

Nicomache (Loxochona) lokii sp. nov. (Annelida: Polychaeta: Maldanidae) from the Loki's Castle vent field: an important structure builder in an Arctic vent system

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Abstract The discovery of the Loki's Castle vent field at 2,350 m depth on the Arctic mid-ocean ridge in 2008 represents the first known black smoker vent system in the Arctic region. Preliminary results on the benthic invertebrates collected at Loki's Castle indicate the presence of an endemic fauna dominated by tube-building polychaetes, melitid amphipods and gastropods. Here, we formally describe and investigate the ecological role of a new maldanid species, *Nicomache (Loxochona) lokii* sp. nov., a species found to be particularly common and regarded as a keystone species in this vent system. The description of the new species is supplemented with a DNA barcode. The subgenus *N. (Loxochona)* includes at present six nominal species, and the new species described herein is the fourth species associated with reducing habitats. A table with diagnostic characters for all species referred to the subgenus is provided. The new species builds tubes up to a length of 20 cm or more, tightly fastened to the substratum. Together with other tube-building species, *N. (L.) lokii* sp. nov. form a complex three-dimensional habitat for a number of free-living invertebrates. Based on the

morphology of the foregut, the microbial community in the gut and the stable isotope values found for this species, it is concluded that it acts as a grazer in this vent system.

Keywords Vent fauna · Norwegian Sea · Arctic mid-ocean ridge · Black smokers · Stable isotopes · *Sphingomonas*

Introduction

Since the discovery of the TAG hydrothermal vent field on the Atlantic mid-ocean ridge, it has been known that hydrothermal vents are not exclusively on ridges with fast spreading rates. The discovery of the Loki's Castle vent field on the Mohn–Knipovich ridge north of Jan Mayen in the Norwegian Sea in 2008 was the first discovery of a black smoker vent field on an ultra-slow spreading ridge and the first along the Arctic ridge systems (Pedersen et al. 2009, 2010). The field comprises several active up to 13-m-tall black smoker chimneys at the top of an extensive mound of hydrothermal sulphide deposits at 2,350 m depth. On the north-eastern flank of the field, there is a sedimentary area with low-temperature diffuse venting and up to 1-m-high barite chimneys (Pedersen et al. 2010).

There has been considerable interest in the nature of an Arctic vent fauna. Previous studies in more shallow waters on the ridge just north of Iceland, including the Kolbeinsey, Grimsey and Jan Mayen vent fields (Fig. 1) have shown that the fauna present mainly consists of shallow and bathyal species from the surrounding waters with few examples of species adapted to reduced habitats (Fricke et al. 1989; Schander et al. 2010). In contrast, exploration of the fauna at Loki's Castle draws a completely different picture of an Arctic vent fauna. All major fauna elements,

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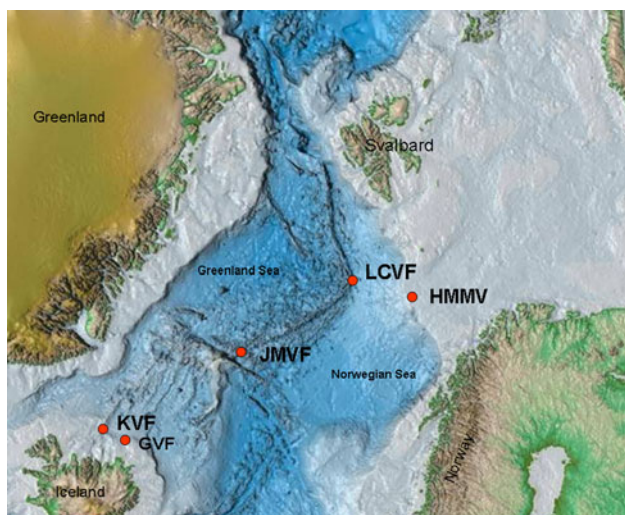


Fig. 1 Map showing the location of the Loki's Castle vent field at 73°33.97'N 08°09.51'E in relation to other known vent fields along the Arctic mid-ocean ridge system. Abbreviations: *HMMV* Haakon Mosby Mud Volcano, *KVF* Kolbeinsey vent field, *GVF* Grimsey vent field, *JMVF* Jan Mayen vent field, *LCVF* Loki's Castle vent field

including amphipods, polychaetes and gastropods, appear to harbour symbiotic microorganisms (Pedersen et al. 2010; Rapp et al. unpublished data). Preliminary results suggest a relatively high degree of endemism and local adaptation within this fauna with apparent links rather to the Pacific vent faunas rather than to the vent sites further south in the Atlantic (Pedersen et al. 2010).

