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Monoculodes bousfieldi sp. n. from the Arctic hydrothermal vent Loki's Castle

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Abstract

In examining the amphipod fauna of the Loki's Castle hydrothermal vent in the north Norwegian Sea, one new species of Oedicerotidae was discovered. This paper describes *Monoculodes bousfieldi* sp. n. (Amphipoda, Oedicerotidae) and includes a short discussion of the blind *Monoculodes*, as well as a key to this subset of the oedicerotids. The description is based on morphology in addition to a sequence of the mitochondrial gene COI (Folmer section). A short discussion on the isotope-signature, giving indications of this species food choice and position in the hydrothermal vent food-web is included.

Keywords *Monoculodes bousfieldi* · Hydrothermal vent · Loki's castle · Amphipod

Abbreviations

A1	Antenna 1
A2	Antenna 2
art	Article (of palps of antennae…)
Ep1 to Ep3	Epimeral plate 1 to epimeral plate 3
Lbi	Labium
Lbr	Labrum
Md	Mandible
Mx1, Mx2	Maxilla 1, maxilla 2
Mxp	Maxilliped
P1 to P7	Pereopod 1 to pereopod 7
T	Telson
U1 to U3	Uropod 1 to uropod 3
Uros	Urosomite

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The new species (*Monoculodes bousfieldi*) is registered in ZooBank under urn:lsid:zoobank.org:act:E9FF0360-F43C-4298-8AD3-20936562226E

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Introduction

Lokis's Castle is located at 2350 m depth at 73° N, 8°E at the Mohns Ridge-Knipovich Ridge transition at the crest of an axial volcanic ridge. It is a black smoker system with five chimney structures up to 11 m tall. The emanating fluids have temperatures up to 320 °C, a pH of 5.5, and a chemical composition that indicates influence of buried sediments, probably from the Bear Island fan. A sedimentary area with more diffuse low-temperature venting with numerous up to 1 m tall barite chimneys is located on the eastern flank of the sulfide mound. The temperature of the fluids in the barite field emanating from the active chimneys is up to 20 °C (Eickmann et al. 2014; Steen et al. 2016; Olsen et al. 2016).

Loki's Castle was the first black smoker vent system ever found on an ultraslow spreading ridge, and it represented the first record of true vent-endemic macroorganisms along the Arctic Mid-Ocean Ridge (AMOR) (Pedersen et al. 2010; Tandberg et al. 2011; Kongsrud and Rapp 2012). The fauna is different from the surrounding deep sea of the Nordic Seas and a preliminary characterization of the field suggest two zones where the first is dominated by black smoker chimneys with microbiota, but also with gastropods and amphipods, and the second is characterized by low-temperature venting with barite chimneys. The first is a hard substrate where the fauna is highly variable in abundance, low in biomass, and generally low in diversity. The second is primarily a soft bottom habitat with a rather diverse and abundant fauna that is characterized by siboglinid tubeworms (*Sclerolinum contortum* Smirnov, 2000), amphipods, gastropods, and tube dwelling polychaetes (Pedersen et al. 2010; Tandberg et al. 2011; Kongsrud and Rapp 2012; Kongsrud et al. 2017; Olsen et al. 2016).

Samples from the low-temperature barite fields around Loki's Castle revealed an until now undescribed species of amphipod, which is placed in the family Oedicerotidae, genus *Monoculodes* Stimpson, 1853. The cosmopolitan family Oedicerotidae contains 224 accepted species within 44 genera, of which all but a very few species of the genus *Monoculodes* are marine. They are found at depths from the intertidal to near 5000 m (Barnard and Karaman 1991).

Bousfield and Chevrier (1996) suggested that *Monoculodes* is a genus complex, and six new genera were split off, leaving 32 species that is now included in *Monoculodes s. str.* (Lowry et al. 2010). Following their key to *Monoculodes s. l.*, our new species fits firmly within the limits of *Monoculodes s. str.* by the shape of the pereopods 1 and 2, both propodal and carpal shapes. Diagnoses to *Monoculodes s. l.* (Barnard and Karaman 1991, p 559) and *Monoculodes s. str.* (Bousfield and Chevrier 1996, pp. 81–82) are still in use. Several authors (e.g., Barnard and Karaman 1991; Bousfield and Chevrier 1996; Brix et al. 2018) have pointed out that both the family Oedicerotidae and the genus *Monoculodes* are in need of a modern revision. As this revision is still not performed, we have to keep to the present slightly confused state of *s. str* and *s. l.*

The present species is one of the two Oedicerotidae ever found on hydrothermal vents, the other (*Monoculodes anophthalma* Bellan-Santini, 2007) was found at the vent Lucky Strike at the Azores. Interestingly, Lucky Strike is one of the presently known vents that is most similar the Loki's Castle with regard to depth and venting temperatures.

