

Two ants (Insecta: Hymenoptera: Formicidae: Formicinae) from the Late Pliocene of Willershausen, Germany, with a nomenclatural note on the genus *Camponotites*

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Abstract Two species of the genus *Camponotites* (Formicidae, Formicinae) are described from the Late Pliocene deposits of Willershausen, Lower Saxony, northern Germany: *C. silvestris* Steinbach, 1967, and *C. steinbachi* n. sp. The generic name *Camponotites* has been established for fossil (Tertiary) ants independently by Steinbach (Bericht der Naturhistorischen Gesellschaft zu Hannover 111:95–102, 1967) and by Dlussky (Trudy paleontologičeskogo instituta, akademiâ nauk SSSR, 1981), each for materials of different stratigraphical and geographical origin. Though poorly described, *Camponotites* Steinbach, 1967, and the single included (type) species *C. silvestris* Steinbach, 1967 (a monotypic species from the Late Pliocene of Willershausen), were based upon indication in the sense of the ICZN. Therefore, both the generic and specific names are valid and available. *Camponotites*

Dlussky, 1981 (and its type species *C. macropterus* Dlussky, 1981) were certainly introduced correctly and are therefore available, too; but due to its homonymy the generic name is not valid. The revision shows that in this rare case both generic names are not only homonyms but also synonyms.

Keywords *Camponotites* · Formicidae · Hymenoptera · Tertiary · Laurussia · Nomenclature

Kurzfassung Aus Ablagerungen des Ober-Pliozän von Willershausen in Niedersachsen (Norddeutschland) werden zwei Arten von *Camponotites* (Formicidae: Formicinae) behandelt: *C. silvestris* Steinbach, 1967 und *C. steinbachi* n. sp. Der Gattungs-Name *Camponotites* wurde unabhängig voneinander zweimal für fossile (Tertiär-zeitliche) Ameisen aufgestellt: von Steinbach (Bericht der Naturhistorischen Gesellschaft zu Hannover 111:95–102, 1967) und von Dlussky (Trudy paleontologičeskogo instituta, akademiâ nauk SSSR, 1981). Beide Namen fußen auf Funden von unterschiedlicher stratigraphischer und geographischer Herkunft. Obwohl nur unzureichend beschrieben, basieren *Camponotites* Steinbach, 1967 sowie die einzige damals eingeschlossene (Typus-) Art *C. silvestris* Steinbach, 1967 (eine monotypische Art aus dem Ober-Pliozän von Willershausen) auf Indikation im Sinne der IRZN. Sowohl der Gattungs- als auch der Art-Name sind daher verfügbar und gültig. *Camponotites* Dlussky, 1981 [und dessen Typus-Art *C. macropterus* Dlussky, 1981] sind zwar korrekt eingeführt worden und somit ebenfalls verfügbar; der Gattungs-Name ist jedoch wegen Homonymie nicht gültig. Die Revision ergibt den seltenen Fall, dass beide Gattungs-Namen nicht nur homonym, sondern gleichzeitig auch synonym sind.

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Schlüsselwörter *Camponotites* · Formicidae · Hymenoptera · Tertiär · Laurussia · Nomenklatur

Introduction

The present article presents comments on the specimens of two formicine ants (Formicidae, Formicinae) from the Late Pliocene of Willershausen in Lower Saxony, northern Germany, which are deposited in the Geoscience Centre of the University of Göttingen and in the Institute of Geology and Palaeontology, Clausthal University of Technology, Germany. While evaluating the literature concerning this locality for a major revision of its fauna, we discovered the homonymy of the generic names *Camponotites* Steinbach, 1967, and *Camponotites* Dlussky, 1981, for fossil ants.

