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A new genus of myrmicine ant (Hymenoptera: Formicidae) from Eocene Baltic amber

*Un nouveau genre de fourmi Myrmicinae (Hymenoptera : Formicidae) dans l'ambre éocène balte*Cédric Chény^{a,b}, Bo Wang^a, Vincent Perrichot^{b,*}^a State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China^b Université de Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France

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ABSTRACT

Examination of fossil ant specimens from various private and institutional German collections of Baltic amber has revealed a new genus and species of Myrmicinae, described here as *Thanacomymex hoffeinsorum* gen. et sp. nov. The new worker morphotype shares some similarities with the coeval extinct genus *Parameranoplus* Wheeler, also from Baltic amber, and the extant genera *Pristomyrmex* Mayr and *Acanthomyrmex* Emery, suggesting placement of the new fossil in the *Myrmecina* genus-group within the tribe Crematogastrini. The new genus highlights the tremendous diversity of ants that evolved in the Palaeogene European forests and composed the first major radiation of crown-group ants.

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R É S U M É

L'examen de fourmis fossiles dans diverses collections privées et institutionnelles allemandes d'ambre balte a révélé un nouveau genre et une nouvelle espèce de Myrmicinae, décrits ici comme *Thanacomymex hoffeinsorum* gen. et sp. nov. Ce nouveau morphotype d'ouvrière partage des similitudes avec le genre éteint *Parameranoplus* Wheeler, également connu de l'ambre balte, et les genres actuels *Pristomyrmex* Mayr et *Acanthomyrmex* Emery, suggérant le placement du nouveau fossile dans le groupe de genres *Myrmecina*, parmi la tribu Crematogastrini. Le nouveau genre souligne la grande diversité de fourmis ayant évolué dans les forêts paléogènes d'Europe et constituant la première radiation majeure du groupe couronne des fourmis.

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* Corresponding author. Géosciences Rennes, Campus de Beaulieu, bât. 15, 263, avenue du Général-Leclerc, 35042 Rennes cedex, France.
E-mail address: vincent.perrichot@univ-rennes1.fr (V. Perrichot).

1. Introduction

The hyperdiverse Myrmicinae is the most speciose subfamily of ants today, composing nearly half of the 13,501 extant valid species (Bolton, 2019). A first major burst of diversification of this subfamily is recorded during the Eocene, 56 to 34 million years ago, and myrmecines were already slightly dominant over the remaining myrmecofauna by the end of this period, composing nearly 30% of the total ant species known for the Late Eocene (Fig. 1). The rise to dominance of the Myrmicinae was thus remarkably fast given their relatively short history compared to the entire Formicidae: molecular phylogenetic studies estimate that crown-group myrmecines originated in the Late Cretaceous, between 73 and 98.6 Ma (age estimates given as “mean values”) or even in the Cenozoic, around 61 Ma (Borowiec et al., 2019; Brady et al., 2014; Moreau and Bell, 2013; Schmidt, 2013; Ward et al., 2015). And the major extant clades should be considerably younger, with age estimates ranging from 52 to 71 Ma (Ward et al., 2015). These estimates are more or less consistent with the fossil record: the earliest representatives of extant myrmecine genera have been described from the Middle Eocene Kishenehn Formation (ca. 46 Ma) of Montana and Sakhalin amber (43–47 Ma), as *Crematogaster aurora* and *Aphaenogaster dluskyana*, respectively (LaPolla and Greenwalt, 2015; Radchenko and Perkovsky, 2016). Earlier specimens described from Chinese Fushun amber (50–53 Ma) were all assigned to extinct genera (Hong, 2002) but a revision of this material is needed. Eocene myrmecines have also been reported, but remain undescribed, from French Oise amber (ca. 53 Ma), Indian Cambay amber (50–52 Ma), and Canadian Hat Creek amber (ca. 52 Ma) (Archibald et al., 2018; Aria et al., 2011; Rust et al., 2010). Definitive myrmecines are yet unknown prior to the Early Eocene.

Baltic amber, here taken in its broad sense including Rovno, Saxonian, and Scandinavian ambers, offers the largest diversity of Myrmicinae from the Eocene (Fig. 1: 60 out of 92 myrmecine species known worldwide). But even after nearly two centuries since the first description of Baltic amber ants by Presl (1822), the discovery of unknown morphotypes in this famous deposit remains possible, as exemplified by the new genus described herein.

