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Phylogeny of the bee family Melittidae (Hymenoptera: Anthophila) based on combined molecular and morphological data

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Abstract. The bee family Melittidae comprises a small, but biologically fascinating, group of mostly oligolectic bees, some of which are oil collecting. Phylogenetic relationships within this family are poorly understood and some genera cannot be placed with confidence at the subfamily level. We analysed melittid phylogeny using a combined dataset of five nuclear genes [28S, elongation factor-1α (EF-1α, F2 copy), long-wavelength rhodopsin, Na-K ATPase and RNA polymerase II] spanning 4842 bp plus 68 adult morphological characters. Our study included 25% of the species-level diversity and 81% of the generic-level diversity and included all previously recognized tribes and subfamilies. We analysed the dataset using parsimony, maximum likelihood and Bayesian methods. All methods yielded congruent results. All topologies recovered the three previously recognized subfamilies (Dasypodainae, Melittinae, Meganomiinae), but two genera (*Afrodasypoda* and *Promelitta*) are transferred from Dasypodainae to Melittinae. On the basis of our tree topologies we identify four tribes (Dasypodaini **comb.n.**, Hesperapini **stat.n.**, Macropidini **comb.n.** and Melittini), only one of which (Melittini) matches a widely used classification. Lastly, we discuss the evolution of host-plant association in the light of our new phylogenetic hypothesis. Our results strongly support multiple independent origins of oil-collecting behaviour in the Melittinae.

Introduction

The family Melittidae is one of the smallest families of bees, with just 16 genera and 200 described species (Michez, 2007; Ascher *et al*., 2008; Table 1). It is a family that includes many rare, geographically restricted species. Melittidae is also an ancient, possibly relictual, bee family that is well represented in the fossil record back to the Oligocene (Michez *et al*., 2007c). Melittid bees are strictly ground nesting and occur in the temperate, xeric, and Mediterranean climate regions of the Old World and the Nearctic (Table 1; Michener, 1979).

In comparison with most other bee families, melittids include a high proportion of host-plant specialists (Michez *et al*., 2008). Pollen specialization, or oligolecty (as defined by Cane & Sipes, 2006), has been inferred from host-plant collection data for many species and has been confirmed for others based on detailed analysis of scopal pollen loads (Westrich, 1990; Michez *et al*., 2008). Host-plant specialization involves both behavioural and sometimes morphological adaptations to collecting, manipulating, and transporting floral resources, such as pollen and floral oils (Steiner & Whitehead, 1991; Michez *et al*., 2008). Although host-plant preferences are restricted, the evolution of host-plant association appears to involve switches among unrelated host plants (Michez *et al*., 2008), suggesting that floral morphology or chemistry, rather than host-plant phylogeny, may drive host switching.

One remarkable aspect of host-plant specialization in melittids involves oil collecting by at least two extant genera: *Rediviva* and *Macropis*. In the Holarctic genus *Macropis*, females use modified, finely branched hairs on the fore and mid-legs to collect floral oils from specialized glandular eliaophores located on the anther column and petals in the genus *Lysimachia* (Primulaceae) (Cane *et al*., 1983; Vogel, 1986; Buchmann, 1987; Michez & Patiny, 2005). Oils are used in cell

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Table 1. Taxonomy, species richness and distribution of the Melittid tribes according to Engel (2005), Michener (2007) and the present study.

Tribes (Engel, 2005)	Tribes (Michener, 2007)	Tribes (present study)	Genera	Diversity (N1–N2)	Distribution	Max. of diversity
Dasypodaini	Dasypodaini	Dasypodaini	*Dasypoda*	4–33	Palaearctic	Mediterranean basin
Dasypodaini	Dasypodaini	Hesperapini	*Eremaphanta*	2–9	Central Asia	Turkestan
Dasypodaini	Dasypodaini	Hesperapini	*Capicola*	1–13	Southern Africa	Cape provinces
Dasypodaini	Dasypodaini	Hesperapini	*Hesperapis*	7–38	Nearctic	California
Sambini	Sambini	Dasypodaini	*Haplomelitta*	5–5	South Africa	South Africa
Sambini	Sambini	Dasypodaini	*Samba*	1–1	Kenya	Kenya
Promelittini	Promelittini	Macropidini[a]	*Promelitta*	1–1	North Africa	North Africa
Afrodasypodini	Promelittini	Macropidini[a]	*Afrodasypoda*	1–1	South Africa	South Africa
Meganomiini	Meganomiini	Meganomiini	*Ceratomonia*	1–1	Namibia	Namibia
Meganomiini	Meganomiini	Meganomiini	*Meganomia*	1–5	Ethiopian	Southern Africa
Meganomiini	Meganomiini	Meganomiini	*Pseudophilanthus*	2–4	Madagascar and Kenya	Kenya
Meganomiini	Meganomiini	Meganomiini	*Uromonia*	2–2	Madagascar, Kenya, Mali	Madagascar, Kenya
Melittini	Melittini	Melittini	*Melitta*[b]	2–44	Old World and Nearctic	Europe
Redivivini	Melittini	Melittini	*Rediviva*	1–24	Southern Africa	South Africa
Redivivini	Melittini	Melittini	*Redivivoides*	1–1	South Africa	South Africa
Eomacropidini	Eomacropidini	Macropidini	*Eomacropis*[c]	1–1	Baltic amber	Baltic amber
Macropidini	Macropidini	Macropidini	*Macropis*[b]	3–16	Holarctic	Eastern Asia
–	–	Macropidini	*Paleomacropis*[c]	1–1	Oise amber	Oise amber

[a]Michener (2007) included the Promelittini in the Dasypodainae. The present study revealed that Promelittini are Melittinae (Macropidini).
[b]Fossil and contemporary taxa.
[c]Fossil taxa.
N1 = number of subgenera; N2 = number of species.

lining and larval provisions (Cane *et al*., 1983). *Rediviva* is a well-known genus of oil-collecting melittid bees restricted to southern Africa. The 24 described *Rediviva* species are known to visit oil-producing flowers in the families Scrophulariaceae, Orchidaceae and Iridaceae (representing 140 species and 14 genera; Whitehead & Steiner, 1993, 2001; Pauw, 2006; Whitehead *et al*., 2008). Accessing oils in some species of *Diascia* (Scrophulariaceae) requires elongate fore legs in female *Rediviva* that in some cases can be nearly twice the length of the bee's body (Steiner & Whitehead, 1990, 1991). Oil collection could be an ancient behaviour in melittid bees because a recently described fossil (*Paleomacropis eocenicus*) from Eocene amber shows the modified hairs typical of oil-collecting *Macropis* (Michez *et al*., 2007c). However, the absence of a robust phylogenetic hypothesis for melittid genera, tribes and subfamilies (see below) did not allow previous authors to distinguish between single or multiple origin(s) of this behaviour.

The phylogeny of the Melittidae is controversial. The monophyly of the family remains poorly supported based on studies of larval and adult morphology (Rozen & McGinley, 1974; Michener, 1981, 2007; Alexander & Michener, 1995; Packer, 2003) and there is no single morphological synapomorphy for the family (Michener, 2007). Figure 1 and Table 1 summarize the previous phylogenetic hypotheses at the subfamily and tribal levels. Some studies have assumed melittids to be monophyletic (e.g. Michener, 1981; Engel, 2001). Other studies (e.g. Alexander & Michener, 1995; Danforth *et al*., 2006a, b), based on morphological and molecular datasets that included extensive sampling across closely related bee families as well as apoid wasps, have failed to support melittid monophyly. Given the uncertainty about melittid monophyly, some authors prefer to recognize three families rather than the three subfamilies traditionally recognized (Alexander & Michener, 1995; Danforth *et al*., 2006b).

Questions also remain about some group membership in Melittidae, from subfamilies to genera. For example, Promelittini (including two monotypic genera, *Promelitta* and *Afrodasypoda*) is currently placed (with weak support) within the subfamily Dasypodainae (Michener, 2007). However, *Promelitta alboclypeata* bears similarities to some genera of Melittinae, including a yellow clypeus in the male (Michez *et al*., 2007b). Michener (2007: 422), while maintaining placement in Dasypodainae, commented that 'in various features *Promelitta* resembles Melittinae at least as much as other Dasypodainae'. Moreover, *Afrodasypoda plumipes*, originally described by Friese (1912) as *Rhinochaetula plumipes*, was placed by Michener (1981) in the genus *Promelitta*, in the tribe Promelittini, 'for lack of a better place to put it' (Michener, 2000). Engel (2005) erected a new genus (*Afrodasypoda*) and tribe (Afrodasypodini) for this species and, like Michener (2000), placed this tribe in the Dasypodainae. Michener (2007) transferred the genus *Afrodasypoda* to the Promelittini, again, in the subfamily Dasypodainae but without strong evidence.

To provide a better understanding of melittid relationships and to establish a robust, cladistically based classification for the family, we conducted a phylogenetic analysis based on a combined dataset of five slowly evolving nuclear genes [28S, elongation factor-1α (EF-1α F2 copy), long-wavelength rhodopsin (opsin), Na-K ATPase (NaK) and RNA polymerase II (RNAp)] plus 68 adult morphological characters.

