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A new extinct ant genus (Hymenoptera: Formicidae: Myrmicinae) from the Late Eocene Rovno amber – a putative ancestor of the *Leptothorax* genus group

Alexander RADCHENKO, Gennady M. DLUSKY† & Ksenia PERFILIEVA



Abstract

A new genus and a new species of ant, *Proleptothorax primitivus*, are described based on two males from the Late Eocene Rovno amber of Ukraine. This genus is characterized by the antennae 13-segmented, with the funiculus filiform without an apical club, by the very short antennal scape, by the short and narrow, bidentate mandibles, and by the forewing with cell 3r closed. We consider these features as obvious plesiomorphies compared with *Leptothorax* MAYR, 1855, *Formicoxenus* MAYR, 1855, and *Harpagoxenus* FOREL, 1893 and assume that *Proleptothorax* could be regarded as a putative ancestor of the extant genera of the *Leptothorax* genus group.

Key words: Ants, palaeontology, *Proleptothorax primitivus* gen.n. et sp.n., new genus, new species, Late Eocene, Rovno amber, evolution.

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Alexander Radchenko (contact author), Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, B. Khmel'nitskogo str., 15, Kiev-30, 01-030, Ukraine. E-mail: rad@izan.kiev.ua; agradchenko@hotmail.com

Gennady M. Dlussky† & Ksenia Perfilieva, Lomonosov Moscow State University, Moscow, 119991, Russia. E-mail: ksenperf@mail.ru

Introduction

The ant fauna of the Late Eocene European ambers (Priabonian stage, 33.9 - 37.2 million years ago, mya) is the best studied among all fossil myrmecofaunas worldwide. The subfamily Myrmicinae is particularly well represented in these ambers, showing a high diversity: Currently, there are an estimated 78 myrmecine species from 27 genera, including several new, yet undescribed taxa (RADCHENKO & DLUSKY 2017a), which is about 40% of both genera and species of the total number of the Late Eocene European amber ants.

Ten out of eleven previously described extinct myrmecine genera from the Late Eocene European ambers are highly specialized morphologically and could not be considered as the ancestors of any extant ant genus (DLUSKY & RADCHENKO 2006a, b, 2009, RADCHENKO & DLUSKY 2012, 2013, 2016, 2017a, b). The sole exception to this is *Parameranoplus* WHEELER, 1915, which might be a putative ancestor of the modern Old World tropical genus *Meranoplus* F. SMITH, 1853. *Parameranoplus* workers possess several plesiomorphies comparable with those of workers of *Meranoplus*, such as 11-segmented antennae, and, perhaps most importantly, a promesonotum that does not form a developed shield overhanging the pleurae laterally and has no long promesonotal spines posteriorly. In contrast, the antennae in *Meranoplus* are 9-segmented, and the promesonotum forms a shield that overhangs the pleurae laterally and has long promesonotal spines posteriorly (see WHEELER 1915, BOLTON 2003). On the other hand, *Parameranoplus* itself possesses a set of apomorphies compared with many less specialized morphologically genera, such as 11-segmented antennae vs.

12-segmented, developed antennal scrobes that are above the eyes, pointed humeral angles, flattened promesonotum, short and clavate femora. Consequently, even if this genus were the putative ancestor of *Meranoplus*, it forms itself a derived lineage relative to a yet unknown precursor.

MAYR (1868) then WHEELER (1915) described six fossil species, initially attributed to the genera *Leptothorax* MAYR, 1855, *Macromischa* ROGER, 1863, and *Nothomyrmica* WHEELER, 1915. However, all these were later transferred to the genus *Temnothorax* MAYR, 1861 (BOLTON 2003, DLUSKY & RADCHENKO 2006b).

