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MORPHOLOGY, CLASSIFICATION, AND ANTIQUITY OF *MELITTOSPHEX BURMENSIS* (APOIDEA: MELITTOSPHECIDAE) AND IMPLICATIONS FOR EARLY BEE EVOLUTION

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ABSTRACT—*Melittosphex burmensis* (Melittosphecidae) is an important apoid fossil from middle Cretaceous (~100 Ma) amber from Myanmar (Burma). *Melittosphex* exhibits a combination of wasp and bee features making it an important transitional form linking bees with crabronid wasps. The presence of branched hairs suggests that it was a pollen-collector and many aspects of the morphology suggest that it is more closely related to bees than to any fossil or extant group of wasps. Here we report additional morphological information on *Melittosphex burmensis*. This specimen remains the earliest body-fossil evidence that pollen-collecting Apoidea (bees) were present approximately 20 million years after the origin of the eudicots (~120 Ma), the major angiosperm lineage with extensive reliance on bee pollination.

INTRODUCTION

BEES ARE among the most important groups of angiosperm-pollinating insects (Schoonhoven et al., 1998). The origin of bees and the appearance of their numerous morphological and behavioral adaptations for pollen collection and transport (Thorp, 1979, 2000) is a key event that may have contributed to the rapid diversification of angiosperms in the early to mid Cretaceous (Regal, 1977; Burger, 1981; Pellmyr, 1992; Grimaldi, 1999). Understanding the role that bees played in angiosperm diversification requires an accurate estimate of bee antiquity as well as a better understanding of bee morphology at the transition from carnivory (wasps) to herbivory (bees). Phylogenetic studies of extant bees and their closest living wasp relatives (Lomholdt, 1982; Prentice, 1998; Melo, 1999; Ohl and Bleidorn 2005; Lohrmann et al., 2008) have established that bees arose from within a group of predatory wasps (referred to as the 'Sphecidae' [Bohart and Menke, 1976], the 'sphecoid wasps' [Melo, 1999], or the 'Spheciformes' [Michener, 2007]) sometime during the Cretaceous (Michener, 2007; Grimaldi and Engel, 2005). The monophyletic group including bees and closely related wasp families (Heterogynaidae, Ampulicidae, Sphecidae and Crabronidae) is referred to as Apoidea (Prentice, 1998; Melo, 1999; Michener, 2007), and the wasp families are referred to as the 'apoid wasps' below. Reconstructing the transition from predatory wasps to pollen-collecting bees is difficult because no transitional forms have been previously identified.

One recently described, transitional form is *Melittosphex burmensis* Poinar and Danforth, 2006, a fossil bee from middle Cretaceous (~100 Ma) amber from Myanmar. This fossil is important because it exhibits a mixture of traits associated with apoid wasps as well as bees. Presence of branched hairs on the head and legs suggests that this fossil represents a pollen-collecting species. The original description was brief and few photographs were provided documenting the morphological details of this important apoid fossil. Here we provide a more complete description of *Melittosphex burmensis.* Our description builds on the previous description and provides additional data and photographs to document the morphology. Since the 2006 publication, one of us (BND) has also examined relevant wasp fossils originally described by Antropov (2000a) from the Myanmar amber. Examination of these important amber wasps as well as examination of representatives of modern Pemphredoninae confirms that *Melittosphex burmensis* is not a pemphredonine wasp. In addition, comparison of *Melittosphex burmensis* to Myanmar amber wasp fossils confirms that *Melittosphex burmensis* bears minutely-branched hairs over much of the body, unlike any fossil or extant apoid wasps. Based on these additional observations, we stand by the argument that *Melittosphex burmensis* presents a unique mix of wasp-like and bee-like features that would make it a likely stem lineage, sister to the modern bees but not nested within the crown group of modern bees. *Melittosphex burmensis* is therefore an important fossil that exhibits a unique suite of traits transitional between bees and the apoid wasps from which they arose.

MATERIALS AND METHODS

Observations and photographs were made with a Nikon SMZ-10 stereoscopic microscope and Nikon Optiphot optical microscope (with magnifications up to ×650).

SYSTEMATIC PALEONTOLOGY

Order HYMENOPTERA Linnaeus, 1758
Superfamily APOIDEA Latreille, 1802
Family MELITTOSPHECIDAE Poinar and Danforth, 2006

Type genus.—*Melittosphex* Poinar and Danforth, 2006.

Description.—Melittosphecidae includes a single genus, *Melittosphex*, described in detail below. The description of *Melittosphex burmensis* serves as a description of the family Melittosphecidae.

Genus *MELITTOSPHEX* Poinar and Danforth, 2006

Type species.—*Melittosphex burmensis* Poinar and Danforth, 2006.

Diagnosis.—As for the species.

Description.—*Melittosphex* includes a single species, *M. burmensis*, described in detail below. The description of *Melittosphex burmensis* serves as a description of the genus *Melittosphex*.

Etymology.—The genus-group name is a combination of '*Melitta*' (Greek, bee) and '*Sphex*' (Greek, wasp), indicating the mix of wasp and bee-like features.

MELITTOSPHEX BURMENSIS Poinar and Danforth, 2006
Figures 1.1–4.3

Diagnosis.—*Melittosphex burmensis* differs from all crown-group bee families in the possession of two mid-tibial spurs and a slender hind basitarsus lacking a hind-leg strigil. All crown-group bee families (including Paleomelittidae Engel, 2001) have a single mid-tibial spur and a basitarsus that is distinctly broader than the subsequent tarsal segments. In overall appearance, Melittosphecidae resembles a small andrenid or halictid bee.