Since the first geological description by Wegele (1914), the now abandoned clay pit of Willershausen has been internationally well-known as an important konservat-lagerstätte for both the exceptional perfect preservation of the fossils and for its unusual young stratigraphic age, close to the end of the Neogene period (Meischner 2000). As already listed by Straus (1979) and Krüger (1979), the fossils include diverse algae, fungi, lichens, many terrestrial plants (mainly leaves), and animals including Bivalvia, Gastropoda, Annelida, Arachnida, Insecta, Crustacea, Teleostei, Amphibia, Reptilia, Aves and Mammalia. More than 500 described species have hitherto been distinguished. Most abundant are leaves and insects. Plant/animal interactions are documented by a large number of galls, mines, and foliage damage by feeding activities. The exceptional importance of the Willershausen site is also mentioned in modern text books on palaeoentomology as, for example, in Rasnitsyn and Quicke (2002: 443).

Most of the insects have been described by several authors in two special “Willershausen” issues of the *Berichte der Naturhistorischen Gesellschaft zu Hannover* (Hiltermann and Gersdorf 1967; Hiltermann and Zobel 1969) as well as in Beiheft 6 of the same series (Gersdorf and Hiltermann 1968), that is to say in a less-known regional scientific journal. Therefore, it is no wonder that these contributions were often overlooked by subsequent authors and are absent in Bolton’s Catalogues (1994, 1995, 2003). Although Carpenter (1992: 602) cited Steinbach (under the incorrect spelling “Steinback”), he did not mention his “*Camponotites*”, but only *Camponotites* Dlussky, 1981. Since some of the authors were amateur scientists while others were profound specialists, the quality of the descriptions varies extremely. In particular, the rules of the International Code of Zoological Nomenclature (ICZN) were evidently unknown to some authors.

This fact sometimes produced imperfection within the descriptions [see for example the comments in Brauckmann et al. (2001) concerning the Lepidoptera]. After a few decades of less scientific activities on Willershausen insects, during the last few years, a new interest in these fossils seems to have arisen (see Brauckmann et al. 2001; Brauckmann and Gröning 2002; Popov 2007).

The fossil Hymenoptera were first studied by Steinbach (1967), who in fact was a specialist on Recent Hymenoptera, but unfortunately shared with other authors on Willershausen fossils the lack of knowledge of the ICZN as well as of taphonomic processes during fossilisation. His descriptions are often only a documentation of the preservation of an individual specimen, but lack diagnostic characters (except for certain measurements). Since he did not include drawings, it is often very difficult to follow his descriptions. Like *Camponotites silvestris* Steinbach, 1967, all the other taxa of the Late Pliocene Hymenoptera from Willershausen distinguished by this author need to be revised.

As compiled by Meischner (2000), many details are now known concerning the konservat-lagerstätte of Willershausen, its development, taphonomy, and hydrography. The Late Pliocene sediments were deposited in a pond which had its origin in a collapse sink of about 10 m depth in a strongly disturbed sequence of the Middle Buntsandstein (= Early Triassic) above subroded salt of the Late Permian Zechstein. Most important climate indicators are the plant remains and the insects. Among the plants there are species which live in disjunct areas in south-eastern Asia and North America today, but the flora and the insect fauna also include species which indicate a warmer climate as in the Mediterranean area and northern Africa. Also controversially discussed is the reconstruction of the landscape of the surroundings. Here, two interpretations are still rivalling: an open, park-like shrub-land vs. a dense, well-stratified forest. Meischner (2000: 227) assumes a continental climate with short but warm and dry summers, cold and dry winters and short transitional periods.

As discussed in Brauckmann and Gröning (2002), for example, the Late Pliocene age of the Willershausen sediments is largely confirmed by Mammalia such as *Mastodon arvernensis* and remains of Cervidae, but also by microfloral components (Mohr 1986).

In 2007, one of us (G.M.D.) registered 111 fossil imprints of ants from Willershausen in the Goettingen collection: 40 *Camponotites* spp., 51 *Lasius* sp., 14 *Aphaenogaster* sp., and 6 Formicidae incertae sedis (fragments of bodies without wings). *Camponotites* species are similar to the recent *Camponotus*, which live in trees. Most of the recent European *Aphaenogaster* forage in the forest litter.

Terminology

The nomenclature of the wing venation (Fig. 1) follows Rasnitsyn (1980), Dlussky et al. (2008), and Dlussky (2009). A detailed modern terminology of the head and body characters accepted by most of the myrmecologists was recently presented by Bolton (1994).

