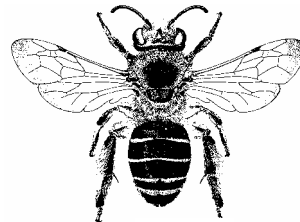
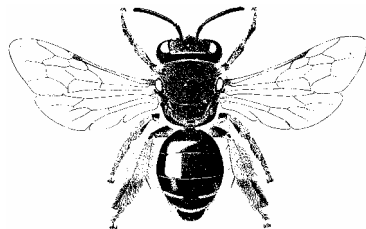


**Monographic revision of the Melittidae *s.l.* (Hymenoptera:
Apoidea: Dasypodaidae, Meganomiidae, Melittidae)**

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Ph-D thesis submitted in fulfilment of the degree of Doctor in Sciences
Mons -September 2007
Supervisor: Prof. P. Rasmont



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*A mes parents,
Brigitte et Albert*

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ABSTRACT

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. 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. 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. This group includes three families: Dasypodaidae, Melittidae *s.str.* and Meganomiidae. This “melittid basal topology” hypothesis calls for further research on the systematics, the 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 15 melittid genera is generally scattered. In this Ph-D, we proposed to fill these gaps by undertaking a thorough systematic revision of the following melittid bee genera: *Capicola*, *Dasypoda*, *Eremaphanta*, *Macropis*, *Melitta* and *Promelitta*. In the same time, we compiled information about the general biology and specially on the host-plants of Melittidae *s.l.*. 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.

RESUME GENERAL

Dans de nombreuses sociétés humaines, les abeilles mellifères (*Apis mellifera*) ont exercé une grande fascination. Elles ont inspiré les hommes qui s'en sont servi comme de puissants symboles. La vie sociale complexe et stable des abeilles nous renvoie l'image d'une société parfaitement organisée, d'une certaine abnégation au travail ou encore d'abondance et de félicité dans la visite des fleurs parfumées et la douceur du miel. Ces chers insectes font aussi partie des espèces domestiquées par l'homme et donc associées quotidiennement à son environnement direct. De plus, elles furent parfois la seule source de sucre directement accessible à l'homme. Elles sont aujourd'hui un des organismes "modèles" les plus étudiés par les scientifiques.

Pourtant, ces abeilles que nous pensons si bien connaître sont bien plus nombreuses et diverses que dans l'imagerie populaire. L'abeille mellifère fait partie d'un genre, le genre *Apis*, qui ne représente que sept espèces parmi les milliers d'espèces d'abeilles déjà décrites. La grande majorité des espèces d'abeilles sont en réalité solitaires et discrètes, les imagos¹ ne vivant que quelques semaines.

Actuellement, les abeilles sont considérées comme un groupe monophylétique (Apoidea Apiformes) qui comprend environ 1200 genres et 16000 espèces répartis sur toute la surface du globe à l'exception des déserts polaires. Elles sont divisées en sept familles (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae et Stenotritidae) associées en deux groupes informels, les abeilles à langue longue, comprenant Apidae et Megachilidae, et les abeilles à langue courte, comprenant toutes les autres familles. Traditionnellement, les abeilles à langue courte et plus particulièrement la famille des Colletidae, sont considérées comme "primitives" c'est-à-dire basales dans le clade des abeilles. Cette hypothèse s'appuie principalement sur la forme bifide de la glosse des Colletidae qui est proche de celle des ancêtres des abeilles, les guêpes fouisseuses (Apoidea Spheciformes). Les abeilles à langue longue seraient alors apparues plus tard, la famille des Melittidae étant considérées comme faisant le lien entre les groupes à langue longue et à langue courte. Cependant, plusieurs analyses phylogénétiques basées dans un premier temps sur des seuls arguments morphologiques, dans un second temps sur des arguments morphologiques et moléculaires, mettent en doute cette hypothèse des "Colletidae basaux" dans la phylogénie des abeilles. Des récentes analyses moléculaires présentent en fait les abeilles à langue courte (Andrenidae, Colletidae, Halictidae et Stenotritidae) comme dérivées d'un groupe paraphylétique formé par les abeilles à langue longue et les Melittidae. Dans

¹ Individu adulte sexué.

cette hypothèse, ce sont les Melittidae qui sont considérées comme basales dans le clade des Apoidea Apiformes. De plus, les mêmes analyses suggèrent la paraphylie de la famille traditionnelle des Melittidae et proposent de considérer trois familles distinctes à partir de cette famille, les Dasypodaidae, les Melittidae *sensu stricto* et les Meganomiidae. Au vu de cette nouvelle hypothèse sur la position basale des Melittidae *sensu lato*² au sein du clade des abeilles, l'étude des melittides devient cruciale pour bien comprendre l'apparition et le début de la diversification des abeilles.

L'objectif principal de cette thèse de doctorat est de présenter une révision monographique des Melittidae *sensu lato*. Cette révision monographique permet de dégager une vue exhaustive de leur diversité, de leur variabilité morphologique, de leur distribution et de leur biologie, ainsi que l'évolution de ces caractéristiques.

Le premier type de recherche à réaliser, incontournable pour pouvoir étudier l'évolution d'un groupe, est son étude systématique et taxonomique. Avant cette thèse, les connaissances sur la systématique des Melittidae *s.l.* étaient pratiquement réduites à la définition des genres, des tribus et de leurs relations phylogénétiques respectives. Seuls quelques genres ont été étudiés de manière exhaustive. Au cours de mes premières années de recherche, j'ai donc revus séparément plusieurs des 15 genres de melittides: le genre *Dasypoda* (annexe I), le genre *Macropis* (annexe II), le genre *Eremaphanta* (annexe III), le genre *Promelitta* (annexe IV), le genre *Capicola* (annexe V) et le genre *Melitta* (annexe VII). Parallèlement, les principaux aspects de leur biologie ont été revus. Une attention plus particulière a été portée sur les choix floraux des Melittidae *s.l.* afin de caractériser l'amplitude du régime alimentaire des femelles en pollen. Pour ce faire, j'ai compilé des données issues d'observations faites directement sur le terrain avec des données issues d'études palynologiques. Dans un second temps, l'évolution de ces choix alimentaires a été analysée en superposant la phylogénie de cinq genres de melittides et de leurs choix floraux respectifs (annexe VIII). Enfin, j'ai proposé une hypothèse globale sur l'origine et la diversification des Melittidae *s.l.*. Pour ce faire, j'ai notamment étudié les spécimens fossiles disponibles (annexe VI).

Dans cette révision, les Melittidae *s.l.* incluent 202 espèces parmi lesquelles 198 espèces contemporaines et 4 espèces fossiles. Elles occupent les zones tempérées et xériques à travers le monde mis à part l'Amérique du Sud, l'Australie et les zones tropicales. La région éthiopienne est la seule région où les trois familles (Dasypodaidae, Melittidae *s.str.* et Meganomiidae) sont présentes. Cette région montre aussi le maximum de diversité générique du groupe mais c'est dans le Paléarctique que l'on trouve le plus d'espèces. Si on considère maintenant le continent africain dans son entièreté (région éthiopienne et Afrique du Nord), on constate que la diversité générique et spécifique y est maximale pour les Melittidae *s.l.*.

² Les Melittidae *sensu lato* (*s.l.*) incluent les trois familles issues de la division de la famille traditionnelle des Melittidae : les Dasypodaidae, les Melittidae *sensu stricto* (*s.str.*) et les Meganomiidae.

Avec 101 espèces, les Dasypodaidae sont les melittides les plus diversifiés. Cette famille inclus huit genres (*Afrodasympoda*, *Capicola*, *Dasypoda*, *Eremaphanta*, *Haplomelitta*, *Hesperapis*, *Promelitta*, *Samba*) répartis dans l'Ancien Monde³ et dans le Néarctique⁴. La richesse spécifique est maximale dans les zones xériques comme les déserts du nord-ouest américains (Californie, Texas, ...), le bassin méditerranéen, le Kysylkum (Asie centrale) et la pointe Sud de l'Afrique. Le genre *Dasypoda* est le seul genre largement répandu. Il est commun dans les zones tempérées et xériques du Paléarctique. Les *Dasypoda* définissent la limite nord de l'aire de répartition des Dasypodaidae au 62^{ème} parallèle.

Les Meganomiidae comprennent quatre genres (*Ceratonomia*, *Meganomia*, *Pseudophilanthus*, *Uromonia*) et seulement 12 espèces répertoriées à ce jour. Cette famille est endémique à l'Afrique mis à part une espèce non décrite connue du Yémen.

La famille des Melittidae *s.str.* inclut aussi quatre genres (*Macropis*, *Melitta*, *Rediviva*, *Redivivoides*) mais avec 85 espèces décrites, elle est beaucoup plus diversifiée que les Meganomiidae. Les Melittidae *s.str.* sont distribuées dans l'Ancien Monde et dans le Néarctique. Leur optimum écologique semble se situer dans les écosystèmes tempérés. *Melitta* et *Macropis* préfèrent en tout cas les écosystèmes tempérés de la région Holarctique. Les deux autres genres, *Rediviva* et *Redivivoides*, ont leur distribution restreinte à la région côtière de l'Afrique.

Concernant leur biologie générale, les melittides présentent un cycle de développement assez semblable entre eux. Les espèces dont la biologie est connue sont solitaires et univoltines⁵. Les mécanismes liés à leur émergence et à leurs comportements sexuels sont très peu connus même si il est généralement admis que leurs phénologies et les lieux de rencontre entre sexes sont au moins partiellement liés aux caractéristiques de leur plante hôte (abondance, période de floraison, ...). Par ailleurs, les melittides sont connues pour nicher dans le sol. Les Dasypodaidae semblent grégaires et limitées aux zones sableuses bien exposées à la lumière. Les femelles de cette famille creusent des nids profonds, jusque un mètre de profondeur, sans appliquer un revêtement imperméable sur les parois du nid. Le comportement de nidification des femelles de Melittidae *s.str.* sont différents des Dasypodaidae. Elles ne sont pas grégaires et creusent leurs nids dans des sols sableux ou argileux à l'abri de la végétation. Les *Macropis* femelles utilisent l'huile issue de fleurs pour tapisser leurs nids là où les femelles de *Melitta* utilisent les sécrétions de leur glande de Dufour. Les Meganomiidae ont un comportement de nidification intermédiaire entre les Dasypodaidae et les Melittidae *s.str.*. Elles sont grégaires et creusent des nids profonds comme les Dasypodaidae mais elles tapissent les parois de leur nid d'une substance imperméable comme les Melittidae *s.str.*. Le développement larvaire est le même chez toutes

³ L'Ancien Monde comprend l'Eurasie et l'Afrique.

⁴ La région néarctique comprend l'Amérique du Nord.

⁵ Espèce avec une seule génération par an.

les Melittidae *s.l.* mis à part les larves de Dasypodaidae qui ne tissent pas de cocon comme le font les larves de Meganomiidae et de Melittidae *s.str.*.

Les observations de terrains et les données palynologiques confirment que la plupart des Melittidae *s.l.* récoltent leur pollen sur quelques taxons de plantes choisis. Seules quelques espèces appartenant aux genres *Dasypoda*, *Hesperapis* et *Melitta* sont probablement généralistes dans leurs choix floraux. Les Dasypodaidae récoltent leur pollen principalement sur des fleurs à morphologie simple comme celles des Aizoaceae, Asteraceae, Brassicaceae, Campanulaceae, Cistaceae ou Dipsacaceae. Les choix floraux des Meganomiidae sont seulement connus pour deux espèces, *Meganomia gigas* et *Ceratonomia rozenorum*, qui collectent uniquement le pollen de Fabaceae. Les genres *Macropis* et *Rediviva* récoltent de l'huile sur quelques plantes particulières appartenant aux familles des Iridaceae, Primulaceae, Orchidaceae et Scrophulariaceae.

En superposant les choix floraux de cinq genres de melittides (*Capicola*, *Dasypoda*, *Hesperapis*, *Macropis* et *Melitta*) sur leur phylogénie respective, on peut caractériser l'évolution de leurs choix floraux. Les résultats montrent que les espèces phylogénétiquement proches présentent des choix floraux similaires. Cependant, quelques changements de choix floraux sont observés au cours de l'évolution. Il y a en effet certains passages sur de nouvelles plantes hôtes qui n'ont parfois aucune affinité phylogénétique ou ressemblance morphologique avec l'hôte ancestral. La plupart de ces passages se font en conservant le comportement spécialiste (passage d'une spécialisation à une autre spécialisation) mais il y a aussi quelques cas de variations dans l'amplitude de la niche alimentaire. Trois patterns d'évolution de choix floraux sont définis: 1. le pattern de la spécialisation conservée (ex. : *Macropis*) ; 2. le pattern de la spécialisation morphologique (ex. : *Dasypoda*) ; 3. le pattern de la spécialisation séquentielle (ex. : *Capicola*, *Hesperapis* et *Melitta*). Par ailleurs, les résultats montrent que les passages d'un comportement spécialiste vers un comportement généraliste sont plus fréquents que les changements d'un comportement généraliste vers un comportement spécialiste. Le comportement spécialiste pourrait donc être ancestral chez les Melittidae *s.l.*. Par ailleurs, d'autres familles d'abeilles présentent des groupes « primitifs » avec des comportements spécialistes (ex. : Lithurginae, Panurginae and Rophitinae). Le fait que la plupart des groupes basaux des familles d'abeilles sont spécialistes pourrait prouver que les comportements généralistes sont globalement des comportements dérivés chez les abeilles.

Finalement, une hypothèse globale sur l'origine et la diversification des Melittidae *s.l.* est présentée. Comme les melittides occupent une position basale dans le clade des abeilles, cette hypothèse porte aussi sur l'origine même des abeilles. Quatre éléments sont considérés : 1. L'origine et l'évolution des Angiospermes⁶ ; 2. La phylogénie et la biogéographie évolutive

⁶ Groupe des plantes à fleurs

des Apoidea (non-melittides) ; 3. Les traces fossiles des Apoidea ; 4. La phylogénie et la biogéographie évolutive des Melittidae *s.l.*.

Le plus vieux fossile d'abeille connu est *Melittosphex burmensis*. Son âge est estimé à ~100 million d'années (MA), à la période mi-Crétacé. Cette donnée fossile est cohérente avec l'estimation sur la période d'apparition des ancêtres des abeilles, les Apoidea Spheciformes⁷ dont le plus vieux fossile connu date de ~130 millions d'années. Cette donnée est aussi cohérente par rapport à l'apparition des plantes à fleurs estimée au plus tard à ~115 MA. L'apparition des abeilles remonte donc très probablement au mi-Crétacé. Concernant l'origine géographique des abeilles, la phylogénie et la distribution des Melittidae *s.l.* indiquent que les abeilles sont probablement apparues sur le continent africain. Enfin, la diversification des abeilles semble avoir été relativement rapide après leur apparition. Plusieurs familles sont déjà présentes au début de l'ère Cénozoïque. De plus, tous les fossiles d'abeilles recensés comme les plus anciens appartiennent au groupe paraphylétique des abeilles à langue longue et des Melittidae *s.l.*, groupe présenté comme basal dans la nouvelle hypothèse phylogénétique « Melittidae basaux ». Les données fossiles renforcent donc l'hypothèse que les Melittidae sont les premières abeilles apparues, suivies des abeilles à langue longue et, enfin, des abeilles à langue courte.

⁷ Communément appelées guêpes fouisseuses (groupe des Sphecidae *s.l.*)

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MAIN PUBLICATIONS

This thesis is based on the following twelve publications (reprints see appendices).

1. Michez D. 2002. *Dasypoda patinyi* sp. nov. (Hymenoptera, Apoidea, Melittidae), espèce nouvelle récoltée en Syrie. *Linzer biologische Beiträge*, 34: 737-742.
2. Michez D., Terzo M. & Rasmont P. 2004. Révision des espèces ouest-paléarctiques du genre *Dasypoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Linzer Biologische Beiträge*, 36: 847-900.
3. Michez D., Terzo M. & Rasmont P. 2004. Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasypoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Annales de la Société entomologique de France (n. s.)*, 40: 421-435.
4. Michez D. 2005. *Dasypoda (Megadasypoda) intermedia* sp. nov. (Hymenoptera, Apoidea, Melittidae), new species from Iran. *Zoologische mededelingen*, 79: 123-127.
5. Michez D. & Patiny S. 2005. World revision of the oil-collecting bee genus *Macropis* Panzer 1809 (Hymenoptera, Apoidea, Melittidae) with a description of a new species from Laos. *Annales de la Société entomologique de France (n. s.)*, 41: 15-28.
6. Michez D. & Patiny S. 2006. Review of the bee genus *Eremaphanta* Popov 1940 (Hymenoptera: Melittidae), with the description of a new species. *Zootaxa*, 1148: 47-68.
7. Michez D., Else G.R. & Roberts S.P.M. 2007. Biogeography, floral choices and redescription of *Promelitta alboclypeata* (Friese 1900) (Hymenoptera, Apoidea, Melittidae). *African Entomology*, 15: 197-203.
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ABBREVIATIONS

myBP = million years before present

LT bees = long-tongued bees

ST bees = short-tongued bees

s.str. = in the strict sense

s.l. = in the broad sense

S1, S2, ... = first, second, etc., metasomal terga

T1, T2, ... = first, second, etc., metasomal sterna

Nomen est numen.
Linné

*Universality and stability in scientific names require that
any legitimately published taxon has a fixed and recognised status.*
A. Nilsson (2007)

*On sait que tout science doit avoir sa philosophie
et que ce n'est que par cette voie qu'elle fait des progrès réels.
En vain, les naturalistes consumeront-ils leur temps
à décrire des nouvelles espèces, à saisir toutes les nuances
et les petites particularités de leurs variations pour agrandir
la liste immense des espèces inscrites, en un mot,
à instituer diversement des genres en changeant sans cesse
l'emploi des considérations pour les caractériser;
si la philosophie de la science est négligée,
ses progrès seront sans réalité,
et l'ouvrage entier restera imparfait.*
Lamarck (1809)

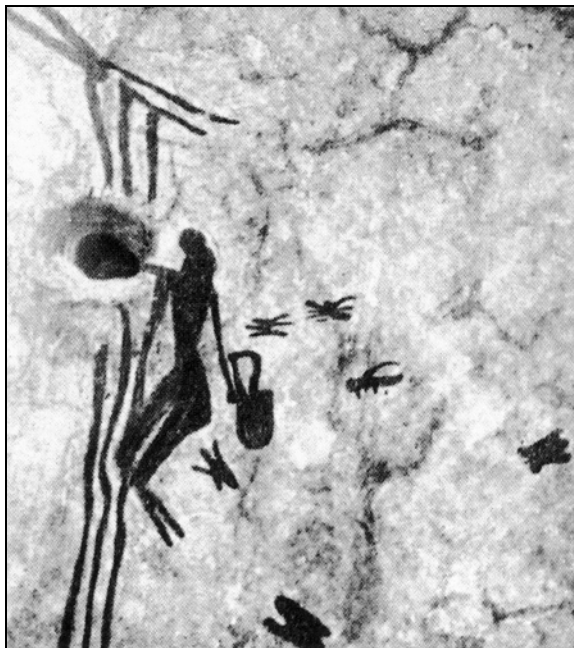
*To do science is to search for repeated patterns,
not simply to accumulate facts.*
Mac Arthur (1972)

GENERAL INTRODUCTION

Images of bees are closely associated with the honeybee, *Apis mellifera* L. 1758. This insect is one of the most investigated animals besides *Drosophila melanogaster* Meigen 1830, the white mice, and of course human beings (Grimaldi & Engel 2005). Honeybees and humans have intimate historical relationships. Humans have domesticated Honeybees but their intrinsic behavioural peculiarities have trigger fascination. In many human civilisations, bees symbolise important values as the spirit of work, the perfect society, the abundance or sweet candies. Honey was the main sweetener in many ancestral human populations (Crane 1999). Five thousand years ago, in one of the first insect's representations, a few bees have been painted on a wall in a Spanish cave of Araña with a woman harvesting honey in cavity (fig. 1).

