

Nematode succession at deep-sea hydrothermal vents after a recent volcanic eruption with the description of two dominant species

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Abstract Nematodes are very common in the deep sea and are an important component of deep-sea hydrothermal vent communities. In early 2006, the eruption of the underwater volcano at 9°50'N East Pacific Rise wiped out almost the entire faunal communities of the area. This provided us with the opportunity to study nematode primary succession at vents as well as on adjacent seafloor basalt. Nematode abundance and richness were extremely low at all studied sites in late 2006 and 2007, and increased only slightly in 2009. Interestingly, the most abundant species during early succession were also prominent in this area prior to the eruption. Our results show that nematodes are extremely influenced by volcanic eruptions and need a long period of time to colonize the lava-flooded area in greater numbers and richness. We hypothesize that low food availability on the young bare basalt and harsh environmental conditions at early succession vent sites might hinder a more successful nematode establishment. In addition to the newly established active vent sites we also studied an inactive vent site that was not directly hit by the eruption but whose vent fluid had ceased after the eruption. At this inactive and older vent, diversity was also relatively low but was higher than at the younger, newly established sites. In addition to the ecological analyses, we here describe the two most abundant species found at inactive vents, namely *Neochromadora* aff. *poecilosoma* De Mann 1893 and *Linhomoeus caudipapillosus* sp. n.

Keywords Nematode · Diversity · Succession · Deep-sea hydrothermal vents · *Linhomoeus* · *Neochromadora*

Introduction

Nematodes are one of the most diverse and abundant meta-zoan taxa, occurring in terrestrial, freshwater and marine environments, from shallow waters to the deep sea (Giere 2009). A very high nematode diversity is found in deep-sea sediments. Other deep-sea settings such as vents, seeps or sea mounts harbor specific nematode assemblages and even increase the total deep-sea nematode diversity. However, many ecological deep-sea studies are at the genus level and/or the majority of the discovered new species remain undescribed (Miljutin et al. 2010; Vanreusel et al. 2010b, a).

Besides the rarity of nematode studies at the species level in the deep sea, also studies on different time scales are scarce, although it is known that diversity and species composition can dramatically change with time, especially when following a disturbance event. Several studies investigated for example the impact of deep-sea mining, and some of them considered the nematode fauna. In general, nematodes in deep-sea sediments are sensitive to disturbance (i.e. trawling, natural physical disturbance) and only recover slowly (Lamshead et al. 2001; Vopel and Thiel 2001; Miljutin et al. 2011). Diversity as well as abundance are usually lower in recently disturbed sites, and in one case even 26 years after trawling the nematode assemblage had not returned to its initial stage (Miljutin et al. 2011).

Deep-sea hydrothermal vents are one of the most extreme and disturbed environments on earth. They are found globally, but patchily distributed along mid-ocean ridges, back-arc basins, rifted arcs and submerged island arc volcanoes (Van Dover 2000). Vents are ephemeral since tectonic events and volcanic activities make them physically and temporally variable. The emerging hot hydrothermal vent fluids are enriched

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with toxic chemicals such as hydrogen sulfide and heavy metals and can change in intensity over time. Interestingly, striking spatial patterns of macrofauna assemblages along a gradient of hydrothermal fluid flux from high temperature communities at sulfide chimneys to diffuse flow are found. Frequent volcanic eruptions can destroy these faunal communities, followed by re-colonization and succession (Van Dover 2000).

At the East Pacific Rise (EPR) 9°50'N, one of the best studied vent regions with a fast spreading rate, a volcanic eruption occurred in 1991 and destroyed the established faunal communities (Haymon et al. 1991; Gregg et al. 1996; Shank et al. 1998). Long-term photo and video observations over a time course of 5 years revealed a rapid and sequential colonization of newly established vent sites from white bacterial mats, to the small tubeworm *Tevnia jerichonana*, to the giant tubeworm *Riftia pachyptila* and to the mussel *Bathymodiolus thermophilus*. In addition, ~3.5 years after the kill-off, about 88 % of associated mega- and large macrofauna species known to inhabit this region were found to have returned. The successional patterns of mega- and macrofauna are mostly explained as a response of species to changes in the composition of hydrothermal vent fluids (Shank et al. 1998), but also biological interactions and recruitment play important roles (e.g., Mullineaux et al. 2003, 2009).

While succession of large animals at vents is relatively well observed, we almost lack information on the associated meiofauna such as nematodes. Nematode studies at well-established vent sites at the 9°50'N EPR revealed that vents were characterized by low nematode diversity and high dominance of single species (Flint et al. 2006; Zekely et al. 2006a; Gollner et al. 2007, 2010). The two most dominant species of the region, *Thalassomonhystera fisheri* Zekely et al. 2006 and *Halomonhystera hickeyi* Zekely et al. 2006b, were described (Zekely et al. 2006b). The species richness was found to be inversely correlated to the intensity of toxic vent fluid emissions (Gollner et al. 2010). A study on different aged mussel beds (4 to >20 years), indicating late succession stages of vents, showed that nematodes were less abundant and diverse at younger sites (Copley et al. 2007).

In early 2006, another eruption, extending approximately >18 km in the axial summit trough (AST) and up to ~1 km off axis, struck the same region at the 9°50'N EPR (Tolstoy et al. 2006). Several research cruises in 2006, 2007 and 2009 made it possible to study the development of the region in great detail. Also this massive lava flooding killed almost the entire faunal communities living in the AST and gave us the opportunity to initiate this study on the nematode succession at deep-sea hydrothermal vents. Here we present the associated nematode assemblages from three newly established active vent sites (Tica, Sketchy, P-Vent) colonized by tubeworms (early stage of succession), but also

from an inactive vent site (East Wall) that was not flooded by lava, but whose megafauna (tubeworms, mussels) were found to be dead in 2006 because of the lack of vent fluids after the eruption. In addition, we observed nematode assemblages on the adjacent bare seafloor basalt next to the vent sites with no direct influence of vent fluids. We hypothesized that the nematode assemblages were strongly affected by the volcanic eruption and that abundance and richness increased with time after this disturbance. We assumed that generalists abundant in the region before the eruption were among the first colonizers after the eruption. We further hypothesize that different species are dominant at active and inactive vent sites. In addition, we describe two dominant nematode species in the region and discuss their occurrence.

Methods

Study area and site description

All study sites are located within the axial summit trough (AST) at the 9°50'N 104°17'W region on the East Pacific Rise (EPR) at ~2,500 m depth. The sites Sketchy (9°50.06' N, 104°17.44'W), P-Vent (9°50.27'N, 104°17.47'W), Tica (9°50.40'N, 104°17.50'W) and East Wall (9°50.55'N, 104°17.51'W) were chosen.

In late 2006, approximately 1 year after the eruption, Sketchy, P-Vent and Tica were already colonized by the small tubeworm *Tevnia jerichonana* and experienced maximal temperatures of up to 28 °C (measured by the submersible *Alvin* temperature probe). In late 2007, 2 years post eruption, at Sketchy vent flux had ceased and the vent site had become inactive (ambient temperature 2 °C, no vent fluid emissions). The sessile tubeworms, which are dependent on a sulfide supply for their diet, had died. At the active sites Tica and P-Vent, in addition to the tubeworm foundation species *T. jerichonana*, also the tubeworm *Riftia pachyptila* had begun to settle. Maximal temperatures at active sites ranged from 15 to 18 °C. In late 2009, 4 years post eruption, also at P-Vent tubeworms had died because of lack of vent fluids. At Tica, the only still active site, the giant tubeworm *R. pachyptila* had almost replaced the small tubeworm *T. jerichonana*, and temperatures ranged from 3 to 15 °C (Table 1).

Tubeworms and mussels colonized the site East Wall prior to the eruption. It was not directly affected by the eruption in 2006 (not covered with lava) but showed no vent fluid emissions (ambient temperature) from 2006 until 2009 (personal observation SG, MB). At East Wall, we studied nematodes associated with dead mussel and tubeworm aggregations, which were well visible as empty tubes and shells in 2006, but were almost completely degraded in 2009.

Table 1 Information on sampling time (years post eruption, year of recovery), number (no.) of experiments (sponges) analyzed per year and site (B4 1+2:1 sponge and 2 in situ collections), maximal measured temperature at site at recovery (in brackets: temp. measured at first deployment, *other two experiments experienced only 3 °C) and state of the site (v = active vent; iv = inactive vent; b = bare basalt; iv old = inactive vent old; b old = bare basalt old; old refers to the fact that the site East Wall was not hit by the volcanic eruption and thus is older than the other sites). Samples were obtained at vent sites Tica (TC), Sketchy (SK), P-Vent (PV), on bare basalt (B) and at the old vent site East Wall (EW), and on bare basalt in the vicinity of East Wall (B-EW). For each site and year mean nematode abundance (\pm SD), mean species richness (\pm SD), total species richness, total identified individuals (ind.) and mean relative species abundance (%) per sponge (\sim 64 cm²) are given. Genus abbreviations used: C. = *Cyatholaimidae*; H. = *Halomonhystera*; L. = *Linhomoeus*; N. = *Neochromadora*; P. = *Parapinnanema*; T. = *Thalassomonhystera*

	TC1	TC2	TC4	SK1	SK2	SK4	PV1	PV2	PV4	B1	B2	B4	EW1	EW2	EW4	B-EW1	B-EW2	B-EW4
Years post eruption	1	2	4	1	2	4	1	2	4	1	2	4	15+1	15+2	15+4	15+1	15+2	15+4
Year of recovery	2006	2007	2009	2006	2007	2009	2006	2007	2009	2006	2007	2009	2006	2007	2009	2006	2007	2009
No. of experiments	3	3	3	3	3	3	3	3	3	3	3	1+2	2	2	2	1	1	1
Max. temp. (°C)	16 (27)	15	19*	3 (12)	2	2	28 (27)	18	2	3	2	2	2	2	2	2	2	2
State	v	v	v	v	iv	iv	v	iv	iv	b	b	b	iv old	iv old	iv old	b old	b old	b old
Mean abundance	0±0	1.5±1	10.2±10.5	1±0.9	0.7±0.3	1.8±0.3	0±0	0±0	13.2±21.1	0.8±0.1	50.1±46.2	38.0±37.2	12.4±0.9	337±23	1,432±938	2.8	50.0	144.5
Mean species richness	0±0	1.7±0.6	2.3±0.6	0.7±0.6	0.3±0.6	1.3±0.6	0±0	0±0	1.3±0.6	1.3±0.6	1.3±1.2	2±0	3±0	4±0	9.5±4.9	2.0	5.0	17.0
Total species richness	0	3	4	1	1	2	0	0	2	2	2	3	3	5	14	2	5	17
Total identified individuals	0	9	61	6	1	11	0	0	79	11	387	224	99	372	383	11	200	196
Mean relative abundance (%)																		
<i>T. fisheri</i>	24			67	33					64	15	4	39	24	2	36	30	14
<i>N. aff. poecilosoma</i>	22	74				50						58	24	38	50	4	19	
<i>H. hickeyi</i>	47	15				26				17	31	4	25	14	2	36	5	30
Nematode juvenile	7	3			28				24	19	21	29	3	11	12	5	5	9
Monhysterid juvenile												5	9	12	1	27	53	12
<i>P. sp. 1</i>						64								0.3	28	2		
<i>L. caudipapillosus</i>		8				8										1		
<i>H. sp. nov. 2</i>																		4
<i>T. sp. nov. 6</i>																		3
<i>T. sp. nov. 9</i>																		3
<i>Leptolaimus sp. 1</i>																		3
<i>Microlaimus sp. 1</i>																		2
<i>Microlaimus/</i>																		2
<i>Aponema sp. 1</i>																		
<i>T. sp. nov. 11</i>																		
Monhysteridae/			1															
Xylyidae sp. 1																		
<i>H. sp. nov. 3</i>																		
<i>Anticomma sp. 1</i>														0.2	0.3			
<i>Chromadora (?) sp. 1</i>																		1
<i>Chromadorita sp. 1</i>																		1
<i>H. sp. nov. 4</i>																		1