All the drawings illustrate actual specimens and were prepared by tracing over photographs. Solid lines trace visible boundaries of sclerites, dotted lines show boundaries of preserved imprint, which are not sclerite boundaries, and dashed lines are supposed sclerite boundaries. In the case when both part and counterpart fossil are available (*C. steinbachi*), a drawing based on the better preserved part is completed with details better preserved on the counterpart.

Systematic palaeontology

Institutional abbreviations GZG.W: Geoscience Centre, Georg-August University of Göttingen, Germany; Willershausen collection (Reich 2008); TU Cl P: Clausthal University of Technology, Germany; Palaeontological collection.

Familia **Formicidae** Latreille, 1802

Subfamilia **Formicinae** Latreille, 1802

Remarks In spite of the fact that *Camponotites* Steinbach, 1967, is habitually similar to *Camponotus*, we cannot formally assign it to the tribe Camponotini because the diagnostic characters of the Camponotini are not visible on the impression. *Camponotites* as used in the present article

is a formal genus (morphogenus) which presumably covers taxa of the tribes Camponotini, Oecophyllini, Plagioplepini, Melophorini and partially Lasiini; therefore it also cannot be assigned to the Camponotini.

Genus *Camponotites* Steinbach, 1967

1967 *Camponotites* Steinbach: 101

1979 *Camponotites*. —Krüger: 406

1981 *Camponotites* Dlussky: 76. syn. nov.

1990 *Camponotites*. —Hölldobler and Wilson: 76 [*sensu* Dlussky 1981]. syn. nov.

1992 *Camponotites*. —Carpenter: 491 [*sensu* Dlussky 1981]. syn. nov.

1994 *Camponotites*. —Bolton: 50 [*sensu* Dlussky 1981]. syn. nov.

1995 *Camponotites*. —Bolton: 23, 83 [*sensu* Dlussky 1981]. syn. nov.

1999 *Camponotites*. —Dlussky and Rasnitsyn: 547 [*sensu* Dlussky 1981]. syn. nov.

2000 *Camponotites*. —Archibald and Mathewes: 1451 [*sensu* Dlussky 1981]. syn. nov.

2002 *Camponotites*. —Dlussky and Rasnitsyn: 418 [*sensu* Dlussky 1981]. syn. nov.

2003 *Camponotites*. —Bolton: 112 [*sensu* Dlussky 1981]. syn. nov.

2003 *Camponotites*. —Fernández: 376 [*sensu* Dlussky 1981]. syn. nov.

Type species *C. silvestris* Steinbach, 1967; Late Pliocene; Willershausen, Lower Saxony, northern Germany.

Diagnosis Impression fossils with *Camponotus*-like forewing venation, which cannot be identified to a genus. Forewing with closed cells 1 + 2r and 3r; cells rm and mcu absent; crossvein r-m absent, and RS5 and M4 branch off

Fig. 1 Wings of the extant *C. saxatilis* Ruzsky with the terminology of the wing venation

