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DISCOVERY OF A SOLDIER OF THE FOSSIL GENUS *DRYMOMYRMEX* (HYMENOPTERA, FORMICIDAE, FORMICINAE) SUPPORTS PHRAGMOTIC BEHAVIOUR IN LATE EOCENE ANTS

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Discovery of a soldier of the fossil genus *Drymomyrmex* (Hymenoptera, Formicidae, Formicinae) supports phragmotic behaviour in Late Eocene ants. Radchenko, A. G. & Ribbecke, H.-W. — A previously unknown soldier of the genus *Drymomyrmex* Wheeler, 1915 is described. This find confirms the dimorphism of the worker caste of this genus, represents the oldest known soldier among ants, and confirms the phragmotic morphology and behaviour of ants in the Late Eocene. The putative life style of the *Drymomyrmex* species and the taxonomic position of this genus are discussed. We propose to assign *Drymomyrmex* to the tribe Lasiini, in particular to the *Cladomyrma* Wheeler, 1920 group.

Key words: Baltic amber, Priabonian, Lasiini, *Drymomyrmex, Cladomyrma*, caste dimorphism.

Introduction

The term “phragmosis” was proposed by Wheeler (1927) to define morphological modifications in living organisms that enable them to close the entrance to a shelter or nest using modified parts of their own body. Such adaptation is widely known in ants and has arisen independently in representatives of several subfamilies due to

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modification of the frontal or dorsal parts of the head. For example, a defence “shield” in soldiers of South American *Cephalotes* Latreille, 1802 or *Blepharidatta* Wheeler, 1915 (Myrmicinae Lepeletier, 1835) forming as follows: first the vertexal area flattens into a semi-circular disc and then the frontal carinae expand first anterolaterally and then join together medially until the cephalic shield becomes complete (De Andrade & Baroni Urbani, 1999). In contrast, in the soldiers and queens of many other genera, such as *Colobopsis* Mayr, 1861 (Formicinae Latreille, 1802), *Tetraponera* F. Smith, 1852 (Pseudomyrmecinae M. Smith, 1952), *Colobostruma* Wheeler, 1915, *Crematogaster* Lund, 1831, *Carebara* Westwood, 1840 or *Pheidole* Westwood, 1839 (Myrmicinae) the anterior part of the clypeus, and often the genae, are truncated and flattened, and together with the mandibles form a shield which is usually much coarsely sculptured than other parts of the head. Mentioned ants live in the cavities of thin branches of various origins and the soldiers plug the entrance to the nest with their modified head (Wheeler, 1927; Wheeler D. E. & Hölldobler, 1985; Fischer et al., 2015; Hosoishi et al., 2022).

Phragmotic head morphology is known also in fossil *Cephalotes* species from Miocene Dominican and Mexican (Chiapas) amber, although their heads are somewhat less specialized than in many modern congeners (Vierbergen & Scheven, 1995; De Andrade & Baroni Urbani, 1999). More ancient fossil ants (from Middle Eocene onwards) were already very diverse taxonomically, many with extremely specialized head structure, but no species had a phragmotic head morphology (e. g., Barden & Grimaldi, 2014; Barden, 2017; Barden & Engel, 2020; Boudinot et al., 2020; Perrichot et al., 2020, and literature cited herein).

However, Wheeler (1915) established a new genus *Drymomyrmex* with two species described based on five gynes from Late Eocene Baltic amber. Their most characteristic feature is a subcylindrical in cross-section head with a truncated and somewhat flattened anterior part of the clypeus. Radchenko (2021) described a new species of *Drymomyrmex* based on a worker from Rovno amber. This ant has a “normal” head, with neither truncated nor flattened clypeus, and Radchenko suggested that *Drymomyrmex* species may have a dimorphic worker caste, such as “normal” workers and soldiers.