Aristotle first studied the social behaviour and the biology of honeybees (d'Aguilar 2006). His studies have been for a long time the only scientific observations on insects. During the 17th century, new major advances have been made thanks to the microscope technology. Frederigo Cesi was the first to draw morphological details of *Apis mellifera* back in 1625 (fig. 2, according to d'Aguilar 2006).

These discoveries were major steps in entomology but the main part of the global diversity of bees remained unknown. In fact, despite their economic and cultural importance, honeybees account only for a tiny part of the global diversity of bees. Honeybees in the genus *Apis* are just seven recognized species among the thousands of bees described (Engel 1999a). That “hidden part of the iceberg”, the description of the wild world of bees, began during the 18th century.



Figures 1-2. 1. Rock painting from the cave of Araña: scene with a woman harvesting honey (Spain, Valencia, 5000BC). 2. *Apis mellifera* drawn by Frederigo Cesi (1625) in his *Apiarium*, first drawing of *Apis mellifera* under microscope (according to d'Aguilar 2006).

Karl von Linné started describing the wild bee fauna of his country (Sweden) in the 18th century. He first published a list containing 14 species (Linné 1742). Later, between 1758 and 1771, Linné described 31 valid species, including *Apis mellifera*, representing around 10% of the currently known Swedish bee fauna (Nilsson 2007).

Kirby and Latreille published independently in 1802 the first two global classifications of wild bees. Kirby described two genera, *Apis* and *Melitta*, roughly representing the long-tongued (LT) bees and the short-tongued (ST) bees, respectively. Latreille recognized the same dichotomy but he described some additional subgroups. During the 19th century, descriptions of new taxa increased exponentially. Among all studies, those by Schenk (1860) and Thomson (1872) were notable in describing a lot of tribes and families [for reviews see Michener (2000) and Engel (2005)]. Nowadays, around 1,200 genera and 16,000 species are included in the Apoidea Apiformes (*i.e.* bees).

It is now widely admitted that bees constitute a monophyletic group sharing a few synapomorphies¹ as plumose hairs, phytophagous alimentation, broad hind basitarsus or basitibial plate² (Michener 2000). Seven bee families are traditionally acknowledged: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae and Stenotritidae (fig. 3; Michener 2000). It has been common to split these families into two major groups based on the morphology of the labial palpus: the LT bees including Apidae and Megachilidae, and the ST bees including the five other families (Kirby 1802, Michener 1944, Engel 2001). Despite this long-standing tradition in classification (two centuries from Kirby to Engel), many points have been debated: (i) the phylogenetic relationships among bee families (Michener & Greenberg 1980, Alexander 1992, Roig-Alsina & Michener 1993, Alexander & Michener 1995); (ii) the basal position of colletid *versus* melittid (Michener & Greenberg 1980, Alexander & Michener 1995); (iii) the monophyly of Melittidae (*sensu* Michener 2000) (Rozen & McGinley 1974, Michener 1981, Alexander & Michener 1995).

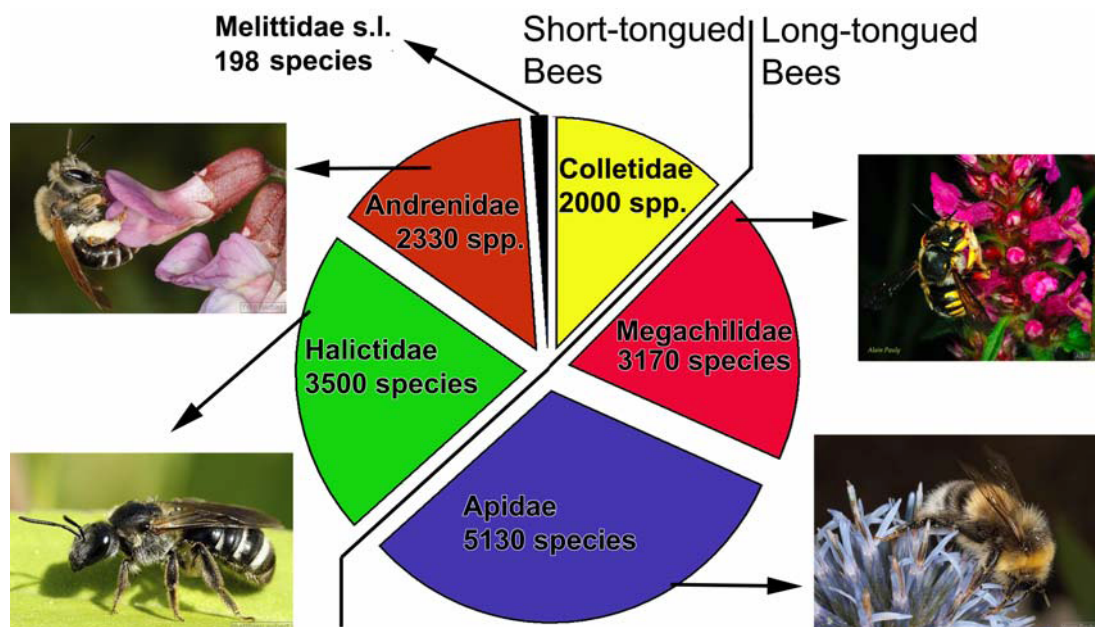
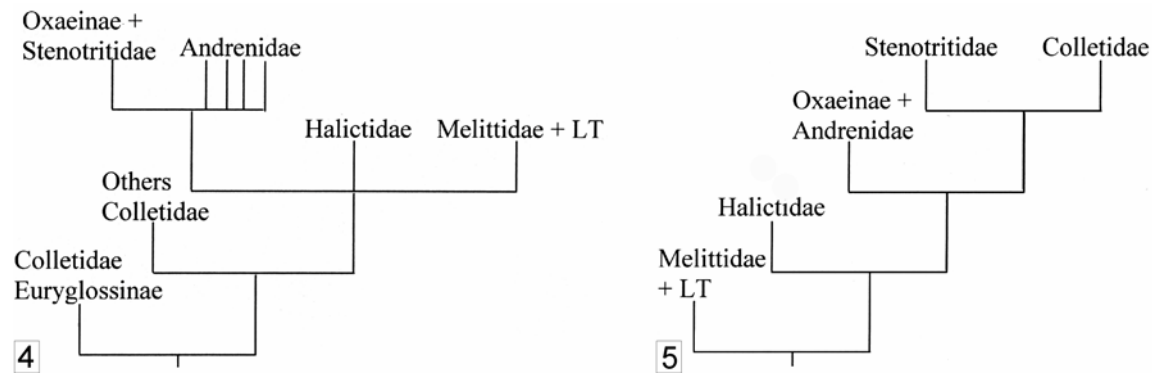


Figure 3. Proportion of species richness of bee families (sum= 16328) except Stenotritidae (21 species) (according to Michener 2000; pictures M. Aubert, Y. Barbier and A. Pauly).

¹ Common ancestral characters

² For a definition of technical terms related to morphology see appendices and Michener (2000).



Figures 4-5. Alternative phylogenetic trees of bee according to Michener (2000). **4.** Traditional phylogenetic tree with Colletidae as basal branch. **5.** Alternative hypothesis with Melittidae+LT as basal branch.

For a long time, ST bees have been considered as primitive in bee phylogeny and the Melittidae as intermediate between ST bees and LT bees groups (fig. 4) (Michener 1944, 2000, Engel 2001). Several phylogenetic analyses based on contemporary taxa actually showed that LT bees derived from the melittid bees (Rozen & McGinley 1974, Michener & Greenberg 1980, Michener 1981, Alexander 1992, Roig-Alsina & Michener 1993, Alexander & Michener 1995). Alternative hypotheses suggested the melittid bees as basal group of the bee clade (fig. 5) (Radchenko & Pesenko 1994, Michener 2000).

The choice between the colletid basal topology (fig. 4) or the melittid basal topology (fig. 5) is crucial to understanding the early diversification of bees. On the one hand, colletid basal topology would indicate that bees originated in Australia - South America and that early bees visited a wide array of flower resources. On the other hand, melittid basal topology would indicate that bees originated in Africa and that early bees visited probably a restricted number of flowers for pollen.

A major breakthrough have been achieved by Danforth *et al.* (2006a, b), who recently consolidated the hypothesis of basal position and paraphyly of Melittidae *s.l.* (fig. 6). These authors presented robust cladistic analyses based on molecular and morphological data. Their results suggested that melittid bees constitute a paraphyletic group from which all other bees are derived, and hence proposed to split the traditional family of Melittidae into three distinct families: Dasypodidae, Melittidae *s.str.* and Meganomiidae.

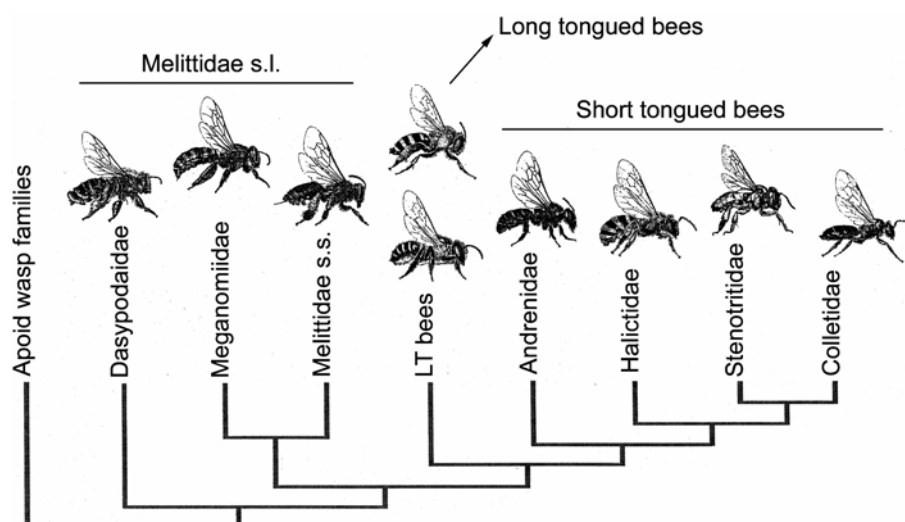


Figure 6. Phylogeny of bee (morphology+ADN data set) from Danforth *et al.* 2006b.

Considering the hypothesis of “melittid basal topology”, the comprehension of the original states and the early diversification of bees need improvement of the knowledge about the systematics, the biogeography, the biology and the host-plant associations of Melittidae *s.l.*.

Comprehensive systematic studies on contemporary and extinct taxa are the first fundamental step to understand the diversity and evolution processes. Unfortunately, systematic sciences are nowadays not very “fashion”. Most scientists consider the systematic studies too descriptive, without reflection or just boring. But, systematics will be always required to name organisms and to speak about this organism. Most biological studies have begun by a description made by a taxonomist.

However, systematic studies are not enough to provide a global picture of the evolutionary processes. Understanding mechanisms and patterns requires additional arguments like biogeographical characteristic, mating behaviour or food preferences. For example, variation in the bee-plant interactions could be a major factor of speciation process, with tight and diffuse coevolution acting to generate taxonomic and genetic diversity. Taxonomists have to become ecologist and biogeograph to understand the origin and the diversification of their groups.

AIMS OF THE THESIS

The knowledge about Melittidae *s.l.* is mainly limited to generic diagnoses and analyses of phylogenetic relationships among tribes and genera (Michener & Greenberg 1980, Michener 1981, Alexander 1992, Roig-Alsina & Michener 1993, Alexander & Michener 1995, Danforth *et al.* 2006a, b). At generic level, there are a few exhaustive reviews available: the revision of all species of the four genera of Meganomiidae by Michener (1981) and the revision of the genus *Hesperapis* by Stage (1966). The information about the other melittid genera is restricted to some general diagnoses (*e.g.* Michener 1981), descriptions of single species and regional revisions [*e.g.* Warncke (1973) for the west-palaearctic melittids; Wu (2000) for the Chinese melittids].

The main aim of this thesis is to fill these gaps by processing a comprehensive systematic revision of the following melittid bee genera:

- *Dasypoda* (appendix I),
- *Macropis* (appendix II),
- *Eremaphanta* (appendix III),
- *Promelitta* (appendix IV),
- *Capicola* (appendix V),
- *Melitta* (appendix VII).

According to the availability of material, we infer the phylogenetic relationships of species within the genera *Dasypoda* (appendix I), *Capicola* (appendix V) and *Melitta* (appendix VII).

In the same time, information about the floral choices of Melittidae *s.l.* is compiled. Records of field observations and palynological studies allow us to characterize the host breadth and the host-plant use of most melittids.

Using these latter advancements on the systematics and floral choices of Melittidae *s.l.*, we examine the inheritance of the host-plant choices throughout melittid evolution by mapping the preferred pollen hosts onto phylogenies of several genera (appendix VIII). We specifically aimed at investigating (i) if host-plant shifts are frequent in these specialized bee clades, (ii) if patterns of host-plant shifts can be observed, and finally (iii) if host-plant specialisation can be regarded as a plesiomorphic (*i.e.*, ancestral) or apomorphic (*i.e.*, derived) condition.

Eventually, we study the global ancestral conditions of Melittidae *s.l.* and the characteristics of their early diversification. We investigate notably a detailed examination of the fossil specimens available. A new fossil specimen is described and we confront these findings to the current state of knowledge of bee systematics (appendix VI).

In the following part of this Ph-D, we review the available information about melittid bees throughout our own works and a synthesis of the literature on this topic.

MONOGRAPHIC REVISION OF THE MELITTIDAE *s.l.*

1. INTRODUCTION

Melittid bees are small, relatively hairless and smooth (*e.g. Macropis*) to large, robust and hairy (*e.g. Dasypoda*). Variation in body size is quite large. The smallest Melittidae *s.l.* is 4 mm in length (*Eremaphanta minuta*) while the biggest is 22 mm (*Meganomia gigas*) (Michener 1981, Michez & Patiny 2006). As far as known, no cleptoparasite or inquiline behaviours have been described in Melittidae *s.l.*. Most melittid bees are probably specialist pollen foragers (*i.e.* oligolectic) (Michener 2000) but a few pollen generalists foragers (*i.e.* polylectic) are recognized in the genera *Dasypoda*, *Hesperapis* and *Melitta* (Stage 1966, Michez *et al.* 2004a, Michez & Eardley in press). Melittid bees are ground nesting, occurring in the temperate and xeric areas of the Old World and the Nearctic region (Michener 1979).

Melittidae *s.l.* is one of the smallest groups of bees (198 species among ~16000 described bees) (Michener 2000). Its monophyly and phylogenetic position in the tree of bees are still debated even if Danforth *et al.* (2006b) recently consolidated the hypotheses of basal position and paraphyly of Melittidae *s.l.* (fig. 7).

The monophyly of melittid bees have been always dubious because of the absence of morphological synapomorphy. Michener (1981), first reviewed this group and characterized the melittid bees only by a diagnostic combination of morphological features: all segments of labial palpus are similar in length (as in other ST bees) and the submentum is V-shaped (as in other LT bees). He distinguished three subfamilies: Dasypodinae, Melittinae and Meganomiinae. By processing global phylogenetic studies of ST bees (including melittid bees) based on a morphological data set, Alexander & Michener (1995) did not find synapomorphy supporting the monophyly of melittid bees either. They consequently proposed to acknowledge the subfamilies described by Michener as genuine families: Dasypodidae, Melittidae *s.str.* and Meganomiidae. The next reviewer, Engel (2001), did not follow Alexander & Michener's suggestions and classically proposed to recognize only one family including four subfamilies: Dasypodinae, Macropidinae, Meganomiinae and Melittinae. Engel (2001) notably resurrected the subfamily Macropidinae Robertson 1904 for the contemporary genus *Macropis* Panzer 1809 and the Baltic amber genus *Eomacropis* Engel 2001. In his last review, Engel (2005) described new tribe and subtribe in collaboration with J. Ascher. Danforth *et al.* (2006a, b) lastly confirmed Alexander & Michener's hypothesis of the melittid paraphyly by developing new molecular analysis. Melittid bees are now split into three families (Dasypodidae, Melittidae *s.str.* and Meganomiidae) which include all taxa previously ranked in the traditional family of Melittidae *sensu* Michener (1981). In the same way, Danforth *et al.* (2006b) argued that Melittidae *s.l.* constitutes a basal group from which other groups of bees are derived (fig. 7).

In this study, we follow the taxonomical hypothesis of Alexander & Michener (1995) and Danforth *et al.* (2006b) about families (three distinct families). However, these authors did not investigate the relationships of Melittidae *s.l.* tribes. Therefore we refer to the designations of tribes proposed by Michener (1981) and Engel (2005). In this review, we consider that Melittidae *s.l.* includes three families (Dasypodidae, Meganomiidae and Melittidae *s.str.*) and eight contemporary tribes (Afrodasypodini, Dasypodini, Macropidini, Meganomiini, Melittini, Promelittini, Redivivini and Sambini) (tab. 1, fig. 7).

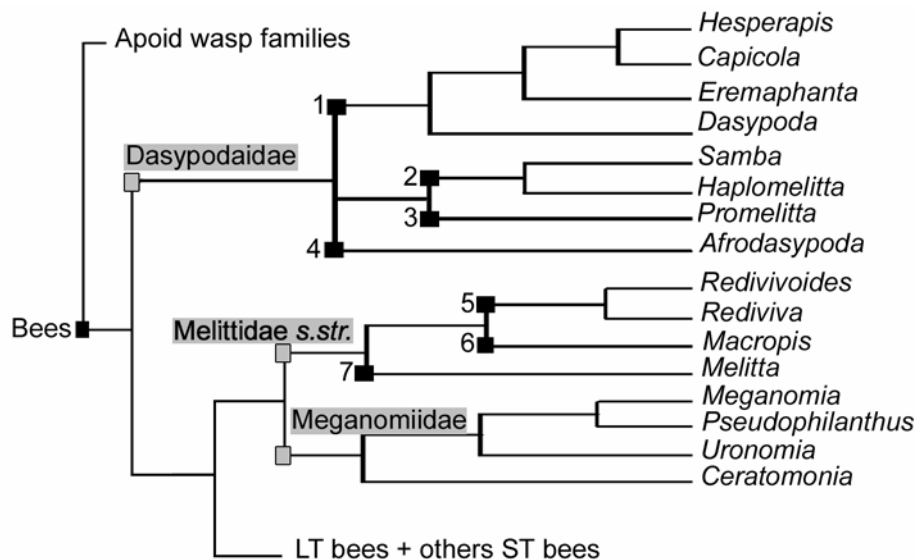


Figure 7. Phylogeny of Melittidae s.l. from Michener (1981) adapted with taxonomical hypothesis of Engel (2005) and Danforth *et al.* (2006b). 1= Dasypodaini Michener 1981, 2= Sambini Michener 1981, 3= Promelittini Michener 1981, 4= Afrodasypodaini Engel 2005, 5= Redivivini Engel 2001, 6= Macropidini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

At the generic level, Michener (1981) recognised 14 genera in the Melittidae s.l.: *Capicola* Friese 1911, *Ceratonomia* Michener 1981, *Dasypoda* Latreille 1802, *Eremaphanta* Popov 1940, *Haplomelitta* Michener 1981, *Hesperapis* Cockerell 1898, *Melitta* Kirby 1802, *Meganomia* Cockerell 1931, *Promelitta* Warncke 1977, *Pseudophilanthus* Alfken 1939, *Rediviva* Friese 1911, *Redivivoides* Michener 1981, *Samba* Friese 1908 and *Uromonia* Michener 1981. Michener (2000) included *Capicola* within *Hesperapis*, *Capicola* and *Capicoloides* being two subgenera among seven other Nearctic subgenera of *Hesperapis*. Michez *et al.* (2007a) demonstrated the monophyly of *Capicola* and acknowledged *Capicola* as a genus. Engel (2005) described a last genus: *Afrodasympoda*. Most of the 15 genera have been recently reviewed (see table 1 for references; **appendices I-V, VII**).

