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Ants of the Genus *Plagiolepis* Mayr (Hymenoptera, Formicidae) from Late Eocene Ambers of Europe

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Abstract—The genus *Plagiolepis* Mayr (Hymenoptera, Formicidae) from the Late Eocene Baltic, Bitterfeld, Rovno, and Scandinavian ambers is revised. Two new species, *Plagiolepis wheeleri* sp. nov. and *P. paradoxa* sp. nov., are described. A lectotype of *Plagiolepis klinsmanni* Mayr, 1868 and neotypes of *P. kuenowi* Mayr, 1868 and *P. solitaria* Mayr, 1868 are designated. *Rhopalomyrmex pygmaeus* Mayr, 1868 (= *Plagiolepis balticus* Dlussky, 1997) is recognized as a new synonym of *P. kuenowi* Mayr, 1868. A key for identification of the Late Eocene species of *Plagiolepis* from the European ambers is provided.

Key words: Ants, Formicinae, *Plagiolepis*, new species, keys, Baltic amber, Bitterfeld amber, Rovno amber, Scandinavian amber, Late Eocene.

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INTRODUCTION

The first thorough revision of the Baltic amber ants has been produced by G. Mayr (1868). It contained descriptions of 50 species, including *Plagiolepis klinsmanni, P. kuenowi, P. squamifera, P. solitaria*, and *P. singularis*, as well as *Rhopalomyrmex pygmaeus*, which has been subsequently transferred to *Plagiolepis* (Dlussky, 1997). Mayr's species descriptions are largely out of date and his drawings are reconstructions rather than illustrations of actual specimens, and are not always precise. Then André (1895) described an additional species, but did not include an illustration. In his classical monograph on the Baltic amber ants Wheeler (1915) redescribed many of Mayr's species and supplied excellent drawings. Unfortunately, the genus *Plagiolepis* was not included in that revision. Wheeler only listed the examined specimens, made a few comments, and included a single drawing of an ant erroneously (see below) identified by him as *Rhopalomyrmex pygmaeus*.

In recent years I have studied extensive collections of ants from the Baltic (Poland and Kaliningrad Region of Russia), Bitterfeld (Germany), Rovno (Ukraine), and Scandinavian (Denmark) ambers, including all the surviving specimens identified by Wheeler. This has allowed to redescribe and illustrate most of the *Plagiolepis* species previously described from the Late Eocene European amber, describe two new species, and compose an identification key.

The following collections were examined: Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (**PIN**), Baltic amber; Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine (**SIZK**), Rovno amber; Museum Ziemi PAN, Warsaw, Poland (**MZPAN**), Baltic amber; Natural History Museum, London, UK (**BMNH**), Baltic amber; Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen, Göttingen, Germany (**GZG.BST**), Baltic amber, a part of the collection formerly owned by the Geological Institute of Königsberg and described by Wheeler (1915)[1]; Humboldt Museum, Berlin, Germany (**HM**), Bitterfeld amber; Zoological Museum of University Copenhagen (**ZMUC**), Scandinavian and Baltic amber; personal collection of Carsten Gröhn, Glinde, Germany (**CGC**), Baltic amber, type specimens from this collection are deposited at Geologisch-Paläontologisches Institut, Universität Hamburg; personal collection of Manfred Kutscher, Sassnitz, Rügen, Germany (**MKC**), bequeathed to Geowissenschaftliches Zentrum, University of Göttingen (**GZG.BST**), Bitterfeld amber.

SYSTEMATIC PALEONTOLOGY

Subfamily Formicinae Latreille, 1802

Genus *Plagiolepis* Mayr, 1861

Type species. *Formica pygmaea* Latreille, 1798.

Composition. Seventy-seven Recent species, in the Palearctic, Oriental, Indo-Australian, and Afro-

[1] In the lists of examined specimens under each species, I indicate both new numbers (preceded by GZG.BST) and old numbers (referring to the Königsberg collection, in parentheses), while giving only the new numbers elsewhere in the text.

tropical regions (Bolton et al., 2006), and 9 previously described fossil species: *Plagiolepis balticus* Dlussky, 1997 (=*Rhopalomyrmex pygmaeus* Mayr, 1868), *P. klinsmanni* Mayr, 1868, *P. kuenowi* Mayr, 1868, *P. singularis* Mayr, 1868, *P. solitaria* Mayr, 1868, *P. squamifera* Mayr, 1968, and *P. succini* André, 1895 from Baltic amber (Late Eocene), *P. minutissima* Dlussky, 2002 from Rovno amber (Late Eocene), and *P. labilis* Emery, 1891 from Sicilian amber (Oligocene). Additionally, one of the specimens described from the Miocene locality Radoboj in Croatia as *Formica fragilis* Heer, 1849 is in fact a gyne *Plagiolepis* (Mayr, 1867).

Remarks. Mayr and Wheeler considered the number of antennal segments as a highly important character. However, it is currently known that this character can vary among small ants even within a single species (Bünzli, 1935). Because, according to its description, the genus *Rhopalomyrmex* Mayr, 1868 differs from *Plagiolepis* only by the number of the antennomeres (10, unlike 11 in *Plagiolepis*), I synonymized it with the latter and proposed for *Rhopalomyrmex pygmaeus* Mayr the name *Plagiolepis balticus* because the name *Plagiolepis pygmaea* was preoccupied (Dlussky, 1997).

The males described as separate species may actually belong to species described based on workers, but proving it is not possible.

PLAGIOLEPIS KLINSMANNI SPECIES GROUP

Diagnosis. Eyes of workers oval, situated approximately at midlength of sides of head. Gena length exceeding maximum eye diameter. Third antennal flagellomere of workers transverse, slightly shorter than fourth. Petiole with node. First segment of gaster shorter than second. Coronula around acidopore very strongly developed, formed by hairs diverging only near apices and close-set more basally, forming solid funnel.