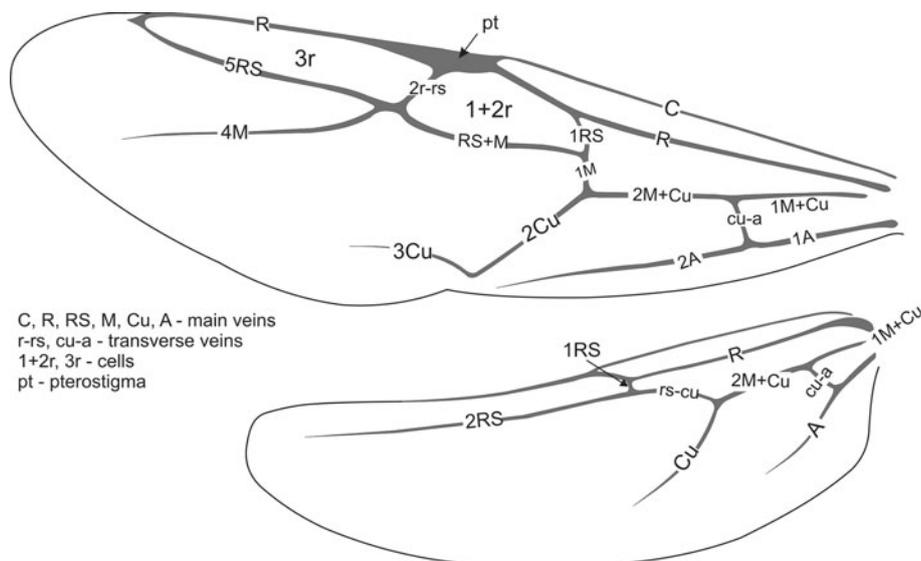
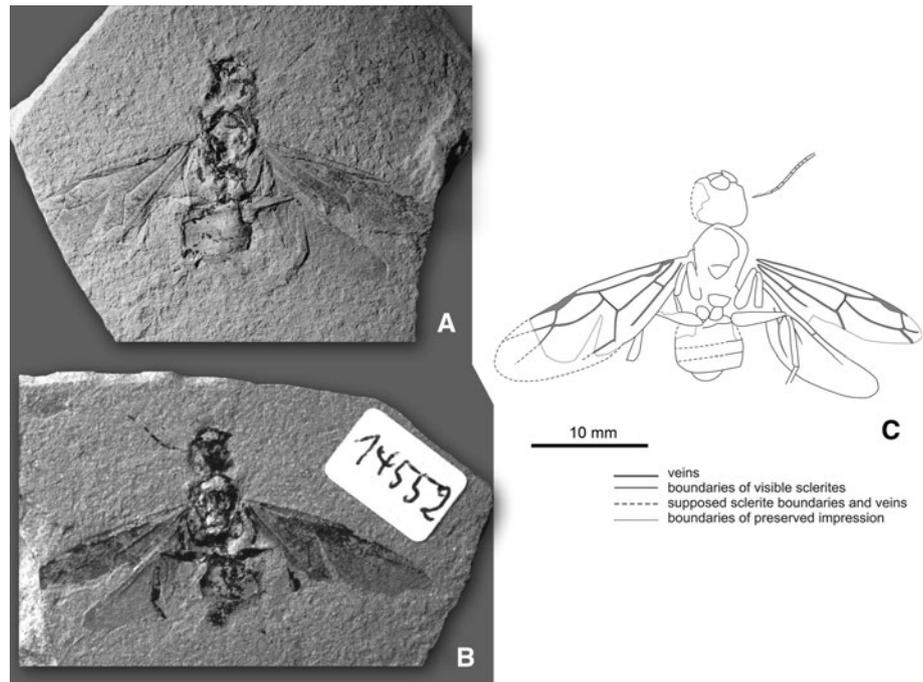


Fig. 2 *Camponotites silvestris* Steinbach, 1967, holotype specimen, gyne (GZG.W.14552a+b); Late Pliocene, Willershausen, Lower Saxony, northern Germany. **a** Photograph of the negative part, **b** photograph of the positive part, **c** drawing



from the same point; crossvein cu-a meeting M + Cu proximal to the junction of 1M and 1Cu for distance subequal to or longer than cu-a long.

Composition *C. silvestris* Steinbach, 1967, and *C. steinbachi* n. sp., described below; both Late Pliocene; Willershausen, Lower Saxony, northern Germany. *C. macropterus* (Dlussky, 1981), new comb.; Middle Miocene: Late Tchokrakian (East Paratethian regional stage of the Neogene period); Vishnevaya Balka near Stavropol, Central North Caucasus, southern European Russia. *C. kraussei* (Dlussky and Rasnitsyn, 1999), new comb.; early Middle Eocene: Klondike Mountain Formation; Golden Promise Mine near Republic, WA, USA [according to Archibald and Mathewes (2000: 1451), their specimens of “Type A” from the Early Eocene of Quilchena, BC, Canada, are similar to this species].

Nomenclatural notes The one and only reference by Steinbach (1967) to generic features of *C. silvestris* is the brief sentence: “Das Flügelgeäder ist gattungstypisch” (=“the venation is typical for the genus”—without exact reference to a particular genus: *Camponotus* or *Camponotites*?), and without further details.

