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A NEW ANT GENUS (HYMENOPTERA, FORMICIDAE) FROM THE LATE EOCENE ROVNO AMBER

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A New Ant Genus (Hymenoptera, Formicidae) from the Late Eocene Rovno Amber. Radchenko, A. G. — Based on workers from the Late Eocene Rovno amber (Ukraine), *Damzenomyrmex* gen. n. (Dolichoderinae) is established to include *Damzenomyrmex ribbeckei* sp. n., which is described here. I consider *Damzenomyrmex* to be a relative of *Dolichoderus* s. l. and assign it to the tribe Dolichoderini. *Damzenomyrmex* differs well from representatives of the previously established subgenera (genera) of *Dolichoderus* s. l., such as *Dolichoderus* s. str., *Karawajewella*, *Acanthoclinea*, *Monoceratoclinea* and *Diceratoclinea* by the nature of the mesosomal armature. It differs from the species of *Hypoclinea* in the presence of horn-like projections on the anterolateral corners of the pronotum. Regarding the last character, *Damzenomyrmex* reminds the species of *Monacis*, but readily differs from them by the non-concave posterior propodeal margin, a different shape of the petiolar scale, a not laterally marginated mesonotum, and some other characters. Furthermore, *Damzenomyrmex* differs from all *Dolichoderus* s. l. species in the cuticular structure and in the serration pattern of the mandibles, with the masticatory margin having 6–7 minor sharp teeth and a much longer apical one, the basal angle distinct and the basal margin lacking teeth or denticles. The comparative composition of Dolichoderinae and representatives of other ant subfamilies in late Eocene European ambers is considered.

Key words: ants, Formicidae, Dolichoderinae, Dolichoderini, new genus, new species, *Damzenomyrmex ribbeckei*, late Eocene, Europe, palaeontology, taxonomy.

Introduction

The ant fauna of the Late Eocene European (i. e. Baltic, Danish, Bitterfeld and Rovno) ambers (Priabonian age, 37.8–33.9 Ma) is the best studied among all fossil myrmecofaunas of the world. In total, about 18,000 ant specimens have been examined, and 178 described species from 64 genera of 12 subfamilies have been recorded so far (Dlussky & Rasnitsyn, 2009; Perkovsky, 2016; Radchenko & Khomych, 2022 a, b; Dubovikoff & Zharkov, 2022; Radchenko, 2023).

The subfamily Dolichoderinae Forel, 1878 was represented in late Eocene European ambers by eight genera and 39 species, or about 13 % and 22 % of all amber ant genera and species, respectively. Among them, the most diverse was the genus *Dolichoderus* Lund, 1831, with 25 species, and the dolichoderine *Ctenobethylus goepperti* (Mayr, 1868) accounted for about 40 % of the collected ant specimens (Dlussky & Rasnitsyn, 2009, with my additions).

At present, there is an opinion about the independent, though coeval, origin of the Rovno and other Late Eocene European ambers (Dlussky & Perkovsky, 2002; Perkovsky et al., 2003; Dlussky & Radchenko, 2006; Dlussky & Rasnitsyn, 2009), and this idea is supported by the character of myrmecofaunas. Thus, among 42 genera and 82 species recorded from Rovno amber till now, six genera and 24 species were found exclusively in this amber (Dlussky & Perkovsky, 2002; Dlussky, 2009; Radchenko & Perkovsky, 2009; Radchenko & Dlussky, 2012, 2013 a, b; 2016; 2018 a, b; 2019; Radchenko et al., 2018, 2021; Perrichot et al., 2019; Radchenko & Khomych, 2020; Radchenko, 2021; Radchenko & Proshchalykin, 2021; Radchenko, 2023). Finding the new genus and species, *Damzenomyrmex ribbeckei* gen. et sp. n., only in the Rovno amber supports the idea of the independent origin of this amber.

I recently received 14 pieces of Rovno amber, containing 16 workers of a previously unknown ant, which is described below as a new genus and species — *Damzenomyrmex ribbeckei* gen. et sp. n.

Material and Methods

I examined 16 specimens (workers) in 14 pieces of amber; the holotype and two paratype specimens are deposited at the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kyiv (SIZK), four paratype specimens are deposited in the collection of J. Damzen (Lithuania), the rest of the specimens are deposited in the collection of M. Khomych (Ukraine).

The photographs were taken by Aleksey Damzen (Lithuania) with a Canon 90D camera, equipped with a macrolens Canon MPE-65 mm and processed with the Helicon Focus software.

The specimens were measured using a Leica MZ6 stereomicroscope with an ocular-micrometer at a maximum magnification x100. Not all features of the specimens examined were properly visible and measurable, so I measured only well visible details (calculated to an accuracy of 0.01 mm), particularly:

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

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

FLW — maximum distance between outer margins of the frontal lobes;

SL — maximum straight-line length of the scape from its apex to the articulation with condylar bulb;

OL — maximum diameter of the eye;

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

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

ML — diagonal length of the mesosoma (seen in profile) from the anterior end of the neck shield to the posterior margin of the propodeal lobes;

MH — height of mesosoma, measured from the upper level of mesonotum perpendicularly to the level of lower margin of mesopleuron;

PNW — maximum width of the pronotum from above;

PNsW — distance between tips of the pronotal teeth from above;

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

PW — maximum width of the petiole from above;

PH — maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole;

HTL — maximum length of the hind tibia;

HTF — maximum length of the hind femur.

