PHYLOGENY AND CLASSIFICATION OF THE BEE TRIBE MEGACHILINI (HYMENOPTERA: APOIDEA, MEGACHILIDAE), WITH EMPHASIS ON THE GENUS *MEGACHILE*

By

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ABSTRACT

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Using a cladistic analysis of adult external morphological characters, I first explore the relationships of the tribes in the bee subfamily Megachilinae. Next, I examine the phylogeny of the subgenera of *Megachile* s. l., and propose a phylogeny-based classification for the genus. This cosmopolitan genus is the largest in the family Megachilidae, which includes economically important species used in crop pollination. The more than 2000 species of *Megachile* s. l. are controversially grouped in 58 subgenera, including a fossil from Dominican amber. Most subgenera have not been revised and many species have not been properly associated with any of the known subgenera. In the phylogenetic analysis of Megachiline tribes, I analyzed 110 characters and selected three outgroups and 38 species (24 genera) of informal generic groups traditionally recognized. In the phylogenetic analysis of *Megachile* s. l., I analyzed 231 characters and used ten outgroup species and 103 ingroup species (53 subgenera). All five tribes currently recognized in Megachilinae were recovered. Lithurgini was the sister group of all other tribes; no synapomorphies were found for Osmiini, and all tribes appeared monophyletic. The cleptoparasitic bee tribe, Dioxyini, was the sister group of the clade formed by Anthidiini, and Osmiini + Megachilini. A single putative synapomorphy (sixth tergum of male with a transverse preapical carina) supported the monophyly of Megachilini. In the phylogenetic analysis of *Megachile*, the cleptoparasitic genera, *Coelioxys* and *Radoszkowskiana*, were the sister group of *Megachile*. Within *Megachile* s. l., most subgenera fall into morphological groups previously associated with differences in nesting behavior. Basal branches included subgenera that use mud or resins as nesting materials (traditionally placed in the genus *Chalicodoma*), whereas a large, more derived clade contained the subgenera *Creightonella*, *Megella*, and *Mitchellapis,* and those groups with flattened abdomen and female mandibles with cutting edges (*i.e.*, leaf-cutter bees). The phylogenetic position of the cleptoparasitic tribe Dioxyini, as sister group of the remaining Megachilinae, supports the distinctness of these bees from other members of the subfamily. It also suggests that those characters shared with Anthidiini, frequently used to place it within that tribe, are likely homoplasies. Further studies including molecular characters and critical taxa that posses a mixture of tribal features, such as the anthidine *Aspidosmia*, will test the sister group relationship of Osmiini + Megachilini. I discuss the monophyly of the subgenera of *Megachile* s. l. and propose alternative classifications that are more morphologically and behaviorally meaningful. I also discuss the evolution of some morphological traits correlated with female nesting behavior and geographical distribution of the subgenera of *Megachile* s. l.

To my mother, Amparo Betancourth Rivera, and to Prof. Charles D. Michener; two good role models in my life

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Introduction to this dissertation

The goals of this dissertation are to explore the relationship of the subgenera of *Megachile* Latreille s. l. using a cladistic analysis of adult external morphological characters and to propose a phylogeny-based classification for the genus. In the first chapter I explore the relationship of Megachilini with the other four tribes of Megachilinae (Anthidiini, Dioxyini, Lithurgini, and Osmiini). The relationships among these tribes as well as among their genera have not yet been studied in detail; such information is also valuable to objectively select outgroup taxa for the analysis of the subgenera of *Megachile* s. l., particularly from the highly diverse Anthidiini and Osmiini. In the second chapter I explore relationships among the subgenera of *Megachile* s. l. I discuss their monophyly and the implications of the phylogenetic results for the current classification of the genus. Using this phylogenetic framework, I briefly discuss the evolution of some characters correlated with nesting behavior and geographical distribution of the subgenera. In the third chapter I propose to synonymize *Radoszkowskiana* with *Coelioxys* and an alternative classification for *Megachile* s. l.; I propose to group its subgenera in four genera (*Chalicodoma*, *Megachile*, *Matangapis*, and *Thaumatosoma*) and to synonymize some that render others paraphyletic. I also present identification keys and, when necessary, comments on each genus and subgenus. In the fourth chapter I study the species of *Argyropile*, a small monophyletic subgenus of *Megachile* that occurs in North and Central America. I describe a new species and unknown males, and propose new synonymies. I also provide a synopsis of its taxonomy and biology and discuss the phylogenetic relationships of the seven species of this subgenus. The results of this chapter have been published (Gonzalez & Griswold 2007).

Chapter I. Phylogenetic relationships of the tribes in the subfamily Megachilinae

INTRODUCTION

The purpose of this chapter is to explore the relationships of the tribes in the subfamily Megachilinae (Anthidiini, Dioxyini, Lithurgini, Megachilini, and Osmiini). The relationships among these tribes as well as among their genera have not yet been studied in detail.

Except for the sister group relationship of Lithurgini to all other tribes, the phylogenetic study of Roig-Alsina & Michener (1993) did not resolve their relationships. Anthidiini, Megachilini, and Osmiini resulted in a polytomy and the cleptoparasitic bee tribe Dioxyini was not included in their analysis. Although these authors used a limited number of species, all tribes seemed monophyletic, except for Osmiini, which may be rendered paraphyletic by Megachilini (Michener 2007). Likewise, while the relationships among the few genera of Lithurgini and Dioxyini has briefly been explored by Michener (1983, 1996) and Engel (2001), the relationships among the numerous and diverse genera of the remaining tribes have not yet been studied. The phylogenetic analysis of Anthidiini by Muller (1996) only included western palearctic non-parasitic species and it was primarily done to study their floral associations.

My phylogenetic analysis recovered all Megachilinae tribes and the position of Lithurgini; all tribes appeared monophyletic, although no synapomorphies supported Osmiini. Dioxyini was the sister group of the clade formed by Anthidiini, and Osmiini + Megachilini. A single putative synapomorphy (sixth tergum of male with a transverse preapical carina) supported the monophyly of Megachilini. I also briefly discuss the position of Dioxyini, which supports the distinctness of this tribe from other Megachilinae.

MATERIALS AND METHODS

Taxa selection

I used species as terminal entities in all phylogenetic analyses. I chose species depending on specimen availability, and tried to cover the maximal morphological and biogeographical diversity (Table 1). I also tried to include representatives of informal species groups or generic groups traditionally recognized in each genus or tribe, as indicated in Michener (2007). When possible, and to account for intraspecific variation, I studied more than one specimen of each sex of each species. Outgroups are taxa with more plesiomorphic characters relative to the ingroup, or studied taxa, and are used to determine the polarity of change of character traits in phylogenetic analysis (Wiley et al. 1991). Based on the phylogeny of Roig-Alsina & Michener (1993), I used one species each of the genera *Xylocopa*, *Fidelia*, and *Pararhophites* as outgroups (Table 1).

Most specimens studied are deposited in the Snow Entomological Collection, University Kansas, although a few rare species were borrowed from the following institutions: United States National Museum of Natural History, The Smithsonian Institute, Washington, D.C.; Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; American Museum of Natural History, New York; USDA-ARS, Bee Biology and Systematics Laboratory; Utah State University, Logan; University of Illinois, Champaign-Urbana; Department of Terrestrial Invertebrates, Western Australian Museum, Welshpool; Hope Entomological Collection, Oxford, United Kingdom; The Natural History Museum, London, United Kingdom.

Table 1. List of species used in the phylogenetic analysis of the subfamily Megachilinae. Locality data associated with examined specimens in square brackets following names. Generic and subgeneric names follow those of Michener (2007). See Table 3 for other species of Megachilini.

APIDAE
Xylocopa Latreille: *X. varians* Smith, 1874 [Brazil]
MEGACHILIDAE
Fideliinae
Fideliini
Fidelia Friese: *F.* (*Parafidelia*) *pallidula* (Cockerell) [South Africa]
Pararhophitini
Pararhophites Friese: *P. orobinus* (Morawitz, 1875) [Pakistan]
Megachilinae
Anthidiini
Afranthidium Michener: *A.* (*Immanthidium*) *repetitum* (Schulz, 1906) [South Africa]
Anthidiellum Cockerell: *A. perplexum* (Smith, 1854) [USA]
Anthidium Fabricius: *A. deceptum* Smith, 1879 [Chile]
Anthodioctes Holmberg: *A. willineri* (Moure, 1947) [USA]
Aztecanthidium Michener & Ordway: *A. tenochtitlanicum* Snelling, 1987 [Mexico]
Dianthidium Cockerell: *Dianthidium* sp. [USA]
Pseudoanthidium Friese: *P. lituratum* (Panzer, 1801) (= *scapulae*) [Slovenia, South Africa]
Serapista Cockerell: *S. denticulata* (Smith, 1854) [Natal, Malawi]
Stelis Panzer: *S. montana* Cresson, 1864 [Canada, USA]
Trachusa Panzer: *T.* (*Ulanthidium*) *mitchelli* Michener, 1948 [Mexico]
Dioxyini
Dioxys Lepeletier & Serville: *D. productus subruber* (Cockerell, 1898) [USA]
Lithurgini
Lithurgus Berthold: *L.* (*Lithurgus*) *apicalis* Cresson, 1875 [Kansas], *L. cornutus fuscipennis* (Lepeletier, 1841) [Turkey], *L. spiniferus* Cameron, 1905 [South Africa]
Microthurge Michener: *M. pharcidonotus* Moure, 1948 [Argentina]
Trichothurgus Moure: *T. wagenknechti* Moure (Chile), *T. holomelan* (Moure, 1948) [Chile]
Osmiini
Ashmeadiella Cockerell: *A. cactorum* (Cockerell, 1897) [USA]
Chelostoma Latreille: *C. rapunculi* (Lepeletier, 1841) [USA]
Heriades Spinola: *H. timberlakei* Michener, 1938 [USA]
Hoplitis Klug: *H.* (*Dasyosmia*) *biscutellae* (Cockerell, 1897) [USA]
Hoplosmia Thomson: *H. bidentata* (Morawitz, 1876) [Greece, Slovakia]
Osmia Panzer: *O. (Cephalosmia) californica* Cresson, 1864 [California], *O.* (*Chalcosmia*) *texana* Cresson, 1872 [USA]
Protosmia Ducke: *P.* (*Chelostomopsis*) *rubifloris* (Cockerell, 1898) [USA]
Megachilini
Coelioxys Latreille: *C.* (*Haplocoelioxys*) *mexicana* Cresson, 1878 [Mexico], *C.* (*Rhinocoelioxys*) *zapoteca* Cresson, 1878 [Argentina, Bolivia, Brazil, Mexico], *C.* (*Synocoelioxys*) *texana* Cresson, 1872 [USA], *C.* (*Neocoelioxys*) *assumptions* Schrottky, 1909 [Mexico, Panama, Costa Rica, Brazil], *C.* (*Platycoelioxys*) *spatuliventer* Cockerell, 1927 [Mexico, Costa Rica]

Character selection

I used or modified many of the characters discussed by Michener & Fraser (1978), Winston (1979), Roig-Alsina & Michener (1993), and Michener (2000, 2007). Other characters were based on my own observations of the adult male and female external morphology. I 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. Then, they were washed with water and stored in glycerin in plastic sorting trays. I examined, measured, and illustrated characters using an Olympus SZ60 stereomicroscope with an ocular micrometer. I used Adobe Illustrator CS® and Adobe Photoshop® to prepare the illustrations. Morphological terminology follows that of Michener (2007). The abbreviations F, OD, PW, S, and T, are used for flagellomere, ocellar diameter, one puncture width, and metasomal sterna and terga, respectively.

Many characters are present in both sexes (*e.g.*, tongue), and I only coded them in one sex to avoid duplication. I only used continuous characters, such as proportions or measurements, when I found distinct gaps in the measured variable among the examined specimens. The majority of characters were binary; some of them, however, are not applicable to all species and these were coded as missing data (-) in the data matrix.

I analyzed 110 characters from three outgroup and 38 ingroup species (placed within 24 genera) (Appendices I, II).

Phylogenetic analysis

I performed a maximum parsimony analysis for the characters using an unconstrained heuristic search [Multiple TBR+TBR (mult*max*) search strategy] in NONA (Goloboff 1993). Under these criteria, the optimal phylogenetic tree(s) is that with the shortest length (*i.e.*, most parsimonious tree). To allow characters to reverse freely and examine possible hypotheses of evolutionary relationships, I treated all characters as unweighted, unordered, and nonadditive. Thus, character-state zero in a given data set does not imply plesiomorphy.

I used the following search and optimization parameters: keep a maximum of 1000000 trees, 1000 replications, 1 starting tree per replication, 0 random time, and DELTRAN optimization; the latter favors, when the choice is equally parsimonious, repeated origins of characters over reversals. Branch robustness was estimated with 10000 bootstrap replicates (Felsenstein 1985) and Bremer support (Bremer 1994) in NONA. The latter search was done by retaining trees that were up to 10 steps longer than the most parsimonious tree. Both methods are commonly used in phylogenetic analyses, especially Bremer support because it is calculated by examining the number of extra steps needed to collapse a branch in a consensus tree based on the original data. Other methods, such as bootstrap or jacknife, distort the original data set when analyzing a new data matrix constructed by resampling or deleting characters from the original data set. Thus, some potential informative character might be omitted or sampled more than once (Bremer 1994). The abbreviations L, CI, and RI are used for tree length, and consistency and retention indices, respectively.

RESULTS

Two most parsimonious trees (L = 398, CI = 33, RI = 71) were obtained from the analysis of the 110 morphological characters of Appendix I. Only two nodes collapsed in the strict consensus tree (Figs. 162; 163a,b). This analysis recovered all five tribes currently recognized in Megachilinae. Lithurgini has the highest values of bootstrap and Bremer support (100/10) and is the sister group of all other tribes (Fig. 162). Dioxyini is the sister group of the clade formed by Anthidiini and Osmiini + Megachilini; the clade containing the last three tribes has low values of bootstrap and Bremer support (< 50%/4) but it is supported by synapomorphies such as: an elongated, not round, anterior tentorial pit (character 3-1), mandible with fimbrial line running parallel to the apical mandibular margin (18-1), and stipes of proboscis (maxilla) with an elongated dististipital process (33-2).

A single putative synapomorphy (character 97-2: S7 of male weakly sclerotized to membranous) supports the clade Osmiini + Megachilini. No synapomorphy supports the Osmiini, and only a single putative synapomorphy (91-1: T6 of male with a transverse preapical carina) supports Megachilini. The tree topology did not change when character 97 was deactivated (five most parsimonious trees, L = 395, CI = 33, RI = 70). Also, tree topology did not change when characters related to cleptoparasitism, namely 43, 50, and 69, were deactivated (five most parsimonious trees, L = 383, CI = 33, RI = 71). When all those characters above (43, 50, 69, and 97) were deactivated at the same time, a total of 19 most parsimonious trees (L = 380, CI = 33, RI = 71) were obtained. Although Dioxyini remained in the same position in the strict consensus tree (16 collapsed nodes), Anthidiini, Osmiini, and Megachilini were in a polytomy. When *Dioxys* was removed from the analysis, the same polytomy was obtained in the strict consensus tree of 126 most parsimonious trees (L = 385, CI = 34, RI = 72).

DISCUSSION

The purposes of this analysis were to explore the phylogenetic relationships of Megachilini, and to objectively choose outgroup taxa for the phylogenetic analysis of subgenera of *Megachile* s. l. As in the phylogenetic study of Roig-Alsina & Michener (1993), and as indicated above, my analysis recovered the two subfamilies of Megachilidae, Fideliinae and Megachilinae, and all five tribes of the latter subfamily (Figs. 162; 163a,b). Lithurgini resulted as the sister group of all remaining tribes and all tribes seemed monophyletic, even though no synapomorphies were found for Osmiini.

Megachilini was closely related to Osmiini, with several homoplastic characters and a single putative synapomorphy (character 97-2: S7of male weakly sclerotized to membranous) supporting this clade. Given the small number of osmiine taxa examined, and that S7 seemed to be more sclerotized in some species (*e.g.*, Mitchell 1960), I suspect that the degree of sclerotization of the S7 might be variable among Osmiini. However, it seems that there is trend in both Osmiini and Megachilini to develop a weakly sclerotized S7, reaching its extreme in the latter tribe, where it is nearly absent. Nonetheless, even when this character of S7 is deactivated from the analysis, the sister group relationship of Osmiini and Megachilini is still supported. Further studies including molecular characters and critical taxa that posses a mixture of tribal features, such as the anthidine *Aspidosmia* Brauns, will test the sister group relationship of Osmiini + Megachilini.

Most characters that support the monophyly of Megachilini are homoplasies; the sixth tergum of male with a transverse preapical carina (Character 91-1, Figs. 106–111) was the only synapomorphy supporting this clade. This carina is present in all Megachilini males, although in some species it is represented by two spines or as a low transverse ridge (Fig. 111), or is nearly absent as in *Megachile* subgenus *Rhodomegachile*.

Another noteworthy result of this analysis was the position of Dioxyini, a distinct group of cleptoparasitic bees that attack species of its sister group tribes (Fig. 162). The median tubercle on the metanotum and the extremely reduced sting, more reduced than that of the stingless bees (Apidae: Meliponini), 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 claws of the female (Michener 1944, 1996).

Given the distinctness 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). Although I included in my analysis those characters shared with Anthidiini (Characters # 52, 62, 67), Dioxyini appeared as the sister group of the clade including Anthidiini, Osmiini, and Megachilini. I obtained the same results when I assumed a hypothetical non-parasitic Dioxyini by excluding from the analysis those characters related to parasitism (43, 50, and 69). Thus, according to this analysis, those characters shared with Anthidiini are likely homoplasies.

The only other study exploring the relationships of Dioxyini is that of Gogala (1995), using nine Megachilinae taxa, no outgroup, and 11 morphological characters. In that study, *Dioxys* 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 polarized. Although my analysis disagrees in the position of Dioxyini from that of Gogala (1995), it also supports the distinctness of this tribe from other Megachilinae.

Chapter II. Phylogenetic relationships of the subgenera of *Megachile* s. l.

INTRODUCTION

In this chapter I explore the relationships of *Megachile* s. l. with *Coelioxys* Latreille and *Radoszkowskiana* Popov, the other two genera of Megachilini, and the relationships among the subgenera of *Megachile* s. l. The genus *Megachile* s. l. is the largest of the family Megachilidae, containing more than 2000 species and 58 currently recognized subgenera, including a fossil from Dominican amber (Michener 2007) (Fig. 1, Table 2). *Megachile* s. l. is ecologically and morphologically very diverse; it is found in a wide diversity of habitats in all continents, except Antarctica, ranging from lowland tropical rain forests, deserts, to high altitude environments. In appearance, species of *Megachile* s. l. range from nearly bare, elongated, parallel-sided bees to robust, hairy bees resembling some bumble bee species; their body length ranges from about 5 mm in *M. rotundata* (Fabricius), the alfalfa bee, to nearly 40 mm in *M. pluto* Smith, the longest bee in the world.

Megachile s. l. nests are built with different materials in a variety of substrates. For example, brood cells can be exposed on the surfaces of walls, stones, and tree branches, or can be constructed inside pre-existing cavities in the ground, wood, stems, or even arboreal termite nests (Michener 2007). Brood cells are made of mud, resin, chewed leaf pulp, wood fibers, leaf or petal pieces, or a combination of these materials; the use of these materials commonly differs among subgenera or species groups. Several species of *Megachile* s. l. (*e.g.*, *M. rotundata*) are able to adapt to different pollen sources and environmental conditions. Such species are intensively used in crop pollination and have been introduced recently in many parts of the world (Michener 2007).

Perhaps such ecological diversity might explain why *Megachile* s. l. bees are so morphologically variable, sometimes with aberrant and bizarre structures not found in other groups of bees. For example, females of the subgenus *Chelostomoides* have distinct modifications on the face and mandibles, and males of several subgenera have modified mandibles and expanded tarsi and coxal spines on their forelegs that are used to hold the female during mating (Wittmann & Blochtein 1995). Also, sexually abnormal individuals exhibiting features of males and females (*i.e.,* gynandromorphs and intersexes) are far more common in *Megachile* s. l. than in other bees (Wcislo et al. 2004), suggesting the possibility of an as yet unknown developmental mechanism that promotes gynandromorphism (Gonzalez 2004).

Despite the ecological and economical importance of *Megachile* s. l., its taxonomy is still poorly understood and its phylogenetic relationships remain unknown. The number of genera or subgenera that should be recognized in *Megachile* s. l. is controversial, the majority of the subgenera have not been revised, and many species have not been properly associated with any of the known subgenera (Michener 2007). The relationships of *Megachile* s. l. with *Coelioxys* and *Radoszkowskiana*, both cleptoparasitic genera, are also unknown. Michener (2000, 2007) suggested that *Coelioxys* may render *Megachile* s. l. paraphyletic because it shares some morphological traits with *Megachile* s. l. subgenus *Chelostomoides*, and that *Coelioxys* and *Radoszkowskiana* may not represent separate origins of parasitism.

Thus, a phylogenetic analysis of *Megachile* s. l. would not only provide insights on its classification but also on its diversity and evolution.

Michener (1962, 1965) initially divided *Megachile* s. l. into three genera (*Chalicodoma* Lepeletier, *Creightonella* Cockerell, and *Megachile*), primarily on the basis of morphological features correlated with their nesting behavior. For example, *Chalicodoma* included those bees with strongly convex and rather parallel-sided abdomen (Fig. 67) and female mandibles without cutting edges between the teeth (as in Fig. 22); those morphological features are associated with narrow burrows and the use of mud or resin as nesting materials. In contrast, *Megachile* included those bees with flattened abdomen (Fig. 1, 68) and female mandibles with cutting edges (Figs. 25–36), features that allow them to cut and use leaf or petal pieces for constructing cells in wider burrows.

Later, when Michener (2000, 2007) considered the fauna of the Eastern Hemisphere, he noted exceptions and intergradations in these morphological features, as well as for almost all other characters he had previously used to characterize these genera. For example, the subgenera *Megella* and *Mitchellapis* combine characters of the genera *Megachile* and *Chalicodoma*. Typical *Megachile* features of these "problem" taxa include the mandible of the female with cutting edges among teeth and the apex of S6 with a fringe of short, dense plumose hairs (Fig. 75); features typical of *Chalicodoma* found in the same subgenera are the elongated, parallel-sided body (Fig. 67), apex of tibia of all legs with a distinct, sharp spine (Fig. 58), and the presence of lateral hairs on S8 of the male (as in Fig. 135).

Thus, he no longer recognized these three genera and synonymized certain subgeneric names that had been created for unusual species; he also organized the subgenera of *Megachile* s. l. into three informal groups that correspond to each previously recognized genus. Groups 1, 2, and 3, are equivalent to the genera *Megachile*, *Chalicodoma*, and *Creightonella*, respectively (Table 2). The subgenera *Megella* and *Mitchellapis*, previously placed in *Megachile* or Group 1, were placed in Group 2 because of the presence of marginal hairs on the S8 of the male. Nonetheless, some authors still follow Michener's earlier classification by recognizing the genera *Chalicodoma*, *Creightonella*, and *Megachile*, and several subgenera proposed for aberrant species (*e.g.*, Silveira et al. 2002, Durante & Abrahamovich 2006, Moure et al. 2007, Ornosa et al. 2007).

My cladistic analysis of 231 adult external morphological characters suggests that the cleptoparasitic taxa *Coelioxys* and *Radoszkowskiana* are the sister group of the free-living *Megachile* s. l. *Radoszkowskiana* seems to be a *Coelioxys* despite its distinctive male characters, and recent biological data also support this idea (Rozen & Kamel 2007). The subgenera *Megella* and *Mitchellapis*, along with *Creightonella*, were consistently placed within a large, monophyletic clade containing all subgenera of Group 1. My analysis also recovered some major phylogenetic lines previously discussed by Michener (1965, 2007) and Mitchell (1980) and confirms the suspicion of Michener (2007) that the recognition of some subgenera renders others paraphyletic. I discuss the implications of these results for the current classification of *Megachile* s. l. Using this phylogenetic framework, I also briefly discuss the evolution of some characters correlated with nesting behavior and geographical distribution of the subgenera.

Table 2. Distribution and number of species of the subgenera of *Megachile* s. l. Groups of subgenera and biogeographical regions are according to Michener (2007). Geographical distribution: AFR = Sub-Saharan Africa, ANT = Greater and Lesser Antilles, ARA = Araucanian region, AUS = Australia, HAW = Hawaii, MAD = Madagascar, NEO = Neotropical, NEA = Nearctic, NZ = New Zealand, ORI = Oriental, PAL = Paleartic, (†) = Fossil

Subgenus	# Sp	Afr	Ant	Ara	Aus	Haw	Mad	Nea	Neo	Nz	Ori	Pal
Group 1												
Acentron Mitchell	21								X			
Aethomegachile Engel	1										X	
Amegachile Friese	30	X			X		X				X	
Argyropile Mitchell	7							X	X			
Austromegachile Mitchell	37		X					X	X			
Austrosarus Raw	3	X										
Chrysosarus Mitchell	51			X					X			
Cressoniella Mitchell	20			X				X	X			
Dasymegachile Mitchell	13			X					X			
Eumegachile Friese	1											X
Eutricharaea Thomson	236	X	X	X	X	X			X	X	X	X
Grosapis Mitchell	1								X			
Leptorachis Mitchell	38			X					X			
Litomegachile Mitchell	6					X		X	X			
Megachile Latreille	9							X				X
Megachiloides Mitchell	60							X				
Melanosarus Mitchell	11		X					X	X			
Moureapis Raw	31			X					X			
Neochelynia Schrottky	17							X	X			
Paracella Michener	39	X									X	
Platysta Michener	2	X										
Pseudocentron Mitchell	73		X	X				X	X			
Ptilosaroides Mitchell	2								X			
Ptilosarus Mitchell	15								X			
Rhyssomegachile Mitchell	3								X			
Sayapis Titus	31		X	X				X	X			
Schrottkyapis Mitchell	1								X			
Steloides Moure	1			X								
Trichurochile Mitchell	3								X			
Tylomegachile Moure	6		X						X			
Xanthosarus Robertson	15							X			X	
Zonomegachile Mitchell	3								X			
Group 2												
Austrochile Michener	10				X							
Callomegachile Michener	91	X	X			X	X				X	
Cestella Pasteels	2						X					
Chalicodoma Lepeletier	31	X									X	X
Chalicodomoides Michener	2				X							

Table 2 (Continued). Distribution and number of species of the subgenera of *Megachile* s. l. Groups of subgenera and biogeographical regions are according to Michener (2007). Geographical distribution: AFR = Sub-Saharan Africa, ANT = Greater and Lesser Antilles, ARA = Araucanian region, AUS = Australia, HAW = Hawaii, MAD = Madagascar, NEO = Neotropical, NEA = Nearctic, NZ = New Zealand, ORI = Oriental, PAL = Paleartic, (†) = Fossil

Subgenus	**# Sp**	**Afr**	**Ant**	**Ara**	**Aus**	**Haw**	**Mad**	**Nea**	**Neo**	**Nz**	**Ori**	**Pal**
Group 2												
Chalicodomopsis † Engel	1								X			
Chelostomoda Michener	14				X						X	
Chelostomoides Robertson	31		X					X	X			
Cuspidella Pasteels	1	X										
Gronoceras Cockerell	10	X										
Hackeriapis Cockerell	90				X						X	
Heriadopsis Cockerell	1	X										
Largella Pasteels	3										X	
Matangapis Baker & Engel	1										X	
Maximegachile Guiglia & Pasteels	3	X										X
Megella Pasteels	3	X									X	
Mitchellapis Michener	6				X							
Neochalicodoma Pasteels	2	X										
Parachalicodoma Pasteels	1											X
Pseudomegachile Friese	80	X	X				X					
Rhodomegachile Michener	3				X							
Schizomegachile Michener	1				X							
Stenomegachile Pasteels	4	X					X					
Thaumatosoma Smith	2				X							
Group 3												
Creightonella Cockerell	50	X			X						X	X
Incertae sedis												
Stellenigris Meunier	1											
Total: 58 subgenera	1231											

MATERIALS AND METHODS

The selection of taxa and characters, and the phylogenetic analysis are as described in the first chapter, except as follows: I chose ten species as outgroups: *Trichothurgus wagenknechti* (Lithurgini), *Dioxys productus* (Dioxyini), *Trachusa mitchelli*, *Aztecanthidium tenochtitlanicum* (Anthidiini), *Chelostoma rapunculi, Hoplosmia bituberculata* (Osmiini), and one species of *Radoszkowskiana* and three of *Coelioxys* (Megachilini) (Table 3, Appendix IV). I chose *Trichothurgus* based on the phylogenetic studies of Michener (1983) and Engel (2001); remaining taxa were chosen based on their positions in the consensus tree produced by prior analysis of relationships among tribes of Megachilinae (Chapter I). As suggested by Prendini (2001), I chose a basal and a more derived species from each tribe to maximize variation in the phylogenetic analysis.

I studied 103 *Megachile* s. l. species belonging to 53 subgenera (Table 3). I included the type species and, to maximize variation, at least one morphologically divergent species from it, or species separated subgenerically but synonymized by Michener (2000, 2007). Eight subgenera of *Megachile* s. l. are monotypic and 16 were represented by a single species in the analysis. I chose only one species of each of the 16 subgenera because each is morphologically uniform (Table 2). Instead, I tried to focus on those highly variable and more specious subgenera such as *Eutricharaea*. I was not able to examine specimens of *Rhyssomegachile* and the newly described subgenus *Austrosarus*.

I analyzed 231 characters (~ 21 % multistate); some of these characters, however, are essentially the same as those listed in Appendix I. Not all characters could be coded for all species because some subgenera are only known from the type specimen and they could not be dissected, and in other cases, they are only known from one sex. Unless sexual dimorphism was suspected, characters were taken from the available sex. Missing information was represented by a question mark in the data matrix. Current computer algorithms make no distinction between the two (inapplicable characters and missing information) but simulation studies suggest that NONA (Goloboff 1993) yields the best results in these cases (*e.g.*, Strong & Lipscomb 1999).

As an attempt to obtain a better resolution, I analyzed this data matrix as follows: i) analysis A, using the full data matrix; ii), analysis B, deactivating characters presumably related to cleptoparasitism, namely characters 70, 71, 80, 101-2, 114, and 117; iii) analysis C, using the full data matrix but excluding *Dioxys*; iv) analysis D and E, deactivating only those characters coded for the male (characters 137–231) or for the female (100 characters deactivated: 1,2, 5–8, 12–51, 59, 69–71, 74, 75, 80, 81, 84, 85, 87–94, 98, 101, 103, 105–136).

Table 3. List of the species used in the phylogenetic analysis and summary of classificatory changes in Megachilini, with emphasis on *Megachile* s. l. Generic names: C = *Coelioxys*, Ch = *Chalicodoma*, Cr = *Cressoniella*, Cy = *Chrysosarus*, E = *Eumegachile*, M = *Megachile*, Mo = *Megachiloides*, P = *Pseudocentron, T* = *Thaumatosoma*. Unless otherwise indicated by an asterisk, listed species are the type species of the genera and subgenera recognized and synonymized by Michener (2007). Previous status: Status according to Pasteels (1965), Michener (1965), Mitchell (1980), and Gupta (1993). For a detailed synonymic list, see account under each group.

Species	Previous status	Michener (2007)	This work
C. zapoteca Cresson, 1878 [Argentina, Bolivia, Brazil, Mexico]	*C*. (*Rhinocoelioxys*)	*C*. (*Rhinocoelioxys*)	*C*. (*Rhinocoelioxys*)
C. decipiens Spinola, 1838* [India]	C. (*Liothyrapis*)	C. (*Liothyrapis*)	C. (*Liothyrapis*)
C. rufiventris Spinola, 1838* [Egypt]	*C. (Radoszkowskiana)*	*Radoszkowskiana*	*C. (Radoszkowskiana)*
Group 1			
M. albitarsis Cresson, 1872 [USA]	*P.* (*Acentron*)	***M.* (*Acentron*)**	***M.* (*Acentron*)**
**M. candida* Smith, 1879 [Costa Rica]	*P.* (*Acentron*)	*M.* (*Acentron*)	*M.* (*Acentron*)
**M.* (*Aethomegachile*) sp. [India]	Unknown at the time	***M.* (*Aethomegachile*)**	***M.* (*Aethomegachile*)**
M. bituberculata Ritsema, 1880 [W. Cameroom]	*M.* (*Amegachile*)	***M.* (*Amegachile*)**	***M.* (*Amegachile*)**
M. ustulatiformis Cockerell, 1910 [Australia]	*M*. (*Callochile*)	*M.* (*Amegachile*)	*M.* (*Amegachile*)
M. parallela Smith, 1853 [USA]	*Mo.* (*Argyropile*)	***M.* (*Argyropile*)**	***M.* (*Argyropile*)**
**M. sabinensis* Mitchell, 1934 [USA]	*Mo.* (*Argyropile*)	*M.* (*Argyropile*)	*M.* (*Argyropile*)
M. montezuma Cresson, 1878 [Brazil]	*Cr.* (*Austromegachile*)	***M.* (*Austromegachile*)**	***M.* (*Austromegachile*)**
M. giraffa Schrottky, 1913 [Brazil]	*Cr.* (*Holcomegachile*)	*M.* (*Austromegachile*)	*M.* (*Austromegachile*)
**M. albopunctata* Jörgensen, 1909 [Argentina]	*M.* (*Chrysosarus*)	***M.* (*Chrysosarus*)**	***M.* (*Chrysosarus*)**
M. guaranitica Schrottky, 1908 [Paraguay]	*Cy.* (*Chrysosarus*)	*M.* (*Chrysosarus*)	*M.* (*Chrysosarus*)
M. parsonsiae Schrottky, 1914 [Argentina]	*Cy.* (*Dactylomegachile*)	*M.* (*Chrysosarus*)	*M.* (*Chrysosarus*)
M. zapoteca Cresson, 1878 [Mexico]	*Cr.* (*Cressoniella*)	***M.* (*Cressoniella*)**	***M.* (*Cressoniella*)**
M. saulcyi Guérin, 1845 [Chile]	*Cr.* (*Dasymegachile*)	***M.* (*Dasymegachile*)**	***M.* (*Dasymegachile*)**
M. mitchelli Raw, 2004 [Argentina, Peru]	*Cr*. (*Chaetochile*)	*M.* (*Dasymegachile*)	*M.* (*Dasymegachile*)
M. bombycina Radoszkowski, 1874 [Finland]	*E.* (*Eumegachile*)	***M.* (*Eumegachile*)**	***M.* (*Eumegachile*)**
M. argentata Fabricius, 1793 [USA]	*M.* (*Eutricharaea*)	***M.* (*Eutricharaea*)**	***M.* (*Eutricharaea*)**
**M. femorata* Smith, 1853 [India]	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
**M. albiscopa* De Saussure, 1890 [Madagascar]	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
M. leachella Curtis, 1828 [Slovakia]	*M.* (*Perezia*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
M. eurymera Smith, 1854 [Kenya, Nigeria]	*M.* (*Eurymella*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
**M. submetallica* Benoist, 1954 [Madagascar]	*M.* (*Eurymella*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
M. digiticauda Cockerell, 1937 [Zimbabwe]	*M.* (*Digitella*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
M. rotundata Fabricius, 1787 [USA]	*M.* (*Neoeutricharaea*)	*M.* (*Eutricharaea*)	*M.* (*Eutricharaea*)
M. cockerelli Rohwer, 1923 [Mexico]	*E*. (*Grosapis*)	***M.* (*Grosapis*)**	***M.* (*Grosapis*)**
M. petulans Cresson, 1878 [USA]	*P.* (*Leptorachis*)	***M.* (*Leptorachis*)**	***M.* (*Leptorachis*)**
M. laeta Smith, 1853 [Brazil]	*P.* (*Leptorachina*)	*M.* (*Leptorachis*)	*M.* (*Leptorachis*)
M. brevis Say, 1837 [USA]	*M.* (*Litomegachile*)	***M.* (*Litomegachile*)**	***M.* (*Litomegachile*)**
**M. gentilis* Cresson, 1872 [USA]	*M.* (*Litomegachile*)	*M.* (*Litomegachile*)	*M.* (*Litomegachile*)
M. centuncularis Linnaeus, 1758 [USA]	*M*. (*Megachile*)	***M*. (*Megachile*)**	***M*. (*Megachile*)**
M. montivaga Cresson, 1878 [USA]	*M*. (*Cyphopyga*)	*M*. (*Megachile*)	*M*. (*Megachile*)

Table 3 (Continued). List of the species used in the phylogenetic analysis and summary of classificatory changes in Megachilini, with emphasis on *Megachile* s. l. Generic names: C = *Coelioxys*, Ch = *Chalicodoma*, Cr = *Cressoniella*, Cy = *Chrysosarus*, E = *Eumegachile*, M = *Megachile*, Mo = *Megachiloides*, P = *Pseudocentron, T* = *Thaumatosoma*. Unless otherwise indicated by an asterisk, listed species are the type species of the genera and subgenera recognized and synonymized by Michener (2007). Previous status: Status according to Pasteels (1965), Michener (1965), Mitchell (1980), and Gupta (1993). For a detailed synonymic list, see account under each group.

Species	Previous status	Michener (2007)	This work
Group 1			
M. oenotherae Mitchell, 1924 [USA]	*Mo*. (*Megachiloides*)	***M*. (*Megachiloides*)**	***M*. (*Megachiloides*)**
M. integra Cresson, 1878 [USA]	*Mo*. (*Xeromegachile*)	*M*. (*Megachiloides*)	*M*. (*Megachiloides*)
M. pascoensis Mitchell, 1934 [USA]	*Mo*. (*Derotropis*)	*M*. (*Megachiloides*)	*M*. (*Megachiloides*)
M. xylocopoides Smith, 1853 [USA]	*P*. (*Melanosarus*)	***M*. (*Melanosarus*)**	***M*. (*Melanosarus*)**
**M. nigripennis* Spinola, 1841 [Brazil]	*P*. (*Melanosarus*)	*M*. (*Melanosarus*)	*M*. (*Melanosarus*)
M. anthidioides Radoszkowski, 1874 [Brazil]	*P*. (*Moureapis*)	***M*. (*Moureapis*)**	***M*. (*Moureapis*)**
M. paulista Schrottky, 1920 [Brazil]	*M*. (*Neochelynia*)	***M*. (*Neochelynia*)**	***M*. (*Neochelynia*)**
M. chichimeca Cresson, 1878 [Mexico]	*Cr*. (*Neomegachile*)	*M*. (*Neochelynia*)	*M*. (*Neochelynia*)
M. carbonaria Smith, 1853 [India]	*Cr*. (*Neocressoniella*)	***M*. (*Neocressoniella*)**	***M*. (*Megella*)**
M. semivenusta Cockerell, 1931 [Malawi]	*M*. (*Paracella*)	***M*. (*Paracella*)**	***M*. (*Paracella*)**
**M. curtula* Gerstaecker, 1857 [Uganda]	*M*. (*Paracella*)	*M*. (*Paracella*)	*M*. (*Paracella*)
M. platystoma Pasteels, 1965 [Congo]	*M*. (*Platysta*)	***M*. (*Platysta*)**	***M*. (*Eutricharaea*)**
M. pruina Smith, 1853 [USA]	*P*. (*Pseudocentron*)	***M*. (*Pseudocentron*)**	***M*. (*Pseudocentron*)**
**M. poeyi* Guérin, 1845 [Cuba]	*P*. (*Pseudocentron*)	*M*. (*Pseudocentron*)	*M*. (*Pseudocentron*)
M. neoxanthoptera Cockerell, 1933 [Panama]	*Cr*. (*Ptilosaroides*)	***M*. (*Ptilosaroides*)**	***M*. (*Ptilosarus*)**
M. bertonii Schrottky, 1908 [Brazil]	*Cr*. (*Ptilosarus*)	***M*. (*Ptilosarus*)**	***M*. (*Ptilosarus*)**
M. pugnata Say, 1837 [USA]	*E*. (*Sayapis*)	***M*. (*Sayapis*)**	***M*. (*Sayapis*)**
**M. coelioxyformis* Schrottky, 1910 [Brazil, Paraguay]	*E*. (*Sayapis*)	*M*. (*Sayapis*)	*M*. (*Sayapis*)
M. assumptionis Schrottky, 1908 [Brazil]	*E*. (*Schrottkyapis*)	***M*. (*Schrottkyapis*)**	***M*. (*Sayapis*)**
M. euzona Pérez, 1899 [Chile]	*Cy*. (*Stelodides*)	***M*. (*Stelodides*)**	***M*. (*Chrysosarus*)**
M. thygaterella Schrottky, 1913 [Peru, Brazil]	*Cr*. (*Trichurochile*)	***M*. (*Trichurochile*)**	***M*. (*Trichurochile*)**
M. orba Schrottky, 1913 [Mexico]	*Cr*. (*Tylomegachile*)	***M*. (*Tylomegachile*)**	***M*. (*Tylomegachile*)**
**M. simplicipes* Friese, 1921 [Mexico]	*Cr*. (*Tylomegachile*)	*M*. (*Tylomegachile*)	*M*. (*Tylomegachile*)
M. latimanus Say, 1823 [USA]	*M*. (*Xanthosarus*)	***M*. (*Xanthosarus*)**	***M*. (*Xanthosarus*)**
M. fortis Cresson, 1872 [USA]	*Mo*. (*Phaenosarus*)	*M*. (*Xanthosarus*)	*M*. (*Xanthosarus*)
M. lagopoda Linnaeus, 1761 [Spain]	*M*. (*Macromegachile*)	*M*. (*Xanthosarus*)	*M*. (*Xanthosarus*)
M. addenda Cresson, 1878 [USA]	*M*. (*Addendella*)	*M*. (*Xanthosarus*)	*M*. (*Xanthosarus*)
Group 2			
M. resinifera Meade-Waldo, 1915 [Australia]	*Ch*. (*Austrochile*)	***M*. (*Austrochile*)**	***T*. (*Austrochile*)**
**M. ignita* Smith, 1853 [Australia]	*Ch*. (*Austrochile*)	*M*. (*Austrochile*)	*T*. (*Austrochile*)
M. mystaceana Michener, 1962 [Australia]	*Ch*. (*Callomegachile*)	***M*. (*Callomegachile*)**	***Ch*. (*Callomegachile*)**
**M. sculpturalis* Smith, 1853 [Japan, USA]	*Ch*. (*Callomegachile*)	*M*. (*Callomegachile*)	*Ch*. (*Callomegachile*)
M. clotho Smith, 1861 [NE. Sulawesi]	*Ch*. (*Eumegachilana*)	*M*. (*Callomegachile*)	*Ch*. (*Callomegachile*)
M. torrida Smith, 1853 [Uganda]	*Ch*. (*Carinula*)	*M*. (*Callomegachile*)	*Ch*. (*Callomegachile*)
**M. decemsignata* Radoszkowski, 1881 [Uganda]	*Ch*. (*Carinula*)	*M*. (*Callomegachile*)	*Ch*. (*Callomegachile*)
M. biseta Vachal, 1903 [Gabon]	*Ch*. (*Morphella*)	*M*. (*Callomegachile*)	*Ch*. (*Callomegachile*)
M. cestifera Benoist, 1954 [Madagascar]	*Ch*. (*Cestella*)	***M*. (*Cestella*)**	***Ch*. (*Cestella*)**

Table 3 (Continued). List of the species used in the phylogenetic analysis and summary of classificatory changes in Megachilini, with emphasis on *Megachile* s. l. Generic names: C = *Coelioxys*, Ch = *Chalicodoma*, Cr = *Cressoniella*, Cy = *Chrysosarus*, E = *Eumegachile*, M = *Megachile*, Mo = *Megachiloides*, P = *Pseudocentron, T* = *Thaumatosoma*. Unless otherwise indicated by an asterisk, listed species are the type species of the genera and subgenera recognized and synonymized by Michener (2007). Previous status: Status according to Pasteels (1965), Michener (1965), Mitchell (1980), and Gupta (1993). For a detailed synonymic list, see account under each group.

Species	Previous status	Michener (2007)	This work
Group 2			
M. parietina Geoffroy, 1785 [Spain]	*Ch.* (*Chalicodoma*)	***M.* (*Chalicodoma*)**	***Ch.* (*Chalicodoma*)**
M. asiatica Morawitz, 1875 [Turkey]	*Ch.* (*Euchalicodoma*)	*M.* (*Chalicodoma*)	*Ch.* (*Chalicodoma*)
M. lefebvrei Lepeletier, 1841 [Greece, Italy]	*Ch.* (*Allochalicodoma*)	*M.* (*Chalicodoma*)	*Ch.* (*Chalicodoma*)
M. manicata Giraud, 1861 [Kazakhstan]	*M.* (*Katamegachile*)	*M.* (*Chalicodoma*)	*Ch.* (*Chalicodoma*)
M. aethiops Smith, 1853 [Australia]	*Ch.* (*Chalicodomoides*)	***M.* (*Chalicodomoides*)**	***Ch.* (*Chalicodomoides*)**
M. spissula Cockerell, 1911 [China]	*Ch*. (*Chelostomoda*)	***M.* (*Chelostomoda*)**	***T.* (*Chelostomoda*)**
**M. ulrica* Nurse, 1901 [India]	*Ch*. (*Chelostomoda*)	*M.* (*Chelostomoda*)	*T.* (*Chelostomoda*)
M. rugifrons Smith, 1854 [USA]	*Ch.* (*Chelostomoides*)	***M.* (*Chelostomoides*)**	***T.* (*Chelostomoides*)**
M. campanulae Robertson, 1903 [USA]	*Ch.* (*Oligotropus*)	*M.* (*Chelostomoides*)	*T.* (*Chelostomoides*)
M. georgica Cresson, 1878 [USA]	*Ch.* (*Gnathodon*)	*M.* (*Chelostomoides*)	*T.* (*Chelostomoides*)
M. spinotulata Mitchell, 1934 [USA]	*Ch.* (*Chelostomoidella*)	*M.* (*Chelostomoides*)	*T.* (*Chelostomoides*)
M. quadraticauda Pasteels, 1965 [Congo]	*Ch*. (*Cuspidella*)	***M*. (*Cuspidella*)**	***Ch*. (*Cuspidella*)**
M. bombiformis Gerstaecker, 1857 [Tanzania]	*Ch.* (*Gronoceras*)	***M.* (*Gronoceras*)**	***Ch.* (*Gronoceras*)**
M. cincta combusta (Smith, 1853) [Tanzania]	*Ch.* (*Digronoceras*)	*M.* (*Gronoceras*)	*Ch.* (*Gronoceras*)
M. rhodura Cockerell, 1906 [Australia]	*Ch*. (*Hackeriapis*)	***M*. (*Hackeriapis*)**	***T*. (*Hackeriapis*)**
**M. ferox* Smith, 1879 [Australia]	*Ch*. (*Hackeriapis*)	*M*. (*Hackeriapis*)	*T*. (*Hackeriapis*)
**M. heriadiformis* Smith, 1853 [Australia]	*Ch*. (*Hackeriapis*)	*M*. (*Hackeriapis*)	*T*. (*Hackeriapis*)
M. striatulus Cockerell, 1931 [Zimbabwe]	*Ch*. (*Heriadopsis*)	***M*. (*Heriadopsis*)**	**T. (*Heriadopsis*)**
M. semivestita Smith, 1853 [C. Java]	*Ch.* (*Largella*)	***M.* (*Largella*)**	***Ch.* (*Largella*)**
M. alticola Cameron, 1902 [Borneo]	Unknown at the time	***M*. (*Matangapis*)**	***Matangapis***
M. maxillosa Guérin, 1845 [Kenya, Natal, Tanzania]	*Ch.* (*Maximegachile*)	***M.* (*Maximegachile*)**	***T.* (*Maximegachile*)**
M. malimbana Strand, 1911 [Zaire]	*M.* (*Megella*)	***M.* (*Megella*)**	***M.* (*Megella*)**
**M. pseudomonticola* Hedicke, 1925 [Japan]	*M.* (*Megella*)	*M.* (*Megella*)	*M.* (*Megella*)
M. fabricator Smith, 1868 [Australia]	*E.* (*Mitchellapis*)	***M.* (*Mitchellapis*)**	***M.* (*Mitchellapis*)**
M. pseudolaminata Pasteels, 1865 [South Africa]	*Ch.* (*Neochalicodoma*)	***M.* (*Neochalicodoma*)**	***Ch.* (*Pseudomegachile*)**
M. incana Friese, 1898 [Egypt]	*Ch.* (*Parachalicodoma*)	***M.* (*Parachalicodoma*)**	***Ch.* (*Chalicodoma*)**
M. ericetorum Lepeletier, 1841 [Spain]	*Ch.* (*Pseudomegachile*)	***M.* (*Pseudomegachile*)**	***Ch.* (*Pseudomegachile*)**
M. flavipes Spinola, 1838 [India]	*Ch*. (*Archimegachile*)	*M.* (*Pseudomegachile*)	*Ch.* (*Pseudomegachile*)
M. armatipes Friese, 1909 [Natal]	*Ch*. (*Neglectella*)	*M.* (*Pseudomegachile*)	*Ch.* (*Pseudomegachile*)
M. muansae Friese, 1911 [Tanzania]	*Ch*. (*Dinavis*)	*M.* (*Pseudomegachile*)	*Ch.* (*Pseudomegachile*)
M. albocincta Radoszkowski, 1874 [Egypt]	*Ch.* (*Xenomegachile*)	*M.* (*Pseudomegachile*)	*Ch.* (*Pseudomegachile*)
M. abdominalis Smith, 1853 [Australia]	*Ch.* (*Rhodomegachile*)	***M.* (*Rhodomegachile*)**	***T.* (*Rhodomegachile*)**
M. monstrosa Smith, 1868 [Australia]	*Ch.* (*Schizomegachile*)	***M.* (*Schizomegachile*)**	***T.* (*Schizomegachile*)**
M. chelostomoides Gribodo, 1894 [Zaire]	*Ch*. (*Stenomegachile*)	***M*. (*Stenomegachile*)**	**T. (*Stenomegachile*)**
**M. dolichosoma* Benoist, 1962 [Madagascar]	*Ch*. (*Stenomegachile*)	*M*. (*Stenomegachile*)	T. (*Stenomegachile*)
M. duboulaii Smith, 1865 [Australia]	*Ch.* (*Thaumatosoma*)	***M.* (*Thaumatosoma*)**	***T.* (*Thaumatosoma*)**
Group 3			
M. cognata Smith, 1853 [Uganda]	*Cg*. (*Creightonella*)	***M.* (*Creightonella*)**	***M.* (*Creightonella*)**
M. albisecta Klug, 1817 [Slovakia]	*M*. (*Metamegachile*)	*M.* (*Creightonella*)	*M.* (*Creightonella*)

RESULTS

Phylogenetic relationships

The 231 morphological characters used in this analysis were coded from all parts of the adult body (Table 4). This data set was not sex-biased because 36 characters, such as those of mouthparts, are present in both sexes and they were only coded in the female. However, even excluding them, the number of characters among body segments was not homogeneous ($X^2_{.05\,[2]} = 32.1$, $P < 0.000$, X^2 test); most characters came from the mandible of the female and the genitalia and associated sterna of the male.

The analysis of the full data matrix (analysis A) yielded 126 most parsimonious trees (L = 2215, CI = 13, RI = 53); 12 nodes collapsed in the consensus tree (Figs. 164a,b) and most branches were weakly supported by homoplastic characters. The clade of cleptoparasitic bees that includes *Dioxys* (an outgroup taxon), *Radoszkowskiana*, and *Coelioxys* is the sister group of *Megachile* s. l. Within the latter genus three large groups resulted in a polytomy; *Gronoceras* and *Cuspidella* remained ungrouped. The largest clade contained all subgenera of Group 1 and also included *Creightonella* (Group 3), *Mitchellapis* (Group 2), and *Megella* (Group 2). The second largest group included the subgenera *Chalicodoma*, *Parachalicodoma*, *Callomegachile*, *Matangapis*, *Chelostomoda* and related subgenera. The remaining subgenera clustered in the third group (Fig. 164a).

Table 4. Number of morphological characters used in the phylogenetic analysis of the subgenera of *Megachile* s. l. (*n* = 231 characters); 22 and 14 characters of the head and mesosoma were present in both sexes but only recorded in the female. (-) = not applicable.

Body structure	**Female (*n* = 136)**	**Male (*n* = 95)**	**Total (%)**
HEAD	**69**	**11**	80 (34.6)
Mandible	24	4	28 (12.1)
Mouthparts	17	0	17(7.4)
MESOSOMA	**31**	**16**	47 (20.3)
METASOMA	**36**	**68**	104 (45.1)
T6	4	10	14 (6.1)
T7	2	6	8(3.5)
S5	0	10	10(4.3)
S6	16	4	20(8.7)
S8	-	9	9(3.9)
Genitalia	2	26	28(12.1)

When those characters presumably related to cleptoparasitism (characters # 70, 71, 80, 101-2, 114, and 117) were deactivated for analysis B, 270 most parsimonious trees were obtained (L = 2177, CI = 13, RI = 53); 16 nodes collapsed in the strict consensus tree. *Dioxys* was now excluded from the ingroup taxa, *Radoszkowskiana* + *Coelioxys* retained the same position, the same three groups of subgenera of *Megachile* were largely recovered, and their relationships mostly solved (Figs. 165, 166). The subgenus *Rhodomegachile* was the sister group of all remaining *Megachile* s. l. A clade that includes the subgenera *Matangapis*, *Chelostomoda* and related taxa, was the sister group of the remaining subgenera of Group 2 and a large clade containing all subgenera of Group 1, including *Creightonella* (Group 3), *Mitchellapis* (Group 2), and *Megella* (Group 2). Because the relationships among the subgenera of *Megachile* s. l. were largely resolved, character numbers and character states are only shown for the consensus tree of this analysis (Fig. 166).

When for analysis C *Dioxys* was excluded, 704 most parsimonious trees (L = 2182, CI = 13, RI = 53) were obtained; 31 nodes collapsed in the strict consensus tree. The main difference from analyses A and B was that all subgenera of Group 2, except for *Mitchellapis* and *Megella*, clustered in the same clade; it also resulted in a large polytomy with the clade that includes the genera *Radoszkowskiana* + *Coelioxys* (Fig. 167).

The exclusion of all 95 male characters for analysis D resulted in a large polytomy that included all ten ingroup taxa in the consensus tree (not shown; 26 nodes collapsed) of 1120 most parsimonious trees (L = 1046, CI = 16, RI = 61). *Rhodomegachile* and *Matangapis* clustered with *Chelostomoda* and related subgenera; *Chelostoma* (outgroup), *Radoszkowskiana*, and *Coelioxys* were included in that clade. Also, the group that included all subgenera of Group 1, *Creightonella*, *Mitchellapis*, and *Megella* was recovered; except as indicated for the first clade, internal relationships in both clades are largely consistent with previous analyses.

Deactivating the 100 female characters (analysis E) yielded 160 most parsimonious trees (L = 1259, CI = 12, RI = 50); 120 nodes collapsed in the consensus tree (not shown). Outgroups were not included within the ingroup and two *Callomegachile* species, *M. torrida* and *M. decemsignata*, were the sister group of all remaining Megachilini. In the latter clade, two large groups were recognized; one included *Coelioxys*, most subgenera of Group 2, *Creightonella*, *Mitchellapis*, and the subgenera of Group 1 *Sayapis* and *Schrottkyapis*. The other group included the remaining subgenera of Group 1, *Gronoceras* (Group 2), two species of the subgenus *Chalicodoma* (*M. asiatica* and *M. manicata*), and the genus *Radoszkowskiana*. In both groups internal branches were largely unresolved.

Monophyly of subgenera

Eight of the 53 subgenera of *Megachile* s. l. included in this study are monotypic. The monophyly of 16 subgenera was either strongly supported (*e.g.*, *Pseudocentron*) or weakly supported but consistently suggested among analyses (*e.g.*, *Litomegachile*). The 16 subgenera containing more than one species but represented in my analyses by single species are also likely monophyletic because each is morphologically uniform (*e.g.*, *Maximegachile*, *Ptilosarus*).

The monophyly of *Pseudomegachile*, and *Chalicodoma* s. str., was suggested in analyses A and C (Figs. 164a, 167a); likewise, *Chrysosarus* was monophyletic only in analysis C (Fig. 167b) and *Megachiloides* and *Leptorachis* in analysis D (not shown). The monophyly of the remaining nine subgenera was not recovered (Table 5).

Table 5. Monotypic, monophyletic, and non-monophyletic subgenera of *Megachile* s. l. **Monotypic:** Subgenera with a single known species. **Monophyletic:** the monophyly of these subgenera was either strongly supported or weakly supported but consistently suggested among analyses. **Likely monophyletic:** these subgenera were represented by a single species in this study but they are likely monophyletic because they seem morphologically uniform (*e.g.*, *Ptilosarus*); *Chalicodoma, Leptorachis*, *Megachiloides*, and *Pseudomegachile* are included here because their monophyly was suggested in at least one of the analyses (see text). **Nonmonophyletic**: The monophyly of these subgenera was not recovered in the analyses.

Monotypic	**Monophyletic**	**Likely monophyletic**	**Nonmonophyletic**
Cuspidella	*Acentron*	*Aethomegachile*	*Callomegachile*
Eumegachile	*Amegachile*	*Cestella*	*Chelostomoides*
Grosapis	*Argyropile*	*Chalicodoma*	*Chrysosarus*
Heriadopsis	*Austrochile*	*Chalicodomoides*	*Dasymegachile*
Matangapis	*Austromegachile*	*Cressoniella*	*Eutricharaea*
Parachalicodoma	*Chelostomoda*	*Largella*	*Hackeriapis*
Schrottkyapis	*Creightonella*	*Leptorachis*	*Sayapis*
Stelodides	*Gronoceras*	*Maximegachile*	*Stenomegachile*
	Litomegachile	*Megachiloides*	*Xanthosarus*
	Megachile	*Mitchellapis*	
	Megella	*Moureapis*	
	Melanosarus	*Neocressoniella*	
	Neochelynia	*Platysta*	
	Paracella	*Pseudomegachile*	
	Pseudocentron	*Ptilosaroides*	
	Tylomegachile	*Ptilosarus*	
		Rhodomegachile	
		Schizomegachile	
		Thaumatosoma	
		Trichurochile	

DISCUSSION

Phylogenetic relationships

The data set used in this analysis was not sex-biased and the combination of characters from both sexes provided a better resolution than the analyses of characters from each sex alone. Therefore, the following comments are focused on the analyses of combined male and female characters, not on analyses D and E.

Most clades were supported by homoplasies and had low Bremer and bootstrap values, but the resulting groups and their relationships seem reasonable; also, most homoplasies might be synapomorphies at lower levels of analyses. Except when *Dioxys* was removed for analysis C, the cleptoparasitic taxa *Coelioxys* and *Radoszkowskiana* were the sister group of the free living *Megachile* s. l. (Fig. 167a). The cleptoparasitic genus *Dioxys* (Tribe Dioxyini) clustered with *Radoszkowskiana* and *Coelioxys* in analysis A (Fig. 164a); however, such a relationship is unlikely because *Dioxys* never fell within Megachilini in the analysis that explored the relationships of the tribes of Megachilinae (Chapter 1, Fig. 162). Thus, this result suggests that they might have grouped because of their morphological similarity given their cleptoparasitic life style. 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 omaulus are usually carinate or lamellate, and the axilla is usually strongly projected (Figs. 1, 57). Probably these features are defensive, serving to counter the sting or jaws of the host

(C. D., Michener, pers. comm.). Thus, cleptoparasitic taxa that are not closely related might be clustered on the basis of these characters, as occurred in this analysis. As suspected, *Dioxys* was excluded from the ingroup taxa in analysis B, when those characters related to cleptoparasitism (Characters # 70, 71, 80, 101-2, 114, and 117) were deactivated (Fig. 165a).

Radoszkowskiana has been separated from *Coelioxys* perhaps because of the short axilla, bare eyes, and the blunt metasoma of the male with a low transverse apical carina on T6; such a carina is distinctive because it is not divided into dorsal and ventral processes as in most *Coelioxys*, but similar to that of males in *Megachile* subgenus *Chelostomoides.* Thus, it has been suggested that cleptoparasitism evolved independently in those two genera. However, *Radoszkowskiana* was consistently the sister group of *Coelioxys*, even when characters related to parasitism were deactivated (Fig. 165a). I have obtained the same sister group relationship between *Radoszkowskiana* and *Coelioxys* in an on-going phylogenetic study of the subgenera of *Coelioxys*.

The characters that distinguish *Radoszkowskiana* from *Coelioxys* are likely plesiomorphic, but they are variable and some species of *Coelioxys* combine characters of both groups. For example, *C.* (*Boreocoelioxys*) *funeraria* Smith and *C.* (*Liothyrapis*) *decipiens* Spinola have short axillae and bare eyes; also, the S6 of the female of *C.* (*Torridapis*) *torrida* Smith is broad and rounded, and entirely sclerotized as in *Radoszkowskiana* whereas it is elongated and pointed with a distinct median weakly sclerotized area in most *Coelioxys* (Figs. 79, 80). Thus, *Radoszkowskiana* seems to be a *Coelioxys* despite the distinctive male characters. Furthermore, the mode of cleptoparasitism in *Radoszkowskiana* seems to fall within the known repertories of parasitism of *Coelioxys* (Rozen & Kamel 2007). Together, the evidence suggests that the two genera had a common parasitic ancestor and thus, that cleptoparasitism evolved only once in Megachilini.

Most subgenera of *Megachile* s. l. fell into morphological groups previously associated with differences in nesting behavior (Figs. 164–167). For example, when characters related to parasitism were deactivated (analysis B), basal branches included those subgenera of Group 2 that use mud or resins as nesting materials; those subgenera with extensive leafcutting behavior clustered in a large, more derived clade containing all subgenera of Group 1, and also included *Creightonella* (Group 3), *Megella* (Group 2), and *Mitchellapis* (Group 2). A similar grouping was obtained when the consensus tree resulted in a polytomy in analyses A and C (Figs. 164b, 167b).

Creightonella, *Megella*, and *Mitchellapis* combine some characters that are typical of both subgenera of Group 1 and 2 and thus, they are difficult to place with confidence in any group on the basis of a few characters. Typical Group 1 features of these “problem” subgenera include the mandible of the female with cutting edges among teeth and the apex of S6 with a fringe of short, dense plumose hairs; typical features of Group 2 are the elongated, parallel-sided body, apex of tibia of all legs with a distinct, sharp spine, and the presence of lateral hairs on the S8 of the male (Michener 2007). These three subgenera were formerly included in Group 1

(*Megachile* sensu Michener 1965), but Michener (2007) later placed *Creightonella* alone in Group 3, and *Megella* and *Mitchellapis* in Group 2; the latter decision seems to be primarily made on the presence of marginal hairs on the S8 of the male (Michener 2007).

My analyses consistently clustered *Sayapis* (Group 1) with *Creightonella* and *Mitchellapis*; they belong to a well supported clade that is the sister group of the remaining subgenera of Group 1 (Figs. 164–167). Likewise, *Megella* was also consistently placed within a primarily Old World clade of subgenera of Group 1. Then, despite having some characters typical of the Group 2, these subgenera are members of the Group 1. Because it is commonly argued that the cost of a character gain is much higher than its loss, the recurrence of characters makes some taxa, such as *Megella*, difficult to place in a given taxonomic category. However, phylogenetic analyses are not only guiding us to make less arbitrary decisions about the placement of those "problem" taxa but also in revealing that character gain is an evolutionary phenomenon more widespread than we previously thought. The recurrence of complex structures, such as eyes and wings, has only been recently appreciated in the light of phylogenetic analyses (***e.g.***, West-Eberhard 2003, Whiting et al. 2003). Thus, the gain of less complex structures such as the marginal hairs of the S8 and arolia, an adhesive pad between pretarsal claws (Fig. 62) in subgenera *Heriadopsis* and *Matangapis*, seems plausible. The nesting biology of *Creightonella* and *Megella*, both of which make extensive use of leaf pieces, also supports their placement in Group 1; the biology of *Mitchellapis* is unknown.

The results presented here recovered some major phylogenetic lines previously discussed by Michener (1965, 2007) and Mitchell (1980), especially when characters related to parasitism were deactivated (analysis B, Fig. 167). For example, among the subgenera of Group 2, two clades are distinguished: one includes *Matangapis* and all the subgenera with heriadiform or hoplitiform bodies (*i.e*., *Chelostomoda*, *Hackeriapis*, etc) whereas the other contains *Chalicodoma* and the remaining subgenera of Group 2. Unlike the clade that includes *Chalicodoma*, the one that includes *Matangapis* was consistently recovered in the analyses and several characters support its monophyly. For example, the integument is usually coarsely and densely punctuated, with usually white fasciate and strong postgradular grooves on T2 and T3, usually pale or grayish pubescence, and with three exposed sterna in the male; the carina of T6 of the male is also usually weak, and little projected in profile.

