



# Cyber catalogue and revision of the nematode genus *Enchodelus* (Dorylaimida, Nordiidae)

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## Abstract

## Background

The genus *Enchodelus* is an intriguing free-living dorylaimid nematode taxon. Its representatives display a distinct distributional pattern as they are mainly spread in high altitudinal enclaves of the Northern Hemisphere, being often associated with mosses and cliff vegetation. Although their feeding habits have not been studied with experimental protocols, it is traditionally assumed that they are omnivorous.

The genus *Enchodelus* has not been recently revised; descriptions of many ‘old species’ (that have been described long ago and have not been reported since their original discovery) are of poor quality, hardly discoverable and do not conform to the nowadays taxonomical standards. Thus, a comprehensive compilation and analysis of their literature data is indispensable to provide new insights into the taxonomy of the genus and to elucidate its evolutionary relationships.

## New information

This contribution provides a cyber catalogue of all *Enchodelus* species, 28 in total. It compiles available information from the key European Research Infrastructures, such as TreatmentBank, Swiss Institute of Bioinformatics Literature Services (SIBiLS), the Catalogue of Life (CoL), Global Biodiversity Information Facility (GBIF), European Nucleotide Archive (ENA) and Biodiversity Literature Repository (BLR). Data about their distribution (geographical records and habitats) are incorporated too and all brought together. It is completed with discussion and notes for some species, along with information on species distributions and microhabitats. Here, all available information on *Enchodelus* species is brought together. This will contribute to a more complete assessment of species diversity and distribution and support further biogeographical and ecological research.

Besides, type material *Enchodelus vestibulifer* Altherr, 1952, deposited in the Museo Cantonale di Storia Naturale di Lugano (Switzerland), is re-examined and the species is considered as *incertae sedis*. Further, a new species of the genus found in Caucasus, Georgia is described after its morphological and molecular study; also morphological and molecular data for *E. macrodorus* (de Man, 1880) Thorne, 1939, the type species of the genus, collected from Spain are provided.

## Keywords

collection, databases, distribution, DNA, new species, research infrastructures

## Introduction

In his monograph devoted to the superfamily Dorylaimoidea, Thorne (1939) erected the genus *Enchodelus* to accommodate five new species, namely *E. arcuatus* Thorne, 1939, *E. brevidentatus* Thorne, 1939, *E. laevis* Thorne, 1939, *E. striatus* Thorne, 1939 and *E. teres* Thorne, 1939, as well as eight transferred from *Dorylaimus* Dujardin, 1845 and *Dorylaimellus* Cobb, 1913, namely *E. analatus* (Ditlevsen, 1927), *E. conicaudatus* (Ditlevsen, 1927), *E. faeroensis* (Ditlevsen, 1928), *E. groenlandicus* (Ditlevsen, 1927), *E. hoppedorus* (Thorne, 1929), *E. macrodorus* (de Man, 1880), *E. macrodoroides* (Steiner, 1914) and *E. vesuvianus* (Cobb, 1893), all of them characterised by having double guiding ring, odontophore with developed flanges and diovarian female genital system. *Enchodelus macrodorus* was proposed as the type species of the new genus.

Several decades later, Ahmad and Jairajpuri (1980) revised the genus and split it into five subgenera (*Enchodelus*, *Heterodorus*, *Nepalus*, *Paraenchodelus* and *Rotundus*), based on some morphological characters, such as lip region shape, odontostyle length, morphology of odontophore, shape of tail and arrangement of ventromedian supplements. At the same time, the authors considered that *Enchodelus* contains two fairly distinct groups of species, one with conoid tails and the other with rounded tails.

Subsequently, *Eliava and Eliashvily (1990)* provided a detailed overview of the family Nordiidae and presented the original descriptions and a key for all previously described species of genus *Enchodelus*.

The new millennium brought new relevant contributions to the study of *Enchodelus* diversity: (i) Guerrero and Peña-Santiago (2007) re-described six species of Thorne's material: *E. arcuatus*, *E. brevidentatus*, *E. geraldii* Winiszewska-Slipinska, 1987 (= *Enchodelus macrodoroides apud* Thorne, 1939), *E. hoppedorus*, *E. macrodorus* and *E. striatus*; (ii) seven new species were described in the period 2008-2012: *E. ameliae* Guerrero, Liebanas & Peña-Santiago, 2008 and *E. longispiculus* Guerrero, Liebanas & Peña-Santiago, 2008 from Spain, *E. babakicus* Pedram, Nicknam, Guerrero, Ye & Robbins, 2009 and *E. sardashtensis* Pedram, Pourjam, Robbins, Ye & Peña-Santiago, 2011 from Iran, *E. parahoppedoroides* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010 and *E. carpaticus* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010 from Romania and *E. makarovae* Elshishka, Lazarova & Peneva, 2012 from the Russian Arctic; (iii) Andrásy (2009a) and Andrásy (2009b) revised the taxonomy of *Enchodelus* species, retrieving the genus *Heterodorus* (= *Nepalus*, *Paraenchodelus*) as a valid genus to include those species displaying conical tail and few ventromedian supplements with hiatus and retaining under *Enchodelus* (= *Rotundus*) the rounded-tailed forms with ventromedian supplements without hiatus; (iv) molecular data (Pedram et al. 2009, Pedram et al. 2011, Pedram et al. 2015) supported the opinion of Andrásy that the species with rounded and conical tail form two different groups (clades); (v) Peña-Santiago (2021b) provided the list of the species of genus *Enchodelus* with their synonyms and geographical records.

The genus *Enchodelus* currently includes 28 species, which are typical components of septentrional (Northern Hemisphere) fauna (Peña-Santiago 2021a), with the exception of *E. brasiliensis* Meyl, 1957, only known to occur in Brazil. The members of the genus inhabit high altitudes (1260-4400 m a.s.l.) and latitudes (northern territories), frequently associated with mosses and rock vegetation (Ahmad and Jairajpuri 1980, Eliava and Eliashvily 1990, Peneva et al. 2009, Elshishka et al. 2012). As the species are found mainly in natural habitats, the genus can be considered to have a conservation value.

No recent revision of *Enchodelus* members has hitherto been published. Descriptions of many 'old species' are of poor quality, hardly discoverable and do not conform to the nowadays taxonomical standards. Actually, information available from databases often is limited to some of the species and usually incomplete as relevant data are missing. Consequently, a comprehensive compilation and analysis of literature data is indispensable to reach new insights into the taxonomy of the genus and to elucidate its evolutionary relationships. Thus, this contribution aims to provide a cyber catalogue of *Enchodelus* species, where all available data for the species are accessible and collected in one place which will greatly facilitate future research. Moreover, a re-examination of type material of *Enchodelus vestibulifer* Altherr, 1952, deposited in [the Museo Cantonale di Storia Naturale di Lugano](https://www.museo.cantonale.ch/en/storia-naturale-di-lugano) (Switzerland), is also presented, as well as the description of a new species of the genus found in Caucasus, Georgia after its

morphological and molecular study and also morphological and molecular data for *E. macrodorus*, collected from Spain.

## Materials and methods

The cyber catalogue compiles all kinds of data (taxonomical, sequences, names, records, tables, figures) provided in some of European Research Infrastructures, such as TreatmentBank, Swiss Institute of Bioinformatics Literature Services (SIBiLS), the Catalogue of Life (CoL), Global Biodiversity Information Facility (GBIF), European Nucleotide Archive (ENA) and Biodiversity Literature Repository (BLR) for the species of the genus *Enchodelus*. This information is completed with records, both geographical and ecological (habitats) and notes or discussion about them. Habitats are reported as in the original paper, with the scientific names of the plants adapted according to their current systematics.

The new species described was collected by one of authors (V. Peneva) from moss on stone (*Tortella squarrosa* (Brid.) Limpr.) in Caucasus, Georgia. Nematodes were extracted by using the Baermann funnel method (van Bezooijen 2006) for 48 hours exposition, killed by gentle heat and fixed in 4% formalin. Specimens were processed in anhydrous glycerine (Seinhorst 1959) and mounted on permanent slides.

Type material of *E. vestibulifer*, belonging to Edmond Altherr's collection, deposited at the [Museo Cantonale di Storia Naturale di Lugano](#) (Switzerland), is re-examined. The single female specimen is preserved in one permanent glycerine slide, in poor condition. The information included on the label is presented in the catalogue and in Fig. 1.



Figure 1. [doi](#)

Slide with original label: *Enchodelus vestibulifer*.

A few specimens of *E. macrodorus* were found in soil samples from grass in Spain. Nematodes were extracted from soil samples by sieving and the sucrose-centrifugation technique (specific gravity = 1.18), following the protocol of California Department of Food and Agriculture (CDFA 2015; based on Jenkins (1964)), killed by gentle heat and fixed in 4% formalin.

Drawings were prepared using an Olympus BX 51 compound microscope 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 CalCom Peripherals, Scottsdale, AZ, USA) and Digitrak 1.0f computer programme (Philip Smith, John Hutton Institute, Dundee, UK). Terminology was adopted according to Peña-Santiago (2021a). The locations of pharyngeal gland nuclei are given following Loof and Coomans (1970) and Andr assy (1998).

### **DNA isolation, PCR and sequencing**

The specimen intended for the molecular study was identified on temporary mounts; a standard set of photomicrographs was taken. Genomic DNA (gDNA) was isolated using 5% suspension of deionised water and Chelex®, containing 0.1 mg/ml proteinase K; samples were incubated at 56°C or overnight, boiled at 90°C for 8 min and centrifuged at 14,000'g for 10 min. A genetic marker sequenced was the large (28S) ribosomal subunit RNA coding regions. Partial fragments of the 28S rRNA gene (domains D1-D3; ~ 1000 bp) were amplified using the forward primer LSU5 (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') (Littlewood et al. 2000) and the reverse primer 1500R (5'-GCT ATC CTG AGG GAA ACT TCG-3') (Tkach et al. 1999). PCR amplifications were performed with 2' MyFi™ DNA Polymerase mix (Bioline Inc., Taunton, USA; Cat. # BIO-25049) in a total volume of 20 µl, containing 8 pmol of each primer and ca. 50 ng of gDNA. The amplification profile for 28S rDNA comprised an initial denaturation at 94°C for 3 min followed by 40 cycles (30 s at 94°C; 30 s at 55°C; and 2 min at 72°C) and a final extension step at 72°C for 7 min. PCR amplicons were purified and sequenced directly for both strands using the PCR primers at Macrogen Europe (Amsterdam, the Netherlands). Contiguous sequences were assembled, quality checked and edited manually using MEGA7 (Kumar et al. 2016) and subjected to a BLASTn search on the NCBI GenBank database. The newly-obtained sequences were submitted to the GenBank database under accession numbers: PP662485, for *Enchodelus enguriensis* sp. nov. - 28S; PP662484, for *E. macrodorus* - 28S; and PP657694, for *E. macrodorus* - 18S.

### **Phylogenetic and sequence analysis**

The newly-obtained sequences were aligned with another fifty-two D2–D3 expansion segments of 28S rRNA gene sequences available in GenBank using ClustalX 1.83 (Chenna 2003). Outgroup taxa were chosen, based on previously-published data ( lvarez-Ortega and Pe a-Santiago 2019,  lvarez-Ortega 2020). The alignment was analysed with Bayesian Inference (BI) at the CIPRES Science Gateway (Miller et al. 2010), using MrBayes 3.2.7a (Ronquist et al. 2012). The best fit model of DNA evolution was obtained using jModelTest 2.1.10 (Darriba et al. 2012) with the Akaike Information Criterion (AIC). The Akaike-supported model, the base frequency, the proportion of invariable sites and the gamma distribution shape parameters and substitution rates in the AIC were then used in phylogenetic analyses. BI analysis under the general time reversible model with a proportion of invariable sites and a gamma-shaped distribution

(GTR+I+G) was initiated with a random starting tree and run with the four Metropolis-coupled Markov Chain Monte Carlo (MCMC) for  $2 \times 10^6$  generations. The topologies were used to generate a 50% majority rule consensus tree. Posterior probabilities (PP) over 70% are given on appropriate clades. The trees were visualised with the programme FigTree v.1.4.3 and drawn with Adobe Illustrator CC.

