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Monograph

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Hidden diversity within the *Nemastoma bidentatum* Roewer, 1914 complex (Opiliones: Nemastomatidae) Part I: Morphological evidence

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Dedicated to our teachers, colleagues and friends Dr Jürgen Gruber and Em. Prof. Dr Jochen Martens.

Abstract. *Nemastoma bidentatum* Roewer, 1914 is a complex of closely related litter-dwelling harvestmen, characterized by a penis glans with two pairs of lateral lancet-like spines, and a femur IV with a saw-like series of pointed tubercles. Here we a) revise the hitherto known taxa within the *N. bidentatum* complex, and b) analyze in detail the relations among the taxa in Slovenia. The study revealed that the *N. bidentatum* complex consists of four species: *N. bidentatum* Roewer, 1914 s. str., *N. relictum* Gruber & Martens, 1968 stat. nov., *N. pluridentatum* (Hadži, 1973) stat. nov. and *N. kozari* Novak, Kozel, Podlesnik & Raspotnig sp. nov. Moreover, *N. bidentatum* s. str. consists of six subspecies: *N. bidentatum bidentatum* Roewer, 1914, *N. bidentatum sparsum* Gruber & Martens, 1968, *N. bidentatum gruberi* Novak, Slana Novak, Kozel & Raspotnig ssp. nov., *N. bidentatum martensi* Novak, Slana Novak & Raspotnig ssp. nov., *N. bidentatum schmidti* Novak, Raspotnig & Slana Novak ssp. nov. and *N. bidentatum sneznikensis* Novak, Komposch, Slana Novak & Raspotnig ssp. nov. In Slovenia, the six subspecies of *N. bidentatum* form a parapatric complex around *N. bidentatum schmidti*. Hybrids occur in the contact zones between adjacent subspecies, but they are missing between distant subspecies. The taxonomic distinction of lineages/subspecies is congruent with their distribution patterns. With six of the nine taxa present, Slovenia is considered the center of the *N. bidentatum* complex speciation. At the time being, this complex is the most diversified harvestman group on a subspecific and young-species level and provides important details on speciation processes in Opiliones.

Keywords. Allopatric speciation, arachnids, Dyspnoi, morphological taxonomy, parapatric speciation.

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Introduction

In recent decades, relations among the higher taxa of harvestmen have become increasingly clear and amenable (Schönhofen 2013; Giribet & Sharma 2015; Fernández *et al.* 2017). However, there is still a need for major revisions in some taxa at the genus and family levels. Dyspnoi Hansen & Sørensen, 1904, e.g., still exhibit many problems with species delineation and assignment (Schönhofen 2013). Except for some Ortholasmatinae Shear & Gruber, 1983, Dyspnoi are restricted to the temperate zones (Gruber 2007). In central Europe, more than a third of harvestman species and subspecies belong to this suborder (Blick & Komposch 2004), while in Slovenia they account for almost half (Novak *et al.* 2006; unpublished own data). One unresolved puzzle within Dyspnoi is the *Nemastoma bidentatum* Roewer, 1914 complex, Nemastomatidae Simon, 1872, distributed in Central and Eastern Europe, with sparse, disjunct localities in northern Europe. These 1.8–2.5 mm long, black or nearly black *Nemastoma* (Fig. 1), have been recorded in Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Germany, Hungary, Italy, Montenegro, Romania, Russia, Serbia, Slovakia, Slovenia and Turkey (Roewer 1914, 1923, 1951; Gruber & Martens 1968; Hadži 1973a; Staręga 1976; Martens 1978, 2006; Mučalica 1988; Ćurčić *et al.* 1999; Klimeš 2000; Novak & Gruber 2000; Blick & Komposch 2004; Komposch & Gruber 2004; Novak 2004a, 2004b; Babalean 2005; Novak *et al.* 2006; Schönhofen & Holle 2007; Komposch 2009, 2011; Schönhofen 2013; Kurt 2014).

Roewer (1914, 1923) cited Comana Vlasca in Romania as the type locality of *N. bidentatum* Roewer, 1914. Hadži (1927) provided the first detailed drawings of *N. bidentatum* from an unknown locality in Slovenia, deposited in the Ferdinand Schmidt Collection at the Natural History Museum in Ljubljana. Gruber & Martens (1968) established that Roewer's illustrations show a taxon living exclusively in the Eastern Alps. Accordingly, they (*ibid.*) redescribed the nominal subspecies *N. b. bidentatum* Roewer, 1914 upon individuals from Bärental in the Karawanken Mts, Carinthia, Austria, along with two new

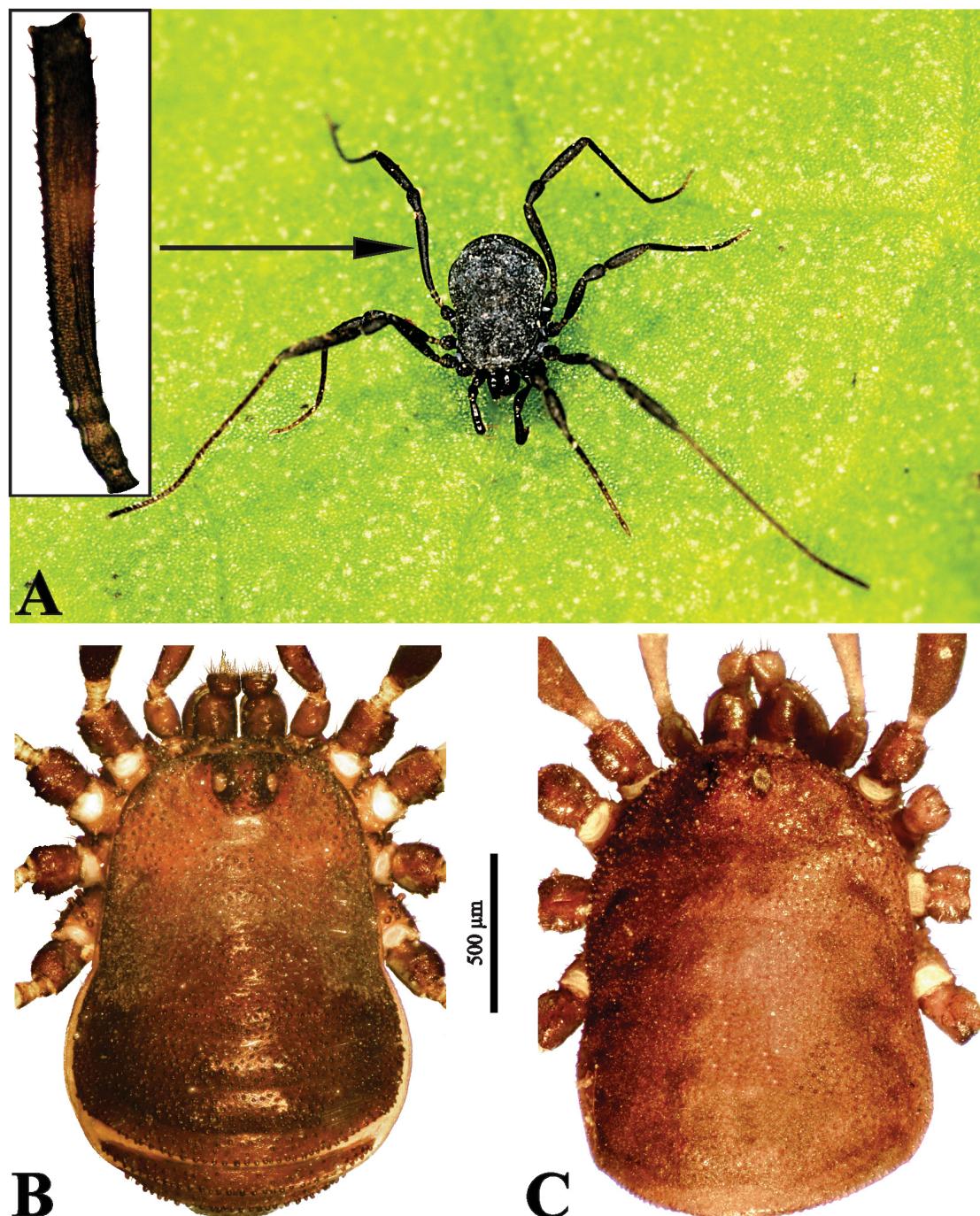


Fig. 1. Representatives of the *Nemastoma bidentatum* Roewer, 1914 complex. **A.** The habitus of a male *Nemastoma bidentatum gruberi* Novak, Slana Novak, Kozel & Raspopnig ssp. nov.; Sveti gori, Slovenia (photo: C. Komposch); inset: femur IV with two pseudo-articulations (apparent articles, i.e., sections delimited with pale, indented rings on the proximal femur portion), and a saw on the latero-posterior margin. **B.** The body of a male *Nemastoma relictum* Gruber & Martens, 1968 stat. nov. showing the tuberculate surface of glittering scutum compositum, and position of the ocular mound (tuber oculorum), supracheliceral lamellae, chelicerae with cheliceral apophysis, and pedipalps and leg. The frontal portion of the scutum is smeared over with a hardened secretum of the integumental glands (cf. Wolff et al. 2016); Mt. Große Karr, the Koralpen Mts, Austria. **C.** The body of a male *Nemastoma bidentatum gruberi* ssp. nov., smeared over with the secretum; Kozje, Slovenia.

subspecies: *N. b. sparsum* Gruber & Martens, 1968 and *N. b. relictum* Gruber & Martens, 1968. They ascribed the subspecies rank to the new taxa, since there were only limited differences in the genital morphology, and hybrids between *N. b. bidentatum* and *N. b. sparsum* probably occurred. They (*ibid.*) also reported *N. b. bidentatum* and *N. b. sparsum* from Slovenia. Later, Hadži (1973a) described two new taxa belonging to the *N. b.* complex: *Nemastoma (Lugubrostoma) triste pluridentatum* Hadži, 1973 and *Nemastoma (Stridulostoma) seliskari* Hadži, 1973. Gruber (1976) synonymized *Stridulostoma* Hadži, 1973 with *Nemastoma* C.L. Koch, 1836, and Martens (1978) synonymized both taxa with *N. b. bidentatum*. Novak (2005a) substantiated *N. ?bidentatum pluridentatum* (the question mark denotes the unresolved subspecific/specific status) from Bosnia as a valid taxon.

Gruber & Martens (1968) explained that, in Austria, *N. b. bidentatum* and *N. b. relictum* do not interbreed in syntopy, and, accordingly, *N. b. relictum* should be raised to the species level if no hybrids were found in the future. Furthermore, Martens (1978) anticipated the syntopic occurrence of *N. b. bidentatum* and *N. b. sparsum* without hybridization. This was later confirmed in Austria, where *N. b. bidentatum*, *N. b. relictum* and *N. b. sparsum* behave as bona fide species (Komposch & Gruber 2004; Komposch 2009). Hybrids between *N. b. bidentatum* and *N. b. sparsum* have been mentioned in Slovenia and Croatia (Gruber & Martens 1968; Martens 1978).

The subspecies category was developed to enhance understanding of geographic variation and speciation, and to refine taxonomic distinction (Mallet 2013; Torstrom *et al.* 2014). There is still much disagreement on this issue, calling for the taxonomic clarification of diagnosability at the subspecies rank level (Patten & Unitt 2002; Isaac *et al.* 2004; Haig *et al.* 2006; Sangster 2009). Genetic techniques, e.g., altered the rules for subspecific designation by applying a phylogeny-based approach, but this should not be to the exclusion of other, traditional lines of evidence; instead, an integrative taxonomic approach, providing a more objective method, has been suggested (Torstrom *et al.* 2014).

Taxa described as subspecies must exhibit their own evolutionary trajectory and not be clinal variants based on a single characteristic (Zink 2004; Oatley *et al.* 2011). When describing new subspecies or revising subspecies taxonomy, detailed description of the concepts and criteria used to determine taxonomic relations should accompany each proposed classification or reclassification (Haig *et al.* 2006). Higher levels of confidence can be obtained by the inclusion of multiple independent sets of characters, such as from morphology, molecular genetics, ecology, behavior and/or physiology (Haig *et al.* 2006; De Queiroz 2007; Miralles *et al.* 2010; Braby *et al.* 2012).

In Dyspnoi, subspecies have been described for seven of the 36 hitherto recognized genera (Schönhofen 2013). Within Nemastomatidae, most subspecies are well defined, while others, e.g., those of *Mitostoma olgae* (Šilhavý, 1939) deserve revision (Novak 2004b; Schönhofen 2013). To date, in the genus *Nemastoma* C.L. Koch, 1836, seven valid species and four subspecies are known (Gruber & Martens 1968; Hadži 1973a; Novak 2005a; Schönhofen 2013). These species are *N. bidentatum* Roewer, 1914, *N. bimaculatum* (Fabricius, 1775), *N. dentigerum* Canestrini, 1873, *N. lugubre* (Müller, 1776), *N. schuelleri* Gruber & Martens, 1968, *N. transylvanicum* Gruber & Martens, 1968 and *N. triste* (C.L. Koch, 1835). All four subspecies ranked within *Nemastoma bidentatum* Roewer, 1914: *N. b. bidentatum* Roewer, 1914, *N. ?b. pluridentatum* (Hadži, 1973), *N. b. relictum* Gruber & Martens, 1968 and *N. b. sparsum* Gruber & Martens, 1968.

Genetic analyses of Nemastomatidae are still scarce, currently providing no reliable model to evaluate relations at the subspecies level (Schönhofen & Holle 2007). Fortunately, chemical analysis of the opilionid scent gland products, which comprise a variety of chemicals, contribute significantly to disentangling specific profiles from higher taxa to the subspecies level (Raspatnig *et al.* 2014). Despite the reluctance of many Dyspnoi to release scent gland substances (Raspatnig *et al.* 2014), the Nemastomatidae appear

to produce easily collectable and highly specific secretions that are very suitable as characters for (chemo) taxonomy (Raspopnig *et al.* 2017). In *Paranemastoma quadripunctatum* Perty, 1833, Raspopnig *et al.* (2010) discovered an exclusively quinonic mixture of seven substances. The secretions of *Nemastoma triste* contained a bouquet of 10 compounds, including quinones and acyclic ketones (Schaider *et al.* 2018).

The taxonomic problems within the *N. b.* complex deserve renewed consideration of the taxa involved. In Slovenia, a systematic collection over several years has provided comprehensive morphological, zoogeographical, chemical and genetic data that allow new insights into the species/subspecies relations in *Nemastoma*. Most of the unresolved questions refer to populations in Slovenia where a number of individuals of the *N. b.* complex cannot be assigned to any of the currently evidenced subspecies: *N. b. bidentatum* and *N. b. sparsum*.

In this revision, we combined morphological, geographical and ecological data. Genetic and chemical data from scent gland secretions were compiled for all species and subspecies of the genus *Nemastoma* and deserve a separate publication. The aims of this contribution are as follows: a) to revise recent knowledge on the *N. b.* complex and b) to analyze relations among the taxa of the complex on the territory of Slovenia in greater detail.

Material and methods

Specimens examined and repositories

Here we mainly consider revised data from Slovenia and, exemplarily, data from Austria, Bosnia and Herzegovina, Croatia and Italy, deposited in the central Opiliones collection, Prirodoslovni Muzej Slovenije, Ljubljana, PMSL (Natural History Museum of Slovenia), and – those collected by S. Polak – in Notranjski muzej, NM (Notranjska Museum, Postojna). The PMSL central Opiliones collection comprises the following collections: IZRK (Karst Research Institute ZRC SAZU, Postojna), NIB (National Institute of Biology), JH (Jovan Hadži), PK (Peter Kozel) and TN-LSN (Tone Novak & Ljuba Slana Novak). Each sample has an individual code number in the brackets, consisting of an acronym of the identifier and the identification number, i.e., the current identification number in the year of identification. The acronyms are as follows: JG Jürgen Gruber, JH Jovan Hadži, CK Christian Komposch, PK Peter Kozel, SL Saška Lipovšek, JM Jochen Martens, TN Tone Novak, GR Günther Raspopnig, ASc Axel Schönhofer, LSN Ljuba Slana Novak, GŽ Gregor Žnidar. Since T. Novak identified most of the samples, these numbers are without acronyms; the acronym is added only for revised samples. In samples from other collections, we have retained the original citations.

Altogether, 4815 individuals were examined: *N. b. bidentatum*: 4 ♂♂, 6 ♀♀, *N. b. gruberi* ssp. nov.: 853 ♂♂, 860 ♀♀, 22 juvs, *N. b. martensi* ssp. nov.: 52 ♂♂, 40 ♀, *N. b. schmidti* ssp. nov.: 823 ♂♂; 1056 ♀♀, 9 juvs, *N. b. sneznikensis* ssp. nov.: 4 ♂♂, 5 ♀♀, *N. b. sparsum*: 173 ♂♂, 188 ♀♀, 4 juvs, *N. kozari* sp. nov.: 7 ♂♂, 11 ♀♀, *N. pluridentatum* stat. nov.: 1 ♂, *N. b. bidentatum* × *N. b. schmidti* ssp. nov.: 19 ♂♂, 20 ♀, 2 juvs, *N. b. gruberi* ssp. nov. × *N. b. martensi* ssp. nov.: 28 ♂♂, 38 ♀♀, *N. b. gruberi* ssp. nov. × *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.: 5 ♂♂, 4 ♀♀, *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov.: 93 ♂♂, 59 ♀♀, *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.: 6 ♂♂, 5 ♀♀, *N. b. schmidti* ssp. nov. × *N. b. sneznikensis* ssp. nov.: 1 ♂ and *N. b. schmidti* ssp. nov. × *N. b. sparsum*: 197 ♂♂, 198 ♀♀, 14 juvs.

Repositories

PMSL = Prirodoslovni Muzej Slovenije, Ljubljana

NM = Notranjski muzej, Postojna

NHMW = Naturhistorisches Museum Wien, Vienna

Abbreviations used

Apo	=	apophysis
Ch	=	chelicera
Fe	=	femur
ibid.	=	same collection data as for preceding
Pa	=	pedipalp
Pe	=	penis
Pt	=	patella
Rec sem	=	receptacula seminis
Ta	=	tarsus
Ti	=	tibia
Tr	=	trochanter

Leg numbering: I–IV.

Sampling area in Slovenia

Prior to this investigation, data on the *N. b.* complex in Slovenia were too scattered to allow proper analysis of variation within the *N. b.* complex. For the purpose of this study, we sampled *N. bidentatum* following the 10 × 10 km UTM grid as the base. In this way, we provided samples in 215 UTM squares (82.4%) covering Slovenia. In the other UTM squares, *N. bidentatum* have not been found. In locality quotations, the UTM codes serve as surrogates for GeoCoordinates. Due to the density of sampling, the UTM codes replace the GeoCoordinates of all localities within the squares. Data for the other countries were presented only exemplarily.

Morphology

The morphology of genitalia, Ch, Pa and the presence of the saw on Fe IV were considered in taxa identification. We followed Gruber's and Martens' (1968) revision of *N. bidentatum* as the basic taxonomic reference. We included all hitherto known *Nemastoma bidentatum* s. lat. in the analysis, i.e., taxa having the Pe with a posteriorly indented, muscular basis, a thin, dorso-ventrally depressed truncus and a triangular glans with two pairs of articulated, lancet-like lateral spines, and a saw-like postero-lateral range of denticles on Fe IV (Fig. 1). In our study, we considered the measurements and shape of the basal Ch article and Ch-Apo (present only in males), the measurements and shape of the Pa, especially the Pa-Fe, including the number and distribution of spines, thorns, denticles, tubercles and setae, as well as characters of the glans and Rec sem. A spine is a long, rigid, acute prominence, a thorn a stout prominence with obtuse to nearly missing terminal point, a denticle is a tooth-like, mostly pointed microstructure (< 10 µm high), a tubercle is a blunt microstructure, and a seta is a hair-like projection of cuticle (terminology according to Gruber & Martens 1968; Martens 1978; Murphree 1988; Schulz & Pinto-da-Roch 2007; Willemart *et al.* 2009, except the thorn, which is our own interpretation). The secretion field is a group of thin openings of the glandular organs on the Ch-Apo, secreting the nuptial gift that roughly coincides with a brush-like field of setae (Gruber & Martens 1968; Martens 1978; Gruber 2007). Ch and Pa were studied in the lateral position, and the Pa armament was additionally examined in a medio-superior view, where this information was of supplementary importance for the presentation. The Pa-Fe minimum width/maximum width is routinely cited for the taxa. The Pa-Fe maximum width is the largest diameter, subterminally or terminally on the Pa-Fe, and the Pa-Fe minimum width is the narrowest diameter of the Pa-Fe at the very proximal portion or a little bit distant from the Tr-Fe joint. In some species, a terminal bonce, i.e., a head-like enlargement, is present. For descriptions, 3–5 females were taken from single-taxon populations, considering their Ch, Pa and Rec sem. Typical male hybrids, i.e., those showing some specific traits beside intermediate traits not present in any subspecies, were briefly described. Since the female hybrids show only intermediate traits, we have not described their morphology separately.

We studied the morphology under a Nikon Eclipse i50 compound microscope (Nikon, Japan), with a mounted digital DS-Fi3 microscope camera, and processed with Nikon NIS-Elements D ver. 5.30.00

software. Transmission light microscopy was combined with illumination from above. Images were manipulated for optimal quality using various applications in GIMP ver. 2.10.22. Drawings were made with a drawing tube mounted on an Olympus CH30 microscope, and then post-processed in the InkScape ver. 0.91 program. We combined glycerol and dry preparations in the procedures. Ovipositors were heated (up to ca 70°C) in lactic acid until the ovipositor became translucent enough to examine the Rec sem. Measurements are in millimeters, if not otherwise indicated.

Ecology

All the taxa within the *N. b.* complex are specialized for living in a loose, humus organic soil horizon and litter. Specific differences in environmental requirements of different taxa deserve a separate study. Here we have roughly assessed the requirements through identification of typical phytocenosis at particular sites. Field notes on the habitat and microhabitat characteristics inhabited by particular taxon of *N. b.* complex were recorded to provide further ecological data. Data on ecology and habitat provide further information that may be of supporting importance in identification in particular cases.

Results

Class Arachnida Lamarck, 1801
Order Opiliones Sundevall, 1833
Suborder Dyspnoi Hansen & Sørensen, 1904
Family Nemastomatidae Simon, 1872
Subfamily Nemastomatinae Simon, 1872

Genus *Nemastoma* C.L. Koch, 1836

Diagnosis (according to Gruber & Martens 1968, slightly modified)

Genus of Nemastomatidae Simon, 1872, with body length 1.5–2.5 mm, with scutum compositum; uniformly black or with silver or golden lateral spots. Pe with base perpendicular to dorso-ventrally flattened truncus, glans bilaterally symmetric or subsymmetric, without or with 1–8 pairs of lateral spines or denticles.

Nemastoma bidentatum Roewer, 1914 complex

Diagnosis

Uniformly black subspecies of *Nemastoma bidentatum* and closely related species, with glans with two pairs of lateral lancet-like, articulated spines, and saw-like series of denticles on Fe IV.

Morphology

The Pe is characterized by a bulbous, muscular, posteriorly medially split basis, a thin truncus and triangular glans, eventually with a shoulder-like truncated tip, either slightly narrower, evenly wide or slightly wider than the truncus, with two pairs of lateral lancet-like, articulated spines. The distal part of the glans is characteristic of some taxa. The shape and size of the Ch basal article and especially of Ch-Apo, and the shape, size and armament of Pa-Fe, and in some taxa Pa-Ti, are further diagnostic characters. Other characters, such as the Pa and leg lengths, may support identification, but are not definitively distinctive. The identification key includes both sexes in the nine pure taxa known to date, except the unknown female of *N. pluridentatum* stat. nov., and typical male hybrids.

Remarks

To date, four additional taxa of the *N. bidentatum* complex have been discovered in Slovenia: *N. b. gruberi* Novak, Slana Novak, Kozel & Raspopnig ssp. nov., *N. b. martensi* Novak, Slana Novak & Raspopnig ssp. nov., *N. b. schmidti* Novak, Raspopnig & Slana Novak ssp. nov. and *N. b. sneznikensis* Novak,

Komposch, Slana Novak & Raspopnig ssp. nov., and one in Bosnia and Herzegovina: *N. kozari* Novak, Kozel, Podlesnik & Raspopnig sp. nov. Within these new taxa, the relatively consistent external morphology of the male Ch-Apo, Pa and glans allows reliable assignment of most individuals. However, *N. b. gruberi* ssp. nov. shows considerable variation in morphology, especially in the Pa-Fe armament, which in some particular cases still raises doubts about the reliability of the assignment (see the description of the taxon for more details). This is because we are still missing a broad review of potentially syntopic hybrids that should be based on data sets independent from morphology, e.g., chemical characters from highly specific scent gland secretions. Such individuals arise from some marginal localities of the area, e.g., from the very south-west of Slovenia, where we still have not been able to exclude the eventual existence of hybrids with *N. b. schmidti* ssp. nov. Morphological differences between females based on the Ch, Pa and Rec sem characters are less conspicuous, but allow correct identification of over 90% of individuals belonging to pure subspecies. Besides, a pairwise vicariance in most neighboring subspecies reveals their different ecological requirements, resulting in niche partitioning. On the other hand, hybrids in the contact zones of adjacent populations of some taxa reveal active gene exchange, supporting the subspecies status of these taxa. *Nemastoma bidentatum* in Austria deserves a separate treatise, while scarce records from the Balkan countries do not allow any further conclusion for the time being.

Thus, to date, there are four species in the *Nemastoma b.* complex in total: *Nemastoma bidentatum* Roewer, 1914, *N. relictum* Gruber & Martens, 1968 stat. nov. and *N. pluridentatum* (Hadži, 1973) stat. nov., both raised to the species level, and the newly discovered *N. kozari* Novak, Kozel, Podlesnik & Raspopnig sp. nov.

***Nemastoma bidentatum* Roewer, 1914**

Nemastoma bidentatum Roewer, 1914: 141, figs 20a–d (original description) [partim; type series also includes *N. triste*].

Nemastoma bidentatum – Roewer 1923: 658, figs 817a–d [partim; type series also includes *N. triste*]. — Gruber & Martens 1968: 141–142 (redescription). — Martens 1978: 106–107. — Schönhofen 2013: 36.

Diagnosis (according to Gruber & Martens 1968, slightly modified)

Species of the *Nemastoma b.* complex with male Pa-Fe having either at least two conspicuous spines or long, rigid setae instead of some spines, or 6–7 irregular tubercles, or 5–11 denticles, and Pa-Fe min:max width 1:2.5–3.5, Rec sem with 1 or none tubular and 12–18 balloon-like vesicles.

Remarks

To date, the species includes six subspecies: *N. b. bidentatum* Roewer, 1914, *N. b. sparsum* Gruber & Martens, 1968, and the newly discovered *N. b. gruberi* Novak, Slana Novak, Kozel & Raspopnig ssp. nov., *N. b. martensi* Novak, Slana Novak & Raspopnig ssp. nov., *N. b. schmidti* Novak, Raspopnig & Slana Novak ssp. nov. and *N. b. sneznikensis* Novak, Komposch, Slana Novak & Raspopnig ssp. nov.

***Nemastoma bidentatum bidentatum* Roewer, 1914**

Figs 2–3, 4A, 5A, 6A, 7B, 8B, 9A, 10A, 11B, 12A, 13A; Tables 1–2

Nemastoma bidentatum Roewer, 1914: 141, figs 20a–d (original description) [partim; type series also includes *N. triste*].

Nemastoma bidentatum – Roewer 1923: 658, figs 817a–d [partim; type series also includes *N. triste*]; 1951: 132 [partim; the description also refers to *N. bidentatum sparsum*].

Nemastoma bidentatum bidentatum – Gruber & Martens 1968: 143–146, figs 4–6, 23 (redescription) [partim; type series also includes *N. bidentatum schmidti* ssp. nov.]. — Martens 1978: 107–111, figs 140–141 [partim; type series also includes *N. bidentatum schmidti* ssp. nov.]. — Komposch & Gruber 2004: 485 [partim; type series also includes *N. bidentatum schmidti* ssp. nov.]. — Novak et al. 2006: 269. — Schönhofner 2013: 36.

Diagnosis (according to Gruber & Martens 1968, slightly modified)

Subspecies of *N. bidentatum* with large, arched dorsal hump on male Ch basal article, and large, apically, sagittally shallowly bifid, quarter moon-like Ch-Apo, ~2.4 times as high as wide. Pa-Fe distinctively club-shaped (Pa-Fe min:max width ~1:3.5), with 3 stout spines in distal Pa-Fe quarter, spine 2 the largest and longest. Pa-Pt Apo equilateral triangular with rounded apex. Pa-Ti with conspicuous proximal dorso-medial hump. Glans isosceles triangular, terminally rounded-truncated. Rec sem of 1 tubular and 12 elongated balloon-like vesicles.

Material examined

AUSTRIA – VM44 • 1 ♀; Bärental; 23 Apr. 2018; L. Slana Novak and T. Novak leg. (6/2018); PMSL.

SLOVENIA – VM44 • 2 ♀♀; Ljubelj; 1 Jun. 1993; S. Brelih leg. (799/1998, rev. 2018); PMSL • 1 ♂, 1 ♀; Ljubeljski prelaz; 20 Jun. 2018; T. Novak leg. (23/2018); PMSL • 3 ♂♂, 2 ♀♀; ibid.; 23 Jul. 2021; L. Slana Novak and T. Novak leg. (298/2021); PMSL.

Description (according to Gruber & Martens 1968, slightly modified)

Male (from Ljubelj)

BODY. Length 1.5–1.7.

CHELICERAE. Ch basal article with large, arched hump in front of dorsal indentation, and large ventral triangular hump; Ch-Apo conspicuously quarter moon-like, Apo apex sagittally bilobed, medial lobe with inconspicuous apical pinnacle (Figs 4A, 6A, 9A). Secretion field apically medially. Proximal article length 0.57, distal article length 0.54, max width 0.17, movable finger length 0.25.

PEDIPALPS. Pa-Tr with high, subequilateral dorsal hump. Pa-Fe distinctively club-shaped (Pa-Fe min:max width ~1:3.5), ventrally bent; with 3, rarely 4 stout spines in distal Pa-Fe quarter; spine 2 the largest, with 2–3 pinnacles. Pa-Pt distinctively ventrally bent, with large, stout, apically rounded medio-ventral Pt-Apo. Pa-Ti straight or slightly bent dorsally, with small, but distinct proximal dorso-medial hump. Pa-Ta terminally narrowing, conically oval (Figs 5A, 6A, 10A). Pa article lengths in Table 1.

PENIS. Pe length 1.7, Pe basis $\frac{1}{3}$ Pe length, glans isosceles triangular, terminally rounded-truncated (Figs 7B, 8B).

LEGS. Leg article lengths in Tables 1–2.

Female (from Ljubelj)

BODY. Length 1.6–1.8.

CHELICERAE. Ch with subparallel dorsal and ventral margins, slightly arched dorsally, Ch length:width ~2.6:1 (Fig. 13A). Proximal article length 0.57, distal article length 0.63, max width 0.21, movable finger length 0.32.

Table 1. Length of appendage-segments in millimeters in *N. bidentatum bidentatum* Roewer, 1914 from Ljubelj, Slovenia: ♂ (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.25 (0.33)	0.76 (0.80)	0.53 (0.56)	0.46 (0.49)	—	0.29 (0.31)	2.29 (2.49)
Leg I	0.23 (0.24)	0.68 (0.70)	0.39 (0.38)	0.61 (0.64)	1.06 (1.05)	0.97 (0.98)	3.94 (3.99)
Leg II	0.27 (0.31)	1.30 (1.56)	0.47 (0.45)	1.13 (1.01)	2.03 (1.68)	0.84 (1.47)	5.98 (6.48)
Leg III	0.19 (0.23)	0.87 (0.96)	0.36 (0.35)	0.61 (0.64)	1.15 (1.17)	0.88 (0.91)	4.06 (4.26)
Leg IV	0.25 (0.25)	1.32 (1.21)	0.39 (0.44)	0.78 (0.89)	1.84 (1.84)	1.18 (1.16)	5.75 (5.79)

Table 2. Length of appendage-segments in millimeters (trochanters not presented) in *N. bidentatum bidentatum* Roewer, 1914 from Bärental, Austria: ♂ (♀) (from Gruber & Martens 1968).

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Leg I	0.75 (0.75)	0.35 (0.35)	0.55 (0.60)	1.00 (0.90)	0.85 (0.85)	3.50 (3.50)
Leg II	1.20 (0.80)	0.35 (0.40)	1.05 (1.05)	1.90 (1.95)	1.55 (1.60)	6.05 (5.80)
Leg III	0.75 (0.85)	0.30 (0.35)	0.60 (0.55)	1.15 (1.05)	0.80 (0.80)	3.60 (3.60)
Leg IV	1.25 (1.30)	0.35 (0.35)	0.75 (0.75)	1.75 (1.70)	1.05 (1.05)	5.15 (5.15)

PEDIPALPS. Pa-Tr long, Pa-Tr length:width ~2.5:1, Pa-Tr dorsal margin with low hump with long, straight posterior portion and stair-like front indentation in distal quarter; Pa-Fe max:min width ~1.9:1; Pa-Ti straight, simply rod-shaped; Pa-Ta narrow long-oval (Fig. 13A). Pa article lengths in Table 1.

OVIPOSITOR. Ovipositor length 1.05, Rec sem with one tubular and 12 elongated balloon-like vesicles (Fig. 11B).

LEGS. Leg article lengths in Tables 1–2.

Remarks

The type locality Comana Vlasca in Romania (Roewer 1914) is erroneous, since besides *N. b. sparsum* (sic! not described by Roewer 1914), the type series also contains *N. b. bidentatum* and *N. triste*, both endemic to the Eastern Alps (Gruber & Martens 1968: 143). Later, Roewer (1951) designated a type specimen from the type series from an unknown locality, but the mixed composition of the type series remained unresolved (Gruber & Martens 1968). Thus, there was a need to clarify the type locality (ICZN 1999: Art. 75.3.1.). Respecting both Roewer's drawing of the male Ch characteristic of individuals in the Karawanken/Karavane Mts and the syntopy of the Roewer's type specimens with *N. triste*, Gruber & Martens (1968) redescribed the nominal subspecies *N. b. bidentatum* upon a neotype (Gruber & Martens 1968: figs 4–6) from Bärental, Carinthia, Austria (not mapped in Gruber & Martens 1968: fig. 24). Bärental is considered the type locality of the type subspecies. However, according to our findings the figured Pe tip from Leutschach/Lučine, Styria, Austria (Gruber & Martens 1968: fig. 3), considered under the type subspecies, belonged to *N. b. schmidti* ssp. nov. All so far published evidence on *N. b. bidentatum* in Slovenia, Croatia and NE Italy (Hadži 1927, 1928; Gruber & Martens 1968; Martens 1978; Novak & Gruber 2000; Komposch & Gruber 2004; Novak 2004a, 2004b, 2005b, 2005c; Novak *et al.* 1984, 1995, 1996, 2002, 2006, 2017) refer to other taxa. The type series deposited in Naturhistorisches Museum Wien (Gruber & Martens 1968) also includes *N. b. schmidti* ssp. nov. See remarks under *N. pluridentatum* stat. nov., *N. b. schmidti* ssp. nov., *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. and *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.

Distribution

The South-Eastern Alps: Austria, Slovenia (Gruber & Martens 1968; Martens 1978), perhaps endemic to the Karawanken/Karavanke Mts. Vertical distribution (incomplete data): 980–1407 m a.s.l. (partly Gruber & Martens 1968 and Martens 1978; this work). Type locality: Bärental/Zavrh–Rute (46.47° N, 14.15° E, 980 m a.s.l.) near Feistritz im Rosental/Bistrica v Rožu, Carinthia, Austria.

Ecology

Montane subspecies of *N. bidentatum* inhabiting submontane and montane neutrophile fir forests within the area of distribution of the montane beech forests, dominated by *Abies alba* Mill., with a great admixture of *Picea abies* (L.) H.Karst. and *Fagus sylvatica* L. Phenology: adults probably eurychronous.

Nemastoma bidentatum sparsum Gruber & Martens, 1968

Figs 2–3, 4B, 5B, 6B, 7C, 8C, 9B, 10B, 11A, C, 12B, 13B; Tables 3–4

Nemastoma bidentatum sparsum Gruber & Martens, 1968: 146–147, figs 1–2, 7–11 (original description) [partim; the type series also includes *N. bidentatum gruberi* ssp. nov.].

Nemastoma bidentatum – Roewer 1914: 141 [partim: type series also includes *N. bidentatum bidentatum* and *N. triste*]. — Šilhavý 1956: 131, figs 243–246. — Loksa 1962: 267, figs 3a–f. — Gruber & Martens 1968: 146–147, figs 1–2, 7–11. — Staręga 1976: 313–315, figs 25–27. — Martens 1978: 111–112, figs 143–145, 147, 150; 2006: 182–184, figs 20, 21c–d, 22a–h. — Novak & Gruber 2000: 286. — Novak et al. 2002: 136 [partim: Radenci]; 2006: 269. — Komposch & Gruber 2004: 485.



Fig. 2. The complete distributional area of the *Nemastoma bidentatum* Roewer, 1914 complex, according to Gruber & Martens (1968), Martens (2006), Schönhöfer & Holle (2007) and own data, with marked positions of the type localities of the taxa.

— Novak 2004b: 245 [partim: Breznica, Slavonski brod, Spačva near Županja]; 2005a: 315 [partim: Bosanski Brod]. — Schönhöfer & Holle 2007: 25, figs 2a–i. — Schönhöfer 2013: 36.

Diagnosis (according to Gruber & Martens 1968, slightly modified)

Male Ch basal article with nearly straight dorsal margin in front of dorsal indentation, and short, roundly oblong Ch-Apo, with small apical pinnacle. Pa-Fe moderately club-shaped (Pa-Fe min:max width ~1:2.5), with 2 distal, pointed spines, spine 2 the largest. Pa-Pt Apo conical. Glans equilaterally triangular. Rec sem with 14 balloon-like vesicles.

