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Phylogeny of the cleptoparasitic Megachilini genera *Coelioxys* and *Radoszkowskiana*, with the description of six new subgenera in *Coelioxys* (Hymenoptera: Megachilidae)

LÉO CORREIA DA ROCHA FILHO[1]* and LAURENCE PACKER[2]

[1]*Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, Ribeirão Preto 14040-901, Brazil*
[2]*Department of Biology, York University, 4700 Keele St, Toronto ON, M3J 1P3, Canada*

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The Megachilini is the most speciose tribe within Megachilidae, comprising four genera: *Coelioxys* Latreille, 1809, *Megachile* Latreille, 1802, *Noteriades* Cockerell, 1931, and *Radoszkowskiana* Popov, 1955. In spite of its high diversity and ubiquity, the phylogenetic relationships both within and among the genera are still obscure. In view of the lack of a phylogenetic analysis for the species of the cleptoparasitic genera *Coelioxys* and *Radoszkowskiana*, a phylogeny using parsimony was inferred based on 239 adult morphological characters. The analyses included the four known species of *Radoszkowskiana* and 72 species of *Coelioxys* as the in-group, representing all subgenera currently recognized. Another 14 species of *Anthidium* Fabricius, 1804, *Aspidosmia* Brauns, 1926, *Dioxys* Lepeletier & Serville, 1825, *Lithurgopsis* Fox, 1902, *Megachile, Noteriades*, *Ochreriades* Mavromoustakis, 1956, and *Osmia* Panzer, 1806 were included as the out group. In the equal-weights analysis, *Coelioxys* and *Radoszkowskiana* formed a clade nested within *Megachile*. Taxonomic implications for the genus *Coelioxys* are as follows: the subgenera *Coelioxys* (*Acrocoelioxys*) Mitchell, 1973, *Coelioxys* (*Haplocoelioxys*) Mitchell, 1973, and *Coelioxys* (*Mesocoelioxys*) Ruszkowski, 1986 are merged with *Coelioxys* (*Neocoelioxys*) Mitchell, 1973, *Coelioxys* (*Glyptocoelioxys*) Mitchell, 1973, and *Coelioxys* (*Allocoelioxys*) Tkalců, 1974, respectively; *Coelioxys* (*Dasycoelioxys*) Mitchell, 1973 and *Coelioxys* (*Paracoelioxys*) Gribodo, 1884 are raised from synonymy with *C.* (*Glyptocoelioxys*) and *Coelioxys* (*Coelioxys s.s.*) Latreille, 1809, respectively. Six new subgenera are described: *Coelioxys* (*Austrocleptria*) Rocha-Filho and *Coelioxys* (*Leuraspidia*) Rocha-Filho from the Neotropical region, *Coelioxys* (*Melissoctonia*) Rocha-Filho and *Coelioxys* (*Rozeniana*) Rocha-Filho from the Palaearctic region, *Coelioxys* (*Eingana*) Rocha-Filho from Australia, and *Coelioxys* (*Callosarissa*) Rocha-Filho from both Australasian and Indomalayan regions. Some taxonomic observations are made and a key to the 20 *Coelioxys* subgenera recognized herein is provided.

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ADDITIONAL KEYWORDS: group support – identification key – implied weighting – morphology – successive approximations character weighting.

INTRODUCTION

The tribe Megachilini is the most diverse of all Megachilidae, corresponding to 49.2% of the species recorded for the family (Ascher & Pickering, 2015). In spite of being considered monophyletic in a phylogeny of all major lineages of long-tongued bees (Roig-Alsina & Michener, 1993), there were no known synapomorphies for the tribe (Gonzalez *et al.*, 2012). In both the molecular analyses of Praz *et al.* (2008) and Litman *et al.* (2011), and the morphological phylogenetic study by Gonzalez *et al.* (2012), the genus *Noteriades* Cockerell, 1931, previously placed in Osmiini, was nested within Megachilini. In view

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*Corresponding author. E-mail: correiadarocha@yahoo.com.br

of this result, Gonzalez *et al.* (2012) transferred the genus to Megachilini, listed three putative synapomorphies for the clade, and established a new classification for the tribe that now encompasses four genera: *Noteriades*, *Megachile* Latreille, 1802, *Coelioxys* Latreille, 1809, and *Radoszkowskiana* Popov, 1955. The tribe includes nest building (*Noteriades* and *Megachile*) and cleptoparasitic (*Coelioxys* and *Radoszkowskiana*) genera, and the latter primarily attack *Megachile* spp. (Mitchell, 1973; Baker, 1975; Michener, 2007; Rozen & Kamel, 2007).

