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ORIGINAL PAPER

Nerillidae (Annelida) from the Corona lava tube, Lanzarote, with description of *Meganerilla cesari* n. sp.

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Abstract Five species of Nerillidae are previously known from Atlantic cave systems. Another four species of Nerillidae are reported here from the Corona lava tube (Lanzarote, Canary Islands) presenting the first records of *Mesonerilla* and *Meganerilla* from anchialine environments. We here describe *Meganerilla cesari* n. sp. which resembles *Meganerilla swedmarki* by the leaf-shaped interramal cirri and lack of median antenna, but differs by the smaller size, shorter chaetae, dense ciliation and presence of ventral lobes on the parapodia. One identified and two unidentified species of *Mesonerilla* are also reported. Updated diagnoses are presented for *Mesonerilla armoricana*, reported here for the first time from the Canary Islands, and *Leptonerilla diatomeophaga*, the only nerillid previously known from the Corona lava tube. The Corona lava tube holds a large variety of benthic habitats, which may explain the high diversity of Nerillidae in this cave system.

Keywords Meiofauna · Interstitial · *Mesonerilla* · *Leptonerilla* · Anchialine cave

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Introduction

The Corona lava tube is a 20,000-year-old cave system on the northeast coast of Lanzarote, Canary Islands (Carracedo et al. 2003). Extending about 7 km from the Corona volcano to the sea, this locality is one of the longest volcanic caves in the world. Although the lava tube was formed under subaereal conditions, the last 1,700 m of the cave were flooded by the sea during the last postglacial period. This last section nowadays extends below sea level and contains a unique anchialine environment with 77 species reported to date, including 37 endemic species and 4 endemic genera (Iliffe et al. 1984, 2000; Martínez et al., this issue).

Crustacea show the highest and Annelida the second highest diversity among the fauna of the Corona lava tube (Martínez et al. this issue). The macro- and meiofaunal annelids recorded comprise species from open waters as well as several endemic species (Hartmann-Schröder 1974, 1988; Bertelsen 1986; Núñez et al. 1997; Iliffe et al. 2000). *Leptonerilla diatomeophaga* (Núñez 1997 in Núñez et al. 1997) was described from a carpet of benthic diatoms at the anchialine lagoon at Jameos del Agua, and is the only nerillid previously recorded from the cave.

The family Nerillidae is, with 50 described species, one of the most species-rich families among interstitial polychaetes, occupying an extreme variety of habitats worldwide (Worsaae 2005). Another four species of Nerillidae have previously been described from anchialine and marine cave systems in the Atlantic: *Leptonerilla prospera* Sterrer and Iliffe, 1982; *Longipalpa saltatrix* Worsaae, Sterrer and Iliffe, 2004; *Nerilla marginalis* Tilzer, 1970; and *Troglochaetus beranecki* Delachaux, 1921. Neither *Mesonerilla* nor *Meganerilla* have been reported previously from anchialine environments, but both nerillid genera have been found in fine silty sediments

and dirty coarse gravel similar to sediments of the Corona lava tube (see, e.g., Müller et al. 2001; Worsaae and Kristensen 2005; Worsaae and Rouse 2009).

During the March 2008 expedition to the Corona lava tube, five species of Nerillidae were collected. We here describe *Meganerilla cesari* n. sp. and briefly present the four other nerillids from the Corona lava tube (Fig. 1).

Materials and methods

Material was collected during the March 2008 international expedition to the Corona lava tube (Wilkens et al. this issue), and three additional surveys in July 1993, July 2006 and May 2008. Sediment samples were collected by snorkeling and scuba diving. Rebreather diving system was necessary for sampling at Montaña de Arena. The amount of sediment collected reflected the spatial range of each habitat in order to minimize the impact on the cave ecosystem. A subsample of each sample was used for analyses of the abiotic parameters of the sediment (Wilkens et al. this issue), before processing it for faunistic studies. Sediment was bulk fixed in 2% formalin in seawater, sieved through a 63-µm mesh and transferred to 70% ethanol. Fauna from the samples collected at Montaña de Arena and Jameos del Agua were studied alive. These samples were first anesthetized by 1:1 addition of isotonic $MgCl_2$, decantated through a 63-µm mesh, and transferred to seawater. Selected live animals were digital video-recorded using a JVC TK-C1381 camera system, mounted on an Olympus CH30 microscope. All material was thereafter re-anesthetized with isotonic $MgCl_2$ solution, fixed in 2% glutaraldehyde in seawater, and stored in cacodylate buffer with 0.3 M sucrose. Specimens selected for scanning electron microscope were postfixed in 1% osmium tetroxide in cacodylate buffer, rinsed and dehydrated through an ethanol series, and transferred to 100% acetone. The specimens were thereafter critical point dried, mounted on stubs, and coated with platinum. Specimens were examined with a JEOL JSM-6335F field emission scanning electron microscope. Permanent glycerol whole mounts were prepared of the remaining material, except for some specimens fixed in ethanol for future molecular studies.

Drawings were made from pictures frame-grabbed from video recordings of live animals. Material is deposited at the Museo de Ciencias Naturales of Tenerife (TFMCBM), Departamento de Biología Animal of the La Laguna University (DBAULL), Canary Islands, and at the Natural History Museum, Copenhagen, Denmark (ZMUC).

Studies on live animals were carried out at the Benthos Laboratory, University of La Laguna (Canary Islands). Studies of fixed material were done at the Marine Biological

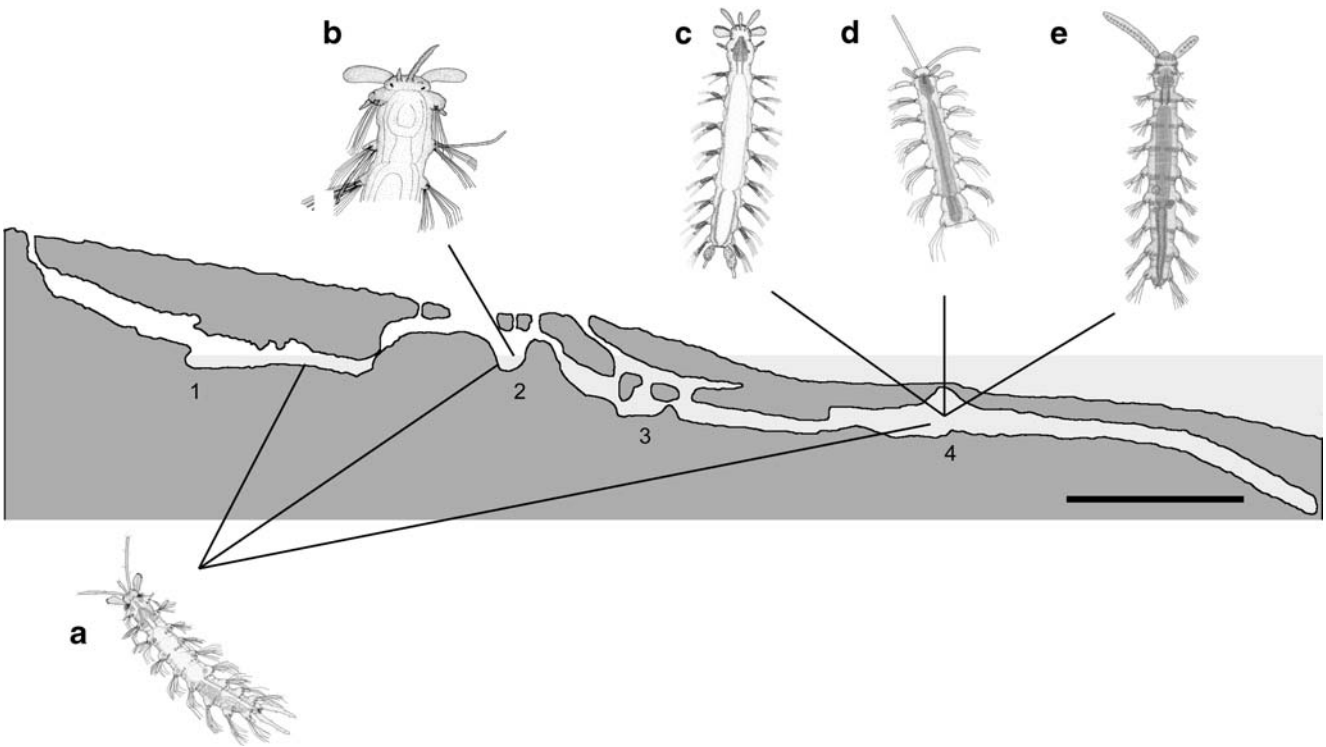


Fig. 1 The Corona lava tunnel, showing the distribution of the Nerillidae along the different sections. *1* Los Lagos cave, *2* Jameos del Agua, *3* Túnel de la Atlántida, *4* position of Montaña de Arena at Túnel de la Atlántida; **a** *Mesonerilla* sp. 1, **b** *Leptonerilla diatomeophaga*, **c** *M. armoricana*, **d** *Mesonerilla* sp. 2, **e** *Meganerilla cesari* n. sp. *Scale bar* 500 m

