Biogeography and phylogenetic position of *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. from Maritime Antarctic (Nematoda, Nordiidae)

Milka Elshishka¹, Stela Lazarova¹, Georgi Radoslavov¹, Peter Hristov¹, Vlada K. Peneva¹

1 Institute of Biodiversity and Ecosystem Research (IBER), Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria

Corresponding author: Vlada K. Peneva (esn.2006@gmail.com)

Academic editor: S. Subbotin | Received 19 May 2017 | Accepted 5 August 2017 | Published 14 September 2017

http://zoobank.org/BF8C5814-46B7-4D05-9853-54BD25CBDBE1

Citation: Elshishka M, Lazarova S, Radoslavov G, Hristov P, Peneva VK (2017) Biogeography and phylogenetic position of *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. from Maritime Antarctic (Nematoda, Nordiidae). ZooKeys 697: 37–58. https://doi.org/10.3897/zookeys.697.13770

Abstract

The taxonomic position of the endemic Antarctic species *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975) is discussed on the basis of morphological study, including SEM, morphometric data, postembryonic observations, and sequence data of 18S rDNA and the D2-D3 expansion fragments of the large subunit rDNA. A number of characters such as the cuticle and stoma structures, including the presence of moderately developed cuticularised ring around the oral aperture, peculiarities of pharynx expansion, size and position of the posterior pair of pharyngeal nuclei, a less complex uterus, and the position of a posterior ventromedian supplement show that this species differs substantially from the other members of the genus *Enchodelus*. Furthermore, both the 18S and 28S rDNA-based phylogenetic trees of the *Enchodelus* sequences available in the GenBank formed two distinct clusters with *E. signyensis* being a part of a well-supported group with species of the genus *Pungentus*; therefore, it is proposed that its taxonomic position should be reconsidered.

Keywords

Distribution, morphology, SEM, SNPs, taxonomy, 18S and D2-D3 rDNA
Introduction

Antarctic represents unique types of habitats – polar deserts, caused by its geological history, harsh climate conditions, and remoteness. Therefore, terrestrial Antarctic biota, including nematodes, is characterised by a very high degree of endemism and low diversity (Nielsen et al. 2011). Besides, distribution of nematodes exhibits clear biogeographical patterns regarding the two Antarctic ecozones, Continental and Maritime Antarctic (Andrássy 1998a). Order Dorylaimida Pearse, 1942 is represented in Antarctic by nineteen species (12 species described from Maritime Antarctic, 7 species, from the continental part, all but one endemics; of six genera reported from this polar region, two are endemic (Elshishka et al. 2015a). *Enchodelus signyensis* Loof, 1975 is the only representative of the genus *Enchodelus* Thorne, 1939 reported from the southern hemisphere and is an endemic for the Maritime Antarctic. This species was recorded from Signy Island (Spaull 1973) as *Enchodelus* sp. Later Loof (1975) studied Spaull’s collections from some of the islands and described this species as *E. signyensis*, naming it after the type locality. Subsequently, Andrássy (1998a) presented a brief description based on a female paratype specimen. Peneva et al. (2002) provided new morphological data about this species from Livingston Island, and described the males. Here new molecular and additional morphological data is presented of adults and juveniles of this species from Livingston and King George Islands, and its taxonomic position discussed.

Materials and methods

Samples were collected from Livingston Island by Dr. N. Chipev (IBER), Dr. R. Mecheva (IBER), D. Apostolova (Sofia University) and from King George Island by Dr. R. Zidarova (Sofia University) during the regular Bulgarian Antarctic Expeditions (2006-2016). Nematodes were extracted from soils and plant materials by a Baerman funnel method (van Bezooijen 2006) for at least 48 hours, killed by gentle heat, and fixed in 4% formalin. For light-microscopy, specimens were processed in anhydrous glycerine (Seinhorst 1959) and mounted on permanent slides. Drawings were prepared using an Olympus BX 51 compound microscope, equipped with a drawing tube. Photographs were taken using an Axio Imager.M2-Carl Zeiss compound microscope equipped with a digital camera (ProgRes C7) and specialised software (CapturePro Software 2.8). Measurements were made using an Olympus BX 41 light microscope with a drawing tube and digitising tablet (CalComp Drawing Board III, GTCO Cal-Com Peripherals, Scottsdale, AZ, USA) and Digitrak 1.0f computer program (Philip Smith, John Hutton Institute, Dundee, UK).

Specimens used for SEM observations were rinsed in 0.1 M cacodylate buffer (twice for 10 min), post-fixed in 1% OsO$_4$ for 2 h, washed twice for 10 min in 0.1 M cacodylate buffer and dehydrated in an ethanol series (Mutafchiev et al. 2013), immersed in hexamethyldisilazane for 30 min and air dried. They were sputter coated with gold in a JEOL JFS 1200 and examined using a JEOL JSM 5510 microscope at 10 kV.
The locations of pharyngeal gland nuclei are given following Loof and Coomans (1970) and Andrássy (1998b).

**DNA extraction, amplification, and sequencing**

Genomic DNA was extracted from two female specimens per species using a standard nematode digestion protocol (Holterman et al. 2006). The specimens used for DNA extraction, amplification, and sequencing were from King George island (*E. signyensis*) and from Rila Mountain (*Enchodelus* sp.). For further details on the procedures used for DNA extraction, amplification, and sequencing, see Nedelchev et al. (2014). Identical sequences were obtained from both individuals of the same species and have been deposited in GenBank with the following accession numbers: for the 18S rDNA KY881720 (*E. signyensis* gen. n., comb. n.) and KY766261 (*Enchodelus* sp.) and for D2-D3 rDNA KY881719 (*E. signyensis* gen. n., comb. n.) and KY766260 (*Enchodelus* sp.).