Melittosphex burmensis differs from all previous described Cretaceous apoid wasp fossils, including Angarosphecidae Rasnitsyn, 1975 (Rasnitsyn, 1975), Ampulicidae Shuckard, 1840 (Ohl, 2003; Ohl and Spahn, 2010), and Crabronidae (Pemphredoninae Dahlbom, 1835) (Antropov, 2000a), and extinct apoid wasp subfamilies Burmastinae Antropov, 2000 and Cirrosphecinae Antropov, 2000 (Antropov, 2000a). For the most part, all these families are represented in the fossil record by much larger wasps and all families except Crabronidae (Pemphredoninae) have three submarginal cells. Some pemphredonine fossils described from Myanmar amber are of approximately the same size, have two submarginal cells, and show some traits similar to *Melittosphex* (Table 1). For example, *Prolemistus apiformis* Antropov, 2000 and *Cretospilomena familiaris* Antropov, 2000 have forewings with two submarginal cells, and *Cretospilomena familiaris* has propodeal spines reminiscent of (although smaller than) those visible on *Melittosphex burmensis*. However, examination of the Myanmar amber pemphredonines described by Antropov (2000a; *Prolemistus apiformis* and *Cretospilomena familiaris*) by BND confirmed they are distinct from *Melittosphex burmensis* in a number of important morphological features. The Myanmar amber pemphredonines all lack branched, plumose hairs visible under high magnification on *Melittosphex*, they lack a pygidial plate, they have an elongate pronotum, an elongate propodeum, and a cylindrical (rather than dorso-ventrally compressed) abdomen. Careful examination of the details of the legs indicates they have a single mid-tibial spur and they show a weakly developed (but visible) hindleg strigil. The wing venation of *Melittosphex burmensis* clearly differs from some previously described pemphredonines in the number of submarginal cells (three submarginal cells in *Palanga succinea* Budrys 1993 and *Archisphex crowsoni* Evans, 1969). For those species with two submarginal cells (*Cretospilomena familiaris* and *Prolemistus apiformis*, Antropov, 2000a), the fossil Pemphredoninae differ from *Melittosphex* in that the first recurrent vein intersects the first submarginal cell rather than being interstitial with the 1st transverse cubital, as in *Melittosphex* (Table 1). None of the extant or fossil Pemphredoninae show evidence of branched (plumose) hairs and none have been interpreted as pollen-collecting Apoidea (Antropov, 2000a, b).

Comparison of *Melittosphex burmensis* to representatives of all modern (extant) tribes and subtribes of Pemphredoninae (based on Pulawski, 2010) confirms that *Melittosphex burmensis* cannot be placed in any of the modern pemphredonine groups (Table 1). All modern Pemphredoninae have a visible (but sometimes weakly developed) hindleg strigil. Examination of the legs of modern Pemphredoninae indicates that they are much less hairy than *Melittosphex* and the apex of the femur is often expanded, unlike that of *Melittosphex*. Most modern (and fossil) Pemphredoninae have an elongate body with an elongate pronotum, an elongate propodeum, and a petiolate, cylindrical abdomen, unlike that of *Melittosphex*. Only

TABLE *1*—Summary of character states useful for diagnosis of Melittosphecidae relative to extant Pemphredoninae and fossil Pemphredoninae from Myanmar. Character states are as follows: (1) number of submarginal cells; (2) intersection of first recurrent vein, 1SM=intersecting first submarginal, 2SM=intersecting second submarginal, intersti=interstitial between first and second submarginal; (3) cylindrical abdomen, yes/no; (4) petiolate abdomen, yes/no; (5) propodeal spine, yes/no; (6) pygidial plate, present in at least one sex/absent; (7) number mid-tibial spurs (note that for most crabronid wasps there are two, well-developed mid-tibial spurs); (8) hindleg strigil present, yes/no; (9) branched, plumose hairs, yes/no. Fossil taxa are indicated with a dagger (†).

Family	Subfamily	Tribe	Genus	(1) no. SM cells	(2) 1st rec. vein	(3) cyl. abd.	(4) pet. abd.	(5) prop. spine	(6) pyg. plate	(7) mid- tibial spurs	(8) hind strigil	(9) plumose hairs
Bees (Anthophila)				var.	var.	no	no	no	var.	1	no	yes
Melittosphecidae			*Melittosphex*†	2	intersti	no	no	yes	pres	2	no	yes
Crabronidae	Pemphredoninae	not assigned	*Cretospilomena*†	2	1SM	yes	yes	yes	abs	1	yes	no
Crabronidae	Pemphredoninae	not assigned	*Prolemistus*†	2	1SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Ammoplanops*	1	1SM	yes	yes	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Diodontus*	2	1SM	yes	no	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Passaloecus*	2	1SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Pemphredon*	2	1SM	yes	yes	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Polemistus*	2	1SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Arpactophilus*	2	intersti	yes	?	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Microstigmus*	1	1SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Spilomena*	2	intersti	yes	no	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Carinostigmus*	2	1SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Paracrabro*	2	1SM	yes	yes	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Pemphredonini	*Stigmus*	2	1SM	yes	yes	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Psenini	*Mimesa*	3	2SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Psenini	*Mimumesa*	3	2SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Psenini	*Pluto*	3	2SM	yes	yes	no	abs	1	yes	no
Crabronidae	Pemphredoninae	Psenini	*Psen*	3	2SM	yes	yes	no	pres	1	yes	no
Crabronidae	Pemphredoninae	Psenini	*Psenulus*	3	2SM	yes	yes	no	pres	1	yes	no

Diodontus Curtis, 1834 and *Spilomena* Shuckard, 1838 lack the petiolate abdomen visible in most pemphredonines. Most modern Pemphredoninae have a first recurrent vein that intersects either the first submarginal or the second submarginal cell. The only observed genera in which the first recurrent is interstitial are *Arpactophilus* F. Smith, 1863 and *Spilomena*. While most Pemphredoninae lack a pygidial plate, some genera have a pygidial plate in at least one sex (e.g., *Ammoplanops* Gussakovskij, 1931, *Diodontus*, *Pemphredon* Latreille, 1796, *Paracrabro* Turner, 1907, and *Stigmus* Panzer, 1804). However, the pygidial plate is elongate, slender, and rather weakly developed compared to *Melittosphex burmensis*. All pemphredonine genera have a single mid-tibial spur (Bohart and Menke, 1976), as opposed to the two spurs visible in *Melittosphex*.

