

The Ant Subfamilies Ponerinae, Cerapachyinae, and Pseudomyrmecinae (Hymenoptera, Formicidae) in the Late Eocene Ambers of Europe

G. M. Dlussky

Moscow State University, Biological Faculty, Moscow, 119899 Russia

e-mail: dlussky@mail.ru

Received May 20, 2008

Abstract—The ant subfamilies Ponerinae, Cerapachyinae and Pseudomyrmecinae are revised in the Baltic, Bitterfeld, Rovno, and Scandinavian ambers of the Late Eocene age. Thirteen new species are described: *Amblyopone groehni* sp. n., *A. electrina* sp. n., *Pachycondyla conservata* sp. n., *P. tristis* sp. n., *Ponera lobulifera* sp. n., *P. mayri* sp. n., *P. wheeleri* sp. n., *Gnamptogenys rohdendorfi* sp. n., *Bradoponera similis* sp. n., *Proceratium eocenicum* sp. n. (Ponerinae), *Procerapachys sulcatus* sp. n. (Cerapachyinae), *Tetraponera europaea* sp. n., and *T. groehni* sp. n. (Pseudomyrmecinae). *Tetraponera angustata* (Mayr) is synonymized with *T. simplex* (Mayr). Keys to species are provided.

DOI: 10.1134/S0031030109090068

Key words: Ants, Ponerinae, Cerapachyinae, Pseudomyrmecinae, *Amblyopone*, *Bradoponera*, *Hypoponera*, *Electroponera*, *Gnamptogenys*, *Pachycondyla*, *Platythyrea*, *Ponera*, *Procerapachys*, *Proceratium*, *Tetraponera*, new species, keys, Baltic amber, Bitterfeld amber, Rovno amber, Scandinavian amber, Late Eocene.

INTRODUCTION

Species from the subfamilies Ponerinae, Cerapachyinae, and Pseudomyrmecinae comprise only a small part of the ant diversity in the Late Eocene ambers: the proportion of their individuals in various ambers does not exceed 5%. However, because each of these species is represented by only a few specimens, the share of these subfamilies in the total number of species is significantly larger, 16.8% (29 out of 173). Yet, by this parameter, too, they are less diverse than the “large” subfamilies, Dolichoderinae, Formicinae, and Myrmicinae (39, 41, and 56 species, respectively). At the same time, Ponerinae, Cerapachyinae, and Pseudomyrmecinae are of particular interest because representatives of these subfamilies display numerous plesiomorphic characters and are highly important for reconstructing the phylogeny of ants.

In the recent years I examined extensive collections of ants preserved in Baltic (Kaliningrad Region of Russia and Poland), Bitterfeld (West Germany), Rovno (Ukraine), and Scandinavian (Denmark) ambers, including all the survived types of the species previously described by Mayr (1868) and Wheeler (1915). In total, more than 5000 ant inclusions were studied, including 140 individuals from the subfamilies revised here. The Late Eocene age, shared by all of the examined ambers, and the assumed independence of their origin are discussed in more detail elsewhere (Perk-

ovsky et al., 2007; Dlussky and Rasnitsyn, 2009, this volume).

The following collections were examined (the abbreviations used in this publication are given in parentheses):

Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN): Baltic amber;

Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev (SIZK): Rovno amber;

Museum Ziemi PAN, Warsaw, Poland (MZ PAN): Baltic amber;

Natural History Museum, London (NHML): Baltic amber;

Naturhistorische Museum in Wien, Austria (NHMW): types of G. Mayr (1868) from the Baltic amber;

Geowissenschaftlicher Zentrum der Georg-August-Universität, Göttingen, Germany (GZG.BST): collection of Baltic amber, which is part of the collection formerly owned by the Geological Institute of Königsberg and described by W. M. Wheeler (1915); contains some of Wheeler’s types. Below, in the lists of examined material for each species I indicated both the new numbers (preceded by GZG.BST) and the old numbers from the Königsberg collection (in parentheses); only the new numbers are given elsewhere in the text.

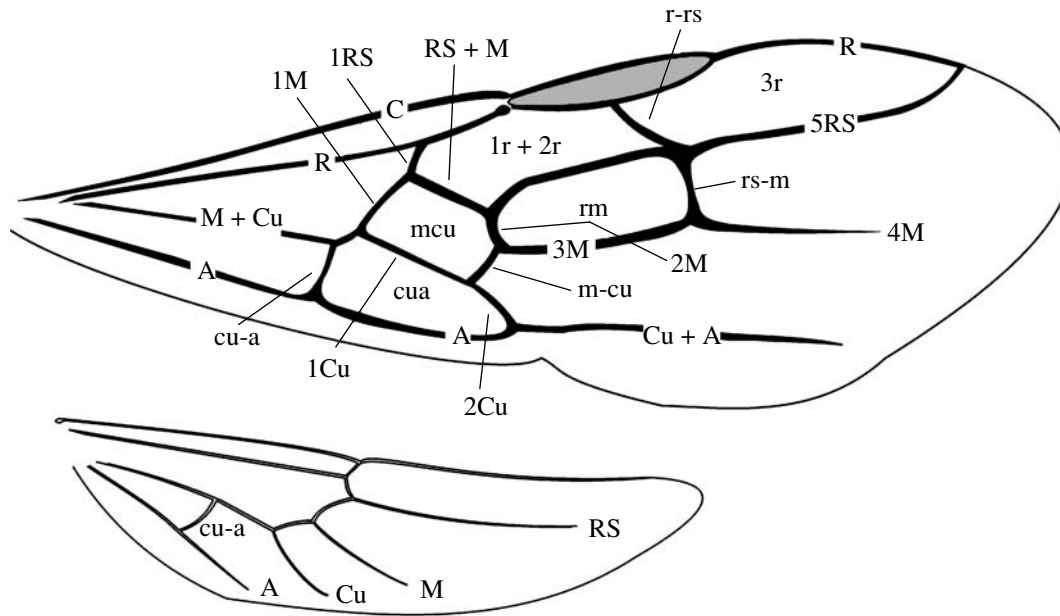


Fig. 1. Wings of a gyne *Gnamptogenys europaea* (Mayr), neotype SIZK, no. UA-822. Designations: (C, R, RS, M, Cu, A) longitudinal veins, (1RS, RS + M, 2M, etc.) their sections, (r-rs, r-m, m-cu, etc.) crossveins, (1r + 2r, rm, m-cu, cua) cells.

Humboldt Museum, Berlin, Germany (HM): Bitterfeld amber;

Zoological Museum of the University of Copenhagen (ZMUC): Scandinavian and Baltic amber;

Personal collection of Carsten Gröhn, Glinde, Germany (CGC): Baltic and Bitterfeld ambers; type specimens from this collection are deposited at the Geological-Paleontological Institute and Museum at the University of Hamburg (Geologische-Paläontologischer Institut der Universität Hamburg) (GPIH);

Personal collection of Manfred Kutscher, Sassnitz, Rügen, Germany (MKC), recently acquired by the Geowissenschaftlicher Zentrum der Universität Göttingen (GZG.BST): Bitterfeld amber;

Personal collection of V. A. Gusakov, Korolev, Moscow Region (VGC): Baltic amber.

All the drawings illustrate actual specimens and were prepared by tracing over photographs, taken using an Olympus SZX9 stereomicroscope equipped with an Olympus Camedia C-3030 digital camera or on a Zeiss Stemi SV11 stereomicroscope equipped with an Axio-Cam HRC camera, using CorelDraw 9 software. The thick continuous lines show margins of tergites; the thin continuous lines, elements of sculpture and hairs; and the dashed lines, folds and assumed margins of tergites by dashed lines. Extraneous objects obstructing the inclusion are represented by filled areas. Only the hairs visible on the inclusion are illustrated. It should be kept in mind that hairs are not always preserved and some are visible only if illuminated at a particular angle.

In the systematics of recent ants, measurements are taken in standard positions: the mesosoma and petiole

are measured strictly in profile, the head from above (in full face view), and the scape so oriented that its measured length is maximal. Because it is often impossible to see certain parts of the inclusion from the proper angle, I could not take measurements from every specimen and, therefore, only those taken more or less precisely are included. The abbreviations for measurements are as follows: **AL**, length of mesosoma from articulation with head to articulation with petiole; **BL**, combined body length; **ED**, maximum eye diameter; **F3**, length of metafemur; **FWL**, length of forewing; **HL**, length of head without mandibles; **HW**, maximum width of head without eyes; **MdL**, length of mandible; **PptL**, length of postpetiole; **PptH**, height of postpetiole; **PptW**, maximum width of postpetiole; **PtL**, length of petiole; **PtH**, maximum height of petiole; **PtW**, maximum width of petiole; **SL**, length of scape.

The body length is reported at the beginning of each species description for the following reasons. First, it cannot be measured precisely, because gastral segments in ants can be drawn into one another. At the same time, in the process of identification, even an approximate size allows to immediately exclude a significantly larger or smaller ant species.

The generic diagnoses and species descriptions below include only those characters that can be seen on specimens enclosed in amber. The problem is that some important diagnostic characters cannot be seen on inclusions. This is particularly true about mouthparts and terminalia. When an ant becomes trapped into resin, it often releases liquid from its mouth and anus. This liquid mixes with the resin to form an opaque "cloud". Pubescence also tends to be preserved incom-

pletely. Descriptions of the previously known species were composed anew, except when I have not seen specimens of a given species. In that case, the original description, somewhat modified and brought into accord with modern terminology, is included.

Data on the number of genera and species are taken from the latest version of the electronic catalogue by Bolton et al. (2006). The complete generic synonymy can be found in that catalogue and is not reproduced here. The nomenclature of the forewing venation used in this paper is illustrated in Fig. 1. Other terms follow Bolton (1994).

Subfamily Ponerinae Lepeletier, 1835

Recently, Bolton (2003) proposed a new higher classification of ants, with 21 subfamilies. He divided the former subfamily Ponerinae into six subfamilies (Amblyoponinae, Ponerinae, Ectatomminae, Heteroponerinae, Paraponerinae, and Proceratiinae) and the former subfamily Myrmicinae into the small subfamily Agroecomyrmecinae Wheeler, with only three genera (the recent *Tatuidris* Brown et Kempf and the fossil *Agroecomyrmex* Wheeler and *Eulithomyrmex* Carpenter), and the giant subfamily Myrmicinae, with 24 tribes and 143 genera. At the same time, recognizing that his newly created subfamilies are closer to each other than to any other ants, Bolton grouped them into novel informal taxonomic categories, not recognized by the International Code of Zoological Nomenclature, such as “the poneromorph subfamilies,” “the myrmicomorph subfamilies,” etc.

If we accept Bolton’s approach, the number of subfamilies in the Formicidae can be increased to infinity, making the classification increasingly unwieldy. In particular, Myrmicinae are significantly more diverse than Ponerinae, and I already suggested that different groups within that subfamily had independent origins (Dlussky and Fedoseeva, 1988). In our opinion, two solutions of this problem are possible: conservative and radical. The conservative approach means using the traditional classification (Dlussky and Fedoseeva, 1988; Bolton, 1994, 1995, etc.), possibly with some adjustments. The other approach is its radical reorganization. In that case, ants should comprise the superfamily Formicoidea with the families Formicidae, Poneridae, Myrmecidae, etc., corresponding to the informal “groups of subfamilies” introduced by Bolton. This solution has already been proposed in the past (Bernard, 1951; Rasnitsyn, 1966), but it has not been accepted by myrmecologists. At least for now, I prefer the more conservative approach and consider Ponerinae as one subfamily with the same composition as in Bolton’s earlier works (Bolton, 1994, 1995).

Defined in this way, the Ponerinae includes 46 recent and 13 extinct genera (Bolton et al., 2006). The oldest fossil Ponerinae, from the genus *Afropone*, have been described from the Turonian deposits in southern Africa (Dlussky et al., 2004). To date, approx-

imately ten species have been described from Baltic amber. Below I describe additional ten species from Baltic and similar ambers.

Unlike other ants, mostly represented by workers, Ponerinae are represented predominantly by alate sexuals. For example, among the 19 amber specimens of *Gnamptogenys europea* known to date, two are alate gynes, 15 are males, and only one is a worker. Among the 33 *Pachycondyla succinea*, 28 are alate gynes and five are males. Among the 59 inclusions of *Hypoponera* and *Ponera* (not differentiated from one another by Mayr and Wheeler), 14 are alate gynes, 42 are males, and only three are workers (Mayr, 1868; Wheeler, 1915, and original data). *Pachycondyla gracillicornis*, *P. baltica*, and the species *Amblyopone electrina*, *Gnamptogenys rohdendorfi*, *Proceratium eocenicum*, *Pachyconyla conservata*, and *P. tristis*, which are described below, are also represented exclusively by sexuals.

This is explained primarily by the fact that the vast majority of Ponerinae live in soil and litter, and almost never climb up the tree trunks. During their nuptial flight, however, the gynes and males first ascend up the grass or tree trunks and only from there they eventually take wing. The only exception is the genus *Bradoponera*, represented in amber mostly by workers.

Traditionally, the systematics of ants is based entirely on workers. Typically, identification of gynes of the Ponerinae poses no difficulties, because many of their characters are similar to those of the workers. At the same time, males differ significantly from both gynes and workers, and their identification is highly difficult even for an expert. Identification keys to males are available only for the European species. For many species and even genera, males are either unknown, or their existing formal descriptions are superficial and useless for identification. In this study I am partly filling in this gap by redescribing males of the previously described and describing those of new species of Ponerinae from the Late Eocene ambers. Because males of ants are poorly studied, we cannot compare males of fossil species with those of recent ones; thus, the new species are compared below only with the previously described fossils.

Tribe Amblyoponini Lepeletier, 1835

Genus *Amblyopone* Erichson, 1842

Type species. *Amblyopone australis* Erichson, 1842, by monotypy.

Diagnosis. Workers and gynes. Head subrectangular or subtrapezoidal, widening towards anterior margin. Eyes, if present, displaced backwards. Frontal carinae broadly separated, frontal lobes partly or completely covering antennal bases. Mandibles elongated, linear, with large teeth, not adhering to the anterior margin of clypeus when closed. Antennae usually 12-segmented, rarely 9- or 11-segmented. Flagellum not flat-

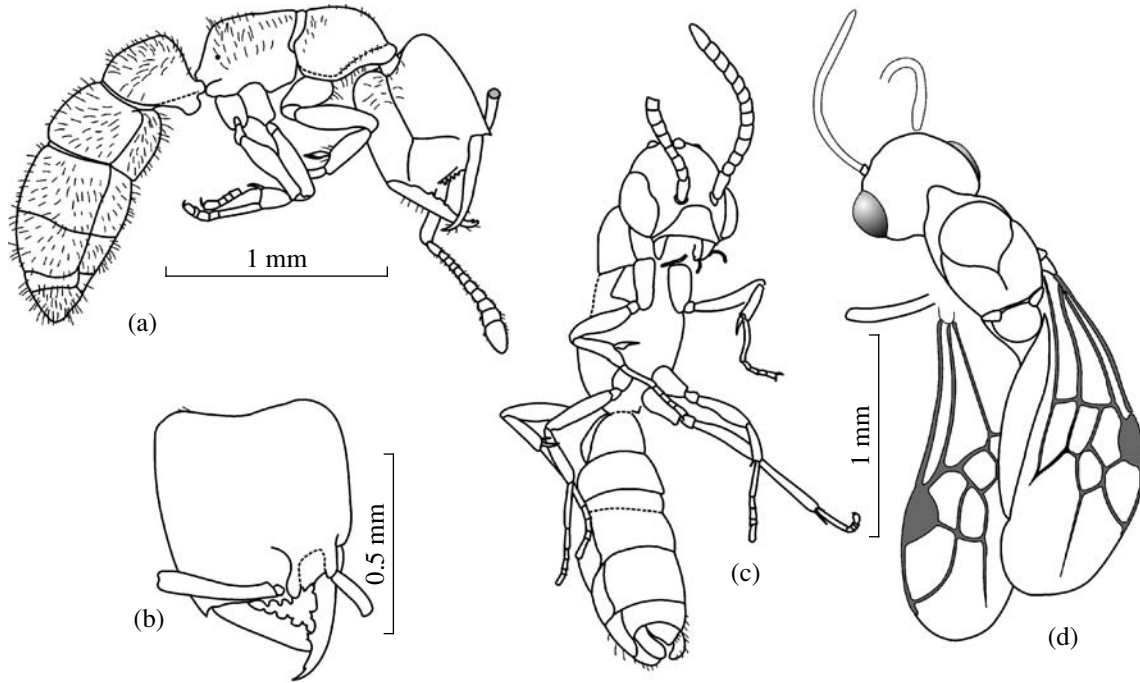


Fig. 2. Species of the genus *Amblyopone*: (a–b) *Amblyopone groehni* sp. n., worker, holotype GPIH, no. 4509 (CGC, no. 3356): a general view of the inclusion (a) and head in dorsal aspect (b); (c–d) *Amblyopone electrina*, male, holotype, GPIH, no. 4508 (CGC, no. 3335): general view of the inclusion in ventral (c) and in dorsal aspects (d).

tened, round in cross section. Metatibia with two spurs, one simple and another pectinate. Petiole without free posterior surface, broadly attached to first gastral segment, in dorsal and lateral views separated from gaster only by constriction. Helcium in profile attached to upper part of anterior surface of first gastral segment.

Males. Head margin behind eyes well-rounded, without distinct occipital corners. Mandibles small, without teeth. Frontal carinae reduced. Antennal insertions exposed, contiguous with posterior margin of clypeus. Antennae 13-segmented, filiform, with short scape. Eyes large, convex. Ocelli well developed. Metatibiae each with two spurs. Petiole as in workers. Pygidium apically without spine. Cerci absent. Forewing usually with complete set of cells. Hindwing without jugal lobe.

Composition and distribution. The modern fauna comprises 69 species occurring on all continents, but predominantly in the tropics. Fifteen species are known from southern Palearctic (Bolton et al., 2006). No fossil representatives of this genus have been previously known.

Amblyopone groehni Dlussky, sp. nov.

Etymology. In honor of Carsten Gröhn, the collector in whose collection the species was discovered.

Holotype. Worker, GPIH, no. 4509 (CGC, no. 3356), excellently preserved inclusion; Baltic amber, Late Eocene.

Description. Worker (Figs. 2a, 2b). BL ca. 3 mm. The head is subtrapezoidal, slightly longer than wide, widened anteriorly, with distinct, rounded occipital corners and a weakly concave occipital margin. Eyes are absent (possibly reduced to a single ommatidium not discernible from the surface sculpture). Frontal carinae are short and strongly diverging. Frontal lobes cover antennal insertions. The central part of the clypeus, between the antennal insertions, with a longitudinal depression. The anterior margin of the clypeus with seven teeth. The antennae are 12-segmented. The scape is short and not nearly reaching the occipital margin of the head. The flagellomeres become conspicuously wider towards the apex of the antenna, but do not form a distinct club. The mandibles are linear, with one apical and one preapical tooth, close-set, followed by three bifid teeth separated from the apical and preapical ones by a diastema, and with two simple denticles at the base. The palpi are not visible. The pronotum is separated from the rest of the mesosoma by a deep suture, other segments of the mesosoma are completely fused. The dorsal surface is smooth. The pronotum is well-rounded anteriorly. The dorsal and the declivous surfaces of the propodeum in profile form an obtuse angle, the declivous surface is straight in profile. The legs are short and thick. The apices of the meso- and metatibiae each with two spurs; one of the two spurs on the metatibia is pectinate. The anterior and the dorsal surfaces of the petiole in profile are weakly convex, forming

together a rounded obtuse angle. The lower side of the petiole anteriorly with a large rounded lobe.

The body is shiny, with delicate shagreened sculpture, sparse decumbent pubescence, and numerous curved erect hairs.

Gynes and males are unknown.

Measurements (mm): AL 0.95, HL 0.60, SL 0.32.

Comparison. The reduced eyes and the structure of mandibles and the anterior margin of clypeus indicate that the new species belongs to the Palearctic species group *A. denticulata* (Roger, 1859) (former genus *Stigmatomma* Roger, 1859). However, no recent species of this group is known to have the same combination of characters. Among species of this group the eyes are reduced, completely or to a single ommatidium, in *A. denticulata* (Roger, 1859) (southern Europe, Libya, Turkey, Transcaucasia), *A. normandi* (Santschi, 1915) (northern Africa, Israel), *A. gaetulica* Baroni Urbani, 1978 (Morocco), *A. pertinax* Baroni Urbani 1978 (India), *A. besucheti* Baroni Urbani, 1978 (Seychelles), and *A. sakaii* Terayama, 1989 (Taiwan), while the bifid mandibular teeth are present only in *A. denticulata* and *A. besucheti*. However, the anterior gastral segments in these species are without long erect hairs. Erect hairs of *A. groehni* are similar to those of *A. sakaii*, but the latter species has the antennae 11-segmented and the mandibles with all the teeth simple, without a preapical tooth.

Material. Holotype.

Amblyopone electrina Dlussky, sp. nov.

Etymology. From the Latin *electrum* (amber).

Holotype. Male, GPIH, no. 4508 (CGC, no. 3335), excellently preserved inclusion; Baltic amber, Late Eocene.

Description. Male (Figs. 2c, 2d). BL ca. 3 mm. The head is widened anteriorly, distinctly longer than wide. The eyes are large, reniform, strongly shifted anteriorly, so that the gena is shorter than the diameter of the scape. The frontal carinae are absent. The clypeus is not dentate, with a weakly concave anterior margin. The antennae are relatively short and, if bent back, not nearly extending to the base of the petiole. The scape is twice as long as wide, somewhat exceeding the combined length of the two more distal antennomeres. The second antennomere is spherical. Each of the more distal antennomeres is somewhat longer than wide. The mandibles are not dentate, short, and not touching when closed. The maxillary and labial palpi are short. The pronotum is transverse. The scutum is weakly convex, with deep parapsidal furrows converging posteriorly to form a Y-shaped furrow. The scutellum is longer than wide. The propodeum is concealed by the wings and is not visible. The legs are relatively long. The meso- and the metatibiae each with two apical spurs. The lower side of the petiole anteriorly with

a small rounded lobe. The constriction between the first and the second gastral segments is distinct. The subgenital plate is triangular. The stipites are thick, curved and strongly rounded at apices.

The body is shiny, with barely visible shagreened sculpture. The unobstructed parts without decumbent pubescence. Erect hairs are visible only on the mandibles and the tip of the gaster.

The wings are broad. The forewing with closed cells 1 + 2r, 3r, rm, mcu, and cua. Cell 3r short and broad, its length only 1.7 times its maximum width, its apex is pointed and lies on the wing margin. On the right wing of the holotype, crossveins rs-m and r-rs meet RS separately, while on the left wing they meet RS at the same point, essentially forming a single crossvein. Cell mcu is pentagonal, on the left wing of the holotype it is approximately as long as wide, while on the right wing it is twice as long as wide. Vein section IRS is approximately half as long as 1M. The meeting of vein cu-a and M + Cu is proximal to the fork of 1M and 1Cu, being separated from it by less than half the length of 1Cu (more precisely, on the left wing by a distance 0.45 times as long as 1Cu, and on the right wing by a distance only slightly exceeding the vein width).

Workers and gynes are unknown.

Measurements (mm): AL 1.0, FWL 1.75.

Comparison. The new species cannot be a male of *A. groehni*. Males from the *A. denticulata* species group, to which *A. groehni* belongs, have the anterior clypeus margin straight or convex and armed with teeth. Moreover, the degree of pilosity is usually similar between the workers and males of one ant species. In the worker of *A. groehni* the entire body bears numerous erect hairs, while the male of *A. electrina* lacks hairs on its head, mesosoma, and most of the gaster.

Remarks. Because for the majority of recent species of the genus males remain unknown and no fossil males of this genus have been described so far, it is not possible to provide a comparison with other species.

Material. Holotype.

Tribe Ponerini Lepeletier, 1835

Genus *Hypoconera* Santschi, 1938

Type species. *Ponera abeillei* André, 1881, by original designation.

Diagnosis. Workers and gynes. Head subrectangular, longer than wide. Eyes, if present, situated in front of lateral midlength of head. Clypeus narrow, transverse, its anterior margin weakly convex and with small median lobe; median part of clypeus narrows posteriorly. Frontal carinae almost covering antennal insertions, forming frontal lobes, close-set in middle part, separated by median furrow. Antennae 12-segmented. Flagellum apically incrassate, without club or with 4- or 5-segmented club. Palpal formula 1.2 or 1.1. Mandibles triangular, with dentate masticatory margin.

Promesonotal suture well developed. Legs short. Meso- and metatibiae each with one spur. Claws simple. Petiole narrowly attached to first gastral segment, with thick scale. Subpetiolar process developed as simple lobe, without acute posteroventral angles and anterior hole or point. Helcium attached very low on high, vertical, anterior surface of first gastral segment.

Males. Occipital margin behind eyes well-rounded. Eyes large. Ocelli relatively small. Clypeus convex, with broadly rounded anterior margin. Antennal insertions exposed, distant from posterior margin of clypeus. Mandibles reduced, not touching, with only apical tooth. Antennae filiform, 13-segmented. Meso- and metatibiae each with one spur. Helcium as in gynes and workers. Pygidium without apical spine. Cerci absent. Forewing with complete set of veins. Hindwing without jugal lobe.

Composition and distribution. In the recent fauna, the genus *Hypoponera* comprises 170 described species, which occur on all continents, but are predominantly associated with the tropics. Eleven species occur in the southern Palearctic (Bolton et al., 2006). Among fossil species, this genus includes with certainty only *H. atavia* (Mayr), described from Baltic amber and found by myself also in Bitterfeld and Scandinavian ambers. It is possible that this genus also includes part of the species previously described by impressions and referred to the genus *Ponera* and the morphogenera *Poneropsis* and *Ponerites*. The generic placement of these impressions is discussed below under the genus *Ponera*.

Remarks. *Hypoponera* is among the least studied ant genera, and in the majority of its species the males are either unknown, or have been described in a formal, perfunctory manner.

***Hypoponera atavia* (Mayr, 1868)**

Ponera atavia Mayr, 1868, p. 72, pl. IV, figs. 66–69 (♀, ♂) (part.); Dalla Torre, 1893, p. 37; Handlirsch, 1907, p. 879; Wheeler, 1915, pp. 38–40, text-fig. 9 (♀); Taylor, 1964, p. 138; Burnham, 1978, p. 109; Bolton, 1995, p. 360; Dlussky, 1997, p. 61.

Hypoponera atavia (Mayr): Dlussky, 2002, pp. 295–297, Figs. 19–22.

LECTOTYPE. Designated by Dlussky (2002): alate gyne, NHMW, no. 1984/31/254, bearing the label “ST *Ponera atavia* Mayr, 1868. Eozoen. Baltischer Bernstein. Kollektion Handlirsch” and a handwritten label by Mayr “Von der jetzt an Europa, Algirer und N. America leb. *P. contracta* kaum zu untersch.”; completely preserved inclusion, partly obscured by extraneous inclusions. Baltic amber, Late Eocene.

DESCRIPTION. Worker (Figs. 3c–3g). BL ca. 3 mm. The head is subrectangular, longer than wide, with its occipital corners rounded and the occipital margin weakly convex. The eyes are strongly reduced, barely distinguishable from the surface sculpture and strongly shifted towards the front. The anterior margin of the clypeus is convex. The scape is short, not nearly

reaching the occipital margin. The first flagellomere is approximately as long as wide. The flagellomeres II to V each is shorter than wide. The four terminal flagellomeres are enlarged, forming a club. The mandibles are triangular, with an obtuse apical tooth, four large teeth in the middle part of the masticatory margin, and several small denticles near the base. The palpi are not visible. The pronotum, mesonotum, and propodeum are separated by shallow yet conspicuous sutures. The dorsum in profile is smooth, weakly convex, with barely noticeable promesonotal and mesopropodeal constrictions. The pronotum in profile is steeply curved anteriorly. The propodeum with declivity nearly straight, slightly shorter than dorsum. The surface of the propodeum is bent abruptly at the transition between the dorsum and the declivity. The legs are short and thick. The mesotibia with one simple, and the metatibia with one pectinate apical spur. The petiole with a high and thick scale. The scale in profile with its apex flattened, the anterior surface weakly concave, and the posterior surface weakly convex. The lower side of the petiole with a small rounded lobe. The gaster is cylindrical, with a distinct constriction between its first and second segments. The sting is well developed.

The body is weakly shiny, with distinct shagreened sculpture, dense decumbent pubescence, and relatively sparse erect and semierect hairs.

Gyne (Figs. 3a, 3b). BL ca. 3.5 mm. The head is subrectangular, longer than wide, with rounded occipital corners and straight occipital margin. The eyes are moderately large, oval, shifted anteriorly. The mandibles are triangular, no teeth are visible. The maxillary palpi are short. The scape is short, not reaching the occipital margin. The flagellomeres II to V each is shorter than wide. The four terminal flagellomeres are enlarged and form a club. The dorsal surface of the scutum is flat, its anterior surface is strongly curved. The propodeum in profile is angular, with its dorsum approximately as long as the declivity. The legs are short and thick. The meso- and metatibiae each with one pectinate spur at apex. The petiole is approximately as high as the propodeum, with a high and thick scale. The anterior surface of the petiole in profile is convex, forming a gradual transition into the dorsal surface, its posterior surface is nearly straight, forming a broadly rounded angle at the transition into the dorsal surface. The ventral view of the petiole is partly obscured by detritus; however, by rotating the specimen it is possible to see a lobe typical of *Hypoponera*: small, unperforated, and without acute posteroventral denticles. The gaster is cylindrical, with a distinct constriction between its first and second segments.

