

A NEW EXTINCT ANT GENUS (HYMENOPTERA: FORMICIDAE) FROM BALTIC AMBER

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Abstract.— A new extinct genus and species from the subfamily Dolichoderinae, *Dlusskyus groehni* gen. et sp. nov., is described based on the single male from Baltic amber (late Eocene, 37.8–33.9 Ma). It differs from all extant and extinct Dolichoderinae genera in the following combination of features: antennae 13-segmented, scape shorter than the second funicular segment, which is the longest; palp formula 6, 4; clypeus not inserted between frontal carinae, frontal triangle well outlined and separated from clypeus by suture; clypeus with longitudinal median carina, its anterior margin very weakly convex, without medial notch; mandibles crossing when closed, masticatory margin long, with two minute sharp apical and preapical teeth and a row of minute sharp denticles, serrate; scutum without notauli; petiole nodiform, with short peduncle; meso- and metatibiae with large simple spur; pretarsal claws without preapical tooth; posterior margin of pygidium with median tooth; subgenital plate with very shallow median notch; pygostyles present; stipites of genitalia very weakly curved, narrow, with rounded apices, telomeres not strongly elongated; forewings with closed cells $1r+2r$, $3r$, rm and mcu ; jugal lobe absent. The taxonomic position of this genus is discussed.



Key words.— *Dlusskyus groehni* gen. et sp. nov., late Eocene, Europe, *Paraneuretus tornquisti*, males, Dolichoderinae, Aneuretiniae, morphology, paleontology

INTRODUCTION

The ant fauna of late Eocene European (i.e. Baltic, Danish, Bitterfeld and Rovno) ambers (37.8–33.9 Ma) is the best studied among all fossil myrmecofaunas of the world. After the publication of Wheeler's (1915) monographic work, almost until the beginning of the 21st century little has been added to the study of ants from late Eocene European ambers, but over the past 20 years 14 new genera and about 90 new species have been described from these ambers (Dlussky 2002a, b, 2008a, b,

2009, 2010; Dlussky and Perkovsky 2002; Dlussky and Radchenko 2006a, b, 2009, 2011; Radchenko and Perkovsky 2009, 2020; Dlussky and Dubovikoff 2013; Dlussky *et al.* 2014; Radchenko *et al.* 2007, 2018, 2019, 2021; Radchenko and Dlussky, 2012, 2013a, b, 2015, 2016, 2017a, b, 2018a, b, c, 2019; Chény *et al.* 2019; Dubovikoff *et al.* 2019, 2020; Radchenko and Khomych 2020; Radchenko 2020, 2021; Radchenko and Proshchalykin 2021; Dubovikoff and Zharkov 2022). As a result, about 18,000 ant specimens have been studied, and 177 described species from 63 genera of 12 subfamilies

have been registered so far (Dlussky and Rasnitsyn 2009; Perkovsky 2016; Radchenko and Khomych 2022).

The subfamily Dolichoderinae was represented in late Eocene European ambers by seven genera and 38 species, which accounted for 11% and 21% of all amber ant genera and species, respectively. Furthermore, the genus *Dolichoderus* Lund, 1831 was the most diverse among all amber genera, numbering 25 species, and dolichoderine *Ctenobethylus goepperti* (Mayr, 1868) accounted for about 45% of the collected specimens (Dlussky and Rasnitsyn 2009, with my additions).

I found one male specimen in a piece of Baltic amber, which clearly differs from all known extinct and extant Dolichoderinae, and decided to describe it as a new genus and species – *Dlusskyus groehni* gen. et sp. nov.

MATERIAL AND METHODS

I examined one male specimen (holotype), belonging to the new genus *Dlusskyus* gen. nov. from Baltic amber. It is stored at the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg (LIB) (former Centre of Natural History of the University of Hamburg; former Geological-palaeontological institute of University Hamburg). The original photographs were taken with a Leica Z16 APO microscope equipped with a Leica DFC 450 camera and processed by LAS Core software, and line drawings were made based on the photographs.