Some lineages previously recognized by Mitchell (1980) were also distinct within the clade that contains all the leafcutter bees (*i.e*., all subgenera of Group 1, *Creightonella*, *Mitchellapis*, and *Megella*). Some of them, such as the *Creightonella* and *Pseudocentron* lines, are distinct and easily recognizable by one or two morphological features; others, like the *Amegachile* and *Cressoniella* lines, lack distinct characters and were only suggested in the analysis. These lineages are briefly discussed below.

***Amegachile* line**. This lineage includes *Aethomegachile*, *Amegachile*, *Megella*, *Neocressoniella*, *Paracella*, and *Tylomegachile*; these taxa, with the exception of *Tylomegachile*, are primarily Old World in distribution.

***Chrysosarus* line**. Mitchell (1980) also recognized this lineage, which included the subgenera *Chrysosarus*, *Stelodides*, and *Zonomegachile*. Based on the description and figures provided by Raw (2007), the newly described subgenus *Austrosarus* seems to belong here.

***Creightonella* line**. This includes the subgenera *Creightonella*, *Mitchellapis*, *Sayapis*, and *Schrottkyapis*. The members of this group have a chalicodomiform body shape and the mandible of the female usually possess incomplete cutting edges between teeth. A remarkable feature of this lineage is the S6 of the female (Fig. 77); at least in the species examined for this study, it is elongated and with a membranous or weakly sclerotized pregradular area (visible only after dissection). Mitchell (1980) recognized this lineage under the generic name of *Eumegachile*; however, he also included the subgenera *Eumegachile* and *Grosapis* but separated *Creightonella* generically.

***Cressoniella* line**. All of the subgenera included here, except for *Tylomegachile*, were included in the genus *Cressoniella* sensu Mitchell (1980). *Austromegachile*, *Cressoniella*, *Dasymegachile*, *Neochelynia*, *Ptilosarus*, *Ptilosaroides*, and *Trichurochile* belong to this New World lineage. The mandible of the female has four teeth, the innermost tooth is blunt, truncated or incised, and has cutting edges in the second and third interspaces.

***Megachiloides* line**. The primarily Nearctic subgenera *Megachiloides* and *Xanthosarus*, and probably *Argyropile* belong here. Mitchell (1980) also suggested this relationship under the generic name *Megachiloides*, but he placed some *Xanthosarus* species in separate genera.

***Pseudocentron* line**. All members of this group of subgenera are primarily Neotropical in distribution; *Acentron*, *Leptorachis*, *Melanosarus*, *Moureapis*, and *Pseudocentron* are included here. Mitchell (1980) recognized this lineage and placed them in the genus *Pseudocentron*. The most distinctive character of this lineage is the S6 of the female that has at least the posterior half bare or nearly so, except for a subapical row of short hairs, behind which there is a bare, smooth rim directed posteriorly (Fig. 75).

Except for the position of *Platysta* within *Eutricharaea*, the relationships among the remaining subgenera are not clear to me. Mitchell (1980) separated *Eutricharaea*, *Litomegachile*, *Megachile* s. str., and some *Xanthosarus* species in the genus *Megachile*; however, these taxa appeared apart from each other in my analyses and may represent independent lineages.

Monophyly of subgenera

The monophyly of 16 subgenera was consistently suggested among analyses, although the relative support for these clades varied (Figs. 164, 165, 167; Table 5). Low branch support in morphological studies is not surprising because species with unusual combinations of character states are selectively chosen to increase variability within subgenera (Packer 2008). The same can be argued for the low branch support of larger clades in the consensus tree.

The 14 subgenera containing more than one species but represented in my analyses by single species are likely monophyletic because each is morphologically uniform (*e.g.*, *Maximegachile*, *Ptilosarus*). *Chalicodoma* and *Pseudomegachile* also seem monophyletic but they appeared paraphyletic when characters related to parasitism were deactivated (analysis B, Fig. 165b). *Chalicodoma* was rendered paraphyletic by *Gronoceras* but the dull mandible and the presence of three large spines on the outer surface of the front tibia in *Gronoceras* suggest a closer relationship to *Callomegachile* or *Largella*. *Pseudomegachile* appeared to be paraphyletic because *M. muansae* clustered with *Callomegachile*; *M. muansae* is the only species placed by Pasteels (1965) in the monotypic subgenus *Dinavis*, and it is known only from the male. The lack of female characters in the data matrix may account for its exclusion from the *Pseudomegachile* clade.

Likewise, *Leptorachis* also seemed monophyletic even though its monophyly was only suggested when for analysis D male characters were deactivated (not shown). The female of *M. laeta*, placed in the subgenus *Leptorachina* by Mitchell (1980), has a distinctive S6 that characterizes all females of *Leptorachis* and those of the *Pseudocentron* group of subgenera: *Acentron*, *Melanosarus*, *Moureapis*, and *Pseudocentron*; such a sternum has at least the posterior half bare or nearly so, except for a subapical row of short hairs, behind which there is a bare, smooth rim directed posteriorly (Fig. 75). However, the female of *M. laeta* is large and robust, and the mandible has a shallower second interspace than in most *Leptorachis*; also unlike most males of *Leptorachis*, the male of *M. laeta* has an expanded front tarsus, large front coxal spine, and a small spine on the middle coxa (as in Fig. 103). A similar case occurs in *Moureapis* where the male of *M. possograndensis* Schrottky has expanded and highly modified front legs unlike any other known male of the subgenus (Raw 2007). With a change in the mating system, it is likely that such modified front legs could have been lost in some males or regained in others (Michener 2007). Thus this one character, like almost any other single character, need not always be considered as subgenerically distinctive. Such an idea is supported for male front tarsi when all male characters are deactivated (analysis D).

Nine subgenera were non-monophyletic (Table 5). It is clear that in some cases recognition of highly derivative species at the subgeneric level render some subgenera paraphyletic. For example, as Michener (2007) suspected, the monotypic subgenus *Schrottkyapis* renders *Sayapis* paraphyletic. Such a relationship is supported by a single putative synapomorphy (character 124-1); S6 of the female has a nearly membranous pregradular area with a distinct invagination parallel to the lateral margin of the sternum (visible only after dissection). *Stelodides* is another monotypic subgenus that rendered *Chrysosarus* paraphyletic, except when *Dioxys* was excluded from the analysis. The subgenus *Platysta* is also clearly derived from the *eurymera* species group (or subgenus *Eurymella* sensu Pasteels 1965), just as *eurymera* is derived from other more ordinary *Eutricharaea*.

In the remaining subgenera, the species used in the analysis either never grouped or at least one was excluded from a cluster containing most of the species. *Stenomegachile* and *Xanthosarus* are examples of the first case; *Hackeriapis* and *Chelostomoides* are of the second. All these subgenera are morphologically heterogeneous and further study is needed.

Outgroup selection for study of subgenera of *Megachile* s. l.

Anthidiini and Osmiini are both speciose and morphologically highly diverse tribes that lack phylogenetic hypotheses; thus, the taxa I selected as outgroups for the phylogenetic analysis of subgenera of *Megachile* s. l. are likely not those most closely related to Megachilini. For practical reasons, I did not include representatives of all genera of both tribes, although species were chosen to cover the maximal morphological and biogeographical diversity, as well as to include representatives of informal generic groups traditionally recognized in each tribe.

The species I selected as outgroups for the phylogenetic analysis of subgenera of *Megachile* s. l. were chosen based on their positions in the strict consensus tree (see Chapter I, Fig. 162); that is, one basal taxon and one more derived taxon within each tribe to maximize variation. Given the limited number of taxa used from each tribe and that most internal branches are poorly supported (bootstrap and Bremer support values of less than 50% and one), the internal relationships within each tribe are likely not accurate. For example, two studies that focused on the internal phylogeny of Lithurgini (Michener 1983, Engel 2001) regarded *Trichothurgus* as the sister group of the other two genera combined (*Microthurge* and *Lithurgus*) whereas in my analysis *Microthurge* was the sister group of the other two. However, *Trachusa* was the sister group of all remaining Anthidiini in my analysis as in the study of Müller (1996). When the relationships among the genera of Anthidiini and Osmiini are studied in detail, further analyses using different outgroups may be desirable.

Nesting behavior and geographical distribution

Some morphological structures are related with differences in nesting substrates. The presence of cutting edges between teeth in the mandible of the female has generally been associated with the use of petal or leaf pieces, although species without such structures (*e.g.*, *Chrysosarus*) still exhibit leafcutting behavior (Zillikens & Steiner 2004). Likewise, the modifications of the female clypeus, labrum, and mandible of *Chelostomoides* and *Hackeriapis* seem to be related to resin, pebble, or sand collection for cell closures. For example, the large head, long and subtriangular labrum, and elongated mandibles of *Megachile rugifrons* are similar to those of *Megachile pluto*, an Oriental species that specializes in resin collection (Messer 1984). The presence of long and stout hairs on the maxillary palpi in some species of Group 2 also seems to be related to resin manipulation because such hairs are rare or absent in subgenera of Group 1 that rarely use resins.

Cutting edges seem to develop from different structures in the mandible. They are clearly extensions of the lower border of a tooth (Figs. 25, 26) or from a transverse ridge at the base of the teeth that runs parallel to the fimbriate line on the inner surface of the mandible. The first type is usually incomplete (*i.e*., does not fill the space between teeth) and its origin is obvious in most cases. Even in species that lack cutting edges (*e.g*., *Schrottkyapis* and *Stelodides*), there still is a hidden small projection from the inferior border of the third tooth that suggests an incomplete cutting edge. The second type is usually complete and its origin is less evident. However, in some species that have secondarily lost cutting edges (*e.g*., *Stelodides*), the transverse ridge is more conspicuous and distinctly elevated compared to that of most species of Group 2 that presumably never developed cutting edges. Thus, it seems that this transverse ridge has been modified into cutting edges in those species with extensive leaf cutting behavior.

The first type of cutting edge has arisen independently in *Chelostomoda* (Group 2) and in the large clade that includes all subgenera of Group 1, *Creightonella*, *Mitchellapis*, and *Megella*; the second type is only present in more derived taxa of the latter clade (Fig. 168). The phylogenetic distribution of both types of cutting edges also indicates that an incomplete cutting edge is more common than a complete cutting edge in the second interspace of the mandible; the opposite occurs in the third interspace.

Cutting edges seem to have evolved after the leaf cutting behavior was already in place. This idea is suggested by the use of chewed leaf pulp in some Osmiini and irregular leaf pieces in some *Callomegachile* species (Michener 2007). Cutting edges have also been secondarily lost in some species of *Chrysosarus*, *Megachile* s. str., and in the monotypic subgenera *Schrottkyapis* and *Stelodides*, although leaf cutting behavior has been retained in some of them. The fossil record for *Megachile* is quite poor and most compression fossils cannot be reliably assigned to the genus (Engel 1999), but a fossil of a dicotyledonous leaf with distinctive, semi-circular cuts into the margin suggests that leaf-cutting behavior started as early as the middle Eocene (Wappler & Engel 2003).

There seems to be great variation within and among species in the degree and manner of leaf use and selection of cell closure materials (*e.g.*, Michener 2007, Armbrust 2004, Zillikens & Steiner 2004). Those might provide additional characters useful for reconstructing the phylogeny of *Megachile* s. l. For example, a few records indicate that some species of the subgenera *Litomegachile*, *Megachiloides*, *Megachile* s. str., and *Xanthosarus* use small circular pieces of leaves to make the bottom of a brood cell (Williams et al. 1986, Krombein & Norden 1995) whereas in other subgenera, such as *Eutricharaea*, the bottom is formed by bending the leaf pieces from the cell cup (Medler 1965, Kim 1992). However, the nesting biology of the vast majority of species of *Megachile* s. l. remains unknown.

Floral relationships are also largely unknown in *Megachile* s. l. The scant information suggests that species in some subgenera may be specialized in pollen collection from several plant families. Some strongly oligolectic species (*e.g.*, *M. campanulae*) have no obvious morphological adaptations to their flowers whereas others have distinctive hairs and brushes on several areas of the body. For example, the female of *M.* (*Dasymegachile*) *mitchelli* has a flat clypeus and supraclypeal area with hooked hairs presumably related to pollen collecting from *Salvia* (Lamiaceae).

Similar hairs are also present in *Matangapis* as in several bee species of unrelated families. Some species of *Megachiloides* seem to be oligolectic on pollen from flowers of several plant families, such as Onagraceae and Cactaceae. Some species have extremely long tongues (*e.g.*, *M. oenotherae*) that may indicate specialization. Probably unique among *Megachile* s. l., and presumably related to pollen-collecting behavior on *Piper* inflorescences, are the long, dense, plumose hairs on the thoracic venter and S2 of the female of *Ptilosarus* (Michener 2007). There are numerous examples of other modified hairs on several body areas in other subgenera but floral records and behavioral studies are still missing.

The geographical distribution of the subgenera of *Megachile* s. l. largely agrees with the proposed phylogenetic hypothesis (Fig. 168). All members of Groups 2 and 3, except for *Chelostomoides*, are native to the Eastern Hemisphere whereas taxa comprising Group 1 occurs in both Eastern and Western Hemispheres. The greatest diversity of Group 1 is in the Western Hemisphere. *Megachile* s. str. and *Xanthosarus* are the only subgenera containing species in both the New and the Old World.

Classificatory considerations

Constructing a useful, practical classification on the basis of phylogenetic hypotheses commonly involves arbitrary or subjective decisions.

My phylogenetic analysis suggests that the cleptoparasitic taxa, *Coelioxys* and *Radoszkowskiana*, are the sister group of the free living *Megachile* s. l. The genus

Radoszkowskiana seems to be a *Coelioxys* despite the distinctive male characters, and recent biological data support this idea (Rozen & Kamel 2007). The three problem subgenera, *Creightonella*, *Megella* and *Mitchellapis*, which combine characters of the three groups and led Michener (2007) to subsume all nonparasitic megachilines in *Megachile*, consistently fell in my analysis within a large, monophyletic clade containing all subgenera of Group 1 (*i.e.*, *Megachile* sensu Michener 1962, 1965). My analysis also supports the suspicion of Michener (2007) that Group 2 (*Chalicodoma* sensu Michener 1962) is nonmonophyletic, and that the recognition of some subgenera renders others paraphyletic; for example, *Schrottkyapis* makes *Sayapis* paraphyletic.

Given these results, one classificatory approach is to recognize only two genera in Megachilini, *Coelioxys* and *Megachile* s. l., while synonymizing those subgenera of the latter genus that render others paraphyletic. The next two classificatory proposals differ from the first in the taxonomic rank given to the major clades of *Megachile* s. l.

In the second proposal, *Megachile* s. l. could be divided into several genera that largely correspond to the groups discussed by Michener (2007: pp. 553–555) and those clades indicated in Fig. 165. For example, the subgenera of Group 2 could be segregated into the genera *Chalicodoma*, *Matangapis* and *Thaumatosoma*; the last is the oldest genus-group name in the clade that includes *Chelostomoda* and related hoplitiform or heriadiform subgenera. Some morphological features indicate that, despite the position in the tree, *Austrochile*, *Chalicodomoides*, and *Rhodomegachile* belong to *Thaumatosoma* (see below). *Matangapis* could also be included within *Thaumatosoma* but it is very different (*i.e*., body shape, presence of arolia in all legs) from the remaining subgenera. *Chalicodoma* would contain the remaining subgenera of Group 2 whereas *Megachile* would be restricted to all subgenera of Group 1, plus the subgenera *Creightonella*, *Megella* and *Mitchellapis*.

The third proposal differs from the second in the generic level given to *Creightonella*. Both sexes of this group are very different from the remaining subgenera of Group 1. It has long been recognized as a genus and retaining this rank maybe appealing for many systematists. However, in all my analyses *Creightonella* clustered with *Mitchellapis* and *Sayapis* (the last includes the monotypic subgenus *Schrottkyapis*, Figs. 164–167). Thus, if one wants to retain the generic rank of *Creightonella*, the status of these subgenera would have to be changed; they are either to be regarded as genera or as subgenera of *Creightonella*. *Mitchellapis* is very distinctive and it could be regarded as a genus, as Michener (2007) suggested. *Sayapis*, however, does not seem to warrant a generic status; it would have to be placed within the genus *Megachile*.

Each of the three proposals has practical advantages and disadvantages. An obvious advantage of retaining the large genus *Megachile* is that even with further knowledge of its phylogeny, the combinations of names created by the second and third proposals would not have to be accepted and perhaps, later, altered again. Phylogenies are always subject to change with the discovery of new taxa or the analysis of new characters (*e.g.*, molecular data, additional morphology, or combined data sets).

Adopting the second or third proposal would create new combinations of names that might seem undesirable, particularly recognizing *Thaumatosoma* and *Creightonella*. However, most published work has been done on members of Group 1 rather than on Group 2 or 3, because of the economic importance and worldwide distribution of species of Group 1. The new combinations of names in Group 2 would not have a major effect in the literature.

The placement of *Austrochile*, *Chalicodomoides*, and *Rhodomegachile* within *Thaumatosoma* seems arbitrary because they did not appear close to *Thaumatosoma* in the consensus tree; however, they have morphological characters that support such a decision. For example, *Austrochile* has nonfasciate postgradular grooves on T2 and T3, usually fulvous pubescence on T5 and T6, and a large subapical spinous process on S1; the latter process is only present in the subgenera *Schizomegachile* and *Thaumatosoma*. Likewise, the distinctive broad, ligulate glossa of *Rhodomegachile*, the very weak to nearly absent carina of T6 of the male, and T2 and T3 without fasciate postgradular grooves are characters that suggest a closer relationship with *Hackeriapis* and its relatives.

One advantage of dividing *Megachile* s. l. into four or six genera is that this may allow a more efficient retrieval of information. Division might also encourage faster taxonomic revisions and comparative biological studies that would in turn increase our understanding of the group. For example, recognition of *Megachile* in a narrower sense than it is now would highlight the differences in nesting behavior and morphology among groups. In other cases, it would highlight unusual distribution patterns. For instance, recognition of the genus *Thaumatosoma* would indicate in more detail the primarily Australian-North American distribution of *Chelostomoides* and *Hackeriapis*. Such information may be easier to remember in several smaller genera rather than in a large genus with numerous subgenera, like *Megachile* s. l.

Chapter III. Classification of the bee tribe Megachilini with emphasis on *Megachile* s. l.

INTRODUCTION

The purpose of a phylogeny-based classification is to develop a system, which in addition to functioning for information storage and retrieval system, is as consistent as possible with the phylogeny (Wiley et al. 1991). In practice, however, it is not always possible to develop a classification that is totally consistent with the phylogeny and therefore, the number of genera or subgenera one wants to recognize is arbitrary and independent of the results and methods (Michener 1957, Mayr 1969). For example, only monophyletic groups should be recognized, but acceptance of paraphyletic groups might sometimes be desirable if it allows a maximum retrieval of information, memorability, easy recognition, or stability with previous classifications (Michener 1957, Mayr 1969). Therefore, in addition to the phylogeny, I also considered the following four criteria that are explained in Materials and Methods: morphological distinctiveness, group size, biology, and stability.

Considering the advantages and disadvantages of each classificatory proposal discussed in the second chapter, I have decided to follow the second approach in recognizing five genera in Megachilini: *Chalicodoma*, *Coelioxys*, *Megachile*, *Matangapis*, and *Thaumatosoma*. Megachilini is highly diverse morphologically and many species with unusual and sometimes bizarre morphologies have been separated as genera or subgenera (*e.g.*, *Schrottkyapis*). Emphasizing differences is sometimes useful in morphologically homogeneous groups (*e.g.*, Augochlorini, Euglossini or Meliponini), but given that excessive splitting conveys little information regarding relationships and considering the high morphological variation present across

Megachilini, I thus have emphasized the similarities rather than the differences among subgenera.

To recognize only monophyletic groups, I propose to synonymize some subgenera that render others paraphyletic (e.g., *Schrottkyapis* and *Sayapis*). To emphasize their relationship and to reduce the number of monotypic subgenera, I propose to synonymize some monotypic or small subgenera with their closest relatives. I have made such decisions only when the grouping is strongly supported by morphological characters (*e.g.*, *Neocressoniella* and *Megella*) or by high values of branch support in the consensus tree.

Although it is straightforward to synonymize monotypic or small subgenera, some of them have either plesiomorphic or highly derived characters that broaden the current subgeneric concepts and make them difficult to diagnose. For example, *Parachalicodoma* is a monotypic subgenus and the sister group of *Chalicodoma*, a subgenus containing about 40 species; *Parachalicodoma* lacks the mandibular and sternal characters that characterize *Chalicodoma*. *Ptilosaroides* is a small subgenus with two or three species and is the sister group of *Ptilosarus*, a subgenus with 15 species; *Ptilosaroides* lacks the distinctive preoccipital carina and specialized pollen-collecting pubescence of *Ptilosarus*. Similar cases appear to be common when developing a phylogeny-based classification in other groups of bees (*e.g.*, Williams et al. 2008); for the present, however, I have decided to synonymize such subgenera.

I have also emphasized female characters because they are less variable than male characters. Some species have been separated subgenerically entirely on male secondary sexual characters when females are clearly associated with an existing subgenus. For example, the female of *M. laeta*, placed in the subgenus *Leptorachina* by Mitchell (1980), is easily assigned to *Leptorachis* based on the mandibular structure and distinctive pubescence of the S6; the male, however, is unlike any other *Leptorachis* in having highly modified front legs that are used to hold the female during mating (Wittmann & Blochtein 1995). A similar case seems to occur with the male *M. possograndensis* Schrottky, a species of the subgenus *Moureapis* (Raw 2007).

As previously noted by Michener (2000), some male characters seem to be consistent in certain subgenera (*e.g*., *Pseudocentron*) but quite variable in others (*e.g*., *Eutricharaea*). The mating behavior of *Megachile* is still poorly known, but a change in the mating system might promote the loss or gain of such structures. Thus, although male characters might provide useful phylogenetic information, there is no need to isolate a species into its own subgenus solely on the male morphology.

I have also retained certain subgenera whose monophyly was not recovered in my analyses (*e.g*., *Eutricharaea* and *Hackeriapis*); they are large and morphologically heterogeneous, and further study is needed. Excluding *Coelioxys*, I recognize a total of seven subgenera in the genus *Chalicodoma*, 29 in *Megachile*, and 11 in *Thaumatosoma*; *Matangapis* is a monotypic genus (Table 3).

MATERIALS AND METHODS

Michener (2000, 2007) provided identification keys and diagnostic characters for the subgenera of *Megachile* s. l. Here, I have modified those keys and included additional comments for each taxon only when needed. Morphological terminology and abbreviations are as explained in the first chapter.

In addition to the phylogeny, I used the following four criteria to develop the classification:

Morphological distinctiveness. I made an effort to recognize species groups that are morphologically distinctive, easy to characterize and to differentiate from close relatives. Mayr (1969) suggested that the larger the species groups, the smaller the morphological discontinuity needed to recognize separate taxa. However, to avoid excessive splitting, I followed the suggestion of Michener (1957, 1963) that such groups should have a reasonably wide morphological discontinuity.

Group size. A classification based on groups containing many species, as well as an excessive number of small groups, reduces its usefulness for information retrieval (Mayr 1969). When possible, I tried to avoid those extremes by lumping monotypic, closely related groups and splitting large, paraphyletic groups. Also, moderate sized groups might promote rapid taxonomic revisions or comparative biological studies, which in turn would increase our understanding of the whole group.

Biology. When available, I used biological information (*e.g.*, nesting biology) to support the recognition of groups. Also, to increase the informative power of their ecological success, I tried to recognize groups that show relationships, rather than uniqueness, among biogeographical regions.

Stability. To avoid excessive nomenclatural changes, I followed the principle of stability that suggests a conservative approach when altering the current classification (Wiley et al. 1991). That is, while implementing a phylogenetic system, I tried to minimize modifications to the current classification.

RESULTS

Key to the New World genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Females) (Partly from Michener 2007)

1\. Scopa absent; metasoma tapering from near base to narrow, often acutely pointed, apex……………………………………………………………………….*Coelioxys*

—. Scopa present on S2 to S5 or S6; metasoma not tapering throughout its length….2

2(1). Mandible with cutting edges between teeth, if in second interspace only, then edge complete (in three-toothed mandible; Fig 23), or mandible clearly five-toothed, with teeth 4 and 5 about as apart as 3 and 4….……………..………………………...3

—. Mandible without or with scarcely evident cutting edges between teeth, or with incomplete cutting edge in second interspace only; mandible with less than five teeth, or, if five-toothed, then upper two teeth (4 and 5) usually closer than teeth 3 and 4….. …………………………………………………………………………………...8

3(2). S6 with at least posterior half bare or nearly so, except for subapical row of short hairs, behind which is a bare, smooth rim directed posteriorly (Fig 75)………… ………………….……………………………………………………………...4

—. S6 with well dispersed scopal hairs (Fig. 76), or, if partly bare, then without bare apical rim behind transverse fringe of short hairs or (in *Argyropile*) rim directed upward, or rim narrow and barely recognizable………………………..…………18

4(3). Mandible five-toothed, a long cutting edge in second interspace, none elsewhere ………………………………………………………*Megachile* (*Melanosarus*)

—. Mandible four-toothed, a well-formed cutting edge in the third interspace ……… ………………………………………………………………….......................5

5(4). Second interspace distinct, with cutting edge usually present…….….………6

—. Second interspace lacking or small, without cutting edge………….……………..7

6(5). Inner angle of mandible truncate, or apical margin of clypeus impressed medially; S6 with distal margin rather narrowly truncate………..…………….…… ……………………………………………………………*Megachile* (*Moureapis*)

—. Inner angle of mandible acute or rounded; clypeal margin straight and entire; S6 with distal margin broadly truncate or rounded ……………………………………… ………………..………………………………….….*Megachile* (*Pseudocentron*)

7(5). Mandible more robust, apical tooth more protuberant, much broader than other teeth; gena usually broader than eye in lateral view…………………………………… ……………………………………………………….….*Megachile* (*Acentron*)

—. Mandible less robust, apical tooth not much broader than second or third; gena usually narrower than eye in lateral view……….…………*Megachile* (*Leptorachis*)

8(3). Mandible with a distinct incomplete cutting edge in second interspace, and no cutting edge elsewhere or with scarcely evident cutting edges in second and third interspaces………..…………………………………………….….……………9

—. Mandible without cutting edges in second and third interspaces.........................12

9(8). Body very large and robust (20 X 10 mm); pubescence entirely fulvous (Mexico)…...…………..…………………………….……………*Megachile* (*Grosapis*)

—. Body not so large and robust; pubescence not entirely fulvous…..……..………10

10(9). Preoccipital carina distinct behind gena……...…*Megachile* (*Rhyssomegachile*)

—. Preoccipital margin of gena not carinate……….…………………………………..11

11(10). T6 straight or nearly so in profile; sterna with incomplete white apical fascia beneath scopa; apex of front tibia without a distinct acute spine on outer surface…… ……………………………...…………………*Megachile* (*Chrysosarus*) (in part)

—. T6 usually strongly concave in profile; sterna without apical hair bands beneath scopa; apex of front tibia with a distinct acute spine on outer surface……………….... ……………………... *Megachile* (*Sayapis*) (in part)

12(8). Apex of front tibia without distinct acute spine on outer surface……..………13

—. Apex of front tibia with at least one distinct acute spine on outer surface (Fig. 58) …….……………………………………………………………………………….14

13(12). T6 distinctly concave in profile, without conspicuous erect pubescence except near base; body pubescence largely white or gray; metasomal sterna without white hair fasciae beneath scopa (Holarctic)……..…..………*Megachile* (*Megachile*) (in part)

—. T6 nearly straight or concave in profile, with abundant erect pubescence; body pubescence of variable color; metasomal sterna with white hair fasciae beneath scopa absent or broadly interrupted medially (Neotropical)…………………………….…… ……………………………………..……………*Megachile* (*Chrysosarus*) (in part)

14(12). Body very large and robust (> 18 mm in length); pubescence with large areas of black or fulvous; apex of front tibia with two or three spines on outer surface (adventive)……………………….……………………….…………………………16

—. Body not so large and robust (~15 mm in length); pubescence largely white, not fulvous; apex of front tibia with only one acute spine on outer surface…………..…15

15(14). Pronotal lobe with transverse hairless lamella hidden among hairs; mandible with third interspace narrowly U-shaped and much deeper than others; clypeus with a strong, bifid median process extending down over the base of labrum (Fig. 5)……….. ……………….…………………………….…………………*Megachile* (*Sayapis*) (in part)

—. Pronotal lobe with transverse, unusually hairy ridge, sometimes with shiny low carina; mandible with third interspace not narrower and deeper than others; clypeus unmodified or not modified as above…...…………*Thaumatosoma* (*Chelostomoides*)

16 (14). Apex of front tibia with three distinct sharp spines or teeth on outer surface; clypeus with longitudinal elevation, highest at lower clypeal margin (? Jamaica)…… …………………………………………………………*Chalicodoma* (*Gronoceras*)

—. Apex of front tibia with two teeth and spines on outer surface; clypeus unmodified or not modified as above…….…………………………………………17

17(16). Mandibular carinae minutely roughened, sometimes dull; adductor interspace of inner surface of mandible covered with very small (≤ 0.2x OD) appressed hairs………………………..……………………*Chalicodoma* (*Callomegachile*)

—. Mandibular carinae shining and smooth (at 40 X); adductor interspace of inner surface of mandible sparsely covered with longer hairs (≥ 0.4x OD)….……………… …………………………………………………*Chalicodoma* (*Pseudomegachile*)

18(3). Mandible three-toothed (Fig. 23) or median tooth weakly divided and mandible thus obscurely four-toothed, with cutting edge limited to upper interspace (second if mandible tridentate, third if mandible quadridentate) (Nearctic)………………………………………………………………..…………*Megachile* (*Megachiloides*) (in part)

—. Mandible four- or five-toothed, with cutting edges in third and usually second interspaces……………..…………………………………….……………………….19

19(18). Mandible robust, apical tooth more protuberant, much broader than other teeth (Fig. 35)..………………………………………………………………………......20

—. Mandible less robust, apical tooth not much broader than second or third…...……………………………………………………………………….……………………..…22

20(19). S6 with apical rim directed upward beyond fringe of hairs, this rim conspicuous if tergum and sternum are spread apart; mid tarsomeres with conspicuously narrow bases, if anterodistal margin is projected, this projection is slender and elongated…………….……………………………*Megachile* (*Argyropile*)

—. S6 without apical rim directed upward beyond fringe of hairs, or, if apical margin is swollen as in *M.* (*Xanthosarus*) *fortis*, bases and anterodistal projections of mid tarsomeres broad and acutely angulated, not elongated...21

21(20). T6 straight in profile; mandible with second tooth often rounded or obtuse; usually no cutting edge in second interspace…….*Megachile* (*Megachiloides*) (in part)

—. T6 straight or concave in profile; mandible with second tooth usually acute; usually with small incomplete cutting edge in second interspace…...............................……………………………………………..……….*Megachile* (*Xanthosarus*)

22(19). Thoracic venter, including leg bases and S2, with dense covering of fine, plumose hairs, sharply differentiated from other scopal hairs……………………………………………………………………….….*Megachile* (*Ptilosarus*) (in part)

—. Thoracic venter and leg bases with ordinary hairs, and scopal hairs all unbranched…………………………………………….…………………………………23

23(22). Metasomal sterna with entire and conspicuous white apical hair fasciae beneath scopa…………………………………………………………………...24

—. Metasomal sterna with white hair fasciae absent or broadly interrupted medially ……….……………………………………………………………………………25

24(23). Mandible four-toothed, not cutting edge in second interspace (adventive, North America, Antilles, Chile, and Argentina)…………………….*M.* (*Eutricharaea*)

—. Mandible with fourth tooth emarginate, thus five-toothed, second interspace with conspicuous but incomplete cutting edge (South America)……..…*M.* (*Trichurochile*)

25(23). Mandible four-toothed, upper tooth acute or right-angular…………..………..26

—. Mandible four- or five-toothed but if four-toothed, then upper tooth rounded, truncate, or incised (sometimes only minutely) and thus approaching the five-toothed condition……………..…………………………………………………………………28

26(25). Metasoma broadly conical, T3 narrower than T1 or T2 (Neotropical)……...… ………………………………………..…….*Megachile* (*Tylomegachile*) (in part)

—. Metasoma more ovoid, T3 as broad as T1…….…………………………………27

27(26). Scopa black; body usually covered with long, dense hairs sometimes obscuring the integument and not forming pale apical tergal fasciae, producing a *Bombus*-like aspect, or if rather ordinary looking species, then clypeus and supraclypeal area flat and dull, with abundant erect, short, and partly hooked hairs (Primarily Andean)……………………..………………..*Megachile* (*Dasymegachile*)

—. Scopa white except on S6; body not densely covered with long, dense hairs; clypeus and supraclypeal area not flat, shiny, and without hooked hairs (Nearctic)… ……………………………………………………..*Megachile* (*Litomegachile*)

28(25). Mandible clearly five-toothed, distance between upper two teeth not or only slightly less than distance between other pairs of teeth (Holarctic)…………………… ……………………………………..………………*Megachile* (*Megachile*) (in part)

—. Mandible four-toothed but upper tooth rounded, truncate, or itself bidentate (sometimes minutely), mandible thus five-toothed but distance between upper two teeth short compared to distances between other pairs of teeth………..…………29

29(28). Metasoma distinctly conical, T1 and T2 broader than T3 (Fig. 68)……..….30

—. Metasoma more ovoid, T3 as broad as or broader than T1……………….……..31

30(29). Metasomal sterna with widely interrupted apical white fasciae beneath scopa; posterior apical angle of hind basitarsus slightly produced, that of segment 2 more conspicuously so (preoccipital margin of gena usually with distinct carina or sharp border)……………………………………….*Megachile* (*Austromegachile*) (in part)

—. Metasomal sterna not at all fasciate; segments 1 and 2 of hind tarsus not or little produced apically……………….……….………….*Megachile* (*Tylomegachile*) (in part)

31(29). Median area of clypeus somewhat elevated and strongly flattened, sloping away on each side (apical margin of clypeus medially emarginate)…………………..
…………………..…………………………….*Megachile* (*Austromegachile*) (in part)

—. Clypeus broadly convex or nearly flat, neither elevated nor flat medially………32

32(31). Pubescence of T6 conspicuous, with many erect hairs as seen in profile; large and robust bees, 9–15 mm in length……………………….….*Megachile* (*Cressoniella*)

—. Pubescence of T6 largely decumbent, with few or no erect hairs visible in profile; small and not so robust bees, 6–11 mm in length………………………………….33

33(32). Thorax and metasoma densely and minutely punctate throughout, largely covered with appressed or suberect tomentum…..…...*Megachile* (*Ptilosarus*) (in part)

—. Thorax and metasoma with punctures distinctly separated, surface not tomentose to any considerable degree……………………………………….*Megachile* (*Neochelynia*)

Key to the New World genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Males)

1. T6 with multispinose preapical carina, with two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair…..*Coelioxys*

—. T6 with preapical carina not as above, often crenulate, medially emarginated, or sometimes reduced to two spines…...2

2(1). Middle tibial spur absent or much shorter than apical width of tibia, sometimes immovably fused to tibia, and middle basitarsus not or little modified……………...3

—. Middle tibial spur present, articulated to tibia, about as long as apical tibial width, or, if absent [as in some *Megachile* (*Xanthosarus*)], then middle basitarsus modified and swollen……………………………………………………………….…..7

3(2). Middle tibial spur present, articulated but small……...*Megachile* (*Leptorachis*)

—. Middle tibial spur absent or represented by prong immovably fused to tibia…..4

4(3). Middle tibial spurlike apical prong (spur presumably fused to tibia), prong sometimes reduced to large, acute tooth…….….……...*Megachile* (*Pseudocentron*)

—. Middle tibial spur without such a process……………………………………...5

5(4). Front and middle tibiae simple and unmodified; front tarsus slender, usually black (except in *M. possograndensis*)..………..……...*Megachile* (*Pseudocentron*)

—. Front and middle tibiae and tarsus modified, middle tibia broadened apically or angulate on lower margin; basitarsus usually excavated along anterior margin; front tarsus dilated and brightly colored………………………………………………...6

6(5). Mesoscutum finely and densely rugoso-punctate, punctures not individually distinguishable; middle coxa usually with small spine (Fig. 103)…………………..…
……………………………………………………………..*Megachile* (*Acentron*)

—. Mesoscutum with punctures usually well separated, but if close, then individually distinguishable; middle coxa without spine…….…….….…*Megachile* (*Melanosarus*)

7(2). S4 not exposed or only its posterior margin exposed; punctuation and vestiture of S4 (except sometimes for posterior margin) reduced and different from those of S3……. …………………………..……………………….…………………..…………8

—. S4 exposed, punctuation and vestiture of S4 similar to those of S3……………..…..9

8(7). Mandible three-toothed, tooth margin much shorter than distance from upper tooth to base of mandible; body not so large and robust (< 17 mm in length); body pubescence largely white or gray.......................……*Thaumatosoma* (*Chelostomoides*)

—. Mandible four-toothed, elongated, toothed margin as long as distance from upper tooth to base of mandible; body very large and robust (20 X 10 mm); pubescence entirely fulvous (only known from Mexico)…………………..…………………….……
……………………………………...…………………….…*Megachile* (*Grosapis*)

9(7). Pronotal lobe with erect, hairless transverse lamella (clypeus protuberant medially; mandible as described above for *Megachile* (*Grosapis*)…………………..…..
……………..…………………*Megachile* (*Sayapis*)

—. Pronotal lobe rounded or with transverse, usually hairy ridge, sometimes with shiny, bare, but low carina………………………….……………………………10

10(9). S8 with hairs on lateral margins (as in Fig. 135); body chalicodomiform with large areas of black and fulvous hairs forming a striking color pattern (except in our species of *Chalicodoma* (*Gronoceras*) (introduced into Caribbean region)…….......11

—. S8 usually without marginal hairs (Fig. 136) but discal hairs sometimes extending laterally beyond margin; body usually megachiliform and usually without striking color pattern [except in *M.* (*Chrysosarus*) *euzona*]…………………………………13

11(10). T6 with preapical brush of long hairs and two long, slender spines representing the preapical carina…………….…………*Chalicodoma* (*Gronoceras*)

—. T6 without brush of long hairs and without long spines……………..…………..12

12(11). T6 with carina short, low, not or shallowly emarginate, not denticulate………
…………..…..*Chalicodoma* (*Callomegachile*)

—. T6 with carina strong, strongly dentate or denticulate, or sometimes scarcely undulate………………………………………………..*Chalicodoma* (*Pseudomegachile*)

13(10). Mandible without inferior projection or tooth (Fig. 93)................................14

—. Mandible with a definite projection, tooth, or angle on lower margin (Figs. 94–96)………………………………………………………………………...............25

14(10). Front coxal spine present (Figs. 99, 100)…...15

—. Front coxal spine absent...20

15(14). Front coxal spine short, inconspicuous; F1 shorter than pedicel; T6 projecting posteriorly, thus nearly horizontal above carina (small, slender species)……………… ………………………………………………….*Megachile* (*Neochelynia*) (in part)

—. Front coxal spine longer, conspicuous; F1 usually longer than pedicel [but short in *Megachile* (*Rhyssomegachile*)]; T6 more nearly vertical, usually not visible from above…...16

16(15). Carina of T6 without emargination but with small median apical point (Neotropical)…. …………………………………………..*Megachile* (*Tylomegachile*)

—. Carina of T6 with a deep, rounded emargination………..……………………...17

17(16). Preoccipital carina strong behind genal area (front tarsus slender, dark)…..… ……………………………………………………….*Megachile* (*Rhyssomegachile*)

—. Preoccipital carina absent………………………………………………………..18

18(17). Anterior end of hypostomal area, immediately behind mandible, with strong, angular projection……………………….………………*Megachile* (*Chrysosarus*) (in part)

—. Anterior end of hypostomal area unmodified……………………………………19

19(18). T6 with preapical carina reduced to two spines, one on each side of emargination; mandible four-toothed; front tarsus slender, black…………………….. ……………………...……...……………………...…*Megachile* (*Ptilosarus*) (in part)

—. T6 with preapical carina better developed, not reduced to two spines; mandible three-toothed; front tarsus usually enlarged, pale….*Megachile* (*Chrysosarus*) (in part)

20(14). F1 and F2 subequal in length (mandible three-toothed, middle tooth sometimes notched, suggesting a four-toothed condition) (primarily Andean)……..… ………………...…………..……………………………*Megachile* (*Dasymegachile*)

—. F1 shorter than F2……………………..………………………………………….21

21(20). Carina of T6 with a pair of acute spines or teeth……..…………………..…22

—. Carina of T6 not bispinose, lateral portions of each side of emargination obtuse, if present…………………………………………………………………………..24

22(21). Large emargination between teeth of carina of T6 filled by dense fringes of long, plumose hairs largely arising from the teeth (mandible three-toothed)………… ……………………...……...………………..……….*Megachile* (*Trichurochile*)

—. Emargination between teeth of carina of T6 not filled by fringe……..………..23

23(22). Mandible four-toothed; body length often 12 mm or more; pubescence erect and rather long…………………...……...……………….*Megachile* (*Cressoniella*)

—. Mandible three-toothed; body smaller, about 7 mm in length; pubescence short, appressed……………………………..…………….*Megachile* (*Ptilosarus*) (in part)

24(21). T6 more nearly horizontal, carina either deeply emarginate, with dorsal surface markedly concave, or surface convex, carina low, with only a small median notch ………………...……...…………………. *Megachile* (*Neochelynia*) (in part)

—. T6 vertical, completely hidden in dorsal view of metasoma, carina low and entire or with small median emargination……..………………….*Megachile* (*Austromegachile*)

25(13). Metasoma about twice as long as wide (carina of T6 usually emarginate medially; front tarsus usually enlarged and pale; front coxa with spine and usually with red bristles)…………………………………………………………………..26

—. Metasoma less than twice as long as wide………………………………………27

26(25). Pubescence of thorax and metasoma black except for broad white band on T3; mandible with small preapical inferior angle……...*Megachile* (*Chrysosarus*) (in part)

—. Pubescence not forming above color pattern; mandible with large basal inferior projection…………………………………………….*Megachile* (*Sayapis*) (in part)

27(25). Carina of T6 entire or crenulate, median part the most produced, with no trace of a median emargination…………………………………………………………28

—. Carina of T6 commonly crenulate, median part emarginate or sometimes irregular but not produced…………………………………………………………………..30

28(27). Front tarsus slender and simple, black or fuscous; apical segment of antenna not at all dilated, fully three times as long as broad; genitalia with apex of gonoforceps simple, usually not dilated and hairless (primarily Nearctic)...................
....*Megachile* (*Argyropile*) (in part)

—. Front tarsus usually dilated, ferruginous or yellowish; apical segment of antenna usually dilated, about twice as long as broad; genitalia with apex of gonoforceps enlarged and bifid, or if simple, usually dilated and with conspicuous hairs………29

29(28). S4 with small but distinct median tubercle on apical margin (large, robust species; Holarctic)……………….………………...*Megachile* (*Xanthosarus*) (in part)

—. S4 without median apical tubercle, apical margin usually broadly membranous (Nearctic)…………………….………………………*Megachile* (*Megachiloides*)

30(27). Mandible four-toothed……….……………………………………………31

—. Mandible three-toothed………………………………………………………..32

31(30). Front tarsus frequently modified, pallid; genitalia with apex of gonoforceps enlarged and bifid, or if simple, usually dilated and with conspicuous hairs (Holarctic)…..…………..…………………………*Megachile* (*Xanthosarus*) (in part)

—. Front tarsus simple, dark-colored; genitalia with apex of gonoforceps simple, usually not dilated and hairless (primarily Nearctic)..
....*Megachile* (*Argyropile*) (in part)

32(30). Mandible with low median or preapical inferior angle in place of usual tooth (Neotropical)….……………………………………*Megachile* (*Chrysosarus*) (in part)

—. Mandible with strong inferior basal tooth..33

34(33). Front tarsus broadly dilated, pale (Holarctic)…………………………………
………………………………..………………*Megachile* (*Xanthosarus*) (in part)

—. Front tarsus simple, black or nearly so…..34

33(32). Front coxal spine reduced to inconspicuous tubercle or absent (Holarctic)…
…………………………………………………………*Megachile* (*Megachile*)

—. Front coxal spine conspicuous, well developed...35

35(34). Morphological apical margin, not carina, of T6 without evident tooth (introduced)……………………..………………………*Megachile* (*Eutricharaea*)

—. Morphological apical margin of T6 with four small but distinct teeth (Nearctic)...*Megachile* (*Litomegachile*)

Key to the Palearctic and Oriental genera and subgenera of Megachilini, excluding *Coelioxys* (Females)

1. Scopa absent; metasoma tapering from near base to narrow, often acutely pointed, apex……………………………………………………………………...*Coelioxys*

—. Scopa present on S2 to S5 or S6; metasoma not tapering throughout its length….2

2(1). Mandible without cutting edges………...3

—. Mandible with cutting edge in at least one interspace, sometimes hidden behind margin of interspace…………………………………………………………………..8

3(2). Arolia present on all legs………………………………...…………...*Matangapis*

—. Arolia absent on all legs…………………………………………………………..4

4(3). Distal margin of clypeus irregularly rounded (rarely weakly emarginate medially), usually strongly crenulate, produced well over base of labrum, not thickened; mandible usually slender with apical margin strongly oblique, except in *C. incana* from northern Africa that has a distinctly five-toothed mandible and less oblique apical margin; head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance……………………*Chalicodoma* (*Chalicodoma*)

—. Distal margin of clypeus truncate or highly modified, usually not crenulate, often not much produced over base of labrum, but if rounded and somewhat crenulate [as in some *Chalicodoma* (*Pseudomegachile*)], then margin thickened and impunctate; head usually much developed posteriorly, ocelloccipital distance thus greater than interocellar distance…….……………………………………………………..…5

5(4). Apex of front tibia with three spines, posterior one less acute and hidden by dense, short hairs; mandible strongly expanded apically, outer margin thus concave in basal half, narrowest part little more than half as wide as apical margin (oriental)…… …………….……………..………………………………*Chalicodoma* (*Largella*)

—. Apex of front tibia with one or usually two spines, posterior one absent; mandible not so expanded apically, outer margin not or weakly concave, narrowest part more than half as wide as apical margin……………………………………..……….6

6(5). Mandible elongate, more or less parallel-sided or narrowest preapically, with teeth across apex and mandibular ridges smooth and shining (at 40X) (southwestern Asia)…………………………………………………*Thaumatosoma* (*Maximegachile*)

—. Mandible of ordinary shape or if elongated as above, then ridges minutely roughened and dull…………………………………………………………………..7

7(6). Mandibular carinae minutely roughened, dulled by microsculpturing; adductor interspace of inner surface of mandible covered with very small (≤ 0.2x OD) appressed hairs……..…………………………………*Chalicodoma* (*Callomegachile*)

—. Mandibular carinae shining and smooth, not dulled by microsculpturing (at 40 X); adductor interspace of inner surface of mandible sparsely covered with longer hairs (≥ 0.4x OD)…..…………………………….………….… *Chalicodoma* (*Pseudomegachile*)

8(2). Mandible with distinct incomplete cutting edge only in second interspace……..
……………………………………………………...…………………………….…9

—. Mandible with cutting edge in third interspace and frequently also in second…….
…………………………………………………………………………………………10

9(8). Metasomal sterna at least laterally with apical fasciae of white hair under scopa; mandible of ordinary shape, five-toothed; small bees (6–10 mm in length)…………
…………………………...……………………….. *Thaumatosoma* (*Chelostomoda*)

—. Metasomal sterna without apical fascia; mandible over twice as long as basal width, four-toothed; large and robust bees (≥ 13 mm in length) (Palearctic).................
……………………..*Megachile* (*Eumegachile*)

10(8). Mandible five- or six-toothed, teeth (except the first) similar and with similarly shaped, incomplete cutting edges in second and third (and sometimes fourth) interspaces (Fig. 25); apices of mandibular teeth roughly equidistant from nearest neighbors; preapical transverse mandibular groove distinct and filled with short, fine, pale hairs……….……………………………………..*Megachile* (*Creightonella*)

—. Mandible four- to five-toothed, teeth above first of different shapes and cutting edges often of different shapes; apices of mandibular teeth commonly separated from nearest neighbors by different distances; preapical transverse mandibular groove, if present, not filled with short, pale hairs……………….……………………..…11

11(10). Mandible with five teeth, distance between fourth and fifth less than half distance between third and forth…….…………………………*Megachile* (*Megachile*)

—. Mandible with four teeth, or if with five, then distance between fourth and fifth little less than half distance between third and fourth……..………………………12

12(11). Mandible with upper interspace as long as or longer than rest of apical margin, cutting edge in upper interspace complete, occupying full length of interspace (hidden or barely visible in facial view in some species), second interspace with incomplete cutting edge…………………………………….………………..13

—. Mandible with upper interspace shorter than rest of apical margin, cutting edges between teeth variable, complete or incomplete….………………………………14

13(12). Head usually much developed posteriorly, ocelloccipital distance thus greater than interocellar distance, usually with preoccipital carina behind gena strong; body 18 mm long or longer……………..…………….………*Megachile* (*Megella*)

—. Head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance, preoccipital carina behind gena absent; body 16 mm long or less ……………………………..…………………………….…… *M.* (*Aethomegachile*)

14(12). Cutting edge large, completely filling second and third interspaces, teeth thus not extending beyond cutting edges and, together with adjacent teeth, forming a thin, generally straight although irregular mandibular margin (Fig. x); cutting edge in second interspace at least in part indistinguishably fused to third tooth (Oriental)…. …………..……………..................…………….………*Megachile* (*Amegachile*)

—. Cutting edges variable but not completely filling interspaces, teeth extending beyond edges at least in some parts of mandibular margin; cutting edges usually nowhere indistinguishably fused to teeth…….…………….………..………………..15

15(14). First mandibular tooth large, ≥ 1.5x wider, at base, than second; sterna without apical hair bands beneath scopa (Palearctic)………………………………… ………………...…………………………………..…*Megachile* (*Xanthosarus*)

—. First mandibular tooth subequal or narrower, at base, than second; sterna frequently with apical white hair bands beneath scopa……..…………………………..16

16(15). Mandible without or with only hidden or very small cutting edge in second interspace but with cutting edge in third interspace (rarely hidden behind interspace margin); inferior margin of upper tooth without laminar projection ….………………. …………………………………………………………*Megachile* (*Eutricharaea*)

—. Mandible with well-developed cutting edges in second and third interspaces; inferior margin of upper tooth usually with a small, tooth-like laminar projection partially hiding cutting edge……………………………………*Megachile* (*Paracella*)

Key to the Palearctic and Oriental genera and subgenera of Megachilini, excluding *Coelioxys* (Males)

1\. T6 with multispinose preapical carina, with two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair...*Coelioxys* (in part)

—. T6 with preapical carina not as above, often crenulate or medially emarginated....2

2(1). Posterior lobe of pronotum with strong transverse lamella extending posterolaterally as flat spine……………………….………………..*Coelioxys* (in part)

—. Posterior lobe of pronotum usually with weak transverse ridge, sometimes with carina or low lamella, but without spine………………………………..…………..3

3(2). S5 and sometimes S6 exposed and generally similar to preceding sterna (sometimes S5 largely hidden but S6 exposed); lateral extremity of carina of T6 directed basad, away from apical margin of tergum………*Megachile* (*Creightonella*)

—. S5 and S6 retracted, variously modified, less sclerotized, less punctate, and less hairy than S1 to S4; lateral extremity of carina of T6 absent or directed toward lateral extremity of apical margin of tergum…………………………………………………4

4(3). Arolia present on all legs……………………………...…………...*Matangapis*

—. Arolia absent on all legs………………………………………………………...5

5(4). S8 with lateral marginal hairs [only one in *Megachile* (*Eumegachile*)]; metasoma commonly strongly convex and twice as long as wide or more………..…..6

—. S8 without marginal hairs but discal hairs sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide………..………………….……………………………….…………15

6(5). S4 largely or wholly retracted, less sclerotized, less punctuate, and less hairy than S2 and S3 (body heriadiform or hoplitiform)..…*Thaumatosoma* (*Chelostomoda*)

—. S4 exposed, similar in punctation and pubescence to preceding sterna……..……7

7(6). T6 with carina dentate or denticulate, sometimes with median emargination but denticulate lateral to it, sometimes bilobed but margin with at least a few faint irregularities; surface of T6 above carina usually without median depression…..…8

—. T6 with carina bilobed or sometimes simple, not at all toothed; surface of T6 above carina usually with median depression……………………………….……..….11

8(7). T7 with narrow, median, apically truncate projection extending well beyond teeth of T6 carina………………………………*Chalicodoma* (*Chalicodoma*) (in part)

—. T7 a low sclerite largely hidden behind T6, sometimes produced to small median spine……………………………..…………………………………………...9

9(8). Front coxa with erect spine……..…..*Chalicodoma* (*Pseudomegachile*) (in part)

—. Front coxa without spine or with tubercle or short spine………………………..10

10(9). Toothed margin of mandible (three-to four-toothed) strongly oblique, nearly as long as distance from upper tooth to mandibular base.. ....*Chalicodoma* (*Chalicodoma*) (in part)

—. Toothed margin of mandible (three-toothed) less oblique, much shorter than distance from upper tooth to mandibular base……………………………….…… ……………………………….………*Chalicodoma* (*Pseudomegachile*) (in part)

11(7). Hairs of middle of T6 above carina extremely long, extending well beyond carina; carina of T6 high, strongly bilobed (T6 conspicuously acute in lateral view)… ……………………………………………………………………………….….....12

—. Hairs of middle of T6 immediately above carina not very long, not extending far beyond carina, although dorsum of T6 may have very long hairs laterally; carina of T6 usually lower, not or rather weakly bilobed……..………………………………14

12(11). Posterior margin of T6 with strong lateral tooth (partly obscured by hair); apex of clypeus with small median nodule continued up clypeus for a distance as a carina (Asia Minor)……..…………………………….…*Thaumatosoma* (*Maximegachile*)

—. Posterior margin of T6 without lateral tooth; clypeus without median nodule and carina………………….………………………………………………………..13

13(12). Front tibia with apical posterior angle, which is obtuse but distinct and covered with short hair……….………………………………*Chalicodoma* (*Largella*)

—. Front tibia without apical posterior angle, or if weakly evident, then angle not covered with short hair………..………….*Chalicodoma* (*Pseudomegachile*) (in part)

14(11). Mandible with strong premedian projection from lower margin at right angles to axis of mandible; T7 with large, exposed, biconvex, punctate surface……..………
…………………………………..…..…………….*Megachile* (*Eumegachile*) (in part)

—. Mandible without inferior projection or with hairy convexity or basal lobe; T7 hidden or exposed as narrow rim (mandibular carinae usually dulled by minute sculpturing)………..…………………………………*Chalicodoma* (*Callomegachile*)

15(5). T7 with large, exposed, biconvex, punctate surface; body chalicodomiform (Palearctic)……...*Megachile* (*Eumegachile*) (in part)

—. T7 hidden or exposed as narrow rim or crescentic sclerite, sometimes prolonged to median spine; body usually megachiliform……….……………………………..16

16(15). Apical margin of T7 deeply, broadly emarginate, forming two prominent teeth………...…………………………………………*Megachile* (*Aethomegachile*)

—. Apical margin of T7 entire or slightly emarginate, not forming two prominent teeth…………………….…………………………………………………………….17

17(16). Front coxal spine absent ………………….……………………………………18

—. Front coxal spine present……………………….……………………………..20

18(17). Head usually with strong preoccipital carina behind gena; species largely black or with fulvous and black coloration suggestive of *C.* (*Callomegachile*); front legs unmodified………...………..…………..…………..…………*Megachile* (*Megella*)

—. Head without preoccipital carina behind gena; species usually dull-colored, gray, often with pale metasomal bands of hair; front legs unmodified or highly modified…
……………….……………………………………………………………..….19

19(18). T6, above preapical carina, usually densely covered with white tomentum (integument not visible); preapical carina of T6 usually toothed or denticulate, usually emarginate medially; gonocoxite of genitalia without dorsal lobe…………..………

……………………….…….………………..…*Megachile* (*Eutricharaea*) (in part)

—. T6 not covered with white tomentum, if present, only medially; preapical carina of T6 medially emarginate, not toothed or denticulate; gonocoxite with dorsal lobe ……………………………………….……………………*Megachile* (*Megachile*)

20(17). Mandible without inferior basal process……….…………………………21

—. Mandible with inferior basal process……………..……………………………22

21(20). Penis valves distinctively enlarged basally; apex of gonostylus simple, not bilobed………..…………………………………*Megachile* (*Paracella*) (in part)

—. Penis valves not distinctively enlarged basally; apex of gonostylus simple or bilobed…………………………………........*Megachile* (*Eutricharaea*) (in part)

22(20). Preapical carina of T6 usually toothed or denticulate, usually emarginate medially……………………………………………………………………23

—. Preapical carina of T6 medially emarginate, not toothed or denticulate…….…24

23(22). Penis valves distinctively enlarged basally…*Megachile* (*Paracella*) (in part)

—. Penis valves not distinctively enlarged basally (apex of gonostylus simple or bilobed)………..……………………………*Megachile* (*Amegachile*, *Eutricharaea*)

24(22). Metasoma with extensive areas of orange tomentum or T6, above preapical carina, usually densely covered with orange or yellowish tomentum (integument not visible)................…..………………..……………*Megachile* (*Amegachile*) (in part)

—. Metasoma without extensive areas of orange tomentum, usually dull-colored, gray, often with pale metasomal bands of hair; T6 not covered with tomentum, if present, only medially but integument largely visible... ……………………..*Megachile* (*Xanthosarus*) (in part)

Key to the Sub-Saharan genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Females)

1. Scopa absent; metasoma tapering from near base to narrow, often acutely pointed, apex……………………..……………………………………………...*Coelioxys*

—. Scopa present on S2 to S5 or S6; metasoma not tapering throughout its length….2

2(1). Mandible without cutting edges; S6 usually with apical hairs like scopal hairs of nearby surface of sternum, sometimes with bare rim; body chalicodomiform, metasoma strongly convex, more or less parallel-sided, and commonly two or more times as wide as long………..3

—. Mandible usually with cutting edge in at least one interspace, sometimes hidden behind margin of interspace; S6 with apical (or preapical if there is a bare rim) fringe of dense, short, often plumose hairs different from scopal hairs; body usually megachiliform [except in *Megachile* (*Megella*)], thus metasoma more or less flattened, cordate, tapering to apical point, usually less than twice as long as wide….. …………………..…………………………………………………...…………….12

3(2). Arolia present on front and middle legs……..……*Thaumatosoma* (*Heriadopsis*)

—. Arolia absent on all legs…………………………………………………………...4

4(3). Distal margin of clypeus rounded (rarely weakly emarginate medially), strongly crenulate, produced well over base of labrum, not thickened; mandible usually slender with apical margin strongly oblique; head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance……………………..… …………………..……………………………………..*Chalicodoma* (*Chalicodoma*)

—. Distal margin of clypeus truncate or highly modified, usually not crenulate, often not much produced over base of labrum, but if rounded and somewhat crenulate [as in some *Chalicodoma* (*Pseudomegachile*)], then margin thickened and impunctate; head usually much developed posteriorly, ocelloccipital distance thus greater than interocellar distance……………….……………………………………………...…5

5(4). Apex of front tibia on outer surface with three distinct, sharp, fully exposed teeth or spines, spaces between them shining…………….*Chalicodoma* (*Gronoceras*)

—. Apex of front tibia with one or two spines, or, if (rarely) with three spines, then posterior spine a mere tubercle or covered by a patch of short hairs, or if distinct and pointed, then spaces between spines with punctures and hairs, not noticeably shining ……………………………………………………………………………………6

6(5). Apex of front tibia with three spines, posterior third one less acute and hidden by dense, short hairs; mandible strongly expanded apically, outer margin thus concave in basal half, narrowest part little more than half as wide as apical margin (Zanzibar)…………………………………………………..…*Chalicodoma* (*Largella*)

—. Apex of front tibia with one or usually two spines, posterior one absent; mandible not so expanded apically, outer margin not or weakly concave, narrowest part more than half as wide as apical margin……………………………………………………7

7(6). Mandible elongate, more o less parallel-sided or narrowest preapically, and mandibular ridges smooth and shining (at 40X); posterior hypostomal area usually with strong tooth..…………………………………………………………………8

—. Mandible of ordinary shape or if elongated as above, then ridges minutely roughened and dull; posterior hypostomal areas without a tooth, sometimes with obtuse angle…………………..……………………………………………………9

8(7). Mandible three-toothed……..…………………...*Thaumatosoma* (*Maximegachile*)

—. Mandible four-toothed……………………………*Thaumatosoma* (*Stenomegachile*)

9(7). Mandible with ridges largely shiny, not dulled by microsculpturing (at 40X)….. ……………………………………………………………………………………10

—. Mandible with ridges dulled by microsculpturing………………………………11

10(9). Apical margin of clypeus broadly and deeply emarginate, lower part of clypeus strongly depressed, separated from upper part by curved ridge……………………….. ……………………………………………………….……………*Chalicodoma* (*Cuspidella*)

—. Clypeus not or little modified, truncate, margin sometimes crenulate………..…… ……………………………………………………*Chalicodoma* (*Pseudomegachile*)

11(9). Mandible five-toothed, with deep, round emargination between third and fourth teeth, fourth and fifth teeth (interpretable jointly as angularly truncate fourth tooth) connected by straight margin basal to level of first three teeth; clypeus with large, deep, triangular, shining, hairless area in middle of which, arising from impunctate surface, is a large tubercle (Madagascar)…..……..*Chalicodoma* (*Cestella*)

—. Mandible three- to seven-toothed, without especially deep emargination and with no teeth displaced basad; clypeus truncate to highly modified, but not as above…… ……………………...………………………………*Chalicodoma* (*Callomegachile*)

12(2). Mandible four to six-toothed, all except lowermost teeth similar in shape with incomplete, similarly shaped cutting edges in second and third (sometimes also forth) interspaces, rarely [*C. cornigera*] in second interspace only, and if mandible four-toothed, then cutting edges sometimes dissimilar; metasoma strongly convex, often twice as long as broad, parallel sided, body chalicodomiform; preapical transverse mandibular groove distinct and filled with short, fine, pale hairs (this is diagnostic in combination with presence of with cutting edges)…………………………………….. ………………………………………...……………….*Megachile* (*Creightonella*)

—. Mandible three- to five-tooth, rarely seven-toothed, without cutting edges, or, if with cutting edges, then second and higher teeth of different shapes and cutting edges of different shapes, or only one cutting edge present; metasomal shape variable; preapical transverse mandibular groove, in forms with cutting edges, absent, or, if present, then not filled with short, pale hairs……………….……………………..13

13(12). Cutting edge large, completely filling second and third interspaces, teeth thus not extending beyond cutting edges and, together with adjacent teeth, forming a thin, generally straight although irregular mandibular margin; cutting edge in second interspace at least in part indistinguishably fused to third tooth (Oriental)……..…… …..………………...…………………………….………*Megachile* (*Amegachile*)

—. Cutting edges variable but not completely filling interspaces, teeth extending beyond edges at least in some parts of mandibular margin; cutting edges usually nowhere indistinguishably fused to teeth……..……….……………………………..14

14(13). Head with strong preoccipital carina behind gena; mandible much broadened apically, outer margin thus strongly convex; metasoma more than twice as long as wide; body 18 mm long or longer………………….………….*Megachile* (*Megella*)

—. Head without preoccipital carina behind gena; mandible of ordinary shape, not strongly concave; metasoma less than twice as long as wide; body usually 16 mm long or less……………………………..……………………………………….15

15(14). Metasomal sterna with complete or incomplete white apical hair fasciae beneath scopa……………………..……………………………………………..16

—. Metasomal sterna without white apical hair fasciae beneath scopa……..……17

16(15). Mandible without or with only hidden or very small cutting edge in second interspace but with cutting edge in third interspace (rarely hidden behind interspace margin); inferior margin of upper tooth without laminar projection………..……..… ……………………………………………….*Megachile* (*Eutricharaea*) (in part)

—. Mandible with well-developed cutting edges in second and third interspaces; inferior margin of upper tooth usually with a small, tooth-like laminar projection partially hiding cutting edge………….………………*Megachile* (*Paracella*) (in part)

17(15). Mandible without or with only hidden cutting edge in second interspace but with cutting edge in third interspace (or upper interspace in a three-toothed mandible), this edge sometimes hidden behind interspace margin…..………..……… ……………………………………………….*Megachile* (*Eutricharaea*) (in part)