We recently found an ant specimen in a piece of Baltic amber. In its main diagnostic features it fits well to *Drymomyrmex*, such as 11-segmented antennae with the short scape, not reaching the occipital margin of the head; a similar shape of the head, which is subcylindrical, distinctly elongated, with subparallel sides, narrowly rounded occipital corners and a straight occipital margin; the appropriate size and position of the eyes; the 6-segmented maxillary palps; the presence of a long simple spur on the middle and hind tibiae; a rather thick petiolar scale with a broadly rounded dorsum, and, most importantly, it has a distinctly truncated and flattened anterior part of clypeus, like in the known gynes of this genus. So, we believe this is a previously unknown *Drymomyrmex* soldier and formally described it for the first time. Based on the antennal structure, we tentatively assign it to *D. fuscipennis* Wheeler, 1915 (see below for details). In our opinion, this finding not only confirms the idea of worker caste dimorphism in this genus, but also indicates the presence of phragmotic behaviour in ants in the Late Eocene.

Material and Methods

We examined one soldier from Baltic amber. The specimen is deposited at the private collection of H.-W. Ribbecke (Germany).

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

The specimen was measured using a Leica MZ6 stereomicroscope with an ocular-micrometre at a maximum magnification x100. Not all features of the specimen examined were properly measurable, so we 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 anteriormost point of clypeus to the mid-point of occipital margin;

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

OL — maximum diameter of the eye;

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

PoL — postocular distance, measured in dorsal view from the level of posterior margin of the eyes to the mid-point of occipital margin;

ML — diagonal length of the mesosoma in lateral view from the anterior margin of the neck shield to the posterior margin of the metapleural lobes;

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

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 lowest point of the petiole;

PW — maximum width of the petiole in dorsal view;

HTL — maximum length of the metatibia.

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).

Definition of metacoxal position:

— metacoxae widely separated — when the coxae are directed perpendicular to the long axis of the body, their inner margins are far apart;

— metacoxae closely approximated — when the coxae are directed perpendicular to the long axis of the body, their inner margins touch or almost touch each other.

Results

Subfamily Formicinae Lepeletier, 1836
Genus *Drymomyrmex* Wheeler, 1915

Diagnosis. With characters of Formicinae. Worker caste dimorphic: ordinary workers and soldiers. Anterior portion of clypeus in gynes and soldiers distinctly flattened and, together with mandibles, forms obliquely truncated rounded plate.

Antennae 11-segmented, inserted close to posterior clypeal margin. Antennal scape short, does not reach occipital margin. Eyes well developed, located at midlength or slightly behind midlength of sides of head. Ocelli in workers and soldiers absent. Mandibles short, massive, subtriangular, masticatory margin with blunt and rather big apical and preapical teeth and three smaller subsequent ones, third tooth appears to be slightly smaller than fourth one (but the latter feature is not so obvious). Palp formula 6, 4. Mesonotum in workers and soldiers completely fused with metanotum and the latter does not form a distinctly separate sclerite. Propodeal spiracles rounded, situated in the dorsal third of propodeum. Petiolar scale distinctly lower than propodeum. Metacoxae widely separated. Metatibiae without row of bristles on inner (flexor) margin. Meso- and metatibiae with well-developed simple spur. Forewing of gynes with closed cells *1+2r* and *3r*, cells *rm* and *mcu* absent.

First description of soldier of *Drymomyrmex fuscipennis* Wheeler, 1915

Material examined. Poland, Baltic amber, Late Eocene, Priabonian age, 37.8–33.9 Ma, No. BS140/213.

Total length *ca*. 5.3 mm. Despite head width not properly measurable, head distinctly elongated, seems at least *ca*. 1.5 times as long as wide; sides of head almost straight, subparallel, occipital corners narrowly rounded, occipital margin straight. Antennae 11-segmented, inserted on head close to posterior margin of clypeus; scape short, about half of head length, not reaching posterior head margin; 1st funicular segment *ca*. twice as long as wide, subsequent segments not strongly elongated, but distinctly longer than width, apical segment the longest, subequal to total length of two preceding ones. Eyes of moderate size (OL/HL 0.19), situated somewhat behind midlength of sides of head, genae much longer than maximum diameter of eye (GL/OL 2.26). Anterior portion of clypeus distinctly flattened and meets basal portion at a somewhat rounded angle, not so abrupt as in many of *Colobopsis* soldiers, while it forms with mandibles an obliquely truncated anterior surface; unlike *Colobopsis*, anterior part of genae lateral to clypeus not truncated; anterior clypeal margin very feebly convex. Mandibles short, massive, subtriangular, masticatory margin with blunt and rather big apical and preapical teeth and three smaller subsequent ones, third tooth appears to be slightly smaller than fourth one, but the latter feature is not so obvious. Maxillary palps 6-segmented, length of segments from 2nd to 6th 0.12, 0.12, 0.16, 0.08, 0.09 mm; labial palps invisible. Frontal carinae short, slightly divergent posteriorly, not reaching level of anterior margin of eyes, clypeus not inserted between frontal carinae; frontal triangle distinct; frons without longitudinal carina or groove.