Table 1 (continued)

	TC1	TC2	TC4	SK1	SK2	SK4	PV1	PV2	PV4	B1	B2	B4	EW1	EW2	EW4	B-EW1	B-EW2	B-EW4		
<i>Microloaimus</i> sp. 2																			1	
<i>Sphaerolaimus</i> sp. 1																				1
<i>T.</i> sp. nov. 10																				1
<i>T.</i> sp. nov. 7																				1
<i>T.</i> sp. nov. 8																				1
<i>Xyalidae</i> sp. 1																				1
<i>C.</i> sp. 1															0.3					
<i>C.</i> sp. 2															0.3					
<i>T.</i> sp. nov. 1															0.3					
<i>T.</i> sp. nov. 4															0.3					

In addition, we also sampled new bare basalt in close vicinity (1–5 m distance) to the newly established vents and old bare basalt adjacent to the East Wall site in the AST, with no direct influence of vent fluid emissions (Table 1, Fig. 1).

Sampling

In order to have a standardized area to compare communities of different sites and ages, we used artificial settlement devices, namely plastic kitchen sponges (referred to as “sponges”). Each single sponge consisted of a single 55-m-long and 1-mm-thin plastic thread woven to a loose net that was furled and fixed with a rubber band. The sponge

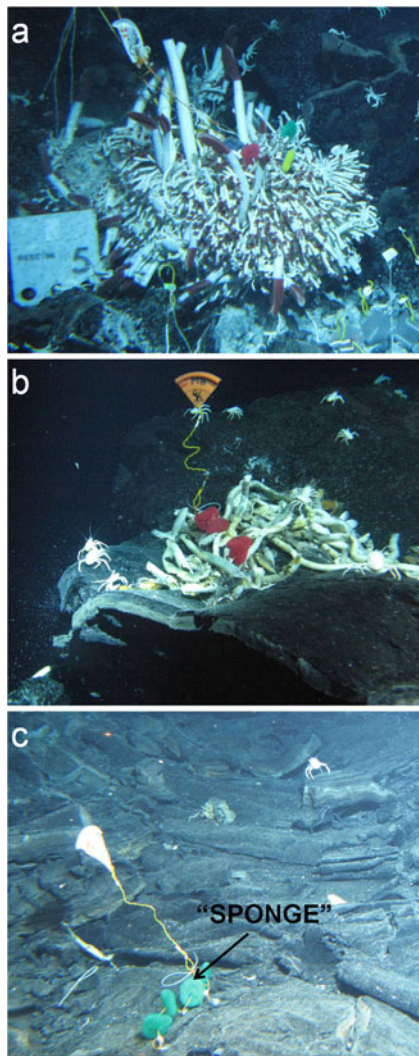


Fig. 1 Examples of habitat types analyzed in this study. **a** Newly established active vent site colonized by the tubeworm foundation species *Tevnia jerichonana* and a few large *Riftia pachyptila* tubeworms at P-Vent in 2007. **b** Old inactive vent at the site East Wall showing empty tubeworm tubes and mussel shells in 2007. **c** Newly bare basalt adjacent to the vent site Tica in 2007. In each habitat artificial settlement devices (referred to as “sponge;” see Fig. 1c) were deployed

had the shape of a cylinder (height ~3 cm) and a circular ground surface area of ~64 cm². The sponges were connected with a rope to markers and a small weight of lead, and were deployed within the vent foundation species (tubeworms, mussels) and on the bare basalt (Fig. 1). To enhance the sample area, we used two sponges per experiment at the Tica, P-Vent and Sketchy vent sites. Three experiments each (with two sponges) were recovered at Tica, P-Vent and Sketchy in November/December 2006 (sponges had been deployed for 1 month), in December 2007 (deployed ~1 year) and in October 2009 (deployed ~2 years). On the new bare basalt, next to the newly established vent sites, four sponges per experiment were used, and three experiments per year (2006, 2007) were recovered. In 2009, only one of these basalt experiments could be recovered, and we therefore took natural *in situ* community samples for comparison. At the East Wall site, two experiments (with four sponges) each could be recovered per year (2006, 2007, 2009). In addition, next to the site East Wall, we recovered one experiment per year (with four sponges) on old bare basalt. Thus, a total of 42 samples were compared in this study (Table 1).

To test the influence of deployment length of sponges we compared 1-week- and 1-month-long deployed sponges, which were recovered in late October and early December 2006 (total of 6 1-week deployments compared to 12 1-month deployments). We found that deployment length had no influence on nematode abundance and species richness (Table 2A). To test the suitability of the artificial colonization devices, we recovered natural *in situ* community samples from basalt and vents throughout the entire experimental program 1 to 4 years post eruption (one per site and habitat and year: total 24). No differences were found between treatments (Table 2A). Also the dominant species were similar in sponges and *in situ* community samples. Therefore, communities collected from sponges reflected the communities naturally colonizing the surfaces in the AST very well.

Artificial settlement devices were deployed and recovered by the submersible *Alvin* and were transported with the submersibles arm into sealed isolated plastic containers on the basket of *Alvin*. The natural *in situ* community samples were collected with the help of the submersibles arm (grabs) and had an average surface area of 208 cm². These samples were also put into isolated boxes. Onboard the research vessel RV *Atlantis*, samples were further processed. Each single sponge was carefully uncoiled and was placed into a container with 32 µm filtered freshwater with 37‰ isotonic MgCl to seawater for 10 min. This treatment relaxed the muscles of the fauna that had colonized the sponge, and the fauna could be washed off with 32 µm cold filtered seawater and sieved through a 32-µm and 1-mm net to separate the meio- from the macrofauna (Higgins and Thiel 1988). The

Table 2 *P*-values of the comparison of nematode abundance (Ab) and species richness (S) between different years, sites and habitat types performed with non-parametric Kruskal-Wallis tests and in case of significant differences (marked in bold) with post-hoc multiple comparisons. 2A CONTROL: Results of testing the influence of

deployment length of sponges (deployed 1 week and 1 month long) and of testing the suitability of the artificial colonization devices (comparison of sponges with *in situ* community collections). 2B SPONGE: Results of testing the influence of time, site and productivity state on nematode abundance and species richness in sponges

	Ab	S
2A CONTROL		
CONTROL deployment length		
Active vent: 1 week – 1 month	0.07	0.24
Bare basalt: 1 week – 1 month	0.51	0.82
CONTROL sponge, <i>in situ</i> community		
Active vent sponge 2006, <i>in situ</i> 2006	0.64	0.6
Active vent sponge 2007, <i>in situ</i> 2007	0.86	0.72
Bare basalt sponge 2006, <i>in situ</i> 2006	0.14	0.11
Bare basalt sponge 2007, <i>in situ</i> 2007	0.38	0.46
2B SPONGE	Ab	S
TIME comparison		
Active vent and time		
Tica 2006 - 2007 - 2009	0.03 (2006-2009:0.03)	0.03 (2006-2009: 0.05)
P-Vent 2006 - 2007	1	1
All active vent sites 2006 - 2007 - 2009	0.01 (06-09:0.02)	0.01 (06-09:0.03)
Inactive vent and time		
Sketchy 2007 - 2009	0.04	0.1
East Wall 2006 - 2007 - 2009	0.1	0.09
Bare basalt and time		
Bare basalt 2006 - 2007 - 2007	0.29	0.35
SITE comparison		
Active vent and site		
Tica 2006 - P-Vent 2006 - Skechty 2006	0.1	0.1
Tica 2007 - P-Vent 2007	0.04	0.04
PRODUCTIVITY comparison		
Active vent (v)- bare basalt (b) - inactive vent (iv)- old inactive vent (iv old)		
v 2006 - b 2006 – iv old 2006	0.03 (v-iv old: 0.05)	0.01 (v-iv old: 0.03)
v 2007 - b 2007 - iv 2007 – iv old 2007	0.08	0.09
v 2009 - b 2009 - iv 2009 – iv old 2009	0.04 (iv-iv old:0.05)	0.02 (iv-iv old:0.04)

procedure was repeated three times to recover all the animals. Also *in situ* community collections were treated the same way as the sponges. Afterwards, the associated fauna of each sample were fixed in 4 % buffered formaldehyde and shipped to Austria or Germany for further processing in the laboratory. Data on other meiofauna than nematodes and on macrofauna will be presented in another manuscript (Gollner et al. in prep).

Faunal analyses

In the laboratory, all nematodes were counted under a binocular using a magnification of up to 10×6 . In 6 out of 72 samples total abundances were very high and were estimated based on the volume of randomly analyzed subsamples. We here present nematode abundance data per sponge based on the circular surface area of $\sim 64 \text{ cm}^2$. The surface area of

in situ community collections was estimated by covering the sampled basalt with aluminum foil, photographing it and calculating its area with the AnalySIS program. Nematode abundance of these *in situ* collections was standardized to 64 cm^2 to allow a rough comparison to the artificial settlement devices.

All or at least 200 randomly picked nematodes per sample were identified to the lowest possible level. Specimens were sorted and transferred into a glycerin-water mixture. After slow evaporation, nematodes were mounted on slides in pure glycerin (Higgins and Thiel 1988). Specimens were studied using a Leica DM2500 and/or a Leica DM750 microscope equipped with a digital camera. Species were discriminated on the morpho-species level in order to reveal the diversity of the nematode assemblages.

