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Description of six new species of *Mesonerilla* (Nerillidae, Annelida) and an emended description of *M. intermedia* Wilke, 1953, from marine and cave environments

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Abstract

Nerillidae is a species-rich family of meiofaunal, mainly interstitial annelids. The genus *Mesonerilla* previously contained eight described species. We here describe six new species of *Mesonerilla* based on detailed morphological light and scanning electron microscopy studies. The new species were collected from coastal subtidal and tidal sediments, as well as from anchialine caves, in the Mediterranean, Canary Islands, Panamá, Trinidad and Tobago and the USA. All species of *Mesonerilla* contain nine segments, two-three antennae, two club-shaped palps, parapodial cirri and compound chaetae in most segments. New species are diagnosed by unique character traits and/or a unique combination of characters involving differences in shape of appendages, reproductive characters and glandular and ciliary patterns. Their validation is further supported by a molecular phylogeny including these and the majority of described species of *Mesonerilla*. With most of the diagnostic characters of the described species being hardly discernible, and with potential additional molecular identifiable species left undescribed, the genus *Mesonerilla*, as many other interstitial groups, show a high degree of cryptic diversity.

Keywords Interstitial · Meiofauna · Anchialine fauna · Microscopy · Molecular phylogeny

Introduction

The meiofaunal genus *Mesonerilla* Remane, 1949 is amongst the most species rich genus within the Nerillidae Levinsen, 1883 and includes eight out of the 54 described nerillid species (Worsaae 2014; Worsaae et al. 2019): *M. luederitzi* Remane, 1949; *M. intermedia* Wilke, 1953; *M. roscovita* Lévi, 1953; *M. armoricana* Swedmark, 1959; *M. fagei* Swedmark, 1959; *M. biantennata* Jouin, 1963; *M. biantennata pacifica* Jouin, 1970; *M. neridae* Worsaae & Rouse, 2009 (Levinsen 1883; Remane 1949; Lévi 1953; Wilke 1953; Swedmark 1959; Jouin 1963, 1970; Worsaae and Rouse 2009). The genus has been reported worldwide in marine waters, mainly from shallow water sediments (Fransen 1983; Bailey-Brock 1999; Besteiro et al. 2012; Curini-Galletti et al. 2012; Worsaae 2014) but also from anchialine caves (Worsaae et al. 2009) and hydrothermal vents (Worsaae and Rouse 2009). All described *Mesonerilla* are interstitial and inhabit the spaces between sandy or gravelly sediments.

The genus presents high interspecific variation and is defined without unique apomorphies, but rather diagnosed by a combination of characters (Worsaae 2005b). All *Mesonerilla* possess nine segments, compound chaetae and two club-shaped palps (Worsaae 2014), but the genus is polymorphic regarding the number of antennae (two or three antennae), reproductive

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mode (hermaphroditic or dioecious), presence or absence of chaetae in segment I, as well as number and position of the spermioducts (Worsaae 2014). They also exhibit a varying degree of parental care. Several species brood their larvae externally, carrying them attached dorsally on segments VIII or IX. A flap-like dorsal outgrow of the posterior trunk, the so-called brooding hood, partially covers the embryos in some, but not all, of these brooding species, supposedly protecting them (Fransen 1983). This variability, as well as the plesiomorphic state of the diagnostic traits, such as nine segments and compound chaetae in Nerillidae raised questions on the monophyly of the genus (Worsaae 2005a), which has also been recovered paraphyletic in a phylogenetic study based on morphology and ribosomal gene fragments (Worsaae 2005b).

During the last 15 years, extensive surveys by the authors for meiofaunal annelids around the world have yielded numerous specimens of *Mesonerilla*, mostly from subtidal environments but also from tidal pools and anchialine caves. Some of these specimens are morphologically indistinguishable from previously described species, despite being collected far from their type localities and exhibiting comparatively large genetic distance in our four sequenced markers. However, other populations present unique combinations of characters unequivocally representing new species. The goal of this paper is to formally describe six of these populations and provide an emended diagnosis and description of *Mesonerilla intermedia*, employing detailed morphological examinations using light and scanning electron microscopy. Our study further identified several morphological species complexes for which further population genetic studies are warranted in order to fully unravel the extensive cryptic diversity within *Mesonerilla*.

Materials and methods

Sample collecting and processing

Specimens of *Mesonerilla* were extracted from samples of intertidal and subtidal marine sediments collected during multiple expeditions, mostly from marine open waters, but also from tidal pools and anchialine caves (Table 1). Sediments, including medium to coarse sand and gravel, were collected manually by snorkel or scuba diving. The specimens were extracted from these sediments using the $MgCl_2$ decantation technique through a 63-μm mesh (Higgins and Thiel 1988). Cave species were collected by scuba divers either from sandy sediment samples or from silty sediments using a plankton net after mechanically stirring the sediments up into the water column of cave pools and flooded passages.

All specimens of the species described herein were sorted out alive in the field using a stereoscope. Light micrographs of living individuals were taken when possible using a Nikon D300 digital camera mounted on an Olympus SZX16 stereoscope. Individuals from each population were then anaesthetised using isotonic $MgCl_2$ and fixed in a 2% paraformaldehyde solution in phosphate buffer with 0.2 M of sucrose (PFA, for 24 h at 4 °C) or in 2% glutaraldehyde in cacodylate buffer (24 h and transferred to 0.1 M cacodylate buffer), as well as preserved in 99% ethanol for DNA analyses.

Morphological examinations

The animals examined using LM were prepared as whole mounts using a glycerol dilution series (20 to 100%). Whole mounts were photographed with an Olympus DP73 camera mounted on an Olympus IX70 inverted compound microscope. Measurements were taken from those scaled pictures using the software CellSens version 1.9.

Specimens examined with SEM were postfixed in 1% osmium tetroxide (1 h), rinsed in milliQ water, dehydrated through an ethanol series and transferred to 100% acetone. Dehydrated animals were then critical point dried and mounted on aluminium stubs before sputter-coating with platinum palladium. Examinations were performed with JEOL JSM-6335F field emission scanning electron microscope at the Natural History Museum of Denmark (NHMD), University of Copenhagen.

The morphological techniques employed for the description of each species are summarised in Table 1. All type material has been deposited in the Natural History Museum of Denmark (NMHD), University of Copenhagen.

Molecular analyses

Representatives of 25 populations of nerillids, including six herein described species of *Mesonerilla*, and six putative undescribed species of *Mesonerilla* were included in the analyses (see Table 1). Most of the molecular data were obtained for the present study, but a few species had published sequences from previous studies (Worsaae 2005b). DNA extraction and amplifications of the ribosomal markers 18SrRNA and 28SrRNA and the protein-coding markers cytochrome c-oxidase subunit I (COI) and histone 3 (H3) was performed following previously optimised protocols for interstitial annelids (Di Domenico et al. 2014; Martínez et al. 2015). PCR amplification products were purified and submitted to Macrogen Europe for sequencing. Quality assessment and contig assemblage was done using Sequencher v. 4.10.1 (GeneCodes Corporation, Ann Arbor, MI, USA). Contigs were subsequently blasted against GenBank databases for possible contamination. Ribosomal markers were aligned using ins-E algorithm in MAFFT v. 2.0 (Katoh and Toh 2008; Katoh

Table 1 Data obtained for *Mesonerilla* spp. and seven outgroups used in the phylogenetic analyses, including the GenBank accession numbers for DNA sequences, as well as the morphological techniques used to investigate each species

Species	Locality of sequenced specimen	GenBank 18S	GenBank 28S	GenBank COI	GenBank H3	Live	LM	SEM
Genus *Mesonerilla*								
M. armoricana	Montaña de Arena, Túnel de la Atlántida, Lanzarote, Canary Islands	MK579423	MK579448	–	–	x	x	x
M. aryae sp. nov.	Punta del Hidalgo, Tenerife, Canary Islands	MK579419	MK579445	MK579466	MK579489	–	–	x
M. biantennata	Spiaggia Paradiso, Sardinia, Italy	MK579421	MK579446	MK579468	MK579491	x	x	x
M. cf. *luederitzi*	Marie Celeste wreck, Bermuda	MK579408	MK579434	MK579458	MK579478	x	–	x
M. cf. *luederitzi*	El Cabron, Arinaga, Gran Canaria, Canary Island, Spain	MK579411	MK579440	MK579462	MK579484	–	x	x
M. cf. *luederitzi*	Charco del Palo, Mala, Lanzarote, Canary Island, Spain	MK579412	MK579439	MK579460	MK579482	x	x	x
M. cf. *luederitzi*	Muro de Playa San Juan, Tenerife, Canary Island, Spain	MK579417	MK579443	MK579465	MK579487	x	x	x
M. fagei	Primel, Roscoff, France	MK579424	MK579449	–	MK579493	–	–	x
M. intermedia	Budelli Island, Cavaliere Bay, La Maddalena, Sardinia, Italy	MK579413	–	MK579461	MK579483	–	x	x
M. intermedia	Cueva del Palo, Colonia de Sant Jordi, Mallorca, Spain	MK579415	MK579441	MK579463	MK579485	x	x	x
M. katharinae sp. nov.	Wild Cane Rock, Bocas del Toro, Panama	MK579416	MK579442	MK579464	MK579486	x	x	x
M. laerkae sp. nov.	Bailey's Hill, Nahant, MA, USA	MK579420	–	MK579467	MK579490	x	x	x
M. peteri sp. nov.	Japanese Garden, Tobago, Trinidad and Tobago	MK579407	MK579433	MK579457	MK579477	–	–	x
M. roscovita	Trezen ar Skoden, Roscoff, France	MK579422	MK579447	–	MK579492	x	x	x
M. runae sp. nov.	Montaña de Arena, Túnel de la Atlántida, Lanzarote, Canary Islands, Spain	MK579418	MK579444	–	MK579488	x	x	x
M. xurxoi sp. nov.	Jameos del Agua, Lanzarote, Canary Island, Spain	MK579410	MK579436	–	MK579480	x	x	x
Mesonerilla sp. 1	Beach of Lizard Island Research Station, Lizard Island, Australia	MK579409	MK579435	MK579459	MK579479	x	–	x
Mesonerilla sp. 2	Roscoff, France	MK579406	MK579432	MK579456	MK579476	–	–	x
Outgroups								
Meganerilla cesari	Montaña de Arena, Túnel de la Atlántida, Lanzarote, Canary Islands, Spain	MK579405	MK579431	–	MK579475	x	x	x
Nerillidium troglochaetoides	Swedmark's Bonden, Kristineberg, Sweden	MK579427	MK579452	MK579471	MK579496	x	x	–
Nerillidium gracile	Swedmark's Bonden, Kristineberg, Sweden	MK579426	MK579451	MK579470	MK579495	x	x	–
Paranerilla sp.	Disko Island, Greenland	AY859539	–	–	MK579497	x	x	x
Leptonerilla diatomeophaga	Jameos del Agua, Lanzarote, Canary Island, Spain	MK579404	MK579429	MK579455	MK579474	x	x	x
Aristonerilla brevis	Düsseldorf Aquarium, Germany	AY859530	MK579428	MK579454	MK579473	x	x	x
Trochonerilla mobilis	Danmark's Aquarium, Denmark	AY834759	MK579453	MK579472	–	x	x	x

live, light microscopy studies on live material; *LM*, light microscopy on fixed material; *SEM*, scanning electron microscopy et al. 2010); protein-coding markers were confirmed to be constant in length and checked for reading frame and absence of stop codons. Alignment was done using the quick algorithm L-INS-I implemented in MAFFT v.2.0 (Katoh et al. 2005).

Bayesian (BA) and maximum likelihood (ML) analyses were conducted using the Cipres Phylogenetic Portal (Miller et al. 2010). Partitioned maximum likelihood analyses were computed with RaxML version 7.2.8 (Stamatakis 2006). A general time-reversible (GTR) model of sequence evolution with corrections for a discrete gamma distribution GTR + Γ was specified for each partition. Nodal support was estimated via non-parametric bootstrap with 1000 replicates and a GTR + Γ model (Felsenstein 1985).

Bayesian analyses were performed using MrBayes version 3.12 (Ronquist and Huelsenbeck 2003). The evolutionary models that minimised the Akaike information criterion (AIC) calculated with jModelTest (Posada and Buckley 2004; Posada 2008) were GTR + Γ for 28S rRNA and GTR + Γ + I for the remaining markers (18S rRNA, COI and H3). Trees were sampled from four independent analyses, each consisting of four chains that were allowed to run for 70,000,000 generations. After proper convergence and mixing of the parameters were confirmed with Tracer 1.4.1, the consensus topology was presented as a 50% majority-rule consensus tree for which the first 20,000,000 samples were discarded as burn-in (Rambaut and Drummond 2007).

Results

Phylogenetic analyses

The maximum likelihood analysis gave a tree topology highly congruent to the Bayesian analysis consensus tree (Fig. 1). Members of *Mesonerilla* were clustered as two non-related clades yielding the genus paraphyletic, as anticipated in previous studies (Worsaae 2005a, b). The systematic implications of this result will be accounted for in ongoing studies with broader taxon sampling (Worsaae and Martínez, in preparation).

The six new species of *Mesonerilla* described here, as well as *M. intermedia* were all recovered within a single major clade, positioned next to *Mesonerilla biantennata* and together with this, found to constitute a sister clade to *Meganerilla cesari* Worsaae et al. 2009.

This major clade of *Mesonerilla* spp. split off into two reciprocally monophyletic branches. One of them yields *M. runae* sp. nov., sister to a major clade containing the subclades *M. intermedia-M. aryae* sp. nov. and *Mesonerilla* sp. 1-*M.* cf. *luederitzi*, and the other containing the two subclades *Mesonerilla* sp. 2-*M. laerkae* sp. nov., sister to *M. xurxoi* sp. nov. and *M. katharinae* sp. nov.-*M. peteri* sp. nov. The geographical distribution of species did not clearly relate to the tree topology.

Two terminals (from Mallorca and Sardinia) in the phylogenetic analyses do not show any noticeable morphological difference to *Mesonerilla intermedia* (described from Napoli). They are therefore considered to belong to this morphospecies, despite that, genetic distances indicate they most likely represent a species complex warranting further research (Table 2). Further morphological information is added to the original description based on fresh material from the type locality. Likewise, four terminals greatly resembling *Mesonerilla luederitzi* were found to be separated by comparatively large genetic distances within the major clade of *Mesonerilla* spp. (Table 2), but since the original description of *M. luederitzi* was based on a fragmented animal and did not include many details (see Table 3), it was not possible to detect whether any of these units truly represented *M. luederitzi* described off Namibia (West Africa). Furthermore, the collected material of several of these populations did not allow for detailed morphological studies, and their description and erection to species awaits future sampling and examinations. For these reasons, and because all of these four terminals were collected far from the type locality, we consider them belonging to the *M. luederitzi* species complex. *Mesonerilla* sp. 1 from Lizard Island, Great Barrier Reef, represented a putative morphologically distinct terminal, as well as the first record of the genus in Australia. However, we prefer not to describe it formally due to the lack of well-preserved material preventing the description of diagnostic morphological features. Finally, the molecular data of *Mesonerilla* sp. 2 from Roscoff, France, did not match the previously described species *M. roscovita*, *M. fagei* and *M. armoricana* (positioned in a separate distant clade on the tree) and there was no sufficient material for further morphological examinations clarifying its species status. All in all, neither terminals identified as *M.* cf. *luederitzi* nor *Mesonerilla* sp. 1 and *Mesonerilla* sp. 2 are morphologically described here but were only included in Table 3 for comparisons.

