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On the cover: A female of *Megachile* sp. preparing to take a freshly cut coinvine [*Dalbergia ecastaphyllum* (L.) Taub. (Fabaceae: Faboideae: Dalbergieae)] leaf section back to her nest (Frenchman's Forest Natural Area, Palm Beach County, Florida; photograph by Bob Peterson; used with permission).

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Morphological phylogeny of Megachilini and the evolution of leaf-cutter behavior in bees (Hymenoptera: Megachilidae)

Victor H. Gonzalez[1,2], Grey T. Gustafson[2,3], & Michael S. Engel[2,3,4]

Abstract. A unique feature among bees is the ability of some species of *Megachile* Latreille *s.l.* to cut and process fresh leaves for nest construction. The presence of a razor between the female mandibular teeth (interdental laminae) to facilitate leaf-cutting (LC) is a morphological novelty that might have triggered a subsequent diversification in this group. However, we have a limited understanding of the phylogeny of this group despite the large number of described species and the origins and patterns of variations of this mandibular structure are unknown. Herein, using a cladistic analysis of adult external morphological characters, we explored the relationships of all genera of Megachilini and the more than 50 subgenera of *Megachile s.l.* We coded 272 characters for 8 outgroups and 114 ingroup species. Depending on the weighting scheme (equal or implied weighting), our parsimony analyses suggested the monophyly of *Megachile s.l.* and that either *Noteriades* Cockerell or the clade *Coelioxys* Latreille + *Radoszkowskiana* Popov is the extant sister group of all other Megachilini. In addition, we conducted Bayesian total-evidence tip-dating analyses to examine other possible hypotheses of relationships and patterns of variation of the interdental lamina. Our analyses suggest that interdental laminae developed asynchronicaly from two different structures in the mandible, and differ in their phenotypic plasticity. Character correlation tests using phylogenetic pairwise comparisons indicated that the presence of interdental lamina is not associated with head size, mandible size and shape, and pubescence on the adductor interspace. We discuss the implications of our findings for the classification of Megachilini and the development of novel evolutionary, ecological, and functional hypotheses on this behavior. New taxa established are **Pseudoheriadini** Gonzalez & Engel, new tribe, **Ochreriadini** Gonzalez & Engel, new tribe, ***Cremnomegachile*** Gonzalez & Engel, new genus, ***Rozenapis*** Gonzalez & Engel, new genus, and ***Saucrochile*** Gonzalez & Engel, new genus, along with the following **new combinations**: *Cremnomegachile dolichosoma* (Benoist), new combination, *Rozenapis ignita* (Smith), new combination, and *Saucrochile heriadiformis* (Smith), new combination.

[1] Undergraduate Biology Program, Haworth Hall, 1200 Sunnyside Avenue, University of Kansas, Lawrence, Kansas 66045, USA (victorgonzab@gmail.com).
[2] Department of Ecology & Evolutionary Biology, Haworth Hall, 1200 Sunnyside Avenue, University of Kansas, Lawrence, Kansas 66045, USA (gtgustafson@gmail.com).
[3] Division of Entomology, Natural History Museum, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045-4415, USA (msengel@ku.edu).
[4] Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA.
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INTRODUCTION

A unique behavior among bees is the ability to cut and process fresh leaves for nest construction. Using their mandibles, the females cut and collect circular to elliptical leaf pieces, leaving distinct excision patterns along the margin of leaves. The bees then use these leaf pieces to line and separate the brood cells, which they build in the ground or inside pre-existing cavities (*e.g*., Michener, 1953). This leaf-cutter (LC) behavior is exclusive to a group of solitary bees in the genus *Megachile* Latreille (Groups 1 and 3 of Michener, 2000, 2007), the most ecologically and morphologically diverse group of the family Megachilidae with a problematic taxonomy (Fig. 1C–G). This genus includes a number of introduced species (*e.g*., Cane, 2004; Rasmussen *et al*., 2012), many highly promising pollinators, and *Megachile* (*Eutricharaea*) *rotundata* (Fabricius), the most intensively managed and produced solitary bee in the world for the production of alfalfa (Pitts-Singer & Cane, 2011).

A good knowledge of LC behavior is essential to gain a better understanding of species' biologies, predict species distributions, and improve current management practices for commercial and conservation purposes (Sinu & Bronstein, 2018). However, limited information is available on which species of plants are used by LC bees and by which bee species. In addition, the majority of records are from common bees in urban or agricultural areas (MacIvor, 2016; Kambli *et al*., 2017; Sinu & Bronstein, 2018). Such limitations are surely a reflection of the challenges associated with finding nests, identifying plants from leaf fragments, and LC bees' taxonomic problems (Michener, 2007; Gonzalez *et al*., 2013). Significantly, less information is yet available on the evolutionary history of this behavior and the mandibular structures involved in leaf cutting.

Unlike other bees, megachilids do not line their cells with hydrophobic secretions of the Dufour's gland; instead, they rely on the physicochemical properties of the foreign material used for nesting (Williams *et al*., 1986). In the case of LC bees, certain phytochemicals (*e.g*., saponins) might increase larval mortality (Horne, 1995), while others (*e.g*., flavonoids, phenols, terpenoids) might decrease it by providing protection against microbes (MacIvor, 2016; Sinu & Bronstein, 2018). Therefore, it is not surprising that available data suggest that LC bees are highly selective in their plant and leaf choices, avoiding latex-producing plants, and preferring species with glabrous leaves, particularly in the families Fabaceae and Rosaceae (Michener, 1953; Kambli *et al*., 2017; Sinu & Bronstein, 2018).

The female mandible of LC bees varies considerably in its overall length and shape, as well as in the number and shape of its teeth (Fig. 2). It also has a distinct lamina in one or more spaces between the teeth, which authors have called 'interdental lamina' (Pasteels, 1965) or 'cutting edges' (Michener, 1962). Doubtless, this structure is an evolutionary novelty among bees because it is unique to this group and its appareance might have triggered a subsequent diversification within LC bees. Presently, the total number of LC bees accounts for about 57% of the species in Megachilini (Michener, 2007).

The presence or absence of this interdental lamina, as well as its size and shape, varies among species and species groups. Available information indicates that such variations correlate with different modes of leaf-cutting behavior and have been useful in the taxonomy of the group. Species with a lamina that entirely fills the space between teeth generally exhibit extensive LC behavior; their brood cells are entirely made of smooth-margined leaf pieces (*e.g*., Kambli *et al*., 2017; Gonzalez *et al*., 2018).

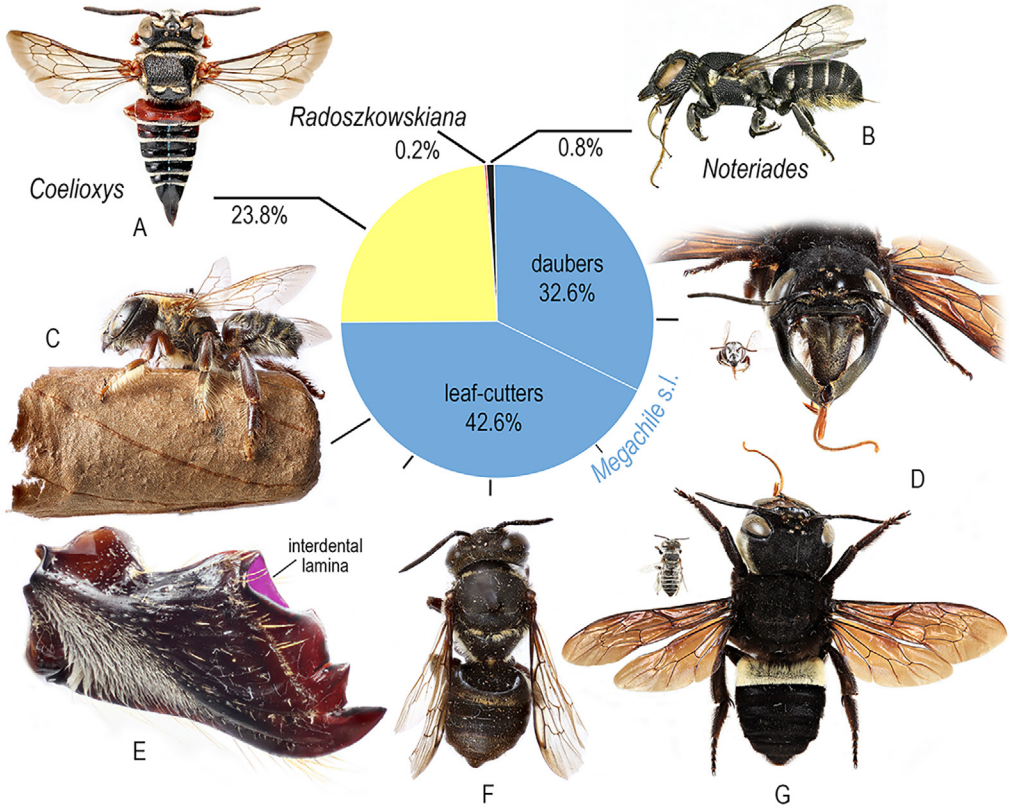

Figure 1. Species richness of currently recognized genera in the bee tribe Megachilini. **A.** Dorsal habitus of a female of *Coelioxys* sp. **B.** Lateral habitus of a female of *Noteriades spinosus* Griswold & Gonzalez. **C.** Male of *Megachile* (*Zonomegachile*) *kalina* Gonzalez, Griswold, & Engel on top of a brood cell built with leaf pieces. **D.** Facial habitus of leaf-cutter *M.* (*Eutricharaea*) *minutissima* Radoszkowski (left) and dauber bee *M.* (*Callomegachile*) *pluto* (Smith) (right). **E.** Outer surface of the female mandible of *M.* (*Leptorachis*) *laeta* Smith, a leaf-cutter bee, showing interdental lamina in pink. **F.** Dorsal habitus of *M.* (*Rhyssomegachile*) *kartaboensis* Mitchell. **G.** Dorsal views of *M.* (*E.*) *minutissima* (upper left) and *M.* (*C.*) *pluto* (right). Photographs are not at the same scale, except for the large and small species compared in figures D and G.

In contrast, species with incomplete lamina (not entirely filling spaces between teeth) or without it, have more limited LC behavior, with their brood cells made of a combination of mud and leaf or petal pieces, which are irregularly cut, often with serrate margins (Michener, 2007; Soh, 2014). The absence of this lamina in the mandible of some species that still exhibit LC behavior indicates that other structures are also involved in leaf cutting. Similarly, the morphological diversity of the mandible also suggests different mechanical solutions to diverse functional problems. However, no one has yet attempted to understand the origins and patterns of variations of these mandibular structures using a phylogenetic framework. To date, the phylogenetic relationships among the four genera of Megachilini (*Coelioxys* Latreille, *Megachile s.l.*, *Noteriades* Cockerell, and *Radoszkowskiana* Popov), as well as that of the more than 50 subgenera of *Megachile s.l.*, are largely unexplored. Besides an unpublished dissertation (Gonzalez, 2008), the only phylogenetic hypothesis available is that of Trunz *et al.* (2016) using molecular data.

Figure 2. Leaf excisions and a sampling of the morphological diversity among the female mandible of leaf-cutter bees. **A.** Leaves of *Rosa* sp. (Rosaceae) from Lesvos, Greece. **B.** Fossil leaf cut (Fabaceae) from Eckfeld Maar, Germany (~43 Ma). **C–J.** Outer view of the mandible showing interdental laminae in green (odontogenic) and pink (ctenogenic). **C.** *Megachile* (*Chrysosarus*) *parsonsiae* Schrottky. **D.** *M.* (*Rhyssomegachile*) *simillima* Smith. **E.** *M.* (*Pseudocentron*) *pruina* Smith. F. *M.* (*Zonomegachile*) sp. **G.** *M.* (*Moureapis*) *maculata* Smith. **H.** *M.* (*Melanosarus*) *xylocopoides* Smith. **I.** *M.* (*Acentron*) *albitarsis* Cresson. **J.** *M.* (*Leptorachis*) *petulans* Cresson. Abbreviations: Mt = mandibular tooth.

Several authors have recorded fossilized dicotyledonous leaves with distinctive cuts along their margins, similar to those caused by LC bees (Figs. 2A, B). Those trace fossils are from deposits in Europe, North and South America, and the oldest is approximately 60 Ma (*e.g.*, Labandeira, 2002; Wedmann *et al*., 2009; Michez *et al*., 2012). Comparative analyses of the ellipse eccentricity between leaf discs of brood cells of living species and fossil excisions, support the attribution of these trace fossils to LC bees (Sarzetti *et al*., 2008). However, molecular analyses using a node-dating approach,

which places the oldest fossil to the youngest internal node and thus imposes the age of the fossil as a minimum age constraint, suggest that LC bees originated around 20–25 Ma (Litman *et al*., 2011; Trunz *et al*., 2016). Other dating approaches might be useful for investigating this temporal discrepancy, such as Bayesian total-evidence tip dating, which utilizes morphological data to infer the placement of fossils within the phylogeny (as terminals or 'tips') in order to calibrate the tree. Therefore, tip-dating does not require the *a priori* constraint of taxa to nodes in order to generate age estimates, and allows the use of all available fossils within a group, extending age estimates beyond the minimum age for clades (Ronquist *et al*., 2012a). Unfortunately, despite the existence of fossil megachilids, such analyses are not yet available for these or any other group of bees.

Considering the biological importance of the LC behavior in the evolution and diversification of this group of pollinators, we set the following goals: First, to explore the relationships of the genera of Megachilini and the subgenera of *Megachile s.l*. using adult morphological data. Second, to determine the possible origins of the interdental lamina in the female mandible. Third, to explore possible patterns of variation of the interdental lamina. Fourth, to examine the implications of our phylogenetic results on the classification of Megachilidae and Megachilini. In addition, to examine other possible patterns of variation of the interdental lamina, we conducted preliminary Bayesian total-evidence tip-dating analyses. We conducted two sets of analyses aimed at obtaining more accurate divergence time estimates because available analyses (*e.g*., Litman *et al*., 2011; Trunz *et al*., 2016) employed a node-dating approach to estimate the origin of LC bees. Thus, we first conducted a phylogenetic analysis of all tribes in Megachilidae and then used the divergence-time estimates generated from that analysis to inform priors for the phylogenetic analysis of the genera of Megachilini. In the following sections, we provide an overview of the diversity, fossil record, and phylogeny of megachilids, highlighting outstanding problems in their classification. Unless otherwise indicated, we followed Michener's (2000, 2007) subgeneric classification of *Megachile s.l*. to facilitate comparisons (Appendix 1).

Diversity of Megachilidae

Megachilidae are the third largest bee family containing more than 4100 species worldwide (Michener, 2007; Ascher & Pickering, 2018). Megachilids utilize a high diversity of nesting materials and substrates. For example, they use mud, petals, leaves (intact pieces or macerated to a pulp), resins, gravel, and plant trichomes to build their brood cells in the soil, attached to twigs, under surfaces of rocks, or inside pre-existing cavities including man-made constructions (*e.g*., Rozen *et al*., 2010; Gonzalez & Griswold, 2013). The most recent higher-level classificatory proposal for the family (Gonzalez *et al*., 2012) recognizes four subfamilies and nine tribes, three of which are extinct (Ctenoplectrellini, Glyptapini, and Protolithurgini). Morphological (Gonzalez *et al*., 2012) and molecular data (Litman *et al*., 2011) support the monophyly of these tribes, except that of Osmiini, which has long been suspected to be paraphyletic (*e.g*., Engel, 2001; Michener, 2007; Praz *et al*., 2008). In these morphological and molecular analyses, either Megachilini or Megachilini + Dioxyini renders Osmiini paraphyletic. The phylogenetic relationships of Dioxyini are also still not clear. This small monophyletic group of cleptoparasitic bees (~36 spp.) appeared as sister of *Aspidosmia* Brauns (Aspidosmiini) in the molecular analysis, but in the morphological analysis it was the sister group of Megachilini.

Diversity and Phylogeny of Megachilini

Megachilini contain about half of the species of the family (~2000 spp.: Michener, 2007; Ascher & Pickering, 2018). The most widely used classificatory proposal for bees worldwide (Michener, 2007) recognizes a free-living genus *Megachile*, and two cleptoparasitic genera, *Coelioxys* (Fig. 1A) and *Radoszkowskiana*. Gonzalez *et al*. (2012) transferred from the Osmiini another free-living genus, *Noteriades* (Fig. 1B). All genera of Megachilini seem monophyletic, except for *Megachile*.

Coelioxys is cosmopolitan in distribution and includes about 470 species grouped in 15 subgenera in the classification of Michener (2007), but several Neotropical taxa synonymized by him are still recognized by some authors (*e.g*., Moure *et al*., 2007). *Coelioxys* are commonly collected bees and frequently found parasitizing other megachilids and some apids. Multiple authors have studied their behavior and immatures (references in Michener, 2007). *Radoszkowskiana* includes only four species restricted to the Palearctic region, which are morphologically and behaviorally similar to *Coelioxys* (Rozen & Kamel, 2007). Rocha Filho & Packer (2017) explored phylogenetic relationships among the subgenera of *Coelioxys*.

Noteriades includes 16 species that occur across tropical and subtropical regions of sub-Saharan Africa, India, and Southeast Asia. The biology of this group of bees is unknown (Griswold & Gonzalez, 2011). Species are small, heriadiform or hoplitiform in body shape, and non-parasitic considering the presence of a metasomal scopa. Griswold (1985) first suggested the close relationship of this genus with Megachilini, which molecular (Praz *et al*., 2008; Litman *et al*., 2011) and morphological analyses (Gonzalez *et al*., 2012) supporting his conclusion.

Remaining species of Megachilini (~1500 spp.) are in *Megachile*, a genus that includes both LC bees and species that primarily use mud or resins as nesting materials. The genus occurs in a wide diversity of habitats on all continents, ranging from lowland tropical rain forests, deserts, to high elevation environments. In appearance, species of *Megachile* range from nearly bare, elongate, parallel-sided bees to robust, setose bees resembling some smaller bumble bee species; their body length ranges from about 4 mm in *M*. (*Eutricharaea*) *minutissima* Radoszkowski, to nearly 40 mm in *M*. (*Callomegachile*) *pluto* Smith, the longest bee in the world (Figs. 1D, G). As we briefly describe below, the taxonomy of *Megachile* is problematic and its phylogenetic relationships largely unexplored.

What is the Genus *Megachile*?

The concept of *Megachile* has changed multiple times since its conception. Latreille (1802) proposed *Megachile* for the European species *Apis centuncularis* Linnaeus, and it initially included not only species of this genus as currently defined, but also species that now belong to different tribes of Megachilidae. Later, Lepeletier de Saint Fargeau (1841) proposed the genus *Chalicodoma* for another European species, *Apis muraria* Olivier. During the second half of the 1800's, as well as during the first decades of the 1900's, several authors (*e.g*., Smith, 1865; Thomson, 1872; Provancher, 1882; Meunier, 1888; Friese, 1899; Robertson, 1901, 1903; Cockerell, 1907, 1922; Mitchell, 1924) proposed a number of generic or subgeneric names for closely allied taxa to *Megachile* from different regions of the world. Until the late 1800's, most authors recognized both *Megachile* and *Chalicodoma* as morphologically and biologically distinct groups, the first consisting of LC bees and the second of species that use mud or resins to build

their nests (*e.g.*, Gerstaecker, 1869; Radoszkowsky, 1874; Taschenberg, 1883). However, Dalla Torre (1896) appears to be the first to have treated *Chalicodoma* as a subgenus of *Megachile*, a position followed by Friese (1898, 1899, 1909, 1911a, 1911b). The latter author (Friese, 1911a) also recognized two previously described taxa, *Thaumatosoma* Smith and *Stellenigris* Meunier, as genera closely related to *Megachile*.

Mitchell (1933) also considered *Megachile* in a broad sense following earlier authors. He regarded *Thaumatosoma* and other generic names proposed until then as subgenera of *Megachile*, including some that Friese (1911a, 1911b) did not mention. In subsequent years, Mitchell (1935a, 1935b, 1936a, 1936b, 1937a, 1937b, 1937c, 1943) proposed several new taxa from the Western Hemisphere and revised their species in a series of monographs that stand until today as major or only resources of regional identification for these bees.

Based on the generic concepts previously used and the discovery of some morphological features that correlated with nesting behavior, Michener (1962, 1965) divided *Megachile* into three genera (*Chalicodoma*, *Creightonella* Cockerell, and *Megachile*). *Chalicodoma* included Eastern Hemisphere species with a strongly convex and rather parallel-sided metasoma and female mandibles without interdental laminae (Figs. 1D, G); those morphological features are associated with narrow burrows and the use of mud or resin as nesting materials. In contrast, *Megachile* included a cosmopolitan group of bees with a flattened metasoma and female mandibles with interdental laminae, features that allow them to cut and use leaf or petal pieces for constructing cells in wider burrows. *Creightonella* combined features of both genera, a female mandible with interdental laminae to cut leaves, and a strongly convex, parallel-sided metasoma. *Creightonella* included a relatively small number of species (50 spp.) restricted to the Eastern Hemisphere. Pasteels (1965) also independently developed the same classificatory scheme of Michener (1962, 1965) when considering the African fauna. Both authors, C.D. Michener and J.J. Pasteels, not only described several subgenera within *Megachile* and *Chalicodoma*, but also rendered as subgenera a few other generic names proposed at the time.

In 1980, when T.B. Mitchell revised the LC bees from the Western Hemisphere, he adopted the multigeneric proposal of Michener (1962, 1965) in recognizing three genera. However, he further divided *Megachile* into six genera, each with multiple subgenera. Although he was not concerned with the Eastern Hemisphere fauna, he made an effort to summarize and place this fauna within his classificatory scheme, which was not widely adopted (Appendix 1).

Despite having divided *Megachile* into three genera in the 1960's, Michener (2000, 2007) no longer recognized them when treating the world fauna because of the exceptions and intergradations he later observed in the main morphological features, as well as for almost all other features he had previously used to characterize these groups. In particular, *Megella* Pasteels and *Mitchellapis* Michener represented major problems within his system. Although Pasteels (1965) and Michener (1965) initially placed both taxa in *Megachile*, they exhibit features of both *Megachile* and *Chalicodoma*. For example, typical *Megachile* characteristics are the interdental laminae in the female mandible and the apex of the female sixth sternum with a fringe of short, dense plumose setae. Features typical of *Chalicodoma* include the elongate, parallel-sided body, apex of the female tibiae with a distinct, sharp spine, and the presence of setae on the lateral margins of the male eighth sternum. Michener (2000, 2007) also synonymized certain subgeneric names that authors created for unusual species and organized the more than 50 subgenera into three informal groups, which corresponded to each genus that

he previously recognized in the 1960's. That is, Groups 1, 2, and 3, are equivalent to the genera *Megachile*, *Chalicodoma*, and *Creightonella*, respectively, in Michener's (1962, 1965) earlier classification (Appendix 1). Because of the presence of marginal setae on the eighth sternum of the male, Michener (2000, 2007) placed these two "problem" taxa (*Mitchellapis* and *Megella*) in Group 2 (*Chalicodoma*), not in Group 1 (*Megachile*) as he (Michener, 1965) and Pasteels (1965) initially assigned them. Another subgenus that also bridged the gap between *Megachile* and *Chalicodoma* was *Chelostomoda* Michener. Michener (1962) described this group as a subgenus of *Chalicodoma* even though it also possesses interdental laminae as in *Megachile*.

Today, there is no consensus in the classification of *Megachile*. Some authors still follow Michener's earlier classification (Michener, 1962, 1965) in recognizing the genera *Chalicodoma*, *Creightonella*, and *Megachile*, including several subgenera that were proposed for species with aberrant or unusual morphologies and that Michener (2000, 2007) synonymized (*e.g*., Silveira *et al*., 2002; Durante & Abrahamovich, 2006; Moure *et al*., 2007; Ornosa *et al*., 2007). Other authors (Trunz *et al*., 2016) recognize a few other taxa at the generic level, as they were initially proposed (*Gronoceras* Cockerell and *Heriadopsis* Cockerell) or were suggested by Michener (2007) as an alternative classification (*Matangapis* Baker & Engel). The species-level systematics of *Megachile s.l*. (*sensu* Michener 2000, 2007) is also problematic and thus species identifications are challenging in most groups. Taxonomic revisions for the majority of the subgenera are not available, keys to species are lacking, and many species have not been properly associated with any of the known subgenera (Michener, 2000, 2007). Even in North America, many species are still known from a single sex or from a small number of specimens (Sheffield & Westby, 2007; Gonzalez *et al*., 2013, 2018).

The phylogenetic relationships among the genera of Megachilini, as well as the subgenera of *Megachile s.l*., are largely unexplored. Michener (2000, 2007) suggested that *Coelioxys* might render *Megachile s.l*. paraphyletic because it shares some morphological traits, particularly with *Chelostomoides* Robertson. Likewise, the recent inclusion of *Noteriades* in Megachilini might also render *Megachile s.l*. paraphyletic considering that this genus shares the presence of arolia (a rare feature in Megachilini, typical of Osmiini) with *Matangapis* and *Heriadopsis*. An unpublished dissertation (Gonzalez, 2008) explored the relationships within Megachilini using morphological data but did not include *Noteriades*. Similarly, the positions of *Matangapis* and *Heriadopsis* were unclear in a recent molecular analysis (Trunz *et al*., 2016), as both taxa nested in a clade consisting of *Coelioxys* and *Radoszkowskiana*. Doubtless, species-level revisionary studies and phylogenetic analyses are required to develop a more stable taxonomy and phylogeny-based classification of *Megachile s.l*.

Fossil Record

Engel (1999, 2001), Engel & Perkovsky (2006), and Michez *et al*. (2012) summarized the fossil record for Megachilidae. The extinct tribes Protolithurgini, Ctenoplectrellini, and Glyptapini contain several species in five genera (*Protolithurgus* Engel, *Ctenoplectrella* Cockerell, *Glaesosmia* Engel, *Friccomelissa* Wedmann *et al*., and *Glyptapis* Cockerell) all from the Eocene (33.9–56 Ma) and many in Baltic amber. The first tribe is sister to all Lithurginae while the remaining two are sisters to all Megachilinae, except Aspidosmiini which might render Ctenoplectrellini paraphyletic (Gonzalez *et al*., 2012). For Megachilini, most records are trace fossils of dicotyledonous leafs with excisions along the margins, similar to those caused by LC bees of the genus *Megachile s.l*. (Wed-

mann *et al*., 2009; Engel & Perkovsky, 2006; Sarzetti *et al*., 2008). Body compressions are few and have not been associated to any subgenus. *Megachile glaesaria* Engel, from the Miocene Dominican amber (*ca*. 17 Ma), is the best-preserved fossil of Megachilini. Engel (1999) noted the close resemblance of this species to some species of the extant North American *Chelostomoides*. However, he placed it in its own subgenus, *Chalicodomopsis* Engel, because of the presence of a small inner tooth in the pretarsal claws and some wing features, which are present in both Megachilini and Anthidiini. He also suggested that *M. glaesaria* might be a basal member of the Group 2 of subgenera or sister to all Megachilini. To date, the phylogenetic position of *M. glaesaria* is unknown.

MATERIAL AND METHODS

Morphological Phylogeny of Megachilini

TAXON SAMPLING: We used eight taxa as outgroups based on the phylogeny of Gonzalez *et al*. (2012) and 114 species of Megachilini as follows: one species of *Noteriades*, one species of *Radoszkowskiana*, three species of *Coelioxys*, and 109 species of *Megachile s.l*. The latter genus is represented by species of 57 subgenera that included those recognized by Michener (2007), the fossil species *M. glaesaria* (Engel, 1999), and four recently described taxa by Baker & Engel (2006), Engel & Baker (2006), Engel & Gonzalez (2011), and Gonzalez & Engel (2012) (Appendix 2). For each subgenus of *Megachile s.l*., we included the type species and, to maximize variation, when available at least one morphologically divergent species from it, or species separated subgenerically but synonymized by Michener (2000, 2007), Gonzalez *et al*. (2010), Gonzalez & Engel (2012), and Gonzalez (2013). About half of the subgenera are represented by one species because they either are monotypic (10 subgenera) or seemed morphologically uniform (20 subgenera). The only three subgenera of *Megachile s.l.* that we were not able to examine are *Austrosarus* Raw, *Neochalicodoma* Pasteels, and *Stellenigris* Meunier. However, Gonzalez & Engel (2012) and Gonzalez (2013) considered the first as a synonym of *Chrysosarus* Mitchell and the second as a synonym of *Pseudomegachile* Friese, subgenera represented by several species in our analyses. The identity and correct taxonomic placement of *Stellenigris* is a mystery. Michener (2000, 2007) suggested that it might belong to large species of the Group 2 of *Megachile s.l*., but the type specimen of *Stellenigris vandeveldii* Meunier, 1888, is probably lost or perhaps destroyed, along with other insects described by F. Meunier (Engel, 2007).

Most specimens studied are in the Snow Entomological Collection, University of Kansas Natural History Museum, although we borrowed specimens of a few rare species from the following institutions (names of the people who kindly arranged these loans are in parentheses): Academy of Natural Sciences of Drexel University, Philadelphia, PA (D. Otte, J. Weintraub); American Museum of Natural History, New York (J.G. Rozen, Jr.); Bee Biology and Systematics Laboratory, USDA-ARS, Utah State University, Logan, UT (T. Griswold, H. Ikerd); the Natural History Museum, London, UK (D. Notton); Department of Terrestrial Invertebrates, Western Australian Museum, Welshpool (T. Houston); Illinois Natural History Survey, Urbana, Illinois, USA (P. Tinerella); Museum of Comparative Zoology, Harvard University, Cambridge, MA (P. Perkins, R.L. Hawkins); Musée Royal de L'Afrique Centrale, Tervuren (A. Pauly, E. De Coninck); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (F. Koch, V. Ritcher); North Carolina State University Insect Museum, Raleigh, NC (Rob Blinn); Oxford University Museum of Natural History, Oxford, UK (J. Hogan); and United States

National Museum of Natural History, Washington, D.C. (D. Furth, B. Harris).

Morphological data: Morphological terminology generally follows that of Michener (2000, 2007) and Engel (2001), except for 'torulus' and 'interdental lamina', which we use herein instead of 'antennal socket' and 'cutting edge'. The first term is in broader application across Hymenoptera while the second describes more accurately the laminae between the teeth of the female mandible that characterizes the majority of LC bee species. 'Cutting edges' have widely been used in the taxonomic literature of *Megachile s.l.* (*e.g.*, Michener, 1962, 2007) but these terms are functionally and structurally ambiguous. They imply that these are the only structures used in cutting leaves and do not inform on their shape nor on their location in the mandible. The absence of interdental laminae in some species of *Megachile s.l.* (*e.g.*, *Chrysosarus*) that also cut leaves or even petals [*e.g.*, *M.* (*Megachile*) *montivaga* Cresson] (*e.g.*, Zillikens & Steiner, 2004; Torretta *et al*., 2014; Orr *et al*., 2015) clearly indicates that these are not the only mandibular structures involved in leaf cutting. For example, the upper and lower margins of each tooth are sometimes thin and sharp, and they might function as razors even when the interdental laminae are present. Thus, as initially proposed by Pasteels (1965), the term interdental laminae seems more appropriate than cutting edges to describe the laminae between the teeth. Terminology for the mandible, proboscis, and female's sting apparatus and associated sterna follows Michener & Fraser (1978), Winston (1979), and Packer (2003, 2004), respectively.

Data compilation: We conceptualized and scored the majority of character statements from searching on all parts of the body of both male and female sexes, including the labiomaxillary complex, mandible, and genitalia with its associated terga and sterna. We also took and modified some character statements from the cladistic analyses of Roig-Alsina & Michener (1993) and Gonzalez *et al*. (2012). During the conception and formulation of character statements, the following comparative studies and taxonomic revisions were useful for charater selection as they mentioned or discussed morphological features of taxonomic importance: Michener (1962, 1965, 2000, 2007), Michener & Fraser (1978), Winston (1979), Mitchell (1980), and Roig-Alsina & Michener (1993).

We examined and measured morphological features using Olympus SZ60 and SZX12 stereomicroscopes with an ocular micrometer. We cleared the labiomaxillary complex and genitalia with 10% KOH at room temperature for about 24h. Then, we washed them with 70% ethanol before storing them in glycerin. To document character states, we prepared line illustrations as well as photomicrographs, which we took with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and assembled with Zerene Stacker™ software package. We processed final figures with Adobe Photoshop® CC.

We built a data matrix in WinClada (Nixon, 1999) and scored 272 characters (Appendix 3). However, we were not able to code all characters for all species because some taxa are known only from the type specimen and we could not dissect them, and in other cases, they are only known from one sex. Unless we suspected sexual dimorphism, we took characters from the available sex. We only used continuous characters, such as proportions or measurements, when we found distinct gaps in the measured variable among the examined specimens. To avoid duplication, we coded only in the female those characters that are unequivocally present in both sexes (*e.g.*, labiomaxillary complex).

To facilitate further comparisons, we formulated character statements following Sereno (2007), in which the most general locator is positioned first (*e.g.*, antennal scape), followed by a variable (*e.g.*, length), a variable qualifier (*e.g.*, length relative to torulocellar distance), and mutually exclusive character states, the latter following a colon.

In some cases, we added a secondary or tertiary locator to clarify the position of the primary locator.

The following are the descriptions of the character statements used in the generic-level analysis of Megachilini. We indicated the original author of a character statement and used the following abbreviations F, OD, PW, Mt, S, and T for flagellomere, median ocellus diameter, one puncture width, mandibular tooth, and metasomal sterna and terga, respectively.

Female

Head

1. Subantennal area (*i.e.*, clypeoantennal distance), length relative to vertical diameter of torulus (Gonzalez *et al*., 2012: char. 4): 0 = short, equal to or shorter than; 1 = long, ≥ 1.2×.
2. Anterior tentorial pit, location (Roig-Alsina & Michener, 1993: char. 2): 0 = at the intersection of subantennal and epistomal sulci; 1 = on epistomal sulcus, below intersection with subantennal sulcus.
3. Anterior tentorial pit, shape: 0 = rounded, about as long as broad; 1 = elongate, about twice as long as broad.
4. Interantennal area (*i.e.*, intertorular distance), length relative to torulorbital distance (Gonzalez *et al*., 2012: char. 9): 0 = equal to or shorter than; 1 = greater than.
5. Antenna, scape, length (excluding basal bulb) relative to torulocellar distance: 0 = equal to or shorter than; 1 = long, ≥ 1.2×.
6. Antenna, pedicel, length relative to length of F1 (modified from Gonzalez *et al*., 2012: char. 13): 0 = short, at most as long as; 1 = long, ≥ 1.5×. In character state 1, the pedicel is often about as long as or longer than length of F1 and F2 combined.
7. Antenna, F1, length relative to F2: 0 = 1.5–2.0× longer than; 1 = about as long as; 2 = shorter than.
8. Vertex, integument, with fine, shining longitudinal line from ocelli to its posterior margin: 0 = absent; 1 = present.
9. Paraocular carina (Roig-Alsina & Michener, 1993: char. 4): 0 = absent; 1 = present.
10. Preoccipital carina (Gonzalez *et al*., 2012: char. 18): 0 = absent; 1 = present.
11. Preoccipital carina, dorsal edge of head behind vertex (modified from Gonzalez *et al*., 2012: char. 19): 0 = present; 1 = absent.
12. Ocelloccipital area, length relative to OD (Gonzalez *et al*., 2012: char. 20): 0 = short, 1.0–3.0×; 1 = long, ≥ 3.1×.
13. Hypostomal area, short transverse carina: 0 = absent; 1 = present. This short carina encloses a small, shiny, depressed area, behind the mandible and is present in the female of *Melanosarus* Mitchell.
14. Hypostomal carina, porterior portion, tooth or strong protuberance: 0 = absent; 1 = present, distinct. In most species, the hypostomal carina gently curves from the base of the mandible (ventral portion) to behind the head (posterior portion), but in some species a distinct tooth or strong protuberance develops where the ventral portion flexes upwards behind the head.
15. Hypostomal carina, ventral portion, orientation relative to margin of mandibular socket (Gonzalez *et al*., 2012: char. 21): 0 = directed to medial margin; 1 = curving towards posterior margin (Griswold & Gonzalez, 2011: fig. 13).
16. Supraclypeal area, lower portion, shape (modified from Gonzalez *et al*., 2012: char. 8): 0 = flat, elevated or modified, not strongly convex in profile; 1 = strongly convex in profile.
17. Clypeus, width relative to mid length: 0 = short, ≥ 3.0×; 1 = long, ≤ 2.8×.
18. Clypeus, basal portion, shape: 0 = flat or convex, not greatly elevated or ornate; 1 = greatly elevated and ornate.
19. Clypeus, disc, shape: 0 = flat or convex, not elevated; 1 = elevated with flat median section.
20. Clypeus, distal margin, degree of projection over labroclypeal articulation (Gonzalez *et al*., 2012: char. 1): 0 = not projected, articulation clearly visible (Fig. 1D; Engel & Gonzalez, 2011:

fig. 8); 1 = slightly projected, articulation not visible (Gonzalez & Engel, 2012: fig. 4); 2 = strongly projected, articulation not visible (Eardley, 2012: fig. 43a). In species having character state 2, the strongly projected distal margin makes the clypeus hexagonal in shape, as in *Chalicodoma*. The clypeus of *M*. (*Schrottkyapis*) *assumptionis* Schrottky has a bifid median process strongly produced over the labrum (Silveira *et al*., 2002: fig. 11.25); however, the apicolateral margins of the clypeus slightly cover the base of labrum; thus, we coded this species as having character state 1.

21. Clypeus, complete longitudinal median carina: 0 = absent; 1 = present (Pasteels, 1965: fig. 1059).
22. Clypeus, pubescence, density: 0 = sparse throughout, integument visible among setae; 1 = dense throughout, integument not visible among setae; 2 = dense on sides of clypeus, sparse to absent on disc (Eardley, 2013: fig. 66a).
23. Clypeus, disc, abundant, erect, short and partially hooked or wavy setae: 0 = absent; 1 = present (Durante & Abrahamovich, 2006: figs. 1–3; Gonzalez & Griswold, 2013: fig. 5E). These modified setae are associated with the passive collection of pollen from nototribic flowers.
24. Labrum, shape: 0 = rectangular, base as wide as apex, lateral margins parallel to each other (Mitchell, 1980: fig. 48); 1 = subtriangular, base ≥ 1.5× apical width, lateral margins converging apically (Mitchell, 1980: fig. 30).
25. Labrum, disc, pubescence: 0 = absent; 1 = present.
26. Labrum, disc, type and length of setae: 0 = consisting only of long (≥ 1.0× OD), erect setae; 1 = consisting of two types of setae, minute, yellowish, appressed setae, and long (≥ 1.0× OD), erect setae; 2 = consisting only of minute, yellowish, appressed setae.
27. Labrum, midapical or subapical protuberance: 0 = absent; 1 = present.
28. Mandible, length relative to length of compound eye in lateral view: 0 = short, ≤ 0.7×; 1 = long, ≥ 0.9× (Fig. 1D; Engel & Gonzalez, 2011: fig. 8).
29. Mandible, outer surface, median root of outer ridge: 0 = absent; 1 = present, extending towards abductor swelling (Gonzalez & Engel, 2012: fig. 5).
30. Mandible, outer surface, upper root of outer ridge: 0 = absent; 1 = present, extending towards acetabulum and joining acetabular carina (Fig. 2F).
31. Mandible, outer surface, secondary transverse ridge: 0 = absent; 1 = present, distinct. King (1994: fig. 8) recognized and illustrated this ridge, which is dorsal and parallel to the acetabular groove. In some species, such as *M*. (*Litomegachile*) *brevis* Say, the acetabular interspace is elevated, flattened or evenly convex, with a distinct edge delimiting the superior margin of the acetabular groove. However, we coded these species as having character state 0 because this is an edge, not a ridge.
32. Mandible, transverse ridge, basal portion joining acetabular carina: 0 = absent; 1 = present (King, 1994: fig. 8).
33. Mandible, apex, width relative to base in lateral view: 0 = narrow, equal to or narrower than (Engel & Gonzalez, 2011: fig. 8); 1 = broad, ≥ 1.5× (Figs. 2C–J).
34. Mandible, distal margin, axis: 0 = straight or nearly so, not strongly oblique (Figs. 2C–J); 1 = strongly oblique as in *Chalicodoma* and *Chalicodomoides* Michener (Michener, 2007: fig. 84-12d).
35. Mandible, outer surface, apex, type of integument: 0 = smooth and shiny, or nearly so, between punctures (Figs. 2C–J; Gonzalez & Engel, 2012: fig. 33); 1 = microreticulate to finely punctate (Fig. 3A; Engel & Gonzalez, 2011: fig. 24).
36. Mandible, outer surface, apex of acetabular mandibular groove, distinct tuft or brush of long golden setae: 0 = absent; 1= present (Fig. 2F). In some species, such as *M*. (*Paracella*) *semivenustella* Cockerell, another brush is also present at the apex of the outer groove. In species with a well-developed outer premarginal fimbria, such as *M*. (*Hackeriapis*) *ferox* Smith, the apices of the acetabular and outer grooves often appeared as having brushes; however, the setae on these areas are about the same length and density as those on the outer premarginal fimbria. Thus, we coded these species as having character state 0.
37. Mandible, outer premarginal impressed fimbria (Gonzalez *et al*., 2012: char. 39): 0 = reduced or absent (Fig. 2E); 1 = present, distinct (Fig. 3E; Michener & Fraser, 1978: fig. 29).

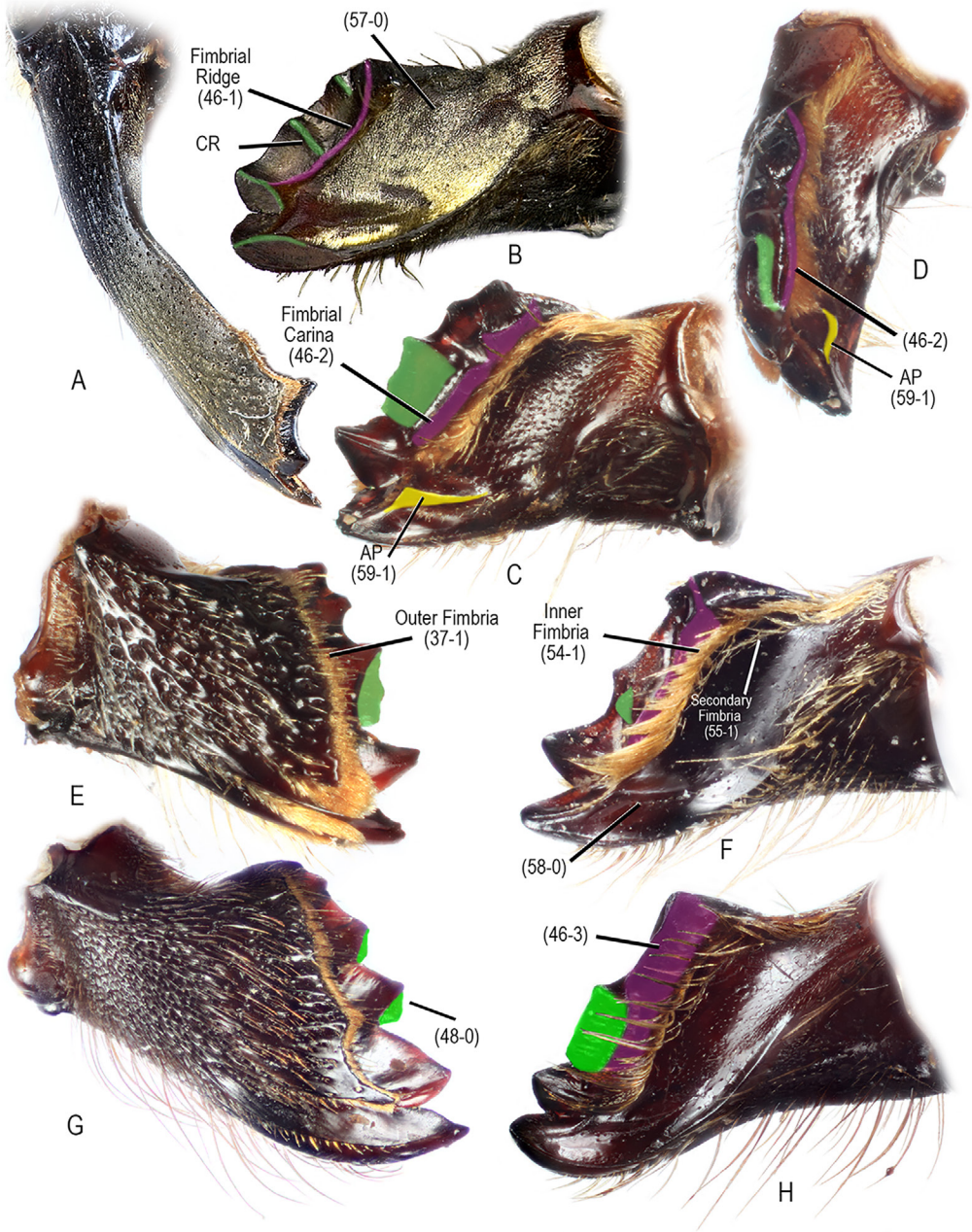

Figure 3. Female mandible of *Megachile* Latreille *s.l.* in outer (A, E, G), frontal (D), and inner views (B, C, F, H). **A.** *Megachile* (*Callomegachile*) *pluto* Smith. **B.** *M.* (*Callomegachile*) sp. **C–E.** *M.* (*Chelostomoda*) *spissula* Cockerell. **F.** *M.* (*Rhyssomegachile*) *simillima* Smith. **G.** *M.* (*Creightonella*) *frontalis* (Fabricius). **H.** *M.* (*Pseudocentron*) *pruina* Smith. Interdental laminae highlighted in green (odontogenic) and pink (ctenogenic). Abbreviations: CR = corono-radicular ridge; AP = adductor apical ridge.