Species richness (S) was calculated from quantitative species abundance data by DIVERSE subroutines in the

PRIMER version 5 package (Clarke and Gorley 2001). To compare the species richness and the abundance of different sites and years, non-parametric Kruskal-Wallis tests were carried out using the program STATISTICA. In case of significant differences, post-hoc multiple comparison z and p values (2-tailed) were obtained. Due to the high number of samples with no nematodes (see results), we did not calculate Shannon diversity index (H'_{\log_e}) and Pielou's evenness index, but instead describe the species dominance (relative abundance %) in more detail. We performed similarity percentage (SIMPER) analyses, analyses of similarity (ANOSIM) and multi-dimensional scaling (MDS), but due to the high number of samples with no nematodes and the high dominance of the very few species present in other samples, these analyses did not add any substantial information other than that already gained by analyzing the species abundance. We therefore did not present these data.

Species description

The two most abundant species from the ecological analyses were selected for the species description. For the species description we used the slides we already had prepared for the ecological analyses. Measurements, drawings and photographs were made with a Leica DM2500 interference contrast microscope equipped with a camera lucida and a digital camera. All type specimens were deposited in the Senckenberg Museum, Frankfurt am Main, Germany.

Abbreviations used are: A, body length divided by maximum body diameter; Amph.diam., body diameter at the level of the amphideal fovea, in μm ; Amph.dist., distance from the cephalic apex to the anterior rim of the amphid; Amph.width, width of the amphideal fovea, in μm ; An.diam., anal body diameter, in μm ; b, body length divided by pharyngeal length; c, body length divided by tail length; c.b.d., corresponding body diameter; Card.diam., body diameter at the level of cardia, in μm ; Ceph.setae, length of cephalic setae, in μm ; Ceph.set.diam, body diameter at the level of cephalic setae, in μm ; Cerv.setae, length of the somatic setae situated on the level of the pharynx, in μm ; Cheil.length, length of the cheilostoma, in μm ; Cheil.width, width of the cheilostoma, in μm ; Dorsal tooth, length of the dorsal tooth, in μm ; Excr.pore, distance from the anterior end to the secretory-excretory pore, in μm ; f, female; Gonad.l., length of the gonad, in μm ; Guber.apoph.l., length of the apophysis of the gubernaculum, in μm ; Gubern.l., length of the gubernaculum, in μm ; L, body length; m, male; Male gonad l., length of the male gonad, in μm ; Max.b.diam., maximal body diameter, in μm ; Midb.diam., midbody diameter, in μm ; Nerve ring, distance from the anterior end to the nerve ring, in μm ; Nerv.r.diam., body diameter on the level of the nerve ring, in μm ; Out.lab.setae, length of the outer labial setae, in μm ;

Phar.l., length of pharynx, in μm ; Pharyng.length, length of the pharyngostoma, in μm ; Pharyng.width, width of pharyngostoma, in μm ; Repr.sys. %, length of the reproductive system as a percentage of total body length, in %; Somat.setae, length of the somatic setae, in μm ; Spic.ch.l., spicule's length along the arch, in μm ; Spic.arc.l., spicule's length along the chord, in μm ; Suppl.num., number of supplements, in μm ; Suppl.size, size of supplement, in μm ; Suppl.dist., distance between supplements, in μm ; Tail.l., length of the tail, in μm ; Tail setae, length of tail setae, in μm ; Ventral tooth, length of the ventral tooth, in μm ; Vulv.dist, distance of vulva from anterior end, in μm ; V%, distance of vulva from anterior end as percentage of body length, in %.

Results

Species descriptions

Neochromadora aff. poecilosoma (De Man 1893); Micoletzky 1924 (Figs. 2, 3 and 4; Table 3)

Material 6 males, 4 females

Locality 9°50'N East Pacific Rise (EPR), bare basalt adjacent to the site Tica (9°50.40'N, 104°17.50'W), collected at 2,510 m depth in 2009, *Alvin* dive no. 4,575 (sponge sample no. RW 84)

Description

Main measurements: Males: L = 1,775–2,122; a = 38.4–39.0; b = 7.1–9.6; 6.9–12.3. Females: L = 1,913–2,069; a = 33.4–41; b = 7.7–9.5; c = 7.4–9.1; V = 44–46.

Body slender, cylindrical with slightly narrowed anterior end and short conical tail. Somatic setae sparse, 5–8 μm length. Cuticle densely dotted, with lateral fields, heterogenic along the body. At the level of the anterior part of the pharynx and from the preanal region to the caudal tip, dots large, round or square in form, arranged very tightly, sometimes fused together. At this part of the body, the lateral field looks like a narrow longitudinal space without dots. It makes an impression of a long, narrow, lateral furrow. At the rest of the body, dots transform into short longitudinal rods. Here the lateral fields look like a row of shorter bars (about 10 shorter bars) and a narrow lateral ridge in the middle of every lateral field. Cuticle ca. 0.7–1 μm thick on the level of cephalic setae, 2–3 μm thick on the level of pharynx, 1–2 μm thick on the level of the midbody and 2–2.5 μm thick on the level of the tail. Only four cephalic setae are visible, being 10–12 μm long in males and 10–14 μm long in females. Amphideal fovea in shape of transversal slit, 7–9 μm wide in males and 8.9–9 μm wide in females, situated 3–4 μm behind the anterior end in males and 2.5–

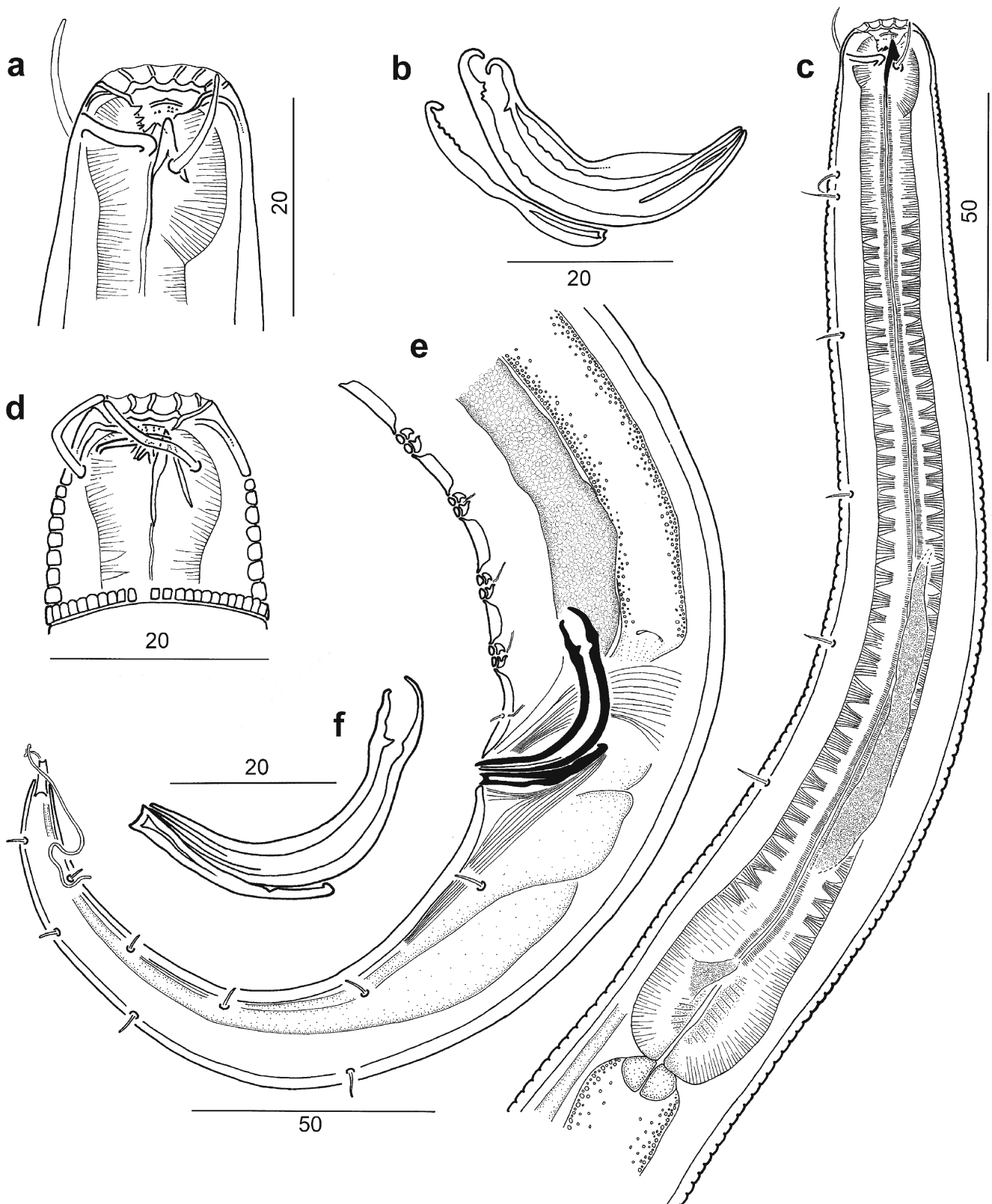


Fig. 2 *Neochromadora* aff. *poecilosoma*, **a** male, specimen no. 1, head region; **b** male, specimen no. 2; **c** male, no. 1, anterior end; **d** female, specimen no. 6; **e** male, no. 1, posterior end; **f** male, no. 1, spicule. Scale in μm

