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Two new species of *Formicoxenus* Mayr 1855 and *Leptothorax* Mayr 1855 from Tibet (Hymenoptera: Formicidae)

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Abstract

The Palaearctic species of the socially parasitic ant genus *Formicoxenus* Mayr 1855 are taxonomically revised. A numeric analysis of phenotypical characters in workers showed a close relatedness of the three Palaearctic *Formicoxenus* species and a strong separation from the six independent Palaearctic species of the genus *Leptothorax* Mayr 1855. *Myrmica laeviuscula* Foerster 1850, *Myrmica lucidula* F. Smith 1858 and *Formicoxenus nitidulus* var. *picea* Wasmann 1906 are synonymized with *Formicoxenus nitidulus* (Nylander 1846) whereas *Formicoxenus orientalis* Dlussky 1963 and *Leptothorax zhengi* Zhou et Chen 2011 are established as junior synonyms of *Formicoxenus sibiricus* (Forel 1899). The new species *Formicoxenus gebaueri* n.sp. is described from NE Tibet. It was found as a guest ant in a nest of an undescribed species of the ant subgenus *Serviformica* Forel 1913. The very plastic host selection of Palaearctic *Formicoxenus* species is explained by the presence of a fully functional worker caste. *Leptothorax tibeticum* n.sp., a species related to *L. muscorum* (Nylander 1846), is described from the high Tibetan Plane. A key to the workers of *Formicoxenus* species and independent *Leptothorax* species of the Palaearctic is provided and each species is depicted by z-stack images in three visual positions.

Keywords Cryptic species | numeric morphology-based alpha-taxonomy | inquilines | host specifity

1. Introduction

Both morphology (Bolton 2003) and genetics (Ward et al. 2015) indicate that the ant genera *Formicoxenus* Mayr 1855 and *Leptothorax* Mayr 1855 are closely related and share a common ancestor. Francoeur et al. (1985), recognizing seven Holarctic species of *Formicoxenus*, noted that the Nearctic species are by morphology closer to *Leptothorax* than the much more derived Palaearctic species. Yet, the presence of ergatoid males and xenobiotic life style in all seven *Formicoxenus* species and absence of this character combination in all known *Leptothorax* species prompted Francoeur et al. to collect the Nearctic and Palaearctic species within the same genus. These species were *Formicoxenus nitidulus* (Nylander 1846) and *F. sibiricus* (Forel 1899) from the Palaearctic and *F. hirticornis* (Emery 1895), *F. provancheri* (Emery 1895) *F. chamberlini* (Wheeler 1904), *F. diversipilosu*s (Smith 1939) and *F. quebecensis* Francoeur et al. 1985 from the Nearctic. This paper does not discuss the problems with this genus concept and will only consider the Palaearctic *Formicoxenus* species of which one species is described here as new. All *Formicoxenus* species are inquilines (guest ants). Considering the Holarctic, ants of the genera *Formica* Linnaeus 1758, *Myrmica* Latreille 1804 and *Manica* Jurine 1807 may serve as hosts. The three Palaearctic species were exclusively observed to live in nests of *Formica* but, on the species level, there is no host specificity. According to Seifert (2018), *Formicoxenus nitidulus* parasitizes in its whole geographic range the subgenera *Formica* s.str, *Coptoformica* Müller 1923 and *Raptiformica* Forel 1913 – making up a total of 12 species. As documented here, *F. sibiricus* uses both the

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subgenera *Serviformica* Forel 1913 and *Coptoformica* and the single finding of *Formicoxenus gebaueri* n.sp. occurred in a nest of *Serviformica*. Plasticity in host selection is probably explained by the presence of a fully functional worker caste, providing some independence, which differs from the situation in workerless inquilines which are more frequently host specific.

The Palaearctic fauna of the genus *Leptothorax* known so far includes the three workerless socially parasitic species *Leptothorax pacis* (Kutter 1945), *L. kutteri* Buschinger 1965 and *L. goesswaldi* Kutter 1967 and the five independent species *L. acervorum* (Fabricius 1793), *L. muscorum* (Nylander 1846), *L. gredleri* Mayr 1855, *L. scamni* Ruzsky 1905 and *L. oceanicus* Kuznetzov-Ugamsky 1928. A sixth independent species, found on the Tibetan Plane, will be described here as new.

2. Material and Methods

2.1 Material

The Palaearctic *Leptothorax* and *Formicoxenus* species have only few, apparently well-separable species. This justifies a rather parsimonious approach. Morphometric data were recorded in *Leptothorax* in 124 samples (usually nest samples) with 247 workers and in *Formicoxenus* in 9 nest samples with 21 workers. With the exception of type specimens and other samples of special relevance, data of this material are not presented in detail in the main text of this paper but are listed up in the electronic supplementary information SI1.

2.2 Equipment and measurement procedures

For spatial adjustment and measuring was used a pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0 planapochromatic objective (resolution 1050 lines/mm) at magnifications of 120-384x. A Schott KL 1500 cold–light source equipped with two flexible, focally mounted light–cables, providing 30°–inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold–light source in combination with a Leica coaxial polarized–light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52 % of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. Images of ants were produced with Keyence VHX 7000 digital microscope.

2.2.1 The morphometric characters

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of hind vertex and/or clypeus reduce CL.

CS – cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.

CW – maximum cephalic width; the maximum is found in *Temnothorax* and *Leptothorax* usually across and including the eyes, exceptionally posterior of the eyes.

EYE – the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye. All structurally visible ommatidia are considered.

FRS – with the area of frontal lobes in visual plane (given when tilting the head caudad), distance of the frontal carinae at the level of the deepest point of the pits taking up the basal scape corners when the scape is tilted caudad. These pits are usually visible by dark shaddows in the frontal lobes. If shaddows are not visible, sufficiently similar measures can be taken at the transverse level of the anterior margin of frontal triangle (Fig. 1).

MGr – depth of metanotal groove or depression, measured from the tangent connecting the dorsalmost points of promesonotum and propodeum; here given as per cent ratio of CS.

MH – with mesosoma in lateral view and measured orthogonal to 'longitudinal mesosomal axis', MH is the longest measurable ***section*** line of mesosoma at mesopleural level (not height above all). 'Longitudinal mesosomal axis' in lateral view is defined as straight line from the center of propodeal lobe (center of dashed circus in Fig. 2) to the border point between anterior pronotal shield and propleuron (dashed line in Fig. 2).

ML – mesosoma length from caudalmost point of propodeal lobe to transition point between anterior pronotal slope and anterior propodeal shield (Fig. 2, preferentially measured in lateral view; if the transition point is not well defined, use dorsal view and take the center of the dark-shaded borderline between pronotal slope and pronotal shield as anterior reference point).

MW –maximum mesosoma width; this is in workers pronotal width, in gynes it is measured anteriorly of the tegulae.

PeH – maximum petiole height. The chord (dashed line in Fig. 3) of ventral petiolar profile at node level (excluding the subpetiolar lobe) is the reference line perpendicular to which the maximum height of petiole is measured.

PeL – diagonal petiolar length in lateral view; measured from anterior corner of subpetiolar process to dorsocaudal corner of caudal cylinder (Fig. 3).

PeW – maximum width of petiole.

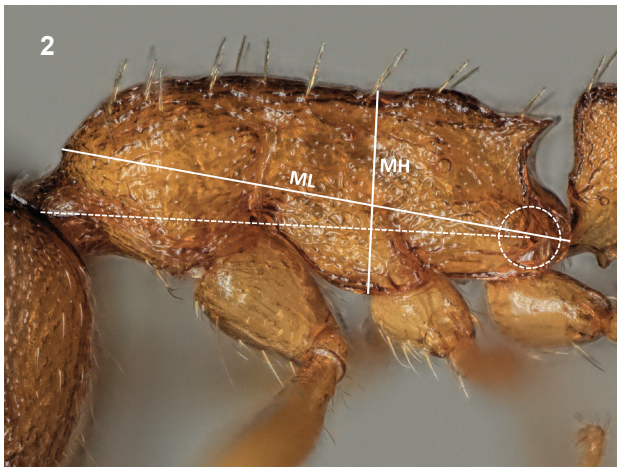
PnHL – length of the longest seta on pronotum.

