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New extinct ant genus (Hymenoptera, Formicidae, Myrmicinae) from late Eocene Rovno amber

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Abstract

A new fossil myrmicine ant genus and species *Lelejus venustus* **gen.** et **sp. nov.**, are described from late Eocene Rovno amber (Priabonian, 33.9–37.8 Ma). This genus differs from all extant and extinct Myrmicinae genera known from the late Eocene European ambers in the combination of morphological features, in particular: 13-segmented antennae with a very short scape and filiform funiculus; 3-segmented maxillary and 2-segmented labial palps; well-developed mandibles with dentate masticatory margin; scutum with broad notauli; forewings with closed cells 1+2r, 3r and mcu, the cell 3r of approximately the same length as cell 1+2r; free vein M branches off from RS approximately at the midlength between the junction of cross-vein 2r-rs with RS and vein m-cu; the cross-vein cu-a is located far from the base of wing, so the branch 1M+Cu is much longer than 2M+Cu. The taxonomic position of the described genus is discussed.

Keywords

Lelejus venustus gen. et sp. nov., fossils, paleontology, taxonomy

Introduction

The diversity of the fossil ant fauna is very rich: more than 800 extinct species, 164 genera and six subfamilies are known now (Bolton 2021; our unpublished data). However, five fossil subfamilies with 20 genera and 45 species became extinct at the end of the Cretaceous. One mysterious subfamily, Formiciinae Lutz, 1986, contained giant ants with a body length of gynes up to 7 cm and wingspan up to 15 cm, known from deposits of the early and middle Eocene of Europe and North America. Thus, all the late Eocene ants already belonged to modern subfamilies.

In general, the ant fauna of the late Eocene (Priabonian, 33.9–37.8 Ma) European (Baltic, Bitterfeld, Scandinavian and Rovno) ambers is probably the best studied among all fossil myrmecofaunas in the world. It includes more than 17,500 specimens belonging to more than 200 extinct species from 34 extinct and 39 modern genera of 12 existing subfamilies (Dlussky and Rasnitsyn 2009; Dlussky et al. 2014; Perkovsky 2016, 2018; our unpublished data).

At present, Myrmicinae is the most diverse ant subfamily, which includes 147 genera with almost 7,000 species. This group therefore represents about 45% ant genera and more than 50% species (calculated from the data from Bolton 2021), but the ratio of subfamilies in the past was different.

The most comprehensive monographic revision of the ants of Baltic amber was published over than 100 years ago (Wheeler 1915), where twelve Myrmicinae genera (28%) and 24 species (27% known amber ants; based on the modern taxonomy) were reported. Interestingly, from 1915 until the beginning of the present century neither new genera nor new species of Myrmicinae were discovered. Two new myrmicine species were described only in 2002 (Dlussky and Perkovsky 2002), soon followed by description of seven new genera and 31 species (Dlussky and Radchenko 2006a, b, 2009; Radchenko and Perkovsky 2009; Radchenko and Dlussky 2012, 2013a, b, 2015, 2016, 2017a, b, 2018a, b, c, 2019; Radchenko et al. 2007, 2018, 2019; Radchenko 2020). Another new genus and species were recently described by Cheny et al. (2019). Thus, together with a new genus established below, the number of Myrmicinae genera in late European ambers reaches 25 (with 13 of them extinct), and if undescribed taxa are included, 85 species, or 34% and 39% amber ant genera and species, respectively.

Material and methods

A new genus and a new species, *Lelejus venustus* gen. et sp. nov., are established on the base of a single male in a piece of Rovno amber. The holotype specimen is deposited in the collection of the I.I. Schmalhausen Institute of Zoology of NAS of Ukraine, Kiev (**SIZK**).

The photographs were taken with a Leica Z16 APO stereomicroscope equipped with Leica DFC 450 camera and processed with LAS Core software.

