

## **Ants of the extinct genus *Cataglyphoides* Dlussky, 2008 (Hymenoptera: Formicidae: Formicinae) from the late Eocene European ambers**

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**ABSTRACT.** A new species from the fossil ant genus *Cataglyphoides* Dlussky, 2008, *C. dluskyi* sp.n., is described from the Rovno amber (Ukraine). A new record of *C. constrictus* (Mayr, 1868) from the Baltic amber (age of both ambers is late Eocene, Priabonian, 33.9–37.2 Ma) and additional diagnostic features of this species are provided. *C. dluskyi* resembles *C. constrictus* but well differs from the latter mainly by the absence of standing hairs on the body, absence of the longitudinal carina on the clypeus, by position of the eyes and the much shorter genae and by character of the standing pilosity on the appendages (*C. dluskyi* has very fine and short whitish subdecumbent to suberect hairs, but *C. constrictus* has coarse brownish bristles). *C. dluskyi* differs from *C. intermedius* Dlussky, 2008 first of all by the shape of petiolar scale and mesosoma, and by the longer antennal scape. A Key for identification of all known *Cataglyphoides* species is compiled.

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**KEY WORDS.** *Cataglyphoides dluskyi* sp.n., *C. constrictus*, *C. intermedius*, Rovno amber, fossils, taxonomy, tribe Formicini, evolution.

## **Муравьи вымершего рода *Cataglyphoides* Dlussky, 2008 (Hymenoptera: Formicidae: Formicinae) из позднеэоценовых янтарей Европы**

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**РЕЗЮМЕ.** Описан новый вид из ископаемого рода муравьев *Cataglyphoides* Dlussky, 2008, *C. dluskyi* sp.n., из ровенского янтаря (Украина). Приведена новая находка *C. constrictus* (Mayr, 1868) из балтийского янтаря и добавлены данные к его диагнозу. Возраст обоих янтарей – поздний эоцен, приабон, 33.9–37.2 Ма. *C. dluskyi* внешне сходен с *C. constrictus*, но хорошо отличается от последнего отсутствием отстоящих волосков на теле, отсутствием продольного срединного киля на наличнике, местом расположения глаз и намного более короткими щеками, характером отстоящего опушения на ногах и скапусе антенн (у *C. dluskyi* очень нежные и короткие

беловатые полуприлежащие или полуютостоящие волоски, а у *C. constrictus* грубые коричневатые отстоящие щетинки). *C. dluskyi* отличается от *C. intermedius* Dlussky, 2008, прежде всего, формой петиолюса и мезосомы, а также более коротким скапусом антенн. Составлена определительная таблица видов *Cataglyphoides*.

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КЛЮЧЕВЫЕ СЛОВА. *Cataglyphoides dluskyi* sp.n., *C. constrictus*, *C. intermedius*, ископаемые, таксономия, триба Formicini, эволюция.

## Introduction

Mayr (1868) described from the Baltic amber a new extinct species, *Camponotus constrictus*. Later on it was transferred to *Formica* Linnaeus, 1758 by Wheeler (1915) and then — to *Cataglyphis* Foerster, 1850 by Dlussky (1967). At last, Dlussky (2008) established a new extinct genus *Cataglyphoides* and designated *C. constrictus* as the type species of this genus.

*Cataglyphoides* belongs to the tribe Formicini of the subfamily Formicinae and morphologically resembles the extant genus *Cataglyphis*. Particularly, *Cataglyphoides* species have long and slender body and appendages, long 6-segmented maxillary and 4-segmented labial palps, long apical mandibular tooth that ca. twice as long as the preapical one, petiole is nodiform or with wide subrectangular scale. Nevertheless, *Cataglyphoides* differs from *Cataglyphis* by the lack of psammophore and relatively shorter, not slit-like propodeal spiracles (Dlussky, 2008).

Till now, two fossil species from the Baltic amber were attributed to *Cataglyphoides*: *C. constrictus* and *C. intermedius* Dlussky, 2008. Recently we found one specimen from the Rovno amber that we describe below as a new species, *C. dluskyi* sp.n. Additionally, we found one more specimen of *C. constrictus* from the Baltic amber and provided some additions to its morphology, as well as measurements and photographs. At last, we compiled a Key for identification of all known species of this genus.