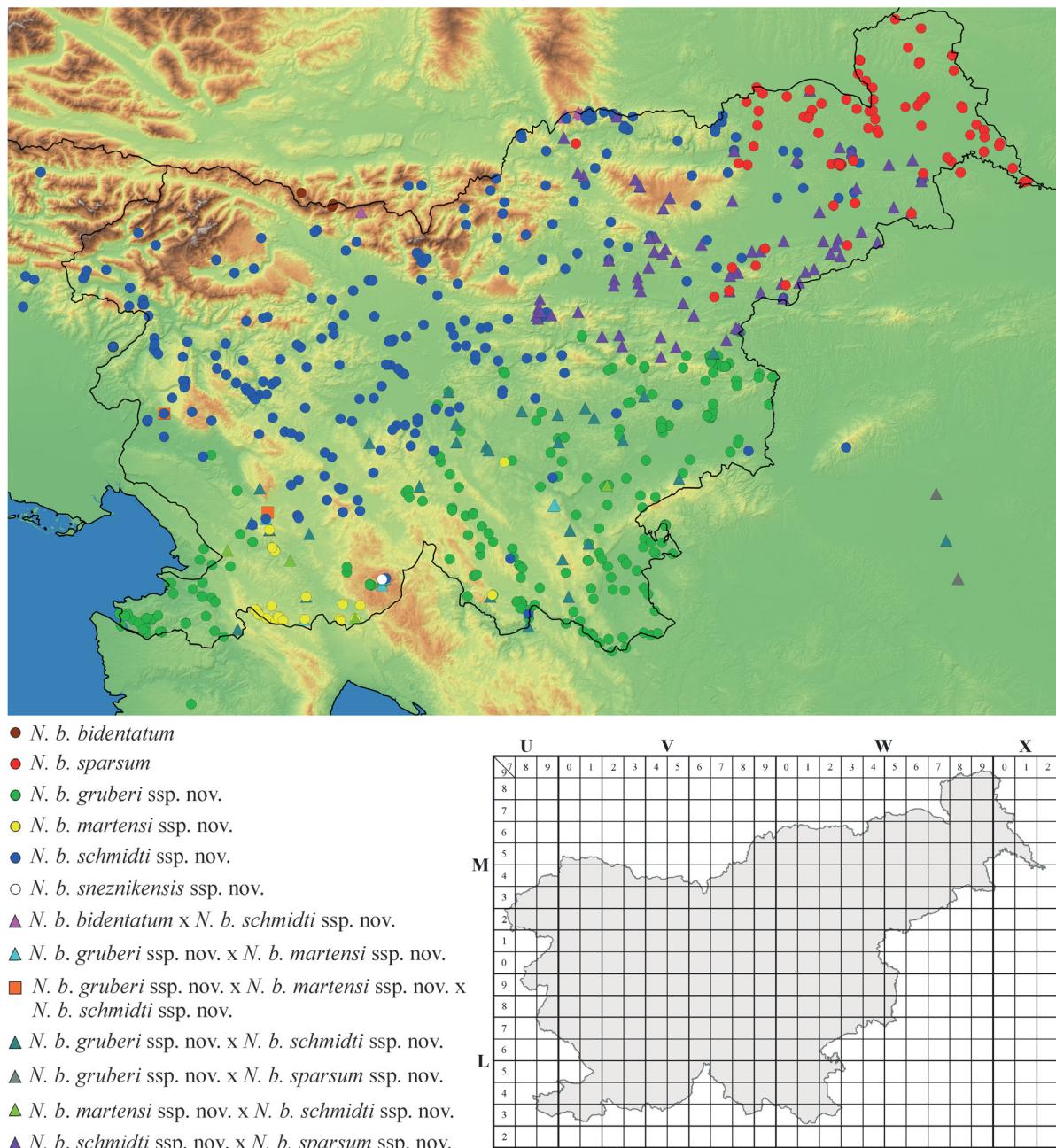


Fig. 3. Distributional areas of six subspecies (circles) and hybrids (triangles, squares) within the *Nemastoma bidentatum* Roewer, 1914 in Slovenia and adjacent regions. Note that many localities overlap on the map.

Material examined

CROATIA – **XM05** • 1 ♀; Jurovčak; 3 Apr. 1983; T. Novak and L. Slana Novak leg. (LSN 7/1983, TN rev. 2008); PMSL.

SLOVENIA – **WM06** • 1 ♂; Cvitrško sedlo, Otiški vrh; 28 May 2008; T. Novak leg. (160/2011); PMSL. – **WM42** • 1 ♂, 2 ♀♀, 1 juv.; Mestinje; 4 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 43/1983); PMSL • 1 ♂, 1 ♀; ibid.; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1138/2002); PMSL • 1 ♀; Šmarje pri Jelšah; 6 Apr. 1986 (1169/1997, rev. 2015); PMSL • 1 ♀; Zgornje Poljčane; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1160/2002); PMSL. – **WM45** • 1 ♂; Ledine; 25 Jul. 1987; F. Janžekovič leg. (7/1999); PMSL • 1 ♂; Maribor; 24 Aug. 1986; Malavašić and Koren leg. (265/2002); PMSL. – **WM47** • 1 ♀; Kresnica; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (162/2011); PMSL. – **WM52** • 1 ♂; Maršečka vas; 11 Oct. 1997; L. Slana Novak and T. Novak leg. (1893/1998); PMSL. – **WM53** • 2 ♂♂, 1 ♀; Pečke; 24 Jun. 2007; T. Novak leg. (45/2007); PMSL • 1 ♂, 2 ♀♀; Šega, Makole; 9 Apr. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 70/1983); PMSL. – **WM56** • 1 ♀; Kaniža; 20 May 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 80/1983); PMSL • 1 ♀; Mt. Piramida, Maribor, 1–30 Nov. 1978; (909/1997, rev. 2015); PMSL • 1 ♀; Spodnje Dobrenje; 23 Apr. 2008; L. Slana Novak and T. Novak leg. (165/2011); PMSL • Ranca, Pesnica. – **WM57** • 1 ♂; Ceršak; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (113/2011); PMSL • 1 ♂; Kozjak pri Ceršaku; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (116/2011); PMSL. – **WM66** • 2 ♀♀; Černetina; 23 Apr. 2008; L. Slana Novak and T. Novak leg. (163/2011); PMSL • 1 ♂; Kremberg; 4 Jun. 1984; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 343/1985); PMSL • 2 ♂♂; ibid.; 23 Apr. 2008; L. Slana Novak and T. Novak leg. (114/2011); PMSL • 1 ♀; Spodnji Žerjavci; 23 Apr. 2008; L. Slana Novak and T. Novak leg. (115/2011); PMSL. – **WM67** • 1 ♂; Sv. Ana; 3 Jul. 2002; T. Novak leg. (799/2002); PMSL • 1 ♀; Nasova; 3 Jun. 1984; L. Slana Novak and T. Novak leg. (314/2002, rev. 2015); PMSL • 1 ♂; Stogovci; 13 Apr. 1984; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 323/1985); PMSL • 1 ♂, 1 ♀; Zgornja Velka; 20 Mar. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 8/1983); PMSL. – **WM73** • 1 ♀; Repišče; 24 Jun. 2007; T. Novak leg. (31/2007, rev. 2015); PMSL. – **WM74** • 1 ♀; Podvinci; 26 Oct. 1994; M. Varžič leg. (21/1999); PMSL • 1 ♂; Žamenci; 22 Oct. 1994; M. Varžič leg. (18/1999); PMSL • 1 ♂; ibid.; (20/1999); PMSL • 1 ♂; ibid.; 23 Oct. 1994; M. Varžič leg. (19/1999, rev. 2015); PMSL. – **WM75** • 1 ♂; Trnovce; 2 Jun. 2002; L. Slana Novak and T. Novak leg. (760/2002); PMSL • 7 ♂♂, 4 ♀♀; Velika Slavšina; 13 Oct. 2005; L. Slana Novak and T. Novak leg. (158/2005, rev. 2018); PMSL • 5 ♂♂, 3 ♀♀; Vitomarci; 30 Jun. 2002; T. Novak leg. (787/2002); PMSL • 1 ♀; ibid.; 3 Jul. 2002; T. Novak leg. (792/2002); PMSL • 1 ♂; ibid.; (797/2002); PMSL • 1 ♀; ibid.; 3 Jul. 2002; T. Novak leg. (794/2002, rev. 2008); PMSL • 1 ♀; ibid.; (796/2002); PMSL • 1 ♂; ibid.; (797/2002); PMSL • 1 ♂; ibid.; (800/2002); PMSL • 1 ♀; ibid.; 2 Oct. 2002; T. Novak leg. (1280/2002); PMSL • 1 ♂; ibid.; (1279/2002); PMSL. – **WM77** • 1 ♀; Črešnjevci; 24 Apr. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 79/1983, TN rev. 2008); PMSL • 1 ♂, 1 ♀; Korovci; 7 Apr. 1984; L. Slana Novak and T. Novak leg. (LSN 191/1985); PMSL • 1 ♂, 1 ♀; Lomanoše; 1 Oct. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 110/1983); PMSL. – **WM78** • 1 ♂; Gerlinci; 11 May 1986; T. Novak and L. Slana Novak leg. (LSN 139/1986); PMSL. – **WM86** • 2 ♂♂, 6 ♀♀; Hrašenski vrh; 9 Sep. 1983; T. Novak and L. Slana Novak leg. (LSN 115/1983); PMSL • 4 ♂♂, 3 ♀♀; Kapelski vrh; 17 Sep. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 112/1983); PMSL • 1 ♂; Murski vrh; 19 May 1984; L. Slana Novak and T. Novak leg. (LSN 240/1984); PMSL • 1 ♀; Radenci; 25 Jul. 1983; M. Slana Novak and L. Slana Novak leg. (LSN 111/1983, TN rev. 2007); PMSL • 2 ♂♂, 2 ♀♀; ibid.; 20 Sep. 1983; L. Slana Novak leg. (LSN 119/1983); PMSL • 1 ♂; Rihtarovci; 26 Feb. 1997; B. Dronenik leg. (94/2001); PMSL. – **WM87** • 3 ♂♂, 3 ♀♀; Cankova; 15 Sep. 1983; T. Novak and L. Slana Novak leg. (LSN 114/1983); PMSL • 3 ♂♂, 3 ♀♀; Skakovci; 27 Mar. 1983; T. Novak and L. Slana Novak leg. (LSN 4/1983); PMSL • 1 ♂; Sodišinci, Radenci; 19 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 68/1983); PMSL. – **WM88** • 1 ♂; Gerlinci; 11 Aug. 1983; L. Slana Novak, M. Slana Novak and T. Novak leg. (1322/1998); PMSL. – **WM89** • 2 ♂♂, 4 ♀♀, 1 juv.; Trdkova; 30 Jul. 1983; T. Novak, M. Slana

Novak and L. Slana Novak leg. (LSN 49/1983); PMSL. – **WM94** • 1 ♀; Pavlovci; 15 Apr. 2000; L. Slana Novak and T. Novak leg. (744/2002); PMSL. – **WM95** • 1 ♀; Podgradje, Ljutomer; 27 May 2001; S. Brelih leg. (125/2001); PMSL. – **WM96** • 1 juv.; Bratonce; 9 Aug. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 335/1985, TN rev. 2008); PMSL. – **WM97** • 1 ♂; Andrejci; 28 Jul. 1981; T. Novak leg. (1188/1981, JG det.); PMSL • 1 ♂; Moravci; 16 Mar. 1984; T. Novak and L. Slana Novak leg. (LSN 243/1984); PMSL • 4 ♂♂; Murska Sobota; 24 Nov. 1982; T. Novak leg. (603/1982); PMSL • 3 ♀♀; Rakičan – Noršinci; 23 Sep. 1984; L. Slana Novak leg. (322/1985); PMSL • 1 ♂, 2 ♀♀; ibid.; 13 Sep. 1981; T. Novak leg. (371/1982, JG det.); PMSL. – **WM98** • 2 ♂♂, 3 ♀♀; Košarovci; 24 Jul. 1982; L. Slana Novak, T. Novak and M. Slana Novak leg. (529/1982, JG det.); PMSL • 1 ♀; ibid.; 1 Sep. 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 318/1985); PMSL • 1 ♂, 3 ♀♀; Mačkovci; 31 Jul. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 67/1983); PMSL. – **WM99** • 2 ♂♂; Lucova; 2 Jun. 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 239/1984); PMSL. – **XM05** • 1 ♀; Bobri; 24 Aug. 1988; F. Velkovrh leg. (13/1995); PMSL • 2 ♂♂, 1 juv.; Dolnja Bistrica; 17 Aug. 1996; I. Kovač leg. (SL 2/1997); PMSL • 2 ♀♀; ibid.; (SL 3/1997); PMSL. – **XM06** • 2 ♂♂, 3 ♀♀; Banuta/Bánuta; 10 Aug. 1996; I. Kovač leg. (SL 5/1997); PMSL • 2 ♂♂, 1 ♀; ibid.; (SL 22/1997); PMSL • 2 ♂♂, 2 ♀♀; ibid.; (SL 21/1997); PMSL • 13 ♂♂, 15 ♀♀; ibid.; 13 Aug. 2012; T. Novak leg. (GR 3837–3849, 3792–3797, TN det.); PMSL • 4 ♂♂, 3 ♀♀; ibid.; (GR 3770–3776); PMSL • several specs; Polanski log, Mala Polana; 17 Jul. 2000; T. Novak leg.; PMSL • 1 ♂, 1 ♀; Radmožanci/Radamos; 17 Mar. 1984; T. Novak and L. Slana Novak leg. (LSN 109/1984); PMSL. – **XM07** • 4 ♂♂, 3 ♀♀; Dobrovnik/Dobronak; 8 Aug. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 57/1983); PMSL • 1 ♀, 1 juv.; ibid.; 18 Aug. 1996; I. Kovač leg. (SL 1/1997); PMSL. – **XM08** • 3 ♂♂, 1 ♀; Prosenjakovci/Pártosfalva; 8 Aug. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 50/1983); PMSL • 2 ♀♀; Središče/Szerdahely; 12 Aug. 1996; I. Kovač leg. (SL 6/1997); PMSL • 4 ♂♂; ibid.; 24 Aug. 1996; I. Kovač leg. (SL 7/1997); PMSL • 2 ♀♀; ibid.; (SL 8/1997); PMSL • 1 ♂, 3 ♀♀; ibid.; (SL 20/1997); PMSL • 4 ♂♂; ibid.; (SL 23/1997); PMSL • 4 ♂♂; ibid.; (SL 61/1997); PMSL • 3 ♂♂; ibid.; (SL 108/1997); PMSL • 12 ♀♀; ibid.; (SL 105/1997); PMSL. – **XM15** • 3 ♀♀; Benica/Benice; 1 Aug. 1996; I. Kovač leg. (SL 11/1997); PMSL • 3 ♀♀; ibid.; (SL 12/1997); PMSL • 2 ♂♂; ibid.; 19 Aug. 1996; I. Kovač leg. (SL 25/1997); PMSL • 2 ♀♀; ibid.; (SL 26/1997); PMSL • 5 ♀♀; ibid.; (SL 28/1997); PMSL • 3 ♂♂; ibid.; (SL 29/1997); PMSL • 2 ♂♂; ibid.; (SL 39/1997); PMSL • 2 ♀♀; ibid.; (SL 64/1997); PMSL • 1 ♂, 1 ♀; ibid.; (SL 65/1997); PMSL • 1 ♂, 3 ♀♀; Gaberje/Gyetyános; 22 Aug. 1996; I. Kovač leg. (SL 9/1997); PMSL • 1 ♀; ibid.; (SL 10/1997); PMSL • 1 ♂; ibid.; (SL 15/1997); PMSL • 3 ♀♀; ibid.; (SL 16/1997); PMSL • 1 ♀; ibid.; 12 Oct. 1996; I. Kovač leg. (SL 30/1997); PMSL • 2 ♀♀; ibid.; (SL 55/1997); PMSL • 5 ♂♂; ibid.; 19 Oct. 1996 (SL 17/1997); PMSL • 4 ♂♂, 4 ♀♀; ibid.; (SL 24/1997); PMSL • 4 ♀♀; ibid.; (SL 103/1997); PMSL • 8 ♀♀; ibid.; (SL 104/1997); PMSL • 2 ♀♀; ibid.; (SL 106/1997); PMSL • 7 ♂♂; ibid.; (SL 107/1997); PMSL • 2 ♂♂; ibid.; (SL 109/1997); PMSL • 14 ♀♀; ibid.; 22 Aug. 1997; I. Kovač leg. (SL 27/1997); PMSL • 1 ♂, 1 juv.; ibid.; (SL 32/1997); PMSL • 1 ♂; ibid.; (SL 68/1997); PMSL • 4 ♂♂; ibid.; 24 Aug. 1997; I. Kovač leg. (SL 19/1997); PMSL • 2 ♀♀; ibid.; 28 Aug. 1997; I. Kovač leg. (SL 13/1997); PMSL • 2 ♂♂; ibid.; (SL 14/1997); PMSL • 1 ♂; ibid.; 12 Oct. 1997; I. Kovač leg. (SL 4/1997); PMSL • 4 ♂♂; ibid.; (SL 20/1997); PMSL • 1 ♀; ibid.; (SL 56/1997); PMSL • 1 ♂; ibid.; (SL 100/1997); PMSL • 4 ♀♀; ibid.; (SL 101/1997); PMSL. – **XM16** • 2 ♂♂; Murska Šuma; 29 Aug. 1998; T. Novak leg. (1538/1998); PMSL • several specs; ibid.; 18 Jun. 2001; T. Novak leg.; PMSL • 1 ♂, 1 ♀; Dolgovaške Gorice/Hossúfaluhegy; 31 Mar. 1984; T. Novak, D. Kuhar and L. Slana Novak leg. (LSN 141/1984); PMSL • 4 ♂♂, 1 ♀; Lendavske gorice/Lendvahegy; 17 Aug. 1996; I. Kovač leg. (SL 31/1997); PMSL. – **XM25** • 1 ♂; Muriša, Murska Šuma; B. Drovenik and A. Pirnat leg. (26/2005); PMSL.

Description (according to Gruber & Martens 1968, slightly modified)

Male (from Prosenjakovci)

BODY. Length 1.5–2.0. Males from Slovenia larger than those from the type locality. Length 1.96, width 1.44.

CHELICERAE. Ch basal article with nearly straight dorsal margin in front of dorsal indentation and small ventral hump, Ch-Apo short, roundly oblong, with convex anterior margin and small apical pinnacle (Figs 4B, 6B, 9B). Secretion field medially. Proximal article length 0.53, distal article length 0.59, max width 0.18, movable finger length 0.25.

PEDIPALPS. Pa-Tr with highly arched dorsal hump. Pa-Fe moderately club-shaped (Pa-Fe min:max width ~1:2.5), slightly ventrally bent, with 2 stout, pointed spines in distal Pa-Fe quarter; spine 2 the largest. Pa-Pt Apo triangular-conical. Pa-Ti simple, straight. Pa-Ta conically tapering (Figs 5B, 6B). Pa article lengths in Table 3.

PENIS. Pe length 1.6, Pe basis ¼ Pe length, glans equilaterally triangular (Figs 7C, 8C).

LEGS. Leg article lengths in Tables 3–4.

Female (from Prosenjakovci)

BODY. Body length 1.6–2.4. Females from Slovenia larger than those from the type locality. Body length 2.40, body width 1.97.

CHELICERAE. Ch basal article with low-arched dorsal margin in front of dorsal indentation, and straight ventral margin with triangular hump, Ch basal article length:width >2.6:1. Proximal article length 0.57, distal article length 0.63, max width 0.21, movable finger length 0.32 (Fig. 13B).

PEDIPALPS. Pa-Tr with moderately high, arched dorsal margin; Pa-Fe with distal bonce, Pa-Fe max:min width ~1.7:1; Pa-Ti elongated-oval (13B). Pa article lengths in Table 3.

OVIPOSITOR. Ovipositor length 1.0, Rec sem with 14 balloon-like vesicles (Fig. 11A, C).

LEGS. Leg article lengths in Tables 3–4.

Remarks

In Slovenia, *N. b. sparsum* lives in the northeast, at the margins of the Pannonian basin (Martens & Gruber 1968; Martens 1978; Kovač 1997). The type series deposited in Naturhistorisches Museum Wien (Gruber & Martens 1968) also includes *N. b. gruberi* ssp. nov. distributed south of the Sava River in Slovenia and Croatia. All prior identifications of *N. b. sparsum* south of the Sava River (Novak et al. 1995, 2002; Novak 2005b) refer to *N. b. gruberi* ssp. nov. Martens (1978: 112) reported a *sparsum*-like population living in the mountain pine association (*Hyperico grisebachii*-*Pinetum mugo* Horvat 1938) on Mt. Veliki Snežnik (the peak at 1796 m) at least up to the altitude of 1650 m a.s.l. These individuals may refer to *N. b. gruberi* ssp. nov., *N. b. martensi* ssp. nov. or *N. b. sneznikensis* ssp. nov. Individuals from Bosnia and Herzegovina (Mt. Plasa, Jajce) and Dalmatia, Croatia (Split) (Gruber & Martens 1968) should be revised for identification. See remarks under *N. b. gruberi* ssp. nov. and *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov., *N. b. martensi* ssp. nov. and *N. b. sneznikensis* ssp. nov.

Distribution

Central and eastern Europe: Austria, Bulgaria, Bosnia and Herzegovina, Czech Republic, Denmark, Hungary, Croatia, Montenegro, Romania, Russia, Slovakia, Slovenia, Serbia and Turkey (Gruber & Martens 1968; Staręga 1976; Martens 1978, 2006; Mučalica 1988; Klimeš 2000; Komposch 2002; Komposch & Gruber 2004; Schönhofer & Holle 2007). Vertical distribution: 120–1650 m a.s.l. (Komposch 1999; Komposch & Gruber 2004), in Slovenia 155–644 m a.s.l. Type locality: Sonnenberg (47.88° N, 16.31° E, 480 m a.s.l.), Leitha Mts, Burgenland, Austria.

Table 3. Length of appendage-segments in millimeters in *N. bidentatum sparsum* Gruber & Martens, 1968 from Prosenjakovci, Slovenia: ♂ (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.25 (0.28)	0.75 (0.74)	0.52 (0.60)	0.45 (0.47)	—	0.29 (0.28)	2.26 (2.37)
Leg I	0.23 (0.24)	0.68 (0.70)	0.39 (0.38)	0.61 (0.64)	1.06 (1.05)	0.97 (0.98)	3.94 (3.99)
Leg II	0.27 (0.31)	1.30 (1.56)	0.47 (0.45)	1.13 (1.01)	2.03 (1.68)	0.84 (1.47)	5.98 (6.48)
Leg III	0.19 (0.23)	0.87 (0.96)	0.36 (0.35)	0.61 (0.64)	1.15 (1.17)	0.88 (0.91)	4.06 (4.26)
Leg IV	0.25 (0.25)	1.32 (1.21)	0.39 (0.44)	0.78 (0.89)	1.84 (1.84)	1.18 (1.16)	5.75 (5.79)

Table 4. Length of appendage-segments in millimeters (trochanters not presented) in *N. bidentatum sparsum* Gruber & Martens, 1968 from Sonnenberg, Austria: ♂ holotype (♀) (from Gruber & Martens 1968).

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Leg I	0.75 (0.75)	0.30 (0.30)	0.55 (0.55)	0.95 (0.95)	0.80 (0.90)	3.35 (3.45)
Leg II	1.30 (1.25)	0.35 (0.40)	1.00 (1.00)	1.95 (1.95)	1.45 (1.45)	6.05 (6.05)
Leg III	0.75 (0.75)	0.30 (0.30)	0.50 (0.50)	1.05 (1.10)	0.60 (0.75)	3.20 (3.40)
Leg IV	1.20 (1.20)	0.35 (0.30)	0.75 (0.75)	1.70 (1.70)	1.05 (1.00)	5.05 (4.95)

Ecology

Nemastoma b. sparsum is a lowland and hilly land subspecies inhabiting various types of acidophilous and neutrophilous forests of *Fagus sylvatica*, *Carpinus betulus* L. and *Quercus petraea* (Matt.) Liebl., riverine forests, and thermophilous scrubs in north-eastern Slovenia, mostly on non-calcareous soils. Phenology: adults eurychronous.

Nemastoma relictum Gruber & Martens, 1968 stat. nov. Komposch
Figs 1B, 2, 4C, 5C, 6C, 7D, 8D, 9C, 10C, 11D, 12C, 13C; Tables 5–6

Nemastoma bidentatum relictum Gruber & Martens, 1968: 147–149, figs 14–16, 24 (original description).

Nemastoma bidentatum relictum – Martens 1978: 112–113, figs 148–150. — Komposch & Gruber 2004: 485. — Komposch 2009: 476; 2011: 65. — Schönhofen 2013: 36.

Diagnosis

Species within the *N. b.* complex with button-shaped Ch-Apo, and secretion field oriented frontally. Pa-Fe without spines, slightly club-shaped (Pa-Fe min:max width ~1:2.3). Rec sem with 5 lobate, tubular-saccular vesicles.

Material examined

AUSTRIA • 2 ♂♂, 3 ♀♀; Großes Kar, the Koralpe Mts; 25 Oct. 2005; C. Komposch leg. (CK det.); PMSL.

Description (according to Gruber & Martens 1968, slightly modified)

Male (from Großes Kar, Salzburg)

BODY. Length 1.55–1.60.

CHELICERAE. Ch with flat triangular dorsal margin in front of dorsal indentation; ventral margin straight, with minute triangular hump. Ch-Apo button-like, inferior and frontal margins straight, embracing a

Table 5. Length of appendage-segments in millimeters in *N. relicum* Gruber & Martens, 1968 stat. nov. from Große Kar, Koralpe, Austria: ♂ (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.25 (0.25)	0.65 (0.63)	0.51 (0.47)	0.41 (0.37)	—	0.32 (0.25)	2.14 (1.97)
Leg I	0.21 (0.23)	0.78 (0.74)	0.34 (0.40)	0.63 (0.52)	0.90 (0.90)	0.89 (0.76)	3.75 (3.55)
Leg II	0.20 (0.23)	1.23 (1.23)	0.42 (0.39)	0.98 (0.98)	1.82 (1.62)	1.21 (1.35)	5.86 (5.80)
Leg III	0.20 (0.20)	0.78 (0.56)	0.31 (0.31)	0.56 (0.54)	1.07 (1.00)	0.67 (0.80)	3.59 (3.41)
Leg IV	0.24 (0.20)	1.13 (1.15)	0.39 (0.38)	0.83 (0.77)	1.56 (1.45)	1.12 (1.04)	5.27 (4.99)

Table 6. Length of appendage-segments in millimeters (trochanters not presented) in *N. relicum* Gruber & Martens, 1968 stat. nov. from the vicinity of Tappenkarsee, Obertauern, Austria: ♂ holotype (♀) (from Gruber & Martens 1968).

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Leg I	0.65 (0.75)	0.30 (0.30)	0.50 (0.50)	0.85 (0.90)	0.80 (0.85)	3.10 (3.30)
Leg II	1.10 (1.15)	0.40 (0.40)	0.95 (0.90)	1.70 (1.65)	1.30 (1.30)	5.45 (5.40)
Leg III	0.70 (0.75)	0.30 (0.30)	0.50 (0.55)	1.00 (1.00)	0.75 (0.80)	3.25 (3.40)
Leg IV	1.10 (1.15)	0.35 (0.30)	0.75 (0.75)	1.50 (1.50)	1.00 (1.00)	4.70 (4.70)

90° angle, Ch-Apo dorsally round, secretion field with dense setae (brush) frontally (Figs 4C, 6C, 9C). Proximal article length 0.54, distal article length 0.53, max width 0.18, movable finger length 0.19.

PEDIPALPS. Pa-Tr dorsal margin high, oval, leaned distally; Pa-Fe distended distally (max:min width ~1.7:1), without spines. Pa-Pt with conspicuously convex ventral margin and finger-like medial Apo. Pa-Ti and Pa-Ta straight (Figs 5C, 6C). Pa article lengths in Table 5.

PENIS. Pe length 1.6, Pe basis ¼ Pe length, glans isosceles triangular (Figs 7C, 8C).

LEGS. Leg article lengths in Tables 5–6.

Female (from Große Kar, Salzburg)

BODY. Length 1.70.

CHELICERAE. Ch basal article with low-arched dorsal margin in front of indentation, and ventral low-arched concavity, Ch basal article length:width ~2.3:1 (Fig. 13C). Proximal article length 0.56, distal article length 0.55, max width 0.19, movable finger length 0.20.

PEDIPALPS. Pa short, ~2 mm long, Pa-Tr with high, isosceles triangular dorsal margin arched on the top, Pa-Fe distended distally (max:min width ~1.6:1), Pa-Ta short, Pa-Ta length:Pa-Ti length ~1:1.6 (Fig. 13C). Pa article lengths in Table 5.

OVIPOSITOR. Rec sem with 5 lobate, tubular-saccular vesicles (Fig. 11D).

LEGS. Leg article lengths in Tables 5–6.

Remarks

We did not examine the original type material; for the current description, we used other specimens from the type location. Rec sem were found much different from the other taxa within the *N. b.* complex.

Distribution

Austria, endemite of eastern Central Alps (Gruber & Martens 1968; Martens 1978; Komposch 1999, 2009). Vertical distribution: 1325–2240 m a.s.l. (Komposch 1999, 2009). Type locality: Großes Kar, near the Tappenkarsee Lake, Kleinartal, Salzburg (47.19° N, 13.32° E, 1760 m a.s.l.), Radstädter Tauern Mts, Austria.

Ecology

Nemastoma relictum stat. nov. is a montane to alpine species within the *N. b.* complex inhabiting forests below the krummholz zone, alpine meadows, spring-areas, and gravel and block heaps in the eastern Central Alps (Gruber & Martens 1968; Martens 1978; Komposch 1999, 2009) in 1325–2240 m a.s.l. (Komposch 1999). Phenology: evidence of adults from the end of May till the end of October, but probably eurychronous.

Nemastoma pluridentatum (Hadži, 1973) stat. nov. Novak

Figs 2, 4D, 5D, 6D, 9D, 10D, 12D; Table 7

Nemastoma (Lugubrostoma) triste pluridentatum Hadži, 1973a: 43, fig 33a (original description) [partim; the description also includes *N. bidentatum schmidti* ssp. nov., *N. bidentatum gruberi* ssp. nov. × *N. bidentatum schmidti* ssp. nov. and *N. bidentatum martensi* ssp. nov. × *N. bidentatum schmidti* ssp. nov.].

Nemastoma bidentatum bidentatum – Martens 1978: 107.

Nemastoma ?bidentatum pluridentatum – Novak 2005a: 314, fig. 34.

Nemastoma bidentatum pluridentatum – Schönhöfer 2013: 36.

Diagnosis (partly according to Hadži 1973a)

Robust, short-legged member of the *Nemastoma b.* complex, with extremely stout Ch and Pa. Ch-Apo small, slightly trapezoid button-like, wider than high, with secretion field in frontal third. Pa-Tr nearly round, Pa-Fe and Pa-Pt very stout, Pa-Fe club-shaped, with 4 large, wide humps.

Material examined

Holotype

BOSNIA AND HERZEGOVINA – YK10 • 1 ♂; Mt. Paljenik, Vlašić planina Mts; 1933 m a.s.l.; 18 Jun. 1962; E. Pretner leg. (4/2005, JH's microscopic preparation); PMSL. (Note: UTM code in Novak (2005a) was erroneously cited as YJ19.)

Partial redescription

Note: male body and penis missing; female unknown.

Male (holotype)

CHELICERAE. Ch basal article length (without Apo) 0.57, stout, 1.8 times as long as wide at Ch max width at dorsal hump, distally rounded. Ch-Apo rounded low trapezoid, with longest margin distally, secretion field frontally. Distal article length 0.57, max width 0.26, movable finger length 0.28 (Figs 4D, 6D, 9D).

PEDIPALPS. Pa stout, Pa-Fe extremely stout, with 4 large, bulky humps (instead of spines), club-shaped (Pa-Fe min:max width ~1:3.6), Pa-Pt extremely stout (length:max width ~1:2.8) (Figs 5D, 6D). Pa article lengths in Table 7.

Table 7. Length of appendage-segments in millimeters in *N. pluridentatum* (Hadži, 1973) stat. nov. from Mt. Paljenik, Bosnia and Herzegovina: ♂ holotype, ♀ unknown.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.27	0.68	0.49	0.38	—	0.29	2.11
Leg I	0.19	0.60	0.31	0.41	0.50	0.49	2.50
Leg II	0.22	1.05	0.28	1.25	1.05	0.80	4.65
Leg III	0.21	0.70	0.25	0.50	0.65	0.65	3.16
Leg IV	0.22	0.95	0.25	0.60	1.20	0.75	3.95

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–2–1–2. Tarsomere formula I–IV: 8–13–5–8. Leg article lengths in Table 7.

Remarks

Under the name *Nemastoma (Lugubrostoma) triste pluridentatum*, Hadži (1973a) described four taxa: a) *N. pluridentatum* (Hadži, 1973) stat. nov. (Hadži 1973a: fig. 33a) from Mt. Paljenik (1943 m a.s.l.) in the Vlašić Mts, Bosnia, b) a hybrid *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. (Hadži 1973a: fig. 33b, č) from the surroundings of Novo mesto, Slovenia, c) a hybrid *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov. (Hadži 1973a: fig. 33c) from the surroundings of Novo mesto, which Hadži (ibid.) erroneously cited for Mt. Vlašić, and d) *Nemastoma b. schmidti* ssp. nov. from Mt. Šmarca gora, Slovenia (Hadži 1973a: fig. 34a), from the surroundings of Ljubljana (Hadži 1973a: fig. 34b), and from the cave Jama Sv. Janeza pri Prestranku near Postojna, Slovenia (Hadži 1973a: fig. 34c). Figs 33 and 34 were drawn freehand; consequently, shapes and dimensions only partly correspond to the real measurements. Hadži's original microscopic preparation labeled “*Nemastoma bidentatum* Roewer pulli, A-1065 (Novo Mesto), legit Karaman” includes two males and a female, but no juveniles. Hadži (ibid.) drew some details of the males, including damaged legs; see remarks on *Nemastoma (Stridulostoma) seliskari* Hadži, 1973 under *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov. Given that some important parts, e.g., Pa of one male, are missing, Hadži probably made this incomplete preparation after observation of the specimens under a microscope. In his original paper (Hadži 1973a), the type specimen and the type locality of *N. pluridentatum* stat. nov. were not designated, but he did that in the catalogue (Hadži 1973b: 13) under a mistyped name: “*N. (L.) triste pleuridentatum* Hadži, 1973”. There he wrote: “Loc. typ.: Novo mesto”. Since the specimens from this locality belong to the above-mentioned hybrids, Novo mesto cannot be the type locality of *N. pluridentatum* stat. nov.; that is the first-mentioned location in Bosnia, as fig. 33a (Hadži 1973a) is the only drawing that refers to this taxon. Unfortunately, only the preparation of one Ch, one Pa and four legs of the male holotype are preserved, while the body, as well as a further male and female mentioned by Hadži (1973a: 44) are missing. Because of the lack of any information on the Pe, the saw on Fe IV in preserved legs is the only available character allowing us to place this taxon into the *N. b.* complex, interpreted as *N. ?bidentatum pluridentatum* (Novak 2005a: fig. 34) or *N. b. pluridentatum* (Schönhofen 2013). In 2019, we visited the type locality Mt. Paljenik, but we did not find further specimens of *N. pluridentatum*. Instead we found a new, much different *N. kozari* sp. nov. there, which unlikely hybridize with *N. pluridentatum* stat. nov. Consequently, we ascribed the species status to *N. pluridentatum*. See remarks under *N. relictum* stat. nov., *N. kozari* sp. nov. and hybrids *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. and *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.

Distribution

Bosnia and Herzegovina, endemic to central Bosnia, probably endemic to the Vlašić Mts. Type locality: Mt. Paljenik in the Vlašić planina Mts, Bosnia, (44.29° N, 17.64° E, 1933 m a.s.l.), Bosnia and Herzegovina.

Ecology

Nemastoma pluridentatum stat. nov. inhabit the highest peak areas with the Mastgrass *Gentianello crispatae-Nardetum strictae* Redžić 1990 communities. Phenology: adults probably eurychronous.

Nemastoma bidentatum gruberi Novak, Slana Novak, Kozel & Raspotnig ssp. nov.

urn:lsid:zoobank.org:act:17EA28A1-5F36-4DFC-9191-9C8680496FAC

Figs 1A, C, 2–3, 4E, 5E, 6E, 7E, 8E, 9E, 10E, 11E, 12E, 13D; Table 8

Nemastoma bidentatum sparsum – Novak *et al.* 2002: 136 [partim: Brežice, Črnomelj, Kočevje, Krško, Litija, Metlika, Novo mesto, Ribnica, Sevnica, Trebnje]. — Novak 2004b: 245 [partim: Buje, Karojba, Vižinada]; 2005b: 105.

Diagnosis

Relatively long-legged subspecies of *Nemastoma bidentatum*, with strait Ch ventral margin, and Pa-Fe with either 4 subequidistantly positioned spines or pointed tubercles or long setae on low protrusions, or their combination in the distal Pa-Fe half, or alternatively, with 2–3 distal stout thorns. Rec sem with one tubular and 12 elongated balloon-like vesicles.

Etymology

The subspecies name ‘*gruberi*’ is dedicated to Jürgen Gruber (Vienna), our teacher, colleague and friend, who generously introduced us to the taxonomy of harvestmen and helped in identifying problematic specimens.

Material examined

Holotype

SLOVENIA – **WL18** • 1 ♂; Dolenje Laknice, Mokronog; 45.93° N, 15.21° E; 237 m a.s.l.; 26 Oct. 2013; L. Slana Novak and T. Novak leg.; mixed forest litter sift; PMSL-Opiliones-GR 4661.

Paratypes

SLOVENIA – **WL18** • 1 ♀; same collection data as for holotype; PMSL-Opiliones-GR 4664 • 5 ♂♂, 4 ♀♀; same collection data as for holotype; PMSL-Opiliones-GR4662, GR4666, GR4667, GR4669, GR4673, GR4676 to GR4679.

Other material

ITALY – **VL05** • 1 ♀; Chiusa/Ricmanje; 29 Sep. 1999; L. Slana Novak and T. Novak leg. (275/1999, rev. 2015); PMSL. – **VL15** • 1 ♀; Basovizza/Bazovica; 29 Sep. 1999; L. Slana Novak and T. Novak leg. (271/1999, rev. 2015); PMSL.

CROATIA – **UL92** • 3 ♂♂, 2 ♀♀ (paratypes of *N. b. sparsum*); vicinity of Buje, and VL02, Vižinada; Sep. 1963; R. Sturany leg.; NHMW 4700. – **VL01** • 1 ♂; Karojba; 28 Feb. 1990; F. Potočnik leg. (1307/1998, rev. 2018); PMSL. – **VL13** • 1 ♀; Mlini; 30 Sep. 1990; L. Slana Novak and T. Novak leg. (32/1990, rev. 2015); PMSL. – **XL90** • 1 ♂, 2 ♀♀; Ponor Sušik, Drežnik; 8 Sep. 2009; A. Schönhofner leg. (Coll. ASc 334, ASc det., TN rev. 5/2012); PMSL.