Steinbach (1967: 101) created his generic name *Camponotites* (with the single and monotypic type species *C. silvestris* Steinbach, 1967, from the Late Pliocene of Willershausen) based upon indication [in accordance with Kraus (2000: Artikel 13 and Artikel 12.2.7); here deliberately cited from the official German translation]. As a “description” of this specimen, he mainly pointed out a

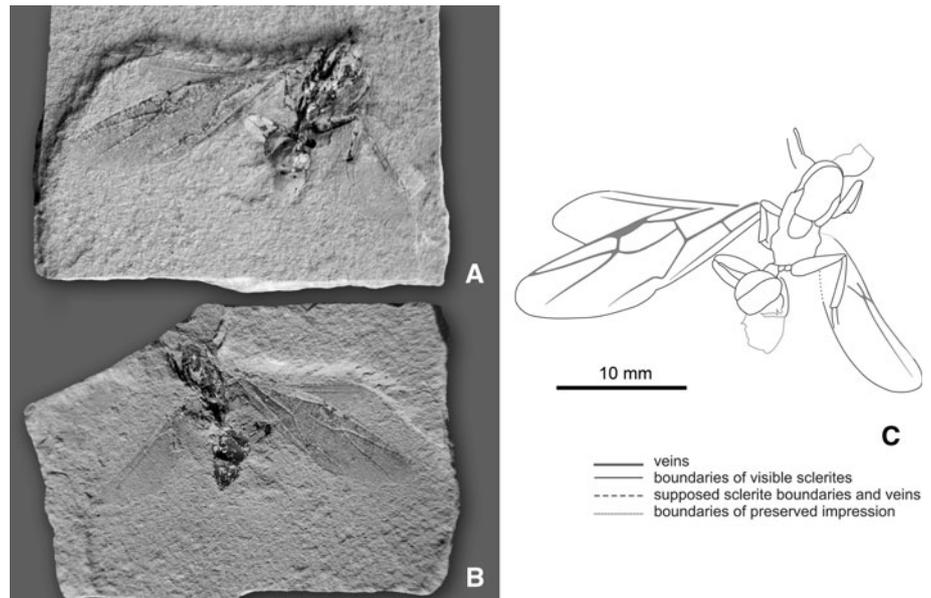
few details of its preservation, accompanied by some measurements—the only characters which can be used as formal combined diagnostic features of the genus and species [in accordance with Kraus (2000: Article 13.4)]. Though poorly described, both the generic and specific names are therefore valid and are available.

Dlussky (1981) independently established the generic name *Camponotites* (with its type species *C. macropterus* Dlussky, 1981) as a formal genus (morphogenus, “collective group”), which is subsequently repeated by Dlussky and Rasnitsyn (2002: 418). Since the author (Dlussky 1981: 76) added a formal and appropriate diagnosis, *Camponotites* Dlussky, 1981, is introduced correctly and therefore available, too. This may be the reason why Carpenter (1992) accepted this generic name. But due to its homonymy, the generic name is not valid under this authorship. As shown by this revision, the genus *Camponotites* also covers the stratigraphically older species *C. macropterus* Dlussky, 1981, and *C. kraussei* Dlussky and Rasnitsyn, 1999. Therefore, *Camponotites* Steinbach, 1967, and *Camponotites* Dlussky, 1981, are not only homonyms but simultaneously subjective synonyms—a rare case in palaeontology.

***Camponotites silvestris* Steinbach, 1967 (Fig. 2)**
v * 1967 *C. silvestris* Steinbach: 101, Fig. 7.
1979 *C. silvestris*. —Krüger: 406.

Holotype (by monotypy) Winged gyne (specimen GZG.W.14552), deposited in the Geoscience Centre,

Fig. 3 *C. steinbachi* n. sp., “Clausthal specimen” (TU Cl P In 191); Late Pliocene, Willershausen, Lower Saxony, northern Germany. **a** Photograph of positive part, **b** photograph of negative part, **c** drawing (combination of positive and negative part)



University of Göttingen, Germany. Originally both the positive and the negative part were collected. The positive part (Fig. 2b) seems now to be missing.

