

## Fossil bees and their plant associates

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### 5.1 Introduction

The bees comprise a derived monophyletic group (Anthophila) of pollen-consuming (secondarily phytophagous) wasps of the superfamily Apoidea, and that diverged from a grade of predatory apoid wasps (formerly “Sphecidae”) sometime in the mid Cretaceous (~120–125 megaannum) (Michener 1944, 1979, 2007; Brothers 1975, 1998; Alexander 1992; Ronquist 1999; Engel 2001a, 2011; Danforth et al. 2006). Seven contemporary families are usually acknowledged: Andrenidae, Apidae, Colletidae, Halictidae, Melittidae, Megachilidae and Stenotritidae, including ~1200 genera and ~20 000 species (Michener 2007; Engel 2005, 2011). Two fossil families are also described: Paleomelittidae from middle Eocene Baltic amber, and a stem-group, Melittosphecidae from Cretaceous Burmese amber which, as discussed below, may or may not be a bee (Engel 2001a; Poinar and Danforth 2006; Ohl and Engel 2007). Bees likely arose concomitantly with the diversification of flowering plants (angiosperms) (Michener 1979; Grimaldi 1999; Engel 1996, 2001a; Crepet et al. 2004; Grimaldi and Engel 2005). Represented by more than 250 000 described species, angiosperms are the most diversified group of vascular plants, covering nearly all terrestrial and many aquatic habitats (Soltis and Soltis 2004). The congruent rise of flowering plants and numerous phytophagous insect lineages, such as bees, ditrysian Lepidoptera, and various flowering-visiting beetles and flies, has fuelled the

notion of coradiation between these lineages. Such a conclusion is supported by the observation of flowers with specific combinations of traits that are correlated with particular pollinators (Bronstein et al. 2006). Selection for insect-pollinated clades is also supported by the fact that deliverance by pollinators of unconsumed pollen to the host plant's female reproductive organs is clearly less stochastic and more efficient than alternative ancestral wind, water or gravity dispersive methods (Labandeira 1998). Lastly, association with pollinators increases opportunities for the evolution of specialization and subsequent diversification (Vamosi and Vamosi 2010).

To test hypotheses regarding the macroevolutionary dynamics of plants and their insect associates, the examination of fossil plant–insect interactions is essential. This chapter is focused on the peculiar mutualistic interactions between angiosperms and their major pollinators, the bees, as well as a consideration of those traces of their past interactions preserved in the geological records. We first describe modern bee–plant interactions and their syndromes. From there we synthesize some methodologies for studying past ecological associations. The bulk of this contribution is an elaboration of the main fossil records for bees in the context of their contemporaneous environmental factors, such as climate, habitat, and likely host plants. A general catalogue of bee fossils is presented in Table 5.1 and constitutes the current state of affairs for paleomelittology. Naturally, much revisionary work remains to be undertaken for all of these deposits, particularly the historical accounts of paleofaunas such as Florissant, and a re-evaluation of these may result in considerable changes of taxonomic affinity. Such changes are beyond the scope of the present work and require careful revisions of historical type material. Relationships between bee fossils and their likely host plants are discussed in the context of higher relationships as proposed in Grimaldi (1999) and Danforth et al. (2006). Refer to Engel (2004b), Grimaldi and Engel (2005), and Ohl and Engel (2007) for an alternative set of phylogenetic relationships in association with the fossil records.

## 5.2 Modern evidence of bee–plant interactions

Pollinators develop adaptative morphological features to forage on plant rewards while plants develop traits to announce such rewards. These adaptative character syndromes are described as “pollination syndromes.” They are morphologically convergent adaptative trends exhibited by both the floral features of pollinated plants and the mouthpart structures as well as other flower-interactive features of their respective pollinators (Proctor et al. 1996; Bronstein et al. 2006). Bees and bee-pollinated angiosperms show obvious pollination syndromes.

**Table 5.1** Bee body fossils and traces are listed by geological eras and then in alphabetical order. All species described from inclusions in amber as well as compressions are extinct. All species described from copal are still extant with the exceptions of *Liotrogona vetula* and *Euglossa cotylisca*. All extinct supraspecific taxa are noted by an asterisk (\*). The classification follows that of Michener (2007). A = Amber. C = Compression. Co = Copal. IN = ichnospecies, nest trace (we do not consider nest traces included in the ichnogenera *Brownichnus*, *Celliforma* and *Palmirachnus* because of their simple structure, poorly relatable to bees). ILD = ichnospecies, leaf damage. F = Female. FW = Female worker. M = Male. Upp = Upper. Low = Lower. Mid = Middle. Num = Numerous. Note that the trace fossil "*Atta praecursor*" from the Late Cretaceous of Bohemia (Frič and Bayer 1901) was considered a *Megachile* trace by Baroni Urbani (1980) but the specimen does not appear to be a bee trace fossil (personal observation).

Family	Subfamily	Tribe	Species (A, C) or Ichnospecies (IN, ILD)	Age	Deposit locality	N	References
<b>Cretaceous</b>							
Apid.	Apinae	Meliponini	<i>Cretotrigona* prisca</i> (Michener and Grimaldi 1988) (A)	-70	Kinkora (USA)	1FW	Michener and Grimaldi (1988a, 1988b); Engel (2000b)
Hal.	Incerta Sedis	Incerta Sedis	<i>Cellicalichnus chubutensis</i> Genise 2000 (IN)	-70	Chubut (Argentina)	Num	Genise (2000); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>C. dakotensis</i> (Elliott and Nations 1998) (IN)	-94	Arizona (USA)	15	Elliott and Nations (1998); Genise (2000); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>Corimbatichnus fernandezi</i> Genise and Verde 2000 (IN)	-70	Nueva Palmira (Urug.)	Num	Genise (2000); Genise and Verde (2000); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>Ellipsoideichnus meyeri</i> Roselli 1987 (IN)	-70	Nueva Palmira (Urug.)	1	Genise (2000); Engel and Peñalver (2006)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Ichnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Hal.	Incerta Sedis	Incerta Sedis	<i>Uruguay auroranormae</i> Roselli 1938 (IN)	-70	Nueva Palmira (Urug.)	Num	Genise (2000); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>Uruguay rivasi</i> (Roselli 1987) (IN)	-70	Nueva Palmira (Urug.)	Num	Genise (2000); Engel and Peñalver (2006)
Melitt.*	Melittosphe.	Melittosphecini	<i>Melittosphehex burmensis</i> Poinar and Danforth 2006 (A)	-100	Hukawng valley (Bur.)	1M	Poinar and Danforth (2006); Ohl and Engel (2007)
<b>Paleocene</b>							
Apid.	Apinae	Anthophorini	<i>Paleohabropoda* oudardi</i> Michez and Rasmont 2009 (C)	-60	Menat (France)	1F	Michez et al. (2009a)
Meg.	Megachiliinae	Incerta Sedis	<i>Probombus* hirsutus</i> Piton 1940 (C)	-60	Menat (France)	1F	Nel and Petrulevicius (2003)
Meg.	Megachiliinae	Megachilini	<i>Phagophytichnus</i> spp. (ILD)	-60	Menat (France)	1	Wedmann et al. (2009)
<b>Eocene – Baltic amber</b>							
Apid.	Apinae	Electrapini*	<i>Electrapis krishnorum</i> Engel 2001 (A)	-48	Baltic basin	4FW	Engel (2001a)
Apid.	Apinae	Electrapini*	<i>E. martialis</i> (Cockerell 1908) (A)	-48	Baltic basin	2FW	Cockerell (1908c); Engel (2001a)
Apid.	Apinae	Electrapini*	<i>E. meliponoides</i> (Buttel- Reepen 1906) (A)	-48	Baltic basin	1FW	Engel (2001a)
Apid.	Apinae	Electrapini*	<i>E. tornquisti</i> Cockerell 1908 (A)	-48	Baltic basin	3FW	Cockerell (1908c); Engel (2001a)

Apid.	Apinae	Electrapini*	<i>Protobombus basilaris</i> Engel 2001 (A)	-48	Baltic basin	1FW	Engel (2001a)
Apid.	Apinae	Electrapini*	<i>P. fatalis</i> (Cockerell 1908) (A)	-48	Baltic basin	2FW	Cockerell (1908c); Engel (2001a)
Apid.	Apinae	Electrapini*	<i>P. hirsutus</i> (Cockerell 1908) (A)	-48	Baltic basin	4FW	Cockerell (1908c); Engel (2001a)
Apid.	Apinae	Electrapini*	<i>P. indecisus</i> (Cockerell 1908) (A)	-48	Baltic basin	4FW	Cockerell (1908c); Engel (2001a)
Apid.	Apinae	Electrapini*	<i>P. tristellus</i> Cockerell 1909 (A)	-48	Baltic basin	1FW	Engel (2001a)
Apid.	Apinae	Electrapini*	<i>Thaumastobombus andreniformis</i> Engel 2001 (A)	-48	Baltic basin	2FW	Engel (2001a); Patiny et al. (2007)
Apid.	Apinae	Electrobombini*	<i>Electrobombus samlandensis</i> Engel 2001 (A)	-48	Baltic basin	2FW	Engel (2001a)
Apid.	Apinae	Melikertini*	<i>Melikertes clypeatus</i> Engel 2001 (A)	-48	Baltic basin	3FW	Engel (2001a, 2004b, unpublished data)
Apid.	Apinae	Melikertini*	<i>M. proavus</i> (Menge 1856) (A)	-48	Baltic basin	2FW	Engel (2001a)
Apid.	Apinae	Melikertini*	<i>M. stilbonotus</i> (Engel 1998) (A)	-48	Baltic basin	9FW	Engel (1998b, 2001a, 2004b)
Apid.	Apinae	Melikertini*	<i>Melissites trigona</i> Engel 2001 (A)	-48	Baltic basin	1FW	Engel (2001a)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Apid.	Apinae	Melikertini*	<i>Roussyana palmnickenensis</i> (Roussy 1937) (A)	-48	Baltic basin	3FW	Engel (2001a)
Apid.	Apinae	Melikertini*	<i>Succinapis goeleti</i> Engel 2001 (A)	-48	Baltic basin	4FW	Engel (2001a, 2004b)
Apid.	Apinae	Melikertini*	<i>S. micheneri</i> Engel 2001 (A)	-48	Baltic basin	30FW	Engel (2001a, 2004b)
Apid.	Apinae	Melikertini*	<i>S. proboscidea</i> Engel 2001 (A)	-48	Baltic basin	3FW	Engel (2001a)
Apid.	Apinae	Meliponini	<i>Liotrigonopsis rozeni</i> Engel 2001 (A)	-48	Baltic basin	1FW	Engel (2001a)
Apid.	Apinae	Meliponini	<i>Kelneriapis eocenica</i> Kelner- Pillault 1969 (A)	-48	Baltic basin	1FW	Engel (2001a)
Apid.	Xylocopinae	Boreallodapini*	<i>Boreallodape baltica</i> Engel 2001 (A)	-48	Baltic basin	9F	Engel (2001a, 2004b)
Apid.	Xylocopinae	Boreallodapini*	<i>B. mollyae</i> Engel 2001 (A)	-48	Baltic basin	6F	Engel (2001a, 2004b)
Apid.	Xylocopinae	Boreallodapini*	<i>B. striebichi</i> Engel 2001 (A)	-48	Baltic basin	14F	Engel (2001a)
Hal.	Halictinae	Halictini	<i>Electrolictus* antiquus</i> Engel 2001 (A)	-48	Baltic basin	1F	Engel (2001a)
Mel.	Melittinae	Macropidini	<i>Eomacropis* glaesaria</i> Engel 2001 (A)	-48	Baltic basin	1F	Engel (2001a); Michez et al. (2009b)

Meg.	Megachilinae	Protolithurgini*	<i>Protolithurgus ditomeus</i> Engel 2001 (A)	-48	Baltic basin	1F	Engel (2001a, 2005); Engel and Perkovsky (2006)
Meg.	Megachilinae	Ctenoplectrellini*	<i>Ctenoplectrella cockerelli</i> Engel 2001 (A)	-48	Baltic basin	3F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Ctenoplectrellini*	<i>C. gorskii</i> Engel 2008 (A)	-48	Baltic basin	2F	Engel (2008)
Meg.	Megachilinae	Ctenoplectrellini*	<i>C. grimaldii</i> Engel 2001 (A)	-48	Baltic basin	1F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Ctenoplectrellini*	<i>C. viridiceps</i> Cockerell 1909 (A)	-48	Baltic basin	12F/2M	Cockerell (1909c); Engel (2001a, 2004b); Engel and Perkovsky (2006)
Meg.	Megachilinae	Ctenoplectrellini*	<i>Glaesosmia* genalis</i> Engel 2001 (A)	-48	Baltic basin	1F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Glyptapini*	<i>Glyptapis densopunctata</i> Engel 2001 (A)	-48	Baltic basin	4F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Glyptapini*	<i>G. disareolata</i> Engel 2001 (A)	-48	Baltic basin	2F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Glyptapini*	<i>G. fuscula</i> Cockerell 1909 (A)	-48	Baltic basin	9F	Engel (2001a); Engel and Perkovsky (2006)
Meg.	Megachilinae	Glyptapini*	<i>G. mirabilis</i> Cockerell 1909 (A)	-48	Baltic basin	5F	Cockerell (1909c); Engel (2001a, 2004b); Engel and Perkovsky (2006)
Pal.*	Paleomettinae	Paleometittini	<i>Paleometitta nigripennis</i> Engel 2001 (A)	-48	Baltic basin	2F	Engel (2001a)

