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## Research article

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# The *Leiobunum rupestre* species group: resolving the taxonomy of four widespread European taxa (Opiliones: Sclerosomatidae)

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**Abstract.** Within the central European opilionid fauna the widely used species names *Leiobunum rupestre* Herbst, 1799 and *Leiobunum tisciae* Avram, 1968 pose taxonomic and distributional problems. In addition, *Nelima apenninica* Martens, 1969 is close to *L. tisciae* in terms of external and genital morphology, but is specifically distinct. While coxal denticulation is largely lacking in *N. apenninica*, the validity of the genus *Nelima* Roewer, 1910 is questioned again. In addition, *Leiobunum subalpinum* Komposch, 1998, a recently described novelty from the eastern Alps, is closely related to *L. rupestre*. The four species are combined as the morphologically defined *Leiobunum rupestre* species group. Except for *L. subalpinum*, they were found to be allopatrically distributed from the Carpathians across central and Northwest Europe to the south-western Alps. The latter species is locally sympatric and partly elevationally parapatric to *L. rupestre*. *Leiobunum tisciae* is a recently introduced name and here recognized as a junior synonym of a number of taxa described much earlier, of which *L. gracile* Thorell, 1876 is re-introduced as oldest available name. Detailed morphological and distributional data for all taxa are presented.

**Keywords.** Taxonomy, synonymy, *Leiobunum*, *Nelima*, Europe.

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## Introduction

A common problem with the Sclerosomatidae Simon, 1879 (harvestmen) is their morphological plasticity as well as their general uniformity, making it often difficult to draw well-recognizable species borders. Even more problematic, especially in the tropics, is the differentiation of higher taxonomic levels from species category upwards (Hedin *et al.* 2012). Applying this difficulty to widespread, closely related and morphologically similar taxa can further hinder discrimination. Here the similar species *Leiobunum rupestre* (Herbst, 1799), *L. subalpinum* Komposch, 1998, *L. tisciae* Avram, 1968 and *Nelima apenninica* Martens, 1969 are investigated and summarized as the *Leiobunum rupestre* species group, though being

generally grouped with two different genera. The four species occupy large parts of central and south-eastern Europe, parts of Scandinavia (Finland, Norway, Sweden), locally Great Britain, continental Italy and south-western France, but sympatric occurrences are unknown (Fig. 2), except for *L. subalpinum* whose distribution is nested within the area of *L. rupestre*. Discrimination of *L. rupestre* and *L. tisciae* has been under debate since Martens (1978) included *L. tisciae* into the central European fauna, even though male genital morphology was properly described and is straightforward. A number of European countries stated the presence of one or two of these species thereafter (e.g., Great Britain: Davidson 2009; Denmark: Enghoff 1988; Czech Republic and Slovak Republic: Šilhavý 1981; Italy: Chemini 1980; Marcelino 1971; Poland: Staręga 2004; Norway: Stol 2003, 2010a, b; Estonia: Staręga 1978; Tomasson *et al.* 2014; Latvia: Tumšs 1963; Spungis 2008), but a complex morphological and taxonomic situation was evident.

The description of *L. tisciae* by Avram (1968) was shortly followed by that of *Nelima apenninica* by Martens (1969), who soon recognized that both species are fairly similar in terms of genital morphology, but he was primarily concerned to discriminate *Leiobunum rupestre* against *L. tisciae* (Martens 1978). Up to today, *N. apenninica* remains poorly known, being recorded from widely scattered localities. These four species raise taxonomic problems and need to be well defined. *L. tisciae* and *N. apenninica* having been described relatively recently, and especially because *L. tisciae* spans a large European area, making it likely that it has been described under an older name before. *L. subalpinum*, a novelty from the eastern Alps, added a further complexity to species recognition in this group of locally common long-legged harvestmen. Taking this argumentation into account and based on representative reference material, we here revalidate the species status, synonymy and distribution of the representatives of the *L. rupestre* species group. The taxa *Leiobunum nigripalpe* Simon, 1879 and “*Leiobunum* sp.”, the latter a recent immigrant to western central Europe (Wijnhoven *et al.* 2006), are not part of the *L. rupestre* species group and are not treated here.

## Material and methods

Material investigated: 54 series of *L. rupestre*, 40 series of *L. tisciae* and 20 series of *N. apenninica* were checked; details are listed in the Material sections (see Appendix). Also literature sources, which we feel present reliable records, are listed there.

### Collection acronyms as used:

- SMNH = Naturhistoriska riksmuseet, Stockholm, Sweden
- AXLS = Coll. Axel Schönhofer, Mainz, Germany
- CIK = Coll. Ivo Karaman, Novi Sad, Serbia
- CJM = Coll. Jochen Martens, Mainz, Germany
- SMF = Arachnology Section, Senckenberg Museum, Gesellschaft für Naturforschung, Frankfurt am Main, Germany

### Abbreviations used in the descriptive parts:

- Abd, abd = Abdomen, abdominal
- Ceph = cephalothorax
- Fe = femur
- Mt = metatarsus
- Palp = palpus, pedipalpus
- Pt = patella
- Ta = tarsus
- Terg = tergite
- thorac = thoracic

Ti = tibia  
 To oc = tuber oculorum, ocularium, eye mound

Original line drawings were produced using a camera lucida attached to a Leitz dissecting Microscope and a Leitz Laborlux Microscope. Measurements were taken by means of a micrometer disc using the same optical devices. All measurements are given in mm.

### Distributional data

From a total of 2600 text-recognized pdf files of opilionid literature, those matching the search strings ‘apenninica’, ‘rupestre’ or ‘tisciae’ were selected. Following our established synonymy further, references were extracted manually and all identifiable distributional records of the *L. rupestre* group were geo-referenced. Of these records only a limited number of the recorded specimens was available to us and geographic reconstructions relied on our representative samplings and sound publication data. We assume Šilhavý (1981) and Staręga (1976, 2004) to have correctly discriminated *L. rupestre* and *L. ‘tisciae’* (*L. glabrum* in Šilhavý 1981) and their data already demarked a North-to-South running borderline between the two species in the Czech Republic and Slovakia (Šilhavý 1981) and in Poland (Staręga 2004). We further interpreted all records east of this line (e.g., *L. rupestre* in Staręga 1978) and north of the central mountain ranges in Germany (e.g., Stol 2010a, b) as *L. ‘tisciae’*, primarily based on investigation of available material. If we found coverage of records sufficiently reliable and indicative of general distributional interpretation we did not map additional records in the relevant area (for these, see in more detail: *L. tisciae*: Denmark: Meinertz 1964; Enghoff 1988; Great Britain: British Arachnological Society 2016; *L. rupestre* and *tisciae* combined: Germany: Staudt 2016). All reconstructed localities are given in Fig. 2 and Appendix 1. Up to-date distributional data of *Leiobunum subalpinum* was available from Komposch (1998, 2009b) and we did not search for any additional records.

### Results

Class Arachnida Cuvier, 1812  
 Order Opiliones Sundevall, 1833  
 Suborder Palpatores Thorell, 1876  
 Family Sclerosomatidae Simon, 1879  
 Subfamily Leiobuninae Banks, 1893  
  
 Genus *Leiobunum* C.L. Koch, 1839

### Type species

Designation by Thorell, 1876: *Opilio fasciatus* Herbst, 1798 = *Leiobunum rotundum* (Latreille, 1798).

### Remark

Of the representative material investigated, we found the four hypothesized species well separable upon a number of somatic and male genital morphological characters, which are summarized in Table 1 for convenient use. Species appear largely allopatric, except for *L. subalpinum*, which is firmly nested within the area of *L. rupestre*. In addition, parapatric and locally sympatric occurrences of two species under discussion in East-Central Europe cannot be excluded, especially in South Poland, the central Alps and close to the Czech/Slovak border area (Fig. 2).

*Leiobunum subalpinum* Komposch, 1998 is considered most closely related to *L. rupestre* (Komposch 1998) and, as such, is also regarded as a member of the *L. rupestre* species group. As it is easily discriminated from all discussed forms by its dark coxal markings and, apart from *L. rupestre*, by its restricted alpine range, it is not featured here (see Komposch 1998; Komposch & Gruber 2004 for

**Table 1.** Comparison of somatic characters of *Leiobunum apennanicum* (Martens, 1969), *L. gracile* Thorell, 1876 and *L. rupestre* Herbst, 1799. *L. subalpinum* Komposch, 1998 is not included, because it is very similar to *L. rupestre* and is easily identified by its black coxal markings. For comparison with *L. rupestre* we refer to Komposch (1998). If not otherwise mentioned, characters apply to males only. Characters outlining a single species are given in bold, more variable characters are given in italics. The combination of several characters for determination is advised. Palpal spination is variable, apparently the appearance in ordered rows is an individual character. Body coloration varies with age and population, aged specimens are darkest.

<i>L. rupestre</i> Herbst, 1799	<i>L. gracile</i> Thorell, 1876	<i>L. apennanicum</i> (Martens, 1969)
<b>in both sexes dorsum smooth, granulation cannot be distinguished with 250×, with a few pointed granules present</b>	in both sexes dorsal granulation consisting of flat, pointed granules, regularly spaced, well visible at 250×	in both sexes dorsal granulation consisting of flat, pointed granules, regularly spaced, well visible at 250×
palp-femur with irregular rows of medium-sized triangular spines on ventral side; dorsal side few on distal part, ventral spines more slender, many pointing downward	palp-femur with irregular rows of large triangular spines on ventral side; dorsal side few on distal part, ventral spines broader, not so slender	<b>palp-femur with few spines, normally restricted to ventro-distal, rarely few large spines on ventral side, only single spines on dorso-distal side</b>
palp-tibia slightly concave in lateral view at ventro-distal end, therefore forming a flat S-bend	palp-tibia slightly concave at ventro-distal end, therefore forming a flat S-bend	<b>palp-tibia not concave at ventro-distal end, therefore forming a flat C-bend</b>
palp-patella appears longer and less massive	palp-patella appears longer and less massive	<b>palp-patella appears shorter and more massive</b>
palp-tarsus bent over its whole length	<b>palp-tarsus mostly straight, bent only in distal third</b>	palp-tarsus bent over its whole length
<b>denticles and hairs on ventral side of palp-tibia darker and therefore well visible</b>	spines and hairs on ventral side of palp-tibia lighter and therefore hard to be seen	spines and hairs on ventral side of palp-tibia lighter and therefore hard to be seen
eye mound in both sexes always without spines	eye mound in both sexes without spines, sometimes one spine present	<b>eye mound in both sexes with 1–3 small spines on each side, rarely absent</b>
<b>in both sexes dorsal coloration without pair of white spots on each area along the median line</b>	in both sexes dorsal coloration with small white spots on each area along the median line	in both sexes dorsal coloration with pair of white spots on each area along the median line
<i>in females no lateral coloration of opisthosoma with a blurred parallel pattern of zigzag lines</i>	<i>in females lateral coloration of opisthosoma with a blurred parallel pattern of zigzag lines, best seen at low magnification</i>	<i>in females lateral coloration of opisthosoma with a blurred parallel pattern of zigzag lines, best seen at low magnification</i>

details) except for general remarks; its geographic range is indicated in Fig. 2. In addition, the poorly known *Leiobunum nigripalpe* Simon, 1889, described from the western Alps (France), was reinvestigated. However, the type series represents a composite collection of at least two different small *Nelima* Roewer species, both unaffiliated to the *L. rupestre* species group. This holds true, too, for the specimen depicted as *Leiobunum nigripalpe* in Martens (1978), representing a yet to be identified *Leiobunum* species.

### Species accounts of the *Leiobunum rupestre* group

#### *Leiobunum rupestre* (Herbst, 1799)

Figs 1A–B, 2, 3A–B, 4A–B, H–G, 5A–C

*Phalangium bicolor* Fabricius, 1793: 429. The name was synonymized with *Gyas annulatus* by Latreille (1804), which was missed by several subsequent authors; some of these used it as valid name, in synonymy of, or in relation to, *L. rupestre* (e.g., C.L. Koch 1847, 16: 56; redescription).

*Opilio rupestris* Herbst, 1799: 4, fig. 1 (material from the type locality Sachsen, i.e., Saxony, examined).

*Leiobunum ovale* C.L. Koch, 1848: 59, fig. 1540.

*Liobunum glabrum* L. Koch, 1869: 4, 6–7.

*Leiobunum ovale* – Roewer 1910: 203. — Šilhavý 1956: 174. — Novak & Gruber 2000: 299.

*Phalangium bicolor* – Simon 1879: 181. — Roewer 1910: 203 (both also listing *Phalangium annulatum* in synonymy). — Lessert 1917: 16.

*Liobunum rupestre* – Simon 1879: 181. — Cantoni 1882: 194. — Hansen 1884: 500. — Kraepelin 1896: 222. — Roewer 1910: 197, 203. — Lessert 1917: 15. — Roewer 1923: 890 (partim). — Hadži 1931: 145. — Šilhavý 1956: 174, figs 437–443.

*Liobunus rupestris* – Müller & Schenkel 1895: 819.

*Liobunum glabrum* – Simon 1879: 181.

*Nelima glabra* – Roewer 1910: 239. — Hadži 1931: 148.

*Leiobunum rupestre* – Šilhavý 1948: 9, 24, table 6, figs 4–6. — Martens 1978: 408–412, figs 778–780, 788. — Komposch 1998: 26–27, 34, figs 5, 10, 14, 21.

### Taxonomic history

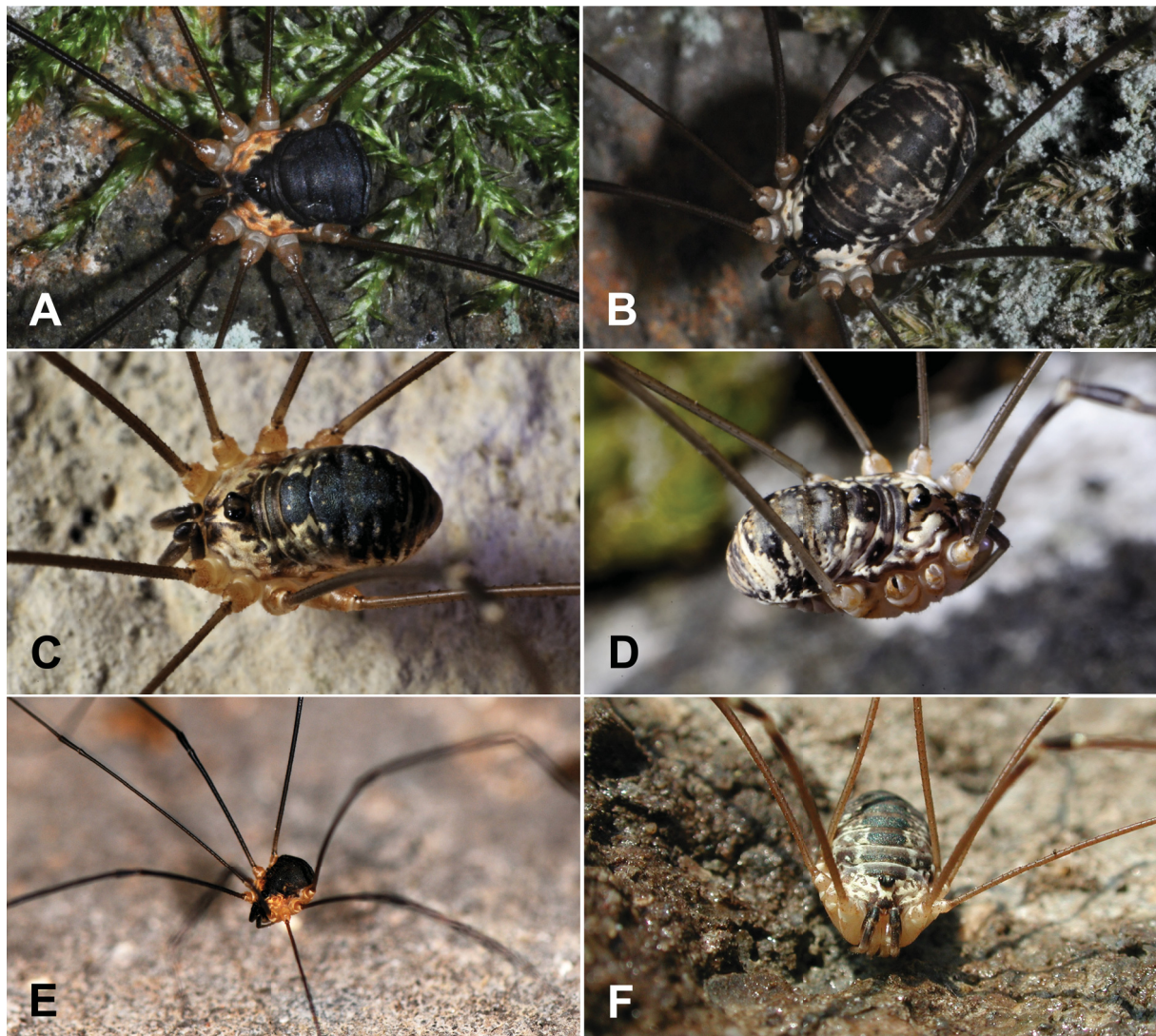
At first glance rather complex, but many distributional records from East central, Northwest and North Europe in reality refer to *Leiobunum 'tisciae'* (see below, *L. gracile*). *L. rupestre* is a montane species and well known from low to mid-altitudes of the central and eastern Alps and mountainous areas in the Czech Republic and north of the Alps in Germany. Its genital morphology is quite characteristic and was first reliably depicted by Šilhavý (1948, figs 4–6; 1956, figs 437–439), fully in accordance with drawings in Martens (1978, fig. 778) and Komposch (1998, figs 9–10). *Leiobunum* populations in the Carpathians, Poland (Staręga 1976), southern Finland (Heinäjäki 1944), along the Baltic coast hinterland and Denmark were also largely affiliated to *L. rupestre* (Martens 1978, fig. 787), though erroneously. These older determinations mostly neglected the genital morphology of these crucial northern populations, which was reconsidered after Avram (1968) published a new species, *L. tisciae*, clearly distinct from *rupestre* but similar in external morphology. Due to its wide distribution, the majority of available names for the eastern and northern populations can be assigned to the synonym of its oldest name *L. gracile* (see below).