## Taxon treatments

### *Enchodelus* Thorne, 1939

- ZooBank [907FC242-EF1E-4072-AF46-FD5BBB4A13D4](https://doi.org/10.21203/rs.3.rs-1000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9CKPN>
- GBIF <https://www.gbif.org/species/2282676>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus&tab=plazi#results-section>

#### Nomenclature

*Enchodelus* (*Enchodelus* Thorne, 1939); Ahmad and Jairajpuri (1980):12-13 [diagnosis; key to species] BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus* (*Enchodelus* Thorne, 1939); Jairajpuri and Ahmad (1992):179 [diagnosis; list] BLR: <https://doi.org/10.5281/zenodo.10849482>

*Enchodelus* (*Rotundus* Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980): 13-14 [diagnosis; key to species] BLR: <https://doi.org/10.5281/zenodo.8144936>

*Enchodelus* (*Rotundus* Ahmad & Jairajpuri, 1980); Jairajpuri and Ahmad (1992):183 [diagnosis; list] BLR: <https://doi.org/10.5281/zenodo.10849492>

*Enchodelus* Thorne, 1939; Thorne (1939):61-62 [diagnosis; key to species] BLR: <https://doi.org/10.5281/zenodo.11003096>

*Enchodelus* Thorne, 1939; Goodey (1951):298, 300-301 [diagnosis; list] BLR: <https://doi.org/10.5281/zenodo.11013374>

*Enchodelus* Thorne, 1939; Andrásy (1958b):324 [diagnosis] BLR: <https://doi.org/10.5281/zenodo.10842858>

*Enchodelus* Thorne, 1939; Goodey (1963):441-443 [diagnosis; list] BLR: <https://doi.org/10.5281/zenodo.10891552>

*Enchodelus* Thorne, 1939; Zullini (1973):406-408 [list; key to species] BLR: <https://doi.org/10.5281/zenodo.10845261>

*Enchodelus* Thorne, 1939; Baqri and Jairajpuri (1974):145-146 [key to species] BLR: <https://doi.org/10.5281/zenodo.8117936>

*Enchodelus* Thorne, 1939; Bongers (1988):324 [diagnosis] BLR: <https://doi.org/10.5281/zenodo.10822196>

*Enchodelus* Thorne, 1939; Eliava and Eliashvily (1990)BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus* Thorne, 1939; Jairajpuri and Ahmad (1992):178-183 [diagnosis; key to subgenera] BLR: <https://doi.org/10.5281/zenodo.10849480>

*Enchodelus* Thorne, 1939; Loof (1999):86 [diagnosis] BLR: <https://doi.org/10.5281/zenodo.11003046>

*Enchodelus* Thorne, 1939; Vinciguerra (2006):457-458 [diagnosis, figure, list]

*Enchodelus* Thorne, 1939; Guerrero et al. (2008a):727, 730-732 [compendium of species of *Enchodelus hoppedorus* group; key to species of *Enchodelus hoppedorus* group]

*Enchodelus* Thorne, 1939; Guerrero et al. (2008b):467-468 [compendium of species of *Enchodelus macrodorus* group; key to species of *Enchodelus macrodorus* group]

*Enchodelus* Thorne, 1939; Andrassy (2009b):382-385 [diagnosis; list; key to European species] BLR: <https://doi.org/10.5281/zenodo.10821943>

*Enchodelus* Thorne, 1939; Elshishka et al. (2012):21 [key to species of *Enchodelus macrodorus* group]

*Enchodelus* Thorne, 1939; Peña-Santiago (2021b):205-212 [list; geographical records]

*Enchodelus* Thorne, 1939; Hodda (2022):28 [list]

### Diagnosis

Nordiidae, Pungentinae. Small- to medium-sized nematodes, 0.6-2.5 mm long. Cuticle dorylamoid. Lip region offset by depression or constriction, with variably amalgamate lips. Amphid fovea cup-like, its aperture occupying ca. one-half of lip region diameter. Odontostyle slender, with narrow lumen and small aperture, longer (1-2 times) than lip region diameter. Guiding ring double, low. Odontophore with developed basal flanges. Pharynx entirely muscular, gradually enlarging into a pharyngeal expansion occupying less than one-half of total neck length, with S<sub>2</sub>N as large as DN and rather anterior in position. Female genital system diovarian, with long and tripartite uterus, distinct *pars refringens vaginae* and transverse vulva. Tail similar in sexes, short and rounded to convex conoid. Spicules dorylaimid. Ventromedian supplements 7-18 in number, spaced, without hiatus.

Type species: *Enchodelus macrodorus* (de Man, 1880) Thorne, 1939

## ***Enchodelus macrodorus* (de Man, 1880) Thorne, 1939**

- ZooBank [7CAD1A7A-726F-4CF0-85F2-B0B5E1B24EB7](https://doi.org/10.3896/AB7-726F-4CF0-85F2-B0B5E1B24EB7)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/886TQ>
- GBIF <https://www.gbif.org/species/2282680>
- ENA <https://www.ebi.ac.uk/ena/browser/view/Taxon:289013>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20macrodorus#results-section>

### **Nomenclature**

*Dorylaimus macrodorus* de Man, 1880; de Man (1880) BLR: <https://doi.org/10.5281/zenodo.10852798>

*Dorylaimus macrodorus*; de Man (1884) BLR: <https://doi.org/10.5281/zenodo.10867883>

*Dorylaimus macrodorus*; de Man (1912):454-456 BLR: <https://doi.org/10.5281/zenodo.11003008>

*Dorylaimus macrodorus*; Menzel (1913) BLR: <https://doi.org/10.5281/zenodo.10797350>

*Dorylaimus macrodorus*; Brakenhoff (1914) BLR: <https://doi.org/10.5281/zenodo.10822895>

*Dorylaimus macrodorus*; Steiner (1914):262 [list] BLR: <https://doi.org/10.5281/zenodo.11003080>

*Dorylaimus macrodorus*; Hofmänner and Menzel (1915):186-187 BLR: <https://doi.org/10.5281/zenodo.11003145>

*Dorylaimus macrodorus*; Steiner (1916a):69-70 BLR: <https://doi.org/10.5281/zenodo.11003157>

*Dorylaimus macrodorus*; Steiner (1916b):345 BLR: <https://doi.org/10.5281/zenodo.11003151>

*Dorylaimus macrodorus*; Micoletzky (1921) BLR: <https://doi.org/10.5281/zenodo.10932729>

*Dorylaimus macrodorus*; Schneider (1923) BLR: <https://doi.org/10.5281/zenodo.10795142>

*Dorylaimus macrodorus*; Kreis (1924) BLR: <https://doi.org/10.5281/zenodo.10892094>

*Dorylaimus macrodorus*; Stefanski (1924):55-57

*Dorylaimus macrodorus*; Micoletzky (1925):181-182



*Dorylaimus macrodorus*; Rahm (1925):182

*Dorylaimus macrodorus*; Stefanski (1927) BLR: <https://doi.org/10.5281/zenodo.10941762>

*Dorylaimus macrodorus*; Soós (1936):61 [list] BLR:<https://doi.org/10.5281/zenodo.10944890>

*Dorylaimus macrodorus*; Allgén (1953) BLR: <https://doi.org/10.5281/zenodo.10809558>

*Dorylaimus (Doryllium) macrodorus* de Man, 1880; Seidenschwarz (1923):42

*Dorylaimus (Doryllium) macrodorus* de Man, 1880; Allgén (1925) BLR: <https://doi.org/10.5281/zenodo.10998093>

*Dorylaimus (Doryllium) macrodorus* de Man, 1880 (Ditlevsen, 1928); Ditlevsen (1928):9

*Dorylaimellus macrodorus* (de Man, 1880) Thorne & Swanger, 1936; Thorne and Swanger (1936) BLR:<https://doi.org/10.5281/zenodo.10845809>

*Dorylaimellus macrodorus*; Altherr (1950) BLR: <https://doi.org/10.5281/zenodo.10810136>

*Dorylaimellus macrodorus*; Altherr (1952):342

*Dorylaimellus macrodorus*; Andrassy (1952) BLR: <https://doi.org/10.5281/zenodo.11012991>

*Dorylaimus (Dorylaimellus) macrodorus* de Man, 1880 (Thorne & Swanger, 1936); Thorne and Swanger (1936) BLR: <https://doi.org/10.5281/zenodo.10845809>

*Dorylaimus (Dorylaimellus) macrodorus*; Schneider (1939) BLR: <https://doi.org/10.5281/zenodo.11028113>

*Enchodelus (Enchodelus) macrodorus* (de Man, 1880) Thorne, 1939

*Enchodelus (Enchodelus) macrodorus*; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144942>

*Enchodelus (Enchodelus) macrodorus*; Jairajpuri and Ahmad (1992): 180 [figure] BLR: <https://doi.org/10.5281/zenodo.10850166>

*Enchodelus (Enchodelus) macrodorus*; Choi et al. (1997) BLR: <https://doi.org/10.5281/zenodo.10822472>

*Enchodelus macrodorus* (de Man, 1880) Thorne, 1939; Thorne (1939) BLR:<https://doi.org/10.5281/zenodo.11003121>

*Enchodelus macrodorus*; Goodey (1951) BLR: <https://doi.org/10.5281/zenodo.11013374>

*Enchodelus macrodorus*; Altherr (1953) BLR: <https://doi.org/10.5281/zenodo.11012949>

*Enchodelus macrodorus*; Andr assy (1958b) BLR: <https://doi.org/10.5281/zenodo.10842858>

*Enchodelus macrodorus*; Meyl (1961) BLR: <https://doi.org/10.5281/zenodo.11015551>

*Enchodelus macrodorus*; van Rossen and Loof (1962) BLR: <https://doi.org/10.5281/zenodo.10845171>

*Enchodelus macrodorus*; Goodey (1963) BLR: <https://doi.org/10.5281/zenodo.10891552>

*Enchodelus macrodorus*; Jairajpuri and Loof (1967) BLR: <https://doi.org/10.5281/zenodo.8122568>

*Enchodelus macrodorus*; Loof and Coomans (1970) BLR: <https://doi.org/10.5281/zenodo.11014428>

*Enchodelus macrodorus*; Zullini (1970) BLR: <https://doi.org/10.5281/zenodo.10850512>

*Enchodelus macrodorus*; Loof (1971) BRL: <https://doi.org/10.5281/zenodo.8152932>

*Enchodelus macrodorus*; Thorne (1974) BLR: <https://doi.org/10.5281/zenodo.10819174>

*Enchodelus macrodorus*; Andr assy (1978):116 [list]

*Enchodelus macrodorus*; Nesterov (1979) BLR: <https://doi.org/10.5281/zenodo.11015718>

*Enchodelus macrodorus*; Vinciguerra (1984) BLR: <https://doi.org/10.5281/zenodo.10818036>

*Enchodelus macrodorus*; Winiszewska-Slipinska (1987) BLR: <https://doi.org/10.5281/zenodo.10854940>

*Enchodelus macrodorus*; Bongers (1988) BLR: <https://doi.org/10.5281/zenodo.10822198>

*Enchodelus macrodorus*; Eliava and Eliashvily (1990):50-51,96 BLR:<https://doi.org/10.5281/zenodo.11003031>

*Enchodelus macrodorus*; Gerber (1991) BLR: <https://doi.org/10.5281/zenodo.10883357>

*Enchodelus macrodorus*; Nasira et al. (1992) BLR: <https://doi.org/10.5281/zenodo.8122525>

*Enchodelus macrodorus*; Popovici (1995a) BLR: <https://doi.org/10.5281/zenodo.8125537>

*Enchodelus macrodorus*; Loof (1999) BLR: <https://doi.org/10.5281/zenodo.11003046>

*Enchodelus macrodorus*; Ahmad et al. (2002) BLR: <https://doi.org/10.5281/zenodo.10683060>

*Enchodelus macrodorus*; Poiras (2006):93 [list] BLR: <https://doi.org/10.5281/zenodo.10717726>

*Enchodelus macrodorus*; Guerrero and Peña-Santiago (2007) BLR: <https://doi.org/10.5281/zenodo.8111782>

*Enchodelus macrodorus*; Guerrero et al. (2008b) BLR: <https://doi.org/10.5281/zenodo.8111849>

*Enchodelus macrodorus*; Pedram et al. (2009) BLR: <https://doi.org/10.5281/zenodo.8114781>

*Enchodelus macrodorus*; Andrásy (2009b)BLR: <https://doi.org/10.5281/zenodo.10821949>

*Enchodelus macrodorus*; Ciobanu et al. (2010a) BLR:<https://doi.org/10.5281/zenodo.8111705>;

*Enchodelus macrodorus*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus macrodorus*; Shahina et al. (2019):223 [list] BLR: <https://doi.org/10.5281/zenodo.10710707>

*Enchodelus macrodorus*; Peña-Santiago (2021b):208-210 BLR: <https://doi.org/10.5281/zenodo.11191905>

## Distribution

A typical member of Palearctic nematode fauna, recorded in a myriad of countries and habitats: **Netherlands** (type habitat: moist soil in meadows and marshes - de Man (1880), de Man (1884) /sandy soil with moss - de Man (1912), Loof and Oostenbrink (1962), Loof and Coomans (1970) Loof and Coomans (1970), Bongers (1988)), **Alps** (moss - Franz (1942), Franz and Gunhold (1954)), **Austria** (moss *Hypnum cupressiforme* Hedw - Steiner (1916b), Micoletzky (1921) / moss - Seidenschwarz (1923)), **Bulgaria** (moss - Andrásy (1958a), Katalan-Gateva (1968)), **China** (grassland and shrubs - Ahmad et al. (2002)), **Czech Republic** (meadow, grassland - Háněl (1998)), **Denmark** (moor - Micoletzky (1925)), **Faroe Islands**