2. Material and methods

2.1. Origin and age of the amber

The new taxon is based on a unique specimen found in the Baltic amber collection of Christel and Hans-Werner Hoffeins (Hamburg, Germany). Baltic amber deposits derive from a wide geographical area along the shores of the Baltic Sea, and even encompass the shores of eastern England and Scotland in their widest acceptance. The main deposits, however, are found on or near the shores of eastern Baltic Sea, particularly on the Samland Peninsula. Unfortunately, the exact provenance of pieces of Baltic amber is rarely documented in collections, so is the case of the piece containing the specimen described herein. Baltic amber predominantly occurs in the Blue Earth Formation (or Blue Earth member of the Prussian Formation), which

was dated as late Bartonian to Priabonian (Upper Eocene, ca. 34–38 Ma) based on palynological data (Aleksandrova and Zaporozhets, 2008; Kosmoswska-Ceranowicz et al., 1997). An older Lutetian age (ca. 41–48 Ma) of the Blue Earth Formation was suggested by Ritzkowski (1997) based on the dating of its glauconite content, but this method can give overestimated ages (Clauer et al., 2005). Smaller amounts of amber also occur in the older Lower Blue Earth Formation (Lutetian) as well as in younger Oligocene sediments. However, Oligocene amber may correspond to redeposited Eocene material (Standke, 2008). In the recent years, several studies have emphasized the similarities and differences between Baltic, Rovno, and Bitterfeld ambers based on shared arthropod and plant species as well as similar $\delta^{13}\text{C}$ signatures, suggesting a close age for these three ambers (Dlussky and Rasnitsyn, 2009; Dunlop et al., 2018; Mänd et al., 2018; Perkovsky, 2018; Perkovsky et al., 2010; Tolkantiz and Perkovsky, 2018). However, Bitterfeld amber is found in a late Oligocene stratum (23.8–25.3 Ma) and there is a continuing debate on whether it is truly Oligocene or late Eocene in age, but an older Eocene age seems excluded (Dunlop et al., 2018; Schmidt and Dörfelt, 2007; Standke, 2008; Wimmer et al., 2008). Altogether, this converges toward a rather late Eocene age for most of the fossiliferous Baltic amber (i.e. that from the Blue Earth layers), leading to an estimated age range of 34 to 38 Ma (Priabonian), which is adopted here, although an older Lutetian age cannot be excluded for at least some amber pieces. Further discussions on the age, geological setting, and paleobiota of Baltic amber can be found in Weitschat and Wichard (2010) and Sadowski et al. (2017).

2.2. Preparation and study of the fossil

The amber piece has been polished, then encased in a block of polyester resin (see detailed method in Hoffeins, 2001). This block has been further polished to facilitate the dorsal view of the ant, and is now measuring $18 \times 12 \times 7$ mm. The ant is exquisitely preserved, although missing the right antenna, right foreleg, left mid and hind legs as well as the apical tarsomeres of all legs. It is preserved with a mite, two ant eggs, and several plant debris including stellate hairs as syninclusions.

Observations, measurements, and photographs were made using a Leica MZ APO stereomicroscope equipped with an ocular micrometer and a Canon 5D Mark II camera. Helicon Focus 6.7 software was used to build composite images from a series of photographs taken at different focal planes. Images and specimen data will be available on AntWeb (<http://www.antweb.org/>) upon publication of the present manuscript.

2.3. Abbreviations used

The measurements and indices used in this study follow Hita Garcia et al. (2017).

EL = Eye length: maximum diameter of the compound eye measured in oblique lateral view (Fig. 2A).

HL = Head length: maximum distance from the midpoint of the anterior clypeal margin to the midpoint of the