Regarding cleptoparasitic and hospicidal behaviours, two distinct modes are recorded for Megachilini: females of *Radoszkowskiana rufiventris* (Spinola, 1838) and *Coelioxys* (*Allocoelioxys*) *coturnix* Pérez, 1884 enter the host nest and oviposit after the host female has deposited her egg (Rozen & Kamel, 2007, 2008). In contrast, species such as *Coelioxys* (*Liothyrapis*) *decipiens* Spinola, 1838, *Coelioxys* (*Boreocoelioxys*) *octodentata* Say, 1824, and *Coelioxys* (*Boreocoelioxys*) *sayi* Robertson, 1897 lay their egg before the host egg is deposited (Baker, 1971; Rozen & Kamel, 2007). These two distinct modes also differ in the host life stage that is attacked, the cleptoparasitic larval instar that performs the attack, the behaviour of the attacking instar, and the mandibular modifications involved in the attack (Rozen & Kamel, 2007). Based on those facts, Rozen & Kamel (2008) pointed out that *Radoszkowskiana* and *Coelioxys* could possibly have had a common parasitic ancestor, and that two modes of cleptoparasitism had evolved in *Coelioxys*. A molecular phylogenetic analysis of the origins of cleptoparasitic lineages in long-tongued bees suggested one or two further origins of cleptoparasitism in the tribe Megachilini (Litman *et al.*, 2013). Thus, the authors stressed the importance of a detailed phylogenetic study in order to clarify the relationship between *Radoszkowskiana* and *Coelioxys*.

Radoszkowskiana is a small genus with only four species and a distribution ranging from northern Africa to India (Schwarz, 2001; Ascher & Pickering, 2015). The only host record for this genus was provided by Rozen & Kamel (2007), who described the biology and immature stages of *R. rufiventris*, a cleptoparasite of *Megachile* (*Pseudomegachile*) *nigripes* (Spinola, 1838). *Coelioxys*, by contrast, is a cosmopolitan, wide-ranging, megadiverse genus with at least 481 species currently recognized and recorded in almost all continents, except Antarctica, and most countries, excepting Iceland, New Zealand, and some small archipelagos and islands in the Indian and Pacific oceans (Mitchell, 1973; Michener, 2007; Ascher & Pickering, 2015). Despite most of the known host records for *Coelioxys* being for *Megachile* species (Mitchell, 1973; Baker, 1975; Michener, 2007), there are some examples of associations with other bee genera: *Anthophora* Latreille, 1803 (Westrich, 1990), *Carloticola* Moure & Urban, 1991 (Rocha-Filho, 2015), *Centris* Fabricius, 1804 (Vinson, Frankie & Rao, 2011), *Epanthidium* Moure, 1947 (C.A. Garófalo, pers. comm.), *Euglossa* Friese, 1802 (Augusto & Garófalo, 2004), *Hoplitis* Klug, 1807 (Westrich, 1990; Voith, 1997), *Osmia* Panzer, 1806 (Alfken, 1928), *Tetraloniella* Ashmead, 1899 (Apidae) (Scheuchl, 1996), and *Trachusa* Panzer, 1804 (Megachilidae) (Westrich, 1990).

Mitchell (1973), considering the high diversity of the *Coelioxys* fauna from the New World, subdivided the genus into 13 subgenera. For the Old World fauna, however, the situation is less straightforward, with various subgenera proposed by different authors (Pasteels, 1968, 1977, 1982; Tkalců, 1974; Ruszkowski *et al.*, 1986; Gupta, 1991, 1992, 1993). Currently at least 15 subgenera are recognized in *Coelioxys* (Mitchell, 1973; Michener, 2007; Moure, Melo & Dalmolin, 2012; Ascher & Pickering, 2015); however, most taxonomic studies of *Coelioxys* have been of local faunas (Holmberg, 1916; Pasteels, 1968, 1977; Mitchell, 1973; Tkalců, 1974; Baker, 1975; Warncke, 1992), and the systematics of this complex, worldwide genus remains unresolved. A phylogenetic analysis is badly needed in order to determine the taxonomic status of the various subgenera currently recognized, and the relationships among them. Of equal importance is the need to resolve the relationship between *Coelioxys* and *Radoszkowskiana*, as well as their relationships to the other genera within the tribe Megachilini.

In view of the above and considering the lack of a phylogenetic study for both the genera *Coelioxys* and *Radoszkowskiana*, this article provides a morphological phylogenetic analysis for both genera, including all four *Radoszkowskiana* species as well as species of all *Coelioxys* subgenera. The taxonomic status of *Coelioxys* subgenera is revised and a key to all subgenera recognized herein is also provided.

