Two New Primitive Ant Genera from the Late Eocene European Ambers

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Two new primitive ant genera from the late Eocene European ambers

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Two extinct genera of ants from the late Eocene (ca. 40 Ma), *Protomyrmica* gen. nov. and *Plesiomyrmex* gen. nov. (family Formicidae, subfamily Myrmicinae), are described based on single specimens (males), from Baltic and Bitterfeld (also called Saxonian) ambers respectively; both genera belong to the tribe Myrmicini. In gross morphology they are similar to modern *Myrmica* but have a series of apomorphies combined with characters that are plesiomorphic not only in the tribe Myrmicini, but also in the subfamily Myrmicinae. The most significant plesiomorphies concern the antennal structure and wing venation of both genera. The antennal scape is short and the funiculus is filiform, having no apical club. Moreover, the antennae of *Protomyrmica* are "sphecoid" with the length of the funicular segments gradually decreasing towards the apex (i.e., the longest is basal, starting from the second, and the shortest is apical); this type of structure is basal for the family Formicidae as a whole. Although we consider the wing venation of *Protomyrmica* to represent the prototype of wings in the subfamily Myrmicinae, it has an apomorphy absent in the modern Myrmicini genera—the antennae are inserted into the head well behind the posterior margin of the clypeus. *Plesiomyrmex* also has a peculiar apomorphy not found in any other genus of Myrmicinae: the antennae are inserted into toruli located on short sub-vertical tube-like or cup-like structures that protrude distinctly above the head surface. As a result, we do not consider either of the newly described genera to be the direct ancestors of modern Myrmicini; nevertheless, the presence of very ancient plesiomorphies may indicate their antiquity, and thus the latest estimated time for the origin of the tribe Myrmicini should be at least the early Eocene.

Key words: Insecta, Hymenoptera, Formicidae, Myrmicinae, evolution, Baltic Amber, Bitterfeld Amber, Eocene.

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Introduction

The ant tribe Myrmicini is considered as the most primitive morphologically in the subfamily Myrmicinae, based on the plesiomorphic states of many features: such as 6-segmented maxillary and 4-segmented labial palps, 11–12-segmented antennae in the female castes and 12–13-segmented antennae in males, the usually well developed pectinate spur on the middle and hind tibiae, the structure of the mesosoma with well defined sutures, etc. It is interesting to notice that this tribe is defined by only plesiomorphic characters and lacks any identifiable morphological apomorphies (e.g., Bolton 2003). Moreover, resulting from one of the modern molecular phylogenetic analysis, the myrmicine genera *Myrmica*, *Manica,* and *Pogonomyrmex* form a sister group to all other Myrmicinae with high support or even "do in fact lie outside the 'core Myrmicinae' (the reminder of the subfamily)" (Brady et al. 2006: 18175). To our opinion, these data may only confirm previous ideas about "primitiveness" of the tribe Myrmicini.

In modern monographs (Bolton 1995, 2003), seven extant genera (*Myrmica*, *Manica*, *Pogonomyrmex*, *Hylomyrma*, *Eutetramorium*, *Huberia*, and *Secostruma*) and one extinct genus (*Nothomyrmica*) were included in this tribe. Recently, *Nothomyrmica* was synonymised with *Myrmica* (Radchenko et al. 2007). Furthermore, a molecular-phylogenetic analysis made very recently by Gunther Jansen (personal communication 2008) suggests that *Eutetramorium* (two species from Madagascar) and *Huberia* (two species from New Zealand) do not form a monophyletic group with the other genera in Myrmicini. While we have no morphological arguments to either support or reject this new idea, it seems quite reasonable from a biogeographical point of view.

The ant fauna of the late Eocene (ca. 40 Ma) European ambers, especially Baltic Amber, is the best studied among all fossil myrmecofaunas worldwide. Currently 119 species belonging to 51 genera are known from the Baltic, Scandinavian, Bitterfeld (also called Saxonian), and Ukrainian (Rovno) ambers (see Dlussky and Radchenko 2006a, b; Radchenko et al. 2007; Dlussky 2008, and literature cited therein). Seventeen ant genera, known from the late Eocene European ambers, belong to the subfamily Myrmicinae, but only *Myrmica* represents tribe Myrmicini.

