

The oldest fossil of a melittid bee (Hymenoptera: Apiformes) from the early Eocene of Oise (France)

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Phylogenetic relationships among and within major groups of bees are still poorly resolved. The main gap is the identification of the basal branch of bee phylogeny. In this context, more information is needed about the early fossil record of bees. Here, we describe *Palaeomacropis eocenicus* gen. nov. sp. nov., discovered in early Eocene amber of Oise (France). It is the oldest record of Melittidae and the fourth oldest fossil bee. The remarkable state of preservation of the specimen allows a detailed description of the cuticle and the setae. A cladistic analysis supports the classification of this species among the Macropidinae (Melittidae). Together with the existing records on a Maastriechian Apidae and a Palaeocene Megachilidae, the discovery of an early Eocene Melittidae supports the hypothesis that Melittidae could constitute the basal branch of bee phylogeny. Moreover, the morphology and disposition of the setae of *P. eocenicus* are similar to those of the contemporary oil-collecting bee *Macropis*. The presence of a bee with such specialized structures would support the hypothesis that a close relationship existed between bees and oil flowers since the early Eocene. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 150, 701–709.

ADDITIONAL KEYWORDS: amber – evolution – insect – oil-collecting bee – phylogeny – pollination – systematic.

INTRODUCTION

Bees belong to a monophyletic group of 16000 species that feed on pollen and plant-derived nutrients (Eickworth & Ginsberg, 1980; Michener, 2000). Seven families are usually recognized: Stenotritidae, Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae, and Apidae (Michener, 2000). Commonly, these families are classified into two major groups based on labial palpal morphology: the long-tongued bees (LT bees), including Apidae and Megachilidae, and the short-tongued bees (ST bees), including the other families (Kirby, 1802; Michener, 1944; Engel, 2001). Despite this long-standing tradition in classification, evolutionary relationships within and between LT bees and

ST bees are poorly resolved. Phylogenetic analysis based on contemporary taxa suggest that Melittidae may be the sister group of the LT bees (Rozen & McGingley, 1974; Michener & Greenberg, 1980; Michener, 1981; Alexander, 1992; Roig-Alsina & Michener, 1993; Alexander & Michener, 1995). Relationships among other families are uncertain. The main missing link is the basal branch of the bee clade. Alexander & Michener (1995) suggested several hypotheses and, in the end, proposed each ST bee family except Andrenidae as possibly being the basal branch. The Colletidae are traditionally considered as the most plesiomorphic family because of their truncated or emarginated glossa, which is similar to that of the spheciform wasp ancestor (Fig. 1A) (Michener, 2000; Engel, 2001). According to this hypothesis, the pointed glossa must be a synapomorphy originating in a noncolletid bee. However, wasps in the genus

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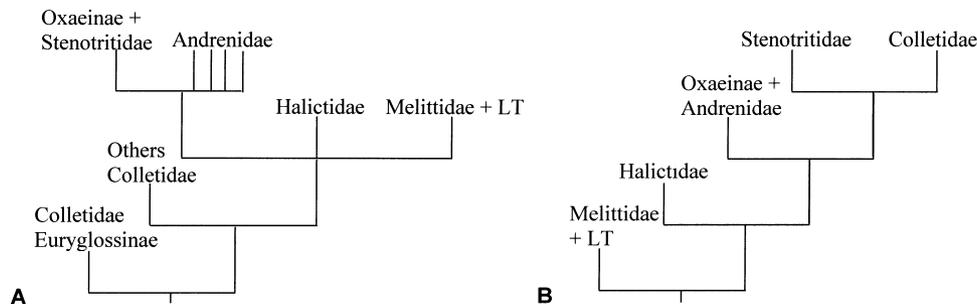


Figure 1. Alternative phylogenetic trees of bee. A, traditional phylogenetic tree with Colletidae as basal branch. B, alternative suggestion with Melittidae as basal branch (Michener, 2000).

Pseudoscolia sp. (Crabonidae) were recently discovered to have a pointed glossa; thus, this character may possibly be homoplastic with Apoidea + spheciform wasps (Michener, 2005). Convincing alternative hypotheses have placed Melittidae near the root of the phylogenetic tree of bees (Fig. 1B) (Michener, 1981; Radchenko & Pesenko, 1989; Michener, 2000; Danforth, Fang & Sipes, 2006a; Danforth *et al.*, 2006b).