The body is weakly shiny, with fine shagreened sculpture and dense decumbent pubescence, including some raised hairs, which appear semierect. True semierect hairs are present only on the mandibles.

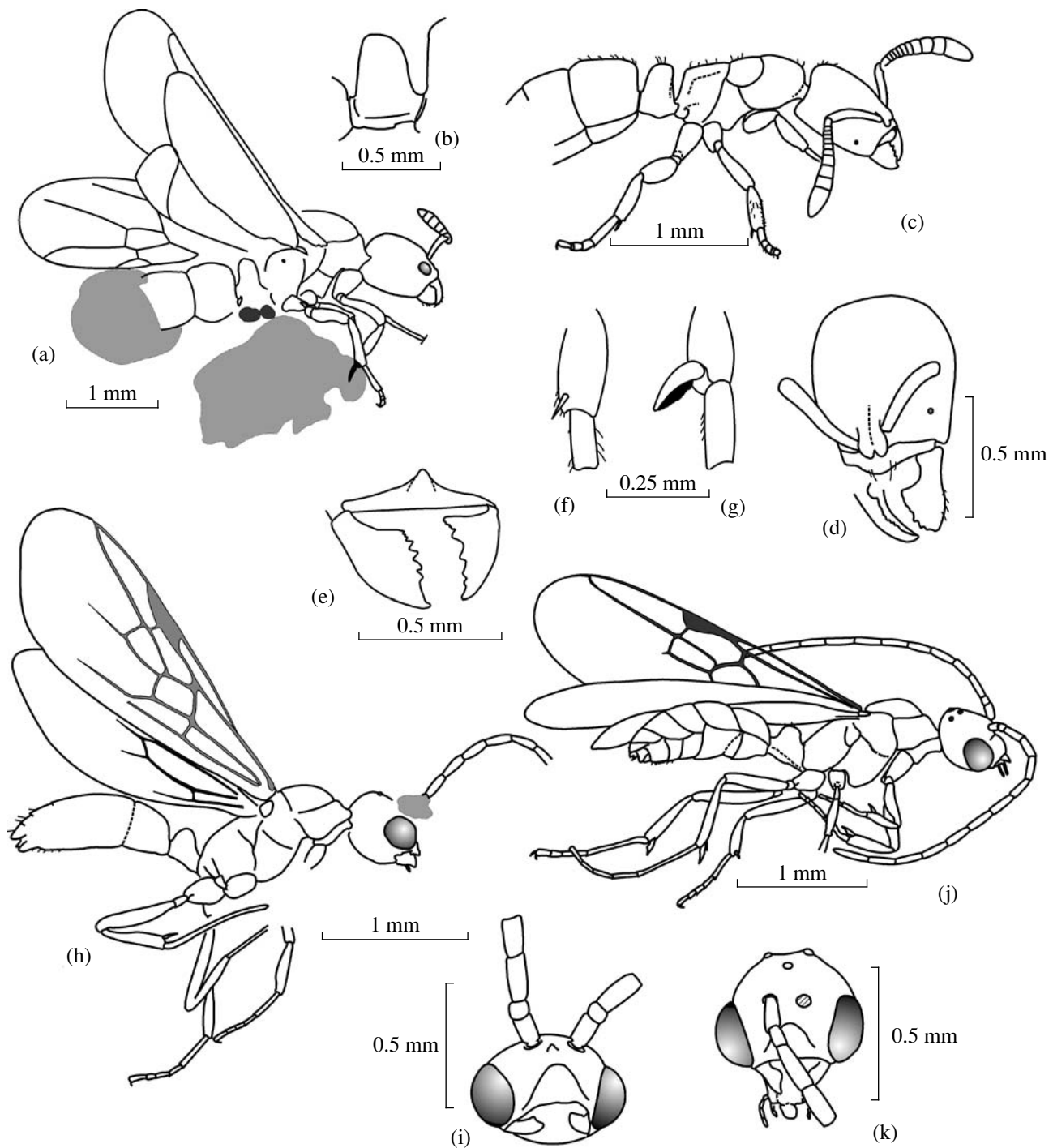


Fig. 3. *Hypoponera atavia* (Mayr): (a–b) gyne, lectotype NHMW, no. 1984/31/254: general view of the inclusion (a) and petiole in profile (b); (c–i) worker, ZMUC, no. 310: general view of the inclusion (c), head (d), mandibles (e), spurs on the mesotibiae (f), and same on the metatibiae (g); (h–i) male, MZ PAN, no. 5821: general view of the inclusion (h) and head (i); (j) male, GZG.BST (MKC), no. 27.019, general view of the inclusion; (k) male, MZ PAN, no. 11492, head.

The forewing with closed cells 1 + 2r, 3r, rm, and mcu. Cell 3r is long, with sides parallel for most of its length, approximately four times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cells rm and mcu are pentagonal. 2M is

short yet distinct. The distance between the points where crossveins rs-m and rs-s meet RS approximately equals to the length of rs-s. 1M is twice as long as 1RS. Cell mcu is approximately 1.5 times as long as wide. The meeting of crossvein cu-a and M + Cu is proximal

to the 1M and 1Cu fork, being separated from it by a distance approximately equal to half of vein width. Cell cua is open at the apex.

Male (Figs. 3h–3k). BL 2.8–3.2 mm. The head is round, approximately as long as wide, without distinct occipital corners, with its occipital margin rounded. The eyes are large, oval, strongly convex, strongly shifted anteriorly, their ventral margins almost touching bases of the mandibles. The ocelli are relatively small, the interocellar distance distinctly exceeds the ocellus diameter. The clypeus with the anterior margin weakly convex, the lateral parts narrow, and the median part extending far behind, yet not reaching the antennal insertions. The scape is short, twice as long as wide; the second antennomere is very short, slightly longer than wide; the third antennomere is the longest, its length exceeds the combined length of the first two antennomeres. The mandibles are short, reduced, without dentation on the masticatory margins, not touching when closed. The palpi are short, not protruding outside the oral cavity. The scutum is convex in its anterior part and flat on its dorsal side. The parapsidal furrows are absent. The propodeum in profile is smoothly curved. The legs are of moderate length. The mesotibiae each with one simple, and the metatibiae each with one pectinate spur. The specimen GZG.BST (MKC), no. 27.019 additionally has a short simple spur on its right metatibia, but not on the left one. The petiole with a scale, which is rounded in profile, and a short peduncle; the ventral side of the petiole without lobes or dentation. The constriction between the first and the second gastral segments is distinct. The stipites are wide and strongly rounded.

The body is weakly shiny, with fine shagreened sculpture, rather abundant decumbent pubescence, and sparse erect hairs. In several areas the pubescence is raised, so that the hairs appear semierect or even erect.

The forewing with venation variable, sometimes varying between the left and the right wings of the same individual. Cells 1 + 2r, 3r, rm, and mcu are always closed, cell cua is closed only in some individuals. Cell 3r is 4–6 times as long as its maximum width, its apex is pointed and lies on the wing margin. Crossveins rs-m and r-rs usually meet RS separately, but the distance between their junction points varies. 2M usually is present, but occasionally RS and 3M meet in a common node. The vein section 1RS is less than half as long as 1M. Cell mcu is 1.4–1.6 times as long as wide. The meeting of cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by a distance exceeding vein width but smaller than one third of the length of 1Cu.

M e a s u r e m e n t s (mm): Workers: spec. ZMUC, no. 310: AL 0.875, HL 0.75, SL 0.40, PtL 0.25; spec. ZMUC, no. 311: AL 0.90, HL 0.625. Gynes: lectotype NHMW, no. 1984/31/254: AL 1.2, FWL 3.3; spec. MZ PAN, no. 6953: HL 0.625, SL 0.40. Males: spec. CGC, no. 90a: AL 1.075; spec. CGC, no. 90b: AL 1.125; spec.

CGC, no. 90c: AL 1.325; spec. GZG.BST (MKC), no. 27.019: AL 1.1, FWL 2.65; spec. GZG.BST (MKC), no. 27.194. AL 1.0, HL 0.575, HW 0.45, FWL 2.4; spec. MZ PAN, no. 5821. AL 0.97, F3L 0.56, FWL 2.4; spec. MZ PAN, no.11492. AL 1.125, HL 0.65, FWL 3.0.

R e m a r k s. The species of Ponerinae most common in Baltic amber has been originally described by Mayr (1868) as *Ponera atavia*, based on 8 gynes and five males. The description of *Ponera atavia* was merely formal and perfunctory. Mayr wrote that this species was practically indistinguishable from the European *Ponera contracta* Latreille (= *Ponera coarctata* Latreille); in his description he used only characters of sculpture and pubescence, which are similar in most species of *Ponera* and *Hypoponera*. In his description of the male, he pointed out the presence of parapsidal furrows on scutum, which, in his opinion, are absent in recent species of *Ponera*, but present in some *Pachycondyla*. However, the drawing of a male that he supplied lacks these furrows, while instead showing a pygidial spine (characteristic of the genus *Ponera*). Later, Wheeler (1915) discovered additional five gynes and 22 males of this species in Königsberg collections, but he did not redescribe the species. Additionally, he found and described a worker specimen that he referred to this species. That worker differed significantly from *Ponera coarctata*, which was specifically emphasized by Wheeler. Later yet, Taylor (1964), in his review of the fossil species described in the genus *Ponera*, wrote that this species should indeed be left in *Ponera*, but did not provide any supporting reasons. Only two syntypes of Mayr at the NHMW and three males identified by Wheeler as *Ponera atavia* at the GZG are known to currently exist. All other specimens, including the worker described by Wheeler, have apparently been lost during the World War II.

My study of the specimens described by Mayr and Wheeler as *Ponera atavia* has demonstrated that these belong to various genera and species. The gyne syntype (designated as the lectotype by Dlussky, 2002) belongs to the genus *Hypoponera*, because it lacks the perforated lobe and posteriorly directed denticles on the ventral side of petiole, which are characteristic of *Ponera*. At the same time, it has to be pointed out that the gyne drawn in Mayr's work has a different wing venation and most probably belongs to a different species of *Ponera* or *Hypoponera*. The male syntype of *P. atavia* turned out to be a male of *Pachycondyla*, because it has two spurs on each meso- and metatibiae, instead of one in *Ponera* and *Hypoponera*. This individual, completely dissimilar from Mayr's drawing and not matching his description (it lacks parapsidal sutures), has been described as *Pachycondyla baltica* (Dlussky, 2002). Three males in the GZG collection, identified by Wheeler as *P. atavia*, in fact belong to two different species of the genus *Ponera*.

Based on Wheeler's drawing, the worker he described must be placed in *Hypoponera*. It is quite possible that it belongs to the same species as the gyne, because both have a similar shape of the propodeum and petiole. The workers I examined differed somewhat from the specimen described by Wheeler. Based on Wheeler's drawing, erect hairs in his specimen were longer and more abundant than in my specimen. Although it is possible that these workers belong to different species, it cannot be proven now because Wheeler's specimen is lost. At the same time, I think my specimens are more similar to workers of *Hypoponera atavia*. The reason is that on ant gynes the pilosity (erect hairs) is developed as well or stronger than on workers. On the specimen described by Wheeler it is distinctly better developed than on the gyne designated as the lectotype, while on our specimens it is more or less the same.

All the *Hypoponera* males I found in the studied collections clearly belong to one species; therefore they can be confidently considered as males of *H. atavia*.

Material. Besides lectotype, from Baltic amber: MZ PAN, nos. 5821 (♂), 6953 (♀), 11492 (♂), CGC, no. 90 (10 ♂ in one amber piece). Bitterfeld amber: GZG.BST (MKC), nos. 27.009 (♂), 27.019 (♂), 27.028 (♂), 27.194 (♂). Scandinavian amber: ZMUC, nos. 307 labeled "V. G. Henningsen, 31.05.61" (2 ♂ in one amber piece); 310 labeled "V. G. Henningsen, 06.03.58" (♀); 311 labeled "Klasskov Andersen, 01.02.59" (♀).

Genus *Pachycondyla* Fr. Smith, 1858

Type species. *Formica crassinoda* Latreille, 1802, by subsequent designation by Emery (1901).

Diagnosis. Workers and gynes. Head subrectangular. Eyes always present in workers, although sometimes small. Eyes situated in front of lateral midlength of head. Clypeus narrow, transverse, with median part narrowing posteriorly. Frontal carinae covering antennal insertions, forming lobes, separated by furrow. Antennae 12-segmented, flagellomeres widening towards apex, but not forming a club. Palpal formula 4.4, 4.3, 3.3, or 2.2. Mandibles triangular, with masticatory margin dentate. Promesonotal suture, in workers, present and well developed. Meso- and metatibiae each with two spurs. Claws simple. Petiole with high node or scale. Helcium attachment very low on first gastral segment, the latter with high vertical anterior surface facing petiole.

Males. Occipital margin behind eyes well-rounded. Eyes large, convex. Ocelli well developed. Antennal insertions exposed. Antennae 13-segmented, filiform, with short scape. Clypeus convex, with anterior margin straight or rounded. Mandibles with masticatory margin not dentate, small, not touching when closed. Tibial spurs and claws as in workers and gynes. Petiole with thick node or scale, more rounded than in workers and

gynes. Subpetiolar process in the form of a tooth or a simple lobe, without acute posteroventral angles or an anterior hole or point. Helcium attachment very low on first gastral segment, but anterior surface of the latter not as strongly truncated as in workers and gynes. Pygidium with well developed apical spine. Cerci absent. Forewing with complete set of veins. Hindwing with jugal lobe in some species.

Composition and distribution. In the recent fauna, the genus *Pachycondyla* comprises 279 species, distributed on all continents, predominantly in the tropics (Bolton et al., 2006). Several species are known from China and Japan, one has been introduced to Caucasus.

The last catalogue by Bolton (Bolton et al., 2006) lists 11 fossil species of this genus: *P. labandeirai* Dlussky and Rasnitsyn, 2003 (Green River, USA, Middle Eocene), *P. rebekkae* Rust et Andersen, 1999 (Fur and Ølst formation, Denmark, Paleocene-Eocene boundary), *P. gracilicornis* (Mayr, 1868), *P. succinea* (Mayr, 1868) (Baltic amber, Late Eocene), *P. baltica* Dlussky, 2002 (Baltic amber, Late Eocene), *P. crawleyi* (Donisthorpe, 1920) (White Island, Great Britain, Oligocene, Donisthorpe, 1920), *P. calcarea* (Théobald, 1937), *P. dubia* (Théobald, 1937), *P. globiventris* (Théobald, 1937) (Haut-Rhin, France, Oligocene), *P. minutansata* (Zhang, 1989), and *P. nuberculata* (Zhang, 1989) (Shanwang, China, Miocene). Some of these species have been originally described in the genera *Ponera* (Mayr, 1868) and *Euponera* (Donisthorpe, 1920; Théobald, 1937; Zhang, 1989). *P. rebekkae* was transferred in the genus *Ypresiomyrma* already after the publication of Bolton's catalogue (Archibald et al., 2006). Additionally, representatives of this genus have been reported from the Miocene Dominican (Hölldobler and Wilson, 1990) and Mexican (Brown 1973) ambers. Below, two additional species of this genus, from Bitterfeld and Rovno ambers (Late Eocene), are described.

Pachycondyla succinea (Mayr, 1868)

Ponera succinea Mayr, 1868, p. 72, (♀); Dalla Torre, 1893, p. 42; Handlirsch, 1907, p. 879.

Euponera (*Trachymesopus*) *succinea* (Mayr): Wheeler, 1915, pp. 37–38, text-fig. 8; Burnham, 1978, p. 109.

Pachycondyla succinea (Mayr): Bolton, 1995, p. 310; Dlussky, 1997, p. 61.

Neotype. The species has been described by Mayr based on three specimens, none of which has survived. The GZG collection holds one specimen identified by Wheeler. To preserve the stability of nomenclature and taking into consideration that Wheeler had seen one of Mayr's syntypes, I am designating that specimen as the neotype. Neotype: alate gyne, GZG.BST.04677, ×11; a completely preserved inclusion, although the amber is somewhat clouded. Baltic amber, Late Eocene.

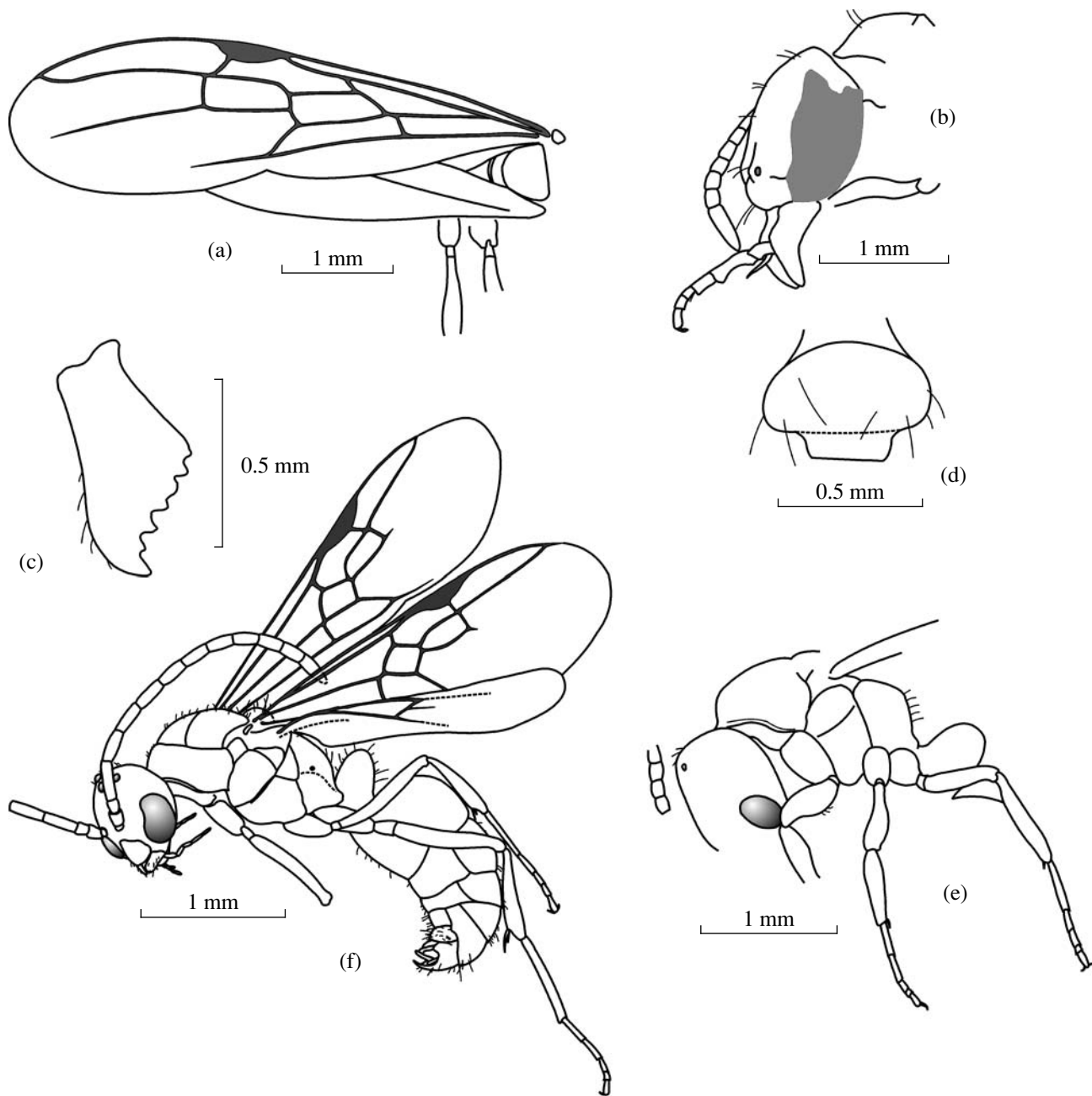


Fig. 4. *Pachycondyla succinea* (Mayr): (a) gyne, neotype no. GZG.BST.04677, forewing; (b) gyne, MZ PAN, no. 15953, head in profile; (c) gyne, PIN, no. 364/552, mandible; (d) gyne, ZMUC, no. 306, petiole in dorsal aspect; (e) gyne, SIZK, no. K-4235, mesosoma in profile; (f) male, GZG.BST (MKC), no. 27.018, general view of the inclusion.

Description. Gyne (Figs. 4a–4e). BL 4–6 mm. The head is slightly longer than wide, with well developed rounded occipital corners and a weakly concave occipital margin. The eyes are oval, weakly convex, strongly shifted anteriorly, so that the gena is half as long as the maximum eye diameter. The ocelli are small but conspicuous. The frontal carinae are close-set. The anterior margin of the clypeus protrudes anteriorly into a rounded lobe. The scape does not reach the occipital margin. Each flagellomere, except the first and the last,

is shorter than wide. The mandibles are triangular, each with 6 large teeth on the masticatory margin, without a tubercle on the outer margin. The dorsal surfaces of the scutum and the scutellum are flat, the constriction between them is almost absent. The propodeum in profile is angular, its dorsum and declivity are of approximately equal size. The legs are relatively short and thick. The meso- and the metatibiae each with two spurs of unequal length, a smaller simple spur and a larger spur, which is serrate on the mesotibiae and pec-

minate on the metatibiae. The petiole with a thick scale, approximately as high as the propodeum, approximately as long as wide, 1.5 times higher than long or wide. The scale in profile with its anterior surface slightly convex, its apex well-rounded, and its posterior surface straight; the petiole on its ventral side with a small rounded lobe. The gaster is cylindrical, with a distinct constriction between its first and second segments.

The head, mesosoma, and petiole are densely punctate, the gaster is smooth. The entire body with rather evenly distributed abundant erect and semierect hairs and with decumbent pubescence. On the gaster, the length of both the decumbent and the semierect hairs significantly exceeds the distance between adjacent hairs.

The forewing with closed cells 1 + 2r, 3r, rm, and mcu. Cell 3r is approximately five times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cell rm is distinctly quadrangular, 2M is approximately half as long as rs-m. Crossveins rs-m and r-rs meet RS separately and do not form a single crossvein. Cell mcu is pentagonal, approximately 1.5 times as long as wide. 1RS is 0.33 times as long as 1M. The meeting of vein cu-a and M + Cu is proximal to the fork of 1M and 1Cu and is separated from it by slightly less than the length of cu-a.

Male (described here for the first time) (Fig. 4f). BL 3.5–4.5 mm. The head is slightly expanding anteriorly, without distinct occipital corners, with a rounded occipital margin. The eyes are large, oval, concave, and shifted anteriorly, so that the gena is approximately as long as half the width of the flagellomeres. The ocelli are rather large, yet their diameter is smaller than the intercellular distance. The frontal carinae are absent. The clypeus with its median part convex and not carinate, with rounded anterior margin; its lateral parts are narrow. The antennae, if bent back, extend (or nearly extend) to the base of the second gastral segment. The scape is very short, only slightly longer than its width, three times shorter than the third antennomere; the second antennomere is 1.5 times shorter than scape, approximately as long as wide; the third antennomere is long, its length exceeds the combined length of the first two antennomeres. The mandibles are triangular, with an apical tooth, but without denticles on the masticatory margins. The maxillary palpi are long, almost reaching the occipital orifice. The mesosoma is robust and rather high. The pronotum is transverse. The scutum is evenly convex, with deep parapsidal furrows. The scutellum is strongly convex. The propodeum in profile is well-rounded. The legs are moderately long. The meso- and the metatibiae each with two spurs of unequal size, a smaller simple spur and a larger spur, which is serrate on the mesotibiae and pectinate on the metatibiae. The petiole with a high and thick scale, which is not as high as the propodeum. The dorsal margin of the scale in profile is rounded. The constriction between the first and

the second gastral segments is distinct. The last gastral tergite with the pygidial process (spine) thin, acute, and bent down. The stipites are wide, rounded at apices.

The body is shiny. The head is densely and the mesosoma and gaster are more sparsely punctate. The sides of the propodeum are rugose longitudinally. The petiole is smooth. The head, dorsal surface of mesosoma, scale, and gaster with numerous erect hairs. The femora and tibiae without erect hairs. The entire body with decumbent pubescence, most conspicuous on the gaster, where the hairs are several times as long as the distances between them.

The forewing with closed cells 1 + 2r, 3r, rm, mcu, and cua. Cell 3r is approximately five times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cell rm is quadrangular, but, in some individuals, 2M is very short. The meeting of crossvein rs-m and RS is distal to r-rs. Cell mcu is pentagonal, longer than wide. 1RS is approximately half as long as 1M. The meeting of crossvein cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by two widths of vein.

Workers are unknown.

Measurements (mm): Gynes: neotype GZG.BST.04677: AL 2.375, HL 1.25, SL 0.75, ED 0.15, PtL 0.55, PtH 0.8, FW 4.9; spec. MZ PAN, no. 15953: AL 2.1, HL 2.1; spec. SIZK, no. K-4235: AL 1.6. Males: spec. HM, no. 7/234: FWL 3; spec. GZG.BST (MKC), no. 27.018: AL 1.3, HL 0.7, FWL 2.7; spec. GZG.BST (MKC), no. 27.021: AL 1.4, HL 0.75, FWL 3.0; spec. NHML, no. In.29202: HL 0.67, HW 0.70, ED 0.37.

Remarks. This species has been described by Mayr in the genus *Ponera*. Later, Wheeler (1915) examined one of the syntypes of *Ponera succinea* and additional 18 gynes in Königsberg collections, redescribed the species, and included it into the subgenus *Trachymesopus* Emery, 1911 of the genus *Euponera* Forel, 1891, which is currently recognized as a junior synonym of *Pachycondyla* F. Smith, 1858. Males of this species are described here for the first time. Although demonstration of a male and a gyne being conspecific is difficult in the case of fossil ants, I believe that the males and gynes described here belong to the same species, because both are the most common *Pachycondyla* ants found in ambers.

The MZ PAN collection contains a strongly oxidized male specimen no. 190, similar in its visible characteristics to males of *P. succinea*, but of larger size (body length 8.5 mm, AL 3.1, HL 1.5, PtL 0.85, PtH 0.95, FWL 6). Most likely it belongs to a new species, but poor preservation precludes its description.

Material. Besides neotype, from Baltic amber: PIN, no. 364/552 (♀); MZ PAN, nos. 190 (♂), 15953 (♀); NHML, no. In. 2902 labeled "A. Thery, 1932" (♂). Bitterfeld amber: HM, no. 7/234 (♂); GZG.BST (MKC), nos. 27.018 (♂), 27.021 (♂). Rovno amber:

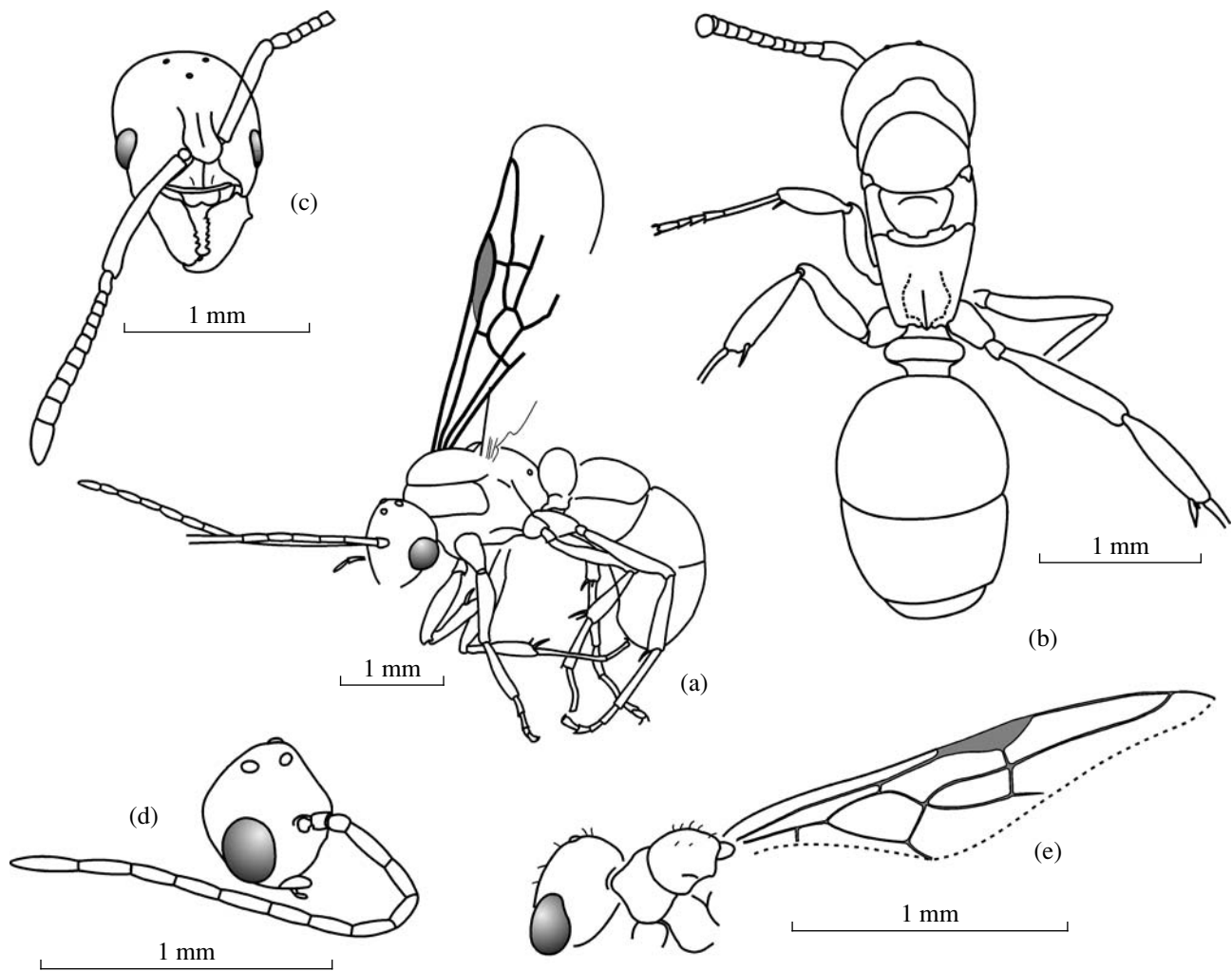


Fig. 5. Species of the genus *Pachycondyla*: (a) *Pachycondyla baltica* Dlussky, holotype NHMW, no. 1984/31/255, general view of the inclusion; (b–c) *Pachycondyla tristis* sp. n., gyne, holotype GZG.BST (MKC), no. 27.131: general view of the inclusion (b) and head (c); (d–e) *Pachycondyla conservata* sp. n., male, holotype SIZK, no. K-4456: head (d) and fragment of the inclusion with wing (e).