Laboratory and Natural History Museum, University of Copenhagen (Denmark).

Results

Genus ***Leptonerilla*** Westheide and Purschke, 1996

Leptonerilla diatomeophaga (Núñez, 1997 in Núñez et al. 1997)

Figures 1 and 2, Table 1.

Type material Holotype (TFMCBM AN/000193) and six paratypes (DBAULL 201–206), Jameos del Agua, the Corona lava tube, carpet of benthic diatoms, 2 m depth, 29°09.43′N, 13°25.51′W, April 1993 and April 1995 (Coll. J. Núñez, L. Núñez and M. Pascual).

Additional material from the Corona lava tube Twenty specimens, Jameos del Agua, same as type locality, July 2006 (Coll. A. Martínez and J. Núñez), fixed in formalin and stored in 70% ethanol (ZMUC-POL-2084).

Additional material from the Canary Islands One whole mount (DBAULL), Agua Dulce marine cave, Los Abrigos (El Médano), Tenerife, February 1993, from the sponge *Neophrissospongia nolitangere* (Schmidt, 1870), 10 m depth, (Coll. M. Pascual and J. Núñez; in Núñez et al. 2005).

Diagnosis (modified from Núñez et al. 1997) Opaque *Leptonerilla* with 9 chaetigerous segments. Prostomium

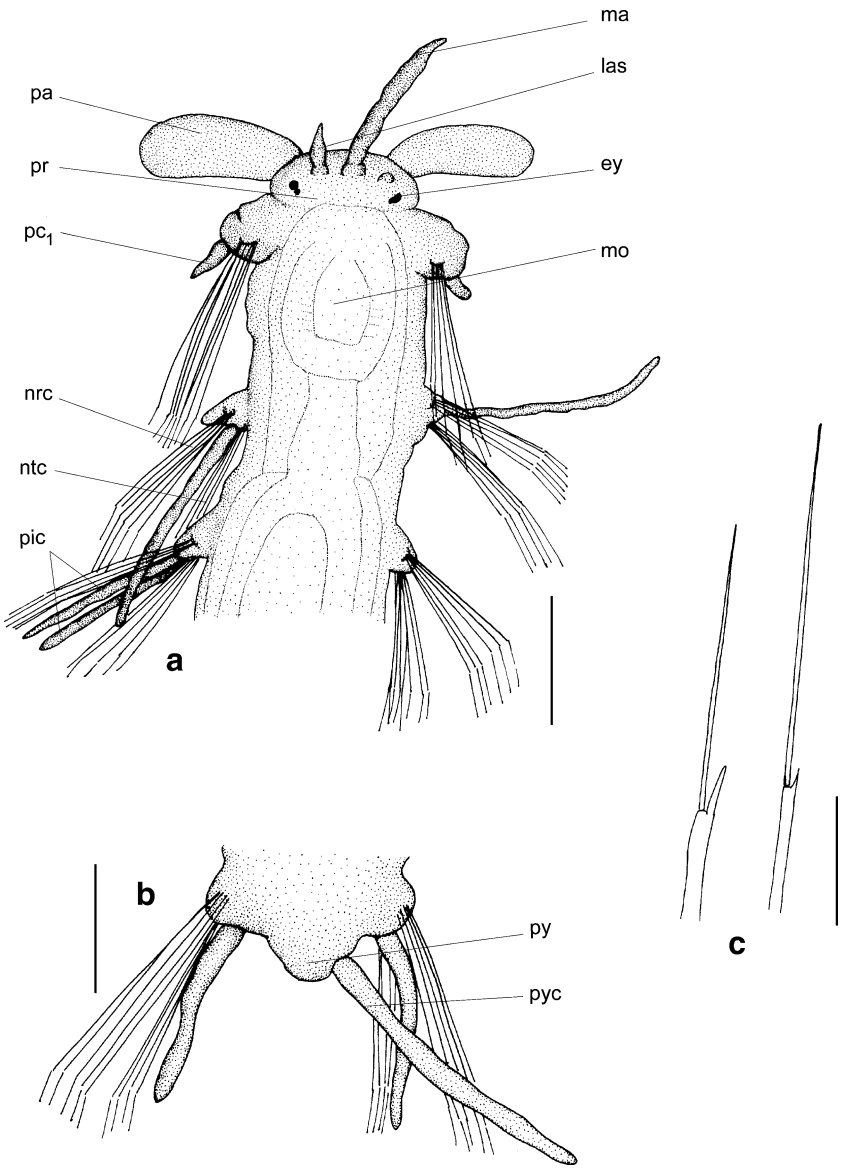


Fig. 2 *Leptonerilla diatomeophaga* (Núñez 1997 in Núñez et al. 1997). Redrawn from Núñez et al. 1997. **a** Prostomium, dorsal view. **b** Pygidium, dorsal view. **c** Compound chaetae, showing different sizes of the distal extension of the shaft. *ey* Eye spot, *las* scar of the lateral antenna, *ma* median antenna, *mo* mouth opening, *nrc* neuropodial chaetae, *ntc* notopodial chaetae, *pa* palp, pc_1 parapodial cirri segment 1, *pic* double interramal cirri, *pr* prostomium, *py* pygidium, *pyc* pygidial cirri. *Scale bars* **a**–**b** 125 μm, **c** 30 μm

Table 1 Diagnostic characters of all nerillids recorded in the Corona lava tube

Nerillidae from the Corona lava tube	L (µm)	Max W ÷ para (µm)	Eyes	Med ant, max L (µm)	Lat ant, max L (µm)	Palp, max L (µm)	Buccal cirri, max L (µm)	Para cirri, max L (µm)	Para cirri, size along body	Para cirri, shape	Pyg cirri, max L (µm)	Pyg cirri, shape	Buc ch, max no.	Buc ch, max L (µm)	Ch segm 2–9, max no.	Ch segm 2–9, max L (µm)	Habitat in the Corona lava tube
Leptonerilla diatomeophaga (Núñez, 1997)	1,200	210	P	200	250	27	30	260	Equal	Filiform	262	Filiform	12	250[a]	24	260[a]	Carpet of benthic diatoms
Meganerilla cesari n. sp.	1,005	125–129	A	A	A	154–288	13–28	80–95	Incr	Tapering	?	?	5	30	17	110	Calcareous sand
Mesonerilla sp.1	610–1,079[b]	70–159[b]	A	52–91	174–317[b]	68–72	20–39[b]	68–142[b]	Incr	Cylindrical or paddle shaped	213	Cylindrical or filiform	11	105	23	171	Lapilli patches, calcareous sand
Mesonerilla sp. 2	465[c]	68	A	180	179	42	47	73	Incr	Cylindrical	?	?	7	71	c. 18	88	Calcareous sand
M. armoricana Swedmark, 1959	1,100	150	A	100	180	80	50	50	Equal	Cylindrical	225	Bottle-shaped	A	A	c. 10[a]	90[a]	Calcareous sand

A Absent, *ant* antenna, *ch* chaetae, *max* maximum, *med* median, *incr* increasing, *L* length, *lat* lateral, *segm* segment, *para* parapodial, *P* present, *pyg* pygidial, *W* width

[a] Estimated from original description

[b] Maximum values measured on squeezed whole mounts

[c] Fragment with 7 segments only

rounded with two club-shaped palps and three filiform antennae. Median antenna slightly shorter than lateral antennae. Two reddish eyes. Compound chaetae in all segments. First segment uniramous with up to 12 chaetae. Following segments biramous with maximum 24 chaetae. Chaetal blades on segments 2–9 increasing in length within each fascicle towards the interramal cirri. Distal extension on chaetal shaft differing in size along segments 2–9 from short and pointed to long and blunt. Filiform parapodial cirri in all segments. Buccal cirri uniramous and shorter than parapodia. Double interramal cirri in segments 2–9, more than double length than chaetae and maximum body width.

