

***Longipalpa saltatrix*, a new genus and species of the meiofaunal family Nerillidae (Annelida: Polychaeta) from an anchihaline cave in Bermuda**

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Abstract.—A new genus and species of the meiofaunal family Nerillidae is described from an anchihaline cave in Bermuda. The description is based on studies of live animals with dissecting and light microscopes, as well as studies of fixed material with light and scanning electron microscopy. *Longipalpa saltatrix*, new species, differs from all other nerillids by possessing a pair of extremely long latero-ventral palps on the prostomium and a pair of ciliated pygidial lobes. It is further characterized by the combination of the following characters: three very short dorsal prostomial antennae, eight chaetigerous body segments, single parapodial cirri from segment three to eight, compound chaetae, and hermaphroditism.

With 48 species in 17 genera (300 μm –2 mm in length), the Nerillidae is the largest meiofaunal family in the Polychaeta. The family has been a member of the now rejected group 'Archiannelida' (e.g., Beauchamp 1910, Goodrich 1912). The Nerillidae are now believed to be more closely related to a macrofauna family among the Aciculata and possibly have evolved by progenesis (Westheide 1990, Westheide & Purschke 1996, Rouse & Fauchald 1997, Rouse & Pleijel 2001).

Nerillids are nearly all marine and distributed worldwide, from the intertidal to abyssal depths (3660 m—see Worsaae & Kristensen 2003). While most nerillids are members of the interstitial sand fauna, some have been found in mud, fine silt, organic debris, bacterial mats, green algae and macrophytes (Jouin & Swedmark 1965, Gelder 1974, Sterrer & Iliffe 1982, Saphonov & Tzetlin 1997, Müller et al. 2001, Worsaae & Kristensen 2003). Several nerillids are known from caves: *Leptonerilla prospera* (Sterrer & Iliffe, 1982) was described from caves in Bermuda with fine silt; *Mesone-*

rilla diatomeophaga Núñez, 1997 in Núñez et al. (1997) was described from a cave in Lanzarote with diatom carpets on lapilli; *Nerilla marginalis* Tilzer, 1970 was described from a marginal cave in Istra; and *Troglochaetus beranecki* Delachaux, 1921 has been reported from various freshwater caves, groundwater reservoirs and mountain rivers in Europe and Colorado, U.S.A. [see Morselli et al. (1995) for review]. Nerillids are known from all continents, except Antarctica, and the wide geographical distribution as well as the diversity in habitats may well reflect an old evolutionary origin of the family.

The anchihaline Bermudian caves are inhabited by a rich and diverse fauna, consisting primarily of crustaceans (Sket & Iliffe 1980; Iliffe et al. 1983; Manning et al. 1986; Iliffe 1993, 1994, 2000). The most abundant stygobiont taxa are copepods and ostracods with 18 species each. Non-crustaceans include two ciliates, two gastropods, and two annelids—the nerillid *Leptonerilla prospera* and the tubificid oligochaete *Phallogriloides macmasterae* (Er-

séus, 1986). Although most of these species are endemic to Bermuda, many of them have cave-adapted congeners from the Caribbean, Mediterranean and the Pacific. Stygobiont taxa with such highly anomalous distributions are believed to be Tethyan relicts.

Materials and Methods

The geology of Bermuda is particularly unusual in that the island consists of a mid-ocean volcanic seamount, capped with marine and eolian limestone of Pleistocene age. The numerous inland caves of Bermuda are totally within this limestone and often contain tidal, anchihaline pools that extend below sea level to a maximum depth of about 25 m. Surface waters in these pools are brackish, with salinity increasing with depth to approach fully marine levels at 3–5 m depths. The island and its caves have been profoundly affected by changes in sea level associated with Pleistocene glaciation. During the Ice Ages, sea level was as much as 100 m lower and the caves of Bermuda were all dry and air filled. Large speleothems (stalactites and stalagmites) formed at this time by rainwater percolating through the ground and dripping into the caves. As glacial periods ended, sea level rose and flooded a substantial portion of the caves such that they are only accessible with the use of specialized cave diving techniques (Iliffe 1993, 1994).

The material was collected in Roadside Cave, a small anchihaline cave located in the Walsingham Tract of Bermuda (32°21'N, 64°43'W) on 15, 20 and 21 Jan 2002. A low entrance crawlway opens to a small dark chamber containing a narrow marine lake, which extends underneath a rock ledge and has a maximum depth of no more than 10 m. Surface salinity and temperature recorded on 28 Oct 1981 were 30‰ and 23°C, respectively. Tidal magnitude in the pool is 57% of that in the open ocean, with a lag of 80 minutes. A number of other anchihaline stygobionts inhabit this

small pool, including the platycopoid copepods *Antriscopia prehensilis* Fosshagen, 1985 in Fosshagen & Iliffe (1985) and *Nanocopia minuta* Fosshagen, 1988 in Fosshagen & Iliffe (1988); the calanoid copepod *Paracyclops naessi* Fosshagen, 1985 in Fosshagen & Iliffe (1985); the misophrioid copepod *Speleophria bivexilla* Boxshall & Iliffe, 1986; the bogidiellid amphipod *Bermudagidiella bermudensis* (Stock, Sket & Iliffe, 1987); the pseudoniphargid amphipod *Pseudoniphargus grandimanus* Stock, Holsinger, Sket & Iliffe, 1986; the halocyprid ostracod *Spelaeoecia bermudensis* Angel & Iliffe, 1987; the mictacean *Mictocaris halope* Bowman & Iliffe, 1985; and the gastropod *Caecum troglodyta* Moolenbeek & Faber, 1987 in Moolenbeek et al. (1987). Similar to the new species of polychaete here described, the copepods *Antriscopia prehensile*, *Nanocopia minuta* and *Speleophria bivexilla* are known only from this cave.