—. Mandible with distinct cutting edges in second and frequently third interspaces.… ……………………..……..…………………………………………………..18

18(17). Mandible with upper interspace as long as or longer than rest of apical margin, cutting edge in upper interspace complete, occupying full length of interspace (hidden or barely visible in facial view); inferior margin of upper tooth without laminar projection…………………………………... *Megachile* (*Aethomegachile*)

—. Mandible with upper interspace shorter than rest of apical margin; cutting edge in upper interspace usually visible in facial view; inferior margin of upper tooth usually

with a small, tooth-like laminar projection partially hiding cutting edge………………
………………………………...………………….. *Megachile* (*Paracella*) (in part)

Key to the Sub-Saharan genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Males)

1. T6 with multispinose preapical carina, with two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair…...*Coelioxys*
—. T6 with preapical carina not as above, often crenulate or medially emarginated....2
2(1). S5 and sometimes S6 exposed and generally similar to preceding sterna (sometimes S5 largely hidden but S6 exposed); lateral extremity of carina of T6 directed basad, away from apical margin of tergum…..……*Megachile* (*Creightonella*)
—. S5 and S6 retracted, variously modified, less sclerotized, less punctate, and less hairy than S2 to S4; lateral extremity of carina of T6 absent or directed toward lateral extremity of apical margin of tergum…………………………………………………3
3(2). Arolia present on front and middle legs……..…...*Thaumatosoma* (*Heriadopsis*)
—. Arolia absent on all legs…………………………………………………………...4
4(3). S8 with lateral marginal hairs; metasoma commonly strongly convex and twice as long as wide or more, chalicodomiform……………………….……………….…..5
—. S8 without marginal hairs but discal hairs sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide, megachiliform……………….……………………………….……………17
5(4). Front tibia on outer surface ending distally in three bare spines or teeth, the posteriormost extending as carina along much of outer posterior margin of tibia; T6 with carina represented by long spines or long lobes, partly hidden by extremely long hairs arising before carina……………………..……..…*Chalicodoma* (*Gronoceras*)
—. Front tibia on outer surface ending in two spines or teeth [posterior tooth of *Chalicodoma* (*Gronoceras*) sometimes represented by angle, which if strong is covered by short hair, see *Chalicodoma* (*Largella*)]; tibia usually without carina along outer posterior margin; T6 with carina variable, not represented by long spines, but if bilobed, then lobes much broader than long, surface of T6 usually without extremely

long hairs, but if present, then such hairs sparse enough that carina almost always easily seen…………………………………………………………………...6

6(5). Preapical carina of T6 strongly produced medially to truncate, untoothed process with longitudinal median carina (T6 with strong lateral tooth)…………..…… ……………………………………………………………..*Chalicodoma* (*Cuspidella*)

—. Preapical carina of T6 dentate or medially emarginate, not produced medially, without longitudinal median carina but sometimes with broad ridge…………………7

7(6). Preapical carina of T6 dentate or denticulate, sometimes with median emargination but denticulate lateral to it, sometimes bilobed but margin with at least a few irregularities, rarely with median emargination forming two large teeth and an additional large lateral tooth (T6 thus four-toothed); surface of T6 above carina commonly without median depression……………………………………………..8

—. Preapical carina of T6 bilobed or sometimes simple, not at all toothed, or sometimes with small lateral tooth; surface of T6 above carina usually with median depression…………………………...……………………………………………11

8(7). Front coxa with erect spine…….……*Chalicodoma* (*Pseudomegachile*) (in part)

—. Front coxa without spine or with tubercle or short spine………………………….9

9(8). Toothed margin of mandible (three- to four-toothed) strongly oblique, nearly as long as distance from upper tooth to mandibular base.....*Chalicodoma* (*Chalicodoma*)

—. Toothed margin of mandible (three-toothed) less oblique, much shorter than distance from upper tooth to mandibular base…….……………………………….10

10(9). Eyes unusually large, ocellocular distance thus much less than interocellar distance; T6 without lateral spine (Madagascar)…….………*Chalicodoma* (*Cestella*)

—. Eyes of ordinary size, ocellocular distance about equal to interocellar distance; T6 with strong lateral spine………………..….*Chalicodoma* (*Pseudomegachile*) (in part)

11(7). Hairs of T6 above middle of preapical carina extremely long, extending well beyond carina……………………..……………………………………………12

—. Hairs of T6 above middle of preapical carina not very long, not extending far beyond carina, although laterally dorsum of T6 may have very long hairs……...…..15

12(11). Hypostoma with large tooth close behind mandibular base; front tibia with longitudinal carina along outer posterior angle; hairs of T6 so long and dense as to almost hide preapical carina……………..…*Thaumatosoma* (*Stenomegachile*) (in part)

—. Hypostoma without large tooth behind mandibular base; front tibia without longitudinal carina; hairs of T6 not at all obscuring preapical carina…………….…13

13(12). Apex of clypeus with small median nodule continued up clypeus as carina; posterior margin of T6 with strong lateral tooth, partially obscured by hair………...…… ……………………………………………….…….*Thaumatosoma* (*Maximegachile*)

—. Clypeus without median nodule and carina; posterior margin of T6 without lateral tooth…………………………….……………..……………………………14

14(13). Apex of front tibia with posterior angle (indicating third apical spine) obtuse but distinct and covered with short hair……….……………..*Chalicodoma* (*Largella*)

—. Apex of front tibia without posterior angle, or, if weakly evident, then not covered with short hair……………………….…….*Chalicodoma* (*Pseudomegachile*) (in part)

15(11). Posterior margin of T6 with slender, mesally directed spine at each extreme side and a mediolateral convexity representing a tooth………..…*Megachile* (*Megella*)

—. Posterior margin of T6 simple………………………………………………...16

16(15). Anterior margin of mesoscutum with median portion anteriorly projected and abruptly bent down, thus forming an anterior vertical smooth surface and a dorsal, punctate surface; mandibular carinae shining and smooth; pubescence giving a gray aspect, forming apical white tergal fasciae; body heriadiform (Madagascar)………… ……………………………………...*Thaumatosoma* (*Stenomegachile*) (in part)

—. Anterior margin of mesoscutum not modified as above; mandibular carinae usually dulled by minute sculpturing; pubescence black, fulvous, or with white patches, not grayish in aspect and not forming tergal fasciae; body chalicodomiform... ....*Chalicodoma* (*Callomegachile*)

17(4). Apical margin of T7 deeply, broadly emarginate, forming two prominent teeth ………………………………….……………………*Megachile* (*Aethomegachile*)

—. Apical margin of T7 entire or slightly emarginate, not forming two prominent teeth…………………………………………………………………………………..18

18(17). Penis valves distinctively enlarged basally; apex of gonostylus simple, not bilobed………………………………………………………*Megachile* (*Paracella*)

—. Penis valves not distinctively enlarged basally; apex of gonostylus simple or bilobed…………………..……………………*Megachile* (*Amegachile*, *Eutricharaea*)

Key to the Australian and Papuan genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Females)

1. Scopa absent; metasoma tapering from near base to narrow, often acutely pointed, apex……………………………..……………………………………...*Coelioxys*

—. Scopa present on S2 to S5 or S6; metasoma not tapering throughout its length….2

2(1). Mandible without cutting edges; body chalicodomiform, metasoma strongly convex, more or less parallel-sided, and commonly two or more times as wide as long …………………...3

—. Mandible usually with cutting edge in at least one interspace, sometimes hidden behind margin of interspace; body usually megachiliform [except in *Megachile* (*Mitchellapis*) and *Thaumatosoma* (*Chelostomoda*)], thus metasoma more or less flattened, cordate, tapering to apical point, usually less than twice as long as wide…. …………………..…………..……………………………………...……………9

3(2). S1 with a large, conspicuous midapical spine (Fig. 74)…..…………….……..…4

—. S1 without apical spine……………………………………………………………6

4(3). Claws each with two teeth on underside (Fig. 66); proboscidial fossa closed posteriorly by process from lower side of each genal area…………………………….. ………………………………………………..*Thaumatosoma* (*Schizomegachile*)

—. Claws without or with but one ventral tooth each; proboscidial fossa open posteriorly……………………………………………………………………..5

5(4). Mandible elongated, approximately parallel-sided, bidentate; T6, as seen from above, with strong, rounded, basolateral shoulders, lateral margins thus strongly concave immediately posterior to shoulders……..….*Thaumatosoma* (*Thaumatosoma*)

—. Mandible of ordinary shape, not elongated or parallel-sided, with three or more teeth; T6 without shoulders, lateral margins gently convex to gently and rather uniformly concave…………………….……………...*Thaumatosoma* (*Austrochile*)

6(3). Metasomal integument red, and T2 and T3 without deep transverse postgradular grooves……….……………………….…..…..*Thaumatosoma* (*Rhodomegachile*)

—. Metasomal integument black, or if red, then with deep transverse postgradular grooves……………..……………………………………………………………7

7(6). Sharp hypostomal tooth behind base of mandible; mandible with apical margin very oblique, as long as distance from basal tooth to base of mandible (Fig. 16)…… …….………………..……………………………..*Thaumatosoma* (*Chalicodomoides*)

—. Sharp tooth behind base of mandible absent; apical margin of mandible not as above…………………………………………………………………………………..8

8(7). Mandible shining, although reticulate; T2 and T3 usually with deep, transverse postgradular grooves, these absent from some middle-sized and large species in which claws have strong basal tooth [except in *T.* (*H*) *semiluctuosa* (Smith)]; pubescence usually giving a gray aspect, often forming apical white tergal fasciae; fulvous pubescence often present but confined to apical part of metasoma, rarely [*T. ustulata* (Smith)] metasoma with extensive fulvous pubescence…………………..…… ……………………………………………….………...*Thaumatosoma* (*Hackeriapis*)

—. Mandible dull with minute roughening; metasomal terga without deep, transverse postgradular grooves [except in *C.* (*Callomegachile*) *mcnamerae* Cockerell and others from New Guinea northwestward]; claws without basal teeth; pubescence black, fulvous, or with white patches, not grayish in aspect and not forming tergal fasciae; fulvous pubescence, if present, not confined to apical part of metasoma……………… ……………………….……………………………..*Chalicodoma* (*Callomegachile*)

9(2). Mandible with distinct incomplete cutting edge only in second interspace...…10

—. Mandible with cutting edge in third interspace and frequently also in second.….11

10(9). S6 with large smooth hairless area before apical fringe; T6 with many long hairs visible in profile, its apex produced and shallowly emarginate; pronotal lobe with rounded transverse ridge; large bees, 12–16 mm long…………………………… ………………………….………………………………*Megachile* (*Mitchellapis*)

—. S6 uniformly punctate and hairy; T6 with only very short hairs in profile, its apex rounded; pronotal lobe with strong transverse carina; small bees, 6.5–10 mm long....... ....*Thaumatosoma* (*Chelostomoda*)

11(9). Coloration fulvous and black suggestive of *C.* (*Callomegachile*); third mandibular tooth broad and irregularly truncate because of fusion with cutting edge of second interspace (Fig. 29), second truncate, sometimes oblique, or sinuate at apex………… ………..…………………...……………..………*Megachile* (*Amegachile*)

—. Usually dull-colored, gray, often with pale metasomal bands of hair; third mandibular tooth as well as second angulate, cutting edge in second interspace usually present although incomplete and not indistinguishably fused to third tooth… …..………………..…………………………………………*Megachile* (*Eutricharaea*)

Key to the Australian and Papuan genera and subgenera of Megachilini, excluding subgenera of *Coelioxys* (Males)

1. T6 multispinose preapical carina, with two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair…...*Coelioxys*
—. T6 with preapical carina not as above, often crenulate or medially emarginated....2
2(1). S5 and sometimes S6 exposed and generally similar to preceding sterna (sometimes S5 largely hidden but S6 exposed); lateral extremity of preapical carina of T6 directed basad, away from apical margin of tergum……………………..……… ……………………………………….…………………..…*Megachile* (*Creightonella*)
—. S5 and S6 retracted, variously modified, less sclerotized, less punctate, and less hairy than S2 to S4; lateral extremity of preapical carina of T6 absent or directed toward lateral extremity of apical margin of tergum…….…………………………3
3(2). Hind tibial spur absent or only one present………..…………………………4
—. Two hind tibial spur present……………………..…………………………...5
4(3). Front tarsus enlarged, pale; mandible with an inferior, basal transparent lamella; clypeus without modified hairs or bristles; flagellum not modified, first segment shorter than others, last segment slightly flattened; large bees, 17–22 mm long……… …………………………..……………………...*Thaumatosoma* (*Schizomegachile*)
—. Front tarsus slender, black; mandible without lamella; clypeus with group of coarse, quill-like bristles arising near middle; flagellum exceedingly attenuate, first segment longer than others, last two segments broadly expanded; small bees, 9–12 mm long………...………………………………..…*Thaumatosoma* (*Thaumatosoma*)
5(3). Metasomal integument red, and T2 and T3 without deep transverse postgradular grooves…….……………………………….…..…..*Thaumatosoma* (*Rhodomegachile*)
—. Metasomal integument black, or if red, then with deep transverse postgradular grooves ………………..……………………………………………………………6
6(5). S1 with large midapical spine (as in Fig. 74)..…......*Thaumatosoma* (*Austrochile*)

—. S1 at most apically tuberculate……………………………………………………7

7(6). S4 retracted, or rear margin in some cases exposed…………………….…….8

—. S4 more or less fully exposed………………………………….……………………10

8(7). Distance between apices of first and third mandibular teeth nearly equal to distance from third tooth to base of mandible (as in Fig. 16); apex of S1 produced as a broad, nearly hairless, median, suberect flap; large, robust species; metasoma without indications of pale tergal bands………………..…*Thaumatosoma* (*Chalicodomoides*)

—. Distance between apices of first and third (or second if two-toothed mandible) mandibular teeth much less than distance from uppermost tooth to base of mandible; apex of S1 not as above; usually smaller and more slender species; metasoma usually with indications of pale tergal bands……………………………………………………….9

9(8). Region of preapical carina of T6 swollen except at median emargination (northern Australia and northward)………………..…*Thaumatosoma* (*Chelostomoda*)

—. Region of preapical carina of T6 not swollen (common throughout Australia and Tasmania, rare in New Guinea, not known elsewhere)………………………..…….
………………………………..…………….*Thaumatosoma* (*Hackeriapis*) (in part)

10(7). Preapical carina of T6, near the untoothed tergal margin, broadly rounded except for median tooth at apex of low, longitudinal median ridge…….……………
………………………………………………….…………..…*Megachile* (*Mitchellapis*)

—. Preapical carina of T6 variable, without median tooth…….……………………..11

11(10). S8 with lateral marginal hairs; metasoma commonly strongly convex and twice as long as wide or more, chalicodomiform………..………….…………….…..12

—. S8 without marginal hairs but discal hairs sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide, megachiliform……………….…………….…………………….……….13

12(11). T2 and T3 usually without deep transverse postgradular grooves; pubescence all black or with pale areas not forming metasomal bands; posterior margin of T6 without teeth………………………………………..*Chalicodoma* (*Callomegachile*)

—. T2 and T3 usually with deep postgradular grooves; pubescence usually giving a gray aspect, often forming apical white tergal fasciae; fulvous pubescence often present but confined to apical part of metasoma; posterior margin of T6 usually with four teeth, median teeth absent in some cases…………………………………………
………………………………………………...*Thaumatosoma* (*Hackeriapis*) (in part)

13(11). Body with fulvous-and-black pubescence suggestive of *Chalicodoma* (*Callomegachile*); apical margin of T6 with four widely separated small teeth……..…
……………………………………….………………….*Megachile* (*Amegachile*)

—. Body usually appearing dull-colored, gray, often with pale metasomal tergal hair bands; apical margin of T6 with small lateral tooth only, or sometimes with weak indication of two submedian teeth………………………….*Megachile* (*Eutricharaea*)

Synopsis of genera and subgenera of Megachilini, excluding subgenera of *Coelioxys*

Genus *Chalicodoma* Lepeletier

Comments. This genus is recognized in a narrower sense than that of Michener (1965). It includes all subgenera of Group 2 of Michener (2007), except for those of heriadiform or hoplitiform bodies with sparse pubescence (*i.e*., *Chelostomoda* and related groups), and *Matangapis* (Table 3). *Megella* and *Mitchellapis*, also placed by Michener (2007) in Group 2, are actually leafcutter bees and belong to the genus *Megachile* as understood in the present work (see below). In my analyses, *Chalicodoma* was monophyletic and the sister group of *Megachile* only when characters related to parasitism were deactivated from the analysis (Fig. 165a); otherwise, the included subgenera resulted in a polytomy (Figs. 164a, 167a). *Chalicodoma* is native to the Old World but a few species of the subgenera *Callomegachile*, *Pseudomegachile*, and probably *Gronoceras*, have been introduced to the Americas. A total of seven subgenera are recognized in this work.

***Chalicodoma* / Subgenus *Callomegachile* Michener**

Chalicodoma (*Callomegachile*) Michener, 1962: 21. Type species: *Chalicodoma mystaceana* Michener, 1962, by original designation.

Chalicodoma (*Eumegachilana*) Michener, 1965: 191. Type species: *Megachile clotho* Smith, 1861, by original designation.

Chalicodoma (*Carinella*) Pasteels, 1965: 447 (not Johnston, 1833). Type species: *Megachile torrida* Smith, 1853, by original designation.

Chalicodoma (*Morphella*) Pasteels, 1965: 537. Type species: *Megachile biseta* Vachal, 1903, by original designation.

Cressoniella (*Orientocressoniella*) Gupta, 1993: 165. Type species: *Megachile relata* Smith, 1879, by original designation.

Megachile (*Carinula*) Michener, McGinley, and Danforth, 1994: 174, replacement for *Carinella* Pasteels, 1965. Type species: *Megachile torrida* Smith, 1853, autobasic.

Comments. *Callomegachile* is the most diverse, morphologically heterogeneous, and widely distributed of all subgenera of *Chalicodoma*. It seems monophyletic in my analysis, except for *M. torrida* and *M. decemsignata*, two of the five species placed by Pasteels (1965) in the subgenus *Carinella* (now *Carinula*) which was synonymized by Michener (2007). The female of this species group differs from most *Callomegachile* in the complete longitudinal median clypeal carina and the less dull mandible; the male is also distinctive in the weakly sclerotized to nearly absent volsella. However, these differences seem to me not to warrant its recognition as a subgenus, and thus, I follow Michener (2007) in retaining the synonymy.

Both sexes of at least two Southeast Asian species, *Chalicodoma* (*Callomegachile*) *aterrimum* (Smith, 1862) and *C.* (*C.*) *funerarium* (Smith, 1863), are remarkable in having the fore wing with a dense patch of black hairs on the posterior half of the first medial cell. This character is unique among Megachilidae, and they could be separated in a new subgenus as Baker (1993) had in mind in his unpublished dissertation. I have not seen the specimens, but Baker (1993) indicated that they are closely related to *C. clotho*. If this wing character is the only one that separates those bizarre species from most *Callomegachile*, it seems best to regard them as a species group rather than separating them as a new subgenus.

***Chalicodoma* / Subgenus *Cestella* Pasteels**

Chalicodoma (*Cestella*) Pasteels, 1965: 547. Type species: *Megachile cestifera* Benoist, 1954, by original designation.

Comments. This subgenus from Madagascar includes two species, *C. cestifera* (Benoist) and *C. tsimbazazae* Pauly, 2001. The modifications of the mandible, clypeus, and supraclypeal area of the female characterize this group. In my phylogenetic analysis, *Cestella* was consistently the sister group of *Largella*, both closely related to *Pseudomegachile* (Figs. 164–167).

***Chalicodoma* / Subgenus *Chalicodoma* Lepeletier s. str.**

Chalicodoma Lepeletier, 1841: 309. Type species: *Apis muraria* Oliver, 1789 = *Apis parietina* Geoffroy, 1785, by designation of Girard, 1879: 778.

Chalicodoma (*Euchalicodoma*) Tkalců, 1969: 358. Type species: *Megachile asatica* Morawitz, 1875, by original designation.

Chalicodoma (*Allochalicodoma*) Tkalců, 1969: 359. Type species: *Chalicodoma lefebvrei* Lepeletier, 1841, by original designation.

Chalicodoma (*Parachalicodoma*) Tkalců, 1969: 363 (not Pasteels, 1966). Type species: *Chalicodoma rufitarsis* Lepeletier, 1841, by original designation.

Megachile (*Heteromegachile*) Rebmann, 1970: 41. Type species: *Chalicodoma lefebvrei* Lepeletier, 1841, by original designation.

Megachile (*Allomegachile*) Rebmann, 1970: 42. Type species: *Megachile asiatica* Morawitz, 1875, by original designation.

Megachile (*Katamegachile*) Rebmann, 1970: 43. Type species: *Megachile manicata* Giraud, 1861, by original designation.

Chalicodoma (*Xenochalicodoma*) Tkalců, 1971: 34, replacement for *Parachalicodoma* Tkalců, 1969. Type species: *Chalicodoma rufitarsis* Lepeletier, 1841, by original designation.

Chalicodoma (*Parachalicodoma*) Pasteels, 1966: 13 (not Tkalců, 1969). Type species: *Chalicodoma incana* Friese, 1898, by original designation. [**New synonymy**]

Comments. The long list of synonymies of this subgenus indicates the great morphological variation of this group, especially in the males. For example, unlike most megachiline males, the genitalia of *C. parietina* and *C. lefebvrei* has long peneal apodemes projecting through the genital foramen; the front coxa is unmodified in most males of this subgenus but it has long, conspicuous spines in *C. asiatica* and *C. manicata*; the S8 of the latter species also lacks the fringe of marginal hairs commonly found in *Chalicodoma* and related genera. Such variation has led to the recognition of several subgenera.

The females, however, are less variable. In all of them, the clypeus is nearly hexagonal, with a convex, unthickened, and denticulate apical margin; the mandibular margin is long, oblique, and edentate, and the S6 is distinctly triangular. Such mandibular and sternal characters fail in *C. incana*, a species separated by Pasteels (1965) in the monotypic subgenus *Parachalicodoma*. In that species, the apical margin of the mandible is less oblique and toothed, and the S6 is broad basally with the distal margin medially emarginate. Despite these differences, *Parachalicodoma* was consistently the sister group of all *Chalicodoma* s. str. I have chosen to show their relationship by synonymizing the former. The denticulated carina of T6 and the long process of T7 of the male of *Parachalicodoma* also support its relationship with *Chalicodoma*.

Nests of *Chalicodoma* consist of hard cells built with clay, sand, and pebbles glued by saliva (Banaszak & Romansenko 1998, Mader 2001, Goff 2007).

Chalicodoma / Subgenus *Cuspidella* Pasteels

Chalicodoma (*Cuspidella*) Pasteels, 1965: 544. Type species: *Chalicodoma quadricaudata* Pasteels, 1965, by original designation.

Comments. This monotypic African subgenus is distinct by the mandible of the female and the truncate process of the carina of T6 of the male. The position of *Cuspidella* is uncertain; it resulted in a polytomy in the analysis of the full data matrix (Fig. 164a) and when *Dioxys* was excluded (Fig. 167a), but it was close to *Callomegachile* when parasitic characters were deactivated (Fig. 165). However, the mandible of the female is shinier than that of *Callomegachile*, and thus, resembles *Pseudomegachile*. The presence of a large spine on the apical margin of T6 of the male is also suggestive of the latter subgenus.

Chalicodoma / Subgenus *Gronoceras* Cockerell

Gronoceras Cockerell, 1907: 65. Type species: *Gronoceras welmani* Cockerell, 1907 = *Megachile bombiformis* Gerstaecker, 1857, by original designation.

Megachile (*Berna*) Friese, 1911: 668, Type species: *Berna africana* Friese, 1911 = *Megachile africanibia* Strand, 1912, monobasic.

Gronoceras (*Digronoceras*) Cockerell, 1931: 134, Type species: *Megachile combusta* Smith, 1853 = *Apis cincta* Fabricius, 1781, by original designation.

Comments. The monophyly of this African subgenus is strongly supported, whereas its relationship with the other subgenera of *Chalicodoma* is not; it was either in a polytomy (Fig. 164a) or included within *Chalicodoma* s. str. (Fig. 165a). A putative synapomorphy of this subgenus is the S6 of the female with a strong recurved border or carina on the lateral surface, near the lateral ridge. The antenal flagellum of the male is also distinctive in some species: it is enlarged and deeply concave in *C. bombiformis* (Fig. 89) but almost normal and barely concave in *C. felina* Gerstaecker.

Gronoceras seems to be closer to *Callomegachile* or *Largella* than to *Chalicodoma* s. str., as suggested by the dull mandible of the female and the presence of three large spines on the outer surface of the front tibia. It also lacks the distinct clypeal and mandibular characters of *Chalicodoma* s. str. (see comments for that subgenus). For these reasons, and in spite of its position within *Chalicodoma* s. str. in one of the analyses, I continue to recognize *Gronoceras*. There are about 10 species of this subgenus; several subspecific names have been given to color variants of *C. bombiformis*, *C. cincta*, and *C. felina*.

***Chalicodoma* / Subgenus *Largella* Pasteels**

Chalicodoma (*Largella*) Pasteels, 1965: 534, Type species: *Chalicodoma semivestita* Smith, 1853, by original designation.

Lagella Wu, 2005: 357. Lapsus calami.

Comments. My analysis suggests that *Largella* is the sister group of *Cestella*, both closely related to *Pseudomegachile*. As indicated in the keys, the mandible of the female is distinct by its strongly expanded apex. Four species have been included in this subgenus (Pasteels 1965, Wu 2005).

***Chalicodoma* / Subgenus *Pseudomegachile* Friese**

Megachile (*Pseudomegachile*) Friese, 1898: 198; species first included by Friese, 1899: 36. Type species: *Megachile ericetorum* Lepeletier, 1841, designated by Alfken, 1933: 56.

Megachile (*Pseudomegalochila*) Schulz, 1906: 71, unjustified emendation of *Pseudomegachile* Friese, 1898.

Megachile (*Archimegachile*) Alfken, 1933: 56. Type species: *Megachile flavipes* Spinola, 1838, by original designation.

Megachile (*Neglectella*) Pasteels, 1965: 431. Type species: *Megachile armatipes* Friese, 1909, by original designation.

Chalicodoma (*Dinavis*) Pasteels, 1965: 549. Type species: *Megachile muansae* Friese, 1911, by original designation.

Megachile (*Xenomegachile*) Rebmann, 1970: 44. Type species: *Megachile albocincta* Radoszkowski, 1874, by original designation.

Chalicodoma (*Neochalicodoma*) Pasteels, 1970: 231. Type species: *Chalicodoma pseudolaminata* Pasteels 1965, by original designation. [**New synonymy**]

Comments. This subgenus is as diverse and morphologically heterogeneous as *Callomegachile*. *Pseudomegachile* seems monophyletic, except for the placement of *C. muansae* when characters related to parasitism were deactivated (Fig. 165a); that species is only known from the male and that may have accounted for such a changed in position.

Neochalicodoma is only known from males of two species, *C. pseudolaminata* and *C. pseudocincta* Pasteels 1970. I examined the holotype of the latter species, and it is a **new junior synonym** of *C.* (*Pseudomegachile*) *scindularia* (Buysson, 1903), a species of the *C. armatipes* species group (subgenus *Neglectella* sensu Pasteels 1965). I was not able to examine the holotype of *C. pseudolaminata*, but judging by the descriptions and illustrations of Pasteels (1965, 1970), it seems this male is closely related to *C. pseudocincta* and therefore, it is male of the *armatipes* species group. For this reason, I have synonymized *Neochalicodoma* with *Pseudomegachile*.

Nests are built in preexisting cavities using mud, and sometimes, a thin layer of resin (Banaszak & Romansenko 1998, Chaudhary & Jain 1978). Luo & Liu (2006) provided information on immature development for *C. lanata* (Fabricius).

Genus *Coelioxys* Latreille

Comments. As herein understood, *Coelioxys* includes *Radoszkowskiana* Popov, 1955, a small group of cleptoparasitic bees that attack *Chalicodoma* subgenus *Pseudomegachile* (Rozen & Kamel 2007). *Coelioxys* is the sister group of all non-parasitic Megachilini. Because cleptoparasitic taxa do not collect pollen to feed their larvae, the scopal hairs on abdomen and legs tend to be reduced or absent. Their integument is also usually coarse, the pronotal lobe and omaulus are carinate or lamellate, and the axillae strongly project. Thus, unrelated cleptoparasitic taxa might be clustered on the basis of these characters that relate to pollen collecting and probably defense. For example, the cleptoparasitic genus *Dioxys* (Tribe Dioxyini) was grouped with *Radoszkowskiana* and *Coelioxys* in the analysis of the full data matrix (Fig. 164a), but it was excluded when those characters related to parasitism were deactivated (Fig. 165a). *Radoszkowskiana,* however, remained as the sister group of *Coelioxys*. I have obtained the same sister group relationship in an on-going phylogenetic study of the subgenera of *Coelioxys*.

Radoszkowskiana has been separated from *Coelioxys*, perhaps because of the short axilla, bare eyes, and the blunt metasoma of the male with a low transverse apical carina on T6; such a carina is distinctive because it is not divided into dorsal and ventral processes as in most *Coelioxys* and thus, it is suggestive of that of males in the genus *Thaumatosoma.* Those characters are likely plesiomorphic in respect to most *Coelioxys*, but they are variable and some species combine characters of both groups. For example, *C.* (*Boreocoelioxys*) *funeraria* Smith and *C.* (*Liothyrapis*) *decipiens* Spinola have short axillae and bare eyes; also, the S6 of the female of *C.* (*Torridapis*) *torrida* Smith is broad and rounded, and entirely sclerotized as in *Radoszkowskiana* whereas it is elongated and pointed with a distinct median weakly sclerotized area in most *Coelioxys* (Figs. 79, 80). Thus, *Radoszkowskiana* seems to be a *Coelioxys* despite the distinctive male characters. In addition, the mode of cleptoparasitism of *Radoszkowskiana* seems to fall within the known repertoire of parasitism of *Coelioxys*, suggesting that both groups have evolved from the same parasitic ancestor (Rozen & Kamel 2007). For these reasons, I think it is best to show their relationship by regarding *Radoszkowskiana* as a subgenus of *Coelioxys*.

Genus *Matangapis* Baker and Engel, New Status

Megachile (*Matangapis*) Baker and Engel, 2006: 2. Type species: *Megachile alticola* Cameron, 1902, by original designation.

Comments. This monotypic genus of megachiliform bees is the only member of the tribe which both sexes have arolia on all legs. My analysis suggests that *Matangapis* is the sister group of the genus *Thaumatosoma*; such a relationship, particularly with *Thaumatosoma* subgenus *Chelostomoda*, was previously noted by Baker & Engel (2006). Both genera have a coarsely and densely punctate bodies, sparsely covered with short pubescence; the mandible of the female is dull, and the carina of the T6 of the male is usually weak, little projected in profile, entire or medially emarginate (Fig. 111).

I have decided to place *Matangapis* in its own genus for no other reason than the presence of arolia in all legs and its megachiliform body, but it could be treated as a subgenus of *Thaumatosoma*. For example, both sexes of *Thaumatosoma* subgenus *Heriadopsis* also have arolia but only on the front and middle legs; the position of *Matangapis*, however, did not change when the presence of arolia was deactivated from the analysis (not shown). Second, a chalicodomiform or hoplitiform body type is related to nesting in narrow burrows and, at least in *Megachile* (see below), a reversion to these body types can occur. The phylogenetic analysis suggests that a megachiliform body shape has been independently acquired in *Matangapis* and *Megachile*, and thus, it seems worth recognizing it.

Matangapis alticola is only known from Borneo and it was fully described and illustrated by Baker & Engel (2006). The hooked hairs on the clypeus and supraclypeal area of the female are like those of bees specialized in pollen collecting from *Salvia* (Lamiaceae); however, these areas of the face are not as conspicuously flat in *M. alticola* as in those known specialist bees.

Genus *Megachile* Latreille

Comments. *Megachile*, as here understood, was monophyletic in all analyses. It includes all subgenera of Group 1, *Creightonella* (the only subgenus of Group 3), and the subgenera *Mitchellapis* and *Megella*; the latter two subgenera were tentatively included by Michener (2007) in Group 2 (Table 3). *Creightonella* is very distinctive and it has long been recognized as a genus. Unlike most subgenera of *Megachile*, as here understood, *Creightonella* has a chalicodomiform body, the mandible of the female has four or five teeth with incomplete cutting edges (Fig. 25), and the male has five or six exposed sterna. Retaining the generic status of *Creightonella* is an appealing option for many systematists.

In my analyses, *Creightonella* clustered with *Mitchellapis* and *Sayapis* in a well supported clade that was the sister group of the remaining *Megachile*. If *Creightonella* is treated at the generic level, the status of those two subgenera would have to be changed; they are either to be regarded as genera or subgenera of *Creightonella*. The latter option would create new combinations of names that seem undesirable at this moment. *Mitchellapis* is very distinctive from remaining subgenera of *Megachile* and it could be regarded as a genus; *Sayapis*, however, does not seem to warrant a generic status and it would have to be place within the genus *Megachile*. Given these problems, for the time being, I have decided to include *Creightonella, Mitchellapis*, and *Sayapis* as subgenera of *Megachile*.

Like *Creightonella* and related groups, *Megella* consists of large, chalicodomiform bees; at least in one species, the S8 of the male has marginal hairs as in the genera *Matangapis*, *Chalicodoma*, and *Thaumatosoma*. Perhaps because of those unusual characters, Michener (2007) doubted that *Megella* was a true leafcutter bee and placed it within his informal Group 2 of subgenera (equivalent to *Chalicodoma* sensu Michener 1965). My phylogenetic analysis consistently placed *Megella* within a primarily Old World clade of *Megachile*. For that reason, despite the resemblance to *Chalicodoma*, *Megella* is a member of *Megachile*. The nesting biology of *M.* (*Megella*) *pseudomonticola* also indicates that *Megella* is a leafcutter bee (see comments on *Megella*).

Megachile ranges worldwide but 21 out of 29 recognized subgenera are restricted to the New World; only six subgenera occur in the Old World. Such differences in diversity might be biased because the Old World fauna, especially that of South East Asia, is still poorly studied. *Megachile* s. str. and *Xanthosarus* are the only subgenera occurring in both New and Old Worlds.

Some phylogenetic lines in *Megachile*, previously recognized by Mitchell (1980), were also recovered in my analysis. Some of them are distinct and easily recognizable by one or two morphological features but others that lack distinctive characters were only suggested in my analyses. Such lineages, also discussed in the first chapter, are listed below accordingly with the new changes.

***Amegachile* line**. It includes the subgenera *Aethomegachile*, *Amegachile*, *Megella*, *Paracella*, and *Tylomegachile*. This lineage is primarily Old World in distribution, except for *Tylomegachile*.

***Chrysosarus* line**. Only *Chrysosarus* is included here; Mitchell (1980) also recognized this lineage but the other subgenera he included (*i.e*., *Stelodides*, *Dactylomegachile*, etc) are here considered species groups of *Chrysosarus*.

***Creightonella* line**. It includes *Creightonella*, *Mitchellapis*, *Sayapis*, and *Schrottkyapis*. The members of this group have a chalicodomiform body shape and the mandible of the female with usually incomplete cutting edges. A remarkable feature of this lineage is the S6 of the female; at least in the examined species, it is elongated with a membranous or weakly sclerotized pregradular area (visible only under dissection). Mitchell (1980) recognized this lineage under the generic name of *Eumegachile* but he included the subgenera *Eumegachile* and *Grosapis*, and separated *Creightonella* generically.

***Cressoniella* line**. All of the subgenera included here, except for *Tylomegachile*, were included in the genus *Cressoniella* sensu Mitchell (1980). *Austromegachile*, *Cressoniella*, *Dasymegachile*, *Neochelynia*, *Ptilosarus*, and *Trichurochile* belong to this New World lineage. The mandible of the female has four teeth (the innermost tooth is blunt, truncated or incised), and has cutting edges in the second and third interspaces.

***Megachiloides* line**. The primarily Nearctic subgenera *Megachiloides* and *Xanthosarus*, and probably *Argyropile*, belong here. Mitchell (1980) also suggested this relationship under the generic name *Megachiloides*, but he placed some *Xanthosarus* species in separated genera.

***Pseudocentron* line**. All members of this group of subgenera are primarily Neotropical in distribution; *Acentron*, *Leptorachis*, *Melanosarus*, *Moureapis*, and *Pseudocentron* are included here. Mitchell (1980) recognized this lineage and placed them in the genus *Pseudocentron*. The most distinctive character of this lineage is the S6 of the female that has at least the posterior half bare or nearly so, except for a subapical row of short hairs, behind which there is a bare, smooth rim directed posteriorly (Fig. 75).

The relationships among the remaining subgenera are not clear to me. Mitchell (1980) separated *Eutricharaea*, *Litomegachile*, *Megachile* s. str., and some *Xanthosarus* species in the genus *Megachile*; these groups, however, appeared apart from each other in my analysis and may represent independent lineages.

***Megachile* / Subgenus *Acentron* Mitchell**

Megachile (*Acentron*) Mitchell, 1934: 307. Type species: *Megachile albitarsis* Cresson, 1872, by original designation.

Comments. The monophyly of *Acentron* is strongly supported; it belongs to the *Pseudocentron* group of subgenera and seems closely related to *Leptorachis* and *Pseudocentron*; it occurs from the southern USA south to Argentina, with its greatest diversity in the tropics. *Acentron* species are apparently polylectic and fly all year round.

***Megachile* / Subgenus *Aethomegachile* Engel & Baker**

Megachile (*Aethomegachile*) Engel & Baker, 2006: 70. Type species: *Megachile trichorhytisma* Engel, 2006, by original designation.

Comments. This subgenus contains ordinary looking *Megachile* species; the mandible of the female has the upper interspace about as long as the rest of apical margin, with a complete cutting edge in the upper interspace and an incomplete cutting edge in the second. T7 of the male is remarkable in having the apical margin deeply, broadly emarginate, forming two prominent teeth.

Aethomegachile was described from a single male from northern Thailand. I examined both sexes of an Indian species identified by Dr. Gupta as *Megachile relata* Smith, the type species of *Orientocressoniella* Gupta. These specimens agree with the descriptions and illustrations provided by Gupta (1993); also, the T7 of the male is as described for *Aethomegachile* and the genitalia posses a strong dorsal lobe as in that subgenus. Without a doubt, these specimens belong to *Aethomegachile*. However, according to the late Dr. D. B. Baker (in Baker & Engel 2006) the type specimen of *M. relata* is a *Callomegachile*, and therefore, Gupta was right in recognizing the subgeneric novelty of his specimens but he misidentified them as *M. relata*. I agree with Baker & Engel (2006) that Gupta's subgeneric name is a synonym of *Callomegachile*.

I have seen at least two other, probably unnamed, species of *Aethomegachile* from Thailand. I have not seen specimens of *M. laticeps* Smith, 1853, but judging by the drawings of its genitalia in Pauly et al. (2001), this species belongs to *Aethomegachile*; *M. conjuncta* Smith, 1853, is a species closely related to *M. laticeps* and thus another member of this subgenus (Pauly et al. 2001). *Aethomegachile* is probably a large, widely distributed group in the oriental region; *M. laticeps* is recorded from Madagascar (Pauly et al. 2001).

Megachile / subgenus *Amegachile* Friese

Megachile (*Amegachile*) Friese, 1909: 326. Type species: *Megachile sjoestedti* Friese, 1901 = *Megachile bituberculata* Ritsema, 1880, by designation of Cockerell, 1931c: 167.

Megachile (*Callochile*) Michener, 1962: 27. Type species: *Megachile ustulatiformis* Cockerell, 1910 = *Apis mystacea* Fabricius, 1775, by original designation.

Megachile (*Platychile*) Michener, 1965: 205, nomen nudum. Type species: *Megachile foliata* Smith, 1861, monobasic.

Comments. This subgenus is monophyletic and was consistently clustered within a clade of primarily Old World *Megachile*. It is widely distributed in Africa, Madagascar, the Oriental region, and Australia. At least two Japanese species, *M. yaeyamaensis* and *M. xanthothrix*, nest in sandy soil (Maeta et al 2004).

Megachile / Subgenus *Argyropile* Mitchell

Megachile (*Argyropile*) Mitchell, 1934: 308. Type species: *Megachile parallela* Smith, 1853, by original designation.

Comments. The mandibular structure of this monophyletic subgenus (Fig. 35) suggests a closer relationship to *Xanthosarus* than to *Litomegachile* as shown in the analyses. *Argyropile* is widely distributed in North and Central America from southwestern Canada as far south as Costa Rica; it has been recorded on many plants, but species appear to show a strong preference for Asteraceae; *M. parallela* makes shallow nests in the ground, and uses entire leaves or leaflets from *Spiraea* (Rosaceae) and *Trifolium* (Fabaceae) to line the cells (Fischer 1951); it has also been recorded using trap-nests (Medler & Lussenhop 1968). Gonzalez & Griswold (2007) revised the seven species of this group.

Megachile / Subgenus *Austromegachile* Mitchell

Megachile (*Austromegachile*) Mitchell, 1943: 666. Type species: *Megachile montezuma* Cresson, 1878, by original designation.

Megachile (*Holcomegachile*) Moure, 1953: 119. Type species: *Megachile giraffa* Schrottky, 1913, by original designation.

Comments. Michener (2007) synonymized *Holcomegachile* with *Austromegachile*, and such synonymy is supported in my cladistic analysis. *Austromegachile* nest in pre-existing cavities; some species appear to be present year-round, founding most nests between October and January, with a peak in November. In some species, the closure of cells containing postdefecating larva or pupa has small perforations (Laroca et al. 1987, Morato 2003); similar perforations have been observed in *M. pseudomonticola*, an Oriental species of the subgenus *Megella* (Katayama 2004).

***Megachile* / Subgenus *Chrysosarus* Mitchell**

Megachile (*Chrysosarus*) Mitchell, 1943: 664. Type species: *Megachile guaranitica* Schrottky, 1908, by original designation.

Megachile (*Dactylomegachile*) Mitchell, 1943: 670. Type species: *Megachile parsonsiae* Schrottky, 1914, by original designation.

Stelodides Moure, 1953: 123. Type species: *Megachile euzona* Pérez, 1899, by original designation. [**New synonymy**]

Chrysosarus (*Zonomegachile*) Mitchell, 1980: 72. Type species: *Megachile mariannae* Dalla Torre, 1896, by original designation. [**New synonymy**]

Megachile (*Austrosarus*) Raw, 2006: 26. Type species: *Megachile frankieana* Raw, 2006, by original designation. [**New synonymy**]

Comments. This subgenus, as here understood, is equivalent to the genus *Chrysosarus* sensu Mitchell (1980); Mitchell's subgeneric names are regarded here as species groups. *Chrysosarus* is a large and diverse subgenus. The mandible of the female lacks cutting edges or has an incomplete cutting edge in the second interspace. *Megachile euzona*, the single species placed in *Stelodides* by Moure (1953), differs from most *Chrysosarus* in its chalicodomiform body, the black body integument contrasting with the orange integument of the antenna and legs; the metasoma has black pubescence except for a band of white hairs on T3. As in most *Chrysosarus*, it lacks cutting edges in the mandible of the female. *Stelodides* rendered *Chrysosarus* paraphyletic, except when *Dioxys* was excluded from the analysis (Fig. 167). This confirms the suspicion of Michener (2000, 2007) that *M. euzona* is a derived species of *Chrysosarus* and does not deserve subgeneric status.

Zonomegachile also seems to be a highly derived *Chrysosarus* species group. I have only seen an unnamed species from Argentina, presumably related to the *parsonsiae* species group (*Dactylomegachile* sensu Mitchell 1943b). Judging by the drawings of Mitchell (1980), this species has a similar mandibular structure to that of *M. mariannae*, the type species of *Dactylomegachile*. In Fig. 51 of Mitchell (1980), there appear to be incomplete cutting edges in the second and third interspaces; however, in the Argentinean specimens these “cutting edges” are thin, translucent extensions of the cuticle on the outer mandibular surface, not from the lower border of the tooth or extensions from a transverse ridge, at the base of the tooth, that runs parallel to the fimbriate line on the inner surface of the mandible as in other *Megachile*. Therefore, as in most species of *Chrysosarus*, as here understood, the mandible of *Zonomegachile* lacks cutting edges as do most species of *Chrysosarus*.

Raw (2006) distinguished *M. frankieana* and other two species subgenerically as *Austrosarus*. The female of this group is distinctive because it has a well developed incomplete cutting edge in the second interspace of the mandible and, as in some species of *Austromegachile*, incomplete white apical fasciae beneath the scopal hairs. I have not seen Raw's specimens but *M.* (*Chrysosarus*) *parsonsiae*, as well as an unnamed species from Argentina, have an indication of an incomplete cutting edge below the inferior border of the third tooth (hidden when the mandible is seen in frontal view), and also broadly interrupted white apical fasciae beneath the metasomal scopa. *Austrosarus* seems to be a derived species group, presumably closely related to the *parsonsiae* group; I tentatively place this name within *Chrysosarus*. Furthermore, the presence of cutting edges in the female mandible and the white apical fasciae beneath the scopa is highly variable among species within *Megachile* subgenera [*e.g.*, see comments for *Eutricharaea* and *Austromegachile* in Michener (2007)].

Chrysosarus nests in pre-existing cavities; cells are built even in the absence of confining walls, and are made of mud, with inner and outer walls covered by petals or leaf pieces (Laroca 1971, Laroca et al. 1992, Zillikens & Steiner 2004).

***Megachile* / Subgenus *Creightonella* Cockerell**

Megachile (*Creightonella*) Cockerell, 1908: 146. Type species: *Megachile mitimia* Cockerell, 1908 = *Megachile cognata* Smith, 1853, by original designation.

Creightoniella Pasteels, 1965. Unjustified emendation of *Creightonella* Cockerell, 1908.

Comments. *Creightonella* was consistently clustered with *Mitchellapis* and *Sayapis* in a well supported clade that was the sister group of the remaining *Megachile*. Comments on the morphological characters that support this clade are given under the accounts of *Mitchellapis* and *Sayapis*. *Creightonella* nest in preexisting cavities in the soil and hollow plant stems; it uses leaves, resin, and foliage mastic to build the cells (Michener & Szent-Ivany 1960, Willmer & Stone 1989). Banaszak & Romasenko (1998) illustrated the postdefecating larva of *M. albisecta*.

***Megachile* / Subgenus *Cressoniella* Mitchell**

Megachile (*Cressoniella*) Mitchell, 1934: 307. Type species: *Megachile zapoteca* Cresson, 1878, by original designation.

Cressioniella Gonzalez, 2006: 93. Lapsus calami.

Comments. *Cressoniella* is the sister group of *Dasymegachile*; species of both subgenera are common at high altitudes in the Andes. *Cressoniella* occurs from southern USA to Chile and Argentina; *M. zapoteca* is the only species reaching the US.

***Megachile* / Subgenus *Dasymegachile* Mitchell**

Megachile (*Dasymegachile*) Mitchell, 1943: 669. Type species: *Megachile saulcyi* Guérin, 1845, by original designation.

Cressoniella (*Chaetochile*) Mitchell, 1980: 63. Type species: *Cressoniella golbachi* Schwimmer, 1980 = *Megachile* (*Dasymegachile*) *mitchelli* Raw, 2004, by original designation.

Comments. This South American subgenus occurs primarily in the Andean region. Unlike other species of the subgenus, the female of *M. mitchelli* has a flat clypeus and supraclypeal area with hooked hairs. The same features, related to pollen collecting on *Salvia* (Lamiaceae), also occur in several bee species from unrelated families. I agree with Michener (2007) that there is no reason to separate this species in a different subgenus, even though *M. mitchelli* did not fall within the *Cressoniella-Dasymegachile* clade. Durante & Abrahamovich (2006) and Durante et al (2006) redescribed and illustrated *M. mitchelli* and revised the nine Argentinean species of this subgenus.

***Megachile* / Subgenus *Eumegachile* Friese**

Eumegachile Friese, 1898b: 198, no included species; Friese, 1899: 36, included species. Type species: *Megachile bombycina* Radoszkowski, 1874, by designation of Cockerell, 1930: 209.

Comments. The female of *M. bombycina*, the single species of this Palearctic subgenus, has a chalicodomiform body form, an elongated, parallel-sided mandible with a large, incomplete cutting edge in the second interspace as in some species of the American subgenus *Sayapis*. The position of *Eumegachile* varied among analyses. It appeared alone as the sister group of *Megachile* s. str. and remaining subgenera of *Megachile* (Fig. 164b), in a polytomy (Fig. Fig. 165b), or as the sister group of *Megachile* s. str. (Fig. 167b). Mitchell (1980) placed *Eumegachile* along with the subgenera *Grosapis*, *Mitchellapis*, *Sayapis*, and *Schrottkyapis* in the genus *Eumegachile*; all these subgenera are close to each other in the analysis but they never clustered in the same clade.

A putative synapomorphy of the clade that includes *Sayapis*, *Creightonella*, and *Mitchellapis* is the elongated S6 of the female with a weak sclerotized pregradular area (visible only after dissection); this sternum is short and well sclerotized in *Eumegachile* as in most *Megachile* subgenera. The nesting biology of *Eumegachile* also does not support a close relationship with *Sayapis*; the former subgenus uses leaves extensively in building cells (Banaszak & Romasenko 1998) whereas the latter has reduced leafcutting behavior, using mostly chewed leaf material and soil to make cell partitions. If *Eumegachile* is in fact related to *Megachile* s. str., as shown in one analysis, it would be worth showing their relationship by synonymizing these subgenera; however, I have decided to maintain its subgeneric status until further studies clarify its phylogenetic relationships.

***Megachile* / Subgenus *Eutricharaea* Thomson**

Megachile (*Eutricharaea*) Thomson, 1872: 228. Type species: *Apis argentata* Fabricius, 1793, monobasic.

Megachile (*Paramegachile*) Friese, 1898: 198. Type species: *Apis argentata* Fabricius, 1793, by designation of Mitchell, 1934: 298.

Megachile (*Paramegalochila*) Schulz, 1906: 71, unjustified emendation of *Paramegachile* Friese, 1898.

Androgynella Cockerell, 1911: 313. Type species: *Megachile detersa* Cockerell, 1910, by original designation.

Perezia Ferton, 1914: 233, not Léger and Dubosc, 1909. Type species: *Perezia maura* Ferton, 1914 = *Megachile leachella* Curtis, 1828, monobasic.

Fertonella Cockerell, 1920: 257, replacement for *Perezia* Ferton, 1914. Type species: *Perezia maura* Ferton, 1914 = *Megachile leachella* Curtis, 1828, autobasic and by original designation.

Megachile (*Eurymella*) Pasteels, 1965: 64. Type species*: Megachile eurymera* Smith, 1854, by original designation.

Megachile (*Digitella*) Pasteels, 1965: 191. Type species*: Megachile digiticauda* Cockerell, 1937, by original designation.

Megachile (*Neoeutricharaea*) Rebmann, 1967: 36. Type species*: Apis rotundata* Fabricius, 1787, by original designation.

Megachile (*Melaneutricharaea*) Tkalců, 1993: 803. Type species: *Megachile hohmanni* Tkalců, 1993, by original, by original designation.

Megachile (*Anodonteutricharaea*) Tkalců, 1993: 807. Type species: *Megachile larochei* Tkalců, 1993 = *Megachile lanigera* Alfken, 1933, by original designation.

Megachile (*Platysta*) Pasteels, 1965: 171. Type species: *Megachile platystoma* Pasteels, 1965, by original designation. [**New synonymy**]

Comments. *Eutricharaea* is the largest subgenus of *Megachile*. It is widespread in the Eastern Hemisphere but a few species have recently been introduced into the Americas. Several subgeneric names, which were synonymized by Michener (2007), have been proposed. My phylogenetic analysis suggests that *Eutricharaea* is likely a non-monophyletic group and, if it is true, some of those subgeneric names should be reestablished to divide this large group into subgenera containing more manageable numbers of species. I considered *Eurymella* as a good candidate; this subgeneric name that was proposed by Pasteels (1965) to accommodate nearly 60 African species. Unlike ordinary *Eutricharaea*, the mandible of the female is more robust, with the apical tooth usually more protuberant, acute, and much broader than other teeth. However, some *Eutricharaea* species such as *M. naevia* Kohl and *M. digiticauda*, the latter placed in the monotypic subgenus *Digitella* by Pasteels (1965), have intermediate mandibular structure that seems to bridge the gap between *Eurymella* and *Eutricharaea*.

The two species placed in the subgenus *Platysta* by Pasteels (1965), *M. platystoma* and *M. khamana* Cockerell, are very large (19–22 mm) and so distinct from most *Eutricharaea* that *Platysta* seems worth recognizing. My cladistic analysis, however, suggests that *Platysta* consists of derived species of *Eurymella*, just as the latter group is likely derived from other more ordinary *Eutricharaea*. In *Platysta*, the female mandible has the upper distal margin incised, resulting in a five-toothed mandible with a complete cutting edge in the upper interspace; the male has a distinct T6 bearing a large median projection, and the apex of gonostylus has a large median lobe. Similar structures are also present in *M. aurilabris* Pasteels and *M. konowiana* Friese, both members of *Eurymella*. Thus, even if one wants to recognize *Eurymella* as a subgenus, *Platysta* should be synonymized under that name. Until a detailed phylogenetic study of *Eutricharaea* is done, I have decided to maintain this large and heterogeneous group, and to synonymize *Platysta* with *Eutricharaea*.

Megachile rotundata is perhaps the best studied *Megachile* because it is widely used for pollination of alfalfa (*e.g.*, Trostle & Torchio 1994, Maeta & Adachi 2005, Maeta & Kitamura 2005). Some species, such as *M. subalbuta* and *M.*

rotundata, nest in pre-existing cavities whereas others, such as *M. kobensis,* nest in sandy soil. Japanese species are partially bivoltine, flying from middle June to late September (Maeta 1999b, Maeta & Minagi 1999).

***Megachile* / Subgenus *Grosapis* Mitchell**

Eumegachile (*Grosapis*) Mitchell, 1980: 46. Type species: *Megachile cockerelli* Rohwer, 1923, by original designation.

Comments. *Megachile cockerelli*, the single chalicodomiform species placed in *Grosapis*, is a very large (20 mm in length), robust, and entirely fulvous bee. This bee is known only from the Cordillera Occidental of northern Mexico and has not been recorded since its description. As in *Eumegachile*, *Mitchellapis*, and *Sayapis*, the female mandible has a large but incomplete cutting edge in the second interspace. Mitchell (1980) placed *Grosapis* near those three subgenera under the genus *Eumegachile*, and Michener (2007) discussed other similarities in the T6 and T7 of the male that shows a relationship to *Sayapis*. According to my phylogenetic analysis, *Grosapis* (as well as *Eumegachile*) does not belong to the same clade as that of *Sayapis* but to its sister clade that includes all remaining *Megachile*. The clade containing *Sayapis* is characterized by having a rather elongated S6 of the female with a weakly sclerotized pregradular area (visible only after dissection); in *Grosapis* this sternum is short and well sclerotized as in most *Megachile* subgenera.

***Megachile* / Subgenus *Leptorachis* Mitchell**

Megachile (*Leptorachis*) Mitchell, 1934: 301, 308. Type species: *Megachile petulans* Cresson, 1878, by original designation.

Pseudocentron (*Grafella*) Mitchell, 1980: 56. Type species: *Pseudocentron crotalariae* Schwimmer, 1980, by original designation.

Pseudocentron (*Leptocharina*) Mitchell, 1980: 56. Type species: *Megachile laeta* Smith, 1853, by original designation.

Comments. The female of *Leptorachis* has the S6 with at least the posterior half bare or nearly so, except for a subapical row of short hairs, behind which there is a bare, smooth rim directed posteriorly. Such S6 characterizes all females of the *Pseudocentron* group of subgenera: *Acentron*, *Melanosarus*, *Moureapis*, and *Pseudocentron*. The monophyly of *Leptorachis* was only recovered when all male characters were deactivated from the analysis (not shown); *M. laeta*, placed in the subgenus *Leptorachina* by Mitchell (1980), was included in the *Pseudocentron* group of subgenera whereas *M. petulans* was placed near to *Litomegachile* and *Argyropile*.

The female of *M. laeta* is large and robust, and the mandible has a shallower second interspace than in most *Leptorachis*; the male has an expanded front tarsus, large front coxal spine, and a small spine in the middle coxa; the latter spine is also only known in *Acentron*. A unique and interesting structure in *M. laeta* is the volsella of the male genitalia; it is large, not fused to the gonocoxite, and with strong transverse ridges (Fig. 160). In *M. petulans*, as in some *Leptorachis* and *Moureapis*, the male also has an unmodified front tarsus and a small front coxal spine. Despite these morphological differences in the males, and the different positions in the consensus tree, the pubescence pattern and presence of the apical bare rim in the S6 of the female are decisive characters that place both species in the same group; this idea is supported when all male characters are deactivated from the analysis. Durante & Diaz (2001) redescribed and illustrated both sexes of *M. laeta*, and presented new geographical records.

***Megachile* / Subgenus *Litomegachile* Mitchell**

Megachile (*Litomegachile*) Mitchell, 1934: 301, 308. Type species: *Megachile brevis* Say, 1837, by original designation.

Comments. *Litomegachile* is a monophyletic group. All analyses resulted in the same unresolved clade containing that subgenus and the subgenera *Argyropile*, *Moureapis*, and *Leptorachis*. This clade is the sister group of a larger clade comprising *Eutricharaea*, *Megachiloides, Xanthosarus*, and *Pseudocentron* group of subgenera. The clade that includes *Litomegachile* is weakly supported and its relationship to the other three included subgenera seems doubtful; for example, *Argyropile* seems to me a close relative of *Xanthosarus* whereas *Moureapis* and *Leptorachis* are definitively members of the *Pseudocentron* group of subgenera.

Although it is not supported in my analysis, *Litomegachile* might be closely related to *Eutricharaea*, as previously noted by Mitchell (1934, 1935, 1980) and Michener (2007). Females of *Litomegachile* can be separated from that subgenus by the lack of bands of white hair beneath the scopa and the conspicuously concave T6, as seen in profile. Also, as far as is known, the cell architecture seems to differs between these subgenera; in *Litomegachile* the bottom of a cell is made of individual circular pieces of leaves whereas in *Eutricharaea* the bottom is formed by bending the leaf pieces from the cell cup (Medler 1965, Kim 1992).

***Megachile* / Subgenus *Megachile* Mitchell s. str.**

Megachile Latreille, 1802: 434. Type species: *Apis centuncularis* Linnaeus, 1758, by designation of Curtis, 1828, pl. 218. [A subsequent designation, *Xylocopa muraria* Fabricius, 1804 = *Apis parietina* Fourcroy, 1785, was by Blanchard, 1840: 408.].

Megalochila Schulz, 1906: 263, unjustified replacement for *Megachile* Latreille, 1802. Type species: *Apis centuncularis* Linnaeus, 1758, autobasic.

Anthemois Robertson, 1903: 168, 172. Type species: *Megachile infragilis* Cresson, 1878 = *Apis centuncularis* Linnaeus 1758, by original designation.

Cyphopyga Robertson, 1903: 169, 172. Type species: *Megachile montivaga* Cresson, 1878, by original designation.

Comments. Although weakly supported, the monophyly of *Megachile* s. str. was suggested in my analysis. Unlike most species of *Megachile* s. str., the female of *M. montivaga* has a mandible without cutting edges and uses petals instead of leaves to make the brood cells. Perhaps because of this, it was initially separated in the monotypic genus *Cyphopyga* by Robertson (1903). Mitchell (1935) first recognized the similarity of *Cyphopyga* with *Megachile* s. str. (as subgenus *Anthemois*) and synonymized these subgenera; however, in his 1980’s revision he regarded it as a subgenus of *Megachile* (sensu Mitchell 1980), along with the subgenera *Eutricharaea* and *Litomegachile*. My phylogenetic analysis confirms the placement of *M.*

montivaga within *Megachile* s. str. but it does not support a close relationship with *Eutricharaea* and *Litomegachile*; it was in the same clade with the monotypic subgenus *Eumegachile*, far apart from *Eutricharaea* and *Litomegachile*.

The nesting biology has been studied for some species (*e.g.*, Medler 1958, Medler 1959, Medler & Koerber 1958, Maeta 1972, 1999a, Maeta et al. 1996, Maeta et al. 1997, Raw 1988). Females are bivoltine or multivoltine, nesting in pre-existing cavities or sandy soil, where they excavate their own tunnels. As in *Litomegachile*, the Japanese *M. humilis* Smith uses small circular pieces of leaves to build the bottom of the cells (Katayama 1997). Sheffield & Westby (2007) provided a synopsis and an updated key to the North American species of the subgenus.

***Megachile* / Subgenus *Megachiloides* Mitchell**

Megachiloides Mitchell, 1924: 154. Type species: *Megachiloides oenotherae* Mitchell, 1924, by original designation.

Megachile (*Xeromegachile*) Mitchell, 1934: 302, 309. Type species: *Megachile integra* Cresson, 1878, by original designation.

Megachile (*Derotropis*) Mitchell, 1936: 156. Type species: *Megachile pascoensis* Mitchell, 1934, by original designation.

Comments. The monophyly of *Megachiloides* was only recovered when all male characters were deactivated from the analysis; however, I have decided to retain the synonymies because the species groups, placed in different subgenera, intergrade with each other. For example, the female of *M. oenotherae* has a mandible that bridges the apparent gap between the truly three-toothed mandible of *Derotropis* and the four-toothed mandible of *Xeromegachile*. In *M. oenotherae*, the mandible has four teeth, but the two median teeth are scarcely separated, resulting in a nearly three-toothed condition. Also, closely related species to *M. oenotherae*, such as *M. xerophila* Cockerell, have short tongues as in *Derotropis* and *Xeromegachile*, and males cannot be separated from males of the latter species group. Thus, unless further evidence supports the non-monophyly of *Megachiloides*, it seems best to keep all these groups together. It is noteworthy that Mitchell (1980) grouped *M. fortis* (subgenus *Xanthosarus*), *M. parallela* (*Argyropile*), and the subgenus *Megachiloides,* as here understood, in the genus *Megachiloides*. Such close relationships among these groups are also weakly suggested in my analysis.

Megachiloides is the largest subgenus of *Megachile* in North America. It comprises about 60 species primarily found in xeric areas; some of them seem to be oligolectic on pollen from flowers of several plant families, such as Onagraceae and Cactaceae. Perhaps because of the oligolectic habits, some *Megachiloides* species have evolved extremely long tongues (*e.g*., *M. oenotherae*), and many species seem to be restricted in distribution (Mitchell, 1937). A phylogenetic study of *Megachiloides* would represent a unique opportunity to understand the evolutionary origins of oligolecty and floral-host switching in bees; however, despite the revisions of Mitchell (1934, 1936, 1937), about half of the species of *Megachiloides* are known from only one sex, the status of several species is doubtful, and no reliable taxonomic identification keys are yet available (Sheffield & Westby 2007).

Some species (*e.g.*, *M. integra*) excavate their own nests in sandy soil, which they may fill with loose soil after cell construction. As in *Litomegachile*, they use small circular pieces of leaves to make the bottoms of brood cells (Williams et al. 1986, Krombein & Norden 1995).

***Megachile* / Subgenus *Megella* Pasteels**

Megachile (*Megella*) Pasteels, 1965: 167. Type species: *Megachile malimbana* Strand, 1911, by original designation.

Cressoniella (*Neocressoniella*) Gupta, 1993: 172. Type species: *Megachile carbonaria* Smith, 1853 = *Anthophora barbata* Fabricius, 1804, by original designation. [**New synonymy**]

Comments. This subgenus consists of large (12–22 mm in body length) megachiliform or chalicodomiform species. In both sexes, the head is usually well developed posteriorly, usually with a strong preoccipital carina behind the gena. The four-toothed mandible of the female has a long upper interspace, longer than the rest of apical margin, with a complete cutting edge (sometimes hidden or barely visible in facial view); there is a small, incomplete cutting edge in the second interspace. The mandible of the male is three- or four-toothed, without an inferior projection; the foreleg, including coxa, is unmodified; the carina of T6 is entire or medially emarginate; S8 usually lacks marginal hairs, except in *M. malimbana*.