38. Mandible, outer surface, acetabular interspace, shape: 0 = not conspicuously flattened or depressed, gently curving towards base of mandible (Fig. 3A); 1 = clearly flattened or depressed, such as outer surface of mandible has a distinguishable basal, lateral surface, and

a distal, anterior surface (Fig. 1E). Character state 1 is typical of most Group 1 of subgenera of *Megachile s.l.*

39. Mandible, tooth count: 0 = two; 1 = three; 2 = four to six; 3 = lower distal margin with one or two large teeth, upper portion edentate or nearly so, or with very small teeth (Michener, 2007: fig. 84-12d, e). In some species, the upper distal margin is incised, resulting in a 5- or 6-toothed mandible (*e.g.*, Figs. 2D, H), with the upper teeth closer than other teeth. We coded these species as having character state 2.
40. Mandible, Mt_1, width relative to basal width of Mt_2: 0 = ≤ 1.4× (Figs. 2C–H); 1 = ≥ 1.5× (Fig. 2I).
41. Mandible, third dental interspace, length relative to combined length of first and second interspaces: 0 = short, ≤ 1.5× or absent; 1 = long, about 2.0× (Michener, 2007: fig. 84-11f).
42. Mandible, upper distal margin, shape: 0 = rounded or pointed with apex anteriorly directed; 1 = pointed, subtriangular, and with apex dorsally directed.
43. Mandible, upper tooth, shape: 0 = acute or right angular (Fig. 2I); 1 = rounded or truncate, not incised (Fig. 2G); 2 = rounded or truncate, incised (Fig. 2H).
44. Mandible, upper margin near distal margin, tooth or projection: 0 = absent; 1 = present.
45. Mandible, upper margin near mandibular base, tooth or projection: 0 = absent; 1 = present (Michener, 1965: fig. 664).
46. Mandible, inner surface preapically: 0 = without a distinct fimbrial ridge or carina; 1 = with a distinct fimbrial ridge running somewhat parallel to the mandibular margin (Fig. 3B); the surface between this ridge and the mandibular margin is sloping; 2 = with a distinct fimbrial carina running parallel to the mandibular margin, usually posterior to the bases of teeth and not apically extended into a lamina; the surface formed between this carina and the mandibular margin somewhat perpendicular (Figs. 3C, D, F); 3 = with a distinct lamina projecting beyond bases of upper teeth (Figs. 2E, 3H).
47. Mandible, second interspace, interdental lamina: 0 = absent; 1 = present (Fig. 2H).
48. Mandible, second interspace, type of interdental lamina: 0 = incomplete, not filling interspace (Fig. 3G); 1 = complete, filling interspace.
49. Mandible, second interspace, origin of interdental lamina: 0 = not arising from inferior border of third tooth and thus interpreted as an apical extension of the fimbrial carina (ctenogenic laminae, see results); 1 = arising from the inferior border of third tooth (odontogenic laminae, Figs. 3C–D). In *M. assumptionis* and *M.* (*Stelodides*) *euzona* Pérez, a very small laminar projection (not visible in frontal view) arises from the inferior border of Mt_3, and thus suggesting an incomplete interdental lamina; however, we coded these species as having character state 0. In *M.* (*Tylomegachile*) *orba* Schrottky and *M.* (*Tylomegachile*) *simplicipes* Friese, the interdental laminae of the second and third interspaces are presumably fused; however, a frontal view of the mandibular margin reveals that these laminae are in different planes. This suggests that the interdental lamina of the second interspace arises from the third tooth and thus we coded these species as having character state 1.
50. Mandible, second interspace, interdental lamina fused with third tooth, thus resulting in a broad, thin tooth with a more or less truncate margin: 0 = absent; 1 = present. Character state 1 is a putative synapomorphy of *Amegachile* Friese (Michener, 2007: fig. 84-11e).
51. Mandible, third interspace, interdental lamina: 0 = absent; 1 = present (Fig. 3G).
52. Mandible, third interspace, type of interdental lamina: 0 = incomplete, not filling interspace; 2 = complete, filling interspace.
53. Mandible, third interspace, origin of interdental lamina: 0 = not arising from inferior border of fourth tooth and thus interpreted as an apical extension of the fimbrial carina; 1 = arising from inferior border of fourth tooth. In *M. semivenustella*, in addition to a complete interdental lamina, there seems to be a small, incomplete interdental lamina arising from Mt_4; thus, we coded this species as having both character states.
54. Mandible, inner surface, inner fimbria, length relative to apical mandibular margin (Gonzalez *et al*., 2012: char. 36): 0 = short, restricted to upper margin (Michener & Fraser, 1978: fig. 25); 1 = long, extending across entire margin (Fig. 3F).
55. Mandible, inner surface, secondary fimbria: 0 = absent; 1 = present (Fig. 3F).
56. Mandible, adductor interspace, setae (Gonzalez *et al*., 2012: char. 37): 0 = absent; 1 = present

(Figs. 3B, C).
57. Mandible, adductor interspace, length of setae relative to OD: 0 = short, ≤ 0.2×; 1 = long, ≥ 0.4×.
58. Mandible, adductor interspace, longitudinal, impressed line below adductor apical ridge marked with a series of setae: 0 = absent (Fig. 3F); 1 = present.
59. Mandible, strong adductor apical ridge (Gonzalez *et al*., 2012; char. 34): 0 = absent; 1 = present (Fig. 3C).
60. Labium, glossa (in repose), length: 0 = short, not reaching metasoma; 1 = long, reaching metasoma.
61. Labium, prementum, subligular process, shape (modified from Gonzalez *et al*., 2012: char. 48): 0 = elongate, long and narrow, styliform (Winston, 1979: fig. 12f); 1 = broad, apex truncated or nearly so (Winston, 1979: fig. 38); 2 = broad, with pointed apex (Winston, 1979: fig. 28).
62. Labium, first palpomere, length relative to length of second palpomere: 0 = short, ≤ 0.5×; 1 = long, ≥ 0.8×.
63. Labium, first palpomere, length relative to width: 0 = ≤ 3.5×; 1 = ≥ 4.0×.
64. Labium, first palpomere, distinct brush of setae on midbasal concavity (Gonzalez *et al*., 2012: char. 51): 0 = absent; 1 = present (Winston, 1979: fig. 11a).
65. Labium, third palpomere, axis relative to second palpomere: 0 = on same plane; 1 = at an angle.
66. Maxilla, stipes, dististipital process (Roig-Alsina & Michener, 1993: char. 31): 0 = absent or reduced (Winston, 1979: fig. 7a); 1 = present, elongated, almost joining stipital sclerite.
67. Labium, glossa, shape: 0 = not broadened or ligulate; 1 = broadened or ligulate (Michener, 1965: fig. 716).
68. Maxilla, palpomere count, including basal palpomere (modified from Gonzalez *et al*., 2012: char. 60): 0 = two or three; 1 = four or five.
69. Maxilla, palpi, setae length relative to palpomere diameter: 0 = short, ≤ 2.0×; 1 = long, ≥ 2.1×.
70. Maxilla, second palpomere, length relative to width: 0 = short, ≤ 1.6×; 1 = long, ≥ 2.0×.
71. Maxilla, third palpomere, length relative to width: 0 = short, ≤ 2.6×; 1 = long, ≥ 3.0×.
72. Maxilla, lacinia, apical setae, length and thickness setae relative to setae on medial margin: 0 = similar in length and thickness; 1 = distinctly longer and thicker.
73. Hypostoma, paramandibular process (Gonzalez *et al*., 2012: char. 22): 0 = short or absent; 1 = present, long (Gonzalez *et al*., 2012: fig. 6).
74. Hypostoma, paramandibular carina, shape and length relative to distance between paramandibular process and hypostomal carina (modified from Gonzalez *et al*., 2012: char. 23): 0 = short, half or less; 1 = long, ending at hypostomal carina; 2 = long, not reaching hypostomal carina, usually curving upwards or downwards; 3 = long, reaching posterior component of the hypostomal carina and forming a strong lobe.

Mesosoma
75. Pronotal lobe, shape (Gonzalez *et al*., 2012: char. 61): 0 = rounded, without carina or strong lamella; 1 = with strong carina or border; 2 = with conspicuously broad, thin lamella.
76. Omaular carina (Gonzalez *et al*., 2012: char. 65): 0 = absent; 1 = present.
77. Mesepisternum, punctation: 0 = finely or coarsely punctate, not forming strong rows with distinct shining ridges among them; 1 = coarsely punctate, forming strong rows with distinct shining ridges among them.
78. Mesoscutum, anterior margin in profile, shape and sculpturing (Gonzalez *et al*., 2012: char. 69): 0 = rounded, without distinctly different surface sculpture; 1 = truncate, perpendicular, or nearly so, shinier and less punctate than dorsal portion.
79. Mesosoma, dorsum, yellow or reddish maculations: 0 = absent; 1 = present.
80. Mesoscutum, disc, length and density of setae: 0 = consisting only of long setae (≥ 3.0–4.0× OD), integument barely visible; 1 = consisting only of very short setae (≤ 0.5× OD), integument sparsely covered to almost bare; 2 = consisting only of short setae (1.5–2.0× OD), integument visible or partially obscured among setae; 3 = consisting of two types of setae, minute, yellowish, appressed setae, and erect longer setae (2.0× OD); 4 = consisting of semi-erect or appressed yellowish tomentum uniformly covering the integument.

81. Mesoscutum, notaulus line, fascia: 0 = absent; 1 = present.
82. Mesoscutum, parapsidal line, length relative to length of tegula in dorsal view (Gonzalez *et al*., 2012: char. 72): 0 = long, ≥ 0.4×; 1 = short, ≤ 0.3× or absent.
83. Mesoscutum, disc, punctation, density and size: 0 = finely and closely (≤ 1.0–2.0× PW) punctate, punctures (≤ 0.2× OD) not in row; 1 = coarsely and densely punctate, punctures (≥ 0.5× OD) arranged in rows, thus giving a striate or wrinkled appearance (Engel & Gonzalez, 2011: fig. 37); 2 = coarsely and densely punctate, punctures (≥ 0.5× OD) not arranged in rows.
84. Mesoscutal-mesoscutellar suture, white fascia: 0 = absent; 1 = present.
85. Preaxilla (below posterolateral angle of mesoscutum), incline and pubescence (Gonzalez *et al*., 2012: char. 73): 0 = sloping, with setae as long as those on adjacent sclerites (Gonzalez *et al*., 2012: fig. 10); 1 = vertical, usually nearly asetose (Gonzalez *et al*., 2012: fig. 11).
86. Axilla, posterior margin, shape (modified from Gonzalez *et al*., 2012: char. 74): 0 = rounded, not projected in acute angle or spine; 1 = weakly projected, not reaching posterior transverse tangent of mesoscutellum; 2 = strongly projected into acute angle or spine, surpassing posterior transverse tangent of mesoscutellum (Michener, 2007: fig. 84-6a).
87. Axilla, lateral surface, shape: 0 = not depressed; 1 = depressed, partially or entirely hidden by dorsal surface.
88. Axilla, lateral surface, sculpturing and pubescence: 0 = similarly punctate and setose as on its dorsal surface; 1 = smooth and shiny, asetose; 2 = micropunctate to strongly imbricate on at least its ventral half, dull, asetose or with sparse setae.
89. Axillar fossa, depth: 0 = shallow, surface behind it subhorizontal, without a high mesoscutellar crest between it and metanotum (Fig. 4A); 1 = deep, its posterior surface usually ascending to strong mesoscutellar crest between fossa and metanotum (Fig. 4B).
90. Mesoscutellum, shape in profile: 0 = flat or convex, forming relatively uninterrupted surface with metanotum, thus without a distinct posterior surface; 1 = elevated from metanotum, with a distinct posterior surface.
91. Metanotal pit: 0 = absent; 1 = present, distinct (Fig. 4B).
92. Metanotum, sublateral length relative to midlength: 0 = about as long as; 1 = narrower than.
93. Metanotum, degree of visibility given by mesoscutellum in dorsal view (modified from Roig-Alsina & Michener, 1993: char. 74): 0 = entirely or partially hidden; 1 = fully exposed (Fig. 4C).
94. Metanotum, median tubercle or spine (Michener, 1996: char. 7): 0 = absent; 1 = present (Michener, 2007: fig. 83-1).
95. Propodeal triangle (= metapostnotum), pubescence (Roig-Alsina & Michener, 1993: char. 79): 0 = present; 1 = absent.
96. Propodeum, shape in profile (Roig-Alsina & Michener, 1993: char. 73): 0 = largely vertical; 1 = entirely slanting or with slanting dorsal portion rounding onto vertical portion.
97. Propodeal pit, shape (Gonzalez *et al*., 2012: char. 87): 0 = rounded or elongate, but not linear; 1 = linear.
98. Legs, color: 0 = dark brown to black, concolor with remaining areas of mesosoma; 1 = reddish or orange, contrasting with dark brown to black mesosoma.
99. Metatibia, outer surface, strong tubercles or spicules that do not end in setae or bristles (Gonzalez *et al*., 2012: char. 102): 0 = absent; 1 = present (Michener, 2007: fig. 80-3b).
100. Mesotibia, outer surface, apically with acute angle and distinct notch anteriorly (Gonzalez *et al*., 2012: char. 92): 0 = absent; 1 = present (Gonzalez *et al*., 2012: fig. 14).
101. Mesotibia, outer surface, long, acute medial spine on apical margin: 0 = absent; 1 = present (Fig. 4D).
102. Mesotibia, outer surface, distinct longitudinal carina on apical one-fourth: 0 = absent; 1 = present (Fig. 4E). This carina joins the distal margin of the tibia, sometimes in a sharp angle, and thus appearing as a spine [*e.g*., *M*. (*Amegachile*) *bituberculata* Ritsema]; however, there is always a concave, bare area posterior to this carina, which is absent in taxa that possess a true spine. In some species, this carina and the distal margin of tibia form a distinct spatulate or spoon-like process, easily visible in posterior view. This carina is apically notched in *Melanosarus*.
103. Mesotibia, outer surface, area behind longitudinal carina, setae: 0 = present; 1 = absent.

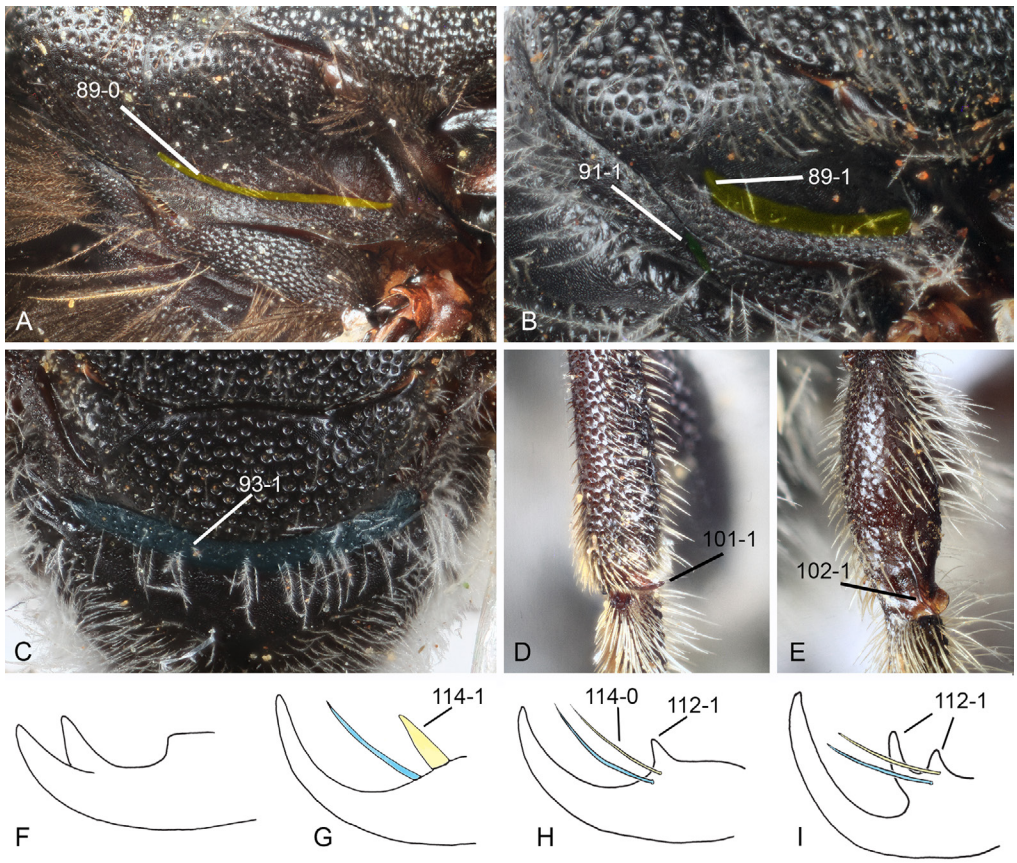

Figure 4. Some female morphological features used in the phylogenetic analysis. **A, B.** Lateral view of axilla. **C.** Dorsal view of mesoscutellum and metanotum. **D, E.** Outer view of apex of mesotibia. **F–I.** Pretarsal claws. *Megachile* (*Melanosarus*) *xylocopoides* Smith (A); *M.* (*Stenomegachile*) *dolichosoma* Benoist (B, C); *M.* (*Chelostomoides*) *rugifrons* (Smith) (D); *M.* (*Megachiloides*) *pascoensis* Mitchell (E); *Dioxys productus* (Cresson) (F); *M.* (*Acentron*) *albitarsis* Cresson (G); *M.* (*Hackeriapis*) *ferox* Smith (H); *M.* (*Schizomegachile*) *monstrosa* Smith (I).

104. Mesotibia, outer surface, posterodistal margin projected into a distinct spine: 0 = absent; 1 = present (Gonzalez & Engel, 2012: fig. 7). In *M.* (*Lophanthedon*) *dimidiata* (Smith) the projection is small and sometimes absent. We coded this species as having character state 0.
105. Mesotibia, outer surface, tuft of stiff setae on posterodistal margin: 0 = absent; 1 = present.
106. Metatibia, basitibial plate (Roig-Alsina & Michener, 1993: char. 84): 0 = absent; 1 = present.
107. Metatibia, scopa consisting of uniformly dispersed long setae on outer surface: 0 = absent; 1 = present.
108. Metatibia, spurs, shape: 0 = pointed, straight or gently curving apically; 1 = pointed, straight with apex strongly curved inward; 2 = not pointed, parallel-sided and with apex blunt.
109. Metabasitarsus, length relative to length of tibia: 0 = short, ≤ 0.5×; 1 = long, ≥ 0.8×.
110. Metabasitarsus, length relative to width (modified from Roig-Alsina & Michener, 1993: char. 90): 0 = ≥ 3.0×; 1 = ≤ 2.8×.
111. Pretarsal claws, shape (Roig-Alsina & Michener, 1993: char. 99): 0 = simple (Fig. 4G–I); 1 = bifurcate (Fig. 4F).
112. Pretarsal claws, one or two basal projections: 0 = absent; 1 = present (Figs. 4H, I).
113. Pretarsal claws, seta count: 0 = one; 1 = two.
114. Pretarsal claws, thickness and length of setae relative to each other: 0 = similar thickness,

one of them at least half length of the other (Fig. 4H, I); 1 = one conspicuously shorter and stouter than the other (Fig. 4G).
115. Propretarsus, arolium (Roig-Alsina & Michener, 1993: char. 98): 0 = reduced or absent; 1 = present.
116. Forewing, first submarginal cell, length relative to second as measured on posterior margin (modified from Gonzalez *et al*., 2012: char. 116): 0 = equal to or shorter than; 1 = longer than.
117. Forewing, basal vein (M), location relative to cu-a (modified from Gonzalez *et al*., 2012: char. 118): 0 = posterior to; 1 = confluent with, or basal to.
118. Forewing, 2m-cu (second recurrent vein), location relative to 2rs-m (second submarginal crossvein) (Michener, 1996: char. 12): 0 = basal to (Michener, 2007: fig. 81-1b); 1 = confluent with, or distal to (Michener, 2007: fig. 82-1).
119. Forewing, pterostigma, length relative to width (Gonzalez *et al*., 2012: char. 112): 0 = long, ≥ 2.1×; 1 = short, ≤ 2.0×.
120. Forewing, 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.
121. Hind wing, second abscissa of vein M+Cu, length relative to length of cu-a (Gonzalez *et al*., 2012: char. 122): 0 = short, ≤ 3.0×; 1 = long, ≥ 3.1×.
122. Hind wing, jugal lobe, length relative to length of vannal lobe (each lobe measured from wing base to apex) (modified from Roig-Alsina & Michener, 1993: char. 105): 0 = ≤ 0.5×; 1 = ≥ 0.6×.

Metasoma
123. Metasoma, shape: 0 = strongly convex dorsally, more or less parallel-sided as in *Chalicodoma* and *Chalicodomoides* (Michener, 2007: fig. 84-9); 1 = not parallel-sided, cordate, triangular, and rather flattened as in *Megachile s.str*. (Michener, 2007: fig. 84-8); 2 = as in *Coelioxys* (Michener, 2007: fig. 84-2).
124. T1, junction of anterior and dorsal surfaces, shape (Gonzalez *et al*., 2012: char. 125): 0 = rounded; 1 = angled; 2 = carinate.
125. T1, disc in profile and posterior margin in dorsal view, shape (Gonzalez *et al*., 2012: char. 124): 0 = flattened, posterior margin rounded, anterior and dorsal surfaces indistinguishable; 1 = convex, posterior margin straight or nearly so, with distinct anterior and dorsal surfaces.
126. T1, pubescence, length, density, and color relative to those on T2 and T3: 0 = about the same length, density, and/or color, not contrasting notoriously with these terga; 1 = not of the same color, distinctly longer (2.0–3.0×) and denser.
127. T1, dorsal surface, length relative to length of T2 (measured at midline): 0 = ≥ 0.7×; 1 = ≤ 0.6×.
128. T2, laterally with distinct oval velvety patch: 0 = absent; 1 = present (Pasteels & Pasteels 1971: fig. 1). This velvety patch is sometimes present also on T3.
129. T3, deep postgradular groove (Gonzalez *et al*., 2012: char. 126): 0 = absent; 1 = present.
130. T3, mid portion, deep postgradular groove: 0 = absent, clearly visible only laterally; 1 = present.
131. T3, fasciate marginal zones: 0 = absent; 1 = present.
132. T3, well marked premarginal line: 0 = absent; 1 = present.
133. T6, pygidial plate (Roig-Alsina & Michener, 1993: char. 116): 0 = present; 1 = absent.
134. T6, pubescence, color relative to that of T1–T4: 0 = concolorous (black, pale, or yellowish); 1 = not concolorous (orange, yellowish, or pale).
135. T6, short (≤ OD), appressed setae: 0 = absent; 1 = present.
136. T6, disc in profile, shape: 0 = straight or slightly concave; 1 = strongly convex, without preapical notch; 2 = strongly convex, with preapical notch.
137. T6, erect setae on disc: 0 = present; 1 = absent.
138. T6, clubbed setae on disc: 0 = absent; 1= present.
139. T6, wide apical hyaline flange (Gonzalez *et al*., 2012: char. 131): 0 = absent; 1 = present (Gonzalez *et al*., 2012: fig. 15).
140. Sternal scopa (Roig-Alsina & Michener, 1993: char. 110): 0 = present; 1 = absent.

141. S1, midapical tooth or spine (Gonzalez *et al*., 2012: char. 137): 0 = absent; 1 = present.
142. S3, apical white fasciae under scopa: 0 = absent; 1 = present.
143. S3, mid portion, apical white fasciae: 0 = absent; 1 = present.
144. S6, length (measured along midline) relative to width (Gonzalez *et al*., 2012: char. 138): 0 = short, as long as or shorter than; 1 = elongated, ≥ 2.0×.
145. S6, shape: 0 = subtriangular or broad basally, not parallel-sided; 1 = somewhat parallel-sided, not subtriangular or broad basally.
146. S6, apodeme, disc between marginal ridge and transapodemal ridge (Gonzalez et al., 2012: char. 139): 0 = present (Gonzalez *et al*., 2012: fig. 18; Packer, 2004: fig. 6a, d); 1 = reduced or absent (Gonzalez *et al*., 2012: figs. 19, 20; Packer, 2004: fig. 7f).
147. S6, anterior margin between apodemes, depth and shape: 0 = shallow, without U- or V-shaped concavity; 1 = deep, with U- or V-shaped concavity.
148. S6, anterior margin, deep and narrow medial furrow: 0 = absent; 1 = present (Gonzalez *et al*., 2012: fig. 19).
149. S6, superior lateral margin just below apodemes, distinct swollen border: 0 = absent; 1 = present.
150. S6, lateral surface near lateral ridge, with a strong recurved border or carina: 0 = absent; 1 = present.
151. S6, pregradular area parallel to lateral margin, with a deep invagination: 0 = absent; 1 = present.
152. S6, pregradular area, degree of sclerotization (modified from Gonzalez *et al*., 2012: char. 142): 0 = well sclerotized; 1 = entirely membranous or weakly sclerotized, often easily broken during dissection (Gonzalez *et al*., 2012: fig. 19); 2 = membranous or weakly sclerotized only medially.
153. S6, apex, shape (modified from Gonzalez *et al*., 2012: char. 144): 0 = truncate to broadly rounded; 1 = V-shaped, pointed.
154. S6, distal margin, shape: 0 = simple, not bilobed; 1 = bilobed.
155. S6, setose area, length of area relative to sternal length, as measured it from base of apodemes to apex of sternum: 0 = covering at most apical fourth; 1 = covering about one-third; 2 = covering at least half.
156. S6, setose area, density of setae: 0 = uniformly covered or nearly so; 1 = bare or nearly so.
157. S6, strong preapical border or carina: 0 = absent; 1 = present.
158. S6, fringe of branched setae on or near apical margin: 0 = absent; 1 = present.
159. S6, smooth, bare rim behind apical fringe of branched setae: 0 = absent; 1 = present.
160. S6, bare rim, thickness and shape: 0 = thin, translucent, posteriorly directed; 1 = thick, rolled or abruptly bent dorsally.
161. Sting apparatus, 7th hemitergite, orientation: 0 = vertical (sting apparatus laterally-compressed); 1 = horizontal (sting apparatus dorso-ventrally compressed).
162. Sting apparatus, apex of gonostylus, setal density and length relative to maximum gonostylar width as seen in lateral view (Gonzalez *et al*., 2012: char. 147): 0 = nearly asetose to sparsely covered by short setae (≤ 1.0×); 1 = densely covered by long plumose setae (≥ 1.2×).
163. 7th hemitergite, lamina spiracularis, sculpturing: 0 = smooth and shiny, not sculptured; 1 = weakly to markedly sculptured (Packer, 2003: fig. 2e).
164. 7th hemitergite, lamina spiracularis with a strong protrusion near base of lateral process (Gonzalez *et al*., 2012: char. 150): 0 = absent or reduced; 1 = present (Packer, 2003: fig. 5b).

Male

Head

165. Clypeus, pubescence, density: 0 = sparse throughout, integument visible among setae; 1 = dense throughout, integument not visible among setae (Gonzalez *et al*., 2018: fig. 5C); 2 = basal half with sparse setae (integument visible) or mostly bare, distal half densely covered by setae (integument not visible) (Gonzalez *et al*., 2018: fig. 5D).
166. Clypeus, coloration: 0 = dark brown to black; 1 = yellow.
167. Antenna, F1, length relative to length of F2: 0 = 1.5–2.0×; 1 = about as long as; 2 = shorter

than.
168. Antenna, F5–F10, shape: 0 = cylindrical, flattened, or crenulate; 1 = deeply concave on one side.
169. Antenna, F11, shape: 0 = cylindrical; 1 = compressed or flattened (Engel & Baker, 2006: fig. 5).
170. Hypostomal area, with a concavity or protuberance: 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 5E).
171. Gena, with an oblique, low, smooth, and shiny carina bordered with a dense row of white branched setae: 0 = absent; 1 = present.
172. Mandible, tooth count: 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 *Chalicodoma*.
173. Mandible, upper distal margin, shape and size relative to length and width as remaining teeth: 0 = rounded or pointed, similar length and width; 1 = triangular, conspicuously broader and longer than.
174. Mandible, inferior border, with tooth, process, or projection (Gonzalez *et al*., 2012: char. 156): 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 5F).
175. Mandible, inferior process, shape and orientation: 0 = broad, subtriangular, posteriorly-directed, on basal third of inferior border (Gonzalez *et al*., 2018: fig. 5E); 1 = slender, posteriorly-directed (Fig. 5A; Praz, 2017: fig. 8); 2 = broad, small or large, anteriorly-directed, on basal two-thirds of inferior border (Fig. 5B); 3 = broad, with a very dense brush of stiff branched setae (Fig. 5C; Gonzalez & Engel, 2012: fig. 42); 4 = with a small angle midapically (Durante & Cabrera, 2009: fig. 6).
176. Mandible, inner surface, degree of concavity: 0 = weak; 1 = strong.

Mesosoma
177. Procoxal spine (Gonzalez *et al*., 2012: char. 157): 0 = absent; 1 = present (Gonzalez & Engel, 2012: fig. 43).
178. Procoxal spine, shape and length relative to OD: 0 = short (≤ 1.5×), pointed or somewhat parallel-sided; 1 = long (≥ 2.0×), not parallel-sided; 2 = long (≥ 2.0), parallel-sided or nearly so.
179. Procoxal spine, ventral surface, pubescence: 0 = very sparse to nearly asetose, integument clearly visible; 1 = densely covered with branched setae, integument barely visible among setae.
180. Procoxa, disc, pubescence: 0 = uniformly covered with branched setae, integument barely visible among setae; 1 = asetose or nearly so, integument clearly visible.
181. Procoxa, tuft of stiff ferruginous setae: 0 = absent; 1 = present.
182. Protrochanter, inferior margin apically produced: 0 = absent; 1 = present.
183. Profemur, shape and color: 0 = not strongly compressed, same color of femora of remaining legs; 1 = antero-posteriorly strongly compressed, bright yellow or pale, contrasting with color of femora of remaining legs.
184. Protibia, shape and length relative to width: 0 = not enlarged or swollen, ≥ 3.0×; 1 = distinctively swollen, enlarged, ≤ 2.8×.
185. Protarsi, shape and color (Gonzalez *et al*., 2012: char. 158): 0 = not enlarged or excavated, without conspicuous dark spots on inner surface; 1 = slightly or distinctly enlarged or excavated, often with conspicuous dark spots on inner surface.
186. Protarsi, degree of excavation and color: 0 = slightly excavated, with dark spots on inner surface, usually of the same color of tarsi of remaining legs (Michener, 2007: fig. 84-19b); 1 = strongly modified, distinctively enlarged or excavated, inner surface with dark spots, bright yellow or pale, contrasting with tarsi of remaining legs (Michener, 2007: fig. 84-19a).
187. Protarsi, basal tarsomere (probasitarsus), shape: 0 = not in the shape of a concave, long, distally directed lobe; 1 = forming a distinctly concave, long, distally directed lobe.
188. Mesocoxa, inner surface, small tooth or protuberance: 0 = absent, 1 = present.
189. Mesotibia, inner surface, tooth or protuberance: 0 = absent, 1 = present.
190. Mesotibial spur: 0 = present; 1 = absent.
191. Mesotibial spur, length relative to apical width of metatibia: 0 = at least as long as; 1 = much

shorter than.
192. Mesotibial spur, articulation with mesotibia: 0 = free, not fused to tibia; 1 = fused to tibia.
193. Mesobasitarsus, length relative to width: 0 = long, ≥ 2.5×; 1 = short, ≤ 2.0×.
194. Metafemur, posterior surface, patch of microtrichia (metafemoral keirotrichia): 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 5I). We coded *M.* (*Leptorachis*) *laeta* Smith as having character state 1 even though this structure is very small.
195. Metatibia, inner spur: 0 = present; 1 = absent.
196. Metabasitarsus, length relative to width: 0 = long, ≥ 2.3×; 1 = short, ≤ 2.0×.
197. Propretarsus, arolium: 0 = present (Baker & Engel, 2006: fig. 5); 1 = reduced or absent.

Metasoma
198. T3, marginal zone, color relative to tergal disc: 0 = concolorous; 1 = not concolorous, semi-translucent to translucent.
199. T6, transverse preapical carina (Gonzalez *et al*., 2012: char. 162): 0 = absent; 1 = present.
200. T6, transverse preapical carina, shape: 0 = strong, medially emarginate, not toothed or denticulate (Fig. 5E); 1 = strong, entire or nearly so (Fig. 5D); 2 = strong, toothed or denticulate, with or without a median emargination (Fig. 5F); 3 = weak, little projected in profile, entire or nearly so (Baker & Engel, 2006: fig. 2).
201. T6, preapical carina divided in two or more dorsal processes, and a pair of ventral processes: 0 = absent; 1 = present (Michener, 2007: fig. 84-7).
202. T6, above preapical carina, with strong longitudinal median ridge or protuberance: 0 = absent; 1 = present.
203. T6, above preapical carina, with distinct median concavity: 0 = absent; 1 = present.
204. T6, region of preapical carina, shape: 0 = not swollen or bulbous; 1 = swollen or bulbous, except medially.
205. T6, dorsal surface, density and length of setae relative to OD: 0 = densely covered (integument not visible) by long (2.0–3.0×) setae; 1 = bare or sparsely covered (integument visible) by long (2.0–3.0×) or short (≤ 1.0×) setae; 2 = densely covered by short (≤ 1.0×), appressed, branched setae.
206. T6, apical margin, with lateral spine or tooth: 0 = absent (Fig. 5D); 1 = present (Fig. 5F).
207. T6, apical margin, with submedian spine or tooth: 0 = absent; 1 = present (Fig. 5E).
208. T6, apical margin, size of lateral spine or tooth: 0 = large; 1 = small (Fig. 5E).
209. T6, apical margin, submedian spine or tooth, size relative to size of lateral spine or tooth: 0 = similar; 1 = conspicuously longer and broader than.
210. T7, degree of visibility in dorsal view and orientation (Gonzalez *et al*., 2012: char. 164): 0 = exposed, posteriorly directed; 1 = hidden, and/or anteriorly or ventrally directed.
211. T7, strongly carinate gradulus: 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 6B).
212. T7, transverse carina, shape: 0 = rounded, truncate, or emarginate (Fig. 5G); 1 = long, acute, spiniform (Fig. 5H); 2 = angular (Fig. 5I).
213. T7, with distinct, strong longitudinal median ridge: 0 = absent; 1 = present.
214. T7, apical margin, shape: 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 (Engel & Baker, 2006: fig. 6); 3 = little projected medially, with small, submedian tooth; 4 = little projected medially, without submedian tooth.
215. T7, pygidial plate (Roig-Alsina & Michener, 1993: char. 118): 0 = present; 1 = absent.
216. Sterna, number of fully exposed sclerites (modified from Gonzalez *et al*., 2012: char. 168): 0 = three; 1 = four; 2 = five or six; 3 = two.
217. S1, midapical spine: 0 = absent; 1 = present.
218. S5, width relative to length (Gonzalez *et al*., 2012: char. 175): 0 = ≤ 2.0×; 1 = ≥ 2.1×.
219. S5, gradulus, degree of sclerotization and definition: 0 = weak, barely distinguishable; 1 = strong, indicated by a well-defined transverse line or border.
220. S5, postgradular area laterally, with setose, sclerotized surface: 0 = absent; 1 = present.
221. S5, apical margin, shape: 0 = straight or nearly so; 1 = deeply or shallowly concave.

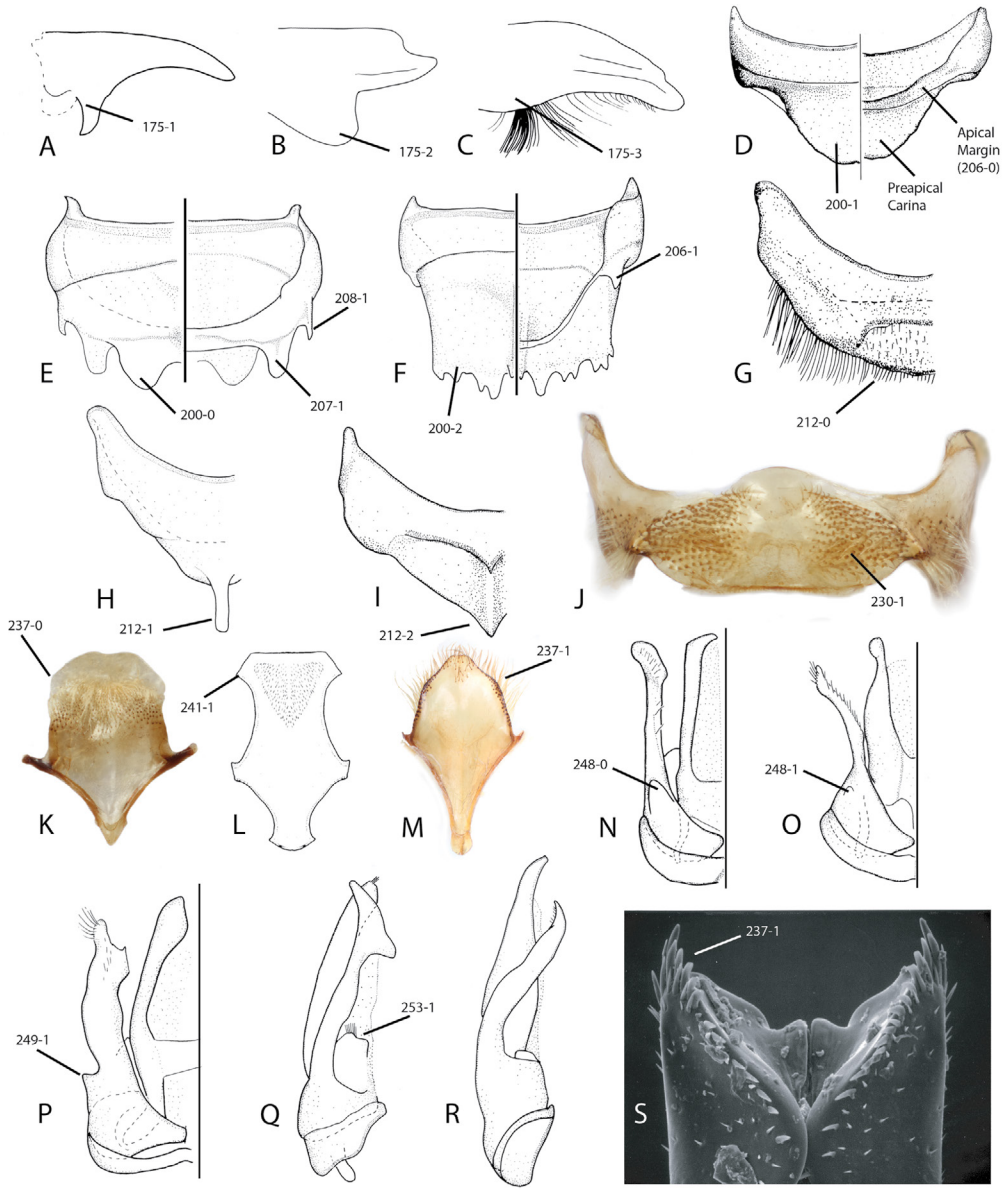

Figure 5. Some male morphological features used in the phylogenetic analysis. **A–C.** Ventral projection of mandible. **D–F.** Dorsal (left half) and ventral (right half) views of sixth tergum. **G–I.** Dorsal view of seventh tergum. **J.** Ventral view of sixth sternum. **K–M.** Ventral view of eighth sternum. **N–P.** Dorsal view of genital capsule. **Q, R.** Profile view of genital capsule. **S.** Apex of penis valves. Taxa: *Megachile* (*Acentron*) *albitarsis* Cresson (**A, L**); *M.* (*Callomegachile*) *biseta* Vachal (**B**); *M.* (*Maximegachile*) *maxillosa* Guérin-Méneville (**C**); *M.* (*Argyropile*) *longuisetosa* Gonzalez & Griswold (**D, G**); *M.* (*Grosapis*) *cockerelli* (**E, H, R**); *M.* (*Creightonella*) *cognata* Smith (**F, I**); *M.* (*Zonomegachile*) *moderata* Smith (**J, K**); *M.* (*Largella*) *donbakeri* Gonzalez & Engel (**M**); *M.* (*Austromegachile*) *montezuma* Cresson (**N**); *M.* (*M.*) *centuncularis* (Linnaeus) (**O**); *M.* (*Moureapis*) *maculata* Smith (**P**); *M.* (*Chalicodoma*) *parietina* (Geoffroy) (**Q**); *M.* (*Chalicodoma*) *sicula* (Rossi) (**S**).