SIZK, nos. K-4235 (♀). Scandinavian amber: ZMUC, no. 306 labeled “G.V. Henningsen, 31.05.61” (♀).

Pachycondyla gracilicornis (Mayr, 1868)

Ponera gracilicornis Mayr, 1868, p. 72, nota (♀); Dalla Torre, 1893, p. 39; Handlirsch, 1907, p. 879.

?*Ponera gracilicornis* (Mayr): Wheeler, 1915, p. 40; Burnham, 1978, p. 110.

Pachycondyla gracilicornis (Mayr): Bolton, 1995, p. 305; Dlussky, 1997 p. 61.

Type s. The species has been described based on a single specimen in Menge’s collection, which has not survived. I have not found this species among the examined material.

Description (Mayr, 1868). **Worker.** BL 10.5 mm. Decumbent pubescence is abundant. The head, mesosoma, and gaster are delicately and densely punctate, with erect hairs short and sparse. The mandibles are sparsely and coarsely punctate. The compound

eyes are oval and rather flat, they are situated very close to the mandible bases and consist of numerous ommatidia. The first five flagellomeres are each longer than wide, the second flagellomere is slightly longer than the first. The gynes and males are unknown.

Remarks. Wheeler had not seen the type of this species, but suggested, judging from its size, that it could not be a *Ponera*. Later Bolton (1995) transferred this species to the genus *Pachycondyla*. The generic affinity of this ant cannot be determined from Mayr’s description, but most probably it, indeed, belongs to the genus *Pachycondyla*. The reason is that, in the late 19th century, researchers classified as *Ponera* the externally similar ants currently placed in the genera *Ponera* Latreille, *Hypoconera* Santschi, *Cryptopone* Emery, and *Pachycondyla* F. Smith. However, in the first three genera, the body length of workers never exceeds 5 mm, while workers of *Pachycondyla* can often be quite large.

Pachycondyla baltica Dlussky, 2002

Ponera atavia Mayr, 1868, p. 72 (part.).

Pachycondyla baltica Dlussky, 2002, p. 7, text-fig. 23 (♂).

H o l o t y p e. Male, MNHW, no. 1984/31/255, labeled "ST *Ponera atavia* Mayr, 1868. Eozaen. Baltischer Bernstein. Kollektion Handlirsch. Syntypus zu Mayr, 1868"; a completely preserved inclusion, partly clouded. Baltic amber, Late Eocene.

D e s c r i p t i o n. Male (Fig. 5a). BL ca. 3.5 mm. The head is suboval, without distinct occipital corners, its occipital margin is rounded. The eyes are large, oval, and convex. The ocelli are small, their diameter is smaller than the interocellar distance. The frontal carinae are absent. The clypeus with a median longitudinal carina. The antennae, if bent back, extend to the first gastral segment. The scape is short, slightly longer than wide; the second antennomere is the shortest, approximately as long as wide; the third antennomere is long, longer than the combined length of the first two antennomeres. The maxillary palpi are short, barely protruding outside the oral cavity. The mandibles are triangular. The mandibular dentation and the anterior margin of the clypeus are obscured by a cloudy film, not visible. The mesosoma is robust and rather high. The pronotum is transverse. The scutum is strongly convex anteriorly and nearly flat dorsally. The parapsidal furrows are absent. The propodeum in profile is angular, its dorsum and declivity are of approximately equal size, forming a rounded obtuse angle. The legs are moderately long. The meso- and the metatibiae each with two spurs of unequal size, a smaller simple spur and a larger spur, which is serrate on the mesotibia and pectinate on the metatibia. The petiole with a high and thick node, which is approximately as high as the propodeum. The scale in profile with its dorsal margin rounded. The constriction between the first and the second gastral segments is distinct. The tip of the gaster is obscured by cloudiness, its structure is not discernible.

The head and mesosoma with shagreened sculpture and without conspicuous decumbent pubescence. The gaster is weakly shiny, with very delicate shallow sculpture and rather dense decumbent pubescence, consisting of very fine hairs. Erect hairs are visible only on the occipital margin of the head and the tip of the gaster.

The forewing with closed cells 1 + 2r, 3r, rm, and mcu. Cell 3r is approximately four times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cell rm is distinctly quadrangular, 2M is approximately half as long as rs-m. Crossveins rs-m and r-rs meet RS almost at one point, appearing as a single crossvein. Cell mcu is pentagonal, 1.7 times as long as wide. 1RS is less than half as long as 1M. Vein cu-a meets M+Cu almost at the 1M and 1Cu fork.

Workers and gynes are unknown.

M e a s u r e m e n t s (mm): Holotype, L 1.3, FWL 3.5.

C o m p a r i s o n. Differs from the male of *P. succinea* in lacking the parapsidal furrows and having sparse erect pilosity.

R e m a r k s. The male described here, designated as a syntype of *Ponera atavia* (Ponomarenko and Schultz, 1988), clearly belongs to the genus *Pachycondyla* since it has two spurs on each meso- and metatibia. It matches neither Mayr's description (lack of parapsidal furrows), nor his drawing.

M a t e r i a l. Holotype.

Pachycondyla conservata Dlussky, sp. n.

E t y m o l o g y. From the Latin *conservatus* (being preserved).

H o l o t y p e. Male, SIZK, no. K-4456; a completely preserved inclusion, partly obscured by cracks; one wing crumpled, the other incompletely preserved. Rovno amber, Late Eocene.

D e s c r i p t i o n. Male (Figs. 5d, 5e). BL 2.4 mm. The head is suboval, without distinct occipital corners, its occipital margin is rounded. The eyes are large, oval, convex, strongly shifted anteriorly, so that their anterior margins almost touch bases of the mandibles. The ocelli are large, their diameter is only slightly less than the interocellar distance. The frontal carinae are absent. The clypeus is medially convex, without a carina, its anterior margin is well-rounded. The antennae, if bent back, extend to the first gastral segment. The scape is short, slightly longer than wide; the second antennomere is the shortest, approximately as long as wide; the third antennomere is long, longer than the combined length of the first two antennomeres. The maxillary palpi are short, barely protruding outside the oral cavity. The mandibles are triangular, each with a pointed apical tooth but without dentation on the masticatory margin. The pronotum is transverse. The scutum is strongly convex anteriorly and nearly flat dorsally. The parapsidal furrows are absent. The propodeum in profile is well-rounded. The legs are moderately long. The meso- and the metatibiae each with two spurs of unequal size, a smaller simple spur and a larger spur, which is serrate on the mesotibiae and pectinate on the metatibiae. The petiole is slightly longer than high, not as high as the propodeum, with a scale, which is triangular in profile and has rounded apex. The constriction between the first and the second gastral segments is poorly distinct. The pygidium with a short spine.

The head and mesosoma are densely and finely punctate, with rather dense decumbent pubescence. A few erect hairs are visible only on the head near the ocelli and on the scutum. Sculpture and hairs on the gastral tergites are obscured, impossible to see.

The forewing with closed cells 1 + 2r, 3r, rm mcu, and cua. Cell 3r is very narrow and long, more than five times longer than wide. Cell rm is triangular. 1M is approximately four times as long as 1RS. Crossvein rs-m meets RS distal of r-rs by approximately the vein

width. Cell mcu is quadrangular. Vein cu-a meets M + Cu proximal to the fork of 1M and 1Cu.

Workers and gynes are unknown.

Measurement (mm): Holotype, AL 0.93, HL 0.45.

Comparison. Differs from males of *P. succinea* and *P. baltica* by its significantly smaller size and by having the cell rm in the forewing triangular. From *P. succinea* it additionally differs in lacking parapsidal furrows.

Material. Holotype.

Pachycondyla tristis Dlussky, sp. n.

Etymology. From the Latin *tristis* (sad).

Holotype. Dealate gyne, MKC, no. 27.131, a completely preserved inclusion. Bitterfeld amber, Late Eocene.

Description. Gyne (Figs. 5b, 5c). BL ca. 4.5 mm. The head is longer than wide, without distinct occipital corners, its occipital margin is convex. The eyes are oval, weakly convex, strongly shifted anteriorly, so that the gena is shorter than the maximum diameter of the eye. The ocelli are small yet conspicuous. The frontal carinae are close-set. The clypeus with a median longitudinal carina, the anterior margin of the clypeus protrudes as a rounded lobe. The antennae without a club. The scape reaches the occipital margin. The length of each flagellomere, except the first and the last, equals to or slightly exceeds its width. The mandibles are triangular, relatively long, each with 7–8 large teeth on the masticatory margin and a tubercle on the outer margin. The palpi are not visible. The upper surfaces of the scutum and the scutellum are flat, the constriction between them is nearly absent. The scutum is longer than wide. The propodeal declivity is bordered by strongly smoothed carinae, with a distinct median longitudinal carina. The meso- and the metatibiae each with two spurs of unequal size, a smaller simple spur and a larger spur, which is serrate on the mesotibia and pectinate on the metatibia. The petiole is twice as wide as long and only 1.3 times shorter than the maximum width of the mesonotum, with a rounded scale, which is high and wide. The constriction between the first and the second gastral segments is poorly distinct.

The entire body with shagreened sculpture. Short erect hairs are present only on the head (one pair near the ocelli and one pair on the clypeus), scutum (four pairs), and the tip of the gaster. Decumbent pubescence is absent.

Workers and males unknown.

Measurements (mm): AL 1.4, AW 0.7, HL 0.8, HL + MdL 1.2, HW 0.8, SL 0.65, PtW 0.525.

Comparison. Differs from the gyne of *P. succinea* in having a wider petiole scale and in lacking abundant erect and semierect hairs on the body.

Material. Holotype.

Genus *Ponera* Latreille, 1938

Type species. *Formica coarctata* Latreille, 1802, by subsequent designation by Westwood (1840).

Diagnosis. Workers and gynes. Head subrectangular, longer than wide. Eyes, if present, situated in front of lateral midlength of head. Clypeus narrow, transverse, with anterior margin weakly convex with small median lobe. Median part of clypeus narrowing posteriorly. Frontal carinae almost covering antennal insertions, forming lobes, close-set medially, separated by longitudinal furrow. Antennae 12-segmented, geniculate. Flagellomeres becoming wider towards apex, not forming club, or forming 4 to 5-segmented club. Mandibles triangular, with masticatory margin dentate, with three apical teeth and series of small denticles in basal part. Palpal formula 2.2. Promesonotal suture well developed in workers. Legs short. Meso- and metatibiae each with one spur. Claws simple. Petiole narrowly attached to gaster, with thick node. Subpetiolar process in profile with acute posteroventral angles and small window or translucent point in anterior part. Helcium attachment on first gastral segment very low, the latter with high vertical anterior surface facing helcium.

Male. Occipital margin behind eyes well-rounded, without distinct occipital corners. Eyes large. Ocelli relatively small. Clypeus convex, with broadly rounded anterior margin. Antennal insertions exposed, distant from posterior clypeal margin. Antennae 13-segmented, filiform, with short scape. Mandibles reduced, not touching when closed. Meso- and metatibiae each with one spur. Petiole with thick and relatively high scale, as in workers, but with more rounded angles. Helcium as in workers and gynes. Pygidium with terminal spine well developed. Cerci absent. Forewing with complete set of veins. Hindwing without jugal lobe.

Composition and distribution. Fifty-two species are known in the recent fauna, distributed in the eastern Palearctic and Indo-Australian region from Russia's Primorsky Krai, Japan, and China to New Guinea. Only five species are known to occur outside that area: three in Europe and two in North America (Bolton et al., 2006). Among fossil ants, only three species described below from the European Late Eocene ambers can be confidently placed in *Ponera*.

Remarks. Twenty-three fossil species have been described in *Ponera* Latreille. However, it subsequently turned out that such species described from Baltic amber belong, in fact, to the genera *Hypoponera* Santschi and *Pachycondyla* F. Smith (Dlussky, 1997, 2002), while the species described by impressions from the Miocene deposits have been either excluded from *Ponerinae* (Mayr, 1867), or placed into the morphogenera *Poneropterus* Heer, 1867 (Taylor, 1964) and *Ponerites* Dlussky et Rasnitsyn, 2002 (Dlussky, 1981; Dlussky and Rasnitsyn, 2002). The reason is that, even on the best preserved impressions, one cannot see the diagnostic characters that distinguish the genera of small *Ponerinae*, such as the shape of the subpetiolar process, tib-

ial spurs, etc. The morphogenus *Ponerites* comprises small Ponerinae similar to *Ponera*, *Hypoconera*, *Cryptopone* Emery, and small *Pachycondyla*. Currently it includes three species from the Middle Eocene of USA (Green River formation) and one species from the Middle Eocene of North Caucasus (Dlussky and Rasnitsyn, 2002). Taylor suggested including ant species described based on impressions with only the wings well preserved in the morphogenus *Poneropterus*, and included into it 21 ant species described earlier from various European Miocene deposits as *Ponera*. Diagnostic of this genus is the presence of closed cells 1 + 2r, 3r, rm, and mcu in the forewing. This character is shared by many ant genera from various subfamilies. The species described by Emery (1891) from Sicilian amber (Lower Miocene) as *Ponera leptocephala*, listed under the same name in Bolton's catalogue (Bolton, 1995), undoubtedly belongs to Ponerinae. However, judging from Emery's description and drawing, this ant is so unusual that I cannot place it in any recent or fossil genus.

Ponera lobulifera Dlussky, sp. n.

E t y m o l o g y. From the Latin *lobulifera* (bearing a small lobe).

H o l o t y p e. Male, GZG.BST.03872 (G2940); an ideally preserved, complete inclusion. Baltic amber, Late Eocene.

D e s c r i p t i o n. Male (Figs. 6a, 6b). BL 3.25–3.75 mm. The head cannot be examined in frontal view. The eyes are oval, convex, strongly shifted anteriorly, so that their ventral margins are almost touching bases of the mandibles. The ocellus diameter is less than the interocellar distance. The clypeus in profile is strongly convex. Antennae, if bent back, extend beyond the midlength of the gaster. The scape is very short, 1.5 times as long as wide and less than half as long as the third antennomere. The second antennomere is the shortest, approximately as long as wide; the third antennomere is the longest, longer than the combined length of the first two antennomeres. The more distal antennomeres become progressively shorter towards the apex of the antenna. The mandibles are short, spatulate, somewhat angulate at apices. Each mandible bears one or several long hairs at its apex. The maxillary palpi extend to the occipital orifice. The pronotum is transverse. The scutum is evenly convex, with poorly developed parapsidal furrows. The scutellum is convex. The propodeum in profile is rounded. The legs are moderately long. The mesotibiae each with one simple spur, the metatibiae with one large pectinate spur and, in one individual, additionally with a very small simple spur. The petiole in profile with a rounded apex, with a high and thick scale; the ventral side of the petiole anteriorly with a small rounded lobe, which is readily conspicuous in profile. The constriction between the first and the second gastral segments is distinct.

The head and pronotum are densely and delicately punctate, weakly shiny. The scutum, mesopleura, and

gaster are shiny, with sparse, barely visible punctation. The sides and the dorsal surface of the propodeum are densely shagreened and with reticulate sculpture formed by strongly smoothed rugae. The propodeal declivity and the posterior surface of the petiole are smooth and shiny. The head, mesosoma, and petiole without decumbent pubescence. The gaster of the holotype without decumbent pubescence. In the paratype GPIH, no. 4506 sparse decumbent pubescence is present, formed by very fine hairs, much longer than distances between them. Short and fine erect hairs are present on the head near the ocelli, as well as on the pronotum, scutum, propodeum, petiole, and the entire tergal and sternal surfaces of the gaster. The tibiae without erect hairs.

The forewing with closed cells 1 + 2r, 3r, rm, mcu, and cua. Cell 3r is 4.5 times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Crossvein r-rs slopes forwards and meets RS somewhat proximal to junction with rs-m; as a result, rs-m and r-rs do not appear as a single crossvein. 2M is present, so that cell rm is quadrangular and mcu is pentagonal. Cell rm is 2.0–2.5 times as long as wide, cell mcu is 1.6–1.7 times as long as wide. 1RS is noticeably shorter than 1M. The meeting of crossvein cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by more than double width of vein.

M e a s u r e m e n t s (mm): Males: holotype GZG.BST.03872: AL 1.325, HL 0.73, ED 0.37; paratype GZG.BST.04678: AL 1.5; paratype GPIH, no. 4506 (CGC, no. 651): AL 1.4; FWL 3.15.

C o m p a r i s o n. Differs from *P. mayri* and *P. wheeleri* in the presence of a lobe on the ventral side of the petiole. It additionally differs from *P. wheeleri* in having the parapsidal furrows developed and the cell rm quadrangular, and from *P. mayri* by the decumbent pubescence being sparse.

R e m a r k s. The specimen GZG.BST.04678 (K7530), designated here as a paratype, has been identified by Wheeler (1915, p. 40) as *Ponera atavia*.

M a t e r i a l. Besides holotype, from Baltic amber: paratypes GZG.BST.04678 (K7530) (♂) and GPIH, no. 4506 (CGC, no. 651) (♂).

Ponera mayri Dlussky, sp. n.

E t y m o l o g y. In honor of the myrmecologist G. Mayr.

H o l o t y p e. Male, MZ PAN, no. 11487, a well preserved complete inclusion with crumpled wings. Baltic amber, Late Eocene.

D e s c r i p t i o n. Male (Figs. 6c–6f). BL 3–4 mm. The head is widened anteriorly, almost as long as wide. The eyes are oval, strongly convex, strongly shifted anteriorly, so that their ventral margins are almost touching bases of the mandibles. The ocellus diameter is less than the interocellar distance. The clypeus is convex medially, with narrow lateral parts, its anterior

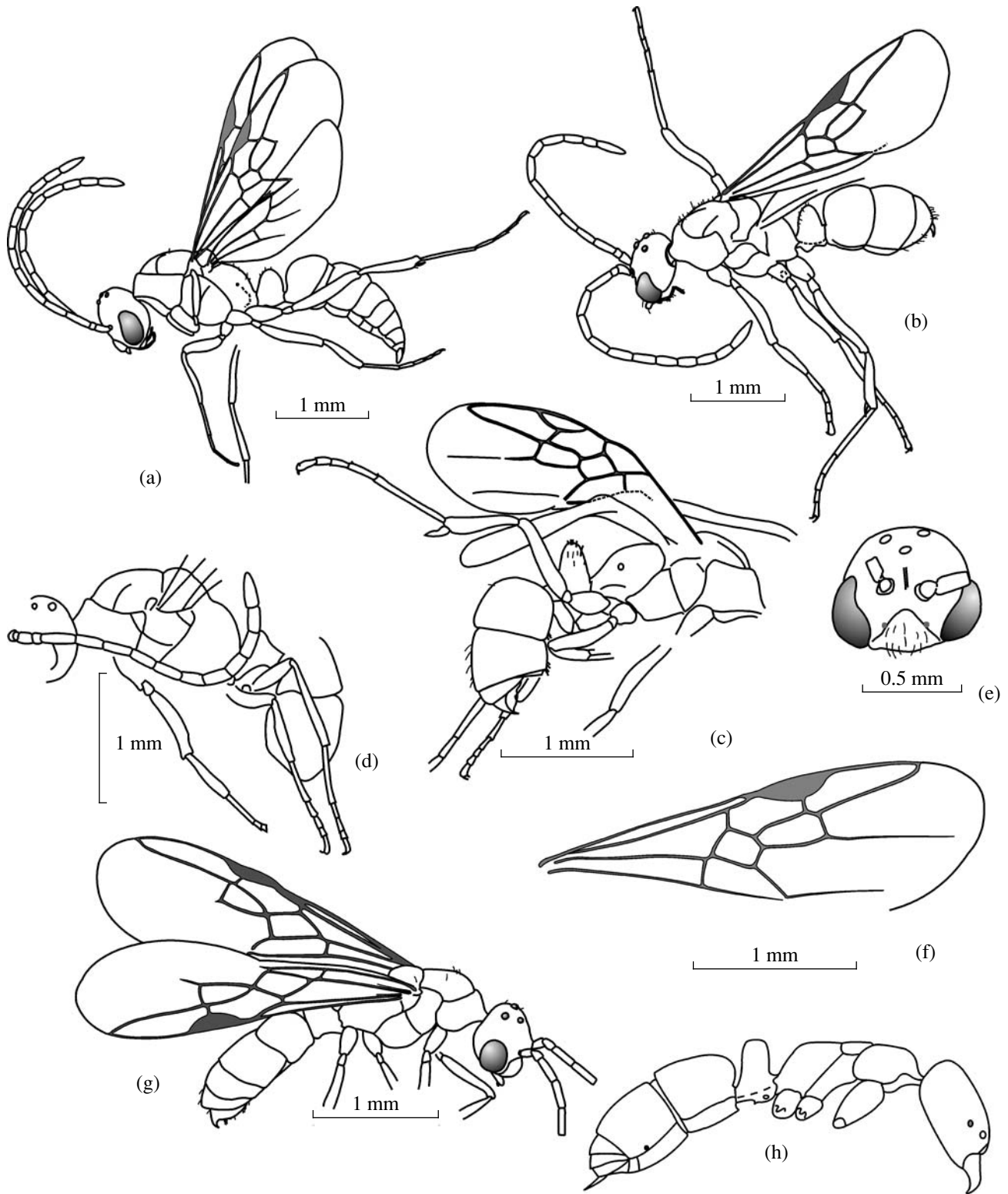


Fig. 6. Species of the genus *Ponera*: (a–b) *Ponera lobulifera* sp. n., males, general views of inclusions: holotype GZG.BST.03872 (a) and paratype GPIH, no. 4506 (CGC, no. 651) (b); (c–f) *Ponera mayri* sp. n., male, holotype MZ PAN, no. 11487: general view of the inclusion from different angles (c, d) and head (e), and male, paratype GZG.BST.04679, forewing (f); (g) *Ponera wheeleri* sp. n., male, holotype HM, no. 11/229, general view of the inclusion; (h) worker of *Ponera coarctata* Latreille (recent).

margin is weakly convex. Between the antennal insertions there is a longitudinal furrow. The antennae, if bent back, extend beyond the midlength of the gaster. The scape is short, twice as long as wide; the second antennomere is very short, shorter than wide; the third antennomere is the longest, exceeding the combined length of the first two antennomeres. The more distal antennomeres progressively become shorter. The maxillary palpi extend beyond midpoint between mouth and occipital orifice. The mandibles are spatulate, without teeth. The pronotum is transverse. The scutum is evenly convex, with weak yet conspicuous parapsidal furrows. The scutellum is convex. The propodeum in profile is rounded. The legs are moderately long, each mesotibia with one simple and each metatibia with one pectinate spur. The petiole in profile with a rounded apex, with a high and thick scale. The ventral side of the petiole without a lobe. The constriction between the first and the second gastral segments is distinct.

The body is weakly shiny, with fine shagreened sculpture and abundant dense decumbent pubescence. Decumbent hairs are significantly longer than distances between them. The clypeus, propodeum, upper margin of scale, and gaster additionally with a few semierect and erect hairs.

The forewing with closed cells 1 + 2r, 3r, rm, and mcu. Cell 3r is 3.5–4.0 times as long as its maximum width. Crossveins rs-m and r-rs meet RS close to each other but still at different points, separated by less than two widths of vein. 2M is present, so that cell rm is quadrangular and mcu is pentagonal. Cell mcu is approximately 1.5 times as long as wide. 1RS is approximately half as long as 1M. The meeting of veins cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by slightly more than two widths of vein. Cell cua is open apically.

Measurements (mm): Males: holotype MZ PAN, no. 11487: AL 1.4, HW 0.64; paratype GZG.BST.04679: AL 1.46, FW 2.8; paratype GZG.BST.04680: HL 0.67; paratype SIZK, no. K-3621: AL 1.6, HL 0.77, ED 0.37, FW 3.0.

Comparison. Differs from *Ponera lobulifera* in the absence of a lobe on the ventral side of petiole and the presence of abundant decumbent pubescence and from *Ponera wheeleri* in the presence of parapsidal furrows and the cell rm being quadrangular.

Remarks. This species better than others matches the characters (presence of parapsidal furrows) and the drawing (wing venation, presence of pygidial spine) in the original description of *Ponera atavia* (Mayr, 1868). Although its petiole differs slightly from the petiole drawn by Mayr, this inconsistency can simply be due to the quality of the drawing. At the same time, the species undoubtedly belongs to the genus *Ponera*, while the lectotype of *Ponera atavia* (gyne) belongs to *Hypoponera* (Dlussky, 2002). The specimens GZG.BST.04679 (K5238) and GZG.BST.04680 (K5252), designated

here as paratypes, have been determined by Wheeler (1915, p. 40) as *Ponera atavia*.

Material. Besides holotype, paratypes GZG.BST.04679 (K5238) (♂) and GZG.BST.04680 (K5252) (♂), Baltic amber; SIZK, no. K-3621 (♂), Rovno amber. Late Eocene.

Ponera wheeleri Dlussky, sp. n.

Etymology. In honor of the myrmecologist W.M. Wheeler.

Holotype. Male, HM, no. 11/229; a completely preserved inclusion. Bitterfeld amber, Late Eocene.

Description. Male (Fig. 6g). BL 2.6–3.0 mm. The eyes are oval, convex, shifted anteriorly, so that the gena is approximately as long as the width of the flagellomeres. The ocellar diameter is less than the interocellar distance. The clypeus in profile is strongly convex. The antennae, if bent back, extend beyond the midlength of the gaster. The scape is very short, 1.5 times as long as wide; the second antennomere is the shortest, approximately as long as wide, half as long as the scape; the third antennomere is the longest, longer than the combined length of the first two antennomeres, approximately twice as long as the scape. Each mandible with a single long hair at the apex. The maxillary palpi are short, not reaching half-way between the mouth and the occipital orifice. The pronotum is transverse. The scutum is evenly convex, without parapsidal furrows. The scutellum is weakly convex. The propodeum in profile is well-rounded. The legs are moderately long, each mesotibia with one simple and each metatibia with one pectinate spur. The petiole in profile with its anterior surface weakly concave and its apex rounded, without a lobe on the ventral side. The constriction between the first and second gastral segments is poorly distinct.

The head and mesosoma are weakly shiny, with fine shagreened sculpture, without decumbent pubescence. The gaster is shiny, with barely visible punctation and relatively sparse decumbent pubescence, consisting of hairs twice as long as distances between them. Erect hairs are present on the head near the ocelli, as well as on the scutum and the tip of the gaster. The femora and tibiae without erect hairs, only with very short semierect hairs.