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In the course of investigation of the ants from late Eocene European ambers, we have found two specimens (males) from the Baltic and Bitterfeld ambers that belong to the tribe Myrmicini, but possess peculiar combinations of plesiomorphic and apomorphic characters. We cannot place them in any known extinct or extant genus, therefore we describe them as two new genera and discuss their taxonomic position and their significance to the understanding of the possible evolutionary trends in the tribe Myrmicini.

Institutional abbreviations.—GZG, Geowissenschaftlicher Zentrum der Georg-August-Universität, Göttingen, Germany (collection of Manfred Kutscher); NHM, The Natural History Museum, London, UK.

Other abbreviations.—AH, height of mesosoma, measured from the upper level of scutum perpendicularly to the level of lower margin of mesopleuron; AL, diagonal length of the mesosoma seen in profile, measured from the anterior-upper margin of pronotum to the posterior margin of propodeal lobes; HL, length of head in full face view, measured in a straight line from the anterior point of median clypeal margin to mid-point of the posterior margin; HW, maximum width of head in full face view behind the eyes; HTL, length of tibia of hind leg; OL, maximum diameter of eye; PH, maximum height of petiole in profile; PL, maximum length of petiole from above from posterodorsal margin of petiole to articulation with propodeum; PW, maximum width of petiole from above; PPH, maximum height of postpetiole in profile; PPL, maximum length of postpetiole from above; PPW, maximum width of postpetiole from above; SCL, maximum length of scutum + scutellum from above; SCW, maximum width of scutum from above; SL, maximum straight-line length of antennal scape seen in profile.

Indices.—AI = AL/AH; CI = HL/HW; HTI = HTL/HL; OI_1 = OL/HL; OI_2 = OL/HW; PI_1 = PL/PH; PI_2 = PL/HW; PI_3 = PW/HW; PPI_1 = PPL/PPH; PPI_2 = PPL/HW; PPI_3 = PPW/HW; PPI_4 = PPW/PW; SCI = SCL/SCW; SI_1 = SL/HL; SI_2 = SL/HW.

For the characteristic of wing venation two indices based the length of several veins were used: Icu = [1Cu+(2M+Cu)]/1Cu; Icua = [(1M+Cu)+(2M+Cu)]/(1M+Cu) (after Dlussky 1981; see also Figs. 1H and 2K).

Material and methods

We investigated two pieces of amber, each containing one male. The piece with *Protomyrmica atavia* is preserved in the BMNH (Baltic Amber), and the piece with *Plesiomyrmex tubulatus* is in GZG (Bitterfeld Amber).

The figures are based on the original drawings of the specimens and photographs made using an Olympus Camedia C-3030 digital camera fitted to an Olympus SZX9 microscope in conjunction with the computer software CorelDraw 8.

The specimens were measured (accurate to 0.01 mm) using a stereomicroscope Leica S6E, and the measurements were used to calculate the various indices (see other abbreviations section). We measured as many features as possible on each specimen, given that not all were easily visible and measurable (see above).

Systematic palaeontology

Family Formicidae Latreille, 1809

Subfamily Myrmicinae Lepeletier, 1835

Tribe Myrmicini Lepeletier, 1835

Genus *Protomyrmica* nov.

Etymology: From Greek "*prôtos*"—primary, initial, and the ant genus *Myrmica*.

Type species: *Protomyrmica atavia* sp. nov., by monotypy.