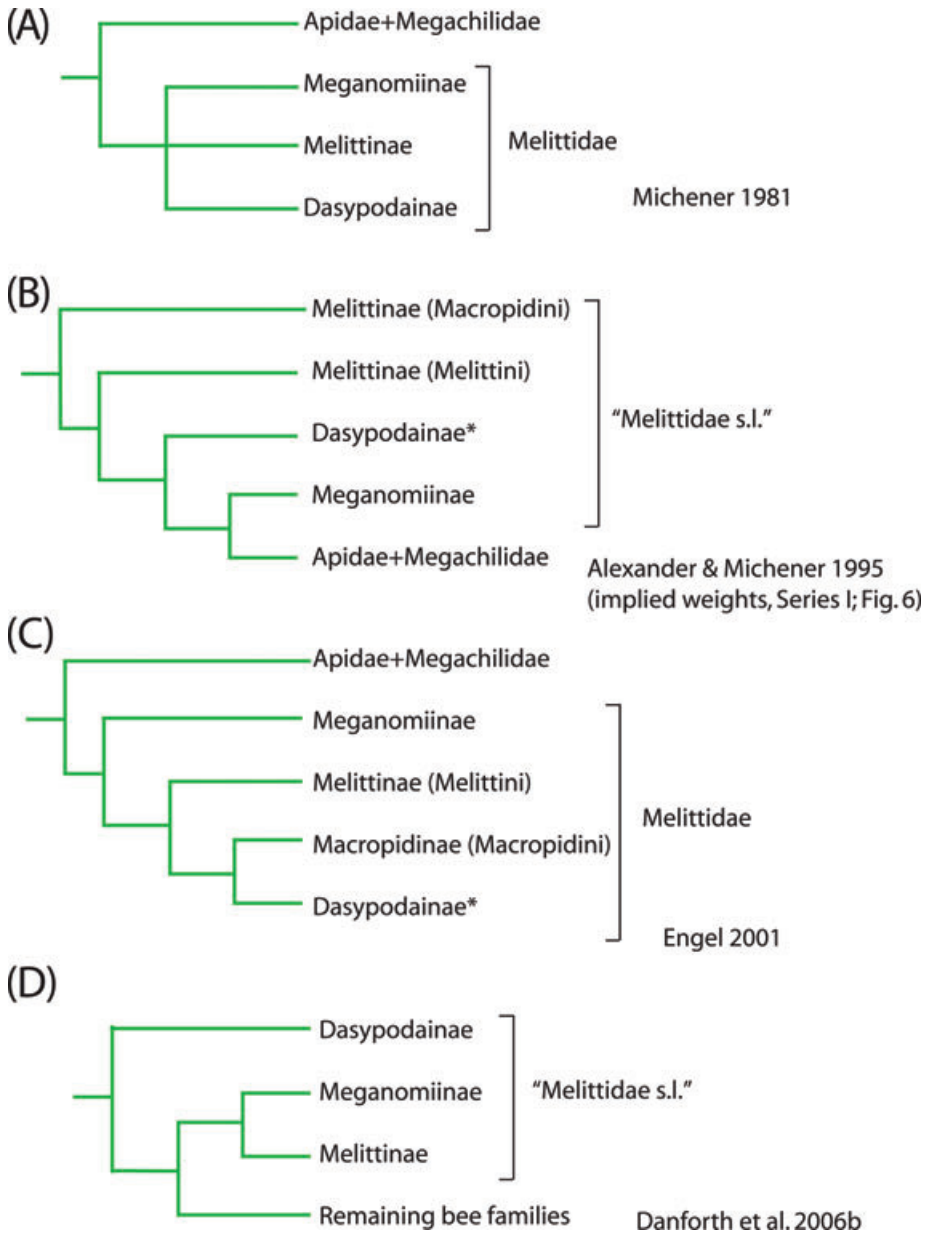

Fig. 1. Summary of previous studies of melittid phylogeny. (A) Analysis of morphological data from extant melittid bees. (B) Analysis of morphological data from extant short-tongued bees. (C) Re-analysis of Alexander & Michener's (1995) dataset by adding fossil taxa. (D) Analysis of five nuclear genes plus the morphological matrix of Alexander & Michener (1995). Placement of *Afrodasypoda* and *Promelitta* is indicated by an asterisk (in cases where these genera were included in the resulting classification).

Our dataset included nearly all the described genera, all tribes, and subfamilies, and a large proportion of the species. Given the rarity of some key taxa (e.g. *Afrodasypoda plumipes, Samba calcarata*), we were unable to include DNA sequence data for all species. However, the combination of molecular and morphological data in our study allowed us to place these key taxa with confidence. The goal of this study was not to resolve the issue of melittid monophyly. Rather, we sought to determine the limits of the melittid subfamilies and tribes. Our results are robust and provide a revised classification for the family and new phylogenetic hypotheses. We consider the evolution of host-plant associations of melittid bees in the light of this new phylogenetic hypothesis.

Materials and methods

Taxon sampling

The taxon sampling of the ingroup included representatives from all six extant tribes recognized by Michener (2007) and all eight extant tribes recognized by Engel (2005) (Table 1). Morphological characters were gathered for 50 species and 13 genera (Appendix 1), representing ~25% of the specific diversity and ~81% of the generic diversity. We included only one species of Meganomiinae because the monophyly of this subfamily is well demonstrated in the morphological analysis of Michener (1981). We generated DNA sequences for 41 species and 11 genera (Table 2), namely ~21% of the melittid

Table 2. Description of the molecular dataset.

Taxon	Collection locality	GenBank accession numbers				
		28S	EF-1α	Opsin	NaK	RNAp
Outgroup						
Andrena brooksi	U.S.A.: NM: Animas	AY654510	AY230129	EF416861	EF646389	AY945092
Colletes inaequalis	U.S.A.: NY: Ithaca	AY654484	AY585123	DQ115542	EF646387	AY945107
Ctenoplectra albolimbata	South Africa: Hluhluwe	AY654538	AY585118	DQ116677	EF646391	AY945111
Halictus rubicundus	U.S.A.: MT: Missoula	AY654510	AF140335	DQ116674	EF646388	AY945120
Lithurgus echinocacti	U.S.A.: AZ: Tucson	AY654541	DQ141116	DQ116702	EF646390	AY945136
Ingroup						
Capicola hantamensis	South Africa: Calvinia	EF594353	EF594329	EF594378	–	EF599276
C. nanula	South Africa: Vanrhynsdorp	EF594351	EF594327	EF594376	EF646412	EF599274
C. nigerrima	South Africa: Nieuwoudtville	EF594352	EF594328	EF594377	EF646413	EF599275
C. richtersveldensis	South Africa: Richtersveld	AY654523	AY585152	DQ116683	EF646414	AY945123
Dasypoda (D.) dusmeti	France: Vidauban	EF594355	EF594331	EF594380	–	–
D. (D.) hirtipes	France: Generac	AY654519	AY585149	DQ116681	EF646416	AY945113
D. (D.) oraniensis	Morocco: Anezal	EF594356	EF594332	EF594381	EF646417	EF599279
D. (D.) pyriformis	Greece: Kato Samiko	EF594360	EF594336	EF594384	EF646422	EF599282
D. (Hetero.) pyrotrichia	France: Eyne	EF594359	EF594335	EF594383	EF646421	EF599281
D. (Mega.) argentata	France: Generac	AY654518	AY585148	DQ116680	EF646418	AY945112
D. (M.) braccata	Italy: Mompanteri	EF594357	EF594333	EF594382	EF646419	EF599280
D. (M.) frieseana	Greece: Kato Samiko	EF594361	EF594337	EF594385	EF646423	EF599283
D. (M.) spinigera	Turkey: Isparate	EF594362	EF594338	EF594386	EF646424	EF599284
D. (M.) suripes	Greece: Kato Samiko	EF594363	EF594339	EF594387	EF646425	–
D. (M.) visnaga	France: Valras plage	AY654520	AY585150	DQ116682	EF646420	AY945181
D. (Micro.) crassicornis	France: La Motte	EF594358	EF594334	–	–	–
Eremaphanta (E.) iranica	Oman: Wadi Quibit	EF594366	EF594341	–	–	–
Haplomelitta (H.) ogilviei	South Africa: Nieuwoudtville	EF594364	–	EF594388	–	EF599285
H. (Prosamba) griseonigra	South Africa: ClanWilliam	AY654524	AY585153	DQ116684	EF646426	AY945125
H. (Prosamba) sp.	South Africa: Nieuwoudtville	EF594365	EF594340	EF594389	EF646427	EF599286
Hesperapis (Ambl.) larrae	U.S.A.: CA: Palmdale	AY654521	AY230131	AF344597	EF646410	AY945121
H. (Carinapis) rhodocerata	U.S.A.: AZ: Willcox	DQ060856	EF594324	EF594373	EF646407	AY045186
H. (Disparapis) cockerelli	U.S.A.: AZ: Willcox	EF594350	EF594326	EF594375	EF646411	EF599273
H. (H.) trochanterata	U.S.A.: AZ: Willcox	EF594349	EF594325	EF594374	EF646408	EF599272
H. (Panurgomia) regularis	U.S.A.: CA: Del Puerto Cyn.	AY654456	AY585151	DQ116692	EF646409	AY945122
Macropis (Macr.) europaea	France: Portiragnes	AY654525	AY585154	DQ116685	EF646403	AY945138
M. (M.) fulvipes	Bulgaria: Kludnitse	EF594348	EF594323	EF594372	EF646405	EF599271
M.(M.) nuda	U.S.A.: NY: Rensselaer	AY654454	AY585155	DQ116686	EF646404	AY945139
Meganomia binghami	South Africa: Vivo	AY654528	DQ141114	DQ116689	EF646406	AY945144
Melitta (Cilissa) arrogans	South Africa: Port Nolloth	AY654526	AY585156	DQ116687	EF646392	AY945140
M. (C.) dimidiata	France: Blandas	EF594342	EF594317	EF594367	EF646395	EF599266
M. (C.) eickworti	U.S.A.: NY: Ithaca	AY654527	AY585157	AF344604	EF646393	AY945141
M. (C.) ezoana	South Korea: Seokdong	EF594346	EF594321	EF594370	EF646399	EF599270
M. (C.) haemorrhoidalis	France: Nohèdes	EF594345	EF594320	EF594369	EF646398	EF599269
M. (M.) leporina	France: Port la Nouvelle	AY654529	AY585158	DQ116688	EF646394	AY945142
M. (M.) nigricans	Belgium: Lens	EF594343	EF594318	EF594368	EF646396	EF599267
M. (M.) tricincta	Belgium: Peronnes	EF594344	EF594319	–	EF646397	EF599268
Promelitta alboclypeata	Morocco: Erfoud	EF594354	EF594330	EF594379	EF646415	EF599277
Rediviva macgregori	South Africa: Kamieskroon	AY654531	AY585159	DQ116690	EF646400	AY945159
R. saetigera	South Africa: Graskop	EF594347	EF594322	EF594371	EF646402	AY945201
Redivivoides simulans	South Africa: Clanwilliam	AY654532	AY585142	DQ116691	EF646401	AY945160

28S, ribosomal 28S subunit; EF-1α, elongation factor-1α F2 copy; Opsin, long-wavelength rhodopsin; NaK, Na-K ATPase; RNAp, RNA polymerase II.

species and ~69% of the melittid genera. Five bee species from five other bee families were selected as outgroups: Andrenidae (*Andrena brooksi*), Colletidae (*Colletes inaequalis*), Halictidae (*Halictus rubicundus*), Megachilidae (*Lithurgus echinocacti*) and Apidae (*Ctenoplectra albolimbata*).

Molecular methods

Total DNA was extracted from single dry or ethanol-preserved specimens, following a phenol/chloroform protocol adapted from Saghai-Maroof *et al*. (1984) (see Danforth, 1999). Vouchers are deposited in the Cornell University Insect Collection and Mons-Hainaut University Collection. Conditions of polymerase chain reaction and primer sequences are given in Table 3. The polymerase chain reaction products were gel purified, following the Promega Wizard protocol and sequenced on an automated 3730xl DNA analyzer (Applied BioSystems, Foster City, CA, USA). The sequences were trimmed and assembled using SEQUENCHER 4.7 (Gene Codes Corporation, 2007). The edited sequences were aligned using CLUSTALW implemented in the program MEGALIGN (DNASTAR, Lasergene). The resulting alignment was checked by eye and edited manually (28S, EF-1α introns, opsin introns) in MACCLADE 4.08 (Maddison & Maddison, 2000) and MESQUITE 2.0 (Maddison & Maddison, 2007). *Apis mellifera* was used as a reference for identifying intron/exon boundaries within EF-1α and opsin and for identifying stem and loop regions within 28S (Cameron & Mardulyn, 2001).

