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Original article

Phylogeny and host-plant evolution in Melittidae *s.l.* (Hymenoptera: Apoidea)*

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Abstract – Bees and the angiosperms they pollinate have developed intimate and often complex interactions over the past 100 million years. As in other insect-plant interactions, host-plant specificity is variable among taxa. While many solitary bee species display an obvious preference for a narrow spectrum of host-plants (oligolecty), others regularly visit a diversified array of pollen hosts (polylecty). Few studies have examined the patterns of host-plant associations in bees using well-resolved phylogenies at the species level combined with accurate and quantitative data on host-plant preferences. In this study, we examined the evolution of bee-plant relationships in several genera of specialist (oligolectic) bees. We used the Melittidae *s.l.* as a model taxon by mapping the preferred pollen hosts onto species-level phylogenies to investigate the frequency and pattern of host-plant switching. Our results suggest that host-plant associations are maintained over time in many lineages, but that host switches to unrelated plant families are also common. We find some evidence that host-switches occur more frequently to morphologically similar, rather than closely-related, host-plants suggesting that floral morphology plays a key role in host-plant evolution in bees.

bees / Melittidae *s.l.* / oligolecty / polylecty / phylogeny / evolution / host-plant

1. INTRODUCTION

Bees constitute a monophyletic group of more than 16000 described species sharing morphological and behavioural adaptations to forage on pollen and nectar from flowers (Linsley, 1958; Thorp, 1979, 2000; Eickwort and Ginsberg, 1980; Michener, 2000). Their exclusive reliance upon floral rewards throughout their life cycle makes bee-flower interactions a textbook case of animal-plant mutualisms. Like many groups of phytophagous insects (Jaenike, 1990), bees show variation in host-plant use as well as host-plant breadth. Whereas many bee species exhibit floral specificity, visiting only a restricted number of suitable and available plant taxa throughout their range (i.e., monolecty or oligolecty), others display a wider spectrum of pollen hosts (i.e., mesolecty or polylecty).

With very few exceptions, morphological, behavioural and physiological constraints are assumed to impact more significantly on pollen than on nectar collection (Westerkamp, 1996). Female bees typically have more nectar

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than pollen host(s) (Robertson, 1925). Hence, characterizing a bee's host breadth is best done by recording the female's pollen host-plant(s).

Roberston (1925) first proposed a classification of host breadth in bees. He described three categories: 1. *Monolecty* (for bees foraging on only one plant species, i.e. extreme specialist bees), 2. *Oligolecty* (for bees foraging on one plant family, i.e. specialist bees), and 3. *Polylecty* (for bees foraging on more than one plant family, i.e. generalist bees). Several studies since then have reported that this dichotomy between specialist and generalist bees reflects an oversimplification. For example, Rasmont (1988) proposed the term *mesolectic* for the medium host breadth. In a recent review, Cane and Sipes (2006) proposed new definitions reflecting better the reality of a continuum in bee host breadth, from extreme specialisation (*monolecty*) on one hand to extreme generalisation (*broad polylecty*) on the other. These authors defined four intermediate states: narrow oligolecty, oligolecty, mesolecty and polylecty.

Host specialisation has evolved multiple times independently in bees (Wcislo and Cane, 1996). Oligolecty is frequent in solitary bees with short life cycles in which bee emergence and host-plant flowering are tightly coupled (Hurd, 1957; Danforth, 1999; Minckley et al., 2000). Oligolecty is rare in eusocial bees. However, specialist bumblebees (*Bombus consobrinus* and *B. gerstaeckeri*; Ponchau et al., 2006) are known to forage exclusively on pollen of *Aconitum* sp. Specialist bees are particularly common in some lineages, such as Andrenidae, non-social Apinae, Lithurgini, Melittidae *s.l.*, Paracolletini and Rophitinae (Linsley, 1958; Wcislo and Cane, 1996; Michener, 2000; Patiny et al., 2007; Larkin et al., 2008).

In most cases, specialist bee species do not show morphological adaptations to their particular host-plants. Accessible rewards, such as the pollen of Asteraceae, do not require special morphological features and there are many oligolectic bees that specialize on Asteraceae. However, some bee species show highly modified morphological structures for gathering pollen from particular host-plants (Thorp, 1979, 2000) or particular floral resources, such as floral oils (Vogel, 1974; Cane et al., 1983; Buchmann, 1987; Michez and Patiny, 2005), flowers with hidden anthers (Müller, 1995, 2006), flowers with large pollen grains (Pasteels and Pasteels, 1979; Thorp, 1979), or nototribic flowers (Müller, 1996b).

Only a few previous studies have examined the pattern of host-plant evolution in specialist bees using phylogenies at the species level (Müller, 1996a; Sipes and Wolf, 2001; Michez et al., 2004b; Sipes and Tepedino, 2005; Larkin et al., 2008). Such studies have generally indicated that host-plant associations are maintained over multiple speciation events (suggesting that host-switching is not always associated with speciation), but that when host switches occur, they occur to distantly related host-plant families.

In this study, we examined host-plant evolution in several genera of Melittidae *s.l.* (families Dasypodaidae, Meganomiidae and Melittidae *s.s.*). We used parsimony to map the preferred pollen hosts onto species-level phylogenies for five genera, all of which include a large proportion of oligolectic species. Our mapping of host-plant use allowed us to examine (i) if host-plant shifts are frequent in these specialist bee clades, (ii) the frequency of host-plant shifts to distantly related hosts, (iii) if host-plant switches involve the evolution of unique morphological adaptations, and (iv) if host-plant specialisation can be regarded as ancestral or derived within each of these genera.