**Sequences and phylogenetic analyses**

The 18S and D2-D3 28S rDNA sequences were compared with those of other nematode species available at the GenBank sequence database using BLASTN similarity search tool. The sequences revealing the highest similarity were used for sequence and phylogenetic analyses (Meldal et al. 2007; Holterman et al. 2008; Pedram et al. 2009, 2011a; Pedram et al. 2011b; Pedram et al. 2015, etc.). Bayesian Inference (BI) algorithm implemented in MrBayes 3.2.5 was used for reconstruction of phylogenetic relationships (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012). For further details on phylogeny analyses and tree visualisation, see Lazarova et al. (2016). Based on previous studies (Holterman et al. 2006; Elshishka et al. 2015a) *Aporcelaimellus* spp. were selected as an outgroup for both phylogenies. The estimates of evolutionary divergences between sequences/species within and between groups (numbers of base differences and p-distances) were performed with MEGA7 (Kumar et al. 2016). The analyses involved nine nucleotide sequences with 790 and 1666 positions in total for D2-D3 and 18S rDNA, respectively.

**Taxon treatment**

*Enchodelus signyensis* Loof, 1975

Figs 1–6

**Material examined.** Twenty-eight females and twenty-one juveniles (J1-J4) from Livingston and King George Islands (Table 1).

**Description.** Measurements. See Table 2–4.
### Table 1. Origin of the examined materials of *Enchodeloides signyensis* gen. n., comb. n.

| Site description                      | Collection year | Abbreviation |
|---------------------------------------|-----------------|--------------|
| King George Island (KGI)              | –               | –            |
| **Fildes Peninsula** / Moist brown soil without vegetation, surrounded by moss | 2013            | KGI_F        |
| Livingston Island (LI)                | –               | –            |
| **Svetilishteto**                     | 2006–2007       | LI_SV        |
| Playa Bulgara / Mosses                | 2008            | LI_M         |
| Punta Hesperides / Soil under moss crust | 2010          | LI_PH        |
| Punta Hesperides / Soil               | 2016            | LI_PH_n      |

### Table 2. Morphometrics of *Enchodeloides signyensis* gen. n., comb. n. (females). All measurements, unless indicated otherwise, are in μm (and in the form: mean±SD (range)).

| Locality                     | King George Island | Livingston Island |
|------------------------------|--------------------|-------------------|
|                              | KG1_F              | KG1_M             |
| n                            | 7                  | 4                 | 12 | 2 |
| L (mm)                       | 1.59±0.1           | 1.45±0.05         | 1.43; 1.51; 1.44 | 1.35±0.1 (1.20–1.45) | 1.27, 1.37 |
| a                            | 28.9±1.9 (26.9–32.8) | 28.1±1.2 (26.7–29.5) | 28.5; 31; 27 | 29.5±1.4 (27.6–32.4) | 26.1, 28.2 |
| b                            | 5.3±0.3 (4.7–5.6)   | 4.8±0.2 (4.6–4.9)  | 5; 5; 4.8   | 4.5±0.2 (4.2–4.8) | 4.1, 4.6 |
| c                            | 43.7±2.1 (40.6–46.9) | 48.2±3.1 (43.8–50.7) | 49.3; 48; 44.8 | 43.7±3.9 (37–50) | 50.1, 53.2 |
| c’                           | 1.0±0.04 (1.0–1.1)  | 1.0±0.1 (0.9–1.0)  | 0.9; 1.0; 1.0 | 1.0±0.1 (0.8–1.1) | 0.9, 0.9 |
| V %                          | 50.4±0.7 (49.5–51.5) | 53.8±1.3 (52–55) | 51; 54; 53 | 54.4±1.0 (52–56) | 55, 56 |
| Lip region diameter          | 14.3±0.4 (14–15)   | 14.2±0.2 (14–14.4) | 14; 14; 15 | 14.1±0.7 (13–15) | 14, 13 |
| Odontostyle length           | 19.9±0.8 (19–21)   | 18.9±0.7 (18–19.5) | 19; 20; 20 | 19.2±0.8 (18–20) | 18, 19 |
| Odontophore length           | 25.2±0.8 (24–26.5) | 26.5±0.4 (26–27)  | 25; 23.5; 25 | 26.4±2.8 (22–32) | 27, 26 |
| Anterior end to guiding ring  | 12.0±0.7 (11–13)   | 12.6±0.3 (12–13)  | 12; 11; 12 | 12.1±0.6 (11–13) | 12, 12 |
| Pharynx length               | 297.8±11.4 (277–310) | 304.0±3.8 (302–308) | 283; 301; 297 | 302.2±11.8 (271–314.5) | 307, 300 |
| Pharyngeal base diameter     | 51.5±3.8 (45–55)   | 46.7±2.4 (44–49)  | 47; 45; 47.5 | 43.3±2.9 (38–46.5) | 45, 45.5 |
| Mid-body diameter            | 55.2±3.5 (50–60)   | 51.8±1.8 (49–54)  | 50; 49; 53 | 45.9±3.8 (39–51) | 48, 48.5 |
| Prerectum length             | 104.2±32.2 (72–166) | –                 | 71           | 84.5±24.5 (62–128) | –, 75 |
| Rectum length                | 36.4±3.0 (32–40)   | 32, 46           | 30.5; 37; 41 | 33.4±2.0 (31–36.5) | –, 37.5 |
| Tail length                  | 36.4±2.1 (32–39)   | 30.3±2.7 (28–34)  | 29; 31.5; 32 | 31.2±3.4 (25–35) | 25, 26 |
Female. Habitus curved ventrally after fixation, adopting a C-shape. Cuticle consisting of four layers with different refraction, the outer two layers thinner, the second outer with stronger refraction, the inner layers thicker, especially at tail region. Cuticle 2–3 µm thick at postlabial region at the level of the guiding ring, 2–4 µm at mid-body and 4–6 µm on tail; outer layer with very fine transverse striations, innermost layer coarsely striated (Figs 1, 2). Lip region 4–5 µm high angular (following terminology adopted by Pena-Santiago (2006)), offset from the adjoining body by a constriction; about 3 times as wide as high. Based on SEM photographs (Fig. 3), perioral area high, disc-like structure with apparently four elevations surrounding oral aperture, oral aperture appearing cross-like in shape in frontal view. Labial and cephalic papillae prominent; labial papillae button-like, each surrounded by a small ring, their openings pore-like. Inner labial papillae located at distinct elevations; separated from each other, and far from oral aperture and outer labial papillae; divided from the outer labial and cephalic papillae by a circular striation (Fig. 3). Cephalic papillae button-like; outer labial and cephalic papillae below the margin of oral field. Six radial striations beginning from the oral field interrupted by inner and ending at outer labial papillae. Amphidial fovea cup-shaped, its aperture approximately half of lip region diameter, its margin curved; under SEM, the amphidial aperture with an operculum, however the presence of this structure should be confirmed with further studies. Cheilostom a truncate cone with weakly developed walls, its anteriormost part representing a moderately cuticularised perioral ring, appearing as small perioral refractive dots. Odontostyle short and slender, straight, 18–20 times as long as wide, 1.2–1.6 times lip region diameter, aperture 14–16% of its length, 1.2–1.7% of body length. Odontophore 1.2–1.6 times as long as odontostyle, with small swellings at its base. Guiding ring double, located at 0.8–1.0 times lip region diameter from anterior end. Anterior region of pharynx enlarging gradually; pharyngeal expansion 112.5–134 µm, occupying 37–45% of total pharynx length. Location of pharyngeal gland nuclei and their orifices is presented in Table 3. Distance DO-DN 14–19 µm, nuclei of dorsal and second ventrosublateral glands clearly visible, nuclei of first ventrosublateral glands in most specimens indistinct, located slightly behind the middle of the distance DN-S\textsubscript{2}N (n = 1). Nuclei of dorsal glands 3.5–5 µm diameter, first and second pair ventrosublateral 1 µm and 2–3 µm, respectively. Excretory pore opposite the nerve ring with slightly cuticularised canal clearly visible at 100–112 µm from the anterior end. Cardia rounded conoid. Prerectum 1.7–4.8, rectum 0.9–1.4 times anal body diameter long. Tail bluntly conoid, 2–3% of body length, with numerous saccate bodies. Hyaline part 4–8 µm wide or 12–25% of tail length. Two pairs of caudal pores present. Both branches of female genital system equally and well-developed (in specimens of Livingston Island shorter: anterior 236.2 ± 23.3 (186–275) µm and posterior 208.2 ± 34.4 (143–259) µm long, in specimens from King George Island anterior 298.3 ± 31.9 (245–330) µm and posterior 323.1 ± 46.4 (243–361) µm long). Ovaries short, rarely reaching sphincter level; oviduct with well-developed pars dilatata. Sphincter well developed. Uteri tubular, thick walled, surrounded by hyaline cells along almost the whole length, anterior uterus 104–152 µm long, posterior 105–156 µm long, 2–3 times correspond-
Figure 1. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). **Female.** A–E Anterior region (A, B specimens from Livingston Island C, D, E specimens from King George Island), black arrows indicate the minute basal swellings F, G Amphideal fovea (E specimen from Livingston Island G specimen from King George Island) H, I Entire body J, K Pharyngeal bulb (J specimen from Livingston Island K specimen from King George Island) L Posterior genital branch (specimen from Livingston Island) M Uterus (specimen from Livingston Island) N–Q Vulval regions (N, O specimens from Livingston Island P, Q specimens from King George Island). Scale bars: 10 μm (A–G, J, K, M–Q); 200 μm (H, I); 20 μm (L).
Biogeography and phylogenetic position of Enchodeloides signyensis (Loof, 1975), gen. n...

