

# Monographic revision of the melittid bees (Hymenoptera, Apoidea, Melittidae *sensu lato*)

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The popularity of bees is mainly due to a single species, the domestic honeybee although there are in fact thousands of different wild bees. Bees constitute a monophyletic group including 16,000 species in seven families. In this presentation, we propose an overview of one key group in the bee phylogeny: the Melittidae *s.l.* We show information about their diversity, biogeography and biology. Moreover, we investigate the origin of Melittidae *s.l.* and the characteristics of their early diversification.

*Keywords:* diversification, monophyletic group, honeybee, biogeography, phylogeny

Bees are among the most common and familiar animals. This popularity is mainly due to a single species, the domestic honeybee (*Apis mellifera*) although there are in fact thousands of other species of wild bees in the world. All bee species constitute together a monophyletic group including more than 16,000 described species and seven families currently acknowledged (Michener 2007). The extensive studies carried out on the honeybee contrast markedly with the global level of knowledge of most wild bees, which have received comparatively little attention so far. The ancestral states, the early diversification and the phylogeny of bees need particularly new advancements to propose a strong hypothesis on their evolution.

The phylogenetic relationships among bee families have been recently deeply reconsidered. Traditional hypothesis presented the colletid bees as basal in the clade of bees (Michener 1944, Engel 2001). This hypothesis was mainly based on a few morphological similarities with the ancestral sphecid wasps. New robust phylogenies including morphological and molecular dataset have provided strong support to define the paraphyletic group of Melittidae *s.l.* as the real sister group of all other contemporary bees (Danforth *et al.* 2006). This group includes three families: Dasypodaidae, Melittidae *s.str.* and Meganomiidae (Fig. 1). This ‘melittid basal topology’ hypothesis calls for further research on the systematics, the

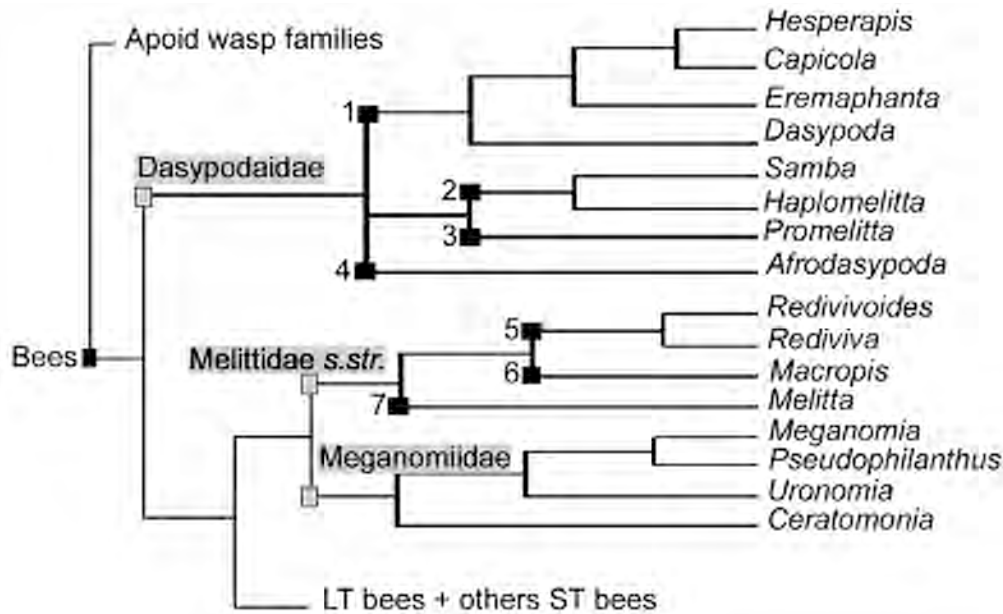


Figure 1. Phylogeny of Melittidae *s.l.* from Michener (1981) adapted with taxonomical hypothesis of Engel (2005) and Danforth *et al.* (2006). 1 = Dasypodaini Michener 1981, 2 = Sambini Michener 1981, 3 = Promelittini Michener 1981, 4 = Afrodasypodaini Engel 2005, 5 = Redivivini Engel 2001, 6 = Macropidini Robertson 1904, 7 = Melittini Schenk 1860.

biogeography, the biology and the host-plant associations of Melittidae *s.l.* to understand the ancestral states and the early diversification of all bees.