Description.—The single male specimen of *Melittosphex burmensis* is embedded in a small trapezoidal piece of amber measuring 7 mm by 5 mm (Fig. 1.1). The specimen is dorsoventrally compressed, thus obscuring some characters that would normally be visible in lateral view. The ventral surface is clearly visible but the dorsal surface of the thorax is obscured by dark areas of the amber specimen. The entire specimen measures just 2.95 mm in length. The appendages of the left side of the body are clearly visible. The specimen bears branched hairs on the undamaged portions of the thorax, legs, abdomen, and head (Fig. 1.2, 1.3). The most clearly visible plumose hairs are those on the hind femur, tibia and basitarsus (Figs. 1.4, 2.1, 2.2). The head is heart shaped (0.24 mm in length) with a covering of short plumose hairs on the vertex (Fig. 1.2). The two antennae originate relatively low on the face (below the midline; Fig. 1.2). Each antenna bears 11 flagellomeres (Fig. 2.3) establishing that this is a male specimen. The scape is long for a bee and the first flagellomere is elongate (nearly twice the length of the second flagellomere). A small portion of the vertex is undamaged and shows relatively coarse, distinct punctures (Fig. 1.2). The mandibles are elongate and acutely tridentate, unlike the mandibles of most extant male bees (Fig. 3.1).

The mesosoma (1.45 mm in length) is largely damaged due to compression and one cannot make out the details of the dorsal or lateral surfaces. It is impossible to determine if the specimen has a rounded pronotal lobe characteristic of Apoidea, but numerous other characters place *Melittosphex* unambiguously within Apoidea. The propodeum bears two distinct posterolateral tubercles (Fig. 1.1) with scattered branched hairs. The forewing is 2.5 mm in length and the venation is typical of many small bees (Danforth, 1989), with a distinct stigma, two submarginal cells, a weakly arcuate basal vein, and an acutely pointed marginal cell with the apex on the wing margin (Fig. 3.2). The forewing venation does not match any of the wasps reported from early Cretaceous compression fossils (e.g., Angarosphecidae [Rasnitsyn, 1975]) nor does it match any of the apoid wasp fossils described from Myanmar amber (Grimaldi et al., 2002; Antropov, 2000a). The hindwing venation is not visible but one can make out the anterior edge of one hindwing based on the presence of the hamuli, which are visible. Important leg characters include the elongate, slender hindtibia (lacking distinct tibial spines characteristic of apoid wasps; Fig. 1.1, 1.4), a narrow hind basitarsus (a characteristic of apoid wasps; Figs. 1.1, 2.1), a weakly developed basitibial plate (Fig. 1.4), and absence of a hindleg strigil (Fig. 2.1). There are two hind-tibial spurs (as in most bees), but one is distorted and appears to be bent around behind the basitarsus (Fig. 2.2). The midtibia clearly shows two spurs (a groundplan feature of the apoid wasps; Fig. 4.1). The foreleg bears a well-developed antennal cleaner (Fig. 4.2) and the pre-tarsal claws are bifid.

The metasoma (1.26 mm in length) is dorso-ventrally compressed but T7 (the last visible metasomal tergum in males) is undamaged (Fig. 1.1). The specimen clearly bears a well-developed pygidial plate (Fig. 4.3) on T7, a character that unites bees with Crabronidae (Melo, 1999). Cerci are apparently absent.

Etymology.—The specific epithet '*burmensis*' is based on the locality where the fossil was found.

Type.—The specimen was obtained from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State (N 26120′, E 96136′) in Myanmar (Burma). Holotype male in amber, deposited in the Poinar amber collection (accession #B-Hy-7) maintained at the Oregon State University.

Occurrence.—Amber mine in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (N 26120′, E 96136′), northern Myanmar (Burma). This amber site, known as the Noije Bum 2001 Summit Site, was assigned to the early Cretaceous, upper Albian, on the basis of paleontological evidence (Cruickshank and Ko, 2003), placing the age at 97 to 110 Ma. Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al., 2007b).

Discussion.—*Melittosphex burmensis* appears to represent an extinct lineage of pollen-collecting Apoidea sister to the extant bee families (Poinar and Danforth, 2006; Ohl and Engel, 2007; Table 2; Fig. 5). The seven extant bee families are united by a total of 14 synapomorphies (Michener, 2007) some of which are present and visible on the fossil specimen: 1) plumose hairs, 2) posterior strigil absent, 3) mid-femoral/tibial brush for cleaning foreleg present, 4) bristles on outer surface of tibia weak or absent, 5) weakly developed basitibial plate, and 6) bifid tarsal claws. *Melittosphex burmensis* bears several character states that resemble some extant groups of bees. However, the possession of two mid-tibial spurs and a slender hind basitarsus are groundplan features of the apoid wasps and these characters suggest that *Melittosphex* is not a member of any currently recognized bee family. Bees and crabronid wasps share eight synapomorphic characters (Melo, 1999). We can assess two of these characters in the fossil and both support the placement of *Melittosphex* within the clade including bees and Crabronidae. First, the fossil lacks abdominal cerci, which is a synapomorphy of Crabronidae + bees. Second, the fossil has a well developed pygidial plate (Fig. 4.3). Presence of a pygidial plate in females is a synapomorphy of Crabronidae + bees (Melo, 1999). While the fossil specimen is a male, the presence of the pygidial plate in males is often associated with its presence in females, thus supporting the view that the female of *Melittosphex* had a pygidial plate. Autapomorphic features of the fossil include large, clearly tridentate mandibles, gracile, slender hindlegs, and distinct tubercles on the propodeum (Fig. 1.1). None of these characters clearly unite this fossil with any extant or fossil group of bees or apoid wasps.