Figure 2. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). Female: A–D Tail ends (A specimen from King George Island; B, C, D specimens from Livingston Island) E–G Tail ends with saccate bodies (E specimen from King George Island F, G specimens from Livingston Island). Scale bar: 10 µm.

...ing body diameter, not differentiated. Vulva a transverse slit. Vagina extending inwards for 54–76% of body diameter; *pars proximalis* 19.5–25×12–15 µm, *pars refringens* with two drop shaped sclerotised pieces, with combined width of 11–13 µm, *pars distalis* 4–5 µm long.

**Juveniles.** Based on morphometrics of juvenile specimens and the relationships between the lengths of their functional and replacement odontostyles and body lengths, four juvenile stages were identified (Figs 4–7). Habitus in first juvenile stage slightly ventrally curved, lip region flat, continuous with the body, genital primordium 11–12 µm long, tail conical elongated with long central peg (Figs 4–6). Tail in J2 and J3 conoid elongated in J4 bluntly conoid as in females with numerous saccate bodies on tail, c’ decreasing during the successive stages to J4 and females.

**Sequences and phylogenetic analyses.** The phylogenies based on both gene regions showed that *Enchodelus* sp. and *E. signyensis* are parts of two distantly related and well-supported groups (I and II), and in both analyses, they revealed similar relationships with other dorylaimid species (Figs 8, 9). With one exception (AY593052, *E. macrodorus* (de Man, 1880) from The Netherlands), *E. signyensis*, was evolutionary close to *Pungentus* spp. (AY593050, AY593052–53 for D2-D3 28S, and AJ966501
Figure 3. SEM micrographs. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). **Female**: A, D, E Lip region, in face view, amphid aperture B, F Lip region, in sublateral view C Cephalic and labial papillae G–I Vulval region J–L Tail ends. Scale bars: 2 µm (A, C, D, E, F, G); 5 µm (B, I, J); 10 µm (L).

and AY284788 for 18S rDNA) while, *Enchodelus* sp. from Bulgaria clustered with other *Enchodelus* spp. from the Netherlands and Iran being a part of well-supported clade including species of various genera (*Eudorylaimus* Andrássy, 1959, *Epidorylaimus* Andrássy, 1986, *Prodorylaimus* Andrássy, 1959 and *Crassolabium* Yeates, 1967).

