

# A new species of *Paranerilla* (Polychaeta: Nerillidae) from Northeast Greenland Waters, Arctic Ocean

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**Abstract:** *Paranerilla cilioscutata* sp. nov. is described from high arctic waters, off Northeast Greenland. It was found in muddy sediments at depths of 32 to 590 m between 77°09'N and 82°11'N and between 8°40.42'W and 30°24'W in Independence Fjord and the Greenland Sea. The new species expands the distribution of Nerillidae into the Arctic. It is compared with *Paranerilla limicola* which is the only other species of the genus. New material of *P. limicola* was collected at the type locality in the Gullmar Fjord, Sweden (58°16'N, 11°28'E). Both species were studied with light microscopy (alive and preserved) and scanning electron microscopy. Both have seven segments with compound chaetae and the characteristic prostomium of *Paranerilla*, with two lateral horns and a dense covering of cilia. The new species differs from *P. limicola* by a much denser dorsal ciliation and lack of prostomial ciliated sensory fields. The dorsal ciliation of *P. cilioscutata* sp. nov., totally covers the prostomium and segment 1, and is seen as ciliary plates on segments 2-6 (versus partly ciliated prostomium and segment 1, and narrow double or single ciliary bands on segments 2-6 in *P. limicola*). The present studies of *P. limicola* revealed two new groups of sensory cilia (absent in *P. cilioscutata* sp. nov.) located on the anterior and posterior part of the prostomium, respectively.

Résumé: Une nouvelle espèce de Paranerilla (Polychaeta: Nerillidae) des eaux du Nord-Est du Groenland, océan Arctique. Paranerilla cilioscutata sp. nov. est décrite des eaux du Nord-Est du Groenland. L'espèce a été récoltée dans des sédiments vaseux à des profondeurs de 32 à 590 m entre 77°09'N à 82°11'N et 8°40.42'W à 30°24'W à Independence Fjord et dans la mer du Groenland. Cette nouvelle espèce étend l'aire de distribution des Nerillidae à l'océan Arctique. Elle est comparée à Paranerilla limicola qui est la seule autre espèce du genre. De nouveaux spécimens de P. limicola ont été récoltés à la localité type dans le Gullmar Fjord, Suède (58°16'N, 11°28'E). Les deux espèces ont été étudiées vivantes et fixées, en microscopie photonique et en microscopie électronique à balayage. Les deux espèces ont sept segments portant des soies composées et un prostomium caractéristique du genre avec deux cornes latérales et une couverture de cils dense. Chez P. cilioscutata, cette ciliature couvre entièrement le prostomium et le segment 1 et forme de larges plages ciliées sur les segments 2-6 (versus prostomium et segment 1 partiellement ciliés et bandes ciliées étroites, doubles ou simples sur les segments 2-6 chez P. limicola). L'étude réalisée sur P. limicola a également révélé deux groupes de cils sensoriels jusqu'ici inconnus, situés sur les parties antérieure et postérieure du prostomium. Ces cils sensoriels sont absents chez P. cilioscutata.

Keywords: high arctic, muddy sediments, Paranerilla cilioscutata sp. nov., P. limicola, SEM.

#### Introduction

The family Nerillidae consists of small polychaetes formerly assigned to the polyphyletic group Archiannelida (Jouin, 1971; Westheide, 1985). In all recent publications the family is included in the class Polychaeta (for reviews see Westheide, 1988, 1990), but the exact phylogenetic position is still enigmatic (Westheide, 1990; Rouse & Fauchald, 1997; Rouse & Pleijel, 2001). The nerillids belong to the meiobenthos and are usually less than 1.5 mm in length. All 49 described species of the 16 genera are short with 7-9 segments and a midventral ciliary band.

The genus *Paranerilla* Jouin & Swedmark, 1965 was established for a single species, *P. limicola* Jouin & Swedmark, 1965 from the Gullmar Fjord, Sweden. The genus has remained monotypic and *P. limicola* has only been recorded from a few other muddy localities off the Norwegian coast and in the northern Adriatic Sea (Sterrer, 1968). *Paranerilla* was defined mainly by the combination of the following characters: seven segments, all with compound chaetae, prostomium with two lateral horns and a dense covering of cilia; pygidium with two cirri (Jouin & Swedmark, 1965).

Recently collected polychaetes from subtidal sediments off Northeast Greenland are here assigned to *Paranerilla*, and described as a new species. It differs from *P. limicola* in a number of characters, several of which are only clearly visible with scanning electron microscopy (SEM). As *P. limicola* has not previously been examined with SEM, we collected it for comparative SEM and LM studies. These studies provided new information on *P. limicola*, which are here included as an emended description of this species.

The genus *Paranerilla* differs ecologically from other nerillids in several ways: Nerillids are predominantly found in the interstitial fauna of shell gravels and sandy sediments. *Paranerilla limicola* is the only nerillid found solely in muddy sediments (Jouin & Swedmark, 1965; Sterrer, 1968). A single other nerillid species, *Meganerilla swedmarki* Boaden, 1961 has been reported once from muddy sediment (Saphonov & Tzetlin, 1997).

Nerillidae have previously been recorded from most of the world, except for the Polar regions. They are mainly found in intertidal and shallow subtidal habitats. Three species are found at greater depths: *Bathychaetus heptapous* Faubel, 1978, at 126 m (Faubel, 1978), *Paranerilla limicola* at 270 m (Sterrer, 1968) and *Xenonerilla bactericola* Müller, Bernhard & Jouin-Toulmond, 2001, at 592 m (Müller et al., 2001). We have also found the genus *Paranerilla* in *Globigerina* sediments in the deep sea (e.g., 3660 m; 46°18.57'N, 12°33.88'W) (R. M. Kristensen, unpubl.), but the material was too poor for species identification.

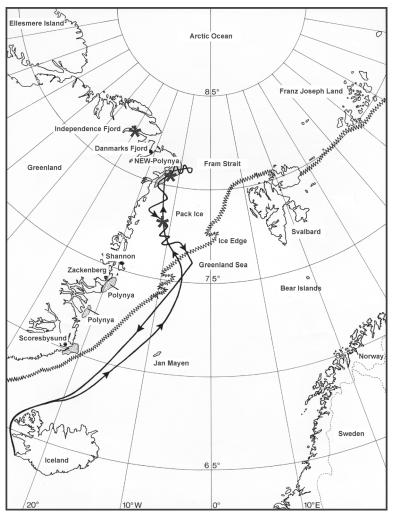
Nerillids generally move by gliding with the help of the midventral ciliary band and, in addition, most species observed alive are also capable of making a quick escape reaction by rapid undulation of the body (e.g., Jouin & Swedmark, 1965). *Paranerilla limicola* has moreover been observed to enter the upper layers of the sediment by moving particles across its dorsal surface (Jouin & Swedmark, 1965). This transport of particles is enabled by the dense covering of cilia on the prostomium and first segment, which is unique for this genus.

# **Materials and methods**

Material from Greenland Sea and Northeast Water Polynya Meiofauna samples were collected during an expedition to the Northeast Water Polynya 15 July - 19 August 1992 with the US Coast Guard icebreaker Polar Sea (Kristensen & Kristensen, 1993). Samples were taken between 76°56'N and 80°49'N and between 7°19'W and 16°47'W (Fig. 1) at depths from 10 m (SCUBA- diving) to 1216 m (gravity core). A total of 26 localities were sampled for meiobenthos using a 1 m<sup>2</sup> spade corer (modified box corer, see fig. 7.6, p. 119 in Fleeger et al., 1988). For each spade core sample, 0.4 m<sup>2</sup> of mud sediment was treated with a modified Higgins' bubbling technique (Higgins & Kristensen, 1988). Mixed sediment and water (1:1) was bubbled with air and the surface screened with a 200 µm mesh net. The meiobenthos was rinsed in seawater, bulk-fixed in 4% formaldehyde (buffered with borax) and stained with Rose Bengal. The new Paranerilla was found in 21 spade cores from 12 stations (see Fig. 2).