**Table 5.1** (cont.)

Family	Subfamily	Tribe	Species (A, C) or Icnospecies (IN, ILD)	Age	Deposit locality	N	References
<b>Eocene – Other than Baltic deposit</b>							
Apid.	Apinae	Electrapini*	<i>Electrapis electrapoides</i> (Lutz 1993) (C)		Messel (Germany)	3FW	Lutz (1993); Wappler and Engel (2003)
Apid.	Apinae	Electrapini*	<i>E. micheneri</i> Wappler and Engel 2003 (C)	-44	Eckfeld (Germany)	1FW	Wappler and Engel (2003)
Apid.	Apinae	Electrapini*	<i>E. prolata</i> Wappler and Engel 2003 (C)	-44	Eckfeld (Germany)	1FW	Wappler and Engel (2003)
Apid.	Apinae	Electrapini*	<i>Protobombus messelensis</i> Wappler and Engel 2003 (C)	-49	Messel (Germany)	1FW	Wappler and Engel (2003)
Apid.	Apinae	Electrapini*	<i>P. pristinus</i> Wappler and Engel 2003 (C)	-44	Eckfeld (Germany)	1FW	Wappler and Engel (2003)
Apid.	Apinae	Electrapini*	<i>P. spp.</i> (A)	-52	Cambay basin (India)	1FW	Rust et al. (2010); Engel (unpublished data)
Apid	Apinae	Melikertini*	<i>Melikertes spp.</i> (A)	-52	Cambay basin (India)	3FW	Rust et al. (2010); Engel (unpublished data)
Apid.	Apinae	Incerta Sedis	<i>Pygomelissa* lutetia</i> Engel and Wappler 2003 (C)	-49	Messel (Germany)	1F	Wappler and Engel (2003)
Hal.	Halictinae	Halictini	<i>Halictus?savenyei</i> Engel and Archibald 2003 (C)	-53	Quilichena (Canada)	1F	Engel and Archibald (2003); Engel and Peñalver (2006)



Mel.	Melittinae	Macropidini	<i>Paleomacropis* eoenicus</i> Michez and Nel 2007 (A)	-53	Oise (France)	1F	Michez et al. (2007)
Meg.	Megachilinae	Ctenoplectrellini*	<i>Friccomelissa schopowi</i> Wedmann et al. 2009 (C)	-49	Messel (Germany)	1F	Wedmann et al. (2009)
Meg.	Megachilinae	Ctenoplectrellini*	<i>Ctenoplectrella zherkhini</i> Engel and Perkovsky 2006 (A)	-48	Rovno (Ukraine)	1F	Engel and Perkovsky (2006)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> <i>pseudocircus</i> Sarzetti et al. 2008 (ILD)	-44	Eckfeld (Germany)	3	Wappler and Engel (2003); Wedmann et al. (2009)
Meg.	Megachilinae	Megachilini	<i>P. pseudocircus</i> Sarzetti et al. 2008 (ILD)	-49	Messel (Germany)	1	Wedmann et al. (2009)
Meg.	Megachilinae	Megachilini	<i>P. pseudocircus</i> Sarzetti et al. 2008 (ILD)	Mid	Puryear (USA)	1	Brooks (1955); Labandeira (2002a); Wedmann et al. (2009)
Meg.	Megachilinae	Megachilini	<i>P. pseudocircus</i> Sarzetti et al. 2008 (ILD)	-48	Rio Pichi-Leufú (Arg.)	1	Sarzetti et al. (2008)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> spp. (ILD)	-44	Eckfeld (Germany)	4	Wappler and Engel (2003); Wedmann et al. (2009)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> spp. (ILD)	-49	Messel (Germany)	4	Wedmann et al. (2009)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> sp. (ILD)	-49	Republic (USA)	2	Labandeira (2002a)

**Table 5.1** (cont.)

Family	Subfamily	Tribe	Species (A, C) or Icnospecies (IN, ILD)	Age	Deposit locality	N	References
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> spp. (ILD)	-49	MacAbee (Canada)	1	Labandeira (2002a)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> spp. (ILD)	Mid	Viola (USA)	1	Wedmann et al. (2009)
<b>Oligocene – Florissant shale</b>							
And.	Andreninae	Andrenini	<i>Andrena?</i> <i>clavula</i> Cockerell 1906 (C)	-32	Florissant (USA)	1F	Cockerell (1906)
And.	Andreninae	Andrenini	<i>A. grandipes</i> Cockerell 1911 (C)	-32	Florissant (USA)	1F	Cockerell (1911b)
And.	Andreninae	Andrenini	<i>A. hypolitha</i> Cockerell 1908 (C)	-32	Florissant (USA)	1F	Cockerell (1908c)
And.	Andreninae	Andrenini	<i>A. percontusa</i> Cockerell 1914 (C)	-32	Florissant (USA)	1F	Cockerell (1914)
And.	Andreninae	Andrenini	<i>A. septula</i> Cockerell 1906 (C)	-32	Florissant (USA)	1F	Cockerell (1906)
And.	Andreninae	?	<i>Lithandrena</i> * <i>saxorum</i> Cockerell 1906 (C)	-32	Florissant (USA)	1F	Cockerell (1906)
And.	Andreninae	?	<i>Pelandrena</i> * <i>reducta</i> Cockerell 1909 (C)	-32	Florissant (USA)	1F	Cockerell (1909b)
And.	Panurginae	?	<i>Libellulapis</i> * <i>antiquorum</i> Cockerell 1906 (C)	-32	Florissant (USA)	2F	Cockerell (1906, 1913b)

And.	Panurginae	?	<i>L.* wilmattae</i> Cockerell 1913 (C)	-32	Florissant (USA) 1F	Cockerell (1913b)
Apid.	Apinae	Anthophorini	<i>Anthophora melfordi</i> Cockerell 1908 (C)	-32	Florissant (USA) 1?	Cockerell (1908c); Michez et al. (2009a)
Apid.	Bombinae	Bombini	<i>Calyptapis* florissantensis</i> Cockerell 1906 (C)	-32	Florissant (USA) 2?	Cockerell (1906, 1908c)
Apid.	Xylocopinae	Ceratinini	<i>Ceratina disrupta</i> Cockerell 1906 (C)	-32	Florissant (USA) 1?	Cockerell (1906); Engel (2001b)
Apid.	Xylocopinae	Xylocopini	<i>Xylocopa gabriellae</i> Engel 2001 (C)	-32	Florissant (USA) 1F	Engel (2001b); Nel and Petruvecius (2003)
Apid.	Apinae	Melectini	<i>Protomelecta* brevipennis</i> Cockerell 1908 (C)	-32	Florissant (USA) 1?	Cockerell (1908a); Engel (2004a)
Hal.	Halictinae	Halictini	<i>Cyrtapis* anomalus</i> (Cockerell 1908) (C)	-32	Florissant (USA) 1?	Cockerell (1908a); Engel (2002a); Engel and Peñalver (2006)
Hal.	Halictinae	Halictini	<i>Kronolictus* scudderiiellus</i> Cockerell 1906 (C)	-32	Florissant (USA) 1F	Cockerell (1906); Engel (2002a); Engel and Peñalver (2006)
Hal.	Halictinae	Halictini	<i>K.* vulcanus</i> Engel 2002 (C)	-32	Florissant (USA) 1F	Engel (2002a); Engel and Peñalver (2006)
Hal.	Halictinae	Halictini	<i>Ocyromormelitta*</i> <i>florissantella</i> Cockerell 1906 (C)	-32	Florissant (USA) 1F	Cockerell (1906); Engel (2002a); Engel and Peñalver (2006)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Hal.	Halictinae	Halictini	<i>O. * miocenica</i> (Cockerell 1909) (C)	-32	Florissant (USA)	1F	Cockerell (1909b); Engel (2002a); Engel and Peñalver (2006)
Hal.	Halictinae	Halictini	<i>O. * sorella</i> Engel 2002 (C)	-32	Florissant (USA)	1F	Engel (2002a); Engel and Peñalver (2006)
Mel.	Melittinae	Melittini	<i>Melitta willardi</i> Cockerell 1909 (C)	-32	Florissant (USA)	1F	Cockerell (1909a); Michez et al. (2007)
Meg.	Megachilinae	Anthidiini	<i>Anthidium exhumatum</i> Cockerell 1906 (C)	-32	Florissant (USA)	1M	Cockerell (1906); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Anthidiini	<i>A. scuderrii</i> Cockerell 1906 (C)	-32	Florissant (USA)	1?	Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Anthidiini	<i>Dianthidium? tertiarium</i> Cockerell 1906 (C)	-32	Florissant (USA)	1M	Cockerell (1906); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Anthidiini	<i>Lithanthidium pertriste</i> Cockerell 1911 (C)	-32	Florissant (USA)	1?	Cockerell (1911a); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Megachilini	<i>Megachile praedicta</i> Cockerell 1908 (C)	-32	Florissant (USA)	1F	Cockerell (1908b); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Megachilini	<i>Phagophytichnus</i> <i>pseudocircus</i> Sarzetti et al. 2008 (ILD)	-32	Florissant (USA)	1	Cockerell (1910); Sarzetti et al. (2008); Wedmann et al. (2009)

Meg.	Megachilinae	Osmiini	<i>Heriades bowditchi</i> 1906 (C)	Cockerell	-32	Florissant (USA)	2F	Cockerell (1906); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. halictinus</i> 1906 (C)	Cockerell	-32	Florissant (USA)	1F	Cockerell (1906); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. laminarum</i> 1906 (C)	Cockerell	-32	Florissant (USA)	1?	Cockerell (1906); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. mersatus</i> 1923 (C)	Cockerell	-32	Florissant (USA)	1?	Cockerell (1923); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. mildredae</i> 1925 (C)	Cockerell	-32	Florissant (USA)	1?	Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. priscus</i> 1917 (C)	Cockerell	-32	Florissant (USA)	1F	Cockerell (1917); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>H. saxosus</i> 1913 (C)	Cockerell	-32	Florissant (USA)	1M	Cockerell (1913a); Engel (1999c); Engel and Perkovsky (2006)
<b>Oligocene – other than Florissant shale</b>								
Apid.	Apinae	Anthophorini?	<i>Anthophora effosa</i> 1862 (C)	Heyden	Upp	Rott (Germany)	1?	Cockerell (1908c); Michez et al. (2009a)

**Table 5.1** (cont.)

Family	Subfamily	Tribe	Species (A, C) or Icnospecies (IN, ILD)	Age	Deposit locality	N	References
Apid.	Apinae	Apini	<i>Apis</i> ( <i>Synapis</i> *) <i>henshawi</i> Cockerell 1907 (C)	Upp	Rott (Germany)	1FW/5?	Cockerell (1907); Meunier (1920); Arillo et al. (1996); Engel (1998a, 1999b, 2006); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (S.)* henshawi</i> Cockerell 1907 (C)	Upp	Marseille (France)	2?	Nel et al. (1999a)
Apid.	Apinae	Apini	<i>A. (S.)* henshawi</i> Cockerell 1907 (C)	Upp	Aix-en-Provence (Fr.)	3FW/2?	Nel et al. (1999a); Engel (1998a, 1999b, 2006)
Apid.	Apinae	Apini	<i>A. (S.)* cuenoti</i> Théobald 1937 (C)	Upp	Céreste (France)	2FW/1?	Engel (1998a); Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (S.)* vetusta</i> Engel 1998 (C)	Upp	Rott (Germany)	1FW	Engel (1998a, 2006)
Apid.	Apinae	Apini	<i>Apis</i> spp. C (C)	Upp	Aix-en-Provence (Fr.)	1?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Eucerini	<i>Tetralonia berlandi</i> Théobald 1937 (C)	Upp	Céreste (France)	1?	Zeuner & Manning (1976)
Apid.	Xylocopinae	Xylocopini	<i>Xylocopa celinae</i> Nel and Petrulevicius 2003 (C)	Upp	Camoins-Is-bains1? (Fr.)		Nel and Petrulevicius (2003)
Apid.	Xylocopinae	Xylocopini	<i>X. friesei</i> Statz 1936 (C)	Upp	Rott (Germany)	1?	Nel and Petrulevicius (2003)

Hal.	Halictinae	Halictini	<i>Halictus? ruissatensis</i> Timon-David 1944 (C)	Upp	Marseilles (France)	1?	Timon-David (1944); Engel (2002a)
Hal.	Halictinae	Halictini	<i>LasioGLOSSUM celinae</i> Nel and Petrulevicius 2003 (C)	Mid	Bois d'Asson (France)	1F	Nel and Petrulevicius (2003); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>Cellicalchnus fcooides</i> (Retallack 1984) (IN)	Upp	Badlians (USA)	Num	Retallack (1984); Engel (1996); Genise (2000); Engel and Peñalver (2006)
Meg.	Megachilinae	Anthidiini	<i>Anthidium mortuum</i> (Meunier 1920) (C)	Upp	Rott (Germany)	1F	Meunier (1920); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini?	<i>Osmia? carbonum</i> Heyden 1862 (C)	Upp	Rott (Germany)	1?	Engel and Perkovsky (2006)
<b>Miocene – Dominican amber</b>							
And.	Panurginae	Protandrenini	<i>Heterosarus (Het.) eickworti</i> Rozen 1996 (A)	-19	Dominican Republic	1M	Rozen (1996)
Apid.	Apinae	Euglossini	<i>Euglossa moronei</i> Engel 1999 (A)	-19	Dominican Republic	1F	Engel (1999d)
Apid.	Apinae	Euglossini	<i>Eufriesea melissiflora</i> (Poinar 1998) (A)	-19	Dominican Republic	2F	Poinar (1998); Engel (2000)
Apid.	Apinae	Euglossini	<i>Paleoeuglossa*</i> undescribed species (A)	-19	Dominican Republic	1F?	Poinar (2010)
Apid.	Apinae	Meliponini	<i>Proplebeia* dominicana</i> (Wille and Chandler 1964) (A)	-19	Dominican Republic	>1000	Engel (2009)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Apid.	Apinae	Meliponini	<i>P.* tantilla</i> Camargo et al. 2000 (A)	-19	Dominican Republic	2M/2F	Camargo et al. (2000)
Apid.	Apinae	Meliponini	<i>P.* vetusta</i> Camargo et al. 2000 (A)	-19	Dominican Republic	3F	Camargo et al. (2000)
Col.	Xeromelissinae	Xeromelissini	<i>Chilicola</i> (Hyl.) <i>electrodominica</i> Engel 1999 (A)	-19	Dominican Republic	1F	Engel (1999a)
Col.	Xeromelissinae	Xeromelissini	<i>C. (H.) gracilis</i> Michener and Poinar 1996 (A)	-19	Dominican Republic	1M	Michener and Poinar (1996)
Hal.	Halictinae	Augochlorini	<i>Augochlora</i> ( <i>Electr.</i> ) <i>leptoloba</i> Engel 2000 (A)	-19	Dominican Republic	1F	Engel (2000a, 2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>Augochloropsis</i> sp. (A)	-19	Dominican Republic	?	Poinar (2004); Engel (2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>Neocorynura electra</i> Engel 1995 (A)	-19	Dominican Republic	1F	Engel (1995, 2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>Oligochlora</i> * ( <i>Oligochlora</i> ) <i>eickworti</i> Engel 1996 (A)	-19	Dominican Republic	1F	Engel (1996, 2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>O.* (O.) grimaldii</i> Engel 1997 (A)	-19	Dominican Republic	2F	Engel (1997, 2002a); Engel and PeñaIver (2006)



