

***Formica* species (Hymenoptera, Formicidae, Formicinae) in late Eocene Rovno amber**

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Abstract

A new species, *Formica ribbeckei* Radchenko & Perkovsky, **sp. nov.**, is described based on four workers from late Eocene Rovno amber (Ukraine). It most resembles *F. flori* Mayr, 1868 but differs from the latter mainly by the 5-segmented maxillary palps with the preapical segment subequal in length to the apical one, and by the shorter first funicular segment. Fossil *F. luteola* Presl, 1822, *F. trigona* Presl, 1822, *F. macrognatha* Presl, 1822 and *F. quadrata* Holl, 1829 are considered *incertae sedis* in Formicidae. Thus, ten valid *Formica* Linnaeus, 1758 species (including *F. ribbeckei*) are known now from late Eocene European ambers. The diversity of *Formica* in the early and middle Eocene deposits of Eurasia and North America is considered. It is assumed that the genus *Formica* most likely arose in the early Eocene.

Keywords

European ambers, *Formica ribbeckei*, new species, paleontology, syninclusions, taxonomy

Introduction

The ant fauna of late Eocene European ambers (Priabonian, 33.9–37.8 Ma) is the best studied among all fossil myrmecofaunas worldwide. More than 17,500 ant specimens

belonging to nearly 220 extinct species from 73 genera (34 extinct and 39 extant) and 12 subfamilies (all extant) have been discovered till now (Dlussky and Rasnitsyn 2009; Dlussky et al. 2014; Radchenko and Dlussky 2012, 2017, 2018; Perkovsky 2016, 2018; our unpublished data). These ambers are: the Baltic amber (Kaliningrad Region of Russia and Baltic coast of Poland), the Bitterfeld (= Saxonian) amber (Germany, Saxony–Anhalt), the Scandinavian (= Danish) amber (mainly from the coast of Denmark), and the Rovno amber (Rovno, Zhitomir and Volyn Regions of Ukraine). Until 2015, almost all scientifically studied inclusions in Rovno amber were mined in Klesov or Dubrovitsa (Rovno Region), and inclusions from Vladimirets and Zarechnoje Districts of the Rovno Region were added later (Martynova et al., 2019). The data on inclusions from the Zhitomir Region have so far been limited to three new genera of Diptera and Coleoptera, one species of mites, and one species of caddisfly (Fedotova and Perkovsky 2015, 2017; Perkovsky 2017; Legalov et al. 2021). *Formica ribbeckei* Radchenko & Perkovsky, sp. nov. and *Plagiolepis klinsmanni* Mayr, 1868 are the first hymenopteran species recorded from amber of the Zhitomir Region.

Sixteen formicine genera are known from late Eocene European ambers, seven of which are extinct. In total, they comprise 39 described extinct species. Of the eight extant genera of the tribe Formicini only *Formica* Linnaeus, 1758 is found in late Eocene European ambers, as well as three extinct genera of this tribe: *Protoformica* Dlussky, 1967b, *Cataglyphoides* Dlussky, 2008 and *Conoformica* Dlussky, 2008 (Dlussky 2008; Bolton 2021).

The genus *Formica* comprises about 180 extant species, distributed almost exclusively in the Holarctic Region (Dlussky 1967a; Radchenko 2016; Bolton 2021), and nine extinct species were known from Eocene European ambers (Dlussky 2008). In total, about 100 fossil species have been attributed to *Formica* so far, but more than half of these names were either synonymized or are unidentifiable and are considered *incertae sedis* in Formicidae, and the actual number of valid species is less than 50; all are known from various Eocene, Oligocene and Miocene deposits of Eurasia and North America (Dlussky 2008; Dlussky and Putyatina 2014; Bolton 2021; our unpublished data). The oldest *Formica* species were described from the early Eocene (Ypresian, ca. 50–52 Ma) deposit of Quesnel (Okanagan Highlands, Canada) (Scudder 1877) and middle Eocene (Lutetian, ca. 46 Ma) deposit of Kishenehn (Montana, United States) (LaPolla and Greenwalt 2015), and several undescribed species have been discovered in the latest Ypresian Messel (47.8 Ma) and Lutetian Eckfeld (44.3 Ma) Lagerstätten of Germany (Dlussky 2008; Dlussky and Putyatina 2014).