Morphological analyses and systematic account

Morphological descriptions below are arranged following the numbers included in Fig. 1.

Genus ***Mesonerilla*** Remane, 1949

(1) ***Mesonerilla runae*** sp. nov..
http://zoobank.org/B24BBE1D-B8FD-4CDB-8105-470392EB875E

Fig. 2, Table 3.

Mesonerilla n. sp. 2: Martínez et al. 2009, 2015; Worsaae et al. 2009

Type of material. Holotype: NHMD- 301540, on SEM-stub, Montaña de Arena, Túnel de la Atlántida, Lanzarote, Canary Islands. Coarse sand, 30–40 m depth, 29.157° N, 13.425° W, 10 October 2011 (Coll: K. Worsaae, A. Martínez,

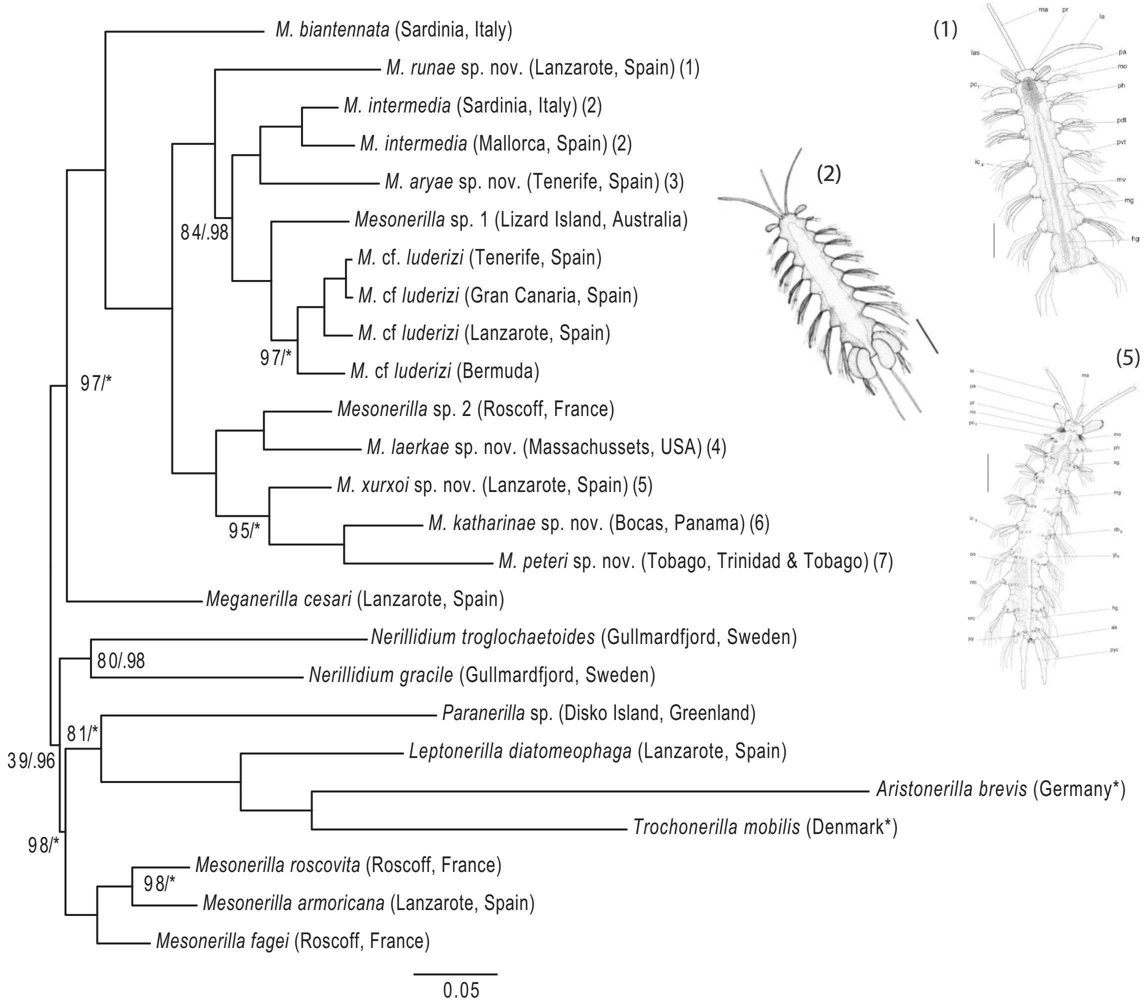


Fig. 1 Phylogeny of *Mesonerilla* spp., using four molecular markers analysed with maximum likelihood and Bayesian methods. Maximum likelihood tree topology highly congruent with Bayesian consensus tree. Maximum likelihood values as well as posterior probabilities showed only when lower than 100/1.00. Numbers in brackets near each terminal refer to the morphological section of the text. Drawings illustrating morphological differences in the genus (from top to bottom): *Mesonerilla runae* sp. nov., redrawn from Worsaae et al. 2009 (1); *Mesonerilla intermedia*. Redrawn from Besteiro et al. 2012 (2); *Mesonerilla xurxoi* sp. nov., redrawn from Worsaae et al. 2009 (5)

E. Domínguez, R. Schoenermark). Paratype: NHMD- 301547, video recorded alive and mounted on an SEM-stub, same locality as holotype, 20 March 2008 (Coll: T. Iliffe, A. Martínez).

Diagnosis. *Mesonerilla* with three long, cylindrical antennae. Segment I uniramous, with broad parapodial cirri, longer than the palps. Segments II–IX biramous, with cylindrical interramal cirri, increasing in length towards pygidium. Dorsolateral transverse ciliation arranged as paired rows of ciliary tufts not fusing at midline of the body. Ventrolateral transverse ciliation consisting of a single paired row of ciliary tufts per segment. Pygidium without terminal prolongation or dorsal row of pores, pygidial cirri unknown. Gonochoristic, brooding hood absent.

Etymology. Named after Runa, oldest daughter of first author Katrine Worsaae, assisting during the collecting at Lanzarote.

Description (measurements from holotype). Trunk transparent, nine segments, 465 μm long and 65 μm wide. Segments of equal size and shape (Fig. 2a). Prostomium with club-shaped palps (max. L. 40 μm) and three cylindrical antennae, approximately equal in length, 180 μm long. Eyes absent. Oesophageal glands small, not easily visible neither in live nor fixed material. Parapodial cirri on segment I conspicuously broader than those in the subsequent segments and longer than the palps (max. L. 35 μm) (pc, Fig. 2b, d); cirri on segments II–IX cylindrical and slightly increasing in length towards pygidium (max. L. 70 μm, from paratype). Pygidium short, pygidial cirri lost. Segment I uniramous, with maximum 7 chaetae (max. L. 70 μm) (ch, Fig. 2b); segments II–IX biramous, with 5–9 chaetae (max. L. 90 μm) (nec, noc, Fig. 2d, e).

Prostomial ciliation with anterior and posterior ciliary fields, as well as paired lateral ciliary rows, extending from insertion of each lateral antenna to palps. Palp ciliation unknown. Trunk with midventral ciliary band as well as

Table 2 Summary of the genetic distances for each marker in all the species included in the phylogeny. Missing data are not counted as differences

Markers	Species	Locality	No.													
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI		
COI	*Mesonerilla* cf. *luderitzi*	Bermuda	I													
		Canary Islands. Tenerife	II	0.830												
		Canary Islands. Lanzarote	III	0.824	0.871											
		Canary Islands. Gran Canaria	IV	0.835	0.970	0.863										
	Mesonerilla intermedia	Italy. Sardinia	V	0.798	0.763	0.778	0.751									
		Spain. Mallorca	VI	0.800	0.763	0.770	0.756	0.868								
	Mesonerilla aryae sp. nov.	Canary Islands. Tenerife	VII	0.747	0.746	0.740	0.747	0.768	0.763							
	Mesonerilla sp. 1	Australia. Lizard Island	VIII	0.838	0.815	0.825	0.813	0.807	0.793	0.770						
	Mesonerilla katharinae sp. nov.	Panama. Bocas del Toro	IX	0.615	0.610	0.635	0.617	0.561	0.580	0.552	0.622					
	Mesonerilla laerkae sp. nov.	MA, USA	X		0.744	0.734	0.727	0.732	0.756	0.754	0.727	0.747	0.601			
	Mesonerilla peteri sp. nov.	Trinidad and Tobago. Tobago	XI		0.538	0.541	0.547	0.552	0.549	0.547	0.514	0.523	0.645	0.582		
	Mesonerilla sp. 2	France. Roscoff	XIV	0.770	0.740	0.713	0.740	0.704	0.747	0.697	0.760	0.620	0.784	0.598		
				I	II	III	IV	V	VI	VII	VIII	IX	XI	XII	XIII	
28S	*Mesonerilla* cf. *luderitzi*	Bermuda	I													
		Canary Islands. Tenerife	II	0.983												
		Canary Islands. Lanzarote	III	0.982	0.998											
		Canary Islands. Gran Canaria	IV	0.982	0.998	0.997										
	Mesonerilla intermedia	Italy. Sardinia	V	0.919	0.919	0.917	0.917									
		Spain. Mallorca	VI	0.919	0.918	0.917	0.916	1.000								
	Mesonerilla aryae sp. nov.	Canary Islands. Tenerife	VII	0.911	0.915	0.913	0.913	0.937	0.937							
	Mesonerilla sp. 1	Australia. Lizard Island	VIII	0.933	0.929	0.928	0.931	0.893	0.892	0.882						
	Mesonerilla katharinae sp. nov.	Panama. Bocas del Toro	IX	0.826	0.815	0.813	0.815	0.836	0.836	0.813	0.807					
	Mesonerilla peteri sp. nov.	Trinidad and Tobago. Tobago	XI	0.813	0.802	0.800	0.802	0.819	0.819	0.807	0.787	0.960				
	Mesonerilla runae sp. nov.	Canary Islands. Lanzarote	XII	0.899	0.902	0.904	0.900	0.902	0.902	0.896	0.871	0.842	0.819			
	Mesonerilla xurxoi sp. nov.	Canary Islands. Lanzarote	XIII	0.845	0.834	0.832	0.834	0.836	0.836	0.830	0.818	0.914	0.903	0.824		
	Mesonerilla sp. 2	France. Roscoff	XIV	0.834	0.829	0.832	0.827	0.831	0.831	0.812	0.803	0.880	0.866	0.831	0.891	
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII

Table 2 (continued)

Markers	Species	Locality	No.													
18S	*Mesonerilla* cf. *luderitzi*	Bermuda	I													
		Canary Islands. Tenerife	II	0.998												
		Canary Islands. Lanzarote	III	0.997	0.999											
		Canary Islands. Gran Canaria	IV	0.998	1.000	0.999										
	Mesonerilla intermedia	Italy. Sardinia	V	0.974	0.974	0.973	0.974									
		Spain. Mallorca	VI	0.976	0.975	0.975	0.975	0.998								
	Mesonerilla aryae sp. nov.	Canary Islands. Tenerife	VII	0.971	0.972	0.971	0.972	0.985	0.985							
	Mesonerilla laerkae sp. nov.	Australia. Lizard Island	VIII	0.988	0.987	0.986	0.987	0.974	0.976	0.973						
	Mesonerilla katharinae sp. nov.	Panama. Bocas del Toro	IX	0.970	0.968	0.967	0.968	0.970	0.970	0.969	0.971					
	Mesonerilla laerkae sp. nov.	MA, USA	X	0.956	0.954	0.953	0.954	0.954	0.956	0.955	0.956	0.958				
	Mesonerilla peteri sp. nov.	Trinidad and Tobago. Tobago	XI	0.961	0.954	0.953	0.954	0.954	0.954	0.955	0.955	0.966	0.952			
	Mesonerilla runae sp. nov.	Canary Islands. Lanzarote	XII	0.941	0.947	0.947	0.947	0.949	0.949	0.937	0.948	0.942	0.912	0.926		
	Mesonerilla xurxoi sp. nov.	Canary Islands. Lanzarote	XIII	0.969	0.961	0.961	0.961	0.965	0.966	0.969	0.963	0.978	0.967	0.960	0.941	
	Mesonerilla sp. 2	France. Roscoff	XIV	0.965	0.960	0.960	0.960	0.962	0.963	0.965	0.961	0.967	0.988	0.954	0.935	0.973
				I	II	III	IV	VI	VII	VIII	IX	X	XI	XII	XIII	
H3	*Mesonerilla* cf. *luderitzi*	Bermuda	I													
		Canary Islands. Tenerife	II	0.944												
		Canary Islands. Lanzarote	III	0.944	0.994											
		Canary Islands. Gran Canaria	IV	0.944	1.000	0.994										
	Mesonerilla intermedia	Spain. Mallorca	VI	0.855	0.851	0.844	0.855									
	Mesonerilla aryae sp. nov.	Canary Islands. Tenerife	VII	0.877	0.877	0.881	0.877	0.859								
	Mesonerilla sp. 1	Australia. Lizard Island	VIII	0.931	0.913	0.913	0.917	0.874	0.888							
	Mesonerilla katharinae sp. nov.	Panama. Bocas del Toro	IX	0.896	0.881	0.884	0.884	0.862	0.870	0.899						
	Mesonerilla laerkae sp. nov.	MA, USA	X	0.906	0.895	0.895	0.898	0.859	0.866	0.914	0.892					
	Mesonerilla peteri sp. nov.	Trinidad and Tobago. Tobago	XI	0.914	0.906	0.906	0.909	0.859	0.866	0.917	0.938	0.924				
	Mesonerilla runae sp. nov.	Canary Islands. Lanzarote	XII	0.873	0.888	0.888	0.891	0.824	0.830	0.878	0.847	0.888	0.869			
	Mesonerilla xurxoi sp. nov.	Canary Islands. Lanzarote	XIII	0.903	0.895	0.899	0.899	0.881	0.910	0.924	0.928	0.914	0.945	0.869		
	Mesonerilla sp. 2	France. Roscoff	XIV	0.920	0.909	0.913	0.913	0.859	0.892	0.927	0.899	0.958	0.917	0.888	0.917	

Table 3 Examined characters used for the diagnosis of each of the morphological species of *Mesonerilla* identified in the study. See text for further information on each character. Cells with bold types indicate diagnostic traits. Abbreviations: segm, segment;?, unknown; -, inapplicable