222. S5, with short, well-sclerotized midapical process: 0 = absent; 1 = present (Mitchell, 1980: fig. 42).
223. S5, postgradular area, size of setose area relative to width of sternum (Gonzalez *et al*., 2012: char. 177): 0 = large, ≥ 0.6×; 1 = small, ≤ 0.5×.
224. S5, postgradular area, type of setae (modified from Gonzalez *et al*., 2012: char. 176): 0 = simple, branched or plumose (Fig. 6A); 1 = lanceolate, ovate-acuminate (Figs. 6B, C); 2 = capitate or spatulate (Figs. 6E, F); 3 = fan-shaped (Fig. 6D). Sometimes we found more than one type of setae, and thus we coded the most abundant type.
225. S5, postgradular area, with broad, asetose, and weakly sclerotized area above pubescence: 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 26D).
226. S5, apicolateral margin, type and length of setae relative to those on postgradular area: 0 = asetose or with short setae of similar length; 1 = with simple or branched longer (2.0–3.0×) setae.
227. S5, midapical margin, with dense tuft of stiff, thickened, simple setae: 0 = absent; 1 = present.
228. S6, width relative to length (Gonzalez *et al*., 2012: char. 183): 0 = ≤ 2.0×; 1 = ≥ 2.1×. Because the midapical margin of S6 is highly variable, we measured the length of S6 on its lateral margin, from the base of the apodeme to the apical margin of the sternum.
229. S6, degree of sclerotization (Gonzalez *et al*., 2012: char. 182): 0 = well-sclerotized; 1 = weakly sclerotized to membranous.
230. S6, postgradular area, pubescence (Gonzalez *et al*., 2012: char. 184): 0 = absent or very sparse (integument clearly visible among setae), without forming distinct patches; 1 = dense, forming distinct patches (Fig. 5J). In *Trichothurgus wagenknechti* (Moure), a mediolongitudinal bare area divides the discal pubescence of S3–S6. Thus, the resulting patches of setae on S6 might not be homologous to those found in other megachiline bees. However, we coded this species as having character-state 1.
231. S6, bare area between setal patches, width relative to one patch width: 0 = wide, ≥ 1.0 ×; 1 = small, ≤ 0.5×.
232. S6, postgradular area, type of setae (modified from Gonzalez *et al*., 2012: char. 185): 0 = unmodified, simple or branched (Fig. 6A); 1 = modified, lanceolate, ovate-acuminate (Figs. 6B, C), capitate, spatulate (Figs. 6E, F), or fan-shaped (Fig. 6D).
233. S7, degree of sclerotization (modified from Gonzalez *et al*., 2012: char. 186): 0 = entirely well-sclerotized, usually setose; 1 = weakly sclerotized, membranous, frequently asetose.
234. S8, length relative to width: 0 = ≤ 2.5×; 1 = ≥ 2.6×.
235. S8, spiculum, shape: 0 = pointed or broadly rounded (Michener, 2007: figs. 77-1b, 80-4d); 1 = subrectangular; 2 = as an elongate, narrow process (Michener, 2007: fig. 82-2i); 3 = as a short process with an expanded apex (Gonzalez & Griswold, 2013: fig. 508).
236. S8, lateral apodemes: 0 = absent or weakly sclerotized (Michener, 2007: fig. 80-4d); 1 = distinct (Michener, 2007: fig. 82-2b).
237. S8, lateral margins, setae: 0 = absent (Figs. 5K, L); 1 = present, forming a distinct fringe (Fig. 5M).
238. S8, apex, length relative to sternal length, as measured from lateral apodemes to distal margin: 0 = short, about ¼ (Michener, 2007: fig. 80-4d); 1 = long, about half.
239. S8, apex, width relative to width of spiculum: 0 = wider; 1 = about as wide as or narrower than.
240. S8, apex, shape: 0 = broadly or narrowly rounded; 1 = subrectangular (Fig. 5L).
241. S8, apex, shape: 0 = not expanded; 1 = expanded (Fig. 5L).
242. S8, distal margin, shape: 0 = entire, straight, broadly rounded or pointed (Michener, 2007: fig. 84-4b); 1 = entire, with a small midapical projection (Michener, 2007: fig. 77-1b); 2 = bilobed (Michener, 2007: fig. 82-2b).
243. Genital capsule, length relative to width: 0 = short, about as long as; 1 = elongate, longer than. We measured maximum total length from the base of the gonobase to apex of the penis valves or gonostylus and maximum width at the base of the gonobase.
244. Genital foramen, orientation: 0 = anteriorly directed or nearly so (Michener, 2007: fig. 80-4c); 1 = ventrally directed (Michener, 2007: fig. 77-1a).

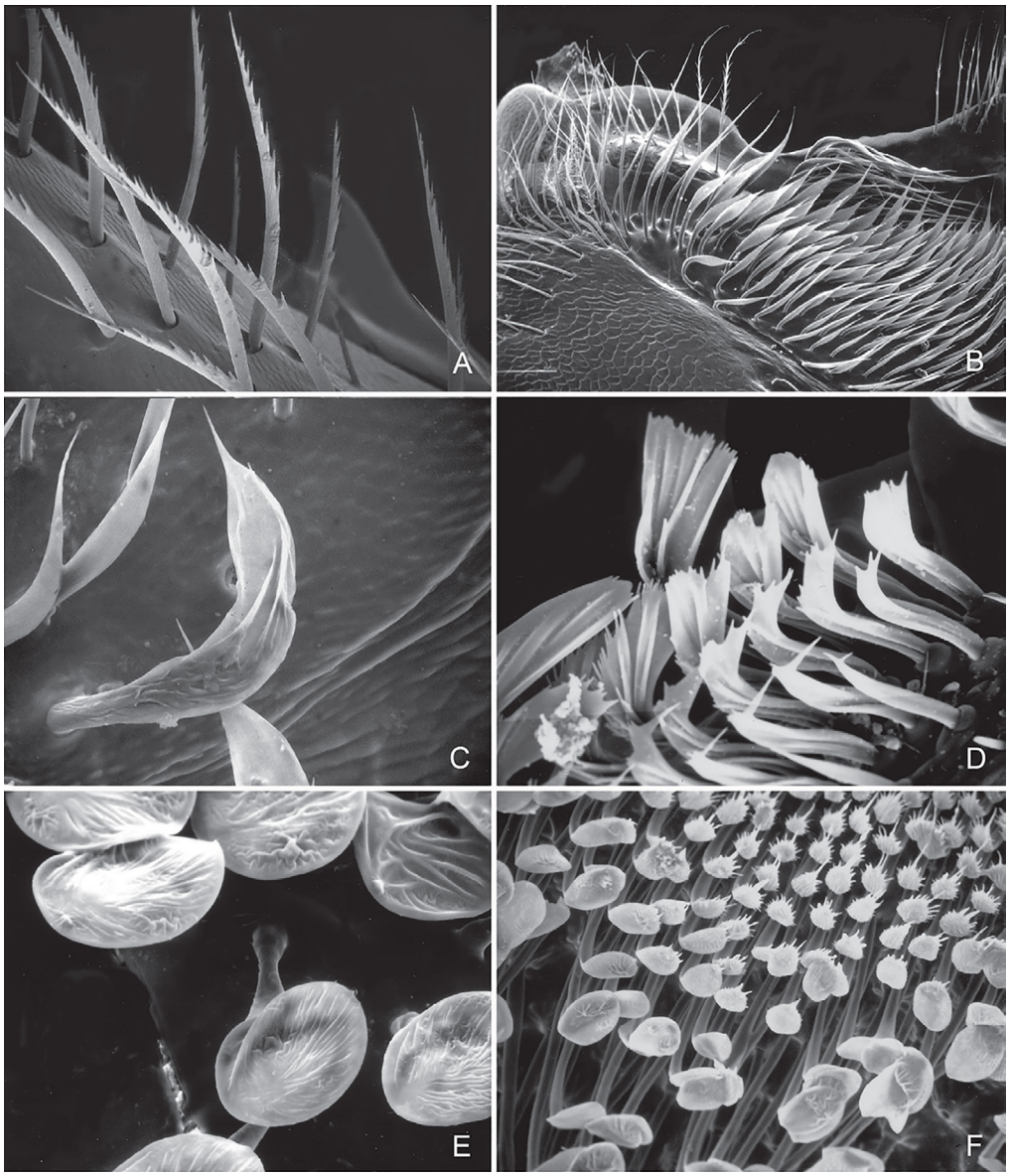

Figure 6. Examples of the types of setae found on the male S4–S6 of *Megachile* Latreille *s.l.* **A.** Branched, unmodified, S4, *Megachile* (*Acentron*) *albitarsis* Cresson. **B.** Acuminate, S4, *M.* (*Megachile*) *centuncularis* (Linnaeus). **C.** Acuminate, S6, *M.* (*Chalicodoma*) *sicula* (Rossi). **D.** Fan-shaped, S6, *M.* (*Chelostomoides*) *exilis* Cresson. **E.** Capitate-spatulate, S5, *M.* (*Chelostomoides*) *rugifrons* (Smith). **F.** Capitate-spatulate, S5, *M.* (*Xanthosarus*) *fortis* Cresson.

245. Gonobase (modified from Roig-Alsina & Michener, 1993: char. 122): 0 = present, distinguishable; 1 = reduced or absent.
246. Articulation between gonostylus and gonocoxite (modified Roig-Alsina & and Michener, 1993: char. 125): 0 = distinct, at least ventrally; 1 = fused, thus forming an unsegmented appendage.
247. Gonocoxite, dorsal lobe: 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 6E).
248. Gonocoxite, dorsal lobe, shape: 0 = large, strong, digitiform (Fig. 5N; Engel & Baker, 2006:

fig. 11); 1 = small, acute (Fig. 5O).
249. Gonocoxite, small sublateral lobe: 0 = absent; 1 = present (Fig. 5P).
250. Volsella (modified from Roig-Alsina & Michener, 1993: char. 126): 0 = absent; 1 = present.
251. Articulation between volsella and gonocoxite: 0 = fused; 1 = articulated, distinguishable as a separated sclerite (Michener, 2007: fig. 77-1a).
252. Volsella, apex, shape: 0 = rounded or pointed; 1 = distinctly notched or bilobed, thus suggesting a medial digitus and a lateral cuspis (Gonzalez & Engel, 2012: fig. 28).
253. Volsella with setae on distal margin: 0 = absent; 1 = present (Fig. 5Q).
254. Gonostylus, length relative to gonocoxite: 0 = equal or shorter than; 1 = ≥ 2.0×.
255. Gonostylus, length relative to penis valves in ventral view (modified from Gonzalez *et al*., 2012: char. 196): 0 = subequal to; 1 = longer than; 2 = shorter than.
256. Gonostylus, shape in lateral view: 0 = curved or arched; 1 = straight or nearly so.
257. Gonostylus, width in lateral view: 0 = not conspicuously narrow, widest at midlength or at apex (Fig. 5Q); 1 = very narrow, about the same width across its entire length (Fig. 5R).
258. Gonostylus, shape in cross section: 0 = not flattened; 1 = flattened.
259. Gonostylus, apex, orientation in dorsal view: 0 = laterally directed; 1 = medially directed; 2 = posteriorly directed.
260. Gonostylus, apex, shape: 0 = not expanded; 1 = clearly expanded.
261. Gonostylus, apical lobes: 0 = absent; 1 = present.
262. Gonostylus, apical lobes, types: 0 = one lateral and one medial (Gonzalez *et al*., 2018: fig. 6D); 1 = one dorsal and one ventral. The gonostylus of *M*. (*Xanthosarus*) *lagopoda* (Linnaeus) has three apical lobes; one on each medial, ventral, and dorsal surfaces. We coded this species as having character states 1 and 2.
263. Gonostylus, medial apical lobe, size: 0 = small, barely indicated; 1 = large and conspicuous (Gonzalez *et al*., 2018: fig. 6D).
264. Gonostylus, apex with large, deep concavity between dorsal and medial lobes: 0 = absent; 1 = present (Gonzalez *et al*., 2018: fig. 6D).
265. Gonostylus, medial surface, pubescence: 0 = absent; 1 = present.
266. Gonostylus, medial surface, length of setae relative to maximum apical gonostylar width: 0 = short, ≤ 2.0×; 1 = long, ≥ 2.1× (Gonzalez & Engel, 2012: fig. 28).
267. Penis valve, apodemes, length relative to their visibility outside genital capsule: 0 = short, not visible; 1 = long, visible as they project through genital foramen (Michener, 2007: fig. 82-2d).
268. Penis valve, shape in dorsal view: 0 = distinctly curved or arched; 1 = straight or nearly so.
269. Penis valve, basal shape: 0 = not enlarged or protuberant; 1 = distinctly expanded.
270. Penis valve, lateral margin, shape: 0 = not enlarged or protuberant; 1 = distinctly enlarged or protuberant.
271. Penis valve, apical shape in ventral view: 0 = straight or nearly so; 1 = distinctly curved or arched inward; 2 = distinctly curved or arch outward (as in *Aztecanthidium* Michener & Ordway).
272. Penis valve, apex with row of thick, spine-like setae: 0 = absent; 1 = present (Fig. 5S).

DATA CHARACTERIZATION: We scored characters from all tagmata of the adult body in both sexes (Fig. 7A). However, more characters were scored from the female than from the male (Chi-squared test, $\chi^2_{[1]} = 5.14$, $p = 0.023$, $n = 252$), even after excluding some characters (~10%) that are present in both sexes but were scored only in the female to avoid duplication. We scored more characters from the metasoma than from other tagmata ($\chi^2_{[2]} = 13.07$, $p = 0.001$, $n = 272$). The number of characters within each sex was significantly different among tagmata (♀: $\chi^2_{[2]} = 10.59$, $p = 0.005$, $n = 164$; ♂: $\chi 2_{[2]} = 64.5$, $p < 0.001$, $n = 108$). In the female, most characters are from the head and mesosoma whereas for the male most characters are from the metasoma.

PHYLOGENETIC ANALYSES: We analyzed this dataset using maximum parsimony under two weighting schemes. We treated all characters as unordered and nonadditive, and used equal weights (EW) and implied weigths (IW) in Tree Analysis Using New

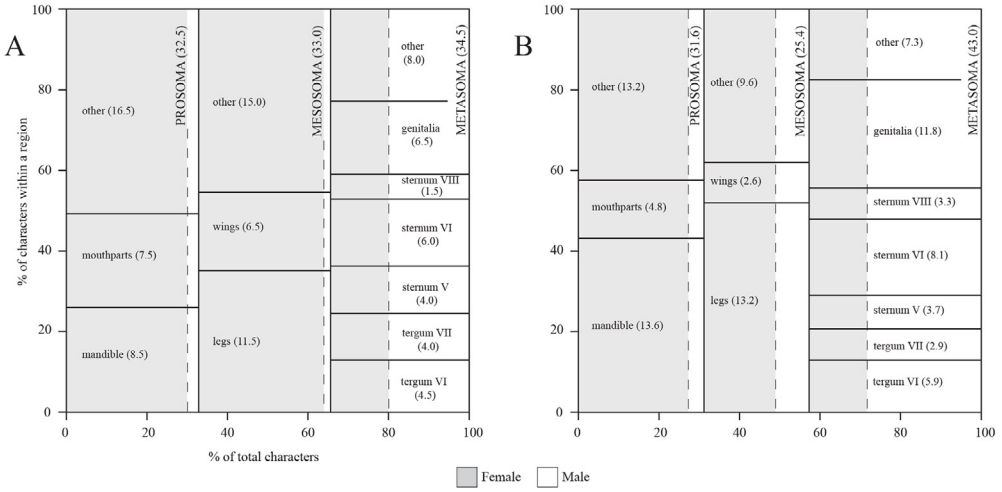

Figure 7. Character distribution maps of the morphological datasets used in the generic-level phylogeny of Megachilini (**A**, $n = 272$ characters) and the tribal-level phylogeny of Megachilidae (**B**, $n = 200$ characters). The *x*-axis represents the percentage of total characters in each tagma or body region (*e.g.*, prosoma) while the *y*-axis represents the percentage of characters of selected structures (*e.g.*, mandible) within a tagma. Percentage in parentheses represents contribution to the total number of characters. See Whitlock & Wilson (2013) for further explanation on character distribution maps.

Techology (TNT; Goloboff *et al.*, 2003a). The IW analysis downweights characters according to their degree of homoplasy (*i.e.*, characters with higher homoplasy have lower weigths) during the heuristic search for parsimonious hypotheses (Goloboff, 1993). In IW analyses, instead of using random *k*-values to vary the strength of the weigthing function, we explored a range of constant *k*-values calculated for average character fits (F) of 50, 54, 58, 62, 66, 70, 74, 78, 82, 86, and 90%. We obtained these *k*-values using the following formula described in Mirande (2009), Reemer (2012), and Reemer & Ståhls (2013): $k = (F \times S)/1\text{-}F$). S is a measure of the average homoplasy per character, calculated as the number of observed steps minus the minimum number of steps divided by the number of characters. The number of observed steps is based on the shortest tree found under EW, which for our dataset is 2364. The minimum number of steps is the cumulative number of minimum character state changes for all 272 characters, which amounts to 323. Thus, the value of S is: (2364-323)/272 = 7.50, while the *k*-value for the character fit of 50% is: (0.5×7.50)/1-0.5) = 7.50. Resulting *k*-values are in Appendix 4. We chose to conduct the IW analysis because studies have proven its effectiveness in recovering topologies congruent with those of total evidence phylogenies (*e.g.*, Reemer, 2012), sometimes outperforming other methods (*e.g.*, Goloboff *et al.*, 2018). This weighting approach is also frequently used in the analysis of morphological datasets along with EW (*e.g.*, Kim & Ahn 2016; Marín *et al.*, 2017; Rocha Filho & Packer, 2017).

We searched for trees under both weighting schemes by implementing sectorial searches with tree drifting (TD) and tree fusing (TF), and ratchet runs with TD and TF. We used the following search: keep a maximum of 10,000 random trees, 500 random addition sequences, and 1000 ratchet iterations, including 100 cycles of TD and 100 rounds of TF per iteration. In EW analysis, we estimated branch robustness using standard bootstrap (sample with replacement) and absolute Bremer support in TNT,

and plotted the values on the strict consensus topology obtained from the final TNT parsimony run. We used 10,000 bootstrap replicates under a heuristic tree search that consisted of 10,000 replicates of Wagner trees with random addition sequences, followed by Tree Bisection Reconnection (TBR) branch swapping (saving 10 trees per replicate). Resulting values per node represent frequency differences GC for Group present/Contradicted (Goloboff *et al*., 2003b). We calculated Bremer support by withholding 10,000 suboptimal trees up to 10 steps longer than the parsimonious trees under a traditional search (10,000 replicates of Wagner trees, followed by TBR, saving 10 trees per replicate).

We assessed the performance of each IW analysis by comparing the number of parsimonious trees, tree length, retention index, and node support. For the latter, we used Jacknife with symmetric resampling expressed as GC frequency-difference values, which Reemer (2012) found useful when determining the reliability of trees under different *k*-values. We searched trees under each *k*-value and used 1000 replicates under a heuristic tree search that consisted of 10 replicates of Wagner trees with random addition sequences, followed by Tree Bisection Reconnection (TBR) branch swapping (saving 10 trees per replicate). We calculated average and median GC frequency-difference from the value displayed at each node, which we plotted on the resulting tree or strict consensus tree (if the analysis yieled more than one parsimonious tree). Groups that are more often contradicted than supported displayed values in brackets, which we considered as having a support of zero and excluded them from the calculations. In addition, we calculated in TNT the SPR distance (Goloboff, 2008) between the resulting topology from each IW analysis and the topology obtained from the analysis of this dataset combined with molecular data (*vide infra*).

We visualized cladograms in WinClada, collapsing unsupported nodes and using DELTRAN (slow) for character optimization; when the choice is equally parsimonious, the latter favours repeated origins of characters over reversals. We used the abbreviations MPT, L, CI, and RI for maximum parsimonious tree, tree length, and consistency and retention indices, respectively. In the text, we referred to characters states in the form 21-1, where 21 is the character and 1 the character state.

PHYLOGENETIC SIGNAL OF MORPHOLOGICAL CHARACTERS: The current trend in evolutionary biology is the analysis of large datasets composed of both molecular and morphological data. Thus, to facilitate future comparative cladistics analyses, we assessed the phylogenetic signal of the scored characters and determined the level of homoplasy among character sets. We compared the median value of RI per character set and conducted partitioned phylogenetic analyses. We grouped characters by sex (male and female characters), tagmata (pro-, meso-, and metasoma), and by the following set of characters of taxonomic importance in the diagnosis and recognition of supraspecific groups: female mandible, female terminalia (T6, S6, and sting apparatus), male legs, and male terminalia (T6, T7, S5–S8, and genitalia). We conducted phylogenetic analyses only to the subset of male and female characters using the settings for EW analyses under parsimony as indicated above. For each analysis, we recorded the number of MPT and tree statistics (L, CI, and RI).

Origin of the Interdental Lamina in the Female Mandible

To determine the possible mandibular structure(s) from which interdental laminae originated, we conducted a comparative study of the female mandible across all taxa of Megachilini used in the phylogenetic analyses. We examined specimens with

unworn mandibles and, whenever possible, we removed one of them from the head capsule, washed it with 95% ethanol, and then mounted it on a card point for examination. We made inferences on the origin of the interdental lamina based on topological correspondence, a robust criteria for recognizing primary homologies (*e.g.*, Remane, 1952; Rieppel & Kearney, 2002; Agnarsson & Coddington, 2008).

Evolutionary Origins of the Interdental Lamina

In addition to using the tree topology inferred from the morphological dataset of Megachilini to examine patterns of variation of the interdental lamina, we also conducted preliminary Bayesian total-evidence tip-dating analyses to explore other hypotheses of relationships. We conducted these preliminary analyses because the phylogenetic hypothesis of Trunz *et al*. (2016) based on molecular data differed from ours (*vide* Results, *infra*), and because these authors employed a node-dating approach to estimate the origin of LC bees. Thus, we conducted two sets of analyses aimed at obtaining more accurate divergence time estimates. First, we conducted a phylogenetic analysis of all tribes in the family Megachilidae. Then, we used the divergence time estimates generated from that analysis to inform priors for the phylogenetic analysis of the genera of Megachilini.

For these combined analyses, we used the morphological data matrix of Gonzalez *et al*. (2012) for the tribal-level analysis of Megachilidae. For the generic-level analysis of Megachilini, we used the newly developed morphological dataset documented in this work. The dataset of Gonzalez *et al*. (2012) includes all tribes, representatives of all fossil taxa, and 80% of the extant generic-level diversity of the family (Appendix 2). It consisted of characters scored from all tagmata of the adult body in both sexes (Fig. 7B), particularly from the female (Chi-squared test, $\chi^2_{[1]} = 52.02$, $p \leq 0.001$, $n = 200$). The number of characters is similar among tagmata ($\chi^2_{[2]} = 0.13$, $p = 0.937$, $n = 200$) but differs between sexes (♀: $\chi^2_{[2]} = 13.60$, $p = 0.001$, $n = 151$; ♂: $\chi^2_{[2]} = 51.47$, $p \leq 0.001$, $n = 49$). In the female, most characters are from the head and mesosoma whereas for the male most characters are from the metasoma.

Molecular data: We used molecular sequences available through GenBank from the following five gene regions generated by Litman *et al*. (2011) and Trunz *et al*. (2016): the protein-coding genes elongation factor 1-α (EF1α), LW-rhodopsin (Opsin), conserved ATPase domanin (CAD), sodium potassium adenosine triphosphatase (NAK), and the ribosomal gene 28S (Appendix 5). We aligned gene fragments using MAFFT ver. 7.305 (Katoh & Standley, 2013), with the secondary structure of 28S accounted for using the Q-INS-I method (Katoh & Toh, 2008). The alignments were then cleaned, frame checked, and concatenated in Mesquite ver. 3.40 (Maddison & Maddison, 2018). Because the gene fragments EF1α, Opsin, and CAD have introns (Trunz *et al*., 2016), we conducted analyses using two approaches. In one analysis, we retained introns, as originally aligned by MAFFT. In the other one, we removed introns and their surrounding variable regions using Gblocks (Castresana, 2000; Talavera & Castresana, 2007) under the less stringent selection options of 'allow gap positions' and 'allow less strict flanking positions'. We also removed the highly variable regions of 28S using Gblocks under these parameters. To find the partition scheme of the molecular data for phylogenetic analysis, we used PartitionFinder ver. 2.1.1 (Lanfear *et al*., 2016) on both approaches of the concatenated molecular datasets under the 'greedy' search algorithm (Lanfear *et al*., 2012), with unlinked branch-lengths, and Akaike information criterion corrected (AICc) model selection.

COMBINED DATA: DNA sequences are available for many of the species used in the morphological analyses. However, they are not available for many others, particularly those species known from the holotype or from a small number of specimens, which in most cases represent the type species of a genus-group name. In those cases, we used available molecular data for closely related species (*i.e.*, same subgenus or species group) to those scored in the morphological analysis. We chose to use these chimeric taxa for pragmatic reasons, in an attempt to increase the taxonomic representation of our analyses. Although we did not assess the differences in the number of character states between the pair of species combined, we are confident that the anatomical overlap is high because closely related taxa tend to share a high number of morphological features. In addition, because our goal was to explore the relationships among tribes and genera, we pursued and scored morphological characters that might reflect those levels of relationships (*i.e.*, morphological features common to a group of genera or subgenera), not characters aimed to reveal relationships among the species within a subgenus. We referred to those chimeric taxa by their generic name, and sometimes subgenus, followed by a combination of the first three letters of both specific epithets in square brackets (Appendix 2). For example, the name for the operational taxonomic unit (OTU) resulting from *Nomada utahensis* Moalif and *N. maculata* Cresson is referred as *Nomada* [uta×mac] in the combined dataset.

For the tribal-level analysis, six taxa with morphological information [*Anthidioma chalicodomoides* Pasteels, *Gnathanthidium prionognathum* (Mavromoustakis), *Indanthidium crenulaticauda* Michener & Griswold, *Osmia* (*Hoplosmia*) *scutellaris* (Morawitz), *Xenoheriades micheneri* Griswold, *Xenostelis polychroma* Baker] did not have closely related species with DNA sequences available and thus we excluded them from the analyses. Six out of the 73 remaining taxa of the original morphological dataset of Gonzalez *et al*. (2012) are Baltic amber fossils and 44 are species with available DNA sequences. Thus, the remaining 23 terminal taxa are chimeric taxa (Appendix 2). The resulting dataset consisted of 73 OTUs, 200 morphological characters, and 5667 aligned nucleotide positions. For the generic-level analysis, the combined dataset consisted of 67 OTUs, 268 morphological characters, and 6981 aligned nucleotide positions. One of the OTUs is a fossil taxon, 34 have available DNA sequences, and the remaining 33 are chimeric taxa. This combined dataset has 45% less the number of taxa used in the morphological analysis because species of many subgenera do not have available molecular data. However, most of these are from a large, well-supported clade (Clade C, see Fig. 8) that includes the LC bees. Thus, reducing the taxonomic representation of this clade does not significantly affect the overall taxonomic coverage of the different lineages of the tribe. After reducing the number of taxa from the original morphological dataset, four characters became inapplicable and thus we excluded them. To explore other hypotheses of generic-level relationships, we also analyzed a combined datataset that had all taxa used in the morphological analysis, even though many of them lacked molecular data. We referred to these datasets as the reduced (67 OTUs) and full datasets (122 OTUs).

PHYLOGENETIC ANALYSES: For the analyses of the molecular datasets and combined molecular and morphological datasets, we used maximum likehood (ML) and Bayesian inference (BI). We conducted ML analyses using the message passing interface (MPI) version of IQ-Tree 1.5.5 (Nguyen *et al*., 2015). We used the command ModelFinder (Kalyaanamoorthy *et al*., 2017) to select the substitution model during the analyses to avoid *a priori* models. To examine the effects of introns on the phylogeny, we first ran ML analyses on the concatenated molecular datasets with and without introns,

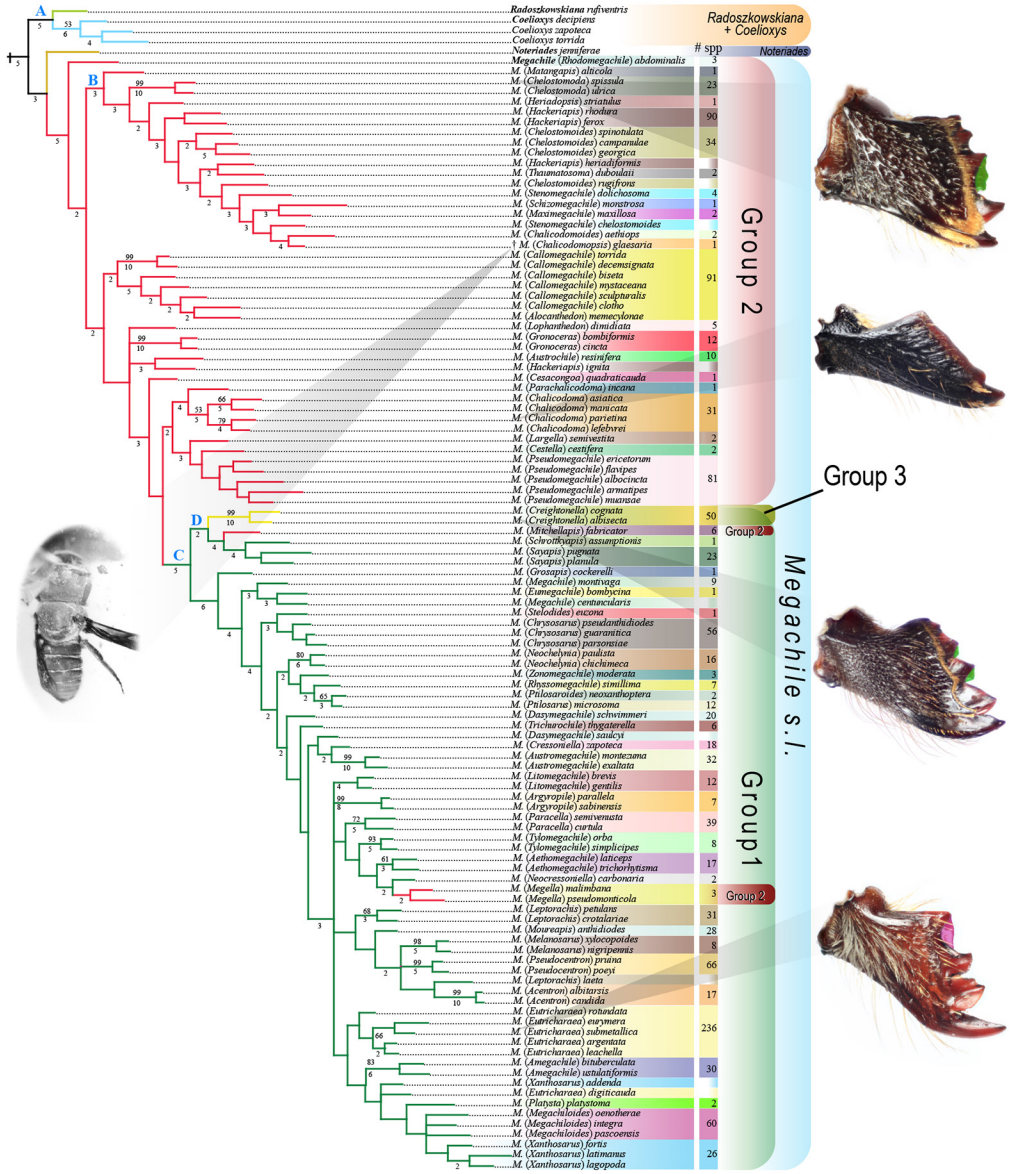

Figure 8. Strict consensus tree of 30 parsimonious trees obtained under equal weighting. Numbers above nodes are standard bootstrap values, numbers below nodes are absolute Bremer values. Branches without numbers indicate bootstrap values below 50% and Bremer values of 1. A capital letter above a node indicates a clade discussed in the text. Species within boxes of the same color correspond to the same subgenus of *Megachile* Latreille *s.l.* following Michener's (2007) classification. The colored column after the species names indicates approximate number of species per subgenus. Half-colored boxes without a number correspond to species that did not cluster with the other species of the same subgenus included in the analysis. Species richness taken from Michener (2007), Moure *et al.* (2007), and Ascher & Pickering (2018). Mandibles with interdental laminae highlighted in green (odontogenic) and pink (ctenogenic).

as described above. While introns had negligible effects on the topology of both the tribal- and generic-level phylogenetic trees, their inclusion resulted in higher support

values in the generic-level analysis. Thus, we used the molecular data without introns in the combined analysis of the tribal-level phylogeny and the dataset with introns in the generic-level study. Then, we conducted ML analyses on these combined datasets, giving the morphological data a separate partition. We estimated branch support using 1,000 replicates of ultrafast bootstrapping (Minh *et al*., 2013).

We conducted BI analyses using the MPI version of MrBayes 3.2.6 (Ronquist *et al*., 2012b; Zhang *et al*., 2016) on the total-evidence datasets described above, with the morphological data given its own partition. We did not select an *a priori* substitution model; instead, we used the reversible-jump Markov chain Monte Carlo (MCMC) method with gamma-distributed rate variation across sites to test the probability of different models *a posteriori* during the analysis (Huelsenbeck *et al*., 2004; Ronquist *et al*., 2012b). We conducted two different types of BI analyses, a time-free and a time-calibrated analysis. For the time-free analysis, we did not add further specifications following the input for the reversible-jump MCMC. We set the MCMC generation to run 10 million generations using four chains (three heated, one cold) with the swap number set to one, and a temperature of 0.1 for the heated chains. We monitored MCMC convergence of both time-free and time-calibrated analyses with Trace v.1.6 (Rambaut *et al*., 2014). We considered a value of ESS ≥ 200 a good indicator of convergence.

We used a tip-dating approach (Pyron, 2011; Ronquist *et al*., 2012a) for the time-calibrated analyses. First, we estimated the base molecular clock rates as outlined by Ronquist *et al*. (2012a). For the tribal-level analysis, the base clock rate and root age were informed using the age of the oldest crown bee fossil (Engel, 2000, 2001) for the minimum age, and 120 Ma for the mean age based on previous estimates for the age of Megachilidae by Cardinal & Danforth (2013). Then, we used the divergence time estimates generated by the tip-dated tribal-level analysis to inform these priors in the generic-level analysis. We used the fossilized birth-death macroevolutionary model (Heath *et al*., 2014) following the methods of Zhang *et al*. (2016). The sampling strategy was set to diversity, with sampling probability set to 0.016 in the tribal-level analysis (66 megachilids sampled from the 4,105 known species) and to 0.029 for the generic-level analysis (59 megachilines of the 2,000 known species of the tribe Megachilini). We assigned an uncorrelated relaxed clock model IGR with the prior on rate variation across lineages set to exponential 10. We gave the fossils a uniform calibration prior based on the dated ages of their amber deposits (Engel, 2001).

To aid convergence in the time-free analyses, we applied several constraints on well-supported groups. In the tribal-level analysis, we constrained both melittine taxa, as well as Apidae and Megachilidae, as sister groups. In the generic-level analysis, we applied constraints to unite taxa representing the following groups: Lithurgini, Osmiini, Megachilini, and Osmiini + Megachilini. We also conducted additional analyses constraining the fossil species *M*. (*Chalicodomopsis*) *glaesaria* with different taxa of *Megachile s.l*. based on the results of the EW parsimony analysis of the morphological dataset.

The MCMC generation settings for the time-calibrated analyses were initially set identically to the time-free analyses, and we completed the preferred tribal-level tip-dated tree under these settings. However, we experienced considerable difficulty getting both the tribal-and generic-level tip-dated analyses to converge. Convergence of the generic-level analysis was accomplished after providing the time-free total-evidence Bayesian tree as a starting tree, lowering the heated chain temperature to 0.010, and increasing the MCMC generations to 50 million. Thus, we applied a similar approach to the tribal-level analysis, increasing the number of chains and swaps, and

increasing MCMC generation to 200 million, but it still did not attain convergence. Furthermore, allowing the tip-dated tribal-level analysis to run longer resulted in unrealistically old divergence time estimates, placing the root of the tree in the Permian with a median age of 256 Ma. Thus, the resulting preferred tip-dated tribal-level tree did not reach convergence, but the topology is identical to that obtained across the different attempts to reach convergence. It has similar support values, but it differs in the age estimates, which are considerably more realistic and in line with previous estimates using node-calibration approaches (Cardinal & Danforth, 2013; Litman *et al.*, 2011).

Patterns of variation of the interdental lamina: We used Mesquite (Maddison & Maddison, 2018) to trace the evolutionary history of the interdental lamina. We reconstructed ancestral character states using a parsimony model with unordered character states and visualized them on the tree topology obtained from the analysis of the combined full dataset using BI.

To test for character association between the LC behavior and some female cephalic and mandibular features, we used the phylogenetic pairwise comparison implemented in Mesquite. We used the option that searches for pairs of taxa contrasting in the state of two characters, with a maximum number of pairings set to 1,000,000 pairs. To maximize the number of pair comparisons, we used the resulting tree topology from the analysis of the combined full dataset using BI. We tested the following five characters that we considered dependent characters: ocelloccipital distance (character #12), mandible length (#28), mandibular apical width (#33), shape of acetabular interspace in the outer surface of mandible (#38), and pubescence on the adductor interspace in the inner surface of mandible (#56). We chose these characters because they appeared to be under the same selective pressure, which is the type of nesting material used (Mitchell, 1980; Williams & Goodell, 2000). The size and shape of the mandible also influences the size and shape of the head, as the latter contains the mandibular musculature. Thus, we used these characters as proxy of the head size and mandibular size and shape. We also included the pubescence on the adductor interspace of the mandible because we observed that setae on this area appears to be absent in many species of LC bees. We tested each of these five characters for association with the presence of interdental laminae, a feature unquestionably indicative of LC behavior. For analysis, we scored each species as having either character state 0 when these laminae are absent, or as having character state 1, when they are present on at least one dental interspace. We did not compare these characters with the presence or absence of LC behavior because the nesting biology of most species in our analysis is unknown. Additionally, some species that lack interdental laminae still cut leaves while others do not (*e.g.*, *M. montivaga*). Thus, assuming an absence of LC behavior in species that lack interdental laminae is not applicable.

RESULTS

Morphological-based Phylogeny of Megachilini

The analysis of the morphological data matrix under EW yielded 30 MPTs (L = 2364, CI = 13, RI = 57); nine nodes collapsed in the consensus tree (Fig. 8) and most branches were weakly supported by homoplastic characters. The clade of cleptoparasitic bees (Clade A) consisting of *Coelioxys* and *Radoszkowskiana* resulted as the sister group of all other Megachilini. *Noteriades* is the sister group to the entire clade con-

taining *Rhodomegachile* Michener (Group 2) and all remaining *Megachile s.l.* Most subgenera of Group 2 clustered in multiple clades along the tree, except for *Mitchellapis* and *Megella*, which were in a large derived clade (Clade C) containing all subgenera of Group 1 and *Creightonella* (Group 3). The fossil taxon, *Chalicodomopsis*, resulted in a clade that included *Matangapis*, *Chelostomoda*, *Hackeriapis* Cockerell, and other hoplitiform or heriadiform taxa of Group 2 (Clade B).

Implied weighting analyses under the 11 *k*-values each resulted in a single MPT, except for two analyses (character fits 66 and 70%) that yielded two MPTs. All resulting trees are longer than the MPTs obtained under EW, but have similar CI and RI values. The topologies obtained with character fits 54 and 62 to 70% have the highest SPR values (Appendix 4). However, the median GC frequency-difference value was similar among analyses (Kruskal-Wallis H test, $H = 0.773$, $p = 0.99$) and it was not associated with SPR values (Spearman's correlation, $r_s = 0.146$, $p = 0.667$). Likewise, the number of supported nodes was similar among analyses [Chi-squared goodness-of-fit test, χ^2 (10, $n = 715$) = 1.139, $p = 1.00$].

The resulting topology from the IW analyses was similar to that of the EW analysis, but the position of several taxa significantly changed among *k*-values (results not shown). For example, *Noteriades* resulted as the sister group of Megachilini in all analyses, except in those with character fits 86 and 90%, in which it appeared as sister of *Megachile s.l.* as in the EW analysis. *Chelostomoda*, a member of Group 2 of subgenera (see Clade B in EW consensus, Fig. 8), clustered with *Creightonella*, *Mitchellapis*, *Sayapis* Titus, and *Schrottkyapis* Mitchell (see Clade D in EW consensus) in analyses with character fits ranging from 50 to 70%. In remaining analyses, *Chelostomoda* clustered within Clade B. *Rhodomegachile* and *Chalicodomopsis* were sister groups, either as part of Clade B (analyses with character fits 50 and 58%), or as the sister group of all other Megachilini (analyses with character fits 62 to 86%) excluding *Noteriades* and Clade A. In the analysis with the highest character fit, both taxa resulted in positions similar to those in the EW consensus topology. Likewise, *Gronoceras* (Group 2) resulted either as the sister group of all other Megachilini, excluding *Noteriades* and Clade A (character fits 50 and 54%), or in the same clade with *Lophanthedon* Gonzalez & Engel (Character fits 58, 70–90%). *Megachile* (*Callomegachile*) *decemsignata* Radoszkowski and *M.* (*Callomegachile*) *torrida* Smith, members of Group 2, clustered with *Lophanthedon* in Clade D (character fits 50–58, 66, 70%) or with other members of *Callomegachile* in the remaining analyses. *Matangapis* was the sister group of *Heriadopsis* and clustered within Clade B (character fits 50–58%). However, in analyses with character fits 62–70, and 86%, *Heriadopsis* remained within the same clade but *Matangapis* resulted singly in a branch after the clade consisting of *Rhodomegachile* and *Chalicodomopsis*. In remaining analyses, *Matangapis* was the sister group of all members of Clade B, as in the EW consensus. Clade C was consistenly recovered, but the arrangement of internal nodes changed among analyses.

PHYLOGENETIC SIGNAL: The female and male character sets were similar in the median RI value (Mann–Whitney test, $U = 13334$, $p = 0.192$), as well as in the percentage of unambiguous synapomorphic characters (Table 1). However, unlike the analysis of the male characters that resulted in a highly unresolved tree, female characters recovered Megachilini and several major lineages (not shown). For both sexes, we did not find statistically significant differences between the median RI values and percentage of unambiguous synapomorphic characters between character sets (♀, RI value: $U = 1452$, $p = 0.183$; % unambiguous synapomorphic characters: Chi-squared goodness-of-fit test, $\chi^2_{[1]} = 0.67$, $p = 0.414$. ♂: $U = 1630$, $p = 0.209$; $\chi^2_{[1]} = 0.014$, $p = 0.907$).

Table 1. Phylogenetic signal of selected character sets used in the morphological phylogeny of Megachilini. Retention index per morphological character set and quantitative descriptors of trees obtained from partitioned analysis using female and male characters. RIc = average retention index of character set followed, in parentheses, by median, standard deviation, and number of characters; % Unambiguous Synapomorphies = Percentage of unambiguous synapomorphic characters in the analysis of the full data matrix; MPT = number of parsimonious trees; Collapsed nodes = number of nodes that collapsed in the consensus strict tree; L = tree length; CI = consistency index; RIt = retention index of MPTs. Non-applicables are indicated by an em dash symbol (—).

Character set	RIc	% Unambigious Synapomorphies	MPT	Collapsed nodes	L	CI	RIt
Female	54.33 (50.0, ± 29.87, *n* = 156)	13.9	310	74	1146	16	64
Mandible	54.63 (59.0, ± 32.19, *n* = 32)	9.4	—	—	—	—	—
Terminalia	54.33 (58.0, ± 35.88, *n* = 24)	16.7	—	—	—	—	—
Male	50.17 (50.0, ± 27.23, *n* = 107)	13.8	340	104	1079	12	55
Legs	54.10 (53.0, ± 25.63, *n* = 29)	15.8	—	—	—	—	—
Terminalia	48.93 (42.0, ± 28.07, *n* = 71)	14.5	—	—	—	—	—

Origin and Evolution of the Interdental Lamina

Combined phylogenies: In the preferred Bayesian analysis for the family Megachilidae (Fig. 9), Pararhophitinae resulted as the sister group of Lithurginae, both taxa sister to Megachilinae. Within the latter subfamily, Dioxyini were the sister group of Glyptapini while Aspidosmiini rendered Ctenoplectrellini paraphyletic. Megachilini also rendered Osmiini paraphyletic, as they clustered with the osmiine genera *Afroheriades* Peters and *Pseudoheriades* Peters. The remaining osmiines are together in another clade (Fig. 9). The origin of crown Megachilidae was estimated at a median age of 111.3 Ma (95% highest posterior density 80.94–127.56 Ma) with crown Megachilini at 42.0 Ma (24.75–49.55 Ma). A similar topology resulted from the ML analysis of the combined dataset with extant taxa only. However, Pararhophitinae were the sister group of Lithurginae + Megachilinae, Aspidosmiini and Dioxyini clustered in the same clade, and the osmiine genus *Ochreriades* Mavromoustakis resulted as the sister group of a clade that contained Megachilini and the remaining Osmiini.