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

Indices: CI = HL/HW, SI1 = SL/HL, SI2 = SL/HW, FLI = FLW/HW, OI1 = OL/HL, OI2 = OL/HW, MdI = MdL/HL, GI = GL/OL, PI1 = PL/PH, PI2 = PW/HW, MI1 = ML/MH, MI2 = ML/PNW, FTI = HFL/HTL.

Taxonomy

Subfamily Dolichoderinae Forel, 1878.

Genus ***Damzenomyrmex*** **gen. n.**

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Type species: ***Damzenomyrmex ribbeckei*** **sp. n.**, by present designation.

Etymology. The genus is dedicated to Mr. Jonas Damzen (Lithuania), who found the holotype and several paratypes and made them available for study.

Diagnosis. Worker. Apex of gaster without circular nozzle-like acidopore. Integument appears rather thin, with very fine microsculpture, appears somewhat dull (at least not shiny). Posterior margin of head concave. Eyes situated somewhat in front (below) midlength of sides of head and set in from sides. Ocelli absent. Antenna 12-segmented, inserted close to posterior clypeal margin; scape long, surpassing occipital margin of head. Maxillary palp 6-segmented, labial palp 4-segmented. Hypostoma without medial notch, its anterior corner with expanded tooth-like flange, directed anteroventrally. Psammophore absent. Propodeal dorsum much lower than promesonotum, so that mesosoma does not form a regular arch in profile; anterolateral corners of pronotum with distinct blunt horn-like projections, directed asides and forward at an angle ca. 45° to longitudinal axis of body. Posterior surface of propodeum straight (not concave). Masticatory margin of mandible with 6–7 minor sharp teeth and much longer apical one; basal angle distinct; basal margin without teeth or denticles.

Damzenomyrmex ribbeckei **sp. n.**

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Material examined. **Types**. Holotype, worker, No. JDC 8918, Rovno amber, Late Eocene, Ukraine, Rivne Reg., deposited in SIZK; **paratypes**: 2 workers in the same piece of amber as holotype (together with 1 worker of *Lasius schiefferdeckeri* Mayr, 1868, 1 Hymenoptera sp., ca. 10 specimens of Diptera spp. in same piece of amber), deposited in SIZK; 1 worker, No. JDC 8955, 1 worker, No. JDC 9947, 2 workers, No. JDC 11388 (together with 1 specimen of Blattoptera sp. in same piece of amber), Rovno amber, Late Eocene, Ukraine, Rivne Reg.; 1 w, No. JDC 9946, 1 worker, No. JDC 9948, both most probably Rovno amber; all deposited in the collection of J. Damzen (Lithuania); 1 worker, No. F-066, Rovno amber, Late Eocene, Ukraine, Rivne Reg.; 1 worker, No. F-406 (together with 3 workers of *Ctenobetylus goepperti* (Mayr, 1868) in same piece of amber); 1 worker, No. F-613, both Rovno amber, Late Eocene, Ukraine, Rivne Reg., Zarichniansky Distr., village Kuhotska Volya, valley of River Veselukha; 1 worker, No. F-140 (together with 1 worker of *Camponotus mengei* Mayr, 1868 and termite in same piece of amber); 1 worker, No. F-141, both Rovno amber, Late Eocene, Ukraine, Rivne Reg., Volodymeretsky Distr., village Voronki. **Non-type**: 1 worker, No. F-059 (together with 1 worker of *Fallomyrma transversa* Dlussky et Radchenko, 2006 in same piece of amber); 1 worker, No. F-142, both Rovno amber, Late Eocene, Ukraine, Rivne Reg., Volodymeretsky Distr., village Voronki, all deposited in the collection of M. Khomych (Ukraine).

Etymology. The species is dedicated to Mr. Hans-Werner Ribbecke (Germany), who kindly donated the piece of amber with the holotype and two paratype specimens of this species to SIZK collection.