Not all features of the examined specimen were properly visible and measurable, hence we measured only well-discernible details (with 0.01 mm resolution), in particular:

HL maximum length of the head in dorsal view, measured in a straight line from the anteriormost point of clypeus to the mid-point of occipital margin;
HW maximum width of the head in dorsal view just behind (above) the eyes;
FW minimum width between the frontal carinae;
SL maximum length of the scape measured in a straight line from its apex to the articulation with condylar bulb;
OL maximum diameter of the eye;
GL length of the genae, measured from the anterior margin of the eyes to the articulation with the mandible;
MdL length of the mandible from the tip of apical tooth to the outer point of insertion with the head;
ML diagonal length of the mesosoma seen in profile from the anterior-upper margin of pronotum to the posterior margin of propodeal lobes;
MH height of the mesosoma, measured from the upper level of scutum perpendicularly to the level of lower margin of mesopleuron;
PL maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;
PH maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole;
PPL maximum length of the postpetiole in profile;
PPH maximum height of the postpetiole in profile;
HTL maximum length of the metatibia;
WL maximum length of the forewing;
WW maximum width of the forewing.

The approximate total length is calculated as the sum of HL + ML + PL + length of the gaster.

Indices:

CI=HL/HW, FI=FW/HW, SI1=SL/HL, SI2=SL/HW, MdI=MdL/HL, OI1=OL/HL, OI2=OL/HW, PI1=PL/HL, PI2=PL/PH, MI=ML/MH, WI=WL/WH.

Nomenclature of the wing venation is given according to Dlussky (2009) and Dlussky and Perfilieva (2014) (see also Fig. 4).

Indices of forewing venation:

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

Taxonomy

Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835

Genus *Lelejus* gen. nov.
http://zoobank.org/BA1BE4FC-8712-4E90-81AD-DCE8F8A021BE

Type species. *Lelejus venustus* sp. nov.

Diagnosis. Antennae 13-segmented, inserted into head very close to posterior clypeal margin; scape very short, less than total length of first and second funicular segments, funiculus filiform, without apical club. Palp formula 3, 2. Mandibles well developed, subtriangular, masticatory margin with larger basal tooth, four minor sharp teeth and much longer sharp apical tooth. Median portion of clypeus evenly convex, without median and lateral carinae, its anterior margin convex, without a notch. Scutum with broad notauli. Propodeum distinctly angulated in profile, its dorsal surface delineated laterally by sharp longitudinal ridges. All meso- and metatibiae with well-developed simple spur, pretarsal claws simple. Forewing with closed cells 1+2r, 3r and mcu; cell 3r relatively short, about the same length as cell 1+2r; free vein M branching off from RS approximately at the midlength between junction of cross-vein 2r-rs with RS and vein m-cu; cross-vein cu-a located far from base of wing, so that branch 1M+Cu much longer than 2M+Cu, Icu = 1.75, Icua = 1.28. Hind wing without jugal lobe; free abscissa M absent; branch 1RS well developed; vein cu-a located close to base of wing, so that branch 1M+Cu much shorter than 2M+Cu, Icua = 2.37.

Etymology. The new genus is named in honor of our colleague and friend Prof. Arkady S. Lelej (Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok, Russia) on the occasion of his 75th birthday and in recognition of his great contributions to the study of Hymenoptera.

Comparative diagnosis. The described genus differs from any extant and extinct myrmicine genera known from the late Eocene European ambers by unique combination of the above mentioned features (for details see Discussion). Among these characters, the broad, foveate notauli and mandibles with six teeth are particularly distinctive of the new genus.

***Lelejus venustus* sp. nov.**
http://zoobank.org/C9378CD0-53D8-447C-8357-A595CDAEEF91
Figures 1–4

Material examined. *Holotype*: male, SIZK No. UA-27845, Ukraine, Rovno Region, Klesov, Rovno amber, late Eocene, 33.9–37.8 Ma; AntWebCASENT0917546.

Diagnosis. As for the genus.