Mesosoma rather long and slender, about 3 times as long as high, promesonotal suture well-marked laterally and dorsally, but mesonotum not raised above pronotum, mesonotum feebly convex and gradually sloping to propodeum; metanotal groove distinct, but not deep; mesonotum fused with metanotum, so that metanotum does not form distinctly separate sclerite; propodeal dorsum lies only slightly lower than mesonotum, its dorsal surface somewhat longer than posterior one, both meet at rounded angle; propodeal spiracles rounded, situated quite close to declivity. Petiole with short anterior and posterior peduncles, scale low, thick, bluntly rounded dorsally and somewhat inclined anteriorly. Legs of moderate length, HTL/ML 0.56;

meso- and metatibiae with well-developed simple spur, which longer than maximum width of tibia; pretarsal claws simple; metatibiae without row of bristles on flexor margin. Apex of gaster with well-visible acidopore and coronula.

Decumbent and standing pilosity on body poorly visible due to nature of preservation of specimen, but numerous and rather long subdecumbent setae visible on tibiae, tarsi, funiculus and gastral tergites. Surface of body with microsculpture, but appears somewhat shiny. Body and appendages blackish-brown.

Workers and males unknown.

Measurements (in mm) and ratios:

HL 1.27, SL 0.65, OL 0.25, GL 0.56, POL 0.44, ML 1.61, MH 0.55, PL 0.22, PH 0.23, PW 0.23, HTL 0.91;

SL/HL 0.51, OL/HL 0.19, GL/OL 2.26, GL/HL 0.44, POL/HL 0.35, PL/PW 0.94, PL/PH 0.94, MH/PH 2.33, ML/MH 2.88, HTL/ML 0.56.

Comparative diagnosis

It is rather problematic to confidently assign the soldier here described to any of the previously described species, since two of them, *D. fuscipennis* and *D. claripennis* Wheeler, 1915, were described based on gynes, and *D. rasnitsyni* Radchenko, 2021 was described from a worker. The shape and proportions of the head and mesosoma or length of the scape in gynes (queens), soldiers and workers of the same ant species can differ so significantly, that representatives of different subcastes can be classified as different species. For example, the scape in gynes and soldiers of *Colobopsis truncata* (Spinola, 1808) is noticeably shorter than that of workers, while the structure of the funicular segments is similar. At the same time, the scape of gynes in *Colobopsis* species is never longer than that of conspecific soldiers. The scape of the worker of *D. rasnitsyni* is significantly longer than that of the described soldier (SL/HL 0.72 vs. 0.51), and its 2nd–9th funicular segments are transversal or subsquare, while in the latter they are somewhat elongated (see Radchenko, 2021) which, most likely, precludes their conspecifity. Moreover, *D. rasnitsyni* was found in Rovno amber and the soldier — in Baltic amber. In terms of the antennal structure, the described soldier has features of both *D. fuscipennis* and *D. claripennis*: its scape is short, like that of the first species, but the proportions of the funicular segments are similar to the latter. However, we hesitate to describe one more new species of this genus from Baltic amber, considering that the length of the scape is more important than the proportion of the funicular segments, we tentatively attribute the described soldier to *D. fuscipennis*.

Discussion

Putative life style of the *Drymomyrmex* species

The ant fauna of Late Eocene European ambers (e. g., Baltic, Bitterfeld, Danish and Rovno, Priabonian age, 37.8–33.9 Ma) is the richest and the best studied fossil myrmecofauna worldwide. So far, more than 19,000 specimens were investigated and 204 species (all extinct) from 70 genera (40 extinct and 30 extant) of 12 subfamilies (all extant) have been discovered (Dlussky & Rasnitsyn 2009; Barden, 2017; Radchenko, 2024, 2025; Radchenko et al., 2024, 2025; Radchenko & Khomych, 2025), and with more than 20 additional species and some genera still awaiting description.