In the generic study of Megachilini, the fossil *M. glaesaria* resulted as the sister group of all other Megachilini using the reduced dataset of Megachilini, Clade A was the sister of some members of Group 2 of subgenera, Clade B was segregated in several clades, and *Chelostomoda* was sister to Clade C (Fig. 10). The origin of Clade C was estimated at a median age of 14.92 Ma (95% highest posterior density 11.83–19.42 Ma) and that of *Chelostomoda* + Clade C at a median age of 15.61 Ma (12.80–19.16 Ma). Constraining the position of *M. glaesaria* to the clade that includes *Thaumatosoma*, as in the EW topology, yielded older estimates for the origin of Clade C (23.63 Ma, 18.96–28.93 Ma) and for that of *Chelostomoda* + Clade C (24.82 Ma, 20.25–30.24 Ma). Likewise,

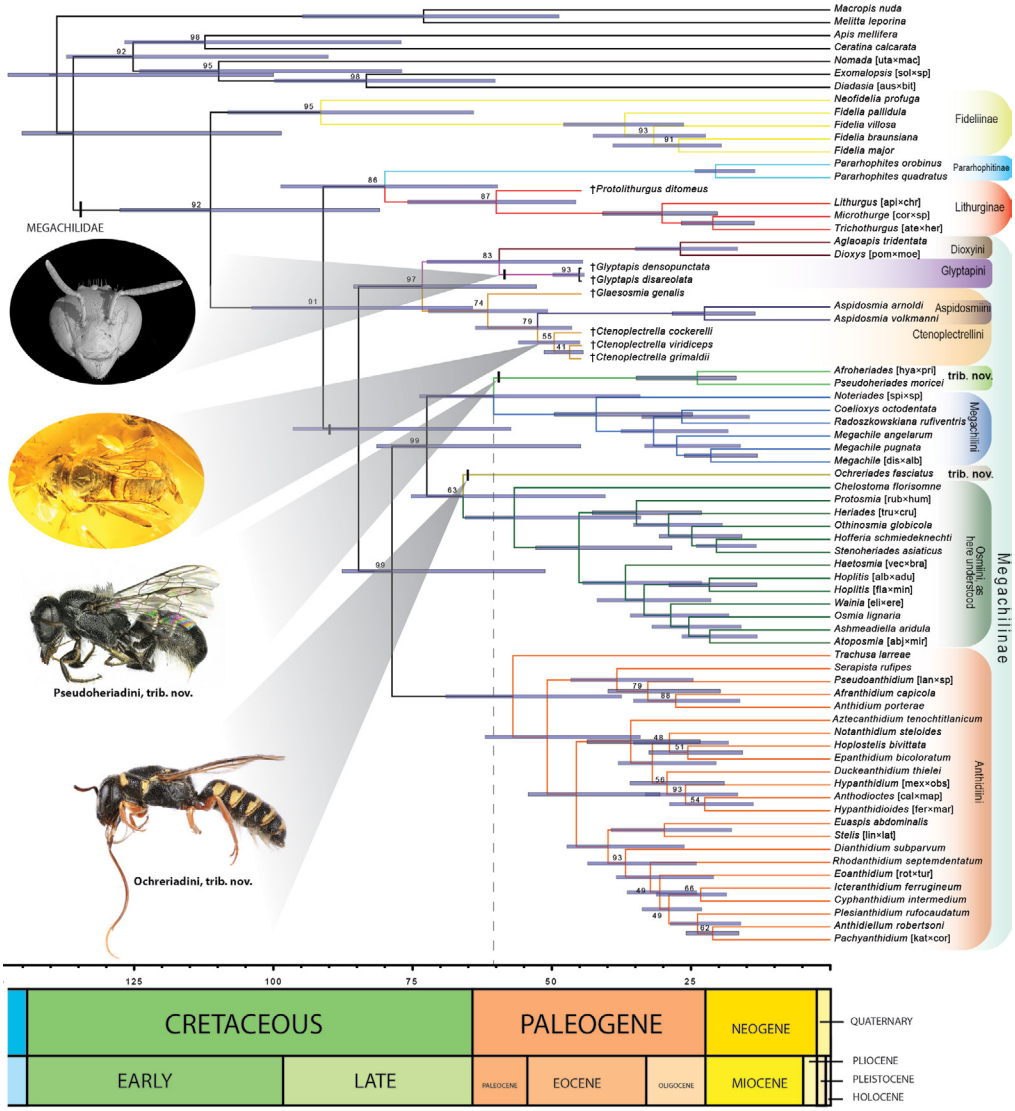

Figure 9. Preferred total evidence dated phylogeny of Megachilidae. Majority-rule consensus tree from Bayesian analysis using fossils as terminals under the FBD tree prior. Blue bar at each node represents the 95% highest posterior density age range. Posterior probability below 100 indicated above each node.

constraining the position of *M. glaesaria* to the clade that includes *Matangapis* yielded older estimates for the origin of Clade C (22.42 Ma, 19.11–26.98 Ma) and for that of *Chelostomoda* + Clade C (23.58 Ma, 20.27–28.24 Ma). We obtained the same topology when we analyzed the full dataset (Fig. 11). However, estimated median ages were older for Clade C (17.6 Ma, 15.22–21.80 Ma) as well as for that of *Chelostomoda* + Clade C (18.6 Ma, 16.12–23.35 Ma). A similar topology resulted from the ML analysis of the reduced dataset, except that *Noteriades* was the sister group of all Megachilini, and *Matangapis* and *Heriadopsis* clustered with members of Clade C.

TYPES OF INTERDENTAL LAMINA: We found two types of interdental laminae that

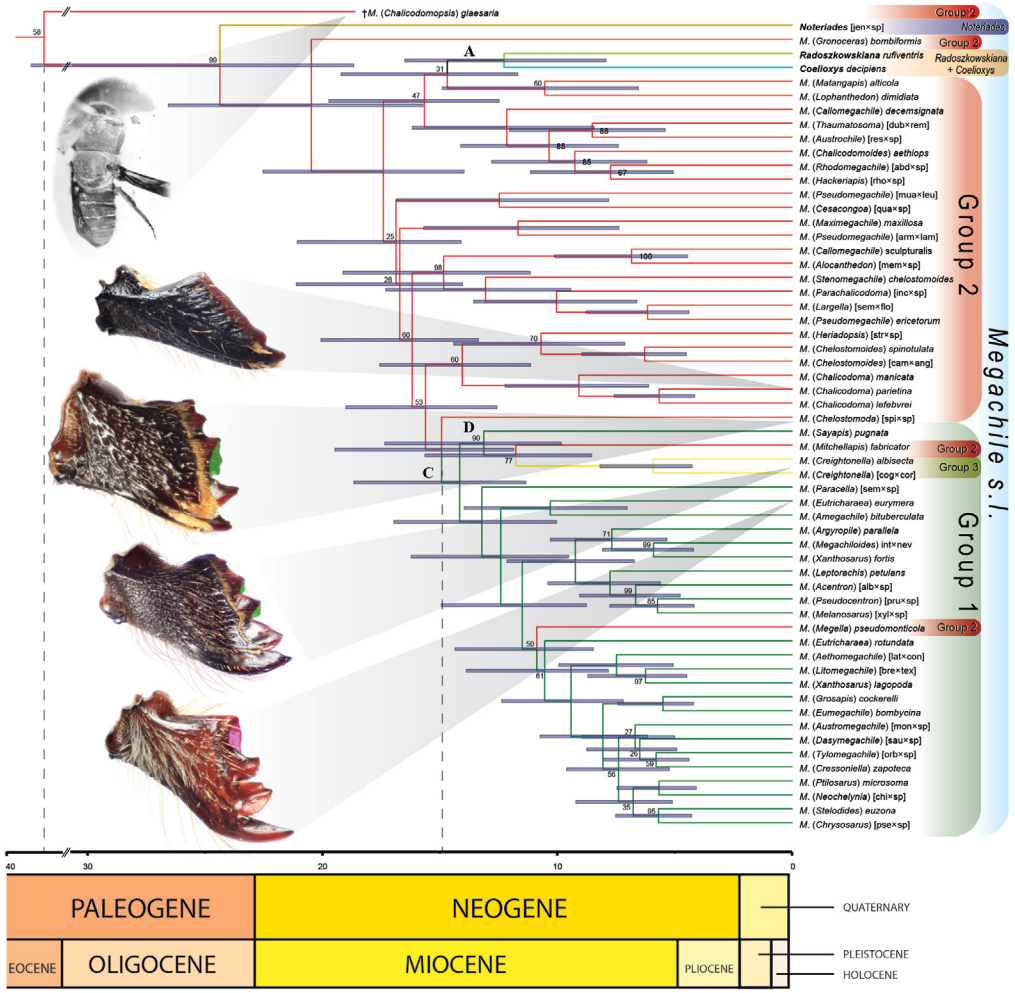

Figure 10. Preferred total evidence dated phylogeny of Megachilini from the analysis of the reduced morphological data matrix (67 OTUs). Majority-rule consensus tree from Bayesian analysis using fossils as terminals under the FBD tree prior. Blue bar at each node represents the 95% highest posterior density age range. Posterior probability below 100 indicated above each node. A capital letter above a node indicates a clade discussed in the text. Mandibles with interdental laminae highlighted in green (odontogenic) and pink (ctenogenic).

likely develop from different structures in the mandible. The first type is clearly a ventral extension of the corono-radicular ridge (CR), a strong ridge that runs basally from the apex or cusp of the inner surface of each tooth (Fig. 3B). This CR ridge is usually strongest on Mt_1, sometimes continuing dorsally into the adductor interspace or curving ventrally, thus running parallel to or towards the adductor ridge (Figs. 3C, D). Gonzalez *et al*. (2012) recognized the portion of this ridge running parallel to or towards the adductor ridge as the adductor apical ridge (AP). Interdental laminae originating from teeth, hence called *odontogenic laminae*, often partially fill the dental interspaces (*i.e*., incomplete). Even in species of *Schrottkyapis* and *Stelodides* Moure, which have secondarily lost interdental laminae, there still is a hidden small projection from the CR ridge of Mt_3 suggestive of a lamina.

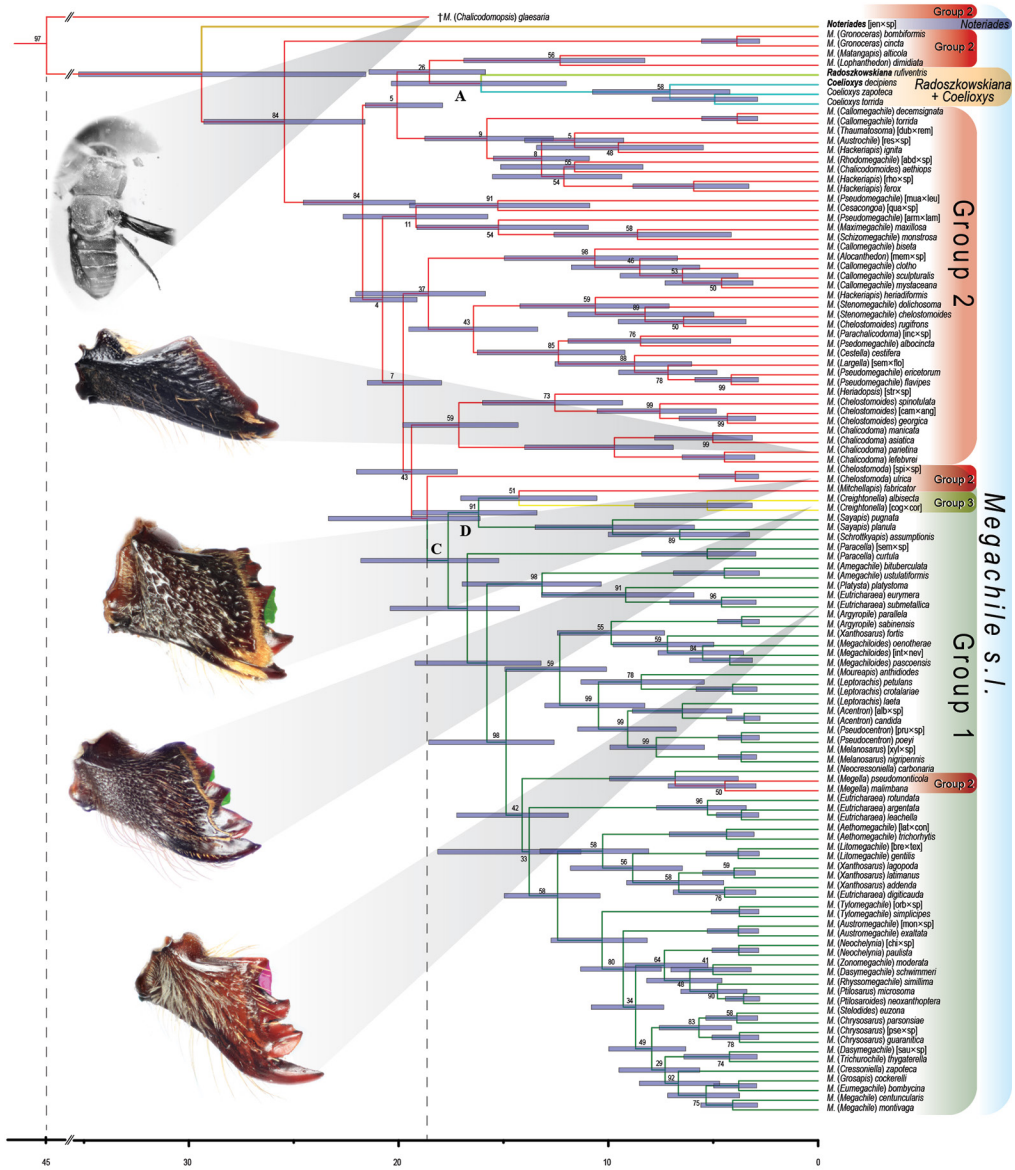

Figure 11. Total evidence dated phylogeny of Megachilini from the analysis of the full morphological data matrix (122 taxa). Majority-rule consensus tree from Bayesian analysis using fossils as terminals under the FBD tree prior. Blue bar at each node represents the 95% highest posterior density age range. Posterior probability below 100 indicated above each node. A capital letter above a node indicates a clade discussed in the text. Mandibles with interdental laminae highlighted in green (odontogenic) and pink (ctenogenic).

The second type of interdental lamina is usually complete and is likely an extension from a transverse ridge at the base of the teeth, which runs parallel to the inner fimbria on the inner surface of the mandible. When this transverse ridge is laminate and apically extended so that it can be seen from the outside of the mandible in between the teeth, it becomes an interdental lamina. In megachiline bees that never developed interdental laminae, this ridge runs from the upper carina to the base of Mt_2,

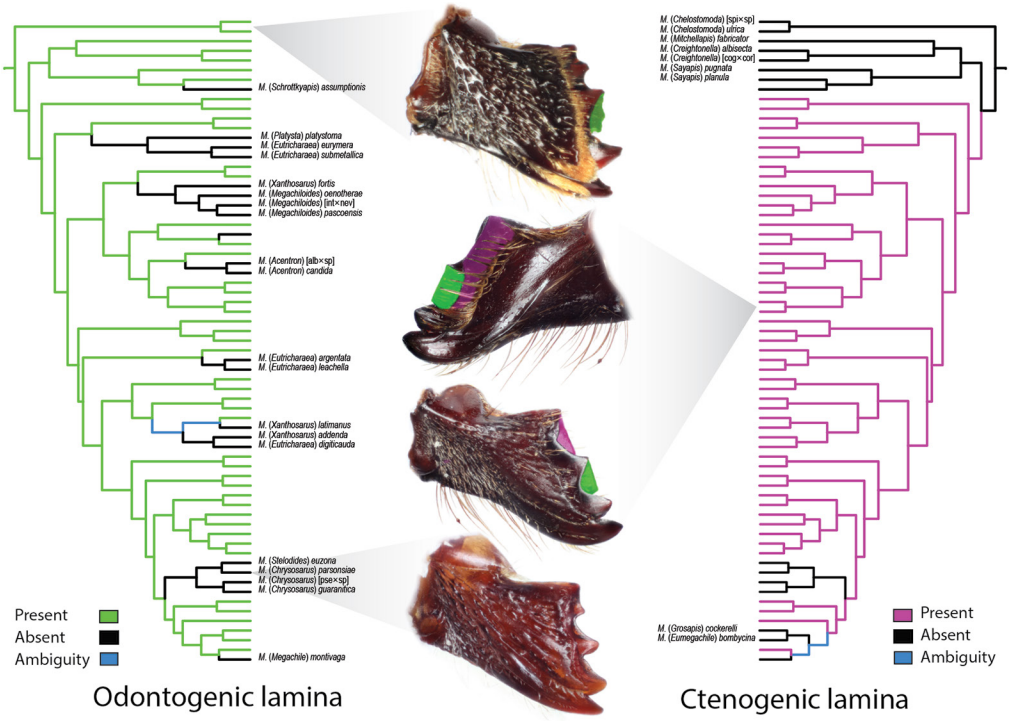

Figure 12. Parsimony reconstruction of the two types of interdental laminae of the leaf-cutter bee mandible. We used the tree topology obtained from the total-evidence analysis of the full data set (122 taxa) to visualize character states on the clade of leaf-cutter bees. All photographs are outer views of the mandibles, except for the second from top to bottom, which is an inner view of the mandible below. Odontogenic lamina highlighted in green and ctenogenic lamina in pink.

merging with the CR of that tooth, and forming a rather concave surface, which sometimes is divided by the CR of the other teeth (Fig. 3B). In *Chelostomoda*, *Creightonella*, and *Sayapis*, such a transverse ridge is laminate or nearly so, but it does not extend enough apically to form an interdental lamina (Fig. 3C–E). In species that have secondarily lost interdental laminae, this transverse ridge is conspicuous and distinctly elevated compared to that of most species of Group 2 that never developed interdental laminae. Michener & Fraser (1978) recognized that the transverse ridge was associated with the inner fimbria and thus named it the *fimbrial ridge* or *fimbrial carina*. Consequently, we referred to the lamina that develops from this fimbrial ridge as either the *fimbrial lamina* or *ctenogenic lamina* (from the Greek κτείς, *kteis*, meaning "comb").

Evolution of the interdental lamina: Odontogenic laminae evolved first and have secondarily been lost or modified multiple times. In constrast, ctenogenic laminae developed once in more derived clades of LC bees and have been lost or modified comparatively fewer times than odontogenic laminae (Fig. 12). Odontogenic laminae are often restricted to Mt_3 and thus visible in the second interdental space only (Figs. 2E–H), except in *Creightonella* where they are also present on $Mt_{4–5}$ (Fig. 3G).

Mandibles of species that only have odontogenic laminae tend to have a thick distal margin with the acetabular interspace of the outer surface gently curving towards the base of the mandible, thus resembling the mandible of species of Group 2 that never developed interdental laminae (Fig. 2C). In contrast, mandibles that have both

Table 2. Phylogenetic pairwise comparisons between the presence of interdental laminae in the female mandible (independent character) and some female cephalic and mandibular characters (dependent characters). See materials and methods for description of each character. # Pairs = number of pairs contrasting in the state of two characters; Relationship = number of pairs with a positive (+) or negative (-) relationship. In a positive relationship, one of the paired species has a character state 1 for both characters and the other species character state 0 for both characters. In a negative relationship, one of the paired species has a character state 1 for one character and a 0 for the other character while the other species has the opposite. P-value: significance value for the number of pairs contrasting in the state of two characters; Range of P-values: range of significance values for all optimal set of pairs of pairwise comparisons.

Compared character #	# Pairs	Relationship	P-value	Range of P-values
12-ocelloccipital distance	4	1+, 3-	0.313	0.313–0.688
28-mandible length	3	2+, 1-	0.5	0.5–0.5
33-mandibular apical width	3	2+, 1-	0.5	0.5–0.5
38-acetabular interspace	4	3+, 1-	0.313	0.313–0.313
56-pubescence on adductor interspace	4	3+, 1-	0.313	0.063–0.313

odontogenic and ctenogenic laminae exhibit a distinct basal, lateral surface and a distal, anterior surface because the acetabular interspace is clearly flattened or depressed (Fig. 2E–J). The mandible is also much broader apically, with the distal margin flattened, and with both types of laminae often at different levels from the mandibular margin and from each other. However, in some species whose mandible is flattened at the apex, both laminae are thin and nearly at the same level with the interspace margin, sometimes fused and indistinguishable. The CR ridges are usually absent in apically flattened mandibles, except for that of Mt_1. In some species with thicker mandibular apex, the ctenogenic interdental laminae are narrow (not reaching apex of teeth), well behind or deeper to the interspace margin, and often hidden by it (Fig. 2D). A mandible of this kind would appear to lack laminae when seen in it from the outside.

According to the phylogenetic pairwise comparisons, the presence of interdental laminae is not associated with characters #12, 28, 33, 38, or 56 (ocelloccipital distance, mandible length, mandibular apical width, shape of acetabular interspace, and pubescence on the adductor interspace, respectively), which we used as proxy of head size and mandible size and shape (Table 2).

DISCUSSION

Phylogenetic Relationships within Megachilini

The morphological phylogeny presented here provides an additional hypothesis that allowed us to place the fossil species as well as some rare megachiline taxa for which DNA is not yet available. Neither our morphological analysis nor the preliminary total-evidence phylogeny supports the proposal of Trunz *et al*. (2016) of recognizing *Heriadopsis* and *Matangapis* at the generic level, while simultaneously retaining other Group 2 taxa within *Megachile*. In our analyses, *Heriadopsis* always clustered near *Chelostomoides*, but the position of *Matangapis* changed from being part of the same clade with *Heriadopsis* to sister of *Lophanthedon* in the combined analysis. Thus,

separating these taxa alone at the generic rank, as Trunz *et al*. (2016) proposed, creates a large paraphyletic *Megachile s.l*.

Although sharing the presence of arolia with both *Heriadopsis* and *Matangapis*, *Noteriades* never clustered with any of these taxa. It resulted either as the sister group of *Megachile s.l*. (EW analysis of morphological data, Fig. 8) or as sister of Megachilini (IW analyses of morphological data and combined analyses, Figs. 10, 11). Thus, our study further supports the placement of *Noteriades* within Megachilini, as well as its recognition at the generic rank.

Michener (2007) suggested that *Coelioxys* might render *Megachile s.l*. paraphylectic because of its shared morphological features, particularly with *Chelostomoides*. He also suggested that cleptoparasitism might have evolved independently in *Radoszkowskiana* and *Coelioxys*. Morphologically, *Radoszkowskiana* differs from *Coelioxys* in the short axilla, bare compound eyes, and the blunt metasoma of the male, which has a low transverse apical carina on T6 that is not divided into dorsal and ventral processes as in most *Coelioxys* (but is similar to that of males in *Chelostomoides*). Some species of *Coelioxys* combine features of both genera. For example, *Coelioxys* (*Boreocoelioxys*) *funeraria* Smith and *C*. (*Liothyrapis*) *decipiens* Spinola have short axillae and bare compound 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 elongate and pointed with a distinct median weakly sclerotized area in most *Coelioxys*. Furthermore, the mode of cleptoparasitism in *Radoszkowskiana* seems to fall within the known repertoire of parasitism of *Coelioxys* (Rozen & Kamel, 2007). Thus, *Radoszkowskiana* seems to be a close relative of *Coelioxys* despite the distinctive male characters. Our analyses consistently placed *Radoszkowskiana* as the sister group to *Coelioxys* (Clade A), a relationship also recovered in the phylogenetic analyses of Rocha Filho & Packer (2017) and Trunz *et al*. (2016). However, the position of this clade of cleptoparasitic bees varied among our analyses.

In the morphological analysis under EW, the clade *Radoszkowskiana* + *Coelioxys* resulted as the sister group of *Noteriades* + *Megachile s.l*. (Fig. 8), but it rendered the latter genus paraphyletic when we analyzed the morphological data under IW. Our preliminary total-evidence phylogeny does not resolve the position of this clade either, as the posterior probabilities values were very low (Figs. 10, 11). Furthermore, our analyses do not support Michener's (2007) view of two independent origins of cleptoparasitism. Behavioral, morphological, and molecular data strongly indicate that cleptoparasitism evolved only once in Megachilini.

Most subgenera of *Megachile s.l*. fell into morphological groups previously associated with differences in nesting behavior. Basal branches included those subgenera of Group 2 that use mud or resins as nesting materials. These subgenera grouped in different clades whose taxonomic composition changed among analyses, except in a few cases (*e.g*., *Maximegachile* Guigla & Pasteels and *Schizomegachile* Michener always resulted as sister groups). Michener (2007: p. 553) discussed some of these relationships, which we mostly recovered in the morphological analysis under EW, but not under IW nor in the combined phylogeny. Thus, our analyses support the suspicion of Michener (2007) that Group 2 [*Chalicodoma sensu* Michener (1962) and Mitchell (1980)] is nonmonophyletic but it does not support the majority of his divisions or phylogenetic lines.

Taxa that exhibit LC behavior clustered in a large, more derived clade containing all subgenera of Group 1, and included *Megella*, *Mitchellapis* (Group 2), and *Creightonella* (Group 3). These taxa combine some features that are typical of Group 1 and 2 and thus, they have been difficult to place with confidence in any group based on a few

morphological features. The basal position *Creightonella* and *Mitchellapis* within the LC clade is in agreement with the fact that they retained some of the Group 2 features (*e.g.*, chalicodiform body, male S8 with marginal setae) whereas the more derived position of *Megella* indicates the recurrence of some features of Group 2. Because the cost of a character gain might be much higher than its loss, the reacquisition of characters makes some taxa, such as *Megella*, difficult to place in a given taxonomic category. However, studies have documented the recurrence of complex structures, such as eyes and wings (*e.g.*, West-Eberhard, 2003; Whiting *et al*., 2003). This is likely the result of turning off controlling genes while retaining the underlying genetic architecture, such that even though a complex trait may not be expressed in a given taxon it can be expressed again later in the evolution of the lineage by reactivating the necessary controlling elements. Thus, the gain of less complex structures, such as the marginal setae of S8 and arolia, seems even more plausible in Megachilini.

Chelostomoda is another group that combines features of Groups 1 and 2 of *Megachile s.l.* In the EW analysis of the morphological data, this subgenus was near *Chelostomoides* in Clade B (Fig. 8), but it resulted as the sister group of LC bees when we analyzed this dataset under IW and in combination with molecular data (Figs. 10, 11). The IW scheme shows that the characteristics of Group 2 (*e.g.*, elongate body, terga with strong postgradular grooves, and S8 with marginal setae) exhibited by *Chelostomoda* are homoplastic features. The nesting biology of *Chelostomoda*, *Creightonella*, and *Megella*, which make extensive use of leaf pieces (*e.g.*, Katayama, 2004; Maeta, 2005; Michener, 2007), also supports their placement in Group 1; the biology of *Mitchellapis* is unknown.

Our results also recovered some major phylogenetic lines or groups of subgenera within the LC clade previously discussed by Michener (1965, 2007) and Mitchell (1980). Some of them, such as the *Creightonella* and *Pseudocentron* groups, are distinct and easily recognizable by one or two morphological features; others lack distinct features. We briefly discussed some of them here.

Chrysosarus group: Mitchell (1980) included in this lineage the subgenera *Chrysosarus*, *Dactylomegachile* Mitchell, *Stelodides*, and *Zonomegachile* Mitchell. Based on the description (Raw, 2006) and photographs of the types, *Austrosarus* seems to belong here. Both type of interdental laminae are secondarily lost in this group, except in *Zonomegachile* (Gonzalez *et al*., 2018). Gonzalez (2013) considered these taxa within a single subgenus, *Chrysosarus*, but our analyses indicate that *Zonomegachile* does not belong to this group.

Creightonella group: This lineage includes the subgenera *Creightonella*, *Mitchellapis*, *Sayapis*, and *Schrottkyapis*. The members of this group have a chalicodomiform body shape and odontogenic interdental laminae only. A remarkable feature of this lineage is the S6 of the female; at least in the species we examined for this study, it is elongate and with a membranous or weakly sclerotized pregradular area (visible only after dissection). Mitchell (1980) recognized this lineage under the generic name of *Eumegachile* Friese; however, he also included the subgenera *Eumegachile* and *Grosapis* Mitchell but separated *Creightonella* generically (Appendix 1).

Megachiloides group: Mitchell (1980) included *Megachiloides* Mitchell, *Argyropile* Mitchell, and three other names that Michener (2000, 2007) synonymized under *Megachiloides* or *Xanthosarus* Robertson. Unlike most species of LC bees, members of this group appear to dig their own nest in the ground (Eickwort *et al*., 1981).

Pseudocentron group: All members of this group of subgenera are primarily Neotropical in distribution; *Acentron* Mitchell, *Leptorachis* Mitchell, *Melanosarus*, *Moureapis*

Table 3. Monotypic, monophyletic, and non-monophyletic subgenera of *Megachile* Latreille *s.l. sensu* Michener (2007). * = subgenera represented by a single species in this study but they are likely monophyletic given their morphological uniformity; † = fossil taxa.

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

Raw, and *Pseudocentron* Mitchell are included here. Mitchell (1980) recognized this lineage and placed them in the genus *Pseudocentron* (Appendix 1). The most distinctive character is the S6 of the female. It has at least the posterior half bare or nearly so, except for a subapical row of short setae, behind which there is a bare, smooth rim directed posteriorly.

Mitchell (1980) grouped the remaining subgenera of LC bees in two genera, *Megachile* and *Cressoniella* Mitchell (Appendix 1). In our analyses, these subgenera resulted in multiple clades but some taxa clustered as suggested by Mitchell. For example, he placed *Ptilosarus* Mitchell, *Ptilosaroides* Mitchell, *Rhyssomegachile* Mitchell, and *Neochelynia* Schrottky in *Cressoniella*. We recovered these subgenera in the same clade but apart from the other subgenera included by Mitchell (1980) in his genus *Cressoniella*.

Unlike the fossil tribes Ctenoplectrellini and Glyptapini, whose phylogenetic positions were consistent among analyses (Fig. 9), that of the Dominican fossil *M. glaesaria* varied from being near *Chelostomoides* (Fig. 8) to be the sister group of all Megachilini (Figs. 10, 11). Interestingly, Engel (1999) discussed the possibility of both phylogenetic positions. Such instability might be the result of the low number of characters that we were able to score from this fossil (75 of 272).

Monophyly of subgenera of *Megachile s.l.*: Ten of the 57 subgenera of *Megachile s.l.* included in this study are monotypic (Table 3). The 19 subgenera containing more than one species but represented in our analyses by a single species are also putatively monophyletic because each is morphologically uniform (*e.g.*, *Maximegachile*, *Ptilosarus*). The monophyly of 18 subgenera was either strongly supported (*e.g.*, *Pseudocentron*) or weakly supported but consistently recovered among analyses. Our analyses support the non-monophyly of several subgenera, which previous authors had already suspected or suggested (Michener, 2007; Trunz *et al.*, 2016). Among the subgenera of Group 2, *M. biseta* Vachal, *M. decemsignata*, *M. memecylonae* (Engel), and *M. torrida*

rendered *Callomegachile* paraphyletic; *M. ignita* Smith and *M. heriadiformis* Smith rendered *Hackeriapis* polyphyletic; *M. muansae* Friese, *M. cestifera* Benoist, and *M. incana* Friese rendered *Pseudomegachile* Friese paraphyletic; *M. dolichosoma* Benoist rendered *Stenomegachile* Pasteels polyphyletic; and *M. rugifrons* (Smith) rendered *Chelostomoides* paraphyletic. Among the clade of LC bees, *M. assumptionis* rendered *Sayapis* paraphyletic; *M. platystoma* Pasteels, *M. eurymera* Smith, *M. submetallica* Benoist, and *M. digiticauda* Cockerell rendered *Eutricharaea* Thomson polyphyletic; *M. fortis* Cresson and *M. addenda* Cresson rendered *Xanthosarus* polyphyletic; *M. laeta* rendered *Leptorachis* polyphyletic; *M. schwimmeri* Engel (a replacement name for *M. mitchelli* Raw: *vide* Engel, 2017) rendered *Dasymegachile* Mitchell polyphyletic; and *M. euzona* rendered *Chrysosarus* paraphyletic.

In some cases, the recognition of highly derived species at the subgeneric level rendered some taxa paraphyletic. For example, as Michener (2007) suspected, the monotypic subgenus *Schrottkyapis* renders *Sayapis* paraphyletic. A single putative synapomorphy supports such a relationship: S6 of the female with a nearly membranous pregradular area and a distinct invagination parallel to the lateral margin of the sternum (visible only after dissection). In other cases, such as in *Eutricharaea*, *Hackeriapis*, and *Callomegachile*, current taxon concepts are broad and Michener (2007) proposed them as practical solutions to show relationships among diverse, poorly known groups. For example, when Michener (2007) synonymized various groups under *Eutricharaea*, as he did for many other bees, he acknowledged the arbitrarity of his decision. He also highlighted morphological features that supported their relationships, which turned out to be homoplastic characters in our analyses (*e.g.*, apical fasciae under scopa, T6 preapical carina toothed or denticulate and medially emarginate). Thus, in several instances breaking up Michener's (2007) heterogeneous circumscriptions into multiple subgenera (*e.g.*, resurrecting *Eumegachilana* Michener and others among *Callomegachile*) aids the recognition of natural groups as well as stimulates revisionary studies which can be undertaken on more manageable units.

PHYLOGENETIC SIGNAL OF MORPHOLOGICAL CHARACTERS: The morphological character sets used in the phylogeny of Megachilini showed different levels of homoplasy (Table 1), as per RI value and percentage of unambiguous synapomorphic characters, but such differences were not statistically significant. Thus, these character sets were equally informative for the phylogeny. However, the analysis of female characters alone, which also excluded those present in the male but coded only for the female to avoid duplication, recovered Megachilini and several major lineages, unlike the analysis of male characters that resulted in a large polytomy. This does not mean that male characters were useless, but rather that our dataset was female-biased (Fig. 7A).

Several authors have recognized important morphological features of taxonomic value in the male (*e.g.*, Mitchell, 1980; Michener, 2007; Engel & Gonzalez, 2011; Gonzalez & Engel, 2012; Gonzalez *et al*., 2018), which appear to show high rates of evolution, as they are sometimes highly variable within and among distinct phylogenetic lineages. For example, secondary sexual features such as the preapical carina of T6, mandibular projection, coxal spine, and modifications of front legs, are associated with particular strategies of mating system (Wittmann & Blochtein, 1995). The morphology of these structures are largely unexplored and, depending on the level of study and finer levels of character conceptualization, they might prove phylogenetically informative as in other group of bees (*e.g.*, *Xylocopa* Latreille; Minckley, 1998). Equally unexplored is the female mandible. We conceptualized a number of characters for our study, but the mandible has a plethora of anatomical features with potential phyloge-

netic and taxonomic values at other levels of study. Michener & Fraser (1978) established terminology and homologies for the various structures of the bee mandible, but they only considered the body, not the apex. Among these ignored structures in the mandibular apex were the interdental laminae, which as we have shown, are relevant for understanding the biology, taxonomy, and phylogeny of Megachilini.

Origin and Patterns of Variation of the Interdental Lamina

We demonstrate for the first time that interdental laminae, the most distinctive and taxonomically significant feature of LC bees, likely developed from two different structures in the female mandible. We also show that odontogenic laminae evolved once and prior to the development of ctenogenic laminae, which developed from the fimbrial ridge and appeared in more derived LC taxa (Fig. 12). These findings have major implications for our understanding of the conection between character evolution and diversification. The most obvious is that interdental laminae represent two characters that evolved in a sequence of evolutionary events, not a single character that evolved once as current dogma surmises (Michener, 2007; Trunz *et al*., 2016).

Our analyses also suggest that the presence of odontogenic laminae is a putative synapomorphy for all LC bees, which exhibits more phenotypic plasticity than ctenogenic laminae. The multiple modifications and secondary losses observed across the phylogeny are more likely in this type of lamina perhaps because of its small size and less involved structural modifications relative to ctenogenic laminae. However, losses in ctenogenic laminae occurred independently in two clades, the *Chrysosarus* and *Megachile s.str*. groups of subgenera, sometimes also with the loss of odontogenic laminae (Fig. 12). While retaining the use of leaves, these groups have incorporated other nesting materials, such as mud or petals (*e.g*., Laroca *et al*., 1992; Banaszak & Romasenko, 1998; Zillikens & Steiner, 2004; Michener, 2007). At least one species, *M*. (*M*.) *montivaga*, makes nests entirely of petals (*e.g*., Mitchell, 1935b; Michener, 2007; Orr *et al*., 2015). The environmental factors that favor the use of mud or petals in LC bees are unknown. As far as we know, species with secondarily lost interdental laminae co-occur in the same habitats with LC bees, and sometimes even occupy a wide range of habitats (*e.g*., *M. montivaga*).

Although the mandible of LC bees appears to be shorter, apically wider, and with rather two distinct outer surfaces than that of dauber bees, pairwise tests for trait correlation revealed no significant associations between each of them and the presence of interdental laminae. Pairwise comparisons also suggest similar independence of trait evolution between a short ocelloccipital distance and the absence of setae on the adductor interspace in the inner surface of the mandible (Table 2). Parsimony reconstructions suggest that these are ancestral character states (not shown). They are also present in some dauber bees in the genus *Megachile s.l*., as well as in some outgroups. Thus, these cephalic and mandibular features, rather than being associated with leaf cutting, are likely the result of a shift in processing and handling foraging materials (leaves, plant hairs, pebbles, resins, *&c*.) as an alternative to using glandular secretions to waterproof cells in the soil (Michener & Fraser, 1978; Eickwort *et al*., 1981).

Origin of Leaf-cutting Behavior

Our preliminary total-evidence tip-dated analyses aimed to provide additional hypotheses of relationships and to assess the temporal discrepancy between the recent

age (20–25 Ma) estimated from molecular analyses using a node-dating approach (Litman *et al*., 2011; Trunz *et al*., 2016) and the much older age (60 Ma) suggested by fossil traces (Michez *et al*., 2012). A tip-dating approach allows the incorporation of all available fossils into phylogenetic analyses, which not only expands the taxonomic coverage and ancentral character states, but also provides more accurate fossil information to the analysis than *ad hoc* node age constraints (*e.g*., Pyron, 2011; Ronquist *et al*., 2012a; Slater & Harmon, 2013; Arcila *et al*., 2015). However, tip-dating analyses tend to estimate much older divergence times when compared to the node-dating approach, sometimes unrealistically (*e.g*., O'Reilly *et al*., 2015; O'Reilly & Donoghue, 2016). In our case, the tip-dated analyses suggested a similar recent divergence time (15–25 Ma) to those obtained from molecular analyses using a node-dating approach (Figs. 10, 11). The position of the fossil *M. glaesaria* as the sister group to all other Megachilini, which differed from that obtained in the morphological analysis (Fig. 8), influenced the divergence time estimates. Constraining the position of this fossil near *Thaumatosoma*, as in the morphological analysis, yielded older estimates for the origin of LC bees, yet these values were never greater than 30 Ma.

Our analyses support the idea that Eocene trace fossils might not be the result of LC bees, but we should interpret these results with caution. First, we used a low number of fossils in our analyses, particularly in the generic-level phylogeny, and studies have shown that including more fossil taxa across different clades increases the precision of tip-dating estimates (Pyron, 2011; Ronquist *et al*., 2012a; Dos Reis & Yang, 2013). Second, if age estimates are correct, they are indicating the origin of taxa within *Megachile s.l*. with interdental laminae, not the origin of the LC behavior itself.

Although the presence of interdental laminae is associated with leaf cutting, these structures are not required to express this behavior. For example, LC bees that secondarily lost these laminae are still able to cut leaves (*e.g*., Laroca *et al*., 1992; Zillikens & Steiner 2004; Torretta *et al*., 2014). Leaf-cutter ants, which never developed interdental laminae (Fig. 13A–C), are also able to cut leaves, petals, and grasses efficiently. Shifts in behavior might act as drivers of evolutionary diversification and phenotypic change (*e.g*., Duckworth, 2009; Lapiedra *et al*., 2013). Thus, it is likely that interdental laminae might have evolved after the LC behavior was already in place. This idea is supported by the use of chewed leaf pulp, large petal pieces, and irregular leaf pieces in some Osmiini and in some *Callomegachile* that lack interdental laminae (Michener, 2007; Rozen *et al*., 2010). Lower costs in handling and processing large leaf pieces when compared with masticated plant material, and a greater access to more readily available vegetative plant resources (flowers are not often continuously available), might have facilitated a transition to leaf cutting.

The development of interdental laminae might have either allowed a more efficient way to cut and process leaves, or allowed access to more leaf types and plants. Bee species with odontogenic laminae only or without it, cut irregularly margined leaf pieces [*e.g*., Soh, 2014: *M*. (*Creightonella*) *atrata* Smith]. In species with both types of laminae, the margins of the leaf pieces are smooth (Michener, 2007). The study of MacIvor (2016) supports the second adaptive hypothesis. For example, *M*. (*Sayapis*) *pugnata* Say, a species with odontogenic lamina only, significantly uses less plant species than *M*. (*Megachile*) *centuncularis* and *M*. (*E*.) *rotundata*, species from lineages that developed both types of laminae. However, leaf choice might not only depend on the ability to cut certain types of leaves, but also on the local availability as well as on their chemichal, mechanical, and antimicrobial properties.