We chose the Melittidae *s.l.* for several reasons. First, melittid bees are mainly distributed in the Old World and they show low species richness. The comprehensive study of specimens in museum collections and institutions across Europe is relatively easy. Second, melittid bees form a specialist group with a key position in the phylogeny of bees (Michener, 2000; Engel, 2001, Danforth et al., 2006a,b). Third, supra-generic revisions are available and most of genera are well-delimited (Michener, 1981, 2000).

From the morphological point of view, the traditional family Melittidae is sometimes considered as paraphyletic (Rozen and McGinley, 1974; Michener, 1981, Alexander and Michener, 1995; Michener, 2000). Using

Figure 1. Map of collecting localities for the 24 515 specimens of Melittidae included in the study.

phylogenetic analyses based on a large morphological data set, Alexander and Michener (1995) divided the traditional Melittidae into three families: Dasypodaidae, Meganomiidae and Melittidae *s.str.*. Danforth et al. (2006a, b) recently supported this hypothesis based on molecular data.

2. MATERIALS AND METHODS

2.1. Specimen data

We studied melittid bee specimens from the collections of major museums (16546 specimens; details see Michez, 2002, 2005; Michez and Patiny, 2005, 2006; Michez and Eardley, 2007; Michez and Kuhlmann, 2007; Michez et al., 2004a, b, 2007a, b). Other data were collected from the literature (3782 specimens) and databases (4187 specimens). We have collected and digitised data from a total of 24515 specimens (Fig. 1).

The present study focused on five genera, selected for the availability of host-plant records and the accuracy of their systematics: *Capicola* Friese (Dasypodaidae, Dasypodaini), *Dasypoda* Latreille (Dasypodaidae, Dasypodaini), *Hesperapis* Cockerell (Dasypodaidae, Dasypodaini), *Macropis* Panzer (Melittidae *s.str.*, Macropidini) and *Melitta* Kirby (Melittidae *s.str.*, Melittini). The distributions and diversity of these taxa are summarised in Table I; 144 species are included.

For the definition of supra-generic level, we referred to Danforth et al. (2006b). Species taxonomy and phylogeny follow Michez et al. (2007a), Michez and Kuhlmann (2007) for *Capicola*; Michez et al. (2004b) for *Dasypoda*; Stage (1966) and Michener (1981) for *Hesperapis*; Michez and Patiny (2005) for *Macropis*; Michez and Eardley (2007) for *Melitta*. All published phylogenies are based on morphological data (Figs. 2–6).

2.2. Host-plant data

We amassed host-plant association data for females of *Capicola*, *Dasypoda*, *Hesperapis*, *Macropis* and *Melitta* (Tabs. II–V). Most host-plant data were based on field records from the literature and labels of pinned specimens (3216 specimens). However, several studies showed that field records are not always reliable enough to confidently determine the host-plant range because field records rarely distinguish between pollen and nectar foraging (e.g. Westrich and Schmidt, 1986; Westrich, 1990; Müller, 1996a; Sipes and Tepedino, 2005; Timmermann and Kuhlmann, unpubl. data.). We have therefore initiated a project on the palynological study of scopal loads of *Capicola* and *Dasypoda* (Michez and Müller, unpubl. data; Michez and Timmermann, unpubl. data) (Tab. II). This method provides an accurate and quantitative estimate of host-plant breadth in bees (Westrich and Schmidt, 1986). Pollen analyses allow the discrimination of pollen and nectar hosts, and the detection of inconspicuous floral choices. As a general rule, we sampled museum specimens in a way that maximised the species' temporal and spatial distribution (see details of method in Müller, 1996a). The pollen was gently removed with an insect pin and embedded in glycerol gelatine on microscope slides.

Table I. Studied taxa and references of dataset. References: 1 = Michez et al. (2007a), 2 = Michez and Kuhlmann (2007), 3 = Michez and Timmermann (unpubl. data), 4–5 = Michez et al. (2004a,b), 6 = Michez and Müller (unpubl. data), 7 = Stage (1966), 8 = Michener (1981), 9 = Rozen (1987), 10 = Rozen and McGinley (1991), 11 = Cane et al. (1997), 12 = Michez and Patiny (2005); 13 = Michez and Eardley (2007).

Taxa	No. of species	Distribution	Main host-plant families	Rf.
Capicola	13	Southern Africa	Aizoaceae, Asteraceae, Campanulaceae, Fabaceae	1–3
Dasypoda	34	Palaearctic	Asteraceae, Cistaceae, Dipsacaceae	4–6
Hesperapis	38	Nearctic	Asteraceae, Boraginaceae, Fabaceae, Loasaceae, Malvaceae, Onagraceae, Papaveraceae	7–11
Macropis	16	Holartic	Primulaceae (*Lysimachia* sp.)	12
Melitta	43	North America and Old World excluding tropical areas	Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Ericaceae, Fabaceae, Lamiaceae, Lythraceae, Malvaceae, Resedaceae Scrophulariaceae, Zygophyllaceae	13

Pollen samples were identified by light microscopy at a magnification of 400×. Pollen composition was investigated by identification of 400 pollen grains randomly chosen from each sample. Pollen grains representing less than 5% per load were assumed to be contamination and neglected (Westrich and Schmidt, 1986). Pollen counts were corrected by volume. We designated a species as oligolectic if more than 90% of the available data (even weak) reveal one host-plant family. If not, we considered the species as mesolectic or polylectic depending on the diversity of the alternative host-plants.