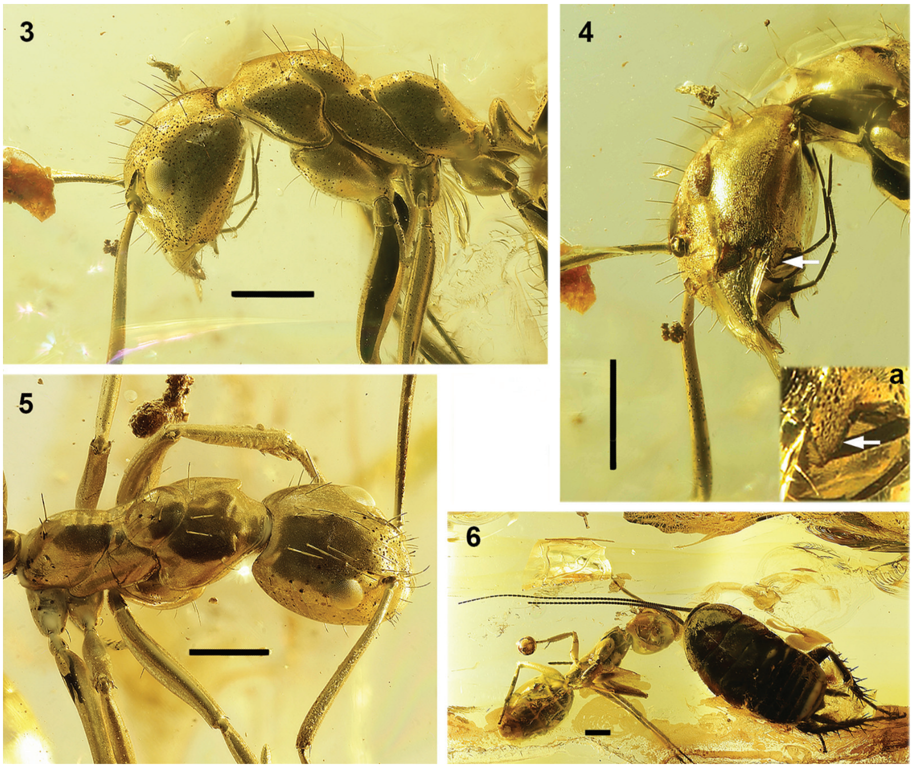
Workers (figs 1–6; tables 1, 2). Body length 8.3–10.7 mm. Head *ca*. 1.2 times as long as wide, with distinctly convex sides and narrowly rounded occipital corners. Frontal triangle weakly defined, not separated from frons by suture, clypeus shallowly insert-

Figs 1–2. Photos of *Damzenomyrmex ribbeckei* gen. et sp. n., workers: 1 — piece of amber with holotype (H) and paratypes (P-1, P-2), No. JDC 8918; 2 — holotype in lateral view. Scale bar 1 mm (photos by Aleksey Damzen).

Table 1. Measurements of the holotype and paratype specimens of *Damzenomyrmex ribbeckei* gen. et sp. nov., in mm

No.	HL	HW	FLW	SL	OL	GL	MdL	ML	MH	PNW	PNsW	PL	PH	PW	HTL	HFL
JDC 8918H	1.87	–	–	2.16	0.51	0.51	0.94	3.24	1.04	–	–	0.65	0.65	–	2.34	2.65
JDC 8918 P-1	1.77	1.46	0.69	2.12	0.44	0.48	0.92	3.11	0.95	1.01	1.07	0.62	0.62	0.52	2.30	2.52
JDC 8918 P-2	1.72	1.43	0.66	2.13	0.43	0.47	0.91	3.17	–	1.01	1.07	0.57	–	0.52	–	–
JDK 8955	1.92	1.59	0.77	2.24	0.48	0.49	0.96	3.28	1.07	1.07	1.09	0.68	0.66	0.53	2.38	2.70
F-066	2.03	1.66	–	2.50	0.49	0.55	1.01	3.30	–	1.12	1.20	0.70	0.68	0.57	2.39	2.72
F-406	1.77	–	–	–	0.44	0.48	–	2.78	–	0.94	1.01	0.62	0.60	–	2.18	2.39
F-140	1.82	–	–	2.26	0.48	0.53	–	2.97	0.94	–	–	0.62	0.61	–	2.35	2.65
F-141	2.07	1.68	–	2.46	–	–	–	3.64	1.18	1.16	–	0.70	0.68	–	2.41	2.73
F-613	1.87	–	–	–	0.48	–	–	3.20	1.02	1.04	1.09	–	–	–	2.16	2.38

H — holotype, P-1, 2 — corresponding paratypes (see fig. 1).



Figs 3–6. Photos of *Damzenomyrmex ribbeckei* gen. et sp. n., workers: 3 — holotype, head, mesosoma and petiole in lateral view; 4 — holotype, head in lateral view; arrows indicate tooth-like flange on anterior corner of hypostoma (a — same, magnified); 5 — paratype P-1, mesosoma and head in dorsal view; 6 — paratype No. JDC 8955 with Blattoptera sp. Scale bars 1 mm (photos by Aleksey Damzen).

ed between frontal lobes. Eye suboval (ratio of max/min diameters ca. 1.15), rather large (OI1 0.24–0.27, OI2 0.30), gena equal or slightly longer than maximum diameter of eyes (GI 1.00–1.11); eye without hairs. Longitudinal medial frontal groove or carina absent. Lateral frontal carina well developed, subvertical and short, somewhat sinuous and subparallel, reaching to level of midline of eye. Clypeus without medial and lateral carinae; central part of its surface convex, lateral parts lay lower than central one; clypeus in profile

Table 2. Morphometric indices of the holotype and paratype specimens of *Damzenomyrmex ribbeckei* gen. et sp. nov.