Systematic studies of Melittidae *s.l.* are limited to a few general revisions. Moreover, the information about all 16 melittid genera is generally scattered. We filled these gaps by undertaking a thorough systematic revision of the following melittid bee genera: *Capicola*, *Dasyпода*, *Eremaphanta*, *Macropis*, *Melitta* and *Promelitta* (Table 1; Michez 2007). In the same time, we compiled information about the general biology and the host-plants of Melittidae *s.l.* (Michez *et al.* 2008). Using phylogenies and host-plants records of several genera, we examined the inheritance of the host-plant choices throughout the evolution of melittid. Finally, we investigated the origin of Melittidae *s.l.* and the characteristics of their early diversification. We carried out notably to a detailed examination of the fossil specimens available and we included a new fossil record that we described and confronted to the current state of knowledge of bee systematics.

We present hereafter a review of the available information about melittid bees throughout our own works and a synthesis of the literature on this topic.

## SYSTEMATICS AND BIOGEOGRAPHY OF THE MELITTIDAE *S.L.*

Melittidae *s.l.* includes 202 species: 198 contemporary species and 4 fossil species (Table 1). Dasypodaidae is the most diverse (101 species) while Meganomiidae comprises only 12 species. Melittid bees occur in temperate and xeric ecosystems

Table 1. Taxonomy, species richness and distribution of the Melittidae s.l. according to Michener (2007) [\* fossil taxa; (\*) fossil and contemporary taxa; N1= subgenera diversity; N2= species diversity; South.= Southern; Mad.= Madagascar, Ken.= Kenya; M.= Mali; OW = Old World; Near.= Nearctic].

Families	Tribes	Genera	Diversity (N1-N2)	Distribution	Max. of diversity	Main references	
Dasypodaidae	Dasypodaini	<i>Dasyoda</i>	4 – 33	Palaearctic	Med.. basin	Warncke (1973), Michez et al. (2004a, b.)	
	Dasypodaini	<i>Eremaphanta</i>	2 – 9	Central Asia	Turkestan	Popov (1957), Michez & Patiny (2006)	
	Dasypodaini	<i>Capicola</i>	1 – 13	South. Africa	Cape province	Michener (2007), Michez et al. (2007a)	
	Dasypodaini	<i>Hesperapis</i>	7 – 38	Nearctic	California	Stage (1966), Michener (1981, 2007)	
	Sambini	<i>Haplomelitta</i>	5 – 5	South Africa	South Africa	Michener (1981, 2007)	
	Sambini	<i>Samba</i>	1 – 1	Kenya	Kenya	Michener (1981, 2007)	
	Promelittini	<i>Promelitta</i>	1 – 1	North Africa	North Africa	Michez et al. (2007b)	
	Promelittini	<i>Afrodasyopoda</i>	1 – 1	South Africa	South Africa	Engel (2005)	
	Meganomiidae	Meganomiini	<i>Geratomonia</i>	1 – 1	Namibia	Namibia	Michener (1981)
		Meganomiini	<i>Meganomia</i>	1 – 5	Ethiopian	South. Africa	Michener (1981)
Meganomiini		<i>Pseudophil.</i>	2 – 4	Mad. and Ken.	Kenya	Michener (1981), Michener et al. (1990)	
Meganomiini		<i>Uromonia</i>	2 – 2	Mad., Ken., M.	Mad., Kenya	Michener & Brooks (1987)	
Melittini		<i>Melitta</i> (*)	2 – 44	OW and Near.	Europe	Michez & Eardley (2007)	
Melittini		<i>Rediviva</i>	1 – 24	South. Africa	South Africa	Whitehead & Steiner (2001), Whitehead et al. (in press)	
Melittidae	Melittini	<i>Redivivoides</i>	1 – 3	South Africa	South Africa	Michener (1981, 2007)	
	Eomacropidini	<i>Eomacropis</i> *	1 – 1	Baltic amber	Baltic amber	Engel (2001)	
	Macropidini	<i>Macropis</i> (*)	3 – 16	Holarctic	Eastern Asia	Michener (1981), Michez & Patiny (2005)	
	Macropidini	<i>Paleomacropis</i> *	1 – 1	Oise amber	Oise amber	Michez et al. (2007c)	

of the Nearctic and the Old World. Ethiopian region is the only region where the distributions of all families overlap. Ethiopian region shows the maximum of generic diversity but the maximum of species diversity is reached in the Palearctic region. The African continent (Ethiopian region + North Africa) lumps clearly the maximum of both generic and specific diversity.