Material and methods

The amphipods were collected during five cruises (2008, 2009, 2010, 2015, 2017) at the Loki's Castle hydrothermal vent (Pedersen et al. 2010). Although *Monoculodes bousfieldi* could be found along the base of the black smoker chimneys, it was much more abundant in lower temperatures, and the vast majority of the samples were collected in the low-temperature barite field (Steen et al. 2016), only 5–20 m away from the high-temperature chimneys, where they were commonly found among tufts of *Sclerolinum contortum* (Kongsrud and Rapp 2012). Sampling was performed with a suction sampler mounted on an ROV. The specimens were immediately sorted after landing on board, fixed in 96% ethanol and kept cold.

Specimens used for the morphological examinations were dissected using a stereo microscope (Leica M125) and mounted on slides with Faure's medium. Illustrations were produced using a Leica DMLB compound microscope fitted with a drawing tube, and pencil-drawings were inked following the methods described by Coleman (2003, 2009).

To supplement the morphological data, we aimed at providing a molecular barcode by targeting CO1, using a degenerated version of the Folmer primers dg-HCO (5-AAA CTT AAA GRA ATT GAC GG-3) and dg-LCO (5-CTA AGG GCA TCA CAG ACC-3) (Folmer et al. 1994). The primers were optimized for PCR amplification including an initial denaturation cycle (3 min at 95 °C), followed by 35 amplification cycles (30 s at 95 °C, 30 s at 57.4 °C, and 1 min at 72 °C). Takara Ex HS Taq amplification rate is 1–2 kb/min, which cover amplicons of 1000 bp, well within the expected range of 650 bp. The amplification cycles were followed by a final extension at 72 °C for 5 min. Amplified gene fragments were visualized by electrophoresis in a 1% agarose gel. Four specimens of varying sizes were sequenced.

Stable isotope analyses (δ13C and δ15N) were conducted at the University of Bergen. Ethanol-preserved samples were dried at 80 °C for 24 h in glass vials and ground to powder using a glass pestle. Lipids were removed by adding 7% methanol in dichloromethane for 2 h to the dried sample and then removed using a glass Pasteur pipette and again dried for 24 h at 80 °C. Inorganic carbon was removed by adding 0.5 M HCl to the samples. The time for the inorganic carbon to dissolve varied, and the HCl was kept at minimum 5 min or until the reaction was finished. Acid waste was washed away by carefully adding and removing water to the sample until the pH reached 6–7. Finally, the samples were dried and weighed in tin capsules and measured using a Delta V Plus isotope ratio mass spectrometer connected to a Flash EA 1112 elemental analyzer (Thermo Scientific). Isotope ratios are expressed in delta notation as ‰ difference in $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios compared to Pee Dee Belemnite (PDB) and air N2, respectively. Samples were calibrated to internationally acknowledge C and N isotope ratio standards.

Results

Taxonomy

Order: Amphipoda Latreille, 1816
Family: Oedicerotidae Lilljeborg, 1865
Monoculodes Stimpson, 1853: 54
Kroyera Bate, 1857: 140
Monoculodes bousfieldi sp. n.