Polychaetes, especially the Siboglinidae, are known to be important structure builders at hydrothermal vents in the Pacific Ocean as well as in cold seep environments in most oceans (e.g. Van Dover 2000). At Loki's Castle, the typically seep-associated siboglinid *Sclerolinum contortum* Smirnov, 2000 forms dense aggregations in the sedimentary area on the lee-side of the hydrothermal deposits and within the area of low-temperature venting ($\sim 20^{\circ}\text{C}$) and barite chimneys (Pedersen et al. 2010). While these tube worms are normally deeply buried in sediments, three-fourth of the tubes are found above the sediment surface at this site, attached to a dense layer of polychaete tubes resting on top of highly anoxic sediments. The main fauna component in this polychaetous mat is a new species of *Nicomache* (*Loxochona*). Three out of five species already assigned to this subgenus are known from reduced habitats. *N. (L.) arwidssoni* Blake, 1985 and *N. (L.) venticola* Blake and Hilbig, 1990 are found at vents in the Pacific, while *N. (L.) ohtai* Miura and Hashimoto, 1991 is found at cold seeps off Japan.

Here, we provide a formal description of the new species of *N. (Loxochona)* and investigate the ecological role of this abundant polychaete in the Loki's Castle vent system.

Materials and methods

Material was collected from the Loki's Castle vent field during the R/V *G. O. Sars* cruises BIODEEP in July 2008, H2DEEP in August 2009 and CGB DEEP in July 2010. Benthic samples were taken using the "Bathysaurus" XL remotely operated vehicle (ROV) provided by Argus Remote Systems. Video was acquired using a high-definition camera, and still photos were subsequently captured from the video. During the 2008 cruise, fauna samples were taken from the chimney walls near the base of black smokers as well as in sedimentary areas on the NE slope of the hydrothermal mound. In 2009 and 2010, sampling was more focused within the dense fields of *Sclerolinum contortum* accompanied with low-temperature barite chimneys. The fauna samples were sorted on board and fixed in either 96% alcohol or 6% buffered formaldehyde solution in seawater.

Type material and additional material have been deposited in the Natural History Collections, Bergen Museum, University of Bergen, Norway (ZMBN). The specimens were examined by use of a Leica MZ Stereomicroscope and a Leica DM 6000 B compound microscope. A Canon 20D camera, with MP-E 65-mm and EF 100-mm macro-lenses, has been used for digital photographs of the species. Drawings were prepared in Adobe Photoshop and Adobe Illustrator CS5. SEM micrographs of gut microbes and the structure of the tube wall were made using a ZEISS Supra 55 V SEM on dried and gold/palladium-coated material. Methyl blue was used for staining in order to study and describe the distribution of glandular tissue of the epidermis (Green 1991).

Preparation of samples for stable isotope analyses was performed following standard protocols as described elsewhere (Levin et al. 2009; Pedersen et al. 2010). The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ stable isotope compositions of the new species were analysed at Institute for Energy Technology (IFE). Approximately 1.0 mg of material was used for the C and N analyses and 2.0 mg for the S analysis. The isotopic measurements were performed using a Nu Instrument Horizon, isotope ratio mass spectrometer. Results were corrected against the international standards IAEA-N-1 and IAEA-N-2 ($\delta^{15}\text{N}$), USGS-24 ($\delta^{13}\text{C}$) and IAEA-S2 ($\delta^{34}\text{S}$). DNA was extracted using the FastDNA[®] SPIN for Soil Kit following the protocols from the supplier. For barcoding purposes, the mitochondrial cytochrome *c* oxidase subunit I (COI) gene (the Folmer fragment) was amplified and sequenced following standard protocols (Folmer et al. 1994). The 16S rDNA clone library of endobionts was obtained using the primers B338f (Lane 1991) and B1392r (modified from Amann et al. 1995) and the Strataclone PCR Cloning Kit from Strategene. DOTUR analysis of microbial sequence data was performed to estimate the

diversity of microbial endobionts (Schloss and Handelsman 2005), and phylogenetic trees (Maximum Likelihood) were constructed using the program ARB.

Results

Systematics

Family Maldanidae Malmgren, 1867

Subfamily Nicomachinae Arwidsson, 1906

Genus *Nicomache* Malmgren, 1865

Subgenus *Loxochona* Arwidsson, 1906

Nicomache (Loxochona) lokii sp. nov. (Figs. 2, 3, 4; Table 1)

Type locality: Loki's Castle vent field, Arctic mid-ocean ridge, 73°33.97'N 08°09.51'E, 2,350 m depth.