3. RESULTS

3.1. Genus *Capicola* Friese

Capicola species seem to be oligolectic on one of the following four plant families: Aizoaceae (six *Capicola* species), Asteraceae (one species), Campanulaceae (four species) and Fabaceae (one species) (Tab. II).

Within the genus *Capicola*, robust monophyletic groups are associated with pollen host specialisation (Fig. 2). For instance all species of the *C. flavicara* and *C. aliciae* groups are oligolectic on Aizoaceae, the only exception being *C. micheneri* which only visits plants of the family Fabaceae. In the group of *C. danforthi*, *C. gessorum* and *C. nigerrima* the host-plants are more diverse (Aizoaceae, Asteraceae and Campanulaceae). Preliminary analyses and observations suggest that *C. rufiventris* and *C. flavitarsis* are oligolectic on Aizoaceae, and they are basal in this group. Collectively, these results suggest that the collection of pollen from Aizoaceae could be an ancestral condition in two species groups of *Capicola* (Fig. 2), whereas shifts in pollen hosts involving pollen specialisation on Fabaceae and Asteraceae could be regarded as derived conditions within the genus.

There are 23 branch segments above the common ancestor of all *Capicola* and only 4 shifts of host-use (Fig. 2).

The host-plants of *Capicola* are very common in South Africa and offer accessible rewards. They are very attractive to many other oligolectic bee species (Gess and Gess, 2004).

3.2. Genus *Dasypoda* Latreille

Most *Dasypoda* species seem to be oligolectic on actinomorphic plant families (i.e. with radiate symmetry) (Tab. II). All *D.* (*Dasypoda*) *s.str.* and *D. visnaga* forage on Asteraceae whereas females of *D.* (*Megadasypoda*) forage exclusively on

Table II. Host-plants of *Capicola* and *Dasypoda*. Field data = 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; pollen counts are corrected by volume; * = Hundred percent of data.

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

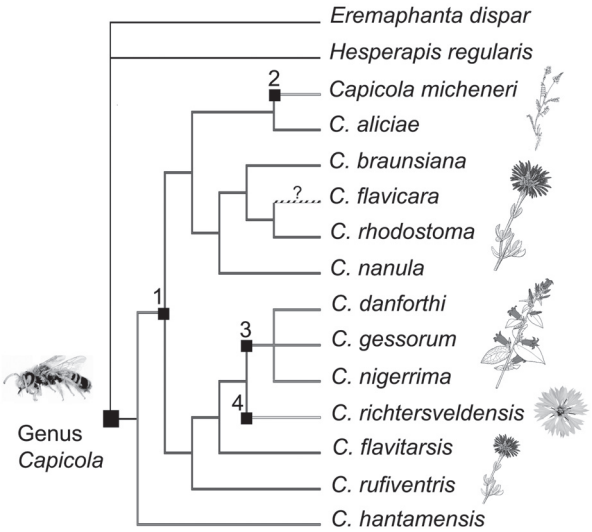

Figure 2. Phylogeny and host-plant associations in *Capicola* (from Michez and Kuhlmann, 2007; Michez and Timmermann unpubl. data). 1 = shift from Campanulaceae to Aizoaceae; 2 = shift from Aizoaceae to Fabaceae; 3 = shift from Aizoaceae to Campanulaceae; 4 = shift from Aizoaceae to Asteraceae.

Dipsacaceae. Females of *D.* (*Microdasypoda*) and *D.* (*Heterodasypoda*) are characterised by a wider host breadth although they are strongly associated with the family Cistaceae (Tab. II). Four species (*D. albimana*, *D. cingulata*, *D. crassicornis*, *D. morotei*) could be described as polylectic with a strong preference for Cistaceae (Müller, 1996a). The fifth species (*D. pyrotrichia*) appears strictly oligolectic on Cistaceae but the sample is too small to conclude definitely. Numerous alternative host-plants have been recorded for the polylectic species of *D.* (*Microdasypoda*) and *D.* (*Heterodasypoda*). For example, *D.* (*Micro.*) *crassicornis* has been recorded on seven different plant families (Asteraceae, Brassicaceae, Cistaceae, Geraniaceae, Linaceae, Ranunculaceae and Rosaceae) and palynological analyses have provided evidence for pollen collection from these plants (Michez et al., 2004b; Michez and Müller, unpubl. data).

By mapping the floral choices onto the phylogeny of contemporary *Dasypoda*, there are 34 branch segments above the common ancestor of all *Dasypoda* species and only two shifts of the main host-plant (Fig. 3). Moreover, there are two shifts of host-breadth.

All main host-plants and alternative host-plants of *Dasypoda* show radiate symmetry. The most parsimonious hypothesis explaining this pattern is that the ancestral host of *Dasypoda* was probably an actinomorphic flower.

As was observed in the genus *Capicola*, the host-plants visited by *Dasypoda* bees are very common in the Palaearctic and offer accessible rewards.

