



***Aristonerilla*: a new nerillid genus (Annelida: Polychaeta) with description of *Aristonerilla (Micronerilla) brevis* comb. nov. from a seawater aquarium**

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Abstract: A nerillid polychaete is described from the organic-filter system of a marine aquarium in the AquaZoo (Düsseldorf, Germany). The body comprises the prostomium, seven segments and the pygidium. With two large, ventrolateral palps and three long, threadlike antennae, the species possesses the maximal number of prostomial appendages present in this taxon. Two small eyes are visible. The first segment (buccal segment, peristomium) contains a pair of small parapodia without cirri but with a few, relatively long chaetae. Segments II to VI possess parapodial cirri, increasing in length posteriorly. In segment VII the cirri are reduced. Each trunk segment has one dorsal and one ventral bundle of chaetae, which are slightly longer than the parapodial cirri. All chaetae are compound; some possess very long blades. The pygidium carries two threadlike anal cirri. Apart from minor morphometrical and anatomical differences, the animals resemble *Micronerilla brevis*. However, the type species *Micronerilla minuta*, does not possess seven but eight segments and because the number of segments is considered a stable character in nerillid genera, the species *brevis*, with seven segments, has to be placed in a new genus, *Aristonerilla*, and named *Aristonerilla brevis* (new comb.).

Résumé : *Un nouveau genre Aristonerilla (Polychaeta : Nerillidae) et description de Aristonerilla (Micronerilla) brevis comb. nov.* Un Nerillidae est décrit dans le sédiment du système de filtration d'un aquarium marin à l'AquaZoo de Düsseldorf en Allemagne. Le corps comprend le prostomium, sept segments et le pygidium. Avec deux grands palpes ventrolatéraux et trois longues antennes filiformes l'espèce possède le nombre maximum d'appendices prostomiaux présents dans la famille des Nerillidae. Deux petits yeux sont visibles. Le premier segment (segment buccal, péristomium) porte une paire de petits parapodes sans cirres, mais avec des soies relativement longues. Les segments II à VI possèdent des cirres parapodiaux, qui augmentent de taille dans la région postérieure. Cependant dans le segment VII les cirres sont réduits. Chaque segment du tronc a un faisceau de soies dorsal et un ventral qui sont légèrement plus longs que les cirres parapodiaux. Toutes les soies sont composées, certaines ont des articles très longs. Le pygidium porte deux cirres anaux filiformes. Mises à part quelques différences morphométriques et anatomiques mineures, les animaux ressemblent à *Micronerilla brevis*, espèce décrite de la Mer Blanche. Ces différences cependant ne justifient pas la création d'une nouvelle espèce. Le nombre de segments étant considéré comme un caractère stable dans les genres de Nerillidae, et le genre *Micronerilla* ayant 8 segments, l'espèce *brevis*, à sept segments, est placée dans le nouveau genre *Aristonerilla* et nommée *Aristonerilla brevis* (comb. nov.).

Keywords: Annelida, Nerillidae, meiofauna, cLSM, enteronephridia

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Introduction

The taxon Nerillidae comprises minute polychaetes that are restricted to the interstitial spaces within sandy marine sediments (Westheide, 1990). Only *Troglochaetus beranecki* Delachaux, 1921 lives in continental groundwater areas. Nerillids are distributed worldwide and the genera *Nerilla*, *Nerillidium* and *Mesonerilla* are regarded as cosmopolitan (Jouin, 1971). Although conditions in marine aquaria often differ from those in nature, *Nerilla* frequently inhabits these artificial biotopes and is able to adapt to new food sources (Schlieper, 1925). *Nerilla jouinae* Saphonov & Tzetlin, 1987 and *Trochonerilla mobilis* Tzetlin & Saphonov, 1992 are species that have been reported only from seawater aquaria. It is assumed that these animals are transferred from the natural localities together with various larger animals, algae or substrate. Determination of their geographical origin is difficult and in many cases impossible (Tzetlin & Saphonov, 1992). This disadvantage is compensated by the fact that the animals can easily be extracted from their surroundings without any damage, an optimal condition for a detailed description of specimens (Riser, 1988; Müller et al., 2001). *Aristonerilla* gen. nov. *brevis* (Saphonov & Tzetlin, 1997), found in the substrate of a seawater filter system (AquaZoo Düsseldorf), is re-described by means of light, electron and confocal laser scanning microscopy (LM, SEM, cLSM, respectively).

Material and methods

Aristonerilla (*Micronerilla*) *brevis* (Saphonov & Tzetlin, 1997) was extracted from the substratum with a solution of 8% MgCl₂ isotonic to sea water (see Westheide & Purschke, 1988 for details).