A total of 36 specimens were sorted out. Six specimens (including the holotype) from two spade cores (SC 32: 450 m, 80°01.41'N, 15°56.85'W and SC 44: 289 m, 80°16.54'N, 08°40.83'W) were sorted out live and examined in detail on board the vessel. They were observed live both with stereo microscope (x 50) and a Zeiss phase contrast microscope. Five specimens from sample SC 44 and one specimen from sample SC 31 were fixed in a trialdehyde solution (Lake, 1973), for 2 hours. Thereafter, specimens were rinsed and stored in 0.1 M sucrose/sodium cacodylate buffer until further treatments. Thirty specimens were sorted out from 4% formaldehyde bulk-fixed samples (see Table 1).

A total of 19 specimens (for light microscopy (LM)) were washed in demineralized water and the fixative was replaced with 2% glycerol in distilled water, which was added under the cover slip. When fully dehydrated after two days, the cover slip was sealed with Glyceel®. All whole mounts were examined and photographed with phase contrast and DIC (Nomarski-technique) in an Olympus BX51 microscope mounted with a digital camera (Olympus c-3030). The holotype was drawn using a Wild drawing tube (camera lucida) mounted on a Wild M20 microscope. Two



**Figure 1.** The cruise (arrows) of NEW-P92 with the icebreaker *Polar Sea* in the summer 1992. Sample sites of *Paranerilla cilioscutata* sp. nov. from Independence Fjord, NEW-Polynya and Fram Strait are indicated with stars. The polynyas (dotted areas) are shown in the pack ice. The ice edge is drawn from a satellite photo mid July, 1992.

**Figure 1.** Trajet (flèches) de la Campagne NEW-P92 du brise-glace *Polar Sea* pendant l'été 1992. Les lieux de récolte de *Paranerilla cilioscutata* sp. nov. de Independence Fjord, NEW-Polynya et Fram Strait sont indiqués par des étoiles. Les polynyes (aires pointillées) sont montrées dans le pack. Le front de glace est dessiné d'après une photographie satellite de mi-juillet 1992.

trialdehyde-fixed and four formaldehyde-fixed specimens for SEM were transferred through an acetone series and critical point dried using carbon dioxide. Thereafter they were mounted on aluminium stubs, sputter coated with gold, and examined with a JEOL JSM-840 scanning electron microscope. Ten specimens were examined with an Olympus SZX12 stereoscope and stored in 4% formaldehyde and one trialdehyde-fixed specimen was embedded for future sectioning and examination in transmission electron microscopy (Table 1).

## Material from Independence Fjord

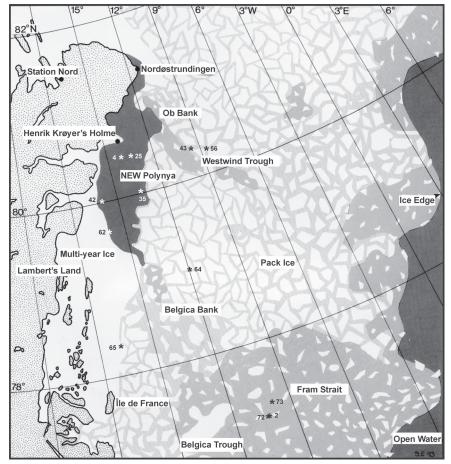
During the Independence Fjord Expedition in 1995 (Klitgaard & Schiøtte, 1998) 13 meiofauna samples were collected for kinorhynchs (bubbling technique) in Jørgen Brøndlund Fjord and Independence Fjord. The samples were taken from seal holes and leads with a 1/50 m<sup>2</sup> van Veen grab in a transect from depths of 20 to 200 m. The detritus and the meiobenthos were subsequently decanted through a 63 µm mesh net and bulk-fixed in 4% formaldehyde (buffered with borax). Surprisingly, one sample from Independence Fjord collected on 9 August 1995 (32 m, 82°11'N, 30°24'W) also contained the new species of Paranerilla. A total of four animals were sorted out. One specimen was used for whole mount, two were prepared for SEM, and one examined with an Olympus SZX12 stereoscope and stored in 4% formaldehyde (Table 1).

## Material from the Gullmar Fjord, Sweden

New material of Paranerilla limicola was collected at the type locality in the Gullmar Fjord near Rödbergsskär at 48-57 m; 58°16'N, 11°28'E. The samples were taken with an Ockelmanndredge on 20 August 2001 on board the R/V Oscar von Südow. The samples were carefully washed in a 100 µm mesh and the animals sorted out alive. Several animals were observed and photographed alive in an Olympus BX51 microscope mounted with a digital camera (Olympus c-3030). Before fixation the animals were anaesthetized in an isotonic solution of MgCl<sub>2</sub>. Four specimens were used for whole mounts with the same method as described above after fixation in a 4% formaldehyde solution buffered with borax. More than ten specimens for SEM were fixed one hour in 1% osmium tetroxide, transferred to distilled water and dehydrated through an acetone series. The material was then critical point dried, mounted on stubs, sputter coated with gold, and examined with a JEOL JSM-840 scanning electron microscope.

#### Measurements and meristics

All measurements were made on fixed material mounted on slides (LM) or stubs (SEM). All segments were measured from the posterior border of the parapodia of the foregoing segment to the posterior border of the parapodia of the next segment. The curling up of several of the chaetae in the SEM-figures is an artefact of the critical point drying. Several of the examined specimens (e.g., the holotype, see Fig. 3) have one or more parapodia with regenerating, broken or lost chaetae. Shafts of these were measured when



**Figure 2.** Map of the ice condition around the NEW-Polynya (23 July 1992). All the localities (NEW-P92 stations) with *Paranerilla cilioscutata* sp. nov. are indicated. Note that the new species is found commonly both inside NEW- Polynya and outside in the Fram Strait.

**Figure 2.** Carte indiquant l'état de la glace autour de NEW-Polynya (23 juillet 1992). Toutes les localités (NEW-P92 stations) avec des *Paranerilla cilioscutata* sp. nov. sont indiquées. Noter que la nouvelle espèce est trouvée aussi bien dans NEW-Polynya qu'à l'extérieur, dans Fram Strait.

possible, and even lost chaetae (insertion visible) are included in the counting and numbering of chaetae in a fascicle. The pygidial cirri were easily lost during handling or fixation.

## Results

NERILLIDAE Levinsen, 1883 Paranerilla Jouin & Swedmark, 1965

#### Emended diagnosis

The genus *Paranerilla* Jouin & Swedmark, 1965 is characterized by the following characters: seven chaetigerous segments between prostomium and pygidium; prostomium without appendages but with two lateral horns; compound chaetae; dorsal and ventral ciliation well developed; segment 1 with cirri fully developed; cirri in

following parapodia rudimentary; two elongate pygidial cirri.

Paranerilla cilioscutata sp. nov. Figs 3-6, 9; Table 2

#### Material examined

The specimens were collected in 1992 and 1995 at 32-590 m between 77°09'N and 82°11'N, and between 8°40.42'W and 30°24'W (Figs 1, 2). Forty specimens were examined for the taxonomic description (Table 1).

#### Type material

Holotype: deposited in the Zoological Museum, University of Copenhagen, (ZMUC), Denmark, ZMUC-Pol-1318, whole mount, female, 678 µm long, USA Coast Guard *Polar Sea*, St.56, SC 44, 289 m, 80°16.54'N, 8°40.83'W, 7 August 1992.

Paratypes: in addition to the holotype, 35 paratypes are deposited in the ZMUC, 2 paratypes are deposited in the Smithsonian Institution, US National Museum of Natural History (USNM), Washington D.C., USA and 2 paratypes are deposited in the Sweden Museum of Natural History (SMNH), Stockholm, Sweden. See Table 1 for detailed information.

#### Diagnosis

A *Paranerilla* with an extended dorsal ciliation: dorsal ciliary covering on prostomium and segment 1; dorsal ciliary plates (or very broad bands) on segment 2-6 and a narrow transverse

ciliary band at the posterior part of segment 7. Prostomial sensory fields with sensory cilia absent.

