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First record of a soldier of the genus *Carebara* Westwood, 1840 (Hymenoptera: Formicidae: Myrmicinae) from Late Eocene Baltic amber

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Abstract

A new species, †*Carebara andrushchenkoi* **sp. nov.** is described and illustrated from Late Eocene Baltic amber. The new species represents the second described species of the genus *Carebara* Westwood, 1840 with a soldier caste from the Late Eocene European ambers and the first in Baltic amber. †*C. andrushchenkoi* **sp. nov.** is distinguished from other fossil *Carebara* species by the following combination of features: In profile view, vertex posteriorly with a pair of acute small horns, dorsum of head slightly convex; meso- and metatibiae without spurs; all body covered with subdecumbent pubescence and long erect to suberect hairs. This discovery is another important evidence that pronounced polymorphism in ants was formed at least in the Late Eocene.

Key words fossil ants, Crematogastrini, †*C. andrushchenkoi*, major worker.

Introduction

The genus *Carebara* Westwood, 1840 (Hymenoptera: Formicidae) is composed of small ants widespread in tropical, subtropical and warm temperate regions of the world (Bolton 2025). Species of this genus are known for their pronounced polymorphism of workers, which is manifested in the presence of tiny workers (minors) and large soldiers (majors) with massive heads. They are poorly represented in the fossil record, mainly by finds in European Eocene ambers (Radchenko *et al.* 2019). To date, nine fossil species have been described. In his landmark monograph, Gustav Mayr (1868) described the species †*Carebara antiqua* (Mayr, 1868) from Late Eocene Baltic amber based on two females. It was originally placed in the genus *Pheidologeton* Mayr, 1862, which is now a junior synonym of *Carebara* (Fischer *et al.* 2014). William M. Wheeler (1915) studied three females (including one of the type specimens of Mayr), and described four workers and three males from Baltic amber. Gennady M. Dlussky described two species of *Carebara* from Late Eocene Rovno amber (in the genus

Oligomyrmex Mayr, 1867, which is now a junior synonym of *Carebara*; Fernández 2004): †*Carebara nitida* (Dlussky, 2002) based on a minor worker and †*Carebara ucrainica* (Dlussky, 2002) based on a female (Dlussky & Perkovsky 2002). Significant contributions were made by Radchenko *et al.* (2019), who described two new species: †*Carebara kutscheri* Radchenko *et al.*, 2019, based on both major and minor workers, and †*Carebara groehni* Radchenko *et al.*, 2019, based on a male specimen. Additionally, they reviewed the taxonomic position of fossil *Carebara*. Notably, their work marked the first description of a soldier caste in a fossil species of *Carebara*. (†*C. kutscheri* from Late Eocene Bitterfeld amber).

Despite the relatively high level of study of the myrmecofauna from Late Eocene European ambers (with nearly 200 species described to date; Zharkov *et al.* 2025), finds of representatives of the genus *Carebara* are exceedingly rare. This is likely due to their predominantly subterranean and litter-dwelling lifestyle, which significantly reduced the likelihood of these ants becoming entrapped in tree resin. This characteristic makes the taxonomy and morphological diversity of extinct *Carebara* particularly intriguing for further research. Here, we describe and illustrate a new species of *Carebara* based on both major and minor workers found in Late Eocene Baltic amber. The soldier ant of the new species is the first evidence of polymorphism of representatives of the genus *Carebara* in Baltic amber.

Materials and Methods

The fossil ant specimens examined (Figure 1) are from the Baltic amber, Priabonian age (Late Eocene, 37.8–33.9 Ma), the Prussian Formation, on the Sambia Peninsula near Kaliningrad, Kaliningrad region, Russia (Iakovleva *et al.* 2022). The holotype (major), paratype (minor) and 2 examined minor workers of the new species are kept in the collection of the Palaeontological Museum of the St. Petersburg State University, Russia, accessioned KA–234. The amber was hand processed for study (cut and polished) at the St. Petersburg State University (PaleoEcoAnt lab).