DISCUSSION

Paleoenvironmental conditions.—Cretaceous-age amber from Myanmar was probably formed under tropical or sub-tropical conditions because temperatures during the Cretaceous are considered some of the highest during the past 500 my (Spicer et al., 1996). The presence of what are normally considered to be tropical and warm temperate taxa (including Onychophora,

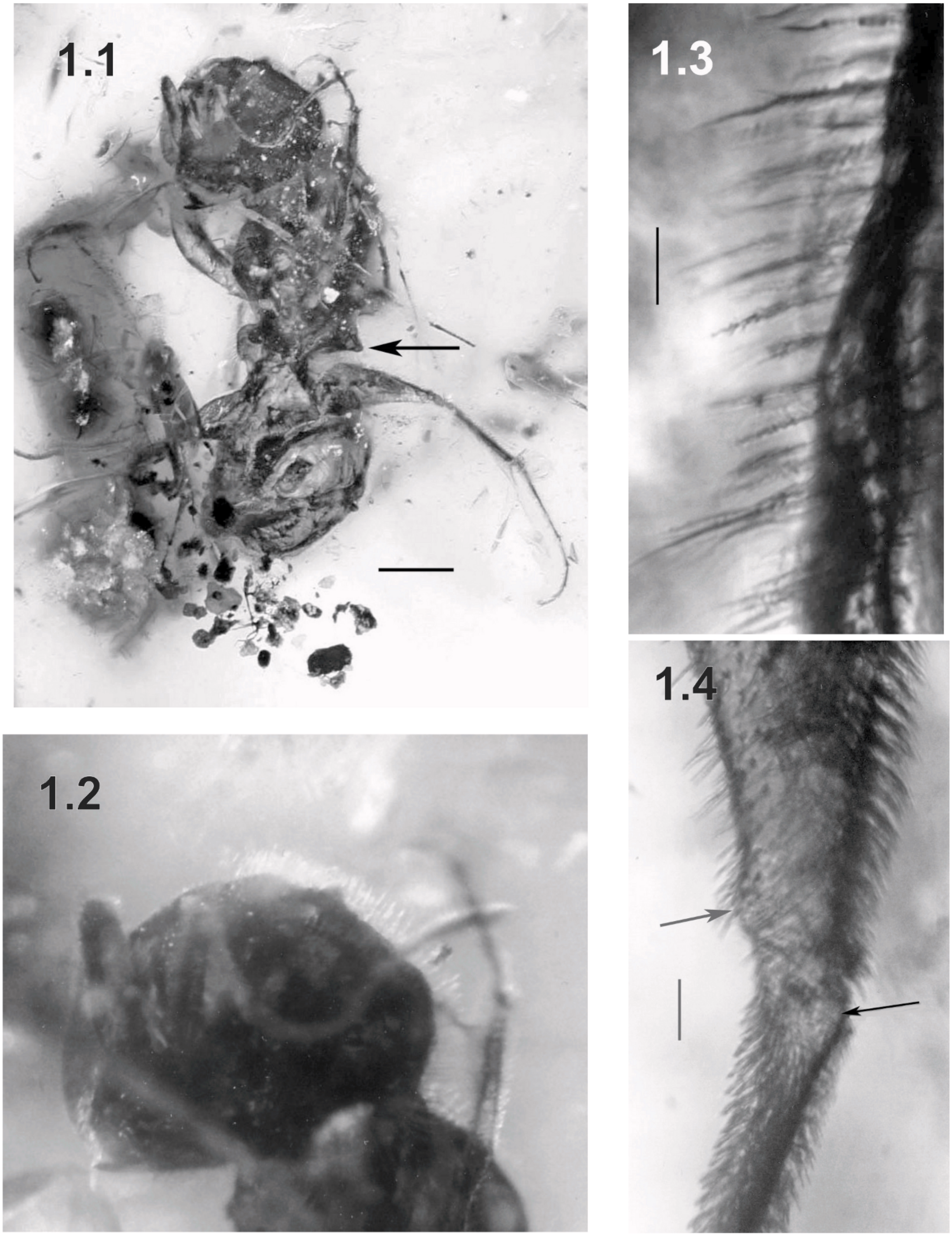

FIGURE *1*—Holotype of *Melittosphex burmensis* Poinar and Danforth, 2006. *1,* arrow shows propodeal projection, scale bar=410 μm; *2,* head capsule showing antennal placement and plumose hairs on vertex; *3,* plumose hairs on hind femur with branches on most of shaft, scale bar=15 μm; *4,* hind femur (upper arrow) and tibia showing weakly developed basitibial plate (lower arrow), scale bar=100 μm.