The estimates of evolutionary divergences (p-distances) between D2-D3 28S rDNA sequences within and between both groups are presented in Table 5. The dis-
### Table 3. Morphometrics of *Enchodeloides signyensis* gen. n., comb. n. (juveniles). All measurements, unless indicated otherwise, are in µm (and in the form: mean±SD (range)).

| Location        | Characters | Livingston Island | King George Island |
|-----------------|------------|-------------------|--------------------|
|                 | LI_S       | LI_M              | LI_PH_n            | KGI      |
| **Stages**      |            |                   |                    |          |
| n               | 6          | 1                 | 1                  | 7        |
| **L (mm)**      | 0.40±0.1   | 0.60, 0.62        | 0.7                | 1.02±0.1 |
|                 | (0.37–0.42)|                   | (0.93–1.13)        | 1.03     |
| **a**           | 26.5±1.1   | 27.0, 27.5        | 27                 | 28.9±1.8 |
|                 | (24.7–27.9)|                   | (26.8–31.7)        | 26.9     |
| **b**           | 3.2±0.5    | 3.6, 3.8          | 3.5                | 3.9±0.2  |
|                 | (2.9–4.2)  |                   | (3.7–4.1)          | –        |
| **c**           | 13.6±0.9   | 24.7, 26.2        | 27.6               | 36.8±2.3 |
|                 | (12.8–14.8)|                   | (33.7–39.6)        | 35.5     |
| **c’**          | 2.8±0.2    | 1.5, 1.5          | 1.4                | 1.1±0.1  |
|                 | (2.6–3.1)  |                   | (1.0–1.2)          | 1.1      |
| **Lip region diameter** | 7.3±0.2 | 8.5, 8            | 11                 | 11.8±0.3 |
|                 | (7–7.5)    |                   | (11–12)            | 11       |
| **Odontostyle length** | 6.6±0.4  | 8, 8              | 11                 | 14.7±0.2 |
|                 | (6–7)      |                   | (14–15)            | 15       |
| **Replacement odontostyle length** | 8.2±0.2  | 11, 10             | 14              | 18.5±0.4 |
|                 | (8–8.3)    |                   | (18–19)            | 20       |
| **Pharynx length** | 126.2±15.9 | 165.5, 163      | 200.5              | 258.8±14.2 |
|                 | (95–140)  |                   |                    | (244–281)|
| **Pharyngeal base diameter** | 16.0±0.3  | 23, 23            | 27               | 35.3±2.5 |
|                 | (15.6–16.3)|                   | (32–40)            | 36       |
| **Mid-body diameter** | 15.0±0.4 | 22, 23            | 26               | 35.4±2.9 |
|                 | (14–15.5) |                   | (31–40)            | 38.5     |
| **Prerectum length** | 35 | –                 | –                | 87, 110  |
| **Rectum length** | 14.5 | –                 | –                | 25.5±2.7 |
|                 |           |                   |                   | (21.5–28.5)|
| **Tail length** | 29.6±2.2  | 24, 24            | 25               | 27.7±1.2 |
|                 | (27–31)   |                   | (26–30)            | 29       |

Similarity between *E. signyensis* and other *Enchodelus* spp. is very high, varying from 16.6% to 17.1% while within **group II** the distances between sequences are between 0.8–7.1%. The dissimilarity within **group I** varies from 0.1% to 7.6% with the highest values (7.4–7.6%) estimated from pair-wise comparison of *E. signyensis* to other sequences within the group. A similar pattern was observed when 18S rDNA evolutionary divergences were analysed. Although having much lower resolution, the 18S rDNA distance of *E. signyensis* to other *Enchodelus* species available at NCBI was 2.6–2.8% (or 44–47 nucleotides). This species was the most closely related to two *Pungentus* spp. from Europe (AJ966501 and AY284788) showing 1.4–1.6% dissimilarity (or 24–26 nucleotides difference). The SNPs analyses of the parsimony-informative sites between sequences for *Enchodeloides* gen. n., *Enchodelus* and *Pungentus* Thorne & Swanger, 1936 and for both genes are given as Suppl. materials 1 and 2.
Figure 4. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975).

Juveniles: **A–D** Anterior ends (J1-J4) (specimens from Livingston Island) **Female** (specimen from Livingston Island) **E** Anterior end **F** Amphideal fovea **G** Pharyngeal bulb. *Enchodelus groenlandicus* (Ditlevsen, 1927) **H** Pharyngeal bulb. Scale bar: 50 µm.
Biogeography and phylogenetic position of *Enchodeloides signyensis* (Loof, 1975), gen. n...

**Table 4.** Pharyngeal characters of *Enchodeloides signyensis* gen. n., comb. n. For abbreviations see Loof & Coomans (1970) and Andrássy, 1998b.

|                | LI | LI\_PH | LI\_S | KGI_F |
|----------------|----|--------|-------|-------|
| DN=D           | 67–70 | 69     | 72, 68 | 63–67 |
| DO             | 64, 64, 62 | 63     | 66, 62 | 55–63 |
| S, N\_1        | –   | –      | 80    | –     |
| S, N\_2        | –   | –      | 79    | –     |
| S, N           | 89–91| 90, 91 | 92, 90 | 89–90 |
| S, O           | 92  | –      | 93    | 90, 91|
| A, S\_1        | –   | –      | 37    | –     |
| A, S\_2        | –   | –      | 35    | –     |
| P, S\_1        | 65–71| 70     | 71, 68 | 67–74 |
| P, S\_2        | 66–72| 68     | 70, 69 | 67–72 |

**Table 5.** Genetic distances using D2-D3 28S rDNA sequence data (p-distances given in percents). Pairwise comparisons are based on alignment with 790 nucleotide positions (all positions containing gaps were eliminated).

| Sequence number/species | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  |
|-------------------------|----|----|----|----|----|----|----|----|----|
| KY881719 *E. signyensis* gen. n., comb. n., Antarctica | 1.0 |     |     |     |     |     |     |     |     |
| 2 AY593050 *Pungentus engadinensis* (Altherr, 1950) Altherr, 1952 | 7.1 | 7.6 |     |     |     |     |     |     |     |
| 3 AY593052 *Pungentus silvestris* (de Man, 1912) Coomans & Geraert, 1962, 1 NL | 7.4 | 2.7 |     |     |     |     |     |     |     |
| 4 AY593053 *P. silvestris* 2, NL | 7.5 | 2.8 | 0.1 |     |     |     |     |     |     |
| 5 AY593054 *Enchodelus macrodorus* (de Man, 1880) Thorne, 1939, NL | 7.5 | 2.8 | 0.1 | 0.3 |     |     |     |     |     |
| 6 KY766260 *Enchodelus* sp., Bulgaria | 17.1 | 17.3 | 16.0 | 16.2 | 16.2 |     |     |     |     |
| 7 EF207240 *Enchodelus* sp., NL | 16.6 | 16.1 | 14.9 | 15.0 | 15.0 | 6.5 |     |     |     |
| 8 KP190119 *E. longispiculus* Guerrero, Liébanas & Peña-Santiago, 2008, Iran | 17.0 | 17.1 | 15.9 | 16.0 | 16.0 | 0.8 | 6.3 |     |     |
| 9 KP190120 *Enchodelus* sp. 1, Iran | 17.1 | 17.3 | 16.0 | 16.2 | 16.2 | 1.5 | 7.1 | 1.2 |     |