Not all features of the examined specimen were properly visible and measurable, hence I measured only the visible details (with an accuracy of 0.01 mm), in particular:

HL – maximum length of the head in dorsal view, measured in a straight line from the anterior-most point of clypeus to the mid-point of occipital margin;

HW – maximum width of the head in dorsal view behind (above) the eyes;

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

OL – maximum diameter (=length) of the eye;

GL – length of the genae, measured from the anterior margin of the eyes to the articulation with the mandible;

CpL – length of the clypeus, measured medially between its anterior and posterior margins;

MdL – length of the mandible, measured from its tip to articulation with the head;

ML – length of the mesosoma in dorsal view from the anterior end of scutum to the point of articulation with petiole;

ScL – length of the scutum+scutellum in dorsal view;

ScW – maximum width of the scutum in dorsal view;

PL – maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;

PNdL – length of the petiolar node;

HTL – maximum length of the metatibia;

FWL – maximal length of the forewing;

FWW – maximal width of the forewing;

GAL – length of the gaster;

FSL-1...12 – length of the funicular segments from 1 to 12;

MPL-3...6 – length of the segments of maxillary palps from 3 to 6.

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

For simplicity, I give ratios of various measurements (e.g. HL/HW) rather than naming and abbreviating various indices (e.g. CI – cephalic index).

The nomenclature of the wing venation is given according to Dlussky (2009) and Dlussky and Perfilieva (2014). Two indices characterizing important features of the venation of the forewings are used: $I_{Cu} = [1Cu + (2M+Cu)] / 1Cu$, $I_{CuA} = [(1M+Cu) + (2M+Cu)] / (1M + Cu)$ (for details see Dlussky and Perfilieva 2014).

TAXONOMY

Subfamily Dolichoderinae Forel, 1878

Genus *Dlusskyus* gen. nov.

Type species. *Dlusskyus groehni* sp. nov., by monotypy.

Diagnosis. Male. Antennae 13-segmented, inserted into head very close to posterior clypeal margin; scape shorter than second funicular segment; funiculus without apical club, first funicular segment not globular, second funicular segment the longest, length of following segments gradually decreased, 5–11 segments subequal in length, apical segment 1.4 times as long as preceding one; whole antennae long, surpassing base of gaster when directed backward. Frontal lobes narrow, subvertical, antennal sockets almost completely exposed. Maxillary palps does not fully visible, but based on length of four terminal segments and position of palps, they seem 6-segmented, labial palps 4-segmented. Clypeus does not insert between frontal carinae, frontal triangle well outlined and separated from clypeus by suture. Clypeus with median longitudinal carina, its anterior margin very slightly convex, without medial notch. Eyes big, situated not far from posterior clypeal margin, their inner margin weakly convex. Mandibles elongate-triangular, crossing when closed; masticatory margin long, with two minute but sharp apical and preapical teeth and row of minute sharp denticles, serrate; masticatory margin well separated

from basal one by angle (but without basal tooth), basal margin without denticles. Scutum without notaui. Petiole nodiform, with short peduncle. Meso- and metatibiae with big simple spur, which is distinctly longer than maximal width of tibia; pretarsal claws without preapical tooth on inner margin. Posterior margin of pygidium with median tooth. Posterior margin of subgenital plate with very shallow median notch. Pygostyles present. Stipites of genitalia very feebly curved, narrow, with rounded apices, telomeres not strongly elongated. Forewing with closed cells $1r+2r$, $3r$, rm and mCu ; jugal lobe absent.

Etymology. The genus is dedicated to the memory of outstanding myrmecologist and paleoentomologist G. M. Dlussky (1937–2014).