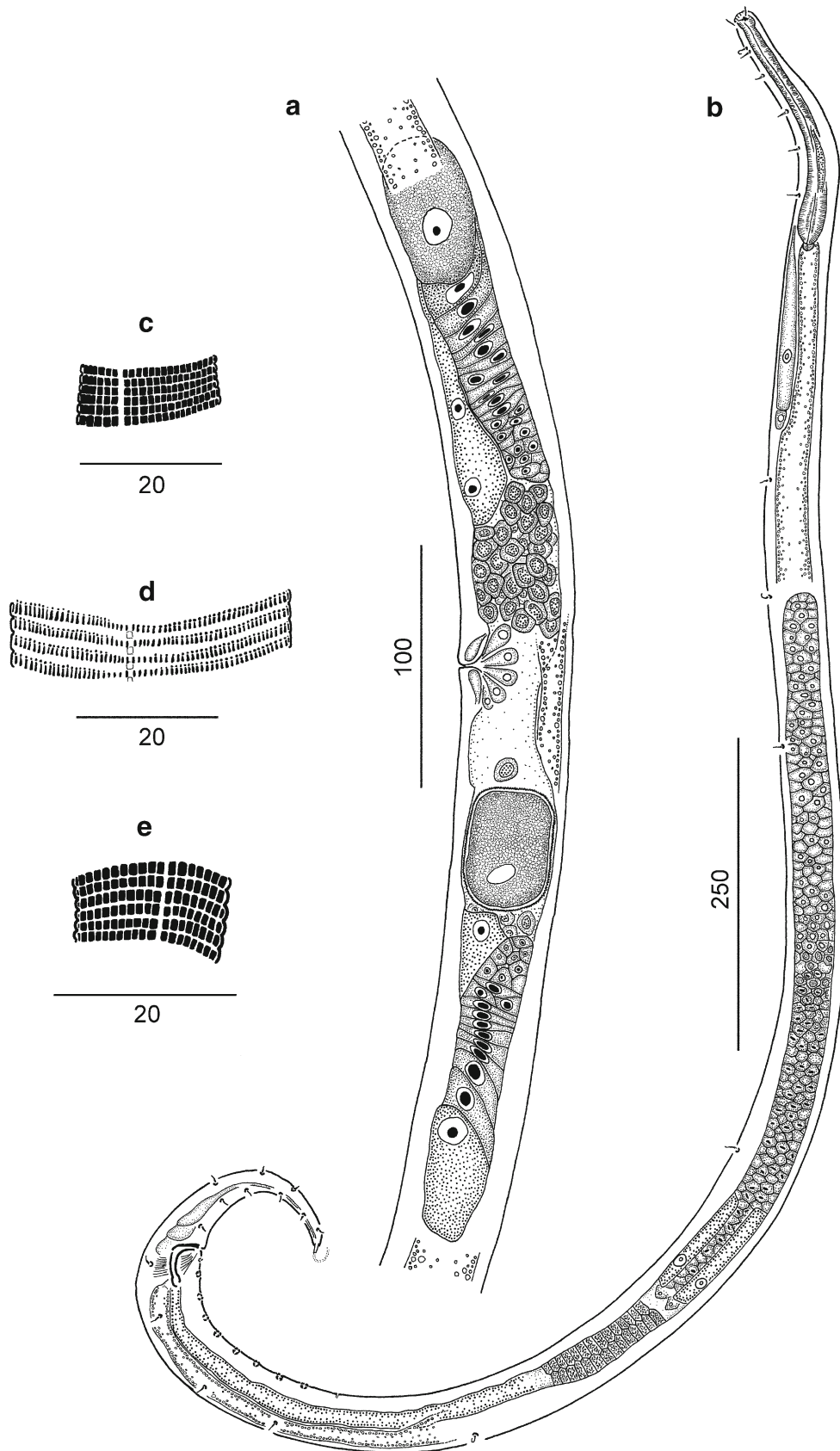


Fig. 3 *Neochromadora* aff. *poecilosoma*, a female, specimen no.7, reproductive system; **b** female, no. 7 total view; **c** male, no. 1, cuticle on the level of the pharynx; **d** male, no. 1, cuticle on the level of the midbody; **e** male, no.1, cuticle on the level of the tail. Scale in μm

4 μm in females. Stoma consisting of wide, cup-shaped cheilostoma and narrow funnel-shaped pharyngostoma. Cheilostoma ca. 5–6 μm long, 4–5 μm wide, possessing 12 well-developed rugae. Pharyngostoma 6–7 μm long with thick cuticular walls, containing three sclerotized onchia and numerous rows of denticles. One large hollow dorsal onchium ca. 5–7 μm long, two small subventral onchia ca. 1.5–3 μm long visible in most specimens. Pharyngeal musculature swollen around the stoma; elsewhere the pharynx is almost cylindrical with a slightly enlarged posterior part, not developing a bulb. Several pharyngeal glands visible in posterior half of pharynx. Cardia small, roundish. Renetta large. Its body is situated behind the cardia. Secretory-excretory pore invisible. Tail conical, short. Males possessing shorter tails than females ($c = 10.1\text{--}12.3$ versus $c = 6.9\text{--}9.1$, respectively). Three large cellular bodies of caudal glands visible at the level of the anus and posterior to it.

Male reproductive system monorchic, occupying 0.55–0.72 of pre-anal body length. Testis directed anterior, outstretched, lying to the right of the intestine. At the level of the posterior part of the testis, walls of the testis having three giant cells containing numerous granules and well visible nuclei. Spicules curved, with cuticular sculpture inside. Gubernaculum long, rod-shaped, with a bifurcated distal end and hook-like proximal end. One short (ca. 3 μm long) precloacal seta and 7–9 conspicuous, complex-looking cup-shaped precloacal supplements visible. The distance between supplements increasing toward the anterior end. Distance between the two posteriormost supplements 9–14 μm and between the two anteriormost ones 13–23 μm . The diameter of supplements increasing toward the anus from 5.0–5.5 μm (for the anteriormost one) to 5.5–7.0 μm (for the posteriormost one).

Female reproductive system consisting of two antidromous, uniformly sized ovaries (anterior ovary lying to the right of the intestine and posterior one lying to the left of the intestine), oviducts and long uterus. Most females have mature oocytes with maximum size about $83 \times 40 \mu\text{m}$ in their ovaries. Oviducts detached from the uterus by constriction. Walls of every oviduct have three very large cells with granular content (these cells resemble three large granular cells in posterior parts of testes in males). Borders of these cells are invisible, but nuclei well discernible. In young females, these cells are also well visible, but without granules inside. Uterus (usually) with one or two fertilized eggs and numerous roundish spermatozoa 10–13 μm in diameter. Eggs covered by a thick knobby shell. Numerous small vulvar glands surrounding the vulva are visible.

Remarks

The found individuals resembled *Neochromadora poecilosoma*. The only differences we could find were the size of

Fig. 4 *Neochromadora* aff. *poecilosoma*, micrographs. **a–c** heads; **d** posterior end of male (supplements marked with arrows); **e** supplement; **f** male spicule region; **g** giant cell of spermaduct wall with granular content; **h** oocyte; **i** cuticle surface at pharyngeal region; **j, k** cuticle surface at midbody (lateral ridge visible); **l** cuticle surface at postcloacal region. Scale bars: **a–c, f–j, l** = 20 μm ; **d, k** = 50 μm ; **e** = 10 μm . Abbreviations: *a.* amphid; *c.s.* cephalic seta; *f.d.* field of denticles in cheilostoma; *on.* onchium; *r.* ruga

the precloacal supplements and their position. Type specimens had relatively small and simple cup-shaped supplements at equal distance to each other, but our individuals possessed prominent and complex ones, and the distance between supplements increased toward the anterior end. Since the species was described in 1893, these observed differences could be explained by the better optical microscopy conditions. The species' geographical distribution is cosmopolitan, and it is found in shallow waters (Gerlach and Riemann 1973) and sometimes in sulfidic sediments (Wieser and Kanwisher 1961). It was also observed at shallow vents in 100-m depth on the subpolar Mid-Atlantic ridge (Fricke et al. 1989), and in a previous study at deep-sea hydrothermal vents at the 9°N East Pacific Rise were the species called *Chromadorida* sp. 1 (Gollner et al. 2010).

Linhomoeus caudipapillosus sp. n. (Figs. 5, 6 and 7; Table 4)

Type material Collection no. SMF 16966–16975. Holotype: male. Paratypes: 4 males, 5 females.

Type locality 9°50'N East Pacific Rise (EPR), East Wall site (9°50.55'N, 104°17.51'W), inactive vent covered by dead tubeworms, collected at 2,500 m depth in 2009, *Alvin* dive no. 4580 (sponge sample no. RW 96; holotype, paratypes 1–6 and 8–9) and bare basalt adjacent to the Tica site (9°50.45'N, 104°17.49'W), collected at 2,500 m depth in 2003, *Alvin* dive no. 3952 (sample B1, see Gollner et al. 2010 Table 1; paratype 7)

Etymology Latin *caudipapillosus* (= bearing papillae on the tail)

Description

Main measurements: Males: $L = 2,283\text{--}2,704$; $a = 78.7\text{--}91.5$; $b = 14.8\text{--}17.2$; $c = 19.3\text{--}25.7$. Females: $L = 1,949\text{--}2,829$; $a = 62.4\text{--}89$; $b = 12.3\text{--}17.6$; $c = 18.9\text{--}22.3$; $V = 47\text{--}53$ %.

Body slender, cylindrical, very long with slightly narrowed anterior end and short tail in shape of a truncated cone. Head truncated and not offset from the body. Cuticle damaged in most individuals. Cuticle finely striated, bearing (presumably) lateral ridges (not clear because of bad condition of the cuticle), 1–1.5 μm thick. Somatic seta scar, short (about 6–7 μm long in holotype), found only at cervical and tail regions. One preanal seta 2 μm long visible in holotype. Inner labial sensilla invisible. Six outer labial setae 3–5 μm long and four cephalic