(Ditlevsen (1928)), **Germany** (river bank - Brakenhoff (1914) / moss - Schneider (1923), Rahm (1925), Schneider (1939) / grassland - Diedrich et al. (1998) / lake, 1136 m a.s.l. - Michiels and Traunspurger (2005)), **Hungary** (moss - Soós (1936), Soós (1940a), Soós (1940b), Andrásy (1952), Andrásy (1958b) / moss, grass, pine - Andrásy (1996), Andrásy (2009b)), **Iran** (grasslands - Pedram et al. (2009), Jabbari et al. (2019)), **Italy** (moss - Zullini (1970) / moss - Vinciguerra (1984)), **Korea** (*Betula platyphylla* var. *japonica* Hara - Choi et al. (1997)), **Moldova** (deciduous forests - Poiras (2006)), **Norway** (Jan Mayen Island - Allgén (1953) / Spitzbergen, grasses - Loof (1971)), **Pakistan** (soil around roots of weeds and grasses - Nasira et al. (1992) / freshwater - Nasira et al. (2016) / freshwater - Nasira and Shamim (2018)), **Poland** (moss - Stefanski (1924), Brzeski (1963b) / *Arrhenatherum* sp. - Winiszewska-Slipinska (1987) / primeval forest - Brzeski and Winiszewska-Slipinska (1996)), **Romania** (freshwater - Stefanski (1926), Stefanski (1927), Popovici (1993), Popovici (1995a) / hornbeam-beech forest, 400 m a.s.l. - Popovici (1995b), Popovici and Ciobanu (1997) / grasslands - Popovici (1998), Ciobanu and Popovici (2001) / hornbeam-beech forest, grasslands, cliff vegetation, 400-1250 m a.s.l. - Ciobanu et al. (2010a) / grass - Ciobanu and Popovici (2017)), **Russia** (Arctic - Novaya Zemlya Archipelago - Steiner (1916a) / Arctic tundra - Kuzmin (1973), Kuzmin and Gagarin (1990) / Novaya Zemlya Archipelago - Gagarin (1997), Gagarin (2001) / polar desert - cape Cheluykin - Chernov et al. (1979), Soloveva et al. (1976)), **Slovakia** (moss - Koniar (1957) / corn - Sabova et al. (1979), Šály (1979) / vineyard - Liskova (1980) / *Alnus glutinosa* Gaertn. - Šály (1980) / *Fagus sylvatica* L., *Abies alba* Mill., *Picea abies* H.Karst., meadow, moss, riverbank, brook, waterfall - Šály (1985) / *Pinus mugo* Turra, *P. abies* - Liskova et al. (1996) / meadow, river bank - Liskova and Čerevkova (2005) / grassland - Čerevková (2006) / grasslands - Čerevková (2008) / *Lariceto-Picetum* - Čerevková and Renčo (2009) / moss, forests, grasslands, potato, cereal, vineyard, riverbank - Liskova and Čerevkova (2011) / spruce forests - Čerevková et al. (2013) / *P. abies*, *Pinus sylvestris* L., *Quercus robur* L., *Acer pseudoplatanus* L., *F. sylvatica* - Renčo (2013) / maize - Čerevková and Cagan (2015) / alpine meadows, 1763-1994 m a.s.l. - Háněl 2017 / *P. abies*, *Larix decidua* - Renčo and Čerevková (2017) / deciduous forest, wetland, *Fallopia japonica* (Houtt.), 386-455 m a.s.l. - Čerevková et al. (2019) / *Asclepias syriaca* L., grassland - Jurová et al. (2020) / deciduous forests, grassland, *Solidago gigantea* Ait. - Čerevková et al. (2020)), **Spain** (Palomo (1979) / wet meadows, soil around poplar, 1400-2925 m a.s.l. - Guerrero et al. (2008b)), **Sweden** (moss - Allgén (1925), van Rossen and Loof (1962)), **Switzerland** (Alps, 2000-4000 m a.s.l. - Menzel (1913), Steiner (1914), Hofmänner and Menzel (1915) / lake with the melting snow water - Kreis (1924) / alpine meadow with *Alchemilla* sp., *Nardus stricta* L., *Trifolium* sp., pine forest, 1900-2200 m a.s.l. - Altherr (1950), Altherr (1952), Altherr (1953)), **UK** (moor, grassland - Banage (1962), Loof and Coomans (1970) / grasslands, 110-160 m a.s.l. - Hodda and Wanless (1994) / spruce forests, 200 m a.s.l. - Ruess et al. (1996)), **Ukraine** (grasses - Nesterov (1979)) and **Uzbekistan** (rice, bean, cotton - Tulaganov (1958) / *Cucumis sativus* L. - Tukhtasinov (2023)).

Very sporadically, this species was also recorded in Nearctic (**USA**, *Sporobolus compositus* (Poir.) Merr. - Orr and Dickerson (1967) / mountain soil - Thorne (1974)) and Indomalayan (**India**, soil near roots of apple - Jairajpuri and Loof (1967) / *Pinus pinea* L. - Ahmad and Jairajpuri (1980)) enclaves.

### Taxon discussion

*Enchodelus macrodorus* was originally described by de Man (1880) from the Netherlands. It is the most widely spread *Enchodelus* species. Guerrero and Peña-Santiago (2007) and Guerrero et al. (2008b) re-described American specimens of *E. macrodorus* studied by Thorne (1939), noted that these specimens apparently fitted very well with those described by de Man (1880), considered that many subsequent records of the species were doubtful or might correspond to other species, provided an emended diagnosis of this species and regarded the populations reported by Thorne (1939), Jairajpuri and Loof (1967), Ahmad and Jairajpuri (1980), Nasira et al. (1992) and Ahmad et al. (2002), also three of the populations reported by Popovici (1995a) to be conspecific with *E. macrodorus*. Later Pedram et al. (2009) reported the species for the first time from Iran and presented the first integrative study of the species.

**Morphological characterisation:** Material examined. One female in good condition, mounted on one slide and collected from Rasquilla, Navalsauz, Avila Province, Spain, in grassland riparian zone close to the Alberche River (N 40° 24.350' W 05° 01.817', elevation 1247 m a.s.l.) in May 2021.

Measurements: Table 1, Fig. 2

Table 1. Measurements of females, males and juveniles of <i>Enchodelus enguriensis</i> sp. nov. from Georgia and <i>Enchodelus macrodorus</i> from Spain. All measurements are in $\mu\text{m}$ (except L in mm) and in the form: mean $\pm$ standard deviation with range.								
Character	<i>E. enguriensis</i> sp. nov.							<i>E. macrodorus</i>
	♀ holotype	Females (n = 3)	Males (n = 5)	J1 (n = 1)	J2 (n = 2)	J3 (n = 3)	J4 (n = 6)	Female (n = 1)
L	1.4	1.4; 1.2; 1.03	1.3 $\pm$ 0.1 (1.2 – 1.4)	0.25	0.45; 0.43	0.52; 0.55; 0.43	0.9 $\pm$ 0.1 (0.75-1.02)	1.44
a	25.6	23.3; 23.7; 20.2	26.0 $\pm$ 0.9 (24.6-27)	16.0	20.3; 17.0	17.2; 18.3; 14.8	22.1 $\pm$ 2.5 (19.2-25.6)	21.1
b	4.8	5.0; 4.2;-	4.6 $\pm$ 0.1 (4.5-4.7)	2.1	2.8; 2.7	2.7; 3.4; -	3.6 $\pm$ 0.5 (2.9-4.1)	4.4

Character	<i>E. enguriensis</i> sp. nov.							<i>E. macrodorus</i>
c	69.1	58.3; 63.6; 54.2	56.6±5.1 (51.3-63.5)	7.7	-; 20.3	27.2; 27.4; 23.9	47.7±6.7 (39.5-57.1)	71.4
c'	0.7	0.6; 0.6; 0.6	0.7±0.1 (0.5-0.8)	2.8	-; 1.2	0.8; 0.9; 0.8	0.7±0.1 (0.5-0.8)	0.5
V%	49	50; 53; 50	-	-	-	-	-	44
Lip region diameter	16	16.5; 16; 16	16.4±0.5 (16-17)	7	9; 9	-; 10; 11	13.1±0.7 (12-13.5)	18.5
Odontostyle length	40	37; 37.5; 38.5	37.1±1.7 (36-40)	7	9; 10	14; 15; 15	25.4±0.9 (24-26.5)	39.0
Replacement odontostyle	-	-	-	8.5	14; 16	23; 23; 24	37.6±0.8 (37-39)	-
Guiding ring	24	-; 25; 26.5	23.2±1.1 (22-25)					25.5
Neck length	285	280; 290; -	283.0±9.7 (270-295)	120	160; 160	190; 160; -	251.3±8.5 (240-260)	326
Body diameter at:								
pharynx base	47	53; 47.5; 47	45.7±1.5 (44-47)	16	22; 24	30; 28; 28	37.6±3.2 (35-43)	60
mid - body	54	60; 51; 51	50.4±2.4 (47.5-53.5)	16	22; 25	30; 30; 29	39.3±3.9 (34-46)	68
anus/cloacal aperture	30	37; 30; 32	35.6±3.6 (31-40)	12	-; 18	23; 22; 24	28.1±1.2 (26-29)	39
Prerectum length	124	-; 90; -	153.9±18.6 (138-174)		-; 60	-; 58; 69	95.8±12.6 (80-110)	185
Rectum length	33	33; 30; 34		10	-; 17	19; 16; -	27.6±2.1 (25-30)	40
Tail length	20	24; 19; 19	23.4±2.9 (19-26)	33	-; 21	19; 20; 18	18.3±2.5 (15-22)	20
Genital primordium	-	-	-	8	14; 15	-; 15; -	38.6±3.6 (34-43)	-
Spicule length	-	-	57.3±2.6 (54-61)	-	-	-	-	-
Ventromedian supplements	-	-	9-10	-	-	-	-	-

Diagnosis (based in examined specimen)

*Enchodelus macrodorus* is characterised by its 1.44 mm long body, lip region 18.5 µm wide and offset by weak depression, odontostyle 39.0 µm long or 2.1 times lip

region diameter, odontophore flanged and 1.1 times as long as odontostyle, neck 326  $\mu\text{m}$  long, pharyngeal expansion occupying two-fifths of the total neck length, female genital system diovarian, uterus short (63, 68  $\mu\text{m}$  long), *pars refringens vaginae* with two rectangular sclerotisations, vulva ( $V = 44\%$ ), tail short and rounded (20  $\mu\text{m}$ ,  $c = 71$ ,  $c' = 0.5$ ) bearing saccate bodies.



Figure 2. [doi](#)

*Enchodelus macrodorus* (de Man, 1880) Thorne, 1939, female. **A** Entire body; **B-D** Anterior region; **E** Neck; **F** Genital system; **G** Pharyngeal dorsal nuclei; **H** Pharyngeal intestinal junction; **I** Uterus and oviduct junction; **J** Vagina; **K** Posterior body region; **L-N** Tail ends (**M** detail of the lateral chord ending; **N** detail of the saccate bodies of tail). Scale bars: **A** 200  $\mu\text{m}$ ; **B-D**, **G**, **H**, **J**, **L-N** 10  $\mu\text{m}$ ; **E**, **F**, **K** 50  $\mu\text{m}$ ; **I** 20  $\mu\text{m}$ .

## Remarks

The studied female perfectly fits, morphologically and morphometrically, with the previous descriptions of this species, especially with the re-description of the Thorne material provided by Guerrero and Peña-Santiago (2007).

**Molecular characterisation:** One partial 18S rRNA and one D2-D3 of 28S rRNA gene sequences were obtained for this species. In the partial 18S rRNA (Fig. 3) gene tree, the sequence of the Spanish *E. macrodorus* clustered together to another sequence of the same species (FJ042953) and inside of a highly-supported clade (PP = 100) with other *Enchodelus* spp. In the D2-D3 of 28S rRNA (Fig. 4) gene tree, the sequence of the Spanish *E. macrodorus* formed a highly-supported clade (PP = 100) with *E. enguriensis* sp. nov. and another three *Enchodelus* sequences from GenBank.

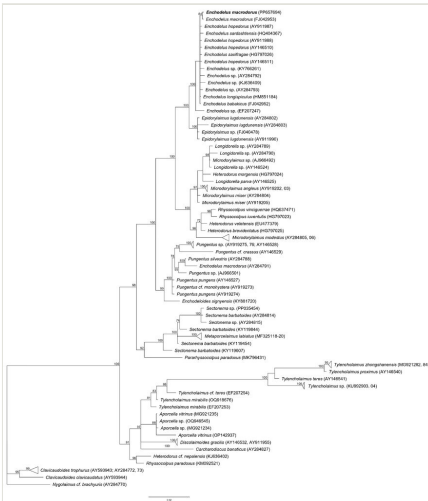


Figure 3. [doi](#)

Bayesian 50% majority rule consensus tree as inferred from the partial 18S rRNA gene sequence alignment under the GTR+I+G model. Posterior probability values more than 70% are given on appropriate clades. New sequences are indicated by bold letters.

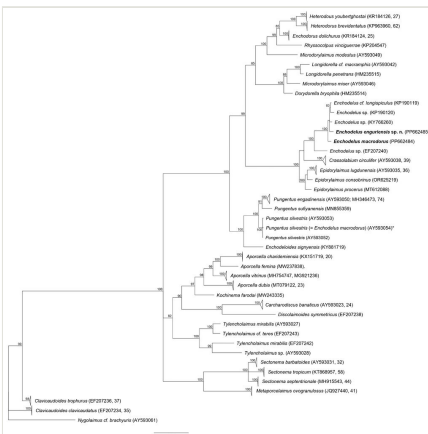


Figure 4. [doi](#)

Bayesian 50% majority rule consensus tree as inferred from the D2-D3 expansion segments of 28S rRNA gene sequence alignment under the GTR+I+G model. Posterior probability values more than 70% are given on appropriate clades. New sequences are indicated by bold letters.

Regarding the molecular data for this species, it appears that the sequence AY593054 available in GenBank was incorrectly identified or labelled. This sequence is herein identified as belonging to *Pungentus silvestris* (Figs 3, 4). Besides, the sequence AY284791, available in GenBank, was incorrectly identified too and most probably belongs to a *Pungentus* species.