In this context, more information is needed about the early fossil record of each clade to validate one phylogenetic hypothesis or another. Unfortunately, the fossil record of the bees is incomplete. Moreover, only amber fossils are preserved well enough to shed light on general phylogeny (Michener, 2000). Three main deposits with bee fossils are known: Dominican amber from the Miocene (20 Mya), Florissant shale from the Oligocene (32 Mya), and Baltic amber from the late Eocene (45 Mya). These deposits have produced a sizeable bee Palaeofauna (Zeuner & Manning, 1976; Poinar, 1999; Engel, 2001). Other bee fossils have been discovered in isolated sites scattered around the world. The oldest known bee fossil, *Cretotrigona prisca* (Michener & Grimaldi, 1988), is an Apinae found in New Jersey amber (Engel, 2000) estimated from the late Maastrichtian (65–70 Mya). The two next oldest bees, *Probombus hirsutus* Piton 1940 and an undescribed fossil, are compressions from the Palaeocene, found in Menat (France). The former was recently attributed to Megachilidae (Nel & Petrulevicius, 2003).

Angiosperm fossils could be used as a second indirect path to understand bee diversification. Indeed, close ecological associations with angiosperms are tied to the origin and subsequent radiation of bees (Grimaldi, 1999; Engel, 2001). First, bees may have arisen at the same time as the earliest unambiguous angiosperm fossils from the early Cretaceous (Michener & Grimaldi, 1988; Crane, Friss & Pedersen, 1995; Danforth & Ascher, 1999; Engel, 2001). Likewise, the diversification of major anthophilic groups of insects in the mid-Cretaceous is consistent with the

rise of entomophilous syndromes in Cretaceous flowers (Grimaldi, 1999). Lastly, the radiation of bilateral flowers in the late Cretaceous is likely to be linked to the simultaneous diversification of LT bees (Dilcher, 2000).

The aim of the present study is to describe *Palaeomacropis eocenicus* gen. nov. sp. nov., a new melittid bee found in early Eocene amber from Oise (France). Detailed description of the morphological structure is possible thanks to the outstanding state of preservation of this fossil. A cladistic analysis is performed to determine the precise phylogenetic position of *Palaeomacropis eocenicus* within Melittidae.

MATERIAL AND METHODS

STUDY AND DESCRIPTION OF *PALAEOMACROPIS EOCENICUS* GEN. NOV. SP. NOV.

The specimen of *Palaeomacropis eocenicus* is embedded in a very clear piece of amber that was carefully polished before this study. The morphological terminology used is consistent with that proposed by Michener (2000).

CLADISTIC ANALYSIS

We used one outgroup and nine ingroup taxa for the cladistic analysis. Following the example of Michener (1981), a nonmelittid ST bee (*Andrena* sp.) was used as the outgroup. For the ingroup, at least one genus was selected among each Melittidae subfamily *sensu* Engel (2001) (see Appendix 1).

We used only female morphological characters because males of the fossil taxa (*Eomacropis glaesaria* Engel 2001 and *Palaeomacropis eocenicus*) are unknown. The data matrix includes 17 discrete morphological characters (Appendices 2 and 3). Sixteen characters have two states, 0 and 1. Only character 8 has three non-additive unordered states. State (0) characterizes the outgroup (*Andrena* sp.) (*sensu* Mad-

dison, Donoghue & Maddison, 1984). The characters were treated as unweighted and unordered.

The minimum length trees were searched using heuristic searches. Analyses were performed using PAUP* 4.0b10 (Swofford, 1998).

SYSTEMATIC PALAEOLOGY

Family: Melittidae Schenck, 1860.

Subfamily: Macropidinae Robertson, 1904.

GENUS *PALAEOMACROPIS* MICHEZ & NEL GEN. NOV.

Type species: *Palaeomacropis eocenicus* gen. nov. sp. nov.

Etymology: From the Greek *Palaeo*, meaning 'old', and *Macropis* referring to the similar contemporary bee genus (see Discussion).

Generic diagnosis: Female: glossa shorter than galea (Fig. 2A, C); paraglossa densely hairy; labial palpal segments similar and cylindrical (Fig. 2A, C); mandible with a very large preapical tooth on the upper margin (Fig. 2A); one subantennal suture branching ventrally on the antennal socket (Fig. 2C); facial foveae absent; vertex enlarged behind lateral ocelli (Fig. 3A); basal width of propodeal triangle longer than four-fifths of basal width of propodeum; propodeal triangle bare; two submarginal cells, the second as long as the first (Figs 3A, 4B); second abscissa of Rs slanting and widely separated from 1m-cu (Figs 3A, 4B); apex of marginal cell pointed (Figs 3A, 4B); mid-basitarsus with dense plumose setae on inner and outer side (Fig. 3B); trochanter with curved setae; no basitibial plate (Fig. 3A); hind tibia and basitarsus with poorly developed scopa (Fig. 2E); hind basitarsus narrower than tibia (Fig. 2E); sterna with long, erect setae (Figs 2D, 4A). Male: unknown.