Locus typicus Abandoned clay pit of Willershausen below the western slope of the Harz Mountains, Lower Saxony, northern Germany.

Stratum typicum Late Pliocene.

Distribution Only known from the stratum typicum and the locus typicus.

Preservation Ventral impression, but on the anterior part of mesosoma the boundaries of the scutum and the scutellum are visible from inside. The following are preserved: head + mesosoma + petiole + gaster, with fore-wings and left hind-wing. The distal parts of both fore-wings are absent. The left antenna is documented by the distal part of its scape and eight funicular joints. The fore-legs are lacking, the middle and posterior pair of legs are documented only by femora and tibiae, only the left hind-leg and the right leg additionally show the first segment of the tarsus. The gaster is complete: the rounded terminal segment is distinctly visible; the gaster only seemingly looks so short because it is longitudinally compressed.

Description Winged gyne. Head sub-quadrate, with rounded occipital angles. Mandibles massive, triangulate, with blunt teeth on the masticatory angle (visible on the right mandible). Scape slightly protrudes beyond the occipital margin of the head. Funicular joints longer than thick. Mesosoma robust, about 1.5 times longer than wide. Scutum about as long as wide. Scutellum 1.5 times wider than long. Hind coxae pull together and adjoin. First gastral segment shorter than wide. Distal parts of both fore-wings

are absent, however, section 5RS seems to be straight. Pterostigma rather long and narrow, asymmetrical, with proximal part longer than distal part. Cell 1 + 2r 2.5–3 times as long as wide. Section 1M 2.3–2.4 times as long as 1RS. 1M + Cu, and 1A + 2A straight; 2Cu long, nearly straight. Section 2M + Cu 4–5 times as long as crossvein cu-a.

Measurements (in mm) Length of head + mesosoma = 12; width of mesosoma between the wings = 4.5; length of gaster = 7; preserved right fore-wing: length = 20, maximum width = 6; left hind-wing: length = 15, maximum width = 4.

Comparison *C. silvestris* differs from *C. macropterus* and *C. kraussei* by the proportions of 1RS and 1M (they are equal in both species) and the form of 5RS (it is distinctly curved toward the anterior wing margin in both species) (Fig. 4a). Furthermore, *C. kraussei* has a more elongate head without distinctive occipital corners.

Camponotites steinbachi Dlussky, Karl and Brauckmann n. sp. (Fig. 3)

Etymology After Gerhard Steinbach, author of the first contribution of the Late Pliocene Hymenoptera of Willershausen.

Holotype “Clausthal specimen”, winged gyne (specimen TU Cl P In 191; Fuhrmann collection, Clausthal University of Technology).

Locus typicus Abandoned clay pit of Willershausen below the western slope of the Harz Mountains, Lower Saxony, northern Germany.

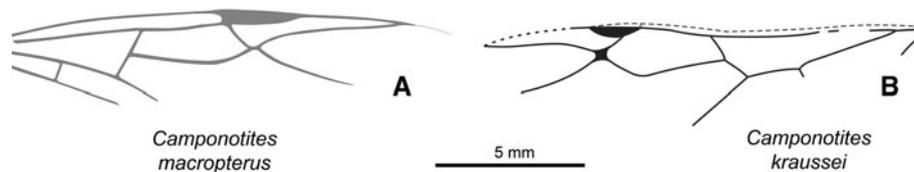


Fig. 4 Fore-wings of other fossil species of *Camponotites*. **a** *C. macropterus* (Dlussky, 1981), new comb., holotype, right fore-wing, new drawing; Middle Miocene, Late Tchokrakian (East Paratethian regional stage of the Neogene period), Vishnevaya Balka near Stavropol, Central North Caucasus, southern European Russia (modified from Dlussky 1981: 76, Fig. 53e; length = 16.8 mm), **b** *Camponotites kraussei*

(Dlussky and Rasnitsyn, 1999), new comb., holotype, left fore-wing, new drawing; early Middle Eocene, Klondike Mountain Formation, Golden Promise Mine near Republic, WA, USA (modified from Dlussky and Rasnitsyn 1999, pp. 547–548, Fig. 2; preserved length = 14.8 mm)

Stratum typicum Late Pliocene.