Samples were collected with a conical plankton net with a diameter of 30 cm and a mesh size of 40 µm. Rocks and projections below the water surface were covered with a thin layer of fine silt. Before the samples were taken, the surface layer was whirled up with hands, fins or loose stones from 0.5–6.5 meter's depth and thereafter the net was dropped and dragged through the suspended material.

More than 70 specimens were sorted out alive from the collected samples. Several of these were observed and video recorded alive with a Hitachi VK C-350 video camera mounted on a Wild M 420 Makroskop dissecting microscope. Fourteen animals were studied and photographed alive with an Olympus BX51 light microscope mounted with a digital camera (Olympus c-3030). Twelve of these were afterwards prepared as permanent whole mounts. Unless otherwise mentioned, measurements were made on live animals. Before fixation, the animals were anesthetized in an isotonic solution of MgCl₂, which was added under the cover slip for the whole mounts. The MgCl₂

of the whole mounts was replaced by a fixative (2% formaldehyde or a trialdehyde solution) and then by a glycerol series from 2–100% (diluted in distilled water). When the glycerol was fully dehydrated after two days, the cover slip was sealed with Glyceel®.

Twenty-six specimens were fixed for scanning electron microscopy (SEM) in a modified trialdehyde solution (Lake 1973) and postfixed in 1% OsO₄, or fixed directly in 1% OsO₄. The specimens were transferred to distilled water, dehydrated through an acetone series, critical point dried, mounted on stubs, sputter coated with palladium, and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

The study of live animals was carried out at the Bermuda Aquarium and Zoo (BAMZ) and the study of fixed material was carried out at the Zoological Museum, University of Copenhagen (ZMUC). Types are deposited in the Zoological Museum, University of Copenhagen (ZMUC), Denmark, and in the Smithsonian Institution, National Museum of Natural History (USNM), Washington D.C., U.S.A.

Family Nerillidae Levinsen, 1883

Longipalpa, new genus

Diagnosis.—*Longipalpa* is unique among nerillids by having two extremely long palps on the prostomium and two densely ciliated lobes on the dorsal side of the pygidium. It is further characterized by the combination of the following characters: eight chaetigerous segments between prostomium and pygidium; prostomium with three very short simple dorsal antennae; compound serrated chaetae; single parapodial cirri from segment three to eight; two pygidial lobes; one anterior and one posterior group of non-motile cilia arranged in distinct patterns and a pair of short bands of motile cilia on prostomium; transverse discontinuous rows of ciliary tufts on dorsal and ventral surface; cuticular

plates in pharyngeal apparatus; two pairs of segmented nephridia from segment II–III and III–IV; hermaphroditic reproduction with one pair of spermiotests from segment VI–VII and one pair of oviducts from segment VII–VIII.

Type species.—*Longipalpa saltatrix*, new species, by present designation.

Gender.—Feminine.

Etymology.—From the Latin *longus* (=long) + English *palp* (=prostomial appendage), in reference to the greater length of these appendages when compared to other genera in the family.

Similarity.—*Longipalpa* differs from the seventeen described nerillid genera by the two extremely long prostomial palps and two ciliated pygidial lobes. It furthermore differs from most genera by the very short length of the prostomial antennae, lack of parapodial cirri in segment 2 and possible lack of pygidial cirri.

Four characters have been important in defining nerillid genera in recent years: number of body segments (7–9), compound or capillary chaetae, number of antennae (0–3), and number of cirri per parapodium (1–2) (Tzetlin & Larionov 1988, Tzetlin & Saphonov 1992, Westheide & Purschke 1996, Müller et al. 2001, Müller 2002). *Longipalpa* resembles eight genera (*Afronerilla*, *Akessonniella*, *Micronerilla*, *Nerillidium*, *Nerillidopsis*, *Thalassochaetus*, *Trochonerilla*, *Troglochaetus*) by having eight segments. It thereby differs from four genera with seven segments (*Aristonerilla*, *Bathychaetus*, *Paranerilla*, *Psammoriedlia*) and five genera with nine segments (*Leptonerilla*, *Meganerilla*, *Mesonerilla*, *Nerilla*, *Xenonerilla*). It resembles seven genera with compound chaetae (*Aristonerilla*, *Leptonerilla*, *Mesonerilla*, *Micronerilla*, *Nerillidopsis*, *Paranerilla*, *Thalassochaetus*) and six genera with three antennae (*Aristonerilla*, *Leptonerilla*, *Mesonerilla*, *Micronerilla*, *Nerilla*, *Trochonerilla*), although only *Trochonerilla* possesses antennae of similar short length. Two genera (*Leptonerilla*, *Micronerilla*) differ from *Longipalpa* by the

presence of two cirri per parapodium (versus one cirrus per parapodium in *Longipalpa*).

