PENSOFT

SENCKENBERG
world of biodiversity

Leibniz Association

Phylogenetic analysis of *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae), including descriptions of four new species

Adrian Smolis[1], Nataliya Kuznetsova[2], Grzegorz Paśnik[3]

1 *University of Wrocław, Faculty of Biological Science, Department of Invertebrate Biology, Evolution and Conservation, Przybyszewskiego 65, 51-148 Wrocław, Poland*

2 *Institute of Biology and Chemistry, Moscow State Pedagogical University, Moscow 129164, Russia*

3 *Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland*

https://zoobank.org/88A70CAC-692F-48EA-99E3-73D4DAEB15FD

Corresponding author: Grzegorz Paśnik (pasnik@isez.pan.krakow.pl)

Received 11 October 2023
Accepted 06 March 2024
Published 25 April 2024

Academic Editors Michael Schmitt, Mónica M. Solórzano Kraemer

Citation: Smolis A, Kuznetsova N, Paśnik G (2024) Phylogenetic analysis of *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae), including descriptions of four new species. Arthropod Systematics & Phylogeny 82: 343–367. https://doi.org/10.3897/asp.82.e114038

Abstract

With 54 described species, *Endonura* is one of the most species-rich genera of the Neanurinae. The taxon is characterised by the presence of 0–2 ocelli, separate tubercles Di and De with the non-crossed type of chaetotaxy on the head, and two or three tubercles on the fifth abdominal tergite. Four new species from the Crimea and the Caucasian region have been described based on adult specimens: *Endonura armeniaca* **sp. nov.**, *E. cochlearifera* **sp. nov.**, *E. crimica* **sp. nov.**, and *E. duplex* **sp. nov.** A phylogenetic analysis of the genus *Endonura* using 70 characters of adult external morphology is presented. Two methods were chosen to examine different approaches to the reconstruction of evolutionary relationships: Maximum Parsimony (MP) and Bayesian Inference (BI). Besides supporting *Endonura* monophyly both analyses failed to resolve any of the deeper relationships within the genus. All known species within the genus are grouped into two main clades, A and D. Both of these clades have members distributed throughout Europe, the Caucasus and the western part of Central Asia. *Endonura crimica* **sp. nov.** can be considered as an intermediate between these two clades.

Keywords

Cladistic analysis, Bayesian inference, Springtails, taxonomy

1. Introduction

Springtails belonging to the subfamily Neanurinae are an example of evolutionary success, with over 800 currently described taxa, representing almost one tenth of all the known Collembola (Bellinger et al. 2023). Members of the subfamily differ significantly from other Collembola in terms of morphology and behaviour. Firstly, they have completely lost the jumping organ (furca or furcula) and their movement can be defined as exceptionally slow compared to the majority of springtails. Another striking difference between members of this subfamily and other

Collembola is that the integument surface has prominent tubercles. In addition, unlike other Collembola, the chaetae that cover the body of Neanurinae are well developed, elongated, widened and covered with numerous teeth.

The evolutionary success of this subfamily is probably due to a number of factors. The first is the presence of body tubercles and well-developed chaetae, which in turn provides an important mechanical barrier for potential predators. The second is protection of toxic volatile chemicals, e.g. phenols (Messer et al. 2000). The third is an apparently narrow feeding specialisation, often on slime moulds, which has recently been observed and experimentally demonstrated (Smolis 2009; Hoskins et al. 2015; Deharveng et al. 2017; Smolis and Greenslade 2020). Slime moulds are cosmopolitan and mostly associated with terrestrial habitats with high humidity. Such habitats are also preferred by Neanurinae, which are almost exclusively springtails of forest ecosystems, with an exceptional diversity of species found in the temperate and tropical forests (e.g. Cassagnau 1988, 1993; Deharveng and Weiner 1984; Deharveng 1989a; Greenslade and Deharveng 1991; Deharveng and Bedos 2000; Simón Benito and Palacios-Vargas 2008; Smolis and Bernard 2017).

The genus *Endonura* Cassagnau, 1979 is one of the most thoroughly studied and the largest genera within Neanuridae, with 54 valid species currently (Bellinger et al. 2023). *Endonura* is a Holarctic genus, with the highest concentration of taxa in some regions of the Western Palearctic, e.g. the Iberian Peninsula, the Caucasus, the Crimea, the Carpathians and northwestern Iran (e.g., Deharveng 1979; Jordana et al. 1997; Smolis et al. 2007; Smolis 2008; Smolis and Kuznetsova 2016; Smolis and Skarżyński 2020). A recent phylogenetic analysis, although based on a very small representation of the genus, showed that *Endonura* is poorly defined and probably consists of not very closely related taxa (Smolis and Paśnik 2020). The objectives of our study were: (1) to analyse and describe the morphology of new, unique taxa; (2) to analyse the phylogenetic relationships among species within the genus *Endonura* based on morphology, and to determine the phylogenetic position of the new taxa; and (3) to evaluate the usefulness of chaetotaxy in resolving relationships within *Endonura*.

2. Materials and methods

2.1. Taxonomic analysis

Material for taxonomic descriptions was collected during field trips to the Crimea (by Alexander Sharikov and Dmitry Shitikov; February 2015 and 2016) and the Caucasus (by: Boris Efeikin, Alexander Kremenitsa, Ivan Kuchiev, Nataliya Kuznetsova and Mikhail Potapov; September 1980, July 2015 and May 2016). Samples were taken from soil, litter and moss and extracted using a Berlese-Tullgren apparatus. After extraction, the specimens were preserved in alcohol. For detailed morphological analysis, they were cleared in Nesbitt's fluid, mounted in Swan's medium and examined using a Nikon Eclipse E600 phase-contrast microscope. Figures were drawn using a camera lucida and prepared for publication using Adobe Photoshop CS3.

Abbreviations used. General morphology: **Abd**. – abdomen; **Ant**. – antenna; **AOIII** – sensory organ of antennal segment III; **Cx** – coxa; Fe – femur; **Scx2** – subcoxa 2; **T** – tibiotarsus; **Th**. – thorax; **Tr** – trochanter; **VT** – ventral tube. Groups of chaetae: **Ag** – antegenital; **An** – chaetae of anal lobes; **ap** – apical; **ca** – centroapical; **cm** – centromedial; **cp** – centroposterior; **d** – dorsal; **Fu** – furcal; **vc** – ventrocentral; **Ve** or **ve** – ventroexternal; **Vea** – ventroexternoanterior; **Vem** – ventroexternomedial; **Vep** – ventroexteroposterior; **Vel** – ventroexternolateral; **Vec** – ventroexternocentral; **Vei** – ventroexternointernal; **Vi** or **vi** – ventrointernal; **Vl** – ventrolateral. Tubercles: **Af** – antenno–frontal; **Cl** – clypeal; **De** – dorsoexternal; **Di** – dorsointernal; **Dl** – dorsolateral; **L** – lateral; **Oc** – ocular; **So** – subocular. Types of chaetae: **Ml** – long macrochaeta; **Mc** – short macrochaeta; **me** – mesochaeta; **mi** – microchaeta; **ms** – s–microchaeta; **S** or **s** – chaeta s; **bs** – s–chaeta on Ant. IV; **miA** – microchaetae on Ant. IV; **iv** – ordinary chaetae on ventral Ant. IV; **or** – organite of Ant. IV; **brs** – border s–chaeta on Ant. IV; **i** – ordinary chaeta on Ant. IV; **mou** – cylindrical s–chaetae on Ant. IV („soies mousses"); **x** – labial papilla x; **L'** – ordinary lateral chaeta on Abd. V; **B4**, **B5** – ordinary chaetae on tibiotarsi.

Terminology. Terminology and layout of the tables used in the paper follow Deharveng (1983), Deharveng and Weiner (1984), Smolis and Deharveng (2006) and Smolis (2008).

Depositories. Department of Invertebrate Biology, Evolution and Conservation, University of Wrocław, Poland (**DIBEC**); Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland (**ISEZ**); Moscow State Pedagogical University, Moscow, Russia (**MSPU**); Muséum d'histoire naturelle, Geneva, Switzerland (**MHNG**); Muséum national d'Histoire naturelle, Paris, France (**MNHN**); Oregon State Arthropod Collection, Zoology Department, Oregon State University, Corvallis, U.S.A. (**OSAC**); Senckenberg Museum of Natural History, Görlitz, Germany (**SMNG**); State Museum of Natural History, Ukrainian National Academy of Sciences, L'viv, Ukraine (**SMNHL**); Zoological Museum of University of Amsterdam, Amsterdam, Netherlands (**ZMA**); U.S. National Museum of Natural History, Washington, D.C. U.S.A (**NMNH**).

2.2. Phylogenetic analysis

To investigate the phylogenetic relationships between species of the genus *Endonura*, 43 of the 54 known species were selected for analyses (Table 1). Because of the unavailability of specimens for examination and insuf-

Table 1. List of examined material.

Species	Number of examined specimens	Status of examined types	Collections	Other sources of data e.g. literature
Endonura agnieskae	24	Holotype, Paratypes	MHNG	—
E. aibgai	12	Holotype, Paratypes	DIBEC, MSPU	—
E. annae	22	Holotype, Paratypes	MHNG	—
E. alavensis	—	—	—	Pozo and Simon 1982
E. alticola	1	Holotype	ISEZ	—
E. arbasensis	—	—	—	Deharveng 1979
E. asiatica	11	Holotype, Paratypes	MNHN, DIBEC	—
E. baculifer	—	—	—	Deharveng 1979
E. cantabrica	—	—	—	Deharveng 1979
E. carpatica	8	Holotype, Paratypes	DIBEC	—
E. centaurea	3	Syntypes	MNHN	—
E. ceratolabralis	7	Holotype, Paratypes	DIBEC	—
E. colorata	—	—	—	Jordana et al. 1997
E. cretensis	7	Holotype	ZMA, DIBEC, SMNHL	—
E. cryptopyga	4	Holotype	MSPU	—
E. dalensi	—	—	—	Deharveng 1979
E. dentifera	7	Holotype, Paratypes	DIBEC, SMNHL	—
E. deharvengi	2	Syntypes	MNHN	—
E. dichaeta	14	Holotype, Paratypes	DIBEC	—
E. diminutichaeta	11	Holotype, Paratypes	MSPU, DIBEC	—
E. dobrolyubovae	8	Holotype, Paratypes	MSPU, DIBEC	—
E. dudichi	40	—	DIBEC	—
E. gracilirostris	5	Holotype, Paratypes	DIBEC, SMNHL	—
E. gladiirostra	1	Holotype	DIBEC	—
E. gladiolifer	—	—	—	Jordana et al. 1997
E. incolorata	26	Lectotype, Paralectotype	ISEZ, DIBEC	—
E. kremenitsai	11	Holotype, Paratypes	MSPU, DIBEC	—
E. levantica	2	Holotype, Paratype	DIBEC, SMNHL	—
E. longirostris	4	Holotype, Paratypes	DIBEC	—
E. lusatica	38	Holotype, Paratype	SMNG	—
E. ossetica	2	Holotype, Paratype	MSPU, DIBEC	—
E. paracantabrica	5	Holotype, Paratypes	MSPU, DIBEC	—
E. paracentaurea	4	Holotype, Paratypes	DIBEC	—
E. persica	14	Holotype, Paratypes	DIBEC	—
E. reticulata	52	—	DIBEC, MNHN	—
E. saleri	—	—	—	Fanciulli and Dallai 2008
E. schwendingeri	9	Holotype, Paratypes	MHNG	—
E. tatricola	162	Lectotype	ISEZ, DIBEC	—
E. taurica	11	Holotype, Paratypes	ISEZ, DIBEC	—
E. transcaucasica	1	Lectotype	ISEZ	—
E. turkmenica	2	Holotype, Paratype	DIBEC	—
E. quadriseta	17	Holotype, Paratype	MNHN, DIBEC	—
E. urotuberculata	2	Holotype, Paratype	MNHN, DIBEC	—
Neanura muscorum	177	—	DIBEC	—
Kalanura babenkoi	34	Holotype, Paratypes	DIBEC, MSPU	—
Xylanura oregonensis	47	Holotype, Paratypes	NMNH, OSAC, DIBEC	—

ficient descriptions, the following species were not included in the analyses: *E. caeca* (Gisin, 1963), *E. granulata* (Cassagnau, Delamare & Deboutteville, 1955), *E. ichnusae* Dallai, 1983, *E. immaculata* Deharveng, 1980, *E. ludovicae* (Denis, 1947), *E. occidentalis* Deharveng, 1979, *E. pejai* Deharveng, 1980, *E. poinsotae* Deharveng, 1980, *E. tartaginensis* (Deharveng, 1980), *E. tetrophthalma* (Stach, 1929) and *E. tyrrhenica* Dallai, 1983.

The four new species described in this paper were included in the phylogenetic analysis. Forty-seven species were analysed out of 58. The trees were rooted using *Neanura muscorum* (Templeton, 1836), *Kalanura babenkoi* Smolis, 2007 and *Xylanura oregonensis* Smolis 2011 as outgroup taxa.

Species were selected based on specimen availability, with a preference for the type-specimens. Most

Table 2. Morphological data matrix used in the analyses.