Excluding the complex synonymy of *L. tisciae* (*gracile*), only one uncertain affiliation remains for *L. rupestre*: the name *Liobunum glabrum* L. Koch, 1869. Šilhavý (1956: fig. 443) originally treated 'glabra' as the juvenile *L. rupestre*, but later used this name to distinguish allopatric populations of western *L. rupestre* and eastern *L. 'glabra'* (later named *L. tisciae*) in former Czechoslovakia (Šilhavý

1981). This was contradicted by Staręga (2004), because the type locality of *L. glabrum*, Meran (northern Italy, southern Alps), is situated deeply within the territory of *L. rupestre* (Martens 1978). We suggest following Hadži (1931) and Martens (1978) to correctly place *Leiobunum glabrum* in the synonymy of *L. rupestre*.

### Diagnosis

A medium-sized *Leiobunum* species with blackish upper side, except for broad, white markings on Ceph disto-laterally in male (Figs 1A, 3A), broad, blackish irregular saddle-like marking all over the length of the body in female with extended white markings laterally from Ceph to abd Area II and a cross stripe all over area V (Figs 1B, 3B). In both sexes series of para-median lines of small white spots on the abd areae I–V are absent. Contrasting yellowish underside including coxae of all appendages. Wings of truncus penis broad, broadest in lower third part of truncus (Fig. 5A–B). Coxa IV with retrolateral row of granules.



**Fig. 1.** Habit of *Leiobunum rupestre* species group. **A–B.** *Leiobunum rupestre* Herbst, 1799, Slovenia, Pohorje Mountains, resting at rock faces. **A.** ♂. **B.** ♀. **C–D.** *Leiobunum apenninicum* (Martens, 1969), Italy, Monesi di Triora, at night. **C.** ♂. **D.** ♀. **E–F.** *Leiobunum gracile* Thorell, 1876, Denmark. **E.** ♂. **F.** ♀. Photographs: A–D by A.L.Schönhofer; E–F by S. Toft, all taken in the field.

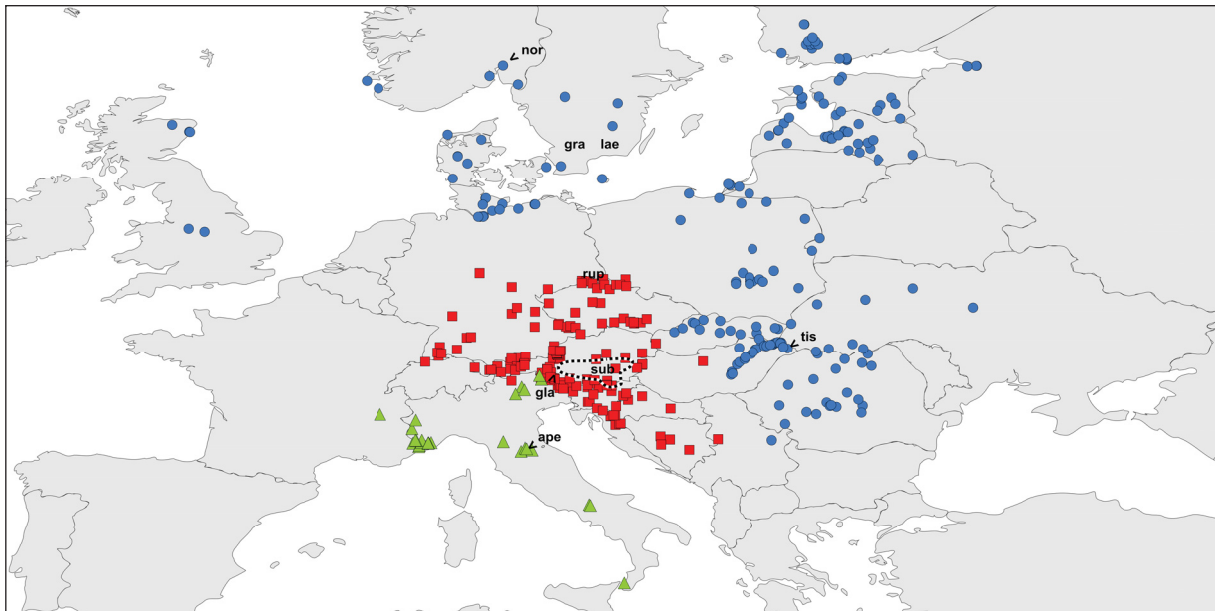
**BODY** (Figs 1A–B, 3A–B). In both sexes dorsum smooth, minute granulation not even to be distinguished with magnification 250 (compare Šilhavý 1981: fig. 4), few scattered pointed granules present; eye mound in both sexes without spines or tubercles.

**DORSAL PATTERN.** Male and female (Figs 1A–B, 3A–B): contrasting black and white (see Diagnosis).

**PEDIPALPS.** Male (Fig. 4A–B): **Fe** with irregular rows of marked triangular spines ventrally; dorsally nearly unarmed, ventral spines more slender than in *L. gracile*; **Pt** slightly armed with pointed denticles laterally; **Ti** markedly convex in basal part and concave at ventro-distal end, therefore forming a well-marked S-bend, field of fine dark coloured granules all over the ventral side, well to be seen; **Ta** continuously and slightly bent to ventral. Female (Fig. 4G–H): similar to male, less spines on Fe and Pt, few spines on Ti proximally and no ventral granulation, Ta straight, slightly bent distally.

**GENITAL MORPHOLOGY** (Fig. 5A–C). Truncus penis stout, in ventral/dorsal view from basal opening to insertion of glans slightly and continuously tapering; distal wings covering less than half of truncus. Wings consist of two independent parts: a ventral shell-like plate, sharply cut off horizontally at upper third of wing structure, from its upper margin continuously extending to lateral side of truncus, thus partly embracing the lateral wings which extend from dorsal side of truncus via lateral side to ventral side. Their lower two thirds are covered by the ventral plate. Surface of the upper margin of the lateral wings and membranes adjacent to the truncus is invaginated forming a long double-walled internal sack. At the very distal end of truncus a small membranous oval sack with a distal opening is attached ventrally.

From lateral view truncus slightly curved (concave on ventral side), slightly tapering towards glans. Wings massively enlarged on ventral side. Glans stout, in lateral view tapering towards stylus.



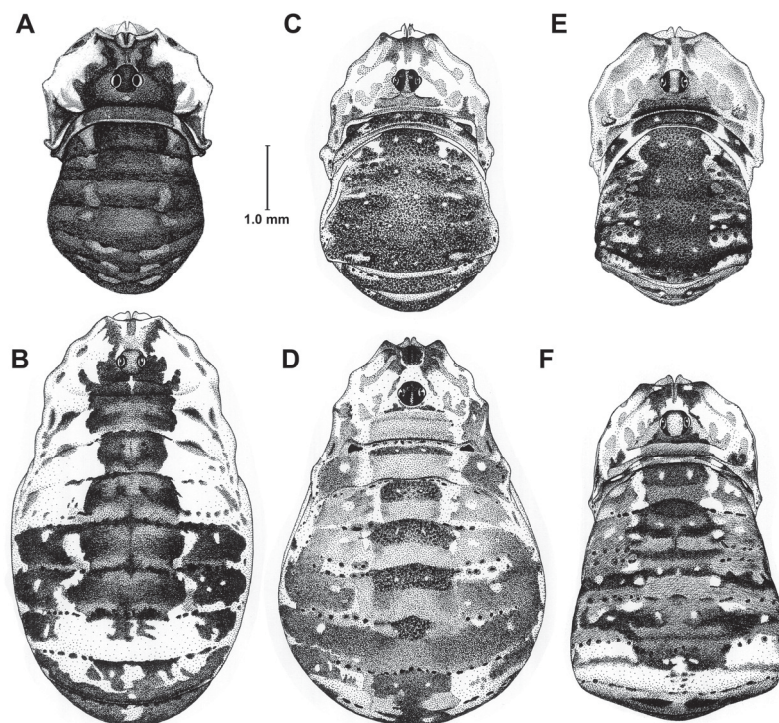
**Fig. 2.** Distribution of the species of the *Leiobunum rupestre* species group. Red squares = *L. rupestre* Herbst, 1799; blue circles = *L. gracile* Thorell, 1876; green triangles = *L. apenninicum* (Martens, 1969); stippled line circumscribes area of *L. subalpinum* Komposch, 1998. Type localities are indicated by abbreviated taxon names (ape = *apenninicum*; gla = *glabrum*; gra = *gracile*; lae = *laeve*; nor = *norvegicum*; rup = *rupestre*; sub = *subalpinum*; tis = *tisciae*). Arrows indicate a specified locality, if unprecisely given, the general area is indicated (*rupestre* = Saxony; *gracile, laeve* = Scania).

**Distribution** (Fig. 2)

Main area are the eastern Alps from the eastern part of Switzerland, all over Austria, the German and Slovenian alpine parts and extending to the north-western Balkan Peninsula. Records extend southwards to Serbia (CJM6363, CIK1336, CIK1337), Croatia (Babić 1916; Novak 2004b) and Bosnia-Herzegovina (Martens 1978; Novak 2005). To the Northeast, the area extends into the Czech Republic: many localities in Bohemia and Moravia, mainly in the northern and southern mountains marking the borders to Austria, Germany and Poland (Šilhavý 1981).

North of the Alps this main Alpine/Balkan area extends in isolated patches towards the northern border of low mountain ranges in Germany (Black Forest, Schwäbische Alb, Frankenalb, Bavarian Forest and Bohemian Forest; all Martens 1978), Fichtelgebirge (Staudt 2016), Thüringer Wald (CJM 5392), Erzgebirge (Büttner 1930), Lausitzer Gebirge (Hiebsch 1972) and northerly up to the Saxonian Elbsandsteingebirge (CJM 4752, 4753). “Sachsen”, i.e., Saxony, is the type locality of *rupestre*, and the type material of Herbst (1799) likely originated from present South Saxony.

For Poland, Staręga (1976) indicated a number of “*rupestre*” records in the southern mountains, the Karkonosze (in German “Riesengebirge”) close to the Czech border. From the opposite Czech side, in the same mountain stock, the Krkonoše, Šilhavý (1981) pinpointed records for (true) *rupestre*, which he compared to “*glabra*” from his country. As these close-to-border Polish localities are situated in mountainous areas, too, they probably belong to *rupestre* as well. Besides, the Polish ‘*tisciae*’ (i.e., *gracile*, below) records are all situated in lower stretches of central and eastern parts of the country (Staręga 1976, 2004), far from any (possible) mountainous *rupestre* record.



**Fig. 3.** Body of *Leiboldunum* C.L. Koch, 1839, dorsal view. A–B. *Leiboldunum rupestre* Herbst, 1799, Germany, Mt. Arber, CJM136. A. ♂. B. ♀. — C–D. *Leiboldunum gracile* Thorell, 1876, Denmark. C. ♂, 2 km N of Skærbæk, CJM3530. D. ♀, Asp, CJM3531. — E–F. *Leiboldunum apenninicum* (Martens, 1969), France, Alpes-Maritimes. E. ♂, CJM1508. F. ♀, CJM2747. Drawings by K. Rehbinder.



The *L. rupestre* area as depicted in Martens (1978: fig. 787) needs to be reduced, subtracting the distribution area of *L. 'tisciae'* (i.e., *gracile*, below), stretching from the Carpathians in a broad northerly area to the Baltic coast up to South Finland and in the West to Denmark and northern Germany (Fig. 2). However, the remaining distribution area of *L. rupestre* slightly changed with respect to the Balkan area, then largely unknown, and new records in central Germany were added.

### Ecology

This is a forest species with a high demand of air moisture. Therefore, it is confined to moist places close to streams and creeks, on tree trunks, under rotten wood and on moist rock faces. It hardly occurs in open areas, in agricultural land, urban gardens or on house walls in villages and towns, if not situated in moist forests (Martens 1978), or at higher altitudes. Martens (1978) indicated height records from 260 m to 2160 m a.s.l. in the Austrian Alps, but likely included localities for the closely related *L. subalpinum*. Komposch & Gruber (2004) set the Austrian uppermost *rupestre* limit at 1680 m a.s.l. and for *subalpinum* at 2100 m a.s.l.

In all cases populations of *rupestre* are confined to mountainous areas of different altitudes. Only in the Saxonian Elbsandsteingebirge does *rupestre* live at the bottom of deeply recessed valleys which are permanently moist and where sun radiation is largely excluded from the narrow valleys by the steep rock faces.

### *Leiobunum subalpinum* Komposch, 1998

Fig. 2

*Leibunum subalpinum* Komposch, 1998: 20.

*Leiobunum rupestre* Gruber, 1966: 46 (partim).

*Nelima religiosa* Roewer, 1910: 912 (in part: series from Tirol, Groß-Glockner).

*Nelima religiosa* Thaler, 1966: 79.

*Leiobunum* sp. – Komposch 1997: 83.

*Leibunum subalpinum* – Komposch 2009b: 487.

### Taxonomic history

Rather uncomplicated. Because of its extreme similarity to *L. rupestre*, including genital morphology, this species went unidentified in many former high-altitude reports on *L. rupestre* until its formal description in 1998. *Leiobunum rupestre* and *L. subalpinum* occur in sympatry and local syntopy, but coxal markings allow easy field identification, so no further misindications were recorded.

### Diagnosis

A medium-sized *Leiobunum* species very similar to *L. rupestre*, except for black coxal markings in both sexes and white markings on Ceph including a white area in front of the tuber oculorum in males. Coxa IV without granules. For further details refer to Komposch (1998).

### Description

BODY. See Diagnosis.

DORSAL PATTERN. Extremely similar to *L. rupestre*.

PEDIPALPS. Very similar to *L. rupestre* except for a medio-basal swelling on Ta in males.