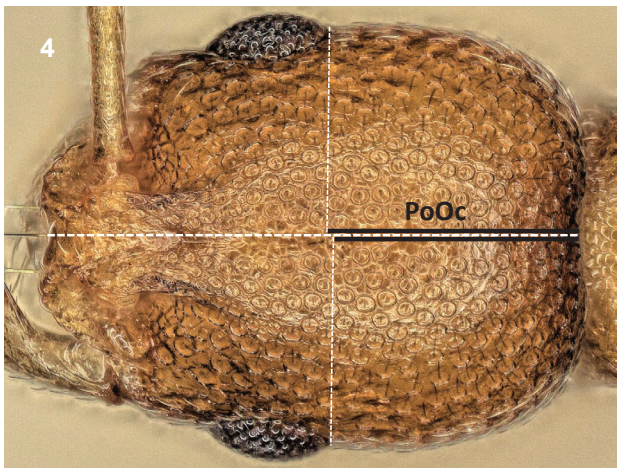
PoOc – postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL (dashed line in Fig. 3). Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin. Note that heads may be asymmetric and average the left and right postocular distance (black bars in Fig. 4).

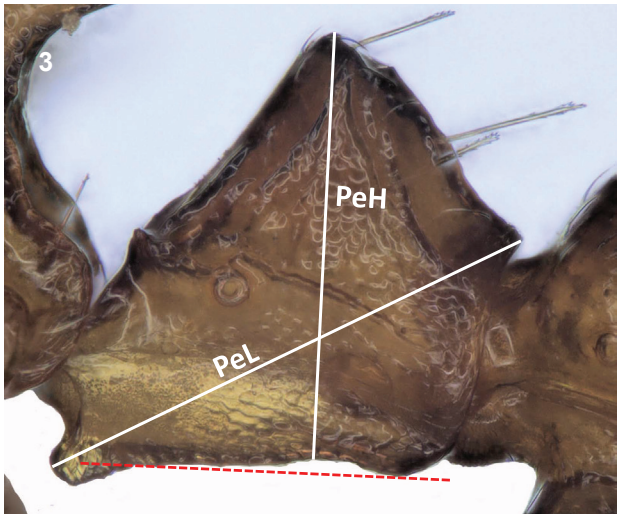
PpW – maximum width of postpetiole.

SL – maximum straight line scape length excluding the articular condyle as arithmetic mean of both scapes.

SP – maximum length of propodeal spines; measured in dorsofrontal view along the long axis of the spine, from







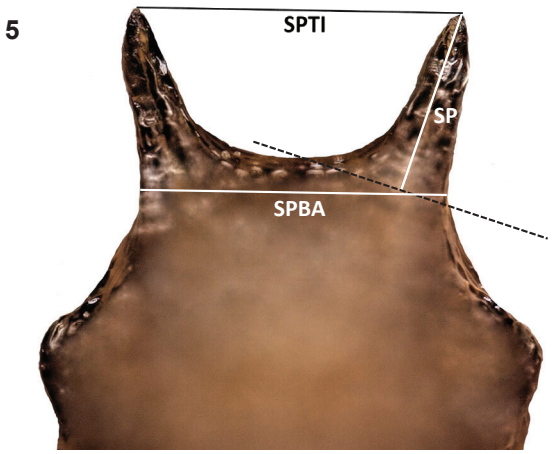


Figure 1–5: (**1**) Measuring FRS. (**2**) The dotted line marks the longitudinal axis of mesosoma in lateral view perpendicular to which MH is measured. (**3**) Measuring PEH perpendicular to but not beginning at the dotted line. (**4**) Bilateral measuring of postocular distance PoOc to correct for head asymmetries. (**5**) Measuring of spine length SP.

spine tip to a line, orthogonal to the long axis, that touches the bottom of the interspinal meniscus (Fig. 5). This mode of measuring is less ambiguous than other methods but it results in some spine length in species with reduced spines.

SPBA – the smallest distance of the lateral margins of the spines at their base. This should be measured in dorsofrontal view, since the wider parts of the ventral propodeum do not interfere with the measurement in this position. If the lateral margins of spines diverge continuously from the tip to the base, a smallest distance at base is not defined. In this case, SPBA is measured at the level of the bottom of the interspinal meniscus.

SPST – distance between the center of propodeal stigma and spine tip. The stigma center refers to the midpoint defined by the outer cuticular ring but not to the center of real stigma opening that may be positioned eccentrically.

SPTI – the distance of spine tips in dorsal view; if spine tips are rounded or truncated, the centers of spine tips are taken as reference points.

3. Results

3.1 Key to the workers of Palaearctic *Leptothorax* and *Formicoxenus*

Specimens of *Leptothorax oceanicus* were not available for investigation – I follow here the original description of Kuznetsov-Ugamsky (1928) and the re-description by Radchenko & Heinze (1997). The three socially parasitic Palaearctic *Leptothorax* species *L. pacis*, *L. goesswaldi* and *L. kutteri* have no workers.

1a Postpetiolar sternite with a well-developed acute spine (Figs 7, 11, 15). Head very narrow but with a broad frons, FRS/CW > 0.464. Eye small, EYE/CL < 0.176. Genus *Formicoxenus*..... **2**

1b Postpetiolar sternite in profile without a well developed spine, at most with small frontal denticle (Figs 20, 32). Head wider, frons narrower, eye larger, FRS/CW <0.464, EYE/CL > 0.176. Genus *Leptothorax*..... **4**

2a Whole dorsum of head smooth and brilliantly shiny, sometimes frontal lobes and genae weakly longitudinally carinulate. Temperate to boreal zone of Palaearctic from Europe to Russian Far East (Figs 6–9) ..... ***F. nitidulus***

2a Whole dorsum of head matt, strongly longitudinally rugulose, the interspaces microreticulate (appearing at lower magnifications punctate) **3**

3a Setae on whole body very short (PnHL/CS < 0.090), widening from base to apex (Fig. 13), apically fringed and in cross-section forming a tridentate star. Frons much broader, FRS/CW >0.533. Middle Asia, Inner Mongolia, Transbaikalia (Figs 10–13) ..... ***F. sibiricus***

3b Setae on whole body much longer (PnHL/CS > 0.90), narrowing from base apex (Fig. 17), and in cross-section cylindrical. Frons much narrower, FRS/CW < 0.533. North of Tibetan Plane (Figs 14–17) ..... ***F. gebaueri* n.sp.**

4a Anterior and posterior slopes of petiole node in lateral view almost linear, forming an acute angle and a sharp dorsal corner; subpetiolar lobe broad (Fig. 18). Anteromedian margin of clypeus without a notch. Erect setae on head and mesosoma sparse. Russian Far East ..... ***L. oceanicus***

4b Dorsum of petiole node in lateral view not forming a sharp, acute corner. Subpetiolar lobe small, dentiform or spiky **5**

5a Scape and tibiae with numerous standing setae (Figs 19–21): Temperate to south arctic zone of whole Palaearctic..... ***L. acervorum***

5b Scape and tibiae without standing setae, occasionally semierect pubescence hairs may be present..... **6**

6a Propodeal spines longer and frons narrower. With all measurements in mm, discriminant 14.66*CW-60.0*FRS+52.06*SPST-7.29 > 2.6 [error 0% in 6 specimens]. Asia Minor and Caucasus (Figs 22–24) ..... ***L. scamni***