Taxon	Characters 1111111111222222222233333333 1234567890123456789012345678901234	Characters 3333444444444455555555556666666667 6789012345678901234567890123456789
N. muscorum	00010100000110001000000010100010100	01010000010100101100000001001101100
K. babenkoi	00010000000110001000000010000010100	01100000000000001100000001000011110
X. oregonensis	00011011110010001030100010000010121	11100101010101100000101?001001011000
E. agnieskae	10011000000110001000000000010110100	01111110000100101110000001101111110
E. aibgai	10011000000111121001?00010010110100	01001111000100101110000001111010110
E. alavensis	10011001100110011020100010010110 2??	?1001?1???0????0??100010?00??011111
E. alticola	10011000000110001000000010010110210	01101111000100111110000??111?11111
E. annae	10011001000110021100110000011200000	01001010010101000001101?001101010110
E. arbasensis	111?10000001100010000000010011111????	?10011110000000?0??100010?000?011111
E. armeniaca	10011001000112121101?001?1?10100200	00001111?111?10111101?0?1111111111
E. asiatica	10001000000110001000000010010110100	00001111000100101110101000111011111
E. baculifer	10011001100111111121?10010011110????	?00010100101012011010100110?0111??
E. cantabrica	10011001000110011001?00010010111????	?10011110001002?0??100000?100?0111??
E. carpatica	111?10001001100211 21?10000011111100	00001010010101001110000001101011111
E. centaurea	11011001001110011101?000000111101 10	00001010010101001110001 0?0101011110
E. ceratolabralis	10011001000110011100100000010110221	11101010010101001110001 0?0101011111
E. cochlearifera	10011000000110011000000000010110200	00001111000100101110100001001111110
E. colorata	10011001110110001021?00000010111????	??001?1???0????0??101000?100?011110
E. cretensis	10011000100012121020000010010111210	01111111?111?10221101?101000111111
E. crimica	10011001000100011001?00000010110100	01001010000100101110000?1000011110
E. cryptopyga	10011000000111121101?00010010100200	01011111000100101110000?1001110010
E. dalensi	10011000000010011000000001001111????	?10011110000000?0??100010?100?011111
E. deharvengi	10011000000111121000000010011?10110	00001010010101001110100001100011111
E. dentifera	10011000000110001100000000010110100	00001111000100101110100001001110001
E. dichaeta	11011001100111121121?00000011?10210	00001010010101001111000000101011111
E. diminutichaeta	10011001000111101000100010010?00200	01101111000100102210001001001111010
E. dobrolyubovae	10011001000111121101?00000010?00100	00001111000100101110100011001?10110
E. dudichi	11011001000110000101?00000011?10100	01001010010101011110000000100111110
E. duplex	10011000000110001000000000010110100	01001111000100101110100001000011110
E. gladiirostra	10011011110110011301000100102002 21	11111010010101000010001 0?1101?11110
E. gladiolifer	10011000100110001021?000?001010????	?11110100111???0111011?0?000?010111
E. gracilirostris	10011000100100011020000000010?10220	00001111000100101110001001101?11010
E. incolorata	11011000000110000101?00000011110100	00001010??0101001120001000100011111
E. kremenitsai	10011000000111101000000010010110100	01101111000100101110000011001111110
E. levantica	10011000000110021000000000011110120	00011010010101001110000?0101011111
E. longirostris	10011000000112121101?00010011110220	00001111000000101210001 0?1100011111
E. lusatica	10011000000111011000000000010110200	00001111000100101110100001001010010
E. ossetica	10011001010110021110100010011100200	01101010000101101010101 0?1001011111
E. paracantabrica	10011000000110001001?00010010110100	01101111000100101110000001001011010
E. paracentaurea	10011001000110021101?00000011110120	01001010010101001110000?0101011111
E. persica	10011000000111121100000010010200100	01001111000100100010000001001010010
E. quadriseta	10011000100110011020000010010110100	00001111000100101110001011000011111
E. reticulata	10011000000110001000000000010110100	00001111000000001110100001000011110
E. saleri	10011000000111111111?00000011111120	00001010000100001110000?1001111111
E. schwendingeri	10011001000111121101?001?1?10100100	00001111000100101110001011111110110
E. tatricola	11011001000110000101?00000011110100	00001010010101001110000000100011111
E. taurica	10011001100100011201000100010110000	00001111000100101110000001001110011
E. transcaucasica	10011001000110021100111000011110210	01001010010101001110001 0?1101011111
E. turkmenica	10011000000110021100000000010110220	00001010010101001110000001101011110
E. urotubercula	111?10000000100111000000000011110100	00001111000000101110001100101011111

characters were based on personal observations of specimens. These observations were supplemented by previous taxonomic/phylogenetic studies (Deharveng 1983; Deharveng and Weiner 1984; Greenslade and Deharveng 1990; Smolis and Deharveng 2006; Smolis 2008).

A total of 70 characters were scored for the study taxa, including 61 binary characters and 9 multistate characters. Missing data were coded as '?' in the matrix (Table 2). All characters were treated as unordered (Fitch 1971) and equally weighted (Wilkinson 1992), thus making no assumptions about character evolution. The character matrix was constructed and characters mapped with WinClada ver. 1.00.08 (Nixon 2002) to observe character state transformation on a tree.

The morphological dataset was analysed using both Maximum Parsimony (MP) and Bayesian Inference (BI).

Parsimony analyses utilized New Technology heuristic searches implemented in the program TNT v. 1.5 (Goloboff and Catalano 2016). New Technology searches (Goloboff 1999) consisted of Tree Fusion, Ratchet, Tree Drifting and Sectorial searches performed, with default parameters applied, until the most-parsimonious tree was found 10 times. All characters were treated as unordered and equally weighted.

Some argue (e.g. Goloboff 1993; Goloboff et al. 2008) that results based on correctly weighted characters are preferable to those where all characters have the same weight. Implied weighting is a commonly used method for assigning different weights during tree searches. It's a good choice because it's independent of previous analyses and weights. The strength against homoplasy under implied weighting is related to a constant k. A lower value of k indicates a higher strength against homoplasy. This value represents the ratio of single extra step to the cost of the most homoplasious character. The value of k was calculated using the TNT script setk.run, written by Salvador Arias (Instituto Miguel Lillo in San Miguel de Tucuman, Argentina), which returned a value of 9.687500 for our dataset.

Clade supports were assessed based on Bremer support (BS) (Bremer 1994) and symmetric resampling (Goloboff et al. 2003). The Bremer support value was calculated by searching suboptimal trees up to 10 steps longer than the shortest one using TBR swapping on the shortest trees. Up to 10,000 suboptimal trees were retained during each turn.

The Symmetric Resampling (SR) support calculated the differences in the frequencies of a given group and its most frequent contradictory group (GC). The analyses were run in TNT with the traditional search, using 10,000 replications, change probability of 0.33, two initial Wagner trees, and holding three trees per replicate.

The following values were applied to support the clades: weak (SR<50%, BS 1–2), moderate (SR 51–75%, BS 3–6), good (SR 76–90%, BS 7–8), and strong (SR>90%, BS 9–10).

The synapomorphies were mapped in WinClada onto the most parsimonious tree using an option showing unambiguous changes only.

Bayesian inferences were performed in MrBayes v3.2.7 (Ronquist et al. 2012) using two simultaneous Markov Chain Monte Carlo runs, with 4 chains of 10 million generations each, sampling trees every 1,000th generation. In this analysis, the dataset was treated as a single partition and analysed under gamma-distribution variation, considering all state frequencies (change rates) set equal, all topologies with equal probabilities, and with unconstrained branch length.

In tree resulting from Bayesian inference, Posterior Probability (PP) was interpreted as statistical support values.

3. Results

3.1. Taxonomic descriptions

Genus *Endonura* Cassagnau, 1979

Neanura (*Endonura*) Cassagnau, 1979: 192.

Type species. *Achorutes tetrophtalmus* Stach, 1929: 282.

Diagnosis. 0–2 + 0–2 eyes, pigmented or not. Colour of body blue, purple brown, white, never yellow or red. Dorsal tubercles present, well developed. Mouthparts feebly developed, maxilla styliform, mandible slender or rarely strong. Labral chaetotaxy: 4/2, 4; sometimes prelabral or labral chaetae reduced. Sensilla S on Ant. IV of similar size. Head with 10 or 12 tubercles. Tubercles Af and Cl separate or fused. Tubercles Di and De on head separate, sometimes Di not differentiated. Arrangement of chaetae Di and De on head of the „non-croisé" type (Deharveng 1983). Tubercles L and So on head fused. S-chaetae present in typical arrangement and number; 22/11111 on each half tergite from th. II to abd. V. Abdomen IV with 8 tubercles: 2 Di, 2 De, 2 Dl and 2 L, or 5 tubercles: (Di+Di), 2 (De+Dl) and 2 L. Abdomen V with 3 tubercles: 2 (De+Dl+L) and (Di+Di) or 2 tubercles: 2 (Di+De+Dl+L). Tubercles Di on abd. V fused or separate. Tibiotarsal chaetotaxy 19, 19, 18. Claw with inner tooth or untoothed.

Endonura armeniaca sp. nov.

https://zoobank.org/554E1A9B-F28D-4ED2-8C7B-4B72DC48CE68

Figs 1–15, Tables 3a–c, 4

Type material. Holotype: adult female on slide, Armenia, road to Agveran village (40°29′32.6′′ N; 44° 35′35.1′′ E), mountain oak forest, litter and soil, 24.V.2016, leg. B. Efeikin (**DIBEC**). Paratype: adult female on slide, same data as holotype.

Diagnosis. 2+2 pigmented eyes. Buccal cone long, labrum ogival. Head with chaetae B, C and D. Chaetae A, O, Ocp and E absent. Tubercles Cl and Af separate. Tubercles Dl and (L+So) on head with 4 and 7 chaetae respectively. Tubercles Di on Th. I absent. Tubercles De on Th. II and III with 3 chaetae. Tubercles L on Abd. III and IV with 3 and 5 chaetae respectively. Abd. IV and V with

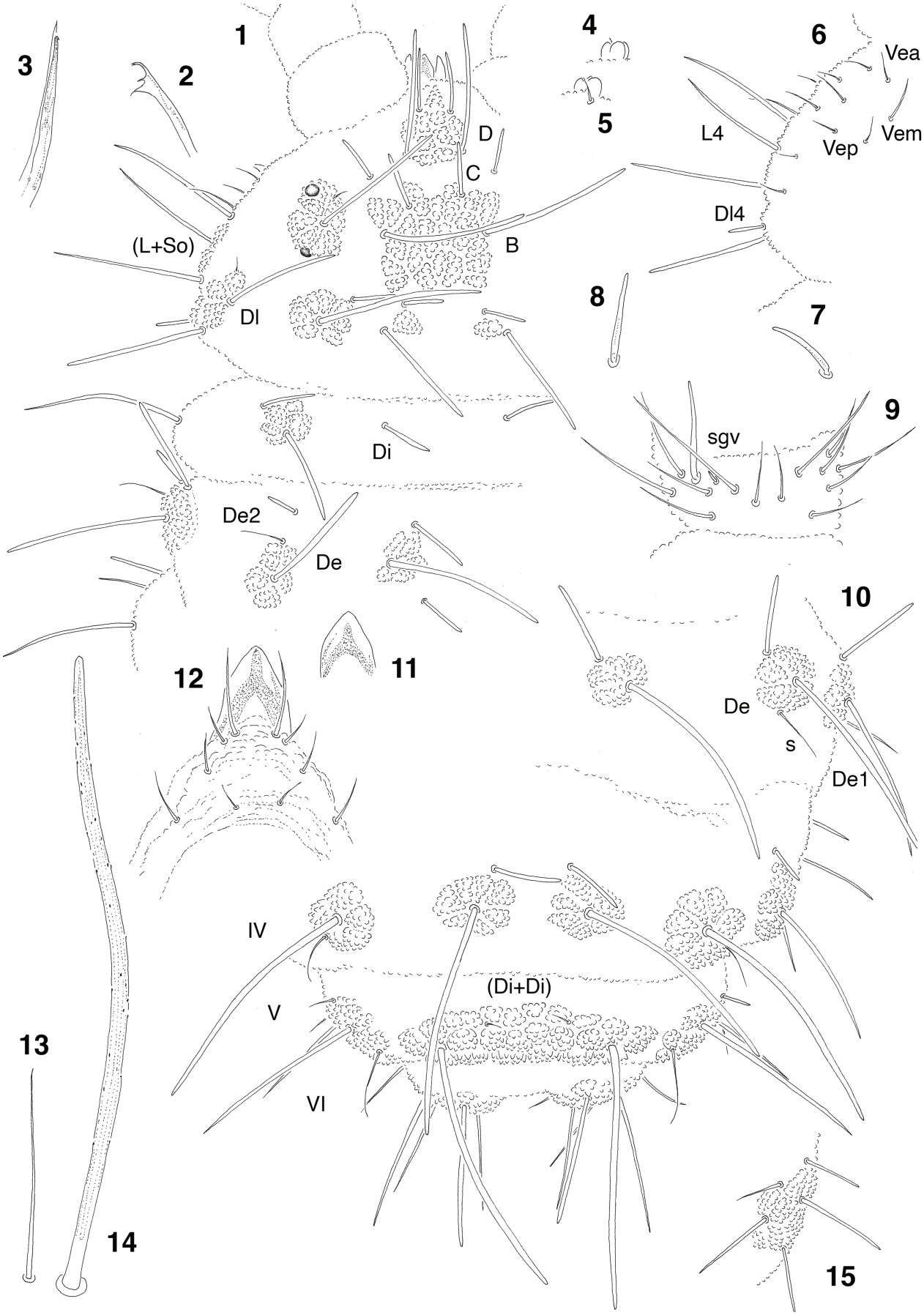

Figure 1–15. *Endonura armeniaca* **sp. nov.: 1** dorsal chaetotaxy of head and Th. I–II; **2** mandible; **3** maxilla; **4** apical bulb, ventral view; **5** apical bulb, dorsal view; **6** ventral chaetotaxy of head; **7** S– chaeta of Ant. IV; **8** sensillum sgd; **9** ventral chaetotaxy of Ant. III; **10** dorsal chaetotaxy of Abd. III–VI; **11** ventral sclerifications of labrum; **12** chaetotaxy of labrum; **13** sensillum of Abd. V; **14** chaeta Di1 of Abd. V; **15** tubercle L of Abd. IV.

Table 3a. Chaetotaxy of *Endonura armeniaca* **sp. nov.**: cephalic chaetotaxy–dorsal side.

Tubercle	Number of chaetae	Types of chaetae	Names of chaetae
Cl	4	Ml	F
		Mc	G
Af	6	Ml	B
		Mc	C, D
Oc	2	Ml	Ocm
		mi	Oca
Di	2	Ml	Di1
		Mc	Di2
De	2	Ml	De1
		Mc	De2
Dl	4	Ml	Dl5, Dl1
		Mc	Dl4
		mi	Dl2
(L+So)	7	Ml	L1, L4, So1
		me	So3–6

Table 3b. Chaetotaxy of *Endonura armeniaca* **sp. nov.**: antennae.

Segment, Group	Number of chaetae	Segment, Group	Number of chaetae adult
I	7	IV	or, 8 S, i, 12 mou, 6 brs, 2 iv
II	11		
III	5 sensilla AO III		
ve	5	ap	8 bs, 5 miA
vc	4	ca	2 bs, 3 miA
vi	4	cm	3 bs, 1 miA
d	5	cp	8 miA, 1 brs

Table 3c. Chaetotaxy of *Endonura armeniaca* **sp. nov.**: postcephalic chaetotaxy.

Terga					**Legs**				
	Di	De	Dl	L	Scx2	Cx	Tr	Fe	T
Th. I	1	2	1	—	0	3	6	13	19
Th. II	3	2+s	3+s+ms	3	2	7	6	12	19
Th. III	3	2+s	3+s	3	2	8	6	11	18
					Sterna				
Abd. I	2	2+s	2	2	VT: 4				
Abd. II	2	2+s	2	2	Ve: 3–6; chaeta Ve1 present				
Abd. III	2	2+s	2	3	Vel: 3–5; Fu: 5 me, 0 mi				
Abd. IV	2	1+s	3	5	Vel: 4; Vec: 1–2; Vei: 2; Vl: 4				
Abd. V	(2+2)	4+s			Ag: 3; Vl: 1				
Abd. VI	7				Ve: 10–11; An: 2mi				

8 and 3 tubercles respectively. Claw without inner tooth. Tibiotarsi with chaetae B4 and B5 short.