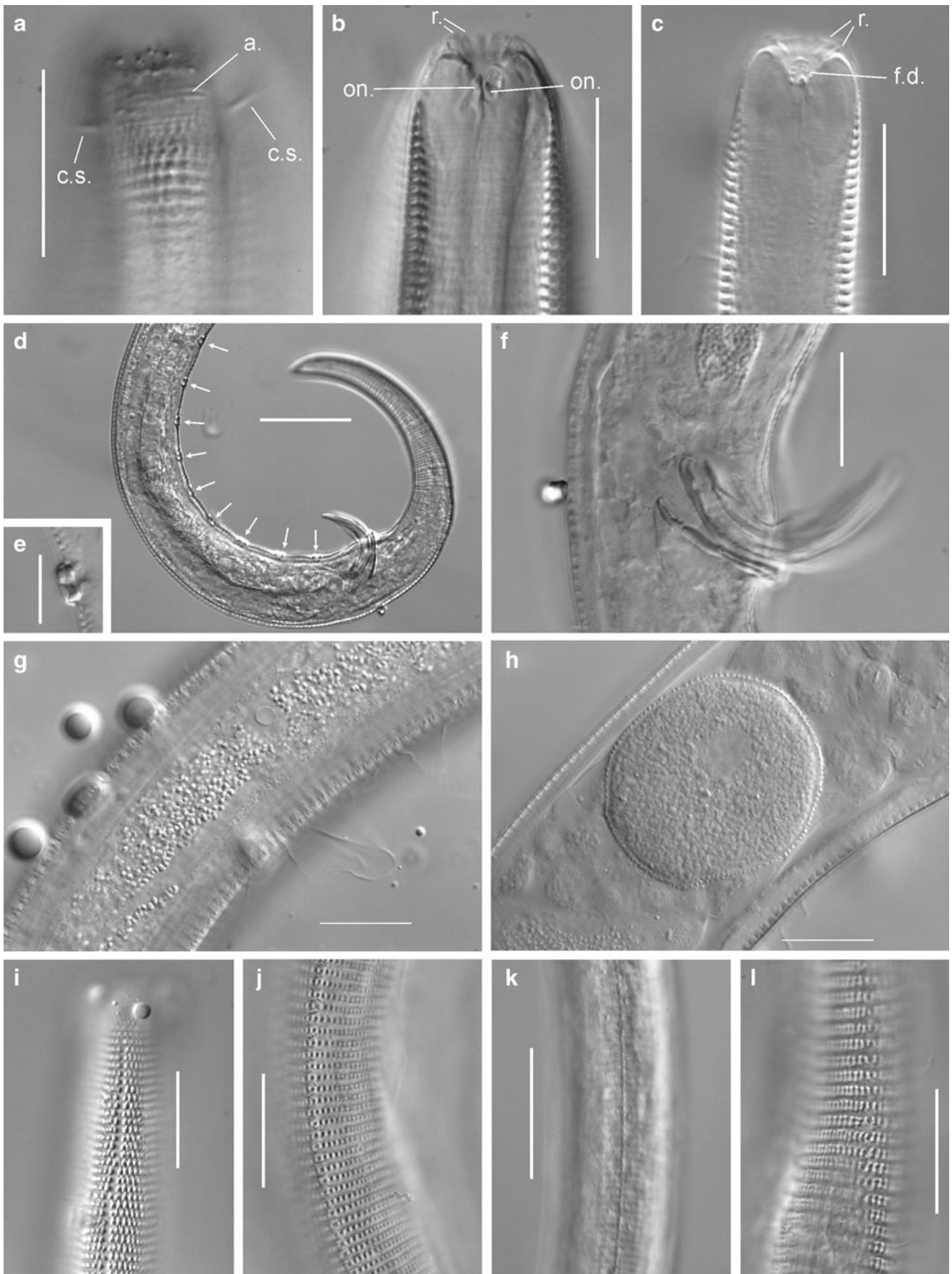


Table 3 *Neochromadora* aff. *poecilosoma*. Measurements (in μm) and body indices

Specimen no.	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
Sample Slide	RW 84 11-20	RW 84 31-40	RW 84 11-20	RW 84 11-20	RW 84 11-20	RW 84 31-40	RW 84 11-20	RW 84 11-20	RW 84 31-40	RW 84 31-40
Gender	m	m	m	m	m	m	f	f	f	f
L	1882	2065	2122	1793	2051	1775	2069	1949	1935	1913
Amph.dist.	4	3.5	?	3.5	3	4	4	?	4	2.5
Phar.l.	232	223	220	232	232	250	218.5	232	252	210
Tail.l.	174	178	188	178	167	259	227.5	239	234	259
Vulv.dist.	-	-	-	-	-	834	923	892	883	847
Male gonad .l.	1173	1351	1342	1106	1039	-	-	-	-	-
Ceph.set.diam	15	17	16	16.5	16	16	16	17	18	15
Amph.diam.	14	15.5	15	15	14	15	13	15	16	13
Card.diam.	34	32	32	31	33	31	35	34	31	33
Midb.diam.	49	42	47	42	48	45	62	56	47	51
An.diam.	38	36.5	41	39	42	28	32	31	30	29
Max.b.diam.	49	42	47	42	48	46	62	56	47	51
Amph.width	8	7	9	?	9	8	8.5	?	9	9
Ceph.setae	11	10	12	11	11	12	10	14	11	11
Cerv.setae	6.5	7	8	7	7	5-6	10	6-10	5-7	6-7
Somat.setae	8	7	?	5-8	6.5	5	?	?	7	?
Tail setae	6	5.5	?	5	5-7	4	?	9	?	4-7
Stoma width	5	?	5	5	5	4	4	?	4.5	4
Cheil.length	6	5	6	5	5.5	5	6	?	5.5	6
Pharyng.length	7	6	6	5	6.5	6	6.5	?	6.5	6
Dorsal tooth	5.5	?	5.5	5.5	6	7	6	?	?	5
Ventral tooth	2	?	1.5	1.5	2	2.5	1.5	?	?	1.5
Spic.ch.l.	37	39	38	36	41	-	-	-	-	-
Spic.arc.l.	54	55	59	50	56	-	-	-	-	-
Gubern.l.	30	26	33	27	33	-	-	-	-	-
Suppl.num.	9+1	8+1	8+1	8+1	8+1	-	-	-	-	-
Suppl.size	5-6	5-5.5	5.5-7	5-6	6-7	-	-	-	-	-
Suppl.dist.	9-18	14-19	9-23	11-15	10-13	-	-	-	-	-
Egg size	-	-	-	-	-	49 × 37	48 × 44	53 × 46	50 × 38	52 × 40
a	38.4	49	45.1	42.7	42.7	39.4	33.4	34.8	41	37.5
b	8.1	9.3	9.6	7.7	8.8	7.1	9.5	8.4	7.7	9.1
c	10.8	11.6	11.3	10.1	12.3	6.9	9.1	8.1	8.3	7.4
V, %	-	-	-	-	-	47	45	46	46	44

setae 13–14 μm long in males and 12–16 μm long in females joined in one circle on the anteriormost part of the head. Subcephalic setae absent. Amphideal fovea circular with very thick cuticular rim. Central spot of amphid well visible. Anterior rim of amphidial fovea situated 10–14 μm (1.3–1.7 c.b.d.) in males and 12–17 μm (1.3–1.8 c.b.d.) in females from anterior end of body. Cheilostoma narrow and short, with thick cuticular walls, 2–3 μm in length and 2.5–3 μm in width. Pharyngostoma cup-shaped, slightly asymmetrical, 3–5 μm in length and 6–7.5 μm in width with thick cuticular walls. Numerous denticles situated in the posterior part of the pharyngostoma. An anteriorly notched cuticular ring surrounding the cheilostoma. Pharynx slender, muscular, with slightly swollen anteriormost and gradually widening posterior parts, without developed bulb. Posteriormost part of pharynx containing plasmatic interruptions. Cardia external, elongate. Its length 33–40 μm in males and 39–43 μm in females. Excretory-secretory pore of the ventral gland situated just posterior to the nerve ring. Length of ventral gland 99 μm in the holotype. In several individuals, intestinal lumen containing numerous thread-like structures resembling bacteria cells. Intestine of the specimen found on bare basalt containing a huge cell resembling a foraminiferan.

Mail gonads paired. Anterior testis straight, posterior one reflexed, their position relative to intestine variable in different specimens. Spicules short, arcuate. Gubernaculum with prominent dorso-caudal apophysis. Two large subventral papillae lying on both sides of the cloacal opening. Three or four medioventral preanal supplementary papillae appearing as very minute tubercles. Supplements seen better in individuals with coiled tail. Several prominent rectal glands surrounding cloacal opening.

Ovaries paired, outstretched, their position relative to intestine variable in different specimens. The size of mature egg, found in paratype no. 10 $12.5 \times 16 \mu\text{m}$.

Tail in shape of truncated cone. Three caudal glands visible; 6–7 pairs of large papillae lying in two subventral rows on the tail of males present. Papillae consisting of wide conical basis and short setoid apical part.

Differential diagnosis

According to NeMys (Deprez et al. 2005) there are 14 valid *Linhomoeus* species. The new species differs considerably from other known *Linhomoeus* species by the presence of 6–7 pairs of prominent subventral papillae on the caudal region of males, precloacal supplements and two papillae on the level of the cloacal opening. Most other species have no similar structures.

Thirteen ventral stiff postanal setae were described in one of the late redescriptions (Wieser 1956) of *L. hirsutus* Bastian 1865, but the structure and locality of these setae differ considerably from the structure and locality of prominent papillae of *L. caudipapillosus* sp. n.. The new species can be

distinguished from *L. hirsutus* by its larger amphideal fovea (36–43 % of c.b.d. vs. 27 % of c.b.d.), its shorter tail ($c = 18.9\text{--}25.7$ vs. $c = 15\text{--}17$) and the absence of precloacal supplements and two subventral papillae at the level of cloacal opening.

L. elongatus Bastian 1865 (Wieser 1956) also possesses numerous long subventral setae, but these setae differ considerably from the papillae of *L. caudipapillosus* sp. n.. The new species also differs from *L. elongatus* by having a shorter body ($L = 1,949\text{--}2,829 \mu\text{m}$ vs. $L = 7,620 \mu\text{m}$) and the size of outer labial and cephalic setae (3–5 μm and 12–16 μm vs. 8–10 μm and 8–10 μm , respectively).

L. undulates Wieser 1959 possesses seven ventral post-cloacal papillae, each with a minute seta, on the tail of males. The shape of these structures is similar to the ones in *L. caudipapillosus* sp. n., but their quantity is higher (12 or 14, i.e. 6–7 pairs). In addition, the new species differs from *L. undulates* by having larger amphideal fovea (36–43 % of c.b.d. vs. 25 % of c.b.d.), a more slender body ($a = 62.4\text{--}91.5$ vs. $a = 46.6$), shorter cephalic setae (12–16 μm vs. 7.5 μm), and the absence of precloacal supplements and two subventral papillae at the level of the cloacal opening.

A small papilla inserts ventrally on the anterior cloacal lip of *L. gittingsi* Jensen 1986b, but this species possesses neither precloacal supplements nor subventral papillae on the caudal region of males. In addition, the new species is shorter ($L = 1,949\text{--}2,829 \mu\text{m}$ vs. $L = 4,243\text{--}5,523 \mu\text{m}$), and the amphideal fovea lies more distant from the anterior part of the body (12–17 μm vs. ca. 7 μm).

The measurements of *L. ponticus* Filipjev 1922 are very similar to the measurements of the new species, but *L. ponticus* was described based on only one female, and it was not possible to compare the most important features developed in males only. Therefore, we decided not to consider this species here.

Remarks

In a previous investigation at the 9°N East Pacific Rise the species was called *Monhystrid* sp. 2 (Gollner et al. 2010).

Nematode succession

Abundance

Nematode abundance was very low at all newly established vent sites. At Tica and P-Vent not a single nematode was found in 2006. Also at Sketchy abundance was extremely low in 2006 (mean 1 ind. 64 cm^{-2}) (Table 1). In 2007, at P-Vent still no nematodes were present, while at Tica on average 2 specimens per sponge were found. At Tica, the only still active vent site in 2009, there was a significant but low increase in abundance from 0 nematodes in 2006 to an average of 10 nematodes per sponge in 2009 (Tables 1, 2).

This increase in abundance over the time period of sampling was also observed when taking all active vent sites into account (Table 2).