Distribution Known only from the Canary Islands and Selvagem Islands (Portugal), from three different habitats (diatom carpet, sponge crevices, and maerl), in marine caves of Lanzarote and Tenerife, and maerl at 16 m depth at Selvagem Pequena (Núñez et al. 2001).

Remarks This species was originally described as *Mesonerilla diatomeophaga* (Núñez et al. 1997). The original description of this species was limited to light microscopy observations, and several details on external ciliation, nephridia and gonoducts are unknown. Additional morphological investigations on new material from the type locality are warranted. Unfortunately, the additional material collected and mentioned above was not fixed appropriately for SEM and CLSM studies. Two other species belong to the genus, *L. prospera* Sterrer and Iliffe, 1982 described from fine silty sediment layers of Walshingham Cave (Bermuda), and *L. diplocirrata* Westheide and Purschke, 1999 described from offshore subtidal patches of coral sand between coral reefs in Hainan Island (South China Sea) at 2–3 m depth. These species differ in body size and relative lengths of median antennae from *L. diatomeophaga*.

Genus ***Mesonerilla*** Remane, 1949

Mesonerilla armoricana Swedmark, 1959

Figures 1 and 3, Table 1.

Material Six whole mounts (TFMCBM AN/00232-AN/000234, ZMUC-POL-2085–2087) from Montaña de Arena, the Corona lava tube, calcareous sand accumulation at 40 m depth, 29°09.43′N, 13°25.51′W, 22 March 2008 (Coll. T. Iliffe, T. Tysall). Additional information obtained from video recordings of six live animals.

Diagnosis (modified after Swedmark 1959 and Jouin 1968) Hyaline *Mesonerilla* with nine segments. Prostomium rounded with two spoon-shaped palps and three relatively

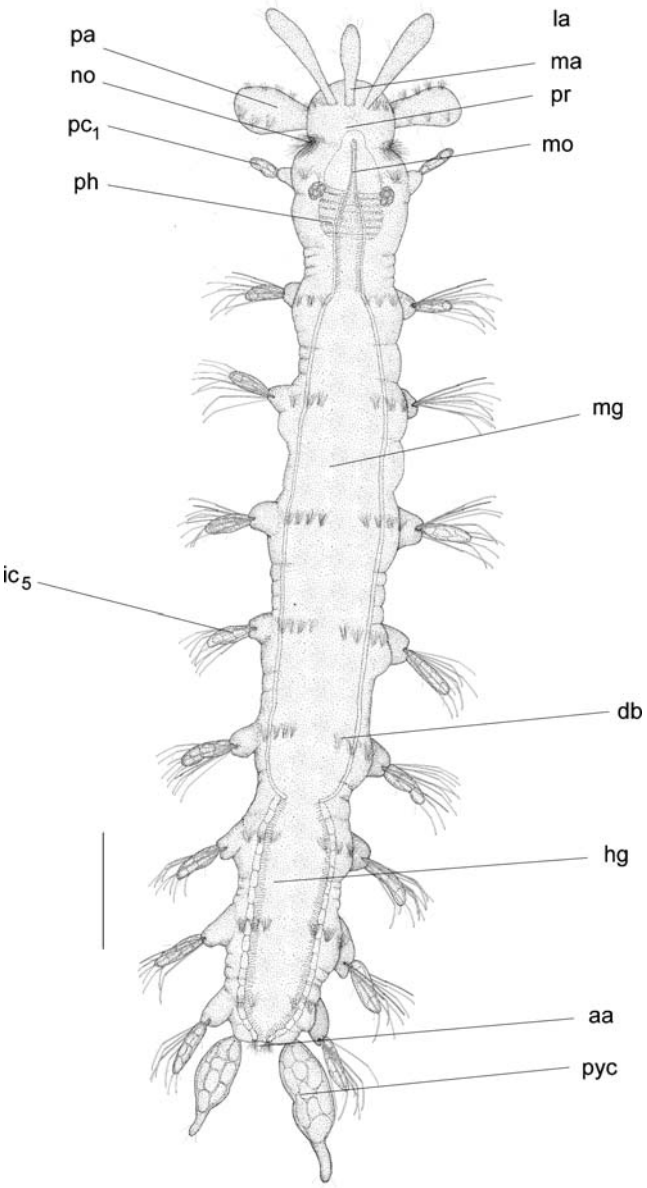


Fig. 3 *Mesonerilla armoricana* Swedmark, 1959. Drawing of live adult specimen, dorsal view. *aa* Anal aperture, *db* dorsal ciliary band, *hg* hindgut, ic_5 interramal cirri on segments 5, *la* lateral antenna, *ma* median antenna, *mg* midgut, *mo* mouth openning, *no* nuchal organ, *pa* palp, pc_1 parapodial cirri segment 1, *ph* pharynx, *pr* prostomium, *pyc* pygidial cirri. *Scale bar* 150 μm

short antennae. Median antenna shorter than lateral antennae. Eyes absent. Compound chaetae on segments 2–9; segment 1 achaetous. All segments with cylindrical parapodial cirri of similar size, less than half maximum body width. Pygidium with two bottle-shaped cirri. Hermaphroditic with two pairs of spermioducts opening in segments 6 and 7, and one pair of oviducts opening in segment 8.

Distribution Both adults and juvenile specimens were collected in the Corona lava tube from calcareous sand at Montaña de Arena (Fig. 1). *Mesonerilla armoricana* has also been found in coarse sand and sandy patches between rocks at several off-shore localities off Tenerife at 10–25 m depth (Martínez, unpublished). It has previously been recorded from the English Channel (Roscoff area) (Swedmark 1959) and Irish Sea (Portaferry) (Boaden 1966).

Remarks Although detailed studies on, e.g., external ciliation could not be conducted on the cave material, there were no noticeable differences from off-shore specimens from Tenerife or the original description. This is thus the first record of *M. armoricana* from the Canary Islands, considerably increasing its distribution range.

Mesonerilla sp. 1

Figures 1 and 4, Table 1.

Material Two whole mounts (TFMCBM AN/00227-AN/00228), Cueva de los Lagos, the Corona lava tuve, lapilli patches at the beginning of the flooded area of the cave, 2 m depth, 29°09.43′N, 13°25.51′W, 12 April 1995 (Coll. J. Núñez). One whole mount (ZMUC-POL-2088), Cueva de los Lagos, accumulation of lapilli at 300 m into the flooded area, 3 m depth, 29°09.43′N, 13°25.51′W, 3 May 2008 (Coll. A. Martínez and J. Núñez). Three whole mounts (TFMCBM AN/00229-AN/00230, ZMUC-POL-2089), Jameos del Agua, the Corona lava tube, lapilli patches at 9 m depth, 29°09.43′N, 13°25.51′W, 6 May and 18 July 2006 (Coll. A. Martínez and J. Núñez). Eleven whole mounts (TFMCBM AN/00231, ZMUC-POL-2090–2099) and 11 specimens on three SEM stubs (ZMUC-POL-2100–2102), Montaña de Arena, Túnel de la Atlántida, the Corona lava tube, calcareous sand dune, 40 m depth, 29°09.43′N, 13°25.51′W, 21 and 23 March 2008 (Coll. T. Iliffe and T. Tysall). Additional information was gathered from video-recordings of two animals.

