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New species of the fossil ant genus *Drymomyrmex* (Hymenoptera, Formicidae, Formicinae) from the late Eocene Rovno amber (Ukraine)

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Abstract

A new species of the fossil ant genus *Drymomyrmex* Wheeler, 1915, *D. rasnitsyni* **sp. nov.**, is described from the late Eocene Rovno amber (Ukraine). This is the first find of a worker of this genus and the first record of *Drymomyrmex* in the Rovno amber. Based on the analysis of the morphological features of gynes and worker it is proposed to attribute *Drymomyrmex* to the tribe Plagiolepidini Forel, 1886.

Keywords: *Drymomyrmex rasnitsyni* **sp. nov.**, Plagiolepidini, worker caste, morphology, taxonomy, palaeontology, first records

Introduction

The ant fauna of the late Eocene (Priabonian, 33.9–37.8 Ma) European ambers is the best studied among all fossil myrmecofaunas worldwide. These ambers are: the Baltic (Kaliningrad Region of Russia and Baltic coast of Poland), the Bitterfeld (= Saxonian) (Germany, Saxony–Anhalt), the Scandinavian (= Danish) (mainly from the coast of Denmark), and the Rovno (Rovno, Zhitomir and Volyn Regions of Ukraine) ambers. More than 17,500 ant specimens belonging to about 220 extinct species from 76 genera (37 of which are extinct) of 12 extant subfamilies are currently known from these ambers (Dlussky & Rasnitsyn, 2009; Perkovsky, 2016; Radchenko & Dlussky, 2018; Radchenko, unpublished).

Formicinae is one of the most diverse ant subfamilies, including 51 extant genera and more than 3,200 species, or 15% of modern ant genera and 23% of species [calculated from Bolton (2021) data)]. The oldest known fossil member of this subfamily, *Kyromyrma neffi* Grimaldi & Agosti, 2000, was found in the Cretaceous (Turonian, *ca.* 92 Ma) New Jersey amber (USA). Fifteen fossil genera, attributed to Formicinae, have been described from the early Eocene (Ypresian, 50–53 Ma) Fushun amber (China) (Hong, 2002). However, the taxa described by Hong requires thorough revision, and even on the basis on the original photos and figures, it can be concluded that only two or three of these genera may belong to Formicinae, while others, apparently, belong to Dolichoderinae, Ponerinae, Aneuretinae, or should be considered *incertae sedis* in the Formicidae (Dlussky, pers. comm. 2012; Radchenko, unpublished).

Sixteen more fossil formicine genera (and morphogenera) have been described from various deposits in Eurasia and North America from the middle Eocene to the Pliocene (Heer, 1850; Wheeler, 1915; Donisthorpe, 1920; Carpenter, 1930; Steinbach, 1967; Wilson, 1985; Dlussky, 1967, 1988, 2008; Dlussky & Putyatina, 2014), and the oldest representatives of the extant genera *Formica* Linnaeus, 1758, *Lasius* Fabricius, 1804 and *Gesomyrmex* Mayr, 1868 are known in the early and middle Eocene deposits (Scudder, 1877; Dlussky, 2008; Dlussky *et al.*, 2009; Dlussky & Perfilieva, 2014; LaPolla & Greenwalt, 2015) (see also Radchenko *et al.*, 2021). However, the richest and most studied fossil Formicinae fauna is known from the late Eocene European ambers: nine extant and seven extinct genera and 39 species (or 21% of all genera of amber ants and 18% of species) were found here. At the same time, only 11 genera (three of which are extinct) and 18 species of this subfamily have been found in the Rovno amber so far. One of these extinct genera, *Drymomyrmex*, was established by Wheeler (1915). It includes two species: *D. fuscipennis* Wheeler, 1915 and *D. claripennis* Wheeler, 1915, described based on gynes; workers of this genus have been unknown.

I found one worker in a piece of Rovno amber, which in its main diagnostic features coincides well with those of *Drymomyrmex*, and decided to describe it as a new species based on the following: there is no real possibility either to assign it to one of the two species of the genus (described by gynes), or refuting this; in addition, gynes and a worker were found in different ambers (Baltic and Rovno). The question of conspecificity of the Rovno worker and one of the Baltic gynes can be resolved only if both castes are found in one piece of amber, but such a chance is scanty, especially considering that only four specimens of gynes

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and a single worker of *Drymomyrmex* were found in the 150-year history of the study of European amber ants. This specimen is the first known worker of this genus and the first record of *Drymomyrmex* in the Rovno amber.