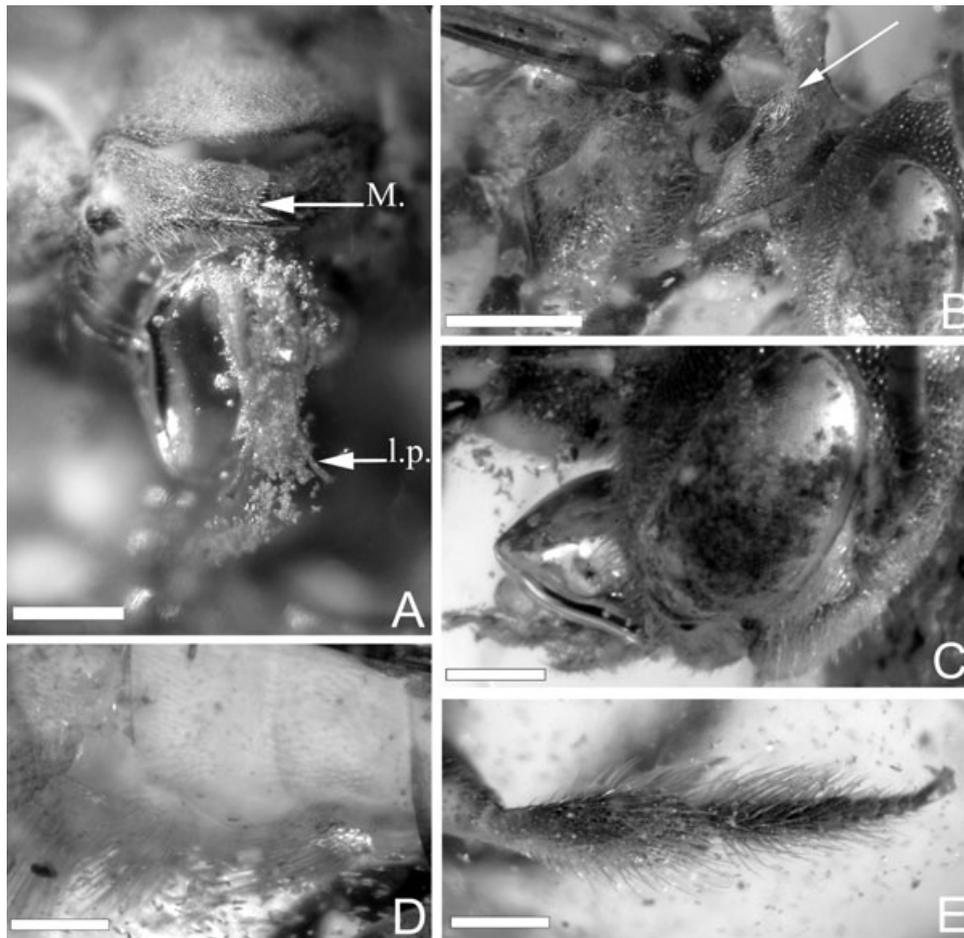


Figure 2. *Palaeomacropis eocenicus* gen. nov. sp. nov. A, facial view of mouthparts (scale = 0.3 mm). B, dorsolateral angle of pronotum with carina (scale = 0.5 mm). C, lateral view of mouthparts (scale = 0.3 mm). D, lateral view of metasoma with long, erect setae on sterna (0.4 mm). E, hind basitarsus (scale = 0.3 mm).