A synthesis of the current knowledge of Melittidae s.l. is presented hereafter providing an overview of their diversity, their distribution and the main characteristics of their biology (general cycle of development and host-plants). Eventually, we discuss these melittid characteristics throughout their macroevolution. As Melittidae s.l. is basal in the bee tree (Danforth *et al.* 2006b), we propose a plausible sketch of the early bee diversification.

This monographic revision is based on our own publications (**appendices I-VIII**) and a synthesis of the literature on melittid bees. Details of methodologies and material of our studies on systematics, biogeography, ecology and evolution are available in appendices. We used the terminology of Harris (1979) for the description of cuticle sculpture and Michener (2000) for the general morphology.

2. SYSTEMATICS AND BIOGEOGRAPHY OF THE MELITTIDAE S.L.

Melittidae *s.l.* includes 202 species: 198 contemporary species and 4 fossil species (tab. 1; Michener 2000, Michez 2005, Michez & Patiny 2005, 2006, Michez & Eardley in press, Michez & Kuhlmann 2007, Michez *et al.*, 2007a, b). Dasypodaidae is the most diverse (101 species) while Meganomiidae comprises only 12 species. Melittid bees occur in temperate and xeric ecosystems 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 Palaearctic region (tab. 2). The African continent (Ethiopian region + North Africa) lumps clearly the maximum of both generic and specific diversity.

2.1. Family Dasypodaidae Börner 1919

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 (tab. 1). The phylogenetic relations among genera and tribes are still dubious.

Dasypodaidae is relatively diverse (101 species) 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 (*Afrodasygoda*, *Capicola* and *Haplomelitta*). *Dasypoda* is the only widespread genus that occurs in the temperate to the xeric areas of the Palaearctic (fig. 8). *Dasypoda* determines the northern limit of Dasypodaidae to the 62nd northern parallel. The other Dasypodaidae genera, *Afrodasygoda*, *Capicola*, *Eremaphanta*, *Hesperapis* and *Promelitta* are each one endemic in different Old World deserts (figs 8, 13).

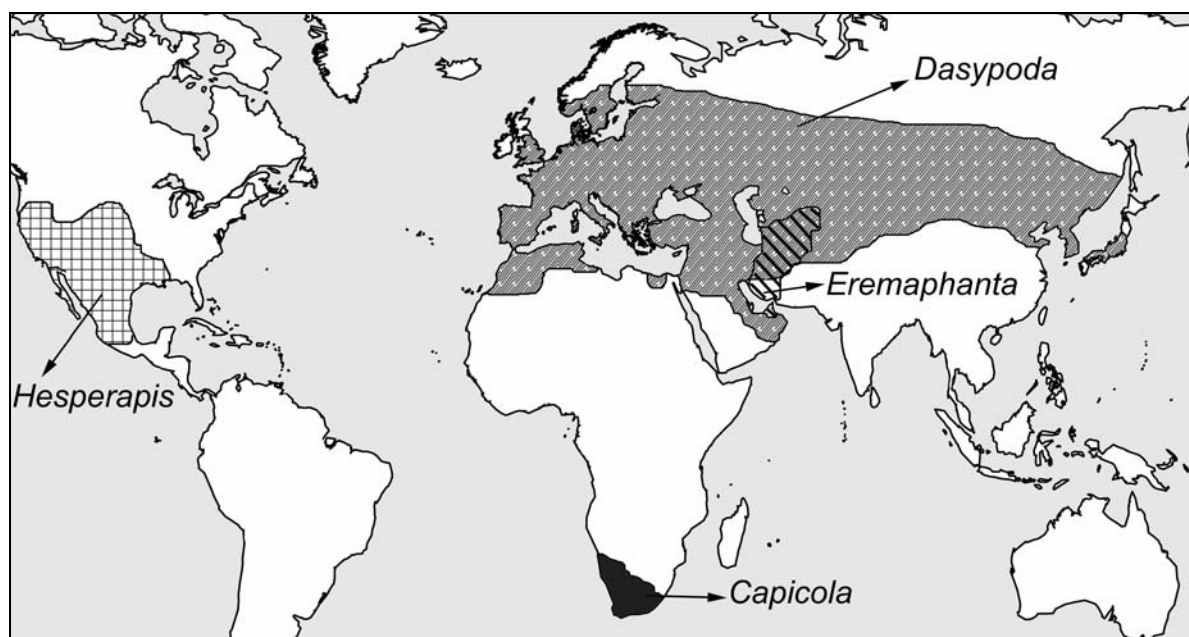


Figure 8. Global distribution of Dasypodaini including the genera *Capicola*, *Dasypoda*, *Eremaphanta* and *Hesperapis* (from Stage 1966, Michez & Patiny 2006, 2007b, Michez *et al.* 2004a, b, 2007a).

Table 1. Taxonomy, species richness and distribution of the Melittidae s.l. [* fossil taxa; (*) fossil taxa; N1= number of species included in the genus (described spp. + undescribed spp.); N2= number of species included in the subgenus (described spp. + undescribed spp.)].

Families	Tribes	Genera	Distribution	N1	Max. of diversity	Subgenera	N2	Main references
Dasypodaidae (101 spp.)	Dasypodaini	<i>Dasyпода</i>	Palaeartic	33	Mediterranean basin	<i>Dasyпода</i> <i>Heterodasyпода</i> <i>Megadasyпода</i> <i>Microdasyпода</i>	16 3 10 4	Warncke (1973), Michez (2002, 2005), Michez <i>et al.</i> (2004a, b,)
		<i>Eremaphanta</i>	Central Asia	9	Turkistan	<i>Eremaphanta</i> <i>Popovapis</i>	7 2	Popov (1940, 1955, 1957), Michez & Patiny (2006)
		<i>Capicola</i>	Southern Africa	13	Cape province	<i>Capicola</i>	13	Michener (1981), Michez & Kuhlmann (2007), Michez <i>et al.</i> (2007a)
		<i>Hesperapis</i>	North America	24+14	California	<i>Amblyapis</i> <i>Carinapis</i> <i>Disparapis</i> <i>Hesperapis</i> <i>Panurgomia</i> <i>Xeralictoides</i> <i>Zacasta</i>	6 8+8 1+2 1+2 6 1+1 1+1	Stage (1966), Michener (1981, 2000)
	Promelittini	<i>Promelitta</i>	North Africa	1	North Africa	<i>Promelitta</i>	1	Michez <i>et al.</i> (2007b)
	Sambini	<i>Haplomelitta</i>	South Africa	5	South Africa	<i>Atrosamba</i> <i>Haplomelitta</i> <i>Haplosamba</i> <i>Metasamba</i> <i>Prosamba</i>	1 1 1 1 1	Michener (1981, 2000)
		<i>Samba</i>	South Africa	1	South Africa	<i>Samba</i>	1	Michener (1981, 2000)
		<i>Afrodasyпода</i>	South Africa	1	South Africa	<i>Afrodasyпода</i>	1	Engel (2005)

Families	Tribes	Genera	Distribution	N1	Max. of diversity	Subgenera	N2	Main references
Meganomiidae (12 spp.)	Meganomiini	<i>Ceratonomia</i>	Namibia	1	Namibia	<i>Ceratonomia</i>	1	Michener (1981)
		<i>Meganomia</i>	Ethiopian	4+1	Southern Africa	<i>Meganomia</i>	4+1	Michener (1981)
		<i>Pseudophilanthus</i>	Madagascar and Kenya	4	Kenya	<i>Pseudophilanthus</i>	3	Michener (1981), Michener <i>et al.</i> (1990)
		<i>Uromonia</i>	Mad., Kenya and Mali	2	Mad., Kenya and Mali	<i>Dicromonia</i> <i>Uromonia</i> <i>Nesomonina</i>	1 1 1	Michener (1981), Michener & Brooks (1987)
Melittidae (89 spp.)	Melittini ^(*)	<i>Melitta</i> ^(*)	Old World and N. Am.	44	W. Palaearctic	<i>Melitta</i>	7	Cockerell (1909), Warncke (1973) Snelling & Stage (1995), Wu (2000), Michez & Eardley (in press)
						<i>Cilissa</i> <i>Incertae sedis</i>	36 1	
	Redivivini	<i>Rediviva</i>	S. Africa	24	South Africa	<i>Rediviva</i>	24	Whitehead & Steiner (2001), Whitehead <i>et al.</i> (in press)
		<i>Redivivoides</i>	South Africa	1+2	South Africa	<i>Redivivoides</i>	1+2	Michener (1981, 2000)
	Eomacropidini*	<i>Eomacropis</i> *	Baltic amber	1	Baltic amber	<i>Eomacropis</i>	1	Engel (2001)
		<i>Macropis</i>	Holarctic	16	Eastern Asia	<i>Macropis</i> <i>Sinomacropis</i> <i>Paramacropis</i> <i>Incertae sedis</i>	10 5 1 1	Warncke (1973), Zhang (1989), Michener (1981), Snelling & Stage (1995), Wu & Michener (1986), Michez & Patiny (2005)
		<i>Paleomacropis</i> *	Oise amber	1	Oise amber	<i>Paleomacropis</i>	1	Michez <i>et al.</i> (2007c)

Genus *Afrodasympoda* Engel 2005

Afrodasympoda is only known from the single female holotype of *Afrodasympoda plumipes* (Fries 1912) collected in Ookiep (29.36°S 17.54°E, South Africa; fig. 13). *Afrodasympoda* is distinct from all other Dasypodaidae in several apomorphies: absence of keitrichia, pygidial plate of female without median elevated area and two equal submarginal cells. This genus shares some characteristics with Promelittini like the basal band on terga 2-3. Michener (1981) first included *Afrodasympoda* in Promelittini. However, Engel (2005) considered that *Afrodasympoda* also displays features of Dasypodaini and Sambini. Therefore, he described a new tribe (Afrodasypodaini) including only *Afrodasympoda*. The taxonomical assignment of *Afrodasympoda* surely requires additional specimens and a global phylogenetic study of the Dasypodaidae.

Genus *Capicola* Friese 1911

The genus *Capicola* is closely related to the Nearctic genus *Hesperapis* (Michener 1981, Engel 2005; **appendix V**) (fig. 7). *Hesperapis* and *Capicola* share synapomorphies, notably the shape of stigma, the two sub-marginal cells (the first longer than the second), the galea comb inserted in front of the maxillary palpus insertion and the scopa restricted to the outer face of hind tibia and basitarsus. On the contrary, the two genera differ in the shape of the male S6 and the pygidial plate of female that displays a strong longitudinal median relief in *Capicola* females.

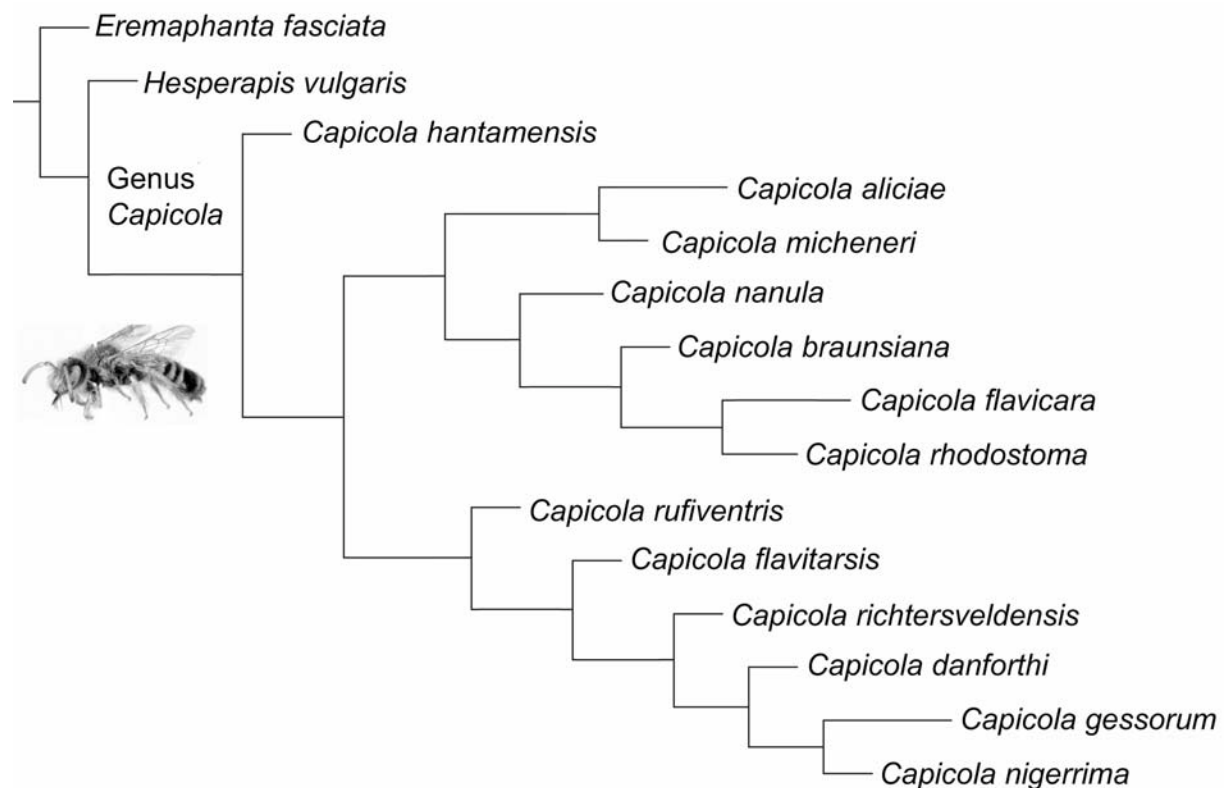


Figure 9. Phylogram of the genus *Capicola* from heuristic search (tree length=54 steps, CI=0.5370 and RI=0.6835; cladogram modified from Michez & Kuhlmann 2007).

Table 2. Repartition of species and genus richness of Melittidae *s.l.* (including undescribed species). S Af= Southern Africa, Md= Madagascar, E Af= Eastern Africa, O= other Ethiopian area (Yemen, Mali), N Af= North Africa, W-P= West Palaearctic region, E-P= East Palaearctic region (including Central Asia); T= regional species and generic diversities.

Taxon	Nearctic Region	Ethiopian Region					Palaearctic Region			
		S Af	Md	E Af	O	T	N Af	W-P	E-P	T
Melittinae	9-2	31-3	-	2-1	-	33-3	4-2	18-2	27-2	42-2
<i>Macropis</i>	4	-	-	-	-	-	1	3	9	12
<i>Melitta</i>	5	5	-	2	-	7	3	15	18	30
<i>Rediviva</i>	-	23	-	-	-	23	-	-	-	-
<i>Redivivoides</i>	-	3	-	-	-	3	-	-	-	-
Meganomiidae	-	3-2	2-2	6-2	2-2	12-4	-	-	-	-
<i>Ceratonomia</i>	-	1	-	-	-	1	-	-	-	-
<i>Meganomia</i>	-	2	-	2	1	5	-	-	-	-
<i>Pseudophilanthus</i>	-	-	1	3	-	4	-	-	-	-
<i>Uromonia</i>	-	-	1	1	1	2	-	-	-	-
Dasypodaidae	38-1	19-3	-	1-1	-	20-4	16-2	20-1	14-2	43-3
<i>Afrodasygoda</i>	-	1	-	-	-	1	-	-	-	-
<i>Capicola</i>	-	13	-	-	-	13	-	-	-	-
<i>Dasypoda</i>	-	-	-	-	-	-	15	20	5	33
<i>Eremaphanta</i>	-	-	-	-	-	-	-	-	9	9
<i>Hesperapis</i>	38	-	-	-	-	-	-	-	-	-
<i>Promelitta</i>	-	-	-	-	-	-	1	-	-	1
<i>Haplomelitta</i>	-	5	-	-	-	5	-	-	-	-
<i>Samba</i>	-	-	-	1	-	1	-	-	-	-
Genus richness	3	8	2	4	2	11	4	3	3	5
Species richness	47	53	2	9	2	65	20	38	41	85

At the species level, the 13 *Capicola* can be unambiguously characterized by a unique morphology of their proboscis proportions, body size, punctuation of clypeus, propodeal triangle, shape of hidden male sterna (S6-S8) or male genitalia (Michez & Kuhlmann 2007, Michez *et al.* 2007a). The shape of the female pygidial plate is also diagnostic for many species, what is notably unusual in Melittidae *s.l.*

Recent cladistic analyses confirm the monophyly of the genus *Capicola* (Michez & Kuhlmann 2007, Michez *et al.* 2007a) (fig. 9). They do not support the former subdivision of *Capicola* into two subgenera *C. (Capicoloides)* and *C. (Capicola)* proposed by Michener (1981). The large species group designated as *Capicola s.str.* is likely not monophyletic. The five species originally included in the latter taxon (*C. braunsiana*, *C. cinctiventris* (= *C. flavitarsis*), *C. flavitarsis*, *C. nanula*, *C. rufiventris*) are associated in two distinct clades.

At a higher taxonomic level, the former results lead to acknowledge seven subgenera (all nearctic) within *Hesperapis*. The phylogenetic relationships among the subgenera of *Hesperapis* and the genus *Capicola* need to be re-evaluated through a global analysis. Interesting preliminary clues on the result of such analysis were suggested by Engel (2005) who grouped *Capicola*, *Hesperapis* and *Eremaphanta* within the subtribe Hesperapina. Several of observations give us additional insights supporting this proposal, notably in the *C. flavicara* morphology (flatness of the female's pygidial plate and the shape of the head).

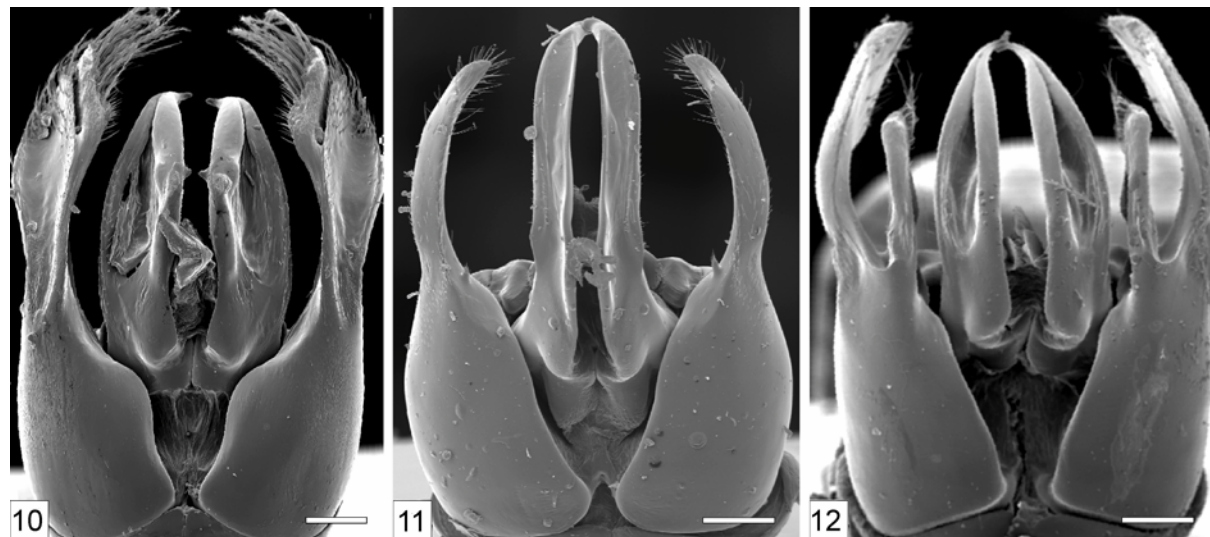
The distribution of *Capicola* is restricted to southwestern Africa (fig. 8). The centre of endemism is clearly in the Western Cape Province's Succulent and Nama Karoo biomes, which have the world's highest floral diversity (Goldblatt & Manning 2002). The distributions of several species extend northward into Namibia and eastward in the Eastern Cape Province. The Namibian endemic species *C. micheneri* is the only *Capicola* recorded outside this area.