The forewing with closed cells 1 + 2r, 3r, rm, and mcu. Cell 3r is approximately four times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Crossveins rs-m and r-rs meet RS very close to each other, yet at different points, separated by slightly more than two vein widths. 2RS and 3M originate from a common node, so that cell rm is triangular and mcu is quadrangular. Cell mcu is longer than wide. 1RS is very short, several times shorter than 1M. The meeting of vein cu-a and M+Cu is proximal to the 1M and 1Cu fork, being separated from it by

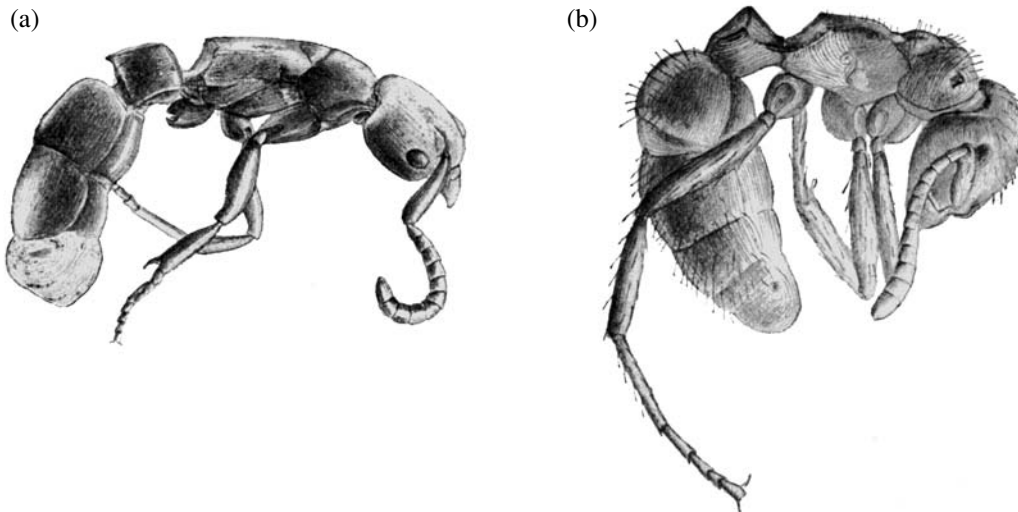


Fig. 7. *Platythyrea primaeva* Wheeler (a) and *Electroponera dubia* Wheeler (b) (from Wheeler, 1915).

slightly more than two widths of vein. Cell cua is apically open.

Measurements (mm): Males: holotype HM, no. 11/229: AL 1.2, FWL 2.8; paratype HM, no. 7/231: AL 1.1; paratype GZG.BST (MKC), no. 27.064: AL 1.05, HL 0.55; FWL 2.55.

Comparison. Differs from *P. lobulifera* and *P. mayri* by the forewing venation (cell rm is triangular, 1RS is very short) and the petiole shape. From *P. lobulifera* it additionally differs in lacking a lobe on the ventral side of petiole, and from *P. mayri* in having sparse decumbent pubescence.

Material. Besides holotype, paratypes GZG.BST (MKC), no. 27.064 (♂) and HM, no. 7/231 (♂), Bitterfeld amber.

Tribe Platythyreini Forel, 1901

Genus *Platythyrea* Roger, 1863

Type species. *Pachycondyla punctata* F. Smith, 1858, by subsequent designation of Bingham, 1903.

Diagnosis. Workers and gynes. Head subrectangular, longer than wide. Eyes situated in front of lateral midlength of head. Frontal carinae widely separated, covering antennal insertions, forming frontal lobes. Frontal lobes not narrowing posteriorly. Antennae 12-segmented, without distinct club. Mandibles triangular, usually with teeth on masticatory margin. Promesonotal suture present. Sculpture pruinose throughout. Meso- and metatibiae each with two pectinate spurs. Claws usually with additional preapical tooth. Petiole node-shaped, not pedunculate, narrowly attached to first gastral segment. Helcium usually attached to middle of anterior surface of first gastral segment.

Males. Mandibles large, touching when closed. Antennae 13-segmented, filiform. Meso- and metatib-

iae each with two pectinate spurs. Claws usually with additional preapical tooth. Helcium usually attached to middle of anterior surface of first gastral segment. Pygidium without terminal spine. Cerci present. Forewing with complete set of veins. Jugal lobe on hindwing present.

Composition and distribution. Thirty-eight species in the recent fauna, distributed circumtropically (Bolton et al., 2006). Five fossil species are known: *Platythyrea primaeva* Wheeler from Baltic amber (Late Eocene), and *P. dentata*, *P. scalprum*, *P. procera* (Lattke, 2003), and *P. pumilio* (De Andrade, 2004) from Dominican amber (Early Miocene).

Platythyrea primaeva Wheeler, 1915

Platythyrea primaeva Wheeler, 1915, p. 36, text-fig. 7 (worker, ♀); Burnham, 1978, p. 110; Bolton, 1995, p. 337; Dlussky, 1997, p. 61, text-fig. 1e.

Type s. The species has been described from Baltic amber based on one worker from the collection of the Geological Institute in Königsberg (without number) and one gyne from Klebs collection (K.5122), neither of which has survived. I have not seen this species among the studied material.

Description (modified from Wheeler, 1915). Worker (Fig. 7a). BL ca. 5.5 mm. The head is distinctly longer than wide, rectangular, with rounded occipital corners. The anterior margin of the clypeus is evenly convex. The scape barely protrudes beyond the occipital margin. The three first flagellomeres are each slightly longer than wide. The other flagellomeres, except the last one, are approximately as long as wide. The mandibles with small denticles. The mesosoma with parallel flattened sides, its dorsal surface is flattened. The promesonotal suture is distinct; the mesopropodeal and the mesopleural sutures are absent. The propodeum with pair of obtuse spines, its declivity is

concave and bordered laterally by carinae. The petiole is as long as wide and as high as long. The petiole in profile is cubic, with pair of obtuse dentiform processes on its posterior margin. The helcium is attached to the middle portion of the first gastral segment. The first gastral tergite in profile is evenly convex. The gaster is cylindrical, with a distinct constriction between the first and the second segments. The body is matte. The sides of the propodeum and of petiole and the base of the first gastral segment with scattered coarse pits. The pronotum and the dorsal side of the head with finer punctation. Erect hairs are present only on the mandibles.

Gyne. Body length ca. 6 mm. Eyes somewhat larger than in worker. Mesosoma distinctly divided by sutures into pronotum, scutum, scutellum, and propodeum, but it is unclear whether the studied specimen had any wings. Propodeum and petiole as in worker. Body matte. Erect pilosity absent.

Males unknown.

Tribe Ectatommini Emery, 1895

Genus *Electroponera* Wheeler, 1915

Type species. *Electroponera dubia* Wheeler, 1915, by monotypy.

Diagnosis. Worker. Head subrectangular. Eyes moderately large, situated behind of lateral midlength of head. Frontal carinae divergent, broadly separated along entire width, lamelliform in profile. Frontal lobes covering antennal insertions. Clypeus broadly extending between frontal lobes. Antennae 12-segmented, flagellum without distinct club. Mandibles triangular. Mesosomal sutures well developed. Pronotum with pair of well developed humeral elevations. Propodeum with pair of obtuse spines and pair of longitudinal carinae associated with spines. Petiole in profile without distinct peduncle, its anterior and posterior surfaces separated from one another and from lateral surfaces with sharp carinae. Helcium attached at middle of anterior surface of first gastral segment; that surface rounded in profile. Gaster with distinct constriction between first and second segments.

Gynes and males unknown.

Composition and distribution. Type species, known only from Baltic amber.

Remarks. Wheeler (1915) tentatively included this genus in the tribe Ectatommini. Bolton (2003) rightly pointed out that the characters listed by Bolton were insufficient to reliably place *Electroponera* in any tribe, and included this genus in Ectatomminae *incertae sedis*. Nevertheless, I think that several characters shared by this ant with recent representatives of the genus *Ectatomma* F. Smith and certain species of *Rhytidoponera* Mayr (in particular, the way its mesosoma is subdivided) allow to leave this genus in the tribe Ectatommini, at least until new material becomes available.

Electroponera dubia Wheeler, 1915

Electroponera dubia Wheeler, 1915, p. 35, text-fig. 6 (♀); Burnham, 1978, p. 110; Bolton, 1995, p. 187; Dlussky, 1997, p. 61, text-fig. 1e.

Type s. The species has been described based on a single specimen (B. 18994) in Baltic amber collection of the Geological Institute in Königsberg, which has not survived. I have not found this species among the studied material.

Description (modified after Wheeler, 1915). Worker (Fig. 7b). BL 7.5 mm. The head is slightly longer than wide, its sides are weakly convex, its occipital corners are rounded, and the occipital margin is weakly concave. The scape reaches the occipital margin of the head. The first flagellomere is slightly longer than wide, the other flagellomeres each as long as wide. The mesopropodeal suture is well developed. The mesonotum is convex, limited by distinct sutures; its anterior part extends anteriorly between the mediolateral parts of the pronotum. The mesopropodeal constriction is distinct. The propodeal dorsum is convex, and the declivity is concave. The petiole in profile with its anterior surface concave and the posterior surface flattened. The mesosoma and the petiole are finely rugose; the pronotum with rugae forming concentric circles around small protuberances; the mesopleura and the sides of the propodeum and of the petiole with longitudinal rugae. The entire body, including the scape and the legs, with rather numerous erect hairs.

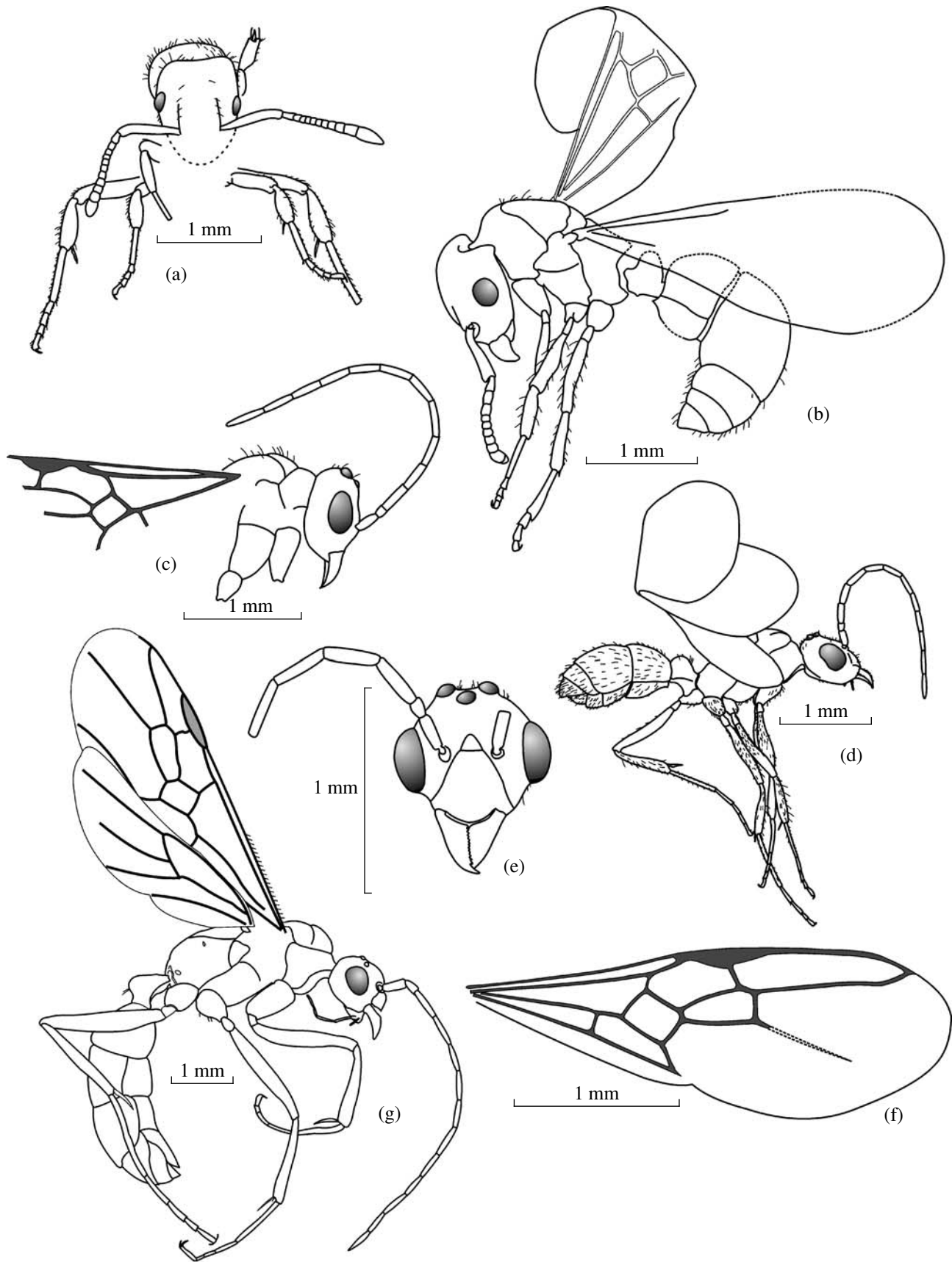
Gynes and males are unknown.

Genus *Gnamptogenys* Roger, 1863

Type species. *Ponera tornata* Roger, 1861, by subsequent designation of Emery, 1911.

Diagnosis. Workers and gynes. The frontal carinae are broadly separated along entire width, lamelliform in profile. Frontal lobes covering antennal insertions. Clypeus broadly extending between frontal lobes, its anterior margin rounded. Mandibles triangular, dentate, touching when closed. Palpal formula 3.2 or 2.2. Antennae 12-segmented, flagellum without distinct club. Anteroventral angles of pronotum without spine, tooth, or acute angle. Promesonotal suture in workers present, but poorly distinct. Meso- and metatibiae each usually with one spur. Claws usually with additional preapical tooth, in some species claws simple. Petiole narrowly attached to gaster. Helcium attached to middle of anterior surface of first gastral segment; that surface rounded in profile. Second gastral segment in profile trapezoidal, with strongly convex dorsal surface, such that entire gaster is bent, its tip being pointed down.

Males. Eyes and ocelli large, convex. Clypeus with broadly rounded anterior margin. Antennal insertions exposed, situated close to but not touching posterior clypeal margin. Antennae 13-segmented, filiform. Mandibles large, triangular, with masticatory margin dentate. Palpal formula 5.3 or 4.3. Meso- and metatib-



iae each with one spur. Claws usually with additional preapical tooth, in some species claws simple. Petiole narrowly attached to gaster. Helcium as in workers and gynes. Pygidium without terminal spine. Cerci absent. Forewing in the Oriental and known fossil species with complete set of veins. Hindwing without jugal lobe.

Composition and distribution. *Gnamptogenys* comprises 132 recent species, 71 of which occur in the Neotropics, five in southern U.S.A. and Mexico, and 56 in the Oriental and Indo-Australian regions (Bolton et al., 2006). Five fossil species have been described: *G. europaea* (Mayr, 1868) from Baltic amber (Late Eocene), and *G. brunoi*, *G. casca* (Lattke, 2002), *G. levinates*, and *G. pristine* (Baroni Urbani, 1980) from Dominican amber (Early Miocene). I have found *G. europaea* not only in Baltic, but also in Rovno, Bitterfeld, and Scandinavian amber. An additional species from Baltic amber is described below. Apparently, the species described as *Ectatomma gracile* Emery, 1891, from Sicilian amber, also belongs to this genus, but this can be confirmed only after the type specimen is examined.

Remarks. *Gnamptogenys europaea* has been originally described by Mayr in the subgenus *Rhytidoponera* Mayr, 1862 of the genus *Ectatomma* F. Smith, 1858. Wheeler shared the same view on the taxonomic affinity of this species. Brown (1958) moved it into the genus *Gnamptogenys* Roger without giving any reasons supporting his decision. He could not have seen the type, and neither Mayr's description, nor the later description of a male, made by Wheeler, contained any characters that could justify placement of this species in *Gnamptogenys*. Therefore, I left it in *Rhytidoponera* (Dlussky, 1997), which is currently considered a separate genus. Only after I had received and examined a gyne and several males of this species it became clear to me that it, indeed, should be placed in *Gnamptogenys*, and not in *Rhytidoponera* (Dlussky and Perkovsky, 2002).

Recent Oriental and both Late Eocene species of *Gnamptogenys* have closed cells 1 + 2r, 3r, rm mcu, and cua in the forewing. At the same time, males of the South American *Gnamptogenys* (at least *G. striatula* Mayr and *G. magnifica* Santschi, which I have seen) have a totally different venation. In those species, the cell cua is not closed, and the cells 1r + 2r and rm have merged into one fused cell, 1r + 2r + rm. Therefore, although males of *Gnamptogenys* remain studied insufficiently to make a comparison between the fossil and the recent species, one can say that the Late Eocene species are close to the recent species from the Oriental region.

Gnamptogenys europaea (Mayr, 1868)

Ectatomma (Rhytidoponera) europaeum Mayr, 1868, p. 76, pl. IV, text-figs. 72 and 73 (♀); Dalla Torre, 1893, p. 24; Handlirsch, 1907, p. 879; Wheeler, 1915, p. 33, Fig. 5 (♂); Burnham, 1978, p. 110.

Gnamptogenys europaea (Mayr): Brown, 1958, p. 181; Bolton, 1995, p. 209; Dlussky and Perkovsky, 2002, p. 17, text-fig. 1.

Rhytidoponera europaeum: Dlussky, 1997, p. 61.

Neotype. The gyne of this species has been described by Mayr based on a single individual from Menge's collection, and the male has been described by Wheeler based on two well preserved inclusions in the collection of the Geological Institute at Königsberg. All these specimens have been lost. In the interest of stability of nomenclature, I am designating here the alate gyne SIZK, no. UA-822 as the neotype; completely preserved inclusion, partly obscured by extraneous material. Rovno amber, Late Eocene.

Description. Worker (described here for the first time) (Fig. 8a). BL ca. 4 mm. The head is subrectangular, slightly longer than wide, with its sides almost parallel, occipital corners well distinct, and occipital margin concave. The eyes are oval, weakly convex, situated slightly behind the lateral midlength of head. The ocelli are absent. The frontal carinae are widely separated, parallel, reaching the mid-level of eyes. The scape almost reaches the occipital margin. The first flagellomere is approximately twice as long as wide, the flagellomeres III to VIII are each slightly longer than wide. The legs are short and thick. The mesotibiae each with one simple, and metatibiae each with one pectinate spur. The teeth on the metatibial spur pecten are very short, shorter than the maximum diameter of the spur. The claws without an additional preapical tooth.

The anterior surface of the pronotum with reticulate sculpture, its dorsal surface with distinct longitudinal rugae. The surface sculpture of the other body parts cannot be seen. The entire body, including legs, is covered in abundant erect and semierect hairs. The scape with short decumbent pubescence, including some hairs partially raised.

Gyne (Figs. 1, 8b). BL 4.0–4.5 mm. The head is slightly longer than wide, with its sides slightly convex, occipital corners rounded, and occipital margin concave. The eyes are round, situated slightly behind the lateral midlength of the head. The ocelli are small. The frontal carinae are nearly straight, reaching the level of the eye midlength. The scape is relatively short, not protruding beyond the occipital margin of the head. The scutum and scutellum are weakly convex. The propodeum is angular in profile, its dorsum is weakly convex and the declivity is concave. The legs are short and thick. The mesotibiae are each with one weakly serrate,

Fig. 8. Species of the genus *Gnamptogenys*: (a–f) *Gnamptogenys europaea* (Mayr): worker, HM, no. 11/393, general view of the inclusion (a), gyne, neotype SIZK, no. UA-822, general view of the inclusion (sculpture not shown) (b), male, HM, no. 1-3/200, general view of the anterior part of body in profile (c), male, MZ PAN, no. 21517, general view of the inclusion (d), male, ZMUC, no. 308, head in dorsal aspect (e), male CGC, no. 3330, forewing (f); (g) *Gnamptogenys rohdendorfi* sp. n., holotype, male, PIN, no. 364/208, general view of the inclusion.

and the metatibiae each with one pectinate spur. The claws are simple, without an additional preapical tooth. The petiole with a high scale, which is trapezoidal in profile and is higher than the propodeum. The petiole is 1.4 times shorter than high. The lower side of the petiole with a small obtuse denticle approximately in the middle. The gaster with a distinct constriction between the first and the second segments. The first gastral sternite on the lower surface with an angulate projection, directed anteriorly.

The entire body surface is distinctly sculptured. The anterior part of the head with longitudinal rugae, blending into reticulate sculpture on its posterior part. The pronotum, sides of the propodeum, and the petiole with reticulate sculpture. The scutum, scutellum, and mesopleura with longitudinal rugae, more or less parallel on the scutum and scutellum, curved on the mesopleura. The gaster with isolated pits and coarsely shagreened surface in between. The entire body with numerous rather short, curved, erect and semierect hairs. The femora and tibiae with numerous semidecumbent and few longer, semierect hairs.

The wings are evenly darkened, with thick veins. The forewing with closed cells 1 + 2r, 3r, rm, mcu, and cua. Cell 3r is approximately four times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cell rm is quadrangular. Cell mcu is pentagonal, but its side formed by 2M is much shorter than the other sides; the length of that cell is approximately two times its maximum width. 1RS is less than half as long as 1M. The meeting of veins cu-a and M + Cu is proximal to the fork 1M and 1Cu, being separated from it by slightly less than two widths of vein.

Male (Figs. 8c–8f). BL 3–4 mm. The head without mandibles is longer than its width above the eyes. The occipital margin is rounded. The occiput with an arched carina. The eyes are large and convex, situated approximately at the lateral midlength of the head, so that the gena is well developed, several times as long as the diameter of the scape. The maximum eye diameter is half as large as the length of head without mandibles. The ocelli are large, convex; the interocellar distance is 1.5 times the diameter of the ocellus. The clypeus is convex, its anterior margin extends as a rounded lobe. The scape is 2.5 times as long as wide. The first flagellomere is half as long as the scape, slightly longer than wide. The other flagellomeres are cylindrical, 1.5–2.0 times as long as the scape, of approximately equal length, 3–4 times as long as wide. The mandibles are well developed, triangular, each with large apical and preapical teeth and 8–10 small denticles on the masticatory margin. The scutum is weakly convex in profile, with deep parapsidal furrows. The propodeum in profile with its dorsum and declivity of approximately equal size, forming an obtuse angle. The legs are thin. The posterior coxae are simple, without a tooth. The claws are simple, without an additional preapical tooth. Each mesotibia with one serrate, and each metatibia with one

pectinate spur. The petiole is approximately twice as long as high; its node is low and rounded posteriorly. The first gastral sternite anteriorly with a small prominence. The genital armature and pygidium are short, rounded.

The mesopleura are smooth and shiny. The rest of the body with shagreened sculpture, coarser on the head and the propodeum, barely visible on the scutum and the gaster. The gaster with scattered piligerous punctures. The entire body, including legs, with numerous erect and semierect hairs. The antennae with dense, short pubescence.

The wings are broad, covered with short hairs. The forewing with closed cells 1+2r, 3r, rm, mcu, and cua. Cell 3r is 4–5 times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Crossveins rs-m and r-rs meet RS separately, not forming a single crossvein. Cell rm is of variable shape; in most specimens it is quadrangular, because a short yet distinct 2M is present; however, in some individuals (GZC.BST, no. 27.017) 3M and 3RS connect in a point, thus 2M is absent and cell rm is triangular. Cell mcu is 1.2–1.5 times as long as its maximum width. 1RS is shorter than 1M. The meeting of veins cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by less than a half length of 1Cu.

Measurements (mm): Gyne: neotype SIZK, no. UA-822: AL 1.4; HL 0.95, PtL 0.37. Males: spec. MZ PAN, no. 9691: FWL 3.1; spec. MZ PAN, no. 21517: BL 3.5, AL 1.2, HL 0.68, HL/EL 2.08; spec. CGC, no. 862: BL~3, FWL 3.1; spec. CGC, no. 3330: HL 0.8, FWL 3.1, HL 0.65, HW 0.575; spec. HM, no. 1-3/200: AL 1.4, HL 0.77; spec. GZG.BST (MKC), no. 27.013: BL~3.8, FWL 3.05; spec. GZG.BST (MKC), no. 27.016: AL 1.2. Worker: spec. HM 11/393: HL~1.0, HW 0.80, SL~0.75.

Remarks. The original description (Mayr, 1868) specifies only characters of the sculpture and pubescence of the gyne. In these characters, as well as in its size, the gyne SIZK, no. UA-822, designated here as the neotype, completely matches the description. At the same time, it strongly differs from Mayr's drawing. The forewing in that drawing has no closed cell cua, the crossvein cu-a situated closer to the wing base than to the cell mcu, and the gaster as in Ponerini (helcium attached to the lower portion of the first gastral segment, the second gastral segment in profile not trapezoidal, but almost rectangular). However, perhaps one should not trust Mayr's drawing. First, the description states that, in the only examined specimen, only the first and part of the second gastral segments were visible, while the rest could not be seen. Secondly, the position of cu-a as illustrated in that drawing never occurs in Ponerinae, suggesting that the author simply could not see well the lower part of the wing. It must be emphasized that the drawings in Mayr's study illustrate not actual individuals, but author's reconstructions, which were not always entirely accurate. The drawing of a

male in Wheeler (1915) shows a wing with the cell *cua* closed and the crossvein *cu-a* situated as is typical of Ponerinae. The left wing of the neotype lacks any preserved veins, and the forewing is folded downwards. However, by rotating the specimen it is possible to see different parts of the wing, which allowed building its reconstruction. The dashed line in my drawing indicates the area that could not be seen. This venation is basically identical to that of the individual illustrated by Wheeler and of all the males of this species that I have examined.

The only discovered worker specimen is poorly preserved: the dorsal surface of most of the mesosoma, petiole, and gaster has been cut off. The head is partly obscured by a cloudy film. Therefore, a complete description is impossible. At the same time, the preserved parts of this specimen are so similar to the corresponding parts of the gyne that I have no doubts it belongs to *Gnamptogenys europaea*.

Material. Besides neotype, from Baltic amber: CGC, nos. 862 (♂), 3330 (2 ♂); MZ PAN, no. 9691 (♂), 21517 (♂). Bitterfeld amber: HM, nos. 1-3/200 (♂), 7/220 (♂), 11/393 (♀); GZG.BST (MKC), nos. 27.013 (♂), 27.016a (♂). Amber of unknown origin: ZMUC, no. 308 labeled "Dr. Jpsen, 01.06.1932" (4 ♂).

Gnamptogenys rohdendorfi Dlussky, sp. nov.

Etymology. In honor of the paleoentomologist B.B. Rohdendorf.

Holotype. Male, PIN, no. 364/208; a completely preserved inclusion, but with minor cracks on the surface. Baltic amber, Late Eocene.

Description. Male (Fig. 8g). BL 8.5–9.0 mm. The head is rounded. The occipital orifice is surrounded with a narrow "collar" formed by a chitinous carina. The eyes are round, convex, not particularly large, situated approximately at the lateral midlength of the head, so that the gena is well developed. The ocelli are large. The mandibles are well developed, triangular, dentate. The anterior part of the clypeus is weakly convex, rounded. The antennae are long and thin; the relative lengths of the basal antennomeres are as follows: I(scape) : II : III : IV : V = 1.0 : 0.5 : 1.1 : 1.05 : 1.0; the scape is 2.5 times as long as wide; the second antennomere is slightly longer than wide; the other antennomeres are cylindrical, the third antennomere is the longest, the more distal antennomeres become progressively shorter. The maxillary palpi appear 5-segmented, they are long and reach the occipital orifice. The labial palpi are very short. The scutum in profile is weakly convex, with well developed parapsidal furrows. The propodeum in profile is well-rounded. The legs are thin and long. The mesotibiae each with a long pectinate and a very short simple spur. The metatibiae each with one pectinate spur. The claws are simple, without an additional preapical tooth. The petiole with a node rounded in profile. The first gastral segment without a prominence. The genital armature is short and rounded.

The entire body is weakly shiny, with poorly developed shagreened sculpture. The mesosoma and the petiole with isolated erect hairs. The legs without erect hairs. The costal vein with oblique setae.

The forewing with closed cells 1 + 2r, 3r, rm, and m_{cu}. Cell 3r is approximately four times as long as its maximum width, its apex is pointed and lies on the anterior wing margin. Cell rm is pentagonal, because crossveins rs-m and r-rs meet RS at different points, which are separated by approximately one length of r-rs. 2M is only slightly shorter than rs-m. Cell m_{cu} is pentagonal, 1.5 times as long as its maximum width. 1RS is slightly shorter than 1M. The meeting point of veins cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by approximately one width of cu-a.

Workers and gynes are unknown.

Measurements (mm): Holotype: HL + MdL 1.7, AL 3.2, F3L 2.25, FWL 5.7, PtL 0.8.

Comparison. Differs from *G. europaea* by its larger size, lack of erect pilosity, and the shape of propodeum. Comparison with recent species is not possible, because males of most species of this genus have not been described.

Material. Holotype.

Tribe Proceratiini Emery, 1895

Genus *Bradoponera* Mayr, 1868

Type species. *Bradoponera meyeri* Mayr, 1868, by monotypy.

Diagnosis. Workers and gynes. Clypeus medially with weakly developed anterior prominence. Antennal insertions distant from clypeus. Frontal carinae widely separated, in profile remarkably thick. Eyes small, flat, with small number of ommatidia. Workers lack ocelli. Antennae 9- or 12-segmented. Flagellomeres becoming wider towards apex; apical flagellomere very large, forming distinct club. Mandibles triangular, without teeth on masticatory margin. Palpal formula 5.4. Maxillary palpi with second segment curved, not hammer-shaped. Mesosoma short and massive, its dorsal surface moderately convex. In workers all the tergites of mesosoma are fused together, and the promesonotal and mesopropodeal sutures are absent. Meso- and metatibiae each with one spur. Claws simple. Petiole with node, which is wedge-shaped in profile, or with scale. Subpetiolar process present. Helcium attached approximately to middle of anterior surface of first gastral segment. Dorsal surface of second gastral tergite arched and domed, so that more distal gastral segments directed anteriorly. Constriction between first and second gastral segments distinct.