Table 3. Polymerase chain reaction conditions and primer sequences.

28S	
Bel-Mar	94°C/1 min; 65°C/1 min;72°C/1 min; 35 cycles
EF-1α	
For1deg-F2rev1	94°C/1 min; 94°C/1 min; 52°C/1 min; 72°C/1 min 30 s; 35 cycles
HaF2For1-F2rev1	94°C/1 min; 94°C/1 min; 54°C/1 min; 72°C/1 min 30 s; 35 cycles
HaF2For1-F2rev3	94°C/1 min; 94°C/1 min; 54°C/1 min; 72°C/1 min 30 s; 35 cycles
F3rho-Cho10	94°C/1 min; 94°C/1 min; 58°C/1 min; 72°C/1 min; 35 cycles
Opsin	
For3mod-Revmod	94°C/1 min; 94°C/1 min; 56°C/1 min; 72°C/1 min; 35 cycles
NaK	
NaKfor2-NaKrev2	94°C/1 min; 94°C/1 min; 58°C/1 min; 72°C/1 min 30 s; 35 cycles
RNAp	
Polfor2a-Polrev2a	94°C/1 min; 94°C/1 min; 52°C/1 min; 72°C/1 min; 35 cycles
Primers	Sequences from 5′ to 3′
28S	
Bel	5′-AGA GAG AGT TCA AGA GTA CGT G−3′
Mar	5′-TAG TTC ACC ATC TTT CGG GTC CC-3′
EF-1α	
For1deg	5′-GY ATC GAC AAR CGT ACS ATY G-3′
HaF2For1	5′-G GGY AAA GGW TCC TTC AAR TAT GC-3′
For3rho	5′-GGY GAC AAY GTT GTT TTY AAY G-3′
F2rev1	5′-A ATC AGC AGC ACC TTT AGG TGG-3′
F2rev3	5′-GTGAAATCASMAGCACCYYAAGGTGG-3′
Cho10(mod)	5′-AC RGC VAC KGT YTG HCK CAT GTC-3′
Opsin	
Opsin For3 (mod)	5′-TTC GAY AGA TAC AAC GTR ATC GTN AAR GG-3′
Opsin Rev (mod)	5′-ATA NGG NGT CCA NGC CAT GAA CCA-3′
NaK	
NaKfor2	5′-GCS TTC TTC TCB ACS AAC GCC GTY GAR GG-3′
NaKrev2	5′-ACC TTG ATR CCG GCY GAW CGG CAC TTG GC-3′
RNAp	
Polfor2a	5′-AAY AAR CCV GTY ATG GGT ATT GTR CA-3′
Polrev2a	5′-AGR TAN GAR TTC TCR ACG AAT CCT CT-3′

Molecular data

We generated DNA sequences for five nuclear genes: 28S, EF-1α (F2 copy), opsin, NaK and RNAp. All genes, except 28S, are protein coding. Except for NaK, these genes have been used in previous studies of bee phylogeny at various levels, including the generic level (e.g. Kawakita *et al*., 2004; Michel-Salzat *et al*., 2004; Hines *et al*., 2006; Larkin *et al*., 2006), the tribal level (e.g. Mardulyn & Cameron, 1999; Cameron & Mardulyn, 2001; Danforth *et al*., 2004; Praz *et al*., 2008) and the family level (e.g. Danforth *et al*., 2006a,b).

For the nuclear 28S ribosomal gene we sequenced an approximately 833 bp region of the D2–D3 region (http://www.entomology.cornell.edu/BeePhylogeny). After manual editing, ambiguities remained within the loop regions of the gene [see secondary structure in Kjer (1995)]. These sites (180) were excluded for the final analysis.

Two copies of EF-1α occur in bees (Danforth & Ji, 1998). Our dataset consisted of a 1571 bp fragment of the F2 copy (Danforth & Ji, 1998). The sequenced fragment included two introns, which were aligned manually. The less-conserved intron regions (247 sites, mainly AT-rich areas) were excluded for the final analysis.

We sequenced a 639 bp region of the opsin paralog (Chang *et al*., 1996), which spanned two introns. We chose to exclude the opsin introns from all analyses because the alignments appeared highly ambiguous. The resulting dataset spanned a 439 bp region of coding sequence.

Table 4. Model selection based on the hierarchical likelihood ratio test (HLrT) and the Akaike information criterion test realized with MRMODELTEST 2.2 on seven distinct partitions defined across the molecular data (one partition by gene with different partitions for introns).

	28S	EF-1α exons	EF-1α introns	EF-1α	Opsin exons	Opsin introns	Opsin	NaK	RNAp
HLrT	G	G	HKY + G	G	SYM + I + G	G	G	G	SYM + I + G
Akaike	G	G	HKY + G	G	SYM + I + G	G	G	G	G

G = GTR + I + G model.

The NaK fragment included in the dataset (~1000 bp) is part of an intronless region coding for the alpha-subunit of the binding part of the trans-membrane Na-K cellular pump (Fagan & Saier, 1993). The primers for this fragment were developed by BND based on published sequences for beetles (Labeyrie & Dobler, 2004) and the complete sequence of the honey bee NaK. For RNAp we analysed a 791 bp intronless region. RNAp has been used in previous studies of family-level bee phylogeny (Danforth *et al*., 2006a, b). Primers, protocols and additional information on these genes are available at http://www.entomology.cornell.edu/BeePhylogeny.

The final molecular dataset for the present study spanned 4842 aligned nucleotide sites and was 94% complete. Sampling localities and GenBank accession numbers are listed in Table 2.

Morphological data

We gathered 68 adult morphological characters from previous studies of higher-level bee phylogeny (Roig-Alsina & Michener, 1993; Alexander & Michener, 1995) and studies of relationships within Melittidae (Stage, 1966; Michener, 1981; Michez *et al*., 2004; Michez & Eardley, 2007; Michez & Kuhlmann, 2007) (Appendix 1). Character states were verified and/or recoded based on examination of specimens from the following institutions: American Museum of Natural History (New York, U.S.A.), Cornell University Insect Collection (Ithaca, U.S.A.), Faculté universitaire des Sciences agronomiques de Gembloux (Gembloux, Belgium), Institute of Zoology (Saint Petersburg, Russia), Museum für Naturkunde der Humboldt-Universität (Berlin, Germany), Oberösterreichisches Landesmuseum (Linz, Austria) and Université de Mons-Hainaut (Mons, Belgium).

Phylogenetic analyses

We performed an extensive analysis of the dataset based on parsimony, maximum likelihood, and Bayesian methods. For parsimony and maximum likelihood we used PAUP 4.0b10 (Swofford, 2002) and for Bayesian analyses we used MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001). Bootstrap values under maximum likelihood were calculated using RAXML 7.0 (Stamatakis, 2006).

Parsimony

We performed a series of parsimony analyses of our dataset, as follows: (1) molecular data (no introns), (2) molecular data + EF-1α introns, (3) molecular data (no introns) + morphology, and (4) molecular data + EF-1α introns + morphology. Combining the molecular and morphological datasets was not trivial because nine species were represented only by morphological data (i.e. *Afrodasypoda plumipes, Samba calcarata, Eremaphanta dispar, Capicola micheneri, Haplomelitta tridentata, Ha. atra, Ha. fasciata, Hesperapis laticeps* and *He. rufipes*). We therefore analysed the combined morphological and molecular dataset in two ways: (4a) we combined the morphological data only for species also characterized in the molecular partition (46 taxa) and (4b) we combined the morphological data leaving the molecular partitions as missing data (55 taxa). The former analysis included fewer taxa but also had less missing data, whereas the latter analysis included the maximum number of taxa with substantial amounts of missing molecular data for nine species.

For all parsimony analyses we coded gaps as a fifth state. How gaps are treated only impacts the analysis of the EF-1α introns and the 28S datasets. Analyses coding gaps as missing data (not shown) did not significantly alter the results nor did inclusion of some regions of the opsin intron. For parsimony analyses we first performed a heuristic search with 10 000 random sequence additions, using tree bisection reconnection branch swapping. All analyses yielded a single most-parsimonious tree. We also used the "Bob Barker" strategy, which implements a wider exploration of tree space (Larkin *et al*., 2006). Ten thousand random addition replicates were performed, saving only the best trees in each replicate (but holding no more than five trees greater than or equal to a length of one). In a second step of the search, the trees in memory were swapped to completion (by tree bisection reconnection). Again, this search procedure yielded a single, most-parsimonious tree. The overall tree topologies were virtually identical, but differed slightly in bootstrap support. Bootstrap support values were computed using 1000 replicates with ten random sequence additions per replicate.

Maximum likelihood

We analysed the performance of 56 substitution models using MODELTEST 3.7 (Posada & Crandall, 1998). The TIM + I + G model (transitional model with proportion of invariable

sites and a gamma distribution for variation among sites) was selected based on its scores in the hierarchical likelihood ratio and Akaike information criterion tests.

The topology obtained by the parsimony analysis was used as a starting tree for an iterative analysis under maximum likelihood using PAUP 4.0b10 (Swofford, 2002). The overall likelihood was estimated on the basis of the selected model and then the topology was submitted to a series of increasingly exhaustive branch-swapping algorithms: nearest neighbour interchange, subtree pruning regrafting and tree bisection reconnection. In each step, the maximum likelihood parameters were re-estimated based on the trees in memory and applied to the next step of branch swapping (Danforth, 1999). We calculated bootstrap support based on a GTR + I + G model and 100 replicates using RAXML 7.0 (Stamatakis, 2006). Maximum likelihood analyses were carried out with EF-1α introns excluded (5) and included (6).

Bayesian methods

For Bayesian analyses we partitioned the dataset by gene and separated EF-1α exons and introns (28S, EF-1α exons, EF-1α introns, opsin exons, NaK, and RNAp). For each gene partition we calculated the likelihood score for 24 possible substitution models using MRMODELTEST 2.2 (Nylander, 2004; in MRMTGUI 1.01). Models were compared based on the hierarchical likelihood ratio test and the Akaike information criterion. These criteria produced different sets of 'best' models (Table 4). We consequently analysed the datasets using both model combinations. An additional analysis was performed using the SSR model, wherein the three codon positions (and introns, when present) were assigned separate rates. This analysis resulted in a model with 14 discrete rate categories (see below).

Analysis of the combined molecular and morphological dataset was performed using six molecular partitions (28S, EF-1α exons, EF-1α introns, opsin exons, NaK, and RNAp). An additional (seventh) partition was dedicated to the morphological data. The 'standard' model implemented in MRBAYES for analysis of the discrete data was used for analysis of this morphological partition. As for the parsimony analysis, we ran separate analyses for molecular data alone with introns excluded (7), molecular data alone with introns included (8), and molecular data (excluding introns) plus morphology (9). Combining the molecular and morphological datasets was, as described above, not trivial because some taxa were represented only by morphological data. We therefore analysed the combined dataset in two ways: (10a) we combined the morphological data only for species also characterized in the molecular partition (46 taxa) and (10b) we combined the morphological data leaving large portions of the data matrix (the molecular partitions) as missing data (55 taxa). The overall tree topologies were very similar irrespective of the dataset analysed.