Etymology: cilioscutata refers to the several ciliary plates on the dorsal surface of the body; "scutum" is Latin for "shield".

*Description* (measurements of holotype and additional measurements in Table 2)

A yellow-whitish, opaque nerillid consisting of prostomium, 7 chaetigerous segments and pygidium (Figs 3, 4, 5A). All examined specimens adults with 7 segments and total length 319-870  $\mu$ m, last segments not fully developed in shortest specimens. Maximum body width always at segment 4, up to 286  $\mu$ m (excluding parapodia). Prostomium with lateral horns and almost fused to segment 1 (Figs 3, 4, 5B, 6A-D). Prostomium up to 59  $\mu$ m long,

**Table 1.** List of site information. Abbreviations: (BC) box corer, (Form.) 4% formaldehyde, (SC) spade corer, (SEM) specimen on SEM-stub, (St.) station, (Triald.) trialdehyde, (WM) whole mount.

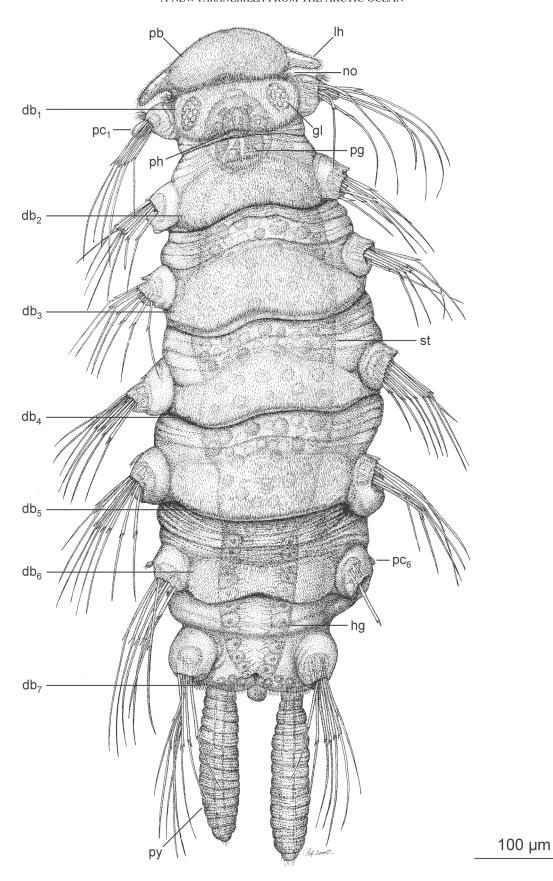
**Tableau 1**. Informations sur les différents échantillons et les lieux de récolte. Abréviations : (*BC*) carottier boîte, (*Form.*) formaldéhyde à 4 %, (*SC*) carottier, (*SEM*) spécimen sur porte-objet pour Microscopie électronique à balayage (MEB), (*St*) station, (*Triald.*) trialdéhyde, (*WM*) montage in toto.

Catalogue No.	Preparation	Fixation	Length (µm)	Station, sample	Water depth (m)	Date	Coordinates (°N, °W)	
ZMUC-POL-1318								
(Holotype)	WM	Triald.	678	St. 56, SC 44	289	07.08.1992	80°16.54', 8°40.83'	
ZMUC-POL-1319	WM	Form.	457	St. 25, SC 05	302	26.07.1992	80°28.05', 13°23.44'	
ZMUC-POL-1320	WM	Form.	501	St. 35, SC 18	105	29.07.1992	80°01.85', 13°26.63'	
ZMUC-POL-1321	WM	Form.	388	St. 35, SC 18	105	29.07.1992	80°01.85', 13°26.63'	
ZMUC-POL-1322	WM	Form.	319	St. 35, SC 18	105	29.07.1992	80°01.85', 13°26.63'	
ZMUC-POL-1323	WM	Form.	707	St. 35, SC 18	105	29.07.1992	80°01.85', 13°26.63'	
USNM	WM	Form.	747	St. 35, SC 18	105	29.07.1992	80°01.85', 13°26.63'	
ZMUC-POL-1324	WM	Form.	381	St. 43, SC 34	316	02.08.1992	80°19.61', 9°34.37'	
ZMUC-POL-1325	WM	Form.	760	St. 43, SC 35	318	02.08.1992	80°19.53', 9°37.40'	
USNM	WM	Form.	420	St. 43, SC 36	316	02.08.1992	80°19.49', 9°31.38'	
SMNH 5740	WM	Form.	461	St. 43, SC 37	310	02.08.1992	80°19.28', 9°28.04'	
ZMUC-POL-1326	WM	Form.	618	St. 43, SC 37	310	02.08.1992	80°19.28', 9°28.04'	
ZMUC-POL-1327	WM	Triald.	728	St. 56, SC 44	289	07.08.1992	80°16.54', 8°40.83'	
ZMUC-POL-1328	WM	Triald.	702	St. 56, SC 44	289	07.08.1992	80°16.54', 8°40.83'	
SMNH 5741	WM	Form.	437	St. 56, SC 45	291	07.08.1992	80°16.27', 8°40.42'	
ZMUC-POL-1329	WM	Form.	512	St. 56, SC 45	291	07.08.1992	80°16.27', 8°40.42'	
ZMUC-POL-1330	WM	Form.	818	St. 64, SC 66	210	09.08.1992	79°00.45′, 11°59.19′	
ZMUC-POL-1331	WM	Form.	623	St. 64, SC 66	210	09.08.1992	79°00.45′, 11°59.19′	
ZMUC-POL-1332	WM	Form.	870	St. 72, SC 74	490	12.08.1992	77°09.07', 10°32.61'	
ZMUC-POL-1333	WM	Form.	672	St. 36	32	09.08.1995	82°11', 30°24'	
ZMUC-POL-1334	SEM	Form.		St. 43, SC 34	316	02.08.1992	80°19.61', 9°34.37'	
ZMUC-POL-1335	SEM	Form.		St. 43, SC 36	316	02.08.1992	80°19.49', 9°31.38'	
ZMUC-POL-1336	SEM	Form.		St. 43, SC 37	310	02.08.1992	80°19.28', 9°28.04'	
ZMUC-POL-1337	SEM	Form.		St. 56, SC 43	285	07.08.1992	80°16.78', 8°41.51'	
ZMUC-POL-1338	SEM	Triald.	652	St. 56, SC 44	289	07.08.1992	80°16.54', 8°40.83'	
ZMUC-POL-1338	SEM	Triald.	744	St. 56, SC 44	289	07.08.1992	80°16.54', 8°40.83'	
ZMUC-POL-1339	SEM	Form.		St. 36	32	09.08.1995	82°11', 30°24'	
ZMUC-POL-1339	SEM	Form.		St. 36	32	09.08.1995	82°11', 30°24'	
-	Embedded	Triald.		St. 42, SC 31	448	30.07.1992	80°01.11', 15°57.31'	
ZMUC-POL-1340	None	Form.		St.02, BC 01	490	19.07.1992	77°09.12', 10°25.30'	
ZMUC-POL-1379	None	Form.		St.04, BC 10	320	21.07.1992	80°26.40', 14°06.77'	
ZMUC-POL-1380	None	Form.		St. 42, SC 32	450	30.07.1992	80°01.41', 15°56.85'	
ZMUC-POL-1381	None	Form.		St. 56, SC 43	285	07.08.1992	80°16.78', 8°41.51'	
ZMUC-POL-1382	None	Form.		St. 62, SC 49	190	08.08.1992	79°37.62', 15°55.90'	
ZMUC-POL-1383	None	Form.		St. 64, SC 61	217	09.08.1992	79°00.46', 11°58.56'	
ZMUC-POL-1384	None	Form.		St. 64, SC 62	215	09.08.1992	79°00.49', 11°58.90'	
ZMUC-POL-1385	None	Form.		St. 65, SC 67	515	10.08.1992	78°19.07', 16°46.65'	
ZMUC-POL-1386	None	Form.		St. 72, SC 72	485	12.08.1992	77°09.00', 10°31.62'	
ZMUC-POL-1387	None	Form.		St. 73, SC 78	355	12.08.1992	77°17.34′, 10°03.92′	
ZMUC-POL-1388	None	Form.		St. 36	32	09.08.1995	82°11', 30°24'	

176 µm wide including lateral horns; maximum length of lateral horns up to 40 µm, measured along posterior edge. Prostomium and segment 1 together about as long as each of the following segments. Segment 7 generally shorter than segments 2-6, pygidium even shorter. The pygidium can be more or less retracted into segment 7 (see Table 2, Figs 3, 5A, 6B). Nuchal organs paired, situated on lateral sides of prostomium, between lateral horns and parapodia of

segment 1 (Figs 3, 6A, C). Parapodia in segment 1 up to 64 µm long (including cirrus), usually more than twice as long as length of following parapodia (Figs 3, 4, 5A, B, 6A-C).