No.	CI	SI1	SI2	FLI	OI1	OI2	MdI	GI	PI1	PI2	MI1	MI2	FTI
JDC 8918 H	–	–	–	–	0.27	–	0.50	1.00	1.00	–	3.11	–	1.13
JDC 8918 P-1	1.21	1.19	1.45	0.47	0.25	0.30	0.52	1.09	1.00	0.29	3.27	3.06	1.10
JDC 8918 P-2	1.20	1.24	1.49	0.46	0.25	0.30	0.53	1.09	–	0.30	–	3.13	–
JDK 8955	1.21	1.16	1.41	0.48	0.25	0.30	0.50	1.03	1.02	0.28	3.07	3.07	1.13
F-066	1.22	1.23	1.50	–	0.24	0.30	0.50	1.11	1.04	0.34	–	2.95	1.14
F-406	–	–	–	–	0.25	–	–	1.09	1.04	–	–	2.97	1.10
F-140	–	1.24	–	–	0.26	–	–	1.10	1.02	–	3.16	–	1.13
F-141	1.23	1.19	–	–	–	–	–	–	1.03	–	3.08	3.14	1.13
F-613	–	–	–	–	0.26	–	–	–	–	–	3.14	3.08	1.10

H — holotype, P-1, 2 — corresponding paratypes (see fig. 1).

slightly depressed; anterior clypeal margin almost straight, without medial notch; anterolateral clypeal margin lays posterior to mediolateral margin; posterior clypeal margin lays between imaginary lines, connecting anteriormost and posteriormost surfaces of antennal sockets. Anterior tentorial pits locate near antennal sockets. Antennal scape surpassing occipital margin for ca. 1/3 of its length. First funicular segment conical, subequal to length of second one; other segments cylindrical, elongated, length of first to tenth segments ca. 3.3–4.3 times as long as wide, apical segment the longest, ca. 4.7–5.0 times as long as wide; second segment 0.90–0.96 times as long as third one; junction of third and fourth segments straight. Maxillary palp very long, reaching occipital foramen, their fifth segment the longest, ratio of length of segments 6 : 5 : 4 = 0.92 : 1.0 : 0.97; third segment subequal in length to fourth one. Labial palp rather short, fourth segment the longest, 1.6–1.7 times as long as third one, first and second segments ca. 0.5 times as long as fourth one. Mandibles rather long, ca. 0.5 times as head length.

Mesosoma slender, 3.07–3.27 times as long as high, mesonotal dorsum slightly raised above pronotum, abruptly sloping posteriorly; pronotal dorsum somewhat flattened; metanotum short, subhorizontal, separated from both mesonotal and propodeal dorsum by sutures; metathoracic spiracles situated dorsally and partly concealed by well developed tubercles. Mesothoracic epimeron near insertion with forecoxa without tooth. Dorsal surface of propodeum feebly convex, posterior one almost straight and inclined posteriorly, both surfaces of subequal length, converging at rounded angle, without teeth or tubercles. Metapleural glands well developed. Propodeal spiracles elongate-oval, less than twice as long as wide, located approximately at midlength of lateral sides of propodeum and quite close to its declivity. Petiole rather high, with long posterior peduncle, its height subequal to length; scale of medium thickness, with narrowly rounded dorsum (seen in profile), not wide, with subparallel sides, gradually rounded and convex dorsum (seen in anterior or posterior views); its anterior surface almost straight, subvertical, posterior surface slightly concave; ventral surface without lobe or tooth. Four gastral tergites visible in dorsal view. Anterior surface of first gastral tergite subvertical, gaster do not conceal petiole in dorsal view. Two apical gastral sternites with distinct longitudinal keel. Meso- and metatibiae with long simple spur, which much longer than maximum width of tibiae.

Head dorsum with 20–26 long, slightly curved coarse setae, ventral surface of head with 6–8 shorter setae, clypeus with ca. 10 setae, pronotum and mesonotum with 8–10, propodeal dorsum with 2–4 similar setae, both gastral tergites and sternites with > 20 similar setae; petiole bare; each coxa with 5–7 somewhat thinner setae; antenna without setae; femora with 3–4 setae on flexor surface, tibiae with 8–12 shorter and coarser setae on flexor surface, tarsi with numerous short coarse bristles on flexor surface. Surface of body and appendages covered with very dense silken silvery decumbent pubescence, distance between hairs much shorter than their length.

Queens and males unknown.

Measurements and indices see in tables 1 and 2.

Comparative diagnosis. Among the 28 extant genera of Dolichoderinae, *Dolichoderus* s. l. (= tribe Dolichoderini Forel, 1878, see Discussion) has two autapomorphies: 1) the anterior corner of the hypostoma with expanded tooth-like flange, directed anteroventrally, and 2) the anteromedial margin of the mesosternum is convex and expanded anteriorly (Shattuck, 1992; Shattuck & Marsden, 2013). *Damzenomyrmex* shares the first apomorphy with *Dolichoderus* s. l. (fig. 4) (the second feature is not visible in fossil specimens, since the forecoxae must be removed to observe it). Based on this, I propose to assign *Damzenomyrmex* to the tribe Dolichoderini.

