A new record of *Thaumastobombus andreniformis* Engel 2001 in Eocene amber (Hymenoptera: Apidae)

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Abstract. A new specimen of the rare fossil bee *Thaumastobombus andreniformis* Engel 2001 (Apidae: Apinae: Electrapini) is reported and figured from middle Eocene (Lutetian) Baltic amber. The new specimen, a female of the worker caste, agrees in every respect with the holotype except some morphometric differences. These minor size differences are likely related to the degree of sociality of *T. andreniformis*.

Resume. **Une nouvelle donnée de *Thaumastobombus andreniformis* Engel 2001 de l'ambre de l'Eocène (Hymenoptera : Apidae).** Un spécimen nouvellement découvert de l'espèce fossile rare, *Thaumastobombus andreniformis* Engel 2001 (Apidae : Apinae : Electrapini), est présenté. Ce spécimen provient de l'ambre de la Baltique du Miocène moyen. Il s'agit d'une femelle de la caste des ouvrières présentant une morphologie similaire à l'holotype excepté quelques différences morphométriques. Ces différences de mineure de taille peuvent probablement être mise en relation avec le degré de socialité de *T. andreniformis*.

Keywords: Eocene, Lutetian, *Thaumastobombus,* Electrapini, Anthophila, Apoidea.

The most widely recognized of bee lineages are those tribes comprising the corbiculate Apinae, commonly known as the corbiculate bees. The lineage includes four modern tribes, with 30 extant genera, these being the familiar honey bees (Apini), bumble or humble bees (Bombini), stingless bees (Meliponini), and orchid bees (Euglossini). The corbiculate bees, as their name implies, share the unique structure of the metatibia in females called corbicula or "pollen basket", among other anatomical features (*e.g.*, Schultz *et al.* 1999, 2001; Michener 2000; Engel 2001a, 2001b). The corbiculate Apinae also includes some of the most complex of social organizations among bees, particularly in the honey bees and stingless bees which occupy the advanced eusocial behavioral grade, exhibiting striking morphological specializations between worker and queen castes and living in large, perennial colonies (*e.g.*, Schultz *et al.* 1999; Michener 2000; Engel 2001b; Noll 2002).

Interestingly, the corbiculate bees have one of the more completely documented fossil records in comparison to other lineages of the Anthophila (*sensu* Engel 2005). In addition to fossil species of the four modern tribes, several extinct genera of Meliponini are known from the Cretaceous through Miocene and three extinct corbiculate tribes are known from the Paleogene, together representing at least 14 additional genera (tab. 1). Like their modern counterparts, these tribes exhibit the suite of synapomorphies for the corbiculate clade but display also unique combinations of characters (Engel 2001a).

The three extinct corbiculate tribes are Electrapini, Electrobombini, and Melikertini. The first includes both species described from fossil compressions as well as inclusions in amber from Europe (Engel 2001a; Wappler & Engel 2003). According to the current knowledge, the electrapines disappeared during the well-documented episode of extinction of the Eocene-Oligocene transition (Engel 2001a, 2004; Prothero 1994; Grimaldi & Engel 2005). To date, three genera and at least 15 species of Electrapini have been recorded from the Paleogene of Europe. All appear to have been of the advanced eusocial behavioral grade, exhibiting morphological differentiation between sterile worker and queen castes (Engel 2001a, 2001b).

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While some electrapines such as *Protobombus indecisus* Cockerell 1908 are not entirely uncommon in Eocene amber, perhaps as a result of their social lifestyle, others remain poorly documented (*e.g.*, Engel 2001a). Indeed, one such rare electrapine is *Thaumastobombus andreniformis* Engel 2001, a species hitherto known only from a single worker female and the only known species of its genus (Engel 2001a).

Table 1. List of corbiculate bee tribes and genera (Apidae: Apinae) according to Engel (2001a). The names of the strictly fossil taxa are preceded by "*", while the notation "(*)" indicates those genera with both living and fossil representatives.