Six genera show resemblance to *Longipalpa* in three out of the four "generic" characters mentioned above: *Aristonerilla*, *Mesonerilla*, *Micronerilla*, *Nerillidopsis*, *Thalassochaetus*, and *Trochonerilla* (see Table 1). *Micronerilla* may show the greatest resemblance with *Longipalpa*, but differs by having two cirri per parapodium, pygidial cirri and two eyes. It furthermore diverges by the much longer antennae; many ciliary tufts on antennae, parapodial and pygidial cirri; parapodial cirri present on segment 2 (and sometimes on segment 1 as well) and absent on the last segment; gonochoristic reproduction and two pairs of spermi ducts (Swedmark 1959, Jouin 1970, Saphonov & Tzetlin 1997, Müller 2002). The other five genera likewise differ from *Longipalpa* in several important characters mentioned in Table 1.

Leptonerilla prospera has previously been described from the caves of Bermuda (Sterrer & Iliffe 1982). The two Bermudian cave species have not been found in the same cave or cave-systems, although Roadside Cave and Walsingham Cave (type locality for *L. prospera*) are separated by only 290 m. Their morphology is very different, and there is no reason to suspect that these two species should be closely related.

Longipalpa saltatrix, new species

Figs. 1–6, Table 2

Gen sp. A in Worsaae & Müller (2004).

Type material.—Holotype: ZMUC-POL 1675 (whole mount), 763 µm long, Roadside Cave, Bermuda (32°21'N, 64°43'W), 0.5–6.5 m depth, 20 Jan 2002. Paratypes: All paratypes with same locality as for holotype, 0.5–6.5 m depth, collected 15, 20 and 21 Jan 2002. Nine specimens as whole mounts (ZMUC-POL 1676–1684) and 26 specimens on nine SEM-stubs (ZMUC-POL 1685–1693) are deposited in the Zoological Museum, University of Copenhagen

Table 1.—Comparison with relevant genera. Abbreviations: (), exceptions from remaining species of a genus; —, not applicable; segm, segment.

Genus	Segm	Antennae	Antennae dimensions ^a	Chaetae	Eyes	Cirri segm	Cirri per parapodium	Pygidial cirri	Sex	Spermi ducts segm	Others
<i>Longipalpa</i>	8	3	short	compound	0	3–8	1	0	hermaphroditic	VI–VII	long palps, pygidial lobes ciliary tufts on antennae
<i>Aristonerilla</i>	7	3	long	compound	2	2–7	1	2	gonochoristic	VI–VII	
<i>Mesonerilla</i>	9	3 (2)	long	compound	(0)	1–9	1	2	gonochoristic, hermaphroditic	IV–V, V–VI + VI–VII	
<i>Micronerilla</i>	8	3	long	compound	2	1–7	2	2	gonochoristic	VI–VII + VII–VIII	ciliary tufts on antennae
<i>Nerillidopsis</i>	8	2	medium	capillary + compound	0	2–7	1	2	hermaphroditic	V–VI	
<i>Thalassochaetus</i>	8	0	—	compound	0	2–7	1	2	?	?	
<i>Trochonerilla</i>	8	3	short	capillary	2	2–7	1	2	gonochoristic	VI–VII + VII–VIII	palps present ^b

^a Short = antennae shorter than prostomium and palps, medium = antennae longer than prostomium but shorter than palps, long = antennae longer than prostomium and palps.

^b Unpublished observations of *Trochonerilla mobilis* with palps (Worsaae, personal observation).

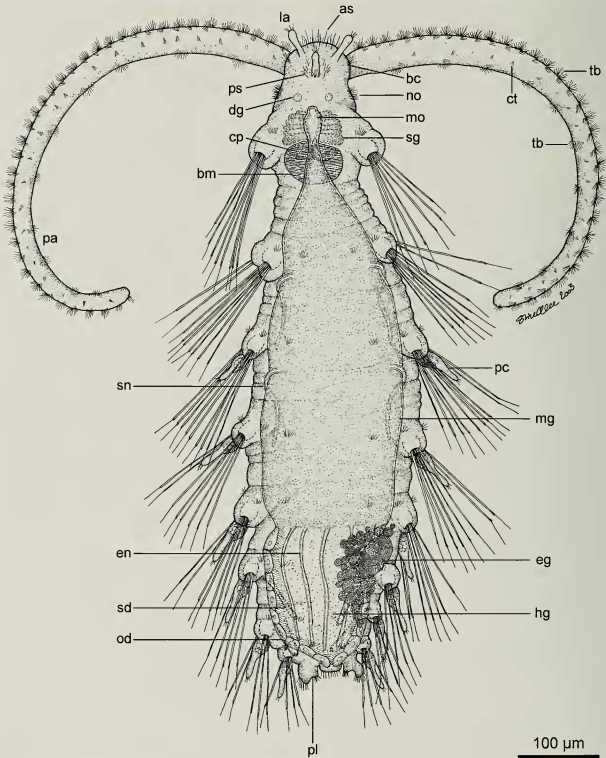


Fig. 1. Reconstruction from light micrograph of live holotype of *Longipalpa saltatrix*, new species, dorsal view. Not all chaetae are drawn. Detailed information on nephridia, gonoducts and external dorsal ciliation is included from confocal laser scanning microscopy and scanning electron microscopy. Abbreviations: as, anterior field of sensory cilia; bc, band of cilia; bm, bulbus muscle; ct, ciliary tuft; cp, cuticular plates; dg, dorsal glands; eg, eggs; en, enteronephridium; hg, hindgut; la, lateral antennae; mg, midgut; mo, mouth; no, nuchal organ; od, oviduct; pa, palp; pc, parapodial cirrus; pl, pygidial lobe; ps, posterior field of sensory cilia; sd, spermiduct; sg, salivary glands; sn, segmented nephridium; tb, transverse ciliary band.

