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Taxonomic comments on *Megachile* subgenus *Chryosarus* (Hymenoptera: Megachilidae)

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Abstract. Comments on the phylogenetic relationships and taxonomy of American leafcutter bees of the genus *Megachile* Latreille subgenus *Chryosarus* Mitchell are provided. The South American subgenera *Austrosarus* Raw, *Stelodides* Moure, and *Zonomegachile* Mitchell are newly synonymized under *Chryosarus* (**new synonymies**).

INTRODUCTION

Megachilidae is one of the seven extant bee families containing more than 4000 described species in 76 genera worldwide (Michener, 2007; Ascher & Pickering, 2013). This family consists of both solitary and cleptoparasitic species and is noteworthy for its astonishing diversity of nesting habits and floral relationships, which collectively are more diverse than any other bee group (e.g., Müller, 1996; Müller & Bansac, 2004; Michener, 2007; Cane *et al.*, 2007), for being the primary source of invasive bees worldwide (e.g., Cane, 2003; Hinojosa-Díaz *et al.*, 2005; Strange *et al.*, 2011), and for including the majority of non-honey bee managed pollinators [e.g., *Megachile* (*Eutricharaea*) *rotundata* (Fabricius), *Osmia* (*Osmia*) *lignaria* Say] now introduced to many parts of the globe (e.g., Pitts-Singer & Cane, 2011). The higher-level phylogeny and classification of the Megachilidae based on adult morphology of extinct and extant taxa were recently revised by Gonzalez *et al.* (2012) and nine tribes and four subfamilies are currently recognized.

The tribe Megachilini is the most common and diverse of all tribes, accounting for about 50% of the species diversity of the family (Michener, 2007). The more than 2000 species have been traditionally grouped in several genera, particularly those non-parasitic taxa placed by Michener (2007) in *Megachile* Latreille. Following Michener's classification, two other genera, *Coelioxys* Latreille and *Radoszkowskiana* Popov, both clep-

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toparasitic, are recognized. The non-parasitic genus *Noteriades* Cockerell was recently transferred from the Osmiini to Megachilini (Gonzalez *et al.*, 2012). Thus, if adopting Michener's (2007) classification, four genera are to be recognized in Megachilini. The phylogenetic relationships within Megachilini, excluding *Noteriades*, were explored by Gonzalez (2008), and the multigeneric classification proposed in that review is adopted herein. The genus *Megachile*, as here understood, is used in a narrower sense than that of Michener (2000, 2007) and refers to a monophyletic, derived clade within *Megachile s.l.* that included all subgenera of "Group 1" of Michener (2000, 2007), *Creightonella* Cockerell (the only subgenus of Michener's "Group 3"), and the subgenera *Mitchellapis* Michener and *Megella* Pasteels; the latter two subgenera tentatively included by Michener (2007) in "Group 2". *Megachile*, as here employed, is characterized by the presence of cutting edges among teeth in the female mandibles, which are generally associated with the use of petal or leaf pieces to build their nest cells. Such leafcutting behavior is unique among bees and it appears to have started as early as the Paleocene, as indicated by fossils of dicotyledonous leaves with distinctive, semi-circular cuts into the margin (Wappler & Engel, 2003; Wedmann *et al.*, 2009). However, cutting edges appear to be secondarily lost in some *Megachile (sensu Gonzalez, 2008)*. In the Americas, these cutting edges are absent in the subgenera *Chrysosarus* Mitchell, some species of *Megachile s.str.*, and in the monotypic subgenera *Schrottkyapis* Mitchell and *Stelodides* Moure, although some still exhibit leafcutting behavior (*e.g.*, Zillikens & Steiner, 2004).

As part of ongoing studies on the systematics of leafcutter bees, herein I provide taxonomic comments on the subgenus *Chrysosarus* and synonymize with this group the South American subgenera *Austrosarus* Raw, *Stelodides*, and *Zonomegachile* Mitchell. This paper is part of a series of recent contributions dealing with the systematics of the Megachilini (*i.e.*, Gonzalez & Griswold, 2007; Gonzalez *et al.*, 2010; Engel & Gonzalez, 2011; Griswold & Gonzalez, 2011; Alqarni *et al.*, 2012; Gonzalez & Engel, 2012; Gonzalez *et al.* 2012), and centered on providing a revised and robust classification.

The relationship of *Chrysosarus* to *Stelodides* and *Zonomegachile* was first indicated by Mitchell (1980). He recognized *Chrysosarus* at the generic level, with *Dactylomegachile* Mitchell, *Stelodides*, and *Zonomegachile* as subgenera. In Michener's (2000) classification, in which a large, all-encompassing genus *Megachile* was recognized, *Dactylomegachile* was synonymized with *Chrysosarus* while *Stelodides* and *Zonomegachile* were treated as separated subgenera. Such a relationship of *Chrysosarus* with *Dactylomegachile* and *Stelodides* has been supported in the cladistic analysis of Gonzalez (2008) and Durante & Cabrera (2009). The synonyms proposed herein are based on these works and are presented at this time to make them available in a forthcoming, updated phylogenetic analysis and classification of the Megachilini (Gonzalez, in prep.).

SYSTEMATICS

Genus *Megachile* Latreille Subgenus *Chrysosarus* Mitchell

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

Megachile (Dactylomegachile) Mitchell, 1943: 670. Type species: *Megachile parsonsiae* Schrottky, 1913, by original designation.

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

New synonymy.