Hal.	Halictinae	Augochlorini	<i>O.* (O.) micheneri</i> Engel 1996 (A)	-19	Dominican Republic	1F	Engel (1996, 2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>O.* (O.) semirugosa</i> Engel 2009 (A)	-19	Dominican Republic	1F	Engel (2009)
Hal.	Halictinae	Augochlorini	<i>O.* (Soliapis) marquetorum</i> Engel & Rightmyer 2000 (A)	-19	Dominican Republic	2F	Engel and Rightmyer (2000); Engel (2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Augochlorini	<i>O.* (S.) rozeni</i> Engel 2000 (A)	-19	Dominican Republic	1F	Engel (2000a, 2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Caenohalictini	<i>Eickwortapis* dominicana</i> Michener and Poinar 1996 (A)	-19	Dominican Republic	1M/2F	Michener and Poinar (1996); Engel (2002a); Engel and PeñaIver (2006)
Hal.	Halictinae	Caenohalictini	<i>Nesagapostemon* moronei</i> Engel 2009 (A)	-19	Dominican Republic	1F	Engel (2009)
Meg.	Megachilinae	Megachilini	<i>Megachile (Chalicod.)</i> <i>glaesaria</i> Engel 1999 (A)	-19	Dominican Republic	1F	Engel (1999c)

#### Miocene – Other than Dominican amber

And.	Andreninae	Andrenini	<i>Andrena? primaeva</i> Cockerell 1909 (C)	Upp	Oeningen (Germany)	1?	Cockerell (1909c)
Apid.	Apinae	Anthophorini?	<i>Anthophorites* longaeva</i> Heer 1867 (C)	Low	Radoboj (Croatia)	5?	Cockerell (1909c); Zeuner and Manning (1976)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Apid.	Apinae	Anthophorini?	<i>A. mellona</i> Heer 1849 (C)	Upp	Oeningen (Germany)	3?	Heer (1849); Engel and Perkovsky (2006)
Apid.	Apinae	Anthophorini?	<i>A. thoracica</i> Heer 1867 (C)	Low	Radoboj (Croatia)	1?	Zeuner and Manning (1976)
Apid.	Apinae	Anthophorini?	<i>A. titiana</i> Heer 1849 (C)	Upp	Oeningen (Germany)	2?	Heer (1849); Cockerell (1909c)
Apid.	Apinae	Anthophorini?	<i>A. tonsa</i> Heer 1849 (C)	Upp	Oeningen (Germany)	1?	Heer (1849)
Apid.	Apinae	Anthophorini?	<i>A. veterana</i> Heer 1849 (C)	Upp	Oeningen (Germany)	2?	Heer (1849)
Apid.	Apinae	Apini	<i>Apis</i> (Caspis*) <i>armbrusteri</i> Zeuner 1931 (C)	Upp	Böttingen (Germany)	>4FW	Engel (1998a, 1999b, 2006); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (C.*) armbrusteri</i> Zeuner 1931 (C)	Low	Rubielos (Spain)	1FW	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (C.*) armbrusteri</i> Zeuner 1931 (C)	Upp	Parschlug (Austria)	2?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (C.*) armbrusteri</i> Zeuner 1931 (C)	Upp	Leida (Spain)	9?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>A. (C.*) armbrusteri</i> Zeuner 1931 (C)	Upp	Sainte-Reine (France)	2?	Nel et al. (1999a); Kotthoff et al. (2011)

Apid.	Apinae	Apini	A. (C. *) <i>armbrusteri</i> Zeuner 1931 (C)	Low	Bilina Mine (Cz. Rep.)	6?	Prokop and Nel (2003); Engel et al. (2009); Kotthoff et al. (2011)
Apid.	Apinae	Apini	A. (C. *) <i>nearctica</i> Engel et al. 2009 (C)	-14	Stewart valley (USA)	1FW	Engel et al. (2009); Kotthoff et al. (2011)
Apid.	Apinae	Apini	A. ( <i>Megapis</i> ) <i>lithothermaea</i> Engel 2006 (C)	Mid	Iki Island (Japan)	1FW	Nel et al. (1999a); Engel (2006); Kotthoff et al. (2011)
Apid.	Apinae	Apini	A. ( <i>Synapis</i> *) <i>longtibia</i> Zhang 1990 (C)	Upp	Shandong (China)	1FW	Engel (1998a, 2006)
Apid.	Apinae	Apini	A. (S. *) <i>miocenica</i> Hong 1983 (C)	Upp	Shandong (China)	4FW	Nel et al. (1999a); Engel (1998a, 2006)
Apid.	Apinae	Apini	A. (S. *) <i>petrefacta</i> (Říha 1973) (C)	Low	Kundratice (Cz. Rep.)	1FW	Nel et al. (1999a); Engel (1998a, 2006)
Apid.	Apinae	Apini	A. (S. *) <i>henshawii</i> Cockerell 1907 (C)	Low	Izarra (Spain)	1FW	Arillo et al. (1996); Engel (1998a, 1999b, 2006); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>Apis</i> "Miocene 1" (C)	Upp	Sainte-Reine (France)	3?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>Apis</i> "Miocene 1" (C)	Upp	Andance (France)	8?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Apini	<i>Apis</i> "Miocene 1" (C)	Upp	Andance (France)	2?	Nel et al. (1999a); Kotthoff et al. (2011)
Apid.	Apinae	Bombini	<i>Bombus</i> spp. (C)	Low	Bilina Mine (Cz. Rep.)	1?	Prokop and Nel (2003)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Apid.	Apinae	Bombini	<i>B. anacolus</i> Zhang et al. 1994 (C)	Upp	Shandong (China)	1F	Zhang et al. (1994)
Apid.	Apinae	Bombini	<i>B. dilectus</i> Zhang et al. 1994 (C)	Upp	Shandong (China)	1F	Prokop and Nel (2003)
Apid.	Apinae	Bombini	<i>B. luianus</i> Zhang 1990 (C)	Upp	Shandong (China)	1F	Rasnitsyn and Michener (1991)
Apid.	Apinae	Bombini	<i>B. proavus</i> Cockerell 1931 (C)	Upp	Latah (USA)	1F	Rasnitsyn and Michener (1991)
Apid.	Apinae	Bombini	<i>B. vetustus</i> Rasnitsyn and Michener 1991 (C)	Upp	Botchi river (Russia)	1M	Rasnitsyn and Michener (1991)
Apid.	Apinae	Bombini	<i>B. ? pristinus</i> Unger 1867 (C)	Low	Euboea (Greece) 1?		Rasnitsyn and Michener (1991)
Apid.	Apinae	Bombini	<i>B. ? crassipes</i> Novak 1877 (C)	Low	Krottensee (Cz. Rep.)	1?	Zeuner and Manning (1976)
Apid.	Apinae	Meliponini	<i>Meliponorytes sicula</i> Tosi 1896 (A)	-20	Sicily (Italy)	1FW	Tosi (1896); Zeuner and Manning (1976); Engel (2001a)
Apid.	Apinae	Meliponini	<i>M. succini</i> Tosi 1896 (A)	-20	Sicily (Italy)	>8	Tosi (1896); Zeuner and Manning (1976); Engel (2001a)
Apid.	Apinae	Meliponini	<i>Nogueirapis silacea</i> Wille 1959 (A)	-20	Chiapas (Mexico)	Num	Wille (1959)

Apid.	Apinae	Incerta Sedis	<i>Paraelectrobombus* patriciae</i> Nel and Petrulevicius 2003 (C)	-22,5	Bes-Konak Basin (Tu.)	1F	Nel and Petrulevicius (2003); likely a synonym of <i>Bombus</i>
Apid.	Apinae	Incerta Sedis	<i>Oligoapis* beskonakensis</i> Nel and Petrulevicius 2003 (C)	-22,5	Bes-Konak Basin (Tu.)	1FW	Nel and Petrulevicius (2003); likely a synonym of <i>Bombus</i>
Apid.	Xylocopinae	Xylocopini	<i>Xylocopa abavus</i> (Heer 1849) (C)	Upp	Oeningen (Germany)	4F	Heer (1849); Cockerell (1909c)
Apid.	Xylocopinae	Xylocopini	<i>X. diatoma</i> Zhang 1990 (C)	Upp	Shandong (China)	1F	Zhang (1990); Engel (2001b)
Apid.	Xylocopinae	Xylocopini	<i>X. hydrobiae</i> Zeuner 1938 (C)	Upp	Biebrich (Germany)	2F	Engel (2001b); Prokop and Nel (2003)
Apid.	Xylocopinae	Xylocopini	<i>X. jurinei</i> (Heer 1865) (C)	Upp	Oeningen (Germany)	2F	Cockerell (1909c); Engel (2001b)
Apid.	Xylocopinae	Xylocopini	<i>X. obata</i> Zhang et al. 1994 (C)	Upp	Shandong (China)	1F	Engel (2001b)
Apid.	Xylocopinae	Xylocopini	<i>X. senilis</i> Heer 1849 (C)	Upp	Oeningen (Germany)	8?	Heer (1849); Zeuner and Manning (1976); Engel (2001b)
Apid.	Xylocopinae	Xylocopini	<i>X. veta</i> Zhang et al. 1994 (C)	Upp	Shandong (China)	1F	Engel (2001b)
Hal.	Halictinae	Halictini	<i>Halictus petrefactus</i> Engel and Peñalver 2006 (C)	Low	Rubielos (Spain)	1F	Engel and Peñalver (2006)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Hal.	Halictinae	Halictini	<i>H. schemppi</i> (Armbuster 1938) (C)	Upp	Randeck (Germany)	4?	Engel (2002a)
Hal.	Halictinae	Halictini	<i>Halictus</i> spp. (C)	Low	Euboea (Greece)	1F	Bachmayer et al. (1971); Engel and Peñalver (2006)
Hal.	Halictinae	Incerta Sedis	<i>Halictinae</i> spp. (C)	Low	Izzara (Spain)	1?	Arillo et al. (1996)
Hal.	Incerta Sedis	Incerta Sedis	<i>Roselichnus patagonicus</i> Genise and Bown 1996 (IN)	Upp	Puesto L.S. (Argen.)	2	Genise and Bown (1996); Genise (2000); Engel and Peñalver (2006)
Hal.	Incerta Sedis	Incerta Sedis	<i>Cellicallchnus habari</i> (Thackray 1994) (IN)	Upp	Rusinga (Kenya)	?	Genise (2000)
Meg.	Lithurginae	Lithurgini	<i>Lithurgus? adamiticus</i> (Heer 1865) (C)	Upp	Oeningen (Germany)	3?	Cockerell (1909c); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachiliinae	Anthidiini	<i>Anthidium basalticum</i> Zhang 1989 (C)	Upp	Shandong (China)	1F	Zhang (1989); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachiliinae	Megachilini	<i>Megachile amaguensis</i> Cockerell 1925 (C)	Low	Kudia river (Russia)	1?	Cockerell (1925); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachiliinae	Megachilini	<i>M. shanwangae</i> Zhang 1989 (C)	Upp	Shandong (China)	1F	Zhang (1989); Engel (1999c); Engel and Perkovsky (2006)

Meg.	Megachilinae	Osmiini	<i>Osmia? antiqua</i> Heer 1849 (C)	Upp	Oeningen (Germany)	1?	Heer (1849); Cockerell (1909C); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	Osmiini	<i>O. nigra</i> Zeuner and Manning 1976 (C)	Upp	Oeningen (Germany)	2?	Zeuner and Manning (1976); Engel (1999c); Engel and Perkovsky (2006)
Meg.	Megachilinae	incertae sedis	Megachilinae spp. Indet (C)	Upp	Latah (USA)	1?	Engel (2004a); Engel and Perkovsky (2006)
Mel.	Melittinae	Macropidini	<i>Macropis basaltica</i> (Zhang 1989) (C)	Upp	Shandong (China)	1F	Zhang (1989); Michez et al. (2007)
<b>Pliocene/Pleistocene</b>							
Apid.	Apinae	Apini	<i>Apis mellifera</i> L. 1758 (Co)	Pleis	East Africa	2FW	Cockerell (1909c); Zeuner and Manning. (1976); Engel (1998a, 2001a)
Apid.	Apinae	Apini	Comb of <i>Apis cerana</i> L. (l, comb)	Pleis	Batu (Malaysia)	1	Engel (1996)
Apid.	Apinae	Meliponini	<i>Hypotrigona gribodoi</i> (Magretti 1884) (Co)	Pleis	East Africa	19?	Zeuner and Manning (1976); Engel (2001a)
Apid.	Apinae	Meliponini	<i>Liotrigona vetula</i> Moure and Camargo 1978 (Co)	Pleis	East Africa	1FW	Moure & Camargo (1978); Engel (2001a)