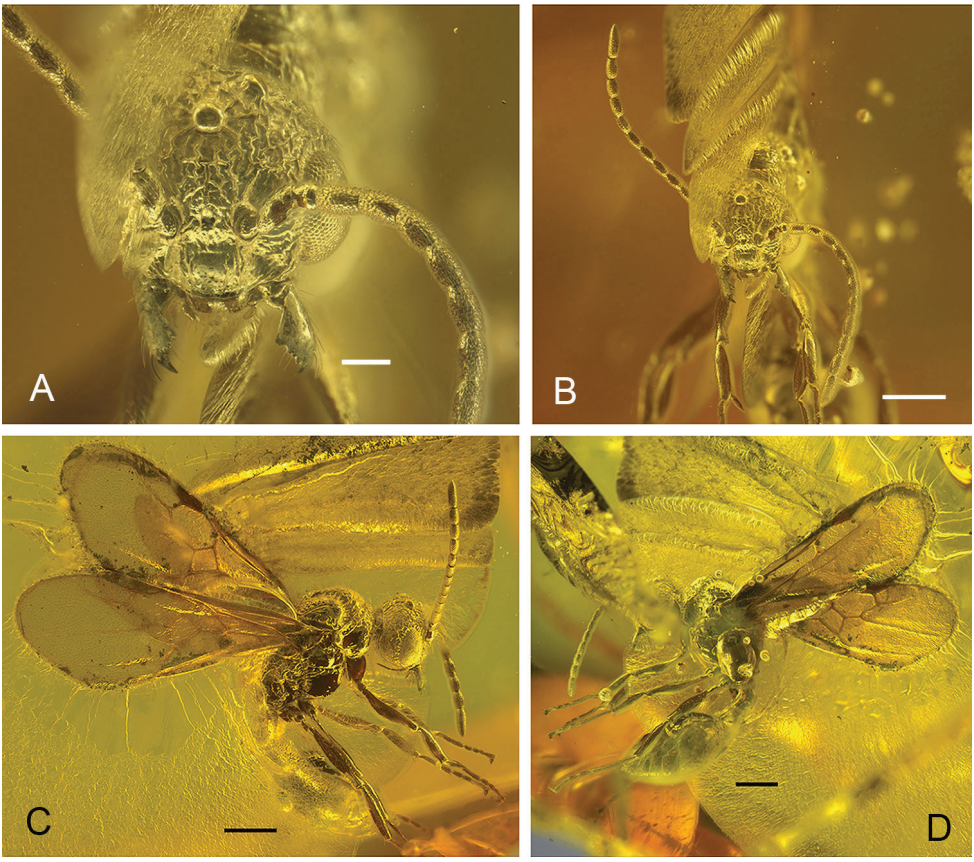

Figure 1. *Lelejus venustus* gen. et sp. nov., holotype, male (AntWebCASENT0917546) **A** head, dorsal view **B** head and antennae, dorsal view **C, D** body, right lateral view (**C**); left dorso-lateral view (**D**). Scale bars: 0.1 mm (**A**); 0.5 mm (**B–D**).

Description. Male. Body length 4.1 mm. Head subglobular, slightly wider than long, gradually rounded behind eyes, without marked occipital corners and with convex occipital margin. Eyes very large, their maximum diameter half of head length, situated distinctly in front of mid-length of sides of head, so genae very short. Ocelli large, forming obtuse triangle, diameter of central ocellus subequal to width of scape. Frons relatively narrow, 0.25 head width, frontal sockets fully exposed. Frontal triangle well marked. Mandibles quite long, ca. 0.4 head length. Apical segment of maxillary palps twice as long as preapical one. Antennal scape ca. twice as long as width and ca. 4.5 times shorter than head. First funicular segment very short, somewhat shorter than wide and half as long as second segment; all subsequent segments of same width; second to 11th segment subequal in length, last segment twice as long as second one. Whole head with coarse reticulation, clypeus with sinuous longitudinal rugae, its central part and mandibles smooth; eyes surrounded by narrow foveate groove. Temples and occipital margin with quite numerous subdecumbent hairs of moderate length;