GENITAL MORPHOLOGY. Very similar to *L. rupestre*. The wing-free basal part of truncus shorter than in *L. rupestre*.

### Distribution (Fig. 2)

Restricted to the eastern Austrian Alps, mainly on the southern macroslope in the federal states of Salzburg, Steiermark and Kärnten (Komposch 1998; Komposch & Gruber 2004; Komposch 2009b) extending into adjacent Slovenia (Novak *et al.* 2006). Type locality is Gößnitztal in the National Park Hohe Tauern in Kärnten.

### Ecology

This a mountainous species of the eastern Alps. Its distributional range extends from about 1500 m to 2100 m a.s.l. with rare outliers down to 430 m in moist and cool ravines and up to 2200 m. Vertical rockfaces mostly of siliceous origin are preferred (Komposch 2009a, b; Komposch & Gruber 1999). There is a zone of sympatric and sometimes even syntopic occurrence together with *L. rupestre* between 500 m and 1400 m. Strongholds of *L. rupestre* in that area extend from 500 m to 1000 m with rare occurrences below (down to 200 m) and above (up to 1400 m) (Komposch 1998).

*Leiobunum gracile* Thorell, 1876  
Figs 2, 3C–D, 4C–D, K–J, 5D–F

Partly refers to the record within the distribution of *L. gracile* according to Fig. 2.

*Phalangium bicolor* Fabricius, 1793: 429.

*Liobunum gracile* Thorell, 1876: 496 (type series SMNH, examined).

*Liobunum laeve* Thorell, 1876: 497 (type series SMNH, examined). **syn. nov.**

*Liobunum norvegicum* Strand, 1900: 7. **syn. nov.**

*Nelima melanogranulata* Morin, 1931 (nomen nudum), 1934 (valid description) syn. to *rupestre* fide Staręga 1978: 208.

*Leiobunum tisciae* Avram, 1968: 115 (neither declaration of type specimens nor depository for specimens, material of the original description dedicated by Avram to J.M., now in CJM3526, examined). **syn. nov.**

*Phalangium bicolor* – Kulczyński 1876: 61. Remark: see *L. rupestre*.

*Liobunum gracile* – Tullgren 1906b: 216 (syn. with *L. rupestre*).

*Liobunum laeve* – Tullgren 1906b: 216–217 (syn. with *L. rupestre*).

*Liobunum norvegicum* – Tullgren 1906b: 217 (syn. *L. rupestre*).

*Leiobunum tisciae* – Martens 1978: 408–412 (partim). — Staręga 2004: 80–81. — Stol 2010b: 35. — Tomasson *et al.* 2014: 153.

*Liobunum rupestre* – Tullgren 1906a: 211; 1906b: 216. — Roewer 1910: 203–204.

*Leiobunum rupestre* – Roewer 1923: 890 (partim). — Heinäjoki 1944: 22–23. — Staręga 1978: 100–103. (partim). — Staręga 1979: 177–178. — Lengyel & Murányi 2006: 121. — Enghoff 1988: 68–69. — Chevrizov 1979: 14. — Spungis 2008: 21.

*Nelima gracilis* – Roewer 1910: 239, 250 (redescription). — Roewer 1923: 916.

*Nelima laevis* – Roewer 1910: 239, 251 (redescription). — Roewer 1923: 916.

*Nelima norvegica* – Roewer 1910: 251 (redescription). — Roewer 1923: 916–917. — Staręga 1976: 100.

*Nelima norvegica* – Roewer 1910: 239. — Staręga 1976: 100 (sic, lapsus calami).

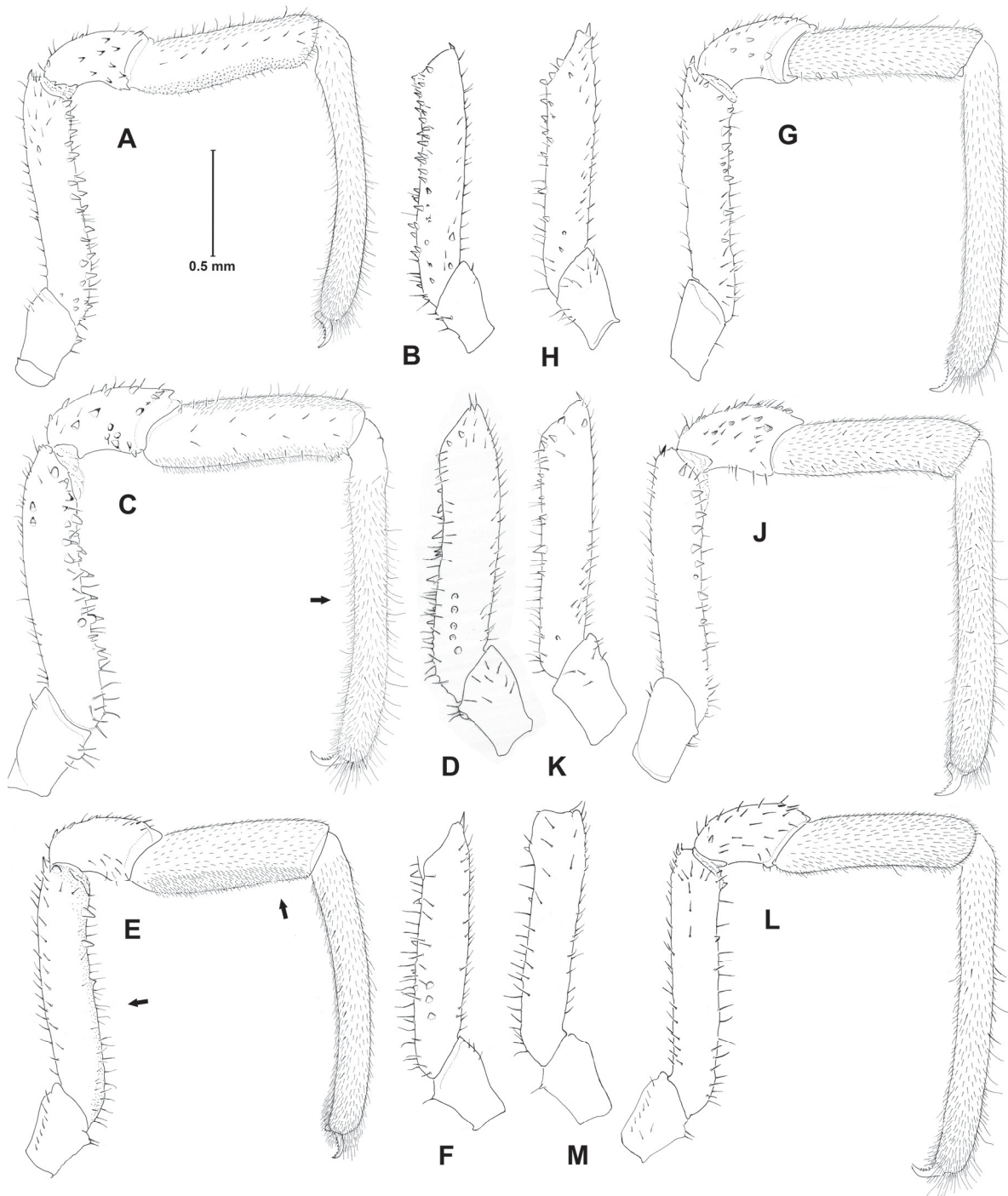
*Liobunum norvegicum* – Müller 1920: 72 (lapsus calami).

*Strandibunus obliquus* – Bartoš 1939: 309.

*Nelima glabra* – Kolosváry 1965: 111–113. — Kolosváry 1966a: 123. — Kolosváry & Homonnay 1967: 77–79.

*Nelima nigripalpis* – Kolosváry 1963: 192. — Kolosváry 1966a, b: 123.

*Leiobunum glabrum* – Šilhavý 1981: 204–207.



**Fig. 4.** Pedipalps of the *Leiobunum rupestre* group, whole pedipalps in lateral view, single femora in medial view. — **A–F.** ♂♂. **A–B.** *Leiobunum rupestre* Herbst, 1799, Germany, Baden-Württemberg, CJM1954. **A.** Pedipalpus lateral. **B.** Femur medial. **C–D.** *L. gracile* Thorell, 1876, Denmark, Asp, CJM3531. **C.** Pedipalpus lateral. **D.** Femur medial. — **E–F.** *Leiobunum apenninicum* (Martens, 1969), France, Alpes-Maritimes, CJM2747. **E.** Pedipalpus lateral. **F.** Femur medial. — **G–M.** ♀♀. **G–H.** *Leiobunum rupestre* Herbst, 1799, Germany, Mt. Arber, CJM136. **G.** Pedipalpus lateral. **H.** Femur medial. **J–K.** *L. gracile* Thorell, 1876, Denmark, Asp, CJM3531. **J.** Pedipalpus lateral. **K.** Femur medial. **L–M.** *L. apenninicum* (Martens, 1969), France, Alpes-Maritimes, CJM2747. **L.** Pedipalpus lateral. **M.** Femur medial. Arrows indicate characters mentioned in the descriptions.

### Taxonomic history

A rather complex situation developed because old species names with type localities in various areas in Scandinavia or in (present) eastern locations were never checked in detail. This is partly due to the fact that names were based on juvenile specimens and partly to the unavailability of former authors to access specimens of northern (Baltic) and southern (Alpine) origin for direct comparison. Consequently, northern populations, originally described as *Liobunum gracile* Thorell, 1876 and *Liobunum laeve* Thorell, 1876, were permanently affiliated to *L. rupestre*, starting with Tullgren (1906a, b), followed by Heinäjoki (1944), Staręga (1976) and Martens (1978). The situation became even worse when Avram (1968) described *L. tisciae* Avram, 1968 from the Tisza valley in Hungary. By external morphology, this species is similar to *L. rupestre*, which Avram did not take into account. Martens (1978) accepted this novelty but at that time lacked suitable fresh material to identify populations from northern Germany and Denmark as conspecific. Instead, he erroneously treated one species under two names, namely North German and Scandinavian populations under *L. 'rupestre'* and those from the Carpathians and single individuals from the British Isles under *L. tisciae*, besides occurrences of *L. 'rupestre'* in the Carpathian Arc as well (Martens 1978). Šilhavý (1981) was the first to recognize two very similar *Leiobunum* species in (former) Czechoslovakia: *L. rupestre* in the West (now Czech Republic) and *L. 'glabrum'* in the East (now Slovakia).

Thorell (1876) based his species *L. gracile* Thorell, 1876 and *L. laeve* Thorell, 1876 on juvenile specimens from South Sweden, although he mentioned only a single male. His original material (kept at the Museum of Natural History Stockholm) definitely concerns the types and was examined. It was found, that it indeed only contains juveniles, as already Tullgren (1906b) assumed they represented juveniles of *L. rupestre*. Likewise, Tullgren (1906b) assumed *L. norvegicum* Strand, 1900 to be identical with *L. rupestre*, but refrained from making a final decision, not having seen the type material. Describing *L. norvegicum*, Strand (1900) depicted a female of the *L. rupestre* complex (from Kristiania [now Oslo]; leg. Sept. 1899) and later Martens (1978) agreed with Tullgren's view, including *L. norvegicum* in the synonymy of a broad species *L. rupestre*.

Considering the allopatric distribution of *L. rupestre* and *L. 'tisciae'* we now can firmly state that all *Leiobunum 'rupestre'*, based on material from Scandinavia, belong to *L. 'tisciae'*. But as *L. 'tisciae'* is a recently proposed name, older names are to be preferred. Albeit *L. gracile* and *L. laeve* are oldest, their description is based on subadults (Tullgren 1906b). Yet, both have been described from Sweden, Province of Scania, from where Tullgren (1906b) confirmed an adult specimen. Therefore, it seems a reasonable decision to re-establish the oldest available name, *Leiobunum gracile* Thorell, 1876, and place *L. laeve* Thorell, 1876, *L. norvegicum* Strand, 1910 and *L. tisciae* Avram, 1968 in its synonymy. *L. gracile* has page and even line priority over *L. laeve*.

### Diagnosis

A medium-sized *Leiobunum* species with blackish upper side, except for broad white markings of Ceph disto-laterally in male (Fig. 3C), broad blackish irregular markings on abd area I–V of the body, in female with mottled white markings laterally from Ceph to posterior areae, white lateral marking on abd area V (Fig. 3D). In both sexes two paramedian small white spots on abd areae I–V, more conspicuous in male (most similar to *L. apenninicum*). Contrasting yellowish underside including coxae of all appendages. Wings of truncus penis slender, slightly tapering proximally.

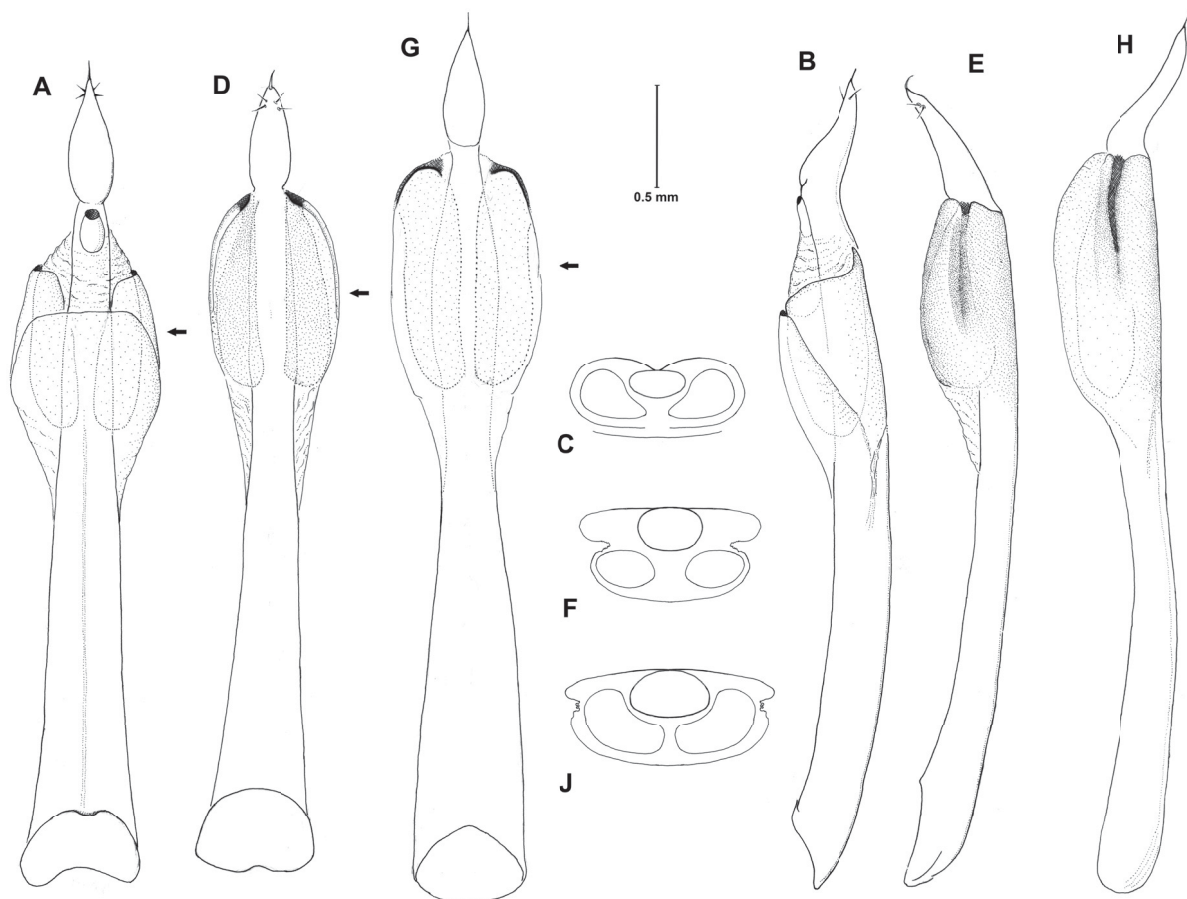
### Description

BODY (Fig. 3C–D). In both sexes dorsal granulation consists of flat, pointed granules, regularly spaced, well visible at 250× (compare Šilhavý 1981: fig. 2).