For each Bayesian analysis, 5 million generations were computed along two simultaneous runs and four chains. Parameters and topologies were sampled every 100 generations and two different lengths of 'burnin' (25 and 50% of the samples) were compared. The 50% majority rule consensus trees were based on 37 500 trees retained after discarding the burnin (25% of the samples). The rates computed for positions among codons while applying a GTR + SSR model were used to analyse relative rates of substitution among codon positions and genes (see below).

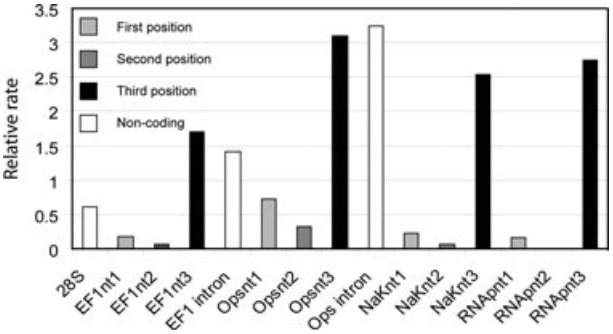

Fig. 2. Relative rates among codon positions (nt1, nt2, nt3) and non-coding regions (28S and introns) for the five genes analysed [18S, elongation factor-1α (EF−1α), long-wavelength rhodopsin (opsin), Na-K ATPase (NaK) and RNA polymerase II (RNAp)]. Rates were computed from the Bayesian GTR + SSR model.

Results

DNA sequences and relative rates

The patterns of relative rates of substitution among codon positions were approximately similar for the four protein-coding genes based on our Bayesian SSR model (Fig. 2). In each, a much higher rate was observed in the third position (nt3) and a much lower rate in the second (nt2). For EF-1α and opsin, the intron rates approximated those of third position sites. Likewise, the patterns observed in NaK and EF-1α were very close, except that NaK had a much higher rate of nt3 substitution. In contrast, opsin and RNAp displayed rather unique patterns, as observed in previous studies (Danforth *et al*., 2004, 2006a). Opsin displayed substantially higher rates in nt1 and nt2, reflecting a higher level of amino acid variation. The rate of substitution in opsin nt1 compared with that of 28S. The level of the nt3 rate in opsin compared with that of RNAp and NaK nt3 (more than 33% higher than EF-1α nt3). The rate pattern in RNAp showed almost no change in nt1 and nt2 and a very high rate in nt3, suggesting that this gene may be a poor choice for very deep divergences in bees (Danforth *et al*., 2006a).

Phylogenetic results

Figures 3–5 and Table 5 summarize our phylogenetic results based on parsimony, maximum likelihood and Bayesian methods. Among the two subfamilies represented by more than one

Table 5. Branch support data for alternative analyses of the dataset.

Method	Parsimony	Parsimony	Parsimony	Parsimony	Parsimony	Maximum likelihood	Maximum likelihood	Bayesian	Bayesian	Bayesian	Bayesian	Bayesian
Dataset	Molecular data No introns	Molecular data +EF introns	Molecular data No introns + morphology	Molecular data +EF introns + morphology	Molecular data +EF introns + morphology	Molecular data No introns	Molecular data +EF introns	Molecular data No introns	Molecular data +EF introns	Molecular data No introns + morphology	Molecular data +EF introns + morphology	Molecular data +EF introns + morphology
Number of taxa	46	46	46	46	55	46	46	46	46	46	46	55
Analysis no.	1	2	3	4a	4b	5	6	7	8	9	10a	10b
Melittidae *sensu lato*	66	53	67	60	46	84	65	1.00	1.00	1.00	1.00	0.99
Melittinae + Mega.	Inc	Inc	Inc	Inc	Inc	75	<50	1.00	1.00	0.99	1.00	0.98
Dasyp. + Mega.	<50	<50	<50	<50	<50	Inc	<50	Inc	Inc	Inc	Inc	Inc
Melittinae	98	99	100	97	86	97	97	1.00	1.00	1.00	1.00	0.98
Dasypodainae	100	100	100	100	85	100	100	1.00	1.00	1.00	1.00	1.00
Melittini	100	100	100	100	93	100	100	1.00	1.00	1.00	1.00	1.00
Macropidini	100	100	100	100	72	100	100	1.00	1.00	1.00	1.00	0.98
Hesperapini	79	81	78	85	85	100	100	1.00	1.00	1.00	1.00	1.00
Dasypodaini	93	92	98	96	85	97	97	1.00	1.00	1.00	1.00	1.00
Melitta	100	100	100	100	100	100	100	1.00	1.00	1.00	1.00	1.00
Rediviva + *Rediviv.*	100	100	100	100	100	100	100	1.00	1.00	1.00	1.00	1.00
Hesperapis	100	100	100	100	96	95	89	1.00	1.00	1.00	1.00	1.00
Capicola	88	87	99	98	97	73	74	0.99	0.99	1.00	1.00	1.00
Dasypoda	100	100	100	100	100	100	100	1.00	1.00	1.00	1.00	1.00
Haplomelitta	100	100	100	100	100	100	100	1.00	1.00	1.00	1.00	0.95
Tree length	5235	5881	5449	6095	6128	–	–	–	–	–	–	–
Number param.	–	–	–	–	–	–	–	22	25	24	27	27
-Ln likelihood	–	–	–	–	–	31 155.95	31 739.88	28 754.32	31 483.14	29 679.67	32 405.44	32 568.82

Inc, incongruent node.

species (Melittinae and Dasypodainae), there was unambiguous support for monophyly (Table 5). However, relationships among subfamilies varied among methods of analysis. Although all parsimony analyses supported a sister-group relationship between Dasypodainae and Meganomiinae, maximum likelihood and Bayesian methods supported (with a high level of support for the Bayesian analysis; Table 5) the sister-group relationship between Melittinae and Meganomiinae (posterior probability = 0.98–1.00).

Our results provide some surprising results in terms of the definitions of some subfamilies, and provide a clearer understanding of tribal and generic relationships within subfamilies. There is strong evidence that *Afrodasypoda* and *Promelitta* belong to Melittinae, whereas they were considered as belonging to Dasypodainae (Michener 2007; Table 1). *Afrodasypoda* and *Promelitta* are apparently closely related to the oil-collecting bee genus *Macropis* (Figs 3–5). We refer to this group of three extant genera (*Macropis, Afrodasypoda, Promelitta*) plus two extinct genera (*Eomacropis* and *Paleomacropis*) as the Macropidini (Appendix 3). Macropidini, in our expanded sense, forms the sister group to the Melittini (sensu Michener, 2007). The monophyly of Macropidini is supported by bootstrap values between 72 (analysis 4b) and 100 (analyses 1–4a, 5 and 6; Table 5) and posterior probabilities between 0.98 and 1.00 (analyses 7–10b; Table 5) as well as several morphological characters. Like *Macropis, Promelitta* and *Afrodasypoda* have two submarginal cells with the second abscissa of Rs slanting and widely separated from 1 m-cu (character 20), and males share a maculate clypeus with the male of Macropis (Fig. 7) (character 26). Appendix 2 provides a description of the male of *Afrodasypoda plumipes*, which corroborates our placement of this genus within the Macropidini. Within the Melittini, *Redivivoides simulans* arises from *Rediviva*, making *Rediviva* paraphyletic (Figs 3, 4). The monophyly of each tribe within Melittinae (Melittini and Macropidini) is well supported based on bootstrap values (Table 5) and several morphological characters, including the structure of the propodeum, the size of the jugal lobe, structures of the male seventh sternum, and the gonostylus (characters 15, 21, 34, 38).

Our tree topologies imply a revised tribal classification for the Dasypodainae. Although Engel (2005) and Michener (2007) excluded *Samba* and *Haplomelitta* from the Dasypodaini (including *Dasypoda, Hesperapis* and *Eremaphanta*), our results suggest that *Samba* + *Haplomelitta* forms the sister group to *Dasypoda* (Figs 3–5), rendering Dasypodaini (sensu Engel, 2005; Michener, 2007) paraphyletic. We recognize a tribe (Hesperapini) for the monophyletic group including *Eremaphanta, Hesperapis* and *Capicola* separate from Dasypodaini (*Dasypoda, Samba, Haplomelitta*). Our results provide the first strong evidence for separating the genus *Hesperapis*, which occurs primarily in arid regions of western North America, from *Capicola* (and *Capicoloides*), which are restricted to arid regions of southern Africa. Finally, the combined dataset shows that *Samba* renders the genus *Haplomelitta* paraphyletic (Figs 4, 5).

Discussion

Phylogeny and revised taxonomy at the tribal and generic levels

Overall, our results provide a strong basis for a revised classification of the melittid genera, tribes and subfamilies (summarized in Table 1). Our revised classification shows some striking differences from previous hypotheses based exclusively on morphology (e.g. Michener, 1981, 2007; Engel, 2001, 2005). Only one of the tribes of Michener (2007), Melittini, is retained intact. All others tribes are synonymized or recombined (Table 1 and Appendix 3). Our tribe Macropidini now includes several genera that were previously placed in two different subfamilies (Dasypodainae and Melittinae; Engel, 2005; Michener, 2007): *Macropis, Afrodasypoda, Promelitta*, and the extinct genera *Eomacropis* and *Paleomacropis*. We have eliminated the tribe Sambini because to recognize this tribe would render Dasypodaini sensu Michener (2007) paraphyletic. Our results suggest that two currently recognized genera (*Haplomelitta* and *Rediviva*) are paraphyletic. *Haplomelitta* is rendered paraphyletic by *Samba* and *Rediviva* is rendered paraphyletic by *Redivivoides*. We are reluctant to revise the generic status at this point without a more detailed and thorough analysis at the species levels. Steiner & Cruz (2006) obtained similar results regarding the placement of *Redivivoides* within *Rediviva*. Detailed anatomical study of the fore and mid-legs of *Redivivoides* suggest that it is descended from an oil-collecting ancestor (Steiner & Cruz, 2006).

Our study strongly supports recognition of *Capicola* as a genus distinct from *Hesperapis*. The taxonomic status of *Capicola*, which is restricted to southern Africa, has remained controversial since originally described by Friese (1911). Additional species were subsequently described in three different genera: *Capicola, Hesperapis* and *Rhinochaetula* (Friese, 1912, 1925; Cockerell, 1932a, b, c, 1934, 1936a, b). Michener (1944, 1981) considered *Capicola* as very close, but separate, from the Nearctic genus *Hesperapis*, whereas later Michener (2000, 2007) included the southern African species as two subgenera of *Hesperapis* (*Capicoloides* and *Capicola*). Our study confirms that *Capicola* (including *Capicoloides*) is the sister group to *Hesperapis*, a conclusion supported by a recent morphological study (Michez *et al*., 2007a). Recognition of *Capicola* at the generic level therefore seems warranted. *Eremaphanta* is the sister group to *Hesperapis* + *Capicola*, as hypothesized by Engel (2005).

