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A new member of Nerillidae (Annelida : Polychaeta), *Xenonerilla bactericola* gen. et sp. nov., collected off California, USA

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Abstract: A new Nerillidae, *Xenonerilla bactericola*, new genus and species, is described from the dysoxic Santa Barbara Basin, off southern California, USA. Common occurrence of the species is restricted to sediments laden with mats of filamentous sulphide-oxidizing bacteria. The body comprises a small prostomium and nine segments; the last is fused with the pygidium. The head has two large, ventrolateral palps, antennae are absent. The first segment (buccal segment) has neither parapodia nor chaetae. Segments II to IX possess parapodial cirri of similar size. Thin capillary chaetae are restricted to posterior segments, only one-two ventral chaetae exist per parapodium. Two pear-shaped anal cirri are present. Distinct characters that separate the new taxon from all hitherto known nerillids are: (1) most specimens completely lack chaetae, while others have only very few chaetae, (2) in the pharyngeal organ, the bulbous muscle is covered anteriorly by an eversible epithelial part. This ventrally located tongue contains intracellular buccal pieces. A brief summary of the 16 known genera of Nerillidae is presented in a tabular form.

Résumé: *Un nouveau membre de la famille des Nerillidae (Annelida: Polychaeta),* Xenonerilla bactericola *gen. et sp. nov., récolté au large de la Californie, USA*.
Un nouveau Nerillidae, *Xenonerilla bactericola*, nouveau genre et nouvelle espèce, est décrit des sédiments hypoxiques du Bassin de Santa Barbara, au large de la Californie sud. L'espèce n'est rencontrée couramment que dans les sédiments riches en mattes de bactéries filamenteuses sulfoxydantes. Le corps comprend un petit prostomium et neuf segments, le dernier fusionné avec le pygidium. La tête a deux larges palpes ventro-latéraux et pas d'antennes. Le premier segment (segment buccal) n'a ni parapodes ni soies. Les segments II à IX possèdent des cirres parapodiaux de taille comparable. Les fines soies capillaires sont limitées aux segments postérieurs où il n'y a qu'une ou deux soies ventrales par parapode. Deux cirres anaux piriformes sont présents. Les caractères distinctifs qui séparent la nouvelle espèce de tous les autres Nerillidae actuellement connus sont: (1) la quasi absence de soies chez la plupart des spécimens, (2) dans le bulbe pharyngien, le muscle bulbaire est recouvert antérieurement par une partie épithéliale éversible. Cette langue, située ventralement, porte des stylets buccaux intracellulaires. Un bref résumé des principaux caractères des 16 genres actuels de Nerillidae est présenté dans un tableau.

Keywords: Annelida, Nerillidae, meiofauna, buccal-pieces, epibiotic bacteria, Santa Barbara Basin

Introduction

Since O. Schmidt described in 1848 *Nerilla antennata*, the first nerillid polychaete, about 30 species and 16 genera

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have been described (Tzetlin & Larionov, 1987; Riser, 1988; Westheide, 1990). It can be expected that there are far more species yet to be discovered because previous research have focused on shallow regions and were rarely directed specifically to the study of meiofauna (Faubel, 1978; Westheide & Purschke, 1996). Furthermore, specimens are often not recovered in a complete state, so that morphological characters necessary for identification cannot be examined (Riser, 1988). This shortcoming can be compensated only by a high number of specimens that, as the present paper demonstrates, are required to enable application of various methods in order to describe the species in detail. The presence or absence of buccal-pieces and their exact location in the pharyngeal bulb for example, can only be shown by TEM. Here, we describe a new genus and species from bathyal, oxygen-depleted sediments by means of light microscopy, electron microscopy (SEM and TEM) and confocal laser scanning microscopy (CLSM), and we briefly discuss its ecology and distribution.

Material and methods

The specimens intended for morphologial study were obtained from the surface ~1-2 cm of sediment collected by a Soutar boxcore. After collection and during transport to South Carolina, sediment samples were maintained at ambient temperature (~5°C). In the laboratory, samples were sieved briefly with chilled artificial seawater over a 63 µm screen and the >63 µm fraction was observed with a stereomicroscope. Individuals were isolated with a small-bore pipette, rinsed in 0.2 µm filtered artificial seawater (FASW), relaxed in 8% $MgCl_2$, rinsed quickly in FASW, and fixed using one of the methods noted below.

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% NaN_3. 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 an 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, ten specimens were analysed with CLSM: six males and four females.

For SEM analyses, paraformaldehyde fixed specimens were dehydrated in an upgraded ethanol series. Subsequently, they were critical-point dried using $C0_2$ as intermedium, mounted on an aluminum tab and sputter-coated with gold. Examination took place in a Zeiss DSM 962. In total, five specimens were investigated by this method.

For TEM investigations, specimens were fixed for 1 h with 3% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.4). After washing with the same buffer they were postfixed for 1 h with 1% osmium tetroxide in 0.1 M sodium cacodylate buffer, subsequently dehydrated in an upgraded ethanol series and embedded in Epon. Ultrathin sections, obtained with a Leica Ultracut UCT, were stained with uranyl acetate and lead citrate and examined with a Jeol JEM-1200EX electron microscope. Two specimens were sectioned and investigated.

For abundance determinations, collections were identical to those described for gastrotrichs in Todaro et al. (2000). Briefly, the surface centimetre of 2.5 cm diameter subcores from Soutar boxcores was fixed in either 3.7% formaldehyde in PBS or 3% glutaraldehyde in 0.1M sodium cacodylate buffer (pH 7.1). In the laboratory, the samples were incubated in a solution of Rose Bengal (ca. 2 g l^{-1}) for at least 12 h, after which they were sieved with the appropriate buffer over a 63 µm screen. Using a stereoscope, all polychaetes (and other metazoans) were isolated and enumerated from the >63 µm fraction.

Dissolved oxygen concentrations of bottom-water samples were determined using microwinkler analysis (Broenkow & Cline, 1969). Water samples were taken with a Niskin bottle that was attached to the boxcore frame and rigged to trip when the boxcorer impacted the seafloor.

Results

Genus *Xenonerilla* gen.nov.

Diagnosis

Nerillidae with two palps on the prostomium. Nine segments; first one without parapodia, cirri and chaetae. Segment II to IX with cirri; no or very few capillary chaetae restricted to hind segments. Two anal cirri. Pharyngeal organ with a ventral tongue containing buccal-pieces.

Etymology: *Xenonerilla* "Xeno-" is a greek prefix for "new, strange, unusual", it refers to the unusual ventral position of a tongue in the pharyngeal bulb.

Xenonerilla bactericola gen. et sp. nov.

Material examined

Specimens were collected in the Santa Barbara Basin off California, USA (SBB) from a water depth between 521 and 592 m (34°13'-16'N, 119°58'-120°2'W). Approximately 30 specimens were investigated for the purpose of taxonomic description.

Type material

The holotype, which is a whole mount of a mature specimen, is deposited in the Smithsonian US National Museum of Natural History, Washington, D. C. (USNM 186784). A paratype is also deposited there (USNM 186785).

Other paratypes are deposited in the Los Angeles County Museum of Natural History: two specimens in alcohol/glycerin, LACM-AHF POLY 1958 and two slide-mounted specimens, LACM-AHF POLY 1959, 1960; in the Muséum National d'Histoire Naturelle, Paris, specimens in 10% neutral formalin: MNHN - POLY 48 - POLY 50 and four slide-mounted specimens, two females (POLY 51) and one male plus one female (POLY 52); in the Senckenberg Museum Frankfurt (SMF 9257).

Description

The animals are not pigmented except for two yellow-brown areas on both sides of the mouth (Fig. 1). The body length ranges from 0.7 to 1.1 mm (without posterior appendages); width 85 to 90 µm (without parapodia).

The small prostomium is separated from the trunk by a dorsal semicircular furrow (Fig. 2C). It bears no eyes and no antennae, but two large, lateroventrally positioned palps, which reach up to 118 µm in length in adults and are much shorter in juveniles (Figs 2B, C, E). The palps are heavily covered with cilia at their ventral inner margin; only a few long cilia in distinct tufts are visible at their dorsal side (Fig. 2G). One pair of nuchal organs, indicated by long cilia originating from a deep groove, is located at the posteriolateral margin of the prostomium (Fig. 2G).