For cLSM analyses, relaxed specimens were fixed on ice at a temperature of 4°C overnight in 4% paraformaldehyde in 0.15 M PBS (phosphate buffered saline; pH 7.4) containing 8% sucrose. After several rinses with PBS for at least 1 h the specimens were pre-incubated for 1 h in PBS containing 0.1% Triton-X-100, 0.25% bovine serum albumin (BSA) and 0.05% NaN₃. The primary antibody, monoclonal mouse-anti-acetylated α -tubulin (Sigma, Heidelberg, Germany; dilution 1:100 in preincubation liquid without BSA) was applied for 12 h at room temperature. Subsequently, specimens were washed in several changes of PBS and incubated with a FITC-conjugated secondary antibody directed against mouse. The secondary antibody was diluted 1:100 in preincubation solution without BSA. Finally, specimens were rinsed in PBS several times and mounted in Citiflour (Plano, Wetzlar) between two cover slides. Preparations were viewed with a confocal laser scanning microscope Zeiss LSM 410. Incubations were

conducted on many specimens to demonstrate reproducibility of the staining. In total, seven specimens were analyzed with cLSM: four males and three females.

For SEM analyses, SPAFG (sucrose-picric acid-paraformaldehyde-glutaraldehyde in 0.1M phosphate buffer) fixed specimens were dehydrated in an upgraded ethanol series. Subsequently, they were critical-point dried using CO₂ as intermedium, mounted on an aluminum tab and sputter-coated with gold. Examination took place in a Zeiss DSM 962. In total, 15 specimens were investigated by this method. The specimens prepared for SEM and further 18 animals stored in alcohol are deposited as additional paratypes in the Senckenberg Museum Frankfurt (SMF 11086, SMF 11087).

Results

Aristonerilla gen. nov. (*Micronerilla*) *brevis*
(Saphonov & Tzetlin, 1997) comb. nov.

Diagnosis

Nerillidae with two palps and three antennae on the prostomium. Seven segments between prostomium and pygidium; first one with parapodia and chaetae but without cirri. Segment II to VI with cirri; cirri in segment VII reduced. Segments II to VII with dorsal and ventral compound chaetae. Two anal cirri. Pharyngeal organ with two pairs of buccal pieces (White Sea specimens).

Etymology: *Aristonerilla*, “*Arist*” is the Greek word for “best, noble, competent”. It is also used to reflect higher development in phylogeny. Referring to a nerillid, “-*nerilla*” is attached. The species name “*brevis*” originates from the first description by Saphonov & Tzetlin (1997).

Material examined. Specimens were extracted from filter-substrate that is a mixture of coral sand of unknown locality and shell fragments from the bay of Brest (France). The small tank is part of a seawater aquarium circuit with a total volume of 25,000 l, operated at 24°C and a salinity of 34 for more than ten years. The center of this circuit is a tropical reef aquarium (17,000 l) that mainly contains species from the Indopacific. Thus, *Aristonerilla brevis* could be an Indopacific species; but it cannot be excluded that the natural geographical locality of the aquarium population is somewhere else. Approximately 50 specimens were fixed in Bouin, 50 in SPAFG and 50 more in 4% paraformaldehyde in PBS.

Description

The animals are transparent with a yellowish to pale green intestine (Fig. 1A, B, C). The body length of adult specimens ranges from 460 to 480 μ m without appendages. Between segments III and IV the body width measures 90 to 100 μ m; within segment III the animals, including parapodia, are approximately 120 μ m wide.

Anterior end. The small prostomium is separated from the peristomium by a gentle furrow (Fig. 2D-F, J); ventrally this border is indicated by a row of ciliary tufts (Fig. 2E). The prostomium carries three long, threadlike antennae and two palps. The lateral antennae (150-200 μm) insert terminally, the median one (160-190 μm) slightly further back and more dorsally (Fig. 2A, F, J). They are loosely trimmed with long sensory cilia, orientated at a right angle to the axis of the antenna (Fig. 2F, G, J). The ventrolaterally inserted palps are ventrally densely covered with cilia, while dorsally single cilia are scarce (Fig. 2B, C). While the palps in adults are club-shaped and 45 to 60 μm long, they measure only 15 μm in juveniles and have a rounded shape (Fig. 2D, G). Two small eyes (fluorescing by reflected light, appearing red under the microscope) are located dorsally near the base of the lateral antennae (Fig. 1A). Nuchal organs are placed dorsolaterally in the furrow between prostomium and peristomium, directly in front of the first parapodium (Fig. 2J).

Trunk. The body comprises seven segments and the pygidium. The parapodia of the first chaetiger (buccal-segment, peristomium) are approximately 21 μm long and 28 μm wide and larger than the following ones (15 μm long, 22 μm wide). They do not carry any cirri but five to ten chaetae each. These are directed conspicuously backwards, may be up to 200 μm long and may reach the third chaetiger (Fig. 2F). The last body segment has no apparent cirri but under higher magnification buds of these appendages are visible (Fig. 3B). Segments II to VI possess long parapodial cirri, increasing in length caudally (II: 76; III: 90; IV: 93; V: 103; VI: 112 μm). In one specimen the sixth parapodial cirri were 176 μm long. Ventrally the parapodial cirri are slightly articulated and each section possesses distally one tuft of sensory cilia (Fig. 3C, D). Segments II to VII have two bundles of chaetae; the dorsal bundle is located above, the ventral one below the cirrus (Fig. 3A). Within one bundle the chaetae are arranged more or less in a vertical row. Only compound chaetae are present, although few chaetae seem to be capillary ones (Fig. 3D-F). The latter are, due to their small diameter, often twisted in SEM preparations. Only under high magnification the articulation of shaft and blade can be noticed (Fig. 3E). The blade of these chaetae is extremely long and can measure up to 50 μm . The shafts of the chaetae are denticulated (Fig. 3B, F, black arrowheads). The small pygidium (30 μm long; 45 μm wide) carries two long (170 μm), slightly wrinkled pygidial cirri (Fig. 2A, I).