Formicinae is one of the most diverse ant subfamilies, including 55 extant genera and more than 3,300 species, or 16% of ant genera and 23% of species (calculated from Bolton, 2025). Representatives of this subfamily were even more relatively diverse in Late Eocene European ambers, with 17 known genera and 43 species, or 24% and 21% of all amber ant taxa, respectively, second only to Myrmicinae (our unpublished data).

Several Formicinae species (*Formica flori* Mayr, 1868, *F. gustawi* Dlussky, 2002 and *Lasius schiefferdeckeri* Mayr, 1868) together with the Dolichoderinae *Ctenobethylus goepperti* (Mayr, 1868) absolutely dominated in number of specimens, accounting for about 70% of all ants collected (Radchenko, 2023; our unpublished data). Such abundance can be explained by the fact that the above-mentioned species had populous colonies, actively tended aphids making foraging trails on the various trees, and, in addition, *C. goepperti* most probably led an arboreal style of life and built nests in branches or hollows in various trees (Wheeler, 1915; Dlussky, 1997). As a result, their workers were trapped in the resin in great number and then preserved in amber. In contrast, only five winged gynes, one worker and one soldier of *Drymomyrmex* were collected, and a question remains: why is the number of *Drymomyrmex* specimens collected so low?

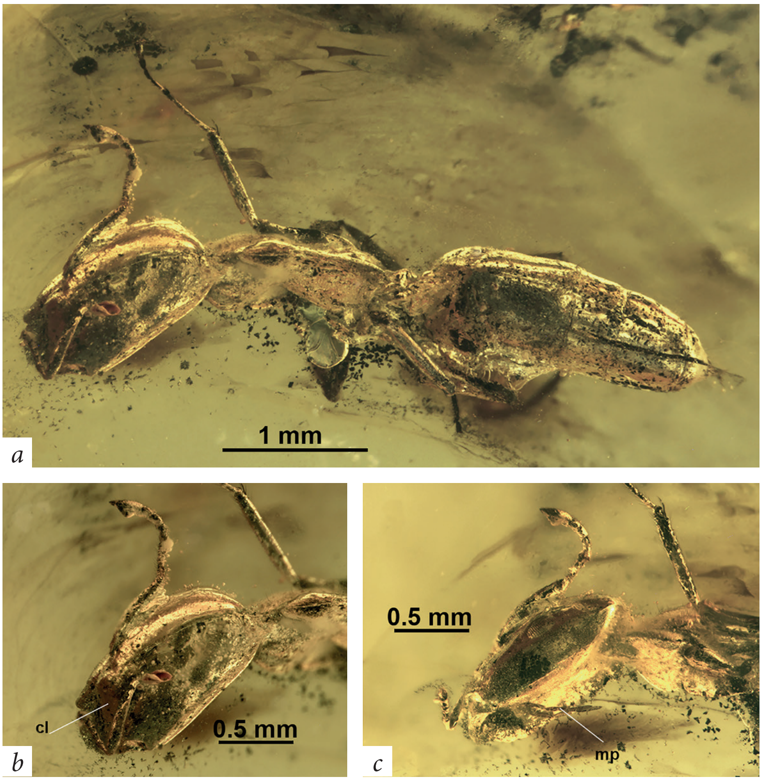
Wheeler (1915, p. 38) noted that "The structure of the head and body [of *Drymomyrmex*] show that it lived in the cavities of twigs, in oak-galls or in abandoned insect galleries in solid wood, like the species of *Colobopsis*", and our discovery of the soldier only confirms this idea.

Several hypotheses can be proposed to explain the rarity of *Drymomyrmex* in amber: 1) colonies were rare; 2) colonies were sparsely populated, similar to modern *Colobopsis* species (Wheeler, 1904, 1910; McArthur, 2012); 3) workers did not actively tend aphids or form foraging trails on the trees; 4) workers built nests and foraged on trees that did not secrete resin (for example, oaks). Perhaps even all of these reasons are true.