The taxonomic history of the generic names *Leptothorax* and *Temnothorax* is quite complicated. MAYR (1855) described *Leptothorax*, based on 12 species. A few years later, he described the closely related genus *Temnothorax* (MAYR 1861) with a single species – *T. recedens* (the type species of this genus by monotypy). For many years, *Temnothorax* was treated by various authors either as a genuine genus or as a subgenus of *Leptothorax*, or even as a junior synonym of *Leptothorax* (see BOLTON 2003).

BINGHAM (1903) designated *Formica acervorum* FABRICIUS, 1793 as the type species of the genus *Leptothorax*. Almost at the same time, RUZSKY (1904) established the genus *Mychothorax*, to which *F. acervorum* was also assigned as the type species (by original designation). EMERY (1912) later designated *Myrmica clypeata* MAYR, 1853 as the type species of *Leptothorax*. Despite the fact that this designation was unjustified, all subsequent authors considered *Mychothorax* as a subgenus of *Leptothorax* and attributed species with 11-segmented antennae in workers



Figs. 1 - 2: Photographs of the holotype male of *Prolepto thorax primitivus* gen.n. et sp.n. (1) Body in dorsal view; (2) head and mesosoma in dorsal view.

and queens to *Mychothorax*, and those with 12-segmented antennae to *Leptothorax* s.str.

Eventually, M.R. SMITH (1950) synonymised *Mychothorax* with *Leptothorax* as they have the same type species (hence, an absolute synonymy) and established *Myrafant* as a new subgenus of *Leptothorax*, with the type species *L. curvispinosus* MAYR, 1866. Then, species from the former subgenus *Leptothorax* s.str. (sensu EMERY 1912) were transferred to the subgenus *Myrafant*, and those that were in *Mychothorax* were considered *Leptothorax* s.str. (sensu BINGHAM 1903).

Essentially, there are many differences between *Leptothorax* s.str. and the subgenus *Myrafant* and the possibility of separating them into two genera was discussed by many myrmecologists. Consequently, BOLTON (2003) formally divided them as different genera, revived several generic names from synonymy, and provided new synonyms. He proposed the following arrangement of the former *Leptothorax* (s.l.) (only Holarctic taxa are given here; for more details, see BOLTON 2003, PREBUS 2017): *Leptothorax* MAYR, 1855 (= *Mychothorax* RUZSKY, 1904; = *Doronomyrmex* KUTTER, 1945); *Temnothorax* MAYR, 1861 (= *Myrafant* M. R. SMITH, 1950).

Lastly, PREBUS (2017) established an informal *Leptothorax* genus group within the tribe Crematogastrini (sensu WARD & al. 2015), including the genera *Leptothorax*, *Formicoxenus* MAYR, 1855, and *Harpagoxenus* FOREL, 1893, and considered this group as a sister clade of *Temnothorax*.

Below, we describe a new fossil genus, *Proleptothorax* gen.n. and assume that it can be the putative ancestor for the genera *Leptothorax*, *Formicoxenus*, and *Harpagoxenus*.

Material and methods

Two males were investigated of the herein described genus and species, *Proleptothorax primitivus* gen.n. et sp.n., from the Rovno amber (Ukraine, Late Eocene, Priabonian stage, 33.9 - 37.2 mya; see PERKOVSKY & al. 2010 for details on the age and deposit). The holotype and paratype specimens were deposited in the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (SIZK). For comparison, we also studied 80 males of 24 extant species of the genera *Leptothorax*, *Temnothorax*, and *Harpagoxenus*, as well as 41 fossil *Temnothorax* specimens from the Late Eocene European ambers.

The figures are based on the original drawings of the specimens and photographs made using an Olympus Camedia C-3030 digital camera fitted to an Olympus SZX9 microscope in conjunction with the computer program CorelDraw 13.