## ***Enchodelus altherri* Vinciguerra & De Francisci, 1973**

- ZooBank [9776ABF8-69E3-462C-A47F-0001DD75B082](https://doi.org/10.3897/zoo.9776ABF8-69E3-462C-A47F-0001DD75B082)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMJX>
- GBIF <https://www.gbif.org/species/12242420>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20altherri#results-section>

### **Nomenclature**

*Enchodelus* (*Enchodelus*) *altherri* Vinciguerra & De Francisci, 1973 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus altherri* Vinciguerra & De Francisci, 1973; Vinciguerra and De Francisci (1973) BLR: <https://doi.org/10.5281/zenodo.8143853>

*Enchodelus altherri*; *Eliava and Eliashvily* (1990):51,96 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus altherri*; *Andrássy* (2009b) BLR: <https://doi.org/10.5281/zenodo.10821947>

*Enchodelus altherri*; *Peña-Santiago* (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11191877>

### **Distribution**

A typical representative of Palearctic nematode fauna, distributed only in Europe: **Italy** (type habitat: moss - Vinciguerra and De Francisci (1973)), **Bulgaria** (*Fagus orientalis* L., *Caprinus betulus* L., with undergrowth of *Daphne pontica* L., *Cyclamen coum* Mill., *Asperula odorata* L., 385 m a.s.l. - Iliev and Ilieva (2014)) and **Hungary** (moss - Andrásy (2009b)).

## ***Enchodelus ameliae* Guerrero, Liébanas & Peña-Santiago, 2008**

- ZooBank [6F323908-ABDA-444D-8A88-0FC39EA230E4](https://doi.org/10.3897/zoo.6F323908-ABDA-444D-8A88-0FC39EA230E4)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8GWTW>
- GBIF <https://www.gbif.org/species/10880151>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20ameliae#results-section>

### **Nomenclature**

*Enchodelus ameliae* Guerrero, Liébanas & Peña-Santiago, 2008; Guerrero et al. (2008a) BLR: <https://doi.org/10.5281/zenodo.8114884>

*Enchodelus ameliae*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11191879>

### Distribution

This species is a part of Western Palearctic nematode fauna, reported only from its type locality in **Spain** (type habitat: hedgehog heath, 1950 m a.s.l. - Guerrero et al. (2008a)).

## *Enchodelus analatus* (Ditlevsen, 1927) Thorne, 1939

- ZooBank [8C88711B-E0E5-4A2D-A8F8-32917C746512](https://doi.org/10.21203/a3.8c88711b-e0e5-4a2d-a8f8-32917c746512)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HDVL>
- GBIF <https://www.gbif.org/species/2282678>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20analatus#results-section>

### Nomenclature

*Dorylaimus* (*Doryllium*) *analatus* Ditlevsen, 1927; Ditlevsen (1927) BLR: <https://doi.org/10.5281/zenodo.10830636>

*Dorylaimellus analatus* (Ditlevsen, 1927) Thorne & Swanger, 1936; Thorne and Swanger (1936) BLR: <https://doi.org/10.5281/zenodo.10845799>

*Enchodelus* (*Rotundus*) *analatus* (Ditlevsen, 1927) Thorne, 1939; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144936>

*Enchodelus analatus* (Ditlevsen, 1927) Thorne, 1939; Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003139>

*Enchodelus analatus*; Loof (1971) BLR: <https://doi.org/10.5281/zenodo.8152928>

*Enchodelus analatus*; Eliava and Eliashvily (1990):51-52,96 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus analatus*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus analatus*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11191883>

### Distribution

This species is a member of Nearctic nematode fauna: **Greenland** (type habitat: moss - Ditlevsen (1927)).

After its discovery, it was reported in Palearctic, mainly in the Arctic: **Norway** (**Spitzbergen**) (bare soil, sand, grasses (*Papaver*, *Silene*, *Saxifraga*, *Draba*, *Oxyria*,

*Polygonum*), 20-350 m a.s.l. - Loof (1971)), **Romania** (beech - Popovici (1989), Popovici (1993)) and **Russia** (Arctic tundra - Kuzmin and Gagarin (1990)).

### Taxon discussion

Originally described by Ditlevsen (1927) from Greenland, it was later reported from Spitzbergen (Loof 1971). Nevertheless, Guerrero et al. (2008a) raised doubt about the true identity of Loof's material, which, in their opinion, was closer to *E. hoppedorus*, this previously having been re-described by Guerrero and Peña-Santiago (2007).

## *Enchodelus arcticus* Nesterov, 1976

- ZooBank [2BDEC04D-338C-4548-8E5F-BD7239F5DBCD](https://doi.org/10.22004/zoobank/2BDEC04D-338C-4548-8E5F-BD7239F5DBCD)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4KY>
- GBIF <https://www.gbif.org/species/7018646>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20arcticus#results-section>

### Nomenclature

*Enchodelus arcticus* Nesterov, 1976; Nesterov (1976) BLR: <https://doi.org/10.5281/zenodo.10849786>

*Enchodelus arcticus*; *Eliava and Eliashvily* (1990):52,97 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus arcticus*; *Peña-Santiago* (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11192261>

### Distribution

*Enchodelus arcticus* is recorded from the Palearctic, more specifically from Arctic Russian territories and high latitudes: **Russia** (type habitat: soil under lichens (Polar Urals) and rhizosphere of herbaceous plants (Yamal Peninsula) - Nesterov (1976)).

### Notes

This is the only described species that lacks male ventromedian supplements, but it should be noted that just one male specimen has been recorded.

## *Enchodelus babakicus* Pedram, Niknam, Guerrero, Ye & Robbins, 2009

- ZooBank [EE731CB2-EB75-4800-B6C3-F3CD87686493](https://doi.org/10.22004/zoobank/EE731CB2-EB75-4800-B6C3-F3CD87686493)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8GPPL>
- GBIF <https://www.gbif.org/species/10704615>
- ENA <https://www.ebi.ac.uk/ena/browser/view/Taxon:592164>

- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus+babakicus&tab=plaz#results-section>

### Nomenclature

*Enchodelus babakicus* Pedram, Niknam, Guerrero, Ye & Robbins, 2009; Pedram et al. (2009) BLR: <https://doi.org/10.5281/zenodo.8114779>

*Enchodelus babakicus*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11192263>

### Distribution

The species is a member of nematode fauna of Eastern Palearctic, found only in mountains of **Iran** (type habitat: rhizosphere of grasses from natural grasslands - Pedram et al. (2009)).

## *Enchodelus brasiliensis* Meyl, 1957

- ZooBank <E425F950-4AD2-41AE-9483-F0C5192396B6>
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J3NZ>
- GBIF <https://www.gbif.org/species/7018530>

### Nomenclature

*Enchodelus brasiliensis* Meyl, 1957; Meyl (1957) BLR: <https://doi.org/10.5281/zenodo.10997965>

*Enchodelus brasiliensis*; Eliava and Eliashvily (1990):53,97 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus brasiliensis*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11191887>

### Distribution

This is the only member of genus *Enchodelus* of Neotropical nematode fauna: **Brazil** (type habitat: wet sand - Meyl (1957)).

### Taxon discussion

This species is the only representative of genus recorded from the Southern Hemisphere (Brazil), an interesting biogeographical singularity. Originally described on the basis of one female and three male specimens, Andrásy (1971) transferred it to *Rhysocolpus*, but it better fits the *Enchodelus* diagnosis (very slender odontostyle, odontophore with flange-like extensions, short pharyngeal bulb, convex conoid tail).

## ***Enchodelus carpaticus* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010**

- ZooBank [8B206EBC-E0E8-433E-85E0-0A881D5B9483](https://doi.org/10.21203/rs.3.rs-1111703)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4Q5>
- GBIF <https://www.gbif.org/species/11820852>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20carpaticus&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus carpaticus* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010; Ciobanu et al. (2010a) BLR: <https://doi.org/10.5281/zenodo.8111703>

*Enchodelus carpaticus*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11192267>

### **Distribution**

This species is recorded in the Palearctic, with only one record from its type locality: **Romania** (type habitat: mountain grassland, 980 m a.s.l. - Ciobanu et al. (2010a)).

## ***Enchodelus decraemerae* Pourjam, Pedram, Vinciguerra & Robbins, 2010**

- ZooBank [015B01B2-199B-48E8-819C-25D8C2F2AB2C](https://doi.org/10.21203/rs.3.rs-1111703)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4HF>
- GBIF <https://www.gbif.org/species/11690414>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20decreaemerae&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus decraemerae* Pourjam, Pedram, Vinciguerra & Robbins, 2010; Pourjam et al. (2010) BLR: <https://doi.org/10.5281/zenodo.10716290>

*Enchodelus decraemerae*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11192271>

### **Distribution**

The species is a member of nematode fauna of West Palearctic: **Iran** (type habitat: rhizosphere of mosses on rocks - Pourjam et al. (2010)).

### **Taxon discussion**

According to Pourjam et al. (2010), this species belongs to a group of species with very long odontostyle (61-67 µm) and conical tail, which Ahmad and Jairajpuri (1980) ascribed to the subgenus *Nepalus*, now regarded identical with *Heterodorus*. Nevertheless, several remarkable traits (distinct flanges at odontophore base,

tripartite uterus, 10-12 irregularly-spaced ventromedian supplements without hiatus) supports its inclusion in *Enchodelus*, although the conical tail with rounded tip is atypical in the genus. Thus, it is provisionally retained under *Enchodelus*, but further study based also on molecular data would elucidate its taxonomic status.

### ***Enchodelus distinctus* Ahmad & Jairajpuri, 1980**

- ZooBank [BF76039B-A151-458A-9041-A3D1B215B4E1](https://doi.org/10.21203/rs.3.rs-11194433/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J3YC>
- GBIF <https://www.gbif.org/species/7018636>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20distinctus&tab=plazi#results-section>

#### **Nomenclature**

*Enchodelus (Enchodelus) distinctus* Ahmad & Jairajpuri, 1980; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144946>

*Enchodelus distinctus*; Eliava and Eliashvily (1990):56,98 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus distinctus*; Peña-Santiago (2021b):206 BLR: <https://doi.org/10.5281/zenodo.11194433>

#### **Distribution**

This species has been recorded only from Indomalayan region: **India** (type habitat: soil around roots of unidentified grasses, 4400 m a.s.l. - Ahmad and Jairajpuri (1980)).

#### **Taxon discussion**

This species is only known to occur in India and was described on the basis of a single female with bipartite uterus.

### ***Enchodelus georgensis* Eliava, Tskitishvili & Bagaturia, 2006**

- ZooBank [EDE1423C-8D44-4CC7-A029-2D76F3DB7C55](https://doi.org/10.21203/rs.3.rs-11194433/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4K6>
- GBIF <https://www.gbif.org/species/7018645>

#### **Nomenclature**

*Enchodelus georgensis* Eliava, Tskitishvili & Bagaturia, 2006; Eliava et al. (2006) BLR: <https://doi.org/10.5281/zenodo.11003168>

*Enchodelus georgensis*; Peña-Santiago (2021b):207 BLR: <https://doi.org/10.5281/zenodo.11193694>

### Distribution

*Enchodelus georgensis* is found only from the Palearctic, with a single report from Georgia (type habitat: deciduous forest, moss, firy forest, soil - Eliava et al. (2006)).

## *Enchodelus groenlandicus* (Ditlevsen, 1927) Thorne, 1939

- ZooBank [867FE891-B62E-4908-8943-4A7B3D922615](https://doi.org/10.26434/chem:867FE891-B62E-4908-8943-4A7B3D922615)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J264>
- GBIF <https://www.gbif.org/species/7018595>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20groenlandicus&tab=plazi#results-section>

### Nomenclature

*Dorylaimus (Doryllium) groenlandicus* Ditlevsen, 1927; Ditlevsen (1927) BLR: <https://doi.org/10.5281/zenodo.10830630>

*Dorylaimellus groenlandicus* (Ditlevsen, 1927) Thorne & Swanger, 1936; Thorne and Swanger (1936) BLR: <https://doi.org/10.5281/zenodo.10845805>

*Enchodelus (Enchodelus) groenlandicus* (Ditlevsen, 1927) Thorne, 1939

*Enchodelus (Enchodelus) groenlandicus*; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus groenlandicus* (Ditlevsen, 1927) Thorne, 1939;  
Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003133>

*Enchodelus groenlandicus*; Eliava and Eliashvily (1990):57;98 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus groenlandicus*; Guerrero et al. (2008b) BLR: <https://doi.org/10.5281/zenodo.8111847>

*Enchodelus groenlandicus*; Andrassy (2009a) BLR: <https://doi.org/10.5281/zenodo.10728535>

*Enchodelus groenlandicus*; Pedram et al. (2011)BLR: <https://doi.org/10.5281/zenodo.8114666>

*Enchodelus groenlandicus*; Elshishka et al. (2012) [Plazi treatment](#)

*Enchodelus groenlandicus*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus groenlandicus*; Peña-Santiago (2021b):207 BLR: <https://doi.org/10.5281/zenodo.11192354>

### Distribution

This species is representative of Holarctic nematode fauna, reported for the first time from **Greenland** (type habitat: a brook - Ditlevsen (1927)) and later from: **Albania** (soil from around beech trees, soil around brook, 950-1500 m a.s.l. - Andrásy (2009a)), **Iran** (the rhizosphere of grasses - Pedram et al. (2011)), **Russia** (Arctic tundra - Kuzmin and Gagarin (1990) / Arctic polygonal nival desert, associated with *Deschampsia borealis* (Trautv.) Roshev., *Gymnomitrium coralloides* Nees., *Cladonia* sp., 750 m a.s.l - Elshishka et al. (2012)), **Spain** (meadow and hedgehog heath, 955-2450 m a.s.l. - Guerrero et al. (2008b)) and **Uzbekistan** (a cotton field - Khakimov (1973)).

