

Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology

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Abstract. Phylogenetic relationships within the bee family Megachilidae are poorly understood. The monophyly of the subfamily Fideliinae is questionable, the relationships among the tribes and subtribes in the subfamily Megachilinae are unknown, and some extant genera cannot be placed with certainty at the tribal level. Using a cladistic analysis of adult external morphological characters, we explore the relationships of the eight tribes and two subtribes currently recognised in Megachilidae. Our dataset included 80% of the extant generic-level diversity, representatives of all fossil taxa, and was analysed using parsimony. We employed 200 characters and selected 7 outgroups and 72 ingroup species of 60 genera, plus 7 species of 4 extinct genera from Baltic amber. Our analysis shows that Fideliinae and the tribes Anthidiini and Osmiini of Megachilinae are paraphyletic; it supports the monophyly of Megachilinae, including the extinct taxa, and the sister group relationship of Lithurgini to the remaining megachilines. The Sub-Saharan genus *Aspidosmia*, a rare group with a mixture of osmiine and anthidiine features, is herein removed from Anthidiini and placed in its own tribe, *Aspidosmiini*, **new tribe**. Protolithurgini is the sister of Lithurgini, both placed herein in the subfamily Lithurginae; the other extinct taxa, Glyptapina and Ctenoplectrellina, are more basally related among Megachilinae than Osmiini, near *Aspidosmia*, and are herein treated at the tribal level. *Noteriades*, a genus presently in the Osmiini, is herein transferred to the Megachilini. Thus, we recognise four subfamilies (Fideliinae, Parahophitinae, Lithurginae and Megachilinae) and nine tribes in Megachilidae. We briefly discuss the evolutionary history and biogeography of the family, present alternative classifications, and provide a revised key to the extant tribes of Megachilinae.

Introduction

Megachilidae is the second largest bee family, containing more than 4000 described species worldwide (Michener, 2007; Ascher & Pickering, 2011). These solitary bees are both ecologically and economically relevant; they include many pollinators of natural, urban and agricultural vegetation. For example, *Megachile rotundata* (Fabricius) has been introduced to many parts of the world as a pollinator of alfalfa (Bohart,

1972; Michener, 2007; Pitts-Singer & Cane, 2011). Megachilid bees are found in a wide diversity of habitats on all continents except Antarctica, ranging from lowland tropical rain forests to deserts to alpine environments. The diversity of nesting biology and floral relationships of Megachilidae is also astonishing. Diverse materials are used in nest building, including mud, petals, leaves (intact pieces or macerated to a pulp), resin, soil particles, gravel and plant trichomes. The inclusion of these foreign materials in nest construction may have promoted a massive range expansion and diversification within the family (Litman *et al.*, 2011). Equally diverse are nesting site choices: surfaces of walls, stones and tree branches; inside pre-existing cavities in the ground, wood, stems, galls and snail

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shells; excavated in soil, wood or even in arboreal termite nests (e.g. Messer, 1984; Cane *et al.*, 2007; Michener, 2007). Some megachilid genera, subgenera or species are oligoleptic (e.g. Weislo & Cane, 1996), collecting pollen exclusively from related plant species or genera, and frequently exhibiting unique associated morphological and behavioral adaptations (e.g. Müller, 1996; Thorp, 2000; Müller & Bansac, 2004). Other interesting adaptations are related to nesting biology. For example, females in several genera in the Anthidiini, commonly known as wool carder bees, make cotton wool-like brood cells from plant hairs or trichomes that they collect with their multidentate mandibles; also, some of them have a dense tomentum on the outer surfaces of their basitarsi, which help them absorb extrafloral trichome secretions that are then added to those plant hairs to waterproof the cell, facilitate manipulation, prevent microbial attack and to deter nest-robbing arthropods (Müller *et al.*, 1996; Michener, 2007). Megachilidae also contains a large number of cleptoparasitic bees (cuckoo bees). Nineteen genera, including an entire tribe (Dioxyini), are cleptoparasites of other bees, thus making Megachilidae an important group for testing hypotheses on the origins of, and adaptations to, cleptoparasitic behaviour amongst bees. Megachilids are also notable as the primary source of invasive bees, including multiple species in the genera *Anthidium* Fabricius and *Megachile* Latreille (e.g. Cane, 2003; Michener, 2007). For instance, *A. manicatum* (Linnaeus) is perhaps the most widely distributed unmanaged bee species in the world. It was unintentionally introduced to North America in the late 1960s from Europe; and it is now established transcontinentally as well as in South America, New Zealand and the Canary Islands (Jaycox, 1967; Smith, 1991; Miller *et al.*, 2002; Hoebeke & Wheeler, 2005; Maier, 2005; Zavortink & Shanks, 2008; Gibbs & Sheffield, 2009; Strange *et al.*, 2011). Despite the ecological importance, evolutionary interest and economic

value of megachilid bees, their higher level classification and phylogeny remain poorly understood.

Classification and phylogeny

The most widely accepted classificatory proposal for bees (Michener, 2007) recognises seven extant families, although other proposals exist (for a discussion see Michener, 2007). In Michener's classification, Megachilidae is organised into two subfamilies, eight tribes (one extinct), two extinct subtribes and 76 genera. An alternative proposal is that of Engel (2005), in which some tribes are given subfamilial rank, some tribes are treated as subtribes and new tribes are proposed (Table 1). Two taxa, now placed in the subfamily Fideliinae, were considered for a long time either as a distinct family or included within the Apidae owing to a number of plesiomorphic features relative not only to Megachilidae, but also to other long-tongued bees (Engel, 2002; Michener, 2007). However, the discovery of the immature stages as well as studies on their nesting biology and ethology suggested their closer affinity to the Megachilidae (Rozen, 1970, 1973, 1977; McGinley & Rozen, 1987).

Roig-Alsina & Michener (1993), in their study of the long-tongued bees using both larval and adult external and internal morphological characters, provided the first exploration of the phylogenetic relationships of Megachilidae. Fideliinae was recovered as the sister group of the remaining megachilids in their analyses, but the subfamily appeared paraphyletic when both larval and adult characters were combined. Fideliinae is a small group with a disjunct distribution in the xeric areas of Asia, Africa and South America. The subfamily is segregated into two very distinct tribes: Fideliini containing 14 species in two genera, and Pararhophitini with three species in a single genus (Engel, 2002, 2004; Michener, 2007).

The other six tribes are currently grouped into the subfamily Megachilinae. The distinctive nature of one tribe, Lithurgini,

Table 1. Hierarchical suprageneric classifications of Megachilidae, including two proposals discussed in the text.

Michener (2007)	Engel (2005)	Proposal 1	Proposal 2 (preferred)
Subfamily Fideliinae Cockerell, 1932	Fideliinae	Fideliinae	Fideliinae
Tribe Fideliini Cockerell, 1932	Fideliini	Pararhophitinae	Pararhophitinae
Tribe Pararhophitini Popov, 1949	Neofideliini Engel, 2004	Megachilinae	Lithurginae
Subfamily Megachilinae Latreille, 1802	Pararhophitinae	Anthidiini	Lithurgini
Tribe Anthidiini Ashmead, 1899	Lithurginae	Aspidosmiini, new tribe	Protolithurgini ^a
Tribe Dioxyini Cockerell, 1902	Lithurgini	Ctenoplectrellini ^a	Megachilinae
Tribe Lithurgini Newman, 1834	Protolithurgini ^a	Dioxyini	Anthidiini
Tribe Megachilini Latreille, 1802	Megachilinae	Glyptapini ^a	Aspidosmiini, new tribe
Tribe Osmiini Newman, 1834	Anthidiini	Lithurgini	Ctenoplectrellini ^a
Subtribe Osmiina Newman, 1834	Anthidiina	Megachilini	Dioxyini
Subtribe Ctenoplectrellina Engel, 2001 ^a	Dioxyina	Osmiini	Glyptapini ^a
Subtribe Glyptapina Cockerell, 1909 ^a	Ctenoplectrellini ^a	Protolithurgini ^a	Megachilini
Tribe Protolithurgini Engel, 2001 ^a	Glyptapini ^a		Osmiini
	Megachilini		
	Osmiini		
	Osmiina		
	Heriadina Michener, 1941		

^aExtinct taxa.

possessing numerous plesiomorphic as well as distinctive apomorphic characters, resulted in subfamilial rank in the past (e.g. Michener, 1944, 1983; Engel, 2005). Lithurgini is a small tribe, with 61 species and 3 genera, found on all continents except Antarctica. The monophyly of the group is not questioned. Except for the sister group relationship of Lithurgini to all other extant tribes of Megachilinae, the phylogenetic study of Roig-Alsina & Michener (1993) did not resolve the relationships among the tribes of Megachilinae. Relationships among Anthidiini, Megachilini and Osmiini were unclear and neither the cleptoparasitic bee tribe Dioxyini nor any fossil taxa were included in their analysis. Although they used a limited number of taxa, their data suggested that all tribes are monophyletic except for Osmiini, which may be rendered paraphyletic by Megachilini (Michener, 2007).

Dioxyini is another unquestionably monophyletic tribe. This small group of cleptoparasitic bees consists of 36 species and eight genera that attack species of Megachilini, Anthidiini and Osmiini (Popov, 1936, 1953; Hurd, 1958). The median tubercle on the metanotum and the extremely reduced sting (Popov, 1953), more reduced than that of the stingless bees (Apidae: Meliponini; Packer, 2003), are some of the characters that support the monophyly of Dioxyini. This tribe also shares some morphological characters with the Anthidiini, such as the depression behind the propodeal spiracle, the short stigma and prestigma (less than twice as long as broad), and the cleft pretarsal claws of the female (Michener, 1944, 1996). Given the distinctive nature of these bees and the characters shared with Anthidiini, Dioxyini has been treated as a separate subfamily or part of Anthidiini (Michener, 1944; Engel, 2001). The characters shared with Anthidiini also suggest that Dioxyini could be its sister group or derived from it, making the former paraphyletic (Michener, 1996, 2007). The only study exploring the relationships of Dioxyini among megachilids is that of Gogala (1995), using nine taxa, no outgroup and 11 morphological characters. In that study, *Dioxys* Lepeletier and Serville came out as the sister group to all other Megachilinae; however, as pointed out by Michener (2007), some of the characters used were highly variable and incorrectly polarised.

The remaining three tribes (Anthidiini, Osmiini and Megachilini) contain most of the species of Megachilidae. While the relationships among the few genera of Fidelini, Lithurgini and Dioxyini have been explored by Michener (1983, 1996) and Engel (2001, 2002, 2004), relationships among the numerous and diverse genera of the remaining tribes have not been studied in detail, except for the molecular analysis of the Osmiini (Praz *et al.*, 2008). The 833 species of Anthidiini (Ascher & Pickering, 2011) have been grouped in 37 genera in the classification of Michener (2007) but numerous neotropical taxa assigned to the subgeneric level by him, many of them monotypic or consisting of a few unusual species, have been accorded generic status (Urban & Moure, 2007). For example, the Neotropical genus *Hypanthidioides* Moure (*sensu* Michener, 2007) contains 51 species grouped into ten subgenera (Michener, 2007; Ascher & Pickering, 2011) that are treated at the generic level

in the classification of Urban & Moure (2007). Some subgenera are monotypic or contain a few species with unusual characters related to adaptations for pollen collecting (e.g. modified hairs on the mouthparts) or secondary sexual characters (e.g. spines on the hind coxa of the male) (Gonzalez & Griswold, 2011). Conversely, in a regional revisionary work, all nonparasitic Anthidiini were included in a single genus *Anthidium* (Warncke, 1980). A worldwide phylogenetic study of the tribe is needed. The phylogenetic analysis of Anthidiini by Müller (1996) only included western Palearctic nonparasitic species and its primary objective was to study floral associations. A recent attempt to explore the generic relationships of the tribe from a global perspective is that of Combey *et al.* (2010).

A total of 1074 species are currently included in the Osmiini (Ascher & Pickering, 2011). No morphological synapomorphies are known for Osmiini and it has long been suspected to be paraphyletic, from which one or all other megachiline tribes originated (e.g. Engel, 2001; Michener, 2007). A comprehensive molecular phylogenetic analysis of the tribe, including representative species of 18 of the 19 currently recognised genera, supported the nonmonophyly of the tribe (Praz *et al.*, 2008) with the genera *Afroheriades* Peters, *Noteriades* Cockerell, *Pseudoheriades* Peters, and possibly *Ochreriades* Mavromoustakis, excluded from the tribe. Interestingly, the resulting position of *Noteriades* within the Megachilini was first suggested by Griswold (1985); the phylogenetic placement of the other four genera remains unclear (Griswold & Gonzalez, 2011).

Another example of a genus that cannot be placed with confidence at the tribal level is that of *Aspidosmia* Brauns (Figs 1–3). This Sub-Saharan genus, initially described as a subgenus of *Osmia* Panzer, and retained within the Osmiini until recently (e.g. Griswold, 1985; Griswold & Michener, 1997), is presently included within the Anthidiini (Michener, 2007). *Aspidosmia* consists of two morphologically distinct species that exhibit a mixture of Osmiini and Anthidiini features as well as unique characters found nowhere else in Megachilidae except in basal lineages. As in many osmiines, it lacks yellow integumental markings on the body (except for the maculate clypeus of the male), the prestigma is longer than the stigma and the second recurrent vein (2m-cu) is basal to 2r-m. However, the pretarsal claws are cleft and the shape of the male genitalia and associated sterna are similar to those of Anthidiini (Peters, 1972; Michener, 2007). The presence of a hind tibial scopa (Fig. 1), in addition to the metasomal scopa of all nonparasitic megachilids, is the most remarkable character of *Aspidosmia*, shared only with *Pararhophites* Friese and the fossil taxa.

Accounting for 2021 species worldwide (Ascher & Pickering, 2011), the Megachilini is the most common and diverse of all Megachilidae. Several genera have been traditionally recognised in this tribe but only three are currently accepted in the classification of Michener (2007). Most species belong to the nonparasitic genus *Megachile*. The phylogenetic relationships among bees in the tribe were recently explored by Gonzalez



Figs 1–3. Lateral habitus (1) and frontal views of female *Aspidosmia* (2, 3) showing pollen on both sternal and tibial scopae. 1, 2, *A. volkmanni*; 3, *A. arnoldi*.