Taking into account the new species described below, *Formica* together with *Plagiolepis* Mayr, 1861 represent the most speciose formicine genera in amber, each containing 10 species (Dlussky 2010). Furthermore, *F. flori* Mayr, 1868 is one of the most common ant species in all late Eocene European ambers: about 1500 specimens were found, and its relative abundance varies in different ambers from ca. 3% to almost 11% of all collected ants (Dlussky and Rasnitsyn 2009; our unpublished data).

We obtained a piece of amber from Gulyanka village (Korosten' District, Zhitomir Region, Ukraine) containing two ant workers assignable to *Formica* and *P. klinsmanni*.

After careful investigation, somewhat unexpectedly we found that this *Formica* specimen differs from the common *F. flori* by many important features, allowing the description of a new species, *F. ribbeckei* Radchenko & Perkovsky, sp. nov.

The discovery of a new *Formica* species in three localities – Gulyanka (Zhitomir region), Klesov and Vladimirets District (Rovno Region) together with *P. klinsmanni*, which was previously known from Klesov, supports a similar, late Eocene age, of all these Rovno amber deposits, since reliably dated late Eocene flora is known from Gulyanka (Pimenova 1937; Sokoloff et al. 2018).

Material and methods

We examined all available *Formica* inclusions from Rovno amber (about 100), four of which belong to *F. ribbeckei* Radchenko & Perkovsky, sp. nov. One piece of amber contains the holotype specimen (worker) of the described species together with a worker of *P. klinsmanni* (Fig. 2), and three other each contain one worker of *F. ribbeckei* Radchenko & Perkovsky, sp. nov. The holotype and two paratype specimens are deposited in the Schmalhausen Institute of Zoology of NAS of Ukraine, Kiev (**SIZK**), the paratype specimen No. KH-F-057 is in the collection of M. Khomych (Ukraine).

The photographs were taken with Leica Z16 APO microscope equipped with Leica DFC 450 camera processed by LAS Core software.

Not all features of the examined specimen were properly visible and measurable, hence we measured only well visible details (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; maxHW – maximum width of the head in dorsal view just behind (above) the eyes; minHW – minimal width of the head in dorsal view at the level of clypeus; 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 gena, measured from the anterior margin of the eye to the articulation with the mandible; ML – diagonal length of the mesosoma in lateral view from the anterior margin of the neck shield to the posterior margin of the metapleuron; MH – height of the mesosoma, measured from the upper level of the mesonotum perpendicularly to the lower margin of mesopleuron; PL – maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum; PW – maximum width of the petiole in dorsal view; PH – maximum height of the petiole in profile, measured from the uppermost point of the petiolar scale perpendicularly to the lowest point of the petiole; HTL – maximum length of the hind tibia; FSL1...2 – length of the funicular segments 1 and 2; FSW1 – width of the funicular segment 1; MP4...5 – length of segments of the maxillary palps from 4 and 5; TL – approximate total length is calculated as the sum of HL + ML + PL + length of the gaster.

Indices: CI=HL/maxHW, HWI= maxHW/minHW, SI1=SL/HL, SI2=SL/maxHW, OI=OL/HL, GI= GL/OL, PI1=PL/HL, PI2=PL/PH, MI=ML/MH, FSI1=FSL1/FSL2, FSI2=FSL1/FSW1, MPI=MP5/MP4.

Results

Taxonomy

Order Hymenoptera Linnaeus, 1758

Family Formicidae Latreille, 1809

Subfamily Formicinae Latreille, 1809

Tribe Formicini Latreille, 1809

Genus *Formica* Linnaeus, 1758

***Formica ribbeckei* Radchenko & Perkovsky, sp. nov.**

<http://zoobank.org/D09EB2FB-8386-49BC-AAFD-6AD1E1A6600A>

Figs 1, 2; Tables 1, 2

Material examined. Holotype: worker, SIZK GU–25, Ukraine, Zhitomir Region, Korosten' District, village Gulyanka, Rovno amber, late Eocene, 33.9–37.8 Ma. **Paratypes:** worker, SIZK K–3566, Ukraine, Rovno Region, Klesov; worker, SIZK K–3514, Ukraine, Rovno Region, Klesov; worker, collection of M. Khomych, No. KH–F–507, Ukraine, Rovno Region, Vladimirets District, vicinity of village Voronky, Rovno amber, late Eocene, 33.9–37.8 Ma.