### Taxon discussion

Originally described by Ditlevsen (1927), based on a single female specimen from Disko Island, Greenland, with Guerrero et al. (2008b) providing a more detailed description of Iberian populations. Later, the species was also reported, along with descriptions, from Albania, Iran and Russian Arctic (polygonal polar desert on Plateau Putorana) (Andrásy 2009a, Pedram et al. 2011, Elshishka et al. 2012, respectively), but Iranian specimens deviate in many morphometric characters from the type population and subsequent records. Besides, the species was recorded in a cotton field in Uzbekistan (Khakimov (1973)), but Guerrero et al. (2008b) suggested that this material belonged to a different species (characterised by a short body and post-equatorial vulva). Further, Andrásy (2009b) suggested that *E. groenlandicus* and *E. saxifragae* are identical.

### Notes

Geographical distribution of *E. groenlandicus* shows a remarkable disjunction pattern as it occurs at high altitudes 950 m - 2450 m a.s.l. in southern Europe and Iran and at high latitudes in the Arctic Polar Region (Putorana Plateau and Greenland). Guerrero et al. (2008b) hypothesised that such distribution might stem from quaternary glacial events.

## *Enchodelus hopedoroides* Altherr, 1963

- ZooBank [4BD2425E-388C-41F1-93EF-D709B1B18CB0](https://zoobank.org/4BD2425E-388C-41F1-93EF-D709B1B18CB0)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMJZ>
- GBIF <https://www.gbif.org/species/4554561>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20hopedoroides&tab=plazi#results-section>



## Nomenclature

*Enchodelus (Enchodelus) hopedoroides* Altherr, 1963 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus hopedoroides* Altherr, 1963; Altherr (1963) BLR: <https://doi.org/10.5281/zenodo.8117912>

*Enchodelus hopedoroides*; Eliava and Eliashvily (1990):57,98 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus hopedoroides*; Guerrero et al. (2008a) BLR: <https://doi.org/10.5281/zenodo.8114882>

*Enchodelus hopedoroides*; Peña-Santiago (2021b):207 BLR: <https://doi.org/10.5281/zenodo.11191895>

## Distribution

*Enchodelus hopedoroides* is a part of Palearctic nematode fauna, reported only from Europe: **Switzerland** (type habitat: subalpine forest, *Calamagrostis villosa* (Chaix) Gmel., grasses, 2170 m a.s.l. - Altherr (1963)) and **Spain** (wet meadow, 2800 m a.s.l. - Guerrero et al. (2008a)).

## Taxon discussion

This species was originally described by Altherr (1963) in Switzerland. Later, Guerrero et al. (2008a) re-examined its type material and studied Iberian specimens.

## *Enchodelus hopedorus* (Thorne, 1929) Thorne, 1939

- ZooBank [BB74D958-FD13-49C9-9D2F-57B8DC1572C3](https://doi.org/10.21203/rs.3.rs-11191895)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HJ34>
- GBIF <https://www.gbif.org/species/4554550>
- ENA <https://www.ebi.ac.uk/ena/browser/view/211319>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20hopedorus&tab=plaz#results-section>

## Nomenclature

*Dorylaimellus hopedorus* Thorne, 1929; Thorne (1929) BLR: <https://doi.org/10.5281/zenodo.10797322>

*Enchodelus (Enchodelus) hopedorus* (Thorne, 1929) Thorne, 1939

*Enchodelus (Enchodelus) hopedorus*; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus (Enchodelus) hopedorus*; Choi et al. (1997) BLR: <https://doi.org/10.5281/zenodo.10822468>

*Enchodelus hopedorus* (Thorne, 1929) Thorne, 1939; Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003129>

*Enchodelus hopedorus*; Brzeski (1963a) BLR: <https://doi.org/10.5281/zenodo.10869685>

*Enchodelus hopedorus*; Zullini (1973) BLR: <https://doi.org/10.5281/zenodo.10845257>

*Enchodelus hopedorus*; Andr ssy (1978):116 [list]

*Enchodelus hopedorus*; Winiszewska-Slipinska (1987) BLR: <https://doi.org/10.5281/zenodo.10854938>

*Enchodelus hopedorus*; Eliava and Eliashvily (1990):58,98 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus hopedorus*; Guerrero and Pe a-Santiago (2007) BLR: <https://doi.org/10.5281/zenodo.8111780>

*Enchodelus hopedorus*; Pe a-Santiago (2021b):207 BLR: <https://doi.org/10.5281/zenodo.11194191>

## Distribution

A member of Holarctic nematode fauna, reported from: **USA** (type habitat: roots of alpine plants and moss, 4344 m a.s.l. - Thorne (1929) / deciduous forests - Johnson et al. (1972)), **North America** (freshwater habitats - Esser and Buckingham (1987)), **Georgia** (Eliava and Eliashvily (1990)), **Korea** (*Pinus densiflora* Siebold & Zucc. - Choi et al. (1997)) and **Poland** (*Sphagnum* spp. - Brzeski (1963a) / oak-hornbeam forest litter and peat bog litter - Winiszewska-Slipinska (1987)), as well as from the high Himalaya, which form part of the boundary between the Palearctic and Indomalayan Regions: **Nepal** (soil from *Rhododendron* spp., *Betula utilis* D. Don, *Abies* sp., 4100 m a.s.l. - Zullini (1973)).

## Taxon discussion

After its original description in the USA, this species was recorded from different locations in Europe and Asia. Guerrero et al. (2008a) raised doubts regarding the identity of non-American material, with the possible exception of Polish material studied by Winiszewska-Slipinska (1987), which might belong to other species.

## *Enchodelus laevis* Thorne, 1939

- ZooBank [E6295909-E23E-42DC-9F97-3E8A9F98B91D](https://doi.org/10.21203/rs.3.rs-10000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8G859>
- GBIF <https://www.gbif.org/species/7018633>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20laevis&tab=plaz#results-section>

### Nomenclature

*Enchodelus (Rotundus) laevis* Thorne, 1939 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144936>

*Enchodelus knuppenburgensis* Altherr in Altherr & Delamare-Deboutteville, 1972; Altherr and Delamare-Deboutteville (1972) BLR: <https://doi.org/10.5281/zenodo.10723432>

*Enchodelus knuppenburgensis*; Eliava and Eliashvily (1990):59 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus laevis* Thorne, 1939; Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003143>

*Enchodelus laevis*; Eliava and Eliashvily (1990):59,99 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus laevis*; Brzeski (1992) BLR: <https://doi.org/10.5281/zenodo.8122483>

*Enchodelus laevis*; Peña-Santiago (2021b):207 BLR: <https://doi.org/10.5281/zenodo.11194193>

### Distribution

Originally recovered from Nearctic: **USA** (type habitat: fresh water stream bank - Thorne (1939) / Altherr and Delamare-Deboutteville (1972)); subsequently, this species is also recorded in Eastern Palearctic: **Korea** (moss - Brzeski (1992)).

### Taxon discussion

This species was briefly described from the USA by Thorne (1939) on the basis of one female specimen. After that, Altherr, in Altherr and Delamare-Deboutteville (1972), studied one male from the USA too that was described as *E. knuppenburgensis*, very close to *E. laevis* in its general morphology. Thus, Altherr suggested that his male might be conspecific with the *E. laevis* female. Brzeski (1992) described five females and one male specimens of *E. laevis* from Korea and regarded both species as identical.

## ***Enchodelus longispiculus* Guerrero, Liébanas & Peña-Santiago, 2008**

- ZooBank [F7B216E2-08F1-4A55-AA31-0F838A47207B](https://doi.org/10.21203/rs.3.rs-1000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8GPPM>
- GBIF <https://www.gbif.org/species/10810810>
- ENA <https://www.ebi.ac.uk/ena/browser/view/Taxon:1068861>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20longispiculus&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus longispiculus* Guerrero, Liébanas & Peña-Santiago, 2008; Guerrero et al. (2008a) BLR: <https://doi.org/10.5281/zenodo.8114886>

*Enchodelus longispiculus*; Ciobanu et al. (2010b) BLR: <https://doi.org/10.5281/zenodo.8111641>

*Enchodelus longispiculus*; Pedram et al. (2011) BLR: <https://doi.org/10.5281/zenodo.8114668>

*Enchodelus longispiculus*; Peña-Santiago (2021b):207-208 BLR: <https://doi.org/10.5281/zenodo.11191897>

### **Distribution**

A typical member of Palearctic nematode fauna: **Spain** (type habitat: wet meadow, 2925 m a.s.l., other microhabitats: gorse scrubland and wet meadows, 2590-2700 m a.s.l. - Guerrero et al. (2008a)), **Iran** (rhizosphere of grasses - Pedram et al. (2011)) and **Romania** (beech forest, cliff vegetation, grassland, 400-2000 m a.s.l. - Ciobanu et al. (2010b)).

### **Taxon discussion**

Originally described from Spain, this species was later recorded in Romania and Iran. Pedram et al. (2011) provided its first molecular characterisation, based on the 18S rDNA, ITS and partial 5.8S gene.

## ***Enchodelus lucinensis* Popovici, 1978**

- ZooBank [573AEEF2-A7E8-4E73-82E8-D24E34F897ED](https://doi.org/10.21203/rs.3.rs-1000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMK3>
- GBIF <https://www.gbif.org/species/4554528>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20lucinensis%C2%A0&tab=plazi#results-section>

## Nomenclature

*Enchodelus lucinensis* Popovici, 1978; Popovici (1978) BLR: <https://doi.org/10.5281/zenodo.8122645>

*Enchodelus lucinensis*; Eliava and Eliashvily (1990):60,99 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus lucinensis*; Ciobanu et al. (2010b) BLR: <https://doi.org/10.5281/zenodo.8111643>

*Enchodelus lucinensis*; Peña-Santiago (2021b):208 BLR: <https://doi.org/10.5281/zenodo.11191899>

## Distribution

*Enchodelus lucinensis* is a member of Palearctic nematode fauna, found in different localities and habitats from: **Romania** (type habitat: peat bog, other habitat: mezohydrophilous meadow\*, 1050-1250 m a.s.l.\* - Popovici (1978), Ciobanu et al. (2010b)\*), **Slovakia** (alpine meadows, 1994-2200 m a.s.l. - Háněl (2017)) and **Turkey** (wildflower meadows, mountain grasslands, riverbed, 2500-4000 m a.s.l. - Çakmak et al. (2021)).

## Taxon discussion

Originally described by Popovici (1978), the type material of this species was later re-examined by Ciobanu et al. (2010b). These authors considered that its separation from *E. teres* (due to brief original description) is very problematic and based on minor differences.

## *Enchodelus makarovae* Elshishka, Lazarova & Peneva, 2012

- ZooBank [FFC630CE-A71F-4361-A611-8CA1862AE381](https://www.zoobank.org/FFC630CE-A71F-4361-A611-8CA1862AE381)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HNCS>
- GBIF <https://www.gbif.org/species/8848341>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus+makarovae&tab=plazi#results-section>

## Nomenclature

*Enchodelus makarovae* Elshishka, Lazarova & Peneva, 2012; Elshishka et al. (2012) [Plazi treatment](#)

*Enchodelus makarovae*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus makarovae*; Peña-Santiago (2021b):210 BLR: <https://doi.org/10.5281/zenodo.11192362>

## Distribution

This species is a part of Palearctic nematode fauna, found only in an Arctic polar desert: **Russia** (Arctic, Severnaya Zemlya Archipelago, type habitat: polygonal polar desert with *Alopecurus alpinus* Sm., *G. coraloides*, *Lopadium* sp., *D. borealis*, black crust - Elshishka et al. (2012)).

## *Enchodelus microdoroides* Baqri & Jairajpuri, 1974

- ZooBank [225D0BC0-58FF-45EB-A48D-243C1780F4AC](https://doi.org/10.22004/zoobank/225D0BC0-58FF-45EB-A48D-243C1780F4AC)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4QR>
- GBIF <https://www.gbif.org/species/7018612>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus+microdoroides&tab=plazi#results-section>

## Nomenclature

*Enchodelus* (*Enchodelus*) *microdoroides* Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144944>

*Enchodelus microdoroides* Baqri & Jairajpuri, 1974; Baqri and Jairajpuri (1974) BLR: <https://doi.org/10.5281/zenodo.8117932>

*Enchodelus microdoroides*; Eliava and Eliashvily (1990):62,100 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus microdoroides*; Eliava and Eliashvily (1990)Brzeski (1992) BLR: <https://doi.org/10.5281/zenodo.8122485>

*Enchodelus microdoroides*; Eliava and Eliashvily (1990)Peña-Santiago (2021b):210 BLR: <https://doi.org/10.5281/zenodo.11198490>

## Distribution

*Enchodelus microdoroides* is a representative of Indomalayan nematode fauna: **India** (type habitat: soil around roots of barley, 549 m a.s.l., other habitat: grasses, 2100 m a.s.l. - Baqri and Jairajpuri (1974) / grasses and mosses - Ahmad and Jairajpuri (1980)); however, there is a single report from the Eastern Palearctic: **Korea** (moss - Brzeski (1992)).

## ***Enchodelus parahopedoroides* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010**

- ZooBank [14062C06-C50A-417C-94B2-5824024030A6](https://zoobank.org/14062C06-C50A-417C-94B2-5824024030A6)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J4BK>
- GBIF <https://www.gbif.org/species/11798772>
- SiBILS <https://sibils.text-analytics.ch/search/?query=enchodelus%20parahopedoroides&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus parahopedoroides* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010; Ciobanu et al. (2010b) BLR: <https://doi.org/10.5281/zenodo.8111645>

*Enchodelus parahopedoroides*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11191909>

### **Distribution**

This species is reported from West Palearctic Region: **Romania** (type habitat: cliff vegetation, 2200 m a.s.l., other habitats: spruce forest, mountain grassland, 1000-2000 m a.s.l. - Ciobanu et al. (2010b)).