Description. ***Body length*****:** 1.1 to 1.2 mm (without antennae) (holotype: 1.2 mm). — ***Colour*****:** pale bluish grey (alive and in alcohol). 2+2 black eyes, in a typical arrangement for the genus (one anterior, one posterior, Fig. 1). — ***Chaetal morphology*****:** Dorsal ordinary chaetae of five types: long macrochaetae (Ml), short macrochaetae (Mc), mesochaetae and microchaetae. Long macrochaetae thick, slightly arched or straight, narrowly sheathed, feebly serrated, apically rounded (Figs 1, 10, 14). Macrochaetae Mc morphologically similar to long macrochaetae, but much shorter. Mesochaetae similar to ventral chaetae, thin, smooth and pointed. Microchaetae similar to mesochaetae, but shorter. S–chaetae of tergites thin, smooth and short, notably shorter than nearby macrochaetae (Figs 1, 10, 13). — ***Antennae*****:** Dorsal chaetotaxy of Ant. as in Table 3b. S–chaetae of Ant. IV of medium length and moderately thickened (Fig. 3), sensillum sgd long and thickened (Fig. 8). Apical vesicle distinct, trilobed (Figs 4, 5). Ventral chaetotaxy of Ant. III with 14 ordinary chaetae, sense organ AOIII with long sensillum sgv and short peg (Fig. 9). — ***Mouthparts*****:** Buccal cone

Table 4. Morphological differences between *E. armeniaca* sp. nov., *E. schwendingeri*, *E. cretensis* and *E. quadriseta*.

Characters	***E. armeniaca* sp. nov.**	***E. schwendingeri***	***E. cretensis***	***E. quadriseta***
Shape of labrum	ogival	not ogival	ogival	not ogival
No. of labial chaetae	11	11	8	11
No. of prelabral chaetae	4	4	2	4
Cephalic chaetae A, E and O	absent	absent	present	present
No. of cephalic chaetae Dl	4	5	3	6
No. of cephalic chaetae (L+So)	7	7	7	9
No. of cephalic chaetae Oc	2	2	3	3
Tubercle Di on Th. I	absent	absent	present	absent
No. of chaetae De on Th. III	2+s	3+s	2+s	3+s
No. of chaetae De on Abd. I–III	2+s	3+s	2+s	3+s
No. of chaetae L on Abd. III and IV	3 and 5	2 and 4	4 and 7	4 and 6–8
No. of chaetae Di on Abd. V	2+2	3+3	2+2	3+3
Cauliflower-like tubercles on Abd. IV–VI	absent	absent	present	absent
Male ventral organ	unknown	present	absent	present
Internal tooth on claws	absent	present	absent	absent

long with labral sclerifications ogival (Fig. 11). Labrum chaetotaxy: 4/2, 4 (Fig. 12). Labium with four basal, three distal and four lateral chaetae, papillae x absent. Maxilla styliform (Fig. 3), mandible thin with two basal and two apical teeth (Fig. 2). — ***Dorsal chaetotaxy and tubercles*:** Chaetotaxy of head reduced, chaetae A, E, O, Ocp, Dl3, Dl6, So2, L2 and L3 absent (Figs 1, 6; Table 3a). Tubercles Di on Th. I not differentiated (Fig. 1). Thorax with chaetae De2 free (Fig. 1). On Abd. I–III, the line of chaetae De1–chaeta s not perpendicular to the dorsomedian line. On Abd. V tubercle (Di+Di) with 2+2 chaetae (Fig. 10). Abd. VI partially visible from above (Fig. 10). — ***Ventral chaetotaxy*:** On head, groups Vea, Vem and Vep with 2, 2, 4 chaetae, respectively (Fig. 6). Group Vi on head with 6 chaetae. On Abd. IV, furca rudimentary without microchaetae. On Abd. IV, tubercle L with 5 chaetae (Fig. 15). On Abd. V, chaetae Vl present and chaetae L' absent. **Legs:** Chaetotaxy of legs as in Table 3c. Claw without internal tooth. On tibiotarsi, chaeta M present, chaetae B4 and B5 relatively short and pointed.

Etymology. The name *armeniaca* is derived from Armenia, the country where the species was found.

Remarks. Among the known members of the genus, *E. armeniaca* **sp. nov.** is distinguished by an extraordinary reduction of dorsal cephalic chaetotaxy. This includes the absence of chaetae A, O, E, Ocp, Dl3, L2, L3 and So2, as well as the presence of an ogival labrum and the absence of an internal tooth on the claws. Morphologically, the new species appears to be most similar to *E. schwendingeri* Smolis and Skarżyński, 2020, a species recently described from northwestern Iran (Smolis and Skarżyński 2020). For instance, both species are identified by the absence of chaetae A and Ocp. However, they differ in several aspects, such as the shape of the labrum (ogival in *armeniaca*, not ogival in *schwendingeri*), the number of chaetae Dl on the head (four in *armeniaca*, five in *schwendingeri*), the number of ordinary chaetae De on Th. III (two in *armeniaca*, three in *schwendingeri*), the number of ordinary chaetae De on Abd. I–III (two in *armeniaca*, three in *schwendingeri*), the number of chaetae L on Abd. III and IV (three and five in *armeniaca* and two and four in *schwendingeri*, respectively), the number of chaetae Di on the penultimate abdominal segment, with *armeniaca* having 2+2 and *schwendingeri* having 3+3. Additionally, *schwendingeri* has an internal tooth on its claws, which is absent in *armeniaca*.

E. armeniaca **sp. nov.** is also similar to *E. cretensis* (Ellis, 1976) and *E. quadriseta* Cassagnau and Peja, 1979, which were described from Greece and recently redescribed (Smolis et al. 2007, Smolis and Kaprus' 2009). The differences between *E. armeniaca* **sp. nov.** and the related species mentioned above are summarised in Table 4.

Endonura cochlearifera sp. nov.

https://zoobank.org/839FDE20-6D6E-4117-8B61-5E9D374603E8

Figs 16–25, Tables 5a–c, 6

Type material. Holotype: adult female on slide, Russia, Caucasus, Northern Ossetia, North Ossetia Nature Reserve, surroundings of the village Tsey, green moss pine forest, in mosses, 23.IX.1980, leg. I. Kuchiev (**DIBEC**). Paratypes: 4 adult females, subadult male and 2 juveniles on slides, same data as holotype (**DIBEC** and **MSPU**).

Diagnosis. 2+2 pigmented eyes. Buccal cone long, labrum ogival. Head with chaetae A, B, C, D, E and O. Tubercles Cl and Af separate. Tubercles Dl and (L+So) on head with 6 and 9 chaetae respectively. Tuberles Di on Th. I absent. Tubercles De on Th. II and III with 3 and 4 chaetae respectively. Tubercles L on Abd. III and IV with 4 and 6–7 chaetae respectively. Abd. IV and V with 8 and 3 tubercles respectively. Claw without inner tooth. Tibiotarsi with chaetae B4 and B5 short.

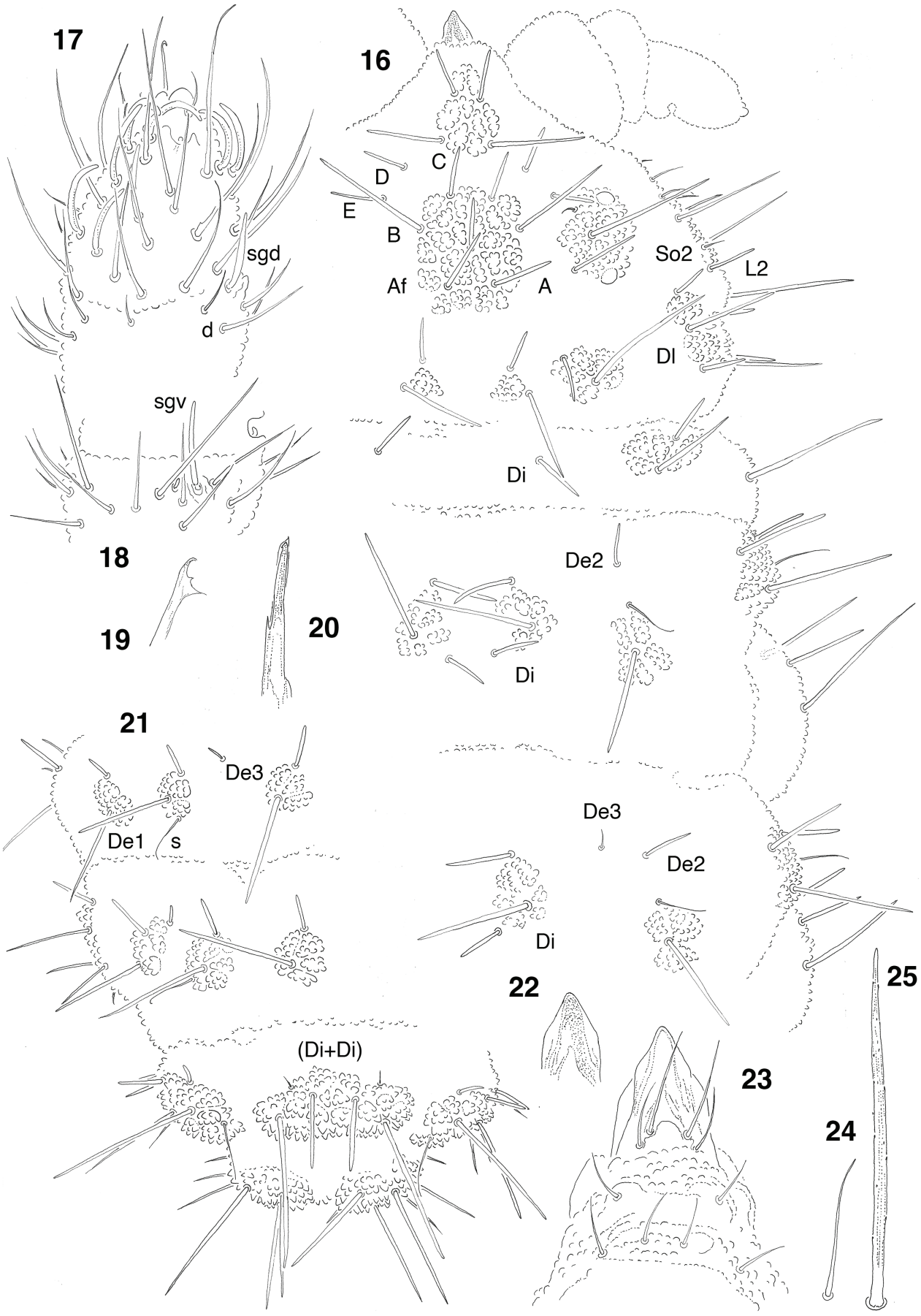

Figure 16–25. *Endonura cochlearifera* **sp. nov.: 16** dorsal chaetotaxy of head and Th.; **17** dorsal chaetotaxy of Ant. III–IV; **18** ventral chaetotaxy of Ant. III; **19** mandible; **20** maxilla; **21** dorsal chaetotaxy of Abd. III–VI; **22** ventral sclerifications of labrum; **23** chaetotaxy of labrum; **24** sensillum of Abd. V; **25** chaeta Di1 of Abd. V.

Table 5a. Chaetotaxy of *Endonura cochlearifera* **sp. nov.**: cephalic chaetotaxy-dorsal side.

Tubercle	Number of chaetae	Types of chaetae	Names of chaetae
Cl	4	Ml	F
		Mc	G
Af	11	Ml	B
		Mc	A, C, D, E, O
Oc	3	Ml	Ocm
		Mc	Ocp
		mi	Oca
Di	2	Ml	Di1
		Mc	Di2
De	2	Ml	De1
		Mc	De2
Dl	6	Ml	Dl5, Dl1
		Mc	Dl2, Dl3, Dl4, Dl6
(L+So)	9	Ml	L1, L4, So1
		Mc	L2
		mi	So2
		me	So3–6

Table 5b. Chaetotaxy of *Endonura cochlearifera* **sp. nov.**: antennae.

Segment, Group	Number of chaetae	Segment, Group	Number of chaetae adult
I	7	IV	or, 8 S, i, 12 mou, 6 brs, 2 iv
II	12		
III	5 sensilla AO III		
ve	5	ap	8 bs, 5 miA
vc	4	ca	2 bs, 3 miA
vi	4	cm	3 bs, 1 miA
d	5	cp	8 miA, 1 brs

Table 5c. Chaetotaxy of *Endonura cochlearifera* **sp. nov.**: postcephalic chaetotaxy.

Terga					Legs				
	Di	De	Dl	L	Scx2	Cx	Tr	Fe	T
Th. I	1	2	1	—	0	3	6	13	19
Th. II	3	2+s	3+s+ms	3	2	7	6	12	19
Th. III	3	3+s	3+s	3	2	8	6	11	18
					Sterna				
Abd. I	2	3+s	2	3	VT: 4				
Abd. II	2	3+s	2	3	Ve: 5; chaeta Ve1 present				
Abd. III	2	3+s	2	4	Vel:5–6; Fu: 5–7 me, 0 mi				
Abd. IV	2	2+s	3	6–7	Vel: 4; Vec: 2; Vei: 2; Vl: 4				
Abd. V	(3+3)	8–9 +s			Ag: 3; Vl: 1				
Abd. VI	7				Ve: 14; An: 2mi				

Description. ***Body length*****:** 0.55 (juvenile) to 1.45 mm (without antennae) (holotype: 1.45 mm). — ***Colour*****:** body pale bluish grey (alive and in alcohol). 2+2 black eyes, in a typical arrangement for the genus (Fig. 16). — ***Chaetal morphology*****:** Dorsal ordinary chaetae of five types: long macrochaetae (Ml), short macrochaetae (Mc), mesochaetae and microchaetae. Long macrochaetae thick, slightly arched or straight, narrowly sheathed, feebly serrated, apically rounded or pointed (Figs 16, 21, 25). Macrochaetae Mc morphologically similar to long macrochaetae, but shorter. Mesochaetae similar to ventral chaetae, thin, smooth and pointed. Microchaetae similar to mesochaetae, but shorter. S–chaetae of tergites thin, smooth and short, notably shorter than nearby macrochaetae (Figs 16, 21, 24). — ***Antennae*****:** Dorsal chaetotaxy of Ant. III–IV as in Fig. 17 and Table 5b. S–chaetae of Ant. IV of medium length and moderately thickened (Fig. 17). Apical vesicle distinct, trilobed. Ventral chaetotaxy of Ant. III with 14 ordinary chaetae, sense organ AOIII with long sensillum sgv and short peg (Fig. 18, Table 5b). —

Table 6. Morphological differences between *E. cochlearifera* **sp. nov.**, *E. lusatica*, *E. dentifera* and *E. annae*.