Photography and morphological analysis of sample was performed using a Leica M205C motorized stereomicroscope. The studies were performed using the equipment of the Research Park of St Petersburg State University (Resource Centre for Microscopy and Microanalysis). Subsequent image processing was carried out using the Helicon Focus Pro 8 and Inkscape 1.2 software. All measurements of morphological structures were carried out in accordance with Zharkov *et al.* (2023, fig. 1).

The dimensional values of morphological structures are given in millimeters. The following designations are used in the text:

HL—head length, maximum length of head in full-face view between lines drawn across anterior margin of clypeus and lines drawn across the posterolateral corners of head;

HW—head width, width of head directly behind the eyes measured in full-face view;

SL—the maximum straight-line length of the scape measured from antennal bulb to the apex;

PdL—pedicel length;

FI1—the length of the first flagellomere;

FI2—the length of the second flagellomere;

MdL—the length of the mandible, measured from the mandibular apex to the anterior clypeus margin, or to the transverse line connecting the anterior-most points in those taxa where the margin is concave medially;

WL—Weber's length, the diagonal length of the mesosoma in profile from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron;

PNW—the maximum width of the pronotum in dorsal view;

ESL—maximum length of propodeal denticles (or spines) in profile, measured along the tubercle/spine from its tip to the deepest point of the propodeal constriction at its base;

ESD—distance between the tips of propodeal tubercles/spines in dorsal view;

PrdL—the maximum length of the propodeum in dorsal view;

PrdH—the height of the propodeum in profile, measured as the perpendicular distance from the ventral edge to the highest point of the propodeum;

PtL—the length of the petiolar node in profile, measured as the distance from the place of attachment to the propodeum to the place of attachment to the postpetiole;

PtH—the height of the petiolar node in profile, measured as the perpendicular distance from the ventral edge to the highest point of the petiolar node;

PtW—the maximum width of the petiolar node in dorsal view;

PPL—the length of the postpetiole in profile, measured as the distance from the place of attachment to the petiolar node to the place of attachment to the gaster;

PPH—the height of the postpetiole in profile, measured as the perpendicular distance from the ventral edge to the highest point of the postpetiole;

PPW—the maximum width of the postpetiole in dorsal view;

HFL—the maximum length of metafemur, measured in anterior view;

HTL—the maximum length of metatibia, measured in anterior view;

GL—the length of the gaster, measured as the distance from the place of attachment of the postpetiole to the top of the gaster in ventral view;

TL—the total length of the ant ($=HL + WL + PtL + PPL + GL$).

Indices:

CI (cephalic index) = HL/HW ;

SI₁ (scape length index) = SL/HL ;

SI₂ (scape width index) = SL/HW ;

MdI (mandible index) = MdL/HL ;

PI₁ (petiole length index) = PtL/PtH ;

PI₂ (petiole width index) = PtL/PtW ;

PI₃ (petiole-cephalic index) = PtW/HW ;

PPI₁ (postpetiole height index) = PPL/PPH ;

PPI₂ (postpetiole width index) = PPH/PPW ;

PPI₃ (postpetiole-petiole index) = PPW/PtW ;

PPI₄ (postpetiole-cephalic index) = PPW/HW ;

ESLI (propodeal spine length index) = ESL/HW ;

ESDI (propodeal spine distance index) = ESD/ESL ;

MI (mesosomal width index) = WL/PNW ;

PRI (propodeal index) = $PrdL/PrdH$.

Results

Systematic palaeontology

Family Formicidae Latreille, 1809

Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835

Genus *Carebara* Westwood, 1840

Type species *Carebara lignata* Westwood, 1840

†*Carebara andrushchenkoi* Zharkov & Dubovikoff **sp. nov.** (Figure 1)

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Etymology. After Konstantin Andrushchenko (Kalinigrad, Russia), our friend and Baltic amber enthusiast, who provided amber for this study and donated it to our Museum.

Type material. Holotype № K-234a (major worker), paratype № K-234b (minor worker) and examined minor workers № K-234c, d were found in a small piece of Late Eocene Baltic amber. The piece is 36.8 mm in length, 3 mm in maximum width, and 9 mm in maximum height. The holotype is an intact specimen, but the pronotum and mesonotum are obscured by bubbles. It was observed in profile, oriented to the right. In profile on the left, it is not completely visible because it is obscured by films. In dorsal views, there is distortion, and in ventral views it is not visible at all. Paratype № K-234b and 2 examined minor workers are deformed to varying degrees and autoclaved. In the same piece of amber, three remains of Diptera were also found, as well as numerous dark bubbles, films and debris.