## Material and methods

We examined two workers from two pieces of amber, belonging to the genus *Cataglyphoides*: one worker of *C. constrictus* (Mayr, 1868) from the Baltic amber, and one worker (the holotype) of *C. dluskyi* sp.n. from the Rovno amber. The first one is deposited in the private collection of Mr. Carsten Gröhn (CCG); this collection will be separately deposited in the Geologisch-Paläontologisches Institut der Universität Hamburg (GPIH; now — Centrum of Natural History, CeNak), and the holotype specimen of *C. dluskyi* is deposited in the Schmalhausen Institute of Zoology of NAS of Ukraine, Kiev (SIZK); the photographs of two specimens of *C. constrictus* taken by G.M. Dlussky in 2007 were also used; these specimens with Nos. 04170 and 04173 are preserved in the collection of Geowissenschaftlichen Zentrum der Georg-August-Universität Göttingen Germany (GZG. BST) (for details see Dlussky, 2008).

The holotype specimen of *C. dluskyi* sp.n. was fossilized in the large piece of amber weighing after primary treatment ca. 210 g together with 11 specimens of Dolichopodidae, four Sciaridae, one Phoridae (Diptera), two Hymenoptera, one Lepidoptera, one Isoptera and two Acari.

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

Not all features of the examined specimens were properly visible and measurable, hence we

measured only visible details (accurate to 0.01 mm), particularly: CL — length of the clypeus, measured medially between its anterior and posterior margins; FSL-1...FSL-11 — length of the funicular segments from 1 to 11; FSW-1...FSW-11 — width of the funicular segments from 1 to 11; GL — length of the genae, measured from the anterior margin of the eyes to the articulation with the mandible; 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; HTL — maximum length of the hind tibia; HW — maximum width of the head in dorsal view behind (above) the eyes; MdL — length of the mandible, measured from its tip to articulation with the head; ML — diagonal length of the mesosoma in lateral view from the anterior margin of the neck shield to the posterior margin of the metapleuron; OL — maximum diameter of the eye; PnW — width of the pronotum in dorsal view; 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 virtual line between the tip of subpetiolar process and posteroventral points of petiole; SL — maximum length of the scape measured in a straight line from its apex to the articulation with condylar bulb.

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

For simplicity, we give ratios of various measurements (e.g. HL/HW) rather than name and abbreviate various indices (e.g. CI — cephalic index).

## Results

### *Cataglyphoides dluskyi* sp.n.

Fig. 1A–E.

**MATERIAL.** Holotype, worker, complete specimen, Ukraine, Rovno Prov., Volodymerets Distr., vicinity of vil. Voronky, Rovno amber, late Eocene, Priabonian, 33.9–37.8 Ma, SIZK No. L-121 (AntWeb CASENT No. 0917593).

**DESCRIPTION.** Worker. Total length ca. 8.65 mm. Head ca. 1.2 times as long as broad, with slightly convex sides, widely rounded but with well marked occipital corners, and almost straight occipital margin. Eyes of moderate size, oval, convex, situate only a little behind midlength of sides of head, so that maximum diameter of eye somewhat longer than genae. Ocelli distinct but quite small, forming equilateral triangle. Frontal carinae slightly divergent, rather short, reaching at most level of midlength of eyes. Frontal triangle distinct. Frons with longitudinal carina, reaching frontal ocellus. Clypeus long, 0.33 of head length, without median longitudinal carina, its surface somewhat depressed laterally, anterior margin gradually widely rounded. Mandibles long, ca. 0.6 times as head length, with eight sharp unequal teeth, apical tooth ca. twice as long as preapical one. Maxillary and labial palps obscured in holotype specimen. Antennae inserted close to posterior clypeal margin. Antennal scapes longer than head, surpassing occipital margin for half of its length; they very smoothly curved at base and somewhat expanded at tips. Antennae without apical club, first funicular segment is longest, subsequent segments gradually decreasing in length, preapical one is shortest, but apical segment subequal to third one; at the same time, they increasing in width starting from eighth one, and apical segment is widest (for more details see measurements and ratios, below).