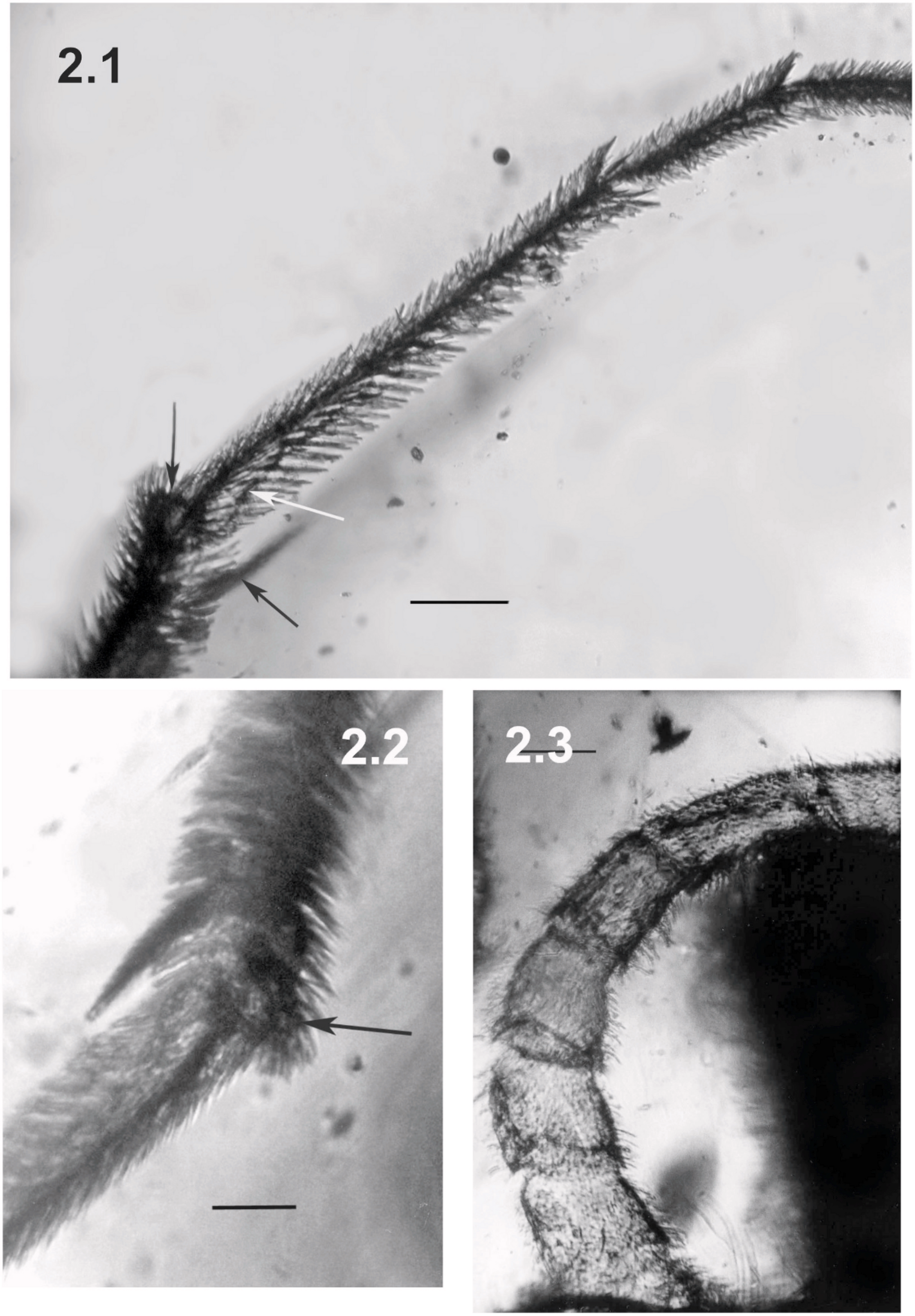

FIGURE 2—*Melittosphex burmensis*. *1,* elongate, slender hind basistarsus, note dense, apparently plumose, hairs, scale bar=100 µm. Black arrows show tibial spurs, white arrow shows region of basistarsus where strigilus would normally be visible in apoid wasps; *2,* hind tibial spurs, arrow shows bent spur, note absence of hindleg strigil, scale bar=48 µm; *3,* detail of the flagellomeres, scale bar=74 µm.

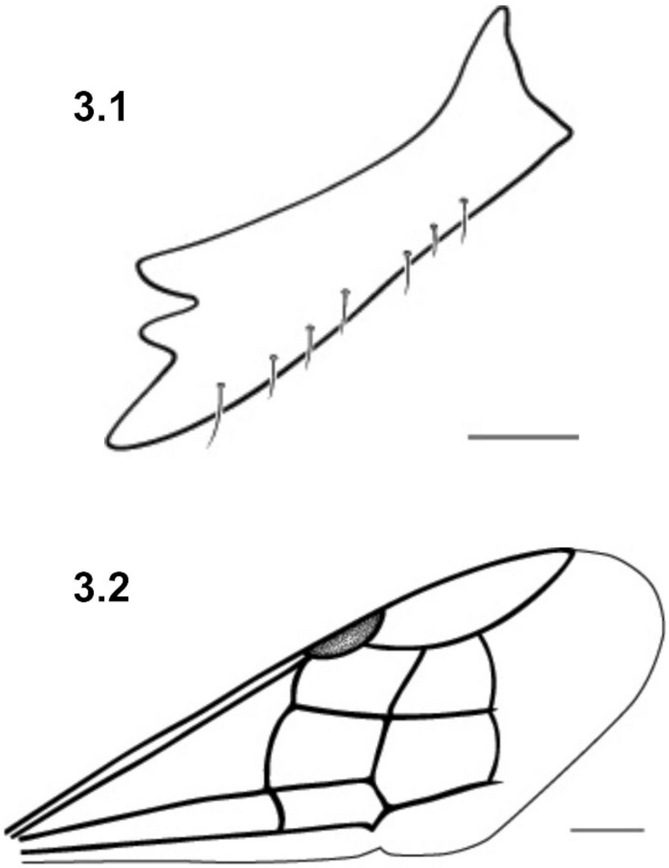

FIGURE 3—*Melittosphex burmensis. 1,* diagram of mandible, scale bar=126 μm; *2,* forewing, scale bar=230 μm.