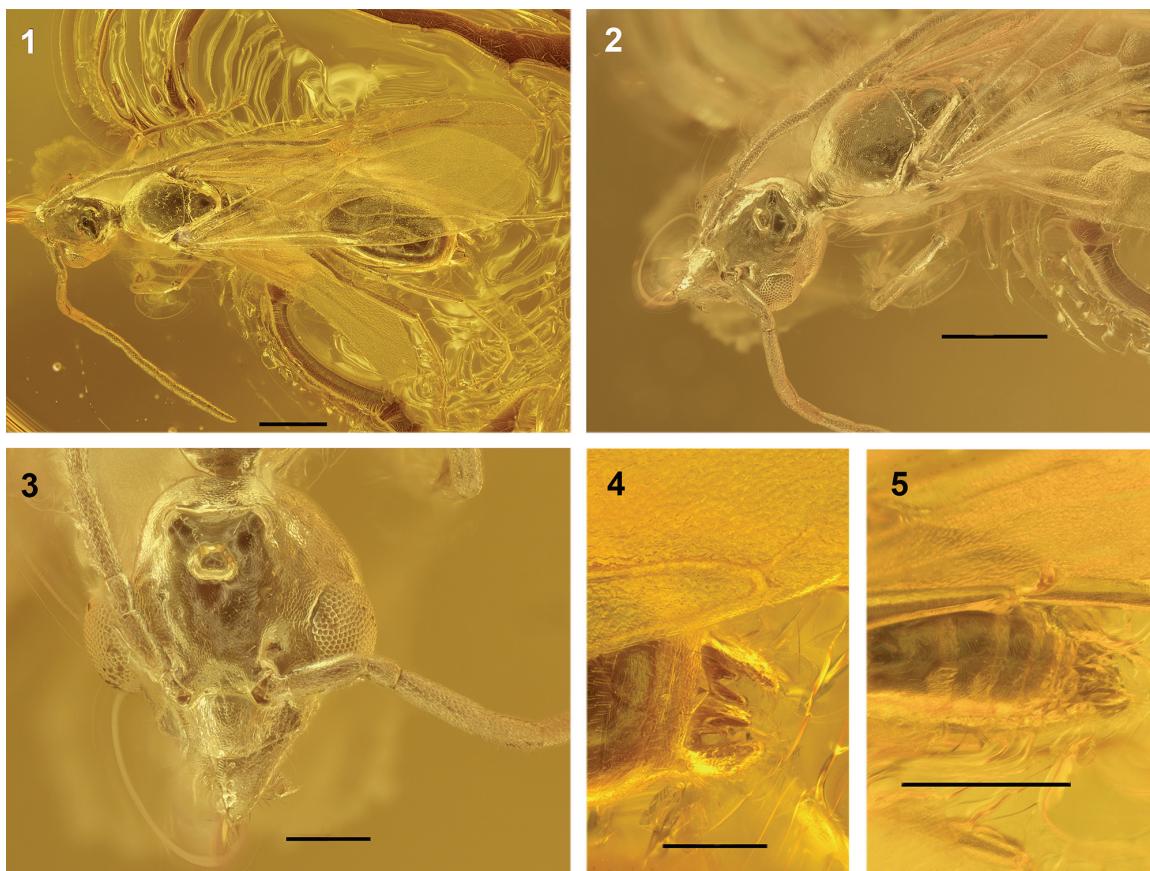
***Dlusskyus groehni* sp. nov.**
(Figs 1–8)

Locality. Poland, Baltic amber, Late Eocene, Priabonian stage, 33.9–37.8 Ma.

Description. Body length ca. 3.3 mm. Head slightly longer than wide, smoothly rounded above eyes,

occipital corners not marked, occipital margin convex. Antennal scape ca. 0.3 times as long as head. Eyes ca. 0.4 times as long as head. Ocelli big, forming equilateral triangle. Genae short, ca. 0.3 times as long as eyes. Mandibles 0.45 times as long as head. Mesonotum slightly convex, propodeum lying somewhat lower than mesonotum (seen in profile). Scutum width ca. 0.75 times the length of scutum+scutellum. Propodeum barely visible, but seems rounded, without tubercles or teeth. Gaster elongate-oval, ca. twice as long as wide. Body finely sculptured. Head dorsum, scutum and scutellum with superficial microreticulation, scutum additionally with scattered piligerous pits, frons, area near ocelli, and gaster almost smooth and shiny. Occipital margin with a few long, erect, somewhat curved hairs, anterior clypeal margin and mandibles with shorter erect to suberect hairs. Head, mesonotum and gaster without decumbent pubescence, clypeus, antennae and legs with a very dense, short depressed pubescence.

Character of forewing venation: vein section $1RS$ vertical, merging with vein R at a right angle; cross-vein $2r+rs$ vertical, merging with vein RS at a right angle; cross-veins $2r+rs$ and $rs-m$ coincide on vein RS



Figures 1–5. Photos of *Dlusskyus groehni* gen. et sp. nov., male, holotype: (1) body, dorsal view; (2) head and mesosoma, dorso-lateral view; (3) head, dorsal view; (4) genitalia, dorsal view; (5) genitalia, ventral view. Scale bars: 1, 2, 5 – 0.5 mm, 3, 4 – 0.2 mm.