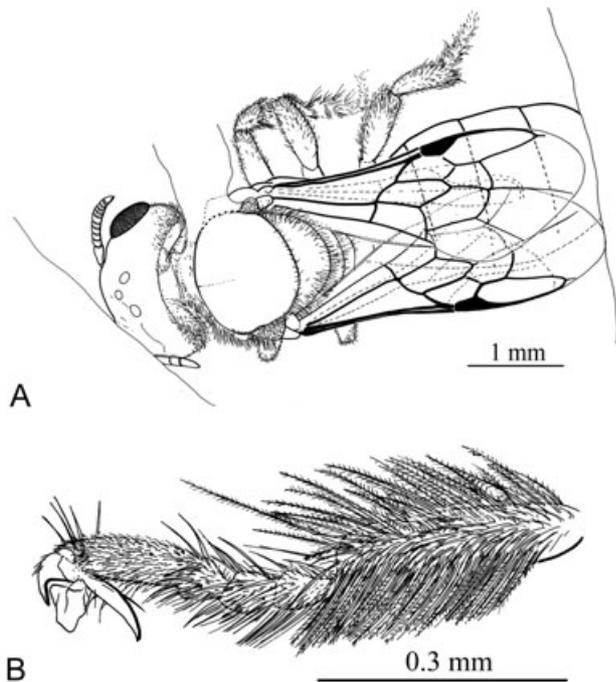


Figure 3. *Palaeomacropis eocenicus* gen. nov. sp. nov. A, drawing of general habitus. B, detail of mesotarsus.

***PALAEOMACROPIS EOCENICUS* MICHEZ & NEL
SP. NOV.**

Etymology: *eocenicus* in reference to the Eocene age of the fossil.

Holotype: Female PA 3190 1/17, with a Nematocera (Diptera), some pollen and 14 male ants, 'Langlois-Meurinne/De Ploëg' collection, mounted in Canada Balsam, deposited in the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

Type locality: Le Quesnoy Farm, Chevrière (49°21'N, 02°41'E), region of Creil, Oise department (northern France).

Type strata: Early Eocene, in amber, approximately 53 Mya, Sparnacian, level MP7 of the mammalian fauna of Dormaal (Feugueur, 1963; Nel *et al.*, 1999).

Specific diagnosis: See diagnosis of the genus.

Description: Head (Figs 2A, B, C, 3A, 4A): 0.90 mm long, 1.70 mm wide, 1.60 mm high. Glossa shorter than galea. Paraglossa densely hairy all over. Labial palpal segments similar and cylindrical. Stipes, prementum and cardo short. Mandible with very large preapical tooth on upper margin, apex pointed. Malar space 0.28 mm wide. Labrum with fringe of six bristles. Clypeus 0.34 mm long, 0.68 mm wide, densely punctured, space between punctures smaller than one diameter, area slightly convex. Face and vertex

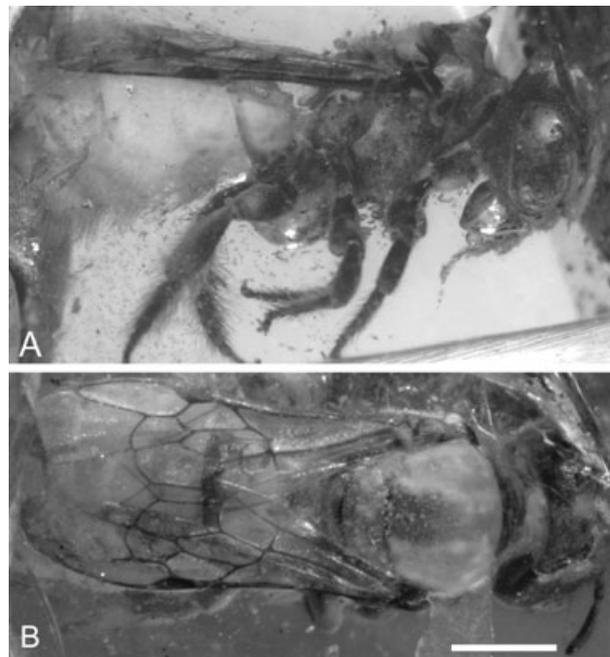


Figure 4. *Palaeomacropis eocenicus* gen. nov. sp. nov. A, lateral view of general habitus. B, dorsal view of general habitus (scale = 1 mm).

densely punctured, space between punctures smaller than one diameter. Facial foveae absent. Paraocular lobe does not extend to clypeus. Only one subantennal suture. Antenna with 12 antennomeres, first flagellar segment 0.02 mm long, scape 0.34 mm long, 0.12 mm wide. Eyes rather broad, 1.20 mm long, 0.60 mm wide, slightly converging towards clypeus.

Mesosoma (Figs 2B, 3A, 4B): 2.20 mm long, 1.90 mm wide, 1.64 mm high. Dorsolateral angle of pronotum with carina. Scutum, scutellum and postsutellum with scattered punctures, space between punctures larger than one diameter. Scrobal groove absent. Episternal groove weak in its dorsal part, almost disappearing ventrally. Propodeal triangle with obtuse lateral margin.