Ciliation. On the prostomium tufts of long cilia are located dorsally between the lateral antennae and the palps (Fig. 2J). In other dorsal areas only few, single cilia are present. The first segment carries two prominent tufts of approximately 10- μm -long cilia, which are directed anteriorly and located just above the parapodium (Fig. 2J, arrow). Ventrally the whole segment is densely covered with

cilia, surrounding the mouth opening (Fig. 2D, E). The ciliation continues backwards into a ventral ciliary band, reaching up to the pygidium (Fig. 2A, D, I). Each trunk segment possesses transversely arranged cilia upon and below the parapodia, but these bands are discontinuous (Figs. 2I, 3A). In juvenile animals the ciliation is less dense.

Pharyngeal organ. The pharyngeal bulb and two lateral folds, shown everted in one juvenile (Fig. 2D, G, H), are free of cilia. No buccal pieces could be observed in the pharyngeal bulb of our specimens.

Nephridia. They were identified by means of cLSM on the basis of their ciliated funnels. Their ducts were discontinuously stained. Nephridia are present in segments I to V (Fig. 1F). Enteronephridia, approximately ten in number, surround the hindgut and project into the intestine at the transition between mid- and hindgut (Fig. 1H).

Mature animals. It is assumed that the new species is gonochoristic. Females had one vitellogenic oocyte (115 μm long, 30 μm wide) in segments V to VI (Fig. 1E). In acetylated α -tubulin-incubated specimens the two oviducts are clearly visible (Fig. 1F). They reach from a dorsal position in segment VI to the ventral integument in segment VII, where they open via a pair of small pores (Fig. 1C). At the level of the female gonopores two pear-shaped glands open midventrally (Fig. 1C, gl). In four other specimens investigated, the gonoducts described above were absent and the posterior half of the body was occupied with filamentous structures, presumably spermatozoa. Male gonoducts could not be detected.

Juveniles. None of the approximately 150 extracted animals carried eggs or juveniles, whereas many free and mobile juveniles were present. In six segmented juveniles the third parapodium was more differentiated than the anterior and posterior ones (Fig. 2D, G). Whereas in segment II the parapodial cirri are short and egg-shaped, they are already elongated in segment III and resemble the condition found in adults.

Discussion

The species of the relatively homogeneous taxon Nerillidae are distinguished taxonomically by such features as number of metamers, type of chaetae, number of prostomial appendages and parapodial cirri and presence of a pharyngeal bulb with or without buccal-elements (Jouin, 1971; Westheide, 1990). Specimens extracted from the filter system of the AquaZoo differ from *Micronerilla brevis* from the White Sea in having 1) no buccal elements, 2) different eye structure, 3) diverse enteronephridial pattern, 4) different morphometric data, 5) different environmental conditions (see Tab. 1, bold surrounded characters). However, the differences in morphometric data, as well as