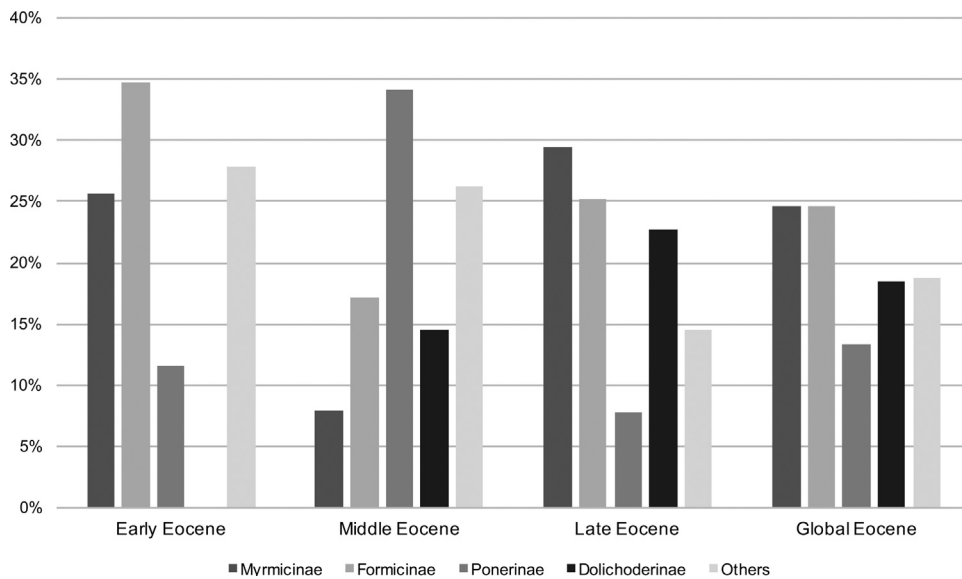


Fig. 1. Relative proportions among described species of the main four subfamilies of ants as recorded in the Eocene, highlighting the rise to dominance of the Myrmicinae. Data compiled from the species list of the fossil ants of the world available at <https://www.antweb.org/> (accessed 10 January 2019). Early Eocene refers to Ypresian records; Middle Eocene refers to Lutetian–Bartonian records; and Late Eocene refers to Priabonian records.

Fig. 1. Proportions relatives des espèces décrites dans les quatre principales sous-familles de fourmis pour l'Éocène, illustrant la dominance progressive des Myrmicinae. Données issues de la liste des espèces de fourmis fossiles du monde, accessible à <https://www.antweb.org/> (consultée le 10 janvier 2019). L'Éocène inférieur comprend les données de l'Yprésien, l'Éocène moyen celles du Lutétien–Bartonian et l'Éocène supérieur celles du Priabonien.

posterior margin of the head, measured in full-face view (Fig. 2B).

HW = Head width: maximum head width measured directly behind the eyes in full-face view (Fig. 2B).

PDL = Peduncular length: length of the petiolar peduncle visible from the propodeal lobes to the anterior limit of the node, in dorsal view (Fig. 2D).

PH = Pronotal height: maximum height of the pronotum measured in lateral view (Fig. 2A).

PL = Petiolar length: maximum median length of the petiole measured in dorsal view, from the propodeum to the postpetiole (Fig. 2D). In details: PL = PDL + PTL + the remaining distance from the posterodorsal angle of the petiolar node to the anterior edge of the postpetiole.

PPH = Postpetiole height: maximum height of the postpetiole measured in lateral view (Fig. 2A).

PPL = Postpetiole length: maximum length of the postpetiole measured in dorsal view (Fig. 2D).

PPW = Postpetiole width: maximum width of the postpetiole measured in dorsal view (Fig. 2D).

PTH = Petiolar node height: maximum height of the petiolar node measured in lateral view from the highest median point of the node to the ventral outline. The measuring line is positioned at an orthogonal angle to the ventral outline of the node (Fig. 2A).

PTL = Petiolar node length: maximum length of the dorsal face of the petiolar node from the anterodorsal to the posterodorsal angle, measured in dorsal view and excluding the peduncle (Fig. 2D).

PTW = Petiolar node width: maximum width of the dorsal face of the petiolar node measured in dorsal view (Fig. 2D).

PW = Pronotal width: maximum width of the pronotum measured in dorsal view (Fig. 2C).

SL = Scape length: maximum straight-line length of the scape, excluding the antennal condyle [= antennal bulb + neck] (Fig. 2B).

WL = Weber's length: diagonal length of the mesosoma in lateral view from the anterior-most point of pronotal slope (excluding the collar) to the posteriormost extension of propodeal lobes (Fig. 2A).

TL = Total body length (excluding the sting) = HL + WL + PL + PPL + gaster length.

CI = Cephalic index: $HW/HL \times 100$.

SI = Scape index: $SL/HW \times 100$.

OI = Ocular index: $EL/HW \times 100$.

DMI = Dorsal mesosoma index: $PW/WL \times 100$.

LMI = Lateral mesosoma index: $PH/WL \times 100$.

LPeI = Lateral petiole index: $PTL/PTH \times 100$.

DPeI = Dorsal petiole index: $PTW/PTL \times 100$.

LPpI = Lateral postpetiole index: $PPL/PPH \times 100$.

DPpI = Dorsal postpetiole index: $PPW/PPL \times 100$.

PPI = Postpetiole index: $PPW/PTW \times 100$.

PTI = Petiolar index: $PTH/PTL \times 100$.

3. Systematic palaeontology

Class Insecta [Linnaeus, 1758](#)

Order Hymenoptera [Linnaeus, 1758](#)

Family Formicidae [Latreille, 1809](#)

Subfamily Myrmicinae [Lepeletier de Saint-Fargeau, 1835](#)

Genus *Thanacomymex* gen. nov.