3.3. Genus *Hesperapis* Cockerell

Within the genus *Hesperapis*, actinomorphic plants host most subgenera or species groups described by Stage (1966) and Michener (1981): *H.* (*Disparapis*) and three species groups of *H.* (*Carinapis*) forage exclusively on Asteraceae, the *Sphaeralceae* species group visits Malvaceae, *H.* (*Hesperapis*) *s.str.* collect pollen on Boraginaceae, whereas *H.* (*Xeralictoides*) and *H.* (*Zacesta*) forage exclusively on Loasaceae and Polemoniaceae, respectively (Fig. 4, Tab. III). Within these clades, all species (except *H. Hurdi*) can be regarded as oligolectic.

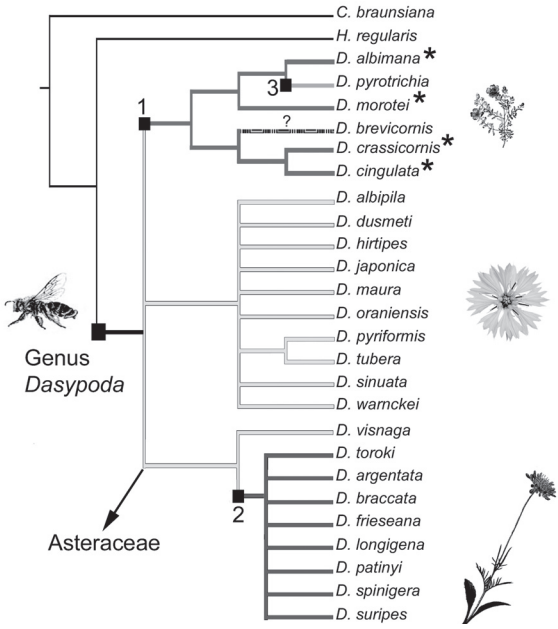

Figure 3. Phylogeny and host-plant associations in *Dasypoda* (from Michez et al., 2004b; Michez and Müller, unpubl. data). 1 = shift from oligolecty on Asteraceae to polylecty with strong preference of Cistaceae; 2 = shift from oligolecty on Asteraceae to oligolecty on Dipsacaceae. 3 = shift from polylecty with strong preference of Cistaceae to oligolecty on Cistaceae. * Polylectic species.

The pattern of host-plant use is different in other parts of the *Hesperapis* clade. *H.* (*Amblyapis*) and *H.* (*Panurgomia*) show "relaxed floral choice" 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. III). Both *H.* (*Amblyapis*) and *H.* (*Panurgomia*) 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.

The phylogeny of *Hesperapis* is not yet fully resolved, which unfortunately does not permit polarising host shifts and their frequency (Fig. 4). However, we are able to conclude that host shifts occurred frequently between as well as within (*Amblyapis*, *Carinapis* and *Panurgomia*) subgenera.

Host-plants of *Hesperapis* bees do not always offer accessible floral rewards. For example, pollen and nectar of tubular flower of *Nama* (Boraginaceae) collected by *H. trochanterata* are not easily accessible.

3.4. Genus *Macropis* Panzer

Macropis bees are apparently all oligolectic on *Lysimachia* (Primulaceae) (Tab. IV). Females collect pollen and oil on *Lysimachia*, whereas nectar is usually collected from a wide variety of host-plants (Vogel, 1986; Pekkarinen et al., 2003; Michez and Patiny, 2005).

Moreover, there is a clear difference in host-plant use between the Western and Eastern Hemisphere species (Fig. 5). In the Palaearctic region, the bees are specialised 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 N. America). We can

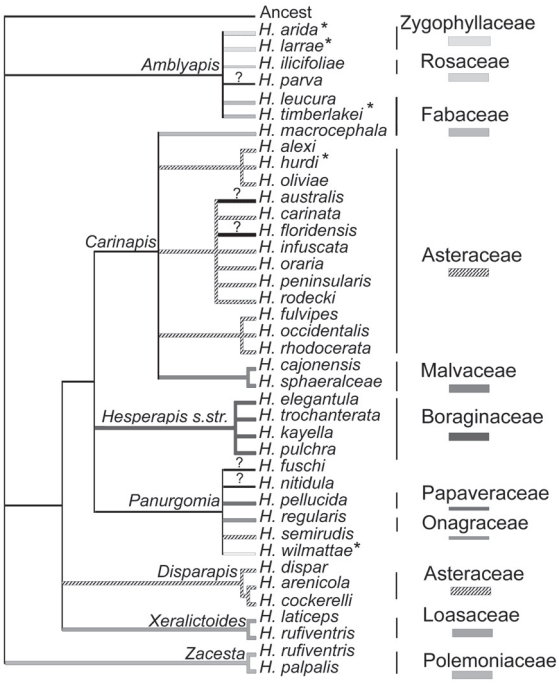

Figure 4. Phylogeny and host-plant associations in *Hesperapis* (from Stage, 1966). * Mesolectic to polylectic species.

hypothesise a biogeographical patterning of the *Macropis* host-plant choices.