Taxonomic position of *Drymomyrmex*

The taxonomic position of the genus *Drymomyrmex* within the subfamily Formicinae remained uncertain for a long time. Wheeler (1915) initially assigned it to the tribe Camponotini Forel, 1878, probably based on the clypeal structure of the gynes, which is similar to that of some species of *Camponotus* Mayr, 1861 (now *Colobopsis* Mayr, 1861). Then Wheeler (1929 b) provisionally transferred *Drymomyrmex* to the tribe Brachymyrmicini Emery, 1925 (now a junior synonym of Myrmelachistini Forel, 1912; see Ward et al., 2016), but did not provide convincing evidence to support this assumption. Later, *Drymomyrmex* was transferred back to the tribe Camponotini without any comments (Donisthorpe, 1943; Dlussky & Fedoseeva, 1988; Bolton, 1994, 1995). Moreover, Dlussky (1997) synonymized the name *Drymomyrmex* with *Camponotus*, but later Dlussky & Rasnitsyn (2009) restored this name from synonymy. Ward et al. (2016) based on exclusively molecular genetic data revised the tribal system of Formicinae, considering *Drymomyrmex* incertae sedis in this subfamily. Finally, Radchenko (2021) described a worker of this genus and tentatively assigned *Drymomyrmex* to the tribe Plagiolepidini Forel, 1886.

Below, we will sequentially exclude the possibility of assigning *Drymomyrmex* to each of the tribes recognized by Ward et al. (2016), before choosing the most appropriate one for this genus.



Photographs of *Drymomyrmex fuscipennis*, soldier: *a* — body in dorso-lateral view; *b* — head in dorso-lateral view (cl — truncated clypeus); *c* — head in ventro-lateral view (mp — maxillary palps) (photos by A. Radchenko)

The morphological characteristics of the tribes are based mainly on Bolton (2003) with the necessary additions in some cases. As not all diagnostic features are visible in fossil specimens, our focus was primarily on the most distinctive structures that distinguish *Drymomyrmex* from various tribes.

Based on the latest arrangement (Ward et al., 2025), the tribe Camponotini includes 11 extant and three extinct genera. The main features that characterise the female castes are: antennae inserted distinctly behind the posterior clypeal margin; antennae 12-segmented; metacoxae closely approximated (see also Bolton, 1994, 2003).

Therefore, *Drymomyrmex* cannot belong to this tribe, as it has 11-segmented antennae, which inserted close to the posterior clypeal margin, and the widely separated metacoxae.

At present, eight modern and three to five fossil genera are assigned to the tribe Formicini Latreille, 1809 (Bolton, 1994, 2003; Blaimer et al., 2015; Ward et al., 2016; Boudinot et al., 2022; Radchenko & Khomych, 2024). Comprehensive morphological characterization of this tribe was proposed by Agosti (1990, 1991, 1994), Bolton (2003) and Dlussky (2008). Among the numerous characters of the female castes, the following can be distinguished: the eyes are located far beyond the midlength of the sides of the head; antennae 12-segmented with a scape extending beyond the occipital margin by at least ¼ of its length; metatibiae with a double row of bristles on the flexor (inner) surface; metacoxae are closely approximated; the propodeal spiracles oval to slit-shaped; finally, the forewing has closed cell *mcu* (with some exceptions in the genus *Cataglyphis* Foerster, 1850).

In contrast, workers and gynes of *Drymomyrmex* have 11-segmented antennae with a relatively short scape, not reaching the occipital margin; the eyes are located at the midlength of the sides of head, or at most slightly further; the metatibiae lack a row of bristles; the propodeal spiracles are rounded; the metacoxae are widely separated; the forewing without cell *mcu*. Consequently, this genus cannot belong to Formicini.

The two tribes, Gigantiopini Ashmead, 1905 and Santschiellini Forel, 1917, each comprise a single, highly specialised monotypic genus. Their representatives clearly differ from *Drymomyrmex* in their 12-segmented antennae and especially by their exceptionally large eyes, which occupy more than ¾ the length of the head.

The tribe Gesomyrmecini Ashmead, 1905 includes one extant (*Gesomyrmex* Mayr, 1868) and two extinct genera (*Sicelomyrmex* Wheeler, 1915 and *Prodimorphomyrmex* Wheeler, 1915) (Ward et al., 2016). The genus *Gesomyrmex* was establishes based on the fossil *G. hoernesi* Mayr, 1868 from Baltic amber, but currently includes 11 extinct and 6 extant highly specialized species. Its workers are highly polymorphic: there are large, medium, and small workers, which differ greatly in size and especially in head shape. Previously, conspecific workers were classified not only as different species, but even as different genera (Wheeler, 1929 a). They have 8-segmented antennae in workers and 10-segmented in gynes, as well as very large eyes, occupying at least half the length of the head in major workers and ¾ in minor ones.