Short cirri with few distal cilia on parapodia of segment 1 (Figs 3, 6C). Rudimentary cirri with few distal cilia usually found on parapodia of segments 2-7, between dorsal and ventral chaetal bundles (Figs 5D, 6E). Two pygidial cirri up to 175 µm long. Two distinctive muscle strands in



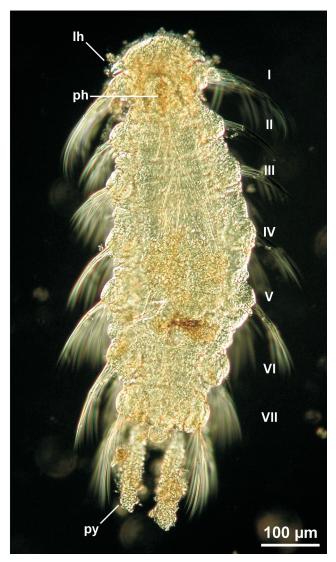
**Table 2.** Measurements and meristic characters of *Paranerilla cilioscutata* sp. nov. and *P. limicola* Jouin & Swedmark, 1965. All measurements, except those given by Jouin & Swedmark (1965) were made on new, fixed material. All measurements are given in  $\mu$ m. \*- measurements obtained from material in SEM. Abbreviations: (*L*) length, (*W*) width, (db<sub>1-7</sub>) dorsal ciliary bands (or plates) on segments 1-7.

**Tableau 2.** Mesures et caractères méristiques de *Paranerilla cilioscutata* sp. nov. et *P. limicola* Jouin & Swedmark, 1965. Toutes les mesures, excepté celles de Jouin & Swedmark, sont faites sur du matériel neuf fixé. Toutes les dimensions sont données en  $\mu$ m. \* mesures obtenues sur du matériel en MEB. Abréviations : (*L*) longueur ; (*W*) largeur ; ( $db_{1-7}$ ) bandes (ou aires) ciliées dorsales des segments 1-7.

	Paranerilla cilioscutata sp. nov.					P. limicola Jouin & Swedmark, 1965				
						Original		New ma		
	Holotype	Min.	Max.	Average	n	descript.	Min.	Max.	Average	n
TOTAL										
L (excl. appendages, chaetae)	678	319	870	599	22	700-900	295	880	701	6
Max. W (incl. parapodia)	262	103	305	190	19	150-200	90	268	209	4
Max. W (excl. parapodia)	232	93	286	171	19		66	236	180	4
No. segm.	7	7	7	7	22	7	7	7	7	6
PROSTOMIUM										
L to non-cil. gap	49	21	59	43	19		39	64	52	5
W (incl. lateral horns)	163	92	176	137	18	c.200	90	197	159	4
W (excl. lateral horns)	120	62	140	98	17		58	144	109	4
Lateral horns	38	13	40	27	18		24	44	35	4
L prost.+ segm. 1	99	48	117	88	19		57	172	111	5
L buccal glandular plates		11	34	20	5		28	28	28	1
BODY										
L segm. 1 (from non-cil. gap										
to end of parapodia)	50	29	70	47	18		18	108	58	5
L segm. 2	89	53	131	80	19		46	120	90	5
L segm. 3	78	47	119	76	19		41	123	87	5
L segm. 4	109	41	130	86	19		40	117	93	5
L segm. 5	99	36	146	89	19		38	120	95	5
L segm. 6	117	30	141	78	19		36	116	89	5
L segm. 7	83	30	126	70	19		30	131	89	5
L pygidium	2	0	45	9	19		0	17	6	5
L anal cirri	175	73	175	117	3		83	83	83	2
Max. L parapodia segm. 1	59	28	64	46	18		52	86	69	2
CILIA										
L db1*		53	53	53	2		26	63	45	2
L db2-db5*		52	61	57	2		8	40	23	2
L db6*		12	43	28	2		6	9	8	2
СНАЕТАЕ										
Max. no. chaetae segm. 1*		13	14		2	13-17	9	13		2
No. chaetae notopodia										
(max. in segm 3-6)*		7	11		2	6-9	6	11		2
No. chaetae neuropodia										
(max. in segm 3-6)*		7	11		2	6-9	7	11		2
Total L chaetae*		54	163		1		63	166		2
L shaft*		5	72		1	33-80	7	64		2
L distal extension shaft*		2	10		1	6.5-9	3	8		2
L blade*		35	111		1	47-75	34	117		2

**Figure 3.** Camera lucida drawing of *Paranerilla cilioscutata* sp. nov.: dorsal view of holotype female (ZMUC-Pol-1318). Abbreviations:  $(db_{1-7})$  dorsal ciliary bands (or plates) on segments 1-7, (gl) glands, (hg) hindgut, (lh) lateral horn, (no) nuchal organ, (pb) prostomial ciliary plate,  $(pc_1)$  parapodial cirrus on segment 1,  $(pc_6)$  rudimentary parapodial cirrus on segment 6, (pg) pharyngeal glands, (ph) pharynx, (py) pygidial cirri, (st) stomach.

Figure 3. Dessin à la chambre claire de *Paranerilla cilioscutata* sp. nov. : vue dorsale de l'holotype femelle (ZMUC-Pol-1318). Abréviations :  $(db_{1-7})$  aires ciliées dorsales des segments 1-7, (gl) glandes, (hg) intestin postérieur, (lh) corne latérale, (no) organe nucal, (pb) aire ciliée du prostomium,  $(pc_1)$  cirre parapodial du segment 1,  $(pc_6)$  cirre parapodial rudimentaire du segment 6, (pg) glandes pharyngiennes, (ph) pharynx, (py) cirres pygidiaux, (st) estomac.



**Figure 4.** Light micrograph of *Paranerilla cilioscutata* sp. nov.. Dorsal view of the holotype female (ZMUC-Pol-1318). Abbreviations: (I-VII) segments 1 to 7, (*lh*) lateral horn, (*ph*) pharynx, (*py*) pygidial cirri.

**Figure 4.** Microphotographie de *Paranerilla cilioscutata* sp. nov.. Vue dorsale de l'holotype femelle (ZMUC-Pol-1318). Abréviations : (I-VII) segments 1 à 7, (*lh*) corne latérale, (*ph*) pharynx, (*py*) cirres pygidiaux.