Pasteels (1965) separated two African species, *M. malimbana* and *M. exsecta* Pasteels, in the subgenus *Megella*. Michener (2007) included *M. pseudomonticola*

Hedicke, an Asian species, and noted that *M. malimbana* has some characters that are typical of the genus *Chalicodoma*, such as the chalicodomiform body and S8 of the male with marginal hairs. The pubescence is also suggestive of some *Chalicodoma* species. For example, the mesosoma and T1 of *M. pseudomonticola* is densely covered with long, yellowish to brownish hairs that contrast with the black pubescence on remaining areas of the body; such a color pattern is similar to that of *Chalicodoma* (*Callomegachile*) *sculpturalis*, another Asian species that has been recently introduced in North America. Both species are superficially so similar such that specimens are sometimes misidentified. Perhaps because of those unusual characters, Michener (2007) doubted that *Megella* was a true leafcutter bee and placed it within his informal Group 2 of subgenera (*Chalicodoma* group).

Gupta (1993) recognized *M. carbonaria*, an Indian species, as the subgenus *Neocressoniella*. Following the generic arrangement proposed by Mitchell (1980), who only considered the New World fauna, Gupta placed *Neocressoniella* within the genus *Cressoniella*. *Neocressoniella* differs from *Megella* in having a megachiliform, but still elongated body, and almost dark brown to black pubescence, including the wings.

My analysis consistently placed *Neocressoniella* and *Megella* as sister groups, along with three other *Megachile* subgenera: *Aethomegachile*, *Amegachile*, and *Tylomegachile*; the first two subgenera are widely spread in the Old World whereas the last one is restricted to the New World. Then, as first suggested by Pasteels (1965), and despite the resemblance to *Chalicodoma*, *Megella* is a member of the genus *Megachile*. Also, given the subtle differences between *Megella* and *Neocressoniella*, I think it is best two regard the latter subgenus as a subgroup of *Megella*. Baker and Engel (2006) regarded *Neocressoniella* as a synonym of *Xanthosarus* but such synonymy is not supported in my analysis; these groups seem to be distantly related.

An elongated, parallel-sided body is typical of *Chalicodoma* and *Thaumatosoma*, but it also occurs in some *Megachile* subgenera, such as *Eumegachile* and *Sayapis*; this body shape is apparently an adaptation to stem-nesting behavior (Michener 2007). Likewise, the marginal hairs of the S8 of the male, usually present in *Chalicodoma* and *Thaumatosoma*, seem to be secondarily lost in some species, such as *Chalicodoma* (*Chalicodoma*) *manicata*, or perhaps regained, as in *M. malimbana*. At least in Megachilini, character loss seems as likely as character gains; for example, the lack of arolia is a usual tribal character but arolia are present in *Thaumatosoma* subgenus *Heriadopsis* and the genus *Matangapis*.

The nesting biology of *M. pseudomonticola* also supports the placement of *Megella* within the genus *Megachile*, as here understood. As in most *Megachile*, that species uses pieces of leaves to make the brood cells; nests are built in preexisting cavities and apparently the same cavity can be used for several nesting seasons (Piel 1933, Katayama 2004). *Megella* occurs in West Africa, India, and Southeast Asia; there are probably seven species in total.

***Megachile* / Subgenus *Melanosarus* Mitchell**

Megachile (*Melanosarus*) Mitchell, 1934: 303, 307. Type species: *Megachile xylocopoides* Smith, 1853, by original designation.

Comments. This primarily Neotropical subgenus consists of largely or entirely black species of the *Pseudocentron* group of subgenera. In addition to the characters indicated in the key, the hypostomal area of the female is depressed, smooth and shiny, and enclosed by short transverse carina. This character seems to be a synapomorphy of this group.

***Megachile* / Subgenus *Mitchellapis* Michener**

Megachile (*Mitchellapis*) Michener, 1965: 211. Type species: *Megachile fabricator* Smith, 1868, by original designation.

Comments. As in *Megella*, this Australian subgenus has some characters that are typical of *Megachile* and *Chalicodoma*. Typical *Megachile* features include the mandible of the female with a large but incomplete cutting edge in the second interspace, the white apical sterna fasciae under the scopa, and the apex of S6 with a fringe of short, dense plumose hairs. Typical characters of *Chalicodoma* include the elongated, parallel-sided body, apex of tibia of all legs with a distinct, sharp spine, and presence of lateral hairs on the S8 of the male.

Michener (1965) placed *Mitchellapis* in the genus *Megachile*, but considering the hairs on the margins of S8 of the male, he later (Michener 2007) regarded it as a member of the Group 2 (*Chalicodoma* group). My phylogenetic analysis consistently placed *Mitchellapis* in the same clade with *Sayapis* and *Creightonella*, within the genus *Megachile*. *Mitchellapis* was either the sister group of *Sayapis* or of *Creightonella*. The most remarkable feature of the females of this clade is the elongated S6 with a weakly sclerotized pregradular area (visible only after dissection). Despite the *Chalicodoma*-like appearance and the hairs on the margins of S8 of the male, *Mitchellapis* is a *Megachile*.

The nesting biology of *Mitchellapis* is unknown but it is likely that it also uses leaves, resin, and foliage mastic to build the brood cells, as do *Sayapis* and *Creightonella*.

***Megachile* / Subgenus *Moureapis* Raw**

Pseudocentron (*Moureana*) Mitchell, 1980: 56; not *Moureana* Zajciw, 1967, a cerambycid beetle. Type species: *Megachile anthidioides* Radoszkowski, 1874, by original designation.

Megachile (*Willinkella*) Laroca, Cure, and Bortoli, 1982: 97, *nomen nudum*.

Megachile (*Acentrina*) Schlindwein, 1995: 97, *nomen nudum*.

Megachile (Moureapis) Raw, 2002: 23, replacement for *Moureana* Mitchell, 1980. Type species: *Megachile anthidioides* Radoszkowski, 1874, autobasic and by original designation.

Comments. This Neotropical subgenus was placed near *Litomegachile* in my analysis, but it belongs to the *Pseudocentron* group of subgenera. As in other subgenera of this group, the S6 of the female has at least the posterior half bare or nearly so, except for a subapical row of short hairs, behind which there is a bare, smooth rim directed posteriorly. The front leg of the male is unmodified, but Raw (2007) noted that if the both sexes are correctly associated, it is expanded and highly modified in *M. possograndensis* Schrottky. This case is similar to that of *M. laeta* in the subgenus *Leptorachis*; males of other species of *Leptorachis* have unmodified front legs. With a change in the mating system, the front leg modifications could have been lost in most males of these subgenera or the modifications could have been regained in these two species. I do not see the need to regard these species in separate subgenus solely on the basis of male foreleg morphology.

Megachile* / Subgenus *Neochelynia

Neochelynia Schrottky, 1920: 187. Type species: *Neochelynia paulista* Schrottky, 1920, monobasic.

Megachile (*Neomegachile*) Mitchell, 1934: 302, 306. Type species: *Megachile chichimeca* Cresson, 1878, by original designation.

Comments. *Neochelynia* is a monophyletic subgenus of small sized bees (6.5–10 mm of body length). Probably because the male of *Neochelynia* has an unusually elongated and tapering metasoma, Schrottky (1920) thought it was related to *Chelynia* Provancher, a cleptoparasitic anthidiine bee placed now in *Stelis* Panzer s. str. Mitchell (1934) proposed *Neomegachile* based on both sexes; as noted by Michener (2007), the name *Neochelynia* has priority. *Neochelynia* is probably related to *Austromegachile*, *Ptilosarus*, *Trichurochile*, and *Rhyssomegachile*. All these groups, including also *Dasymegachile* and *Cressoniella*, were included as subgenera of *Cressoniella* by Mitchell (1980); such a relationship among these groups is indicated in my analyses, especially when *Dioxys* was excluded from the data matrix (Fig. 167b).

***Megachile* / Subgenus *Paracella* Michener**

Megachile (*Paracella*) Pasteels, 1965: 277, no type species designated.

Megachile (*Paracella*) Michener, 1997: 44. Type species: *Megachile semivenusta* Cockerell, 1931, by original designation.

Comments. In this subgenus of ordinary looking *Megachile* species, the mandible of the female is usually four- toothed, or five-toothed if the upper distal margin is incised. There are distinct cutting edges in the second and third interspaces, sometimes incomplete in both interspaces or hidden behind the mandibular margin in the third. At least in *M. curtula*, the cutting edge in the third interspace is as in the second, entirely formed by an extension of the upper tooth, but in *M. semivenusta*, there is another cutting edge behind it; this extra cutting edge is an extension from the fimbriate line as in *Eutricharaea*. Also, at least in those two species, the incomplete cutting edge in the third interspace is unusually acute, not truncated. Under the comparative comments on *Neocressoniella*, Michener (2007, p. 580) mentioned a strong preoccipital carina behind the gena in *Paracella*; he probably meant *Megella* because the preoccipital border is rounded in *Paracella*.

The phylogenetic position of *Paracella* varied among analyses; it appeared within a group of mostly Old World subgenera, or close to *Litomegachile* and *Eutricharaea*. In both cases, these relationships were weakly supported.

***Megachile* / Subgenus *Pseudocentron* Mitchell**

Pseudocentron Mitchell, 1934: 303, 307. Type species: *Megachile pruina* Smith, 1853, by original designation.

Comments. *Pseudocentron* is the largest subgenus of *Megachile* in Central and South America. It is closely related to *Acentron* and *Leptorachis*; as in *Acentron* and *Melanosarus*, the males of this subgenus have modified mandibles, large front coxal spines, and greatly expanded front legs.

***Megachile* / Subgenus *Ptilosarus* Mitchell**

Megachile (*Ptilosarus*) Mitchell, 1943: 667. Type species: *Megachile bertonii* Schrottky, 1908, by original designation.

Cressoniella (*Ptilosaroides*) Mitchell, 1980: 63. Type species: *Megachile neoxanthoptera* Cockerell, 1933, by original designation. [**New synonym**]

Comments. This Neotropical subgenus consists of small megachiliform bees with abundant, short, appressed golden pubescence. The mandible of the female is four-toothed, with the upper distal margin blunt or truncate; it also has distinct cutting edges in the second and third interspaces. Most species have a strong preoccipital carina, and long, dense, plumose pubescence on the thoracic venter and S2 of the female; such distinctive pubescence is presumably related to pollen-collecting behavior on *Piper* inflorescences (Michener 2007). The costal margin of forewing is also usually dusky. The male has a three- or four-toothed mandible and the carina of T6 is reduced to a pair of teeth or spines.

Mitchell (1980) proposed the subgenus *Ptilosaroides* for *M. neoxanthoptera*, a species that lacks distinctive features of *Ptilosarus*, namely, the strong preoccipital carina and the abundant plumose pubescence on the thoracic venter and S2 of the female; the carina of T6 of the male is also more slender than that of *Ptilosarus*. The pubescence on the thoracic venter and S2 that characterize the female of *Ptilosarus* could have been reversed with a change in floral preference. Also, the strong preoccipital carina seems to vary in distinctiveness in *Austromegachile*, the sister group of *Ptilosarus*. For these reasons, I considered *Ptilosaroides* as a species group of *Ptilosarus*. Both subgenera are not large in species number (probably 18 in total) and for the present, it seems to me best to show their relationship rather than their differences.

Ptilosarus uses leaves to make cells and nests in pre-existing cavities; at least one species, *M. neoxanthoptera*, uses abandoned nests of *Ptilothrix plumata* Smith and *Diadasina distincta* (Holmberg) (Apidae, Emphorini); it also uses empty cavities within active termite nests (Martins & Almeida 1994, Almeida et al. 1997).

***Megachile* / Subgenus *Rhyssomegachile* Mitchell**

Cressoniella (*Rhyssomegachile*) Mitchell, 1980: 63. Type species: *Megachile simillima* Smith, 1853, by original designation.

Comments. This monotypic subgenus is restricted to Brazil. I have not seen specimens of this group but Michener (2007) suggested that it may be close to *Ptilosarus* or *Austromegachile*.

***Megachile* / Subgenus *Sayapis* Titus**

Gnathocera Provancher, 1882: 232 (not Kirby, 1825). Type species: *Gnathocera cephalica* Provancher, 1882 = *Megachile pugnata* Say, 1837, monobasic.

Ceratias Robertson, 1903: 172 (not Kroyer, 1845). Type species: *Megachile pugnata* Say, 1837, by original designation.

Sayapis Titus, 1906: 154, replacement for *Gnathocera* Provancher, 1882, and *Ceratias* Robertson, 1903. Type species: *Megachile pugnata* Say, 1837, autobasic.

Eumegachile (*Schrottkyapis*) Mitchell, 1980: 46. Type species: *Megachile assumptionis* Schrottky, 1908, by original designation. [**New synonymy**]

Comments. No doubt because of the distinctive features of *M. assumptionis*, Mitchell (1980) separated it subgenerically as *Schrottkyapis*. The female has a strong, bifid median process in the clypeus (Fig. 5), and the mandible lacks cutting edges. This species is also unique in nesting exclusively in abandoned burrows of *Ptilothrix plumata* Smith (Apidae, Emphorini) (Martins & Almeida 1994, Almeida et al. 1997). Despite its distinctiveness, my phylogenetic analysis confirms the suspicion of

Michener (2007) that *M. assumptionis* is a specialized derivative of *Sayapis*. As in *Sayapis*, the S6 of the female has a pregradular area weakly sclerotized with a distinct invagination (visible only after dissection), parallel to the lateral margin of the sternum. Such an invagination is a putative synapomorphy that support the placement of *M. assumptionis* within *Sayapis.* The lack of a cutting edge in the second interspace in the mandible of the female and the inferior process in the mandible of the male of *M. assumptionis* seem to be secondarily lost in this species.

Sayapis nests in preexisting cavities; cell partitions are made of a mixture of chewed leaf material, clay or sandy soil.

***Megachile* / subgenus *Trichurochile* Mitchell**

Cressoniella (*Trichurochile*) Mitchell, 1980: 63. Type species: *Megachile thygaterella* Schrottky, 1913, by original designation.

Comments. The female of this South American subgenus is easily recognized by the four-toothed mandible with distinct cutting edges in the second and third interspaces, and the white apical fasciae beneath the sterna scopa. In the male, the medially emarginate carina of T6 is filled with long hairs that arise from the inner margin of each tooth. Mitchell (1980) placed *Trichurochile* as a subgenus of *Cressoniella*, along with *Austromegachile*, *Ptilosarus*, and *Neochelynia*; the relationship with the latter two subgenera is also indicated in my analysis.

***Megachile* / subgenus *Tylomegachile* Moure**

Megachile (*Tylomegachile*) Moure, 1953: 120. Type species: *Megachile orba* Schrottky, 1913, by original designation.

Comments. Perhaps because of the four-tooth mandible of the female, with an incomplete cutting edge in the second interspace (sometimes hidden by the mandibular margin in frontal view) and a complete edge in the third, Mitchell (1980) placed this monophyletic subgenus within his genus *Cressoniella*; he also grouped it with the American subgenera *Austromegachile*, *Cressoniella*, *Ptilosarus*, and *Neochelynia*. However, in the current study *Tylomegachile* consistently clustered as the sister group of *Amegachile*, within an Old World clade of *Megachile*. Nevertheless, given the mandibular structure of the female of *Tylomegachile*, it seems more closely related to *Austromegachile* than to *Amegachile*. Further study may clarify the phylogenetic position of *Tylomegachile.*

***Megachile* / subgenus *Xanthosarus* Robertson**

Xanthosarus Robertson, 1903: 168, 169, 172. Type species: *Megachile latimanus* Say, 1823, by original designation.

Megachile (*Delomegachile*) Viereck, 1916: 745. Type species: *Megachile viuda* Smith, 1853, = *M. latimanus* Say, 1823, monobasic.

Megachile (*Phaenosarus*) Mitchell, 1934: 303, 309. Type species: *Megachile fortis* Cresson, 1872, by original designation.

Megachile (*Macromegachile*) Noskiewicz, 1948: 48. Type species: *Apis lagopoda* Linnaeus, 1761, by original designation.

Megachile (*Addendella*) Mitchell, 1980: 24. Type species: *Megachile addenda* Cresson, 1878, by original designation.

Comments. As in *Eutricharaea* and *Megachiloides*, the monophyly of this Holarctic subgenus was not recovered. Males are highly variable and there are intergradations among species in the mandibular structure of the female. Until further evidence supports the non-monophyly of *Xanthosarus*, I follow Michener (2007) in retaining the synonymies above.

Xanthosarus nests in pre-existing cavities in wood or sandy soil; as in *Megachiloides*, it also uses small circular pieces of leaves to make the bottom of a brood cell. Some species seem to be oligolectic on Fabaceae (*e.g.*, *M. nigriventris* Schenck) or Asteraceae (*e.g.*, *M. fortis*). Biological accounts for some North American and European species are by Neff & Simpson (1991), Celary (1995), Cane et al. (1996), and Hartmann & Arens (1998). Maeta (1979) and Maeta et al. (1996) briefly described the nesting biology of two Japanese species.

Genus *Thaumatosoma* Smith

Thaumatosoma Smith, 1865: 394. Type species: *Thaumatosoma duboulaii* Smith, 1865, monobasic.

Comments. This generic name associates to all subgenera of the large clade containing *Chelostomoda* and related groups. *Thaumatosoma* is the oldest name. According to my analysis, *Thaumatosoma* is the sister group of the genus

Matangapis. *Thaumatosoma* includes heriadiform or hoplitiform bees with integument usually coarsely and densely punctuate, usually with white fasciate and strong postgradular grooves in T2 and T3; the pubescence is usually pale or grayish, except in some species with fulvous pubescence on apical terga; the mandible of the female lacks cutting edges except in the subgenus *Chelostomoda* with an incomplete cutting edge in the second interspace. The male usually has three exposed metasomal sterna, the carina of T6 is entire or medially emarginate, and usually weak, little projected in profile or nearly absent as in *Rhodomegachile*.

Relationships among the 11 subgenera of *Thaumatosoma* need to be studied in more detail. *Chelostomoda* was consistently the sister group of all *Thaumatosoma*, but the positions of the remaining subgenera varied among analyses (Fig. x). Most of these subgenera, presumably derived from *Hackeriapis*, contain a single or few species with unusual characters (*e.g*., the presence of arolia in *Heriadopsis* or the modified clypeus and mandibles in *Stenomegachile*); their recognition may render *Hackeriapis* paraphyletic.

***Thaumatosoma* / Subgenus *Austrochile* Michener, New Combination**

Chalicodoma (*Austrochile*) Michener, 1965b: 202. Type species: *Megachile resinifera* Meade-Waldo, 1915, by original designation.

Comments. This Australian subgenus is monophyletic in my analyses; it was placed near *Chalicodoma*, but some characters suggest a closer relationship to *Thaumatosoma*. For example, both sexes have nonfasciate postgradular grooves on

T2 and T3, usually fulvous pubescence on T5 and T6, and a large subapical spinous process on S1. The latter process is otherwise present only in *Thaumatosoma* subgenera *Schizomegachile* and *Thaumatosoma* s. str. Such combinations of characters are rarely found in *Chalicodoma*, and for the present, I have decided to place *Austrochile* within the genus *Thaumatosoma*.

***Thaumatosoma* / Subgenus *Chalicodomoides* Michener, New Combination**

Chalicodoma (*Chalicodomoides*) Michener, 1962: 24, Type species: *Megachile aethiops* Smith, 1853, by original designation.

Comments. This is another small Australian subgenus (two species) that did not cluster with *Thaumatosoma* in my analysis; however, it seems to belong to that genus despite the oblique mandibular margin of the female that resembles that of *Chalicodoma* s. str. Unlike the latter group, there are only three teeth in the mandible of *Chalicodomoides*. The large size of *Chalicodomoides*, the strongly but finely punctuate integument, the sharp tooth on the inferior genal area, the head well developed posteriorly, and S1 of the female slightly projecting medioapically (not as conspicuous as in *Austrochile*), are some characters that suggest a close relationship with *Schizomegachile*, a subgenus of *Thaumatosoma*. S4 of the male is also retracted as in other subgenera of *Thaumatosoma*. Michener (1965) also mentioned that the shape of clypeus and mandible of some *Hackeriapis*, another subgenus of *Thaumatosoma*, approach those of *Chalicodomoides*. Thus, it seems that

Chalicodomoides is another highly derived species group of *Hackeriapis*. For the present, I regard *Chalicodomoides* as a subgenus of *Thaumatosoma*.

Thaumatosoma / subgenus *Chelostomoda* Michener, New Combination

Chalicodoma (*Chelostomoda*) Michener, 1962: 24. Type species: *Megachile spissula parvula* Strand, 1913 = *M. spissula* Cockerell, 1911, by original designation.

Ashmeadiella (*Neoashmeadiella*) Gupta, 1990: 56. Type species: *Ashmeadiella indica* Gupta, 1990, by original designation [for characters of *Thaumatosoma indica* (Gupta) see Michener, 2000]

Comments. This monophyletic subgenus is the sister group to all remaining *Thaumatosoma*. It is the only subgenus with an incomplete cutting edge in the second interspace of the female mandible, as in some groups of the genus *Megachile*. *Chelostomoda* nest in preexisting cavities; it only uses irregular pieces of leaves and leaf pulp to make cell closures because cell walls are omitted as in other *Thaumatosoma* (Michener 2007). Maeta (2005) studied the nesting biology and foraging behavior of *M. spissula* on alfalfa.

Thaumatosoma / Subgenus *Chelostomoides* Robertson, New Combination

Chelostomoides Robertson, 1901: 231. Type species: *Megachile rufimanus* Robertson, 1891 = *Chelostoma rugifrons* Smith, 1854, monobasic.

Oligotropus Robertson, 1903: 168. Type species: *Oligotropus campanulae* Robertson, 1903, monobasic.

Gnathodon Robertson, 1903: 168 (not Oken, 1816, etc). Type species: *Megachile georgica* Cresson, 1878, monobasic.

Sarogaster Robertson, 1918: 92, replacement for *Gnathodon* Robertson, 1903. Type species: *Megachile georgica* Cresson, 1878, autobasic.

Chalicodoma (*Chelostomoidella*) Snelling, 1990: 36. Type species: *Megachile spinotulata* Mitchell, 1934, by original designation.

Comments. Despite the position of *T. rugifrons* in my analysis, this American subgenus seems monophyletic. *Chelostomoides* was either in a polytomy or was the sister group of the clade containing *Thaumatosoma* s. str. As discussed by King (1994) and Michener (1965, 2007), it is very similar to *Hackeriapis* and it is probably closely related to it.

Michener (2007) noted that in *Chelostomoides* the clypeus and mandible of the female are highly variable and several generic and subgeneric names have been proposed for species with aberrant morphology. Such modifications may be related to collecting and transport of nest materials. For example, the large head, long and subtriangular labrum, and elongated mandibles of *T. rugifrons* are similar to those of *Chalicodoma* (*Callomegachile*) *pluto*, an Oriental species that specializes in resin collection (Messer 1984). Males are also variable in those structures related to mating behavior such as the front coxal spine (small, large, or even absent), front tarsi (highly modified to normal), and carina of T6 (usually small, medially emarginate or large and with long teeth as in *T. spinotulata*).

Armbrust (2004) studied in detailed the nesting biology of some North American species, provided new parasite records, and summarized the nesting biology of the subgenus.

***Thaumatosoma* / subgenus *Hackeriapis* Cockerell, New Combination**

Megachile (*Hackeriapis*) Cockerell, 1922: 267. Type species: *Megachile rhodura* Cockerell, 1906, by original designation.

Comments. *Hackeriapis* is the largest subgenus of *Thaumatosoma*; it is likely non-monophyletic form from which *Thaumatosoma* s. str. and related groups might have evolved. Michener (1965, 2007) discussed the variation of some female and male characters that appear to intergrade among species. As in *Chelostomoides*, the modifications of the female clypeus, labrum, and mandible seem to be related to resin, pebble, or sand collection for cell closures. In some species (*e.g*., *T. heriadiformis*), the mandibles are long and slender whereas in others (*e.g*., *T. hackeri*) they are short and broad. Males are also highly variable as in *Chelostomoides*.

King (1994) considered *Hackeriapis* in a very narrow sense, leaving the majority of species unplaced. She probably intended to move those species into several undescribed subgenera; some specimens of species, such as *T*. (*Hackeriapis*) *turneri* (Meade-Waldo, 1913), are found in collections under the generic name *Torridapis*. This name is preoccupied by an Old World subgenus of *Coelioxys* (*Torridapis* Pasteels, 1977), but it has been used at least once by Heard et al. (1990). Until a proper phylogenetic study is done, it seems best to keep recognizing this large and heterogeneous subgenus.

Paini (2004) studied in detail the nesting biology of an unnamed species.

Thaumatosoma / Subgenus *Heriadopsis* Cockerell, New Combination

Heriadopsis Cockerell, 1931: 338. Type species: *Heriadopsis striatulus* Cockerell, 1931, by original designation.

Comments. Unlike *Matangapis alticola*, the only other megachiline species with arolia, both sexes of *Heriadopsis* have arolia only in the front and middle legs; otherwise, *Heriadopsis* looks like an ordinary species of *Hackeriapis*, but unlike *Hackeriapis* it is found in Africa.

Thaumatosoma / Subgenus *Maximegachile* Guiglia and Pasteels, New Combination

Megachile (*Maximegachile*) Guiglia and Pasteels, 1961: 27. Type species: *Megachile maxillosa* Guérin, 1845, by original designation.

Comments. This subgenus is the sister group of *Schizomegachile*; both taxa resulted in a polytomy with *Stenomegachile*. There are apparently only three species.

Thaumatosoma / Subgenus *Rhodomegachile* Michener, New Combination

Chalicodoma (*Rhodomegachile*) Michener, 1965: 201. Type species: *Megachile abdominalis* Smith, 1853, by original designation.

Comments. The position of *Rhodomegachile* varied among analyses; it was the sister group of *Austrochile*, the sister group of all non-parasitic Megachilini, or resulted in a polytomy. However, some characters suggest a close relationship to *Hackeriapis*. For example, the distinctive broad, ligulate glossa of *Rhodomegachile* is also present only in *T.* (*Hackeriapis*) *ferox* and *T.* (*H*) *rhodura*. The carina of T6 of the male of *Rhodomegachile* is very weak to nearly absent, and that subgenus also lacks the fasciate postgradular grooves in T2 and T3 found in some *Hackeriapis*. Michener (2007) also discussed other characters that support the placement of *Rhodomegachile* within *Thaumatosoma*. Three species are known in this subgenus.

Thaumatosoma / Subgenus *Schizomegachile* Michener, new combination

Chalicodoma (*Schizomegachile*) Michener, 1965: 199. Type species: *Megachile monstrosa* Smith, 1868, by original designation.

Comments. *Schizomegachile* and *Maximegachile* are sister groups; both sexes have unusual characters that were described and illustrated by Michener (1965, 2007).

Thaumatosoma / Subgenus *Stenomegachile* Pasteels, new combination

Chalicodoma (*Stenomegachile*) Pasteels, 1965: 507. Type species: *Megachile chelostomoides* Gribodo, 1894, by original designation.

Comments. Although the monophyly of *Stenomegachile* was not recovered, this subgenus consistently clustered with *Maximegachile* and *Schizomegachile*. The four species placed in *Stenomegachile* are morphologically very distinct; for example, the mandible of the female is long and strongly bent apically in *T.* (*Stenomegachile*) *chelostomoides* but short and straight in *T.* (*Stenomegachile*) *dawensis* (Pasteels

1965) and in *T.* (*Stenomegachile*) *dolichosoma*; the posterior hypostomal area is toothed in both sexes of the former species but unmodified in the last. In the male, the fore and middle tarsi are highly modified and the volsella of the genitalia has a long and slender lateral lobe in *T. chelostomoides* but the legs are normal and the volsella without lobes in *T. dolichosoma*.

***Thaumatosoma* / Subgenus *Thaumatosoma* s. str. Smith, New Combination**

Thaumatosoma Smith, 1865: 394. Type species: *Thaumatosoma duboulaii* Smith, 1865, monobasic.

Comments. This Australian subgenus seems to be a derived species group of *Hackeriapis*. As in *Austrochile* and *Schizomegachile*, both sexes of *Thaumatosoma* s. str. have a large subapical spinous process on S1 (less developed in the male). Unique characters in the female include the bidentate mandible and the T6 with strong basolateral shoulders; the male is also distinctive by the swollen scape, long and attenuate flagellum, and clypeus with a central tuft of long, stiff bristles (Michener 2007).

Incertae sedis

Stellenigris Meunier, 1888: 152. Type species: *Stellenigris vandeveldii* Meunier, 1888, monobasic.

Comments. I was not able to examine this species but, as indicated by Michener (2007), it may be a member of the genus *Chalicodoma* as here understood.

Chapter IV. Systematics of the North and Central American *Megachile* subgenus *Argyropile* Mitchell

INTRODUCTION

The majority of the subgenera of *Megachile* have not been revised. One of the North and Central American subgenera, *Argyropile* Mitchell, was revised by Mitchell (1937), who later described an additional species and provided a revised key to the females (Mitchell 1943a). Subsequently he described yet another new species (Mitchell 1944). Despite this work, two species remain known in only one sex.

I review *Argyropile*, describe a new species and the two previously unknown males, provide a synopsis, present new synonymies, a cladistic analysis, an illustrated key to the species and summarize what is known of the biology of these bees. This review has been published by Gonzalez & Griswold (2007).

MATERIAL AND METHODS

Taxonomic description

The morphological descriptions and illustrations were made using an Olympus SZ microscope. Morphological terminology follows Michener (2000) and terminology for surface sculpturing follows Harris (1979). Setal length is given relative to the diameter of the median ocellus. The abbreviations F, MT, OD, PW, S, and T, are used for flagellomere, mandibular teeth (enumerated from apex to base of mandible), ocellar diameter, one puncture width, metasomal sterna and terga, respectively. Measurements are given with standard errors.

Acronyms for collections where specimens are placed are:

ANSP- Academy of Natural Sciences, Philadelphia, Pennsylvania
BBSL- Bee Biology and Systematic Laboratory, Logan, Utah
BNHM-British Natural History Museum, London
CAS-California Academy of Sciences, San Francisco, California
CUIC-Cornell University Insect Collection, Ithaca, New York
INHS-Illinois Natural History Survey, Urbana, Illinois
SEM-Snow Entomological Museum, University of Kansas, Lawrence, Kansas
UNAM-Colección Nacional de Insectos, Universidad Nacional Autónoma de México, D. F., México
UNSM-University of Nebraska State Museum, Lincoln, Nebraska
USNM-National Museum of Natural History, Washington DC, USA

Distribution and floral records

Information on distribution and floral records were extracted from literature and data from specimen labels examined at SEM and BBSL. Most floral records belong to the family Asteraceae. Plant family is given only for floral records from other families.

Phylogeny

In order to explore the internal phylogeny of *Argyropile*, a data matrix for a phylogenetic analysis was constructed in *Winclada* (Nixon 1999) and analyzed using the *wh** and *max** commands in *Nona* (Goloboff 1993). All characters were considered non-additive. Trees were visualized and printed using *Winclada* (Nixon 1999, slow optimization). Preliminary cladistic analyses of *Megachile* subgenera done by one of us (VG) suggest that the subgenus *Acentron* Mitchell is probably the closest relative of *Argyropile*; therefore, we used *Megachile* (*Acentron*) *albitarsis* Cresson as the outgroup. The abbreviations L, CI, RI are used for tree length and consistency and retention indices, respectively.

RESULTS

Subgenus *Argyropile* Mitchell 1934: 308

Type species: *Megachile parallela* Smith 1853 by original designation

Diagnosis. Bees of the subgenus *Argyropile* belong to the Group 1 of subgenera *sensu* Michener (2000), which consist of largely megachiliform species. *Argyropile* can be recognized by the combination of the following characters: Females with S6 nearly bare or scarcely setose (Figs. 6, 7), with apical margin thickened, rolled (Fig. 10) or abruptly bent dorsally (Fig. 11); mandible with four teeth (Fig. 4), or inner tooth incised, resulting in a 5-toothed mandible (Fig. 5), emargination between 3rd and 4th teeth evenly concave; simple cutting edge between 3rd and 4th teeth, sometimes incomplete between 2nd and 3rd; MT1 about 1.3 times wider at base than second (Figs. 4, 5). Males can be separated from other subgenera by the combination of inferior process of mandible small (Figs. 14, 17, 20), basitarsi of all legs slender and unmodified, front coxal spine small (Figs. 25–27), gonoforceps of genitalia narrowed above base in lateral view, slender, compressed apically, shorter than penis valves (Figs. 42–47). Females of some species in the subgenera *Acentron* Mitchell and *Pseudocentron* Mitchell resemble *Argyropile* by having a S6 with an apical rim bent dorsally; however, this rim is usually thinner and translucent, and their mandibular structure is not as described above. In *Acentron* the mandible is more robust, with MT1 about 2.0 times wider at base than MT2, whereas in *Pseudocentron* the second interspace is small, without cutting edge. .

Description. Body length: 9–16 mm. *Female*. Head broader than long. Eyes parallel. Mandible 1.7 times apically wider than long, 4 toothed, inner tooth sometimes incised, resulting in a 5-toothed mandible (Fig. 5); emargination between MT 3 and MT4 evenly concave; simple cutting edge between MT 3 and MT4, sometimes an incomplete edge between MT2 and MT3; MT1 1.3 times wider than MT2 (Figs. 4, 5). Vertex flat in frontal view. Labrum rectangular, 1.2 times longer than wide. Lacinia pointed, with long setae along inner margin (Fig. 21); three maxillary palpomeres; first and second about same length, setae shorter than palpomere diameter. Clypeus with distal margin impunctate, smooth, sinuous and denticulate; clypeal margin entire or with short incurved area medially (Figs. 8–9). Inner margin of fore tibia with dense row of thick setae, longer towards tibial apex. Pretarsal claws simple, with two thick setae at base. Mid tibial spur serrate, straight. Mid tarsomeres with anterodistal margin projected downward (Figs. 1, 2). Hind tibia with spurs serrate, teeth broader than long, inner spur gently curved, outer spur straight. Hind basitarsus wide, slightly narrower to slightly wider than maximum tibial width; anterior margin gently convex, posterior margin straight; outer surface flat or slightly convex. T6, in profile, straight, or nearly so with no erect setae, uniformly and entirely covered with extremely fine pale tomentum, except in *M. sabinensis* which has some erect setae at the base of T6. Scopal setae whitish to ferruginous, 8OD to 9OD in length; S6 with sparse pubescence except along margin (Figs. 6, 7); apical margin rolled (Fig. 10) or abruptly bent dorsally (Figs. 11). Integument black. T1–T5 with apical margins covered by dense, appressed, very short (< 0.5 OD), minutely branched white setae forming fasciae. Mesoscutal-mesoscutellar suture with or without fascia. *Male*. Mandible with 3 or 4 teeth, with a small, slender, , basal, inferior process (Figs. 12–20). Fore coxa with small, slender, acute spine (Figs. 25–27); disc above spine, with or without dense patch of erect, simple, stiff ferruginous setae. Fore femur antero-posteriorly compressed, more than twice as long as wide, dorsal margin almost straight, ventral margin broadly convex, carinate. Fore tibia, somewhat compressed, about 2.5 times longer than wide. Basitarsi of all legs slender, unmodified. Mid tibia with apical spur as in Fig. 3. T5 with preapical margin crenulate. T6 with preapical carina emarginate or entire; apical margin simple or with two acute projections on each side of median line (Figs. 33–35). T7 with preapical margin carinate, median projection truncate, pointed, rounded or emarginate (Figs. 36–38). Gonoforceps shorter than penis valves (Figs. 42–47), narrowed above base in lateral view, slender, compressed apically, slightly sinuate with setae short (shorter than maximum width of gonoforceps) or absent.

Distribution. *Megachile* (*Argyropile*) is widely distributed in North and Central America from southwestern Canada as far south as Costa Rica.

Biology. Little is known about the biology of these species. The only information on nesting is a brief account indicating that at least *M. parallela* makes shallow nests in the ground, and uses entire leaves or leaflets from *Spiraea* (Rosaceae) and *Trifolium*

(Fabaceae) to line the cells (Fischer 1951). *Megachile parallela* has also been recorded using trap-nests (Medler & Lussenhop 1968). *Argyropile* have been recorded on many plants, but they appear to show a strong preference for Asteraceae.

***Megachile* (*Argyropile*) *flavihirsuta* Mitchell**

Mitchell 1930: 225, ♂ (Figures of mandible and carina of T6, Pls. X and XII). Type locality: Guadalajara, Mexico. Type repository: ANSP

Mitchell 1943a: 16 [taxonomic placement]

Ayala *et al.* 1997: 454 [distribution in Mexico]

Yañez-Ordóñez & Hinojosa-Díaz 2004: 188 [distribution in Mexico]

DISTRIBUTION: Central Mexico to Costa Rica.

FLORAL RECORDS: *Bidens, Coreopsis.*

***Megachile* (*Argyropile*) *parallela* Smith**

Smith 1853: 191, ♂. Type Locality: Georgia, USA. Type repository: BNHM.

Mitchell 1937: 48 [mandible, genitalia and associated sterna, Pls. V and VI]; 1941: 167 [intersex]; 1943a: 12; 1943b: 661 (♀ S6, Fig. 18); 1962: 159 [♂ genitalia and associated sterna, Fig. 50, 52 and 55; Fig. 51, mandible of ♀ and ♂]

Fischer 1951: 49; 1953: 47 [nesting biology]

Medler & Lussenhop 1968 [nesting biology]

Ayala *et al.* 1997: 454 [distribution in Mexico]

Yañez-Ordóñez & Hinojosa-Díaz 2004: 188 [distribution in Mexico]

facunda Cresson 1872: 266, ♂. Type locality: Texas, USA. Type repository: ANSP.

Cresson 1916: 118 [lectotype designation]

Hurd 1979: 2066 [synonymy with *parallela*]

6-dentata Robertson 1895: 125, ♂. Type locality: Illinois, USA. Type repository: INHS.

verbesinae Cockerell 1908: 264, ♀. Mitchell, 1937: 57. Type locality: Sonoita, Arizona, USA. Type repository: CAS.

Mitchell 1944: 132 [synonymy with *parallela*]

parallela rita Mitchell 1937: 53, ♀. Type locality: Mt. Santiago, California, USA. Type repository: USNM.

parallela reta Mitchell 1937: 48, 1943a: 16; misspelling of *parallela rita.*

asterae Mitchell 1943a: 13, ♀. Type locality: Kaibab Forest, Utah, USA. Type repository: CAS. [N. Syn.]

tulariana Mitchell 1937: 53, ♀. Type locality: Tulare, California, USA. Type repository: CUIC. [N. Syn.]

DISTRIBUTION: Southwestern Canada (British Columbia – Saskatchewan), western USA to North Dakota, Indiana, North Carolina and Florida; Mexico and Costa Rica.

FLORAL RECORDS: *Aplopappus*, *Agoseris, Asclepias*—Asclepiadaceae*, Aster, Baccharis, Baileya multiradiata, Boltonia, Brassica geniculata*—Brassicaceae*, Calycadenia multiglandulosa, Ceanothus*—Rhamnaceae*, Centaurea melitensis, C. solstitialis, Cephalanthus*—Rubiaceae*, Chrysanthemum, Chrysothamnus paniculatus, C. nauseosus, C. viscidiflorus, Cirsium, Clarkia williamsonii*—Onagraceae, *Coreopsis grandiflora, C. lanceolata, C. tinctoria, C. palmata, Corethrogyne, Chilopsis linearis*—Bignoniaceae, *Dyssodia, Encelia virginensis, E. farinosa, Ericameria parishii, Erigeron pygmaeus, Eriophyllum confertiflorum, Gaillardia pulchella, G. suavis, Gilia*—Polemoniaceae, *Gossypium*—Malvaceae, *Grindelia camporum, G. inuloides, G. squamosa, Gutierrezia californica, G. sarothrae, Haplopappus squarrosus, H. vernonioides, Helenium bigelovii, Helianthus annus, H. atrorubens, H. gracilentus, H. nuttallii, H. petiolaris, Heliopsis, Hemizonia lobbii, H. wrightii, Heterotheca grandiflora, H. subaxillaris, Hypericum*—Clusiaceae, *Lepachys, Lippia cuneifolia*—Verbenaceae, *Lotus scoparius*—Fabaceae, *Malacothrix tenuifolia, Medicago sativa*—Fabaceae, *Melilotus alba*—Fabaceae, *Nepeta cataria*—Lamiaceae, *Palafoxia linearis, Phaseolus*—Fabaceae, *Petalostemon*—Fabaceae, *Ratibida columnaris, R. columnifera pulcherrima, Rudbeckia bicolor, Sapindus drummondi*—Sapindaceae, *Senecio douglasii, S. flaccidus, Solidago, Silphium, Stephanomeria exigua, Verbena stricta*—Verbenaceae, *Verbesina, Viguiera, Xanthocephalum, Zexmenia, Zinnia.*

ASSOCIATED ORGANISMS: The mite *Trochometridium tribulatum* Cross (Acari, Trochometridiidae) has been taken from legs, propodeum and metasoma of females. The same mite species has also been recorded from other ground-nesting bees (P. Klimov, Pers. com).

***Megachile* (*Argyropile*) *rossi* Mitchell**

Mitchell 1943a: 14, ♀. Type locality: Tombstone, Arizona, USA. Type repository: CAS.

Ayala *et al.* 1997: 455 [distribution in Mexico]

Yañez-Ordóñez & Hinojosa-Díaz 2004: 188 [distribution in Mexico]

Description: Male. Body length, 12.3 mm (± 0.26, 11.2–13, *n* = 8); forewing length, 8.4 mm (± 0.2, 7.5–8.8, *n* = 6). *Structure*. Head 1.6 times as wide as long; inner orbits converging below, upper interocular distance 1.2 times greater than inferior interocular distance; interalveolar distance 1.4 times longer than alveolorbital distance, the latter about 2.5 times diameter of antennal socket; interocellar distance 2.4 times OD, about as long as ocellocular; ocelloccipital distance 1.2 times longer than interocellar distance, about 2.8 times greater than OD; compound eye about 2.1 times as long as wide; gena slightly narrower than width of compound eye in profile; clypeus about twice as broad as long, gently protuberant and convex in profile, apical margin as in Fig. 23; mandible tridentate as in Fig. 15–17; scape 2.5 times longer than broad, pedicel slightly wider than long, about as broad as F1–F3; F1 slightly longer than broad, about 1.3 timer longer than pedicel, shorter (0.7 times) than F2 and F3, individually. Front coxal spine small, slender, acute, slightly curving anteriorly in lateral view (Fig. 26); fore femur compressed antero-posteriorly, 2.4 times longer than wide, dorsal margin almost straight, ventral margin broadly convex, carinate;

fore tibia 0.8 times length of femur, somewhat compressed, about 2.5 times longer than wide; basitarsi of all legs slender and unmodified; hind tibia 3.4 times longer than wide; hind basitarsus about 3.3 times longer than wide, about half tibial length. T6, T7, S4–S6, S8, genitalia as in Figs. 29, 31, 34, 37, 40, 43, 46, 49. *Coloration*. Black, except: apex of mandible, flagellum, legs dark reddish brown; tegula, wing veins yellowish ferruginous; wings subhyaline. *Pubescence*. White, except apex of anterior surface of front coxal spine, inner surface of tarsi of all legs, inner margin of fore and mid tibiae with ferruginous setae. Basal third of mandible densely covered with very short (< 0.5 OD), minutely branched setae, lower margin with longer (> 2OD) setae; face with dense (integument not visible), long (> 2OD), minutely branched setae; area above ocelli, vertex with shorter setae than on face, intermixed with some light ferruginous setae; outer surface of scape with dense, long (> diameter of scape), minutely branched setae; upper half of gena with sparse, short (≤ OD) setae, denser, longer (> 2 OD) on lower gena. Mesosoma with long (> 2 OD), dense setae (integument visible) as on face, shorter, sparser on mesoscutum; mesoscutum-scutellum groove with dense, very short (< 0.5 OD), minutely branched setae forming a fascia. Fore leg with coxa, lower margin of trochanter, posterior margin of femur, basitarsus, first tarsomere with long, dense(> 2OD) setae, longer, denser than on other legs. Sides of T1 and T5, apical margins of T2–T4 and base of T6 except for median projection, with dense, appressed, very short (< 0.5 OD), minutely branched setae; S1–S4 and remainder of terga with sparser, erect, whitish to pale grey setae , longer on sterna and sides of terga; longest (> 2OD) and densest on T1. *Punctation.*

Clypeus finely, closely (1 PW) punctate throughout, except for apical margin smooth, shining; paraocular and supraclypeal areas with smaller, closer punctures than clypeus, integument otherwise smooth, shiny; ocellar area, vertex, gena with coarser, larger, sparser (≥ PW) punctures than on face, integument otherwise imbricate. Mesoscutum, mesoscutellum as vertex, but punctures slightly larger, coarser; mesepisternum, metepisternum, sides of propodeum coarsely punctate, punctures larger, closer (< 0.5 PW) than on mesoscutum; basal area of propodeum minutely rugose. Terga densely (≤ PW), coarsely punctate, integument otherwise weakly imbricate to lineolate, punctures closer, coarser on T6. S1 and S2 finely, closely (< PW) punctate, discs of S3, S4 with shallow, sparser (1–2 PW) punctures, except for premarginal area of S4 coarsely, densely (< 0.5 PW) punctured, almost rugose; S1–S4 with thin, impunctate, translucent, narrow (< OD) marginal zones (Fig. 29).

Material Examined: MEXICO. *Chihuahua*: 4♂, Reserva Biosfera Mapimi, dunes N estacion., E of Ceballos, 22 Aug 1991, T. Griswold; 3♂, 65 km NE of Ceballos, 21 23 Aug 1991, ex: *Larrea tridentata* (Zygophyllaceae), R. L. Minckley. *Coahuila*: 1♂, Zapata, 9 km W, 25 Aug 1991, ex: *Verbesina encelioides*, R. L. Minckley. *Durango*: 1♂, Canutillo, 8 mi S, 9 Aug 1951, H. E. Evans [SEMC].

DISTRIBUTION: Southwestern United States to northern Mexico.

FLORAL RECORDS: *Aster, Baileya multiradiata, Bebbia juncea, Bidens, Cercidium*—Caesalpiniaceae, *Encelia virginensis*, *Ericameria nauseosa nauseosa*, *Eriodictyon*—Hydrophyllaceae, *Helianthus annuus, Heliomeris multiflora, Larrea tridentata*—

Zygophyllaceae*,* *Psorothamnus scoparius*—Fabaceae*,* *Senecio flaccidus, S. sparttioides, Verbesina encelioides*, *Viguiera.*

***Megachile* (*Argyropile*) *sabinensis* Mitchell**

Mitchell 1934: 348, ♀. Type locality: Sabinal, Texas, USA. Type repository: USNM.

Mitchell, 1937: 57; 1943a: 13.

Ayala *et al.* 1997: 455 [distribution in Mexico]

Yañez-Ordóñez & Hinojosa-Díaz 2004: 188 [distribution in Mexico]

Description: Male. As described for *M. rossi*, except: body length, 11.2 mm (± 0.44, 10.4–11.9); forewing length, 7.3 mm (± 0.1, 7.1–7.5). Interalveolar distance 1.5 times longer than alveolorbital distance, the latter about twice as long as antennal socket diameter; interocellar distance slightly longer than ocellocular; ocelloccipital distance slightly shorter than interocellar distance, about 2.5 times greater than OD; clypeus 1.9 times wider than long, slightly elevated, flat in profile, apical margin as in Fig. 24; mandible tridentate as in Figs. 18–20; scape 2.4 times longer than broad, pedicel 1.2 times wider than long, slightly narrower than F1–F3; F1 about 1.5 times longer than pedicel, shorter (0.8) than F2 and F3 individually. Front coxal spine as in Fig. 27; fore femur twice as long as wide; fore tibia about 2.4 times longer than wide; hind tibia 3.2 longer than wide; hind basitarsus about 2.3 times longer than wide. T6, T7, S5, S6, S8, genitalia as in Figs. 32, 35, 38, 41, 44, 47, 50. *Pubescence*. In general, shorter than in *M. rossi*; disc of front coxa with dense patch of erect, simple, stiff ferruginous setae. *Punctation.* Clypeus with punctures coarser than, and T6 with punctures sparser (especially on center of disc) than in *M. rossi*.

Material Examined: USA. *Arizona*: 1♂, Portal, 10 mi E, 15 Sep 1955, G. E. Bohart. MEXICO. *Chihuahua*: 1♂, Reserva Biosfera Mapimi, dunes N estacion., E of Ceballos, 22 Aug 1991, T. Griswold; 1♂, Samalayuca, 9 km S, 30 Aug 1991, R. L. Minckley; 1♂, Janos, 35 km NW, ex: *Dyssodia*, 31 Aug 1991, R. L. Minckley [SEMC].

DISTRIBUTION: Southwestern United States to northern Mexico.

FLORAL RECORDS: *Aster, Baileya multiradiata, Dyssodia, Encelia virginensis, Eriogonum*—Polygonaceae*, Haplopappus, Helianthus*, *Hymenothrix wizlizeni, Larrea tridentata*— Zygophyllaceae*, Machaeranthera pinnatifida, M. canescens, Pectis papposa, Tamarix gallica*—Tamariaceae.

***Megachile* (*Argyropile*) *subparallela* Mitchell**

Mitchell 1944: 132, ♀. Type locality: Douglas, Arizona, USA (male also described). Type repository: CAS.

DISTRIBUTION: Southwestern United States to northern Mexico.

FLORAL RECORDS: *Eriogonum*—Polygonaceae*, Haplopappus, Heterotheca*, *Malpighia mexicana*—Malpighiaceae.

***Megachile* (*Argyropile*) *townsendiana* Cockerell**

Cockerell 1898: 129, ♂. Type locality: Las Cruces, Mexico. Type repository: CAS.

Ayala *et al.* 1997: 455 [distribution in Mexico]

Yañez-Ordóñez & Hinojosa-Díaz 2004: 188 [distribution in Mexico]

bishoppi Cockerell, 1915: 535, ♂. Type locality: Paris, Texas, USA. Type repository: USNM.

Mitchell 1937: 54 (Figs. mandible, genitalia and associated sterna, Pls. V and VI); 1943a: 13; 1962: 161 [♂ genitalia and associated sterna, Fig. 50, 52 and 55; Fig. 51, mandible of ♀ and ♂]

DISTRIBUTION: Southwestern United States to northern Mexico.

FLORAL RECORDS: *Actinella, Baileya multiradiata, B. pleniradiata, Encelia frutescens, Geraea canescens, Chrysopsis villosa, Haplopappus acuadenius, Helianthus debilis, Hoffmanseggia*—Leguminosae, *Hymenopappus filifolius, Larrea tridentata*— Zygophyllaceae, *Lepidium montanum*—Brassicaceae, *Medicago sativa*—Fabaceae, *Melanthera parviflora, Pectis papposa, Phacelia robusta*—Hydrophyllaceae, *Prosopis*—Leguminosae, *Verbesina encelioides, Wislizenia refracta*—Capparaceae.

***Megachile* (*Argyropile*) *longuisetosa*, Gonzalez & Griswold, new species**

(Figs. 1, 3, 4, 6–8, 12–14, 21, 22, 25, 30, 33, 36, 39, 42, 45, 48)

Diagnosis: Females can be recognized by the following combination of characters: mid tarsomeres with anterodistal margin strongly acutely produced (Fig. 1), mesoscutal-mesoscutellar suture with distinct pubescent fascia, T5 finely and densely punctate (≤ PW), and apical margin of S6 abruptly bent dorsally. Males can be distinguished by the combination of T6 with preapical carina and apical margin entire (Fig. 33), S5 and S6 with simple, unmodified setae (Figs. 30, 39), and apex of gonoforceps with long setae (Figs. 42, 45).

Description: Female. Body length 11 mm; forewing length 7.1 mm. *Structure*. Head 1.5 times as wide as long; inner orbits slightly converging below, upper interocular distance 1.2 times inferior interocular distance; interalveolar distance 1.4 times alveolorbital distance; interocellar distance 2.6 times OD, slightly shorter than ocellocular distance; ocelloccipital distance about twice as long as OD; compound eye about 2.7 times as long as wide; maximum width of gena approximately equal to maximum width of compound eye in profile, narrower above; clypeus 2.4 times wider than long, apical margin sinuous (Fig. 8); mandible as in Fig. 4; scape 3.2 times longer than broad, pedicel about as broad as long, F1 1.5 times longer than broad, 1.5 times longer than pedicel, only slightly longer than F2 and F3, individually, F2–F10 slightly longer than broad. Mid tarsi as in Fig. 1; hind tibia three times longer than broad, 1.2 times longer than hind basitarsus; hind basitarsus 2.7 times longer than broad, slightly narrower than tibia. *Coloration*. Black except: dark reddish brown on labrum, apical half of mandible, flagellum, tegula, all legs except for spurs; distitarsi and pretarsal claws yellowish ferruginous; wings subhyaline, veins dark brown. *Pubescence*. White, unless indicated otherwise. Basal half of outer surface of mandible densely covered with very short (< 0.5 OD), minutely branched setae, lower margin of mandible with longer (> 2 OD) setae. Face with dense (integument barely visible), long (1–1.5 OD), minutely branched setae; sparser on clypeus; gena with setae as on face, longest on lower gena (> 2 OD); area above ocelli and vertex with shorter (OD), sparser dark brown setae. Scape with outer surface uniformly covered (integument visible) with very short (< 0.5 OD) dark brown to light ferruginous setae. Mesosoma with long (> 2 OD) setae as on face, shorter, sparser on margins of mesoscutum; disc of mesoscutum and mesoscutellum with sparse, poorly branched dark brown setae, longest (> OD) on mesoscutellum; inner surface of tarsi of all legs with light ferruginous setae; posterior margin of fore basitarsus with long setae, longer than twice width of segment. T1 with long (≥ 2 OD), branched setae, denser on sides; T1–T5 with apical margins densely covered with dense, appressed, very short (< 0.5 OD), minutely branched setae; dorsal surfaces of T2–T5 with sparse, semi-erect, mostly simple, short (0.5 OD) dark brown setae, longest on T5; T6 densely covered (integument not visible) with appressed, very short, light ferruginous setae, with longer (1.5 OD), semi-erect, poorly branched, dark brown setae anterolaterally. Pubescence of S6 as in Figs. 6, 7. *Punctation.* Face finely and closely punctate (≤ PW), punctures larger on clypeus, integument smooth and shiny; vertex with integument imbricate between punctures; gena with shallow, larger punctures than face, integument weakly imbricate. Mesoscutum, mesoscutellum as on vertex, punctures coarser and larger on mesoscutellum, mesepisternum and metepisternum coarsely punctate, punctures larger, closer (< 0.5 PW) than mesoscutum; basal area of propodeum strongly imbricate. Terga densely, finely punctate (≤ PW). Sterna with punctures coarser, larger than on terga.

Male. As in female except for: Body length, 12 mm; forewing length, 7.7 mm. *Structure*. Head 1.6 times as wide as long; interalveolar distance 1.6 times longer than alveolorbital distance; interocellar distance 2.4 times OD; ocelloccipital distance 2.5OD; gena narrower than width of compound eye in profile; clypeus 2.3 times broader than long, apical margin as in Fig. 22; mandible tridentate as in Figs. 12–14; scape 2.4 times longer than broad, pedicel slightly wider than long, F1 slightly longer than broad, slightly longer than pedicel, F2 1.6 times longer than F1. Front coxal spine as in Fig. 25; fore femur compressed antero-posteriorly, 2.5 times longer than wide, dorsal margin almost straight, ventral margin broadly convex, carinate; fore tibia 0.8 times length of femur, somewhat compressed, about 3 times longer than wide; basitarsi of all legs slender and unmodified; hind tibia 3.2 longer than wide; hind basitarsus about 3.9 times longer than wide, about half tibial length. T6, T7, S5, S6, S8, genitalia as in Figs. 30, 33, 36, 39, 42, 45, 48. *Pubescence*. In general, longer, denser than in female. Face, mesoscutum, terga with yellowish to light ferruginous setae. Sides of scape with dense, long (> diameter of scape), minutely branched setae; upper half of gena with sparse, short (≤ OD) setae, denser, longer (2–3 OD) on lower gena. Apex of anterior surface of fore coxal spine with patch of dense, short (0.5 OD) ferruginous setae. *Punctation*. Coarser than in female. S1–S4 with thin, impunctate, translucent, wide (< OD) marginal zones (as in Fig. 28 for *M. flavihirsuta*).

Type Material: Holotype: MEXICO, *Veracruz*: 1♀, 31 KM SE Xajala, 7 Nov 1991, 400 m., along hwy, steep hill to fallow field, [R.] Ayala [UNAM]; Paratypes: 1♀, 8 km S Carrizal, 5 Nov 1991, 140 m hot spring resort, along river, R. Ayala [SEMC]; 1♀, *idem*, T. Griswold [BBSL]; 1♂, Catemaco, 6 Sep 1974, W. Hanson & G. Bohart [BBSL]. GUATEMALA, *Mixto Viejo*: 1♂, 30 Oct 1982, H. Suzuki [BBSL].

Etymology. The specific name means “long setae”, in reference to the long setae on the apex of the gonoforceps in the male genitalia.

Internal phylogeny of *Argyropile*

The following characters were used in the phylogenic analysis: *Female.* 1. Anterodistal margin of mid basitarsus: 0 = strongly projecting (Fig. 1). 1 = not strongly projecting (Fig. 2). 2. Length of setae on ventral fringe on hind basitarsus: 0 = short (one-fourth or less width of segment); 1 = long (one-third or more). 3. Fascia on mesoscutal-mesoscutellar suture: 0 = absent; 1 = present. 4. Apical margin of S6: 0 = posteriorly directed; 1 = rolled (Fig. 10); 2 = bent dorsally (Fig. 11). 5. Pubescence on posterior half of S6: 0 = entirely absent; 1 = scarcely pubescent. *Male*. 6. Number of mandibular teeth: 0 = three; 1 = four. 7. Preapical carina of T6: 0 = entire; 1 = emarginate. 8. Lamellate marginal zone of sterna: 0 = wide (Fig. 28); 1 = narrow (Fig. 29). 9. Mid tibial spur: 0 = modified; 1 = normal. 10. Apical margin of T7: 0 = not angled (Figs. 36, 37); 1 = angled (Fig. 38). 11. Stiff ferruginous setae on fore coxa: 0 = absent (Fig. 26); 1 = present (Fig. 27). 12. Apical margin of T6: 0 = simple (Fig. 33); 1 = with two acute projections on each side of mid line (Fig. 34). 13. Hind basitarsus length: 0 = short (about 2.0 times longer than broad); 1 = long and slender (more than 2.0 times longer than broad).

Cladogram. Two most parsimonious trees (L = 21, CI = 66, RI = 50) were obtained from the analysis of the characters described above (Table 6). Two clades were clearly differentiated in those trees: the first includes *Megachile sabinensis* and *M. subparallela*, and the second includes the rest of species (Fig. 51).

Table 6. Character matrix used in cladistic analysis of the internal phylogeny of *Megachile* subgenus *Argyropile*. *Megachile* (*Acentron*) *albitarsis* was used as outgroup. Data for the male of *M. subparallela* were taken from Mitchell's (1944) description. States of characters that could not be drawn from the description were coded as (–).

Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
M. albitarsis	0	1	1	0	0	1	1	1	0	0	1	1	0
Megachile flavihirsuta	0	0	0	2	1	0	0	1	1	1	1	1	1
M. parallela	0	0	0	2	1	1	1	0	1	0	0	1	1
M. rossi	0	1	0	2	1	0	1	0	1	0	0	1	1
M. sabinensis	1	0	1	1	1	1	1	0	1	1	1	1	0
M. subparallela	1	1	1	1	1	0	1	–	1	0	–	1	–
M. townsendiana	0	1	1	2	1	1	1	0	1	0	1	1	1
M. longuisetosa sp. nov.	0	1	1	2	1	1	1	1	1	0	0	0	1

DISCUSSION

Little is known about the biology of *Argyropile* species. Though these bees have been recorded on many plants, they appear to show a strong preference for Asteraceae. In a four-year study of the bee fauna of Grand Staircase-Escalante National Monument in southern Utah (Messinger & Griswold unpub.), 97% of the 62 females collected were found on Asteraceae. The majority of these were visiting *Helianthus*. In a study of bees in Clark County, Nevada 15 of 16 female *M. rossi* were visiting Asteraceae.

Females of *Megachile* (*Megachile*) *pilicrus* Morawitz, which are oligolectic on Asteraceae of the tribe Cardueae, have a dense brush of apically wavy stiff bristles on the ventral side of the hind trochanter and femur for combing pollen from inflorescences. The same brushes are less developed in species of the subgenus *Eutricharaea* with a more polylectic habit (*i.e*., collecting pollen from additional tribes of Asteraceae and other plant families) than *M. pilicrus* (Müller & Bansac 2004). *Argyropile* species lack such specialized brushes on the hind legs, which agrees with their more polylectic diet.

Females of various *Megachile* subgenera have distinct setae and brushes on several areas of their body that might be related to pollen collection from a particular plant source (Michener 2000). However, biological information is extensive only for a few very common species used in agricultural pollination, especially *Megachile rotundata* (Fabricius), and scarce or absent in many other species. Floral records and behavioral observations for a wider array of species are needed to fill this gap, and to reach a definitive interpretation of the diversity, evolution, and ecology of *Megachile*.

Males and females of *Argyropile* exhibit several external morphological characters, which seem taxonomically reliable in species recognition but are not phylogenetically informative, as suggested by the present analysis; in fact, most of these characters seem to be homoplastic. The dorsally bent apical margin of the female S6 (character 4), the long and slender hind basitarsus, and the absence of stiff ferruginous setae on fore coxa in the male (13, 11) support the inclusion of *Megachile longuisetosa* sp. nov., within the clade comprised by *M. townsendiana* and the remaining species (Fig. 51). Furthermore, only the males of *M. longuisetosa* sp. nov. and *M. flavihirsuta* have a sixth tergum with an entire pre-apical carina and setae on the apex of the gonoforceps. Other species either lack these setae or, if the setae are present, they are shorter and barely visible.

Key to species of the subgenus *Argyropile* (Females)

1. Midbasitarsus with anterodistal margin not strongly projecting, rounded (Fig. 2); apical margin of S6 rolled (Fig. 10)……………………………………………2

—. Midbasitarsus with anterodistal margin strongly, acutely projecting (Fig. 1); apical margin of S6 abruptly bent dorsally (Fig. 11)……………………………..3

2(1). S6 covered with pale setae; T6 with dense appressed light setae apically, absent medially; mesoscutum dull with punctures contiguous……….…*M. subparallela*

—. S6 with mostly brown to black setae; T6 with dense appressed setae white medially, dark apically; mesoscutum shiny between dense and fine but not contiguous punctures…………………………………………….*M. sabinensis*

3(1). Inner tooth incised, resulting in a 5-toothed mandible (Fig. 5); body with bright fulvous pubescence; hind basitarsus wider than tibia, its outer surface largely concave……………………………………………………….*M. flavihirsuta*

—. Inner tooth without incision, typical 4-toothed mandible (Fig. 4); body covered with mostly white to yellowish pubescence; hind basitarsus of variable width……………………………………………………………….…..…4

4(3). Clypeal margin with median denticle (Fig. 8); S6 apical flange strongly bent dorsally………………………………………………………………………5

—. Clypeal margin without median denticle (Fig. 9); S6 apical flange not strongly bent dorsally………….……………………………………………..*M. rossi*

5(4). Mesoscutal-mesoscutellar suture with distinct dense white pubescent fascia; hind basitarsus with long ventral fringe, length of setae one-third or more width of segment……………………………………………………………….…6

—.Mesoscutal-mesoscutellar suture without pubescent fascia; hind basitarsus with short ventral fringe, length of setae one-fourth or less width of segment…………………………………………………...…*M. parallela*

6(5). T5 finely and densely punctate (≤ 1 PW); southern Mexico to Guatemala…………………………………………….*M. longuisetosa* sp. nov

—. T5 coarsely punctate; punctures separated by ≥ 1 puncture width; southwestern United States to northern Mexico…………………………..…*M. townsendiana*

Key to species of the subgenus *Argyropile* (Males)

1. Preapical carina of T6 emarginate (Figs. 34, 35); sterna with narrow (< OD) lamellate marginal zone (Fig. 29)……………………………………..…2

—. Preapical carina of T6 entire (Figs. 33); sterna with wide (>> OD) lamellate marginal zone (Fig. 28)……………………………………………………....6

2(1). T7 truncate, rounded or emarginate (Fig. 37); preapical carina of T6 with wide emargination (Fig. 34); T6 densely pubescent throughout………………………3

—. T7 angled, usually acutely (Fig. 38); preapical carina of T6 with narrow emargination (Fig. 35); T6 densely pubescent only basally………………………5

3(2). Mandible with 3 teeth (Fig. 15); mesoscutal-mesoscutellar suture with distinct fascia……………………………………………………………………………4

—. Mandible with 4 teeth; mesoscutal-mesoscutellar suture without fascia……………………………………………………………..…*M. parallela*

4(3). Apical margin of T6 with robust subtruncate carinate submedian teeth; apical margin of T7 rounded…………………………………………..…*M. subparallela*

—. Apical margin of T6 with acute submedian teeth (Fig. 34); T7 with apical margin truncate (Fig. 37)……………………………………………………….*M. rossi*

5(2). Hind basitarsus thickened, about twice as long as broad; fore coxa with patch of reddish setae (Fig. 27); fore basitarsus with dense fringe no longer than width of segment……………………………………………………….…*M. sabinensis*

—. Hind basitarsus long and slender, nearly four times as long as broad; fore coxa without patch of reddish setae; fore basitarsus with loose fringe longer than width of segment…………………………………………………*M. townsendiana*

6(1). Body covered with black and white pubescence; T7 rounded (Fig. 36)…………………………………………………*M. longuisetosa* sp. nov

—. Body covered with reddish pubescence; T7 with median spine as in Fig. 38…………………………………………………………….…*M. flavihirsuta*

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APPENDIX I

Characters used in the phylogenetic analysis of Megachilinae tribes. Character-state zero is not necessarily plesiomorphic.