Mesosoma long, low and slender, pronotum moderately convex, mesonotum somewhat flattened, slightly raised over level of pronotum, sloping posteriorly; metanotum short, horizontal, confluent with propodeal dorsum. Metathoracic spiracles situated dorsally and partly concealed by well developed tubercles. Propodeal spiracles big, elongate-oval (but not slit-shaped), they located not close to margin between lateral and posterior surfaces of propodeum. Petiole with very short anterior peduncle, slightly longer than height, nodiform, with convex anterior surface that gradually merges with almost flat posterior one. Legs long and slender, length of hind tibia subequal to length of mesosoma and ca. 1.4 times as head length. Middle and hind tibiae

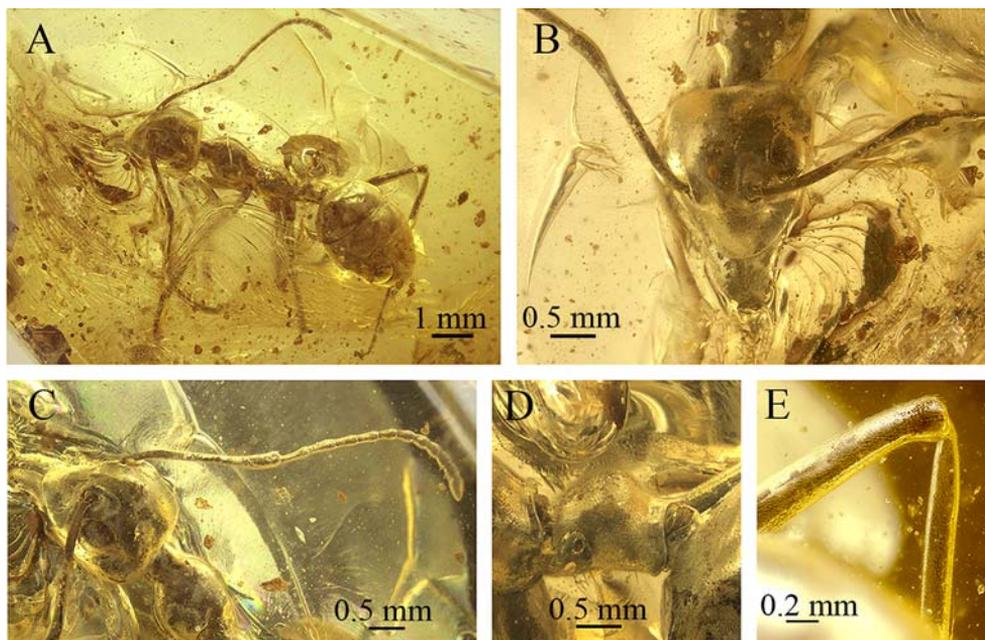


Fig. 1. Microphotographs of details of structures of *Cataglyphoides dlusskyi* sp.n., holotype worker. A — body in dorso-lateral view; B — head in dorsal view; C — head and antenna in dorso-lateral view; D — petiole in dorso-lateral view; E — part of hind femur and tibia (photo by E. Martynova).

Рис. 1. Микрофотографии деталей строения *Cataglyphoides dlusskyi* sp.n., голотип, рабочий. А — тело в верхне-боковом положении; В — голова сверху; С — голова и антенна в верхне-боковом положении; D — петиолюс в верхне-боковом положении; E — часть заднего бедра и голени (фото Е. Мартыновой).

with simple spur. Hind coxae close together in ventral view, when coxae directed outwards their inner margins touch or almost touch each other. Tarsal claws simple, without additional tooth, pulvillae well developed.

Whole body and appendages with very fine but dense decumbent pubescence. Body surface densely but not coarsely superficially punctated, mandibles with very dense and quite coarse longitudinal rugulosity. Head, mesosoma, petiole and gaster without standing hairs. Scapes, femora and tibiae with very fine, short, whitish subdecumbent to suberect hairs, only tarsal segments with coarse short bristles on inner (flexor) margin.

MEASUREMENTS (in mm) and RATIOS: HL 1.95, HW — ca. 1.63 (barely measurable), SL — 2.24, OL — 0.62, GL — 0.52, CL — 0.65, MdL 1.14, ML — 2.86, PnW — ca. 1.04 (barely measurable), PL — 0.65, PH — ca. 0.55 (barely measurable), HTL — 2.68, gaster L — ca. 3.20,

FSL-1 0.43, FSL-2 0.39, FSL-3 0.33, FSL-4 0.29, FSL-5 0.26, FSL-6 0.22, FSL-7 0.22, FSL-8 0.22, FSL-9 0.21, FSL-10 0.21, FSL-11 0.31, FSW-1 0.14, FSW-2 0.16, FSW-3 0.15, FSW-4 0.14, FSW-5 0.14, FSW-6 0.14, FSW-7 0.14, FSW-8 0.18, FSW-9 0.20, FSW-10 0.20, FSW-11 0.21;