DORSAL PATTERN (Fig. 3C–D). See Diagnosis. Tu oc in both sexes smooth, without spines, in rare cases one spine present.

PEDIPALPS. Male (Fig. 4C–D): **Fe** with irregular rows of large triangular spines ventrally often with single hair on top; dorsally few on distal part, ventral spines broader and more massive than in *L. rupestre*, where they are more slender and without hair on top. **Pt** with scattered denticles la and do; **Ti** slightly concave ventro-distally, forming a flat S-bend, denticles and hairs on ventral side of palpal tibia light-coloured, hard to be seen; **Ta** mostly straight, bent only in distal third. Female (Fig. 4J–K): in all members similar to male, but armament less conspicuous, Ti more slender, Ta straight.

GENITAL MORPHOLOGY (Fig. 5D–F). Penis similar to that of *L. apenninicum*. Truncus stout, from ventral/dorsal view from basal opening to insertion of glans slightly and continuously tapering to the internal sac of the wings; lateral wings (ventral view) markedly enlarged, smoothly rounded thus nearly egg-shaped (irrespective the lateral membranes running down the truncus). At its very distal end the wing structure close to the glans insertion opens to a small opening, extending into two long nearly parallel-sided double-walled sacks to the lower end of the wings. A lateral somewhat invaginated discharged membrane in the distal half of the wings unites the dorso-lateral and the latero-ventral part of the wings



**Fig. 5.** *Leiobunum*, male genitalia. A–C. *L. rupestre* Herbst, 1799, Germany, Baden-Württemberg, CJM1954. A. Ventral view. B. Lateral view. C. Cross-section. — D–F. *L. gracile* Thorell, 1876, Denmark, 2 km N of Skærbæk, CJM3530. D. Ventral view. E. Lateral view. F. Cross-section. — G–I. *L. apenninicum* (Martens, 1969), France, Alpes-Maritimes, CJM1508. G. Ventral view. H. Lateral view. I. Cross-section. Arrows indicate the area of the respective cross-sections.

(lateral view) allowing for a possible inflation of the wing structure when the sacs are filled with secretion. From lateral view truncus slightly curved (concave on ventral side), slightly tapering towards basis of stylus. Wings enlarged on ventral side, slightly rounded convexly. Glans broad at truncus insertion, in lateral view continuously tapering towards stylus.

### Distribution (Fig. 2)

From Slovakia (Šilhavý 1981, *glabra*), northern Hungary including the Tisza valley (type locality of *L. tisciae* Avram; various records documented by Kolosváry 1963, 1965, 1966a, b, 1969 as *nigripalpis* and *glabra*, and Kolosváry & Homonnay 1967), no additional records in Komposch (2004) for Hungary. Carpathian Arc with many localities documented in collections, but few published papers available, not very far eastward and not in the southern lowlands (Murányi & Lengyel 2006; Weiss 1996; Cîrdei 1960). In the Southwest the area extends into Serbia (Bor Dubasnica, Mala tisnica, CJM 6363). There are scattered records for the western part of Ukraine, mainly as an extension of the Carpathian area (Bartoš 1939; Cîrdei 1960; Staręga 1978; Morin 1931, 1934; L. Koch 1870). The many records in Poland pertain to the eastern two thirds of the country, extending to the Baltic Sea (Staręga 1978, 2004, *rupestre*; for true Polish *rupestre* see above) and including former Westpreußen. Occurrences in Russia are reported from former Ostpreußen (Le Roi 1914) and from St. Petersburg (CJM 3032), extending to Northeast Poland (Staręga 1976, 2004). Estonia: records along the Baltic Sea Coast (Tomasson *et al.* 2014). Latvia: partly detailed locality maps (Tumšs 1963; Spunģis 2008). Finland: only in the southern part, with detailed map based on monitoring records (Heinäjäki 1944), presence confirmed by Uddström *et al.* (2013). Germany: records along the Baltic Sea Coast and its hinterland (up to Hamburg), dating back to Kraepelin (1896), Le Roi (1914) and Rabeler (1929), but apparently presently very rare, last record in Schleswig-Holstein, Lübeck in 2007 (CJM 6111; see Martens 1978). Denmark: early records by Hansen (1884), more recent records from all over the country remained largely unchanged between about 1960 (Meinertz 1964) and 1987 (Enghoff 1988), with slight distributional differences, formerly missing from Funen and rare in South Jutland and Himmerland, but very common and abundant there in 1987 (Enghoff 1988), including Funen, South Jutland and Himmerland. Since then, it has vanished, has not been recorded for many years, but it was rediscovered recently and is presently extremely rare. In 2008, four individuals were present on four out of 64 sites (Enghoff *et al.* 2014). Sweden: except for the early records of Thorell (1876) in Västergötland, Östergötland, Skåne and Småland, there is a single new one from Uppsala in 2009 (examined, H. Enghoff leg.). Norway: Stavanger (SMF) and Oslo (= Kristiania; Strand 1900, *norvegicum*). Great Britain: Derbyshire (Martens 1978), unrecorded until 2008 when it was found around Aberdeen and Dunbennan, Huntly (Davidson 2009, CJM 6358-6361), in Scotland apparently spreading and in Great Britain presently known from seven counties (British Arachnological Society 2016).

The present distribution of *L. gracile* and that in the recent past obviously represent two different ecological-defined origins. One belongs from lowland to montane and riverine forests, the other one comprises secondary urban habitats to which the species was (most likely) transferred by human activity. Such “anthropogenic” populations may suddenly increase, occupy a large area and sometimes collapse again, for reasons little understood. Others are spot-like with little influence on local faunas. At least for a period of roughly 120 years such dynamics can tentatively be reconstructed (see Discussion).

### Ecology

A euryoecious species. In Slovakia, including the Carpathian Arc, recorded from sheltered places in old-growth forests on tree trunks and on rock faces (Šilhavý 1981). It is common in the inundation zone of rivers like the Tisza, e.g., frequently reported from tree hollows of *Populus* (Avram 1968, *tisciae*) and *Salix* trunks (Avram 1968; Csizmazia *et al.* 1966, *nigripalpis*; Kolosváry 1963, 1965, 1966a, b). This also holds true for East Poland where *gracile* lives in forested habitats (Neple, Bug River, AXLS 958). Weiss (1996) indicated its occurrence from Romanian Transylvania forests of the hilly and montane belt.

In all other areas, which we believe to be secondary, *L. gracile* is confined to strongly modified and human-influenced habitats. There it competes with other species preferring house walls like *Opilio saxatilis* C.L. Koch, 1839, *O. parietinus* (Degeer, 1778) and recently with *O. canestrinii* Thorell, 1876. In central Europe the latter presently is by far the dominant species in human habitats and may have partly caused the noticeable decline of *O. saxatilis*, *O. parietinus* and *L. gracile* (see Discussion).

***Leiobunum apenninicum*** (Martens, 1969)

Figs 1C–D, 2, 3E–F, 4E–F, M–L, 5G–J

*Nelima apenninica* Martens, 1969: 409 (type series SMF, examined).

*Leiobunum rupestre* – Trossarelli 1943: 54. — Gozo 1908: 135.

*Nelima apenninica* – Martens 1978: 424, figs 803–804, 809. — Chemini 1980: 79 (description of female). — Komposch 2009: 457.

**Taxonomic history**

Though only recently described, the status of this large species was accepted by subsequent authors (Chemini 1980; Komposch 2009). However, similarity of genital morphology with *L. 'tisciae'* (now *L. gracile*, Martens 1978) later led Martens to the assumption that the scattered distribution of *apenninica* might represent disjunct area parts of *L. gracile*. This remained unpublished due to the emerging complex taxonomic situation in *L. gracile/L. rupestre*. Yet, many details separate both species as is further confirmed by molecular genetic analysis (J. Martens, unpublished data).

The generic affiliation of *apenninica* is difficult to establish. Certainly, it does not belong to the European bulk of small-bodied *Nelima* species like *N. sylvatica* Simon, 1879, *N. gothica* Lohmander, 1945 and *N. sempronii* Szalay, 1951, but is a large and long-legged species similar to *L. gracile*, less to *L. rupestre*. Due to the lack of coxal denticles in the type material and according to the present definition of sclerosomatid genera it was originally placed in *Nelima*. However, based on only a single external character, this is an artificial affiliation, that we find especially compromised in the species-pair *gracile* and *apenninica*. *Leiobunum gracile* shows a strong variation of number and placement of coxal denticles down to zero (CJM6357, female) and their frequent appearance in *Nelima apenninica* (AXLS1739 two to seven on coxa IV, in both sexes) underlines the false generic placement of *apenninica*. Consequently, in accordance with similar genital morphology and external characters we prefer to place *apenninica* in *Leiobunum*.

**Diagnosis**

A medium-sized *Leiobunum* species with blackish upper side, except for broad white markings of Ceph disto-laterally in male (Figs 1C, 3E), broad blackish irregular markings on abd areae I–V of the body. In female with mottled white markings laterally from Ceph to posterior areae, white lateral marking on abd area V and a white cross stripe all over areae VI (Figs 1D, 3F). In both sexes a series of para-median small white spots on the abd areae I–V, more conspicuous in male (a character similar to *L. gracile*). Contrasting yellowish under side including coxae of all appendages. Wings of truncus penis robust, slightly tapering proximally.

**Description**

**BODY** (Figs 1C–D, 3E–F). In both sexes dorsal granulation consisting of flat, pointed granules, regularly spaced, well to be seen with 250× (comparable to *L. gracile*, see Šilhavý 1981: fig. 2); eye mound in both sexes with 1–3 small spines on each side, rarely absent.

**DORSAL PATTERN** (Figs 1C–D, 3E–F). See Diagnosis.

**PEDIPALPS.** Male (Fig. 4E–F): **Fe** with few massive spines, normally restricted to third ventro-distal part, only single spines on dorso-distal side or absent; **Pt** unarmed except for few small spines dorsally; **Ti** slightly inflated, rather short thus appearing pretty massive, brush-like hair field on ventral side, a peculiar character of its own; no spines clearly visible, likely for being of the same light colour as the embedding hair field; **Ta** continuously bent ventrally over its whole length. Female (Fig. 4M–L): Similar to male. **Fe** nearly smooth, spines even less than in male, tibia less inflated and slightly concave ventrally, no hair field; tarsus straight, distally inconspicuously bent ventrally, more slender and slightly longer than in male.

**GENITAL MORPHOLOGY** (Fig. 5G–J). Penis similar to *L. gracile*. Truncus stout and parallel-sided in the basal half from where slightly and continuously tapering to the lateral lowest parts of the wings, from there slightly enlarged to middle of the wings, then tapering to basis of glans. Lateral wings (ventral view) markedly enlarged, nearly parallel-sided over nearly their total length, pretty sharply merging to distal part of truncus. At the disto-lateral margin of the wings (close to the truncus/glans joint) wings open to a narrow slit leading to two ventro-lateral pockets. A lateral membrane in the distal half of the wings unites the dorso-lateral and the ventro-lateral part of the wings which allows for a possible inflation of the wing structure when the pockets are filled with secretion. From lateral view truncus slightly curved (concave on ventral side), slightly tapering towards middle part, then enlarging again. Wings massively enlarged on ventral side, slightly rounded convexly. Glans slender, in lateral view tapering towards stylus.

### **Distribution** (Fig. 2)

It was long considered a rare and local species (Martens 1969; Komposch & Gruber 2004; Komposch 2009; Chemini 1980) and only a few specimens were available for the original description from the Apennines (Martens 1969). Even fewer became known from the apparently isolated area at the Italian border to Austria (Chemini 1980) and in Austria itself (Martens 1978; Komposch 2009) and the Southwest Alps (Martens 1978). Presently, the area seems to be subdivided into three major parts, viz., French and Italian southwestern Alps, southern Austrian (eastern Tyrol) and Italian Alps (South Tyrol), and scattered records in the Apennines chain. Type locality is Pratovecchio in the Apennines. Yet, there was little additional locality information since its original description until the species was recently rediscovered in the Southwest French Alps in high frequency, namely in the Mercantour National Park and the Vallée des Merveilles (CJM; ALS leg., JM leg). Disregarding its specific habitats and general low sampling activity for long-legged species in the Northwest Alps, the species might have been neglected in large parts of its distributional area. Prior to its description, *L. apenninicum* has likely been confused with *L. rupestre*, as is obvious from Trossarelli's (1943) records for the southwest Alps. The isolated record from Calabria (Gozo 1908, *L. rupestre*; included in Fig. 2) requires confirmation.

### **Ecology**

This is a forest species. During the day males rest on tree trunks and rock faces; females, though not exclusively, prefer to hide on the ground in leaf litter and thus are not easy to locate. Consequently, only males have long been known, because they are easier to spot and collect. The species is locally pretty common wherever the daytime microhabitats of females are found. Otherwise, it is readily encountered at night, and this technique revealed large populations in the Mercantour National Park in the French Alps.

### **Discussion**

Systematics of the four central European species *Leiobunum rupestre*, *L. subalpinum*, *L. gracile* and *L. apenninicum* highlights general problems related to European sclerosomatid taxonomy. Firstly, in this case old, but available names, have been largely neglected and were not compared to species known from the area. Subsequent species proposals, i.e., *Leiobunum norvegicum* or *Leiobunum tisciae* ignored this



point and caused considerable taxonomic confusion. Old names, though available, were not considered in detail and simply put aside. On the other hand, *Leiobunum subalpinum*, a species very similar to *L. rupestre* but not rare at all in its limited alpine area, escaped taxonomic recognition for about 200 years. Furthermore, the artificial division of *Leiobunum* into *Leiobunum* s. str. and *Nelima* proposed by Roewer (1910) and maintained for a century seems to be inappropriate in the case presented here. The Roewerian separation is based solely on the presence (*Leiobunum*) or absence (*Nelima*) of coxal denticles, but does not place “*Leiobunum*” and “*Nelima*” species into reasonable morphological and much less preferably monophyletic units, which is substantiated by results of modern molecular genetics (Hedin *et al.* 2012). In our example, “*Nelima*” *apenninica* normally does not generally bear such denticles, but its male genital morphology is astonishingly similar to that of *L. gracile* to an extent that one might even suppose conspecificity. “*Leiobunum*” *gracile* is reported to have highly variable numbers of coxal denticles (Avram 1968) and partly none, while our material also revealed several individuals of “*Nelima*” *apenninica* to have few denticles, too. Molecular genetic analyses indeed demonstrate close relations (J. Martens, unpublished data), confirming the specific differences. The taxon *apenninica* belongs to *Nelima* only by Roewer’s genus definition, genetically and genital-morphologically it is affiliated to a group of central European *Leiobunum*. However, “*Leiobunum*”, presently a holarctically distributed genus, is heterogeneous as well and refers to a number of morphologically and genetically distinct lineages, which are far from being disentangled (Hedin *et al.* 2012). From our material it is also apparent that an increase of the number of denticles, as well as their presence on more than one coxa is linked to an increased body size of the individual, at least in *apenninica* and *gracile*. Such a variable character is certainly inappropriate to serve for differentiation of higher level taxa within a highly heterogeneous phylogenetic group. A molecular-based re-organization, not only of the European *Leiobunum/Nelima* complex, is in urgent need.

The distributional analysis revealed that *Leiobunum gracile* and *L. apenninicum*, though closely related, show a very different distributional pattern. *Leiobunum apenninicum* is a conservative forest species, apparently confined to a few scattered areas and presently with little perceivable tendencies to enlarge its distribution.

The closely related *L. gracile*, however, massively enlarged its area in close affinity to man-made habitats around the Baltic Sea coast. In this area of expansion its populations considerably fluctuate in numbers and it can constrict its area down to local disappearance. Parts of the Carpathian Arc and the adjacent mountains in Southwest Poland and Slovakia and low-altitude riverine forests in Hungary may represent the original area of the species, though this is difficult to substantiate. “Natural” populations may be indicated by hilly and montane forests, also riverine localities where high population densities are obvious (Avram 1968; Csizmazia & Kolosváry 1966; Kolosváry 1963, 1965, 1966a, b, 1969; Kolosváry & Homonnay 1967).