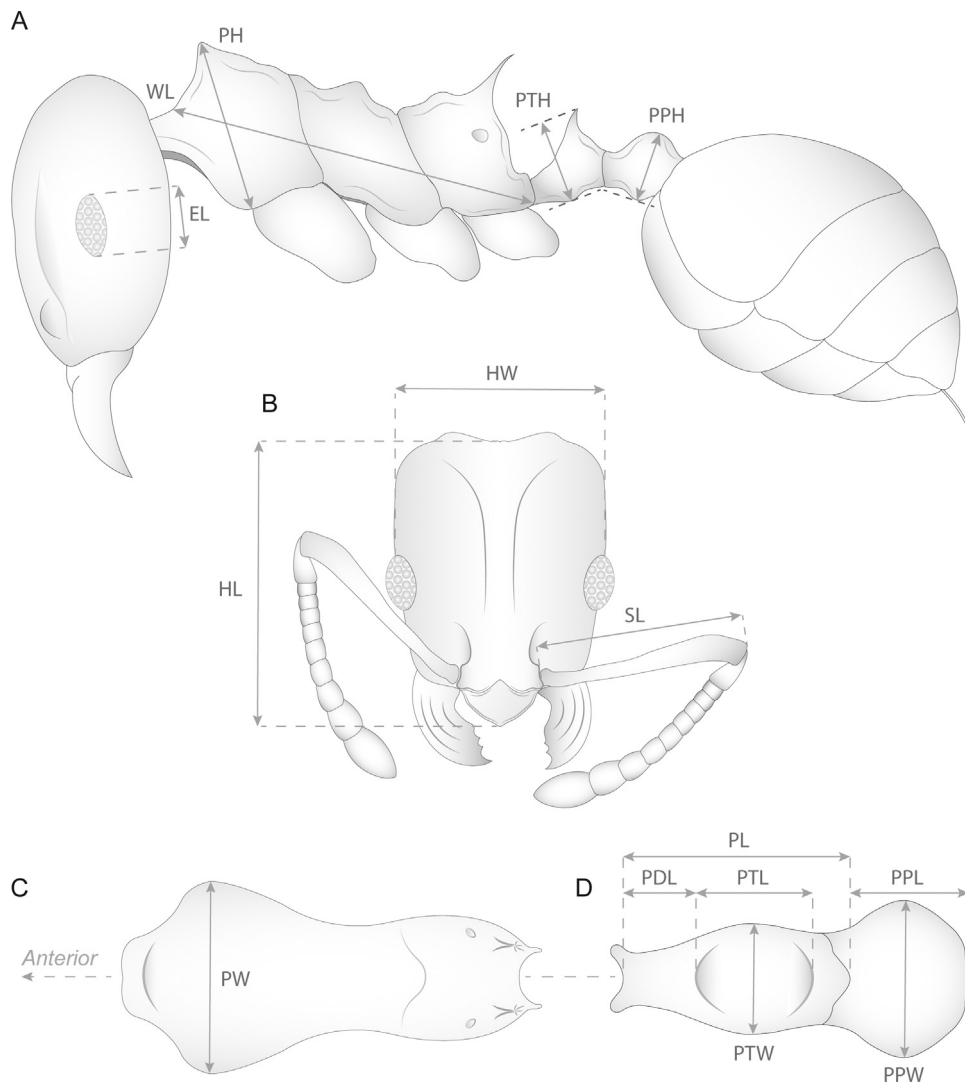


Fig. 2. Schematic line drawings of a generalized myrmicine ant, illustrating the measurements used in this study. A. Body in profile view. B. Head in full-face view. C. Mesosoma in dorsal view. D. Petiole and postpetiole in dorsal view. (Illustration: C. Chény; B–D modified from Hita Garcia et al., 2017).

Fig. 2. Schéma général d'une fourmi Myrmicinae, avec indication des mesures utilisées dans ce travail. A. Corps en vue latérale. B. Tête en vue de face. C. Mésosome en vue dorsale. D. Pétiole et post-pétiole en vue dorsale. (Illustration: C. Chény; B–D modifiées d'après Hita Garcia et al., 2017).

Type species. *Thanacomyrme hoffeinsorum* sp. nov., by monotypy.

Diagnosis (worker). With characters of the Myrmicinae, plus the following unique combination of characters: frontal lobes absent (antennal sockets and torular lobes clearly exposed in frontal view); antennal scrobes and ocelli absent; antennae 11-segmented, with weakly defined 3-segmented club; clypeus posteriorly broadly inserted between antennae, with median portion flat and longitudinally bicarinate; anterior clypeal margin weakly convex laterally, weakly concave medially, the median portion with paired setae; masticatory margin of mandibles with 2 small teeth followed by 7 widely spaced, blunt denticles; compound eyes small; pronotal humeri tuberculate; promesonotal suture absent dorsally; propodeum and petiole bispinose; propodeal lobes present; petiole with short peduncle,

postpetiole broadly rounded dorsally; hind tibia with one short simple spur; head and mesosoma coarsely rugose to areolate rugose; petiole and postpetiole reticulate rugose. Main pilosity of dorsum of head and body simple, sparse.