(2008). A new multigeneric classification and nomenclatural changes were proposed in that review.

A recent molecular phylogenetic analysis of the Megachilidae, primarily done to trace the evolution of nesting biology, indicates that the family had a Gondwanan origin, arising relatively rapidly after the origin of bees about 100 Ma (Litman *et al.*, 2011). That study also suggests that Fideliinae, Fideliini, Anthidiini and Osmiini are not monophyletic.

Fossil record

The fossil record of Megachilidae is relatively good in comparison to that for other bee families. The available material is restricted to Cenozoic deposits of the Northern Hemisphere

(reviewed by Engel & Perkovsky, 2006). Particularly interesting, owing to the many plesiomorphic or unusual characters, are the extinct genera from the Eocene Baltic amber: *Protolithurgus* Engel, *Ctenoplectrella* Cockerell, *Glaeosmia* Engel and *Glyptapis* Cockerell. *Protolithurgus* has the distinctive flattened first metasomal tergum that characterises the extant Lithurgini but the hind basitarsus is flattened, there are long hairs on the outer surface of the hind tibia suggesting a pollen collecting scopa, there are two rather than three teeth on the mandible, and the typical spicules found on the outer surfaces of the lithurgine tibiae are absent. As shown by Engel (2001), *Protolithurgus* is likely the sister group to the remaining lithurgines.

The remaining genera are puzzling because unique combinations of features make them challenging to fit among their

extant relatives. Cockerell (1909), in erecting the subfamily Glyptapinae for *Glyptapis* and *Ctenoplectrella*, commented on its likely basal position within the Megachilidae and its resemblance to the apid genus *Ctenoplectra* Kirby. The latter comment was used by subsequent authors to erroneously include them in the same apine tribe, Ctenoplectrini Cockerell. Engel (2001) was the first to recognise this error and tentatively transferred them to the Osmiini, placing *Glyptapis* in the subtribe Glyptapina and *Ctenoplectrella* and *Glaesomia* in the subtribe Ctenoplectrellina. All of these genera have aroliae and cleft pretarsal claws on all legs and, unlike all members of the subfamily Megachilinae, an apparently short labrum, much broader than long. The four species of *Glyptapis* are remarkable in having hairy compound eyes (as in the megachiline genus *Coelioxys* Latreille and the anthidiine *Pachyanthidium* of the subgenera *Trichanthidium* Cockerell and *Trichanthidioides* Michener and Griswold) and foveolate mesepisterna. Later, Engel (2005) elevated them to tribal rank within Megachilinae (Table 1). To date, the phylogenetic position of these genera remains unknown and their taxonomic placement unresolved.

The purpose of this paper is to explore the relationships of the tribes in Megachilidae based on adult morphological data, to validate the tribal assignment for included genera, and to develop a robust phylogeny-based classification of the family. Our phylogenetic analyses included adult external morphological characters for representative taxa of about 80% of the extant generic-level diversity of the family. We include in the taxa analysed representatives of all of the puzzling extinct and extant genera of uncertain affinities (e.g. *Aspidosmia*) in an attempt to resolve their phylogenetic positions and taxonomic placements. In addition we discuss the evolutionary history and biogeography of the family, propose alternative classifications, and provide a revised key to the extant tribes of Megachilinae.

Materials and methods

Taxon selection

We used species as terminals in all phylogenetic analyses. We attempted to include representatives of all megachilid genera, choosing species that cover the maximal morphological and biogeographical diversity of the group. When possible, and to account for intraspecific variation, we studied more than one specimen of each sex of each species, and other species of the included genera. We examined the primary types of *Xeroheriades micheneri* Griswold, *Xenostelis polychroma* Baker and all seven fossil taxa included in the analysis. Based on the phylogeny of Roig-Alsina & Michener (1993), we used one species each of two genera of the family Melittidae and eight genera of Apidae as outgroups (Table 2). With the exception of the holotype of *X. polychroma* in the Snow Entomological Museum, University of Kansas, Lawrence, KS, and the fossils in the American Museum of Natural History, New York, all specimens studied are in the U.S. National

Table 2. List of species used in the phylogenetic analysis of the family Megachilidae.

MELITTIDAE
<i>Macropis (Macropis) nuda</i> (Provancher, 1882) [U.S.A.: Idaho]
<i>Melitta (Melitta) leporina</i> (Panzer, 1799) [France; Spain; Iran]
APIDAE
APINAE
<i>Apis mellifera</i> Linnaeus, 1758 [U.S.A.: Utah]
<i>Exomalopsis (Stilbomalopsis) solani</i> Cockerell, 1896 [Mexico: Sinaloa; U.S.A.: Arizona]
<i>Diadasia (Coquillettapis) australis</i> (Cresson, 1878) [U.S.A.: Arizona, Utah]
NOMADINAE
<i>Nomada utahensis</i> Moalif, 1988 [U.S.A.: Utah]
XYLOCOPINAE
<i>Ceratina calcarata</i> Robertson, 1900 [U.S.A.: Illinois, North Carolina]
MEGACHILIDAE
FIDELIINAE
Fideliini
<i>Fidelia (Parafidelia) pallidula</i> (Cockerell, 1935) [South Africa: Cape Province]; <i>F. (Fidelia) villosa</i> Brauns, 1902 [South Africa: Cape Province]; <i>F. (Fideliana) braunsiana</i> Friese, 1905 [South Africa: Cape Province]; <i>F. (Fideliopsis) major</i> Friese, 1911 [South Africa: Cape Province]
<i>Neofidelia profuga</i> Moure & Michener, 1955 [Chile: Huasco Province]
Pararhophitini
<i>Pararhophites orobinus</i> (Morawitz, 1875) [Karakalpakstan; Pakistan]; <i>P. quadratus</i> (Friese, 1898) [Egypt]
MEGACHILINAE
Anthidiini
<i>Afranthidium (Capanthidium) capicola</i> (Brauns, 1905) [South Africa: Cape Province]
<i>Anthidiellum (Loyolanthidium) robertsoni</i> (Cockerell, 1904) [U.S.A.: Utah]
<i>Anthidioma chalicodomoides</i> Pasteels (1984) [South Africa: Cape Province]
<i>Anthidium (Anthidium) porterae</i> Cockerell, 1900 [U.S.A.: Arizona, New Mexico]
<i>Anthodioctes (Anthodioctes) calcaratus</i> (Friese, 1921) [Costa Rica: Guanacaste]
<i>Aspidosmia arnoldi</i> (Brauns, 1926); <i>A. volkmanni</i> (Friese, 1909) [South Africa: Cape Province]
<i>Aztecanthidium tenochtitlanicum</i> Snelling, 1987 [Mexico: Jalisco]
<i>Cyphanthidium intermedium</i> Pasteels, 1969 [Namibia: Karibib]
<i>Dianthidium (Dianthidium) subparvum</i> Swenk, 1914 [U.S.A.: California, Utah]
<i>Duckeanthidium thielei</i> Michener [Costa Rica: Heredia]
<i>Eoanthidium (Clistanthidium) rothschildi</i> (Vachal, 1909) [South Africa: Limpopo; Tanzania]
<i>Epanthidium (Epanthidium) bicoloratum</i> (Smith, 1879) [Argentina: Catamarca, Salta]
<i>Euasps abdominalis</i> (Fabricius, 1773) [Zambia]
<i>Gnathanthidium prionognathum</i> (Mavromoustakis, 1935) [South Africa: Cape Province]
<i>Hoplostelis (Hoplostelis) bivittata</i> (Cresson, 1878) [Costa Rica: Guanacaste]
<i>Hypanthidioides (Michanthidium) ferrugineum</i> (Urban, 1992 [1994]) [Argentina: Tucuman]
<i>Hypanthidium (Hypanthidium) mexicanum</i> (Cresson, 1878) [Mexico: Jalisco]

Table 2. Continued

Icteranthidium ferrugineum (Fabricius, 1787) [Egypt: Fayum Province; Tunisia]

Indanthidium crenulaticauda Michener & Griswold, 1994 [India: Poona]

Notanthidium (Notanthidium) steloides (Spinola, 1851) [Chile: Regions IV and VIII]

Pachyanthidium (Pachyanthidium) katangense Cockerell, 1930 [Zimbabwe, Congo]

Plesianthidium (Spinanthidiellum) rufocaudatum (Friese, 1909) [South Africa: Cape Province]

Pseudoanthidium (Micranthidium) lanificum (Smith, 1879) [Cameroon: Fako Province; Congo: Kama]

Rhodanthidium (Rhodanthidium) septemdentatum (Latreille, 1809) [Greece: Lesvos]

Serapista rufipes (Friese, 1904) [South Africa: Cape Province]

Stelis (Stelis) linsleyi Timberlake, 1941 [U.S.A.: California]

Trachusa (Heteranthidium) larreae (Cockerell, 1897) [U.S.A.: Arizona, California, Utah]

Xenostelis polychroma Baker, 1999 [Yemen: Socotra Island]

Dioxyini

Aglaopis tridentata (Nylander, 1848) [Austria: Burgenland]

Dioxys pomonae Cockerell, 19010 [U.S.A.: California, Utah]

Lithurgini

Lithurgus (Lithurgopsis) apicalis Cresson, 1875 [U.S.A.: Arizona, New Mexico, Utah]

Microthurge corumbae (Cockerell, 1901) [Bolivia: Santa Cruz]

Trichothurgus aterrimus (Cockerell, 1914) [Chile: Atacama]

Megachilini

Coelioxys (Boreocoelioxys) octodentata Say, 1824 [U.S.A.: California, Kansas, Nevada, Utah]

Megachile (Chelostomoides) angularum Cockerell, 1902 [U.S.A.: California, Nevada]; *M. (Creightonella) discolor* Smith, 1853 [South Africa: Cape Province]; *M. (Sayapis) pugnata* Say, 1873 [U.S.A.: Virginia, Utah]

Radoszkowskiana rufiventris (Spinola, 1838) [Egypt: Cairo, Mariut]

Osmiini

Osmiina

Afroheriades hyalinus Griswold & Gonzalez, 2011 [South Africa: Cape Province]

Ashmeadiella (Ashmeadiella) aridula Cockerell, 1910 [U.S.A.: Nevada, Texas, Utah]

Atoposmia (Atoposmia) abjecta (Cresson, 1878) [U.S.A.: California]

Chelostoma (Chelostoma) florissonne (Linnaeus, 1758) [Hungary: Békés; Sweden: Öland Island]

Haetosmia vechti (Peters, 1974) [Israel: Beersheba; Pakistan: Baluchistan]

Heriades (Heriades) truncorum (Linnaeus, 1758) [Austria, Sweden]

Hofferia schmiedeknechti (Schletterer, 1889) [Bulgaria: Albena; Greece: Crete]

Hoplitis (Monumetha) albifrons (Kirby, 1873) [U.S.A.: Utah]; *H. (Stenosmia) flavicornis* (Morawitz, 1877) [Mongolia, Uzbekistan]

Noteriades spinosus Griswold & Gonzalez, 2011 [Thailand: Chiang Mai Province]

Ochreeriades fasciatus (Friese, 1899) [Israel: Ramot Naftali, Galilee]

Osmia (Osmia) lignaria Say, 1837 [U.S.A.: Utah, Nevada]; *O. (Odontanthocopa) scutellaris* (Morawitz, 1868) [Bulgaria: Albena, Galata]

Table 2. continued

Othinosmia (Megaloheriades) globicola (Stadelmann, 1892) [South Africa: Cape Province]

Protosmia (Chelostomopsis) rubifloris (Cockerell, 1898) [U.S.A.: California]

Pseudoheriade moricei (Friese, 1897) [Egypt: Ismalia, Mariut]

Stenoheriades asiaticus (Friese, 1921) [Turkey: Antalya]

Wainia (Caposmia) elizabethae (Friese, 1909) [South Africa: Cape Province]

Xeroheriades micheneri Griswold, 1986 [U.S.A.: California]

Glyptapina^a

Glyptapis densopunctata Engel, 2001; *G. disareolata* Engel, 2001

Ctenoplectrellina^a

Ctenoplectrella cockerelli Engel, 2001; *C. grimaldii* Engel, 2001; *C. viridiceps* Cockerell, 1909

Glaesosmia genalis Engel, 2001

Protolithurgini^a

Protolithurgus ditomeus Engel, 2001.

^aExtinct taxa from Baltic amber.

Locality data associated with examined specimens in square brackets following names. Generic and subgeneric names follow those of Michener (2007).