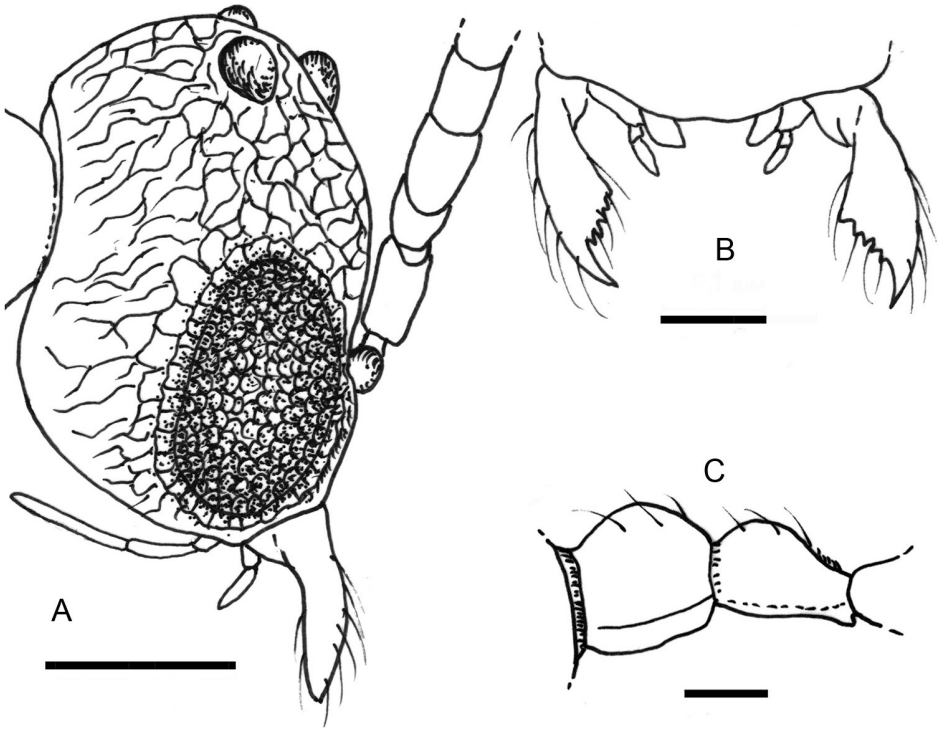

Figure 2. *Lelejus venustus* gen. et sp. nov., holotype, male **A** head, lateral view **B** mandibles **C** petiole and postpetiole, lateral view. Scale bars: 0.25 mm (**A**); 0.1 mm (**B, C**).