Diagnosis. Worker: maxillary palps 5-segmented, long, reaching occipital foramen, its apical and preapical segments subequal in length; gastral tergites with sparse decumbent pubescence, distance between setae greater than their length; first funicular segment ≤ 1.2 times as long as second one, and ≤ 2.25 times as long as broad.

Description. Body length 4.7–6.5 mm. Head slightly longer than wide, distinctly narrowing anteriorly (maxHW/minHW 1.31–1.36), with broadly rounded occipital corners and weakly convex occipital margin. Frontal area well defined, sculptured similarly to frons. Eyes large (OI 0.3–0.35), situated distinctly behind (above) midlength of sides of head, genae distinctly longer than maximum diameter of eyes (GI 1.10–1.15). Ocelli distinct, forming equilateral triangle. Frontal groove weakly developed, short and very shallow. Clypeus with distinct longitudinal medial carina, its anterior margin slightly angulated. Antennal scape longer than head, somewhat widened apically, surpassing occipital margin for ca. 1/4 of its length. First funicular segment 1.1–1.2 times as long as second one and ca. twice as long as wide, second and third segments of same length and 1.7 times as long as wide. Maxillary palps 5-segmented but long, reaching occipital foramen, their third segment the longest, apical segment subequal to preapical one; labial palps 4-segmented. Mandibles with 6–8 sharp teeth, apical tooth distinctly larger, but less than twice as long as preapical one.

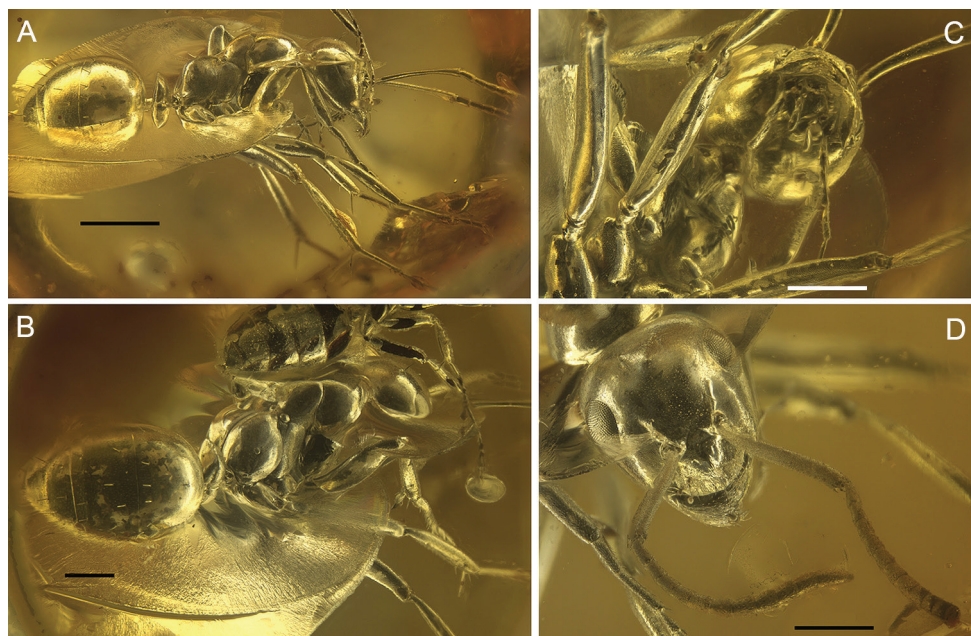


Figure 1. *Formica ribbeckei* Radchenko & Perkovsky, sp. nov., holotype, worker (ANTWEB:casent 0917590) **A** body, lateral view **B** body dorso-lateral view **C** head, maxillary and labial palps, ventral view **D** head, dorsal view. Scale bars: 1.0 mm (**A**); 0.5 mm (**B–D**).