Characters	***E. cochlearifera* sp. nov.**	***E. lusatica***	***E. dentifera***	***E. annae***
Shape of apical labral sclerifications	spoon-like	ogival	not ogival	not ogival
Shape of labrum	elongated and narrow	elongated and narrow	rather long and narrow	short and wide
Cephalic chaeta O	present	present	absent	absent
Cephalic chaetae C	present	present	present	absent
No. of cephalic chaetae Dl	6	5	6	6
No. of cephalic chaetae (L+So)	9	9	10	8
No. of chaetae L on Abd. IV	6–7	7	8–9	6
No. of chaetae Di on Abd. V	3+3	3+3	3+3	2+2
No. of ordinary chaetae (De+Dl+L) on Abd. V	8–9	7	8	5
Chaeta L' on Abd. V	absent	present	absent	present
Length and shape of tibiotarsal chaetae B4 and B5	short and pointed	elongated and clavate	elongated and clavate	short and pointed
Internal tooth on claws	absent	present	present	present

Mouthparts*:** Buccal cone long with labral sclerifications ogival and spoon-like (Figs 16, 22). Labral chaetotaxy: 4/2, 4 (Fig. 23). Labium with four basal, three distal and four lateral chaetae, papillae x absent. Maxilla relatively thick and styliform (Fig. 20). Mandible thin with two basal and two apical teeth (Fig. 19). — ***Dorsal chaetotaxy and tubercles: Head without chaetae L3 (Fig. 16, Table 5a). Tubercles Di on Th. I not differentiated. Thorax with chaetae De2 and De3 free (Fig. 16). On Abd. I–III, the line of chaetae De1–chaeta s non perpendicular to the dorsomedian line. Abd. I–III with chaetae De3 free (Fig. 21). On Abd. V tubercle (Di+Di) with 3+3 chaetae. Abd. VI well visible from above (Fig. 21). — ***Ventral chaetotaxy*:** On head, groups Vea, Vem and Vep with 3, 4, 4 chaetae respectively. Group Vi on head with 6 chaetae. On Abd. IV, furca rudimentary without microchaetae. On Abd. V, chaetae Vl present and chaetae L' absent. **Legs:** Chaetotaxy of legs as in Table 5c. Claw without internal tooth. On tibiotarsi, chaeta M present and chaetae B4 and B5 relatively short and pointed.

Etymology. The name *cochlearifera* refers to the spoon-like shape of the labral sclerifications of this species.

Remarks. *E. cochlearifera* **sp. nov.** is unique and differs from other species of the genus by the spoon-like shape of the apical labral sclerifications. In general appearance (e.g. dorsal chaetotaxy of head and thorax) the new species strongly resembles *E. annae* Smolis & Skarżyński, 2020, *E. dentifera* Smolis et al., 2007 and *E. lusatica* (Dunger, 1979). However, they can be easily distinguished by the following characters: number of chaetae Dl on the head (six in *cochlearifera*, *annae* and *dentifera*, five in *lusatica*), number of chaetae (L+So) on the head (eight in *annae*, nine in *cochlearifera* and *lusatica*, 10 in *dentifera*), number of ordinary chaetae (De+Dl+L) on Abd. V (8–9 in *cochlearifera*, 5 in *annae*, 7 in *lusatica*, 8 in *dentifera*), presence of chaetae L' on Abd. V (absent in *cochlearifera* and *dentifera*, present in *annae* and *lusatica*), length and shape of chaetae B4 and B5 on tibiotarsi (short and acute in *cochlearifera* and *annae*, elongate and clavate in *lusatica* and *dentifera*) and presence of internal tooth on claw (absent in *cochlearifera*, present in *lusatica* and *dentifera*). All differences between *E. cochlearifera* **sp. nov.** and the related species mentioned above are summarised in Table 6.

Endonura crimica sp. nov.

https://zoobank.org/B2C84D73-4B5A-467A-B206-9B7064B04234

Figs 26–36, Tables 7a–c, 8

Type material. Holotype: adult female on slide, Crimea, Jaltynskyi Nature Reserve (34 24.344 N; 44 55.137 E), 570 m alt., mixed forest (pine, beech), 3.II.2016, leg. D. Shitikov, A. Szarikov (**DIBEC**). Paratype: subadult male on slide, Crimea, Ajudag near Gurzuf, 450 m alt., oak forest, 6.II.2015, leg. D. Shitikov, A. Szarikov (**MSPU**).

Diagnosis. 2+2 pigmented eyes. Buccal cone relatively short and narrow, labrum not ogival. Head with chaetae A, B, C, D and O. Tubercles Cl and Af separate. Tubercles Dl and (L+So) on head with 6 and 9 chaetae respectively. Tuberles Di on Th. I present. Tubercles De on Th. II and III with 3 and 4 chaetae respectively. Tubercles L on Abd. III and IV with 4 and 6–7 chaetae respectively. Abd. IV and V with 8 and 3 tubercles respectively. Claw without inner tooth. Tibiotarsi with chaetae B4 and B5 short.

Description. ***Body length*:** 1.05 (subadult male) to 1.15 mm (holotype) (without antennae). — ***Colour*:** body pale bluish grey (alive and in alcohol). 2+2 black eyes, in a typical arrangement for the genus (Fig. 28). — ***Chaetal morphology*:** Dorsal ordinary chaetae of five types: long macrochaetae (Ml), short macrochaetae (Mc), mesochaetae and microchaetae. Long macrochaetae thick, slightly arched or straight, narrowly sheathed, feebly serrated, apically rounded or pointed (Figs 28, 29, 34). Macrochaetae Mc morphologically similar to long macrochaetae, but shorter. Mesochaetae similar to ventral chaetae, thin, smooth and pointed. Microchaetae similar to mesochaetae, but shorter. S–chaetae of tergites thin, smooth and short, notably shorter than nearby macrochaetae (Figs 28,

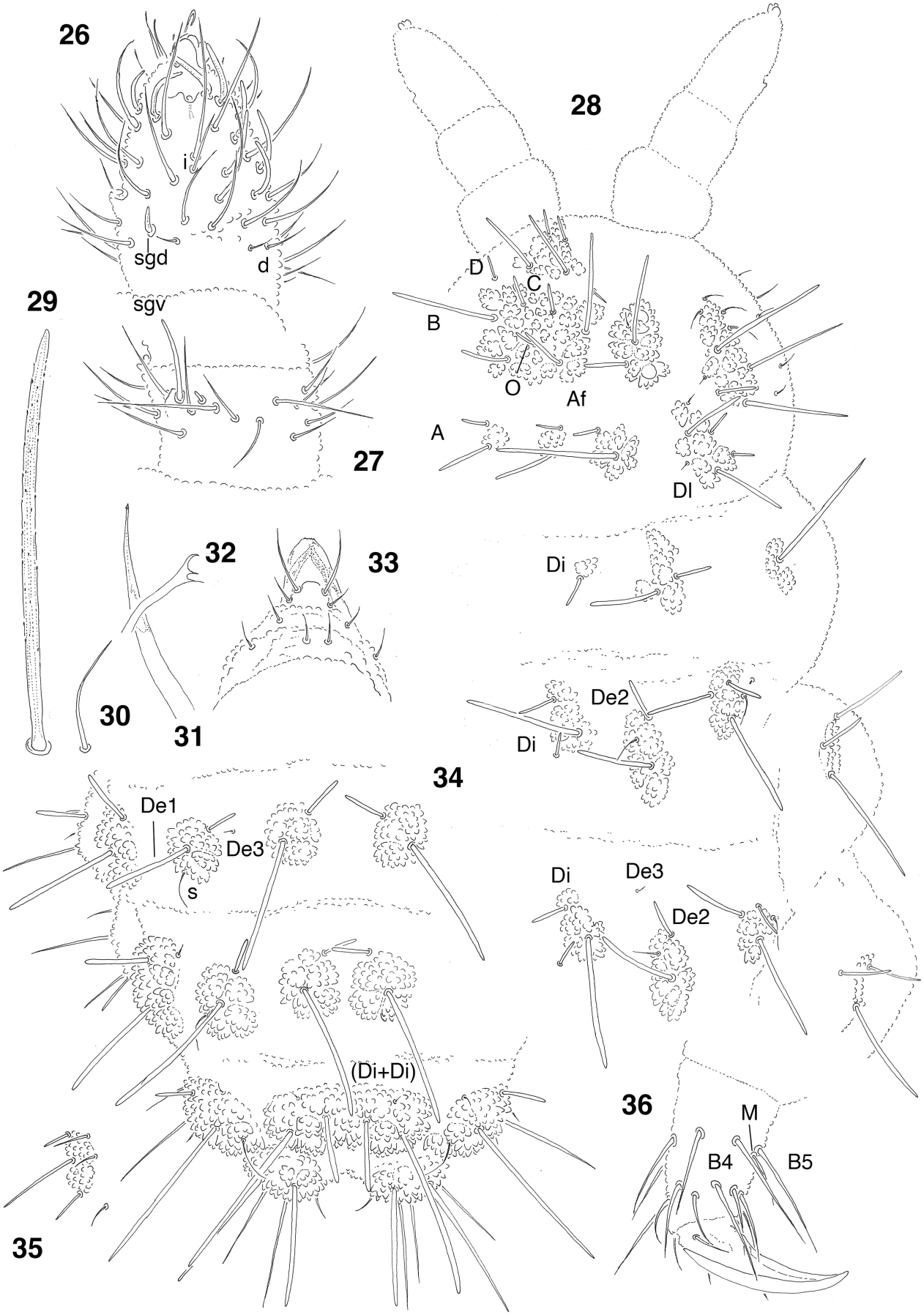

Figure 26–36. *Endonura crimica* **sp. nov.: 26** dorsal chaetotaxy of Ant. III–IV; **27** ventral chaetotaxy of Ant. III; **28** dorsal chaetotaxy of head and Th.; **29** chaeta Di1 of Abd. V; **30** sensillum of Abd. V; **31** maxilla; **32** mandible; **33** chaetotaxy and ventral sclerifications of labrum; **34** dorsal chaetotaxy of Abd. III–VI; **35** tubercle L of Abd. IV; **36** tibiotarsus and claw of leg III, lateral view.

Table 7a. Chaetotaxy of *Endonura crimica* **sp. nov.**: cephalic chaetotaxy–dorsal side.

Tubercle	Number of chaetae	Types of chaetae	Names of chaetae
Cl	4	Ml	F
		Mc	G
Af	9	Ml	B
		Mc	A, C, D, O
Oc	3	Ml	Ocm
		Mc	Ocp
		mi	Oca
Di	2	Ml	Di1
		Mc	Di2
De	2	Ml	De1
		Mc	De2
Dl	6	Ml	Dl5, Dl1
		Mc	Dl3, Dl4
		mi	Dl2, Dl6
(L+So)	9	Ml	L1, L4, So1
		Mc	L2
		mi	So2
		me	So3–6

Table 7b. Chaetotaxy of *Endonura crimica* **sp. nov.**: antennae.

Segment, Group	Number of chaetae	Segment, Group	Number of chaetae adult
I	7	IV	or, 8 S, i, 12 mou, 6 brs, 2 iv
II	12		
III	5 sensilla AO III		
ve	5	ap	8 bs, 5 miA
vc	4	ca	2 bs, 3 miA
vi	4	cm	3 bs, 1 miA
d	5	cp	8 miA, 1 brs

Table 7c. Chaetotaxy of *Endonura crimica* **sp. nov.**: postcephalic chaetotaxy.

Terga					Legs				
	Di	De	Dl	L	Scx2	Cx	Tr	Fe	T
Th. I	1	2	1	—	0	3	6	13	19
Th. II	3	2+s	3+s+ms	3	2	7	6	12	19
Th. III	3	3+s	3+s	3	2	8	6	11	18
					Sterna				
Abd. I	2	3+s	2	3	VT: 4				
Abd. II	2	3+s	2	3	Ve: 5; chaeta Ve1 present				
Abd. III	2	3+s	2	4	Vel: 4–5; Fu: 5–7 me, 0 mi				
Abd. IV	2	2+s	3	6–7	Vel: 4; Vec: 2; Vei: 2; Vl: 4				
Abd. V	(3+3)	7+s			Ag: 2–3; Vl: 1 L‘: 1				
Abd. VI	7				Ve: 14; An: 2mi				

30, 34). — ***Antennae*****:** Dorsal chaetotaxy of Ant. III–IV as Fig. 26 and Table 7b. S–chaetae of Ant. IV of medium length and moderately thickened (Fig. 26), sensillum sgd notably short. Apical vesicle distinct, trilobed. Ventral chaetotaxy of Ant. III with 14 ordinary chaetae, sense organ AOIII with long sensillum sgv and short peg (Fig. 27, Table 7b). — ***Mouthparts*****:** Buccal cone relatively short with labral sclerifications not ogival (Fig. 33). Labral chaetotaxy: 4/2, 4 (Fig. 33). Labium with four basal, three distal and four lateral chaetae, papillae x absent. Maxilla styliform (Fig. 31), mandible thin and tridentate (Fig. 32). — ***Dorsal chaetotaxy and tubercles*****:** Head without chaetae E and L3 (Fig. 28, Table 7a). Tubercles Di on Th. I developed. Th. III with chaetae De3 free (Fig. 28). On Abd. I–III, the line of chaetae De1–chaeta s non perpendicular to the dorsomedian line. Abd. I–III with chaetae De3 free (Fig. 34). On Abd. V tubercle (Di+Di) with 3+3 chaetae. Abd. VI partially visible from above (Fig. 34). — ***Ventral***

Table 8. Morphological differences between *E. crimica* **sp. nov.**, *E. taurica*, *E. gracilirostris* and *E. colorata*.

Characters	*E. crimica* sp. nov.	*E. taurica*	*E. gracilirostris*	*E. colorata*
Shape of labrum	not ogival	not ogival	ogival	not ogival
Prelabral chaetae	present	present	absent	present
Shape of manible	thin	thick	thin	thin
Shape of cephalic tubercle AF	wide	wide	wide	narrow
Length of cephalic tubercle AF	equal or shorter than tubercle Oc	equal or shorter than tubercle Oc	equal or shorter than tubercle Oc	longer than tubercle Oc
Cephalic chaetae E	present	absent	absent	present
Cephalic chaeta O	present	absent	present	present
Position of cephalic chaetae D	free	located within tubercle Cl	located within tubercle Cl	located within tubercle Cl
Tubercle Di on Th. I	present	absent	absent	present
Position of chaetae De2 on Th. II–III	located within tubercle De	free	free	located within tubercle De
No. of ordinary chaetae (De+Dl+L) on Abd. V	7	8	8	6
Ratio Di1/Di2/Di3 on Abd. V	50:21:3	48:18:2	46:11:2	40:22:10
No. of mesochaetae on furca rudimentary	5–7	5	5–6	8–9
Length and shape of tibiotarsal chaeta B4	short and pointed	elongated and clavate	elongated and clavate	short and pointed

***chaetotaxy*:** On head, groups Vea, Vem and Vep with 3, 4, 4 chaetae respectively. Group Vi on head with 6 chaetae. On Abd. IV, furca rudimentary without microchaetae. One chaeta L on Abd. IV free (Fig. 35). On Abd. V, chaetae Vl and chaetae L' present. **Legs:** Chaetotaxy of legs as in Fig. 36 and Table 7c. Claw without internal tooth (Fig. 36). On tibiotarsi, chaeta M present and chaetae B4 and B5 relatively short and pointed.

Etymology. The name *crimica* refers to the geographic area of its collecting.