**Table 5.1** (cont.)

<b>Family</b>	<b>Subfamily</b>	<b>Tribe</b>	<b>Species (A, C) or Icnospecies (IN, ILD)</b>	<b>Age</b>	<b>Deposit locality</b>	<b>N</b>	<b>References</b>
Apid.	Apinae	Meliponini	<i>Meliponula erythra</i> (Schletterer 1891) (Co)	Pleis	East Africa	1FW	Zeuner and Manning (1976); Engel (2001a)
Apid.	Apinae	Meliponini	<i>Trigona iridipennis</i> Smith 1854 (Co)	Pleis	Hukong (Myanmar)	2FW	Zeuner and Manning (1976); Engel (2001a)
Apid.	Apinae	Meliponini	<i>T. lurida</i> Smith 1854 (Co)	-2,5	Santander (Colombia)	2FW	Engel (2001a)
Apid.	Apinae	Meliponini	<i>Trigonisca</i> spp. (Co)	-2,5	Santander (Colombia)	>5FW	Engel (2001a)
Apid.	Apinae	Euglossini	<i>Euglossa cotylisca</i> Hinojosa- Diaz and Engel 2007 (Co)	-2,5	Santander (Colombia)	1M	Hinojosa-Diaz and Engel (2007)
Hal.	Halictinae	Halictini	<i>Dialictus coeruleus</i> (Robertson 1893) (C)	Pleis	Lockport (USA)	Num	Miller and Morgan (1982); Engel (2002a); Nel and Petrulevicius (2003)
Hal.	Incerta Sedis	Incerta Sedis	<i>Roselichnus arabicus</i> Genise and Bown 1996 (IN)	0.28	Abu Dhabi (U.A.E.)	5	Genise and Bown (1996); Genise (2000); Engel and Peñalver (2006)
Meg.	Megachilinae	Osmiini	<i>Heriades</i> spp. (Co)	Pleis	East Africa	1?	Engel (2001a)

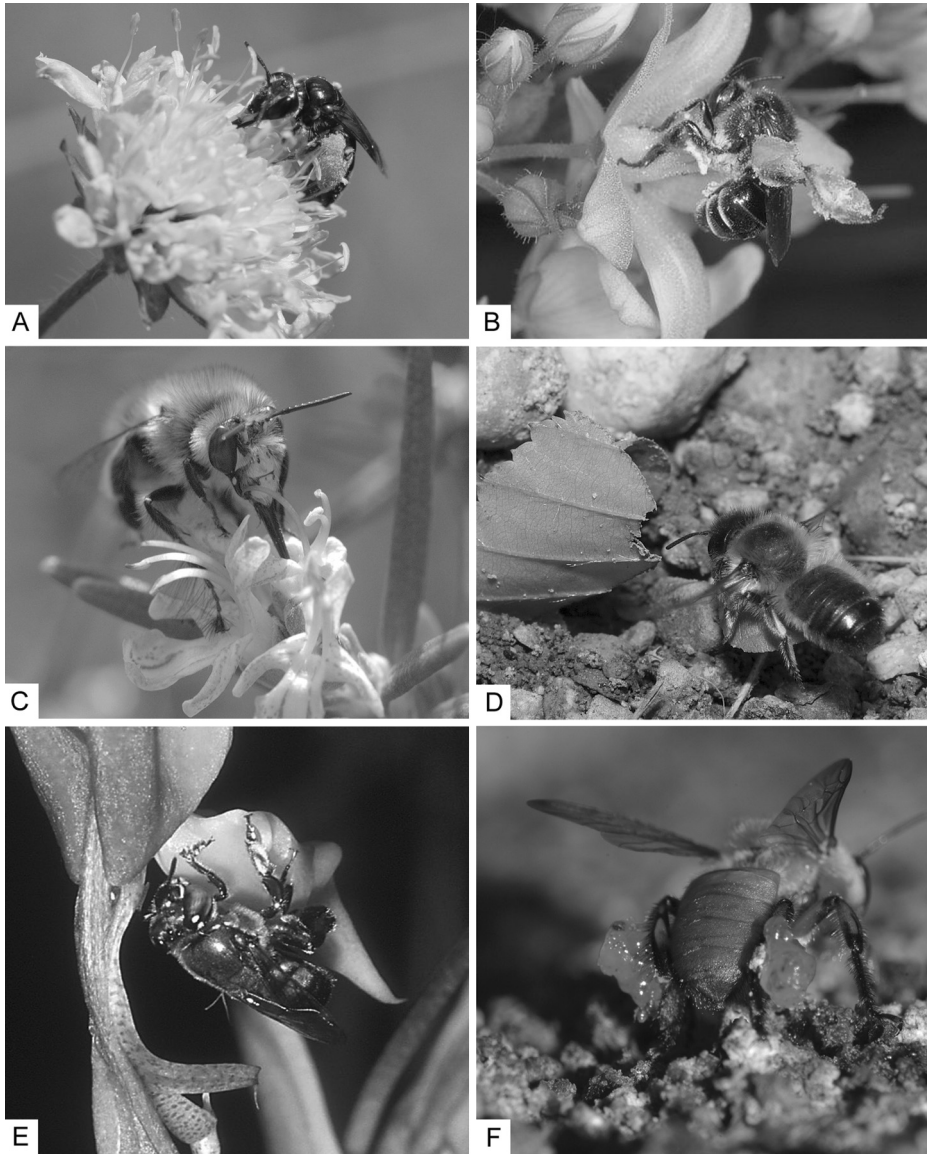


### 5.2.1 Bee adaptations

Bees forage on plants to collect various rewards: pollen, nectar, oil, perfumes, resin, and some material for nesting like pieces of leaves and petals (Fig 5.1; Wcislo and Cane 1996; Labandeira 2000; Pouvreau 2004; Michener 2007). Foraging on plant rewards is a mechanically complex activity that requires certain handling skills, which differ from species to species (Westerkamp and Claßen-Bockhoff 2007). Various foraging strategies have been described among bees mainly based on pollen foraging behavior. Some taxa display floral specificity, restricting their flower visits to closely related plant taxa (pollen specialists) while other bee species are more opportunistic, exploiting a wide range of different flowers (pollen generalists) (Roberston 1925; Westrich 1989; Müller 1996a; Cane and Sipes 2006; Müller and Kuhlmann 2008; Dötterl and Vereecken 2010). To characterize the degree of bee-host plant specialization, different terms were progressively introduced by several authors to better reflect the reality of a continuum in bee-host breadth, from extreme specialization to extreme generalization (Roberston 1925; Rasmont 1988; Cane and Sipes 2006; Müller and Kuhlmann 2008). According to Müller and Kuhlmann (2008), the three main categories are:

- (1) monolecty
- (2) oligolecty, which is differentiated into three subcategories – narrow oligolecty, broad oligolecty, and eclectic oligolecty
- (3) polylecty *sensu lato* which is also differentiated into three subcategories – polylecty with strong preference, mesolecty and polylecty *sensu stricto*.

Females have a wide range of morphological and behavioral features for collecting and transporting pollen. Although some females carry pollen internally in the crop, most exhibit external modifications and behaviors for capturing pollen, and for grooming it from their bodies and loading into scopae (*sensu* Engel 2001a, *contra* Michener 1999) for transport. Several studies have demonstrated that oligolectic species often have specific structures for gathering pollen (Thorp 1979, 2000). These highly modified morphological structures are used by bees to gather pollen that is otherwise difficult to access (Müller 2006) or of large size (Pasteels and Pasteels 1979; Thorp 1979). For example, some species possess hooked hairs on their mouthparts or forelegs to collect pollen from hidden anthers (Shinn 1967; Thorp 1979; Parker and Tepedino 1982; Houston 1990, 1991; Harder and Barrett 1993; Müller 1995; Thorp 2000). Others have additional clusters of hairs, usually on the head, to accumulate pollen from nototribic flowers (Thorp 2000). Some specialized behaviors, such as vibration of flowers (buzz pollination), are also displayed by females to enhance the uptake of pollen, especially in plants with poricidal anthers like Ericaceae or Solanaceae (Michener 1962; Macior 1986, 1995; Buchmann 1983; Houston and Thorp 1984; Gottsberger and Silberbauer-Gottsberger 1988; Neff and



**Fig 5.1** Modern bee–plant interactions. A. *Andrena hattorfiana* female foraging on pollen of *Scabiosa* sp. (Schrophulariaceae) (picture Edith Tempez). B. *Macropis europaea* female foraging on oil and pollen of *Lysimachia vulgaris* (Myrsinaceae) (picture Yvan Barbier). C. *Anthophora plumipes* male foraging on nectar of Lamiaceae (picture Jean-Marc Michalowski). D. *Megachile circumcincta* with peace of leaf for cell lining (picture Nicolas J. Vereecken). E. Male of orchid bee collecting fragrances (picture Günter Gerlach). F. Worker of stingless bee *Melipona* cf. *rufiventris* (Meliponini) carrying resin (picture Claus Rasmussen). See plate section for color version.

Simpson 1988; Proença 1992; Müller et al. 1997). These specialized morphological structures and behaviors have evolved several times independently during the evolution of bees and in widely divergent taxa of both oligolectic and polylectic forms (Thorp 2000). However, many oligolectic bees do not show any evident morphological adaptations. Oligolecty is more often based on a combination of restricted phenology and behavior rather than any particular morphology attribute (Michez et al. 2008).

Pollen is not the only source of rewards for insects. Vascular plants produce fluid rewards such as nectar and oils. Their extraction and gathering can also require morphological adaptations. The morphological feature used for nectar collection is the labiomaxillary complex that may be differentially shortened or elongated to reach nectar reserves in shallow flowers or concealed in tubular corollas (Wcislo and Cane 1996). The bee mouthparts consist of a glossa and associated clasping structures from the labium and maxillae, and represent one of the most complicated apparatuses for fluid feeding among insects (Labandeira 2000). Moreover a rich diversity of prominent morphological specializations has originated for gathering floral oils, such as conspicuous setal brushes and combs on the bee's tarsi and sometimes, abdominal sterna (Vogel 1981, 1986). One of the more amazing innovations is the elongate forelegs of some *Rediviva* species, which are used to collect oils from the twinned elongate spurs of *Diascia* flowers (Vogel and Michener 1985; Steiner and Whitehead 1990; Wcislo and Cane 1996). Morphological specializations for the processes of floral fluids are also well known in bees, particularly the collection of floral components and their transfer to male metatibial organs in orchid bees (Sakagami 1965; Vogel 1966; Whitten et al. 1989; Kimsey 1984; Cruz-Landim and Franco 2001). Such structures are not also without their independent origin elsewhere among bees, such as the metafemoral organs of Arabian *Eoanthidium*, which have a remarkably similar morphological structure and may also be used for processing of plant fragrances (Engel 2004c).

Another resource for bees is the plant itself, especially its tissues. Some bee species are closely associated with plants as a source of materials for nest construction e.g. corbiculate bees and Megachilinae (Wedmann et al. 2009). They use resins, masticated leaves, cut petals, trichomes, or other plant materials sometimes along with mud to construct nests in cavities or in the soil (Müller 2011). Females can also use plant fragments like circular excisions of leaves and petals to line their brood cells e.g. some *Megachile* s.l. species, and some Osmiini, or masticated leaves to hide the nest e.g. some *Osmia* species (Rozen et al. 2010).

### 5.2.2 Plant adaptations

As pollen plays a predominant role in plant reproductive processes, repeated returns to the same plant species not only provide advantages for the forager but

are also an inevitable prerequisite for reliable cross-pollination (Westerkamp and Claßen-Bockhoff 2007). However, the pollen grains are removed in great quantity by bees to ensure their own reproduction (as nest cell provisions for their developing brood). Moreover, the pollen-gathering efficiency can be such that all pollen is entirely removed from a flower, leaving next to nothing for pollination (Westrich 1989; Müller 1996a; Müller et al. 2006; Westerkamp and Claßen-Bockhoff 2007). For example, Schindwein et al. (2005) reported that 95.5 % of the pollen produced by flowers of *Campanula rapunculus* were collected by its oligolectic pollinators, while only 3.7 % contributed to pollination. Another study showed that among 41 bee species, 85 % required the whole pollen content of more than 30 flowers to rear a single larva. The pollen of more than 1000 flowers is needed for some species (Müller et al. 2006). After each flower visitation, the female bee carefully grooms her body and transfers the pollen grains into the scopae, making them inaccessible for pollination (Westerkamp 1996). This huge quantity of pollen withdrawn from flowers for bee reproduction conflicts with the successful pollination of the host plant, resulting in a strong rivalry. Accordingly, the ecological relationship between bees and flowers may not be merely mutualistic (Inouye 1980; Westerkamp 1996, 1997; Thorp 2000; Irwin et al. 2001) but may be better viewed as a "balanced mutual exploitation" (Westerkamp 1996) wherein flowers must continually balance the need to attract bees for pollination on the one hand, and to restrict pollen losses on the other (Praz et al. 2008). Plants must therefore minimize pollen loss by narrowing the spectrum of their pollen-feeding visitors.

Plant and flower size, color and constriction of the corolla, presence of a landing platform, quantity and quality of nectar, scent, timing of flowering as well as morphology of the reproductive system are the consequences of selective pressure imposed by particular pollinators attracted by floral rewards. Several morphological traits of flowers are currently considered adaptations to prevent excessive pollen harvesting:

- (1) heteranthery (Vogel 1993)
- (2) anther dissimulation in nototribic flowers (Müller 1996a; Houston 2000; Thorp 2000), in narrow floral tubes (Thorp 1979, 2000; Parker and Tepedino 1982; Müller 1995; Müller and Kuhlmann 2003; Neff 2004; Müller 2006) or in keel flowers (Westerkamp 1997)
- (3) concealment of pollen in poricidal anthers (Buchmann 1983; Harder and Barclay 1994)
- (4) progressive pollen release (Erbar and Leins 1995; Schindwein et al. 2005)
- (5) zygomorphy (Vamosi and Vamosi 2010).