Tribe	Genus
(*) Apini Latreille	(*) *Apis* L. 1758
(*) Bombini Latreille	(*) *Bombus* Latreille 1802
	* *Oligoapis* Nel & Petrulevicius 2003
	* *Paraelectrobombus* Nel & Petrulevicius 2003
* Electrapini Engel	* *Electrapis* Cockerell 1908
	* *Protobombus* Cockerell 1908
	* *Thaumastobombus* Engel 2001
* Electrobombini Engel	* *Electrobombus* Engel 2001
(*) Euglossini Latreille	*Aglae* Lepeletier and Serville 1825
	Eufriesea Cockerell 1908
	(*) *Euglossa* Latreille 1802
	Eulaema Lepeletier 1841
	Exaerete Hoffmannsegg 1817
* Melikertini Engel	* *Melissites* Engel 2001
	* *Melikertes* Engel 1998
	* *Roussyana* Manning 1960
	* *Succinapis* Engel 2001
(*) Meliponini Lepeletier	*Austroplebeia* Moure 1961
	Cephalotrigona Schwarz 1940
	Cleptotrigona Moure 1961
	* *Cretotrigona* Engel 2000
	Dactylurina Cockerell 1934
	(*) *Hypotrigona* Cockerell 1934
	* *Kelneriapis* Sakagami 1978
	(*) *Lestrimelitta* Friese 1903
	(*) *Liotrigona* Moure 1961
	* *Liotrigonopsis* Engel 2001
	Lisotrigona Moure 1961
	Melipona Illiger 1806
	(*) *Meliponula* Cockerell 1934
	* *Meliponorytes* Tosi 1896
	Meliwillea Roubik, Segura & Camargo 1997
	Nannotrigona Cockerell 1922
	(*) *Nogueirapis* Moure 1953
	Oxytrigona Cockerell 1917
	Paratrigona Schwarz 1938
	Pariotrigona Moure 1961
	Patramona Schwarz 1938
	Plebeia Schwarz 1938
	Plebeina Moure 1961
	* *Proplebeia* Michener 1982
	Scaptotrigona Moure 1942
	Trichotrigona Camargo & Moure 1983
	(*) *Trigona* Jurine 1807
	(*) *Trigonisca* Moure 1950

T. andreniformis is perhaps the rarest of the Eocene amber species in this tribe. The present paper aims at reporting the discovery of a second specimen of *T. andreniformis*. A morphometric comparison is made with the holotype and additional comments are made about the geographical dispersion of specimens.

Material and methods

The new material reported herein is deposited in the private collection of P. Vanmarsenille (Diest, Belgium). It consists in an inclusion in Baltic amber from Poland, likely of middle Eocene (Lutetian). The studied specimen is included at one end of an approximately 3.3 cm long piece, with a maximal width of 1.6 cm at the end with the bee and tapering to 1.2 cm before more precipitously tapering to a bluntly rounded apex at the opposite end. The depth of the piece is approximately 0.8 cm. The bee is positioned obliquely in the piece with its head and anterior legs meeting the amber surface and its length paralleling the widest end of the piece (figs 1–2).

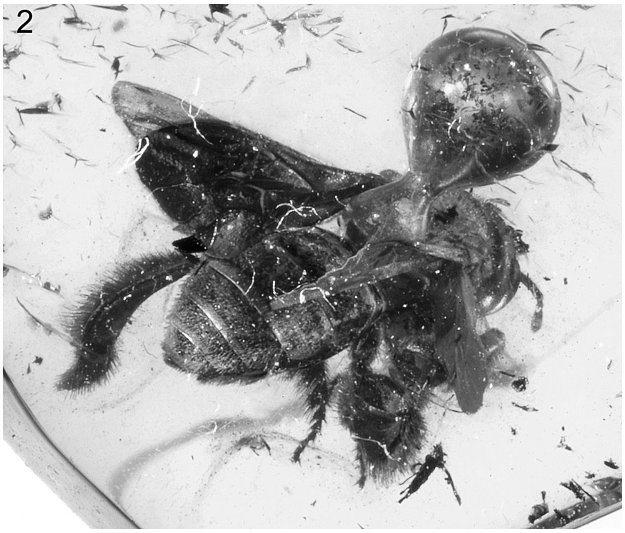
Metrics of the specimen (tab. 2) were made using an ocular micrometer on an Olympus SZX9 Stereomicroscope and must be considered approximate since the optimal angle for measurement was not achievable. Microphotographs of the specimen were made with a MicrOptics Digital Imaging System using an Infinity K-2 Lens (prepared by M.S.E.).

Results

The specimen described herein agrees in all respects with the holotype and original description as presented by Engel (2001a). The apical most portion of the head is obliterated at the surface with much of the clypeus. The apical half of the prementum and more distal labiomaxillary components, most of the flagella, the left mandible, the lowermost portion of the left compound eye, and the right mandible beyond the base are lost. In addition, the left pro-pretarsus, the

Table 2. Comparison of the main morphometric features in the two known specimens of *Thaumastobombus andreniformis*. Measurements of the holotype are extracted from Engel (2001a). NA is used for not accessible measurements due to the conditions of preservation of the specimen.

Character	*T. andreniformis*, holotype (a)	New specimen (b)	Ratio a/b
Total body length	6.92 mm	8.31 mm	0.83
Forewing length	4.45 mm	5.60 mm	0.79
Head length	1.62 mm	NA	NA
Head width	1.70 mm	2.29 mm	0.74
Upper interorbital distance	1.10 mm	1.54 mm	0.71
Lower interorbital distance	0.80 mm	NA	NA
Interocellar distance	0.45 mm	0.53 mm	0.85
Ocello-ocular distance	0.25 mm	0.32 mm	0.78
Median – Lateral ocellus	0.14 mm	0.16 mm	0.88
Intertegular distance	1.20 mm	1.71 mm	0.70



Figures 1–2
Photomicrographs of the specimen (female, worker caste) of *Thaumastobombus andreniformis* Engel 2001 discussed herein; **1,** ventral habitus showing damage to apex of head and portions of legs (scale = 1.5 mm); **2,** dorsal habitus showing large bubble.