Remarks. *E. crimica* **sp. nov.** belongs to a very small group of *Endonura* characterised by a broad and short (equal to or shorter than tubercle Oc) cephalic tubercle Af. In addition to the new species, this group includes *E. taurica* (Stach, 1951) and *E. gracilirostris* Smolis et al., 2007. *E. crimica* sp. nov. can be reliably distinguished from these Crimean species by the following characters: presence/absence of cephalic chaetae E (present in *crimica*, absent in *taurica* and *gracilirostris*), presence/absence of cephalic chaeta O (present in *crimica* and *gracilirostris*, absent in *taurica*), shape of labrum (not ogival in *crimica* and *taurica*, ogival in *gracilirostris*), presence/absence of tubercle Di on Th. I (present in *crimica*, absent in *taurica* and *gracilirostris*), position of chaetae De2 on Th. II and III (within tubercle in *crimica*, free in *taurica* and *gracilirostris*), and length and shape of tibiotarsal chaeta B4 (short and acute in *crimica*, elongated and clavate in *taurica* and *gracilirostris*). Morphologically, *E. crimica* sp. nov. also closely resembles *E. colorata* (Gama, 1964), a species known only from Portugal (Jordana et al. 1997). However, these species differ in several crucial characters: position of cephalic chaetae D (free in *crimica*, located inside tubercle Cl in *colorata*), number of me chaetae on furca rudimentary (5–7 chaetae in *crimica*, 8–9 chaetae in *colorata*), number of ordinary chaetae (De+Dl+L) on Abd. V (7 in *crimica*, 6 in *colorata*). Furthermore, the ratio Di1/Di2/Di3 on Abd. V is 50:21:3 in *crimica* and 40:22:10 in *colorata*. A summary of the differences between these species is given in Table 8.

Endonura duplex sp. nov.

https://zoobank.org/EF8EDEA5-F506-440B-A958-32624FFD6AE8

Figs 37–47, Tables 9a–c, 10

Type material. Holotype: adult female on slide, Russia, NW Caucasus, Adygeya, Caucasus Nature Reserve, 'Kamennoye More' ridge, southern slope, 1850 m. alt., mixed forest (pine, birch), coniferous litter, 21.VII.2015, leg. M. Potapov, N. Kuznetsova, A. Kremenitsa, L.Vanyavina (**DIBEC**). Paratype: subadult male and 2 juveniles on slides, same data as holotype (**DIBEC** and **MSPU**).

Diagnosis. 2+2 pigmented eyes. Buccal cone short, labrum not ogival. Head with chaetae A, B, C, D and E. Two chaetae O present. Tubercles Cl and Af separate. Tubercles Dl and (L+So) on head with 6 and 10 chaetae respectively. Tuberles Di on Th. I present. Tubercles De on Th. II and III with 3 and 4 chaetae respectively. Tubercles L on Abd. III and IV with 4 and 7 chaetae respectively. Abd. IV and V with 8 and 3 tubercles respectively. Claw without inner tooth. Tibiotarsi with chaetae B4 and B5 short.

Description. ***Body length*:** 0.55 (juvenile) to 1.55 mm (holotype) (without antennae). — ***Colour*:** body pale bluish grey (alive and in alcohol). 2+2 black eyes, in a typical arrangement for the genus (Fig. 38). — ***Chaetal morphology*:** Dorsal ordinary chaetae of five types: long macrochaetae (Ml), short macrochaetae (Mc), mesochae-

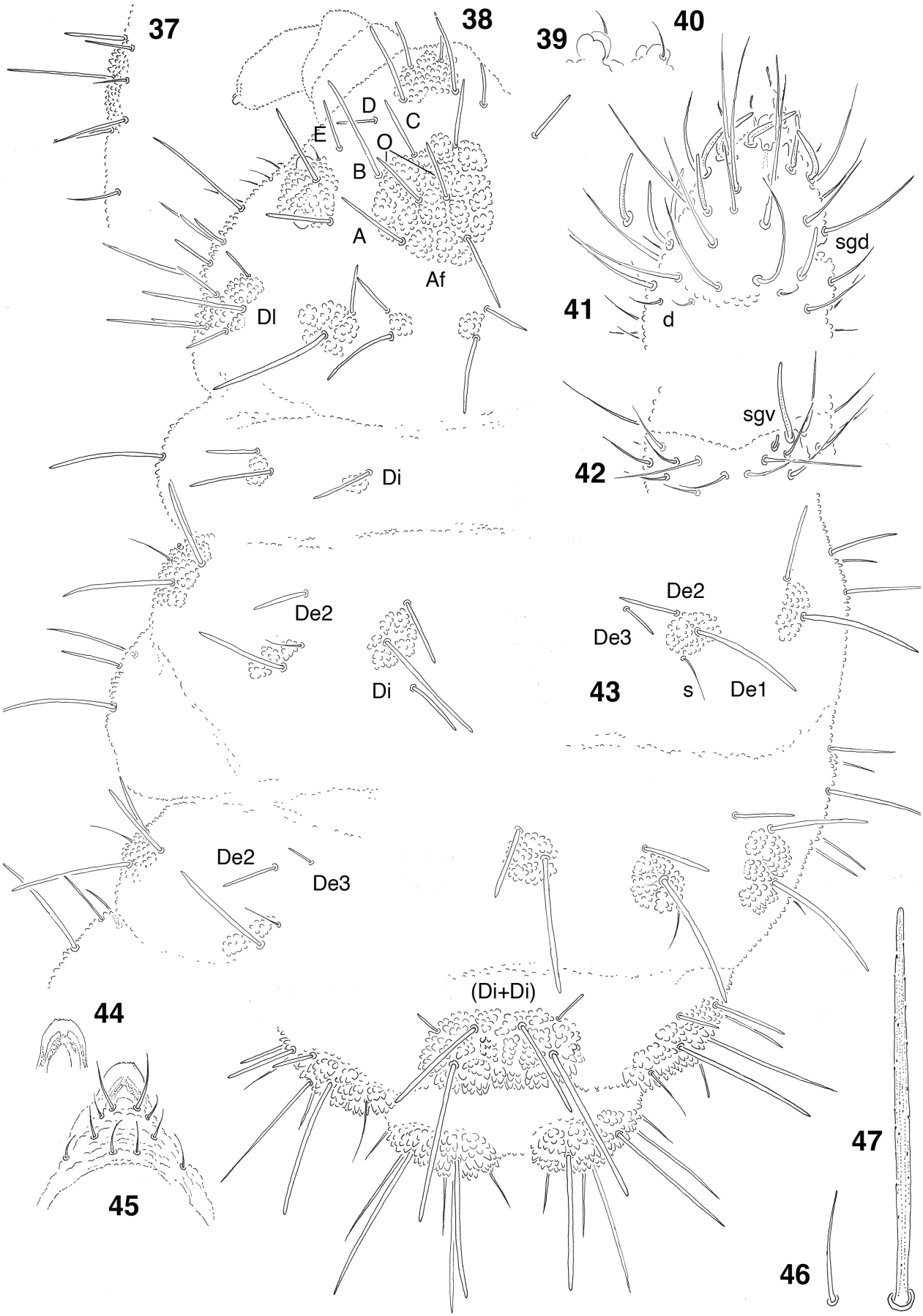

Figure 37–47. *Endonura duplex* **sp. nov.: 37** tubercle L of Abd. IV; **38** dorsal chaetotaxy of head and Th.; **39** apical bulb, ventral view; **40** apical bulb, dorsal view; **41** dorsal chaetotaxy of Ant. III–IV; **42** ventral chaetotaxy of Ant. III; **43** dorsal chaetotaxy of Abd. III–VI; **44** ventral sclerifications of labrum; **45** chaetotaxy of labrum; **46** sensillum of Abd. V; **47** chaeta Di1 of Abd. V.

Table 9a. Chaetotaxy of *Endonura duplex* **sp. nov.**: cephalic chaetotaxy–dorsal side.

Tubercle	Number of chaetae	Types of chaetae	Names of chaetae
Cl	4	Ml	F
		Mc	G
Af	12	Ml	B
		Mc	A, C, D, E, O
Oc	3	Ml	Ocm
		Mc	Ocp
		mi	Oca
Di	2	Ml	Di1
		Mc	Di2
De	2	Mc	De1, De2
Dl	6	Ml	Dl5, Dl1
		Mc	Dl2, Dl3, Dl4, Dl6
(L+So)	10	Ml	L1, L4, So1
		Mc	L2, L3, So2
		me	So3–6

Table 9b. Chaetotaxy of *Endonura duplex* **sp. nov.**: antennae.

Segment, Group	Number of chaetae	Segment, Group	Number of chaetae adult
I	7	IV	or, 8 S, i, 12 mou, 6 brs, 2 iv
II	12		
III	5 sensilla AO III		
ve	5	ap	8 bs, 5 miA
vc	4	ca	2 bs, 3 miA
vi	4	cm	3 bs, 1 miA
d	5	cp	8 miA, 1 brs

Table 9c. Chaetotaxy of *Endonura duplex* **sp. nov.**: postcephalic chaetotaxy.

Terga					**Legs**				
	Di	De	Dl	L	Scx2	Cx	Tr	Fe	T
Th. I	1	2	1	—	0	3	6	13	19
Th. II	3	2+s	3+s+ms	3	2	7	6	12	19
Th. III	3	3+s	3+s	3	2	8	6	11	18
					Sterna				
Abd. I	2	3+s	2	2–3	VT: 4				
Abd. II	2	3+s	2	3	Ve: 5; chaeta Ve1 present				
Abd. III	2	3+s	2	4	Vel: 5; Fu: 5 me, 0 mi				
Abd. IV	2	2+s	3	7	Vel: 4; Vec: 2; Vei: 2; Vl: 4				
Abd. V	(3+3)	7+s			Ag: 3; Vl: 1 L‘: 1				
Abd. VI	7				Ve: 14; An: 2mi				

tae and microchaetae. Long macrochaetae thick, slightly arc-like or straight, narrowly sheathed, feebly serrated, apically rounded or pointed (Figs 38, 43, 47). Macrochaetae Mc morphologically similar to long macrochaetae, but shorter. Mesochaetae similar to ventral chaetae, thin, smooth and pointed. Microchaetae similar to mesochaetae, but shorter. S–chaetae of tergites thin, smooth and short, notably shorter than nearby macrochaetae (Figs 38, 43, 46). — ***Antennae*****:** Dorsal chaetotaxy of Ant. III–IV as Fig. 41 and Table 9b. S–chaetae of Ant. IV of medium length and moderately thickened (Fig. 41), sensillum sgd relatively long. Apical vesicle distinct, trilobed (Figs 39, 40). Ventral chaetotaxy of Ant. III with 14 ordinary chaetae, sense organ AOIII with long sensillum sgv and short peg (Fig. 42, Table 9b). — ***Mouthparts*****:** Buccal cone short with labral sclerifications not ogival (Fig. 44). Labral chaetotaxy: 4/2, 4 (Fig. 45). Labium with four basal, three distal and four lateral chaetae, papillae x absent. Maxilla styliform, mandible thin and tridentate. — ***Dorsal chaetotaxy and tubercles*****:** Head with two chaetae O (Fig. 38, Table 9a). Tubercles Di on Th. I developed. Th. II–III with chaetae De2 and De3 free (Fig. 38). On Abd. I–III, the line of chaetae De1–chaeta s not perpendicular to the dorsomedian line. Abd. I–III with chaetae De3 free

Table 10. Morphological differences between *E. duplex* **sp. nov.**, *E. agnieskae*, *E. alticola* and *E. reticulata*.

Characters	***E. duplex* sp. nov.**	***E. agnieskae***	***E. alticola***	***E. reticulata***
Shape of labrum	not ogival	not ogival	ogival	not ogival
No. of prelabral chaetae	4	4	2	4
No. of lateral labial chaetae	4	3	4	4
No. of cephalic chaetae O	2	1	1	1
Length of cephalic chaetae A and Ocp	chaeta A longer than Ocp	equal in lenght	chaeta A longer than Ocp	chaeta A shorter than Ocp
Tubercle Di on Th. I	present and not fused with De	present and fused with De	present and fused with De	usually absent
Position of chaetae Di3 on Th. II–III	free	free	located within tubercle Di	free
Position of chaeta De2 on Abd. I–III	located within tubercle De	located within tubercle De	located within tubercle De	free
Position of chaeta De2 on Abd. I–III	line of chaeta De1–chaeta s parallel to dorsomedial line	line of chaeta De1–chaeta s parallel to dorsomedial line	line of chaeta De1–chaeta s parallel to dorsomedial line	line of chaeta De1–chaeta s not parallel to dorsomedial line
Fusion of tubercles Di on Abd. IV	absent	absent	present	absent
Number of chaetae Lon Abd. III and IV	4 and 7	3 and 5–6	4 and 6	4 and 6–9
Free chaeta L on Abd. IV	present	absent	absent	absent

(Fig. 43). On Abd. V tubercle (Di+Di) with 3+3 chaetae. Abd. VI well visible from above (Fig. 43). — ***Ventral chaetotaxy*:** On head, groups Vea, Vem and Vep with 3, 4, 4 chaetae respectively. Group Vi on head with 6 chaetae. On Abd. IV, furca rudimentary without microchaetae. One chaeta L on Abd. IV free (Fig. 37). On Abd. V, chaetae Vl and chaetae L' present. **Legs:** Chaetotaxy of legs as in Table 9c. Claw without internal tooth. On tibiotarsi, chaeta M present and chaetae B4 and B5 relatively short and pointed.

Etymology. The name *duplex* is derived from the presence of two chaetae O on head.

Remarks. *E. duplex* **sp. nov.** differs from all other *Endonura* by the presence of two cephalic chaetae O. Besides this character, the new species strongly resembles *E. agnieskae* Smolis & Skarżyński, 2020, *E. alticola* (Stach, 1951) and *E. reticulata* (Axelson, 1905). However, the differences between the new species and the outlined taxa include a number of characters: Shape of labrum (ogival in *alticola*, not ogival in others), number of prelabral chaetae (two in *alticola*, four in others), number of lateral labial chaetae (three in *agnieskae*, four in others), length of cephalic chaetae A and Ocp (chaeta A longer than Ocp in *duplex* and *alticola*, chaeta A shorter than Ocp in *reticulata*, equal in *agnieskae*), presence of tubercle Di on Th. I (present in *duplex*, present and fused with tubercle De in *agnieskae* and *alticola*, usually absent in *reticulata*), position of chaeta Di3 on Th. II–III (within tubercle Di in *alticola*, free in others), position of chaeta De2 on Abd. I–III (free in *reticulata*, within tubercle De in others), position of chaeta s on Abd. I–III (line of chaeta De1-chaeta s not parallel to dorsomedial line in *reticulata*, parallel in others), fusion of tubercles Di on Abd. IV (present in *alticola*, absent in others) and presence of free chaeta L on Abd. IV (present in *duplex*, absent in others). The differences between the species mentioned in the remarks are summarised in Table 10.

3.2. Phylogeny

List of morphological characters

Head eyes

1. **Number of eyes on each side of head:** (0) 3 eyes present; (1) 0–2 eyes present.
2. **Pigmentation of eyes:** (0) present; (1) absent.
3. **Presence of anterior eyes:** (0) present (Fig. 1); (1) absent.
4. **Position of anterior eyes:** (0) outside tubercle Oc (Fig. 2, Smolis 2011); (1) within tubercle Oc (Fig. 1).