Type material: Type locality from sedimentary area with low-temperature diffuse venting with barite chimneys, R/V "G.O. Sars" H2DEEP cruise 2009 sample ROV-8, 07 August 2009, fixed in 96% alcohol: *Holotype* (ZMBN 86266) and *10 paratypes*, all complete specimens (ZMBN 86267–86269, 86271–86272, 86274, 86276–86279).

Fig. 2 *Nicomache (Loxochona) lokii* sp. nov., holotype (ZMBN 86266). **a** Anterior part of body, dorsal view. **b** Head and setigers 1–2, dorsal view. **c** The same, lateral view. **d** Posterior end, lateral view. Scale bars 1.0 mm

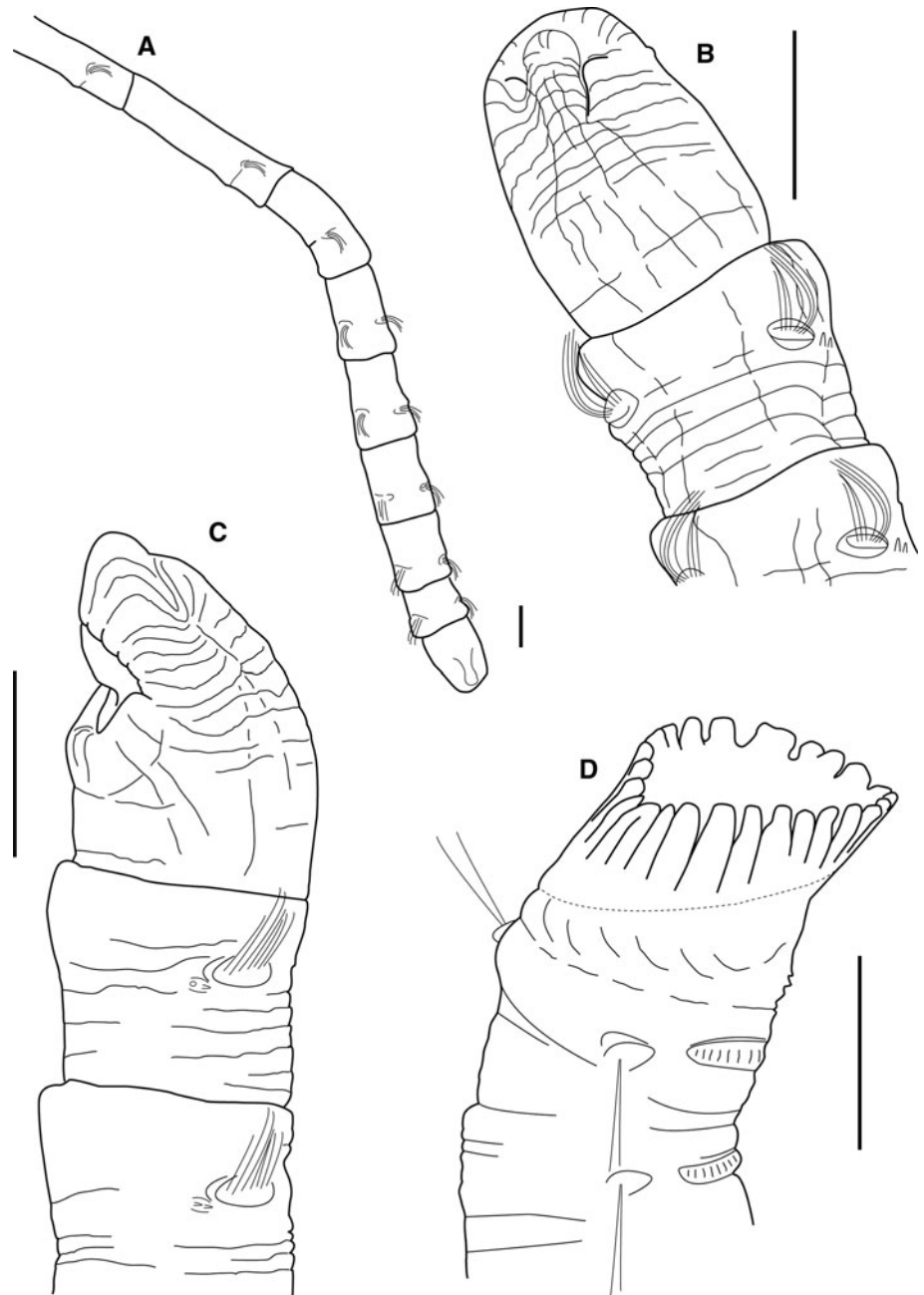




Fig. 3 *Nicomache (Loxochona) lokii* sp. nov. (ZMBN 86276). **a** Capillary setae from setiger 1. **b** Capillary setae from setiger 17. **c** Acicular spine from setiger 2. **d** Rostrate hook from setiger 4. **e** Rostrate hook from setiger 15. Scale bars 50 μ m