Genus *Dasypoda* Latreille 1802

Dasypoda species are the biggest species among the Dasypodaidae. Most species are longer than 15 mm while the other Dasypodaidae are less than 10 mm (figs 22-24). *Dasypoda* share a few apomorphies: black body, vertex elevated, no basitibial plate, female scopae strongly developed and absence of keirotrichia (Michener 1981; **appendix I**).

Michez *et al.* (2004a, b) and Michez (2005) listed 33 species and described four subgenera based on morphological cladistic analysis: *Dasypoda s.str.*, *Heterodasypoda*, *Microdasypoda* and *Megadasypoda*. Diagnostic features are numerous at specific level: sculpture of outer surface of galea, punctation of clypeus, length of malar area, scopae colour, appressed setae on female pygidial plate, shape of male S6-8 and shape of male genitalia (figs 10-12).

Dasypoda species are common in the Palaearctic region from Morocco to Japan (tab. 1, fig. 8) but most species are west-palaearctic (Michez 2002, 2005, Michez *et al.* 2004a, b). The four subgenera diversity centres are restricted to one of the following Mediterranean peninsula: Balkan, Morocco and Spain. Cycles of repeated expansions and fragmentations of ecosystems during the Quaternary Era (Hewitt 1999) could explain these ranges.



Figures 10-12. Male genitalia of *Dasypoda* showing morphological variations (scales=100µm). **10.** *Dasypoda hirtipes*. **11.** *Dasypoda cingulata*. **12.** *Dasypoda argentata*.

Genus *Eremaphanta* Popov 1940

Morphologically, the genus *Eremaphanta* is characterized by some unique features like the presence of extensive yellow markings in both sexes, the stigma as long as the first submarginal cell, the second submarginal cell twice as long as the first and the weak differentiation of male S7 (Popov 1940, Michener 1981; **appendix III**). Some species are among the smallest bees (*e.g.* *E. minuta* female is 4 mm in length).

Characters supporting the specific status for the nine *Eremaphanta* species are found in: the ratio between palpi and glossa lengths, the development of apical bands on terga and the appearance (sculpture, coloration) of the propodeal triangle. Colour patterns of the integument are also specific. On the contrary, the morphology of genitalia and hidden male sterna (S6-8) are strictly uniform among species, whereas these structures are diagnostic in most groups of Apoidea, notably in other Melittidae *s.l.* (Michener 2000). The yellow markings constitute a major characteristic of *Eremaphanta*. In most species, the integument coloration provides evidence for the association of the sexes. In the five species for which both sexes are described: *E. convolvuli*, *E. dispar*, *E. fasciata*, *E. popovi* and *E. vitellinus*, the coloration patterns are quite similar in males and females. However, these yellow markings are notably wider in *Eremaphanta* females than in males, unlike the other Melittidae *s.l.* (*Macropis*, *Meganomiinae* and *Promelitta*).

From a biogeographical point of view, most *Eremaphanta* are endemic and sympatric in Turkestan (Kazakhstan, Tajikistan, Turkmenistan, Uzbekistan; fig. 8) (Popov 1955, Michez & Patiny 2006). Two species were recorded outside these limits: *E. iranica* in the south of Iran and north of Oman, and *E. dispar* in Pakistani Baluchistan.

Genera *Haplomelitta* Cockerell 1934 and *Samba* Friese 1908

Haplomelitta and *Samba* are included in the small tribe of Sambini. The Sambini genera share some unique features: head wider than long, shallow upper metapleural pit, shape of spur of median tibia (short, robust and strongly hooked apically), terga generally without apical hair bands, male gonocoxite with mesoapical lobe apically produced and male gonostylus apically enlarged (Michener 1981).

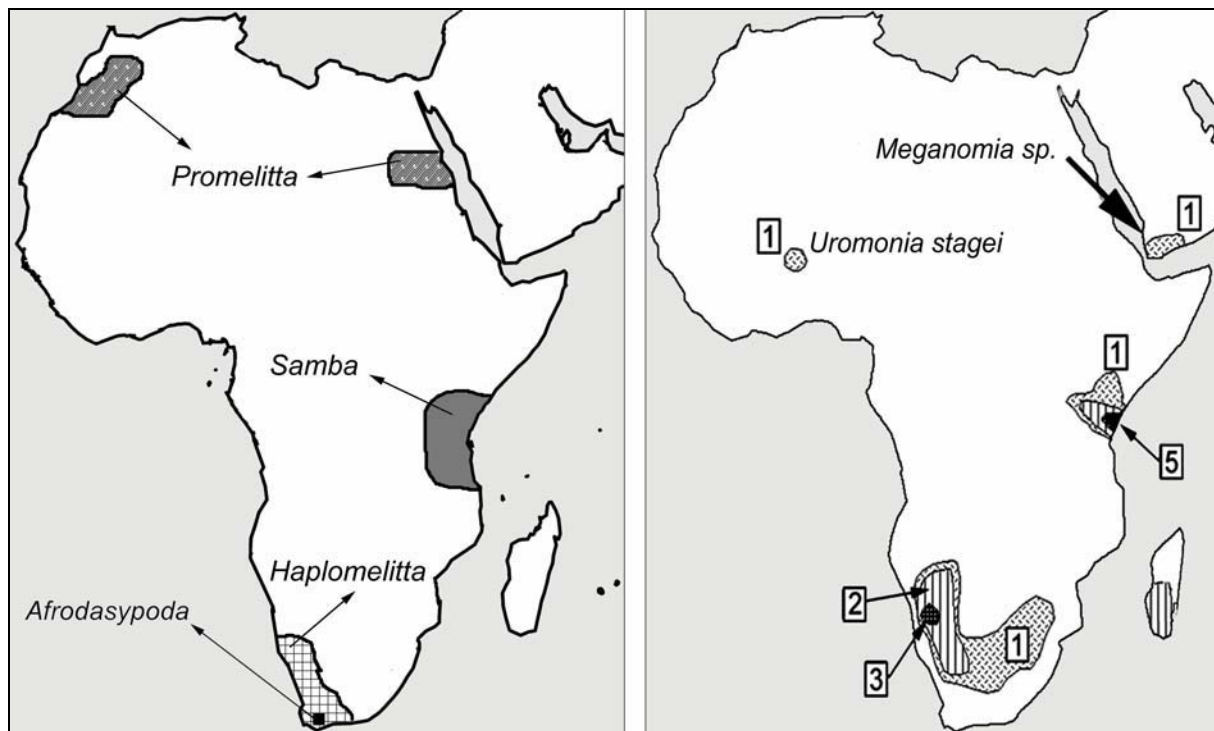
Haplomelitta includes six South African species (fig. 13): *H. (Atrosamba) atra* Michener 1981, *H. (H.) ogilviei* Cockerell 1932, *H. (Haplosamba) tridentata* Michener 1981, *H. (Metasamba) fasciata* Michener 1981, *H. (Prosamba) griseonigra* Michener 1981 and *H. (?) diversipes* (Cockerell 1932). *Samba* includes only one Eastern African species (fig. 13): *S. calcarata* Friese 1908. This species shows numerous autapomorphies: membranous mentum, clypeus with median ridge, concave vertex, female hind tibia with only one hind apical spur.

Genus *Hesperapis* Cockerell 1898

Hesperapis is restricted to the deserts of southwestern North America (fig. 8) (Stage 1966, Michener 1979, Rozen 1987, Cane *et al.* 1997). The flat abdomen, the inner marginal fringe of the gonostylus and the flat pygidial plate of female are characteristic of this genus.

Michener (2000) considered nine subgenera in the genus *Hesperapis* but Michez *et al.* (2007a) proposed to place the Southern African species in a separate monophyletic genus (*Capicola*). The seven nearctic subgenera of *Hesperapis* are namely: *Amblyapis* Cockerell 1910, *Carinapis* Stage 1981, *Disparapis* Stage 1981, *Hesperapis s.str.*, *Panurgomia* Viereck 1909, *Xeralictoides* Stage 1981 and *Zacesta* Ashmead 1899.

Hesperapis includes 27 described species but numerous additional species are still undescribed [Stage (1966) recorded 14 new species in his unpublished Ph-D dissertation].



Figures 13-14. 13. Global distribution of Afrodasypodaini including the genus *Afrodasyopoda* (from Engel 2005), Promelittini including the genus *Promelitta* (from Michez *et al.* 2007b), and Sambini including the genera *Haplomelitta* and *Samba* (from Michener 1981). 14. Global distribution and species richness of Meganomiidae (from Patiny & Michez 2007).

Genus *Promelitta* Warncke 1977

To date, *Promelitta alboclypeata* is the only known species for the genus *Promelitta* and the tribe Promelittini. *Promelitta* presents a few apomorphies: metasomal terga with basal hair bands, shape of propodeum, female hind basitarsus with expanded apical blade, shape of hidden male sterna (S6-8) and male genitalia (Michener 1981; **appendix IV**). *Promelitta* shares also many morphological features with other genera of Melittidae s.l.. For instance, the female keirotrichia and its setae are like those of *Eremaphanta* (Dasypodaini) and *Capicola* (Dasypodaini) (Michener 1981, Engel 2005, Michez & Patiny 2006). The female pygidial plate has a median elevated area like in *Capicola* (Dasypodaini) and Sambini. The clypeus of male is coloured as in some *Eremaphanta* (Dasypodaini) and *Macropis* (Macropidini) (Michez & Patiny 2005, 2006). The outer margin of stipes and the apicolateral structure of male S7 are similar to *Dasypoda* (Dasypodaini) and Sambini (Michener 1981, Michez *et al.* 2004a). The gonostylus is articulated as in Sambini and Macropidini (Michener 1981). Like *Afrodasyopoda*, the phylogenetical affinities of *Promelitta* are still unclear.

The distribution of *Promelitta alboclypeata* shows a disjunction of about 4,200km between the Moroccan and Egyptian/Sudanese populations (fig. 13). In Morocco, the species is known mostly in sub-desertic areas. The vegetation is typically sparse in sandy hollows near temporary water, and with linear growth of the spiny shrub *Convolvulus trautmanianus* Schweinf. & Muschl. (Convolvulaceae) in the shallow flash-flood runnels on the hillside slopes.

2.2. Family Meganomiidae Michener 1981

Meganomiidae is the smallest family of Melittidae *s.l.* (tab. 1). In light of recent molecular analyses, Meganomiidae is probably the sister group of the Melittidae *s.str.* (Danforth *et al.* 2006a, b). Meganomiide species are robust bees with 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 (fig. 14). 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.

2.3. Family Melittidae *s.str.* Schenk 1860

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) (tab. 1, fig. 7).

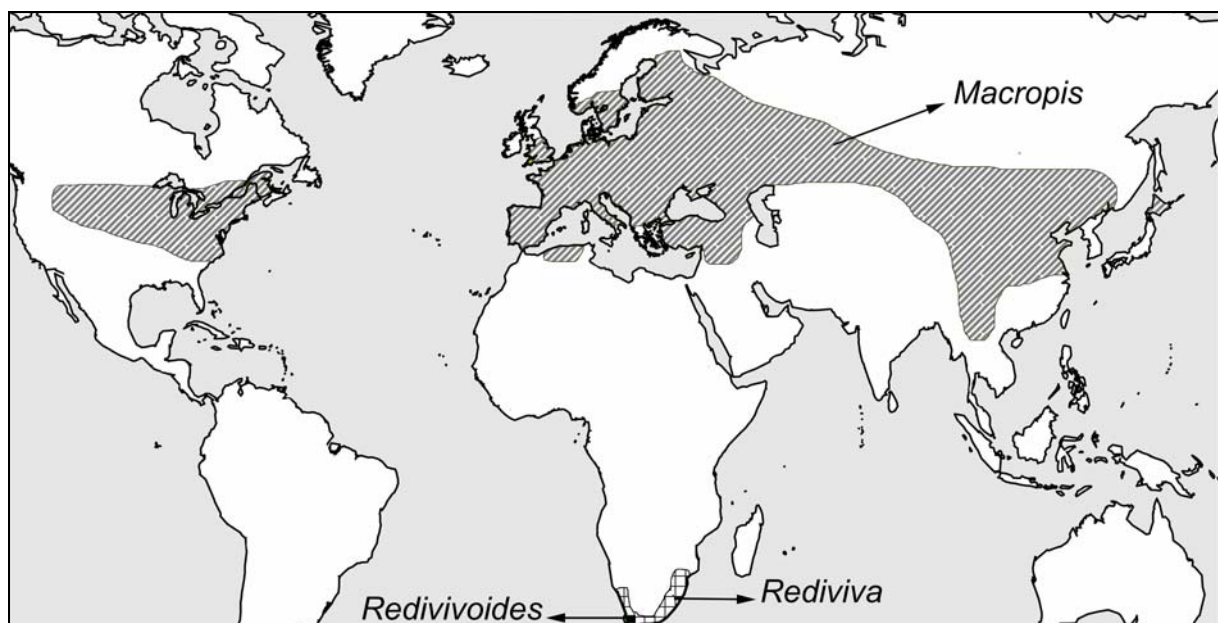


Figure 15. Global distribution of the genera *Macropis*, *Rediviva* and *Redivivoides* (from Michener 1981, Snelling & Stage 1995, Whitehead & Steiner 2001, Whitehead *et al.* in press and Michez & Patiny 2005).

Melittidae s.str. is diverse (86 species) in the Old World and the Nearctic region (tab. 1, figs 15, 18). Unlike the other melittid bees, the Melittidae s.str. show notable climatic preferences. As written above, most Dasypodidae (*Afrodasyptoda*, *Capicola*, *Dasypoda*, *Eremaphanta* and *Promelitta*) and all Meganomiidae are restricted to the xeric areas of the Old World (Michener 1981, Michez & Patiny 2006, Michez *et al.* 2007a, b, c). 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 (Michez & Patiny 2005, Michez & Eardley in press). Both genera, *Rediviva* and *Redivivoides*, are restricted to the coastal area of South Africa.

Genus *Macropis* Panzer 1809

Among Melittidae s.str., the genus *Macropis* is characterized notably by the yellow markings of the male (fig. 25), the two submarginal cells (while the other Melittidae s.str. have three) and the well-developed pygidial plate of both sexes (Michener 1981; **appendix II**). The morphological adaptations to collect oil (velvety hairs on the female fore legs) are also characteristic.

Macropis includes 16 species into three subgenera: *Macropis* s.str., *Paramacropis* Popov & Guiglia 1936 and *Sinomacropis* Michener 1981. Each species can be defined by a unique combination of a few features: shape of male yellow facial marking, pilosity of propodeal triangle, punctuation of terga, shape of pygidial plate, shape of hidden male sterna and shape of male genitalia (Michener 1981, Wu & Michener 1986, Michez & Patiny 2005).

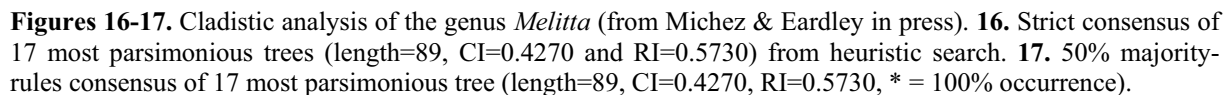
The genus *Macropis* is Holarctic (fig. 15). In East-Palaearctic, *Paramacropis* is distributed Northern the Yellow Sea and *Sinomacropis* Southern. The subgenus *Macropis* s.str. is also Holarctic. Three well-distinct species groups can be considered: (i) a West-Palaearctic group (three species) reaching Altai (Russia), Northern Kazakhstan; (ii) an Asian group which includes nine Chinese, East-Siberian and Japanese species; (iii) a Nearctic group with four species mainly distributed along the Eastern coast of the USA and Canada.

Genus *Melitta* Kirby 1802

Melitta differs from the other Melittidae s.str. by several plesiomorphic features. The males are characterized by the structure of S7 with a large disc and by lateral processes weakly developed. This conformation is similar to the structure observed in Apoidea Spheciformes (Michener 1981). *Melitta* species also share a few additional apomorphies, like lateral tubercles on the labrum, apical projection on the posterior basitarsus and volsella with elongated digitis (Michener 1981; **appendix VII**).

The cladistic analyses of Michez & Eardley (in press) supported the monophyly of the genus *Melitta* (figs 16-17). Moreover, two subgenera have been defined: the subgenus *Melitta* Kirby s.str. (7 species) and the subgenus *Cilissa* Leach (36 species).

At the species level, the *Melitta* are unambiguously characterized by a combination of a few morphological structures, like proboscis proportions, punctuation of clypeus and mesonotum, sculpture of propodeal triangle, shape of hidden male sterna (S6-8) and male genitalia (Michez & Eardley in press). In general, the different species of *Melitta* are morphologically very similar when compared with other Melittidae s.l. (Michener 1981, Michez & Patiny 2005, 2006, Michez *et al.* 2004a, b, 2007a). Most *Melitta* show equivalent size and vestiture (figs 27-29), while the largest *Dasypoda* is twice as large as the smallest species (Michez *et al.* 2004b).



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The diagnostic characters are numerous at the species level: colour of metasome, shape of

D. divius is restricted to Southern Africa (fig. 15). Whitehead & Steiner (2001) and Whitehead

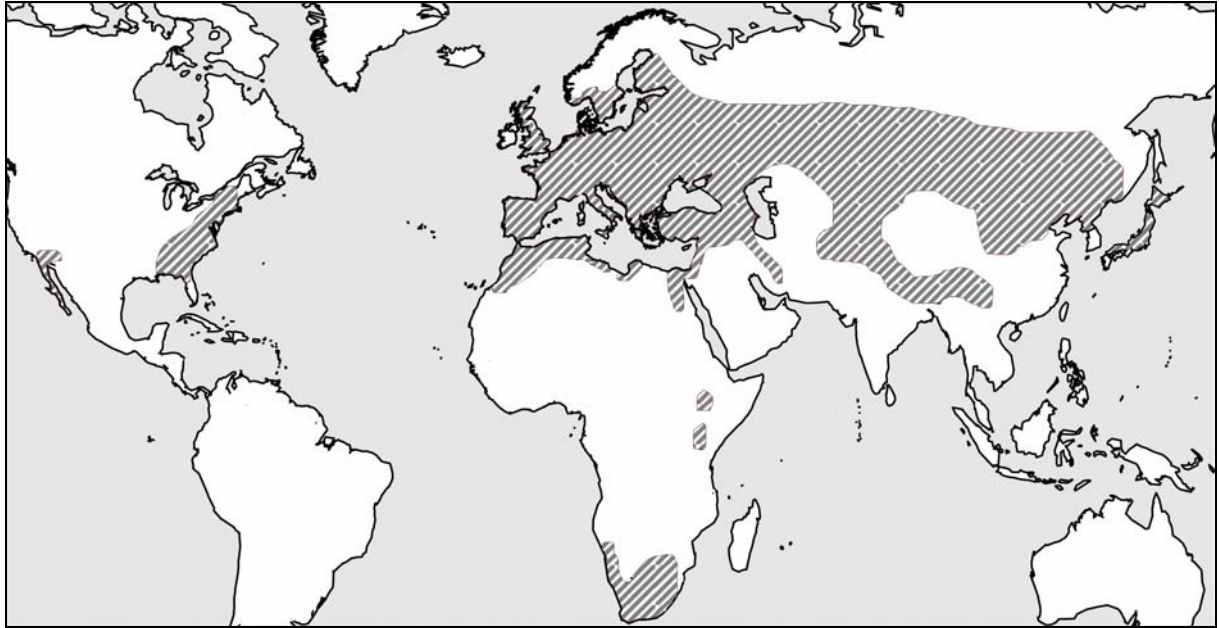
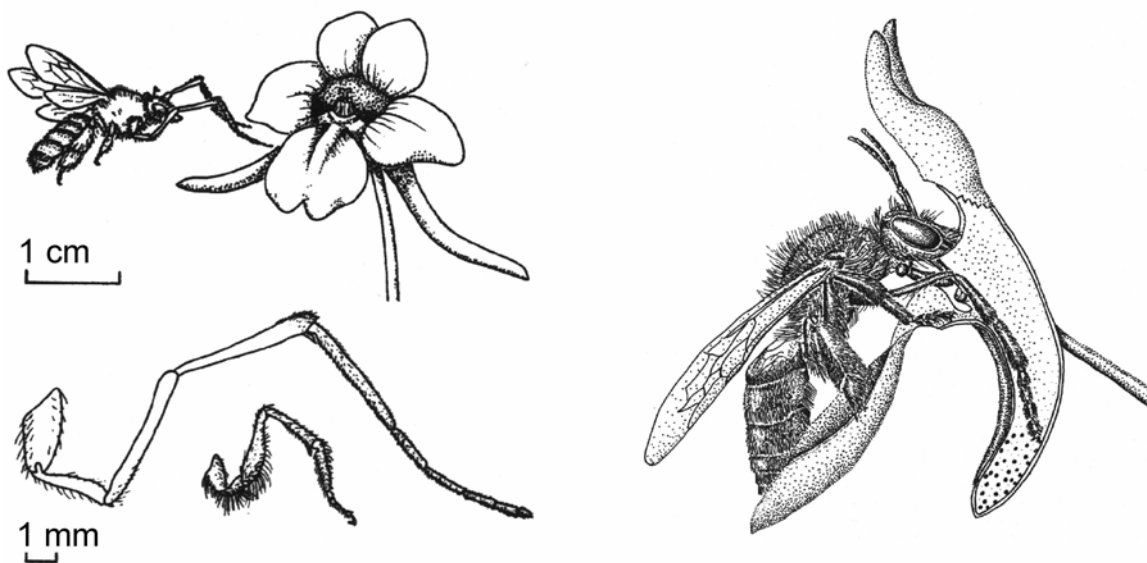


Figure 18. Global distribution of the genus *Melitta* (from Snelling & Stage 1995, Eardley & Kuhlmann 2006, Michez & Eardley in press).