Diagnosis.—Antennae 13-segmented, without apical club, inserted into the head well behind the posterior margin of the clypeus; scape short, length of funicular segments decreases from the second segment to the apex. Frontal triangle absent (at least not separated from the head surface by sutures). Clypeus relatively long, gradually convex across its width, not inserted posteriorly between frontal lobes, its anterior margin widely rounded, without medial notch. Scutum with Mayrian furrows, propodeum somewhat angulated, with very short blunt tubercles. Middle and hind tibiae with big, distinctly pectinate spur, pretarsal claws simple. Mandibles elongate-triangular, with distinct, quite long masticatory margin, which has six small sharp teeth and long apical tooth; length of mandibles, measured from the outer point of insertion with head to the tip of apical tooth, subequal to head width (that is distinctly longer than in males of modern *Myrmica* species, where length of mandibles is much shorter than the head width). Forewing with closed cells 1+2r, 3r, rm, and mcu. Vein section 1RS is vertical, merging with vein R at a right angle. Cross-vein 2r+rs distinctly declined in respect to vein RS. Cross-vein rs-m is far distal with respect to 2r+rs (vein section 4RS present). Cell rm is pentagonal, reaching distally the level of the pterostigmal apex. Vein section 2+3RS has short fenestra proximally, on flexion line. Cell mcu is pentagonal (the vein section 2M is present) and generally trapezoid, reaching distally the level of the pterostigmal base. Cross-vein cu-a merging with the vein section 1M+Cu close to the cell mcu (vein section 2M+Cu is short, subequal to cross-vein cu-a). Cell cua is absent, vein sections 1Cu and 2Cu forming more or less straight line, section 2Cu does not sharply angulate distally and does not confluent with vein A. Hind wing with vein sections 1M and 2M.

Remarks.—Despite the maxillary and labial palps in the investigated holotype specimen being invisible, based on the general shape of the mesosoma, presence of the Mayrian furrows, the well developed and pectinate spur on the hind tibiae, structure of the antennae and general character of the wing venation we place *Protomyrmica* into tribe Myrmicini.

By the antennal structure, *Protomyrmica* resembles *Manica*, but clearly differs from all other genera of Myrmicini, whose males have funicular segments that gradually increase in their length from the second segment to apex. On the other hand, *Protomyrmica* well differs from all genera of this tribe by the antennal insertions being situated well behind the posterior clypeal margin, and especially by its wing venation (for details see Discussion below).

Protomyrmica atavia sp. nov.

Fig. 1.

Etymology: From Latin *atavus*—ancestor, which means presence of the many primitive morphological features in this species.

Holotype: NHM In. 65422 (the label says: "Königsberg, E Prussia, purchased W. Kuhne, 1971, MNH Paleontol. Dept. In. 65422"), male, complete specimen.

Type locality: Unknown locality in the vicinity of Kalliningrad, Russia formely Königsberg in E Prussia, Germany.

Type horizon: Baltic Amber, late Eocene.

Diagnosis.—As for genus.

Description.—Total length: ca. 4–4.5 mm. The new species is characterised by the following features: head ca. 1.3 times longer than broad, steeply rounded above the eyes, occipital corners not marked. Eyes big, their maximal diameter ca. 2.5 times smaller than length of head, situated somewhat in front of sides of head, genae short, ca. 1.5 times longer than diameter of the scape. Ocelli well developed though not very big. Scape shorter than the length of each of the 2nd to 4th funicular segments. First funicular segment not globular, ca. 1.3 times longer than broad; subsequent segments elongated, cylindrical, apical segment is the shortest, length of the 2nd to 12th funicular segments are 0.28, 0.25, 0.23, 0.20, 0.18, 0.16, 0.15, 0.13, 0.13, 0.13, 0.10 mm. Maxillary and labial palps are invisible. Mesosoma relatively long, scutum slightly convex (seen in profile). Dorsal surface of propodeum declined posteriorly, shorter than its declivitous face, propodeal lobes rounded. Scutum wide (in dorsal view), only ca. 1.25 times longer than length of scutum and scutellum. Shape of petiole and postpetiole barely visible, but petiole seems quite big and massive, with relatively short peduncle, its anterior face not steep and almost straight, node widely rounded dorsally; postpetiole also big and massive, not lower than the petiole, subglobular. Pygidium and genitalia are invisible. Legs quite long and slender. Frontal carinae well developed, quite coarse, running posteriorly approximately to the level of central ocellus; frons additionally with distinct, coarse longitudinal median carina. Head dorsum finely longitudinally striato-rugulose. Scutum and scutellum smooth, mesopleura generally smooth, only partly with very fine short striation; sides of propodeum longitudinally rugulose. Sculpture of petiole and postpetiole barely visible, though they seem to be quite smooth (at least without coarse sculpture). Gaster smooth and shiny. Head and mesosoma with abundant, often very long and curved, fine standing hairs. Legs with long hairs, longest hairs much longer than maximal diameter of leg's segments. Forewing: cell 3r long, more than 5 times longer than wide. Vein section 4RS is about as long as cross-vein rs-m. Vein section 1RS very short, much shorter than the vein section 1M. Cell rm 2.4 times longer than wide. Workers and queens are unknown.