MATERIAL AND METHODS

Specimens studied

Most of the material examined in this study was from the Packer Collection, York University, Toronto, Canada (PCYU), but some specimens were borrowed from the following institutions: Australian National Insect Collection, Canberra, Australia (ANIC); Maximilian Schwarz' personal collection, Ansfelden, Austria (Ansfelden); United States National Pollinating Insects Collection, Bee Biology and Systematics Laboratory, Utah State University, Logan, USA (BBSL); Coleção de Abelhas e Vespas Solitárias, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Ribeirão Preto, Brazil (CAVS); Departamento de Zoologia, Universidade Federal de

Minas Gerais, Belo Horizonte, Brazil (DZMG); Essig Museum of Entomology, University of California, Berkeley, USA (EMEC); Luonnontieteellinen keskusmuseo, Helsinki, Finland (LK); Coleção Camargo, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Ribeirão Preto, Brazil (RPSP); National Museum of Natural History, Smithsonian Institute, Washington D.C., USA (USNM); and Zoologische Staatssammlung München, Munich, Germany (ZSM).

TAXA

All four recognized species of *Radoszkowskiana* and 72 species of *Coelioxys* were selected and included in the analysis as the in-group (Table 1). The

Table 1. List of the species used in the phylogenetic analysis

Species	Collection localities	Institute(s)
Lithurgopsis apicalis (Cresson, 1875)	USA	PCYU
Anthidium (*Anthidium*) *utahense* (Swenk, 1914)	USA	PCYU
Aspidosmia volkmanni (Friese, 1909)	South Africa	PCYU
Dioxys cincta (Jurine, 1807)	Morocco, Turkey	Ansfelden
Ochreriades fasciata (Friese, 1899)	Israel	PCYU
Osmia (*Cephalosmia*) *californica* (Cresson, 1864)	Canada	PCYU
Noteriades chapini (Cockerell, 1933)	Kenya	PCYU
Noteriades cf. *clypeata* (Friese, 1904)	Rep. of Congo	PCYU
Megachile (*Chelostomoides*) *angelarum* (Cockerell, 1902)	Canada, USA	PCYU
Megachile (*Creightonella*) *discolor* (Smith, 1853)	Kenya, South Africa	PCYU
Megachile (*Eutricharaea*) *rotundata* (Fabricius , 1787)	Canada	PCYU
Megachile (*Gronoceras*) *felina* (Gerstäcker, 1857)	Kenya	PCYU
Megachile (*Pseudomegachile*) *fulva* (Smith, 1853)	South Africa	PCYU
Megachile (*Sayapis*) *pugnata* (Say 1837)	Canada	PCYU
Radoszkowskiana barrei (Radoszkowski, 1893)*	Iran, Turkey	Ansfelden
Radoszkowskiana gusevi (Schwarz, 2001)	Syria	Ansfelden
Radoszkowskiana rufiventris (Spinola, 1838)	Egypt	Ansfelden
Radoszkowskiana tkalcui (Schwarz, 2001)	Turkey	Ansfelden
Coelioxys (*Acrocoelioxys*) *azteca* (Cresson , 1878)	Costa Rica, Honduras	EMEC
Coelioxys (*Acrocoelioxys*) *dinellii* (Holmberg, 1916)	Argentina, Peru	PCYU
Coelioxys (*Acrocoelioxys*) *dolichos* (Fox, 1890)	USA	PCYU
Coelioxys (*Acrocoelioxys*) *otomita* (Cresson, 1878)*	Mexico	EMEC
Coelioxys (*Acrocoelioxys*) *tolteca* (Cresson, 1878)*[1]	Mexico, Paraguay	EMEC, PCYU
Coelioxys (*Allocoelioxys*) *acanthura* (Illiger, 1806)	Kazakhstan	Ansfelden
Coelioxys (*Allocoelioxys*) *afra* (Lepeletier, 1841)*[2]	Bulgaria, Slovakia	Ansfelden
Coelioxys (*Allocoelioxys*) *caudata* (Spinola, 1838)	Turkey	Ansfelden
Coelioxys (*Allocoelioxys*) *echinata* (Förster, 1853)*[3]	Bulgaria, Slovakia	Ansfelden
Coelioxys (*Allocoelioxys*) *erythrura* (Spinola, 1838)	Kenya	PCYU
Coelioxys (*Allocoelioxys*) *nasuta* (Friese, 1904)	Kenya	PCYU
Coelioxys (*Allocoelioxys*) *polycentris* (Förster, 1853)	Slovakia	Ansfelden
Coelioxys (*Boreocoelioxys*) *alata* (Förster, 1853)*[4]	Germany, Russia	LK, ZSM
Coelioxys (*Boreocoelioxys*) *banksi* (Crawford, 1914)	Canada, USA	PCYU
Coelioxys (*Boreocoelioxys*) *funeraria* (Smith, 1854)*[5]	Canada	PCYU
Coelioxys (*Boreocoelioxys*) *moesta* (Cresson, 1864)	Canada	PCYU
Coelioxys (*Boreocoelioxys*) *porterae* (Cockerell, 1900)	Canada	PCYU
Coelioxys (*Boreocoelioxys*) *rufescens* (Lepeletier & Serville, 1825)	United Kingdom	PCYU
Coelioxys (*Boreocoelioxys*) *rufitarsis* (Smith, 1854)*	Canada	PCYU
Coelioxys (*Boreocoelioxys*) *sayi* (Robertson, 1897)	Canada, USA	PCYU
Coelioxys (*Coelioxys*) *albolineata* (Cockerell, 1905)	Australia	ANIC
Coelioxys (*Coelioxys*) *conoidea* (Illiger, 1806)	United Kingdom	PCYU
Coelioxys (*Coelioxys*) *froggatti* (Cockerell, 1911)	Australia	ANIC
Coelioxys (*Coelioxys*) *quadridentata* (Linnaeus, 1758)*	Czech Rep., Slovakia	Ansfelden
Coelioxys (*Coelioxys*) *reginae* (Cockerell, 1905)	Australia	ANIC, PCYU
Coelioxys (*Coelioxys*) *serricaudata* (Baker, 1975)	USA	EMEC