(vein section $4RS$ is absent); cell $3r$ relatively short, 1.15 times as long as cell $1+2r$ and 0.24 times as long as wing, far not reaching distal wing margin; cell rm subtriangular (vein section $2M$ is absent), ca. 3 times as long as wide, not pedicellate, far not reaching distally level of pterostigmal apex; cell mcu almost trapezoid, ca. 1.2 times as long as wide, not reaching distally level of pterostigmal base; cell cua absent; vein section $2Cu$ very long, almost reaching posterior margin of wing, curved but not angulated basally and does not confluent with vein A ; vein section $4M$ straight and long, almost reaching posterior margin of wing; cross-vein $cu-a$ merging with vein section $1M+Cu$ not too close to cell mcu , vein section $2M+Cu$ subequal to $1Cu$ and 1.7 times as long as cross-vein $cu-a$; $Icu = 1.94$, $Icua = 1.36$.

Hind wings venation: free medial section Cu slightly curved; cross-vein $rs-cu$ very slightly curved; veins $R1$ absent; vein R , cross-vein $rs-cu$ and vein section $2RS$ diverge from same knot; cross-vein $cu-a$ located approximately at midlength between base of wing and branching of $rs-cu$ and Cu , so that vein sections $1M-Cu$ and $2M-Cu$ subequal in length.

Measurements (in mm) and ratios: HL 0.73, HW

0.65, SL 0.21, OL 31, GL 0.10, CpL 0.20, MdL 0.33, PL 0.23, PNdL 0.13, ML 1.17, ScW 0.56, Sc+SctL 0.75, HTL 0.62, FWL 2.63, FWW 0.86, GAL 1.15, FSL-1 0.10, FSL-2 0.30, FSL-3 0.21, FSL-4 0.20, FSL-5...7 0.17, FSL-8...11 0.16, FSL-12 0.22, width of all antennal segments ca. 0.08, MPL-3 0.10, MPL-4 0.14, MPL-5 0.13, MPL-6 0.8;

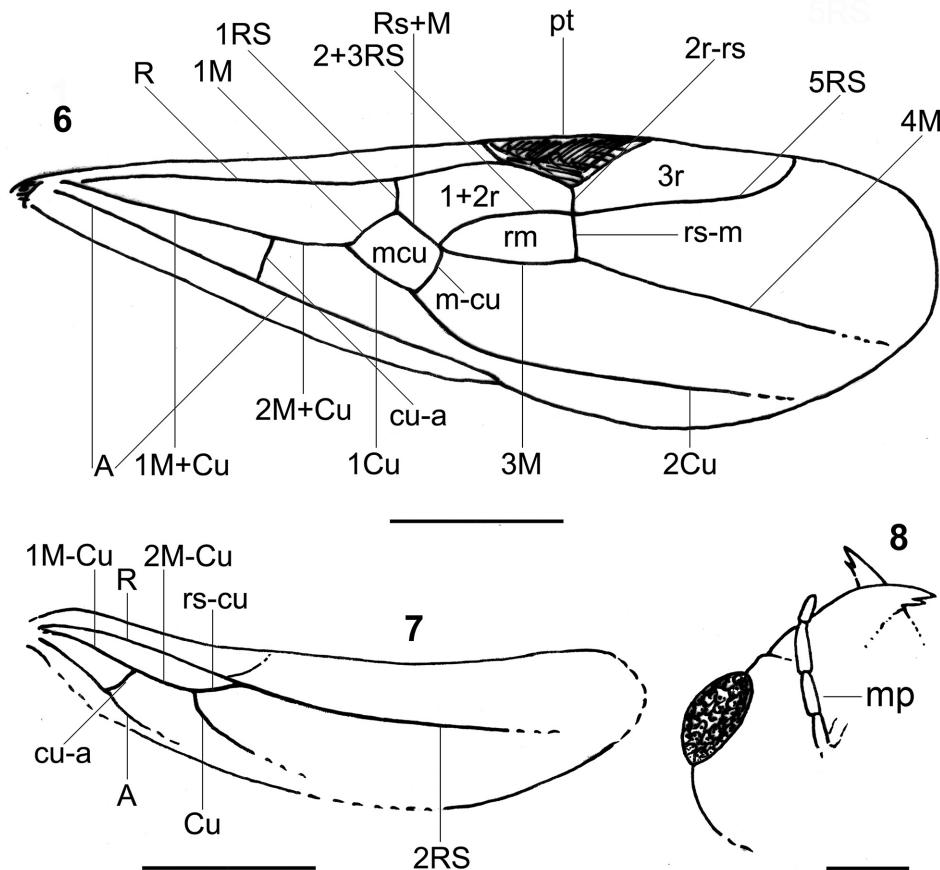
HL/HW 1.12, SL/HW 0.29, SL/FSL-2 0.70, OL/HW 0.43, GL/OL 0.33, CpL/HW 0.27, MdL/HW 0.45, PL/HW 0.32, PL/PNdL 1.8, ML/ScW 2.09, ScL/ScW 1.35, ML/HTL 1.88, HTL/HW 0.86.