HL/HW — ca. 1.2, SL/HL — 1.15, SL/HW — ca. 1.35, OL/HL — 0.32, GL/OL — 0.83, CL/HL — 0.33, MdL/HL 0.59, PL/PH — ca. 1.20, PL/HL — 0.33, ML/PnW — ca. 2.75, ML/HTL 1.07, HTL/HL 1.37; FSL-1/FSW-1 — 3.00, FSL-2/FSW-2 — 2.50, FSL-3/FSW-3 — 2.17, FSL-4/FSW-4 — 2.00, FSL-5/FSW-5 — 1.82, FSL-6/FSW-6 — 1.55, FSL-7/FSW-7 — 1.55, FSL-8/FSW-8 — 1.21, FSL-9/FSW-9 — 1.07, FSL-10/FSW-10 — 1.07, FSL-11/FSW-11 — 1.50.

Queens and males unknown.

ETYMOLOGY. The species is dedicated to eminent Russian myrmecologist Prof. G.M.

Dlussky (1937–2014), who established genus *Cataglyphoides*.

COMPARISON. *C. dlusskyi* well differs from *C. intermedius* by the shape of the petiolar node: it is nodiform in the first species, and much higher, subrectangular in the latter one; the scapes in *C. dlusskyi* are longer than head, but they are shorter than head in *C. intermedius* (SL/HL 1.15 vs. 0.91); the body of *C. dlusskyi* is more slender with the shallow metanotal groove, which is much deeper in the latter species. On the other hand, by the general shape of the body *C. dlusskyi* resembles *C. constrictus*, but differs from it by a set of morphological features, particularly: the eyes situated more anteriorly so that the genae are shorter than maximum diameter of the eye: GL/OL 0.83 vs. 1.3 in *C. constrictus*; the clypeus lacks medial carina; the apical funicular segment is shorter than first to third segments each, but it is the longest in *C. constrictus*; the head, mesosoma, waist and gaster of *C. dlusskyi* are without standing hairs, the scapes, femora and tibiae with very fine, short, whitish subdecumbent to suberect hairs, but the head of *C. constrictus* possess several quite long coarse erect standing hairs, the gaster covered by the more abundant similar hairs, scapes and legs with shorter suberect to erect coarse, bristle-like hairs.

***Cataglyphoides constrictus* (Mayr, 1868)**

Fig. 2A–D.

MATERIAL. 1 worker, Baltic amber, Priabonian stage, 33.9–37.8 Ma, collection of Mr. Carsten Gröhn No. F-6572.

Mayr (1868) described *C. constrictus* based on five workers, but Wheeler (1915) supposed that one of them probably belongs to the genus *Pseudolasius* Emery, 1887 and named this specimen *P. seltatus* sp. nov., although this name is nomen nudum. Andre (1895) recorded two more specimens, and Wheeler (1915) investigated 12 additional workers of this species. Dlussky (2008) re-examined two of the Mayr's type specimens and designated one of them as the lectotype, as well as 10 workers, part of which were previously identified by Wheeler as *C.*

*constrictus*. Thus, 18 specimens of this species were known till now.

We investigated one worker from the Baltic amber from the collection of Mr. Carsten Gröhn, which was determined by Dlussky in 2013 as *C. constrictus*, and confirm this identification. It seems the first new finding of this species in more than 100 years.

Mayr (1868) provided quite comprehensive description of this species, and later it was redescribed twice: by Wheeler (1915) and by Dlussky (2008), but there are some discrepancies in the descriptions of Mayr and Wheeler on the one hand, and of Dlussky on the other hand.

Thus, Mayr (1868) noted that the body of *C. constrictus* is with the very fine decumbent pilosity (“Die anliegende Pubescenz ist Sehr fein”; loc. cit.: 29), but Wheeler (loc. cit.: 129) wrote only that “Surface shining, finely shagreened and sparsely and superficially punctate”, and Dlussky (loc. cit.: 47) noted that “The decumbent pubescence is not visible on any of the studied specimens”. However, the whole body of the investigated by us specimen covered by the dense and fine decumbent pubescence.

Both Mayr and Wheeler noted that the clypeus of *C. constrictus* is with the distinct longitudinal medial carina, but Dlussky (loc. cit.: 46) stressed that “The clypeus is with rounded anterior margin, without medial carina”. We may only suppose that this was a simple typing error, since the medial clypeal carina is very clearly visible on the Dlussky's original photos of the specimen with number 04170 (= B5195 in the Wheeler's paper), which he kindly gave us at the end of the 2000s. Anyway, the medial clypeal carina well developed in the specimen investigated by us.