Morphospecies	Locality	Antennae, shape	Parapodial cirri, relative lengths	Parapodial cirri, shape	Pygidial cirri, shape	Dark oesophageal glands	Dark oesophageal glands, shape	Cirri segm I (buccal cirri)	Buccal cirri, shape	Brooding hood	Brooding hood, shape
M. runae sp. nov.	Lanzarote, Canary Island, NE Atlantic	Cylindrical, not tapering	Slightly increasing towards pygidium	Cylindrical	?	Inconspicuous	–	Present	**Larger than palps**	Absent	–
M. intermedia	Naples, Italy, Mediterranean Sea	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicuous	–	Present	Cylindrical	Present	Rounded
	Sardinia, Italy, Mediterranean Sea	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicious	–	Present	Cylindrical	?	?
	Mallorca, Spain, Mediterranean sea	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicious	–	Present	Cylindrical	Present	Rounded
M. aryae sp. nov.	Tenerife, Canary Island, NE Atlantic	?	?	Bottle-shaped	?	Inconspicuous	–	Present	Cylindrical	Absent	–
Mesonerilla sp. 1	Lizard Island, Australia, SW Pacific	Cylindrical, not tapering	Increasing towards pygidium	Cylindrical	?	?	?	Present	Cylindrical	Absent	–
M. cf. *luderitzi*	Tenerife, Canary Island, NE Atlantic	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicuous	–	Present	Cylindrical	Absent	–
	Gran Canaria, Canary Island, NE Atlantic	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicuous	–	Present	Cylindrical	Absent	–
	Lanzarote, Canary Island, NE Atlantic	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicuous	–	Present	Cylindrical	Absent	–
	Bermuda, NW Atlantic	Cylindrical; tapering	Increasing towards pygidium	Bottle-shaped	Bottle-shaped	Inconspicuous	–	Present	Cylindrical	Absent	–
Mesonerilla sp. 2	Roscoff, France, NE Atlantic	Cylindrical, not tapering	?	Bottle-shaped	?	?	?	Present	Cylindrical	?	?
M. laerkae sp. nov.	Nahant, Massachusetts, USA, NW Atlantic	Bottle-shaped, tapering	Equal size	Bottle-shaped	Bottle-shaped	Present	**Large, elongated along segm. II-III**	Present	Cylindrical	Present	**Fan-shaped with median pointed tip**
M. xurxoi sp. nov.	Lanzarote, Canary Island, NE Atlantic	Cylindrical, not tapering	**Equal size segm II-VIII; longer in segm IX**	Cylindrical	Filiform	Present	Small in segment I; large, collar-like in segm II	Present	Cylindrical	Absent	–
M. katharinae sp. nov.	Bocas del Toro, Panama, NW Atlantic	Cylindrical, not tapering	Equal size in segments II-IV, increasing from V-IX	Cylindrical	Filiform	Present	Small in segment I; large, collar-like in segm. II	Present	Cylindrical	Absent	–
M. peteri sp. nov.	Tobago, Trinidad and Tobago, NW Atlantic	Cylindrical, not tapering	Equal size	Cylindrical	?	?	?	Present	Cylindrical	Absent	–

Table 3 (continued)

Pygidial mid-dorsal band of pores	Pygidial terminal prolongation	Pygidial terminal prolongation, length	Dorsolateral ciliation; transverse row at level of parapodia	Continuous dorsolateral ciliation	Ventrolateral ciliation; number of paired rows per segment	Ventrolateral ciliation; transverse row between parapodia	Ventrolateral ciliation; transverse row at level of parapodia	Paired bundles of cilia on segm III	Lateral ciliation
Absent	Absent	–	3–4 tufts on each side; 1 tuft on parapodia	No	1	Absent	1–3 tufts on each side, never connected	Absent	Absent
Absent	Absent	–	6–9 tufts on each side; 1 tuft on parapodia	Continuous in all segments	2	2–5 tufts on each side; connected medially segm VIII–IX	5–11 tufts on each side; connected medially segm IX	Absent	Absent
Absent	Absent	–	?	?	?	?	?	Absent	Absent
Absent	Absent	–	6-11 tufts on each side	Continous in all segments	?	?	?	Absent	Absent
Present	Absent	–	5–9 tufts on each side; 1–2 tufts on parapodia	Continuous in all segments	2	2–5 tufts on each side; never connected	4–8 tufts on each side; never connected	Absent	**Present**
Absent	Absent	–	2–4 tufts on each side; 1 tuft on parapodia	No	?	?	3–5 tufts on each side	Absent	Absent
Absent	Absent	–	Continuous row of 6–11 tufts; 1–2 tufts on parapodia	Continuous in all segments	2	2–5 tufts on each side; never connected	4–8 tufts on each side; connected medially segm VIII-IX	Absent	Absent
Absent	Absent	–	Continuous row of 6–11 tufts; 1–2 tufts on parapodia	Continuous in all segments	2	2–5 tufts on each side; never connected	4–8 tufts per row on each side; connected medially segm VIII-IX	Absent	Absent
Absent	Absent	–	Continuous row of 6–11 tufts; 1–2 tufts on parapodia	Continuous in all segments	2	2–5 tufts on each side; never connected	4–7 tufts on each side; connected medially segm VIII-IX	Absent	Absent
Absent	Absent	–	?	?	?	?	?	Absent	Absent
?	?	?	?	?	?	?	?	?	?
Absent	Absent	–	3-4 tufts on each side; 1 tuft on parapodia	No	?	?	?	Absent	Absent
Present	Present	**Long**	3–4 tufts on each side; 1–2 tuft on parapodia	No	1	Absent	3–4 tufts on each side; never connected	Absent	Absent
Absent	Present	Short	1–2 tufts on each side; 1 tuft on parapodia	No	1	Absent	2 tufts only on parapodia; never connected	**Present**	Absent
?	Present	Short	3–5 tufts on each side; 1 tuft on parapodia	Possibly continuous in all segments	1	Absent	2–4 tufts on each side; never connected	Absent	Absent

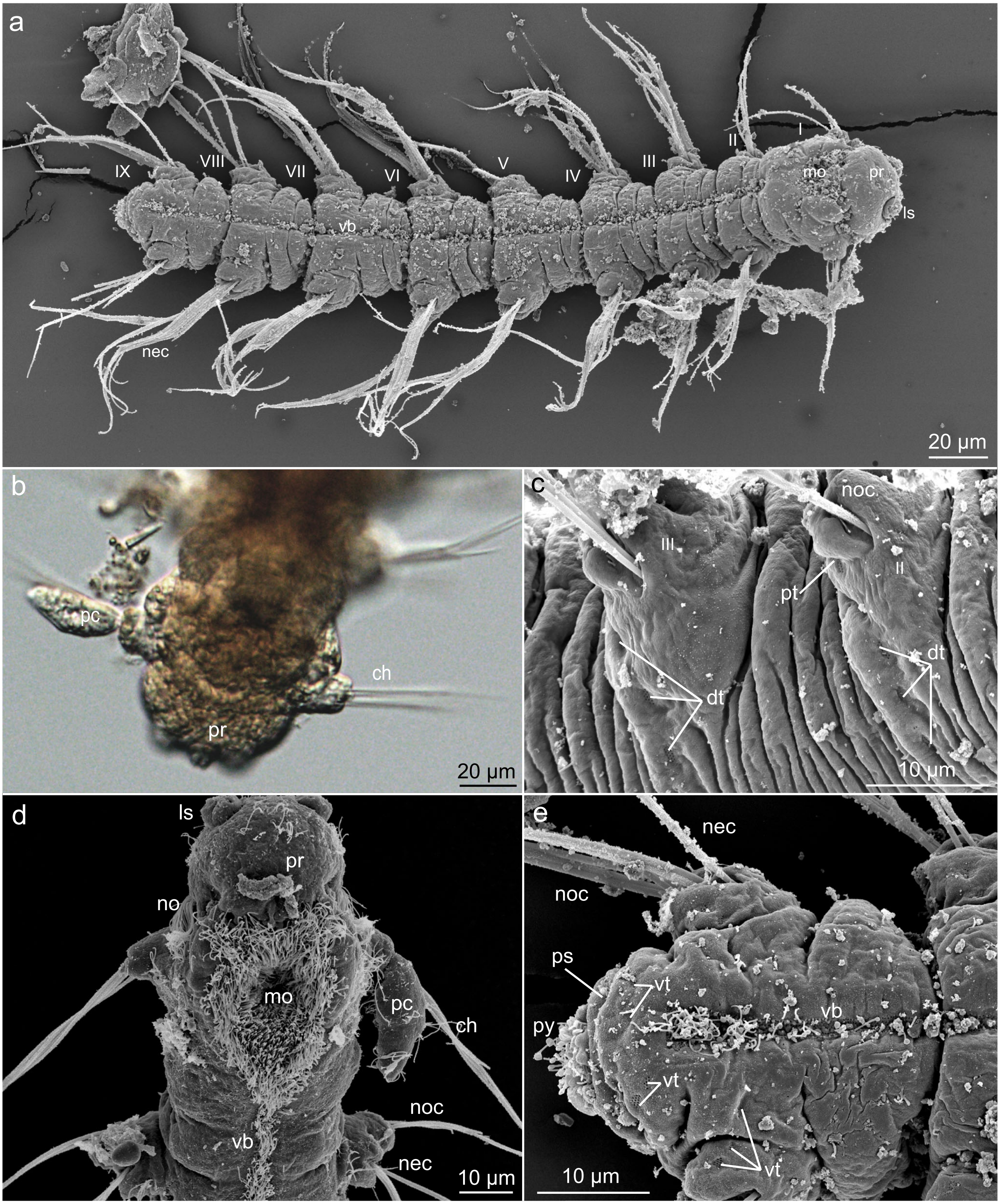


Fig. 2 *Mesonerilla runae* sp. nov. Scanning electron micrograph of **a** whole holotype in ventral view; **b** light micrograph of the prostomium in ventral view showing buccal cirrus; scanning electron micrographs of **c** dorsal trunk ciliation on segments II–III; **d** ventral view of the anterior end; **e** ventral view of the posterior end showing scars form ventral transverse ciliation. ch, chaetae; dt, dorsolateral transverse ciliary row; ls, lateral antenna scar; mo, mouth; nec, neurochaetae; no, nuchal organ; noc, notochaetae; pc, parapodial cirrus; pt., parapodial ciliary tuft; pr, prostomium; py, pygidium; vb, midventral ciliary band; vt, ventrolateral transverse ciliary rows. Segment numbers in roman numerals

dorsolateral and ventrolateral transverse rows of ciliary tufts on segments I–IX, extending from parapodia and not fusing at midline of the body. Dorsolateral transverse ciliary rows with 3–4 tufts on each side of the body (dt, Fig. 2c); ventrolateral transverse rows with 1–3 ciliary tufts on each side of the body (vt, Fig. 2e). One ciliary tuft is present dorsally on parapodia of segments I–IX (pt, Fig. 2c).

Gonochoristic, with separate males and females. Brooding hood absent. Arrangement of gonoducts unknown.

Distribution and habitat. Exclusively known from Montaña de Arena, an accumulation of sand at 750 m inside Túnel de la Atlántida, La Corona lava tube, Lanzarote, 30–40 m depth (Martínez et al. 2016). Accompanying interstitial fauna includes rich assemblage of annelids, including *Meganerilla cesari* and *Claudrilus* sp. (Worsaae et al. 2009; Martínez et al. 2015), as well as several species of Platyhelminthes, gastrotrichs, mollusks and cnidarians (García-Valdecasas 1985; Martínez et al. 2009, 2019; Gobert et al. 2019).

Remarks. *Mesonerilla runae* sp. nov. differs from all described *Mesonerilla* in the presence of very broad and long buccal cirri, longer than the palps, as well as cylindrical interramal cirri increasing in size towards the pygidium (see also Table 3).

(2) ***Mesonerilla intermedia*** Wilke, 1953

Fig. 3, Table 3.

Mesonerilla intermedia Wilke, 1953: Jouin 1968; Bailey-Brock 1999; Müller 1999; Worsaae and Müller 2004; Worsaae 2005a, b; Worsaae and Kristensen 2005

Examined material. NHMD-301558, whole mount, Casamicciola, Ischia Island, Gulf of Naples, Italy. Very coarse and gravel in a *Posidonia* meadow at 12 m depth. 40° 45′ 18 N 13° 53′38 E. Date: October 10, 2013 (Coll: Maikon Di Domenico, Alejandro Martínez). NHMD-301554-301557, four SEM-stubs. Ischia Island, Gulf of Naples, Italy. Coll: Greg Rouse.

Diagnosis. *Mesonerilla* with three cylindrical, tapering antennae. Segment I uniramous, with short, cylindrical buccal cirri; segments II–IX, biramous, with bottle-shaped interramal cirri, increasing in length towards the pygidium. Pygidium with paired, filiform cirri, without terminal prolongation or dorsal row of pores. Dorsolateral transverse ciliation arranged as continuous rows of ciliary tufts. Ventrolateral transverse ciliation consisting of two paired rows of ciliary tufts per segment not connected to the midventral ciliary band. Gonochoristic. Females with fan-shaped, rounded, brooding hood outgrowing from dorsal epidermis on segment VIII.

Emended description (measurements and description based on specimens from the Gulf of Naples). Trunk hyaline with nine segments 900–1645 μm long (without anterior and posterior appendages) and 125–250 μm wide (excluding parapodia). All trunk segments of equal length and shape (Fig. 3a). Prostomium with two club-shaped palps (max. L. 210 μm), two lateral antennae (max. L. 770 μm) and one shorter median antenna (max. L. 355 μm) (pa, la, Fig. 3a). Eyes absent. Parapodial cirri bottle-shaped with long pointed tips and increasing in length towards the pygidium (max. L. 360 μm) (pc, Fig. 3a, e); cirri on buccal segment shorter (max. L. 90 μm) and less elongated. Compound chaetae in all parapodia; buccal segment uniramous with one bundle of maximum 13 chaetae (max. L. 195 μm); segments II-IX biramous with 7–16 chaetae arranged in two bundles. Chaetae on segments II–IX increase in length towards pygidium (max. L. 345 μm). Pygidium with two filiform cirri (max. L. 330 μm).

Prostomium with anterior and posterior ciliated fields, as well as paired lateral ciliary bands extending from each lateral antenna to palps. Palps with ventral and dorsal ciliation: ventral ciliation consisting of a dense and continuous band extending from the basis to tip of palp, dorsal row with 5–10 tufts of cilia (dpc, Fig. 3d). Trunk segments with one dorsolateral and two ventrolateral paired transverse rows of cilia on each segment and longitudinal mid-ventral ciliary band extending from mouth to pygidium. Dorsolateral transverse rows with 6–9 ciliary tufts extending from basis of parapodia to mid-dorsal line (dt, Fig. 3b). Ventrolateral transverse ciliation consisting of two paired rows of ciliary tufts at each side of the midventral ciliary band (vt1, vt2, Fig. 3c, h). One paired ventrolateral row with 2–5 tufts on each side of midventral ciliary band extending along the anterior constriction of each segment (vt1, Fig. 3c, h); another with 5–11 tufts on each side of the body extending on the parapodia (vt2, Fig. 3c, h). One single tuft of cilia dorsally on each parapodia (pt, Fig. 3b).