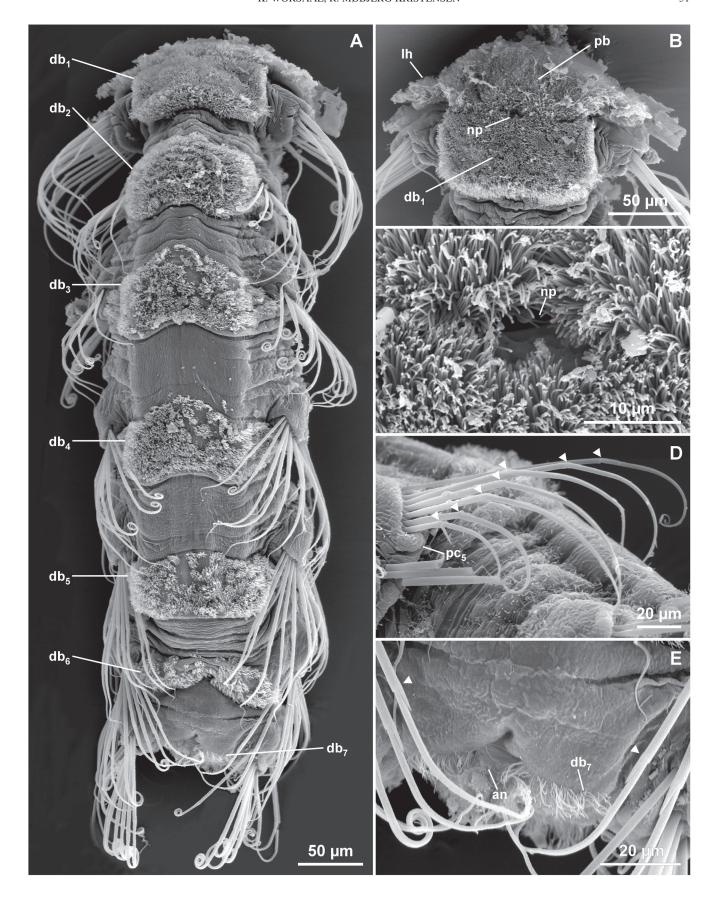
each cirrus, retracted strongly upon fixation (Figs 3, 4). The cirri are easily lost, only 3 of 28 examined specimens (holotype ZMUC-Pol-1318, paratypes ZMUC-Pol-1322 and 1325) had one or both pygidial cirri. Live specimens were observed to discard their cirri upon a slight touch.

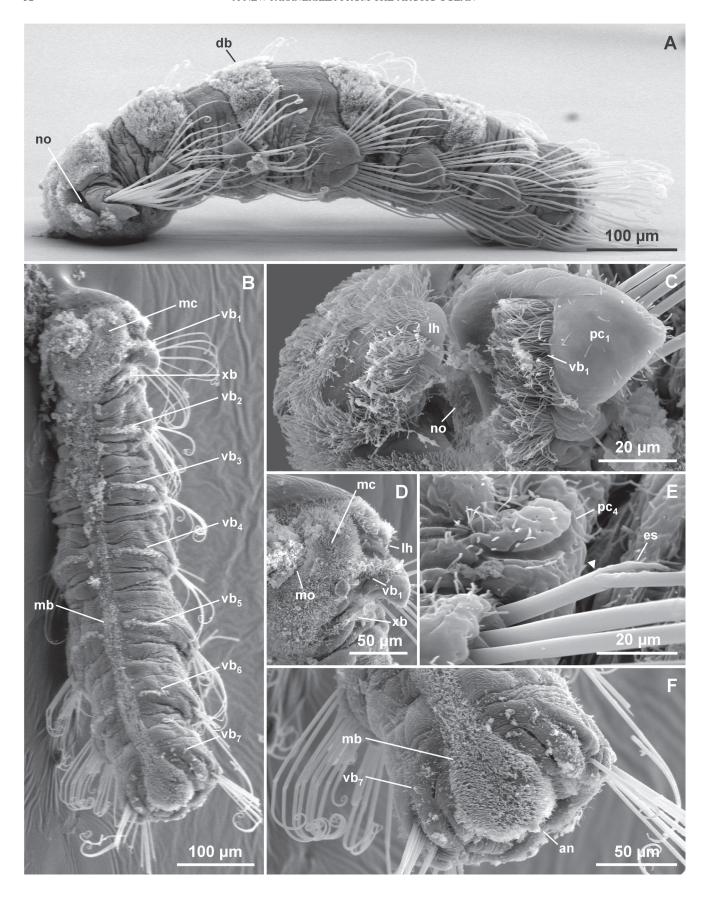
All chaetae compound, shaft with pointed distal extension (Figs 5D-E, 6E). Segment 1 uniramous, with only one chaetal fascicle, with maximum of 14 chaetae; segments 2-7 biramous, with dorsal and ventral fascicles comprising 7-11 chaetae each, highest number in segments 3-6. No noticeable differences between dorsal and ventral chaetae in number and measurements. Measurements of chaetae obtained with SEM from ZMUC-Pol-1338, animal length 652 µm, are given in Table 2 and Fig. 9. Lengths of shaft, distal extension and blade as well as total length of chaetae increase from segment 2 (max. total length 107 µm) to segment 7 (max. total length 163 µm) (Fig. 9A). However, chaetae of segment 1 are among the longest found (max. total length 153 µm), although shafts are often shorter than in segments 4-7 (Fig. 9A, B). Chaetae closest to rudimentary cirrus in dorsal and ventral chaetal fascicles generally much shorter in total length than remaining chaetae (Fig. 9B, C). In each of segments 2-7 an ontogenetic pattern of the chaetae can be detected as the shafts lengthen the farther away from the rudimentary cirrus the dorsal and ventral chaetae are situated (Fig. 9B). The length of the blades shows another pattern: they are shortest near the middle of the parapodium, then gradually lengthen, but afterwards decrease in length farthest away from the rudimentary cirrus (Fig. 9C). The decrease in length may be due to longer exposure to hard wear for these "older" chaetae. More likely, these chaetal blades were formed during maturation, and longer blades are formed when the animal is mature. The developmental patterns of shafts and blades cannot be detected in segment 1, where only one chaetal bundle is present and several of the chaetae are broken off. However, the shafts of the middle chaetae tend to be shorter than the rest, and the relatively few blades measured are of similar length (Fig. 9B, C).

Entire dorsal surface of prostomium and segment 1 covered with cilia, except for minor non-ciliated area on frontal surface of each lateral horn, a very narrow non-

**Figure 5.** Scanning electron micrographs of *Paranerilla cilioscutata* sp. nov. (ZMUC-Pol-1338) (SEM-stub with two specimens). Note that the pygidial cirri are missing. **A.** Dorsal view of whole animal with six ciliary plates on segments 1-6  $(db_{1-6})$  and a ciliary band on segment 7  $(db_7)$ . **B.** Dorsal view of the head region with the two ciliated areas: dorsal ciliary plate of prostomium (pb) and segment 1  $(db_1)$ . **C.** Close up of non-ciliated pit (np) between pb and  $db_1$ . **D.** Lateral view of segment 5 with rudimentary parapodial cirrus  $(pc_5)$ . Arrowheads indicate joints of compound notochaetae. **E.** Close-up of segment 7 and pygidium. Arrowheads indicate joints of compound notochaetae. Abbreviations: (an) anus, (lh) lateral horn.

**Figure 5.** Paranerilla cilioscutata sp. nov. vue au Microscope électronique à balayage (MEB) (ZMUC-Pol-1338, porte-objet MEB avec 2 spécimens). Les lobes pygidiaux manquent. **A.** Vue dorsale d'un spécimen entier montrant les 6 plages ciliées des segments 1-6  $(db_{1-6})$  et une bande ciliée sur le segment 7  $(db_7)$ . **B.** Vue dorsale de la tête avec deux aires ciliées, celles du prostomium (pb) et du segment 1  $(db_1)$ . **C.** Détail de la fossette non ciliée entre pb et  $db_1$ . **D.** Vue latérale du segment 5 avec un cirre parapodial rudimentaire  $(pc_5)$ . Les têtes de flèches indiquent les articulations des soies composées dorsales. **E.** Détail du segment 7 et du pygidium. Têtes de flèches comme en D. Abréviations : (an) anus, (lh) corne latérale.





ciliated gap on borderline between the two elements, and a small non-ciliated pit in the middle of this (Figs 3, 5A-C, 6C). No sensory cilia or other external structures could be identified within this pit (Fig. 5C).