Zoraptera, and Embiidina) in Myanmar amber deposits further supports this view (Grimaldi et al., 2002). *Melittosphex burmensis*, therefore, lived in a hot, most-likely tropical, environment.

Chronological appearance of Apoidea in the fossil record.—The fossil record of Apoidea extends to the early Cretaceous, some 140 Ma. Extinct stem group lineages referred to as Angarosphecidae (Rasnitsyn, 1975, 1980, 2000; Rasnitsyn et al., 1998, 1999; Rasnitsyn and Ansorge, 2000; Rasnitsyn and Martínez-Delclòs, 2000; Darling and Sharkey, 1990; Rasnitsyn and Quicke, 2002) are known from Barremian (140 Ma) up until early Eocene (52–54 Ma) (Pulawski et al., 2000) sites in Europe, South America, and Canada. Angarosphecidae are considered a paraphyletic assemblage presumed to represent the early stem lineages of Apoidea (Pulawski et al., 2000). They are large wasps with three submarginal cells (Rasnitsyn et al., 1999; Pulawski et al., 2000) known only from compression fossils.

Apoid wasps (but not bees) have been described previously from Myanmar amber (Grimaldi et al., 2002; Antropov 2000a). Myanmar amber apoid wasps fall into two extant families: Ampulicidae and Crabronidae (Pemphredoninae) and two extinct subfamilies (Burmastatinae and Cirrosphecinae) of uncertain affinity (Antropov, 2000a). Fossil Apoidea have also been described from New Jersey amber (estimated to be ~90 my old). Antropov (2000b) described a pemphredonine with two submarginal cells (*Psolimena electra* Antropov 2000) and provided a brief review of fossil Pemphredoninae. An important fossil bee, *Cretotrigona prisca* (Michener and Grimaldi, 1988) was described by Michener and Grimaldi (1988a,1988b) and later re-described by Engel (2000). This fossil is of uncertain age, for reasons outlined in (Rasnitsyn and Michener, 1991), but is estimated to be ~65 my old based on the most recent study (Engel, 2000). Bennet and Engel (2006) provide a review of apoid wasp fossils preserved in amber from the early Cretaceous through the Paleogene.

Recently described melittid and apid fossils (Michez et al., 2007, 2009) have established that these two families were clearly present shortly after (and most likely before) the K/T boundary. Michez et al. (2007) described *Palaeomacropis eocenicus* Michez and Nel, 2007 (Melittidae) from early Eocene amber obtained in northern France (Oise, France). This specimen is estimated to be 53 Myr old and represents the oldest fossil melittid and the first evidence of oil-collecting in bees. Most recently, Michez et al., (2009) described *Paleohabropoda oudardi* Michez and Rasmont 2009 (Apidae) based on a compression fossil from the Paleocene of Menat, France (Puy-de-Dôme). This bee is estimated to be 60 Myr old and was attributable based on morphometric analysis of the wing venation to the tribe Anthophorini.

A diverse assemblage of Apoidea (including wasps and bees) are known from the Baltic amber deposits (estimated to be ~42 my old). Both Crabronidae (Pemphredoninae; Sorg, 1986; Antropov and Pulawski, 1989; Budrys, 1993) and Ampulicidae (Nemkov, 1988) have been described from the Baltic amber. The bee fauna of Baltic amber has been carefully documented by Engel (2001) and includes representatives of several extant bee families (Apidae, Megachilidae, Halictidae and Melittidae) as well as one fossil bee family (Paleomelittidae). The predominance of Pemphredoninae in amber deposits (see Bennet and Engel, 2006) is presumably due to their habit of nesting in pithy stems and wood, where sap flows may be common (O'Neill, 2001).

Size of Cretaceous fossil flowers in relation to Melittosphex.—One seemingly remarkable aspect of the *Melittosphex* fossil is its small size. At approximately 3 mm the specimen corresponds to the size of some of the smallest bee species, including small *Perdita* (Andrenidae), Euryglossinae (Colletidae), Hylainae (Colletidae), and Nomioidinae (Halictidae). Interestingly, many of the fossil flowers recorded from the Cretaceous are also very small. We examined flower descriptions from the most recent extensive review of fossil flowers (Crepet et al., 2004) and found that the vast majority of Cretaceous flowers in the range of 0.5–3.0 mm. Only two previously described fossil flowers (Basinger and Dilcher, 1984; Krassikov et al., 1983) are greater than 1 cm in diameter. Likewise, flowers described from Myanmar amber all range in size from 1.0–6.0 mm (Poinar, 2004; Poinar and Chambers, 2005; Poinar et al., 2007a, 2008; Chambers et al., 2010). The small size of *Melittosphex burmensis* may be at least partially explained by the small size of the flowers present during the mid-Cretaceous.

The importance of Melittosphex *for understanding bee origins.*—*Melittosphex burmensis* provides important insights into the early evolution of the bees and the transition from predatory wasps to pollen-collecting bees. Most importantly, it reveals the morphology of what may have been a transitional, now extinct, stem lineage that bridges a morphological gap between extant apoid wasps and modern bees. Indeed, the mix of morphological traits raises important questions about how we define 'bee' (Ohl and Engel, 2007). Admittedly, in the absence of the female, we cannot be sure that *Melittosphex* was a pollen-collector. Unfortunately, even if the female were discovered, it might not be easy to determine if the female collected and provisioned her brood cells with pollen because some modern, non-parasitic bee groups (Euglossinae, Hylaeinae, some Paracolletini, Ceratinini) carry pollen internally (Michener, 2007).