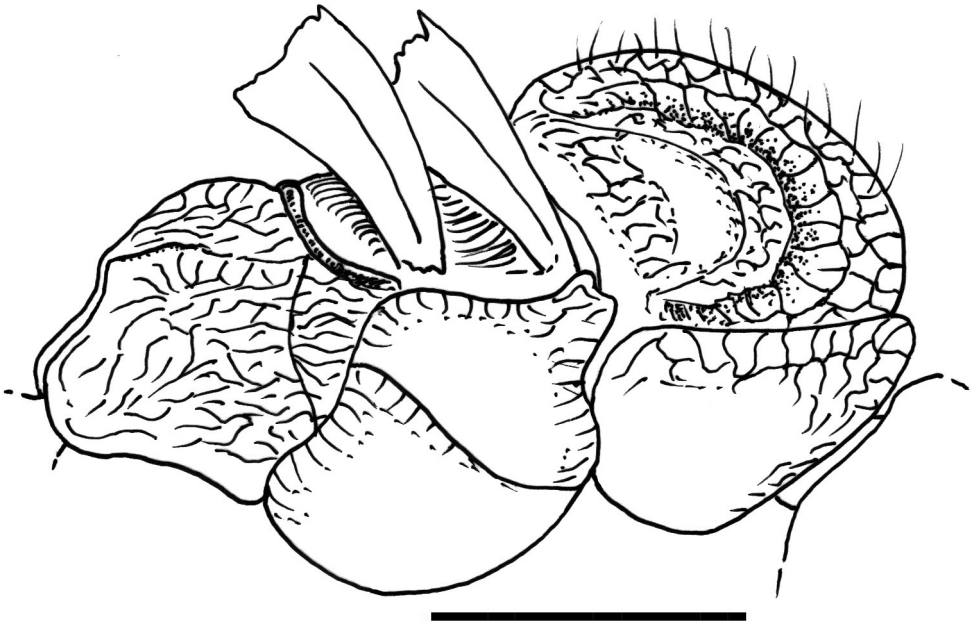

Figure 3. *Lelejus venustus* gen. et sp. nov., holotype, male, mesosoma, lateral view. Scale bar: 0.5 mm.

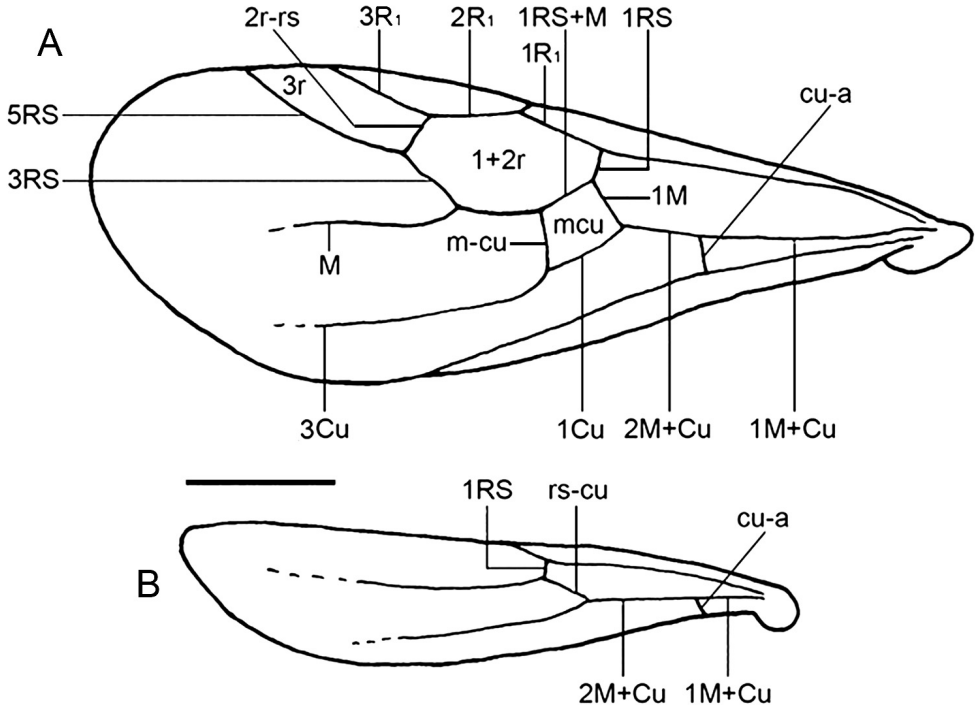

Figure 4. *Lelejus venustus* gen. et sp. nov., holotype, male **A** forewing **B** hind wing. Scale bar: 0.5 mm.

antennal scape with sparse subdecumbent, but quite long hairs; funicular segments with very short and abundant decumbent to subdecumbent pilosity; anterior clypeal margin without long setae, with only a few short, thin hairs; mandibles with quite long semierect hairs.

