

FIRST RECORD OF THE ANT GENUS *CREMATOGASTER* (HYMENOPTERA: FORMICIDAE) FROM THE LATE EOCENE EUROPEAN AMBERS

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Abstract.— The ant genus *Crematogaster* Lund, 1831 is recorded for the first time from the Late Eocene Rovno amber, Ukraine (Priabonian stage, 33.9–37.8 Ma). *C. primitiva* sp. nov. is described based on single male. It well differs from males of the extant species by the 13-segmented antennae (vs. 11–12-segmented in modern species). By this feature it resembles the fossil *C. praecursor* Emery, 1891 described from the Sicilian amber (Early Oligocene, Rupelian stage, 27.8–34.9 Ma), but differs from that species by its distinctly longer antennal scape and by some details of the forewing venation. Only one other fossil *Crematogaster* species is known – *C. aurora* LaPolla et Greenwalt, 2015, which was described based on the imprints of two queens from the Middle Eocene Kishenehn Formation, USA (ca. 46 Ma); however, we consider that the ascription of this species to *Crematogaster* is somewhat questionable.



Key words.— Paleontology, Late Eocene, Rovno amber, *Crematogaster primitiva*, new species

INTRODUCTION

The modern cosmopolitan genus *Crematogaster* Lund, 1831 is among the most speciose ant genera, consisting of about 500 described species and more than 250 subspecies. Its primary characteristic that is unique among myrmicine ants is having its postpetiole articulated on the dorsal surface of the first gastral segment. Additionally (but not uniquely), the petiole of workers and queens is somewhat flattened dorsoventrally, without a node. Males of all extant *Crematogaster* species have 11- or 12-segmented antennae with very short scape that is not longer than two basal funicular segments.

Previously, only two fossil *Crematogaster* species were known: *C. praecursor* Emery, 1891 described based on a male from the Sicilian amber (Early Oligocene, Rupelian, ca. 27.8–33.9 Ma; about a modern dating of the Sicilian amber see Skalski & Veggiani

1990), and *C. aurora* LaPolla et Greenwalt, 2015, based on the imprints of two queens from the Middle Eocene Kishenehn Formation (USA) (ca. 46 Ma). We described here the third fossil species, *C. primitiva* sp. nov. (male) recorded from the Ukrainian Rovno amber (Late Eocene, Priabonian stage, 33.9–37.8 Ma). Two undescribed *Crematogaster* species were previously recorded from the Rovno (“sp. A”) and Baltic (“sp. B”) ambers (Perkovsky 2016), but specimen “sp. B” really originates not from Baltic amber, but from Central American copal (Dubovikoff, personal communication, 2019). That is, *Crematogaster* is the single extant myrmicine genus from the Rovno amber that is not known from the other Late Eocene European ambers. Both known fossil males have 13-segmented antennae, a feature that we consider to be plesiomorphic compared to extant *Crematogaster* males. The taxonomic status of *C. aurora* is less clear, and, to our minds, its ascription to the genus *Crematogaster*

seems somewhat dubious (see Discussion section, below).

MATERIAL AND METHODS

We examined one specimen (male) of *C. primitiva* sp. nov. from the Rovno amber; it is deposited in the Schmalhausen Institute of zoology of the National Academy of Science of Ukraine, Kiev (SIZK). The photographs were taken with Leica Z16 APO microscope equipped with Leica DFC 450 camera and processed by LAS Core software. The line drawings are based on the original photographs in conjunction with the computer program CorelDraw 8. Not all features of the examined specimens were clearly visible and measurable, hence we measured only visible details (accurate to 0.01 mm), particularly:

- SL – maximum straight-line length of the scape from its apex to the articulation with condylar bulb;
- ML – diagonal length of the mesosoma (seen in profile) from the anterior end of the neck shield to the posterior margin of the propodeal lobes;
- MH – height of 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 petiole to the articulation with propodeum;
- PH – maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the imaginary line between the tip of subpetiolar process and posteroventral points of petiole;
- PPL – maximum length of the postpetiole between its visible anterior and posterior margins;
- PPH – maximal height of the postpetiole in profile;
- HTL – maximum length of the hind tibia.

For simplicity, we give ratios of various measurements (e.g. ML/MH) rather than name and abbreviate various indices (e.g. MI) as we have done elsewhere.

TAXONOMY

Crematogaster primitiva sp. nov. (Figs 1–2)

= *Crematogaster* sp. A: Perkovsky, 2016: 115.

Localities. Pugach quarry, Klesov deposit, Rovno Region, Ukraine.