The body comprises 9 segments that are, apart from segment IX, all divided equally by distinct ventral furrows in anterior and posterior regions, the latter bearing the

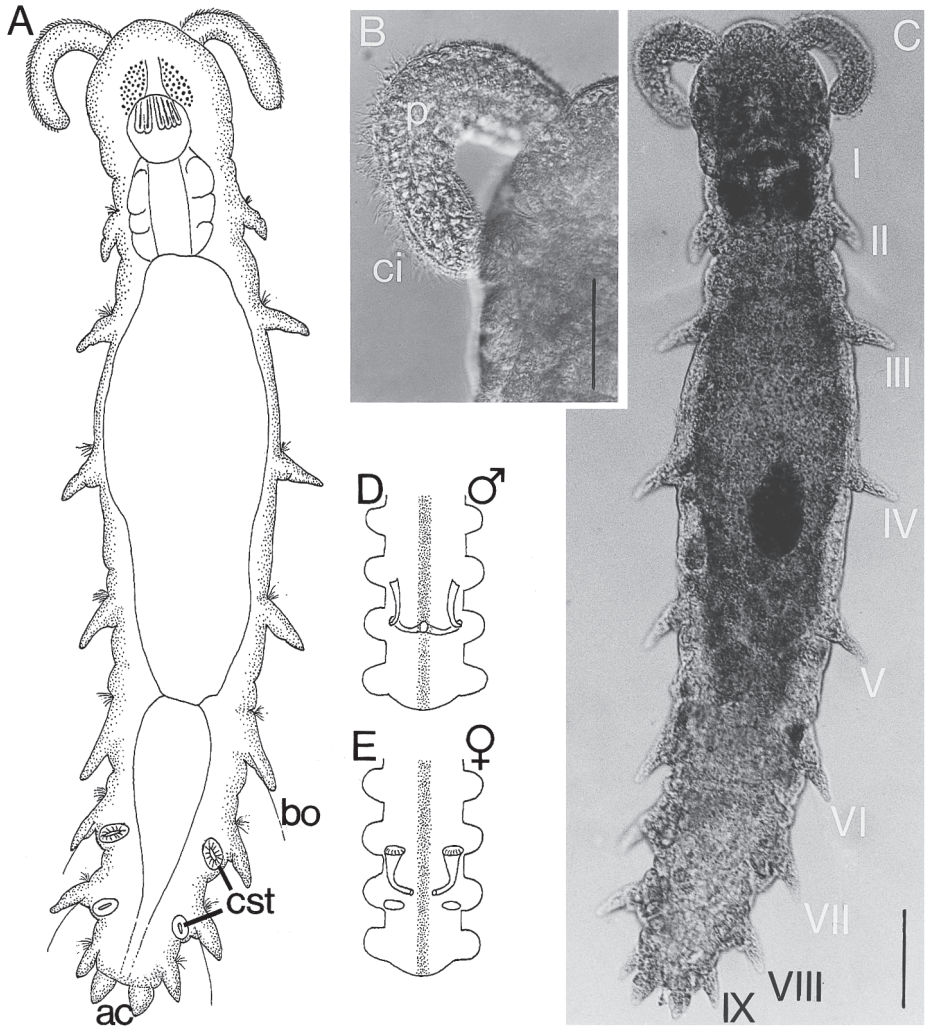
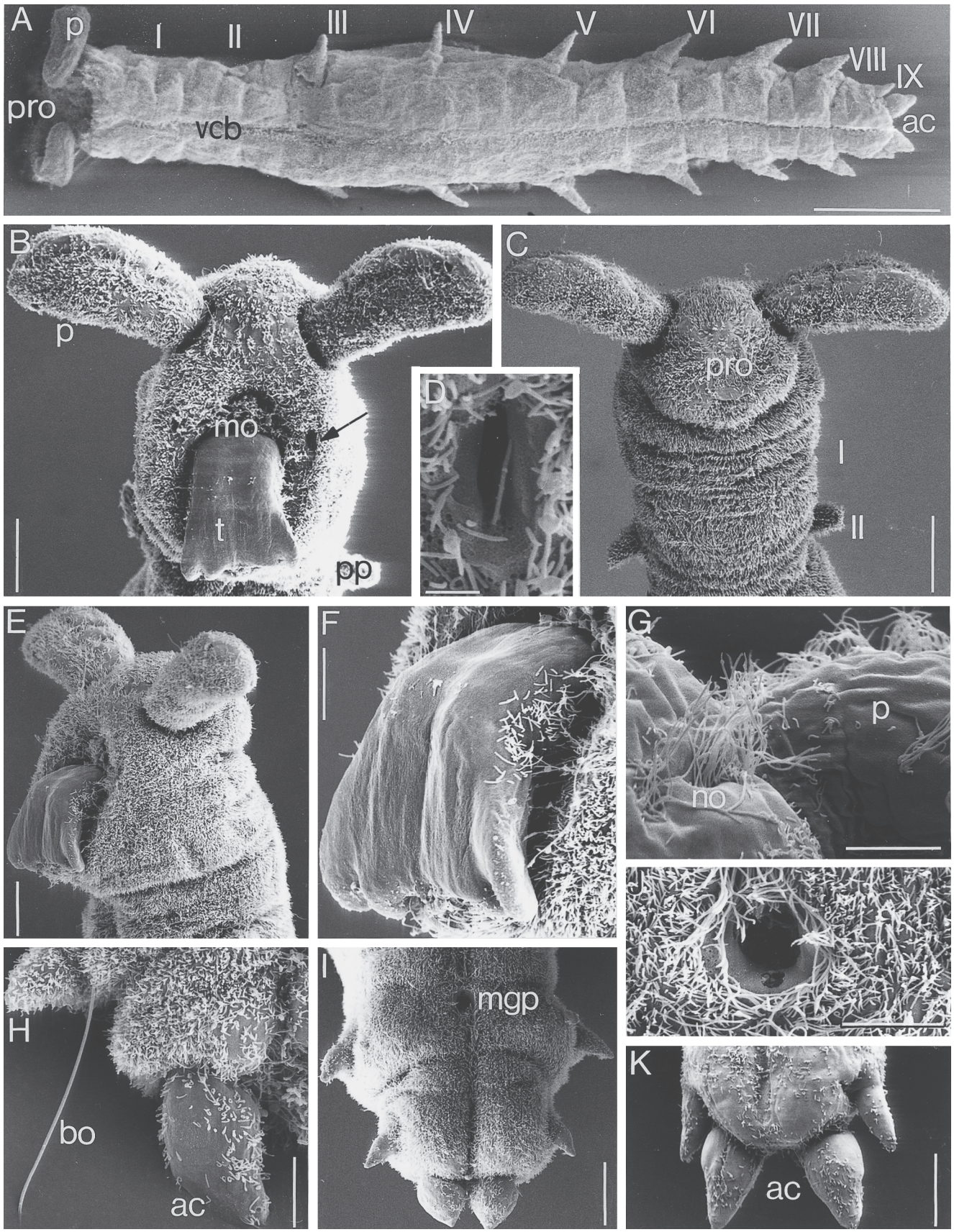


Figure 1. *Xenonerilla bactericola* gen. et sp. nov. **A.** Schematic drawing of a whole female organism. **B.** Micrograph of a palp with marginal ciliation. **C.** Micrograph of a fixed female. (Segments numbered I-IX). **D, E** Schematic drawing of the gonoducts and genital pores, ventral view. **D.** Male. **E**. Female. (*ac*) anal cirri; (*bo*) chaeta; (*ci*) ciliation; (*cst*) coelomostomes; (*p*) palp.

Scale bars: B**:** 50 µm; C: 100 µm.

Figure 1. *Xenonerilla bactericola* gen. et sp. nov. **A.** dessin semi-schématique de l'habitus d'une femelle. **B.** Micrographie d'un palpe montrant la ciliature marginale. **C.** Micrographie d'une femelle fixée et comprimée (segments numérotés de I à IX). **D**, **E** schémas en vue ventrale de l'emplacement des gonoductes et des pores génitaux, **D.** mâle. **E.** femelle. (*ac*) cirres anaux ; (*bo*) soie ; (*ci*) ciliature ; (*cst*) coelomostomes ; (*p*) palpe.