These adaptations can also maximize the contact between the stigma and the visitors e.g. nototribic flowers. These highly specialized bee flowers are mechanically

complex, and gathering pollen from such flowers requires some force and a coordinated movement of many external bee structures. Their access is thus limited to a guild of specialized and faithful pollinators (Westerkamp 1997).

### 5.3 Palaeoecology of bees and plants

Ancient associations can be explored in two principle ways: phylogeny linked to ecology and palaeobiology linked to modern biology. Under the first, a cladogram derived from diverse data sources can be used to reconstruct ecological or behavioral attributes such as relationships with host plants, insect herbivores, degree of sociality, nest architecture, etc. (Engel 2001c; Michez et al. 2007, 2008; Sedivy et al. 2008). However phylogenetic data are not always required to shed light on past plant–insect associations. Ecological interactions can be inferred through morphological analogies with extant organisms and systems. For example, the presence of palm bugs (Heteroptera: Thaumastocoridae) and fig wasps (Hymenoptera: Agaonidae) indicates the presence of palm and fig trees, respectively (Grimaldi 1996; Peñalver et al. 2006). Similarly, the presence of orchid bee fossils in a fauna can indicate the presence of Orchidaceae even in the absence of definitive orchid fossils (Engel 1999d). This secondary approach relies on both a detailed knowledge of modern biology coupled with paleobiology, and is centered around comparisons between fossil and extant material. Evidence of past plant–insect associations consists of three distinct but linked fossil records: insect body-fossils, plant body-fossils, and trace fossils of their associations. This latter archive of associations is based on six principal types of evidence:

- (1) plant reproductive biology indicating insect association
- (2) insect-mediated plant damage
- (3) dispersed insect coprolites
- (4) insect gut contents
- (5) plant-related structure of insect mouthparts and ovipositors
- (6) taxonomic assignment to a modern descendant for which reliable ecological data exist (Labandeira 2000).

Unlike the trilobite that has left a prodigious fossil record, insects are more limited to numerous Lagerstätte and form a highly discontinuous record despite the tremendous number that could have been preserved. In many cases, the fossils are fragmentary showing few critical characters, so that studying them is often frustrating. Nonetheless, the fossil record of insects is growing and sheds considerable insight into the various phases of hexapod evolution (Grimaldi and Engel 2005). The reason for the relative scarcity of insect remains is their more infrequent

preservation in sedimentary matrix owing to various taphonomic factors, the degradation of the exoskeleton in some oxygenated environments, their diminutive proportions relative to the sediment grain size, and the generally lower number of freshwater (e.g. lacustrine) relative to marine deposits. The most notable exception is preservation in amber, which constitutes the most valuable record for insect fossils owing to its unique fidelity of preservation, with even the finest (even life-like) details faithfully conserved (Grimaldi and Engel 2005). Given that many insects were too small to escape entrapment when coming into contact with sticky plant exudates, their frequent preservation as biological inclusions is easily understood. Although amber is known from as far back as the Carboniferous, the earliest fossiliferous resins with insect inclusions date to the Early Cretaceous and about 125 megaannum. The amber record represents the last 30 % of terrestrial plant and arthropod history, and is useful for the earlier evolution of otherwise extant clades. To investigate earlier episodes of insect history, deposits with greater geochronological persistence are necessary, such as lacustrine sediments, extending into the Late Palaeozoic (Labandeira 2002b; Grimaldi and Engel 2005). The earliest evidence of pollination is provided by compression-type material but this mutualism remains difficult to demonstrate because of the very indirect nature of the evidence for plant entomophily and insect pollen transfer (Labandeira 2002b). During the Late Jurassic to Early Cretaceous, the first pollinators of early angiosperms were probably generalized insects without adaptations for flower feeding, such as wasps, moths, thrips, beetles, and flies, from other seed plants possessing flower-like structures (Gnetales, Bennettitales and cycads). More plant-dependent insects followed in later stages such as bees in the Cretaceous and butterflies in the Tertiary. Unfortunately, fossils of bees are exceptionally rare, particularly in Cretaceous deposits (Table 5.1 and following sections). The scarcity of bees can be at least partially explained by their habitat preferences (Bennett and Engel 2006). Most species live in xeric areas outside of those forests that typically produced amber, or outside of anoxic areas that produce most Lagerstätte (Michener 1979, 2007; Engel 2001a, 2004b; Grimaldi and Engel 2005). Fossil records of Apoidea are therefore too patchy to give great precision into the origin of each clade of bees. However, they are very useful for documenting minimal ages for particular clades and for studying their morphological and ecological evolution. The major deposits with bee fossils are known from the Cenozoic:

Dominican amber from the Early Miocene (~19 megaannum)

Florissant shale from the Oligocene (~34 megaannum)

Baltic amber from the middle Eocene (~45 megaannum)

These three deposits have produced the largest bee paleofaunas (Zeuner and Manning 1976; Engel 2001a, 2004b). Excluding these, only six older body fossils

have been discovered from isolated sites scattered around the world, and only two of which are from the Mesozoic era. Accordingly, plant body fossil morphology is critical for assessing the possibility of insect-mediated pollination, especially the structure of reproductive units. Many attributes in the plant fossil record have been inferred to indicate the presence of biotic pollination: accessibility and modifications of flower reproductive structures to attract insects, presence of rewards such as food, nesting material or others to lure potential pollinators, features that promote transfer of pollen or enhance certain pollination types, and the size and surface properties of pollen provide circumstantial evidence for insect pollination (Labandeira 2000, but see previous chapter).

Direct reliable trace fossils of bee–plant associations are quite rare. In many herbivorous clades, the insect-mediated plant damages are the most useful and common records of past relationships, e.g. galling, mining. But bee damages are very uncommon except for damages for nest construction. Given their interesting relationship with plants as nesting resources, the diversity of megachiline bees (*Megachile* and related genera and tribes) in past epochs can be ascertained from not only the remains of actual bee specimens but also from the record of their activities on the surrounding flora (Sarzetti et al. 2008; Wedmann et al. 2009). Such evidence may further help to expand our current understanding of the diversity of these tribes in the past, despite the usual paucity of bee specimens in the fossil records (Wedmann et al. 2009). Preservation of nesting activities is also observed for some lineages like Halictidae digging nests in the soil (described in the ichnofamily Celliformidae, for a review see Genise 2000). However, such paleoichnological data (leaf damage, fossil nests) must be carefully considered before any definitive conclusions from misidentifications become common (Engel 2001a, 2004a).

Records of pollen grains on fossil insects and in coprolites provide additional circumstantial evidence for ancient bee–flower interactions. But the presence of pollen on the fossilized body does not exclude the possibility of flower visitation without pollination. Because evidence of plant–pollinator interactions is exceedingly rare in the fossil record, our current knowledge of ancient pollination is mainly indirectly inferred from specialized morphological features of fossilized insects (Grimaldi 1999; Ramirez et al. 2007; Michez et al. 2007) and flowers (Crepet 1979; Crepet et al. 1991; Gandolfo et al. 2004).

## 5.4 The “proto-bee” and the Cretaceous record of bees

### 5.4.1 The “proto-bee”

Hypotheses about the origin of the first bee are based on (i) the oldest bee fossil records, (ii) the origin and fossil record of their closest relatives (Crabronidae,

spheciform Apoidea), and (iii) the origin of their likely host plants (Angiosperm). While the oldest spheciforms are those species of *Angarosphex* from the Barremian of Brazil's Crato Formation (~125–130 megaannum) and other Early Cretaceous deposits (Grimaldi and Engel 2005), the putative sister group of bees, Crabronidae, are not known until the Early mid Cretaceous (Antropov 2000; Bennett and Engel 2006). The diversification of spheciform Apoidea occurred during the Early Cretaceous (Grimaldi and Engel 2005; Bennett and Engel 2006) (Fig 5.2). Based on the record of fossil Crabronidae (Antropov 2000; Bennett and Engel 2006) and these other factors, a rational timing supposes the origin of bees around the Early mid Cretaceous, or about 125–120 megaannum (Engel 2001a, 2004b, 2011; Grimaldi and Engel 2005; Ohl and Engel 2007). The oldest bee trace is from the Cenomanian of Arizona (94 megaannum), although *Cellicalichnus dakotensis* is quite contemporary in its form (Table 5.1, Elliott and Nations 1998). The descriptions of fossil bee nests from the Triassic were incorrect (Lucas et al. 2010). Angiosperms are hypothesized as having first originated in the xeric interior of Gondwanaland and during the earliest Cretaceous (Raven and Axelrod 1974; Taylor and Hickey 1992), and this is likely also where bees first diverged from their common ancestor with Crabronidae (Engel 2001a, 2004b). In summary, bees likely diverged from among the apoid wasps sometime in the late Early Cretaceous and in the Southern Hemisphere (Engel 2001a, 2004b; Grimaldi and Engel 2005). Molecular phylogenies of Apidae and Halictidae associated with estimates of divergence times support this conclusion and also that bee diversification took place during the Early mid Cretaceous (Danforth et al. 2004; Cardinal et al. 2010; Ware et al. 2010).

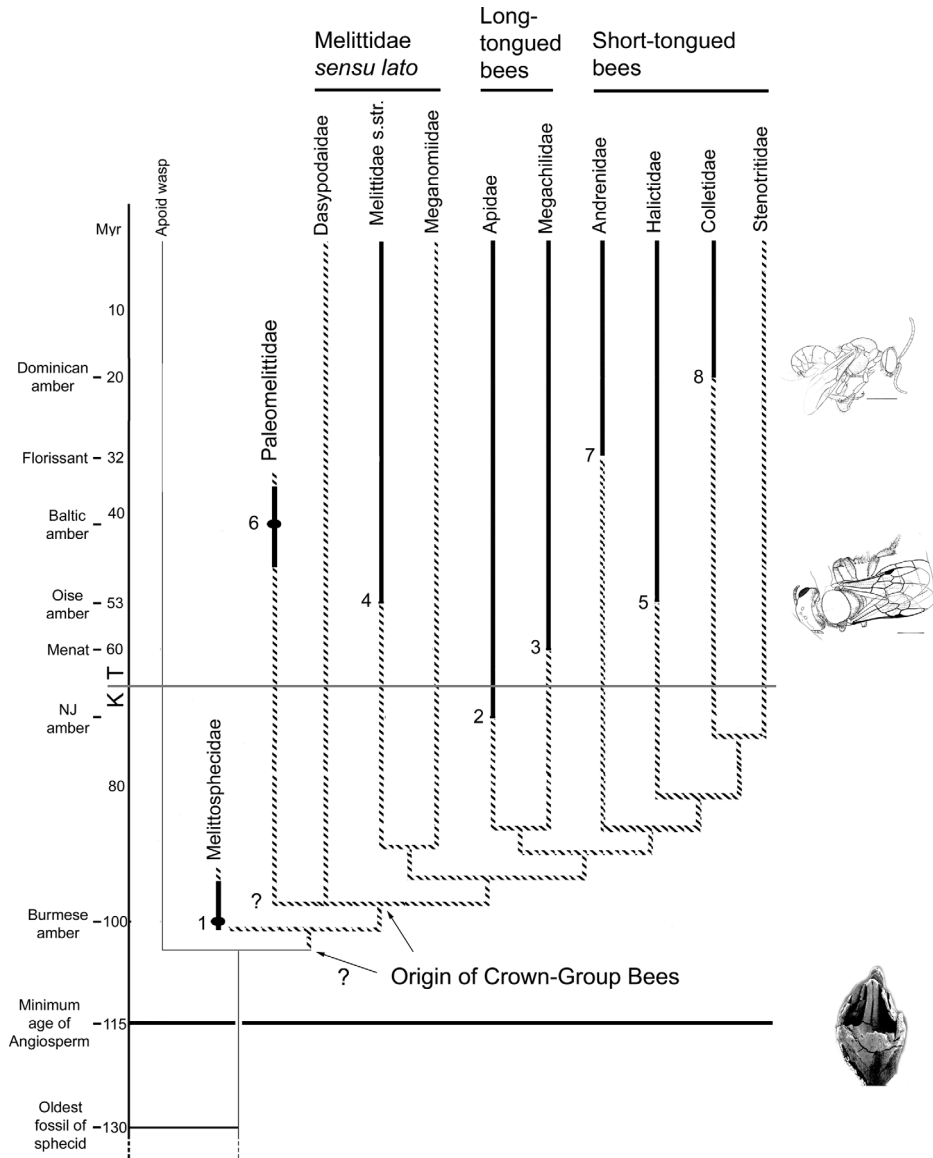
#### 5.4.2 From carnivorous predator to phytophagous pollen forager

Pollen consumption has generally been the evolutionary precursor to pollination (Labandeira 1998). Pollen contains vitamins, starch, lipids, proteins, and amino acids, which provide nutritional requirements for most animal species (Roulston and Cane 2000). Apoid wasps have a predatory diet high in protein. The protein value of pollen is high enough for apoid wasp nutritional requirements, ranging from 12–60 % (Roulston et al. 2000). They also assimilate cholesterol from their prey, and some pollen contains equivalent sterols (Dötterl and Vereecken 2010). Moreover, several bodies of evidence suggest that apoid wasps already displayed attributes suitable to becoming pollen consumers and foragers, as well as pollinators of angiosperms.

Apoid wasps existed and diversified when the first angiosperms appeared. The niche of pollen food was probably not yet overexploited when some spheciforms initially diverged to become bees.

Apoid wasps had mandibulate mouthparts more suitable for chewing pollen than piercing–sucking mouthparts (Crepet 1979).





**Fig 5.2** Hypotheses of bee evolution according to Danforth et al. (2006) with bee fossils mapped on. For an alternative interpretation, refer to Engel (2004b) and Ohl and Engel (2007). 1. *Melittosphecius burmensis*. 2. *Cretotrigona prisca*. 3. *Probombus hirsutus*. 4. *Paleomacropis eocenicus*. 5. *Halictus? savenyei*. 6. *Paleomelitta nigripennis*. 7. *Andrena? clavula*. 8. *Chilicola electrodominica*. Drawings from the top to the bottom: *Proplebeia dominicana* (from Camargo et al. 2000; scale = 1mm); *Paleomacropis eocenicus* (from Michez et al. 2007; scale = 1mm); *Divisestylus brevistamineus* (from Crepet et al. 2004).