Dimensions and indices.—HL = 0.73, HW = 0.55, SL = 0.20, OL = 0.31, AL = 1.40, AH = 0.75, SCL = 0.78, SCW = 0.63, HTL = 0.85 mm; CI = 1.32, SI_1 = 0.28, SI_2 = 0.36, OI_1 = 0.43, OI_2 = 0.57, AI = 1.87, SCI = 1.24; Icu = 1.4; Icua = 1.17.

Genus *Plesiomyrmex* nov.

Etymology: After Greek *plesios*—close, similar, which means in biological terminology prior, initial, and *myrmecos*—ant.

Type species: *Plesiomyrmex tubulatus* sp. nov., by monotypy.

Diagnosis.—Palp formula 6, 4. Antennae 13-segmented, having no apical club, inserted into head close to the posterior margin of the clypeus, however, the nature of the insertions is unusual: toruli are on the tops of short sub-vertical tube-like or cup-like structures that distinctly project above the head surface; scape very short, shorter than each of the 2nd to 12th funicular segments. The first funicular segment not globular, ca. 1.2 times longer than broad, subsequent segments elongated, ca. 3–3.3 times longer than broad; segment's length somewhat increased from 2nd to 5th, and then their length gradually decreased to the 11th segment, apical one is the longest. Frontal triangle is absent. Clypeus does not insert posteriorly between frontal carinae, its median portion elevated, distinctly raised over level of the rest of clypeal surface (seen in profile). Scutum with Mayrian furrows, propodeum angulated, with very short blunt tubercles. Middle and hind tibiae with a big, distinctly pectinate spur, pretarsal claws simple. Mandibles elongate-triangular, with distinct masticatory margin, which has seven small sharp teeth. Forewing with closed cells 1+2r, rm, and mcu. Cell 3r is opened at the apex. Vein section 1RS is vertical, merging with vein R at a right angle. Cross-vein 2r+rs distinctly declined in respect to vein RS. Cross-veins 2r+rs and rs-m coincide on vein RS (vein section 4RS is absent). Cell rm is triangular (vein section 2M is absent), with distinct short stem. Cell mcu is trapezoid, reaching the level of pterostigmal base. Cross-vein cu-a displaced proximally, so that vein section 2M+Cu is long, much longer than the cross-vein cu-a, as usual in Myrmicinae. Cell cua is absent, vein sections 1Cu and 2Cu forming more or less straight line, section 2Cu does not angulate distally and does not confluent with vein A. Hind wing without vein sections 1M and 2M.

Remarks.—We place *Plesiomyrmex* in the tribe Myrmicini based on the general shape of the mesosoma, the presence of Mayrian furrows on the scutum, 6-segmented maxillary and 4-segmented labial palps, middle and hind tibiae with a well developed pectinate spur, and the antennal structure. However, the wing venation in *Plesiomyrmex* is more primitive than in any known Myrmicini genera (see also Discussion below). *Plesiomyrmex* well differs from all extant genera of Myrmicini by its wing venation, by the structure of funiculus, and by the peculiar character of the antennal insertions.