Table 1. *Continued*

Species	Collection localities	Institute(s)
Coelioxys (*Coelioxys*) *sodalis* (Cresson, 1878)	Canada, USA	PCYU
Coelioxys (*Cyrtocoelioxys*) *chichimeca* (Cresson, 1878)	Costa Rica, Mexico	EMEC
Coelioxys (*Cyrtocoelioxys*) *costaricensis* (Cockerell, 1914)*	Costa Rica, Mexico	PCYU, USNM
Coelioxys (*Cyrtocoelioxys*) *gonaspis* (Cockerell, 1924)	Mexico, USA	EMEC
Coelioxys (*Cyrtocoelioxys*) *modesta* (Smith, 1854)	Canada	PCYU
Coelioxys (*Cyrtocoelioxys*) *paraguaya* (Moure, 1943)	Brazil	CAVS
Coelioxys (*Cyrtocoelioxys*) *speculifera* (Cockerell, 1931)	Colombia, Mexico	PCYU
Coelioxys (*Glyptocoelioxys*) *cayennensis* (Spinola, 1841) *[6]	Argentina	PCYU
Coelioxys (*Glyptocoelioxys*) *cerasiopleura* (Holmberg, 1903)	Argentina	PCYU
Coelioxys (*Glyptocoelioxys*) *chilensis* (Reed, 1892)	Chile	PCYU
Coelioxys (*Glyptocoelioxys*) *germana* (Cresson, 1878)	USA	EMEC, PCYU
Coelioxys (*Glyptocoelioxys*) *kuscheli* (Moure, 1951)	Chile	PCYU
Coelioxys (*Glyptocoelioxys*) *pergandei* (Schletterer, 1890)*	Chile	PCYU
Coelioxys (*Glyptocoelioxys*) *praetextata* (Haliday, 1836)	Argentina	PCYU
Coelioxys (*Haplocoelioxys*) *mexicana* (Cresson, 1878)*	USA	EMEC, PCYU
Coelioxys (*Liothyrapis*) *apicata* (Smith, 1854)*	India, Nepal	Ansfelden
Coelioxys (*Liothyrapis*) *decipiens* (Spinola, 1838)	Egypt, Tunisia	Ansfelden
Coelioxys (*Liothyrapis*) *rotundicauda* (Cockerell, 1935)	Namibia	Ansfelden
Coelioxys (*Liothyrapis*) *scioensis* (Gribodo, 1879)	Malawi	PCYU
Coelioxys (*Mesocoelioxys*) *argentea* (Lepeletier, 1841)*	Kyrgyzstan	Ansfelden
Coelioxys (*Neocoelioxys*) *abdominalis* (Guérin, 1844)	Puerto Rico	PCYU
Coelioxys (*Neocoelioxys*) *simillima* (Smith, 1854)*[7]	Argentina, Mexico	PCYU
Coelioxys (*Neocoelioxys*) *slossoni* (Viereck, 1902)	USA	PCYU
Coelioxys (*Neocoelioxys*) *vigilans* (Smith, 1879)	Dominican Rep.	PCYU
Coelioxys (*Platycoelioxys*) *alatiformis* (Friese, 1921)*	Costa Rica, Peru	PCYU, BBSL
Coelioxys (*Rhinocoelioxys*) *agilis* (Smith, 1879)	Brazil	DZMG, RPSP
Coelioxys (*Rhinocoelioxys*) *barbata* (Schwarz & Michener, 1954)	Venezuela	USNM
Coelioxys (*Rhinocoelioxys*) *clypearis* (Friese, 1921)	Brazil	DZMG, RPSP
Coelioxys (*Rhinocoelioxys*) *nasidens* (Friese, 1921)	Bolivia, Brazil	BBSL, USNM
Coelioxys (*Rhinocoelioxys*) *paraguayensis* (Schrottky, 1909)	Bolivia, Brazil	RPSP, BBSL
Coelioxys (*Rhinocoelioxys*) *zapoteca* (Cresson, 1878)*	Brazil, Costa Rica	DZMG, BBSL
Coelioxys (*Synocoelioxys*) *alternata* (Say, 1837)	USA	PCYU
Coelioxys (*Synocoelioxys*) *apacheorum* (Cockerell, 1900)	Canada	PCYU
Coelioxys (*Synocoelioxys*) *hunteri* (Crawford, 1914)	USA	PCYU
Coelioxys (*Synocoelioxys*) *texana* (Cresson, 1872)*	USA	EMEC, PCYU
Coelioxys (*Torridapis*) *ducalis* (Smith, 1854)	Indonesia, Malaysia	Ansfelden
Coelioxys (*Torridapis*) *torrida* (Smith, 1854)*	Comoros, Mali	Ansfelden
Coelioxys (*Torridapis*) *weinlandi* (Schulz, 1904)	Papua New Guinea	Ansfelden
Coelioxys (*Xerocoelioxys*) *aperta* (Cresson, 1878)	Mexico, USA	PCYU
Coelioxys (*Xerocoelioxys*) *bisoncornua* (Hill, 1936)	USA	EMEC
Coelioxys (*Xerocoelioxys*) *edita* (Cresson, 1872)*	USA	PCYU
Coelioxys (*Xerocoelioxys*) *grindeliae* (Cockerell, 1900)	USA	PCYU
Coelioxys (*Xerocoelioxys*) *mesae* (Cockerell, 1921)	Mexico, USA	PCYU
Coelioxys bertonii (Schrottky, 1909)	Brazil	CAVS
Coelioxys confusa (Smith, 1875	Thailand, Vietnam	PCYU
Coelioxys odin (Strand, 1912)	Kenya	PCYU