In 2007 and 2009, abundances at new active sites were similarly low compared to the new inactive vent sites Sketchy and P-Vent (mean 1–13 ind. 64 cm⁻²), whose vent fluid emissions ceased in 2007 and 2009, respectively. Also, abundances on the new bare basalt were similarly low (mean 1–2 ind. 64 cm⁻²) to vents throughout the years regardless of vent activity. Only at East Wall, the inactive vent site that was not directly hit by the eruption, abundances were higher (mean ind. 64 cm⁻² in 2006: 12; in 2007: 337; in 2009: 1,432). At East Wall, abundance was higher than at new active vents in 2006 and higher compared to new inactive vents in 2009 (Tables 1, 2).

Species richness

Nematode species richness was extremely low at all new active vent sites, at new inactive vents sites and on newly established bare basalt (mean S: 0–2; total S per site and time: 0–4 from 2006 to 2009). In general, at active vents species richness slightly increased from 0 to 2 species from 2006 to 2009.

Only at East Wall, the site that was not directly flooded with lava, a few more species were present (mean S: 2006: 3; 2007: 4; 2009: 10). Richness was significantly higher compared to new active vents in 2006 and to new inactive vents in 2009. On the bare basalt next to East Wall (also not flooded with lava), richness was similar to values typical for the inactive vent site East Wall colonized by dead mussels and tubeworms (total S: 2006: 2 on basalt and 3 at an inactive vent; 2007: 5 and 5; 2009: 17 and 14) (Tables 1, 2).

Species dominance

The most dominant species at newly established vents and on bare basalt were *Halomonhystera hickeyi* Zekely 2006b and *Thalassomonhystera fisheri* Zekely 2006b in 2006 and 2007. In 2009, at the active vent site Tica, in addition to *H. hickeyi* also the two described species *Neochromadora* aff. *poecilosoma* and *Linhomoeus caudipapillosus* sp. n. occurred. At Sketchy (inactive in 2009), *Parapinnanema* sp.1 was dominant. At P-Vent (inactive in 2009), *N.* aff. *poecilosoma* and *H. hickeyi* were prominent. On the bare basalt *N.* aff. *poecilosoma*, *H. hickeyi*, and *T. fisheri* were most abundant (Table 1).

At the old inactive vent site East Wall, the species *N.* aff. *poecilosoma*, *H. hickeyi* and *T. fisheri* were about equally dominant in 2006. One year later, in addition *L. caudipapillosus* sp. n. and *Anticomma* sp.1 occurred, although in low relative abundance. In 2009, total richness increased to 14 species, but *N.* aff. *poecilosoma* (50 %) and *L.*

Fig. 5 *Linhomoeus caudipapillosus* sp. n., **a** male, holotype, anterior end; **b** male, holotype, head region; **c** male, holotype, spicule; **d** male, holotype, posterior end; **e** female, paratype no. 7; **f** male, paratype no. 4, spicule. Scale in μm

caudipapillosus sp. n. (28 %) clearly dominated the nematode communities. On the old bare basalt next to the inactive vent site at East Wall, similar species occurred, but *H. hickeyi* and *T. fisheri* were more abundant than *N.* aff. *poecilosoma* and *L. caudipapillosus* sp. n. (Table 1).

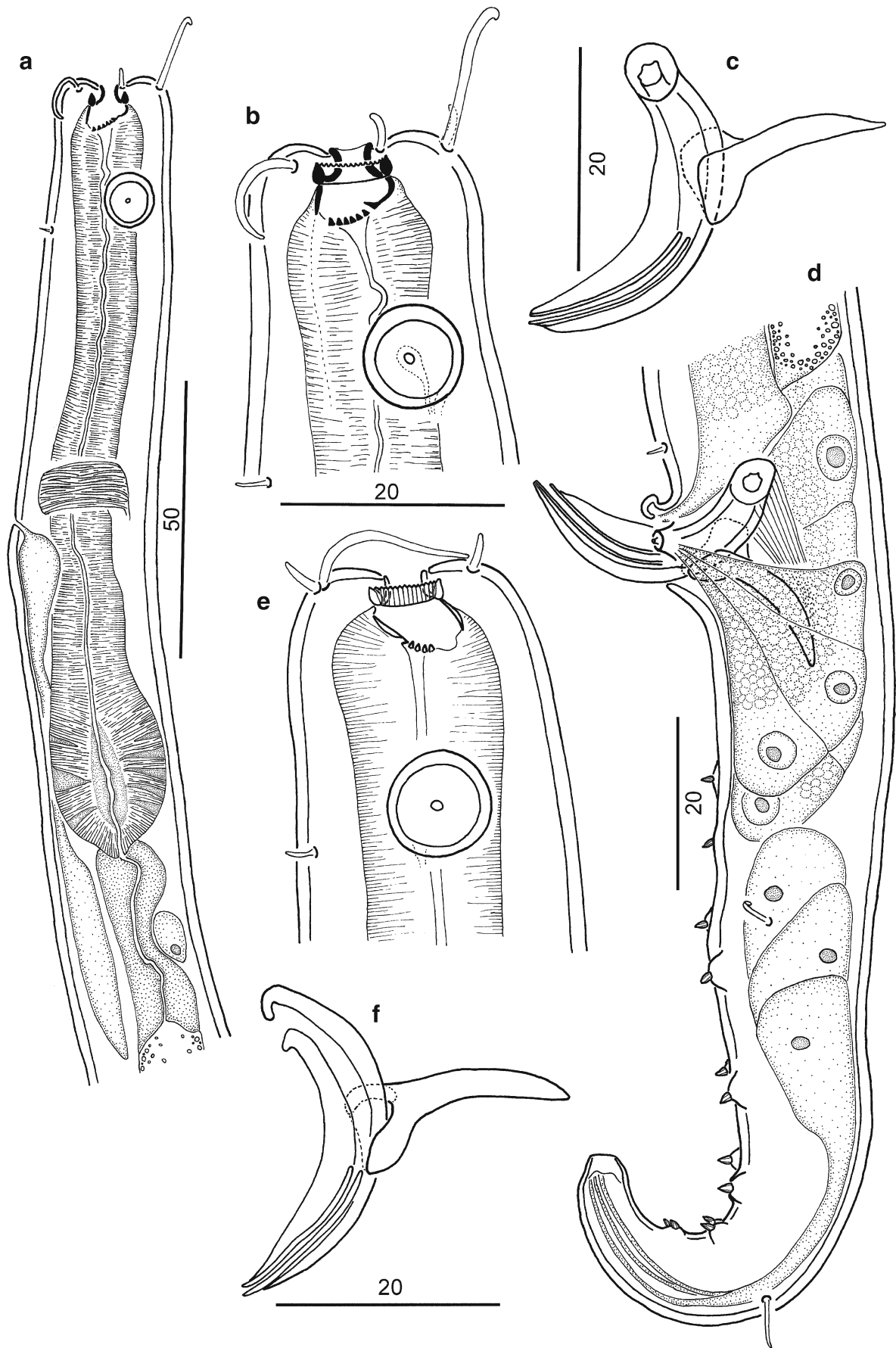
Discussion

After a volcanic eruption struck the 9°50'N EPR region in early 2006, nematode abundance and richness were very low at newly established deep-sea hydrothermal vents and on the bare basalt within the AST in late 2006 and 2007, and they increased only slightly in 2009. In many samples not even a single nematode occurred. Although nematode abundance and richness were also not very high prior to the eruption at well-established vent sites in the same area (Flint et al. 2006; Zekely et al. 2006c; Gollner et al. 2010), our results show that nematodes are extremely influenced by volcanic eruptions and need a long period of time to recolonize the lava-flooded AST in greater numbers and richness. Our finding that nematode abundance and richness increased during early succession is in accordance with other ecological studies (Odum 1969; Dean and Connel 1987; Sousa 2001). However, many different factors might influence nematode abundance, richness and species composition in the AST.

Low nematode abundance and richness during early succession

During the volcanic eruption, a large area of approximately >18 km in the axial summit trough (AST) and up to ~1 km off-axis was flooded (Tolstoy et al. 2006) and must have wiped out almost the entire nematode assemblage. It is known that the effect of patch size can influence the recolonization pattern after a disturbance (Sousa 2001). The here-studied disturbance was not patchy and local, but a whole region was affected, and the majority of potential close-by nematode species pools for recolonization of our observed sites died out. Thus, nematodes had to immigrate from distant areas, which could explain the low nematode abundance and richness during early succession stages.

In addition, the harsh physico-chemical conditions at newly established vents might have prevented nematode establishment during early succession. At the active vent sites Tica and P-Vent, not a single nematode was found in 2006, but at Sketchy, the active vent site, which was characterized by more moderate temperature regimes (see Table 1), and on the new bare basalt with no vent fluid



emissions and ambient deep-sea temperature at least a few nematodes were present early on. In 2006, the vent sites of the studied area were dominated by the tubeworm foundation species *Tevnia jerichonana*, a species that is known to occur at high temperatures, but also at high and toxic sulfide regimes and low oxygen concentrations (Nees et al. 2009). The physico-chemical conditions found associated with the early colonizer *T. jerichonana* are even more extreme than those typical for the later occurring tubeworm *Riftia pachyptila*, which replaces *T. jerichonana* after ~1–2 years (Shank et al. 1998; Nees et al. 2009). Interestingly, nematode diversity associated with *R. pachyptila* in the same area prior to the eruption was very low, which was explained by the more extreme environmental conditions of the habitat compared to mussel beds (Gollner et al. 2007). At the even more extreme Pompeii worm habitat on sulfide chimneys, with occasional temperature peaks of >100 °C, no nematodes were found in this area prior to the eruption (Gollner et al. 2010). Nematodes that have been detected in previous studies at vents have no obvious morphological adaptations to the environment (Gollner et al. 2010; Vanreusel et al. 2010a), and thus the very extreme physicochemical conditions during early stages of succession might be too harsh for nematodes to colonize tubeworm habitats.

Low amounts or poor quality of available food present at the newly established vent sites and on new bare basalt might have caused low nematode abundance in the AST during early succession. When the AST was struck by the volcanic eruption in early 2006 (Tolstoy et al. 2006), all previously accumulated organic material deriving from either *in situ* chemosynthetic primary production at vents or downward flux of photosynthetic production of surface waters (Van Dover 2000) was covered with lava and thus might become unavailable for animals. The large majority of vent nematode species are primary consumers, feeding presumably on bacteria and particulate organic matter (Zekely et al. 2006a). In consequence, an important food source of nematodes immediately disappeared. At newly established vents sites with *in situ* primary production, the flourishing chemoautotroph bacteria might not be of appropriate quality for nematodes, or the vent habitat itself might be too extreme for nematodes to use this food source. In addition, the relatively slow nematodes might be outcompeted by other faster meiofauna (i.e. copepods) or by the larger macrofauna, both of which occurred in higher abundance in the same samples (SG, MB personal observation).