Lastly, both Mayr and Wheeler noted that the body (or at least gaster) of this species covered by the coarse erect hairs, while they did not specify more detail what parts of body have hairs. Dlussky (2008) pointed out that there are some hairs on the head, but “The mesosoma, petiole and two basal gastral tergites lack standing hairs” (loc. cit.: 47). Character of the body pilosity of the investigated by us specimen mostly

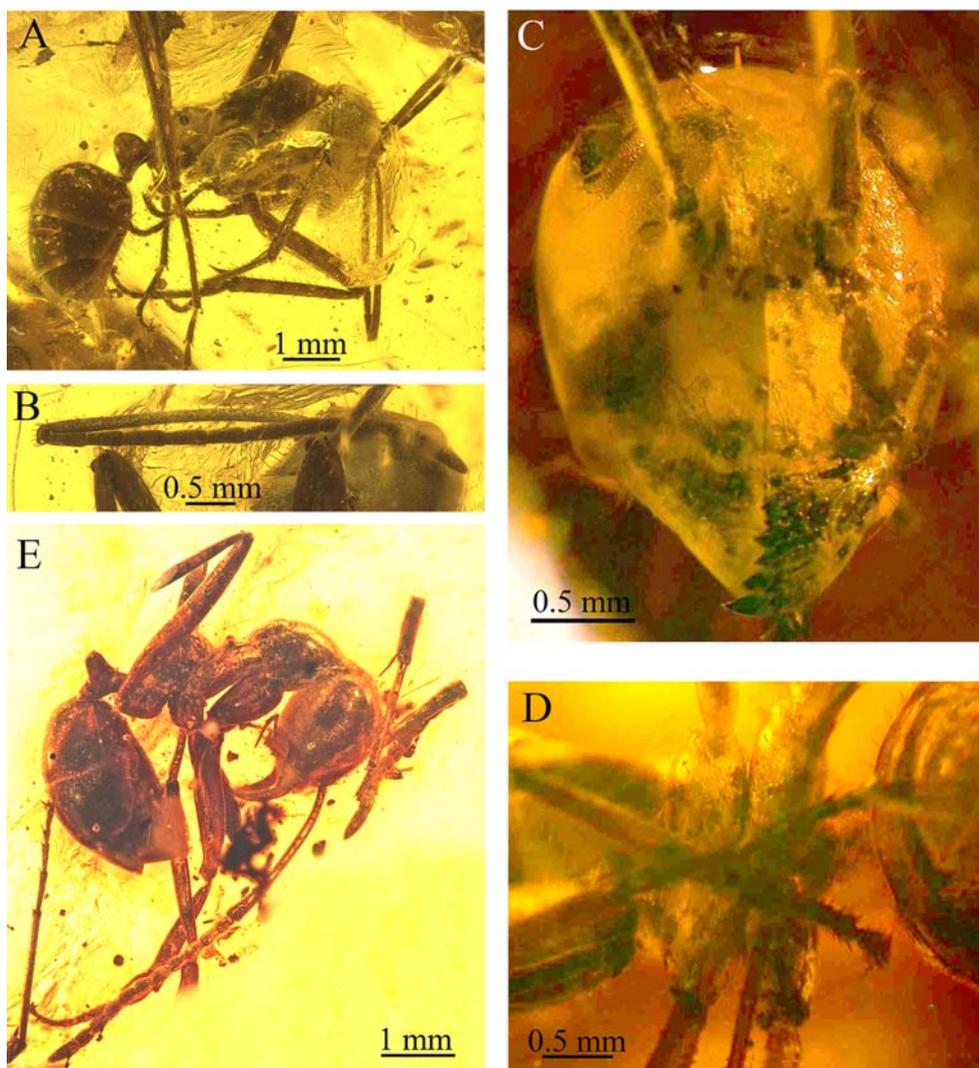


Fig. 2. Microphotographs of details of structures of *Cataglyphoides constrictus* (Mayr, 1868), workers (A–D; A, B — specimen No. F-6572 CCG; C — specimen No. 04170 GZG.BST, D — specimen No. 04173 GZG.BST) and *C. intermedius* Dlussky, 2008 (E), holotype worker. A, E — body in lateral view; B — antenna; C — head in dorsal view; D — middle and hind coxae in ventral view (A, B — photo by E. Martynova; C–E — photo by G. Dlussky, 2007).