Dasypodaidae can be distinguished by an original combination of several features: short tongue with all segments of the labial palpus similar to one another, paraglossa reduced, submentum V-shaped and two submarginal cells with the first submarginal crossvein at right angles to longitudinal vein (Michener 1981). They include four tribes and eight genera (Table 1). The phylogenetic relations among genera and tribes are still dubious.

Dasypodaidae occur in both the Old World and the Nearctic region. This family is absent in South America, Australia and tropical areas. The specific diversity is maximal in xeric areas: the southwestern deserts of North America (*Hesperapis*), the Mediterranean basin (*Dasypoda* and *Promelitta*), the Kyzyl kum in Central Asia (*Eremaphanta*) and the Southern Africa (*Afrodasyroda*, *Capicola* and *Haplomelitta*). *Dasypoda* is the only widespread genus that occurs in the temperate to the xeric areas of the Palearctic (Fig. 2). *Dasypoda* determines the northern limit of Dasypodaidae to the 62<sup>nd</sup> northern parallel. The other Dasypodaidae genera, *Afrodasyroda*, *Capicola*, *Eremaphanta*, *Hesperapis* and *Promelitta* are each one endemic in different Old World deserts.

Meganomiidae is the smallest family of Melittidae *s.l.* (Table 1). In light of recent molecular analyses, Meganomiidae is probably the sister group of the Melittidae *s.str.* (Danforth *et al.* 2006). Meganomiide species are robust bees with

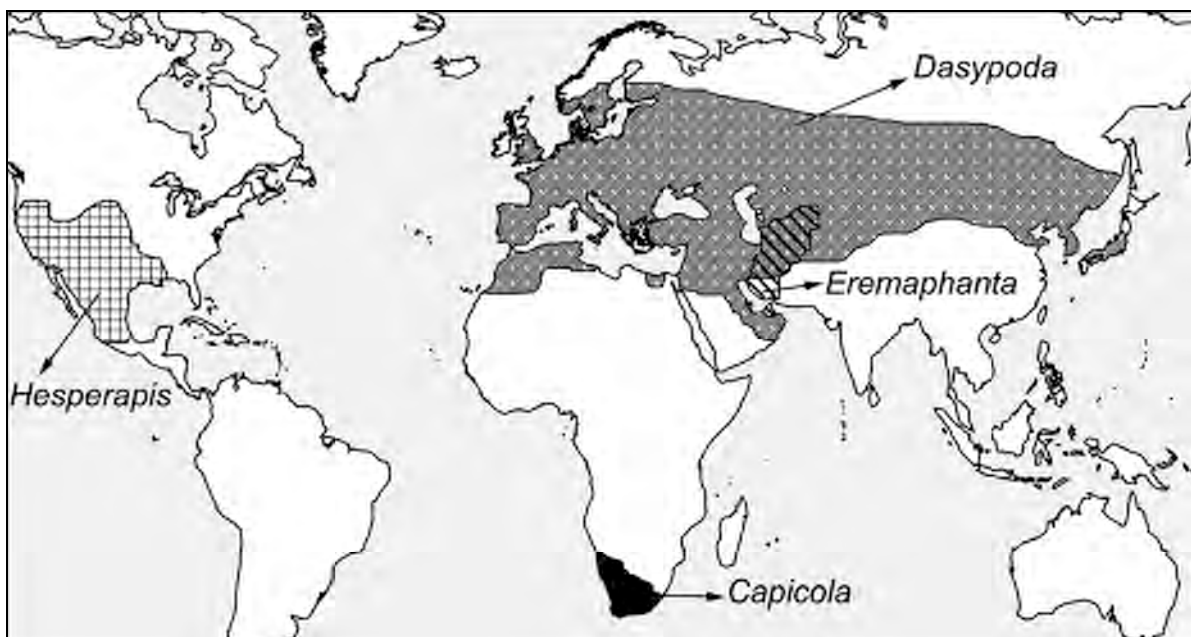


Figure 2. Global distribution of Dasypodaini including the genera *Capicola*, *Dasypoda*, *Eremaphanta* and *Hesperapis*.