SLOVENIA – **UL93** • 4 ♀♀, 1 juv.; Abrami; 19 Jul. 1999; L. Slana Novak and T. Novak leg. (148/1999, rev. 2018); PMSL • 2 ♀♀; ibid.; 20 Jul. 1999; L. Slana Novak and T. Novak leg. (188/1999, rev. 2015); PMSL • 1 ♀; Dragonja; 14 Sep. 2000; L. Slana Novak and T. Novak leg. (154/2001, rev. 2015); PMSL • 4 ♂♂, 4 ♀♀; Dragonja valley; 26 Jun. 2015; T. Novak leg. (78/2015 = GR 5123–5130); PMSL • 2 ♂♂, 3 ♀♀; Ivankovec; 23 Sep. 1998; L. Slana Novak and T. Novak leg. (1791/1998, rev. 2018); PMSL • 1 ♀;

Lucija–Seča – Debernardo; 22 Sep. 1998; L. Slana Novak and T. Novak leg. (1817/1998, rev. 2019); PMSL • 1 ♂; Korte; 23 Sep. 1998; L. Slana Novak and T. Novak leg. (1821/1998, rev. 2018); PMSL • 33 ♂♂, 30 ♀♀; Medljan, Korte; 21 Aug. 1999; T. Novak leg. (239/1999, rev. 2018); PMSL • 1 juv.; ibid.; 22 Jun. 2000; B. Bertoncelj, B. Ogrizek and T. Novak leg. (217/2000, rev. 2018); PMSL • 1 ♀; ibid.; (218/2000, TN rev. 2019); PMSL • 1 ♂; Padna; 19 Jul. 1999; L. Slana Novak and T. Novak leg. (168/1999, rev. 2017); PMSL • 2 ♀♀; Parecag; 23 Sep. 1998; L. Slana Novak and T. Novak leg. (1788/1998, rev. 2018); PMSL • 1 ♀; Seča; 10 Oct. 1998; L. Slana Novak and T. Novak leg. (1844/1998, rev. 2008); PMSL • 1 ♂, 1 ♀; ibid.; 24 Oct. 1998, L. Slana Novak and T. Novak leg. (1881/1998, rev. 2007); PMSL • 3 ♀♀; ibid.; 21 Aug. 1999; M. Štangelj and T. Novak leg. (236/1999, rev. 2008); PMSL • 15 ♂♂, 21 ♀♀; ibid.; 21 Aug. 1999; M. Štangelj and T. Novak leg. (231/1999, rev. 2015); PMSL • 1 ♂, 6 ♀♀; Sečovlje; 1 Mar. 2009; L. Slana Novak and T. Novak leg. (1/2015); PMSL • 1 ♂; Sv. Peter; 11 Oct. 1998; L. Slana Novak and T. Novak leg. (1850/1998, rev. 2015); PMSL • 4 ♂♂, 2 ♀♀; Sv. Sab, Padna; 19 Jul. 1999; L. Slana Novak and T. Novak leg. (151/1999, rev. 2009); PMSL • 1 ♀; Škrline, Dragonja; 20 Jul. 1999; L. Slana Novak and T. Novak leg. (194/1999, rev. 2015); PMSL. – **VL03** • 2 ♂♂, 1 ♀; Boršt; 14 Apr. 2011; T. Novak leg. (76/2011, rev. 2015); PMSL • 2 ♀♀; ibid.; (81/2011, rev. 2015); PMSL. – **VL04** • 1 ♀; Ankaran; 29 Sep. 1999; L. Slana Novak and T. Novak leg. (276/1999, rev. 2015); PMSL • 1 ♂, 1 ♀; Kolombini, Spodnje Škofije; 26 Sep. 2007; L. Slana Novak and T. Novak leg. (94/2007, rev. 2018); PMSL • 5 ♂♂; Mlinarji – Osp; 26 Sep. 2007; L. Slana Novak and T. Novak leg. (97/2007, rev. 2017); PMSL • 1 ♂, 1 ♀; Rižana; 24 Sep. 2016; L. Slana Novak and T. Novak leg. (18/2018); PMSL • 1 ♀; Škocjanski zatok, Koper; 15 Oct. 2009; S. Polak leg. (PK 1/2015); NM • 4 ♂♂, 3 ♀♀; Zgornje Škofije – Tinjan; 26 Sep. 2007; L. Slana Novak and T. Novak leg. (88/2007); PMSL. – **VL07** • 4 ♀♀; Hrastje, Šmarje; 17 Aug. 2000 (674/2000, rev. 2015); PMSL. – **VL13** • 1 ♂; Poletiči, Kubed; 4 Sep. 2016; T. Marinko leg. (27/2016); PMSL • 1 ♂, 1 ♀; Sočerga; 28 Sep. 1990; L. Slana Novak and T. Novak leg. (31/1990, rev. 2015); PMSL. – **VL14** • 4 ♂♂, 4 ♀♀; Bezovica; 29 Sep. 1990; L. Slana Novak and T. Novak leg. (LSN 1/1990, TN rev. 2018); PMSL • 1 ♂; Hrpelje, Kozina; 2 Apr. 1993; S. Brelih leg. (651/1998, rev. 2018); PMSL • 2 ♂♂; Predloka; 29 Sep. 1990; L. Slana Novak and T. Novak leg. (35/1990, rev. 2015); PMSL • 2 ♂♂, 1 ♀; Rižana; 29 Sep. 1990; L. Slana Novak and T. Novak leg. (33/1990, rev. 2015); PMSL. – **VL15** • 1 ♀; Botač; 22 Mar. 1990; M. Černila, B. Horvat and I. Sivec leg. (1246/1997); PMSL. – **VL16** • 1 ♂; Divača; 2 Apr. 1993; S. Brelih leg. (174/2001, rev. 2015); PMSL. – **VL17** • 1 ♂; Vrabče, Podnanos; 10 Mar. 1994; S. Brelih leg. (632/1998, rev. 2017); PMSL. – **VL18** • 1 ♂; Uhanje; 3 Sep. 2001; T. Novak leg. (329/2001, rev. 2018); PMSL. – **VL23** • 1 ♂, 1 ♀; Poljane pri Podgradu; 18 Aug. 2011; L. Slana Novak and T. Novak leg. (166/2012, rev. 2019); PMSL. – **VL25** • 3 ♀♀; Buje; 10 Mar. 1994; S. Brelih leg. (163/2001, rev. 2018); PMSL • 1 ♂, 2 ♀♀; Goriče pri Framljah; L. Slana Novak and T. Novak leg. (343/2011); PMSL • 1 ♀; ibid.; (344/2011); PMSL. – **VL28** • 1 ♂, 1 ♀; Podvrh, Raka; 18 Jul. 2012; P. Kozel, T. Kozel and T. Novak leg. (55/2012); PMSL • 9 ♂♂, 7 ♀♀; ibid.; (GR 3734–3746); PMSL • 3 ♀♀; ibid.; (GR 3791); PMSL. – **VL29** • 6 ♂♂, 12 ♀♀; Dolnje Brezovo, Sevnica; 30 Jun. 2012; (GR 3670–3683); PMSL. – **VL36** • 1 ♂, 1 ♀; Palče – Mt. Javorniki; 1 Oct. 2011; L. Slana Novak and T. Novak leg. (361/2011, rev. 2019); PMSL. – **VL45** • 1 ♀; Koritnice – Mašun; 2 Oct. 2011; L. Slana Novak and T. Novak leg. (329/2011, rev. 2014); PMSL. – **VL47** • 1 ♀; Suha reber, Koritnice; 21 Jan. 2007; S. Polak leg. (107/2007); NM. – **VL54** • 1 ♀; Svičaki; 20 May 1989; T. Trilar leg. (271/2000, rev. 2017); PMSL • 1 ♀; ibid.; 25 May 1989; T. Trilar leg. (275/2000, rev. 2017); PMSL • 1 ♀; ibid.; 21 Jul. 2001; B. Bertoncelj, U. Bertoncelj and T. Novak leg. (29/2001, rev. 2018); PMSL • 1 ♀; ibid.; (34/2001, rev. 2011); PMSL • 1 ♂, 3 ♀♀; Travni Dolci, Mt. Snežnik; 12 Aug. 2001; L. Slana Novak and T. Novak leg. (195a/2001, rev. 2020); PMSL • 2 ♂♂, 4 ♀♀; Mt. Veliki Snežnik; 20 Jul. 1999; L. Slana Novak and T. Novak leg. (185a/1999, rev. 2020); PMSL • 1 ♂; ibid.; 12 Sep. 2018; L. Slana Novak and T. Novak leg. (116/2018); PMSL. – **VL36** • 1 ♂, 1 ♀; Palče – Javorniki; L. Slana Novak and T. Novak leg. (361/2011, rev. 2015); PMSL. – **VL66** • 1 ♀; Benete, Runarsko; 31 May 2004; L. Slana Novak and T. Novak leg. (33/2004, rev. 2015); PMSL. – **VL67** • 5 ♂♂, 3 ♀♀; Nova vas – Volče; 26 Sep. 2006; L. Slana Novak and T. Novak leg. (25/2006, rev. 2019); PMSL • 1 ♂; Runarsko; 26 Sep. 2006; L. Slana Novak and T. Novak leg. (38/2006, rev. 2015); PMSL • 1 ♂, 1 ♀; Veliki vrh, Runarsko; 26 Sep. 2006;

L. Slana Novak and T. Novak leg. (36/2006, rev. 2015); PMSL • 7 ♂♂, 5 ♀♀; Volčje; 26 Sep. 2006; L. Slana Novak and T. Novak leg. (28/2006, rev. 2015); PMSL. – **VL69** • 1 ♂; Veliki vrh pri Šmarju; 10 May 2008; L. Slana Novak and T. Novak leg. (156/2011); PMSL. – **VL74** • 1 ♂, 1 ♀; Mt. Goteniški Snežnik; 28 May 2000; L. Slana Novak and T. Novak leg. (247/2000, rev. 2007); PMSL • 1 ♀; Strma reber, Zgornji Čačiči; 27 Sep. 1996; L. Slana Novak and T. Novak leg. (LSN 126/1996, TN rev. 2008); PMSL. – **VL75** • 2 ♂♂; Draga; 17 Aug. 2011; L. Slana Novak and T. Novak leg. (94/2011); PMSL • 1 ♂, 2 ♀♀; Mt. Goteniški Snežnik; 28 May 2000; L. Slana Novak and T. Novak leg. (253/2000, rev. 2007); PMSL. – **VL76** • 1 ♂; Bukovica, Ribnica; Jul. 1994; B. Oven leg. (LSN 25/1996, TN rev. 2009); PMSL • 2 ♂♂, 1 ♀; Lipovšica, Sodražica; 22 Aug. 2011; L. Slana Novak and T. Novak leg. (100/2011, rev. 2018); PMSL • 1 ♂; Nova Štifta; 22 Aug. 2011; L. Slana Novak and T. Novak leg. (105/2011); PMSL • 2 ♂♂, 3 ♀♀; Ribnica; 6 Sep. 2000; M. Mlakar leg. (828/2000, rev. 2008); PMSL • 1 ♂, 2 ♀♀; ibid.; (831/2000, rev. 2019); PMSL • 1 ♀; Mt. Turn; 27 Jun. 1980; B. Drovenik leg. (383/2002, rev. 2018); PMSL • 1 ♂; ibid.; 28 Aug. 1980; B. Drovenik leg. (394/2002, rev. 2009); PMSL. – **VL77** • 1 ♂; Dolnje Retje; 3 May 2008; L. Slana Novak and T. Novak leg. (161/2011); PMSL • 1 ♀; Rašica, Velike Lašče; 16 Jun. 1986 (261/2002, rev. 2015); PMSL • 1 ♂, 1 ♀; Velike Poljane, Ortnek; 3 May 2008; L. Slana Novak and T. Novak leg. (142/2011, rev. 2019); PMSL. – **VL78** • 1 ♂; Laporje; 3 May 2008; L. Slana Novak and T. Novak leg. (151/2011); PMSL • 1 ♀; Zagradec pri Grosupljem; 7 Jul. 1986; L. Slana Novak and T. Novak leg. (500/2002, rev. 2015); PMSL. – **VL79** • 1 ♀; Veliki Lipoglav – Dobrinje; 8 Jul. 1986; L. Slana Novak and T. Novak leg. (467/2002, rev. 2015); PMSL. – **VL83** • 2 ♂♂; Vršič, Banjaloka; 24 Apr. 2001; S. Brelih leg. (121/2001, rev. 2019); PMSL. – **VL84** • 1 ♂; Jelenja vas; 3 May 2008; L. Slana Novak and T. Novak leg. (137a/2011); PMSL • 1 ♂; ibid.; (153/2011); PMSL • 1 ♂; Pleš, Borovec pri Kočevski Reki; 19 Sep. 2013; P. Kozel and T. Novak leg. (71/2013, rev. 2018); PMSL. – **VL85** • 1 ♀; Grčarice; 18 Oct. 2013; T. Novak leg. (63/2013, rev. 2015); PMSL • 1 ♂, 2 ♀♀; Grčarske Ravne; 18 Oct. 2013; T. Novak leg. (66/2013, TN rev. 2019); PMSL • 3 ♀♀; Kočevje; 6 Sep. 2000; M. Mlakar leg. (822/2000, rev. 2008); PMSL • 1 ♂, 1 ♀; ibid.; (825/2000, rev. 2007); PMSL • 2 ♂♂, 1 ♀; Mt. Stojna, Kočevje; 25 Oct. 1996; S. Brelih leg. (92/2001, rev. 2008); PMSL. – **VL86** • 1 ♀; Dolenja vas; 3 May 2008; L. Slana Novak and T. Novak leg. (110/2011); PMSL • 1 ♂, 1 ♀; ibid.; (154/2012, rev. 2018); PMSL. – **VL87** • 1 ♂; Breg pri Zagradcu; 4 Nov. 1993; S. Brelih leg. (805/1998, rev. 2007); PMSL. – **VL89** • 1 ♀; Potok, Stična; 4 Mar. 1994; S. Brelih leg. (658/1998, rev. 2015); PMSL. – **VL93** • 1 ♂; Brsnik, Fara; 3 May 2008; L. Slana Novak and T. Novak leg. (157/2011, rev. 2018); PMSL. – **VL94** • 1 ♂, 1 ♀; Dolenja Žaga; 29 Apr. 2001; S. Brelih leg. (131/2001, rev. 2015); PMSL • 1 ♀; Dolenja Žaga – Podstene; 26 Jun. 1999; L. Slana Novak and T. Novak leg. (90/1999, rev. 2008); PMSL • 1 ♂, 1 ♀; Gorenja Žaga; 3 May 2008; L. Slana Novak and T. Novak leg. (111a/2011); PMSL • 1 ♂, 1 ♀; ibid.; (159/2011); PMSL • 1 ♀; Ograja; 3 May 2008; L. Slana Novak and T. Novak leg. (109a/2011); PMSL • 1 ♀; ibid.; (121a/2011); PMSL • 1 ♀; ibid.; (144/2011); PMSL • 1 ♀; ibid.; (148/2011); PMSL • 1 ♂, 1 ♀; Ograja – Suhor – Morava; 3 May 2008; L. Slana Novak and T. Novak leg. (120a/2011); PMSL • 1 ♂, 1 ♀; ibid.; (138a/2011); PMSL • 1 ♂, 1 ♀; ibid.; (152/2011); PMSL • 1 ♂; Ograja – Zdihovo; 26 Jun. 1999; L. Slana Novak and T. Novak leg. (76/1999, rev. 2008); PMSL • 3 juvs; ibid.; 12 Jun. 1999; L. Slana Novak and T. Novak leg. (32/1999, rev. 2008); PMSL • 2 juvs; Podstene pri Kostelu; 12 Jun. 1999; L. Slana Novak and T. Novak leg. (24/1999, rev. 2008); PMSL • 1 ♂; Rajndol; 21 Mar. 1994; S. Brelih leg. (821/1998, rev. 2008); PMSL • 5 ♂♂, 3 ♀♀; Srednji Potok, Banja Loka; 8 Oct. 2012; P. Kozel and T. Novak leg. (68/2015); PMSL • 1 ♂, 1 ♀, 2 juvs; Štalcerski preval; 12 Jun. 1999; L. Slana Novak and T. Novak leg. (33/1999, rev. 2008); PMSL. – **VL95** • 1 ♂, 2 ♀♀; Dolga vas; 17 Aug. 1985; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 97/1986, TN rev. 2007); PMSL • 1 ♂, 1 ♀; Livold; 3 May 2008; L. Slana Novak and T. Novak leg. (123a/2011); PMSL • 1 ♂, 1 ♀; ibid.; (158/2011); PMSL. – **VL97** • 1 ♀; Dvor, Lašče; 10 May 2008; L. Slana Novak and T. Novak leg. (112/2011); PMSL • 1 ♂, 2 ♀♀; Železno, Dobrnič; 4 Nov. 1993; S. Brelih leg. (812/1998, rev. 2007); PMSL. – **VL99** • 3 ♀♀; Nova gora, Čatež; 15 Aug. 2007; L. Slana Novak and T. Novak leg. (61/2007, rev. 2015); PMSL. – **VM80** • 1 ♂; Litija; 10 Sep. 2000; M. Mlakar leg. (809/2000, rev. 2008); PMSL • 1 ♂, 1 ♀; ibid.; (834/2000, rev. 2015); PMSL. – **WL03** • 2 ♂♂; Dolenje Kozice; 18 Apr.–13 May 2002; B. Drovenik and A. Gergeli leg.

(509/2018); PMSL • 1 ♂; ibid.; 18 Apr.–13 May 2002; B. Drozenik and A. Gergeli leg. (550/2018); PMSL • 1 ♂; ibid.; 5 Jul. 2002; B. Drozenik and A. Pirnat leg. (1135/2018); PMSL • 1 ♀; ibid.; 6 Aug. 2002; B. Drozenik and A. Pirnat leg. (1090/2018); PMSL • 1 ♀; ibid.; 30 Sep.–28 Oct. 2002; B. Drozenik and A. Gergeli leg. (PK 64/2012); PMSL • 1 ♀; ibid.; 25 Nov. 2002; B. Drozenik and A. Pirnat leg. (270/2018); PMSL • 2 ♀♀; ibid.; 25 Nov.–23 Dec. 2002; B. Drozenik and A. Gergeli leg. (1027/2018); PMSL • 4 ♂♂, 5 ♀♀; Srednji Radenci; 17 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 51/1986, rev. 2008); PMSL • 3 ♂♂, 4 ♀♀; Stari trg ob Kolpi; 21 Mar. 1994; S. Brelih leg. (851/1998, rev. 2008); PMSL • 5 ♂♂, 5 ♀♀; Dolenji Radenci – Breg pri Sinjem vrhu; 3 May 2008; L. Slana Novak and T. Novak leg. (135a/2011); PMSL • 5 ♂♂, 2 ♀♀; ibid.; (149/2011); PMSL. – **WL05** • 1 ♂, 3 ♀♀, 1 juv.; Črmošnjice; 16 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (160/1997); PMSL • 1 ♀; Koprivnik, Kočevski Rog; 21 Mar. 1994; S. Brelih leg. (867/1998, rev. 2008); PMSL • 1 ♂, 2 ♀♀; Mt. Mirna gora; 8 Oct. 2012; P. Kozel and T. Novak leg. (59/2015); PMSL • 4 ♂♂, 4 ♀♀; ibid.; 8 Oct. 2012; P. Kozel and T. Novak leg. (66/2015); PMSL. – **WL06** • 1 ♂; Cerovec – Selišče, Podturn pri Dolenjskih toplicah; 10 May 2008; L. Slana Novak and T. Novak leg. (145/2011, rev. 2017); PMSL. – **WL07** • 1 ♂; Boršt pri Dvoru; 10 May 2008; L. Slana Novak and T. Novak leg. (113/2012); PMSL • 1 ♀; Prečna, Mirna; Jun. 2000; V. Jaćimović leg. (PK and TN 100/2020); PMSL. – **WL08** • 1 ♂; Rdeči kal, Dobrnič; 4 Nov. 1993; S. Brelih leg. (872/1998, rev. 2007); PMSL • 1 ♂, 1 ♀; Trebnje; 29 Aug. 2000; M. Mlakar leg. (787/2000, rev. 2018); PMSL • 1 ♂; ibid.; (787a/2000, rev. 2018); PMSL • 1 ♀; ibid.; (788/2000, rev. 2008); PMSL. – **WL13** • 4 ♀♀; Balkovci, Vinica; 15 Aug. 1999; M. Štangelj and T. Novak leg. (212/1999, rev. 2008); PMSL • 2 ♂♂, 2 ♀♀; Dolenji Radenci – Breg pri Sinjem vrhu; 3 May 2008; L. Slana Novak and T. Novak leg. (146/2011); PMSL • 4 ♂♂, 1 ♀; Kot pri Dramlju; 16 Aug. 1999; M. Štangelj and T. Novak leg. (207/1999, rev. 2015); PMSL • 3 ♂♂, 2 ♀♀; Špeharji, Vinica; 16 Aug. 1999; M. Štangelj and T. Novak leg. (201/1999, rev. 2006); PMSL • 6 ♂♂, 5 ♀♀; Vinica – Sinji vrh; 17 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 59/1986, TN rev. 2007); PMSL • 2 ♂♂; Vukovci; 18 Apr. 1996; S. Brelih leg. (764/1998, rev. 2007); PMSL. – **WL14** • 1 ♂, 1 ♀; Bistrica, Črnomelj; 26 Jun. 1999; L. Slana Novak and T. Novak leg. (65/1999, rev. 2017); PMSL • 1 ♀; Črnomelj; 15 Aug. 1999; M. Štangelj and T. Novak leg. (221/1999, rev. 2008); PMSL • 3 ♂♂, 3 ♀♀, 2 juvs; Desinec – Črnomelj; 17 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (385/1998, rev. 2007); PMSL • 2 ♂♂, 2 ♀♀; Tanča gora; 21 Mar. 1994; S. Brelih leg. (861/1998, rev. 2015); PMSL • 5 ♂♂, 2 ♀♀; Sinji vrh, Vinica; 16 Aug. 1999; M. Štangelj and T. Novak leg. (205/1999, rev. 2007); PMSL. – **WL15** • 1 ♀; Krupa spring; 10 Mar. 1994; S. Brelih leg. (808/1998, rev. 2007); PMSL • 6 ♂♂, 3 ♀♀, 3 juvs; Lokve, Črnomelj; 2 Jul. 1995; L. Slana Novak and T. Novak leg. (105/1997, rev. 2009); PMSL • 3 ♂♂, 2 ♀♀; Mihelja vas; 18 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 55/1986, TN rev. 2017); PMSL • 1 ♀; Praprot; 6 Aug. 1997; T. Novak leg. (418/1998, rev. 2008); PMSL • 1 ♀; ibid.; (432/1998, rev. 2008); PMSL • 1 ♀; ibid.; 22 Jul. 1999; L. Slana Novak and T. Novak leg. (37/1999, rev. 2008); PMSL • 1 ♀; ibid.; (110/1999, rev. 2008); PMSL • 2 ♂♂, 2 ♀♀; Stranska vas; 22 Jul. 1999; L. Slana Novak and T. Novak leg. (108/1999, rev. 2007); PMSL • 2 ♂♂, 1 ♀; Vrčice; 10 May 2008; L. Slana Novak and T. Novak leg. (110/2012); PMSL • 1 ♂, 3 ♀♀; Vrčice – Semič; 8 Oct. 2012; P. Kozel and T. Novak leg. (64/2015); PMSL. – **WL16** • 2 ♀♀; Laze, Uršna Sela; 10 May 2008; L. Slana Novak and T. Novak leg. (103/2012, rev. 2015); PMSL • 1 ♀; ibid.; (108/2012, rev. 2018); PMSL. – **WL17** • 1 ♂, 1 ♀; Brod, Novo Mesto; 31 Aug. 2000; M. Mlakar leg. (811/2000, rev. 2007); PMSL • 1 ♂; Novo mesto; Karaman leg. (87/1983 microscopic preparation, JH det., TN rev. 2011); PMSL • 1 ♂, 1 ♀; ibid.; Karaman leg. (108/1983 microscopic preparation, JH det., TN rev. 2011); PMSL • 1 ♀; ibid.; (814/2000); PMSL • 1 ♂; ibid.; (153/2018 microscopic preparation, JH det., TN rev. 2018); PMSL • 1 ♀, 1 ♀; ibid.; 31 Aug. 2000; M. Mlakar leg. (811/2000, rev. 2007); PMSL • 1 ♂, 2 ♀♀; Ratež; 29 Apr. 1995; S. Brelih leg. (750/1998, rev. 2007); PMSL. – **WL18** • 6 ♂♂, 5 ♀♀; Dolenje Laknice; 26 Oct. 2013; T. Novak leg. (GR 4661, 4662, 4664, 4666, 4667, 4669, 4673, 4676, 4677–4679); PMSL. – **WL19** • 1 ♀; Boštanj – Mokronog – Križ; L. Slana Novak and T. Novak leg. (70/2007, rev. 2011); PMSL • 1 ♂; Jelovec; 15 Aug. 2007; L. Slana Novak and T. Novak leg. (56/2007); PMSL. – **WL23** • 1 ♂; Zilje; 18 Apr. 1996; S. Brelih leg. (767/1998, rev. 2007); PMSL • 1 ♂, 2 ♀♀; Zilje – Vinica; 17 Aug. 1985; L. Slana Novak,

M. Slana Novak and T. Novak leg. (364/1998, rev. 2007); PMSL. – **WL24** • 5 ♂♂, 1 ♀, 1 juv.; Gorenjci pri Adlešičih; 15 Aug. 1999; M. Štangelj and T. Novak leg. (218/1999, rev. 2007); PMSL • 1 ♂; Dragoši, Griblje; 18 Apr. 1994; S. Brelih leg. (733/1998, rev. 2007); PMSL • 4 ♂♂, 2 ♀♀; Griblje – Desinec; 16 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (161/1997, rev. 2009); PMSL. – **WL25** • 1 ♂; Bečka jama cave, Cad. No. 6275, Boldraž; 9 Jun. 2004; V. Germovšek, T. Tkavc, A. Kocuvan and T. Novak leg. (21/2004, rev. 2007); PMSL • 1 ♂; Božakovo; 3 May 2004; L. Slana Novak and T. Novak leg. (48/2004, rev. 2007); PMSL • 2 ♂♂, 3 ♀♀; Bušinja vas; 18 Apr. 1996; S. Brelih leg. (743/1998, rev. 2007); PMSL • 1 ♂, 4 ♀♀; Kapljišče; 16 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 113/1986, TN rev. 2007); PMSL • 2 ♂♂, 1 juv.; ibid. (LSN 119/1986, TN rev. 2007); PMSL • 3 ♀♀; Metlika; 31 Aug. 2000; M. Mlakar leg. (816/2000, rev. 2007); PMSL • 1 ♂; ibid.; (818/2000, rev. 2015); PMSL • 7 ♂♂, 9 ♀♀; Trnovec, Metlika; 23 Jul. 1999; L. Slana Novak and T. Novak leg. (141/1999, rev. 2008); PMSL • 1 ♂, 2 ♀♀; Sv. Urban, Metlika; 18 Apr. 1996; S. Brelih leg. (784/1998, rev. 2007); PMSL. – **WL26** • 1 ♂; Krašnji vrh; 9 Jun. 2004; V. Germovšek, T. Tkavc, A. Kocuvan and T. Novak leg. (37/2004, rev. 2007); PMSL • 1 ♂; Markučev Mlin, Krašnji vrh; 1 Jul. 2007; L. Slana Novak and T. Novak leg. (21/2007); PMSL • 4 ♀♀; ibid.; (17/2007, rev. 2011); PMSL. – **WL27** • 1 ♂; Gabrje, Novo Mesto; 11 Apr. 1984; I. Sivec leg. (875/1997, rev. 2018); PMSL • 1 ♀; Gabrje – Sv. Miklavž – Krvavi kamen, Gorjanci Mts; 22 Jul. 1999; L. Slana Novak and T. Novak leg. (123/1999, rev. 2019); PMSL • 5 ♂♂, 6 ♀♀; Glažarica, Mt. Gorjanci; 22 Jul. 1999; L. Slana Novak and T. Novak leg. (118/1999, rev. 2015); PMSL • 1 ♂, 1 ♀; ibid.; (134/1999, rev. 2018); PMSL • 1 ♀; Golo, Šentjernej; 29 Apr. 1995; S. Brelih leg. (757/1998, rev. 2007); PMSL • 1 ♀; Sv. Miklavž, Gorjanci Mts; 22 Jul. 1999; L. Slana Novak and T. Novak leg. (128/1999, rev. 2019); PMSL. – **WL28** • 3 ♂♂, 7 ♀♀; Brezje pri Raki; 27 Jul. 2012; S. Samu, P. Kozel and T. Novak leg. (115/2012); PMSL • 1 ♂, 1 ♀; Podvrh, Raka; 18 Jul. 2012; P. Kozel, T. Kozel and T. Novak leg. (55/2012); PMSL • 9 ♂♂, 10 ♀♀; ibid.; (GR 3734–3746, 3791, TN det.); PMSL • 4 ♂♂, 11 ♀♀; Škocjan; 26 Oct. 2013; T. Novak leg. (GR 4680–4694, TN det.); PMSL. – **WL29** • 3 ♂♂, 1 juv.; Boštanj; 5 Jul. 1987; L. Slana Novak, M. Slana Novak and T. Novak leg. (433/1998, rev. 2007); PMSL • 6 ♂♂, 12 ♀♀; Dolnje Brezovo; 30 Jun. 2012; T. Novak leg. (GR 3670–3683, TN det.); PMSL • 1 ♂, 1 ♀; Sevnica; 29 Aug. 2000; M. Mlakar leg. (785/2000, rev. 2009); PMSL. – **WL37** • 1 ♂, 1 ♀; Grič; 29 Apr. 1995; S. Brelih leg. (763/1998, rev. 2008); PMSL • 2 ♂♂, 2 ♀♀; Velike Vodenice – Opatova gora; 15 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (144/1997, rev. 2015); PMSL. – **WL38** • 3 ♀♀; Krakovski gozd, Sajevce; 5 May 1993; S. Brelih leg. (792/1998, rev. 2015); PMSL • 68 ♂♂, 59 ♀♀; Dolenje Radulje – Raški vrh; 5 Sep. 2012; P. Kozel and T. Novak leg. (PK 98/2012); PMSL • 84 ♂♂, 78 ♀♀; ibid.; 17 Sep. 2012; P. Kozel and T. Novak leg. (PK 99/2012); PMSL • 73 ♂♂, 83 ♀♀; ibid.; 4 Oct. 2012; P. Kozel and T. Novak leg. (PK 100/2012); PMSL • 44 ♂♂, 38 ♀♀; ibid.; 29 Apr. 2013; P. Kozel and T. Novak leg. (PK 43/2013); PMSL • 74 ♂♂, 71 ♀; Podulce – Zabukovje pri Raki; 20 Aug. 2012; P. Kozel and T. Novak leg. (PK 96/2012); PMSL. – **WL39** • 1 ♂, 1 ♀; Arto, Brestanica; 18 Nov. 1994; S. Brelih leg. (189/2001, rev. 2017); PMSL • 3 ♂♂, 3 ♀♀; ibid.; 1 Jul. 2007; L. Slana Novak and T. Novak leg. (28/2007); PMSL • 5 ♂♂, 3 ♀♀; Kremen; 12 Oct. 2005; L. Slana Novak and T. Novak leg. (141/2005, rev. 2008); PMSL • 1 ♂; Krško; 11 Apr. 1978 (42/2019); PMSL • 1 ♂, 5 ♀♀; ibid.; (47/2019); PMSL • 2 ♀♀; ibid.; (63/2019); PMSL • 1 ♀; ibid.; M. Mlakar leg. (704/2000, rev. 2008); PMSL • 1 ♂; Stara vas; 24 Aug. 2000; M. Mlakar leg. (709/2000, rev. 2007); PMSL • 2 ♂♂; Stolovnik – Anže; 9 Oct. 2005; L. Slana Novak and T. Novak leg. (134/2005, rev. 2008); PMSL • 5 ♂♂, 7 ♀♀; ibid.; 14 Oct. 2005; L. Slana Novak and T. Novak leg. (154/2005, rev. 2007); PMSL. – **WL48** • 1 ♂; Brežice; 30 Aug. 2000; M. Mlakar leg. (794/2000, rev. 2008); PMSL • 1 ♂; ibid.; 30 Aug. 2000; M. Mlakar leg. (792/2000, rev. 2007); PMSL • 1 ♀; Vitovec, Velike Malence; Jul. 1994; M. Potokar leg. (289/1995, rev. 2008); PMSL. – **WL49** • 6 ♂♂, 1 ♀; Podsreda castle; 17 Jun. 2001; L. Slana Novak and T. Novak leg. (145/2001, rev. 2008); PMSL. – **WL59** • 3 ♂♂, 4 ♀♀; Stara vas; 14 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (141/1997, rev. 2007); PMSL • 1 ♂; ibid.; 24 Aug. 2000; M. Mlakar leg. (709/2000, rev. 2007); PMSL • 1 ♂; ibid.; (714/2000, rev. 2007); PMSL • 1 ♂; ibid.; (716/2000, rev. 2007); PMSL. – **WM01** • 3 ♀♀; Hrastnik; 30 Aug. 2000; M. Mlakar leg. (802/2000, rev. 2018); PMSL • 2 ♀♀; ibid.; (806/2000, rev. 2018); PMSL. – **WM10** • 1 ♂, 1 ♀; Lokavec, Zidani most;

26 May 2004; A. Kapla leg. (56/2004, rev. 2007); PMSL • 2 ♀♀; Radeče; 29 Aug. 2000; M. Mlakar leg. (796/2000, rev. 2015); PMSL • 1 ♀; ibid.; (801/2000, rev. 2015); PMSL. – **WM20** • 1 ♂; Mt. Lisca; 26 May 2004; A. Kapla leg. (54/2004, rev. 2007); PMSL • 1 ♂; ibid.; (62/2004, rev. 2007); PMSL. – **WM30** • 7 ♂♂, 8 ♀♀, 1 juv.; Šentvid pri Planini; 14 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 52/1983, TN rev. 2007); PMSL • 10 ♂♂, 4 ♀♀; Mt. Bohor; 20 Aug. 1994, L. Slana Novak and T. Novak leg. (66/1997, rev. 2008); PMSL • 3 ♂♂, 2 ♀♀; Tovornik, Mt. Bohor; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1134/2002, TN rev. 2007); PMSL • 1 ♂, 1 ♀; ibid.; (1149/2002, rev. 2007); PMSL • 4 ♂♂, 1 ♀; Zgornji Reštanj, Senovo; 20 May 2012; T. Novak leg. (53/2012); PMSL. – **WM40** • 1 ♂; Bistri graben, Kozje; 11 Jul. 2003; T. Novak leg. (160/2003, rev. 2007); PMSL • 2 ♀♀; ibid.; (162/2003, rev. 2018); PMSL • 1 ♂; ibid.; (170/2003, rev. 2007); PMSL • 1 ♂; ibid.; (165/2003, rev. 2007); PMSL • 1 ♂; ibid.; (170/2003, rev. 2007); PMSL • 3 ♂♂, 4 ♀♀, 1 juv.; ibid.; 16 Jun. 2019; L. Slana Novak and T. Novak leg. (6/2019); PMSL • 1 ♂, 1 juv.; ibid.; (11/2019); PMSL • 1 ♀; ibid.; (12/2019); PMSL • 1 ♂, 1 ♀, 1 juv.; ibid.; (13/2019); PMSL • 2 ♂♂, 2 ♀♀; Kozje; 14 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 72/1983, TN rev. 2011); PMSL • 1 ♀; ibid.; 31 Jul. 1995; S. Polak leg. (177/2001, rev. 2015); NM • 1 ♀; ibid.; 1 Aug. 1995; S. Polak leg. (168/2001); NM • 3 ♂♂, 2 ♀♀; ibid.; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1150/2002, rev. 2007); PMSL • 3 ♂♂, 5 ♀♀; Podsreda; 14 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 71/1983, TN rev. 2007); PMSL • 2 ♂♂, 3 ♀♀; Stara Glažuta; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1145/2002, rev. 2007); PMSL. – **WM41** • 1 ♂, 1 ♀; Podčetrtek; 10 Aug. 1996; L. Slana Novak and T. Novak leg. (64/1997, rev. 2018); PMSL. – **WM50** • 4 ♂♂, 1 ♀; Bistrica ob Sotli; 13 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 46/1983, TN rev. 2007); PMSL • 1 ♂, 1 ♀; Sveti gore; 17 May 1997; L. Slana Novak and T. Novak leg. (2/1997, rev. 2008); PMSL • 1 ♂; ibid.; 29 Aug. 2009; C. Komposch leg.; PMSL • 11 ♂♂, 9 ♀♀; Orešje na Bizejskem; 10 Aug. 1996; L. Slana Novak and T. Novak leg. (82/1997, rev. 2009); PMSL.

Description

Male (holotype)

BODY. Length 1.99, body width 1.48.

CHELICERAE. Ch basal article (without Apo) length 0.60, relatively long, 2.4 times as long as wide at Ch max width at dorsal hump. Ch-Apo small, 0.3 times as high as basal article long, rounded-trapezoid, widest distally and highest posteriorly; Ch-Apo 0.18 high, max width 0.17, min width 0.10 (at the base), ventral margin straight, with 0.70 long and 0.02 deep indentation with 10–20 μm high tipped tubercles and denticles constituting a saw. Secretion field fronto-medially, apically. Distal article length 0.67, max width 0.24, movable finger length 0.29 (Figs 4E, 6E, 9E).

PEDIPALPS. Pa-Fe relatively thin (Pa-Fe min:max width ~1:2.8), with variable armament: either (the main population) with 4 subequidistant tubercles, spines or long setae, or their combination in the distal Pa-Fe half, or alternatively (marginal population in SW Slovenia), with 2–3 distal stout thorns. Pa-Pt relatively thin (length:max width ~1:4.2) (Figs 5E, 6E, 10E). Pa article lengths in Table 8.

PENIS. Pe length 1.57, base 0.57, glans 0.18, stylus 0.07 (Figs 7E, 8E).

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–1–1–2. Tarsomere leg-Fe formula I–IV: 10–16–9–10. Leg article lengths in Table 8.

Female

BODY. Body length 2.49, body width 1.76.

Table 8. Length of appendage-segments in millimeters in *N. bidentatum gruberi* Novak, Slana Novak, Kozel & Raspopnig ssp. nov. from Dolenje Laknice, Slovenia: ♂ holotype (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.28 (0.31)	0.77 (0.81)	0.56 (0.63)	0.47 (0.49)	—	0.30 (0.31)	2.38 (2.55)
Leg I	0.26 (0.27)	0.94 (0.83)	0.39 (0.35)	0.67 (0.63)	1.11 (1.04)	1.10 (0.98)	4.47 (4.10)
Leg II	0.23 (0.23)	1.55 (1.40)	0.47 (0.50)	0.91 (1.16)	2.21 (2.24)	1.80 (1.61)	7.17 (7.14)
Leg III	0.22 (0.22)	0.82 (0.83)	0.36 (0.35)	0.63 (0.63)	1.22 (1.19)	0.97 (0.95)	4.22 (4.17)
Leg IV	0.23 (0.23)	1.43 (1.35)	0.39 (0.41)	0.79 (0.91)	1.94 (1.90)	1.45 (1.23)	6.23 (6.03)

CHELICERAE. Ch basal article length 0.65, 2.6 times as long as wide at dorsal hump, with low-arched dorsal margin in front of dorsal indentation, and low ventral round-triangular hump (Fig. 13D). Distal article length 0.67, max width 0.20, movable finger length 0.31.

PEDIPALPS. Pa-Tr with relatively high, symmetrically, slightly knee-like arched dorsal margin, Pa-Fe with conspicuous distal bance, Pa-Ti elongated ellipsoid (Fig. 13D). Pa article lengths in Table 8.

OVIPOSITOR. Ovipositor length 0.81, Rec sem with one tubular and 12 elongated balloon-like vesicles (Fig. 11E).

LEGS. Leg article lengths in Table 8.

Variability

In eastern Slovenia, males mostly have four thin medio-ventral spines of similar size on the Pa-Fe, the proximal one placed approximately in the middle of the Pa-Fe. In south-eastern Slovenia, some spines can be very small or diminished to a tubercle with a seta. In contrast, in south-western Slovenia, males have three or rarely two large, stout thorns, sometimes resembling those in *N. b. bidentatum*. Further investigation in Croatian Istria is required to elucidate the whole range of morphological variation and the expected transition between the tender eastern and robust western armament of the Pa-Fe.

Remarks

Nemastoma b. gruberi ssp. nov. is the most variable subspecies within *N. bidentatum*. Prior to this study, a few collected individuals had been considered within the variability range of *N. b. sparsum*, e.g., individuals from Buje and Vižinada considered as paratypes of *N. b. sparsum* (NHMW 4700). Accordingly, Novak *et al.* (2002) and Novak (2004b, 2005b) misidentified specimens, and those from SW Slovenia were erroneously reported (Novak 2005b) as a disjunctive population of *N. b. sparsum* in the Sub Mediterranean region in Slovenia. Near the border of its distribution area in SW Slovenia, *N. b. gruberi* ssp. nov. has relatively uniform, robust Pa-Fe, with 3 subequidistant, rarely 2, large, stout thorns, much different from the armament in the main population.

Distribution

Croatia, Italy, Slovenia. Vertical distribution in Slovenia: 4–1619 m a.s.l. Type locality: Dolenje Laknice, Mokronog (45.93° N, 15.21° E, 237 m a.s.l.), Slovenia.

Ecology

Nemastoma b. gruberi ssp. nov. inhabits various habitat types in lowland and hilly land, from thermophile shrub and *Quercetalia pubescenti-petraeae* Klika 1928 communities in southwestern regions to riverine, floodplain and submontane woods in southern and south-eastern Slovenia. Phenology: adults eurychronous.