Echelles B : 50 µm, C : 100 µm.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parapodia (Fig. 2A). The length of segments increases from segment I to V (40 µm vs. 88 µm, respectively) but decreases in the caudal region (segment IX: 42 µm). The first segment (buccal-segment, peristomium) has neither parapodia nor chaetae. One small cavity of unknown function is located at each side of the mouth (Figs 2B, D). On the following segments, there are small conical cirri, approximately all of similar size (32-45 µm in length); those of segments III to V are slightly longer (around 55 µm). On most specimens chaetae are absent; on some individuals only a few capillary, very thin chaetae occur, being restricted to segments V to VII. These chaetae emerge ventrally to the parapodial cirri and are two to three times longer than the cirrus (Fig. 2H). The pygidium is fused with the last segment. Two pear shaped anal cirri are inserted on the pygidium, pointing slightly dorsally. Apart from a wider proximal part they resemble the parapodial cirri in shape and length (Figs 2I, K). In juveniles, the anal cirri are more squat (Fig. 2I).

Due to the presence of a dense and uniform cover of small epibiotic bacteria all over the body (Fig. 3), observation of the ciliation pattern is difficult, even with SEM (Fig. 2). In spite of this difficulty, two transversal ciliated peribuccal bands and a longitudinal midventral groove protruding anteriorly into the ventral buccal ciliated field, as observed in other Nerillidae, could be observed. Some bacteria can also be found in the stomodeal region.

The pharyngeal apparatus (or pharyngeal bulb, Figs 4, 5) is a muscular and epithelial organ, that measures about 70 µm in length by 70 µm in width and 36 µm in dorso-ventral thickness. As in other nerillids, it is located in the posterior part of the buccal cavity and formed around three invaginations of the stomodeal epithelium: the median invagination, which is the larger one, a ventral invagination and a smaller dorsal one. Besides this epithelial lining, it comprises a bulbous muscle, an investing muscle and an eversible tongue (Fig. 2, B, E, F). The tongue of *Xenonerilla bactericola* is the anterior part of the stomodeal epithelium that covers the bulbous muscle (Fig. 4A). It is located in the ventral part of the pharyngeal bulb whereas the tongue-like organ, in all other nerillids, is located in the dorsal part of the bulb.

The bulbous muscle (Figs 4A, B) comprises nine muscle cells, transversally oriented; five muscle fibres are located ventrally to the median invagination and four fibres form a posterior arc around the end of the median invagination. Each fibre has two very thin peripheral layers of myofilaments (ca. 0.40 µm in thickness) with A and I bands and Z elements, transversally arranged, and a rather large central vacuolar myoplasm containing few mitochondria; peripheral tonofilaments are sometimes present in these muscle cells. These fibres are attached to the stomodeal epithelium by desmosomes (Z elements of the fibres, facing tonofilaments in the stomodeal epithelium) (Fig. 4B).

The investing muscle (Figs 4A, 5B) is thin and exhibits dorsally a bilateral symmetry (Fig. 5B). It comprises five layers of thin muscle cells (ca. 0.60 µm in thickness), with longitudinally arranged myofilaments. A few additional wedge shaped muscle fibers are present medio-dorsally. The investing muscle is connected both dorsally and ventrally to the stomodeal epithelium.

In the anterior part of the pharyngeal bulb, the ventral epithelium lying between the median and the ventral invaginations is enlarged and forms the tongue (Figs 4A) abutting posteriorly on the bulbous muscle (Fig. 4C), while its apical part is located in the buccal cavity (Fig. 4E). This flat and rather large tongue is bridge-shaped and can be everted through the mouth opening (Figs 2B, E, F). It has a bilateral symmetry and comprises two layers of stomodeal epithelial cells separated by a layer of longitudinal muscle

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Figure 2. *Xenonerilla bactericola* gen. et sp. nov. SEM-micrographs. **A.** Whole organism, ventral view. **B.** Head, ventral view. Two cavities (*arrow*) at both side next to the mouth with the extruded tongue. **C.** Anterior end, dorsal view. Body densely covered with bacteria, as in B. **D.** Detail of the cavity (arrowed in B) with a cuticular border. **E.** Lateral view of the head. **F.** One median and two lateral longitudinal furrows subdivide the tongue. **G.** Right nuchal organ. **H.** Capillary chaeta in segment *IX*. **I.** Male genital pore at segment *VIII*. **J.** Detail of the male pore with a distinct border. **K.** Last segment, pygidium and anal cirri. (*ac*) anal cirri; (*bo*) chaeta; (*mgp*) male genital pore; (*mo*) mouth; (*no*) nuchal organ; (*p*) palps; (*pp*) parapodial cirrus of segment 2; (*pro*) prostomium; (*I*) peristomium, (*II-IX*) segments 2-9; (*t*) tongue; (*vcb*) ventral ciliated band.

Scale bars: A: 100 µm; B, D, I : 25 µm; C: 5 µm; E, K: 20 µm; F, G, H, J: 10 µm.

Figure 2. *Xenonerilla bactericola* gen. et sp. nov. Microscopie électronique à balayage. **A.** organisme entier, vue ventrale. **B.** Vue ventrale de la tête montrant la langue, sortant de la bouche, et deux petites cavités péribuccales symétriques (*flèche*). **C.** vue dorsale de la tête. Le corps est entièrement recouvert de bactéries, comme en B. **D.** détail d'une des cavités péribuccale (fléchée en B). **E.** vue latérale de la tête. **F.** détail de la langue sortie, montrant à sa surface un sillon médian et deux latéraux. **G.** organe nucal droit. **H.** soie capillaire du sétigère *IX*. **I.** orifice génital mâle médioventral sur le segment *VIII*. **J.** détail de l'orifice mâle avec un bord net. **K.** Dernier segment, pygidium et cirres anaux, vue ventrale. (*ac*) cirres anaux; (*bo*) soie; (*mgp*) pore génital mâle ; (*mo*) bouche; (*no*) organe nucal ; (*p*) palpe; (*pp*) cirre parapodial du segment 2 ; (*pro*) prostomium; (I) peristomium, (II-IX) segments 2-9 ; (*t*) langue; (*vcb*) sillon cilié médio-ventral.

Echelles A : 100 µm, B, D, I : 25 µm, C : 5 µm, E, K : 20 µm, F, G, H, J : 10 µm.

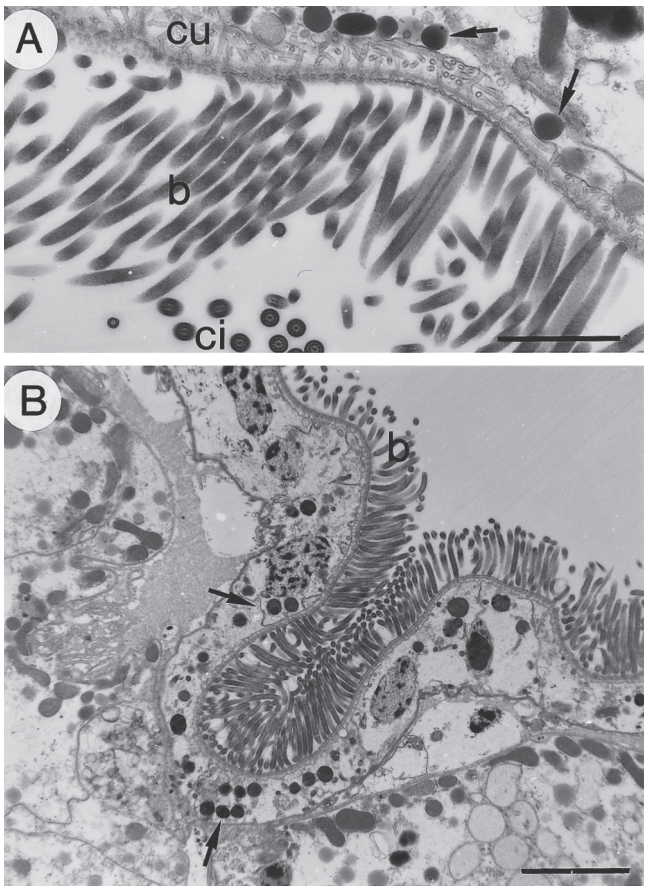


Figure 3. *Xenonerilla bactericola* gen. et sp. nov.. **A, B.** TEM-micrographs of the body surface. The small epibiotic bacteria cover the body surface but do not penetrate the cuticle. Electron dense vesicles (*arrows*) are located in the epidermis, directly beneath the cuticle. (*b*) bacteria ; (*ci*) cilia ; (*cu*) cuticle.

Scale bars: A: 2 µm; B: 4 µm.

Figure 3. *Xenonerilla bactericola* gen. et sp. nov.. **A**, **B.** Microscopie électronique à transmission (MET). Coupes de la paroi du corps. Les bactéries épibiotiques recouvrent la surface du corps mais ne pénètrent pas dans la cuticule. Des vésicules denses (*flèches*) sont situées dans l'épiderme, immédiatement sous la cuticule. (*b*) bactéries ; (*ci*) cils ; (*cu*) cuticule.