Characteristics Mesonerilla with nine chaetigerous segments. Prostomium with two club-shaped palps and three antennae. Median antenna cylindrical and shorter than filiform lateral antennae. No eyes. Two distinct large esophageal glands in segment two; parapodial glandular structures in segments 3–6. Compound chaetae in all segments; increasing in size towards pygidium. Buccal cirri short and cylindrical; remaining segments with slightly tapering interramal cirri, increasing in length towards pygidium. Pygidium sometimes with glandular preanal zone, dorsal anus, and two cylindrical or filiform cirri. A dorsal brooding hood with ciliated rim at segment 8 was observed on three specimens.

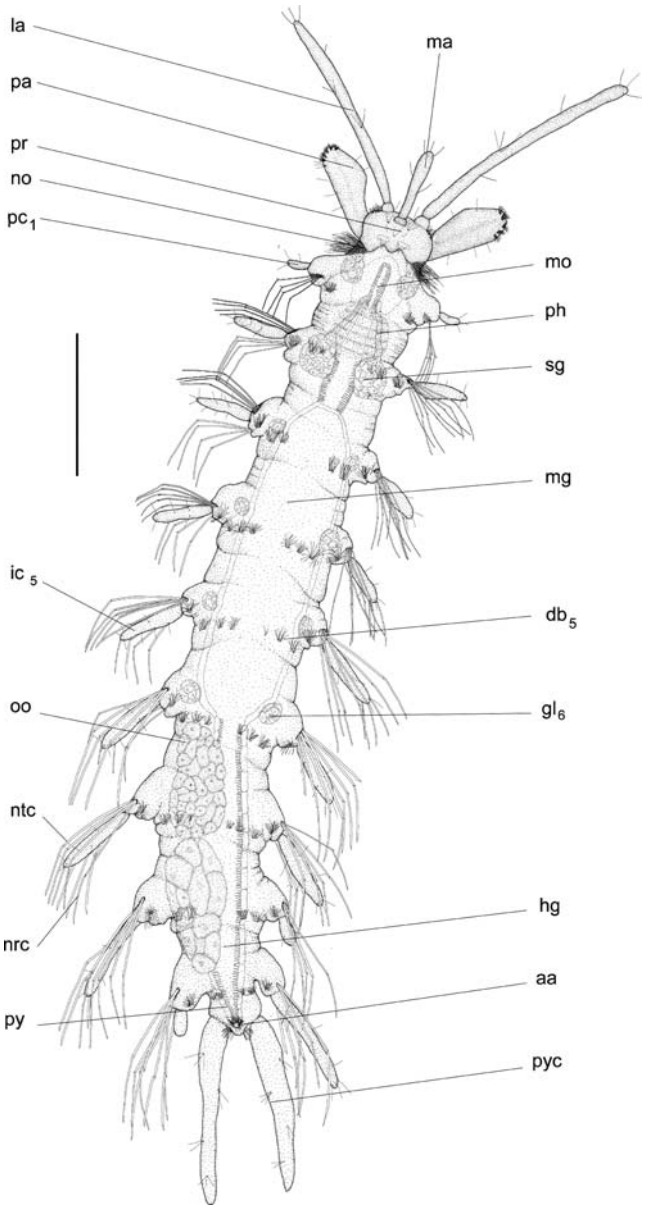


Fig. 4 *Mesonerilla* sp. 1. Drawing of live adult specimen, dorsal view. *aa* Anal aperture, db_5 dorsal transverse ciliary band segment 5, gl_6 glandular area parapodium 6, *hg* hindgut, ic_5 interramal cirri on segment 5, *la* lateral antenna, *ma* median antenna, *mg* midgut, *mo* mouth opening, *no* nuchal organ, *nrc* neurochaetae, *ntc* notochaetae, *oo* oocytes, *pa* palp, pc_1 parapodial cirri segment 1, *ph* pharynx, *pr* prostomium, *py* pygidium, *pyc* pygidial cirri, *sg* salivary glands. *Scale bar* 100 μm

Distribution *Mesonerilla* sp. 1 was collected interstitially in all sections of the Corona lava tube, from lapilli patches in Cueva de los Lagos and Jameos del Agua anchialine lagoon, and from coarse sediments in *Montaña de Arena* (Fig. 1). This is the only species collected from the lapilli patches and the only nerillid which have been found in all sections of the cave.

Remarks Unfortunately, the preserved material is generally in bad condition preventing further examinations, and our few measurements on body size and appendages varied a lot. Additional new material is necessary to properly identify or describe this possibly new species. The species shows greatest resemblance to *M. intermedia* Wilke, 1953 by the presence of a brooding hood, but seems to differ from this by the short median antenna (see Table 1). However, material from the northeast and northwest Atlantic previously assigned to *M. intermedia* also vary in shape and size of appendages and brooding hood (Westheide 2008). *Mesonerilla* sp. 1 seems to differ from all described species of *Mesonerilla* by the presence of large rounded esophageal glands in segment 2, and parapodial glandular areas in segments 3–6.

Mesonerilla sp. 2

Figures 1 and 5, Table 1.

Material Montaña de Arena, Túnel de la Atlántida, calcareous sand accumulation, 40 m depth, 29°09.43′N, 13°25.51′W, 23 March 2008 (Coll. T. Iliffe and T. Tysall). The single specimen was video-recorded alive, and subsequently lost.

Characteristics Small *Mesonerilla* recorded from a single anterior fragment with seven segments. Prostomium rounded with two club-shaped palps and three long filiform antennae of similar length. Eyes absent. Compound chaetae in all segments with single extension on shaft; chaetal length slightly increasing posteriorly. All segments with cylindrical parapodial cirri; buccal cirri of similar length as following, but broader.

Distribution The single specimen was sorted out from coarse sand collected at *Montaña de Arena* (Fig. 1) in the Corona lava tube, Lanzarote (Canary Islands).

Remarks New and complete material is necessary to verify and describe this possibly new species. However, the broad and long buccal cirri are considered a unique character within *Mesonerilla*. *Mesonerilla* sp. 2 otherwise shows closest resemblance to *M. luederitzi* Remane, 1949, but differs by the equal sized antennae. *Mesonerilla intermedia* and *M. equadoriensis* Schmidt & Westheide, 1977 both have longer interramal cirri and chaetae. In addition to various size differences of chaetae and cirri, *Mesonerilla* sp. 2 differs from *Mesonerilla* sp. 1, *M. fagei* Swedmark 1959 and *M. neridae* Worsaae and Rouse 2009 by presence of equal sized antennae and from *M. armoricana* and *M. roscovita* Lévi, 1953 by presence of buccal chaetae as well as equal sized antennae. *M. biantennata biantennata* Jouin, 1963 and *M. biantennata pacifica* Jouin, 1970 lack a median antenna.