The nomenclature of the wing venation follows DLUSSKY & PERFILIEVA (2014; see also Fig. 3). Two indices that characterize important features of venation of the forewings were used:

$$Icu = [1Cu + (2M+Cu)] / 1Cu$$

$$Icu_a = [(1M+Cu) + (2M+Cu)] / (1M+Cu) \text{ (for details, see DLUSSKY & PERFILIEVA 2014).}$$

Morphometrics: The holotype specimen of *P. primitivus* was measured (accurate to 0.01 mm), and the measurements were used to calculate the various ratios defined below. Additionally, we measured head length, scape length, and length of the first funicular segment of males of modern *Leptothorax*, *Harpagoxenus*, and *Temnothorax* species.

2FSL	length of second funicular segment
GL	length of genae, measured from anterior margin of eyes to mandibular insertion
HTL	maximum length of hind tibia
HL	maximum length of head in dorsal view, measured in a straight line from anteriormost point of clypeus to mid-point of occipital margin
HW	maximum width of head in dorsal view behind (above) the eyes
ML	length of mesosoma in dorsal view from anterior end of scutum to the point of articulation with petiole
OL	maximum diameter of eye
PL	maximum length of petiole in dorsal view, measured from posterodorsal margin of petiole to articulation with propodeum
PH	maximum height of petiole in profile, measured from uppermost point of petiolar node perpendicularly to a virtual line between tip of subpetiolar process and posteroventral points of petiole
PPH	maximal height of postpetiole in profile
PPL	maximum length of postpetiole in dorsal view between its visible anterior and posterior margins
PPW	maximum width of postpetiole in dorsal view
PW	maximum width of petiole in dorsal view
ScL	length of the scutum + scutellum in dorsal view
ScW	maximum width of scutum in dorsal view
SL	maximum straight-line length of scape from its apex to the articulation with condylar bulb

For simplicity, in this paper ratios of various measurements are used (e.g., HL / HW) rather than indices and their abbreviations (e.g., CI) as done elsewhere previously.

Systematic palaeontology

Family Formicidae LATREILLE, 1809

Subfamily Myrmicinae LEPELETIER DE SAINT-FARGEAU, 1835

Genus *Proleptothorax* gen.n.

Type species: *Proleptothorax primitivus* sp.n.

Derivation of name: from Greek “pro” – before, prior to, and the ant genus *Leptothorax*.

Diagnosis:

- antennae 13-segmented
- antennal scape very short (SL / HL 0.16, SL / HW 0.18)
- antennal funiculus filiform, without apical club
- length of the second funicular segment subequal to the third one, while distinctly longer than scape, the longest segments are 5th, 6th and 7th
- mandibles short and narrow, bidentate
- forewing with cell 3r closed by vein 5RS
- maxillary palps 5-segmented, labial palps 3-segmented
- scutum with deeply impressed and crenulated notauli

***Proleptothorax primitivus* sp.n.** (Figures 1 - 8)

Derivation of name: from Latin “primitivus” – primitive, primal, which means presence of the many primitive morphological features in this species.

Material examined: holotype: SIZK No. K-26591, male, complete specimen; **paratype:** SIZK No. K-18699, male, complete specimen.

Type locality: Ukraine, Rovno Prov., vicinity of Klesov.

Type horizon: Rovno amber, Late Eocene (Priabonian stage).

Diagnosis: As for genus.