Genus *Redivivoides* Michener 1981

Redivivoides is very closely related to *Rediviva* (males with reduced disk of S7 and small propodeal triangle) and could represent a less derived group branching at the base of *Rediviva* (Michener 1981). *Redivivoides* does not collect floral oil and lacks the morphological adaptation of front legs. *Redivivoides* present some plesiomorphies like the shape of volsella and pygidial plate present in male.

Three species of *Redivivoides* are recognized but only one was described by Michener (1981), *Redivivoides simulans*. This species is endemic in western Cape Province (fig. 15).



Figures 19-21. 19. *Rediviva longimanus* foraging on *Diascia longicornis* (from Buchmann 1987). 20. Comparison between the fore leg of *Rediviva longimanus* and *Apis mellifera* (from Buchmann 1987). 21. *Rediviva neliana* with its fore leg in the spur of *Diascia capsularis* (from Steiner & Whitehead 1990).



Figures 22-25. Pictures of melittid bees. **22.** Female of *Dasygaster hirtipes* on *Hypochoeris radicata* L. (picture N.J. Vereecken). **23.** Male of *Dasygaster hirtipes* on *Hypochoeris radicata* L. (picture N.J. Vereecken). **24.** Female of *Dasygaster hirtipes* (picture N.J. Vereecken). **25.** Male of *Macropis europaea* on *Lysimachia vulgaris* L. (picture N.J. Vereecken).



Figures 26-29. Pictures of melittid bees. **26.** Female of *Macropis europaea* on *Lysimachia vulgaris* (picture Y. Barbier). **27.** Female of *Melitta tricincta* on *Odonites verna* (Bell.) Dumort. (picture N.J. Vereecken). **28.** Female of *Melitta nigricans* landing on *Lythrum salicaria* L. (picture Y. Barbier). **29.** Male of *Melitta dimidiata* on *Onobrychis viciifolia* Scopoli (picture N.J. Vereecken).

3. BIOLOGY OF THE MELITTIDAE *s.l.*

3.1. General cycle of development

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. 30). 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. 30D). 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. 30E). After consuming all the pollen and after defecation, larva overwinters and becomes pupa the following year (fig. 30F).

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, Joris (2006) showed that the emergence of *Melitta nigricans* females (Melittidae *s.str.*) overlaps the blooming peak of its host-plant, *Lythrum salicaria* L. (fig. 31). However, she did not study the factors eliciting the emergence of *M. nigricans*.

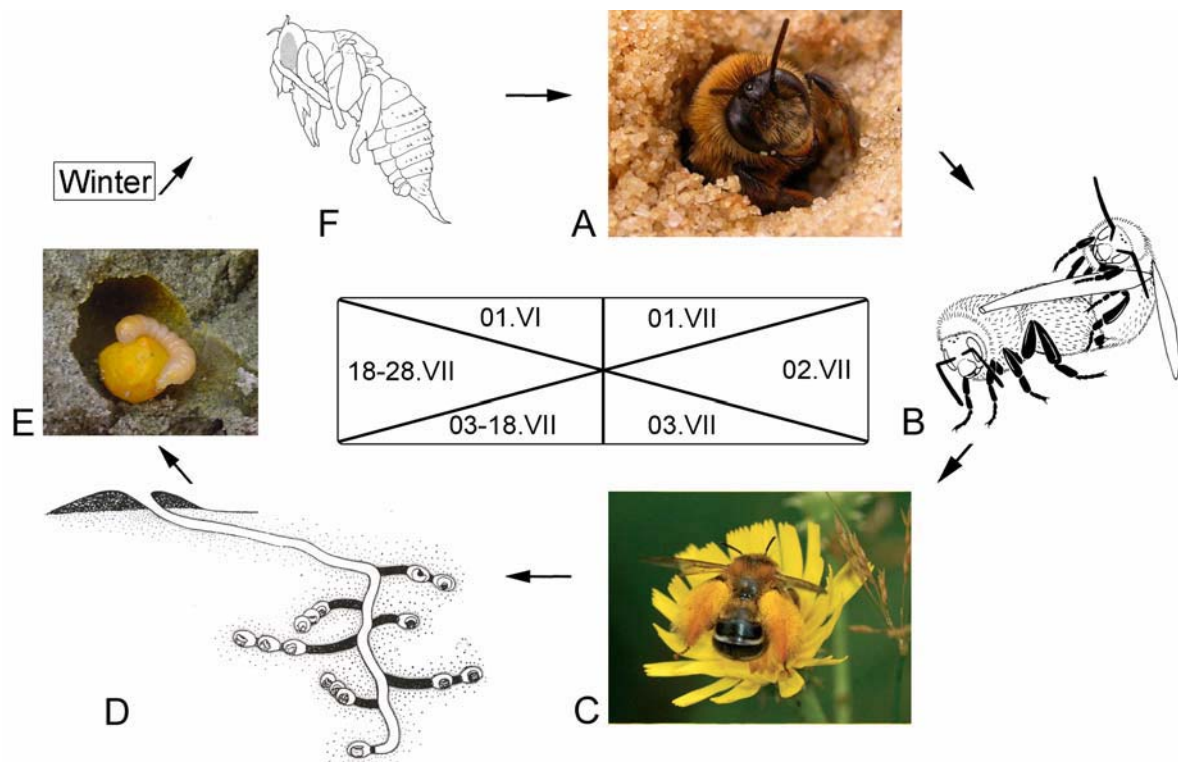


Figure 30. General cycle of development of Melittidae *s.l.*. **A.** Emergence of *Dasygaster hirtipes* female (picture N. J. Vereecken). **B.** Copulation of a pair of bees (drawing M. Terzo). **C.** Female of *D. hirtipes* foraging on *Hypochaeris radicata* L. (picture N. J. Vereecken). **D.** Nest of *Dasygaster braccata* (from Radchenko 1987). **E.** Larva of *D. hirtipes* (picture M. Gosselin). **F.** Pupa of *Hesperapis trochanterata* (from Rozen 1987).

Mating behaviour is only described for *Dasypoda hirtipes* (Dasypodidae) (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, Pouvreau & Loublier 1995, Vereecken *et al.* 2006). 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”.

Nesting and provisioning behaviours have been studied for a few species in the genera *Capicola* (Rozen 1974), *Dasypoda* (Saunders 1908, Maruyama 1953, Blagovestchenskaya 1963, Lind 1968, Radchenko 1987, Pouvreau & Loublier 1995, Chmurzynsky *et al.* 1998, Celary 2002, Vereecken *et al.* 2006), *Haplomelitta* (Rozen 1974), *Hesperapis* (Stage 1966, Rozen 1987, Rozen & McGinley 1991, Cane 1997, Cane *et al.* 1997), *Macropis* (Malyshev 1929, Phipps 1948, Rozen & Jacobson 1980, Cane *et al.* 1983, Pekkarinen *et al.* 2003, Celary 2004), *Meganomia* (Rozen 1977) and *Melitta* (Tirgari 1968, Litt 1999, Celary 2006).

Dasypodaide bees seem gregarious and associated with sandy soils. Females nest in habitats like inland dunes, sandy coast, drifts or silty flood plains. They excavate individual tunnels to depths that can exceed one meter. The burrow is surmounted with a regular tumulus resulting from the excavation of the sand. The main tunnel penetrates the surface at a low angle and comes down vertically after some decimetres. Chambers (*i.e.* cells) are burrowed in the end of lateral tunnels (fig. 30D). The cells are either single like in *Haplomelitta* and *Hesperapis* (except *H. larrae*), or arranged in linear series like in *Capicola* and *Dasypoda*. The tunnels and the cells are unlined and non-waterproof but the walls are more solid than the substrate. Females forage pollen moistened with nectar to fill the cells. The provisions are moulded in different shapes, spherical in *Capicola*, *Haplomelitta* and *Hesperapis*, or with basal cones in *Dasypoda*. The female lays one egg on the top of the pollen ball and closes the cell with fine soil material. After hatching, the larva quickly consumes its provisions (during 15 days). After defecation, the mature larva overwinters as prepupa. The postdefecating larva does not spin any cocoon.

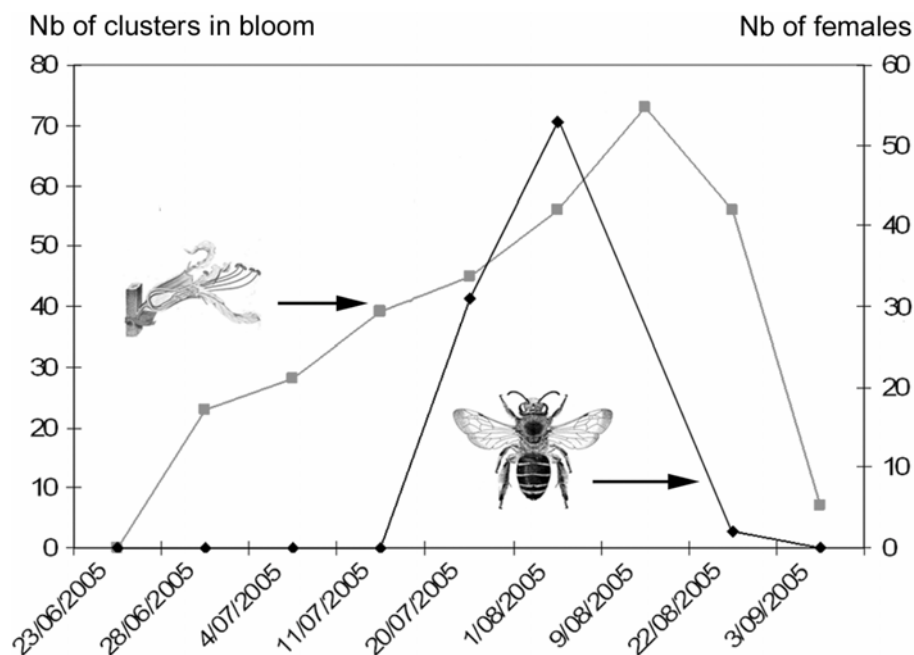


Figure 31. Phenology of *Lythrum salicaria* and *Melitta nigricans* during summer 2005 in Hensies (Belgium) (according to Joris 2006).

The nests of Melittidae *s.str.* are usually not aggregated. At least, the nests of *Melitta* and *Macropis* are known to be isolated. Females dig in clay or sandy soil where the entrance is concealed by vegetation. A low tumulus surrounds the entrance. The main tunnel is about 20 to 40 cm in depth, clearly less deep than those of Dasypodaidae. The lateral tunnels run horizontally leading to one or two cells. *Melitta* females carry dry pollen and *Macropis* females moisten pollen with oil. *Macropis* uses oil-flower as cell lining (Cane *et al.* 1983) whereas *Melitta* uses Dufour's gland secretion (Celary 2006). The development of larvae is similar to Dasypodaidae but the larvae spin cocoon.

Meganomia gigas is the only Meganomiidae for which nesting and provisioning behaviours are described (Rozen 1977). This species presents intermediate nesting behaviour between Dasypodaidae and Melittidae *s.str.*. Females are gregarious and dig a deep nest (120 cm) in sandy soil like Dasypodaidae but they apply waterproof lining like Melittidae *s.str.*. Females of *Meganomia* moist the pollen with nectar during their foraging trips as females of Dasypodaidae do but larvae spin cocoons like females of Melittidae *s.str.* do.

3.2. Host-plants

Dasypodaidae

Most Dasypodaidae are specialised on easily accessible flowers like those of Aizoaceae, Asteraceae, Brassicaceae, Campanulaceae, Cistaceae or Dipsacaceae (tabs 3-4). Only a few species of *Dasypoda* and *Hesperapis* are likely polylectic (Stage 1966, Michez *et al.* 2004a, submitted).

Capicola species seem to be oligolectic on one of following four plant families: Aizoaceae (six *Capicola* species), Asteraceae (one *Capicola* species), Campanulaceae (three *Capicola* species) and Fabaceae (one *Capicola* species) (tab. 3; Michez *et al.* 2007a). The host-plants of *Capicola* are very common in South Africa and offer accessible rewards. The families Aizoaceae, Asteraceae and Fabaceae are also very attractive to many other oligolectic bee species (Gess & Gess 2004).

Likewise, most *Dasypoda* species appear to be oligolectic on actinomorph plant families (*i.e.* showing flowers with radiate symmetry) (tab. 3; Michez *et al.* 2004a, submitted). All *D. (Dasypoda) s.str.* and *D. visnaga* forage on Asteraceae (figs 22-23) whereas females of *D. (Megadasypoda)* forage exclusively on Dipsacaceae. Females of *D. (Microdasypoda)* and *D. (Heterodasypoda)* are characterized by a wider host breadth although they are strongly associated with the family Cistaceae (tab. 3). Four species (*D. albimana*, *D. cingulata*, *D. crassicornis*, *D. morotei*) could be described as polylectic with a strong preference for Cistaceae (Müller 1996). The fifth species (*D. pyrotrichia*) appears strictly oligolectic on Cistaceae but the sample is too small to definitely conclude on its host preferences. Numerous alternative host-plants are recorded for the polylectic species of *D. (Microdasypoda)* and *D. (Heterodasypoda)*. For instance, *D. crassicornis* visits at least seven different plant families (Asteraceae, Brassicaceae, Cistaceae, Geraniaceae, Linaceae, Ranunculaceae and Rosaceae). The palynological analyses provide additional evidence of pollen collection from these plants.

The floral choices of *Promelitta alboclypeata* are unclear. The field observations differ from the palynological studies of the female scopal loads. All observed females of *Promelitta* forage on yellow Brassicaceae (Michez *et al.* 2007b) but preliminary palynological analyses show that females collect mainly pollen from Resedaceae (tab. 3).

Table 3. Host-plants of the females of *Capicola*, *Dasypoda*, *Eremaphanta* and *Promelitta*. Field= number of specimens with field data; number of localities. Pollen= number of specimens with palynological data; number of sampled localities. Between brackets, percentage of the main host-plants family; pollen counts are corrected by volume; * = Hundred percent of data. ¹= Preliminary palynological analysis.

Taxon	Field	Main host-plants	Pollen	Main host-plants
Genus <i>Capicola</i> Friese				
<i>C. (Capicola) aliciae</i>	4;2	Aizoaceae*	6;2	Aizoaceae*
<i>C. braunsiana</i>	20;9	Aizoaceae*	21;9	Aizoaceae*
<i>C. danforthi</i>	23;7	Campanulaceae*	-	-
<i>C. flavicara</i>	-	-	-	-
<i>C. flavitarsis</i>	-	-	1;1	Aizoaceae*
<i>C. gessorum</i>	3;2	Campanulaceae*	-	-
<i>C. hantamensis</i>	3;1	Campanulaceae*	-	-
<i>C. micheneri</i>	47;6	Fabaceae*	16;3	Fabaceae*
<i>C. nanula</i>	12;3	Aizoaceae (92%)	3;2	Aizoaceae*
<i>C. nigerrima</i>	32;7	Campanulaceae*	-	-
<i>C. rhodostoma</i>	9;5	Aizoaceae (89%)	-	-
<i>C. richtersveldensis</i>	23;3	Asteraceae (96%)	-	-
<i>C. rufiventris</i>	15;5	Aizoaceae*	5;1	Aizoaceae*
Genus <i>Dasypoda</i> Latreille				
<i>D. (Dasypoda) albipila</i>	-	-	15;8	Asteraceae (88%)
<i>D. (D.) chinensis</i>	-	-	-	-
<i>D. (D.) cockerelli</i>	-	-	1;1	Asteraceae*
<i>D. (D.) dusmeti</i>	8;2	Asteraceae*	31;23	Asteraceae (97%)
<i>D. (D.) gusenleitneri</i>	-	-	-	-
<i>D. (D.) hirtipes</i>	152;52	Asteraceae*	66;47	Asteraceae (99%)
<i>D. (D.) japonica</i>	?	Asteraceae	2;2	Asteraceae*
<i>D. (D.) litigator</i>	-	-	-	-
<i>D. (D.) maura</i>	4;1	Asteraceae*	21;8	Asteraceae (99%)
<i>D. (D.) oraniensis</i>	1;1	Asteraceae*	17;7	Asteraceae (94%)
<i>D. (D.) pyriformis</i>	-	-	27;16	Asteraceae*
<i>D. (D.) sichuanensis</i>	-	-	-	-
<i>D. (D.) sinuata</i>	1;1	Asteraceae*	19;15	Asteraceae (95%)
<i>D. (D.) syriensis</i>	-	-	-	-
<i>D. (D.) tubera</i>	-	-	17;11	Asteraceae*
<i>D. (D.) warnckeii</i>	-	-	4;3	Asteraceae*
<i>D. (Megadasypoda) argentata</i>	191;41	Dipsacaceae*	54;40	Dipsacaceae*
<i>D. (M.) braccata</i>	285;18	Dipsacaceae*	38;19	Dipsacaceae (99%)
<i>D. (M.) frieseana</i>	-	-	4;3	Dipsacaceae (91%)
<i>D. (M.) longigena</i>	-	-	3;3	Dipsacaceae*
<i>D. (M.) patinyi</i>	-	-	-	-
<i>D. (M.) spinigera</i>	-	-	44;25	Dipsacaceae*
<i>D. (M.) suripes</i>	3;3	Dipsacaceae*	32;24	Dipsacaceae*
<i>D. (M.) toroki</i>	1;1	Asteraceae*	1;1	Dipsacaceae*
<i>D. (M.) visnaga</i>	22;5	Asteraceae*	49;34	Asteraceae*
<i>D. (Heterodasy.) albimana</i>	3;1	Rosaceae*	17;9	Cistaceae (43%)
<i>D. (H.) morotei</i>	3;1	Cistaceae*	25;12	Cistaceae (88%)
<i>D. (H.) pyrotrichia</i>	5;3	Cistaceae*	11;4	Cistaceae*
<i>D. (Microdasy.) brevicornis</i>	-	-	-	-
<i>D. (M.) cingulata</i>	9;2	Malvaceae (55%)	30;20	Cistaceae (67%)
<i>D. (M.) crassicornis</i>	44;23	Asteraceae (36%)	30;22	Cistaceae (81%)
Genus <i>Eremaphanta</i> Popov				
<i>E. (Popovapis) dispar</i>	9 ; 3	Asteraceae (67%)	5 ; 1	Asteraceae (96%)
<i>E. (P.) zhelochovtsevi</i>	-	-	-	-
<i>E. (Eremaphanta) convolvuli</i>	2 ; 1	Convolvulaceae*	-	-
<i>E. (E.) fasciata</i>	-	-	2 ; 1	Cistaceae*
<i>E. (E.) iranica</i>	-	-	-	-
<i>E. (E.) minuta</i>	-	-	-	-
<i>E. (E.) popovi</i>	-	-	-	-
<i>E. (E.) turcomanica</i>	-	-	-	-
<i>E. (E.) vitellina</i>	-	-	-	-
Genus <i>Promelitta</i> Friese				
<i>Promelitta alboclypeata</i>	15 ; 6	Brassicaceae	-	Resedaceae ¹

Table 4. Host-plants of the females of *Haplomelitta*, *Hesperapis* and *Samba*. Field= number of specimens with field data; number of localities. Between brackets, percentage of the main host-plant family. * = Hundred percent of data. ¹ = Preliminary palynological analysis.