Mesosoma quite slender, 2.34–2.43 times as long as high, mesonotum slightly raised above pronotum. Dorsal surface of propodeum convex, posterior one almost straight and inclined posteriorly, both surfaces converging at rounded angle. Propodeal spiracles elongate-oval, ca. twice as long as wide. Petiolar scale rather high, its anterior surface convex, posterior one flat and almost straight, sides very slightly convex; its upper margin convex, without notch (seen in anterior or posterior views), in profile quite narrow, with crest. Meso- and metatibiae each with a single, long simple spur.

Body surface with very fine microsculpture, appears quite shiny, especially on gena. Mesosoma, petiole, legs and antennae without standing setae. Several coarse semierect setae present on vertex, frons and clypeus; gastral tergites and sternites with similar setae. Meso- and metatibiae usually without row of coarse bristles, only with 2–4 bristles on distal third of flexor surface. Mesosoma and petiole with very fine, short and dense whitish decumbent pubescence, setae longer than distance between them; head dorsum with sparse pilosity, distance between setae greater than their length. Gastral tergites with sparse decumbent pilosity, distance between setae greater or at most equal to their length. Eyes bare.

Measurements (in mm) and indices are given in the Tables 1, 2.

Queens and males. Unknown.

Etymology. The species is dedicated to Mr Hans-Werner Ribbecke (Mecklenburg–Vorpommern, Germany), who donated us the holotype specimen.

Table 1. Measurements of *Formica ribbeckei* Radchenko & Perkovsky, sp. nov. (in mm).

Specimens	HL	max	min	SL	OL	GL	ML	MH	PL	PW	PH	HTL	FSL1	FSW1	FSL2	MP4	MP5	TL
	HW	HW																
holotype	1.14	1.07	0.78	1.26	0.40	0.44	1.77	0.75	0.26	–	0.56	1.26	0.20	0.10	0.17	0.21	0.22	4.7
K-3566	1.12	0.99	0.73	1.25	0.38	0.43	1.79	–	0.26	0.49	–	1.25	0.23	0.12	0.20	0.30	0.31	4.8
K-3514	1.40	1.22	0.94	1.52	0.44	0.51	2.34	0.99	0.39	–	–	1.87	0.36	0.12	0.23	–	–	6.5
KH-F-507	1.30	1.20	–	1.47	0.40	0.46	2.21	0.91	0.38	–	–	1.82	0.27	0.12	0.23	0.34	0.31	6.1

Table 2. Morphometric indices of *Formica ribbeckei* Radchenko & Perkovsky, sp. nov.

Specimens	CI	HWI	SI1	SI2	OI	GI	PI1	PI2	MI	FSI1	FSI2	MPI
holotype	1.07	1.36	1.10	1.18	0.35	1.10	0.23	0.47	2.34	1.15	2.00	1.06
K-3566	1.13	1.36	1.12	1.26	0.34	1.14	0.23	–	–	1.20	2.00	1.04
K-3514	1.15	1.31	1.08	1.24	0.31	1.15	0.27	–	2.37	1.11	2.11	–
KH-F-507	1.09	–	1.13	1.23	0.34	1.13	0.29	–	2.43	1.17	2.21	0.92

Comparative diagnosis. Nine undoubted *Formica* species are known from late Eocene European ambers (Dlussky 2008). *F. ribbeckei* Radchenko & Perkovsky, sp. nov. clearly differs from *F. horrida* Wheeler, 1915, *F. kutscheri* Dlussky 2008, *F. palaeopolonica* Dlussky, 2008 and *F. zherikhini* Dlussky, 2008 by the absence of erect or suberect setae on the tibiae and antennal scape. Among other species with bare tibiae and scape, *F. ribbeckei* Radchenko & Perkovsky, sp. nov. differs from *F. radchenkoi* Dlussky, 2008 by the absence of notch on the anterior clypeal margin. It resembles *F. phaethusa* Wheeler, 1915 by the 5-segmented maxillary palps, but its palps are much longer and reach the occipital foramen; additionally, it differs by the longer antennal scape and by the angulated anterior clypeal margin. New species differs from *F. strangulata* Wheeler, 1915 by the clypeal shape, the first funicular segment shorter, and the promesonotal and propodeal shape. Both *F. flori* and *F. gustawi* Dlussky, 2002 have 6-segmented maxillary