Gonochoristic. Males with two pairs of spermioducts in segments IV–V and V–VI, with unpaired midventral openings on segment V and VI. Females with one pair of oviducts in segments VII–VIII. A maximum of two vitellogenic oocytes (200 μm long) found in same specimen. Up to four embryos reported, attached dorsally on segments VIII–IX. Juveniles partly covered by brooding hood, formed by outgrowing of dorsal epidermis on segment VIII at level of parapodia and rising above dorsal surface of posterior end (bh, Fig. 3g). Brooding hood up to 60 μm wide and 20 μm long. Fan-shaped brooding hood with rounded outer margin and only partly covering segment IX. Outer line of brooding hood ciliated with small tufts of cilia on dorsal side (ct, Fig. 3g).

Distribution and habitat. Gulf of Naples, Italy, Mediterranean Sea (Jouin 1968; Wilke 1953; Müller 1999). Other records for the species require confirmation. Coarse and gravelly sand in *Posidonia oceanica* meadows from the lower water line to shallow subtidal depths (Wilke 1953).

Remarks. The morphological observations on new material of *M. intermedia* Wilke, 1953 from the type locality is in accordance with the original description (Wilke 1953), allowing us to add new morphological information to the original description, such as details on ciliary patterns and brooding hood. The brooding hood of *M. intermedia* differs

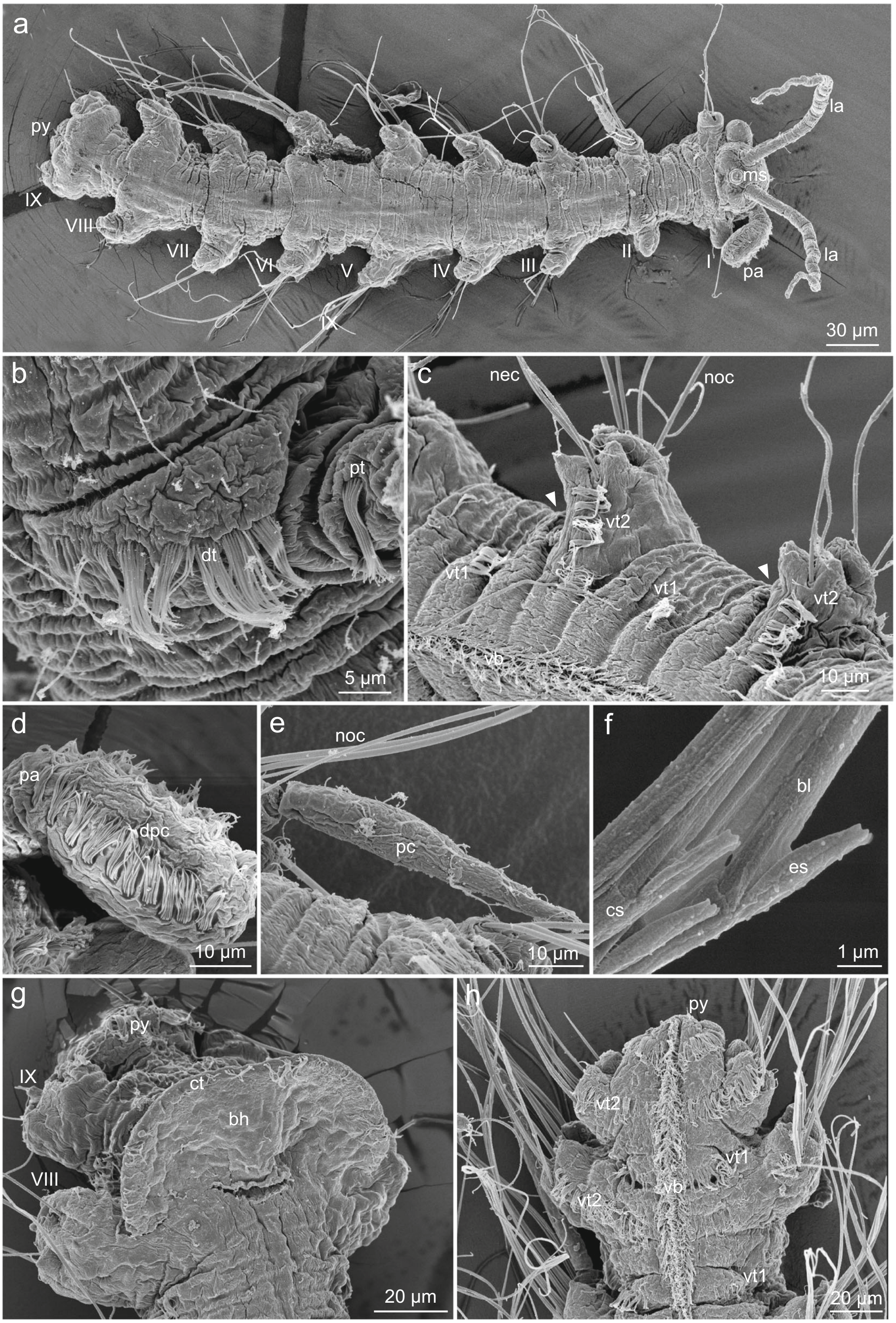


Fig. 3 *Mesonerilla intermedia*. Scanning electron micrographs of **a** whole male specimen in dorsal view; **b** dorsal trunk ciliation on segment III; **c** ventral trunk ciliation on segments I–III; **d** dorsal view of the palp showing dorsal palp ciliation; **e** bottle-shaped parapodial cirrus on segment VII; **f** detail of chaetae on segment IV with shaft, extension of shaft and blade; **g** dorsal view of the posterior end of a female with brooding hood; **h** ventral view of segments VIII–IX and pygidium showing ventral ciliation. bh, brooding hood; bl, chaetael blade; cs, chaetal shaft; ct, ciliary tufts; dpc, dorsal palp ciliation; dt, dorsolateral transverse ciliary row; es, extension shaft; la, lateral antenna; ms, antenna scar; nec, neurochaetae; noc, notochaetae; pa, palp; pc, parapodial ciliary tuft; py, pygidium; vb, midventral ciliary band; vt1–2, ventral transverse ciliary rows. Segment numbers in roman numerals

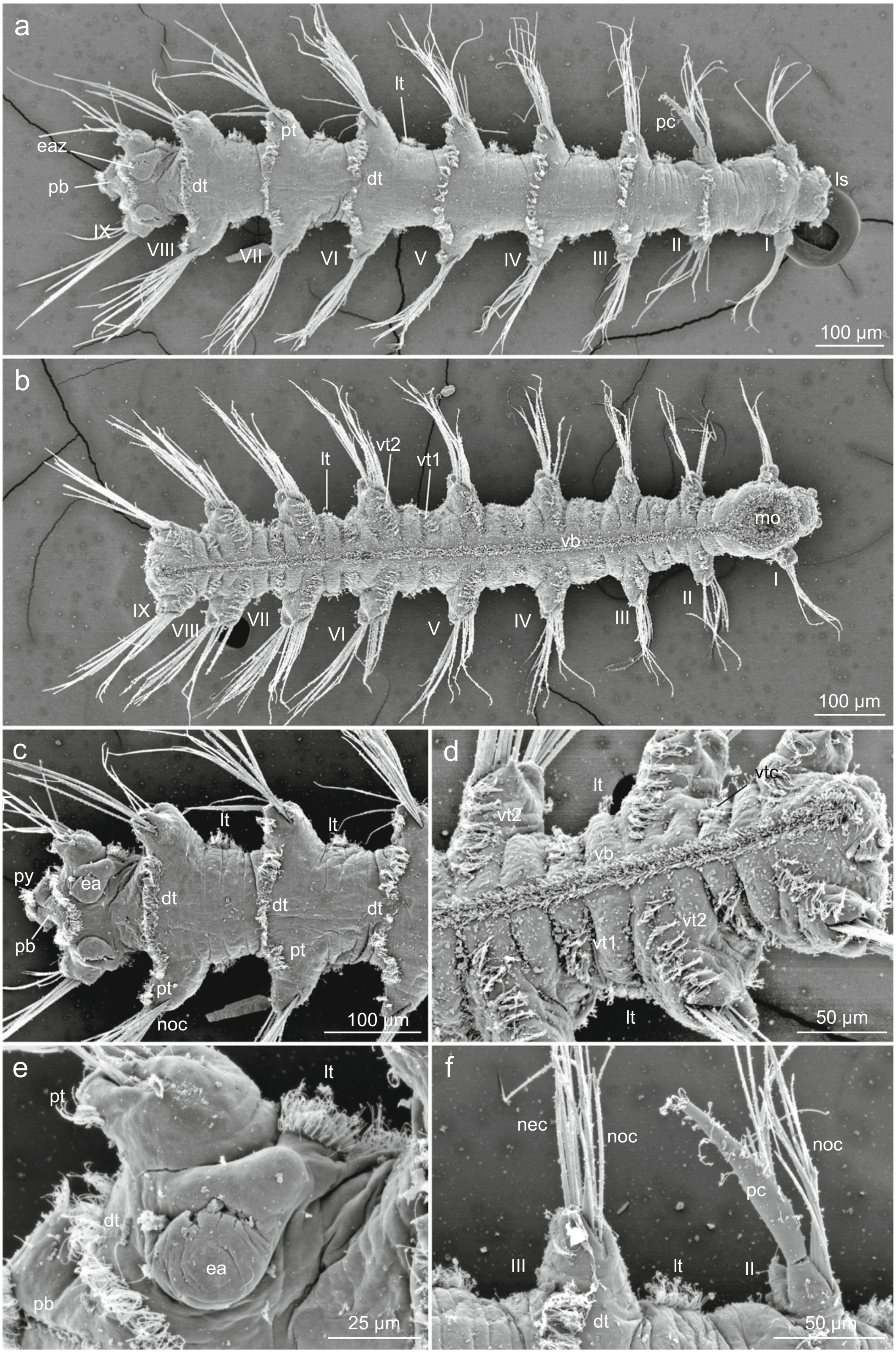


Fig. 4 *Mesonerilla aryae* sp. nov. Scanning electron micrographs of **a** whole specimen in dorsal view; **b** whole specimen in ventral view; **c** dorsal view of segments VI–IX of a female showing the attachment zone for two embryos and dorsal transverse ciliation; **d** ventral transverse ciliation on segments VII–IX; **e** attachment zone of an embryo on segment IX; **f** dorsal view of parapodial cirri on segments II–III. dt, dorsolateral transverse ciliary row; ea, embryo attachment; eaz, embryo attachment zone; ls, lateral antenna scar; lt, lateral ciliary row; mo, mouth; nec, neurochaetae; noc, notochaetae; pb, pygidial band of pores; pc, parapodial cirrus; pt, parapodial ciliary tuft; py, pygidium; vb, midventral ciliary band; vt1–2, ventral transverse ciliary rows. Segment numbers in roman numerals

from the brooding hood earlier described for specimens of *Mesonerilla* collected from Massachusetts (USA) (Fransen 1980, 1983) and Isles of Scilly (English Channel) (Westheide 2008). The attribution of the latter two populations to *M. intermedia* is doubtful and requires further examinations.

Specimens examined from Mallorca and Sardinia only differ from those collected in the Gulf of Naples in the number of ciliary tufts in the dorsal and ventral transverse ciliary rows (see Table 3). Despite the overall morphological similarities, the comparatively large genetic distances between sequenced specimens from each population suggest that they might represent a complex of cryptic species.

(3) ***Mesonerilla aryae*** sp. nov.

http://zoobank.org/C0BD704C-C269-4448-BFDA-6958A7AA4278

Fig. 4, Table 3.

Type material. Holotype: NHMD-301589, mounted on SEM-stub, dorsal view. Punta del Hidalgo, Tenerife, Canary Islands. 28.576° N; 16.328° W. Cinder and gravel deposits in a supratidal pool, about 100 m above the HW line, 0–30 cm depth, 4 July 2011. Coll: A. Martínez and C. Abreu. Paratype: NHMD-301594, one specimen mounted on same SEM-stub, ventral view, same date and locality as holotype.

Etymology. Named after Arya Cañadas Montelongo, daughter of diver Luis E. Cañadas. Both assisted the authors during several field trips around the Canary Islands, including those leading to the discovery of the material used to describe this species.

Diagnosis. *Mesonerilla* with three antennae, unknown shape. Segment I uniramous, with cylindrical buccal cirri; segments II–IX biramous, with bottle-shaped parapodial cirri. Pygidium without terminal prolongation and with dorsal row of pores, pygidial cirri unknown. Dorsolateral transverse ciliation arranged as continuous rows of ciliary tufts. Ventrolateral transverse ciliation consisting of two paired rows of ciliary tufts per segment. Lateral ciliation as a short oblique row of tufts on each segment between parapodia. Gonochoristic. Females without brooding hood.

Description (measurements from holotype). Trunk consisting of nine chaetigerous segments; maximum 1000 μm long and 125 μm wide (without appendages or parapodia). All segments of equal size and shape (Fig. 4a). Prostomium with two palps, two lateral antennae and one median antenna (all lost). Eyes absent. Glands unknown. Parapodial cirri bottle-shaped (max. L. 95 μm (on segment II)) (pc, Fig. 4a, f), relative length unknown. Segment I uniramous, with maximum 8 chaetae per bundle (max. L. 145 μm); segments II–IX with maximum 29 chaetae, slightly increasing in length from segment I–VII (max L. 200 μm), equal in length on segments VIII–IX. All chaetae compound. Pygidium with a mid-dorsal longitudinal band of pores (pb, Fig. 4c). Pygidial cirri lost.

Prostomial ciliation organised in two fields, anterior and posterior to median antenna, respectively. Paired lateral ciliary rows extends from each lateral antenna to the palps. Palp ciliation unknown. Trunk ciliation with one dorsolateral and two ventrolateral paired transverse rows on each segment and a midventral ciliary band. Dorsolateral transverse rows with 5–9 ciliary tufts extending from basis of parapodia, connecting in dorsal midline on each segment (dt, Fig. 4a, c). Ventrolateral transverse ciliation consists of two paired rows of cilia per segment (vt1, vt2, Fig. 4b), one extending between parapodia and with 2–5 tufts on each side of the body (vt1, Fig. 4d), another at the level of the parapodia with 4–8 tufts on each side of the midventral ciliary band (vt2, Fig. 4b, d). Number of tufts per row increasing posteriorly from segment I–IX. Lateral ciliation consisting of a short row of 2–3 tufts extending obliquely between parapodia (lt, Fig. 4a–f). Each parapodium with 1–2 dorsal tufts of cilia (pt, Fig. 4c, e).

Gonochoristic, with separate males and females. Two embryos may be attached at each dorsolateral side at segment IX at level of parapodia. Brooding hood absent (Fig. 4e).