Multiple origins of oil-collecting structures

By establishing the relationships among *Macropis* and *Rediviva*, our phylogeny provides a basis for an analysis of the evolution of oil-collecting behaviour in Melittinae. Oil collecting is known from three genera of Melittinae. Morphological adaptations for oil collection have been described from two extant genera (*Macropis* and *Rediviva*) and one fossil genus (*Paleomacropis*) (Vogel, 1974; Michez & Patiny, 2005; Michez *et al*.,

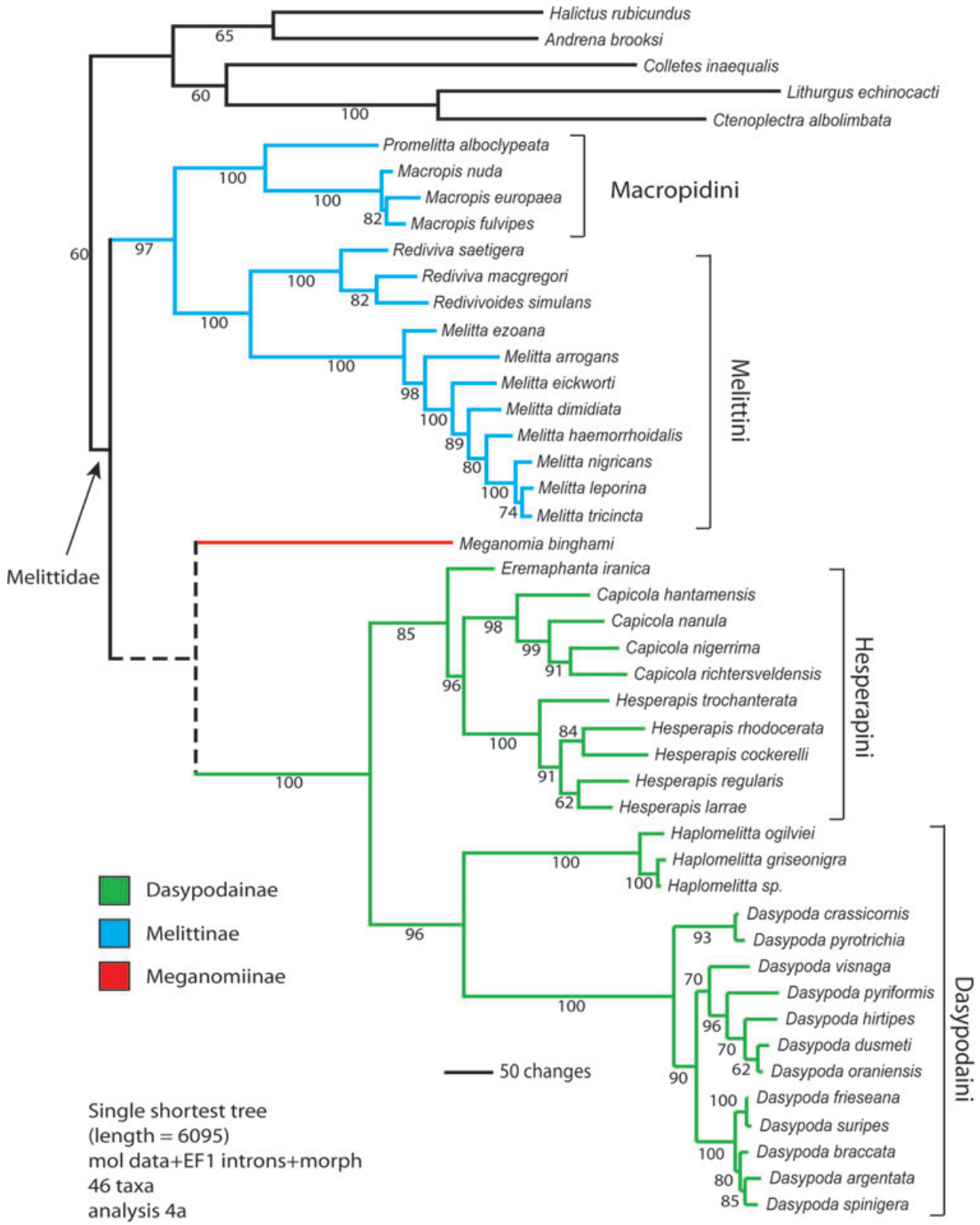

Fig. 3. Single most-parsimonious tree based on combined analysis of five genes [with elongation factor-1α (EF-1α introns included] and morphology for the 46 taxon matrix (analysis 4a). The numbers below the nodes are bootstrap values. Major clades (families, subfamilies, tribes) are labelled. Coloured branches refer to the three subfamilies: blue: Melittinae; red: Meganomiinae; green: Dasypodainae. Dashed lines indicate weakly supported nodes.

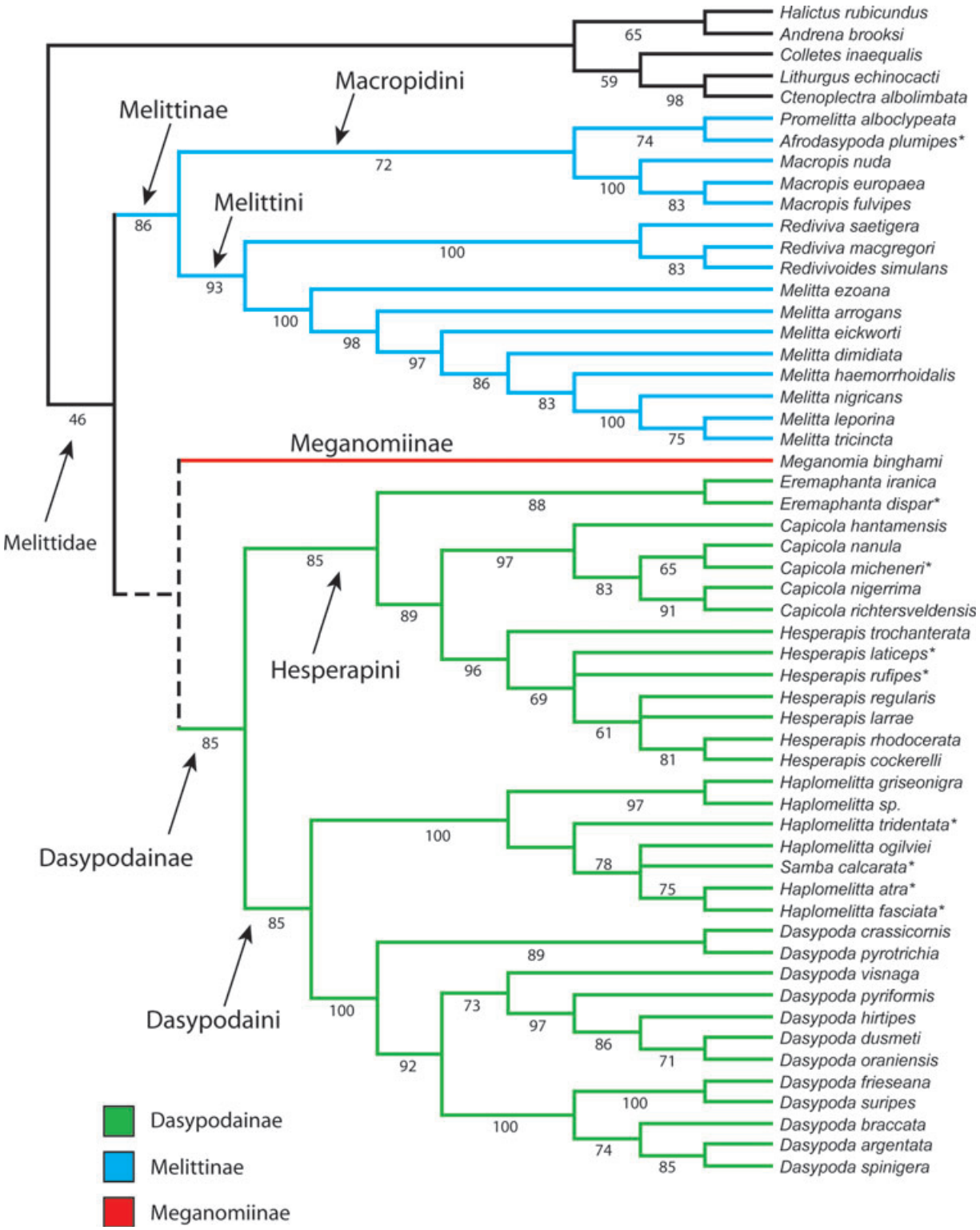

Fig. 4. Consensus of eight equally parsimonious trees based on combined analysis of five genes [with elongation factor-1α (EF-1α introns included] and morphology for the 55 taxon matrix (analysis 4b). The numbers below the nodes are bootstrap values. Major clades (families, subfamilies, tribes) are labelled. Coloured branches refer to the three subfamilies: blue: Melittinae; red: Meganomiinae; green: Dasypodainae. Dashed lines indicate weakly supported nodes based on bootstrap values. Taxa indicated with an asterisk are those for which we only have morphological data.