<i>F. ribbeckei</i>	<i>F. flori</i>
Maxillary palps 5-segmented; apical and preapical segments subequal in length	Maxillary palps 6-segmented; preapical segment about 1.5 times as long as apical one
First funicular segment ≤ 1.20 times as long as second one and ≤ 2.25 times as long as broad	First funicular segment ≥ 1.35 times as long as second one and ≥ 3 times as long as broad
Upper margin of petiolar scale thin and with distinct crest Mesosoma with dense decumbent pubescence	Upper margin of petiolar scale quite thick and rounded Mesosoma with sparse decumbent pubescence

palps. In addition, the latter species has dense decumbent pubescence on the gastral segments, which distinguishes it well from *F. ribbeckei* Radchenko & Perkovsky, sp. nov.

Formica ribbeckei Radchenko & Perkovsky, sp. nov. most resembles *F. flori*, particularly in the sparse decumbent pilosity on the gastral tergites. The main differences between it and *F. flori* are:

We examined approximately 100 *Formica* specimens of five species from Rovno amber in varying degrees of preservation: *F. flori* (38), *F. gustawi* (15), *F. palaeopolonica* (1), *F. radchenkoi* (2, including the holotype) and *F. ribbeckei* Radchenko & Perkovsky, sp. nov. (5). These represent half of the known amber *Formica* species.

The most abundant species in all ambers is *F. flori*, followed by *F. gustawi*. The latter clearly differs from *F. flori* by the dense decumbent pubescence on the gastral ter-



Figure 2. General view of the synclusion of *Formica ribbeckei* Radchenko & Perkovsky, sp. nov., holotype, worker (A) and *Plagiolepis klinmanni*, worker (B). Scale bar: 1.0 mm (ANTWEB:casent0917590).

gites. Thirty three specimens of *F. gustawi* have been recorded from all ambers (Dlussky 2002b, 2008; Dlussky and Rasnitsyn 2009; Perkovsky 2016), but its separation with *F. flori* was not agreed upon by all researchers until 2002 when *F. gustawi* was described. Therefore, when previously examined *Formica* material will be re-evaluated, the abundance of *F. gustawi* may increase. The situation with *F. ribbeckei* Radchenko & Perkovsky, sp. nov. may be similar, as this species is very similar to *F. flori*, and we cannot rule out that *F. ribbeckei* Radchenko & Perkovsky, sp. nov. can be found in other late Eocene European ambers after re-investigation of corresponding material.

Nine fossil species originally assigned to genus *Formica* were first described from Baltic amber in the first half of 19th century (Presl 1822; Holl 1829; Giebel 1856). However, the type specimens of these species have been lost, and based on their inadequate descriptions, it is impossible to attribute these species to *Formica* or any other ant genera. As a result, Mayr (1868) suggested that *F. cordata* Holl, 1829 belongs to *Pheidole* Westwood, 1839, and *F. lucida* Giebel, 1856 is not an ant, but a parasitoid Braconidae wasp, and Handlirsch (1907) proposed to consider most of them *incertae sedis* in Formicidae.

Bolton (2021) agreed with Handlirsch (1907) and excluded *F. nigra* Presl, 1822, *F. gibbosa* Presl, 1822 and *F. parvula* Presl, 1822 from *Formica*. It is unclear why

F. luteola Presl, 1822, *F. trigona* Presl, 1822 and *F. macrognatha* Presl, 1822 were not excluded. These species do not belong to the genus *Formica* for the following reasons.