Additional material: Type locality from chimney walls near the base of black smokers: R/V “G.O. Sars” BIODDEEP cruise 2008, sample ROV-11, 14 July 2008, fixed in 96% alcohol: 1 spm. (ZMBN 86283); 1 spm. (ZMBN 86284) and 14 spms (ZMBN 86285). Type locality from sedimentary area with low-temperature diffuse venting with barite chimneys: R/V “G.O. Sars” H2DEEP cruise 2009, sample ROV-8, 07 August 2009, fixed in 96% alcohol: 1 spm. (ZMBN 86267); 1 spm. (ZMBN 86270); 2 spms (ZMBN 86273); 4 spms (ZMBN 86275); 10 spms (ZMBN 86280); 4 spms (ZMBN 86281) and 1 spm. (ZMBN 86282). R/V “G.O. Sars” CGB DEEP cruise 2010: Sample ROV-04, 15 July 2010, fixed in 6% formaldehyde and preserved in 80% alcohol: 3 spms (ZMBN 86286); 6 spms (ZMBN 86287); 20 spms (ZMBN 86288); several spms in block of tubes (ZMBN 86289). Sample ROV-05, 16 July 2010, fixed in 96% alcohol: 7 spms (ZMBN 86290). Sample ROV-09, 18 July 2010, fixed in 96% alcohol: 2 spms (ZMBN 86291).

Diagnosis: A large species, up to 125 mm long and 1.8 mm wide, for 22–25 setigerous segments. Asetous preanal segments absent, Pygidial funnel asymmetric, with anal opening ventrally inside anal funnel. First three setigers with 1–2 (3) straight neuropodial spine(s). From setiger four, neurosetae as rostrate hooks; up to 20 hooks in mid-body setigers. Hooks with maximum four apical teeth above main fang and several subrostral hairs. Spiral notosetae absent. 3–4 pairs of nephridial papillae, starting on setiger 7 or 8.

Molecular identification: CO1 sequences (DNA barcodes): ZMBN 86269, paratype (Genbank accession nr FR877579) and ZMBN 86270 (Genbank accession nr FR877578).

Description: Body long, cylindrical with asetigerous head, 22–25 setigerous segments and pygidial funnel. Holotype 100 mm long and 1.2 mm wide, with 23 setigerous segments. Paratypes 22–125 mm long and 0.5–1.8 mm wide (Table 1). Prostomium and peristomium fused to form a well-defined head, about 1.5–2 times longer than wide, anteriorly rounded, with wide anterior part (prostomial palpode) (Fig. 2b, c). Cephalic keel well defined, arched. Paired nuchal grooves moderately long, on each side of cephalic keel; posterior part of nuchal grooves parallel, anterior part curving laterally (Fig. 2b). Ocelli not observed. Mouth large, oval, with thick lower lip. Transverse epidermal furrow presents ventrally and laterally slightly posterior to mouth. Dissection of head revealed a foregut with well-developed ventral pharynx and dorso-lateral folds.

Anterior seven setigers with swollen anterior margin. Segmental borders distinct in anterior and posterior setigers and indistinct in middle setigers, from about setigers 8–14. Anterior 6 setigers all relatively short, about 1–2 times as long as wide (Fig. 2a). Setiger seven longer, about 2–3 times as long as wide. Length of setigers 8–9 uncertain due to indistinct segmental borders, but setiger 8 probably short and setiger 9 comparatively long. Setiger 10 and following setigers four times as long as wide or longer. Posterior setigers progressively shorter, with last 1–2 setigers shorter than wide. Parapodia located on anterior half of segments in setigers 1–8, and near posterior end of setiger 9 and remaining setigers.

Pygidial funnel slightly shorter than wide and asymmetrical, with ventral part longer than dorsal part and somewhat curved outward (Fig. 2d). Posterior rim of pygidium with 20–30 small cirri/papillae (Table 1), exceptionally up to 38 (ZMBN 86280), some of which are bilobed. Mid-ventral cirrus absent. Base of pygidium oblique, with dorsal part of pygidial funnel deeper than ventral part (indicated by stippled line in Fig. 2d). Anus