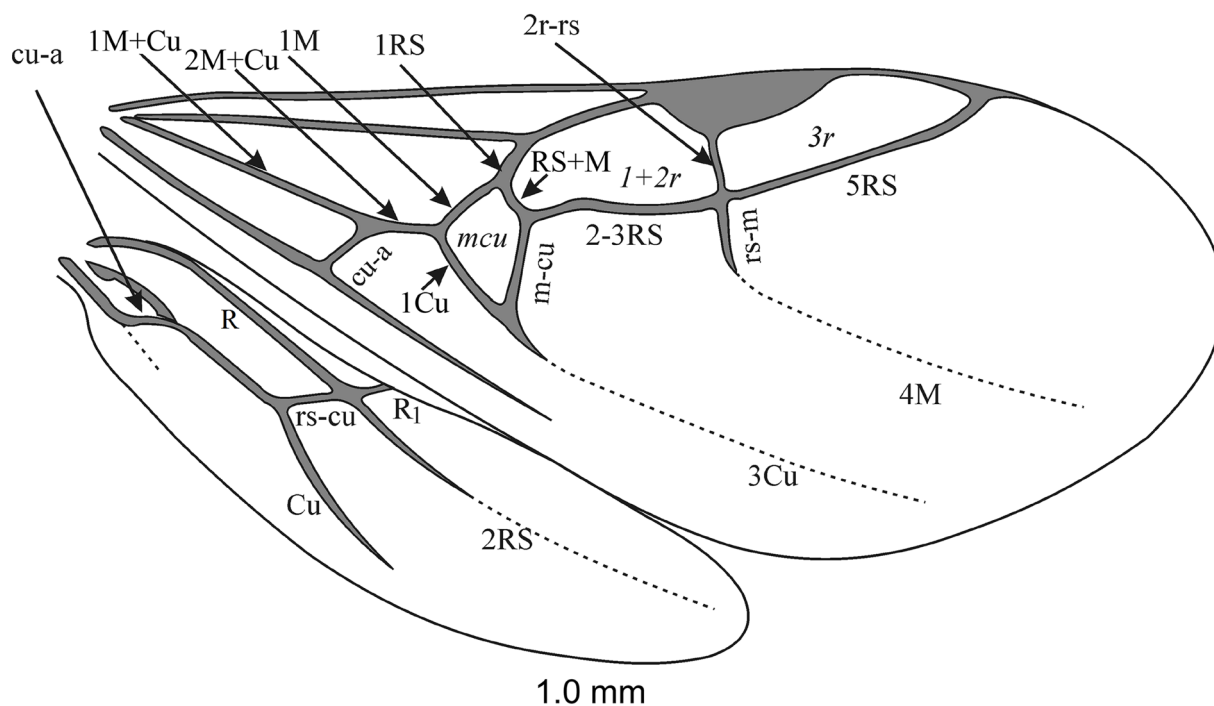


Fig. 3: Forewing venation and hind wing of *Proleptothorax primitivus* gen.n. et sp.n. with designation of cells and veins.

Description: Total length ca. 2.2 - 2.3 mm. Head slightly longer than wide, widely and gradually rounded above eyes and with strongly convex occipital margin as seen dorsally. Frons slightly longitudinally depressed; frontal carinae and frontal lobes not developed. Distance between antennal insertions 0.08 mm. Torulus subvertical. Clypeal surface gradually convex along its width, without longitudinal carinae, anterior margin of clypeus slightly convex, without medial notch. Eyes large, bulging, their maximal diameter about half of head length, situated distinctly in front of midlength of sides of head, so that temples longer than maximum diameter of eye. Genae very short, four times shorter than maximum diameter of eyes. Ocelli well developed and large, diameter of central ocellus 0.06 mm, distance between posterior ocelli 0.09 mm; lower edge of central ocellus lays slightly posteriorly of imaginary line connecting posterior margins of eyes. Length of mandibles 0.12 mm.

Mesosoma relatively long and rather narrow, scutum quite strongly convex as seen laterally, scutellum much less convex, lays distinctly lower than surface of scutum, scutoscutellar sulcus wide, deep and crenulated. Propodeum angulate, without teeth, its dorsal surface subequal to posterior one. Petiole with quite long peduncle, twice longer than high, anterior surface of petiolar node very weakly concave, posterior one slightly convex, node dorsum widely rounded; postpetiole subglobular. Legs long and slender, femora not swollen. Hind coxae widely separated in ventral view, when coxae directed outward, their inner margins far apart. Pretarsal claws simple. Middle and hind tibiae with short simple spur.