The body length of *F. luteola* is ca. 3.2 mm (too small for *Formica*), the body is light yellow (“Flavescenti-alba”) and the head is rounded and somewhat cordate (“Caput rotundatum, fere cordatum”). These features are not known to be present in either extant or extinct *Formica* species. *F. trigona* is also too small for *Formica* (ca. 2.5 mm) with a triangular head (“Caput trigonum”) and long antennae (“antennae longitudine capitis et thoracis”). These features raise doubts that this species should even be included to the family Formicidae. *F. macrognatha* is also quite small (ca. 3.7 mm), with short legs (“Pedes breves”), and its head is large and triangular (“Caput... magnum, trigonum”), precluding its placement in *Formica*.

Our data also confirm the exclusion of the following species from *Formica*: *F. nigra* and *F. parvula* are too small, with body lengths of 2.1 and 1.5 mm, respectively. *F. gibbosa* is too large: ca. 10.5 mm, its head is ovoid (“ovoideum”) and the mesosoma is extremely elevated (“Thorax ovoideus, eximie elevates”). And, based on the original description, *F. quadrata* Holl, 1829 cannot be unambiguously assigned to any ant genus, and we agree with its exclusion from *Formica*.

Discussion

Accordingly, only ten *Formica* species are reliably known from late Eocene European ambers. Dlussky (2008) suggested that most of these species are quite specialized and only *F. flori* and *F. gustawi* can be considered the putative ancestors of extant *Formica* species. They belong to the *F. fusca* Linnaeus, 1758 species-group. Despite that *F. ribbeckei* Radchenko & Perkovsky, sp. nov. resembles *F. flori*, it has a reduced number of maxillary palps, and therefore we do not consider it to be one of the ancestors of the extant species of the *F. fusca* group.

The *Formica fusca*-group is considered ancestral to other extant *Formica* species (Dlussky 1967a; Radchenko 2016). Its representatives are characterized by a non-specialized head structure, mesosoma, petiole, maxillary palps, funicular segments, as well as a weakly developed polymorphism and a low level of social organization. Their gynes are large, which is associated with the independent founding of new colonies.

Formica radchenkoi most likely belongs to the more derived subgenus *Raptiformica* Forel, 1913, which includes slave-making species. Similarly, *F. parexsecta* Dlussky & Putyatina, 2014, described from the early Miocene deposits of Radoboj (Croatia), resembles extant species from the morphologically specialized subgenus *Coptoformica* Müller, 1923. Representatives of this subgenus have an emarginated occipital margin, short maxillary palps and often reduced body pubescence. Queens are quite small compared to those of the other *Formica* subgenera (Dlussky 1967a; Radchenko 2016). The emarginated occipital margin of the head allows an increase in the mass and strength of the mandibular muscles, which is associated with their nesting habits: workers cut grass to build nesting mounds. The small body size of gynes is associated with their biology: they are unable to independently establish a new colony and are temporary social parasites of *Serviformica* Forel, 1913 species (Dlussky 1967a).

Until recently, the oldest undoubted *Formica* species were known from the late Eocene. These are 10 species known from European amber: 8 species from Baltic amber and 7 from Scandinavian, Bitterfeld and Rovno ambers taken together. Cockerell (1920) described *F. heteroptera* from the Bagshot Beds in Bournemouth (Dorset, England) (Lutetian) based on a forewing, but the described features of this wing indicate that this specimen does not belong to *Formica* (Perfilieva, personal communication), from which it is formally excluded here. Théobald (1937) described three new *Formica* species and recorded impressions of *F. flori* (gyne) from the Upper Rhine Graben of Kleinkems (Baden–Württemberg, Germany) (latest Eocene); however, because the short antennal scape does not reach the occipital margin, this specimen differs not only from *F. flori* but also from all extinct and extant *Formica* species. The affinities of *F. tripartita* Théobald, 1937, *F. alsatica* Théobald, 1937 and *F. cf. septula* Théobald, 1937 with *Formica* from late Eocene ambers remains uncertain. Interestingly, *Formica* ants have not been found in the Bembridge Marls, Isle of Wight, England (late Eocene) (Dlussky and Perfilieva 2014). This could be due to unsuitable environmental conditions at Bembridge for *Formica* and other epigeic ants (Radchenko and Perkovsky 2021).