Although the phylogeny and the plant associations of *Macropis* are not fully resolved, the data show that all *Macropis* species are all associated with *Lysimachia* (Popov, 1958; Vogel, 1974, 1986; Michez and Patiny, 2005), which suggests that this bee-flower relation is ancient. All contemporary *Macropis* females possess specialised arrays of setae on their fore- and mid-tarsi that are used to collect floral oils (Michez and Patiny, 2005; Fig. 7). Likewise, one of the oldest bee fossils, the Eocene fossil *Palaeomacropis eocenicus* (Melittidae *s.str.*, Macropidini) was also characterised by dense plumose setae on the inner and outer surfaces of the mid basitarsus and long, erect setae on the metasoma (Michez et al., 2007c). *Lysimachia* are probably too modern to have been the host-plant of *Paleomacropis eocenicus* but other potential oil-producing families, such as Malpighiaceae (Davis et al., 2002), are known from the Eocene and could have been the host-plant of *Palaeomacropis eocenicus*.

3.5. Genus *Melitta* Kirby

Many species of *Melitta* appear to be oligolectic on varied plant families (Tab. V). Fabaceae are the main floral resources for ten *Melitta* species (including all species of the *Dimidiata* species group). Ericaceae hosts three North American species. Five *Melitta* species belonging to the *Haemorrhoidalis* species group forage mainly on Campanulaceae. Another six *Melitta* species are variously associated with the Brassicaceae, Iridaceae, Lythraceae, Malvaceae, Resedaceae and Scrophulariaceae.

In the Old World, seven species are probably mesolectic to polylectic (Tab. V) among which at least four are from temperate areas (*M. haemorrhoidalis*, *M. harrietae*, *M. ezoana* and *M. sibirica*) and another three species are

Table III. Host-plants of *Hesperapis*. Field data = number of female specimens with field data; number of localities. Between brackets, percentage of the main host-plant family. * = Hundred percent of data.

Taxon	Field data	Main host-plants
H. (*Amblyapis*) *arida*	3;3	Zygophyllaceae (66%)
H. (*A.*) *ilicifoliae*	33;2	Rosaceae (91%)
H. (*A.*) *larrae*	13;6	Zygophyllaceae (69%)
H. (*A.*) *leucura*	19;3	Fabaceae*
H. (*A.*) *parva*	–	–
H. (*A.*) *timberlakei*	28;10	Fabaceae (71%)
H. (*Carinapis*) *alexi*	21;9	Asteraceae*
H. (*C.*) *australis*	–	–
H. (*C.*) *cajonensis*	1;1	Malvaceae*
H. (*C.*) *carinata*	46;7	Asteraceae*
H. (*C.*) *floridensis*	–	–
H. (*C.*) *fulvipes*	38;8	Asteraceae*
H. (*C.*) *hurdi*	35;14	Asteraceae (80%)
H. (*C.*) *infuscata*	38;13	Asteraceae (97%)
H. (*C.*) *macrocephala*	34;2	Fabaceae (97%)
H. (*C.*) *occidentalis*	32;11	Asteraceae*
H. (*C.*) *oliviae*	1;1	Asteraceae*
H. (*C.*) *oraria*	–	Asteraceae*
H. (*C.*) *peninsularis*	8;3	Asteraceae*
H. (*C.*) *rhodocerata*	105;12	Asteraceae*
H. (*C.*) *rodecki*	4;2	Asteraceae*
H. (*C.*) *sphaeralceae*	1;1	Malvaceae*
H. (*Disparapis*) *arenicola*	41;12	Asteraceae (90%)
H. (*D.*) *cockerelli*	41;7	Asteraceae*
H. (*D.*) *dispar*	3;1	Asteraceae*
H.(*Hesperapis*) *elegantula*	–	Boraginaceae*
H. (*H.*) *kayella*	22;6	Boraginaceae (91%)
H. (*H.*) *pulchra*	7;3	Boraginaceae*
H. (*H.*) *trochanterata*	–	Boraginaceae*
H. (*Panurgomia*) *fuchsi*	–	–
H. (*P.*) *nitidula*	–	–
H. (*P.*) *pellucida*	–	Papaveraceae*
H. (*P.*) *regularis*	373;43	Onagraceae (91%)
H. (*P.*) *semirudis*	3;2	Asteraceae*
H. (*P.*) *willmattae*	–	Polylectic
H. (*Xeralictoides*) *laticeps*	74;7	Loasaceae (97%)
H. (*X.*) *rufiventris*	18;6	Loasaceae (94%)
H. (*Zacesta*) *rufipes*	76;5	Polemoniaceae (99%)
H. (*Z.*) *palpalis*	48;9	Polemoniaceae*

from xeric areas (*M. aegyptiaca*, *M. arrogans* and *M. schmiedeknechti*).

As was observed in *Macropis*, there is a divergence in host-plant use between the Western and Eastern Hemisphere *Melitta* species (Tab. V, Fig. 6). In the New World, *Melitta* are specialists on Ericaceae (*M. americana*, *M. eickworti* and *M. melittoides*) and Malvaceae (*M. californica*) whereas these plant families are not exploited in the Old World. These results suggest original resource exploitation by *Melitta* in the Nearctic area.

To date, the phylogeny of *Melitta* is not sufficiently resolved to document the polarity of shifts and their frequency. For example, more data are required to test whether the polylectic

Table IV. Host-plants of *Macropis*. Field data = number of female specimens with field data; number of localities. *L.*(*S.*) = *Lysimachia* (*Seleucia*), *L.*(*L.*) = *Lysimachia* (*Lysimachia*). * = Hundred percent of data.