Legs (Figs 2E, 3B, 4A): fore femur 0.80 mm long, tibia 0.76 mm long, tarsi 0.86 mm long. Mid femur 0.76 mm long, tibia 0.64 mm long, tarsi 0.80 mm long. Middle coxa fully exposed laterally. Hind femur 0.80 mm long, tibia 0.94 mm long, 0.32 mm wide, tarsi 1.04 mm long, basitarsus 0.60 mm long, 0.16 mm wide. Hind tibial spurs slender and nearly straight, only slightly curved at apex. Hind tibia without basitibial plate, without tooth on inner face. Hind basitarsus narrower than femur, reaching second tarsomere at apex. Claws simple.

Forewing (Figs 3A, 4B): 3.60 mm long, 1.28 mm wide. Stigma present, longer than prestigma. Vein r arising well before apical margin of stigma. Margin of

stigma convex on marginal cell. Marginal cell 0.98 mm long, 0.30 mm wide, tapering towards apex. Two submarginal cells, first submarginal cell 0.60 mm long, second submarginal cell 0.52 mm long, not much shorter than the first, second submarginal cell extending well beyond apex of stigma. Stigma basal to vein r with margins diverging apically. Beyond vein r, inner margin of stigma convex. Second submarginal cross-vein not sinuated, at obtuse angle to distal part of radial sector. Basal vein M strongly curved.

Hindwing (Figs 3A, 4B): 2.50 mm long, 0.70 mm wide. Jugal lobe 0.60 mm long, much shorter than vannal lobe, 1.10 mm long.

Metasoma (Figs 2D, 4A): 2.76 mm long, 1.80 mm wide. Six exposed metasomal terga and sterna 1–4 with apex straight. Sternum 5 with concave apex. Terga and sterna punctured on base of setae.

Pilosity (Figs 2A, B, C, D, E, 3A, B, 4A, B): face and clypeus with simple, scattered, short, appressed setae. Scutum with very short, simple, suberect setae. Scutellum with apical fringe of simple, erect setae. Mesepisternum and dorsal part of metepisternum covered with plumose setae. Sides of propodeum with numerous long, simple setae, not forming corbicula. Propodeal triangle bare. Front and mid-femora with short, simple setae. Front basitarsus with dense plumose setae on inner side and scattered plumose setae on outer side. Mid basitarsus with dense plumose setae on inner and outer side. Scopa present on hind legs, with setae apparently not plumose. Hind trochanter with curved setae. Long, erect, simple setae on sterna S1, S2, S3, S4, and S5, distinctly longer on S2 than on other sterna. Terga with very short, simple, suberect setae.

DISCUSSION

POSITION OF *PALAEOMACROPIS EOCENICUS* GEN.

NOV. SP. NOV. IN APOIDEA

Palaeomacropis eocenicus is an ST bee because of its similar cylindrical labial palpal segments (Michener, 2000). Thus, *P. eocenicus* is not a Megachilidae or an Apidae. The attribution to a precise taxon within ST bees is complicated by the poor preservation of the glossa.

Palaeomacropis eocenicus cannot be included in the Australian family Stenotritidae because of its antennal structure. The first flagellar segment of Stenotritidae is longer than the scape, unlike the case of *P. eocenicus*.

Palaeomacropis eocenicus does not have glossa with bifid apex. This would exclude it from Colletidae. However, Xeromelissinae (Colletidae) has the same kind of metasomal setae as *P. eocenicus*. It has long, erect to suberect setae on S1, S2, S3, S4, and S5, distinctly longer on S2 than on the other sterna (Michener,

2000). Xeromelissinae is strictly Neotropical, with two fossils currently included in this group, *Chilicola (Hylaeosoma) electrodominicana* Engel, 2000 and *Chilicola gracilis* Michener & Poinar, 1996, both found in Dominican amber (Michener & Poinar, 1996; Engel, 2000). *Palaeomacropis eocenicus* differs from the Xeromelissinae as follows: the episternal groove is ventrally inconspicuous; the stipes, prementum and cardo are not very long; the second submarginal cell is not much shorter than the first; the setae on S2 and the other sterna are apparently not branched or plumose; the stigma is basal to vein r with margins apically diverging (this latter character is present in Chilicolini and *Geodiscelis* Michener & Rozen, 1999) (Michener & Rozen, 1999; Engel, 2000). Therefore, *Palaeomacropis eocenicus* cannot be considered as a Xeromelissinae.

Specialized metasomal setae are also present on the metasoma in the halictid genus *Homalictus* Cockerell 1919 (Alexander & Michener, 1995). *Homalictus* differs from *P. eocenicus* in the enormous scopal hairs that it has on the sterna and the ventral part of the terga, and the plumose scopal hairs on its hind femora and tibia (Michener, 2000).