Forewing with closed cells *mcu*, *1+2r* and *3r*, cells *cua* and *rm* are absent. Pterostigma quite big, somewhat rounded. Cell *3r* relatively short, its length subequal to length of cell *1+2r*, apex of cell *3r* touches wing margin. Cell *mcu* small, trapezoid, high, its height equal to length

of midline, section 2-3RS more than 3 times longer than RS+M. Vein 5RS very feebly curved, almost straight, vein section 2-3RS S-shaped. Cross-vein *rs-m* merging with vein section 4M at a blunt angle, it diverges with cross-vein 2r-rs and vein 5RS from same knot so that vein section 4RS is absent. Vein 3Cu feebly marked, not sclerotized. Wing length 1.87 mm, distance from wing base to pterostigma 0.82 mm. $Icu = 1.57$, $Icua = 1.27$.

Hind wing without free section of medial vein, free section of cubital vein (Cu) very slightly curved, almost straight. Cross-vein *rs-cu* not curved. Veins R, *rs-cu*, 2RS and R_1 diverge from same knot. Cross-vein *cu-a* located approximately at the midlength between base of wing and branching of *rs-cu* and Cu. Wing length 1.21 mm.

Since wings of the specimen were somewhat deformed (curved down) during fossilization, the shape of the cells *mcu* and *1+2r* appear slightly distorted.

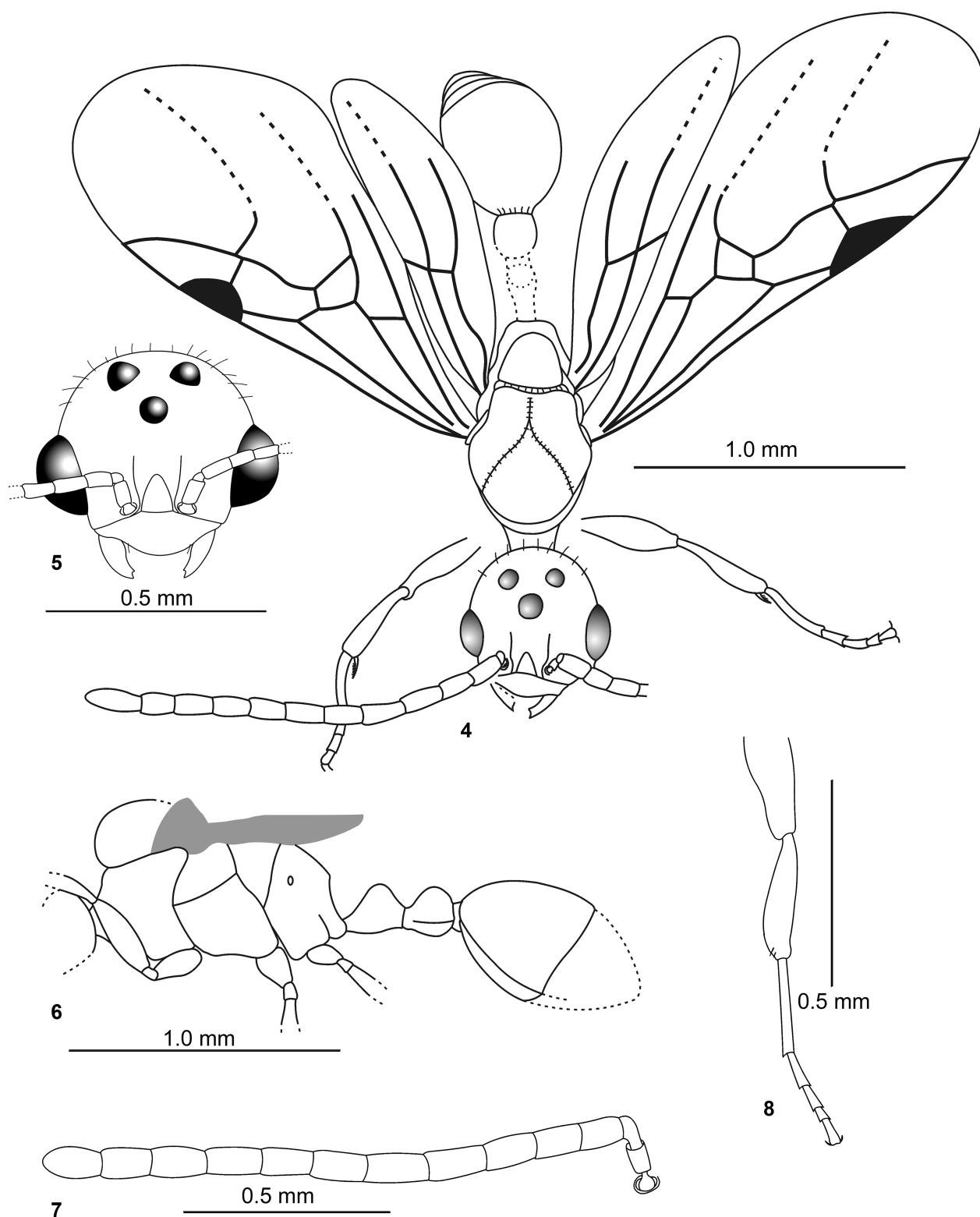
Head dorsum quite coarsely and densely punctated, frons laterally also with longitudinal striation. Scutum, scutellum, propodeal dorsum waist and gaster smooth and shiny; pronotum, mesopleura and sides of propodeum finely superficially punctated, appears dull. Whole body with quite abundant, thin erect to suberect hairs, scapes and legs with dense decumbent pubescence.