However, it remains arbitrary to solidify area limits of an original and an expansive population based on ecological comparison of historical records. It is thus only hypothesized that starting from the Carpathians the Baltic coast area and its hinterland have been colonized, possibly by help of human-mediated transport. All Baltic authors (Rabeler 1929; Kraepelin 1896; Le Roi 1914; Heinäjoki 1944; Tumšs 1963; Meinertz 1964; Enghoff 1988; Enghoff *et al.* 2014; Staręga 1978, 2004) emphasize the close proximity to human settlements in their area, such as in gardens, specifically on house walls and similar environments, while forest habitats played a minor role in all ecological characterisations. In the Baltic area, this presumed invasion of new areas was successful, but to the West, the North Sea coast was not reached, at least not in a continuous belt, with the westernmost localities around Hamburg (Kraepelin 1896). Isolated outposts are known from the British Isles (Martens 1978) including Scotland (British Arachnological Society 2016), where the population seems to prosper.

A reasonable proof of newly gained territories is the fact that in the newly colonized areas population densities are high in “disturbed” habitats, remain stable for a certain period and after years or even decades collapse or finally completely disappear. This holds true for the population in Denmark, stable at least from the mid 1960s (Meinertz 1964) to 1987, when Enghoff (1988) undertook another monitoring and found an even more extended territory inhabited. Presently, *L. gracile* has largely disappeared from Denmark (Enghoff *et al.* 2014). Likewise in northern Germany only a few isolated records were reported between 2000 and 2009 (Staudt 2016), while the species appeared common at the beginning of the last century (Kraepelin 1896; Rabeler 1929; Le Roi 1914). Other occurrences remained spot-like from the very beginning and apparently disappeared soon after the first discovery in Great Britain (Martens 1978, *tisciae*) or gained new area spots far away in Scotland and other parts of the U.K. (British Arachnological Society 2016).

Reasons for such extreme population fluctuations are unclear and have not been surveyed in detail. Population decline was obvious for long prior to the invasion of *Opilio canestrinii* to central Europe, which started about 1970 (Martens 1978, as *ravennae*, first German records in Stuttgart 1974 CJM1619; Mainz 1975 CJM1525; Berlin 1976 CJM1553). For the year 1987 Enghoff (1988) stated that *L. gracile* and *O. canestrinii* lived side by side in high population densities in Denmark. Only *gracile* disappeared, *canestrinii* remained to the present and is common everywhere (Toft 2004, pers. comm.). However, it must be taken into account that long-lasting effects of high population density of *O. canestrinii* may have caused the decline of *L. gracile*. The same is assumed for *Opilio parietinus* in central Europe.

The temporal invasion of the Baltic dates back for at least 120 years, probably considerably longer. Kraepelin (1896) mentioned *gracile* as not being rare for the Hamburg area whereas Heinäjoki (1944) stated that *gracile* invaded Finland and gained northward territory only in the 1920s. Monitoring of the Finnish arachnid fauna was pretty detailed at that time and earlier occurrences would have been certainly noticed as indicated by Heinäjoki (1944), who documented the extension to about 61.6° N up to Hämeenkyrö, until today the northernmost known record (Uddström *et al.* 2013). For Denmark records date back to the 19<sup>th</sup> century, when Hansen (1884) mentioned the species.

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## Appendix 1 – List of material and distributional data

### Remarks

The list incorporates investigated material and references, which we judged sufficiently reliable. Old or alternative locality names, interpretations and accuracy of coordinate-reconstruction are indicated in parenthesis. Important taxonomic material, such as types, are indicated in bold.

Acronyms of institutions cited in the list

AXLS	=	Coll. A. Schönhofer, Mainz, Germany
BGZM	=	Biozentrum Grindel and Zoologisches Museum, Universität Hamburg, Germany
CIK	=	Coll. Ivo Karaman, Novi Sad, Serbia
CJM	=	Coll. Jochen Martens, Mainz, Germany
MBN	=	Museum Bergen, Norway
MFSNU	=	Museo Friulano di Storia Naturale, Udine, Italy
MNHN	=	Muséum national d'histoire Naturelle, Paris, France
MTSN	=	Museo Tridentino di Scienze Naturali, Trento, Italy
MNV	=	Museo Civico di Storia Naturale di Verona, Italy
SMF	=	Senckenberg Forschungsinstitut Frankfurt a. Main, Germany
UNILAT	=	Department of Zoology and Animal Ecology, Faculty of Biology, University of Latvia
ZMB	=	Museum für Naturkunde Berlin, Germany

### *Leiobunum apenninicum* (Martens, 1969)

AUSTRIA: Osttirol, Arnbach near Sillian, 1100 m, 46.74° N, 12.39° E, leg. A. Ausobsky, 15 Jun. 19?? (Martens 1978); Defereggental, banks of river Schwarzach below Mariahilf, 1670 m, 46.913° N, 12.31° E, leg. 31 Aug. and 1 Sep. 2007 (Komposch 2009).

FRANCE: 5 ♂♂, 4 ♀♀, 2 juv., Dép. Isère, Le-Sappey-en-Chartreuse, direction to Sarqueñas, 1158 m, mixed coniferous and *Fagus* forest, under bark and logs, 45.273° N, 5.766° E, leg. 31 Aug. 2008 (AXLS30); 3 juv., Dép. Alpes-Maritimes, buffer area of the Mercantour National Park, focal site La Minière de Valaura (9), 1476 m, mixed forest on north facing slope, under stones and logs, 44.069° N, 7.132° E, leg. 5 Sep. 2008 (MNHN); 4 juv., same locality, below Col de Turini, 1513 m, coniferous forest, under logs and bark, 43.977° N, 7.386° E, leg. 3 Sep. 2008 (AXLS85); 1 ♂, Forêt de Peira Cava, 1500 m, 43.93° N, 7.37° E, leg. 18 Aug. 1972 (CJM1508; Martens 1978); 2 ♂♂, 1 ♀, Col de Turini, 1500 m, *Picea* forest, below pass, 43.978° N, 7.390° E, leg. 19 Sep. 1982 (CJM2747); 28 ♂♂, 2 ♀♀, 15 juv., Mercantour National Park, focal site Valmasque (7), 1905 m, NW exposed slope, very humid, indicated by predominance of *Alnus viridis*, at stems of *Larix*, 44.111° N, 7.473° E, leg. 6 Sep. 2008 (CJM6295).

ITALY: 6 ♂♂, Prov. Arezzo, Casentino, Bibbiena vicinity, P. di Mandioli (interpreted as Passo di Mandrioli), 1050 m, rivulet in *Fagus* forest, 43.78° N, 12.01° E, leg. 18 Oct. 1975 (CJM3287); 2 ♂♂, Central Apennin, Matese Mts., Roccamandolfi, 820 m, 41.50° N, 14.35° E, leg. 27 Jun. 1967 (MV; Marcellino 1971; Martens 1978); 1 ♂, Sotto Rifugio Campitello, 1250 m, 41.463° N, 14.394° E, leg. 22 Sep. 1967 (MV; Marcellino 1971; Martens 1978); Emilia Romagna, Prov. Bologna, 1 ♀, “Corno alle Scale” Park (coordinates inaccurate), 44.14° N, 10.83° E, leg. 2005 (online source Tree of Life, photographic evidence ID11332); 1 ♂, Forli-Cesena, Parco Nazionale Foreste Casentinesi, Poggio Scali, Monte Falterone, 1520 m, 43.845° N, 11.79° E, leg. Sept. 1963 (SMF16433; Martens 1969; cf. Kirchner & Salzer 1967; **holotype of *Leiobunum apenninicum* (Martens, 1969)**); 2 ♂♂, same locality, Campigna, 1050 m, 43.87° N, 11.73° E, leg. Sept. 1963 (SMF16434; Martens 1969, **paratypes**); 1 ♂, 1 ♀, Pratomagno, E Firenze, Vallombrosa (interpreted as the abbey), 1100 m, *Abies* forest, 43.732° N,

11.558° E, leg. 17 Oct. 1975 (CJM3282); Prov. Imperia, 9 ad., 1 juv., Monesi di Triora, 1300 m, stream valley before village, night catch, 44.081° N, 7.761° E, leg. 30 Aug. 2014 (AXLS1733); 1 ♂, first stream valley before village, 1400 m, in deep stony gravel and sieved from litter in-between, 44.071° N, 7.748° E, leg. 30–31 Aug. 2014 (AXLS1701); 20 ♂♂, 31 ♀♀, 3 juv., last valley before Monesi di Triora, 1287 m, sitting on dry leaf litter (often under fallen twigs) in mixed forest, 44.081° N, 7.767° E, leg. 9 Sep. 2008 (CJM6308); 1 ♂, Monesi di Triora, 1304 m, deciduous forest (*Fagus*), under stones, 44.082° N, 7.771° E, leg. 8–9 Sep. 2008 (AXLS111); 1 ♀, c/o Monesi, 1320 m, 7.761° N, 44.081° E, leg. 24 Jun. 2011 (AXLS1150); 1 ♂, Alpi Cozie, Crissolo, Monviso, 1300 m, 44.67° N, 7.10° E, leg. July 1967 (MV; Marcellino 1975); 1 ♂, N Pinerolo, Giaveno, W Forno (interpreted as Forno), 950 m, 45.04° N, 7.24° E, leg. 9 Oct. 1972 (CJM1576; Martens 1978); 8 ♂♂, 4 ♀♀, 4 juv., Alpi Marittimi, National Park Alpi Marittime, focal site Palanfré, 1501 m, old N-exposed *Fagus sylvatica* forest, sitting on leaf litter, 44.195° N, 7.494° E, leg. 10 Sep. 2008 (MNHN); 1 juv., focal site Vallone d' Argentera, 1580 m, coniferous forest, under stones, 44.185° N, 7.269° E, leg. 12 Sep. 2008 (MNHN); 2 ♂♂, 2 ♀♀, Nava, 888 m, night catch alongside deciduous forest and stream, mostly on road, 44.099° N, 7.874° E, leg. 7 Sep. 2008 (AXLS108); 4 ♂♂, 2 ♀♀, Val de Valasco, Rifugio Valasco, 1800 m, N-facing slope with large boulders, *Alnus viridis* and *Myrtillus* shrubs, under stones and in crevices, 44.196° N, 7.233° E, leg. 28 Aug. 2014 (AXLS1739); 3 ♂♂, Trentino-Südtirol, betw. Niglerpass and Karerpass, E Welschnofen, 1720 m, 46.43° N, 11.58° E, leg. 28 Aug. 2005 (CJM4670); 1 ♂, 1 ♀, surroundings of Palù del Fersina, 1300–1400 m, 46.13° N, 11.34° E, leg. 8 Sep. 1973 (MTSN, Chemini 1980); 1 ♂, surroundings of Paneveggio, 1500 m, 46.31° N, 11.70° E, leg. 28 Aug. 1973 (MTSN, Chemini 1980). Calabria, Valletta della grotta della Melia, 38.23° N, 15.76° E (Cantoni 1882; Gozo 1908; orig. det. as *L. rupestre* and is here affiliated to *L. apenninicum*; requires confirmation).

***Leiobunum gracile* Thorell, 1876**

**Remarks**

*Leiobunum gracile* was mostly considered under the names *L. rupestre* and *L. tisciae*. These names we used for the original identification of records in the literature. The repetitive information was omitted, while more unusual species taxa names and identifications (*glabra*, *nigripalpe*, etc.) are given. If necessary, please refer to the respective publication.

DENMARK: 3 ♂♂, 2 ♀♀, 1 juv., 2 km N of Skærbæk, coniferous forest, 55.17° N, 8.76° E, leg. 16–30 Sep. 1987 (CJM3530); 1 ♂, 3 ♀♀, Asp, indoors, 56.824° N, 9.936° E, leg. 19 Sep.–6 Oct. 1987 (CJM3531); Bornholm, 55.16° N, 14.87° E (Meinertz 1964); 4 ♀♀, Givskud, 55.82° N, 9.37° E, leg. 16 Sep. 1987 (CJM6232); 2 ♂♂, 3 ♀♀, Herning, 56.13° N, 8.97° E, leg. 16 Oct. 1987 (CJM6230); 1 ♂, 2 ♀♀, Copenhagen (coordinates inaccurate), 55.66° N, 12.59° E (ZMB12642); 2 ♂♂, 1 ♀, Copenhagen, leg. 10 Sep. 1984 (CJM4799); 14 ad, Stjæ, 56.12° N, 8.97° E, leg. 30 Sep. 1987 (CJM6231); 1 ♂, Tørvekjær v. Klitmøller, 57.03° N, 8.55° E, leg. 2 Dec. 2006 (CJM6229).

ESTONIA: All Estonian records refer to Tomasson *et al.* 2014 based on 3–4 sampling periods of 4–7 months in 2008–2011. 3 ex., Harju, Üksnurme, unmanaged old apple orchard next to cultivated grassland, 59.295° N, 24.628° E; 15 ex., Hiiu, Kerema, moist alvar grassland with juniper brush, 58.891° N, 22.948° E; 116 ex., Jõgeva, Pataste, moist forest dominated by alder, birch, bird cherry, spruce, 58.581° N, 26.778° E; 18 ex., Lääne, Kunila, Moist broad-leaved forest, 58.631° N, 23.811° E; 1 ex., Pärnu, Nigula NR, paludified pine forest with *Polytrichum*, 58.007° N, 24.712° E; 11 ex., Pärnu, Tõstamaa, next to brush covered ditch bank surr. by fallow grassland, 58.336° N, 24.006° E; 56 ex., Saare, Igaküla, Pine forest with *Corylus*, 58.601° N, 23.128° E; 18 ex., Saare, Orissaare, patch of deciduous managed forest in an urban area, 58.555° N, 23.087° E; 1 ex., Saare, Viidumäe, edge of a spring fen, 58.294° N, 23.089° E; 108 ex., Tallin, 59.44° N, 24.75° E (Staręga 1978); 108 ex., Tartu, Maiorg, spruce and aspen dominated old forest along a rivulet valley, 58.278° N, 26.334° E; 136 ex., Tartu, Sudaste, *Oxalis*-type

drained spruce forest, 58.329° N, 26.940° E; 11 ex., Valga, Puka, edge of paludified forest, *Filipendula* type, 58.041° N, 26.207° E; 48 ex., Võru, Leoski, edge of dry boreal forest, *Vaccinium myrtillus* type, 57.709° N, 27.139° E.

FINLAND: 2 juv., Espoo, 60.21° N, 24.65° E, leg. 17–18 Jul. 1940 (Heinäjoki 1944); Häme, Forssa, 60.82° N, 23.63° E (Hippan 1975); Tammela, 60.80° N, 23.77° E (Hippan 1975); Ypäjä, 60.80° N, 23.28° E (Hippan 1975); Hämeenkyrö, 1 ♀, 61.64° N, 23.20° E, leg. 1943 (Heinäjoki 1944); Köijärvi, 60.94° N, 23.66° E (Hippan 1975); N. Helsinki, 30 ♂♂, 150 ♀♀, 173 juv., Eläintarhanhuvila 6, 60.18° N, 24.94° E, leg. 1935–40 (Heinäjoki 1944); 1 juv., Käpylä, indoors at wall, 60.21° N, 24.95° E, leg. 3 Aug. 1925 (Heinäjoki 1944); Oulunkylä and Pakinkylä, on path and indoors, 60.23° N, 24.94° E, leg. late summer 1943 (Heinäjoki 1944); 1 ♂, Ullanlinna, indoors at wall, 60.16° N, 24.95° E, leg. 25 Sep. 1926 (Heinäjoki 1944); Southern Finland, Humppila, 60.93° N, 23.37° E (Hippan 1975); Jokioinen, 60.80° N, 23.48° E (Hippan 1975); St. Hämeenkyrö, 1 ad., on a path, 61.635° N, 23.193° E, leg. 20 Sep. 1943 (Heinäjoki 1944); Turku (coordinates inaccurate), 1 ♂, 1 ♀, 60.45° N, 22.26° E, leg. 25 Sep. 1926, 9 May 1927 (Heinäjoki 1944); Western Finland, Somero, 60.63° N, 23.52° E (Hippan 1975); Urjala, 61.08° N, 23.54° E (Hippan 1975).