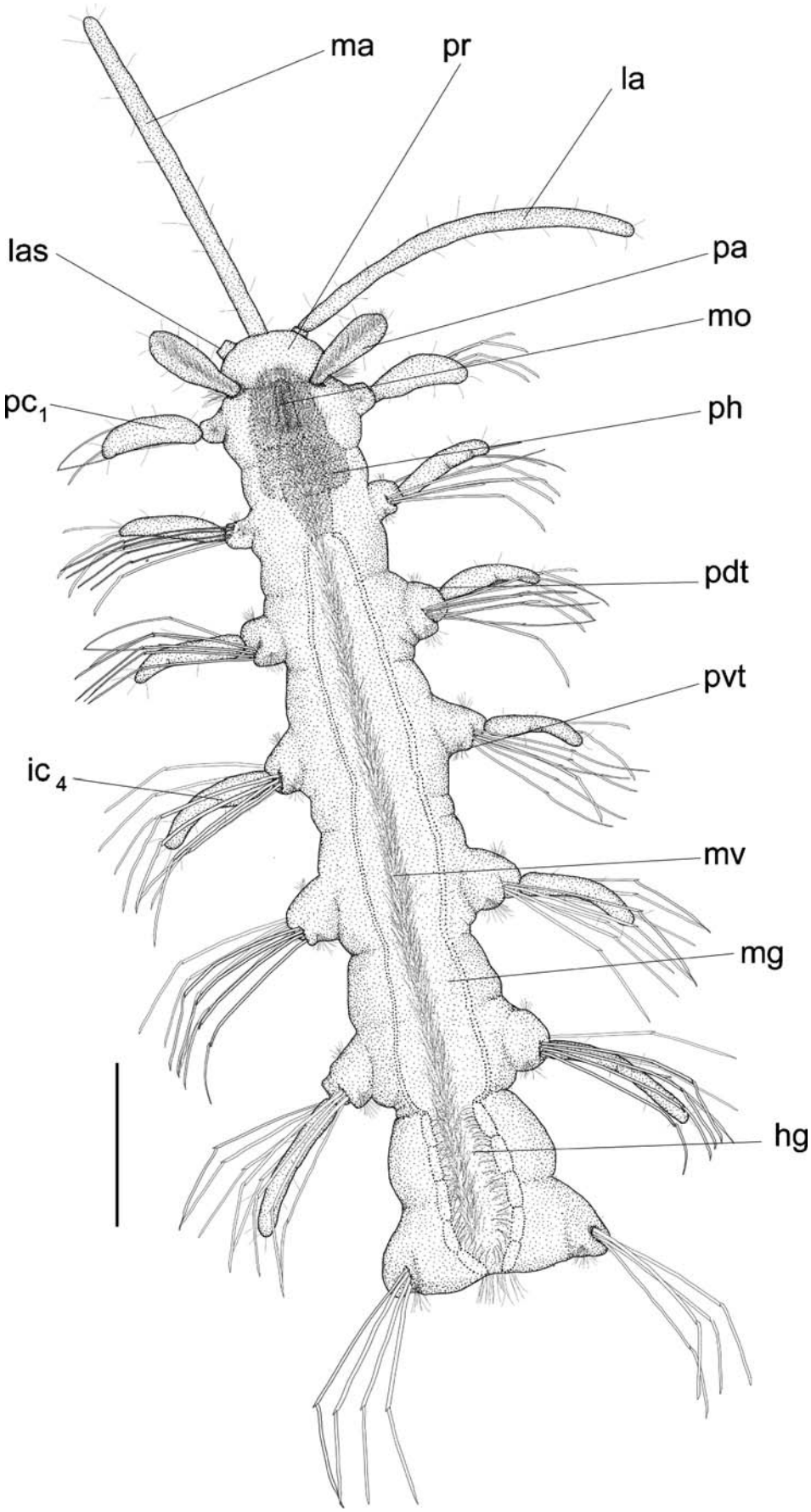


Fig. 5 *Mesonerilla* sp. 2. Drawing of live adult specimen, ventral view. *hg* Hindgut, ic_4 interramal cirri on segment 4, *la* lateral antenna, *las* scar of the lateral antenna, *ma* median antenna, *mg* midgut, *mo* mouth opening, *mv* midventral ciliary band, *pa* palp, pc_1 parapodial cirri segment 1, *pdt* parapodial dorsal tuft, *ph* pharynx, *pr* prostomium, *pvt* parapodial ventral tuft. *Scale bar* 100 μm

Genus ***Meganerilla*** Boaden, 1961

***Meganerilla cesari* n. sp.**

Figures 1, 6, 7 and 8, Tables 1 and 2.

Type material Holotype: female (whole mount, ZMUC-POL-2103), Montaña de Arena, the Corona lava tube, calcareous sand accumulation at 40 m depth, 29°09.43′N, 13°25.51′W, 23 March 2008 (Coll. T. Iliffe and T. Tysall). Paratypes: Two whole mounts (one juvenile, TFMCBM AN/00235; one adult, TFMCBM AN/00236) and two SEM specimens on stubs (one juvenile and one adult, ZMUC-POL-2104), all with same locality data as for holotype. Additional information was gathered from video-recordings of several live animals.