Distribution and habitat. Exclusively known from the type locality at Punta del Hidalgo, Tenerife, Canary Island. Cinder and gravel deposits in saltwater pools, presumably not anchialine, above the high tide level, probably receiving seawater from waves during the storms. Depth of about 0.1–0.3 m. Accompanying fauna consisted of cyclopoid copepods as well as a new species of *Nerilla* (Nerillidae) (Martínez and Worsaae, unpublished).

Remarks. *Mesonerilla aryae* sp. nov. resembles *Mesonerilla intermedia* and *M. luederitzi* in the presence of bottle-shaped parapodial cirri and continuous segmental dorsal transverse ciliary bands. However, *Mesonerilla aryae* sp. nov. differs from both species in the presence of lateral ciliation and the presence of a mid-dorsal longitudinal band of pores at the pygidium. Pygidial pores are otherwise only observed in *Mesonerilla xurxoi* sp. nov., from which *M. aryae* sp. nov. differs in the presence of bottle-shaped parapodial cirri (cylindrical in *M. xurxoi* sp. nov.), continuous dorsal segmental ciliary bands (discontinuous in *M. xurxoi* sp. nov.), lack of pygidial prolongation (present in *M. xurxoi* sp. nov.) and presence of a lateral ciliary tufts on each trunk segment (absent in *M. xurxoi* sp. nov.). *Mesonerilla aryae* sp. nov. further differs form *M. intermedia* in the absence of brooding hood.

(4) ***Mesonerilla laerkae*** sp. nov.

http://zoobank.org/CFB24218-DDCB-408D-B4CC-BC98BC4AF1EA

Fig. 5, Table 3.

Mesonerilla intermedia (non Wilke, 1953): Fransen 1980, 1983; Riser 1988; Westheide and Riser 1983; Westheide 2008

Type material. Holotype: NHMD- 301607, on SEM-stub. Bailey's Hill, Nahant, MA, USA, coarse sand, 8–15 m depth, 42.427° N, 70.919° W, April 2012 (Coll: C. Laumer). Two additional specimens from same locality as the holotype were

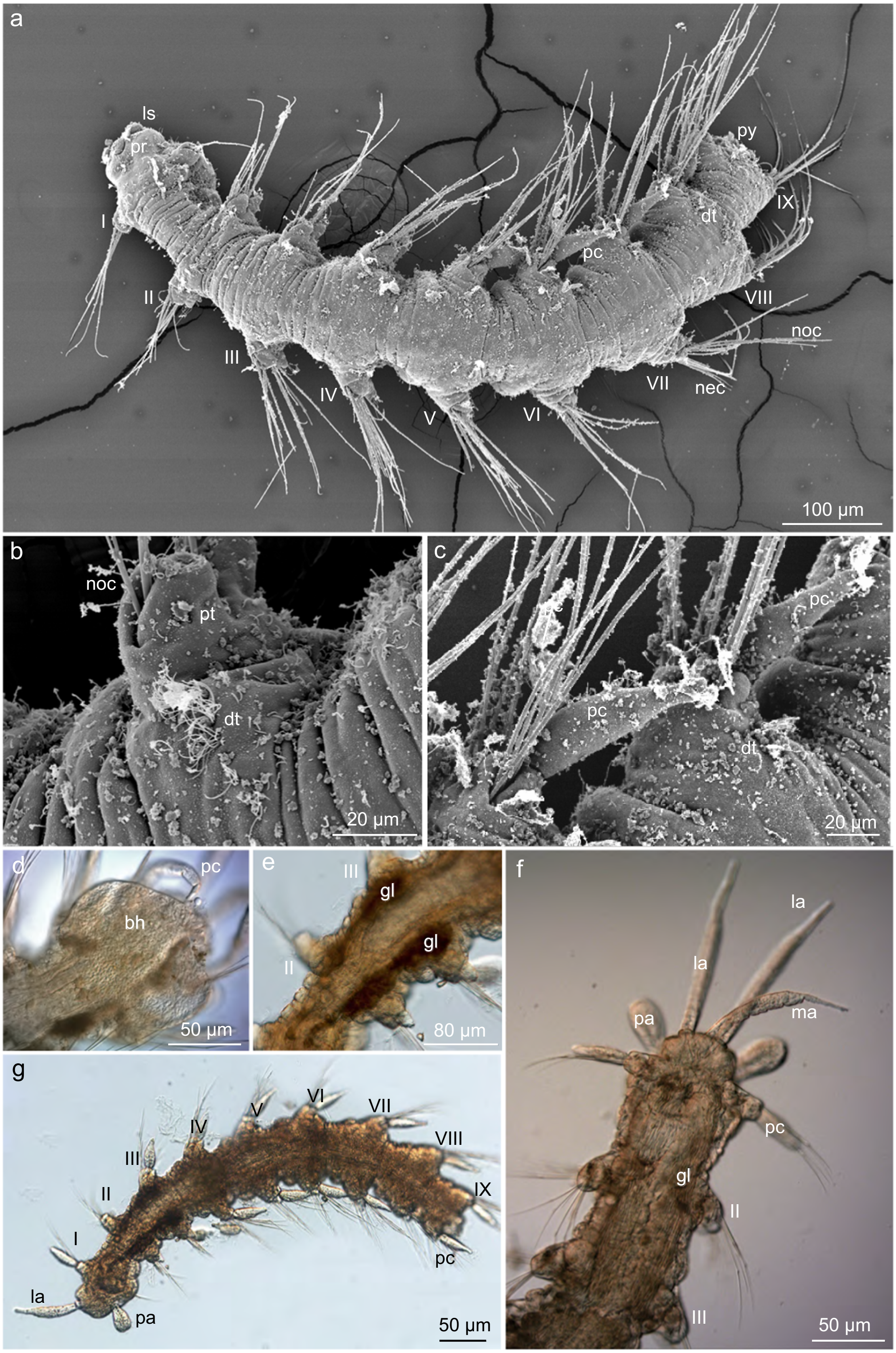


Fig. 5 *Mesonerilla laerkae* sp. nov. Scanning electron micrographs of **a** whole specimen in dorsal view; **b** dorsal view of parapodium on segment III; **c** parapodial cirri on segments V–VI; light micrographs of **d** posterior end of a female showing dorsal brooding hood; **e** oesophageal glands in segments II–III; **f** ventral view of the anterior end showing palps and antennae; **g** whole specimen in ventral view. bh, brooding hood; dt, dorsolateral transverse ciliary row; gl, glands; la, lateral antenna; ls, lateral antenna scar; ma, medina antenna; nec, neurochaetae; noc, notochaetae; pa, palp; pc, parapodial cirrus; pt, parapodial ciliary tuft; pr, prostomium; py, pygidium. Segment numbers in roman numerals

photographed with light microscopy (by C. Laumer) and data were included in the description.

Etymology. Named after Laerke, youngest daughter of first author Katrine Worsaae, who has helped in collecting several of the other species though not this one, which was collected by Christopher Laumer (see Acknowledgements).

Diagnosis. *Mesonerilla* with three bottle-shaped antennae. Segment I uniramous with rounded cirri, segments II–IX biramous, interramal cirri bottle-shaped equal in size along the body. Pygidium with paired elongated bottle-shaped cirri, without terminal prolongation or dorsal row of pores. Oesophageal glands large along segments II–III. Gonochoristic. Females with large fan-shaped medially pointed brooding hood on segment VIII–IX.

Description (measurements from holotype). Trunk transparent, with nine chaetigerous segments; maximum 1170 μm long and 125 μm wide (without appendages or parapodia) (Fig. 5a). All trunk segments of similar size and shape. Prostomium with two club-shaped palps (max. L. 70 μm) and three bottle-shaped antennae, medium antenna slightly shorter (L. 125 μm) than lateral antennae (max L. 160 μm) (la, ma, Fig. 5f). Eyes absent. Oesophageal glands large, extending along segments II–III (gl, Fig. 5e). Parapodial cirri on segment I round (max. L. 80 μm), cirri on segments II–IX, bottle-shaped and equal in size along the body (max. L. 90 μm). Segment I uniramous, with a maximum of 4 chaetae (max. L. 80 μm), segments II–IX biramous, with 5–15 chaetae (max. L. 180 μm). Pygidial cirri elongated and bottle-shaped (max. L. 170 μm). All chaetae compound.

Prostomium with anterior and posterior ciliary fields, as well as paired lateral ciliary bands extending from insertion of each lateral antenna to palps. Palp ciliation unknown. Trunk ciliation with dorsolateral and ventrolateral paired transverse rows on each segment and midventral ciliary band. Dorsolateral paired rows at level of parapodia with 3–4 tufts each, extending from base of each parapodium towards dorsal midline of trunk, leaving midline unciliated (dt, Fig. 5b); number of paired rows as well as number of tufts in each of them are unknown. A single ciliary tuft dorsally on each parapodium (pt, Fig. 5b).

Gonochoristic. Gonoducts position unknown. Females with up to six embryos attached dorsally on segments VIII–IX. Brooding hood as dorsal outgrowing of segment VIII, attaching laterally to dorsal surfaces of parapodia and covering segments VIII–IX and pygidium (bh, Fig. 5d); ca. 100 μm long. Band of ciliary tufts extends along dorsal margin of brooding hood.

Distribution and habitat. Nahant, MA, USA. Coarse sand, 8–15 m deep. Accompanying fauna included the interstitial annelids *Meganerilla penicillicauda* (Riser, 1988), *Diurodrilus* sp., *Nerilla* sp. (Fransen, 1980, 1983; Riser 1988; Worsaae and Martínez, unpublished).

Remarks. *Mesonerilla laerkae* sp. nov. differs from all described species of *Mesonerilla* in the presence of very large oesophageal glands, extending along segments I–III. Otherwise, it resembles *Mesonerilla intermedia*, in the presence of bottle-shaped cirri and brooding hood, but differs in the presence of a larger brooding hood and discontinuous dorsolateral ciliary rows (continuous in *M. intermedia*). *Mesonerilla laerkae* sp. nov. also resembles *M. luederitzi* in the shape of appendages, but differs in the presence of a brooding hood, morphology of glands and discontinuous dorsolateral ciliary rows.

(5) ***Mesonerilla xurxoi*** sp. nov.

http://zoobank.org/B36EDDBF-64DF-4632-8DC9-F1C2CBFC91F6

Mesonerilla sp. nov. in Martínez et al. 2009, 2016; Worsaae et al. 2009

Type material. Holotype NHMD-109880, whole mount. Montaña Arena, Túnel de la Atlántida, Lanzarote, Canary Islands, coarse sand, 30–40 m depth, 29.157° N, 13.425° W, 23 March 2008 (Coll: T. Iliffe and A. Martínez). Paratypes NHMD-109871-72, two whole mounts. Cueva de Los Lagos, Lanzarote. Cinder patches at the second lake, 2 m depth, 29.156° N, 13.438° W, 3 March 2008 (Coll: J. Núñez and A. Martínez) and 10 January 2010 (Coll: A. Martínez, E. Domínguez and R. Schoenermark). Paratype NHMD-109881, whole mount. Cueva de Los Lagos, Lanzarote. Cinder patches in the first lake, 29.156° N, 13.438° W, 12 April 1995 (Coll: J Núñez and M. C. Brito). Paratypes NHMD-109873-79, seven whole mounts, same locality as holotype, 21 March 2008 (Coll: T. Iliffe and A. Martínez). Paratypes NHMD-109882-84, three whole mounts. Los Jameos del Agua, Lanzarote. 29.157° N, 13.425°W. Cinder patches, 9 m depth, 21 March 2008. (Coll: T. Iliffe, J. Núñez and A. Martínez). Paratypes NHMD-109885, 301530, 301531, 301533, four SEM-stubs, same locality as previous, lapilli sediment, 2 m depth, 14 and 21 January 2010 (Coll: A. Martínez, E. Domínguez and R. Schoenermark). Paratype NHMD-301536 on SEM stub, same locality as holotype, 22 March 2008 (Coll: T. Iliffe and A. Martínez).

Diagnosis. *Mesonerilla* with three cylindrical antennae, median shorter. Segment I uniramous, with ovoid cirri. Segments II–IX biramous, with cylindrical interramal cirri, equal on segments II–VIII, longer on segment IX. Pygidium with paired cylindrical cirri and short mid-ventral terminal prolongation and a mid-dorsal longitudinal band of pores. Trunk dorsolateral transverse ciliation as paired dorsolateral rows on each segment, not connecting medially. Ventrolateral transverse ciliation consisting of paired rows on each segment at the level of the parapodia. Gonochoristic. Large rounded oesophageal glands in segment I–II. Females without brooding hood.

Etymology. Named after the zoologist Jorge Núñez, Xurxo, to honour his pioneering work in the meiobenthic annelids in the Canary Islands. His early research in Los Jameos del Agua inspired the authors to study the interstitial meiobenthic communities in other anchialine caves. The first material of the species was found by Jorge and María del Carmen Brito in Cueva de los Lagos in 1997.