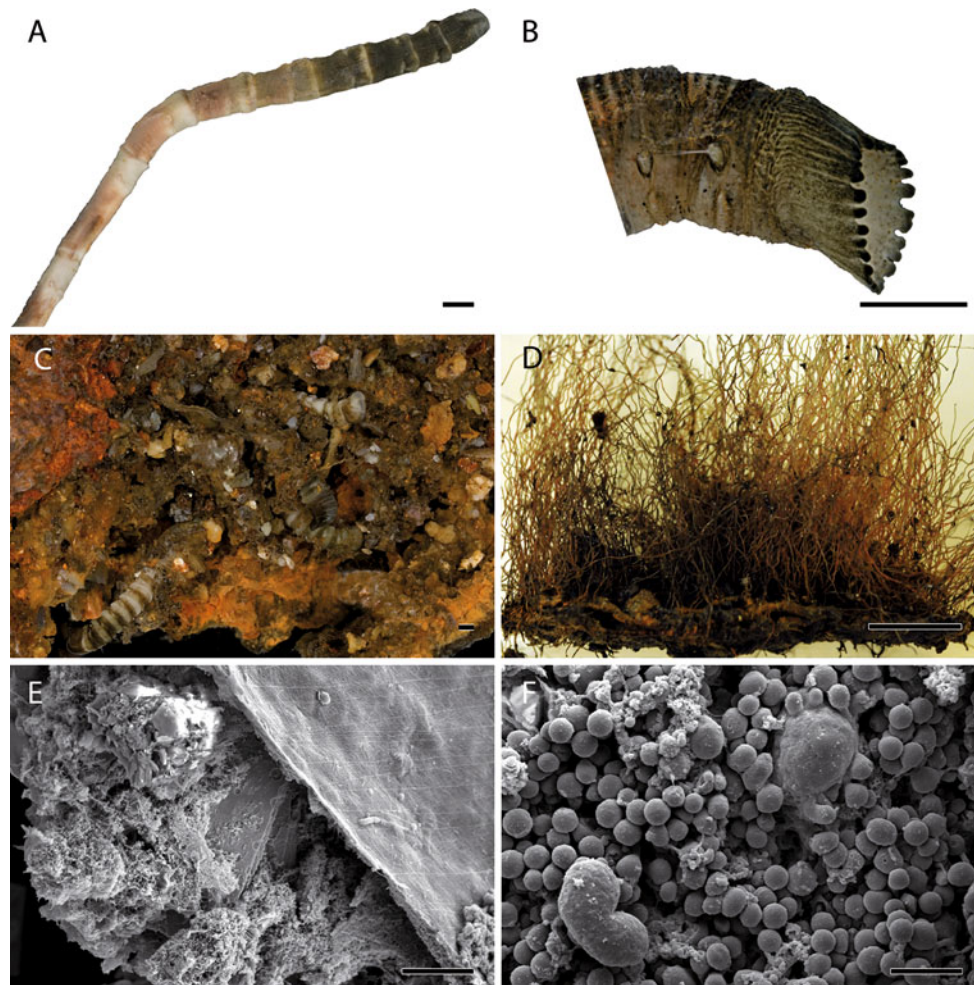


Fig. 4 *Nicomache (Loxochona) lokii* sp. nov. **a** Holotype, anterior part of body, dorso-lateral view. **b** Holotype, posterior part of body, lateral view. **c** Specimens in ferrous crust on wall of a *black smoker*. **d** *Nicomache*-Pogonophora mat from sedimentary areas with diffuse venting. **e** SEM micrograph of the tube wall of *N. (L.) lokii* sp. nov.

The outer surface is covered by barite crystals. The tube wall itself is composed of a very fine and regularly woven mesh of fibres. **f** SEM micrograph of gut microbes in *N. (L.) lokii* sp. nov. Scale bars: **a, b** 1.0 mm; **c** 0.5 mm; **d** 50 mm; **e, f** 10 μ m

situated ventrally inside pygidial funnel. Base of anal funnel with longitudinal folds from pygidial rim towards anal opening; each fold with several small papillae. Anal valve absent.

Distribution of glandular tissue characteristic and well stained by methyl blue. Head uniformly stained, except for the nuchal organs. First nine setigers with complete band anteriorly; staining less distinct dorsally in setigers 7–9. Remaining setigers with staining restricted to parapodia and, in posterior setigers, a narrow transverse band dorsally between the parapodia. Pygidial funnel uniformly stained.