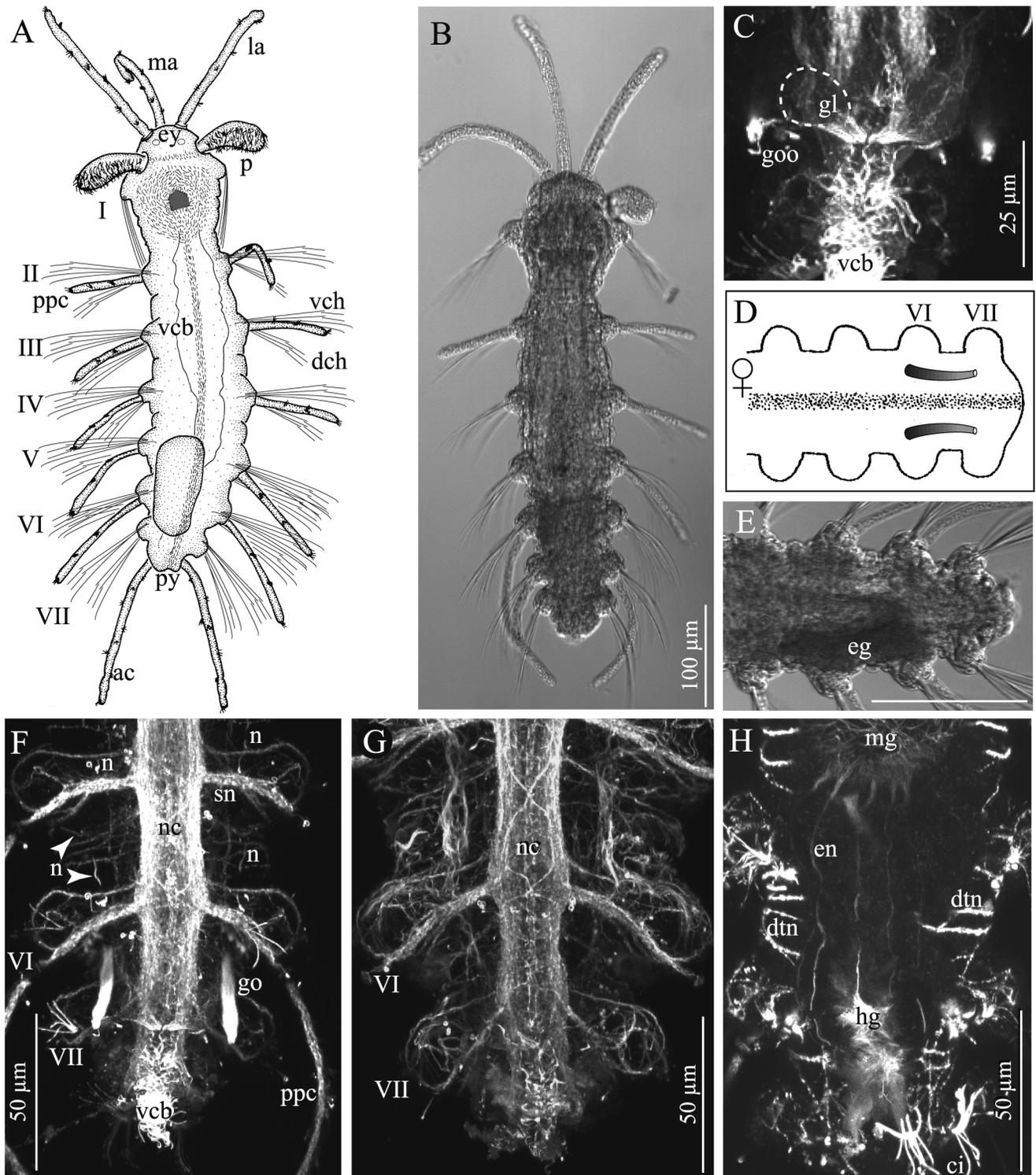


Figure 1. *Aristonerilla brevis*. **A.** Schematic drawing of a whole organism, ventral view. **B.** Female, whole mount, light micrography. One palp, the anal cirri and several parapodial cirri broken off. **C, F-H.** cLSM micrographs; acetylated α -tubulin immunoreactivity. **C.** Glands opening midventrally on segment VII. Shape of left gland indicated. **D.** Schema indicating the location of the female gonoducts in segments VI-VII. **E.** Female posterior end with an egg. Scale bar: 100 μ m. **F.** Female posterior end with pair of gonoducts. **G.** Male

eye-configuration, are not significant and the structure of the pharyngeal organ as well as the enteronephridia distribution pattern have to be studied in detail by TEM investigations in specimens of both populations, so that, at present, the specimens from the White Sea and from the AquaZoo are regarded as belonging to only one species. Subsequently, DNA studies could solve the question concerning the existence of one or two species.

In contrast to Saphonov & Tzetlin (1997) many other authors consider the segment number a stable character in nerillid genera (Jouin, 1970; Westheide 1990; Westheide & Purschke, 1996). Following the latter argumentation, the reduced segment number in *Micronerilla brevis* (7 segments) is regarded as being more important than the striking similarities with *M. minuta* (8 segments) (see Table 1) and justifies to place it into a the new genus *Aristonerilla*. Therefore the species name will be changed into *Aristonerilla brevis* (Saphonov & Tzetlin, 1997) comb. nov.. For the same reasons *Micronerilla minuta* (*Mesonerilla minuta* Swedmark, 1959) was taken out of the genus *Mesonerilla* (9 segments) and placed into the genus *Micronerilla* (8 segments) created by Jouin in 1970.

Out of the hitherto 17 known genera four are seven-segmented (including the new genus *Aristonerilla*), eight are eight-segmented and five are nine-segmented (Tzetlin and Saphonov, 1992; Müller et al. 2001). The taxon presented here differs from all other seven-segmented nerillids in possessing three antennae and two pigmented eyes, whereas *Bathychaetus* Faubel, 1978, *Paranerilla* Jouin & Swedmark, 1965 and *Psammoriedlia* Kirsteuer, 1966 have no antennae and no eyes. Furthermore, *Bathychaetus* is different from *Aristonerilla* in being much smaller (300 µm versus 500 µm) and having only capillary chaetae and relatively short anal cirri (42 µm versus 170 µm) (Faubel, 1978). *Paranerilla* is different from the new genus in size (700-900 µm), lack of palps and antennae and in possessing only very short parapodial cirri. *Psammoriedlia* differs from *Aristonerilla* in that it has only capillary chaetae, in a smaller number (Kirsteuer, 1966).