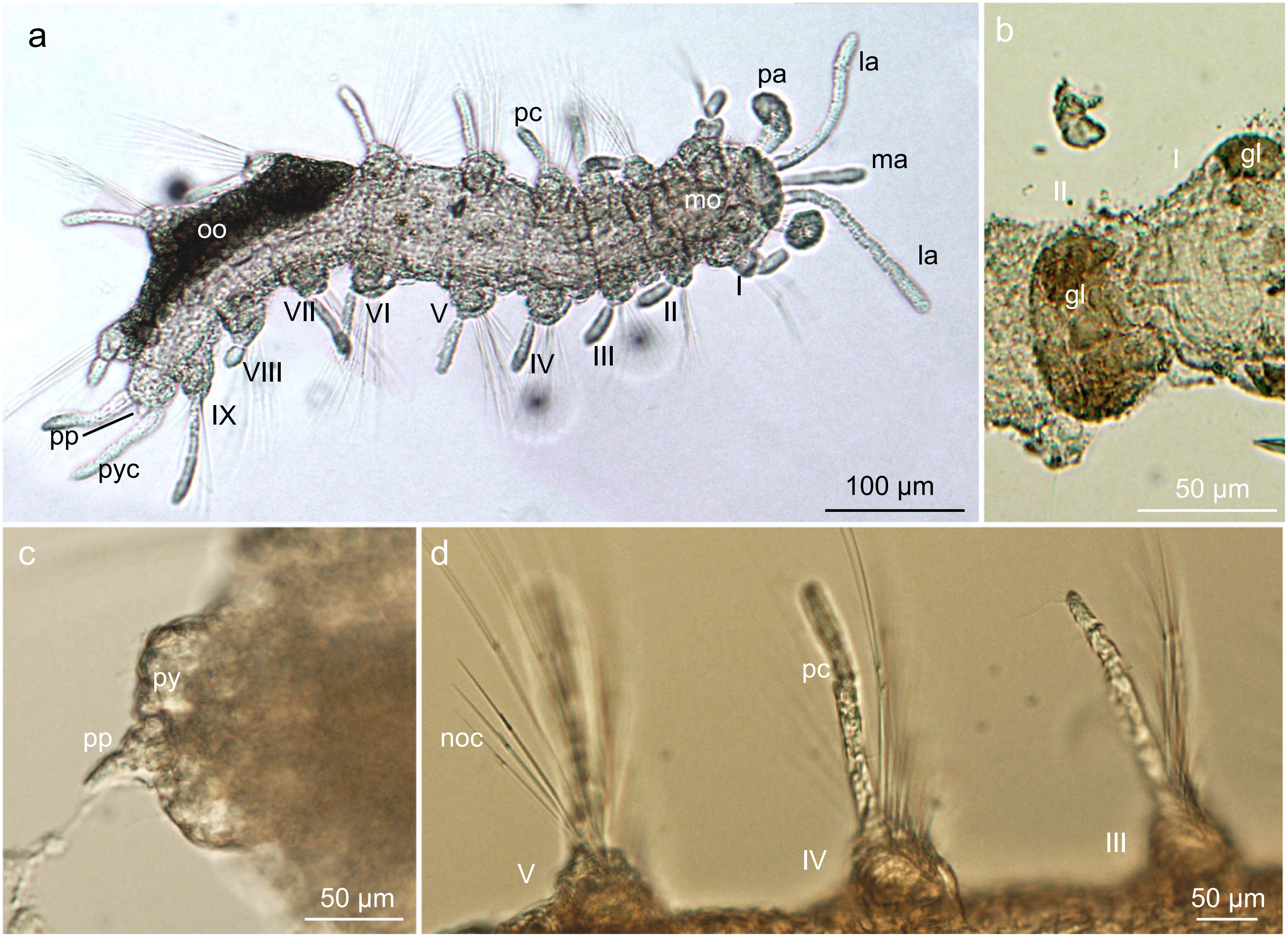
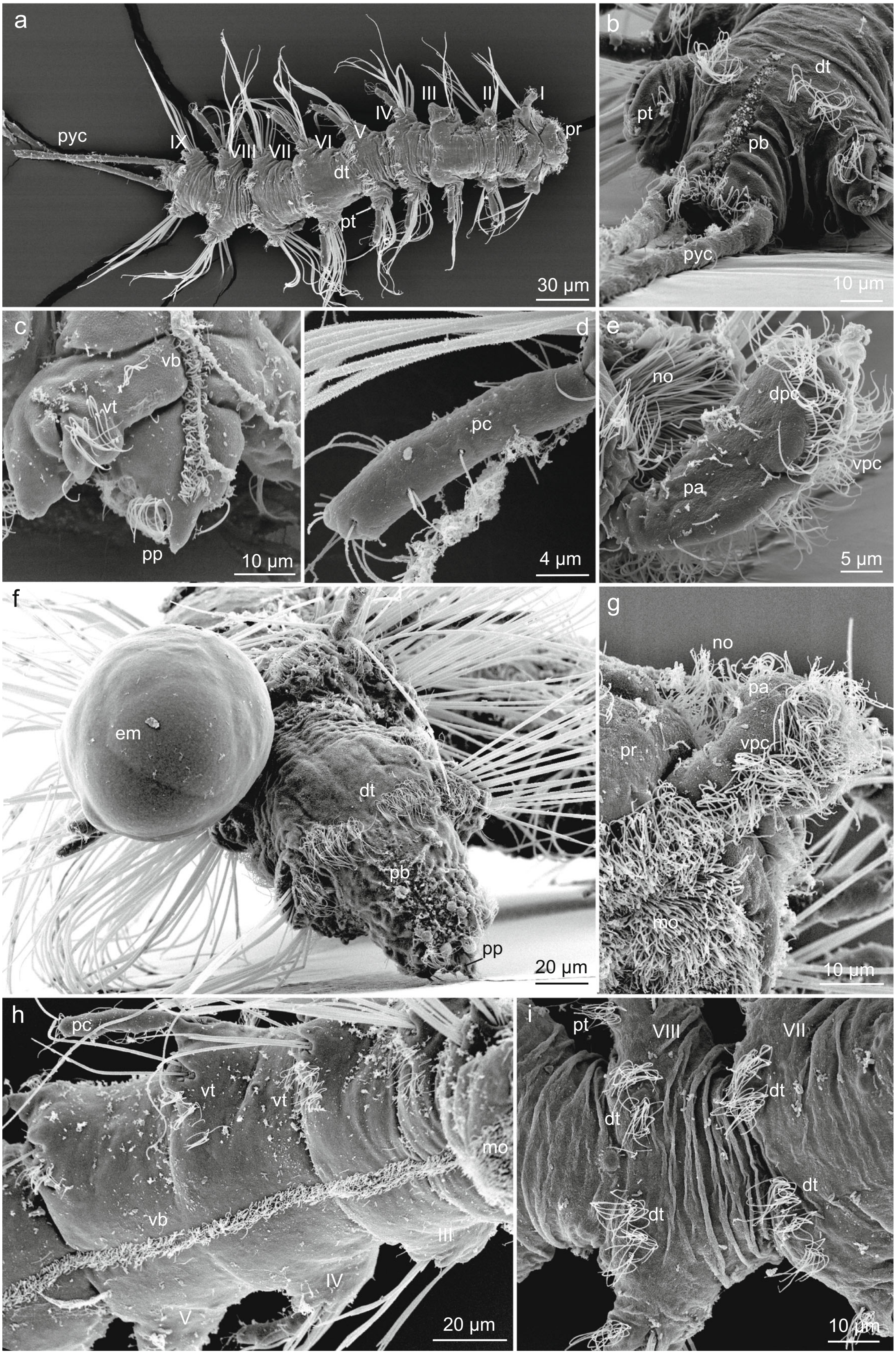


Fig. 6 *Mesonerilla xurxoi* sp. nov. Light micrographs of **a** whole holotype in ventral view; **b** detail of the glands in segments I–II of a paratype from Cueva de los Lagos; **c** detail of the posterior end showing the pygidial prolongation on a live specimen from Montaña de Arena; **d** parapodial cirri on segments III–V on a live specimen from Montaña de Arena. gl, glands; la, lateral antenna; ma, median antenna; mo, mouth; noc, notochaetae; oo, oocyte; pc, parapodial cirrus; pp, prolongation on the pygidium; py, pygidium; pyc, pygidial cirri. Segment numbers in roman numerals

Description (based on holotype, measurements from paratypes in parentheses). Trunk hyaline, with nine chaetigerous segments; maximum 660 µm long and 80 µm wide (without appendages or parapodia). All segments of equal size and shape (Fig. 6a). Prostomium with two club-shaped palps (max. L. 75 µm), two lateral antennae (max. L. 110 µm) and one median antenna (max. L. 75 µm); all antennae cylindrical with blunt tips (la, ma, Fig. 6a). Eyes absent. Two large rounded oesophageal glands in segment II (gl, Fig. 6b), smaller glands visible laterally on segment I. Parapodial cirri on segment I short and ovoid (max. 20 µm long); parapodial cirri on segments II–VIII cylindrical and of equal length (max. L. 70 µm) (Figs. 6d and 7d), cirri on segment IX slightly longer (Fig. 6a). Segment I uniramous, with 5–12 chaetae per bundle (max. L. 95 µm); segment II–IX biramous with maximum 23 chaetae (max. L. 95 µm) (Fig. 7f). Pygidium with two filiform cirri (max. 120 µm long) (pyc, Fig. 6a) and a terminal tapering prolongation outgrowing posteriorly (pp, Fig. 6c and 7c). A longitudinal band of pores present mid-dorsally from the posterior end of pygidium to segment IX (pb, Fig. 7b, f).

Prostomium with anterior and posterior ciliated fields, as well as paired lateral ciliary rows extending from each lateral antenna to palps. Palp ventral ciliary band dense and continuous, extending longitudinal from insertion to tip of palp (vpc, Fig. 7e). Palp dorsal ciliary row short, consisting of four tufts extending transversely on tip of palp (dpc, Fig. 7e). Trunk dorsolateral ciliation consisting of paired transverse rows extending from base of each parapodium towards dorsal midline of trunk, leaving midline unciliated (dt, Fig. 7a, i). Each row consists of 3–4 tufts of cilia. Dorsolateral transverse rows are more developed towards pygidium (Fig. 7i), almost connected in dorsal midline on segment IX (dt, Fig. 7f). Trunk ventrolateral ciliation as one paired transverse row of 3–4 tufts each, extending from each parapodium towards midventral ciliary band; never connected at midventral line (vt, Fig. 7h). Dorsal parapodial ciliation consists of 1–2 tufts of cilia (Fig. 7b).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◀ **Fig. 7** *Mesonerilla xurxoi* sp. nov. Scanning electron micrographs of **a** whole specimen in dorsal view; **b** dorsal view of the pygidium showing the longitudinal band of pores; **c** ventral view of the pygidium showing the ventral pygidial prolongation; **d** parapodial cirrus on segment IV; **e** dorsal view of the palp; **f** posterior end of a female with a dorsally attached embryo; **g** ventral view of the palp; **h** ventral trunk ciliation on segments III–V; **i** dorsal trunk ciliation on segments VII-VIII. dpc, dorsal palp ciliation; dt, dorsolateral transverse ciliation; em, embryo; mo, mouth; no, nuchal organ; pa, palp; pb, pygidial band of pores; pc, parapodial cirrus; pr, prostomium; pp, prolongation on the pygidium; pt, parapodial ciliary tuft; pyc, pygidial cirri; vb, midventral ciliary band; vpc, ventral palp ciliation; vt, ventral transverse ciliary row. Segment numbers in roman numerals

Gonochoristic. Males with one pair of spermioducts with fused midventral gonopore in segment V. Females with one pair of oviducts opening in segment VIII. Vitellogenic oocytes laterally in segment VII–IX (oo, Fig. 6a). Females with one embryo attached dorsally on segments VIII–IX, observed at least in two specimens (em, Fig. 7f). Brooding hood absent.

Distribution and habitat. La Corona lava tube, Lanzarote, Canary Islands, Northeast Atlantic Ocean (Wilkens et al. 2009). Coarse sand and cinder patches in anchialine caves from 2 to 40 m depth. Accompanying interstitial fauna in Los Jameos del Agua consists of several species of annelids, including the stygobitic species *Leptonerilla diatomeophaga* Núñez, 1997, *Fauveliopsis jameoaquensis* Núñez, 1997, *Macrochaeta* sp. nov. (Núñez et al. 1997), as well as several species of crustaceans (Martínez et al. 2009, 2016). *Mesonerilla xurxoi* sp. nov. was the only annelid found in the cinders at Cueva de los Lagos, rarely found together with the isopod *Curassanthura canariensis* Wägele, 1985. See description of *Mesonerilla runae* sp. nov. for more details on Montaña de Arena.

Remarks. *Mesonerilla xurxoi* sp. nov. presents a combination of features only resembling those in *M. katharinae* and *M. peteri*, except for a very elongated pygidium. See discussion under *M. peteri* for a detailed comparison amongst these species.

(6) ***Mesonerilla katharinae*** sp. nov.

http://zoobank.org/D4443669-4740-46D4-9156-63E1C416FF50

Fig. 8, Table 3.

Type material. Holotype: (NHMD-301622) as a permanent whole mount. Wild Cane Rock, Bocas del Toro, Panamá, coarse sand, 14 m depth, 9.350° N, 82.172° W, 8 June 2010 (Coll: D. Gouge, K. Worsaae and A. Martínez). Paratypes: (NHMD-301627, 301629), two SEM-stubs, same date and locality as holotype. Additional unpreserved material video recorded alive. Tiger Rock, Bocas del Toro, Panamá, coarse sand, 28 m depth, 9.350° N, 82.172° W, 6 June 2010 (Coll: D. Gouge, K. Worsaae and A. Martínez).

Etymology. Named after the zoologist Katharina Jörger in gratitude for her friendship and continuous effort in sampling interstitial annelids during her own and collaborative field trips.

Diagnosis. *Mesonerilla* with three cylindrical antennae, median shorter. Segment I uniramous, with short cirri; segments II–IX biramous, interramal cirri cylindrical and blunt; with equal length on segments II–IV and increasing on segment V–IX. Pygidium with long filiform cirri and mid-ventral tapering prolongation. Dorsolateral transverse ciliation arranged as paired rows on each segment, not connecting medially. Ventrolateral transverse ciliation consisting of one paired row per segment at the level of the parapodia. Paired bundle of cilia on segment III at each side of midventral ciliary band. Dark oesophageal glands visible in segments I–II. Gonochoristic. Females without brooding hood.

Description (based on holotype, measurements from paratypes in parentheses). Trunk transparent, with nine segments; maximum 1000 μm long and 100 μm wide (without appendages or parapodia). All segments of equal size and shape (Fig. 8a). Prostomium with two club-shaped palps (max. L. 80 μm), two lateral antennae (max. L. 260 μm) and one median antenna (max. L. 75 μm), all antennae cylindrical with blunt tips (Fig. 8a). Eyes absent. Paired rounded oesophageal glands in segment II. Parapodial cirri on segment I–III ovoid (40 μm long); cirri on segments IV–IX, cylindrical (max. L. 95 μm) (Fig. 8a–c). Segment I uniramous, with maximum 7 chaetae per bundle (max. L. 90 μm); segments II–IX biramous with maximum 16 chaetae per parapodium, increasing in length posteriorly (L. 90–160 μm) (Fig. 8d). Pygidium with two filiform cirri (max. L. 350 μm) and short terminal tapering prolongation outgrowing posteriorly (max. L. 10 μm) (Fig. 8b).

Prostomium with anterior and posterior ciliated fields, as well as paired lateral ciliary rows, extending from each lateral antenna to palps (Fig. 8f). Palp ventral ciliary band dense and continuous, extending longitudinally from insertion of palp to palp tip (Fig. 8h). Palp dorsal ciliary row short, extending along tip of palp (dpc, Fig. 8h). Trunk dorsolateral ciliation as paired transverse rows, each with 1–2 ciliary tufts, extending from base of each parapodium towards dorsal midline of trunk leaving the mid-body line unciliated (dt, Fig. 8f). Each parapodium with one dorsal ciliary tuft (Fig. 8f). Trunk ventrolateral ciliation only found as 2 ciliary tufts on each parapodium (vt, Fig. 8c). Characteristic paired bundles of cilia situated ventrally in the centre of segment III; one at each side of midventral ciliary band (pbc, Fig. 8e). Each bundle slightly fuses with midventral cilia band and consists of 30–50 long cilia whose function remains unknown.

Gonochoristic. Brooding hood absent in mature females with large oocytes. Embryos not observed.

Distribution and habitat. Bocas del Toro, Panamá, Caribbean Sea. Sandy bottom with medium-coarse sand between 14 and 28 m depth. Accompanying fauna including *Lobatocerebrum*, Protodrilidae, Saccocirridae, Psammodrilidae (Martínez et al. 2013; Di Domenico et al. 2014; Kerbl et al. 2015; Worsaae et al. 2018).