Material and methods

I examined one worker in a piece of Rovno amber. The holotype is an intact, well-preserved specimen, but partially covered with an opaque film. It is deposited in the I. I. Schmalhausen Institute of Zoology of NAS of Ukraine, Kiev (SIZK). The piece of amber was processed as an irregular polyhedron block with flat faces (Fig. 2). Photographs of the specimen were taken with a Leica Z16 APO stereomicroscope equipped with Leica DFC 450 camera and processed by LAS Core software. Measurements of the specimen were made using Leica MZ6 stereomicroscope with an ocular micrometer, with maximum magnification ×100. Not all features of the examined specimen were properly visible and measurable, hence I measured only well visible details (calculated accurate to 0.01 mm), particularly:

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;

SL – maximum length of the scape measured in a straight line from its apex to the articulation with condylar bulb;

OL – maximum longitudinal diameter of the eye;

GL – length of the genae (sensu Bolton, 1994), measured from the anterior margin of the eyes to the articulation with the mandible;

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;

HTL – maximum length of the hind tibia.

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

Indices: SI = SL/HL, OI = OL/HL, GI = GL/OL, MI = ML/MH.

The terms "hairs" and "pubescence" are given according to Bolton (1994); "subdecumbent" mean hairs, outstanding from the surface at an angle < 30°.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Formicinae Latreille, 1809
Genus *Drymomyrmex* Wheeler, 1915

***Drymomyrmex rasnitsyni* sp. nov.**
(Figs 1–3)

Holotype. Worker, SIZK No. DO-136, Ukraine, Rovno Prov., Dubrovitsy Distr., village Osova, Rovno amber, late Eocene.

Etymology. The new species is named in honour of Professor Alexander P. Rasnitsyn, famous Russian paleoentomologist.

Diagnosis. Head elongated; antennae 11-segmented; mesonotum completely fused with metanotum and the latter does not form a distinctly separate sclerite; meso- and metatibiae with well developed simple spurs.

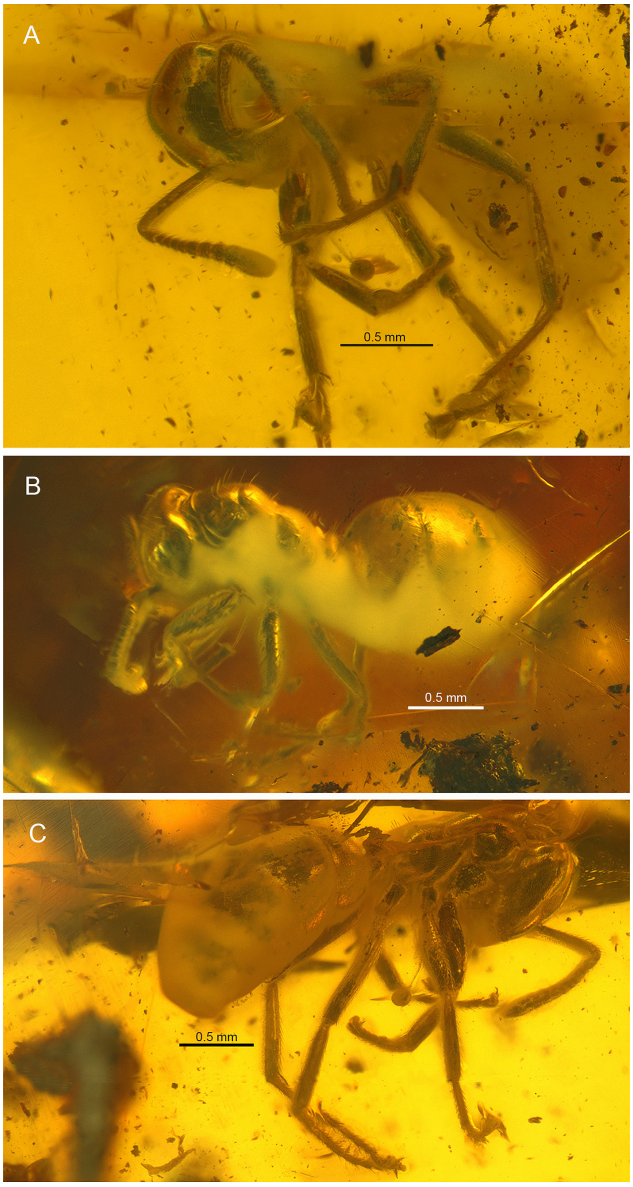

FIGURE 1. Photographs of *Drymomyrmex rasnitsyni* **sp. nov.**, holotype, SIZK No. DO-136. **A**, Anterolateral view. **B**, Left dorsolateral view. **C**, Right dorsolateral view.