Fig. 2. Микрофотографии деталей строения *Cataglyphoides constrictus* (Mayr, 1868), рабочие (A–D; A, B — экземпляр No. F-6572 CCG; C — экземпляр No. 04170 GZG.BST, D — экземпляр No. 04173 GZG.BST) и *C. intermedius* Dlussky, 2008 (E), голотип, рабочий. A, E — тело сбоку; B — антенна; C — голова сверху; D — средние и задние коксы снизу (A, B — фото Е. Мартыновой; C–E — фото Г.М. Длусского, 2007 г.).

agree with Dlussky's description, but all gastral tergites and sternites covered by the coarse standing hairs.

Summarizing all available data we propose the brief diagnosis of *C. constrictus*:

– hind coxae close together in ventral view, when coxae directed outwards their inner margins touch or almost touch each other (Fig. 2, D).

– head suboval, with barely marked occipital corners;

– eyes situate far behind the midlength of the sides of head, length of the genae 1.3–1.4 times of the maximum diameter of the eyes;

– antennal scapes ca. 1.5 times as the head length, surpassing the occipital margin more than half of its own length;

– first to fifth funicular segments more than 2.5 times as their width, apical segment the longest;

– clypeus with the distinct median longitudinal carina;

– petiole nodiform;

– whole body with the dense and fine decumbent pilosity;

– head with the several coarse standing hairs, mesosoma and petiole without hairs, all gastral tergites and sternites with coarse standing hairs;

– antennal scapes and legs with abundant, short, coarse bristle-like standing hairs that are especially abundant on the tarsi.

Below are measurement (in mm) and ratios of the investigated specimen: total length 9.36, HL 2.08, SL 3.04, OL 0.30, GL 0.83, MdL 0.88, ML 3.38, PL 0.78, PH 0.70, HTL 3.38, FSL-1 0.39, FSL-2 0.35, FSL-3 0.39, FSL-4 0.37, FSL-5 0.37, FSL-6 0.35, FSL-7 0.34, FSL-8 0.34, FSL-9 0.33, FSL-10 0.29, FSL-11 0.57, FSW-1 0.13, FSW-2 0.13, FSW-3 0.13, FSW-4 0.14, FSW-5 0.14, FSW-6 0.14, FSW-7 0.16, FSW-8 0.16, FSW-9 0.16, FSW-10 0.16, FSW-11 0.16; SL/HL 1.46, OL/HL 0.29, GL/OL 1.39, MdL/HL 0.43, PL/PH 1.11, PL/HL 0.38, ML/HTL 0.95, FSL-1/FSW-1 — 3.00, FSL-2/FSW-2 — 2.70, FSL-3/FSW-3 — 3.00, FSL-4/FSW-4 — 2.64, FSL-5/FSW-5 — 2.64, FSL-6/FSW-6 — 2.45, FSL-7/FSW-7 — 2.17, FSL-8/FSW-8 — 2.17, FSL-9/FSW-9 — 2.08, FSL-10/FSW-10 — 1.83, FSL-11/FSW-11 — 3.67.

#### KEY FOR IDENTIFICATION OF *CATAGLYPHOIDES* SPECIES (WORKERS)

1. Petiole with thick, quite high, subrectangular scale.

Antennal scapes shorter than head, surpass occipital margin less than half of its own length.

Mesosoma shorter and stouter, pronotum more convex, metanotal groove deep (Fig. 2E) .....

..... *C. intermedius* Dlussky

– Petiole nodiform. Antennal scapes longer than head, surpass occipital margin more than half of its own length. Mesosoma longer and more slender, pronotum less convex, metanotal groove shallow (Figs 1A–D, 2A, B) ..... 2

2(1) Head suboval, with barely marked occipital corners; eyes situate far behind the midlength of sides of head, genae longer than maximum diameter of eyes (GL/OL 1.3–1.4); clypeus with distinct median longitudinal carina (Fig. 2C).