Species composition during succession

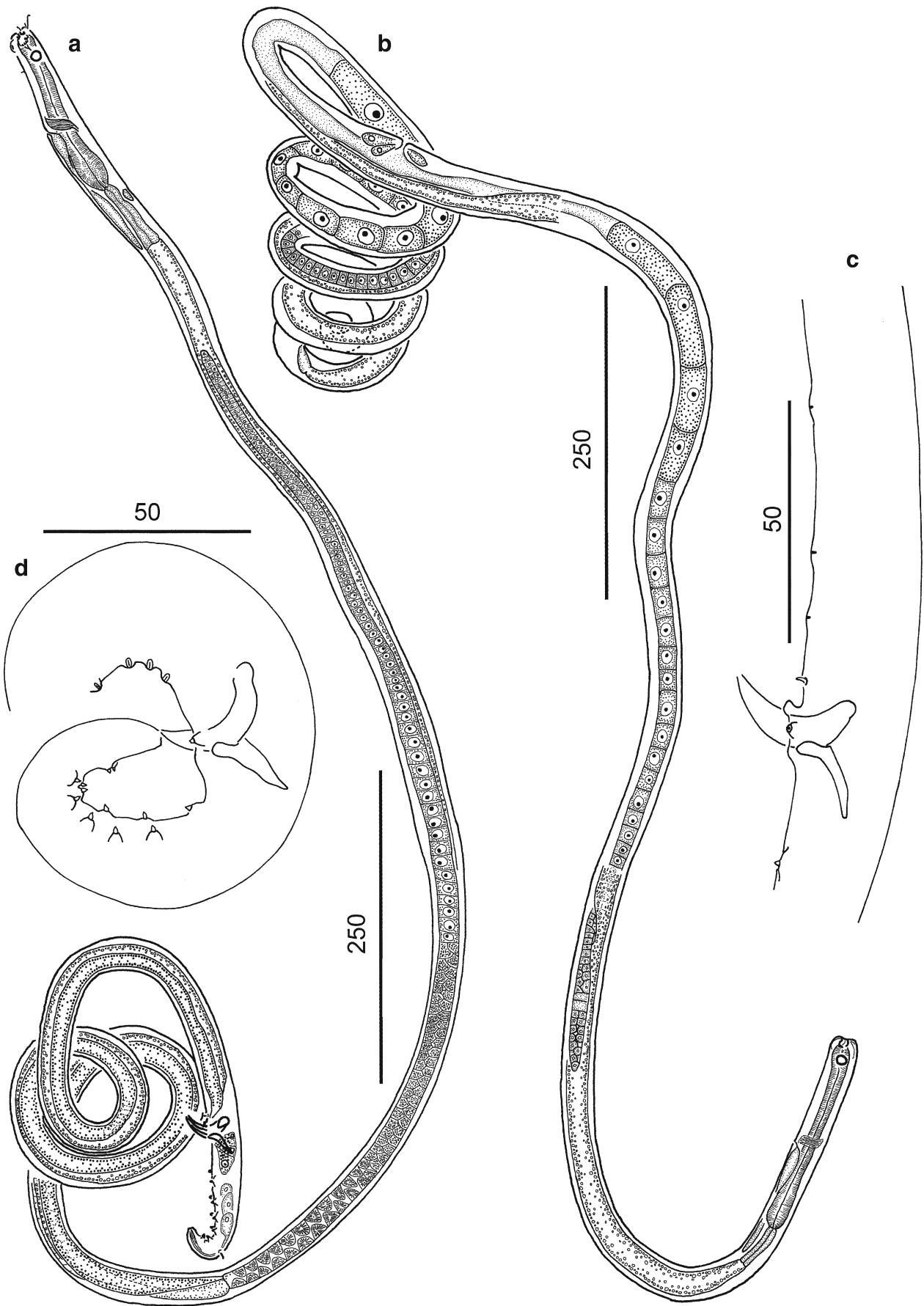
Interestingly, species dominating prior to the eruption were the first colonizers after the eruption. *Thalassomonhystera fisheri* and *Halomonhystera hickeyi* were abundant at active vent sites in the 9°50'N EPR area prior to the eruption and

Fig. 6 *Linhomoeus caudipapillosus* sp. n., **a** male, holotype, total view; **b** female, paratype no. 6, total view; **c** male, holotype, cloacal region with precloacal supplements; **d** male, paratype no. 2, posterior end. Scale in μm

occurred also, although in lower abundance, on the bare basalt (Zekely et al. 2006a; Gollner et al. 2010). Those two species were the first invaders at newly established active vent sites and on the new bare basalt, and they also remained very dominant in 2007. This suggests that generalists with a broad ecological niche, which can live in highly productive and extremely abiotic environments but also in poorly productive and moderate environments, are the most successful colonizers after major disturbances.

In contrast, rare specialists with a narrow ecological niche were most influenced by the volcanic eruption. Rare species typically occurred on the bare basalt prior to the eruption, while the active vent sites were dominated by a few generalists. Prior to the eruption 26 nematode species were reported from the 9°50'N EPR region by Gollner et al. (2010): 7 were classified as AST generalists (species that occurred at vents and on bare basalt), and 6 of them had returned after the eruption by 2009. In contrast, from the 19 species with a more restricted distribution prior to eruption at either vents or bare basalt, only three species returned after the eruption during the sampling time. These three species were found prior to the eruption only on bare basalt, but after the eruption we detected them also at vents; thus they also can now be considered as AST generalists. Among these three species are the here-described species *Neochromadora* aff. *poecilosoma* and *Linhomoeus caudipapillosus* sp. n. In summary, only AST generalist species were apparently able to recolonize the AST after the major disturbance until 2009.

The study of nematode succession in tubeworm habitats revealed similar species composition at very young and older tubeworm aggregations. The most dominant species at early succession tubeworm sites (this study: 1–2 years old) and at older tubeworm sites (>5 years) studied prior to the eruption at the same site were *T. fisheri* and *H. hickeyi* (Gollner et al. 2007). Also, species richness was similarly low at young and older sites (always <5 total species). Unfortunately in 2009 (4-year-old tubeworm aggregation at Tica), the sponges we had deployed were not directly placed within tubeworms but at the edge of the aggregation. In these samples, *N. aff. poecilosoma* and *H. hickeyi* dominated; however, species richness was similarly low compared to all other tubeworm samples, and in the control sample from 2009 *T. fisheri* was dominant. This indicates that nematode assemblages associated with active vent sites colonized by tubeworms at the 9°50'N EPR region remain similar, regardless of age. The harsh physico-chemical conditions, which are typical for such vent habitats, might cause the constantly low nematode diversity.



Different nematode species were dominant at active and inactive vents. While *T. fisheri* and *H. hickeyi* were abundant at active vent sites, *Neochromadora* aff. *poecilosoma* and *Linhomoeus caudipapillosus* were prominent at inactive vent sites. Interestingly, members of the genus *Thalassomonhystera* and *Halomonhystera* were also dominant at other active vent sites in the West and East Pacific and in the Atlantic (Vanreusel et al. 1997; Flint et al. 2006; Zekely et al. 2006c), and a *Halomonhystera* species was very abundant in the most sulfidic area of a cold seep at Hakon Mosby Mud Volcano (Van Gaever et al. 2009). *Thalassomonhystera* and *Halomonhystera* species are usually not very large (Fonseca and Decraemer 2008). In contrast, members of *Neochromadora* and *Linhomoeus* are usually larger, and in our samples, they were at least twice as large as *Thalassomonhystera* and *Halomonhystera*. Reasons for the opposing species patterns at active and inactive vents are difficult to decipher, but availability and quality of food can be important factors controlling species occurrence (Danovaro and Gambi 2002; Vanaverbeke et al. 2004). Also species characteristics such as size and motility could influence the colonization pattern, as could be shown in a study of deep-sea sediments, where larger and more motile nematodes dominated in disturbed sediments (Gallucci et al. 2008). While the larger and potentially faster nematodes might be able to outcompete the smaller ones at inactive vents, we suggest that at active vents only species that are able to tolerate the harsh physico-chemical conditions can survive and dominate (Gollner et al. 2010).

Influence of local patches not directly affected by extinction events

Another important aspect of recolonization of nematodes at deep-sea hydrothermal vents after volcanic eruptions might be the local survival of populations in some undisturbed, local patches due to topographic features (Sousa 2001). The East Wall site, which is located on a ~8-m-high wall within the AST, was not flooded during the eruption and was thus not directly affected by the eruption (SG, MB personal observation). Instead, it was indirectly influenced since its vent flux had ceased, because during the eruption the lava might have clogged the channels in the earth's crust through which the hydrothermal fluids had emerged. In consequence, nematodes at East Wall were only indirectly affected by the eruption, were not killed by the lava flooding but could potentially survive the eruption. Survivor sites such as East Wall can harbor important local source populations, which might be important for recolonization of species.

Fig. 7 *Linhomoeus caudipapillosus* sp. n., micrographs. **a, b** Heads; **c, h** posterior end of male; **d** region of male spicule; **e** foraminifera (?) in intestine; **f** midbody region of female; **g** content of intestine; **i** postanal subventral papillum (enlarged); **j** bacteria-like content of intestine. Scale bars: **a–c, e, j** = 20 μ m; **d, i** = 5 μ m. Abbreviations: *b.* bacteria; *c.s.* cephalic seta; *c.p.* near-cloacal subventral papilla; *cu.r.* cuticular ring; *d.* denticles; *gu.a.* apophysis of gubernaculum; *o.* oocyte; *o.l.s.* outer labial seta; *o.n.* nucleus of oocyte; *p.p.* postanal subventral papilla; *s.* supplement

Importance of inactive vent sites in the AST

Inactive vent sites, whose vent flux had ceased, might be important refuges for nematode species living in the AST in general. On one hand, such inactive sites offer high amounts of organic matter because of decaying chemoautotroph foundation species. With the exception of active vents and their *in situ* primary production, the vast majority of the AST is a food-poor deep-sea region (Van Dover 2000; Etter and Mullineaux 2001). On the other hand, there is no toxic hydrothermal vent fluid at inactive sites, which could hinder the establishment of more sensitive species. Due to constant waxing and waning of local vent patches in a hydrothermal vent region (Van Dover 2000), such inactive vent patches might be important for maintaining nematode diversity in the AST.