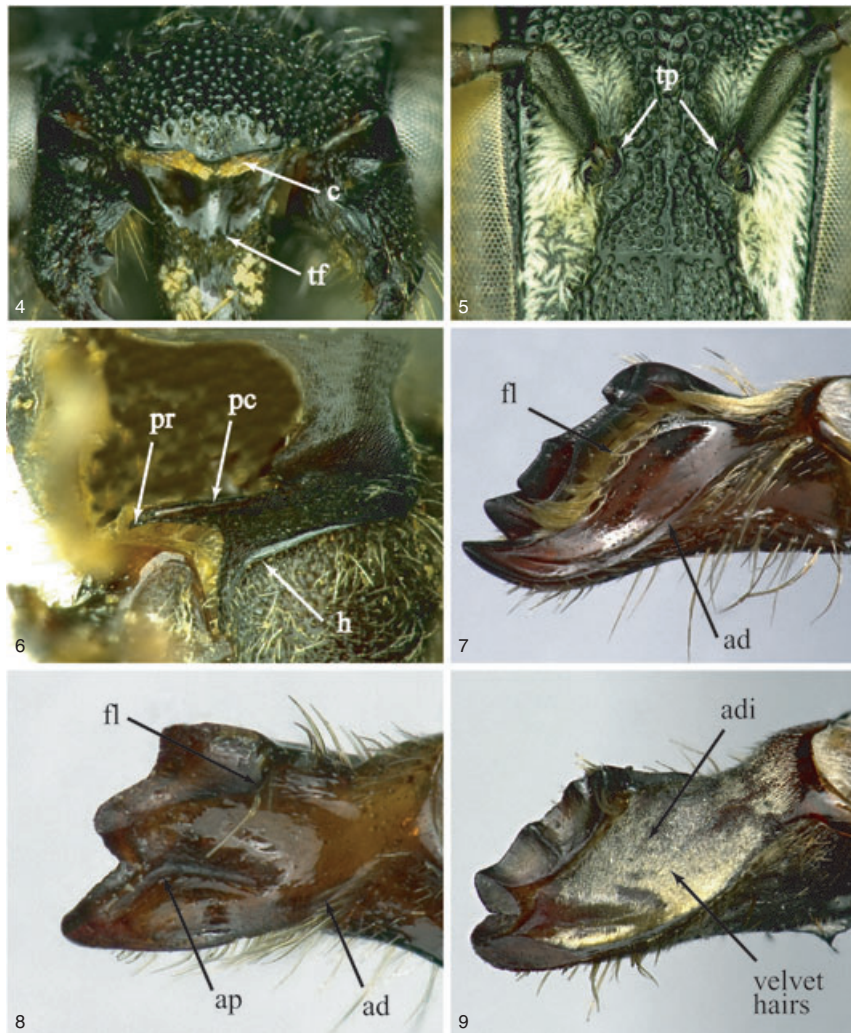
Pollinating Insects Collection, Bee Biology and Systematics Laboratory, Utah State University, Logan, UT.

Morphological characters

We used or modified many of the characters discussed by Michener & Fraser (1978), Winston (1979), Roig-Alsina & Michener (1993) and Michener (2007). Other characters were based on our own observations of the adult male and female external morphology. We also dissected and studied the tongue, mandible and the male and female genitalia with their associated sterna. These structures were cleared with 10% KOH at room temperature for about 24 h and then washed with 70% ethanol before storing in glycerin.

A total of 200 characters were coded. Many characters are present in both sexes (e.g. those of the tongue); these were coded in only the female sex to avoid duplication. The majority of characters were binary (87.5%) and were coded from all parts of the adult body in the female; in contrast, most characters of the male were coded from the metasoma (40 of 49 characters). Not all characters could be coded for all species because some are only known from the type specimen (e.g. *Xenostelis* Baker), few specimens (e.g. *Indanthidium* Michener and Griswold) or from one sex (e.g. *Anthidioma* Pasteels) and could not be dissected. Also, most fossil Megachilidae from Baltic amber are known only from the female and many external characters could not be seen due to the position of the specimen or the condition of the amber matrix. This missing information was represented by a question mark in the data matrix. Some characters are not applicable to all species and these were coded as missing data (-). In the discussion, characters are referenced in the form 78-2, where 78 is the character and 2 the character state.

We examined, measured and illustrated character states using a Leica MZ12 stereomicroscope with an ocular micrometer.



Figs 4–9. Clypeus, labrum and mandibles (4), detail of face (5), hypostomal area (6) (labiomaxillary complex removed from head), and inner views of mandibles of female (7–9). 4, *Osmia scutellaris*; 5, *Noteriades spinosus*; 6, *Stelis linsleyi*; 7, *Megachile* sp.; 8, *Atoposmia abjecta*; 9, *Megachile* (*Callomegachile*) sp. Abbreviations: ad, adductor ridge; adi, adductor interspace; ap, adductor apical ridge; c, clypeal brush; fl, inner fimbriate line; h, hypostomal carina; pc, paramandibular carina; pr, paramandibular process; tf, transverse fringe of labrum; tp, torular process.

Morphological terminology follows that of Michener (1944, 2007) and Engel (2001). The abbreviations F, OD, S and T, are used for flagellomere, median ocellar diameter, and metasomal sterna and terga, respectively. Photomicrographs were taken using a Keyence® VHX-500F Digital Imaging System and processed with Adobe® Photoshop® 7.0.

The following are the morphological characters used in the phylogenetic analysis.

Females

Head

1. Clypeal margin: 0 = not overhanging base of labrum; 1 = slightly overhanging labral base; 2 = strongly produced, distinctly overhanging labral base.

2. Clypeus with well-developed lateral brush of hairs beneath distal margin: 0 = absent; 1 = present (Fig. 4).
3. Clypeus with a slender, midapical projection: 0 = absent; 1 = present.
4. Clypeoantennal distance: 0 = short (equal to or shorter than vertical diameter of antennal socket); 1 = long ($\geq 1.2 \times$ antennal socket).
5. Position of anterior tentorial pit: 0 = at the intersection of subantennal and epistomal sulci; 1 = on epistomal sulcus below intersection with subantennal sulcus.
6. Insertion of the subantennal sulcus: 0 = directed toward lower margin of antennal socket; 1 = directed toward outer margin of antennal socket.
7. Subantennal sulcus: 0 = straight or curved inward, not distinctly arcuate outward; 1 = distinctly arcuate outward.

8. Supraclypeal area: 0 = flat or nearly so, at about the same level as the clypeus; 1 = distinctly elevated or with median prominence.
9. Interantennal distance: 0 = equal or shorter than antennocular distance; 1 = greater than antennocular distance.
10. Juxtantennal carina: 0 = absent; 1 = present.
11. Juxtantennal swelling: 0 = absent; 1 = present.
12. Antennal socket (torulus) with a distinct mesal projection on upper half: 0 = absent; 1 = present (Fig. 5). *Protosmia rubifloris* seems to have a similar projection but it is not as developed as in Megachilini. We coded that species as having character state 0.
13. Length of pedicel: 0 = distinctly shorter than F1; 1 = about as long as F1; 2 = much longer than F1 (sometimes about as long as or longer than combined lengths of F1 and F2).
14. Length of F1: 0 = shorter than combined lengths of F2 and F3; 1 = as long as or longer than combined lengths of F2 and F3.
15. Paraocular area integumental punctation: 0 = not differentiated from more median part of frons; 1 = narrow area bordering eye with punctures sparser and smaller than on frons; 2 = broad, ovoid, sharply delimited area with sparser, smaller punctures.
16. Paraocular carina: 0 = absent; 1 = present.
17. Color of paraocular area: 0 = concolorous with rest of face; 1 = not concolorous with rest of face, with yellow or pale maculations.
18. Preoccipital carina: 0 = absent; 1 = present.
19. Preoccipital carina: 0 = continuous, present on gena and dorsal edge of head behind vertex; 2 = discontinuous, present on gena only; 3 = discontinuous, present on vertex only.
20. Ocelloccipital distance: 0 = short ($1-3 \times OD$); 1 = long ($\geq 3.1 \times OD$).
21. Ventral portion of hypostomal carina, near mandible: 0 = directed to medial margin of mandibular socket; 1 = curving toward posterior margin of mandibular socket.
22. Paramandibular process: 0 = short or absent; 1 = long (Fig. 6).
23. Paramandibular carina: 0 = short, ending about half or less the distance between paramandibular process and hypostomal carina; 1 = long, ending at or close to the hypostomal carina (Fig. 6).
24. Labrum: 0 = broader than long; 1 = much longer than broad. Engel (2001) mentioned that in all extinct genera of Megachilidae the labrum appears to be broader than long; however, the apex of the labrum, obscurely visible in the holotype of *Glyptapis densopunctata* and paratype of *G. disareolata*, appears to be longer than broad. We coded those two species as having character state 1 while the remaining extinct taxa were coded as missing data. Coding all extinct taxa as having either character 0, 1, or as missing data did not change the resulting topology.
25. Labrum anterior surface: 0 = with basal polished area, sometimes elevated, clearly delimited from punctate and hairy disc; 1 = without basal polished area.
26. Basal projections of labrum: 0 = absent; 1 = present, distinct.
27. Labral fossa: 0 = absent; 1 = present (Michener, 1944: fig. 124).
28. Labrum with a distinct transverse fringe of erect hairs on basal third: 0 = absent; 1 = present (Fig. 4).
29. Labral erect hairs: 0 = not forming a U- or V-shaped row; 1 = forming U- or V-shaped row with midpoint near apex of labrum and arms extending basad nearly to lateral margins of labrum.
30. Labrum with a distinctly long, strong apical or subapical tight tuft of hairs: 0 = absent; 1 = present.
31. Labrum with minute, yellowish, appressed or erect hairs covering anterior surface: 0 = absent; 1 = present.
32. Mandible with cranial condyle: 0 = contiguous with lateral clypeal margin; 1 = partly covered by lateral clypeal margin, which is usually elevated over condyle (Roig-Alsina & Michener, 1993: fig. 4).
33. Mandible with upper carina, trimmal carina and fimbriate line united in a Y-shaped pattern: 0 = absent; 1 = present (Michener & Fraser, 1978: fig. 25).
34. Strong adductor apical ridge of mandible: 0 = absent; 1 = present. The *adductor apical ridge* (Fig. 8) is a new name for a ridge found on the inner surface of the mandible that extends close to the upper margin of the apical tooth and distal to the adductor ridge. The ridge corresponds to one of the unnamed secondary ridges indicated by the letter R in Michener & Fraser (1978: e.g. figs 33, 34).
35. Adductor apical ridge basally: 0 = not merging with the adductor ridge (Fig. 8); 1 = merging with the adductor ridge.
36. Inner fimbriate line of mandible: 0 = short, extending somewhat parallel to upper mandibular margin (Michener & Fraser, 1978: fig. 25); 1 = long, extending somewhat parallel to apical margin of mandible (Fig. 7).
37. Hairs on adductor interspace of mandible: 0 = absent (Figs 7, 8); 1 = present.
38. Hairs on adductor interspace of mandible forming velvet mat: 0 = absent; 1 = present (Fig. 9).
39. Mandible with outer premarginal impressed fimbria: 0 = reduced or absent; 1 = present, distinct (Michener & Fraser, 1978: fig. 33).
40. Mandibular apex: 0 = simple or with single tooth or with ventral tooth longest; 1 = with ventral tooth shorter than next tooth (Michener & Fraser, 1978: fig. 29).
41. Mandible with pollex region: 0 = not expanded distally; 1 = expanded to form two to several teeth (Michener & Fraser, 1978: fig. 34).
42. Mandible with basal tooth (tooth of pollex): 0 = smaller than rutellum; 1 = as large as the rutellum (Michener & Fraser, 1978: fig. 25).
43. Mandible with basal tooth: 0 = anteriorly directed, at most as wide as remaining teeth; 1 = posteriorly

- directed, distinctly broader than remaining teeth, except apical tooth (Michener, 2007: fig. 82-3a).
44. Mandible with two to several small teeth on pollex region: 0 = absent; 1 = present (Michener, 2007: fig. 82-3a).
 45. Mandible with cutting edge between teeth: 0 = absent; 1 = present in the second or third mandibular interspace, or both (Michener, 2007: fig. 84-11).
 46. Distal end of mentum: 0 = entire; 1 = concave (Winston, 1979: fig. 10b); 2 = notched (Winston, 1979: fig. 10d); 3 = not sclerotised.
 47. Subligular process of prementum (Winston, 1979: fig. 2c): 0 = fully sclerotised and united to rest of prementum (Roig-Alsina & Michener, 1993: fig. 16); 1 = separated from rest of prementum by weak line.
 48. Shape of subligular process of prementum: 0 = elongated, long and narrow, styliiform (Winston, 1979: fig. 12f); 1 = broader, apex truncated or nearly so (Winston, 1979: fig. 38); 2 = broad, with pointed apex (Winston, 1979: fig. 28); 3 = membranous (Winston, 1979: fig. 40); 4 = weakly sclerotised distally, appearing bilobed.
 49. Ligular arms: 0 = fused with prementum (Winston, 1979: fig. 14c); 1 = distinct from prementum, with no region of continuous sclerotization between them (Winston, 1979: fig. 14a, b).
 50. First and second labial palpomeres: 0 = not particularly flattened, similar in form and length to third and fourth palpomeres; 1 = greatly elongated compared to third and fourth palpomeres.
 51. First labial palpomere with a distinct basal concavity on inner margin: 0 = absent; 1 = present (Winston, 1979: fig. 11a).
 52. Length of first labial palpomere: 0 = at least twice as long as the second; 1 = about as long as second; 2 = short, 0.8–0.5 × length of the second; 3 = very short, 0.17–0.3 × length of second.
 53. Third labial palpomere: 0 = flattened, apically directed as is second; 1 = not flattened, laterally directed from second. The mouthparts of *Protolithurgus ditomeus* are not visible in the holotype, as in all other fossil taxa examined, and could not be coded. The statement indicating that the third labial palpomere is on the same axis as the second in the original description of *P. ditomeus* seems to be a typographical error because such a character was not coded in the data matrix presented in the same publication (c.f. Engel, 2001; p. 140).
 54. Basistipital process of stipes: 0 = absent or reduced; 1 = present (Winston, 1979: fig. 5a).
 55. Dististipital process of stipes: 0 = absent; 1 = present (Winston, 1979: fig. 7b).
 56. Stipital comb: 0 = absent; 1 = present (Winston, 1979: fig. 4a).
 57. Galea: 0 = without row of bristles; 1 = with longitudinal row of bristles on anterior margin of inner surface (Roig-Alsina & Michener, 1993: fig. 15b).
 58. Galeal blade: 0 = uniformly sclerotised or only narrowly desclerotised near apex; 1 = with posterior margin broadly desclerotised almost to base (Roig-Alsina & Michener, 1993: fig. 15).
 59. Galeal blade at midpoint with internal sclerotised surface: 0 = as wide as external surface; 1 = at most two-thirds as wide as external surface (Roig-Alsina & Michener, 1993: fig. 15b, c); 2 = three fourths or more as wide as external surface but narrower than external surface.
 60. Number of maxillary palpomeres, including basal segment: 0 = two; 1 = three; 2 = four; 3 = five; 4 = six. Although the generic descriptions of Engel (2001) indicate that the maxillary palpus of *Glyptapis*, *Ctenoplectrella* and *Glaesosmia* is four-segmented, we coded these taxa as having missing data because we could not see this structure in the examined specimens.
- ### Mesosoma
61. Pronotal lobe with strong carina or lamella: 0 = absent; 1 = present.
 62. Dorsal margin of pronotal collar: 0 = not swollen laterally; 1 = distinctly swollen laterally (Griswold, 1994; fig. 1).
 63. Tegula with margins: 0 = not distinctly thickened; 1 = distinctly thickened.
 64. Episternal groove: 0 = absent; 1 = present. There is no explicit mention of this character in the original description of the fossil *P. ditomeus* but an examination of the holotype revealed that the episternal groove is present, forming with the scrobal groove a distinct convex area, the hypopimeron, characterised by having shorter hairs than on adjacent areas of the mesepisternum as described by Engel (2001).
 65. Omaulus: 0 = rounded; 1 = angular, carinate, or lamellate.
 66. Omaular carina: 0 = complete, reaching midventer or nearly so; 1 = incomplete, limited to upper half of mesepisternum.
 67. Metepisternum width at level of upper metepisternal pit divided by height of metepisternum measured from lower end to apex of wing process: 0 = 0.20 or more; 1 = 0.19 or less. In both sides of the holotype of *P. ditomeus* the anterior margin of the metepisternum is strong and well-defined, whereas the posterior margin is much weaker and difficult to see because of debris and internal fractures of the amber. The metepisternum appears to be broad dorsally, becoming narrower below as in *Trichothurgus* Moure (e.g., Griswold, 1985; fig. 3). We have tentatively coded this species as having character state 1.
 68. Metepisternum with dorsal carina: 0 = absent; 1 = present.
 69. Anterior margin of scutum in profile: 0 = rounded, without distinctly different surface sculpture; 1 = truncate, perpendicular, or nearly so, shinier and less punctate than dorsal portion.