Modern species of *Dolichoderus* s. l. are highly variable morphologically. They may have denticles or spines of various shapes and lengths on the pronotum, mesonotum, propodeum, or petiole, which led to the description of a number of subgenera within *Dolichoderus* or separate genera in a past (see Discussion). At the same time, the posterior surface of the propodeum in the vast majority of species is concave to varying degrees. Similarly, some extinct *Dolichoderus* s. l. species may have differently developed denticles or spines on the mesosoma, but all of them (with one exception, see Discussion) have a distinctly concave posterior propodeal margin.

Damzenomyrmex differs well from representatives of the previously established subgenera (genera) of *Dolichoderus* s. l., such as *Dolichoderus* s. str., *Karawajewella* Donisthorpe, 1944, *Acanthoclinea* Wheeler, 1935, *Monoceratoclinea* Wheeler, 1935 and *Diceratoclinea* Wheeler, 1935 by the nature of the mesosomal armature (see Karawajew, 1926; Wheeler, 1935; Shattuck, 1992). It differs from the species of *Hypoclinea* Mayr, 1855 in the presence of horn-like projections on the anterolateral corners of the pronotum. In terms of the last character, *Damzenomyrmex* is similar to the species of *Monacis* Roger, 1862, but differs well from them in the non-concave posterior propodeal margin, a different shape of the petiolar scale, a not laterally marginate mesonotum, and some other features (see Kempf, 1959).

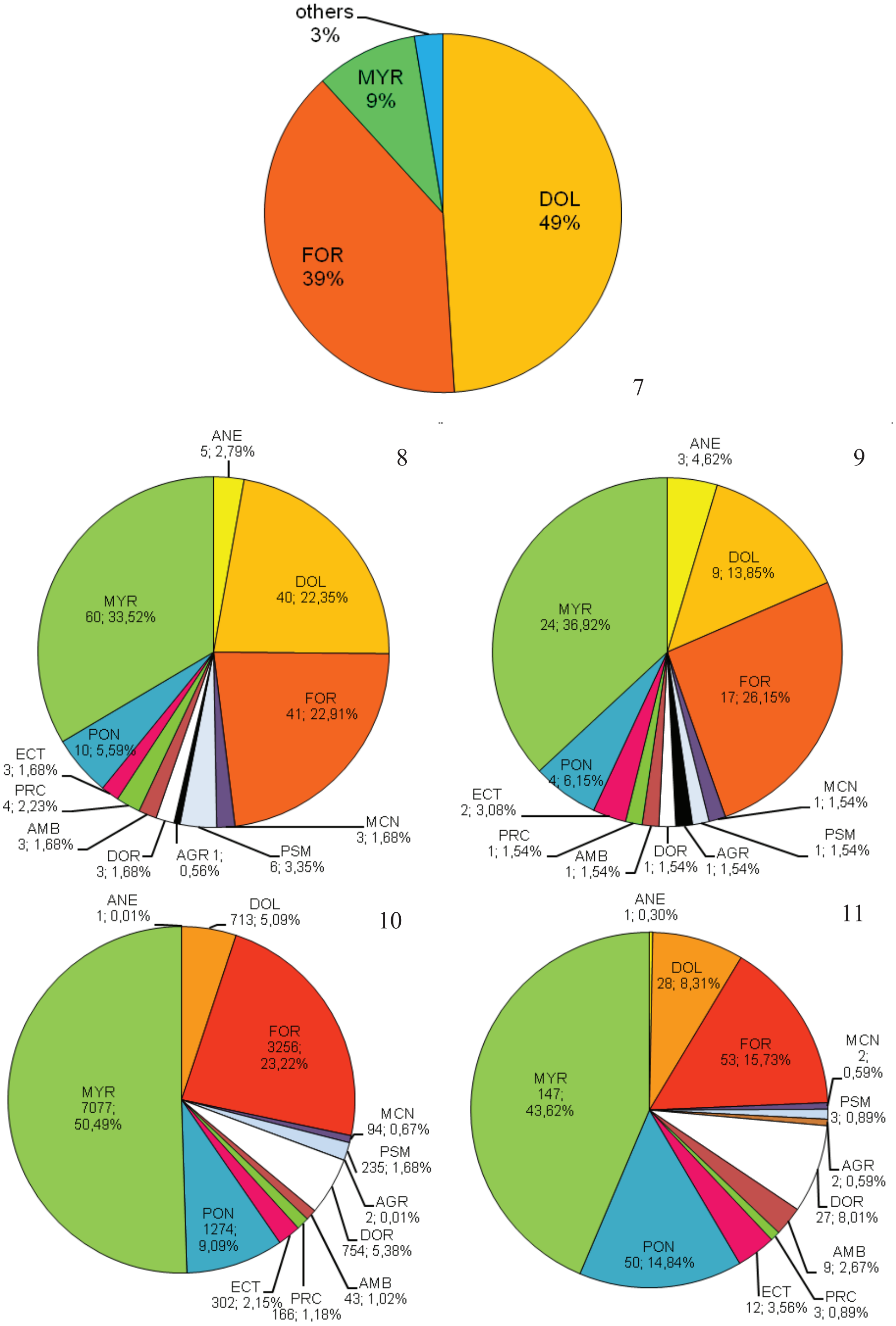
Besides, *Damzenomyrmex* differs from all *Dolichoderus* s. l. species in the cuticular structure and in the serration pattern of the mandibles, with the masticatory margin having 6–7 minor sharp teeth and a much longer apical one, the basal angle distinct and the basal margin has no teeth or denticles *vs*. mandibles have ≥ 9 teeth with an apical tooth nearly as long as the preapical one, the basal angle is indistinct and the basal margin is serrated over the entire surface in modern *Dolichoderus* species. I have also observed a serrated basal margin of mandibles in a number of fossil *Dolichoderus* species from Late Eocene European ambers, in which the state of preservation and position in the amber allowed this feature to be seen, such as *D. balticus* (Mayr, 1868), *D. tertiartius* (Mayr, 1868), *D. sculpturatus* (Mayr, 1868), *D. lucidus* Dlussky, 2008, and *D. pilipes* Dlussky, 2008.