Composition. *Plagiolepis klinsmanni* Mayr, 1868 and two species described below from the Late Eocene amber of Europe, *P. wheeleri* sp. nov. and *P. paradoxus* sp. nov.

Remarks. The peculiar shape of the petiole in these ants is associated with their capability of holding the gaster vertically up. Rather often these ants become preserved in amber in this very posture. The ability to raise the gaster straight up evolves in Formicinae and Dolichoderinae in three cases. First of all it is found in diurnal predators/scavengers of deserts (*Cataglyphis* Förster, *Dorymyrmex* Mayr) and in large canopy-dwelling ants (*Oecophylla* F. Smith, *Leptomyrmex* Mayr). In these ants the habit of raising the gaster vertically is associated with peculiarities of their locomotion and correlates with slenderness of the body and great length of the legs (Dlussky, 1981). Some more robust ants with relatively short legs display a similar behavior, but use it to release defensive volatiles. This behavior is rather common in Dolichoderinae (in particular, it is highly typical of *Liometopum* Mayr), but I know of no such examples among recent Formicinae. The latter usually spray their venom not by raising the gaster, but by instead bending it down between the legs and pointing its tip forwards. The presence of the scale on the petioles of these ants is also associated with this behavior (Dlussky and Fedoseeva, 1988). The extinct *Plagiolepis* of the *klinsmanni* group appear to be an exception from this rule. An exceptionally strong development of the acidopore's coronula corroborates this interpretation. This structure protects the ant from its own venom, released through the acidopore.

***Plagiolepis klinsmanni* Mayr, 1868**

Plagiolepis klinsmanni: Mayr, 1868, p. 37, plate I, figs. 19 and 20 (worker); Dalla Torre, 1893, p. 172; André, 1895, p. 82; Handlirsch, 1908, p. 859; Wheeler, 1915, p. 101 (male); Burnham, 1978, p. 113, Ponomarenko and Schultz, 1988, p. 27; Bolton, 1995, p. 335; Dlussky, 1997, p. 59; Dlussky and Perkovsky, 2002, p. 12.

Lectotype (designated here to ensure the stability of nomenclature). No. 1984/31/183 (worker, Mayr's syntype), in the Natural History Museum of Vienna (Ponomarenko and Schultz, 1988); Baltic amber; Late Eocene.

Description (Figs. 1a–1c). Worker. Body length, 2.5–3.85 mm. The head is rectangular, with the occipital angles rounded and the occipital margin straight, slightly convex, or slightly concave. The clypeus usually with a weak smoothed-out carina and a rounded anterior margin. The antennae are 11-segmented. The scape is not quite reaching the head's occipital margin. The apical flagellomeres are thickened, but not forming a distinct club. The first flagellomere is approximately as long as the combined length of the two next ones. The second and third flagellomeres each are slightly longer than wide, the seventh to ninth are distinctly wider than long. The terminal flagellomere is approximately as long as the two more proximal ones combined. The mandibles are triangular, relatively narrow, with 5 to 6 teeth on the masticatory margin. The palpal formula is 6.4. The maxillary palpi are reaching the occipital orifice. The sutures delimiting the pronotum, mesonotum, and propodeum are distinct; the mesopleural suture is absent. The pronotum is strongly convex, without humeral prominences, separated from the mesonotum by a constriction, shallow yet well visible in profile. The prosternum between the fore coxae with a triangular projection, which is wider than long. The mesonotum is slightly convex, except in its posterior part, where it is concave. The mesopropodeal constriction is wide. The propodeum in profile is very smoothly rounded, without distinct dorsum and declivity. This undivided upper surface is separated from the lateral surfaces by rather sharp edges. The propodeal spiracles are widely oval, situated at the edges. The petiole is more than 1.5 times as long as high, almost as wide as high. The node of the petiole in