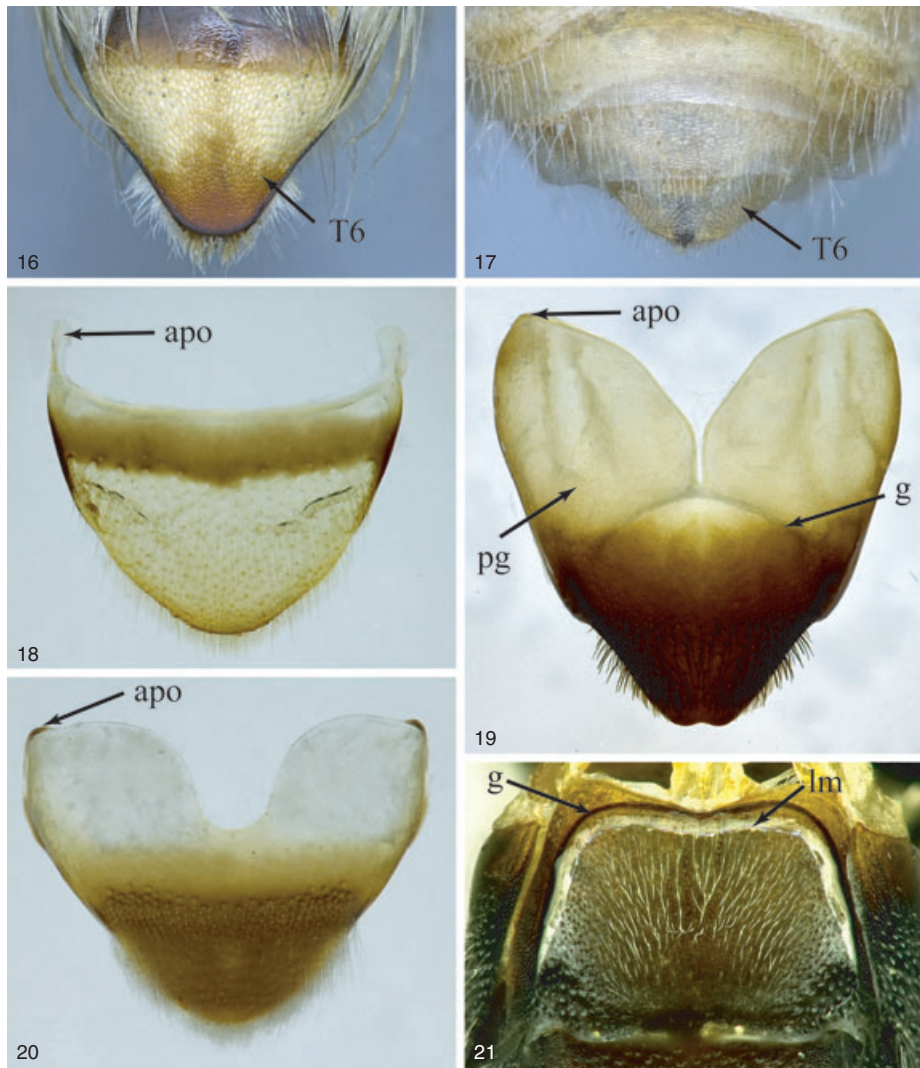


Figs 10–15. Lateral views of scutum (10, 11), dorsal and posterodorsal views of propodeum (12, 13), outer surface of fore tibia (14), and sixth metasomal tergum of female (15). 10, *Aspidosmia arnoldi*; 11, *Pachyanthidium katangense*; 12, *Fidelia pallidula*; 13, *Afranthidium capicola*; 14, *Noteriades spinosus*; 15, *Hofferia schmiedeknechti*. Abbreviations: aop, articulating orifice of propodeum; ma, posterior marginal area of propodeum; pa, preaxilla; pp, propodeal pit; sg, submarginal groove of propodeum.

70. Disc of scutum in profile: 0 = convex; 1 = flat or nearly so.
71. Dorsum of mesosoma with yellow or reddish maculations: 0 = absent; 1 = present.
72. Parapsidal line: 0 = long ($\geq 0.4 \times$ tegula length); 1 = short ($\leq 0.3 \times$ tegula length).
73. Preaxilla (below the posterolateral angle of scutum): 0 = sloping, with hairs as long as those on adjacent sclerites (Fig. 10); 1 = vertical, usually nearly hairless (Fig. 11).
74. Axilla: 0 = without posteriorly oriented acute angle or spine; 1 = with posteriorly oriented acute angle or spine.
75. Axilla laterally: 0 = not carinate; 1 = carinate.
76. Scutellum in profile: 0 = not projecting over metanotum; 1 = projecting over metanotum.
77. Distal margin of scutellum as seen from above: 0 = convex, not truncate; 1 = truncate.
78. Scutellum with posterior margin: 0 = not carinate or lamellate; 1 = distinctly carinate or lamellate, at least laterally.
79. Scutoscutellar suture: 0 = narrow, without smooth and hairless bottom; 1 = wide and deep, with smooth and hairless bottom.
80. Metanotum in profile: 0 = subhorizontal or slanting on same plane as scutellum, scutellum also subhorizontal or slanting; 1 = vertical, not overhung by convex

- scutellum whose posterior margin is more or less vertical; 2 = vertical, strongly overhung by scutellum whose posterior margin faces downward.
81. Metanotum with median tubercle or spine: 0 = absent; 1 = present (Michener, 2007; fig. 83-1).
 82. Propodeum in profile: 0 = with a nearly horizontal basal zone, behind which it rather abruptly turns downward to form the declivous posterior surface; 1 = with a steeply slanting or sometimes convex basal zone or entirely declivous.
 83. Basal zone of propodeum with distinct row of pits: 0 = absent; 1 = present (Michener, 2007; fig. 82-14).
 84. Propodeal basal zone: 0 = not bounded by a posterior carina or carina incomplete; 1 = bounded by a complete posterior carina.
 85. Propodeal triangle with hairs: 0 = absent; 1 = present, widespread.
 86. Propodeal triangle with integument: 0 = largely smooth and shiny; 1 = dull, lineolate, imbricate, minutely punctate or rugose.
 87. Propodeal pit: 0 = rounded or elongate, but not linear; 1 = linear.
 88. Propodeum with a shiny fovea behind spiracle defined by posterior carina: 0 = absent; 1 = present (Michener, 2007; fig. 82-8).
 89. Posterior marginal area of propodeum dorsomedially: 0 = rounded or flat, not carinate in lateral view, distinctly projecting posteriorly, submarginal groove usually shallow (Fig. 12); 1 = carinate or sharply angulated, not distinctly projecting posteriorly, submarginal groove usually deep (Fig. 13).
 90. Submarginal groove of propodeum: 0 = continuous, not submedially interrupted; 1 = not continuous, submedially interrupted by a distinct wall, forming a deep pit.
 91. Fore coxa with oblique carina or lamella medially: 0 = absent; 1 = present.
 92. Outer surfaces of fore and mid tibiae apically with acute angle and distinct notch anteriorly: 0 = absent; 1 = present (Fig. 14). In some species the acute angle is well-developed and it could be considered a spine, giving the impression of having an anterior and medial spine on the fore and mid tibiae. Some Anthidiini, such as *Euasps abdominalis*, *Pachyanthidium katangense* and *Stelis linsleyi*, also have two apical spines on the outer surface of the fore and mid tibiae; however, the other spine is on the posterior margin. In *Aztecantidium tenochtitlanicum* the anterior margin is developed into a small spine similar to that of Megachilini. However, the notch is absent and the apical margin is densely covered by hairs; such area is usually bare in Megachilini. We coded all these species as having character state 0.
 93. Fore tibial spur (antennal cleaner) with malus: 0 = simple, without a distinct projecting ridge on its anterior side; 1 = with low expansion at right angle to velum, curving apically into spine of malus; 2 = with strong expansion at right angles to velum, ending in strong angle or prong (Schönitzer & Renner, 1980; fig. 19).
 94. Length of apical portion of malus of fore tibial spur: 0 = long, at least half length of base of malus; 1 = short, less than half length of base of malus.
 95. Fore tibial spur with apical row of teeth on apex of malus (along same margin of velum): 0 = absent; 1 = present (Schönitzer, 1986; figs 1–10).
 96. Mid tibia outer apical margin: 0 = with a medial spine (Michener, 2007; fig. 82-6b); 1 = with medial and posterior spines (Michener, 2007; fig. 82-6a). In *Plesianthidium rufocaudatum*, *Epanthidium bicoloratum* and *Cyphanthidium intermedium* the medial spine is emarginate thus forming two spines; in *Xenostelis* there are two spines, but one is anterior and the other medial. Thus, we coded these species as having character state 0. The generic description of *Ctenoplectrella* in Engel (2001) indicates the absence of a spine on the outer surface of the mid tibia; however, such a spine is barely visible in the holotype of *C. cockerelli* and clearly visible in that of *C. viridiceps* and *C. phaeton* Gonzalez & Engel (2011). We coded these species as having character state 1.
 97. Mid tibial spur: 0 = finely serrate or ciliate; 1 = coarsely serrate.
 98. Hind coxa with ventral carina: 0 = absent; 1 = present.
 99. Hind tibia with basitibial plate: 0 = absent; 1 = present.
 100. Hind tibia with smooth, shiny, elevated bare area basally: 0 = absent; 1 = present.
 101. Hind tibia with distinct longitudinal carina on outer surface: 0 = absent; 1 = present.
 102. Hind tibia with strong tubercles or spicules on outer surface that do not end in hairs or bristles: 0 = absent; 1 = present (Michener, 2007; fig. 80-3b).
 103. Hind tibial scopae consisting of uniformly dispersed long hairs on outer surface: 0 = absent; 1 = present. We do not know if the long tibial hairs of the examined fossil taxa are functional scopae but we coded these species as having character state 1. Coding these species as having character state 0, as missing information, or excluding this character from the analyses did not change the resulting topology (see results).
 104. Inner hind tibial spur: 0 = with apex straight or nearly so; 1 = with apex strongly curved.
 105. Outer hind tibial spur: 0 = about as long as inner spur; 1 = distinctly shorter than inner spur.
 106. Hind basitarsus: 0 = $\geq 3\times$ longer than broad; 1 = $\leq 1.5\times$ longer than broad; 2 = 1.6–2.9 \times longer than wide.
 107. Hind basitarsus with distinctly long, simple hairs on posterior margin (as in *Fidelia*): 0 = absent; 1 = present.
 108. Pretarsal claws: 0 = bifurcate or cleft, inner ramus sometimes reduced; 1 = simple.
 109. Arolia: 0 = present; 1 = absent.
 110. Wing vestiture: 0 = hairy throughout (Michener, 2007; fig. 85-2); 1 = partly absent.
 111. Fore wing with distal papillae: 0 = absent; 1 = present. In *Anthidium porterae*, *Megachile pugnata* and *Megachile discolor* the papillae are more pointed and apically curved than the typical papillae found in apids,