In their attempt to explain the assumed progenetic origin of the nerillids, Westheide (1987) and Westheide & Purschke (1996) postulated that a nerillid species close to the stem species ought to have a relatively complex configuration: many segments, maximum number of prostomial appendages, compound and many chaetae, two cirri per parapodium etc.. According to these authors the nerillid genera could be arranged in a morphological series in order of decreasing segment number (nine-eight-seven) and complexity. Saphonov & Tzetlin (1997) postulated the morphological series *Mesonerilla* – *Micronerilla minuta* – *Aristonerilla* (*Micronerilla*) *brevis* in which complexity is stable but the segment number is decreasing. In this series *Mesonerilla* Remane, 1949 should be replaced by *Leptonerilla* Westheide & Purschke, 1996 because the latter one is the most complex and primitive nerillid yet known (Westheide & Purschke, 1996). Furthermore complexity is decreasing in this series as well: *Leptonerilla* possesses two cirri per parapodium, in *Micronerilla* 50% of the specimens show this character whereas single cirri occur in *Aristonerilla*. Cirri in segment I (peristomium) are present always in *Leptonerilla*, sometimes in *Micronerilla* and never in *Aristonerilla*. In the taxon Nerillidae, however, the presence of cirri in segment I is inconsistently distributed: they are present in all nine-segmented (exception: *Xenonerilla*), missing in all eight-segmented (exception: *Nerillidium*) and present in all seven-segmented genera (exception *Aristonerilla*). The same is true for other major characters, such as compound or capillary chaetae. Further molecular investigations should focus on the question, whether close relationships within the Nerillidae are defined by segment-number or by other characters.

Mature animals. Whereas Saphonov & Tzetlin (1997) had no problems to distinguish males and females, gonochorism of *Aristonerilla brevis* can here be inferred only indirectly. Only females were identified without doubt, by the presence of eggs and oviducts. The lack of normal segmental nephridia in this section suggests that the excretory function of these organs has been lost and that

posterior end. **H.** Female posterior end with enteronephridia. (*ac*) anal cirri; (*ci*) cilia; (*dch*) dorsal chaetae; (*dm*) dorsal transverse nerves; (*eg*) egg; (*en*) enteronephridia; (*ey*) eye; (*gl*) gland; (*go*) gonoduct; (*goo*) gonoduct opening; (*hg*) hind gut; (*la*) lateral antenna; (*ma*) median antenna; (*mg*) mid gut; (*n*) nephridia; (*nc*) nerve cord; (*p*) palp; (*ppc*) parapodial cirrus; (*py*) pygidium; (*sn*) segmental nerve; (*vcb*) ventral ciliary band; (*vch*) ventral chaetae; (*I-VII*) segments I-VII.

Figure 1. *Aristonerilla brevis*. **A.** Dessin schématique d'un spécimen entier, vue ventrale. **B.** Femelle, photomicrographie: un palpe, les cirres anaux et plusieurs cirres parapodiaux manquent. **C, F-H.** micrographies en microscopie confocale; immunoréactivité anti- α -tubuline acétylée. **C.** Glandes s'ouvrant médioventralement sur le segment VII. La forme de la glande gauche est indiquée. **D.** Schéma montrant l'emplacement des oviductes chez la femelle dans les segments VI-VII. **E.** Photomicrographie de la partie postérieure d'une femelle portant un œuf. Echelle : 100 µm. **F.** Extrémité postérieure d'une femelle montrant la paire d'oviductes. **G.** Extrémité postérieure d'un mâle. **H.** Extrémité postérieure d'une femelle montrant les entéronéphridies. (*ac*) cirres anaux; (*ci*) cils; (*dch*) soies dorsales; (*dm*) nerfs dorsaux transverses; (*eg*) œuf; (*en*) entéronéphridie; (*ey*) œil; (*gl*) glande; (*go*) oviducte; (*goo*) ouverture de l'oviducte; (*hg*) intestin postérieur; (*la*) antenne latérale; (*ma*) antenne médiane; (*mg*) intestin moyen; (*n*) néphridie; (*nc*) chaîne nerveuse; (*p*) palpe; (*ppc*) cirre parapodial; (*py*) pygidium; (*sn*) nerf segmentaire; (*vcb*) bande ciliée ventrale; (*vch*) soies ventrales; (*I-VII*) segments I-VII.