Measurements (in mm): GL 0.06, HL 0.51, HTL 0.27, HW 0.46, ML 0.67, OL 0.24, PH 0.16, PL 0.32, PPH 0.16, PPL 0.16, PPW 0.13, PW 0.11, ScL 0.57, ScW 0.43, SL 0.08.

Ratios: GL/OL 0.25, HL/HW 1.12, OL/HL 0.47, PL/HL 0.63, PL/PH 2.00, PPL/PPH 1.20, ScL/ScW 1.34, SL/HL 0.16, SL/HW 0.18.

Workers and queens unknown.

Note: The paratype specimen is mostly concealed by turbid film and hardly measurable, though the forewing venation, antennal structure and general shape of the body (in profile) are visible. Its body length is ca. 2.2 mm.

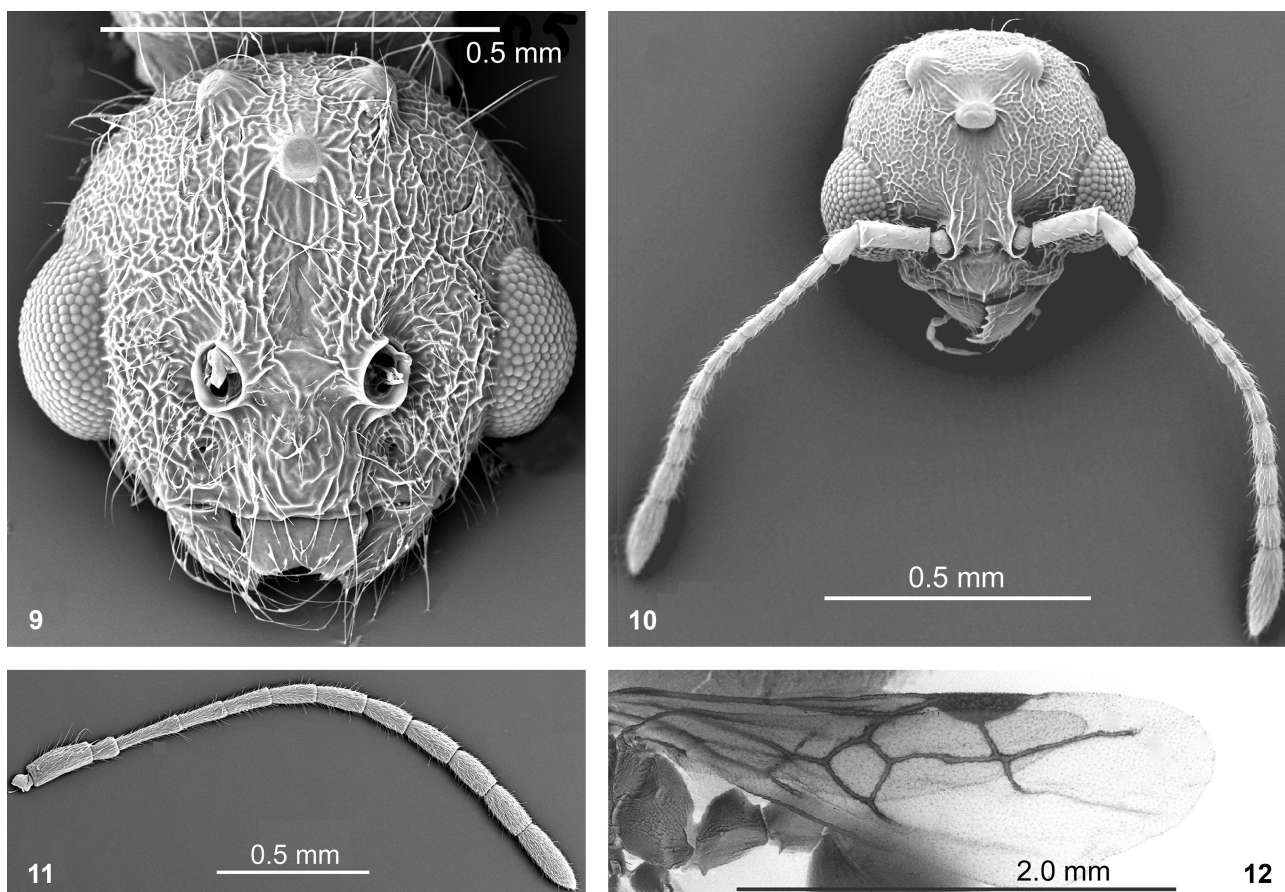


Figs. 4 - 8: Line drawings of the holotype male of *Proleptothorax primitivus* gen.n. et sp.n. (4) Body in dorsal view; (5) head in dorsal view; (6) mesosoma, waist, and gaster in lateral view; (7) antenna; (8) hind tibia and tarsus.

Discussion

Males of the genera of the *Leptothorax* genus group (sensu PREBUS 2017) (i.e., *Leptothorax*, *Harpagoxenus*, and non-ergatoid *Formicoxenus*) have mandibles with the short, blunt, edentate masticatory margin, 12-segmented an-

tennae with the filiform funiculus without an apical club; the second funicular segment long, obviously longer than each of the remainder ones except for the apical one and nearly the same length as the antennal scape in *Leptothorax* and *Harpagoxenus* (ratio 2FSL / SL 0.857 – 1.056, mean 0.988 ± 0.044) (Figs. 9, 11), while it is somewhat longer in



Figs. 9 - 12: SEM photographs of the details of structure of *Leptothorax* and *Temnothorax* males. (9, 11) *Leptothorax muscorum*; (10) *Temnothorax unifasciatus*; (12) *Leptothorax kutteri*; (9) head in dorsal view; (10) head and antennae in dorsal view; (11) antenna; (12) forewing.

the non-ergatoid males of *Formicoxenus* and subequal to the total length of the first and second funicular segments (for more details, see FRANCOEUR & al. 1985). In contrast, males of the genus *Temnothorax* have mandibles with a well developed masticatory margin and with 5 - 7 teeth, 13-segmented antennae (very rarely 12-segmented), the antennal funiculus with a distinct 4-segmented apical club, and a short second funicular segment, at least twice shorter than the length of scape (Fig. 10).