Description. Male (Figs 1–2). Total length ca. 3.4 mm. Head in the specimen is deformed during fossilization (fattened dorso-ventrally) but definitely small. Eyes quite big, situated approximately at midlength of sides of head. Ocelli well developed though not big.

Antennae 13-segmented, without defined club, scape relatively long, subequal to total length of 1st to 3rd funicular segments. Mandibles elongate-triangular, with quite narrow but distinct masticatory margin, with is with three small acute teeth.

Mesosoma relatively high, ca. 1.3 times longer than height, scutum high, slightly convex, without Mayrian furrows. Propodeum widely rounded (seen in profile), its dorsal surface ca. 3 times shorter than posterior one. Petiole with short peduncle and massive, quite high node, its dorsum long, convex, declined anteriorly. Postpetiole small, articulated on dorsal surface of first gastral segment. Middle and hind tibiae with simple spur, pretarsal claws simple.

Forewing with closed cells *1r+2r* and *mcu*, cell *3r* open distally, cell *rm* is absent. Cell *1r+2r* big, hexagonal, more than twice longer than width; cell *mcu* trapezoid (not pentagonal), ca. 1.5 times longer than width, reaching distally level of pterostigmal base. Cross-vein *cu-a* merging with vein section *1M+Cu* far proximally than cell *mcu* (vein section *2M+Cu* much longer than cross-vein *cu-a*).

Body seems smooth and shiny (sculpture on head obscured). Whole body with not abundant, quite long suberect hairs; scape with sparse decumbent pubescence; coxae, inner margins of trochanters and femora with not abundant, long erect to suberect hairs; both inner and outer margins of tibiae and tarsi with short suberect to subdecumbent hairs.

Measurements. SL 0.32, ML 1.04, MH 0.77, PL 0.32, PH 0.21, PPL 0.16, PPH 0.15, HTL 0.67, total length 3.4 mm.

Ratios. ML/MH 1.34, PL/PH 1.54, PPL/PPH 1.09.

Workers and queens. Unknown.

Type material. Holotype male, Rovno amber, Late Eocene, No. K-25850 (SIZK), AntWeb CASENT No. 17566.

Etymology. From the Latin word “*primitiva*” (feminine gender) – primitive, that means the primitive structure of the antennae compare to modern species.

DISCUSSION

Based on the structure of the waist, mesosoma and head, as well as on the character of the forewing venation, we have no doubt that *C. primitiva* belongs to the genus *Crematogaster*. Nevertheless, it well differs from all known males of the extant *Crematogaster* species by its 13-segmented antennae and by its much longer antennal scape that is subequal to the total length of the 1st to 3rd funicular segments (*vs.* modern species, where antennae are 11- or 12-segmented and the scape length is subequal to the total length of only the 1st and 2nd segments).



Figure 1. *Crematogaster primitiva* sp. nov., photos of holotype male, body in lateral view; AntWeb CASENT No. 17566.

Similarly, based on the general structure of its body the male of *C. praecursor* belongs to *Crematogaster*, but like *C. primitiva* it has 13-segmented antennae, although these have short scape similar to the modern species of this genus (see Emery 1891, plate II, figure 19). Consequently, we suggest that *C. primitiva* and *C. praecursor* demonstrate an evolutionary trend in the male antennal structure in genus *Crematogaster*. The most plesiomorphic character is a 13-segmented antennae with a relatively long scape (*C. primitiva*), with the more “advanced” condition being 13-segmented, but with short scape (*C. praecursor*), and the most recent condition being an 11- or 12-segmented antenna with a short scape (all extant species). This idea fully corresponds with the geological age of both species: *C. primitiva* living 33.9–37.8 Ma and *C. praecursor* – 27.8–33.9 Ma.

The taxonomic position of *C. aurora* is less clear. LaPolla and Greenwalt (2015, p. 169) gave as the diagnosis of this species “Presence of a 2-segmented club on antennae, and petiole with distinct subpetiolar process directed anteriorly”. Neither of these features actually “diagnose” *Crematogaster*. Despite the general structure of the petiole of *C. aurora* being similar to modern *Crematogaster* (it is without a distinct node), contrary to modern species it is quite short, not so strongly flattened, and possess well developed, quite wide ventral process. Furthermore, neither the original description of *C. aurora* (*loc. cit.*, p. 169) nor the high quality photograph of the holotype specimen, indicates

the presence of the core diagnostic feature of *Crematogaster*: a postpetiole that articulates on the dorsal surface of the first gastral segment (opposed to the “normal” myrmecine condition articulating on the anterior surface of the first gastral segment).