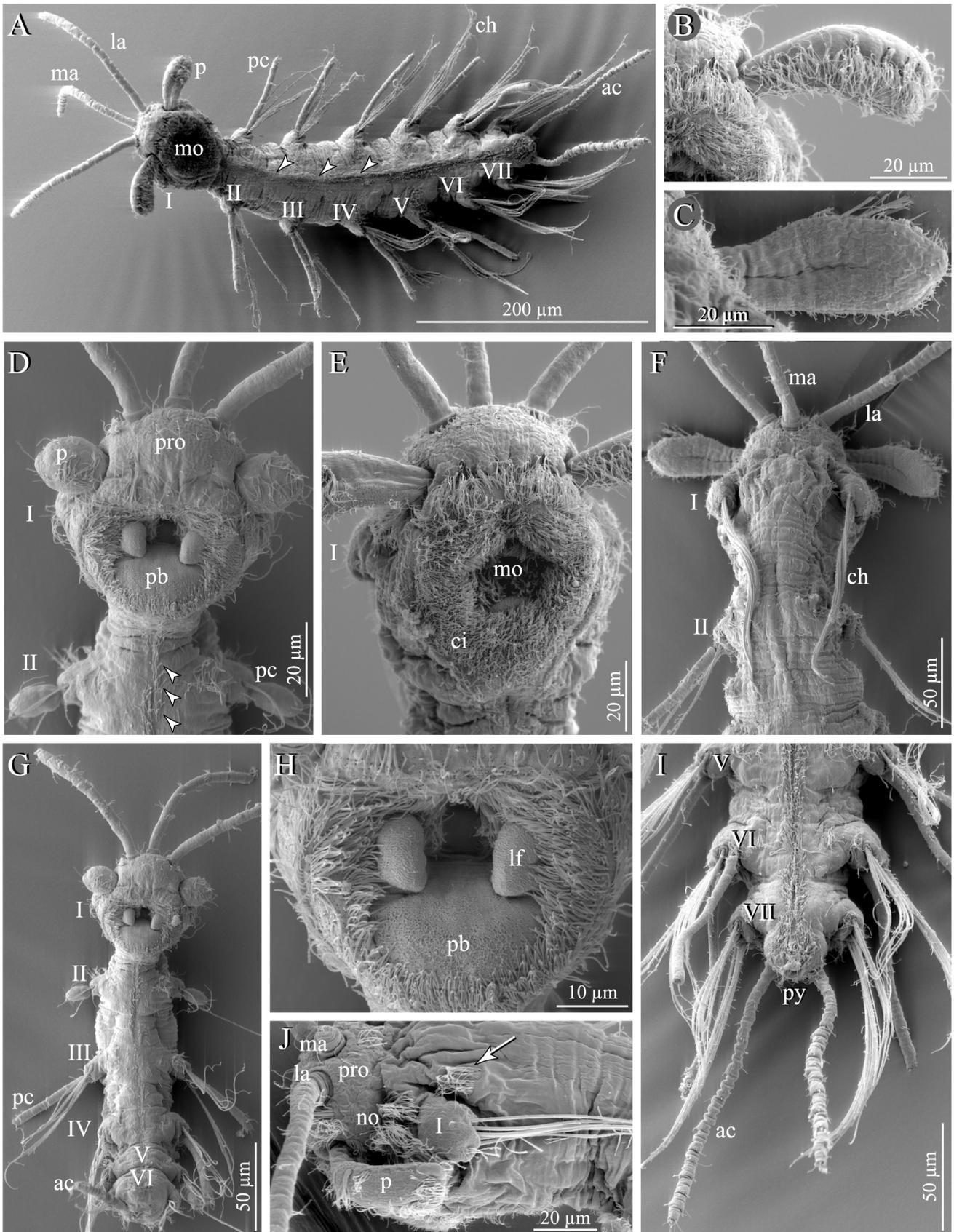


Table 1: Comparison of main characters between *Micronerilla minuta* (Swedmark, 1959) and *Aristonerilla brevis* (Saphonov & Tzetlin, 1997) from the White Sea (WS) and from the AquaZoo (AZ) (ca = capillary; co = compound; hg = hindgut; la = lateral antenna; mg = midgut; + = present; - = absent; I-VIII = segment number; * = personal communication A. Tzetlin; grey = differences between *Aristonerilla* and *Micronerilla*; bold delimited = differences between *Aristonerilla brevis* from the White Sea (WS) and the AquaZoo (AZ)).

Tableau 1 : Comparaison des principaux caractères de *Micronerilla minuta* (Swedmark, 1959), et d'*Aristonerilla brevis* (Saphonov & Tzetlin, 1997) de la Mer Blanche (WS) et de l'AquaZoo (AZ). (ca = soies capillaires ; co = soies composées ; hg = intestin postérieur ; la = antenne latérale ; mg = intestin moyen ; + = présent ; - = absent ; I-VIII = numéros des segments ; * = communication personnelle de A. Tzetlin ; en gris = différences entre *Aristonerilla* et *Micronerilla* ; encadrés = différences entre les spécimens de la Mer Blanche (WS) et ceux de l'AquaZoo (AZ)).