Apoid wasps flew very well and are good at hovering, allowing them to forage rapidly on many flowers.

Apoid wasps constructed nests and transported food (arthropod prey) to feed their offspring. They were then able to substitute prey transport for pollen transport.

Plumose setae, often integral in pollen-collecting structures, may have been present in spheciforms before subsequent cooption of their original function. For example, plumose setae were likely originally used for thermoregulation (Heinrich 1996).

Plesiomorphically apoid wasps, like most aculeate Hymenoptera, are cold-blooded and live mainly in hot xeric climates. Plumose setae are useful for capturing heat and permitting the body to warm up more quickly after the torpor of cold desert nights. This character would have appeared randomly and could be considered an exaptation. Much like the origin of feathers among theropod dinosaurs for thermoregulation prior to their eventual use in flight by their descendents – the birds, so too, does it appear that branched hairs may have predated pollen collection and even bees, representing an earlier evolutionary solution to a completely different problem.

Ancestral specialist behavior could have been a key feature allowing the proto-bee to promote fixation of its new foraging behavior i.e. pollen foraging. Indeed, a bee's foraging behavior exhibits particular constraints:

pollen-collecting behavior is very complex (Wcislo and Cane 1996) and proto-bees could have been cognitively limited to use a large range of hosts

bees invest strongly in their offspring. Females of bees lay only a few eggs and generalist risk-takers could have been selected against. Many pollen contents could have been unsuitable for adult and larval feeding (Praz et al. 2008).

host perception seems more complex than in other phytophagous insects. Bees detect color, shape, size and scent of flowers (Raine et al. 2006).

specialization can increase the selection of pollen-foraging efficiency (Strickler 1979).

All these characteristics have probably forced the specialization and its inheritance.

Although there does exist some clear examples of transitions from polylecty to oligolecty, growing evidence suggests that oligolecty might be the ancestral state in bees (Danforth et al. 2006). Firstly, many generalist bee species have evolved from oligolectic ancestors. For example, in several anthidiine bees as well as in pollen-collecting masarine wasps, polylecty appears to be a derived trait (Müller 1996b; Mauss et al. 2006). In the genus *Andrena*, oligolecty is also assumed

to be the plesiomorphic condition and polylecty has evolved independently several times (Larkin et al. 2008). Shifts from oligolecty to polylecty are more frequent than the reverse (Müller 1996b; Michez et al. 2008). Secondly, basal clades of most bee lineages such as Dasypodainae, Melittinae, Fideiinae, Rophitinae etc. include a high proportion of oligolectes (McGinley and Rozen 1987; Westrich 1989; Wcliso and Cane 1996; Engel 2004d; Danforth et al. 2006; Patiny et al. 2008; Michez et al. 2008). These facts could be a hint that, in general, polylecty is a derived foraging strategy that has evolved multiple times among bees. Plant associations mapped across bee phylogenies have only recently begun to become more and more prominent in studies (Müller 1996b; Engel 2002b, 2004d; Michez et al. 2008; Sedivy et al. 2008) so the body of evidence for this is continuing to grow but it does appear that the Danforth et al. (2006) hypothesis of polarity is widely supported.

Once foraging behaviors took place and larvae were able to digest the pollen as protein and lipid resources, it was perhaps not long before pollen foraging became a significant advantage for survival. Searching for regularly and conspicuously displayed pollen rewards would have been easier than seeking and subduing mobile prey, which generally tried to conceal itself (Engel 2001a, 2004b). Under this scenario, strong selective pressures would quickly stabilize any lineage toward becoming “bees”.

#### **5.4.3 To bee or not to bee? Burmese amber and the conceptual challenge of stem groups**

The report of the Burmese amber apoid, *Melittosphex*, is an immensely interesting and important contribution to the fossil history of the superfamily, alongside the detailed monographic treatment of Antropov (2000). This particular fossil was introduced with much fanfare and bravado as the “oldest fossil bee.” However, several conceptual challenges make it difficult to determine whether this species truly provisioned its nests with pollen and nectar, and that its larva was an obligate consumer of such resources. As noted many times before, bees are those ecologically dominant, apoid wasps that, as adults, collect pollen and nectar for exclusive consumption by their larvae. Accordingly, any lineage after the evolutionary novelty of obligate pollen-feeding larvae is a bee, while any lineage diverging before this is not. Thus, is this fossil species actually a bee, or rather a predatory apoid wasp sister to bees? This is not a specific criticism of *Melittosphex* but instead a philosophical question highlighting the difficulty of identifying any true, stem-group bee. At what point must we accept ignorance as our answer rather than a definitive attribution to the ecological clade we recognize as bees? As noted by Ohl and Engel (2007), it would appear that in order to make *Melittosphex* a bee, the definition of “bee” has to be set on a restricted set of features, expanding “bees” to include organisms that may or may not actually

perform the ecological role that has made the group so very famous – namely, their mutualistic association with flowering plants. Rather than the traditional concept of bees as essentially vegetarian derivatives of the apoid wasps, that is, adults collecting pollen and nectar which are then consumed by the larvae (features entirely unknown for the fossil), the attribution as a “bee” is based solely on branched hairs and a slightly enlarged hind tarsal article, rather than positive evidence of pollen feeding. Thus, *Melittosphex*, which may have been predatory like other wasps, is accorded bee status simply by its close relation to actual bees rather than for an exhibition of true bee-like habits or ecology. The assertion that branched-hairs automatically indicates pollen collection is erroneous as some predatory wasps, such as sapygids, have identical hairs while masarine wasps and a crabronid wasp (*Krombeinictus*) lack them, yet successfully collect and provision pollen. Moreover, some bees, like hylaeines and euryglossines, effectively lack such plumose hairs and transport pollen in the crop (Michener 1965, 2007; Torchio 1984). The only available specimen of *Melittosphex* is a poorly preserved male, the sex that does not collect pollen and provision if it was a bee, and so any pollen (if actually present) on its body must be incidental, just as occurs on many specimens of male and female apoid wasps. Male and female apoid wasps are often captured with pollen on their bodies since they visit flowers to consume nectar, but they do not store pollen or feed the pollen to their larvae (otherwise they would be no different from bees). There is no evidence that *Melittosphex* provisioned its brood cells with pollen. Naturally, this is an issue with all stem-group fossils and begs the question as to at what point we arbitrarily decide what is and what is not a “bee” (Ohl and Engel 2007). Interestingly, this trap with regard to Cretaceous, stem-group Anthophila was predicted by Engel (2001a, p. 155–8), and this represents a critical conceptual and practical challenge to the designation of any stem-group Anthophila as being “bees” rather than predatory wasps. In our estimation, the sole feature that distinguishes a bee from the wasps they evolved from is the specialization of the larva for consumption of a mixture of pollen, nectar, and/or floral oils; and the subsequent morphological adaptation of the female to provision the larva, otherwise they are merely anatomically peculiar wasps. Thus, in the absence of data on larval feeding (including features of the female conclusively associated with provisioning the larva with such resources), any fossil with a placement outside of the crown-group clade of true bees must be considered for what it truly is ... merely an apoid wasp that resembles and is allied to bees, and which may or may not be a “bee.” From a conservative epistemological position, we cannot deem any stem group as a “bee” without such positive evidence and must remain agnostic as to their biological/ecological identity.

Regardless of these challenges, Burmese amber is dated as to near the Albian–Cenomanian boundary (~100 megaannum) (Grimaldi et al. 2002; Cruickshank

and Ko 2003; Ross et al. 2010). Grimaldi et al. (2002) consider that the environment was tropical within an average temperature range of 32–55 °C. Ross et al. (2010) listed arthropod records of 36 orders, 216 families, and 228 species, mainly Diptera, Coleoptera and Hymenoptera. *Melittosphex burmensis* from these deposits has been placed in the monospecific family Melittosphecidae, apparently sharing only some synapomorphies with contemporary bees (Poinar and Danforth 2006). Branched hairs are putatively present on the body which, as mentioned, the authors use as a proxy for indicating pollen foraging behavior, but the only known specimen is a male and so this is a speculative conclusion. Nonetheless, the small size of *M. burmensis*, at around 3 mm, is consistent with the small size of contemporary angiosperms (Poinar and Danforth 2006; Crepet et al. 2004). Further exploration of mid Cretaceous deposits in Myanmar and elsewhere will hopefully bring evidence to more positively resolve the identity of this and any other stem-group Anthophila.

#### 5.4.4 Raritan amber: the first definitive bee remains

Raritan amber occurs throughout Cretaceous outcrops of the Atlantic Coastal Plain of eastern North America and is Turonian (~90 megaannum) in age (Grimaldi et al. 2000; Grimaldi and Nascimbene 2010). Origin of the amber is now understood to be from the Cupressaceae. The paleohabitat was an inter-distributary system of shallow, brackish water channels that formed a delta in the mid to Late Cretaceous (Grimaldi and Nascimbene 2010). The proximity of freshwater is indicated by the diversity of adult insects that breed in freshwater such as Trichoptera. All indications are that New Jersey was at this time tropical or subtropical in climate and that angiosperms comprised a substantial part of the flora. Based on macrofossils and pollen analyses, there were more than 130 angiosperm taxa, including some entomophilous lineages like Clusiaceae, Ericales, Lauraceae, Palmae and Protaceae (Michener and Grimaldi 1988a). There is a total of 104 described species and 59 families of arthropods (Grimaldi and Nascimbene 2010). Only one bee fossil is described from these deposits, *Cretotrigona prisca* (Michener and Grimaldi 1988a, 1988b; Engel 2000b; but see Rasnitsyn and Michener 1991). This species is included in a derived taxon of the corbiculate Apinae – the Meliponini. This tribe includes extant eusocial species showing polylectic and resin-foraging behaviors. The presence of a corbicula indicates that *C. prisca* likely shared the same foraging and carrying behavior as its modern meliponine counterparts. Specific relationships to any plant family described from the deposit is unlikely as *C. prisca* would have been a generalist pollinator of many entomophilous taxa, like its modern relatives. Nonetheless, *C. prisca* demonstrates that bees with highly modified and specialized structures were already well-established by the Late Cretaceous.

## 5.5 Paleocene and Eocene bee fossils

### 5.5.1 Paleocene and Eocene characteristics

The Cenozoic began with the Paleocene epoch (65–55 megaannum) and was one of the warmest periods in Earth’s history. At this time, “tropical” lineages were nearly ubiquitous in geographic distribution (Grimaldi and Engel 2005). Europe was composed of multiple land masses and archipelagos separated from Asia by an epicontinental seaway (Turgai Strait). Southern Europe bordered the northwestern bays of the Tethys Ocean, which later formed the Mediterranean Sea to its west. North America was also crossed by a deep sea and India was still isolated from the other continents. Climatically, the Eocene (55–38 megaannum) was the most dramatic episode in the Tertiary. During the Early Eocene, no large, standing regions of ice were present, even at the poles, but by the end of this epoch, the glaciation of Antarctica had begun. This global cooling had a critical impact on the global distributions of many plants and animals, including bees. There are presently thirteen documented deposits with bee fossils from the Paleocene and Eocene: Menat (-60 megaannum, France), Oise (-53 megaannum, France), Quilchena (-53 megaannum, Canada), Cambay (-52 megaannum, India), Messel/Eckfel (-49/-44 megaannum, Germany), MacBee/Republic (-49 megaannum, Canada/USA), Baltic region (-48/-45 megaannum, northern Europe), Rovno (-48/-45 megaannum, Ukraine), Rio Pichi-Leufú (-48 megaannum, Argentina), Puryear/Viola (middle Eocene, USA). Four contemporary bee families (Apidae, Halictidae, Melittidae and Megachilidae) and one extinct family (Paleomelittidae) have been described from these deposits based on 51 species and 178 body fossils specimens. It appears that the K/T transition had little effect on bee diversity at a higher level, although certainly those bees in the zones of the various extraterrestrial impacts would have been considerably effected, leading to perhaps localized extinctions of particular faunal elements but without global alterations of the families or subfamilies of Apoidea. However, the global cooling at the end of the Eocene, a noted period of mass extinction (Eocene–Oligocene transition), probably caused the extinction of many corbiculate lineages principally known from Baltic amber (Engel 2001c), as well as from Cambay amber (Rust et al. 2010; Engel, unpublished data).

### 5.5.2 Menat, France: an ancient “bee community”

The Menat deposit is of primary importance because it is the oldest deposit with more than one isolated bee fossil and it is the only one presently with such material from the Paleocene. Two fossils of long-tongued bees, *Probombus hirsutus* (Megachilidae) and *Paleohabropoda oudardi* (Apidae) and one ichnospecies have been described from this deposit (Table 5.1). These taxa probably lived in a wet and very warm climate. The area of Menat (~60 megaannum) was likely characterized by a forest of oak and willow trees distributed around a crater

lake (Piton 1940). The fauna comprized crocodiles, numerous large Mantodea (Chaeteessidae), Blattodea, Coleoptera (Buprestidae and Cerambycidae), Odonata (Megapodagrionidae) and very diverse Hemiptera (Fulgoroidea); all indicative of a warm palaeoclimate and a forest palaeoenvironment (Piton 1940; Nel and Roy 1996; Nel et al. 1997). *Paleohabropoda oudardi* was included in the Anthophorini, an old lineage where polylectic species are dominant (Iuga 1958; Michez et al. 2009a; Cardinal et al. 2010). Thus, association with a particular pollen host is unlikely. The presence of Megachilidae is more informative about potential host-plant associations. The description of one typical *Megachile* excision on a willow leaf could indicate a potential association between Megachilidae and Salicaceae at this time (Wedmann et al. 2009). Salicaceae could have been as an important a pollen resource for these fossil species as willow pollen is today for contemporary spring bees in Europe (Westrich 1989).