Echelles A : 2 µm, B : 4 µm.

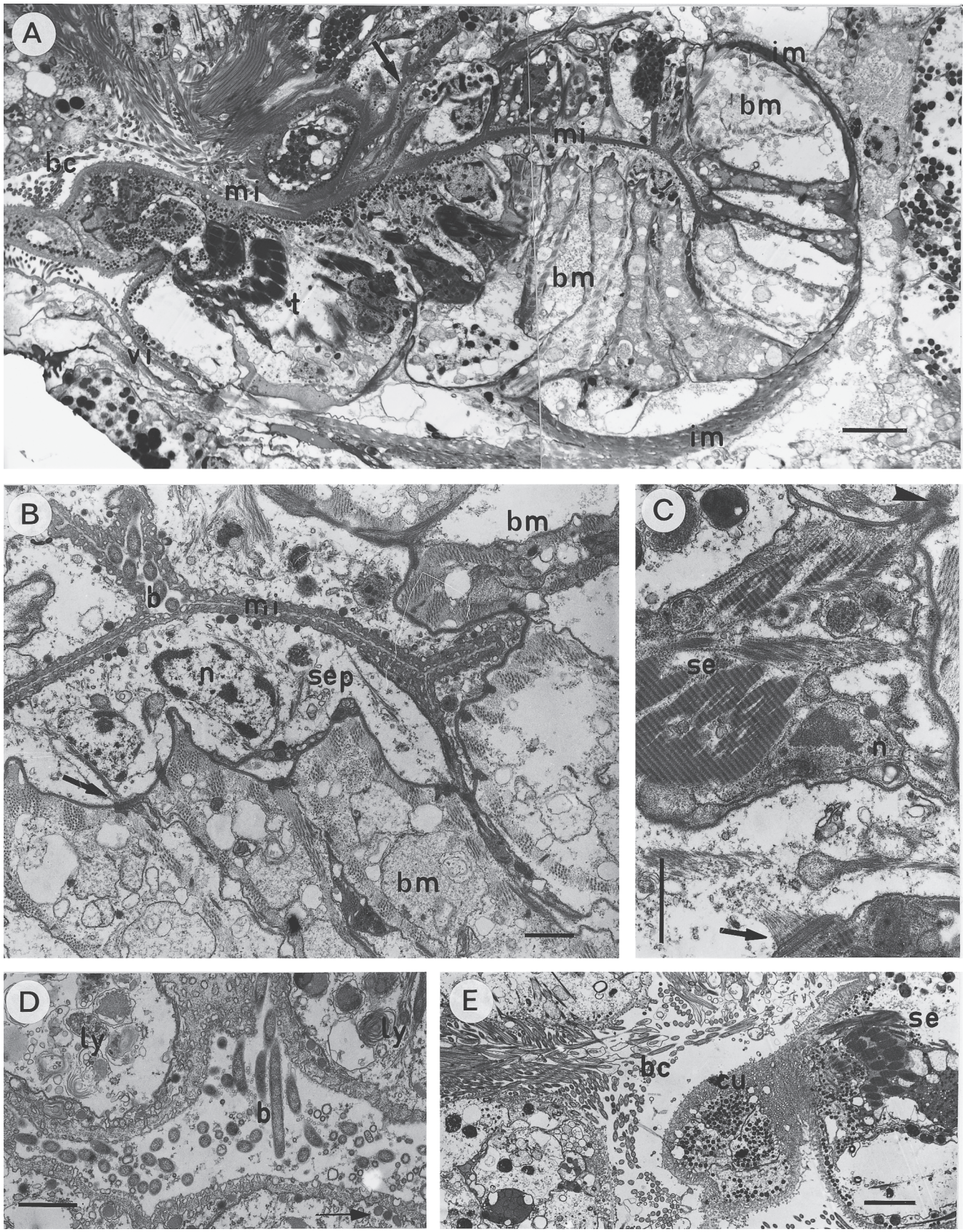
fibers (Fig. 5A). The upper epithelial layer lines the median stomodeal invagination, the lower layer lines the ventral stomodeal invagination. The stomodeal cells of the two layers are characterized by numerous large secondary lysosomes (ca. 750 nm in diameter) and subcuticular electron-dense granules (ca. 250 nm in diameter) (Figs 4A, 5A). Moreover, the upper layer of cells comprises four to five pairs of cells, each secreting several (up to five) longitudinal skeletal rods (stylets) reaching a length of about 30 µm and a diameter of about 2.2 µm by 1.4 µm (Figs 4A, C, 5A). The secretory cells of the stylets have nuclei located caudally in the tongue, near the adjacent bulbous muscle (Figs 4A, C), and an electron dense cytoplasm that contains electron-dense secretory granules, about 270 nm in diameter, which appear to fuse with the skeletal rods. Each skeletal rod, initially made of smaller bundles of tonofilaments that fuse (Fig. 4C), has a typical striated structure, which appears on longitudinal sections, with a period of ca. 70 nm (Fig. 4C). A striation appears also on transverse sections, with periods of 125 to 235 nm, but these striations may vary according to the orientation of the sections and are likely an artifact (Fig. 5A).

Figure 4. *Xenonerilla bactericola* gen. et sp. nov. TEM-micrographs of the pharyngeal organ; **A**, **B**, **C**, **E** Parasagittal sections; **D** Transverse section. **A.** Thick parasagittal section of the organ showing three stomodeal invaginations, dorsal (*arrow*), median and ventral invaginations, the bulbous muscle, investing muscle and the tongue containing electron-dense skeletal element. Buccal cavity on the left. **B.** Parts of six muscle fibres of the bulbous muscle covered by the stomodeal epithelium of the median invagination. *Arrow* points to a myoepithelial junction. **C.** Caudal part of cells of the tongue, one containing striated skeletal elements. Arrow points to desmosome uniting these cells to each other, or with muscle cell (*arrow head*). **D.** Bacteria and numerous small membrane bound vesicles are enclosed laterally within the median invagination. The stomodeal epithelium contains numerous secondary lysosomes and electron-dense subcuticular vesicles (*arrow*). **E.** Anterior part of the tongue showing a simple cuticle and numerous electron-dense subcuticular vesicles. (*b*) bacteria ; (*bc*) buccal cavity ; (*bm*) bulbous muscle ; (*cu*) cuticle ; (*im*) investing muscle ; (*ly*) secondary lysosomes ; (*mi*) median invagination ; (*n*) nucleus ; (*se*) skeletal elements ; (*sep*) stomodeal epithelium ; (*t*) tongue ; (*vi*) ventral invaginations.

Scale bars : A: 5 µm; B, D: 1 µm; C: 0.5 µm; E: 2 µm.

Figure 4. *Xenonerilla bactericola* gen. et sp. nov. Micrographies MET du bulbe pharyngien ; **A**, **B**, **C**, **E**, coupes parasagittales, **D** coupe transversale. **A.** Coupe parasagittale épaisse du bulbe montrant trois invaginations stomodéales : dorsale (flèche), médiane et ventrale. La cavité buccale est à gauche; **B.** une partie de six fibres musculaires du muscle bulbaire recouvertes par l'épithélium de l'invagination médiane ; la *flèche* indique une jonction myoépithéliale ; **C.** région postérieure de cellules de la langue, l'une d'entre elles contenant des stylets striés. La *flèche* indique un desmosome unissant ces cellules entre elles et la *tête de flèche* une jonction avec une cellule musculaire. **D.** bactéries et nombreuses petites vésicules enfermées latéralement dans l'invagination stomodéale médiane. L'épithélium stomodéal contient de nombreux lysosomes secondaires et des vésicules denses sous-cuticulaires (*flèche*). **E.** partie antérieure de la langue montrant une cuticule simple et de nombreuses vésicules denses sous-cuticulaires. (*b*) bactéries ; (*bc*) cavité buccale ciliée ; (*bm*) muscle bulbaire; (*cu*) cuticule ; (*im*) muscle d'enveloppe ; (*ly*) lysosomes secondaires ; (*mi*) invagination médiane ; (*n*) noyau ; (*se*) stylets ; (*sep*) épithélium stomodéal ; (*t*) langue ; (*vi*) invagination ventrale.