Character		<i>Aristonerilla brevis</i> (WS)	<i>Aristonerilla brevis</i> (AZ)	<i>Micronerilla minuta</i>
body:	segment number	VII	VII	VIII
	length (µm)	550-670	460-480	520-600
	width (µm)	100	90-100	90
eyes:	location	base la	base la	base la
	colour	none	red	red
buccal pieces:		2 pairs	?	1 pair
appendages:	median antenna (µm)	270-330	160-190	125-150
	lateral antenna (µm)	260-320	150-200	150-175
	palps (µm)	40-60	45-60	70-80
	cirri I	-	-	+ / -
	cirri II-VII(I), number/segm.	1	1	1 / 2
	cirri II-VII(I) (µm)	100-140	75-175	100-150
	cirri last segment (µm)	-	bud	-
chaetae: (adult)	anal cirri (µm)	300	170	305
		co	co	co
	length of blade (µm)	25-30	30-50	
	juvenile	?	co	co / ca
	shaft compound chaetae	denticulated	denticulated	denticulated
	in I, number	9-12	5-10	?
	in I, length (µm)	120-140	200	?
in II-VII, number	10-16	?	?	
ciliation:	ventral ciliary band	continuous	continuous	continuous
	transverse segmental cilia	band	band	ring
gonoducts:	female	?	VI-VII	VII-VIII
	male	?	?	VI-VII+VII-VIII
nephridia:		?	II-VI	?
enteronephridia:		?	ca. 10	?
	location	mg/hg *	hg	?



Figure 2. *Aristonerilla brevis*. SEM-micrographs. **A.** Whole organism, ventral view. **B.** Left palp, ventrally densely covered with cilia. **C.** Right palp, dorsally devoid of cilia. Long cilia are attached to the anterior margin. **D.** Anterior end up to the second segment of a six-segmented juvenile with everted pharyngeal bulb, ventral view. **E.** Prostomium and first segment (= peristomium) of an adult specimen, ventral view. **F.** Anterior end up to the second segment of an adult animal, dorsal view. **G.** Six-segmented juvenile, ventral view. **H.** Enlargement of the everted buccal part. **I.** Posterior end of an adult animal, ventral view. **J.** Dorsolateral view of the anterior end of an adult organism with the median antenna broken off. (*ac*) anal cirri; (*ch*) chaetae; (*ci*) cilia; (*lf*) lateral fold; (*la*) lateral and (*ma*) median antenna; (*mo*) mouth opening; (*no*) nuchal organ; (*p*) palp; (*pb*) pharyngeal bulb; (*pc*) parapodial cirrus; (*pro*) prostomium; (*py*) pygidium; (*arrow*) tufts of long, anteriorly directed cilia; (*arrowheads*) ventral ciliary band; (*I-VII*) segments I to VII;

Figure 2. *Aristonerilla brevis*. Micrographies MEB. **A.** organisme entier, vue ventrale. **B.** Palpe (gauche), abondamment cilié ventralement. **C.** Palpe (droit) dépourvu de cils dorsalement. De longs cils sont implantés sur son bord antérieur. **D.** Vue ventrale de la région antérieure, jusqu'au deuxième segment, d'un juvénile de six segments, bulbe pharyngien éversé. **E.** Prostomium et premier segment (= péristomium) d'un spécimen adulte, vue ventrale. **F.** Extrémité antérieure d'un spécimen adulte, vue dorsale. **G.** Juvénile de six segments, vue ventrale. **H.** Détail du bulbe pharyngien éversé. **I.** Partie postérieure d'un adulte, vue ventrale. **J.** Vue dorso-latérale du prostomium et du péristomium d'un adulte, avec l'antenne médiane cassée. (*ac*) cirres anaux ; (*ch*) soies ; (*ci*) cils ; (*lf*) repli latéral ; (*la*) antenne latérale et (*ma*) médiane ; (*mo*) bouche ; (*no*) organe nuchal ; (*p*) palpe ; (*pb*) bulbe pharyngien ; (*pc*) cirre parapodial ; (*pro*) prostomium ; (*py*) pygidium ; (*flèche*) touffes de longs cils ; (*têtes de flèches*) bande ciliée ventrale ; (*I-VII*) segments I à VII.