Males. Head round, without distinct occipital corners, with convex occipital margin. Frontal carinae short. Antennal insertions exposed, not touching posterior margin of clypeus. Clypeus in profile convex. Eyes and ocelli large. Mandibles triangular, not touching

when closed, without teeth on masticatory margin. Antennae 13-segmented, geniculate, with short scape and filiform flagellum. Maxillary palpi 5-segmented, their second segment curved, not hammer-shaped. Parapsidal furrows present. Mesotibiae each with one, and metatibiae each with two spurs. Claws simple. Helcium attached approximately to middle of anterior surface of first gastral segment. Second gastral segment in profile trapezoidal, with strongly convex dorsal surface, such that entire gaster is bent and its apex is directed down. Pygidium without terminal spine. Forewing with incomplete set of veins, closed cells *rm* and *mcu* absent. Hindwing without jugal lobe.

Composition and distribution. Three species of *Bradoponera* have been described so far, all from Baltic amber (Late Eocene): *B. meyeri* Mayr, *B. wunderlichii* Baroni Urbani et de Andrade, and *B. electrina* Baroni Urbani. The last two species, which I have not seen, have been described very thoroughly (De Andrade and Baroni Urbani, 2003), so I am not giving their descriptions here, while still including these species in the identification key. The above-mentioned paper also contains a detailed redescription of the genus and of *B. meyeri*, as well as a thorough discussion of the affinities of *Bradoponera* within the tribe Proceratini.

I have discovered *B. meyeri* also in Bitterfeld and Rovno ambers. Additionally, in Bitterfeld amber I have discovered one new species of *Bradoponera*, which is described below.

***Bradoponera meyeri* Mayr, 1868**

Bradoponera meyeri Mayr, 1868, p. 74, pl. IV, figs. 70 and 71 (♂); André 1895, p. 82; Wheeler, 1915, p. 32, text-fig. 4 (♀); Burnham, 1978, p. 110; Bolton, 1995, p. 82; Dlussky, 1997, p. 61, text-fig. 1g; De Andrade and Baroni Urbani, 2003, pp. 935–936, text-figs. 3–5, 10.

Bradyponera meyeri: Dalla Torre, 1893, p. 18; Handlirsch, 1907, p. 879; Ponomarenko and Schultz, 1988, p. 26 (misspelling).

Lectotype. The species has been described by Mayr based on five specimens, only one of which has survived. In the interests of stability of nomenclature, I am designating here that specimen as lectotype. Lectotype: worker, NHMW, no. 1984/31/356 labeled “*ST Bradyponera meyeri* Mayr, 1868. Eozoen. Baltischer Bernstein. Kollektion Handlirsch”. Baltic amber, Late Eocene.

Description. Worker (Fig. 9a). Body length 2.0–2.5 mm. The head is slightly longer than wide, rectangular, with rounded occipital corners and straight or weakly concave occipital margin. The occipital orifice is bordered by a low chitinous carina. The eyes are round, weakly convex. The gena is distinctly longer than the maximum diameter of the eye. The clypeus is distinctly subdivided into a median and two lateral parts. The median part has no carina and appears like a segment of a sphere; it is slightly longer than wide, protruding anteriorly farther than the lateral parts, posteriorly it is contiguous with the anterior parts of the frontal carinae and with the antennal insertions, becoming here

an acute frontal area. The anterior margin of the clypeus is rounded. The lateral parts of the clypeus are very narrow, extending as two narrow lateral stripes from its median part down to bases of the mandibles. The frontal carinae originate at the sides of the median clypeal part, behind the midpoint between the frontal area and the antennal pit, and extending posteriorly, strongly diverging, not reaching the level of eyes. The antennae are 12-segmented. The scape is broadened and flattened, extending beyond the eyes but not reaching the occipital margin. The flagellum is attached somewhat below the apex of the scape. The apex of the scape on the lower side with a groove, which possibly received the base of the flagellum at rest. The first flagellomere is approximately as long as wide. Each of the more distal flagellomeres, except the terminal one, is distinctly shorter than wide. The terminal flagellomere is very large, its length is approximately equal to the combined lengths of the flagellomeres III to X. The mandibles are short, triangular, with the interior and the masticatory margins approximately equally long; the masticatory margin is not dentate, cutting, forming a flat arch; the apical angle of the mandible is acute, the internal angle (at the base of the masticatory margin) is rectangular. The maxillary palpi are 5-segmented, each with a long terminal segment. The mesosoma is robust, compressed laterally, without sutures. The dorsal surface of the mesosoma is evenly convex, without mesopropodeal constriction. The propodeum with pair of well rounded teeth at the transition between the dorsum and the declivity. The posterior surface of the propodeum is concave, laterally bordered by indistinct chitinous carinae, extending from those teeth. Legs are short and thick. The meso- and the metatibiae with short spurs.

The petiole in profile is wedge-shaped, with a very short peduncle. The anterior surface of the petiole in profile is weakly convex, its posterior surface is weakly concave and the apex is narrowly rounded. The petiole is distinctly shorter than high. The subpetiolar projection is developed as a rounded lobe. Most of the gaster comprise the first two gastral segments, separated by a constriction. The first gastral tergite in profile is evenly convex. The lower surface of the first gastral sternite, below its articulation with the petiole, with a short obtuse conical tooth. The dorsal surface of the second tergite is strongly rounded, several times as long as the sternite, so that the second tergite is arched in profile. The other segments form a short cone, directed anteriorly. The sting is short.

Long erect hairs are absent. The entire body, including the legs and the antennae, with numerous very short decumbent or partially raised hairs. The sculpture is formed by isolated rounded pits. On the head and the dorsal mesosoma the diameter of the pits approximately equals the distances between them. The gaster with smaller and sparser pits, poorly visible under dense decumbent pubescence.

Gyne (Fig. 9b). Body length 2.8–3.5 mm. Differs from the worker by the presence of ocelli, the larger

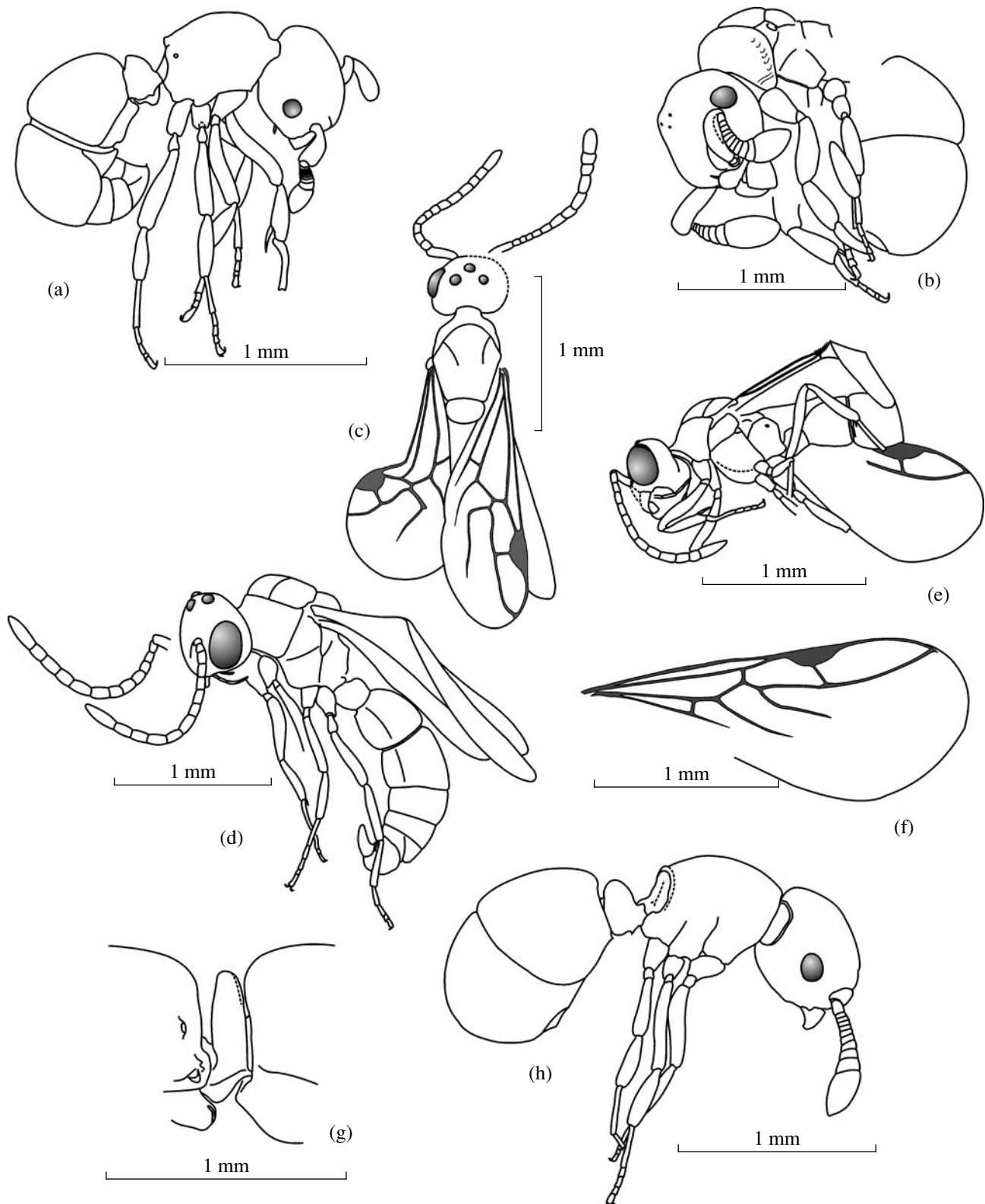


Fig. 9. Species of the genus *Bradoponera*: (a–h) *Bradoponera meyeri* Mayr: worker, CGC, no. 3343, general view of the inclusion (a), gyne, MZ PAN, no. 15444, general view of the inclusion (b), male, SIZK, no. K-3569, general view of the inclusions from different angles (c–d), male, MZ PAN, no. 14764, general view of the inclusion (e) and forewing (f); (g) *Bradoponera electrina* Baroni Urbani, worker, holotype (modified from De Andrade and Baroni Urbani, 2003); (h) *Bradoponera similis* sp. n., holotype HM, no. 11/388, general view of the inclusion.

eyes, the complete subdivision of mesosoma, and a better developed surface sculpture. The sides of the pronotum with a row of large elongate pits along the posterior margins.

Male (described here for the first time) (Figs. 9c–9f). BL 2.0–2.5 mm. The head is slightly shorter than wide. The eyes are very large, convex, almost completely occupying sides of head, but shifted anteriorly; the length of the gena is approximately equal to the width of the flagellum. The ocelli are very large, the interocellar distance is approximately equal to the diameter of the ocellus. The mandibles are small, triangular; the masticatory margin without teeth. The antennae, if bent back, reach the posterior margin of the mesosoma. The scape is distinctly longer than the first two flagellomeres combined. The first flagellomere is the shortest, yet it is still approximately twice as long as wide. The third flagellomere is 2.0–2.5 times as long as the second. The more distal flagellomeres gradually become longer and thicker. The maxillary palpi are long, almost reaching the occipital orifice. The labial palpi are short, almost as long as the longest segment of the maxillary palpi. The lateroposterior margins of the pronotum are somewhat pointed. The scutum is convex, longer than wide, with deep parapsidal furrows, not fusing together posteriorly. The scutellum is convex. The mesopleura are convex, with deep longitudinal suture. The propodeum in profile is angular, with its dorsum shorter than the declivity. The legs are short and thick. Each mesotibia with one simple spur; the metatibiae in the specimen SIZK, no. K-3569 each with one pectinate spur and in the specimen MZ PAN, no. 14764 each with a larger pectinate and a very small, bristlelike simple spur. The petiole is low, approximately as high as wide, with the node angular in profile. The subpetiolar projection is absent. The constriction between the first and the second gastral segments is deep and distinct. The stipites are long, slightly curved, with rounded apices.

The head, pronotum, scutum, and scutellum with isolated pits, separated by coarsely shagreened surface. The mesopleura with only coarse shagreened sculpture, without pits. The sides of the propodeum and the entire petiole are rugose. The gaster is shiny, with delicate shagreened sculpture. Erect hairs on the body are absent. Decumbent pubescence is sparse, consisting of very short fine hairs.

Wings with a large pterostigma, with closed cells 1 + 2r and 3r. Cell 3r is approximately three times as long as wide, its apex is pointed and lies on the wing margin. Cell 1 + 2r is more than twice as long as wide, the free 4M comes off near its base. RS and the free branch of M connect to cell 1 + 2r at widely separated points, which indicates that cell rm has disappeared due to reduction of crossvein rs-m. The meeting of veins cu-a and M + Cu is proximal to the split of 1M and free branch of Cu, being separated from it by 1.5 lengths of cu-a.

Measurements (mm): Workers: spec. MZ PAN, no. 10360: AL 0.85, HL 0.58, SL 0.40; spec. CGC, no. 3343: AL 0.65, HL 0.50, F3L 0.42, PtL 0.18, PtH 0.27; spec. HM, no. 11/296: AL 0.675, HL 0.60, SL 0.275; spec. GZG.BST (MKC), no. 27.101: AL 0.90. Gyne: spec. MZ PAN, no. 15444: AL 1.0, HL 0.7, SL 0.45, ED 0.15. Males: spec. MZ PAN, no. 14764: AL 0.775, FWL 2.0; spec. SIZK, no. K-3569: AL 0.83, HL 0.51, HW 0.53, ED 0.29, FWL 1.65.

Remarks. *Bradoponera meyeri* is the most abundant species of Ponerinae in the Late Eocene ambers. In total, 32 specimens have been examined thus far: five workers by Mayr (1868), two workers by André (1895), ten workers and one dealate gyne by Wheeler (1915), three workers by De Andrade and Baroni Urbani (2003), and 8 workers, two males, and one dealate gyne by myself. It is striking that, unlike other species of Ponerinae abundantly represented in ambers (*Hypoconera atavia*, *Pachycondyla succinea*, *Gnamp-togenys europaea*, and species of *Ponera*), which are mostly represented in ambers by alate gynes and males, most discovered specimens of *B. meyeri* (30 out of 32) are workers and dealate gynes. As was mentioned above, the strong prevalence of alate individuals in most fossil Ponerinae indicates that those ants lived in litter or upper soil, climbing up the trees only during their nuptial flight. The prevalence of wingless individuals in *B. meyeri* suggests that these ants routinely walked on tree trunks. At the same time, these ants are similar in their appearance to other representatives of Proceratiini: *Proceratium* and, particularly, *Discothyrea*, the recent species of which dwell in litter. The shapes of their head capsule (lack of distinct occipital corners, usually associated with strong mandibular muscles) and mandibles contradict the hypothesis that *Bradoponera* workers were capable of building nests in a dense substrate, such as wood. Therefore, it is probable that they made nests inside natural cavities in dead wood or (more likely) in the detritus accumulating on epiphytes, as is the case with some recent tropical Ponerinae.

There is no doubt that the described males belong to *Bradoponera meyeri*. This is indicated by their size, sculpture, structure of palpi, and general appearance.

Material. Baltic amber: MZ PAN, nos. 10360 (♀), 14764 (♂), 15444 (♀); NHML, nos. In.17965 (♀), PI II.1100 labeled “J. Gerber, 1969” (♀); CGC, no. 3343 (♀); GZG.BST.03956 (G2954) (♀). Bitterfeld amber: HM, no. 11/296 (♀); GZG.BST (MKC), no. 27.101 (♀). Rovno amber: SIZK, nos. K-3569 (♂), K-4248 (♀).

Bradoponera similis Dlussky, sp. n.

Holotype. Worker HM, no. 11/388. Bitterfeld amber, Late Eocene.

Description. Worker (Fig. 9h). BL ca. 2.5 mm. The head is longer than wide, rectangular, with rounded occipital corners, its occipital margin is straight or slightly concave. The occipital orifice is bordered by a

distinct chitinous carina. The gena length is approximately equal to the eye diameter. The anterior margin of the clypeus is rounded. The frontal carinae are short, divergent. The antennae are 12-segmented. The scape does not reach the occipital margin. The first flagellomere is longer than wide. The more distal flagellomeres, except the terminal, each is distinctly shorter than wide. The terminal flagellomere is very large, slightly shorter than the combined length of the flagellomeres II to X. The mandibles are triangular. The palpi and the masticatory margin of the mandibles cannot be seen. The mesosoma is robust, compressed laterally, without sutures. The dorsal surface of mesosoma is evenly convex, without the mesopropodeal constriction. The propodeum without denticles, its declivity is concave, bordered with a relatively thick chitinous carina. Looking exactly in profile, one can see a depressed line between that carina and the propodeal dorsum. The legs are short and thick. The petiole is relatively thick, on its lower surface with a small pointed tooth, which is directed ventrad. Petiole in profile with upper margin well-rounded. The petiole is distinctly shorter than high. The gaster is as in the preceding species.

Long erect hairs are absent. Sculpture is formed by isolated round pits, which are deeper on the upper side of the head and the lateral sides of the mesosoma.

Gynes and males are unknown.

Measurements (mm): Holotype: AL 0.68, HL 0.59, ED 0.14, PtL 0.20, PtH 0.27.

Comparison. The new species is similar to *Bradoponera meyeri* Mayr, from which it differs by the shapes of its propodeum and the petiole, the larger eyes, and the coarser sculpture.

Material. Holotype.

***Bradoponera wunderlichi* Baroni Urbani et De Andrade, 2003**

Bradoponera wunderlichi Baroni Urbani et De Andrade: De Andrade and Baroni Urbani, 2003, pp. 931–934, text-figs. 1 and 8 (dealate ♀).

Holotype. Dealate gyne, Museo Regionale di Scienze Naturali of Turin, no. BB-1. Baltic amber, Late Eocene.

***Bradoponera electrina* Baroni Urbani, 2003**

Bradoponera electrina Baroni Urbani: De Andrade and Baroni Urbani, 2003, pp. 934–935, text-figs. 2 and 9.

Holotype. Worker, Museo Regionale di Scienze Naturali of Turin, no. BB-6. Baltic amber, Late Eocene.

Genus *Proceratium* Roger, 1863

Type species. *Proceratium silaceum* Roger, 1863, by monotypy.

Diagnosis. Workers and gynes. Clypeus transverse, its anterior margin straight or with median prominence. Frontal carinae thin, widely separated, lamelliform in profile, partly covering antennal insertions.

Antennal insertions shifted anteriorly. Eyes present, but in workers reduced to small pigmented spots. Antennae 6- to 12-segmented, flagellomeres becoming thicker towards apex; terminal flagellomere larger, but not forming distinct club. Mandibles triangular, with teeth on masticatory margin. Palpal formula from 2.2 to 4.2. Second segment of maxillary palpi hammer-shaped. Mesosoma short and robust, its dorsal surface moderately convex. Promesonotal suture in workers rudimentary or completely absent. Posterior surface of propodeum bordered with more or less distinct carinae. Each tibia with one pectinate spur. Petiole of variable shape, with thick scale or node-shaped. Projection on lower surface of petiole present. Helcium attached approximately to center of anterior surface of first gastral segment. Dorsal surface of second gastral tergite arched, so that more distal gastral segments are directed anteriorly. Constriction between first and second gastral segments moderately developed.

Males. Eyes large, rounded. Ocelli relatively small. Clypeus narrow, with weakly produced anterior margin. Frontal carinae short. Antennal insertions exposed, close to posterior clypeal margin. Antennae 13-segmented, filiform, with short scape. Mandibles triangular, touching when closed, without teeth on masticatory margin. Second segment of maxillary palpi hammer-shaped. Parapsidal furrows present. Each tibia with one spur. Petiole with node lower and more rounded than in workers and gynes. Helcium attached approximately to center of anterior surface of first gastral segment. Second gastral segment in profile trapezoidal, with strongly convex dorsal surface, such that entire body is arched, its tip directed down. Pygidium without terminal spine. Forewing with incomplete set of veins: closed cell rm absent. Hindwing without jugal lobe.

Composition and distribution. Seventy-six species in the recent fauna, distributed on all continents, but predominantly in the tropics. Five species are known in the southern Palearctic (Bolton et al., 2006). Up until now, four fossil species have been described, all from Dominican amber (Early Miocene): *P. denticulatum* (Lattke, 1991), *P. dominicanus*, *P. gibberum*, and *P. poinari* (Baroni Urbani and De Andrade, 2003). The new species described below is the first representative of this genus found in the Baltic amber.

***Proceratium eocenicum* Dlussky, sp. nov.**

Etymology. From the name of the epoch (Eocene).

Holotype. Male, MZ PAN, no. 18097; a completely preserved inclusion, partly obscured by cloudy extraneous matter. Baltic amber, Late Eocene.

Description. Male (Fig. 10). Body length 2.2–2.7 mm. The head is round, longer than wide, with barely visible, strongly rounded occipital corners and a convex occipital margin. The eyes are shifted anteriorly; the length of the gena is slightly less than the width of the scape. The interocellar distance is less than

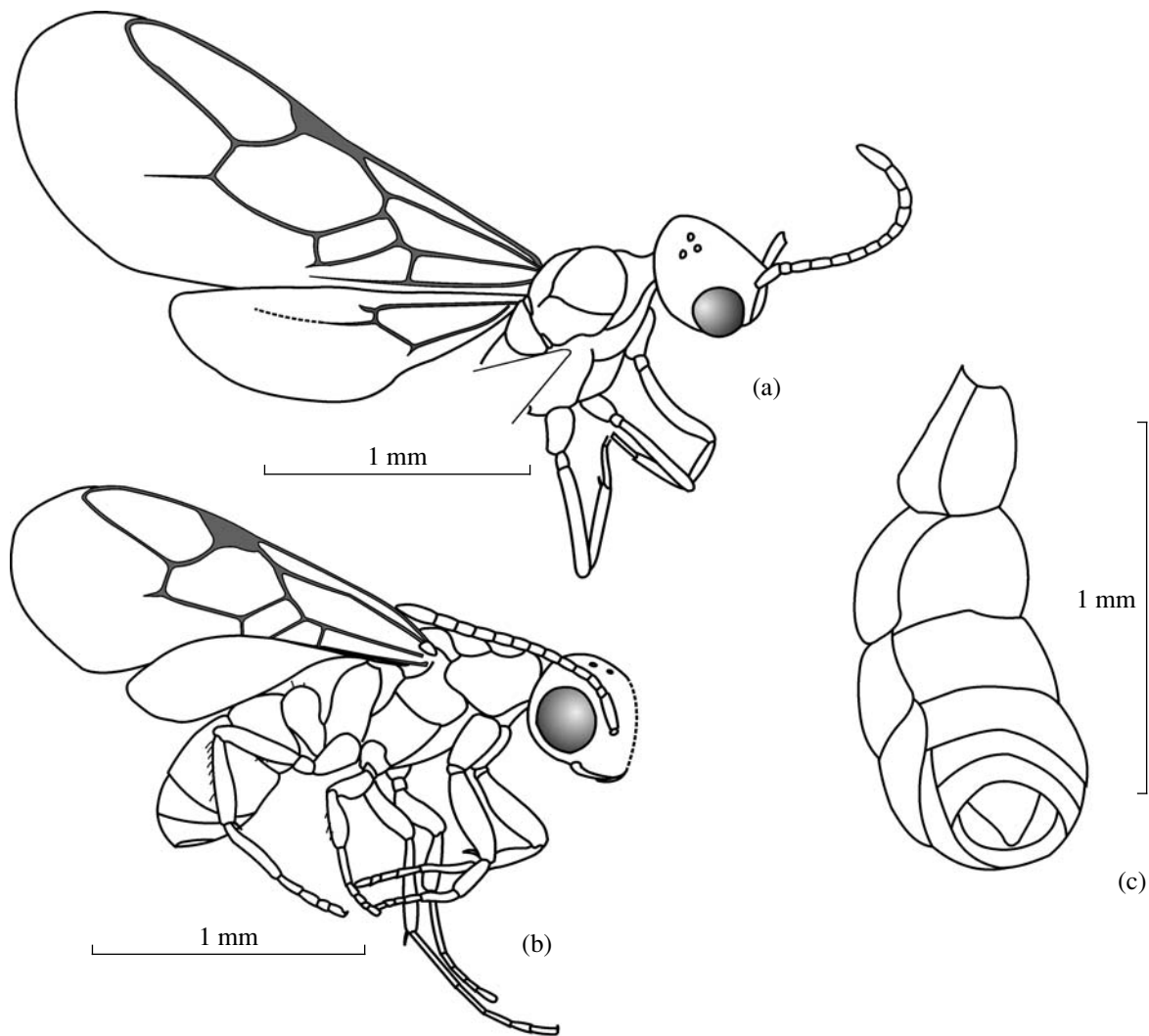


Fig. 10. *Proceratium eocenicum* sp. n.: (a) male, holotype MZ PAN, no. 18097; (b–c) male, paratype GPIH, no. 4507 (CGC, no. 3306); general view of the inclusion (b) and gaster in ventral view (c).

the ocellar diameter. The clypeus in profile is weakly convex. The antennae, if bent back, do not reach the posterior margin of the mesosoma. The scape is twice as long as wide, approximately as long as the two next antennomeres combined; the second antennomere is the shortest, as long as wide. The more distal antennomeres progressively become longer, each longer than wide. The pronotum is narrow, transverse, with rounded posterolateral angles. The scutum is slightly longer than wide, weakly convex, with distinct parapsidal furrows, converging posteriorly into a single Y-shaped furrow. The mesopleural suture is shallow yet conspicuous. The propodeum in profile is rounded. Each mesotibia with one simple and each metatibia with one pectinate spur. The petiole is low, not as high as long, with the node rounded in profile. The lower side of the petiole with a small rounded projection. The constriction between the first and the second gastral

segments is deep and distinct. The subgenital plate is triangular. The genitalia are drawn in, not visible.

The body is shiny, with sculpture consisting of shallow isolated pits, separated by distances smaller than their diameter, conspicuous on the propodeum and the mesopleura, barely developed on the upper surface of the head and on the scutum. Decumbent pubescence is short and sparse, the hairs are shorter than distances between them. Erect and semierect hairs are visible on the meso- and metatibiae and on the tip of the gaster.

The wings are broad, with a distinct fringe of fine hairs along their posterior margins. The forewing with $2 + 3RS$ reduced, cells $1 + 2r$ and rm are fused into a single large cell. Therefore, the forewing has closed cells $1 + 2r + rm$, $3r$, and mcu . Cell $3r$ is 2.9 times as long as its maximum width in the holotype and 2.4 times in the paratype; its apex is rounded, not quite reaching the wing margin. Cell $1 + 2r + rm$ is very large,

1.7–1.8 times as long as wide; free 4M comes off its distal part. The meeting of veins cu-a and M + Cu is proximal to the 1M and 1Cu fork, being separated from it by less than half the length of 1Cu (2.6 times in the holotype, 2.2 times in the paratype). Cell cua is open at the apex.

Workers and gynes are unknown.

M e a s u r e m e n t s (mm): Males: holotype MZ PAN, no. 18097: AL 1.0, HL 0.55, FWL 2.1; paratype CGC, no. 3306: AL 0.80, HL 0.50, HW 0.5, FWL 1.75.

C o m p a r i s o n. A comparison with the recent species of *Proceratium* is not possible because males of this genus are poorly known. The new species can be easily differentiated from the male of *Bradoponera meyeri* by its forewing venation and lack of coarse sculpturing.

M a t e r i a l. Besides holotype, paratype male, GPIH, no. 4507 (CGC, no. 3306). Baltic amber.

Key to Species of Ponerinae from the Late Eocene Ambers of Europe

Workers and gynes

1. Petiole broadly attached to first gastral segment, in profile separated from it only by constrictions on dorsal and ventral sides. Helcium in profile attached to upper portion of anterior surface of first gastral segment (Fig. 2a). Head subtrapezoidal, widened anteriorly. Mandibles elongated, linear, with large teeth, in closed state not contiguous with anterior margin of clypeus (Fig. 2b). Eyes in workers absent or reduced to a single ommatidium. Entire body with numerous erect hairs. 3 mm.....*Amblyopone groehni* sp. n.

—Petiole nodiform or with vertical scale. Helcium attached to first gastral segment in its middle or lower parts (Figs. 3c, 6h, 7a, 7b, 8b, 9a, 9g, 9h). Mandibles triangular (Figs. 3e, 5c).....2.

2. Helcium attached to first gastral segment in its lower part. Anterior surface of first gastral segment, facing petiole, vertical (Figs. 3c, 6h). Frontal carinae close-set (Figs. 3d, 5c). Promesonotal suture distinct. Gaster cylindrical.....3.

—Helcium attached to first gastral segment in its middle part. First gastral tergite in profile more or less evenly convex (Figs. 7a, 7b, 8b, 9a, 9g, 9h). Frontal carinae widely separated (Figs. 7a, 8a).....7.

3. Subpetiolar process anteriorly with pair of acute teeth or angles, posteriorly with round semitransparent “window” or perforation (Fig. 6h). Meso- and metatibiae each with one spur *Ponera* spp. (workers and gynes unknown in amber)

—Subpetiolar process (if present) is simple rounded lobe (Fig. 3b).....4.