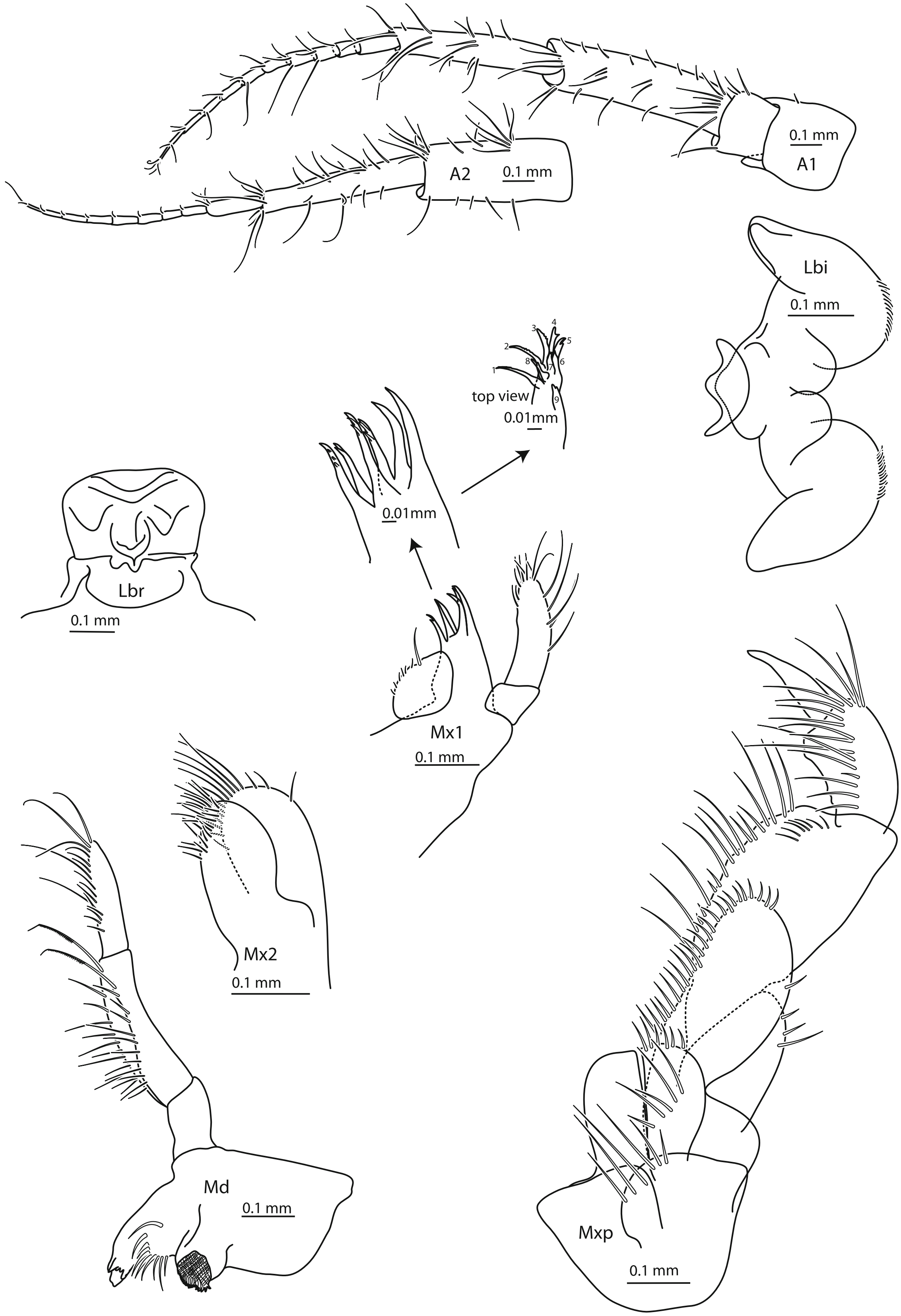

Fig. 1 Head appendages of *Monoculodes bousfieldi* sp. n. All scale bars 0.1 mm, except on enlargement of Mx1 outer plate tip: 0.01 mm. Holotype