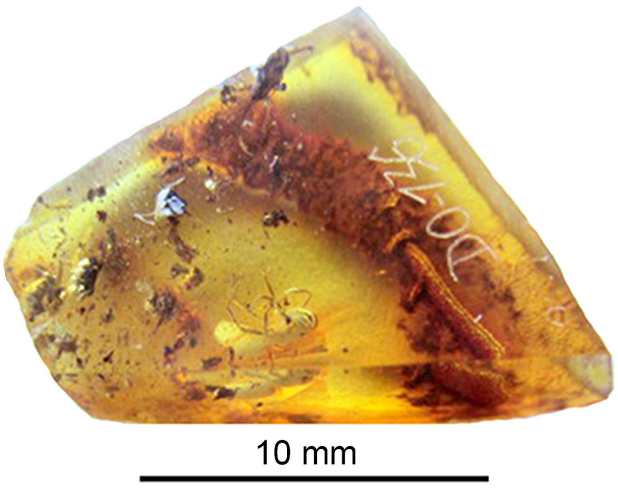

FIGURE 2. Photograph of piece of amber with the holotype worker of *Drymomyrmex rasnitsyni* **sp. nov.**

Type locality and horizon. Ukraine, Rovno Prov., Dubrovitsy Distr., village Osova, Rovno amber, late Eocene, Priabonian, 33.9–37.8 Ma.

Description. Total length *ca*. 3.5 mm. Despite head width not properly measurable, head definitely elongated, seems at least *ca*. 1.4 times as long as wide; sides of head very slightly convex, subparallel, occipital corners narrowly rounded, occipital margin straight. Antennae 11-segmented, inserted to head just near posterior margin of clypeus; scape relatively short, slightly does not reach occipital margin; funicular segments gradually enlarged from 2nd to apical, 1st segment *ca*. twice as long as wide, 2–5th transversal, 6–9th subsquare, 10th the longest, *ca*. 1.5 times as long as two preceding segments together. Eyes of moderate size (OI 0.26), situated approximately at midlength of sides of head, genae distinctly longer than maximum diameter of eye (GI 1.29). Ocelli absent. Surface of median portion of clypeus evenly convex, not truncated anteriorly over mandibles, its anterior margin feebly convex. Frontal carinae very short, not reaching level of anterior margin of eyes, clypeus not inserted between frontal carinae; anterior part of frons with not coarse longitudinal carina (instead of groove); frontal triangle small, but distinct. Mandibles triangular, but obscured, number of teeth cannot be counted. Maxillary and labial palps not visible.

Mesosoma relatively stout, *ca*. 1.3 times as long as high, pro-mesonotal suture very clear and deep, mesonotum slightly raised above pronotum, inclined to propodeum; mesonotum fused with metanotum, so that metanotum does not form distinctly separate sclerite (seen from above); propodeal dorsum much lower than promesonotum (*i.e*., mesosoma does not form regular arch in profile); propodeum gradually rounded, without teeth or tubercles, its dorsal surface somewhat shorter than declivous one; propodeal spiracles rounded, located quite close to declivity. Petiole with short posterior peduncle, its scale slightly inclined forward, thick, relatively low, with subparallel anterior and posterior surfaces and widely rounded dorsum; gaster partially overhangs posterior petiolar peduncle. Metacoxae widely separated (seen from below). Legs of moderate length, fore femora quite wide, *ca*. 3 times as long as width; middle and hind tibiae with well developed simple spur, which longer than maximum width of tibia; pretarsal claws simple.

Head dorsum and appendages with short and relatively sparse decumbent pubescence, length of appressed hairs subequal to distance between them, but such pubescence much denser in ventral and lateral surfaces of head, mesosoma and gaster, where hairs much longer than distance between them. Frons and occiput with infrequent quite long erect to suberect hairs, occipital margin and margin of temples also with very dense short subdecumbent hairs; mesosoma and petiole with rather long, often curved erect to suberect hairs, gaster with similar, but shorter hairs; antennae and legs with numerous quite short subdecumbent hairs, tarsi additionally with numerous coarse bristles. Body and appendages brownish-black.

Gynes and males. Unknown.

Measurements (in mm)**.** HL 0.69, SL 0.49, OL 0.18, GL 0.23, ML 0.98, MH 0.43, HTL 0.74.

Indices: SI 0.72, OI 0.26, GI 1.29, MI 2.27.