three sub-marginal cells, extending yellow marking on the whole body and many unique modifications of legs and hidden sterna of male (Michener 1981). Meganomiidae is restricted to the Sub-Saharan Africa except one undescribed *Meganomia* species recorded in Yemen. Michener (1981), Michener & Brooks (1987) and Michener *et al.* (1990) reviewed the four included genera: *Ceratonomia* Michener 1981, *Meganomia* Cockerell 1931, *Pseudophilanthus* Alfken 1939 and *Uromonia* Michener 1981.

Like Meganomiidae, most Melittidae *s.str.* have three submarginal cells (except *Macropis*), which set apart from the Dasypodidae. Melittidae *s.str.* is always smaller than Meganomiidae. The largest Melittidae *s.str.* is 15 mm long while the smallest Meganomiidae is 17 mm. The body of Melittidae *s.str.* is mainly black but some males of *Macropis* display yellow markings on the head. Designations of tribe are still unfixed in the Melittidae *s.str.* Michener (1981) did not distinguish any tribe and included all genera in the Melittini. Engel (2005) considered two different subfamilies: Macropidinae and Melittinae. The Macropidinae have been split into two tribes: Eomacropidini (including the fossil *Eomacropis* Engel 2001) and Macropidini (including the contemporary *Macropis* Panzer 1809 and the fossil *Paleomacropis* Michez & Nel 2007). Two tribes have been recognized in the Melittinae, on the one hand the Redivivini with genera *Rediviva* and *Redivivoides*, on the other hand the Melittini with the genus *Melitta*. We follow the tribe designation of Engel (2005). Melittidae *s.str.* is diverse (86 species) in the Old World and the Nearctic region (Table 1). Unlike the other melittid bees, the Melittidae *s.str.* show notable climatic preferences. As written above, most Dasypodidae (*Afrodasyppoda*, *Capicola*, *Dasypoda*, *Eremaphanta* and *Promelitta*) and all Meganomiidae are restricted to the xeric areas of the Old World. By contrast the ecological optimum for Melittidae *s.str.* seems to live in cooler temperate climate. At least *Melitta* and *Macropis* prefer the cool temperate ecosystems. Both genera, *Rediviva* and *Redivivoides*, are restricted to the coastal area of South Africa.

## **BIOLOGY OF THE MELITTIDAE S.L.**

As far as known, all Melittidae *s.l.* are solitary and univoltine. All females can produce offspring and each species completes one cycle of development during one year. The general cycle of development is therefore relatively unchanged (Fig. 3). Males emerge from the ground some days before females. After female emergences, males mate with virgin females generally on host-plants around emergence site (*i.e. rendez-vous flowers*, Alcock *et al.* 1978). After mating, gravid females begin to dig a nest. At the bottom of lateral tunnels, females build one or a few chambers where they bring pollen (Fig. 3D). When the pollen ball is formed, they lay one egg on the top. The larva eats the pollen during about ten days and grows fastly (Fig. 3E). After consuming all the pollen and after defecation, larva overwinters and becomes pupa the following year (Fig. 3F).