Fig. 2 P1-P4 of *Monoculodes bousfieldi* sp. n. All scale bars 0.1 mm. Holotype

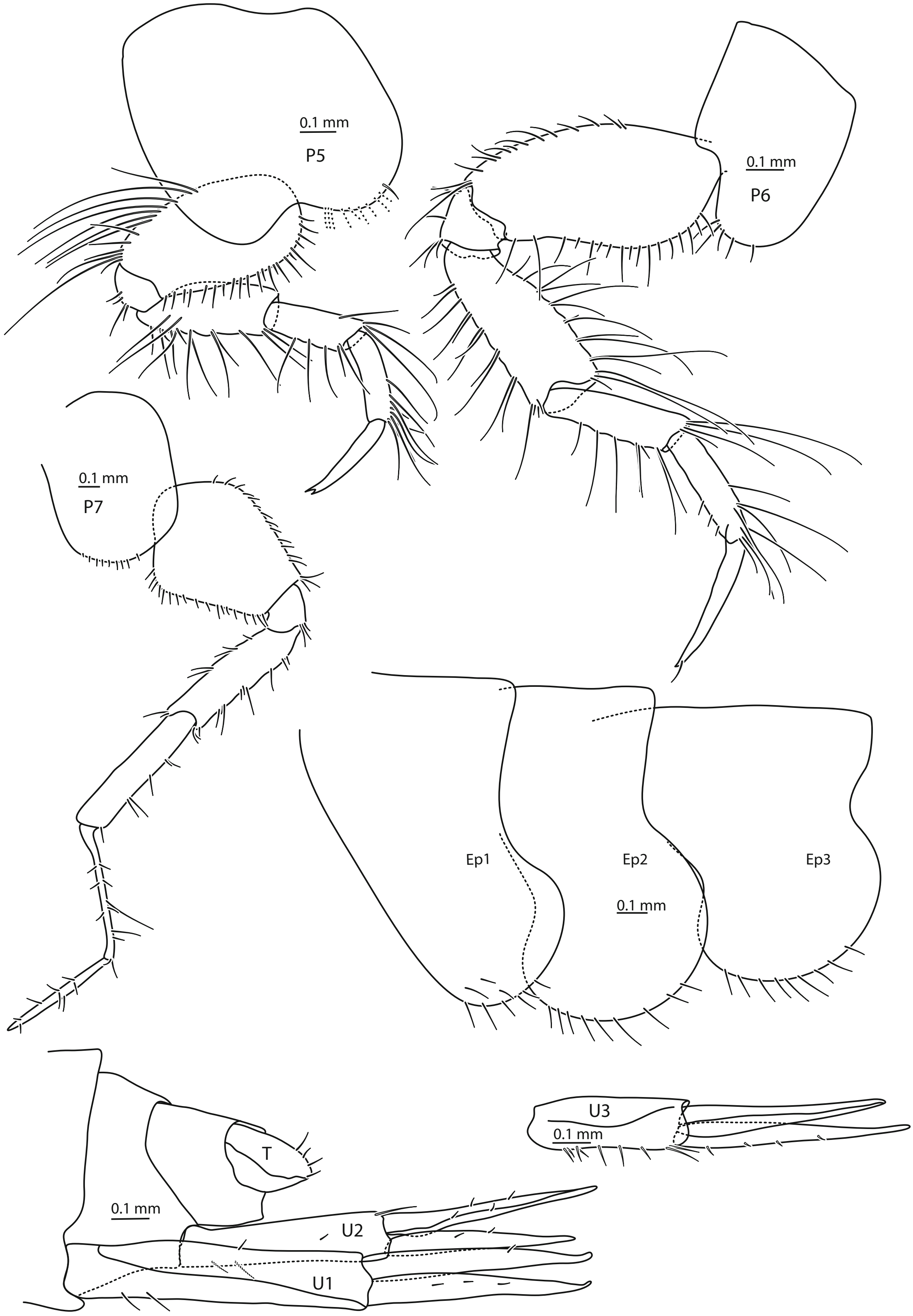

Fig. 3 P5-P7, epimeral plates and urosomal appendages of *Monoculodes bousfieldi* sp. n. All scale bars 0.1 mm. Holotype