Table 2.—Meristics and morphometric characters of holotype and total type material (measurements on juveniles in parentheses). Abbreviations: excl., exclusive; incl., inclusive; L, length; min., minimum; max., maximum; segm., segment; W, width.

	Holotype	Min.	Max.	Average	n
<i>Total</i>					
L excl. appendages, chaetae	763	624 (471)	985	788	14
max. W incl. parapodia	224	127 (116)	285	202	13
max. W excl. parapodia	192	108 (99)	268	173	13
<i>prostomium</i>					
L	72	59	77	68	12
W	81	67 (66)	90	80	12
max. L palps	696	680 (660)	718	696	6
L median antenna	43	24 (17)	43	33	7
max. L lateral antennae	56	41 (31)	65	53	10
<i>trunk</i>					
L segm. 1	80	55 (46)	97	74	12
L segm. 2	123	98 (77)	150	126	12
L segm. 3	113	76 (71)	152	108	12
L segm. 4	109	73	121	104	12
L segm. 5	103	71 (69)	103	93	12
L segm. 6	67	54	106	80	12
L segm. 7	56	54	89	68	11
L segm. 8	35	25	58	42	11
L pygidium	8	8	37	20	12
max. L parapodia segm. 1	63	35	63	53	13
max. L other parapodia	48	30	50	40	12
max. L parapodial cirri	67	41	73	60	13
max. L pygidial lobes	42	30	50	41	9
<i>chaetae</i>					
max. no. chaetae segm. 1 ^a		7 (6)	13	10	8
max. no. chaetae notopodia ^a		7	10	8	6
max. no. chaetae neuropodia ^a		6	10	8	6
max. total L chaetae ^b		135	145	139	8
max. L shaft ^b		86	109	103	5
L distal extension shaft ^b		0	2	1	5
L blade ^b		33	41	37	5

^a Measured on fixed material by SEM.

^b Measured alive by LM and on fixed material by SEM.

(ZMUC), Denmark. Two paratypes as whole mounts (USNM 1022181-1022182) are deposited in the Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A.

Diagnosis.—Characters of the genus.

Etymology.—From the Latin *saltator* (=dancer), in reference to the swimming skills of the species, which may swim in loops while waving and twisting the long palps.

Description (see Table 2 for principle counts and measurements).—A relatively

hyaline nerillid with brown pigmentation, especially along intestinal wall. The body consists of prostomium, eight chaetigerous segments and pygidium (Figs. 1, 2A, 4). Adults with eight segments and a total length of 624–985 μm (only 454–825 μm when fixed); juveniles with six to seven segments and a total length of about 500 μm . Maximum body width generally at segment five, up to 268/285 μm (excl./incl. parapodia); narrow restriction between segment one and two, posterior to the esophagus. Prostomium up to 77 μm long, 90 μm

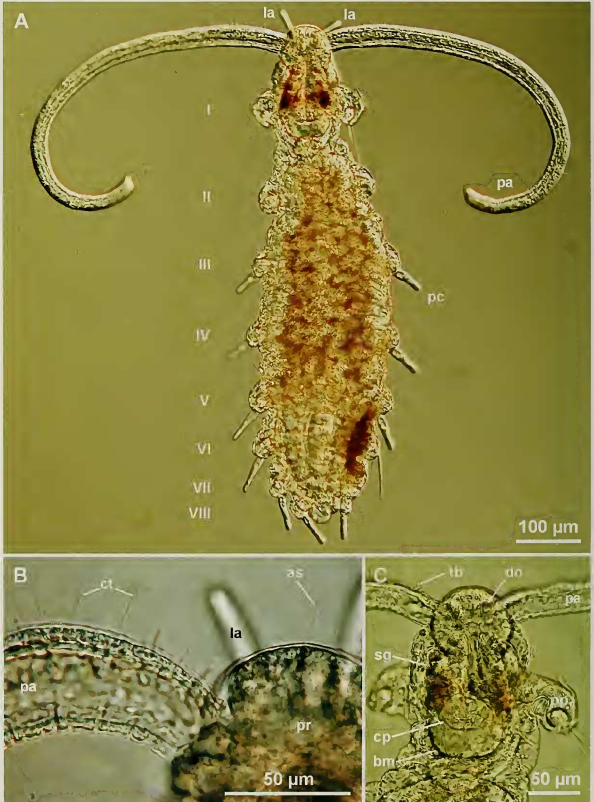


Fig. 2. Light micrographs of live holotype of *Longipalpa saltatrix*, new species. A, Whole specimen with two palps. B, Closer view of ciliation on palp and prostomium. C, Closer view of prostomium and segment one. Abbreviations: see Fig. 1; pp., parapodium of segment one; pr, prostomium; I-VIII, segments one to eight.