In general, the antennal scape is somewhat shorter in males of *Leptothorax* and *Harpagoxenus* species than in *Temnothorax* ones: means SL / HL are 0.342 ± 0.014 [$n = 23$, five species of *Leptothorax* and *H. sublaevis* (NYLANDER, 1849)] vs. 0.361 ± 0.037 ($n = 57$, 18 species of *Temnothorax*), while these ratios highly overlap between the mentioned genera: minimum - maximum are 0.310 - 0.383 in *Leptothorax* and *H. sublaevis* vs. 0.290 - 0.439 in *Temnothorax*.

Additionally, the cell 3r on the forewing is open in the *Leptothorax* group genera (Fig. 12) as well as in *Temnothorax* males, though this cell occasionally might be closed in some *Temnothorax* species [e.g., *T. unifasciatus* (LATREILLE, 1798), *T. crassispinus* (KARAWAJEW, 1926), *T. rottenbergii* (EMERY, 1870)], sometimes even only on one forewing, but this feature varies within the same species, which have normally an open cell 3r (A. Radchenko, G.M. Dlussky† & K. Perfilieva, unpubl.).

WARD & al. (2015) and then PREBUS (2017) based on molecular analysis considered clades of (*Leptothorax* +

Harpagoxenus + *Formicoxenus*) and *Temnothorax* (including synonymised generic names *Chalepoxenus* MENOZZI, 1923 and *Myrmoxenus* RUZSKY, 1902) as sister groups, with the time of their divergence between 45 and 50 mya (Middle to Early Eocene). As for the genera of the *Leptothorax* genus group, separation of the subclades *Harpagoxenus* and (*Formicoxenus* + *Leptothorax*) from the common ancestor occurred ca. 10 mya (Late Miocene), and divergence of the genera *Formicoxenus* and *Leptothorax* took place even later, ca. 5 mya (Late Miocene or even Pliocene), however not many species were included in the analysis.

Males of *Proleptothorax* have 13-segmented antennae with a filiform funiculus without an apical club, a very short antennal scape, short and narrow, bidentate mandibles, and, which is very important, a closed cell 3r on the forewing. Interestingly, the second funicular segment in *Proleptothorax* is not the longest and is subequal to the third one (although distinctly longer than the scape), while the longest segments are 5th, 6th and 7th. The differences in structure of the basal funicular segments between *Leptothorax* genus group and *Proleptothorax* can be explained by the fusion of the 2nd and 3rd segments in the genera of *Leptothorax* genus group, which makes the 2nd segment the longest. A similar fusion of the second and third funicular segments was noted in ants from different subfamilies, for example in males of some species of *Leptomyrmex* MAYR, 1862 (Dolichoderinae) and in males of *Tetramorium* MAYR, 1855 and *Strongylognathus*

MAYR, 1853 (Myrmicinae) (DLUSSKY & al. 2014, RADCHENKO 2016). On the other hand, *Proleptothorax* males have 5-segmented maxillary palps and 3-segmented labial palps. These features as well as the general shape and structure of the head, mesosoma and waist, and the presence of the notauli fully match the diagnostic characters of males of the *Leptothorax* genus group.

It should be noted that the short and narrow bidentate mandibles in all castes are a plesiomorphy in the family Formicidae (WILSON & al. 1967, DLUSSKY 1983, DLUSSKY & RASNITSYN 2007), and a closed cell *3r* on the forewing is a plesiomorphy in the subfamily Myrmicinae (DLUSSKY & RADCHENKO 2009, RADCHENKO & DLUSSKY 2013).

Thus, we may state that the above-mentioned diagnostic characters of *Proleptothorax* are obvious plesiomorphies, and it has no apomorphic features compared with the genera of the *Leptothorax* genus group. Moreover, the time when *Proleptothorax* existed is much older than the estimated time of separation of the genera *Leptothorax*, *Harpagoxenus*, and *Formicoxenus* but younger than the divergence of the *Leptothorax* genus group and *Temnothorax*. Consequently, we assume that *Proleptothorax* might be considered a putative ancestor of the genera of the *Leptothorax* genus-group but not of *Temnothorax*.

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