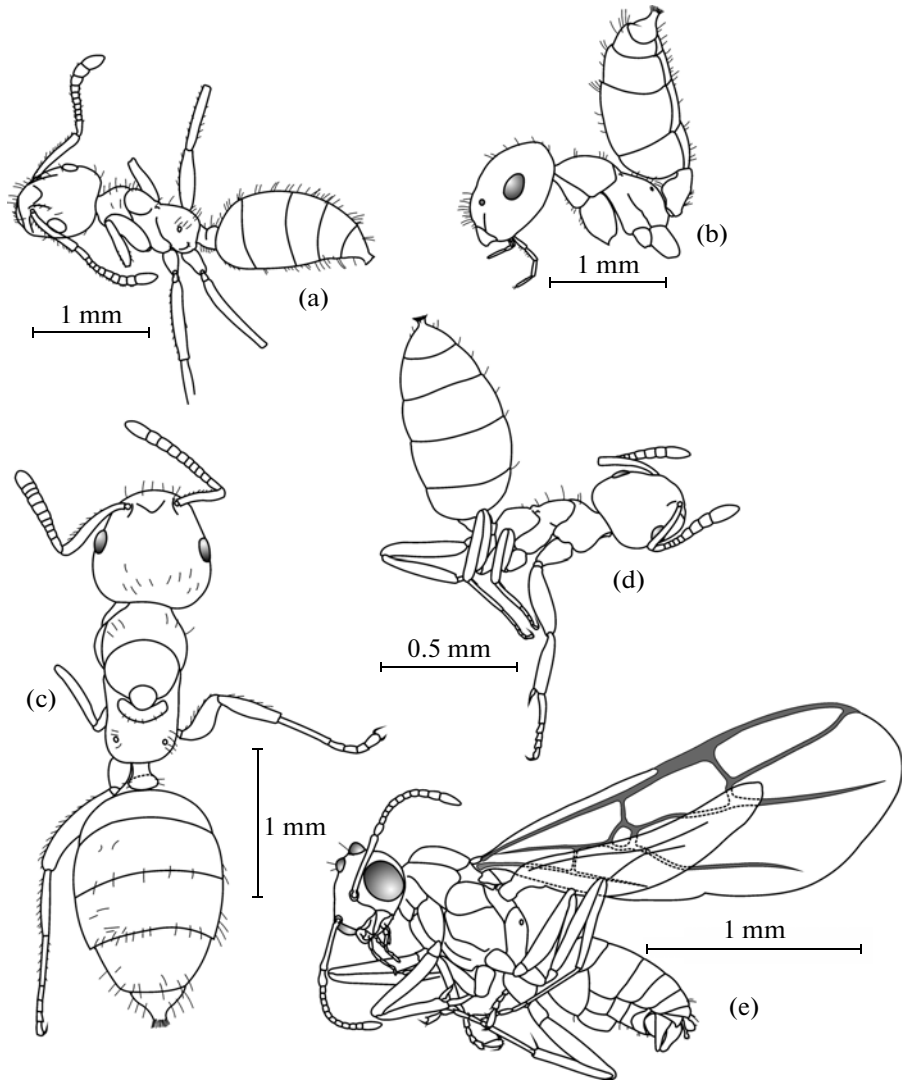

Fig. 1. Species of the *Plagiolepis klinsmanni* species group: (a–c) *P. klinsmanni* Mayr: (a) MZPAN, no. 11471, worker; (b) ZMUC, no. 347, worker; (c) MZPAN, no. 282, ergatoid gyne; (d) *P. wheeleri* sp. nov., holotype GZG.BST, no. 04651, worker; (e) *P. paradoxa* sp. nov., holotype GZG/BST, no. 25.012, male. Baltic (a–d) and Bitterfeld (e) amber; Late Eocene.

profile is triangular, with its apex well rounded. The body is smooth, with numerous piligerous punctures. The decumbent pubescence is variable: in specimens where it is best developed the decumbent hairs are considerably longer than distances between them, and in the least pubescent specimens distinctly shorter than those distances; there is a complete spectrum of intermediate conditions between these two extreme cases. Erect hairs are present on the entire upper surface of the head, on the occipital angles, sometimes on the occipital margin and also on the lower side of the head. The pronotum with 3–6, mesonotum with 2–4, and propodeum with 6–7 pairs of erect hairs. The petiole with erect hairs. The gaster with erect hairs on the entire surface of tergites and sternites. The scape and the legs with erect and semierect hairs.

Ergatoid gyne (described for the first time). The body length is ca. 3.5 mm. The head and gaster as in workers. The mesosoma is not as wide as the head. The scutum is oval, slightly convex, approximately 1.5 times as wide as long. The scutellum is very small, transverse. The petiole with a node, as in workers. The upper surface of the node with a shallow longitudinal depression. Punctures and decumbent pubescence on the scutum and scutellum are sparse. The legs and scape with numerous semierect hairs.

Measurements (mm): workers: mesosoma length, 0.8–1.5 (mean 0.96), head length, 0.65–0.95 (mean 0.76), scape length, 0.45–0.65 (mean 0.54); ergatoid gyne MZPAN, no. 282: mesosoma length, 1.0, mesosoma width, 0.75, head length, 0.875.

Comparison. See below, in the Table with key to these ants.

R e m a r k s. Mayr has described this species based on eight workers; the only surviving syntype is being designated here as a lectotype.

Wheeler (1915) wrote that he saw a male (K.1020 from Klebs collection), which probably belonged to this species, but he did not describe it, except for the size (2.5 mm) and some characters typical of other *Plagiolepis* (12-segmented antennae and the absence of the forewing cells rm and mcu). It is unclear which characters, besides the size, differentiated this male from *P. solitaria*. The specimen is missing from the GZG.BST collection. I have found in that collection only a single male, *Plagiolepis minutissima* Dlussky, identified by Wheeler as *Prenolepis henschei* Mayr.

The specimen described by Wheeler as *Rhopalomyrmex pygmaeus* (Wheeler, 1915, p. 103), based on his description, most probably belongs to the *P. klinsmanni* group because it has a nodelike petiole. Wheeler has placed it into *Rhopalomyrmex* on the account of 11-segmented instead of 12-segmented antennae. At the same time, the relatively large size (3 mm) and the presence of numerous semierect hairs on the legs and the scape may indicate that this specimen was a male *P. klinsmanni*. Because the specimen is not preserved, it cannot now be identified with certainty.

M a t e r i a l. *Baltic* amber: GZG.BST nos. 04039 (K909), 040093 (K911), 04615 (K4262), 04616 (K4313), 04619 (K4045), 04622 (K2649) (workers, identified by Wheeler as *Plagiolepis klinsmanni*), 04565 (K4180) (worker, identified by Wheeler as *Prenolepis henschei*), 05064 (K812), 05190 (K2639) (workers, identified by Wheeler as *Bothriomyrmex goepperti*), 04101 (2 workers); MZPAN nos. 282 (ergatoid gyne), 2000/1, 8794, 11471, 11583, 15441, 15450, 15685 (3 workers), 18742; BMNH, no. In.17791 (Samland), PI.II.1091 (J. Gerber, 1969); ZMUC nos. 347 (Danzig. D. Jacobsen, 24.03.1916); 348 (Min. Mus.). *Bitterfeld* amber: HM nos. 14/202, 16/239 (workers). *Rovno* amber: SIZK nos. UA-59, K-44, K-193, K-5103 (workers). *Scandinavian* amber: worker ZMUC, no. 396 (A.K. Andersen, 28.03.1968).

Plagiolepis wheeleri Dlussky, sp. nov.

Rhopalomyrmex pygmaeus: Wheeler, 1915, p. 104, fig. 49 (nec. *Rhopalomyrmex pygmaeus* Mayr, 1868).

E t y m o l o g y. In honor of the myrmecologist W.M. Wheeler.

H o l o t y p e. GZG.BST.04651 (K789), worker, identified by Wheeler as *Rhopalomyrmex pygmaeus*; Baltic amber; Late Eocene.