All setigers biramous. Setigers 1–3 with comparatively small noto- and neuropodia. Mid-body and posterior setigers with well-developed notopodial lobes and neuropodial tori. Posterior setigers distinctly swollen at level of parapodia. Anterior setigers with notosetae in single row. From setiger 4, notosetae arranged in double rows. Notosetal rows in dorso-ventral direction in all setigers. All notosetae simple

winged capillaries (Fig. 3a, b); capillaries from anterior row shorter and more slender than capillaries from posterior row. Setigers 1–3 with 1–2 (3) straight acicular spines per neuropodium (Fig. 3c). Setiger 4 and following setigers with single vertical row of rostrate hooks (Fig. 3d, e). Number of rostrate hooks varies along body and with body size increasing to a maximum in mid-body setigers and thereafter decreases progressively towards the last setiger. Large specimens with 4–5 hooks in setiger 4, up to 20 hooks in mid-body setigers, and 8–10 hooks in the posterior most setiger. Rostrate hooks of setiger 4 with 2–3 apical teeth above the main fang and few, short subrostral fibrils, or fibrils absent (Fig. 3d). Fully developed hooks from setiger 5, each with four apical teeth above the main fang and several strongly curved subrostral fibrils (Fig. 3e).

Anterior part of body with six internal septa separating setigers 1–7. Three–four pairs of nephridia present, with

Table 1 Measurements of type specimens of *Nicomache (Loxochona) lokii* sp. nov.

Specimen	Body length (mm)	Body width (mm, max)	Number of setigers	Number of nephridia (and setigers with nephridiopores)	Number of anal cirri	Sex
Holotype (ZMBN 86266)	100	1.2	23	4 (7–10)	27	Male
Paratype (ZMBN 86267)	96	1.8	24	4 (7–10)	28	Female
Paratype (ZMBN 86268)	22	0.5	23	4 (8–11)	20	
Paratype (ZMBN 86269)	51	0.9	24	4 (7–10)	22	
Paratype (ZMBN 86271)	112	1.5	22	3 (7–9)	20	Female
Paratype (ZMBN 86272)	125	1.8	24	3 (7–9)	30	Male
Paratype (ZMBN 86274)	45	0.9	23	3 (7–9)	24	Male
Paratype (ZMBN 86276)	82	1.2	22	4 (7–10)	22	Male
Paratype (ZMBN 86277)	35	0.8	23	4 (7–10)	15	
Paratype (ZMBN 86278)	43	1.0	25	4 (8–11)	23	
Paratype (ZMBN 86279)	47	1.0	24	4 (7–10)	22	

nephridiopores located ventrally beneath row of hooks on setigers 7–11 (Table 1).

Pigmentation: Dark-green-to-black pigmentation on head, anterior and posterior setigers and on pygidium. Some specimens with reddish pigmentation on posterior part of setigers 3–7 (Fig. 4a, b).

Tube: Flexible, attached, up to about 200 mm long, with inner thin transparent organic layer of fine and regular woven mesh of fibres, incrustated with fine-particulate material (Fig. 4e). The tubes of several specimens are often tightly felted into a thick crust (Fig. 4c, d).

Reproduction: Sexes are separate and several females with oocytes in mid-body setigers and males with sperm were observed (Table 1). Oocytes of variable size, discoid, up to about 240 µm in diameter. Asexual reproduction by architomy was observed. A specimen divides into two fragments at setiger 12/13, each of which subsequently regenerates the lost parts. The two specimens, after undergoing architomic division, were found in the same tube. Several specimens regenerating posterior or anterior end were also observed separately.

Etymology: The species is named after the Norse god Loki and subsequently the Loki's Castle vent field.

Remarks: The new species is referred to the subgenus *N. (Loxochona)* based on presence of an asymmetric pygidial funnel, with the base of the funnel being oblique with a ventrally placed anal opening, and the absence of nephridial papillae on setiger 6 (Arwidsson 1906). Some confusion about the number of species referred to the subgenus *N. (Loxochona)* exists in the literature. De Assis et al. (2007a) referred the following six species to the subgenus: *N. arwidssoni* Blake, 1985; *N. quadrispinata* Arwidsson, 1906; *N. trispinata* Arwidsson, 1906; *N. canadensis*

McIntosh, 1913; *N. ohtai* Miura and Hashimoto, 1991; and *N. venticola* Blake and Hilbig, 1990. De Assis et al. (2007b) referred, in addition, two more species, *N. personata* Johnson, 1901 and *N. maculata* Arwidsson, 1911, to the subgenus. However, *N. canadensis*, *N. maculata* and *N. personata* are all well-documented members of the subgenus *N. (Nicomache)* Arwidsson, 1906, as they all possess a more or less symmetrical pygidial funnel with a centrally placed anus within the funnel, and nephridial papillae present on setiger 6 (not known for *N. canadensis*) (Johnson 1901; Arwidsson 1911; McIntosh 1913; Arwidsson 1922; Imajima and Shiraki 1982). To summarize, the subgenus *N. (Loxochona)* comprises at present six species, including the new species described herein (Table 2). *N. (L.) lokii* sp. nov. differs from *N. (L.) ohtai*, *N. (L.) quadrispinata* and *N. (L.) trispinata* in the absence of an asetous preanal segment and the absence of spiral notosetae. Further, it differs from *N. (L.) arwidssoni* and *N. (L.) venticola*, both known from hydrothermal vent habitats, in the number of setigerous segments and in maximum number of hooks per setiger. *N. (L.) venticola* differs from both *N. (L.) arwidssoni* and *N. (L.) lokii* sp. nov in the number of acicular spines per neuropodium in setigers 1–3.