6b Propodeal spines shorter and frons wider. Discriminant < 2.6 [error 0% in 90 specimens]..... **7**

7a Postocular distance smaller, scape relatively longer and head width on average larger. With all measurements in mm, discriminant 37.13*CW+46.90*SL-127.92* PoOc-12.72 > 0.25 [error 0% in 40 specimens]. Lateral vertex with pronounced longitudinal sculpture, reticular structures in comparison much less obvious. Temperate and submediterranean zone of Europe and Caucasus (Figs 25–27) ..... ***L. gredleri***

7b Postocular distance larger, scape relatively shorter and head width on average smaller. Discriminant < 0.25 [error 0% in 50 specimens]. Lateral vertex with a more reticular sculpture..... **8**

8a Frontal carinae not or only very slightly diverging frontad (FL/FR < 1.025). Petiole relatively lower (PEH/PEL 0.803 ± 0.023) and in profile with a broader dorsal crest. Sculpture weaker. Temperate to south boreal zone of Palaearctic (Figs 28–30)..... ***L. muscorum***

8b Frontal carinae notably diverging frontad (FL/FR > 1.025). Petiole relatively higher (PEH/PEL 0.870 ± 0.021) and in profile with a narrow (but not acute) dorsal crest. Sculpture stronger. Tibetan Plane (Figs 31–33)..... ***L. tibeticum* n.sp.**

3.2 Taxonomic treatment on genus level – the strong morphological disparity of Palaearctic *Leptothorax* and *Formicoxenus*

The workers of the three Palaearctic *Formicoxenus* species differ clearly from those of *Leptothorax* by a much more developed subpostpetiolar spine, a much more elongated head, a broader frons, by the genae in dorsal view appearing parallel or even diverging frontad and by smaller eyes. A principal component analysis of the characters CL/CW, FRS/CS, EYE/CS, SP/CS, MW/CS and PEL/CS provides a very clear separation on the individual level (Fig. 34). These data suggest a close relatedness of the Palaearctic *Formicoxenus* species. Yet, it appears questionable if the Nearctic species collected by Francoeur et al. (1985) under *Formicoxenus* will turn out as the next relatives after a whole-genome analysis has been done. The *Formicoxenus* concept of Francouer et al. is based on the sharing of a syndrome that is not known in *Leptothorax* species: (a) presence of ergatoid males, (b) development of multiple female intercastes and (c) xenobiotic life style. It would not be a big surprise if this syndrome is inherited by a single nonrecombinant supergene that might be transmitted in evolutionary networks as a block of coadapted genes. A genetic mechanism that works in the development of supercoloniality (Chapuisat 2023) might also work in expression of xenobiotic life style.

3.3 Taxonomic treatment by species

The reasons for identification of a taxon are given in square brackets after taxonomic name, author and year.

***Formicoxenus nitidulus* (Nylander 1846)**

Myrmica nitidula Nylander 1846 [type investigation]
The species has been described in an ergatoid male from Helsingfors (=Helsinki), leg F.W. Maeklin. Investigated were two syntypes on different pins. The first is labelled 'H: fors', 'W. Nyland.', 'Mus. Fenn', 'Mus. Zool. H: fors Spec. typ. No. 5072 *Myrmica nitidula* Nyl.' and the second one with equal labels except for '... Spec. typ. No. 5073...'.

Myrmica laeviuscula Foerster 1850 [original description]
This taxon has been described from Aachen in a gyne. Types are probably lost but the original description clearly indicates a synonymy with *F. nitidulus*. Foerster already considered a possible synonymy but decided to describe a new species because his gyne had 11 antennal segments whereas Nylander's 'worker' (in fact an ergatoid male!) was reported to have 12 segments.

Myrmica lucidula F. Smith 1858 [original description]
This taxon has been described from Weybridge, Surrey (leg. Waterhouse). The only descriptive statement was that the ants '...appear always to inhabit the nest of the wood-ant, never constructing a nest of their own'. As there is in Europe only a single shiny ('*lucidula*') ant living in nests of *Formica rufa* group ants, there is little doubt on a synonymy.

Formicoxenus nitidulus var. *picea* Wasmann 1906 [original description]
This taxon was described from Luxembourg as a very dark (nearly blackish brown) color variant found in a nest of *Formica pratensis* Retzius 1783. The synonymy is obvious.

Material examined. Morphometric data were taken in seven samples with 10 workers from Czech Republic, Germany and Finland. For details see supplementary information SI1. The material subjectively inspected is from the whole Westpalaearctic.

Geographic range. Eurosiberian, temperate-boreal. The very wide host spectrum allows continuous distribution from Scotland and France to Russian Far East. In Fennoscandia up to 70°N, in the Alps ascending to 2300 m.

Diagnosis: --Worker (Figs 6–9, key). Numeric data given are arithmetic means based on measurement of 10 specimens (for standard deviation, minimum and maximum values see Tab. 1). Rather small size, CS 642 µm . Head much elongated, CL/CW 1.270. Clypeus extended caudad, semiglobular, in dorsal view with a semicircular anterior margin. Posterior margin of head straight. Frons extremely broad (FRS/CS 0.513). Scape rather short, SL/CS 0.677. Eye small, EYE/CS 0.186, with long setae (Fig. 9). Dorsal profile of promesonotum and propodeum weakly convex, metanotal depression shallow (MGr/CS 1.34 %). Spines rather short (SP/CS 0.143) and not very acute, their bases rather distant (SPBA/CS 0.324). Petiole with strong anterolateral corners, in

Table 1. Measurements of workers of the genera *Leptothorax* and *Formicoxenus*. Data are given in the sequence arithmetic mean ± standard deviation [minimum, maximum].