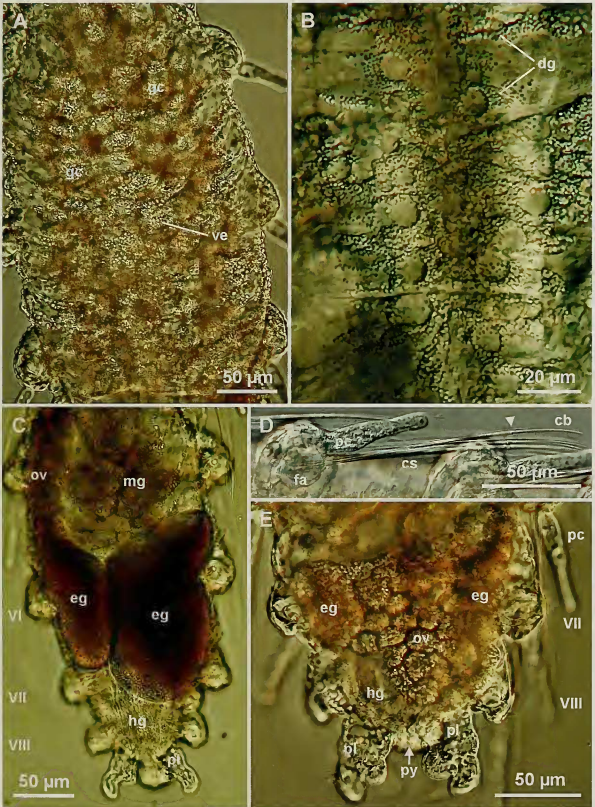


Fig. 3. Light micrographs of live specimens of *Longipalpa saltatrix*, new species. A, Dorsal view of segment three to six showing midgut lining of glandular cells with vesicles. B, Ventral view of middle segments showing diffuse glandular pattern. C, Posterior part of animal. D, Parapodium. E, Segments seven-eight and pygidium. Abbreviations: see Fig. 1; arrowhead, extension of shaft; cb, chaetal blade; cs, chaetal shaft; dg, diffuse glandular pattern; fa, fascicle; gc, glandular cells; ov, ovoids; py, pygidium; VI-VIII, segments six to eight; ve, vesicles.

wide; first four segments longest, decreasing in length posteriorly, pygidium even shorter.

Prostomium short, with two ventro-lateral palps and three dorsal antennae. Palps filiform and long, up to 718 μm (up to about 90% of body length in adults, and up to about 130% in juveniles), and with complex ciliation (see below) (Figs. 1, 2, 5A). Antennae short, filiform, with few distal cilia. Medium antenna up to 43 μm long, lateral antennae up to 65 μm long (Figs. 1, 4A, B, 5A). Nuchal organs paired, situated between palps and parapodia of segment one on a round elevated bulge on each lateral side of the prostomium (Figs. 1, 5A, C). Parapodia of segment one very large (up to 63 μm long), up to twice the length of the following parapodia (Figs. 1, 2A, 4A, C).

Parapodial cirri (with few distal cilia) between dorsal and ventral chaetal bundles of parapodia of segment three to eight; length up to 73 μm , increasing towards the posterior segments (Fig. 4A). No trace of attachment of parapodial cirri on segment one and two, neither of scars from detached cirri, or rudimentary cirri. Appendages like cirri and palps, and even chaetae, were easily lost during handling and fixing of the animals. Of the more than 70 specimens observed alive, none possessed parapodial cirri on segment one and two and scars were not found with SEM. Pygidial cirri were never observed, but it was difficult to examine the pygidium thoroughly for scars of cirri with SEM. On one specimen, a pair of scar-like structures was found at the pygidium, which could be scars from lost pygidial cirri or just an artifact (Fig. 6G). All adult (but no juvenile) animals possessed two very special structures, here named pygidial lobes due to their location on the dorsal side of the pygidium. Each lobe is up to 50 μm long, with two projections and a dense ciliation (Figs. 1, 3E, 4A, 6G, H).

All chaetae compound and relatively straight, shaft with minor pointed distal extension, less than 2 μm long (Figs. 3D, 6B).

Chaetae very slightly serrated and generally with a hairy appearance (Fig. 6A–C). Segment one uniramous, with up to thirteen chaetae in one chaetal fascicle; segments two to eight biramous, with dorsal and ventral fascicles comprising up to ten chaetae each. Similar numbers of chaetae in segments two to six, somewhat fewer chaetae in the last two segments. No noticeable differences in number or length between dorsal and ventral chaetae. Similar lengths in all segments of shaft, blade and total length of chaeta. Shaft up to 109 μm , blade up to 41 μm , total length up to 145 μm (Figs. 3D, 4, 6A).

Dorsal surface of prostomium with very specific ciliation characterized by three different groups of cilia: a pair of short bands with motile cilia (>20 cilia, up to 20 μm long), one on each dorso-lateral surface next to the lateral antennae (Figs. 1, 5A); two transverse rows of non-motile cilia in front of antennae on the anterior most part of the prostomium (Fig. 5A, B), the last of which arranged in a distinct pattern; and a posterior group of twenty non-motile cilia (Fig. 5D, E), arranged in complex pattern near the origin of median antenna on posterior part of the prostomium.

The patterns of the anterior field of cilia (probably sensory in function, see Discussion) and the posterior fields of cilia (probably sensory) are characteristic of the species and are here given in detail: anterior field of cilia (5–15 μm long) with two transverse rows of cilia (Fig. 5B). Posterior row contains about 5 cilia, spaced 2–5 μm apart (cilia no. 1–5 in Fig. 5B). Anterior row with about 20 cilia (no. 6–25 in Fig. 5B). Cilia arranged in distinct pattern mirrored halfway along the row. Moving towards the middle from the lateral sides, the first cilia are two groups of four cilia (no. 6–9 and 10–13), a single cilium next to them (no. 14 and 15), two groups of three cilia (no. 16–18 and 19–21), three cilia in the middle (no. 22–24), and one cilium (no. 25) in front of the middle cilium.