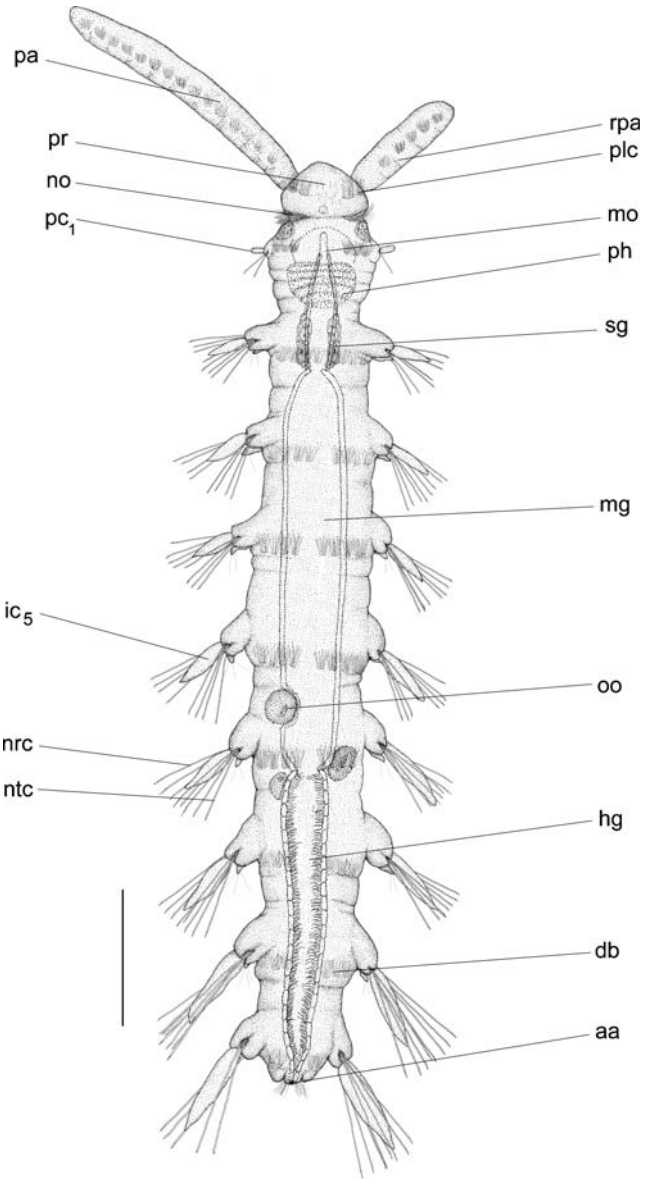


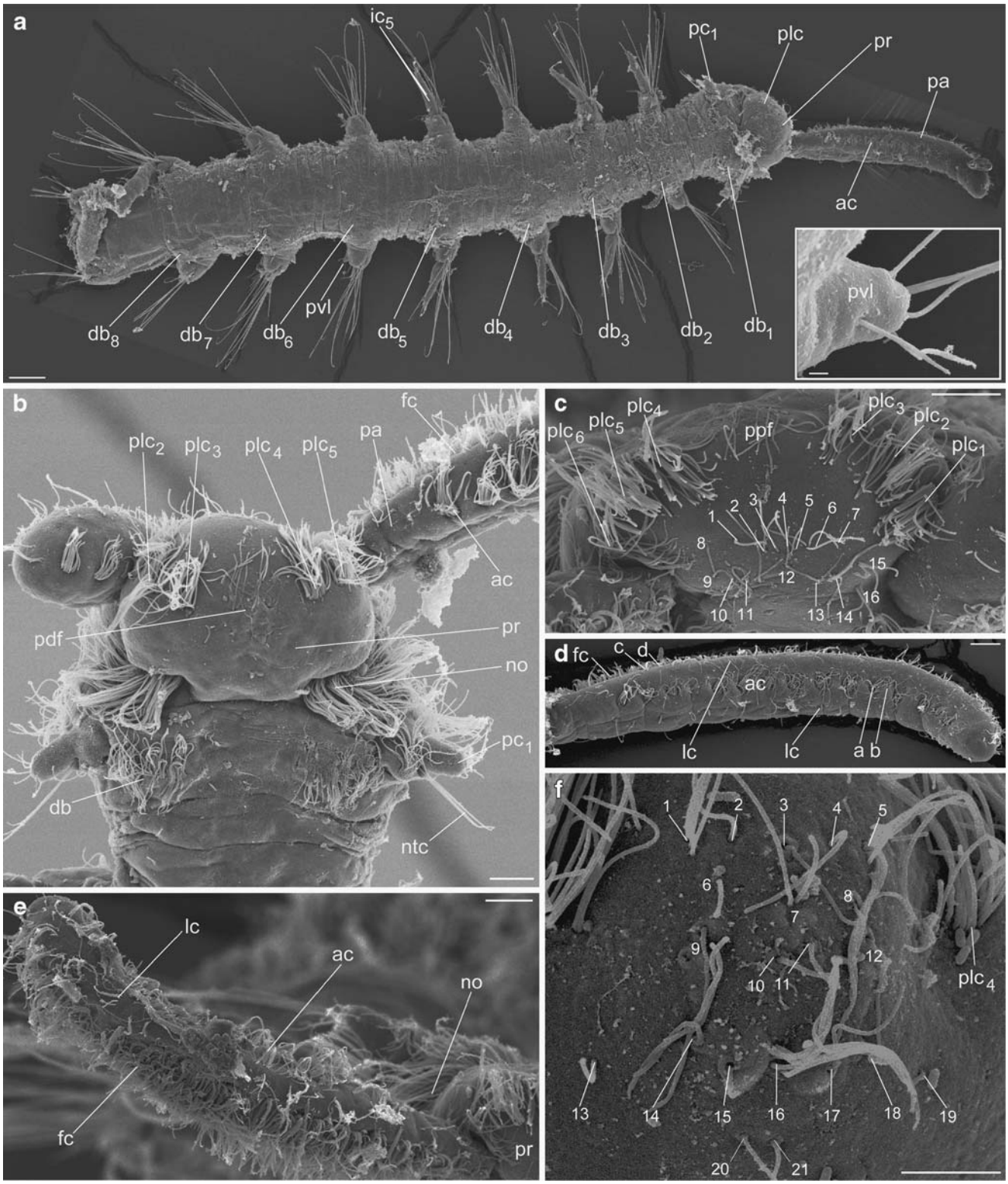
Fig. 6 *Meganerilla cesari* n. sp. Drawing made from live holotype, dorsal view. *aa* Anal aperture, *db* dorsal ciliation, *hg* hindgut, ic_5 interramal cirri on segment 5, *mg* midgut, *mo* mouth opening, *no* nuchal organ, *nrc* neurochaeta, *ntc* notochaeta, *oo* oocyte, *pa* palp, pc_1 parapodial cirri on segment 1, *ph* pharynx, *plc* prostomial lateral ciliation, *pr* prostomium, *rpa* regenerating palp, *sg* salivary glands. *Scale bar* 200 μm

Fig. 7 *Meganerilla cesari*, n. sp., scanning electron micrographs. **a** ▶ Dorsal view of whole specimen. *Inset* Detail of the parapodial ventral lobe on segment 6. **b** Dorsal view of prostomium. **c** Frontal view of prostomium, showing arrangement of anterior ciliated field (no. 1–16). **d** Dorsal view of palp, showing arrangement of cilia (**a–d**). **e** Frontal view of palp. **f** Dorsal view of prostomium, showing arrangement of posterior ciliated field (nos. 1–19). *a* Large tuft of abfrontal band, *b* small tuft of abfrontal band, *ac* abfrontal ciliary band, *c* small tuft of lateral band, *d* intermediate cilium of lateral band, $db_{1–8}$ dorsal ciliation, *fc* frontal ciliary band, ic_5 interramal cirri on segment 5, *lc* lateral ciliary band, *no* nuchal organ, *ntc* notochaetae, *pa* palp, pc_1 parapodial cirri on segment 1, *pdf* prostomium dorsal ciliary field, $plc_{1–6}$ prostomium lateral ciliary bands tufts 1–6, *ppf* prostomium posterior ciliated field, *pr* prostomium, *pvl* parapodial ventral lobe. *Scale bars* **a** 30 μm (inset 1 μm), **b** 10 μm, **c** 10 μm, **d** 10 μm, **e** 10 μm, **f** 10 μm

Diagnosis A *Meganerilla* with nine chaetigerous segments and no antennae. Prostomium with two cylindrical palps and no eyes. Elongated palps with rounded tips and dense ciliation, arranged in four longitudinal bands. Prostomium with paired lateral ciliary bands, each comprising 3 tufts, between the palps and the posterior ciliary field. Dorsal and ventral ciliation on body arranged in transverse rows at the level of the parapodia; each row comprising up to 10 ciliary tufts. Simple serrated chaetae in all segments. Buccal segment uniramous, with up to 5 short chaetae. Segment 2–9 biramous with up to 11 chaetae in each chaetal bundle. Maximum length of chaetae in buccal segment less than half maximum length of chaetae in segment 9. Chaetae in segment 2–9 increasing in length towards pygidium. Short parapodial cirri on segment 1; interramal, tapering cirri in segment 2–9, increasing in size posteriorly. Pygidium rounded with terminal ciliation. Pygidial cirri unknown.

Etymology Named after the artist César Manrique, who devoted his life to Lanzarote and the protection of the unique Natural Heritage of the island promoting a sustainable development of tourisms in the 1960s–1970s. Los Jameos del Agua touristic complex is part of his heritage.

Description (based on observations of live holotype, Fig. 6) Hyaline 1,005 μm long, 125 μm wide *Meganerilla* with 9 chaetigerous segments, increasing in length from segment 2–6. Prostomium 50 μm long and 80 μm wide, with two 290-μm-long cylindrical ventro-lateral palps with blunt tips, reaching almost one-third of body length. Nuchal organs with dense long cilia in paired lateral pits between prostomium and segment 1. Pharynx with ventral slit-like



mouth opening and ventral muscular bulb in segment 1. Paired, lateral, round glands in segment 1, possibly entering pharyngeal lumen laterally. Paired brown salivary glands line the esophagus in segment 2, comprising several spherical cells and opening through paired lateral ducts into anterior esophagus. Midgut extends from segment 2 to 6; hindgut extends from segment 7 to pygidium. Pygidium short and rounded (16 μm) with terminal anus and ciliary band.