Two new *Formica* species, *F. biamoensis* Dlussky et al., 2015 (worker) and *F. paleosibirica* Dlussky et al., 2015 (male), have recently been described from the latest Eocene deposit of the Russian Far East (Bol'shaya Svetlovodnaya) (Dlussky et al. 2015). *F. biamoensis* resembles *F. flori* and *F. gustawi* in general appearance, but the affinity of the second species to other known *Formica* is uncertain. Four species have also been recorded from the United States: *F. eoptera* Cockerell, 1923 (described based on a forewing) from Texas, and three species have been described based on winged gynes from Florissant, Colorado (latest Eocene) by Carpenter (1930). Although Carpenter (1930) doubted the attribution of *F. eoptera* to *Formica* and suggested considering it *incertae sedis* in Formicidae, Bolton (2021) concurred with Cockerell (1923). Based on the original description and illustration, there is no evidence to contradict the assignment of this species to *Formica*, and thus, we agree with Bolton.

The oldest species, assigned to *Formica*, *F. arcana* Scudder, 1877, was described by Scudder (1877) based on a forewing from the early Eocene of Quesnel (Okanagan Highlands, Canada), but Archibald et al. (2018) doubted that this species belonged to *Formica* or even Hymenoptera. However, the original description of the wing venation does not contradict the main features of *Formica* wing venation (Perfilieva, personal communication). Another undescribed *Formica* species was recently recorded from the early Eocene Palana Formation (India) (Patel et al. 2019). However, the interpretation of this specimen seems to be incorrect, and based on a photograph of the imprint (loc. cit., Fig. 10) we believe that this specimen does not exactly belong to *Formica* and, most likely it is not an ant at all.

Recently, Dlussky (2008) and Dlussky and Perfilieva (2014) indicated that there are some *Formica* compression fossils from the latest Ypresian Messel (47.8 Ma) and Lutetian Eckfeld (44.3 Ma) Lagerstätten (Germany). LaPolla and Greenwalt (2015) described males of *F. annosa* from the Kishenehn Formation (Lutetian, ca. 46 Ma) in northwestern Montana, USA. Despite that many important diagnostic details are usually unrecognizable from imprints (in contrast to amber fossils), the described males resemble extant males of

the *F. fusca*-group in general appearance and visible features. This observation may serve as confirmation of its ancestral position in the genus.

Extant *Formica* species are one of the dominant groups of ants in the temperate humid zones of the Northern Hemisphere, where they mainly inhabit forests and meadows. Some species live in semi-arid regions (steppes, Mediterranean landscapes), but in deserts and semi-deserts, they occur only in intrazonal wet places. The distribution of many species extends beyond the Arctic Circle, and species can be found at elevations of 3600 m in the Alps, 3950 m in the Pamir, 4300 m in the North American Cordillera and even up to 4800 m in the Himalayas. Some species are also distributed in the mountains of tropical regions (Mexico, Taiwan, Myanmar), and *F. fusca* has been introduced and naturalized in Cuba (Dlussky 1967a; Gregg 1969; Radchenko 2016).

Ecologically, *Formica* is a keystone genus (together with *Lasius* Fabricius, 1804 and *Myrmica* Latreille, 1804) in the temperate zone of the Holarctic. Many species (e.g. members of the subgenera *Formica* s. str., *Coptoformica*, some *Serviformica*) dominate in ant communities (Dlussky 1967a; Zakharov et al 2013; Zakharov 2018). All *Formica* species are epigeic ants; they build nests in the ground, often with soil mounds, or make “ant-hills” from small pieces of branches, conifer needles or grass. They actively forage not only on the ground but also in the grass and on trees and bushes where they collect honeydew of aphids and other homopterans and prey on a variety of invertebrates.

It can be assumed that the extinct *Formica* species had a similar lifestyle. Homopteran insects were common by the late Eocene and are present in European ambers, and numerous syninclusions of aphids and ants have been recorded (Perkovsky 2006, 2007, 2008, 2009, 2010, 2011a, b; Perkovsky and Wegierek 2018). Most likely, workers of one of the most numerous amber ants, *F. flori* (as well as other *Formica* species), were trapped in resin during foraging on tree trunks when collecting honeydew.