The piece of amber containing the ants is stored in the collection of the Paleontological Museum of the St. Petersburg State University, St. Petersburg city, Russia, accessioned KA-234.

Type locality and age. The piece of amber was found by Konstantin Andrushchenko (<https://paleoamber.ru/>) in Baltic amber. The material originated from Yantarny, on the Sambia Peninsula, Kaliningrad region, Russia. Late Eocene, Priabonian age (37.8–33.9 Ma), the Prussian Formation, (Iakovleva *et al.* 2022).

Diagnosis. *Major worker:* Holotype soldier № K-234a is distinguished from other fossil *Carebara* species by the following combination of features: In profile view, vertex posteriorly with a pair of acute small horns, dorsum of head slightly convex; mandible with 6 teeth; median portion of clypeus depressed longitudinally, biconvex and divergent forward; well-developed mesoscutellum; metanotal groove wide and deep; meso- and metatibiae without spurs; all body covered with subdecumbent pubescence and long erect to suberect hairs.

Minor workers: Paratype № K-234b is distinguished from other fossil *Carebara* species by the following combination of features: Propodeum without teeth, dorsum convex; meso- and metatibiae without spurs; all body covered with subdecumbent pubescence and long erect to suberect hairs.

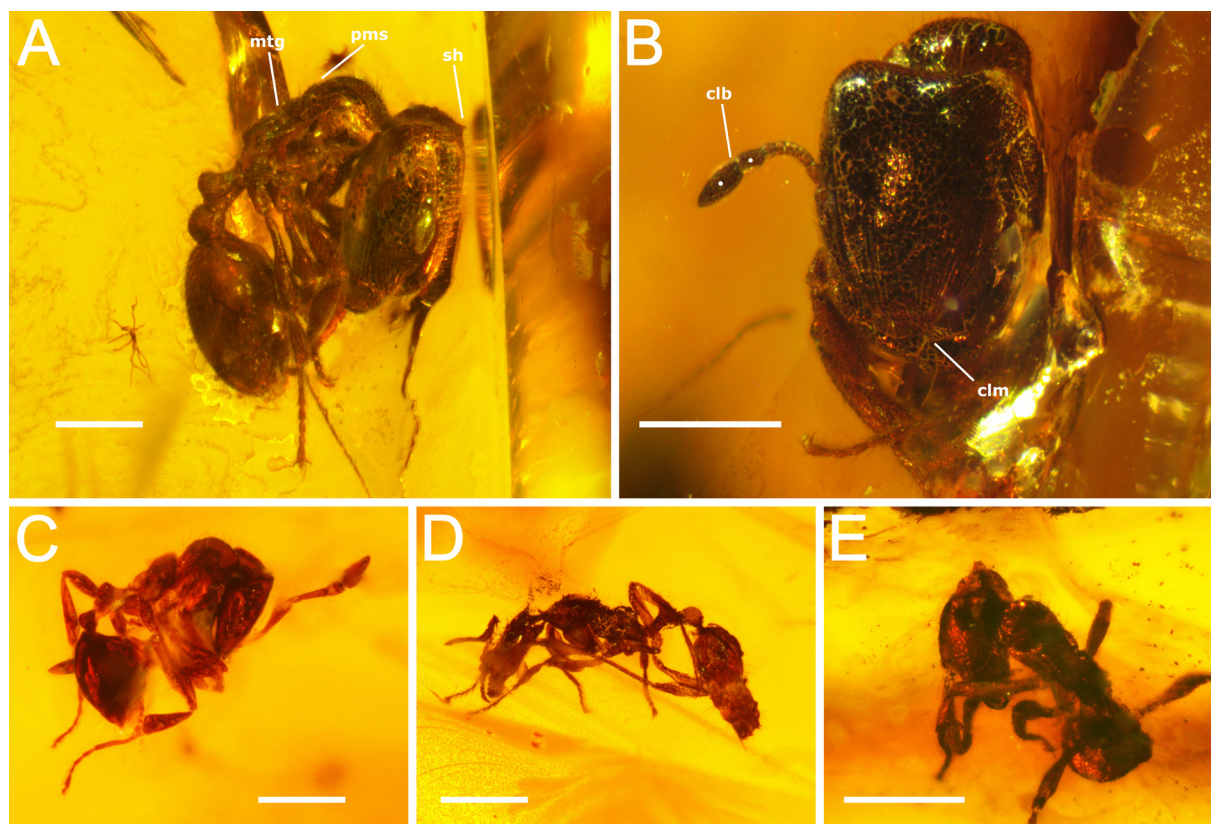


Figure 1. †*Carebara andrushchenkoi* sp. nov., photomicrographs showing certain key features. Holotype soldier KA-234a (major worker): A— lateral view; B— head in full-face view. Paratype minor worker KA-234b: C— lateral oblique view. Minor workers: D— KA-234c, lateral view; E— KA-234d, lateral oblique view. Abbreviations: antennal club (clb), clypeal margin (clm), metanotal groove (mtg), promesonotal suture (pms), small horns (sh). Scale bar – 0.5 mm.

Measurements (in mm) and indices. *Holotype № K-234a (major worker):* HL – 0.97; HW – 0.82; SL – 0.40; PdL – 0.10; Fl1 – 0.02; Fl2 – 0.01; MdL – 0.14; WL – 0.90; PNW – 0.47; ESL – 0.01; ESD – 0.19; PrdL – 0.24; PrdH – 0.30; PtL – 0.24; PtH – 0.24; PtW – 0.17; PPL – 0.18; PPH – 0.20; PPW – 0.21; HFL – 0.57; HTL – 0.59; GL – 0.87; TL – 3.16.