Echelles A : 5 µm, B, D : 1 µm, C : 0,5 µm, E : 2 µm.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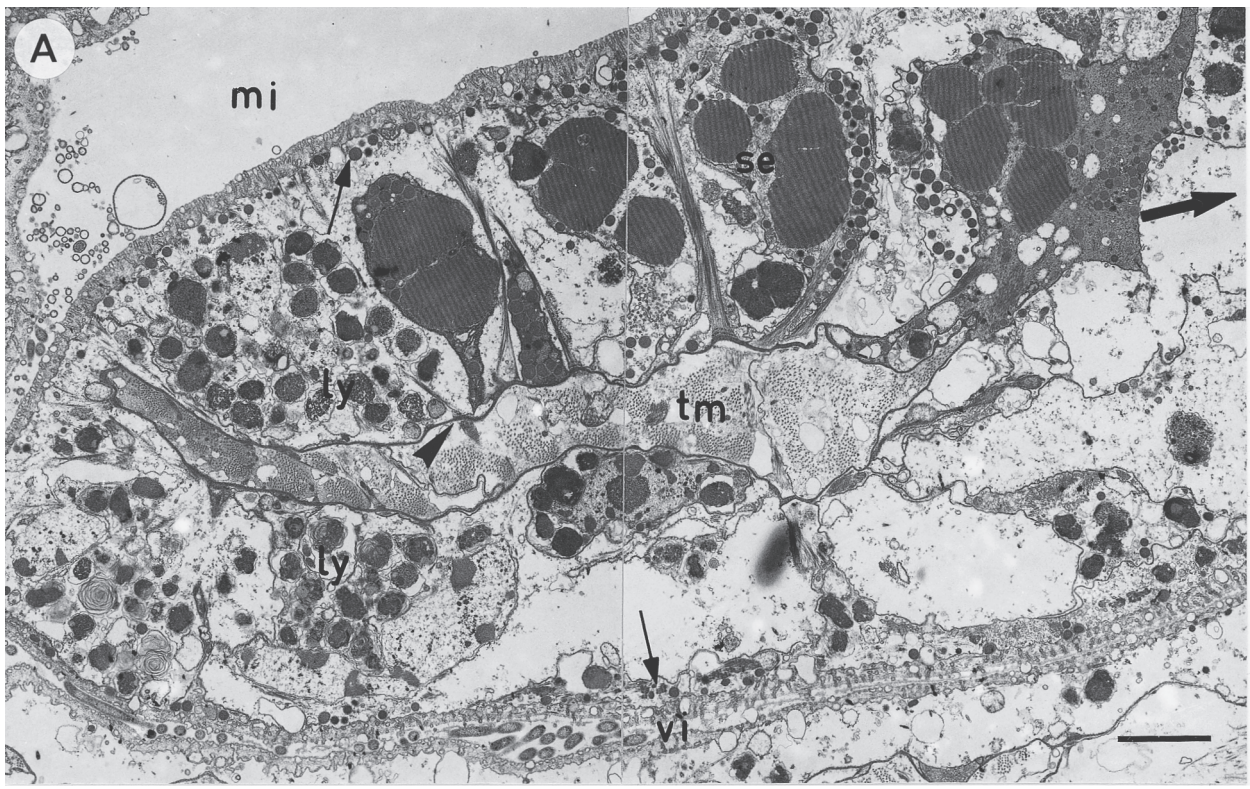
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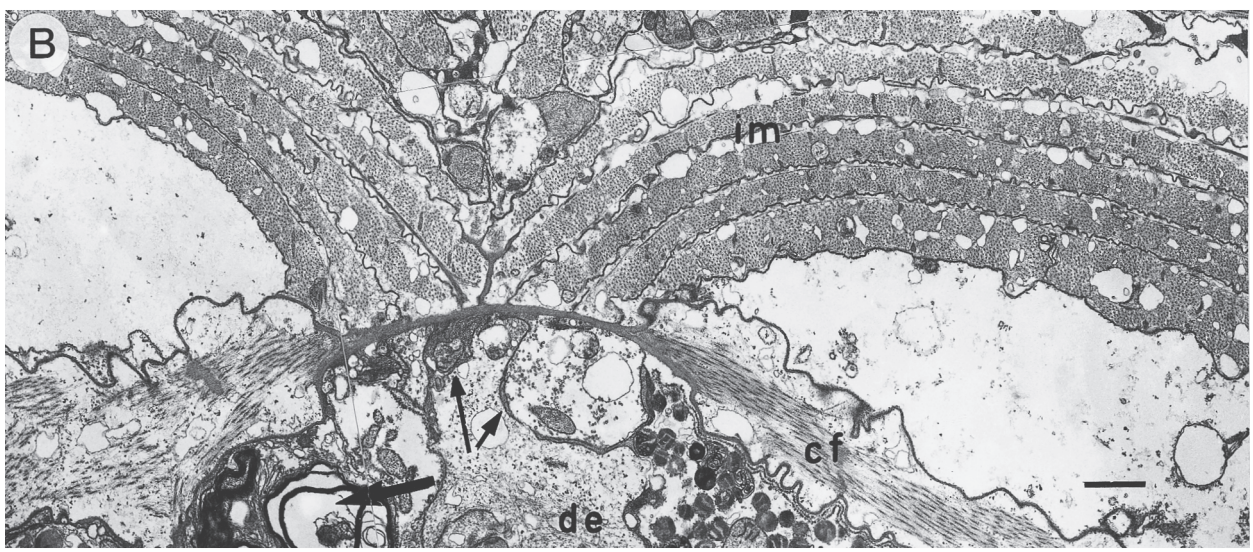
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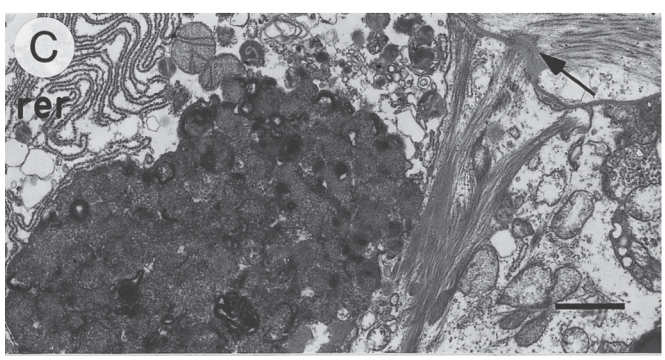
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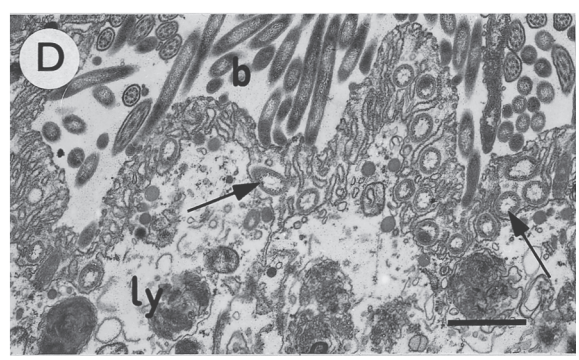
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The secretory cells alternate with epithelial cells devoid of skeletal rods. Large electron-dense secondary lysosomes, as well as a regular sub-cuticular layer of electron-dense membrane-bounded vesicles (ca. 200-250 nm), characterize this second cell type. These cells are also crossed by bundles of tonofilaments which attach apically below the cuticle by small hemidesmosomes and on the basal matrix by desmosomes formed with Z elements of the tongue muscle (Fig. 5A). The stylets secretory cells also contain tonofilaments forming desmosomes with Z elements apposed to the plasma membrane of the bulbous muscle (Fig. 4C) and the tongue muscle. They are also united to adjacent cells by well-developed desmosomes (Fig. 4C).

The cells lining the ventral part of the tongue belong to the same cell type, devoid of skeletal elements, being characterized by large secondary lysosomes, a sub-cuticular layer of electron-dense vesicles and tonofilaments.

The epithelium dorsal to the median invagination (Figs 4A, 5B, C) is developed in a cell cluster comprising mainly secretory cells with a well-developed rough endoplasmic reticulum, different types of secretory granules, tonofilaments and large autophagosomes (Fig. 5B). Two nerves are present dorsally in the middle of this cell cluster, below a thick basal matrix that borders this cell cluster separating it from the investing muscle (Fig. 5B). These epithelial cells extend anteriorly along the median invagination in the buccal cavity and do not contain skeletal elements.

The cuticles lining the three stomodeal invaginations are not specialized, even at the level of the tongue: the cuticle is generally thin (0.2 to 0.3 µm) and crossed by numerous short microvilli that terminate at the cuticle surface in rounded tips (Fig. 4B). The cuticle of the tongue does not differ from that of the other parts, however, it is twice thicker (~0.6 µm) in the upper layer lining the median invagination.