Etymology. The genus name is an anagram of *Acanthomyrmex*, which shares many morphological similarities with the new taxon. The gender is masculine.

***Thanacomyrme hoffeinsorum* sp. nov.**

(Figs. 3 and 4)

Type material. Holotype CCHH 1628-6 (worker); housed in the Senckenberg Deutsches Entomologisches Institut Münchenberg, Germany (SDEI).

Type locality and horizon. In Baltic amber, late Eocene (likely Priabonian, ca. 34–38 Ma).

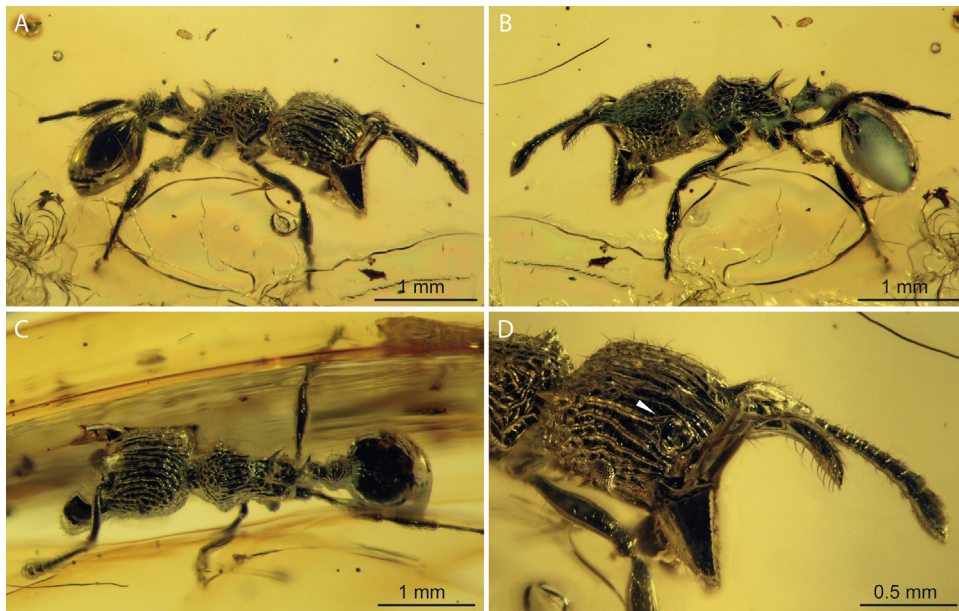


Fig. 3. Photographs of the holotype worker (CCHH 1628-6) of *Thanacomyrmex hoffeinsorum* gen. et sp. nov. from Baltic amber. A. Right dorsolateral view. B. Left ventrolateral view. C. Dorsal view. D. Detail of head. The white arrow indicates the posterior portion of the frontal carina.

Fig. 3. Photographies de l'holotype (CCHH 1628-6) de *Thanacomyrmex hoffeinsorum* gen. et sp. nov., dans l'ambre balte. A. Vue dorsolatérale droite. B. Vue ventrolatérale gauche. C. Vue dorsale. D. Détail de la tête. La flèche blanche indique la partie postérieure de la carène frontale.

Etymology. The specific epithet is a patronym for Christel and Hans-Werner Hoffeins who generously provided access to the specimen for study.

Diagnosis. As for the genus (see above).

Description. Worker. Entire body including legs and antennae sparsely covered with simple short setae; may be very sparse or absent in places on propodeum, petiole, and gaster.

Head. In full-face view, with sides subparallel, posterior corners broadly rounded, posterior margin shallowly concave. Compound eye subcircular, small and weakly bulging, inserted on the laterodorsal boundary slightly anterior to midlength of head. Frontal carinae present, short, terminating just behind the antennal fossae against a longitudinal ruga (see head's sculpture below), and strongly divergent posteriorly. Antennal sockets and torular lobes exposed, the antennal fossae clearly visible, located close to the anterior margin of head (i.e. lateral portions of clypeus reduced to a thin cuticular bridge in front of antennal sockets); antennal scape bent almost at right angle in its basal part, not surpassing occipital margin, about 5.5× as long as pedicel; first flagellomere half as long as pedicel, following flagellomeres gradually incrassate toward apex; apical flagellomere with acute tip. Median clypeal portion anteriorly with two short setae, with sides longitudinally carinate. Mandibles stoutly triangular, with basal angle acute, basal margin smooth; masticatory margin with apical and preapical teeth subequal in size, small, followed by a distinct diastema and 7 blunt denticles each widely separated; fine rugose sculpture present basally on lateral outer surface of mandibles; outer edge of mandible bearing one row of fine suberect setae; inner surface of mandible bearing one row of similar setae along