Head tuberculation

5. **Tubercle L:** (0) separate (Fig. 5, Smolis 2007); (1) fused with tubercle So (Fig. 28).
6. **Tubercle Dl:** (0) separate (Fig. 16); (1) fused with tubercle L (Fig. 5E, Smolis and Deharveng 2017).
7. **Tubercle Af:** (0) separate (Fig. 16); (1) fused with tubercle Cl (Fig. 5, Smolis and Kaprus' 2003).
8. **Elementary tubercles BE:** (0) absent; (1) present (Fig. 5, Smolis et al. 2015).
9. **Elementary tubercles DF:** (0) absent; (1) present (Fig. 1, Smolis et al. 2015).
10. **Elementary tubercles DE:** (0) absent; (1) present (Fig. 5, Smolis and Kaprus' 2003).
11. **Non-reticulate area within tubercle Af:** (0) absent; (1) present (Fig. 9, Smolis 2016).
12. **Tubercles Di:** (0) tubercles absent; (1) tubercles present (Fig. 1).

13. **Length of tubercle Af:** (0) longer than tubercle Oc (Fig. 1); (1) equal or shorter than tubercle Oc (Fig. 20, Smolis et al. 2007).

Head chaetotaxy

14. **Number of chaetae Dl (on half of head):** (0) 6 chaetae present (Fig. 5, Smolis 2007); (1) 5 chaetae present (Fig. 13, Smolis 2016); (2) 4 or fewer chaetae present (Fig. 1).
15. **Chaeta Dl3:** (0) present (Fig. 5, Smolis 2007); (1) absent.
16. **Number of chaetae L+So (on half of head):** (0) 10 chaetae present (Fig. 5, Smolis 2007); (1) 9 chaetae present (Fig. 16); (2) 8 or fewer chaetae present (Fig. 1).
17. **Position of chaeta L4:** (0) included within tubercle L+So (Fig. 37, Smolis 2008); (1) free.
18. **Chaeta O:** (0) present (Fig. 16); (1) absent.
19. **Chaetae D:** (0) free (not included in tubercle Af or Cl) (Fig. 1); (1) included in tubercle Af (Fig. 58, Smolis and Kuznetsova 2016); (3) included in tubercle Cl (Fig. 1, Smolis et al. 2015); (4) included in tubercle Af+Cl (Fig. 5, Smolis & Kaprus' 2003).
20. **Chaetae E:** (0) present (Fig. 5, Smolis 2007); (1) absent.
21. **Position of chaetae E:** (0) free, not included in tubercle Af (Fig. 5, Smolis 2007); (1) included in tubercle Af (Fig. 58, Smolis and Kuznetsova 2016).
22. **Chaetae C:** (0) present (Fig. 1); (1) absent.
23. **Chaetae Oca:** (0) present (Fig. 1); (1) absent.
24. **Chaetae Ocp:** (0) present (Fig. 16); (1) absent.
25. **Length of chaetae Ocp:** (0) longer than chaeta A (Fig. 9, Smolis 2016); (1) shorter than chaeta A (Fig. 38).
26. **Chaetae A:** (0) present (Fig. 28); (1) absent.
27. **Length of chaetae A:** (0) shorter than chaetae B (Fig. 28); (1) equal to chaetae B (Fig. 1B, Smolis and Deharveng 2017).
28. **Arrangement of chaetae Di2 and De2:** (0) "croisée" (line between chaetae Di 2 and De2 crosses line between Di1 and De1, Deharveng 1983) (Fig. 5, Smolis 2007); (1) "non croisée" (line between chaetae Di 2 and De2 does not cross line between Di1 and De1) (Fig. 1).

Body

29. **Color in alive:** (0) blue, bluish grey or purple brown; (1) white.
30. **Placement of the longest macrochaetae:** (0) Abd. VI (Fig. 7, Smolis 2007); (1) Abd. V (Fig. 1); (2) Abd. IV (Fig. 1, Smolis and Kaprus' 2003).
31. **Cryptopygy:** (0) present (Fig. 1, Smolis and Kaprus' 2003); (1) absent.

Mouthparts

32. **Labial chaeta f:** (0) present (Fig. 14, Smolis 2008); (1) absent.
33. **Shape of labial apex:** (0) truncate (Fig. 2, Smolis et al. 2007); (1) rounded (Fig. 33); (2) ogival (Fig. 12).
34. **Number of prelabral chaetae:** (0) 4 chaetae present (Fig. 12); (1) 2 chaetae present (Fig. 2, Smolis and Kaprus' 2009); (2) chaetae absent.
35. **Number of labral chaetae:** (0) 6 chaetae present (Fig. 1); (1) 4 chaetae present (Fig. 3, Smolis and Kaprus' 2003).
36. **Number of apical labral chaetae:** (0) 4 chaetae present (Fig. 1); (1) 2 chaetae present (Fig. 3, Smolis and Kaprus' 2003).

Thorax

37. **Tubercles Di on the first tergite:** (0) absent; (1) present (Fig. 28).
38. **Tubercles Di and De on the first tergite:** (0) separate (Fig. 28); (1) fused (Fig. 1, Smolis and Kaprus' 2003).
39. **Position of chaetae Di3 on the second and third tergites:** (0) free (Fig. 1); (1) included in tubercle Di (Fig. 1, Smolis and Kaprus' 2003).
40. **Number of ordinary chaetae De on the second tergite (on half of tergite):** (0) 3 chaetae present (Fig. 5, Smolis 2007); (1) 2 chaetae present (Fig. 1).
41. **Position of chaeta De2 on the second tergite:** (0) free (Fig. 1); (1) included in tubercle De (Fig. 28).
42. **Number of ordinary chaetae De on the third tergite (on half of tergite):** (0) 4 chaetae present (Fig. 6, Smolis 2007); (1) 3 or fewer chaetae present (Fig. 16).
43. **Position of chaeta De2 on the third tergite:** (0) free (Fig. 6, Smolis 2007); (1) included in tubercle De (Fig. 28).
44. **Presence of chaeta De3 on the third tergite:** (0) present (Fig. 6, Smolis 2007); (1) absent.
45. **Position of chaeta De3 on the third tergite:** (0) free (Fig. 6, Smolis 2007); (1) included in tubercle De (Fig. 8, Smolis 2016).

Abdomen dorsal

46. **Number of ordinary chaetae De on tergites I–III:** (on half of tergite): (0) 3 chaetae present (Fig. 21); (1) 2 chaetae present (Fig. 10).
47. **Position of chaeta De2 on tergites I–III:** (0) free (Fig. 13, Smolis 2011); (1) included in tubercle De (Fig. 10).
48. **Presence of chaeta De3 on tergites I–III:** (0) present (Fig. 21); (1) absent.
49. **Position of chaeta De3 on tergites I–III:** (0) free (Fig. 21); (1) included in tubercle De (Fig. 66, Smolis and Kuznetsova 2016).
50. **Line of chaetae De1 and s-chaeta on each of tergites I–III:** (0) perpendicular to midline (Figs 31, 33; Fig. 5, Smolis 2008); (1) parallel to midline (Figs 16, 17; Smolis 2008).
51. **Number of tubercles on tergite IV (excluding tubercles L):** (0) 5 or fewer tubercles present (Fig. 5, Smolis and Kuznetsova 2016); (2) 6 tubercles present (Fig. 21).

52. **Length of chaeta Di1 on tergite III:** (0) longer than chaeta Di1 on tergite V (Fig. 1, Smolis and Kaprus' 2003); (1) slightly shorter than chaeta Di1 on tergite V (Fig. 1, Smolis 2007); (2) no more than half the length of chaeta Di1 on tergite V (Fig. 1, Smolis and Kaprus' 2009).
53. **Length of chaeta Di1 on tergite IV:** (0) longer than chaeta Di1 on tergite V (Fig. 1, Smolis and Kaprus' 2003); (1) slightly shorter than chaeta Di1 on tergite V (Fig. 10); (2) no more than half the length of chaeta Di1 on tergite V (Fig. 1, Smolis and Kaprus' 2009).
54. **Number of tubercles on tergite V:** (0) 4 tubercles present (Fig. 7, Smolis 2007); (1) 3 tubercles present (Fig. 10); (2) 2 tubercles present (Fig. 57, Smolis 2008).
55. **Number of chaetae Di on tergite V (on half of tergite):** (0) 3 chaetae present (Fig. 21); (1) 2 or fewer chaetae present (Fig. 10).
56. **Length of chaeta Di2 on tergite V:** (0) less than half the length of chaeta Di1 on tergite V (Fig. 10); (1) half the length of chaeta Di1 on tergite V (Fig. 21).
57. **Presence of chaeta Di3 on tergite V:** (0) present (Fig. 21); (1) absent.
58. **Length of chaeta Di3 on tergite V:** (0) more than twice shorter than chaeta Di2 on tergite V (Fig. 21); (1) maximum twice shorter than chaeta Di2 on tergite V (Fig. 12, Smolis 2011).
59. **Shape of tubercles on two last segments:** (0) normal (Fig. 10); (1) cauliflower-like (Fig. 6, Smolis and Kaprus' 2009).

Abdomen ventral

60. **Male ventral organ (secretory structure composed of modified chaetae, Simiczyjew et al. 2018):** (0) absent; (1) present (Fig. 34, Smolis and Kuznetsova 2016).
61. **Microchaetae on furcal remnant:** (0) present (Fig. 38, Smolis 2008); (1) absent.
62. **Number of chaetae L on segment III:** (0) more than 3 chaetae present (Fig. 12, Smolis 2011); (1) fewer than 3 chaetae present.
63. **Number of chaetae L on segment IV:** (0) more than 5 chaetae present (Fig. 4, Smolis 2007); (1) 5 or fewer chaetae present (Fig. 15).
64. **Position of chaetae L on segment IV:** (0) at least 1 chaeta free (Fig. 4, Smolis 2007); (1) all chaetae included in tubercle L (Fig. 15).
65. **Chaeta L':** (0) present (Fig. 4, Smolis 2007); (1) absent.
66. **Number of chaetae Vei:** (0) 6 chaetae (Fig. 6D, Smolis and Deharveng 2017); (1) 4 or fewer chaetae (Fig. 21, Smolis 2008).

Legs

67. **Tooth on claw:** (0) present (Fig. 13, Smolis 2008); (1) absent.
68. **Clavate chaetae B4 and B5 on tibiotarsus:** (0) present (Fig. 13, Smolis 2008); (1) absent.

Antennae

69. **Number of chaetae on antennal segment I:** (0) 8 chaetae (Fig. 1F, Deharveng 1981); (1) 7 chaetae (Fig. 1D, Deharveng 1981).
70. **Number of chaetae on antennal segment II:** (0) 12 chaetae (Fig. 2, Wang et al. 2016) 11 chaetae (Fig. 2, Ji-Gang Jiang et al. 2018).

3.3. Phylogenetic analysis

Phylogenetic analysis with TNT under an equal weighting scheme produced nineteen most parsimonious trees, with a length of 310 steps, consistency index of 36, and a retention index of 69.

Implied character weighting analyses resulted in a single most parsimonious cladogram with k = 9.687500 (Best score: 14.85760, tree length: 319, total fit: 49.14240) (Fig. 48). The phylogenetic topology obtained through Bayesian inference is presented in Figure 49. The trees resulting from both Bayesian and maximum parsimony analyses produced a similar topology. Both analyses supported *Endonura* monophyly, but failed to resolve deeper relationships within the genus. The resulting trees showed two main clades containing the same species, but with different internal relationships between them.

We use the most parsimonious tree obtained under implied weighting as a hypothetical reconstruction to discuss character transformations and relationships within the ingroup (Fig. 50). For arguments on the benefits of character weighting in morphological data sets, see Goloboff et al. (2008).

In the analyses, the species of *Endonura* have been classified into two primary clades (A and D). Both contains several different subclades (B–C and E–H respectively). (Fig. 48).

Clade A includes nineteen species, and it is supported by four character state but none of them represent synapomorphy (Fig. 50): the head with 9 chaetae L+So (character 16:1), the body colour white in alive (character 29:1), the prelabral chaetae absent (character 34:2) and the antennal segment II with 11 chaetae (character 70:1). The *E. saleri* is placed in the basal position within the clade, but this grouping has very low support. The remaining species are grouped into two subclades.

Subclade B includes 8 species and is supported only by one character: the labial apex ogival in shape (character 33:2, ambiguous). The remaining species form subclade C and this grouping is supported by the presence of microchaetae on furcal remnant (character 61:0, ambiguous).

Clade D comprises twenty eight remaining species, and it is supported by three character state: the head chaeta 'O' present (character 18:0, ambiguous), the presence of tubercle 'Di' on first thoracic tergite (character 37:1, ambiguous) and by the line of chaetae De1 and s-chaeta on abdominal tergites I–III parallel to midline (character 50:1, ambiguous).

The phylogenetic position and affiliation of the two species, *Endonura colorata* and *E. crimica* within this

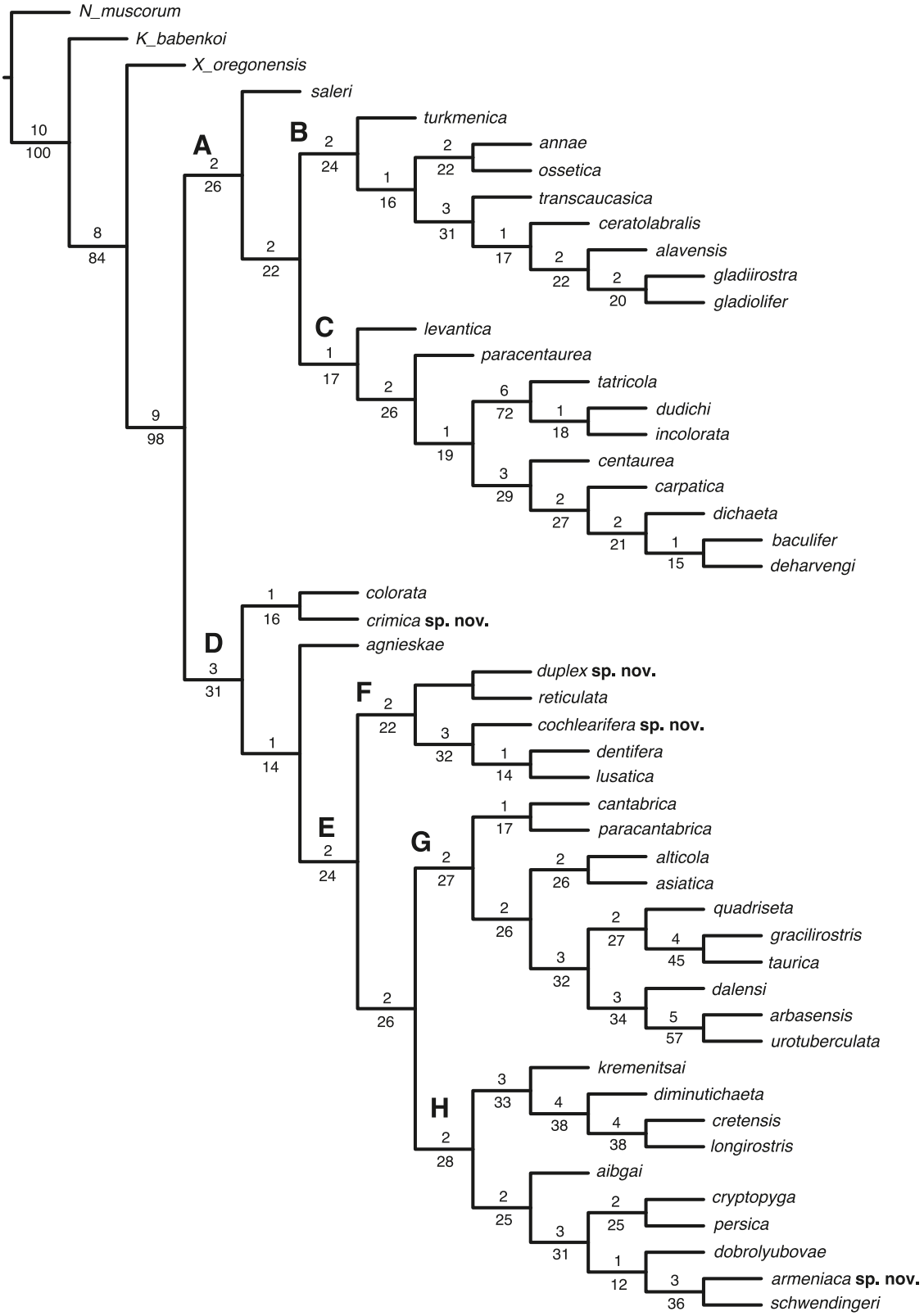

Figure 48. Single cladogram obtained in the analysis of morphology under implied weights k = 9.687500 (Length = 319; Fit = 49.14240). Node values indicate the frequency of GC groups derived from Bremer support (above) and symmetric resampling (below). The main clades are indicated with capital letters (A–H) on branches.