The type species of *Radoszkowskiana* and of each subgenus of *Coelioxys* are indicated with an asterisk. The superscript numbers indicate type species of synonymized subgenera: [1]*C.* (*Melanocoelioxys*); [2]both *C.* (*Allocoelioxys*) and *C.* (*Coelioxita*); [3]both *C.* (*Coelioxula*) and *C.* (*Intercoelioxys*); [4]*C.* (*Paracoelioxys*); [5]*C.* (*Schizocoelioxys*); [6]Mitchell (1973) considered *Coelioxys vidua* Smith, 1854 a synonym of *Coelioxys praetextata* Haliday, 1836, as the type species of *C.* (*Glyptocoelioxys*); however, Moure, Melo & Dalmolin (2007), by subsequent designation, fixed *C. chacoensis* as the type species, which is a synonym of *C. cayennensis*; [7]*C. assumptionis* is the type species of *C.* (*Neocoelioxys*), but was considered a synonym of *Coelioxys simillima* Smith, 1854 by both Ascher & Pickering (2015) and Moure *et al.* (2012).

classification of *Coelioxys* subgenera initially followed Michener (2007). Thus, 15 subgenera (nine exclusive to the New World, one Holarctic, one cosmopolitan, and four from the Old World) were initially recognized. The type species of each of the 15 subgenera was included in the analysis, as were any additional species available to us (Table 1, and see details in the table legend). Three species considered as *incertae sedis* by Ascher & Pickering (2015) were also added to the analysis (Table 1): *Coelioxys bertonii* Schrottky, 1909, *Coelioxys confusa* Smith, 1875, and *Coelioxys odin* Strand, 1912. Species of the other two genera of the tribe Megachilini, *Megachile*, and *Noteriades*, were included as out-groups. Likewise, the other four tribes within the subfamily Megachilinae, as proposed by Gonzalez *et al.* (2012) – Anthidiini, Aspidosmiini, Dioxyini, and Osmiini – were represented by one species each (Table 1). Lastly, *Ochreriades fasciata* (Friese, 1899) was included because the position of this genus within the subfamily remains unclear (Praz *et al.*, 2008). *Lithurgopsis apicalis* (Cresson, 1875) (Lithurginae) was used to root the tree.