- such as *Anthophora* Latreille. However, we coded these species as having character state 1.
112. Prestigma: 0 = elongate, more than twice as long as broad (Michener, 2007; fig. 76-1a); 1 = short, at most twice as long as broad (Michener, 2007; fig. 82-1c). The width of the prestigma was measured to its margin, not to the wing margin as shown in fig. 10-8 of Michener (2007), that is, we excluded the width of the costal vein in this measurement. In *Ctenoplectrella cockerelli* the prestigma is more elongate than shown in fig. 43 of Engel (2001); we coded this species as having character state 1.
 113. Stigma: 0 = longer than broad, length beyond vein r at least half as long as margin basal to vein r, margin within marginal cell convex or sometimes straight (Michener, 2007; fig. 68-1); 1 = longer than broad, length beyond vein r less than half as long as margin basal to vein r, margin within marginal cell concave (Michener, 2007; fig. 76-1b); 2 = not longer than broad, almost parallel-sided (Michener, 2007; fig. 82-1a); 3 = narrow, almost parallel-sided (as in *Apis mellifera*).
 114. Apex of marginal cell: 0 = pointed, on wing margin; 1 = separated from wing margin, pointed; 2 = separated from wing margin, rounded.
 115. Number of submarginal cells: 0 = three; 1 = two.
 116. Length of second submarginal cell on posterior margin: 0 = equal or longer than first on posterior margin; 1 = shorter than first on posterior margin.
 117. Basal vein: 0 = straight or nearly so, meeting Cu at acute angle; 1 = curved, meeting Cu at right angle (Engel, 2001; fig. 37).
 118. Basal vein: 0 = confluent or distal to cu-v (Engel, 2001; fig. 37); 1 = basal to cu-v.
 119. Vein 2m-cu (second recurrent vein): 0 = distinctly diagonal, strongly or gently curved before meeting with 2r-m; 1 = straight, or nearly so, for entire length (Michener, 2007; fig. 81-1b).
 120. Vein 2m-cu: 0 = basal to 2r-m (Michener, 2007; fig. 81-1b); 1 = confluent with, or distal to, 2r-m (Michener, 2007; fig. 82-1). In species with only two submarginal cells we are assuming that either the second abscissa of Rs (first submarginal crossvein) or the first r-m (second submarginal crossvein) is missing. Although the original description of *Ctenoplectrella cockerelli* indicates that 2m-cu is basal to 2r-m (Engel, 2001; fig. 43), a reexamination of the holotype revealed that these two veins are in fact confluent; thus, this species was coded as having character state 1.
 121. Jugal lobe of hind wing: 0 = long, one-half or more vernal lobe length; 1 = short, more than one-fourth but less than half, vernal lobe length; 2 = very short, less than one-fourth vernal lobe length. Both lobes were measured from the wing base to the apices of the lobes as indicated in Michener (2007).
 122. Hind wing with second abscissa of vein M + Cu: 0 = short, $\leq 3.0 \times$ length of vein cu-v; 1 = long, $\geq 3.1 \times$ length of vein cu-v.
- Metasoma
123. Coloration of metasomal terga: 0 = entirely of one color; 1 = not entirely of one color, with distinct white, yellow, or reddish maculations.
 124. T1: 0 = long, convex in profile, with posterior margin straight or nearly so, and with distinct anterior and dorsal surfaces; 1 = small, flattened, with posterior margin rounded, anterior and dorsal surfaces indistinguishable.
 125. Junction of anterior and dorsal surfaces of T1: 0 = rounded; 1 = angled; 2 = carinate.
 126. T2–T3 with deep postgradular grooves: 0 = absent; 1 = present.
 127. T2–T5 with distinct depressed marginal zones: 0 = absent; 1 = present.
 128. T5 with polished apical margin: 0 = absent or narrow and parallel-sided; 1 = broad, wider in middle, basal margin with long, stiff setae (Fig. 17).
 129. T6 with transverse preapical carina: 0 = absent; 1 = present.
 130. T6 in profile with dorsal surface: 0 = horizontal or subhorizontal; 1 = vertical or convex.
 131. T6 with wide apical hyaline flange: 0 = absent; 1 = present (Fig. 15).
 132. Pygidial plate: 0 = present; 1 = absent.
 133. Integument of pygidial plate: 0 = not papillate; 1 = papillate or minutely roughened (Fig. 16). The integument of the pygidial plate of *Melitta leporina* is strongly imbricate, thus somewhat resembling that of *Fidelia* Friese and *Neofidelia* Moure and Michener. We coded this species as having character state 0. This character does not apply to the two species of *Pararhophites* because they do not have a distinct pygidial plate (Fig. 17).
 134. Pygidial plate shape: 0 = triangular or nearly so, basally occupying about median one-third to one-fourth of tergal width (Michener, 2007; fig. 10-13); 1 = triangular or nearly so, basally occupying at least median two-thirds of tergal width (Fig. 16); 2 = elongate, very narrow, not triangular (Michener, 2007; fig. 80-2).
 135. T6 with sublateral teeth on apical margin: 0 = absent; 1 = present.
 136. Metasomal sternal scopa: 0 = absent; 1 = present.
 137. S1 with subapical tooth, spine or projection: 0 = absent; 1 = present.
 138. Length of S6: 0 = short, about as long as wide or shorter (length measured from apodeme to distal margin laterally); 1 = elongate, $\geq 1.2 \times$ longer than wide.
 139. Apodeme of S6: 0 = with distinct disc between marginal ridge and transapodemal ridge (Fig. 18; see also Packer, 2004; fig. 6a, d); 1 = with disc reduced or absent (Figs 19, 20; see also Packer, 2004; fig. 7f).
 140. Pregradular area of S6: 0 = not elongate laterally (Fig. 18); 1 = elongate laterally (Figs 19, 20).
 141. Width of elongated pregradular area of S6 (width measured just posterior to apodeme, in ventral view):



Figs 16–21. Dorsal apex of metasoma (16, 17) and sixth metasomal sternum of female (18–20) and third sternum of male (21). 16, *Fidelia villosa*; 17, *Pararhophites orobinus*; 18, *Hoplostelis bivittata*; 19, *Megachile pugnata*; 20, *Afranthidium capicola*; 21, *Stenoheriades asiaticus*. Abbreviations: apo, apodeme; g, gradulus; lm, lamella of gradulus; pg, pregradular area; T6, sixth tergum.

- 0 = narrow, one-fourth or less of concavity width; 1 = broad, at least half of concavity width (Figs 19, 20).
142. Pregradular area of S6: 0 = entirely or almost entirely sclerotised; 1 = entirely membranous or weakly sclerotised (often easily broken during dissection) (Figs 19, 20). In *Coelioxys octodentata* the pregradular area is membranous or weakly sclerotised only medially. We coded this species as having character state 0.
143. Concavity on basal margin of S6: 0 = deep, $\leq 2.0 \times$ wider than deep (Figs 19, 20); 1 = shallow, $\geq 2.1 \times$ wider than deep (Fig. 18).
144. Apex of S6: 0 = truncate; 1 = broadly to narrowly rounded; 2 = pointed.
145. S6 with apical spine: 0 = absent; 1 = present.
146. Stylet of sting apparatus: 0 = normal, distinct; 1 = reduced or absent.
147. Pubescence of apex of sting gonostylus: 0 = nearly hairless to sparsely covered by short hairs (\leq maximum gonostylus width in lateral view); 1 = densely covered by long plumose hairs ($\geq 1.2 \times$ gonostylar width).
148. Medial and lateral portions of marginal ridge of T7 hemitergite: 0 = not parallel-sided (e.g. Packer, 2003; fig. 5c); 1 = parallel to each other or nearly so (Packer, 2003; fig. 5a, b).
149. Lamina spiracularis of T7 hemitergite: 0 = smooth and shiny, not sculptured; 1 = weakly to markedly sculptured (Packer, 2003; fig. 2e).
150. T7 hemitergite with strong protrusion on the lamina spiracularis, near base of lateral process: 0 = absent or weak; 1 = present (Packer, 2003; fig. 5b).

151. Spiracle of T7 hemitergite: 0 = located on the basal two-thirds of hemitergite length; 1 = located at or near apical third of hemitergite length.

Male

Head

152. Colour of clypeus: 0 = concolorous with rest of face; 1 = yellow or pale, not concolorous with rest of face.
 153. Median flagellomeres (F5–F7): 0 = short ($\leq 1.3\times$ longer than broad); 1 = long ($\geq 1.6\times$ longer than broad).
 154. Mandible: 0 = edentate (i.e. without subapical tooth); 1 = with two teeth; 2 = with three or more teeth.
 155. Basal tooth of mandible: 0 = pointed; 1 = truncate.
 156. Inferior process of mandible: 0 = reduced or absent; 1 = present (e.g., Gonzalez & Griswold, 2007; figs 14, 17).

Mesosoma

157. Front coxal spine: 0 = absent; 1 = present (e.g., Gonzalez & Griswold, 2007; figs 25–27).
 158. Front tarsi: 0 = unmodified; 1 = modified, distinctively enlarged, excavated, inner surface frequently with dark spots (Michener, 2007; fig. 84-19a).
 159. Hind basitarsus: 0 = elongate, $\geq 4.0\times$ longer than broad; 1 = not elongate, $\leq 3.5\times$ longer than broad.
 160. Arolia: 0 = absent or minute; 1 = present, large.

Metasoma

161. T5 with lateral spine: 0 = absent; 1 = present.
 162. T6 with transverse preapical carina: 0 = absent; 1 = present, at least laterally.
 163. T6 with lateral spine: 0 = absent; 1 = present.
 164. T7: 0 = exposed, posteriorly directed; 1 = hidden, and/or anteriorly or ventrally directed.
 165. T7 with pygidial plate: 0 = present, distinct; 1 = absent, but sclerotised apical rim suggests apex of plate; 2 = absent, without apical rim.
 166. T7 with distinct lateral lobe: 0 = absent; 1 = present.
 167. T7 with median apical spine: 0 = absent; 1 = present.
 168. Number of fully exposed metasomal sterna: 0 = two or three; 1 = four; 2 = five or six.
 169. S1 subapically: 0 = not produced, without a distinct double margin; 1 = produced, forming a distinct double margin.
 170. S3: 0 = not concealed by S2; 1 = concealed by S2.
 171. S3 with gradulus: 0 = not produced into a thin, hyaline lamella; 1 = produced into a thin, hyaline lamella (Fig. 21). This is the same character referred to by Griswold (1985) and Michener (2007) as lateral hyaline flaps of S3. Lamella may cover most of disc.
 172. S3 with disc: 0 = bare or sparsely pubescent; 1 = densely covered with velvety pubescence (Fig. 21).

173. Fringe on apical margin of S3: 0 = absent; 1 = present, medially directed.
 174. S5: 0 = well sclerotised as in the preceding sterna; 1 = poorly sclerotised, translucent to membranous, not as preceding terga.
 175. S5 length: 0 = $\leq 2\times$ wider than long; 1 = $\geq 2.1\times$ wider than long. Because the midapical margin of S5 as well as of S6 is highly variable, we measured the length of these sterna on the lateral margin, from the base of the apodeme to apical margin of the sternum.
 176. S5 with hairs on disc: 0 = simple or plumose; 1 = apically modified (e.g. lanceolate, ovate-acuminate, capitate or spatulate).
 177. Pilose postgradular area of S5: 0 = large, maximum width $\geq 0.6\times$ sternal width; 1 = small, $\leq 0.5\times$ sternal width.
 178. S5 with small lateral spine: 0 = absent; 1 = present.
 179. S5 with medial emargination: 0 = absent; 1 = present.
 180. S5 with fringe of modified hairs on margin lateral to median emargination: 0 = absent; 1 = present. In *Pseudanthidium lanificum* S5 is deeply concave medially, with a distinct postgradular lateral extension distally, bearing a comb of ciliate cuticular processes, these are not modified hairs. We coded this species as having character state 0.
 181. S5 with medial comb of heavily sclerotised, simple black setae on distal margin: 0 = absent; 1 = present (Pasteels, 1984; fig. 266).
 182. S6: 0 = well sclerotised as in the preceding sterna; 1 = poorly sclerotised, translucent to membranous.
 183. Length of S6: 0 = $\leq 2\times$ wider than long; 1 = $\geq 2.1\times$ wider than long.
 184. Hairs of postgradular area of S6: 0 = sparse to dense, but not forming distinct sublateral patches; 1 = forming distinct sublateral patches.
 185. S6 with hairs on postgradular area: 0 = simple or plumose; 1 = apically modified (e.g. lanceolate, ovate-acuminate, capitate or spatulate).
 186. S7: 0 = well sclerotised throughout, usually pilose (Michener, 2007; fig. 80-4e); 1 = weakly sclerotised medially, thus forming two separated, sclerotised sclerites; 2 = mostly membranous, frequently hairless, at most barely indicated by weakly sclerotised apodemes.
 187. Length of S8: 0 = about as long as broad or shorter (Michener, 2007; fig. 82-2g); 1 = $\geq 1.3\times$ longer than broad (Michener, 2007; fig. 81-11b).
 188. Spiculum of S8: 0 = short, broad, parallel-sided (Michener, 2007; fig. 88-6c); 1 = long, narrow, parallel-sided (Michener, 2007; fig. 82-2g, i); 2 = narrowly rounded or V-shaped (Michener, 2007; fig. 81-11b); 3 = broadly rounded (Michener, 2007; fig. 77-1b); 4 = bifid. Character state 4 is only present in *Plesianthidium rufocaudatum* and *Icteranthidium ferrugineum*.
 189. Distal margin of S8: 0 = not medially produced as a lobe; 1 = medially produced as a lobe (Michener, 2007; fig. 81-11b).

190. Gonobase: 0 = present, ventrally absent (Michener, 2007; fig. 88-6a ,b); 1 = present, forming a complete ring, ventrally narrower (Michener, 2007; fig. 84-10a); 2 = present, forming a complete ring, well developed ventrally (Michener, 2007; fig. 80-4c); 3 = entirely reduced or absent (Michener, 2007; fig. 82-2h).
191. Gonocoxite length: 0 = subequal to, or longer than, gonostylus (Michener, 2007; fig. 77-1a); 1 = short, $\leq 0.5 \times$ gonostylar length (Michener, 2007; fig. 84-10a).
192. Volsella: 0 = absent; 1 = present.
193. Apex of volsella with clearly differentiated medial digitus and lateral cuspis: 0 = absent; 1 = present (Michener, 2007; fig. 77-1a).
194. Volsella located: 0 = not in the same plane as gonocoxite; 1 = in the same plane as gonocoxite.
195. Articulation between gonostylus and gonocoxite: 0 = fused, thus forming an unsegmented appendage; 1 = distinct, at least ventrally.
196. Gonostylus with apex (in ventral view): 0 = reaching about the same level as apex of penis valves; 1 = well surpassing apex of penis valves; 2 = short, not reaching apex of penis valves.
197. Apex of gonostylus (in ventral view): 0 = curved, laterally directed; 1 = curved, medially directed; 2 = straight, posteriorly directed.
198. Shape of gonostylus: 0 = not distinctly enlarged apically; 1 = distinctly enlarged apically.
199. Bridge of penis valves: 0 = absent; 1 = present.
200. Apodemes of the penis valve: 0 = not projecting through genital foramen; 1 = projecting through genital foramen (Michener, 2007; fig. 82-2a).