clade are obscure, despite their basal positions. It is uncertain whether they belong to clade D. These species exhibit the position of 'De3' chaetae on the third tergite of the thorax (character 45) and of 'De1' chaetae on thoracic tergites I–II (character 50), similar to taxa of this clade. However, they also share the same position of 'De2' chaetae on the thorax (characters 41 and 43) as species belonging to clade A. The *Endonura agnieskae* is placed in the basal position to the remaining species of this clade, but it shares certain characters with species of

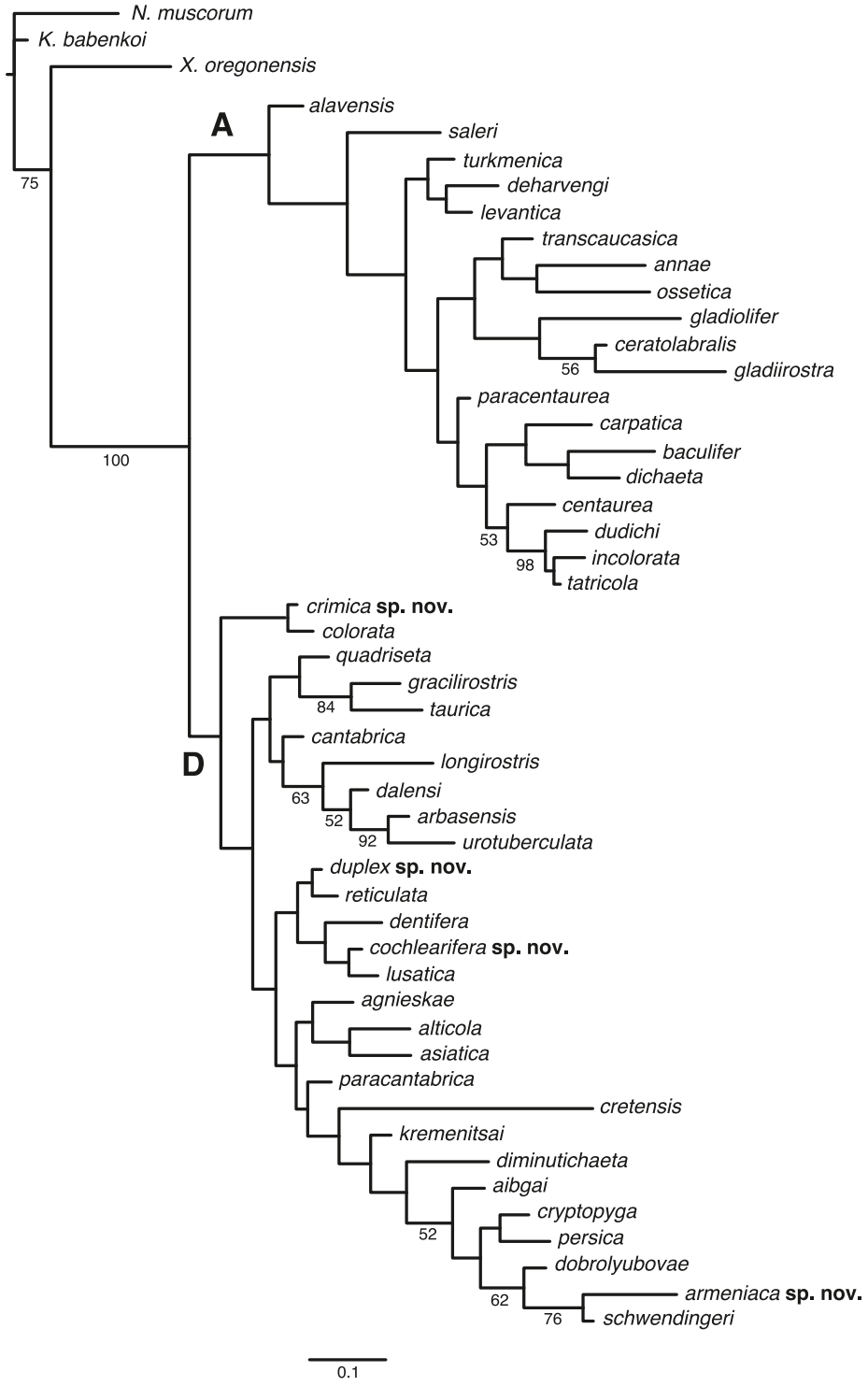

Figure 49. Bayesian consensus phylogram of *Endonura*. Numbers below branches are Bayesian posterior probability (PP) values (>50%). The main clades are indicated with capital letters on branches and correspond to this of Fig. 48.

clade A, as do the two species mentioned above and this grouping has very low support.

The remaining species constitute a distinct group (clade E), which is characterized by the one character: thoracic chaeta 'De2' included in tubercle 'De' (character 43:1, ambiguous). This group forms 3 separate subclades. The species of subclade F are supported by the following characters: the absence of tubercles 'Di' on first thoracic tergite (character 37:0) and the chaeta 'Di2' on fifth abdominal tergite shorter than chaeta 'Di1' (character 56:1). This group comprises two newly described species. *Endonura duplex* was clustered with *E. reticulata*, while *E. cochlearifera* was placed as a similar species to *E. dentifera* and *E. lusatica*.

Subclade G includes ten species, and it is supported by one character state: the presence of chaeta L' on ventral abdominal sternites (character 65: 0).

Subclade H comprises 10 species that share two common characters: the presence of 5 chaetae 'Dl' on head (character 14:1) and the absence of chaeta 'Dl3' on the

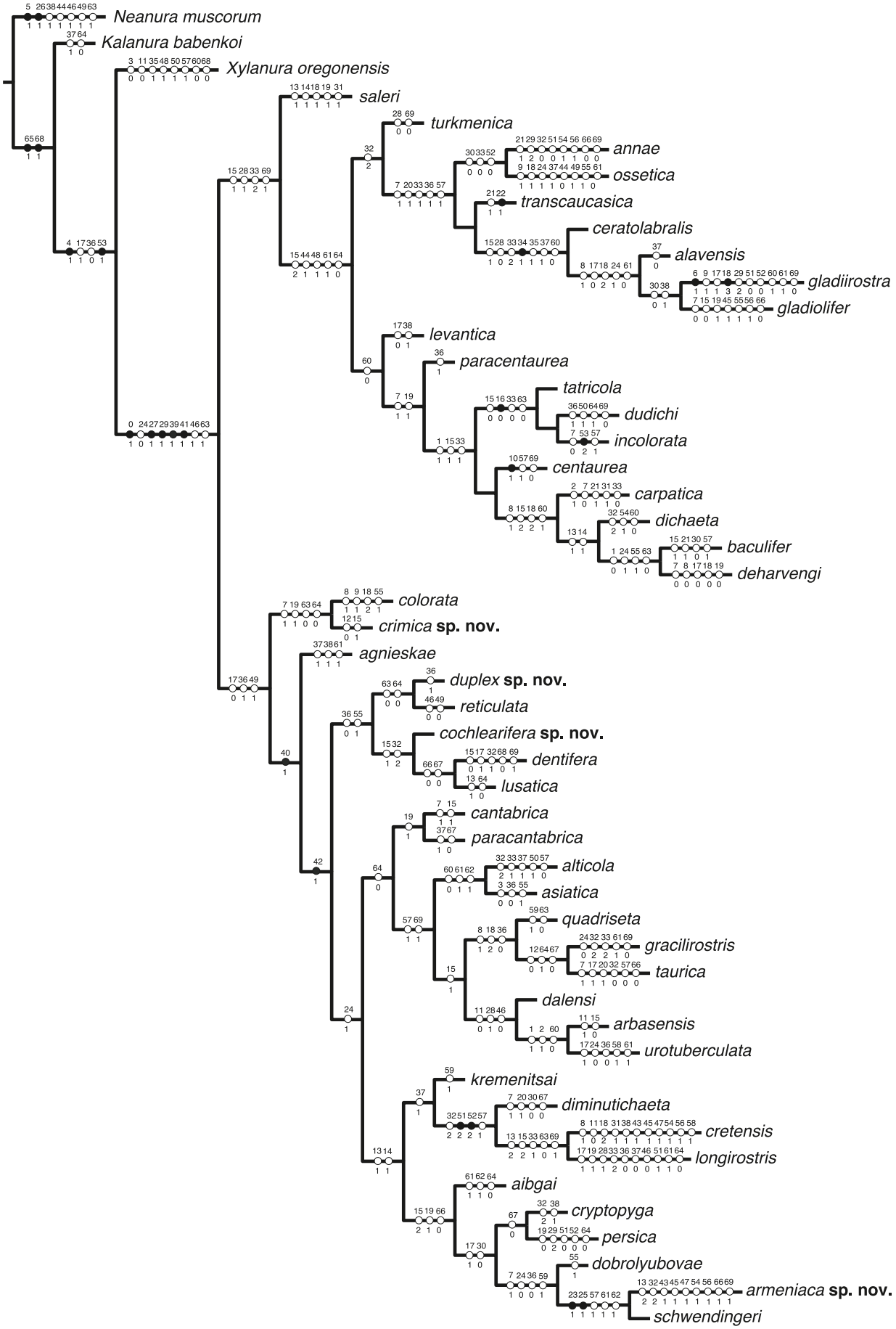

Figure 50. Unambiguous morphological character optimization obtained from analysis of the data (**Table 1**) under implied weights. The numbers above and below circles on the branches indicate character numbers and states, respectively. White and black circles represent homoplasious and nonhomoplasious character state transformations, respectively.

head (character 15:1). The group comprises a newly described species, *E. armeniaca*, which has been clustered with *E. schwendingeri*.

4. Discussion

In terms of species richness, *Endonura* is the third most abundant genus in the subfamily. Only two other genera, *Deutonura* Cassagnau, 1979 and *Pronura* Dellamare Debouteville, 1953 contain more taxa, 62 and 58 species, respectively (Bellinger et al. 2023).

It is common taxonomic practice in large genera to create informal groups of species within them, as opposed to subdividing them into subgenera. The formation and naming of these groups are usually on the basis of both geographical and morphological features. *Deutonura*, the genus referred to above, has five such groups, *fodinarum*, *alticola*, *centralis*, *conjuncta* and *phlegrea* (Deharveng 1982). It should be noted, however, that further cladistic analysis of the genus has failed to confirm that such morphological groups exist (Deharveng 1989b).

The genus *Endonura* has not yet been phylogenetically analysed. The obtained results indicate *Endonura* to be non-homogeneous genus and all considered species can be grouped into two major clades, A and D (Fig. 48). While distinct species groups are apparent within each clade, their low support precludes their formal designation.

In most Collembola groups, including the subfamily Neanurinae to which the analysed genus belongs, chaetotaxy is the main source of characters used in taxonomic and phylogenetic analyses at different levels of classification, as demonstrated by several studies (e.g. Deharveng 1983, 1986; Bedos and Deharveng 1998; Palacios-Vargas et al. 2010; Smolis and Paśnik 2020), and in the present analysis chaetotaxy-based characters account for almost two thirds of the characters used (see List of characters). As chaetae primarily function as sensory organs, usually as mechanoreceptors (Crouau et al. 1987) or less commonly, with glandular function (Simiczyjew et al. 2018), their presence or absence and position is treated as a phylogenetic signal. The value of individual chaetae is uncertain, given the limited number of phylogenetic analyses based on morphological characters. For instance, Cassagnau (1974) claims that the phylogenetic weight is not uniform across all dorsal chaetae and that axial and subaxial chaetae in the anterior segments, i.e. the head and thoracic segments 2 and 3, are most informative. In addition to confirming the latter statement, our analysis shows that most of the synapomorphies concern the head (characters 17, 24, 26, 28) and thoracic (characters 40, 41, 42, 43) chaetae.

However, chaetotaxy is identified by some authors (e.g. Deharveng 1989b; Palacios-Vargas et al. 2010) as a major source of homoplasy. This is often linked to the widespread process of reduction of individual chaetae, which often occurs in parallel in different evolutionary lineages (e.g., Fjellberg 1984). The cladistic analysis presented here supports this view, indicating a significant amount of homoplasy, particularly with regard to chaetotaxy-related characters.

Although all Collembola have chaetae, only a few, such as the Neanurinae, are characterised by the presence of cuticular protrusions known as tubercles. These tubercles rank second in importance as a source of characters in our analysis. However, the majority of the characters analysed are homoplasies. The only character representing a synapomorphy specific to the *E. tatricola*, *E. dudichi* and *E. incolorata* group is the 'L4' chaeta within the 'So+L' tubercle.

The insufficient support for the various clades can be attributed to the limited number of morphological characters available for phylogenetic analysis. This problem is prevalent in both the taxonomy of Neanurinae and Collembola as a whole. This issue is unsurprising because springtails are relatively small organisms with a restricted number of morphological characters. The increase in recently described species results in an insufficient number of characters that can be used in taxonomy to identify species and in phylogenetic analyses to infer relationships. In the systematics of springtails, it is now prevalent to use a combination of multiple characters to identify taxa. While this approach remains effective in systematics, it poses significant challenges in phylogenetic analyses. Such an approach results in a deficiency of defining synapomorphies for taxa. Consequently, the support for cladistic analyses is weakened. As a result, the systematics of Collembola (including Neanuridae) is based on the Linnaean system rather than the phylogenetic relationships. The analysis that is presented in this paper is also subject to the same issues. The analysis divides the species of *Endonura* into distinct groups, however, it is challenging to determine the extent to which this is a result of relationships or similarities among species.

Further research is needed to clarify the relationships among *Endonura* species, especially through the use of a combination of morphological characters and molecular methods.