4. Meso- and metatibiae each with one spur (Figs. 3f, 3g). Petiole with high and thick scale (Figs. 3a–3c). Workers with eyes reduced to several ommatidia, inconspicuous against surface sculpture.

Worker 3.0, gyne 3.5 mm.....*Hypoponera atavia* (Mayr)

—Meso- and metatibiae each with two spurs, large pectinate and short simple. Workers with eyes normally developed. Body length exceeds 4 mm.....5.

5. Body length of worker 10.5 mm.....*Pachycondyla gracilis* (Mayr)

—Smaller, gyne body length 4–6 mm, workers unknown.....6.

6. Petiole approximately as long as wide, with thick scale (Figs. 4d, 4e). Entire body with numerous erect hairs.....*Pachycondyla succinea* (Mayr)

—Petiole twice as wide as long, with scale broad and thin (Fig. 5b). Erect hairs short, not numerous, present only on head, scutum, and gaster tip.....*Pachycondyla tristis* sp. n.

7. Propodeum with pair of obtuse teeth, each associated with longitudinal carina. Petiole triangular in profile, without distinct peduncle, its anterior and posterior surfaces separated from each other and from lateral surfaces with sharp crests (Fig. 7b). Worker 7.5 mm.....*Electroponera dubia* Wheeler

—Propodeum and petiole without distinct longitudinal carinae or crests. If propodeum with carinae extending from teeth, then petiole not triangular and without transverse crest along upper margin.....8.

8. Gaster cylindrical. Petiole in profile cubical, with pair of obtuse dentiform projections at posterior margin (Fig. 7a). 5.5–6.0 mm...*Platythyrea primaeva* Wheeler

—Second gastral segment in profile trapezoidal or triangular, its dorsal surface strongly convex, so that entire body curved, its rear end pointed down or even forward (Figs. 8b, 9a, 9b, 9h).....9.

9. Head and mesosoma with distinct reticulate and rugose sculpture. Entire body, including legs, with numerous erect hairs. Promesonotal suture in workers present. Gaster tip directed down. Worker 4.0, gynes 4.0–4.5 mm.....*Gnamptogenys europaea* (Mayr)

—Head and mesosoma with sculpture consisting of coarse pits. Erect hairs on body absent. All segments of mesosoma fused, sutures absent. Gaster very strongly bent, its tip pointed forward.....10.

10. Antennae 9-segmented. Gyne 2.5 mm.....*Bradoponera wunderlichi* Baroni Urbani et de Andrade

—Antennae 12-segmented.....11.

11. Propodeal dorsum and declivity forming rounded angle, without teeth or transverse carina at bend. Petiole with high and thin scale (Fig. 9g). Worker 3.5 mm.....*Bradoponera electrina* Baroni Urbani

—Propodeum and petiole different. Workers 2.0–2.5, gynes 3.0–3.5 mm.....12.

12. Propodeum with pair of strongly rounded teeth at transition between its dorsum and declivity. Petiole in profile wedge-shaped (Fig. 9a).....*Bradoponera meyeri* Mayr

—Propodeum with transverse carina at transition between its dorsum and declivity. Upper margin of petiole in profile well-rounded (Fig. 9h).....
.....*Bradoponera similis* sp. n.

Males

1. Petiole broadly attached to gaster, in profile separated from it only by constrictions on dorsal and ventral sides (Fig. 2c). Forewings with closed cells 1 + 2r, 3r, rm, mcu, and cua (Fig. 2d). Mandibles reduced, not touching when closed, without teeth on masticatory margin (Fig. 2c). Parapsidal furrows, fusing in posterior part of scutum. Ca. 3 mm...*Amblyopone electrina* sp. n.

—Petiole nodiform or with vertical scale, narrowly articulated to gaster.....2.

2. Forewing without isolated cell rm (Figs. 9c, 9e). Meso- and metatibiae usually each with single spur. Parapsidal furrows present (Figs. 9c, 10a). Pygidium without terminal spine (Figs. 9d, 10c).....3.

—Forewing with closed cells 1 + 2r, 3r, rm, mcu and usually also cua (Figs. 1, 3h, 4a, 4f, 6a, 6b, 6g, 8f, 8g)...4.

3. Forewing with isolated cell mcu. Cell 1 + 2r + rm very large, 1.7–1.8 times as long as wide; section 4M connected to distal part of that cell (Figs. 10a, 10b). Parapsidal furrows fused in posterior part of scutum (Fig. 10a). 2.2–2.7 mm...*Proceratium eocenicum* sp. n.

—Forewing without closed mcu. Cell 1 + 2r smaller and narrower, more than two times as long as wide; section 4M connected near base of that cell (Figs. 9c, 9f). Parapsidal furrows not fused in posterior part of scutum (Fig. 9c). 2.0–2.5 mm.....*Bradoponera meyeri* Mayr

4. Mandibles large, triangular, touching when closed, with teeth on masticatory margin. Antennal insertions situated close to posterior margin of clypeus (Fig. 8e). Helcium attached to middle of first gastral segment (Figs. 8d, 8e). Meso- and metatibiae each with one spur. Parapsidal furrows present. Pygidium without terminal spine.....5.

—Mandibles reduced, not touching when closed, without teeth on masticatory margin (Figs. 3i, 3k). Antennal insertions distant from posterior margin of clypeus (Figs. 3k, 6e). Helcium attached to bottom part of first gastral segment (Figs. 3h, 3j, 4f, 6a–6c).....6.

5. Entire body, including legs, with numerous erect hairs. Propodeum in profile with its dorsum and declivity approximately equal, forming obtuse angle. Smaller, body length 3.0–4.0 mm.....
.....*Gnamptogenys europaeva* (Mayr)

—Mesosoma and petiole with isolated erect hairs. Legs without erect hairs. Propodeum in profile well-rounded. Larger, 8.5–9.0 mm.....
.....*Gnamptogenys rohdendorfi* sp. n.

6. Meso- and metatibiae each with two spurs: smaller, simple, and larger, pectinate on metatibia and pectinate or serrate on mesotibia. Pygidium with terminal spine.....7

—Meso- and metatibiae each with one pectinate or serrate spur. Very rarely metatibia with very small, bristle-like second spur.....9

7. Parapsidal furrows well developed (Fig. 4f). Entire body with numerous erect hairs. 3.5–4.5 mm.....
.....*Pachycondyla succinea* (Mayr)

—Parapsidal furrows absent (Figs. 5a, 5e). Erect hairs sparser.....8

8. Smaller: body length ca. 2.5 mm. Forewing with cell rm triangular. Propodeum in profile well-rounded.....
.....*Pachycondyla conservata* sp. n.

—Larger: body length ca. 3.5 mm. Forewing with cell rm quadrangular. Dorsal and posterior surfaces of propodeum in profile forming rounded angle.....
.....*Pachycondyla baltica* Dlussky

9. Pygidium with rounded apex, without terminal spine (Figs. 3h, 3f). Parapsidal furrows absent. Decumbent pubescence relatively abundant. Erect hairs sparse. 2.8–3.2 mm.....
.....*Hypoconera atavia* (Mayr)

—Pygidium with terminal spine.....10

10. Parapsidal furrows absent. Forewing with cell rm triangular (Fig. 6g). Head and mesosoma weakly shiny, with fine shagreened sculpture, without decumbent pubescence. Sparse erect hairs present on head near ocelli, scutum, and gaster tip. 2.6–3.0 mm.....
.....*Ponera wheeleri* sp. n.

—Parapsidal furrows present. Forewing with cell rm quadrangular (Figs. 6a–6c).....11

11. Petiole below with small rounded lobe (Fig. 6b). Head and pronotum with delicate dense punctation, weakly shiny. Scutum, mesopleura, and gaster shiny, with sparse, barely visible punctation. Sides and dorsum of propodeum with dense shagreened sculpture and reticulate sculpture formed by strongly smoothed rugae. Decumbent pubescence absent or gaster with very short decumbent hairs, much shorter than distances between them. Short, fine, erect hairs present on head near ocelli, on clypeus, pronotum, scutum, propodeum, petiole, and entire surface or gastral tergites and sternites. 3.2–3.8 mm.....
.....*Ponera lobulifera* sp. n.

—Petiole below without lobe. Body weakly shiny, with fine shagreened sculpture and abundant decumbent pubescence. Decumbent hairs significantly longer than distances between them. Clypeus, propodeum, upper margin of scale, and gaster with isolated semierect and erect hairs. 3.0–3.5 mm.....
.....*Ponera mayri* sp. n.

Subfamily Cerapachyinae Forel, 1893

In the modern fauna the subfamily Cerapachyinae is represented by six genera containing the total of 212 species, distributed throughout the tropical zone (Bolton et al., 2006). Two fossil species, *Procerapachys annosus* and *P. favosus*, have been described from Baltic amber (Late Eocene) (Wheeler, 1915), and additional four, *Acanthostychus hispaniolicus*

(De Andrade, 1998a), *Cylindromyrmex antillianus*, *C. electrinus* (De Andrade, 1998b), and *C. inopinatus* (De Andrade, 2001), from Dominican amber (Early Miocene).

For a long time most myrmecologists included the tribes Acanthostichini, Cerapachyini, and Cylindromyrmecini in Ponerinae. In particular, Brown (1975) followed this classification in his revision of Ponerinae. Wilson (1958a) demonstrated that these species were specialized myrmecophages: they organize group raids, attack nests of other ant species, and steal their larvae and pupae, which serve as the main diet for the larvae of *Cerapachys*. He suggested that this behavior could have been ancestral to the peculiar behavior of army ants from the subfamilies Ecitoninae, Dorylinae, and Aenictinae (Wilson, 1958b). Later, Bolton (1990a) pointed out several similarities in the morphology of the gastral region of Cerapachyini and army ants. Based on these, he proposed treating Cerapachyinae as a separate subfamily including the tribes Acanthostichini, Cerapachyini, and Cylindromyrmecini (Bolton, 1990b). Currently he includes this subfamily in the dorylomorph group of subfamilies, along with Ecitoninae, Leptanilloidinae, Aenictinae, Dorylinae, and Aenictogitoninae (Bolton, 2003).

Most myrmecologists consider Cerapachyinae as the common ancestor of all other dorylomorph subfamilies (Baroni Urbani et al., 1992, etc.). However, recently Perfilieva (2002) demonstrated that wings of Cerapachyinae (only recent species were studied) show advanced features and could not be ancestral for the venation characteristic of Ecitoninae, Aenictinae, and Dorylinae. However, the venation of the *Procerapachys* wing, described below for the first time, is rather primitive, which obviates several of Perfilieva's objections.

Tribe Cerapachyini Forel, 1893

Genus *Procerapachys* Wheeler, 1915

Type species. *Procerapachys annosus* Wheeler, 1915, by the original designation.

Diagnosis. Workers. Head subrectangular. Eyes relatively large, convex, comprising numerous ommatidia. Antennal insertions exposed. Frontal carinae close-set, parallel, shaped as thin vertical lamellae. Genae with distinct carina. Clypeus narrow, transverse. Antennae short, 12-segmented. Width of flagellomeres gradually increasing towards apex of antenna, distinct club absent. Mandibles large, triangular, without teeth on masticatory edge. Palpal formula 5.4. Pronotum anteriorly with transverse carina along fold. Promesonotal suture present, other sutures on mesosoma reduced. Propodeal declivity curved by carina. Each tibia with single pectinate spur. Petiole one-segmented; first and second gastral segments separated by constriction. Helcium attached to middle part of first gastral segment. Sculpture of first gastral segment (postpetiole) similar to that of the rest of gaster, differing mark-

edly from sculpture of petiole. More terminal gastral segments without constrictions in between. Pygidium unmodified, with convex and slightly flattened dorsal surface, its posterior margin without teeth or denticles.

Males. Head with distinct occipital carina. Eyes relatively small. Ocelli large. Antennal insertions exposed. Frontal carinae long, straight, weakly divergent. Clypeus transverse, with broadly rounded anterior margin and distinct median carina. Antennae 13-segmented, filiform, with short scape. Mandibles triangular, touching when closed, without teeth on masticatory margin. Parapsidal furrows distinct. Tibial spurs as in workers. Petiole one-segmented; first and second gastral segments separated by constriction. Helcium attached to middle part of first gastral segment. Sculpture of first gastral segment (postpetiole) similar to that of the rest of gaster, differing markedly from sculpture of petiole. Forewing with complete set of veins. Hindwing without jugal lobe.

Gynes unknown.

Composition and distribution. To date, two species have been described from Baltic amber (Late Eocene): *Cerapachys annosus* (Wheeler, 1915) and *C. favosus* (Wheeler, 1915). I have found the first species also in Bitterfeld amber. One additional species is being described below.

Remarks. Brown (1975) synonymized the genus *Procerapachys* Wheeler to *Cerapachys* F. Smith. Having not seen the ants, he based this decision only upon the description and Wheeler's drawings. In my opinion, this synonymy is erroneous. Even the description of *Procerapachys* by Wheeler (1915) indicates the presence of promesonotal suture, 5-segmented maxillary palpi, and 4-segmented labial palpi. Among Cerapachyinae, traces of the promesonotal suture are present, besides *Procerapachys*, only in the African *Cerapachys wroughtoni* Forel. In other representatives of this subfamily the promesonotal suture is reduced. Maxillary palpi in workers and gynes of *Cerapachys* are 3- to 4-segmented, labial palpi 2- to 3-segmented. Additionally, one can point out the complete wing venation and the structure of pygidium of *Procerapachys*. In all known recent species of Cerapachyinae wing venation is more or less reduced (Perfilieva, 2002). In recent Cerapachyinae, pygidium is flattened, and the flattened areola is curved laterally or/and posteriorly by a series of short teeth of denticles, while in *Procerapachys* the dorsal surface of pygidium is convex and slightly flattened, without teeth or denticles. All these characters of *Procerapachys* are plesiomorphic with respect to other Cerapachyinae, which corroborates Wheeler's hypothesis that this genus is the most primitive in the subfamily.

Procerapachys annosus Wheeler, 1915

Procerapachys annosus Wheeler, 1915, p. 28–31, fig. 2 (worker, ♂); Burnham, 1978, p. 110.

Cerapachys annosus (Wheeler): Brown, 1975, p. 22; Bolton, 1995, p. 142; Dlussky, 1997, p. 57.

Neotype. Wheeler based his description upon six specimens, one worker (holotype) from Klebs's collection (K.5793) and three workers (IV.7.8094/702 and B.225) from the collection of the Geological Institute of Königsberg. None of these specimens has survived. Therefore, to ensure the stability of nomenclature, a neotype is being designated here: worker, HM, no. 7/225, fully corresponding to Wheeler's description and his Fig. 2b. A completely preserved inclusion, partly obscured with cloudy material. Bitterfeld amber, Late Eocene.

Description. Worker (Figs. 11a, 11b). BL 6–9 mm. The head is slightly longer than wide, slightly widened anteriorly, with almost straight sides in full-face view, rounded occipital corners, and a weakly concave occipital margin. The occiput with an arcuate carina. The eyes are oval, weakly convex, situated slightly behind the lateral midlength of the head. The gena is longer than the maximum eye diameter. The ocelli are present in some individuals. The frontal carinae reach to almost 1/3 of the head length, they are parallel in the anterior and convergent in the posterior part. The surface between the carinae is concave. The scape is short and thick, not nearly reaching the occipital margin of the head. The flagellomeres II to V each is shorter than wide. The terminal flagellomere is shorter than the combined length of the two preceding flagellomeres. The dorsal surface and the sides of the mesosoma are weakly concave medially. The dorsal and the anterior surfaces of the pronotum are separated by a chitinous carina. A similar carina borders the posterior margin of the propodeum. The legs are thick. The petiole is massive, cylindrical, its length distinctly exceeds both its width and height. The anterior surface of the petiole is vertical, bordered by a carina, similarly to the propodeal declivity. The petiole in profile with its anterior and posterior surfaces forming a rounded right angle. The subpetiolar process is developed as a pointed tooth. The postpetiole is 1.5 times wider than the petiole, in profile with its dorsal and ventral surfaces nearly parallel; it is separated from the rest of the gaster by a deep constriction, which is anteriorly narrower than posteriorly. The sting is well developed.

The head is densely punctate, sculptured with large shallow pits. Additionally, the genae with several coarse rugae. The mandibles are smooth. The mesosoma and the sides of the petiole with coarse longitudinal rugae. The propodeal declivity and the anterior surface of the petiole are smooth, shiny. The rugae on the dorsal surface of the petiole are anastomosing, forming reticulate sculpture. Postpetiolar sculpture consists of shallow pits, which are sparser and shallower than those on the head. The gaster is finely punctate. The entire body, including the legs and the scape, with erect

and semierect hairs. The gaster with fine and rather dense decumbent pubescence.

Male (Figs. 11c, 11d). BL 8–9 mm. The body is slender. The head is subtrapezoidal, narrowing anteriorly, with strongly rounded occipital corners and a convex occipital margin. The eyes are shifted anteriorly; the length of the gena is less than the maximum eye diameter, but approximately two times greater than the width of the flagellomeres. The ocelli are large, the interocellar distance exceeds the ocellus diameter. The frontal carinae are long and straight, divergent. The clypeus with a broadly rounded anterior margin and a distinct median carina. The antennae, if bent back, reach slightly beyond the posterior margin of the mesosoma. The scape is cylindrical, somewhat thickened, longer than the combined length of the two first flagellomeres. The first flagellomere is the shortest, shorter than wide. The more distal flagellomeres, except the terminal one, are approximately equal in size, two times as long as wide. The mesosoma is approximately 1.8 times as long as high. The propodeum in profile is angular; its dorsum and declivity are weakly convex, the fold between them with a transverse carina, which is serrate in its middle part. The petiole in profile with straight anterior and slightly rounded dorsal surfaces, its length almost equal to its height. The subpetiolar process is developed as a pointed tooth. The postpetiole is campaniform, longer and slightly wider than the petiole.

The head, mesosoma, and petiole are very coarsely reticulately rugose. The gaster (including the postpetiole) is smooth, with scattered piligerous punctures. The entire body, including legs, with rather numerous erect and semierect hairs.

The forewing with closed cells 1 + 2r, 3r, rm, mcu, and cua. Cell 3r is relatively short, three times as long as its maximum width. Crossveins r-rs and rs-m meet RS at the points separated from each other by a distance exceeding the length of r-rs. Cell rm is quadrangular, but 2M is very short. 1M and 1RS are approximately equal. Crossvein cu-a meets M + Cu very close to the 1M and 1Cu fork.

Gyne is unknown.

Measurements (mm): Workers: neotype HM, no. 7/225: BL 7.2, AL 1.7, HL 1.6, SL 0.9, ED 0.35, PtL 1.0, PtH 0.9; spec. CGC, no. 3348: BL 9.0, AL 1.9, HL 1.7, ED 0.35; spec. GZG.BST. (MKC), no. 27.103: HL 0.92, SL 0.49, ED 0.25. Males: spec. VGC, no. 6a: AL, HL 1.125, F3 1.25; spec. VGC, no. 6b: AL 2.375, HL 1.025, PtL 0.775; spec. VGC, no. 6c: AL 2.55; spec. VGC, no. 6d: PtL 0.75, PtH 0.625.

Material. Besides neotype, from Baltic amber: CGC, no. 3348 (two workers in one piece); VGC, no. 6 (7 ♂♂ in one piece). Bitterfeld amber: HM, no. 16/233 (♀); GZG.BST (MKC), no. 27.103 (♀). Late Eocene.

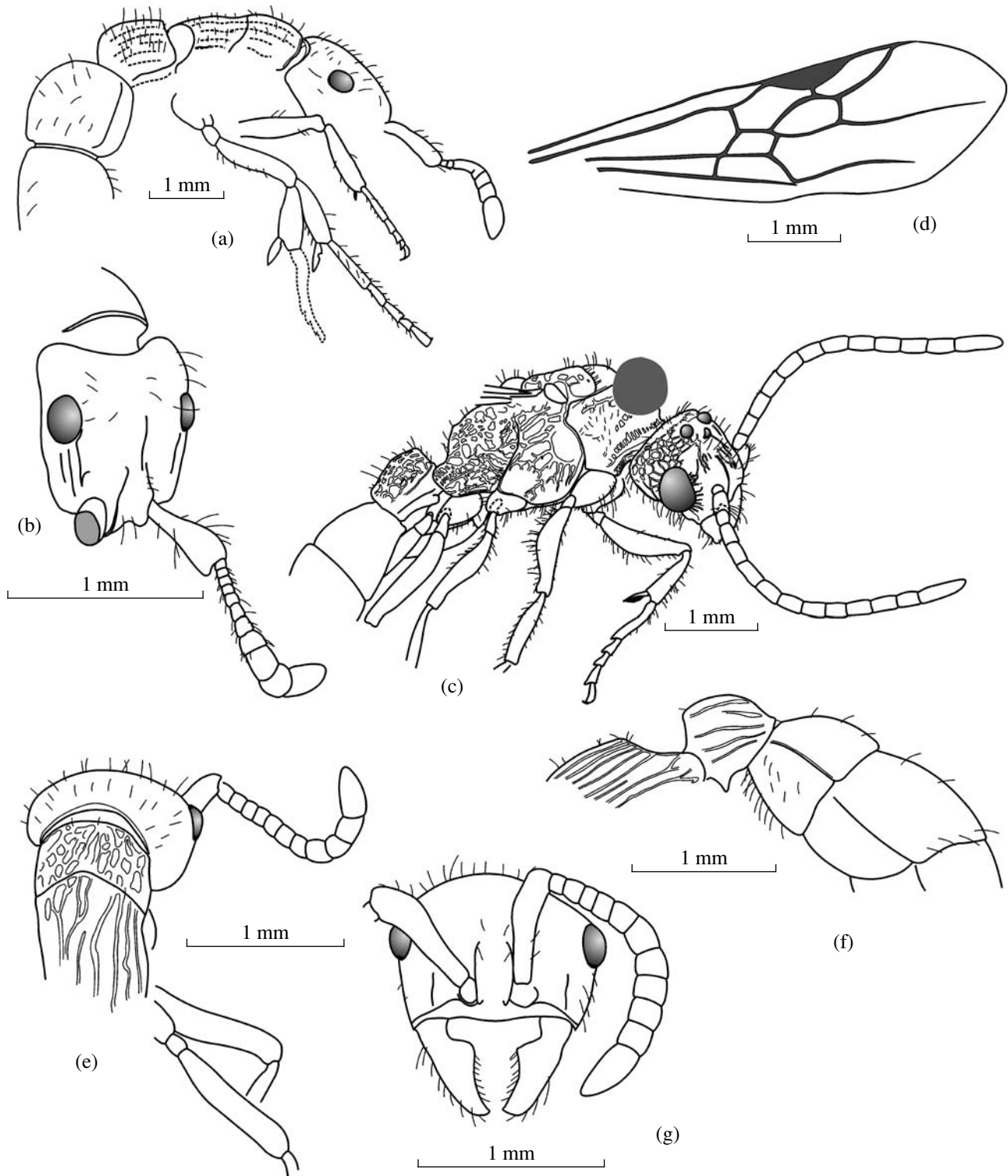


Fig. 11. Species of the genus *Procerapachys*: (a–d) *P. amosus* Wheeler: neotype HM, no. 7/225, worker, inclusion in profile (a), worker, GZG.BST (MKC), no. 27.103, head (b), male, VGC, no. 6, general view of the inclusion (c) and forewing (d); (e–g) *P. sulcatus* sp. n., holotype MZ PAN, no. 23537, worker: head and mesosoma in dorsal aspect (e), propodeum, petiole, and base of gaster in profile (f), and head (g).

Procerapachys favosus (Wheeler, 1915)

Procerapachys favosus Wheeler, 1915, p. 31–31, fig. 3 (♀); Burnham, 1978, p. 110.

Cerapachys favosus (Wheeler): Brown, 1975, p. 22; Bolton, 1995, p. 143; Dlussky, 1997, p. 57.

H o l o t y p e. Wheeler described this species based upon a single specimen (B-1839) from the collection of the Geological Institute of Königsberg, which has not survived. I have found no representatives of this species among the examined material.

Description (modified after Wheeler, 1915). Worker. BL 6 mm. Similar in its appearance to *C. annosus*, but with a different surface sculpture. The ocelli are present. The sides of the mesosoma and of the petiole are flatter than in *C. annosus*. The eyes are less convex. The head, mesosoma, petiole, and postpetiole are coarsely reticulately rugose. The head and the postpetiole with sculpture less developed than on the mesosoma; in addition to the rugae, these parts are densely and finely punctate. The propodeal declivity is bordered by a carina, smooth. The erect pilosity is sparser and the hairs are coarser than in *C. annosus*. The legs and the scape without erect hairs.

Procerapachys sulcatus Dlussky, sp. n.

E t y m o l o g y. From the Latin *sulcus* (furrow).

H o l o t y p e. Worker, MZ PAN, no. 23537. Baltic amber, Late Eocene.

Description. Worker (Figs. 11e–11g). BL ca. 3 mm. The head is subrectangular, with rounded occipital corners and a weakly concave occipital margin. A chitinous carina surrounding the occipital orifice is visible in posterior view. The eyes are oval, weakly convex, situated slightly behind the lateral midlength of the head. The gena is longer than the maximum eye diameter. The ocelli are absent. The frontal carinae reach the mid-level of eyes, they are parallel anteriorly and divergent posteriorly. The surface between the carinae is concave. The scape is short and wide, not nearly reaching the occipital margin of the head. The flagellomeres II to V each is shorter than wide. The last four flagellomeres are enlarged, but do not form a distinct club. The dorsal surface of the mesosoma is weakly and evenly convex. The dorsal and the anterior surfaces of the pronotum are separated by a distinct chitinous carina. A similar carina curbs the posterior surface of the propodeum. The legs are thick. The petiole is massive, only slightly longer than high. The anterior surface of the petiole is vertical, curbed by a carina, similarly to the propodeal declivity. The dorsal and the posterior surfaces of the petiole form a smooth transition, their fold in profile is more or less smoothly arcuate. The subpetiolar process is developed as a pointed tooth. The postpetiole is campaniform, separated from the rest of the gaster by a shallow constriction.

The head is densely punctate, sculpted with large shallow pits. The mandibles are smooth. The sides of the mesosoma and the petiole with coarse longitudinal

rugae; on the dorsal surface parallel rugae extend to the promesonotal suture, on the pronotum they smoothly blend with reticulate sculpture. The gaster, including the postpetiole, is finely punctate. The head, mesosoma, and anterior gastral segments with rather numerous erect and semi-erect hairs. The scape with isolated erect hairs. The legs without erect hairs.

Gynes and males are unknown.

M e a s u r e m e n t s (mm): AL 1.6, HW 1.15, SL 0.65, PtL 0.6, PtH 0.75.

C o m p a r i s o n. Similar to *P. annosus*, from which it differs by smaller size, a different shape of the petiole, and the lack of erect hairs on the legs.

M a t e r i a l. Holotype.

Key to Workers of *Procerapachys*

1. Mesosoma and petiole with reticulate sculpture. 6 mm.....*Procerapachys favosus* (Wheeler)
 - At least sides of mesosoma and petiole with coarse longitudinal rugae.....2
2. Entire mesosoma with rough longitudinal rugae. Legs with erect hairs. Petiole in profile with posterior and dorsal surfaces forming rounded right angle. 6–9 mm*Procerapachys annosus* (Wheeler)
 - Pronotum with reticulate sculpture. Legs without erect hairs. Petiole in profile with posterior and dorsal surfaces forming more or less smooth arch. Smaller, body length ca. 3 mm.....*Procerapachys sulcatus* sp. n.

Subfamily Pseudomyrmecinae M. R. Smith, 1952

In the modern fauna, the subfamily Pseudomyrmecinae includes 255 species, distributed mostly in the tropics (Bolton et al., 2006). All the New World species are placed in the genera *Pseudomyrmex* Lund, containing 142 species, and the monotypic *Myrcidris* Ward, 1990. In the past, the Old World species have been divided between the genera *Tetraoponera* F. Smith, 1852, *Sima* Roger, 1863, *Pachysima* Emery, 1912, *Viticicola* Wheeler, 1919, and *Parasima* Donisthorpe, 1948, but currently all are included in the genus *Tetraoponera* (Ward, 1990). All the recent representatives of Pseudomyrmecinae are specialized for living in wood. Their long, narrow bodies with short and thick legs and shortened antennae are perfectly adapted to moving along narrow passages in dense wood. Their large eyes indicate that in hunting insects they rely on vision. Many species live in dead wood, but some live in symbiosis with live plants (Hocking, 1970; Janzen, 1969, 1972; Klein et al., 1993; Ward, 1991; Young et al., 1997).

19 fossil representatives of this subfamily have been described to date. One species of *Pseudomyrmex* have been described from Florissant (U.S.A., Lower Oligocene) (Carpenter, 1930) and 12 from Dominican amber (Early Miocene) (Ward, 1991). Six species from Europe have been described in the genus *Sima*, cur-

rently considered a junior synonym of *Tetraponera* F. Smith (Donisthorpe, 1916; Ward, 1990).

Genus *Tetraponera* F. Smith, 1852

Type species. *Tetraponera atrata* F. Smith, 1852 (= *Eciton nigrum* (Jerdon, 1851)) by subsequent designation by Wheeler (1911).