## ***Enchodelus parateres* Baqri & Jairajpuri, 1974**

- ZooBank [5E901204-F5D0-44EB-86CC-57850518D76E](https://zoobank.org/5E901204-F5D0-44EB-86CC-57850518D76E)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9J3QS>
- GBIF <https://www.gbif.org/species/7018643>
- SiBILS <https://sibils.text-analytics.ch/search/?query=enchodelus+parateres&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus (Rotundus) parateres* Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) [Plazi treatment](#)

*Enchodelus parateres* Baqri & Jairajpuri, 1974; Baqri and Jairajpuri (1974) BLR: <https://doi.org/10.5281/zenodo.8117930>

*Enchodelus parateres*; Eliava and Eliashvily (1990):64,100 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus parateres*; Jairajpuri and Ahmad (1992):182 [figure] BLR: <https://doi.org/10.5281/zenodo.10850166>

*Enchodelus parateres*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus parateres*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11191913>

### Distribution

*Enchodelus parateres* is a member of Indomalayan nematode fauna: **India** (type habitat: soil around roots of weeds and mosses, 2600 m a.s.l. - Baqri and Jairajpuri (1974) / soil around the roots of wild fruit trees, 1415 m a.s.l. - Ahmad and Jairajpuri (1980)).

The species was also recorded in Palearctic: **Romania** (grassland, mix forest, 1050 m a.s.l. - Ciobanu and Popovici (2017)) and **Russia** (Arctic tundra - Kuzmin (1986), Kuzmin and Gagarin (1990)).

### *Enchodelus parvus* Loof, 1971

- ZooBank [66A06F84-3034-47C8-828C-880B6885AF3F](https://www.zoobank.org/66A06F84-3034-47C8-828C-880B6885AF3F)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8GNN3>
- GBIF <https://www.gbif.org/species/4554531>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20parvus#results-section>

### Nomenclature

*Enchodelus (Rotundus) parvus* Loof, 1971 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144936>

*Enchodelus parvus* Loof, 1971; Loof (1971) BLR: <https://doi.org/10.5281/zenodo.8152930>

*Enchodelus parvus*; Eliava and Eliashvily (1990):65,101 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus parvus*; Holovachov (2014):22 [list] [Plazi treatment](#)

*Enchodelus parvus*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11191917>

### Distribution

This species was reported in Palearctic, mainly in Arctic tundra: **Norway (Spitzbergen)** (type habitat: bare soil, 150 m a.s.l., other habitats: grass tufts and mosses, *Saxifraga* sp. - Loof (1971)), **Russia** (Arctic tundra - Kuzmin (1986), Kuzmin and Gagarin (1990) and **Uzbekistan** (cotton - Mavlyanov et al. 1989). The last record requires confirmation.



## ***Enchodelus ponorensis* Popovici, 1995**

- ZooBank [E1EC7E6D-6D62-46AA-888B-65E7CDD3BCD5](https://doi.org/10.21203/rs.3.rs-10000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMK6>
- GBIF <https://www.gbif.org/species/4554555>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20ponorensis#results-section>

### **Nomenclature**

*Enchodelus ponorensis* Popovici, 1995; Popovici (1995a) BLR: <https://doi.org/10.5281/zenodo.8125533>

*Enchodelus ponorensis*; Ciobanu et al. (2010b) BLR: <https://doi.org/10.5281/zenodo.8111647>

*Enchodelus ponorensis*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11191919>

### **Distribution**

This species is reported from Western Palearctic Region: **Romania** (type habitat: mountain grassland, 1000 m a.s.l. - Popovici (1995a)).

### **Taxon discussion**

Ciobanu et al. (2010b) re-examined type material of this species only known to occur in Romania. It is an atypical representative of the genus due to its short bipartite uterus, long pharyngeal expansion (ca. two-fifths of pharynx length) and longer and conoid tail, but other relevant traits (lip region shape, double guiding ring, flanged odontophore etc.) fit well the *Enchodelus* diagnosis.

## ***Enchodelus sardashtensis* Pedram, Pourjam, Robbins, Ye & Peña-Santiago, 2011**

- ZooBank [89A41CD5-08E3-4C72-A003-C205D15FD8B9](https://doi.org/10.21203/rs.3.rs-10000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/8GPPN>
- GBIF <https://www.gbif.org/species/10787556>
- ENA <https://www.ebi.ac.uk/ena/browser/view/Taxon:1068862>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20sardashtensis%20&tab=plazi#results-section>

### **Nomenclature**

*Enchodelus sardashtensis* Pedram, Pourjam, Robbins, Ye & Peña-Santiago, 2011; Pedram et al. (2011) BLR: <https://doi.org/10.5281/zenodo.8114670>

*Enchodelus sardashtensis*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11194197>

### Distribution

This species is reported from Eastern Palearctic, only known from its type locality: **Iran** (type habitat: rhizosphere soil of grasses - Pedram et al. (2011)).

## *Enchodelus saxifragae* Popovici, 1995

- ZooBank [8F559D50-234C-48A9-B99A-D49E70C99EAB](https://doi.org/10.5281/zenodo.11194197)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HJ35>
- GBIF <https://www.gbif.org/species/4554544>
- ENA <https://www.ebi.ac.uk/ena/browser/view/Taxon:1440451>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20saxifragae#results-section>

### Nomenclature

*Enchodelus saxifragae* Popovici, 1995; Popovici (1995a) BLR: <https://doi.org/10.5281/zenodo.8125535>

*Enchodelus saxifragae*; Guerrero et al. (2008b) BLR: <https://doi.org/10.5281/zenodo.811185>

*Enchodelus saxifragae*; Ciobanu et al. (2010a) BLR: <https://doi.org/10.5281/zenodo.8111707>

*Enchodelus saxifragae*; Peña-Santiago et al. (2015):147 [figure] BLR: <https://doi.org/10.5281/zenodo.10698092>

*Enchodelus saxifragae*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11191923>

### Distribution

*Enchodelus saxifragae* is distributed in Western Palearctic, reported from different localities and habitats: **Romania** (type habitat: subalpine grassland on limestone, under *Saxifraga moschata* Wulf., 1950-2000 m a.s.l. - Popovici (1995a), Popovici and Ciobanu (1997) / grasslands - Popovici (1998), Ciobanu and Popovici (2001) / cliff vegetation, subalpine meadow, 1450-2000 m a.s.l. - Ciobanu et al. (2010a)) and **Spain** (hedgehog heath, psychroserophilous pasture, pine forest with savin juniper, 1550-3350 m a.s.l. - Guerrero et al. (2008b), Peña-Santiago et al. (2015)).

### Taxon discussion

This species, originally described and later repeatedly recorded in Romania, is also known to occur in Spain. Ciobanu et al. (2010a) re-examined its type material and

noted the peculiar shape of the lateral guiding pieces, which was regarded as a relevant diagnostic feature. It is very close to *E. groenlandicus*, but it differs from this in lip region shape, degree of sclerotisations of the *pars refringens vaginae* and the presence of males. Peña-Santiago et al. (2015) provided its first molecular (18S rDNA) study.

## ***Enchodelus teres* Thorne, 1939**

- ZooBank [8711F9F6-2790-4774-B3CD-8865203DBAD3](https://www.zoobank.org/8711F9F6-2790-4774-B3CD-8865203DBAD3)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMK7>
- GBIF <https://www.gbif.org/species/4554532>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20teres#results-section>

### **Nomenclature**

*Enchodelus (Rotundus) teres* Thorne, 1939 (Ahmad & Jairajpuri, 1980); Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144936>

*Enchodelus teres* Thorne, 1939; Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003135>

*Enchodelus teres*; Zullini (1970) BLR: <https://doi.org/10.5281/zenodo.10850514>

*Enchodelus teres*; Eliava and Eliashvili (1990):67,101 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus teres*; Holovachov (2014):23 [list] [Plazi treatment](#)

*Enchodelus teres*; Peña-Santiago (2021b):211 BLR: <https://doi.org/10.5281/zenodo.11194199>

### **Distribution**

Holarctic species. First recovered in Nearctic: **USA** (type habitat: soil around root of alpine plants, 3440 m a.s.l. - Thorne (1939) / *Ambrosia psilostachya* DC. - Orr and Dickerson (1967)) and also reported from few localities of Palearctic: **Italy** (moss, 1340 m a.s.l. - Zullini (1970)) and **Russia** (Arctic tundra - Kuzmin (1973), Kuzmin and Gagarin (1990)).

### **Taxon discussion**

Available information about this species is very limited. On the one hand, the original description of American specimens lacks many details. On the other hand, its later records only provided some Demanian indices, if anything.

## ***Enchodelus vestibulifer* Altherr, 1952**

- ZooBank [7376F631-5490-452C-A770-2268F6245BEF](https://doi.org/10.21203/rs.3.rs-10000000/v1)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMK9>
- GBIF <https://www.gbif.org/species/4554545>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=Enchodelus%20vestibulifer#results-section>

### **Nomenclature**

*Enchodelus vestibulifer* Altherr, 1952; Altherr (1952) BLR: <https://doi.org/10.5281/zenodo.10813922>

*Enchodelus vestibulifer*, Meyl (1961) BLR: <https://doi.org/10.5281/zenodo.11015551>

*Enchodelus vestibulifer*, Eliava and Eliashvily (1990):68,102 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus vestibulifer*, Peña-Santiago (2021b):211

### **Description**

Material examined. One female in poor condition, mounted on one slide labelled *Enchodelus vestibulifer* n. sp., and collected from Parc National, st. 39 in July 1948 (Fig. 1).

Measurements: L = 1.36 mm, a = 32.4, b = 3.8, c = 61.8, c' = 1.0, V = 53%, neck length = 355 µm (Fig. 5).

Habitus curved ventrally after fixation, adopting an open C-shape (Fig. 6). Cuticle consisting of two layers, its outer layer provided with distinct transverse striations. Lip region 16 µm wide, offset by a shallow depression (Fig. 7). Cheilostom a wide cavity. Amphidial fovea funnel shape. Odontostyle 24 µm long, strong with wide lumen, straight, 1.5 times lip region diameter, 1.8% of body length. Guiding ring double. Anterior region of pharynx enlarging gradually; pharyngeal basal expansion 174 µm, occupying about half of total neck length, bearing muscular sheath (Fig. 8). Pharyngeal gland nuclei not visible, their orifices obscure. Cardia rounded. A disc-like structure separating the pharyngeal base from cardia present. Female genital system diovarian. Uteri not differentiated. Vagina extending inwards for 62% of body diameter, *pars refringens vaginae* not well preserved (Fig. 9). Prerectum 1.4, rectum 1.3 times anal body diameter long. Tail conical with rounded tip, 22 µm long, 1.8% of body length (Fig. 10).

### **Distribution**

This species is a part of Palearctic nematode fauna, currently known only from **Switzerland** (type habitat: soil of grasses; 1900 m a.s.l. - Altherr (1952)).

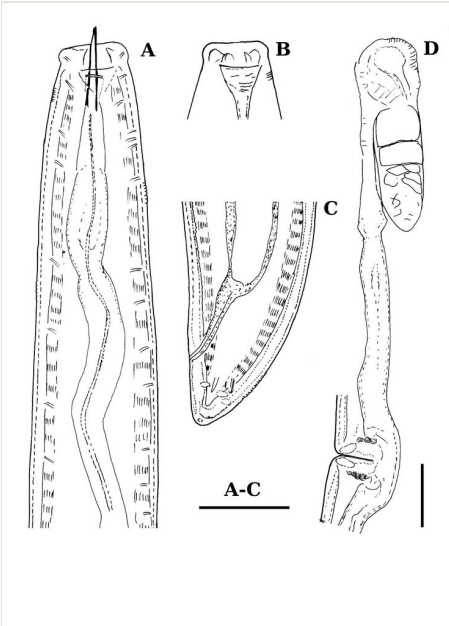


Figure 5. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, female. **A** Anterior region; **B** Amphid; **C** Tail end; **D** Anterior genital branch. Scale bars: **A-C** 25 µm; **D** 25 µm.

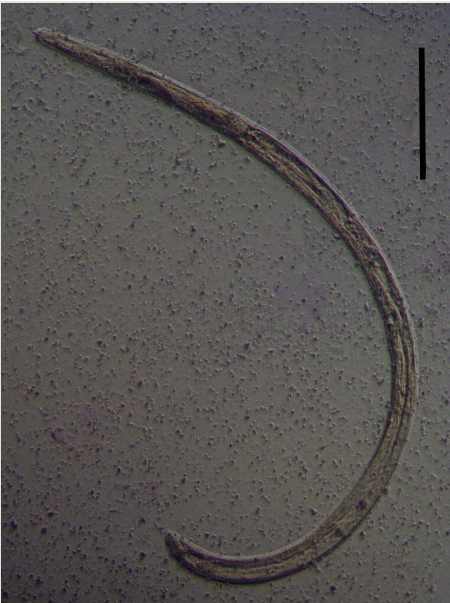


Figure 6. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, entire body. Scale bar: 200 µm.

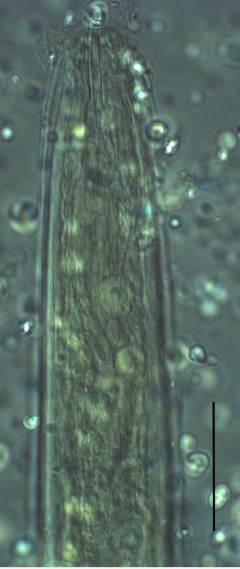


Figure 7. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, anterior end. Scale bar: 30  $\mu$ m.