	Leptothorax					**Formicoxenus**		
	L. scamni (n=6)	***L. gredleri*** (n=40)	***L. muscorum*** (n=37)	***L. tibeticum*** (n=13)	***L. acervorum*** (n=151)	***F. nitidulus*** (n=10)	***F. sibiricus*** (n=5)	***F. gebaueri*** n.sp. (n=5)
CS	0.832 ± 0.039 [0.778,0.882]	0.706 ± 0.035 [0.641,0.763]	0.647 ± 0.027 [0.593,0.700]	0.618 ± 0.030 [0.575,0.698]	0.813 ± 0.041 [0.701,0.946]	0.642 ± 0.038 [0.568,0.689]	0.676 ± 0.007 [0.670,0.688]	0.738 ± 0.021 [0.708,0.756]
CL/ CW	1.074 ± 0.031 [1.028,1.109]	1.100 ± 0.019 [1.064,1.138]	1.135 ± 0.016 [1.102,1.161]	1.115 ± 0.016 [1.086,1.146]	1.109 ± 0.025 [1.020,1.176]	1.270 ± 0.024 [1.230,1.302]	1.333 ± 0.022 [1.312,1.362]	1.253 ± 0.024 [1.226,1.279]
SL/CS	0.710 ± 0.011 [0.690,0.722]	0.705 ± 0.016 [0.667,0.736]	0.691 ± 0.013 [0.662,0.713]	0.689 ± 0.010 [0.673,0.705]	0.695 ± 0.014 [0.650,0.727]	0.677 ± 0.010 [0.653,0.687]	0.737 ± 0.008 [0.726,0.749]	0.712 ± 0.011 [0.696,0.723]
PoOc/ CL	0.369 ± 0.007 [0.360,0.379]	0.349 ± 0.008 [0.333,0.364]	0.373 ± 0.008 [0.362,0.397]	0.370 ± 0.009 [0.354,0.383]	0.379 ± 0.009 [0.352,0.402]	0.368 ± 0.007 [0.353,0.378]	0.375 ± 0.003 [0.371,0.378]	0.379 ± 0.003 [0.375,0.384]
EYE/ CS	0.211 ± 0.014 [0.195,0.230]	0.220 ± 0.008 [0.208,0.239]	0.218 ± 0.006 [0.204,0.230]	0.220 ± 0.004 [0.211,0.228]	0.203 ± 0.006 [0.187,0.223]	0.186 ± 0.008 [0.172,0.196]	0.173 ± 0.003 [0.168,0.177]	0.164 ± 0.005 [0.156,0.169]
FRS/ CS	0.360 ± 0.009 [0.345,0.369]	0.392 ± 0.010 [0.372,0.416]	0.382 ± 0.010 [0.362,0.397]	0.411 ± 0.014 [0.381,0.427]	0.384 ± 0.011 [0.356,0.413]	0.513 ± 0.013 [0.487,0.531]	0.478 ± 0.004 [0.474,0.484]	0.432 ± 0.005 [0.426,0.439
MW/ CS	0.587 ± 0.003 [0.581,0.590]	0.621 ± 0.011 [0.604,0.643]	0.621 ± 0.010 [0.597,0.648]	0.618 ± 0.016 [0.591,0.648]	0.624 ± 0.011 [0.600,0.654]	0.574 ± 0.010 [0.552,0.584]	0.581 ± 0.004 [0.576,0.587]	0.578 ± 0.008 [0.565,0.585]
MH/ CS	0.519 ± 0.025 [0.492,0.549]	0.535 ± 0.021 [0.486,0.582]	0.544 ± 0.014 [0.512,0.579]	0.544 ± 0.020 [0.496,0.571]	0.546 ± 0.020 [0.523,0.570]	0.524 ± 0.015 [0.499,0.552]	0.545 ± 0.010 [0.532,0.557]	0.515 ± 0.026 [0.484,0.553]
ML/ CS	1.323 ± 0.031 [1.286,1.355]	1.326 ± 0.022 [1.274,1.368]	1.293 ± 0.021 [1.250,1.331]	1.266 ± 0.026 [1.226,1.302]	1.326 ± 0.022 [1.270,1.372]	1.257 ± 0.036 [1.198,1.314]	1.307 ± 0.082 [1.293,1.315]	1.307 ± 0.023 [1.274,1.336]
SPBA/ CS	0.266 ± 0.010 [0.251,0.276]	0.282 ± 0.014 [0.260,0.315]	0.289 ± 0.014 [0.260,0.315]	0.301 ± 0.017 [0.273,0.330]	0.298 ± 0.014 [0.257,0.336]	0.324 ± 0.004 [0.318,0.331]	0.294 ± 0.008 [0.285,0.304]	0.289 ± 0.014 [0.268,0.301]
SPTI/ CS	0.340 ± 0.012 [0.323,0.355]	0.304 ± 0.018 [0.260,0.341]	0.322 ± 0.012 [0.297,0.346]	0.344 ± 0.016 [0.317,0.372]	0.346 ± 0.019 [0.288,0.413]	0.298 ± 0.010 [0.276,0.312]	0.276 ± 0.012 [0.262,0.294]	0.280 ± 0.011 [0.268,0.291]
SPST/ CS	0.376 ± 0.012 [0.363,0.397]	0.313 ± 0.017 [0.279,0.346]	0.319 ± 0.013 [0.293,0.347]	0.308 ± 0.018 [0.279,0.336]	0.346 ± 0.015 [0.300,0.386]	0.296 ± 0.020 [0.256,0.323]	0.314 ± 0.004 [0.311,0.320]	0.299 ± 0.017 [0.284,0.326]
SP/CS	0.248 ± 0.007 [0.240,0.256]	0.183 ± 0.016 [0.138,0.218]	0.196 ± 0.015 [0.173,0.228]	0.213 ± 0.016 [0.188,0.239]	0.221 ± 0.013 [0.176,0.253]	0.143 ± 0.017 [0.104,0.162]	0.144 ± 0.007 [0.138,0.155]	0.153 ± 0.017 [0.136,0.178]
PeW/ CS	0.249 ± 0.013 [0.233,0.264]	0.263 ± 0.013 [0.247,0.301]	0.266 ± 0.009 [0.245,0.286]	0.270 ± 0.012 [0.256,0.293]	0.270 ± 0.012 [0.247,0.310]	0.300 ± 0.008 [0.291,0.316]	0.267 ± 0.008 [0.258,0.279]	0.271 ± 0.013 [0.256,0.289]
PpW/ CS	0.388 ± 0.019 [0.354,0.408]	0.417 ± 0.017 [0.388,0.446]	0.406 ± 0.014 [0.371,0.427]	0.417 ± 0.018 [0.397,0.460]	0.430 ± 0.018 [0.389,0.493]	0.405 ± 0.013 [0.384,0.426]	0.344 ± 0.003 [0.341,0.349]	0.379 ± 0.016 [0.356,0.399]
PeH/ CS	0.372 ± 0.014 [0.352,0.383]	0.390 ± 0.015 [0.350,0.417]	0.397 ± 0.010 [0.371,0.417]	0.402 ± 0.014 [0.381,0.422]	0.393 ± 0.013 [0.363,0.427]	0.394 ± 0.011 [0.379,0.418]	0.362 ± 0.003 [0.358,0.364]	0.365 ± 0.014 [0.351,0.384]
PeL/ CS	0.495 ± 0.010 [0.482,0.506]	0.474 ± 0.014 [0.448,0.502]	0.494 ± 0.015 [0.468,0.520]	0.463 ± 0.021 [0.430,0.512]	0.502 ± 0.018 [0.462,0.552]	0.487 ± 0.019 [0.457,0.508]	0.506 ± 0.008 [0.493,0.513]	0.507 ± 0.021 [0.475,0.532]
MGr/ CS	2.78 ± 0.98 [1.53,4.36]	2.47 ± 0.67 [1.37,3.94]	1.99 ± 0.49 [1.21,2.89]	1.48 ± 0.72 [0.52,3.51]	2.15 ± 0.49 [1.10,3.46]	1.34 ± 0.47 [0.87,2.05]	2.69 ± 0.20 [2.42,2.89]	2.95 ± 0.36 [2.39,3.40]
PnHL/ CS	0.112 ± 0.007 [0.104,0.120]	0.146 ± 0.011 [0.129,0.181	0.141 ± 0.012 [0.118,0.162]	0.146 ± 0.014 [0.114,0.161]	0.132 ± 0.011 [0.106,0.155]	0.077 ± 0.014 [0.045,0.093]	0.062 ± 0.005 [0.054,0.067]	0.128 ± 0.008 [0.116,0.137]
FL/FR	1.022 ± 0.013 [1.000,1.034]	1.004 ± 0.006 [1.000,1.019]	1.003 ± 0.005 [1.000,1.019]	1.090 ± 0.023 [1.045,1.131]	1.013 ± 0.014 [1.000,1.063]	1.000 ± 0.000 [1.000,1.000]	1.005 ± 0.011 [1.000,1.025]	1.000 ± 0.000 [1.000,1.000]