CHARACTERS

The sting apparatus of females as well as the hidden sterna and genital capsule of males were dissected and cleared in a 10% KOH solution, and then stored in glycerine, except for females of *Coelioxys weinlandi* Schulz, 1904, *Radoszkowskiana barrei* (Radoszkowski, 1893), *Radoszkowskiana gusevi* Schwarz, 2001, and *Radoszkowskiana tkalcui* Schwarz, 2001, , because of the scarcity of individuals of those species in collections. The female of *Coelioxys costaricensis* Cockerell, 1914 was also not dissected because the only specimen available was the holotype (on loan from the USNM). *Noteriades chapini* (Cockerell, 1933) was represented only by the female.

In total, 239 morphological characters (numbered 0–238) were scored for the 90 terminal taxa (see also Supporting Information, Table S2). Thirty-three characters used by Gonzalez *et al.* (2012) were included because they varied among our terminals; seven of them were modified as needed for the different suite of taxa we used (see comments on the relevant characters in the Character List). Characters considered diagnostic and/or used in taxonomic studies of *Coelioxys* by Pasteels (1968, 1977), Baker (1975), or Mitchell (1973) were added. Other characters are new and are based on the study of the morphology of our material. In order to avoid duplication, characters present in both sexes were coded only in the females because we did not have males of one of our terminals (*N. chapini*). Characters that were not applicable were coded as missing data (–), whereas question marks (?) were used when the male was absent or when females were not dissected, as noted above. Morphological terminology follows Mitchell (1973), with one exception: Mitchell (1973) used the term ‘apical rim’ for what we call the apical impressed area of the male sterna. The term midocellar area refers to the area immediately surrounding the mid ocellus and anteriorly to it. The following abbreviations were used: T, S, H, and F for metasomal terga, sterna, hemiterga, and flagellomeres, respectively. All measurements are in millimetres (mm).

IMAGES

Some of the morphological characters were illustrated using a Visionary Digital BK Plus imaging system using a Canon EOS 40D digital SLR camera. The photographs were then processed with Adobe PHOTOSHOP. The characteristics used in the key are shown in Figures 4–93. Figure 94 illustrates some of the less well-known characters/character states that were used in the phylogenetic analysis.

PHYLOGENETIC ANALYSIS

Parsimony analyses were performed using equally weighted characters, implied weighting, and successive weighting with TNT1.1 (Goloboff, Farris & Nixon, 2008b). Weighted analyses were performed because they reduce the impact of the more homoplasious characters on the results (Goloboff *et al.*, 2008a), and we chose implied weighting (Goloboff, 1993) because it weights characters during tree search (Goloboff *et al.*, 2008a). Tree searches were conducted using heuristic methods with a driven search and with default parameters, except as follows: we performed 10 000 and 100 000 replications, drift and ratchet (both with default parameters), random seed = 0, saving ten trees per replicate, and not collapsing trees after search. Branch support was estimated by absolute group frequencies through Bootstrapping (Felsenstein, 1985) and by frequency-group differences through symmetric resampling (Goloboff *et al.*, 2003), with 10 000 replicates. Bremer support values (Bremer, 1994; Goloboff & Farris, 2001) were calculated using TNT.

WinClada 1.00.08 (Nixon, 2002) was used to map the characters for visual inspection, tree editing, and figure generation.

CHARACTER LIST

Female

0. **First flagellomere (F1):** 0, at least 1.2× as long as second flagellomere (F2); 1, less than 1× but more

than 0.8× as long as F2; 2, at most 0.8× as long as F2.

1. **Interantennal distance:** 0, equal to or shorter than antennocular distance; 1, longer than antennocular distance (Gonzalez *et al.*, 2012).

2. **Antennal socket with a distinct mesal process on upper half:** 0, absent; 1, present (Gonzalez *et al.*, 2012: fig. 5).

3. **Compound eye:** 0, bare (Fig. 4); 1, hairy (Fig. 5).

4. **Compound eye pilosity:** 0, sparse (as in Fig. 16); 1, dense (as in Fig. 5). Not applicable for taxa with bare eyes.

5. **Ocular hairs:** 0, very short (<0.07 mm); 1, short (0.07–0.08 mm); 2, long (~0.12 mm); 3, very long (~0.17 mm or longer). Not applicable for taxa with bare eyes.