### **5.5.3 Cambay Basin, India: Early Eocene bees from an “isolated” subcontinent**

Recently abundant Ypresian-aged amber has been discovered and reported on from the Cambay Basin in western India (Rust et al. 2010). This amber is rich in biological inclusions and comes from a time almost immediately before the complete connection of the Indian subcontinent with Asia when the subcontinent was still separated from Asia by oceanic waters and connecting archipelagos. This amber is of dipterocarp origin and is quite chemically distinctive (Rust et al. 2010). Interestingly, while work has only just begun on these deposits, four bee specimens are already known from such a limited sampling of inclusions (Rust et al. 2010; Engel, unpublished data). What is more interesting, is that the available material is representative of taxa otherwise known in Baltic amber, including a large fragmentary electrapine (perhaps of the genus *Protobombus*) and three melikertines of perhaps two distinct species. These are all eusocial lineages of corbiculate Apinae (Engel 2001a), and as such were likely polylectic and resin-collecting. Indeed, given the abundance of dipterocarps in this forest, it is highly probable that these species visited Dipterocarpaceae among other plant families for numerous resources including resins for nest construction. Given the immensity of the Cambay amber deposits (Rust et al. 2010), the potential for critical insights into Paleogene bees from a biogeographically and floristically distinct region is considerable.

### **5.5.4 Oise, France: early oil-collecting bees**

Until relatively recently, fossil resins were poorly known from France (Nel and Brasero 2010). The situation changed dramatically after the discovery of an important 53 megaannum amber deposit in the department of Oise (Nel et al. 1999b). The dominance of an arborescent amber-producing species and the presence of freshwater in the French Eocene environs suggest a semi-deciduous forest

with a mosaic of gallery-forest mixed with dryer plant communities, in a deltaic paratropical region (De Franceschi and De Ploëg 2003). The amber-producing tree was deduced as *Aulacoxylon sparnacense* (Combretaceae or Fabaceae-Caesalpinaceae). Brasero et al. (2009) provided an inventory of insects already described from the Oise deposit, with 59 families and 78 species, among them one female bee of *Paleomacropis eocenicus* (Melittidae, Macropidini) (Michez et al. 2007). *Paleomacropis eocenicus* was characterized by dense plumose setae on the inner and outer surfaces of the mesobasitarsus and long, erect setae on the metasoma. These kinds of setae could be linked to the collection of oil and pollen, as in the contemporary oil-collecting bee genus *Macropis*. Indeed, the oil of *Lysimachia* flowers (Primulaceae) is harvested by *Macropis* females using specialized setae on the inner surface of their pro- and mesobasitarsi (Vogel 1976; Cane et al. 1983; Michez and Patiny 2005). Moreover, dry pollen is initially held at the same time by the simple, long, erect setae of the metasomal sterna (Cane et al. 1983). Based on molecular clock analyses, the stem of *Lysimachia* was dated to around 41 megannum (28–52 megannum) (Renner and Schaeffer 2010). The plausible temporal coincidence between *Paleomacropis* and proto-*Lysimachia* could support the notion that *Macropis* and *Lysimachia* coevolved from the onset, even if the oldest fossil record of *Lysimachia* consists of fossil seeds from late mid Miocene of Jutland, Denmark (Hao et al. 2004). Other plant families producing oil, like Malpighiaceae (Davis et al. 2002), are known from the Eocene and could have been alternative host plants for *Paleomacropis eocenicus*.

### 5.5.5 Baltic amber: a diverse and abundant paleofauna for bees

Baltic amber represents the most diverse paleofauna and paleoflora described in the world (Weitschat and Wichard 2010). The dating of this deposit was debated for a long time, but today most evidence support Baltic amber as either middle Eocene (~45 megannum) or late mid Eocene to Early Eocene (48–50 megannum). The source plant of the amber has also been debated, with evidence supporting either a Pinaceae producer (based on inclusions such as wood remains, male cones and needles) or Sciadopityaceae (based on FTIR chemotaxonomic inferences) (Engel 2001a; Wolfe et al. 2009). The palaeohabitat was probably very similar to contemporary pine forests of the South Atlantic Coastal Plain of North America (from North Carolina to Florida). At lower elevations the amber forest was adapted to paratropical climates (savannah woods) with a population of conifer and palm trees. Moreover, the forest must have had lightly wooded areas with various different habitat types (Weitschat and Wichard 2010). Among plant inclusions, branched epidermal trichomes of oak tree leaves and flower buds are very common. With more than 98 % of all embedded animal inclusions, the Arthropoda are most frequently represented in Baltic amber. Weitschat and Wichard (2010) listed 539 families including 1535 genera and 3068 species. Engel (2001a) listed



36 species and 18 genera of bees, with one species of *Ctenoplectrella* subsequently added (Engel 2008). These descriptions were based on 160 specimens (Table 5.1), although even more are known in collections today, which represent the second most important and abundant deposit for bee body fossils after Dominican amber. Only four specimens, representing three species, are short-tongued bees; perhaps not surprising as most are not resin collectors, typically nest in the soil, and are often more diverse in xeric habitats. Most are long-tongued taxa of the Apidae or Megachilidae, and all are known from females except *Ctenoplectrella viridiceps*, where both sexes are known. All species from Baltic amber exhibit morphological structures for pollen collection:

- a corbicula for those Electrapini, Electrobombini, Melikertini and Meliponini
- a metasomal scopa for those Ctenoplectrellini, Glyptapini and Prolithurgini
- a hind leg scopa for those Boreallodapini, Halictini, Macropidini and Paleomelittidae.

Based on comparisons with extant taxa, the eusocial species (Electrapini, Electrobombini, Melikertini), the solitary Xylocopinae (Boreallodapini) and Halictini from Baltic amber were probably polylectic while *Eomacropis* could have been oligolectic as modern Melittidae (Michez et al. 2008). Engel (2001a) describes *Eomacropis* without any particular morphological adaptation to collect oil as the actual *Macropis* do, but the unusual long glossa of the female could have been a particular adaptation to a special host plant. Just as extant polylectic taxa are dominant in tropical and subtropical regions (Michener 1979), so too were these groups apparently dominant in number and diversity during the middle Eocene of Europe (Engel 2001a, 2004b; Wappler and Engel 2003).

## 5.6 Oligocene bee fossils

### 5.6.1 Oligocene characteristics

The Eocene–Oligocene transition is a well-documented episode of climate change and extinction. Average global temperature dropped from near 22 °C to 12 °C. Many lineages of corbiculate bees disappeared during this global cooling event (Engel 2001c), and it appears that the bee fauna underwent a considerable shift around this time, from principally ancient lineages to largely modern forms (Engel 2004b). Eight deposits with bee remains or traces have been documented: Florissant (-34 megaannum, USA), Badlands (Upper Oligocene, USA), the French deposits of Aix-en-Provence, Bois d'Asson, Camoins-les-Bains, Céreste and Marseille (Middle to Upper Oligocene, France), and Rott (Upper Oligocene, Germany). Total material represents 62 body fossil specimens, 47 species, and two ichnospecies. All extant

families are present in these faunas with the exception of Stenotritidae, for which there is no fossil record, and all are preserved as compressions with little to no relief, particularly those from the diverse and prolific Florissant deposits of Colorado.

### **5.6.2 Florissant, Colorado: glimpses into the first “modern” bee fauna**

Fossils from Florissant, Colorado, USA are compressions with low to no relief, formed in fine volcanic ash (Engel 2001a). This deposit is dated about 34 megaannum (Epis and Chapin 1974). The extant bee families represented in the Baltic amber (Apidae, Halictidae, Melittidae and Megachilidae) have also been described from this deposit with the addition of Andrenidae. Engel (2002a) revised the Florissant fauna of Halictidae, but the primary information for this fauna comes from the publications of T. D. A. Cockerell and is quite dated (see list in Table 5.1). Even if numerous and diverse taxa are present in the deposit – at least 36 body fossils, 34 species, 19 genera (Table 5.1) – body fossils are typically preserved only by wing venation or some structures of the legs and thorax, so accurate comparisons with living species as well as other fossil deposits are not entirely possible. Some attributions of species to extant genera are quite speculative and some, such as *Ceratina disrupta*, may be assignable only to Apoidea or even Aculeata incertae sedis. Furthermore, morphological structures associated with pollen collection are not discernible in the available material except under uncommon circumstances. Some species considered as cleptoparasites, based on the apparent absence of setae patches recognizable as scopae, need confirmation (e.g. *Protomelecta brevipennis*) and may represent poor preservation rather than definitive absence.

## **5.7 Neogene and quaternary bee fossils**

### **5.7.1 Neogene and quaternary characteristics**

The Neogene began 23.8 megaannum ago with the Miocene epoch. Climatic conditions were similar to the end of the Oligocene. As far as known, bee body fossils or traces have been described from 27 Miocene deposits: Bes-Konak Basin (22.5 megaannum, Turkey), Dominican amber (20 megaannum, Dominican Republic), Mexican amber (20 megaannum, Mexico), Sicilian amber (20 megaannum, Italy), Stewart valley (-14 megaannum, USA), Bilina Mine (Lower Miocene (LM), Czech Republic), Euboea (LM, Greece), Izarra (LM, Spain), Krottensee (LM, Czech Republic), Kudia River (LM, Russia), Kundratice (LM, Czech Republic), Radoboj (LM, Croatia), Rubielos (LM, Spain), Iki Island (Middle Miocene, Japan), Andance (Upper Miocene (UM), France), Biebrich (UM, Germany), Botchi river (UM, Russia), Böttingen (UM, Germany), Latah (UM, USA), Lleida (UM, Spain), Oeningen (UM, Germany), Parschlug (UM, Austria), Puesto Los Sauces (UM, Argentina), Randeck

(UM, Germany), Rusinga (UM, Kenya), Sainte-Reine (UM, France), Shandong (UM, China); and six Pliocene/Pleistocene deposits: Santander (2.5 megaannum, Colombia), Abu Dhabi (0.28 megaannum, UAE), Batu (Pleistocene, Malaysia), Eastern African copal (Pleistocene), Hukong (Pleistocene, Myanmar), Lockport (Pleistocene, USA). Based on the description of 84 species and 5 ichnospecies, all extant families are present except Stenotritidae with no described fossil at all (Table 5.1). The bee fauna is clearly modern in the Miocene deposits. As most of described species from Copal still exist, evolutionary significance of the Pliocene and Pleistocene concerns the origins of modern species.

### 5.7.2 Dominican and Mexican amber: the most recent paleofauna of bees

Dominican amber has been dated as Burdigalian in age (between  $20.43 \pm 0.05$  megaannum and  $15.97 \pm 0.05$  megaannum), the first and longest warming period of the Miocene (Poinar 2010). Dominican amber preserves the most diverse described bee fauna among Miocene deposits. All bee families have been recorded with the exception of Melittidae *s.l.* and Stenotritidae (Engel 2009). Among the twelve-recorded genera, only three genera (*Augochlora*, *Euglossa* and *Megachile*) are still present in the Greater Antilles, but only four are now extinct at a global scale (*Eickwortapis*, *Nesagapostemon*, *Oligochlora* and *Proplebeia*), although with close relatives among Central and South American taxa. The absence of Melittidae and Stenotritidae in Dominican amber is expected as they are also absent today in Central and South America (Michener 2007; Michez et al. 2009b; Almeida and Danforth 2009). The bee fauna preserved in Dominican amber is largely equivalent to the modern Neotropical fauna, and quite distinct from those of Asia, Europe, and Africa. Mexican amber is roughly contemporaneous age and similarly harbors an abundant bee fauna, albeit mostly representing a single species, *Nogueirapis silacea* (Solórzano-Kraemer 2007).

Apidae are the most numerous in number of specimens (among the thousands) but only five species have been described (Table 5.1; Poinar 1998; Camargo et al. 2000; Engel 2009). All described apids that were probably resin collectors, but the high number of apine specimens is truly due to only one eusocial species, *Proplebeia dominicana*. Presence of foraged resin on the corbiculae of some specimens is indirect evidence that *Proplebeia* species routinely and actively gathered resin from extinct *Hymenaea* (Fabaceae, resin source of Dominican amber) (Camargo et al. 2000). Moreover, one specimen was described with an attached pollinium of *Meliorchis caribea* (Orchidaceae) (Ramirez et al. 2007). This fossil constitutes a rare, direct observation of plant–pollinator interaction. Moreover, as the staminal filaments are fused to the style in the Orchidaceae, the anatomical match required for a pollinator to remove the pollinium is nearly identical to that necessary for its subsequent delivery (Ramirez et al. 2007). *Proplebeia dominicana* was therefore probably a pollinator

of *Meliorchis caribea*. But pollinia do not constitute an alimentary resource for stingless bee workers. Visitors of orchids forage on nectar or fragrances. But orchids can also deceive their visitors by not producing rewards and only mimicking alternative alimentary rewards of neighboring host plants (Vereecken and McNeil 2010). As *M. caribea* is included in the subtribe Goodyerinae, the fossil species probably offered nectar similar to some modern species of this tribe (Singer and Sazima 2001). Two other fossils probably foraged on Orchidaceae during the Miocene, *Euglossa moro- nei* and *Eufriesea melissiflora* (Engel 1999d). These bees are orchid bees (Euglossini) where the males of contemporary species mainly forage on orchids to collect fragrances (Dressler 1982; Michener 2007; Ramirez 2009). However, *M. caribea* is not a good candidate as a fragrance host plant for euglossines since Goodyerinae do not produce suitable scents. Euglossini instead are mainly associated with the orchid taxa Gongoreae, Catasetinae, Zygopetallinae, Lycastinae, Bifrenariinae and Oncidiinae (Dressler 1982).

In their degree of pollen specialization, all apid lineages described from Dominican amber are polylectic clades (Dressler 1982; Michener 2007). Among short-tongued bees, Halictidae are the most diverse with 11 species but known from only 13 specimens. The rarity of halictids in the Dominican amber record may be partly due to the fact that most species nest in the ground and do not collect resin as other bees, thus making contact and preservation unlikely. This is also true for the sole panurgine (Andrenidae) in Dominican amber (Rozen 1996). Although Panurginae are greatly oligolectic, the Anthemurgini show little diversification in such behavior.