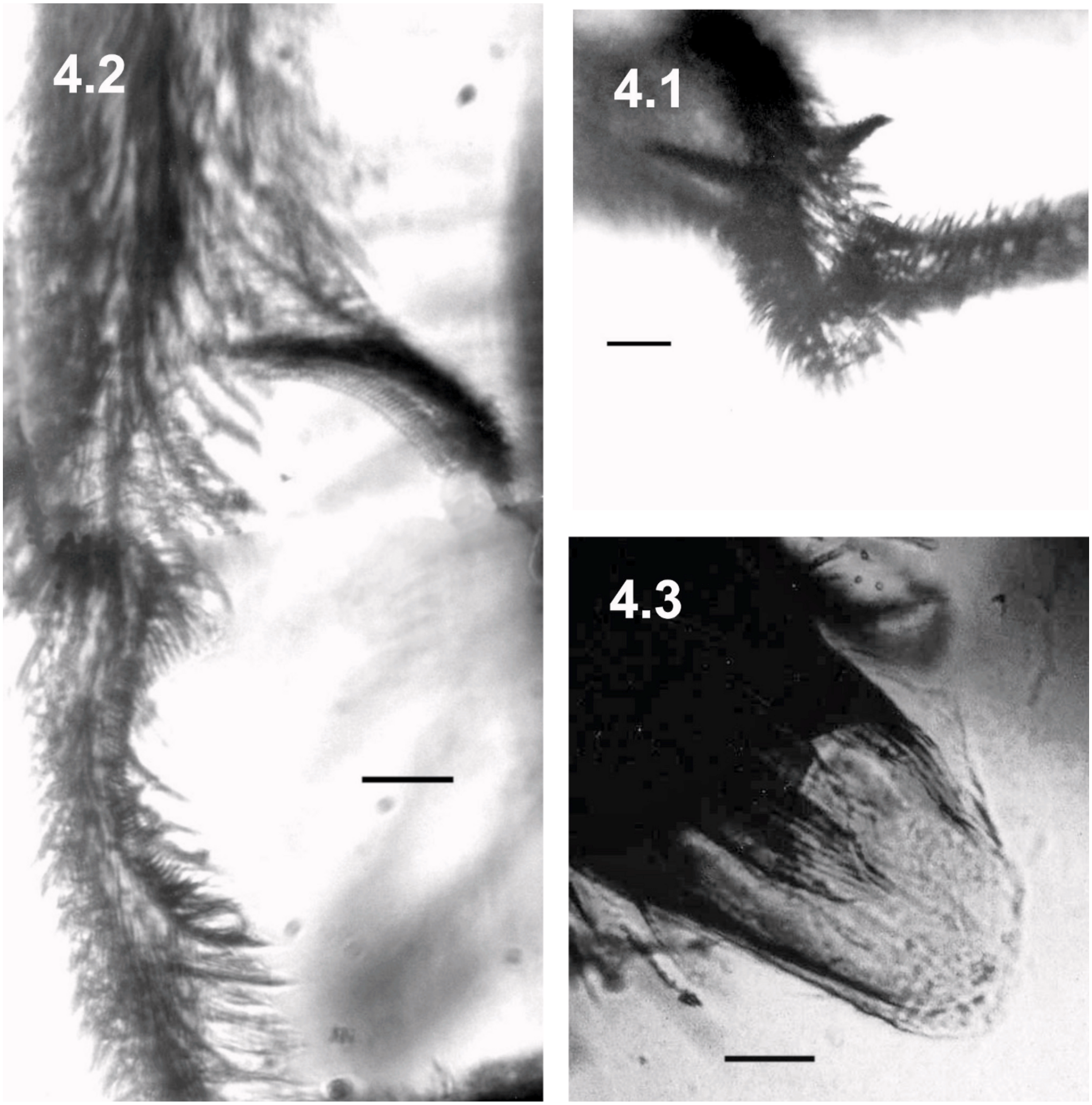

FIGURE 4—*Melittosphex burmensi. 1,* midtibial spurs, scale bar=32 µm; *2,* foreleg antennal cleaner showing tibial spur (fibula) and the concave inner surface of the forebasitarsus (the stridular concavity), scale bar=21 µm; *3,* pygidial plate, scale bar=40 µm.

TABLE *2*—Summary of character states useful for assessing the phylogenetic affinities of Melittosphecidae.

Character	Crabronidae	Melittosphecidae	Bees	Source
plumose hairs	absent	present	present	Michener, 2007
bifid tarsal claws	no	yes	yes	Michener, 2007
hind basitarsus	narrow	narrow	broad	Michener, 2007
hind-leg strigil	present	absent	absent	Michener, 2007
mid-femoral/tibial brush	absent	present	present	Michener, 2007
mid-tibial spur	2 (groundplan*)	2	1	Melo, 1999
submarginal (SM) cells	variable	2	variable	Michener, 2007
tarsal claws	simple	bifid	bifid	Michener, 2007
outer surface hind tibia	spines present	spines absent	spines absent	Michener, 2007
male cerci	absent	absent	absent	Melo, 1999
pygidial plate	variable	present	variable	Melo, 1999

* Two mid-tibial spurs is considered the ground-plan feature for apoid wasps. However, some groups, including Pemphredoninae, Larrinae and Philanthinae show a reduction to a single mid-tibial spur, as in bees (Michener, 2007).