6. **Eye surface:** 0, not or weakly convex ventrally (Fig. 76); 1, distinctly convex ventrally (Fig. 74).

7. **Midocellar area sculpturing, anterior to and immediately surrounding mid ocellus:** 0, punctate or densely punctate throughout (Fig. 54); 1, densely punctate only around mid ocellus, rest impunctate (Fig. 52); 2, impunctate around mid ocellus and densely punctate elsewhere (Fig. 4); 3, sparsely punctate throughout (Fig. 53). In *Lithurgopsis apicalis* the impunctate area is only anterior to the mid ocellus, and thus it was coded 2. In *Coelioxys alatiformis* there are a few punctures anterior to the mid ocellus, but it was coded as 2 because the anterior area is clearly different in sculpture from the rest of the area around the midocellus.

8. **Area around mid ocellus (carinate edge to swelling absent, unless stated otherwise):** 0, flat, not swollen (Fig. 54); 1, swollen around the entire circumference of mid ocellus (Fig. 53); 2, swollen only anteriorly (Rocha-Filho & Packer, 2015: fig. 3G); 3, swollen only posteriorly (Rocha-Filho & Packer, 2015: fig. 19B); 4, swollen around the entire circumference, with a carinate edge (Fig. 4).

9. **Supraclypeal area:** 0, raised above surrounding face but surface otherwise flat; 1, elevated medially, forming a rounded ridge (Fig. 53); 2, elevated medially, forming a sharp keel at least apically (Fig. 54); 3, with a tubercle between antennal sockets; 4, not elevated or keeled (Fig. 54).

10. **Apex of clypeus, hair fringe:** 0, absent; 1, present (Fig. 48).

11. **Clypeal surface:** 0, flat or nearly so (Fig. 54); 1, swollen or produced apically (Fig. 5); 2, apicoventrally reflexed (Fig. 48).

12. **Clypeal pilosity density:** 0, disc densely covered with hairs, integument not visible or barely visible (Fig. 4); 1, disc not densely covered with hairs, with at least the integument of the medial area of the disc visible (Fig. 81).

13. **Clypeal pilosity length:** 0, disc with long, appressed/subappressed hairs or long, suberect hairs (Fig. 4); 1, disc with short/minute, appressed/subappressed hairs (Fig. 82).

14. **Clypeal erect, sparse hairs:** 0, thick, erect hairs throughout the disc, contrasting with the appressed or subappressed hairs (Rocha-Filho & Packer, 2015: fig. 7B); 1, thin, erect, long hairs throughout the disc, contrasting with appressed or subappressed hairs (Fig. 81); 2, without thick or long hairs (Fig. 48). In *Coelioxys edita* there are sparse suberect, short, plumose hairs, and thus it was coded as 2.

15. **Clypeus apical margin:** 0, simple or indented (Fig. 48); 1, emarginate (Fig. 5) or strongly indented; 2, convex. In *Coelioxys zapoteca* females the clypeus shape can vary from truncate to strongly bilobed (Rocha-Filho & Packer, 2015), hence this species was coded as polymorphic even though the female studied herein has the apical margin simple.

16. **Clypeus medially with paired, longitudinal medial ridges:** 0, absent (Fig. 48); 1, present (Rocha-Filho & Packer, 2015: fig. 19B).

17. **Clypeus with dorsal carina medially:** 0, absent (Fig. 48); 1, present.

18. **Ventral portion of hypostomal carina, near mandible:** 0, directed to medial margin of mandibular socket; 1, curving towards posterior margin of mandibular socket (Gonzalez *et al.*, 2012).

19. **Mandible, number of teeth:** 0, three or less; 1, more than three.

20. **Mandible shape:** 0, modified, with distinct flange on outer surface (Baker, 1975: fig. 36C); 1, normal, lacking distinct flange (Figs 81, 82).

21. **Mandible shape dorsally:** 0, straight, not conspicuously curved medially on outer surface (Baker, 1975: fig. 11B); 1, conspicuously curved medially on outer surface (Fig. 82); 2, angled medially on outer surface (Fig. 81).

22. **Mandible with conspicuous, thick, long, erect hairs dorsally:** 0, present (Rocha-Filho & Packer, 2015: fig. 7B); 1, absent (Fig. 82).

23. **Mandible pilosity with sparse, erect, long golden hairs dorsally:** 0, present (Fig. 82); 1, absent. These hairs are entirely different from those of the previous character.

24. **Mandible dorsal surface:** 0, nearly bare or hairy only basally; 1, densely covered with hairs except subapically.