This unique structure of the waist in all modern *Crematogaster* species is believed to be closely connected with defense and hunting behaviors. The sting in *Crematogaster* species is well developed, but with a blunt, spatulate tip that is unsuitable for pricking (Buren 1959, Kugler 1978), and the venom is applied topically by wiping on a victim instead of injecting it inside the body (Buren 1959, Longino 1993). By holding its gaster raised up and even somewhat forward, over its head, a worker can attack prey or enemies in a 360° radius.

While many of the visible characteristic features of the imprints of the specimens (queens) that were described by the authors are found in genus *Crematogaster*, they are also common for many other myrmecine genera, e.g. “Head longer than wide; posterior margin apparently straight; posterolateral corners broadly rounded; scapes short, not surpassing posterior margin by length of at least 2 funicular segments; ... declivity [of propodeum] steep, with two small spines directed slightly entad... petiole without node, longer than postpetiole; petiole with distinct subpetiolar process directed anteriorly; postpetiole short, without node, with smaller subpetiolar process than on petiole; postpetiole narrowly attached to gaster“ (*loc. cit.*, p. 169).

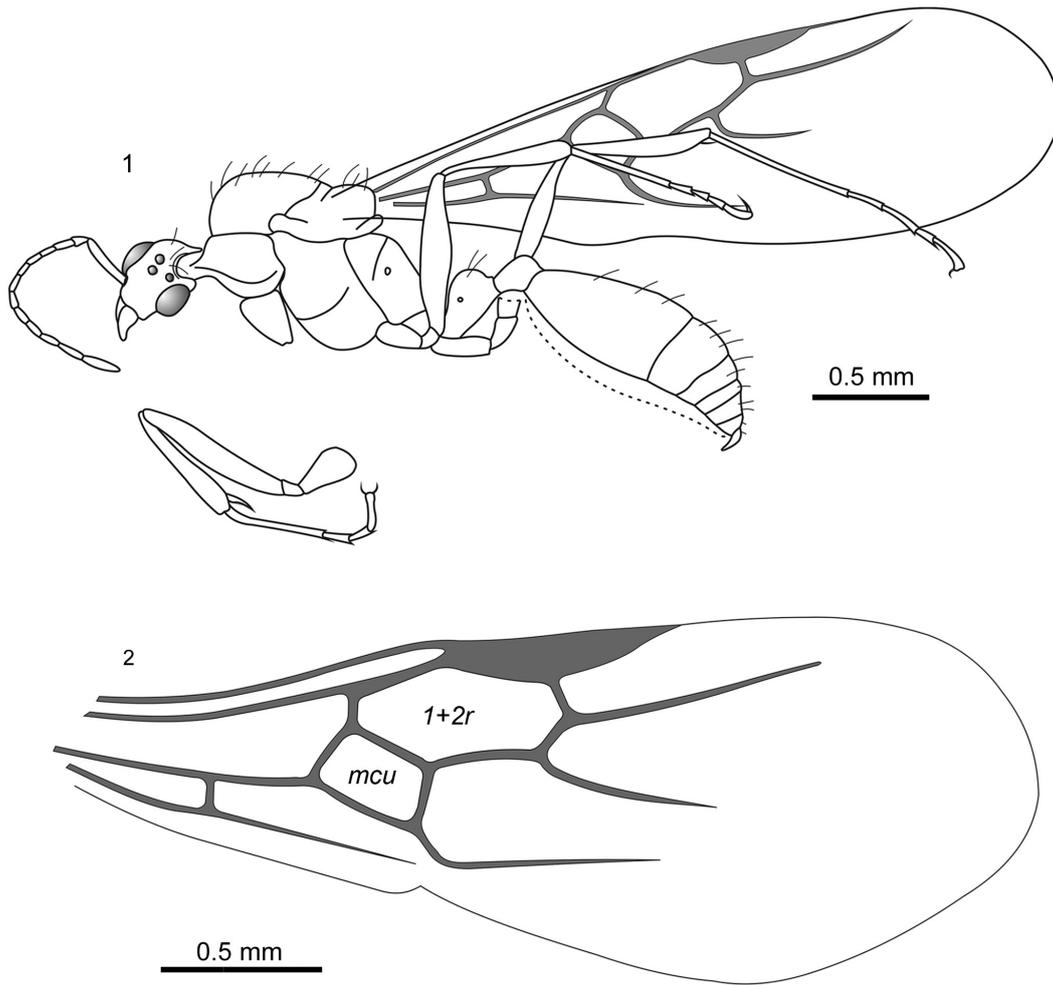


Figure 2. Line drawings made on original photo of *Crematogaster primitiva* sp. nov., holotype male. 1 – body in lateral view; 2 – forewing.