Phylogenetic analysis

We built a data matrix in WinClada (Nixon, 1999) consisting of 200 characters for seven outgroup species and 72 representative ingroup taxa (Table 2, Appendix S1). Parsimony analyses were carried out in Tree Analysis Using New Technology (TNT; Goloboff *et al.*, 2003). All characters were treated as nonadditive and equally weighted. Tree search in TNT was done by implementing sectorial searches with tree drifting (TD) and tree fusing (TF) and ratchet runs with TD and TF. We used the following search: keep a maximum of 10 000 random trees, 500 random addition sequences, and 1000 ratchet iterations, including 100 cycles of TD and 100 rounds of TF per iteration. Branch robustness was estimated with 10 000 bootstrap replicates (Felsenstein, 1985) and absolute Bremer support (Bremer, 1994) in TNT. The latter search was done by withholding 10 000 suboptimal trees up to 10 steps longer than the most parsimonious trees and plotting the values on the strict consensus tree obtained from the final TNT parsimony run. We used the strict consensus tree to trace the possible evolutionary pattern of those characters of particular evolutionary or taxonomic interest, namely the coarsely serrate hind tibial spur and the female hind tibial scopa. Trees were visualised and printed in WinClada, collapsing unsupported

nodes and using DELTRAN (slow) for character optimisation; the latter favours, when the choices are equally parsimonious, repeated origins of characters over reversals. The abbreviations MPT, L, CI and RI are used for most parsimonious trees, tree length, and consistency and retention indices, respectively.

Results

The analysis of the data matrix including 79 taxa and 200 characters yielded four most parsimonious trees (MPTs) (L = 1494, CI = 15, RI = 57); five nodes collapsed in the consensus tree and most branches were poorly supported by both bootstrap and Bremer values. The analysis recovered the subfamily Megachilinae, including the fossil taxa, but not the Fideliinae (Figs 22, 23); the latter subfamily is paraphyletic as applied in Michener (2007) but both of its tribes are monophyletic. Fideliini is the sister group of the remaining megachilids. The following five putative synapomorphies support the monophyly of the Fideliini: mandible with upper carina, trimmal carina and fimbriate line united in a Y-shaped pattern (33-1); maxillary galea without row of bristles on anterior margin of internal surface (57-0); maxillary galeal blade at midpoint with internal sclerotised surface about three-quarters or more as wide as external surface but narrower than external surface (59-2); pygidial plate of female with papillate or minutely roughened integument (133-1) and triangular or nearly so, basally occupying at least median two-thirds of tergal width (134-1). A single putative synapomorphy, the presence of dististipital process in the maxillary stipes (55-1), supports the sister group relationship of *Pararhophites* with Megachilinae. The monophyly of Megachilinae is supported by the subantennal sulcus inserting on the outer margin of the antennal socket (6-1) and the volsella of the male genitalia, when present, located at the same level as the gonocoxite (194-1). Within Megachilinae, Protolithurgini + Lithurgini constitute the sister group of the remaining megachilines; *Aspidosmia* did not cluster with the Anthidiini; *Glaeosmia* did not cluster with *Ctenoplectrella*; and Megachilini and Dioxyini were nested within the Osmiini. The genus *Noteriades* that has previously been placed in Osmiini was nested within Megachilini; this clade is supported by the following three synapomorphies: antennal socket with a distinct mesal projection on upper half (12-1; Fig. 5); outer surfaces of fore and mid tibia apically with acute angle and distinct notch anteriorly (92-1; Fig. 14); and male S7 mostly membranous, frequently hairless, at most barely indicated by weakly sclerotised apodemes (186-2).

Discussion

Phylogenetic relationships

As in the phylogenetic study of Roig-Alsina & Michener (1993), our analysis supports the monophyly of Megachilinae as well as the sister group relationship of Lithurgini to the

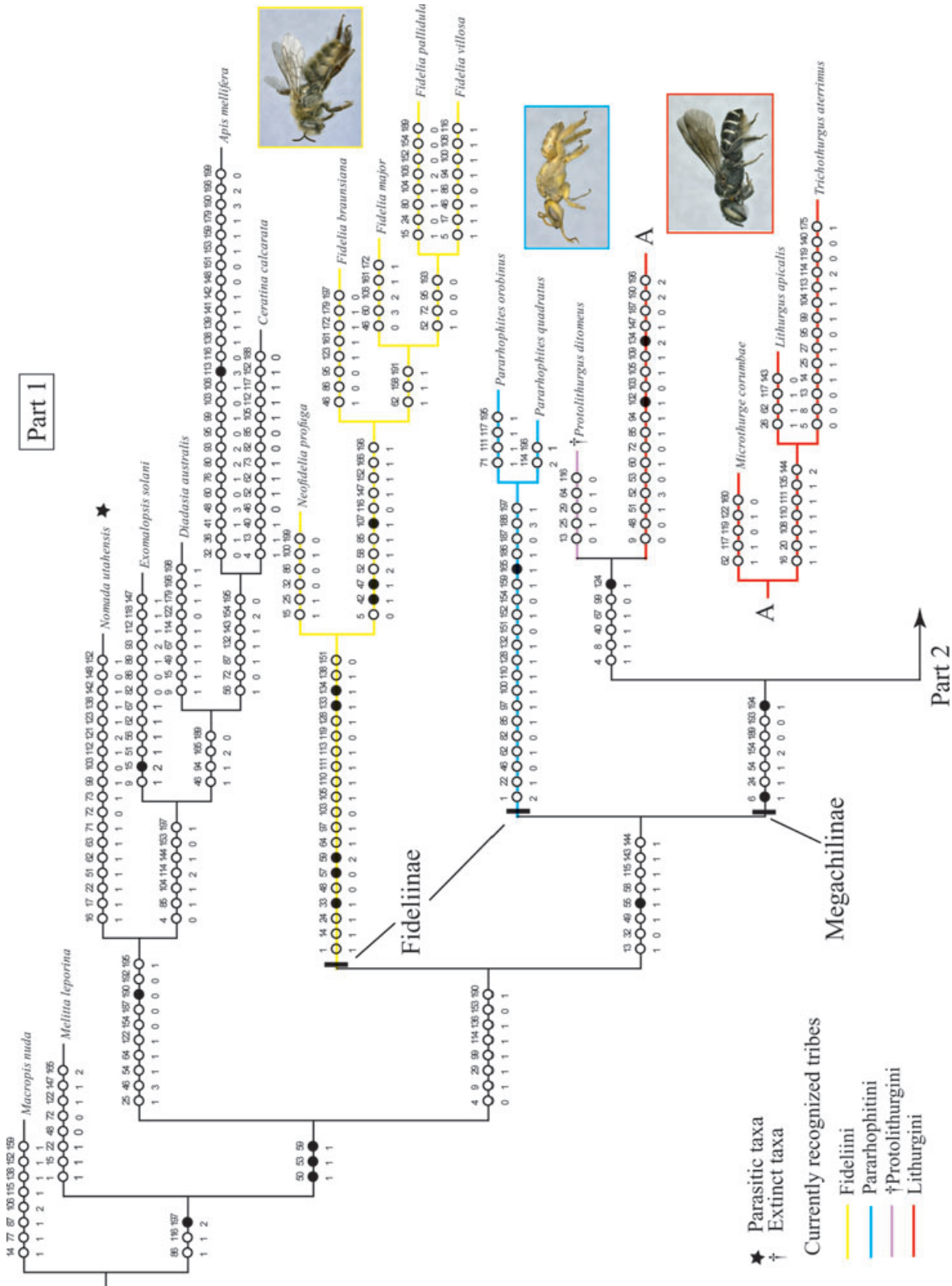


Fig. 22. Strict consensus tree of four most parsimonious trees. Black circles indicate unique characters; white circles indicate homoplastic changes; character numbers are placed above each change, character-states below.

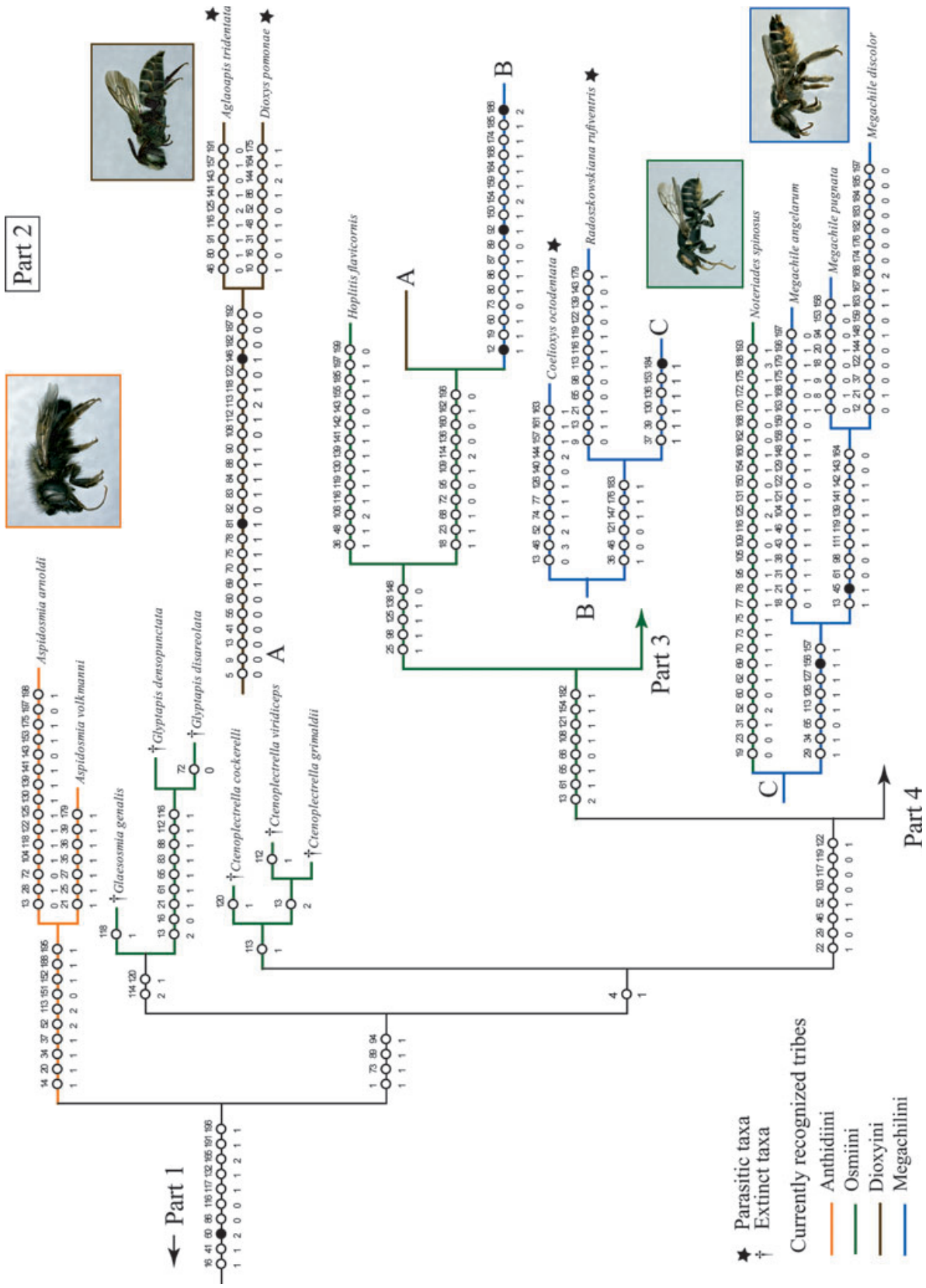
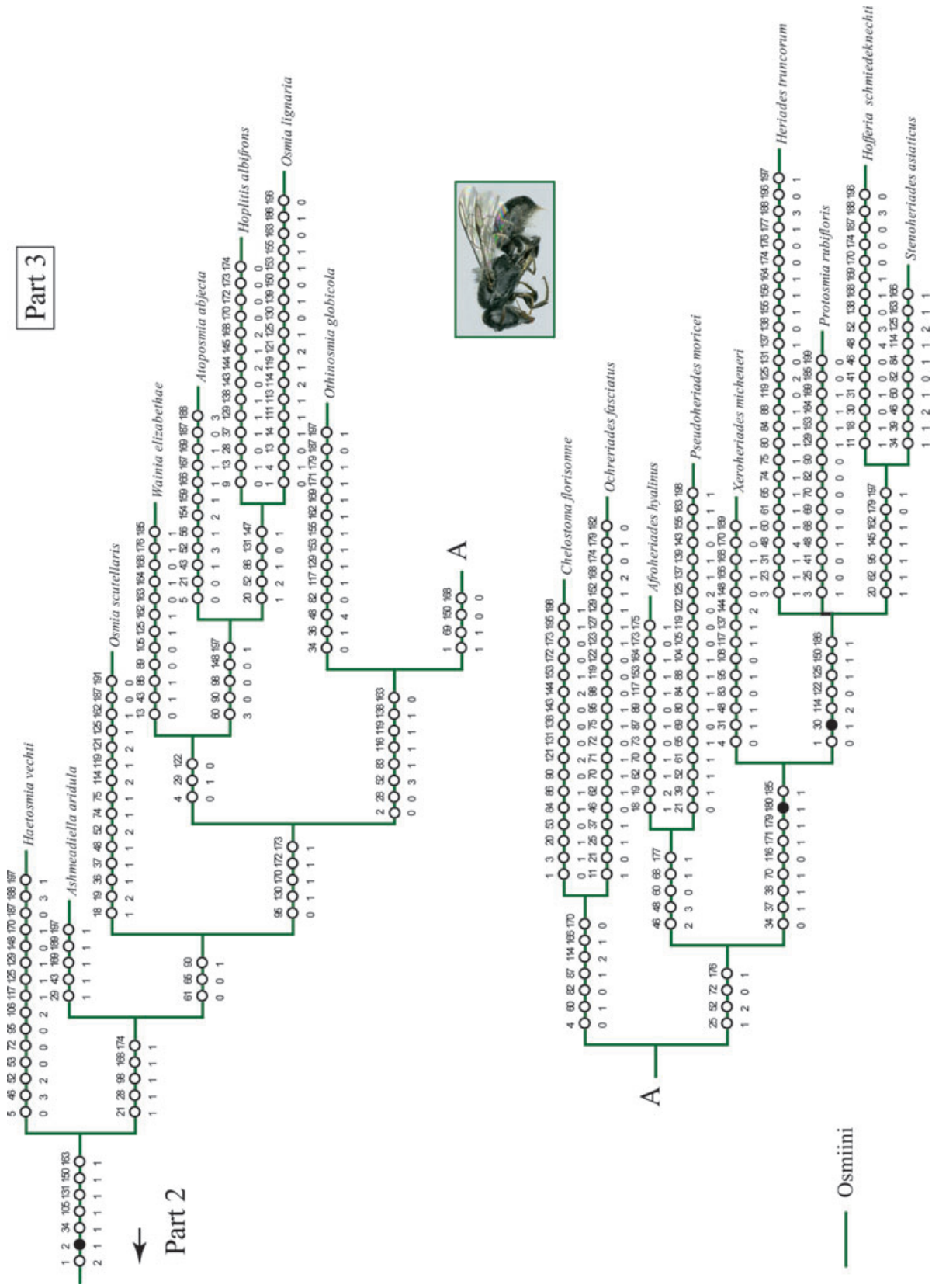