GERMANY: Hamburg (three localities), large numbers (coordinates inaccurate), 53.56° N, 9.87° E (BGZM); Barmbeck, 53.58° N, 10.03° E (Kraepelin 1896); Bahrenfeld, 1 ♂, Stadtteil von Hamburg, 53.57° N, 9.91° E (SMF-R.1255); St. Georger Kirchhof, 53.557° N, 10.007° E (Kraepelin 1896); Blankenese, 53.56° N, 9.81° E (Kraepelin 1896); Mecklenburg-Vorpommern, 1 ex., Rostock, house garden in nesting box (Rabeler 1929); 4 ex., Rostock, old cemetery at Saarpfatz (now abandoned), at houses and walls, 54.085° N, 12.117° E, leg. 8 Oct. 1927–1929 (Rabeler 1929); 1 ex., Rostock, yard of the Entomology Seminar, 54.088° N, 12.134° E, leg. 7 Oct. 1927–1929 (Rabeler 1929); 1 ex., Rostock, indoors, leg. 7 Nov. 1927–1929 (Rabeler 1929); 3 ex., Rostock, Wallanlagen, in cracks of wall, 54.087° N, 12.132° E, leg. 13 Sep. 1927–1929 (Rabeler 1929); Wismar, 53.89° N, 11.45° E (Le Roi 1914); Schleswig-Holstein, Bad Oldesloe, 54.10° N, 10.79° E (BGZM; Kraepelin 1896); 1 ♀, 2 ♀♀, Kiel, Institute of Zoology, 54.33° N, 10.1° E, leg. 1 Sep. 1964 (CJM949, CJM6172); 1 ♂, 1 ♀, Lübeck, former School of Navigation, on wall, 53.861° N, 10.689° E, leg. 9 Oct. 2007 (CJM6111); 1 ♂, 4 ♀♀, Neumünster (72), 20 m, 54.07° N, 9.99° E, leg. 17 + 27 Sep. 1964 (CJM6171); Neumünster(?) (coordinates inaccurate), 1 ♂, 54.07° N, 9.99° E, leg. Sep. 1967 (CJM948).

GREAT BRITAIN: Scotland, Aberdeenshire, 2 ♂♂, 1 ♀, Aberdeen, Botanic garden, 57.16° N, 2.09° W, leg. 20 Sep. 2008 (CJM6359); 2 ♀♀, same data (CJM6358); 4 ♂♂, 1 ♀, same data (CJM6357); 2 ♂♂, 1 ♀, Aberdeen, Torry, Greyhope House, 57.142° N, 2.062° W, leg. 9 Oct. 2008 (CJM6361); 1 ♂, 3 ♀♀, same data, leg. 4 Oct. 2008 (CJM6360); 1 ♂, Dunbennan, Huntly, Cemetery, 57.45° N, 2.79° W, leg. 12 Sep. 2008 (CJM6362); Derbyshire, 13 ex., between Leek and Stoke on Trent (coordinates inaccurate), 53.06° N, 2.12° W, leg. Sep. 1971 (CJM1739) (Martens 1978).

HUNGARY: All Hungarian records of Kolosváry (1963, 1966a, b), Kolosváry & Homonnay (1967) and Csizmazia *et al.* (1966) are originally det. as *Nelima nigripalpe*, of Kolosváry (1965) orig. det. as *Nelima glabra* and of Kolosváry (1969) orig. det. as *Nelima glabra* and *N. nigripalpe* considered as syn. Northern Hungary: Bükk Mts., Bánkút, Veres sár bérc, 48.09° N, 20.49° E, leg. 2 Nov. 2005 (Lengyel & Murányi 2006, orig. det. as *L. rupestre*); Tisza River and surroundings, Kisköre, 47.49° N, 20.51° E, leg. Aug. 1968 (Kolosváry 1969); 1 ex., Komoró, inundation zone, *Salix* forest, in humus, 48.31° N, 22.09° E, leg. 18–31 Jul. 1965 (Kolosváry 1965); Nagyrév, 46.94° N, 20.15° E, leg. Aug. 1968 (Kolosváry 1969); river kilometre 507, „Koldus“ forest near Tiszadob, inundation zone, tree hollows of *Salix* stem, 48.03° N, 21.18° E, leg. 18–19+23+31 Jul. 1964 (Csizmazia *et al.* 1966); many ex. river kilometre 601–602 (near Dombrád), inundation zone, tree hollows of *Salix*, 48.24° N, 21.92° E, leg. 18–31 Jul. 1965 (Kolosváry 1965); river kilometre 602–604 (1–3 km NE Dombrád), inundation zone, at walls of cottage, 48.26° N, 21.94° E, leg. 18–31 Jul. 1965 (Kolosváry 1965); 1 ex. river kilometre 620, Tuzsér, inundation zone, moulting at branch of *Salix*, 48.34° N, 22.11° E, leg. 18–31 Jul. 1965 (Kolosváry

1965); 1 ex., Szabolcsveresmart, inundation zone, *Quercus* forest, under log, 48.31° N, 22.02° E, leg. 18–31 Jul. 1965 (Kolosváry 1965); Tiszabercel, 48.17° N, 21.66° E, leg. Aug. 1968 (Kolosváry 1969); Tiszacsermely, 48.23° N, 21.81° E, leg. Aug. 1968 (Kolosváry 1969); Tiszadada, inundation zone, listed as terricole species, 48.04° N, 21.24° E, leg. 1963–1964 (Kolosváry 1966b); 1 ex., Tiszadob, inundation zone, listed as terricole species, 48.03° N, 21.18° E (Kolosváry 1963); Tiszaföldvár, 46.99° N, 20.22° E, leg. Aug. 1968 (Kolosváry 1969); Tiszahát, Endes-Puszta, on *Rubus* leaves, 48.29° N, 22.23° E, leg. 1 Aug. 1966 (Kolosváry & Homonnay 1967); Tiszahát, Gergelyiugornya, river kilometre 698, in forest, 48.13° N, 22.34° E, leg. 27 Jul. 1966 (Kolosváry & Homonnay 1967); Tiszahát, Gergelyiugornya, river kilometre 698, in forest, skins in tree hollows of *Salix* and *Quercus*, 48.13° N, 22.34° E, leg. 27 Jul. 1966 (Kolosváry & Homonnay 1967); Tiszahát, Lónya, inundation zone, 48.32° N, 22.25° E, leg. 21 Jul. 1966 (Kolosváry & Homonnay 1967); Tiszahát, Mátyus, on *Rubus* leaves, 48.29° N, 22.27° E, leg. 21 Jul. 1966 (Kolosváry & Homonnay 1967); Tiszahát, Tiszamogyorós, in tree hollows, 48.32° N, 22.25° E, leg. 1 Aug. 1966 (Kolosváry & Homonnay 1967); Tiszaörvény, 47.61° N, 20.72° E, leg. Aug. 1968 (Kolosváry 1969); Tizasüly, 47.39° N, 20.41° E, leg. Aug. 1968 (Kolosváry 1969); Tiszaszederkény, 47.91° N, 21.08° E, leg. Aug. 1968 (Kolosváry 1969); Tiszatarján, 47.82° N, 21.01° E, leg. Aug. 1968 (Kolosváry 1969); Tiszavalk, 47.68° N, 20.75° E, leg. Aug. 1968 (Kolosváry 1969); Tiszavárkony, 47.07° N, 20.19° E, leg. Aug. 1968 (Kolosváry 1969); Vencsellő, 48.18° N, 21.56° E, leg. Aug. 1968 (Kolosváry 1969); Tisza-völgye, Tiszabercel, Babócsa-szög, 48.16° N, 21.63° E, leg. 20 Jul. 2002 (Lengyel & Muranyi 2006); Tisza-völgye, Tiszabercel, Babócsa-szög, 48.16° N, 21.64° E, leg. 20 Jul. 2002 (Lengyel & Muranyi 2006); Tur River estuary into Tisza River (km 715–744, GPS placed at Tivadar), 48.06° N, 22.52° E (Avram 1968, **type locality of *Leiobunum tisciae***); 1 ♂, 1 ♀, likely same locality: Tisza River, left banks, leg. 21 Jul. 1967 (CJM3526, det. by Avram, **likely part of the type series of *Leiobunum tisciae***, the remainder of specimens not specified, likely in Bucharest Museum but no data accessible); Zemplén, Erdőhorváti, Tolcsva-patak part, 48.29° N, 21.45° E, leg. 3.11.2001 (Lengyel & Muranyi 2006, orig. det. as *L. rupestre*); Telkibánya, Cserenkő (oberlauf), 48.48° N, 21.35° E, leg. 30 Sep. 2001 (Lengyel & Muranyi 2006, orig. det. as *L. rupestre*).

LATVIA: All Latvian records refer to UNILAT, Spuņģis 2008, if not otherwise indicated. Aizkraukle Distr., 1 ex., Ērberģe, rotten birch wood, 56.37° N, 25.02° E, leg. 15 Oct. 2006; 1 ex., Koknese, rotten deciduous wood, 56.66° N, 25.41° E, leg. 11 Oct. 2003; 2 ex., Krasti, deciduous forest, 56.44° N, 25.92° E, leg. 15 Oct. 2006; 1 ex., Vesetas paliene fen, on tree trunk, 56.70° N, 25.81° E, leg. 15 Jun. 2005; 4 ♂♂, 1 ♀, Bergī, pie Bukultiem, 56.99° N, 24.28° E, leg. 25 Sep. 1960 (Tumšs 1963); Daugavpils Distr., 1 ex., Pilskalnes Siguldiņa, rotten deciduous wood, 55.98° N, 26.25° E, leg. 15 Oct. 2005; 3 ex., Krāslava Distr., Ezernieki, on building, 56.18° N, 27.66° E, leg. 9 Oct. 2005; 6 ♀♀, Krimulda, 57.19° N, 24.85° E, leg. 27 Jul. 1937 (Tumšs 1963); 2 ex., Kuldīga Distr., Īvande, on building, 56.99° N, 21.76° E, leg. 22 Oct. 2006; 1 ex., Limbaži Distr., Mērnīeki, on wooden building, 57.86° N, 24.51° E, leg. 14 Aug. 2007; 3 ex., Madona Distr., Bērzaune, on building, 56.81° N, 26.04° E, leg. 8 Aug. 2007; 2 ♂♂, Moricsala, 57.21° N, 22.14° E, leg. 22 Oct. 1960 (Tumšs 1963); Rīga Distr., 3 ex., Salaspils, deciduous forest, 56.87° N, 24.35° E, 21 Sep. 2005; 5 ex., Tumšupe river valley (GPS not accurate), on white alder trunk, 57.01° N, 24.61° E, 22 Aug. 2007; 1 ex., Botanical garden of University of Latvia, greenhouse, pitfall traps, 56.950° N, 24.058° E, leg. 15–29 Nov. 2004; 1 ex., Dārziņi, on wooden building, 56.87° N, 24.28° E, leg. 24 Sep. 2006; 4 ex., Nordeķi, deciduous park, 56.96° N, 24.17° E, leg. 24 Sep. 2005 (3 ex.), leg. 5 Oct. 2003 (1 ex.); 9 ex., Saldus Distr., Saldus, Ciecere river valley, on wooden building, 56.67° N, 22.49° E, leg. 22 Oct. 2005; 1 ♂, Sauka, 56.28° N, 25.48° E, leg. 10 Aug. 1937 (Tumšs 1963); 1 ♂, 1 ♀, Sigulda, 57.15° N, 24.85° E, leg. 21 Oct. 1960 (Tumšs 1963); 5 ♂♂, Sudas purvs, 57.15° N, 25.00° E, leg. 1 Oct. 1960 (Tumšs 1963); 1 ex., Talsi Distr., Dundaga, deciduous park, 57.51° N, 22.36° E, leg. 28 Oct. 2007; 8 ex., Kolka, on wooden building, 57.75° N, 22.58° E, leg. 28 Aug. 2005 (7 ex.), 31 Aug. 2007 (1 ex.); 1 ex., Valmiera Distr., Kauguri, garden, 57.49° N, 25.44° E, leg. 8 Aug. 2004; Ventspils Distr., 9 ex., Usma, rotten deciduous wood, 57.22° N, 22.15° E, leg. 13 Aug. 2006.

NORWAY: Oslo (=Kristiania, coordinates inaccurate), 59.92° N, 10.82° E, **type locality of *Leiobunum norvegicum*** Strand, 1900, 1 ♀ (Strand 1900); 1 ♀, 7 juv., Østlandet, Tistedalen, 59.13° N, 11.44° E, leg. 22 Aug. 1977 (Stol 2010b); 1 ♀, Rogaland, Karmøy, 59.28° N, E5.21° E, leg. 1977 (Stol 2010a); Stavanger, 58.97° N, E5.70° E, leg. ? (SMF, Schönhofer 2005); Vestfold, Botne, 59.482° N, 10.275° E, leg. 13 Sep. 1964 (MBN-A3575, Stol 2010b).

POLAND: 2 juv., Białowies (no further data, coordinates inaccurate), 52.67° N, 23.83° E, leg. 15 Aug. 1916 (SMF1603, Müller 1920); 1 ♂, 1 ♀, Bieszczady Mts., Distr. Mstrzyki Dolne, Mstrzyki Górne, “zarośla blehowe” along small stream Terebowiec, 49.10° N, 22.67° E, leg. 25 Sep. 1964 (CJM6368, I.Z.PAN-Warszawa, 35/64); 11 ♀♀, 14 juv., Bug River Valley, landscape park N Neple, aggregations under branches close to floor of riverine forest, 100 m, 52.135° N, 23.519° E, leg. 14 Jul. 2010 (AXLS958); Chylonia (formerly Kielau), 54.53° N, 18.44° E (Le Roi 1914); Frombork (formerly Frauenburg), 54.35° N, 19.68° E (Le Roi 1914); Janów, 53.47° N, 23.23° E (Wajgel 1874), orig. Z4612, det. as *Leiobunum bicolor*; Masurian Lake District, Lidzbark Warmiński, 54.12° N, 20.58° E (Staręga 1963); 2 ♀♀, 1 juv., Memerki near Wegorzewo, Tilio-Carpinetum, 54.18° N, 21.65° E, leg. 4 Aug. 1983 (SMF36129); Świekatowo (formerly Westpreußen, Johannisberg), 53.42° N, 18.09° E (Le Roi 1914); Warschau vicinity (GPS not accurate), 52.21° N, 21.06° E (Staręga 1963); Wyżynie Lubelskiej, Kazimierz Dolny, 51.317° N, 21.95° E (Staręga 1963).

The following records of Staręga (2004) share the same data: Lysa Góra Mts., different forest communities (Dentario glandulosae-Fagetum, Tilio-Carpinetum, Pino-Quercetum), xerophilic dry grassland, boulders, caves, buildings, leg. Jul. 1981–Aug. 1985. Data differ in: Kakonin, 50.867° N, 20.929° E; Miejska Góra, 50.957° N, 20.929° E; NSG Chelmowa Góra, 50.867° N, 21.071° E; NSG Góra Miedzianka, 50.865° N, 20.361° E; NSG Milechowy, 50.775° N, 20.362° E; NSG Skalki Piekło pod Niekłaniem, 51.226° N, 20.642° E; NSG Święty Krzyż, 50.867° N, 21.071° E; NSG Wykus, 51.047° N, 20.929° E; NSG Zamczysko, 50.777° N, 20.929° E; Szewna, 50.956° N, 21.356° E; 4 ♂♂, 4 ♀♀, Lysa Góra Mts., NSG Lisiny Bodzechowskie, beo Ostrowiec Swietokryskiz, 50.866° N, 21.497° E, leg. 9 Sep. 1981 (SMF, Staręga 2004); 1 ♂, 1 ♀, Roztoczański National Park, NSG Nart (coordinates inaccurate), Dentario glandulosae-Fagetum, 50.60° N, 22.97° E, leg. 15 Oct. 1986 (SMF); 1 ♀, Roztoczański, R.N., rez. Bukowa Go'ra FB30, leg. 5 Aug. 1981, subadult (SMF).