masticatory margin. Head capsule coarsely rugose, the dorsal surface between compound eyes with 20 longitudinal, irregular rugae reaching to posterior margin of head, the rugae rarely reticulated; lateral and ventral sides of head areolate rugose, flame-shaped anteriorly then progressively foveate subcircular pits.

Mesosoma. In dorsal view, mesosoma anteriorly swollen, promesonotal suture absent (but suture is conspicuous from lateral view); pronotum with a pair of tubercles on humeral angles; metanotal groove shallow; propodeum with a pair of long sharp spines directed backward, upward and outward, and distinctly curved toward acute tip; propodeal lobes well developed as a subrectangular lamella with rounded ventral corners and slightly angulate dorsal corners; legs relatively short, metacoxa not distinctly larger than pro- and mesocoxae; profemur only weakly swollen, protibia progressively swollen toward apex; metatibia and metafemur distinctly swollen around two thirds of length; cuticle ornamented dorsally and laterally by longitudinal irregular ridges forming a network with pits more or less elongate.

Waist segments and gaster. In profile view, petiole with short anterior peduncle; petiolar tergite forming a distinct triangular node with short acute spines at apex (= petiole bispinose), with anterior and posterior surfaces strongly inclined, nearly flat, the posterior surface about half as long as anterior one; subpetiolar process developed as a thin and straight lamella; postpetiole globular, slightly shorter and broader than petiole, the tergite broadly rounded; helcium positioned at the anterior face of abdominal segment IV; gaster ovoid, the first tergite much larger than following ones; petiole and postpetiole finely reticulate; postpetiole transversely rugose.