Females

Head

1. Clypeoantennal distance: 0 = short (equal to or shorter than vertical diameter of antennal socket, Figs. 2, 4); 1 = long (≥ 1.2x antennal socket, Figs. 3, 5).
2. Insertion of the subantennal suture: 0 = directed toward lower margin of antennal socket (Figs. 2, 4); 1 = directed toward outer margin of antennal socket (Figs. 3, 5).
3. Shape of anterior tentorial pit: 0 = rounded; 1 = elongated, ≥ 2x longer than broad.
4. Thickening of secondary tentorial bridge: 0 = uniting to head wall at or below antennal socket; 1 = merging with eutentorial arm before reaching head wall. See character 15 of Roig-Alsina & Michener (1993).
5. Fan-shaped posterior sheets of tentorium, sometimes represented externally by the occipital sulci: 0 = well developed; 1 = small to absent. See character 22 of Roig-Alsina & Michener (1993).
6. Antennal scape length, excluding basal bulb: 0 = long (≥ 1.2x alveolocellar distance, Fig. 4); 1 = short (equal to or shorter than alveolocellar distance, Figs. 2, 3).
7. Length of F1: 0 = as long as or longer than length of F2 and F3 combined (Figs. 2, 4); 1 = shorter than length of F2 and F3 combined.
8. Supraclypeal area: 0 = flat or nearly so; 1 = elevated, with a median prominence (Fig. 6).
9. Juxtantennal carina: 0 = absent (Figs. 2, 4, 5); 1 = present (Fig. 3).
10. Inner paraocular carina: 0 = absent; 1 = present. The paraocular carina of *Microthurge pharcidontus* and *Trichothurgus wagenknechti* is very low and barely visible, thus I coded them as having character-state 0.
11. Short, erect hairs on compound eye: 0 = absent; 1 = present (Fig. 57).
12. Preoccipital carina: 0 = absent; 1 = continuous, present on gena and dorsal edge of head behind vertex; 2 = discontinuous, present either on gena or vertex.
13. Occipital distance: 0 = short (1–3x OD); 1 = long (≥ 3.1x OD).

14. Labrum: 0 = broader than long (Figs. 10); 1 = much longer than broad, rectangular, base as wide as apex, lateral margins parallel to each other (Fig. 11); 2 = subtriangular, base at least 1.5x apical width, lateral margins converging apically (Fig. 12).
15. Apical margin of labrum: 0 = bifid; 1 = broadly rounded; 2 = straight or nearly so.
16. Mandible with upper carina of trimma (UCT): 0 = absent; 1 = present, forming a Y-shaped system (Fig. 18); 2 = present, not forming a Y-shaped system (Fig. 20).
17. Inner fimbriate line of mandible (FL): 0 = running somewhat parallel to upper mandibular margin (Fig. 18); it is reduced to a tuff of thick hairs on the upper mandibular margin in Lithurgini, and I coded as having character-state 0; 1 = running somewhat parallel to apical margin of mandible (Figs. 20–22).
18. Hairs on adductor interspace of mandible: 0 = absent (Fig. 21); 1 = present (Fig. 22).
19. Adductor ridge distally with a tooth-like projection: 0 = absent; 1 = present (Fig. 19).
20. Mandible with outer premarginal impressed line (OIL): 0 = reduced or absent; 1 = present (Fig. 15).
21. Lower preapical tooth of mandible: 0 = absent; 1 = present (Fig. 13).
22. Mandible with small denticles between large teeth: 0 = absent; 1 = present (Fig. 14).
23. Mandible with cutting edge between teeth: 0 = absent (Figs. 13, 14, 16, 17, 19, 22); 1 = present in the second or third mandibular interspace, or both (Figs. 15, 20, 21, 23–36).
24. Proboscis length (in repose): 0 = short, not reaching metasoma; 1 = long, reaching metasoma.
25. Distal end of mentum: 0 = entire (Figs. 38, 39, 42); 1 = concave (Fig. 41); 2 = notched (Fig. 44); 3 = not sclerotized (Fig. 43).
26. Ligular arms of prementum: 0 = fused with prementum (Fig. 48); 1 = free, not fused with prementum (Fig. 49).
27. Subligular process of prementum: 0 = elongated, long and narrow, styliform (Fig. 45); 1 = broad, apex truncated (Fig. 47); 2 = broad and with pointed apex (Fig. 38, 46); 3 = membranous.
28. First labial palpomere: 0 = short, ≤ 0.5x second segment (Fig. 50); 1 = long, ≥ 0.8x second segment (Figs. 38, 39, 51).
29. First labial palpomere with a brush of hairs on midbasal concavity: 0 = absent; 1 = present (Fig. 50).

30. Third labial palpomere: 0 = apically directed as is second (Fig. 50); 1 = laterally directed from second (Figs. 38, 39, 51, 52).

31. Basistipital process of stipes: 0 = absent or reduced; 1 = present (Fig. 40).

32. Hairs on the anterobasal surface of stipes: 0 = short, ≤ 2x maximum stipital width in lateral view (Figs. 37, 40, 53); 1 = long, ≥ 2.1x stipital width (Figs. 55, 56). I consider the proboscis to be projected downward.

33. Dististipital process of stipes: 0 = absent; 1 = reduced; 2 = elongated, almost joining to stipital sclerite (Fig. 40).

34. Stipital comb along well-sclerotized concavity on posterior distal margin of stipes: 0 = present (Figs. 55, 56); 1 = absent.

35. Sclerotization of maxillary lacinia: 0 = strongly sclerotized, all borders clearly differentiated; 1 = weakly sclerotized, borders barely discernible; 2 = membranous, whitish, translucent, no borders noticeable.

36. Hairs on disc of lacinia: 0 = present (Fig. 54); 1 = absent.

37. Stipital sclerite: 0 = with distal end expanded; 1 = with no distal end expanded.

38. Maxillary galeal blade: 0 = uniformly sclerotized or only narrowly desclerotized near apex; 1 = with posterior margin broadly desclerotized almost to base.

39. Number of maxillary palpal segments, including basal segment: 0 = two; 1 = three; 2 = four; 3 = five; 4 = six.

40. Hair on maxillary palpi: 0 = short, ≤ 2x palpomere diameter (Figs. 37, 40); 1 = long, ≥ 2.1x palpomere diameter (Fig. 53).

41. Paramandibular process: 0 = short or absent (Fig. 9); 1 = long (Fig. 8).

42. Integument of head: 0 = black or dark brown, without yellow, reddish, or cream maculations; 1 = entirely yellowish, or black to dark brown, with yellow, reddish, or cream maculations; 2 = dark brown with blue metallic highlights or entirely metallic blue.

Mesosoma

43. Pronotal lobe with strong carina or lamella: 0 = absent; 1 = present (Fig. 57).

44. Episternal groove: 0 = absent; 1 = present.

45. Omaulus: 0 = rounded; 1 = angular, carinate, or lamellate.

46. Metapleuron with dorsal lamella: 0 = absent; 1 = present.

47. Parapsidal line: 0 = long (≥ 0.4x tegula length, in dorsal view); 1 = short (≤ 0.3x tegula length) or absent.
48. Mesoscutellum: 0 = not projected over metanotum in profile; 1 = projected over metanotum.
49. Preaxilla: 0 = sloping, with long hairs; 1 = vertical, nearly hairless.
50. Axilla: 0 = rounded, not posteriorly projected in acute angle or spine; 1 = posteriorly projected in acute angle or spine (Fig. 57).
51. Shape of propodeum in profile: 0 = divided in a subhorizontal or slopping basal surface, and a declivous posterior surface; 1 = entirely declivous or nearly so.
52. Propodeal spiracle: 0 = without a shiny, hairless fovea behind spiracle; 1 = with a shiny, hairless fovea defined by carina behind spiracle.
53. Dorsum of mesosoma with yellow or reddish maculations: 0 = absent; 1 = present.
54. Front coxal spine: 0 = absent; 1 = present.
55. Pubescence of fore and mid basitarsi: 0 = sparse, integument visible; 1 = densely covered (integument not visible) by white, branched hairs.
56. Middle tibial spur: 0 = finely serrate or ciliate (as in Fig. 59); 1 = coarsely serrate (as in Fig. 60).
57. Basitibial plate: 0 = absent; 1 = present.
58. Outer hind tibial spur: 0 = finely serrate or ciliate (Fig. 59); 1 = coarsely serrate (Fig. 60).
59. Hind basitarsus: 0 = ≥ 6x longer than broad, rounded; 1 = ≤ 5x longer than broad, flattened.
60. Strong tubercles or spicules on outer surfaces of tibiae: 0 = absent; 1 = present.
61. Pretarsal claws: 0 = simple (Fig. 62); 1 = bifurcate (Fig. 63).
62. Arolia: 0 = reduced or absent; 1 = present (Fig. 62).
63. Wing vestiture: 0 = hairy throughout; 1 = partly bare.
64. Number of submarginal cells: 0 = three; 1 = two.
65. Length of second submarginal cell: 0 = equal or longer than first on posterior margin; 1 = shorter than first on posterior margin.
66. Vein 2m-cu of fore wing: 0 = anterior to 2nd submarginal crossvein; 1 = confluent with or posterior to 2nd submarginal crossvein.
67. Stigma: 0 = long (≥ 2.1x longer than broad); 1 = short (≤ 2x longer than broad).

68. Jugal lobe of hind wing: 0 = ≤ 0.5x vanal lobe length; 1 = ≥ 0.6x vanal lobe length.

Metasoma

69. Location of pollen-collecting structures: 0 = hind tibia and basitarsus; 1 = sterna; 2 = absent.
70. Coloration of metasomal terga: 0 = entirely metallic, reddish, yellowish, or dark brown to black; 1 = dark brown to black with yellow, cream, or reddish maculations.
71. T1: 0 = long, convex in profile, with posterior margin straight or nearly so, and with distinct anterior and dorsal surfaces (Fig. 74); 1 = small, flattened, with posterior margin rounded, undistinguishable anterior and dorsal surfaces (Fig. 69).
72. Pygidial plate: 0 = present; 1 = absent, midapical tergal area with integument hairless, papillate or minutely roughened; 2 = absent, tergal area pilose, integument not papillate nor minutely roughened.
73. Short (≤ OD), appressed hairs on T6: 0 = absent; 1 = present.
74. Sublateral teeth on apical margin of T6: 0 = absent; 1 = present (Fig. 70).
75. Length of S6: 0 = short (Fig. 75), as long as wide or shorter (length measured along midline); 1 = elongated, ≥ 2x longer than wide (Figs. 79, 80).
76. Basal margin of S6, between apodemes: 0 = convex or straight (Figs. 78–80); 1 = broadly or deeply concave (Figs. 75–77).
77. Median longitudinal weakly sclerotized area on S6: 0 = absent; 1 = present (Figs. 79, 80).
78. Apex of S6: 0 = short, pointed or broadly rounded (Figs. 75–78); 1 = long, acutely pointed (Figs. 79, 80).
79. Subapical margin of S6: 0 = straight or unmodified; 1 = with a sublateral tooth or angle (Fig. 79).
80. Sting apparatus: 0 = laterally compressed, T7 and T8 hemitergites, and second valvifers vertically oriented; 1 = dorso-ventrally compressed, T7 and T8 hemitergites, and second valvifers horizontally oriented (Fig. 81).
81. Pubescence of apex of sting gonostylus: 0 = nearly hairless to sparsely covered by short hairs (≤ maximum gonostylus width in lateral view, Fig. 84); 1 = densely covered by long plumose hairs (≥ 1.2x gonostylar width, Fig. 83).
82. Medial and lateral portions of marginal ridge of T7 hemitergite: 0 = converging or diverging apically; 1 = parallel to each other or nearly so.

83. Lamina spiracularis of T7 hemitergite: 0 = smooth and shiny, not sculptured; 1 = weakly to markedly sculptured (Fig. 82).

84. T7 hemitergite with a strong protrusion on the lamina spiracularis, near base of lateral process: 0 = absent or reduced (Figs. 85, 86); 1 = present (Figs. 87, 88).

85. Spiracle of T7 hemitergite: 0 = located on the basal two thirds of hemitergite length (Fig. 81); 1 = located at or near apical third of hemitergite length (Figs. 85, 87).

Male

Head

86. Inferior process of mandible: 0 = reduced or absent (Fig. 93); 1 = present (Fig. 91, 94–96).

Mesosoma

87. Front coxal spine: 0 = absent; 1 = present (Figs. 99, 100).

88. Front tarsi: 0 = unmodified; 1 = modified, distinctively enlarged, excavated, inner surface with dark sports (Figs. 101, 102).

89. Arolia: 0 = absent or reduced; 1 = present (as in Fig. 62).

Metasoma

90. T5 with one or two sublateral hooks: 0 = absent; 1 = present.

91. T6 with transverse preapical carina: 0 = absent; 1 = present.

92. Sublateral spines on apical margin of T6: 0 = absent; 1 = present.

93. T7: 0 = exposed, posteriorly directed; 1 = hidden, and/or anteriorly or ventrally directed.

94. Pygidial plate: 0 = present; 1 = absent.

95. Number of fully exposed metasomal sterna: 0 = three; 1= four; 2 = five or six.

96. S3 with a median hairless, polished area: 0 = absent; 1 = present (only in *Trichoturgus*).

97. Sclerotization of S7: 0 = entirely well-sclerotized, usually pilose (Fig. 132); 1 = weakly sclerotized medially, thus forming two separated, sclerotized sclerites (Fig. 131); 2 = weakly sclerotized, membranous, frequently hairless.

98. Shape of S8: 0 = elongated, triangular, not square-shaped (Figs. 133–139); 1 = square-shaped (Fig. 140).

99. Spiculum of S8: 0 = broadly rounded or V-shaped (Fig. 134); 1 = long, pointed, rectangular (Fig. 133); 2 = absent or reduced.

100. Lateral apodemes of S8: 0 = absent or weakly sclerotized (Fig. 134); 1 = distinct (Figs. 135–140).

101. Apical margin of S8: 0 = concave, thus forming two lobes (Figs. 133, 134, 137, 140); 1 = with a small, midapical lobe (Figs. 135, 138, 139); 2 = straight, rounded, or pointed (Fig. 136).

102. Simple or branched hairs on or near lateral margins of S8: 0 = absent (Figs. 133, 136); 1 = present (Figs. 134, 135).

103. Genital foramen: 0 = anteriorly directed or nearly so (Fig. 141); 1 = ventrally directed (Fig. 142).

104. Gonobase: 0 = present, distinguishable (Figs. 141, 142); 1 = reduced or absent (Fig. 144).

105. Articulation between gonostylus and gonocoxite: 0 = distinct, at least ventrally (Fig. 142); 1 = fused, thus forming an unsegmented appendage or gonoforceps (Fig. 143–152).

106. Volsella: 0 = small, articulated, distinguishable as separated sclerite (Fig. 142); 1 = small, fused to gonocoxite (Figs. 145–152); 2 = long (≥ one-third of gonoforceps length), fused to gonocoxite, broad (Fig. 143); 3 = reduced or absent.

107. Apex of volsella: 0 = rounded or pointed (Figs. 145–152); 1 = clearly differentiated in medial digitus and lateral cuspis (Fig. 142).

108. Gonostylus (in ventral view): 0 = subequal to penis valves (Fig. 142); 1 = longer than penis valves (Fig. 143); 2 = shorter than penis valves (Fig. 149).

109. Apex of gonostylus: 0 = laterally directed (Figs. 149–152); 1 = medially directed (Figs. 142, 143); 2 = posteriorly directed (Fig.141).

110. Apodemes of the penis valve: 0 = not projecting through genital foramen (Figs. 141, 142, 145–152, 156–161); 1 = projecting through genital foramen (Figs. 143, 144, 153, 154).

Appendix II. Character matrix used in cladistic analysis of Megachilinae tribes; (-) = not applicable

	Characters																																																							
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**
Xylocopa varians	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	1	0	0	0	0	0	0	0	4	0	0	2	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1
Pararhophites orobinus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	1	0	1	1	0	0	1	0	1	0	1	4	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Fidelia pallidula	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0	0	1	4	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1
Lithurgus apicalis	1	1	0	1	1	0	1	1	0	1	0	0	0	1	1	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
L. cornutus fuscipennis	1	1	0	1	1	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
L. spiniferus	1	1	0	1	1	0	0	1	0	1	0	0	1	1	1	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Microthurge pharcidontus	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trichoturgus wagenknechti	1	1	0	1	1	0	0	0	0	0	0	0	1	2	0	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	2	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
T. holomelan	1	1	0	1	1	0	0	1	0	1	0	0	1	2	1	2	0	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0	1	1	2	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Osmia californica	0	1	1	1	1	1	1	0	0	1	0	0	0	1	1	2	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	3	0	0	2	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
O. texana	0	1	1	1	1	1	1	0	0	1	0	0	1	1	2	2	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	3	0	0	2	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Chelostoma rapunculi	1	1	1	1	1	1	1	0	0	1	0	1	0	1	0	2	1	1	0	1	0	0	0	0	0	1	1	0	0	1	1	0	2	1	1	1	1	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Hoplitis biscutellae	0	1	1	1	1	1	1	0	0	1	0	0	1	1	1	2	1	0	0	1	0	0	0	0	1	1	1	1	0	1	1	1	2	1	1	1	1	1	3	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0
Ashmeadiella cactorum	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	2	1	1	0	1	0	0	0	0	1	1	1	1	0	1	1	1	2	1	1	1	1	1	2	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0
Hoplosmia bituberculata	1	1	1	1	1	1	1	0	0	1	0	0	1	1	2	2	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	2	1	1	1	1	1	2	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0
Heriades timberlakei	1	1	1	1	1	1	1	0	0	1	0	0	0	1	1	2	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	2	1	1	1	2	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0
Protosmia rubifloris	1	1	1	1	1	1	1	0	0	1	0	0	0	2	2	2	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	2	1	1	1	2	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Anthidiellum perplexum	1	1	0	1	1	1	1	0	0	0	0	2	0	1	2	2	0	1	0	1	0	0	0	0	1	1	2	1	0	1	1	1	2	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0
Anthodioctes willineri	1	1	0	1	1	1	1	0	1	1	0	0	0	1	1	2	0	1	0	1	0	0	0	0	1	1	2	1	0	1	1	0	2	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	0
Aztecanthidium tenochtitlanieum	0	1	1	1	1	0	1	0	1	1	0	1	1	1	0	2	1	1	0	1	0	0	0	0	1	1	2	1	0	1	1	0	2	1	1	1	1	1	2	1	1	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0
Dianthidium sp.	1	1	0	1	1	1	1	0	0	0	0	1	1	1	2	2	1	1	0	1	0	0	0	0	1	1	2	0	0	1	1	1	2	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	0	0	0
Trachusa mitchelli	0	1	1	1	1	1	0	0	0	1	0	0	1	1	1	2	1	1	0	1	0	0	0	0	1	1	2	1	0	1	1	1	2	1	1	1	1	1	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0
Stelis montana	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	2	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	1	1	1	1	1	1	1	0	0	1	2	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0
Anthidium deceptum	1	1	1	1	1	1	1	0	0	0	0	0	0	1	2	2	1	0	0	0	0	1	0	0	1	1	2	1	0	1	1	1	2	0	1	1	1	1	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	0
Afranthidium repetitum	1	1	1	1	1	1	1	0	0	0	0	0	0	1	2	2	1	0	0	0	0	1	0	0	1	1	2	1	0	1	1	1	2	1	1	1	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	0
Pseudoanthidium lituratum	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	0	1	1	2	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0
Serapista denticulata	0	1	1	1	1	1	0	0	0	1	0	0	0	1	2	2	1	0	0	0	0	1	0	0	1	1	2	0	0	1	1	1	2	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0
Dioxys productus subruber	1	1	1	1	1	1	1	0	0	0	0	1	0	1	2	2	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	1	2	1	1	1	0	0	1	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	0
Megachile albitarsis	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	2	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
M. xylocopoides	1	1	1	1	1	1	1	0	0	1	0	0	1	1	2	2	1	0	0	1	0	0	1	0	1	1	2	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
M. rhodura	1	1	1	1	1	1	1	0	0	1	0	0	1	1	2	2	1	1	0	1	0	0	0	0	1	1	2	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
M. georgica	1	1	1	1	1	1	1	0	0	1	0	0	1	1	2	2	1	1	0	1	0	0	0	0	1	1	2	1	0	1	1	0	2	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
M. cognata	1	1	1	1	1	0	1	0	0	1	0	0	1	1	2	2	1	0	0	1	0	0	1	0	1	1	2	1	0	1	1	1	2	1	1	1	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Coelioxys torrida	1	1	1	1	1	1	1	0	0	1	0	2	0	1	2	2	1	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0
C. apicata	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	2	0	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0
C. mexicana	1	1	1	1	1	1	1	0	0	1	1	2	0	1	2	2	0	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0
C. zapoteca	1	1	1	1	1	1	1	0	0	1	1	1	0	1	2	2	0	0	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0
C. texana	1	1	1	1	1	1	1	0	0	1	1	1	0	1	2	2	0	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0
C. assumptionis	1	1	1	1	1	1	1	0	0	1	1	1	0	1	2	2	0	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0
C. spatuliventer	1	1	1	1	1	1	1	0	0	1	1	1	0	1	2	2	0	1	0	0	0	0	0	0	3	1	3	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	1	0	0	0
Radoszkowskiana rufiventris	1	1	1	1	1	1	1	0	0	1	0	0	0	1	2	2	1	1	0	0	0	0	0	0	0	1	2	1	0	1	1	0	2	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0

Appendix II (Continued). Character matrix used in cladistic analysis of Megachilinae tribes; (-) = not applicable

Taxa	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
Xylocopa varians	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	2	0	1	0	0	1	0	0	2	0
Pararhophites orobinus	1	1	0	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	0	1	0	2	0
Fidelia pallidula	1	1	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	0	1	0	0	0	1	1	2	0
Lithurgus apicalis	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0
L. cornutus fuscipennis	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0
L. spiniferus	0	0	1	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0
Microthurge pharcidontus	0	0	1	1	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	2	0
Trichoturgus wagenknechti	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	0	0	0	0	1	0	0	2	0
T. holomelan	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	0	0	0	0	1	0	0	2	0
Osmia californica	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	1	0	2	0	0	0	1	0	1	0	0	1	0	1	2	0
O. texana	0	1	1	0	1	0	1	1	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	1	0	2	0	0	0	1	0	1	0	0	1	0	1	2	0
Chelostoma rapunculi	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	2	0	0	0	0	0	1	0	0	1	0	1	1	0
Hoplitis biscutellae	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	2	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0
Ashmeadiella cactorum	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	2	0	0	0	1	0	0	0	1	1	0	1	1	0
Hoplosmia bituberculata	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	2	0	0	0	1	0	1	0	0	1	0	0	1	0
Heriades timberlakei	0	1	1	0	1	0	1	1	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	2	0	0	0	2	0	0	0	1	2	0	1	2	1
Protosmia rubifloris	0	1	1	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	2	0	0	0	1	0	1	0	1	2	0	1	2	0
Anthidiellum perplexum	0	1	1	1	1	0	1	0	1	1	0	1	1	0	2	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	1	1	3	-	0	0	1
Anthodioctes willineri	0	1	1	1	1	0	1	1	1	1	0	1	1	0	2	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	2	0	0	0	1	0	0	0	0	1	1	3	-	2	2	1
Aztecanthidium tenochtitlanieum	0	1	1	1	1	0	1	1	1	1	1	1	1	0	2	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	1	1	2	0	0	0	1	0	0	0	0	1	0	0	0	2	2	1
Dianthidium sp.	0	1	1	1	1	0	1	0	1	1	0	1	1	0	2	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	1	1	2	0	0	0	1	0	0	0	0	1	0	0	0	2	2	1
Trachusa mitchelli	0	1	0	1	0	0	1	0	1	1	0	1	0	0	2	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1	1	0	0	0	1	1	0	0	0	0	0	2
Stelis montana	0	1	0	1	1	0	1	0	1	1	0	2	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1
Anthidium deceptum	0	1	0	1	0	0	1	0	1	1	0	1	1	0	2	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	2	0	1	1	1	0	1	0	0	1	0	1	0	0	0	2
Afranthidium repetitum	0	1	0	1	0	0	1	0	1	1	0	1	1	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2	0	1	1	1	0	2	0	0	1	0	1	0	0	1	1
Pseudoanthidium lituratum	0	1	0	1	0	0	1	0	1	1	0	1	1	0	2	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1	1	0	2	0	1	1	1	1	0	0	1	2
Serapista denticulata	0	1	0	1	0	0	1	1	1	1	1	2	0	0	2	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	2	0	1	0	2	0	2	0	0	1	0	1	0	0	1	2
Dioxys productus subruber	0	1	0	1	0	0	1	1	0	1	0	2	0	0	2	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	2	0	2	0	1	1	1	3	-	0	0	2
Megachile albitarsis	0	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	0	2	0	0	0	2	0	1	1	1	1	0	0	0	2
M. xylocopoides	0	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	2	0	0	0	2	0	1	1	1	1	0	0	0	2
M. rhodura	0	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	2	0	1	0	2	1	0	1	1	0	0	0	2	2
M. georgica	0	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	2	0	0	0	2	1	0	1	1	0	0	0	1	0
M. cognata	0	1	0	0	0	0	1	1	0	0	1	1	0	0	2	1	0	0	1	0	0	0	0	1	1	0	0	1	1	1	0	0	0	1	1	1	1	2	0	2	0	1	0	0	0	0	0	1	1	0	0	0	0
Coelioxys torrida	0	1	0	0	0	0	1	0	0	0	1	2	0	0	2	1	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	1	2	0	2	0	1	0	2	0	0	1	1	1	0	0	1	2
C. apicata	0	1	0	0	0	0	1	0	0	0	1	2	0	0	2	1	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	2	0	2	0	0	0	2	1	0	0	1	0	0	0	0	2
C. mexicana	0	1	0	0	0	0	1	1	0	0	0	2	0	0	2	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	2	0	2	0	0	0	2	1	0	1	1	1	0	0	0	2
C. zapoteca	0	1	0	0	0	0	1	0	0	0	0	2	0	0	2	1	0	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	2	0	2	0	0	0	2	1	0	1	1	1	0	0	0	2
C. texana	0	1	0	0	0	0	1	0	0	0	0	2	0	0	2	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	2	0	2	0	1	0	2	1	1	0	1	1	0	0	0	2
C. assumptionis	0	1	0	0	0	0	1	0	0	0	0	2	0	0	2	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	2	0	2	0	0	0	2	1	0	1	1	1	0	0	0	2
C. spatuliventer	0	1	0	0	0	0	1	1	0	0	0	2	0	0	2	1	0	1	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	2	0	2	0	0	0	2	1	0	1	1	1	0	0	0	2
Radoszkowskiana rufiventris	0	1	0	0	0	0	1	1	0	0	1	2	0	0	2	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	0	2	0	0	0	2	1	1	0	1	1	0	0	0	2

APPENDIX III

Characters used in the phylogenetic analysis of *Megachile* s. l. subgenera. As noted in Material and Methods, some characters are essentially the same as those listed in Appendix I. Character-state zero is not necessarily plesiomorphic.

Females

Head

1. Compound eyes: 0 = slightly converging ventrally, parallel or nearly so; 1 = strongly diverging ventrally.
2. Clypeoantennal distance: 0 = short (equal to or shorter than vertical diameter of antennal socket, Figs. 2, 4); 1 = long (≥ 1.2x antennal socket, Figs. 3, 5).
3. Anterior tentorial pit: 0 = located at the intersection of subantennal and epistomal sutures; 1 = located on epistomal suture, below intersection with subantennal suture.
4. Shape of anterior tentorial pit: 0 = rounded, about as long as broad; 1 = elongated, about twice as long as broad.
5. Interantennal distance: 0 = equal or shorter than antennocular distance; 1 = greater than antennocular distance.
6. Antennal scape length, excluding basal bulb: 0 = short (equal to or shorter than alveolocellar distance, Figs. 2, 3); 1 = long (≥ 1.2x alveolocellar distance, Fig. 4).
7. Length of pedicel: 0 = short, about as long as F1; 1 = long, about as long as or longer than length of F1 and F2 combined.
8. Length of F1: 0 = 1.5–2x longer than F2; 1 = about as long as F2; 2 = shorter than F2.
9. Vertex in frontal view: 0 = convex; 1 = flat or nearly so.
10. Vertex with a fine, shining longitudinal line from ocelli to posterior margin of vertex: 0 = absent; 1 = present.
11. Preoccipital carina: 0 = absent; 1 = continuous, present on gena and dorsal edge of head behind vertex; 2 = discontinuous, present on gena only.
12. Occipital distance: 0 = short (1–3 OD); 1 = long (≥ 3.1 OD).
13. Hypostomal area, near mandible: 0 = flat, or if depressed, not enclosed by short transverse carina; 1 = depressed and enclosed by short transverse carina. Character state 1 is only present in the female of *Megachile* subgenus *Melanosarus*.

14. Hypostomal carina: 0 = unmodified, gently curving from base of mandible (ventral portion) to behind head (posterior portion); 1 = modified, with a tooth or strong protuberance where the ventral portion flexes upwards behind head.
15. Ventral portion of hypostomal carina, near mandible: 0 = directed to medial margin of mandibular socket; 1 = curving towards posterior margin of mandibular socket.
16. Lower part of supraclypeal area: 0 = flat, elevated or modified, not strongly convex in profile; 1 = strongly convex in profile.
17. Clypeus length: 0 = short (≥ 3x wider than long); 1 = long (≤ 2.8x wider than long).
18. Base of clypeus: 0 = flat or convex, not greatly elevated or ornate; 1 = greatly elevated and ornate.
19. Disc of clypeus: 0 = flat or convex, not elevated; 1 = elevated with flat median section.
20. Distal margin of clypeus: 0 = not overhanging labrum, labroclypeal articulation clearly visible; 1 = slightly overhanging labrum, labroclypeal articulation not visible; 2 = strongly produced over base of labrum, clypeus then appearing hexagonal in shape as in *Megachile* subgenus *Chalicodoma*. The clypeus of *M. assumptionis* has a bifid median process strongly produced over labrum (Fig. 5); however, the apicolateral margins of the clypeus slightly cover the base of labrum; thus, I coded this species as having character state 1.
21. Complete longitudinal median clypeal carina: 0 = absent; 1 = present.
22. Pubescence of clypeus: 0 = sparse throughout, integument visible among hairs; 1 = dense throughout, integument not visible among hairs; 2 = dense on sides of clypeus, sparse to absent on disc.
23. Disc of clypeus with abundant, erect, short and partially hooked or wavy hairs: 0 = absent; 1 = present.
24. Shape of labrum: 0 = rectangular, base as wide as apex, lateral margins parallel to each other (Fig. 11); 1 = subtriangular, base ≥ 1.5x apical width, lateral margins converging apically (Fig. 12).
25. Pubescence of disc of labrum: 0 = absent; 1 = consisting only of long (≥ 1x OD), erect hairs; 2 = consisting of two types of hairs, minute, yellowish, appressed hairs, and long (≥ 1 OD), erect hairs; 3 = consisting only of minute, yellowish, appressed hairs.

26. Apex of labrum: 0 = unmodified, without midapical or subapical protuberance; 1 = with a midapical or subapical protuberance.
27. Mandible length: 0 = short (≤ 0.7x eye length in lateral view, Fig. 4); 1 = long (≥ 0.9x eye length, Fig. 7).
28. Apex of mandible: 0 = narrow, equal to or narrower than base in lateral view (Fig. 17); 1 = broad (≥ 1.5x basal width, Figs. 15, 20).
29. Integument of mandibular apex (outer surface): 0 = smooth and shiny, or nearly so, between punctures; 1 = microreticulate to finely punctuate.
30. Pubescence on apex of outer mandibular groove: 0 = absent or apex of groove sparsely covered with long or short hairs, integument clearly visible; 1= dense, covered with very short, golden hairs, integument not visible; 2 = with a distinct tuft or brush of long golden hairs.
31. Mandible with outer premarginal fimbria: 0 = reduced or absent; 1 = present (Fig. 15).
32. Acetabular interspace of mandible: 0 = not conspicuously flattened or depressed, gently curving towards base of mandible; 1 = clearly flattened or depressed, such as outer surface of mandible with a distinguishable basal, lateral surface, and a distal, anterior surface.
33. Number of mandibular teeth: 0 = two; 1 = three (Fig. 23); 2 = four to six (Figs. 25–36); 3 = lower distal margin with one or two large teeth, upper portion edentate or nearly so, or with very small teeth (Fig. 16). The upper distal margin is incised in some species, resulting in a 5 or 6-toothed mandible, with upper teeth closer than other teeth.
34. Distal margin of mandible: 0 = straight or nearly so, not strongly oblique (Fig. 20); 1 = strongly oblique as in *Megachile* subgenus *Chalicodoma* (Fig. 16).
35. First mandibular tooth: 0 = subequal or narrower, at base, than second (Figs. 25, 29); 1 = ≥ 1.5x wider, at base, than second (Figs. 20, 23, 35).
36. Mandible with cutting edge in second interspace: 0 = absent (Figs. 15–17); 1 = present, incomplete (Figs. 25–27); 2 = present, complete (Figs. 33, 35).
37. Mandible with cutting edge in third interspace: 0 = absent (Figs. 16, 17); 1 = present, incomplete (Fig. 25); 2 = present, complete (Figs. 29, 31, 35).

38. Cutting edge on second mandibular interspace: 0 = not fused with third tooth or absent; 1 = fused with third tooth, thus resulting in a broad, thin tooth with a more or less truncate margin (Figs. 29, 30).
39. Origin of cutting edge on second mandibular interspace: 0 = not arising from inferior border of third tooth (Figs. 33, 35); 1 = arising from inferior border of third tooth (Figs. 25–28, 31, 32). There is a very small projection (not visible in frontal view) from the inferior border of the third tooth in the mandible of *Megachile* subgenera *Schrottkyapis* and *Stelodides* that suggest an incomplete cutting edge; however, I coded them as having character state 0.
40. Origin of cutting edge on third mandibular interspace: 0 = not arising from inferior border of fourth tooth (Figs. 29–32); 1 = arising from inferior border of fourth tooth (Figs. 25, 26). In addition to a complete cutting edge, there seems to be a small incomplete cutting edge, arising from the fourth tooth, in the mandible of *M*. (*Paracella*) *semivenusta*; thus, I coded this species as having both character states.
41. Third mandibular interspace: 0 = absent or short (≤ 1.5x the combined length of first and second interspaces; 1 = long, about 2x the combined length of first and second interspaces.
42. Upper distal margin of mandible: 0 = rounded or pointed with apex anteriorly directed; 1 = pointed, subtriangular, and with apex dorsally directed.
43. Upper margin of mandible, just near distal margin: 0 = unmodified, without a tooth; 1 = modified, with a large or small tooth.
44. Upper margin, near mandibular base: 0 = unmodified, without a tooth; 1 = modified, with an acute tooth.
45. Inner fimbriate line of mandible (FL): 0 = absent or reduced; 1 = present (Fig. 20).
46. Abductor ridge, near the base of mandible: 0 = strong; 1 = low or weakly indicated.
47. Hairs on adductor interspace of mandible: 0 = absent (Fig. 21); 1 = present, short (≤ 0.2 OD); 2 = present, long (≥ 0.4 DO, Fig. 22).
48. Adductor interspace with a longitudinal, median impressed line marked with a series of hairs along its lower margin: 0 = absent; 1 = present.
49. Adductor interspace with a longitudinal, median ridge: 0 = absent; 1 = present.

50. Condylar interspace: 0 = mostly horizontal (*i.e.,* facing ventrally) when mandibles are open; 1 = oblique or vertical (*i.e.*, facing medially or nearly so), when mandibles are open.
51. Proboscis length (in repose): 0 = short, not reaching metasoma; 1 = long, reaching metasoma.
52. Distal end of mentum: 0 = entire (Figs. 38, 39, 42); 1 = concave or notched (Figs. 41, 44); 2 = not sclerotized (Fig. 43).
53. Subligular process of prementum: 0 = elongated, long and narrow, styliform (Fig. 45); 1 = broad, apex truncated (Fig. 47); 2 = broad and with pointed apex (Figs. 38, 46).
54. First labial palpomere: 0 = short, ≤ 0.5x second segment (Fig. 50); 1 = long, ≥ 0.8x second segment (Figs. 38, 39, 51).
55. First labial palpomere length/width: 0 = ≤ 3.5x; 1 = ≥ 4 x.
56. First labial palpomere with a brush of hairs on midbasal concavity: 0 = absent; 1 = present (Fig. 50).
57. Third labial palpomere: 0 = apically directed as is second (Fig. 50); 1 = laterally directed from second (Figs. 38, 39, 51, 52).
58. Dististipital process of stipes: 0 = absent or reduced; 1 = elongated, almost joining stipital sclerite (Fig. 40).
59. Glossa: 0 = not broadened or ligulate (Figs. 38, 39); 1 = broadened or ligulate (Fig. 52).
60. Number of maxillary palpal segments, including basal segment: 0 = two or three; 1 = four or five.
61. Hairs of maxillary palpi: 0 = short, ≤ 2x palpomere diameter (Figs. 37, 40); 1 = long, ≥ 2.1x palpomere diameter (Fig. 53).
62. Length of second maxillary palpomere: 0 = short, ≤ 1.6x longer than broad; 1 = long, ≥ 2x longer than broad.
63. Length of third maxillary palpomere: 0 = short, ≤ 2.6x longer than broad; 1 = long, ≥ 3x longer than broad.
64. Apex of lacinia: 0 = rounded (Figs. 54, 56); 1 = acutely pointed (Figs. 37, 40).
65. Apex of lacinia with a hair distinctly longer and thicker hair than hairs on the medial margin: 0 = absent; 1 = present (Fig. 53).

66. Hairs on the anterobasal surface of stipes: 0 = short, ≤ 2x maximum stipital width in lateral view (Figs. 37, 40); 1 = long, ≥ 2.1x stipital width (Figs. 55, 56).
67. Stipes with posterolateral border with a row of long hairs, as long as or longer than half of stipital width in lateral view: 0 = absent; 1 = present (Fig. 53).
68. Paramandibular process: 0 = short or absent (Fig. 9); 1 = long (Fig. 8).
69. Paramandibular carina: 0 = short, ending about half distance between paramandibular process and hypostomal carina; 1 = long, ending at the hypostomal carina; 2 = long, ending right before the hypostomal carina, and usually curving upwards or downwards; 3 = long, forming a strong lobe with the posterior component of the hypostomal carina.

Mesosoma

70. Pronotal lobe: 0 = rounded, without carina or strong lamella; 1 = with strong carina or border; 2 = with conspicuously broad, thin lamella (Fig. 57).
71. Omaulus: 0 = rounded; 1 = weakly angular to carinate.
72. Punctuation of mesepisternum: 0 = finely or coarsely punctuate, not forming strong rows with distinct shining ridges among them; 1 = coarsely punctuate, forming strong rows with distinct shining ridges among them.
73. Anterior margin of mesoscutum in profile: 0 = rounded; 1 = truncate, perpendicular, or nearly so, shinier and less punctuate than dorsal portion.
74. Disc of mesoscutum in profile: 0 = convex; 1 = flat or nearly so.
75. Pubescence of disc of mesoscutum: 0 = consisting only of long hairs (≥ 3–4x OD), integument barely visible; 1 = consisting only of very short hairs (≤ 0.5x OD), integument sparsely covered to almost bare; 2 = consisting only of short hairs (1.5–2.0x OD), integument visible or partially obscured among hairs; 3 = consisting of two types of hairs, minute, yellowish, appressed hairs, and erect longer hairs (2x OD); 4 = consisting of semierect or appressed yellowish tomentum uniformly covering the integument.
76. Notalus line with fascia: 0 = absent; 1 = present.
77. Parapsidal line: 0 = long (≥ 0.4x tegula length, in dorsal view); 1 = short (≤ 0.3x tegula length) or absent.
78. Punctation of mesoscutal disc: 0 = finely and closely (≤ 1–2x PW) punctate, punctures (≤ 0.2x OD) not in row; 1 = coarsely and densely punctured, punctures (≥ 0.5x OD)

arranged in rows, thus giving a striate appearance; 2 = coarsely and densely punctured, punctures (≥ 0.5x OD) not arranged in rows.

79. Mesoscutal-mesoscutellar suture with white fascia: 0 = absent; 1 = present.
80. Axilla: 0 = rounded, not posteriorly projected in acute angle or spine; 1 = angulated, short, not reaching posterior transverse tangent of mesoscutellum; 2 = strongly projected in acute angle or spine (Fig. 57).
81. Mesoscutellum: 0 = not triangular or pointed medially on posterior margin; 1 = triangular, pointed medially on posterior margin.
82. Metanotum: 0 = entirely or partially hidden, as seen from above, by mesoscutellum; 1 = fully exposed, not hidden by mesoscutellum.
83. Hairs on propodeal triangle: 0 = present; 1 = absent.
84. Propodeal profile: 0 = largely vertical; 1 = entirely slanting or with slanting dorsal portion rounding onto vertical portion.
85. Color of legs: 0 = dark brown to black like other areas of mesosoma; 1 = reddish or orange contrasting with the dark brown to black mesosoma.
86. Apex of fore tibia with one to three long, acute spines on outer surface: 0 = absent; 1 = present (Fig. 58).
87. Basitibial plate: 0 = absent; 1 = present.
88. Hind tibial spurs: 0 = pointed, straight or gently curving apically (Fig. 59); 1 = pointed, straight with apex strongly curved inward; 2 = not pointed, parallel-sided and with apex blunt (Fig. 61).
89. Length of hind basitarsus: 0 = short, ≤ 0.5x tibial length; 1 = long, ≥ 0.8x tibial length.
90. Hind basitarsus length/width: 0 = narrow, ≥ 3x; 1 = broad, ≤ 2.8x.
91. Strong tubercles or spicules on outer surface of tibiae: 0 = absent; 1 = present.
92. Pretarsal claws: 0 = simple, without basal projection (Fig. 62); 1 = simple, with one or two basal projections (Figs. 65, 66); 2 = bifurcate (Fig. 63).
93. Hairs on pretarsal claws: 0 = about the same thickness (Fig. 62, 65, 66); 1 = one of the hairs conspicuously shorter and stouter than the other (Fig. 64).
94. Arolia: 0 = reduced or absent on all legs; 1 = present on at least front legs (Fig. 62).
95. Length of second submarginal cell: 0 = equal or longer than first on posterior margin; 1 = shorter than first on posterior margin.

96. Vein 2m-cu of fore wing: 0 = basal to 2nd submarginal crossvein; 1 = confluent with or distal to 2nd submarginal crossvein.

97. Stigma: 0 = long (≥ 2.1x longer than broad); 1 = short (≤ 2x longer than broad).

98. Fore wing coloration: 0 = entirely hyaline, yellowish, or dusky; 1 = apical half dusky, contrasting with hyaline or yellowish basal half; 2 = yellowish wing base with dusky costal margin.

99. Hind wing with second abscissa of vein M+Cu: 0 = short, ≤ 3.0x length of vein cu-v; 1 = long, ≥ 3.1x length of vein cu-v.

100. Jugal lobe of hind wing: 0 = ≤ 0.5x vanal lobe length; 1 = ≥ 0.6x vanal lobe length

Metasoma

101. Metasoma shape: 0 = strongly convex dorsally, more or less parallel sided as in *Megachile* subgenera *Chalicodoma* and *Chalicodomoides* (Fig. 1); 1 = not parallel-sided, cordate, triangular, and rather flattened as in Megachile subgenus *Megachile* (Fig. 1); 2 = as in *Coelioxys* (Fig. 1).

102. T1: 0 = small, flattened in profile with posterior margin rounded, and without distinct anterior and dorsal surfaces (Fig. 69); 1 = long, convex in profile with posterior margin straight, and distinct anterior and dorsal surfaces (Fig. 74).

103. Pubescence of T1: 0 = about the same length, density, and color as on other terga; 1 = not of the same color, and distinctly longer (2–3x) and denser than on remaining terga.

104. Length of dorsal part of T1/T2 (measured at midline): 0 = ≥ 0.7; 1 = ≤ 0.6.

105. T2 and T3 with deep postgradular groove: 0 = absent; 1 = present, medially interrupted, clearly visible only laterally; 2 = present, complete, clearly evident at midline.

106. T2 and T3 with fasciate marginal zones: 0 = absent; 1 = present.

107. T3 and T4 with well marked premarginal line: 0 = absent; 1 = present.

108. Pygidial plate: 0 = present; 1 = absent.

109. Pubescence of T5: 0 = black, pale or yellowish, as on preceding terga; 1 = orange, yellowish, or pale as on T6, contrasting with that of T1–T4.

110. T6 with short (≤ OD), appressed hairs: 0 = absent; 1 = present.

111. Dorsum of T6 in profile: 0 = straight or slightly concave (Fig. 71); 1 = strongly convex, without preapical notch (Fig. 72); 2 = strongly convex, with preapical notch (Fig. 73).

112. T6 with erect hairs on disc: 0 = present; 1 = absent.

113. T6 with clubbed hairs on disc: 0 = absent; 1= present.

114. Sternal scopa: 0 = present; 1 = absent.

115. S1 with midapical tooth or spine: 0 = absent; 1 = present (Fig. 74).

116. Apical white fasciae under scopal hairs of S2 and S3: 0 = absent; 1 = present, medially interrupted, thus restricted to the sides; 2 = present, complete.

117. Length of S6: 0 = short (Figs. 75–78), as long as wide or shorter (length measured along midline); 1 = elongated, ≥ 2x longer than wide (Figs. 79, 80).

118. Shape of S6: 0 = subtriangular or broad basally, not parallel-sided (Figs. 75–78); 1 = somewhat parallel-sided, not subtriangular or broad basally (Figs. 79, 80).

119. Apodemes of S6: 0 = present, large (Figs. 75, 78); 1 = reduced or absent (Figs. 76, 77).

120. Anterior margin of S6, between apodemes: 0 = with a shallow, not U or V-shaped concavity; 1 = with deep U or V-shaped concavity.

121. Anterior margin of S6 with a very deep and narrow medial furrow: 0 = absent; 1 = present (Fig. 75).

122. Superior lateral margin of S6, just below apodemes, with a strong border or carina: 0 = absent; 1 = present.

123. Lateral surface of S6, near lateral ridge, with a strong recurved border or carina: 0 = absent; 1 = present.

124. Pregradular area of S6, parallel to lateral margin, with a deep invagination: 0 = absent; 1 = present.

125. Sclerotization of pregradular area of S6: 0 = well sclerotized or nearly so; 1 = entirely membranous or weakly sclerotized; 2 = membranous or weakly sclerotized only medially (Figs. 79, 80).

126. Apex of S6: 0 = truncate or broadly rounded (Figs. 75–77); 1 = V-shaped, pointed (as in Fig. 78).

127. Distal margin of S6: 0= simple, not bilobed; 1 = bilobed (Fig. 76).

128. Pilose area of S6: 0 = restricted to the apical fourth or less of sternal length, as measured from base of apodemes to apex of sternum (Fig. 77); 1 = covering about one-third of sternal length (Fig. 75); 2 = large, covering half or more of sternal length (Fig. 78).

129. Pilose area of S6: 0 = uniformly covered with hairs or nearly so (Figs. 76–78); 1 = bare or nearly so (Fig. 75). The S6 of *Coelioxys apicata* is densely covered with very short, appressed pubescence; I coded it as having character state 0.

130. S6 with a strong preapical border or carina: 0 = absent; 1 = present.

131. S6 with a fringe of branched hairs on or near apical margin: 0 = absent; 1 = present (Fig. 75).

132. S6 with smooth, bare rim behind apical fringe of branched hairs: 0 = absent (Figs. 76–80); 1 = present, thin and translucent (Fig. 75); 2 = present, thick, rolled or abruptly bent dorsally.

133. Sting apparatus: 0 = laterally compressed, T7 and T8 hemitergites, and second valvifers vertically oriented; 1 = dorso-ventrally compressed, T7 and T8 hemitergites, and second valvifers horizontally oriented (Fig. 81).

134. Pubescence of apex of sting gonostylus: 0 = nearly hairless to sparsely covered by short hairs (≤ maximum gonostylar width as seen in lateral view, Fig. 84); 1 = densely covered by long plumose hairs (≥ 1.2x gonostylar width, Fig. 83).

135. Lamina spiracularis of T7 hemitergite: 0 = smooth and shiny, not sculptured; 1 = weakly to markedly sculptured (Fig. 82).

136. T7 hemitergite with a strong protrusion on the lamina spiracularis, near base of lateral process: 0 = absent or reduced (Figs. 85, 86); 1 = present (Figs. 87, 88).

Males

Head

137. Pubescence of clypeus: 0 = sparse throughout, integument visible among hairs; 1 = dense throughout, integument not visible among hairs; 2 = basal half with sparse hairs (integument visible) or mostly bare, distal half densely covered by hairs (integument not visible).

138. Coloration of clypeus: 0 = dark brown to black; 1 = yellow.

139. Length of F1: 0 = 1.5x–2x longer than F2; 1 = about as long as F2; 2 = shorter than F2.

140. F5–F10: 0 = cylindrical, flattened, or crenulate; 1 = deeply concave on one side (Fig. 89).

141. F11 compressed or flattened: 0 = absent; 1 = present (Fig. 90).

142. Hypostomal area: 0 = unmodified; 1 = slightly depressed; 2 = strongly concave (Fig. 91).

143. Gena: 0 = unmodified, without a distinct carina or patch of hairs; 1 = modified, with an oblique, low, smooth, and shiny carina bordered with a dense row of white branched hairs (Fig. 92).

144. Mandibular teeth: 0 = two; 1 = three; 2 = four; 3 = distal margin of mandible with basal two-thirds edentate or nearly so, at most, one or two very small teeth as in *Megachile* subgenus *Chalicodoma*.

145. Upper distal margin of mandible: 0 = rounded or pointed, about the same length and width like remaining teeth; 1 = with a large triangular tooth, conspicuously broader and longer than remaining teeth.

146. Inferior border of mandible: 0 = unmodified (Fig. 93); 1 = with a broad, subtriangular, posteriorly-directed process on basal third (Fig. 91); 2 = with a slender, posteriorly-directed process (Figs. 94, 95); 3 = with a broad, small or large, anteriorly-directed process on basal two-thirds (Fig. 96); 4 = with a very dense brush of stiff branched hairs (Figs. 97, 98).

147. Inner surface of mandible: 0 = weakly concave; 1 = strongly concave.

Mesosoma

148. Front coxal spine: 0 = absent; 1 = small (≤ 1.5x OD), pointed or somewhat parallel-sided (Fig. 99); 2 = long (≥ 2x OD), not parallel-sided (Fig. 100); 3 = long (≥ 2x OD), tapering apically, parallel-sided or nearly so.

149. Pubescence on ventral surface of front coxal spine: 0 = very sparse to nearly hairless, integument clearly visible; 1 = densely covered with branched hairs, integument barely visible among hairs.

150. Disc of front coxa: 0 = uniformly covered with branched hairs, integument barely visible among hairs; 1 = hairless or nearly so, integument clearly visible.

151. Front coxa with a tuft of stiff ferruginous hairs: 0 = absent; 1 = present.

152. Front trochanter: 0 = unmodified, without spine or tooth; 1 = modified, with an apical spine or tooth.

153. Front femur: 0 = unmodified, not strongly compressed, same color of femora of remaining legs; 1 = modified, antero-posteriorly strongly compressed, bright yellow or pale, contrasting with color of femora of remaining legs.

154. Front tibia: 0 = unmodified, not enlarged or swollen, ≥ 3x longer than broad; 1 = modified, distinctively swollen, enlarged, ≤ 2.8x longer than broad.

155. Fore tarsi: 0 = unmodified, not enlarged or excavated, without conspicuous dark spots on inner surface; 1 = little modified, slightly excavated, with dark spots on inner surface, usually of the same color of tarsi of remaining legs; 2 = strongly modified, distinctively enlarged or excavated, inner surface with dark spots, bright yellow or pale, contrasting with tarsi of remaining legs (Figs. 101, 102).

156. Shape of front first tarsomere: 0 = unmodified or modified, without concave, long, distally directed lobe; 1 = strongly concave, with long distally directed lobe.

157. Small tooth or protuberance on inner surface of mid coxa: 0 = absent, 1 = present (Fig. 103).

158. Tooth or protuberance on inner surface of mid tibia: 0 = absent, 1 = present (Fig. 103).

159. Mid tibial spur: 0 = present; 1 = fused to tibia; 2 = absent.

160. Mid basitarsus length: 0 = long, ≥ 2.5x longer than broad; 1 = short, ≤ 2x longer than broad (Fig. 104).

161. Inner hind tibial spur: 0 = present; 1= absent.

162. Hind basitarsus length: 0 = long, ≥ 2.3x longer than broad; 1 = short, ≤ 2x longer than broad (Fig. 105).

163. Arolia: 0 = present (Fig. 62) on at least front legs; 1 = reduced or absent on all legs.

Metasoma

164. Transverse preapical carina of T6: 0 = absent; 1 = strong, medially emarginate, not toothed or denticulate (Figs. 106, 107); 2 = strong, entire or nearly so (Fig. 108); 3 = strong, toothed or denticulate, with or without a median emargination (Fig. 109); 4 = weak, little projected in profile, entire or nearly so (Fig. 111).

165. T6 with preapical carina divided in two or more dorsal processes, and a pair of ventral processes: 0 = absent; 1 = present.

166. T6, above preapical carina, with strong longitudinal median ridge or protuberance: 0 = absent (Fig. 111); 1 = present (Fig. 110).

167. T6, above preapical carina, with distinct median concavity: 0 = absent; 1 = present.

168. Region of preapical carina of T6: 0 = not swollen or bulbous; 1 = swollen or bulbous, except medially.

169. Dorsal surface of T6: 0 = densely covered (integument not visible) by long (2–3x OD) hairs; 1 = bare or sparsely covered (integument visible) by long (2–3x OD) or short (≤ OD) hairs; 2 = densely covered by short (≤ OD), appressed branched hairs.

170. Apical margin of T6 with lateral spine or tooth: 0 = absent (Fig. 108); 1 = present (Figs. 106, 109).

171. Apical margin of T6 with submedian spine or tooth: 0 = absent (Fig. 108); 1 = present (Fig. 106).

172. Lateral spine or tooth of apical margin of T6: 0 = large; 1 = small (Fig. 106).

173. Submedian spine or tooth of apical margin of T6: 0 = about the same size as lateral spine or tooth; 1 = conspicuously longer and broader than lateral spine or tooth (Fig. 106).

174. T7: 0 = exposed, posteriorly directed; 1 = hidden, and/or anteriorly or ventrally directed.

175. Gradulus of T7: 0 = without carina or weakly carinate; 1 = strongly carinate (Fig. 114).

176. Transverse carina of T7: 0 = rounded, truncate, or emarginate (Fig. 112); 1 = with a long, acute spinous process (Fig. 113); 2 = angular (Fig. 114).

177. T7 with a strong longitudinal median ridge: 0 = absent; 1 = present.

178. Apical margin of T7: 0 = straight or nearly so, not emarginate or strongly projecting; 1 = with a small median tooth; 2 = deeply and broadly emarginate, forming two prominent teeth; 3 = with midapical, rectangular, sharply angulate projection; 4 = with midapical, rectangular, not sharply angulate projection.

179. Pygidial plate: 0 = present (Fig. 115); 1 = absent.

180. Number of fully exposed metasomal sterna: 0 = three; 1 = four; 2 = five or six.

181. S1 with midapical spine: 0 = absent; 1 = present (as in Fig. 74).

182. S5 length: 0 = ≤ 2x wider than long (Fig. 116); 1 = ≥ 2.1x wider than long (Fig. 121).

183. Gradulus of S5: 0 = strongly sclerotized, indicated by a well-defined transverse line or border (Fig. 119); 1 = weakly sclerotized, barely distinguishable (Fig. 120).

184. Pilose, sclerotized lateral plate on each side of postgradular area of S5: 0 = absent (Fig. 116); 1 = present (Figs.118, 119).

185. Apical margin of S5: 0 = straight or nearly so (Fig. 120); 1 = deeply or shallowly concave (Figs. 117, 118).

186. Short, well-sclerotized midapical process of S5: 0 = absent (Fig. 120); 1 = present (Fig. 121).

187. Pilose postgradular area of S5: 0 = large, maximum width ≥ 0.6x sternal width (Fig. 118); 1 = small, ≤ 0.5x sternal width (Fig. 120).

188. Hairs on postgradular disc of S5: 0 = simple, branched or plumose (as in Fig. 122); 1 = lanceolate, ovate-acuminate (Figs. 123, 124); 2 = capitate or spatulate (Figs. 126, 127); 3 = fan-shaped (Figs. 125).

189. Broad, hairless, and weakly sclerotized area above pubescence of postgradular area of S5: 0 = absent (Fig. 116); 1 = present (Fig. 117).

190. Apicolateral margin of S5: 0 = hairless or with short hairs, similar in length to those on postgradular area (Figs. 119–121); 1 = with simple or branched long hairs, 2–3x longer than those on postgradular area (Fig. 118).

191. Dense tuft of stiff, thickened, simple hairs on midapical margin of S5: 0 = absent (Fig. 120); 1 = present (Fig. 119).

192. Length of S6: 0 = short, ≤ 2x wider than long (Fig. 128); 1 = long, ≥ 2.1x wider than long (Figs. 129, 130). Because the midapical margin of S6 is highly variable, I measured the length of S6 on its lateral margin, from the base of the apodeme to apical margin of the sternum.

193. Sclerotization of S6: 0 = well-sclerotized; 1 = weakly sclerotized to membranous.

194. Hairs of postgradular area of S6: 0 = absent or very sparse (integument clearly visible among hairs) without forming distinct patches (Fig. 130); 1 = forming distinct patches widely separated from each other by at least one patch width (Fig. 129); 2 = hairs forming patches very close from each other, separated by ≤ 0.5x patch width.

195. Hairs on postgradular disc of S6: 0 = unmodified [simple or branched (as in Fig. 122)]; 1 = modified [lanceolate, ovate-acuminate (Figs. 123, 124), capitate, spatulate (Figs. 126, 127), or fan-shaped (Fig. 125)].

196. Sclerotization of S7: 0 = entirely well-sclerotized, usually pilose (Fig. 132); 1 = weakly sclerotized, membranous, frequently hairless.

197. Length of S8: 0 = short, ≤ 2.5x longer than broad (Figs. 134, 140); 1 = long, ≥ 2.6x longer than broad (Fig. 136).

198. Spiculum of S8: 0 = pointed or broadly rounded (Figs. 134, 139); 1 = subrectangular; 2 = as an elongated, narrow process; 3 = as a short process with an expanded apex (Figs. 138, 140).

199. Lateral apodemes of S8: 0 = absent or weakly sclerotized (Fig. 134); 1 = distinct (Figs. 133, 136, 140).

200. S8 with simple or branched hairs on or near lateral margin: 0 = absent (Fig. 136); 1 = present (Figs. 134, 135).

201. Apex of S8: 0 = short, about ¼ of total sternal length (Fig. 134); 1 = long, about half of total sternal length (Fig. 136).

202. S8 with small apex as in *M. semivenusta*: 0 = absent; 1 = present.

203. S8 with subrectangular apex as in Fig. 136: 0 = absent; 1 = present.

204. S8 with apex somewhat expanded as in Fig. 136: 0 = absent; 1 = present.

205. Distal margin of S8: 0 = entire, straight, broadly rounded or pointed (Fig. 136); 1 = entire, with a small midapical projection (Figs. 138, 139); 2 = bilobed (Figs. 133, 134, 140).

206. Genital capsule: 0 = short, about as wide as long (Fig. 141); 1 = elongated, longer than wide (Fig. 145). I measured maximum total length from base of gonobase to apex of penis valves or gonostylus; maximum width was measured at base of gonobase.

207. Genital foramen: 0 = anteriorly directed or nearly so (Fig. 141); 1 = ventrally directed (Fig. 145).

208. Gonobase: 0 = present, distinguishable (Figs. 141, 142); 1 = reduced or absent (Fig. 144).

209. Articulation between gonostylus and gonocoxite: 0 = distinct, at least ventrally (Fig. 142); 1 = fused, thus forming an unsegmented appendage (Figs. 145–152).

210. Gonocoxite length: 0 = equal or longer than gonostylus (Figs. 141, 142); 1 = short, ≤ 0.5x gonostylar length (Figs. 143–154).

211. Dorsal lobe of gonocoxite: 0 = absent (Fig. 145); 1 = present, large, strong, digitiform (Figs. 151, 152); 2 = present, small, acute (Figs. 149, 150).

212. Small sublateral lobe of gonocoxite: 0 = absent (Fig. 145); 1 = present (Figs. 147, 148).

213. Volsella: 0 = fused to gonocoxite (Figs. 141, 143–154); 1 = articulated, distinguishable as a separated sclerite (Fig. 142).

214. Apex of volsella: 0 = rounded or pointed (Fig. 142); 1 = distinctly notched or bilobed, thus suggesting a medial digitus and a lateral cuspis (Figs. 142, 153, 154, 158, 159).

215. Volsella with hairs on distal margin: 0 = absent (Figs. 156, 157, 160, 161); 1 = present (Figs. 153, 154, 158, 159).

216. Length of gonostylus, in ventral view: 0 = subequal to penis valves (Fig. 142); 1 = longer than penis valves (Fig. 143); 2 = shorter than penis valves (Fig. 149).

217. Shape of gonostylus, in lateral view: 0 = curved or arched (Figs. 146, 148, 150, 152, 154, 157, 159); 1 = straight or nearly so (Fig. 161).

218. Width of gonostylus, in lateral view: 0 = not conspicuously narrow, widest at midlength or at apex (Fig. 146); 1 = very narrow, about the same width across its entire length (Fig. 157).

219. Shape of gonostylus, in cross section: 0 = not flattened; 1 = flattened.

220. Orientation of apex of gonostylus, in dorsal view: 0 = laterally directed (Figs. 149–152); 1 = medially directed (Figs. 142, 143); 2 = posteriorly directed (Fig. 141).

221. Apex of gonostylus: 0 = not expanded; 1 = clearly expanded.

222. Apical lobes of gonostylus: 0 = absent; 1 = present, one lateral and one medial (Figs. 145, 147, 160); 2 = present, one dorsal and one ventral. The gonostylus of *M. lagopoda* has three apical lobes; one on each medial, ventral, and dorsal surfaces. I coded this species as having character states 1 and 2.

223. Medial apical lobe of gonostylus: 0 = small, barely indicated (Fig. 147); 1 = large and conspicuous (Figs. 145, 160).

224. Apex of gonostylus with large, deep concavity between dorsal and medial lobes: 0 = absent; 1 = present (Figs. 145, 160).

225. Hairs on medial surface of gonostylus: 0 = absent (Fig. 145); 1 = present, short, ≤ 2x maximum apical gonostylar width (Fig. 149); 2 = present, long, ≥ 2.1x apical gonostylar width (Fig. 158).

226. Apodemes of the penis: 0 = not projecting through genital foramen (Figs. 141, 142, 145–152, 156–161); 1 = projecting through genital foramen (Figs. 143, 144, 153, 154).