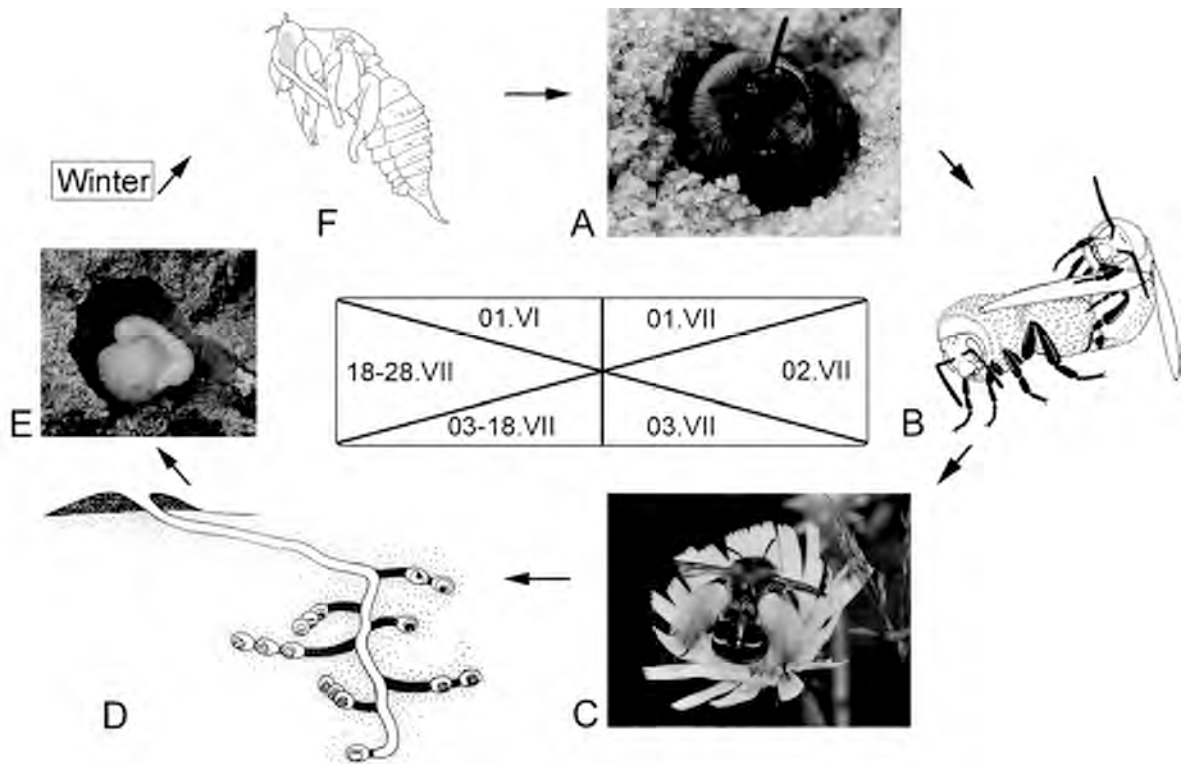


Figure 3. General cycle of development of Melittidae s.l.. A. Emergence of *Dasygoda hirtipes* female (picture N.J. Vereecken). B. Copulation of a pair of bees (drawing M. Terzo). C. Female of *D. hirtipes* foraging on *Hypochoeris radicata* L. (picture N.J. Vereecken). D. Nest of *Dasygoda braccata* (from Radchenko 1987). E. Larva of *D. hirtipes* (picture M. Gosselin). F. Pupa of *Hesperapis trochanterata* (from Rozen 1987).

The mechanisms of the emergence are unexplored in Melittidae s.l.. However, like most other specialist bees, the melittid bees probably need a minimal overlap between their flight period and the host-plant(s) blooming (Thorp 1979, 2000, Danforth 1999, Minckley *et al.* 2000). Flight collecting period must be long enough to produce the brood cells. In xeric areas like the southwestern American desert, synchronisation between *Hesperapis* emergence and their respective host-plant blooming is probably possible thanks to the abilities of *Hesperapis* to feel the variation of the soil humidity after raining (Hurd 1957). In mesic areas, Michez *et al.* (in press) showed that the emergence of *Melitta nigricans* females (Melittidae s.str.) overlaps the blooming peak of its host-plant, *Lythrum salicaria* L. However, they did not study the factors eliciting the emergence of *M. nigricans*.

Mating behaviour is only described for *Dasygoda hirtipes* (Dasypodaidae) (review of mating behaviour of bees see Ayasse *et al.* 2001). Males and females of *D. hirtipes* mate on their exclusive host-plants, yellow Asteraceae, (Bergmark *et al.* 1984). Bergmark *et al.* (1984) highlighted that mate recognition of male in *D. hirtipes* is driven by multiple factors as presence of scopae, scent of female and scent of host-plant. The other Melittidae s.l. could have the same kind of mating behaviour on 'rendez-vous flowers'.