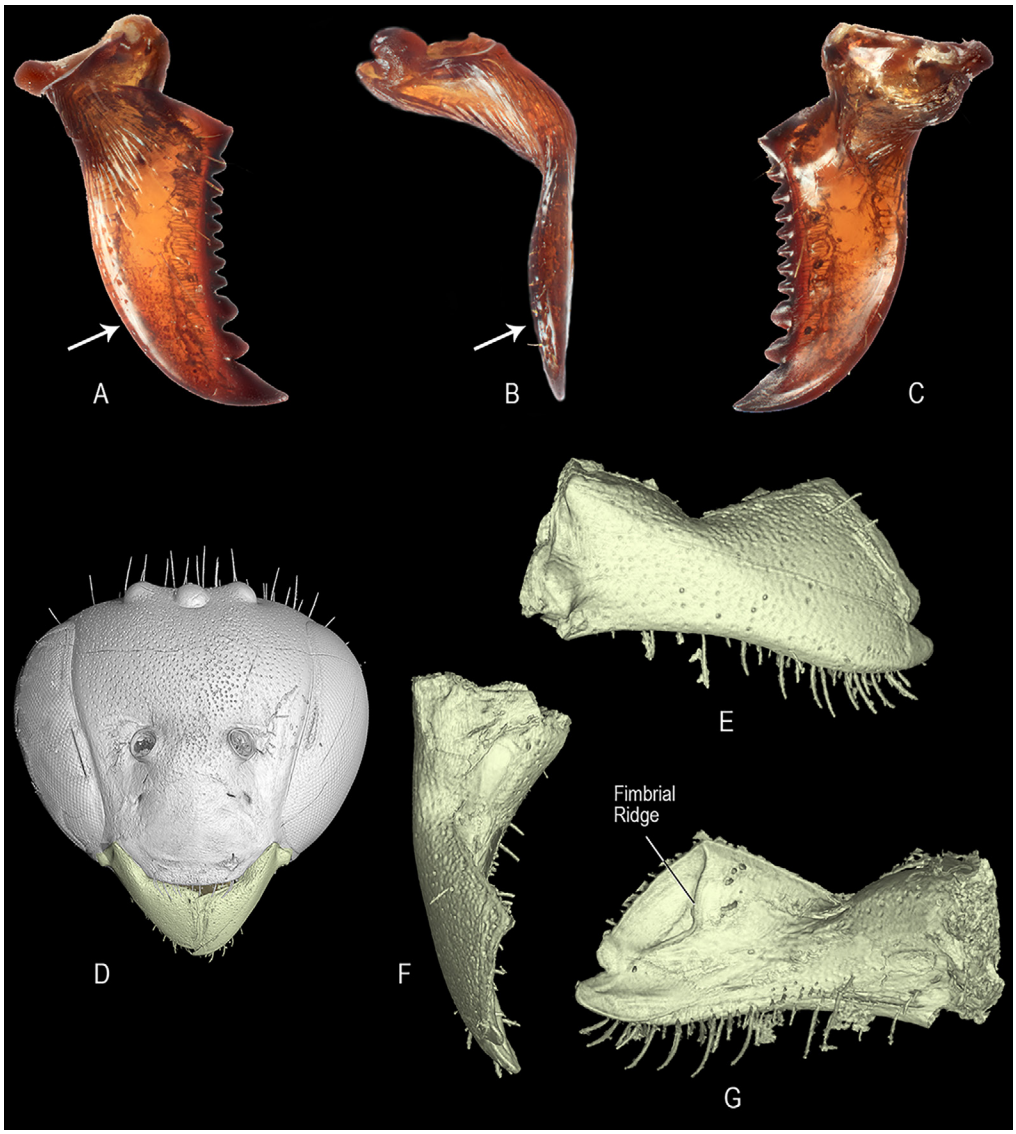

Figure 13. Female mandible of leaf-cutter ants and extinct Baltic amber megachilids. **A–C.** Right mandible of leaf-cutter ant (Formicidae: Attini: *Atta* sp.) in frontal, lateral, and inner views, respectively. Arrow points to the lower margin. **D–G.** Synchrotron-radiation μCT scan of *Glyptapis* sp. (Glyptapini) from Eocene Baltic amber; facial view of the head and right mandible in outer, superior, and inner views, respectively [note that the scan resolution could not resolve the finest setae, such as those of the compound eyes which are present in this specimen as in all species of *Glyptapis* Cockerell (Engel, 2001)].

If the derived clade of LC bees evolved recently, and interdental laminae are not required for and likely evolved after the LC behavior, which insects are then responsible for the Eocene fossil leaf excisions? There are few insects capable of leaving similar cuts on leaf margins (for a discussion see Wedmann *et al*., 2009) and one of them are LC ants. However, LC ants are restricted to the Neotropics and they evolved even more recently (8–12 Ma) than LC bees (Schultz & Brady, 2008). Larval sawflies, larval lepi-

dopterans, and adult and larval beetles also produce arcuate excisions on leaf margins, but these are quite different from megachilids, as they are uniformly cuspate, sharp, and entire (Labandeira, 2002: fig. 6m, n). Another possibility is that extinct lineages of megachilid bees from the Eocene (*e.g.*, Ctenoplectrellini and Glyptapini) also cut leaves, or even extinct lineages within Osmiini or stem-group Megachilini.

An examination of the mandibular structure of fossils from Ctenoplectrellini and Glyptapini, both using light microscopy and CT scans, showed two different types of mandibles. In Glyptapini, the lateral surface of the mandible gently curves towards the apex; its distal margin has a single apical tooth and a long, edentate upper margin (trimmal expansion); and the inner surface of the mandible possesses a distinct fimbrial ridge apically, which is long and parallel to the edentate upper margin (Figs. 13D–G). Thus, the mandible of Glyptapini resembles that of some species of Anthidiini that use resins, as well as that of some species of Group 2 of *Megachile s.l.* Unlike Glyptapini, the female mandible of Ctenoplectrellini is tridentate (males are bidentate) and has two distinct outer surfaces that merge rather abruptly with each other, one lateral basally and one anterior distally (Engel, 2001). Thus, the mandible of Ctenoplectrellini is somewhat similar to that of some species of *Osmia* Panzer. Finally, interdental laminae and fimbrial carinae are completely absent in both tribes.

Based on the mandibular structure, it is therefore unlikely that these particular extinct taxa might have cut leaves, principally Glyptapini. However, it is likely that Ctenoplectrellini might have used plant resources as nesting materials because *Aspidosmia*, its extant closest relative, uses masticated leaf pulp to build their nests (Brauns, 1926). Thus, the identity of the Eocene LC insects remains elusive, and may or may not have included extinct Megachilinae or stem-group Osmiini or Megachilini. Alternatively, the estimated dates of divergence may be grossly underestimated. For now, the only direct evidence from the Eocene and other deposits demonstrates that some taxon, either a LC bee or LC bee-like relative, was present and capable of producing cuts indistinguishable from those of modern LC bees and different from those other insects that cut or chew leaves.

Classificatory Implications

FAMILY MEGACHILIDAE: The phylogenetic relationships obtained from our preliminary total-evidence analyses were generally congruent with previous phylogenetic hypotheses (Litman *et al*., 2011; Gonzalez *et al*., 2012). However, they revealed new relationships that might help to resolve phylogenetic positions of problematic taxa and adjust current classificatory proposals. For example, our analysis suggests that both Dioxyini and Aspidosmiini are extant relatives of the extinct tribes Ctenoplectrellini and Glyptapini. Previous authors placed all these tribes whitin either Anthiidini or Osmiini (*e.g.*, Engel, 2001; Michener, 2007), but our analyses clearly show them in a well-supported clade, sister to the remaining Megachilinae. The relationship of Dioxyini with these fossil taxa is a new phylogenetic hypothesis for this distinctive taxon. All four of these tribes have aroliae, cleft pretarsal claws, and the crossvein 2m-cu basal to 2rs-m, but these features are also present in other Megachilinae. Aspidosmiini rendered Ctenoplectrellini paraphyletic in our analysis, and in that case, it would be appropriate to synonymize the former under the latter tribe. Gonzalez *et al*. (2012) discussed this option but ultimately decided to recognize it in its own tribe because of the limited number of scored characters for these fossils, which could have biased the results. Thus, we suggest recognizing Aspidosmiini until further analyses test these relationships using a larger number of characters for the fossil taxa.

Table 4. Hierarchichal suprageneric classification of Megachilidae including two new tribes described in the text (*vide infra*). Classification follows Engel (2005) and Gonzalez *et al*. (2012). † = fossil taxa.

Subfamily Fideliinae Cockerell
Tribe Neofideliini Engel
Tribe Fideliini Cockerell
Subfamily Pararhophitinae Popov
Subfamily Lithurginae Newman
Tribe †Protolithurgini Engel
Tribe Lithurgini Newman
Subfamily Megachilinae Latreille
Tribe †Glyptapini Cockerell
Tribe Dioxyini Cockerell
Tribe †Ctenoplectrellini Engel
Tribe Aspidosmiini Gonzalez *& al*.
Tribe Pseudoheriadini Gonzalez & Engel, new tribe
Tribe Megachilini Latreille
Tribe Ochreriadini Gonzalez & Engel, new tribe
Tribe Osmiini Newman
Subtribe Chelostomina Kirby
Subtribe Heriadina Michener
Subtribe Osmiina Newman
Tribe Anthidiini Ashmead
Subtribe Trachusina Robertson
Subtribe Anthidiina Ashmead

The osmiines *Afroheriades* and *Pseudoheriades* are sister genera that form a well-supported clade. The morphological analysis of Gonzalez *et al*. (2012) placed them among the *Heriades*-group of genera of Osmiini whereas the molecular analysis of Praz *et al*. (2008) placed them either as sister of either Anthidiini or Megachilini. Griswold (1985) also suggested a relationship with Megachilini based on the modified setae on the fifth sternum of the male. Our analyses consistently placed these two genera and Megachilini in a well-supported clade (Fig. 9). All other Osmiini clustered in another clade. Thus, in order to recognize a monophyletic Osmiini, we would need to either transfer them to Megachilini or distinguish them in their own tribe. Tranferring them to Megachilini weakens the recognition and diagnosis of this tribe because a morphological synapomorphy unambiguously present in that clade is unknown. In contrast, recognizing *Afroheriades* and *Pseudoheriades* in their own tribe might highlight their distinctiveness while maintaining the current taxon concept for Megachilini. The tribe Osmiini will thus contain those taxa clustered in the other clade, which is sister to Megachilini + (*Afroheriades* + *Pseudoheriades*), except for *Ochreriades*.

The phylogenetic position of *Ochreriades* has varied among morphological (Gonzalez *et al*., 2012), molecular (Praz *et al*., 2008), and our combined analyses. For example, it resulted among the *Heriades*-group of genera, as sister to all of Megachilinae, or as sister to Megachilini and Osmiini. In our Bayesian analysis, *Ochreriades* clustered with the majority of osmiines (excluding *Afroheriades* + *Pseudoheriades*) in a clade with low support. *Ochreriades* is morphologically distinctive among megachilids. It has yellow integumental markings as in the Anthidiini, a very long body with an elevated pronotum that surrounds the mesoscutum anteriorly, and long mouthparts that reach the tip of the metasoma. Thus, *Ochreriades* is a taxon with distinctive features whose separation from Osmiini might be desirable. Based on these results, we propose to

recognize two new tribes (Pseudoheriadini and Ochreriadini, *vide infra*), thus, narrowing and strengthening the taxon concept of Osmiini. Our preliminary analyses also support the recognition of three subtribes or genus groups within Osmiini and two within Anthidiini (Table 4).

TRIBE MEGACHILINI: Our morphological phylogeny suggests that recognizing *Gronoceras*, *Heriadopsis*, and *Matangapis* as genera distinct from *Megachile s.l.*, but not other Group 2 subgenera, renders that latter genus paraphyletic. Our preliminary total-evidence analyses also support this idea, although branch support is low. We discuss three possible phylogeny-based solutions, but advocate for one that maximizes information storage and retrieval, memorability, and congruence with modern classification in other bee taxa.

The first classificatory proposal is to recognize only two extant genera in Megachilini, *Noteriades* and *Megachile*. The cleptoparasitic genera *Coelioxys* and *Radoszkowskiana*, would be subgenera of *Megachile*. The fossil subgenus *Chalicodomopsis* could be treated either as a subgenus of *Megachile* given its position in the morphological analysis under EW or as a genus, as suggested in the IW and combined analyses.

The second proposal recognizes some of the subgenera of Group 2 at the generic rank, namely those taxa that clustered in a large clade with *Coelioxys* and *Radoszkowskiana*. All of these taxa are Old World in distribution and the majority of them are hoplitiform or heriadiform in body shape (*e.g.*, *Thaumatosoma*, *Rhodomegachile*, *Hackeriapis*). Thus, this proposal would recognize about 15 genera alongside *Megachile*, the latter including a mixture of Groups 1, 2, and 3.

The third proposal differs from the second in that *Megachile* would be restricted to the derived, well-supported clade that includes the LC bees only (Clade C in Figs. 8, 10, 11). This proposal would treat the remaining taxa at the generic level, thus recognizing about 28 genera total (Table 5, Fig. 14). Therefore, our proposals are somewhat similar to those discussed by Trunz *et al*. (2016), but differ in the number and identity of the taxa recognized at the generic level due to differences in the clade composition with our total-evidence phylogeny.

All three proposals imply new combinations of names and each proposal has practical advantages and disadvantages. An obvious advantage of retaining a large genus *Megachile s.l.*, as in the first proposal, 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 morphological, behavioral, and molecular data. For example, features of immature stages might provide additional informative characters, but available information suggests little morphological variation in the major lineages of *Megachile s.l.* (Rozen *et al*., 2016). However, the first proposal also requires the inclusion of *Coelioxys* and *Radoszkowskiana* in *Megachile*, which would create more than 470 combinations of names and perhaps many new homonyms. *Megachile* would be an enormous genus with nearly 2000 species, more than 75 subgenera, and a wide range of biologies and morphologies. Such a retrograde classification is therefore highly undesirable.

Adopting the second or third proposal would not create as many new combinations of names as in the first proposal. As previously outlined in the introduction, several authors initially described some taxa of Group 2 at the generic rank (*e.g.*, *Chelostomoides*, *Gronoceras*, *Heriadopsis*, *Thaumatosoma*), which others subsequently treated first as subgenera of *Chalicodoma* and then of *Megachile*. Furthermore, because of the economic importance and worldwide distribution of Group 1, most published work

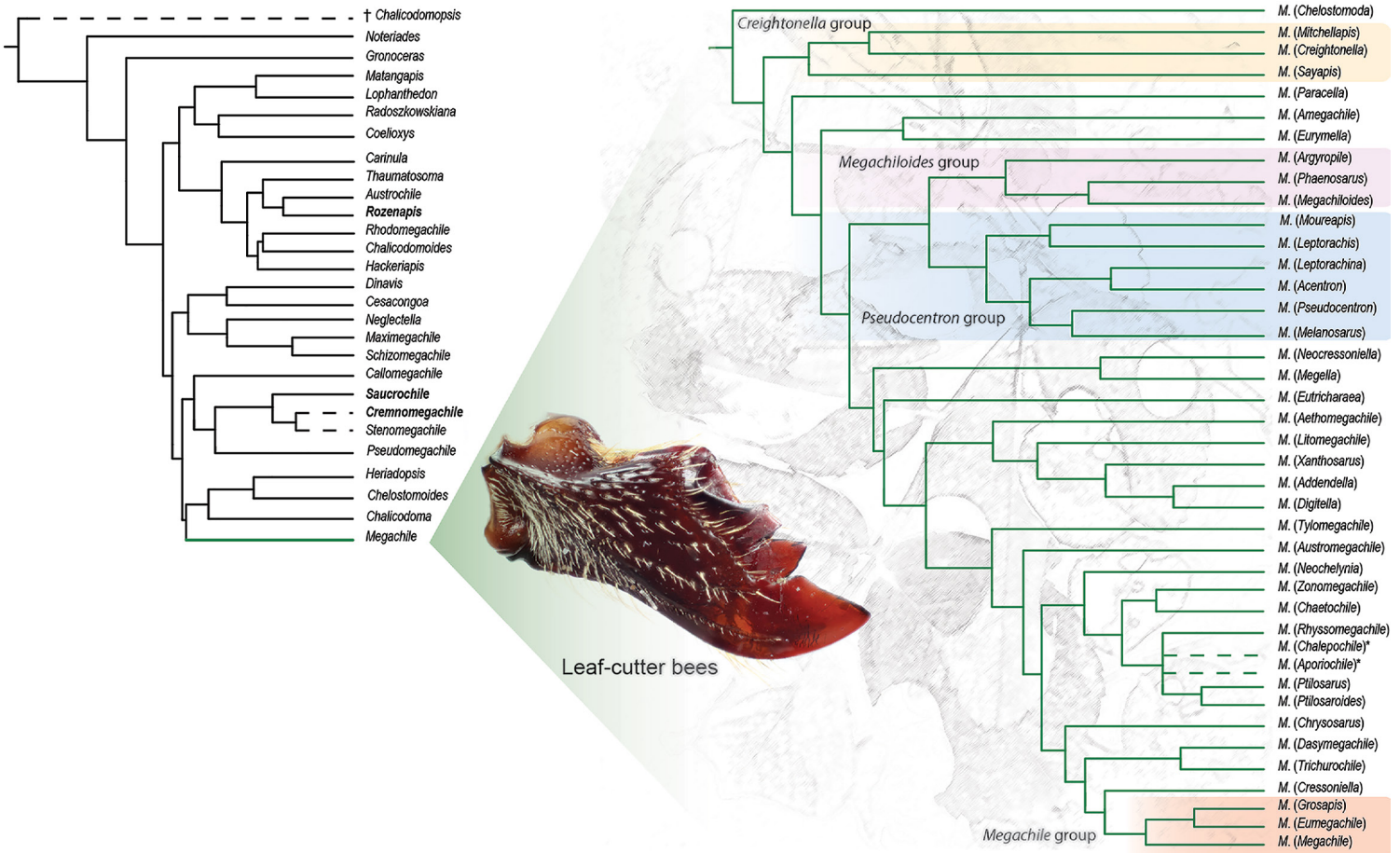

Figure 14. Summary of the proposed classification for Megachilini (Table 5 and Appendices 6, 7). Broken lines indicate uncertain positions. New taxa described herein are bold faced. Gonzalez *et al*. (2018) recognized and described two new subgenera of *Megachile* after this work was completed (indicated with an asterisk) and were not included in the analyses. Groups of subgenera of *Megachile* highlighted in color are discussed in the text.

Table 5. New classification of Megachilini following Proposal #3 (see text). The list follows the order of taxa according to the phylogeny represented in figure 11. It does not includes the subgenera of *Coelioxys* Latreille. † = fossil taxa; * = new status.

Genus †*Chalicodomopsis* Engel*	Genus *Megachile* Latreille
Genus *Noteriades* Cockerell	Subgenus *Chelostomoda* Michener
Genus *Gronoceras* Cockerell	Subgenus *Mitchellapis* Michener
Genus *Matangapis* Baker & Engel	Subgenus *Creightonella* Cockerell
Genus *Lophanthedon* Gonzalez & Engel*	Subgenus *Sayapis* Titus
Genus *Coelioxys* Latreille	Subgenus *Paracella* Michener
Genus *Radoszkowskiana* Popov	Subgenus *Amegachile* Friese
Genus *Carinula* Michener *& al*.*	Subgenus *Eurymella* Pasteels
Genus *Thaumatosoma* Smith	Subgenus *Argyropile* Mitchell
Genus *Austrochile* Michener*	Subgenus *Phaenosarus* Mitchell
Genus *Rozenapis* Gonzalez & Engel, n. gen.	Subgenus *Megachiloides* Mitchell
Genus *Rhodomegachile* Michener*	Subgenus *Moureapis* Raw
Genus *Chalicodomoides* Michener*	Subgenus *Leptorachis* Mitchell
Genus *Hackeriapis* Cockerell*	Subgenus *Leptorachina* Mitchell
Genus *Dinavis* Pasteels*	Subgenus *Acentron* Mitchell
Genus *Cesacongoa* Koçak & Kemal*	Subgenus *Pseudocentron* Mitchell
Genus *Neglectella* Pasteels*	Subgenus *Melanosarus* Mitchell
Genus *Maximegachile* Guiglia & Pasteels*	Subgenus *Neocressoniella* Gupta
Genus *Schizomegachile* Michener*	Subgenus *Megella* Pasteels
Genus *Callomegachile* Michener*	Subgenus *Eutricharaea* Thomson
Subgenus *Alocanthedon* Engel & Gonzalez	Subgenus *Aethomegachile* Engel & Baker
Subgenus *Callomegachile* Michener	Subgenus *Litomegachile* Mitchell
Subgenus *Eumegachilana* Michener	Subgenus *Xanthosarus* Robertson
Subgenus *Morphella* Pasteels	Subgenus *Addendella* Mitchell
Genus *Saucrochile* Gonzalez & Engel, n. gen.	Subgenus *Digitella* Pasteels
Genus *Cremnochile* Gonzalez & Engel, n. gen.	Subgenus *Tylomegachile* Moure
Genus *Stenomegachile* Pasteels*	Subgenus *Austromegachile* Mitchell
Genus *Pseudomegachile* Friese*	Subgenus *Neochelynia* Schrottky
Subgenus *Archimegachile* Alfken	Subgenus *Zonomegachile* Mitchell
Subgenus *Cestella* Pasteels	Subgenus *Chaetochile* Mitchell
Subgenus *Largella* Pasteels	Subgenus *Rhyssomegachile* Mitchell
Subgenus *Parachalicodoma* Pasteels	Subgenus *Chalepochile* Gonzalez & Engel
Subgenus *Pseudomegachile* Friese	Subgenus *Aporiochile* Gonzalez & Engel
Subgenus *Xenomegachile* Rebmann	Subgenus *Ptilosarus* Mitchell
Genus *Heriadopsis* Cockerell	Subgenus *Ptilosaroides* Mitchell
Genus *Chelostomoides* Robertson*	Subgenus *Chrysosarus* Mitchell
Subgenus *Chelostomoides* Robertson	Subgenus *Dasymegachile* Mitchell
Subgenus *Chelostomoidella* Snelling	Subgenus *Trichurochile* Mitchell
Genus *Chalicodoma* Lepeletier de Saint Fargeau	Subgenus *Cressionella* Mitchell
	Subgenus *Grosapis* Mitchell
Incertae sedis	Subgenus *Eumegachile* Friese
Genus *Stellenigris* Meunier	Subgenus *Megachile* Latreille

has been done on members of this group rather than on Group 2 or 3. Thus, the new combinations of names resulting from treating the subgenera of Group 2 at the generic level would not have a major effect in the literature.

Recognizing some subgenera of Group 2 at the generic rank while others as subgenera of *Megachile*, as in the second proposal, would still make *Megachile* highly heterogeneous morphologically and biologically, rendering the genus difficult to diag-

nose as well as differentiate from remaining Megachilini. However, the third proposal allows a more efficient retrieval of information and significantly improves the recognition and diagnosability of *Megachile* when the genus only consists of groups that cut leaves and developed interdental laminae. For example, recognizing *Megachile* in a narrower sense than in the second proposal would highlight the differences in nesting behavior and morphology among groups. This division may also encourage faster taxonomic revisions and comparative biological studies that would in turn increase our understanding of Megachilini.

The multigeneric classification of the third proposal might seem like an extreme change, but upon inspection, is not. First, authors have previously recognized several subgenera within Group 2 at the genus rank, and the need for a multigeneric classification in Megachilini has repeatedly been voiced (*e.g*., Mitchell, 1980; Engel & Baker, 2006; Michener, 2007; Trunz *et al*., 2016). The problem at the time had been in choosing the best approach to picking which taxa to recognize at the genus rank in the absence of phylogenetic hypotheses. Second, the morphological differences among the subgenera of Group 2 are comparable or even greater than that among other genera of bees, including other megachilid tribes. For example, the morphological differences between the stingless bee genera *Trigona* Jurine and *Partamona* Schwarz (Apidae: Meliponini), or between the wool carder bee genera *Anthidium* Fabricius and *Afranthidium* Michener (Megachilidae: Anthidiini), seem trivial when we compare that between *Hackeriapis* and *Chalicodoma*. Such a difference in the breadth of generic concepts among bee groups might be a reflection of the levels of taxonomic, phylogenetic, and morphological knowledge within each group. Third, many bee taxa now widely accepted as genera today, were treated in the past as subgenera of much larger genera, just like in the case of *Megachile s.l*. For example, Michener (1944) and Schwarz (1948) treated the more than 20 genera of Meliponini recognized today as subgenera of *Trigona*. Fourth, other authors (*e.g*., Almeida, 2008; Almeida & Danforth, 2009) have recently proposed to elevate at the genus rank numerous subgenera of other similarly diverse bee genera, such as *Leioproctus* Smith *s.l*. (Colletidae) *sensu* Michener (2007). For these reasons, we advocate the third proposal given its practical adavantages, its hierarchichal arragement, and congruence with modern generic concepts of bees.

In addition to elevating the status of subgenera of Group 2 to the genus level following the third proposal (Table 5), one might need to create some new genera for species that rendered some taxa paraphyletic, as well as new synonymies and taxonomic arrangements (*vide infra*). For example, if one wishes to recognize *Callomegachile* Michener at the generic level, several genus-group names are available and could be treated as subgenera (*e.g*., *Alocanthedon* Engel & Gonzalez). The five species placed in *Carinula* Michener *et al*. are more related to *Hackeriapis* than *Callomegachile*. The presence of translucent distal margins in the male terga reinforces their affinity to *Hackeriapis*. The species placed in *Parachalicodoma* Pasteels, *Largella* Pasteels, and *Cestella* Pasteels showed a close relationship with *Pseudomegachile*, rendering the latter paraphyletic in some analyses. They could be regarded as species groups or subgenera of *Pseudomegachile* (Table 5). *Dinavis* Pasteels and *Negletella* Pasteels did not cluster with *Pseudomegachile* and thus they could be treated as separate genera. *Megachile* (*Chelostomoides*) *rugifrons* rendered *Chelostomoides* paraphyletic in all analyses, clustering closer to groups such as *Schizomegachile*. However, the morphology of both sexes is highly variable among the species of this group and we were not able to find a single morphological feature that consistently separated *M. rugifrons* from the remaining *Chelostomoi-*

des. Thus, we suggest retaining this species in *Chelostomoides* despite its position in the analyses until a finer analysis can be undertaken on this clade.

In the genus *Megachile*, according to the third proposal, we would recommend resurrecting the following subgenera: *Eurymella* Pasteels and *Digitella* Pasteels from *Eutricharaea* Thomson; *Phaenosarus* Mitchell and *Addendella* Mitchell from *Xanthosarus*; *Leptorachina* Mitchell from *Leptorachis*; and *Chaetochile* Mitchell from *Dasymegachile*. We also newly synonymize *Schrottkyapis* under *Sayapis* (new synonymy), while *Stelodides* was previously placed under *Chrysosarus* and our results corroborate such a synonymy (Gonzalez, 2013) (Appendices 6, 7). While Trunz *et al*. (2016) already established some of the changes indicated above (*e.g*., *Parachalicodoma* as a synonym of *Pseudomegachile*), some other authors (*e.g*., Durante & Abrahamovich, 2006; Moure *et al*., 2007) never adopted Michener's (2007) classification and still recognize some of the subgenera (*e.g*., *Leptorachina*, *Chaetochile*) that we recovered as independent lineages in our analyses.

Finally, Trunz *et al*. (2016) proposed to synonymize *Grosapis* and *Eumegachile* under *Megachile s.str*., and *Paracella* Michener under *Anodonteutricharaea* Tkalců, the order of the latter synonym corrected by Praz (2017). Such taxonomic changes might be correct but we do not recommend following these changes at this time because *Eumegachile* only rendered *Megachile s.str*. in the morphological analysis under EW, and both groups resulted as the sister group to *Megachile s.str*. in the combined analysis. *Grosapis* and *Eumegachile* are each morphologically distinctive and, although we included a few species of *Megachile s.str*. in our analyses, synonymyzing these taxa under *Megachile s.str*. would make it difficult to diagnose and recognize. Trunz *et al*. (2016) suggested the synonymy of *Paracella* under *Anodonteutricharaea* (*vide etiam* Praz, 2017) based on the phylogenetic position of *M. villipes* Morawitz, a species assigned to *Anodonteutricharaea*, a subgenus already synonymized under *Eutricharaea* by Michener (2007). However, neither these authors nor we were able to include the type species of *Anodonteutricharaea*, *M. lanigera* Alfken, in the analyses, and thus the phylogenetic position of this species remains uncertain along with such a synonymy. It cannot be presumed at this time that *M. lanigera* would fall into the same phylogenetic position as *M. villipes*.

Conclusions and Future Directions

Interdental laminae, the most distinctive and taxonomically significant feature of LC bees, developed from two different structures in the female mandible (Figs. 3B–H). One type of lamina developed from the tooth (odontogenic laminae) while the other from the fimbrial ridge (ctenogenic laminae). Odontogenic laminae, a putative synapomorphy for all LC bees, evolved first and exhibited more phenotypic plasticity than ctenogenic laminae (Fig. 12).

Our preliminary total-evidence tip dating analyses favor the hypothesis of a recent origin (15–25 Ma) for LC bees with interdental lamina (Figs. 8, 10, 11). Based on this estimate, Eocene trace fossil excissions would not likely to be the result of the activity of bees within this particular clade (Clade C in Figs. 8, 10, 11). Our observations on the mandibular morphology of Glyptapini and Ctenoplectrellini, extinct lineages from the Eocene, also indicate these taxa were unlikely to cut leaves (Figs. 13E–G). Thus, the identity of the Eocene LC insects remains elusive. However, considering that interdental laminae are not necessary for cutting leaves and the behavior certainly predated the origin of cutting structures, these traces may represent the activity of as-of-yet un-

identified stem-group Megachilini or Osmiini. A greater number of fossils are needed to more accurately and finely calibrate future phylogenetic studies of Megachilidae.

Citing Labandeira (2002: p. 50) as evidence, Trunz *et al*. (2016: p. 255) indicated that Eocene leaf trace fossils are hypothetical because many other hervibore insects produce similar cuts. However, reading Labandeira's (2002) paper, it is clear that he never doubted that megachilids were responsible for the Eocene leaf traces he examined, except for those of an unidentified fern that were clearly different (Labandeira, 2002: fig. 6m-n). Furthermore, the study of Sarzetti *et al*. (2008) supports the idea that many Eocene trace fossils are the product of megachilid bees based on analyses of the ellipse eccentricity of the excisions and leaf discs of brood cells from living bees.

Our preliminary total evidence analyses support the proposal of Gonzalez *et al*. (2012) in recognizing four subfamilies within Megachilidae, each with several tribes. It also provide insights on long-standing issues in the systematics of Megachilidae, namely the non-monophyly of Osmiini, phylogenetic position of Dioxyini, and the internal relationships of Megachilini. The IW analyses of the morphological dataset of Megachilini, using a range of constant *k*-values calculated for average character fits (Appendix 4), support the effectiveness of this weighting scheme in recovering topologies congruent with total evidence phylogenies. As in Reemer (2012), we found that tree topologies obtained with *k*-values calculated for character fits near 70% are highly congruent with the preliminary total-evidence phylogeny.

Finally, our study provides a framework to formulate and address novel and interesting evolutionary questions regarding the LC behavior in bees. For example, is there a phylogenetic pattern between the type of interdental laminae and the plants used by LC bees? Do mandibular shape and interdental laminae correlate with any leaf feature (*e.g*., toughness) or any particular cutting and handling process? Are interdental laminae stronger and more resistant to abrasion when compared with each other as well as with teeth? Do interdental laminae contain heavy metals and halogens to increase hardness as in the mandible of other insects? Certainly, plants vary in leaf traits and the variable morphology of the mandible of LC bees suggest mechanical solutions to some functional problems. In LC ants, for example, the mandible and the LC behavior of species that cut edicot leaves are different from those that cut grasses (*e.g*., Camargo *et al*., 2015). In addition, the mandibular teeth of LC ants have heavy metals (*e.g*., Schofield *et al*., 2002), which increase their hardness and influence their ability to cut leaves. These aspects are unknown for LC bees, although there seems to be great variation within and among species in the degree and manner of leaf use. For example, a few records indicate that some species of *Litomegachile* Mitchell, *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). In other subgenera, such as *Eutricharaea*, bees make the bottom of the cell 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.

Limitations of the Study

Our work has several limitations. First, we were not able to code all morphological characters for all species because some taxa are accessible only from the type specimen or a small number of specimens, and thus we could not dissect them. In other cases, only one of the sexes was available to us. Second, a large number of the taxa we coded for morphology do not have available DNA sequences or when available, they

are incomplete. For example, sequence data from a single gene (28S) are only available for *Matangapis* and *Heriadopsis*. For practical purposes, we included chimeric taxa to increase the taxonomic representation in our analysis. Although we are confident that the anatomical overlap is high between the pair of chosen species given that the morphological characters we pursued and scored reflect higher levels of relationships, this approach is not ideal. Some of the taxa with available information in GenBank are from specimens identified only to species groups within a subgenus or tentatively assigned to a subgenus (see supplemental Table S1 of Trunz *et al*., 2016). Thus, our total-evidence analyses are preliminary in nature. The support of many clades is weak and the monophyly of several groups need to be tested using more taxa. Further studies should attempt to score morphological data from the hologenophore (Astrin *et al*., 2013), as well as to employ non-destructive extraction of DNA from museum specimens, such as Ultraconserved Elements (UCEs) (*e.g*., Blaimer *et al*., 2016).

Descriptions of New Taxa

Family Megachilidae Latreille
Subfamily Megachilinae Latreille

Key to Extant Tribes of Megachilinae
(modified from Michener, 2007)

1. Metanotum with median spine or tubercle (except in *Allodioxys* Popov and *Ensliniana* Alfken); mandible of female slender apically, bidentate, similar to that of male; pronotum (except in *Prodioxys* Friese) with prominent obtuse or right-angular dorsolateral angle, below which a vertical ridge extends downward; sting and associated structures greatly reduced (scopa absent) ..... Dioxyini
—. Metanotum without median spine or tubercle; mandible of female usually wider apically, with three or more teeth, except rarely bidentate when mandible is greatly enlarged and porrect and clypeus is also modified; pronotum with dorsolateral angle weak or absent (or produced to a tooth in some *Chelostoma* Latreille but without vertical ridge below it); sting and associated structures well developed 2
2(1). Pterostigma less than twice as long as broad, inner margin basal to r-rs usually little if any longer than width, rarely about 1.5× width; pretarsal claws of female cleft or with an inner tooth (except in *Trachusoides* Michener & Griswold); body commonly with yellow or ivory integumental marks 3
—. Pterostigma over twice as long as broad, inner margin basal to r-rs longer than width; pretarsal claws of female simple (except in *Osmia* subgenus *Metalinella* Tkalců, Palaearctic); body without yellow or white integumental marks, except in Ochreriadini 4
3(2). Outer surface of metatibia with long setae forming a distinct scopa; prestigma much more than twice as long as broad; preaxilla, below posterolateral angle of mesoscutum, sloping and with small patch of setae, these as long as those of adjacent sclerites ..... Aspidosmiini
—. Outer surface of metatibia usually with abundant simple bristles, not forming a distinct scopa; prestigma commonly short, usually less than twice as long as broad; preaxilla vertical, smooth and shining, usually without setae .... Anthidiini

4(2). Body distinctly elongate with enlarged pronotum surrounding mesoscutum anteriorly, thus practically eliminating omaular surface of mesepisternum and anterior surface of mesoscutum; body with yellow or ivory integumental markings at least on metasoma ..... Ochreriadini, n. trib.
—. Body not as elongate and slender as above, pronotum not enlarged nor surrounding mesoscutum anteriorly, mesepisternum with distinct omaular surface; body without yellow or white integumental marks 5
5(4). Outer surfaces of pro- and mesotibiae apically with an acute angle (usually produced into a spine) and distinct notch anteriorly; male T6 with preapical carina often present; arolia normally absent, except in a few tropical Old World taxa (*Noteriades*, *Matangapis*, and *Heriadopsis*); body nonmetallic or nearly so ..... Megachilini
—. Outer surfaces of pro- and mesotibiae apically without an acute angle or spine and lacking distinct notch anteriorly; male T6 without preapical carina; arolia present; body sometimes metallic green, blue, or brassy 6
6(5). Maxillary palpus with two palpomeres; propodeum with basal area not marked posteriorly by a strong carina, if present, it does not extend laterally behind propodeal spiracle; male T7 large, exposed, quadrately surrounded by T6; male S5 with modified discal setae (female: T6 with wide apical hyaline rim, S1 with slender, erect spine, posterolateral angle of mesoscutum with marginal ridge rounded or carinate, if rounded, with dense patch of long setae laterally) ..... Pseudoheriadini, n. trib.
—. Maxillary palpus with at least with three palpomeres; propodeum with basal area not marked posteriorly by carina, or if present, then extending laterally behind propodeal spiracle; male T7 small, usually hidden, not quadrately surrounded by T6; male S5 with branched or simple discal setae ..... Osmiini

Pseudoheriadini Gonzalez & Engel, new tribe

ZooBank: urn:lsid:zoobank.org:act:DEC53F0B-8A55-418B-B72D-840B9F388F09

(Fig. 15)

Type genus: *Pseudoheriades* Peters, 1970.

Diagnosis: This tribe can be readily separated from all other tribes of Megachilinae by the following combination of features: small body size (4.0–8.5 mm in length); heriadiform (Fig. 15A); maxillary palpus dimerous (two palpomeres); propodeum with basal area not marked posteriorly by a strong carina, but if present, it does not extend laterally behind propodeal spiracle; outer surfaces of pro- and mesotibiae without a distinct notch on distal margin; arolia present; female T6 with wide apical hyaline rim; male T7 large, exposed, quadrately surrounded by T6 (Fig. 15B); male S3 with gradulus projecting into thin, basal hyaline lamella; male S5 with capitate discal setae.

Description: ♀: Preoccipital carina present (laterally in *Pseudoheriades*, dorsally in *Afroheriades*); clypeus little to not overhanging labral base; labrum not elongate, margin without fringe or apical tuft of setae; maxillary palpi dimerous (two palpomeres); mesoscutellum flat or slightly convex, not overhanging metanotum; metepisternum with dorsal carina or lamella (weakly present in *Afroheriades*); T6 with wide apical hyaline rim; S6 without lateral or apical projection.

♂: Metasoma with two or three sterna visible; T7 large, exposed, quadrately surrounded by T6; S3 with gradulus projecting into thin, basal hyaline lamella; S5 with capitate discal setae.

COMMENTS: This tribe contains at least 15 species (Griswold & Gonzalez, 2011; Ascher & Pickering, 2018) grouped in two Eastern Hemisphere genera, *Afroheriades* and *Pseudoheriades*. The first genus is restricted to the Cape Province of South Africa whereas the second is more widespread, occurring across Africa, the Middle East, and India. Griswold (1985) provided detailed descriptions and diagnostic features of both genera, some of which Griswold & Gonzalez (2011) illustrated.

Ochreriadini Gonzalez & Engel, new tribe
ZooBank: urn:lsid:zoobank.org:act:D70C4AF0-CE03-4A89-9881-AA8ABAE29225
(Fig. 15)

TYPE GENUS: *Ochreriades* Mavromoustakis, 1956.

DIAGNOSIS: This tribe is readily separated from all other tribes of Megachilinae by the following combination of features: body elongate and with yellow or ivory integumental markings; pronotum distinctly elevated and surrounding mesoscutum anteriorly; mouthparts elongate, reaching tip of metasoma.

DESCRIPTION: ♀: Clypeus not overhanging labral base; labrum not elongate, margin without fringe or apical tuft of setae; maxillary palpus trimerous (three palpomeres); metepisternum with dorsal carina or lamella; pronotum enlarged and surrounding mesoscutum anteriorly, practically eliminating omaular surface of mesepisternum and anterior surface of mesoscutum; mesoscutellum flat, on same plane with metanonum and propodeal base, as seen in profile; T6 without wide apical hyaline rim; S6 without lateral or apical projection.

♂: Metasoma with six sterna visible; S2 and S3, each with disc swollen; S4 with dense pubescence on disc; S5 not emarginate, with branched or simple discal setae; T7 exposed, inferiorly directed.

COMMENTS: This tribe contains a single genus, *Ochreriades*, which consists of two species. *Ochreriades fasciatus* (Friese) occurs in the Middle East whereas *O. rozeni* Griswold occurs in Namibia, Africa (Griswold, 1994; Ascher & Pickering, 2018).

Tribe Megachilini Latreille

Cremnomegachile Gonzalez & Engel, new genus
ZooBank: urn:lsid:zoobank.org:act:9B13591A-A7C6-4781-AF42-4B131460E1B5
(Fig. 16)

TYPE SPECIES: *Megachile dolichosoma* Benoist, 1962.

DIAGNOSIS: This genus resembles *Stenomegachile* in the elongate, shiny female mandible (Fig. 16A), female hypostomal area toothed, and male preapical carina of T6 bilobed (Fig. 16E). It can easily be separated by the shape of the mesoscutum, which is midanteriorly projected and truncate, thus forming an anterior-facing area (Fig. 16B).

DESCRIPTION: Small to moderate sized-bees (10.0–12.0 mm in body length). Integument shiny, with punctures coarse and spaced. Preoccipital border strongly carinate on gena; ocelloccipital distance distinctly greater than ocellocular distance.

♀: Mandible without interdental laminae, elongate, outer surface shiny, with apex about as broad as base, four-toothed, Mt_4 on upper margin and clearly separated from Mt_{1-3}, which are on distal margin; clypeus not covering base of labrum; labrum elongate, triangular, with distinct preapical protuberance bearing long, stiff tuft of setae; hypostomal carina with posterior portion ending in a tooth. Pronotal lobe with trans-

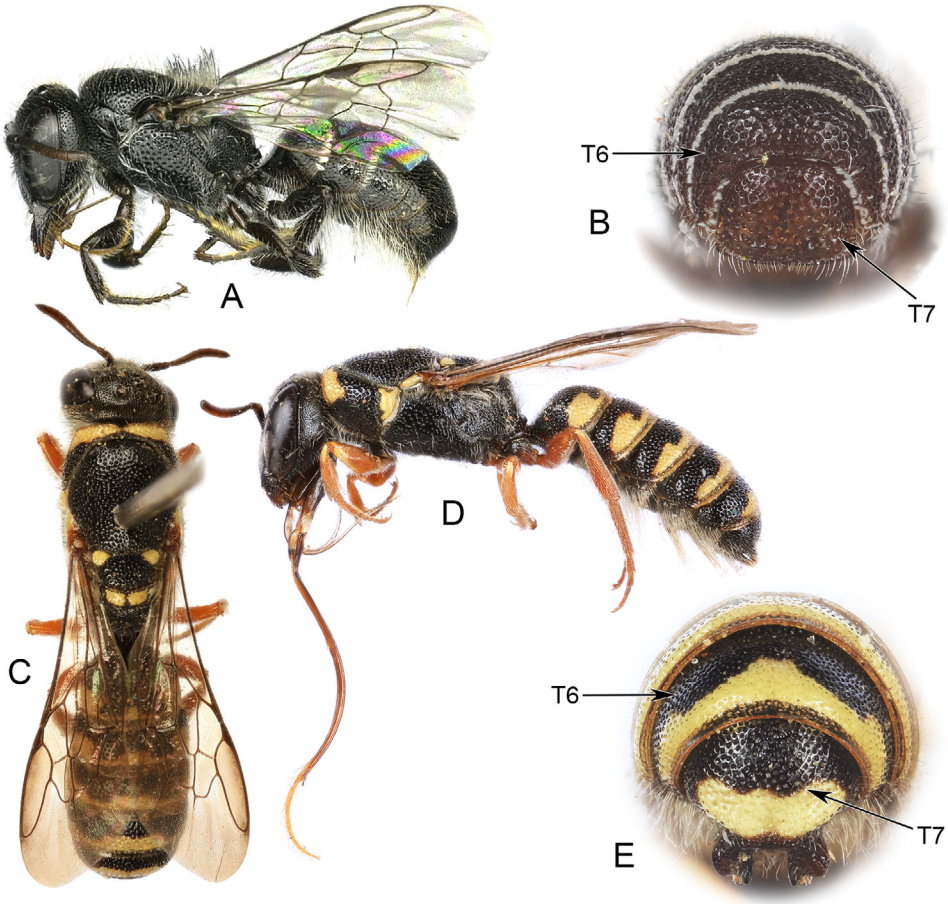

Figure 15. Tribes Pseudoheriadini and Ochreriadini. **A.** Female of *Afroheriades hyalinus* Griswold & Gonzalez in lateral view. **B.** Male terminal terga of *Pseudoheriades moricei* (Friese). **C, D.** Female of *Ochreriades fasciatus* (Friese) in dorsal and lateral views. **E.** Male terminal terga of *O. fasciatus*.

verse lamella; mesoscutum flat on disc, midanteriorly projected and truncate, thus forming an anterior-facing area; mesoscutellum flat, not overhanging metanotum in dorsal view (Fig. 4C). Metasoma narrow, parallel-sided, with white apical fasciae and distinct postgradular grooves on T2–T4; sterna without apical fasciae beneath scopa; T6 straight (vertical) in profile.