Head with a few standing hairs, gaster with abundant similar hairs; antennal scapes and legs with abundant, short, coarse bristle-like standing hairs (Fig. 2A, B) .... *C. constrictus* (Mayr)

– Head with widely rounded but well marked occipital corners; eyes situate only a little behind midlength of sides of head, genae shorter than maximum diameter of eyes (GL/OL 0.83); clypeus without median longitudinal carina (Fig. 1B). Head and gaster without standing hairs (Fig. 1A–C). Antennal scapes, femora and tibiae with very fine, short, whitish subdecumbent to suberect hairs, only tarsal segments with row of coarse short bristles on inner margin (Fig. 1A, E)

..... *C. dluskyi* sp.n.

## Discussion

Dlussky (2008) attributed *Cataglyphoides* to the tribe Formicini. This tribe includes eight extant (*Alloformica* Dlussky, 1969, *Bajcaridris* Agosti, 1994, *Cataglyphis* Foerster, 1850, *Formica* Linnaeus, 1758, *Iberoformica* Tinaut, 1990, *Polyergus* Latreille, 1804, *Proformica* Ruzsky, 1902 and *Rossomyrmex* Arnoldi, 1928), and three extinct (*Cataglyphoides*, *Conoformica* Dlussky, 2008 and *Protoformica* Dlussky, 1967) genera from the late Eocene European ambers.

Different authors have diagnosed Formicini by a combination of various morphological features (Agosti, 1990, 1994; Agosti, Bolton, 1990; Bolton, 2003; Dlussky, 2008; Ward *et al.*, 2016), the most distinctive of which, to our opinion, are: metacoxae are closely approximated, when coxae directed outward, their inner margins touch or almost touch each other; metatibiae are with a double row of stout setae (bristles); propodeal spiracles are elliptical to slit-shaped and located on a distance from the margin between the lateral and posterior surfaces of propodeum; eyes located behind the midlength of sides of head; ocelli in workers present; antennae 12-segmented (13-segmented in males), inserted close to the posterior margin of clypeus.

Nevertheless, any of the mentioned characters cannot be considered as a true synapomor-

phy for this tribe, and occurred in various combinations in other tribes of Formicinae. Moreover, some of these traits are absent in the extant socially parasitic genera (*Polyergus* and *Rossomyrmex*); in *Conoformica* ocelli are absent and propodeal spiracles are small and rounded, and tibiae lack row of the coarse setae in *C. intermedius* and *C. dluskyi* sp.n.

Beside three extinct Formicini genera, nine “good” fossil *Formica* species are known from the late Eocene European ambers. Despite some of them are superficially similar to several extant species, in general all late Eocene *Formica* constitute quite an archaic group and any of them most probably cannot be considered as a direct ancestor of modern species. *Protoformica* by the set of characters is intermediate between the extant genera *Alloformica*, *Formica*, *Proformica* and *Cataglyphis* and also cannot be considered as an ancestor of any of the mentioned genera; *Conoformica* has no analogues in the modern fauna at all (Dlussky, 2008).

At the same time, Dlussky (2008) supposed that *Cataglyphoides* may well be regarded as the ancestral with respect to *Cataglyphis*, but we disagree with this opinion.

*Cataglyphoides* species are quite specialized compare to contemporaneous Formicini genera. Particularly, *C. constrictus* and *C. dluskyi* have nodiform petiole; although the petiole of *C. intermedius* is less specialized having thick, high, subrectangular scale, by its structure it is also well differs from any other late Eocene Formicini genera.

That is *Cataglyphoides* by the structure of petiole resembles species from the some species-groups of *Cataglyphis*. Particularly, *C. constrictus* and *C. dluskyi* are similar to or even intermediate between advanced *bicolor*- and *albicans*-groups, and *C. intermedius* resembles species of quite specialized *altisquamis*-group. But the fact is that the most primitive *Cataglyphis* species have petiole with the vertical, often quite thin, scale (Dlussky, 1981; Radchenko, 2001). Thus, fossil *Cataglyphoides* species cannot be considered as ancestral of the basic modern *Cataglyphis* species, and, consequently, of this genus at all.

*Cataglyphoides* seems to be specialized extinct genus and morphological similarity with

*Cataglyphis* could be result of convergent evolution. Based on the main morphological features of it species (the long body and appendages, petiolar structure) we may speculate that they were arboreal.

Relative scarcity (totally only 23 specimens) could be due to two reasons: real rarity and small colonies, and large size of workers, which more rarely trapped to resin than much smaller other arboreal dwellers with big colonies, e.g. *Lasius* Fabricius, 1804, *Ctenobethylus* Brues, 1939, *Yantaromyrmex* Dlussky et Dubovikoff, 2013, etc.

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