Nemastoma kozari Novak, Kozel, Podlesnik & Raspopnig sp. nov.

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Figs 2, 4F, 5F, 6F, 7F, 8F, 9F, 10F, 11F, 12F, 13E; Table 9

Diagnosis

Species of the *N. b.* complex with highly arched, symmetrical Pa-Tr dorsal margin, concave dorsal margin of Pa-Ti and equilateral triangular glans, and Rec sem of 5 elongated vesicles attached to a bladder.

Etymology

The species name ‘*kozari*’ is dedicated to Senad Kozar (Travnik), whose friendship and hospitality helped us in a searching expedition on the Vlašić planina Mts.

Material examined

Holotype

BOSNIA AND HERZEGOVINA – YK10 • 1 ♂; Mrazišće, the Vlašić planina Mts, Travnik; 44.28° E, 17.63° N; 1550 m a.s.l.; 1 Oct. 2019; S. Kozar, J. Podlesnik, P. Kozel and T. Novak leg.; light submontane beech and fir forest litter; PMSL-Opiliones-TN 137/2019.

Paratypes

BOSNIA AND HERZEGOVINA – YK10 • 2 ♂♂, 1 ♀; same collection data as for holotype; PMSL-Opiliones-TN 137/2019.

Other material

BOSNIA AND HERZEGOVINA – YK10 • 4 ♂♂, 10 ♀♀; Oštrike, Vlašić Planina Mts; 1 Oct. 2019, S. Kozar, J. Podlesnik, P. Kozel and T. Novak leg. (GR5534–5543, GR5547–5550); PMSL.

Description

Male (holotype)

BODY. Length 1.90, body width: 1.41.

CHELICERAE. Ch basal article (without Apo) length 0.61, 2.0 times as long as wide at Ch max width at dorsal hump. Ch-Apo small, 0.24 times as high as basal article length, rounded-trapezoid, widest distally; Ch-Apo height 0.14, max width 0.12, min width 0.09 (at the base), ventral margin slightly concave. Secretion field apically. Distal article length 0.60, max width 0.19, movable finger length 0.23 (Figs 4F, 6F, 9F).

PEDIPALPS. Pa-Tr relatively very high (Pa-Tr height:length ~0.7:1), Pa-Fe moderately robust (Pa-Fe min:max width ~1:2.7), with 4 subequidistant stout spines in the distal Pa-Fe third. Pa-Pt relatively thin (length:max width ~1:4.5), Pa-Ti dorsally conspicuously concave (Figs 5F, 6F). Pa article lengths in Table 9.

PENIS. Pe length 1.55, base 0.60, glans 0.13, stylus 0.04 (Figs 7F, 8F).

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–1–1–2. Tarsomere leg formula I–IV: 8–14–8–9. Leg article lengths in Table 9.

Female

BODY. Length 2.03, body width 1.67.

Table 9. Length of appendage-segments in millimeters in *N. kozari* Novak, Kozel, Podlesnik & Raspopnig sp. nov. from Vlašić planina, Bosnia and Herzegovina: ♂ holotype (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.25 (0.28)	0.74 (0.69)	0.51 (0.55)	0.41 (0.43)	—	0.28 (0.29)	2.19 (2.24)
Leg I	0.22 (0.23)	0.87 (0.76)	0.35 (0.30)	0.59 (0.62)	0.97 (0.91)	0.82 (0.88)	3.82 (3.70)
Leg II	0.24 (0.24)	1.32 (1.22)	0.44 (0.36)	1.08 (1.00)	1.87 (1.72)	1.46 (1.37)	6.41 (5.91)
Leg III	0.23 (0.26)	0.82 (0.78)	0.33 (0.31)	0.53 (0.51)	1.09 (1.06)	0.82 (0.72)	3.82 (3.64)
Leg IV	0.27 (0.26)	1.28 (1.23)	0.43 (0.38)	0.88 (0.77)	1.74 (1.69)	1.04 (0.79)	5.64 (5.12)

CHELICERAE. Ch basal article length 0.63, 2.4 times as long as wide at dorsal hump, with slightly arched dorsal margin in front of indentation, and slightly concave ventral margin (Fig. 13E). Distal article length 0.66, max width 0.23, movable finger length 0.28.

PEDIPALPS. Pa-Tr with moderately high, arched dorsal margin, Pa-Fe with conspicuous distal bionce, Pa-Pt and Pa-Ti elongated (Fig. 13E). Pa article lengths in Table 9.

OVIPOSITOR. Ovipositor length 0.93, Rec sem consisted of bladder and 5 elongated sac-like vesicles (Fig. 11F).

LEGS. Leg lengths in Table 9.

Distribution

Bosnia and Herzegovina, probably endemic to the Vlašić planina Mts. Vertical distribution: 1550–1630 m a.s.l. Type locality: Mrazišće, Mt. Paljenik in the Vlašić planina Mts, Travnik (44.28° N, 17.63° E, 1550 m a.s.l.), Bosnia.

Ecology

Nemastoma kozari sp. nov. individuals have been found in light submontane beech and fir forests, but may inhabit also other vegetation types. Phenology: adults probably eurychronous.

Nemastoma bidentatum martensi Novak, Slana Novak & Raspopnig ssp. nov.

urn:lsid:zoobank.org:act:CCDC54EF-D41A-4547-A4D4-50370212C243

Figs 2–3, 4G, 5G, 6G, 7G, 8G, 9G, 10G, 11G, 12G, 13F; Table 10

Diagnosis

Subspecies of *Nemastoma bidentatum* with Ch basal article with a saw-like series of 1–3 µm high denticles on anterior margin of ventral hump, and a row of 5–11 denticles and tubercles in the distal half of Pa-Fe. Rec sem of 12–14 slightly elongated balloon-like vesicles.

Etymology

The subspecies name ‘*martensi*’ is dedicated to Jochen Martens (Mainz), our teacher, colleague and friend, who provided the first modern revision of harvestmen in Slovenia.

Material examined

Holotype

SLOVENIA – VL23 • 1 ♂; Poljane pri Podgradu; 45.50° N, 14.10° E; 597 m a.s.l.; 25 Sep. 2011; L. Slana Novak and T. Novak leg.; thermophile scrub and mixed forest litter sift; PMSL-Opiliones-TN 287/2011.

Paratypes

SLOVENIA – VL23 • 8 ♂♂, 5 ♀♀; same collection data as for holotype; PMSL-Opiliones-TN 287/2011.

Other material

SLOVENIA – VL15 • 3 ♂♂, 8 ♀♀; Buje; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (316/2011, rev. 2015); PMSL • 2 ♂♂; ibid.; (316a/2011); PMSL • 1 ♀; Mt. Ostrič; 29 Aug. 2014; L. Slana Novak and T. Novak leg. (32/2014); PMSL. – VL23 • 4 ♂♂, 1 ♀; Poljane pri Podgradu; 15 May 2011; L. Slana Novak and T. Novak leg. (40/2012); PMSL • 1 ♂; ibid.; 18 Aug. 2011; (165/2012); PMSL • 3 ♂♂, 2 ♀♀; ibid.; 20 May 2012; L. Slana Novak and T. Novak leg. (GR 3597–3601, TN det.); PMSL • 1 ♂, 2 ♀♀; ibid.; 24 Oct. 2013; L. Slana Novak and T. Novak leg. (GR 6017, 6018, 6020, TN det.); PMSL • 2 ♂♂, 4 ♀♀; ibid.; 28 Oct. 2013; L. Slana Novak and T. Novak leg. (GR 4651, 4653, 4654, 4656, 4657, 4659, TN det.); PMSL • 1 ♂, 1 ♀; Mt. Velika Medvižica; 18 Jul. 2014; L. Slana Novak and T. Novak leg. (15/2014); PMSL. – VL24 • 1 ♂; Mala Plešivica, Golac; 20 Sep. 2012; T. Novak leg. (169/2012); PMSL • 1 ♂; ibid.; 5 Oct. 2012; L. Slana Novak and T. Novak leg. (PK 20/2012, TN rev. 2018); PMSL • 1 ♀; ibid.; 21 May 2014; P. Kozel and T. Novak leg. (PK 18/2014); PMSL • 1 ♀; ibid.; (PK 18/2014); PMSL • 1 ♂; Mt. Mala Pleševica – Mt. Lipica; 19 Oct. 2014; T. Novak leg. (26/2015); PMSL • 1 ♂; Obrov – Golac; 19 Sep. 2011; L. Slana Novak and T. Novak leg. (253/2011); PMSL • 1 ♂; Mt. Velika Pleševica; 19 Oct. 2014; T. Novak leg. (14/2015); PMSL • 1 ♂, 1 ♀; ibid.; (16/2015); PMSL • 1 ♂; Velika vrata, Mt. Velika Pleševica; 6 Oct. 2012; L. Slana Novak and T. Novak leg. (186/2012); PMSL • 4 ♂♂, 2 ♀♀; ibid.; (PK 16/2012, TN rev. 2018); PMSL. – VL25 • 1 ♀; Buje – Suhorje; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (298/2011); PMSL. – VL26 • 3 ♂♂; Fameljska loza, Senožeče; 1 Oct. 2011; L. Slana Novak and T. Novak leg. (351/2011); PMSL. – VL33; PMSL • 3 ♂♂; Starod; 25 Sep. 2011; L. Slana Novak and T. Novak leg. (269/2011); PMSL. – VL34 • 1 ♂, 1 ♀; Harije; 19 Sep. 2011; L. Slana Novak and T. Novak leg. (224a/2011); PMSL. – VL43 • 2 ♀♀; Novokrajska jama cave, Cad. No. 810, Novokračine; 21 Jul. 2006; P. Trontelj and M. Zagnajster leg. (PK and TN 96/2020); PMSL • Novokračine; 2 ♂♂, 2 ♀♀; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (307/2011, rev. 2015); PMSL. – VL44 • 1 ♂, 1 ♀; Jablanica – Trpčane; 9 Sep. 2011; L. Slana Novak and T. Novak leg. (252/2011, rev. 2015); PMSL. – VL53 • 1 ♂, 1 ♀; Mt. Šešnovica; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (300/2011); PMSL. – VL54 • 1 ♀; Bezgovec, Zabiče; 13 Nov.–10 Dec. 2002; B. Drovenik and A. Gergeli leg. (PK 50/2012; TN rev. 2018); PMSL • 1 ♀; ibid.; 16 Oct.–13 Nov. 2002; B. Drovenik and A. Gergeli leg. (PK 58/2012; TN rev. 2018); PMSL • 1 ♂; Mt. Snežnik; 12 Sep. 2018; L. Slana Novak and T. Novak leg. (116b/2018); PMSL. – VL84 • 1 ♂, 1 ♀; Pleš, Borovec pri Kočevski Reki; 19 Sep. 2013; T. Novak leg. (60/2013, rev. 2015); PMSL. – VL87 • 1 ♂; Veliki Grintovec, Zagradec, Žužemberk; 10 May 2008; L. Slana Novak and T. Novak leg. (117/2011, rev. 2015); PMSL.

Description**Male (holotype)**

BODY. Length 1.63, width 1.26.

CHELICERAE. Ch basal article (without Apo) length 0.57, 2.5 times as long as wide at Ch max width at dorsal hump, and with a saw-like series of 1–3 μm high denticles on anterior margin of ventral hump (not visible on Figs). Ch-Apo small, 0.31 times as high as basal article length, rounded-trapezoid, widest distally, highest posteriorly; Ch-Apo height 0.18, max width 0.15, min width 0.09 (at the base), frontal margin quarter moon-like. Secretion field medially. Distal article length 0.58, max width 0.19, movable finger length 0.23 (Figs 4G, 5G, 6G).

PEDIPALPS. Pa-Tr oval-trapezoid, moderately high (Pa-Tr height:length ~0.6:1), Pa-Fe moderately robust (Pa-Fe min:max width ~1:3.0), with 7 subequidistant low, stout, irregularly shaped tubercles and denticles in the distal Pa-Fe half. Pa-Pt moderately robust (length: max width ~1:4.0) (Figs 5G, 6G). Pa article lengths in Table 10.

Table 10. Length of appendage-segments in millimeters in *N. bidentatum martensi* Novak, Slana Novak & Raspopnig ssp. nov. from Poljane pri Podgradu, Slovenia: ♂ holotype (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.27 (0.26)	0.73 (0.76)	0.48 (0.55)	0.44 (0.47)	—	0.27 (0.29)	2.19 (2.33)
Leg I	0.23 (0.23)	0.93 (0.80)	0.35 (0.35)	0.60 (0.56)	1.03 (0.94)	0.78 (0.89)	3.92 (3.88)
Leg II	0.22 (0.23)	1.43 (1.35)	0.48 (0.45)	1.15 (1.25)	1.93 (1.80)	1.69 (1.65)	6.88 (6.63)
Leg III	0.24 (0.21)	0.83 (0.80)	0.33 (0.33)	0.60 (0.59)	1.09 (1.05)	0.83 (0.83)	3.93 (3.81)
Leg IV	0.23 (0.21)	1.33 (1.30)	0.48 (0.38)	0.83 (0.83)	1.59 (1.63)	0.84 (0.83)	5.30 (5.18)

PENIS. Pe length 1.44, base 0.45, glans 0.12, stylus 0.07 (Figs 7G, 8G).

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–1–1–2. Tarsomere leg-Fe formula I–IV: 8–17–8–9. Leg article lengths in Table 10.

Female

BODY. Length 2.23, width 1.60.

CHELICERAE. Ch basal article length 0.60, 2.9 times as long as wide at dorsal hump, with slightly, evenly arched dorsal margin in front dorsal indentation, and medial straight portion in middle of slightly concave ventral margin (Fig. 13F). Distal article length 0.63, max width 0.20, movable finger length 0.23.

PEDIPALPS. Pa-Tr with moderately high, arched, with straight posterior portion of dorsal margin, Pa-Fe slightly widened distally; Pa-Pt, Pa-Ti and Pa-Ta elongated (Fig. 13F). Pa article lengths in Table 10.

OVIPOSITOR. Ovipositor length 0.94, Rec sem of 12–14 slightly elongated vesicles (Fig. 11G).

LEGS. Leg article lengths in Table 10.

Distribution

Croatia, Slovenia. Vertical distribution in Slovenia: 320–1030 m a.s.l. Type locality: Poljane pri Podgradu (45.50° N, 14.10° E, 597 m a.s.l.), Slovenia.

Ecology

Nemastoma b. martensi ssp. nov. is native to lowland to submontane habitats with thermophile scrub and *Quercetalia pubescenti-petraeae* and *Tilia platyphyllos* Scop. forest communities, with partly substantial admixture of *Fagus sylvatica* and *Corylus avellana* L. in southwestern Slovenia. Phenology: adults probably eurychronous.

Nemastoma bidentatum schmidti Novak, Raspopnig & Slana Novak ssp. nov.

urn:lsid:zoobank.org:act:389E4C27-24B9-44F9-A724-11475CB9E12B

Figs 2–3, 4H, 5H, 6H, 7A, H, 8A, H, 9H, 10H, 11H, 12H, 13G; Table 11

Nemastoma triste – Roewer 1917: 149 [partim: Maribor/Marburg], 151 [partim: Postojna/Adelsberg, Divača/Divaca, Ljubljana/Laibach, Zagreb/Agram].

Nemastoma bidentatum – Roewer 1923: 658 [partim: Postojna/Adelsberg, Ljubljana/Laibach, Zagreb/Agram; the other localities refer to *N. bidentatum sparsum*]. — Hadži 1927: 11–14, figs 81–93; 1928: 9; 1931: 108–109 [partim: Podkoren, Peričnik, Bled].

Nemastoma bidentatum bidentatum — Gruber & Martens 1968: 141, figs 3, 23 [partim: Leutscach]. — Marcellino 1973: 194. — Martens 1978: 107, fig 142 [partim: HR: Dugo selo, Zagreb; I: Laghi di Fusine; SLO: Bled, Cerknica, Ljubljana, Mt. Nanos, Postojna]. — Novak 2004a: 218.

Nemastoma quadripunctatum humerale — Hadži 1931: 41, figs 94–98 (by lapsus).

Nemastoma (Lugubrostoma) triste pluridentatum — Hadži 1973a: 43 figs 34a–c [partim: Mt. Šmarca gora, Prestranek].

?*Nemastoma bidentatum bidentatum* × *N. bidentatum sparsum* — Novak & Gruber 2000: 285.

Diagnosis

Subspecies of *Nemastoma bidentatum* with elongated oval-trapezoid Ch-Apo, sagittally shallowly bilobed apically, wider distally, with a prominent apical pinnacle posteriorly, and conspicuously club-shaped Pa-Fe, with dorsal margin bent in the middle and nearly straight anterior and posterior portions, and evenly arched ventral margin, with 3 stout spines in distal fourth, and low, inconspicuous Pa-Ti hump. Rec sem of one tubular and 12 slightly elongated vesicles.

Etymology

The subspecies name ‘schmidti’ is dedicated to Ferdinand Joseph Schmidt (1791–1878; Ljubljana), who collected the first specimens of this taxon preserved in his arthropod collection in the Slovenian Museum of Natural History, Ljubljana.

Material examined

Holotype

SLOVENIA — VM31 • 1 ♂; Dolenja Sevnica, Poljane nad Škofjo Loko; 46.12° N, 14.15° E; 517 m a.s.l.; 27 Mar. 2018; T. Novak leg.; mixed forest litter; PMSL-Opiliones-TN 1145/2018.

Paratypes

SLOVENIA — VM31 • 2 ♀♀; same collection data as for holotype; PMSL-Opiliones-GR 3809.

Other material

AUSTRIA — VM74 • 1 ♂; Eisenkappel/Železna Kapla — Ebriach/Obirsko, Carinthia; 7 May 2018; T. Novak leg. (38/2018); PMSL • 1 ♀; Seilach/Sele — Ebriach/Obirsko, Carinthia; 7 May 2018; T. Novak leg. (41/2018); PMSL.

CROATIA — WL67 • 1 ♂, 1 ♀; Mt. Medvednica; A. Schönhofer leg. (6/2012, rev. 2019); PMSL.

ITALY — UM52 • 7 ♂♂, 7 ♀♀; Artegna; 4 Mar.–11 Aug. 1992; F. Gasparo leg. (64/2002, rev. 2017); PMSL. — UM62 • 1 ♂; Alta Val Torre; 5 Aug. 1992; G. Governatori leg. (1062/2003, rev. 2017); PMSL • 1 ♂, 1 ♀; Villanova, Lusevera; 23 Oct. 1997; G. Governatori leg. (244/2003); PMSL • 3 ♂♂, 4 ♀♀; Tarcento/Čenta; 19 Aug. 2001; L. Slana Novak and T. Novak leg. (259/2001, rev. 2017); PMSL • 1 ♂, 5 ♀♀; ibid.; (257/2001, rev. 2018); PMSL • 1 ♂; Valle del Torre Vedronca valley; 5 Aug. 1992; G. Governatori leg. (1062/2003, rev. 2017); PMSL. — UM65 • 2 ♂♂, 1 ♀; Pontebba; 19 Aug. 2001; L. Slana Novak and T. Novak leg. (240/2001, rev. 2017); PMSL. — UM80 • 4 ♂♂; Altana/Utana; 26 Aug. 2001; L. Slana Novak and T. Novak leg. (283/2001, rev. 2017); PMSL.

SLOVENIA • 1 ♂, 1 ♀ (Schmidt’s collection); (84/1985 microscopic preparation, JH det. sub *N. triste*, TN rev.); PMSL • 1 ♂, 1 ♀ (Schmidt’s collection); (89/1985 microscopic preparation, JH det. sub *N. triste*, TN rev.); PMSL. — UL99 • 1 ♂, 2 ♀♀; Panovec; 17 Aug. 2000; T. Novak leg. (668/2000, rev. 2017); PMSL • 1 ♀; ibid.; 18 Mar. 2001; S. Brelih leg. (63/2001, TN rev. 2019); PMSL • 9 ♂♂, 5 ♀♀; ibid.; 11 Nov. 2006; L. Slana Novak and T. Novak leg. (152/2006, rev. 2017); PMSL • 1 ♂; Replje; 8 Apr. 1992; S. Brelih leg. (649/1998, rev. 2017); PMSL. — UM72 • 1 ♂; Mt. Kobariški Stol; 24 May 2003; L. Slana

Novak and T. Novak leg. (720a/2003, TN and SL rev. 2017); PMSL. – **UM73** • 1 ♂; Mt. Kobariški Stol; 8 Jun. 2017; T. Novak leg. (6/2017); PMSL. – **UL82** • 1 ♀; Tavenica, Bela; 10 Oct. 1995; S. Brelih leg. (789/1998, rev. 2018); PMSL • 1 ♂; Sedlo – Mt. Kobariški Stol; 1 Aug. 1998; L. Slana Novak and T. Novak leg. (52/1999, rev. 2018); PMSL. – **UM90** • 2 ♀♀; Avče; 2 Aug. 2000; T. Novak leg. (298/2000, rev. 2019); PMSL • 2 ♂♂; Doblar; 2 Aug. 2000; leg. T. Novak (285/2000, rev. 2017); PMSL • 1 ♀; ibid.; 17 Jun. 2001; L. Slana Novak and T. Novak leg. (151/2001, rev. 2017); PMSL • 1 ♂; Lepenka valley, Doblar; 25 Sep. 1998; L. Slana Novak and T. Novak leg. (1795/1998, rev. 2017); PMSL • 1 ♂; Levpa – Seniški breg; 2 Aug. 2000; T. Novak leg. (319/2000, rev. 2017); PMSL • 1 ♀; Marija Snežna, Avče; 2 Aug. 2000; T. Novak leg. (293/2000; rev. 2019); PMSL. – **UL91** • 1 ♂; Kamno; 31 Jul. 1998; L. Slana Novak and T. Novak leg. (1337/1998, rev. 2018); PMSL • 1 ♂, 1 ♀; ibid.; 25 Sep. 1998; L. Slana Novak and T. Novak leg. (1809/1998, rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; Solarji, Livške Ravne; 8 Aug. 2000; T. Novak leg. (562/2000, TN and SL rev. 2017); PMSL. – **UM92** • 6 ♂♂, 1 ♀; Ladrski vrh; 14 May–11 Jun. 2002; B. Drovenik and A. Gergeli leg. (482/2018); PMSL • 1 ♀; ibid.; 11 Jun.–7 Aug. 2002; B. Drovenik and A. Pirnat leg. (792/2018); PMSL • 2 ♂♂, 3 ♀♀; ibid.; 8 Jul.–7 Aug. 2002; B. Drovenik and A. Pirnat leg. (PK 9/2013, TN rev. 2019); PMSL • 1 ♀; ibid.; (PK 10/2013, TN rev. 2019); PMSL • 1 ♀; ibid.; (585/2018); PMSL • 1 ♀; ibid.; 7 Aug.–4 Sep. 2002; B. Drovenik and A. Pirnat leg. (780/2018); PMSL • 1 ♂; ibid.; (787/2018); PMSL • 2 ♂♂, 6 ♀♀; ibid.; 4 Sep.–1 Oct. 2002; B. Drovenik and A. Pirnat leg. (827/2018); PMSL • 2 ♂♂; ibid.; (910/2018); PMSL • 4 ♀♀; ibid.; (915/2018); PMSL • 3 ♀♀; ibid.; (923/2018); PMSL • 2 ♀♀; ibid.; (928/2018); PMSL • 1 ♂; ibid.; (933/2018); PMSL • 3 ♂♂, 5 ♀♀; ibid.; 1–29 Oct. 2002; B. Drovenik and A. Pirnat leg. (959/2018); PMSL • 1 ♂, 3 ♀♀; ibid.; (961/2018); PMSL • 10 ♀♀; ibid.; (965/2018); PMSL • 4 ♀♀, 1 juv.; ibid.; (971/2018); PMSL • 1 ♂, 1 ♀; ibid.; (974/2018); PMSL • 3 ♂♂, 6 ♀♀; ibid.; (981/2018); PMSL • 8 ♀♀; ibid.; (1003/2018); PMSL • 1 ♂; ibid.; 29 Oct.–7 Nov. 2002; B. Drovenik and A. Gergeli leg. (PK 36/2013, TN rev. 2019); PMSL • 3 ♀♀; ibid.; (PK 37/2013, TN rev. 2019); PMSL • 2 ♂♂, 13 ♀♀; ibid.; (871/2018); PMSL • 2 ♀♀; ibid.; (877/2018); PMSL • 1 ♂, 3 ♀♀; ibid.; (880/2018); PMSL • 2 ♀♀; ibid.; (881/2018); PMSL • 3 ♂♂, 4 ♀♀; ibid.; (897/2018); PMSL • 4 ♂♂, 6 ♀♀; ibid.; (900/2018); PMSL • 3 ♂♂, 1 ♀; ibid.; (939/2018); PMSL • 2 ♀♀; ibid.; 27 Nov.–21 Dec. 2002; B. Drovenik and A. Gergeli leg. (948/2018); PMSL • 3 ♂♂, 2 ♀♀; ibid.; (950/2018); PMSL • 1 ♂; ibid.; (1010/2018); PMSL • 3 ♀♀; ibid.; (1014/2018); PMSL • 2 ♀♀; ibid.; (1019/2018); PMSL • 1 ♂; ibid.; (1026/2018); PMSL • 1 ♂, 2 ♀♀; ibid.; 21 Dec. 2002–28 Jan. 2003; B. Drovenik and A. Pirnat leg. (718/2018); PMSL • 1 ♂, 2 ♀♀; ibid.; (742/2018); PMSL • 2 ♂♂, 1 ♀; ibid.; (772/2018); PMSL • 3 ♀♀; ibid.; (778/2018); PMSL • 3 ♂♂, 2 ♀♀; ibid.; (813/2018); PMSL • 2 ♂♂, 3 ♀♀; ibid.; (1007/2018); PMSL • 1 ♂; ibid.; (1013/2018); PMSL. – **UL92** • 1 ♂, 1 ♀; near Kamno; Sep. 1915; Andreini leg.; PMSL • 1 ♂, 2 ♀♀; Selce; 10 Oct. 1995; S. Brelih leg. (786/1998, rev. 2017); PMSL • 1 ♂; Šturm; 8 Aug. 2000; T. Novak leg. (545/2000, rev. 2017); PMSL. – **UL93** • 1 ♀; Bavšica; 9 Aug. 1996; S. Brelih leg. (744/1998, rev. 2018); PMSL • 3 ♀♀; Brvce; 11 Oct. 1995; S. Brelih leg. (745/1998, rev. 2018); PMSL. – **VL07** • 1 ♀; Velike Žablje; 17 Aug. 2000; T. Novak leg. (677/2000, rev. 2017); PMSL. – **VL09** • 1 ♂, 2 ♀♀; Čepovanska reber; 2 Aug. 2000; T. Novak leg. (344/2000, rev. 2017); PMSL • 1 ♂; Lijak spring, Ozeljan; 17 Apr. 2002; B. Drovenik and A. Gergeli leg. (219/2011, rev. 2017); PMSL • 1 ♂; ibid.; 17 Apr.–14 May 2002; B. Drovenik and A. Pirnat leg. (540/2018); PMSL • 2 ♂♂; ibid.; (553/2018); PMSL • 2 ♂♂, 3 ♀♀; ibid.; 14 May–11 Jun. 2002; B. Drovenik and A. Gergeli leg. (503/2018); PMSL • 1 ♀; ibid.; (518/2018); PMSL • 1 ♂; ibid.; 11 Jun. 2002; B. Drovenik and A. Pirnat leg. (212/2011, rev. 2017); PMSL • 1 ♂; ibid.; 8 Jul. 2002; B. Drovenik and A. Pirnat leg. (1093/2018); PMSL • 1 ♀; ibid.; (1097/2018); PMSL • 1 ♀; ibid.; 7 Aug.–4 Sep. 2002; B. Drovenik and A. Gergeli leg. (567/2018); PMSL • 1 ♂; ibid.; 1 Oct. 2002; B. Drovenik and A. Pirnat leg. (313/2018); PMSL • 1 ♂, 1 ♀; ibid.; 18 Feb. 2003; B. Drovenik and A. Gergeli leg. (200/2011, TN rev. 2017); PMSL • 1 ♂; Lokve; 2 Aug. 2000; T. Novak leg. (350/2000, rev. 2017); PMSL • 1 ♀; ibid.; (364/2000, rev. 2017); PMSL • 1 ♀; Smrečje, Trnovski gozd; 18 Aug. 1973; I. Sivec leg. (519/1981, JG det. 1982, TN rev. 2018); PMSL. – **VL16** • Divača – **VL19** • 1 ♂; Gorenja Kanomlja; 1 Aug. 2000; T. Novak leg. (401/2000, rev. 2017); PMSL • 1 ♀; Predmeja; 21 Aug. 2006; L. Slana Novak and T. Novak leg. (4/2006, rev. 2017); PMSL • 2 ♀♀; Srednja Kanomlja; 1 Aug. 2000; T. Novak leg. (391/2000, rev. 2017); PMSL. – **VL26** •

3 ♂♂, 3 ♀♀; Senožeče; 20 Sep. 2011; L. Slana Novak and T. Novak leg. (262/2011, rev. 2017); PMSL • 1 ♀; Mt. Vremščica; 10 Mar. 1994; S. Brelih leg. (680/1998, rev. 2017); PMSL. – **VL28** • 2 ♂♂, 1 ♀; Črni vrh – Col; L. Slana Novak and T. Novak leg. (239/2011, rev. 2017); PMSL. – **VL29** • 3 ♂♂, 3 ♀♀; Godovič – Črni vrh; 11 Sep. 2011; L. Slana Novak and T. Novak leg. (241/2011, rev. 2017); PMSL • 2 ♂♂, 1 ♀; Gore; 10 Jun. 2000; L. Slana Novak and T. Novak leg. (155/2000, rev. 2017); PMSL • 1 ♀; Idrija; Jun. 1997; M. Vončina leg. (1702/1998, rev. 2017); PMSL • 1 ♂; ibid.; 10 Jun. 2000; L. Slana Novak and T. Novak leg. (137/2000, rev. 2017); PMSL • 8 ♂♂, 1 ♀; ibid.; (229/2000, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; 1 Aug. 2000; T. Novak leg. (382/2000, rev. 2017); PMSL • 2 ♂♂; Razpotje; 1 Aug. 2000; T. Novak leg. (408/2000, rev. 2017); PMSL • 1 ♂; Spodnja Idrija; 10 Jun. 2000; L. Slana Novak and T. Novak leg. (143/2000, rev. 2017); PMSL • 2 ♂♂; Srednja Kanomlja; 1 Aug. 2000; T. Novak leg. (389/2000, rev. 2017); PMSL • 1 ♀; ibid.; (397/2000, rev. 2017); PMSL • 1 ♂; Urbanovec; 10 Jun. 2000; L. Slana Novak and T. Novak leg. (149/2000, rev. 2017); PMSL. – **VL36** • 1 ♂; Jama Sv. Janeza cave, Cad. No. 897, Prestranek; 11 Aug. 1952; E. Pretner leg. (56/1983, JH det., TN rev. 2017); PMSL • 1 ♀; ibid.; 29 Aug. 1954; E. Pretner leg. (174/1984, JH det., TN rev. 2018); PMSL • 1 ♂; ibid.; 11 Aug. 1957; E. Pretner leg. (221/1984, TN rev. 2017); PMSL • 3 ♀♀; Jernejeva jama cave, Cad. No. 929, Koče; 22 Apr. 2001; S. Vidmar, S. Polak, T. Novak leg. (157/2001, rev. 2008); PMSL • Postojna – **VL37** • 1 ♂; Belsko; 14 Apr. 2011; L. Slana Novak and T. Novak leg. (86/2011); PMSL • 1 ♂; Landol; 9 May 1994; S. Brelih leg. (888/1998); PMSL. – **VL38** • 2 ♂♂, 3 ♀♀; Dolenji Novi Svet; L. Slana Novak and T. Novak leg. (230/2011); PMSL • 1 ♀; Novi svet, Hotederšica; 22 Mar. 1993; S. Brelih leg. (855/1998, rev. 2019); PMSL. – **VL39** • 3 ♂♂, 3 ♀♀; Kugu, Rovte; 11 Sep. 2011; L. Slana Novak and T. Novak leg. (244/2011); PMSL. – **VL46** • 1 ♂, 1 ♀; Mt. Javorniki; 9 May 1994; S. Brelih leg. (836/1998); PMSL • 2 ♂♂, 8 ♀♀; Mali Kožljek, Mt. Javorniki; 2 Oct. 2011; L. Slana Novak and T. Novak leg. (336/2011); PMSL. – **VL47** • 1 ♂, 2 ♀♀; Planina pri Rakeku; 24 Mar. 1992; F. Velkovrh leg. (221/1995, rev. 2017); PMSL • 1 ♂; Rakov Škocjan; Jul. 1994; K. Musar leg. (79/1995, rev. 2017); PMSL • 1 ♂; ibid.; 12.–15 May 1994; S. Polak leg. (640/1998, rev. 2018); NM • 7 ♂♂, 17 ♀♀; ibid.; 10 Sep. 2009; A. Schönhofer leg. (3/2012, rev. 2017); PMSL. – **VL48** • 1 ♀; Bistra; 29 Mar. 1993; S. Brelih leg. (641/1998, rev. 2017); PMSL • 1 ♂; Laze; 16 Oct.–21 Nov. 1994; M. Kuntner leg. (176/1995, rev. 2017); PMSL • 1 ♀; ibid.; Jul.–Aug. 1994; M. Kuntner leg. (20/1997, rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; Aug. 1994; M. Kuntner leg. (183/1995, rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; Dec. 1994–Mar. 1995; M. Kuntner leg. (170/1995, rev. 2017); PMSL • 1 ♀; Vranja jama cave, Cad. No. 88, Laze pri Planini; 7 Jun. 1994; stud. biol. leg. (101/2019); PMSL. – **VL49** • 1 ♀; Retovje, Vrhnika; Jul. 1994, A. Valenčak leg. (17/1997, rev. 2017); PMSL • 1 ♂; ibid.; Jun. 1998; M. Zagmajster leg. (1493/1998, rev. 2017); PMSL • 1 ♀; Vrhnika; Jul. 1994; A. Valenčak leg. (17/1997, rev. 2017); PMSL. – **VL54** • 1 ♂; Mt. Snežnik; 21 Jul. 2001; B. Bertoncelj, U. Bertoncelj and T. Novak leg. (150/2001, rev. 2017); PMSL • 1 ♀; ibid.; 24 Nov. 2003; S. Polak leg. (120/2006, rev. 2018); NM; PMSL. – **VL56** • 1 ♂, 3 ♀♀; Cerkniško jezero; 19 Oct. 1994; S. Polak leg. (721/1998, rev. 2017); NM • 1 ♀; ibid.; 20 Nov. 1994; S. Polak leg. (687/1998, rev. 2017); NM • 2 ♂♂, 1 ♀; ibid.; 24 Apr. 2001; S. Brelih leg. (72/2001, rev. 2017); PMSL. – **VL57** • 2 ♂♂, 4 ♀♀; Dolenje Otave – Selšček; 14 Aug. 2011; L. Slana Novak and T. Novak leg. (36/2011, rev. 2017); PMSL. – **VL58** • 1 ♂; Mt. Krim; 14 Aug. 2011; L. Slana Novak and T. Novak leg. (42/2011, rev. 2017); PMSL • 2 ♀♀; Rakitna; 14 Aug. 2011; L. Slana Novak and T. Novak leg. (40/2011, rev. 2017); PMSL. – **VL59** • 2 ♂♂, 1 ♀; Bevke; 20 Oct. 2018; L. Slana Novak and T. Novak leg. (136/2018); PMSL • 1 ♂; Brezovica pri Ljubljani; 25 May 1997; L. Slana Novak and T. Novak leg. (14/1997, rev. 2018); PMSL • 1 ♀; Draga pri Igu; 13 Apr. 1995; S. Brelih leg. (732/1998, rev. 2018); PMSL • 3 ♂♂, 10 ♀♀; Žabnica; 14 Aug. 2011; L. Slana Novak and T. Novak leg. (33/2011, rev. 2017); PMSL. – **VL68** • 1 ♂, 3 ♀♀; Iška vas – Mt. Krim; 14 Aug. 2011; L. Slana Novak and T. Novak leg. (48/2011, rev. 2017); PMSL • 1 ♂; ibid.; 31 Mar. 1997; S. Brelih leg. (53/2001, rev. 2017); PMSL • 1 ♀; Kremenica, Ig; 29 Jun. 1980 (1155/1981, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; 2 Mar. 1996; S. Brelih leg. (45/2001, rev. 2017); PMSL • 1 ♂; ibid.; 1 May 1997; S. Brelih leg. (101/2001, rev. 2017); PMSL • 1 ♂; ibid.; 7 Jun. 1997; S. Brelih leg. (117/2001, rev. 2017); PMSL • 1 ♂; ibid.; 10 Jul. 1997; S. Brelih leg. (139/2001, rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; 25 Aug. 1997; S. Brelih leg. (113/2001, rev. 2017); PMSL • 1 ♀; Mt. Mokrec; 18 Jul. 1980 (LSN 151/1984,

TN rev. 2017); PMSL • 1 ♀; Ščurki, Turjak; 3 May 2008; L. Slana Novak and T. Novak leg. (155/2011, rev. 2017); PMSL • 1 ♀; ibid.; 20 Jun. 1980; (1149/1981, JG det., TN rev. 2018); PMSL • 1 ♀; Škrilje; 20 Jun. 1980; (1159/1981, JG det., TN rev. 2018); PMSL – **VL69** • 2 ♀♀; Šmarje Sap; 10 May 2008; L. Slana Novak and T. Novak leg. (119a/2011, rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; (147/2011, rev. 2018); PMSL – **VL79** • 1 ♂, 4 ♀♀; Brinjski hrib; L. Slana Novak and T. Novak leg. (99/2012, TN and SL rev. 2017); PMSL • 1 ♂; Stara vas; 16 Mar. 1993; S. Brelih leg. (665/1998, rev. 2017); PMSL – **VL85** • 1 ♀; Mt. Stojna; 21 Oct. 1996; S. Brelih leg. (90/2001, rev. 2017); PMSL – **VL89** • 1 ♂, 4 ♀♀; Vintarjevec; T. Novak leg. (173/2011, rev. 2017); PMSL • 2 ♂♂, 4 ♀♀; ibid.; (178/2011, rev. 2017); PMSL – **VL93** • 1 ♀; Kostel, Dolenja Žaga; 16 Apr. 1996; S. Brelih leg. (737/1998, rev. 2018); PMSL – **VL99** • 1 ♀; Cerovec, Gabrovka; L. Slana Novak and T. Novak leg. (74/2007, rev. 2017); PMSL – **VM00** • 1 ♂, 2 ♀♀; Cvretrež, Voglarji; 2 Aug. 2000; T. Novak leg. (324/2000, TN and SL rev. 2017); PMSL • 5 ♂♂, 4 ♀♀; Čepovan; 1 Aug. 2000; T. Novak leg. (361/2000, rev. 2017); PMSL • 1 ♂; Čepovan – Most na Soči; 10 Jun. 1997; S. Brelih leg. (110/2001, rev. 2017); PMSL • 1 ♂; Preval, Lokovec, Čepovan; 2 Aug. 2000; T. Novak leg. (329/2000, rev. 2017); PMSL – **VM05** • several specs; Podkoren; J. Hadži leg.; PMSL – **VM09** • 1 ♀; Smrečje; 18 Aug. 1973; I. Sivec leg. (519/1981, JG det., TN rev. 2018); PMSL – **VM10** • 1 ♂; Bukovo; 8 Aug. 2000; T. Novak leg. (501/2000, rev. 2017); PMSL • 3 ♂♂, 5 ♀♀; Oblakov vrh; 1 Aug. 2000; T. Novak leg. (377/2000, rev. 2017); PMSL • 1 ♂; Stopnik; 8 Aug. 2000; T. Novak leg. (492/2000, rev. 2018); PMSL – **VM12** • 1 ♀; Šavnica, Bohinjska Bistrica; 26 Jul. 2002; B. Drozenik and A. Pirnat leg. (1094/2018); PMSL – **VM13** • 1 ♀; Suha; 25 Oct. 1993; S. Brelih leg. (868/1998, rev. 2018); PMSL – **VM14** • 1 ♀; Peričnik waterfall, Vrata valley; 14 Aug. 1928; J. Hadži leg.; PMSL – **VM20** • 1 ♀; Fužine; 8 Aug. 2000; T. Novak leg. (484/2000, rev. 2017); PMSL • 1 ♂, 1 ♀; Govejk; 8 Aug. 2000; T. Novak leg. (486/2000, rev. 2017); PMSL • 1 ♀; Osojnica; 8 Aug. 2000; T. Novak leg. (498/2000, rev. 2017); PMSL • 2 ♂♂; Otalež; 8 Aug. 2000; T. Novak leg. (479/2000, rev. 2017); PMSL – **VM21** • 3 ♂♂, 1 ♀; Davča; 27 Jul. 2003; L. Slana Novak and T. Novak leg. (703/2003, rev. 2017); PMSL • 1 ♀; ibid.; (706/2003, rev. 2017); PMSL • 1 ♂; Velbnik, Mt. Porezen; 7 Jul. 2003; L. Slana Novak and T. Novak leg. (700/2003); PMSL – **VM22** • 1 ♀; Nomenj; 25 Oct. 1993; S. Brelih leg. (849/1998, rev. 2018); PMSL – **VM23** • 2 ♀♀; the Pokljuka Mts; 19 Jul. 1940; J. Hadži leg. (323/1983, rev. 2017); PMSL – **VM30** • 1 ♂, 1 ♀; Gorenja vas – Lučine; 15 May 1994; S. Brelih leg. (862/1998, rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; Srednja vas – Poljane; 8 Aug. 2000; T. Novak leg. (483/2000, rev. 2017); PMSL – **VM31** • 15 ♂♂, 14 ♀♀; Dolenja Sevnica, Poljane; 15 Aug. 2012; L. Slana Novak and T. Novak leg. (GR 3777–3783, 3805–3811, 3819–3825, 3833–3835); PMSL – **VM32** • 1 ♂, 2 ♀♀; Selca; 15 Aug. 2012; L. Slana Novak and T. Novak leg. (139/2012, TN and SL rev. 2017); PMSL – **VM33** • 1 ♂; Begunje; 12 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (166/1997, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; (374/1998, rev. 2017); PMSL • Bled. – **VM40** • 5 ♂♂, 5 ♀♀; Polhov Gradec – Črni vrh; 11 Sep. 2011; L. Slana Novak and T. Novak leg. (235/2011, rev. 2017); PMSL – **VM41** • 2 ♀♀; Log nad Škofjo Loko; 8 Aug. 2000; T. Novak leg. (475/2000, rev. 2017); PMSL • 1 ♂; Mt. Lubnik; Jul. 1998; R. Potočnik leg. (1666/1998, rev. 2017); PMSL • 2 ♂♂, 6 ♀♀; Sopotniška grapa; 8 Aug. 2000; T. Novak leg. (505/2000, rev. 2017); PMSL • 1 ♂; Štinetova jama cave, Cad. No. 240, Crngrob, Škofja Loka; 25 Jul. 1980; T. Novak, I. Sivec leg. (LSN 214/1984, TN rev. 2019); PMSL – **VM42** • 1 ♂; Bukovščica; 15 May 1994; S. Brelih leg. (881/1998, rev. 2017); PMSL • 1 ♂; Mt. Šmarjetna gora; 27 Apr.–4 May 1987; A. Ziherl, T. Trilar leg. (492/1998, rev. 2017); PMSL • 1 ♀; ibid.; 18–24 Oct. 1987; A. Ziherl, T. Trilar leg. (483/1998, rev. 2017); PMSL • 1 ♂; ibid.; (513/1998, TN and SL rev. 2017); PMSL – **VM43** • 1 ♀; Kriška planina; May 1968; (1218/1981, JG det., TN rev. 2017); PMSL • 1 ♂; Križe, Tržič; 6 Aug. 2015; L. Slana Novak and T. Novak leg. (101/2015, rev. 2017); PMSL – **VM50** • 1 ♀; Ljubljana; Nov. 1986; (631/2002, rev. 2017); PMSL • 1 ♀; ibid.; Nov. 1987; (125/1997, TN and SL rev. 2017); PMSL • 1 ♂, 2 ♀♀; ibid.; Dec. 1987; F. Velkovrh leg. (106/1997, rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; Mar. 1990; F. Velkovrh leg. (285/1995, rev. 2017); PMSL • 1 ♀; Podutik; Jun. 1998; (1648/1998, rev. 2017); PMSL • 1 ♀; ibid.; Oct. 1928; J. Staudacher leg. (16/1983 microscopic preparation, rev. 2017); PMSL • 1 ♀; ibid.; May–Jun. 2000; A. Pokrivač leg. (PK and TN 74/2020); PMSL • 1 ♀; Preval, Ljubljana; 18 Mar. 1993; S. Brelih leg. (664/1998, rev. 2017); PMSL – **VM51** • 1 ♂; Mt. Grmada, Medno; 28 Jul.