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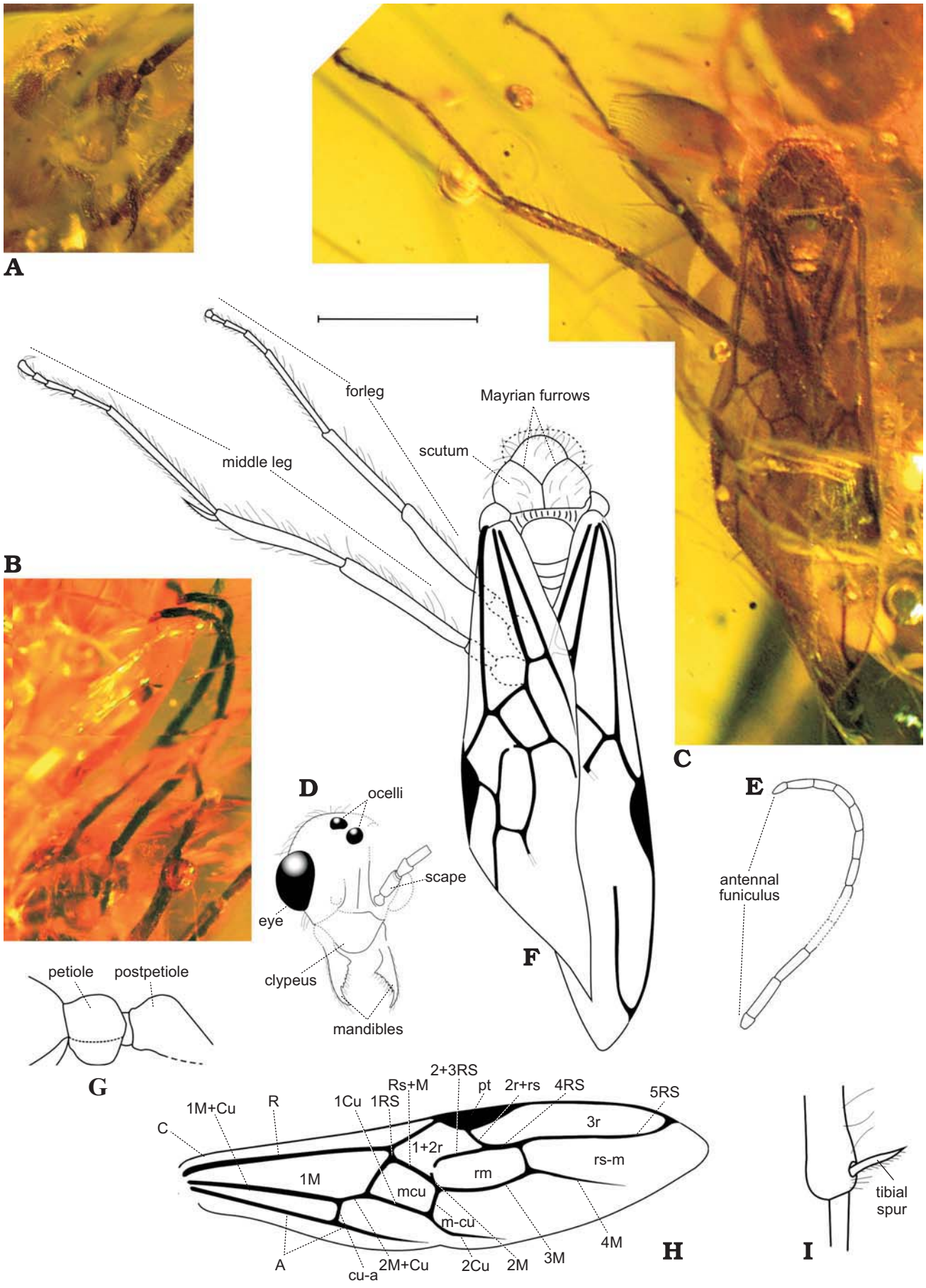

Plesiomyrmex tubulatus sp. nov.

Fig. 2.

Etymology: From Latin *tuba*—tube, which refers to the peculiar character of the antennal insertion.

Holotype: GZG.BST.27.193, male, complete specimen.

Type locality and horizon: Unknown locality in Saxony, Germany.

Type horizon: Bitterfeld Amber, late Eocene.

Diagnosis.—As for genus.