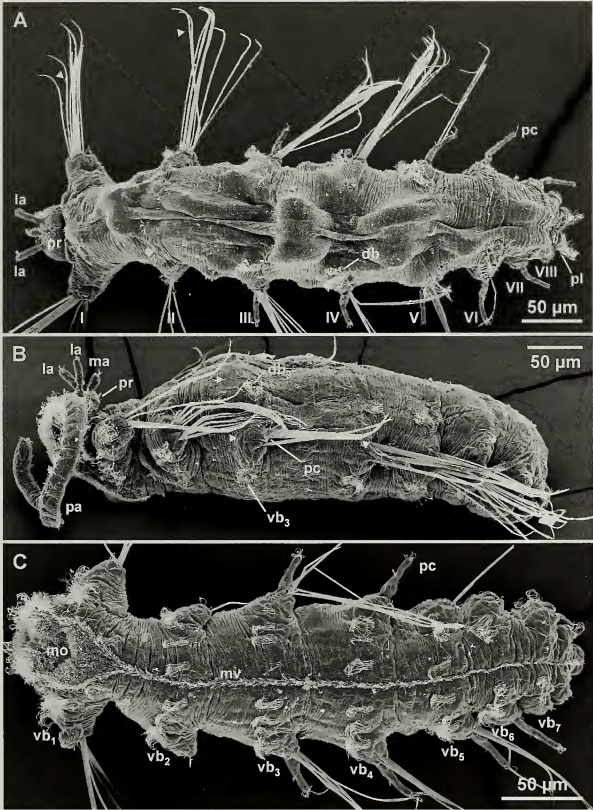


Fig. 4. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Dorsal view of whole specimen with both palps lost. B, Lateral view of specimen with one palp lost. C, Ventral view of specimen with two palps lost. Abbreviations: see Figs. 1, 2; arrowhead, connection of chaetal shaft and blade; db₃, dorsal ciliary band of segment three; ma, median antennae; mv, midventral ciliary band; vb₁-vb₇, ventral ciliary band on segments one to seven.

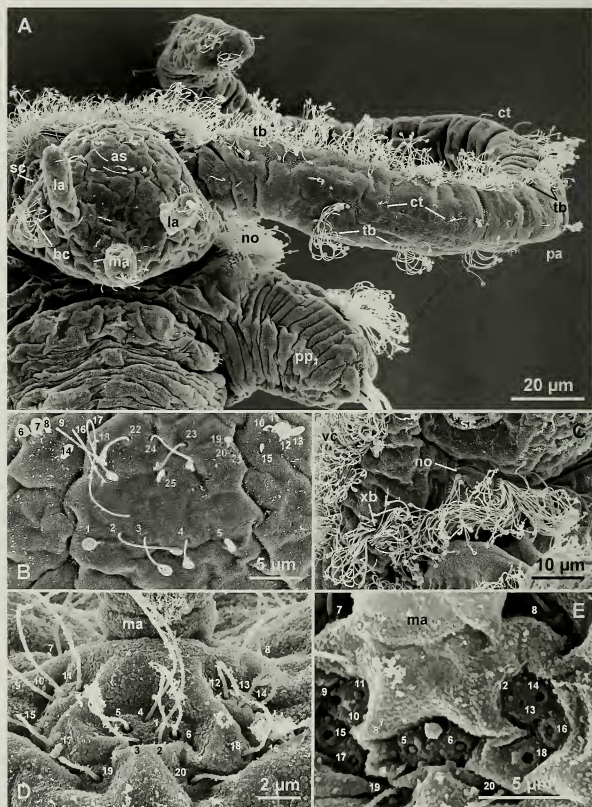


Fig. 5. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Dorsal view of prostomium, right palp, and segment one. B, Closer view of anterior field of twenty-five cilia. C, Closer lateral view of nuchal organ and extra ventral ciliary band. D, E, Close dorsal view of posterior field of twenty cilia from two specimens. Abbreviations: see Figs. 1, 2, 4; bc, band of cilia; sc, scar from lost palp; vc, ventral ciliation around mouth; xb, extra ventral ciliary band.