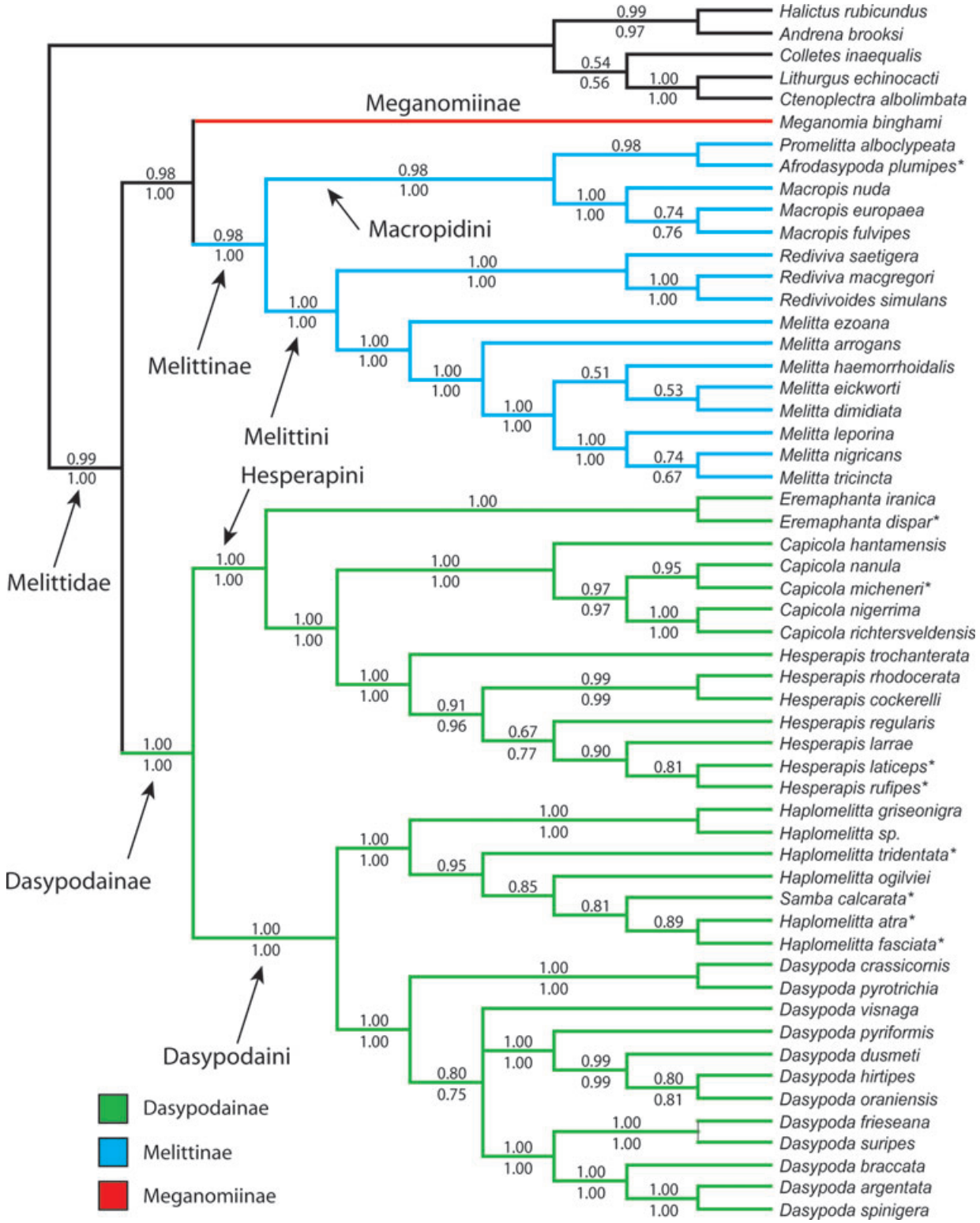

Fig. 5. Bayesian tree topology based on combined analysis of five genes [with elongation factor-1α (EF-1α introns included] and morphology (for Bayesian) for the 55 taxon matrix (analysis 10b) and the 46 taxon matrix (analysis 10a). Posterior probabilities are indicated below the nodes for the 46 taxon analysis and above the nodes for the 55 taxon analysis. Major clades (families, subfamilies, tribes) are labelled. Coloured branches refer to the three subfamilies: blue: Melittinae; red: Meganomiinae; green: Dasypodainae.

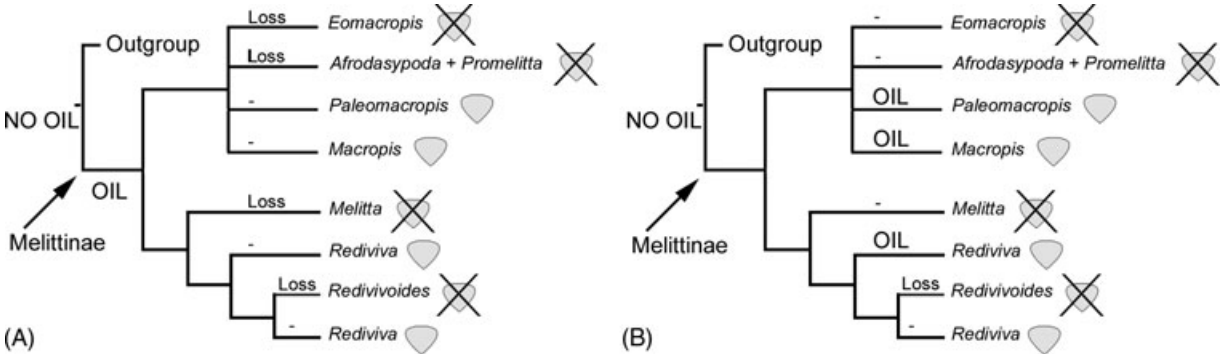

Fig. 6. Evolution of oil-collecting structures in Melittinae. (A) First hypothesis with oil-collecting ancestor (five evolutionary steps). (B) Second hypothesis with non oil-collecting ancestor (four evolutionary steps).

2007c; Whitehead *et al*., 2008). Other extant genera (*Afrodasypoda, Melitta, Promelitta* and *Redivivoides*) and the fossil *Eomacropis* do not share these morphological adaptations and they probably collect(ed) only pollen and nectar (Michez & Eardley, 2007; Michez *et al*., 2007a). Given our phylogeny, and assuming gains and losses of oil-collecting behaviour are equally probable, the scenario of independent origin of oil-collecting structures in *Rediviva* and Macropidini appears to be more parsimonious than multiple losses (Fig. 6A, B). Indeed, assuming that oil collecting arose in the common ancestor of Melittinae, we would have to hypothesize a total of five steps to explain the current distribution of oil-collecting behaviour: one gain (in the common ancestor) and four independent losses (Fig. 6A). Assuming a non oil-collecting common ancestor, we would have to hypothesize at most a total of four steps: three gains of oil collecting (*Macropis, Paleomacropis* and *Rediviva*) and one loss (*Redivivoides*) (Fig. 6B). Moreover, given that *Macropis* and *Paleomacropis* are probably sister groups (Michez *et al*., 2007c), they may share a common ancestor that was oil collecting. If this is the case, we would hypothesize a total of three steps: two gains (in the common ancestor of *Macropis* + *Paleomacropis* and *Rediviva*) and one loss (*Redivivoides*). The scenario of multiple origins of oil-collecting behaviour in Melittidae is congruent with the evolution of oil-collecting behaviour in other groups of bees. Except melittid bees, this particular behaviour appears to have arisen at least four times in unrelated tribes of Apidae: Centridini, Ctenoplectrini, Exomalopsini and Tetrapediini (Buchmann, 1987).

Future research

In the present study we developed an important molecular dataset in the ingroup (melittid bees) resolving some key taxonomic problems in Melittidae. However, the monophyly of Melittidae remains problematic. Recent molecular studies at the family level (Danforth *et al*., 2006a, b) have found evidence that melittids form a paraphyletic grade at the base of the bees (with Dasypodainae sister to all other bees). However, the basal nodes of this phylogeny were not well supported and statistical tests using the Bayes Factor did not show strong statistical support for the paraphyly of the family.

Further studies will have to add broader sampling of melittid species, sphecid wasps and non-melittid bees combining molecular data for common taxa and morphological data for some rare key taxa.

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Appendix 1. Morphological dataset (50 taxa × 68 characters)

The final morphological dataset included 68 characters, 17 of which are multistate. We used the glossary of Harris (1979) to describe the surface sculpture and Michener (2007) for morphological terms.

Female and male imago

1 Body size: (0) longer than 5 mm; (1) equal or shorter than 5 mm.
2 Flabellum: (0) absent; (1) present.
3 Paraglossa: (0) densely hairy; (1) with reduced pubescence.
4 Paraglossa: (0) as long as suspensorium; (1) shorter than suspensorium; (2) absent.
5 Posterior margin of stipe: (0) without flange; (1) with flange along posterior margin.

6 Posterior margin of stipe: (0) without preapical concavity; (1) with preapical concavity.
7 Mandible: (0) one colour or darker basally; (1) basally yellowish to brownish, apically brownish to reddish.
8 Tuft on apical area of labrum: (0) absent; (1) present.
9 Malar area: (0) shorter than scape; (1) longer than scape.
10 Compound eyes: (0) converging below; (1) parallel; (2) diverging below.
11 Vertex seen from front: (0) flat or weakly convex; (1) convex and elevated well above summits of eyes; (2) concave.
12 Postoccipital pouch below foramen magnum: (0) shallow; (1) distinct and deep.
13 Internal scrobal ridge from mesepisternal scrobe posteriorly to intersegmental suture: (0) absent; (1) present.
14 Upper metapleural pit: (0) widely separated from the lower pit; (1) very close to the lower pit (difficult to recognize).
15 Profile of propodeum: (0) anterior third to fifth more nearly horizontal than the posterior or declivous part; (1) anterior half part horizontal and posterior half part slanting; (2) anterior and posterior part more or less in one sloping plane.
16 Propodeal triangle: (0) sculptured or carinate; (1) smooth.
17 Fore wing, stigma: (0) shorter than the first submarginal cell; (1) as long as the first submarginal cell.
18 Fore wing, stigma: (0) length beyond vein r at least half as long as margin basal to vein r; (1) length beyond vein r less than half as long as part basal to vein r.
19 Fore wing, submarginal cells: (0) three; (1) two, first longer than second; (2) two, first and second of equal length.
20 Fore wing, second abscissa of Rs: (0) slanting; (1) at right angles to longitudinal veins.
21 Hind wing, jugal lobe: (0) two thirds as long as vannal lobe; (1) about half as long as vannal lobe; (2) less than half as long as vannal lobe.
22 Inner mid-tibial spur: (0) finely serrate or ciliate; (1) coarsely serrate; (2) with sharp outstanding spines (pectinate).
23 Inner hind tibial spur: (0) with row of stout serrate setae; (1) with sharp outstanding spines.
24 Tergal graduli: (0) laterally curved; (1) bent posteriorly at each side, but terminating approximately half-way from bend to marginal zone of tergum.

Male imago

25 Galeal comb: (0) present, with 3–18 teeth; (1) absent.
26 Clypeus: (0) black; (1) at least apically with yellow or white maculation.
27 Basitarsus 3: (0) flat; (1) inflated.
28 Pygidial plate: (0) present; (1) absent.
29 Marginal zone of sterna 3–5: (0) nearly hairless; (1) with white apical fringes.
30 Apical margin of sternum 6: (0) not bilobed; (1) bilobed.
31 Sternum 6: (0) with sparse hairs to nearly hairless; (1) with bushy medio-apical hairs.
32 Sternum 6: (0) without apicolateral processes, sometimes with reduced small medio-apical plate; (1) with two pairs of apical processes, one median and one lateral.
33 Sternum 7: (0) with apicolateral processes; (1) with reduced apicolateral processes; (2) without distinct apicolateral processes.
34 Medio-apical lobes of sternum 7: (0) without reduced spiny apicolateral processes; (1) with reduced spiny apicolateral processes.
35 Ventral side of sternum 8: (0) without carina; (1) with one median carina; (2) with two median carinae; (3) with two lateral carinae.
36 Disc of sternum 8: (0) without hook; (1) with mediolateral hook; (2) with mediolateral teeth.
37 Gonocoxite: (0) without meso-apical lobe; (1) with meso-apical lobe.
38 Gonostylus: (0) moveable, articulated to gonocoxite; (1) broadly fused to gonocoxite.
39 Gonostylus: (0) not biangulate apically; (1) biangulate apically.
40 Gonostylus: (0) simple; (1) double, with two processes linked with median membrane; (2) double, with two processes without median membrane; (3) triple, with three independent processes.
41 Inner lobe of gonostylus: (1) nearly hairless; (1) with fringe on margin.
42 Outer surface of gonostylus: (0) without dense short setae; (1) with defined area of dense short setae.
43 Lobes of volsella: (0) digitis as long as cuspis; (1) digitis longer than cuspis.
44 Digitis: (0) apically rounded; (1) apically pointed.
45 Cuspis: (0) apically rounded; (1) apically pointed.