Remarks on *Neochromadora* aff. *poecilosoma* and *Linhomoeus caudipapillosus*

Neochromadora aff. *poecilosoma* is a species typically found in high abundance at inactive vent sites in the 9° 50'N EPR region. Interestingly, this species was already detected prior to the eruption in this region on bare basalt (Gollner et al. 2010). At East Wall, the site that was not flooded by lava, the species already occurred in 2006 and was a prominent component of the assemblage in all post-eruption years. This shows that this species has perhaps survived the eruption locally and could therefore colonize other inactive vents relatively quickly.

Linhomoeus caudipapillosus also occurs mostly at inactive vent sites, but in lower dominance than *N.* aff. *poecilosoma*. *L. caudipapillosus* was found at and near East Wall at the inactive vent site and on the bare basalt in 2007 and 2009. Also this species was already known from before the eruption (Gollner et al. 2010). Fascinatingly, *L. caudipapillosus* was larger, the gonads were longer, and the guts of several individuals were probably full of filamentous bacteria when the species was found associated with inactive vent sites. In contrast, the studied specimen from the bare basalt was smaller and the gut likely contained only one big foraminiferan. Previous studies observed that several nematode species showed an increase in body size at maturity when food availability was experimentally enriched (Dos Santos et al. 2008). Thus, the food-enriched environment of

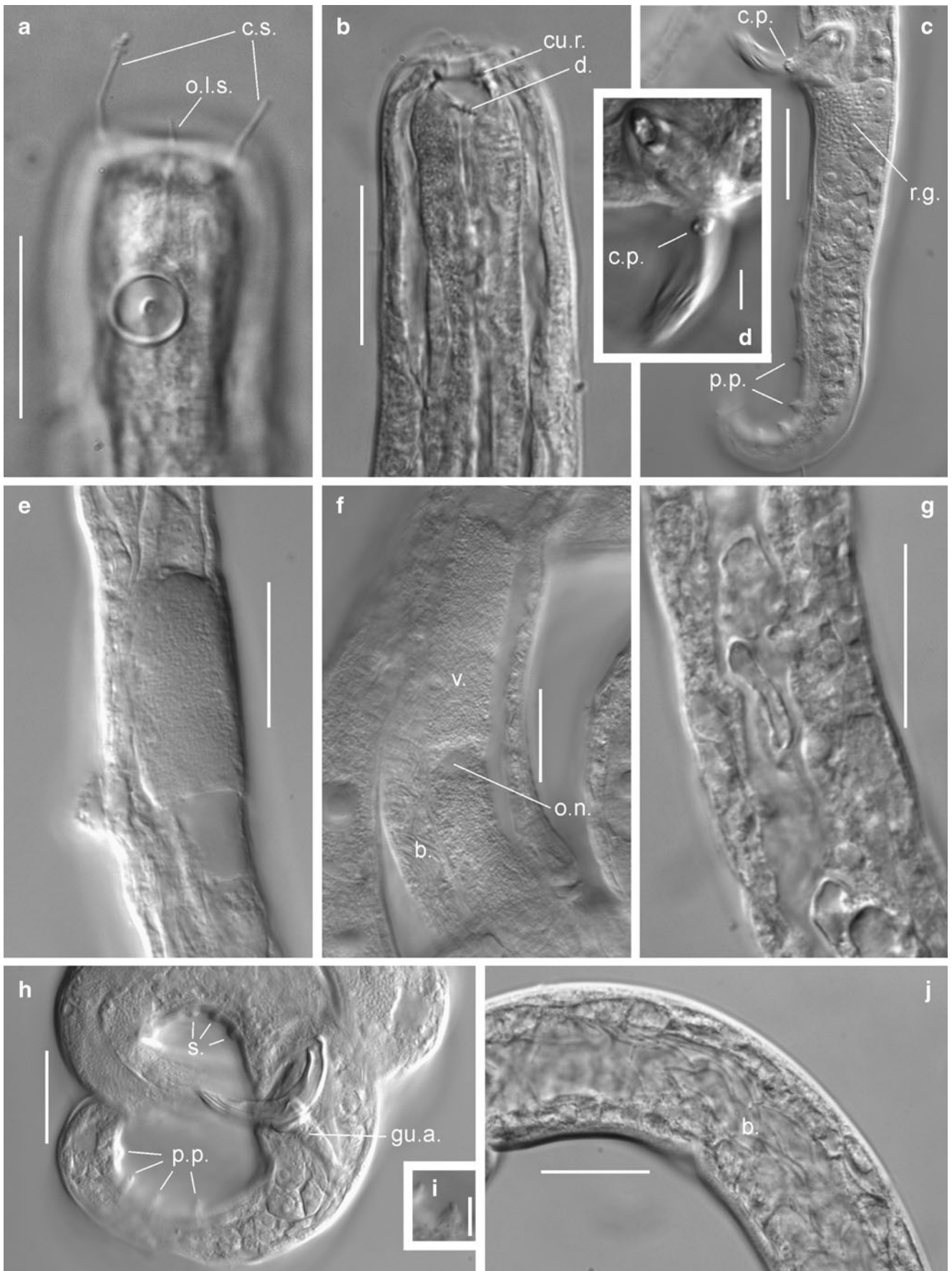


Table 4 *Linhomoeus caudipapillosus* sp.n. Measurements (in μm) and body indices

Specimen No.	Holotype	Paratype no. 1	Paratype no. 2	Paratype no. 3	Paratype no. 4	Paratype no. 5	Paratype no. 6	Paratype no. 7	Paratype no. 8	Paratype no. 9
Collection no.	SMF 16966	SMF 16967	SMF 16968	SMF 16970	SMF 16971	SMF 16969	SMF 16972	SMF 16973	SMF 16974	SMF 16975
Sample	RW 96	RW 96	RW 96	RW 96	RW 96	RW 96	RW 96	B1	RW 96	RW 96
Gender	M	M	M	M	M	F	F	F	F	F
L	2,425	2,704	2,283	2,543	?	2,829	2,438	1,949	2,435	2,525
Amph.dist.	16	16	14	15	?	13	17	10	15	12
Nerve ring	66	84.5	74.8	77	?	86	82	75	92.5	82
Excr.pore	82	?	92.5	?	?	95	93	84	?	93
Phar.l.	141	159	154	155	?	161	165	158	162	165
Tail.l.	116	105	118	114	128.5	127	129	103	112	117
Vulv.dist.	-	-	-	-	-	1,332	1,138	1,039	1,221	1,212
Gonad .l.	872/757	?	?	?	?	714/ 684	?	461/324	671/655	581/662
Repr.sys., %	89	85	85	?	?	62	?	56	66	65
Ceph.set.diam	18	20	18	18	?	15	16	14	17	17
Amph.diam.	21	25	23	25	?	22	22	17	24	22
Nerv.r.diam.	26	26	25	26	?	24	28	18.5	26	26
Card.diam.	24.5	32	25	27	?	25	32	19	26	27
An.diam.	26.5	29	29	29	27	26	24	17	39	40
Max.b.diam.	26.5	34	29	31	31	41	34	22	26	25
Amph.diam.	9	9	8.5	10	?	9	9	7	10	9
Out.lab.setae	5	4	4	5	?	4	4	3	5	4
Ceph.setae	14	13	?	14	?	?	?	12	16	?
Cheil. width	2.5	2.5	2.5	2.5	?	3	2.5	3	2.5	3
Cheil.length	2.5	2	2.5	2	?	2.5	3	2.5	3	3
Pharyng.width	7.5	6.5	7	7.5	?	6	7	6.5	6	6.5
Pharyng.length	4	5	3	4.5	?	4	4	3.5	4	3.5
Spic.ch.l.	26.8	25.2	31.3	27.9	27.1	-	-	-	-	-
Spic.arc.l.	35.6	40.8	40.8	34.7	35.3	-	-	-	-	-
Guber.apoph.l.	16.9	18.4	17.7	?	16.1	-	-	-	-	-
a	91.5	79.5	78.7	82.0	?	69	72	89	62.4	63.1
b	17.2	17.0	14.8	16.4	?	17.6	14.8	12.3	15.0	15.3
c	20.9	25.7	19.3	22.3	?	22.3	18.9	18.9	21.7	21.6
V, %	-	-	-	-	-	47	47	53	50	48

inactive vent sites might have a positive influence on the maximal size that can be reached as an adult.

The origin of vent nematode species is not clear yet, but the taxonomic similarity between several vent species and adjacent regular deep-sea sediment species is quite high, which supports the importance of local adaptation (e.g., the abundant deep-sea genus *Thalassomonhystera*) rather than long distance distribution (Vanreusel 2010a). However, both here-described species, occurring in high abundance at inactive vents, belong to genera typical in shallow, coastal waters and are rarely found in deep-sea sediments, suggesting that these species might have originated in shallow waters.

Representatives of the genus *Neochromadora* are regular members of the shallow-water assemblages and can dominate in intertidal and estuarine environments (Vincx 1986; Pavlyuk 2004), but are rare in deep-sea sediments (Gambi et al. 2003; Lamshead et al. 2003). *Neochromadora poecilosoma* is a cosmopolitan species and was found in very different geographic regions, but usually in shallow waters (Gerlach and Riemann 1973), sometimes inhabiting anoxic, sulfidic sediments (Wieser and Kanwisher 1961). It was also found at shallow vents in 100-m depth on the subpolar Mid-Atlantic ridge (Fricke et al. 1989). Another species, *Neochromadora* sp., dominated a typical sulfidic, deep-sea vent associated with mussels in the Iheya Ridge area (Shirayama 1992). It appears as if several members of the genus in general might be associated with reduced environments, which are abundant in coastal sediments, or at vents, but in general not present in the deep sea.

The genus *Linhomoeus* can be found in shallow coastal waters, in either subtidal sediments, associated with sediments that accumulated in seagrass beds (i.e. *Zostera*, *Posidonia*), or associated with algae (Schuurmans Stekhoven 1950; Wieser 1954; Lorenzen 1973; Adao et al. 2004). The genus has been also considered indicative for reduced sediments rich in hydrogen sulfide (Jensen 1987). It was reported from shallow vents at the subpolar Mid-Atlantic Ridge (Fricke et al. 1989) and from shallow (72 m depth) sulfide-rich brine seeps in the Gulf of Mexico (Jensen 1986a). There are, to our knowledge, no reports of *Linhomoeus* from greater depths. The deepest occurrence of a described *Linhomoeus* species is reported off North Carolina at a depth of 100 to 400 m (Tietjen 1976). The species *L. brevisetosus* has a reported depth occurrence of 5 to 218 m (Schuurmans Stekhoven 1946). Thus, *Linhomoeus caudipapillosus* sp.n. is currently the deepest found member of the genus. The occurrence of several *Linhomoeus* species in shallow water but its rare occurrence in the deep-sea suggests that this vent species might have originated in shallow waters. Similar to *Neochromadora*, also *Linhomoeus* seems to have affinities to reducing environments.

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