**Discussion.** Based on the main morphological characters, the studied populations are very similar, but specimens from King George Island differ by a somewhat longer (average 1.47–1.66 vs 1.20–1.51 mm), and wider body (55.2 ± 3.5 (50–60) μm vs 48.0±3.9 (39–54) μm), longer female genital branches (anterior 298.3±31.9 (245–330) μm and posterior 323.1 ± 46.4 (243–361) μm vs 236.2 ± 23.3 (186–275) μm and 208.2 ± 34.4 (143–259) μm, respectively, vulva position (V=50.4 ± 0.7 (49.5–51.5)% vs V=54.1±1.3 (51–56)%), and tail (32–39 vs 25–35 μm). The specimens examined generally agree well with data previously reported for this species (Loof 1975; Andrássy 1998a; Peneva et al. 2002), although some minor differences occurred: our populations have somewhat shorter body length (1.20–1.66 vs 1.37–1.88 mm) and the presence of a moderately developed cuticularised ring around the oral aperture has
Figure 5. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). 
*Juveniles* (specimens from Livingston Island): **A–D** Tail ends (J1) **E–G** Tail ends (J2–J4) **Female** (specimen from Livingston Island) **H** Tail end. Scale bar: 50 µm.

Figure 6. *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). 
*Juveniles* (specimens from Livingston Island): **A–D** Anterior ends (J1–J4) **F–I** Tail ends (J1–J4) **Female** (specimen from Livingston Island) **E** Anterior end **J** Tail end. Scale bar: 10 µm.

not been described in those studies. Although *E. signyensis* resembles members of the genus *Enchodelus* in many respects, this structure has not been reported for any of its species. The number of morphological characters (see below), as well as molecular data, do not support the current taxonomic position of this species as a member of the genus *Enchodelus* and therefore a new genus *Enchodeloides* gen. n. is proposed.
Biogeography and phylogenetic position of *Enchodeloides signyensis* (Loof, 1975), gen. n...

**Figure 7.** *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975). Scatter plot of the functional (○) and replacement odontostyle (∇) in relation to the body length of the juvenile stages and females.

*Enchodeloides* gen. n.
http://zoobank.org/0AFC0BD5-CA16-4A19-9165-16CD7EE71176

**Diagnosis.** Nordiidae. Nematodes of medium size. Cuticle dorylaimoid, consisting of four layers, outer layer finely, inner layer coarsely transversally striated. Lip region angular; stoma entrance surrounded by a moderately developed cuticularised ring, appearing as small perioral refractive dots. Amphidial fovea cup-shaped, its aperture about half of lip region diameter, curved. Odontostyle short and slender, straight. Odontophore with small swellings. Guiding ring double. Anterior region of pharynx enlarging gradually into pharyngeal expansion. Posterior pair of pharyngeal nuclei smaller than dorsal nucleus, located posteriorly in pharyngeal expansion. Cardia rounded conoid. Female genital system amphidelpthic. Uterus not differentiated. Vagina moderately sclerotised. Vulva a transverse slit. Males rare. Spicula stout ventrally curved. Lateral guiding pieces present. Sperm cells spindle-shaped. Supplements 2 to 4 in number preceded by an ad-cloacal pair of papillae, starting far behind the level of the spicules. Tail bluntly conoid, with numerous saccate bodies on tail. First juvenile stage with elongate conical tail with long central peg.

**Relationships.** The new genus resembles members of the subfamily Pungentinae Siddiqi, 1969, especially the genera *Enchodelus*, *Pungentella* Andrássy, 2009, *Pungentus* and *Stenodorylaimus* Álvarez-Ortega & Peña-Santiago, 2011. It differs from *Enchodelus* by having lip region with six radial striae starting from inner and ending at outer labial papillae *vs* absent (seen under SEM), four *vs* three layered cuticle, two *vs* one thicker inner layer at tail region (under light microscopy), cheilostom thin walled *vs* thick walled, a moderately developed cuticularised ring around the oral ap-
Figure 8. Phylogenetic relationships of *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975) based on 18S rDNA inferred from a Bayesian analysis (GTR+G model) and two *Aporcelaimellus* species used as an outgroup. *Thonus* is currently considered a synonym of *Cras-solabium* (Peña-Santiago and Ciobanu, 2008).

erture vs absent; less developed vs well developed basal swellings; a pharynx enlargement gradually expanding vs abruptly expanding into basal expansion (Fig. 4G, H), the posterior pair of pharyngeal nuclei generally smaller than dorsal nucleus vs as
Figure 9. Phylogenetic relationships of *Enchodeloides signyensis* (Loof, 1975), gen. n., comb. n. (= *Enchodelus signyensis* Loof, 1975) based on 28S rDNA D2-D3 inferred from a Bayesian analysis (GTR+G model) and two *Aporcelaimellus* species used as an outgroup. *Thonus* is currently considered a synonym of *Crassolabium* (Peña-Santiago & Ciobanu, 2008).