Ecology

A pronounced difference in size and abundance of *N. (L.) lokii* sp. nov. was observed when comparing samples from the black smoker chimney walls and the low-temperature sedimentary area. On the chimney walls, small specimens (generally smaller than 25 mm) form thin crusts of tubes heavily incrustated by ferrous material (Fig. 4c). In the sedimentary *Sclerolinum* field, large specimens (up to 125 mm) form an up to 5-cm-thick mat in the upper part of

Table 2 Species referred to the subgenus *Nicomache* (*Loxochona*) Arwidsson, 1906, with information on type locality, habitat preference, geographical distribution and selected morphological characters

Characters/species	<i>lokii</i> sp. nov.	<i>arwidsoni</i> Blake, 1985	<i>ohiai</i> Miura and Hashimoto, 1991	<i>quadrispinata</i> Arwidsson, 1906	<i>trispinata</i> Arwidsson, 1906	<i>venticola</i> Blake and Hilbig, 1990
Source of information	Present investigation	Blake 1985; 1991; Gebruk et al. 2000; Blake and Desbruyères 2006	Miura and Hashimoto 1991	Arwidsson 1906; own observation	Arwidsson 1906; own observation	Blake and Hilbig 1990; Blake 2006
Type locality	Loke's Castle vent site, Arctic, in 2,350 m depth	East Pacific Rise vent area, in 2,600 m depth	Off Hatsushima, Sagami Bay, Japan, in 1,163 m depth	Not specified, Spitsbergen and East Greenland, in 25–425 m depth	Trondhjemfjord, Norway, in 30–350 m depth	Hell Vent. Juan de Fuca ridge, NE Pacific, in 1,550 m depth
Habitat	Hydrothermal vents	Hydrothermal vents	Cold seeps	Soft bottom habitats	Sandy to mixed bottom habitats	Hydrothermal vents
Distribution	Only known from type locality	East and central Pacific, and mid-Atlantic ridge at 14°45'N, 2,450–3,650 m depth	Only known from type locality	North Atlantic and Arctic to about 1,000 m depth	North Atlantic and Arctic in coastal areas	North-east Pacific, 1545–2,200 m depth
Body size, max length/width (mm) recorded for complete spms.	125/1.8	84/3	187/3.5	45/1	55/1	130/2.5
Number of setigers	23 (22–25)	21 (19–21)	32 (31–35)	22	23	32 (27–32)
Number of asetous preanal segments	0	0	1 (0–2)	1	1	0
Number of setigers with neuropodial spines	3	3	3	4	3	3
Number of neuropodial spines per setiger	1–2 (3)	1–2	5 (3–6)	1–2	1–2	4–6
Maximum number of hooks per setiger	20	10	19	11	17	10
Hooks, max number of apical teeth above main fang	4	4	4	3	4	3
Hooks, subrostral fibrils	Present	Present	Present	Absent	Present	Present
Spiral notosetae	Absent	Absent	Present, short	Present, long	Present, long	Absent

the sediment (Fig. 4d). Just below this mat, the sediment is anoxic, and a minor part of the *Sclerolinum* tubes penetrate this deep into the sediment. The observed stable isotope values of $\delta^{13}\text{C} = -22.5$ and $\delta^{15}\text{N} = 3.8$ suggest that *N. (L.) lokei* sp. nov. is a grazer, utilizing both the bacterial mats found on the chimney walls and on the sediment surface as well as sinking particles from the water column. This is supported by the morphology of the foregut in *N. (L.) lokei* sp. nov., where the ventral pharynx is well developed and may be used for scraping off food particles from the substrate (Tzetlin and Purschke 2005). However, the sulphur isotope signal ($\delta^{34}\text{S} = 11.1$) indicate a trophic relationship with the microbial community (Kennicutt et al. 1992).