Discussion

The generic attribution of this worker specimen is somewhat uncertain because it represents a unique phenotype not presently known from taxa preserved in Baltic ambers. Based on morphological comparisons, the most reasonable placement that does not require definition of a new supraspecific taxon is in the genus *Drymomyrmex*. The new species matches it in having 11-segmented antennae with the relatively short scape, not reaching the occipital margin of the head, and the same structure of the funiculus; a similar shape of the head, which is subrectangular, distinctly elongated, with subparallel sides, narrowly rounded occipital corners and a straight occipital margin; the same size and position of the eyes; the presence of a long simple spur on the middle and hind tibiae; a rather thick petiolar scale with a broadly rounded dorsum; a similar character of the body pilosity (unfortunately, the maxillary and labial palps are not visible in the worker specimen), but differs from known *Drymomyrmex* gynes in the shape of clypeus, which it is evenly convex, not truncated, and does not form a flattened rounded plate with the mandibles. However,

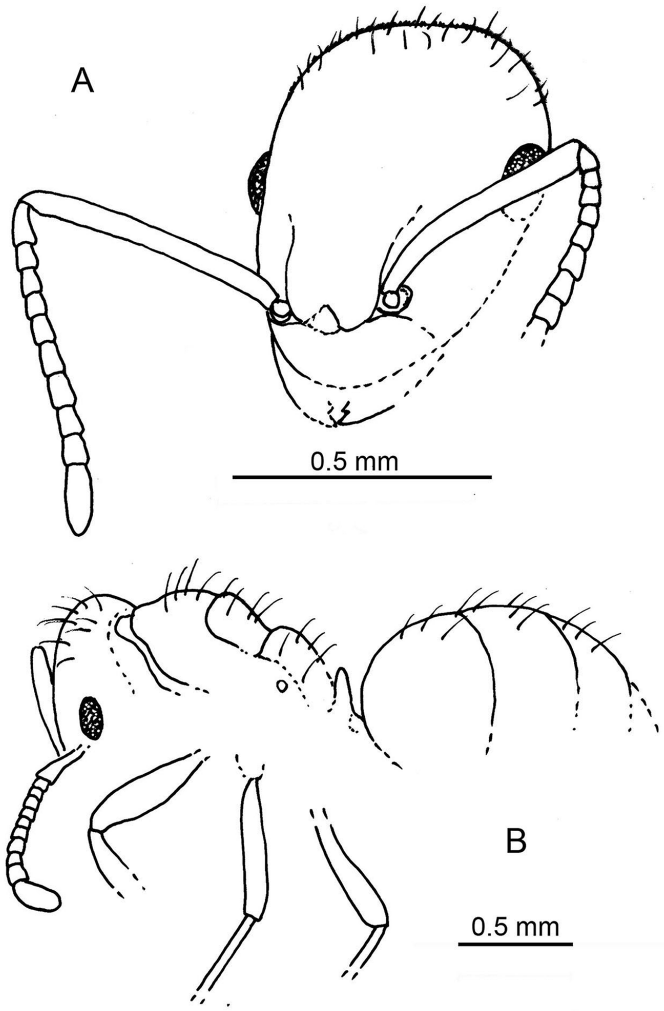

FIGURE 3. Line drawings of *Drymomyrmex rasnitsyni* **sp. nov.**, holotype. **A**, Head, dorsal view. **B** and **C**, Right dorsolateral view.

similar differences in the head structure are found in other genera of ants (for example, *Colobopsis* Mayr, 1861 or some *Tetraponera* F. Smith, 1852): gynes and soldiers may have a truncated head, but workers have the usual head shape. Thus, one can only assume that the worker caste of *Drymomyrmex* may be dimorphic with soldiers and workers.

Gynes of *Drymomyrmex* differ from those of any of the Formicinae genera known in late Eocene European ambers in a combination of features, particularly: the 11-segmented antennae with a relatively short scape that does not reach occipital margin of the head; the 6-segmented maxillary and 4-segmented labial palps; the long simple spur on the middle and hind tibiae; the clypeus is truncated to a variable extent, forming together with mandibles a flattened rounded plate (somewhat similar to some *Colobopsis* species). *Plagiolepis* Mayr, 1861 is the only other formicine genus from late Eocene European ambers with 11-segmented antennae, but its gynes differ from *Drymomyrmex* by the smaller body size (< 5 mm *vs*. 6–7 mm), a longer antennal scape that exceeds the posterior margin of the head, absence of spurs on the middle and hind tibiae, and a non-truncated clypeus.

The described worker of *Drymomyrmex* differs well from *Plagiolepis* in the structure of the mesosoma: in the latter species, the mesonotum is separated from the metanotum by a conspicuous transversal groove, so that the metanotum forms an isolated narrow sclerite, but in *Drymomyrmex* the mesonotum is completely fused with the metanotum and the latter does not form a distinctly separate sclerite (*e.g*., see Bolton, 1994; Czechowski *et al*., 2012).