Mesosoma 1.6 times as long as high, scutum moderately convex, posterior surface of propodeum 1.2 times as long as dorsal one. Notauli deep and wide, distinctively arched in profile view, with coarse short transverse rugae (foveate). Petiole with distinct peduncle, 1.6 times as long as high, its node with widely rounded dorsum; postpetiole subglobular, slightly higher than petiole. Spurs on meso- and metatibiae relatively long, equal to width of tibia at point of their articulation. Scutum, scutellum and propodeal dorsum with coarse reticulation; sides of pronotum, mesopleura and lower part of sides of propodeum smooth; gaster smooth.

Mesosoma, waist and gaster with moderately dense erect to semierect hairs, legs with decumbent to subdecumbent pilosity, femora with additional longer suberect hairs. Genitalia small and barely visible. Forewings: pterostigma rather long and narrow; cross-vein rs-m completely reduced, so that cell rm absent; cell mcu of moderate size, trapezoidal, its height subequal to midline, its distal point does not reach level of basal end of pterostigma, vein section 1RS+M somewhat shorter than 1Cu; cell 1+2r heptagonal, relatively short, veins $1R_1$, $2R_1$ and $3R_1$ of nearly equal length; vein sections 2RS+M and 3RS subequal in length; cross-veins 2r-rs and 1RS well developed,

1RS slightly inclined toward base of wing, 2r-rs almost perpendicular to $2R_1$ and $3R_1$ at the point of their junction.

Measurements (in mm). HL 0.73, HW 0.77, FW 0.19, SL 0.16, OL 0.36, GL 0.06, MdL 0.30, ML 1.43, MH 0.88, PL 0.39, PH 0.27, PPL 0.27, PPH 0.29, HTL 0.60, WL 3.18, WW 1.13; length of funicular segments from second to 11th: 0.13, 0.13, 0.14, 0.14, 0.14, 0.14, 0.14, 0.14, 0.16, 0.26.

Indices: CI 0.95, SI1 0.22, SI2 0.21, FI 0.25, MdI 0.41, OI1 0.50, OI2 0.47, PI1 0.54, PI2 1.58, PPI1 0.39, PPI2 0.95, MI 1.62, WI 2.83.

Workers and queens. Unknown.

Etymology. From Latin *venustus* – pretty, nice, fine, which means that the described specimen has a fine general appearance.

Discussion

Males are known for 17 of 24 Myrmicinae genera (six of which are extinct), previously found in late Eocene European ambers. *Lelejus* gen. nov. can be easily distinguished from the extant *Aphaenogaster* Mayr, 1853, *Carebara* Westwood, 1840, *Crematogaster* Lund, 1831, *Monomorium* Mayr, 1855, *Solenopsis* Westwood, 1840 and *Vollenhovia* Mayr, 1865 by the presence of notauli (not to mention many other features). It also differs well from other modern genera that have notauli, particularly: in *Myrmica* Latreille, 1804 the palp formula is 6, 4; forewings have closed cell 1+2r+rm, partially separated by a short vein, and cell 3r is always open; *Pristomyrmex* Mayr, 1866 has 12-segmented antennae, reduced mandibles and an open cell 3r on the forewings; *Stenamma* Westwood, 1839 has a much longer antennal scape (SI1 ≥ 0.40), a noticeably longer head (CI > 1.20), and cell 3r on the forewing open; similarly to *Stenamma*, *Temnothorax* Mayr, 1861 also has a longer antennal scape (SI1 ≥ 0.30), cell 3r on the forewing open, meso- and metatibiae have no spurs, and the palp formula is 5, 3; finally, *Tetramorium* Mayr, 1855 has 10-segmented antennae with a very long second funicular segment, which is markedly longer than the three subsequent segments together.