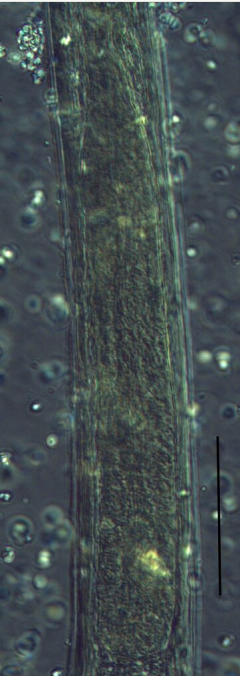


Figure 8. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, pharyngeal expansion. Scale bar: 50  $\mu$ m.

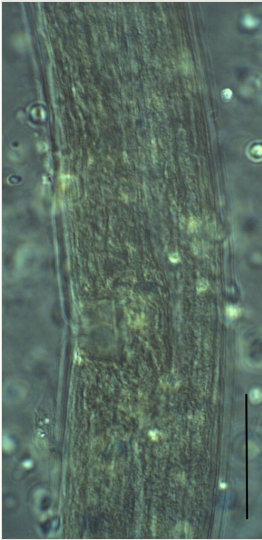


Figure 9. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, vulval region. Scale bar: 30  $\mu$ m.



Figure 10. [doi](#)

*Enchodelus vestibulifer* Altherr, 1952, posterior end. Scale bar: 30  $\mu$ m.

### Taxon discussion

Altherr (1952) described this species on the basis of a single female from Switzerland and no later record exists. The female forms part of Altherr's collection, deposited in [the Museo Cantonale di Storia Naturale di Lugano](#) (Switzerland). Its state of preservation is not good, so that some morphological features are difficult to appreciate with accuracy.

The re-examination of this material has provided some differences from Altherr's original description - shorter body length ( $L = 1.36$  vs.  $1.55$  mm), values of de Man indices "c" are lower, "a", c', V are higher, size of vagina, saccate bodies described and illustrated in the original description are hardly visible, most likely due to flattening of the specimen and conservation.

Meyl (1961) considered this species as *species inquirenda*. New observations reveal that several relevant traits (strong odontostyle with wide lumen, comparatively long pharyngeal expansion occupying ca. one-half of the total neck length, tail conical with rounded tip) are not compatible with those characterising the genus *Enchodelus*. Thus, this species is herein regarded as *incertae sedis*.

### ***Enchodelus vesuvianus* (Cobb, 1893) Thorne, 1939**

- ZooBank [BA5F7F84-F01C-4874-AE74-0E352B5A2A3A](https://doi.org/10.26007/2522-2029-BA5F7F84-F01C-4874-AE74-0E352B5A2A3A)
- Catalogue of Life <https://www.catalogueoflife.org/data/taxon/9HMKB>
- GBIF <https://www.gbif.org/species/4554533>
- SIBiLS <https://sibils.text-analytics.ch/search/?query=enchodelus%20vesuvianus#results-section>

#### **Nomenclature**

*Dorylaimus vesuvianus* Cobb, 1893; Cobb (1893) BLR: <https://doi.org/10.5281/zenodo.10853995>

*Dorylaimus vesuvianus*; Steiner (1914):262 [list] BLR: <https://doi.org/10.5281/zenodo.11003080>

*Dorylaimellus vesuvianus* (Cobb, 1893) Thorne & Swanger, 1936; Thorne and Swanger (1936) BLR: <https://doi.org/10.5281/zenodo.10845811>

*Enchodelus* (*Enchodelus*) *vesuvianus* (Cobb, 1893) Thorne, 1939; Ahmad and Jairajpuri (1980) BLR: <https://doi.org/10.5281/zenodo.8144934>

*Enchodelus vesuvianus* (Cobb, 1893) Thorne, 1939; Thorne (1939) BLR: <https://doi.org/10.5281/zenodo.11003126>

*Enchodelus vesuvianus*; Meyl (1954) BLR: <https://doi.org/10.5281/zenodo.10928057>

*Enchodelus vesuvianus*; Meyl (1961) BLR: <https://doi.org/10.5281/zenodo.11015551>

*Enchodelus vesuvianus*; Zullini (1970) BLR: <https://doi.org/10.5281/zenodo.10850516>

*Enchodelus vesuvianus*; Vinciguerra (1972) BRL: <https://doi.org/10.5281/zenodo.11028268>



*Enchodelus vesuvianus*; Vinciguerra and De Francisci (1973) BLR: <https://doi.org/10.5281/zenodo.8143851>

*Enchodelus vesuvianus*; Zullini (1978) BLR: <https://doi.org/10.5281/zenodo.10814618>

*Enchodelus vesuvianus*; Winiszewska-Slipinska (1987) BLR: <https://doi.org/10.5281/zenodo.10854942>

*Enchodelus vesuvianus*; Eliava and Eliashvily (1990):69,102 BLR: <https://doi.org/10.5281/zenodo.11003031>

*Enchodelus vesuvianus*; Andrásy (2009b) BLR: <https://doi.org/10.5281/zenodo.10821951>

*Enchodelus vesuvianus*; Peña-Santiago (2021b):211-212 BLR: <https://doi.org/10.5281/zenodo.11191929>

### Distribution

The species is widespread in southern and central parts of Western Palearctic: **Italy** (type habitat: moss - Cobb (1893) / moss - Meyl (1954), moss - Zullini (1970), Zullini (1971), Vinciguerra (1972) / moss - Vinciguerra and De Francisci (1973) / moss - Zullini (1978) / moss on rock - Barbuto and Zullini (2006) / alpine springs - sediments, mosses - Zullini et al. (2011)), **Hungary** (Andrásy (1973), Andrásy (2009b)), **Poland** (*Festucetalia valesiaca* Soó, *Arrhenatherum* sp. - Winiszewska-Slipinska (1987)) and **Switzerland** (Steiner (1914)).

In Nearctic, it is reported from **the USA** (*Schizachyrium scoparium* (Michx.) Nash, *Symphoricarpos orbiculatus* Moench - Orr and Dickerson (1967)).

### Notes

*Enchodelus vesuvianus* was found and described for the first time from Mount Vesuvius, Italy. This species is widespread in Europe, mainly associated with mosses. It has also been reported from the USA, but without morphological and morphometric data.

## *Enchodelus enguriensis* Elshishka, Mladenov, Altash, Tskitishvili, Álvarez-Ortega, Peña-Santiago & Peneva, sp. nov.

- ZooBank [92281C43-6B4F-47D0-B1DE-B957B7439CFF](https://zoobank.org/92281C43-6B4F-47D0-B1DE-B957B7439CFF)

### Description

Material examined. Four females, five males and twelve juveniles (J1-J4) from Georgia.

## Measurements (see Table 1)

**Adult** (Figs 11, 12, 13, 14, 15). Moderately slender ( $a = 20-27$ ) nematodes of medium size, 1.03-1.40 mm long. Body cylindrical, tapering towards the ends. Upon fixation, habitus regularly curved ventrad, C-shaped. Cuticle two-layered, 3-3.5  $\mu\text{m}$  thick at level of the guiding ring, 2.5  $\mu\text{m}$  at mid-body and 6-8  $\mu\text{m}$  on tail, layers with different refraction, the outer one visibly thinner than the inner one and bearing very fine transverse striation, inner layer with slight radial striation, especially visible at tail. Lateral chord very narrow, with granular aspect and lacking any differentiation. Several dorsal and ventral body pores are present at cervical region. Lip region rounded, offset from the adjoining body by a weak, but distinct depression, 2.7-3.6 times as wide as high, with mostly amalgamated lips and distinct papillae visibly protruding above the lip region contour. Amphidial fovea funnel-like, its aperture more than half of lip region diameter. Cheilostom a truncate cone to almost cylindrical, thick-walled. Odontostyle long and slender, straight, 2.1-2.5 times the lip region diameter, 18-20 times as long as wide and 2.6-3.7% of body length, with very narrow lumen and minute aperture occupying hardly 5% of its length. Guiding ring double, located at 1.3-1.7 times lip region diameter from anterior end. Odontophore 1.1-1.2 times as long as odontostyle, thickened, bearing flange-like extensions at its base. Pharynx entirely muscular, gradually enlarging into the basal expansion 87-94  $\mu\text{m}$  long that occupies one-third of the total neck length, pharyngeal gland nuclei and their orifices located as follows: DO = 69-70%, DN = 71-74%, SN = 87-89%, PS1 = 41-48%, PS2 = 40-46%. Nerve ring located at 160  $\mu\text{m}$  from the anterior end. Pharyngo-intestinal junction consisting of a short and rounded cardia and a weak ring-like structure surrounding pharyngeal base.

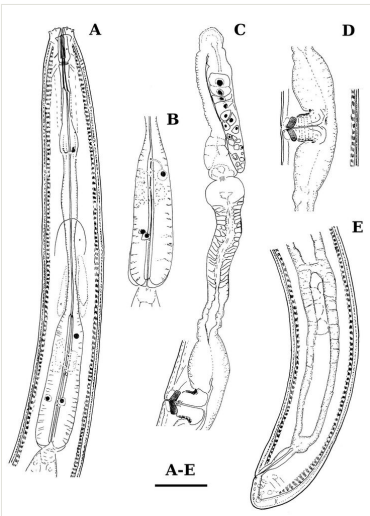
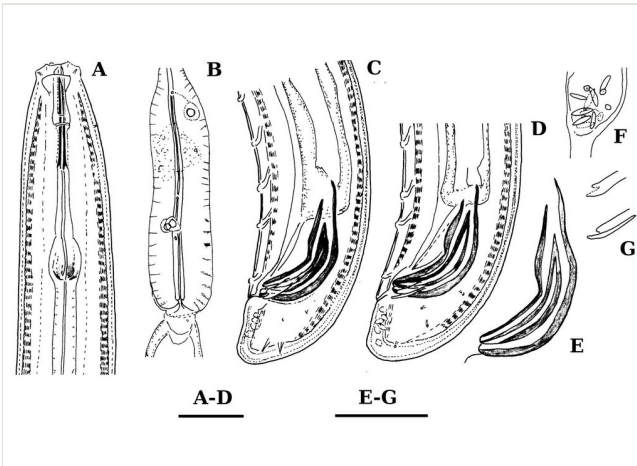
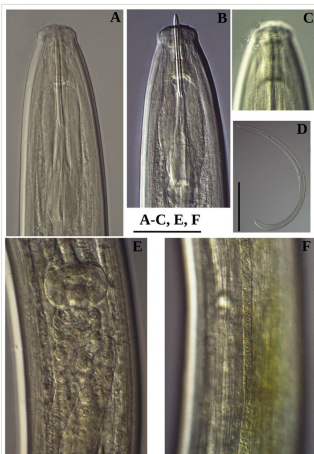


Figure 11. [doi](#)

*Enchodelus enguriensis* sp. nov., female (Holotype). **A** Anterior region; **B** Pharyngeal expansion; **C** Anterior genital branch; **D** Vulval region; **E** Tail end. Scale bar: **A-E** 25  $\mu\text{m}$ .

Figure 12. [doi](#)

*Enchodelus enguriensis* sp. nov., male. **A** Lip region; **B** Pharyngeal expansion; **C**, **D** Posterior end; **E** Spicules; **F** Sperm cells; **G** Lateral pieces. Scale bars: **A-D** 25  $\mu$ m, **E-G** 25  $\mu$ m.

Figure 13. [doi](#)

*Enchodelus enguriensis* sp. nov., female. **A**, **B** Lip region; **C** Amphid; **D** Entire body; **E** *Pars dilatata distalis uteri*; **F** Lateral field. Scale bars: **A-C**, **E**, **F** 30  $\mu$ m **D** 400  $\mu$ m.

**Female.** Genital system diovarian, with both branches equally developed, the anterior 250  $\mu$ m long, the posterior 240  $\mu$ m ( $n = 1$ ). Ovaries relatively short, often not reaching the sphincter level. Oviduct with well-developed *pars dilatata* bearing distinct lumen. Sphincter between oviduct and uterus well developed. Uterus long, 126-152  $\mu$ m or 2.5-2.8 times the corresponding body diameter, tripartite, consisting of a wider proximal portion, a longer and much more slender intermediate section with a narrow lumen and surrounded by cluster of hyaline cells and a well-developed, spheroid, distal *pars dilatata*. Vagina extending inwards to 57-59% of body diameter: *pars*

*proximalis* 19-20 x 18.5-19  $\mu\text{m}$ , *pars refringens* with (in lateral view) two rectangular sclerotised pieces whose combined width is 14-17  $\mu\text{m}$ , *pars distalis* 3-5  $\mu\text{m}$  long. Vulva a transverse slit. Prerectum 3.0-4.1, rectum 0.9-1.1 times anal body diameter length. Tail convex conoid, 1.5-1.9% of body length, with bubble-like or saccate bodies mostly on ventral side, inner core occupying 50-70% of tail length, caudal pores two pairs.



Figure 14. [doi](#)

*Enchodelus enguriensis* sp. nov., female. **A, B** Vulval region; **C, D** Tails; **E** Saccate bodies. Scale bar: **A-E** 30  $\mu\text{m}$ .

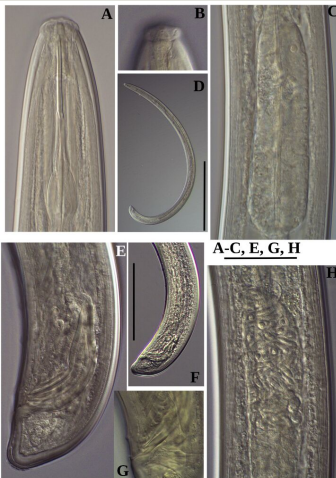


Figure 15. [doi](#)

*Enchodelus enguriensis* sp. nov., male. **A** Lip region; **B** Amphid; **C** Pharyngeal expansion, dorsal gland; **D** Entire body; **E** Tail end and spicules; **F** Posterior end; **G** Lateral piece; **H** Sperm cells in testis. Scale bars: **A-C, E, G, H** 30  $\mu\text{m}$ ; **D** 400  $\mu\text{m}$ ; **F** 100  $\mu\text{m}$ .