5. Declarations

Funding statement: The authors have no funding to report.

Conflict of Interest: The authors have no conflicts of interests to declare.**Authors' contributions:** A.S. was responsible for the identification of the species, the preparation of the taxonomic section of the paper, interpretation of data and the revision of the manuscript. N.K. collected and determined material for the study and contributed to the present research's conception and design. G.P. conducted the phylogenetic analyses with constructive discussions and made suggestions and revisions to the manuscript. All authors read and approved the final manuscript.

6. Acknowledgements

We wish to express our sincere thanks to Collectors: Boris Efeikin, Dmitry Shitikov, Alexander Sharikov, Mikhail Potapov (Moscow), Alexander Kremenitsa (Essentuki). Ivan Kuchiev (Alagir).

7. References

Bellinger PF, Christiansen KA, Janssens F (2023) Checklist of the Collembola of the World. Available from: http://www.collembola.org (accessed 5 June 2023).

Bremer K (1994) Branch support and tree stability. Cladistics 10: 295–304. https://doi.org/10.1111/j.1096-0031.1994.tb00179.x

Bedos A, Deharveng L (1998) A taxonomic and cladistic analysis of the west European genus *Monobella* (Collembola, Neanuridae). Zoologica Scripta 27(4): 291–309.

Cassagnau P (1974) Chétotaxie et phylogénie chez les Collemboles Poduromorphes. Pedobiologia 14: 300–312.

Cassagnau P (1979) Les Collemboles Neanuridae des Pays Dinaro-Balkaniques: leur interêt phylogénétique et biogéographique. Biologia Gallo-Hellenica 8: 185–203.

Cassagnau P (1988) Les Collemboles Neanurinae des Masif du sud de l'Inde et de Ceylan. Travaux du Laboratoire d'écobiologie des Arthropodes Edaphiques, Toulouse 5(4): 21–51.

Cassagnau P (1993) Les Collemboles Neanurinae de l'Himalaya; III – Genre *Nepalimeria*. Revue suisse de Zoologie 100(1): 91–112.

Cassagnau P, Delamare Deboutteville C (1955) Mission Henri Coiffait (1951). 3. Collemboles. Archives de Zoologie Expérimentale et Génerale 91: 365–395.

Cassagnau P, Péja N (1979) Diagnoses préliminaries de quelques Neanuridae de Grèce et d'Albanie. Biologia Gallo – Hellenica 8: 205–222.

Crouau Y, Bauby A, Deharveng L (1987) Fine structure of the tibiotarsal and pretarsal sensory organs in *Monobella grassei banyulensis* Deharveng (Collembola, Neanuridae). International Journal of Insect Morphology and Embryology 16: 245–261.

Deharveng L (1979) Contribution à la connaissance des Collemboles Neanurinae de France et de la Péninsule Ibérique. Travaux du Laboratoire d'écobiologie des Arthropodes édaphiques, Toulouse 1(4): 1–61.

Deharveng L (1980) Contribution à la connaissance systématique, écologique et biogéographique des collemboles Neanurinae de Corse. Revue d'écologie et de biologie du sol 17(3): 419–435.

Deharveng L (1981) Nouvelles espèces de Neanurinae européens appurtenant aux genres Bilobella et Monobella. Bulletin de la Société d'histoire naturelle de Toulouse 117(1–4): 95–102.

Deharveng L (1982) Cle de determination des genres de Neanurinae (Collemboles) d'Europe et de la Region Mediterraneenne, avec description de deux nouveaux genres. Travaux du Laboratoire d'écobiologie des Arthropodes édaphiques, Toulouse 3(4): 7–13.

Deharveng L (1983) Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée Neanurienne. Travaux du Laboratoire d'écobiologie des Arthropodes édaphiques, Toulouse: 4(2): 1–63.

Deharveng L (1986) Analyse phylogénétique du genre *Deutonura*. In: Dallai R (Ed.) Proceedings of the 2nd International Seminar on Apterygota, Siena, 23–28.

Deharveng L (1989a) The genus *Paranura* Axelson, 1902 in Thailand (Collembola Neanurinae). Tropical Zoology 2: 103–121. https://doi.org/10.1080/03946975.1989.10539432

Deharveng L (1989b) The problem of homoplasies in Neanurinae (Insecta: Collembola): microcomputer assisted phylogeny of the genus *Deutonura*. In: Dallai R. (Ed.) 3rd International Seminar on Apterygota. University of Siena, Siena, Italy, 183–193.

Deharveng L, Bedos A (1992) *Blasconurella*, a new genus of Neanurinae from Thailand, with five new species. Tropical Zoology 5: 299–311. https://doi.org/10.1080/03946975.1992.10539201

Deharveng L, Palacios-Vargas JG, Bedos A (2017) A list of Yuukianura Yosii, 1955 species of the world (Collembola: Neanuridae: Neanurinae: Lobellini), with description of a new species of unusual ecology from Santo Island (Vanuatu). Zoosystema 39(1): 55–67. https://doi.org/10.5252/z2017n1a7

Deharveng L, Weiner WM (1984) Collemboles de Coree du Nord. III. Morulinae et Neanurinae. Travaux du Laboratoire d'écobiologie des Arthropodes édaphiques, Toulouse 4: 1–61.

Denis JR (1947) Sur la faune Française des Aptérygotes (XXIV enote). Étude du matériel récolté en Corse par P. et L. Rémy en 1942. Annales des Sciences Naturelles Zoologie 11 e série 9: 1–12.

Ellis WN (1976) Autumn fauna of Collembola from Central Crete. Tijdschrift voor Entomologie 119: 221–236.

Fanciulli PP, Dallai R. (2008) Three new species of Collembola from north-east Italy. Zootaxa 1701: 15–28.

Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20(4): 406. https://doi.org/10.2307/2412116

Fjellberg A (1984) Elements of dorsal chaetotaxy in Neanuridae with descriptions of two new species of Anurida (Collembola). Entomologica Scandinavica 15: 349–362.

Gisin H (1963) Sieben neue Arten von Collembolen aus Bosnien and Wiederbeschreibung von *Onychiurus serratotuberculatus* Stach. Extrait du Godišnjak Biološkog Istituta Universiteta u Sarajevu 14: 477–525.

Goloboff PA (1993) Estimating character weights during tree search. Cladistics 9(1): 83–91. https://doi.org/10.1111/j.1096-0031.1993.tb00209.x

Goloboff PA (1999) Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428.

Goloboff PA, Farris JS, Källersjö M, Oxelman B, Ramıacuterez MJ, Szumik CA (2003) Improvements to resampling measures of group support. Cladistics 19(4): 324–332. https://doi.org/10.1111/j.1096-0031.2003.tb00376.x

Goloboff PA, Carpenter JM, Arias JS, Esquivel DRM (2008) Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics 24: 758–773. https://doi.org/10.1111/j.1096-0031.2008.00209.x

Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32(3): 221–238. https://doi.org/10.1111/cla.12160

Greenslade P, Deharveng L (1991) *Phradmon*, a New genus of Paleonurini (Collembola: Neanuridae) from Australia with a Key to the Genera from Southern Regions and Notes on *Pronura*. Invertebrate Taxonomy 5: 837–54. http://dx.doi.org/10.1071/IT9910837

Hoskins JL, Janion-Scheepers Ch, Chown SL, Duffy GA (2015) Growth and reproduction of laboratory-reared neanurid Collembola using a novel slime mould diet. Scientific Reports 5: 11957: 1–8. https://doi.org/10.1038/srep11957

Jiang JG, Wang WB, Xia H (2018) Two new species of Lobellini from Tianmu Mountain, China (Collembola, Neanuridae). ZooKeys 726: 1–14. https://doi.org/10.3897/zookeys.726.11934

Jordana R, Arbea JI, Simón C, Luciáñez MJ (1997) Collembola, Poduromorpha. In: Ramos MA, Alba J, Bellés X, Gosálbez J, Guerra A, Macpherson E, Martín F, Serrano & Templado J. (Eds.) Fauna Ibérica. Vol. 8. Museo Nacional de Ciencias Naturales. CSIC, Madrid, 1–807.

Messer C, Walther J, Dettner K, Schulz S (2000) Chemical deterrents in podurid Collembola. Pedobiologia 44: 210–220.

Nixon KC (2002) WinClada, version 1.00.08. Published by the author, Ithaca, New York. http://www.cladistics.com. Accessed Sep 2019.

Palacios-Vargas JG, García-Barros E, Simón Benito JC (2010) Phylogeny of the genus *Palmanura* (Collembola: Neanuridae). Cladistics 26: 482–496. https://doi.org/10.1111/j.1096-0031.2009.00299.x

Pozo J, Simón JC (1982) Colémbolos del Pais Vasco I. *Neanura* (*Endonura*) *occidentalis alawensis* nov. ssp. y *Neanura* (*Deutonura*) *plena* ssp. *plena* Stach, 1951. Eos 57: 221–229.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.

Simiczyjew B, Skarżyński D, Smolis A, Pomorski RJ, Mazurkiewicz-Kania M (2018) Structure and function of the male ventral organ in *Onychiuroides granulosus* (Collembola: Onychiuridae). European Journal of Entomology 115: 134–139. https://doi.org/10.14411/eje.2018.012

Simón Benito JC, Palacios-Vargas JG (2008) Two new species of *Paranura* (Collembola: Neanuridae) from Southeastern Mexico. Annals of the Entomological Society of America 101(4): 683–688.

Smolis A (2007) *Kalanura*–a new genus of Neanurini (Collembola, Neanuridae, Neanurinae) from Siberia, with description of four new species. Zootaxa 1511: 1–16.

Smolis A (2008) Redescription of four Polish *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae), with a nomenclature of the ventral chaetae of antennae. Zootaxa 1858: 9–36.

Smolis A (2009) Redescription and lectotype designation of *Thaumanura carolii* (Stach, 1920) (Collembola, Neanuridae), with remarks on its biology. Deutsche Entomologische Zeitschrift 56(1): 73–83.

Smolis A (2011) *Xylanura oregonensis*, a new genus and species of saproxylic springtail (Collembola: Neanuridae: Neanurinae) from North America, with a key to genera of the tribe Neanurini. Pan-Pacific Entomologist 87(1): 15–26.

Smolis A (2016) On the identity of some poorly known species of the genus *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae). Zootaxa 4173 (3): 237–250. http://doi.org/10.11646/zootaxa.4173.3.3

Smolis A, Bernard EC (2017) *Intricatonura fjellbergi*, a new peculiar genus and species of Neanurini (Collembola: Neanuridae: Neanurinae) from Great Smoky Mountains National Park. Florida Entomologist 100(4): 725–730. https://doi.org/10.1653/024.100.0419

Smolis A, Deharveng L (2006) *Vitronura mascula*, a new species of Neanurinae (Collembola: Neanuridae) from northern Vietnam, with a key to the species of the genus. Revue Suisse de Zoologie 113(2): 263–268.

Smolis A, Deharveng L (2017) *Neanura judithae* n. sp. from Polish Carpathians, with an updated and illustrated key to all species of the genus *Neanura* MacGillivray, 1893 (Collembola: Neanuridae). Zoosystema 39(1): 37–47. https://doi.org/10.5252/z2017n1a5

Smolis A, Deharveng L, Kaprus' IJ (2011) Studies on the non-European *Endonura* Cassagnau, 1979 (Collembola, Neanuridae, Neanurinae). Zootaxa 3004: 45–56.

Smolis A, Greenslade P (2020) New Lobellini (Collembola: Neanuridae) from Queensland contribute to understanding distribution and ecology of Australian fauna. Austral Entomology 59: 253–264. https://doi.org/10.1111/aen.12460

Smolis A, Kaprus' I (2003) A new species of the genus *Endonura* Cassagnau, 1979 from Israel (Collembola: Neanuridae). Genus 14: 325–329.

Smolis A, Kaprus' I (2009) Redescription of *Endonura cretensis* (Ellis, 1976) (Collembola: Neanuridae: Neanurinae) with a new record from Israel. Annales Zoologici 59: 1–6. https://doi.org/10.3161/000345409X432538

Smolis A, Kuznetsova N (2016) Remarkable diversity of the genus *Endonura* Cassagnau, 1979 (Collembola: Neanuridae: Neanurinae) in the Caucasus. Zootaxa 4200(1): 47–82. https://doi.org/10.11646/zootaxa.4200.1.2

Smolis A, Kuznetsova N (2018) The genera *Albanura* Deharveng, 1982 and *Persanura* Mayvan et al., 2015 are no longer monotypic: description of new species from the Caucasus (Collembola, Neanuridae, Neanurinae, Neanurini). ZooKeys 737: 1–12. https://doi.org/10.3897/zookeys.737.21191

Smolis A, Paśnik G (2020) Phylogenetic analysis of the tribe Neanurini questions tribal classification of the subfamily Neanurinae (Collembola: Neanuridae). Organisms Diversity & Evolution 20: 497–509 https://doi.org/10.1007/s13127-020-00446-z

Smolis A, Shayanmehr M, Kuznetsova N, Lafooraki EY (2017) Three new remarkable species of the genus *Endonura* Cassagnau from the Middle East and Central Asia (Collembola, Neanuridae, Neanurinae, Neanurini). ZooKeys 673: 135–151. https://doi.org/10.3897/zookeys.673.12084

Smolis A, Skarżyński D, Kahrarian M, Kaprus IJ (2016). Redescription of *Protanura papillata* Cassagnau and Delamare Deboutteville, 1955 (Collembola, Neanuridae, Neanurinae), with new records from Middle East, and with supplemented diagnosis and key to the genus. Zootaxa 4092(2): 293–300. https://doi.org/10.11646/zootaxa.4092.2.11

Smolis A, Skarżyński D, Pomorski RJ, Kaprus' I (2007). Redescription of *Endonura taurica* (Stach, 1951) and *E. quadriseta* Cassagnau & Péja, 1979, and description of two new species of the genus *Endonura* Cassagnau, 1979 (Collembola: Neanuridae: Neanurinae) from the Crimea (Ukraine). Zootaxa 1442: 19–35.

Smolis A, Skarżyński D (2020) Contribution to the knowledge of Neanurinae of northwestern Iran with description of seven new species (Collembola, Neanuridae). ZooKeys 992: 105–138. https://doi.org/10.3897/zookeys.992.56921

Stach J (1929) Verzeichnis der Apterygogenea Ungarns. Annales Musei Nationalis Hungarici, Budapest 26: 282–283.

Templeton R (1836) *Thysanura hiberbnicae*, or descriptions of such species of springtailed insects (Podura and Lepisma, Lin.) as have been observed in Ireland. Transactions of the Entomological Society of London 1(2): 89–98. https://doi.org/10.1111/j.1365-2311.1838.tb00147.x

Wang YR, Wang WB, Jiang JG (2016) New Neanurinae (Collembola: Neanuridae) form Central China. Zootaxa 4139(2): 183–196. https://doi.org/10.11646/zootaxa.4139.2.3

Wilkinson M (1992) Ordered versus unordered characters. Cladistics 8(4): 375–385. https://doi.org/10.1111/j.1096-0031.1992.tb00079.x