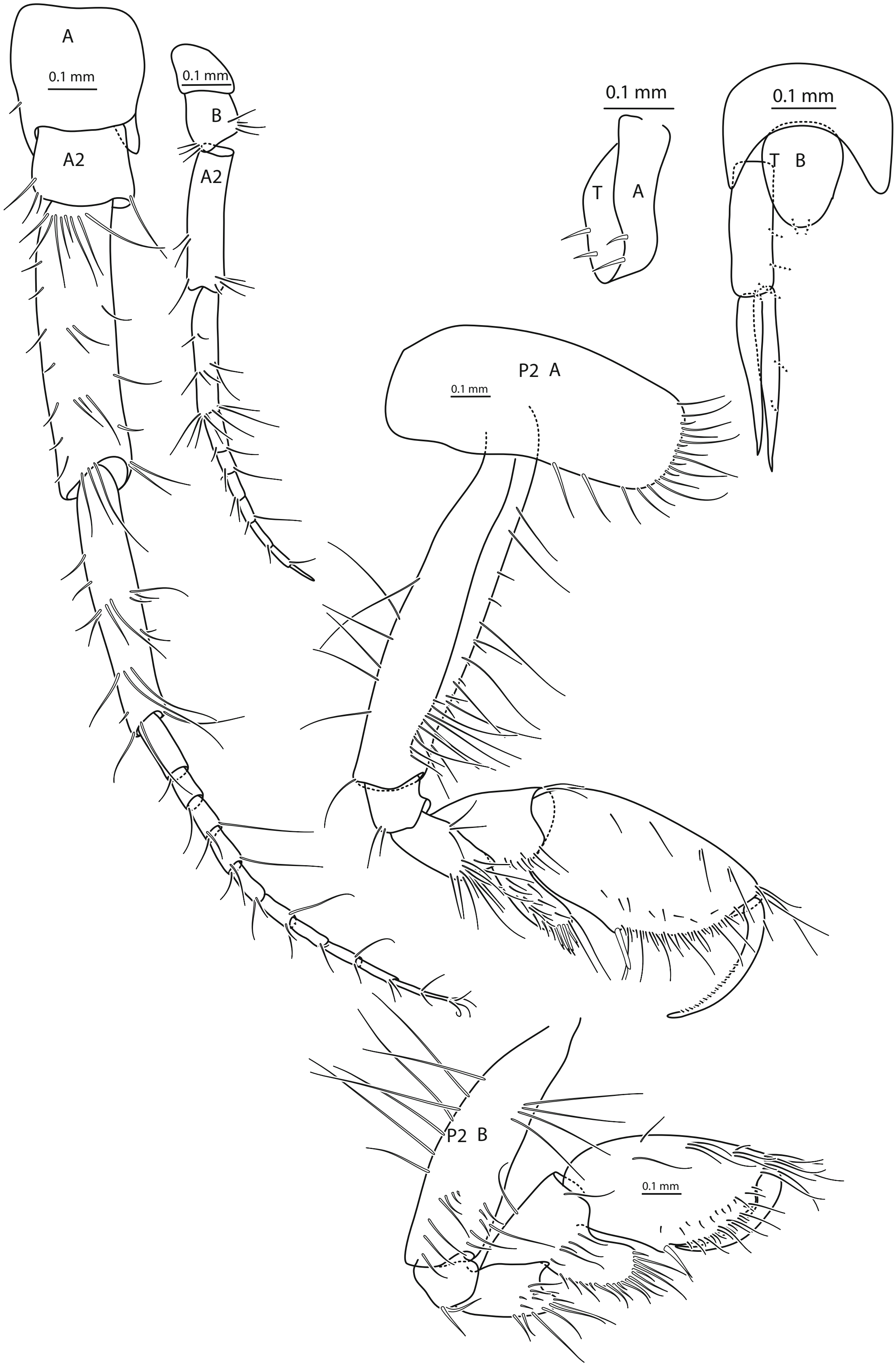

Fig. 4 Intraspecific variations and allometric differences of *Monoculodes bousfieldi* sp. n. Holotype (**a**) and paratype (**b**) of A1, P2, and T

Fig. 5 Map of distribution of blind *Monoculodes s. l.* in the North Atlantic/Arctic Ocean

Type locality: Loki's Castle Hydrothermal Vent in area with diffuse and low-temperature venting (i.e., barite field with turf forming tubeworms like e.g., *Sclerolinum contortum* and *Nichomache lokii*, at appr. 20 °C, 73° 33.9 N 08° 09.7 E, 2350 m depth).

Type material: ZMBN 116915 (holotype: female, 7 mm, slides), ZMBN 116916 (paratype, female, 4 mm, slides), ZMBN 116917 (paratype, slide), ZMBN 116918 (paratype, slide), ZMBN 116919 - ZMBN 116921 ((3 vials: 5 specimens, 2 specimens, 3 specimens) paratypes, wet-material (EtOH)).

Other material: ZMBN 116922 – ZMBN 116929 (8 vials, approximately 30 specimens) wet-material (EtOH) from ROV samples during cruises 2010, 2015, and 2017. Material from ROV samples from cruises 2008 and 2009 (6 vials, EtOH material) was also examined; these have not yet been incorporated in the museum collections. All examined material is from an area of 50 m diameter from the type locality.

Morphological description (holotype) (Figs. 1, 2, and 3):

Body: smooth.

Head: rostrum short, reaching barely 1/3 of article 1 A1, slightly longer than cephalic lobe, slightly curved, subacute; cephalic lobe truncate. Antennae short; A1 half length of A2, articles 1–2 relatively long; both antennae setose. No eyes.

Mouthparts: labrum rounded, mandible with 3-articulate palp, articles 2–3 with setose inner margin, strongly triturative molar, small, serrate incisor; labium bilobed, slightly setose outer lobes; maxilla 1 palp 2-articulate, outer plate with 9 dentate spines, inner plate with one strong and several smaller setae; maxilla 2 lobes subequal, setose inner margin; maxilliped palp 4-articulate, broad, strongly setose inner margin, inner plates separate, outer plates long (reaching half article 2 of palp), nearly as broad as palp article 2.