Discussion

Modern representatives of the subfamily Dolichoderinae are distributed throughout the world, but the greatest generic and species diversity is observed in the Neotropical, Australasian and Oriental Regions (Shattuck, 1992). In total, this subfamily includes 28 extant genera, numbering more than 710 species; 20 fossil genera and about 140 species are also known (Bolton, 2023).

Dolichoderinae is one of the oldest evolutionary lineages of the modern ant subfamilies: its oldest members are known from the Late Cretaceous Canadian ambers (Campanian, 78–79 Ma), e. g. *Eotapinoma macalpini* Dlussky, 1999 and *Chronomyrmex medicinehatensis* McKellar, Glasier et Engel, 2013 (Dlussky, 1999; McKellar et al., 2013; see also Boudinot et al., 2022). Moreover, in Kachin amber (Myanmar the earliest Cenomanian, ca. 100 Ma), another undescribed dolichoderine genus and species were discovered (Boudinot et al., 2020, 2022).

The extant genera of Dolichoderinae were first found in the middle Eocene deposits (*ca*. 45 Ma) (Wilson, 1985; Dlussky & Rasnitsyn, 2002), but diversity of this subfamily considerably increased since the Late Eocene. Thus, in Late Eocene European ambers Dolichoderinae dominated in terms of the number of specimens (fig. 7), and were among the taxonomically most diverse subfamilies, inferior in this respect only to Myrmicinae Lepele-



Figs 7–11. Diagrams of the ratio of the number of specimens to number of taxa of ant subfamilies, found in Late Eocene European ambers: 7 — by number of amber specimens; 8 — by number of amber species; 9 — by number of amber genera; 10 — by number of modern species; 11 — by number of modern genera; ANE — Aneuretinae, DOL — Dolichoderinae, FOR — Formicinae, MCN — Myrmeciinae, PSM — Pseudomyrmecinae, AGR — Agroecomyrmecinae, DOR — Dorylinae, AMB — Amblyoponinae, PRC — Proceratiinae, ECT — Ectatomminae, PON — Ponerinae, MYR — Myrmicinae.

tier, 1835 and Formicinae Latreille, 1809 (figs 8, 9). However, starting from the Oligocene their proportion began to decrease significantly (Dlussky, 2002, 2008; Dlussky & Rasnitsyn, 2002, 2007) and at present they are inferior to more subfamilies in the number of species and genera (figs 10, 11) (calculated based on Bolton, 2023).

Dolichoderus s. l. is the most speciose genus of Dolichoderinae with more than 130 extant species, or about 20 % of the known species of this subfamily. It has worldwide distribution, except for the Afrotropics and Madagascar, and is most diverse in the tropical forests of the Oriental and Neotropical Regions.

Dolichoderus s. l. has a rather complicated taxonomic history. The type species of the genus *Dolichoderus* is *Formica attelaboides* Fabricius, 1775 from Brazil. Mayr (1855) established the genus *Hypoclinea* and assigned to it *H. frauenfeldti* Mayr, 1855 (now transferred to *Lepisiota* Santschi, 1926) and *H. quadripunctata* (Linnaeus, 1771); the latter was subsequently designated by Wheeler (1911) as the type species of this genus. The Neotropical genus *Monacis* was established by Roger (1862), but Mayr (1862) noted that he received species intermediate between *Hypoclinea* and *Monacis* and proposed to consider the latter name a junior synonym of *Hypoclinea*. Later, Karawajew (1926) established a new subgenus of *Dolichoderus*, *Diabolus* (replacement name *Karawajewella*) from Southeast Asia. Finally, Wheeler (1935) established three more subgenera in this genus: Australasian *Acanthoclinea* and *Monoceratoclinea*, and Indo-Australian *Diceratoclinea*. As a result, he divided *Dolichoderus* s. l. into seven subgenera: *Dolichoderus* s. str., *Monacis* (both Neotropical), nearly cosmopolitan *Hypoclinea*, and the four remaining subgenera mentioned above.