large as dorsal nucleus (Andrássy 2009), except for *E. macrodorus* Thorne, 1939 (Guerrero and Peña-Santiago 2007) and located more posteriorly, more than 89% vs 83–88% of the pharyngeal expansion (Loof and Coomans 1970); less complex uterus vs tripartite (bipartite in *E. distinctus* Ahmad & Jairajpuri, 1980 and *E. pono-rens* Popovici, 1995); posteriormost ventromedian supplement located at a considerable distance from the adcloacal pair and outside of the spicule range vs posteriormost one or two ventromedian supplements rather close to the adcloacal pair.
and inside the spicule range, 2–4 vs 7–16 in number, and finally, all representatives of the genus *Enchodelus* have been reported only from the northern hemisphere. *Enchodeloides* gen. n. differs from *Pungentella* by having transversally striated cuticle vs smooth; a longer odontostyle (much longer vs equal to or slightly longer than lip region diam.) with a smaller aperture (up to one-sixth vs one-fourth to one-third its length); a moderately developed cuticularised ring vs four small platelets around the oral aperture and the guiding ring double vs simple. From *Pungentus* it differs in having a moderately developed cuticularised ring vs four distinct circumoral platelets around the oral aperture; a straight vs arcuate odontostyle; shorter odontostyle (1.2–1.6 times vs 2–3 times lip region diameter (Andrásy 2009a); the first pair of ventrosublateral pharyngeal gland nuclei indistinct, difficult to observe vs well developed; a long distance DO-DN (5–6% vs 2–4% (Loof and Coomans 1970)); ventromedian supplements located at a considerable distance from the adcloacal pair and outside of the spicule range vs posteriormost 1–4 supplements lying within the spicule range, and with vs without hiatus. From the genus *Stenodorylaimus* it differs by having a shorter body (L=1.2–1.9 vs 3.7–5.1 mm), and a slender vs more robust odontostyle (1.2–1.7 vs 0.51–0.87% of body length); a longer pharynx (b-ratio up to 6 vs more than 7); saccate bodies present vs absent; the first pair of ventrosublateral pharyngeal gland nuclei indistinct, difficult to observe vs well developed; ventromedian supplements spaced vs irregularly spaced, 2–4 vs 14–19 in number, and with vs without hiatus.

Consequently, the new combination *Enchodeloides signyensis* (Loof, 1975) is proposed to accommodate the only nordiid species occurring in Maritime Antarctic.

**Distribution**

*Enchodeloides signyensis* is a widespread endemic for the Maritime Antarctic, occurring in several islands: Signy (Loof 1975; Maslen 1981; Caldwell 1981), Coronation, Elephant, Galindez, Blaiklock (Loof 1975), Alamode (Loof 1975; Maslen and Convey 2006), Dream (Shishida and Ohyama 1989), Charcot (Convey et al. 2000; Maslen and Convey 2006), Livingston (Peneva et al. 2002, 2004; Elshishka et al. 2015b), Alexander (Maslen and Convey 2006), and King George Islands (Russell et al. 2014). It has been recorded from various microhabitats, different moss and algae communities, and in association with species of higher plants, reported from Maritime Antarctic (*D. antarctica* and *C. quitensis*) (Table 6). Data from previous records and the present study show that *E. signyensis* is associated with different type of microhabitats. Like other terrestrial nematodes in extreme polar conditions, a majority of which colonise all microhabitats, this species does not show specific biotope preferences. According to Chernov et al. (2011) the major life strategy of organisms inhabiting extreme environments is the development of tolerance and plasticity, not specialisation and competitiveness, which is typical of other biomes.
Table 6. Distribution of *Enchodeloides signyensis* gen. n., comb. n. in Antarctic islands and habitats.

| Island        | Microhabitats and plant associations                                                                 | References         |
|---------------|------------------------------------------------------------------------------------------------------|--------------------|
| Signy         | *Tortula excelsa* Card (type host)                                                                  | Loof 1975          |
|               | *Deschampsia antarctica* Desv.                                                                     |                    |
|               | *Colobanthus quitensis* (Kunth) Bartr.                                                              |                    |
|               | *Polytrichastrum alpinum* (Hedwig). *Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth., *Sanionia uncinata* (Hedw.), *Calliergon seretosum* (Wahlenb.), *Calliergidium austro-stramineum* (C. Muell.) Bartr. | Maslen 1981        |
| Coronation    | *D. antarctica*                                                                                     | Loof 1975          |
| Elephant      | *D. antarctica*                                                                                      |                    |
|               | *Polytrichum* sp.                                                                                    |                    |
| Galindez      | *D. antarctica*                                                                                      |                    |
| Blaiklock     | *P. alpinum, Poblia nutans* (Hedw.)                                                                 |                    |
| Alamode       | *S. uncinata*                                                                                        | Maslen and Convey 2006 |
|               | Moss                                                                                                |                    |
| Dream         | Moss mats with green algae                                                                         | Shishida and Ohyama 1989 |
| Charcot       | Soil, moss clumps, algae, various lichens                                                           | Convey et al. 2000 |
|               | Moss, lichen and soil                                                                               | Maslen and Convey 2006 |
| Livingston    | *D. antarctica, S. uncinata, Sanionia georgico-uncinata* (Müll. Hal.) Ochyra & Hedenäss, *C. quitensis, P. alpinum, Bryum sp., Usnea sp., Cladonia sp.*, *Polytrichum juniperinum* Hedw., *Bartramia patens* Brid. | Peneva et al. 2002 |
|               | Moss; soil under moss crust; soil                                                                   | Present study       |
| Alexander     | Moss; lichen; soil; microbial mat                                                                    | Maslen and Convey 2006 |
| King George   | *D. antarctica, C. quitensis, Sanionia sp., Syntrichia filaris* (Müll.Hal.), *Syntrichia magellanica* (Mont.) | Russell et al. 2014 |
|               | Moist brown soil without vegetation, surrounded by moss                                             | Present study       |

Acknowledgements

This study was funded by the project № 64/27.04.2016, the program for career development of young scientists, Bulgarian Academy of Sciences. The authors are thankful to Dr. R. Zidarova, Dr. N. Chipev, Dr. R. Mecheva, and D. Apostolova for collecting the samples, to Mr. N. Dimitrov (Faculty of Chemistry and Pharmacy, Sofia University) for his assistance with SEM photographs. The authors are thankful to Dr Nathalie Yonow from Swansea University, Wales, UK for critical reading of the manuscript and helpful suggestions.