227. Penis valve, in dorsal view: 0 = distinctly curved or arched (Fig. 146); 1 = straight or nearly so (Fig. 145).

228. Medial margin of penis valves: 0 = not enlarged or protuberant; 1 = distinctly expanded basally.

229. Lateral margin of penis valve: 0 = not enlarged or protuberant; 1 = distinctly enlarged or protuberant.

230. Apex of penis valve: 0 = straight or nearly so; 1 = distinctly curved or arched inward.

231. Apex of penis valve with row of thick, spine-like hairs: 0 = absent; 1 = present (Fig. 155).

Appendix IV. Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**
Trichoturgus wagenknechti	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0
Dioxys productus subruber	-	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	0	0	1	1	1	1	0	1	0
Trachusa (Ulanthidium) mitchelli	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	2	0	0	1	0	2	0	0	1	1	1	0	1	3	0	1	0	0	0	-	-	0	0	0	0	1	0	1	1	0	0	0	1	2	1	1	0	1	1
Aztecanthidium tenochtitlanieum	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	1	0	1	0	1	2	1	1	0	1	1
Chelostoma rapunculi	0	0	1	1	1	0	1	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	0	0	0	1	0	0	0	1	1
Hoplitis (Dasyosmia) biscutellae	0	0	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	2	0	1	1	0	1	1	1	0	0	1	1
M.(Acentron) albitarsis	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Acentron) candida	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Amegachile) bituberculata	0	1	1	1	1	0	0	1	1	0	2	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	0	2	2	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Callochile) ustulatiformis	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	0	2	2	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Argyropile) parallela	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Argyropile) sabinensis	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Austromegachile) montezuma	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	2	0	0	1	0	0	1	1	1	0	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Holcomegachile) giraffa	0	1	1	1	1	0	0	2	0	0	2	0	0	0	1	0	1	0	1	1	0	2	0	0	1	0	0	1	1	1	0	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Chrysosarus) guaranitica	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Chrysosarus) albopunctata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Dactylomegachile) parsonsiae	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	1	0	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Cressoniella) zapoteca	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	1	1	0	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Dasymegachile)saulcyi	0	1	1	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Chaetochile) mitchelli	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	1	2	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	2	1	1	0	1	1
M. (Eumegachile) bombycina	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	1	0	0	0	0	1	1	1	2	0	0	1	0	0	1	-	0	0	0	0	1	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Eutricharaea) argentata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	2	1	1	0	1	1
M. (Eutricharaea) femorata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Perezia) leachella	0	1	1	1	1	0	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	2	1	1	0	1	1
M. (Eurymella) eurymera	0	1	1	1	1	0	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Eurymella) submetallica	0	1	1	1	1	0	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Digitella) digiticauda	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Platysta) platystoma	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	1	0	1	1	1	0	1	2	1	1	0	1	1
M. (Neoeutricharaea) rotundata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	2	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Grosapis) cockerelli	0	0	1	1	1	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	2	0	0	1	0	0	1	-	0	0	0	0	1	1	2	0	1	1	0	0	2	1	1	0	1	1
M. (Leptorachis) petulans	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	1	0	0	1	1	0	1	2	1	1	0	1	1
M. (Leptorachina) laeta	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	0	0	2	0	-	0	0	0	0	0	1	1	0	0	1	1	0	1	2	1	1	0	1	1
M. (Litomegachile) brevis	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	0	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Litomegachile) gentilis	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	0	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	2	2	1	1	0	1	1
M. (Megachile) centuncularis	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	1	0	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Cyphopyga) montivaga	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Megachiloides) oenotherae	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	1	0	1	2	0	0	0	-	0	0	0	0	1	0	1	0	1	1	0	1	2	0	1	0	1	1
M. (Xeromegachile) integra	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Derotropis) pascoensis	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	0	0	0	-	0	0	0	0	1	0	0	0	0	1	0	1	2	1	1	0	1	1
M. (Melanosarus) xylocopoides	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	2	0	0	1	0	0	1	1	1	0	1	2	0	0	1	0	0	1	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Melanosarus) nigripennis	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	1	1	0	1	2	0	0	1	0	0	1	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Moureapis) anthidiodes	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	1	1	0	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**
Trichoturgus wagenknechti	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dioxys productus subruber	0	0	0	0	-	0	0	0	0	1	1	2	1	0	1	0	1	0	1	2	0	2	0	0	1	0	1	1	0	0	0	0	0	2	0	0	1	0	1	0	0	0	2	1	0	0	0	1	0	1	0	1	0	0	0	1	0	-
Trachusa (Ulanthidium) mitchelli	0	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Aztecanthidium tenochtitlanieum	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Chelostoma rapunculi	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	1	0	1	0	1	0	0	0	0	0	0
Hoplitis (Dasyosmia) biscutellae	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M.(Acentron) albitarsis	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	0	1	0	1	0	1	0	0	0	0
M. (Acentron) candida	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	0	1	0	1	0	1	0	0	0	0
M. (Amegachile) bituberculata	0	0	0	1	1	0	0	0	1	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	2	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0
M. (Callochile) ustulatiformis	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	2	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0
M. (Argyropile) parallela	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Argyropile) sabinensis	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Austromegachile) montezuma	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1
M. (Holcomegachile) giraffa	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	2	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1
M. (Chrysosarus) guaranitica	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M. (Chrysosarus) albopunctata	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M. (Dactylomegachile) parsonsiae	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Cressoniella) zapoteca	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Dasymegachile)saulcyi	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Chaetochile) mitchelli	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0
M. (Eumegachile) bombycina	0	0	0	1	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Eutricharaea) argentata	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	$	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	2	0	1	1	0	1	0	0	0	0	0	2
M. (Eutricharaea) femorata	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	$	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0	2
M. (Perezia) leachella	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	0	1	1	0	1	0	0	0	0	0	2
M. (Eurymella) eurymera	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	2	0	1	1	0	1	0	0	0	0	0	2
M. (Eurymella) submetallica	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	1	1	1	0	1	0	0	0	0	0	2
M. (Digitella) digiticauda	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0	2
M. (Platysta) platystoma	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
M. (Neoeutricharaea) rotundata	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	2	0	1	1	0	1	0	0	0	0	0	2
M. (Grosapis) cockerelli	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Leptorachis) petulans	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	0	1	0	1	0	0	0	0	0	0
M. (Leptorachina) laeta	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	1	2	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0
M. (Litomegachile) brevis	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	0	1	0	1	0	0	0	0	0	0
M. (Litomegachile) gentilis	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Megachile) centuncularis	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Cyphopyga) montivaga	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	2	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Megachiloides) oenotherae	0	0	0	1	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Xeromegachile) integra	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Derotropis) pascoensis	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Melanosarus) xylocopoides	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0
M. (Melanosarus) nigripennis	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0
M. (Moureapis) anthidiodes	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**
Trichoturgus wagenknechti	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-	-	0
Dioxys productus subruber	0	1	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	1	0	0	-	-	1
Trachusa (Ulanthidium) mitchelli	0	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	-	-	1
Aztecanthidium tenochtitlanieum	0	0	0	1	0	0	0	0	0	1	0	2	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	-	1
Chelostoma rapunculi	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	-	-	1
Hoplitis (Dasyosmia) biscutellae	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	-	1
M.(Acentron) albitarsis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	2	1	2	0	2	1	2	0	1	1	1	1	1	2	0	1	1	2	1	0	1	1	1	0	0	1	0	2	0	0	-	-	1
M. (Acentron) candida	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	2	1	2	0	2	1	2	0	1	1	1	1	1	2	0	1	1	2	1	0	1	1	1	0	0	0	0	2	0	0	-	-	1
M. (Amegachile) bituberculata	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	1	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	0	0	-	-	1
M. (Callochile) ustulatiformis	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	2	0	2	1	1	0	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	3	0	1	1	0	2	1	1	1	1	1
M. (Argyropile) parallela	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	2	0	1	0	1	1	0	2	0	0	0	0	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	1	0	-	1
M. (Argyropile) sabinensis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	2	0	1	0	1	1	0	2	0	0	0	0	2	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	-	1
M. (Austromegachile) montezuma	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	-	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	1	-	1
M. (Holcomegachile) giraffa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	2	0	0	0	1	2	0	1	0	0	1	1	0	1	-	1
M. (Chrysosarus) guaranitica	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	-	1
M. (Chrysosarus) albopunctata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	3	0	1	0	0	1	1	1	1	0	1
M. (Dactylomegachile) parsonsiae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	1	-	1
M. (Cressoniella) zapoteca	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	1	1	1	0	1
M. (Dasymegachile)saulcyi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1
M. (Chaetochile) mitchelli	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1
M. (Eumegachile) bombycina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1
M. (Eutricharaea) argentata	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	1	1	0	2	0	0	1	-	1
M. (Eutricharaea) femorata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	0	2	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3	0	1	1	0	2	1	0	1	-	1
M. (Perezia) leachella	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	1	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	2	1	0	1	-	1
M. (Eurymella) eurymera	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	0	1	0	3	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	2	0	1	1	0	2	1	1	1	1	1
M. (Eurymella) submetallica	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	1	0	1	1	2	0	1	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1	2	0	1	1	0	2	1	0	1	-	1
M. (Digitella) digiticauda	0	0	0	0	-	0	-	0	-	0	0	1	0	0	1	0	0	1	0	-	1	0	1	0	1	2	0	1	1	2	0	3	0	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	0	1	-	1
M. (Platysta) platystoma	0	-	-	-	-	-	-	-	-	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	2	0	2	0	2	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	2	0	0	0	0	2	1	1	1	1	1
M. (Neoeutricharaea) rotundata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	2	0	0	-	-	1
M. (Grosapis) cockerelli	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	2	0	3	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1
M. (Leptorachis) petulans	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	2	0	0	0	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	0	1	-	1
M. (Leptorachina) laeta	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	0	2	1	2	0	1	1	2	0	1	1	1	1	1	2	0	1	1	0	1	0	1	1	1	0	1	1	0	1	1	1	1	0	1
M. (Litomegachile) brevis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	2	1	1	1	0	1
M. (Litomegachile) gentilis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	1	1	1	0	1
M. (Megachile) centuncularis	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	0	1	0	0	2	0	1	0	2	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	1	0	1	1	1	1	0	1
M. (Cyphopyga) montivaga	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	1	0	2	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1
M. (Megachiloides) oenotherae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	2	0	3	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0	1	1	1	1	1	1
M. (Xeromegachile) integra	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	1	2	1	1	1	1	0	3	1	1	0	0	1	0	2	0	0	0	0	0	0	1	1	2	0	0	0	0	1	1	1	1	1	1
M. (Derotropis) pascoensis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	1	2	1	1	0	2	1	3	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	1	1	1	1
M. (Melanosarus) xylocopoides	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	2	0	1	2	0	2	0	1	1	3	0	1	1	0	1	1	2	0	0	1	2	0	0	1	1	1	0	0	1	0	1	1	0	1	-	1
M. (Melanosarus) nigripennis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	2	0	1	2	1	2	0	1	1	3	0	0	1	0	1	1	2	0	0	1	2	0	0	1	1	1	0	0	1	0	1	1	0	1	-	1
M. (Moureapis) anthidiodes	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	2	0	0	1	0	2	1	2	0	1	1	0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	1	1	0	1	-	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**175**	**176**	**177**	**178**	**179**	**180**	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**	**191**	**192**	**193**	**194**	**195**	**196**	**197**	**198**	**199**	**200**	**201**	**202**	**203**	**204**	**205**	**206**	**207**	**208**	**209**	**210**	**211**	**212**	**213**	**214**	**215**	**216**	**217**	**218**	**219**	**220**	**221**	**222**	**223**	**224**	**225**	**226**	**227**	**228**	**229**	**230**	**231**
Trichoturgus wagenknechti	0	1	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	0	2	0	0	0	0	0	0
Dioxys productus subruber	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0		0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	-	-	-	0	0	0	1	2	0	0	-	0	1	0	0	0	0	0	0
Trachusa (Ulanthidium) mitchelli	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	1	0	1	0	0	0	2	1	1	1	0	1	0	0	1	1	0	0	0	0	1	2	0	1	0	0	0	1	1	0	0	0	0
Aztecanthidium tenochtitlanieum	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	1	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	2	1	0	0	2	0	0	-	0	2	1	0	1	0	-	0
Chelostoma rapunculi	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	2	1	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	-	0	0	0	1	1	0	0	0
Hoplitis (Dasyosmia) biscutellae	0	1	0	0	1	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	2	1	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	-	0	0	0	1	0	0	1	0
M.(Acentron) albitarsis	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	1	1	1	1	1	1	0	3	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	1	1	1	0	1	0	1	0	0	1	0
M. (Acentron) candida	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	1	1	1	1	1	1	0	3	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	1	1	1	0	1	0	1	0	0	1	0
M. (Amegachile) bituberculata	0	0	0	0	1	1	0	1	0	0	1	0	0	2	0	0	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	0	0	-	0	0	0	1	0	0	0	0
M. (Callochile) ustulatiformis	1	0	0	0	1	1	0	1	0	0	1	0	0	2	1	0	0	1	1	1	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	2	1	0	1	1	0	0	-	0	1	0	1	0	1	0	0
M. (Argyropile) parallela	0	0	0	0	1	1	0	1	0	0	0	0	1	2	0	0	0	1	1	2	1	1	0	3	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	1	0	-	0	0	0	1	0	0	0	0
M. (Argyropile) sabinensis	0	1	0	0	1	1	0	1	0	0	0	0	1	2	0	0	0	1	1	2	1	1	0	3	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	1	0	-	0	0	0	1	0	0	0	0
M. (Austromegachile) montezuma	1	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	2	0	1	0	3	1	1	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	-	0	1	0	1	0	0	1	0
M. (Holcomegachile) giraffa	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	2	0	1	0	3	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	-	0	1	0	1	0	0	1	0
M. (Chrysosarus) guaranitica	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	0	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
M. (Chrysosarus) albopunctata	0	2	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	2	0	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
M. (Dactylomegachile) parsonsiae	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	0	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
M. (Cressoniella) zapoteca	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	0	1	0	1	1	2	0	0	0	0	0	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Dasymegachile)saulcyi	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Chaetochile) mitchelli	1	2	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
M. (Eumegachile) bombycina	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	1	0	0	0
M. (Eutricharaea) argentata	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	2	0	1	0	0	1	0	1	0	0	0	0
M. (Eutricharaea) femorata	0	0	0	0	1	1	0	1	0	0	1	0	0	2	0	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
M. (Perezia) leachella	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	2	1	2	-	0	1	0	1	0	0	0	0
M. (Eurymella) eurymera	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	0	1	0	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	2	0	0	0	2	0	1	0	0	1	0	1	0	0	0	0
M. (Eurymella) submetallica	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1	1	2	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	2	0	1	0	0	1	0	1	0	0	0	0
M. (Digitella) digiticauda	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	0	0	0
M. (Platysta) platystoma	0	0	0	0	1	1	0	0	1	0	1	0	0	1	1	0	0	1	1	2	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	1	0	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Neoeutricharaea) rotundata	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	0	0	0
M. (Grosapis) cockerelli	0	1	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	0	0	0	2	1	1	0	1	1	0	0	1	0	0	2	0	1	1	0	0	0	-	0	1	0	1	0	0	0	0
M. (Leptorachis) petulans	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	3	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0
M. (Leptorachina) laeta	0	0	0	0	1	1	0	1	1	1	1	0	0	2	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	2	0	1	1	0	1	0	1	0	1	0	0
M. (Litomegachile) brevis	0	0	0	0	1	1	0	1	0	0	0	0	1	2	0	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	1	0	0
M. (Litomegachile) gentilis	0	0	0	0	1	1	0	1	1	0	0	0	1	2	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	0	0	0	-	0	1	0	1	0	0	0	0
M. (Megachile) centuncularis	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	2	0	1	0	0	2	0	0	1	2	0	0	-	0	1	0	1	1	0	0	0
M. (Cyphopyga) montivaga	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	-	0	1	0	1	1	0	0	0
M. (Megachiloides) oenotherae	0	2	0	0	1	1	0	1	1	1	0	0	1	3	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Xeromegachile) integra	0	0	0	0	1	1	0	1	1	1	1	0	0	3	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Derotropis) pascoensis	1	1	0	0	1	1	0	1	1	0	1	0	0	3	1	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	-	0	2	0	1	0	0	0	0
M. (Melanosarus) xylocopoides	0	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	2	1	1	1	0	1	0	1	0	0	0	0
M. (Melanosarus) nigripennis	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	1	2	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	2	1	1	1	0	1	0	1	0	0	0	0
M. (Moureapis) anthidiodes	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	2	1	1	0	0	1	0	1	0	0	0	0

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**
M. (Neochelynia) paulista	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	2	0	1	2	0	0	2	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Neomegachile) chichimeca	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	2	0	1	2	0	0	2	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Paracella) semivenusta	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	2	0	1	2	0	0	1	2	0	1	#	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Paracella) curtula	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	2	0	1	2	0	0	1	2	0	1	1	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Pseudocentron) pruina	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	1	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Pseudocentron) poeyi	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	1	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Ptilosaroides) neoxanthoptera	0	1	1	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	2	0	1	2	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Ptilosarus) bertonii	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	2	0	1	2	0	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Sayapis) pugnata	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	2	1	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	2	0	1	0	0	1	2	1	1	0	1	1
M. (Sayapis) coleoxyformis	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	1	0	1	1	0	2	2	1	1	0	1	1
M. (Schrottkyapis) assumptions	0	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	0	0	2	1	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Stelodides) euzona	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	2	1	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Trichurochile) thygaterella	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	2	0	1	2	0	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Tylomegachile) orba	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	2	0	1	2	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Tylomegachile) simplicipes	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	2	0	1	2	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Xanthosarus) latimanus	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	0	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Addendella) addenda	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	0	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Macromegachile) lagopoda	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	1	1	2	0	1	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Phaenosarus) fortis	0	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	1	1	2	0	1	0	2	0	-	0	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Neocressoniella) carbonaria	0	0	1	1	1	0	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	1	0	1	1	2	0	0	1	2	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Aethomegachile) sp.	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	1	1	2	0	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Austrochile) resinifera	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	0	0	0	0	0	1	1	1	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	1	1	0	1	2	1	1	0	1	1
M. (Austrochile) ignita	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	3	0	0	1	1	1	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	1	1	1	0	0	2	1	1	0	1	1
M. (Callomegachile) mystaceana	0	1	1	1	1	0	0	2	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	3	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1	0	1	1
M. (Callomegachile) sculpturalis	1	0	1	1	1	1	0	2	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	2	0	1	0	1	1	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	1	1	1	1	0	1	2	1	1	0	1	1
M. (Eumegachilana) clotho	1	0	1	0	1	1	0	2	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	1	1	1	1	0	0	1	0	0	0	0	0	-	-	0	1	0	1	1	0	1	1	0	0	0	1	2	1	1	0	1	1
M. (Carinula) torrida	0	1	1	1	1	0	0	1	0	0	2	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	3	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	1	1	0	1	2	1	1	0	1	1
M. (Carinula) decemsignata	0	1	1	1	1	0	0	1	0	0	2	0	0	0	0	0	1	0	0	1	1	0	0	0	2	0	0	1	1	1	0	0	3	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	1	1	0	1	2	1	1	0	1	1
M. (Morphella) biseta	0	1	1	1	1	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	1	0	0	0	1	2	1	1	0	1	1
M. (Cestella) cestifera	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	2	1	0	1	0	0	0	0	0	-	-	0	1	1	0	1	0	2	1	0	0	0	1	2	1	1	0	1	1
M. (Chalicodoma) parietina	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	1	1	0	2	1	1	3	1	0	0	0	0	-	-	0	0	0	0	1	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Euchalicodoma) asiatica	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	0	1	1	2	1	1	3	1	0	0	0	0	-	-	0	0	0	0	0	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Allochalicodoma) lefebvrei	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	0	1	1	2	1	1	3	1	0	0	0	0	-	-	0	0	0	0	0	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Katamegachile) manicata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	0	1	1	2	1	1	3	1	0	0	0	0	-	-	0	0	0	0	1	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Parachalicodoma) incana	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	0	1	1	2	0	0	2	0	0	0	0	0	-	-	0	0	0	0	1	0	2	0	1	1	0	1	2	1	1	0	1	1
M. (Chalicodomoides) aethiops	1	1	1	1	1	0	0	1	0	0	2	1	0	1	0	0	1	0	0	2	0	0	0	0	1	0	0	1	0	0	1	1	3	1	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	1	0	1	2	1	1	0	1	1
M. (Chelostomoda) spissula parvula	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	1	0	2	0	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	1	0	1	1	0	1	2	1	0	0	1	1
M. (Chelostomoda) ulrica	0	1	1	1	1	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	1	0	2	0	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	1	0	1	1	0	1	2	1	0	0	1	1
M. (Chelostomoides) rugifrons	1	0	1	1	1	0	0	2	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	2	1	1	0	0	1	1	0	1	0	0	0	0	0	-	-	0	1	0	1	1	0	1	0	1	0	0	1	2	1	1	0	1	1
M. (Oligotropus) campanulae	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	1	0	1	0	0	2	0	0	0	0	0	-	-	0	1	0	0	1	0	1	0	1	1	0	2	2	1	1	0	1	1
M. (Gnathodon) georgica	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	2	0	0	1	0	1	1	0	2	0	0	0	0	0	-	-	0	1	0	0	1	0	1	0	1	0	0	1	2	1	1	0	1	1
M. (Chelostomoidella) spinotulata	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	2	0	0	1	0	1	1	0	2	0	0	0	0	0	-	-	0	1	1	0	1	0	1	0	1	0	0	1	2	1	1	0	1	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**
M. (Neochelynia) paulista	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	2	0	1	1	0	1	0	0	0	0	0	0
M. (Neomegachile) chichimeca	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	2	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Paracella) semivenusta	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	1	1	0	1	0	0	0	0	0	1
M. (Paracella) curtula	0	0	0	1	1	0	0	0	0	1	2	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Pseudocentron) pruina	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Pseudocentron) poeyi	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Ptilosaroides) neoxanthoptera	0	0	0	0	1	1	0	0	0	1	2	0	1	0	0	0	4	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	2	1	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0
M. (Ptilosarus) bertonii	0	0	0	0	1	1	0	0	0	1	2	0	1	0	0	0	4	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	2	1	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0
M. (Sayapis) pugnata	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	1	0	0	0	0	0
M. (Sayapis) coleoxyformis	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	1	0	1	2	0	1	1	0	1	0	0	1	0	0	1
M. (Schrottkyapis) assumptions	0	0	0	0	1	0	0	0	0	1	2	1	0	0	0	0	2	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	1	1	1	0	1	0	0	0	0	0	1
M. (Stelodides) euzona	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Trichurochile) thygaterella	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	0	0	1	0	1	0	0	1	0	0	1
M. (Tylomegachile) orba	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
M. (Tylomegachile) simplicipes	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	2	0	0	0	1	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
M. (Xanthosarus) latimanus	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Addendella) addenda	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Macromegachile) lagopoda	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Phaenosarus) fortis	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Neocressoniella) carbonaria	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0
M. (Aethomegachile) sp.	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0
M. (Austrochile) resinifera	0	0	1	1	1	0	0	1	1	1	2	1	1	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	2	0	1	1	1	1	1	0	0	0	1	0
M. (Austrochile) ignita	0	0	1	1	1	0	0	0	1	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	0	1	1	1	0	0	0	0	1	0
M. (Callomegachile) mystaceana	0	0	1	1	1	1	1	0	1	1	1	0	1	1	0	1	2	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Callomegachile) sculpturalis	0	0	1	1	1	1	0	0	1	1	1	0	0	1	0	0	2	0	0	2	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Eumegachilana) clotho	0	0	1	1	1	1	1	0	1	1	3	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0
M. (Carinula) torrida	0	0	1	1	1	0	0	0	1	1	2	0	1	1	0	1	4	0	0	1	0	0	0	0	1	0	0	1	0	2	1	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0
M. (Carinula) decemsignata	0	0	1	1	1	0	1	0	1	1	2	0	1	1	0	1	4	0	0	1	0	0	0	0	1	0	0	1	0	2	0	1	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0
M. (Morphella) biseta	0	0	1	1	1	0	0	0	1	1	2	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M. (Cestella) cestifera	0	0	1	1	1	0	0	1	1	1	1	1	1	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	1	2	0	1	1	0	1	1	0	1	0	0	0
M. (Chalicodoma) parietina	0	0	1	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Euchalicodoma) asiatica	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Allochalicodoma) lefebvrei	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Katamegachile) manicata	0	0	1	1	1	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Parachalicodoma) incana	0	0	1	1	1	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	0
M. (Chalicodomoides) aethiops	0	0	1	1	1	0	0	1	1	1	2	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	1	0	1	1	0	0	0	0	0
M. (Chelostomoda) spissula parvula	0	0	0	0	1	0	0	0	1	1	2	1	1	0	1	1	1	0	0	2	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	1	0	0	0	0	0
M. (Chelostomoda) ulrica	0	0	0	0	1	0	0	0	1	1	2	1	1	0	1	1	1	0	0	2	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	1	1	1	0	1	1	0	0	0	0	0
M. (Chelostomoides) rugifrons	0	0	1	1	1	0	0	0	1	1	3	1	1	0	1	1	1	1	0	2	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	1	1	1	0	1	2	0	1	0	0	0
M. (Oligotropus) campanulae	0	0	1	1	1	1	0	0	1	1	2	0	0	0	1	0	1	0	0	2	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	1	1	1	0	1	2	0	1	0	0	0
M. (Gnathodon) georgica	0	0	1	1	1	0	0	0	1	1	2	0	0	0	0	0	1	0	0	2	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	1	1	1	0	1	2	0	0	0	0	0
M. (Chelostomoidella) spinotulata	0	0	1	1	1	1	0	0	1	1	2	1	0	0	0	1	1	1	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	2	0	0	0	0	0

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**
M. (Neochelynia) paulista	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	-	1
M. (Neomegachile) chichimeca	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	-	1
M. (Paracella) semivenusta	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	0	0	-	-	1
M. (Paracella) curtula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	0	0	-	-	1
M. (Pseudocentron) pruina	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	2	1	1	1	3	0	1	0	0	1	1	2	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	-	1
M. (Pseudocentron) poeyi	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	-	1	1	0	1	0	0	2	0	2	1	1	1	3	0	1	0	0	1	1	2	0	0	1	1	0	0	0	1	1	0	0	1	0	1	1	0	1	-	1
M. (Ptilosaroides) neoxanthoptera	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	-	-	1
M. (Ptilosarus) bertonii	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	1	0	1	-	1
M. (Sayapis) pugnata	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	1	2	0	1	0	2	0	3	1	1	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	-	-	1
M. (Sayapis) coleoxyformis	1	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	2	0	2	0	0	2	0	1	0	1	0	3	1	1	1	0	0	0	2	0	0	0	0	0	0	0	1	3	0	0	1	0	1	0	0	-	-	1
M. (Schrottkyapis) assumptions	0	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	2	0	1	0	0	1	0	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	1	0	0	-	-	1
M. (Stelodides) euzona	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	2	0	1	0	0	0	3	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	1	-	1
M. (Trichurochile) thygaterella	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	2	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	-	1
M. (Tylomegachile) orba	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	1	0	2	1	1	1	0	1
M. (Tylomegachile) simplicipes	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	2	1	1	1	0	1
M. (Xanthosarus) latimanus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	1	2	1	1	0	2	1	3	0	1	1	0	1	1	2	0	0	0	2	1	0	1	1	1	0	0	1	0	1	1	1	1	1	1
M. (Addendella) addenda	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	2	0	1	0	2	0	3	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	-	1
M. (Macromegachile) lagopoda	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	2	1	1	0	2	1	3	1	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	0	1
M. (Phaenosarus) fortis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	1	0	1	1	0	1	0	0	2	1	1	0	2	0	3	0	1	1	0	1	1	2	0	0	0	0	0	0	1	1	2	0	0	0	0	1	1	1	1	1	1
M. (Neocressoniella) carbonaria	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1
M. (Aethomegachile) sp.	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	-	1
M. (Austrochile) resinifera	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	2	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0	1	1	1	0	1	1
M. (Austrochile) ignita	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	0	1
M. (Callomegachile) mystaceana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	2	0	2	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	2	0	0	-	-	1
M. (Callomegachile) sculpturalis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	2	0	-	0	0	2	0	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	$	0	1	1	0	1	0	0	-	-	1
M. (Eumegachilana) clotho	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	2	0	2	0	0	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	-	-	1
M. (Carinula) torrida	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	-	1
M. (Carinula) decemsignata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	2	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	$	0	0	0	0	1	0	0	-	-	1
M. (Morphella) biseta	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	2	0	2	0	0	1	0	1	0	3	0	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0	2	0	0	-	-	1
M. (Cestella) cestifera	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	2	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	-	-	1
M. (Chalicodoma) parietina	0	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	3	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	1	0	0	-	-	1
M. (Euchalicodoma) asiatica	0	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	2	0	1	0	0	0	3	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	0	-	1
M. (Allochalicodoma) lefebvrei	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	3	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	1	0	1	1	0	0	-	1
M. (Katamegachile) manicata	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	0	0	1	0	1	1	0	1	0	0	2	0	3	0	0	0	3	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	0	-	1
M. (Parachalicodoma) incana	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	0	-	1
M. (Chalicodomoides) aethiops	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	-	1
M. (Chelostomoda) spissula parvula	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	2	0	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	4	0	0	1	1	2	0	0	-	-	1
M. (Chelostomoda) ulrica	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	2	0	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	4	0	0	1	1	1	0	0	-	-	1
M. (Chelostomoides) rugifrons	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	1	1	1	1	0	1
M. (Oligotropus) campanulae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	2	0	0	2	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	1
M. (Gnathodon) georgica	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1
M. (Chelostomoidella) spinotulata	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	2	0	1	0	1	0	3	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																							
Taxa	**175**	**176**	**177**	**178**	**179**	**180**	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**	**191**	**192**	**193**	**194**	**195**	**196**	**197**	**198**	**199**	**200**	**201**	**202**	**203**	**204**	**205**	**206**	**207**	**208**	**209**	**210**	**211**	**212**	**213**	**214**	**215**	**216**	**217**	**218**	**219**	**220**	**221**	**222**	**223**	**224**	**225**	**226**	**227**	**228**	**229**	**230**	**231**
M. (Neochelynia) paulista	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	1	2	0	1	0	3	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Neomegachile) chichimeca	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Paracella) semivenusta	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	0	0	1	1	2	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	2	1	0	-	0	1	0	1	0	1	0	0
M. (Paracella) curtula	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	-	0	0	0	1	0	1	0	0
M. (Pseudocentron) pruina	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	2	1	1	1	1	0	0	0	0	0	0	0
M. (Pseudocentron) poeyi	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	2	1	1	1	1	0	0	0	0	0	0	0
M. (Ptilosaroides) neoxanthoptera	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Ptilosarus) bertonii	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	1	0	0	0	2	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0
M. (Sayapis) pugnata	1	2	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	2	1	1	0	3	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	0	1	0
M. (Sayapis) coleoxyformis	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	-	0	0	0	1	0	0	1	0
M. (Schrottkyapis) assumptions	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	-	0	0	0	1	0	0	1	0
M. (Stelodides) euzona	1	2	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	0	0	0	0	0
M. (Trichurochile) thygaterella	0	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	2	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Tylomegachile) orba	0	2	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	0	0	0	-	0	1	0	1	0	1	1	0
M. (Tylomegachile) simplicipes	0	2	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	2	0	0	1	2	0	0	-	0	1	0	0	0	1	1	0
M. (Xanthosarus) latimanus	1	2	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	1	2	0	1	0	0	1	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	2	-	0	1	0	0	0	0	0	0
M. (Addendella) addenda	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	2	0	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	2	0	0	1	0	0	0	-	0	1	0	1	0	0	0	0
M. (Macromegachile) lagopoda	1	2	0	0	1	1	0	1	1	0	0	0	1	2	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	2	0	0	0	2	0	$	1	0	1	0	1	0	0	0	0
M. (Phaenosarus) fortis	1	0	0	0	1	1	0	1	1	1	0	0	0	2	1	0	0	1	1	2	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	-	0	1	0	1	0	0	1	0
M. (Neocressoniella) carbonaria	1	0	0	0	1	2	0	1	1	0	0	0	0	2	1	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	1	1	0
M. (Aethomegachile) sp.	1	0	0	2	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	0	1	0
M. (Austrochile) resinifera	0	0	0	1	1	1	1	1	1	0	1	0	0	2	0	0	0	1	1	2	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	2	0	0	-	0	0	0	0	0	0	0	0
M. (Austrochile) ignita	0	2	0	3	1	0	0	0	1	0	0	0	0	2	1	0	0	0	1	2	1	1	0	0	1	0	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	0	0	0	1	2	1	0	-	0	1	0	0	0	0	0	0
M. (Callomegachile) mystaceana	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	2	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	-	0	2	0	1	0	0	1	0
M. (Callomegachile) sculpturalis	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	2	0	0	-	0	1	0	0	0	0	1	0
M. (Eumegachilana) clotho	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	2	1	1	0	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	-	0	1	0	1	0	0	1	0
M. (Carinula) torrida	0	2	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	-	0	1	0	0	0	0	0	0
M. (Carinula) decemsignata	0	2	0	0	1	1	0	1	1	0	1	0	1	1	1	0	0	0	1	2	0	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0
M. (Morphella) biseta	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	1	1	2	0	0	-	0	0	0	1	0	0	1	0
M. (Cestella) cestifera	0	0	0	0	1	1	0	0	1	0	0	0	0	3	0	0	0	0	1	0	1	1	0	3	1	1	1	0	0	0	1	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	-	0	2	0	0	0	0	0	0
M. (Chalicodoma) parietina	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	0	1	2	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	0	0	0	1	2	1	0	-	0	0	1	1	0	0	0	1
M. (Euchalicodoma) asiatica	0	1	0	3	1	1	0	1	1	0	0	0	0	3	0	1	0	0	1	2	1	1	1	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	2	0	0	1	0	0	0	-	0	0	0	1	0	0	0	0
M. (Allochalicodoma) lefebvrei	0	0	0	0	1	1	0	1	1	1	0	0	0	2	0	0	0	1	1	2	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	1	0	1	1	0	0	1	1	1	0	-	0	1	1	1	0	0	0	1
M. (Katamegachile) manicata	1	1	0	3	1	1	0	1	1	0	0	0	0	0	0	1	0	1	1	2	0	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Parachalicodoma) incana	0	1	0	2	1	0	0	1	1	0	0	0	1	2	0	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	2	0	0	-	0	2	0	1	1	1	0	0
M. (Chalicodomoides) aethiops	0	0	0	0	1	1	0	0	1	0	0	0	0	2	0	0	0	1	1	2	1	1	1	3	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	2	1	0	-	0	0	0	1	0	0	0	0
M. (Chelostomoda) spissula parvula	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	-	0	1	0	1	0	0	0	0
M. (Chelostomoda) ulrica	0	0	0	1	1	0	0	1	0	0	0	0	0	3	1	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	1	2	0	0	-	0	1	0	-	0	1	0	1	0	0	0	0
M. (Chelostomoides) rugifrons	1	0	0	4	1	0	0	1	0	0	0	0	0	2	0	0	0	1	1	2	1	1	0	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	-	0	1	0	0	0	1	0	0
M. (Oligotropus) campanulae	1	0	0	4	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	2	1	1	0	3	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	1	0	-	0	1	0	1	0	0	0	0
M. (Gnathodon) georgica	1	0	0	4	1	1	0	0	1	0	0	0	0	1	0	1	0	0	1	2	1	1	0	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	-	0	1	0	0	0	1	0	0
M. (Chelostomoidella) spinotulata	1	0	0	4	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	2	1	1	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	-	0	2	0	0	0	0	1	0

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**
M. (Gronoceras) bombiformis	0	1	1	1	1	1	0	1	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	3	0	0	1	1	2	1	1	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	1	1
M. (Digronoceras) cincta combusta	0	1	1	1	1	1	0	1	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	3	0	0	1	1	2	1	1	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	1	1
M. (Hackeriapis) rhodura	0	1	1	1	1	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	1	0	1	1	0	2	0	0	0	0	0	-	-	0	1	0	0	1	0	1	0	0	0	0	1	2	1	0	0	1	1
M. (Hackeriapis) ferox	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	2	0	0	1	0	1	0	0	2	0	0	0	0	0	-	-	0	1	0	0	1	0	0	0	1	1	0	1	2	1	0	0	1	1
M. (Hackeriapis) heriadiformis	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	1	0	1	0	0	0	0	0	-	-	0	0	0	0	1	1	2	1	1	0	0	1	2	1	1	0	1	1
M. (Heriadopsis) striatulus	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	1	0	0	1	2	1	1	0	1	1
M. (Largella) semivestita	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	2	0	0	1	0	2	1	1	3	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	1	0	1	2	1	1	0	1	1
M. (Maximegachile) maxillosa	1	0	1	1	1	1	0	1	0	1	2	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	2	0	0	1	0	0	0	0	0	-	-	0	0	0	0	0	0	2	0	1	0	0	0	2	1	1	0	1	1
M. (Megella) malimbana	0	1	1	1	1	1	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	2	0	1	2	0	0	1	2	0	1	0	1	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Megella) pseudomonticola	0	1	1	1	1	1	0	1	1	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	2	0	1	2	0	0	1	2	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	2	1	1	0	1	1
M. (Mitchellapis) fabricator	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	2	0	0	1	0	0	1	-	0	0	0	0	1	0	1	0	1	1	0	0	2	1	1	0	1	1
M. (Pseudomegachile) ericetorum	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	0	0	1	0	0	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	1	0	1	2	1	1	0	1	1
M. (Archimegachile) flavipes	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	1	0	1	2	1	1	0	1	1
M. (Neglectella) armatipes	0	1	1	0	1	0	0	1	1	0	2	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	2	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	1	1	0	1	2	1	1	0	1	1
M. (Xenomegachile) albocincta	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	-	1	0	3	0	0	0	0	0	-	-	0	0	0	0	1	0	2	1	0	1	0	1	2	1	1	0	1	1
M. (Dinavis) muansae	?	1	?	1	?	0	?	?	0	0	0	1	?	0	0	?	1	?	?	?	0	?	0	0	2	0	?	?	0	?	0	?	?	-	-	0	0	0	?	-	?	?	?	?	1	0	1	1	0	0	0	1	2	1	1	0	1	1
M. (Rhodomegachile) abdominalis	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	1	1	1	1	0	2	0	0	0	0	0	-	-	0	1	0	0	1	0	1	0	1	1	0	0	2	1	0	0	1	1
M. (Schizomegachile) mostrosa	1	0	1	1	1	0	0	2	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1	0	0	0	0	0	-	-	0	1	0	0	1	1	2	1	1	0	0	1	2	1	0	0	1	1
M. (Stenomegachile) chelostomoides	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	2	0	1	1	1	1	0	0	2	1	0	2	0	0	0	0	0	-	-	0	1	0	0	1	1	2	1	1	0	0	1	2	1	1	0	1	1
M. (Stenomegachile) dolichosoma	1	0	1	1	1	0	1	1	0	0	2	1	0	1	0	0	0	1	0	0	0	2	0	1	2	1	1	0	0	2	1	0	1	0	0	0	0	0	-	-	0	1	1	0	1	1	2	1	1	0	0	1	2	1	1	0	1	1
M. (Thaumatosoma) duboulaii	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	-	-	0	1	0	0	1	1	2	1	1	0	0	0	2	1	1	0	1	1
M. (Creightonella) cognata	0	1	1	1	1	1	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	2	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Creightonella) albisecta	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	2	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	1	1
M. (Matangapis) alticola	0	1	1	1	1	0	1	2	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	3	0	0	0	0	1	0	0	3	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	1	1	0	0	2	1	1	0	1	1
M. (Cuspidella) quadraticauda	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	2	0	0	1	0	0	1	0	0	1	0	3	0	1	0	0	0	-	-	0	0	0	0	1	0	1	0	0	0	0	1	2	1	1	0	1	1
Radoszkowskiana rufiventris	0	1	1	1	0	0	0	1	0	0	2	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	1	1	1	1	0	0	0	2	1	1	0	1	1
C. (Liothyrapis) decipiens	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	1	1	0	0	0	2	2	1	1	0	1	1
C. (Rhinocoelioxys) zapoteca	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	0	1	1
C. (Torridapis) torrida	0	1	1	1	1	0	0	2	1	0	2	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	3	0	1	0	0	0	-	-	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Material and Methods for explanation).

	Characters																																																								
Taxa	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**
M. (Gronoceras) bombiformis	0	0	1	1	1	0	1	1	1	1	2	0	1	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M. (Digronoceras) cincta combusta	0	0	1	1	1	0	1	1	1	1	2	0	1	0	0	0	2	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
M. (Hackeriapis) rhodura	1	0	0	0	1	0	0	0	1	1	2	2	0	0	1	1	1	0	0	2	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	0	0
M. (Hackeriapis) ferox	1	0	1	1	1	0	0	0	1	1	2	0	0	0	1	0	2	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	0	0
M. (Hackeriapis) heriadiformis	0	0	1	1	1	1	0	0	1	1	2	0	0	0	1	1	2	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	0	1	1	1	0	0	0	0	0	0
M. (Heriadopsis) striatulus	0	0	0	0	1	1	0	0	1	1	2	0	0	0	1	1	1	0	0	2	0	0	0	1	1	1	0	1	0	2	1	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0	2	1	1	1	0	1	0	1	0	0	0	0
M. (Largella) semivestita	0	0	1	1	1	0	0	1	1	1	2	1	1	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0	0
M. (Maximegachile) maxillosa	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	2	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Megella) malimbana	0	0	0	0	1	1	0	0	1	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	1	1	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Megella) pseudomonticola	0	0	1	0	1	1	0	0	1	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	1	0	0	0	2	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Mitchellapis) fabricator	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	0	1
M. (Pseudomegachile) ericetorum	0	0	1	1	1	0	0	1	1	1	2	1	1	0	0	1	2	0	0	2	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Archimegachile) flavipes	0	0	1	0	1	0	0	1	1	1	2	1	1	0	0	0	2	0	0	2	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	2	1	1	1	0	1	0	1	0	0	0	1
M. (Neglectella) armatipes	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	2	0	0	2	0	0	0	0	1	1	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	2	1	1	1	0	1	1	0	0	0	0	0
M. (Xenomegachile) albocincta	0	0	1	1	1	0	0	1	1	1	2	0	1	0	0	0	2	0	0	2	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0
M. (Dinavis) muansae	0	0	0	1	0	1	0	0	0	1	?	1	0	0	?	?	?	?	0	0	0	0	?	?	?	?	0	1	0	?	?	?	0	0	0	0	1	0	0	0	0	1	0	1	?	?	?	0	1	1	0	1	?	?	?	0	?	?
M. (Rhodomegachile) abdominalis	1	0	0	0	1	0	0	1	1	1	2	2	1	0	0	0	2	0	1	2	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0
M. (Schizomegachile) mostrosa	1	0	1	0	0	0	0	1	1	1	1	2	0	0	1	1	1	1	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	2	0	1	1	0	1	1	0	0	0	1	0
M. (Stenomegachile) chelostomoides	0	0	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	1	0	1	0	0	0
M. (Stenomegachile) dolichosoma	0	0	1	1	1	0	0	0	1	1	2	2	1	0	1	1	1	0	0	2	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0
M. (Thaumatosoma) duboulaii	0	0	1	1	1	1	0	0	1	1	2	0	0	0	1	1	2	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	2	0	0	1	1	1	0	0	0	0	1	0
M. (Creightonella) cognata	0	0	1	0	1	0	0	1	0	1	2	0	0	0	0	0	2	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2	0	1	1	0	1	0	0	0	0	0	0
M. (Creightonella) albisecta	0	0	0	0	1	0	0	1	0	1	2	1	0	0	0	0	2	0	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	2	1	1	1	0	1	0	0	0	0	0	0
M. (Matangapis) alticola	0	0	1	0	1	1	0	0	1	1	2	0	1	0	0	0	1	0	0	2	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0
M. (Cuspidella) quadraticauda	0	0	1	1	1	1	0	0	1	1	2	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0
Radoszkowskiana rufiventris	0	0	0	0	1	0	0	0	0	1	2	2	1	0	1	1	1	0	1	2	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	1	0	1	0	1	0	1	0	1	0	0	0	1	0	-
C. (Liothyrapis) decipiens	0	0	0	0	0	1	0	0	1	1	2	1	1	0	1	1	1	0	0	2	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	1	1	0	1	0	1	0	1	0	1	0	-
C. (Rhinocoelioxys) zapoteca	0	0	0	0	0	0	0	0	0	1	2	2	1	0	1	1	1	0	1	2	1	2	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	1	1	1	1	0	1	0	1	0	1	0	-
C. (Torridapis) torrida	0	0	0	0	1	0	0	0	0	1	2	2	1	1	1	1	1	0	0	0	1	2	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	2	1	0	0	1	1	1	1	0	1	0	1	0	1	0	-

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Materials and Methods for explanation).

	Characters																																																								
Taxa	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**
M. (Gronoceras) bombiformis	0	0	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	1	0	1	2	0	1	1	0	2	0	3	0	3	0	3	1	1	0	0	1	1	2	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	1
M. (Digronoceras) cincta combusta	0	0	0	1	0	0	1	0	0	0	0	2	0	0	0	0	0	1	0	1	2	0	1	1	0	2	1	1	0	3	0	2	0	1	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1
M. (Hackeriapis) rhodura	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	1	0	2	1	1	1	0	1
M. (Hackeriapis) ferox	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	2	0	1	2	0	1	1	1	1	3	0	1	0	0	0	0	2	0	0	0	0	1	0	0	1	4	0	0	0	1	1	1	1	1	0	1
M. (Hackeriapis) heriadiformis	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	1	2	1	1	1	0	1
M. (Heriadopsis) striatulus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	2	1	1	1	0	1
M. (Largella) semivestita	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	-	-	1
M. (Maximegachile) maxillosa	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	2	0	2	0	0	0	0	1	0	4	0	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	-	1
M. (Megella) malimbana	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	1	1	0	1	-	1
M. (Megella) pseudomonticola	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	1	0	0	1	1	1	1	0	1
M. (Mitchellapis) fabricator	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	2	0	0	2	0	1	0	4	0	3	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	2	0	0	1	0	1	0	0	-	-	1
M. (Pseudomegachile) ericetorum	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	-	-	1
M. (Archimegachile) flavipes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3	0	0	0	0	2	0	0	-	-	1
M. (Neglectella) armatipes	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	1	1	1	0	0	1	3	0	1	0	0	0	0	2	0	0	0	0	0	0	0	1	3	0	0	1	0	2	1	0	0	-	1
M. (Xenomegachile) albocincta	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	2	0	3	0	3	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	3	0	0	0	0	1	1	0	1	-	1
M. (Dinavis) muansae	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	0	2	0	0	1	0	1	0	4	0	3	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	2	1	0	0	-	1
M. (Rhodomegachile) abdominalis	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	2	0	0	-	-	1
M. (Schizomegachile) mostrosa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	1	0	0	0	0	4	0	3	1	0	0	0	0	0	2	0	0	0	0	0	1	0	1	2	0	0	1	0	1	0	0	-	-	1
M. (Stenomegachile) chelostomoides	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	0	1	2	0	2	0	0	0	0	-	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	-	1
M. (Stenomegachile) dolichosoma	0	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	0	0	-	-	1
M. (Thaumatosoma) duboulaii	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	1	1	1	1	1
M. (Creightonella) cognata	0	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	1	1	0	0	1	0	0	-	1
M. (Creightonella) albisecta	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	3	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	3	0	1	1	0	1	1	0	0	-	1
M. (Matangapis) alticola	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	2	0	2	0	0	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	1	1	0	0	-	-	1
M. (Cuspidella) quadraticauda	0	0	?	?	0	?	?	?	?	0	0	1	0	0	0	0	0	1	0	1	1	0	2	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	1	0	0	1	1	0	0	-	1
Radoszkowskiana rufiventris	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	1	0	0	2	0	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	1	0	1	-	1
C. (Liothyrapis) decipiens	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	-	1
C. (Rhinocoelioxys) zapoteca	1	0	0	1	0	0	0	0	2	1	0	2	-	0	0	0	0	1	0	0	1	0	1	0	0	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	-	1
C. (Torridapis) torrida	1	0	0	1	0	0	0	0	2	1	0	1	-	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	2	0	1	0	1	1	1	0	1	0	1	0	0	-	-	1

Appendix IV (Continued). Character matrix used in cladistic analysis of *Megachile* subgenera; (-) = not applicable, # = multistate (0, 1), $ = multistate (1, 2), ? = state of characters that could not be recorded (see Materials and Methods for explanation).

Taxa	Characters 175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231
M. (Gronoceras) bombiformis	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Digronoceras) cincta combusta	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	0	1	2	1	0	-	0	1	0	1	0	0	0	0
M. (Hackeriapis) rhodura	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	0	2	0	1	1	2	0	0	-	0	1	0	0	0	0	1	0
M. (Hackeriapis) ferox	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Hackeriapis) heriadiformis	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	-	0	1	0	1	0	0	0	0
M. (Heriadopsis) striatulus	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0	1	2	0	0	-	0	1	0	0	0	0	0	0
M. (Largella) semivestita	0	2	0	0	1	1	0	1	1	1	0	0	1	2	0	1	0	0	1	2	1	1	0	2	1	1	1	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	1	2	0	0	-	0	2	0	1	0	0	0	0
M. (Maximegachile) maxillosa	0	0	0	0	1	1	0	0	1	0	0	0	0	2	0	0	0	1	1	2	1	1	0	3	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	2	1	0	-	0	1	0	0	0	0	0	0
M. (Megella) malimbana	1	0	0	4	1	1	0	1	1	0	1	0	0	2	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	1	0	0	0	0
M. (Megella) pseudomonticola	0	2	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	2	1	1	0	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	2	0	0	1	2	0	0	-	0	1	0	0	0	1	1	0
M. (Mitchellapis) fabricator	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	1	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	1	0	0
M. (Pseudomegachile) ericetorum	0	1	1	0	1	1	0	1	1	0	1	1	0	2	0	0	0	0	1	2	1	1	0	2	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	2	0	0	-	0	2	0	0	0	0	0	0
M. (Archimegachile) flavipes	0	1	1	0	1	1	0	1	1	0	1	0	1	2	0	0	0	0	1	2	1	1	0	2	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	-	0	2	0	0	0	0	0	0
M. (Neglectella) armatipes	0	0	0	0	1	1	0	1	1	0	1	0	0	2	0	1	0	0	1	2	1	1	0	1	1	1	1	0	0	0	2	1	1	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0	-	0	1	0	0	0	0	0	0
M. (Xenomegachile) albocincta	0	1	0	0	1	1	0	1	1	0	1	1	0	1	0	1	0	1	1	2	1	1	0	2	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	1	2	0	0	-	0	2	0	0	0	1	0	0
M. (Dinavis) muansae	0	0	0	4	1	1	0	1	1	0	0	0	0	2	0	1	0	0	1	2	1	1	0	2	1	1	0	0	0	0	2	1	1	0	1	1	0	0	1	1	0	0	0	0	1	2	0	0	-	0	1	0	0	0	1	0	0
M. (Rhodomegachile) abdominalis	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	2	0	1	0	0	1	1	1	0	0	0	2	0	1	0	1	1	0	0	1	0	1	0	0	0	0	2	0	0	-	0	1	0	0	0	0	0	0
M. (Schizomegachile) mostrosa	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	1	2	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	0	2	0	0	-	0	0	0	0	0	0	0	0
M. (Stenomegachile) chelostomoides	0	0	0	0	1	1	0	0	1	0	0	0	0	2	0	0	0	0	1	2	1	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	2	0	0	-	0	0	0	1	0	0	0	0
M. (Stenomegachile) dolichosoma	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	1	1	0	0	0	1	1	1	0	1	1	0	0	0	1	1	2	0	0	1	1	0	0	-	0	1	0	1	0	0	1	0
M. (Thaumatosoma) duboulaii	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0	1	1	2	1	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0	-	0	0	0	1	0	0	0	0
M. (Creightonella) cognata	1	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	2	1	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	-	0	0	0	1	0	1	0	0
M. (Creightonella) albisecta	0	1	1	0	1	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	2	0	1	1	0	0	0	-	0	0	0	1	0	1	0	0
M. (Matangapis) alticola	0	0	0	0	1	0	0	1	1	0	0	0	0	2	0	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	2	0	1	1	0	0	0	0	1	0	1	0	-	0	0	0	1	0	0	0	0
M. (Cuspidella) quadraticauda	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	1	0	1	2	0	0	-	0	2	0	1	0	0	0	0
Radoszkowskiana rufiventris	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	-	0	1	0	1	0	0	0	0
C. (Liothyrapis) decipiens	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	2	1	0	-	0	1	0	1	0	0	0	0
C. (Rhinocoelioxys) zapoteca	0	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	1	2	1	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	2	1	0	-	0	1	1	1	0	0	0	0
C. (Torridapis) torrida	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0	2	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	1	2	0	0	-	0	1	0	1	0	0	0	0

FIGURES USED IN CHAPTERS I-III

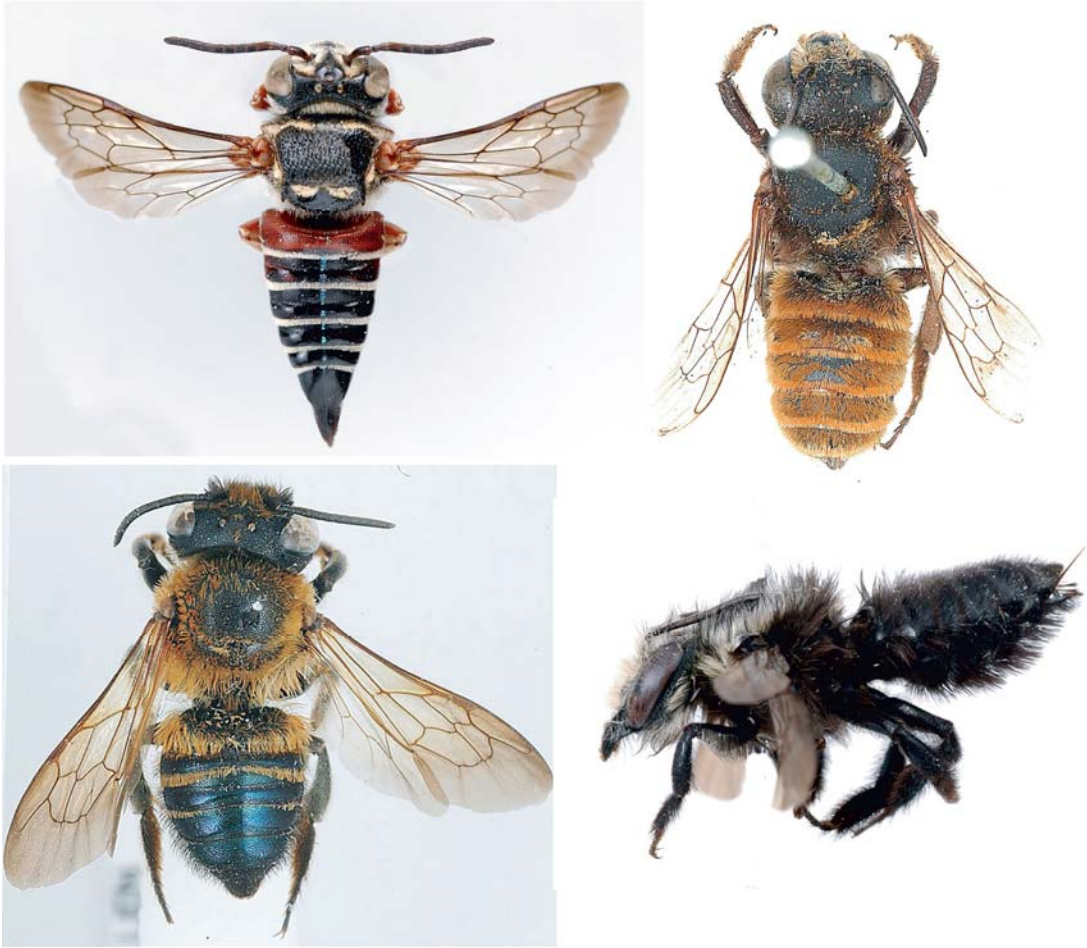
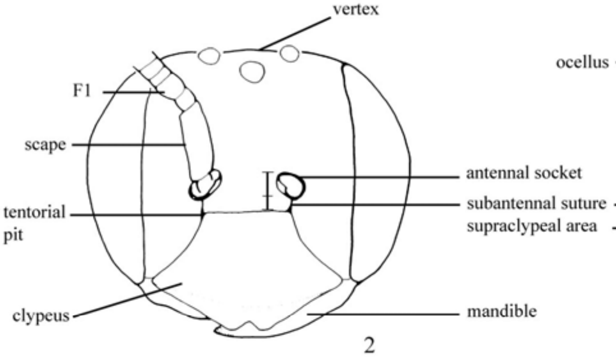


Fig. 1. *Coelioxys* sp. (upper left) and *Megachile* (remaining figures). Male paratype of *M.* (*Cuspidella*) *quadricaudata* (upper right), and females of *M. laticeps* (bottom left) and *M.* (*Cressoniella*) *amparo* Gonzalez, 2006 (bottom right). Photos by Alain Pauly and Daniel Bennett.



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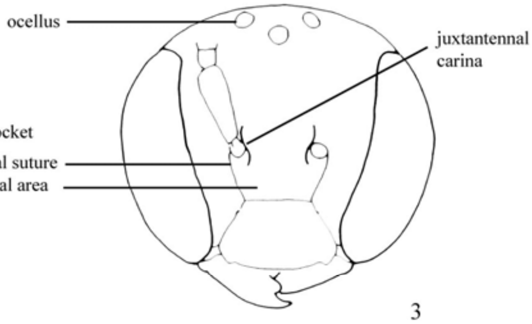

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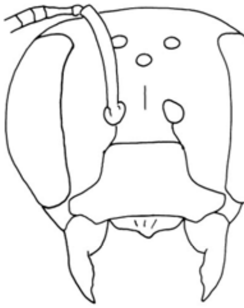

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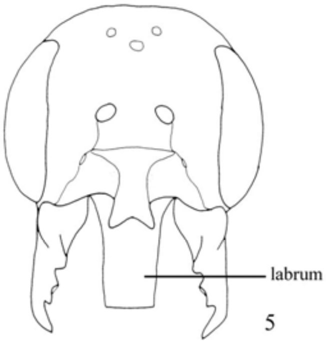

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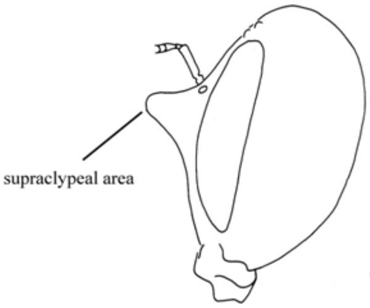

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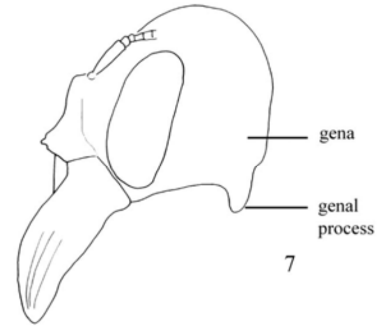

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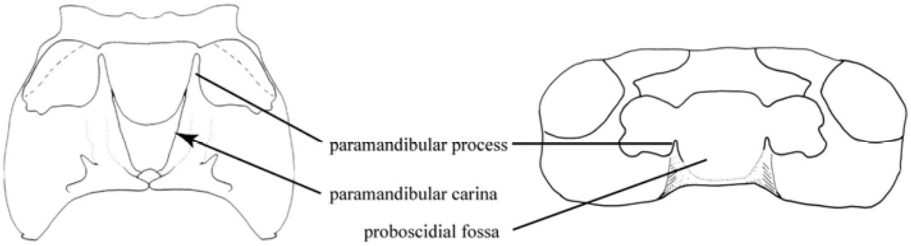
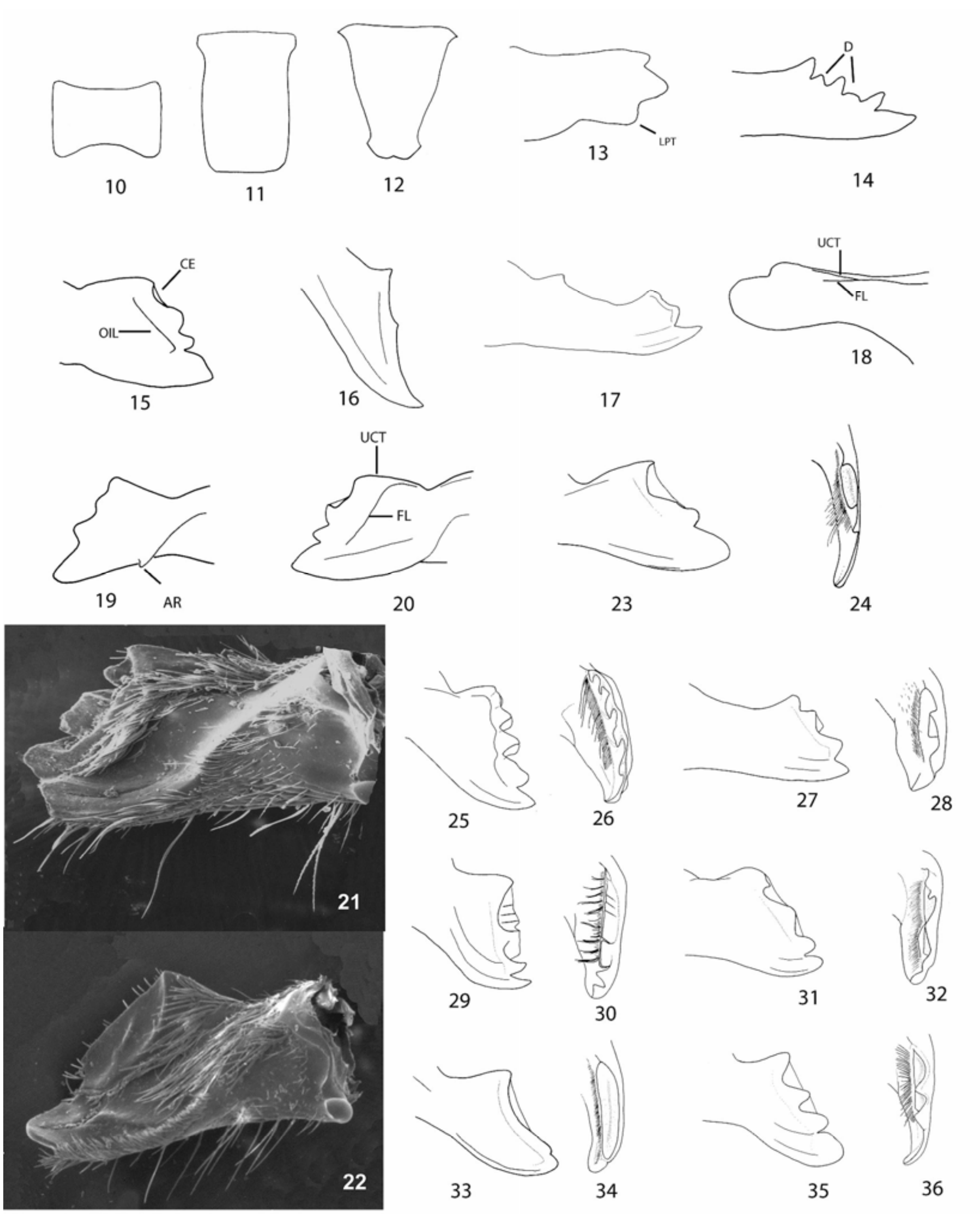


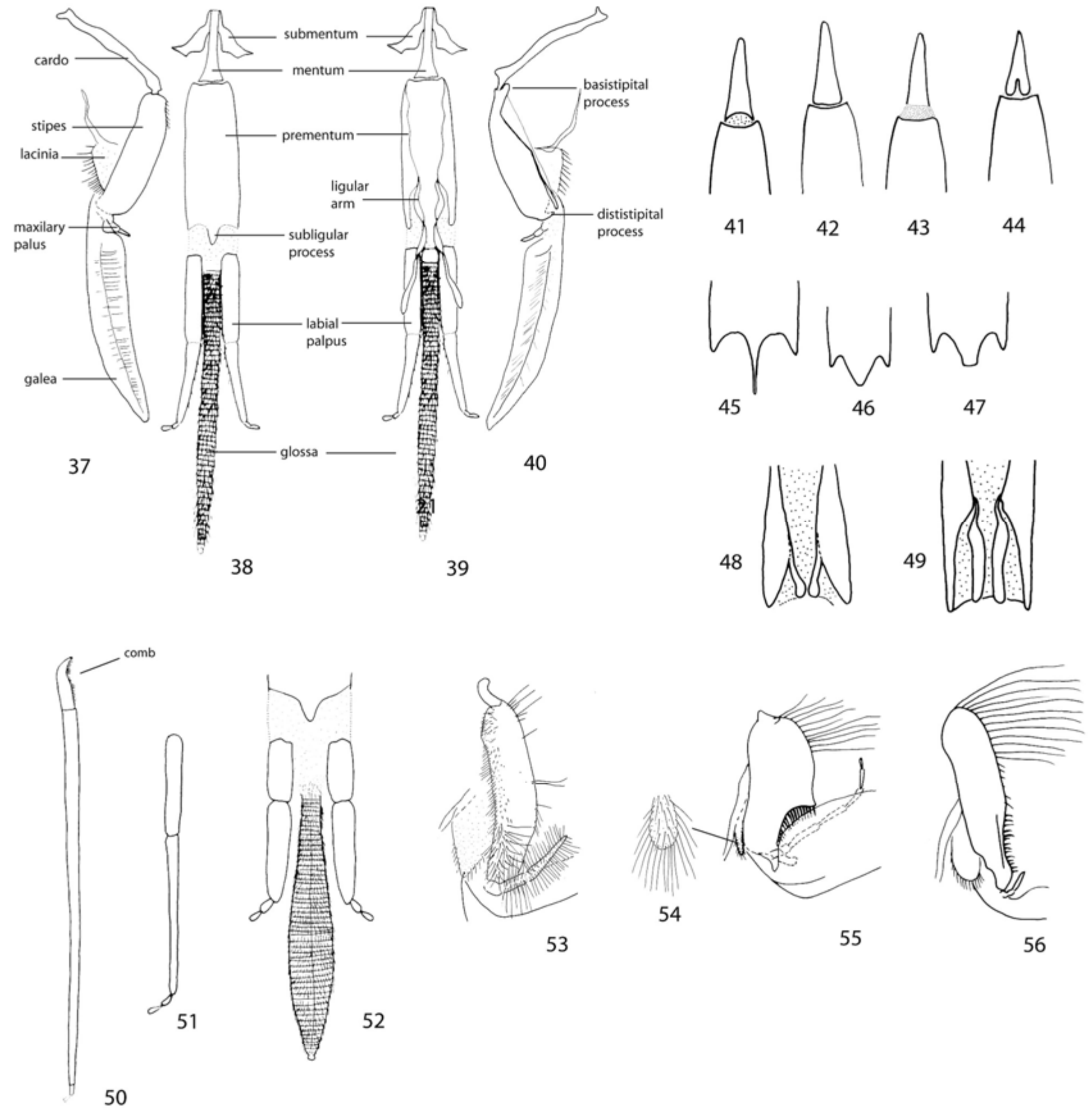
8

9

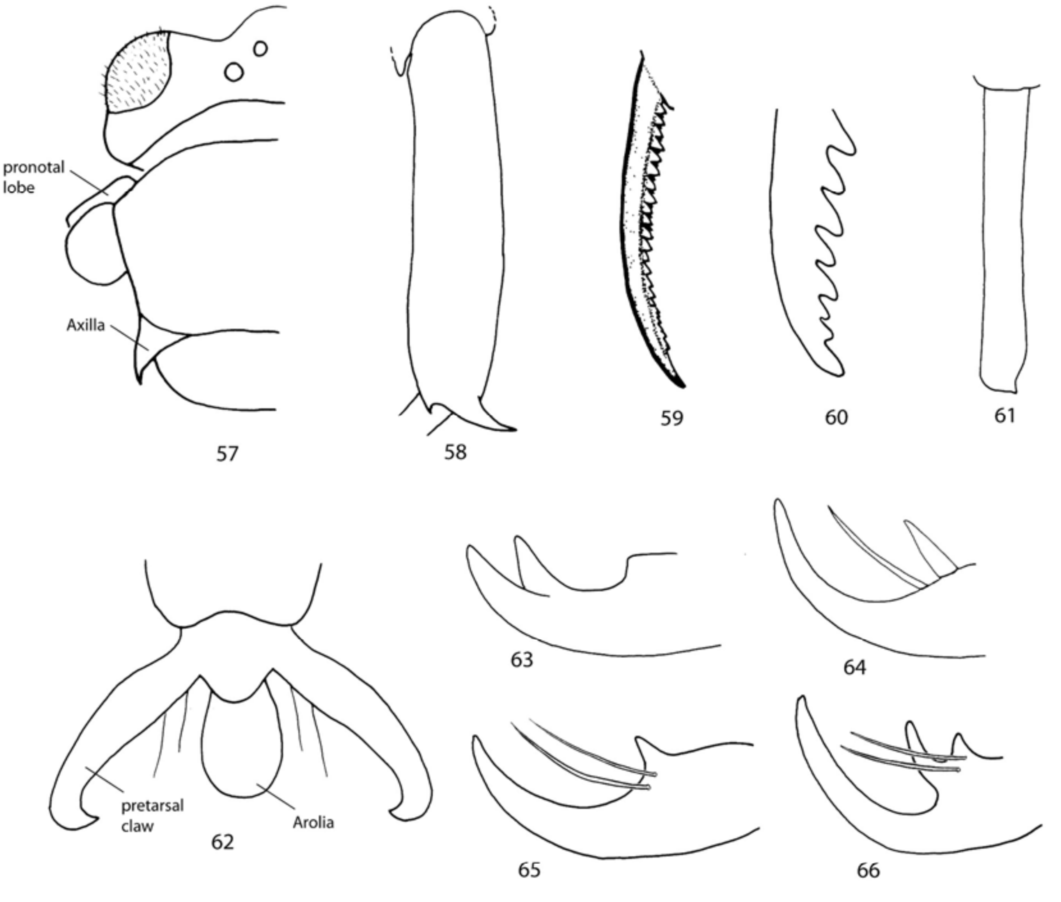
Figs. 2-9. Female heads in frontal (2-5), profile (6, 7), and inferior views (8, 9). *P. orobinus* (2), *Hypanthidiodes currani* (Schwarz) (3), *Xylocopa varians* (4, 9), *M. assumptionis* (5), *Lithurgus* sp. (6), *M. pugnata* (7), *M. monstrosa* (8). Labrum and mandibles are not shown in Figs. 8 and 9.