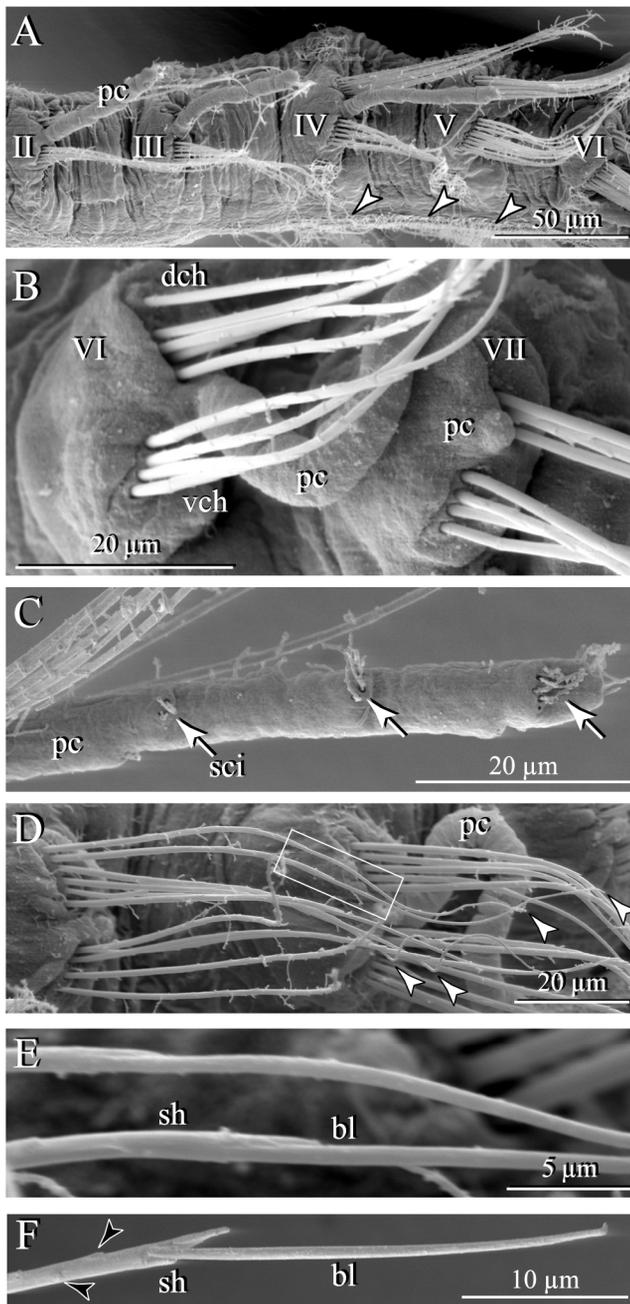


Figure 3. *Aristonerilla brevis*. SEM-micrographs. **A.** Lateral view of an adult animal from segment II to VI (*arrowheads*: ventral ciliary band). **B.** Lateral view of segments VI and VII with the bud of parapodial cirrus in VII. **C.** Enlargement of the second parapodial cirrus, on which three tufts of sensory cilia are visible. **D.** Chaetal bundle with “pseudocapillary” chaetae (*arrowheads*). **E:** Enlargement of D. **F:** Compound chaeta with a short blade. The shaft carries small denticles (*black arrowheads*). (*bl*) blade; (*dch*) dorsal and (*vch*) ventral chaetal bundles; (*pc*) parapodial cirrus; (*sci*, *arrows*) sensory cilia; (*sh*) shaft; (*II-VI*) segments II to VI.

Figure 3. *Aristonerilla brevis*. Micrographies MEB. **A.** Vue latérale des segments II à VI d'un adulte (*têtes de flèches* : bande ciliée ventrale). **B.** Vue latérale des segments VI et VII avec ébauche de cirre parapodiale sur VII. **C.** Détail du deuxième cirre parapodiale montrant trois touffes de cils sensoriels. **D.** Faisceaux de soies “pseudocapillaires” (*têtes de flèches*). **E :** Détail du cadre en D. **F :** Soie composée avec un article court. La hampe est denticulée (*têtes de flèches noires*). (*bl*) article ; (*dch*) faisceau de soies dorsal et (*vch*) cirre parapodiale ; (*pc*) cirre parapodiale ; (*sci*, et *flèches*) cils sensoriels ; (*sh*) hampe ; (*II-VI*) segments II à VI.



implies that the anterior three segments do not differentiate continuously in an antero-posterior gradient. Jouin & Swedmark (1965) observed that in *Paranerilla limicola* Jouin & Swedmark, 1965 a three-segmented larva hatches from the egg. In these larvae the third and last chaetiger is more developed than the two preceding ones. Whether the embryonic development of *A. brevis* performs in the same way has to be investigated in further studies.

Enteronephridia. Enteronephridia have been described for *Nerillidopsis hyalina* Jouin, 1966 and several species of *Nerillidium* (Jouin, 1967), *Meganerilla clavata* Magagnini 1966, *Mesonerilla armoricana* Swedmark, 1959 and *M. biantennata* Jouin, 1963 (Jouin, 1967, 1968), *Akesioniella orientalis* Tzetlin & Larionov, 1988, *Trochonerilla mobilis* Tzetlin & Saphonov, 1992 (Tzetlin et al., 1992) and *Nerillidium troglochaetoides* Remane, 1925 (Tzetlin et al., 1992). They were first demonstrated by tubulin incubation and cLSM for *T. mobilis* by Müller (1999). Future studies should focus on whether the occurrence and the number of these organs (*Nerillidopsis hyalina*: 4, *Mesonerilla intermedia*: 6, *M. biantennata*: 2; *Nerillidium troglochaetoides*: 3, *Trochonerilla mobilis*: 13; *Aristonerilla brevis*: ca. 10) are taxonomically valuable.

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they are enlarged in order to lay eggs. Males could be identified only by the lack of oviducts and the presence of tubulin-containing filaments, interpreted as spermatozoa. The situation has to be clarified by TEM investigations.

Juveniles. Since no juveniles attached to a mother, but many free-living and mobile young specimens, with four to six segments, were extracted from the substratum, *Aristonerilla brevis* is considered not to exhibit brood protection, as documented in several other species of the taxon (Jouin, 1968). That the third segment in juveniles is further developed than the anterior two metamers (Fig. 2G)

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