References

Ahmad M, Jairajpuri MS (1980) A review of the genus *Enchodelus* Thorne, 1939 with descriptions of species from India. Records of the Zoological Survey of India, Miscellaneous Publication Occasional Paper 15: 1–42.
Altherr E (1952) Les nématodes du Parc National Suisse. 2e partie. Ergebnisse der wissenschaftlichen Untersuchung des schweizerischen Nationalparks 3: 315–356.
Altherr E (1950) Les nématodes du Parc National Suisse. Ergebnisse der wissenschaftlichen Untersuchung des schweizerischen Nationalparks 1: 1–46.
Álvarez-Ortega S, Peña-Santiago R (2011) Re-description of two atypical species of Pungentus Thorne & Swanger, 1936, with proposal of Stenodorylaimus gen. n. (Nematoda, Dorylaimida, Nordiidae). Zootaxa 2799: 49–62. https://doi.org/10.5281/zenodo.203129
Andrássy I (1959) Taxonomische Übersicht der Dorylaimen (Nematoda), I. Acta Zoologica Budapest 5: 191–240.
Andrássy I (1986) The genus Eudorylaimus Andrássy, 1959 and the present status of its species (Nematoda: Qudsianematidae). Opusculla Zoologica Budapest 22: 3–42.
Andrássy I (1998a) Nematodes in the Sixth Continent. Journal of Nematode Morphology and Systematics 1: 107–186.
Andrássy I (1998b) Once more: the oesophageal gland nuclei in the dorylaimoid nematodes. Opuscula Zoologica, Institutio zoosystematici Universitatis Budapestinensis 31: 165–170.
Andrássy I (2009) Free-living nematodes of Hungary (Nematoda errantia), III. (Csuzdi C, Mahunka S (Eds.) Pedozoologica Hungarica No 5. Budapest, Hungary, Hungarian Natural History Museum and Systematic Zoology Research Group of the Hungarian Academy of Sciences, 608 pp.
Caldwell J R (1981) The Signy Island terrestrial reference sites: XIII. Population dynamics of the nematode fauna. British Antarctic Survey 54: 33–46.
Chernov YuI, Matveeva NV, Makarova OL (2011) Polar deserts: At the limit of life. Priroda 9: 31–43. [In Russian]
Convey P, Smith RIL, Peat HJ, Pugh PJA (2000) The terrestrial biota of Charcot Island, eastern Bellingshausen Sea, Antarctica: an example of extreme isolation. Antarctic Science 12: 406–413. https://doi.org/10.1017/S095410200000047X
Coomans A, Geraert E (1962) Some species of Dorylaimoidea found in Belgium. Nematologica 8: 233–241. https://doi.org/10.1163/187529262X00495
de Man JG (1880) Die einheimischen, frei in der reinen Erde und im sussen Wasser lebenden Nematoden. Tijdschrift Nederlandsche Dierkundige Vereeniging 5: 1–104.
de Man JG (1912) Helminthologische Beiträge. Zoologischer Jaarbuch, Jena 15: 439–464.
Ditlevsen H (1927) Free-living nematodes from Greenland, Land and Freshwaters. Meddelejer om Grønland 23: 159–178.
Elshishka M, Lazarova S, Radoslavov G, Hristov P, Peneva VK (2015a) New data on two remarkable Antarctic species Amblydorylaimus isokaryon (Loof, 1975) Andrássy, 1998 and Pararhyssocolpus paradoxus (Loof, 1975), gen. n., comb. n. (Nematoda, Dorylaimida). ZooKeys 511: 25–68. https://doi.org/10.3897/zookeys.511.9793
Elshishka M, Lazarova S, Peneva V (2015b) Terrestrial nematodes of Livingston Island, Maritime Antarctica. In: Pimpirev Ch, Chipev N (Eds) Bulgarian Antarctic Research. A Synthesis. “St Kliment Ohridski” University Press, Sofia, 320–334.
Guerrero P, Peña-Santiago R (2007) Redescription of Enchodelus species studied by Thorne in 1939 (Dorylaimida, Nordiidae). Nematology 9: 93–121. https://doi.org/10.1163/1568-54107779969646
Guerrero P, Liébanas G, Peña-Santiago R (2008) Nematodes of the order Dorylaimida from Andalucía Oriental, Spain. The genus Enchodelus Thorne, 1939. 3. Description of two new and one known species with rounded tail and medium-sized odontostyle. Nematology 10: 711–733. https://doi.org/10.1163/156854108785787208

Holterman M, Rybarczyk K, Van den Essen S, van Megen H, Mooyman P, Peña-Santiago R, Bongers T, Bakker J, Helder J (2008) A ribosomal DNA-based framework for the detection and quantification of stress-sensitive nematode families in terrestrial habitats. Molecular Ecology Resources 8: 23–34. https://doi.org/10.1111/j.1471-8286.2007.01963.x

Holterman M, Wurff AVD, Elsen SVD, Megen HV, Bongers T, Holovachov O, Bakker J, Helder J (2006) Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clades. Molecular Biology and Evolution 23: 1792–1800. https://doi.org/10.1093/molbev/msl044

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger data sets. Molecular Biology and Evolution 33 (7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lazarova S, Peneva V, Kumari S (2016) Morphological and molecular characterisation, and phylogenetic position of X. browni sp. n., X. penevi sp. n. and two known species of Xiphinema americanum-group (Nematoda, Longidoridae). ZooKeys 574: 1–42. https://doi.org/10.3897/zookeys.574.8037

Loof PAA (1975) Dorylaimoidea from some subantarctic islands. Nematologica 21: 219–255. https://doi.org/10.1163/187529275X00581

Loof PAA, Coomans A (1970) On the development and location of the oesophageal gland nuclei in the Dorylaimina. Proceedings IX International Nematology Symposium (Warsaw 1967) Zeszyty Problemowe Postępów Nauk Rolniczych 92: 79–161.

Maslen NR (1981) The Signy Island terrestrial reference sites: XII. Population ecology of nematodes with additions to the fauna. British Antarctic Survey Bulletin 53: 57–75.