Workers and gynes. Unknown.

Type material. Holotype male, complete specimen, GPIH 5072 (CCGG 6742) (AntWeb CASENT0917557) (LIB).

Etymology. The species is dedicated to Mr. Carsten Gröhn (Glinde, Germany), who kindly provided the holotype specimen for investigation.

Comparative diagnosis. Based on the combination of one-segmented petiole and the gaster without constriction between the first and second segments (= III and IV abdominal segments) *Dlusskyus* belongs to the formicomorph group of subfamilies (sensu Bolton 2003), which include the Formicinae Latreille,



Figures 6–8. Line drawings of *Dlusskyus groehni* gen. et sp. nov., male, holotype: (6) forewing; (7) hind wing; (8) part of head, ventral view, mp – maxillary palps. Scale bars: 6, 7 – 0.5 mm, 8 – 0.2 mm.

1809, Dolichoderinae and Aneuretinae Emery, 1913. The forewings of *Dlusskyus* have closed cells $1+2r$, $3r$, rm and mCu , which are found in all known extant and extinct genera of Aneuretinae and in many Dolichoderinae. On the contrary, the closed cell rm is absent in all Formicinae genera what rules out *Dlusskyus* belonging to this subfamily.

The forewings with the four closed cells mentioned are found, at least in part, in males of the eight extant Dolichoderinae genera: *Anillidris* Santschi, 1936, *Aptinoma*, Fisher, 2009, *Azteca* Forel, 1878, *Dolichoderus*, *Leptomyrmex* Mayr, 1862 (group ‘micro-*Leptomyrmex*’), *Linepithema* Mayr, 1866 and *Liometopum* Mayr, 1861, but *Dlusskyus* distinguishes from each of them by a combination of other features. Thus, the mandibles of *Anillidris* and *Azteca* are not serrate, with no more than eight teeth. *Aptinoma* has much longer antennal scape, SL/HL ca. 0.5 vs. 0.29 in *Dlusskyus*. *Liometopum* not only more than twice as large as *Dlusskyus*, but also has somewhat longer antennal scape, which is longer than the second antennal segment (SL/HL > 0.4). *Linepithema* has a different antennal structure, e.g. scape is extremely short (SL/HL < 0.25), second funicular segment is very long, more than five times as long as wide vs. less than four times as long as wide in *Dlusskyus*, SL/FSL-2 ca. 0.5 (vs. 0.7), total length of second to six segments distinctly longer than the rest of funiculus (subequal in *Dlusskyus*). The inner margin of the eyes of *Dolichoderus* is distinctly concave (the eyes are reniform). Finally, among the 28 known species of *Leptomyrmex*, only the males *L. burwelli* Smith et Shattuck, 2009 from the group ‘micro-*Leptomyrmex*’, have forewings with four closed cells, but it differs from *Dlusskyus* in the non-notched medially posterior margin of the subgenital plate, and in the shape of the posterior clypeal margin, which lays at the level of the anterior surface of the antennal sockets; furthermore, it also differs from *Dlusskyus* in having a longer head (HL/HW > 1.30 vs. 1.12) and larger eyes (OL/HL > 0.50 vs. 0.43) (Shattuck 1992 a; Smith and Shattuck 2009; see also Dlussky et al. 2014).

Beside this, males are described in nine fossil genera assigned to Dolichoderinae. Three of them, *Ctenobethylus* Brues, 1939, *Yantaromyrmex* Dlussky et Dubovikoff, 2013 and *Usomyrma* Dlussky, Radchenko et Dubovikoff, 2014 were found in late Eocene European ambers. *Leptomyrmula* (Emery, 1913) was found in Oligocene Sicilian amber, and the others are known from imprints: *Miomyrmex* Carpenter, 1930 and *Protazteca* Carpenter, 1930 from early Oligocene deposits (USA, Florissant), *Alloiomma* Zhang, 1989 and *Elaphrodites* Zhang, 1989 from late Miocene deposits (Shandong, China), and morphotaxon *Emplastus* Donisthorpe, 1920 from deposits of USA (Florissant), England (Isl. Wight) and Russian Far East (all –

late Eocene), and Croatia (Radoboj, early Miocene) (Dlussky and Perfilieva 2014; Dlussky et al. 2014, 2015).