Female imago

46 Shape of head: (0) nearly as long as wide ($1.25 > L/W \geqslant 0.75$); (1) longer than wide ($L/W > 1.25$); (2) wider than long ($L/W < 0.75$).
47 Integument of paraocular area: (0) not differentiated from median part of vertex; (1) with punctures sparser and smaller than rest of vertex; (2) with scattered or velvety hairs.
48 Legs 2–3: (0) black; (1) with yellow markings.
49 Base of mid-femur: (0) with undifferentiated sparse hairs; (1) with short conspicuous brush of yellow stiff on the trochanter-femur.
50 Undersurface of mid-tibia: (0) with longitudinal ridge bearing a longitudinal brush; (1) flat, with more scattered hairs.
51 Mid-tibial spur: (0) slender; (1) robust, enlarged at base.
52 Mid-tibial spur: (0) nearly straight; (1) strongly curved apically.
53 Mid-tibial spur: (0) less than half as long as inner margin of tibia 2 ($L/L < 0.5$); (1) nearly as long as inner margin of tibia 2 ($L/L > 0.9$).
54 Basitibial plate: (0) present; (1) absent.

55 Inner surface of hind tibia: (0) with keirotrichia; (1) without keirotrichia.
56 Scopae (hairs on hind leg): (0) unicolour; (1) bicolour.
57 Scopae: (0) with one kind of seta; (1) with limited plumose hairs under long simple hairs.
58 Scopal setae: (0) shorter than tibia width; (1) twice as long as tibia width.
59 Structure of longest scopal setae: (0) simple; (1) a few lateral setae weakly plumose; (2) spatulate; (3) densely plumose.
60 Shape of hind basitarsus: (0) over three times as long as wide; (1) 1.6–2.9 times as long as wide; (2) 1.5 times as long as wide or less.
61 Apex of hind basitarsus: (0) without small projection or tooth above articulation of second tarsal segment; (1) with small projection or tooth above articulation of second tarsal segment; (2) with large external apical plate above articulation of second tarsal segment.
62 Hind basitarsus: (0) simple; (1) apically divided.
63 Terga 1–2: (0) black; (1) partially red to reddish; (2) partially yellow.
64 Terga 2–4: (0) with apical hair bands; (1) without apical hair bands; (2) with basal hair bands.
65 Tergum 5: (0) with prepygidial fimbria distinct from other terga; (1) without prepygidial fimbria; (2) with apical hair band similar to those of preceding segments.
66 Pygidial plate: (0) hairless; (1) with short appressed hairs.
67 Pygidial plate: (0) flat; (1) with a strongly elevated median area.
68 Metasomal sterna: (0) nearly hairless, with sparse simple setae; (1) with dense plumose hairs; (2) with dense simple hairs.

Morphological data matrix.

Characters	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Outgroup																																				
Andrena brooksi	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	0	2	0	0	0
Colletes inaequalis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenoplectra albolimbata	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Halictus rubicundus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	2	0	0	0
Lithurgus echinocacti	0	1	0	0	0	1	0	0	1	0	1	0	0	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	0
Ingroup																																				
Afrodasypoda plumipes	0	0	1	0	0	0	0	1	0	2	1	1	?	0	2	1	0	0	2	0	1	0	0	1	?	1	0	1	0	1	1	0	0	0	0	0
Capicola hantamensis	1	0	1	1	0	0	1	1	0	0	1	1	?	0	0	0	0	0	1	1	0	2	1	0	0	1	0	1	0	1	0	1	2	0	0	0
C. micheneri	1	0	1	1	0	0	1	1	0	0	1	1	?	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	1	2	0	0	0
C. namula	1	0	1	1	0	0	1	1	0	0	1	1	?	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	1	2	0	0	0
C. nigerrima	0	0	1	1	0	0	0	1	0	0	1	1	?	0	2	0	0	0	1	1	0	2	1	0	0	0	0	1	0	1	0	1	2	0	0	0
C. richtersveldensis	0	0	1	1	0	0	0	1	0	0	1	1	?	0	2	0	0	0	1	1	0	2	1	0	0	0	0	1	0	1	0	1	2	0	0	0
Dasypoda argentata	0	1	1	1	0	0	0	1	1	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	1	3	0
D. braccata	0	1	1	1	0	0	0	1	1	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	1	3	0
D. crassicornis	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	2	0	1	0
D. dusmeti	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	1	1	0	0	1	0	2	1
D. frieseana	0	1	1	1	0	0	0	1	1	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	1	3	0
D. hirtipes	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	0	2	1
D. oraniensis	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	0	2	1
D. pyrtiformis	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	0	2	1
D. pyrotrichia	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	2	0
D. spinigera	0	1	1	1	0	0	0	1	1	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	1	3	0
D. suripes	0	1	1	1	0	0	0	1	1	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	1	3	0
D. visnaga	0	1	1	1	0	0	0	1	0	0	1	1	1	0	2	0	0	1	1	1	2	0	0	0	1	0	0	1	0	1	0	0	1	0	2	0
Eremaphanta dispar	1	0	1	1	0	1	1	0	0	1	1	1	?	0	1	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	2	0	0	0
E. iranica	1	0	1	1	0	1	1	0	0	0	0	1	?	0	1	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	2	0	0	0
Haplomelitta atra	0	0	1	2	1	0	0	1	0	1	0	0	1	1	2	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0

Morphological data matrix (*Continued*).

Characters	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
H. fasciata	0	0	1	2	1	0	0	1	0	0	0	0	1	1	2	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0
H. griseonigra	0	0	1	1	1	0	0	1	0	1	0	0	1	1	2	1	0	0	1	1	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0
H. ogilviei	0	0	1	2	1	0	0	1	0	1	2	0	1	1	2	0	0	0	1	1	2	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0
H. sp.	0	0	1	1	1	0	0	1	0	1	0	0	1	1	2	1	0	0	1	1	2	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0
H. tridentata	0	0	1	2	1	0	0	1	0	2	0	0	1	1	2	1	0	0	1	1	2	1	0	0	?	?	?	?	?	1	?	?	?	?	?	?
Hesperapis cockerelli	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	2	0	0	0
H. larrae	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	0
H. laticeps	0	0	1	1	0	0	1	0	0	0	2	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	2	0	0	0
H. regularis	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0
H. rhodocerata	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	1	0	2	0	0	0	0	0	0	1	1	1	0	2	0	0	0
H. rufipes	0	0	1	1	0	0	1	1	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	2	0	0	0
H. trochantera	1	0	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0
Macropis europaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	2
M. fulvipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	2
M. nuda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	2
Melitta arrogans	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. dimidiata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. eickworti	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. ezoana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. haemorrhoidalis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. leporina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. nigricans	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
M. tricincta	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Meganomia binghami	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	2
Promelitta alboclypeata	0	0	1	0	0	0	0	0	0	0	0	?	?	0	0	1	0	0	2	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	2
Rediviva macgregori	0	0	0	0	0	0	0	0	0	0	0	?	?	0	2	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
R. saetigera	0	0	0	0	0	0	0	0	0	0	0	?	?	0	2	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Redivivoides simulans	0	0	0	0	0	0	0	0	0	0	0	?	?	0	2	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Samba calcarata	0	0	1	2	1	0	0	1	0	1	2	0	?	1	2	1	0	0	1	0	2	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0

Morphological data matrix (*Continued*).

Characters	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
Outgroup																																
Andrena brooksi	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Colletes inaequalis	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Ctenoplectra albolimbata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	2
Halictus rubicundus	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lithurgus echinocacti	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ingroup																																
Afrodasypoda plumipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	2	0	0	0	2
Capicola hantamensis	0	1	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0
C. micheneri	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0
C. namula	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0
C. nigerrima	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
C. richtersveldensis	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Dasypoda argentata	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	0	1	0	1
D. braccata	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	0	1	0	1
D. crassicornis	0	0	0	2	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1
D. dusmeti	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0	0	1
D. frieseana	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	0	1	0	1
D. hirtipes	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	2	0	0	0	0	0	0	0	0	1
D. oraniensis	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	2	0	0	0	0	0	0	0	0	1
D. pyrifformis	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	2	0	0	0	0	0	0	0	0	1
D. pyrotrichia	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0	0	0	0	1	0	0	0	1
D. spinigera	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	0	1	0	1
D. suripes	0	0	0	3	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	0	1	0	1
D. visnaga	0	0	0	3	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	2	0	0	0	0	0	0	0	0	1
Eremaphanta dispar	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0
E. iranica	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplomelitta atra	1	0	1	0	0	0	1	1	0	2	0	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0
H. fasciata	1	0	1	0	0	0	1	1	0	2	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0

Morphological data matrix (*Continued*).

Characters	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
H. griseonigra	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0
H. ogilviei	1	0	1	0	0	0	1	1	0	2	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0
H. sp.	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0
H. tridentata	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Hesperapis cockerelli	0	1	0	2	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	2	0	0	0
H. larrae	0	1	0	2	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
H. laticeps	0	1	0	2	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
H. regularis	0	1	0	2	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0
H. rhodocerata	0	1	0	2	1	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0	0	0
H. rufipes	0	1	0	2	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
H. trochantera	0	1	0	2	1	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	2	0	0	0
Macropis europaea	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	2
M. fulvipes	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	2
M. nuda	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Melitta arrogans	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
M. dimidiata	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. eickworti	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. ezoana	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. haemorrhoidalis	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. leporina	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. nigricans	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
M. tricincta	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Meganomia binghami	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Promelitta alboclypeata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	1	2
Rediviva macgregori	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
R. saetigera	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Redivivoides simulans	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1
Samba calcarata	1	0	1	0	0	0	1	0	0	2	0	0	1	0	1	1	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0

Appendix 2. Description of the male of *Afrodasypoda plumipes*

We describe below the previously unknown male of *Afrodasypoda plumipes*. *Afrodasypoda plumipes* was only known from one female specimen (Michener, 2007). This enigmatic species was included in the Afrodasypodini (monobasic) and Promelittini (with the genus *Promelitta*), both Dasypodainae. The present study transfers *Afrodasypoda plumipes* to the Macropidini (Melittinae).

Material examined

One male, South Africa, Richtersveld (28.18°S 16.58°S), 09.ix.1986, leg. Struck, collection of Iziko South African Museum (Cape Town, South Africa). One male, South Africa, Richtersveld, Foot of Hells Kloof, 10.ix.1974, leg. R.H. Watmough, collection of Plant Protection Research Institute (Pretoria, South Africa).