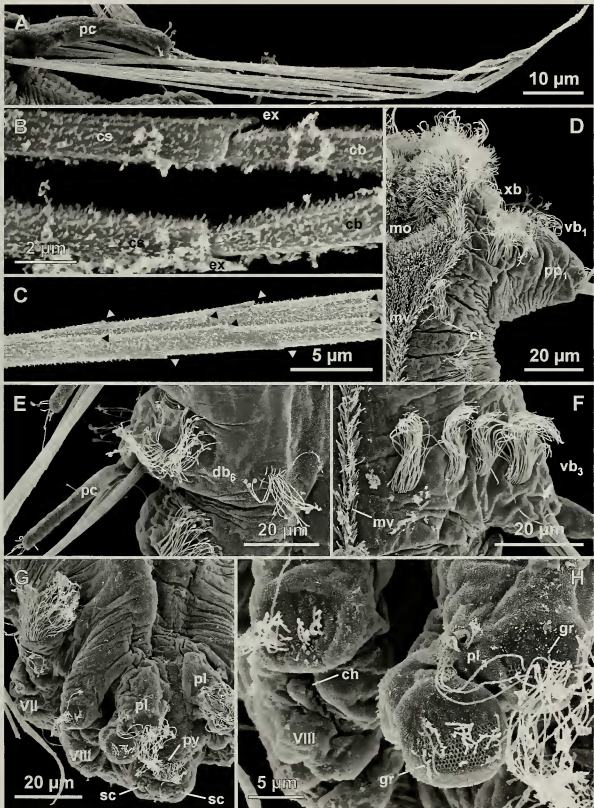


Fig. 6. Scanning electron micrographs of *Longipalpa saltatrix*, new species. A, Chaetal bundle and parapodial cirrus. B, Closer view of chaetae with microvillar hairy appearance. C, Two hairy chaetae showing serration pattern (indicated by arrowheads). D, Left ventral side of prostomium and segment one. E, Right side of segment six with half dorsal ciliary band. F, Left ventral side of segment three with half ventral ciliary band. G, Left dorsal side of posteriormost segments. H, Closer view of left pygidial lobe. Abbreviations: see Figs. 1-5; ch, holes after lost chaetae; db₆, dorsal ciliary band of segment six; ex, extension of shaft; gr, dense ciliary groups; sc, scars from lost pygidial cirri or an artifact.

Posterior field of twenty cilia (3–15 μm long) covers an area about 12 μm wide and 8 μm long (Fig. 5D, E). Four cilia in a close square (no. 1–4 in Fig. 5D) surrounded by a common elevation of the cuticle, are found in the center of the field, posterior to the basal part of the antenna. Right next to these four cilia one cilium is found on each lateral side (no. 5–6), which as all the single situated cilia in the pattern, is surrounded by a cuticular collar. On each lateral side of the antenna is one cilium (no. 7–8). About 3 μm posterior of these two clusters are found, each with three cilia in a transverse line, surrounded by a common elevation of the cuticle (no. 9–14). Next to these, on the level of the 4 central cilia, are found 2 pairs of cilia next to each other on each lateral side (no. 15–18). The last pair of cilia (no. 19–20) is located a few micrometers posteriorly with about 5 μm in between the cilia.

Palps with complex ciliation containing transverse ciliary bandlets in a longitudinal row on the inner and outer lateral surfaces of the palp, respectively. More than 20 cilia, up to 20 μm long in each ciliary bandlet, positioned 5–20 μm apart in a row extending to the tip. Farthest distance between bandlets on outer lateral surface of the palp. Longitudinal row of single ciliary tufts on both dorsal and ventral surface between the longitudinal rows of bandlets (Figs. 1, 5A). Less than 5 cilia, up to 7 μm long in each ciliary tuft, located in a row extending to the tip. Ciliary bandlets beat in metacronal waves, creating a water current leading particles towards the base of the palp. Motility of ciliary tufts not clearly distinguishable due to intense beating of ciliary bandlets. However, we suspect these cilia to be non-motile due to their small number and short length.

Dorsal surface of body segments not ciliated, except for few ciliary tufts. Two to four tufts of motile cilia are situated in a transverse line across each segment between the parapodia on each side (Figs. 4A, B, 6E). Each tuft contains 20–200 motile cilia, up to ca. 25 μm long. Each pygidial lobe possess-

es two large groups of cilia, one on each of the two projections of the lobe (Figs. 1, 4A, 6G, H). Each group contains more than 100 cilia, up to ca. 25 μm long.

Ventral surface with dense ciliation around mouth on ventral side of prostomium, continuous with relatively narrow mid-ventral ciliary band extending to the anus on the dorsal side of the pygidium. Transverse rows of ventral ciliary tufts on each segments at the level of the parapodia: four pairs on segments one to three, three pairs on segments four to seven, two pairs on segment 8. Three additional pairs of ciliary tufts: one pair between prostomium and segment one, almost connecting ciliation around mouth with that of the nuchal organs; and two pairs between segment one and two (Figs. 4C, 6D).

Pharynx with ventral opening between prostomium and segment one, and muscular bulb in segment one (Figs. 1, 2A, C). About six pairs of ventral brown glands (may have salivary function) open into buccal cavity on ventral side of pharynx (Figs. 1, 2A, C). Two additional dark brown, round cell-groups (probably glandular in function) dorsally of pharynx in prostomium. All groups contain several cells with relatively large round vesicles. A pair of triangular cuticular plates on ventral side of pharyngeal bulb in anterior part of pharyngeal organ (Figs. 1, 2C). Large round glandular cells with many small vesicles and brown pigmentation line stomach wall (Figs. 1, 3A); large ciliated cells line hindgut (Figs. 1, 3C). Diffuse superficial glands create a unique pattern in the ventro-caudal epithelium (Fig. 3B).

Studies by confocal scanning microscopy showed the distribution of nephridia and gonoducts in this and other species (Worsaae & Müller 2004). *Longipalpa saltatrix* is hermaphroditic with one pair of spermiducts in segments six to seven and one pair of oviducts in segments seven to eight (see Fig. 1 and Worsaae & Müller 2004, fig. 2J). Two pairs of segmented nephridia are present, from segments two to three, and

from segments three to four, respectively (see Fig. 1, and Worsaae & Müller 2004, fig. 2G-I). Several enteronephridia line the hindgut (see Fig. 1, and Worsaae & Müller 2004, fig. 2G, J). Fertile animals contain a maximum of two large eggs with diameters up to 170 μm , and an additional large number (up to ca. 40 has been counted) of smaller ovoids with a diameter about 10–20 μm .

Distribution.—Presently known only from a certain anchihaline cave pool in Bermuda.