Fig. 22. Continued



Part 4

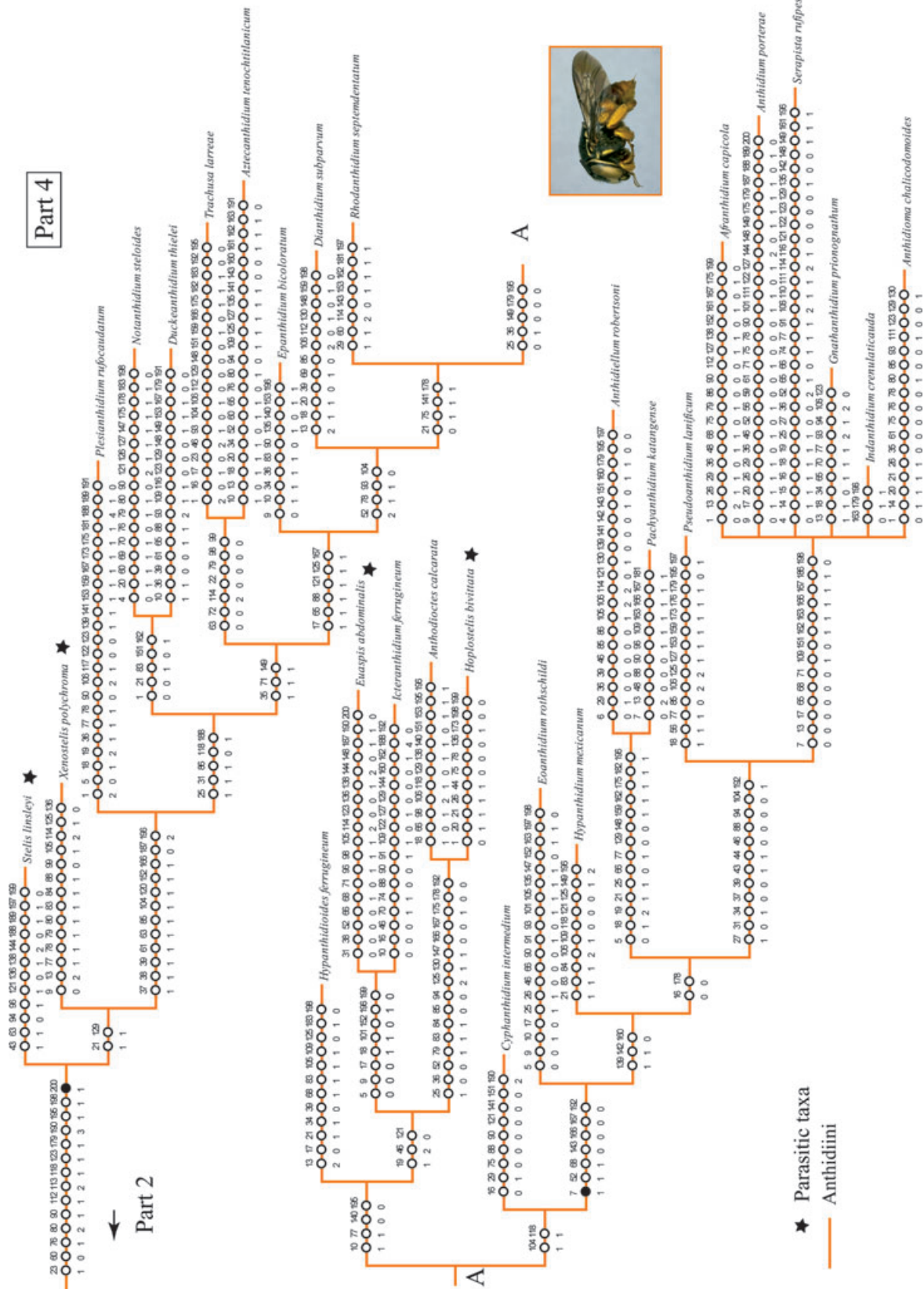


Fig. 22. Continued

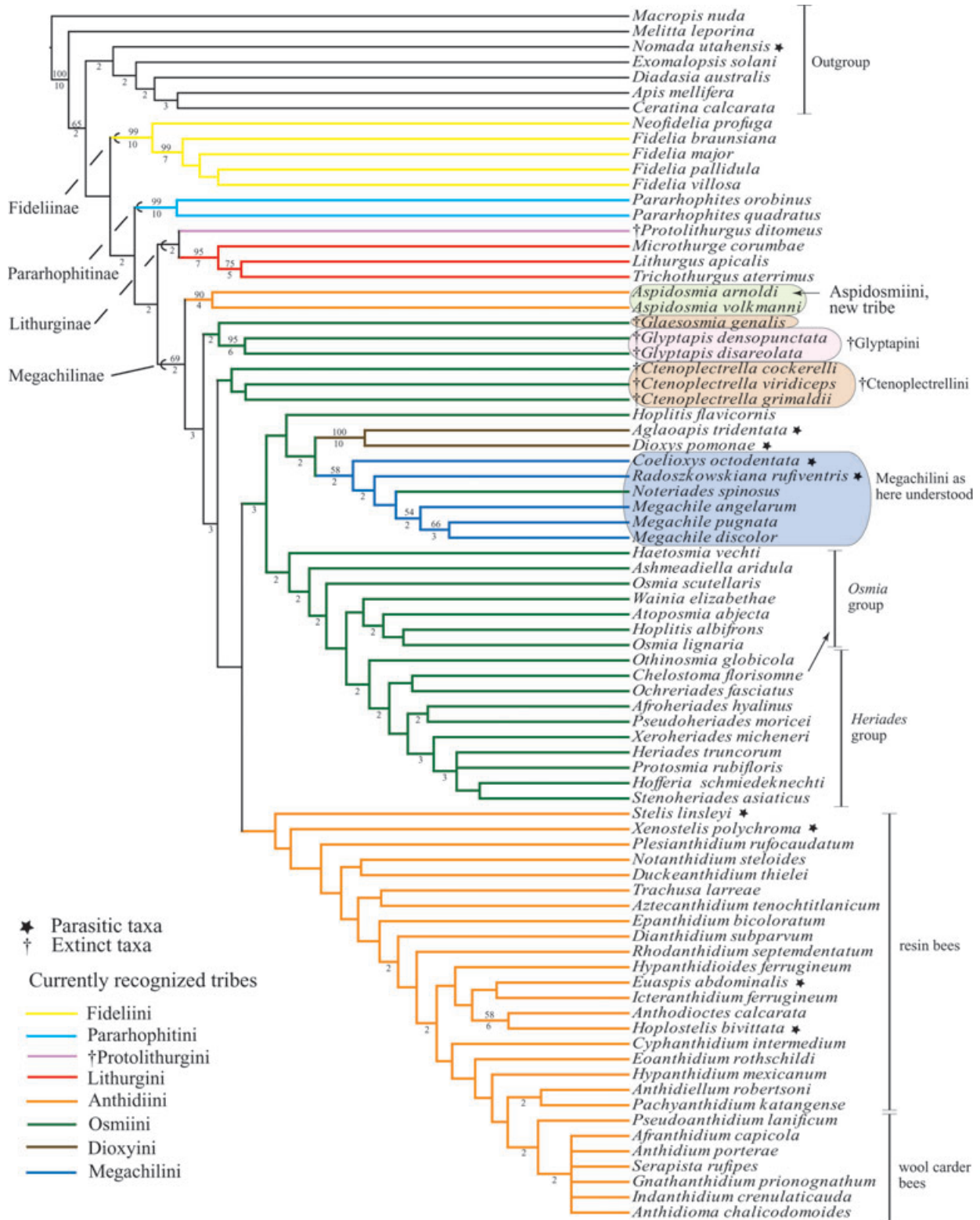


Fig. 23. Strict consensus tree of four most parsimonious trees with proposed classificatory changes. Numbers above nodes are bootstrap values, numbers below are absolute Bremer values. Branches without numbers indicate bootstrap values below 50% and Bremer values of 1. Currently recognised tribes in the legend are those of Michener (2007). Subfamilies shown are those recognised herein. *Chelostoma florissomme* is presently included in the *Osmia* group, as indicated by an arrow.

remaining megachilines. It also supports the sister group relationship of Protolithurgini to Lithurgini as indicated by Engel (2001). However, unlike the study of Roig-Alsina & Michener (1993), our analysis does not support the monophyly of Fideliinae. In their study, two synapomorphies supported the subfamily: the outer hind tibial spur coarsely serrate and the papillate or minutely roughened dorsal surface of the female sixth tergum. Mapping the presence of a coarsely serrate outer hind tibial spur onto the consensus trees resulted in ambiguous choices. It was either an ancestral character retained in both Fideliini and Pararhophitini when favouring character reversals over convergences in the analysis, or gained independently in both taxa when favouring repeated origins over reversals. The papillate or minutely roughened dorsal surface of the female sixth tergum in both taxa may not be homologous. In Fideliini, this integument is present on the well-defined pygidial plate only (Fig. 16) whereas in Pararhophitini, which lacks a pygidial plate, it is present on the entire distal half of the tergum (Fig. 17). Thus, by coding both taxa as having the same type of integument we are failing to assess the primary homology based on the positional criterion (e.g. De Pinna, 1991). For this reason, we did not code this character as in Roig-Alsina & Michener (1993); instead, we redefined this character by coding its presence or absent on a well-defined pygidial plate. Given that such a plate is absent in *Pararhophites*, this character does not apply to this taxon. However, one could argue that the pygidial plate is secondarily reduced in *Pararhophites* and, in that case, it would be reasonable to assume the primary homology of the surface sculpture. This idea is not supported by the fact that this type of integument is not restricted to the dorsal surface of the tergum, where it should be limited if a pygidial plate was present, but is found along the entire distal half of the segment. Nonetheless, coding this character as present in both Fideliini and Pararhophitini, as in Roig-Alsina & Michener (1993), did not change the resulting topology.

The nonmonophyly of Fideliinae *sensu* Michener (2007) was suggested in the analysis of Roig-Alsina & Michener (1993) when larval characters were analysed alone or combined with adult characters. Recent molecular analyses support the paraphyly of this subfamily as well as an ancient origin of both Fideliini and Pararhophitini of at least 100 Ma (Litman *et al.*, 2011). That analysis also suggests the paraphyly of Fideliini. In contrast, the monophyly of the tribe is strongly supported by high bootstrap (99%) and Bremer (10) values and five synapomorphies in our analysis. Both Fideliini and Pararhophitini have some distinctive biological features not known in other bees but commonly found among apoid wasps. In both groups the cells are unlined with walls no smoother than the burrow and the cocoon tapers at each end, incorporating sand eaten by the mature larva and voided in strips tending to run on the inside of the cocoon (Rozen, 1970, 1973; McGinley & Rozen, 1987; Michener, 2007). Such behavioural traits have been suggested as additional synapomorphies for Fideliinae (Michener, 2007) but it seems they are likely plesiomorphic features retained by those groups, perhaps as adaptations to nesting in sandy soils in strongly seasonal deserts (Litman *et al.*, 2011).

The sister group relationship of Pararhophitini and Megachilinae is weakly supported by bootstrap (<50%) and Bremer (2) values, as well as by a questionable synapomorphy: the presence of the dististipital process on the maxillary stipes (55-1). Although McGinley & Rozen (1987) indicated that this process is present as a very short distal bulge similar to that found in *Lithurgus*, Roig-Alsina & Michener (1993) coded it as absent in their analysis. The dististipital process of Lithurgini seems to us slightly more distinct and sclerotised than that of *Pararhophites*. Although we coded *Pararhophites* as having this process (character-state 1), coding it as if it were absent or as missing data did not change the resulting topology.

Aspidosmia, presently in the Anthidiini but characterised by a combination of both osmiine and anthidiine features, does not belong to either tribe. Rather it is a well-supported clade (90 bootstrap and 4 in Bremer values; Fig. 23) that is sister to the remaining megachiline tribes excluding Lithurgini. A recent molecular analysis also supports this basal position of *Aspidosmia* among the Megachilinae (Litman *et al.*, 2011). Thus, the current taxonomic placement of *Aspidosmia* within the Anthidiini renders this tribe paraphyletic. Interestingly, such a phylogenetic position was first suggested by Peters (1972) and discussed by Michener (2007) when assuming the hind tibial scopa to be an 'ancestral' (plesiomorphic) feature in *Aspidosmia*. Our results support this view. Whether favouring repeated origins over reversals or favouring character reversals over convergences, the analyses suggest that the presence of a hind tibial scopa is an ancestral character retained in *Pararhophites*, *Protolithurgus*, *Aspidosmia*, *Glaesosmia*, *Glyptapis* and *Ctenoplectrella* (results not shown).