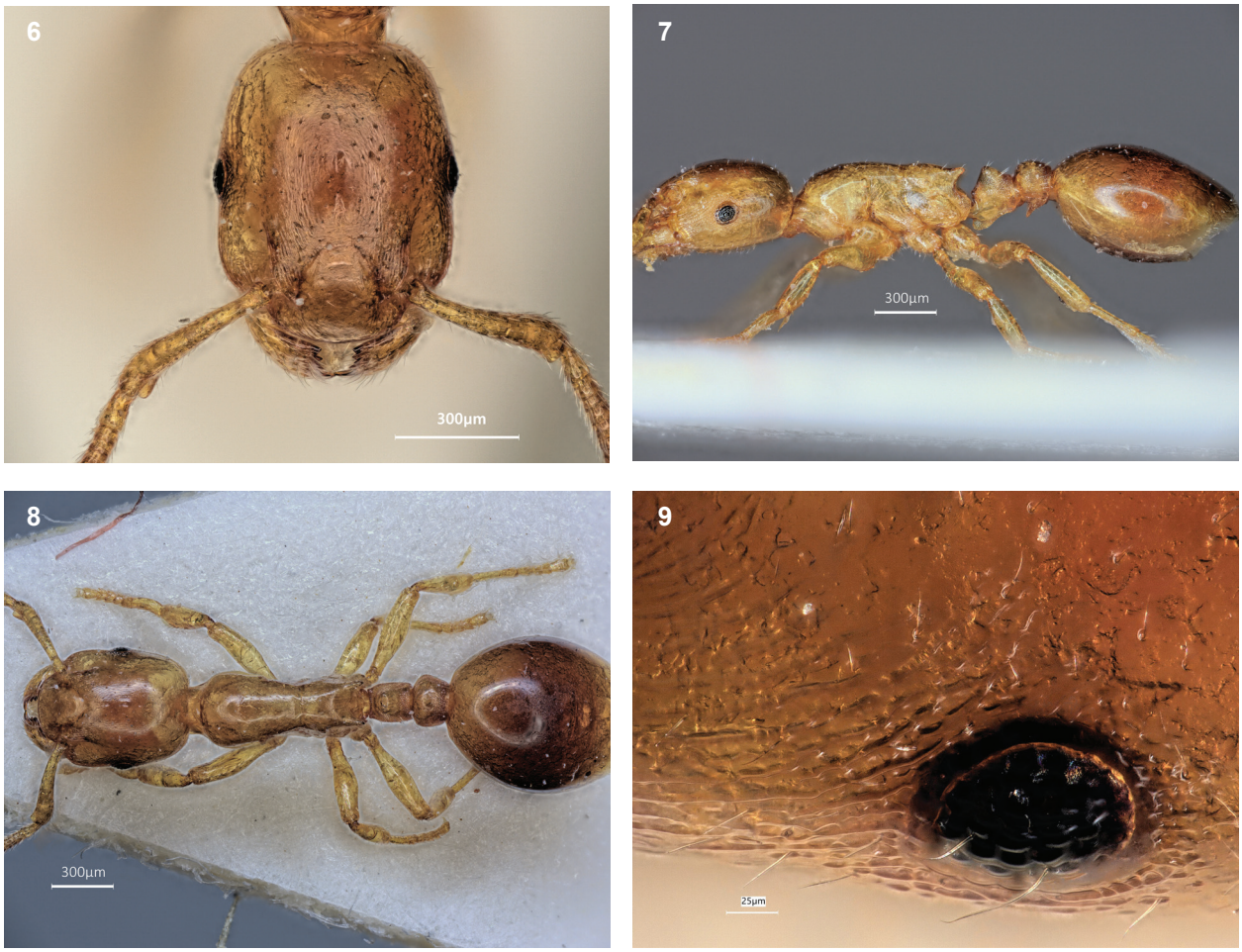


Figure 6–9. *Formicoxenus nitidulus*; (**6**) head in dorsal view; (**7**) lateral view; (**8**) dorsal view; (**9**) dorsolateral view on eye. Germany: Altdöbern, 1992.02.09

profile without peduncle and with a broad subpetiolar lobe. Postpetiolar sternite with a well-developed spine. All surfaces of head, mesosoma, waist and appendages smooth and very shiny, sometimes frontal lobes and genae weakly longitudinally carinulate. Gaster glabrous and with very dilute pubescence. Head, mesosoma, waist, scape, femora and tibiae with scattered and short (PnHL/CS 0.077) setae, tapering apicad and round in cross-section. Color variable from light yellowish brown to nearly blackish brown.

Taxonomic comments. As a combination of smooth and shiny body surfaces, very broad frons, elongated head and extended semiglobular clypeus not to confuse.

Biology. See the condensed description of life history in Seifert (2018).

Formicoxenus sibiricus (Forel 1899)

Leptothorax sibiricus Forel 1899 [images of type specimen]

Forel (1899) described this taxon from East Siberia without giving a more precise type locality: 'Sibérie orientale (recu de M. Nassonow).' Investigated were the images of the lectotype worker, designated by A. Francoeur and labelled 'L. sibiricus For', 'L. sibiricus For Nassonov', 'Siberie orient.', 'Typus', 'LECTOTYPE Formicoxenus sibiricus (FOREL) A.F.-1984' and 'ANTWEB CASENT 0909066'. This lectotype fixation was published by Francoeur et al.(1985). Depository: Muséum d'histoire naturelle de Genève, Genève, Switzerland. We have a very good idea of the morphological characters of this species as the images of the type correspond very well to the characters of my own sample from East Kazakhstan on the basis of which the species is re-described below.

Formicoxenus orientalis Dlussky 1963 [original description]

Dlussky (1963) described this taxon from East Siberia based on workers collected within a nest of *Formica pressilabris*. He gave the data: „Golotyp. 1 rabotschi iz gnezda *Formica pressilabris*. No 288, 9 IX 1957,

Chitinskaya obl., Sretenskij raiyon, Dunayevskoje lesnichestvo, pad' Kulinda." Type-depository: Zoological Museum of Moscow Lomonossov University, Moskva / Russia.

Dlussky's description is very detailed and is in no character in disagreement with the re-description of *Formicoxenus sibiricus* presented below. This refers to any feature of body shape, sculpture and the characteristic shape of setae.

Leptothorax zhengi Zhou et Chen 2011 [original description]

Zhou et al. (2011) gave the following collecting data: 'Holotype locality: Inner Mongolia: Shantangzi Monitoring Station, Helanshan National Nature Reserve, 29 July 2010, leg. Chen Zhi-Lin.' The type depository was not specified but is possibly the collection of Guangxi Normal University, Guilin, China. As mean measurements of three type workers in mm can be derived from the data of Zhou et al. (2011) CL = 0.790, CW 0.581 (adapted to the measuring mode used here), SL 0.460, MW 0.385, ML 0.845. This translates into CS 0.686, CL/CW 1.360, SL/CS 0.671, MW/CS 0.560, ML/CS 1.230 (compare with Tab. 1). Even if considering some measuring inaccuracy, these measurements as well as images given in the original description indicate a junior synonymy with *F. sibiricus*. This refers in particular to the much elongated head, the small eyes, the mesosoma and waist profile with a very broad subpetiolar process and an acute, well-developed spine of postpetiolar sternite, the characteristic sculpture on head, mesosoma and waist, and the short blunt setae on whole body. Hence there is in no character a disagreement with the re-description of *Formicoxenus sibiricus* presented below. No data on the circumstances of collecting were given.

Material examined. Direct investigation was performed in a sample of five workers, collected from a nest of *Formica clara* Forel 1886, and labelled 'KAZ: 47.17.39 N, 85.37.03 E, 1486 m, Saur Mts. Steppe, mit Serviformica, leg. Seifert 2001.07.24 – 179'. Depository: SMN Görlitz.