Pereon: all coxal plates with setal row along distal margin, coxa 1 expanded distally, broader than coxa 2; pereopod 1 propodus subtriangular and broad, palm oblique, and longer than hind margin, carpal lobe broad and 2/3 length of hind propodus margin, dactylus with setule row outer 2/3; pereopod 2 propodus roughly same size as propodus P1 but more elongate, with almost parallel margins, carpal lobe 2/3 length of hind margin propodus, slightly narrow, rounded, dactylus with outer 2/3 setule row; coxa 4 broad and bilobed; Pereopods 5 to 7 with dactylus longer than propodus. (Distal part of P7 of holotype probably damaged, very thin, see Fig. 3. P7 is a very long leg in all Oedicerotids and is typically missing or broken in most specimens. Sadly, this was the case also in our material.)

Table 1 Synoptic table of the blind *Monoculodes* (s. l.)

Species, author	Rostrum length	Lateral cephalic lobe shape	Propodus P1	Carpal lobe P1	Propodus P2	Carpal lobe P2	T shape	T setation	Other details	Eyes	Antennae	Type locality	Geographic distribution
Deflexilodes rostratus (Stephensen, 1931)	Half art 2 A1	Subacute	Subtriangular, more elongate than others	Broad, almost as long as hind margin prop	Elongate	As long as hind margin propodus, broadish	Emarginate	2 setae	Long dactyli	Absent	Aa1 half of a2	S of Iceland, 957 m, ThorStation 166	Norwegian Sea (S of Iceland)
Monoculodes abacus Barnard, 1961	Equal art 1 A1	Slightly round ed truncate	Subtriangular, broad	Short (0.5 prop hind margin) broad, blunt	Subtriangular, broad	Short (0.5 propodus hind margin), broad	Rounded	4 setae		Absent	A1 much shorter than a2	Tasman sea, 610 m (Galathea station 626: 42°10’ S, 170°10′ E)	Tasman sea
M. anophthalma Bellan-Santini, 2007	Shorter than art 1 A1	Subacute	Subtriangular	Short, broad	Subtriangular	Short (0.5 propodus hind margin), narrower than P1	Emarginate (slight excavation)	2 setae		Absent	Equal length, short	Lucky Strike (Menez Hom), 2200 m	Hydrothermal vent, Azores
Monoculodes bousfieldi sp. n.	1/3 of art1 A 1, slightly longer than cephalic lobe	Truncate	Subtriangular, broad	Broad, as long as hind margin prop	Elongate triangular	Narrow, 0.6 hind margin propodus	Rounded	2–4 setae	Slightly shorter than prop, thin	Absent	A1 half of A2, both relatively short – A1, Art1 long	Loki’s Castle	Hydrothermal vent Norwegian sea
M. coecus Gurjanova, 1946	Subequal to art 1, A1	Subacute	Subovate, broad	0.7 hind margin prop, broad	Narrow with parallel margins	Narrow, 0.5 of hind margin propodus, tapering	Truncate, slightly emarginate	None	P3–7 long dactyli	Absent		Cedov stations (1035) 6, 60 & 64: 610–698 m	Arctic Ocean
M. diversisexus JL Barnard, 1967	Short, almost 0.1 of art1, A1 (not exceeding cephalic lobes)	Truncate	Subtriangular, broad	Less than 0.5 prop hind margin, broad, rounded	Slightly elongate subtriangular	Narrow, 0.3 of hind margin propodus	Truncate	2 strong, 4 thin setae	Longer than propodus	Absent		Station 7229, 1720 m (27 N, 115 W)	Cedros Tranch, Baja California
M. latissimanus Stephensen, 1931	3/4 of length art 1 A1	Slightly rounded truncate	Subtriangular, very broad	0.5 length of prop hind margin, broad, sharply cut off	Subtriangular	0.3 propodus hind margin, broad	Truncate	2 strong, 2 thin setae	P3–7 dactlyli very long	Absent	A1 shorter than a2	W. Greenland, 1090 m, Ingolf station 25	W. Greenland
M. neocopinus JL Barnard, 1967	Small, 0.5 art1, A1, as long as cephalic lobe	Truncate	Subovate slightly broad	Broad, as long as hind margin prop	Subovate, slightly broad	Elongate, narrow - as long as hind margin propodus	Truncate	2 strong, 4 thin setae	As long as propodus	Absent	Equal length	Station 7229, 1720 m (27 N, 115 W)	Cedros Tranch, Baja California
M. recandesco JL Barnard, 1967	Not exceeding lateral cephalic lobe	Truncate	Subtriangular, broad	0.7 hind margin prop, broad, rounded	Elongate subtrianguar, slightly broad	0.5 hind margin prop, tapering	Slightly rounded	4 setae	As long as propodus	Absent		Station 7231, 2475 m, (27 N, 115 W)	Cedros Tranch, Baja California
Monoculodes sudor Barnard, 1967	As long as art1 A1	Subacute, with small dent	Rounded triangular, broad	Short (0.2 hind margin prop, broad, rounded	Elongate triangular	Short (0.2 hind margin prop), truncate	Rounded	4 setae	Dactyli as long as propodus, thin	Absent	Subequal, slender	Station 7234, 840 m, (27 N,115 W)	Cedros trench, Baja California