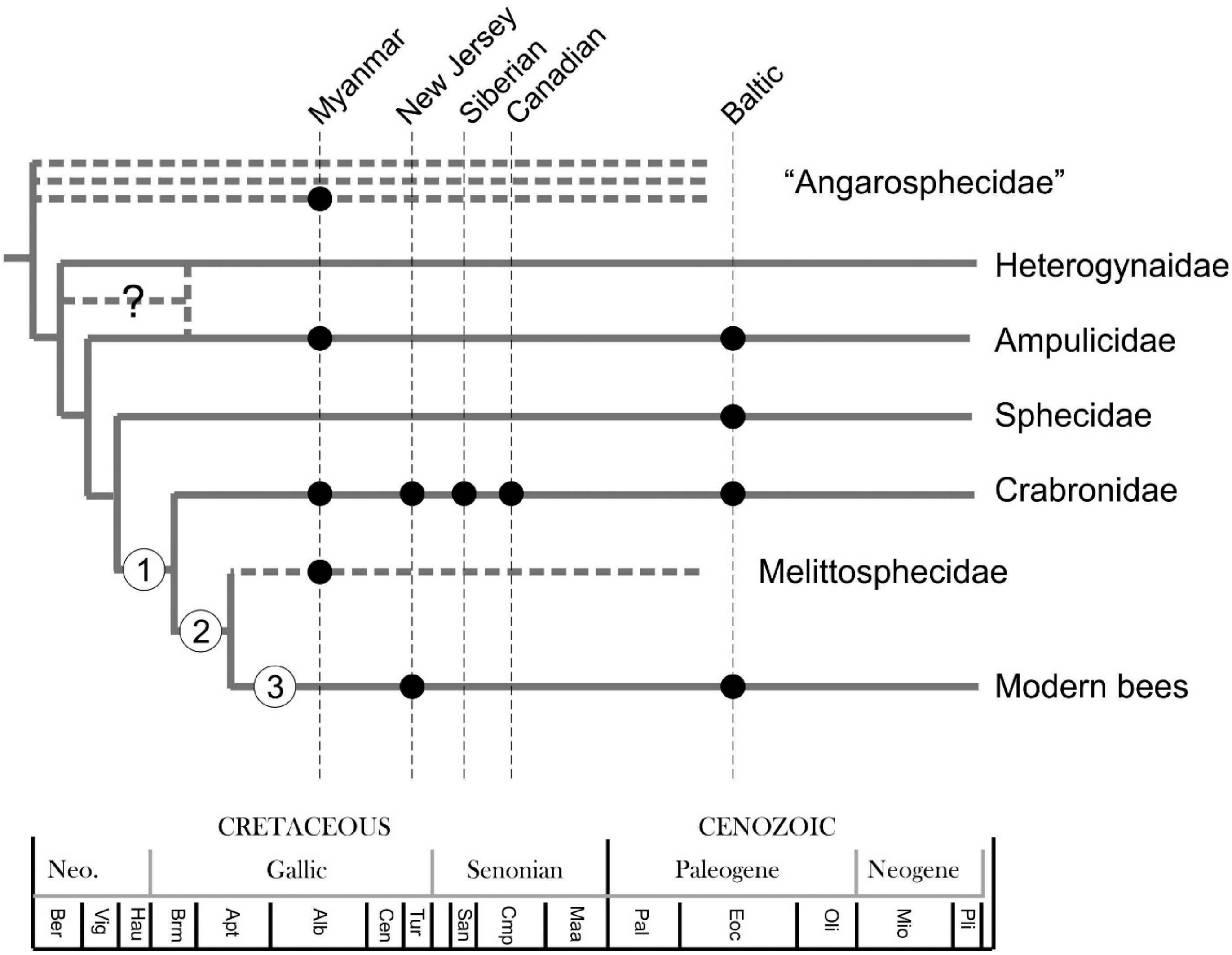

FIGURE 5—Presumed phylogeny and chronological appearance of apoid families in amber deposits. Relationships among extant Apoidea based on Melo (1999). Note that in some of Melo's analyses Ampulicidae was placed as sister to the Heterogynaidae (Melo's fig. 8), and that in some recent molecular studies (Ohl and Bleidorn, 2005) Heterogynaidae is placed within Crabronidae. Information on the presence of apoid wasp lineages in the fossil record was recently summarized in Bennet and Engel (2006; Table 1). Characters uniting nodes are as follows. Node 1 (synapomorphies of Crabronidae + (Melittosphecidae + extant bees): (a) male cerci absent, (b) pygidial plate present (Melo [1999] lists six additional characters that cannot be seen in the fossil). Node 2 (synapomorphies of Melittosphecidae + extant bees): (a) plumose hairs, (b) posterior strigil absent, (c) mid-femoral/tibial brush for cleaning foreleg present, (d) bristles on outer surface of tibia weak or absent, (e) cleft tarsal claws (Michener [2007] lists additional bee synapomorphies that cannot be seen in the fossil). Node 3 (synapomorphies of extant bees): (a) reduction from two to one mid-tibial spurs, (b) expansion of hind basitarsus (Michener [2007] lists additional bee synapomorphies).

However, we believe the clearly visible branched, plumose hairs on the head and legs of *Melittosphex* provide support for the hypothesis that this species was a pollen collector. These hairs are very different from those of extant and fossil crabronid wasps (Antropov 2000a, 2000b; Bennet and Engel, 2006). In addition, the absence of a hind-leg strigil and bristles on the outer surface of the hind tibia, and the bee-like wing venation are all traits suggestive of a bee rather than an apoid wasp. The presence of a distinct pygidial plate and a weakly developed basitibial plate in the male suggests that the female would most-likely have been a ground-nesting species.

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