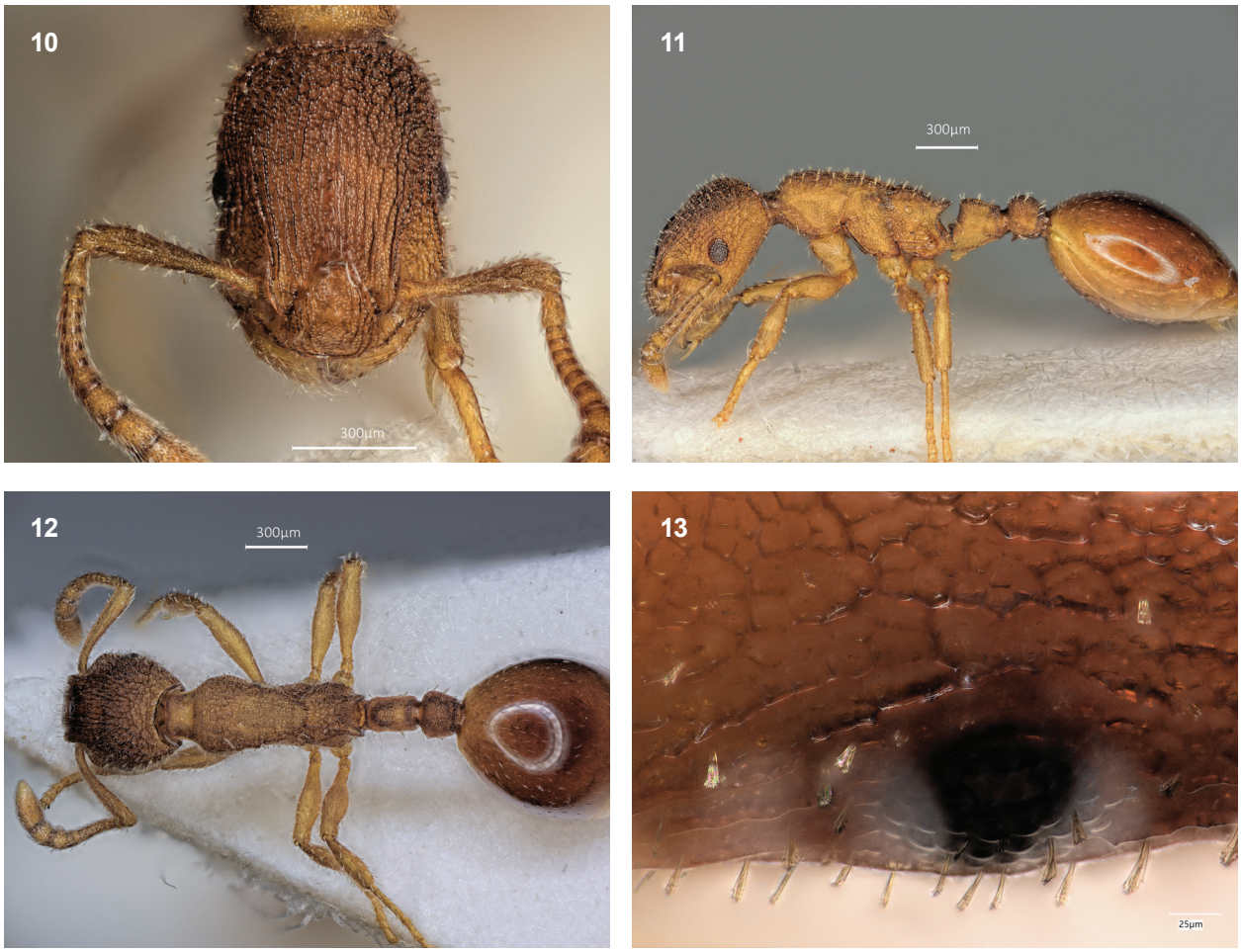


Figure 10–13. *Formicoxenus sibiricus*; (**10**) head in dorsal view; (**11**) lateral view; (**12**) dorsal view; (**13**) dorsolateral view on eye. Kazakhstan: Saur Mountains, 2001.07.24

Geographic range. Southern Central to East Siberia. The three collecting sites with useful geographical data are in the Saur Mountains (47.2933°N 85.6177°E), the Helanshan National Nature Reserve (38.7°N 105.9°E) and Kulinda waterfall near Dunayevo (52.501°N 116.720°E).

Diagnosis: --Worker (Figs 10–13, key; pictures CASENT 0909066 in www.antweb.org). Numeric data given are arithmetic means based on measurement of 5 specimens (for standard deviation, minimum and maximum values see Tab. 1). Rather small size, CS 676 µm. Head much elongated, CL/CW 1.333. Genae in dorsal view parallel or even slightly diverging frontad. Anterior margin of clypeus in dorsal view semicircular. Occipital margin straight to weakly concave. Frons very broad (FRS/CS 0.478). Scape comparably long, SL/CS 0.737. Eye very small, EYE/CS 0.173, with notable microsetae. Dorsal profile of promesonotum largely linear, propodeum convex, metanotal depression moderately deep (MGr/CS 2.69%). Spines rather short and acute (SP/CS 0.144), their bases moderately distant (SPBA/CS 0.294). Petiole with strong anterolateral corners, in profile without peduncle and with a broad subpetiolar lobe. Postpetiole narrower than in other species (PpW/CS 0.344), its sternite with a well-developed spine. All surfaces of head, mesosoma, waist and appendages matt due to a reticulate microsculpture. Dorsal vertex strongly longitudinally carinulate-rugulose. Gaster glabrous and with very dilute pubescence. Head, mesosoma, waist, scape, femora and tibiae with very short (PnHL/CS 0.062) setae, which widen from base to apex, are apically fringed (Fig. 13) and form in cross-section a tridentate star. Color of head, mesosoma, waist and gaster homogenously yellowish brown.

Taxonomic comments. As a combination of short, blunt and fringed setae with a well-developed sculpture on head, mesosoma, waist and appendages, *Formicoxenus sibiricus* is unmistakable.

Biology. Similar to the situation in *Formicoxenus nitidulus*, there is obviously no host specificity in this xenobiotic ant. Confirmed host species are *Formica (Serviformica) clara* Forel 1886 and *Formica (Coptoformica) pisarskii* Dlussky 1964. The latter host had originally been determined by Dlussky (1963) as *F. (Coptoformica) pressilabris* Nylander 1846 but later he corrected the identification (Dlussky 1964). The mistake becomes already apparent by zoogeography: the site near Dunayevo (52.07°N, 117.06°E) should exclude *F. pressilabris* the known range of which does not extend east of 61°E (Seifert & Schultz 2021).

***Formicoxenus gebaueri* n.sp.**

Etymology: dedicated to the collector Axel Gebauer.

Type material:

Holotype and 7 paratype workers from the same nest labelled 'CHINA: 36.82°N, 102.53°E, Beishan Nat. Park, 2600 m, Picea-Pinus-Wald, Geröllhang. A. Gebauer 1996.05.30'

Diagnosis: --Worker (Figs 14–17, key). Numeric data given are arithmetic means based on measurement of 5 specimens (for standard deviation, minimum and maximum values see Tab. 1). Medium-sized, CS 738 µm.Head elongated, CL/CW 1.253. Genae in dorsal view nearly parallel. Median third of anterior margin of clypeus and hind margin of vertex in dorsal view straight. Frons narrower than in *F. sibiricus* (FRS/CS 0.432), scape slightly shorter (SL/CS 0.712. Eye very small, EYE/CS 0.164. Dorsal profile of promesonotum and propodeum slightly convex, metanotal depression moderately deep (MGr/CS 2.95%). Spines rather short and acute (SP/CS 0.153), their bases moderately distant (SPBA/CS 0.289). Petiole with strong anterolateral corners, in profile without peduncle and with a less broad subpetiolar lobe. Postpetiolar sternite with a well-developed spine. All surfaces of head, mesosoma, waist and appendages matt due to a reticulate microsculpture. Dorsal vertex strongly longitudinally carinulate-rugulose. Gaster smooth and shiny but in contrast to *F. sibiricus* with subdecumbent to semierect setae. Head, mesosoma, waist, and gaster with long (PnHL/CS 0.128) setae, tapering apicad (Fig. 17) and round in cross-section. Color of head, mesosoma, waist and gaster homogenously yellowish brown.

Taxonomic comments. As a combination of long, tapering setae, well-developed sculpture on head, mesosoma, waist and appendages and narrower frons, *Formicoxenus gebaueri* n.sp. is unmistakable among the Palaearctic *Formicoxenus* species.

Biology. The type sample was collected below a stone within a *Picea-Pinus* forest on a slope with rubble. The host species was an undescribed species of the subgenus *Serviformica* Forel 1913.