Several bacteria are present along the cuticle of the median and ventral invaginations (Figs 4B, D, 5A) and enclosed in invaginated areas, especially in the lateral pockets of the median invagination, where these bacteria are surrounded by numerous small vesicles, suggesting a possible lysis process. They do not penetrate the cuticular layer. Numerous bacteria are also present in the lumen of the oesophagus (Fig. 5D): here the bacteria penetrate the cuticle, whereas this has not been observed in the stomodeal epithelium. The oesophageal cells exhibit the same secondary lysosomes as the stomodeal epithelium.

Mature animals

The new species is gonochoristic. In the males, bundles of spermatozoa are visible in the coelom at the base of the parapodial cirri in segments V, VI and VII (Fig. 6A). One pair of spermioducts is present; coelomostomes are located in the posterior part of segment VII. After running about 60 µm posteriorly, the spermioducts form a loop and stretch transversely towards the midventral ciliated groove. Here in

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Figure 5. *Xenonerilla bactericola* gen. et sp. nov. **A-C** TEM-micrographs of the pharyngeal organ, transverse sections. **D.** oesophagus. **A.** Transverse section through the left half of the tongue showing in the upper part four cells containing each several skeletal elements. Below a thin muscular layer, the epithelium of the lower part has no skeletal elements and contains secondary lysosomes. *Large Arrow* points towards the sagittal plane of the tongue. *Small arrows* indicate the subcuticular layer of dense vesicles. *Arrow head*: myoepithelial junction. **B.** Transverse section of the dorsal part of the pharyngeal bulb showing the bilateral symmetry of the investing muscle and a small part of the epithelial cluster of cells that is dorsal to the median invagination. *Large arrow* : autophagosome. *Small arrows* point to nerves. **C.** A secretory cell of the dorsal cell cluster contains a well developed endoplasmic reticulum and several types of secretory granules. Tonofilaments cross the cell and forms desmosomes (*arrow*) with a surrounding muscle cell. **D.** Transverse section of the oesophagus, above the pharyngeal bulb, shows numerous bacteria in the ciliated lumen. Several bacteria (*arrows*) are enclosed in the oesophageal cuticle and numerous secondary lysosomes are present in the oesophageal cells. (*b*) bacteria, (*cf*) semicircular muscle fibres; (*de*) dorsal cell cluster; (*im*) investing muscle; (*ly*) secondary lysosomes; (*mi*) median invagination, (*rer*) rough endoplasmic reticulum; (*tm*) tongue muscle; (*vi*) ventral invagination.

Scale bars: A: 2 µm; B-D: 1 µm.

Figure 5. *Xenonerilla bactericola* gen. et sp. nov. Micrographies MET. **A - C** coupes transversales du bulbe pharyngien. **D.** œsophage. **A.** Coupe à travers la moitié gauche de la langue montrant dans sa partie supérieure quatre cellules contenant chacune plusieurs stylets. Au-dessous d'une mince couche musculaire, l'épithélium de la partie inférieure n'a pas de stylets et contient de nombreux lysosomes secondaires. *Grande flèche* : vers le plan sagittal de la langue. *Petites flèches* : couche sous-cuticulaire de vésicules denses. *Tête de flèche* : jonction myoépithéliale. **B.** Partie dorsale du bulbe pharyngien montrant la symétrie bilatérale du muscle d'enveloppe et une petite partie du massif cellulaire épithélial dorsal à l'invagination médiane. G*rande flèche* : autophagosome. *Petites flèches* : nerfs. **C.** Une cellule sécrétrice du massif cellulaire dorsal avec un réticulum endoplasmique rugueux bien développé et plusieurs types de granules de sécrétion. Des tonofilaments traversent la cellule et rejoignent des desmosomes (*flèches*) au contact d'une fibre musculaire bordante. **D.** Coupe transversale de l'œsophage, au dessus du bulbe pharyngien ; il héberge de nombreuses bactéries. Plusieurs bactéries (*flèches*) sont incluses dans la cuticule œsophagienne et de nombreux lysosomes secondaires sont présents dans les cellules œsophagiennes. (*b*) bactéries, (*cf*) fibres musculaires semicirculaires; (*de*) massif cellulaire dorsal ; (*im*) muscle d'enveloppe ; (*ly*) lysosomes secondaires ; (*mi*) invagination médiane ; (*rer*) réticulum endoplasmique rugueux; (*tm*) muscle de la langue ; (*vi*) invagination ventrale.

Echelles A: 2 µm, B-D : 1 µm.

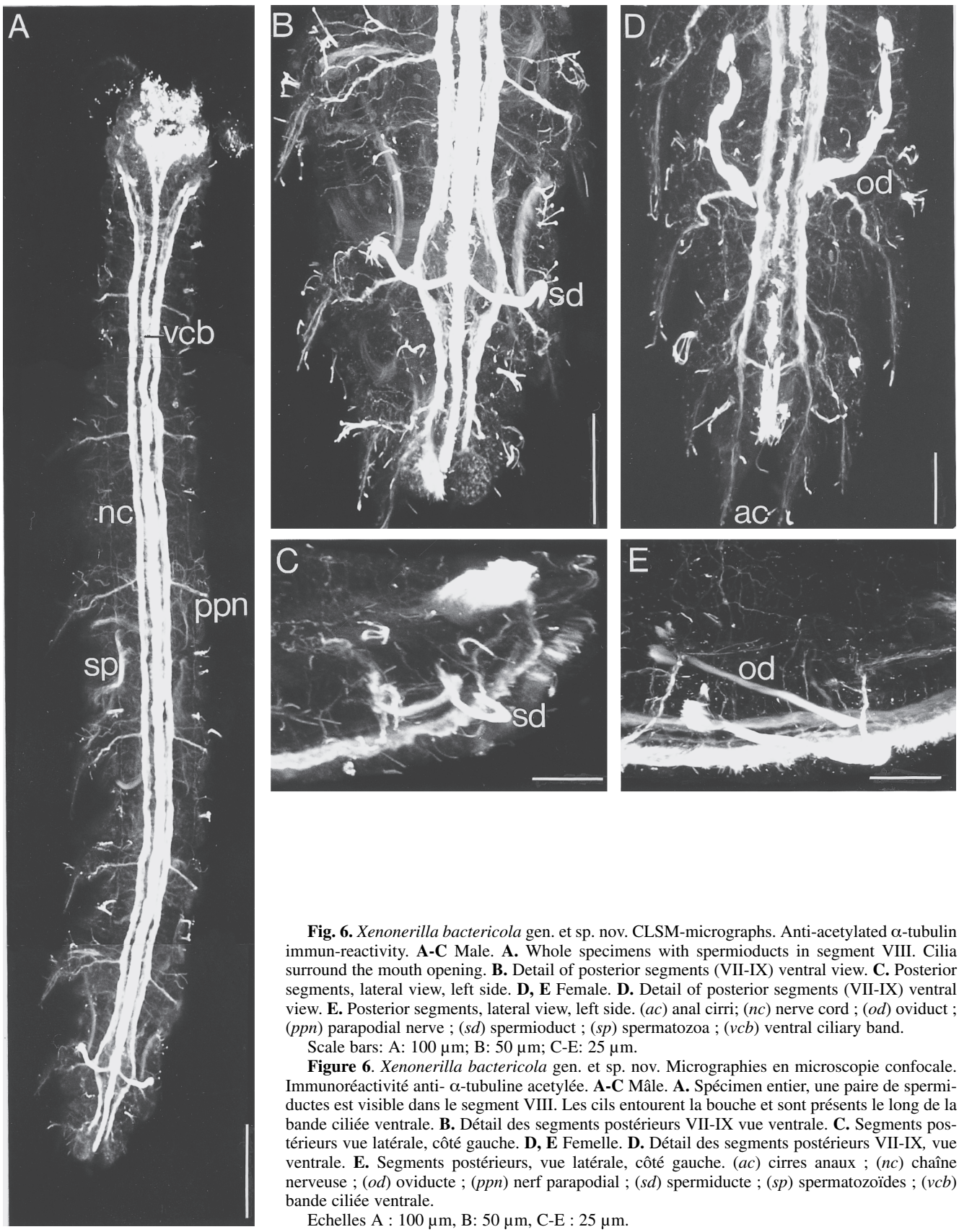

Fig. 6. *Xenonerilla bactericola* gen. et sp. nov. CLSM-micrographs. Anti-acetylated α-tubulin immun-reactivity. **A-C** Male. **A.** Whole specimens with spermioducts in segment VIII. Cilia surround the mouth opening. **B.** Detail of posterior segments (VII-IX) ventral view. **C.** Posterior segments, lateral view, left side. **D, E** Female. **D.** Detail of posterior segments (VII-IX) ventral view. **E.** Posterior segments, lateral view, left side. (*ac*) anal cirri; (*nc*) nerve cord ; (*od*) oviduct ; (*ppn*) parapodial nerve ; (*sd*) spermioduct ; (*sp*) spermatozoa ; (*vcb*) ventral ciliary band.