ROMANIA: 1 ♀, Băile Herculane, 44.88° N, 22.42° E, leg. 25 Jun. 1956 (CJM6420); 1 ♂, Bihor Mts., valley around Sighiștel, 46.52° N, 22.54° E, leg. 26 Sep. 1958 (Avram & Dumitrescu 1969); Bistritz, Dealul Târgului, 47.19° N, 24.50° E (Weiss 1996); 2 ♂♂, Cabana Negoiul, 1540 m, 45.59° N, 24.52° E, leg. 24 Jul. 1950 (CJM6426); Fogarasch Mts., Bălea-Tal, Roter Turm, 45.63° N, 24.26° E (Weiss 1996); 3 ad., Hunedoara, Vulcan, 45.38° N, 23.29° E, leg. 16.11.1999 (CJM6460); 1 ♂, 1 ♀, Hunedoara, Vulcan, 45.38° N, 23.29° E, leg. 16 Nov. 1996 (CJM3770); Klausenburg, Botanical Garden, 46.759° N, 23.586° E (Weiss 1996); 1 ♂, 1 ♀, Nădrag, 45.65° N, 22.18° E, leg. 30 Aug. 2001 (CJM3768); 1 ♂, Parâng Mountains, Râncea, 45.29° N, 23.69° E, leg. 17 Aug. 1997 (CJM3769); 1 ♂, 2 ♀♀, Perșani Mts., Valea Siclău (coordinates inaccurate, valid for mountains!), 45.90° N, 25.43° E, leg. 4 Aug. 1967 (from literature); 1 ♂, Piatra (Köhát) Mts., Săpânța (Szaplönca), Brazi valley, 841 m, 47.830° N, 23.743° E, leg. 2 Sep. 2004 (Muranyi & Lengyel 2006); 8 juv., Piatra (Köhát) Mts., Săpânța (Szaplönca), mineral water springs in the lower valley of the Săpânța (Szaplönca) stream, 408 m, 47.9349° N, 23.6781° E, leg. 30 Jun. 2005 (Muranyi & Lengyel 2006); 1 juv., Piatra (Köhát) Mts., Săpânța (Szaplönca), valley of the Săpânța (Szaplönca) Stream, 500 m, leg. 30 Jun. 2005 (Muranyi & Lengyel 2006); 1 ♂, Prahova, Sinaia, 45.35° N, 25.55° E, leg. 25 Sep. 1949 (CJM6183, H. Franz, 938); 1 ♂, 1 ♀, Rodna (Radnai) Mts., Săcel (Izaszacsal), Iza spring, 900 m, leg. 22 Sep. 2005 (Muranyi & Lengyel 2006, was described as *L. rupestre* but doubtful record); 1 ♂, 1 ♀, Rodna Mts., Pasul Prislop, 47.609° N, 24.855° E, leg. 25 Jun. 1968 (Avram & Dumitrescu 1969); Saschiz, Keisd, 46.194° N, 24.960° E (Weiss 1996); Sebeș Olt (GPS might not be correct), 45.67° N, 24.31° E (Weiss 1996); Suceava, Horodnicu de Sus (Russian translation

and GPS might not be correct), 47.84° N, 25.82° E (Cîrdei 1960); Suceava, Măgura Mt. 47.32° N, 25.96° E (Roșca 1930); Suceava, Rarău Mt., 47.45° N, 25.58° E (Roșca 1930); 2 ♂♂, Kronstadt, Kapellenberg, 45.635° N, 25.597° E (ZMB12634, orig. det. as *L. rupestre*); 2 ♂♂, Sibiu (Hermannstadt), 45.78° N, 24.12° E, leg. 29 Aug. 1896 (ZMB12636, orig. det. as *L. rupestre*).

RUSSIA: Oblast St Petersburg (Leningrad), Petrodvorec, 59.886° N, 29.896° E (Roewer 1957); Primorje (formerly Groß Kuhren), 54.94° N, 20.04° E (Le Roi 1914); Rjabinowka (formerly Groß Raum), 54.83° N, 20.50° E (Le Roi 1914); Sankt Petersburg (Leningrad), 59.90° N, 30.25° E (Staręga 1978); 1 ♂, St. Petersburg, City, (coordinates inaccurate), wall of house, 59.90° N, 30.28° E, leg. 10 Aug. 2003 (CJM3032); Svetlogorsk (formerly Warnicken), 54.90° N, 20.11° E (Le Roi 1914); Swetlogorsk (formerly Rauschen), 54.89° N, 20.11° E (Le Roi 1914); Alt-Peterhof (St. Petersburg), 6 ♂ 6 ♀ (SMFR11/1201, Roewer 1957).

SERBIA: 1 ♂, Bor Dubašnica, Mala Tisnica, 44.200° N, 21.867° E, leg. 12 Aug. 1994 (CJM6363).

SLOVAK REPUBLIC: Červená skala (Dobšiná), 48.82° N, 20.13° E (Šilhavý 1981); Dobroč (Brezno nad Hronom), 48.73° N, 19.69° E (Šilhavý 1981, all following records from this reference orig. det as *L. glabrum*); Gornasek (Rožnava; used for GPS), 48.66° N, 20.54° E (Šilhavý 1981); Kamenica nad Cir (Kamenica nad Cirochou: GPS), 48.93° N, 22.00° E (Šilhavý 1981); Košice, 48.72° N, 21.25° E (Šilhavý 1981) did not discriminate betw. *L. rupestre* and *L. tisciae* for this record); Nové Mesto nad Váhom, 48.75° N, 17.83° E (Šilhavý 1981); Pajštún (Bratislava), 48.27° N, 17.08° E (Šilhavý did not discriminate betw. *L. rupestre* or *L. tisciae* for this record); Prešov, 48.99° N, 21.24° E (Šilhavý 1981) did not discriminate betw. *L. rupestre* and *L. tisciae* for this record); Rájecké Teplice, 49.13° N, 18.68° E (Šilhavý 1981); Roháče Mts. (coordinates inaccurate), 49.23° N, 19.72° E (Šilhavý 1981); Štubnianské Teplice (today Turčianske Teplice), 48.86° N, 18.86° E (Šilhavý 1981); Súlov, 49.16° N, 18.59° E (Šilhavý 1981); Trenčianske Teplice, 48.91° N, 18.17° E (Šilhavý 1981); Vihorlat Mts. (coordinates inaccurate), 48.89° N, 22.13° E (Šilhavý 1981); Vrátna dolina (Žilina), 49.26° N, 19.03° E (Šilhavý 1981).

SWEDEN: Östergötland (coordinates inaccurate, just for the map!), 58.35° N, 15.51° E (Tullgren 1906a, b); Västergötland, Råbäck, 58.61° N, 13.36° E (Tullgren 1906a, b); Skåne County, Lund, 55.70° N, 13.19° E, leg. Aug. 1872 (Tullgren 1906a, b); Småland (coordinates very inaccurate!), 57.4° N, 15.3° E (Tullgren 1906a, b).

UKRAINE: Bez. Černovcy, Ciudei, 48.05° N, 25.62° E, leg. 1935 (Cîrdei 1960); Bez. Kiev, Bila Tserkva (orig.: Belaja Cerkov), 49.78° N, 30.13° E (Morin 1934); Bez. Užgorod, Rachov, 48.05° N, 24.21° E (Bartoš 1939); Bez. Žitomir, Novograd-Volynskij, 50.58° N, 27.66° E (Morin 1934); Chernivets'ka, Vijnja, 48.25° N, 25.19° E (Roșca 1930); L'vovskaya oblast' (orig.: Bez. L'vov), Ivano-Frankovo, 49.92° N, 23.73° E (L. Koch 1870); Ternopil, Kremeneč, 50.11° N, 25.72° E (Staręga 1978).

#### *Leiobunum rupestre* (Herbst, 1790)

AUSTRIA: Vorarlberg: 1 ♂, Übersaxen, Baschghöhle, 785 m, 47.25° N, 9.67° E, leg. October (Breuss 1995); Salzburg (all records if not otherwise indicated refer to Ausobsky 1987), Bergheim bei Salzburg, Hochgitzten, 47.850° N, 13.034° E; Buchberg, 47.942° N, 13.092° E; Haunsberg, 47.92° N, 12.99° E; Heuberg, 47.82° N, 13.11° E; Moosachtal bei St. Georgen an der Salzach, 47.98° N, 12.88° E; Plain, Plainberg, 47.837° N, 13.044° E; Salzburg, Festungsberg, 47.795° N, 13.048° E; Salzburg, Kapuzinerberg, 47.803° N, 13.056° E; Salzburg, Mönchsberg, 47.799° N, 13.039° E; Salzburger Becken, Elsbethen, Elsbethener Hügel, 47.76° N, 13.10° E, Georgenberg near Kuchl, 47.635° N, 13.161° E; Hellbrunner Berg, 47.758° N, 13.066° E; Morzger Hügel, 47.768° N, 13.055° E; Tannberg, 47.973° N, 13.188° E; Tiefstein gorge near Schleedorf, 47.947° N, 13.158° E; Stubachtal, Weissee, 47.16° N, 12.64° E (Mazzucco 1967); 4 ♂♂, 2 ♀♀, Stubachtal, N Enzingerboden, 1420–1460 m, 47.184° N, 12.625° E, leg. 7 Oct.

1966 (CJM496); 11 ♂♂, 5 ♀♀, Pinzgau, Kaprun, entrance of Sigmund-Thun-Klamm (Alp12\_04), 800 m, 47.258517° N, 12.738571° E, leg. 10 Sep. 2012 (AXLS1283); Oberösterreich, Weilhartsforst, 48.16° N, 12.91° E (Ausobsky 1987); 1 ♂, vicinity of Stifterherberge at Bärenstein, 900–950 m, upper coniferous forest, 48.660° N, 13.991° E (SMF16343/1); 1 ♂, Steiermark, Koralpe, Soboth, 900 m, wet slopes near stream, *Salix* and *Abies*, 46.67650° N, 15.08331° E, leg. 30 Aug. 2009 (AXLS277); 1 ♂, Gesäuse, coniferous forest, 47.58° N, 14.64° E, leg. 16 Sep. unknown year (ZMB12640); Kärnten, Baldersdorf, way to Egelsee, 46.78° N, 13.56° E (Komposch 2008); Saualpe, Löllingbach, 1100 m, 46.55° N, 14.37° E (Komposch & Gruber 2004); 5 juv., Flaschberg near Oberdrauburg, 46.75° N, 12.94° E, leg. 28 Jul. 1982 (Kofler & Mildner 1986); Klagenfurt, Sattnitz, boulders betw. Bad and Hanswirt, leg. 3 Sep. 1985 (Kofler & Mildner 1986); Klagenfurt, Sattnitz, Höllgraben, 46.49° N, 14.28° E, leg. 10 Sep. 1985 (Kofler & Mildner 1986); 5 ♂♂, 1 ♀, near Klebas, road 111, subway, 46.696° N, 12.802° E, leg. 1 Sep. 2012 (AXLS1356); Ruin Obertrixen, 46.702° N, 14.575° E, leg. 19 Aug. 1985 (Kofler & Mildner 1986); St. Leonhard near Liebenfels, 46.74° N, 14.26° E, leg. 30 Jul. 1985 (Kofler & Mildner 1986); 1 ♂, Tröpolach, Gailtal, 900 m, 46.62° N, 13.28° E, leg. 30 Sep. 1975 (CJM1411); Ulrichsberg, 46.71° N, 14.31° E, leg. 3 Oct. 1968 (Kofler & Mildner 1986); 6 ♂♂, 2 ♀♀, N Graz, Hinterreitenwald, SE Glettwieber, Glettbach, 870 m, 47.201° N, 15.428° E, leg. 14 Sep. 2012 (AXLS1301); Hohe Tauern, Gössnitztal (Gössnitz=Goessnitz), 1700 m, 47.031° N, 12.792° E (Komposch & Gruber 1999); Niederösterreich, Lunz am See, forests around Untersee, 47.85° N, 15.05° E (Thaler 1963); 1 ♂, Semmering (M2), 47.63° N, 15.83° E, leg. Oct. 1899 (ZMB12644); 1 ♂, Tirol, Innsbruck, in the city, Weierburggasse, 730–800 m, at housewall, 47.278° N, 11.396° E, leg. 27 Sep.–1 Oct. 1986 (CJM3523); Innsbruck surroundings, *Picea* forests S of Inn River, Hußlhof-Natters-Amras-Igls-Ampass-Hall, 580 m, in moss (Stipperger 1928); 1 ex., Forellenhof near Lavant, at limestone boulders, 46.79° N, 12.84° E, leg. 7 Sep. 1971 (Kofler 1984); 3 juv., Nikolsdorf, Tal-Trasse, right side of Drau River, 46.78° N, 12.91° E, leg. 28 Jul. 1982 (Kofler 1984); 1 ♀, Nörsach (Kärntner Grenze), 46.78° N, 12.93° E, leg. 28 Aug. 1969 (Kofler 1984); Villgrater Tal (GPS not accurate), 46.80° N, 12.38° E (Werner 1931); 1 ♀, Virgental, Iselschlucht near Welzelach, 47.017° N, 12.413° E, leg. 2 Aug. 1978 (Kofler 1984); Windisch-Matrei, 47.00° N, 12.53° E (Dalla-Torre 1882); Bärenbadalm above Achensee, 1400–1500 m, caves in *Picea* forest, 47.42° N, 11.70° E (Stipperger 1928); Hungerburg, 860 m, Sand- and Schotterquarry at border of *Picea* forest, 47.29° N, 11.40° E (Stipperger 1928); Maldontal, betw. Boden and Bsclabs, 1350 m, Fichten- und Föhrenwald, 47.30° N, 10.59° E (Stipperger 1928); Stallental, 800–1600 m, *Picea* forest with *Fagus*, 47.38° N, 11.69° E (Stipperger 1928); Kaunertal from Kaltenbrunn and Feuchten to Gepatschhaus (coordinates inaccurate), 1260–1700 m, *Picea* forest, humid cliffs along stream and path, 47.05° N, 10.75° E (Stipperger 1928); Oberbergtal from Milders im Stubai to Stöcklenalm (coordinates inaccurate), 1100–1600 m, *Picea* forest, at boulders, 47.12° N, 11.32° E (Stipperger 1928); S St. Anton am Arlberg, 1310 m, cliffs in *Picea* forest, 47.13° N, 10.27° E (Stipperger 1928); Schwaz, betw. Schloß Freundsberg and Rodlhütte, 540–1600 m, *Picea* forest mixed with *Abies* and *Fagus*, under leaf litter, in moss, at stones and trunks, 47.34° N, 11.71° E (Stipperger 1928); Sellraintal betw. Kematen, Gries and Praxmar, 610–1600 m, humid, shaded cliffs and moss at stream in *Picea* forest, 47.17° N, 11.14° E (Stipperger 1928); between Pettneu and Malfontal, 1200–1300 m, *Picea* forest, 47.140° N, 10.343° E (Stipperger 1928); betw. Volders and Volderer Wildbad, 600–1100 m, wet *Picea* forest with *Alnus*; 3 ♂♂, 47.27° N, 11.56° E (Stipperger 1928); Lienz (GPS not accurate), 46.83° N, 12.76° E, (SMFR11/1184, Roewer 1957); 3 ♂♂, 1 ♀, Lienz Dolomiten, Hohenstein (SMFR11/701, Roewer 1957); Burgenland, 1 ♂, southern Leithagebirge, „Kürschnergrube“ (abandoned chalk quarry) N of Eisenstadt, 435 m, in man made cavity at steep humid cliff, 47.86° N, 16.52° E, leg. 7 Nov. 1996 (NMW17922, Gruber 2000).