The fossil genera *Glaesosmia*, *Glyptapis* and *Ctenoplectrella*, presently in Osmiini, were consistently placed among basal Megachilinae, near *Aspidosmia*. Particularly interesting is the resemblance of *Ctenoplectrella* and *Aspidosmia*. Despite having a labrum broader than long, the wing venation of *Ctenoplectrella* (e.g. fore wing with vein 2m-cu basal to 2r-m, basal vein curved, meeting Cu at right angle) seems similar to that of *Aspidosmia*. Also, it appears that the hairs on the hind tibia are long, suggestive of a scopa. We do not know whether the long hind tibial hairs of the Baltic megachilid genera constitute functional scopae but the phylogenetic position of these taxa, as well as that of *Aspidosmia*, did not change when this character was excluded from the analysis, indicating that their position in the tree does not depend entirely on the presence of the hind tibial scopa. Biogeographically, it is interesting to note that Sub-Saharan taxa, such as *Aspidosmia*, often show relationships to taxa in Baltic amber (Engel, 2001; Grimaldi & Engel, 2005). According to our analysis *Aspidosmia* and *Ctenoplectrella* are not sister groups but such a conclusion may be biased given the limited number of characters (less than half) that could be coded for *Ctenoplectrella*. If, in fact, these groups are sister taxa, *Aspidosmia* is likely the only survivor of this lineage. In that case, it would be more meaningful to place both genera in a single tribe Ctenoplectrellini to highlight the unique biogeographical and phylogenetic connections.

Additional fossil material may resolve this question, but with available data such a decision would be premature. The position of *Glaesosmia*, as sister of *Glyptapis*, is doubtless due to absence of data. *Glaesosmia* is only known from the female holotype, which is in poor condition. Additional material that shows a large number of characters of these fossil taxa, including those of the male, will help to test their relationship to *Aspidosmia*.

The remaining anthidiine taxa clustered in a clade with low bootstrap (<50%) and Bremer (1) support values. The penis valves with long apodemes projecting through the genital foramen in the male (200-1) was the single putative synapomorphy supporting this clade. This character appears to be secondarily lost in some Anthidiini genera such as *Anthidium* and *Euaspsis* Gerstäcker and is also present in some species of *Megachile* subgenus *Chalicodoma* (Gonzalez, 2008). Our analysis shows that parasitism has evolved multiple times in Anthidiini and that the wool carder bees or series B of genera (*sensu* Michener, 2007) represent a derived clade within the paraphyletic resin bees or series A (Fig. 23). The series B clade includes the following eight genera *Afranthidium* Michener, *Anthidioma* Pasteels, *Anthidium*, *Gnathanthidium* Pasteels, *Indanthidium* Michener and Griswold, *Neanthidium* Pasteels, *Pseudoanthidium* Friese and *Serapista* Cockerell. It is characterised by the female mandible with at least four small, acute teeth on the distal margin and by the absence of velvety hairs on the outer surface of the labrum and the inner surface of the mandible. These anthidiines are commonly known as wool carder bees because such multidentate mandibles, as well as the absence of velvety hairs, is presumably associated with the use of plant hairs or trichomes to build their cotton-like brood cells (Michener, 2007).

The analysis also supports the long suspected nonmonophyly of Osmiini, which is mainly caused by the placement of *Hoplitis* (in part) as sister group of the clade consisting of Dioxyini, Megachilini and *Noteriades*; no unique synapomorphies or high bootstrap and Bremer values support such a relationship (Figs 22, 23). Two groups of genera have traditionally been recognised in the 19 genera of Osmiini, sometimes treated at the subtribal level: the *Osmia* group or subtribe Osmiina and the *Heriades* group or subtribe Heriadina. Both groups can be roughly characterised by a combination of characters, but intermediate taxa such as *Protosmia* Ducke and *Othinosmia* Michener bridge the gap between the two (Griswold & Michener, 1997; Michener, 2007). Although we included a representative of each osmiine genus and scored the characters listed by Griswold (1985) and Michener (2007) in their recognition of each group of genera, the analysis does not support the monophyly of either group. Yet neither were the results concordant with the molecular analysis of Praz *et al.* (2008), except for *Noteriades* (see below); *Afroheriades*, *Pseudoheriades* and *Ochreriades* appeared close to other 'Osmiini', within a clade of most of the *Heriades* group. In fact, it is interesting that results place the rare genus *Ochreriades* as the sister group of *Chelostoma*, a relationship previously suspected by Mavroustakis (1956) and Griswold (1985, 1994) but not supported by molecular analyses (Praz *et al.*, 2008).

The position of Dioxyini within the Osmiini, and sister to the clade that includes *Noteriades* and Megachilini, was an unanticipated result. Although the monophyly of Dioxyini is unquestionable given a number of derived characters (e.g. reduced sting in the female, metanotum with median spine) and high bootstrap and Bremer values (Figs 22, 23), the phylogenetic position of this parasitic tribe is puzzling. Dioxyini has been long thought to be related to the Anthidiini because it exhibits typical features of that tribe, namely a depression behind the propodeal spiracle, short stigma and prestigma, and cleft pretarsal claws in the female (Michener, 1944, 1996, 2007). The position of Dioxyini in our consensus tree suggests that it might have grouped with Megachilini because of their morphological similarity to *Coelioxys* and *Radoszkowskiana* Popov resulting from their shared cleptoparasitic lifestyle. Cleptoparasites do not collect pollen to feed their larvae, and therefore the scopal hairs on abdomen and legs tend to be reduced or absent, their integument is also usually coarse, the pronotal lobe and omanus are usually carinate or lamellate, and the axilla is usually strongly projected. Thus, cleptoparasitic taxa that are not closely related might be clustered on the basis of these characters. However, when we excluded either the two parasitic megachiline genera or deactivated three characters related to cleptoparasitism from the analysis (characters 61, 66, and 74: pronotal lobe with strong carina or lamella, omanus carina, and axilla projected in acute angle or spine, respectively), we obtained a much higher number of MPTs (59 and 81) and a large number of branches (25 and 22) collapsed in the consensus trees; Dioxyini was the sister group of *Xenostelis* and was either in a large polytomy with other Osmiini and Anthidiini or was nested in the latter tribe. Our results also contrast with those of Gogala (1995), the only other study exploring the relationships of Dioxyini among megachilids. In Gogala's study *Dioxys* came out as the sister group to all other Megachilinae but his analysis included a limited number of taxa and characters (nine taxa, no outgroup and 11 morphological characters). While the phylogenetic relationships of Dioxyini need to be further explored, our results support a distinct Dioxyini within the Megachilinae.

Another significant result of our analysis was the position of *Noteriades* within Megachilini. Such a result confirms the idea of its close relationship to this tribe first mentioned by Griswold (1985) and more recently supported by the molecular analysis of Praz *et al.* (2008). In fact, when including *Noteriades* in the dataset of Gonzalez (2008) for the phylogeny of Megachilini (6 outgroup species, 107 ingroup species and 231 morphological characters), it was consistently included in that tribe but its position was not consistent among analyses. *Noteriades* appeared either as the sister group of *Megachile* s. l. or in a polytomy with *Matangapis* Baker & Engel and the clade that contains *Chelostomoda* Michener and related *Megachile* subgenera (V.H. Gonzalez and T.L. Griswold, in preparation). Independent of the position of *Noteriades* within Megachilini, its inclusion in Megachilini renders a more easily recognised

and diagnosed tribe. To date, there are no known synapomorphies for Megachilini; however, at least one of the three putative synapomorphies for the clade *Noteriades* + Megachilini found in this analysis seems to be unambiguously present: the presence of an anterior angle or spine followed by a notch on the apical margin of the outer surfaces of both fore and mid tibiae (92-1; Fig. 14). Thus, the recognition of *Noteriades* within Megachilini is warranted and is formally established herein. Concerning the other two putative synapomorphies (both found in *Noteriades*), the torular process (12-1; Fig. 5) is reduced to nearly absent in some *Megachile* (e.g. *M. discolor*) and the mostly membranous S7 of the male (186-2) is a condition also present in some Osmiini.

Classificatory considerations

Independently of the suprageneric classification followed, our analysis suggests four classificatory changes. First, our analysis indicates that Fideiini and Pararhophitini are not sister taxa but form successive sister taxa to the remaining Megachilidae. Thus, herein each is recognised in its own subfamily, as presently recognised by some authors (Table 1; Fig. 21). Second, the current placement of *Aspidosmia* within the Anthidiini would result in a paraphyletic taxon. Given the phylogenetic position and distinctive characters of *Aspidosmia*, such as the presence of a hind tibial scopa in the female, we herein place it in its own tribe, Aspidosmiini, new tribe (see below).

Third, our analysis indicates that the inclusion of *Noteriades* within Megachilini strengthens the recognition and diagnosis of this tribe. Thus, it is formally transferred to that tribe from Osmiini. We do not recommend synonymising Osmiini and Dioxyini under Megachilini (the oldest name of these three tribes). That decision should await a more rigorous study of the osmiines, including more taxa and characters (molecular as well as morphological). Such a study could also shed light on the monophyly of the *Osmia* and *Heriades* groups. Until then, we recommend continued treatment of them as informal units rather than as subtribes.

Fourth, and finally, the current taxonomic placement of the fossil genera *Glaesosmia*, *Glyptapis* and *Ctenoplectrella* into two subtribes of Osmiini, renders this tribe paraphyletic. Thus, herein they are treated at the tribal level, as presently recognised by Engel (2005).

Given the results, two classificatory approaches are plausible (Table 1). The first one (Proposal 1) closely follows the current classification of Michener (2007) but with Pararhophitini elevated to the subfamily level and the fossil subtribes Ctenoplectrellina and Glyptapina treated at the tribal level. The second approach (Proposal 2) follows that of Engel (2005) in recognising Fideiini, Pararhophitini and Lithurgini at the subfamilial level. It differs from Engel (2005) in not recognizing two tribes within Fideiinae and in recognising Dioxyini at the tribal level. Of course, the number of suprageneric categories one wants to recognise in Megachilidae is arbitrary; herein we prefer to follow Proposal 2 (Fig. 23).

Aspidosmiini, new tribe

Type genus: *Aspidosmia Brauns*
(Figs 1–3, 10)

Diagnosis. This tribe can be readily separated from all other tribes of Megachilinae by the presence of scopal hairs on the outer surface of the female hind tibia (in addition to the sternal scopa; Fig. 1), and by the forewing with a long prestigma, about as long as the stigma, a short stigma (less than twice as long as broad), and the vein 2m-cu basal to 2r-m.

Description. Female. Clypeus not covering labral base (Figs 2, 3); first labial palpomere short, about half length of second; maxillary palpi four-segmented. Preaxilla, below posterolateral angle of scutum, sloping, with small patch of hairs as long as those of adjacent sclerites (Fig. 10); propodeal triangle smooth and shiny, hairless; fore tibial spur (antennal cleaner) with malus simple, without a distinct projecting ridge on its anterior side, apex long, at least half length of base of malus, with distinct row of teeth on inner and outer margins; outer surface of hind tibia with long simple hairs forming a distinct scopa; hind basitarsus elongate, more than five times longer than broad; forewing with prestigma about as long as stigma; stigma less than twice as long as broad; vein 2m-cu basal to 2r-m, basal vein curved, meeting Cu at right angle; hind wing with jugal lobe about half as long as vannal lobe. *Male.* T6 without preapical carina; T7 exposed, posteriorly directed, sparsely covered by long hairs; S7 well-sclerotised, not medially divided; gonoforceps dorsolaterally weakly sclerotised; volsella present.

Comments. The novelty of this tribe was recognised by C. J. P. and B. N. D. based on the phylogenetic position of *Aspidosmia* in a recent molecular analysis of Megachilidae (Litman *et al.*, 2011). Such a result is supported by the present morphological study. Therefore, the authorship of this tribe is attributed to all four authors of this paper to reflect the equal intellectual contribution in the recognition and diagnosis of this lineage.

Key to the extant tribes of the Megachilinae

(Modified from Michener, 2007)

1. Metanotum with median spine or tubercle (except in *Allodioxys* and *Ensliniana*); mandible of female slender apically, bidentate, similar to that of male; pronotum (except in *Prodioxys*) with prominent obtuse or right-angular dorsolateral angle, below which a vertical ridge extends downward; sting and associated structures greatly reduced (scopa absent) Dioxyini
- Metanotum without median spine or tubercle; mandible of female usually wider apically, with three or more teeth, except rarely bidentate when mandible is greatly enlarged and porrect

and clypeus is also modified; pronotum with dorsolateral angle weak or absent (or produced to a tooth in some *Chelostoma* but without vertical ridge below it); sting and associated structures well developed 2

2(1). Stigma less than twice as long as broad, inner margin basal to vein r usually little if any longer than width, rarely about 1.5 times width; claws of female cleft or with an inner tooth (except in *Trachusoides*); body commonly with yellow or white integumental marks 3

– Stigma over twice as long as broad, inner margin basal to vein r longer than width; claws of female simple (except in *Osmia* subgenus *Metalinella*, Palearctic); body without yellow or white integumental marks (except in *Ochreriades*). 4

3(2). Outer surface of hind tibia with long hairs forming a distinct scopa; prestigma much more than twice as long as broad; preaxilla, below posterolateral angle of scutum, sloping and with small patch of hairs, these as long as those of adjacent sclerites (Fig. 10) **Aspidosmiini, new tribe**

– Outer surface of hind tibia usually with abundant simple bristles, not forming a distinct scopa; prestigma commonly short, usually less than twice as long as broad; preaxilla vertical, smooth and shining, usually without hairs (Fig. 11) **Anthidiini**

4(2). Outer surfaces of fore and mid tibiae apically with an acute angle (usually produced into a spine) and distinct notch anteriorly (Fig. 14); arolia absent, except in a few tropical Old World taxa (*Noteriades*, *Matangapis* and *Megachile* subgenus *Heriadopsis*); body nonmetallic or nearly so **Megachilini**

– Outer surfaces of fore and mid tibiae apically without an acute angle or spine and lacking distinct notch anteriorly; arolia present; body sometimes metallic green, blue, or brassy **Osmiini**

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Appendix S1. Character matrix used in cladistic analysis of the family Megachilidae. -, not applicable; ?, state of character that could not be recorded (see Materials and methods); *, multistate (0,1).

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