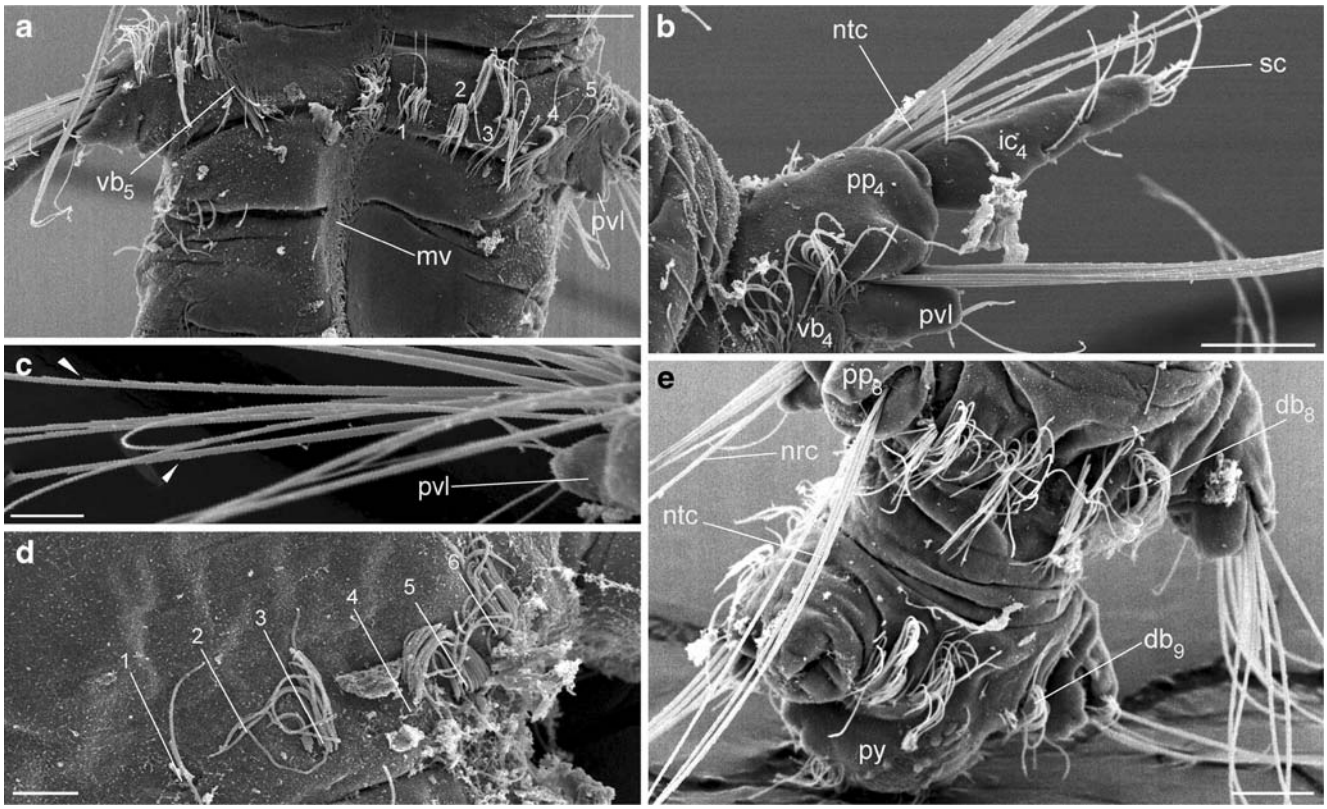


Fig. 8 *Meganerilla cesari* n. sp., scanning electron micrographs. **a** Ventral view of segments 5–6, showing the arrangement of the ventral ciliation. **b** Parapodium on segment 4, ventral view. **c** Detail of the capillary chaetae in segment 7, arrowhead indicate the serration. **d** Dorsal view of segment 6, showing arrangement of dorsal cilæairy band; number indicates each tuft. **e** Dorsal view of segments 7–8 of juvenile with 8 chaetigers. db_{8-9} Dorsal transvcerse ciliary band segment 8–9, ic_4 interramal cirri segment 4, *mv* midventral ciliary band, *nrc* neurochaetae, *ntc* notochaetae, pp_4 parapodium segment 4, *pvl* parapodial ventral lobe, *pvl* parapodial ventral lobe, *py* pygidium, *sc* cilia on interramal cirri, vb_5 ventral ciliary band segments 4 and 5. *Scale bars* **a** 5 μm, **b** 10 μm, **c** 10 μm, **d** 5 μm, **e** 10 μm

Parapodia at segment 1 minute (13 μm); subsequent parapodia longer and increasing in size towards pygidium, reaching maximum length (53 μm) around segments 6–8. Ventral conical lobe with few terminal cilia (up to 14 μm long) present on each parapodium of segments 2–8. Parapodial cirri on first segment minute (18 μm) and cylindrical (Fig. 7b); parapodial cirri on segments 2–9 interramal, slightly tapering and increasing in size towards the pygidium (up to 95 μm long). Pygidial cirri unknown.

Simple serrated chaetae present in all segments. Parapodia of segment 1 uniramous with 4 chaetae (up to 24 μm long). Parapodia of segments 2–9 biramous with dorsal and ventral bundles of chaetae. Chaetae arranged in a row within each fascicle, comprising up to 11 chaetae (several chaetae are usually lost). Same number of chaetae in dorsal and ventral fascicles as well as along body. Chaetae slightly longer than corresponding parapodial cirri, and increasing in length towards segment 8 (up to 110 μm).

Three oocytes observed in segment 5–7 (most developed in segment 7), nephridia and gonoducts not studied.

The animal moves slowly by midventral ciliary gliding.

Additional information from paratypes (including detailed SEM observations on ciliation, Figs. 7 and 8, Table 2) Besides three juveniles observed alive (347, 385,793 μm long), fixed paratypes comprise two juveniles (TFMCBM AN/00235, 377 μm long; ZMUC-POL-2104, 452 μm long), and two mature specimens with 9 segments (TFMCBM AN/00236, 560 μm long; ZMUC-POL-2104, 787 μm long), none of which generally exceed the lengths or numbers provided for the holotype above. The only three exceptions are (1) the cirri on segment 1 with a maximum length of 28 μm (versus 18 μm), (2) the buccal chaetae with a maximum length of 30 μm (versus 24 μm), (3) max number of buccal chaetae 5 (versus 4).

Prostomium with three ciliated areas: paired lateral ciliary band extending from base of palps to dorsal ciliary field; an anterior field of cilia on frontal surface of prostomium; and a dorsal field of cilia, positioned dorsally between the lateral ciliary bands and extending to border of first segment. Each lateral ciliary band with 3 tufts of 15–20 long cilia (up to 17 μm) (Fig. 7b, c). Anterior ciliated field with cilia arranged in two transverse rows (rows up to 4 μm

Table 2 Comparison of diagnostic characters of *Meganerilla*

Meganerilla Boaden 1961	Max L (µm)	Max W minus para (µm)	Eyes	Med ant, max L (µm)	Palp, max L (µm)	Buc cirri, max L (µm)	Para cirri, max L (µm)	Para cirri, size along body	Para lobe	Pyg cirri, max L (µm)	Pyg cirri, shape	Buc ch, max no.	Buc ch, max L (µm)	Ch segm 2–9, max no.	Ch segm 2–9, max L (µm)	Spermio-ducts
Meganerilla cesari n. sp.	1,005	129	A	A	288	28	95	Increasing	P	?	?	5	30	17	110	?
Meganerilla bactericola (Müller, Bernhard & Jouin-Toulmond, 2001)	1,100	90	A	A	118	A	55	Equal	?	ca. 55	Leaf-shaped	A	A	Few	165[a]	Fused
Meganerilla clavata Magagnini, 1966	1,500	190	A	115	400	20	116	Increasing	P	290	Cylindrical	6	25[a]	20	130[a]	Paired
Meganerilla penicillicauda Riser, 1988	2,000	250	A	100	300	30	100	Equal, 8–9 longer	P	140	Leaf-shaped	4	140[a]	16	270	Paired
Meganerilla swedmarki Boaden, 1961	2,100	250	P	A	520	30	152	Increasing	A	350	Cylindrical	5	110	23	220	Paired

A Absent, *ant* antenna, *ch* chaetae, *max* maximum, *med* median, *L* length, *lat* lateral, *segm* segment, *para* parapodial, *P* present, *pyg* pygidial, *W* width