Gynes and workers of only seven extant Formicinae genera have 11-segmented antennae: *Acropyga* Roger, 1862, *Anoplolepis* Santschi, 1914, *Lepisiota* Santschi, 1926, *Plagiolepis*, *Pseudolasius* Emery, 1877 (antennae are usually 12-segmented, but some species have 11-segmented ones), *Stigmacros* Forel, 1905 and *Tapinolepis* Emery, 1925, but gynes of *Drymomyrmex* clearly differ from each of them primarily by the structure of the clypeus.

In addition, worker differs from each these genera by a combination of other features.

Thus, the eyes of *Acropyga* workers are overwhelmingly very small, but even if they are relatively large, they are located distinctly in front of the midlength of the sided of head (in both workers and gynes), and the palp formula is 5, 3 or less. The legs and antennal scape of *Anoplolepis* are long, the latter exceeding the occipital margin, and the eyes are located distinctly behind the midlength of the sided of head. Like the previous genus, *Lepisiota* has long legs and scape, the propodeum of its workers has a pair of the sharp short teeth, and all castes have no spurs on the middle and hind tibiae. The antennae of *Pseudolasius* surpassing the occipital margin, and the palp formula is 5, 3 or less (moreover, amber *P. boreus* Wheeler, 1915 has 12-segmented antennae). The antennal scape of workers and gynes of the Australian genus *Stigmacros* also exceeds the occipital margin, and their body is without erect hairs. The African *Tapinolepis* has a long antennal scape and no spurs on the middle and hind tibiae. In addition, the venation of the forewings of *Drymomyrmex* is generally similar to that of all mentioned genera, in particular, by the presence of only two closed cells, 1+2r and 3r, but the cell 1+2r in *Drymomyrmex* is much wider and relatively shorter than in other genera. The taxonomic position *Drymomyrmex* is still uncertain. Wheeler (1915) provisionally considered it to be intermediate between the monotypic Afrotropical genus *Aphomomyrmex* Emery, 1899 and *Colobopsis* and placed it to the tribe Camponotini Forel, 1878, but later attributed it to the tribe Brachymyrmecini Emery, 1925 (Wheeler, 1929). Donisthorpe (1943), Dlussky & Fedoseeva (1988) and Bolton (1994) again attributed it to Camponotini. Dlussky (1997) synonymized *Drymomyrmex* with *Camponotus* Mayr, 1861, which was repeated by Bolton (2003). Finally, Dlussky & Rasnitsyn (2009) revived this name from synonymy and considered *Drymomyrmex incertae sedis* in Formicinae (see also Ward *et al*., 2016).

Bolton (2003) offered the most comprehensive morphological characteristic of Plagiolepidini Forel, 1886 and included 14 genera in it. Later, Blaimer *et al*. (2015) and Ward *et al*. (2016) revised the tribal system of the subfamily Formicidae, transferred a couple of genera from Plagiolepidini to other tribes, and assigned the genera *Acropyga* Roger, 1862 and *Anoplolepis* Santschi, 1914 to it.

As a result, nine genera are included in this tribe now, three of which are monotypic (*Aphomomyrmex* Emery, 1899, *Petalomyrmex* Snelling, 1979 and *Bregmatomyrma* Wheeler, 1929). Moreover, the assignment of the last genus to Plagiolepidini is provisional and "a taxonomic revision of the plagiolepidine genera is overdue" (Ward *et al*., 2016: 348). Since their studies were carried out only on the basis of molecular genetics approaches, they did not provide any morphological confirmation of the exclusion or inclusion of genera in this tribe.

I thus propose only preliminary morphological characteristic of this tribe, based on Emery (1925), Bolton (2003) and my own data: antennae 9–11-segmented (except for *Bregmatomyrma*) (9–12 in males), without apical club, inserted close to posterior clypeal margin. Propodeal spiracles rounded, situate at or near the declivity. Metacoxae widely separated (seen from below). Petiolar scale (node) somewhat inclined anteriorly, often with distinct posterior peduncle, at least partly overhands by the first gastral segment (the latter feature is absent in *Drymomyrmex* and *P. klinsmanni* Mayr, 1868). Forewing of males and gynes with closed cells 1+2R and 3R, cells rm and mcu are absent.

After the discovery of the worker of *Drymomyrmex*, I believe that most of the diagnostic features this genus is quite consistent with the characteristics of Plagiolepidini and presumably attribute *Drymomyrmex* to this tribe.

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