During a long period from the last third of the 19th century until the 1990s, various authors treated the mentioned genus-group taxa as good genera, subgenera or synonyms of *Dolichoderus* s. l. Finally, Shattuck (1992) summed up this discussion by treating all subgeneric names as junior synonyms of *Dolichoderus* s. l., which has hitherto been simply repeated by all subsequent authors (for more details see Shattuck, 1992, fig. 61; Bolton, 2023). However, this issue cannot be considered definitively resolved.

First of all, it should be emphasised that none of the authors who have synonymised any of the mentioned subgeneric/generic names with *Dolichoderus* has provided any sufficient, or in most cases, no arguments for this. Thus, *Acanthoclinea*, *Diceratoclinea*, *Karawajewella*, *Monacis* and *Hypoclinea* were synonymised with *Dolichoderus* by all authors prior to Shattuck's (1992) revision only formally in the texts without any arguments (e. g. Forel, 1878; Emery & Forel, 1879; Dalla Torre, 1893; Bingham, 1903; Ruzsky, 1905; Brown, 1973; Taylor & Brown, 1985).

Shattuck (1992) then pointed out that some species assigned to *Hypoclinea* form a transitional cline linking them to *Karawajewella*, and in general, he "…can find no character by which to define *Hypoclinea*, other than as an assemblage of taxa left after all distinctive groups are removed" (loc. cit., p. 72). Consequently, he considered *Hypoclinea* to be a paraphyletic. At the same time, he emphasised that the former subgenera/genera *Dolichoderus* s. str., *Acanthoclinea*, *Monoceraloclinea* and *Diceratoclinea* are morphologically distinct and well distinguishable units. On the basis of this he drew a somewhat unexpected and rather contradictory conclusion: "While these groups are discernible their treatment as genera is still unacceptable as this would leave *Hypoclinea* paraphyletic. Therefore all groups are treated as members of the single genus *Dolichoderus*" (Shattuck, 1992, p. 75).

Based on the molecular-based phylogenetic analysis of Dolichoderinae Ward et al. (2010) considered four tribes in this subfamily: Bothriomyrmecini Dubovikoff, 2005, Tapinomini Emery, 1913, Leptomyrmecini Emery, 1913 and Dolichoderini; the latter includes the only genus *Dolichoderus* s. l. However, these data also do not provide an unambiguous answer to the question about the composition of *Dolichoderus*, at least, they do not confirm the synonymy proposed by Shattuck (1992).

Ward et al. (2010) used only six *Dolichoderus* species for molecular phylogenetic analysis, but even in this case the results are quite interesting and, to a certain extent, indicative, since representatives of different former subgenera/genera form unequally spaced sister clades. When assigning the species used for analysis to the previously established subgenera/genera of *Dolichoderus* s. l., the phylogenetic scheme (fig. 2 in Ward et al., 2010) is as follows: (((*Dolichoderus* s. str. + (Hypoclinea sp. A + Hypoclinea sp. B)) + ((Diceratoclinea + (Monacis sp. A + Monacis sp. B))). That is, the species in the phylogram are not arranged randomly, but are grouped according to previously established subgenera (genera).

Although Ward et al. (2010) made no attempt to separate *Dolichoderus* s. l. into subgenera/genera, it is clear from the text of the article that such a broad interpretation of this taxon, unlike other genera of Dolichoderinae, creates difficulties in resolving a number of issues. For example, they wrote: “Based on the current state of *Dolichoderus* systematics, we believe that this is an appropriately conservative assignment that takes into account uncertainty about the relationship of Southeast Asian species … to those of other regions” (loc. cit., p. 348); “Because we treat the genus *Dolichoderus* (= tribe Dolichoderini) as a single entity, we cannot make a statement about crown-group distribution” (ibid., p. 352); “We made no attempt to estimate the geographic origin of Dolichoderini because we treated the sole genus, *Dolichoderus*, as a single unit” (ibid., p. 356).

In my opinion, in such a situation it would be quite logical to consider *Dolichoderus* s. str., *Acanthoclinea*, *Monoceraloclinea*, *Diceratoclinea* and, most probably, *Monacis* as good genera, and in the future to carry out a thorough revision of the remaining “genera” to clarify their composition and phylogenetic relationships. With this approach, the five genera mentioned plus “*Hypoclinea*” and, probably, “*Karawajewella*”, form the monophyletic group, i.e. the tribe Dolichoderini.