Usomyrma has a completely different forewing venation with only two closed cell, $(1+2r)+mCu$ and $3r$ (Dlussky et al. 2014). The forewings venation of *Leptomyrmula* is even more specialized: they have only one closed cell $3r$ (Emery 1891; see also Dlussky et al. 2014). The forewing venation of males of *Yantaromyrmex geinitzi* (Mayr, 1868) and *Ctenobethylus goepperti* (Mayr, 1868) is similar to that of *Dlusskyus*, but they differ from the latter genus in a longer antennal scape, which is not shorter than two basal funicular segments combined (SL/HL > 0.35 vs. 0.29), and by the not serrate mandibles with at most 10 teeth on the masticatory margin; in addition, males of *geinitzi* are larger (body length > 4.5 mm vs. 3.3 mm in *Dlusskyus*).

The forewing venation of males of the remainder genera is similar to that of *Dlusskyus* (at least they have four closed cells), but *Miomyrmex*, *Protazteca* and *Emplastus* males are much larger (body length 6–9 mm), their mandible are not long, with not serrate masticatory margin, and the funicular segments are short, only slightly longer than wide. *Alloiomma changweiensis* Zhang, 1989 was described by one imprint specimen, which was considered as male. However, based on the original description and drawings (Zhang 1989, Fig. 283), I believe that it is rather gyne. Anyhow, it has 11-segmented antennae, long scape, surpassing occipital margin, short funicular segments, extremely big eyes, and its body length is more than 8 mm. Two species of *Elaphrodites* are probably males, but they have 8-segmented antennae. Thus, all known males of the extant and extinct Dolichoderinae genera well differ from *Dlusskyus*.

The subfamily Aneuretinae currently includes the only monotypic extant genus *Aneuretus* Emery, 1893 and seven fossil genera (Bolton 2022; see also Boudinot et al. 2022), but males are known only from two of them – *Aneuretus* and *Paraneuretus* Wheeler, 1915. *Dlusskyus* differs well from the males of *Aneuretus simoni* Emery, 1893 in a much shorter petiole, the shape of mandibles, which have a relatively short masticatory margin with one sharp apical tooth and less than 10 minute denticles in *A. simoni*, and also in a palp formula: the maxillary palps in *A. simoni* are 3-segmented (Wilson et al. 1956).

Males of *Paraneuretus* well differs from those of both *A. simoni* and *D. groehni* in a number of characters, in particular, in the presence of well developed notauli and by the much larger size: their body length is 7 or 10 mm vs. < 4 mm in *A. simoni* and *D. groehni*.

Theoretically, the male described here may belong to one of three genera from late Eocene European ambers, in which males are unknown: *Eldermymex* Shattuck,

2011 (Dolichoderinae), and *Protaneuretus* Wheeler, 1915 or *Pityomyrmex* Wheeler, 1915 (Aneuretinae). However, the workers of the last two genera are not smaller than 5.5 mm, while the male of *Dlusskyus* is much smaller, 3.3 mm. Since the males of virtually all known ants are at least as large as conspecific workers (often larger), it is possible to exclude the belonging of the described male to *Protaneuretus* or *Pityomyrmex*. It can be assumed that the described male may belong to *Eldermyrmex*, but such a conclusion is not confirmed by anything and is absolutely speculative.