Taxon	Field data	Main host-plants
M. (*Macropis*) *ciliata*	2;2	*L.*(*S.*)*
M. (*M.*) *dimidiata*	5;1	*L.*(*L.*)*
M. (*M.*) *europaea*	84;27	*L.*(*L.*)*
M. (*M.*) *fridvaldskyi*	–	*L.*(*L.*)*
M. (*M.*) *fulvipes*	64;18	*L.*(*L.*)*
M. (*M.*) *kiangsuensis*	–	–
M. (*M.*) *nuda*	–	*L.*(*S.*)*
M. (*M.*) *patella*	–	*L.*(*S.*)*
M. (*M.*) *steironematis*	–	*L.*(*S.*)*
M. (*M.*) *tibialis*	–	–
M. (*Paramacropis*) *ussuriana*	–	–
M. (*Sinomacropis*) *hedini*	–	*L.*(*L.*)*
M. (*S.*) *immaculata*	–	*L.*(*L.*)*
M. (*S.*) *orientalis*	–	–
M. (*S.*) *micheneri*	–	–
M. (*S.*) *omeiensis*	–	–

condition of *M. schmiedeknechti* is plesiomorphic or apomorphic.

As in *Hesperapis*, the rewards presented by the host-plants of *Melitta* are not always readily accessible. For example, *M. tricincta* is a specialist on the nototribic flowers *Odontites* (Scrophulariaceae).

4. DISCUSSION

4.1. Degree of host-plant specialization in Melittidae *s.l.*

Most of the species of melittid bees for which we have host-plant data show narrow host-plant associations that would be described as "oligolectic." Among the 108 species with host-plant records, we recorded only 16 putative mesolectic or polylectic species (Tabs. II–V; Figs. 2–6) making oligolecty the predominant condition within Melittidae *s.l.*. Our results suggest that there are few cases of increased host-plant breadth. Most cases of host-plant variation involve *shifts* in the host-plant visited with little change in diet *breadth*. This pattern is consistent with previous studies on the evolution of host-plant associations in bees (Müller, 1996a; Sipes and Tepedino, 2005; Patiny et al., 2007; Larkin et al., 2008).

4.2. Pattern of host breadth variation

In the genera we studied, shifts from specialist behaviour to generalist behaviour seem more frequent than the reverse. Müller (1996a) described a similar pattern in the West-Palaearctic tribe Anthidiini (Megachilidae) and Larkin et al. (2008) observed the same pattern in the *Andrena* subgenus *Callandrena*. However, our data show that the evolution of dietary breadth in melittid bees is not unidirectional. Oligolecty appears to be the plesiomorphic condition for *Capicola*, *Hesperapis* and *Macropis*. However, polylecty or oligolecty (we are unable to distinguish unambiguously) could be the primitive condition for *Melitta* and *Dasypoda*.

4.3. Pattern of shifts among host-plants

Our results provide interesting insights into the mode of host-plant switching in bees. Some genera (e.g., *Dasypoda*) appear to specialize on morphologically similar but unrelated host-plant families. Oligolectic and polylectic *Dasypoda* usually forage on simple, radially symmetrical flowers like those of Asteraceae, Cistaceae, Dipsacaceae, Geraniaceae, Linaceae, Malvaceae or Rosaceae, which produce abundant and easily accessible rewards. In the genus *Dasypoda*, the ancestral host-plant (probably with radial symmetry) has seemingly had a strong influence on the contemporary host-plant choice of these bees. The potential alternative host-plant species seem to be restricted to the actinomorphic plant taxa. Host switches based on morphological similarity among host-plants has been demonstrated in some previous studies. For example, several genera within the subfamily Rophitinae (Halictidae) (*Penapis*, *Protodufourea* and *Xeralictus*; reviewed by Patiny et al., 2007), *Diadasia* (Apidae; Sipes and Wolf, 2001; Sipes and Tepedino, 2005) and *Macrotera* (Andrenidae; Danforth, 1996)

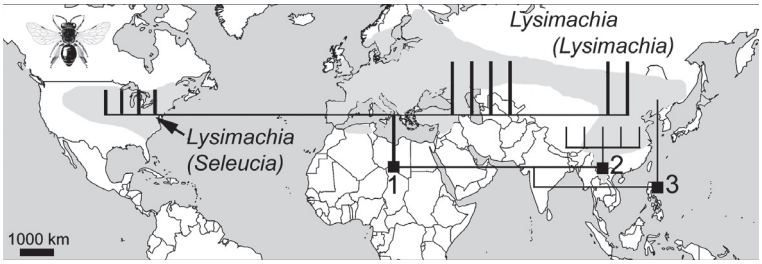

Figure 5. Distribution, phylogeny and host-plant associations in *Macropis* (from Michez and Patiny, 2005). 1 = subgenus *Macropis s.str.*; 2 = subgenus *Sinomacropis*; 3 = subgenus *Paramacropis*.

present equivalent shifts to unrelated, but morphologically similar, host-plants.