Diagnosis. Workers and gynes. Body elongated, with legs and antennae short. Head subrectangular. Eyes of moderate size. Frontal carinae partly covering antennal bases. Clypeus with median part not protruding between frontal carinae. Antennae 12-segmented. Mandibles triangular, massive, with 3–6 large teeth. Palpal formula 6.4, 4.3, or 3.3. Promesonotal suture well developed. Meso- and metatibiae usually each with two spurs. Claws with additional, preapical tooth on internal margin. Petiole and postpetiole present. Sting well developed.

Males. Body elongated. Antennae 12-segmented, filiform, with short scape. Mandibles triangular, with 2–6 teeth on masticatory margin. Palpal formula 6.4, 4.3, or 3.3. Meso- and metatibiae each with one large pectinate and one small simple spurs. Claws with additional, preapical tooth on internal margin. Petiole and postpetiole present. Wings with complete set of veins. Hindwing without jugal lobe.

Composition and distribution. The modern fauna comprises 113 species, 33 of which occur in the Oriental and Australian regions and the rest in the Afrotropical region (Bolton et al., 2006). Six fossil species have been described in the genus *Sima*, currently considered a synonym of *Tetraponera*: *T. angustata* (Mayr), *T. simplex* (Mayr), *T. ocellata* (Mayr), *T. klebsi* (Wheeler), and *T. lacrimarum* (Wheeler) from Baltic amber (Mayr, 1868; Wheeler, 1915) and *T. oligocenica* (Théobald) from the Oligocene deposits of Le Bassin d'Alés (Gard) in France (Théobald, 1937). Judging from the venation of its forewing, illustrated by Théobald (1937), the latter species not only does not belong to this genus, but is not even an ant, and should be considered Hymenoptera incertae sedis. Below, two new fossil genera are described. Additionally, previously unknown sexuals of *T. simplex* are described, and it is demonstrated that *T. angustata* is a junior synonym of *T. simplex*.

Remarks. The recent Asian and Australian species of *Tetraponera* are divided into four groups: *T. allaborans* (Walker, 1859) (11 spp.), *T. nigra* (Jerdon, 1851) (20 spp.), *T. pilosa* (F. Smith, 1858) (1 sp.), and *T. rufonigra* (Jerdon, 1851) (1 sp.) (Ward, 2001). In his discussion of relationships between the fossil and the modern species of the genus, Ward (2001) suggested, based on Wheeler's drawing of *T. lacrimarum*, that that species might belong to the *T. nigra* group. The affinities of the other Baltic amber species remained obscure. The new data allow to conclude that the Late Eocene amber species of *Tetraponera* belong to two groups,

T. simplex group and *T. ocellata* group. Differences between the two groups are given in the diagnoses. Clearly, none of these species can be referred to the *T. pilosa* or *T. rufonigra* groups, because representatives of those groups have well developed humeral prominences, or to the *T. allaborans* group, because its representatives have narrow mandibles with three teeth on the masticatory margin and a peculiar type of articulation between the petiole and the postpetiole. In the ants of the latter group, the semicircular margin of the petiolar sternite, to which the postpetiolar sternite is articulated, is shifted inwards (dorsomedially). Therefore, the actual posterior margin of the sternite is formed by its hood-shaped expansion. As a result, in profile, a distinct notch is visible between the lower margin of the postpetiolar sternite and the posteroventral part of the petiole. In its external characters (the number of teeth on the masticatory margin of the mandibles, the shape of the medial lobe of the clypeus, the structure of the articulation between the petiole and the postpetiole), *T. simplex* is similar to species from the recent *T. nigra* group. At the same time, in none of the specimens of *T. simplex*, *T. lacrimarum*, and *T. europaea* one can clearly see such important diagnostic characters of that group as the lack of the metanotal plate and the characteristic details of the structure of the metabasitarsal furrow, pubescence on the mesosternum, and male genitalia. Therefore, at this point, I cannot confidently refer these species to the *T. nigra* group; consequently, I am placing them in a separate group, *T. simplex*. Species of the *T. ocellata* group have no analogues in the modern fauna.

GROUP *TETRAPONERA SIMPLEX*

Diagnosis. Workers. Ocelli absent. Mandibles with four teeth on masticatory margin. Pronotum without humeral prominences. Anterior margin of postpetiolar sternite articulated directly to posteroventral margin of petiole.

Composition and distribution. *Tetraponera simplex* (Mayr) (Baltic, Bitterfeld, Rovno, and Scandinavian ambers, Late Eocene), *T. lacrimarum* (Wheeler) (Baltic and Bitterfeld ambers, Late Eocene), *T. europaea* sp. n. (Rovno and Bitterfeld ambers, Late Eocene).

Tetraponera simplex (Mayr, 1868)

Sima simplex Mayr, 1868, p. 102 (♀); Dalla Torre, 1893, p. 54; Handlirsch, 1907, p. 872; Burnham, 1978, p. 110.

Tetraponera simplex: Ward, 1990, p. 489; Bolton, 1995, p. 419; Dlussky, 1997, p. 62.

Sima angustata Mayr, 1868, p. 102, pl. V, fig. 106 (♀); Dalla Torre, 1893, p. 53; Handlirsch, 1907, p. 872; Wheeler, 1915, p. 43, fig. 12. Burnham, 1978, p. 110. **syn. nov.**

Tetraponera angustata: Ward, 1990, p. 489; Bolton, 1995, p. 417; Dlussky, 1997, p. 62, fig. 1a; Dlussky and Perkovsky, 2002, p. 18. **syn. nov.**

Lectotype. The species has been described by Mayr based on four specimens, only one of which has survived and which, in the interests of stability of nomenclature, I propose to recognize as the lectotype: a worker, NHMW, no. 1984/31/261; a completely preserved inclusion (a photograph has been examined). Baltic amber, Late Eocene.

Description. Worker (Figs. 12a, 12b). Body length 3.5–6.0 mm. The head is subrectangular, with rounded occipital corners and a straight or a weakly concave occipital margin. The head is 1.2 times as long as wide. The eyes are oval, weakly convex; the maximum eye diameter is 0.36–0.42 times the head width. The gena length approximately equals or slightly exceeds the maximum eye diameter. The clypeus with a weakly protruding median lobe, the anterior margin of which is straight or weakly convex. The scape is short, not nearly reaching the occipital margin, approximately half as short as the width of the head. The first flagellomere is approximately as long as the two more distal ones. Each of the more distal flagellomeres, except the terminal one, is distinctly shorter than wide. Each mandible has an additional obtuse tooth (or a prominence) on the basal margin. The masticatory margin of the mandible is approximately as long as the basal margin. The pronotum with a convex dorsal surface. The promesonotal constriction is barely visible, the mesopropodeal one is distinct, extending onto the lateral surfaces of the mesosoma. The propodeum is longer than high, in profile with a poorly developed, strongly rounded angle between the dorsum and the declivity. The petiole is longer than either wide or high, with a rounded node and a short peduncle, without a posteroventral tooth. The postpetiole is campaniform, slightly longer than high, approximately as long as wide.

In most specimens the head and the mesosoma are punctate, but in the largest ones the pronotum has shagreened sculpture. The gaster is smooth, with sparse punctation, and sometimes with very fine shallow shagreened sculpture. Erect and semierect hairs are always present on the clypeus and mandibles, and on the ventral surface and the tip of the gaster. Most specimens have one pair of erect hairs on the pronotum and 2–4 hairs along the posterior margins of the three basal gastral tergites. The entire body with fine decumbent pubescence, the hairs on the gaster are longer than distances between them.

Gyne (described here for the first time). (Fig. 12c). Body length 5.6 mm. The head is 1.3–1.4 times as long as wide, rectangular, with rounded occipital corners and a weakly concave occipital margin. The ocelli are present. The eyes are oval, weakly convex. The maximum eye diameter is 0.4 times the head width. The scape is not nearly reaching the occipital margin, its length is 0.55 times the head width. The mandibles and the anterior margin of the clypeus are as in workers. The maxillary palpi are short, barely protruding outside the oral cavity. The mesosoma is narrow and long, 2.3

times as long as wide. The pronotum in dorsal view with a trapezoidal dorsal part and an abruptly constricted neck part. The dorsal part, measured along the median, is 2.5 times shorter than the maximum width of the pronotum. The scutum is flat, 1.5 times shorter than wide. The petiole is nodiform, 1.7 times as long as wide, with a distinct peduncle. The postpetiole is approximately as long as wide. Sparse erect hairs are present on the anterior margin of the clypeus, on the pronotum (two pairs), petiole (two pairs), and gastral sternites and tergites. The body is smooth and shiny, finely punctate. Decumbent pubescence is very sparse on mesosoma and is denser on the gaster. Decumbent hairs on the gaster are longer than distances between them.

Male (described here for the first time, Figs. 12e–12d). Body length 3.5–4.0 mm. The body is narrow. The head is approximately as long as wide, its sides are strongly convex, the occipital margin is concave, and the occipital corners are somewhat pointed. The mandibles and the anterior margin of the head are not visible. The ocelli form an obtuse triangle. The distance between the central and the lateral ocelli is approximately equal to the ocellar diameter. The eyes are convex, occupying half of each side of the head, strongly shifted forward, almost touching bases of the mandibles, so that the gena is conspicuously shorter than the scape diameter. The scape is short and wide, twice as long as wide. The second antennomere is half as long as the scape, as long as wide. The third and the more distal antennomeres, except the terminal, are 1.75 times as long as the scape and 3.5 times as long as wide. The maxillary palpi are short and thick, not reaching half-way between the mouth and the occipital orifice. The mesosoma is elongated, 2.5 times as long as its maximum width. The pronotum is transverse, without humeral prominences or carinae. The scutum does not cover the pronotum from above and is distinctly longer than wide. Parapsidal furrows are absent. The scutellum is flat and, consequently, the constriction between the scutum and the scutellum is poorly developed. The propodeum in profile is well-rounded. In both specimens each mesotibia with two simple spurs of unequal length. In the specimen ZMUC, no. 303, each metatibia with two spurs, one simple and one pectinate. In the specimen GZG.BST (MKC), no. 27.142, the left metatibia with only one spur, thick and serrate, without a simple spur; the apex of the right metatibia of the same specimen is obscured by a bubble, so that one cannot see the spurs. The petiole is nearly cylindrical, slightly expanding posteriorly, without a node, 2.3 times as long as its maximum width. The postpetiole is campaniform, 1.2 times as long as wide.

The body is shiny, with barely visible shallow shagreened surface sculpture and sparse decumbent pubescence comprised of very short, fine hairs. Erect hairs are present only on the clypeus (one pair) and the tip of the gaster.

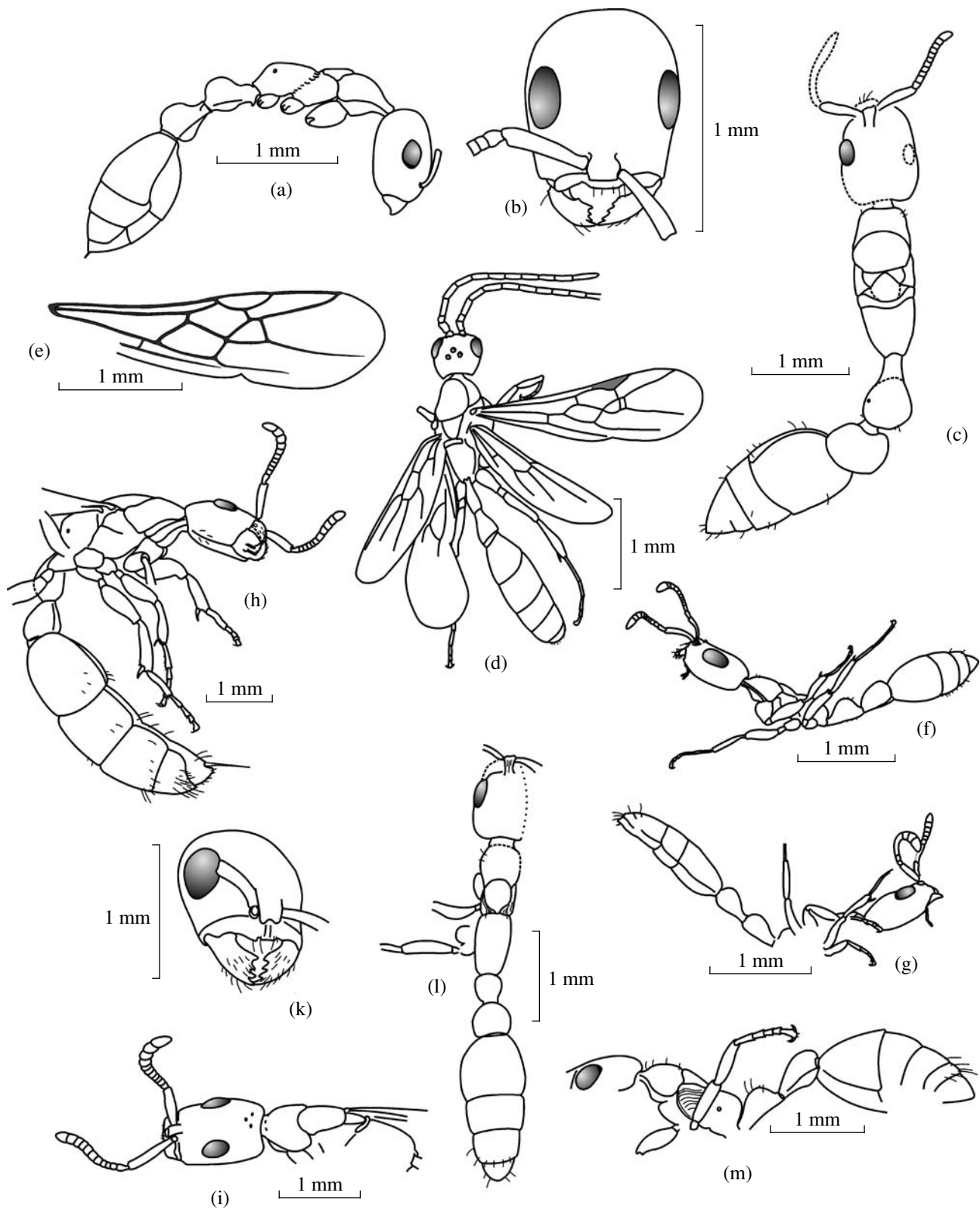


Fig. 12. Species of the *Tetraponera simplex* group: (a–e) *Tetraponera simplex* (Mayr): worker PIN, no. 364/01, general view of the inclusion (a), head of worker, ZMUC, no. 294 (b), gyne, CGC, no. 3317, general view of the inclusion (c), male, GZG.BST (MKC), no. 37.142, general view of the inclusion (d), forewing of male, ZMUC, no. 303 (e); (f–g) *Tetraponera lacrimarum* (Wheeler): worker, holotype GZG.BST, no. 04670, general view of the inclusion (f), worker, GZG.BST (MKC), no. 27.172, general view of the inclusion (g); (h–m) *Tetraponera europaea* sp. n., gyne, holotype SIZK, no. 3626: general views of the inclusion from different angles (h–i), head (k), worker, paratype HM, no. 10/207, general view of the inclusion from different angles (l–m).

In the specimen ZMUC, no. 303, forewing has closed cells 1 + 2r, 3r, rm, and mcu; cell cua is open. Veins 2RS and 3M arise from the same node of cell mcu, therefore cell rm is triangular. Crossveins rs-m and 2r-rs meet RS at points separated by approximately the length of r-rs. Vein cu-a is proximal to the 1M and 1Cu fork, being separated from it by approximately its own length. The specimen GZG.BST (MKC), no. 27.142 has clearly aberrant wings, showing different aberrations on the left and on the right sides. Both forewings have the supernumerary vein 2rs-m: on the right wing it is distal to the true rs-m, and on the left wing it is situated inside cell rm. Location of the crossveins also differs between the two hindwings of that specimen.

Measurements (mm): Workers: spec. PIN, no. 964/001: BL 3.9, AL 1.2, HL 0.775, PtL 0.45; spec. GZG.BST.04672: BL 3.75, AL 1.10, HL 0.70, HW 0.54, ED 0.22, SL 0.30; spec. HM, no. 14/203: BL 4.0, AL 1.1, HL 0.79, HW 0.64; spec. SIZK, no. K-3620: AL 1.8, HL 1.05, SL 0.45, ED 0.42, PtL 0.61, PtW 0.5, PptL 0.5, PptW 0.66; spec. SIZK, no. UA-478: BL 4.3, AL 1.3, HL 0.93, PtL 0.47; spec. ZMUC, no. 294a: BL 4.85, AL 1.4, HL 0.925, HW 0.775, SL 0.4; spec. ZMUC, no. 297: BL 4.0, AL 1.2, PtL 0.40; spec. ZMUC, no. 302: AL 1.5, PtL 0.50. Gyne: spec. CGC, no. 3317: AL 1.6, HL 1.07, HW 0.79, SL 0.45, PtL 0.8, PptL 0.58. Males: spec. GZG.BST (MKC), no. 27.142: BL 3.6, AL 1.05, HL 0.475, HW 0.5, PtL 0.35, PptL 0.34, FWL 2.55; spec. ZMUC, no. 303 BL ca. 4, AL 1.1, HL 0.58, HW 0.60, FWL 2.85.

Remarks. Mayr (1868) described two species of *Sima* on the same page: *simplex*, based on four workers, and *angustata*, based on three workers. Only one syntype of *Sima simplex*, in the NHMW collection, has survived, and I am designating it as the lectotype; other specimens are lost. For the first species, Mayr gave a short description, while for *S. angustata* he gave only differences from *S. simplex*, noting that the two species were very similar. Mayr differentiated the two species by the following characters: (1) in *S. simplex* mandibles have masticatory margins wider, and in *S. angustata* narrower than their bases; (2) in *S. simplex* flagellomere I is shorter, and in *S. angustata* as long as or longer than II and III combined; (3) in *S. angustata* punctation of head and mesosoma is sparser than in *S. simplex*; (4) in *S. angustata* decumbent pubescence is sparser than in *S. simplex*. The first character is virtually impossible to use in practice. First, the vast majority of specimens have the mandibles tightly closed, so that their structure cannot be seen. Secondly, even when the mandibles are open, in order to see this character, one has to orient them precisely, which is not usually possible with inclusions. The relative size of antennomeres is a highly unreliable character, because antennomeres can be drawn into one another, and even in the same individual the first flagellomere can be longer than the next two combined in one antenna and shorter in the other. The density of punctation and decumbent pubescence

varies significantly within a species, and I failed finding consistent differences in these characters in a large series of examined individuals.

Wheeler (1915) had not seen the types of *S. simplex*, but among the material he examined he identified four individuals as *S. simplex* and 10 as *S. angustata* (one of these specimens is currently held in the Göttingen collection under the identifier GZG.BST.04672 (K 794)). He remarked that he could not see the structure of the mandibles and, therefore, relied on the relative size of antennomeres and on the sculpture. At the same time, in his description of *S. simplex*, Mayr pointed out that, in that species, erect hairs were “almost absent” (“die abstehende Behaarung fehlt fast”), while Wheeler’s drawing shows an ant with numerous erect hairs on its head, mesosoma, petiole, postpetiole, and gastral tergites. Examination of a photograph of the lectotype of *T. simplex*, kindly provided to me by Dr. Ortwin Schultz, has demonstrated that, in this species, erect hairs are present only on the clypeus and the gaster tip. Therefore, Wheeler obviously dealt with a different species, most probably with small workers of *Tetraponera ocellata*. Workers of that species, unlike *T. simplex*, have ocelli, but in some individuals they are poorly developed, blending in with the surface sculpture of the head.

Because neither the types of *Sima angustata*, nor the specimens identified by Wheeler as *Sima simplex* have survived, in my opinion, it will be expedient to consider *Sima angustata* Mayr, 1868 as a junior synonym of *Tetraponera simplex* (Mayr, 1868), and *Sima simplex* sensu Wheeler, 1915 as a junior synonym of *Tetraponera ocellata* (Mayr, 1868).

Tetraponera simplex is the most common species of the genus in the Late Eocene ambers. Seven workers have been studied by Mayr, 10 workers (including one of Mayr’s syntypes) by Wheeler, and 25 workers (including one of the specimens identified by Wheeler), two males, and one gyne by myself. The amber piece containing the specimen ZMUC, no. 294a also contains two workers of *Ctenobethylus goepperti* (Mayr).

Material. Besides lectotype, from Baltic amber: PIN, no. 964/001 (♀); GZG.BST.04672 (K.794) (♀); MZ PAN, nos. 9192 (♀), 20847 (♀); CGC, no. 3317 (♀); ZMUC, no. 303, “Ostpreussen, G.V. Henningsen, 1.07.66” (♂); VGC, no. 33 (♀). Bitterfeld amber: HM, nos. 7/227 (♀), 11/218 (♀), 14/203 (♀), 15/223 (♀); GZG.BST (MKC), nos. 27.142 (♂), 27.157 (♀), 27.180 (♀). Rovno amber: SIZK, nos. K-2620 (♀), K-2851 (♀), K-3620 (♀), SC-10 (♀), UA-478 (♀), UA-681 (♀), UA-2233 (♀). Scandinavian amber: ZMUC, nos. 297 labeled “G.V. Henningsen, 27.05.63” (♀); 298 labeled “G.V. Henningsen, 26.02.65” (♀); 301 labeled “A.K. Andersen, 28.03.68” (♀); 312, labeled “Borge Mortensen, 12.10.60” (♀). Amber of unknown origin: ZMUC, nos. 294 labeled “Min. Mus., Nordjyll. Vestkysd, Guldsmed Henningsen, 1952”; 300 labeled “Storebalt ud for Tiisso Baron Wedell, 6.08. 1896”; 302 labeled “Dr. Jpsen, no 118”. The poorly preserved spec-

imen HM, no. 11/218 from Bitterfeld amber also possibly belongs to this species.

Tetraoponera lacrimarum (Wheeler, 1915)

Sima lacrimarum Wheeler, p. 44, fig. 13 (♀); Burnham, 1978, p. 110.

Tetraoponera lacrimarum (Wheeler): Ward, 1990, p. 489; Bolton, 1995, p. 418.

Tetraoponera angustata (Mayr): Dlussky, 1997, p. 62 (part.); Dlussky and Perkovsky, 2002, p. 18 (part.).

H o l o t y p e. Worker, GZG.BST.04670, ×2; a completely preserved inclusion. Late Eocene, Baltic amber.

D e s c r i p t i o n. Worker (Figs. 12f–12g). Length, 3.0–3.5 mm. The head is longer than wide, rectangular, with rounded occipital corners. The eyes are oval, convex, somewhat shifted anteriorly. The maximum diameter of the eye slightly exceeds the length of the gena. The scape is short and curved, not extending to the occipital margin of the head. The first flagellomere is relatively long, as long as the two to three more distal flagellomeres combined. The flagellomeres II–XI each is shorter than wide. The mandibles and the anterior margin of the clypeus are not visible in any known specimen. The maxillary palpi are short, not reaching half-way to the occipital orifice. The dorsal surface of the pronotum in profile is flattened; the humeral prominences are absent. The promesonotal and the mesopropodeal constrictions are distinct. The propodeum is short, approximately as long as high; in profile its dorsum and declivity form together a rounded right angle. The petiole without a posteroventral tooth, in profile triangular, with a rounded apex, without a distinct peduncle, with a declivous, weakly concave anterior surface and an almost vertical posterior surface. The postpetiole rather abruptly narrows towards its base, campaniform. The petiole and postpetiole are longer than high.

The body is smooth and shiny, with sparse punctation. Decumbent pubescence is sparse. The head, mesosoma, and petiole with a few erect hairs. The gaster with erect hairs on its ventral surface and the tip.

Gynes and males unknown.

M e a s u r e m e n t s (mm): Holotype, GZG.BST.04670: BL 3.4, AL 0.94, HL 0.68, SL 0.30, ED 0.22; spec. GZG.BST (MKC), no. 27.172: AL 0.95, HL 0.78, SL 0.24, ED 0.20, PtL 0.37, PtH 0.21, PptL 0.38, PptH 0.23.

R e m a r k s. Previously I believed, based only on the description, that *T. lacrimarum* (Wheeler) was a synonym of *T. angustata* (Mayr) (Dlussky, 1997; Dlussky and Perkovsky, 2002). The fact is that Wheeler in his description stated that “This species appears to be closely related to *S. angustata*, but I have described it as distinct, on account of its very small size, the larger and more anteriorly placed eyes and the shortness of joints 2–5 of the funiculus.” Because the size of *T. angustata* varies considerably, as Wheeler himself pointed out, and the size ratio of flagellomeres cannot be considered

a reliable character, I decided that these characters were insufficient to differentiate between the two species. Later, having examined the holotype, I became convinced that this is a separate species, well differentiated from all the Eocene ambers *Tetraoponera* in the shape of its petiole and other important characters.

M a t e r i a l. Besides holotype, from Bitterfeld amber: GZG.BST (MKC), no. 27.172. It is possible that the poorly preserved HM, no. 15/221 from Bitterfeld amber also belongs to this species.

Tetraoponera europaea Dlussky, sp. n.

E t y m o l o g y. From the country of origin (Europe).

H o l o t y p e. SIZK, no. K-3626. A well preserved gyne with crumpled wings, partly obscured by cracks. Rovno amber, Late Eocene.

D e s c r i p t i o n. Gyne (Figs. 12h–12k). BL 7.5 mm. The head is 1.5–1.6 times as long as wide, rectangular, with rounded occipital corners and a weakly concave occipital margin. The ocelli are present. The eyes are oval, weakly convex. The maximum eye diameter is 0.5 times the width of the head. The length of gena is approximately equal to the maximum eye diameter. The scape is not nearly extending to the occipital margin of the head, 0.6 times the head width. The first flagellomere is approximately 1.5 times as long as wide, as long as the two more distal flagellomeres combined. The more distal flagellomeres, except the terminal, are distinctly shorter than wide. The mandibles without an additional tooth or a prominence on the basal margin. The maxillary palpi are short, barely protruding beyond the oral cavity. The mesosoma is narrow and long, approximately twice as long as high. The dorsal portion of the pronotum with anterior margin smoothly rounded. The scutum is flat. The outline of the propodeum in profile is almost rectangular, with the angle rounded; the propodeal dorsum is somewhat longer than the declivity. The petiole in profile is almost triangular, without a distinct peduncle, without a posteroventral tooth; the anterior surface of the petiole in profile is very slightly concave, the posterior surface is weakly convex, and the upper angle is strongly rounded. The length of the petiole is 1.7–1.8 times its height or width. The postpetiole is as long as high, 0.83 times as long as wide.

The body is smooth, shiny, with rather dense, fine punctation. Isolated erect hairs are present on the anterior margin of the clypeus as well as on the frons, mandibles, lower surface of head (two pairs), pronotum, petiole, postpetiole, and the first two gastral tergites and sternites. Erect hairs on the more distal gastral tergites and sternites are denser, thicker, and longer. The entire body with rather dense decumbent pubescence consisting of very short hairs. The wings are crumpled, the venation is obscure.

Worker (Figs. 12l, 12m). BL 4.6 mm. The head is longer than wide, rectangular, with distinct rounded occipital corners and a weakly concave occipital margin. The scape is short, not nearly reaching the occipital margin of the head. The pronotum, mesonotum, and propodeum are each longer than wide. The pronotum in profile is well-rounded. The dorsal surface of the mesonotum is flattened. The promesonotal and mesopropodeal constrictions are distinct. The propodeal dorsum and the declivity are of approximately equal size, forming a rounded right angle in profile. The petiole is almost twice as long as either wide or high, without a distinct peduncle, without a posteroventral tooth, in profile almost triangular, with the anterior surface very weakly concave, the posterior surface weakly convex, and the upper angle strongly rounded. The postpetiole is approximately as long as wide, 1.5 times as long as high. A few erect hairs are visible on the pronotum, petiole, postpetiole, and caudal gastral tergites. The femora, tibiae, and scape without erect hairs.

The head is shiny, with sparse, delicate punctation, with a few thin longitudinal rugae present only between the frontal carinae. The dorsal surface of the mesosoma with denser punctation, the mesopleura with thin longitudinal rugae. The gaster is smooth and shiny. The entire body with very fine decumbent pubescence. The decumbent hairs on the gaster are longer than distances between them.

Males are unknown.

Measurements (mm): Holotype SIZK, no. 3626 (gyne): AL 2.0, HL 1.25, HW 0.8, SL 0.5, ED 0.4, PtL 0.79, PtW 0.45, PptL 0.6, PptH 0.55, PptW 0.65. Paratype HM, no. 10/207 (♀) AL 1.3, HL 0.9, HW 0.78, SL 0.54, ED 0.42, PtL 0.58, PtH 0.31, PtW 0.31.

Comparison. In the structure of petiole, the new species is similar to *T. lacrimarum*, from which it differs by its larger size, details of pilosity, and by the presence of striation on the mesopleura of the worker.

Remarks. The worker from Bitterfeld amber is similar to the gyne from Rovno amber in the shape of its petiole and propodeum, details of sculpture, and the development of pilosity; therefore, I have no doubts that the two are conspecific.

Material. Besides holotype, paratype HM, no. 10/207. A completely preserved worker specimen, partly obscured by cracks. Bitterfeld amber, Late Eocene.