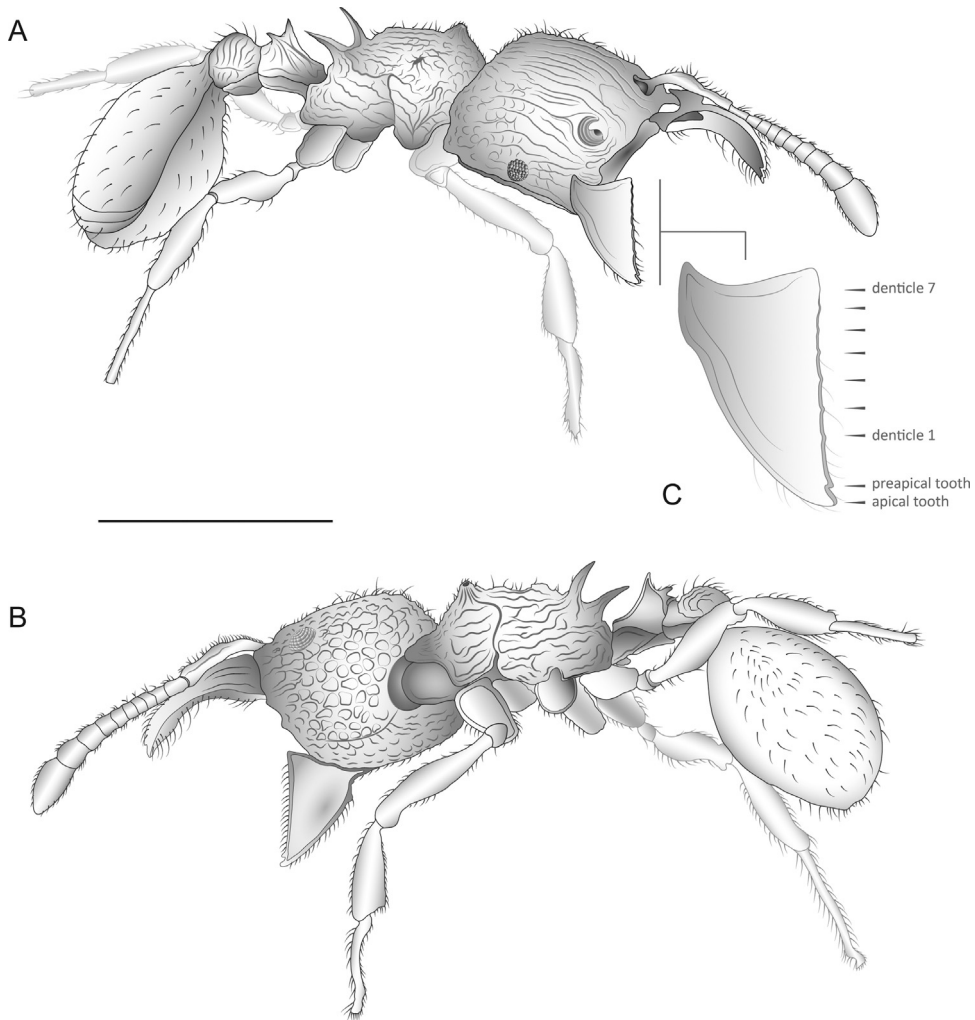


Fig. 4. Drawings of holotype worker (CCHH 1628-6) of *Thanacomymex hoffeinsorum* gen. et sp. nov. from Baltic amber (Illustration: C. Chény). A. Right dorsolateral view. B. Left ventrolateral view. C. Detail of the right mandible in dorsal view. Scale bar (A, B): 1 mm.

Fig. 4. Dessins de l'holotype (CCHH 1628-6) de *Thanacomymex hoffeinsorum* gen. et sp. nov. dans l'ambre balte (Illustration: C. Chény). A. Vue dorsolatérale droite. B. Vue ventrolatérale gauche. C. Détail de la mandibule droite en vue dorsale. Barre d'échelle (A, B) : 1 mm.

Measurements (in mm) and indices. TL 3.5; HL 0.9; HW 0.8; SL 0.5; EL 0.2; PH 0.5; PL 0.4; PW 0.7; WL 0.8; PDL 0.1; PTL 0.3; PTH 0.4; PTW 0.2; PPL 0.2; PPH 0.3; PPW 0.3; CI 89; SI 62.5; OI 25; DMI 87; LMI 62; LPeI 12; DPeI 67; LPpI 67; DPpI 100; PPI 150; PTI 133.

4. Discussion

The new fossil looks superficially similar to the extant genus *Acanthomyrmex*; however, it differs by the antennae with 11 segments (vs. 12 segments in *Acanthomyrmex*), the antennal scrobes absent (vs. present), the basal angle of mandibles acute (vs. straight or obtuse), the anterior clypeal margin smooth and without an unpaired seta (vs. 2 clypeal processes and an unpaired median seta present), the pronotum with humeral tubercles (vs. pronotum bispinose), the petiole with a short anterior peduncle (vs. elongate peduncle), the suture between first gastral tergite and sternite regularly curved (vs. M-shaped basally),

and the presence of short standing hairs (vs. long standing hairs). Fossils of *Acanthomyrmex* are yet unknown.

The fossil morphotype also shares some features with the extant genus *Pristomyrmex*, such as the antennae with 11 segments and a weakly defined club, the frontal lobes vestigial or absent and antennal scrobes indistinct, the absence of an unpaired median seta on the anterior clypeal margin, the compound eyes of medium size, the absence of promesonotal suture dorsally, the presence of propodeal lobes, and the suture between first gastral tergite and sternite regularly curved. But the new fossil differs from *Pristomyrmex* by the clypeus, which is medially carinate and anteriorly simple (vs. not carinate and anteriorly denticulate in *Pristomyrmex*), the masticatory margin with 2 small teeth and 7 blunt denticles (vs. 3–5 distinct teeth in *Pristomyrmex*), the pronotum tuberculate (usually with teeth or spines in *Pristomyrmex*), the projecting mesopleural flange absent in *Thanacomymex*, and the petiole bispinose and with short anterior peduncle

(usually nodiform and with elongate peduncle in *Pristomyrmex*). Our fossil compares similarly with the extinct species of *Pristomyrmex* described to date: *P. elmesi* Radchenko & Dlussky from Rovno amber, and *P. rasnitsyni* Dlussky & Radchenko from Danish (=Baltic) amber (Dlussky and Radchenko, 2011; Radchenko and Dlussky, 2018a). A third species, *Pristomyrmex archaios* Radchenko & Dlussky, was described from Bitterfeld amber based on male specimens (Radchenko and Dlussky, 2018a) and is thus not directly comparable to our worker specimen.

Finally, the new fossil looks rather similar to *Parameranoplus primaevus* Wheeler, which was also described from Baltic amber (Wheeler, 1915). Indeed, they both have the antennae 11-segmented and terminating in a weakly defined 3-segmented club, with the scape distinctly curved at its base, large triangular mandibles apparently bluntly dentate (although unclear in *P. primaevus*), the propodeum bispinose, and a similar dorsal sculpture of the head, postpetiole, and gaster. But *P. primaevus* differs by the presence of conspicuous antennal scrobes and a promesonotal suture distinct dorsally, the humeral angles armed with pointed teeth (instead of rounded tubercles), the petiole nodiform (instead of bispinose), and the gaster with dense long pubescence (instead of sparse short setae in our fossil).

