammerlynck 1992 ; San Vicente et al. 1993; Dauvin et al. 1994) and Antarctica (San Vicente et al. 2007, 2009). It is likely that a more widespread use of this gear may result in a different picture of the distribution of the genus *Axiokebuita*.

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