Taxon	Field	Main host-plants	Taxon (continuation)	Field	Main host-plants
Genus <i>Haplomelitta</i> Michener			<i>H. (C.) peninsularis</i>	8;3	Asteraceae*
<i>Haplomelitta (H.) ogilviei</i>	-	Campanulaceae ¹	<i>H. (C.) rhodocera</i>	105;12	Asteraceae*
<i>H. (Atrosamba) atra</i>	-	-	<i>H. (C.) rodecki</i>	4;2	Asteraceae*
<i>H. (Metasamba) fasciata</i>	-	Fabaceae ¹	<i>H. (C.) sphaeralceae</i>	1;1	Malvaceae*
<i>H. (Prosamba) griseonigra</i>	-	Crassulaceae ¹	<i>H. (Disparapis) arenicola</i>	41;12	Asteraceae (90%)
<i>H. (Haplosamba) tridentata</i>	-	-	<i>H. (D.) cockerelli</i>	41;7	Asteraceae*
Genus <i>Hesperapis</i> Cockerell			<i>H. (D.) dispar</i>	3;1	Asteraceae*
<i>H. (Amblyapis) arida</i>	3;3	Zygophyllaceae (66%)	<i>H. (Hesperapis) elegantula</i>	-	Boraginaceae*
<i>H. (A.) ilicifoliae</i>	33;2	Rosaceae (91%)	<i>H. (H.) kayella</i>	22;6	Boraginaceae (91%)
<i>H. (A.) larrae</i>	13;6	Zygophyllaceae (69%)	<i>H. (H.) pulchra</i>	7;3	Boraginaceae*
<i>H. (A.) leucura</i>	19;3	Fabaceae*	<i>H. (H.) trochanterata</i>	-	Boraginaceae*
<i>H. (A.) parva</i>	-	-	<i>H. (Panurgomia) fuchsi</i>	-	-
<i>H. (A.) timberlakei</i>	28;10	Fabaceae (71%)	<i>H. (P.) nitidula</i>	-	-
<i>H. (Carinapis) alexi</i>	21;9	Asteraceae*	<i>H. (P.) pellucida</i>	-	Papaveraceae*
<i>H. (C.) australis</i>	-	-	<i>H. (P.) regularis</i>	373;43	Onagraceae (91%)
<i>H. (C.) cajonensis</i>	1;1	Malvaceae*	<i>H. (P.) semirudis</i>	3;2	Asteraceae*
<i>H. (C.) carinata</i>	46;7	Asteraceae*	<i>H. (P.) willmattae</i>	-	Polylectic
<i>H. (C.) floridensis</i>	-	-	<i>H. (Xeralictoides) laticeps</i>	74;7	Loasaceae (97%)
<i>H. (C.) fulvipes</i>	38;8	Asteraceae*	<i>H. (X.) rufiventris</i>	18;6	Loasaceae (94%)
<i>H. (C.) hurdi</i>	35;14	Asteraceae (80%)	<i>H. (Zacesta) rufipes</i>	76;5	Polemoniaceae (99%)
<i>H. (C.) infusata</i>	38;13	Asteraceae (97%)	<i>H. (Z.) palpalis</i>	48;9	Polemoniaceae*
<i>H. (C.) macrocephala</i>	34;2	Fabaceae (97%)	Genus <i>Samba</i> Friese		
<i>H. (C.) occidentalis</i>	32;11	Asteraceae*	<i>Samba calcarata</i>	-	-
<i>H. (C.) oliviae</i>	1;1	Asteraceae*			
<i>H. (C.) oraria</i>	-	Asteraceae*			

Eremaphanta species seem also oligolectic on various plant families (tab. 3). The field observations recorded in literature and our studies of the available series suggest a strong orientation of floral choices toward different plant taxa in Euasteridae. *Convolvulus* sp. (Convolvulaceae) and *Cousinia* sp. (Asteraceae) seem to be the main resources for *E. convolvuli* and *E. dispar* respectively (Popov 1940, 1957, Michez & Patiny 2006). The association of *E. dispar* with Asteraceae is confirmed in palynological analyses and pollen of Cistaceae-like are found in the scopal loads of *E. fasciata* (tab. 3; Michez & Müller unpublished data). *Eremaphanta* could be therefore associated with at least three plant families: Asteraceae, Cistaceae and Convolvulaceae.

Within the genus *Hesperapis*, actinomorphic plants host most subgenera or species groups described by Stage (1966) and Michener (1981): (i) three species groups of *H. (Carinapis)* and *H. (Disparapis)* forage exclusively on Asteraceae; (ii) the *Sphaeralceae* species group visits Malvaceae; (iii) *H. (Hesperapis) s.str.* collect pollen on Boraginaceae; (iv) *H. (Xeralictoides)* and *H. (Zacesta)* forage exclusively on Loasaceae and Polemoniaceae, respectively (tab. 4; Stage 1966, Rozen 1987, Cane *et al.* 1997). Within these groups, all species (except *H. hurdi*) can be considered reasonably as oligolectic.

The pattern of host-plants use is different in other parts of the *Hesperapis* clade. *H. (Amblyapis)* and *H. (Panurgomia)* both include six species foraging on very different plant families (Asteraceae, Fabaceae, Onagraceae, Papaveraceae, Rosaceae and Zygophyllaceae). *H. timberlakei* is probably mesolectic on Fabaceae (mainly on *Dalea* spp.) and Zygophyllaceae (mainly on *Larrea* spp.). Stage (1966) described *H. (P.) wilmattae* as the only polylectic *Hesperapis* species. *H. (Amblyapis)* and *H. (Panurgomia)* show “relaxed floral choices” with a wider host-breadth. The occurrence of the main host-plant is relatively low

compared with *H. (Disparapis)*, *H. (Hesperapis) s.str.*, *H. (Xeralictoides)* and *H. (Zacesta)* (tab. 4).

The knowledge of the Sambini host-plants is sketchy. Rozen (1974) studied the provisioning behaviour of *H. ogilviei* and reported the specialisation of females on Campanulaceae. Gess & Gess (2004) described the floral visits of three species of *Haplomelitta*: *H. ogilviei* is described as specialist on Campanulaceae (as observed by Rozen 1974), one undetermined *Haplomelitta* species forages on *Indigofera* sp. (Fabaceae) and one other undetermined species collect pollen exclusively on Crassulaceae. Our preliminary palynological studies indicate that *H. ogilviei* females show in fact a strong preference to Campanulaceae but forage also actively pollen on Asteraceae (Michez & Timmermann unpublished data). *H. ogilviei* could be therefore mesolectic on Asteraceae and Campanulaceae. Our palynological studies confirm the other observations of Gess & Gess (2004): *H. fasciata* is probably oligolectic on Fabaceae and *H. griseonigra* is specialized on Crassulaceae (Michez & Timmermann unpublished data).

Meganomiidae

The floral choices of Meganomiidae have only been investigated by Rozen (1977). Females of *Meganomia gigas* and *Ceratonomia rozenorum* have been observed to forage exclusively on Fabaceae, respectively on the genera *Indigofera* sp. and *Crotalaria* sp..

Table 5. Host-plants of females of Meganomiidae, *Macropis*, *Rediviva* and *Redivivoides*. Field data= number of specimens with field data; number of localities. *L. (S.)*= *Lysimachia (Seleucia)*, *L. (L.)*= *Lysimachia (Lysimachia)*. * = Hundred percent of data. ²= Observations from literature without specimen counts.

Taxon	Field data	Main host-plants	Taxon	Field data	Main host-plants
Meganomiidae			<i>M. (S.) orientalis</i>	-	-
Genus <i>Ceratonomia</i> Michener	-	-	<i>M. (S.) micheneri</i>	-	-
<i>C. rozenorum</i>	-	Fabaceae ²	<i>M. (S.) omeiensis</i>	-	-
Genus <i>Meganomia</i> Cockerell			Genus <i>Redivivoides</i> Michener		
<i>M. andersoni</i>	-	-	<i>R. simulans</i>	-	-
<i>M. binghami</i>	-	-	Genus <i>Rediviva</i> Friese		
<i>M. gigas</i>	-	Fabaceae ²	<i>R. albifasciata</i>	-	Schrophulariaceae ²
<i>M. rossi</i>	-	-	<i>R. alonsoae</i>	-	<i>Alonsoa</i> sp. ²
Genus <i>Pseudophilanthus</i> Alfken			<i>R. aurata</i>	-	Schrophulariaceae ²
<i>P. stavoensis</i>	-	-	<i>R. autumnalis</i>	-	<i>Diascia</i> spp. ²
<i>P. taeniatus</i>	-	-	<i>R. brunnea</i>	-	<i>Diascia</i> spp. ²
<i>P. tavetensis</i>	-	-	<i>R. colorata</i>	-	Schrophulariaceae ²
Genus <i>Uromonia</i> Michener			<i>R. emdeorum</i>	-	<i>Diascia</i> spp. ²
<i>U. (Uromonia) stagei</i>	-	-	<i>R. gigas</i>	-	Orch., Schroph. ²
<i>U. (Nesomonina) flaviventris</i>	-	-	<i>R. intermedia</i>	-	Schrophulariaceae ²
Melittidae s.str.			<i>R. intermixta</i>	-	Schrophulariaceae ²
Genus <i>Macropis</i> Panzer			<i>R. longimanus</i>	-	Orch., Schroph. ²
<i>M. (Macropis) ciliata</i>	2;2	<i>L. (S.)*</i>	<i>R. macgregori</i>	-	Orch., Schroph. ²
<i>M. (M.) dimidiata</i>	5;1	<i>L. (L.)*</i>	<i>R. micheneri</i>	-	<i>Diascia</i> sp. ²
<i>M. (M.) europaea</i>	84;27	<i>L. (L.)*</i>	<i>R. neliana</i>	-	Schrophulariaceae ²
<i>M. (M.) fridvaldskyi</i>	-	<i>L. (L.)*</i>	<i>R. nitida</i>	-	Schrophulariaceae ²
<i>M. (M.) fulvipes</i>	64;18	<i>L. (L.)*</i>	<i>R. pallidula</i>	-	<i>Diascia</i> sp. ²
<i>M. (M.) kiangsuenensis</i>	-	-	<i>R. parva</i>	-	Orch., Schroph. ²
<i>M. (M.) nuda</i>	-	<i>L. (S.)*</i>	<i>R. peringueyi</i>	-	Orch., Schroph. ²
<i>M. (M.) patella</i>	-	<i>L. (S.)*</i>	<i>R. rhodosoma</i>	-	<i>Diascia</i> sp. ²
<i>M. (M.) steironematis</i>	-	<i>L. (S.)*</i>	<i>R. ruficornis</i>	-	Schrophulariaceae ²
<i>M. (M.) tibialis</i>	-	-	<i>R. rufipes</i>	-	Schrophulariaceae ²
<i>M. (Paramacropis) ussuriensis</i>	-	-	<i>R. rufocincta</i>	-	<i>Bowkeria</i> sp. ²
<i>M. (Sinomacropis) hedini</i>	-	<i>L. (L.)*</i>	<i>R. saetigera</i>	-	Schrophulariaceae ²
<i>M. (S.) immaculata</i>	-	<i>L. (L.)*</i>	<i>R. transkeiana</i>	-	<i>Diascia</i> sp. ²

Table 6. Host-plants of females of *Melitta*. Field= number of female specimens with field data; number of localities. Pal. data= number of female specimens with palynological data; number of sampled localities. Between brackets, percentage of the main host-plant family; * = Hundred percent of data. ¹= Preliminary palynological analysis. ²= Observations from literature without specimen counts.

Taxon	Field	Main host-plants	Taxon	Field	Main host-plants
<i>M. (Melitta) aegyptiaca</i>	10;9	Fabaceae (50%)	<i>M. (C.) harrietae</i>	-	Polylectic ¹
<i>M. (M.) changmuensis</i>	-	-	<i>M. (C.) heilungkiangensis</i>	-	-
<i>M. (M.) leporina</i>	387;59	Fabaceae (91%)	<i>M. (C.) hispanica</i>	-	-
<i>M. (M.) maura</i>	11;5	Brassicaceae (91%)	<i>M. (C.) iberica</i>	-	-
<i>M. (M.) nigricans</i>	66;17	Lythraceae*	<i>M. (C.) japonica</i>	8;2	Fabaceae*
<i>M. (M.) schmiedeknechti</i>	9;4	Resedaceae (77%)	<i>M. (C.) kastiliensis</i>	-	-
<i>M. (M.) tricineta</i>	187;24	Scrophulariaceae (97%)	<i>M. (C.) katherinae</i>	-	-
<i>M. (Cilissa) albida</i>	-	-	<i>M. (C.) latronis</i>	-	-
<i>M. (C.) americana</i>	2;2	Ericaceae*	<i>M. (C.) melittoides</i>	-	Ericaceae ¹
<i>M. (C.) arrogans</i>	10;8	Zygophyllaceae (50%)	<i>M. (C.) mongolica</i>	-	-
<i>M. (C.) barbarae</i>	-	Fabaceae ²	<i>M. (C.) montana</i>	-	-
<i>M. (C.) bicollaris</i>	6;4	Fabaceae*	<i>M. (C.) murciana</i>	-	Fabaceae ¹
<i>M. (C.) budensis</i>	-	Campanulaceae*	<i>M. (C.) nigrabdominalis</i>	-	-
<i>M. (C.) californica</i>	22;3	Malvaceae*	<i>M. (C.) sp. nov. 2</i>	-	Campanulaceae ¹
<i>M. (C.) cameroni</i>	-	-	<i>M. (C.) schultzei</i>	1;1	Iridaceae*
<i>M. (C.) danae</i>	-	-	<i>M. (C.) seitzi</i>	-	-
<i>M. (C.) dimidiata</i>	31;11	Fabaceae*	<i>M. (C.) sibirica</i>	-	Polylectic ¹
<i>M. (C.) eickworti</i>	22;4	Ericaceae*	<i>M. (C.) tomentosa</i>	-	Campanulaceae ¹
<i>M. (C.) ezoana</i>	9;3	Fabaceae (77%)	<i>M. (C.) udmurtiaca</i>	-	Fabaceae ¹
<i>M. (C.) fulvescenta</i>	-	-	<i>M. (C.) wankowiczi</i>	35;12	Campanulaceae*
<i>M. (C.) sp. nov. 1</i>	-	-	<i>M. (C.) whiteheadi</i>	4;2	Fabaceae*
<i>M. (C.) haemorrhoidalis</i>	152;59	Campanulaceae (88%)			

Melittidae s.str.

As Dasypodaidae and Meganomiidae, most Melittidae s.str. are known to be specialist (tab. 5). The oil-collecting genera *Macropis* and *Rediviva* are associated with a few plant families producing oil (Iridaceae, Primulaceae, Orchidaceae and Scrophulariaceae). A few *Melitta* species seem to be polylectic (Michez & Eardley in press).

Macropis bees are probably all oligolectic on *Lysimachia* (Primulaceae) (Cane *et al.* 1983, Popov 1958, Rozen & Jacobson 1980, Vogel 1976, Wu 2000). Females forage pollen and oil on *Lysimachia*, whereas nectar is usually collected from a wide variety of host-plants (fig. 26; Pekkarinen *et al.* 2003, Michez & Patiny 2005). They display morphological adaptations to oil collecting (such as typical hairs on tarsi) suggesting a very tight insect-plant association (Michener 1981). Cane *et al.* (1983) observed that females use the oil to coat their cell walls, but oil is also mixed with the pollen for larval provisions. In any part of their distribution, *Macropis* forage on *Lysimachia* for pollen and oil. Moreover, the data point out the vicariance in the floral choices of bees between the Western and Eastern Hemisphere populations (tab. 5). In the Palaearctic region, the bees are specialized on the subgenus *Lysimachia* s.str., while they are exclusively associated with the subgenus *Seleucia* in North America (although the two plant subgenera are sympatric in this area). We can assume a biogeographical patterning of the *Macropis* host-plant choices

The *Melitta* host-plants are known for 27 species (tab. 6). Females of *Melitta* visit more than 20 different plant families to collect nectar and pollen (Snelling & Stage 1995, Eardley & Kuhlmann 2006, Michez & Eardley in press) (figs 27-29). However, only 13 of these plant families constitute more than 5% percent of the visits for at least one *Melitta* species (Michez & Eardley in press). Likewise, only ten plant families seem to be the exclusive floral resource for at least one oligolectic *Melitta* species (tab. 6). Fabaceae are the main floral resources for ten *Melitta* (including all species of the *Dimidiata* species group). Ericaceae host three North

American species. Five *Melitta* species belonging to the *Haemorrhoidalis* species group forage exclusively on Campanulaceae. Another five *Melitta* species are variously associated with Brassicaceae, Iridaceae, Lythraceae, Malvaceae and Scrophulariaceae.

In the Old World, seven *Melitta* species are probably mesolectic to polylectic (tab. 6) among which at least four are from temperate areas (*M. ezoana*, *M. haemorrhoidalis*, *M. harrietae* and *M. sibirica*) and another three species are from xeric areas (*M. aegyptiaca*, *M. schmiedeknehti* and *M. arrogans*). As it is observed in *Macropis*, we show a shift in host-plant use of *Melitta* species between the Western and Eastern Hemisphere species (tab. 6). In the New World, *Melitta* are specialists on Ericaceae (*M. americana*, *M. eickworti* and *M. melittoides*) and Malvaceae (*M. californica*) whereas these pollen resources are not exploited in the Old World. These results suggest an original resource exploitation by *Melitta* in the Nearctic area.

As *Macropis*, the Southern African genus *Rediviva* collects unusual oil rewards. The main host-plants are *Diascia* (Scrophulariaceae) but some *Rediviva* forage on oil of other Scrophulariaceae (*Hemimeris* and *Bowkeria*), Iridaceae and Orchidaceae (tab. 5; Manning & Brothers 1986, Steiner & Whitehead 1990, Whitehead & Steiner 2001, Whitehead *et al.* in press). Oil-collecting bees of the genus *Rediviva* and South African oil-flowers show a rare plant-pollinator relationships, some plants species depending exclusively on one *Rediviva* species for their pollination (Steiner & Whitehead 1990, 1991, 2002, Pauw 2006). Females use their fore legs to collect oil-secreting secreted by floral trichomes. In *Diascia*, these trichomes are hidden within deep spurs (fig. 21).

4. EVOLUTION OF THE MELITTIDAE *s.l.*

4.1. Phylogeny and host-plants of the Melittidae *s.l.*

Most phytophagous insects are host-specialist (Jaenike 1990, Schoonhoven *et al.* 1998). Estimations of the specialisation in main lineages of insect conclude that more than 70% of species consume only one or a few chemically similar host-plants (Bernays & Chapman 1994). Like the other phytophagous insects, melittid bees are mainly specialists (see previous chapter; tabs 3-6). However, they show sometimes variations in host-plant breadth and host-plant use: (i) a few melittids exhibit a wider spectrum of pollen hosts (*i.e.* mesolecty or polylecty); (ii) different specialist species can forage on different host-plants.