***Leptothorax tibeticum* n.sp.**

Etymology: belonging to Tibet since all known findings were from there.

Type material:

Holotype and plus 4 paratype workers on the same pin, labelled 'CHI: 36.6911°N, 99.7968°E, Heimahe-4 km SSE, 3288 m, Viehweide, 2011.07.26-KoZ2-Bleg'; one

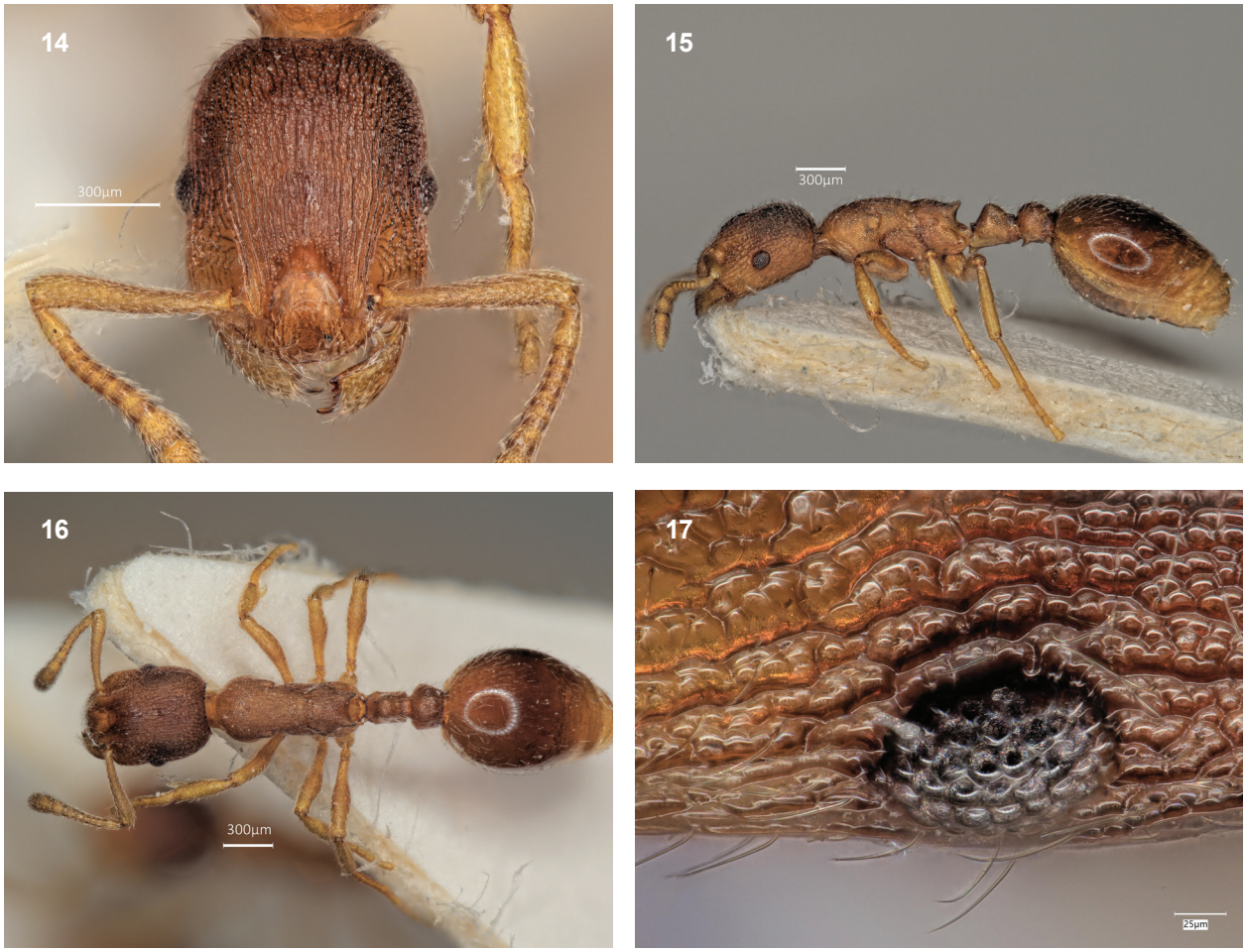


Figure 14–17: *Formicoxenus gebaueri* n.sp., holotype; (**14**) head in dorsal view; (**15**) lateral view (flipped horizontally); (**16**) dorsal view; (**17**) dorsolateral view on eye. China: Beishan National Park, 1995.05.30

paratype worker labelled 'CHI: 36.6959°N, 99.8119°E, Heimahe-4.7 km SE, 3262 m, Viehweide, Seifert 2011.07.23-KoA-BPs'; two paratype workers on the same pin, labelled 'CHI: 37.1796°N, 102.7775°E, Tianzhu, 3039 m, Rand Weide / Buschland, Seifert 2011.08.04-82'; five paratype workers on two pins, labelled 'CHI: 37.1770°N, 102.7731°E, Tianshu, 3146 m, Gipfel, Weide mit Büschen, Seifert 2011.08.04'; four paratype workers, labelled 'CHI: 38.0370°N, 101.5896°E, Xinchengzizhen, 3114 m, Weide an Waldrand, Seifert 2001.07.31-74'; all five samples were collected by the author and are deposited in SMN Görlitz.

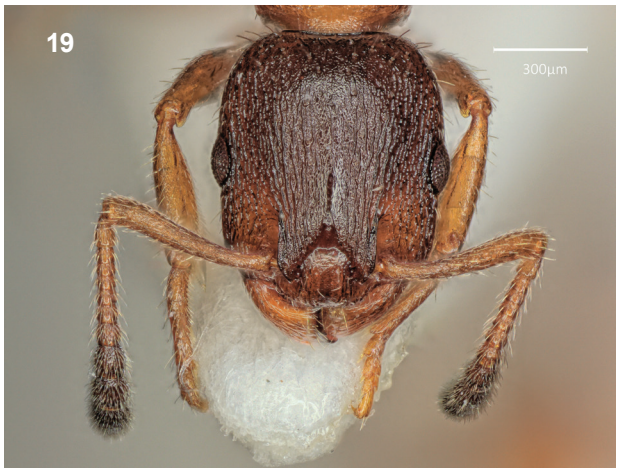
Geographic range. So far only found during collections of the PADEMOS project in the three NE Tibetan sites reported above. This ant was not found during collections of the same project performed in similar habitats farther south and southwest.

Diagnosis: --Worker (Figs 31–33, key). Numeric data given are arithmetic means based on measurement of 13 specimens (for standard deviation, minimum and maximum values see Tab. 1). Rather small, CS 618 µm.