Besides the ciliated prostomium and segment 1, the remaining dorsal surface of *P. cilioscutata* sp. nov. is extraordinary densely ciliated. On segments 2-6, very broad ciliary bands appearing as ciliary plates cover almost half the length of each segment and stretch across segments between parapodia on each lateral side (Figs 3, 5A, 6A). The plates are densely ciliated with slightly elevated borders (Figs 5A, 6A). Maximum width (longitudinal direction of worm) about 60  $\mu$ m in segments 2-5, somewhat less in segment 6 (found on a specimen with total length 744  $\mu$ m). On segment 7, narrow band of cilia instead of plate (Fig. 5A, E).

Ventral surface of prostomium and segment 1 fully covered with cilia (Fig. 6B, D). Midventral double ciliary band from pharyngeal region to pygidium, and further on to anus on dorsal side (Fig. 6B). Band broadens on segment 7 and pygidium (Fig. 6B, F). Transverse ventral ciliary bands on segments 2-7 from parapodia to very near midventral band (Fig. 6B). On segment 1, this band fuses with pharyngeal ciliation (Fig. 6B-D). An extra ventral transverse band between segments 1 and 2 (Fig. 6B, D).

Pharynx muscular, with pharyngeal bulb in segment 1 (Figs 3, 4). Pharynx opening ventrally between prostomium and segment 1. Many reddish salivary glands, most likely opening into buccal cavity on dorsal side of pharynx (Fig. 3). Two large, hyaline to blue glands in segment 1, one on each side of pharyngeal organ (Fig. 3). They consist of several cells with relatively large round vesicles. A pair of short peanut-shaped glandular plates (11-34 µm long) in middle of pharyngeal organ. Measurements may be somewhat defective as it was difficult to interpret the structure because of underlying bundles of pharyngeal muscle fibres. Large round glandular and microvillar cells line stomach wall; large ciliated cells line hindgut (Fig. 3).

Nephridia, sperm and eggs were difficult to detect in fixed material. However, we believe we have found

nephridia and aggregations of sperm in 3 specimens (paratypes ZMUC-Pol-1319, 1325 and 1330) in segments 2-7. Small eggs (max. dia. 23  $\mu$ m) were found in 3 other specimens (paratypes ZMUC-Pol-1318, 1326 and 1327) in front of the parapodia in segments 5 and 6.

#### Motility

The animals studied alive were observed to enter upper layers of sediments as well as make quick escape reactions by undulation of the body. Animals enter sediment by moving particles over the prostomium and dorsal body surface with the heavy ciliation. Furthermore, they often leave the substratum to swim into the water column with help of the dorsal ciliary plates and the midventral ciliary band. When they enter the sediment and while swimming gently through the water, parapodia and chaetae are compressed along the body.

#### Associated meiofauna

A rich hard-bodied meiofauna was observed in two mud samples sorted out live on board the vessel (see Materials and methods). This included harpacticoid copepods, nematodes, kinorhynchs (*Echinoderes* sp., *Pycnophyes* sp.), tanaids, tardigrades (e.g., *Styraconux qivitoq* Kristensen & Higgins, 1984), and a tantulocarid (*Polynyapodella ambrosei* Huys, Møbjerg & Kristensen, 1997). In addition, several soft-bodied taxa were found such as gastrotrichs, gnathostomulids, hydrozoans (*Protohydra* sp.), nemertines, turbellarians and small polychaetes (Kristensen & Kristensen, 1993; Møbjerg et al., 1995; Huys et al., 1997).

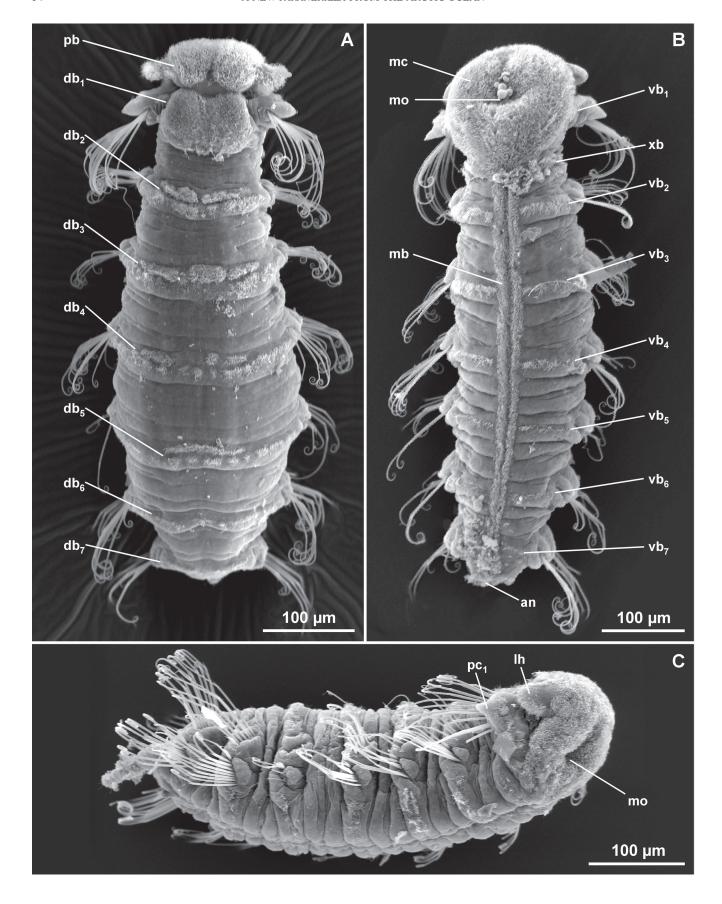
Paranerilla limicola Jouin & Swedmark, 1965 Paranerilla limicola Jouin and Swedmark, 1965: 201-218; Sterrer 1968: 65-68.

## Material examined

The specimens were collected 20 August 2001 at 48-57 m at the type locality in the Gullmar Fjord near Rödbergsskär, 58°16'N, 11°28'E. Thirteen specimens were examined for the emended description. Four whole mounts (ZMUC-Pol-1389 to ZMUC-Pol-1392) and nine specimens on two stubs

**Figure 6.** Scanning electron micrographs of *Paranerilla cilioscutata* sp. nov. (ZMUC-Pol-1338 (SEM-stub with two specimens)). Note that the pygidial cirri are missing. **A.** Lateral view of whole animal (same specimen as in Fig. 5A). **B.** Ventral view of whole animal (other specimen than in Fig. 6A). **C.** Lateral view of the prostomium with lateral horn (lh) and the parapodium on segment 1 with cirrus ( $pc_I$ ). **D.** Ventral view of prostomium and segment 1. **E.** Close-up of rudimentary parapodial cirrus ( $pc_I$ ) and distal extension of neurochaetal shaft (es) on segment 4, lateral view. Arrowhead indicates joint of compound chaeta. **F.** Ventral view of the segment 7 and the pygidium. Abbreviations: (an) anus, (ab) dorsal ciliary plate, (ab) midventral ciliary band, (ab) ciliary field around mouth, (ab) mouth, (ab) nuchal organ, (ab) ventral ciliary bands on segments 1 to 7, (ab) extra ventral ciliary band.

Figure 6. Paranerilla cilioscutata sp. nov. vue au MEB (ZMUC-Pol-1338, porte-objet MEB avec 2 spécimens). Les lobes pygidiaux manquent. A. Vue latérale du spécimen entier de la Figure 5A. B. Vue ventrale d'un autre spécimen entier. C. Vue latérale du prostomium, avec une corne latérale (lh), et d'un parapode du segment 1 avec un cirre ( $pc_1$ ). D. Vue ventrale du prostomium et du segment 1. E. Agrandissement du cirre parapodial rudimentaire ( $pc_4$ ) et du crochet distal (es) de la hampe d'une soie ventrale composée du segment 4, vue latérale. La tête de flèche indique l'articulation de la soie. F. Vue ventrale du segment 7 et du pygidium. Abréviations : (an) anus, (db) plage ciliée dorsale, (mb) bande ciliée médio-ventrale, (mc) ciliature péribuccale, (mo) bouche, (no) organe nucal, ( $vb_{1-7}$ ) bandes ciliées ventrales sur les segments 1-7, (xb) bande ciliée ventrale additionnelle sur le segment 1.