Similarly to *Lelejus* gen. nov., known males of all extinct Myrmicinae genera from late Eocene European ambers have notauli. However, these are never as broad and foveate as in *Lelejus* gen. nov., except for *Proleptothorax* Radchenko, Dlussky & Perfilieva, 2018 (see below). Additionally, *Lelejus* gen. nov. well differs from any of these genera in a set of other features. Thus, the anterior clypeal margin in *Bilobomyrma* Radchenko & Dlussky, 2013 is strongly notched medially and with two lateral lobes, the head is much longer (CI > 1.20), and meso- and metatibiae without spur; *Electromyrmex* Wheeler, 1915 has a distinctly longer antennal scape (SI1 > 0.45) and funiculus with a distinct 4-segmented club, a very long petiole without a node (PI2 > 3.30), meso- and metatibiae without spur, and forewing with closed cells 1+2r, rm and mcu, but cell 3r open; *Eocenomyrma* Dlussky & Radchenko, 2006 has a much longer antennal scape (SI1 0.50), a rather long head (CI 1.18), relatively smaller eyes (OI1 0.35), meso- and metatibiae without spur, and cell 3r on the forewing open; both *Plesiomyrmex*

Dlussky & Radchenko, 2009 and *Protomyrmica* Dlussky & Radchenko, 2009 have pectinate meso- and metatibial spurs and closed cells 1+2r, rm and mcu on the forewing; *Proleptothorax* Radchenko, Dlussky & Perfilieva, 2018 resembles *Lelejus* gen. nov. by the general pattern of forewing venation, antennal structure, shape of the head, presence of simple spurs on the middle and hind tibiae, but well differs by the short and narrow bidentate mandibles, longer head (CI 1.12), shorter and higher petiole (PI2 2.00), and by the 5-segmented maxillary and 3-segmented labial palps. Both these genera have wide foveate notauli, but they are Y-shaped in *Proleptothorax* and V-shaped in *Lelejus* gen. nov. (for a more detailed comparison see Dlussky and Radchenko 2009; Radchenko and Dlussky 2013a, 2016, 2018c; Radchenko et al. 2018).

Most of the morphological features of *Lelejus* gen. nov. can be considered as plesiomorphies in Myrmicinae. These are 13-segmented antennae with the short scape and filiform funiculus without an apical club; head without marked occipital corners and with convex occipital margin; subtriangular mandibles with a well-developed and dentate masticatory margin; unmodified clypeus; scutum with notauli; unmodified petiole and postpetiole; simple pretarsal claws; closed cell 3r on the forewing. On the other hand, the reduced number of segments of maxillary and labial palps (3, 2), presence of the simple spur (instead of pectinate) on the meso- and metatibiae, and reduced cell rm on the forewing are apomorphies. Nevertheless, based on the above, we cannot attribute *Lelejus* gen. nov. to any Myrmicinae tribe, and we cannot consider it as an ancestor of any known extinct or extant genera.

Of the 11 extant genera found in late Eocene European ambers, fossil males are known in six of them. These of *Stenamma*, *Aphaenogaster* and *Carebara* do not differ from extant species in the main diagnostic features (Wheeler 1915; Radchenko et al. 2019), but others possess a set of plesiomorphies compared to modern species. Thus, *Crematogaster primitiva* Radchenko & Dlussky, 2019 has 13-segmented antennae in contrast to 11- or 12-segmented ones in modern species. The forewings of *Pristomyrmex archaios* Radchenko & Dlussky, 2018 have closed cells 1+2r and mcu, while the cell mcu is completely reduced in extant species. Antennae in males of extinct *Temnothorax* species have an almost indistinct apical club instead of 4-segmented in modern species (Radchenko and Dlussky 2018b, 2019; Radchenko et al. 2018).

In general, the majority of the extinct amber genera of Myrmicinae are quite specialized and cannot be considered the ancestors of modern ants. Only two genera might be treated as the putative ancestors of extant genera: *Parameranoplus* Wheeler, 1915 of *Meranoplus* Smith, 1853, and *Proleptothorax* of the genera of the *Leptothorax* genus-group, but not of *Temnothorax* (Wheeler 1915; Radchenko et al. 2018).

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