♂: Antennal flagellum unmodified, F1 shorter than F2; mandible tridentate, without basal projection or tooth on lower margin; hypostomal carina unmodified, area behind mandible unmodified, without a projection or concavity; procoxa aspinose; pro- and mesotibiae and tarsi unmodified; metabasitarsus elongate, about 4.0× longer than broad; mesotibial spur present, articulated to mesotibia, about as long as apical width of mesotibia. T6 vertical in profile, with deep concavity above broad, medially emarginate preapical carina, distal margin without a distinct tooth or projection; T7 with preapical carina broadly rounded; S4 exposed, with punctation and vestiture similar to those of preceding sterna; S8 with marginal setae. Genital capsule elongate, 1.9× longer than wide; gonostylus straight or nearly so in ventral view, apically simple

(not bifid), much narrower than base in lateral view, with long setae along its medial margin; volsella present, apically truncate.

ETYMOLOGY: The new genus-group name is a combination of of the Greek word, *kremnos*, meaning "overhanging wall", in reference to the projected and anterior-facing surface of the mesoscutum, and the generic name *Megachile*. The gender of the name is feminine [as noted by Gonzalez *et al*. (2018: p. 19), although *Megachile* is a neuter pleural and should be nomenclaturally considered masculine, precedence is to consider names based on *chile* (χεῖλος), meaning, "lip" or "rim", to be feminine].

COMMENTS: The genus is known from the type species only, which occurs in southern Madagascar (Pauly *et al*., 2001). This results in the **new combination**, *Cremnomegachile dolichosoma* (Benoist).

In addition to the features indicated in the diagnosis, the male of *Stenomegachile* differs from that of *Cremnomegachile* in the four-toothed mandible (tridentate in *Cremnomegachile*); the hypostomal area, behind the mandible, which is strongly projected into a tooth (unmodified in *Cremnomegachile*); and the pro- and mesotarsi that are expanded (normal in *Cremnomegachile*). The genital morphology is quite different, particularly in the shape of the volsella, which is narrow and apically notched (*vide* Pasteels, 1965: p. 513). In the female of *Stenomegachile* the mandible is more elongate and apically curved, and the labrum is long but parallel-sided. The hypostomal projection of *Stenomegachile* might not be homologous to the hypostomal tooth of *Cremnomegachile* because it is not part of the posterior portion of the hypostomal carina as in the latter genus.

Rozenapis Gonzalez & Engel, new genus
ZooBank: urn:lsid:zoobank.org:act:6CD5BAC1-311E-4476-8F26-755312E57364

TYPE SPECIES: *Megachile ignita* Smith, 1853.

DIAGNOSIS: This genus superficially resembles some robust species of *Hackeriapis* with the terminal terga reddish and thus contrasting with the preceeding black terga. The female shares with *Austrochile* a large, conspicuous midapical spine on S1 (absent in *Hackeriapis*), but it differs in the mandible. In *Austrochile* the transverse ridge is strong and extends basally to merge with the acetabular carina, whereas in *Rozenapis* such a ridge is entirely absent. The male differs from *Austrochile* in the absence of the midapical spine of S1 and the shape of T6, which has four equally distant teeth on its distal margin and a preapical carina that extends almost across the entire width of the tergum. In *Austrochile* the spine of S1 is present, the preapical carina of T6 is restricted to the median third, and the median projections of the distal margin are closer than the distance from one of them to a lateral tooth. The male of *Rozenapis* differs from *Hackeriapis* (*sensu* King, 1994) in the impunctate distal margins of T2–T4, which are narrow and nearly concolorous with the discal areas (broad, distinctive, and hyaline in *Hackeriapis*). It also differs in the pretarsal claws, which lack a basal tooth (present in *Hackeriapis*).

DESCRIPTION: Moderate-sized bees (12.0–15.0 mm in body length). Integument shiny, with punctures coarse and nearly contiguous. Preoccipital border rounded, not carinate; ocelloccipital distance slightly longer than ocellocular distance in female, much longer in male.

♀: Mandible without interdental laminae, short, outer surface dulled without transverse ridge, with apex about as broad as base, four-toothed; clypeus barely covering base of labrum; labrum rectangular. Pronotal lobe with transverse carina; me-

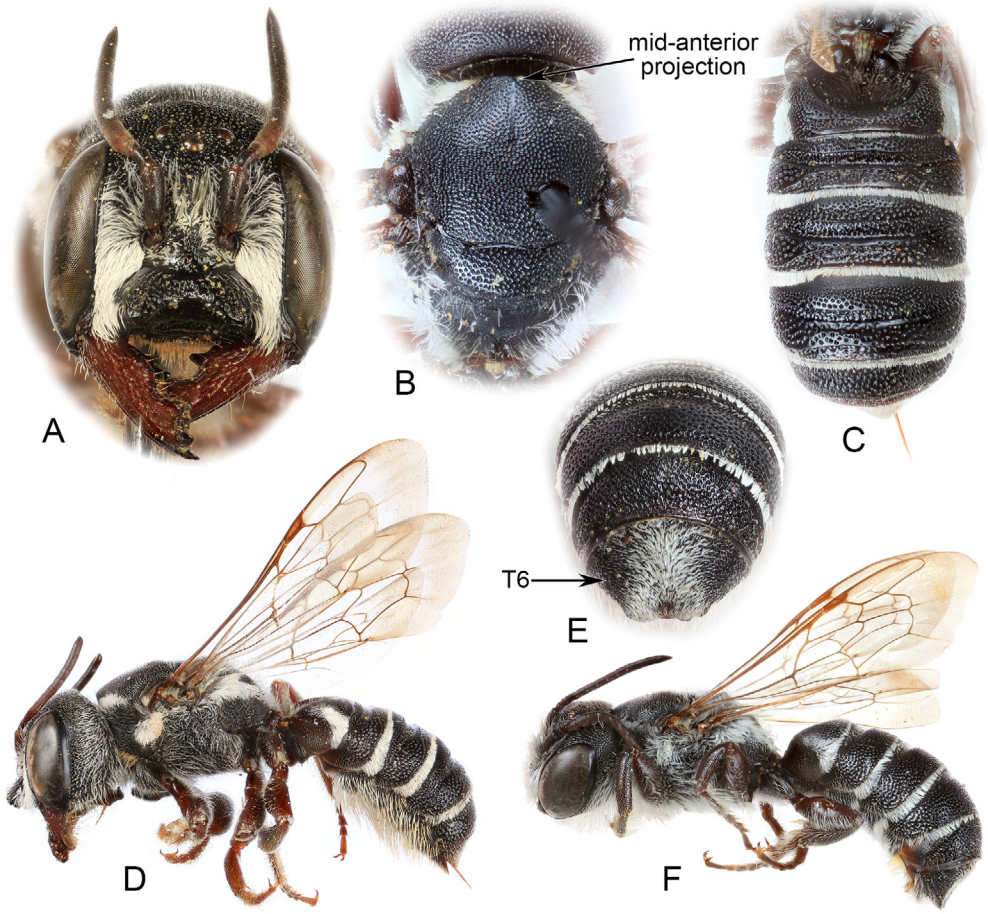

Figure 16. *Cremnomegachile dolichosoma* (Benoist), new combination. **A.** Facial view of female. **B.** Detail of female mesoscutum. **C.** Female metasoma in dorsal view. **D.** Lateral view of female. **E.** Male terminal terga. **F.** Lateral view of male.

soscutellum not overhanging metanotum in dorsal view. Metasoma robust, parallel-sided, with white apical fasciae laterally only and weak postgradular grooves on basal terga; S1 with long, distinct midapical projection; sterna without apical fasciae beneath scopa; T6 gently convex in profile, slightly concave preapically.

♂: Antennal flagellum unmodified, F1 shorter than F2; mandible tridentate, without basal projection or tooth on lower margin; hypostomal area behind mandible unmodified, without a projection or concavity; procoxal spine small; pro- and mesotibiae and tarsi slightly expanded; metabasitarsus elongate, about 4.0× longer than broad; mesotibial spur present, articulated to mesotibia, about as long as apical width of mesotibia. T6 vertical in profile, with deep concavity above broad, medially emarginate preapical carina, distal margin with four small, equidistant teeth or projections; T7 with preapical carina slightly projecting medially; S4 apically exposed, with punctation and vestiture similar to those of preceding sterna; S8 with marginal setae. Genital capsule elongate, 1.4× longer than wide; gonostylus straight or nearly so in ventral view, apically simple, truncate, much broader than base in lateral view, with short setae along its medial margin; volsella present, apically notched.

ETYMOLOGY: The new genus-group name is a patronymic honoring Dr. Jerome G. Rozen, Jr., of the American Museum of Natural History, for his significant contributions to the biology and systematics of bees, and his many years of dear friendship and mentorship to M.S.E. The name is a combination of his surname and *Apis* Linnaeus (Latin, meaning, "bee"). The gender of the name is feminine.

COMMENTS: This genus resulted as the sister group of *Austrochile* in our analyses. Only the type species from western Australia is known, which Michener (1965) listed in *Hackeriapis* as a member of species group 'A'. This results in the **new combination**, *Rozenapis ignita* (Smith).

Saucrochile Gonzalez & Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:395871FD-1354-4660-ACDD-1DF694882441

TYPE SPECIES: *Megachile heriadiformis* Smith, 1853.

DIAGNOSIS: This genus is most similar to *Hackeriapis* (*sensu* King, 1994). It differs in the pretarsal claws, which lack of a basal tooth, and in the distal margins of male T2–T4, which are punctate and concolorous with the discal areas. In *Hackeriapis*, the pretarsal claws have a distinct basal tooth and the distal margins of male T2–T4 are impunctate, broad, and hyaline. In addition, the pronotal lobe is distinctly carinate or lamellate, at least dorsally, in *Hackeriapis*, while the pronotal lobe is completely rounded in *Saucrochile*.

DESCRIPTION: Small sized-bees (8.0–11.0 mm in body length). Integument shiny, with punctures coarse and spaced. Preoccipital border rounded, not carinate; ocelloccipital distance much longer than ocellocular distance.

♀: Mandible without interdental laminae, elongate, outer surface shiny, with sparse punctures, outer ridge weak, extending basally to acetabular carina, three teeth on distal margin; clypeus not covering base of labrum; labrum elongate, parallel-sided, without preapical protuberance. Pronotal lobe without transverse carina or lamella; mesoscutellum flat, not overhanging metanotum in dorsal view. Metasoma elongate, parallel-sided, with white apical fasciae and strong postgradular grooves on basal terga; sterna without apical fasciae beneath scopa; T6 gently convex in profile.

♂: Antennal flagellum unmodified, F1 shorter than F2; mandible tridentate, without basal projection or tooth on lower margin; hypostomal area behind mandible unmodified, without a projection or concavity; procoxal spine small; pro- and mesotibiae and tarsi unmodified; metabasitarsus elongate, about 4.0× longer than broad; mesotibial spur present, articulated to mesotibia, about as long as apical width of mesotibia. T6 vertical in profile, with weak concavity above narrow, medially emarginate preapical carina, distal margin with four small, equidistant teeth or projections; T7 with preapical carina slightly projecting medially; S4 hidden, with punctation and vestiture different to those of preceding sterna; S8 with marginal setae. Genital capsule elongate, about 2.0× longer than wide; gonostylus straight or nearly so in ventral view, slightly narrower basally in lateral view, apically simple, with short setae along its medial margin; volsella present, apically notched.

ETYMOLOGY: The new genus-group name is a combination of of the Greek words, *saukros*, meaning "graceful", in reference to the general elegant aspect of this group, and *chile*, meaning "lip" or "rim". The gender of the name is feminine (*vide* Etymology for *Cremnomegachile*, *supra*).

Comment: Only the type species from the southern half of Australia is known, which Michener (1965) listed in *Hackeriapis* as a member of species group 'A'. This results in the **new combination**, *Saucrochile heriadiformis* (Smith).

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Appendix 1. Summary of major proposals in the classification of the genus *Megachile s.l.*, as discussed in the text (*vide supra*). Original names of subgenera are under each genus. Green shaded cells include the leaf-cutter taxa. * = A few recently described taxa are included within this classificatory scheme. † = Extinct taxa. § = *Cesacongoa* Koçak & Kemal is a replacement name for *Cuspidella* Pasteels.

Michener (1965) & Pasteels (1965)	Mitchell (1980)	Michener (2000, 2007)*
Genus *Chalicodoma*: *Archimegachile, Austrochile, Callomegachile, Carinella, Cestella, Chalicodoma, Chalicodomoides, Chelostomoda, Chelostomoides, Cuspidella, Digronoceras, Dinavis, Eumegachilana, Gronoceras, Hackeriapis, Largella, Maximegachile, Morphella, Neglectella, Pseudomegachile, Rhodomegachile, Schizomegachile, Stelodides, Stenomegachile, Thaumatosoma*	**Genus *Chalicodoma*:** *Archimegachile, Austrochile, Callomegachile, Carinella, Cestella, Chalicodoma, Chalicodomoides, Chelostomoda, Chelostomoides, Cuspidella, Digronoceras, Dinavis, Eumegachilana, Gronoceras, Hackeriapis, Largella, Maximegachile, Morphella, Neglectella, Pseudomegachile, Rhodomegachile, Schizomegachile, Stelodides, Stenomegachile, Thaumatosoma*	**Genus *Megachile*:** Group 2: *Alocanthedon, Austrochile, Callomegachile, §Cesacongoa, Cestella, Chalicodoma, Chalicodomoides, †Chalicodomopsis, Chelostomoda, Chelostomoides, Gronoceras, Hackeriapis, Heriadopsis, Largella, Lophanthedon, Matangapis, Maximegachile, Megella, Mitchellapis, Neochalicodoma, Parachalicodoma, Pseudomegachile, Rhodomegachile, Schizomegachile, Stellenigris, Stenomegachile, Thaumatosoma*
Genus *Creightonella*	**Genus *Creightonella***	Group 3: *Creightonella*
Genus *Megachile*: *Acentron, Amegachile, Argyropile, Austromegachile, Callochile, Chrysosarus, Cressoniella, Dactylomegachile, Dasymegachile, Delomegachile, Derotropis, Digitella, Eumegachile, Eurymella, Eutricharaea, Holcomegachile, Leptorachis, Litomegachile, Megachile, Megachiloides, Megella, Melanosarus, Mitchellapis, Neomegachile, Paracella, Phaenosarus, Platysta, Pseudocentron, Ptilosarus, Sayapis, Tylomegachile, Xanthosarus, Xeromegachile*	**Genus *Chrysosarus*:** *Chrysosarus, Dactylomegachile, Stelodides, Zonomegachile*	Group 1: *Acentron, Aethomegachile, Amegachile, Aporiochile, Argyropile, Austrosarus, Austromegachile, Chalepochile, Chrysosarus, Cressoniella, Dasymegachile, Eumegachile, Eutricharaea, Grosapis, Leptorachis, Litomegachile, Megachile, Megachiloides, Melanosarus, Moureapis, Neochelynia, Neocressoniella, Paracella, Platysta, Pseudocentron, Ptilosaroides, Ptilosarus, Rhyssomegachile, Sayapis, Schrottkyapis, Stelodides, Trichurochile, Tylomegachile, Xanthosarus, Zonomegachile*
	Genus *Cressoniella*: *Austromegachile, Chaetochile, Cressoniella, Dasymegachile, Holcomegachile, Neomegachile, Ptilosaroides, Ptilosarus, Rhyssomegachile, Trichurochile, Tylomegachile*	

Appendix 1. Continued.

Michener (1965) & Pasteels (1965)	Mitchell (1980)	Michener (2000, 2007)*
	Genus *Eumegachile*: *Eumegachile, Grosapis, Mitchellapis, Sayapis, Schrottkyapis* **Genus *Megachile*:** *Addendella, Amegachile, Callochile, Delomegachile, Digitella, Eurymella, Eutricharaea, Litomegachile, Macromegachile, Megachile, Megella, Paracella, Platysta, Xanthosarus* **Genus *Megachiloides*:** *Argyropile, Derotropis, Megachiloides, Phaenosarus, Xeromegachile* **Genus *Pseudocentron*:** *Acentron, Grafella, Leptorachina, Leptorachis, Melanosarus, Moureana, Pseudocentron*	

Appendix 2. List of taxa included in the morphological and molecular analyses of the family Megachilidae and tribe Megachilini. We followed the classifications of Gonzalez *et al*. (2012) for the tribes of Megachilidae and that of Michener (2007) for the subgenera of *Megachile s.l.*, which also includes recently described taxa. In the combined analyses, we used closely related species to those used in the morphological analyses when molecular data were not available for the same species. We referred to those chimeric taxa by their generic name, and sometimes subgenus, followed by a combination of the first three letters of both specific epithets in square brackets. For example, the name for the operational taxonomic unit (OTU) resulting from *Trichothurgus wagenknechti* (Moure) and *T. herbsti* (Friese) is referred herein as *Trichothurgus* [wag×her] (see text for explanation). GenBank accession numbers for specimens of included species in the analyses are in Appendix 4. * = Type species of the particular subgenus indicated within *Megachile s.l.*, as recognized by Michener (2007). † = Extinct species. — = Species not included in the analysis.

Phylogeny of Megachilidae		
Morphological analysis	**Molecular analysis**	**Combined analysis**
Outgroups		
Family MELITTIDAE Kawall		
Macropis (*Macropis*) *nuda* (Provancher) [USA]	*Macropis nuda*	*Macropis nuda*
Melitta (*Melitta*) *leporina* (Panzer) [France, Spain, Iran]	*Melitta leporina*	*Melitta leporina*
Family APIDAE Latreille		
Apis mellifera Linnaeus [USA]	*Apis mellifera*	*Apis mellifera*
Exomalopsis (*Stilbomalopsis*) *solani* Cockerell [USA, Mexico]	*Exomalopsis* sp.	*Exomalopsis* [sol×sp]
Diadasia (*Coquillettapis*) *australis* (Cresson) [USA]	*Diadasia bituberculata* (Cresson)	*Diadasia* [aus×bit]
Nomada utahensis Moalif [USA]	*Nomada maculata* Cresson	*Nomada* [uta×mac]
Ceratina calcarata Robertson [USA]	*Ceratina calcarata*	*Ceratina calcarata*
Ingroup		
Family MEGACHILIDAE Latreille		
Subfamily FIDELIINAE Cockerell		
Fidelia (*Parafidelia*) *pallidula* (Cockerell) [South Africa]	*Fidelia pallidula*	*Fidelia pallidula*
F. (*Fidelia*) *villosa* Brauns [South Africa]	*F. villosa*	*F. villosa*
F. (*Fideliana*) *braunsiana* Friese [South Africa]	*F. braunsiana*	*F. braunsiana*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
Subfamily Pararhophitinae Popov		
Pararhophites orobinus (Morawitz) [Pakistan]	*Pararhophites orobinus*	*Pararhophites orobinus*
P. quadratus (Friese) [Egypt]	*P. quadratus*	*P. quadratus*
Subfamily Lithurginae Newman		
Tribe Lithurgini Newman		
Lithurgus (*Lithurgopsis*) *apicalis* Cresson [USA]	*Lithurgus chrysurus* Fonscolombe	*Lithurgus* [api×chr]
Microthurge corumbae (Cockerell) [Bolivia]	*Microthurge* sp.	*Microthurge* [cor×sp]
Trichothurgus aterrimus (Cockerell) [Chile]	*Trichothurgus herbsti* (Friese)	*Trichothurgus* [ate×her]
Tribe †Protolithurgini Engel		
†*Protolithurgus ditomeus* Engel		
Subfamily Megachilinae Latreille		
Tribe Anthidiini Ashmead		
Afranthidium (*Capanthidium*) *capicola* (Brauns) [South Africa]	*Afranthidium capicola*	*Afranthidium capicola*
Anthidiellum (*Loyolanthidium*) *robertsoni* (Cockerell) [USA]	*Anthidiellum robertsoni*	*Anthidiellum robertsoni*
Anthidium (*Anthidium*) *porterae* Cockerell [USA]	*Anthidium porterae*	*Anthidium porterae*
Anthodioctes (*Anthodioctes*) *calcaratus* (Friese) [Costa Rica]	*Anthodioctes* (*Anthodioctes*) *mapirensis* (Cockerell)	*Anthodioctes* [cal×map]
Aztecanthidium tenochtitlanicum Snelling [Mexico]	*Aztecanthidium tenochtitlanicum*	*Aztecanthidium tenochtitlanicum*
Cyphanthidium intermedium Pasteels [Namibia]	*Cyphanthidium intermedium*	*Cyphanthidium intermedium*
Dianthidium (*Dianthidium*) *subparvum* Swenk [USA]	*Dianthidium subparvum*	*Dianthidium subparvum*
Duckeanthidium thielei Michener [Costa Rica: Heredia]	*Duckeanthidium thielei*	*Duckeanthidium thielei*
Eoanthidium (*Clistanthidium*) *rothschildi* (Vachal) [South Africa]	*Eoanthidium* (*Clistanthidium*) *turnericum* (Mavromoustakis)	*Eoanthidium* [rot×tur]

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
Epanthidium (*Epanthidium*) *bicoloratum* (Smith) [Argentina]	*Epanthidium bicoloratum*	*Epanthidium bicoloratum*
Euaspis abdominalis (Fabricius) [Zambia]	*Euaspis abdominalis*	*Euaspis abdominalis*
Hoplostelis (*Hoplostelis*) *bivittata* (Cresson) [Costa Rica]	*Hoplostelis bivittata*	*Hoplostelis bivittata*
Hypanthidioides (*Michanthidium*) *ferrugineum* (Urban) [Argentina]	*Hypanthidioides* (*Saranthidium*) *marginata* (Moure & Urban)	*Hypanthidioides* [fer×mar]
Hypanthidium (*Hypanthidium*) *mexicanum* (Cresson) [Mexico]	*Hypanthidium* (*Hypanthidium*) *obscurius* Schrottky	*Hypanthidium* [mex×obs]
Icteranthidium ferrugineum (Fabricius) [Egypt, Tunisia]	*Icteranthidium ferrugineum*	*Icteranthidium ferrugineum*
Notanthidium (*Notanthidium*) *steloides* (Spinola) [Chile]	*Notanthidium steloides*	*Notanthidium steloides*
Pachyanthidium (*Pachyanthidium*) *katangense* Cockerell [Congo]	*Pachyanthidium* (*Pachyanthidium*) *cordatum* (Smith)	*Pachyanthidium* [kat×cor]
Plesianthidium (*Spinanthidiellum*) *rufocaudatum* (Friese) [South Africa]	*Plesianthidium rufocaudatum*	*Plesianthidium rufocaudatum*
Pseudoanthidium (*Micranthidium*) *lanificum* (Smith) [Cameroon, Congo]	*Pseudoanthidium* sp.	*Pseudoanthidium* [lan×sp]
Rhodanthidium (*Rhodanthidium*) *septemdentatum* (Latreille) [Greece]	*Rhodanthidium septemdentatum*	*Rhodanthidium septemdentatum*
Serapista rufipes (Friese) [South Africa]	*Serapista rufipes*	*Serapista rufipes*
Stelis (*Stelis*) *linsleyi* Timberlake [USA]	*Stelis* (*Stelis*) *lateralis* Cresson	*Stelis* [lin×lat]
Trachusa (*Heteranthidium*) *larreae* (Cockerell) [USA]	*Trachusa larreae*	*Trachusa larreae*
Tribe Aspidosmiini Gonzalez *& al.*		
Aspidosmia arnoldi (Brauns) [South Africa]	*Aspidosmia arnoldi*	*Aspidosmia arnoldi*
Aspidosmia volkmanni (Friese) [South Africa]	*A. volkmanni*	*A. volkmanni*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
Tribe †Ctenoplectrellini Engel		
†*Ctenoplectrella cockerelli* Engel		
†*C. grimaldii* Engel		
†*C. viridiceps* Cockerell		
†*Glaesosmia genalis* Engel		
Tribe Dioxyini Cockerell		
Aglaoapis tridentata (Nylander) [Austria]	*Aglaoapis tridentata*	*Aglaoapis tridentata*
Dioxys pomonae Cockerell [USA]	*Dioxys moesta* Costa	*Dioxys* [pom×moe]
Tribe †Glyptapini Cockerell		
†*Glyptapis densopunctata* Engel		
†*G. disareolata* Engel		
Tribe Megachilini Latreille		
Coelioxys (*Boreocoelioxys*) *octodentata* Say [USA]	*Coelioxys octodentata*	*Coelioxys octodentata*
Megachile (*Chelostomoides*) *angelarum* Cockerell [USA]	*Megachile* (*Chelostomoides*) *angelarum*	*Megachile* (*Chelostomoides*) *angelarum*
M. (*Creightonella*) *discolor* Smith [South Africa]	*M.* (*Creightonella*) *albisecta* Klug	*M.* (*Creightonella*) [dis×alb]
M. (*Sayapis*) *pugnata* Say [USA]	*M.* (*Sayapis*) *pugnata*	*M.* (*Sayapis*) *pugnata*
Noteriades spinosus Griswold & Gonzalez [Thailand]	*Noteriades* sp.	*Noteriades* [spi×sp]
Radoszkowskiana rufiventris (Spinola) [Egypt]	*Radoszkowskiana rufiventris*	*Radoszkowskiana rufiventris*
Tribe Osmiini Newman		
Afroheriades hyalinus Griswold & Gonzalez [South Africa]	*Afroheriades primus* (Peters)	*Afroheriades* [hya×pri]
Ashmeadiella (*Ashmeadiella*) *aridula* Cockerell [USA]	*Ashmeadiella aridula*	*Ashmeadiella aridula*
Atoposmia (*Atoposmia*) *abjecta* (Cresson) [USA]	*Atoposmia* (*Eremosmia*) *mirifica* (Michener)	*Atoposmia* [abj×mir]

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
Chelostoma (*Chelostoma*) *florisomne* (Linnaeus) [Hungry, Sweden]	*Chelostoma florisomne*	*Chelostoma florisomne*
Haetosmia vechti (Peters) [Israel, Pakistan]	*Haetosmia brachyura* (Morawitz)	*Haetosmia* [vec×bra]
Heriades (*Heriades*) *truncorum* (Linnaeus) [Austria, Sweden]	*Heriades crucifer* Cockerell	*Heriades* [tru×cru]
Hofferia schmiedeknechti (Schletterer) [Bulgaria, Greece]	*Hofferia schmiedeknechti*	*Hofferia schmiedeknechti*
Hoplitis (*Monumetha*) *albifrons* (Kirby) [USA: Utah]	*Hoplitis* (*Hoplitis*) *adunca* (Panzer)	*Hoplitis* [alb×adu]
H. (*Stenosmia*) *flavicornis* (Morawitz) [Mongolia, Uzbekistan]	*H.* (*Stenosmia*) *minima* (Schulthess)	*Hoplitis* [fla×min]
Ochreriades fasciatus (Friese) [Israel]	*Ochreriades fasciatus*	*Ochreriades fasciatus*
Osmia (*Osmia*) *lignaria* Say [USA]	*Osmia lignaria*	*Osmia lignaria*
Othinosmia (*Megaloheriades*) *globicola* (Stadelmann) [South Africa]	*Othinosmia globicola*	*Othinosmia globicola*
Protosmia (*Chelostomopsis*) *rubifloris* (Cockerell) [USA]	*Protosmia* (*Protosmia*) *humeralis* (Pérez)	*Protosmia* [rub×hum]
Pseudoheriades moricei (Friese) [Egypt]	*Pseudoheriades moricei*	*Pseudoheriades moricei*
Stenoheriades asiaticus (Friese) [Turkey]	*Stenoheriades asiaticus*	*Stenoheriades asiaticus*
Wainia (*Caposmia*) *elizabethae* (Friese) [South Africa]	*Wainia* (*Caposmia*) *eremoplana* (Mavromoustakis)	*Wainia* [eli×ere]
Phylogeny of Megachilini		
Outgroups		
Subfamily Lithurginae Newman		
Tribe Lithurgini Newman		
Microthurge friesei (Ducke) [Argentina]	*Microthurge* sp.	*Microthurge* [fri×sp]
Trichothurgus wagenknechti (Moure) [Chile]	*Trichothurgus herbsti* (Friese)	*Trichothurgus* [wag×her]
Subfamily Megachilinae Latreille		
Tribe Aspidosmiini Gonzalez *& al.*		
Aspidosmia volkmanni (Friese) [South Africa]	*A. volkmanni*	*A. volkmanni*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
Tribe Anthidiini Ashmead		
Aztecanthidium tenochtitlanicum Snelling [Mexico]	*A. tenochtitlanicum*	*A. tenochtitlanicum*
Trachusa mitchelli (Michener) [Mexico]	*T. larreae* (Cockerell)	*Trachusa* [mit×lar]
Tribe Dioxyini Cockerell		
Dioxys producta (Cresson) [USA]	*Dioxys moesta* Costa	*Dioxys* [pro×moe]
Tribe Osmiini Newman		
Chelostoma rapunculi (Lepeletier) [USA]	*Chelostoma florisomne* (Linnaeus)	*Chelostoma* [rap×flo]
Hoplitis biscutellae (Cockerell) [USA]	*Hoplitis adunca* (Panzer)	*Hoplitis* [rap×flo]
Ingroup		
Tribe Megachilini Latreille		
Coelioxys (*Rhinocoelioxys*) *zapoteca* Cresson [Argentina, Bolivia, Brazil, Mexico]	—	—
C. (*Liothyrapis*) *decipiens* Spinola [India]	*Coelioxys decipiens*	*Coelioxys decipiens*
C. (*Torridapis*) *torrida* Smith [South Africa]	—	—
Noteriades jenniferae Griswold & Gonzalez [Thailand, Myanmar]	*Noteriades* sp.	*Noteriades* [jen×sp]
Radoszkowskiana rufiventris Spinola [Egypt]	*R. rufiventris*	*R. rufiventris*
Genus *Megachile* Latreille *s.l.*		
GROUP 1		
**M.* (*Acentron*) *albitarsis* Cresson [USA]	*M.* (*Acentron*) sp.	*M.* (*Acentron*) [alb×sp]
M. (*Acentron*) *candida* Smith [Costa Rica]	—	—
M. (*Aethomegachile*) *laticeps* Smith [India]	*M.* (*Aethomegachile*) *conjuncta* Smith	*M.* (*Aethomegachile*) [lat×con]
**M.* (*Aethomegachile*) *trichorhytisma* Engel [Thailand]	—	—
**M.* (*Amegachile*) *bituberculata* Ritsema [Cameroon]	*M.* (*Amegachile*) *cf. bituberculata*	*M.* (*Amegachile*) *bituberculata*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
M. (*Amegachile*) *ustulatiformis* Cockerell [Australia]	—	—
**M.* (*Argyropile*) *parallela* Smith [USA]	*M.* (*Argyropile*) *parallela*	*M.* (*Argyropile*) *parallela*
M. (*Argyropile*) *sabinensis* Mitchell [USA]	—	—
M. (*Austromegachile*) *exaltata* Smith [Brazil]	—	—
**M.* (*Austromegachile*) *montezuma* Cresson [Brazil]	*M.* (*Austromegachile*) sp.	*M.* (*Austromegachile*) [mon×sp]
**M.* (*Chrysosarus*) *guaranitica* Schrottky [Paraguay]	*M.* (*Chrysosarus*) sp.	*M.* (*Chrysosarus*) [pse×sp]
M. (*Chrysosarus*) *parsonsiae* Schrottky [Argentina]	—	—
M. (*Chrysosarus*) *pseudanthidioides* Moure [Brazil]	—	—
**M.* (*Cressoniella*) *zapoteca* Cresson [Mexico]	*M.* (*Cressoniella*) *zapoteca*	*M.* (*Cressoniella*) *zapoteca*
M. (*Dasymegachile*) *schwimmeri* Engel [Argentina, Peru] (= *M. mitchelli* Raw, *nomen praeoccupatum*)	—	—
**M.* (*Dasymegachile*) *saulcyi* Guérin-Méneville [Chile]	*M.* (*Dasymegachile*) sp.	*M.* (*Dasymegachile*) [sau×sp]
**M.* (*Eumegachile*) *bombycina* Radoszkowski [Finland]	*M.* (*Eumegachile*) *bombycina*	*M.* (*Eumegachile*) *bombycina*
**M.* (*Eutricharaea*) *argentata* Fabricius [USA]	—	—
M. (*Eutricharaea*) *digiticauda* Cockerell [Zimbabwe]	—	—
M. (*Eutricharaea*) *eurymera* Smith [Kenya, Nigeria]	*M.* (*Eutricharaea*) *aff. eurymera*	*M.* (*Eutricharaea*) *eurymera*
M. (*Eutricharaea*) *femorata* Smith [India]	—	—
M. (*Eutricharaea*) *leachella* Curtis [Slovakia]	—	—
M. (*Eutricharaea*) *rotundata* Fabricius [USA]	*M.* (*Eutricharaea*) *rotundata*	*M.* (*Eutricharaea*) *rotundata*
M. (*Eutricharaea*) *submetallica* Benoist [Madagascar]	—	—
**M.* (*Grosapis*) *cockerelli* Rohwer [Mexico]	*M.* (*Grosapis*) *cockerelli*	*M.* (*Grosapis*) *cockerelli*
M. (*Leptorachis*) *crotalariae* Schwimmer [Brazil]	—	—
M. (*Leptorachis*) *laeta* Smith [Brazil]	—	—
**M.* (*Leptorachis*) *petulans* Cresson [USA]	*M.* (*Leptorachis*) *petulans*	*M.* (*Leptorachis*) *petulans*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
*M. (*Litomegachile*) *brevis* Say [USA]	M. (*Litomegachile*) *texana* Cresson	M. (*Litomegachile*) [bre×tex]
M. (*Litomegachile*) *gentilis* Cresson [USA]	—	—
*M. (*Megachile*) *centuncularis* Linnaeus [USA]	—	—
M. (*Megachile*) *montivaga* Cresson [USA]	—	—
M. (*Megachiloides*) *integra* Cresson [USA]	M. (Megachiloides) nevadensis Cresson	M. (*Megachiloides*) [int×nev]
*M. (*Megachiloides*) *oenotherae* Mitchell [USA]	—	—
M. (*Megachiloides*) *pascoensis* Mitchell [USA]	—	—
M. (*Melanosarus*) *nigripennis* Spinola [Brazil]	—	—
*M. (*Melanosarus*) *xylocopoides* Smith [USA]	M. (*Melanosarus*) sp.	M. (*Melanosarus*) [xyl×sp]
*M. (*Moureapis*) *anthidioides* Radoszkowski [Brazil]	—	—
M. (*Neochelynia*) *chichimeca* Cresson [Mexico]	M. (*Neochelynia*?) sp.	M. (*Neochelynia*) [chi×sp]
*M. (*Neochelynia*) *paulista* Schrottky [Brazil]	—	—
*M. (*Neocressoniella*) *carbonaria* Smith [India]	—	—
M. (*Paracella*) *curtula* Gerstaecker [Uganda]	—	—
*M. (*Paracella*) *semivenusta* Cockerell [Malawi]	M. (*Paracella*) sp.	M. (*Paracella*) [sem×sp]
*M. (*Platysta*) *platystoma* Pasteels [Congo]	—	—
M. (*Pseudocentron*) *poeyi* Guérin-Méneville [Cuba]	—	—
*M. (*Pseudocentron*) *pruina* Smith [USA]	M. (*Pseudocentron*) sp.	M. (*Pseudocentron*) [pru×sp]
*M. (*Ptilosaroides*) *neoxanthoptera* Cockerell [Panama]	—	—
M. (*Ptilosarus*) *microsoma* Cockerell [Trinidad and Tobago]	M. (*Ptilosarus*) *microsoma*	M. (*Ptilosarus*) *microsoma*
*M. (*Rhyssomegachile*) *simillima* Smith [Brazil]	—	—
M. (*Sayapis*) *planula* Vachal [Brazil, Paraguay]	—	—
*M. (*Sayapis*) *pugnata* Say [USA]	M. (*Sayapis*) *pugnata*	M. (*Sayapis*) *pugnata*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
**M.* (*Schrottkyapis*) *assumptionis* Schrottky [Brazil]	—	—
**M.* (*Stelodides*) *euzona* Pérez [Chile]	*M.* (*Steloides*) *euzona*	*M.* (*Steloides*) *euzona*
**M.* (*Trichurochile*) *thygaterella* Schrottky [Peru, Brazil]	—	—
**M.* (*Tylomegachile*) *orba* Schrottky [Mexico]	*M.* (*Tylomegachile*) sp.	*M.* (*Tylomegachile*) [orb×sp]
M. (*Tylomegachile*) *simplicipes* Friese [Mexico]	—	—
M. (*Xanthosarus*) *addenda* Cresson [USA]	—	—
M. (*Xanthosarus*) *fortis* Cresson [USA]	*M.* (*Xanthosarus*) *fortis*	*M.* (*Xanthosarus*) *fortis*
M. (*Xanthosarus*) *lagopoda* Linnaeus [Spain]	*M.* (*Xanthosarus*) *lagopoda*	*M.* (*Xanthosarus*) *lagopoda*
**M.* (*Xanthosarus*) *latimanus* Say [USA]	—	—
**M.* (*Zonomegachile*) *moderata* Smith [Brazil]	—	—
GROUP 2		
M. (*Alocanthedon*) *memecylonae* (Engel) [Malaysia]	*M.* (*Alocanthedon*) sp.	*M.* (*Alocanthedon*) [mem×sp]
**M.* (*Austrochile*) *resinifera* Meade-Waldo [Australia]	*M.* (*Austrochile*) sp.	*M.* (*Austrochile*) [res×sp]
M. (*Callomegachile*) *biseta* Vachal [Gabon]	—	—
M. (*Callomegachile*) *clotho* Smith [NE. Sulawesi]	—	—
M. (*Callomegachile*) *decemsignata* Radoszkowski [Uganda]	*M.* (*Callomegachile*) *decemsignata*	*M.* (*Callomegachile*) *decemsignata*
**M.* (*Callomegachile*) *mystaceana* Michener [Australia]	—	—
M. (*Callomegachile*) *sculpturalis* Smith [Japan, USA]	*M.* (*Callomegachile*) *sculpturalis*	*M.* (*Callomegachile*) *sculpturalis*
M. (*Callomegachile*) *torrida* Smith [Uganda]	—	—
**M.* (*Cesacongoa*) *quadraticauda* Pasteels [Congo]	*M.* (*Cesacongoa*) sp.	*M.* (*Cesacongoa*) [qua×sp]
**M.* (*Cestella*) *cestifera* Benoist [Madagascar]	—	—
M. (*Chalicodoma*) *asiatica* Morawitz [Turkey]	—	—
M. (*Chalicodoma*) *lefebvrei* Lepeletier [Greece, Italy]	*M.* (*Chalicodoma*) *lefebvrei*	*M.* (*Chalicodoma*) *lefebvrei*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
M. (*Chalicodoma*) *manicata* Giraud [Kazakhstan]	*M.* (*Chalicodoma*) *manicata*	*M.* (*Chalicodoma*) *manicata*
**M.* (*Chalicodoma*) *parietina* Geoffroy [Spain]	*M.* (*Chalicodoma*) *parietina*	*M.* (*Chalicodoma*) *parietina*
**M.* (*Chalicodomoides*) *aethiops* Smith [Australia]	*M.* (*Chalicodomoides*) *aethiops*	*M.* (*Chalicodomoides*) *aethiops*
*†*M.* (*Chalicodomopsis*) *glaesaria* Engel [Dominican Republic]		
**M.* (*Chelostomoda*) *spissula* Cockerell [China]	*M.* (*Chelostomoda*) sp.	*M.* (*Chelostomoda*) [spi×sp]
M. (*Chelostomoda*) *ulrica* Nurse [India]	—	—
M. (*Chelostomoides*) *campanulae* Robertson [USA]	*M.* (*Chelostomoides*) *angelarum* Cockerell	*M.* (*Chelostomoides*) [cam×ang]
M. (*Chelostomoides*) *georgica* Cresson [USA]	—	—
**M.* (*Chelostomoides*) *rugifrons* Smith [USA]	—	—
M. (*Chelostomoides*) *spinotulata* Mitchell [USA]	*M.* (*Chelostomoides*) spinotulata	*M.* (*Chelostomoides*) *spinotulata*
**M.* (*Gronoceras*) *bombiformis* Gerstaecker [Tanzania]	*M.* (*Gronoceras*) *bombiformis*	*M.* (*Gronoceras*) *bombiformis*
M. (*Gronoceras*) *cincta combusta* (Smith) [Tanzania]	—	—
M. (*Hackeriapis*) *ferox* Smith [Australia]	—	—
M. (*Hackeriapis*) *heriadiformis* Smith [Australia]	—	—
M. (*Hackeriapis*) *ignita* Smith [Australia]	—	—
**M.* (*Hackeriapis*) *rhodura* Cockerell [Australia]	*M.* (*Hackeriapis*) sp. 1	*M.* (*Hackeriapis*) [rho×sp]
**M.* (*Heriadopsis*) *striatulus* Cockerell [Zimbabwe]	*M.* (*Heriadopsis*) sp.	*M.* (*Heriadopsis*) [str×sp]
**M.* (*Largella*) *semivestita* Smith [C. Java]	*M.* (*Largella*) *floralis* (Fabricius)	*M.* (*Largella*) [sem×flo]
M. (*Lophanthedon*) *dimidiata* Smith [Malaysia]	*M.* (*Lophanthedon*) *dimidiata*	*M.* (*Lophanthedon*) *dimidiata*
**M.* (*Matangapis*) *alticola* Cameron [Borneo]	*M.* (*Matangapis*) *alticola*	*M.* (*Matangapis*) *alticola*
**M.* (*Maximegachile*) *maxillosa* Guérin-Méneville [Kenya, Natal, Tanzania]	*M.* (*Maximegachile*) *maxillosa*	*M.* (*Maximegachile*) *maxillosa*
**M.* (*Megella*) *malimbana* Strand [Zaire]	—	—
M. (*Megella*) *pseudomonticola* Hedicke [Japan]	*M.* (*Megella*) *pseudomonticola*	*M.* (*Megella*) *pseudomonticola*

Appendix 2. Continued.

Morphological analysis	Molecular analysis	Combined analysis
**M.* (*Mitchellapis*) *fabricator* Smith [Australia]	*M.* (*Mitchellapis*) *fabricator*	*M.* (*Mitchellapis*) *fabricator*
**M.* (*Parachalicodoma*) *incana* Friese [Egypt]	*M.* (*Parachalicodoma*) sp.	*M.* (*Parachalicodoma*) [inc×sp]
M. (*Pseudomegachile*) *albocincta* Radoszkowski [Egypt]	—	—
M. (*Pseudomegachile*) *armatipes* Friese [Natal]	*M.* (*Pseudomegachile*) *laminata* Friese	*M.* (*Pseudomegachile*) [arm×lam]
**M.* (*Pseudomegachile*) *ericetorum* Lepeletier [Spain]	*M.* (*Pseudomegachile*) *ericetorum*	*M.* (*Pseudomegachile*) *ericetorum*
M. (*Pseudomegachile*) *flavipes* Spinola [India]	—	—
M. (*Pseudomegachile*) *muansae* Friese [Tanzania]	*M.* (*Pseudomegachile*) *leucospilura* Cockerell	*M.* (*Pseudomegachile*) [mua×leu]
**M.* (*Rhodomegachile*) *abdominalis* Smith [Australia]	*M.* (*Rhodomegachile*) sp.	*M.* (*Rhodomegachile*) [abd×sp]
**M.* (*Schizomegachile*) *monstrosa* Smith [Australia]	—	—
**M.* (*Stenomegachile*) *chelostomoides* Gribodo [Zaire]	*M.* (*Stenomegachile*) *chelostomoides*	*M.* (*Stenomegachile*) *chelostomoides*
M. (*Stenomegachile*) *dolichosoma* Benoist [Madagascar]	—	—
**M.* (*Thaumatosoma*) *duboulaii* Smith [Australia]	*M.* (*Thaumatosoma*) *remeata* Cockerell	*M.* (*Thaumatosoma*) [dub×rem]
GROUP 3		
M. (*Creightonella*) *albisecta* Klug [Slovakia]	*M.* (*Creightonella*) *albisecta*	*M.* (*Creightonella*) *albisecta*
**M.* (*Creightonella*) *cognata* Smith [Uganda]	*M.* (*Creightonella*) *cornigera* Friese	*M.* (*Creightonella*) [cog×cor]

Appendix 3. Morphological data matrix used in the cladistics analysis of Megachilini. –, not applicable; ?, state of character that could not be recorded; *, $ multistate (see material and methods).