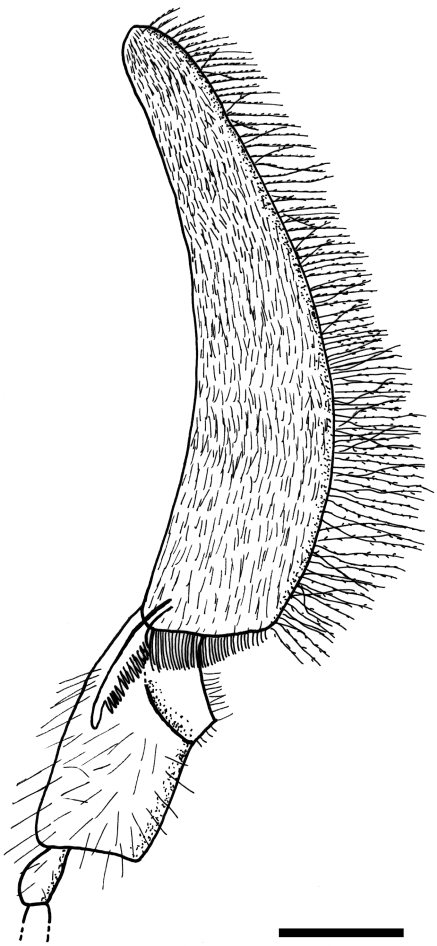


Figure 3
Line drawing of the inner surface of the metatibia and metabasitarsus of *Thaumastobombus andreniformis* Engel 2001 (scale = 0.7 mm).

right leg beyond the middle of the protibia, and the apicalmost margin of the metabasitarsus and beyond are similarly lost at the amber surface. Some portions of the posterior mesosomal dorsum are obscured by a large, elongate bubble that emanates likely from the propodeal spiracles (fig. 1). Despite these minor imperfections, the individual is exceptionally well-preserved and display many of the species diagnostic characters. The wing venation (three sub-marginal cells, marginal cell not truncate, vein 1m-cu long and oblique, pterostigma much greater than the prestigma) and the metatibial spur pectination are typical and particularly clearly observable in the described specimen (figs 1–4). The new specimen is a female (likely of worker caste in front of its reduced

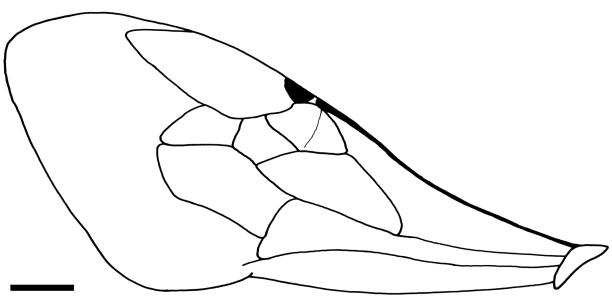


Figure 4
Line drawing of the forewing of *Thaumastobombus andreniformis* Engel 2001 (scale = 0.8 mm).

metasomal structures), of which metrics are provided in tab. 2 (compared with those of the holotype as recorded by Engel 2001a).

All specimens of *T. andreniformis* discovered to date are from the southern Baltic Sea amber deposits, the so-called *blaue Erde*. The genus is presently unknown in other amber deposits or as compression fossils from either New or Old World localities.

Discussion

Like the earlier record of the species (holotype), as well as two suspected individuals of *T. andreniformis* reported by Engel (2001a), the present material is also preserved as an inclusion in Baltic amber. The genus and species, therefore, remains confined to amber deposits of the northern European coast, while the other electrapine genera appear to be more widespread or abundant (Engel 2001a; Wappler & Engel 2003). Continued exploration in Eocene deposits, both amber and compression sites, will hopefully eventually uncover more material of *T. andreniformis* and perhaps even additional species.

In addition, comparison of the holotype and the new individual in various observable morphometric features highlights a light (averaged difference = 21%) but significant divergence between the specimens. This size polymorphism, observed for all the metrics independent of the orientation of the structures in the amber piece, is likely not an artifact resulting from less than optimal viewing of specific traits during measurement (*i.e.*, a direct view for any given feature was not possible owing to the position of the individual in the amber relative to the amber surface). Such differences in the body size and proportions of workers are common in social insects (i.e. Knee & Medler 1965). Among most contemporary social species the individuals in the worker caste display strong divergences in body size, notably following the relative age of their brood of origin (Cumber 1949), while metasomal structures are usually reduced (Michener 2000; Engel 2001a). This size polymorphism in *T. andreniformis*, as well as the obviously reduced metasomal structures, likely constitutes additional clues to support the hypothesis of advanced eusociality in this species, as well as others of the Electrapini.

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