GROUP *TETRAPONERA OCELLATA*

Diagnosis. Workers. Ocelli present, at least in large workers. Mandibles with five teeth on masticatory margin. Pronotum without humeral prominences. Anterior margin of postpetiolar sternite attached directly to posteroventral margin of petiole.

Composition and distribution. *T. ocellata* (Mayr) (Baltic, Bitterfeld, Rovno, and Scandina-

vian ambers, Late Eocene), *T. klebsi* (Wheeler) (Baltic amber, Late Eocene), and *T. groehni* sp. nov. (Baltic amber, Late Eocene).

Tetraponera ocellata (Mayr, 1868)

Sima ocellata Mayr, 1868, p. 101, pl. V, fig. 104, 105 (♀); Dalla Torre, 1893, p. 54; Handlirsch, 1907, p. 872; Wheeler, 1915, p. 42; Burnham, 1978, p. 110.

Tetraponera ocellata (Mayr): Ward, 1990, p. 489; Bolton, 1995, p. 419; Dlussky, 1997, p. 62.

Sima simplex (Mayr): Wheeler, 1915, p. 42–43, fig. 11 (nec. Mayr, 1868). **syn. nov.**

Neotype. Mayr described this species based on six workers, none of which has survived. Therefore, in the interests of stability of nomenclature, here a neotype is being designated: worker SIZK, no. K-630; the gaster of the inclusion is cut away, but the other parts are beautifully preserved and match completely the description by Mayr. Rovno amber, Late Eocene.

Description. Worker (Fig. 13a). BL 5.0–9.5 mm. The head is longer than wide, with distinct rounded occipital corners and a weakly concave occipital margin. The anterior margin of the clypeus protrudes as a small lobe with somewhat pointed angles and a weakly concave anterior margin. The ocelli are present. The eyes are oval, flat. The gena is approximately as long as the maximum eye diameter. The scape is short, not nearly reaching the occipital margin of the head. The first flagellomere is longer than the second, but shorter than the second and the third combined. The maxillary palpi extend farther than half-way to the occipital orifice. The dorsal surface of the pronotum is convex. The promesonotal constriction is barely visible, while the mesopropodeal one is distinct, extending onto the lateral surfaces of the mesosoma. The pronotum, mesonotum, and propodeum are each longer than wide. The propodeum in profile is well-rounded. The petiole is approximately 1.5 times as long as high, with a high and thick node and a distinct peduncle. The node is compressed laterally, the petiole is 1.8 times as long as its maximum width. The postpetiole is campaniform, approximately as long as high and as long as wide.

The head, pronotum, mesonotum, petiole, postpetiole, and gaster with a few erect hairs. The tip of the gaster additionally with long thick setae. The femora and tibiae without erect hairs, the scape with a few hairs. The body is weakly shiny. The mandibles with coarse longitudinal rugae. The head is densely punctate. The pronotum is coarsely shagreened, and the rest of the mesosoma and the petiole are finely shagreened. The gaster is smooth, with sparse punctation, poorly visible under decumbent pubescence. The mesosoma, petiole, postpetiole, and gaster with dense decumbent pubescence; the decumbent hairs are longer than distances between them. The dorsal surface of the head with very short and fine decumbent hairs, shorter than distances between them.

Gynes and males are unknown.

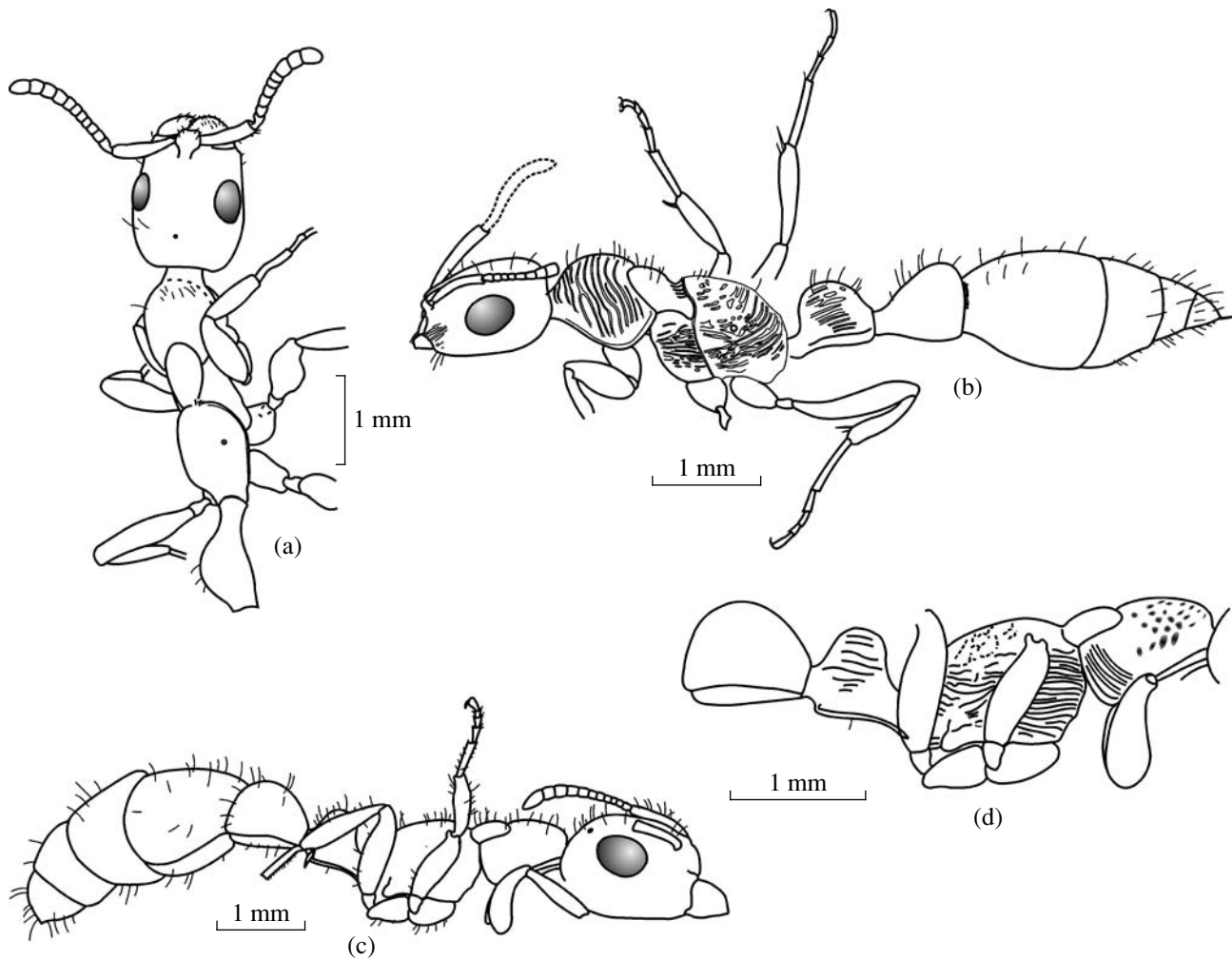


Fig. 13. Species of the *Tetraponera ocellata* group: (a) *Tetraponera ocellata* (Mayr), worker, neotype SIZK, no. K-630; (b) *Tetraponera klebsi* (Wheeler), worker, holotype GZG.BST, no. 04671; (c–d) *Tetraponera groehni* sp. n., worker, holotype GPIH, no. 4510 (CGC, no. 3357): general view of the inclusion (sculpture not shown) (c), sculpture of mesosoma and petiole (d).

Measurements (mm): Workers: neotype SIZK, no. K-630: AL 2.75, HL 1.55, HW 1.25, SL 0.75, ED 0.45, PtL 1.25, PtH 0.6; spec. PIN, no. 964/002: BL 7, AL 1.8, HW 0.85, PtL 0.75, PtH 0.42, PptL 0.50, PptH 0.50; spec. ZMUC, no. 296: HL 1.8, SL 0.8, ED 0.5; spec. ZMUC, no. 299: BL 5.0, AL 1.25, HL 0.95, HW 0.70, SL 0.40, PtL 0.50, PtW 0.28, PptL 0.50.

Remarks. Mayr described this species based on five workers. Wheeler examined one of those types and saw one additional specimen in the collection in Berlin, but did not add anything to Mayr's description. None of the types is currently present in Vienna or Göttingen; apparently they have been lost. The specimens I examined match Mayr's description in every detail, except the size. Some of these specimens are smaller than the size indicated in the description, while otherwise fully agreeing with it.

For synonymy see above, under *T. simplex*.

Material. Besides neotype, from Baltic amber: PIN, no. 364/01 (♀), CGC, no. 3355 (♀). Bitterfeld amber: HM, nos. 11/217 (♀), 12/226 (♀). Scandinavian amber: ZMUC:, nos. 295 labeled "G. V. Henningsen, 3.05.60" (♀); 296 labeled "J. Flauensgaard, 22.10.65" (♀); 299 labeled "G. V. Henningsen, 1.08.62" (♀). The poorly preserved specimens HM, no. 11/248 and 11/276 (workers) from Bitterfeld amber also possibly belong to this species.

Tetraponera klebsi (Wheeler, 1915)

Sima klebsi Wheeler, 1915, p. 41–42, fig. 10 (♀); Burnham, 1978, p. 110.

Tetraponera klebsi (Wheeler): Ward, 1990, p. 489; Bolton, 1995, p. 418; Dlussky, 1997, p. 61.

Holotype. Worker, GZG.BST.04671, ×8; a completely preserved inclusion. Baltic amber, Late Eocene.

Description. Worker (Fig. 13b). BL 8.5 mm. The head is longer than wide, with distinct rounded

occipital corners and a weakly concave occipital margin. The ocelli are present. The eyes are oval, flat. The gena is slightly shorter than the maximum eye diameter. The mandibles and the anterior margin of the clypeus are not visible. The scape is short, not nearly reaching the occipital margin of the head. The first flagellomere is slightly shorter than the combined length of the two more distal flagellomeres. The pronotum, mesonotum, and propodeum are each longer than wide. The pronotum with a weakly convex dorsal surface, without humeral prominences. The mesopropodeal constriction is distinct. The propodeum in profile is well-rounded. The petiole is longer than high, with a high and thick node, with a distinct short peduncle. The node is compressed laterally. The postpetiole is campaniform, longer than wide.

The entire body with rather numerous erect hairs. The scape and the tibiae with isolated hairs. The body is weakly shiny. The mandibles with coarse longitudinal rugae. The head is coarsely shagreened, with indistinct longitudinal rugae on the genae. The pronotum with coarse arcuate rugae. The mesonotum, mesopleura, and the dorsal and lateral surfaces of the propodeum with finer longitudinal rugae. The propodeal declivity with transverse rugae connected to the longitudinal rugae on the lateral parts of the propodeum. The petiole with coarse longitudinal rugae. The postpetiole and the gaster are smooth and shiny. The dorsal surface of the head with decumbent pubescence, consisting of very short and fine hairs. Other body parts without decumbent pubescence.

Gynes and males are unknown.

Measurements of holotype (mm): BL 8.5, AL 2.35, HL 1.65, ED 0.6, SL 0.75.

Material. Holotype.

Tetraponera groehni Dlussky, sp. nov.

Etymology. In honor of Mr. Carsten Gröhn (Glinde), from whose collection this species is being described.

Holotype. Worker, GPIH, no. 4510 (CGC, no. 3357). A well preserved complete inclusion. Baltic amber, Late Eocene.

Description. Worker. Body length 8 mm. The head is longer than wide, with distinct rounded occipital corners and a weakly concave occipital margin. The ocelli are present. The eyes are oval, flat. The gena is 1.1 times shorter than the maximum eye diameter. The scape is short, not nearly reaching the occipital margin of the head. The first flagellomere is approximately as long as the combined length of the two more distal flagellomeres. The pronotum with the dorsal surface convex. The promesonotal and the mesopropodeal constrictions are distinct. The propodeum in profile is well-rounded. The petiole is approximately as long as high, with a high and thick node, with a distinct short pedun-

cle. The postpetiole is campaniform, 1.25 times as long as high.

The head, pronotum, mesonotum, petiole, postpetiole, and gaster with numerous erect hairs. The tip of the gaster additionally with long thick setae. The scape, femora, and tibiae with erect hairs. The mandibles with coarse longitudinal rugae. The head is coarsely shagreened, without longitudinal rugae on the genae. The dorsal surface of the pronotum with large isolated pits and shallow shagreened sculpture in between, its posterior corners with thin arcuate rugae. The mesonotum with shagreened sculpture. The propodeal dorsum with smoothed reticulate sculpture. The mesopleura, lateral surfaces of propodeum, and petiolar node with coarse longitudinal rugae. The postpetiole and the gaster are smooth, shiny, with scattered piligerous punctures. Decumbent pubescence is absent.

Gynes and males are unknown.

Measurements of holotype (mm): AL 2.25, HL 1.5, SL 0.625, ED 0.55, PtH 0.625, PptL 0.875, PptH 0.70.

Comparison. In its general appearance, the species is similar to *T. klebsi* (Wheeler) and *T. ocellata* (Mayr), from both of which it differs by details of its sculpturing and a denser pilosity.

Material. Holotype.

Key to Workers of *Tetraponera* in the Late Eocene Ambers of Europe

1. Petiole in profile triangular, without distinct peduncle (Figs. 12e, 12f, 12l). Ocelli absent. Mandibles with four teeth on masticatory margin (Fig. 13k).....2
 - Petiole with node and well distinct peduncle (Figs. 12a, 13a–13d).....3
2. Smaller: 3.0–3.5 mm. Mesopleura smooth. Head, mesosoma, and petiole with very short isolated erect hairs (Figs. 12e–12f).....*T. lacrimarum* (Wheeler)
 - Larger: body length ca. 4.5 mm. Mesopleura with thin longitudinal rugae. Head, mesosoma, and petiole with erect hairs (Fig. 12l).....*T. europaea* sp. n.
3. Pilosity sparse. Hairs always present on clypeus, mandibles, and ventral surface and tip of gaster. Most specimens with one pair of erect hairs on pronotum and 2–4 hairs along posterior margins of each of first three gastral tergites. Mandibles with 4 teeth (Fig. 12b). Ocelli absent. Body length 3.5–6.0 mm.....*T. simplex* (Mayr)
 - Body with more numerous erect and semierect hairs: dorsal side of mesosoma always with more than two pairs of erect hairs (Figs. 13a–13c). Mandibles with 5 teeth. Ocelli present, at least in large workers...4
4. Pronotum coarsely and the rest of mesosoma and petiole finely shagreened, without rugose sculpture. Head densely punctate. Scape and legs without erect hairs. 5.0–9.5 mm.....*T. ocellata* (Mayr)

—Mesosoma, at least laterally, with rugose sculpture (Figs. 13b, 13d). Scape and legs at least with isolated erect hairs. 8–9 mm.....5

5. Pronotum with coarse arcuate rugae; mesonotum, mesopleura, and dorsal and lateral surfaces of propodeum with finer longitudinal rugae. Posterior surface of petiole with transverse rugae, connected with longitudinal rugae on its lateral surfaces. Petiole with coarse longitudinal rugae (Fig. 13b). Head coarsely shagreened, with indistinct longitudinal rugae on genae.....*T. klebsi* (Wheeler)

—Dorsal surface of pronotum with large isolated pits and shallow shagreened sculpture in between; its posterior corners with thin arcuate rugae. Mesonotum with shagreened sculpture. Propodeal dorsum with smoothed reticulate sculpture. Mesopleura, propodeum laterally, and petiolar node with coarse longitudinal rugae (Fig. 13d). Head coarsely shagreened, without longitudinal rugae on genae.....*T. groehni* sp. n.

ACKNOWLEDGMENTS

For the opportunities to study and describe ants from various amber collections I am indebted to A.P. Rasnitsyn (PIN), E.E. Perkovsky (SIZK), the late R. Kulicka (MZ PAN), A.J. Ross (NHML), O. Schultz (NHMW), M. Reich (GZG), C. Gröhn (Glinde, Germany), M. Kutscher (Sassnitz, Rügen, Germany), L.B. Vilhelmsen (ZMUC), V.A. Gusakov (Korolev, Moscow Region), A. Wiszniewski (Warsaw, Poland), and S.A. Suvorkin (Kiev, Ukraine). I am also grateful to S. Perfilieva for her assistance in interpreting wing venation of ants. The study has been partially funded by the Russian Foundation for Basic Research grants (nos. 05-04-49419 and 08-04-00701) and the Deutsche Forschungsgemeinschaft (DFG) grant no. 436 RUS 17/17/07.

REFERENCES

1. E. André, "Notice sur les fourmis fossiles de l'ambre de la Baltique et description de deux espèces nouvelles," *Bull. Soc. Zool. Fr.* **20**, 80–84 (1895).
2. S. B. Archibald, S. P. Cover, and C. S. Moreau, "Bulldog Ants of the Eocene Okanagan Highlands and History of the Subfamily (Hymenoptera: Formicidae: Myrmecinae)," *Ann. Entomol. Soc. Am.* **99** (3), 487–52 (2006).
3. C. Baroni Urbani, "The Ant Genus *Gnamptogenys* in Dominican Amber (Amber Collection Stuttgart: Hymenoptera, Formicidae. IV: Ectatommini)," *Stuttg. Beitr. Naturkd. Ser. B, Geol. Paläontol.* **67**, 1–10 (1980).
4. C. Baroni Urbani and M. L. De Andrade, "The Ant Genus *Proceratium* in the Extant and Fossil Record (Hymenoptera: Formicidae)," *Mus. Reg. Sci. Nat. Monogr. (Turin)* **36**, 1–492 (2003).
5. C. Baroni Urbani, B. Bolton, and P. Ward, "The Internal Phylogeny of Ants (Hymenoptera: Formicidae)," *Syst. Entomol.* **17**, 301–329 (1992).
6. F. Bernard, "Hyménoptères, super-famille des Formicoidea Ashmead 1905," in *Traité de Zoologie*, Ed. by

- P. P. Grassé (Masson et Cie, Paris, 1951), Vol. 10, Issue 2, pp. 997–1104.
7. C. T. Bingham, *The Fauna of British India, Including Ceylon and Burma. Hymenoptera*, Vol. 2. Ants and Cuckoo-wasps (Taylor and Francis, London, 1903).
8. B. Bolton, "Abdominal Characters and Status of the Cerapachyine Ants (Hymenoptera, Formicidae)," *J. Nat. Hist.* **24**, 53–68 (1990a).
9. B. Bolton, "Army Ants Reassessed: The Phylogeny and Classification of the Doryline Section (Hymenoptera, Formicidae)," *J. Nat. Hist.* **24**, 1339–1364 (1990b).
10. B. Bolton, *Identification Guide to the Ant Genera of the World* (Harvard Univer. Press, Cambridge, Mass., 1994).
11. B. Bolton, *A New General Catalogue of the Ants of the World* (Harvard Univer. Press, Cambridge, Mass., 1995).
12. B. Bolton, "Synopsis and Classification of Formicidae," *Mem. Am. Entomol. Inst.* **71**, 1–370 (2003).
13. B. Bolton, G. Alpert, P. S. Ward, and P. Nasrecki, *Bolton's Catalogue of Ants of the World* (Harvard Univer. Press, Cambridge, Mass., CD-ROM, 2006).
14. W. L. Brown, Jr., "Contributions toward a Reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera)," *Bull. Mus. Compar. Zool.* **118**, 175–362 (1958).
15. W. L. Brown, Jr., "A Comparison of the Hylean and Congo-West African Rain Forest Ant Faunas", in *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, Ed. by B. J. Meggers, E. S. Ayensu, and W. D. Duckworth (Smithsonian Institution Press, Washington, D.C., 1973), pp. 161–185.
16. W. L. Brown, Jr., "Contributions toward a Reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini," *Search Agric. (Ithaca N. Y.)* **5** (1), 1–115 (1975).
17. L. Burnham, "Survey of Social Insects in the Fossil Records," *Psyche* **89**, 85–133 (1978).
18. F. M. Carpenter, "The Fossil Ants of North America," *Bull. Mus. Compar. Zool. Harvard* **70**, 1–66 (1930).
19. C. G. Dalla Torre, *Catalogus Hymenopterorum, hucusque descriptorum systematicus et synonymicus*, Vol. 7 (W. Engelmann, Lipsiae (Leipzig), 1893).
20. M. L. De Andrade, "Fossil and Extant Species of *Cylindromyrmex* (Hymenoptera: Formicidae)," *Rev. Suisse Zool.* **105**, 581–664 (1998a).
21. M. L. De Andrade, "First Description of Fossil *Acanthostichus* from Dominican Amber (Hymenoptera: Formicidae)," *Mitt. Schweiz. Entomol. Ges.* **71**, 269–274 (1998b).
22. M. L. De Andrade, "A Remarkable Dominican Amber Species of *Cylindromyrmex* with Brazilian Affinities and Additions to the Generic Revision (Hymenoptera: Formicidae)," *Beitr. Entomol.* **51**, 51–63 (2001).
23. M. L. De Andrade and C. Baroni Urbani, "The Baltic Amber Ant Genus *Bradoponera* (Hymenoptera: Formicidae), with Description of Two New Species and a Reassessment of the Proceratiini Genera," *Rev. Suisse Zool.* **110** (4), 913–938 (2003).
24. G. M. Dlussky, "Miocene Ants (Hymenoptera, Formicidae) of the USSR," in *New Fossil Insects from the Territory of the USSR*, Ed. by V. N. Vishnjakova, G. M. Dlussky, and L. N. Pritykina (Nauka, Moscow, 1981), pp. 64–83 [in Russian].

25. G. M. Dlussky, "Genera of Ants (Hymenoptera: Formicidae) from Baltic Amber," *Paleontol. Zh.*, No. 6, 50–62 (1997) [*Paleontol. J.* **31** (6), 616–627 (1997)].
26. G. M. Dlussky, "Syntypes of Baltic Amber Ants *Formica flori* Mayr and *Ponera atavia* Mayr (Hymenoptera: Formicidae)," *Russ. Entomol. J.* **11**, 291–298 (2002).
27. G. M. Dlussky and E. B. Fedoseeva, "The Origin and Early Evolutional Steps of Ants (Hymenoptera: Formicidae)," in *Cretaceous Biocenotic Crisis and Evolution of the Insects*, Ed. by A. G. Ponomarenko (Nauka, Moscow, 1988), pp. 70–144 [in Russian].
28. G. M. Dlussky and E. E. Perkovsky, "Ants (Hymenoptera, Formicidae) from the Rovno Amber," *Vestn. Zool.* **36** (5), 3–20 (2002).
29. G. M. Dlussky and A. P. Rasnitsyn, "Ants (Hymenoptera: Formicidae) of Formation Green River and Some Other Middle Eocene Deposits of North America," *Russ. Entomol. J.* **11** (4), 411–436 (2003 [for 2002]).
30. G. M. Dlussky, D. J. Brothers, and A. P. Rasnitsyn, "The First Late Cretaceous Ants (Hymenoptera: Formicidae) from Southern Africa, with Comments on the Origin of the Myrmicinae," *Insect Systematics and Evolution* **35**, 1–13 (2004).
31. H. Donisthorpe, "Synonymy of Some Genera of Ants," *Entomol. Rec. J. Var.* **28**, 241–244 (1916).
32. H. Donisthorpe, "British Oligocene Ants," *Ann. Mag. Nat. Hist.* **9** (6), 81–94 (1920).
33. C. Emery, "Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Università di Bologna," *Mem. R. Accad. Sci. Ist. Bologna* **5** (1), 141–165 (1891).
34. C. Emery, "Notes sur les sous-familles des Dorylines et Ponerines (Famille des Formicides)," *Ann. Soc. Entomol. Belg.* **45**, 32–54 (1901).
35. C. Emery, "Hymenoptera. Fam. Formicidae. Subfam. Ponerinae", *Genera Insectorum* **118**, 1–125 (1911).
36. A. Handlirsch, *Die fossilen Insekten und die Phylogenie der rezenten Formen* (Wilhelm Engelmann, Leipzig, 1906–1908).
37. B. Hocking, "Insects Associations with the Swollen Thorn Acacias," *Trans. R. Entomol. Soc. London* **122**, 211–255 (1970).
38. B. Hölldobler and E. O. Wilson, *The Ants* (Harvard Univ. Press, Cambridge, Mass., 1990).
39. D. H. Janzen, "Birds and the Ants Acacia Interaction in Central America, with Notes on Birds and Other Myrmecophytes," *Condor* **71** (3), 240–256 (1969).
40. D. H. Janzen, "Protection of *Barteria* (Passifloraceae) by *Pachysima* Ants (Pseudomyrmecinae) in a Nigerian Rain Forest," *Ecology* **53**, 885–893 (1972).
41. R. W. Klein, U. Maschwitz, and D. Kovac, "Flood Control by Ants: A Southeast Asian Bamboo-dwelling *Tetraponera* (Formicidae, Pseudomyrmecinae) Bails Water from Its Internode Nests," *Insectes Sociaux* **40**, 115–118 (1993).
42. J. E. Lattke, "The Genus *Proceratium* Roger in Dominican Amber (Hymenoptera: Formicidae)," *Caribb. J. Sci.* **26**, 101–103 (1991 [for 1990]).
43. J. E. Lattke, "Nuevas especies de *Gnamptogenys* Roger, 1863 de América (Hymenoptera: Formicidae: Ponerinae)," *Entomotropica* **17**, 135–144 (2002).
44. G. L. Mayr, "Vorläufige studien über die Radoboj-formiciden in der Sammlung der k. k. geologischen Reichsanstalt," *Jb. K. K. Geol. Reichsanst. Wien* **17**, 47–62 (1867).
45. G. L. Mayr, "Die Ameisen des Baltischen Bernstein," *Beitr. Naturk. Preuss., Phys.-Ökon. Ges. Königsberg* **1**, 1–102 (1868).
46. K. S. Perfilieva, "Wing Venation in Army Ants (Hymenoptera, Formicidae) and Its Importance for Phylogenetic Analysis," *Zool. Zh.* **81**, 1239–1250 (2002) [*Entomol. Rev.* **82**, 1065–1076 (2002)].
47. E. E. Perkovsky, A. P. Rasnitsyn, A. P. Vlaskin, and M. V. Taraschuk, "A Comparative Analysis of the Baltic and Rovno Amber Arthropod Faunas: Representative Samples," *Afr. Invertebr.* **47**, 229–245 (2007).
48. A. G. Ponomarenko and O. Schultz, "Typen der Geologisch-Paläontologischen Abteilung: Fossile Insekten," *Kataloge der wissenschaften Sammlung des Naturhistorischen Museum in Wien. Paläozoologie* **6** (1), 1–30 (1988).
49. A. P. Rasnitsyn, "The Key of Superfamilies and Families of Hymenoptera," *Rev. Entomol. USSR* **45**, 599–611 (1966).
50. J. Rust and N. M. Andersen, "Giant Ants from the Paleogene of Denmark with a Discussion of the Fossil History and Early Evolution of Ants (Hymenoptera: Formicidae)," *Zool. J. Linn. Soc.* **125**, 331–348 (1999).
51. R. W. Taylor "Taxonomy and Parataxonomy of Some Fossil Ants (Hymenoptera-Formicidae)," *Psyche* **71**, 134–141 (1964).
52. N. Théobald, *Les insectes fossiles des terrain oligocène de France* (G. Thomas, Nancy, 1937).
53. P. S. Ward, "The Ant Subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): Generic Revision and Relationship to Other Formicids," *Syst. Entomol.* **15**, 449–489 (1990).
54. P. S. Ward, "Phylogenetic Analysis of Pseudomyrmecine Ants Associated with Domatia-bearing Plants," in *Ant-Plant Interactions*, Ed. by C. R. Huxley and D. F. Cutler (Oxford Univ. Press, Oxford, 1991), pp. 335–352.
55. P. S. Ward, "Ants of the Genus *Pseudomyrmex* (Hymenoptera, Formicidae) from Dominican Amber, with a Synopsis of the Extant Antillean Species," *Psyche* **99**, 55–85 (1992).
56. P. S. Ward, "Taxonomy, Phylogeny, and Biogeography of the Ant Genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian Regions," *Invertebr. Taxonomy* **15**, 589–665 (2001).
57. J. O. Westwood, "Observations on the Genus *Typhlopone*, with Descriptions of Several Exotic Species of Ants," *Ann. Mag. Nat. Hist.* **6**, 81–89 (1840).
58. W. M. Wheeler, "A List of the Type Species of the Genera and Subgenera of Formicidae," *Ann. N. Y. Acad. Sci.* **21**, 157–175 (1911).
59. W. M. Wheeler, "The Ants of the Baltic Amber," *Schrift. Phys.-Ökon. Ges., Königsberg* **55**, 1–142 (1915).
60. E. O. Wilson, "Observations on the Behavior of the Cerapachyine Ants," *Insectes Sociaux* **5**, 129–140 (1958a).
61. E. O. Wilson, "The Beginning of Nomadic and Group-predatory Behavior in the Ponerine Ants," *Evolution* **12**, 14–31 (1958b).
62. T. P. Young, C. H. Stubblefield, and L. A. Isbell., "Ants on Swollen-thorn Acacias: Species Coexistence in a Simple System," *Oecologia (Berlin)* **109**, 98–107 (1997).
63. J. Zhang, *Fossil Insects from Shanwang, Shandong, China* (Shandong Sci. and Technol. Publishing House, Jinan, 1989).