The unique combination of characters described above sets this specimen apart from other known myrmicine genera, hence the assignment to a new genus. Its affinities with *Acanthomyrmex*, *Pristomyrmex*, and *Parameranoplus*, all grouped within the Crematogastrini according to Ward et al. (2015) and Blaimer et al. (2018), suggest placement of *Thanacomymex* in this tribe, and possibly in the *Myrmecina* genus-group to which *Acanthomyrmex* and *Pristomyrmex* belong. According to Ward et al. (2015), however, these two genera are not closely related to each other within the genus-group, and a phylogenetic analysis will be needed to determine whether *Thanacomymex* could be an extinct sister taxon to one of them, or a possible ancestor to the entire genus-group (= a stem *Myrmecina* genus-group).

5. Biogeography and palaeohabitat

The ant fauna from the Eocene Baltic amber shows remarkable affinities with the modern fauna from the Indomalayan and Australasian bioregions, with strong similarities in their generic composition (Guénard et al., 2015). *Thanacomymex* well agrees with this biogeographical pattern, being morphologically close to *Acanthomyrmex* and *Pristomyrmex*, two extant genera with a mostly Indomalayan distribution today. *Acanthomyrmex* is currently restricted to Southeast Asia (South China, Vietnam, Thailand, Malaysia, and Borneo), while *Pristomyrmex* is further widespread in Eastern Asia, from Japan to Australia, and in the Afrotropics (Guénard et al., 2017; Janicki et al., 2016), but also occurred in Europe during the Eocene (Dlussky and Radchenko, 2011; Radchenko and Dlussky, 2018a). Both genera have a maximum diversity in the Asian tropics today: in Borneo, Sumatra, and Sulawesi for *Acanthomyrmex* (7, 3, and 3 out of the total 17 extant species, respectively); and in Borneo, the Philippines and New Guinea for *Pristomyrmex* (11, 19, and 15 out of 61 extant species). Therefore, we may assume that *Thanacomymex*,

Pristomyrmex and other ants composing the Baltic amber fauna lived in similar tropical habitats in Europe during the Eocene. But the numerous plant remains found fossilized in Baltic amber merely indicate a warm/temperate climate and heterogeneous forests with diverse types of habitats, from coastal and lowland swamps to humid mesophytic conifer-angiosperm forests interspersed with drier patches (Sadowski et al., 2017). In our opinion, this supports a Priabonian rather than Lutetian age for Baltic amber, since the Lutetian coincided with the Middle Eocene Climatic Optimum (MECO, ~40 million years ago), which was a transient period of global warming during the Palaeogene cooling trend, favoring the extension of tropical biomes in high latitudes (Bijl et al., 2010; Bohaty et al., 2009). We tentatively assume that the tropical affinities of Baltic amber ants were inherited from the MECO and previous hyperthermal events that occurred in the Early Eocene (PETM, ETM 2 and ETM 3), and these ants later vanished from Europe during the Late Eocene cooling. Yet, it is unknown whether the affinities of the modern Indomalayan and Australasian ant fauna with the extinct West Palearctic fauna result from contractions of historically wider-ranged genera (=relictual distribution), or whether some ranges have shifted into different bioregions over the Late Palaeogene and Neogene. The recent discovery of ant-rich amber deposits from the Early Eocene of India (Barden et al., 2016; Rust et al., 2010) and the Miocene of China (Chény et al., 2018; Zheng et al., 2019), both originating from tropical dipterocarp rainforests, will help elucidating this question.

6. Conclusion

It is striking that new ant morphotypes are still being discovered from Baltic amber despite over 150 years of study since Mayr's landmark monograph (1868), and tens of thousands of specimens examined since then (Dlussky and Rasnitsyn, 2009; Wheeler, 1915). Although more than 200 extinct species have been described from Baltic amber to date, Penney and Preziosi (2014) estimated that about 30% of ant species are yet to be found from this highly fossiliferous amber. This holds particularly true with regards to male morphotypes that have long remained overlooked compared to females, but the recent description of several new species based on males, particularly in myrmicines, are progressively filling this gap (Dlussky and Radchenko, 2009; Radchenko and Dlussky, 2013, 2016, 2018a, b). Some treasures are also left within the worker ants, though, as shown by the new genus described herein. Thorough studies of institutional and private Baltic amber collections worldwide may allow for additional new findings and improve our understanding of the evolutionary history of ants.

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