Among other groups, *P. eocenicus* differs from Andreninae due to its lack of paired subantennal sutures or facial foveae. It differs from the Oxaeinae (Andrenidae) and Diphaglossinae (Colletidae) in the presence of a stigma longer than the prestigma, with vein r arising well before the apical margin of the stigma, and the convex margin of the stigma in the marginal cell. *Palaeomacropis eocenicus* differs from the Colletinae (Colletidae), Halictinae (Halictidae), and Nomioidinae (Halictidae) in its weak episternal groove, mainly dorsal and almost disappearing ventrally (this structure is also absent in the colletine *Hesperocolletes* Michener, 1965). The Nomiinae (Halictidae) also have a reduced episternal groove, as is the case in *P. eocenicus*. Nevertheless, their marginal cell usually does not taper much toward the apex, unlike *P. eocenicus* (Michener, 2000), although some nomiine species do have pointed marginal cells. The Nomiinae typically have a labrum with a strong apical process in the female, unlike *P. eocenicus*.

Unlike *P. eocenicus*, the Baltic amber family Palaeomelittidae Engel, 2001 has no long, erect setae on the metasomal sterna. However it does have a well developed jugal lobe (Engel, 2001), which *P. eocenicus* does not.

Palaeomacropis eocenicus and Melittidae are ST bees and they have in common the absence (or near absence) of episternal and scrobal grooves. Their jugal lobe (on the hindwing) is clearly shorter than the vannal lobe (characters shared with LT bees). The middle coxa of *Palaeomacropis eocenicus* is fully exposed laterally and nearly reaches the lower metapleural pit,

Lutz, 1993 discovered in Eocene shales from Germany (Lutz, 1993). All of these taxa are included in the monophyletic clade of 'Melittidae + LT bees'. The first nonmelittid ST bee fossil is *Electroictus antiquus* Engel 2001 from more recent Baltic amber (Engel, 2001). These fossil data support one of the hypotheses put forth by Alexander & Michener (1995) and Danforth *et al.* (2006a, b): Melittidae could be the most basal group of the Apoidea (Fig. 1B). They also support the Perkins–McGinley hypothesis, namely that obtuse or bilobed glossa of Colletidae could be apomorphic (Michener, 2000).

PALAEOMACROPIS EOCENICUS GEN. NOV. SP. NOV.:
A FOSSIL OF THE FIRST SPECIALIZED
OIL-COLLECTING BEE?

Palaeomacropis eocenicus is characterized by dense plumose setae on the inner and outer surfaces of the mid basitarsus and long, erect setae on the metasoma (see description). These kinds of setae could be linked to the collection of oil and pollen, as in the contemporary oil-collecting bee genus *Macropis*. Indeed, the oil of *Lysimachia* sp. flowers (Primulaceae) is harvested by the *Macropis* females using specialized setae on the inner surface of their fore and mid basitarsi (Popov, 1958; Vogel, 1976; Cane *et al.*, 1983; Michez & Patiny, 2005). Moreover, dry pollen is initially held on the same simple, long, erect setae of the metasomal sterna (Cane *et al.*, 1983).

Lysimachia are probably too modern to have been the host-plant of *Palaeomacropis eocenicus*. The oldest fossil record of *Lysimachia* consists of the fossil seeds from late Middle Miocene of Jutland Denmark (Hao *et al.*, 2004). *Lysimachia* L. constitute a derived genus included in a derived family of which origin is likely posterior to *P. eocenicus* (Judd *et al.*, 2002). However, others plant families producing oil, like Malpighiaceae (Davis *et al.*, 2002), are known from the Eocene and could have been the host-plant of *Palaeomacropis eocenicus*.

Oil flowers (e.g. *Lysimachia* L.) are visited and pollinated by highly specialized bees (Buchmann, 1987). The close relationship between oil flowers and their pollinators presents an example of insect-plant coevolution. For example, the tight relationship between *Rediviva* sp. (Melittidae) and *Diascia* sp. (Scrophulariaceae) is well known (Steiner & Whitehead, 1991, 2002). The presence of a bee with such specialized structures, such as *P. eocenicus* in the early Eocene, could support the hypothesis that a close relationship had already existed between bees and oil flowers.

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as in contemporary species *Melitta* (character shared with LT bees) (Michener, 2000).