1969; (531/1981, rev. 2018); PMSL • 2 ♂♂; ibid.; 3 Jun. 1986; (242/2002, rev. 2017); PMSL • 1 ♂; ibid.; 28 Jul. 1969; (531/1981, rev. 2018); PMSL • 1 ♂; ibid.; 15 May 1970; (526/1981, rev. 2018); PMSL • 1 ♀; ibid.; 19 Apr.–15 May 2002; B. Droveník and A. Gergeli leg. (188/2011, rev. 2017); PMSL • 1 ♀; ibid.; (446/2018); PMSL • 1 ♀; ibid.; 15 May 2002; B. Droveník and A. Pirnat leg. (216/2011, rev. 2017); PMSL • 1 ♂; ibid.; 15 May–12 Jun. 2002; B. Droveník and A. Gergeli leg. (427/2018); PMSL • 1 ♂, 1 ♀; ibid.; (523/2018); PMSL • 1 ♂; ibid.; (558/2018); PMSL • 1 ♀; ibid.; 12 Jun.–9 Jul. 2002; B. Droveník and A. Gergeli leg. (602/2018); PMSL • 1 ♀; ibid.; (PK 34/2014, TN rev. 2019); PMSL • 2 ♂♂, 1 ♀; ibid.; 8 Aug.–6 Sep. 2002; B. Droveník and A. Gergeli leg. (PK 86/2012; TN rev. 2019); PMSL • 1 ♂; ibid.; 6 Sep. 2002; B. Droveník and A. Pirnat leg. (354/2018); PMSL • 1 ♀; ibid.; 2 Oct. 2002 (173/2003, rev. 2017); PMSL • 1 ♀; ibid.; (1100/2018); PMSL • 2 ♀♀; ibid.; (1124/2018); PMSL • 1 ♀; ibid.; 28 Oct.–25 Nov. 2002; B. Droveník and A. Gergeli leg. (PK 28/2012, TN rev. 2019); PMSL • 1 ♂; ibid.; (264/2018); PMSL • 1 ♀; ibid.; 25 Nov. 2002; B. Droveník and A. Pirnat leg. (277/2018); PMSL • 4 ♀♀; ibid.; (279/2018); PMSL • 1 ♂; ibid.; 19 Mar. 2003; B. Droveník and A. Pirnat leg. (330/2018); PMSL • 1 ♀; ibid.; (375/2018); PMSL • 3 ♂♂, 2 ♀♀; Mavčiče; Jun. 1998; A. Žunič leg. (1568/1998, rev. 2017); PMSL – VM52 • 14 ♂♂, 12 ♀♀; Predoslje; 29 Jan. 1954; A. Polenec leg. (263/1984, rev. 2017); PMSL • 11 ♂♂, 23 ♀♀; ibid.; 31 Mar. 1954; A. Polenec leg. (337/1984, rev. 2017); PMSL • 8 ♂♂, 7 ♀♀; ibid.; 10 Oct. 1954; A. Polenec leg. (106/1984, rev. 2017); PMSL • 3 ♂♂, 2 ♀♀; ibid.; 15 Oct. 1954; A. Polenec leg. (351/1984, TN and SL rev. 2017); PMSL • 6 ♂♂, 14 ♀♀; ibid.; 24 Oct. 1954; A. Polenec leg. (63/1984, rev. 2017); PMSL • 4 ♂♂, 7 ♀♀; ibid.; 30 Oct. 1954; A. Polenec leg. (416/1984, TN and SL rev. 2017); PMSL • 2 ♂♂, 4 ♀♀; ibid.; 6 Nov. 1954; A. Polenec leg. (556/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 11 ♀♀; ibid.; (319/1984, rev. 2017); PMSL • 2 ♂♂; ibid.; 14 Nov. 1954; A. Polenec leg. (345/1984, TN and SL rev. 2017); PMSL • 3 ♂♂, 9 ♀♀; ibid.; (393/1984, TN and SL rev. 2017); PMSL • 3 ♂♂, 1 ♀; ibid.; 28 Nov. 1954; A. Polenec leg. (364/1984, TN and SL rev. 2017); PMSL • 1 ♂, 4 ♀♀; ibid.; (410/1984, TN and SL rev. 2017); PMSL • 28 ♂♂, 32 ♀♀; ibid.; 5 Dec. 1954; A. Polenec leg. (382/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; 18 Dec. 1954; A. Polenec leg. (20/1984, rev. 2017); PMSL • 32 ♂♂, 34 ♀♀; ibid.; (58/1984, rev. 2017); PMSL • 1 ♀; ibid.; 31 Dec. 1954; A. Polenec leg. (24/1984, rev. 2017); PMSL • 9 ♂♂, 21 ♀; ibid.; 9 Jan. 1955; A. Polenec leg. (324/1984, TN and SL rev. 2017); PMSL • 12 ♂♂, 8 ♀♀; ibid.; 15 Jan. 1955; A. Polenec leg. (209/1984, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; (210/1984, TN and SL rev. 2017); PMSL • 6 ♂♂, 17 ♀♀; ibid.; 22 Jan. 1955; A. Polenec leg. (342/1984, TN and SL rev. 2017); PMSL • 18 ♂♂, 15 ♀♀; ibid.; 7 Feb. 1955; A. Polenec leg. (103/1984, TN and SL rev. 2017); PMSL • 20 ♂, 27 ♀♀; ibid.; 12 Feb. 1955; A. Polenec leg. (242/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; 15 Feb. 1955; A. Polenec leg. (328/1984, TN and SL rev. 2017); PMSL • 7 ♂♂, 14 ♀♀; ibid.; 19 Feb. 1955; A. Polenec leg. (390/1984, TN and SL rev. 2017); PMSL • 2 ♀♀; ibid.; 25 Mar. 1955; A. Polenec leg. (29/1984, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; (33/1984, TN and SL rev. 2017); PMSL • 7 ♂♂, 7 ♀♀; ibid.; 27 Mar. 1955; A. Polenec leg. (285/1984, TN and SL rev. 2017); PMSL • 8 ♂♂, 12 ♀♀; ibid.; 29 Mar. 1955; A. Polenec leg. (99/1984, TN and SL rev. 2017); PMSL • 9 ♂♂, 10 ♀♀; ibid.; (277/1984, TN and SL rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; ibid.; 6 Apr. 1955; A. Polenec leg. (90/1984); PMSL • 2 ♂♂, 2 ♀♀; ibid.; 9 Apr. 1955; A. Polenec leg. (229/1984, TN and SL rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; 8 May 1955; A. Polenec leg. (69/1984, TN and SL rev. 2017); PMSL • 4 ♂♂, 6 ♀♀; ibid.; (247/1984, TN and SL rev. 2017); PMSL • 7 ♂♂, 5 ♀♀; ibid.; 21 May 1955; A. Polenec leg. (279/1984, TN and SL rev. 2017); PMSL • 9 ♂♂, 3 ♀♀; ibid.; 4 Jun. 1955; A. Polenec leg. (298/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; (333/1984, TN and SL rev. 2017); PMSL • 2 ♀♀; ibid.; 23 Apr. 1955; A. Polenec leg. (313/1984, TN and SL rev. 2017); PMSL • 13 ♂♂, 11 ♀♀; ibid.; 21 Jun. 1955; A. Polenec leg. (50/1984, TN and SL rev. 2017); PMSL • 3 ♀♀; ibid.; 2 Jul. 1955 (379/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; 27 Aug. 1955; A. Polenec leg. (253/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; (305/1984, TN and SL rev. 2017); PMSL • 2 ♀♀; ibid.; 8 Sep. 1955; A. Polenec leg. (258/1984, TN and SL rev. 2017); PMSL • 7 ♂♂, 12 ♀♀; ibid.; 8 Oct. 1955; A. Polenec leg. (362/1983, TN and SL rev. 2017); PMSL • 1 ♂, 2 ♀♀; ibid.; 22 Oct. 1955; A. Polenec leg. (383/1983, TN and SL rev. 2017); PMSL • 3 ♂♂, 4 ♀♀; ibid.; (389/1983, rev. 2017); PMSL • 11 ♂♂, 9 ♀♀; ibid.; 9 Nov. 1955; A. Polenec leg. (91/1984, TN and SL rev. 2017); PMSL •

2 ♂♂, 3 ♀♀; ibid.; 16 Apr. 1956; A. Polenec leg. (482/1983, TN and SL rev. 2017); PMSL • 1 ♂, 2 ♀♀; ibid.; 22 Apr. 1956; A. Polenec leg. (280/1983, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; 26 May 1957; A. Polenec leg. (441/1983, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; 4 Jun. 1956; A. Polenec leg. (289/1984, TN and SL rev. 2017); PMSL • 1 ♀; ibid.; 22 Jun. 1956; A. Polenec leg. (472/1983); PMSL • 1 ♂; ibid.; 8 Jul. 1956; A. Polenec leg. (208/1983, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; 22 Jul. 1956; A. Polenec leg. (LSN 9/1983, TN rev. 2018); PMSL • 1 ♂; ibid.; (532/1983, TN and SL rev. 2017); PMSL • 1 ♂; ibid.; 10 Aug. 1956; A. Polenec leg. (256/1983, TN and SL rev. 2017); PMSL • 1 ♂, 1 ♀; ibid.; 24 Oct. 1956; A. Polenec leg. (537/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 11 ♀♀; ibid.; 29 Oct. 1956; A. Polenec leg. (508/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 1 ♀; ibid.; 30 Nov. 1956; A. Polenec leg. (423/1983, TN and SL rev. 2017); PMSL • 1 ♂, 5 ♀♀; ibid.; 16 Dec. 1956; A. Polenec leg. (196/1983, TN and SL rev. 2017); PMSL • 7 ♂♂, 11 ♀♀; ibid.; (544/1983, TN and SL rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; ibid.; 30 Dec. 1956; A. Polenec leg. (214/1983, TN and SL rev. 2017); PMSL • 4 ♀♀; ibid.; (295/1984, TN and SL rev. 2017); PMSL • 8 ♂♂, 10 ♀♀; ibid.; 20 Feb. 1957; A. Polenec leg. (449/1983, TN and SL rev. 2017); PMSL • 4 ♂♂, 10 ♀♀; ibid.; 23 Feb. 1957; A. Polenec leg. (418/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 5 ♀♀; ibid.; (215/1984, JH det., TN and SL rev. 2017); PMSL • 4 ♂♂, 10 ♀♀; ibid.; 8 Mar. 1957; A. Polenec leg. (247/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 12 ♀♀; ibid.; 6 Apr. 1957; A. Polenec leg. (491/1983, TN and SL rev. 2017); PMSL • 10 ♂♂, 11 ♀♀; ibid.; 9 Mar. 1957; A. Polenec leg. (465/1983, TN and SL rev. 2017); PMSL • 12 ♂♂, 4 ♀♀; ibid.; 3 May 1957; A. Polenec leg. (506/1983, TN and SL rev. 2017); PMSL • 5 ♂♂, 5 ♀♀; ibid.; 18 May 1957; A. Polenec leg. (551/1983, TN and SL rev. 2017); PMSL. – VM60 • 12 ♂♂, 29 ♀♀; Ljubljana; Jun. 1972; (518/1981, JG det., TN rev. 2020); PMSL • 1 ♂; ibid.; 26 May 1986; Hribernik, Koren and Mencinger leg. (255/2002, rev. 2017); PMSL. – VM61 • 4 ♂♂, 1 ♀; Mt. Gobavica, Mengeš; 22 Aug. 2011; L. Slana Novak and T. Novak leg. (97/2011, rev. 2017); PMSL • 1 ♀; Rašica; Jun. 1994; H. Urbas leg. (241/1995, TN rev. 2017); PMSL. – VM62 • 1 ♂, 1 ♀; Stahovica – Ambrož; 17 Aug. 2011; L. Slana Novak and T. Novak leg. (61/2011, rev. 2017); PMSL. – VM63 • 1 ♀; Mt. Kalški greben; 12 Aug. 2009; L. Slana Novak and T. Novak leg. (28/2009, rev. 2017); PMSL • 1 juv.; ibid.; (31/2009, rev. 2017); PMSL • 1 ♂, 2 ♀♀; Kamnik; 29 Oct. 2000; N. Žmaher leg. (885/2000, rev. 2017); PMSL • 1 ♀; Mt. Koren; 8 Sep. 2009; L. Slana Novak and T. Novak leg. (50/2009, rev. 2017); PMSL • 1 ♂; Mt. Košutna; 22 Sep. 2009; L. Slana Novak and T. Novak leg. (68/2009, rev. 2017); PMSL • 1 ♀; Mt. Mokrica; 22 Sep. 2009; L. Slana Novak and T. Novak leg. (80/2009, rev. 2017); PMSL. – VM70 • 1 ♂, 3 ♀♀; Jevnica; 8 Jul. 1986; L. Slana Novak and T. Novak leg. (538/2002, rev. 2017); PMSL • 5 ♂♂, 3 ♀♀; Senožeti – Velika vas; 17 Aug. 2011; L. Slana Novak and T. Novak leg. (55/2011, rev. 2017); PMSL • 2 ♂♂, 3 ♀♀; Spodnja Javoršica; 16 Aug. 2000; T. Novak leg. (603/2000, rev. 2017); PMSL • 1 ♂; Vinje; 16 Aug. 2000; T. Novak leg. (693/2000, rev. 2017); PMSL. – VM71 • 1 ♂; Brezje pri Dobu; 16 Aug. 2000; T. Novak leg. (605/2000, rev. 2017); PMSL • 5 ♂♂, 1 juv.; Lukovica pri Domžalah; L. Slana Novak and T. Novak leg. (64/2011, rev. 2017); PMSL • 1 ♀; Prevoje pri Šentvidu, Šentvid pri Lukovici; 30 Mar. 1993; S. Brelih leg. (637/1998, rev. 2018); PMSL. – VM72 • 7 ♂♂; Smrečje v Črni; L. Slana Novak and T. Novak leg. (73/2011, rev. 2017); PMSL. – VM73 • 1 ♂, 1 ♀; Robanov kot; 4 Aug. 2015; T. Novak leg. (85/2015, rev. 2017); PMSL. – VM74 • 2 ♀♀; Podolševa; 4 Aug. 2015; T. Novak leg. (83/2015, rev. 2017); PMSL. – VM80 • 3 ♂♂, 3 ♀♀; Kresnice – Litija; 9 Jul. 1986; L. Slana Novak and T. Novak leg. (496/2002, rev. 2017); PMSL • 1 ♀; Ribče; 20 Nov. 1992; S. Brelih leg. (724/1998, rev. 2017); PMSL. – VM81 • 6 ♂♂, 4 ♀♀; Mt. Limbarska gora; 17 Aug. 2011; L. Slana Novak and T. Novak leg. (68/2011, rev. 2017); PMSL • 1 ♀; Negastern; 16 Aug. 2000; T. Novak leg. (593/2000, rev. 2017); PMSL • 1 ♀; Podmilj; 10 May 2008; L. Slana Novak and T. Novak leg. (106/2012, rev. 2017); PMSL. – VM82 • 3 ♂♂, 1 ♀; Mt. Gradišče, Bočna, Gornji Grad; 17 Aug. 2011; L. Slana Novak and T. Novak leg. (75/2011, rev. 2017); PMSL. – VM83 • 1 ♂; Primož pri Ljubnem; 31 Mar. 1994; S. Brelih leg. (875/1998, rev. 2017); PMSL. – VM84 • 1 ♀; Bistra; 4 Aug. 2015; T. Novak leg. (89/2015, rev. 2017); PMSL. – VM85 • 1 ♂, 1 ♀; Najbrževo, Mt. Peca; 10 Aug. 1999; F. Janžekovič leg. (82/2002, JG det., TN rev. 2018); PMSL • 1 ♂; ibid.; 21 Oct. 1999; F. Janžekovič leg. (45/2003, rev. 2018); PMSL • 1 ♂, 2 ♀♀; Topla valley; 12 Jul. 2003; L. Slana Novak and T. Novak leg. (187/2003, rev. 2017); PMSL. – VM90 • 1 ♀; Cerovec, Gabrovka; 15 Aug.

2007; L. Slana Novak and T. Novak leg. (74/2007, rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; Renke; 9 Jul. 1986; L. Slana Novak and T. Novak leg. (518/2002, rev. 2017); PMSL • 3 ♂♂, 2 ♀♀; Sava; 15 Aug. 2007; L. Slana Novak and T. Novak leg. (55/2007, rev. 2017); PMSL. – **VM91** • 1 ♂, 4 ♀♀; Mt. Čemšenik; 1 Jul. 2002; L. Slana Novak and T. Novak leg. (1202/2002, rev. 2018); PMSL • 5 ♂♂, 1 ♀; Mt. Črni vrh, Mt. Čemšeniška planina; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1171/2002, rev. 2018); PMSL • 1 ♀; Sv. Primož in Felicijan, Mt. Čemšeniška planina; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1197/2002, rev. 2017); PMSL. – **VM93** • 1 ♂, 1 ♀; Mt. Golte; 14 Dec. 1984; A. Polenec leg. (LSN 57/1985, TN rev. 2018); PMSL • 1 ♂; Žlabor; 31 Mar. 1994; S. Brelih leg. (886/1998, rev. 2017); PMSL. – **VM94** • 1 ♂, 1 ♀; Florjan; 6 Jul. 2003; L. Slana Novak and T. Novak leg. (196/2003, rev. 2018); PMSL • 1 ♂; Mt. Smrekovec; 18 Sep. 2000; (579/2002, rev. 2017); PMSL. – **VM95** • 3 ♂♂; Tolsti vrh, Ravne na Koroškem; 11 Oct. 2006; T. Novak leg. (55/2006, rev. 2019); PMSL • 4 ♂♂, 3 ♀♀; Mt. Uršlja gora; L. Slana Novak and T. Novak leg. (65/2006, TN and SL rev. 2017); PMSL. – **VM96** • 2 ♂♂, 3 ♀♀; Jamnica; 10 Oct. 2006; T. Novak leg. (11/2006, rev. 2019); PMSL • 1 ♂, 1 ♀; Zgornja Jamnica; Ravne na Koroškem; 10 Oct. 2006; T. Novak leg. (13/2006, rev. 2018); PMSL. – **WL07** • 1 ♂; Mali Lipovec; 10 May 2008; L. Slana Novak and T. Novak leg. (107/2011, rev. 2017); PMSL. – **WL19** • 1 ♂; Krmelj – Tržiče; 15 Aug. 2007; L. Slana Novak and T. Novak leg. (66/2007, rev. 2017); PMSL. – **WL39** • 1 ♂; Arto; 18 Nov. 1994; S. Brelih leg. (188/2001, rev. 2017); PMSL. – **WL48** • 1 ♂, 4 ♀♀; Prilipe, Brežice; 26 May 1984; L. Slana Novak and T. Novak leg. (LSN 228/1984, TN rev. 2018); PMSL. – **WM00** • 1 ♀; Sopota valley, Podkum; 1 Apr. – 6 May 2002; B. Drovenik and A. Pirnat leg. (642/2018); PMSL • 1 ♀; ibid.; (648/2018); PMSL • 1 ♂; ibid.; 27 May 2002; B. Drovenik and A. Pirnat leg. (214/2011, ver. 2017); PMSL • 1 ♂; ibid.; 27 May–1 Jul. 2002; B. Drovenik and A. Gergeli leg. (185/2011, rev. 2017); PMSL • 3 ♀♀; ibid.; (187/2011, rev. 2017); PMSL • 1 ♀; ibid.; (189/2011, rev. 2017); PMSL • 2 ♀♀; ibid.; 20 Aug.–19 Sep. 2002; B. Drovenik and A. Gergeli leg. (PK 24/2012, TN rev. 2018); PMSL • 1 ♀; ibid.; (858/2018); PMSL • 1 ♂, 2 ♀♀; ibid.; (888/2018); PMSL • 1 ♂; ibid.; 19. Sep. 2002; B. Drovenik and A. Pirnat leg. (256/2018); PMSL • 1 ♀; ibid.; 19 Sep.–15 Oct. 2002; B. Drovenik and A. Pirnat leg. (943/2018); PMSL • 1 ♀; ibid.; (985/2018); PMSL • 1 ♀; ibid.; 15 Oct. 2002; B. Drovenik and A. Pirnat leg. (1030/2018); PMSL • 1 ♀; ibid.; (1078/2018); PMSL • 2 ♀♀; ibid.; 15 Oct. 2002–12 Nov. 2002; B. Drovenik and A. Gergeli leg. (PK 81/2012, TN rev. 2018); PMSL • 1 ♂; ibid.; (898/2018); PMSL • 3 ♂♂, 2 ♀♀; ibid.; 12 Nov. 2002–6 Mar. 2003; B. Drovenik and A. Pirnat leg. (685/2018); PMSL • 1 ♂; ibid.; (713/2018); PMSL • 1 ♀, 1 juv.; ibid.; (736/2018); PMSL • 1 ♂, 3 ♀♀; ibid.; (743/2018); PMSL • 1 juv.; ibid.; 6 Mar. 2003; B. Drovenik and A. Pirnat leg. (212/2018); PMSL • 1 ♀; ibid.; (238/2018); PMSL • 1 ♂; Šklendrovec, Mt. Kum; 22 Apr. 1992; S. Brelih leg. (727/1998, rev. 2017); PMSL. – **WM02** • 3 ♂♂, 1 ♀; Braslovško jezero, Braslovče; 26 Oct. 2013; T. Novak leg. (35/2013, rev. 2017); PMSL. – **WM03** • 3 ♂♂, 3 ♀♀; Andraž nad Polzelo; 26 Oct. 2013; T. Novak leg. (47/2013, rev. 2017); PMSL. – **WM04** • 6 ♂♂; Mislinjska Dobrava; 26 Oct. 2013; T. Novak leg. (37/2013, rev. 2018); PMSL • 1 ♀; Rdečka jama cave, Cad. No. 3488, Mt. Rdečki vrh; 10 Jul. 1977; V. Kuštor, T. Novak leg. (1119/1981, JG det., TN rev. 2018); PMSL. – **WM06** • 1 ♂, 1 ♀; Dom na Košenjaku; 14 Oct. 1995; S. Hudrap and M. Pavlin leg. (LSN 103/1996, TN rev. 2004); PMSL • 1 ♂, 1 ♀; Mt. Košenjak; 14 Oct. 1995; S. Hudrap and M. Pavlin leg. (LSN 103/1996, TN rev. 2019); PMSL • 2 ♂♂; Pernice; 18 Aug. 2005; T. Novak leg. (57/2005, rev. 2018); PMSL • 1 ♂; ibid.; 18 Aug. 2005; T. Novak leg. (66a/2005, rev. 2017); PMSL • 1 ♂; ibid.; 1 Aug. 2005; T. Novak leg. (69/2005, rev. 2019); PMSL • 2 ♂♂, 3 ♀♀; ibid.; 20 Aug. 2005; L. Slana Novak and T. Novak leg. (86/2005, rev. 2017); PMSL • 1 ♂; ibid.; 22 Aug. 2005; L. Slana Novak and T. Novak leg. (108/2005, rev. 2017); PMSL • 1 ♂; ibid.; (110/2005, rev. 2017); PMSL • 1 ♀; ibid.; (112/2005, rev. 2017); PMSL • 2 ♂♂, 1 ♀; ibid.; (114/2005, rev. 2018); PMSL. – **WM13** • 1 ♂, 1 ♀; Lipje, Vinska Gora; 21 Apr. 2002; L. Slana Novak and T. Novak leg. (741/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; Vodosteč, Črnova; 21 Apr. 2002; L. Slana Novak and T. Novak leg. (737/2002, rev. 2019); PMSL • 1 ♂, 1 ♀; Zavrh nad Dobrno; 22 Apr. 1995; S. Brelih leg. (770/1998, rev. 2018); PMSL. – **WM14** • 2 ♀♀; Paka pri Velenju; 9 Jun. 2015; T. Novak leg. (50/2015, rev. 2018); PMSL. – **WM15** • 3 ♂♂, 1 ♀; Sv. Primož; 22 Oct. 1995; S. Hudrap and M. Pavlin leg. (LSN 104/1996, TN rev. 2018); PMSL • 1 ♂, 1 ♀; Mt. Kremžarjev vrh; 26 May 2005; L. Slana Novak and T. Novak leg. (187/2005, rev. 2017); PMSL.

- **WM16** • 2 ♂♂; Mt. Kapunar; 20 Aug. 2005; L. Slana Novak and T. Novak leg. (60/2005, rev. 2018); PMSL • 1 ♂; Pernice; 20 Aug. 2005; L. Slana Novak and T. Novak leg. (75/2005, rev. 2018); PMSL • 1 ♀; ibid.; 27 Apr. 2008; L. Slana Novak and T. Novak leg. (167/2011, rev. 2017); PMSL • 1 ♀; Prevalov graben, Muta; 27 Apr. 2008; L. Slana Novak and T. Novak leg. (150/2011, rev. 2017); PMSL • 1 ♀; Radlje ob Dravi; 2 Jul. 1939; (334/1983, rev. 2017); PMSL • 1 ♀; ibid.; 15 May 1966; I. Leitinger leg. (510/1981, rev. 2018); PMSL • 1 ♀; ibid.; (513/1981, JG det., TN rev. 2018); PMSL • 1 ♂; ibid.; 12 Jun. 1966; I. Leitinger leg. (514/1981, rev. 2018); PMSL • 1 ♂; ibid.; (517/1981, rev. 2018); PMSL • 1 ♀; ibid.; 10 Jul. 1966; I. Leitinger leg. (525/1981, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; 8 Aug. 1966; I. Leitinger leg. (1222/1981, JG det., TN rev. 2018); PMSL • 3 ♂♂; ibid.; 26 Aug. 1966; I. Leitinger leg. (511/1981, rev. 2018); PMSL • 1 ♀; ibid.; (512/1981, JG det., TN rev. 2018); PMSL • 2 ♀♀; ibid.; (515/1981, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; (524/1981, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; 9 Sep. 1966; I. Leitinger leg. (516/1981, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; (671/1981, rev. 2017); PMSL • 1 ♀; ibid.; (152/1982, JG det., TN rev. 2018); PMSL • 1 ♀; ibid.; 8 Oct. 1973; T. Novak leg. (994/1981, rev. 2018); PMSL • 3 ♂♂, 1 ♀; Sv. Trije Kralji; 19 Aug. 2005; T. Novak leg. (97/2005, rev. 2017); PMSL • 1 ♀; ibid.; 20 Aug. 2005; L. Slana Novak and T. Novak leg. (82/2005, rev. 2017); PMSL • 2 ♂♂; ibid.; (73/2005, rev. 2018); PMSL. – **WM23** • 2 ♂♂, 1 ♀; Mt. Stenica; 25 Apr. 1982; T. Novak; G. Kolar leg. (267/1982, JG det., TN rev. 2018); PMSL. – **WM32** • 1 ♂; Razbor, Ponikva; 9 Jun. 2015; T. Novak leg. (54/2015, rev. 2017); PMSL. – **WM33** • 6 ♂♂, 7 ♀♀; Preloge; 17 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 73/1983, TN rev. 2018); PMSL. – **WM34** • 1 ♀; Sv. Trije Kralji, the Pohorje Mts; 10 Aug. 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 250/1984, TN rev. 2018); PMSL. – **WM35** • 1 ♀; Smolnik; 8 Aug. 2015; L. Slana Novak and T. Novak leg. (108/2015, TN rev. 2017); PMSL. – **WM36** • 2 ♂♂, 2 ♀♀; Ožbalt; 25 Oct. 2013; T. Novak leg. (45/2013, rev. 2017); PMSL. – **WM43** • 1 ♀; Brezje pri Poljčanah; 10 Apr. 1995; S. Brelih leg. (714/1998, rev. 2017); PMSL • 1 ♀; Zbelovo; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1158/2002, rev. 2018); PMSL. – **WM45** • 1 ♀; Sv. Bolfenk, the Pohorje Mts; 27 Jul. 1987; F. Janžekovič leg. (5/1999, TN rev. 2018); PMSL • 1 ♂; Limbuš; 11 Oct. 2001; D. Kos leg. (217/2004, rev. 2017); PMSL • 16 ♂♂, 36 ♀♀; ibid.; (224/2004, rev. 2017); PMSL • 1 ♂; ibid.; (218/2004, rev. 2018); PMSL • 7 ♂♂; ibid.; (225/2004, rev. 2018); PMSL. – **WM46** • 1 ♀; Gaj nad Mariborom; 16 Apr. 1983; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 64/1983, TN rev. 2018); PMSL • 1 ♀; ibid.; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (164/2011, rev. 2018); PMSL • 1 juv.; Gaj nad Mariborom – Žavcarjev vrh; 1 Aug. 1981; T. Novak leg. (1084/1981, rev. 2019); PMSL • 1 ♀; Jurski vrh; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (166/2011, rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; Kamniška graba; 20 Apr. 2008; L. Slana Novak and T. Novak leg. (129/2011, rev. 2018); PMSL • 5 ♂♂, 1 ♀; Zgornji Slemen; 16 Apr. 1983; T. Novak, M. Slana Novak, L. Slana Novak and M. Štangelj leg. (LSN 10/1983, TN rev. 2018); PMSL. – **WM54** • 1 ♂, 1 ♀; Marjeta na Dravskem polju; 8 Jun. 2015; P. Kozel leg. (57/2015, rev. 2017); PMSL. – **WM55** • 1 ♀; Maribor – Ruperče; 20 Apr. 1993; S. Brelih leg. (852/1998, rev. 2018); PMSL. – **WM64** • 1 ♂; Krčevina pri Vurbergu; 15 Sep. 2015; T. Marinko leg. (134/2015, TN rev. 2017); PMSL • 1 ♂; Placar; 16 Oct. 1994; M. Varžič leg. (17/1999, rev. 2018); PMSL. – **WM65** • 1 ♂; Hum; 23 Apr. 2008; L. Slana Novak and T. Novak leg (130/2011, rev. 2017); PMSL • 2 ♂♂, 2 ♀♀; Zgornja Voličina – Hrastovec; 2 Oct. 2002; T. Novak leg. (1284/2002, rev. 2018); PMSL. – **WM74** • 1 ♂; Hlaponci; 23 Apr. 1998; S. Brelih leg. (73/2001, rev. 2017); PMSL • 1 ♂; ibid.; (74/2001, rev. 2017); PMSL • 3 ♂♂, 2 ♀♀; Pacinje; 13 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 60/1983, T. Novak rev. 2018); PMSL. – **WM75** • 2 ♀♀; Drbetinci; 28 Apr. 2002; L. Slana Novak and T. Novak leg. (731/2002, rev. 2017); PMSL • 1 ♂, 1 ♀; Kokolanjšček; 26 Sep. 2005; L. Slana Novak and T. Novak leg. (121/2005, rev. 2017); PMSL • 1 ♂, 1 ♀; Velika Slavšina; 13 Oct. 2005; L. Slana Novak and T. Novak leg. (149/2005, rev. 2017); PMSL • 3 ♂♂; Vitomarci; 2 Jun. 2002; L. Slana Novak and T. Novak leg. (756/2002, rev. 2018); PMSL. – **WM76** • 1 ♂; Kočki vrh; 30 Jun. 2002; T. Novak leg. (784/2002, rev. 2017); PMSL. – **WM95** • 1 ♂; Gresovščak; L. Slana Novak and T. Novak leg. (162/2012, TN and SL rev. 2017); PMSL.

Description

Male (holotype)

BODY. Length 1.94, width 1.43.

CHELICERAE. Ch basal article (without Apo) length 0.58, 2.0 times as long as wide at Ch max width at dorsal hump. Ch-Apo elongated oval-trapezoid, shallowly bilobe apically, wider distally, with a prominent apical pinnacle posteriorly. Ch-Apo height 0.21, min width 0.08 (at the base) and max width 0.15. Secretion field frontally. Distal article length 0.60, max width 0.25, movable finger length 0.28 (Figs 4H, 6H, 9H).

PEDIPALPS. Pa-Tr with dorsal margin conspicuously inclined distally. Pa-Fe conspicuously club-shaped (Pa-Fe min:max width ~1:2.8) with dorsal margin bent in the middle and nearly straight anterior and posterior portions, and evenly arched ventral margin, with 3 stout spines in distal fourth. Pa-Ti hump low, inconspicuous (Figs 5H, 6H). Pa-Pt length:max width ~1:4.1. Pa article lengths in Table 11.

PENIS. Pe length 1.47, base 0.48, glans 0.09, stylus 0.07 (Figs.7A, H, 8H).

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–1–1–2. Tarsomere leg-Fe formula I–IV: 10–17–10–10. Leg article lengths in Table 11.

Female

BODY. Length 2.11, width 1.65.

CHELICERAE. Ch basal article width 0.63, 2.7 times as long as wide at dorsal hump, with nearly straight dorsal margin in front of indentation and ventral margin (Fig. 13G). Distal article length 0.64, max width 0.23, movable finger length 0.27.

PEDIPALPS. Pa-Tr with low dorsal margin, highest in the first third and straight posteriorly. Pa-Fe with conspicuous distal bance, Pa-Pt, Pa-Ti and Pa-Ta elongated (Fig. 13G). Pa article lengths in Table 11.

OVIPOSITOR. Ovipositor length 0.84, Rec sem of one tubular and 12 slightly elongated vesicles (Fig. 11G).

LEGS. Leg article lengths in Table 11.

Remarks

Hadži (1927, sub *N. bidentatum*) made the first detailed drawings of *N. b. schmidti* ssp. nov. from Schmidt's collection. Prior to this study, all published evidence citing either *N. bidentatum* or *N. b. bidentatum* in Slovenia (all localities), Croatia (Zagreb) and NE Italy (all localities) refers to *N. b. schmidti* ssp. nov. Previously, all authors considered this subspecies to be within the range of variability of *N. b. bidentatum* (Roewer 1917, 1923; Hadži 1927, 1928, 1931; Gruber & Martens 1968; Marcellino 1973; Martens 1978; Novak et al. 1984, 1995, 1996, 2002, 2017; Novak & Gruber 2000; Komposch & Gruber 2004; Novak 2004a, 2005b, 2005c). However, Roewer (1951) noticed that Hadži's individuals designated as *N. bidentatum* probably belonged to another species, while Novak & Gruber (2000) considered *N. b. schmidti* ssp. nov. a possible hybrid *N. b. bidentatum* × *N. b. sparsum*. The glans tip of a specimen from Leutschach/Lučane, (46.67° N, 15.47° E, 350 m a.s.l.; Gruber & Martens 1968: fig. 24; Martens 1978: fig. 142), Austria, is the first detailed drawing of the glans in *N. b. schmidti* ssp. nov. See remarks under *N. pluridentatum* stat. nov., *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. and *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.