Pleon: Epimeral plates 1–3 rounded, distal margin setose.

Urosome: Uropods 1–3 normal for genus: all uropods biramous, well developed and the tips of all rami reaching as long as the other tips. Telson rounded four thin setae apically.

Intraspecific variation (Figs. 4 and 5): differences between small (young) specimens and larger (older) manifests mainly in an increase in setation of most appendages including antennae, pereopods, and telson. Several smaller specimens (3–5 mm) had only two setae on telson, as well as much less setose antennae, pereopods, coxae, and epimeral plates. Antenna 1 is relatively longer compared with the length of antenna 2 in smaller specimens. The carpal lobe of pereopod 2 seems broader in some of the smaller specimens.

Etymology

This species is named in honor of Edward (Ed) Lloyd Bousfield, a leading Canadian amphipod researcher over many years. Ed reviewed the genus *Monoculodes s. l.* (pp 77–82 in Bousfield and Chevrier, 1996). He passed away September 2016.

Molecular data

Analyses of the COI gene fragment revealed 100% identical sequences in all four specimens, including both smaller and larger specimens. Blast search placed our specimens firmly within the Oedicerotidae, but well separated from other species in the family. Sequences have been submitted to Genbank under the accession numbers MH063526, MH063527, MH063528 and MH063529.

Stable isotopes

The overall stable isotope values for the studied amphipods from Loki's Castle Vent Field (*Exitomelita sigynae*, Calliopiidae indet., and *Laothoes* sp.) have been shown to be quite similar for δ13C values and relatively similar for δ15N, with average values of − 23.47‰ (± 1.1‰ S.D.) for δ13C and − 0.49‰ (± 0.82‰ S.D.) for δ15N (Berntsen 2017). Our data on *Monoculodes bousfeldi* sp. n. fit into the same main values with δ13C the range of − 24.12‰ min (− 23.46‰ mean), − 21.08‰ (max) ± 1.34‰ S.D. and δ15N in the range of − 0.44‰ min (− 0.03‰ mean), 0.82‰ (max) ± 0.54‰ S.D. ($n = 6$).

Discussion

Eleven species of amphipods belonging to five families have so far been identified from the material collected at the Loki's Castle (Tandberg et al. 2017). One other *Monoculodes* species has been described from hydrothermal vents, albeit much further south in the Atlantic: *Monoculodes anophthalma* Bellan-Santini, 2007. Both Lucky Strike and Loki's Castle vent fields have low levels of sulfur and high levels of methane. As is at Loki's Castle, most of the fauna at Lucky Strike seems to be connected to the low-temperature (30–90 °C) areas (Cuvelier et al. 2011), giving relatively similar habitats for the two vent-associated *Monoculodes* species.

Both species are also blind. There are three other blind *Monoculodes s. l.* species described from the same general area as the present species: *Monoculodes latissimanus* Stephensen, 1931 (from W. Greenland), *Monoculodes coecus* Gurjanova, 1946 (Arctic Ocean), and *Deflexilodes rostratus* (Stephensen, 1931) (Norwegian Sea) (Fig. 5). There are very few blind *Monoculodes* species, and a synoptic table (Table 1) clearly shows that the new species does not fit any of the previously described; none of the blind species agrees with the morphology of the present species. The blindness of the *Monoculodes* discussed above does not necessarily mean that these species are phylogenetically close, but it is a good morphological character to use in species identification. For most of the blind species, there is only the type-material, and that often consists of a single specimen. Having examined several specimens of *Monoculodes bousfieldi* sp. n., we see that there are several allometric differences, especially in setosity, and to some degree in the length of the carpal lobe of the gnatopods.