Figure 18. *Leptothorax oceanicus*, propodeum and waist (from Kuznetzov-Ugamsky 1928), Russian Far East

Head less elongated than in *muscorum*, CL/CW 1.115. Anterior margin of clypeus in dorsal view convex. Paramedian clypeus with 2-3 curved carinulae on each side; median clypeal surface smooth and shiny, its contour in dorsocaudal view plane. Genae and postocular head sides in dorsal view slightly convex, posterior margin of

head straight and feebly concave in median third. Frons broader than in *muscorum* (FRS/CS 0.411); frontal carinae, as difference to any other Palaearctic *Leptothorax* species, strongly diverging frontad (FL/FR 1.090). Scape moderately long, SL/CS 0.689. Eye relatively large, EYE/CS 0.220, with notable microsetae. Mesosoma shorter than in other species (ML/CS 1.266). Dorsal profile of mesosoma in overall impression feebly but rather evenly convex, with a shallow metanotal depression (MGr/CS 1.48 %). Spines rather long and acute (SP/CS 0.213), their



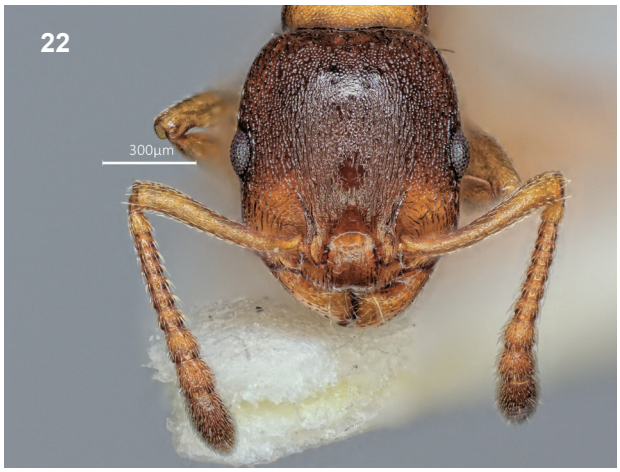


Figure 19–21. *Leptothorax acervorum*; (**19**) head in dorsal view; (**20**) lateral view; (**21**) dorsal view. Spain: Valdelinares-2.6 km SSW, 2009.05-SG10

Figure 22–24. *Leptothorax scamni*; (**22**) head in dorsal view; (**23**) lateral view; (**24**) dorsal view. Georgia: Abastumani Observatory, 2010.08.27-JH21

axis in lateral view directed caudad, their bases more distant than in *muscorum* (SPBA/CS 0.301). Petiole in lateral view without peduncle, deviating from the situation in *muscorum* (compare Figs. 29 and 32) by a steep and rather straight frontal face, a rather straight caudal slope of the node and the narrow dorsal crest of the node. Petiole relatively higher than in *muscorum* (PEH/PEL 0.870). Sculpture on nearly all surfaces stronger than in *muscorum*; frontal laminae and large parts of vertex more strongly longitudinally carinulate-rugulose,

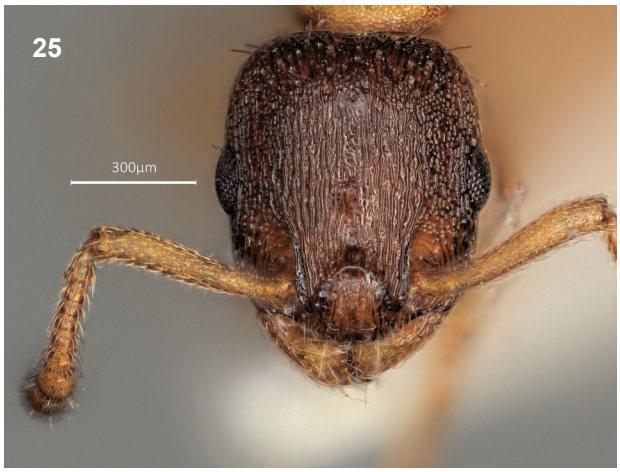
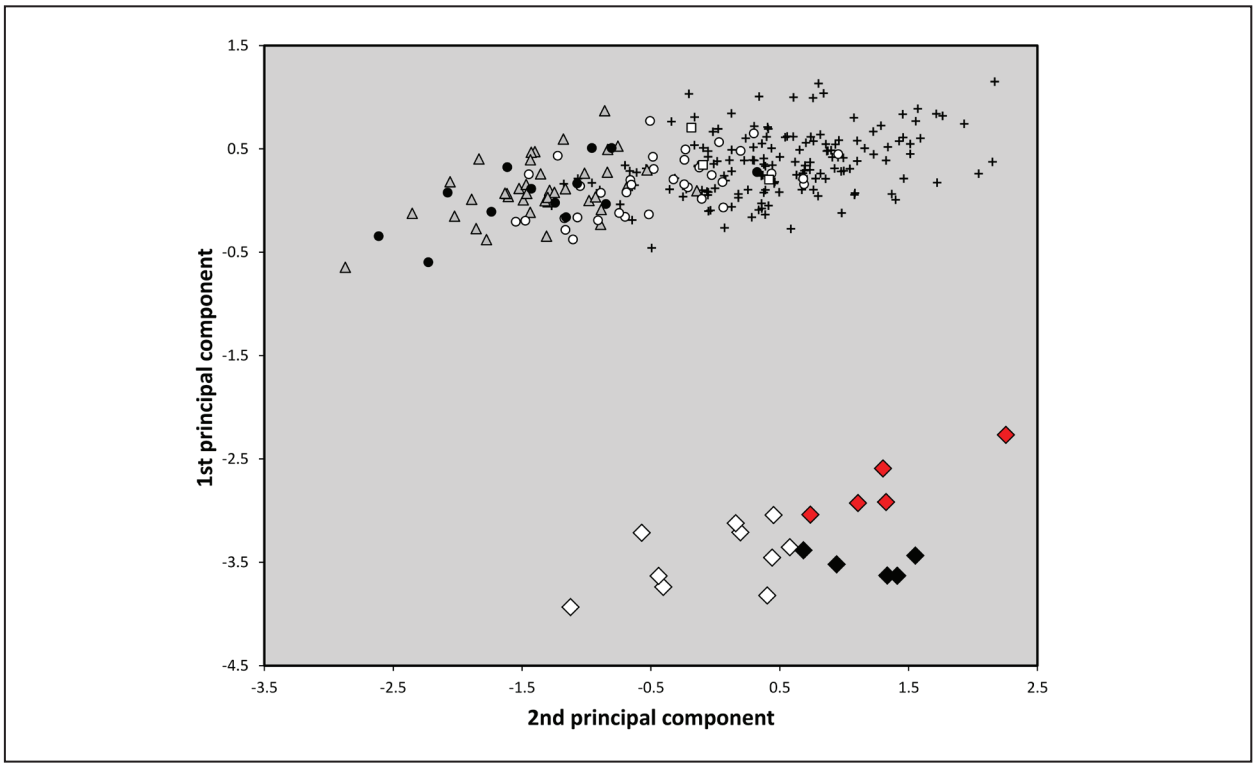


Figure 25–27. *Leptothorax gredleri*; (**25**) head in dorsal view; (**26**) lateral view; (**27**) dorsal view. Germany: Trebsen-0.36 km E, 2012.06.07

Figures 28–30. *Leptothorax muscorum*; (**28**) head in dorsal view; (**29**) lateral view; (**30**) dorsal view. Germany: Dubring-2.6 km NNW, 2012.07.21.

Figures 31–33. *Leptothorax tibeticum* n.sp., holotype; (**31**) head in dorsal view; (**32**) lateral view (flipped horizontally); (**33**) dorsal view. China: Heimahe-4.4 km SSE, 2011.07.26.

▼**Figure 34**. Principal component analysis of the six morphometric characters CL/CW, FRS/CS, EYE/CS, SP/CS, MW/CS and PEL/CS in workers of *Formicoxenus nitidulus* (white rhombs), *F. sibiricus* (black rhombs), *F. gebaueri* n.sp. (red rhombs), *Leptothorax acervorum* (black crosses), *L. muscorum* (white dots), *L. gredleri* (grey triangles), *L. scamni* (white squares) and *L. tibeticum* n.sp. (black dots).



mesosoma more strongly rugulose. Head, mesosoma, waist and gaster with rather long setae which do not taper from base to apex (PnHL/CS 0.146). Head and gaster dark to blackish brown. Mesosoma, waist, all appendages and mandibles light yellowish brown.

Taxonomic comments. As a combination of bulging frontal carinae, characteristic petiole profile and several morphometric differences not to confuse with any known Palaearctic species. Following the available descriptions, the East Siberian *L. oceanicus s*hould be well separable by the almost linear anterior and posterior slopes of petiole node, forming in lateral view an acute angle, by the broader subpetiolar process and by the sparser setae on all body parts.

Biology. Unknown. The five samples were collected on short-grassy high-altitude pastures or in ecotones between pasture and woodland.

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