DISCUSSION

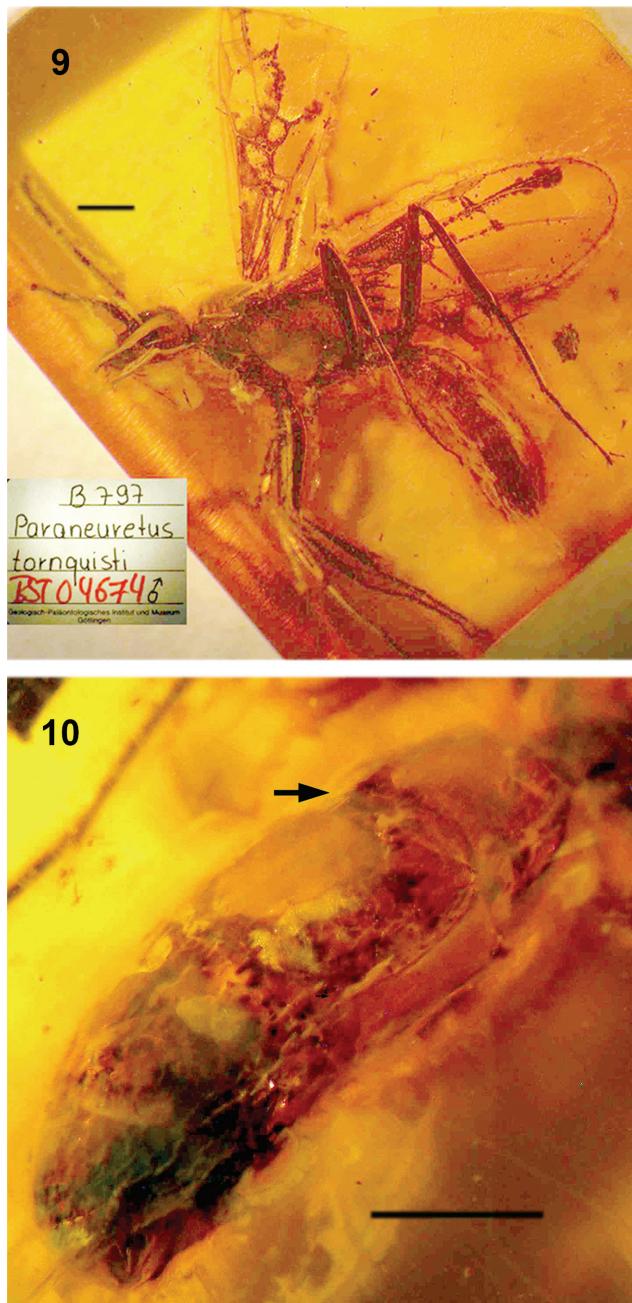
The question remains: how do males of Dolichoderinae differ from males of Aneuretinae, and to which of these subfamilies does *Dlusskyus* belong?

Overall, Aneuretinae is a rather enigmatic taxon with loosely defined morphological boundaries. The proposed diagnosis of Aneuretinae (Wilson *et al.* 1956; Bolton 2003) is based primarily on the workers and queens of extant *Aneuretus simoni* and includes only two autapomorphies compared to Formicinae and Dolichoderinae: 1) petiole with a long anterior peduncle; 2) helcium is attached high on the anterior face of the first gastral segment (abdominal segment III); beside these, they have a well developed and functional sting. However, the location of helcium in many fossil species of Aneuretinae is not high, and the assignment of some extinct genera to this subfamily seems somewhat doubtful (Boudinot 2015; LaPolla and Barden 2018; Boudinot *et al.* 2022; Radchenko and Khomych 2022). Additionally, Shattuck (1992b) proposed only one synapomorphy for imago stages of Aneuretinae, an elongated anterior petiolar peduncle.

Males of Aneuretinae and Formicinae are well differentiated by the forewing venation (see above), but the separating males of Aneuretinae and Dolichoderinae is much more problematic (Shattuck 1992a). Boudinot (2015) proposed a more detailed distinction between Aneuretinae and Dolichoderinae males, but only based on *A. simoni*. In particular, he again considered the long petiolar peduncle in *Aneuretus* as the main difference, as well as the level of development of basimeres and telomeres in the genitalia.

Apart from *Aneuretus*, two males were described in a single fossil genus: *Paraneuretus tornquisti* Wheeler, 1915 and *P. longicornis* Wheeler, 1915. As in *Aneuretus*, the forewings of these males have closed cells $1+2r$, $3r$, rm and mcu , a rather short antennal scape, subequal to the total length of the 1st and 2nd funicular segments, and a nodiform petiole with distinct peduncle, although it is considerably shorter than in *Aneuretus*. However, males of *Paraneuretus* have well-developed notaulari on the scutum, clearly

distinguishing them from *Aneuretus* and Dolichoderinae. At the same time, Wheeler (1915, p. 76) noted that "They closely resemble the males of the Ponerinae... There is, however, not race of a constriction between the first and second gastric segments", but unfortunately he did not provide drawings of these males. However, I possess the photographs of the syntype ('androtype' according to Wheeler, 1915) specimen of *P. tornquisti*, taken by Dlussky and kindly provided



Figures 9–10. Photos of *Paraneuretus tornquisti* Wheeler, 1915, male, syntype: (9) body, lateral view; (10) gaster, lateral view. Scale bars: 1 mm. Photos of G. M. Dlussky.