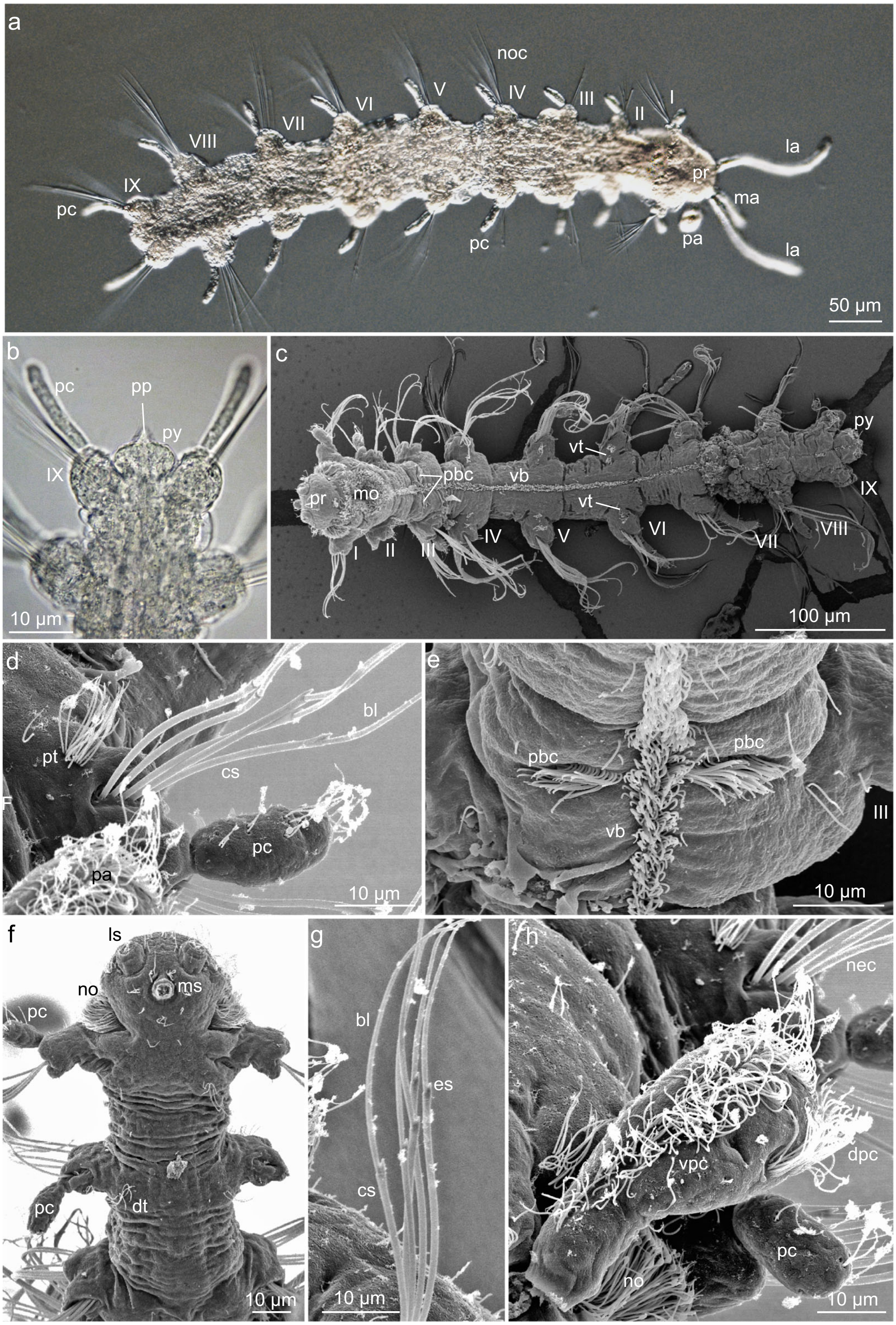
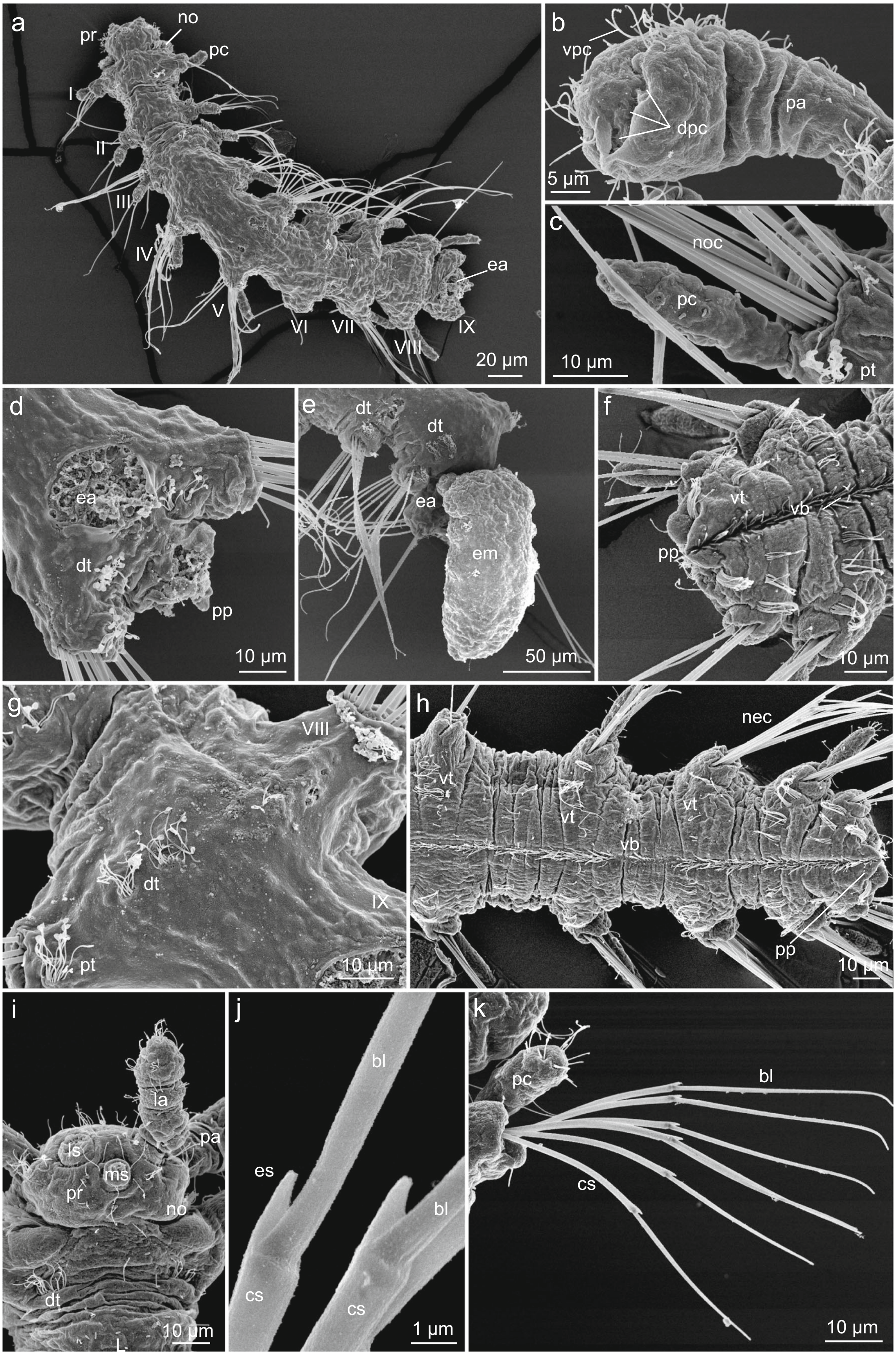


Fig. 8 *Mesonerilla katharinae* sp. nov. Light micrograph of **a** whole holotype in dorsal view; **b** ventral view of the pygidium showing pygidial prolongation in a living animal; scanning electron micrographs of **c** whole specimen in ventral view; **d** detail of the cirrus and compound chaetae on segment I; **e** ventral view of segment III with paired bundle of cilia; **f** dorsal view of the anterior end showing dorsal trunk ciliation; **g** neurochaetae on segment II; **h** ventral view of the palp. bl, chaetal blade; cs, chaetal shaft; dpc, dorsal palp ciliation; dt, dorsolateral transverse ciliary row; es, extension of the shaft; la, lateral antenna; ls, lateral antenna scar; ma, median antenna; mo, mouth; ms, median antenna scar; nec, neurochaetae; no, nuchal organ; noc, notochaetae; pa, palp; pbc, paired ventral ciliary bundles; pc, parapodial cirrus; pp, prolongation on the pygidium; pr, prostomium; pt, parapodial ciliary tuft; py, pygidium; vb, midventral ciliary band; vpc, ventral palp ciliation; vt, ventral transverse ciliary row. Segment numbers in roman numerals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◀ **Fig. 9** *Mesonerilla peteri* sp. nov. Scanning electron micrographs of **a** whole holotype on dorsal view; **b** palp in dorsal view; **c** parapodial cirrus on segment VI; **d** posterior end of female in dorsal view showing the embryo attachment zone; **e** posterior end of female with embryo attached dorsally; **f** pygidium in ventral view with a pygidial prolongation; **g** dorsal transverse trunk ciliation on segment VIII; **h** ventral view of segments V–IX showing ventral transverse ciliation and pygidial prolongation; **i** dorsal view of the prostomium; **j** chaetal shaft extension on segment I; **k** chaetae on segment I. bl, chaetal blade; cs, chaetal shaft; dpc, dorsal palp ciliation; dt, dorsolateral transverse ciliary row; ea, embryo attachment; em, embryo; es, extension of the shaft; la, lateral antenna; ls, lateral antenna scar; ms, median antenna scar; nec, neurochaetae; no, nuchal organ; noc, notochaetae; pa, palp; pc, parapodial cirrus; pp, prolongation on the pygidium; pr, prostomium; pt, parapodial ciliary tuft; vb, midventral ciliary band; vpc, ventral palp ciliation; vt, ventral transverse ciliary row. Segment numbers in roman numerals

Remarks. *Mesonerilla katharinae* sp. nov. presents a combination of characters only resembling *M. xurxoi* and *M. peteri* except for unique ventral paired bundles of cilia on segment III. See discussion under *M. peteri* for detailed comparison amongst these species.

(7) ***Mesonerilla peteri*** sp. nov.

http://zoobank.org/E0C8296D-EB73-4067-82F8-7840918941CD

Fig. 9, Table 3.

Type material. Holotype: NHMD-301637, mounted on SEM-stub. Japanese garden, Tobago, Trinidad and Tobago. Coarse sand at 10 m depth, 27 December 2002. Coll: K Worsaae and PR Møller. Paratypes: NHMD-301638, eight specimens mounted on one SEM-stub. Same date and locality as holotype.

Etymology. Named after zoologist Peter R. Møller in gratitude for his continuous collecting assistance during multiple field trips sampling Nerillidae, including this to Trinidad and Tobago.

Diagnosis. *Mesonerilla* with two lateral antennae and one median antenna; cylindrical with blunt tips. Segment I uniramous, with short cirri; segments II–IX biramous with cylindrical interramal cirri; slightly ovoid in segment I–III, approximately equal in length on segments II–VIII, longer on segment IX. Pygidium with mid-ventral tapering prolongation, without dorsal row of pores. Dorsolateral transverse ciliation arranged as one paired dorsolateral row on each segment, not connecting medially. Ventrolateral transverse ciliation consisting of one paired row per segment at level of the parapodia. Gonochoristic. Brooding hood absent. Embryos attached dorsally on segments IX.

Description. (based on holotype) Body hyaline, with nine chaetigerous segments, 415 μm long and maximum 50 μm wide (not including appendages or parapodia). All segments of equal size and shape. Prostomium with two club-shaped palps (max. L. 45 μm) (Fig. 9b), two lateral antennae (max. L. 35 μm) and one median antenna (length unknown); cylindrical with blunt tips. Eyes absent. Glands unknown. Parapodial cirri on all segments, equal in length (20–25 μm long). Cirri on segment I–III ovoid; cirri on segments IV–IX, cylindrical and elongated (Fig. 9a). Segment I uniramous, with maximum 6 chaetae (max. 65 μm long) (Fig. 9k); segments II–IX biramous with maximum 13 chaetae (max. 80 μm long). Pygidium with terminal tapering prolongation (Fig. 9f), without dorsal band of pores. Two dense tufts of cilia situated at each lateral side of prolongation. Pygidial cirri lost.

Prostomium with anterior and posterior ciliated fields, as well as paired lateral ciliary bands extending from each lateral antenna to palps. Palp ventral ciliary band dense and continuous, extending longitudinally from insertion to tip of palp. Palp dorsal ciliary row consisting of a short longitudinal row of tufts extending at tip of palp (Fig. 9b). Trunk dorsolateral ciliation as paired transverse rows of 2–4 tufts extending from base of each parapodium to dorsal midline of trunk, leaving midline unciliated (dt, Fig. 9d–i). Trunk ventrolateral ciliation as paired transverse rows of 3–5 tufts each, extending from parapodia towards midventral ciliary band (vt, Fig. 9h). Dorsal parapodial ciliation consisting of single tuft of cilia (pt, Fig. 9g).

Gonochoristic. One embryo found attached dorsolaterally on segments VIII–IX (em, Fig. 9e) in one female specimen. Brooding hood absent.

Distribution and habitat. Tobago, Caribbean Sea, Northwest Atlantic Coarse, well-sorted sand at 10 m depth. Accompanying annelid fauna consisted of *Aristonerilla* sp. (Worsaae, unpublished).

Remarks. *Mesonerilla peteri* sp. nov. was recovered next to *Mesonerilla xurxoi* sp. nov. and *M. katharinae* sp. nov. in our phylogeny. The three species share a unique combination of features including presence of cylindrical antennae, cylindrical interramal cirri—equal in length on the anterior segments and presence of a ventral tapering prolongation on the pygidium. Furthermore, they all share the presence of discontinuous transverse dorsolateral ciliary rows and paired short ventrolateral ciliary rows on each trunk segment. However, *Mesonerilla xurxoi* sp. nov. is distinguished by a more elongated pygidium, a mid-dorsal longitudinal band of pores on the pygidium, as well as dorsolateral ciliation consisting of 3–4 tufts per row and 1–2 tufts on the parapodia and ventrolateral ciliation consisting of 3–4 tufts per row.

Mesonerilla katharinae sp. nov. is diagnosed by the presence of paired ventral ciliary bundles on segment III (Fig. 8c, e), and only two ciliary tufts on the ventral transverse ciliary rows. Interramal cirri in these species also start increasing in length from segment V (versus segment IX on *M. peteri* sp. nov. and *M. xurxoi* sp. nov.).

Finally, *Mesonerilla peteri* sp. nov. can be identified by the presence of a short terminal pygidial prolongation (as in *M. katharinae* sp. nov.), in combination with dorsolateral transverse rows consisting of 3–4 ciliary tufts each (as in *M. xurxoi* sp. nov.). Both pygidial mid-dorsal longitudinal band of pores and paired ventral ciliary bundles are absent in the species.