Description.—Total length: ca. 5.2 mm. The new species is characterised by the following features: head length subequal to its width, widely and regularly rounded above the eyes. Clypeus wide and short, its anterior margin slightly convex and very shallowly notched medially, but not bicarinate. Eyes big, their maximal diameter ca. 2.5 times smaller than length of head. Ocelli well developed, big. Lengths of 2nd to 12th funicular segments are 0.24, 0.25, 0.26, 0.28, 0.26, 0.25, 0.25, 0.24, 0.20, 0.20, 0.35 mm. Mesosoma relatively long, scutum slightly convex (seen in profile); dorsal surface of propodeum declined posteriorly, somewhat longer than its declivitous face, propodeal lobes rounded. Scutum not wide, 1.5 times longer than total length of scutum and scutellum. Petiole quite long and low, 1.75 times longer than height, its anterior face not steep, almost straight, so that peduncle does not distinctly separate from widely rounded node; postpetiole subglobular, somewhat longer than its height and higher than petiole. Pygidium convex, without any additional structures, stipes of genitalia wide, not curved, broadly rounded at the apex, with numerous short erect hairs. Cerci are absent. Legs are long and slender. Lower part of frons between antennal insertions with 3 transversal rugulae, frons with longitudinal striation, surface between clypeus and lateral ocelli with semiconcentric rugulae; whole head dorsum additionally with fine superficial reticulation. Scutum and scutellum with fine reticulation. Sculpture of mesopleura, propodeum and waist is barely visible, but seems to be striato-punctated, nevertheless not coarse. Gaster is smooth and shiny. Head margins, scutum and scutellum with quite long, abundant semierect hairs. Petiole with a few standing hairs (those on postpetiole are invisible), gaster with sparse standing hairs. Legs with short subdecumbent pilosity. Forewing: vein section 1RS is much shorter than section 1M. Cells rm and mcu about twice longer than wide. Workers and queens are unknown.

Dimensions and indices.—HL = 0.80, HW = 0.79, SL = 0.18, OL = 0.33, PL = 0.53, PW = 0.25, PH = 0.30, PPL = 0.33, PPW = 0.30, PPH = 0.40, AL = 1.88, AH = 1.40, SCW = 0.85, SCL = 1.28, HTL = 1.23 mm; CI = 1.01, SI_1 = 0.219, SI_2 = 0.222, OI_1 = 0.406, OI_2 = 0.413, PI_1 = 1.75, PI_2 = 0.67, PI_3 = 0.32, PPI_1 = 0.81, PPI_2 = 0.41, PPI_3 = 0.38, PPI_4 = 1.20, AI = 1.34, SCI = 1.51, HTI = 1.53; Icu = 1.7; Icua = 1.5.

Discussion

Protomyrmica and *Plesiomyrmex* by their general appearance are similar to modern species of *Myrmica*. However, both have a series of apomorphies combined with characters that are plesiomorphic not only in the tribe Myrmicini, but also in the subfamily Myrmicinae. These plesiomorphies are 6-segmented maxillary and 4-segmented labial palps (this feature is visible only in *Plesiomyrmex*), well developed and pectinate spur on the middle and hind tibiae, 13-segmented antennae with a short scape but without a developed club, mandibles with the well defined masticatory margin, possessing a set of distinct sharp teeth and a scutum with Mayrian furrows.

On the other hand, there are several structures in both genera forming a mosaic of plesiomorphic and apomorphic characters. Thus, antennal scape is short in both genera (plesiomorphic state), in *Plesiomyrmex* it is even definitely shorter than in *Protomyrmica* (SI_2 = 0.22 versus 0.36), while antennal funiculus in both genera is filiform, having no apical club. *Protomyrmica* has so-called "sphecoid" antennae that are basal for ant males as a whole: the proximal (starting from the second) funicular segments are the longest and their length decreases towards the apex, with the apical segment being the shortest. Such an antennal structure is characteristic for the poneroid genera, and it is known only in the genus *Manica* among Myrmicini.

However, the most remarkable feature of both newly described genera is the wing venation. Brown and Nutting (1950) believed genus *Pogonomyrmex* represents the primary or initial type of the wing venation in the subfamily Myrmicinae: at least in some its species forewings have the most complete set of closed cells (1+2r, 3r, rm, and mcu), found in this subfamily.

Additionally, the cell rm in the most of extant Myrmicinae genera is triangular, but Brown and Nutting (1950) recorded quadrangular cell rm in some *Pogonomyrmex* males. Also Barry Bolton (personal communication 2008) found quadrangular or even pentagonal cell rm in some species of *Myrmica*, *Pogonomyrmex*, *Messor*, and *Aphaenogaster*, and recorded many examples of closed cell 3r in more than 30 Myrmicinae genera. Nevertheless, we believe that forewings with closed cells 1+2r, 3r, rm, and mcu, and with quadrangular cell rm are archaic for Myrmicinae, while are common in the Ponerinae and some other subfamilies preserving primitive morphological traits.