(ZMUC-Pol-1393 and ZMUC-Pol-1394). Six syntypes from the Swedish Museum of Natural History, Stockholm were compared, but not examined in detail.

### Diagnosis

A *Paranerilla* with large ciliated areas on prostomium and segment 1 and transverse ciliary bands on following segments. Anterior sensory field with group of sensory cilia; posterior sensory field with several sensory cilia arranged in characteristic pattern.

#### Emended description (Table 2, Figs 7-8)

The original description (Jouin & Swedmark, 1965) is excellent and the following emended description will therefore focus on additional information and two new characters found mainly from using SEM.

Two new groups of cilia were found in the present study of P. limicola. They are situated on the anterior and the posterior part of the prostomium, respectively, and we suggest them to be sensory (Fig. 8A-D). One group is found in the otherwise non-ciliated small pit on the anterior edge (frontal side) of the prostomium (Fig. 8A-C). It consists of 4-6 cilia situated right next to each other, with each cilium surrounded by a collar-like elevation of the cuticle. General ciliation on prostomium found relatively close to the pit. The anterior sensory cilia were easily distinguished on live animals (observed in LM), being non-motile and stiff among the constantly beating general ciliation on the prostomium. On each side of this group of sensory cilia, along the non-ciliated anterior edge of prostomium, are a few additional non-motile cilia. These cilia, which might also be sensory, could not be recognized with SEM as the general dense ciliation on the prostomium covers them. The group of anterior sensory cilia are indicated in the camera lucida drawing, but not mentioned in the text of the description by Jouin & Swedmark (1965).

Another undescribed group of cilia is not as easily seen on live animals with LM, but very obvious with SEM. This group is found on the posteriormost part of the prostomium, in an otherwise non-ciliated area on the borderline between prostomium and segment 1 (Fig. 8A-B, D). The cilia vary in length from 4 to 12  $\mu$ m and are also suggested to be sensory because of their non-motility as well as because of the

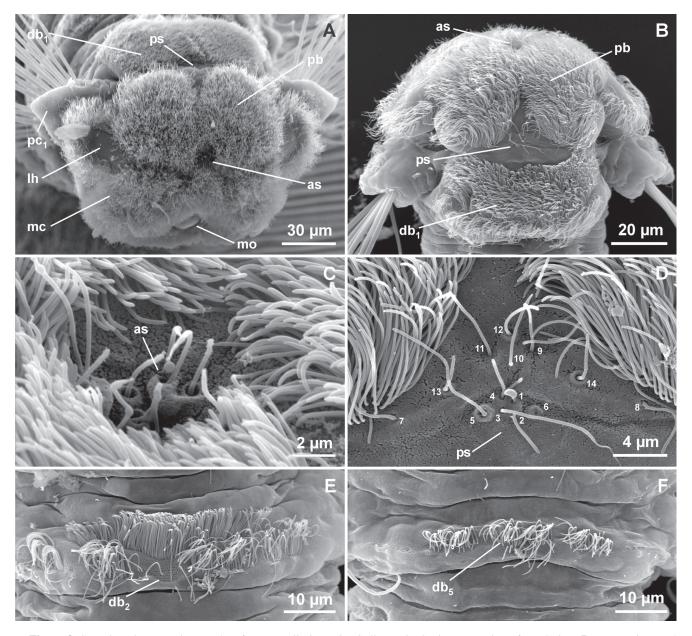
cuticular collar surrounding one or more cilia. This new autapomorphy of P. limicola deserves a detailed description because of the very specific pattern in which the cilia are arranged. The group consists of about 14 cilia arranged in a pattern covering an area about 20 µm wide and 10 µm long (no. 1-14 in Fig. 8D). Four cilia (1-4 in Fig. 8D) are situated in the centre (in the median line of the prostomium), right next to each other forming a square, surrounded by a common elevation of the cuticle. The remaining ten cilia are each surrounded by a more or less obvious collar elevation of the cuticle. On each lateral side of the four central cilia is found one cilium (5-6 in Fig. 8D). Lateral to these, less than 10 µm from the median line, almost next to the general ciliation of the prostomium, is found one more cilium on each lateral side (7-8 in Fig. 8D). Less than 4 µm anterior to the four central cilia four additional cilia are found (9-12 in Fig. 8D) relatively close to each other (orientated in each corner of a rhomb, the centre of which is in the median line). Between these and the four central cilia one cilium is found on each lateral side (13-14 in Fig. 8D), 4-5 µm from the median line.

The original description mentioned 13-17 chaetae in segment 1, 6-9 chaetae in both dorsal and in ventral chaetal bundle in the following segments. The present study found 6-11 chaetae in each bundle in segments 2-7, with highest number present in segments 4-7. The chaetae of two specimens were measured on pictures from SEM, expanding some of the ranges given in the original description: min. length of extension of shaft 3  $\mu$ m, max. length of blade 117  $\mu$ m (Table 2).

Jouin & Swedmark (1965) described double transverse bands on the dorsal surface on segments 2-4 and single bands on the following segments. The additional material here studied showed most specimens to possess double bands on segment 2-5 and single bands on segments 6-7 (Figs 7A, 8E). However, one small specimen (295  $\mu$ m long) had a single band on segment 5 (Fig. 8F). The anterior of the two bands in the double bands is generally somewhat shorter than the posterior one. In segments 4 and 5 the anterior band is only about 1/3 the length of the posterior one (Fig. 7A).

**Figure 7.** Scanning electron micrographs of *Paranerilla limicola* (Gullmar Fjord). Note that the pygidial cirri are missing in **A** and **B**, and only one cirrus is present in **C**. **A.** Dorsal view of the whole animal. **B.** Ventral view of whole animal. **C.** Lateral view of the whole animal. Abbreviations: (an) anus,  $(db_{1-7})$  dorsal ciliary bands (or plates) on segments 1 to 7, (lh) lateral horn, (mb) midventral ciliary band, (mc) ciliary field around mouth, (mo) mouth, (pb) prostomial ciliary plate,  $(pc_1)$  parapodial cirrus on segment 1,  $(vb_{1-7})$  ventral ciliary bands on segments 1 to 7, (xb) extra ventral ciliary band.

**Figure 7.** Paranerilla limicola (Gullmar Fjord), vue au MEB. Spécimens entiers, mais les cirres pygidiaux manquent en A et B et un seul cirre est présent en C. **A.** Vue dorsale. **B.** Vue ventrale. **C.** Vue latérale. Abréviations : (an) anus,  $(db_{1-7})$  bandes (ou aires) ciliées dorsales des segments 1-7, (lh) cornes latérales, (mb) bande ciliée médio-ventrale, (mc) ciliature péribuccale, (mo) bouche, (pb) aire ciliée du prostomium,  $(pc_1)$  cirre parapodial du segment 1  $(vb_{1-7})$  bandes ciliées ventrales sur les segments 1-7, (xb) bande ciliée ventrale additionnelle sur le segment 1.



**Figure 8.** Scanning electron micrographs of *Paranerilla limicola* (Gullmar Fjord). **A.** Prostomium, frontal view. **B.** Prostomium and segment 1, dorsal view. **C.** Close-up of anterior sensory cilia (as) in Fig. 8A. **D.** Close-up of posterior sensory cilia in Fig. 8B (ps, numbered 1-14). Note the collar around the sensory cilia. **E.** Dorsal ciliary band on segment 2 ( $db_2$ ). **F.** Dorsal ciliary band on segment 5 ( $db_5$ ), dorsal view. Abbreviations: (lh) lateral horn, (mc) ciliary field around mouth, (mo) mouth, (pb) prostomial ciliary plate, ( $pc_1$ ) parapodial cirrus on segment 1.