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

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

DISCUSSION

Chrysosarus, as here circumscribed, is equivalent to the genus *Chrysosarus sensu* Mitchell (1980); Mitchell's subgeneric names are regarded here as synonyms and informal species groups. *Chrysosarus* is a large and diverse subgenus. It comprises about 60 species that occur from Honduras to Argentina and central Chile, although it is most diverse in South America (Michener, 2007; Moure *et al.*, 2007). The mandible of the female lacks cutting edges, except in a few species with an incomplete cutting edge in the second interspace (the *frankieana* species group).

Megachile euzona, the single species placed in *Stelodides* by Moure (1953), differs from most *Chrysosarus* in its chalicodomiform body, the black body integument contrasting with the orange integument of the antenna and legs, and the black pubescence on the metasoma with a band of white setae on the third tergum. Its distinctive body color is unique among *Chrysosarus*, but it is similar to that found in many other unrelated groups of bees (e.g., *Leioproctus* Smith subgenus *Perditomorpha* Ashmead of the family Colletidae) and wasps that occur in Chile and Argentina, suggesting a geographical convergence in color pattern. As in most *Chrysosarus*, it lacks cutting edges in the female mandible. *Stelodides* rendered *Chrysosarus* paraphyletic in some of the cladistic analyses of Gonzalez (2008), confirming the suspicion of Michener (2000, 2007) that *M. euzona* is merely a derived species of *Chrysosarus* and does not deserve subgeneric status.

Zonomegachile consists of three described species (Moure *et al.*, 2007) and also seems to be a highly derived species group within *Chrysosarus*. An unnamed species from Argentina, presumably related to the *parsonsiae* species group (*Dactylomegachile sensu* Mitchell, 1943), was examined. Judging by the drawings of Mitchell (1980), this species has a similar mandibular structure to that of *M. mariannae*, the type species of *Dactylomegachile*. In Mitchell's (1980) figure 51, there appear to be incomplete cutting edges in the second and third interspaces; however, in the Argentinean specimens these "cutting edges" are thin, translucent extensions of the cuticle on the outer mandibular surface, not from the lower border of the tooth or extensions from a transverse ridge, at the base of the tooth, that runs parallel to the fimbriate line on the inner surface of the mandible as in other *Megachile* (Gonzalez, 2008). Therefore, the mandible of *Zonomegachile* lacks cutting edges as do most species of *Chrysosarus*.

Raw (2006) distinguished *M. frankieana* and two other species subgenerically as *Austrosarus*. The female of this group is distinctive because it has a well developed incomplete cutting edge in the second interspace of the mandible and, as in some species of *Austromegachile* Mitchell, incomplete white apical fasciae beneath the scopal setae. I have not been able to examine Raw's specimens, but *M. (Chrysosarus) parsonsiae*, as well as an unnamed species from Argentina, have an indication of an incomplete cutting edge below the inferior border of the third tooth (hidden when the mandible is seen in frontal view), and also broadly interrupted white apical fasciae beneath the metasomal scopa. *Austrosarus* is clearly a derived species group, presumably closely related to the *parsonsiae* species group. Thus, the name *Austrosarus* is tentatively placed within *Chrysosarus*. Furthermore, the presence of cutting edges in the female

mandible and the white apical fasciae beneath the scopa are highly variable among species within subgenera of *Megachile* [e.g., refer to comments for *Eutricharaea* Thomson and *Austromegachile* in Michener (2007)].

Durante & Cabrera (2009) also explored the phylogenetic relationships of *Chrysosarus*. In their study, 63 morphological characters of 17 species were analyzed (1 *Dasymegachile*, 1 *Zonomegachile*, *Stelodides*, 9 *Dactylomegachile*, and 5 *Chrysosarus*). A single most parsimonious tree was obtained and *Stelodides* was sister to the remaining species. In the next branch was *Zonomegachile*, sister to a clade consisting of *Dactylomegachile* and *Chrysosarus*, each as a monophyletic group. Based on these results, the authors resurrected *Dactylomegachile*. However, *Dasymegachile*, *Zonomegachile*, and *Stelodides* were treated as outgroups, characters were only coded for the male of *Zonomegachile*, and many characters could not be recorded; thus, the position of *Zonomegachile* and *Stelodides* were likely affected by treating them as outgroups in the analysis, instead of permitting them to move freely among the ingroup species, as well as by the absence of pertinent data. Furthermore, *Austrosarus* was excluded from their study. Despite these limitations, the analysis of Durante & Cabrera (2009) supports the relationship of *Chrysosarus* with the other subgenera discussed here and does not alter the taxonomic decisions presented above.

The biology of *Dactylomegachile* and *Chrysosarus* also supports their phylogenetic relationship. Species of both groups nest in pre-existing cavities, cells are made of mud, with the inner and outer walls covered by petals or leaf pieces, and are built even in the absence of confining walls (Laroca, 1971; Laroca *et al.*, 1992; Zillikens & Steiner, 2004).

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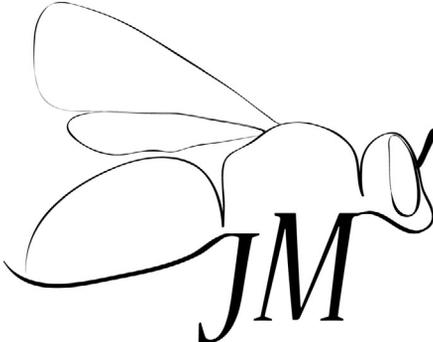
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