**Male.** General morphology similar to that of female. Genital system diorchic, with opposite testes. Sperm cells spindle-shaped,  $8\text{--}9 \times 2 \mu\text{m}$ . In addition to the ad-cloacal pair, located at  $7\text{--}9 \mu\text{m}$  from the cloacal aperture, there is a series of 9–10 spaced ventromedian supplements, one or two within the range of spicules, thus without hiatus. Spicules dorylaimoid, 1.4–1.9 times the body diameter at level of the cloacal aperture, 4–5 times as long as wide its maximum width: head occupying 20–25% of total length, ventral side bearing prominent hump and hollow, posterior end  $6\text{--}7 \mu\text{m}$  wide. Lateral guiding pieces cylindrical with asymmetrical bifurcate end (Figs 12, 15), reaching the spicule terminal tip, measuring  $13\text{--}15 \times 2\text{--}3 \mu\text{m}$ . Tail convex conoid, with two pairs of caudal pores.

**Juveniles** (Figs 16, 17). Based on morphometric of juvenile specimens and the relationships between the lengths of their functional and replacement odontostyles and body lengths, four juvenile stages were identified. Habitus in first juvenile stage almost straight, lip region flat, continuous with the body, genital primordium  $8 \mu\text{m}$  long, tail ventrally curved with long central peg,  $20 \mu\text{m}$  long.

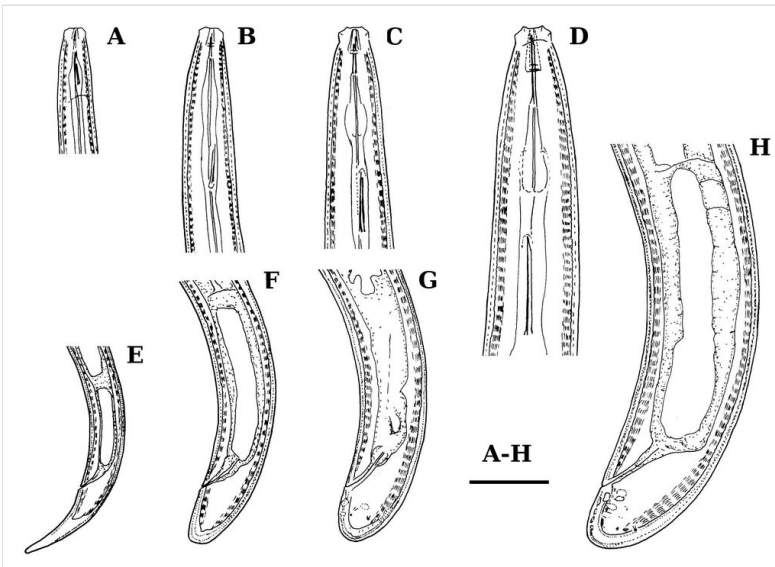


Figure 16. [doi](#)

*Enchodelus enguriensis* sp. nov. juveniles. **A–D** Anterior region (A J1, B J2, C J3, D J4); **E–H** Tail ends (E J1, F J2, G J3, H J4). Scale bar: **A–H**  $25 \mu\text{m}$ .

Tail in J2 and J3 conoid elongated in J4 bluntly conoid as in females,  $c'$  decreasing during the successive stages to J4 and females.

**Molecular characterisation:** One D2–D3 of 28S rRNA gene sequences was obtained for this species. In the D2–D3 of 28S rRNA (Fig. 4) gene tree, this sequence formed a highly-supported clade (PP = 100) with *E. macrodorus* and other three *Enchodelus* sequences from GenBank.

## Diagnosis

*Enchodelus enguriensis* sp. nov. is characterised by its 1.03-1.40 mm long body, lip region 16-17  $\mu\text{m}$  wide and offset by weak depression, odontostyle 37–40  $\mu\text{m}$  long or 2.1-2.5 times lip region diameter, odontophore flanged and 1.1–1.2 times as long as odontostyle, neck 270-290  $\mu\text{m}$  long, pharyngeal expansion occupying one-third of the total neck length, female genital system diovarian, uterus tripartite, *pars refringens vaginae* with two rectangular sclerotisations, vulva ( $V = 49\text{--}53\%$ ), tail convex conoid (19-26  $\mu\text{m}$ ,  $c = 51\text{--}69$ ,  $c' = 0.5\text{--}0.8$ ) bearing abundant saccate bodies; males abundant, spicules 54–61  $\mu\text{m}$  long and 9-10 spaced ventromedian supplements without hiatus.

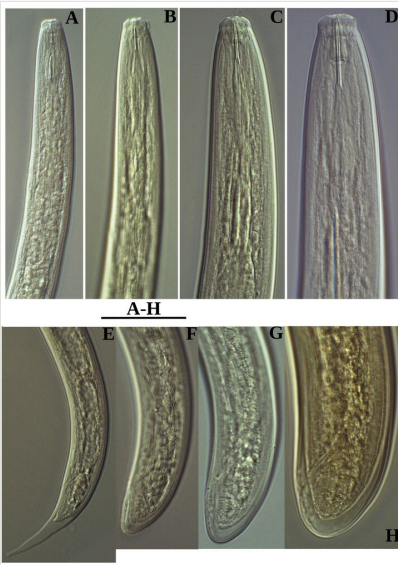


Figure 17. [doi](#)

*Enchodelus enguriensis* sp. nov., juveniles. **A-D** Anterior region (A J1, B J2, C J3, D J4); **E-H** Tail ends (E J1, F J2, G J3, H J4). Scale bar: **A-H** 30  $\mu\text{m}$ .

**Relationships:** Based on tail morphology and odontostyle length, this species can be assigned to the *E. macrodorus* – group as defined by Guerrero et al. (2008b). This group includes *E. babakicus*, *E. carpaticus*, *E. distinctus*, *E. groenlandicus*, *E. macrodorus*, *E. makarovae*, *E. microdoroides* and *E. saxifragae*. This homogeneous group is characterised by the presence of a rather long odontostyle ( $> 35 \mu\text{m}$ ), odontophore with well-developed flanges, uterus tripartite (except for *E. distinctus*, which has been described with a bipartite uterus (Ahmad and Jairajpuri 1980) and hemispheroid to rounded conoid tail.

In having a lip region offset by a depression, the new species is most similar to *E. carpaticus*, *E. groenlandicus*, *E. macrodorus*, *E. makarovae* and *E. microdoroides*. The new species differs from:

*Enchodelus carpaticus* by its by slightly shorter odontostyle (37–40 vs. 39.5–47  $\mu\text{m}$ ), shorter neck length (280–290 vs. 336–388  $\mu\text{m}$ ) and pharyngeal expansion (87–94 vs. 136–167  $\mu\text{m}$ ), absence of dorsal cell mass near cardia vs. presence, shorter prerectum (90–124 vs. 164–272  $\mu\text{m}$ ) and tail (av. 20.5 (19–24) vs. av. 23.7 (21–29)  $\mu\text{m}$ ), saccate bodies present vs. absent, males present vs. absent (males not found, but sperm cells were observed in one female) (Ciobanu et al. 2010a);

*Enchodelus groenlandicus* by its shorter body ( $L = 1.03\text{--}1.4$  vs.  $1.54\text{--}2.5$  mm) and odontostyle (37–40 vs. 43–53  $\mu\text{m}$ ), somewhat more anteriorly located guiding ring (24–26.5 vs. 27–37  $\mu\text{m}$ ), narrower lip region (16–16.5 vs. 19–22  $\mu\text{m}$ ), more posterior vulva position ( $V = 49\text{--}53$  vs.  $40\text{--}49\%$ ), males present vs. absent (Ditlevsen 1927, Andrásy 2009a, Elshishka et al. 2012). A record from Iran (Pedram et al. 2011) largely deviates from the morphometrics of other data for *E. groenlandicus* (e.g. lip region width, tail length) and is not included in the comparison.

*Enchodelus macrodorus* in having a shorter body ( $L = 1.03\text{--}1.4$  vs.  $1.38\text{--}1.92$  mm) and pharyngeal expansion (87–94 vs. 110–145  $\mu\text{m}$ ), more posterior vulva position ( $V = 49\text{--}53$  vs.  $37\text{--}47\%$ ), a longer and more differentiated uterus (2.5–2.8 times longer than body diameter with long intermediate portion and well developed *pars distalis* vs. 0.9–2.0 times body diam. with very short intermediate region and poorly developed *pars distalis*), tail differently shaped (convex conoid vs. rounded to hemispherical), males abundant vs. males rare (Guerrero et al. 2008b).

*Enchodelus makarovae* by its shorter body ( $L = 1.03\text{--}1.4$  vs.  $1.57\text{--}2.00$  mm), shorter odontophore (1.1–1.2 vs. 1.2–1.4 times as long as odontostyle), shorter neck length and pharyngeal expansion (280–290 vs. 320–377  $\mu\text{m}$  and 87–94 vs. 113–130  $\mu\text{m}$  long, respectively) and uterus (126–152 vs. 220–346  $\mu\text{m}$ ), males with shorter spicules (54–61 vs. 65–74  $\mu\text{m}$  long), lateral piece shape (asymmetrically vs. symmetrically bifurcated) (Elshishka et al. 2012);

*Enchodelus microdoroides* by having a wider lip region (16–16.5 vs. 13–14  $\mu\text{m}$ ), relatively shorter odontostyle (2.3–2.5 vs. 3 times lip region diameter), guiding ring located more anteriorly (24–26.5 vs. 28–39  $\mu\text{m}$  from anterior end), differently-shaped *pars refringens vaginae* (rectangular vs. quadrangular), males abundant vs. males rare, longer spicules (54–61 vs. 45–50  $\mu\text{m}$ ) (Baqri and Jairajpuri 1974, Ahmad and Jairajpuri 1980, Brzeski 1992).

The new species can be distinguished from the remaining three species of *E. macrodorus* group by its lip differentiation: lip region set off by depression vs. set off by a deep constriction. Further, it differs from:

*Enchodelus babakicus* by having cuticle smooth vs. striated, a slightly shorter and thinner odontostyle (37–40 vs. 40–45  $\mu\text{m}$  and 18–20 vs. 13.6–15.3 times as long as wide, respectively), guiding ring located slightly more anterior (24–26.5 vs. 25–30  $\mu\text{m}$  from anterior end), more posteriorly located vulva ( $V = 49\text{--}53$  vs.  $44\text{--}49\%$ ), differently-shaped *pars refringens vaginae* (rectangular vs. trapezoidal), thinner hyaline part of

tail (29-47 vs. 42-57% of tail length), differently-shaped lateral piece (asymmetrically vs. symmetrically bilobed) (Pedram et al. 2011).

*Enchodelus distinctus* in having a shorter body length (L = 1.03-1.4 vs. 1.85 mm), longer odontostyle (37–40 vs. 36  $\mu\text{m}$ ), more posteriorly located guiding ring (1.5-1.7 vs. 1.4 times lip region diameter), pharyngo-intestinal disc present vs. absent, different structure of uterus (tripartite vs. bipartite), shorter tail (19-24 vs. 32  $\mu\text{m}$ ,  $c' = 0.6-0.7$  vs.  $c' = 0.8$ ), saccate bodies present vs. absent, males present vs. absent (Ahmad and Jairajpuri 1980).

*Enchodelus saxifragae* by its shorter body length (L = 1.03-1.4 vs. 1.61-2.38 mm), a narrower lip region (16-16.5 vs. 18–22  $\mu\text{m}$ ), shorter neck length and pharyngeal expansion (280-290 vs. 319-490  $\mu\text{m}$  and 87-94 vs. 116–186  $\mu\text{m}$  long, respectively), shorter prerectum (90-124 vs. 140–294  $\mu\text{m}$ ) and fewer ventromedian supplements (9-10 vs. 13–16 in number) (Popovici 1995a, Guerrero et al. 2008b, Ciobanu et al. 2010a).

**Type-locality and habitat:** Georgia, Samegrelo-Zemo Svaneti Region, Bogreshi, Enguri River, Tower of Love, moss *Tortella squarrosa* (Brid.) Limpr., geographical coordinates: 43°00'01N 42°50'04"E, 1544 m a.s.l.

**Type material:** The holotype female, three paratype males and four paratype juveniles are deposited in the Nematode Collection of Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Bulgaria, under the accession numbers IBER-BAS NTC 107-109. Other paratypes are deposited as follows: one female, one male and three juveniles (accession numbers ISUZI0010581, ISUZI0010582) – in the Nematode Collection of the Department of Nematology, Institute of Zoology, Ilia State University, Tbilisi, Georgia; one female, one male and three juveniles (accession numbers 0714, 0715) – in the Nematode Collections of the Universidad de Jaén, Jaén, Spain; one female, two males and one juvenile (accession numbers T-8075p, T-8076p) – in the USDA Nematode Collection, Beltsville, Maryland, USA.

### Etymology

The species is named after the River Enguri; it was recovered from the stone next to the Tower of Love on the bank of the river.

### Distribution

Georgia

### Notes

Morphometric data of all species (28) of genus *Enchodelus* are provided in *Suppl. material 1*.



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## Supplementary material

### Suppl. material 1: Morphometric data of the species of genus *Enchodelus* [doi](#)

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**Data type:** morphometrics

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