CI – 1.18; SI₁ – 0.41; SI₂ – 0.49; MdI – 0.14; PI₁ – 1.00; PI₂ – 1.41; PI₃ – 0.21; PPI₁ – 0.90; PPI₂ – 0.95; PPI₃ – 1.24; PPI₄ – 0.26; ESLI – 0.01; ESDI – 19.00; MI – 1.91; PRI – 0.80.

Paratype № K-234b (minor worker): HL – 0.43; SL – 0.33; PdL – 0.01; WL – 0.58; PtL – 0.16; PtH – 0.14; PPL – 0.10; PPH – 0.11; HFL – 0.41; GL – 0.47; TL – 1.74.

Minor worker № K-234c: HL – 0.44; SL – 0.29; PdL – 0.08; MdL – 0.17; WL – 0.64; PrdL – 0.17; PrdH – 0.21; PtL – 0.26; PtH – 0.14; PPL – 0.17; PPH – 0.11; HFL – 0.44; HTL – 0.40; GL – 0.71; TL – 2.22.

Minor worker № K-234d: WL – 0.46; PtL – 0.20; PPW – 0.09; HTL – 0.31.

Description. Holotype soldier № K-234a (major worker). *Head*: Head clearly longer than broad, roughly rectangular in full face view. Posterior margin moderately concave. Posterolateral corners roundly prominent. In profile view, vertex posteriorly with a pair of acute small horns, dorsum of head slightly convex. Mandibles with 6 teeth. Median portion of clypeus depressed longitudinally, biconvex and divergent forward. Antennae 11-merous with distinct two-segmented club. Pedicel long, approximately two times as long as wide. Second to eighth flagellomeres distinctly broader than long. Antennal scape short, clearly not reaching posterior margin of head. Ocelli absent, eyes very small, situated at anterior one-third of lateral head. Mandibles smooth and shiny. Anterior 2/3 of head surface longitudinally finely striate, posterior 1/3 of head surface and lateral sides smooth and shiny.

Mesosoma: Promesonotum weakly convex. Promesonotal suture weak, observed in dorsal view. Mesoscutum and mesoscutellum differentiated, metanotal groove wide and deep. Dorsal face of propodeum short, flat, sloping backwards, densely foveolate-punctate. Lateral surface of propodeum transversally rugose. Propodeal teeth very short, triangular.