Distribution

Austria, Italy, Croatia, Slovenia. Vertical distribution in Slovenia: 77–2108 m a.s.l. Type locality: Dolenja Sevnica, Poljane nad Škofjo Loko (46.12° N, 14.15° E, 517 m a.s.l.), Slovenia.

Table 11. Length of appendage-segments in millimeters in *N. bidentatum schmidti* Novak, Raspopnig & Slana Novak ssp. nov. from Dolenja Sevnica, Slovenia: ♂ holotype (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.28 (0.30)	0.77 (0.83)	0.45 (0.60)	0.46 (0.48)	—	0.26 (0.33)	2.22 (2.54)
Leg I	0.21 (0.25)	0.86 (0.85)	0.33 (0.35)	0.63 (0.60)	0.93 (1.01)	0.95 (0.99)	3.91 (4.05)
Leg II	0.23 (0.29)	1.35 (1.35)	0.41 (0.49)	1.12 (1.08)	1.98 (1.95)	1.58 (1.63)	6.67 (6.79)
Leg III	0.22 (0.18)	0.86 (0.85)	0.35 (0.35)	0.59 (0.60)	1.08 (1.04)	0.87 (0.78)	3.97 (3.80)
Leg IV	0.22 (0.26)	1.32 (1.33)	0.41 (0.40)	0.82 (0.81)	1.60 (1.81)	1.11 (1.08)	5.48 (5.69)

Ecology

Nemastoma b. schmidti ssp. nov. is a mesophilous colline to montane subspecies occupying most regions of Slovenia, except the southern and eastern territory, inhabiting various forest and scrub communities, from mixed hardwood riverine forests in the lowland to subalpine *Nardion strictae* Br.-Bl. 1926 with isolated patches of *Pinus mugo* Turra and low-growing or krummholz communities. Phenology: adults eurychronous.

Nemastoma bidentatum sneznikensis Novak, Komposch, Slana Novak & Raspopnig ssp. nov.

urn:lsid:zoobank.org:act:7690FA07-5D60-4545-8660-282ADED3F576

Figs 2–3, 4I, 5I, 6I, 7I, 8I, 9I, 10I, 11I, 12I, 13H; Table 11

Etymology

The subspecies name ‘*sneznikensis*’ references Mt. Snežnik, southern Slovenia.

Diagnosis

Short-legged (leg II <6 mm) species of the *N. b.* complex, with slightly elongated-trapezoidal Ch-Apo, with row of low tubercles on Pa-Fe and with equilateral triangular glans. Rec sem of 18 balloon-like vesicles.

Material examined

Holotype

SLOVENIA – VL54 • 1 ♂; Mt. Snežnik; 45.59° N, 14.44° E; 1553 m a.s.l.; 21 Aug. 1998; Ljuba Slana Novak and Tone Novak leg.; deep-humus in Dinaric *Pinus mugo* scrub in contact with the Dinaric *Fagus sylvatica*–*Abies alba* treeline litter sift; PMSL-Opiliones-TN 1494/1998.

Paratypes

SLOVENIA – VL54 • 2 ♂♂, 1 ♀; same collection data as for holotype; PMSL-Opiliones-TN 1494/1998.

Other material

SLOVENIA – VL54 • 3 ♂♂, 4 ♀♀; Mt. Snežnik; 20 Jul. 1999; L. Slana Novak and T. Novak leg. (185/1999, rev. 2009); PMSL.

Description

Male (holotype)

BODY. Length 1.81, width 1.18.

CHELICERAE. Ch basal article (without Apo) length 0.53, 2.7 times as long as wide at Ch max width at dorsal hump. Ch-Apo oval-trapezoid, wider distally, without apical pinnacle. Ch-Apo height 0.13, max width 0.13, min width 0.08 (at the base). Secretion field frontally. Distal article length 0.51, max width 0.17, movable finger length 0.22 (Figs 4I, 6I, 9I).

Table 12. Length of appendage-segments in millimeters in *Nemastoma bidentatum sneznikensis* ssp. nov. from Mt. Snežnik, Slovenia: ♂ holotype (♀).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.20 (0.15)	0.59 (0.58)	0.43 (0.48)	0.33 (0.38)	—	0.24 (0.25)	1.79 (1.84)
Leg I	0.19 (0.18)	0.73 (0.62)	0.31 (0.28)	0.52 (0.51)	0.79 (0.96)	0.74 (0.63)	3.28 (3.18)
Leg II	0.19 (0.23)	1.16 (0.95)	0.38 (0.38)	1.03 (0.93)	1.46 (1.61)	1.27 (1.24)	5.49 (5.34)
Leg III	0.18 (0.17)	0.70 (0.78)	0.29 (0.27)	0.53 (0.52)	0.86 (1.04)	0.63 (0.57)	3.19 (3.35)
Leg IV	0.17 (0.18)	1.06 (0.98)	0.33 (0.28)	0.74 (0.73)	1.42 (1.44)	1.01 (0.92)	4.73 (4.53)

PEDIPALPS. Pa-Tr with dorsal margin slightly inclined distally. Pa-Fe slightly club-shaped (Pa-Fe min:max width ~1:2.6) with terminal bonce, and 7 irregular granula in distal third. Pa-Pt length:max width ~1:4.3. Pa-Ti slender (Figs 5I, 6I, 10I). Pa article lengths in Table 12.

PENIS. Pe length 1.22, base 0.46, glans 0.09, stylus 0.04 (Figs 7I, 8I).

LEGS. Pseudoarticle leg-Fe formula I–IV: 0–1–1–2. Tarsomere leg formula I–IV: 9–14–6–8. Leg article lengths in Table 12.

Female

BODY. Length 2.11, width 1.43.

CHELICERAE. Ch basal article length 0.59, 2.7 times as long as wide at dorsal hump, with low-arched dorsal margin in front of indentation and straight ventral margin (Fig. 13H). Distal article length 0.66, max width 0.20, movable finger length 0.30.

PEDIPALPS. Pa-Tr low, with roof-like broken dorsal margin, highest in the first two fifths. Pa-Fe distally with low ventral hump, Pa-Pt, Pa-Ti and Pa-Ta elongated (Fig. 13H). Pa article lengths in Table 12.

OVIPOSITOR. Ovipositor length 0.62, Rec sem of 18 balloon-like vesicles (Fig. 11I).

LEGS. Leg article lengths in Table 12.

Remarks

Regarding external morphology, *N. b. sneznikensis* ssp. nov. is very similar to *N. relictum*, including the habitus, the similarly shaped Pa and relatively short legs. No individuals belonging to the subspecies were found in the last decade. See remarks on taxa of *Nemastoma* on Mt. Snežnik under *N. b. gruberi* ssp. nov.

Distribution

Despite over 30 collections, this taxon has been recorded only in a limited area on Mt. Snežnik. Endemic to Mt. Snežnik, southern Slovenia. Type locality: Mt. Snežnik (45.59° N, 14.44° E, 1553 m a.s.l.), Slovenia.

Ecology

Nemastoma b. sneznikensis ssp. nov. is a psychrophilous subspecies. To date it has been recorded only in a cold, well-drained, deep mull humus Dinaric *Pinus mugo* scrub in contact with the Dinaric *Fagus sylvatica*–*Abies alba* treeline on calcareous soils. Likely, it inhabits other cold habitats, like scree and stone heap edges in contact with humus accumulations, as is known for *N. relictum* (Komposch 1999; Komposch & Gruber 2004), and perhaps a humus-rich shallow subterranean habitat (SSH), i.e., Milieu Souterrain Superficiel (MSS) (Mammola *et al.* 2016; Halse 2018). Since this habitat is restricted to an area of less than 1 km² on Mt. Snežnik, this subspecies is considered highly endangered. Phenology: probably eurychronous.

Hybrids among the subspecies of *Nemastoma bidentatum*

Remarks

In Austria, a few localities are known where *N. b. bidentatum* lives in syntopy with *N. relictum* (Gruber & Martens 1968; Martens 1978; in both papers sub *N. b. relictum*), and with *N. b. sparsum* (Komposch & Gruber 2004; Komposch 2009). However, individuals of these three taxa do not interbreed and have been considered as potential species (Gruber & Martens 1968; Martens 1978; Komposch & Gruber 2004; Komposch 2009). In Slovenia, *N. b. schmidti* ssp. nov., with its central geographic position, interbreeds with all other adjacent subspecies: *N. b. bidentatum* in the North, and *N. b. martensi* ssp. nov., *N. b. sneznikensis* ssp. nov., *N. b. gruberi* ssp. nov. and *N. b. sparsum* from the Southwest to the Northeast of the country. Besides, *N. b. gruberi* ssp. nov. interbreed with *N. b. martensi* ssp. nov., and with *N. b. sparsum*. In Bosnia, *N. pluridentatum* stat. nov. has not been found; consequently, the genitalia have not been examined. Despite this, major differences from all the other known taxa within the *N. b.* complex allow it to be considered a separate species. This is because interbreeding of *N. pluridentatum* stat. nov., which might be a subalpine species, with the montane *N. kozari* sp. nov. from the same mountain is quite unlikely, given their great dissimilarity. However, data on taxa of *Nemastoma* in Bosnia and Herzegovina are nearly completely missing, allowing no further conclusions.

Although being morphologically variable, hybrids possess larger Ch-Apo than pure subspecies and are well distinguishable from these. In interbreeding subspecies, hybrids between the two subspecies frequently occur syntopically with individuals belonging to pure subspecies. Consequently, such a collection consists of either one or two pure subspecies and a series of hybrids with varying Ch-Apo shapes.

An overview of interbreeding relations among the taxa of the *N. b.* complex is presented in Table 13. In Slovenia, *N. b. bidentatum* and *N. b. sparsum* do not interbreed, since the areas are several tens of kilometres distant from each other. In contrast, we have found hybrids between all the adjacent subspecies (Fig. 3), except *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. × *N. b. sparsum*, which is expected in the meeting area of the three taxa. Besides, data on hybridization of *N. b. sneznikensis* ssp. nov. are too scarce to be properly evaluated in full. The zone of hybridization between *N. b. schmidti* ssp. nov. and *N. b. sparsum* is the widest, measuring up to 100 km in north-eastern Slovenia, while these zones are narrow to virtually non-identifiable among the others, and hybrids are accordingly scarce. Hybrids *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. were found in a zone up to 10 km wide, while *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov. and *N. b. gruberi* ssp. nov. × *N. b. martensi* ssp. nov. are limited to zones a few kilometers wide. In Slovenia, there are no hybrids between allopatric *N. b. martensi* ssp. nov. and *N. b. sparsum*, while these are expected in Croatia.

Hybridization patterns were not simple clines in the transition zones between two subspecies. Instead, in some cases, morphologically various hybrids between the neighboring subspecies, sharing various ratios of the hybridizing subspecies characters (cf. Gruber & Martens 1968; Martens 1978), appeared scattered across the whole width of the transition zone. In some places in the hybridization zone, individuals of both subspecies, together with hybrids of various intermittent stages, occurred syntopically.

***Nemastoma bidentatum bidentatum* Roewer, 1914 × *N. bidentatum schmidti* ssp. nov.**
Figs 3, 9J, 10J.

Diagnosis

Typically, males with narrow quarter moon-like, apically bifid Ch-Apo, ~2.4 times as high as wide, with wide, inconspicuous apical pinnacle posteriorly, and Pa-Fe ~intermediate between both subspecies.

Material examined

SLOVENIA – VM44 • 1 ♂, 1 ♀; Gromov rob, Jelendol, Tržič; 23 Aug. 2017; T. Novak leg. (GR 5339, GR 5338); PMSL. – WM06 • 1 ♂, 1 ♀; Mt. Košenjak; 27 Sep. 1981; T. Novak leg. (520/1981, rev.

Table 13. Confirmed hybrids among the taxa of the *N. bidentatum* complex.

	<i>bidentatum</i>	<i>gruberi</i>	<i>kozari</i>	<i>martensi</i>	<i>pluridentatum</i>	<i>relictum</i>	<i>schmidti</i>	<i>sneznikensis</i>
<i>gruberi</i>								
<i>kozari</i>								
<i>martensi</i>	+							
<i>pluridentatum</i>								
<i>relictum</i>								
<i>schmidti</i>	+	+		+				
<i>sneznikensis</i>						+		
<i>sparsum</i>		+				+		

2018); PMSL • 4 ♂♂, 2 ♀♀; ibid.; 14 Aug. 2012; T. Novak leg. (GR 3784, GR 3799, GR 3800, GR 3826, GR 3830, GR 3832); PMSL • 2 ♀♀; ibid.; 24 Aug. 2012; T. Novak leg. (153/2012, rev. 2018); PMSL • 1 ♂; Sv. Simon, Pernice; 18 Aug. 2005; T. Novak leg. (66b/2005, rev. 2018); PMSL • 7 ♂♂, 5 ♀♀; Sv. Urban, Kozji vrh nad Dravogradom; 24 Sep. 2005; L. Slana Novak and T. Novak leg. (127/2005, rev. 2019); PMSL • 3 ♂♂, 7 ♀♀; ibid.; 9 Aug. 2017; S. Lipovšek and T. Novak leg. (GR M1021, GR M1024, GR M1025, GR M1027, GR M1033, GR M1035–GR M1039); PMSL.

Nemastoma bidentatum bidentatum Roewer, 1914 × *N. bidentatum sparsum* Gruber & Martens, 1968

Remarks

Every allegation of hybrids *N. b. bidentatum* × *N. b. sparsum* in Slovenia and Croatia (Gruber & Martens 1968; Martens 1978; Novak & Gruber 2000; Novak *et al.* 2002; Novak 2004b) refer either to *N. b. schmidti* ssp. nov. × *N. b. sparsum* or *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov.; see these references for further remarks.

Nemastoma bidentatum gruberi ssp. nov. × *N. bidentatum martensi* ssp. nov. Figs 3, 9K, 10K

Diagnosis

Typical male hybrids are characterized by Ch basal article with large hump in front of dorsal indentation, and broad, low quarter moon-like Ch-Apo, ~1.6 times as high as wide, and slightly club-shaped, relatively thin Pa-Fe, and five, subequidistant, simple ventral Pa-Fe denticles in the frontal half of the Pa-Fe.

Material examined

CROATIA – **WL00** • 8 ♂♂, 11 ♀♀; Debeli Lug, Jasenak; 8 Sep. 2009; (2/2012); PMSL. – **WL20** • 7 ♂♂, 13 ♀♀; Ambarac sinkhole, Ogulin; 7 Sep. 2009; R. Ozimec and A. Schönhöfer leg. (Coll. ASC 324, 1/2012); PMSL.

SLOVENIA – **VL26** • 3 ♂♂, 1 ♀; Senožeče – Laže; 20 May 2012; L. Slana Novak and T. Novak leg. (50/2012, rev. 2019); PMSL. – **VL33** • 2 ♂♂, 3 ♀♀; Plazine, Starod; 25 Oct. 2012; L. Slana Novak and T. Novak leg. (194/2012, rev. 2018); PMSL. – **VL54** • 1 ♂; Travni Dolci, Mt. Snežnik; 12 Aug.

2001; L. Slana Novak and T. Novak leg. (195b/2001, rev. 2020); PMSL • 1 ♂; Mt. Snežnik; 12 Sep. 2018; L. Slana Novak and T. Novak leg. (116a/2018); PMSL • 1 ♂; ibid.; 25 Oct. 2019; T. Novak. leg. (138/2019); PMSL. – **VL95** • 1 ♂, 2 ♀♀; Mt. Kočevska Mala gora; 17 Aug. 1985; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 98/1986, TN rev. 2019); PMSL. – **VL96** • 1 ♂; Pečke – Mali vrh, Kočevski Rog; 20 Sep. 2001; B. Drozenik and A. Pirnat leg. (10/2005, rev. 2015); PMSL • 1 ♀; ibid.; (16/2005, rev. 2015); PMSL. – **WL37** • 3 ♂♂, 2 ♀♀; Mirčev grič, Mt. Gorjanci; 29 Apr. 1995; S. Brelih leg. (780/1998, rev. 2019); PMSL.

Nemastoma bidentatum gruberi ssp. nov. × *N. bidentatum martensi* ssp. nov.

× *N. bidentatum schmidti* ssp. nov.

Figs 3, 9L, 10L

Diagnosis

Typical male hybrids are characterized by Ch-Apo with nearly symmetrically convex ventro-anterior margin and straight posterior margin, and club-shaped, robust Pa-Fe with five simple, more or less equidistant ventral Pa-Fe spines in the frontal half, and Pa-Ti with small dorsal hump.

Material examined

SLOVENIA – **VL09** • 2 ♂♂; Ozeljan; 17 Apr. 2002; B. Drozenik and A. Pirnat leg. (218/2011, rev. 2017); PMSL. – **VL26** • 3 ♂♂, 4 ♀♀; Laže, Razdrto; 1 Oct. 2011; L. Slana Novak and T. Novak leg. (358/2011, rev. 2017); PMSL.

Nemastoma bidentatum gruberi ssp. nov. × *N. bidentatum schmidti* ssp. nov.

Figs 3, 9M, 10M

Nemastoma bidentatum bidentatum – Gruber & Martens 1968: 141 [partim: Dugo selo]. — Martens 1978: 107 [partim: Županja, Mt. Snežnik].

Nemastoma bidentatum bidentatum × *Nemastoma bidentatum sparsum* – Novak & Gruber 2000: 285 [partim: Mt. Snežnik]. — Novak 2004b: 246 [partim: Dugo selo].

Diagnosis

In typical male hybrids, Ch-Apo is boomerang-shaped, Pa-Fe club-shaped, but relatively thin, with four simple, equidistant ventral Pa-Fe spines in the frontal half, Pa-Ti without proximal dorso-medial hump.

Material examined

CROATIA – **WL97** • 1 ♂, 1 ♀; Zagreb – Dugo selo; J. Martens *et al.* leg. (JM 837); PMSL • 16 ♂♂, 13 ♀♀; ibid.; 9 Sep. 2009; A. Schönhofer leg. (ASc 342, 4/2012, ASc det., TN rev. 2018); PMSL. – **XL06** • 3 ♂♂, 2 ♀♀; Prevlaka; (826/2002, rev. 2018); PMSL • 4 ♂♂, 6 ♀♀; ibid.; Oct. 1984; (236/2002, rev. 2018); PMSL • 2 ♂♂, 2 ♀♀; ibid.; (278/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; ibid.; (280/2002, rev. 2018) • 1 ♂, 1 ♀; ibid.; 15 Aug. 1985; (LSN 28/1996, TN rev. 2018); PMSL • 1 ♀; ibid.; (891/2002, rev. 2018); PMSL • 1 ♂; ibid.; 30 Aug. 1985; (609/2002, rev. 2019); PMSL • 2 ♂♂; ibid.; (861/2002, rev. 2018); PMSL • 2 ♂♂, 1 ♀; ibid.; Oct. 1985; (896/2002); PMSL • 1 ♀; ibid.; 7 Apr. 1986; I. Kos leg. (328/2002, rev. 2018); PMSL • 1 ♂; ibid.; (843/2002, rev. 2018); PMSL.

SLOVENIA – **VL13** • 3 ♂♂, 3 ♀♀; Rakitovec; 21 Sep. 2011; L. Slana Novak and T. Novak leg. (263/2011, rev. 2017); PMSL. – **VL26** • 5 ♂♂, 2 ♀♀; Fameljska loza, Senožeče; 1 Oct. 2011; L. Slana Novak and T. Novak leg. (350/2011, rev. 2017); PMSL • 1 ♂; Senožeče – Vremščica; 1 Oct. 2011; L. Slana Novak and T. Novak leg. (355/2011, rev. 2017); PMSL. – **VL27** • 3 ♂♂, 1 ♀; Mt. Nanos; 1 Sep.

2011; T. Novak leg. (198/2011, rev. 2018); PMSL. – **VL34** • 1 ♂, 3 ♀♀; Harije; 19 Sep. 2011; L. Slana Novak and T. Novak leg. (224/2011, rev. 2015); PMSL • 1 ♀; Petelinje; 27 Apr. 1994; S. Brelih leg. (815/1998, rev. 2015); PMSL. – **VL58** • 2 ♂♂; Brezovica pri Borovnici; 12 May 1997; S. Brelih leg. (83/2001, rev. 2015); PMSL. – **VL67** • 1 ♂, 2 ♀♀; Lužarji; 25 Aug. 2011; T. Novak leg. (168/2011, rev. 2018); PMSL. – **VL78** • 1 ♀; Mt. Limberk; Jun. 1998; I. Bertoncelj leg. (1544/1998, rev. 2009); PMSL • 1 ♂; Veliko Mlačevo; 13 Mar. 1992; S. Brelih leg. (813/1998, rev. 2018); PMSL. – **VL79** • 1 ♂; Veliki Lipoglav; 8 Jul. 1986; L. Slana Novak and T. Novak leg. (472/2002, rev. 2018); PMSL. – **VL84** • 1 ♂, 2 ♀♀; Pleš, Borovec pri Kočevski Reki; 19 Sep. 2013; P. Kozel and T. Novak leg. (27/2013, rev. 2015); PMSL. – **VL88** • 1 ♂, 1 ♀; Krka, Krška vas pri Muljavi; 7 Jul. 1986; L. Slana Novak and T. Novak leg. (474/2002, rev. 2018); PMSL • 1 ♀; ibid.; Jun. 1998; V. Kovačič leg. (1444/1998, rev. 2017); PMSL. – **VL93** • 1 ♂; Slavski Laz; 29 Apr. 2001; S. Brelih leg. (79/2001, rev. 2018); PMSL. – **VL99** • 5 ♂♂, 1 ♀; Cirnik; 27 May 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 249/1984, TN rev. 2015); PMSL • 1 ♀; Temenica; 4 Mar. 1994; S. Brelih leg. (680a/1998, rev. 2018); PMSL. – **WL04** • 5 ♂♂; Brezovica pri Predgradu; 17 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (147/1997, rev. 2018); PMSL. – **WL05** • 5 ♂♂; Črmošnjice; 18 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (152/1997, rev. 2018); PMSL. – **WL06** • 1 ♂, 1 ♀; Baza 20, Kočevske Poljane; 17 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 76/1986, TN rev. 2018); PMSL • 2 ♂♂; Podstene, Kočevski Rog; 19 Jun. 1986 (672/2002, rev. 2017); PMSL. – **WL08** • 1 ♀; Velika jama nad Trebnjem cave, Cad. No. 104, Mokronog; 28 Jul. 2009; M. Zagmajster leg. (PK and TN 6/2020); PMSL. – **WL09** • 1 ♂; Šentrupert; 28 Feb. 1994; S. Brelih leg. (825/1998, rev. 2018); PMSL. – **WL19** • 3 ♂♂; Puščava, Mokronog; 28 Feb. 1994; S. Brelih leg. (801/1998, rev. 2018); PMSL. – **VL28** • 1 ♂; Mt. Homski hrib, Sela pri Zburah; Jun. 1997; D. Vrček leg. (1709/1998); PMSL. – **WL29** • 1 ♂, 2 ♀♀; Dolenji Boštanj; 15 Aug. 2007; L. Slana Novak and T. Novak leg. (73/2007, rev. 2015); PMSL. – **WM01** • 1 ♂, 6 ♀♀; Mt. Javor, Znojile; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1194/2002, rev. 2018); PMSL. – **WM40** • 1 ♂; Lesično; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1130/2002, rev. 2018); PMSL • 5 ♂♂; ibid.; (1132/2002, rev. 2018); PMSL. – **WM42** • 1 ♂; Mestinje; 4 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 44/1983, TN rev. 2015); PMSL.

Nemastoma bidentatum gruberi ssp. nov. × *N. bidentatum sparsum* Gruber & Martens, 1968
Figs 3, 9N, 10N

Diagnosis

Typical male hybrids with elongated Ch-Apo with knee-like flexion of frontal margin, and equidistant triangular upper portion, and club-shaped, but relatively thin Pa-Fe, with tubercle tightly in front of the first spine of four simple, equidistant ventral spines in distal Pa-Fe half, either pointed or almost without the tip.

Material examined

CROATIA – **XL03** • 1 ♂; Jezero Posavsko, Suša; 3 Dec. 1985; (61/2019); PMSL.

Nemastoma bidentatum martensi ssp. nov. × *N. bidentatum schmidti* ssp. nov.
Figs 3, 9O

Nemastoma (Stridulostoma) seliskari Hadži, 1973a: 48, figs 33c, 37a–e.

Nemastoma bidentatum bidentatum – Martens 1978: 107 [partim: *Nemastoma (Stridulostoma) seliskari* Hadži, 1973].

Nemastoma bidentatum bidentatum × *N. bidentatum sparsum* – Novak & Gruber 2000: 286 [partim: Novo mesto, Mt. Mirna gora].

Nemastoma bidentatum pluridentatum – Schönhofer 2013: 36 [partim: *Nemastoma (Stridulostoma) seliskari* Hadži, 1973, and *Nemastoma seliskari* Hadži, 1973].

Diagnosis

Typical male hybrids with Ch basal article with large hump in front of dorsal indentation, Ch-Apo with knee-like frontal flexion and narrowly drawn out upper portion, Pa-Fe club-shaped, but thinner than in *N. b. schmidti* ssp. nov., with four simple, equidistant ventral spines in distal Pa-Fe half, and Pa-Ti with minute hump.

Material examined

SLOVENIA – VL15 • 1 ♂; Prelože pri Lokvi; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (310/2011); PMSL. – VL35 • 3 ♂♂, 5 ♀♀; Ribnica – Ostrožno Brdo; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (324/2011, rev. 2015); PMSL. – VL53 • 1 ♂; Zabiče; 27 Sep. 2011; L. Slana Novak and T. Novak leg. (301/2011, rev. 2015); PMSL. – WL05 • 1 ♂; Mt. Mirna gora; 28 Jul. 1948; A. Seliškar leg; PMSL. – WL17 • 1 ♂; Novo Mesto; Karaman leg. (107/1983 microscopic preparation, JH det., TN rev. 2017); PMSL.

Remarks

In Hadži's original preparation, labelled “*Nemastoma bidentatum* Roewer pulli”, with two cover glasses on the same microscope slide, there are two males and a female. One male corresponds to the type specimen of *Nemastoma (Stridulostoma) seliskari* Hadži, 1973 (Hadži 1973a). For this species, Hadži (ibid.) founded a new subgenus *Stridulostoma* based on the existence of an alleged “stridulatory organ” on the Fe III (Hadži 1973a: figs 37c–d). Gruber (1976: 797) explained that the stridulatory organ alone does not justify establishing of a new subgenus, especially because this new species differs from *N. (Lugubrostoma) triste pluridentatum* Hadži, 1973 exclusively by possession of this organ, and accordingly, synonymized *Stridulostoma* with *Nemastoma*. Following these remarks, Schönhofer (2013: 36) synonymized *N. seliskari* with *N. b. pluridentatum*. We found that the portion of the Fe III, identified by Hadži (1973a) as a stridulatory organ in the type specimen, is in fact a depression-damage, caused by desiccation. Moreover, such damage is present in nearly all (sic!) the other femora of this freshly moulted specimen, but nothing resembles the fine lamellated structure shown in Hadži's drawing (1973a: figs 37c–d). No similar structure was found in the specimens of *Nemastoma* collected later on Mt. Mirna gora. One might imagine that a careless inspection under a microscope at low magnification could result in the illusion of a ‘stridulatory organ’. However, the drawing of its lamellae cannot be considered anything but a pure fabrication. Moreover, Pa-Fe in Hadži (1973a: fig. 33c), being under the same cover glass in the preparation, belongs to the same specimen, although Hadži (ibid.) ascribed it to *N. (Lugubrostoma) triste pluridentatum*. See remark under *N. pluridentatum* stat. nov.

Nemastoma bidentatum schmidti ssp. nov. × *N. bidentatum sneznikensis* ssp. nov.

Diagnosis

In typical male hybrids, Ch basal article oblong, *sneznikensis*-like, with Ch-Apo with small apical pinnacle posteriorly, Pa-Fe club-shaped, thinner than in *N. b. schmidti* ssp. nov., with three simple ventral spines in distal Pa-Fe half, Pa-Pt *schmidti*-like, Pa-Ti with inconspicuous tubercle.

Material examined

SLOVENIA – VL54 • 1 ♂; Mt. Snežnik; 14 Sep. 2019; L. Slana Novak and T. Novak leg. (GR 5468); PMSL.

Remarks

To date, only one male has been found.

Nemastoma bidentatum schmidti ssp. nov. × *N. bidentatum sparsum* Gruber & Martens, 1968
Figs 3, 9P, 10O

Nemastoma triste – Roewer 1917: 149: [partim: Celje/Cilli, Maribor/Marburg].

Nemastoma bidentatum bidentatum × *N. bidentatum sparsum* – Gruber & Martens 1968: 142, 147, figs 12–13 [partim: Novo mesto; Županja]. — Martens 1978: 107, fig 146 [partim: Županja; Novo mesto, Mt. Snežnik]. — Novak & Gruber 2000: 286 [partim: Novo mesto]. — Novak et al. 2002: 136 [partim: Ptuj]. — Novak 2004b: 246 [partim: Županja].

Nemastoma bidentatum ssp. – Novak & Gruber 2000: 286 [partim: Celje, Maribor].

Diagnosis

Hybrids exhibiting varying Ch-Apo morphology, but with knee-like flexion of anterior margin, and either being relatively tiny with more or less elongated superior portion or more massive with superior portion drawn out in tiny apical portion, and club-shaped Pa-Fe with intermediate form with respect to both subspecies.

Material examined

SLOVENIA – VM91 • 2 ♂♂, 4 ♀♀; Čemšemik; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1183/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; Jesenovo – Znojile; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1187/2002, TN rev. 2018); PMSL • 6 ♂♂, 5 ♀♀; Mt. Čemšeniška planina; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1191/2002, rev. 2018); PMSL • 2 ♀♀; Zaplanina, Ločica pri Vranskem; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1210/2002, rev. 2018); PMSL • 1 ♂, 5 ♀♀; ibid.; (1179/2002, rev. 2018); PMSL. – VM92 • 4 ♂♂, 9 ♀♀; Ločica pri Vranskem; 10 Aug. 1985; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 101/1986, TN rev. 2018); PMSL. – WM01 • 7 ♂♂, 5 ♀♀; Marija Reka; 21 Jul. 2002; L. Slana Novak and T. Novak leg. (1186/2002, rev. 2018); PMSL. – WM05 • 4 ♂♂, 7 ♀♀; Slovenj Gradec; 9 Oct. 1983; T. Novak and L. Slana Novak leg. (LSN 113/1983, TN rev. 2018); 3 ♂♂, 4 ♀♀; ibid.; 6 Jul. 2003; L. Slana Novak and T. Novak leg. (190/2003, rev. 2018); PMSL. – WM06 • 1 ♂, 2 ♀♀; Dravograd; 25 Oct. 1995; S. Hudrap and M. Pavlin leg. (11/1996, rev. 2018); PMSL. – WM10 • 4 ♂♂, 1 ♀; Lože – Globoko; 14 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 45/1983, TN rev. 2018); PMSL. – WM11 • 1 ♂, 2 ♀♀; Brdce; 22 Apr. 1995; S. Brelih leg. (758/1998, rev. 2018); PMSL • 1 ♂, 3 ♀♀; Udomat; 15 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 47/1983, TN rev. 2018); PMSL. – WM12 • 7 ♂♂, 3 ♀♀; Arja vas; 10 Jul. 1986; L. Slana Novak and T. Novak leg. (513/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; Velika Pirešica; 10 Jul. 1986; L. Slana Novak and T. Novak leg. (452/2002, rev. 2018); PMSL • 1 ♂, 4 juvs; ibid.; (470/2002, rev. 2018); PMSL. – WM13 • 4 ♂♂, 3 ♀♀; Vodosteč, Črnova; 10 Jul. 1986; L. Slana Novak and T. Novak leg. (453/2002, rev. 2018); PMSL • 2 ♂♂; ibid.; 22 Apr. 1995; S. Brelih leg. (772/1998, rev. 2018); PMSL • 1 ♂, 1 ♀; ibid.; 21 Apr. 2002; L. Slana Novak and T. Novak leg. (737/2002, rev. 2019); PMSL. – WM16 • 2 ♂♂, 3 ♀♀; Sv. Trije Kralji, Muta; 20 Aug. 2005; L. Slana Novak and T. Novak leg. (79/2005, rev. 20018); PMSL. – WM20 • 2 ♂♂, 3 ♀♀; Jurklošter; 15 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 53/1983, TN rev. 2018); PMSL. – WM21 • 1 ♂, 2 ♀♀; Lahovna; 22 Apr. 1995; S. Brelih leg. (740/1998, TN rev. 2018); PMSL • 2 ♂♂, 3 ♀♀, 1 juv.; Trobni dol; 16 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 48/1983, TN rev. 2018); PMSL. – WM22 • Celje • 1 ♂; ibid.; 30 Oct. 2000; N. Žmaher leg. (881/2000, rev. 2018); PMSL • 7 ♂♂, 2 ♀♀; Šmartinsko jezero; 25 Mar. 1995; S. Brelih leg. (704/1998, rev. 2018); PMSL • 1 ♂, 4 ♀♀; Vojnik; 17 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 58/1983, TN rev. 2018); PMSL. – WM23 • 1 ♂, 1 ♀; Črešnjice; 25 Mar. 1995; S. Brelih leg. (709/1998, rev. 2018); PMSL • 3 ♂♂, 3 ♀♀, 1 juv.; Frankolovo; 17 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 76/1983, TN rev. 2018); PMSL • 1 ♂; Mt. Konjiška

gora; 14 Jun. 1981; V. Kuštor, T. Novak leg. (1120/1981, rev. 2018); PMSL • 1 ♂, 2 ♀♀; Mt. Stenica; 30 May 1981; T. Novak, V. Kuštor leg. (228/1981, rev. 2018); PMSL • 1 ♀; Stenica; 24 Jul. 2002; B. Drovenik and A. Gergeli leg. (1138/2018); PMSL • 1 ♀; ibid.; 24 Jul.–21 Aug. 2002; B. Drovenik and A. Gergeli leg. (PK 73/2012, TN rev. 2018); PMSL • 1 ♀; ibid.; (PK 12/2013, TN rev. 2018); PMSL • 1 ♂; ibid.; 21 Aug. 2002; B. Drovenik and A. Gergeli leg. (1071/2018); PMSL • 1 ♀; ibid.; 21 Aug.–16 Sep. 2002; B. Drovenik and A. Gergeli leg. (782/2018); PMSL • 1 ♂, 1 ♀; ibid.; (819/2018); PMSL • 1 ♀; ibid.; (856/2018); PMSL • 1 ♂, 1 ♀; ibid.; (804/2018); PMSL • 1 ♀; ibid.; 16 Sep.–14 Oct. 2002; B. Drovenik and A. Gergeli leg. (817/2018); PMSL • 1 ♀; ibid.; 14 Oct. 2002; B. Drovenik and A. Gergeli leg. (361/2018); PMSL • 1 ♀; ibid.; (783/2018); PMSL • 1 ♂, 1 ♀; ibid.; (794/2018); PMSL • 1 ♂, 1 ♀; ibid.; (814/2018); PMSL • 1 ♀; ibid.; (824/2018); PMSL • 1 ♀; ibid.; (831/2018); PMSL • 1 ♀; ibid.; (846/2018); PMSL • 1 ♂; ibid.; 11 Nov. 2002; B. Drovenik and A. Gergeli leg. (208/2018); PMSL • 1 juv.; ibid.; (266/2018); PMSL • 1 ♂; ibid.; 11 Nov. 2002–4 Mar. 2003; B. Drovenik and A. Gergeli leg. (694/2018); PMSL • 1 ♀; ibid.; (698/2018); PMSL • 2 ♀♀; ibid.; (701/2018); PMSL • 1 ♂, 1 ♀; ibid.; (710/2018); PMSL • 1 ♀; ibid.; (716/2018); PMSL • 1 ♀; ibid.; (721/2018); PMSL • 1 ♂; ibid.; (724/2018); PMSL • 3 ♂♂, 2 ♀♀; ibid.; (729/2018); PMSL • 1 ♂; ibid.; 8 Apr. 2003; B. Drovenik and A. Gergeli leg. (267/2018); PMSL • 3 juvs; ibid.; (271/2018); PMSL • 1 ♂; ibid.; 8 Apr. 2003; B. Drovenik and A. Gergeli leg. (189/2018); PMSL • 1 juv.; ibid.; (266/2018); PMSL – **WM24** • 1 ♂, 1 ♀; Jurgovo; 24 Jul.–3 Aug. 2005; A. Kapla leg. (178/2005, rev. 2018); PMSL • 3 ♂♂; Resnik; 12 Aug. 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 252/1984, TN rev. 2018); PMSL – **WM25** • 3 ♂♂; Glažuta, Mislinjski jarek; 9 Sep. 2017; M. Delakorda, S. Lipovšek, L. Slana Novak and T. Novak leg. (107/2018); PMSL • 1 ♀; ibid.; 19 Sep. 2018; S. Lipovšek, P. Kozel and T. Novak leg. (132/2018); PMSL • 1 ♂; Ribnica na Pohorju; 4 Jul. 1939; J. Hadži leg. (145/1984, rev. 2018); PMSL – **WM30** • 1 ♂, 1 ♀; Loke – Lažiše; 11 Jul. 2003; T. Novak leg. (154/2003, rev. 2018); PMSL – **WM31** • 3 ♂♂, 2 ♀♀; Bezovje pri Šentjurju; 16 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 56/1983, TN rev. 2018); PMSL • 1 ♂; Slivniško jezero; 7 Apr. 1995; S. Brelih leg. (701/1998, rev. 2018); PMSL – **WM33** • 3 ♂♂, 2 ♀♀, 1 juv.; Tepanje; 17 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 62/1983, TN rev. 2018); PMSL • 2 ♂♂; Žiče monastery; 25 Mar. 1995; S. Brelih leg. (706/1998, rev. 2018); PMSL – **WM40** • 1 ♂; Lesično; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1130/2002, rev. 2018); PMSL – **WM41** • 1 ♂, 5 ♀♀; Podčetrtek; 13 Aug. 1983; L. Slana Novak and T. Novak leg. (LSN 51/1983, TN rev. 2018); PMSL • 2 ♂♂, 3 ♀♀; ibid.; 7 Jul. 2012; T. Novak leg. (51/2012, rev. 2018); PMSL • 2 ♂♂, 3 ♀♀; Virštajn; 7 Apr. 1995; S. Brelih leg. (699/1998, rev. 2018); PMSL – **WM42** • 1 ♀; Mt. Boč; 17 Apr. 1982; T. Novak and G. Kolar leg. (125/1982, rev. 2018); PMSL • 2 ♂♂, 1 ♀; ibid.; 16 Oct. 1983; L. Slana Novak and T. Novak leg. (LSN 118/1983, TN rev. 2018); PMSL • 2 ♂♂; Mestinje; 13 Jul. 2002; L. Slana Novak and T. Novak leg. (1165/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; ibid.; (1168/2002, rev. 2018); PMSL • 1 ♂, 1 ♀; Zgornji Gabrnik; 11 Oct. 1997; L. Slana Novak and T. Novak leg. (412/1998, rev. 2018); PMSL – **WM43** • 4 ♂♂, 1 ♀; Ložnica; 17 Aug. 1983; T. Novak and L. Slana Novak leg. (LSN 75/1983, TN rev. 2018); PMSL – **WM44** • 2 ♂♂, 4 ♀♀; Kočno pri Polskavi; 8 Aug. 2015; L. Slana Novak and T. Novak leg. (110/2018); PMSL – **WM45** • 1 ♂; Limbuš; 11 Oct. 2001; D. Kos leg. (226/2004, rev. 2018); PMSL – **WM52** • 1 ♀; Sv. Donat, Donačka gora; 16 Sep. 2002; B. Drovenik and A. Pirnat leg. (247/2018); PMSL • 1 ♀; ibid.; (248/2018); PMSL • 1 ♀; ibid.; 14 Oct. 2002; B. Drovenik and A. Pirnat leg. (1032/2018); PMSL • 6 ♂♂, 2 ♀♀, 2 juvs; Tuncovec; 4 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 66/1983, TN rev. 20018); PMSL – **WM53** • 4 ♂♂, 1 ♀; Majšperk; 24 Jun. 2007; T. Novak leg. (43/2018); PMSL • 4 ♂♂, 1 ♀; Pečke; 10 Apr. 1995; S. Brelih leg. (713/1998, rev. 2018); PMSL • 1 ♂; Stogovci; 24 Jun. 2007; T. Novak leg. (50/2007, rev. 2018); PMSL – **WM62** • 1 ♂, 2 ♀♀; Dobovec pri Rogatcu; 7 Oct. 2001; T. Novak leg. (605/2002, rev. 2007); PMSL • 2 ♂♂; ibid.; 16 Aug. 2003; J. Ravljen and T. Novak leg. (807/2003, rev. 2018); PMSL • 4 ♂♂; ibid.; 16 Aug. 2003; J. Ravljen, L. Slana Novak and T. Novak leg. (812/2003, rev. 2007); PMSL • 1 ♂, 2 ♀♀; ibid.; 30 Sep. 2012; T. Novak leg. (63/2015); PMSL • 7 ♂♂, 4 ♀♀, 1 juv.; Kozminci; 6 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 61/1983, TN rev. 2018); PMSL • 1 ♀; Mt. Macelj; Jun. 1980; V. Kuštor and T. Novak leg. (LSN 5/1983, TN rev. 2018); PMSL • 2 ♀♀; Žale, Dobrina; 24 Apr. 1998; S. Brelih leg. (85/2001,

rev. 2018); PMSL. – **WM63** • 4 ♂♂, 1 ♀; Majski vrh – Tržec; 6 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 65/1983, TN rev. 2018); PMSL. – **WM64** • 3 ♂♂, 3 ♀♀; Ptuj; 6 Aug. 1983, T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 77/1983, TN rev. 2018); PMSL. – **WM65** • 2 ♂♂; Selca; 14 Jun. 1984; L. Slana Novak, M. Slana Novak and T. Novak leg. (LSN 238/1984, TN rev. 2018); PMSL • 1 ♂, 2 ♀♀; Zgornja Voličina; 23 Apr. 1998; S. Brelih leg. (124/2001, rev. 2018); PMSL. – **WM73** • 1 ♂, 4 ♀♀; Berinjak; 24 Jun. 2007; T. Novak leg. (36/2007, rev. 2018); PMSL • 1 ♂, 8 ♀♀; Borl castle, Dolane; 7 Aug. 1983; L. Slana Novak, M. Štangelj and T. Novak leg. (LSN 59/1983, TN rev. 2018); PMSL • 1 ♂, 2 ♀♀; Ljubslava, Podlehnik; 24 Jun. 2007; T. Novak leg. (49/2007, TN rev. 2018); PMSL • 5 ♂♂; Spodje Gruškovje, Podlehnik; 24 Jun. 2007; T. Novak leg. (13/2007, rev. 2018); PMSL • 4 ♂♂, 1 ♀; Vareja; 6 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 78/1983, TN rev. 2018); PMSL. – **WM76** • 4 ♂♂, 3 ♀♀; Brengova; 26 Jul. 1983; T. Novak and L. Slana Novak leg. (LSN 63/1983, TN rev. 2018); PMSL • 2 ♂♂, 1 ♀; Kočki vrh; 30 Jun. 2002; T. Novak leg. (783/2002, rev. 2018); PMSL • 1 ♂, 2 ♀♀; ibid.; (789/2002, rev. 2018); PMSL. – **WM83** • 3 ♂♂, 5 ♀♀; Korenjak – Turški vrh; 7 Aug. 1983; T. Novak, M. Štangelj and L. Slana Novak leg. (LSN 55/1983, TN rev. 2018); PMSL. – **WM84** • 4 ♂♂, 3 ♀♀; Vudina, Velika Nedelja; 29 May 2001; P. Igerc and T. Novak leg. (22/2001, rev. 2018); PMSL. – **WM85** • 2 ♀♀; Radoslavci; 10 Sep. 1983; T. Novak, M. Slana Novak and L. Slana Novak leg. (LSN 117/1983, TN rev. 2018); PMSL. – **WM94** • 2 ♂♂, 3 ♀♀; Pavlovci; 2 Apr. 1983; T. Novak and L. Slana Novak leg. (LSN 6/1983, TN rev. 2018); PMSL. – **WM95** • Noršinci pri Ljutomeru; 27 Aug. 1983; T. Novak and L. Slana Novak leg. 2 ♂♂, 2 ♀♀ (LSN 109/1983, TN rev. 2018); PMSL. – **WM95** • 3 ♂♂, 3 ♀♀; Gresovščak; L. Slana Novak and T. Novak leg. (163/2012, rev. 2018); PMSL • 2 ♂♂, 2 ♀♀; Slamnjak, Ljutomer; 10 Jun. 1984; L. Slana Novak and T. Novak leg. (LSN 241/1984, rev. 2018); PMSL.