The genus *Dolichoderus* was also diverse in a past, with 50 extinct species described. The oldest ones, *Dolichoderus kohlsi* Dlussky et Rasnitsyn, 2002 and *Dolichoderus dlusskyi* LaPolla et Greenwalt, 2015, were described from imprints from the USA (Green River and Kishenehn Formations, respectively), dating by the middle Eocene (Lutetian, 47.8–41.2 Ma). Six species were described by imprints from the Late Eocene deposits of North America, Europe and East Asia (Scudder, 1877; Deichmüller, 1881; Donisthorpe, 1920; Carpenter, 1930; Dlussky et al., 2015), and five from the Oligocene deposits of Germany and France (Förster, 1891; Théobald, 1937), but the richest fauna of this genus, numbering 25 species, is known from the Late Eocene European ambers (Mayr, 1868; Wheeler, 1915; Dlussky, 2002, 2008; Dlussky & Perkovsky, 2002; Dubovikoff & Zharkov, 2022). Seven species were described by imprints from the Miocene deposits of China, Croatia and Crimea (Hong, 1984; Zhang, 1989; Zhang et al., 1994; Dlussky & Putyatina, 2014; Perfilieva et al., 2017), and four from the Miocene Dominican amber (Wilson, 1985).

Dlussky (2002) placed *Dolichoderus* species from the Late Eocene European ambers into five species groups, three of which (*quadripunctatus*, *balticus* and most probably *palassoma* group) can be assigned to the former genus *Hypoclinea*, one (*cornutus*-group) corresponds to the gubgenus *Diceratoclinea*, and one, probably, to the subgenus *Monoceratoclinea*. Interestingly, the recently described species from Rovno amber, *D. jonasi* Dubovikoff et Zharkov, 2022, resembles species from the subgenus *Monacis* in many ways. At the same time, all species described from imprints from the Late Eocene and Oligocene deposits, as well as Miocene *Dolichoderus heeri* Dlussky & Putyatina, 2014 from Croatia correspond to *Hypoclinea*. *Dolichoderus tavridus* Perfilieva, Dubovikoff et Dlussky, 2017 from Crimea was described only from the forewing, and the morphological features of the Chinese fossil species are difficult to interpret based on the drawings in the relevant papers (Hong, 1985; Zhang, 1989; Zhang et al., 1994), but the described gynes are at least morphologically unspecialised and may probably also belong to the *Hypoclinea*. Finally, Wilson (1985) assigned one species from the Dominican amber to the genus *Dolichoderus* s. str., two to *Monacis*, and one to *Hypoclinea* (*H. primitiva* Wilson, 1985). The latter species have a smoothly rounded propodeum with a non- concave posterior margin (seen in profile), and the outer margin of the eyes extends beyond the lateral outline of the head (seen from above). Based on a very brief original description and drawings, the assignment of *H. primitiva* to *Hypoclinea* seems quite doubtful, at least Wilson did not provide sufficient justification for assigning this species to *Dolichoderus* s. l. or even to Dolichoderinae.

In general, the vast majority of fossil *Dolichoderus* species are characterised by dense integument, often rather strongly sculptured, and the posterior surface of the propodeum is distinctly concave, and all of them can be assigned to known modern "subgenera/genera" or species-groups.

The genus *Dolichoderus* s. l. (= tribe Dolichoderini) was previously considered by many authors to be quite primitive, sometimes basal in relation to the rest of the Dolichoderinae (Emery, 1888; Forel, 1917; Brown, 1973; Brady et al., 2006), but was later placed in phylograms with other genera (tribes) of this subfamily (Shattuck, 1995; Brandão et al., 1999; Chiotis et al., 2000; Ward et al., 2010). Ward et al. (2010, p. 354) also noted: "Given that *Dolichoderus* is nested within the dolichoderine tree, the thin flexible cuticle and reduced body sculpture typical of most dolichoderines — as well as their sister group, the Aneuretinae — is most parsimoniously interpreted as the ancestral condition for the subfamily. The thick cuticular sculpture and armament of Dolichoderus is therefore likely to represent a convergence with well-armored ants in other subfamilies". In addition, the estimated mean divergence time of the tribe Dolichoderini is 52 Ma, which is less than that of the tribe Tapinomini (57 Ma) (Ward et al., 2010), which is consistent with the palaeontological evidence. I agree with this opinion and also consider the formation of a dense, often coarsely sculptured cuticle, the development of variously shaped spines in many species, the concave posterior surface of the propodeum of the *Dolichoderus* s. l. to be secondary to other Dolichoderinae. The absence of denticles on the basal margin of the mandibles in *Damzenomyrmex* can be regarded as a secondary loss, but their development in *Dolichoderus* s. l. is rather an apomorphy, since the absence of such a dentition in ants is generally an ancestral trait (Dlussky & Fedoseeva, 1988).

Thus, the autapomorphies proposed by Shattuck (1992) for the genus *Dolichoderus* s. l. are quite acceptable to consider as synapomorphies for all members of the tribe Dolichoderini, including *Damzenomyrmex*, and at the same time, as autapomorphies for this tribe as a whole, in relation to other Dolichoderinae. With that, *Damzenomyrmex* cannot be considered a direct ancestor of *Dolichoderus* s. l., but can probably be placed within the stem lineage of Dolichoderini.

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