D e s c r i p t i o n (Fig. 1d). Worker. Body length, 2.3 mm. The head is rectangular, slightly longer than wide, with the occipital angles rounded and occipital margin slightly convex. The clypeus is slightly convex, without a carina, with the anterior margin rounded. The antennae are 10-segmented. The scape is not quite reaching the occipital margin of the head. The first flagellomere is longer than the second and third combined. The flagellomeres 2–6 are approximately as long as wide; the flagellomeres 7–10 are significantly larger than other flagellomeres, forming an indistinct club. The mandibles are triangular, relatively narrow, with 5 teeth on the masticatory margin. The maxillary palpi are 6-segmented, long, reaching the occipital orifice. The sutures delimiting the pronotum, mesonotum, and propodeum are distinct; the mesopleural suture is absent. The promesonotal constriction is not developed. The mesopropodeal constriction is wide and shallow. The propodeum is very smoothly rounded in profile, without distinct dorsum and declivity. The propodeal spiracles are widely oval, situated at the edges. The petiole is longer than high, with the node uniformly rounded in profile. The body is smooth, with sparse piligerous punctures. No decumbent pubescence is visible. The head with erect hairs on the clypeus. The pronotum with 2, mesonotum with 3, and propodeum with 2 pairs of erect hairs. The three basal gastral tergites with sparse erect hairs, mostly along posterior margins. The more distal gastral tergites and all the sternites with erect hairs on the entire surface. The scape and the legs without erect hairs.

M e a s u r e m e n t s (mm): holotype: mesosoma length, 0.64; head length, 0.50; scape length, 0.37.

C o m p a r i s o n. The species is similar to *P. klinsmanni*, from which it differs by the 10-segmented antennae and the absence of erect or semierect hairs on the legs and the scape.

R e m a r k s. The specimen described and illustrated by Wheeler (1915, fig. 49) as *Rhopalomyrmex pygmaeus*, although it has 10-segmented antennae, cannot belong to that species. It has a nodelike petiole, similar to that of *P. klinsmanni*, while Mayr's description clearly indicates that *Rh. pygmaeus* has a petiole similar to that of *P. kuenowi*, with a scale: "Das Stielchen hat oben eine, wie bei Plagiolepis Künowi geformte Schuppe, welche niedrig, queroval und schief nach vorne geneigt ist." It should also be noted that, on the above-mentioned drawing (Wheeler, 1915: fig. 49), the propodeum is illustrated with much more numerous erect hairs than actually present.

M a t e r i a l. Holotype.

Plagiolepis paradoxa sp. nov.

E t y m o l o g y. From the Latin *paradoxus* (strange, unusual).

H o l o t y p e. GZG.BST, no. 25.012 (MKC), male; Bitterfeld amber; Late Eocene.

D e s c r i p t i o n (Fig. 1e). Male. Body length, 1.9 mm. The head is rounded, without distinct occipital angles. The eyes are large, almost round; the maximum eye diameter is half the length of the lead. The length of gena approximately equaling the width of the mandibular base. The ocelli are large and prominent, the ocellar diameter is greater than the interocellar distance. The mandibles are narrow, curved, with a

sharp apical tooth, without small teeth on the masticatory margin. The maxillary palpi are 6-segmented, relatively short, not reaching to the occipital orifice. The clypeus is rather flat, with a slightly protruding rounded lobe in the middle of its anterior margin. The antennae are geniculate, 12-segmented. The scape is relatively long, longer than half-length of the flagellum, its tip is extending beyond the occipital margin of the head. The first flagellomere is long and thick, 1.7 times as long and 1.4 times as wide as the second flagellomere, 1.8 times as long as wide. The second flagellomere is 1.5 times as long as wide. The third flagellomere is slightly shorter than the second; more distal flagellomeres gradually become shorter towards the tip. The penultimate flagellomere is only slightly shorter than and the terminal one is 1.7 times as long as the first flagellomere. The scutum in profile is convex, without parapsidal sutures, not covering the pronotum from above. The propodeal dorsum and declivity in profile form a rounded yet distinct obtuse angle. The forewing with closed cells 3r, 1r+2r+rm, and mcu. The apex of 3r lies on the wing's margin. Sections 5RS and 4M extending from cell 1r+2r+rm independently from one another, separated by section r-m, which is more than twice longer than the vein width. Vein cu-a is separated from the discoidal cell by a distance greater than the length of section 1Cu. The petiole in profile is triangular, with a rounded apex. The subgenital plate is uniformly concave. The stipes is triangular, narrow, twice as long as wide basally, with a rounded apex. The squamula with a dentiform projection on its posterior margin. The entire body is smooth and shiny. Isolated erect hairs are present on the head (near ocelli) and the sternites and apical tergites of the gaster. Decumbent pubescence is absent.

Measurements (mm): holotype: —body length, 1.9; mesosoma length, 0.71; head length, 0.41; scape length, 0.55; forewing length, 2.05.

Comparison. The described specimen differs from all the known males of *Plagiolepis* by the presence of the closed cell mcu in the forewing. However, this character potentially can be an individual aberration. The species differs from *P. minutissima* Dlussky and *P. solitaria* Mayr, also described from Late Eocene amber, by the shape of the petiole.

Remarks. The forewing venation of the described male (cell mcu present and 5RS and 4M independently originating from cell 1r+2r+rm) is unusual for *Plagiolepis*. At the same time, in the forewings of all the known Formicinae 5RS and 4M originate at a common node, while all the known *Plagiolepis* lack a closed mcu. Still, because of the considerable similarity between the new species and the known *Plagiolepis* in all characters other than wing venation I believe it should be placed in *Plagiolepis*. Small ant males often display abnormalities in wing venation (Perfilieva, 2000), and it is possible that we have such an individual aberration in this case.

Based on correlations between characters observed in recent species, we can expect the males of *P. klinsmanni* to have erect or semierect hairs on the legs, and the males of *P. wheeleri* to have 11-segmented antennae. Because in the described male of *P. paradoxa* there are no hairs on the legs and the antennae are 12-segmented, it is unlikely that it belongs to any of the *P. klinsmanni* group species described based on workers.