BOSNIA AND HERZEGOVINA: 11 ♂♂, 1 ♀, Jaice (=Jajce), tufa walls, waterfall, 44.342° N, 17.266° E (ZMB12639); 2 ♂♂, Kupreška vrata, Bugojno, 1384 m, 44.00° N, 17.31° E (Novak 2005); Travnik, 44.22° N, 17.66° E (Martens 1978); 2 ♂♂, Trebević (National Park and mountain S of Sarajevo, coordinates accurate), *Corylus* forest, 43.8° N, 18.45° E, leg. Sep.–Oct. (ZMB12638); 4 ♂♂, 1 juv., Vilinska jama cave, 42.73° N, 17.89° E, leg. 1916 (Novak 2005).



CROATIA: 1 ♂, Bijeli vrh, Vrhovine, 1074 m, 44.84° N, 15.44° E (Novak 2004b); 1 juv., Kamengrad, Papuk Mt., beside the Orlava river, 528m, 45.53° N, 17.50° E (Novak 2004b); 5 ♂♂, 2 ♀♀, 2 juv., Kamenica Skradnička, beside the Rudnica brook (WL30), 260 m, 45.20° N, 15.45° E, leg. May 1985 (Novak 2004b); 3 ♂♂, 1 ♀, Kameniti vrh Mt., Plitvice, 934 m, 44.88° N, 15.57° E (Novak 2004b); 1 ♂, Klanjec, 170 m, 46.05° N, 15.74° E (Babić 1916); 1 ♂, Krapina, 290 m, 46.16° N, 15.87° E, leg. Aug. 1914 (Babić 1916); Križevci, 140 m, 46.03° N, 16.52° E (Daday 1896), orig. det. as *Leiobunum glabrum*); 2 ♂♂, Ledenjača u Čudinoj uvali cave (WK46), Veliki Javornik, 44.84° N, 15.57° E (Novak 2004b); Maksimova pećina cave, Jankovac, 657 m, 45.52° N, 17.68° E (Babić 1916); 2 ♂♂, Medvedak Mt., Plitvice, 889 m, 44.89° N, 15.64° E (Novak 2004b); 2 ♂♂, 1 ♀, E Sveti Jakob, stream valley of river Medveščak, 600 m, under stones and wet logs near river, 45.884° N, 15.945° E, leg. 9 Sep. 2009 (AXLS345); 1 juv., near Vrilo Rudnice, Kamenica Skradnička, 260 m, 45.23° N, 15.35° E, leg. Jul. 1987 (Novak 2004b); 1 juv., Ozalj, Karlovac, Kordun, Ozaljska spilja cave, 45.62° N, 15.45° E, leg. 6378 (Novak 2004b); 13 juv., Pećina pri Tržiću (=Pećina kod mlina), Tržić Tounjski, beside the Mrežnica River, 45.23° N, 15.41° E, leg. Jul. 1983 (Novak 2004b); 1 juv., Plitvice (coordinates inaccurate), 677 m, 44.88° N, 15.62° E (Babić 1916); 6 ♂♂, Sagorije, Ogulinsko, Ivancij, hunter house at Smitowo jezero, 351 m, at large rocks in *Fagus* forest, 45.188° N, 15.223° E, leg. 7 Sep. 2009 (AXLS319); 1 ♂, 1 ♀, Sagorije, Ogulinsko, Ivancij, Sagorska peč, 326 m, at wall in cave entrance, 45.197° N, 15.222° E, leg. 7 Sep. 2009 (AXLS322); 1 ♂, Skrad, 700 m, 45.43° N, 14.91° E, leg. May 1905 (Babić 1916); 1 juv., Sveta gora, 580 m, 45.53° N, 14.67° E (Novak 2004b, Babić det. as *O. alpinus*); 1 ♂, 1 ♀, Vilinska jama cave (=Vilina jama, Volina-Volinjska jama, one hour away from Krapina), leg. 11 Aug. 1885 (Jurinac 1886, Novak 2004b), orig. det. as *Leiobunum religiosum*).

CZECH REPUBLIC: All records originate from Šilhavý (1981) so far not otherwise indicated. Šumava, Boubín, 48.94° N, 13.79° E; Holná (maybe wrong), 49.12° N, 14.87° E; Horní Smrčné, 49.33° N, 15.76° E; Hrubá Skála, 50.54° N, 15.19° E; Ještěd Mt., 50.73° N, 14.98° E; Jevany, 49.97° N, 14.81° E (Šilhavý did not discriminate betw. *L. rupestre* or *L. tisciae* for this record); 2 ♂♂, 1 ♀, limestone caves near Brunn (Brno), leg. 17 Sep. 1971 (CJM982); Klučky (mountain ridge near Nový Bor), 50.78° N, 14.50° E; Koněšín, 49.19° N, 16.04° E; Kunratice, 50.01° N, 14.48° E (Šilhavý did not discriminate betw. *L. rupestre* or *L. tisciae* for this record); Kvilda, 49.02° N, 13.58° E; Lamberk (Náměšť nad Oslavou), 49.17° N, 16.18° E; Máchovo jezero (Dosky), 50.58° N, 14.67° E; Mariánské Lázně, 49.96° N, 12.70° E; Mohelno (Třebíč), 49.11° N, 16.19° E; Moravský kras, 49.31° N, 16.70° E; Olší (Jindřichův Hradec), 49.16° N, 15.37° E; Pravčická brána (Hřensko), 50.88° N, 14.28° E; Rokytnice nad Jizerou, 50.73° N, 15.45° E; Rýchory, 50.67° N, 15.87° E; Špindleruv Mlýn, 50.73° N, 15.61° E; Tiské skály (Děčín), 50.80° N, 14.04° E; Tremšín (Rožmitál), 49.57° N, 13.78° E (Šilhavý did not discriminate betw. *L. rupestre* or *L. tisciae* for this record); Vlčí kopec, 49.15° N, 16.45° E.

GERMANY: Baden-Württemberg, 2 ♀♀, Nature Reserve Wutachschlucht, Stigelesfels, 48.0166° N, 8.9333° E, leg. 1 Oct. 1980 (CJM1954); 4 ♂♂, Lotenbachklamm, rock face, 47.85° N, 8.3° E, leg. 25 Jul. 1964 (CJM123); 1 ♂, Schwäbische Alb, Höllochschacht bei Dettingen, 48.513° N, 9.346° E, leg. 2.12.1967 (CJM1198); 2 ♂♂, Tiefental, Kreis Nürtingen, Gutenberg, Gußmannshöhle, 680 m, 48.543° N, 9.520° E, leg. 18 Feb. 1962 (SMF13067/2, Dobat 1963); 2 ♂♂, 11 ♀♀, Schwarzwald, Triberg, 48.13° N, 8.23° E, leg. Aug. 1959 (SMF11173/12); 5 ♂♂, 3 ♀♀, S-Schwarzwald, Schwarzatal S Schluchsee, Schwarzahalden, 600 m, Bannwald, 47.74° N, 8.19° E, leg. 14 Sep. 2008 (CJM6207); 2 ♂♂, 1 juv., Schwarzwald, Titisee, 865 m, 47.89° N, 8.14° E, leg. 29 Sep. 2013 (AXLS1626); Wolfsbrunn near Heidelberg, 49.412° N, 8.746° E (C. Koch 1871; Le Roi 1914); Bayern, Benediktenwand, 47.65° N, 11.47° E (L. Koch 1861); Berchtesgaden, Jenner, 800 m, forest, 47.58° N, 13.00° E (Hammelbacher 1986); 1 ♂, 1 ♀, Ramsau / Wachterl, 1000 m, mixed forest, 47.65° N, 12.866° E, leg. 11 Jul. 1986 (CJM2804); 3 ♂♂, Tegernsee, ascend to Wallberg, 700–1000 m, coniferous forest, at cliff, 47.68° N, 11.75° E, leg. 31 Sep. 2006 (CJM5318); near Regensburg (GPS for the city), 48.97° N, 12.13° E (Martens 1978); 4 ♂♂, Bavarian Forest, N Finsternau, Siebensteinkopf, 1130–1200 m, 48.95° N, 13.566° E, leg. 23 Aug. 1992 (CJM4358); 2 ♀♀, Arber, in the cirque-wall (Karwand), 49.10° N, 13.12° E, leg. 19

Aug. 1964 (CJM136); 20 juv., Lusen, Arber, Riesloch Falls, 48.933° N, 13.50° E, leg. 14–17 Aug. 1964 (CJM143); 1 ♂, 6 juv., Rachelsee, under stones, 48.975° N, 13.402° E, leg. 16 Aug. 1964 (CJM113, CJM109); 6 ♂♂, Riesloch-Fälle near Bodenmais, 49.05° N, 13.083° E, leg. 18 Aug. 1964 (CJM101); 1 ♂, 1 ♀, Garmisch-Partenkirchen, Partnachklamm, 850 m, 47.466° N, 11.116° E, leg. 14 Oct. 1978 (CJM1856); 1 ♀, NSG Murnauer Moos, 47.64° N, 11.17° E, leg. 1977/78 (SMF33105, Löser *et al.* 1982); Nürnberg, betw. Bruck and Happburg (coordinates inaccurate), 49.52° N, 11.18° E (L. Koch 1877, as *L. bicolor*); Pottenstein, Fränkische Schweiz, 49.77° N, 11.40° E, leg. 1 Oct. 1948 (SMF59294, Schönhofer 2005); 2 ♂♂, Waldnaabtal, Oberfranken, 49.6° N, 12.133° E, leg. 22 Aug. 1964 (CJM86). Hessen, 1 ♂, Werra-Meißner-Kreis, Meißner, stone cellar near Neuen Schwalbenthaler Erbstollen (No. 4725/58), 580 m, Mittlerer Buntsandstein, 51.2056° N, 9.87 09° E, leg. 25 Oct. 2005 (CJM4802, S. Zänker, WK 211); Thüringen, 2 ♂♂, Schwarzta Valley near Schwarzburg, 50.633° N, 11.183° E, leg. 28 Sep. 2006 (CJM5392); Sachsen, 1 ♀, Erzgebirge (Ore Mountains), at Floßgraben betw. Aue and Bockau, 50.55° N, 12.67° E, leg. 21 Nov. 1926 (Büttner 1930); Lausitzer Mts., Neiße Valley betw. Östritz and Hirschfelde, 50.97° N, 14.92° E (Hiebsch 1972); 8 ♂♂, 1 ♀, S Königstein, stream valley before junction to Cunnersdorf, Biela Stream, 150 m, at stone bridge, 50.903° N, 14.064° E, leg. 9 Sep. 2006 (CJM5293); 7 ♂♂, Schöna, near border to Czech Republic, 100 m, coniferous and mixed forest, at night at wood and stones, 50.867° N, 14.217° E, leg. 13 Oct. 2005 (CJM4752); 2 ♀♀, same data (CJM4753).

HUNGARY: Budapest, Mecsek Mts. (coordinates inaccurate), 47.51° N, 19.01° E (Kolosváry 1929, 1964); 10 ex., Geschriebenstein Nature Park, beside road to Velem (St. Veit), NNE Óház, WSW Kőszeg (Güns), 400 m, scree in a fresh deciduous forest with maple, linden, hombeam and beech, 47.22° N, 16.30° E (Komposch 2004); Kőszegi-hegység, Kőszeg, Hét-forrás, 47.39° N, 16.53° E, leg. 31 Aug. 2005 (Lengyel & Muranyi 2006); Kőszegi-hegység, Velem, Szerdahelyi-patak-part, 47.345° N, 16.514° E, leg. 17 Sep. 2005 (Lengyel & Muranyi 2006).

ITALY: Carnia, 46.37° N, 13.14° E (Caporiacco 1922); 1 ♂, Friuli-Venezia Giulia, Prov. Udine, Carnic Alps near Tarvisio, 800 m, 46.50° N, 13.57° E, leg. 1 Oct. 1975 (CJM1456); 2 juv., Moggio Udinese, Stavoli Cuel Lung alto, Mt. Zovet (UM53), 700 m, Fagetum, pitfall traps, 46.48° N, 13.19° E, leg. 16 Jul. –20 Aug. 2001 (MFSNU, Novak 2004a); 1 ♂, SE Arta Terme, path in forest, 46.478° N, 13.069° E, leg. 1 Sep. 2012 (AXLS1349); 1 ♀, Resia, above Clen, between Casera Coot and Slatina superiore (UM73), 1000 m, Fagetum, pitfall traps, leg. 20 Aug.–26 Sep. 2001 (MFSNU, Novak 2004a); 3 juv., Resia, between Berdo di Sopra and Rio Malidul (UM73), 1260 m, 46.34° N, 13.29° E, leg. 12 Jun. 2003 (MFSNU, Novak 2004a); Südtirol, Meran, 46.68° N, 11.17° E (L.Koch 1869, **type locality of *Leiobunum glabrum* L. Koch, 1869**).

POLAND: 3 ♂♂, Kitz....? (maybe Kitzelberg; label not legible) Bober Katzbach Mts. (GPS not accurate), 50.96° N, 15.84° E, leg. 6 Sep. 1924 (ZMB12643). Karkonosze Mts. (Staręga 2004).

SERBIA: 1 ♀, Valjevo, planina Medvenik, 44.24° N, 19.63° E, leg. 1 Aug. 1998 (CIK1337); 1 ♂, Valjevo, planina Medvenik, Drenaička pecina, leg. 20 Oct. 1999 (CIK1336).

SLOVENIA: Alto Isonzo, Monte Merzli, 46.22° N, 13.70° E, leg. Nov. 1915 (Marcellino 1973); 1 ♂, Celje (Cilli), deciduous forest, 46.24° N, 15.26° E, leg. 25 Oct. (ZMB12635); 7 ♂♂, Huda Luknaja Cave, Tisnick Mt. SE Slownej Gradec, 46.48° N, 15.07° E, leg. 16 Oct. 2004 (CJM4203); 3 ♀♀, Huda Luknaja Cave, Tisnick Mt., SE Slownej Gradec (GPS S of city), 46.48° N, 15.07° E, leg. 16 Oct. 2004 (CJM4204); 15 ♂♂, 4 ♀♀, Julian Alps, road to Mount Mangert, upper end of village Strmec na Predelu, 1013 m, 46.41769° N, 13.60833° E, leg. 28 Aug. 2009 (AXLS264); 4 ♂♂, Karawanken, road to Loibl Pass, 650 m, 46.40° N, 14.28° E, leg. 2 Oct. 1975 (CJM1445); 6 ♂♂, 1 ♀, Ljubljana, small forest at northern city limit, 46.10530556° N, 14.51822° E, leg. 3–4 Sep. 2012 (AXLS1389); 9 ♂♂, 1 ♀, Pohorje Mts., Mislinja, locality Glažuta, 1013 m, stream valley, on cliff-faces in coniferous forest, 46.480° N, 15.280° E, leg. 26 Aug. 2009 (AXLS237); 3 ♂♂, Savinje valley, Erjavčeva Jama, entrance zone, 700 m,

46.383° N, 14.717° E, leg. 2 Oct. 1994 (CJM3161); 1 ♀, Slowenj Gradec, at housewall, 46.51° N, 15.07° E, leg. 13–17 Oct. 2004 (CJM4140); Triglav, Martuljuk, 46.46° N, 13.83° E, leg. 15 Aug. 1928 (Hadži 1931); 1 juv., vicinity of Zirknitz (=Cerknica), 650 m, *Fagus* forest, 45.79° N, 14.37° E, leg. 17 Jul. 1974 (CJM1260); 3 ♂♂, 1 ♀, Unec, Rakov Škocjan, at border of river Rak, 520 m, at cliff in *Fagus* forest, leg., 45.796° N, 14.293° E, leg. 10 Sep. 2009 (AXLS352); 1 ♂, Wochein (=Bohinj, Julian Alps) (ZMB12637).

SWITZERLAND: Basel-Landschaft, Arlesheim, 47.49° N, 7.63° E (Müller & Schenkel 1895; Lessert 1917).

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