The only known worker of the fossil species *Sicelomyrmex corniger* (Emery, 1891) from Oligocene Sicilian amber looks even more bizarre, having a highly modified head with long spines on the occipital corners, long propodeal spines, 10-segmented antennae, etc. (see Emery, 1891). The single known worker of *Prodimorphomyrmex* is clearly differentiated from that of *Drymomyrmex* in the 10-segmented antennae, very short maxillary palps, much bigger size (ca. 8 mm vs. ca. 3.5 mm), lacks of standing setae on mesosoma and gaster, etc. (see Wheeler, 1915; Radchenko, 2021). Consequently, *Drymomyrmex* cannot be attributed to this tribe.

The highly specialized morphologically genus *Oecophylla* F. Smith, 1850 (weaver ants) represents a monotypic tribe Oecophyllini Emery, 1895. It differs significantly from *Drymomyrmex* in the shape of the head, rather long mandibles with 9–16 sharp teeth crossing apically, long 12-segmented antenna with the scape exceeding the occipital margin by more than 1/3 of its length, long and slender body and legs, etc. Moreover, *Oecophylla* has a behaviour that is unique among ants: its workers construct nests from leaves, stuck together with silk produced by their larvae.

The tribe Myrmelachistini Forel, 1912 includes two genera, *Brachymyrmex* Mayr, 1868 and *Myrmelachista* Roger, 1863. Their workers and gynes differ from *Drymomyrmex* in having 9- or 10-segmented antennae. Moreover, both are distributed in the Neotropics, and their relationship to the genus from Late Eocene European ambers seems highly unlikely.

The tribe Myrmoteratini Emery, 1895 includes the extremely specialized genus *Myrmoteras* Forel, 1893 with a mandibular structure unique for the subfamily Formicinae: they are trap-jaw, very long and linear, equipped with numerous sharp teeth.

Based on morphology, Bolton (2003) included a single genus, *Melophorus* Lubbock, 1883, in the tribe Melophorini Forel, 2012. However, Ward et al. (2016) showed, based on molecular study, that this genus belongs to a fairly large and well-supported clade, and assigned nine morphologically diverse genera to this tribe. Eight of them are distributed in Australia, New Zealand and New Guinea, and one, *Lasiophanes* Emery, 1895, with six species, is restricted to Patagonia. All Australasian genera are clearly distinguished from *Drymomyrmex* by their12-segmented antennae and closely approximated metacoxae. On the other hand, the metacoxae of *Lasiophanes* are widely separated, but their antennae are 12-segmented and scape clearly exceeds the occipital margin. Therefore, morphologically *Drymomyrmex* differs significantly from all representatives of this tribe and cannot be included in it.

Bolton (2003) established an informal lasiine tribe group assigning to it the tribes Lasiini Ashmead, 1905, Plagiolepidini Forel, 1886 and the monotypic tribe Myrmoteratini, and considered widely separated metacoxae as a putative synapomorphy of this group. Later, Ward et al. (2016) transferred several genera from Lasiini to other tribes, and two among them, *Acropyga* Roger, 1862 and *Anoplolepis* Santschi, 1914, were assigned to Plagiolepidini. On the contrary, the genera *Euprenolepis* Emery, 1906, *Prenolepis* Mayr, 1861, *Pseudolasius* Emery, 1887, *Paratrechina* Motschoulsky, 1863, *Nylanderia* Emery, 1906, *Paraparatrechina* Donisthorpe, 1947 and *Zatania* LaPolla, Kallal & Brady, 2012 (species from the last three genera were previously attributed to *Paratrechina*) were transferred from Pladiolepidini to Lasiini. As a result, the diagnostic features proposed by Bolton (2003) to separate these two tribes have practically lost their value. Nevertheless, all genera of both tribes (sensu Ward et al., 2016) share an important diagnostic feature of the former lasiine tribe group: they have widely separated metacoxae.