Material. Holotype.

PLAGIOLEPIS PYGMAEA SPECIES GROUP

Diagnosis. Eyes of workers oval, shifted slightly forwards from the midlength of sides of head. Gena approximately as long as maximum eye diameter. Third flagellomere of workers transverse or quadrate, distinctly shorter than fourth. Petiole with scale. First segment of gaster as long as or longer than second segment. Coronula of acidopore of regular shape.

Composition. The recent *Plagiolepis pygmaea* (Latreille, 1798) (Europe), *P. flavescens* Collingwood, 1976 (eastern Palearctic), and *P. karawajewi* Radchenko, 1989 (Crimea) (Radchenko, 1996) and the fossil *P. kuenowi* Mayr, *P. minutissima* Dlussky, *P. solitaria* Mayr, and *P. squamifera* Mayr from Late Eocene amber of Europe.

***Plagiolepis kuenowi* Mayr, 1868**

Plagiolepis künowi: Mayr, 1868, p. 39, Pl. I, fig. 22, 23 (worker); Dalla Torre, 1893, p. 172; André, 1895, p. 82; Handlirsch, 1907, p. 859; Wheeler, 1915, p. 101.

Plagiolepis kuenowi: Mayr: Burnham, 1978, p. 113; Bolton, 1995, p. 335; Dlussky, 1997, p. 59.

Rhopalomyrmex pygmaeus: Mayr, 1868, p. 42, Pl. II, figs. 25, 26 (worker); Dalla Torre, 1893, p. 175; André, 1895, p. 82; Handlirsch, 1908, p. 859; Wheeler, 1915, p. 103–104, (worker); Burnham, 1978, p. 113; Bolton, 1995, p. 377. Syn. nov.

Plagiolepis balticus: Dlussky, 1997, p. 59 (replacement name for *Rhopalomyrmex pygmaeus*). Syn. nov.

Neotype (designated here to ensure the stability of nomenclature). GZG.BST, no. 04275 (K5775), worker, identified and compared to Mayr's holotype by Wheeler; Baltic amber; Late Eocene.

Description (Figs. 2a and 2b). Worker. Body length, 1.4–2.7 mm. The head is rectangular, slightly longer than wide, with the occipital angles rounded and the occipital margin straight, slightly convex, or slightly concave. The frontal carinae are short, diverging. Frontal area is delimited. The clypeus is convex, without a carina, with the anterior margin rounded. The antennae are 10- or 11-segmented. The scape is reaching the occipital margin of the head. The apical flagellomeres are thickened, but not forming a distinct club. The first flagellomere is slightly shorter than the second and third combined. All the flagellomeres are longer than wide. The terminal flagellomere is shorter than the two preceding flagellomeres combined. The mandibles are triangular, relatively narrow. The maxillary palpi are reaching the occipital orifice. The sutures delimiting the pronotum, mesonotum, and