Discussion

All species of *Mesonerilla* here described present very similar body plans, with nine trunk segments, compound chaetae and three antennae and club-shaped palps, while they differ mostly in the relative size of those appendages as well as in details of their ciliary patterns, glands and reproductive features.

The shape and relative size of the body appendages have been introduced as the main diagnostic feature in the genus. However, these features should be treated with caution since they vary during development from juvenile to adults, and appendages are easily lost during the extraction and fixation of collected specimens. The presence of specific glands is here used for the first time as a diagnostic feature of *M. laerkae* sp. nov., *M. katharinae* sp. nov. and *M. xurxoi* sp. nov., which present large and very conspicuous glands in the anterior segments, observable even in fixed material. The presence of a brooding hood has here been used to distinguish *M. intermedia* and *M. laerkae* sp. nov. from the remaining species of the genus, lacking a brooding hood. However, only sexually mature females may possess a brooding hood, so one has to be aware of having examined sexually mature females when interpreting the absence of this in a species. In other instances, ciliary patterns showed useful interspecific variation. However, the study of ciliary patterns requires SEM examination on carefully preserved specimens, which are often difficult to obtain given the low population densities of many of the species in most studied localities. Furthermore, possible intraspecific variation in body ciliation cannot be ruled out for species, where only few specimens have been observed. Nevertheless, all species described herein were with great support found to represent separate taxonomic units in the molecular phylogeny presented.

We speculate whether these difficulties in identifying useful characters for species identification may be the reason why the vast majority of records of *Mesonerilla* have previously been attributed to described species (Westheide 2008; Worsaae 2014). In fact, additional molecular distinct populations found in our samples were morphologically and virtually identical to previously described species, even after conducting detailed SEM and light microscopy investigations and for a few populations we did not have sufficient material for morphological examinations. These concerns the four species of *M.* cf. *luederitzi* from the Canary Islands and Bermuda and one species of *Mesonerilla* sp. from Roscoff, France. The lack of major differences in morphology also concerns the several cave species of the genus, which have always been found living in cave sediments of relatively similar properties as the habitats of their non-cave relatives (Worsaae et al. 2009). They do not present adaptations to swimming and suspension feeding in the water column of the caves, which is the case for other more radically different cave specialised meiofaunal annelids, including species of the nerillid genus *Speleonerilla* (Martínez et al. 2013, 2017; Worsaae et al. 2019). Less distinct shift of ecological niches, e.g. in sediment with different granulometry or levels of organic content, or across wider geographical distances with varying degree of isolation has not yet been examined in relation to the molecular diversification of *Mesonerilla*.

The lack of morphological changes has been long discussed in other meiofaunal groups, in which subsequent molecular studies have revealed a large diversity of cryptic species (Jörger et al. 2012; Martínez et al. 2015; Mills et al. 2017; Worsaae et al. 2018, 2019; Struck et al. 2018). All species of *Mesonerilla* lack pelagic larvae and are restricted to the interstitial environments, both traits being recognised as predictors for poor dispersal capabilities in most meiofaunal groups (Curini-Galletti et al. 2012). Though isolation may hence be an important driver for speciation in this group, it contradicts the 'everything is everywhere' hypothesis (Fenchel and Finlay 2004), which has been highly debated for meiofauna (Fontaneto 2011; Curini-Galletti et al. 2012). This again highlights the necessity of more comprehensive population genetic analyses to fully understand the diversity, distribution and evolutionary history of this genus. Moreover, several of both non-cryptic and cryptic species are found in the same area, which underlines our apparent lack of understanding of diverging adaptations to the environment in these minute and morphologically relatively similar species.

Acknowledgements First of all, we would like to thank Christopher Laumer for collecting and photographing the specimens of the new species *M. laerkae* and Greg Rouse for collecting some of the examined material of *M. intermedia*. We greatly acknowledge the many colleagues and students who have helped over more than 10 years of specimen collection for this study, during trips arranged by KW and AM. We are grateful to Elena Mateo and Leopoldo Moro for assistance with obtaining the permissions to sample in Lanzarote, as well as to divers Luis E. Cañadas, Enrique Domínguez, Carola D. Jorge, Ralf Schoenemark and a larger group of international students and colleagues in helping us collect and sort out the animals during the First International Workshop to Marine and Anchialine Meiofauna, Lanzarote 2011. The workshop was funded by Consejería de Medio Ambiente del Cabildo de Lanzarote and Reserva de la Biosfera. We thank Thomas M Iliffe, Terence Tysall, Tim Rozzi and Jill Heinerth for collecting samples from Montaña de Arena in 2008, as well as to Jorge Núñez Fraga for the donation of his material from Los Jameos del Agua. Finally, we are also grateful for the invitation to participate in trips organised by our colleagues Jon Norenburg (to STRI, Panamá), Greg Rouse (to the Great Barrier Reef, Australia), Marco Curini-Galletti (to Sardinia, Italy) and Maikon Di Domenico (to Napoli, Italy).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

Data availability All data generated or analysed during this study are included in this published article.

References

Bailey-Brock JH (1999) Nerillidae of Hawai’i: two new records of interstitial polychaetes. Pac Sci 53:299–304

Besteiro C, Núñez J, Martínez A (2012) Familia Nerillidae Levinsen, 1883 In *Annelida Polychaeta* III. Parapar J, Alós C, Núñez J, Moreira J, López E, Aguirrezabalaga F, Besteiro C, Martínez. *A. fauna Ibérica* vol. 36. MA Ramos et al. (Eds.). Museo Nacional de Ciencias Naturales. CSIC. Madrid:335–345

Curini-Galletti M, Artois T, Delogu V, De Smet WH, Fontaneto D, Jondelius U, Leasi F, Martínez A, Meyer-Wachsmuth I, Nilsson KS, Tongiorgi P, Worsaae K, Todaro MA (2012) Patterns of diversity in soft-bodied meiofauna: dispersal ability and body size matter. PLoS One 7(3):e33801

Di Domenico M, Martínez A, Lana PC, Worsaae K (2014) Molecular and morphological phylogeny of Saccocirridae (Annelida) reveals two cosmopolitan clades with specific habitat preferences. Mol Phylogenet Evol 75:202–218

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39(4):783–791

Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. BioScience 54:777

Fontaneto D (2011) Biogeography of microscopic organisms: is everything small everywhere? Cambridge University Press

Fransen ME (1980) Ultrastructure of coelomic organization in annelids. Zoomorphologie 95:235–249

Fransen ME (1983) Fine structure of the brooding apparatus of the Archiannelid *Mesonerilla intermedia*: maternal connections to brooded eggs. Trans Am Microsc Soc 102:25–37

García-Valdecasas A (1985) Estudio faunístico de la cueva submarina "Túnel de la Atlántida", Jameos del Agua, Lanzarote. Nat Hisp 27: 1–56

Gobert S, Reygel P, Artois T (2019) Schizorhynchia (Platyhelminthes Rhabdocoela) of Lanzarote (Canary Islands), with the description of eight new species. Mar Biodivers 49(5) https://doi.org/10.1007/s12526-017-0736-x

Higgins RP, Thiel H (1988) Introduction to the study of Meiofauna. Smithsonian Institution Press, Washington, DC 488 pages

Jörger KM, Norenburg JL, Wilson NG, Schrödl M (2012) Barcoding against a paradox? Combined molecular species delineations reveal multiple cryptic lineages in elusive meiofaunal sea slugs. BMC Evol Biol 12:245

Jouin C (1963) *Mesonerilla biantennata* n. sp. nouvelle Archiannélide Nerillidae de la region de Roscoff. CR Acad Sci (Paris) D 257: 4057–4060

Jouin C (1968) Sexualité et biologie de la reproduction chez *Mesonerilla* Remane et *Meganerilla* Boaden (Archiannélides, Nerillidae). Cah Biol Mar 6:31–52

Jouin C (1970) Archiannélides interstitielles de Nouvelle- Calédonie. Editions de la Fondation Singer-Polignac 4:149–167

Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. Brief Bioinform 9(4):286–298

Katoh K, Kuma KI, TohH MT (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Res 33(2): 511–518

Katoh K, Asimenos G, Toh H (2010) Multiple alignment of DNA sequences with MAFFT. In: Posada D (ed) Bioinformatics for DNA sequence analysis. Methods in molecular biology (methods and protocols) 537. Humana, New York, pp 39–64

Kerbl A, Bekkouche N, Worsaae K (2015) Detailed reconstruction of the nervous and muscular system of Lobatocerebridae with an evaluation of its annelid affinity. BMC Evol Biol 15:277

Lévi C (1953) Archiannélides Nerillidae de la region de Roscoff. Arch Zool Exp Gén 90:64–70

Levinsen GMR (1883) Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. Første Halvdel. Vid Medd Dansk Naturh For

Martínez A, Palmero AM, Brito MC, Núñez J, Worsaae K (2009) Anchialine fauna of the Corona lava tube (Lanzarote, Canary Islands): diversity, endemism and distribution. Mar Biodivers 39: 169–187

Martínez A, Di Domenico M, Leasi F, Curini-Galletti M, Todaro MA, Dal Zotto M, Artois T, Norenburg J, Jörger KM, Núñez J, Fontaneto D, Worsaae K (2019) Patterns of diversity and endemismof soft-bodied meiofauna in an oceanic island, Lanzarote, Canary Islands. Mar Biodivers 49(5). https://doi.org/10.1007/s12526-019-01007-0

Martínez A, Di Domenico M, Jörger K, Norenburg J, Worsaae K (2013) Description of three new species of *Protodrilus* (Annelida, Protodrilidae) from Central America. Mar Biol Res 9(7):676–691

Martínez A, Di Domenico M, Rouse GW, Worsaae K (2015) Phylogeny of Protodrilidae (Annelida) inferred by total evidence analyses. Cladistics 31:250–276

Martínez A, Gonzalez BC, Núñez J, Wilkens H, Oromí P, Iliffe TM, Worsaae K (2016) Guide to the anchialine ecosystems of Los Jameos del Agua and Túnel de la Atlántida. Medio Ambiente, Cabildo de Lanzarote, Arrecife, Lanzarote, Spain, 310 pages, ISBN-13: 978-84-95938-92-3

Martínez A, Kvindebjerg K, Iliffe TM, Worsaae K (2017) Evolution of cave suspension feeding in Protodrilidae (Annelida). Zool Scr 46(2): 214–226

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Gateway Computing Environments Workshop (GCE)

Mills S, Alcántara-Rodríguez JA, Ciros-Pérez J et al (2017) Fifteen species in one: deciphering the *Brachionus plicatilis* species complex (Rotifera, Monogononta) through DNA taxonomy. Hydrobiologia 796:39–58

Müller MCM (1999) Das Nervensystem der Polychaeten: Immunohistochemische Untersuchungen an ausgewählten Taxa. PhD thesis, University of Osnabrück: 402 pages

Núñez J, Ocaña Ó, Brito MC (1997) Two new species (Polychaeta: Fauveliopsidae and Nerillidae) and other polychaetes from the marine lagoon cave of Jameos del Agua, Lanzarote (Canary Islands). Bull Mar Sci 60(2):252–260

Posada D (2008) jModelTest: phylogenetic model averaging. Mol Biol Evol 25(7):1253–1256

Posada D, Buckley TR (2004) Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. Syst Biol 53(5): 793–808

Rambaut A, Drummond AJ (2007) Tracer v1. 4: MCMC trace analyses tool. In http://tree.bio.ed.ac.uk/software/tracer. Accessed 19 Dec 2016

Remane A (1949) Archianneliden der Familie Nerillidae aus Südwest-Afrika. Kiel Meeresfors 6:45–50

Riser NW (1988) Morphology of a new species of Nerillid Polychaete from the north shore of Massachusetts Bay, U.S.A. Trans Am Microsc Soc 107:171–179

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12):1572–1574

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21):2688–2690

Struck TH, Feder JL, Bendiksby M, Birkeland S, Cerca J, Gusarov VI, Kistenich S, Larsson KH, Liow LH, Nowak MD, Stedje B, Bachmann L, Dimitrov D (2018) Finding evolutionary processes hidden in cryptic species. Trends Ecol Evol 33(3):153–163

Swedmark B (1959) Archiannélides Nerillidae des côtes du Finistère. Arch Zool Exp Gén 98:26–42

Westheide W (2008) Polychaetes: Interstitial Families. Synopsis of the British Fauna (New Series), 44 (second edition). Field Studies Council: Shrewsbury, UK. ISBN 978–1–85153-271-1. VII, 169 pp

Westheide W, Riser NW (1983) Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n. gen., n. sp. (Annelida). Zoomorphology 103:67–87

Wilke U (1953) *Mesonerilla intermedia* nov. sp., ein neuer Archiannelide aus dem Golf von Neapel. Zool Anz 150:211–215

Wilkens H, Iliffe TM, Oromí P, Martínez A, Tysall TN, Koenemann S (2009) The Corona lava tube, Lanzarote: geology, habitat diversity and biogeography. Mar Biodivers 39(3):155–167

Worsaae K (2005a) Systematics of Nerillidae (Polychaeta, Annelida). Meiofauna Mar 14:49–74

Worsaae K (2005b) Phylogeny of Nerillidae (Polychaeta, Annelida) as inferred from combined 18S rDNA and morphological data. Cladistics 21:143–162

Worsaae K (2014) Nerillidae Levinsen, 1883. In: Beutel RG, Kristensen NP, Leschen R, Purschke W, Westheide W, Zachos F (eds) Handbook of Zoology online. Walter de Gruyter, Berlin

Worsaae K, Kristensen RM (2005) Evolution of interstitial Polychaeta (Annelida). Hydrobiol 535:319–340

Worsaae K, Müller MCM (2004) Nephridial and gonoduct distribution patterns in Nerillidae (Annelida: Polychaeta) examined by tubulin staining and cLSM. J Morph 261:259–269

Worsaae K, Rouse GW (2009) *Mesonerilla neridae* sp. nov. (Nerillidae): first meiofaunal annelid from deep-sea hydrothermal vents. Zoosymposia 2:297–303

Worsaae K, Martínez A, Núñez J (2009) Nerillidae (Annelida) from the Corona lava tube, Lanzarote with description of *Meganerilla cesari* n. sp. Mar Biodivers 39:195–207

Worsaae K, Gonzalez BC, Kerbl A, Nielsen SH, Jørgensen JT, Armenteros M, Iliffe TM, Martínez A (2019). Diversity and evolution of the stygobitic *Speleonerilla* nom. nov. (Nerillidae, Annelida) with description of three new species from anchialine caves in the Caribbean and Lanzarote. Mar Biodivers 49(5) https://doi.org/10.1007/s12526-018-0906-5

Worsaae K, Giribet G, Martínez A (2018) The role of progenesis in the diversification of the interstitial annelid lineage Psammodrilidae. Invert Syst 32:774–793