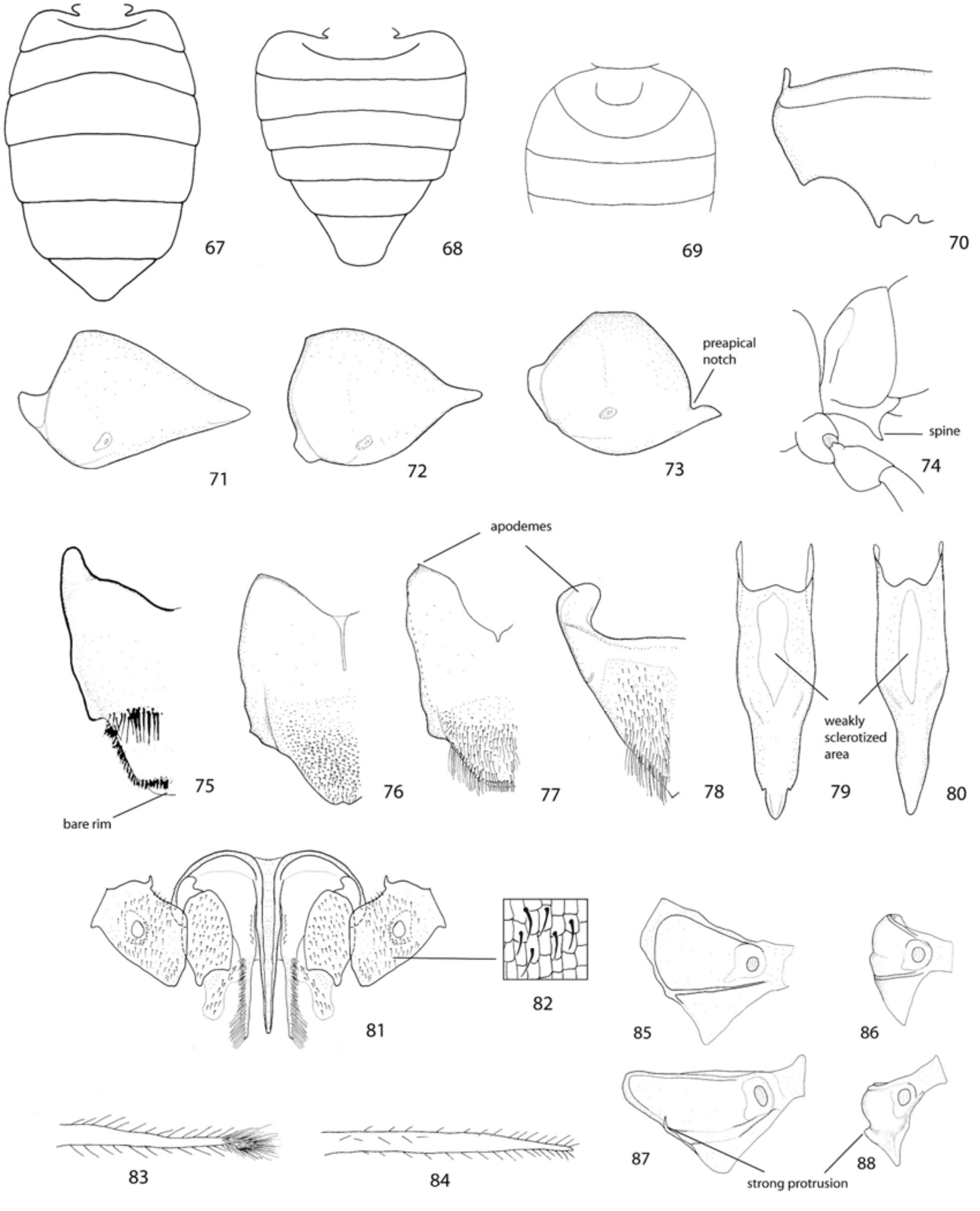
Figs. 10-36 Labrum and mandible of female. Outer view of labrum (10-12) and outer (13-17, 23, 25, 27, 29, 31, 33, 35), inner (18-22), and frontal view of the distal margin (24, 26, 28, 30, 32, 34, 36) of the mandible. *A. manicatum* (14), *F. pallidula* (10, 18), *M. aethiops* (16), *M. albitarsis* (11, 15, 20, 21), *M. bituberculata* (29, 30), *M. bombycina* (27, 28), *M. clotho* (17), *M. cognata* (25, 26), *M. montezuma* (31, 32), *M. oenotherae* (23, 24), *M. parallela* (35, 36), *M. pascoensis* (33, 34), *M. sicula* (22), and *T. wagenknechti* (12, 13). Abbreviations. AR: adductor ridge, CE: cutting edge, D: denticles, LPT: lower preapical tooth, OIL: outer premarginal impressed line, and UCT: upper carina of trimma.



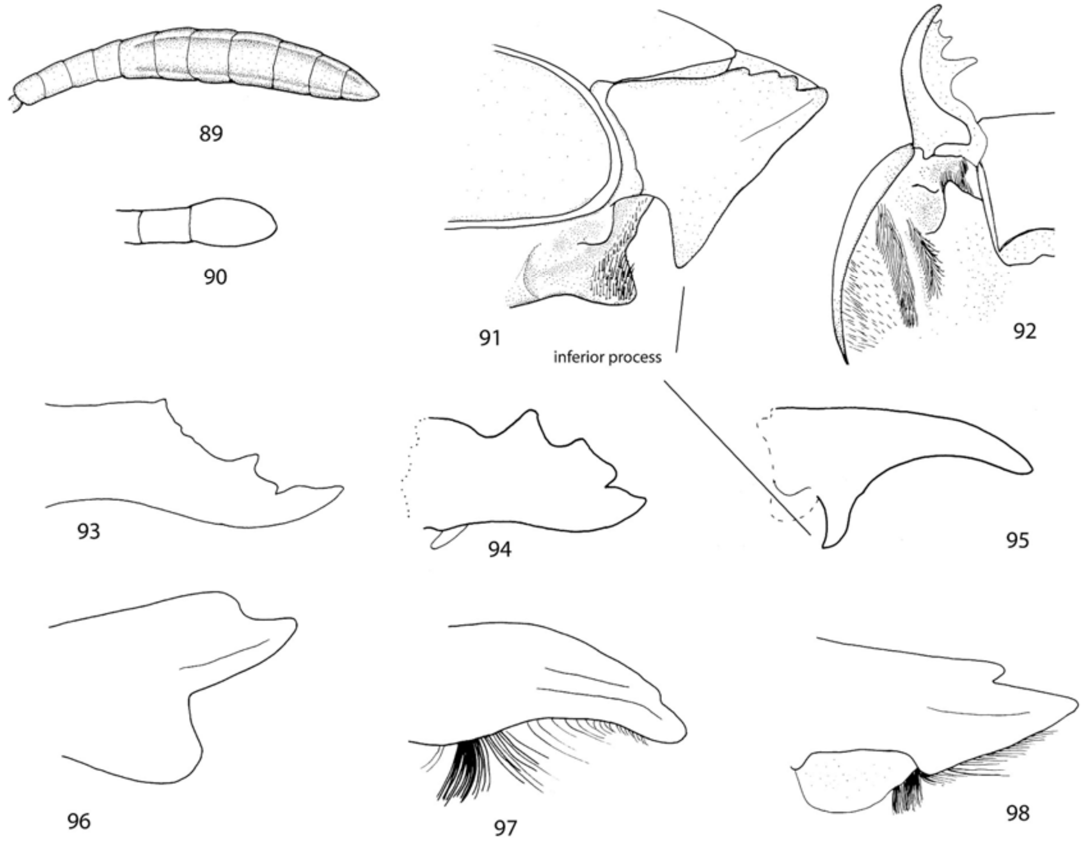
Figs. 37-56. Female mouthparts. Outer and inner views of maxilla (37, 40), anterior and posterior views of labium (38, 39), details of mentum (41-44), subligular process (45-47), ligular arm (48, 49), labial palpi (50, 51), glossa (52), lacinia (54), and outer view of stipes (53, 55, 56). *A. deceptum* (46, 56), *C. zapoteca* (43), *F. pallidula* (41), *L. apicalis* (44, 48, 50), *M. abdominalis* (52), *M. albitarsis* (47, 49), *M. clotho* (53), *M. parallela* (37-40), *O. californica* (51), *P. orobinus* (42), *T. wagenknechti* (45), and *X. varians* (54, 55).



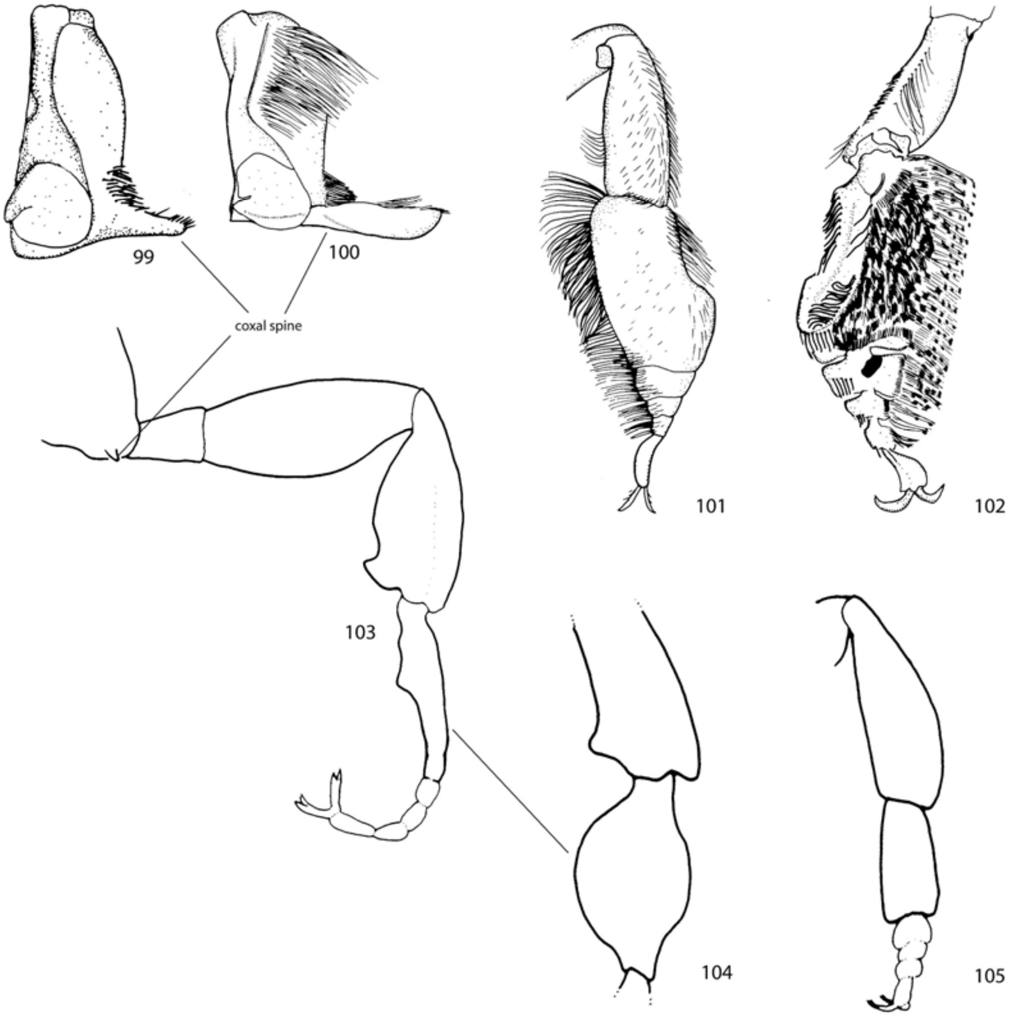
Figs. 57-66. Female mesosoma. Dorsal view of head and mesosoma (57), outer view of fore tibia (58), outer hind tibial spur (59-61), pretarsal claws in frontal (62) and profile views (63-66). *Coelioxys* sp. (57), *D. productus* (63), *M. albitarsis* (64), *M. ferox* (65), *M. monstrosa* (66), *M. parallela* (59), *M. pseudomonticola* (61), *M. pugnata* (58), *M. striatulus* (62), and *P. orobinus* (60).



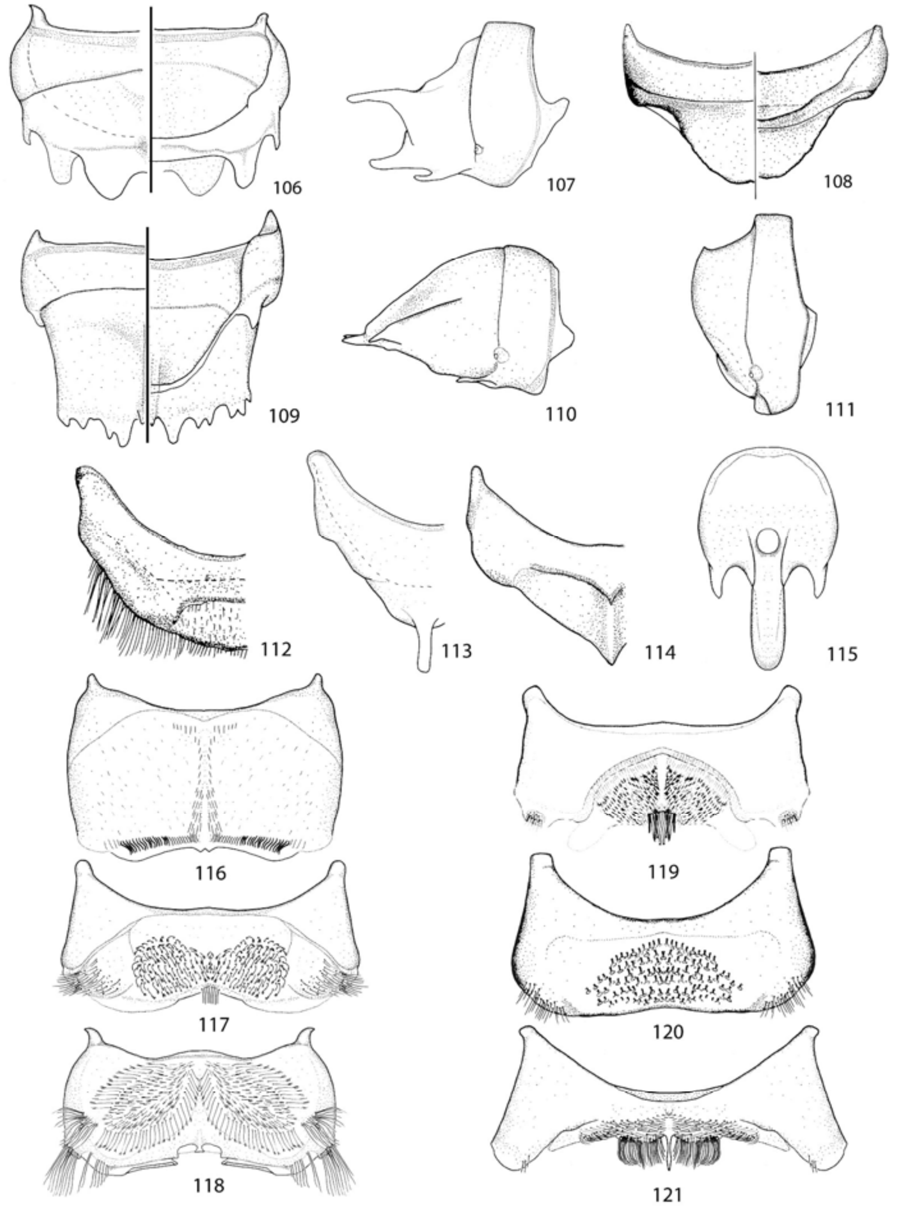
Figs. 67-88. Female metasoma. Dorsal views of metasoma (67, 68), T1-T3 (69), T6 in dorsal (70) and profile views (71-73), T1 and S1 in profile (74), S6 (75-80), sting apparatus and detail of sculpturation of lamina spiracularis (81, 82), detail of gonostylus (83-84), and lateral (85, 87) and profile (86, 88) views of T7 hemitergite. *A. deceptum* (70), *A. repetitum* (84), *C. zapoteca* (80), *C. assumptionis* (79), *L. spiniferus* (69), *M. aethiops* (72), *M. albitarsis* (75, 83, 87, 88), *M. assumptionis* (67), *M. cognata* (77), *M. georgica* (73), *M. monstrosa* (74), *M. montezuma* (71), *M. spissula* (76), *M.* (*Tylomegachile*) sp. (68), *O. texana* (85, 86), *T. mitchelli* (81, 82), and *X. varians* (78).



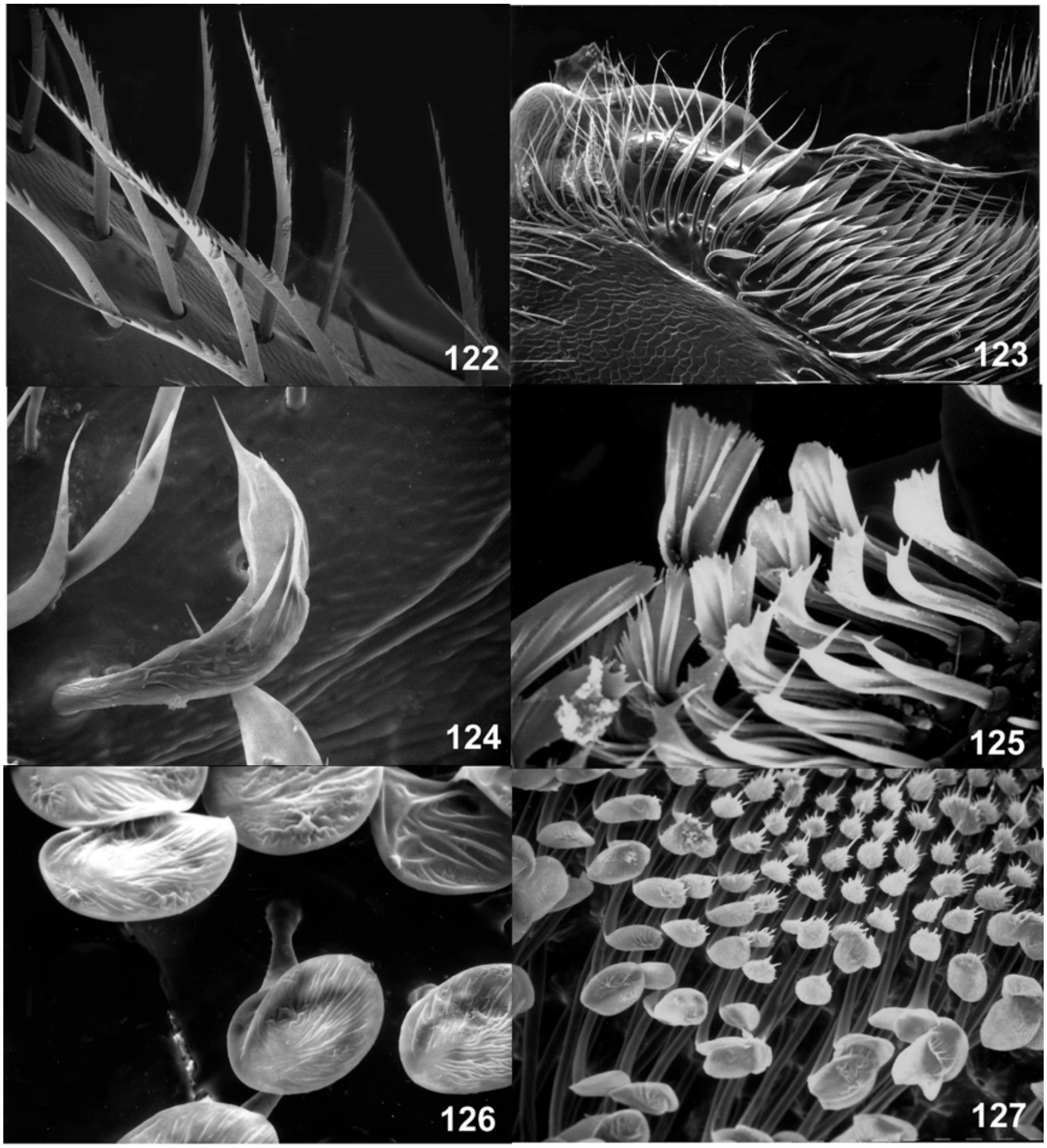
Figs. 89-98. Males. Ventral view of antennal flagellum (89), last two flagellomeres (90), profile and ventral views of head (91, 92), and outer (93, 94, 96-98) and inferior (95) views of mandibles. *M. albitarsis* (90-92), *M. biseta* (96), *M. bombiformis* (89), *M. cockerelli* (93), *M. longuisetosa* (89, 90), *M. maxillosa* (92), and *M. monstrosa* (93).



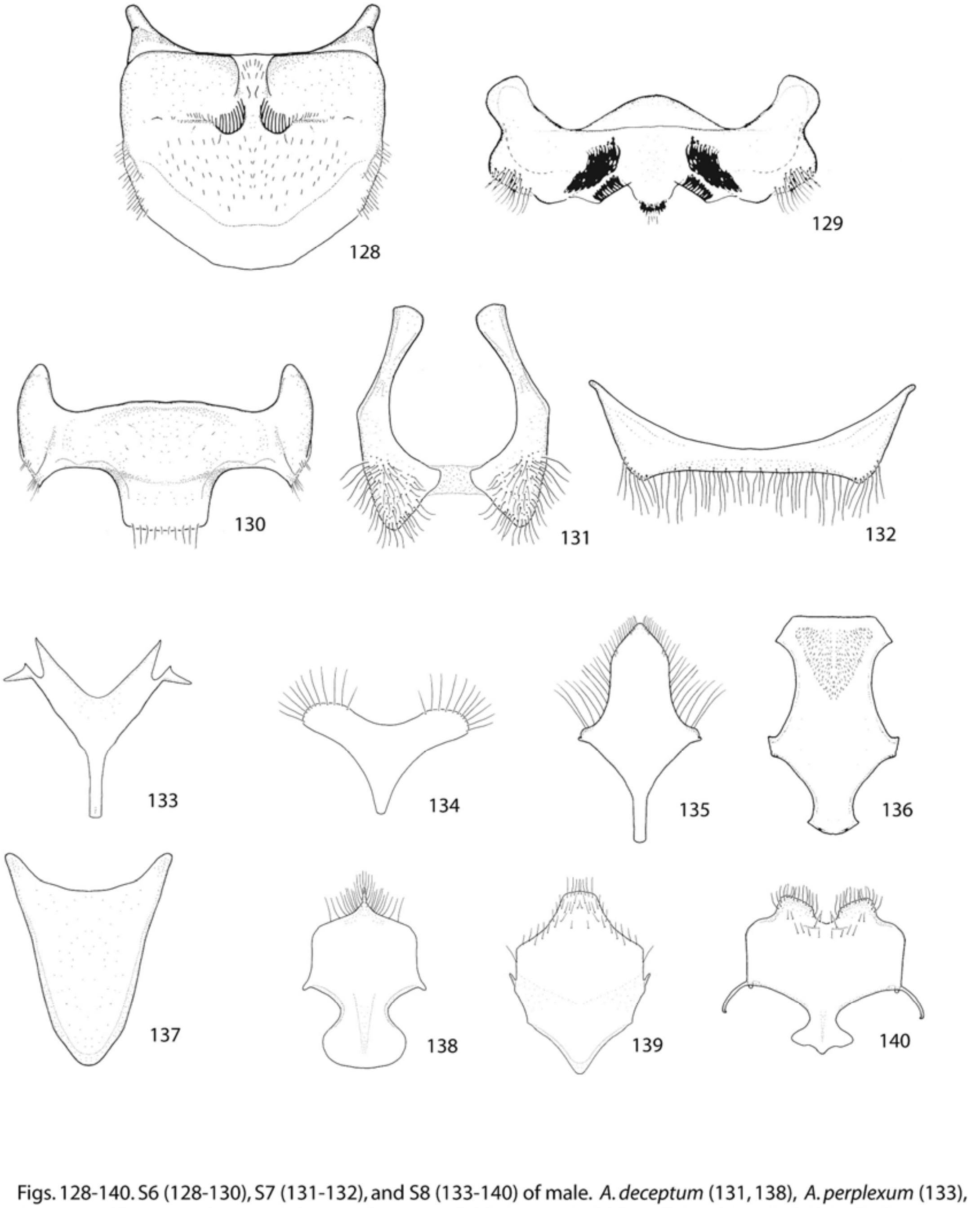
Figs. 99-105. Legs of Males. Front coxa (99, 100), outer and inner views of front leg (101, 102), mid leg in profile (103), outer view of mid basitarsus (104), and hind tibia and tarsi (105). *M. albitarsis* (100-105) and *M. longuisetosa* sp. nov. (99).



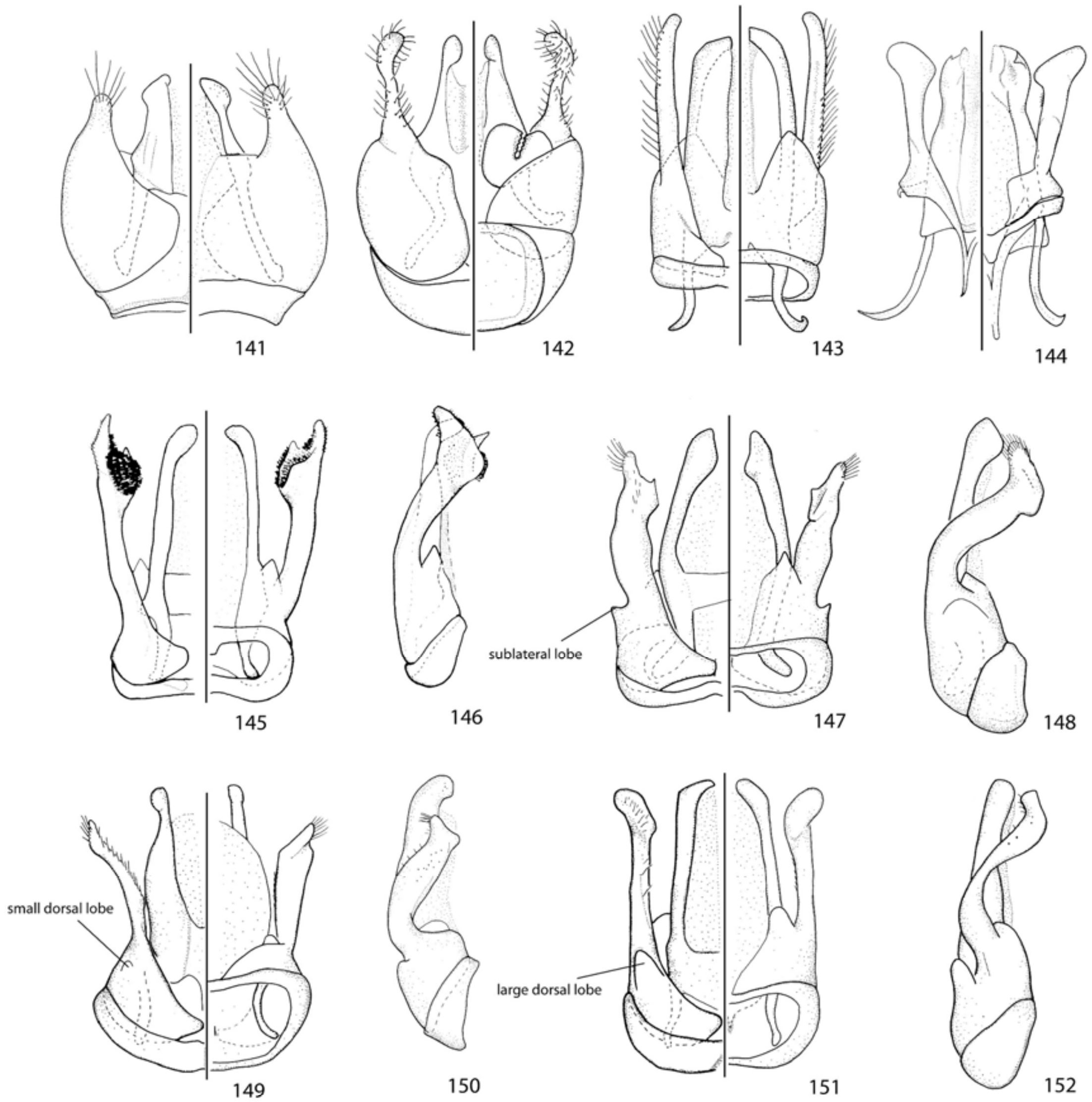
Figs. 106-121. Terminal segments of male metasoma. Dorsal (left half), ventral (right half) (106, 108, 109), and profile views (107, 110, 111) of T6, dorsal view of T7 (112-115), and S5 (116-121). *F. pallidula* (115), *M. albitarsis* (119), *M. albocincta* (118), *M. alticola* (111), *M. cockerelli* (106, 107, 113), *M. cognata* (109, 110, 114,116), *M. longuisetosa* sp. nov. (108, 112), *M. oenotherae* (117), *M. sabinensis* (120), and *M. pruina* (121).



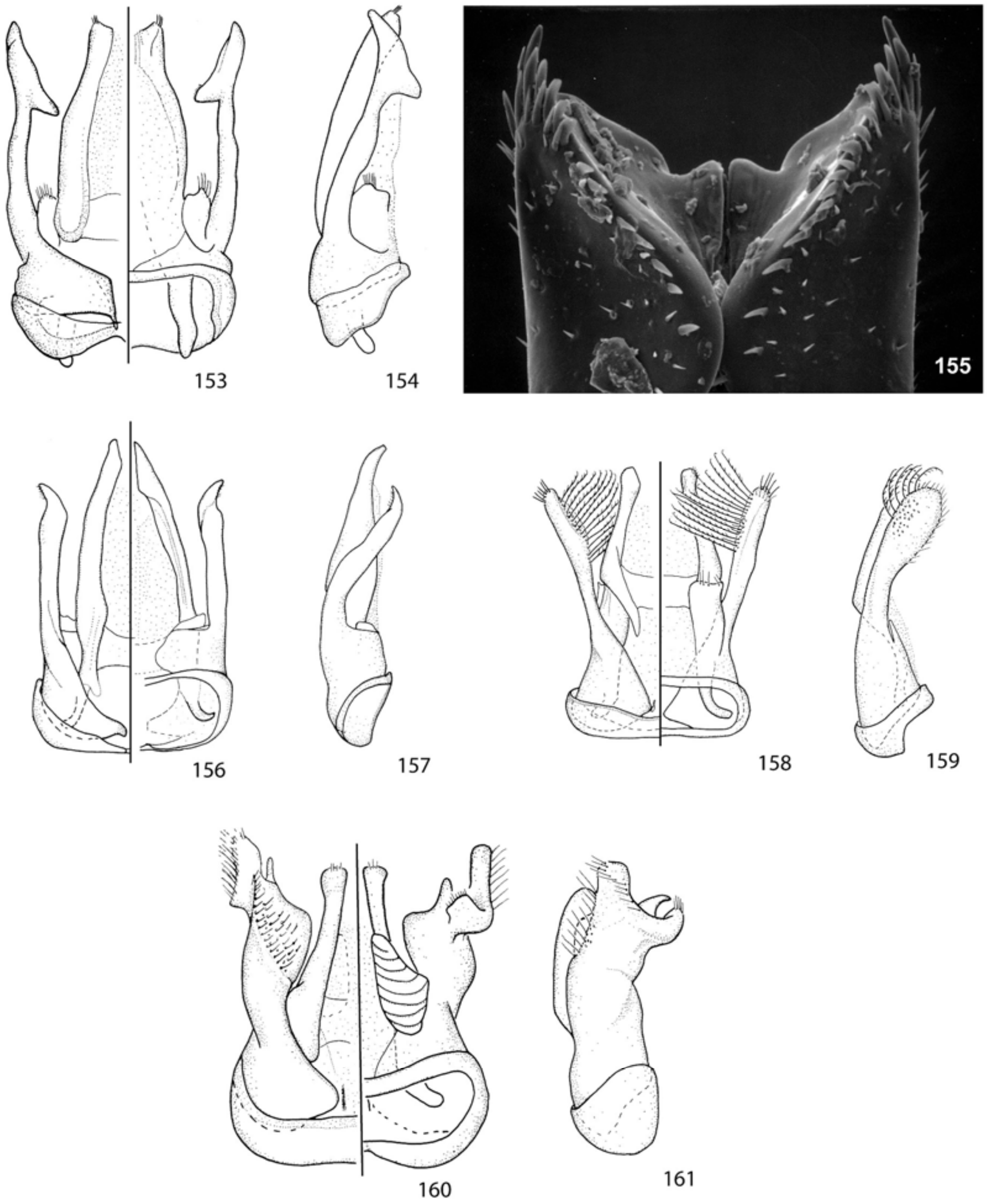
Figs. 122-127. Types of hairs found on the S4-S6 of malea. Branched, unmodified (122), acuminate (123, 124), fan-shaped (125), and capitate-spatulate (126, 127). *M. albitarsis* (122), *M. centuncularis*, S4 (123), *M. exilis*, S6 (125), *M. fortis*, S5 (127), *M. sicula*, S6 (124), and *M. rugifrons*, S5 (126).



Figs. 128-140. S6 (128-130), S7 (131-132), and S8 (133-140) of male. *A. deceptum* (131, 138), *A. perplexum* (133), *C. texana* (135), *D. productus* (137), *H. bituberculata* (139), *L. apicalis* (132, 134), *M. albitarsis* (129, 136), *M. cognata* (128), *M. petulans* (130), and *T. mitchelli* (140).



Figs. 141-152. Male genitalia in dorsal and ventral (lefth and right half, 141-145, 147, 149, 151), and profile views (146, 148, 150, 152). *A. perplexum* (144), *H. timberlakei* (143), *L. apicalis* (141), M. anthidioides (147, 148), *M. albitarsis* (145, 146), *M. centuncularis* (149, 150), *M. montezuma* (151, 152), and *P. orobinus* (142).



Figs. 153-161. Male genitalia in dorsal and ventral (lefth and right half, 153, 156, 158, 160), and profile views (154, 157, 159, 161), and detail of the apex of penis valvae (155). *M. albocincta* (158, 159), *M. cockerelli* (156, 157), *M. laeta* (160, 161), *M. parietina* (153, 154), and M. sicula (155).

Fig. 162. Phylogenetic analysis of the tribes of Megachilinae. Strict consensus tree based on the analysis of 110 morphological characters (Appendix I) (L = 402, CI = 33, RI = 71). Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

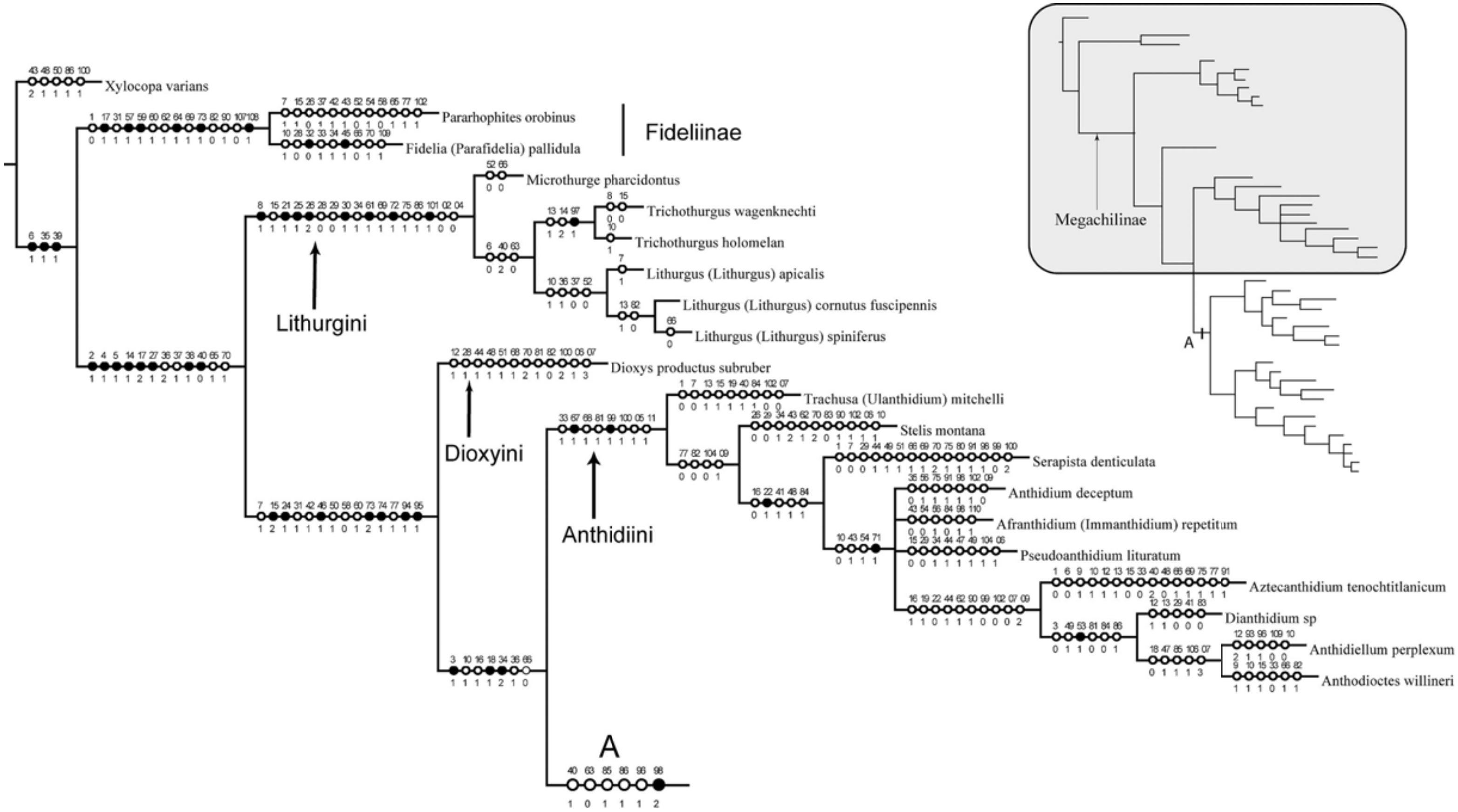


Fig. 163a. Phylogenetic analysis of the tribes of Megachilinae. The part of the tree within the shaded area of upper right figure is shown. Strict consensus tree based on the analysis of 110 morphological characters (Appendix I) (L = 402, CI = 33, RI = 71). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix II, are placed above and below each change.

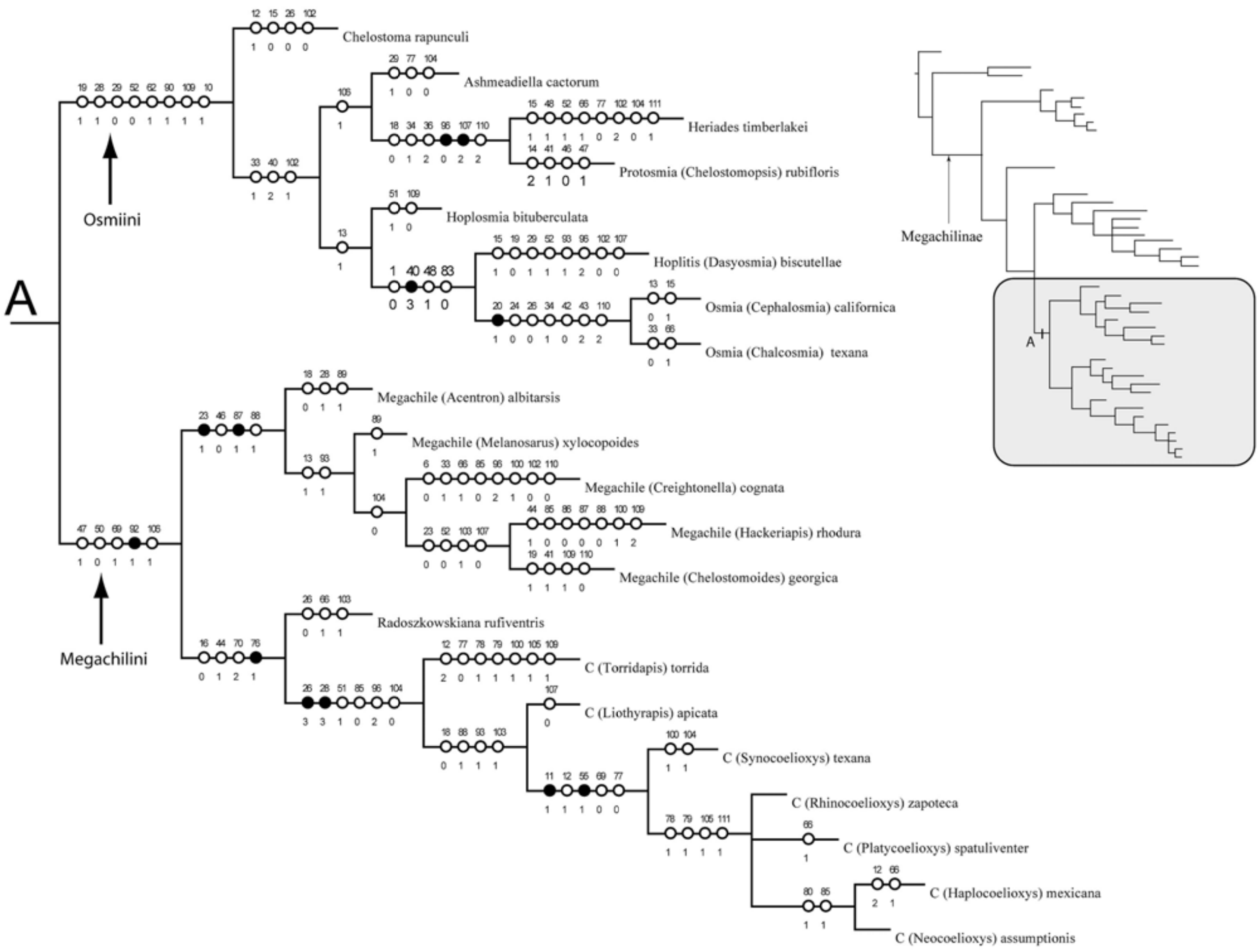


Fig. 163b. Phylogenetic analysis of the tribes of Megachilinae. The part of the tree within the shaded area of upper right figure is shown. Strict consensus tree based on the analysis of 110 morphological characters (Appendix I) (L = 402, CI = 33, RI = 71). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix II, are placed above and below each change.

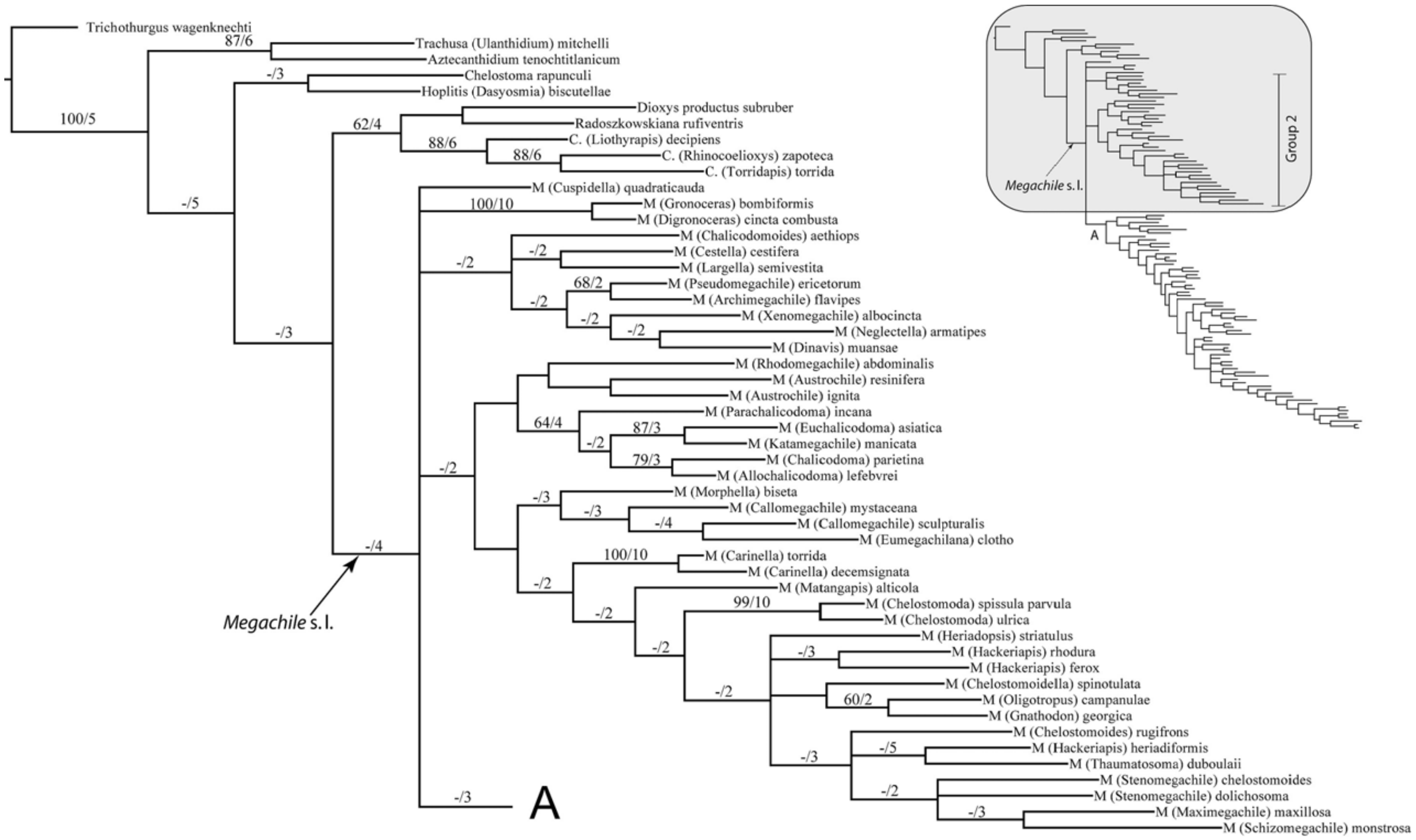


Fig. 164a. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Analysis A; strict consensus tree based on the full data matrix of 231 morphological characters (L = 2249, CI = 13, RI = 52) . Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

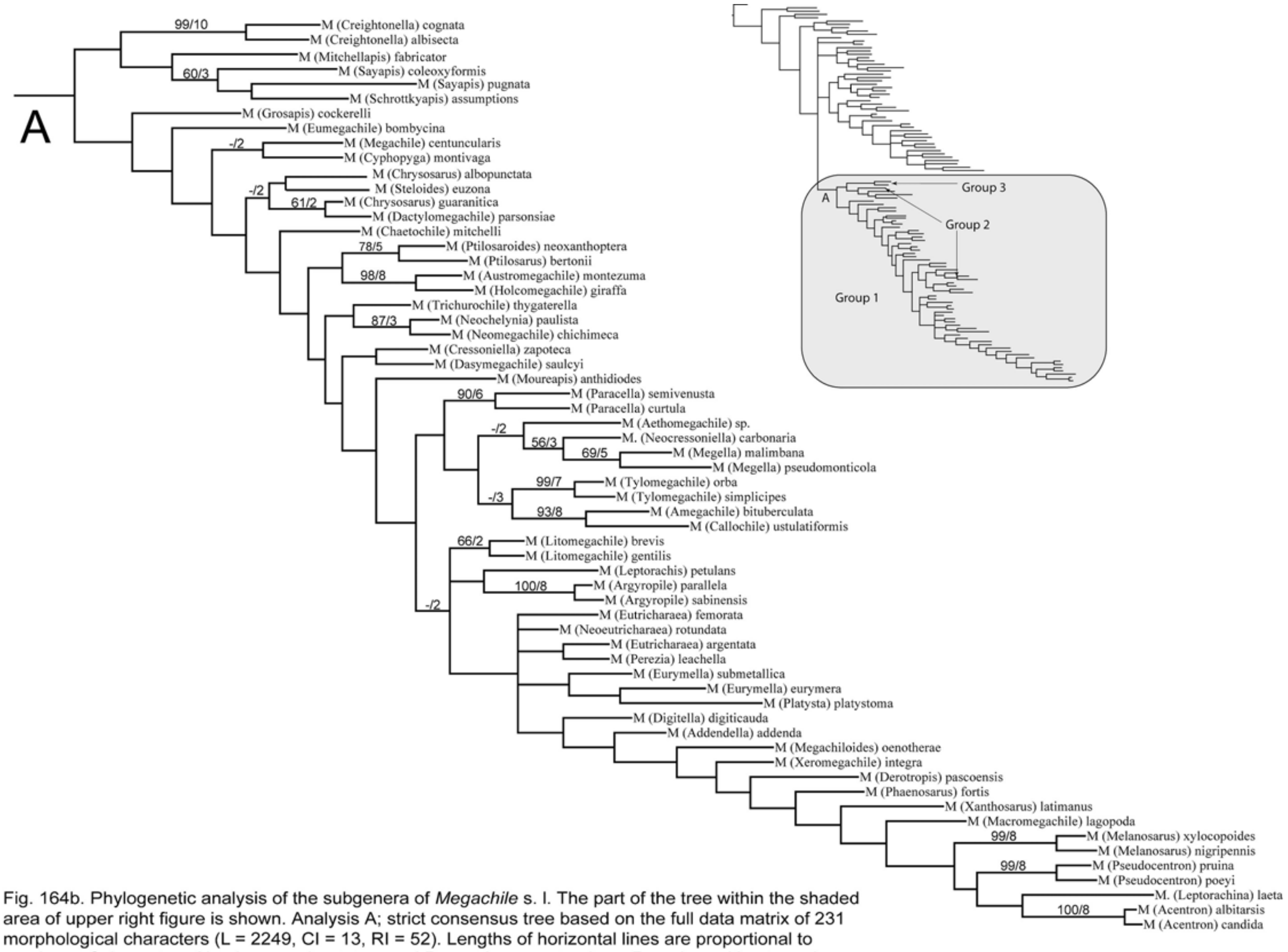


Fig. 164b. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Analysis A; strict consensus tree based on the full data matrix of 231 morphological characters (L = 2249, CI = 13, RI = 52). Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

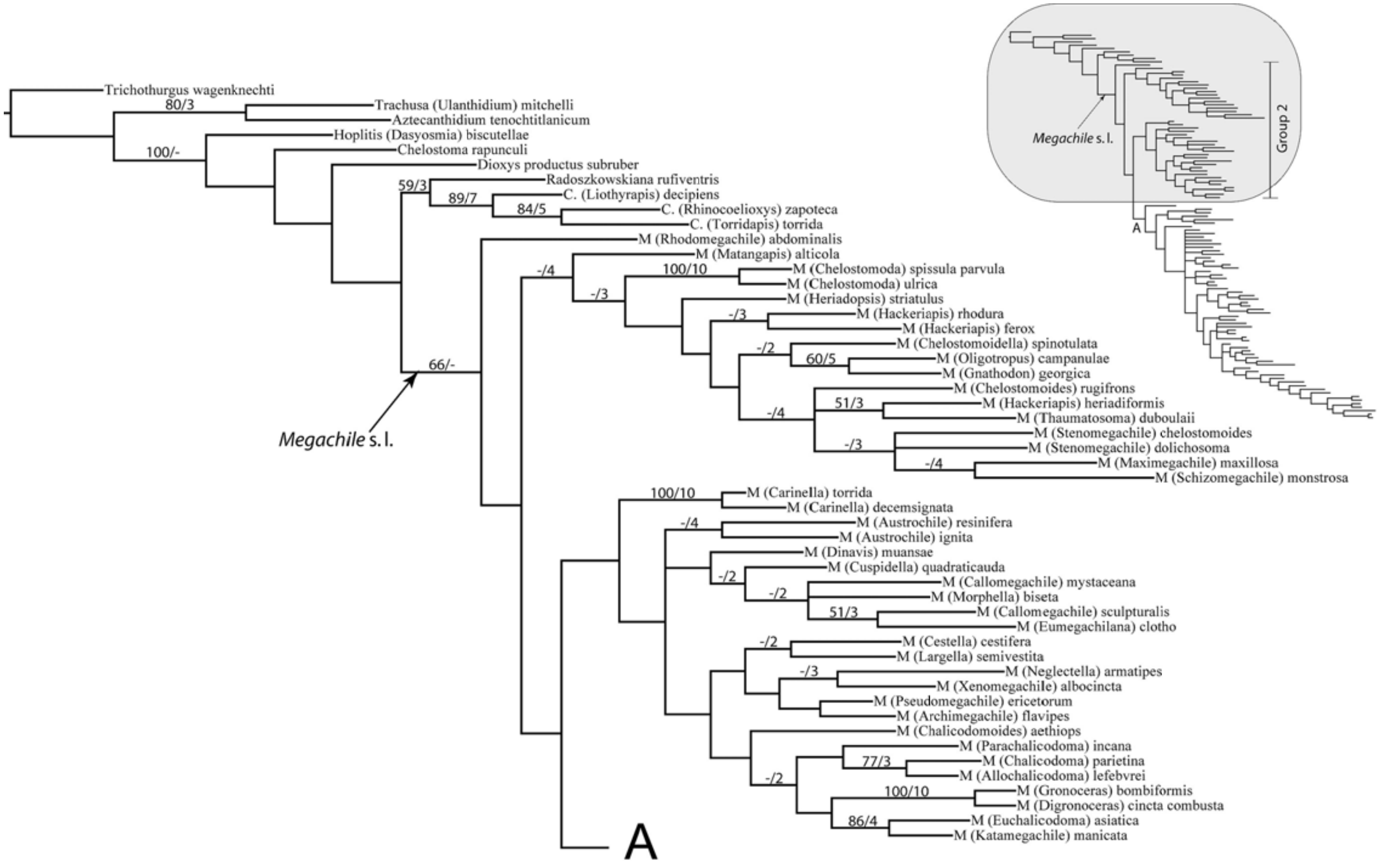


Fig. 165a. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

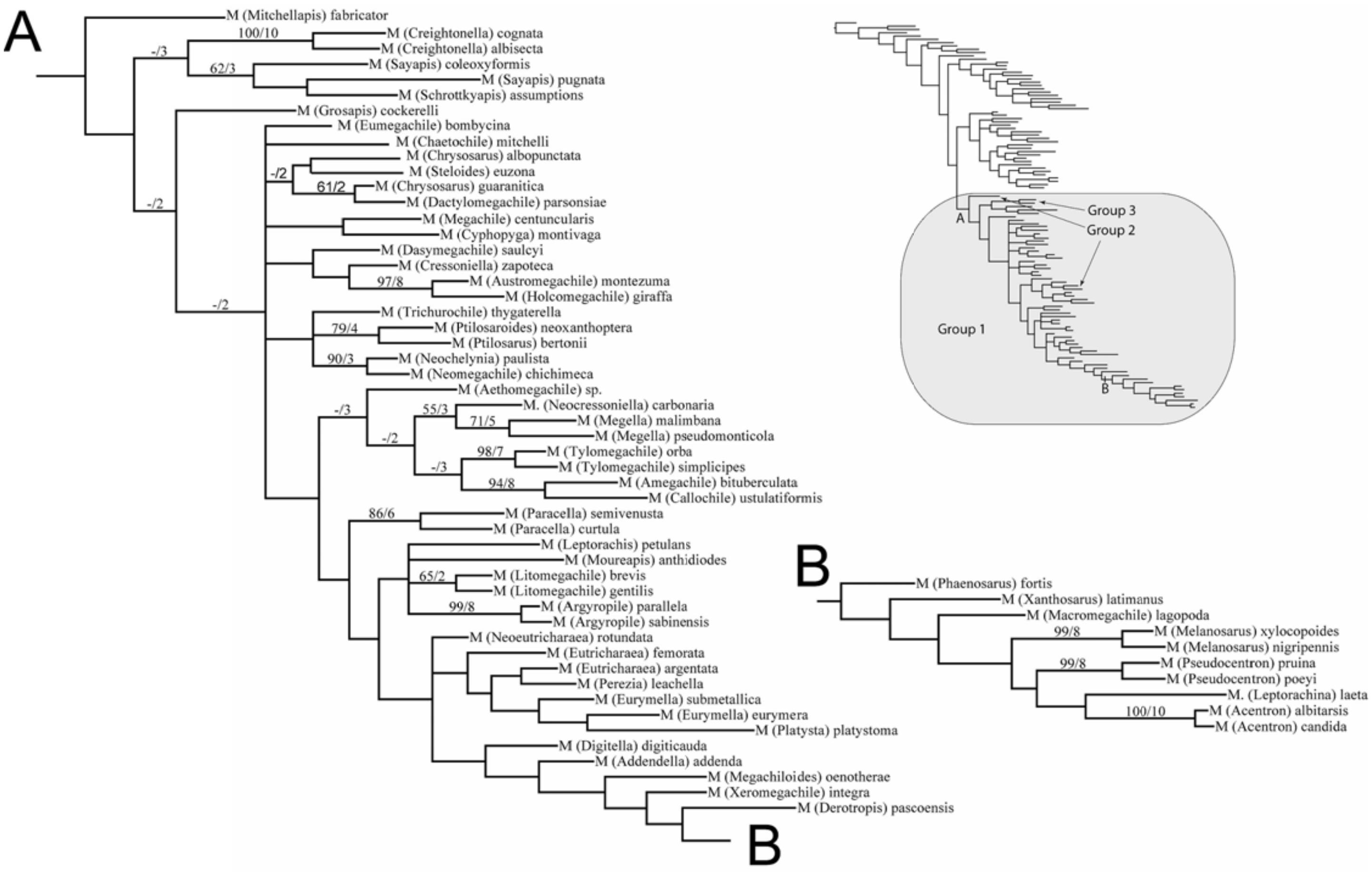


Fig. 165b. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51) . Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