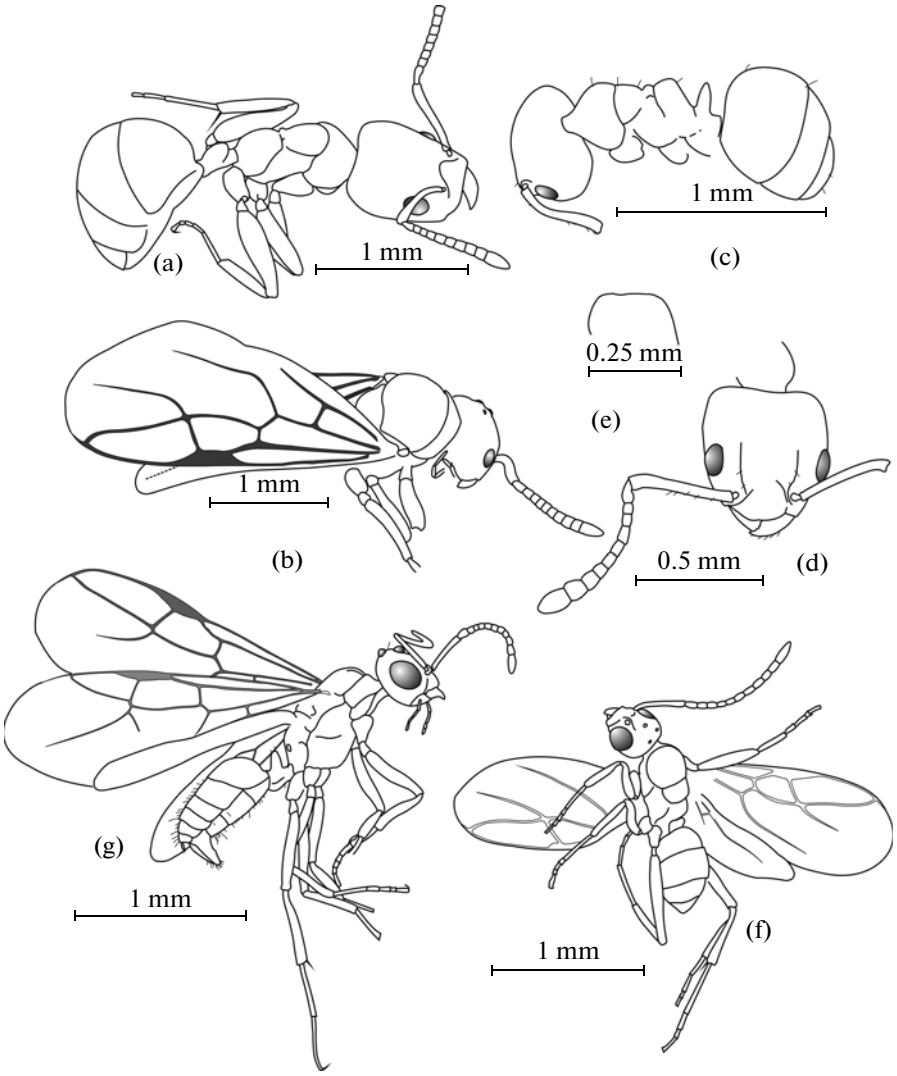

Fig. 2. Species of the *Plagiolepis pygmaea* species group: (a–b) *P. kuenowi* Mayr: (a) neotype GZG.BST, no. 04275, worker; (b) CGC, no. 3345, female; (c–e) *P. squamifera* Mayr: (c) neotype GZG.BST, no. 04621, worker; (d–e) HM, no. 10/203, worker: (d) head, (e) upper margin of scale; (f) *P. minutissima* Dlussky, holotype SIZK, no. UA-1066, male; (g) *P. solitaria* Mayr, neotype HM, no. 13/218, male. Baltic (a–c), Bitterfeld (d, e, g), and Rovno (f) amber; Late Eocene.

propodeum are distinct; the mesopleural carina is absent. The pronotum is convex, without humeral prominences, in profile forming a continuous arc with the slightly convex mesonotum; the promesonotal constriction is not developed. The prosternum without a projection between the fore coxae. The propodeum in profile is angular, with distinct dorsum and declivity. The dorsum is very short and convex in cross-section. The declivity is flat in cross-section, straight in profile, separated from the dorsal and lateral surfaces by a sharp edge, at which the propodeal spiracles are situated. The petiole is higher than long. The scale of the petiole is oblique, relatively narrow, with its sides convex and the upper marring rounded, distinctly higher than wide. The body is smooth and shiny. The decumbent hairs are very thin, visible not on all specimens and only at high magnifications and with a proper lighting. The head with erect hairs on the clypeus, frons (2 or 3 pairs along the frontal carinae), and very seldom on the vertex. Most specimens without erect hairs on the mesonotum and the scale, at most with 2 pairs of hairs on the pronotum, 2 pairs on the mesonotum, and 1 pair on the upper angles of the scale. On the gastral segments 1–3 erect hairs are typically present along the posterior margins only, but in some specimens sparse hairs are present on the entire surface. The scape and the legs without erect or semierect hairs.

Gyne (described for the first time). Body length, ca. 3 mm. The eyes are oval, shifted slightly forwards. The gena is as long as the maximum eye diameter or slightly shorter. The scutum is approximately 1.2 times as wide as long, convex, without paranotal sutures, in profile separated from the scutellum with a distinct

constriction. The scutellum is slightly convex, transverse. At least the scutum, scutellum, legs, and scape without erect hairs.

Measurements (mm): workers: neotype: mesosoma length, 0.81, head length, 0.73, scape length, 0.49; PIN, no. 964/487: mesosoma length, 0.625, head length, 0.525, head width, 0.475, scape length, 0.425; SIZK, no. K-1008: mesosoma length, 0.575, head length, 0.525, scape length, 0.425; SIZK, no. K-5152: mesosoma length, 0.59, head length, 0.48, scape length, 0.40; SIZK, no. K-5269: head length, 0.43, head width, 0.37, scape length, 0.32; MZPAN, no. 16471: mesosoma length, 0.475; ZMUC, no. 343: mesosoma length, 0.65; ZMUC, no. 344: mesosoma length, 0.50, head length, 0.525, head width, 0.375; ZMUC, no. 346: mesosoma length, 0.60; no. ZMUC, no. 355a: mesosoma length, 0.55, scape length, 0.375; ZMUC, no. 355b: head width, 0.35; gyne: CGC, no. 3345: scutum length, 0.55, scutum width, 0.67, scutellum length, 0.23, scutellum width, 0.40, forewing length, 1.8.

Material. *Baltic* amber: neotype, GZG.BST nos. 04059 (K5779), 04104 (K5790), 04344 (B960); PIN 964/487; MZPAN no, 16471 (workers); CGC, no. 3345 (gyne). *Bitterfeld* amber (workers): HM, no. 14/260 (worker), GZG.BST, no. 25.081 (MKC) (3 workers). *Rovno* amber (workers): SIZK nos. K-1008, K-2583, K-3512, K-5152, K-5269. *Scandinavian* amber (workers): ZMUC nos. 343 (G.V. Henningsen, 12.04.1957), 344 (G.V. Henningsen, 08.12.1954), 345 (A.K. Andersen, 28.03.1968), 346 (Borge Mortensen, 21.03.1961), 351 (A. Henningsen, 09.09.1974), 353 (G.V. Henningsen, 08.12.1954), 355 (2 workers) (Borge Mortensen, 01.09.1960).

Remarks. The single specimen on which the description of *Plagiolepis kuenowi* was based is not preserved. Similarly is not preserved the only specimen on which the description of *Rhopalomyrmex pygmaeus* was based. Mayr pointed out in his description that *Rhopalomyrmex pygmaeus* is very similar to *Plagiolepis kuenowi*, differing from it by 10-segmented antennae with a distinct club and a more convex clypeus. Wheeler (1915) also wrote about a similarity between this species and *P. kuenowi*. Because it is currently known that the number of antennal segments in small ants is subject to variation and because no other characters differentiating *Rhopalomyrmex* from *Plagiolepis* have been described, I have synonymized the two genera (Dlussky, 1997). I preserved the identity of *Rh. pygmaeus* as a separate species under the name *Plagiolepis balticus* because *Plagiolepis pygmaea* (Latreille, 1798) had already been described earlier. Examination of a series of workers of *P. kuenowi* revealed that *Rh. pygmaeus* was a junior synonym of that species. Most of the examined specimens have 11-segmented antennae, while in two of them (ZMUC, no. 344 and GZG.B5T, no. 27.081b) the antennae are 10-segmented. The specimen GZG.BST, no. 27.081 contains three workers, one of which has 10-segmented and two others 11-segmented antennae.