Molecular analysis of our material indicates that all *Monoculodes* specimens from Loki's Castle are conspecific. Comparisons with available molecular data of amphipods (BOLD, GenBank) indicate a close relationship with other Oedicerotidae. There are, however, very few Oedicerotidae sequences available, and only one other COI sequence from a *Monoculodes s. str.* was available prior to this study. All available materials of the morphologically closest species of *Monoculodes* mentioned above have unfortunately been preserved in formalin and are unavailable for molecular analysis. Therefore, we cannot at this stage say anything about genetic distance between morphospecies within this group.

Previous studies of *Exitomelita sigynae* from Loki's Castle have proposed that this amphipod has ectosymbiotic bacteria on the gills and that energy acquisition is through chemosynthetic bacteria (Pedersen et al. 2010; Tandberg et al. 2011). However, stable isotope values from a range of amphipods from Loki's Castle have been studied, among those *Monoculodes bousfeldi* sp. n., and these studies find no direct evidence for symbiosis between amphipods and chemosynthetic bacteria. On the other hand, most species appear to be bacterial consumers, with a possible preference for thiotrophic bacteria (Berntsen 2017). Thus, the primary energy source of for the amphipods at Loki's Castle is most likely bacteria in the sediment and from the chimney walls. The isotope ratios from both large (7–8 mm) and smaller (3–4 mm) specimens are the same—indicating that there is no change in food choice through life.

Monoculodes is a genus/genus complex with a predominantly arctic-arctoboreal distribution; few species are found in warmer waters, and in the southern hemisphere, it is only found at bathyal depths (Bousfield and Chevrier 1996). This distributional pattern fits well with the type locality of our new species, being on an arctoboreal ridge and at 2350 m depth, but maybe not so much with the bottom temperature of 20 °C (sediment surface). There are, however, sharp thermal gradients around the vents, and with negative temperatures only 1 m above the seafloor where the diffuse venting takes place, it is possible that *Monoculodes bousfieldi* lives in ambient temperatures closer to its generic normal.

Key to blind *Monoculodes* s. l.

1. Rostrum very long, reaching halfways along A1 article 2.
   Deflexilodes rostratus (Stephensen, 1931) (Norwegian Sea (S of Iceland)) (7 mm)
   Rostrum shorter than or as long as A1 art1. **2**

2. Gn1 carpal lobe as long as hind margin propodus
   M. neocopinus JL Barnard, 1967 (Cedros Trench, Baja California) (6.5 mm)
   Gn1 carpal lobe clearly shorter than hind margin propodus* (*lobe might be *almost* as long as the hind margin) **3**

3. Rostrum nearly or fully as long as A1 article 1 **4**
   Rostrum reaches not longer than 1/2 A1 article 1 **7**

4. Gn1 carpal lobe very short. Propodus palm extremely oblique, hind margin very short.
   ?*M. sudor* JL Barnard, 1967 (Cedros Trench, Baja California) (11 mm)
   Gn1 carpal lobe at least 1/2 of hind margin propodus **5**

5. Rostrum reaches to end of A1 article 1. Telson rounded or emarginate **6**
   Rostrum reaches to 3/4 of A1 art1. Telson truncate.
   M. latissimanus Stephensen, 1931 (W. Greenland) (7 mm)

6. Telson rounded, with 4 setae.
   M. abacus Barnard, 1961 (Tasman Sea) (4 mm)
   Telson emarginate, bare
   M. coecus Gurjanova, 1946 (Arctic Ocean) (5.5 mm)

7. Rostrum reaches ca 1/2 A1 art1.
   M. anophthalma Bellan-Santini, 2007 (Hydrothermal vent, Azores) (4 mm)
   Rostrum very short, not or scarcely exceeding lateral lobe **8**

8. Rostrum reaches 1/3 of A1 art.1, slightly longer than cephalic lobe. P5–7 dactylus slightly shorter than propodus
   Monoculodes bousfieldi sp. n. (Hydrothermal vent Loki Castle) (3–8 mm)
   Rostrum very short not exceeding lateral lobes. P5–7 dactylus at least as long as propodus **9**

9. Gn 1 carpal lobe 1/2 of hind margin propodus; Gn2 carpal lobe 1/3 of hind margin
   M. diversisexus JL Barnard, 1967 (Cedros Trench, Baja California) (8.5 mm)
   Gn 1 carpal lobe 2/3 of hind margin propodus; Gn 2 carpal lobe 1/2 of hind margin.
   M. recandesco JL Barnard, 1967 (Cedros Trench, Baja California) (6.5 mm)

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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 by the authors.

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.

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