In conclusion, *P. eocenicus* is an ST bee, with a fully exposed middle coxa, without facial foveae or paired subantennal sutures, and with the jugal lobe shorter than the vannal lobe. Therefore, we include *P. eocenicus* in Melittidae.

POSITION OF *PALAEOMACROPIS EOCENICUS* GEN.

NOV. SP. NOV. IN MELITTIDAE

Engel (2001) distinguishes four subfamilies within Melittidae: Dasypodinae, Macropidinae, Meganomiinae, and Melittinae. Engel (2001) notably resurrects the subfamily Macropidinae Robertson 1904 for the contemporary genus *Macropis* Panzer 1809 and the Baltic amber genus *Eomacropis* Engel, 2001, both with two submarginal cells. He excludes Macropidinae from the Dasypodinae on the basis of the hairy paraglossa and the second abscissa of Rs that is slanting and widely separated from 1m-cu. He excludes them from the Melittinae on the basis of the presence of only two submarginal cells, the presence of yellow maculations on the face of the male, and the presence of a pygidial plate in the male. Macropidinae differs from the Meganomiinae due to its two submarginal cells, the pointed apex of its marginal cell, and its mandible with a very large preapical tooth on the upper margin.

In relation to this diagnosis, it appears that *P. eocenicus* must be considered as a Macropidinae. However, *P. eocenicus* shares some apomorphic characters with other melittid genera: no basitibial plate (like *Dasyпода*), a propodeal structure like that of *Meganomia* and mid-basitarsal setae like those of *Rediviva*. Thus, cladistic analysis helps us find the most parsimonious solution for classification.

The cladistic analysis yielded one shortest tree length (23 steps, CI = 0.78, RI = 0.76) (Fig. 5). This confirms the position of *P. eocenicus* in Macropidinae *sensu* Engel (2001). The subfamily is characterized by the venation of the forewing (character 8^a). *Palaeomacropis eocenicus* differs from *Eomacropis* in the long, erect setae on its metasomal sterna (character 17) and dense plumose setae on its mesotarsus (character 12). It differs from *Macropis* by lacking dense plumose setae on each side of its protarsus (character 11). *Palaeomacropis eocenicus* differs from other Macropidinae genera (*Macropis* and *Eomacropis*) in the curved setae on its trochanter (character 13), and the absence of a basitibial plate (character 14). The originality of *P. eocenicus* is such that it can fall within a new monobasic genus included in Macropidinae.

FOSSILS OF MELITTIDAE

In common with other bee families, fossils of Melittidae are very rare. *Dasyпода basaltica* Zhang 1989 is a

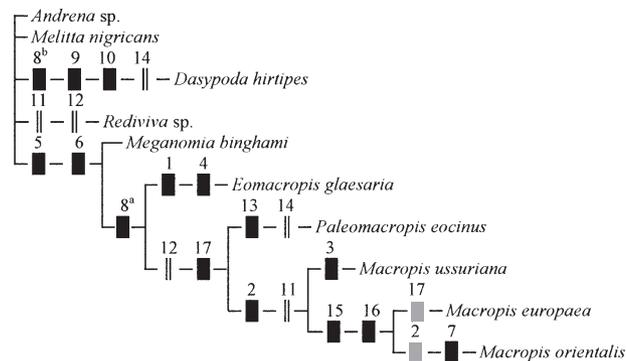


Figure 5. Best tree of cladistic analysis (length = 23 steps, CI = 0.78, RI = 0.76). Black square, apomorphy; double line, possible convergency; grey square, possible reversion. The state of character 8 is indicated by a (state 1) and b (state 2).

compression fossil only recognizable by its forewing. It strongly resembles the Macropidinae and differs from the Dasypodinae on the basis of its second abscissa of Rs widely separated from 1m-cu (Zhang, 1989). Therefore, we include it in the Macropidinae and in the genus *Macropis* *s.l.*, under the name *Macropis basaltica* comb. nov. *Melitta willardi* Cockerell 1909 is also a compression fossil. It is characterized by the scopa of the hind tibia and basitarsus, three submarginal cells and their diagnostic shape (Cockerell, 1909). Without any other indications, it appears that *M. willardi* is indeed a Melittidae: Melittinae. *Eomacropis glaesaria* Engel 2001 is from Baltic amber of the late Eocene. It is characterized by two submarginal cells subequal in length and its slanting second abscissa of Rs widely separated from 1m-cu. This bee is indeed a Melittidae: Macropidinae. The Baltic amber genera *Glyptapis* Cockerell 1909 and *Ctenoplectrella* Cockerell 1909 were previously included in the Melittidae together with the contemporary genus *Ctenoplectra* Kirby 1826 (Zeuner & Manning, 1976; Burnham, 1978). These two fossil genera are now included in Megachilidae: Osmiini (Engel, 2001). Likewise, Gerlach (1989) described an unnamed *Dasyпода* species from Baltic amber (Dasypodinae) that Engel (2001) designated as a *Glyptapis* (Megachilidae).