Although the specimen GZG.BST, 04651 (K789), identified by Wheeler as *Rhopalomyrmex pygmaeus* and illustrated on his Figure 49 (Wheeler, 1915) has 10-segmented antennae, it differs from *Plagiolepis kuenowi* by the structure of its propodeum and petiole. It is described above under the name *P. wheeleri*.

Plagiolepis minutissima Dlussky, 2002

Plagiolepis minutissima: Dlussky: Dlussky and Perkovsky, 2002, pp. 12–13, fig. 3d (male).

Holotype. SIZK, no. UA-1066. male; Rovno amber; Late Eocene.

Description (Fig. 2f). Male. Body length, 1.4–1.5 mm. The head is slightly longer than wide, slightly narrowing anteriorly, with the occipital angles strongly rounded and the occipital margin slightly convex. The eyes are large, round, strongly convex, shifted forwards. The gena length is approximately equal to the scape diameter. The ocelli are relatively small, the interocellar distance is less that the ocellar diameter. The clypeus is strongly convex in the middle, with the anterior margin rounded. The antennae are 12-segmented. The scape is extending far beyond the occipital margin of the head. The first flagellomere is slightly longer that the second, the flagellomeres 2 to 6 are of approximately equal length. The maxillary palpi are 6-segmented, long, reaching beyond the occipital orifice. The scutum and scutellum are convex, separated by a deep transverse constriction. The propodeum in profile is angular, its outline forming a strongly rounded angle. The scale of the petiole is high, slightly convex on the upper margin. The forewing with closed cells 3r and 1r+2r+rm; cell mcu is reduced. Free branches of RS and M originate from a common node. The body is smooth and shiny, without a noticeable sculpturing. The body and appendages without erect pilosity.

Measurements (mm): holotype: mesosoma length, 0.56, head length, 0.33, head width, 0.32, scape length, 0.35, forewing length, 1.46, metafemur length, 0.59; paratype SIZK, no. UA-1066: mesosoma length, 0.62, scape length, 0.35, forewing length, 1.62; SIZK, no. K-5372: mesosoma length, 0.64, head width, 0.40, scape length, 0.37, forewing length, 1.85; PIN no, 964/238: head length, 0.425, head width, 0.40, scape length, 0.375.

Remarks. Judging from its size, it can be a male *Plagiolepis kuenowi* or *P. squamifera*, but it is impossible to determine to which of the two species it has to be referred.

Material. Besides holotype, paratype SIZK, no. UA-1064; Rovno amber; Late Eocene. Other specimens (males): Rovno amber: SIZK, no. K-5372; Baltic amber: GZG.BST, no. 04556 (G2931); PIN, no. 964/238.

***Plagiolepis solitaria* Mayr, 1868**

Plagiolepis solitaria: Mayr, 1868, p. 40 (male); Dalla Torre, 1893, p. 173; André, 1895, p. 82; Handlirsch, 1908, p. 859; Wheeler, 1915, p. 102; Burnham, 1978, p. 113; Bolton, 1995, p. 336; Dlussky, 1997, p. 59.

Neotype (designated here to ensure the stability of nomenclature). HM no, 13/218, a male, completely matching the description by Mayr; Bitterfeld amber; Late Eocene.

Description (Fig. 2g). Male. Body length, 2–3 mm. The head is slightly longer than wide, slightly narrowing anteriorly, with the occipital angles strongly rounded and the occipital margin convex. The eyes are large, round, strongly convex, shifted forwards. The gena length is approximately 1.5 times the scape diameter. The ocelli are large, the interocellar distance approximately equals the ocellar diameter. The clypeus is strongly convex, somewhat angular in cross-section, but without a distinct median carina, with the anterior margin rounded. The antennae are 12-segmented. The scape is rather thick, extending beyond the occipital margin of the head. The first flagellomere is twice as long as the second. The mandibles are rather long, with 5 to 6 teeth, four of which are well developed and the other two are barely distinct. The maxillary palpi are almost reaching the occipital orifice. The scutum is flat dorsally and smoothly rounded anteriorly. The propodeum in profile is angular, its outline forming a strongly rounded angle. The scale of the petiole is high, with the upper margin rounded. The forewing with closed cells 3r and 1r+2r+rm; cell mcu is reduced. Free branches of RS and M originate from a common node. In the genitalia, the stipites are long, 1.7 times as long as wide basally. The body is smooth and shiny, without a noticeable sculpturing. Erect hairs are visible on the vertex, the scale, and the entire surface of gastral tergites and sternites. The legs and the scape without erect or semierect hairs.

Measurements (mm): neotype HM, no. 13/218: body length, 2.0, mesosoma length, 0.72, head length, 0.38, maximum eye diameter, 0.20, scape length, 0.24, forewing length, 1.85; GZG.BST, 25.024: body length, ca. 2.5, scape length, 0.48, forewing length, 2.54.

Remarks. The only specimen from Menge collection, on which the description of this species was based, is not preserved. The specimens I examined match the description of *P. solitaria*, except the size (2 to 2.5 mm, compared to 3 mm in the description). The size of this ant matches the size expected for males of *Plagiolepis klinsmanni*. Yet, based on correlations between characters observed in the recent species, males of that species are expected to have the petiole with a node, instead of a scale, and abundant erect pilosity.

Material: neotype. Other specimens (males): Baltic amber: GPC, no. 3316; Bitterfeld amber: HM, no. 11/250, GZG.BST, no. 25.024 (MKC); Rovno amber: SIZK, no. K-2564.

***Plagiolepis squamifera* Mayr, 1868**

Plagiolepis squamifera: Mayr, 1868, p. 40, Pl. I, fig. 24 (worker); Dalla Torre, 1893, p. 173; André, 1895, p. 82; Handlirsch, 1907, p. 859; Wheeler, 1915, p. 102; Burnham, 1978, p. 113; Bolton, 1995, p. 336; Dlussky, 1997, p. 59.

Neotype (designated here to ensure the stability of nomenclature). GZG.BST, no. 04621 (K.905), worker, identified by Wheeler and compared by him with Mayr's type. Baltic amber.