Characters 1–46

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                                  1   5    10   15   20   25   30   35   40   45
                                  |   |    |    |    |    |    |    |    |    |
Trichothurgus wagenknechti        1000100000-10010000000010-01010-00000010000000
Microthurge friesei               1100000000-10010100000011000010-00000010000000
Dioxys productus subruber         1100001001000000000100001200010-00000000000000
Trachusa (Ulanthidium) mitchelli  0111100010-10010100200101100000-10101131000000
Aztecanthidium tenochtitlanicum   0111000011010010000000001100000-10101030000000
Chelostoma rapunculi              0111011011000010100100000-00001100001010000000
Hoplitis (Dasyosmia) biscutellae  0111001010-10010100200001000000-10000010000001
Aspidosmia volkmanni              0111000010-10010100000001000000-00001020000000
Noteriades jenniferae             1111011011000010100110001100100-00101020000000
Radoszkowskiana rufiventris       1110001011100010100101001000010-00000010000000
C (Liothyrapis) decipiens         1111001010-00010100101001000001100000010000000
C (Rhinocoelioxys) zapoteca       1111001011000000100101001000000-00000010000000
C (Torridapis) torrida            1111002011100000100101001000000-00101031000000
M (Austrochile) resinifera        1111001010-00010100102000-00001110101030000001
M (Hackeriapis) rhodura           1111011010-10010000100001100010-10001020010001
M (Hackeriapis) ferox             1111011010-00010100100001100001110001020010001
M (Hackeriapis) heriadiformis     1111001010-10000000000011001010-00001010000001
M (Hackeriapis) ignita            1111001010-00000100100001200000-10101030000001
M (Heriadopsis) striatulus        1111011010-00010100100001100000-10101030000001
M (Rhodomegachile) abdominalis    1111001010-10000010001001100001110101020010001
M (Schizomegachile) monstrosa     0111002110-10100010000001001000-00001010010001
M (Stenomegachile) chelostomoides 0111001010-10100000002011011000-00001020010001
M (Stenomegachile) dolichosoma    0111011011110100010002011111001100001010010101
M (Thaumatosoma) duboulaii        0111000010-10000000000001101001000001000010001
M (Chalicodomoides) aethiops      1111001011110100100200010000111110011300000001
M (Matangapis) alticola           1111012010-00010100100101200001100000030000001
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Appendix 3. Continued.

Characters 1–46

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                                  1   5    10   15   20   25   30   35   40   45
                                  |   |    |    |    |    |    |    |    |    |
M (Chelostomoides) rugifrons      0111002010-1000001000011111000-00001010010011
M (Oligotropus) campanulae        1111001010-0001000010000110010-10001020010001
M (Gnathodon) georgica            1111001010-1001010010000110010-10001020010001
M (Chelostomoidella) spinotulata  1111001010-0001010010000110010111000102001000 1
M (Callomegachile) mystaceana     1111002110-10010100100000-00000-00101030000001
M (Callomegachile) sculpturalis   0111102110-1000000010001110100 0-00101010000001
M (Eumegachilana) clotho          0101102110-1010000000000110100 0-10101010010011
M (Carinula) torrida              1111001011100000100110001000000-10101030000001
M (Carinula) decemsignata         1111001011100000100110001100000-10101030000001
M (Morphella) biseta              1111002010-0000010010000100000 0-00101030000001
M (Alocanthedon) memecylonae      0110102011110010000000001100000-10101021000001
M (Cestella) cestifera            0111001010-0000010010000100000 0-10101010010101
M (Chalicodoma) parietina         1111101010-0000010020000110100 0-11011131000001
M (Euchalicodoma) asiatica        1111001010-0000010020000110001101111131000001
M (Allochalicodoma) lefebvrei     1111001010-0000010020000110000101101113100000 1
M (Katamegachile) manicata        1111001010-0000010020000110000111111113100000 1
M (Parachalicodoma) incana        1111001010-0000010020000110000 0-10000020000001
M (Gronoceras) bombiformis        1111101011100000100100001200001110101130000001
M (Digronoceras) cincta combusta  1111101011100000100100001200011110101130000001
M (Largella) semivestita          0101001010-0000010011000110000 0-10001130000001
M (Lophanthedon) dimidiata        1111002010-0001010011000120010101010103000000 1
M (Maximegachile) maxillosa       0111101111110100010000011001000-00001010000001
M (Pseudomegachile) ericetorum    0111001010-0000010010000110000 0-10001030000001
M (Archimegachile) flavipes       1111001010-00000100101000-00000-10001030000001
M (Neglectella) armatipes         1101001011110110000100001000100-10001030000001
M (Xenomegachile) albocincta      1111001010-0000010010000100000 0-10001030000001
M (Dinavis) muansae               ??1????010-??????????????????????0???????????
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Appendix 3. Continued.

Characters 1–46

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                                  1   5    10   15   20   25   30   35   40   45
                                  |   |    |    |    |    |    |    |    |    |
M (Cesacongoa) quadraticauda      1111001010-1001010010200100000-10001031000001
M (Chelostomoda) spissula parvula 1111001010-1001110010000100000-10001020000002
M (Chelostomoda) ulrica           1111011010-1001110010000100000-10001020000002
M (Creightonella) cognata         1111101010-1001010010000100000-10001020000002
M (Creightonella) albisecta       1111001010-1001010010000100000-10001020000002
M (Sayapis) pugnata               0110001010-1000001000001100100-10001020000002
M (Sayapis) planula               1110001010-0001010010000100000-10001020000002
M (Schrottkyapis) assumptionis    0110001010-1001010010200100000-00001020002001
M (Mitchellapis) fabricator       1111001010-1001010010000100000-10001020000002
M (Acentron) albitarsis           1111001010-0001010010200100000-10000121000003
M (Acentron) candida              1111001010-0001010010200100000-10000121000003
M (Leptorachis) petulans          1111001010-0000010010200100000-10100120000003
M (Leptorachina) laeta            1111001010-0000010110200100000-10100120000003
M (Leptorachis) crotalariae       1111000010-0000010010200100000-10100120000003
M (Melanosarus) xylocopoides      1111001010-1100010110200100000-10100120002003
M (Melanosarus) nigripennis       1111001010-1100010110000100000-10100120002003
M (Moureapis) anthidiodes         1111001010-0001010010200100000-10100120000003
M (Pseudocentron) pruina          1111000010-0000010010200100000-10100120000003
M (Pseudocentron) poeyi           1111000010-0000010010200100000-10100120000003
M (Chrysosarus) guaranitica       1111001010-0000010010200100000-10000020001002
M (Chrysosarus) pseudanthidiodes  1111101010-0001010010000100000-10000020001002
M (Dactylomegachile) parsonsiae   1111001010-0000010010200100010-10100020002002
M (Stelodides) euzona             1111001010-0001010010000100000-10001020002002
M (Zonomegachile) moderata        1111101010-0001010010000100010-10010120000003
M (Amegachile) bituberculata      1111001011100000101102001000011110100120000003
M (Callochile) ustulatiformis     1111001010-0000010110200100001111000120000003
M (Paracella) semivenusta         1111001010-0001010010200100000101001012000 1003
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Appendix 3. Continued.

Characters 1–46

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                                  1   5    10   15   20   25   30   35   40   45
                                  |   |    |    |    |    |    |    |    |    |
M (Paracella) curtula             1111001010-0000010010200100000-10110120001003
M (Neocressoniella) carbonaria    0111001011100000100102001000010-10111120100003
M (Aethomegachile) laticeps       1111001010-0000010010200100001-0-10001120001003
M (Aethomegachile) trichorhytisma ???1???010-??????????0?????????????????????????
M (Megella) malimbana             1111101011100000100100001000000-10110120101003
M (Megella) pseudomonticola       1111101011100000100100001000010-10100120100003
M (Austromegachile) montezuma     1111001010-0001010110200100000-10110120002003
M (Holcomegachile) exaltata       1111002011100010101102001000000-10110120002003
M (Cressoniella) zapoteca         1111001010-0001010010200100000-10110120002003
M (Dasymegachile) saulcyi         1101001010-0001010010200100000-10010120002003
M (Chaetochile) schwimmeri        1101001010-0001010010010100001-0-10110120001003
M (Neochelynia) paulista          1111001010-0001010010200100001-0-10010120001003
M (Neomegachile) chichimeca       1111001010-0001010010200100001-0-10010120001003
M (Ptilosaroides) neoxanthoptera  1111001010-0001010010000100001-0-10010120001003
M (Ptilosarus) microsoma          1111001011000010100100001000010-10010120001003
M (Rhyssomegachile) simillima     1111001011000010100100001000000-10010120002002
M (Trichurochile) thygaterella    1111001010-0001010010200100000-10110120001003
M (Eumegachile) bombycina         1110101010-1000010000200100000-00001120000002
M (Grosapis) cockerelli           0111101010-1001010000000100100-10011020001002
M (Argyropile) parallela          1111001010-0000010010200100000111000012100000 3
M (Argyropile) sabinensis         1111001010-0000010010200100000111000012100000 3
M (Megachiloides) oenotherae      1111001010-0001010010200100000-10000111000003
M (Xeromegachile) integra         1111001010-0001010010200100001-0-10000121000003
M (Derotropis) pascoensis         1111001010-0001010010000100000-10000110000003
M (Xanthosarus) latimanus         1101101010-0000010010200100001-0-10100121002003
M (Addendella) addenda            1111001010-1000010010200100001-0-10000121000003
M (Macromegachile) lagopoda       1111001010-0000010010200100001111010012100200 3
```

Appendix 3. Continued.

Characters 1–46

```
                                1   5    10   15   20   25   30   35   40   45
                                |   |    |    |    |    |    |    |    |    |
M (Phaenosarus) fortis          1111001010-1000010010200100001101000012100 2003
M (Eutricharaea) argentata      1111001010-0000010010200100000-10010120000003
M (Perezia) leachella           1111001011100000100102001000000-10010120000003
M (Eurymella) eurymera          1111001011100000100102001000000-10000120000003
M (Eurymella) submetallica      1111001011100000100102001000000-10000120000003
M (Digitella) digiticauda       1111001010-0001010010200100???-10000120000003
M (Platysta) platystoma         1111001010-0000010010200100???-10000120000003
M (Neoeutricharaea) rotundata   1111001010-0000010010200100000-10010120000003
M (Litomegachile) brevis        1111001010-0000010010200100000-10010020000003
M (Litomegachile) gentilis      1111001010-0000010010200100010-10010020000003
M (Megachile) centuncularis     1111001010-0000010010200100000-10010020001003
M (Cyphopyga) montivaga         1111001010-1000010010000100000111001002000 1002
M (Tylomegachile) orba          1111001010-0000010010200100010-10110120002003
M (Tylomegachile) simplicipes   1111001010-0000010010000100010-10110120002003
M (Chalicodomopsis) glaesaria   0??1??1010-1???000000001 1?01????000??02000000?
```

Appendix 3. Continued.

Characters 47–92

```
                                47  51   56   61   66   71   76   81   86   91
                                |   |    |    |    |    |    |    |    |    |
Trichothurgus wagenknechti      0------000-0010001000101100000000000000001010
Microthurge friesei             0------000-0000001000001100000010100200001010
Dioxys productus subruber       -------0011000111010000-0112101010120101110 10
Trachusa (Ulanthidium) mitchelli 0---0--1010100211011000100100000000000100 00
Aztecanthidium tenochtitlanicum 0---0--0010000211011011110111100110020100 0111
Chelostoma rapunculi            0------0011100100011000000100001010020101110 10
Hoplitis (Dasyosmia) biscutellae 0------1011010110011010110100000000100101110 10
Aspidosmia volkmanni            0---0--1011010201011010110000000000100000110 10
Noteriades jenniferae           0---0--1010000211011000 1-0101100010021101111 10
Radoszkowskiana rufiventris     0------1010100211011000010122001010120011111 10
C (Liothyrapis) decipiens       0------0010100211011000000121101010020011011 10
C (Rhinocoelioxys) zapoteca     0------000-0002110110000000122101010121021111 10
C (Torridapis) torrida          0---0--1010000011011000010122111010001021011 10
M (Austrochile) resinifera      0---0--1010010211011001110121000020000000211 10
M (Hackeriapis) rhodura         0---0--1010000210011100010122001010020000210 10
M (Hackeriapis) ferox           0---0--100-0102100111011101200010200000002101 0
M (Hackeriapis) heriadiformis   0------1011000211011001110120001020000000210 10
M (Hackeriapis) ignita          0---0--1010100211011001110120000020000000211 10
M (Heriadopsis) striatulus      0---0--1010010211011000010120001010020000210 10
M (Rhodomegachile) abdominalis  0---0--1010000210011100010122000020120000211 10
M (Schizomegachile) monstrosa   0------1011110210011101000112001011010000110 10
M (Stenomegachile) chelostomoides 0---0--1011100211011001110112001011000000110 10
M (Stenomegachile) dolichosoma  0------1011100211011001110122001010020000210 10
M (Thaumatosoma) duboulaii      -------1011110211011001110120001020000000210 10
M (Chalicodomoides) aethiops    0---0--1011100211011001110121000010000000211 10
M (Matangapis) alticola         0---0--1010010211011001010120000010020000211 10
M (Chelostomoides) rugifrons    0------1010100211011001110131001011021000210 10
```

Appendix 3. Continued.

Characters 47–92

	47 51 56 61 66 71 76 81 86 91
M (*Oligotropus*) *campanulae*	0---0--10100102110110011101200010100200021010
M (*Gnathodon*) *georgica*	0---0--10100102110110011101200000100210021010
M (*Chelostomoidella*) *spinotulata*	0---0--10100102110110011101210000110010021010
M (*Callomegachile*) *mystaceana*	0---0--10100102110110011111100100200100021100
M (*Callomegachile*) *sculpturalis*	0------10101102110110011101100100200200021100
M (*Eumegachilana*) *clotho*	0------10101102110110011111300000300000021100
M (*Carinula*) *torrida*	0---0--10100102110110011101200100400100020100
M (*Carinula*) *decemsignata*	0---0--10100102110110011111200100400100020100
M (*Morphella*) *biseta*	0---0--10101002110110011101200100100100021100
M (*Alocanthedon*) *memecylonae*	0---0--1010110211011001?1?111001001000021100
M (*Cestella*) *cestifera*	0------10111002110110011101110002000000000000
M (*Chalicodoma*) *parietina*	0---0--10110102110110010001200000000000021000
M (*Euchalicodoma*) *asiatica*	0---0--10110102110110011101200000000000021000
M (*Allochalicodoma*) *lefebvrei*	0---0--10110102110110011101200000000000021000
M (*Katamegachile*) *manicata*	0---0--10110102110110011101200000000000021000
M (*Parachalicodoma*) *incana*	0---0--10110102110110011101200000000000000100
M (*Gronoceras*) *bombiformis*	0---0--10100100110110011111201000200100000110
M (*Digronoceras*) *cincta combusta*	0---0--10100100110110011111201000200100000110
M (*Largella*) *semivestita*	0---0--10111002110110011101210000200000000110
M (*Lophanthedon*) *dimidiata*	0---0--10101102110110011101210000200100000110
M (*Maximegachile*) *maxillosa*	0------10110102110110011101110010200000021000
M (*Pseudomegachile*) *ericetorum*	0---0--10111002110110011101210000200200020000
M (*Archimegachile*) *flavipes*	0---0--10111002110110010101210000200200001000
M (*Neglectella*) *armatipes*	0---0--10111102110110011101110002002000000010
M (*Xenomegachile*) *albocincta*	0---0--10111002110110011101200000200200001000
M (*Dinavis*) *muansae*	????????????0???????001001?100?0??0?000?????0
M (*Cesacongoa*) *quadraticauda*	0---0--10100002110110011101200000200000000010

Appendix 3. Continued.

Characters 47–92

```
                                47  51   56   61   66   71   76   81   86   91
                                |   |    |    |    |    |    |    |    |    |
M (Chelostomoda) spissula parvula 10100--10100102100110000101210010100200002101 0
M (Chelostomoda) ulrica           10100--10100102100110000101210010100200002101 0
M (Creightonella) cognata         1010101100-01021101100101012000002002000000001
M (Creightonella) albisecta       1010101100-01021101100001012100002002000000001
M (Sayapis) pugnata               10100--10110102110110001101200000200000000001
M (Sayapis) planula               10100--10100102110110000101200000100000000011
M (Schrottkyapis) assumptionis    0---0--100-11021101100001012100002000100000001
M (Mitchellapis) fabricator       10100--10100102110110000101200000200000000101
M (Acentron) albitarsis           0---110100-01021101100000012000003000100020101
M (Acentron) candida              0---110100-01021101100000012000003000100020101
M (Leptorachis) petulans          0---110100-01021101100011012000002000100020111
M (Leptorachina) laeta            1010110100-01021101100011012000002000100020101
M (Leptorachis) crotalariae       1010110100-010????1?000?????000002000100020101
M (Melanosarus) xylocopoides      10100--110-01021101100001012000002000000000101
M (Melanosarus) nigripennis       10100--110-01021101100001012000002000000020101
M (Moureapis) anthidiodes         1010110110-01021101100000012000002000000020101
M (Pseudocentron) pruina          1010110110-01021101100000012000002000000020101
M (Pseudocentron) poeyi           1010110110-01021101100000012000002100100020101
M (Chrysosarus) guaranitica       0---0--110-01021101100001012000002000000020001
M (Chrysosarus) pseudanthidiodes  0---0--110-01021101100001012000002000000020001
M (Dactylomegachile) parsonsiae   0---0--110-01021101100001012000002000000020001
M (Stelodides) euzona             0---0--110-01021101100001012000002000000020001
M (Zonomegachile) moderata        1010110110-01021101100001012000002000000020001
M (Amegachile) bituberculata      1111110100-01021101100011012000002000000000101
M (Callochile) ustulatiformis     1111110100-01021101100001012000002000000000101
M (Paracella) semivenusta         101011*110-01021101100000012000003000000000001
M (Paracella) curtula             1010111110-01021101100011012000003000000000001
```

Appendix 3. Continued.

Characters 47–92

```
                                47  51   56   61   66   71   76   81   86   91
                                |   |    |    |    |    |    |    |    |    |
M (Neocressoniella) carbonaria  1010110100-0102110110000101200000200000000101
M (Aethomegachile) laticeps     1010110100-0102110110000101200000200000000101
M (Aethomegachile) trichorhytisma ??????????????????????????????????????000?0??1
M (Megella) malimbana           1010110100-0102110110000101200000200000020101
M (Megella) pseudomonticola     1010110100-0102110110010101200000200000000001
M (Austromegachile) montezuma   1010110100-0102110110001101200000200000020111
M (Holcomegachile) exaltata     1010110100-0102110110001101200000200100020111
M (Cressoniella) zapoteca       1010110110-0102110110001101200000200000020001
M (Dasymegachile) saulcyi       1010110110-0102110110001101200000000000020101
M (Chaetochile) schwimmeri      1010110110-0002110110000101200000200000020001
M (Neochelynia) paulista        1110110110-0102110110001101200000100100020001
M (Neomegachile) chichimeca     1110110110-0102110110001101200000100100020001
M (Ptilosaroides) neoxanthoptera 1010110110-0102110110000101200000400100020001
M (Ptilosarus) microsoma        1110110110-0102110110000101200000400000020011
M (Rhyssomegachile) simillima   1010110110-0102110110000001200000100000020011
M (Trichurochile) thygaterella  1110110110-0102110110000101200000000000020101
M (Eumegachile) bombycina       10100--1011010211011000110120000020000000020011
M (Grosapis) cockerelli         1010101101101021101100001012000002000000020011
M (Argyropile) parallela        1110110100-0102110110000101200000200100000001
M (Argyropile) sabinensis       1110110100-0102110110000101200000200100000001
M (Megachiloides) oenotherae    1100---1010010201011000110120000020000000000111
M (Xeromegachile) integra       0---110100-0102110110000001200000200100000011
M (Derotropis) pascoensis       1100---100-0002110110000001200000200000000001
M (Xanthosarus) latimanus       0---110100-0102110110000001200000200000020111
M (Addendella) addenda          0---110100-0102110110000101200000200000000101
M (Macromegachile) lagopoda     1010110100-0102110110000101200000200000000101
M (Phaenosarus) fortis          0---110100-0102110110000001200000200000000001
```

Appendix 3. Continued.

Characters 47–92

```
                                47  51   56   61   66   71   76   81   86   91
                                |   |    |    |    |    |    |    |    |    |
M (Eutricharaea) argentata      0---110110-0002110110000101200000200010000000 1
M (Perezia) leachella           0---110110-0002110110000101200000200010000000 1
M (Eurymella) eurymera          0---110100-0102110110001101200000200000000010 1
M (Eurymella) submetallica      0---110100-0102110110000101200000200000000010 1
M (Digitella) digiticauda       0---110100-0102110110000101200000200010000010 1
M (Platysta) platystoma         0---110100-1102110110001101200000200000000010 1
M (Neoeutricharaea) rotundata   1010110110-0102110110000101200000200000000010 1
M (Litomegachile) brevis        1010110110-0102110110000001200000200010000011 1
M (Litomegachile) gentilis      1010110110-0102110110000001200000200010002011 1
M (Megachile) centuncularis     10100--110-0102110110000101200000200000002011 1
M (Cyphopyga) montivaga         0---0--110-0102110110001101200000200000002000 1
M (Tylomegachile) orba          1010110110-0102110110001101200000200000000010 1
M (Tylomegachile) simplicipes   1010110110-0102110110000101200000200010000010 1
M (Chalicodomopsis) glaesaria   0---0--?????????????????????0000?0?2000???10?
```

Appendix 3. Continued.

Characters 93–138

	93 97 102 107 112 117 122 127 132 137
Trichothurgus wagenknechti	0000001000-0010010000-0100000100000000-00000000
Microthurge friesei	0001001000-0000010100-0000001100000000-00000000
Dioxys productus subruber	0111010010-000-0001010011010002110000-10101000
Trachusa (*Ulanthidium*) *mitchelli*	0000000000-0000011101000111000011000-00111000
Aztecanthidium tenochtitlanicum	0000000000-0000010101011111001011000-01101000
Chelostoma rapunculi	1011000010-0000010001010100010001000111010100
Hoplitis (*Dasyosmia*) *biscutellae*	1011000010-0000010001010000000010100-00101000
Aspidosmia volkmanni	1011100010-0001110101011100001001000-00100000
Noteriades jenniferae	0010100110-0000010001011000011021010-10101110
Radoszkowskiana rufiventris	0011110110-000-0000010010000012110100-10101000
C (*Liothyrapis*) *decipiens*	0010100110-000-0100010000000012110001010101010
C (*Rhinocoelioxys*) *zapoteca*	0010110110-000-0000010000000112110001011101010
C (*Torridapis*) *torrida*	0000100110-000-0100011000000112110001011101010
M (*Austrochile*) *resinifera*	0010100110-0000200001000000011011010110111100
M (*Hackeriapis*) *rhodura*	1011100110-0000010011000000011011010111111000
M (*Hackeriapis*) *ferox*	1011100110-0000010011000000011011010111111000
M (*Hackeriapis*) *heriadiformis*	1011100110-0000011001000000011011010111011000
M (*Hackeriapis*) *ignita*	0010100110-0000210001000000011011010111011000
M (*Heriadopsis*) *striatulus*	1011100110-0000211001010000011011000111101010
M (*Rhodomegachile*) *abdominalis*	0010100110-0000010011000010011011000-00101001
M (*Schizomegachile*) *monstrosa*	0011100110-0000010001101000101011100110110100
M (*Stenomegachile*) *chelostomoides*	1011100110-0000010001000000011011010111101101
M (*Stenomegachile*) *dolichosoma*	1011100110-0000010001000000011011010111101010
M (*Thaumatosoma*) *duboulaii*	1011100110-0000010001000000011011010110011000
M (*Chalicodomoides*) *aethiops*	0010100110-0000010011000000001011000110110100
M (*Matangapis*) *alticola*	0010100110-0000011001010000011011000-00101000
M (*Chelostomoides*) *rugifrons*	1011100110-0000010001000000011011000111101201

Appendix 3. Continued.

Characters 93–138

```
                                93  97   102  107  112  117  122  127  132  137
                                |   |    |    |    |    |    |    |    |    |
M (Oligotropus) campanulae      1011100110-0000110001001000001011010111110120 1
M (Gnathodon) georgica          0010100110-0000110001000000001011010111110120 0
M (Chelostomoidella) spinotulata 1011100110-0000010001000000011011010111110120 0
M (Callomegachile) mystaceana   0010100110-0000010001001000001011010110110100 0
M (Callomegachile) sculpturalis 0010100110-0000010001001000001011110110110100 0
M (Eumegachilana) clotho        0010100110-0000011001001000001011010-01101000
M (Carinula) torrida            0010100110-0000211001000000101011010-01101000
M (Carinula) decemsignata       0010100110-0000201001000000101011000-01101000
M (Morphella) biseta            0010100111000000100010010000110110100-00101000
M (Alocanthedon) memecylonae    0010100110-0000010001101000001011000110010100 0
M (Cestella) cestifera          0010100110-0000000001001000101011110110110110 1
M (Chalicodoma) parietina       0010100110-0000010001001000001011010110010100 0
M (Euchalicodoma) asiatica      1011100110-0000110001000000001011010110010100 0
M (Allochalicodoma) lefebvrei   0010100110-0000011001001000001011010110010100 0
M (Katamegachile) manicata      0010100110-0000010001001000011011010110010100 0
M (Parachalicodoma) incana      0010100100-0000011001001000001011000110010100 0
M (Gronoceras) bombiformis      0010100110-1000010001000000001011010-00101000
M (Digronoceras) cincta combusta 0010100110-1000010001000000001011010-00101000
M (Largella) semivestita        0010100110-0100200001001000001011010110010100 0
M (Lophanthedon) dimidiata      0010110110-0000000001000000001011000-00100000
M (Maximegachile) maxillosa     1011100110-0000010001101000101011110110110100 0
M (Pseudomegachile) ericetorum  0011100110-0100010001001000001011010111110100 0
M (Archimegachile) flavipes     0011110110-0100010001001000101011010111110101 0
M (Neglectella) armatipes       0011100110-0000211001000000001011100111110110 0
M (Xenomegachile) albocincta    0011110100-0000011001001000001011110-01101000
M (Dinavis) muansae             ?01?10011????00???001001000001 0?1??0????1?????
M (Cesacongoa) quadraticauda    0010100110-0000010001001000001011010-00101000
```

Appendix 3. Continued.

Characters 93–138

```
                                  93  97   102  107  112  117  122  127  132  137
                                  |   |    |    |    |    |    |    |    |    |
M (Chelostomoda) spissula parvula 0011100110-0000011001000000011011010111110 1100
M (Chelostomoda) ulrica           0011100110-0000011001000000011011000111110 1100
M (Creightonella) cognata         0010100101100000100 00-0100000101101011011010 00
M (Creightonella) albisecta       0010100101100000100 00-0100000101101011111010 00
M (Sayapis) pugnata               1011100110-0000010011001000011011010111110 1100
M (Sayapis) planula               0011100110-0000011001001000011111010110110 1001
M (Schrottkyapis) assumptionis    1011100110-0000010001000000000101101011111010 00
M (Mitchellapis) fabricator       0010100110-0000010011001000101011110 0-01101001
M (Acentron) albitarsis           0010100101100000110011000000111110101110101010
M (Acentron) candida              0010100101100000110011000000111110101110101010
M (Leptorachis) petulans          0010100101100002110011000000111110101110101000
M (Leptorachina) laeta            0010100101100000110011000000111110 100-11101000
M (Leptorachis) crotalariae       0010100101100000111001100000011111010111010 1010
M (Melanosarus) xylocopoides      0010100101100000110011000000111110000-01101010
M (Melanosarus) nigripennis       0010100101100000110011000000111110000-00101010
M (Moureapis) anthidiodes         0010100101100000110011000000111110 100-01101010
M (Pseudocentron) pruina          0010100101100000110011010000111110101111101000
M (Pseudocentron) poeyi           0010110101100000100011000000011110101111101000
M (Chrysosarus) guaranitica       0010100101100000110011000000111110 100-00101000
M (Chrysosarus) pseudanthidiodes  0010100101100000110011000000101110 100-00101000
M (Dactylomegachile) parsonsiae   0010100101100000110011000000111110101100101000
M (Stelodides) euzona             0010110101100000110011000000110110101100101000
M (Zonomegachile) moderata        0010100101100000110011000000111110 100-10101000
M (Amegachile) bituberculata      0010100101100002110011000001011111100-01101000
M (Callochile) ustulatiformis     0010100101100002110011000000011110 100-01101010
M (Paracella) semivenusta         0010100101100002110010000000011110001101101000
M (Paracella) curtula             0010100101100002110010000000011110101111101000
```

Appendix 3. Continued.

Characters 93–138

```
                                93  97   102  107  112  117  122  127  132  137
                                |   |    |    |    |    |    |    |    |    |
M (Neocressoniella) carbonaria  00101001011000021100100000000010110100-01101000
M (Aethomegachile) laticeps     00101001011000011100110000000011111000-01101000
M (Aethomegachile) trichorhytisma ?01?10010????00????????0?0???????1???????1?????
M (Megella) malimbana           00101001011000021100110000011101101101101101000
M (Megella) pseudomonticola     00111001011000021100100000010101111101101101000
M (Austromegachile) montezuma   00101101011000000110011000000111110000-10101000
M (Holcomegachile) exaltata     00101101011000021100110000000111110000-10101010
M (Cressoniella) zapoteca       00101001011000011100110000000111110101100101000
M (Dasymegachile) saulcyi       00101001011000011100110000000111110101100101000
M (Chaetochile) schwimmeri      00101001011000011100110000000011110000-00101000
M (Neochelynia) paulista        10111001011000001100110000000111110001101101000
M (Neomegachile) chichimeca     10111001011000021100110000000111110101100101000
M (Ptilosaroides) neoxanthoptera 00111001011000001100110000002111110000-00111000
M (Ptilosarus) microsoma        00111001011000001100110000002111110000-10111000
M (Rhyssomegachile) simillima   00111001011000001100110000000101110000-10101000
M (Trichurochile) thygaterella  00101001011000011100110000000111110101100101000
M (Eumegachile) bombycina       00111001011000001000110000000111101101101101000
M (Grosapis) cockerelli         00101001011000001000110100000110110101101101000
M (Argyropile) parallela        00101001011000001100110000000111101011111101010
M (Argyropile) sabinensis       00101001011000001100110000000111110101111101010
M (Megachiloides) oenotherae    00101001011000001000100000000111110101111101010
M (Xeromegachile) integra       00101001011000021100100000000111110101111101000
M (Derotropis) pascoensis       00101001011000001100100000000111110101111101000
M (Xanthosarus) latimanus       00101001011000011100110000000111101101101101000
M (Addendella) addenda          00101001011000011100110000000111101011111101000
M (Macromegachile) lagopoda     00101001011000001100110100000111110101101101000
M (Phaenosarus) fortis          00101001011000001100110000000111110101111101000
```

Appendix 3. Continued.

Characters 93–138

```
                                93  97   102  107  112  117  122  127  132  137
                                |   |    |    |    |    |    |    |    |    |
M (Eutricharaea) argentata      0010100101100000$1100110000000011110111101101000
M (Perezia) leachella           0010100101100000111001100000000111101111101101000
M (Eurymella) eurymera          0010100101100000111001001000000111101011101101000
M (Eurymella) submetallica      0010100101100000111001000000000111100011111101000
M (Digitella) digiticauda       0010100101100000111001100000000111100000-11101000
M (Platysta) platystoma         0010100101100000011001001000000111100000-01101000
M (Neoeutricharaea) rotundata   0010100101100000111001100000000111100111101101000
M (Litomegachile) brevis        0010100101100000011001100000000111101011110101000
M (Litomegachile) gentilis      0010100101100000011001100000000111101011111101000
M (Megachile) centuncularis     0010100101100000010001100000000111101011111101000
M (Cyphopyga) montivaga         0010100101100002100011000000000111101011111101010
M (Tylomegachile) orba          0010100101100002110011000000000111100000-01101000
M (Tylomegachile) simplicipes   0010100101100002110011000000000111100000-01101000
M (Chalicodomopsis) glaesaria   00???00??????000??01??00?110??0?10??110?101200
```

Appendix 3. Continued.

Characters 139–184

```
                                 139 143  148  153  158  163  168  173  178  183
                                 |   |    |    |    |    |    |    |    |    |
Trichothurgus wagenknechti       0000-00000000010100000-01000000000100-00--00000
Microthurge friesei              00011000000000010200000-01000000000100-00--00000
Dioxys productus subruber        010--0101000000020000-10000010000000-00--00000
Trachusa (Ulanthidium) mitchelli 0000-0001000001020000-11100100000100-00--00000
Aztecanthidium tenochtitlanicum  0000-0001000001020010-10100110000100-00--00000
Chelostoma rapunculi             0000-0001000000020000-01010010000100-00--00000
Hoplitis (Dasyosmia) biscutellae 0000-0001000000010000-01011010000000-00--00000
Aspidosmia volkmanni             0000-0000000000020000-00000100000200-00--00000
Noteriades jenniferae            1000-0001000000020000-01010020000000-00--00000
Radoszkowskiana rufiventris      010--1101000000110000-01011010010100-00--00000
C (Liothyrapis) decipiens        010--1101000000010000-01001010010100-010100000
C (Rhinocoelioxys) zapoteca      010--100100002102-000-01001010010100-010100000
C (Torridapis) torrida           010--100100002101-000-01000010000000-00--00000
M (Austrochile) resinifera       0010-0000000000010000-01011020010200-010101000
M (Hackeriapis) rhodura          0000-0001000001110000-01001020000110-00--00000
M (Hackeriapis) ferox            0000-0000000000010000-0100102011011101120100000
M (Hackeriapis) heriadiformis    0000-0001000001010000-01001020000010-010100000
M (Hackeriapis) ignita           0010-0000000000020000-01011010000110-010100000
M (Heriadopsis) striatulus       0000-0001000001010000-0101102000010120120000000
M (Rhodomegachile) abdominalis   0000-0000000000020000-01001020000100-00--00000
M (Schizomegachile) monstrosa    0010-0000000000010000-0101102010000130121000000
M (Stenomegachile) chelostomoides 0000-0101000001010000-01011020110200-00--00000
M (Stenomegachile) dolichosoma   0000-0001000001020000-01011020000100-00--00000
M (Thaumatosoma) duboulaii       0010-0000000001020000-01011010100100-00--00000
M (Chalicodomoides) aethiops     0000-0001000000010100-01011020000110-00--00000
M (Matangapis) alticola          0000-0000000000010010-01012020000100-00--00000
M (Chelostomoides) rugifrons     0000-0000000001010000-01001020000110-00--00000
```

Appendix 3. Continued.

Characters 139–184

```
                                  139 143  148  153  158  163  168  173  178  183
                                  |   |    |    |    |    |    |    |    |    |
M (Oligotropus) campanulae        0000-0000000000010000-0101002001010100101000000
M (Gnathodon) georgica            0000-0001000001010000-0101102001011100101000000
M (Chelostomoidella) spinotulata  0000-0000000001010000-0101102001010100121100000
M (Callomegachile) mystaceana     0000-0000000000010010-0101202001010-010100000
M (Callomegachile) sculpturalis   0000-0000000000010010-0101202001010110101000000
M (Eumegachilana) clotho          0000-0101000000010000-0101202001020100101000000
M (Carinula) torrida              0000-0000000000010000-0101002000020-00--00000
M (Carinula) decemsignata         0000-0000000000010000-0101002000020-00--00000
M (Morphella) biseta              0000-0000000000010000-0101202001010120121000000
M (Alocanthedon) memecylonae      0000-0001000000010000-0101202001010100100100000
M (Cestella) cestifera            0000-0001000000010000-0101202000010-00--00000
M (Chalicodoma) parietina         0000-0001000001020000-0101101000030-00--00000
M (Euchalicodoma) asiatica        0000-0001000001020000-0101101001010-012111000
M (Allochalicodoma) lefebvrei     0000-0000000001020000-0101101000030-00--00000
M (Katamegachile) manicata        0000-0001000001020100-0101101001030-012110000
M (Parachalicodoma) incana        0000-0000000000020000-0101101000010-00--00000
M (Gronoceras) bombiformis        0000-0001001000020000-0101201101030120121100 11
M (Digronoceras) cincta combusta  0000-0001001000020000-0101201101111012011010000
M (Largella) semivestita          0000-0001000000010000-0101101000030-010100000
M (Lophanthedon) dimidiata        0000-0001000000010000-0101102000030-00--00000
M (Maximegachile) maxillosa       0000-0001000001110000-0101202000010130 0--00000
M (Pseudomegachile) ericetorum    0000-0001000000010010-0101102000010-010100000
M (Archimegachile) flavipes       0001000000000000010000-0101102000010-010100000
M (Neglectella) armatipes         0000-0001000000010000-0101102001110 0-112010000
M (Xenomegachile) albocincta      0000-0000000000010010-0101101001020120120000000
M (Dinavis) muansae               ??????????????????????????1020010101301210 0000
M (Cesacongoa) quadraticauda      0000-00????????0010000-0101102001010 0-010100000
```

Appendix 3. Continued.

Characters 139–184

```
                                  139 143  148  153  158  163  168  173  178  183
                                  |   |    |    |    |    |    |    |    |    |
M (Chelostomoda) spissula parvula 0001000101000110100 00-01012020000100-010100000
M (Chelostomoda) ulrica           0001000101000110100 00-01012020000100-010100000
M (Creightonella) cognata         0000-0011000010010001001001010000101211 0100000
M (Creightonella) albisecta       0000-0011000010010011001011010010101211 0101000
M (Sayapis) pugnata               0000-0010100111100010-0101101011010110121110 01
M (Sayapis) planula               0001010101001100000 10-0101202001010100121110 00
M (Schrottkyapis) assumptionis    0001000101001100000 10-0101201001030 0-010100000
M (Mitchellapis) fabricator       0001000101000100000 10-0101102001010130121000 00
M (Acentron) albitarsis           0000-0000000000011011001011010111201111101111 1
M (Acentron) candida              0000-0000000000011011001011010111201111101111 1
M (Leptorachis) petulans          0000-0000000000011011001011020000111101010000 0
M (Leptorachina) laeta            0000-0000000000011011001011010011201011101111 1
M (Leptorachis) crotalariae       0000-00????????00?10110?1??10100001?11012110000
M (Melanosarus) xylocopoides      0000-0000000000011011001011020111201011200101 1
M (Melanosarus) nigripennis       0000-0000000000011011001011020111201011200101 1
M (Moureapis) anthidiodes         0000-0000000000011011001011020010211101010001 0
M (Pseudocentron) pruina          0000-0000000000011011001011010010211011201001 1
M (Pseudocentron) poeyi           0000-0000000000011011001011010010211011201001 1
M (Chrysosarus) guaranitica       0000-0000000000010010-0101102000010 0-010100000
M (Chrysosarus) pseudanthidiodes  0000-0000000000010010-0101002000010 0-010100000
M (Dactylomegachile) parsonsiae   0000-0000000000010010-0101102000010 14010111000
M (Stelodides) euzona             0000-0000000000010010-0101101001010 14012111000
M (Zonomegachile) moderata        0000-0000000000010010-0101102001010 0-012100000
M (Amegachile) bituberculata      0000-0101000000010010-0101101001011 10012000000
M (Callochile) ustulatiformis     0000-0001000000010010-0101101001021 10012010000
M (Paracella) semivenusta         0001000000100000 10010-0101101000021 0-010100000
M (Paracella) curtula             0000-0000000000010010-0101102000021 0-010100000
```

Appendix 3. Continued.

Characters 139–184

```
                                  139 143  148  153  158  163  168  173  178  183
                                  |   |    |    |    |    |    |    |    |    |
M (Neocressoniella) carbonaria    0000-0101000000010010-01011020000200-00--00000
M (Aethomegachile) laticeps       0000-0101000000010010-01011020000200-00--00000
M (Aethomegachile) trichorhytisma ?0??????????????????????????1020100200-00--00000
M (Megella) malimbana             0000-0101000000010010-01011020000100-00--00000
M (Megella) pseudomonticola       0000-0000000000010010-01011020000100-00--00000
M (Austromegachile) montezuma     0001000000000000010010-01011020000110-00--00001
M (Holcomegachile) exaltata       0001000000000000010010-01011020000100-00--00000
M (Cressoniella) zapoteca         0000-0000000000010010-01011020000210-00--00000
M (Dasymegachile) saulcyi         0000-0000000000010010-01011010000110-00--00000
M (Chaetochile) schwimmeri        0000-0000000000010010-01011010000100-00--00000
M (Neochelynia) paulista          0000-0100000000010010-01011020000100-00--00000
M (Neomegachile) chichimeca       0000-0100000000010010-01011020000200-010100000
M (Ptilosaroides) neoxanthoptera  0000-0000000000010010-01012020000200-010100000
M (Ptilosarus) microsoma          0000-0000000000010010-01012020000100-00--00000
M (Rhyssomegachile) simillima     0000-0000000000010010-01012020000100-00--00000
M (Trichurochile) thygaterella    0001000000000000010010-01012020000100-00--00000
M (Eumegachile) bombycina         0000-0000000000010010-01011010010100-00--00000
M (Grosapis) cockerelli           0000-0001000000010010-01010010010300-00--00000
M (Argyropile) parallela          0000-0000000000010011101011020000201101010000 0
M (Argyropile) sabinensis         0000-0000000000010011101011020000201101010000 0
M (Megachiloides) oenotherae      0000-0000000000010010-0101101000010110121100 10
M (Xeromegachile) integra         0000-0000000000010010-0101101011111100121100 10
M (Derotropis) pascoensis         0000-0000000000010010-0101101011110111121010 11
M (Xanthosarus) latimanus         0000-0000000000010010-0101102011110111120110 11
M (Addendella) addenda            0000-0000000000010010-0101101001010110121110 10
M (Macromegachile) lagopoda       0000-0000000000010010-0101101001110111121110 11
M (Phaenosarus) fortis            0000-0000000000010011101011010011101120110 11
```

Appendix 3. Continued.

Characters 139–184

```
                                  139 143  148  153  158  163  168  173  178  183
                                  |   |    |    |    |    |    |    |    |    |
M (Eutricharaea) argentata        0001100000100000010010-0101102001011111010100000
M (Perezia) leachella             0001100000000000010010-0101102001011111010100010
M (Eurymella) eurymera            0001100010000000010010-0101102001010100012010001
M (Eurymella) submetallica        0001100000000000010010-0101102001011111010100000
M (Digitella) digiticauda         000110000?0?0?0010010-010-1010110111012011010
M (Platysta) platystoma           0000-0?????????0010010-0101101001020110111101001
M (Neoeutricharaea) rotundata     0001100000000000010010-0101102001011111010100000
M (Litomegachile) brevis          0000-0000000000010010-0101102000011111010100000
M (Litomegachile) gentilis        0000-0000000000010010-0101102001011111010100000
M (Megachile) centuncularis       0000-0001000000010011001011010010101100--00000
M (Cyphopyga) montivaga           0000-0000000000010010-0101101001010110--00000
M (Tylomegachile) orba            0000-0100000000010010-0101102000011O-012100000
M (Tylomegachile) simplicipes     0000-0100000000010010-0101102000011O-012100000
M (Chalicodomopsis) glaesaria     0000-????????????-000-??????????????????????
```

Appendix 3. Continued.

Characters 185–230