The mixed character of the Baltic amber ant fauna, including both extant temperate and tropical genera, was already mentioned by Wheeler (1910, 1915). The same can be said about all other late Eocene European ambers (e.g. see Dlussky and Rasnitsyn 2009). The composition of amber fauna can be explained by the climate of the late Eocene, which was equable and has no current analogues (Radchenko and Perkovsky 2021 and references therein).

The ant genera and some species found in late Eocene European ambers that are classified as Holarctic (temperate) are: *Formica*, *Lasius*, *Temnothorax* Mayr, 1861 and *Camponotus mengei* Mayr, 1858, but *Gesomyrmex* Mayr, 1868, *Yantaromyrmex* Dlussky et Dubovikoff, 2013, *Dolichoderus robustus* Dlussky, 2002 and *Bradoponera* Mayr, 1868 are classified as tropical (Dlussky 2002a; Dlussky and Rasnitsyn 2009; Dubovikoff 2012; Radchenko and Perkovsky 2021). We cannot attribute the extinct taxa *Ctenobethylus* Brues, 1939, *Monomorium mayrianum* Wheeler, 1915 and *Plagiolepis klinmanni* to either Holarctic or tropical groups (Radchenko and Perkovsky 2021).

More than 60 ant syninclusions have been found in late Eocene European ambers, and about 20 contain *Formica* (Dlussky, pers. comm. 2013; Radchenko and Perkovsky 2021). Wheeler (1915) reported three *Formica* syninclusions: *F. flori* with *Ctenobethylus goepperti* (Mayr, 1868), *F. flori* with *Camponotus mengei* and *F. horrida* with *Temnothorax gracilis* (Mayr, 1868) (names of species and genera are given according to

modern taxonomy). Fifteen more *Formica* syninclusions are now known from Baltic, Bitterfeld and Rovno ambers, and only four include Holarctic species: three with *Lasius schiefferdeckeri* Mayr, 1868 and one with *C. menzei*. Five syninclusions represent mixed Holarctic and tropical fauna: one *F. flori* with *Gesomyrmex hoernesii* Mayr, 1868, one with *D. robustus*, one with *Bradoponera meyeri* Mayr, 1868, one with *Yantaromyrmex geinitzi* (Mayr, 1868) and one *F. gustawi* with *Y. geinitzi*. Finally, six pieces of amber contain *F. flori* with ants of unknown geographic affiliation: four with *C. goepperti*, one with *M. mayrianum* and one with *P. klinsmanni*.

The genus *Formica* most likely arose in the early Eocene, diversified in the late Eocene, and its species became dominant in ant communities. Then they continuously evolved to the present and have now become the dominant group of ants in the temperate zone of the Northern Hemisphere.

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Supplementary material 1

***Formica* species (Hymenoptera, Formicidae, Formicinae) in late Eocene Rovno amber**

Authors: Alexander G. Radchenko, Evgeny E. Perkovsky, Dmitry V. Vasilenko

Data type: new species, fossils, paleontology

Explanation note: A new species, *Formica ribbeckei* Radchenko & Perkovsky, sp. nov., is described based on four workers from late Eocene Rovno amber (Ukraine). It the most resembles *F. flori* Mayr, 1868 but differs from the latter mainly by the 5-segmented maxillary palps with the preapical segment subequal in length to the apical one, and by the shorter first funicular segment that is ≤ 1.20 times as long as the second, and ≤ 2.25 times as long as broad.

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Supplementary material 2

***Formica* species (Hymenoptera, Formicidae, Formicinae) in late Eocene Rovno amber**

Authors: Alexander G. Radchenko, Evgeny E. Perkovsky, Dmitry V. Vasilenko

Data type: COL

Explanation note: A new species, *Formica ribbeckei* Radchenko & Perkovsky, sp. nov., is described based on four workers from late Eocene Rovno amber (Ukraine). It the most resembles *F. flori* Mayr, 1868 but differs from the latter mainly by the 5-segmented maxillary palps with the preapical segment subequal in length to the apical one, and by the shorter first funicular segment that is ≤ 1.20 times as long as the second, and ≤ 2.25 times as long as broad.

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