Motility.—The animals swim beautifully in the water column, describing loops and turns. Less frequently, they glide over the surface and if provoked make an escape reaction or quick turn by undulation of the body and fast curling up of the palps in a narrow spiral. When swimming, they are capable of bending the prostomium and body as well as waving, bending and curling the long palps. The pygidial lobes are flapped between positions flat along the body to an almost right angle to the dorsal surface, thereby using the densely ciliated lobes as helms. The forward drift seems to be created mainly by the ventral ciliation, possibly with additional force from the cilia on palps and pygidial lobes.

Remarks.—The description of *Longipalpa saltatrix* not only adds a new genus to the family Nerillidae, but also expands the definition of the family. The extremely long palps of this species are not only unusual in their length but probably also in their function. The longitudinal rows of ciliary bandlets create a water current propelling particles towards the mouth opening, which has never been observed in other nerillids. It seems possible that the animals collect food particles by help of the palps, thereby increasing their feeding radius extensively. Foraging could happen when gliding over or through the substrate as well as when swimming through and above the sediment collecting particles in suspension. In several species of nerillids, the ciliation of the much shorter palps creates a water current

transporting particles away from the mouth (Worsaae, personal observations). This transport may indicate that other nerillid palps may also be functional in feeding behavior, however, by transporting rejected particles away from the mouth and not by gathering them. The previous understanding of the nerillid palps as being mainly sensory in function should probably be expanded to include a function in feeding behavior. This view stands in contrast to the general comprehension of the ventral palps of the major taxon group Aciculata (see Rouse & Fauchald 1997) with which the family has the most apparent resemblance (see e.g., Schmidt 1848, Quatrefages 1866, Westheide 1990, Westheide & Purschke 1996, Rouse & Fauchald 1997, Rouse & Pleijel 2001). Aciculates are generally characterized by short sensory palps with no direct function in food collecting. If the nerillids truly belong to the Aciculata, then the long palps of *Longipalpa saltatrix* may also influence the conception of the conservativeness of the palps in this taxon group.

The extremely long palps would probably be disadvantageous in the interstitial habitat from which many nerillids are described. This disadvantage may be one of the reasons why these long palps have not been found in other nerillids. In the Bermudian caves with only a sparse layer of very fine silt on top of bare rocks, it may even be an advantage to be able to actively swim and perhaps also feed on suspended particles with the aid of the palps. However, *Leptonerilla prospera* which lives under rather similar conditions, except from more light in the Walsingham Caves in Bermuda, does not possess long feeding palps. Differences in habitat characteristics between cave and interstitial habitats include more space in caves, thus allowing for swimming as opposed to crawling, and different types of food, hence different feeding mechanisms. Many other anchihaline species are most commonly found within the water column rather than on the sediments, implying that this is where food is primarily located.

The motile ciliary bands and the anterior field of cilia on the prostomium could easily be detected on live animals with light microscopy (LM), whereas the posterior field of cilia could only be detected with SEM. The motile ciliary bands (bc in Figs. 1, 5A) are most likely not mechanoreceptors because of their long length, motility, and dense grouping. However, the anterior and posterior fields of cilia are probably sensory in function because of their non-motility, shorter length, and single appearance of cilia—each with a cuticular collar. Two fields of cilia (suggested to be sensory in function) have also been described for the nerillid *Paranerilla limicola* Jouin & Swedmark, 1965 (Worsaae & Kristensen 2003). The anterior field of cilia in *P. limicola* consists of a little group of cilia and, except for the anterior position; it is very different from the two transverse rows of cilia arranged in a pattern found in *L. saltatrix*. The posterior field in *P. limicola* is more similar with 14 cilia arranged in a distinct pattern. However, this pattern differs some from the pattern of 20 cilia found in *L. saltatrix*. It seems very possible that the two systematically significant prostomial fields of cilia (probably sensory in function) are a common feature of nerillids, which just demands SEM techniques to be described.

A few of the unusual characteristics of *L. saltatrix* have previously been found in single occasions in otherwise very different nerillid species. Structures remarkably similar to the special triangular cuticular plates on the ventral part of the pharynx have been described for *Thalassochaetus palpifoliaceus* Ax, 1954. A different, although also distinct pattern of diffuse superficial ventral glands are described for *Nerillidium renaudae* Jouin, 1970. Pygidial lobes have been described for the aberrant *Nerillidium simplex* Levi, 1953 (see also Jouin 1966, Swedmark 1959). These lobes are apparently not double-lobed or ciliated as in *L. saltatrix*; however, their position and square, non-cirriiform appearance is very similar to *L. saltatrix*. The pygidial lobes

found in *N. simplex* have been interpreted as modified pygidial cirri (Levi 1953, Swedmark 1959), which may also count for the lobes of *L. saltatrix*. The superficial resemblance with the lobes of *N. simplex* is probably a matter of convergence; however, the lobes may be functionally comparable. The two groups of cilia on each pygidial lobe of *L. saltatrix* show great resemblance in number and length with the two ciliary tufts found on each side of the body segment dorsal to the parapodia. Furthermore, examined juveniles did not possess pygidial lobes, which would be expected if the lobes were modified pygidial cirri. These observations could mean that the pygidial lobes are modified rudiments of a strongly reduced ninth body segment. However, studies with LM and SEM of *L. saltatrix* show that there are no remains of chaetae or parapodial muscles and cLSM studies show that there are no segmental nerves posterior to the eighth body segment. Further examination of the development of *L. saltatrix* is needed to clarify the origin of the pygidial lobes.

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