Unfortunately, there is no modern taxonomic revision of Plagiolepidini, and the composition of this tribe proposed by Ward et al. (2016) is not supported (or refuted?) by morphological data. The genera of this tribe are morphologically quite diverse, while almost all have a reduced number of antennal segments (from 7 to 11). Practically, *Drymomyrmex* shares with all Plagiolepidini genera only structure of the metacoxae and the reduced number of antennal segments. The only rather enigmatic monotypic, presumably socially parasitic genus *Bregmatomyrma* Wheeler, 1929, known from several dealate queens from Borneo and Malesia has 12-segmented antennae (Wheeler, 1929 b; Bolton, 2003, 2025), but its assignment to this tribe is not supported by molecular data and is provisional, and a taxonomic revision of the plagiolepidine genera is overdue (Ward et al., 2016). Thus, based on such insufficient and somewhat contradictory morphological data, we do not currently dare to assign *Drymomyrmex* to the tribe Plagiolepidini.

More recently, Boudinot et al. (2022) provided a comprehensive phylogenetic and taxonomic analysis of the genus *Lasius* Fabricius, 1804 and the tribe Lasiini based on both morphological and molecular approaches. They retained generic composition of this tribe proposed by Ward et al. (2016) with the addition of the genus *Metalasius*, described by them in the mentioned paper, with the type species of that genus *Lasius myrmidon* Mei, 1998. They proposed a detail morphological characterization of Lasiini, using 23 morphological features. Unfortunately, many of them are not visible in the studied specimens of *Drymomyrmex* (e. g., structures of the petiolar foramen and apodeme, the third abdominal segment, and, naturally, the anatomy of the proventriculus). However, none of the visible features contradict the proposed characteristics of Lasiini, e.g., the mandibular structure, the nature of the antennal articulation, the palp formula, the shape of the propodeal spiracles, the widely separated metacoxae, the absence of a row of bristles on inner (flexor) margin of the metatibiae, etc. (for more details, see the diagnosis of *Drymomyrmex* above).

The small Oriental genus *Cladomyrma* Wheeler, 1920 forms separate clade in relation to other Lasiini genera (Blaimer et al., 2015; Ward et al., 2016; Boudinot et al., 2022). Morphologically, it is clearly distinguished from them by the 8-segmented antennae of workers and queens, very short frontal carinae, undifferentiated metanotum, and the position of the propodeal spiracle, which are clearly located in the dorsal third of the propodeum (Boudinot et al., 2022). In addition, its worker caste is dimorphic, with "normal" (minor) workers and soldiers. The latter, as well as the queens, have truncated and flattened clypeus (although these characters are less developed than in *Drymomyrmex* or *Colobopsis* species), which may indicate phragmotic behaviour. Lastly, its representatives lead a strictly arboreal lifestyle, nesting in the twig's hollows of myrmecophytic lianas or trees (Agosti, 1991; Agosti et al., 1999).

In contrast, workers and queens of other Lasiini genera have 12-segmented antennae (a few species have 11-segmented antennae in the genus *Preudolasius* Emery, 1887), longer frontal carinae, a differentiated metanotum, and propodeal spiracle located at or below its dorsal third (Boudinot et al., 2022). Their workers are not dimorphic, with the exception of the genus *Pseudolasius*. However, its soldiers do not have phragmotic morphology. Beside this, their representatives are epigean or hypogean, nesting in the ground or leaf litter, very rarely in wood remnants or under the bark of dead trees, but never in branch holes.

Thus, in terms of both morphology and biology, the genus *Drymomyrmex* is more similar to *Cladomyrma* than to other Lasiini genera. According to Boudinot et al. (2022), the first deep split in the Lasiini (*Cladomyrma* + core Lasiini) occurred between the Late Cretaceous (Santonian) and the Late Paleocene (Thanetian). That is, the genus *Cladomyrma* should have already existed before the Late Eocene, and we may suggest that *Drymomyrmex* forms a sister group to it, originated from a common ancestor, but cannot be its direct descendant, since its female castes have 11-segmented antennae instead of 8-segmented ones in *Cladomyrma*.

As a result, we propose to assign *Drymomyrmex* to the tribe Lasiini, in particular to the *Cladomyrma* group.

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