Scale bars: A: 100 µm; B: 50 µm; C-E: 25 µm.

Figure 6. *Xenonerilla bactericola* gen. et sp. nov. Micrographies en microscopie confocale. Immunoréactivité anti- α-tubuline acetylée. **A-C** Mâle. **A.** Spécimen entier, une paire de spermiductes est visible dans le segment VIII. Les cils entourent la bouche et sont présents le long de la bande ciliée ventrale. **B.** Détail des segments postérieurs VII-IX vue ventrale. **C.** Segments postérieurs vue latérale, côté gauche. **D, E** Femelle. **D.** Détail des segments postérieurs VII-IX, vue ventrale. **E.** Segments postérieurs, vue latérale, côté gauche. (*ac*) cirres anaux ; (*nc*) chaîne nerveuse ; (*od*) oviducte ; (*ppn*) nerf parapodial ; (*sd*) spermiducte ; (*sp*) spermatozoïdes ; (*vcb*) bande ciliée ventrale.

Echelles A : 100 µm, B: 50 µm, C-E : 25 µm.

segment VIII, they converge and open together in a common midventral genital pore (Figs 6A, B, C). At higher magnification, this male pore is visible as a distinct hole with a distinct margin (Figs 2I, J).

In the females, two pairs of large pockets are located laterally to the hindgut, just behind the parapodial cirri in posterior parts of segments VII and VIII. They represent the coelomostomes of two pairs of oviducts. The oviducts of the posterior pair could not be traced, whereas those of the anterior pair are clearly visible at CLSM micrographs (Figs 6D, E). They run from the posterior margin of segment VII caudally, bend towards the midventral sagittal line and end with separate pores located on segment VIII, laterally to the ventral ciliated groove. No oocytes were visible in those specimens. Clusters of small cells (oogonia?) were present in the coelom more dorsally, in front of the coelomostomes in segment VII and VIII, but also in segments IV to VI. Neither segmentally-arranged nephridia nor hindgut surrounding enteronephrida could be detected.

Habitat

The type locality, Santa Barbara Basin (SBB), is a depression in the seafloor between the California mainland and the northern Channel Islands. The basin, which has a sill depth of about 475 m, has dysoxic bottom waters due to local bathymetry, circulation, and a well-developed oxygen minimum zone. Pore waters of sediments in the central SBB are even more oxygen-depleted ($[O_2] < 1$ µM within the top 5 mm; Reimers et al. 1996) and sulphide concentrations in the surface centimeter can be > 0.1 µM (Kuwabara et al., 1999). These conditions support a mat of the filamentous sulphide-oxidizing bacteria *Beggiatoa* (Soutar & Crill, 1977). In the dysoxic, bacteria-laden SBB sediments, *Xenonerilla bactericola* occurs in densities as high as 6.5 cm^{-2} (Tab. 1). The abundance of *X. bactericola* is highest in samples where $O_2 < 4$ µM, while densities were extremely low in samples with bottom water $O_2 > 5$ µM. Other metazoans that co-occur with *X. bactericola* are the gastrotrich *Urodasys anorektoxys* Todaro et al., 2000, the nematode *Desmodora masira* Warwick, 1973 and the epifaunal gastropod *Astryx permodesta* (*Mitrella permodesta*) Dall, 1890 (Bernhard et al., 2000; Todaro et al., 2000). A variety of protists also occur in the *Beggiatoa* mats of the SBB. Most SBB eukaryotes have putative symbioses with prokaryotes (Bernhard et al., 2000).

Table 1. List of site information, including bottom water oxygen concentrations (O_2) and number of *Xenonerilla bactericola* cm^{-2} (# cm^{-2}). Sample designations are coded with month and year information (i.e., 998G collected in September 1998). ND = no data.

Table 1. Informations sur les lieux de récolte des échantillons, y compris la concentration en O_2 du milieu (O_2) et le nombre de *Xenonerilla bacteriola* cm^{-2} (#cm^{-2}). Les numéros des échantillons comprennent le mois et l'année de récolte (i.e. 998G : récolté en septembre 1998). ND = pas de données.

Sample	Coordinates (°N, °W)	Water Depth (m)	O_2 (µM)	# cm^{-2}
998G	34°13.522, 120°02.285	589	1.4	4.9
299L	34°13.423, 120°02.065	592	2.4	6.5
299C	34°15.939, 120°01.990	588	3.8	5.1
299P	34°17.476, 120°01.896	581	ND	0.8
299X	34°16.845, 119°58.561	555	5.1	1.2
299U	34°17.817, 119°56.886	521	5.1	0.2

Discussion

In the taxon Nerillidae, out of the hitherto 16 known genera three are seven-segmented, eight are eight-segmented and, including the new genus, five are nine-segmented (Tab. 2). Tzetlin and Saphonov (1992) counted nine genera with eight segments, but *Bathychaetus* only comprises seven segments (Faubel, 1978; Westheide, 1990).

From the nine-segmented genera, *Mesonerilla* Wilke, 1953 and *Leptonerilla* Westheide & Purschke, 1996 are distinct from *Xenonerilla* in having compound chaetae. Of the remaining taxa with capillary chaetae, *Nerilla* differs from *Xenonerilla* in having a larger size (1.5-1.7 mm vs. 0.7-1.1 mm), numerous chaetae all along the body (versus almost no chaetae in *Xenonerilla*), three antennae, four pigmented eyes, jointed peristomial cirri, jointed anal cirri and well developed parapodial cirri except at segment IX.

The nine-segmented *Meganerilla* Boaden, 1961 and the new genus *Xenonerilla* share some common features: prostomium with no antennae (in *Meganerilla swedmarki* Boaden, 1961, but *M. clavata* Magagnini, 1966 has a reduced median antenna), two large, lateroventral palps, no eyes (apart from *M. swedmarki*, where two eyes are present), all trunk segments bear cirri, and the species are gonochoristic (Tab. 2, grey fields).

The main differences between *Xenonerilla* and *Meganerilla* are the absence, in *Xenonerilla,* of chaetae in most parapodia and the buccal segment without parapodial cirri. The species is also of a smaller size (maximum size 1.1 mm) when compared to *Meganerilla swedmarki*, *M. clavata* and *M. penicillicauda* (1.5, 2.1 and 2 mm, respectively; see Boaden, 1961; Magagnini, 1966; Riser, 1988). In the males of *X. bactericola*, the spermioducts have a position similar to those in *Meganerilla clavata* and *M. penicillicauda* (in segments VII-VIII), but are confluent, opening by a unique genital pore located medio-ventrally on segment VIII (vs. being separate in *M. clavata* and *M. penicillicauda*; see Jouin, 1968; Riser, 1988). *Xenonerilla* females have one pair of oviducts (segm. VII-VIII), as does *M. clavata,* but the two pore openings are located on both sides of the mid-ventral ciliated band (vs. latero-ventral pores in *M. clavata*). Furthermore,

Table 2. Main characteristics of the hitherto known 16 nerillid genera; gono = gonochoristic; herma = hermaphroditic; mic. = microvillar; n = number of segments; pigm. = pigmented; sens. org. = sensory organ; * = unpublished data M. C. Müller.