Other genera showed evidence of host switching to both unrelated and morphologically divergent host-plants. In *Capicola*, *Hesperapis* and *Melitta* species forage on distantly related but widespread plant families such as Aizoaceae, Brassicaceae, Campanulaceae, Fabaceae or Scrophulariaceae. Moreover, many species are specialists on rare plant families such as Lythraceae or Resedaceae. For these three melittid genera, the ancestral floral choice apparently does not influence the host-plant choice of extant species. The coexistence and co-occurrence of potential hosts in a given habitat that is home to such bees has probably facilitated shifts from one host to another. Consequently, these oligolectic genera could be regarded as ecological opportunists, with the ability to shift among hosts with equivalent floral resources. Specialisation is associated with the exploitation of highly attractive, readily accessible flowers, rather than under-utilised flowers of plant species whose rewards are inaccessible to generalist pollinators.

Other oligolectic bee genera associated with multiple, unrelated plant families include *Colletes* (species group of *C. succintus*; Kuhlmann et al., 2007); *Dufourea* (Ebmer, 1984; Patiny et al., 2007), *Micralictoides* (Bohart and Griswold, 1987) and *Rophites* (Ebmer and Schwammberger, 1986). Note that the presence of closely-related bee species on distantly related host-plants could also be explained by extinction of bee lineages on intermediate host-plant families.

4.4. Morphological adaptation and host-plant specialisation

Morphological adaptations for the collection of floral rewards are evident in some of the melittid genera we examined. In *Macropis*, for example, the females possess specialized morphologies (dense plumose setae on the fore- and mid-leg; Fig. 7) for collecting oils from their host-plants, *Lysimachia* (Primulaceae). Although this morphological adaptation is particularly efficient for oil collection, it can hardly be used for any other purpose. Fossil evidence (*Palaeomacropis eocenicus*, Michez et al., 2007c) indicates that oil-collecting behaviour and the associated morphological structures occurred as far back as the Eocene but another closely related fossil (*Eomacropis glaesaria*, Engel 2001) from Baltic amber did not present specialised oil-collecting structures (Engel, 2001). A similar case of extreme morphological adaptation is observed in the genus *Rediviva* where females use their elongated fore legs to collect oil produced at the bottom of long floral spurs of the South African *Diascia* species (Scrophulariaceae) (Steiner and Whitehead, 1990).

Other cases of morphological adaptations to particular host-plants are found in the genus *Hesperapis*. The four species included in the subgenus *Hesperapis s.str.* forage on deep tubular flowers of Boraginaceae. Three species (*H. elegantula*, *H. kayella* and *H. pulchra*) share a specialised morphological device to collect pollen (Stage, 1966; Michener, 1981). Their mouthparts bear wavy hairs used to access the pollen on hidden anthers (e.g. Müller, 1995; Thorp, 2000). *H. trochanterata* collects

Table V. Host-plants of *Melitta*. Field data = 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.

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

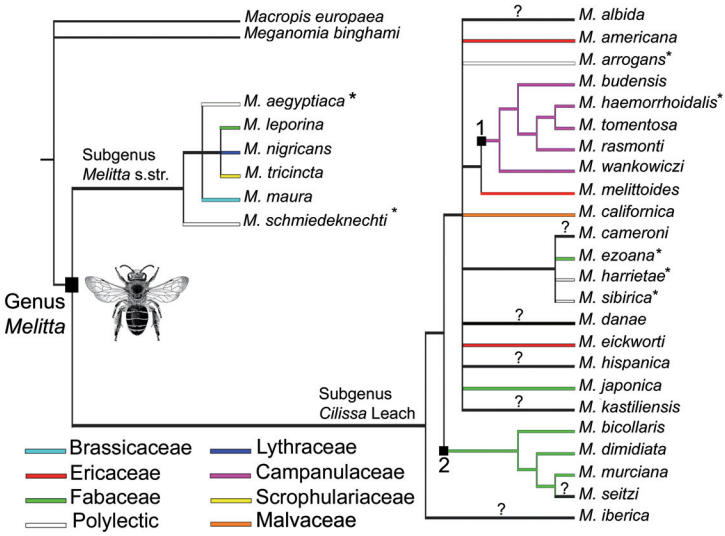

Figure 6. Phylogeny and host-plant associations in *Melitta* (from Michez and Eardley, 2007; clade including only species with both sexes described). 1 = *Haemorrhoidalis* species group; 2 = *Dimidiata* species group. * Mesolectic to polylectic species.

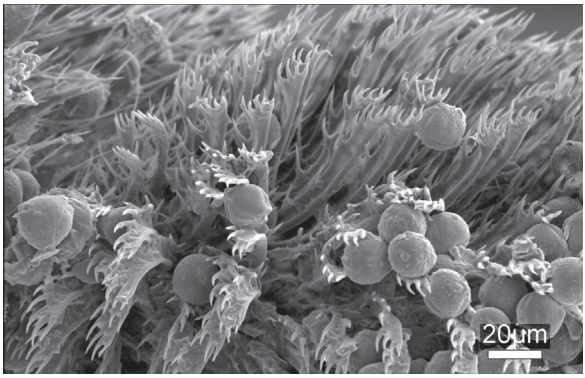

Figure 7. Setae of the protarsus of female *Macropis europaea* with pollen of *Lysimachia vulgaris*.

pollen and nectar of *Nama* (Boraginaceae). Both sexes of *H. trochanterata* display an elongate head and projecting clypeus, which allows the bees to enter the narrow, tubular corollas (Rozen, 1987).