SEM micrographs of the inner gut show that the inner wall is densely populated by bacteria (Fig. 4f). From our 16SrDNA clone library of the endobiont community, a total of 53 sequences were obtained. Through DOTUR analysis, we obtained four OTUs with a distance level of 1%. A pronounced dominance of bacteria clustering within the *Sphingomonas* was found (43 out of 53 sequences), with more than 99% sequence similarity with *Sphingomonas melonis* Buonauro et al., 2002. Further phylogenetic analysis using ARB confirmed these results as all the sequences clustered within the phylum Proteobacteria, where the majority clustered within the alphaproteobacteria and the genus *Sphingomonas*, a group generally known as decomposers (data not shown).

The mat of polychaete tubes provides both a shelter and substrate for a rich and specialized polychaete assemblage as well as clusters of nematodes and dense populations of gastropods of the genera *Pseudosetia* and *Skenea*.

Discussion

The Norwegian–Greenland Seas are known for hosting a deep water fauna with a species composition that is quite different from the fauna found south of the Greenland–Iceland–Faroe ridge (e.g. Svavarsson et al. 1993) and with a high degree of endemism (Gage et al. 2004; Stuart and Rex 2009). Similarities to the Polar Basin indicate a possible connection between the faunas of the northernmost Pacific and the Norwegian–Greenland Seas (Rapp 2004; MacDonald et al. 2010). Preliminary results of the fauna composition at the Loki's Castle vent field indicate that the fauna have developed by local specialization, as well as by migration of fauna from cold seeps and the Pacific (Pedersen et al. 2010). Blake and Hilbig (1990) stated that the genus *Nicomache* is represented at hydrothermal vents and cold seeps by a group of species lacking the long spiral notosetae characteristic for their shallow-water relatives. The long spiral notosetae are also lacking in *N. (L.) lokii* sp.

nov., suggesting a close relationship with the species associated with reducing habitats in the north Pacific. However, the unexpected record of the Pacific species *N. (L.) arwidssoni* from the Logatchev area on the mid-Atlantic ridge (Gebruk et al. 2000) clearly indicates the presence of a closely related species also in the Atlantic. A thorough taxonomic and phylogeographical study of material from different vent sites is needed in order to understand the true geographical distribution and relationships between the different species of this group.

The stable isotope data fall within values previously published for maldanids from vent and seep systems (Van Dover 1994; MacAvoy et al. 2005; Bergquist et al. 2007), and in combination with the dominating endobionts as well as the morphology of the foregut with a well-developed ventral pharynx, it is suggested that *N. (L.) lokii* sp. nov. acts as a grazer in the vent system, utilizing the bacterial mats partly mixed with particles sinking from above. In the Loki's Castle vent system, *N. (L.) lokii* thus seems to fill a very similar niche as the specialized bacteriovore *N. (L.) venticola* at the Juan de Fuca ridge in the NE Pacific (Bergquist et al. 2007). The sulphur isotope signal ($\delta^{34}\text{S} = 11.1$) indicates a trophic relationship with the microbial community. However, it cannot be concluded whether it is due to sulphur oxidizing endobionts or bacterial mats being the main food source.

The difference in size between individuals growing on chimney walls and in sedimentary areas may be explained by differences in food availability and longevity of the substrate. On the chimney walls, they probably rely on grazing bacterial mats and are easily covered by chimney material as the chimneys grow, while in the more stable sedimentary areas, the 20-cm-long *Sclerolinum* tubes act as efficient sediment traps and thus provide an additional food source for *N. (L.) lokii* sp. nov.

The reproduction biology of *N. (L.) lokii* sp. nov. and ability to carry out asexual reproduction may be one of the explanations for the high abundance of this species in the Loki's Castle Vent community. Although rarely reported in the maldanids, asexual reproduction by architomic division has been reported for *Nicomache (Nicomache) minor* Arwidsson, 1906 (Tzetlin and Markelova 1985) and *Maldane sarsi* Malmgren, 1867 (Tzetlin and Markelova 1986; Wrzesinski and Hartmann-Schröder 1994). In all three of these species, architomic division seems to be frequent and may contribute significantly to recruitment.

In the genus *Nicomache*, several species are known to occur in dense populations forming aggregations or galleries of tubes in favourable habitats (e.g. De Assis et al. 2007a; Tzetlin and Markelova 1985). However, *N. (L.) lokii* sp. nov. seems to be the only vent-species to build large populations, as the two other species, *N. (L.) arwidssoni* and *N. (L.) venticola*, only occur as epifauna on and

between other vent-organisms (Blake and Desbruyères 2006; Blake 2006). In the Loki's Castle vent community, the densely felted mats of polychaete tubes aid in stabilizing the very soft and anoxic sediments surrounding the vent field and thus provide a stable substrate for a range of invertebrates adapted to reduced habitats. Hence, *N. (L.) lokii* sp. nov. should be regarded as a keystone species in this Arctic vent system.

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