```
                                185 189  194  199  204  209  214  219  224  229
                                |   |    |    |    |    |    |    |    |    |
Trichothurgus wagenknechti      0--000000000000-----000--00100020010000000001
Microthurge friesei             0--000000000100-----100--00100020010000000000
Dioxys productus subruber       0--000000000100-----100--10000120110000000100
Trachusa (Ulanthidium) mitchelli 0--000000000000-----100--10000120110000000100
Aztecanthidium tenochtitlanicum 0--000000000000-----100--10000120110000000001
Chelostoma rapunculi            0--000000000000-----100--10000110110000000000
Hoplitis (Dasyosmia) biscutellae 0--000000000000-----1100-10100121010000000000
Aspidosmia volkmanni            0--000000000000-----100--00-02120010101000000
Noteriades jenniferae           0--000000000000-----100--10000130100000000111
Radoszkowskiana rufiventris     0--00000000010120000 1101-10000110100100000110
C (Liothyrapis) decipiens       0--00000000010101010 1100-10100110010000000010
C (Rhinocoelioxys) zapoteca     0--00000000010101010 1100-10000120010000000011
C (Torridapis) torrida          0--0010-001010101010100--10000110010000000011
M (Austrochile) resinifera      10000000000011110000111011000111111010020001 11
M (Hackeriapis) rhodura         0--00000000011130000211101000010001000010001 10
M (Hackeriapis) ferox           11000000100011130001111101000010001000000000111
M (Hackeriapis) heriadiformis   0--00000000010130001211101000110010010010001 11
M (Hackeriapis) ignita          0--00000000010100010111001020310001000021000 11
M (Heriadopsis) striatulus      0--00000100011300002111110000100110000100011 1
M (Rhodomegachile) abdominalis  0--000000000100-----200--10000110110000000111
M (Schizomegachile) monstrosa   11000000001011110000100--10000110110100000 1111
M (Stenomegachile) chelostomoides 11000000010011100000010 1-10000110010000200001 1
M (Stenomegachile) dolichosoma  0--00000000010100010200--10000110011000000001 1
M (Thaumatosoma) duboulaii      0--00000010111000001111110000101110101000011 1
M (Chalicodomoides) aethiops    10000000000011100000110 1-10000110010000200011 1
M (Matangapis) alticola         0--00000000000130001100--10000100110000200011 1
M (Chelostomoides) rugifrons    0--00000000011130000111101100410010000020001 11
```

Appendix 3. Continued.

Characters 185–230

```
                                  185 189  194  199  204  209  214  219  224  229
                                  |   |    |    |    |    |    |    |    |    |
M (Oligotropus) campanulae        10000000000011100000111101100410001010010000 11
M (Gnathodon) georgica            10000000000011100000111101100411001000010100 11
M (Chelostomoidella) spinotulata  10100000000011100000111001100410011010000001 11
M (Callomegachile) mystaceana     0--0000000001011001020 0--1000011001000001001 11
M (Callomegachile) sculpturalis   0--000000000101$011010 0--1000011001000001001 11
M (Eumegachilana) clotho          0--000000000101000101 00--1000011001000010000 11
M (Carinula) torrida              0--000000000111000001 00--1020011011000010000 10
M (Carinula) decemsignata         0--000000000111$000010 0--1020011011010111000 11
M (Morphella) biseta              10000000000010110000200--1000011011010000001 10
M (Alocanthedon) memecylonae      10000000000010110000100--1?00?120???????????1?
M (Cestella) cestifera            0--0000000001010000010 0--1000011001000030000 10
M (Chalicodoma) parietina         0--0000000001012001010 0--1000011011110000100 11
M (Euchalicodoma) asiatica        10000000000010120000110 0-1010311011000030100 11
M (Allochalicodoma) lefebvrei     0--0000000001012001011 00-1000011011100020001 11
M (Katamegachile) manicata        10000000000010120000110 0-1110311011000000101 11
M (Parachalicodoma) incana        0--000000000101200001100-1010210011000000001 11
M (Gronoceras) bombiformis        11000000100110100000011011000211001000000000 11
M (Digronoceras) cincta combusta  11000000000010100000011011000211001000000000 11
M (Largella) semivestita          0--000000000101000001 00--1020011011100120100 11
M (Lophanthedon) dimidiata        0--0000000001010000010 1-1100001100100000000 00
M (Maximegachile) maxillosa       10000000000001110000011 00-1000011001000020001 11
M (Pseudomegachile) ericetorum    10000000000011120000100--1011011011011020000 11
M (Archimegachile) flavipes       10000000000010120000200--1011011011010120000 11
M (Neglectella) armatipes         11000000000011120010210 0-1000011011010020100 11
M (Xenomegachile) albocincta      1000010000001?1200001101-1010011011011010101 11
M (Dinavis) muansae               10100000000011100000210 0-1000411011000020100 11
M (Cesacongoa) quadraticauda      1000000000001?1101001100-1000011001000000000 00
```

Appendix 3. Continued.

Characters 185–230

```
                                  185 189  194  199  204  209  214  219  224  229
                                  |   |    |    |    |    |    |    |    |    |
M (Chelostomoda) spissula parvula 1000000010011113001120 0--1000110001010010001 10
M (Chelostomoda) ulrica           1000000010011113001110 0--1000110010000031001 11
M (Creightonella) cognata         0--0000001001012010001 00-1111012001000000000 01
M (Creightonella) albisecta       1000000001001012011011 00-1011012001000010000 00
M (Sayapis) pugnata               1010000000001110001010 0--1120011001000000001 11
M (Sayapis) planula               1100000000001112001010 0--1100011001010000000 11
M (Schrottkyapis) assumptionis    0--0000000001112001010 0--1110011011000000000 11
M (Mitchellapis) fabricator       1010001000001011000010 0--1000011011000010001 11
M (Acentron) albitarsis           110111--110110100010200--1000011011000110011 11
M (Acentron) candida              110111--110110100000200--1000011011000110011 11
M (Leptorachis) petulans          0--0001001001010001021 01-1100011010000000001 10
M (Leptorachina) laeta            1101101011011010011011110100001101111002000 110
M (Leptorachis) crotalariae       0--0001001001010001021 1101?0001101000?000111
M (Melanosarus) xylocopoides      110011--0001101000101101-1000011011000111001 11
M (Melanosarus) nigripennis       110011--0001101000101101-1000011011000010001 11
M (Moureapis) anthidiodes         0--001--0100101000001101-1000011011000110001 11
M (Pseudocentron) pruina          1100001100001010001011 01-1000011011111110001 11
M (Pseudocentron) poeyi           1100101100001010001011 01-1000011011111110001 11
M (Chrysosarus) guaranitica       1000000001001010000011 01-1000011011000100001 10
M (Chrysosarus) pseudanthidiodes  1000000001001010000011 01-1100011010000110001 10
M (Dactylomegachile) parsonsiae   1000000001001012000011 01-1000011011000100001 10
M (Stelodides) euzona             1000000000001012000011 01-1120011011010000011 11
M (Zonomegachile) moderata        1000000000001010000010 0--1120011001010001001 11
M (Amegachile) bituberculata      0--0000000001010001020 0--1000011010010020001 11
M (Callochile) ustulatiformis     1000000000001012011021 1111110001101001002100 111
M (Paracella) semivenusta         0--0000001011010001020 0--1000011011000020001 11
M (Paracella) curtula             0--0000001011010001020 0--1000011011010110001 11
```

Appendix 3. Continued.

Characters 185–230

```
                                  185 189  194  199  204  209  214  219  224  229
                                  |   |    |    |    |    |    |    |    |    |
M (Neocressoniella) carbonaria    0--0000001001010000011110110001101100002100111
M (Aethomegachile) laticeps       0--000000100101000101101-1100211011000011000110
M (Aethomegachile) trichorhytisma 1000000011011011001110 0--1100211001000110001 11
M (Megella) malimbana             0--0000000001011001011 01-1100411011010020001 11
M (Megella) pseudomonticola       0--0000000001012010011111010200110110100100011 1
M (Austromegachile) montezuma     0--0000001001010010011 01-1100011011010000001 11
M (Holcomegachile) exaltata       0--001--0100101101001101-1000011011010000001 11
M (Cressoniella) zapoteca         0--0000001001010010021110100001101001010000111
M (Dasymegachile) saulcyi         0--0000000001010001011110100001101100000100111
M (Chaetochile) schwimmeri        0--0000000001010001011110112001101100011000111
M (Neochelynia) paulista          0--000000000101000001 00--1000011011000100001 11
M (Neomegachile) chichimeca       0--000000000101000001 00--1100011010000100001 11
M (Ptilosaroides) neoxanthoptera  0--000000000101000002 00--1100011010010100001 11
M (Ptilosarus) microsoma          0--000000000101000002 00--1100011010010100001 11
M (Rhyssomegachile) simillima     0--000000000101000011 00--1100011010010110001 11
M (Trichurochile) thygaterella    0--000000000101000001 00--1000011011010111001 11
M (Eumegachile) bombycina         0--0000001001010001011110100001101101011000111
M (Grosapis) cockerelli           0--0000000001010000011101101001101100010000111
M (Argyropile) parallela          0--000000100101000102110-1000011010000120001 11
M (Argyropile) sabinensis         0--000000100101000101110-1010011010000120001 11
M (Megachiloides) oenotherae      1000000001001011000011111102001101110013100111
M (Xeromegachile) integra         1100000000011011000011111100001101111003100111
M (Derotropis) pascoensis         1000000001001011000001111111001101101003100111
M (Xanthosarus) latimanus         110001--1001101000101111111200110110001 0100111
M (Addendella) addenda            0--000000100101000101101-1000011011000110001 11
M (Macromegachile) lagopoda       1010000001011010001011110112001101100012000111
M (Phaenosarus) fortis            1100000001011011000011111110001101110002100111
```

Appendix 3. Continued.

Characters 185–230

```
                                185 189  194  199  204  209  214  219  224  229
                                |   |    |    |    |    |    |    |    |    |
M (Eutricharaea) argentata      0--0000001001012011020 0--1000011010000111001 11
M (Perezia) leachella           0--0000001001012001021 01-1000011010000111001 11
M (Eurymella) eurymera          1010001001011011011021111100001101000011100111
M (Eurymella) submetallica      100001--0000101101102101-1000011010000100101 11
M (Digitella) digiticauda       1000000001001010001021 01-1000011010000111001 11
M (Platysta) platystoma         10101000?00101100002111110000110010100110011 11
M (Neoeutricharaea) rotundata   0--0000000001012001020 0--1000011010000111001 11
M (Litomegachile) brevis        0--0000010010120010211101000011010000120001 11
M (Litomegachile) gentilis      0--0000010010100010211101000011011000121001 11
M (Megachile) centuncularis     0--0000010010110110111101100011011010110001 11
M (Cyphopyga) montivaga         0--0000010010100110111101000011010000000001 11
M (Tylomegachile) orba          0--0000010010110110211101020011010000100001 11
M (Tylomegachile) simplicipes   0--0000010010110010211101020011010000101001 11
M (Chalicodomopsis) glaesaria   ??????-????????????????????????????????????
```

Appendix 3. Continued.

Characters 231–272

```
                                231 235  240  245  250  255  260  265  270
                                |   |    |    |    |    |    |    |    |
Trichothurgus wagenknechti      1000000000210000-0100100000000---11000000
Microthurge friesei             -000000000010000-0100000100000---11000000
Dioxys productus subruber       -0100100000011010-00---10001200---10000000
Trachusa (Ulanthidium) mitchelli -0003101000211100-01110100012010000-110000
Aztecanthidium tenochtitlanicum 1000210000200100-0110002100200---11101020
Chelostoma rapunculi            -0100101000211000-0100011100100---0-011000
Hoplitis (Dasyosmia) biscutellae -0100101000211000-0110010001100---0-010010
Aspidosmia volkmanni            -0001101000211000-0110011111000---11010000
Noteriades jenniferae           1110011000011010-0111010101210---10010000
Radoszkowskiana rufiventris     -0100111000011010-0110010000200---10010000
C (Liothyrapis) decipiens       -0100111000011010-0100011100210---10010000
C (Rhinocoelioxys) zapoteca     1111011100011010-0100010100210---10110000
C (Torridapis) torrida          1010210100011010-0100011101200---10010000
M (Austrochile) resinifera      1111111100011010-0111010000200---0-000000
M (Hackeriapis) rhodura         -1100111010011010-0110012011200---10000010
M (Hackeriapis) ferox           1110011100011010-0111010001200---10010000
M (Hackeriapis) heriadiformis   1110011100011010-0111010000000---10010000
M (Hackeriapis) ignita          1110010100011010-0111110001210---10000000
M (Heriadopsis) striatulus      1110011100011010-0101011101200---10000000
M (Rhodomegachile) abdominalis  1010011100020101 0-0110110000200---10000000
M (Schizomegachile) monstrosa   1110011100011010-0110110010200---0-000000
M (Stenomegachile) chelostomoides 1111011100011010-0111011000200---0-010000
M (Stenomegachile) dolichosoma  1010011100011101 0-0101112001100---10000010
M (Thaumatosoma) duboulaii      1111011100011010-0111110000010---0-010000
M (Chalicodomoides) aethiops    1111311101001101 0-0111011000210---0-010000
M (Matangapis) alticola         1110011100000101110111010001010---0-010000
M (Chelostomoides) rugifrons    1110111100011010-0100011000010---10000100
```

Appendix 3. Continued.

Characters 231–272

```
                                231 235  240  245  250  255  260  265  270
                                |   |    |    |    |    |    |    |    |
M (Oligotropus) campanulae      11103111010011010-0111010001010---10010000
M (Gnathodon) georgica          11101111010011010-0110010000010---10000100
M (Chelostomoidella) spinotulata11100111000211010-0111011001000---11000010
M (Callomegachile) mystaceana   10110111000011010-0100010000200---11010010
M (Callomegachile) sculpturalis 11100111000011010-0110011001200---10000010
M (Eumegachilana) clotho        11101111000011010-0111010000000---10010010
M (Carinula) torrida            -0101111010011010-0101010001000---10000000
M (Carinula) decemsignata       10100111010011010-0101010000000---10000000
M (Morphella) biseta            -1100111000011010-0100010111200---0-010010
M (Alocanthedon) memecylonae    -?1???1?000011010-0110011011000---11000010
M (Cestella) cestifera          -1103111000111010-0111010001000---11000000
M (Chalicodoma) parietina       11110111000111010-0111110001210---0-110001
M (Euchalicodoma) asiatica      11110111010011010-0110012001000---0-010000
M (Allochalicodoma) lefebvrei   11110111000111010-0110111001110---10110001
M (Katamegachile) manicata      10100101010011010-0101011001200---10010000
M (Parachalicodoma) incana      01100111000111011001111111001200---11011100
M (Gronoceras) bombiformis      10100111000011010-0110010001200---10010000
M (Digronoceras) cincta combusta10100111000011010-0110110001210---10010000
M (Largella) semivestita        11102111010111010-0110010001200---11010000
M (Lophanthedon) dimidiata      -1100111000011010-1111010010200---0-000000
M (Maximegachile) maxillosa     11103111010011010-0111011000210---10000000
M (Pseudomegachile) ericetorum  11102111000011010-0101010000200---11000000
M (Archimegachile) flavipes     11102111000011010-0111010001000---11000000
M (Neglectella) armatipes       11101111000211010-0111110000010---10000000
M (Xenomegachile) albocincta    11102111010011010-0111110001200---11000100
M (Dinavis) muansae             11102110000211010-0111010001200---10000100
M (Cesacongoa) quadraticauda    -1100111000011010-0111010101200---11010000
```

Appendix 3. Continued.

Characters 231–272

```
                                  231 235  240  245  250  255  260  265  270
                                  |   |    |    |    |    |    |    |    |
M (Chelostomoda) spissula parvula -1100111000011010-0101010000000---10010000
M (Chelostomoda) ulrica           1110011100001l010-010111200-010---10010000
M (Creightonella) cognata         1110210000021l010-0100010111000---0-000100
M (Creightonella) albisecta       -1100111000011010-0100012011000---0-000100
M (Sayapis) pugnata               1110310100001l010-0100010001000---10010010
M (Sayapis) planula               0110010100001l010-0100010001200---0-010010
M (Schrottkyapis) assumptionis    0110010100001l010-0100010101000---0-010010
M (Mitchellapis) fabricator       1110011101001l010-0100010001000---10010100
M (Acentron) albitarsis           0110310101101l010-0100010001211010010010010
M (Acentron) candida              0110310101101l010-0100010001211010010010010
M (Leptorachis) petulans          -0103101010011010-0100012001001000010011000
M (Leptorachina) laeta            -0100101011011010-0110111100201010010010100
M (Leptorachis) crotalariae       0010010101001l010-110001??010?????10010000
M (Melanosarus) xylocopoides      0110010100001l010-0100010100211010010010000
M (Melanosarus) nigripennis       1110010100001l010-0100011100211010010010000
M (Moureapis) anthidiodes         1110010101000l010-1100010001211000010010000
M (Pseudocentron) pruina          1110010101101l010-0100010100211011O-000000
M (Pseudocentron) poeyi           1110010101101l010-0100010100211011O-000000
M (Chrysosarus) guaranitica       -0100101010011011101000100002O0---10010000
M (Chrysosarus) pseudanthidiodes  -0100101010011011101000100012O0---10010000
M (Dactylomegachile) parsonsiae   -0100101010011011101000100002O0---10010000
M (Stelodides) euzona             1010010101001l011101000120012O0---10000000
M (Zonomegachile) moderata        1010010101001l011001000100012O0---10010000
M (Amegachile) bituberculata      0110010101001l010-0100012001200---0-010000
M (Callochile) ustulatiformis     0110010101001l010-0110012101100---10010100
M (Paracella) semivenusta         1110010110001l010-0100012000210---10010100
M (Paracella) curtula             1010010101001l010-0111011000000---0-010100
```

Appendix 3. Continued.

Characters 231–272

```
                                  231 235  240  245  250  255  260  265  270
                                  |   |    |    |    |    |    |    |    |
M (Neocressoniella) carbonaria    11100101010011010-0100012001200---10010110
M (Aethomegachile) laticeps       -0100101011011011001000100010000---10010010
M (Aethomegachile) trichorhytisma 11100101011011011000---11001100---10010010
M (Megella) malimbana             11100111010011010-0100012001200---10010000
M (Megella) pseudomonticola       11100101010011010-0100012001200---10000110
M (Austromegachile) montezuma     10103101010011011001000100000010---10010010
M (Holcomegachile) exaltata       10103101010011011001000100000000---10010010
M (Cressoniella) zapoteca         10100101010000101110100010001200---10010000
M (Dasymegachile) saulcyi         10100101010011011101000120012000---10010000
M (Chaetochile) schwimmeri        10100101010011011101000120002000---10010000
M (Neochelynia) paulista          10103101010011011001000120012000---10010000
M (Neomegachile) chichimeca       10100101010011011001000120012000---10010000
M (Ptilosaroides) neoxanthoptera  10100101010011011001000120010000---10010010
M (Ptilosarus) microsoma          10100101010011011001000120010000---10010010
M (Rhyssomegachile) simillima     10100101010011011101000120012000---10010000
M (Trichurochile) thygaterella    10100101010011011101000120012000---10010000
M (Eumegachile) bombycina         01100101000011011101000120012000---10011000
M (Grosapis) cockerelli           10100101000211010-0110012011000---10010000
M (Argyropile) parallela          11103101011011010-0100010001210---0-010000
M (Argyropile) sabinensis         11103101011011010-0100012001210---0-010000
M (Megachiloides) oenotherae      11100101011011010-0100010001200---10010000
M (Xeromegachile) integra         11100101010011010-0100010001200---10010000
M (Derotropis) pascoensis         11100101010011010-0100010000010---11010000
M (Xanthosarus) latimanus         10100101000111010-0100010000101---10000000
M (Addendella) addenda            10100101010011010-0101012001000---10010000
M (Macromegachile) lagopoda       11100101010011010-0111012000201*1010010000
M (Phaenosarus) fortis            10100101011011010-0100010000210---10010010
```

Appendix 3. Continued.

Characters 231–272

```
                                231 235  240  245  250  255  260  265  270
                                |   |    |    |    |    |    |    |    |
M (Eutricharaea) argentata      1110010100001101 0-0100012000201000100100 00
M (Perezia) leachella           1110010100001101 0-0100012000211 --100100 00
M (Eurymella) eurymera          1010010110000101 0-0100012000201000100100 00
M (Eurymella) submetallica      1010010100001101 0-0100012000201000100100 00
M (Digitella) digiticauda       1110010101101101 0-0100010001000---100100 00
M (Platysta) platystoma         1010010101101101 0-0100110101211010100100 00
M (Neoeutricharaea) rotundata   1110010101001101 0-0100010001000---100100 00
M (Litomegachile) brevis        1110010101001101 0-0100010001000---100101 00
M (Litomegachile) gentilis      1110010101001101 0-0100012001000---100100 00
M (Megachile) centuncularis     0110010100001101 1101100120012000---100110 00
M (Cyphopyga) montivaga         1010010100000101 0-0100010001200---100110 00
M (Tylomegachile) orba          0110010101001101 0-0100012001000---100101 10
M (Tylomegachile) simplicipes   0110010101001101 0-0101012001200---100001 10
M (Chalicodomopsis) glaesaria   ????????????????????????????????????????
```

Appendix 4. Quantitative descriptors of trees obtained from implied weighting (IW) analyses. F = total fit of characters to tree (Goloboff, 1993); K = concavity factor determining weighting strength; MPT = number of parsimonious trees; L = tree length; RI = retention index; GC Observed = average GC frequency-difference, as calculated from displayed support at each node in the resulting tree. Average value followed, in parentheses, by median, standard deviation, and number of nodes. * = a single node collapsed in the consensus tree. In all analyses, the Consistency Index was 13. Avg. SPR-dist. EW consensus = SPR distance between the resulting topology of each IW analysis and the topology obtained from the consensus tree of the equal weighting analysis. Avg. SPR-dist. Total evidence = SPR distance between the resulting topology of each IW analysis and the topology obtained from the Bayesian inference analysis of the full dataset. High values in bold face.

F	K	MPT	L	RI	GC Observed	Avg. SPR-dist EW consensus	Avg. SPR-dist Total Evidence
0.5	7.50	1	2434	56	**50.24** (48.0, ± 35.11, n = 63)	0.5966	0.4538
0.54	8.81	1	2421	56	**50.97** (54.5, ± 35.36, n = 60)	0.6134	**0.4874**
0.58	10.40	1	2415	56	**51.03** (55.0, ± 35.87, n = 62)	0.6387	0.4622
0.62	12.20	1	2397	57	49.31 (42.0, ± 36.27, n = 65)	0.6891	**0.4874**
0.66	14.60	2*	2393	57	**50.19** (46.5, ± 36.08, n = 64)	0.6807	**0.4874**
0.7	17.50	2*	2389	57	48.15 (40.0, ± 36.37, n = 67)	0.6639	**0.4874**
0.74	21.40	1	2378	57	48.03 (40.0, ± 35.79, n = 68)	0.7815	0.4790
0.78	26.60	1	2377	57	48.73 (41.0, ± 35.18, n = 67)	0.7899	0.4538
0.82	34.20	1	2377	57	47.38 (38.0, ± 35.43, n = 69)	0.7899	0.4538
0.86	46.10	1	2372	57	48.27 (38.5, ± 35.33, n = 66)	0.7563	0.4286
0.9	67.50	1	2366	57	49.67 (41.0, ± 34.88, n = 64)	**0.8824**	0.3782

Appendix 5. GenBank accession numbers for sequences used in this study.

Phylogeny of Megachilidae					
Taxa	**EF1α**	**Opsin**	**CAD**	**NAK**	**28S**
Macropis nuda	AY585155	DQ116686	DQ067171	HQ995917	HQ996008
Melitta leporina	AY585158	DQ116688	DQ067174	EF646394	AY654529
Apis mellifera	AF015267	AMU26026	DQ067178	XM_623142	AY703551
Exomalopsis sp.	GU244989	HM211835	—	GU245110	GU244802
Diadasia bituberculata	GU244927	AF344594	—	GU245074	GU244768
Nomada maculata	GU245030	AF344609	—	GU245206	GU244890
Ceratina calcarata	AY585108	AF344620	DQ067190	GU245213	HQ996011
Fidelia pallidula	HQ995686	HQ995756	HQ995831	HQ995929	HQ996025
Fidelia villosa	HQ995682	HQ995752	HQ995827	HQ995925	HQ996021
Fidelia braunsiana	HQ995683	HQ995753	HQ995828	HQ995926	HQ996022
Fideliopsis major	DQ141113	EU851628	HQ995833	HQ995931	HQ996027
Fidelia profuga	GU244990	HQ995760	HQ995836	GU245151	HQ996030
Pararhophites orobinus	HQ995679	HQ995749	HQ995823	HQ995922	HQ996018
Pararhophites quadratus	EU851522	EU851627	HQ995824	GU245153	GU244841
Afranthidium (*Capanthidium*) *capicola*	KX060937	KX060813	KX060879	KU976158	KU976218
Aspidosmia arnoldi	HQ995701	HQ995773	HQ995850	HQ995945	HQ996042
Aspidosmia volkmanni	HQ995702	HQ995774	HQ995851	HQ995946	HQ996043
Anthidiellum (*Loyolanthidium*) *robertsoni*	KX060952	KX060830	KX060894	KU976175	KU976235
Anthidium (*Anthidium*) *porterae*	GU244996	AF344619	—	GU245158	GU244846
Anthodioctes (*Anthodioctes*) *mapirensis*	HQ995700	HQ995772	HQ995849	HQ995944	HQ996041
Dianthidium (*Dianthidium*) *subparvum*	GU244993	KX060847	KX060909	GU245155	GU244843
Euaspis abdominalis	JX869703	JX869735	JX869627	JX869769	JX869662

Appendix 5. Continued.

Taxa	EF1α	Opsin	CAD	NAK	28S
Hoplostelis bivittata	JX869705	JX869737	—	JX869771	JX869671
Pachyanthidium (*Pachyanthidium*) *cordatum*	KX060971	KX060852	KX060915	KU976196	KU976257
Serapista rufipes	HQ995716	HQ995789	HQ995866	HQ995960	HQ996057
Stelis lateralis	JX869718	JX869751	JX869643	JX869784	JX869685
Trachusa larreae	HQ995719	HQ995791	HQ995868	GU245154	GU244842
Notanthidium steloides	HQ995712	HQ995784	HQ995861	HQ995956	HQ996053
Plesianthidium (*Spinanthidiellum*) *rufocaudatum*	KX060976	KX060857	KX060920	KU976201	KU976262
Icteranthidium ferrugineum flavum	HQ995711	HQ995783	HQ995860	HQ995955	HQ996052
Hypanthidium obscurius	HQ995710	HQ995782	HQ995859	HQ995954	HQ996051
Hypanthidioides marginata	HQ995709	HQ995781	HQ995858	HQ995953	HQ996050
Eoanthidium turnericum	HQ995707	HQ995779	HQ995856	HQ995951	HQ996048
Rhodanthidium septemdentatum	HQ995715	HQ995788	HQ995865	HQ995959	HQ996056
Epanthidium bicoloratum	HQ995708	HQ995780	HQ995857	HQ995952	HQ996049
Pseudoanthidium (*Micranthidium*) sp.	KX060982	KX060862	KX060926	KU976206	KU976268
Aztecanthidium tenochtitlanicum	—	KX060844	KX060906	KU976189	KU976249
Duckeanthidium thielei	HQ995706	HQ995778	HQ995855	HQ995950	HQ996047
Cyphanthidium intermedium	KX060966	KX060845	KX060907	KU976190	KU976250
Aglaoapis tridentata	EU851524	EU851630	HQ995844	HQ995939	HQ996036
Dioxys moesta	HQ995696	HQ995768	HQ995845	HQ995940	HQ996037
Lithurgus chrysurus	EU851523	EU851629	HQ995837	HQ995934	HQ996031
Microthurge sp.	HQ995694	HQ995766	HQ995842	GU245161	GU244849
Trichothurgus herbsti	HQ995695	HQ995767	HQ995843	GU245160	GU244848
Afroheriades primus	EU851532	EU851638	HQ995902	HQ995995	HQ996092

Appendix 5. Continued.

Taxa	EF1α	Opsin	CAD	NAK	28S
Ashmeadiella aridula	EU851535	EU851641	HQ995903	GU245171	GU244858
Atoposmia mirifica	EU851541	EU851647	HQ995904	HQ995996	HQ996093
Chelostoma florisomne	EU851546	EU851652	HQ995905	HQ995997	HQ996094
Haetosmia brachyura	HQ995748	HQ995822	HQ995906	HQ995998	HQ996095
Heriades crucifer	EU851555	EU851661	DQ067194	GU245168	GU244855
Hofferia schmiedeknechti	EU851556	EU851662	HQ995907	HQ995999	HQ996096
Hoplitis adunca	EU851572	EU851678	HQ995908	HQ996000	HQ996097
Ochreriades fasciatus	EU851590	EU851696	HQ995909	HQ996001	HQ996098
Osmia lignaria	EU851610	EU851715	HQ995910	GU245169	GU244856
Othinosmia globicola	EU851616	EU851721	HQ995911	HQ996002	HQ996099
Protosmia humeralis	EU851621	EU851726	HQ995913	HQ996004	HQ996101
Pseudoheriades moricei	EU851622	EU851727	HQ995914	HQ996005	HQ996102
Stenoheriades asiaticus	EU851623	EU851728	HQ995915	HQ996006	HQ996103
Hoplitis minima	EU851625	EU851730	EU851520	—	—
Wainia eremoplana	EU851626	EU851731	HQ995916	HQ996007	HQ996104
Noteriades sp.	EU851589	EU851695	HQ995900	HQ995993	HQ996090
Coelioxys octodentata	KX428310	KX428056	KX428226	KX428394	KX428151
Megachile pugnata	AY585147	HQ995818	DQ067196	HQ995990	HQ996087
Megachile angelarum	HQ995727	HQ995800	HQ995878	GU245163	GU244851
Megachile albisecta	EU851529	EU851635	HQ995881	HQ995974	HQ996071
Radoszkowskiana rufiventris	HQ995747	HQ995821	HQ995901	HQ995994	HQ996091

Appendix 5. Continued.

Phylogeny of Megachilini					
Taxa	**EF1α**	**Opsin**	**CAD**	**NAK**	**28S**
Trichothurgus herbsti	HQ995695	HQ995767	HQ995843	GU245160	GU244848
Microthurge sp.	HQ995694	HQ995766	HQ995842	GU245161	GU244849
Aspidosmia volkmanni	HQ995702	HQ995774	HQ995851	HQ995946	HQ996043
Trachusa larreae	HQ995719	HQ995791	HQ995868	GU245154	GU244842
Hoplitis adunca	EU851572	EU851678	HQ995908	HQ996000	HQ996097
Chelostoma florisomne	EU851546	EU851652	HQ995905	HQ995997	HQ996094
Dioxys moesta	HQ995696	HQ995768	HQ995845	HQ995940	HQ996037
Aztecanthidium tenochtitlanicum	—	KX060844	KX060906	KU976189	KU976249
Radoszkowskiana rufiventris	HQ995747	HQ995821	HQ995901	HQ995994	HQ996091
Coelioxys decipiens	KX428313	KX428059	KX428229	KX428397	KX428154
Noteriades sp.	EU851589	EU851695	HQ995900	HQ995993	HQ996090
Megachile (*Rhodomegachile*) sp.	HQ995744	HQ995817	HQ995897	HQ995989	HQ996086
M. (*Matangapis*) *alticola*	—	—	—	—	KX580315
M. (*Chelostomoda*) sp.	HQ995726	HQ995799	—	HQ995971	HQ996068
M. (*Heriadopsis*) sp.	—	—	—	—	KX580316
M. (*Hackeriapis*) sp. 1	KX428356	KX428102	KX428272	KX428438	KX428195
M. (*Chelostomoidella*) *spinotulata*	HQ995728	HQ995801	HQ995879	HQ995972	HQ996069
M. (*Chelostomoides*) *angelarum*	HQ995727	HQ995800	HQ995878	GU245163	GU244851
M. (*Thaumatosoma*) *remeata*	HQ995745	HQ995819	HQ995898	HQ995991	HQ996088
M. (*Stenomegachile*) *chelostomoides*	KX428383	KX428129	KX428299	KX428461	KX428218
M. (*Maximegachile*) *maxillosa*	HQ995737	HQ995810	HQ995890	HQ995983	HQ996080
M. (*Chalicodomoides*) *aethiops*	HQ995725	HQ995798	HQ995877	HQ995970	HQ996067

Appendix 5. Continued.

Taxa	EF1α	Opsin	CAD	NAK	28S
M. (*Carinula*) *decemsignata*	KX428325	KX428071	KX428242	KX428409	KX428166
M. (*Callomegachile*) *sculpturalis*	HQ995724	HQ995797	HQ995875	HQ995968	HQ996065
M. (*Alocanthedon*) sp.	KX428318	KX428064	KX428235	KX428402	KX428159
M. (*Gronoceras*) *bombiformis*	HQ995733	HQ995806	HQ995886	HQ995979	HQ996076
M. (*Lophanthedon*) *dimidiata*	KX428359	KX428105	KX428275	KX428441	KX428198
M. (*Austrochile*) sp.	HQ995723	HQ995796	HQ995874	HQ995967	HQ996064
M. (*Parachalicodoma*) sp.	KX428370	KX428116	KX428286	KX428448	KX428205
M. manicata	KX428330	KX428076	KX428247	KX428413	KX428170
M. (*Chalicodoma*) *parietina*	EU851530	EU851636	HQ995876	HQ995969	HQ996066
M. (*Allochalicodoma*) *lefebvrei*	KX428329	KX428075	KX428246	KX428412	KX428169
M. (*Largella*) *floralis*	HQ995735	HQ995808	HQ995888	HQ995981	HQ996078
M. (*Pseudomegachile*) *ericetorum*	HQ995742	HQ995815	HQ995895	GU245165	GU244853
M. (*Neglectella*) *laminata*	KX428366	KX428112	KX428282	KX428444	KX428201
M. (*Dinavis*) *leucospilura*	KX428336	KX428082	KX428252	KX428418	KX428175
M. (*Cesacongoa*) sp.	KX428328	KX428074	KX428245	KX428411	—
M. (*Creightonella*) *albisecta*	EU851529	EU851635	HQ995881	HQ995974	HQ996071
M. (*Creightonella*) *cornigera*	KX428334	KX428080	KX428250	KX428416	KX428173
M. (*Mitchellapis*) *fabricator*	HQ995740	HQ995813	HQ995893	HQ995986	HQ996083
M. pugnata	AY585147	HQ995818	DQ067196	HQ995990	HQ996087
M. (*Grosapis*) *cockerelli*	KX428355	KX428101	KX428271	KX428437	KX428194
M. (*Eumegachile*) *bombycina*	KX428337	KX428083	KX428253	KX428419	KX428176
M. (*Litomegachile*) *texana*	HQ995736	HQ995809	HQ995889	HQ995982	HQ996079
M. (*Neoeutricharaea*) *rotundata*	XM003705302	XM003705921	XM012287299	XM012290255	—

Appendix 5. Continued.

Taxa	EF1α	Opsin	CAD	NAK	28S
M. (*Eurymella*) *aff. eurymera*	KX428338	KX428084	KX428254	KX428420	KX428177
M. (*Argyropile*) *parallela*	HQ995722	HQ995795	HQ995873	HQ995966	HQ996063
M. (*Amegachile*) *cf. bituberculata*	KX428319	KX428065	KX428236	KX428403	KX428160
M. (*Xeromegachile*) *nevadensis*	HQ995739	HQ995812	HQ995892	HQ995985	HQ996082
M. (*Phaenosarus*) *fortis*	KX428371	KX428117	KX428287	KX428449	KX428206
M. (*Xanthosarus*) *lagopoda*	KX428390	KX428136	KX428306	—	—
M. (*Leptorachis*) *petulans*	KX428357	KX428103	KX428273	KX428439	KX428196
M. (*Pseudocentron*) sp.	KX428372	KX428118	KX428288	KX428450	KX428207
M. (*Melanosarus*) sp.	KX428365	KX428111	KX428281	KX428443	KX428200
M. (*Acentron*) sp.	KX428316	KX428062	KX428233	KX428400	KX428157
M. (*Paracella*) sp.	KX428368	KX428114	KX428284	KX428446	KX428203
M. (*Tylomegachile*?) sp.	KX428384	KX428130	KX428300	KX428462	KX428219
M. (*Aethomegachile*) *conjuncta*	HQ995720	HQ995793	HQ995871	HQ995964	HQ996061
M. (*Megella*) *pseudomonticola*	KX428364	KX428110	KX428280	KX428442	KX428199
M. (*Dasymegachile*) sp.	KX428335	KX428081	KX428251	KX428417	KX428174
M. (*Cressoniella*) *zapoteca*	HQ995730	HQ995803	HQ995882	HQ995975	HQ996072
M. (*Austromegachile*) sp.	KX428322	KX428068	KX428239	KX428406	KX428163
M. (*Ptilosarus*) *microsoma*	HQ995743	HQ995816	HQ995896	HQ995988	HQ996085
M. (*Neochelynia*?) sp.	KX428367	KX428113	KX428283	KX428445	KX428202
M. (*Stelodides*) *euzona*	KX428382	KX428128	KX428298	KX428460	KX428217
M. (*Chrysosarus*) sp.	HQ995729	HQ995802	HQ995880	HQ995973	HQ996070

Appendix 6. Organization of genera in tribe Megachilini, with synonyms indicated. For subgenera of *Megachile* refer to Appendix 7.

Genus †*Chalicodomopsis* Engel
Genus *Noteriades* Cockerell
Genus *Gronoceras* Cockerell
  =*Berna* Friese
  =*Digronoceras* Cockerell
Genus *Matangapis* Baker & Engel
Genus *Lophanthedon* Gonzalez & Engel
Genus *Coelioxys* Latreille
Genus *Radoszkowskiana* Popov
Genus *Carinula* Michener *& al.*
  =*Carinella* Pasteels, *nomen praeoccupatum*
Genus *Thaumatosoma* Smith
Genus *Austrochile* Michener
Genus *Rozenapis* Gonzalez & Engel, n. gen.
Genus *Rhodomegachile* Michener
Genus *Chalicodomoides* Michener
Genus *Hackeriapis* Cockerell
Genus *Dinavis* Pasteels
Genus *Cesacongoa* Koçak & Kemal
  =*Cuspidella* Pasteels, *nomen praeoccupatum*
Genus *Neglectella* Pasteels
  =*Neochalicodoma* Pasteels
Genus *Maximegachile* Guiglia & Pasteels
Genus *Schizomegachile* Michener
Genus *Callomegachile* Michener
  Subgenus *Alocanthedon* Engel & Gonzalez
  Subgenus *Callomegachile* Michener
    =*Orientocressonliella* Gupta
  Subgenus *Eumegachilana* Michener
  Subgenus *Morphella* Pasteels
Genus *Saucrochile* Gonzalez & Engel, n. gen.
Genus *Cremnochile* Gonzalez & Engel, n. gen.
Genus *Stenomegachile* Pasteels
Genus *Pseudomegachile* Friese
  Subgenus *Archimegachile* Alfken
  Subgenus *Cestella* Pasteels
  Subgenus *Largella* Pasteels
  Subgenus *Parachalicodoma* Pasteels
  Subgenus *Pseudomegachile* Friese
    =*Pseudomegalochila* Schulz, *nomen vanum*
  Subgenus *Xenomegachile* Rebmann
Genus *Heriadopsis* Cockerell
Genus *Chelostomoides* Robertson
  Subgenus *Chelostomoides* Robertson
    =*Oligotropus* Robertson
    =*Gnathodon* Robertson
    =*Sarogaster* Robertson
  Subgenus *Chelostomoidella* Snelling
Genus *Chalicodoma* Lepeletier de Saint Fargeau
  =*Euchalicodoma* Tkalců
  =*Allochalicodoma* Tkalců
  =*Parachalicodoma* Tkalců, *nomen praeoccupatum*
  =*Heteromegachile* Rebmann
  =*Katamegachile* Rebmann
  =*Xenochalicodoma* Tkalců
Genus *Megachile* Latreille (*vide* Appendix 7)

Incertae sedis
Genus *Stellenigris* Meunier

Appendix 7. Organization of genus *Megachile* Latreille, with synonyms of subgenera indicated.

Subgenus *Chelostomoda* Michener
=*Neoashmeadiella* Gupta
Subgenus *Mitchellapis* Michener
Subgenus *Creightonella* Cockerell
=*Creightoniella* Pasteels, *nomen vanum*
Subgenus *Sayapis* Titus
=*Gnathocera* Provancher, *nomen praeoccupatum*
=*Ceratias* Robertson
=*Schrottkyapis* Mitchell, n. syn.
Subgenus *Paracella* Michener
=*Paracella* Pasteels, *nomen invalidum*
Subgenus *Amegachile* Friese
=*Callochila* Michener
=*Platychile* Michener, *nomen nudum*
Subgenus *Eurymella* Pasteels
=*Platysta* Pasteels
Subgenus *Argyropile* Mitchell
Subgenus *Phaenosarus* Mitchell
Subgenus *Megachiloides* Mitchell
=*Xeromegachile* Mitchell
=*Derotropis* Mitchell
Subgenus *Moureapis* Raw
=*Moureana* Mitchell, *nomen praeoccupatum*
=*Willinkella* Laroca *et al*., *nomen nudum*
=*Acentrina* Schlindwein, *nomen nudum*
Subgenus *Leptorachis* Mitchell
=*Grafella* Mitchell
Subgenus *Leptorachina* Mitchell
Subgenus *Acentron* Mitchell
Subgenus *Pseudocentron* Mitchell
Subgenus *Melanosarus* Mitchell
Subgenus *Neocressoniella* Gupta
Subgenus *Megella* Pasteels
Subgenus *Eutricharaea* Thomson
=*Paramegachile* Friese
=*Paramegalochila* Schulz, *nomen vanum*
=*Andrygonella* Cockerell
=*Perezia* Ferton
=*Fertonella* Cockerell
=*Neoeutricharaea* Rebmann
=*Melanoeutricharaea* Tkalců
=*Anodonteutricharaea* Tkalců
Subgenus *Aethomegachile* Engel & Baker
Subgenus *Litomegachile* Mitchell
Subgenus *Xanthosarus* Robertson
=*Delomegachile* Viereck
=*Macromegachile* Noskiewicz
Subgenus *Addendella* Mitchell
Subgenus *Digitella* Pasteels
Subgenus *Tylomegachile* Moure
Subgenus *Austromegachile* Mitchell
=*Holcomegachile* Moure
Subgenus *Neochelynia* Schrottky
=*Neomegachile* Mitchell
Subgenus *Zonomegachile* Mitchell
Subgenus *Chaetochile* Mitchell
Subgenus *Rhyssomegachile* Mitchell
Subgenus *Chalepochile* Gonzalez & Engel
Subgenus *Aporiochile* Gonzalez & Engel
Subgenus *Ptilosarus* Mitchell
Subgenus *Ptilosaroides* Mitchell
Subgenus *Chrysosarus* Mitchell
=*Dactylomegachile* Mitchell
=*Stelodides* Moure
Subgenus *Dasymegachile* Mitchell
Subgenus *Trichurochile* Mitchell
Subgenus *Cressionella* Mitchell
Subgenus *Grosapis* Mitchell
Subgenus *Eumegachile* Friese
Subgenus *Megachile* Latreille
=*Megalochila* Schulz, *nomen vanum*
=*Anthemois* Robertson
=*Cyphopyga* Robertson

Journal of Melittology

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