Table 2. Principales caractéristiques des 16 genres de Nerillidae connus ; gono = gonochorique ; herma = hermaphrodite ; mic. = à microvillosités ; n = nombre de segments ; pigm. = pigmentés ; sens. org. = organes sensoriels ; * = données M.C. Müller non publiées.

n	Genus	length (mm)	palps	antennae	eyes	cirri segm I	chaetae segm I	chaetae	trunk cirri	pygidial cirri	buccal pieces	sex	unique features
7	***Bathychaetus*** Faubel, 1978	0.3	2	0	0	+	+	capillary	2-7	2	2 lateral	gono	
	Paranerilla Jouin & Swedmark, 1965	0.7-0.9	0	0	0	short	+	compound	2-7 reduced	2 long	glandular plates	gono	mud pelagic development
	Psammoriedlia Kirsteuer, 1966	0.4-0.5	2	0	0	+	+	capillary	2-6	2	2/4 dorsal?	?	
8	***Troglochaetus*** Delachaux, 1921	0.5-0.6	2	0	0	0	0	capillary	2-7 reduced	2 reduced	dorsal	herma	Only genus in fresh water
	Nerillidium Remane, 1925	0.3-0.6	2	0-2	0 or 2 mic.*	+-0	+	capillary	0 or 2-7	2	4 dorsal	herma	
	Thalassochaetus Ax, 1954	0.5-0.6	2	0	0	0	+	compound	2-7	2 palpif.	cuticular plates	?	
	Nerillidopsis Jouin, 1966	0.5-0.6	2	2	0	0	+	compound + capillary	2-7	2	8 dorsal	herma	
	Micronerilla Jouin, 1970	0.5-0.6	2	3 wrinkled	2 pigm.	0	+	compound	2-7	2 wrinkled	2 dorsal	gono	wrinkled antennae and pygidial cirri; 2 cirri/parapodium
	Afronerilla Faubel, 1978	0.36	0	0	0	0	0	capillary	2-7	-----	-----	?	
	Akessoniella Tzetlin & Larionov, 1987	0.4	2	2	0	0	+	capillary	2-7	-----	2 lateral	herma	unpaired dorsal sens. org.
	Trochonerilla Tzetlin & Saphonov, 1992	0.62	0	3	2 pigm.	0	+	capillary	2-8	2 wrinkled	2 dorsal	gono.	trochus
9	***Nerilla*** Schmidt, 1848	1.5-1.7	2	3 jointed	4 pigm.	+ jointed	+	capillary	2-8	2 jointed	dorsal	gono.	
	Mesonerilla Wilke, 1953	1.2	2	2-3	0 or 2 ciliary *	+	+/-	compound	2-8 2-9	2	? dorsal	gono.+ herma	brood hood (only in *M. intermedia)*
	Leptonerilla Westheide & Purschke, 1996	0.7	2	3	2 pigm.	+	+	compound + capillary	2-9	2	2 (?) dorsal -----	?	2 cirri/parapodium
	Meganerilla Boaden, 1961	1.2-1.5	2 large	0-1	0 or 2	+	+	capillary	2-9	2	----- 10-12	gono	
	Xenonerilla gen. et sp. nov.	0.7-1.1	2 large	0	0	0	0	capillary very few	2-9	2	ventral	gono	very few chaetae; ventral buccal pieces

Xenonerilla possesses a second posterior pair of oviducts, which is incomplete and apparently reduced to a pair of coelomostomes, that does not exist in *Meganerilla* nor in other Nerillidae (Jouin, 1968; Westheide, 1990).

The pharyngeal bulb of *X. bactericola* exhibits several autapomorphic characters: (1) the transformation of the anterior epithelial part that covers the bulbous muscle into a ventral tongue, distinct from the dorsal tongue-like organ of other nerillids; (2) this tongue is large, bridge shaped, eversible and contains numerous skeletal elements; (3) the reduced number of fibres in both the bulbous and the investing muscle, in comparison with other Nerillidae; (4) the secretory dorsal part of the pharyngeal epithelium; and (5) the presence of numerous secondary lysosomes in the stomodeal and oesophageal epithelium.

The tongue of *Xenonerilla bactericola*, in spite of its unique position in the ventral part of the pharyngeal bulb, possesses typical intracellular skeletal elements, or stylets, that are similar in structure and thus, are homologous to those of other Nerillidae. According to Purschke (1988), four skeletal elements represent the basic plan in this family. This is realized in *Nerillidium troglochaetoides,* where the tongue-like organ comprises four cells, each with one skeletal rod. In *Nerilla* there are 16 cells, each containing one skeletal element. In *X. bactericola*, the symmetrically arranged tongue comprises four to five pairs of cells, each containing several (5-11) skeletal elements.

The muscle cells are reduced in comparison with other Nerillidae; the number of fibres in the bulbous muscle is only 10 in *X. bactericola*, versus 13 in *Nerillidium* and 19 in *Nerilla*. On cross section, the layers of myofilaments are very thin in each fibre of *X. bactericola*: 0.33 µm, versus 0.77 µm in *Nerillidium* and 2.5 µm in *Nerilla*. Moreover the curved shape of the bulbous muscle in *X. bactericola* is unusual. As in other nerillids the mitochondria have an axial position in the fibres.

A secretory activity of the stomodeal epithelium has already been noted in other Nerillidae, for example, in *Nerilla antennata* (Purschke, 1985). Such activity, however, is limited in comparison with *X. bactericola,* that has well-developed secretory granules in the dorsal cluster of cells of the pharyngeal bulb**.**

The most striking feature of the *X. bactericola* stomodeal epithelium is the regular presence of a subcuticular layer of electron-dense vesicles and of numerous secondary lysosomes not observed with such an abundance in the stomodeal epithelium of other Nerillidae. Such lysosomes are also present in the oesophageal cells. It is possible that, as the subcuticular layer of vesicles, they are related to the presence of bacteria, which are located in the invaginations of the pharyngeal organ. However, we never observed bacteria inside the epithelial cells and so the hypothesis of an intracellular digestive process of the bacteria appears unlikely.

Xenonerilla bactericola lives in a dysoxic and sulphide-rich environment. The presence of abundant lysosomes observed in the stomodeal and oesophageal epithelia, as well as in the ventral epidermis of the head, is a peculiar feature of *X. bactericola* among the Nerillidae. These lysosomes could be morphologically compared to the sulfide-oxidizing bodies described in *Urechis caupo* (Menon & Arp, 1998). The latter are assumed to form a peripheral defense on all exposed surface and enable the worm to live in a sulphide-rich environment. Whether or not the numerous secondary lysosomes present in different epithelial layers of *X. bactericola* are really related to the sulfide-rich environment and able to protect all the tissues of the worm against sulphide toxicity has to be proven. A complete TEM investigation of the epidermal layer of the entire animal, along with characterization of these lysosomes is needed to resolve these issues.

Bacterial associations, or symbioses, are reported for gutless oligochaetes (Giere et al. 1988, 1991, 1995) but are uncommon in polychaetes. To date, only two nerillid species, *Trochonerilla mobilis* Tzetlin & Saphonov, 1995 and *Micronerilla brevis* Saphonov & Tzetlin 1997 are known to have endosymbiotic bacteria located in epidermal bacteriocytes and another genus of polychaetes, the genus *Alvinella*, with *A. pompejana* Desbruyères & Laubier, 1980 and *A. caudata* Desbruyères & Laubier, 1986, has bacterial epibionts (Gaill et al., 1987; Desbruyères et al., 1998). In *Trochonerilla mobilis* and *Micronerilla brevis*, the presence of electron-dense residual bodies in cytoplasmic parts of the bacteriocytes suggests that there is probably an endocytosis of bacteria in these nerillids. Moreover the presence of bacteria in adults, juveniles and embryos shows that the symbiosis is obligate (Tzetlin & Saphonov, 1995). In *Xenonerilla bactericola*, although we regularly observed undeterminable food residuals in the gut lumen, it is possible that the bacteria are phagocytozed either by epidermal cells or by the digestive epithelium and used as supplementary food source. But until now no endocytosis has been observed in or below the epithelial cells, although bacteria penetrate the oesophageal cuticle (Fig. 5D). The metabolic relationships between the two nerillid hosts *T. mobilis* and *M. brevis* and the bacteria remain unclear, as do the relationships between *Xenonerilla bactericola* and its epibionts. Only additional molecular, biological and physiological studies will elucidate these relationships.

One of the most striking characters of the taxon Nerillidae is that the peristomium bears chaetae (Westheide, 1990; Westheide & Rieger, 1996), which are only lacking in *Troglochaetus*, *Afronerilla,* some *Mesonerilla* species and *Xenonerilla*. The latter is the first known nerillid genus in

which chaetae are either totally lacking or reduced dramatically in number and restricted to few posterior segments (V-VII). In their attempt to explain the inferred progenetic origin of Nerillidae Westheide (1987) and Westheide & Purschke (1996) postulated that the stem species ought to have numerous head appendages, a maximum number of nine segments, segments with parapodia, dorsal and ventral cirri, jointed chaetae and anal cirri (see also Ax, 1953). By these criteria the new described species can be regarded as highly evolved, even though showing the nerillid maximum number of segments.

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