## 5.8 General conclusion

### 5.8.1 Bee fossil diversity

Knowledge about bee fossils has improved dramatically during the last 15 years. About one-third of the 184 described fossil species have been documented within this time period, and historical species discovered prior to this are gradually undergoing revision and reassessment (Engel 2000b, 2002a; Nel and Petruvelicius 2003; Michez et al. 2009a; Kotthoff et al. 2011). As paleontology continues to experience a current Renaissance among the entomological community, the value of such data will only become more significant and refined. Even for lineages with relatively sparse records, such as bees (in comparison to the more prolific records of flies or beetles), profound improvements are undoubtedly in store as more and more deposits are discovered and more attention is focused on these resources. Already the scant data is overturning some elements of current dogma, such as the discovery of native fossil honeybees in North America (Engel et al. 2009). The revelation that *Apis* was once native to the New World during the Neogene with subsequent

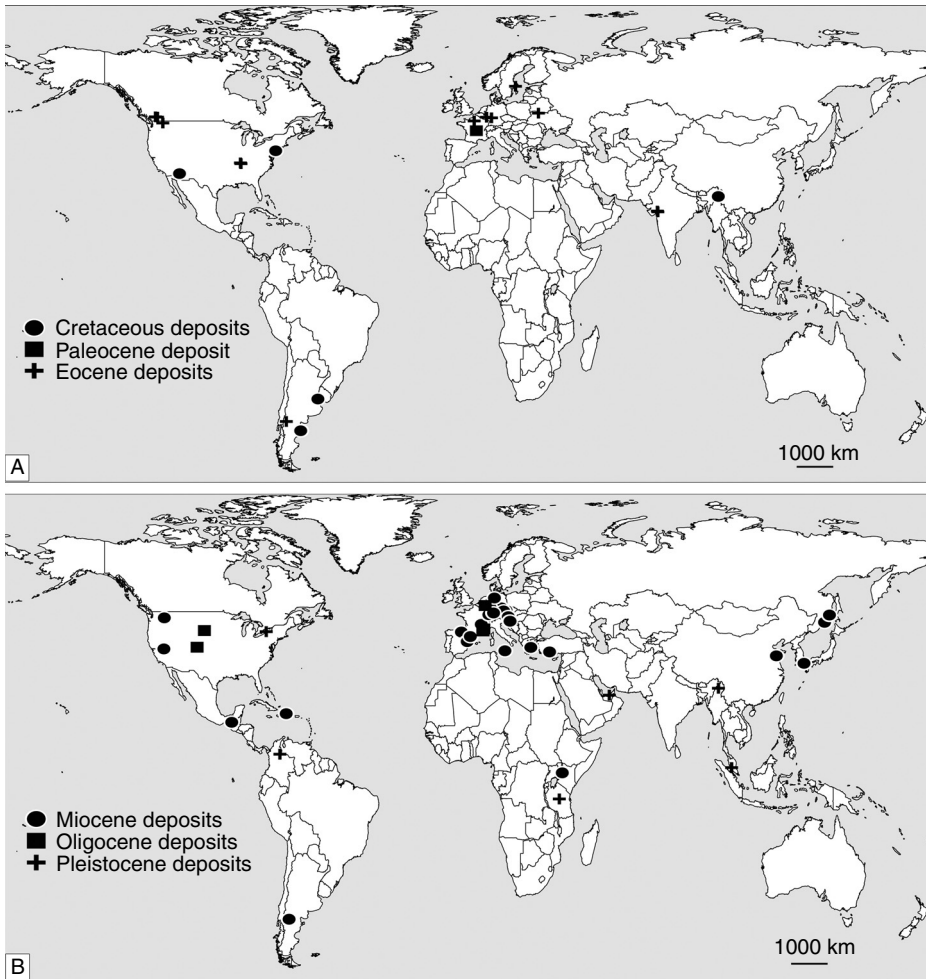
post-Miocene extinction, revises traditional concepts of apine biogeography, with honeybees mimicking the pattern observed in the more completely understood records of horses (*Equus caballus*), ginkgos, and the Chinese Tree of Heaven (*Ailanthus*), among many others. The prospect for future revelations of similar nature, ones perhaps entirely unexpected, is considerable. Accordingly, any study ignoring the fossil record, regardless of how meager, does so to its own jeopardy. If concerted efforts during such a brief span of time as 15 years can increase the available record by 33 %, then it is staggering to conceive how much more fully complete this record may be 15–25 years from today. Truly we are only at the earliest dawn of paleomelittology.

While 59 deposits include at least one bee fossil and/or one likely bee trace, only ten deposits have revealed more than three bee fossils, highlighting the scarcity of bees in fossil deposits (Table 5.1). Moreover, there are presently three principle biases in this record: geographical, biological, and habitat based.

Firstly, the geological history of bees is “northern biased” (Fig 5.3; Engel 2004b; Engel and Peñalver 2006). There are merely five deposits in the Southern Hemisphere (Table 5.1), with all other localities distributed in the Northern Hemisphere. A growing number of suitable deposits are continuously being discovered in the Southern Hemisphere or from regions that were once south of the Equator but are no longer. Aside from suitable compression sites already known from South American and southern Africa (e.g. Late Cretaceous of Botswana), perhaps the most exciting are those southern amber locales such as Peru, Ecuador, Ethiopia (which during the Cenomanian was obviously more southerly), and the rich outcrops of Australia. Intense exploration of these and others is only just beginning. As already noted, our record of fossil bees will change profoundly in the years to come, hopefully eliminating at least this first bias.

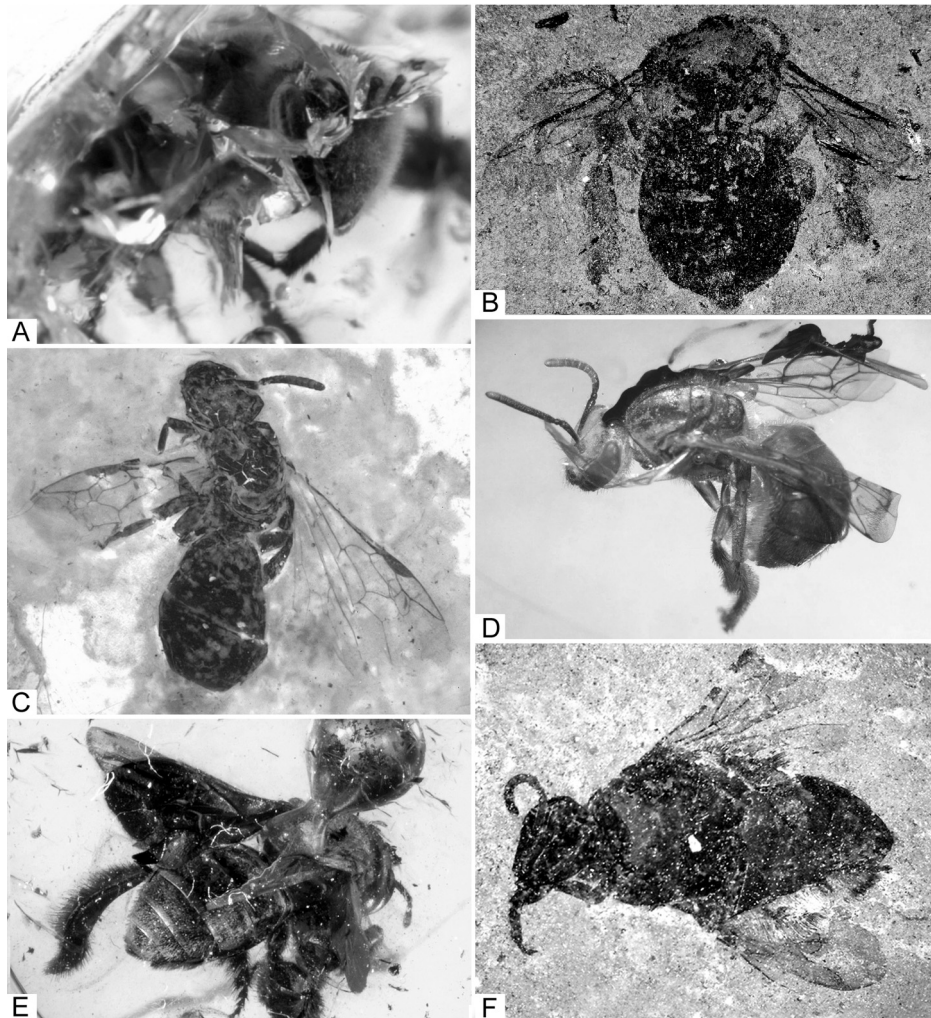
Secondly, resin-foraging bees are likely to be over-represented in amber and copal deposits, which include both 41 % of the described bee fossils (see examples in Fig 5.4). Excluding the hyperabundant stingless bee, *Proplebeia dominicana*, apids still represent 61 % of species and 71 % of specimens in amber and copal. In the modern fauna, apids represent 29 % of species globally and can represent 35 % or more of the species in some tropical habitats (Gonzalez and Engel 2004). Resin collectors more frequently come into contact with such substances and, although they are more adept at handling this resource, they are still significantly more likely to become entrapped, particularly when considering eusocial species where the increased numbers of individuals make the potential for “accidents” greater, pushing the numbers of such bees in amber higher. As such, resin foraging behavior could explain a large portion of this bias, although some component certainly does reside in the third, and last, obvious bias.

Unfortunately, the last bias may represent a hurdle more difficult to clear than the others. Large components of bee diversity are found in xeric habitats,



**Fig 5.3** Mapping of the deposits including bee body fossils and traces. A. Deposits from Cretaceous, Paleocene and Eocene. B. Deposits from Oligocene, Miocene and Pleistocene.

regions not frequently represented in suitable fossil deposits and, when they are, they frequently lack the fine-scale sedimentary deposition necessary to preserve remains with sufficient detail to permit confident identification and comparison with modern counterparts. The small size of many bees, at least relative to many sedimentary sites that faithfully preserve larger animals such as vertebrates, and particularly the diminutive proportions predicted for the earliest of bees, may mean that the elimination of this habitat bias will be a long time in the works. For the foreseeable future, our record may be largely confined to more tropical, even wet tropical, habitats rather than the deserts that harbor our beloved objects of investigation.



**Fig 5.4** Representative fossil bees. A. *Cretotrigona prisca* (New Jersey amber, USA, late Cretaceous; Engel 2000b). B. *Paleohabropoda oudardi* (Menat, France, Paleocene; Michez et al. 2009). C. *Halictus petrefactus* (Rubielos de Mora basin, Spain, Early Miocene; Engel & Peñalver 2006). D. *Oligochlora eickworti* (Dominican amber, Early Miocene; Engel 1996). E. *Thaumastobombus andreniformis* (Baltic amber, middle Eocene; Patiny et al. 2007). F. *Protobombus messelensis* (Messel, Germany, middle Miocene; Wappler & Engel 2003).

### 5.8.2 Evidence of bee–plant interactions

Among the six principal types of evidence of past association between insects and plants (see previous chapter), two are quite common in bee fossil records: bee-mediated plant damage (Megachile damage for nest construction) and plant-related

structure of bee-body fossil (morphological structure associated to pollen, nectar and oil foraging). We can synthesize the succession of plant-associated features:

- (1) first evidence of plumose hairs in *Melittosphex burmensis* (-100 megaannum). This feature is present in all following bees (Michener 2007).
- (2) small size likely adapted to small flower in *Melittosphex burmensis* (-100 megaannum). The size increased maybe linked to the evolution of polylecty (Thorp 1979).
- (3) long tongue in *Cretotrigona prisca* (-70 megaannum) to collect nectar in deep flower. This feature is present in all extant Megachilidae and Apidae and some “short-tongued bees” (Roig-Alsina and Michener 1993; Alexander and Michener 1995).
- (4) first corbicula in *Cretotrigona prisca* (-70 megaannum). This feature likely derived from hind-leg scopa and is present in the clade of corbiculate bees (Kawakita et al. 2008).
- (5) earliest evidence of scopa in *Paleohabropoda oudardi* (-60 megaannum). Hind-leg scopa is present in most non-cleptoparasite taxa (Michener 2007).
- (6) first evidence of oil-collecting setae in *Paleomacropis eocenicus* (-53 megaannum). Features associated with oil foraging are present in some unrelated clades of modern bees like Melittidae and Apidae (Renner and Schaefer 2010).
- (7) metasomal scopae in Baltic Megachilid bees
- (8) earliest evidence of modified male hind tibia in *Euglossa cotylisca* (2.5 megaannum). This feature is present in all males of extant orchid bees (Ramirez et al. 2010).

We also characterize past association thanks to taxonomic assignment to a modern descendant for which reliable ecological data exists, but this evidence is more speculative. The other archives of associations, plant reproductive biology indicating narrow bee-association, dispersed coprolites, and gut contents are no longer available in the present records.

### 5.8.3 Importance of paleobiological studies

Fossils provide a rare opportunity to study not only the origin and (co)-evolution of clades, but also their ecology, offering a unique window on past interactions. The functioning of ancient ecosystems has a direct bearing on the evolution of entire guilds, the diversification of specific lineages, and the ability of communities to respond to extrinsic changes such as climatic shifts. While much can be deduced from extending knowledge of current ecosystem operations and plant-host-herbivore associations into past epochs, at least for those in which the individual operators are presumed to have functioned similar to their modern counterparts,



the power of this exercise pales in comparison to any direct views into ancient communities themselves. This is all the more critical with progressively more antique ecologies in which there may be guilds and lineages represented that left no survivors or ecologically-analogous taxa. The paleontological forefront is as important today as is the application of tools such as molecular and developmental biology, comparative anatomy and physiology, and the biochemistry and energy flow of entire ecosystems. Ignoring fossils compromises understanding of evolution.

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