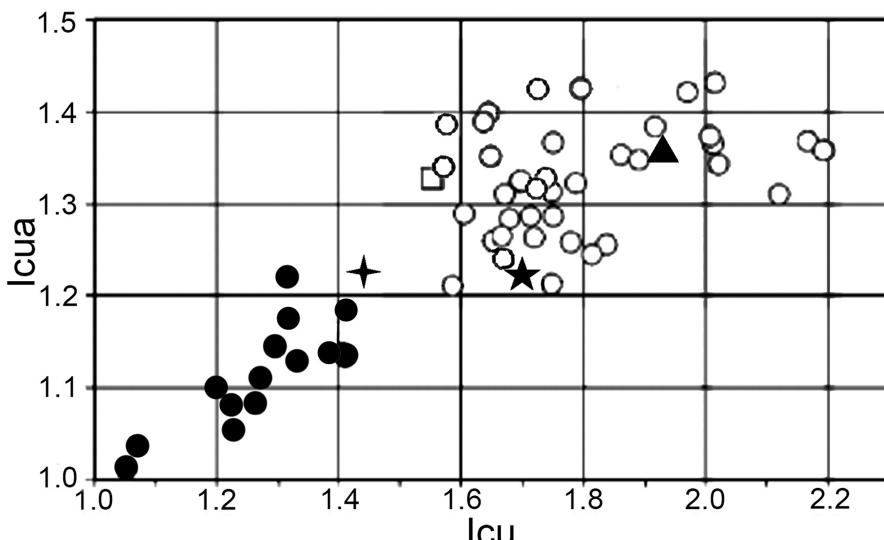


Figure 11. Differences in the values of the indices Icu and Icua in the males of Aneuretinae, Dolichoderinae and Ponerinae (after Dlussky and Perfilieva 2014, with modifications and additions). Legend: white square – *Britaneuretus anglicus* (Cockerel, 1915), black cross – *Aneuretus simoni* Emery, 1893, black star – *Paraeneuretus tornquisti* Wheeler, 1915 (Aneuretinae); transparent dots – Dolichoderinae; black triangle – *Dlusskyus groehni* gen. et sp. nov.; black dots – Ponerinae.

to me by him in 2012. This specimen with collection numbers “B 797 BST 04674” is preserved in the collection of Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen (GZG.BST) (former Geologisch-Paläontologisches Institut und Museum Göttingen).

In general appearance and especially in the shape of the gaster, this specimen really resembles the males of Ponerinae more than *Aneuretus* or Dolichoderinae, and in some images the constriction between the 1st and 2nd gastral segments is quite clearly visible (Figs 9, 10). On the other hand, the indices Icu = 1.71 and Icua = 1.22, which is in good agreement with those in Aneuretinae and Dolichoderinae, but not in poneroids (see Dlussky and Perfilieva 2014). Further, each meso- and metatibiae in the male *P. tornquisti* has one large simple spur, but poneroids often have two spurs on each tibia, and if there is only one spur, then it is pectinate, at least on the metatibiae. Thus, *P. tornquisti* males have rather mosaic characters between Aneuretinae and poneroids, and their correct taxonomic position can be definitely clarified after a more detailed study of the ‘androtype’ specimen.

On the whole, the male of *Dlusskyus* appears to be Dolichoderinae rather than Aneuretinae. In particular, it has a distinctly shorter petiole with a short peduncle (PL/HL 0.32 vs. > 0.5 in *A. simoni*), which is even shorter than in many Dolichoderinae males; then, the telomeres in the genitalia are also distinctly shorter than in *Aneuretus*. It is practically impossible to separate *Aneuretus* from Dolichoderinae by the forewings venation (see Cantone 2017), but taking in account the

indices Icu and Icua, *Dlusskyus* lies within most of the Dolichoderinae (Fig. 11).

So, based on all of the above, I decided to classify *Dlusskyus* as Dolichoderinae. Nevertheless, this genus is well distinguished from all known Dolichoderinae and its position within this subfamily remains unclear.

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