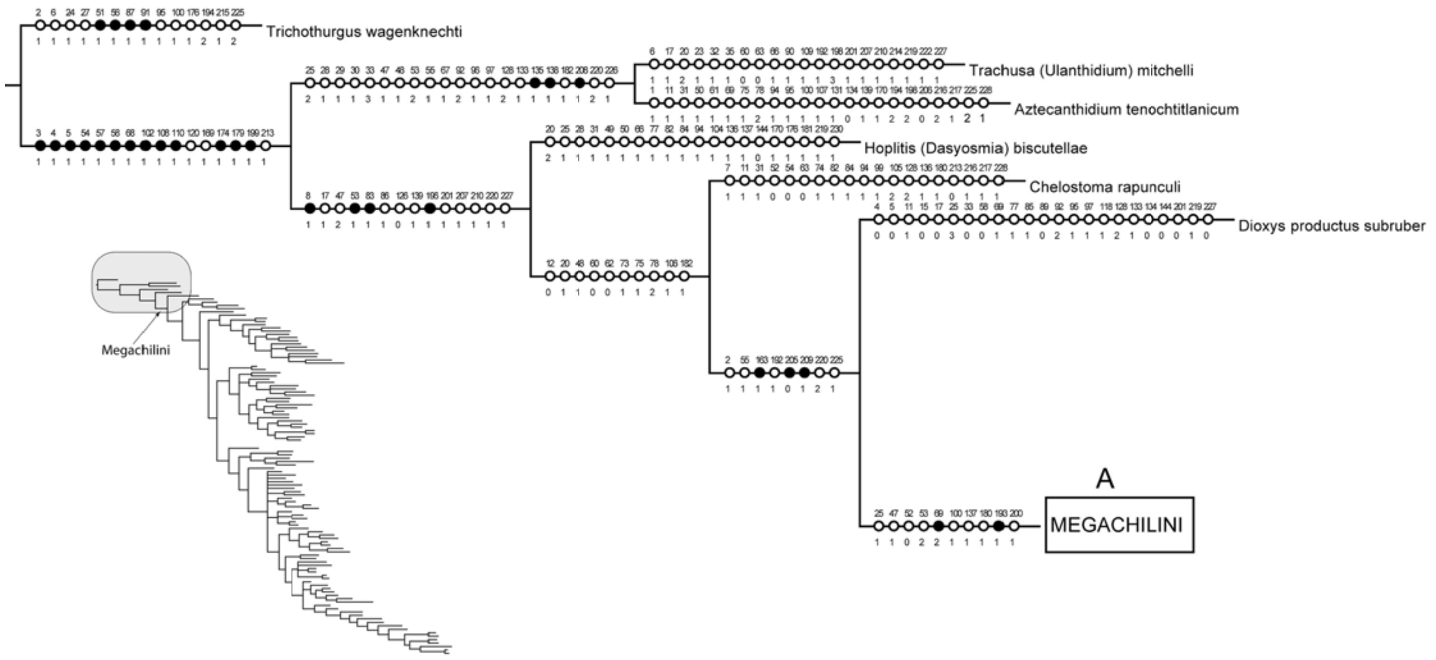


Fig. 166a. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower left figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

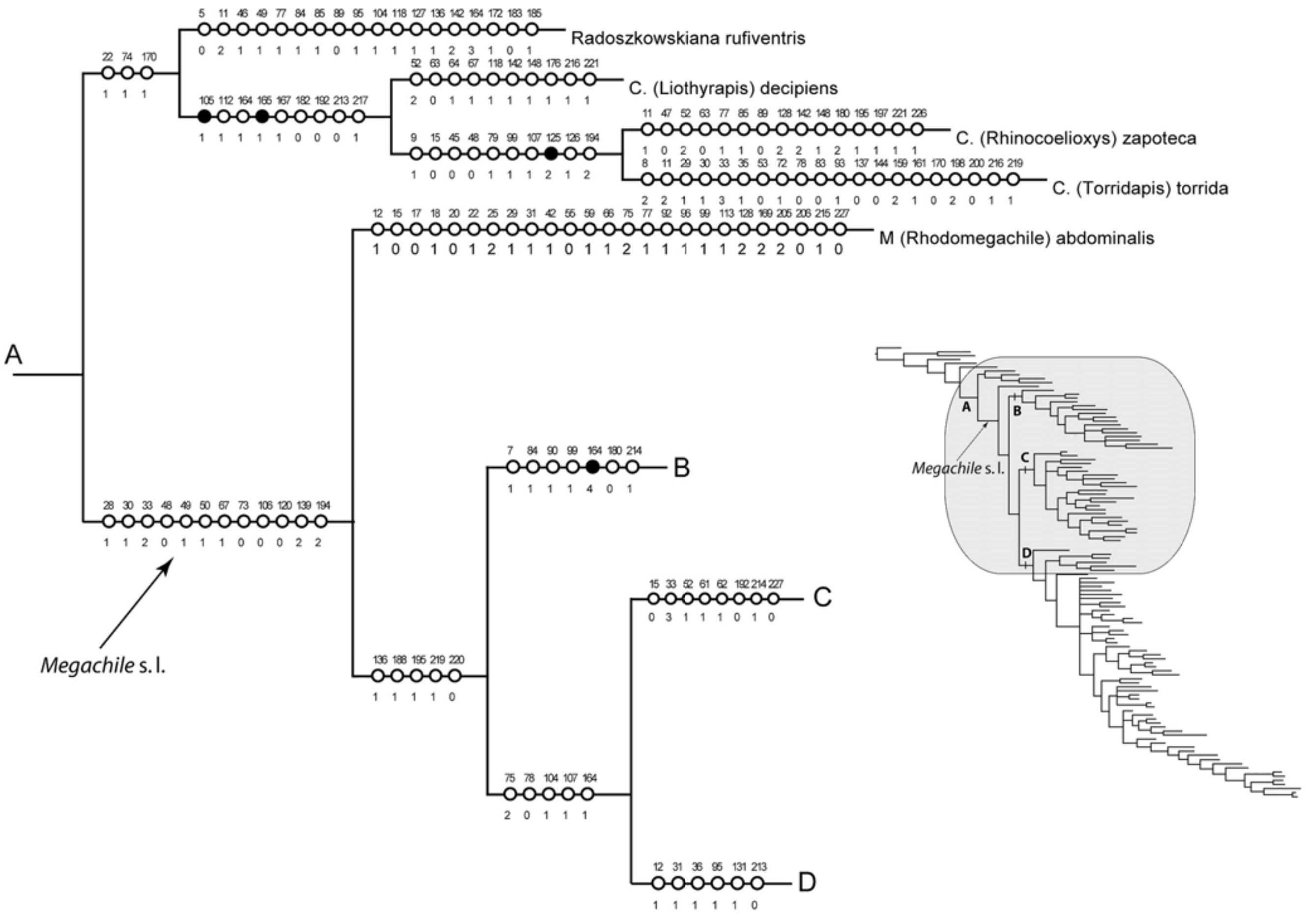


Fig. 166b. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

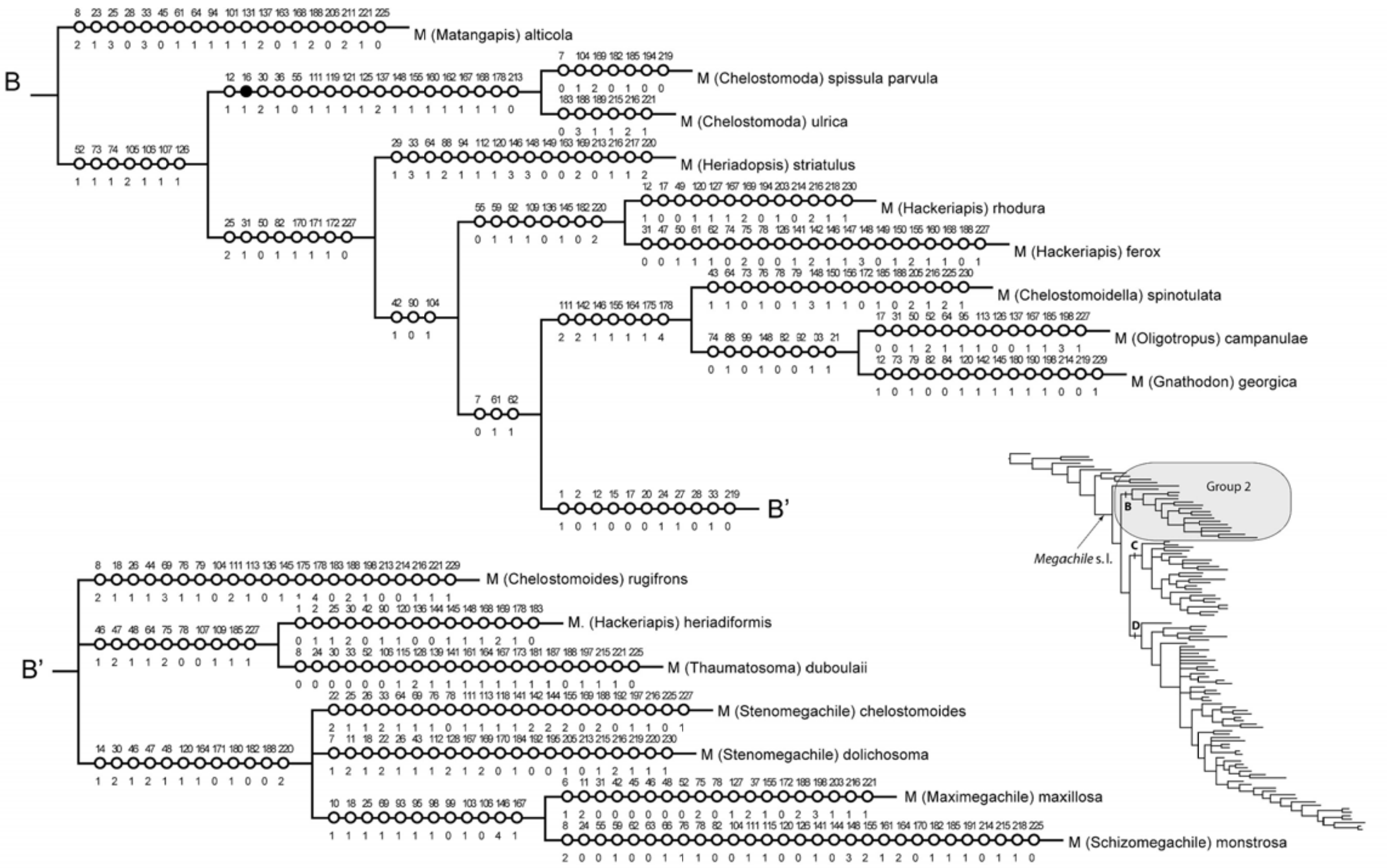


Fig. 166c. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

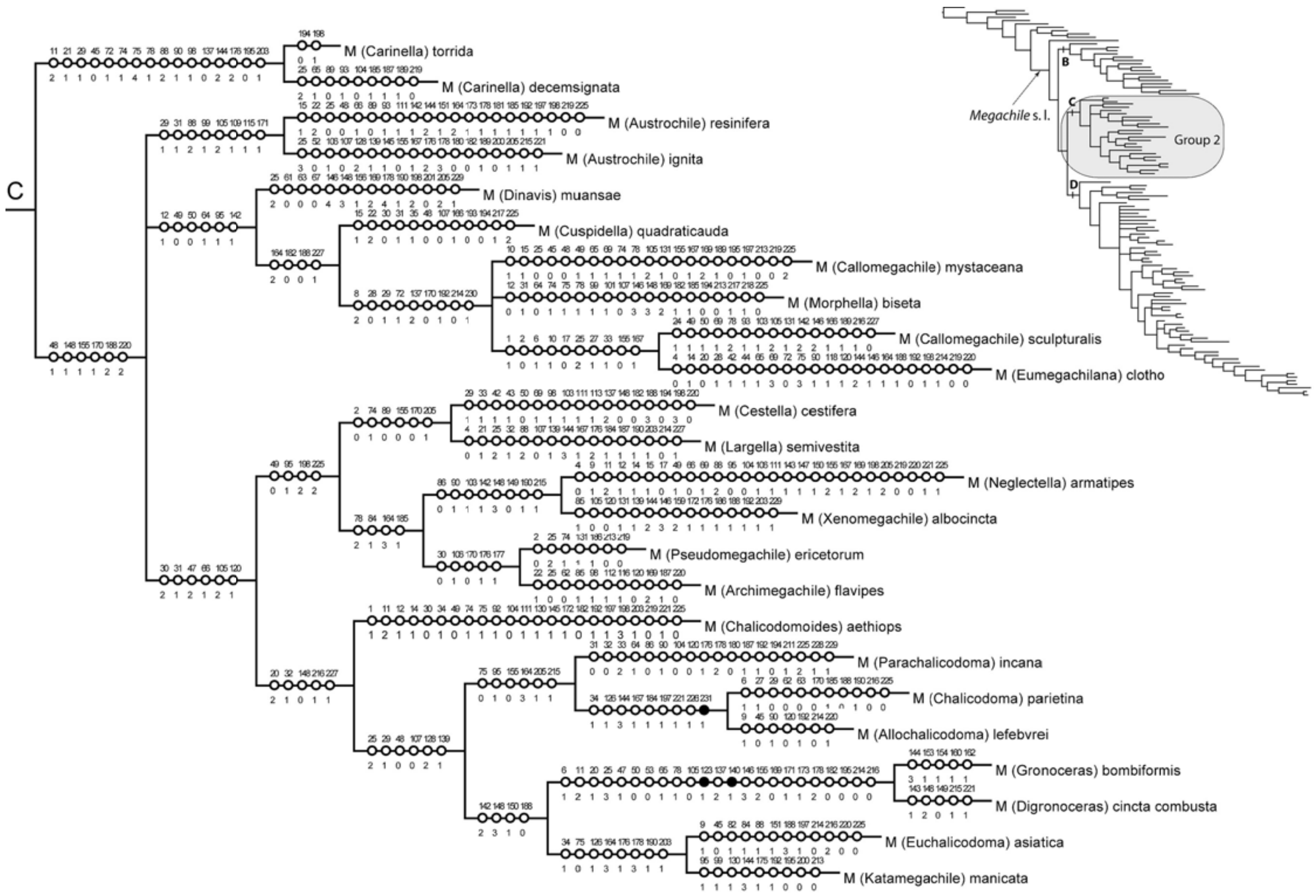


Fig. 166d. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

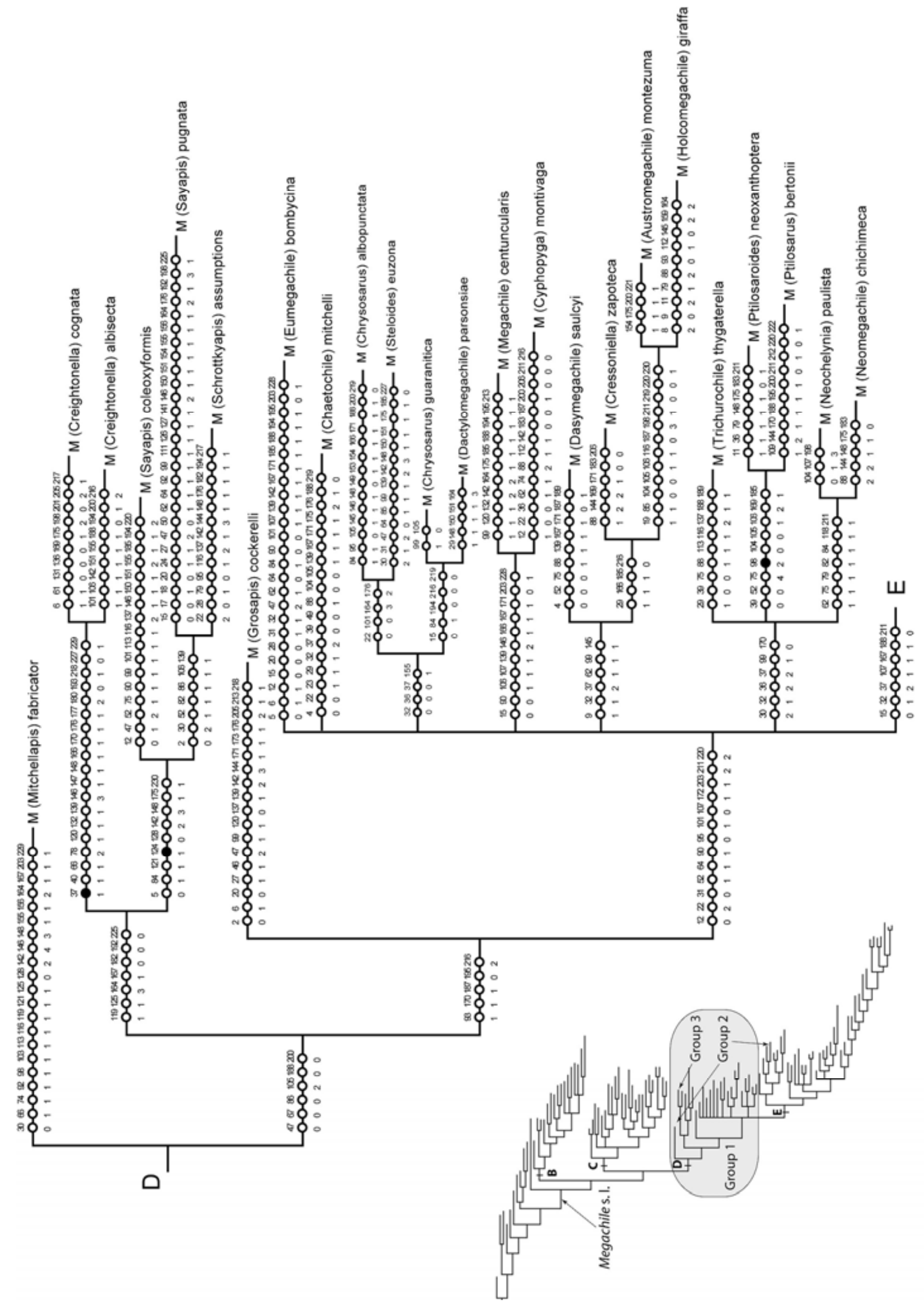


Fig. 166e. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower left figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; changes; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

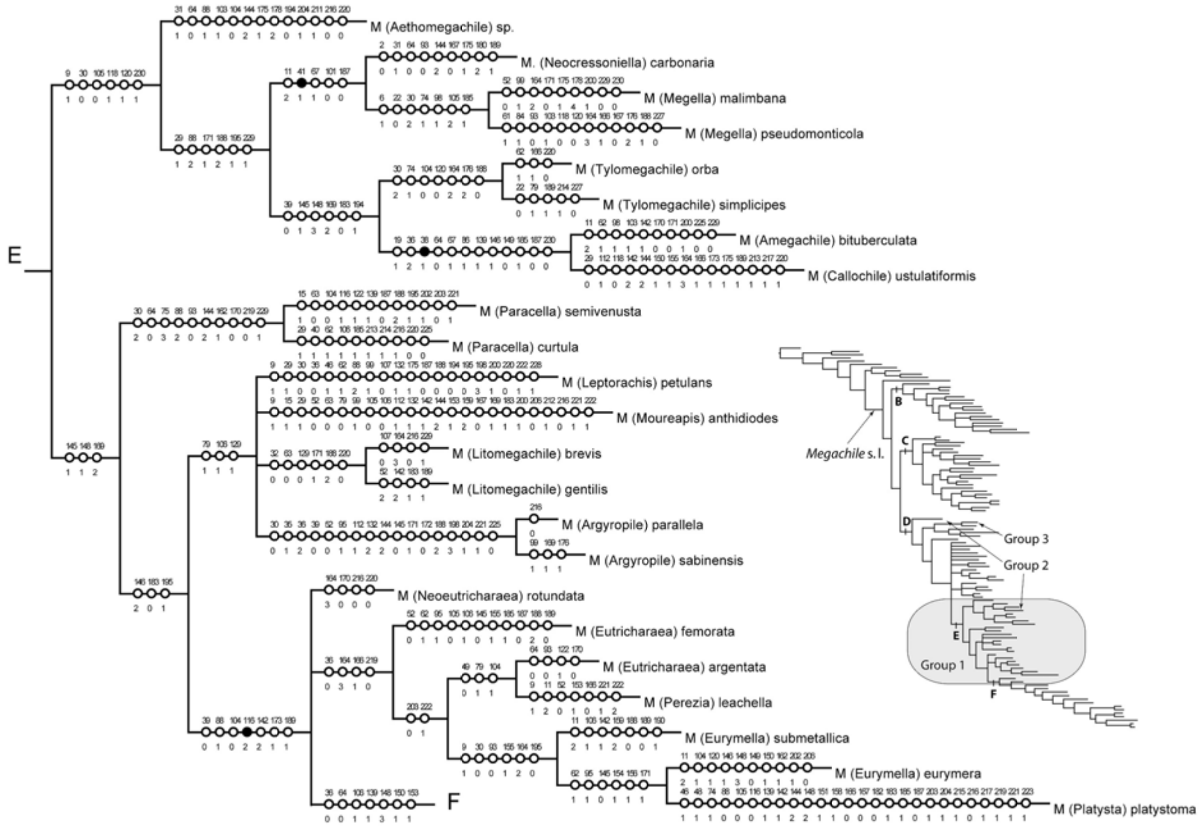


Fig. 166f. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower right figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

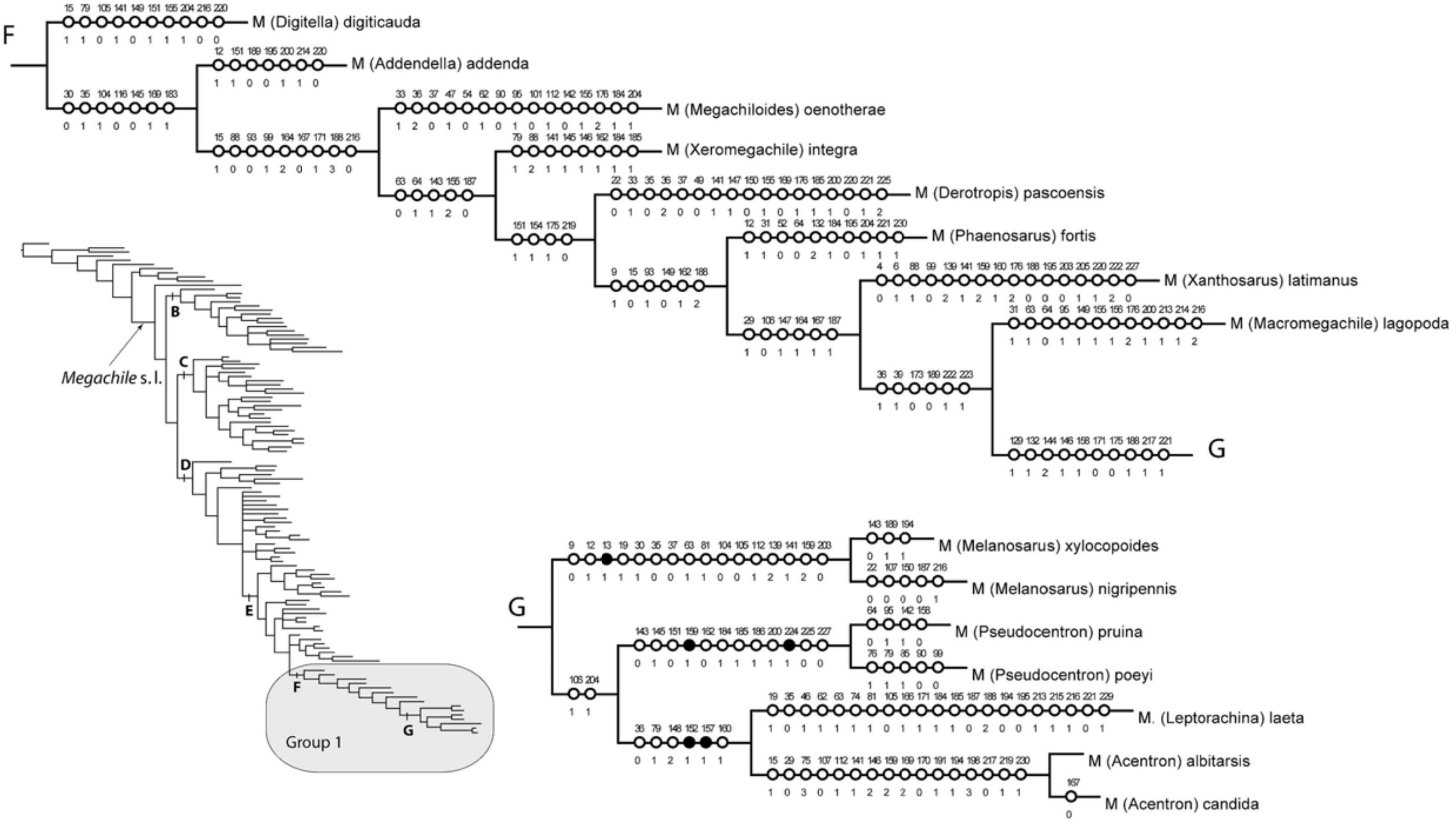


Fig. 166g. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower left figure is shown. Analysis B; strict consensus tree based on the analysis of 225 morphological characters; characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers and character-states, according to Appendix IV, are placed above and below each change.

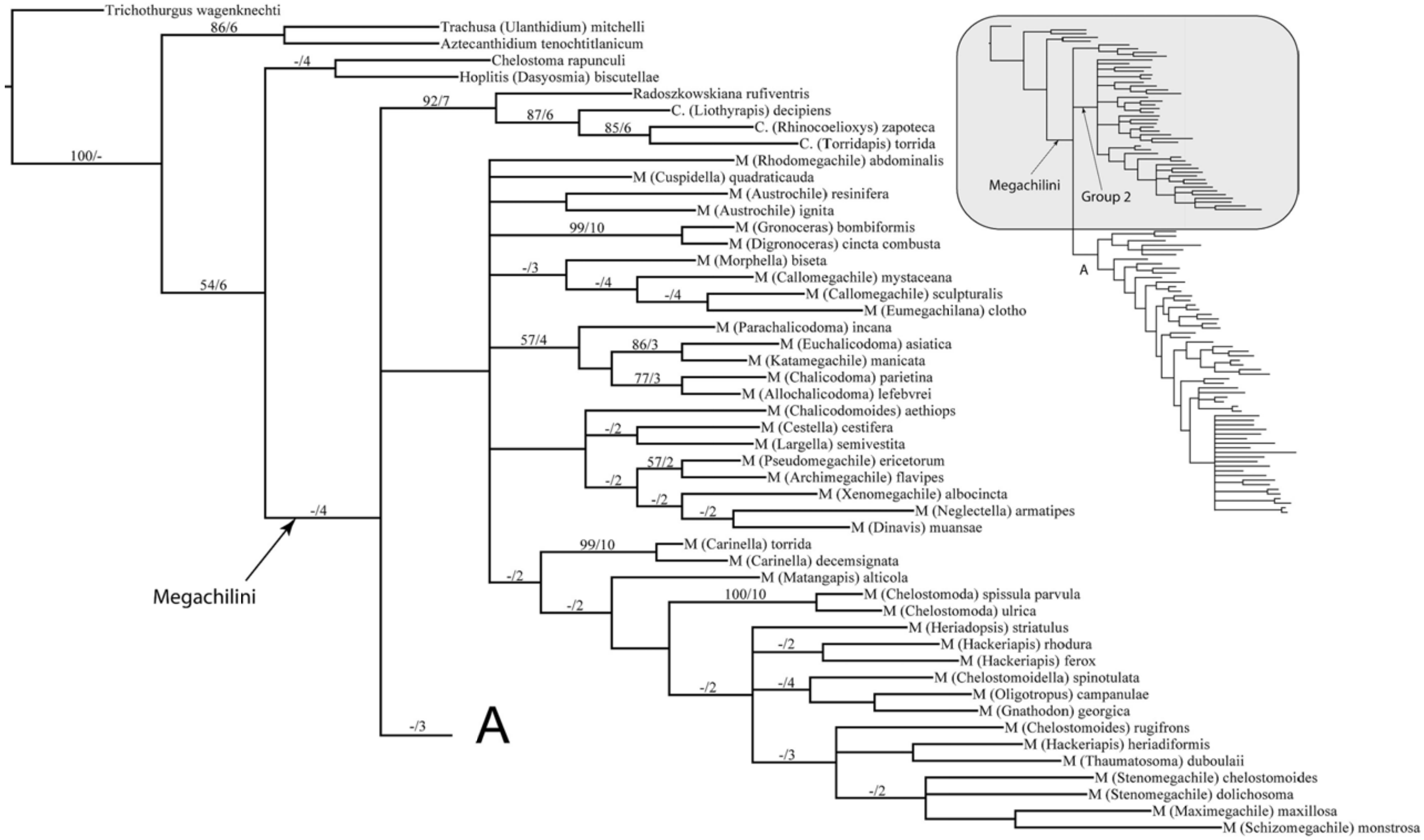


Fig. 167a. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Analysis C; strict consensus tree based on the full data matrix (231 morphological characters), excluding the cleptoparasitic genus *Dioxys* (L = 2409, CI = 12, RI = 47). Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

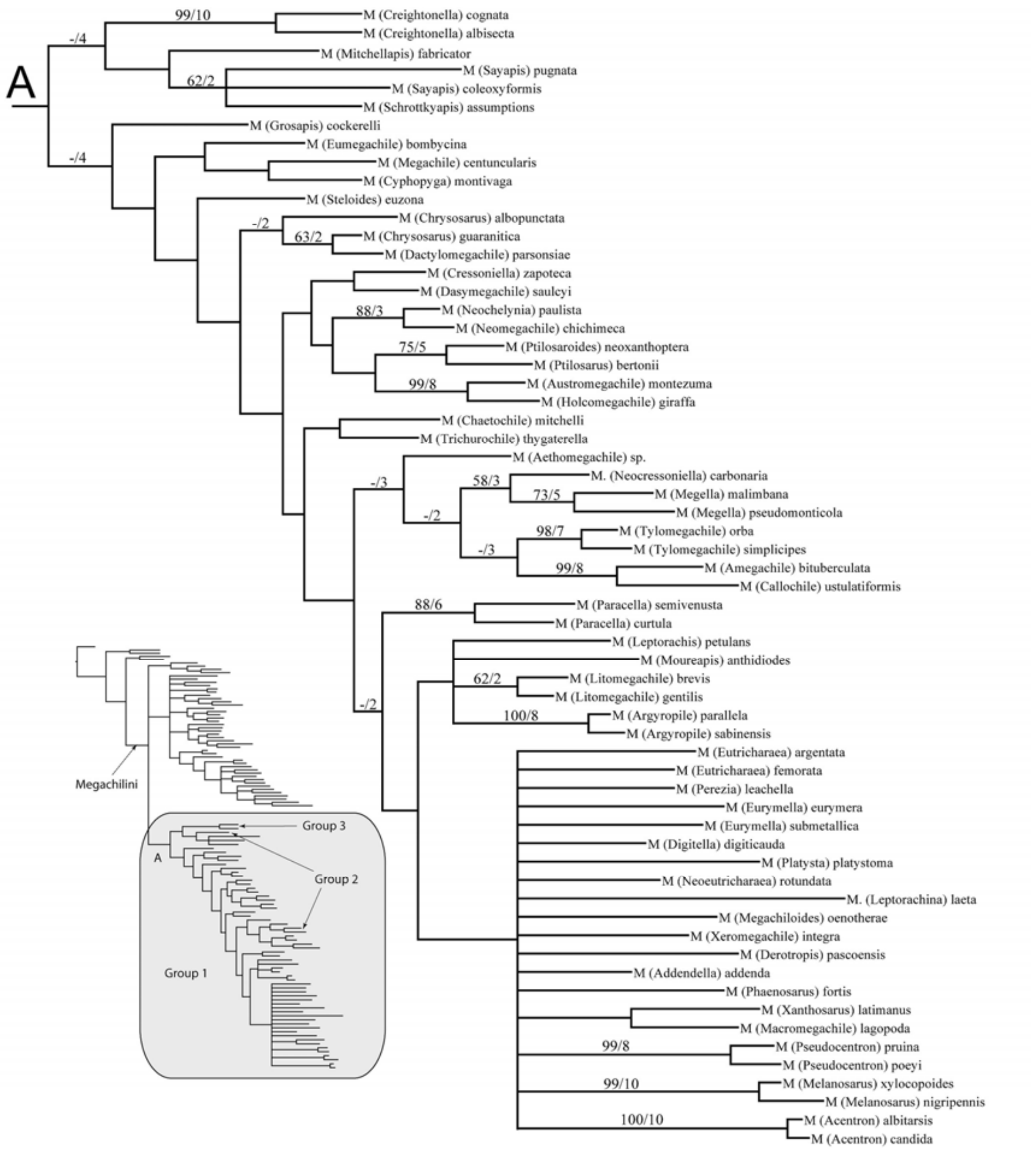


Fig. 167b. Phylogenetic analysis of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of lower left figure is shown. Analysis C; strict consensus tree based on the full data matrix (231 morphological characters), excluding the cleptoparasitic genus *Dioxys* (L = 2409, CI = 12, RI = 47). Lengths of horizontal lines are proportional to numbers of characters. Numbers are bootstrap and Bremer's support values. Branches without numbers or with a dash indicate bootstrap values below 50% and Bremer values of one.

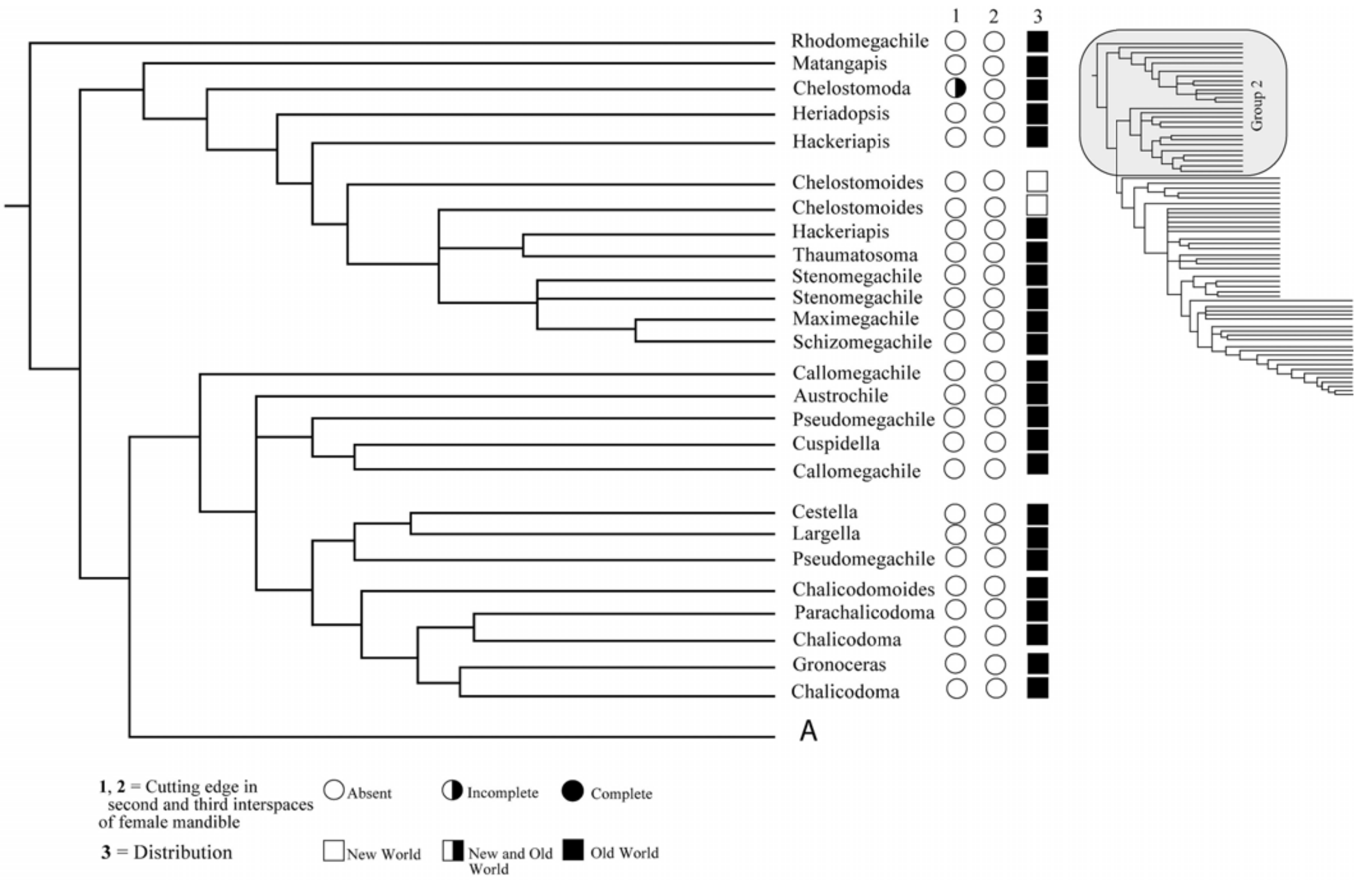


Fig. 168a. Presence and absence of cutting edges in the second and third interspaces of the female mandible and geographical distribution of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Strict consensus tree based on the analysis of 225 morphological characters (analysis B); characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51) .

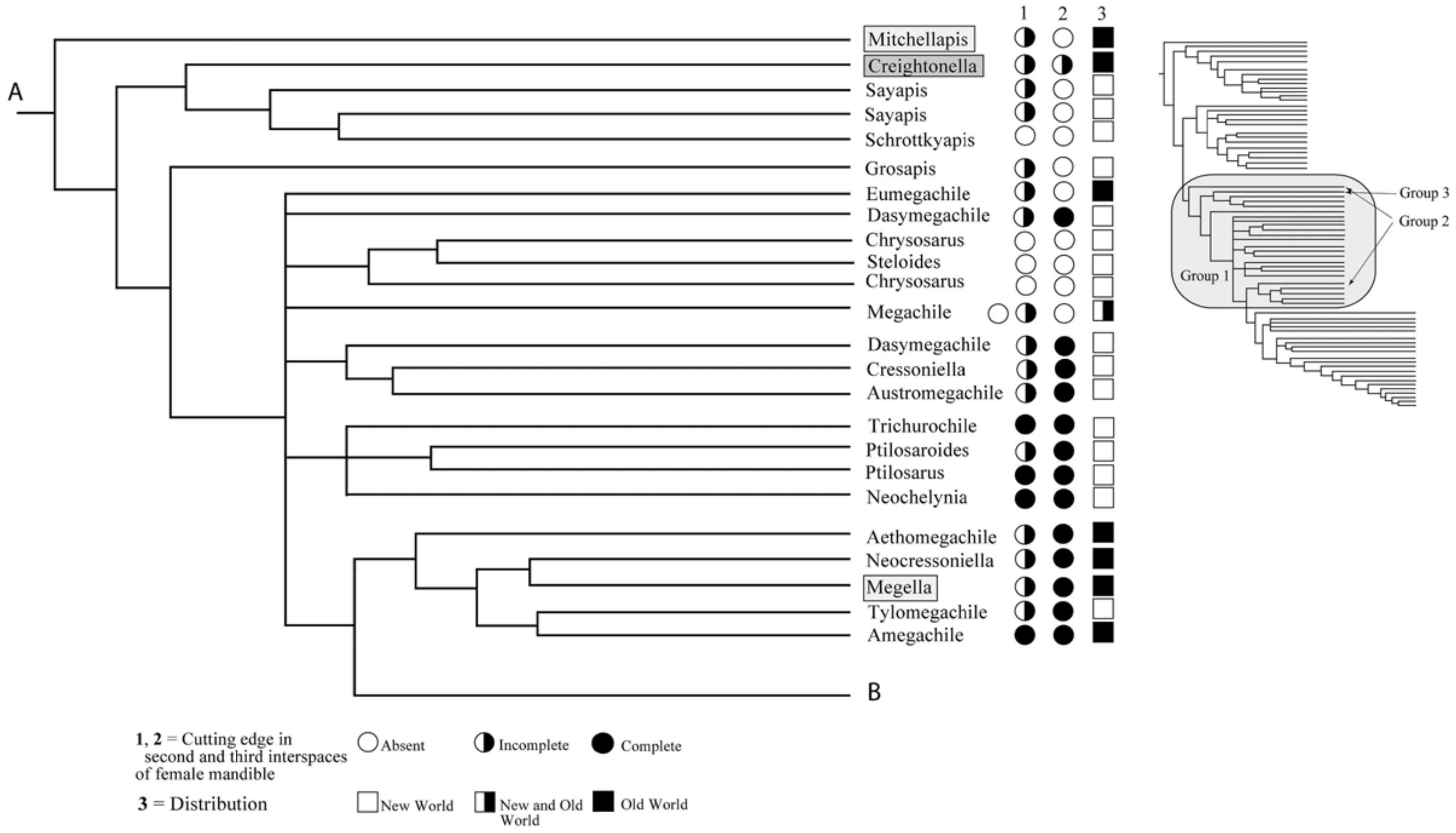


Fig. 168b. Presence and absence of cutting edges in the second and third interspaces of the female mandible and geographical distribution of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Strict consensus tree based on the analysis of 225 morphological characters (analysis B); characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51) .

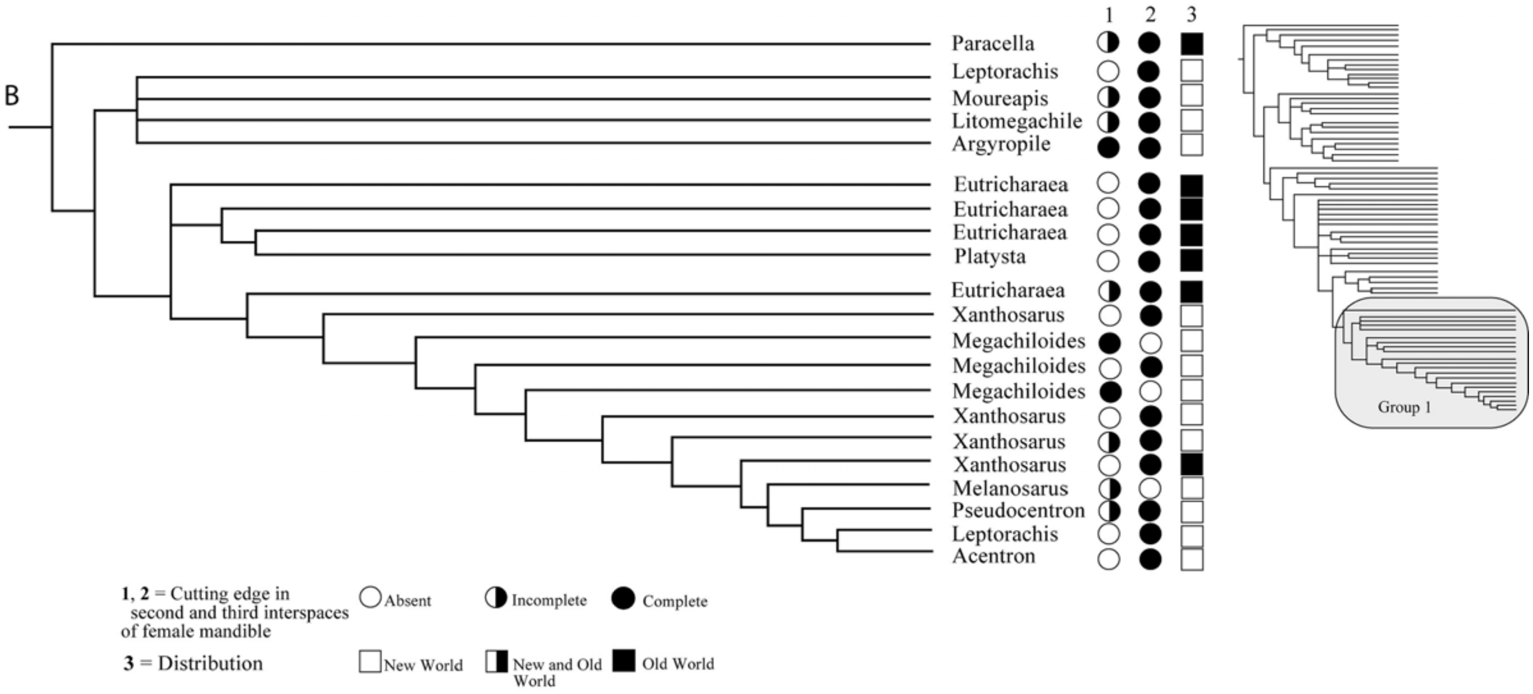
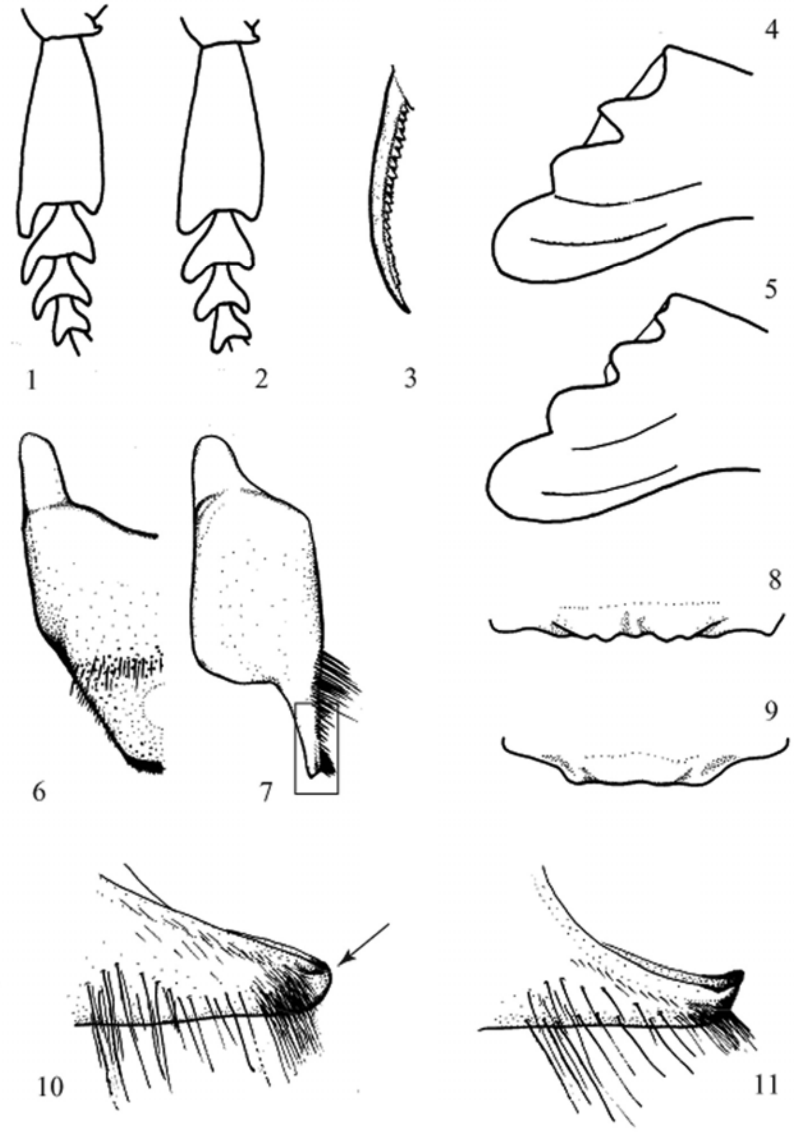
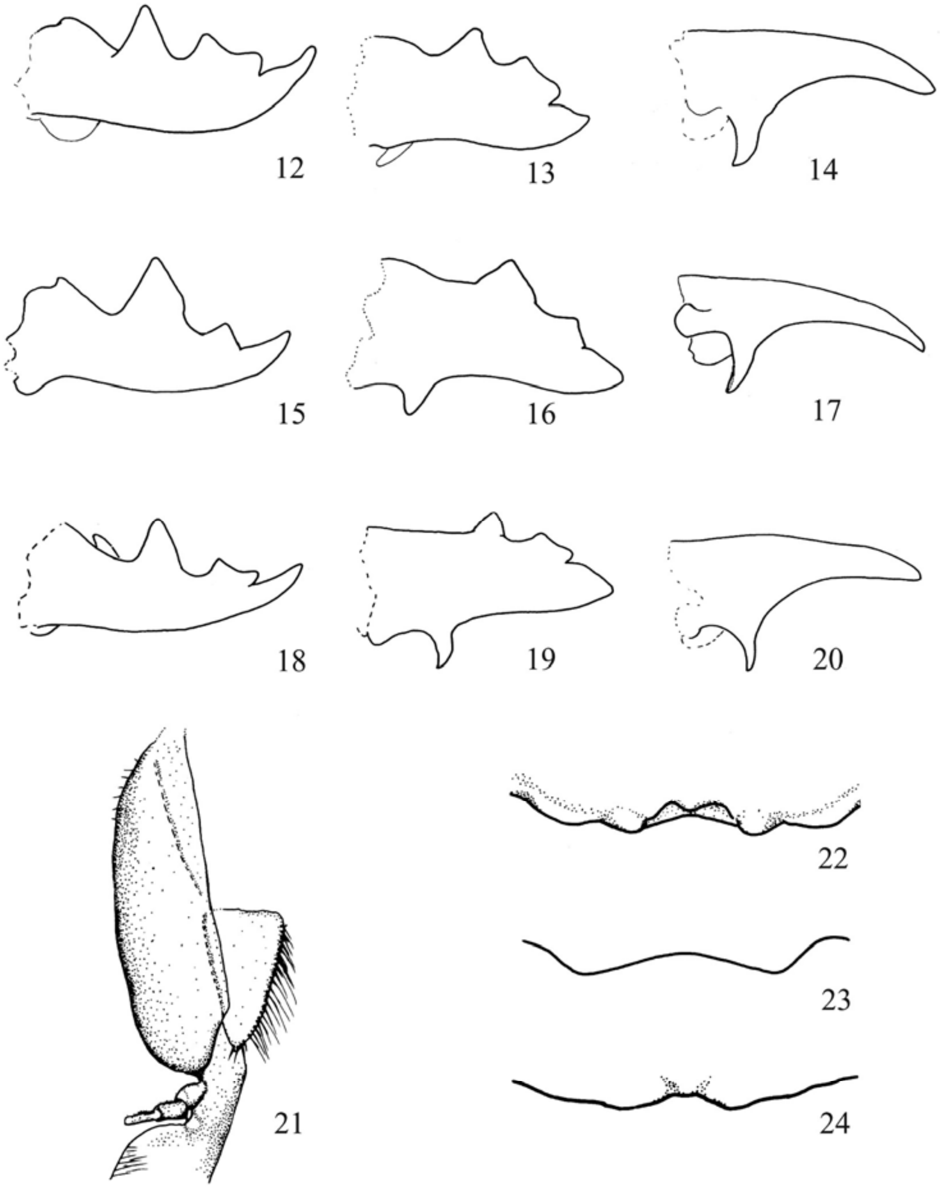


Fig. 168c. Presence and absence of cutting edges in the second and third interspaces of the female mandible and geographical distribution of the subgenera of *Megachile* s. l. The part of the tree within the shaded area of upper right figure is shown. Strict consensus tree based on the analysis of 225 morphological characters (analysis B); characters 70, 71, 80, 101-2, 114, and 117, related to cleptoparasitism, were deactivated (L = 2243, CI = 12, RI = 51) .

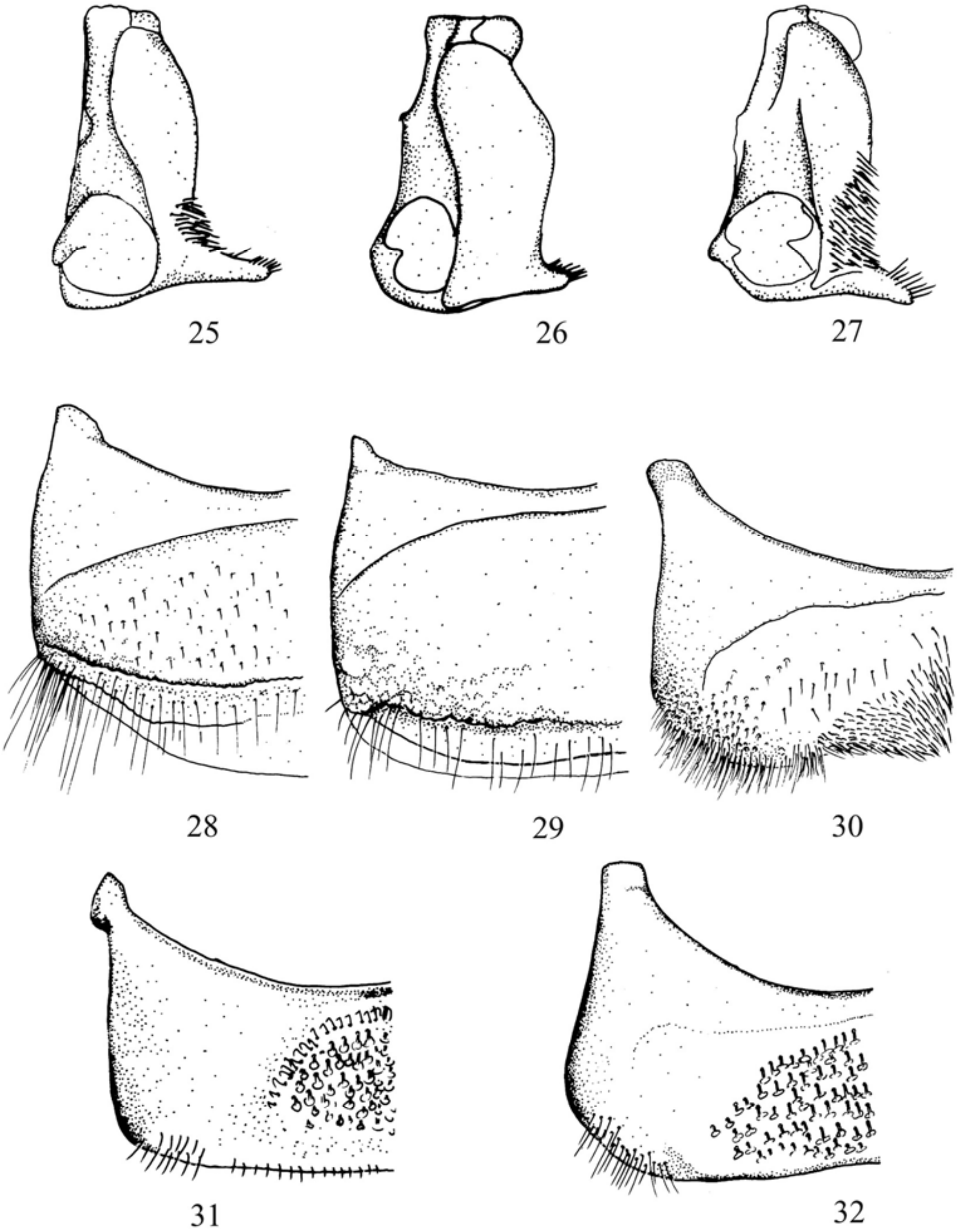
FIGURES USED IN CHAPTER IV



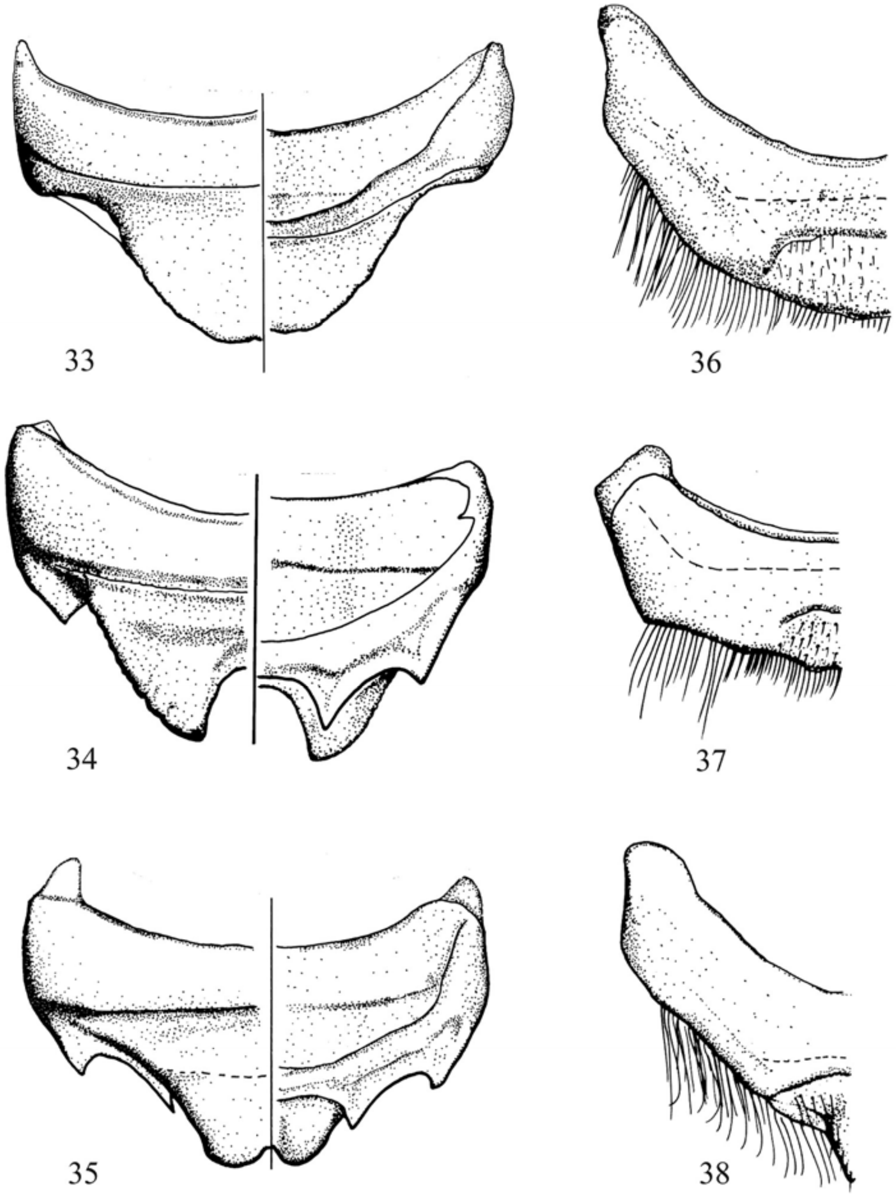
Figs. 1–11. Mid tarsomeres of females (1, 2); male mid tibial spur (3); female mandible (4, 5); sternum six of female, ventral and lateral views (6, 7); apical margin of clypeus of females (8, 9); apex of sternum six (close-up of selected area in Fig. 7) in lateral view (10, 11). *Megachile longuisetosa* sp. nov. (1, 3, 4, 6–8), *M. flavihirsuta* (5), *M. sabinensis* (10), and *M. rossi* (9, 11).



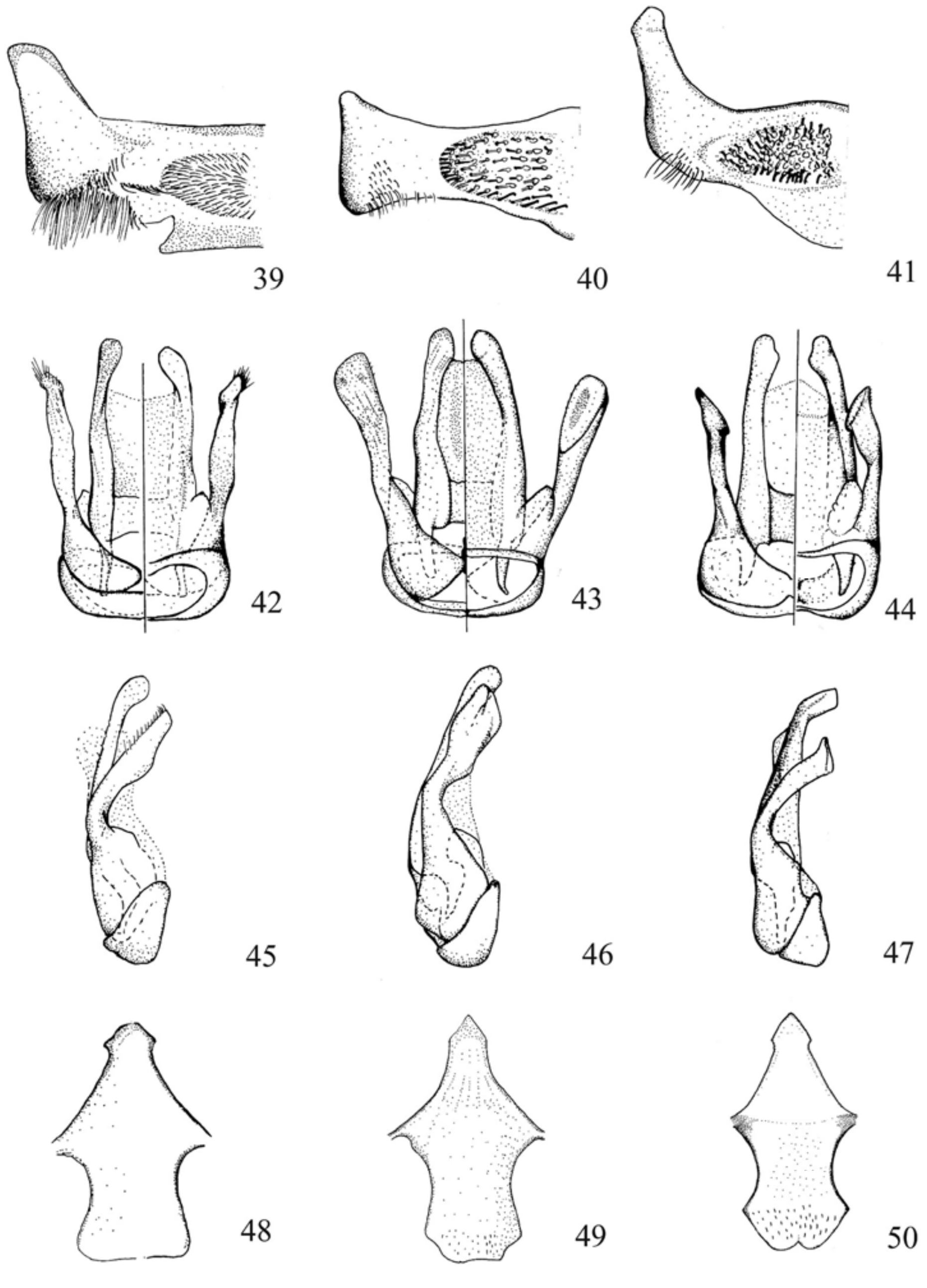
Figs. 12–24. Superior, lateral and inferior views of male mandible (12–20), detail of lacinia of female and male mouthparts (21), and apical margin of clypeus of males (22–24). *Megachile longuisetosa* sp. nov. (12–14, 21, 22), *M. rossi* (15–17, 23), and *M. sabinensis* (18–20, 24).



Figs. 25–32. Fore coxa (25–27), sterna four (28–29), and five (30–32) of males. *Megachile longuisetosa* sp. nov. (25, 30), *M. rossi* (26, 29, 31), *M. sabinensis* (27, 32), and *M. flavihirsuta* (28).



Figs. 33–38. Terga six, dorsal and ventral views (33–35) and seven, dorsal view (36–38) of males. *Megachile longuisetosa* sp. nov. (33, 36), *M. rossi* (34, 37), and *M. sabinensis* (35, 38).



Figs. 39–50. Male genitalia and associated sterna. Sternum six (39–41), genitalia, dorsal and ventral (42–44), and lateral views (45–47), and sternum eight (48–50). *Megachile longuisetosa* sp. nov. (39, 42, 45, 48), *M. rossi* (40, 43, 46, 49), and *M. sabinensis* (41, 44, 47, 50).

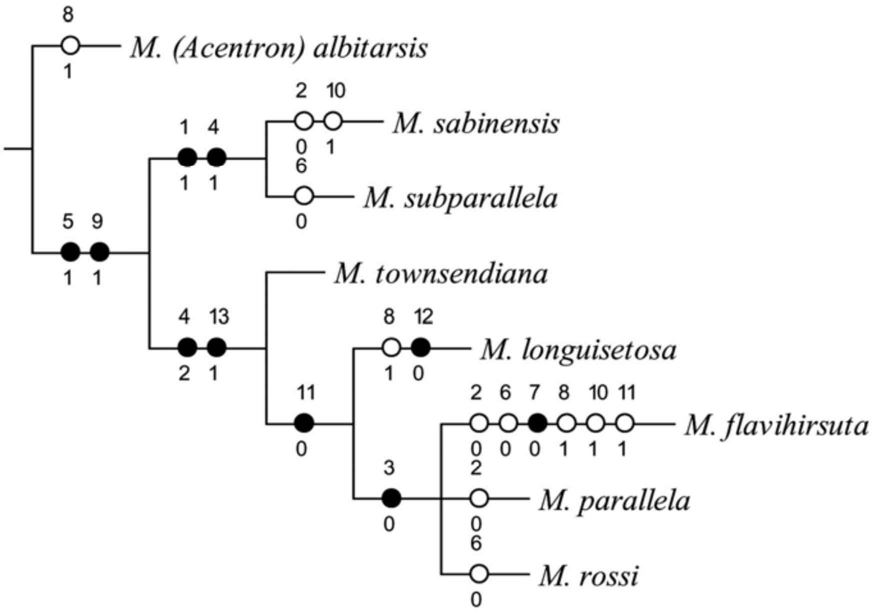


Fig. 51. Internal phylogeny of Megachile subgenus *Argyropile* species (strict consensus tree, length = 22, CI = 63, RI = 42). Black circles indicate unique changes; white circles indicate homoplastic changes; character numbers are placed above each change, character-states below (Table 6).