We can only speculate that big (about 10 mm long) and robust queens of *C. aurora* might belong to a new fossil genus that could represent the extinct ancestral lineage of the genus *Crematogaster* or even the whole tribe Crematogastrini (sensu Bolton, 2003).

Finally, there is an interesting and unresolved question: if the known age of *Crematogaster* is not less than 34 Ma (or even 40 Ma taking in account *C. aurora*), why are examples of this genus, one the most speciose among modern ants, absent in the contemporary or even much younger, Oligocene and Miocene deposits?

The numerous fossil-containing Oligocene-Miocene deposits throughout the World are sediments and it might be predicted that almost all ant specimens falling into the ancient shallow waters and becoming fossilized in their sediments would be alates. Indeed,

almost all the known Oligocene-Miocene ant specimens are alate gynes and males (very often only their wings were fossilized), and many specimens from the morphotaxon *Paraphaenogaster* Dlussky have been recorded in these deposits. The forewing venation of *Paraphaenogaster* is similar or even identical to that of many other modern myrmicine genera, including *Crematogaster* (e.g. see Dlussky 1981, Dlussky & Perfilieva 2014, Dlussky & Putyatina 2014, Radchenko & Perkovsky 2016). So, we can speculate that at least some of the *Paraphaenogaster* records may belong to *Crematogaster*, and this genus could have been relatively common in the Oligocene-Miocene time.

On the other hand, there is a distinct absence of *Crematogaster* workers in the very well studied Late Eocene European ambers as well as in the Middle Miocene Mexican ambers, while only two undescribed

yet *Crematogaster* species from two subgenera were recorded from the Middle Miocene Dominican amber (Wilson 1985). So either *Crematogaster* species were very rare in the amber-bearing forests, or they were not arboreal and did not climb up trees, or even by both reasons. Although the majority of modern *Crematogaster* species are typical arboreal dwellers, some species build nests in the soil and forage on the ground surface, tending aphids on herbs and do not climb up trees. If this was the normal life style in the Eocene and Middle Miocene, it would suggest quite a significant change towards an arboreal life-style since the amber formations.

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REFERENCES

- Bolton, B. 2003. Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71: 1–370.
- Buren, W. F. 1959 (1958). A review of the species of *Crematogaster*, sensu stricto, in North America (Hymenoptera: Formicidae). Part I. *Journal of the New York Entomological Society*, 66: 119–134.
- Dlussky, G. M. 1981. Miocenovye murav'i, pp. 64–83. *In*: Vishniakova V. N., Dlussky G. M. and Pritykina L. N. *Novye iskopaemye nasekomye s territorii SSSR*. Nauka, Moskva. [In Russian].
- Dlussky, G. M. and K. S. Perfilieva. 2014. Superfamily Formicoidea Latreille, 1802, pp. 410–438. *In*: Antropov, A. V., Belokobylskij, S. A., Compton, S. G. *et al.* The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 104: 335–446.
- Dlussky, G. M. and T. S. Putyatina. 2014. Early Miocene ants (Hymenoptera, Formicidae) from Radoboj, Croatia. *Neues Jahrbuch für Geologie und Paläontologie*, 272: 237–285.
- Emery, C. 1891. Le formiche dell'Ambra Siciliana nel Museo Mineralogico dell'Università di Bologna. *Memoire della Reale Accademia delle Scienze dell'Istituto di Bologna. Serie 5*, 1: 567–594.
- Kugler, C. 1978. A comparative study of the Myrmicine sting apparatus (Hymenoptera, Formicidae). *Studia Entomologica*, 20: 413–548.
- LaPolla, J. S. and D. E. Greenwalt. 2015. Fossil Ants (Hymenoptera: Formicidae) of the Middle Eocene Kishenehn Formation. *Sociobiology*, 62: 163–174.
- Longino, J. T. 1993. The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, 151: 1–150.
- Perkovsky, E. E. 2016. Tropical and Holarctic ants in Late Eocene Ambers. *Vestnik zoologii*, 50(2): 111–122.
- Radchenko, A. G. and E. E. Perkovsky. 2016. The ant *Aphaenogaster dlusskyana* sp. nov. (Hymenoptera, Formicidae) from the Sakhalin amber – the earliest described species of an extant genus of Myrmicinae. *Paleontological Journal*, 50: 936–946.
- Skalski, A. W. and A. Veggiani. 1990. Fossil resin in Sicily and the Northern Apennines: geology and organic content. *Prace Muzeu Ziemi*, 41: 37–49.
- Wilson, E. O. 1985. Ants of the Dominican amber (Hymenoptera: Formicidae). 1. Two new myrmicine genera and an aberrant Pheidole. *Psyche*, 92(1): 1–9.

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