Hereafter, we examined some genera of Melittidae *s.l.* with special emphasis on the origin and the evolution of their interactions with flowering plants by mapping the preferred pollen hosts onto bee phylogeny (figs 32-34; **appendix VIII**).

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

In most cases, closely related species visit similar host plants (figs 32-34). 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. 34), *Dasypoda* (fig. 33), *Hesperapis*, *Macropis* (fig. 32) and *Melitta*.

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 (tabs 3-6; **appendix VIII**) 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).

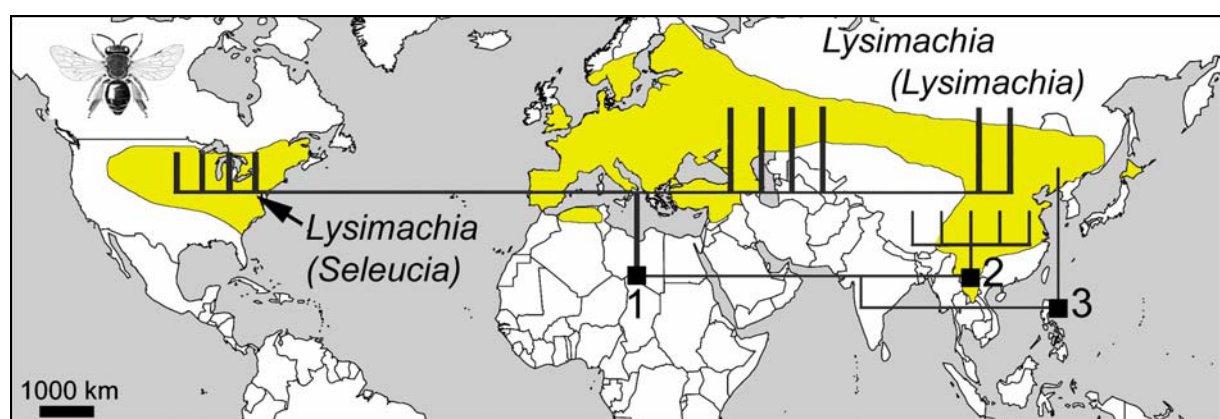


Figure 32. Distribution, phylogeny and host-plants of *Macropis*. 1= subgenus *Macropis s.str.*; 2= subgenus *Sinomacropis*; 3= subgenus *Paramacropis*.

Pattern of host breadth variation

Evolution of dietary breadth in melittid bees is not unidirectional. Oligolecty could be the plesiomorphic condition for the genera *Capicola*, *Hesperapis* and *Macropis*. However,

according to the data available for the phylogeny and floral choices for the genera *Melitta* and *Dasypoda*, polylecty can be put forward as a plesiomorphic condition. Host breadth of Melittidae s.l. could therefore have evolved both ways (toward generalisation and toward specialisation).

In the studied genera, shifts from specialisation to generalisation seem to be more frequent than shifts from generalisation to specialisation. Müller (1996) described a similar pattern in the West-Palaeartic tribe Anthidiini (Megachilidae). However, this pattern could be an artefact. If specialist behaviour is more frequent and the dietary breadth randomly labile, it is expected that the occurrence of generalisation has to be more frequent.

Pattern of shifts among host-plants

Three major patterns of alternative host-plant use can be described in melittid bees: 1. Fixed-specialist pattern (e.g. *Macropis*; fig. 32), 2. Morphological-specialist pattern (e.g. *Dasypoda*; fig. 33), 3. Sequential-specialist pattern (e.g. *Capicola*, *Hesperapis* and *Melitta*; fig. 34).

In the fixed-specialist pattern, the ancestral host-plant seems inherited throughout the evolution of the genus. In some cases, abilities to shift on an alternative host-plant are probably strongly reduced by particular morphological adaptations to the pollen collection (e.g. velvety setae of *Macropis*).

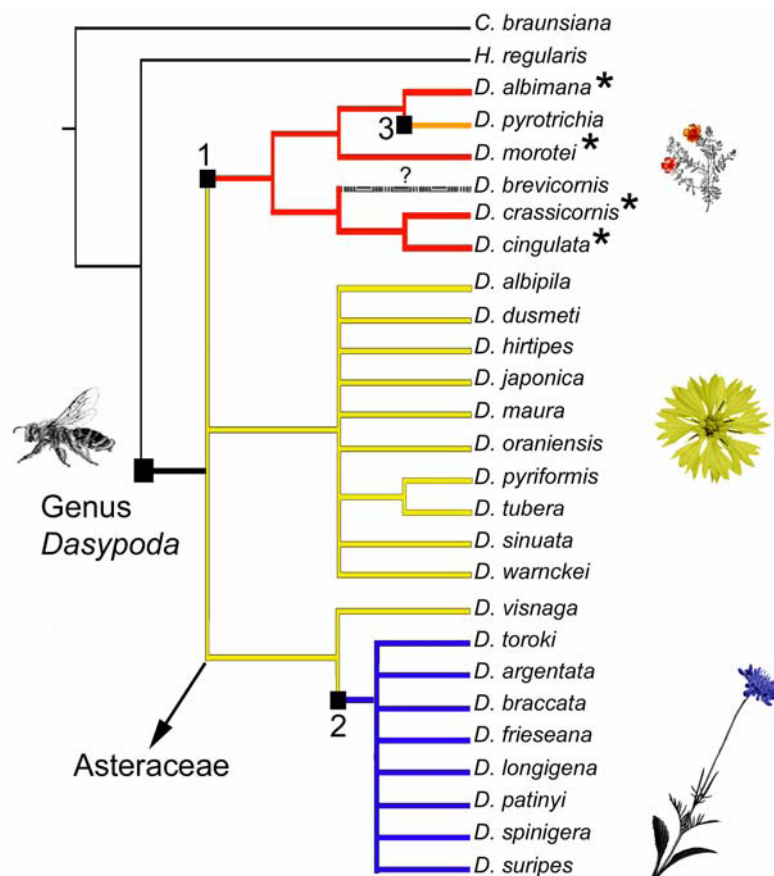


Figure 33. Phylogeny and host-plants of *Dasypoda*. 1= shift from oligolecty on Asteraceae to polylecty with strong preference of Cistaceae; 2= shift from oligolecty on Asteraceae to oligolecty on Dipsacaceae. 3= shift from polylecty with strong preference of Cistaceae to oligolecty on Cistaceae. * polylectic species.

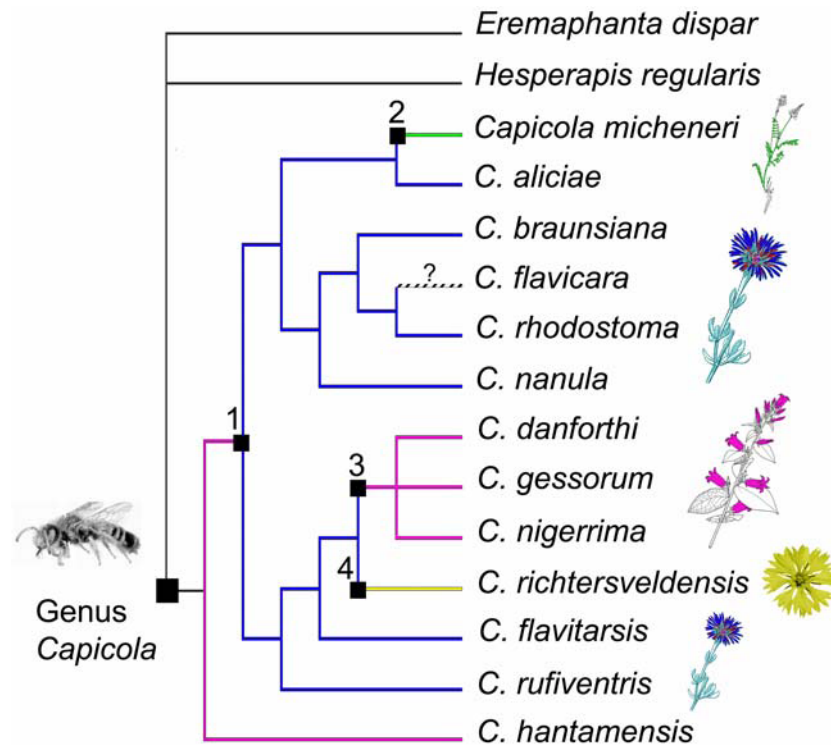


Figure 34. Phylogeny and host-plants of *Capicola* (from Michez & Kuhlmann 2007; Michez & Timmermann unpublished data). 1= shift from Campanulaceae to Aizoaceae; 2= shift from Aizoaceae to Fabaceae; 3= shift from Aizoaceae to Campanulaceae; 4= shift from Aizoaceae to Asteraceae.

Genera characterized by a morphological-specialist pattern presents shifts of hosts. However, the ancestral host-plant has seemingly a strong influence on the present host-plants visited by contemporary species. The potential alternative host-plants seem to be restricted to plant taxa with equivalent morphology.

To the contrary, the selection of alternative host-plants is not atavistic (*i.e.* linked with the earlier ancestral host-plant) within genera showing a sequential-specialist pattern. The co-existence and co-occurrence of potential hosts in a given habitat of such bees facilitate probably shifts from one host to another. Consequently, these oligolectic genera could be regarded as ecological opportunists, with the ability of shifting among hosts with similar floral resources.

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.* 2006b). 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.

4.2. Origin and diversification of the Melittidae s.l.

As written above, *Melittidae s.l.* is a key group in bee evolution. Danforth *et al.* (2006a, b) recently provided strong support to define *Melittidae s.l.* as the sister group of other contemporary bees (fig. 6). Therefore, a discussion about the origin of *Melittidae* is *de facto* a discussions about the early diversification of bees.

Four main sources of arguments have to be considered to understanding the origin and early diversification: (A) the origin and evolution of the exclusive bee hosts, the flowering plants; (B) the phylogeny and the historical biogeography of Apoidea (non-melittid), (C) the fossil records of Apoidea, (D) the direct evidence in the phylogeny and the historical biogeography of *Melittidae s.l.* (*i.e.* present-day distributions of contemporary taxa, plate tectonic development and paleoclimatology). By summarising these four arguments, we propose a plausible picture of the early diversification of bees (E).

A. Origin and evolution of flowering plants

Angiosperm evolution can be used as an indirect way to understand the evolution of bees. Indeed, bees and angiosperms developed close ecological associations that are tied to the origin of bees and their subsequent radiations (Crepet 1979, Michener & Grimaldi 1988, Crane *et al.* 1995, Danforth & Ascher 1999, Grimaldi 1999, Engel 2001). Bees may have arisen at the same time as the earliest obvious angiosperm. On one side, Crepet *et al.* (2004) estimated the minimum age of flowering plant at ~113 myBP (fig. 38). Bees may have appeared during this period at the earliest. On the other side, the diversification of major anthophilic groups of insects in the mid-Cretaceous is consistent with the rise of entomophilous syndromes in Cretaceous flowers (Crepet & Nixon 1998, Grimaldi 1999). Crepet (1996) highlighted that 36 reproductive features indicating entomophilous syndromes appeared in Angiosperm from Aptian (125-112 myBP) to Turonian (115-90 myBP). Moreover, Crane & Ligard (1990) found that generic diversity of Angiosperm was deeply increased during the Albian (112-99 myBP) to the Turonian (94-89 myBP) which could correspond to the period of the early radiation of bees (Grimaldi 1999).

To summarise, the appearance and radiation of Angiosperm during the mid-Cretaceous has been accompanied and probably paralleled by evolution in pollinator insects (including bees).

B. Phylogeny and historical biogeography of Apoidea

Traditionally, colletid have been considered as basal in contemporary bee phylogeny and the Melittidae as intermediate between ST bees and LT bees (fig. 4) (Michener 1944, Grimaldi 1999, Engel 2001). The main argument supporting this “colletid basal” topology, is the bifid glossa morphology of colletid being superficially similar to the ancestral Spheciformes (Alexander & Michener 1995, Michener 2000). Based on family-level inferences supported by extensive data set (molecular + morphology), Danforth *et al.* (2006b) proposed alternative phylogenetic hypothesis and classification. Molecular analyses confirmed the monophyly of six contemporary families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae and Stenotritidae) such as in previous morphological studies by Roig-Alsina & Michener (1993) and Alexander & Michener (1995). However, Danforth *et al.* (2006b) acknowledged the paraphyly of the Melittidae (*sensu* Michener 2000) and split the family into Dasypodaidae, Meganomiidae and Melittidae *s.str.*. In Danforth’s hypothesis, *Melittidae s.l.* is a basal paraphyletic group from which other bee groups arose (fig. 38). The

“Melittid basal” topology could indicate an African origin of bees but Danforth *et al.* (2006b) did not develop a comprehensive phylogenetic or biogeographic argument (see next chapter).

Additionally, some other researches focused accurately on the phylogeny and historical biogeography of one high-level taxa of bees (family, subfamily or tribe). These studies allow us to propose a scenario of the early diversification of bees.

Danforth *et al.* (2004) investigated molecular phylogeny of Halictidae with comprehensive biogeographical analysis. Their results suggested an early radiation in Southern continents (Africa and South America). The subfamilies of Halictidae likely appeared between ~127 myBP and ~90 myBP, before the K/T boundary³. Other lower level taxa in Halictidae have been investigated accurating the results of Danforth *et al.* (2004) (*e.g.* Rophitinae, Patiny *et al.* in press).

By processing similar data set, Ascher (2004) and Almeida (2007) proposed new topologies for Andrenidae and Colletidae + Stenotritidae, respectively. These last authors proposed also a hypothesis on familial biogeographical history. The results in Ascher (2004) and Almeida (2007): (i) confirmed the monophyly of the Andrenidae, Colletidae and Stenotritidae; (ii) suggested that the Andrenidae are probably originated from Western continents, rather from South America as suggested by the distribution of the genera *Alocandrena*, *Euherbsia* and *Orphana* (Patiny 2001); (iii) indicated that colletid bees appeared probably in Australia prior to the separation of the Antarctide (*i.e.* the paleocontinent lumping Australia + Antarctic + South America) but after the separation between Africa and South America. The origin of Colletidae is probably not in Gondwanaland as suggested by previous authors (Michener 1979, Grimaldi 1999, Engel 2001); (iv) the main lineages of colletid bees probably appeared between the late Cretaceous and the early Cenozoic (fig. 38).

There are no equivalent familial revisions for the long-tongued bees (Apidae and Megachilidae). Taxa have been investigated at lower level taxa within genera (*e.g.* *Bombus*: Kawakita *et al.* 2004, Hines *et al.* 2006, Cameron *et al.* 2007; *Diadasia*: Sipes & Wolf 2001; *Xylocopa*: Leys *et al.* 2000, 2002), tribe (*e.g.* Allodapini: Schwarz *et al.* 2006; Ceratinini: Terzo 2000; Euglossini: Michel-Salzat *et al.* 2006; Meliponini: Costa *et al.* 2003, Rasmussen & Cameron 2007) or group of close tribes (*e.g.* Corbiculate bees: Mardulyn & Cameron 1999, 2003, Ascher *et al.* 2001, Cameron & Mardulyn 2001). No accurate hypotheses on the historical biogeography of Apidae and Megachilidae have been made available.

To summarise, the group of “Melittidae *s.l.* + LT bees” is basal in the bee clade and the ST bees are derived. Molecular clock and biogeographical data predict that Halictidae and Colletidae (*i.e.* two derived ST bee families) probably appeared during the late Cretaceous. Therefore, all families of bees must have appeared before the K/T boundary (fig. 38).

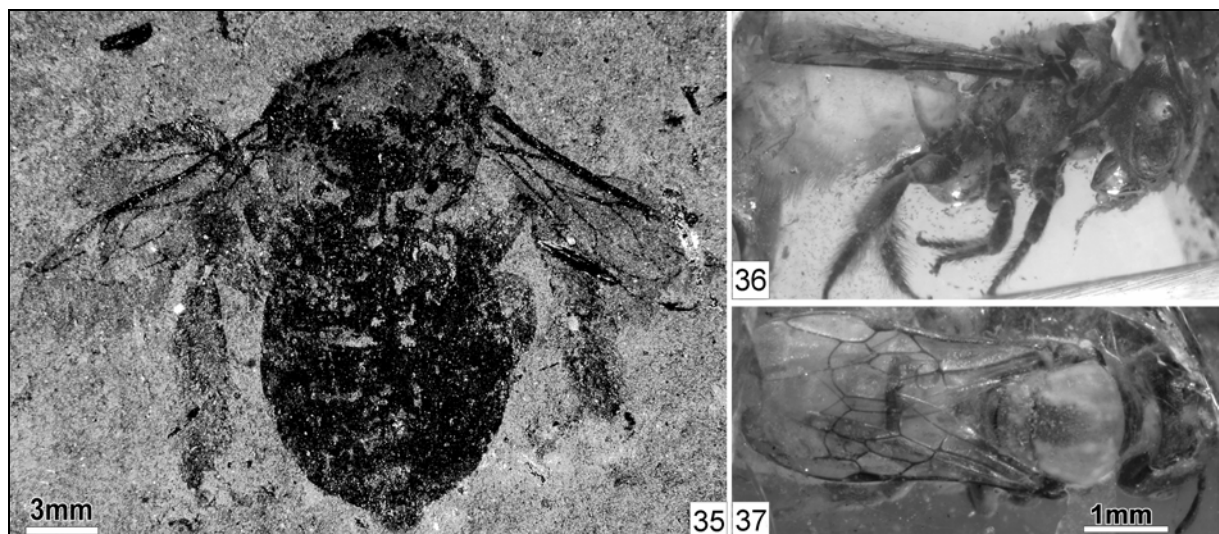
C. Fossil records of Apoidea

The main widespread and useful records of insect fossils are for sure amber fossils. Unfortunately, amber fossils of Apoidea are very rare. The scarcity of Apoidea in amber can be at least partially explained by their habitat preferences (Bennett & Engel 2006). Most species of Apoidea (Apiformes and Spheciformes) live in xeric areas outside of the forest which produces amber (Grimaldi & Engel 2005, Michener 1979, 2000). Fossil records of Apoidea are therefore too patchy to precise the origin of bees. However, they are very useful to recall the minimal age for some clades.

³ Limit between the Cretaceous and the Cenozoic (65 myBP)

Numerous fossil records of Spheciformes wasps have been described from Cretaceous deposits (Grimaldi & Engel 2005, Bennet & Engel 2006). For example, Antropov (2000) described eight species from Burmese amber (upper Albian, ~100 myBP). According to Grimaldi & Engel (2005), the oldest Spheciformes is *Angarosphex magnus*, a compression from the Barremian of Brazil's Santana formation (~125–130 myBP) (fig. 38). Probably more important, the derived sphecid family of Crabonidae has been recorded in mid-Cretaceous showing that diversification of Apoidea Spheciformes occurred during the Lower Cretaceous (Bennet & Engel 2006).

Unlike the Apoidea Spheciformes, bees have been rarely recorded in Cretaceous deposits. Three main deposits with bee fossils are known, all from Cenozoic: Dominican amber from the Miocene (~20 myBP), Florissant shale from the Oligocene (~32 myBP) and Baltic amber from the late Eocene (~45 myBP). These deposits produced a sizeable bee Paleofauna (Zeuner & Manning 1976, Poinar 1999, Engel 2001). Excluding these three deposits, only six older bee fossils have been discovered in isolated sites scattered around the World (fig. 38). The oldest bee fossil (*Melittosphex burmensis* Poinar & Danforth 2006) has been described from the Upper Albian of the early Cretaceous (~100 myBP). This fossil represents an extinct lineage (the Melittosphecidae) sharing only some synapomorphies with the contemporary bees like plumose setae (Poinar & Danforth 2006). The next oldest fossil, *Cretotrigona prisca* (Michener & Grimaldi 1988), is ~35 myBP younger and obviously belonging to the contemporary Apidae family (Apinae, Meliponini). It has been discovered in the New Jersey amber and dated from the late Maastrichtian (~65 to 70 myBP) (Engel 2000). Chronologically, *Probombus hirsutus* Piton 1940 and *Paleohabropoda menatensis* Michez & Nel are the third and the fourth oldest bee fossil (fig. 35). They consist in compressions from the Palaeocene of Menat (France, ~60 myBP) (Nel & Petrulėvičius 2003, Michez *et al.* in prep.). *P. hirsutus* has been recently revised and attributed to Megachilidae (Nel & Petrulėvičius 2003). *Paleomacropis eocenicus* Michez & Nel 2007 has been described from the amber of Oise (France, ~53 myBP) (figs 36-37; **appendix VI**). That latter fossil is particularly interesting with regard to the specialized collecting structures close to those of the contemporary *Macropis*. The corbiculate Apini *Eckfeldapis electrapoides* Lutz 1993 has been discovered in the Eocene shales of Eckfeld (Germany) and constitutes the last noticeable fossil older than the paleofauna of Baltic amber (Lutz 1993).