Therefore, all the fossils attributed to Melittidae are from the middle Eocene or later, and *P. eocenicus* is thus the oldest record of a melittid bee.

FOSSIL RECORDS AND PHYLOGENY OF APOIDEA

Palaeomacropis eocenicus highlights the gap between fossil data and the traditional phylogenetic tree of bees (Fig. 1A). Presently, the three oldest described bee fossils are an Apidae (*C. prisca*), a Megachilidae (*P. hirsutus*) and a Melittidae (*P. eocenicus*). We can add the corbiculate Apini *Eckfeldapis electrapoides*

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APPENDIX 1

Taxa are studied with material from the collection of the University of Mons-Hainaut (Mons, Belgium), the Oberösterreichisches Landesmuseums (Linz, Austria) and the Zoological Institute of St Petersburg (Federation of Russia). The character states of *Eomacropis glaesaria* are established based on Engel (2001).

OUTGROUP

Andrena sp.

INGROUP

Dasypoda hirtipes (Fabricius 1793) (Dasypodainae); *Meganomia binghami* (Cockerell, 1909) (Meganomiinae); *Melitta nigricans* (Alfken 1905) and *Rediviva* sp. (Melittinae); *Eomacropis glaesaria* Engel, 2001, *Macropis* (*Macropis*) *europaea* Warncke 1973, *Macropis* (*Sinomacropis*) *orientalis* Michez 2005 and *Macropis* (*Paramacropis*) *ussuriana* (Popov, 1936) (Macropidinae).

APPENDIX 2

Our cladistic analysis is based on morphological features of adults.

1. Glossa: shorter than galea = 0; longer than galea = 1.
2. Labrum: with subapical crest = 0; without subapical crest = 1.
3. Vertex behind ocelli: narrow = 0; well extended with a carina = 1.
4. Metanotum: not carinated = 0; carinated = 1.
5. Basal width of propodeal triangle: equal to less than four-fifths of basal width of propodeum = 0;

- longer than four-fifths of basal width of propodeum = 1.
6. Upper lateral margin of propodeal triangle: acute = 0; obtuse = 1.
7. Propodeal triangle: hairless = 0; hairy = 1.
8. Forewing, submarginal cells: three = 0; two, second as long as or longer than first = 1; two, second shorter than first = 2.
9. Forewing, second abscissa of Rs: widely separated from 1m-cu = 0; not widely separated from 1 m-cu = 1.
10. Forewing, second abscissa of Rs: slanting = 0; at right angles to longitudinal veins = 1.
11. Fore basitarsus: with normal setae = 0; with dense plumose setae on inner and outer side = 1.
12. Mid basitarsus: normal setae = 0; dense plumose setae on inner and outer side = 1.
13. Curved setae on trochanter: absent = 0; present = 1.
14. Basitibial plate: present = 0; absent = 1.
15. Length of metabasitarsus: half as long as tibia = 0; less than half as long as tibia = 1.
16. Width of metabasitarsus: over four times as long as broad = 0; less than four times as long as broad = 1.
17. Setae on apex of metasomal sternum 2 (S2): shorter than disc of S2 = 0; longer than disc of S2 = 1.

APPENDIX 3

Table A1. Character-state matrix for cladistic analysis

Taxons	Characters																
	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17
Outgroup																	
<i>Andrena</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ingroup																	
<i>Dasypoda hirtipes</i>	0	0	0	0	0	0	0	2	1	1	0	0	0	1	0	0	0
<i>Eomacropis glaesaria</i>	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>Macropis</i> (<i>Macropis</i>) <i>europaea</i>	0	1	0	0	1	1	0	1	0	0	1	1	0	0	1	1	0
<i>Macropis</i> (<i>Paramacropis</i>) <i>ussuriana</i>	0	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	1
<i>Macropis</i> (<i>Sinomacropis</i>) <i>orientalis</i>	0	0	0	0	1	1	1	1	0	0	1	1	0	0	1	1	1
<i>Meganomia binghami</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Melitta nigricans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Palaeomacropis eocenicus</i> sp. nov.	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	1
<i>Rediviva</i> sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0