Remarks

To date, *N. b. schmidti* ssp. nov. has been reported under *N. b. bidentatum*, and *N. b. gruberi* ssp. nov. under *N. b. sparsum*. Since hybrids *N. b. bidentatum* × *N. b. sparsum* have not been identified in any locality, all these published data likely refer either to *N. b. schmidti* ssp. nov. × *N. b. sparsum* or *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov. *Nemastoma b. bidentatum* referred from Germany (Schönhofner & Holle 2007) is a hybrid, probably *N. b. schmidti* ssp. nov. × *N. b. sparsum*. Since both *N. b. sparsum* and *N. b. gruberi* ssp. nov. inhabit the lowland in Croatia, hybrids south of the Sava River or nearby probably belong to *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov.

Identification key to taxa within the *Nemastoma bidentatum* Roewer, 1914 complex

The identification key refers to species of the *N. bidentatum* complex, and subspecies of *N. bidentatum* s. str. including typical male hybrids. Female hybrids show intermediate traits and are not considered in the key. Figs 4–5 summarize the written information visually throughout the key, and are therefore not referred in the key. Detailed morphology is presented in Figs 6–13. Consult characters presented in Figs 6–10 and 13 (pure taxa), and Figs 11–12 (pure taxa and hybrids, males) in support.

1. ♂ 2
- ♀ 16

2. Ch and Pa slender to robust, Pa-Pt > 3.5 times as long as wide 3
- Ch and Pa very robust, Pa-Pt < 2.8 times as long as wide (Fig. 12D) *N. pluridentatum* (Hadži, 1973) stat. nov.

3. Pa-Fe unarmed or with series of small tubercles, glans isosceles triangular 4
- Pa-Fe with either spines, thorns, pointed tubercles or 4 long, rigid, subequidistant setae, glans variously shaped 5

4. Ch-Apo comb-like, Pa-Fe unarmed, without terminal bonce, Pa-Pt ~4.0 times as long as wide (Fig. 12C) *N. relicturn* Gruber & Martens, 1968 stat. nov.
- Ch-Apo rounded-trapezoidal, Pa-Fe with series of ~7 minute irregular tubercles, with terminal bonce, Pa-Pt >4.8 times as long as wide (Fig. 12I) *N. b. sneznikensis* ssp. nov.
5. Ch-Apo variously shaped, Pa-Fe with spines, thorns, pointed denticles or 4 long, rigid setae on low protrusions 6
- Ch-Apo low-trapezoid, Pa-Fe slightly club-shaped, with 6–11 medio-ventral pointed denticles, glans isosceles triangular (Fig. 12G) *N. b. martensi* ssp. nov.
6. Pa-Fe robust, very club-shaped (Pa-Fe max:min width >2.5:1) and ventrally bent (e.g., Figs 10J, O, 12A, F, H) 7
- Pa-Fe moderately club-shaped (Pa-Fe max:min width <2.4:1) and ventrally bent 13
7. Pa-Ti with small medio-dorsal hump, glans truncated terminally 8
- Pa-Ti without hump, glans isosceles triangular 10
8. Ch-Apo either broadly quarter moon-like or elongated oval-trapezoid 9
- Ch-Apo narrowly quarter moon-like, ~2.0 times as high as wide (Fig. 9J) *N. b. bidentatum* Roewer, 1914 × *N. b. schmidti* ssp. nov.
9. Ch-Apo high, broadly quarter moon-like, ~2.4 times as high as wide, apically sagittally shallowly bifid, Pa-Fe with evenly arched dorsal and ventral margins, Pa-Ti medio-dorsal hump conspicuous, glans terminally roundly truncated (Fig. 12A) *N. b. bidentatum* Roewer, 1914
- Ch-Apo elongated oval-trapezoid, with apical pinnacle posteriorly, apically sagittally shallowly bifid, Pa-Fe with knee-like bent dorsal margin and evenly arched ventral margin, with 3 stout spines in distal fourth, Pa-Ti with low medio-dorsal hump, and glans terminally evenly truncated (Fig. 12H) *N. b. schmidti* ssp. nov.
10. Pa-Fe with knee-like bent dorsal and ventral margins 11
- Pa-Fe with evenly bent dorsal and ventral margins 12
11. Ch-Apo very high, Pa-Fe with 4 stout spines in distal half (Figs 9M, 10M) *N. b. gruberi* ssp. nov. × *N. b. schmidti* ssp. nov.
- Ch-Apo high to very high, Pa-Fe with 2–3 stout spines in distal third, frontal margin bent approximately in lower quarter (Figs 9P, 10O) *N. b. schmidti* ssp. nov. × *N. b. sparsum* Gruber & Martens, 1968
12. Pa-Tr with high, evenly arched dorsal margin, Pa-Fe with evenly arched dorsal and ventral margins, with 4 stout, equidistant spines, Pa-Ti dorsally concave, without hump, glans isosceles triangular (Fig. 12F) *N. kozari* sp. nov.
- Ch-Apo thumb-like, Pa-Fe evenly club-shaped, with 5 small denticles in distal half (Figs 9L, 10L) *N. b. gruberi* ssp. nov. × *N. b. martensi* ssp. nov. × *N. b. schmidti* ssp. nov.
13. Ch-Apo rhomboidal or apically extended 14
- Ch-Apo oblong with pinnacle or distinctive angle, Pa-Fe with either 2 stout spines or tubercle and pointed thorn, glans equilateral triangle (Fig. 12B) *N. b. sparsum* Gruber & Martens, 1968
14. Ch-Apo apically extended 15
- Ch-Apo rhomboidal, Pa-Fe with either 4 subequidistantly positioned spines or pointed tubercles or long setae on low protrusions, or their combination in the distal Pa-Fe half, or, alternatively, with 2–3 stout thorns distally, glans isosceles triangle with width 80% of length (Fig. 12E) *N. b. gruberi* ssp. nov.

15. Ch-Apo apically extended in spire, Pa-Fe with 2 simple denticles (Figs 9N, 10N)
 *N. b. gruberi* ssp. nov. × *N. b. sparsum* Gruber & Martens, 1968
- Ch-Apo apically extended in narrow, finger-like protrusion, Pa-Fe with 5 equidistant denticles
 *N. b. gruberi* ssp. nov. × *N. b. martensi* ssp. nov.
16. Pa-Tr dorsal margin arched, Pa-Ti dorsal margin straight or negligibly concave 17
 – Pa-Tr dorsal margin isosceles obtuse-triangular, Pa-Fe with ventral hump distally, Pa-Ti dorsal margin slightly, but conspicuously concave (Fig. 13H) *N. b. sneznikensis* ssp. nov.
17. Apex of Pa-Tr dorsal margin conspicuously leaned anteriorly 18
 – Apex of Pa-Tr dorsal margin ~in middle 19
18. Frontal margin of Ch basal article ~straight, Pa-Tr conspicuously step-wise broken anteriorly, Pa-Pt relatively robust (Pa-Pt length:width ~4.1:1) strait, Pa-Tr with conspicuous step-wise indentation anteriorly, Pa-Pt relatively robust (Pa-Pt length:width ~4.1:1) (Fig. 13A)
 *N. b. bidentatum* Roewer, 1914
- Frontal margin of Ch basal article convex, Pa-Tr inconspicuously broken-bent anteriorly, Pa-Pt relatively normally proportioned (Pa-Pt length:width ~4.9:1) (Fig. 13G)
 *N. b. schmidti* sp. nov.
19. Rec sem elongated saccular-like 20
 – Rec sem balloon-like 21
20. Ch basal article length:width ~2.6:1, Pa-Pt length:width ~4.7:1, Rec sem of 5 irregularly-saccular alveolus (Fig. 13C) *N. relictum* Gruber & Martens, 1968 stat. nov.
 – Ch basal article length:width ~2.9:1, Pa-Pt length:width ~4.7:1, Rec sem of 5 regularly-saccular alveolus originating in bladder-like structure (Fig. 13E) *N. kozari* sp. nov.
21. Dorsal margin of Pa-Tr moderately high arched, Pa-Fe with conspicuous terminal widening 22
 – Dorsal margin of Pa-Tr highly arched, Pa-Fe in whole length equally widening (Fig. 13F)
 *N. b. martensi* ssp. nov.
22. Dorsal margin of Pa-Tr equally arched, Pa-Fe max width behind terminal widening vs min width ~2.3:1 (Fig. 13B) *N. b. sparsum* Gruber & Martens, 1968
 – Dorsal margin of Pa-Tr with knee-like medial flexion, Pa-Fe max width behind terminal widening vs min width ~1.9:1 (Fig. 13D) *N. b. gruberi* ssp. nov.

Biogeography

In Slovenia, six taxa of the *N. b.* complex, namely six subspecies of *N. bidentatum* exist: *N. b. bidentatum*, *N. b. gruberi* ssp. nov., *N. b. martensi* ssp. nov., *N. b. schmidti* ssp. nov., *N. b. sparsum* and *N. b. sneznikensis* ssp. nov. The distributional areas of these taxa cover most of the country (Fig. 3). Southern Austria with hitherto known three subspecies of *N. bidentatum* and one more species: *N. b. bidentatum*, *N. b. schmidti* ssp. nov., *N. b. sparsum* and *N. relictum* stat. nov., and north-western Croatia with four subspecies: *N. b. gruberi* ssp. nov., *N. b. martensi* ssp. nov., *N. b. schmidti* ssp. nov. and *N. b. sparsum* additionally contribute to the bulk of the *N. b.* complex diversity. At the time being, three species of the complex are known in Bosnia and Herzegovina: *N. b. sparsum*, *N. pluridentatum* stat. nov. and *N. kozari* sp. nov., two subspecies: *N. b. gruberi* ssp. nov. and *N. b. schmidti* ssp. nov. occur in Italy, *N. b. sparsum* and, potentially, *N. b. schmidti* ssp. nov. in Germany, while only *N. b. sparsum* occurs in all the other mentioned countries. In Slovenia, the main areas of the pure taxa are well defined, while the borders between the subspecies areas are not simple lines.

Discussion

Although the process of dividing the initially single genus *Nemastoma* C.L. Koch, 1836 (Koch 1836), as started by Roewer (1951), into valid genera proceeded step by step (Schönhöfer 2013), it was Gruber & Martens (1968) who redefined the genus *Nemastoma* s. str. and began the revision of the *N. b.* complex. Prior to the present study, many problems regarding the *N. b.* complex were identified and discussed (Gruber 1976; Gruber & Martens 1968; Martens 1978; Novak & Gruber 2000; Komposch & Gruber 2004; Komposch 2009), leading to the conclusion that there were four valid taxa within the complex, some of these with an uncertain status: *N. b. bidentatum*, *N. b. sparsum*, *N. b. relictum* and *N. b. pluridentatum* (Schönhöfer 2013). Further research in Slovenia led to further taxonomic challenges, particularly with respect to the existence of new taxa and various hybrid forms, which additionally blurred the relations among the taxa, demanding a systematic and detailed reconsideration of the whole complex. So far, six subspecies of *N. bidentatum* s. str. have been identified in Slovenia, three subspecies of *N. bidentatum* and one species in Austria and four subspecies of *N. bidentatum* in Croatia. Only one or two taxa sojourn in all the other mentioned countries. Accordingly, Slovenia is the most diverse country with respect to the *N. bidentatum* s. str. However, Bosnia and Herzegovina with three species within the *N. bidentatum* complex and nearly unexplored *Nemastoma* fauna might be the center of the *N. bidentatum* complex species diversity.

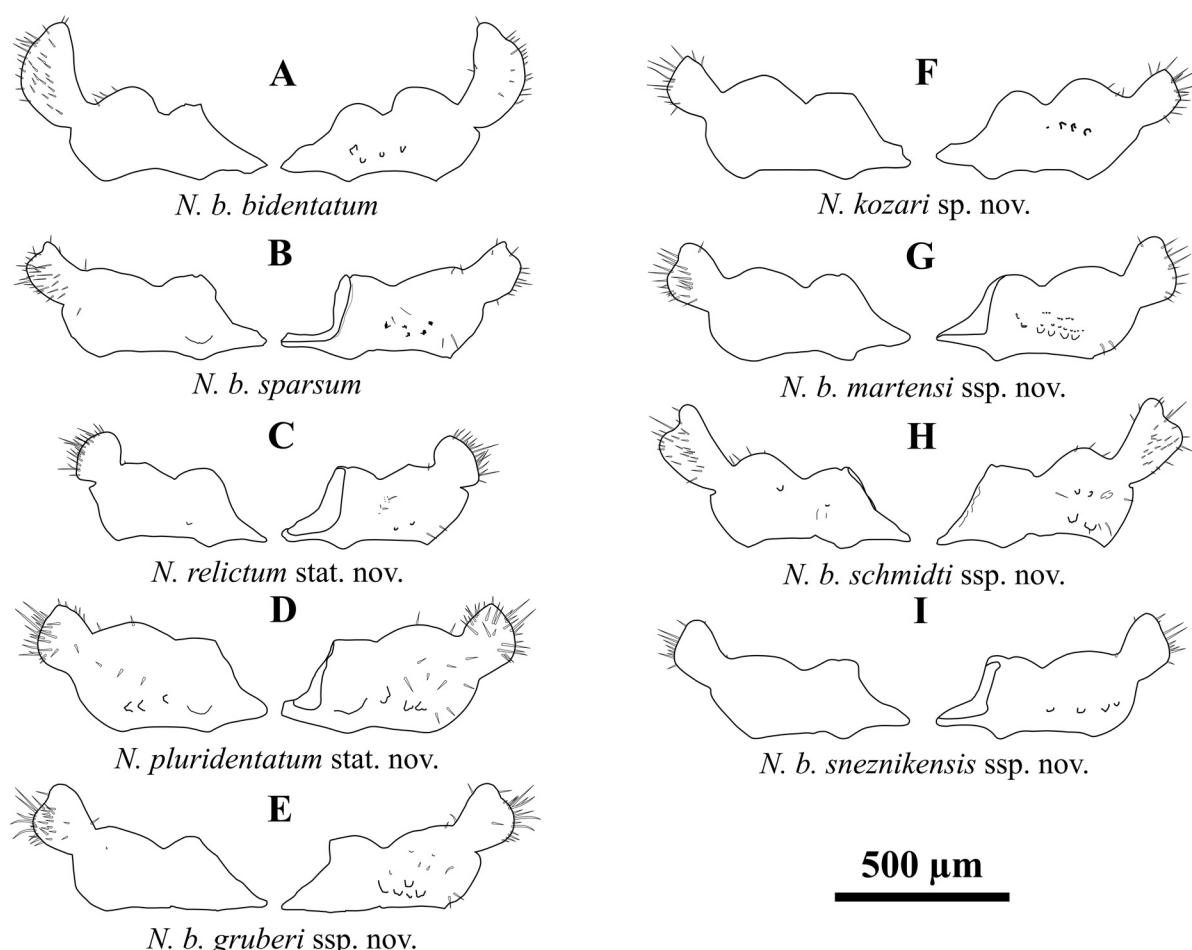


Fig. 4. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. Ch basal articles (medial, lateral views).

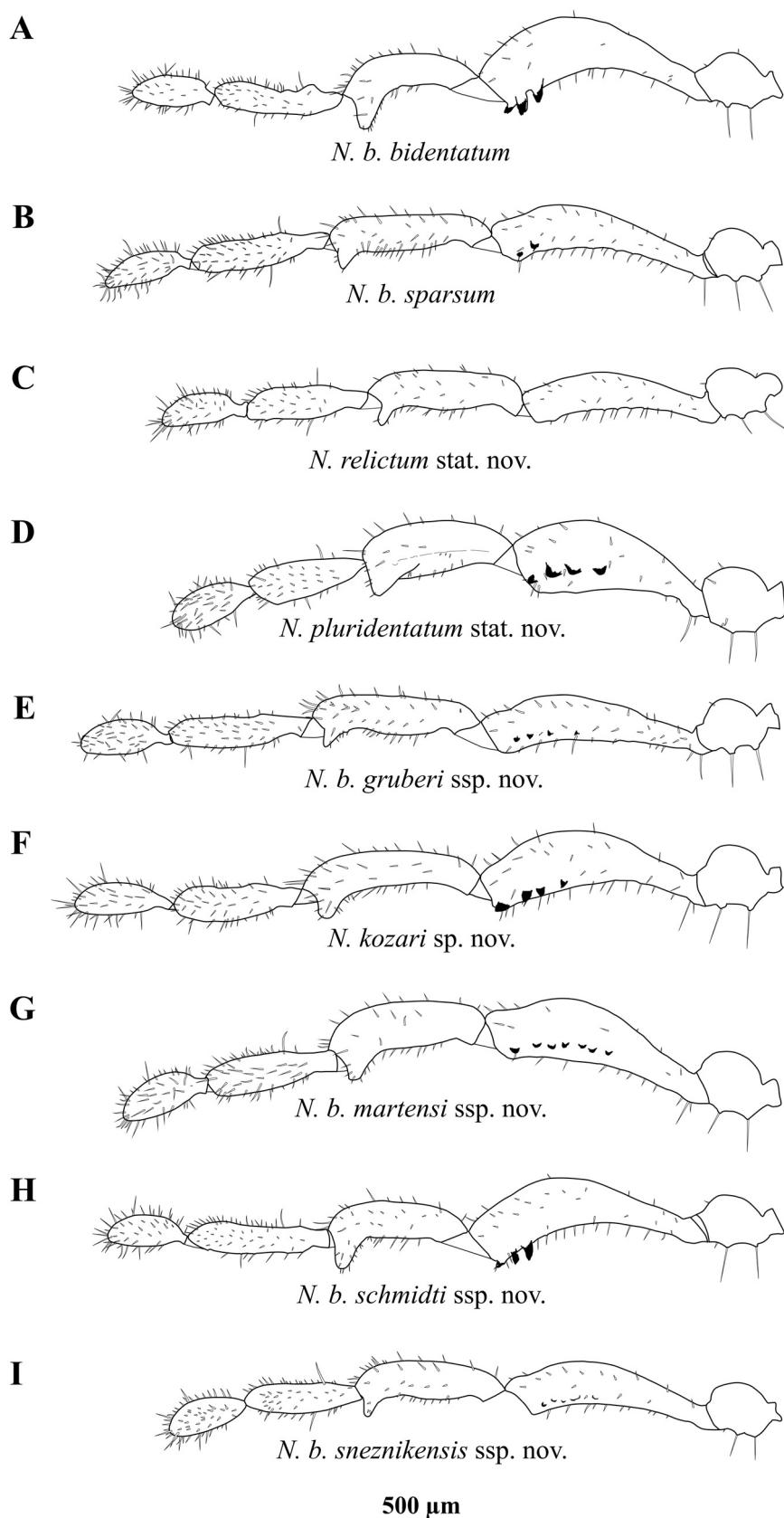


Fig. 5. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. Pa (medial view).

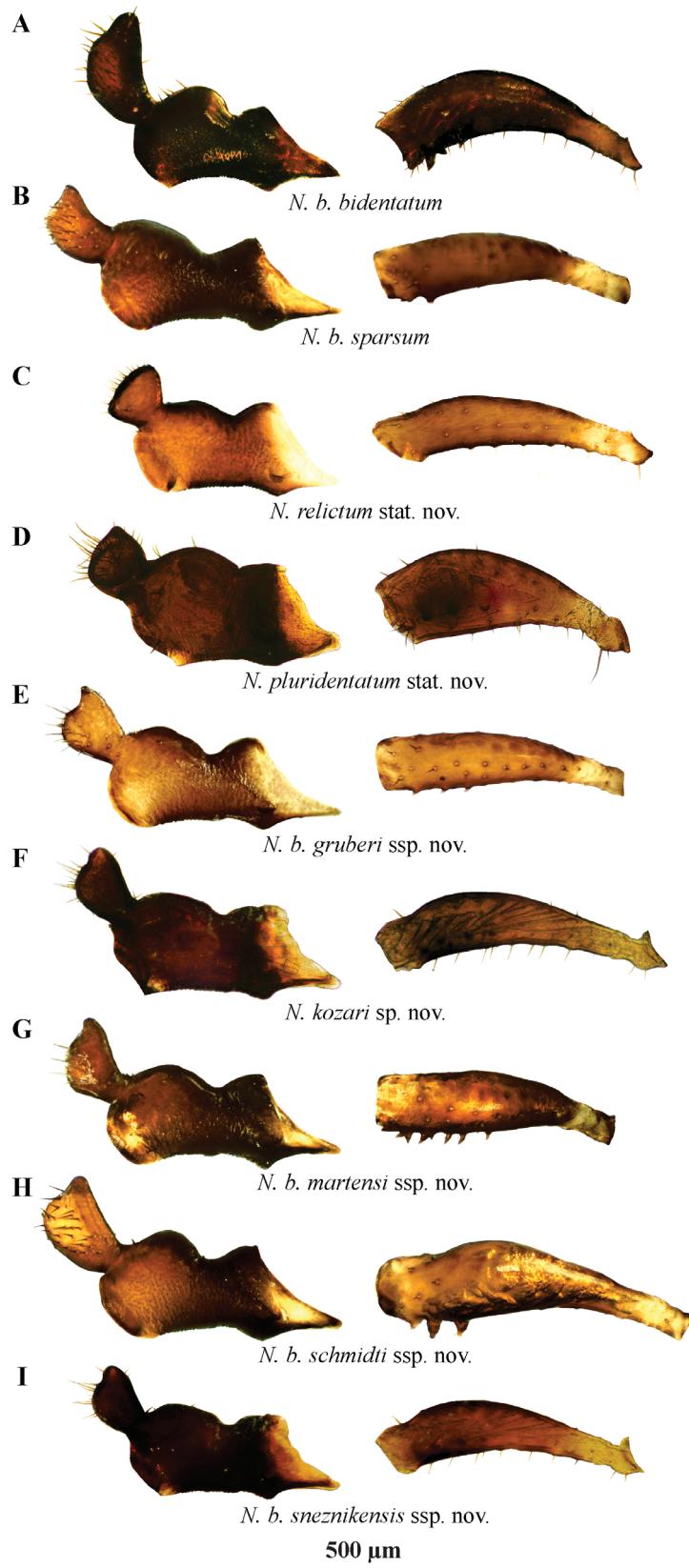


Fig. 6. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. Synchroscopic images of the male Ch basal article and Pa-Fe (medial views, except G, right figure, which is in dorso-medial view).

The largest, western and central portion of Slovenia is occupied by *N. b. schmidti* ssp. nov., which meets *N. b. bidentatum* in the north, and *N. b. martensi* ssp. nov., *N. b. gruberi* ssp. nov., *N. b. sneznikensis* ssp. nov. and *N. b. sparsum* in the southwest to the northeast of the country. The central position of *N. b. schmidti* ssp. nov. in this ongoing parapatric speciation, with hybrid zones between any two subspecies in contact, is congruent with the distinct regional and geomorphological characteristics of the subspecies areas, reflecting the ecological optima of the different subspecies. On the other hand, it is probably the genetic distance between non-neighboring taxa that hinders their hybridization, e.g., in the *bidentatum* – *schmidti* ssp. nov. – *sparsum* taxa. While *N. b. schmidti* ssp. nov. interbreeds with both other taxa, no hybrids are known between *N. b. bidentatum* and *N. b. sparsum* (Gruber & Martens 1968; Martens 1978; Komposch & Gruber 2004; Komposch 2009). This indicates a speciation process reminiscent of that in the ring species (Irwin 2012), with a chain of interbreeding populations in contact, i.e., those acting as subspecies, and reproductively isolated populations, i.e., those acting as species to distant populations if co-occurring secondarily in syntopy.

For credible, morphologically-based identification of taxa within the *N. b.* complex, combined inspection of Ch, Pa, Pe and Rec sem is required; the morphology and length of the extendable ovipositor yield no useful information. This is because of the varying stability of particular characters across the taxa. The

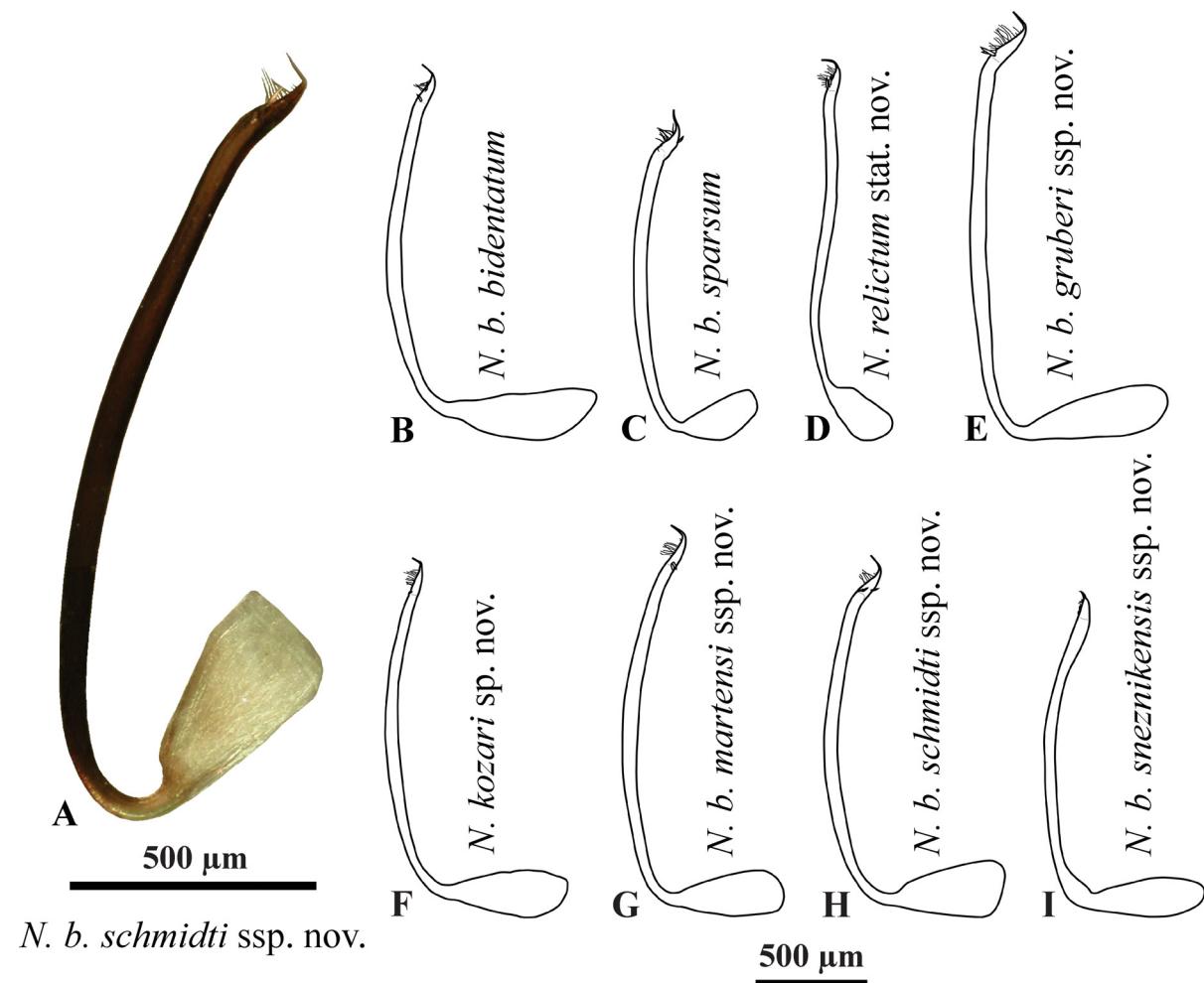


Fig. 7. *Nemastoma bidentatum* Roewer, 1914 complex. Penes (lateral view). Note: The penis of *N. pluridentatum* (Hadži, 1973) stat. nov. is unknown.

shape of the basal Ch article varies considerably, while the Ch-Apo vary to a limited extent, thus being useful for identification. Only *N. b. bidentatum* and *N. b. schmidti* ssp. nov. can be identified on the basis of the Ch-Apo shape alone. The Pa morphology is much less stable. Gruber & Martens (1968) identified morphological variation in the male Fe-Pa in *N. b. bidentatum*, which has two or three distal medio-ventral spines, one of which may be bifid. In *N. b. martensi* ssp. nov., the number and shape of denticles vary from 5 to 11, and from pointed denticles alone to irregularly shaped, blunt tubercles instead of denticles in a row. Instead, *N. b. sneznikensis* ssp. nov. has a row of minute, irregularly shaped tubercles. Such moderate variation is usual in all subspecies, but in *N. b. gruberi* ssp. nov. it is excessive. In this subspecies, the Pa-Fe armament varies from four equidistant, relatively thin medio-ventral spines of subequal sizes in individuals from central-eastern Slovenia, to very small spines or ones diminished to a tubercle with a seta in the corresponding position in the south, or 2 to 3 large, stout thorns in the southwest. Furthermore, the presence of a hump on the Pa-Ti indicates either *N. bidentatum* b. or *N. b. schmidti* ssp. nov. As for the genital characters, the whole Pe size and shape, including the glans shape, are rather unsuitable for

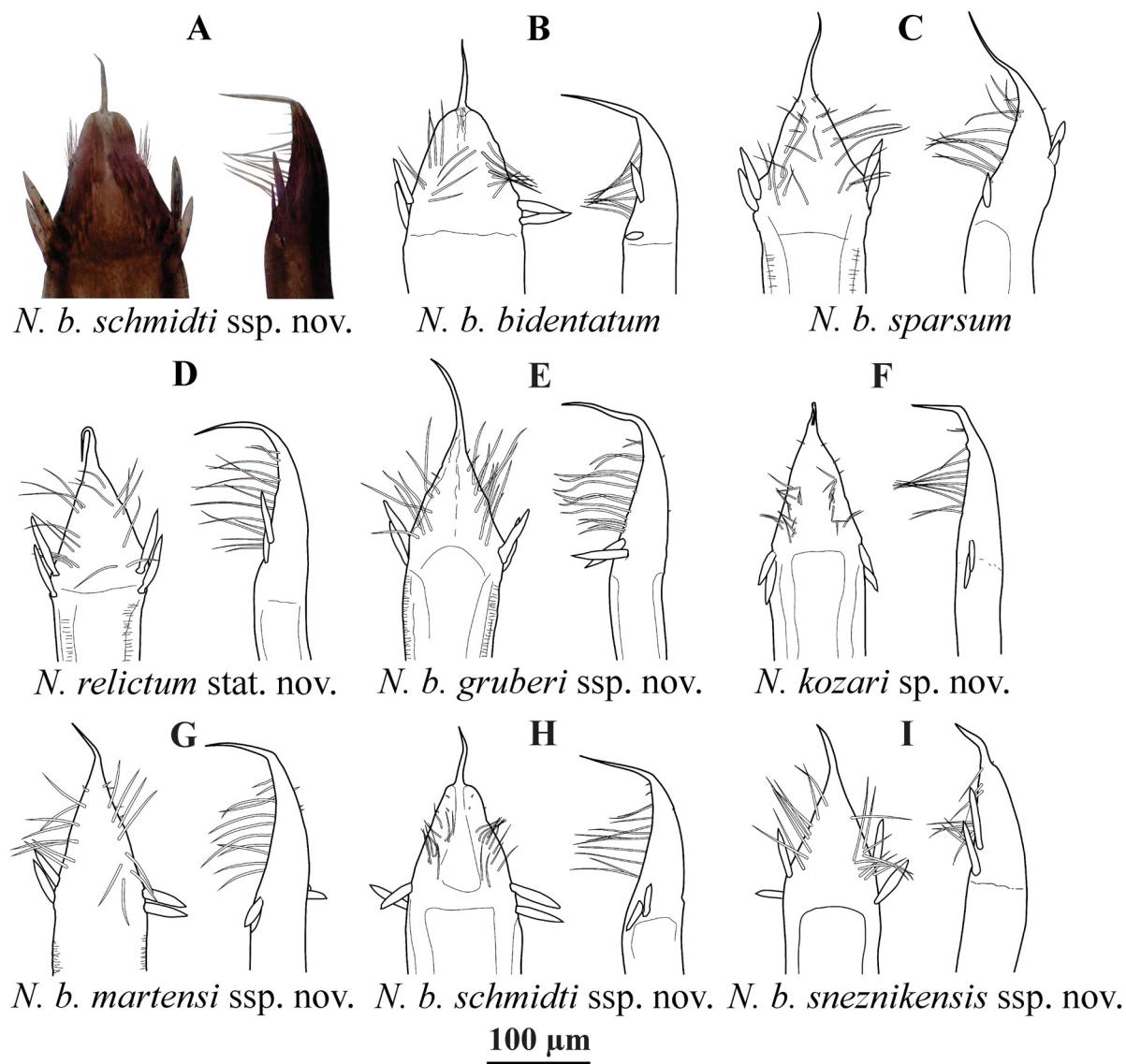


Fig. 8. *Nemastoma bidentatum* Roewer, 1914 complex. Glans (dorsal and lateral views). Note: The penis of *N. pluridentatum* (Hadži, 1973) stat. nov. is unknown.

identification, with the exception of the truncated tip in *N. b. bidentatum* and *N. b. schmidti* ssp. nov. On the other hand, the Rec sem in *N. relictum* stat. nov. and *N. kozari* sp. nov. alone allow credible identification. Otherwise, the genital characters in combination with Ch and Pa characters together allow credible identification in males, and the Ch, Pa and Rec sem in females. In previous studies, females have routinely been ascribed to a taxon in accordance with males identified in the sample (Gruber pers. com.).