[a] Estimated from original description

apart) on frontal surface of prostomium (Fig. 7c). Dorsal row with 7 groups of cilia spaced ca. 10 µm apart, distributed as one central cilium (no. 4, Fig. 7c), a pair of cilia dorso-lateral to this (no. 3 and 5, Fig. 7c), and pair of lateral groups (no. 2 and 6, Fig. 7c) with about 3 cilia each, and a pair of distal groups with 1–2 cilia each (no. 1–7, Fig. 7c), respectively. Ventral row comprising 9 groups of cilia spaced ca. 20 µm apart, with a central group of 1–2 cilia (no. 12, Fig. 7c), lined by a pair with 2 cilia each (no. 11 and 13, Fig. 7c), followed by another pair with about 4–5 cilia each (no. 10 and 14, Fig. 7c); further lateral are two paired groups (each with 3 cilia), positioned dorsally and ventrally to the ventral row (no. 8–9 and 15–16, Fig. 7c). Prostomial posterior ciliated field with 21 groups of cilia arranged in 4 transverse rows, with cilia mirrored in distinct pattern through sagittal median axis, covering an area about 16 µm wide and 18 µm long (Fig. 7f). Anterior row with 5 groups of cilia, 10 µm apart (Fig. 7f: one central cilium, no. 3; a pair of single lateral cilia, no. 2 and 4; a pair of lateral groups with 3 cilia each, no. 1 and 5). Mid-anterior row with 3 groups of cilia spaced 8 µm apart (Fig. 7f: one central cilium, no. 7; two lateral, single cilia, no. 6 and 8). Mid-posterior row with 4 groups spaced 9 µm apart (Fig. 7f: two central cilia, no. 10, 11; two lateral groups with up to 5 cilia each, no. 9 and 12). Posterior row with 7 groups of cilia spaced 15 µm apart (Fig. 7f: central group of about 4 cilia, no. 16; a pair of single cilia (no. 15 and 17); two other groups of cilia, no. 14 and 18; and a pair of lateral single cilia, no. 13 and 19). Two additional cilia are present, between the posterior row and the insertion of the first segment (no. 20–21).

Palps with complex ciliation arranged in four longitudinal bands (Fig. 7d, e). Continuous frontal ciliary band of continuously beating cilia extends from mouth to palp tip. Abfrontal ciliary band beating in intense metachronal waves originates about 30 µm from insertion of palp (ca. 20% of total palp length) and extends towards tip along abfrontal palp surface. The abfrontal band comprises up to 15 large tufts, each with 15–20 long motile cilia, up to 14 µm long ("a" in Fig. 7d). Smaller tufts present between the large ones, each with 3–4 cilia ("b" in Fig. 7d). Two lateral ciliary band extends from insertion of palp along each lateral surface to tip. The one lateral band comprises up to 25 small tufts (of 4–5 cilia; "c" in Fig. 7d) with intermediate single or double non-motile cilia ("d" in Fig. 7d). The other lateral band comprises a single row of non-motile cilia.

Dorsal body surface with well developed single transverse ciliary band situated at the level of the parapodia on each segment; clearly visible on live animals due to intense ciliary action. Each transverse band with up to 10 ciliary tufts (Fig. 8e). Each tuft comprises 20–25 cilia, 12–14 µm long (Fig. 8d). Dense transverse band on segment 1 (Fig. 7b). Ventral surface of body with dense ciliation around mouth,

continuing anteriorly into frontal ciliary bands of palps and posteriorly into midventral ciliary band. Ventral transverse bands with up to 10 tufts of motile cilia present on each segment at the level of the parapodia (Fig. 8c). Small groups of non-motile cilia (up to 14 μm long) present on parapodial cirri, more concentrated towards the distal end (Fig. 8b). A similar ciliary pattern is present on the conical ventral lobe at each parapodium (Fig. 7a, inset).

Distribution *Meganerilla cesari* n. sp. is so far only found in the Corona lava tube (Lanzarote, Canary Islands), where it is restricted to the coarse calcareous sediments of Montaña de Arena (Fig. 1). The existence of a permanent population at this locality is supported by the presence of animals in all subsamples including both juvenile and mature specimens.

Remarks (see also Table 2 for Meganerilla spp. comparisons) *Mesonerilla cesari* n. sp. shows greatest resemblance to *M. swedmarki* Boaden, 1961 but differs by well-developed ventral parapodial lobes, shorter body length, and longer relative length of buccal cirri. The presence of serrated chaetae in *M. cesari* n. sp. may be unique within *Meganerilla*; however, this feature warrants detailed SEM studies of the other species. *Meganerilla cesari* n. sp. differs from *M. bactericola* (Müller et al 2001) by the presence of chaetae and parapodial cirri on segment 1, increasing size of interramal cirri along body and longer palps. The lack of median antenna, smaller body size, and longer relative length of buccal cirri distinguishes *M. cesari* n. sp. from *M. clavata* Magagnini, 1966 and *M. penicillicauda* Riser, 1988.

Discussion

Five species of Nerillidae are recorded from the Corona lava tube exhibiting different distributions and habitat preferences (Fig. 1). The highest diversity was found in Montaña de Arena, where four of the five species have been collected. Montaña de Arena is a sand dune at 700 m penetration and 40 m depth at Túnel de la Atlántida (Wilkens et al. this issue). It was formed after the flooding of the cave by slow entering of coarse calcareous sand from offshore through a fissure in the ceiling. The offshore origin of this sediment is supported by the high percentage of carbonates (Wilkens et al. this issue) as well as the high sphericity and low angularity of the grains, suggesting erosion due to offshore marine dynamics. It is colonized by a complex assemblage of meiobenthic interstitial taxa such as several annelid families, nematodes, halacarids, priapulids, cnidarians and solenogastres as well as several macrofaunal species including annelids and sipunculans (García-Valdecasas 1985; Martínez et al. this issue). Forty-nine species in total have now been recorded from this locality (Martínez et al. this issue). Several of these taxa may have entered the cave together with the sand and colonized the dune due to its resemblance to their offshore environments. Ongoing colonization may take place in this part of the cave (Fig. 1). Nerillidae, favoring the coarse sandy subtidal interstitial environment offshore (Worsaae and Kristensen 2005; Westheide 2008), here exhibit the highest diversity among the annelid families. Two of the four nerillids recorded here, *Mesonerilla armoricana* and *Meganerilla cesari* n. sp., have been recorded offshore (Westheide 2008; A. Martínez, personal observation). Limited sampling offshore and at the subterranean coastline of Lanzarote makes it difficult to determine whether the two other species, *Mesonerilla* sp. 1 and *Mesonerilla* sp. 2, are truly endemic and to predict how they have colonized the cave.

Leptonerilla diatomeophaga is restricted to the carpet of benthic diatoms in Jameos del Agua. However, since it is found in different habitats (sponge and maerl) in another cave at Tenerife (Canary Islands) and Selvagem Islands (Portugal), the lack of coastal records as well as of records from other parts of the cave is surprising. This may be explained by limited offshore sampling off the Canary Islands, as well as indicating that this species is adapted to the high organic content of the diatom carpet of Jameos del Agua.

Mesonerilla sp. 1 is the only nerillid found in the lapilli patches at the Jameos del Agua and the Cueva de los Lagos. Patches of lapilli are found scattered all along the tube and constitute well aerated interstitial habitats. Lapilli sediment is of volcanic origin and was probably accumulated by small collapse events and erosion of the ceiling and the walls during the history of the tube. Persistence of sediment with very coarse grains of high angularity and porosity, low sphericity, and a low percentage of fine particles is possible within the cave due to low sedimentation and lack of marine dynamics (Wilkens et al. this issue). Trophic resources in the lapilli patches are generally low and restricted to organic matter sedimented from the water column, possibly reflected in its scarce and highly endemic fauna (Martínez et al. this issue). However, the organic content is higher in the lapilli sediment of the Jameos del Agua, having a primary production, which may explain the more abundant interstitial fauna and higher percentage of offshore species recorded here (Núñez et al. 1997). Lapilli patches are not limited to the cave but spread around the subterranean flooded areas of the coast line of Lanzarote, where stygobiontic species of the Corona lava tube have also been found (Wilkens et al. 1986, 1993). *Mesonerilla* sp. 1 inhabiting the lapilli sediment may have evolved in this subterranean environment and colonized the cave subsequent to the formation and flooding of the Corona lava tube.

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