4.5. Implication for the evolution of bees

Melittid bees constitute a group of specialist taxa that occupies a basal position in the bee phylogeny. Likewise, we observe that a lot of other basal groups are also oligolectic (e.g. Lithurginae, Panurginae and Rophitinae; Fig. 8) (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 myr) (Michez et al., 2007c). This melittid bee (Melittidae *s.str.*, Macropidini) presents oil-collecting structures on its legs (like Fig. 7) similar to those observed in contemporary oil-collecting bees. In

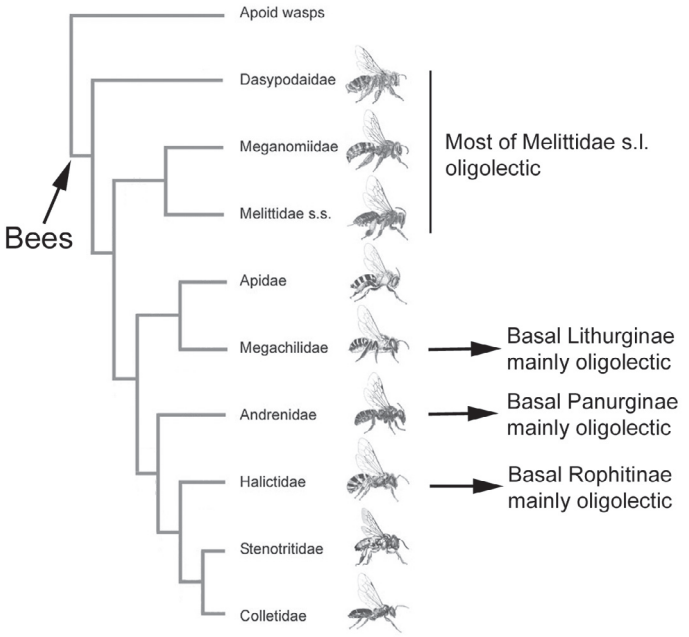

Figure 8. Phylogeny of bees showing broad-scale patterns of host-plant specialisation (according to Danforth et al., 2006b).

light of these records, and since many extant oil-collecting bees are oligolectic, it can be reasonably assumed that this fossil bee was a specialist taxon, which increases the likelihood for oligolecty to constitute an ancestral condition in bees.

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Phylogénie et évolution des plantes hôtes chez les Melittidae *s.l.* (Hymenoptera : Apoidea).

Melittidae / oligolectie / polylectie / phylogénie / évolution hôte-plante / abeille

Zusammenfassung – Phylogenie und Wirtspflanzenevolution bei den Melittidae *s.l.* (Hymenoptera: Apoidea). Wie viele Gruppen pflanzenfressender Insekten zeigen auch Bienen Variation sowohl in der Wirtspflanzenwahl als auch in der Breite ihrer Wirtspflanzen. Einige Bienen zeigen eine hohe Spezifität in der Blütenwahl (Oligolektie; viele Solitärbienen), während andere ein weites Spektrum in der Blütenwahl aufweisen (Polylektie; die meisten eusozialen Bienen). Nur wenige frühere Studien haben die Muster der Wirtspflanzenwahl in Beziehung zu einer gut aufgelösten Phylogenie auf dem Artniveau untersucht.

Wir untersuchten die Vererbung der Wirtspflanzenwahl über ihre evolutionäre Geschichte bei fünf Gattungen von spezialisierten Bienen innerhalb der Melittidae *s.l.* (Tab. II–V, *Capicola*, *Dasypoda*, *Hesperapis*, *Macropis* und *Melitta*). Wir kartierten die bevorzugten Pollenwirte über den Phylogenien auf dem Artniveau (Abb. 2–6). Wir versuchten insbesondere zu ermitteln, ob (i) Verschiebungen der Wirtspflanzen in diesen Kladen spezialisierter Bienen häufig sind, (ii) ob Wirtspflanzenverschiebungen zu entfernt verwandten Wirten vorkommen,

(iii) ob Wirtspflanzenverschiebungen mit der Entstehung besonderer morphologischer Anpassungen einhergehen, und (iv) ob die Wirtspflanzenspezialisierung in diesen Gattungen als ursprünglich oder als abgeleitet angesehen werden kann.

Wir zeigen, dass nahverwandte Arten in den meisten Fällen ähnliche Wirtspflanzen aufsuchen. Allerdings beobachteten wir in vier der fünf Gattungen Verschiebungen zu nichtverwandten Wirtspflanzen (mit *Macropis* als der einzigen Ausnahme). Die meisten Wechsel beinhalteten Umstellung von einer Wirtspflanzenfamilie zu einer anderen, nicht verwandten Wirtsfamilie, mit wenig Änderung der Auswahlbreite. Wechsel der Auswahlbreite, wenn sie beobachtet wurden, fanden hauptsächlich von Oligolektie zu Polylektie statt. Wirtspflanzenspezifität erscheint daher bei den melittiden Bienen ein ursprüngliches Verhalten zu sein. In mehreren anderen Bienenfamilien sind die basalen Gruppen ebenfalls oligolektisch (z. B. Lithurginae, Panurginae und Rophitinae). Dies legt den Schluss nahe, dass der ursprüngliche Zustand der Bienen oligolektisch war.

Bienen / Melittidae *s.l.* / Oligolektie / Polylektie / Phylogenie / Evolution / Wirtspflanzen

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