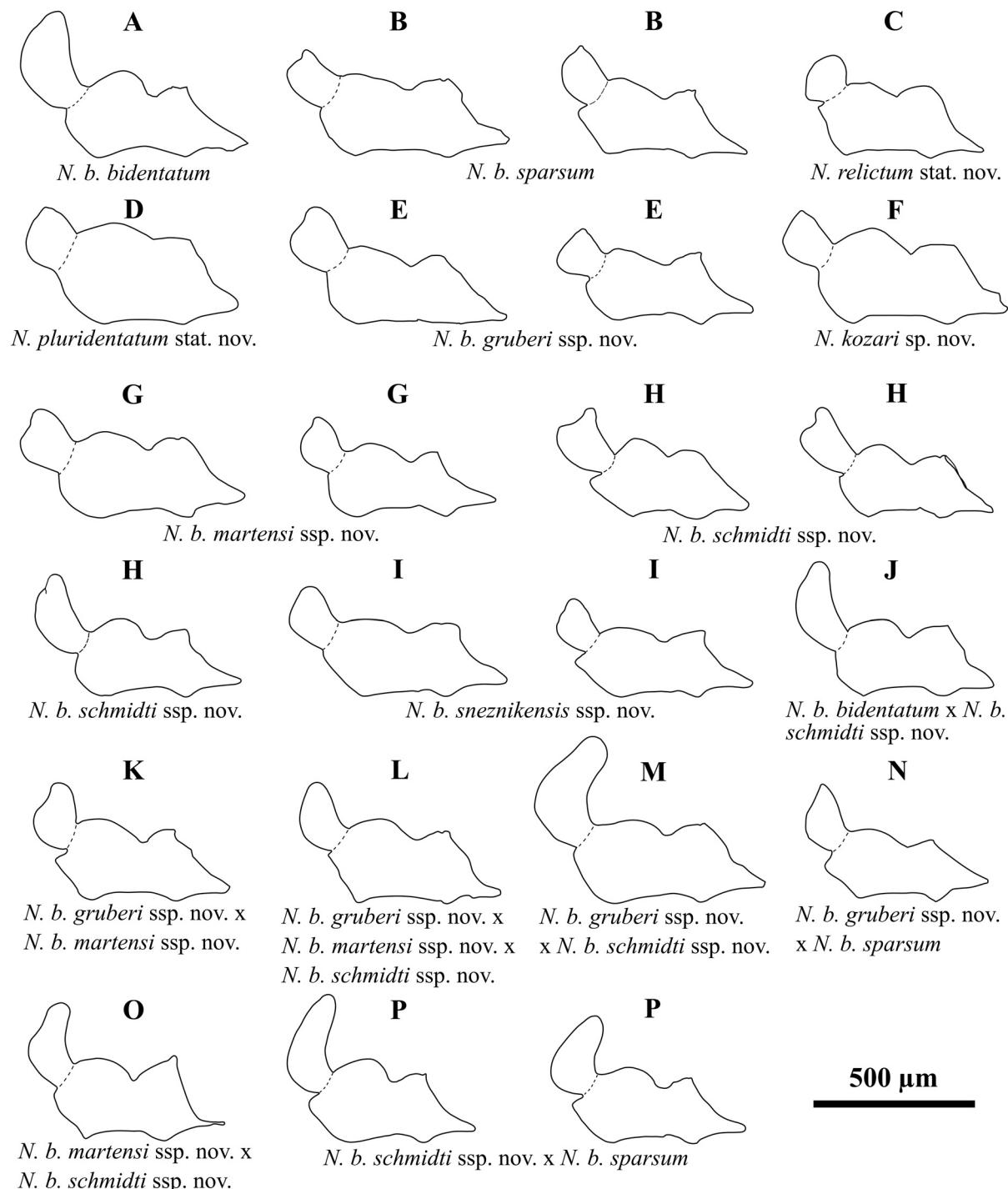


Fig. 9. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. Variation of the Ch basal article (medial view) in species, subspecies and hybrids.

However, the Rec sem, and the Ch basal article, Pa-Tr and Pa-Fe shapes are diagnostic to a varying extent, but always in combination. Males of pure subspecies are easy to identify, while in few cases, identification of females with Rec sem consisting of balloon-like vesicles alone is not certain.

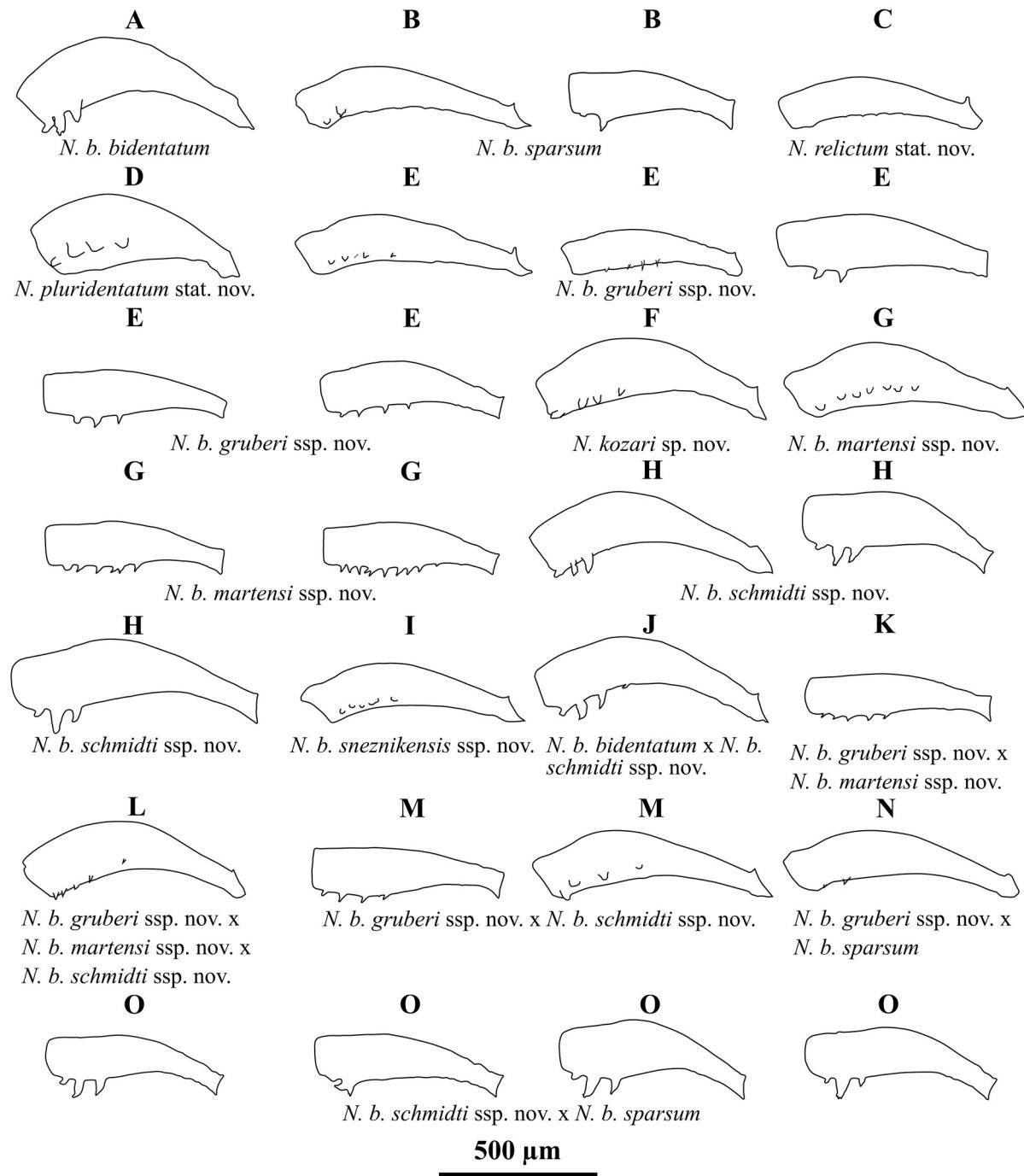


Fig. 10. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. Variation of the Pa-Fe (A–B first image, C, D–E first image, F–G first image; H–J, L–M right, N–O: lateral view; the others in dorso-medial view to show the armament).

We applied the subspecies concept to all relatively uniform populations that exhibit constant differences with respect to other such adjacent populations while interbreeding with them. The standard quantitative level for defining a subspecies is the 75% rule (Patten & Unitt 2002), which states that a subspecies is valid if at least 75% of a population lies outside 99% of the range of the overlapping population for a given character. However, there is disagreement about the 75% threshold and the number of characters that should be used when comparing populations (Patten & Unitt 2002). In subspecies of *N. bidentatum*, this rule can easily be confirmed for all the subspecies, except the polymorphic *N. b. gruberi* ssp. nov. All these taxa fulfill the Braby *et al.* (2012) recommendation for subspecies status. This states that under the unified species lineage, the subspecies are extant groups representing partially isolated lineages of a species that are allopatric, phenotypically distinct, and have one fixed, diagnosable character state. Beside pure subspecies, most typical hybrid males can be easily identified, while hybrids with prevailing characters of one subspecies, and hybrid females are poorly identifiable. In most subspecies combinations, typical hybrid males are characterized by their elongated Ch-Apo, mostly without an apical pinnacle, and usually with a more or less expressed, knee-like flexion of the frontal margin. In contrast, *N. b. gruberi* ssp. nov. × *N. b. sparsum* males have a low, quarter moon-like Ch-Apo, which can only be evaluated in combination with the Pa characters. In any doubtful cases, biogeographical data allow a credible check.

The status of the four species is argued according to combined criteria. The first described *N. bidentatum* is a complex of six subspecies; however, the nominal *N. b. bidentatum* is markedly distinctive from all other taxa within the complex. We gave the species status to *N. relictum* stat. nov. because it has Rec sem with five elongated, sack-like vesicles, which makes it distinctly different from all the subspecies of *N. bidentatum*, in which the Rec sem consists of 12 to 18 balloon-like vesicles. Besides, it lives syntopically with another taxon of the *N. b.* complex, without hybridization. In the case of *N. pluridentatum* stat. nov., we took into account that this taxon shows explicit morphological difference from any other taxon of the *N. b.* complex, including the recently discovered *N. kozari* sp. nov. inhabiting the same mountain.

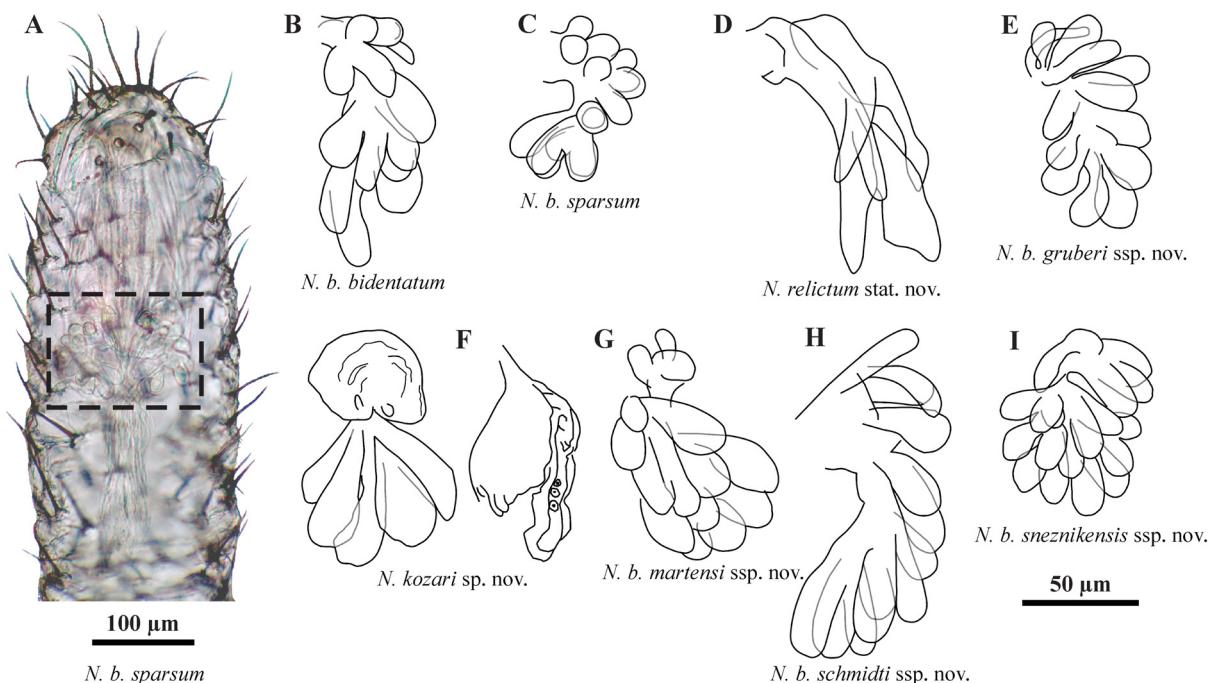


Fig. 11. *Nemastoma bidentatum* Roewer, 1914 complex, ♀♀; Rec sem (lateral view, right portion, except F left figure, which is in dorsal view). A. The frame encloses the ovipositor portion with Rec sem. Note: Female *N. pluridentatum* (Hadži, 1973) stat. nov. is unknown.

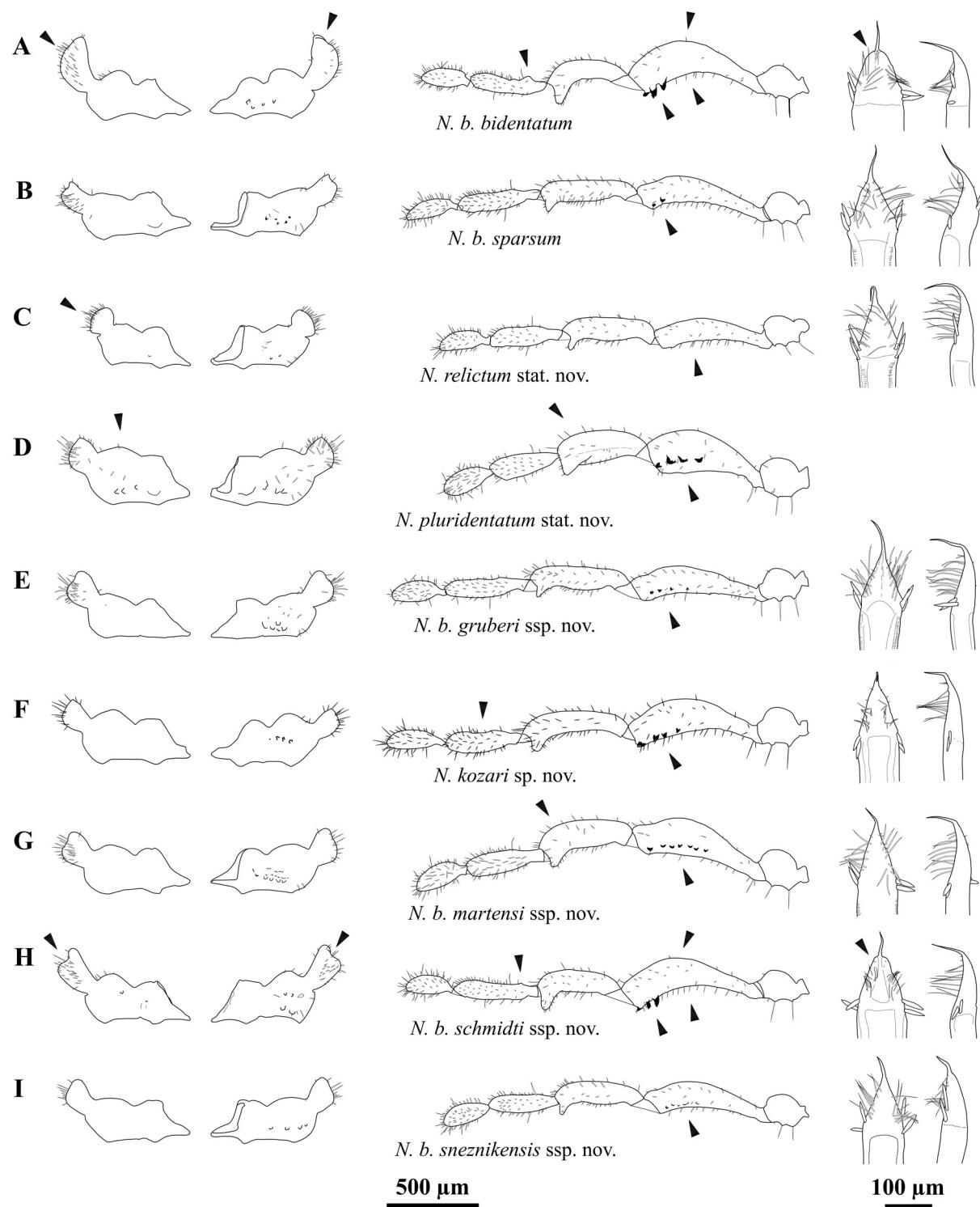


Fig. 12. *Nemastoma bidentatum* Roewer, 1914 complex, ♂♂. From left to right: Ch basal article (medial, lateral views), Pa (medial view) and Pe tip (dorsal, lateral views). Arrows indicate the most identifying characters. Note: Pe of *N. pluridentatum* (Hadži, 1973) stat. nov. is unknown.

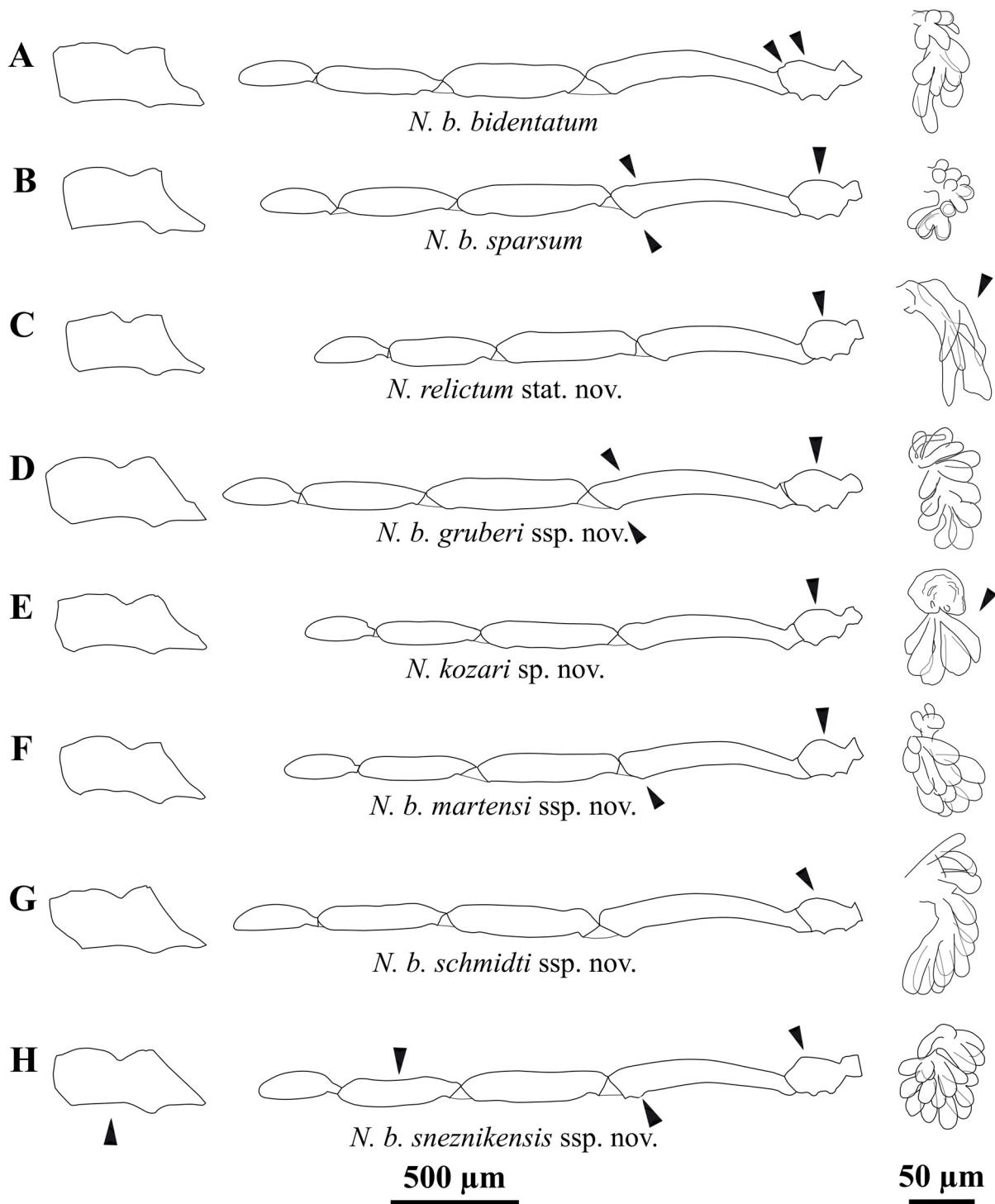


Fig. 13. *Nemastoma bidentatum* Roewer, 1914 complex, ♀♀. From left to right: Silhouettes of the Chelicerae basal article, Pa (both medial view) and Rec sem. Arrows indicate the most identifying characters. Note: female *N. pluridentatum* (Hadži, 1973) stat. nov. is unknown.

Nemastoma relictum stat. nov., *N. pluridentatum* stat. nov. and *N. b. sneznikensis* ssp. nov. are relic taxa inhabiting montane to alpine habitats.

All the morphological findings in this study are supported by chemotaxonomic investigation of the scent gland profiles of the taxa under consideration and by genetics (to be published separately), but these are currently lacking for *N. b. sneznikensis* ssp. nov. due to its sparseness. Further taxa within the *N. b.* complex are expected in the Balkans, especially in the Dinarides.

A clear-cut contact zone between the subspecies of *N. bidentatum* has not been found. Sharp boundaries, such as referred to by Gruber & Martens (1968) and Martens (1978), may occur due to a barrier habitat between the two populations (cf. Monahan *et al.* 2012), such as a wide brook with pebble, sand or clay banks, representing an unsuitable habitat for both subspecies. Otherwise, the contact zones between areas of vicariant subspecies follow the geomorphological variation, or there are narrow or wider hybrid zones in between. Individuals of adjacent subspecies that usually live vicariantly in the contact zone, live syntopically in a contact area of various habitats, e.g., a riparian and an adjacent steep dry forest, or *Nardion strictae* and *Hyperico grisebachii-Pinetum mugo* associations, which might comprise zones only a few meters wide. In most localities in the hybrid zones, hybrids of varying intermediate stages are present, and in some places they live in syntopy with individuals showing pure characters of one or both neighboring subspecies. Most interbreeding zones are a few to 20 km wide, while the overlapping area of *N. b. schmidti* ssp. nov. and *N. b. sparsum* is over 100 km wide in eastern Slovenia. Taking into account various environmental conditions related to the subspecies requirements in the main distribution areas, such flexible borders could be understood.

Field notes on microhabitats inhabited by individual taxa of *N. b.* complex allowed us to conclude that all these taxa – with the exception of *N. pluridentatum* with unknown habitat preferences – are specialized for living in loose litter, deep cushion moss and similar loose microhabitats in riparian, deciduous and pine forests, various scrublands, orchards and high-turf grasslands, and maybe a humus-rich, shallow subterranean habitat (SSH), originally named Milieu Souterrain Superficiel (MSS) (Mammola *et al.* 2016; Halse 2018). Typically, the loose, organic substrate is at least a few centimeters deep, moist, not dry or wet, and with at least a small amount of mull humus. In humid, calm conditions, individuals move on the surface and sometimes climb mushrooms, rotten wood and similar objects. However, individuals are very scarce or lacking at sites with compact litter due to abundant precipitation or the formation of macroaggregates by fungal activity (Coleman *et al.* 2018). This is true for any habitat type, including natural and moderately managed habitats. Thus, the taxa of *N. b.* complex are indicators of loose organic substrate producing humus soils, which indicates a type of pedological process with rich organic strata rather than a specific plant community.

We consider the *N. b.* complex a perfect opportunity to study speciation in Opiliones in general, and Dyspnoi in particular. In the following contributions we shall present chemotaxonomy based on the scent gland profiles and the genetics of the taxa under study. Despite the taxonomic complexity of the *N. bidentatum* group we conclude that morphological approach, based on detailed morphological study and supported by another taxonomic approaches, allows credible identification, which might importantly alleviate current faunistic and ecological investigations.

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Competing interests

The authors declare no competing interests.

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References

- Babalean A.F. 2005. General overview of the opilionid fauna (Arachnida, Opiliones) in Romania. *Scientific Annals of „Alexandru Ioan Cuza” University of Iasi. (New Series), Section 1. Animal Biology* 51: 47–54.
- Blick T. & Komposch C. 2004. Checkliste der Webspinnen Mittel- und Nordeuropas. Checklist of the harvestmen of Central and Northern Europe (Arachnida: Opiliones). Version 27. December 2004. Available from https://arages.de/fileadmin/Pdf/checklist2004_opiliones.pdf [accessed 25 Feb. 2021].
- Braby M.F., Eastwood R. & Murray R. 2012. The subspecies concept in butterflies: has its application in taxonomy and conservation biology outlived its usefulness? *Biological Journal of the Linnean Society* 106: 699–716. <https://doi.org/10.1111/j.1095-8312.2012.01909.x>
- Coleman D.C., Callaham Jr. M.A. & Crossley Jr. D.A. 2018. *Fundamentals of Soil Ecology*. 3rd Ed. Elsevier Academic Press.
- Ćurčić B.P.M., Karaman I.M. & Tomić V.T. 1999. On some new and little known epigean harvestmen (Opiliones, Arachnida) from west Serbia, Yugoslavia. *Arches of Biological Sciences, Belgrade* 51 (4): 61–62.
- De Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/10635150701701083>
- Fernández R., Sharma P.P., Tourinho A.L. & Giribet G. 2017. The Opiliones tree of life: shedding light on harvestmen relationships through transcriptomics. *Proceedings of the Royal Society B* 284: e20162340. <https://doi.org/10.1098/rspb.2016.2340>
- Giribet G. & Sharma P.P. 2015. Evolutionary biology of harvestmen (Arachnida, Opiliones). *Annual Review in Entomology* 60: 157–175. <https://doi.org/10.1146/annurev-ento-010814-021028>
- Gruber J. 1976. Ergebnisse zoologischer Sammelreisen in der Türkei: Zwei neue Nemastomatidenarten mit Stridulationsorganen, nebst Anmerkungen zur systematischen Gliederung der Familie (Opiliones, Arachnida). *Annalen des Naturhistorischen Museums in Wien* 80: 781–801.

- Gruber J. 2007. Dyspnoi – Historical systematic synopsis and family chapters. In: Pinto-da-Rocha R., Machado G. & Giribet G. (eds) *Harvestmen: the Biology of Opiliones*: 131–159. Harvard University Press, Cambridge MA.
- Gruber J. & Martens J. 1968. Morphologie, Systematik und Ökologie der Gattung *Nemastoma* C.L. Koch (s. str.) (Opiliones, Nemastomatidae). *Senckenbergiana Biologica* 49 (2): 137–172.
- Hadži J. 1927. Opilioni Schmidtové zbirke. *Glasnik Muzejskega Društva za Slovenijo* 7–8: 1–41 + VIII.
- Hadži J. 1928. Beitrag zur Kenntnis der Opilioniden-Fauna von Slowenien (Jugoslawien). *Zoologischer Anzeiger* 77 (1–2): 5–19.
- Hadži J. 1931. Opilioni Triglavskoga masiva. *Prirodoslovne razprave* 1: 107–154.
- Hadži J. 1973a. Novi taksoni suhih južin (Opilionidea) v Jugoslaviji. *Razprave SAZU, IV. razred* 16 (1): 1–120.
- Hadži J. 1973b. Opilionidea. In: Hadži J., Lorković Z., Horvatić S., Bole J. & Martinčič A. (Consilium JAZU, eds) *Catalogus Faunae Jugoslaviae III/4*: 1–24. SAZU, Ljubljana.
- Haig M., Beever E.A., Chambers S.M., Draheuim H.M., Dugger B.D., Dunham S., Elliot-Smith E., Fontaine J.B., Kesler D.C., Knaus B.J., Lopes I.F., Loschl P., Mullins T.D. & Sheffield L.M. 2006. Taxonomic considerations in listing subspecies under the U.S. Endangered Species Act. *Conservation Biology* 20 (6): 1584–1594. <https://doi.org/10.1111/j.1523-1739.2006.00530.x>
- Halse S. 2018. Research in calcretes and other deep subterranean habitats outside caves. In: Moldovan O.T., Kováč L. & Halse S. (eds) *Cave Ecology*: 415–434. Springer, Cham. <https://doi.org/10.1007/978-3-319-98852-8>
- ICZN, International Commission on Zoological Nomenclature 1999. *International Code of Zoological Nomenclature (fourth edition)*. The International Trust for Zoological Nomenclature, c/o The Natural History Museum, London.
- Irwin D.E. 2012. A novel approach for finding ring species: look for barriers rather than rings. *BMC Biology* 10: 21. <https://doi.org/10.1186/1741-7007-10-21>
- Isaac N.J.B., Mallet J. & Mace G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology and Evolution* 19: 464–469. <https://doi.org/10.1016/j.tree.2004.06.004>
- Klimeš L. 2000. Checklist of harvestmen (Opiliones) of Czechia and Slovakia. *Ekológia Bratislava* 19, Suppl. 3: 125–128.
- Koch C.L. 1836. *Die Arachniden getreu nach der Natur abgebildet und beschrieben. Vol. 3*. C.H. Zeh'sche Buchhandlung, Nürnberg.
- Komposch C. 1999. Rote Liste der Webspinnen (Arachnida: Opiliones). In: Rottenburg T., Wieser Ch., Mildner P. & Holzinger W.E. (eds): *Rote Listen gefährdeter Tiere Kärntens. Naturschutz in Kärnten* 15: 547–565. Amt der Kärntner Landesregierung, Abt. 20, Landesplanung, Klagenfurt.
- Komposch C. 2002. The harvestmen fauna of Hungary (Arachnida, Opiliones). In: Samu F. & Szinetár Cs. (eds) *Proceedings of the 20th European Colloquium of Arachnology*: 227–242. Szombathely.
- Komposch C. 2009. Opiliones (Webspinnen). In: Rabitsch W. & Essl F. (eds) *Endemiten – Kostbarkeiten in Österreichs Pflanzen- und Tierwelt*: 476–500. Naturwissenschaftlicher Verein für Kärnten & Umweltbundesamt.
- Komposch C. 2011. Endemic harvestmen and spiders of Austria (Arachnida: Opiliones, Araneae). *Arachnologische Mitteilungen* 40: 65–79. <https://doi.org/10.5431/aramit4008>
- Komposch C. & Gruber J. 2004. Die Webspinnen Österreichs (Arachnida, Opiliones). *Denisia* 12, zugleich *Kataloge der Österreichischen Landesmuseen Neue Serie* 14: 485–534.

- Kovač I. 1997. *Suhe južine (Opiliones) v različnih habitatih v Prekmurju. (Harvestmen (Opiliones) in various habitats in Prekmurje.)* Diploma work, Department of Biology, Faculty of Education, University of Maribor.
- Kurt K. 2014. Updated checklist of harvestmen (Arachnida, Opiliones) in Turkey. *Archives of Biological Sciences* 66 (4): 1617–1631. <https://doi.org/10.2298/ABS1404617K>
- Loksa I. 1962. Beiträge zur Kenntnis der Webergnechte-Fauna Ungarns, I. *Zoologischer Anzeiger* 168: 256–269.
- Mallet J. 2013. Subspecies, semispecies, superspecies. In: Levin A.S. (ed.) *Encyclopedia of Biodiversity* 7: 46–48. Elsevier, Academic Press, San Diego. <http://doi.org/10.1016/B978-0-12-384719-5.00138-6>
- Mammola S., Giachino P.M., Piano E., Jones A., Barberis M., Badino G. & Isaia M. 2016. Ecology and sampling techniques of an understudied subterranean habitat: the Milieu Souterrain Superficiel (MSS). *The Science of Nature* 103: e88. <https://doi.org/10.1007/s00114-016-1413-9>
- Marcellino I. 1973. Notizie su Opilioni (Arachnida) italiani e dell'Alto Isonzo. *Annali del Museo Civico di Storia Naturale di Genova* 79: 192–205.
- Martens J. 1978. Spinnentiere, Arachnida: Webergnechte, Opiliones. In: Senglaub F., Hannemann H. & Schumann H. (eds) *Die Tierwelt Deutschlands* 64: 1–464. Fischer Verlag, Jena.
- Martens J. 2006. Webergnechte aus dem Kaukasus (Arachnida, Opiliones, Nemastomatidae). *Senckenbergiana Biologica* 86 (2): 145–210.
- Miralles A., Vasconcelos R., Perela A., Harris D.J. & Carranza S. 2010. An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). *Zoologica Scripta* 10: 1–29. <https://doi.org/10.1111/j.1463-6409.2010.00453.x>
- Monahan W.B., Pereira R.J. & Wake D.B. 2012. Ring distributions leading to species formation: a global topographic analysis of geographic barriers associated with ring species. *BMC Biology* 10: e20. <https://doi.org/10.1186/1741-7007-10-20>
- Mučalica M. 1988. A contribution to the study of harvestmen (Opiliones, Arachnida) on the mountains Avala and Fruska gora (Serbia, Yugoslavia). *Glasnik Prirodnjačkog muzeja srpske zemlje. Serija B, Biološke nauke* 43/44: 193–198.
- Murphree C.S. 1988. Morphology of the dorsal integument of ten opilionid species. *Journal of Arachnology* 16 (2): 237–252.
- Novak T. 2004a. Harvestmen of the Museo Friulano di Storia Naturale in Udine (Arachnida: Opiliones). Part 1. *Gortania* 26: 211–241.
- Novak T. 2004b. An overview of harvestmen (Arachnida: Opiliones) in Croatia. *Natura Croatica* 13: 231–296.
- Novak T. 2005a. An overview of harvestmen (Arachnida: Opiliones) in Bosnia and Herzegovina. *Natura Croatica* 14: 301–350.
- Novak T. 2005b. The harvestmen fauna (Arachnida: Opiliones) from the Sub Mediterranean region of Slovenia – II. *Annales, Series historiae naturalis* 15: 103–114.
- Novak T. 2005c. Terrestrial fauna from cavities in Northern and Central Slovenia, and a review of systematically ecologically investigated cavities. *Acta Carsologica* 34: 169–210. <https://doi.org/10.3986/ac.v34i1.285>
- Novak T. & Gruber J. 2000. Remarks on published data on harvestmen (Arachnida: Opiliones) from Slovenia. *Annales, Series historiae naturalis* 10: 281–308.
- Novak T., Gruber J. & Slana L. 1984. Remarks on Opiliones from cavities in Slovenia (Yugoslavia). *Mémoires de Biospéologie* 11: 185–197.

- Novak T., Gruber J. & Slana L. 1995. A contribution to the knowledge of the harvestmen (Opiliones) from the submediterranean region of Slovenia. *Annales, Series historiae naturalis* 5: 181–192.
- Novak T., Gruber J. & Slana L. 1996. Webergnachte (Opiliones) des Zentral-Europäischen zoogeographischen Gebietes Sloweniens. *Znanstvena revija, Maribor* 7: 47–60.
- Novak T., Slana L., Červek N., Mlakar M., Žmaher N. & Gruber J. 2002. Harvestmen (Opiliones) in human settlements of Slovenia. *Acta Entomologica Slovenica* 10: 131–154.
- Novak T., Lipovšek Delakorda S. & Slana L. 2006. A review of harvestmen (Arachnida: Opiliones) in Slovenia. *Zootaxa* 1325 (1): 267–276. <https://doi.org/10.11646/zootaxa.1325.1.17>
- Novak T., Janžekovič F., Rak M., Ivajnšič D., Kozel P., Slana Novak L. & Škornik S. 2017. Can highland habitat type distributions replace mapping of harvestman species? *Journal of Insect Conservation* 21 (2): 331–343. <https://doi.org/10.1007/s10841-017-9979-x>
- Oatley G., Bowie R.C.K. & Crowe T.M. 2011. The use of subspecies in the systematics of southern African white-eyes: historical entities or eco-geographic variants. *Journal of Zoology* 284: 21–30. <https://doi.org/10.1111/j.1469-7998.2010.00772.x>
- Patten M.A. & Unitt P. 2002. Diagnosability versus mean differences of sage sparrow subspecies. *The Auk* 119 (1): 26–35. <https://doi.org/10.1093/auk/119.1.26>
- Rasputnig G., Leutgeb V., Schaider M. & Komposch C. 2010. Naphthoquinones and anthraquinones from scent glands of a dyspnoid harvestman, *Paranemastoma quadripunctatum*. *Journal of Chemical Ecology* 36: 158–162. <https://doi.org/10.1007/s10886-010-9745-y>
- Rasputnig G., Bodner M., Schäffer S., Koblmüller S., Schönhofer A. & Karaman I. 2014. Chemosystematics in the Opiliones (Arachnida): a comment on the evolutionary history of alkylphenols and benzoquinones in the scent gland secretions of Laniatores. *Cladistics* 30: 1–8. <https://doi.org/10.1111/cla.12079>
- Rasputnig G., Schaider M., Föttinger P. & Schönhofer A. 2017. A model for phylogenetic chemosystematics: Evolutionary history of quinones in the scent gland secretions of harvestmen. *Frontiers in Ecology and Evolution* 5: 139. <https://doi.org/10.3389/fevo.2017.00139>
- Roewer C.F. 1914. Die Familien der Ischyropsalidae und Nemastomatidae der Opiliones–Palpatores. *Archives für Naturgeschichte* 80 A (3): 99–169.
- Roewer C.F. 1917. Über Nemastomatiden und ihre Verbreitung. *Archives für Naturgeschichte* 83 A (2): 140–160.
- Roewer C.F. 1923. *Die Webergnachte der Erde*. Gustav Fischer, Jena.
- Roewer C.F. 1951. Über Nemastomatiden. Weitere Webergnachte XVI. *Senckenbergiana* 32: 95–153.
- Sangster G. 2009. Number of bird species result from taxonomic progress, not taxonomic inflation. *Proceedings of the Royal Society B* 276 (1670): 3185–3191. <https://doi.org/10.1098/rspb.2009.0582>
- Schaider M., Novak T., Komposch C., Leis H.-J. & Rasputnig G. 2018. Methyl-ketones in the scent glands of Opiliones: a chemical trait of cyphophthalmi retrieved in the dyspnoan *Nemastoma triste*. *Chemoecology* 28: 61–67. <https://doi.org/10.1007/s00049-018-0257-5>
- Schönhofer A.L. 2013. A taxonomic catalogue of the Dyspnoi Hansen and Sørensen, 1904 (Arachnida: Opiliones). *Zootaxa* 3679 (1): 1–68. <https://doi.org/10.11646/zootaxa.3679.1.1>
- Schönhofer A.L. & Holle T. 2007. *Nemastoma bidentatum* (Arachnida: Opiliones: Nemastomatidae): neu für Deutschland und die Tschechische Republik. *Arachnologische Mitteilungen* 33: 25–30. <https://doi.org/10.5431/aramit3306>

- Schulz J.W. & Pinto-da-Rocha R. 2007. Morphology and functional anatomy. In: Pinto-da-Rocha R., Machado G. & Giribet G. (eds) *Harvestmen: the Biology of Opiliones*: 14–61. Harvard University Press, Cambridge MA.
- Staręga W. 1976. Webergnechte (Opiliones, excl. Sironidae) Bulgariens. *Annales Zoologici* 33(18): 287–433.
- Šilhavý V. 1956. Sekáči – *Opilionidea*. In: *Fauna ČSR* 7. Nakladatelství Československé akademie věd, Praha.
- Torstrom S.M., Pangle K.L. & Swanson B.J. 2014. Shedding subspecies: The influence of genetics on reptile subspecies taxonomy. *Molecular Phylogenetics and Evolution* 76: 134–143.
<https://doi.org/10.1016/j.ympev.2014.03.011>
- Willemart R.H., Farine J.-P. & Gnaspi P. 2009. Sensory biology of Phalangida harvestmen (Arachnida, Opiliones): a review, with new morphological data on 18 species. *Acta Zoologica* 90: 209–227.
<https://doi.org/10.1111/j.1463-6395.2008.00341.x>
- Wolff J.O., García-Hernández S. & Gorb S.N. 2016. Adhesive secretions in harvestmen (Arachnida: Opiliones). In: Smith A.M. (ed.) *Biological Adhesives*: 281–301. Springer.
<https://doi.org/10.1007/978-3-319-46082-6>
- Zink R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society London B* 271: 561–564. <https://doi.org/10.1098/rspb.2003.2617>

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