Figures 35-37. Bee fossils. **35.** *Paleohabropoda menatensis*, general habitus (according to Michez *et al.* in prep.). **36.** *Paleomacropis eocenicus*, lateral view of general habitus. **37.** *Paleomacropis eocenicus*, dorsal view of general habitus.

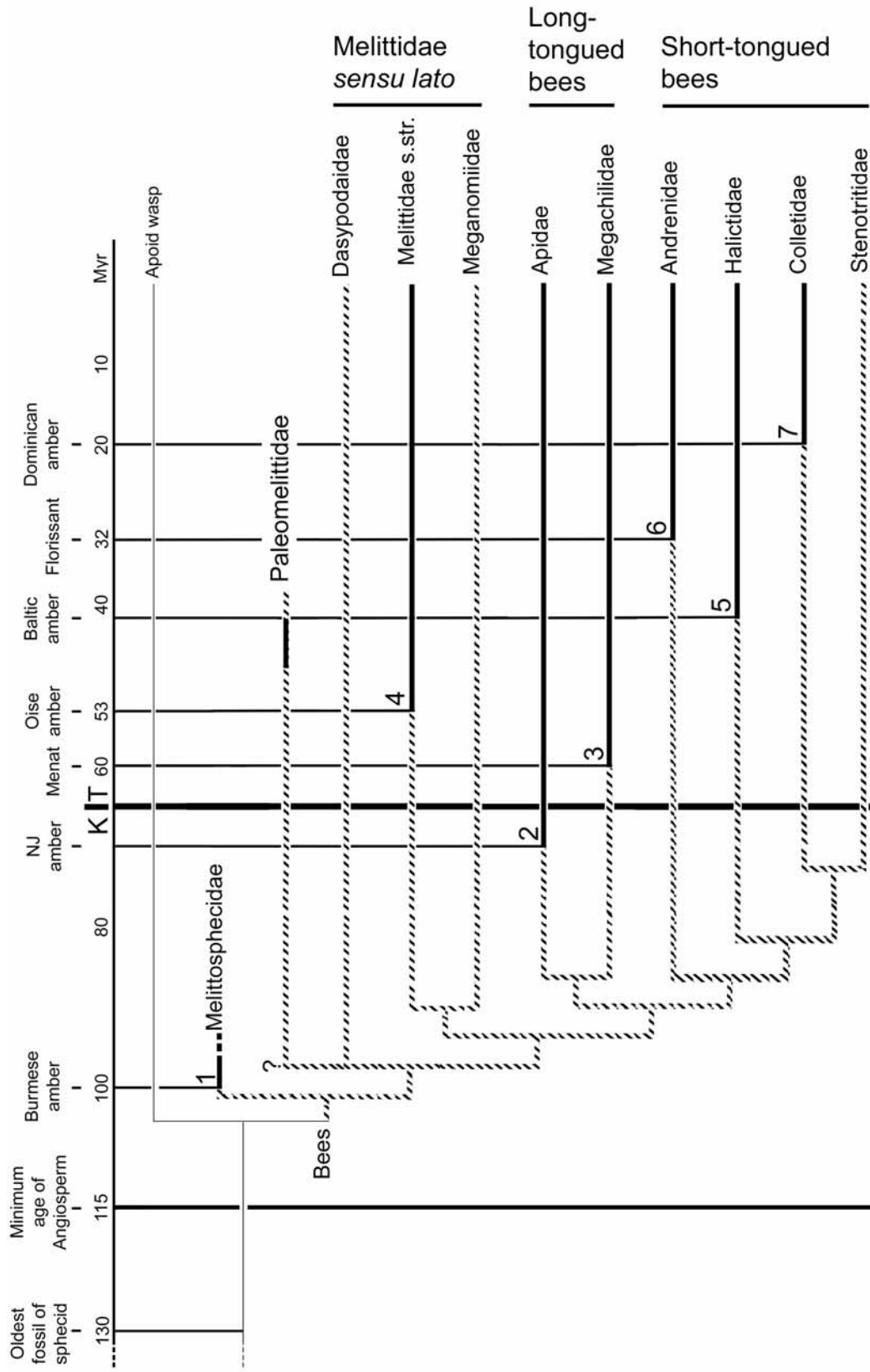


Figure 38. Chronogram of the bee families according to Danforth *et al.* (2006b) with mapping of oldest Apoidea fossils, the position of Paleomelittidae Engel 2001 is not resolved (age of the oldest fossil of sphecids according to Grimaldi & Engel 2005; minimum age of Angiosperm according to Crepet *et al.* 2004). 1 = *Melittosphecid burmensis* Poinar & Danforth 2006 (~100 myBP); 2 = *Cretostrigona prisca* (Grimaldi & Grimaldi 1988) (~65 to 70 myBP); 3 = *Probombus hirsutus* Piton 1940 (~60 myBP); 4 = *Paleomacropis eocenicus* Michez & Nel 2007 (~53 myBP); 5 = *Electrodictus antiquus* Engel 2001 (~45 myBP); 6 = *Andrena* spp., (~32 myBP); 7 = *Chilicola electrodromica* Engel 1999 (~20 myBP).

Three additional fossils of Melittidae s.str. are known: *Macropis basaltica* (Zhang 1989), *Eomacropis glaesaria* Engel 2001 and *Melitta willardi* Cockerell 1909. These fossils come from the middle Eocene or later. The absence of Dasypodaidae and Meganomiidae fossils could be explained by their habitat preferences. In fact, most species are restricted to xeric environment where amber is not produced (figs 8, 13-14). Unlike most other bees, the Melittidae s.str. (specially the genera *Melitta* and *Macropis*) is more diverse in mesic environment like temperate forest producing amber.

The oldest non-melittid ST bee is *Electrolictus antiquus* Engel 2001 (Halictidae) from the Eocene Baltic amber (~45 myBP) (Engel 2001). The records of the other families are much more recent: *Andrena* spp. (Andrenidae, shale of Florissant, ~32 myBP; Zeuner & Manning 1976), *Chilicola gracilis*, and *Chilicola electrodominica* (Colletidae, Dominican amber, 20 myBP; Michener & Poinar 1996, Engel 1999b) (fig. 38).

To summarise, Apoidea fossils support the hypothesis that Apoid Spheciformes appeared surely during Lower Cretaceous. The fossil records of Apiformes are coherently older. The oldest bee fossils are all included in the group of “Melittidae + LT bees” (fig. 38). The resulting temporal distribution of the fossil archives for bees provides additional evidence to the hypothesis of Alexander & Michener (1995) and Danforth *et al.* (2006a, b) designating “Melittidae + LT bees” group as the most basal group of Apoidea (figs 4, 6). It also matches with the correlate “Perkins-McGinley hypothesis”, i.e. bilobed glossa of Colletidae could be derived in the bee clade (Michener 2000).

D. Historical biogeography of Melittidae s.l.

The present knowledge of phylogeny and historical biogeography of Melittidae s.l. does not allow us to determine the definitive localisation of their origin. Melittid distributions are characterized by having two equal centres of diversity (i.e. areas with higher generic endemism), one in Africa and one in the Palaearctic (fig. 39). In the clade of Dasypodaidae, two basal groups (Afrodasyopodaini and Sambini + Promelittini) are restricted to Africa and the last group, the Dasypodaini, is widespread in the Palaearctic. In the clade of Meganomiidae + Melittidae s.str., Meganomiidae is endemic to Africa and the Melittidae s.str. occurs mainly in the Palaearctic. Therefore, melittid bees could have originated: (i) in Africa; (ii) in Africa + Palaearctic. In the first hypothesis, melittid families would have appeared in xeric area of Africa. Melittidae s.str. and Dasypodaidae could have colonised later the Palaearctic region (fig. 39). In the second hypothesis, the Palaearctic group and African group could be vicariant. This vicariance would result in the split of Africa and Europe. The first hypothesis seems more probable *a priori*, as Africa (included in Gondwanaland) and the Palaearctic (included in Laurasia) were separated during Jurassic (~200 myBP) before the appearing of Angiosperm.

The biogeographical disjunction of Hesperapina [*Eremaphanta* + (*Hesperapis* + *Capicola*)] is one of the best arguments to validate the ancestral origin of Dasypodaidae. The three genera are isolated in xeric regions of Central Asia (Kyzyl kum), Southern Africa and North America (Stage 1966, Michener 1981, Michez & Patiny 2006, Michez *et al.* 2007a). Hesperapina were probably widely distributed in the past and undergone significant extinctions. A potential cause driving these drastic extinctions could have been the global climate changes occurring during the Quaternary period (Marchant & Hooghiemstra 2004). Moreover, as Hesperapina includes mainly specialist species (tabs 3-4), it can be assumed that some elements of this group could have disappeared during the K/T boundary (65 myBP) which mainly drove to the extinction of specialist groups (Labandeira *et al.* 2002).

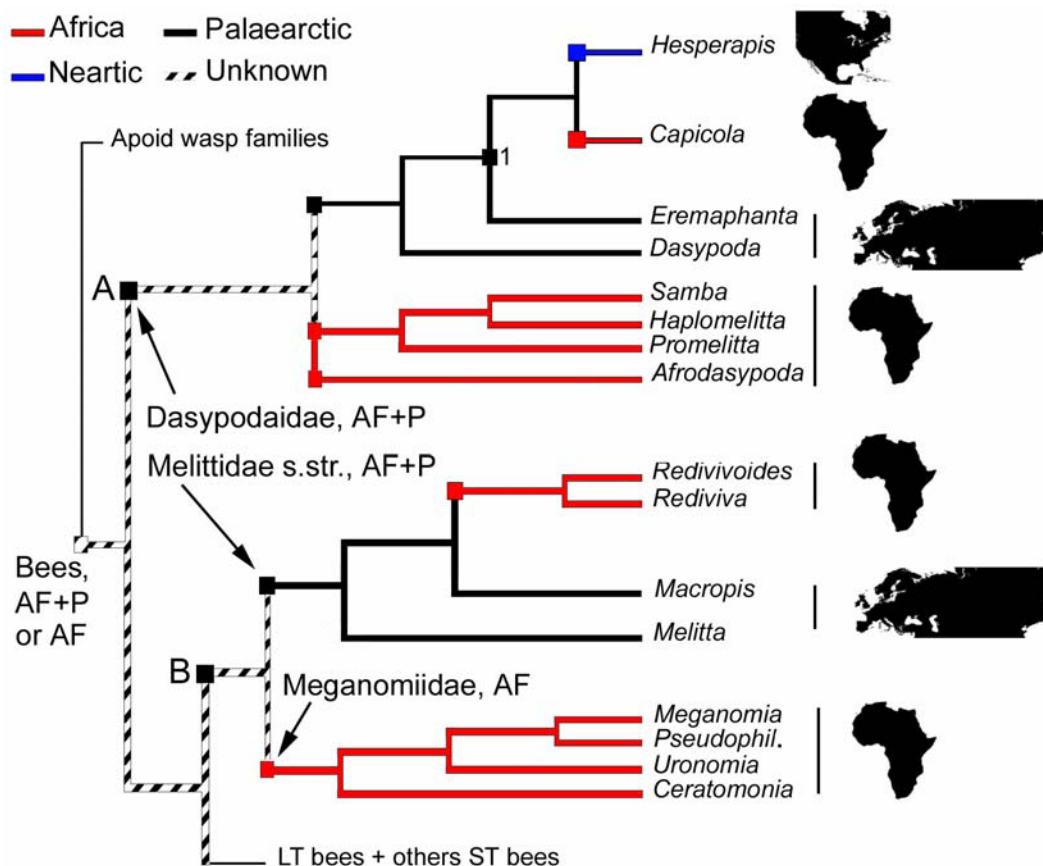


Figure 39. Historical biogeography of Melittidae *s.l.*. A= larvae without cocoon; B= larvae with cocoon; 1= subtribe Hesperapina.

Promelittini, Afrodasydopaini, Sambini, Meganomiidae and Redivini originated probably from Africa (tab. 2, fig. 39). They remained restricted to this area. Melittini and Macropidini are more diverse in the temperate climate by comparison with the Dasypodaidae and Meganomiidae. The fact that the species of Melittidae *s.str.* build their nests with cell lining, while the species of Dasypodaidae do not, could be a significant advantage to inhabit the moister areas.

Melitta and *Macropis* probably originated in Palaeartic where they show the maximum of their specific and subgeneric diversities (tab. 2; Michez & Patiny 2005, Michez & Eardley in press). The occurrence of *Macropis* in North America and *Melitta* in Africa and North America (figs 15, 18) could result from a secondary colonisation from the Palaeartic.

E. Global hypothesis on the origin and early diversification of bees

Collectively, the four latter sources of arguments allow us to propose a global picture of the origin (temporal and geographical) and early diversification of bees.

The oldest fossil of bee is *Melittosphex burmensis*, from early Cretaceous (~100 myBP). This fossil is logically younger than the oldest fossil of the bee ancestor (the Apoidea Spheciformes) recorded from ~130 myBP. This fossil is also logically younger than the Angiosperms. The Angiosperms origin is estimated ~115 myBP at the latest. We can therefore assume that bees are originated from the mid-Cretaceous.

Phylogeny and biogeography of contemporary taxa of Melittidae *s.l.* seem to indicate that bees have appeared in Africa.

Finally, all oldest bee-fossil records indicate that the derived clade of the LT bees and the Melittidae *s.str.* were present in the late Cretaceous or early Cenozoic. Following the phylogenetic hypothesis of Danforth *et al.* (2006b), the diversification of the “Melittidae *s.l.* + LT bees” was probably fast considering their basal position and the constraint of mid-Cretaceous diversification of Angiosperm. The diversification of the derived ST bees would have happened much more lately, during the Cenozoic, explaining the absence of old fossil records from this group. However, molecular clock predicts that Halictidae have appeared during Cretaceous (Danforth *et al.* 2004). In this hypothesis, the appearing of high-level taxa of Apoidea Apiformes could have been “*explosive*” (Grimaldi 1999). The short tongued bees were maybe very rare during the Cretaceous which explains their absence in fossil records. They could have benefited from the K/T boundary, which was harmful for the specialist group like Melittidae *s.l.*, basal Megachilidae and basal Apinae (Labandera *et al.* 2002).

4.3. How to become a bee?

Drawing a global picture of the early diversification of bees, we would like to address the crucial question, how did the ancestral Spheciformes predators become phytophagous pollinators?

The Spheciformes had already several abilities to become a pollinator of Angiosperm: (i) Spheciformes existed when first angiosperms appeared (fig. 38). The niche of pollen food was probably not yet overexploited when some sphecids wasps became bees. (ii) Spheciformes had mandibulate mouthparts more suitable for chewing pollen than piercing-sucking mouthparts (Crepet 1979). (iii) Spheciformes had a predator diet high in protein. Pollen is also high in protein and may content from 12 % to 60 % protein (Roulston & Cane 2000, Roulston *et al.* 2000). (iv) Spheciformes flew very well, that allowed them to forage rapidly on many flowers. (v) Spheciformes brought and transported food (arthropod prey) to feed their offspring. They have been then able to substitute prey transport to pollen transport.

Moreover, use by bees of plumose setae as pollen-collecting structure could have been an exaptation. It means that the plumose setae would have appeared in Spheciformes before pollen collecting behaviour. Indeed, plumose setae would have been firstly used to thermoregulate the body because Spheciformes lived mainly in hot xeric climate and there are, like most of Hymenoptera Aculeate, warm blooded (Heinrich 1996). However, this character would have appeared randomly.

Lastly, the ancestral specialist behaviour (see previous chapter) could have been a key feature to allow the new pollinator to inherit and to promote the new foraging behaviour. Indeed, bee's foraging behaviour exhibits particular constraints. (i) Pollen collecting behaviour is very complex (Weislo & Cane 1996). Bees could have been cognitively limited to use a few hosts. (ii) Bees invest strongly in their offsprings. Females of bees lay only a few eggs and generalist risk-takers could have been selected against. (iii) Host perception seems more complex than in other phytophagous insects. Bees detect colour, shape, size and odour of flowers (Raine *et al.* 2006).

All these characteristics have probably promoted the specialisation and its inheritance. Strong inheritance of specialisation reduces the opportunity to use alternative hosts and increases quickly the selection of pollen-foraging efficiency.

5. FUTURE RESEARCH

Such as all scientific explorations, our modest new studies on Melittidae *s.l.* bring some answers on bee diversity but they drive many additional questions. We distinguish three main directions for future research: (i) development of bee systematics; (ii) exploration of wild bee physiology; (iii) investigations in chemical ecology.

First, the systematic of bee families need additional phylogenetic studies including comprehensive sample of taxa to complete the first global molecular studies of Danforth *et al.* (2006a, b). These kinds of studies are particularly needed for the long-tongued bees and the Melittidae *s.l.*. New robust phylogeny of Melittidae *s.l.* could define accurately the relationship among the tribes, notably the position of Afrodasyopodaini and Promelittini. New fossil records, molecular clock and biogeographical analyses could confirm or reject actual hypothesis on the early diversification of bees.

Bee systematic knowledge presents a few monographic revisions of genera (including phylogeny) despite this taxonomical level is probably the most interesting level to well understand the evolution of bee-plant interactions. Described patterns of host-plant evolution need confirmation processing phylogeny (including morphological and molecular data) and specific floral choices (including field and palynological data) of numerous bee genera. The selected genera should include both specialist and generalist species (*e.g.* *Andrena*, *Anthophora* or *Dufourea*). Additionally, these studies will bring new evidences in the controversial question, how specialisation could affect the speciation and diversity of insects?

If the description of evolutionary patterns needs improvement in bee systematic knowledge, the understanding of their mechanisms needs developments in physiology, molecular ecology and behavioural ecology.

Constraints in becoming phytophagous are still unknown in bees. The primitive bee, probably close to the contemporary Melittidae *s.l.*, must have found equivalent alimentary resources (lipid, glucid and protein) than its carnivorous ancestor. Moreover, digestion of pollen shows different processes in adult (digestion with crop) and larvae (digestion without crop) (Roulston & Cane 2000). There were two potential solutions: (i) females have been found equivalent diet in their new host (for itself and larvae); (ii) females and larvae have been develop new physiological pathway to digest their new alimentary resource. Both hypotheses remain to be tested.

Eventually, the mechanisms of host switches and host breadth variations have to be explored. Bees like many insects can probably eat on a larger variety of plants than are actually used in nature (Praz *et al.* in press). Likewise, host choices are known to depend mainly on adult behaviour than physiological (digestion) ability of larvae (Williams 2003). Shift of foraging behaviour could depend on flower morphology (*e.g.* shape, colour), pollen nutritional rewards (*e.g.* diversity and quality of protein and/or lipid; Roulston & Cane 2000), pollen digestion of larvae and adult, flower scent (*e.g.* odour of pollenkit; Dobson & Bergström 2000, Dötterl *et al.* 2005), adult abilities to learn new floral manipulation, mating constrain (*i.e.* *rendez-vous* flowers), larvae imprinting or on a combinations of these previous features. Many of theses hypotheses are still untested.

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