Maslen NR, Convey P (2006) Nematode diversity and distribution in southern maritime Antarctic – clues to history? Soil Biology and Biochemistry 38: 3141–3151. https://doi.org/10.1016/j.soilbio.2005.12.007

Meldal BH, Debenham NJ, De Ley P, De Ley IT, Vanfleteren JR, Vierstraete AR, Bert W, Borgonie G, Moens T, Tyler PA, Austen MC, Blaxter ML, Rogers AD, Lambshead PJ (2007) An improved molecular phylogeny of the Nematoda with special emphasis on marine taxa. Molecular Phylogenetics and Evolution 42: 622–636. https://doi.org/10.1016/j.ympev.2006.08.025

Mutafchiev Y, Kontrimavichus VL, Georgiev BB (2013) Redescriptions and comments on the validity of Acuaria subula and A. skrjabini (Nematoda, Spirurida, Acuariidae), parasites of passerine birds. Acta Parasitologica 53: 284–296. https://doi.org/10.2478/aapa.2008.0013

Nedelchev S, Elshishka M, Lazarova S, Radoslavov G, Hristov P, Peneva V (2014) Calcaridorylaimus castaneae sp. n. (Nematoda: Dorylaimidae) from Bulgaria with an identification key to the species of the genus. ZooKeys 410: 41–61. https://doi.org/10.3897/zookeys.410.6955
Nielsen UN, Wall DH, Adams BJ, Virginia RA (2011) Antarctic nematode communities: observed and predicted responses to climate change. Polar Biology 34: 1701–1711.

Pearse AS (1942) Introduction to parasitology Springfield, Ill., Baltimore, Md., 357 pp.

Pedram M, Niknam G, Guerrero P, Ye W, Robbins RT (2009) Morphological and molecular characterisation of Enchodelus babakicus n. sp. and E. macrodorus Throne, 1939 (Nematoda: Nordiidae) from Iran. Nematology 11:895–907. https://doi.org/10.1163/156854109X430563

Pedram M, Niknam G, Vinciguerra MT, Ye W, Robbins RT (2011a) Morphological and molecular characterization of Paractinolaimus sahandi n. sp. (Nematoda: Actinolaimidae) from the Sahand Mountains in Iran. Journal of Helminthology 85: 276–282. https://doi.org/10.1017/S0022149X10000556

Pedram M, Pourjam E, Atighe MR, Panahandeh Y (2015) Further studies on soil nematode fauna in north Western Iran with the description of one new species. Journal of Nematology 47: 148–152.

Pedram M, Pourjam E, Robbins R, Ye W, Peña-Santiago R (2011b) Description of Rhyssocolpus vinciguerrae sp. n. (Dorylaimida, Nordiidae) from Iran and the first molecular study of this genus. Nematology 13: 927–937. https://doi.org/10.1163/138854111X565224

Peña-Santiago R (2006) Dorylaimida Part I: Superfamilies Belondiroidea, Nygolaimoidea and Tylencholaimoidea. In: Abebe-Eyualem, Andrássy I, Traunspurger W (Eds) Freshwater nematodes. CAB International, Cambridge, UK, 326–391. https://doi.org/10.1079/9780851990095.0326

Peña-Santiago R, Ciobanu M (2008) The genus Crassolabium Yeates, 1967 (Dorylaimida: Qud-sianematidae): Diagnosis, list and compendium of species, and key to their identification. Russian Journal of Nematology 16(2): 77–95.

Peneva V, Lazarova S, Chipev N (2002) Description of the male of Enchodelus (Rotundus) signyensis Loof, 1975 (Nematoda, Nordiidae) from Livingston Island, Antarctica, and notes on its morphology and distribution. In: Golemansky V, Chipev N (Eds) Bulgarian Antarctic Research. Life Sciences, Pensoft, Sofia-Moscow 3, 83–90.

Peneva VK, Lazarova SS, Mladenov AG, Nedelchev S, Chipev N H (2004) Patterns of spatial distribution of omnivorous and predatory nematodes on Livingston Island, Antarctica. (Abstract). Proceedings of 27th ESN International Symposium, 14–18 June, 2004, Rome, Italy, 33 pp.

Popovici I (1995) New species of Tubixaba and Enchodelus (Nematoda: Dorylaimida) from Romania. Nematologica 41: 435–448. https://doi.org/10.1163/003925995X00396

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Russell DJ, Hohberg K, Potapov M, Brückner A, Otte V, Christian A (2014) Native terrestrial invertebrate fauna from the northern Antarctic Peninsula: new records, state of current knowledge and ecological preferences. Summary of a German federal study. Soil organisms 86: 1–58.
Seinhorst JW (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. Nematologica 4: 67–69. https://doi.org/10.1163/187529259X00381
Shishida Y, Ohyama Y (1989) A note on the terrestrial nematodes around Palmer Station, Antarctica (Extend abstract). Proceeding of the NIPR Symposium on Polar Biology 2: 223–224.
Siddiqi MR (1969) Crateronema n. gen. (Crateronematidae n. fam.), Poronemella n. gen. (Lordellonematinae n. subfam.) and Chrysonemoides n. gen. (Chrysonematidae n. fam.) with a revised classification of Dorylaimoidea (Nematoda). Nematologica 15: 234–240.
Spaull VW (1973) Distribution of nematode feeding group at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. British Antarctic Survey Bulletin 37: 21–32.
Thorne G (1939) A monograph of the nematodes of the superfamily Dorylaimoidea. Capita Zoologica 8: 1–261.
Thorne G, Swanger H (1936) A monograph of the nematode genera Dorylaimus Dujardin, Aporcelaimus n. g., Dorylaimoides n. g. and Pungentus n. g. Capita Zoologica 6: 1–223.
van Bezooijen J (2006) Methods and techniques for nematology. Wageningen University, 112 pp.
Yeates G (1967) Studies on nematodes from dune sands. 6. Dorylaimoidea. New Zealand Journal of Science 10: 773–777.

Supplementary material I

18S Parsimoni informative sites TemporaryMEGA17
Authors: Milka Elshishka, Stela Lazarova, Georgi Radoslavov, Peter Hristov, Vlada K. Peneva
Data type: (nucleotide)
Explanation note: 18S rDNA Phylogenetic analysis between tree Genus based on Parsimony informative nucleotide sites.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zookeys.697.13770.suppl1
Supplementary material 2

28S Parsimony informative sites Temporary MEGA15
Authors: Milka Elshishka, Stela Lazarova, Georgi Radoslavov, Peter Hristov, Vlada K. Peneva
Data type: (nucleotide)
Explanation note: 28S rDNA Phylogenetic analysis between tree Genus based on Parsimony informative nucleotide sites.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/zookeys.697.13770.suppl1