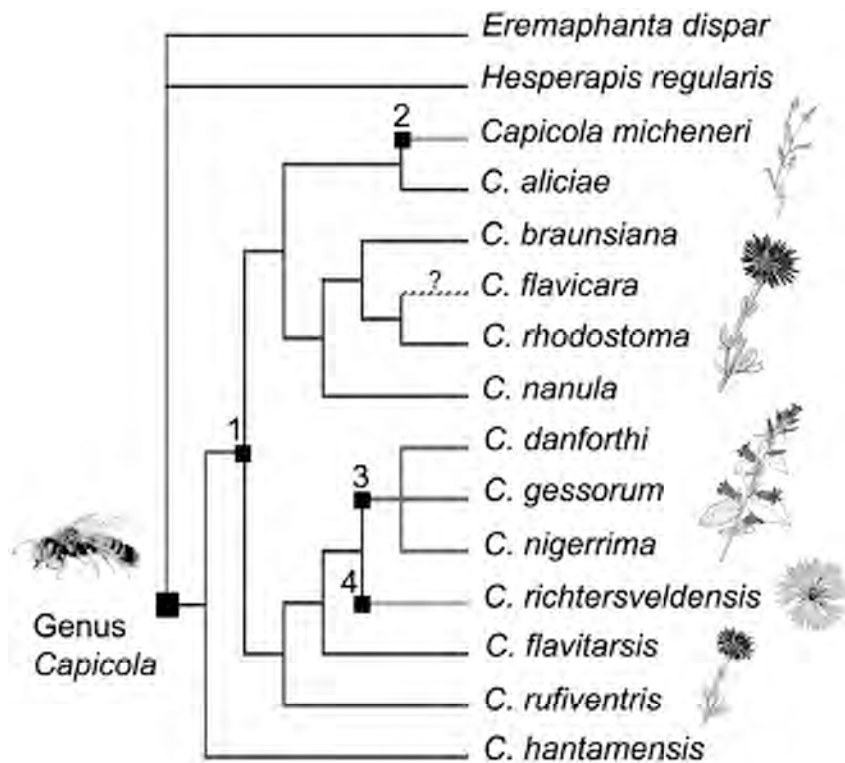


Figure 4. Phylogeny and host-plants of *Capicola* (from Michez & Kuhlmann 2007; Michez & Timmermann unpublished data). 1 = shift from Campanulaceae to Aizoaceae; 2 = shift from Aizoaceae to Fabaceae; 3 = shift from Aizoaceae to Campanulaceae; 4 = shift from Aizoaceae to Asteraceae.

## EVOLUTION OF THE MELITTIDAE S.L.

### Inheritance of host-plants in the Melittidae s.l.

In most cases, closely related species visit similar host plants. These results confirm previous studies on the evolution of flower relationships in non-melittid bees [Müller 1996 for Anthidiini (Megachilidae); Sipes & Tepedino 2005 for the genus *Diadasia* (Apidae)]. However, floral choices have interestingly not always been inherited among species in the course of the evolution of melittid bees. We observe independent shifts to different host plants (related or not) in the genera *Capicola* (Fig. 4), *Dasypoda*, *Hesperapis*, *Macropis* and *Melitta* (Michez *et al.* 2008).

Most Melittidae s.l. have a relatively narrow host range. Among the 108 species with host-plant records, we record only 16 mesolectic or polylectic species making oligolecty a dominant condition within most groups. Our data provide strong evidence for the rarity of host breadth variations. Most cases of host-plant shifts involve shifts of host-plant use (shift from one specialisation to another one).

### Implication for the understanding of the early diversification of bees

Melittids constitute a group of specialist taxa, which are basal in the bee phylogeny (see previous chapter). Likewise, we observe that a lot of other basal

groups are also oligolectic (*i.e.* Lithurginae, Panurginae and Rophitinae) (Danforth *et al.* 2006). The fact that the most primitive taxa within several bee families are oligolectic could be a hint that, in general, polylecty is the derived foraging strategy that has evolved in bees. This hypothesis is supported by the recent discovery of the bee fossil, *Paleomacropis eocenicus* from the early Eocene (~53 myBP) (Michez *et al.* 2007c). This Melittidae *s.str.* presents oil-collecting structures on its legs similar to those observed in contemporary oil-collecting bees. In light of these records, and since most contemporary oil-collecting bees are oligolectic, it can be reasonably assumed that this fossil bee was a specialist taxon, which increases the likelihood for oligolecty to constitute an ancestral condition in bees.

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