**Figure 8.** Paranerilla limicola (Gullmar Fjord), vue en MEB. **A.** Prostomium, vue frontale. **B.** Prostomium et segment 1, vue dorsale. **C.** Détail des cils sensoriels antérieurs (as) de la Fig. 8A. **D.** Détail des cils sensoriels postérieurs (ps, numérotés 1-14) de la Fig. 8B. Noter le collier à la base des cils. **E.** Bande ciliée dorsale du segment 2 ( $db_2$ ). **F.** Bande ciliée dorsale du segment 5 ( $db_5$ ).

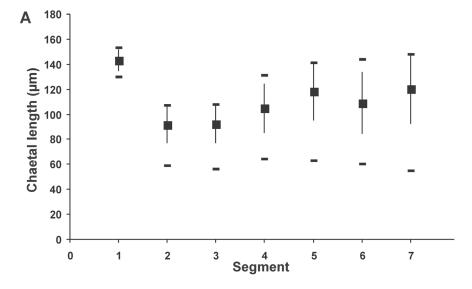
Abréviations : (lh) corne latérale, (mc) ciliature péribuccale, (mo) bouche, (pb) plage ciliée du prostomium,  $(pc_I)$  cirre parapodial du segment 1.

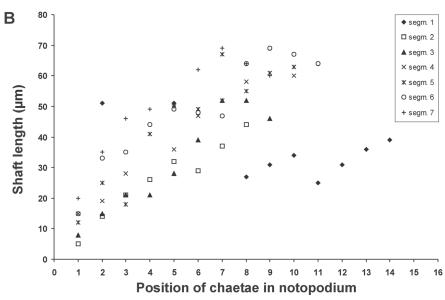
The midventral ciliary band, extending from the pharyngeal cilated area to the pygidium, broadens on segment 7 and the pygidium (Fig. 7B).

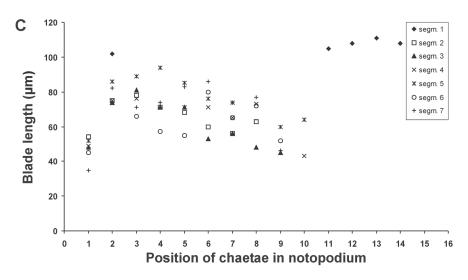
In all other details and characters we could confirm the description by Jouin & Swedmark (1965).

# Motility

The same motility patterns were observed for this species as the ones mentioned above for *P. cilioscutata* sp. nov. These patterns were also recognized and carefully described by Jouin & Swedmark (1965).







### Discussion

# Morphology

Until now Paranerilla has been monotypic, with P. limicola as the only species. The new Arctic species resembles P. limicola in having seven segments with compound chaetae, pygidium and the characteristic prostomium of Paranerilla, with two lateral horns and a covering of cilia. The new species sustains the generic diagnosis, and verifies that the genus lacks the prostomial appendages (antennae and palps) normally present in Nerillidae. The present with LM and SEM studies emphasized that the lateral horns of Paranerilla are continuous with the prostomium and not inserted (and discardable) appendages like e.g. However, transmission palps. electron microscopy of innervations is necessary to finally prove that the lateral horns are not homologous with palps or antennae.

Figure 9. Diagrams of measurements of notochaetae in *Paranerilla cilioscutata* sp. nov. Measurements are given as an average of chaetae on left and right side. A. Total length of notochaetae found in each segment (average, standard deviation, minimum and maximum values indicated). B-C. Lengths of shafts (B) and blades (C) of notochaetae as a function of their position from ventral to dorsal side (chaetae nos. 1-14) in each parapodium of segments 1-7 (marked as series with same signature).

Figure 9. Diagrammes des mesures effectuées sur les soies dorsales de *Paranerilla cilioscutata* sp. nov. Les mesures correspondent à des moyennes sur les soies des côtés droit et gauche pour chaque segment. A. Longueur totale des soies dorsales dans chaque segment (moyenne, écart type, valeurs minimum et maximum sont indiquées). B-C. Longueur des hampes (B) et des articles (C) des soies dorsales en fonction de leur position (1-14), depuis la face ventrale jusqu'à la face dorsale, dans chaque parapode des segments 1-7.

The dorsal ciliation of *P. cilioscutata* sp. nov. differs from P. limicola in several ways. The ciliation of P. cilioscutata sp. nov. covers almost the entire dorsal surface on both the prostomium and the first segment, except for a narrow nonciliated gap with a small non-ciliated pit in the middle, along the borderline between prostomium and segment 1 (versus partly ciliated prostomium and segment 1 in P. limicola). Ciliary plates are found on the dorsal surface on segment 2-6 in *P. cilioscutata* sp. nov. versus the double or single transverse ciliary bands found in P. limicola. The plates could also be interpreted as very broad densely ciliated "single bands" and are most likely homologous to the bands found in P. limicola. When two animals of about the same length are compared, the ciliary plates on segments 2-6 in P. cilioscutata sp. nov. are about twice as broad (longitudinal direction of worm) as the transverse bands in P. limicola.

The anterior and posterior groups of sensory cilia found in the non-ciliated areas on the prostomium of *P. limicola* are absent in *P. cilioscutata* sp. nov. However, the non-ciliated pit on *P. cilioscutata* sp. nov. on the borderline between the prostomium and segment 1 is situated in exactly the same area as the posterior group of sensory cilia on *P. limicola*.

The ventral transverse ciliary bands on the parapodia of segment 1 do not connect with the ventral ciliation of the pharyngeal area in *P. limicola* as they do in *P. cilioscutata* sp. nov. (Figs 6D, 7C).

The parapodia (including cirri) on segment 1 are somewhat shorter in *P. cilioscutata* sp. nov. than in *P. limicola* (Table 2), but this character may be affected by fixation and preparation. The pygidial cirri in both species were obviously strongly affected by fixation, which made it difficult to compare their lengths. Furthermore, both species very easily discard their pygidial cirri and only few were available for measurements.

The maximum number of chaetae found in a parapodium of *P. cilioscutata* sp. nov. differs from the number given in the original description of *P. limicola*. However, our additional studies of *P. limicola* showed that both species have up to 11 chaetae in a fascicle of segments 2-7 and 13-14 chaetae in segment 1 (Table 2). Similarly, our measurements showed the chaetae to be within the same length ranges in the two species (Table 2).

# Habitat, motility and distribution

Paranerilla cilioscutata sp. nov. is the first nerillid described from high arctic waters. The species is found both inside and outside the North East Water Polynya in muddy sediments. It is one of the deepest (down to 590 m) recorded nerillids. As mentioned in the introduction, a Paranerilla sp. has also been collected in the deep sea in muddy sediments (3660 m; Kristensen, unpubl.).

Paranerilla limicola and P. cilioscutata sp. nov. are the only nerillids found solely in muddy sediments (Jouin & Swedmark, 1965; Sterrer, 1968), the most common substratum of the arctic and deep-sea bottoms. The morphology of both species of Paranerilla deviates from other nerillids in many ways: they lack palps and antennae on the prostomium and furthermore only possess rudimentary parapodial cirri on most of the body. The pygidial cirri are the only true discardable appendages, and these contain very thick longitudinal muscles, which may contract during burrowing. Even though these cirri are easily shed during handling of the animals, they will not be directly exposed during burrowing. The lack of discardable appendages on the prostomium may be an advantage when burrowing in mud.

Within the Nerillidae, the ciliary covering of the prostomium and segment 1 is unique for Paranerilla. The aberrant morphology of Paranerilla, together with the unique motility pattern of the cilia used for entering the sediment, have to be considered as adaptations to muddy sediments. Relatively unusual for nerillids, P. cilioscutata sp. nov. and P. limicola were both observed leaving the substratum to swim gently into the water column. The freshwater nerillid Troglochaetus beranecki Delachaux, 1921 has also been observed to swim into the water column. but according to Delachaux (1921) it did this by help of the ciliation on the palps. The ability to swim could provide faster access to the most suitable substratum, which may be an important feature when living in nutrient-poor caves, arctic- or deep- sea waters. It is reasonable to assume that the nerillid genus Paranerilla, adapted to muddy sediment and being an elegant swimmer, can be found elsewhere in the muddy arctic- and deep-sea habitats.

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