Compared to other Myrmicinae genera, the forewing of *Protomyrmica* seems even more primitive. Its overall pattern of venation is unknown in any Myrmicinae genera, but is quite common in the subfamily Ponerinae. Hence, we propose that the wing of *Protomyrmica* represents the prototype

← Fig. 1. Myrmicine ant *Protomyrmica atavia* gen et sp. nov., the holotype male, NHM In. 65422, from the Baltic Amber, late Eocene. **A**–**C**. Photograph of head in dorso-lateral view (**A**), antennae (**B**), and body in dorsal view (**C**). **D**–**I**. Explanatory drawing, based on the original photographs, head in dorso-lateral view (**D**), antennal funiculus (**E**), body in dorsal view (**F**), petiole and postpetiole in lateral view (**G**), forewing (reconstruction based on the visible feature of the right and left wings) (**H**), and spur of hind tibia (**I**). Scale bar: G and I 0.5 mm; for all others 1 mm.

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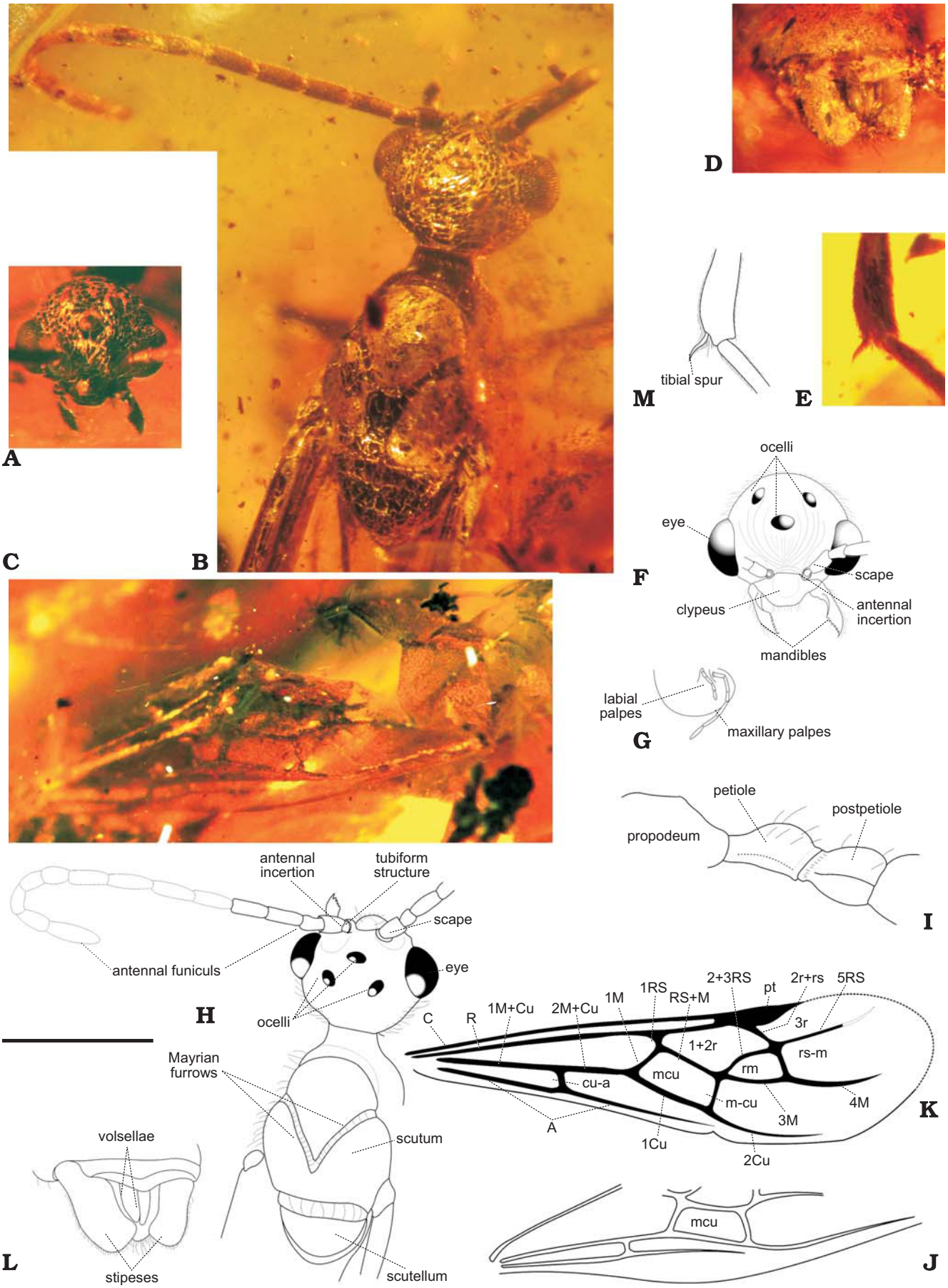

of wings in the subfamily Myrmicinae. We consider the following wing characters of *Protomyrmica* as plesiomorphies:

Cross-veins 2r+rs and rs-m merging with the vein RS on the far distal points, so that vein section 4RS is present; in other Myrmicinae genera they, as a rule, merge with vein RS on the same point and cross-veins 2r+rs and rs-m appear as a single cross-vein (compare Figs. 1H and 2K) (however, there are several examples in *Myrmica*, *Pogonomyrmex*, *Messor*, *Aphaenogaster*, and *Pheidole*, where section 4RS is also present [Barry Bolton, personal communication 2008]).

Cell rm is big and pentagonal, distally reaching the level of the pterostigmal apex.

Cross-vein cu-a lies close to the cell mcu (Icua = 1.17), the length of cu-a subequal to the vein section 2M+Cu. In other Myrmicinae genera cross-vein cu-a is displaced proximally, cu-a much shorter than 2M+Cu. As a result, Icua usually >1.20, while in Ponerinae and other primitive subfamilies it is <1.20.

Cell mcu is placed distally and reaches the level of the base of pterostigma.

Hind wing with free longitudinal median vein and well developed vein sections 1M and 2M.

The wing venation of *Plesiomyrmex* is also rather primitive for the Myrmicinae. However, wings with the similar venation are quite common in the Pheidolini genera (*Pheidole*, *Messor*, many species of *Aphaenogaster*), and among Myrmicini—in *Pogonomyrmex* species. Wing venation of *Plesiomyrmex* could easily arise from the *Pogonomyrmex*-like wing, when the vein RS is reduced distally and cell 3r became open.

Despite the presence of the set of plesiomorphies in the wing venation and antennal structure of *Protomyrmica* and *Plesiomyrmex*, we do not consider either genus to be the direct ancestor of modern Myrmicini genera, because both have peculiar apomorphies not found in any genus of Myrmicinae: e.g., the antennae of *Protomyrmica* that are inserted distinctly behind the posterior clypeal margin, and the toruli of *Plesiomyrmex* that are located on the tops of short subvertical tube-like structures, which distinctly rise above the level of the head surface.

However, the discovery of these extinct genera supports the idea that the Myrmicini had already evolved a rather high diversity of morphological features by the late Eocene. *Protomyrmica* and *Plesiomyrmex* were probably derivates of the ancient, basal stem of this tribe that persisted long enough to co-exist with more modern genera of Myrmicini, such as *Myrmica*. Moreover, the presence of plesiomorphies in *Protomyrmica* and *Plesiomyrmex*, especially in the antennal structure and wing venation that are associated with "old" lineages of ants, suggests that basal stem of the tribe Myrmicini might already had great antiquity. If so, the Myrmicini should already have been well established by the early Eocene.

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← Fig. 2. Myrmicine ant *Plesiomyrmex tubulatus* gen et sp. nov., the holotype male, GZG.BST.27.193, from the Bitterfeld Amber, late Eocene. **A**–**E**. Photograph of head in dorsal view (**A**), mesosoma and head in dorsal view (**B**), right wing (**C**), genitalia in dorso-caudal view (**D**), and spur of hind tibia in lateral view (**E**). **F**–**M**. Explanatory drawings, based on the original photographs, head in dorsal view (**F**), maxillary and labial palpes in ventral view (**G**), mesosoma and head in dorsal view (**H**), propodeum, petiole and postpetiole in lateral view (**I**), part of right forewing (**J**), forewing (reconstruction based on the visible feature of the right and left wings) (**K**), genitalia in dorso-caudal view (**L**), and spur of hind tibia in lateral view (**M**). Scale bar: D, E, G, L, and M 0.5 mm; for all others 1 mm.

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