Description

Body length = 11.9 mm (n=2). Head. Integument: black except clypeus with yellow maculation and mandible with red apex (Fig. 7F). Glossa pointed (Fig. 7F). Labial palpus with four subequal segments. Outer surface of galea punctate. Maxillary palpus with six segments, the first with long setae. Mandible with one preapical tooth. Labrum flat and smooth. Malar area short. Clypeus, face and vertex flat, densely punctate (punctures contiguous), smooth between punctures. Compound eyes parallel. Antenna with 13 segments (AT), AT3 as long as AT3 + 4, AT4–13 ventrally inflated. Vestiture: clypeus, face, vertex and genal area with sparse, short, erect, white setae.

Mesosoma. Integument: black. Pronotum, scutum, scutellum and metanotum densely punctate (punctures nearly contiguous), cuticle smooth between punctures. Propodeum smooth, anterior and posterior part in one gradually sloping plane. Vestiture: whitish short erected setae. Legs. Integument: fore leg reddish. Mid- and hind legs black. Legs without tooth or spine. Hind femur with keirotrichia. Vestiture: whitish short apressed setae. Wings. Hyaline. Two submarginal cells, the first as long as the second. Stigma shorter than the first submarginal cell. Jugal lobe about half as long as vannal lobe. Metasoma. Integument: black. Terga 2–5 with basal depression. Disc of terga and sterna densely punctate (punctures nearly contiguous), smooth between punctures. Stenum 6 apically bifid (Fig. 7A). Sternum 7 with long latero-apical processes (Fig. 7B, C). Apical column of sternum 8 without carina (Fig. 7D). Gonostylus simple, articulated to gonocoxite, apically truncated (Fig. 7E). Vestiture: terga with basal band of whitish setae. Disc of terga with black erected setae. Marginal zone of terga hairless. Disc of sterna with sparse apical setae.

Appendix 3. Systematics of Melittidae

Dasypodainae Latreille, 1802 **comb.n**

Included genera. Capicola Friese, 1911, *Dasypoda* Latreille, 1802, *Eremaphanta* Popov, 1940, *Haplomelitta* Cockerell, 1934, *Hesperapis* Cockerell, 1898 and *Samba* Friese, 1908.

Diagnosis. Paraglossa absent or shorter than the suspensorium, such reduced paraglossa is unique among bees (Michener, 2007). Body black except in a few males of Hesperapini (*Eremaphanta, Capicola hantamensis* and *Hesperapis rufipes*).

Fig. 7. *Afrodasypoda plumipes* male (black scale= 250 μm; white scale = 1 mm). (A) Sternum 6 in ventral view, (B) sternum 7 in ventral view, (C) sternum 7 in lateral view, (D) sternum 8 in ventral view, (E) genitalia in dorsal view, (F) head in frontal view.

Two submarginal cells with the first submarginal crossvein at right angles to longitudinal vein. Male without pygidial plate. Volsella with distinct digitis and cuspis. Larvae do not spin a cocoon.

Biology. As far as is known, the Dasypodainae are gregarious and associated with sandy soils. Females nest in habitats such as inland dunes, sandy coast, drifts or silty flood plains (Stage, 1966; Rozen, 1974, 1987; Celary, 2002). They excavate individual tunnels to depths that could exceed 1 m. The burrows are surrounded by a symmetrical tumulus resulting from the excavation of the sand. The main tunnel penetrates the surface at a low angle and descends vertically after approximately 10 cm. Brood chambers (i.e. cells) are placed at the ends of long lateral tunnels. The cells are sometimes placed singly, as in *Hesperapis* (except *H. larrae*) and *Haplomelitta*, and sometimes arranged in linear series, as in *Capicola* and *Dasypoda*. The tunnels and the cells are unlined and apparently not waterproofed, but the walls are more consolidated than the substrate. Cells are provisioned with a pollen/nectar mix and females moisten the pollen loads with nectar. The provisions are moulded in different shapes. *Hesperapis, Capicola* and *Haplomelitta* make spherical pollen balls, whereas *Dasypoda* pollen balls are supported above the cell surface on three small, conical 'feet'. Females put one egg on the top of the pollen ball and close the cell with fine soil material. After hatching, the larvae consume their provisions quickly (15 days). The mature larva overwinters as a prepupa. The postdefecating larvae do not spin a cocoon.

Diversity and biogeography. Dasypodainae occur in both the Old World and the Nearctic region (Table 1). This family is absent in South America, Australia and tropical areas. The species level diversity of Dasypodainae is maximal in the xeric areas: southwestern North American semideserts (*Hesperapis*), Mediterranean basin (*Dasypoda*), Kyzylkum in Central Asia (*Eremaphanta*) and Southern Africa (*Capicola* and *Haplomelitta*). *Dasypoda* is the only widespread genus that occurs in both temperate and xeric parts of the Palaearctic. *Dasypoda* determines the northern limit of Dasypodainae to the 62nd northern parallel. The other genera of Dasypodainae, *Capicola, Eremaphanta, Haplomelitta, Hesperapis* and *Samba*, are each endemic to different semideserts (Table 1).

As stated previously, Dasypodainae is the most robustly supported clade of the displayed topologies. It is supported by nearly all individual genes, morphological characters and the combined dataset. Two tribes are distinguished: Dasypodaini and Hesperapini (Figs 3–5).

Dasypodaini Latreille, 1802 **comb.n**

= Sambini Michener, 1981 **syn.n.**

Included genera. Dasypoda, Haplomelitta and *Samba*.

Diagnosis. Head black. Anterior and posterior part of propodeum more or less in one sloping plane. Jugal lobe of hind wing two-thirds as long as vannal lobe. Gonostylus of male long, flexibly joined or articulated to gonocoxite. Sternum 7 of male with small to expanded latero-apical processes.

Distribution. Old World.

Comment. Although our results suggest that *Samba* arises from within *Haplomelitta* (rendering *Haplomelitta* paraphyletic; Figs 3–5), we do not propose to change the generic status of these genera. Future studies, including more species of *Haplomelitta*, will be needed to corroborate these results.

Hesperapini Ascher and Engel, 2005 **stat.n**

Included genera. Capicola, Eremaphanta and *Hesperapis*.

Diagnosis. Clypeus and mandibles sometimes with yellow marking. Profile of propodeum nearly horizontal at base than elsewhere. Jugal lobe of hind wing less than half as long as vannal lobe. Gonostylus of male robust, broadly fused to gonocoxite. Sternum 7 of male without latero-apical processes.

Distribution. Holarctic and Southern Africa.

Melittinae Kirby, 1802 **comb.n**

Included genera. Afrodasypoda Engel, 2005, *Eomacropis* Engel, 2001, *Macropis* Klug, 1809, *Melitta* Kirby, 1802, *Paleomacropis* Michez & Nel, 2007, *Promelitta* Warncke, 1977, *Rediviva* Friese, 1911 and *Redivivoides* Michener, 1981.

Diagnosis. Paraglossa as long as suspensorium. Body mainly black except male of Macropidini, which has yellow or white clypeus. Two or three submarginal cells. Male with or without pygidial plate. Volsella with distinct digitis and cuspis. Larvae spin a cocoon.

Biology. The nests of Melittinae are usually not aggregated (Celary, 2004, 2006). 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 20–40 cm in depth, clearly less deep than those of Dasypodainae. 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 floral oils to line the cells (Cane et al., 1983), whereas *Melitta* should use Dufour's gland secretions (Celary, 2006; but this author did not provide precise details on the source of the cell lining). The development of larvae is similar to Dasypodainae, but the larvae spin a cocoon.

Diversity and biogeography. Melittinae occur in the Old World and the Neartic region (Table 1). Genera of Melittinae show divergent climatic preferences. *Melitta* and *Macropis* prefer cool, temperate ecosystems (Michez & Patiny, 2005; Michez & Eardley, 2007). Others genera, *Afrodasypoda, Promelitta, Rediviva* and *Redivivoides*, are distributed in more xeric areas of South and North Africa.

Two tribes are distinguished: Melittini and Macropidini (Figs 3–5).

Melittini Kirby, 1802

= Redivivini Engel, 2001

Included genera. Melitta Kirby, 1802, *Rediviva* Friese, 1991 and *Redivivoides* Michener, 1981.

Diagnosis. Clypeus male black. Three submarginal cells. Gonostylus of male short, broadly fused to gonocoxite. Digitis longer than cuspis.

Distribution. Holarctic and Southern Africa.

Comment. Although our results suggest that *Redivivoides* arises within *Rediviva* (making *Rediviva*, as currently defined, paraphyletic), we do not propose to alter the taxonomy at this time. Conclusions about the placement of *Redivivoides* should await studies including a broader sample of *Rediviva* species.

Macropidini Robertson, 1904 **comb.n**

= Promelittini Michener, 1981 **syn.n.**
= Afrodasypodini **syn.n.**
= Eomacropidini Engel, 2001 **syn.n.**

Included genera. Afrodasypoda Engel, 2005, *Eomacropis* Engel, 2001, *Macropis* Panzer, 1809, *Paleomacropis* Michez & Nel, 2007 and *Promelitta* Warncke, 1977.

Diagnosis. Clypeus of male with white or yellow maculation. Two submarginal cells with the second abscissa of Rs slanting and widely separated from 1 m-cu. Apex of marginal cell pointed. Gonostylus of male long, flexibly joined or articulated to gonocoxite. Digitis as long as cuspis.

Distribution. Holarctic and Southern Africa.

Meganomiinae Michener, 1981

Included genera. Ceratomonia Michener, 1981, *Meganomia* Cockerell, 1931, *Pseudophilanthus* Alfken, 1939, *Uromonia* Michener, 1981.

Diagnosis. Paraglossa as long as suspensorium. Extensive yellow markings on the whole body (male and female). Three submarginal cells. Many unique modifications of legs and hidden sterna of male. Male with pygidial plate. Reduced volsella without recognizable digitis and cuspis. Larvae spin cocoon.

Biology. Meganomia gigas is the only Meganomiinae in which nesting behaviour has been described (Rozen, 1977). This species presents intermediate nesting behaviours in comparison with other melittid bees. Females are gregarious and dig a deep nest (120 cm) in sandy soil, as in Dasypodainae, but they apply a waterproof cell lining, as in Melittinae. *Meganomia* moisten the pollen with nectar during foraging as Dasypodainae, but larvae spin a cocoon like Melittinae

Diversity and biogeography. Meganomiinae is the least speciose subfamily of Melittidae sensu lato (Table 1). Meganomiinae is restricted to Sub-Saharan Africa except one undescribed *Meganomia* species recorded in Yemen. Michener (1981), Michener & Brooks (1987) and Michener *et al*. (1990) reviewed the four included genera. These authors did not propose tribes. According to the topologies yielded by Bayesian analyses, the Meganomiinae (represented in the dataset by *M. binghami*) form the sister group to the Melittinae. This is also supported by morphological data)