Description (Figs. 2c–2e). Worker. Body length, 1.6–1.8 mm. The head is slightly longer than wide, rectangular, with its sides convex, the occipital angles rounded, and the occipital margin weakly concave. The gena length approximately equals the maximum eye diameter. The frontal carinae are short, diverging. The clypeus is convex, without a carina, with the anterior margin rounded. The antennae are 11-segmented. The scape is reaching to or slightly beyond the occipital margin of the head. The first flagellomere is slightly longer than the second and third combined. The apical flagellomeres are thickened, but not forming a distinct club. The terminal flagellomere is approximately as long as the two more basal ones combined. The mandibles are triangular, comparatively narrow. The maxillary palpi are reaching the occipital orifice. The sutures delimiting the pronotum, mesonotum, and propodeum are distinct; the mesopleural carina is absent. The propodeum in profile is angular, its dorsum is much shorter than the declivity. The petiole is higher than long. The scale of the petiole is high, with its sides weakly convex, almost parallel, and its upper margin slightly concave. The body is smooth and shiny, with sparse piligerous punctures. The specimens I examined (as well as those described by Mayr) are without visible decumbent pubescence. The head with erect hairs on the clypeus, frons (2 to 3 pairs along the frontal carinae), and, very rarely, vertex. The mesosoma with a few isolated hairs. The first to third gastral segments with erect hairs on the entire surface. The scape and the legs with sparse semierect hairs.

Measurements (mm): neotype: mesosoma length, 0.60, scape length, 0.41; HM 10/203: head length, 0.52, head width, 0.49, scape length, 0.41.

Remarks. The species has been described based on two specimens, which are not preserved.

Material. Neotype. Other specimens (males): Bitterfeld amber: HM, no. 10/203, HM, no. 16/266-2.

Key to Species of Plagiolepis from Late Eocene Amber of Europe

1. Workers and gynes 2
—Males 5
2. The petiole with a scale. The first gastral s egment is not shorter than the second. The eyes are situated anteriorly of the midlength of sides of the head 3

—The petiole is longer than high, with a node. The first gastral segment is distinctly shorter than the second. The ants are often preserved with their gasters raised straight up. The eyes are situated at the midlength of sides of the head 4

3. The legs and the scape without erect or semierect hairs. The scale of the petiole is narrow, with rounded apex, higher than wide. Body length: workers, 1.4–2.7 mm; gynes, ca. 3 mm. *P. kuenowi* Mayr

—The scape and usually also the legs with semierect hairs. The scale of the petiole is wide, with the upper margin weakly concave. Body length: workers, 1.6–1.8 mm; gynes are unknown *P. squamifera* Mayr

4. The scape and the legs with erect and semierect hairs. The antennae are 11-segmented. Body length: workers, 2.5–3.85 mm; ergatoid gyne, 3.5 mm. *P. klinsmanni* Mayr

—The scape and the legs without erect or semierect. The antennae are 10-segmented. Body length: worker, 2.3 mm; gynes are unknown *P. wheeleri* sp. nov.

5. The petiole with a node. The forewing with closed cell mcu. Body length: ca. 2 mm. *P. paradoxa* sp. nov.

—The petiole with a scale. The forewing without closed cell mcu. 6

6. Body length: ca. 1.5 mm. The upper margin of the scale is slightly concave. The first flagellomere is slightly longer than the second *P. minutissima* Dlussky

—Body length: ca. 2–3 mm. The upper margin of the scale is rounded. The first flagellomere is twice as long as the second *P. solitaria* Mayr

Species of unknown taxonomic position

Plagiolepis succini: Ern. André, 1895

Plagiolepis succini: Ern. André, 1895, pp. 81 and 83 (worker); Handlirsch, 1908, p. 859; Wheeler, 1915, p. 100; Burnham, 1978, p. 113; Bolton, 1995, p. 336; Dlussky, 1997, p. 59.

The species has been described from Baltic amber. The location of the type is unknown to me. Wheeler (1915) did not see this species and only included a translation of the original description. I did not encounter it among examined material either. According to the description, the species is very similar to the recent *Anoplolepis custodiens* (F. Smith). With the exception of *Anoplolepis gracilipes* (F. Smith), which has currently become widespread in anthropogenic landscapes across the entire tropical zone, all representatives of the genus occur in Africa only. This prompted Wheeler (1915) to suggest that perhaps *P. succini* had been described not from Baltic amber, but from African copal. Determination of the generic affinity of this species is currently impossible.

***Plagiolepis singularis* Mayr, 1868**

Plagiolepis singularis: Mayr, 1868, p. 38, Pl. I, fig. 21 (gyne); Dalla Torre, 1893, p. 173; André, 1895, p. 82; Handlirsch, 1908, p. 859; Wheeler, 1915, p. 102; Burnham, 1978, p. 113; Bolton, 1995, p. 336; Dlussky, 1997, p. 59.

The species has been described from Baltic amber based on a single specimen (gyne), which is not preserved. Wheeler found no specimens similar to Mayr's description among the material he examined. I did not encounter this species among the specimens I examined either. Mayr (1868) and Wheeler (1915) correctly believed that this female could not be placed in any of the species described based on workers. The length of that specimen was 5.7 mm, while in all other known recent (Radchenko, 1989, 1996) or fossil species of *Plagiolepis* the body length of gynes does not exceed 4 mm. This led Wheeler to suggest that the specimen could have been a female *Drymomyrmex* Wheeler, 1915. In the latter genus the antennae are also 11-segmented, as in *Plagiolepis*. However, neither the description, nor the drawing corroborate placement of *P. singularis* into that genus. The shape of the petiole in that ant is also unusual. On the drawing, showing the specimen in profile, the petiole has a very thick and high vertical scale, which has its anterior and posterior surfaces parallel, which is completely atypical of *Plagiolepis*. Therefore, determination of the generic affinity of this species is currently impossible.

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