Distribution Only known from the stratum typicum and the locus typicus.

Preservation Fragment of head + mesosoma + anterior fragment of gaster, with left fore-wing and both hind-wings; anterior part of left hind-wing covered by left fore-wing, visible part lying closely in front of fore-wing; venation of right hind-wing incompletely preserved. Left middle and hind legs, partly covered by body; right fore femur and hind femur and tibia.

Description Winged gyne. Mesosoma elongate, about 2.5 times longer than wide. Scutum 1.8 times longer than wide. Scutellum nearly as long as wide. First gastral segment shorter than wide. Fore-wing 3.3 times as long as wide, apex narrow, nearly pointed, asymmetrical, close to the anterior margin; indentation of the posterior margin (at distal ends of 2Cu and 2A) nearly at mid-wing. Pterostigma nearly at mid-wing, rather long and narrow, asymmetrical, with proximal part longer than distal part. Cell 3r long and narrow, 6.5 times as long as wide. Section 5RS nearly straight. Cell 1 + 2r 2.8 times as long as wide. Section 1M 1.7 times as long as 1RS. 3Cu moderately and asymmetrically curved; 1M + Cu, and 1A + 2A straight; 2Cu long, nearly straight, ending at posterior margin in a relatively narrow angle; claval fold distinctly marked. Section 2M+ Cu 2.9 times as long than cross-vein cu-a.

Measurements (in mm, approximately) Length of mesosoma = 9.1, preserved length of fore-wing = 20.5, estimated total length of fore-wing = 22–23, length of hind-wing = 14.3, length of hind femur = 4.3, length of hind tibia = 4.2.

Comparison The new species differs from *C. silvestris* by its more elongated mesosoma. The fore-wing venation in general is similar to *C. silvestris*, but it differs in some details: proportion of 1RS and 1M, more distal position of cu-a and maybe in the shape of 3r.

Discussion

Both described species are habitually similar to the extant species of *Camponotus* Mayr, a usual component of the recent entomofauna in Europe. However the key characters of *Camponotus* are not visible in imprints, therefore we prefer to include them in the formal genus *Camponotites*. As already expressed for the Late Pliocene Lepidoptera and Cicadidae (Brauckmann et al. 2001 and Brauckmann and Gröning 2002, respectively), it is extremely difficult to decide whether such stratigraphically young fossil insects can be grouped with Recent species or if they should be separated. The only comparable characters are usually restricted to the venation of the wings; but in most cases, these characters are not sufficient for an exact specific determination. Additionally, the infraspecific variation is often poorly known. However, in this case we can assume with sufficient confidence that *C. silvestris* and *C. steinbachi* are not conspecific with any of modern species of *Camponotus*. They are larger than any of the modern *Camponotus* of the Palaearctic region. The fore-wing length of gynes of the largest modern species [*Camponotus herculeanus* (L.), *C. saxatilis* Ruzsky, *C. xerxes* Forel, etc.] is 13–16 mm, whereas the fore-wing length of *Camponotites silvestris*, judging from the single fragment, was more than 19 mm and the fore-wing length of *C. steinbachi* was about 22–23 mm.

The only characters for distinguishing *C. silvestris* from the other described fossil species of *Camponotites* (*C. macropterus* and *C. kraussei*) are the different proportions of 1RS and 1M and the straight (not curved) 5RS, which are not sufficient generic features. Therefore, we prefer to extend the genus *Camponotites* Steinbach to include the hitherto distinguished species of *Camponotites sensu* Dlussky. In this case the diagnosis as used by Dlussky (1981) and Dlussky and Rasnitsyn (2002) becomes relevant for the whole genus. This also creates the rare situation in which two homonyms subsequently also become synonyms.

Judging from the only comparable wing venation, *C. macropterus* (Fig. 4a) and *C. kraussei* (Fig. 4b) undoubtedly present different species and maybe even different genera. However, the poor preservation of the imprints does not allow a precise definition of a new genus for the two latter species. That is the reason why we include them in *Camponotites* Steinbach.

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