Metasoma: Petiole (abdominal segment II) with relatively short and thick node, anterior and posterior faces sloping, dorsal face roundly convex. Postpetiole (abdominal segment III) subglobular. Petiole and postpetiole densely foveolate-punctate. Gaster ovoid, smooth and shiny, the first tergite much larger than following one.

Legs: Meso- and metatibiae without spurs.

Total length ca. 3.16 mm. Entire body covered with subdecumbent pubescence and long erect to suberect hairs; scape, middle and hind tibiae with short subdecumbent hairs only.

Paratype minor worker № K-234b: *Head*: Head longer than broad, not much massive; vertex posteriorly without small horns in profile. Eyes not observed. Antennae 11-merous with distinct two-segmented club. Scape relatively short, its apex reaching 3/4 of the distance from socket to posterolateral corner of head. Pedicel long, approximately two times as long as wide.

Mesosoma: Promesonotum moderately convex. Propodeum without teeth, dorsum convex.

Metasoma: Petiole (abdominal segment II) with relatively long peduncle, node high, with rounded dorsum. Postpetiole (abdominal segment III) with gradually rounded dorsum, lower than petiole, somewhat longer than high.

Legs: Meso- and metatibiae without spurs.

Total length ca. 1.74 mm. The pubescence is approximately the same as that of the major worker. Males and females are unknown.

Notes. The minor workers are deformed and autoclaved to varying degrees, but most likely belong to the same species as the soldier. This is supported by the fact that all specimens have the same type of pubescence and lack spurs on their tibiae. However, since the minor workers № K-234c, d are too severely deformed, we decided not to designate them as paratypes, but rather as simply examined specimens. †*Carebara andrushchenkoi* **sp. nov.** is well distinguished from all other fossil *Carebara* species by the following of features: (1) The soldier of †*C. andrushchenkoi* **sp. nov.** differs from that of †*C. kutscheri* by being half the size, possessing horns on the vertex posteriorly, lacking spurs on the tibiae, having smaller eyes, more pronounced body sculpture, and a more pilose body; (2) The minor worker of †*C. andrushchenkoi* **sp. nov.** differs from that of †*C. nitida* and †*C. antiqua* by the absence of teeth on the propodeum posterodorsally and a more pilose body; (3) The species †*C. groehni*, which is described based on the male, cannot be directly compared to the new species; (4) Since the character of sculpture and pilosity of body in females (queens) and worker castes is generally correlated, the female of †*C. ucrainica* can be a different species according to a smoother head and reduced pilosity compared to the new species, as well as a shorter postpetiole and the absence of vertex horns.

Discussion

At present, it is impossible to assign or compare the new species with any species group within the genus *Carebara*, as its taxonomy has not yet been fully developed. There are taxonomic classifications at the

regional level: North America (Fernández 2004), Colombia (Fernández & Serna 2019), Afrotropics (Fischer *et al.* 2014), Malagasy (Azorsa & Fisher 2018), India (Bharti & Kumar 2013, Akbar & Bharti 2017), Arabian Peninsula (Sharaf & Aldawood 2013), China (Liu *et al.* 2024), Thailand (Wimolsuthikul *et al.* 2024), Cambodia (Hosoishi *et al.* 2022), Australia (Heterick 2021), although many regions still require attention. The horns on the occipital region of †*Carebara andrushchenkoi* sp. nov. are an interesting feature, but they are widely encountered across species around the globe.

Radchenko *et al.* (2019) reported the first discovery of a soldier subcaste in the species †*Carebara kutscheri* from Late Eocene Bitterfeld amber. Thus, we have discovered the second species with a soldier subcaste and for the first time from Late Eocene Baltic amber. These findings provide direct evidence of significant polymorphism and, consequently, of complex social organization within ant colonies, which was already present in Europe at least by the Late Eocene. Given the rarity of *Carebara* species found in Late Eocene European ambers, it is likely that they did not lead an arboreal lifestyle and, similar to recent species, inhabiting soil or leaf litter. The discovery expands our knowledge of the morphological diversity of the genus *Carebara* in the Eocene.

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