25. **Mandible with outer premarginal impressed fimbria:** 0, reduced or absent; 1, present, distinct (Gonzalez *et al.*, 2012).

26. **Paraocular area:** 0, covered predominantly with subappressed or erect hairs, underlying integument visible (Fig. 81); 1, conspicuously covered with

appressed hairs at least on lower margin where integument not visible beneath hairs (Fig. 5).

27. **Pilosity of punctures on vertex:** 0, with only long suberect hairs, appressed plumose or scale-like hairs absent (Fig. 52); 1, a mixture of appressed plumose and long suberect hairs; 2, a mixture of appressed scale-like hairs and long suberect hairs (Fig. 32).

28. **Vertex:** 0, coarsely and densely punctate, no flat interspaces between punctures; 1, punctate, flat interspaces between punctures shorter than puncture diameters (Fig. 52); 2, shining, sparsely punctate, interspaces greater than puncture diameters (Fig. 53).

29. **Ocellocular distance:** 0, clearly shorter than ocelloccipital distance (Fig. 32); 1, subequal to ocelloccipital distance; 2, clearly longer than ocelloccipital distance (Fig. 53).

30. **Preoccipital carina:** 0, absent; 1, present (Fig. 32) (Gonzalez *et al.*, 2012).

31. **Preoccipital carina interrupted on vertex:** 0, no (Fig. 32); 1, yes (Gonzalez *et al.*, 2012; modified). Not applicable for taxa without a carina.

32. **Omaulus:** 0, absent, lateral and anterior surfaces of mesopleuron evenly rounded onto each other; 1, present, angulate, carinate, or lamellate (Gonzalez *et al.*, 2012).

33. **Pronotal tubercle:** 0, nearly straight, not forming distinct lobes (Fig. 31); 1, emarginate, forming two distinct lobes (Fig. 73).

34. **Outer margin of pronotal lobe:** 0, carinate or lamellate (Fig. 31); 1, distinctly rounded, not carinate (Fig. 30).

35. **Carina of pronotal tubercle:** 0, conspicuously elevated, forming a distinct lamella (Figs 31, 73); 1, sharply carinate but not forming lamella, distinct except normally hidden by long hairs (Fig. 75). Not applicable for taxa with a rounded outer margin of pronotal lobe.

36. **Fascia on anterior margin of mesoscutum:** 0, absent or inconspicuous (Fig. 83); 1, conspicuous, not interrupted medially (Fig. 51); 2, conspicuous, interrupted medially (Fig. 6).

37. **Fascia on anterior margin of mesoscutum, pilosity:** 0, elongate and/or plumose hairs (Fig. 51); 1, scale-like or elliptical hairs (Fig. 6). Not applicable for taxa without fascia or with an inconspicuous fascia.

38. **Fascia on anterior margin of mesoscutum, shape:** 0, extending towards the mesoscutal disc medially (Fig. 6); 1, fascia nearly straight, not extending towards mesoscutal disc (Fig. 51). Only applicable for taxa with a conspicuous fascia.

39. **Medial area of mesoscutum:** 0, not swollen (Fig. 55); 1, conspicuously swollen (Fig. 58).

40. **Mesoscutal sculpturing:** 0, coarsely and densely punctate, no interspaces between punctures or interspaces clearly shorter than puncture diameters (Fig. 7); 1, densely punctate, interspaces between punctures subequal to or longer than puncture diameters (Fig. 51); 2, sparsely punctate, interspaces between punctures much larger than puncture diameters (Fig. 50).

41. **Mesoscutal punctures:** 0, punctures of the same size throughout (Fig. 7), 1, punctures larger towards the lateral margins, smaller on disc (Fig. 50).

42. **Mesoscutum with carina medioposteriorly:** 0, strong, carina extending from apex to midlength of mesoscutum (Fig. 11); 1, weak, a rounded elevated area not attaining midlength of mesoscutum; 2, not carinate (Fig. 50).

43. **Mesosomal pilosity:** 0, long, erect hairs, without spots of appressed hairs (Figs 30, 83); 1, short, subappressed hairs, without spots of appressed hairs; 2, short, subappressed hairs as well as spots of appressed hairs (Fig. 50); 3, long, erect hairs as well as spots of appressed hairs; 4, bare.

44. **Pubescence of body:** 0, predominantly hairs (Fig. 39); 1, with both scale-like hairs and hairs abundant; 2, predominantly scale-like hairs.

45. **Preaxilla:** 0, sloping, with hairs (Gonzalez *et al.*, 2012: fig. 10); 1, vertical, usually hairless (Gonzalez *et al.*, 2012: fig. 11).

46. **Mesoscutellum:** 0, not produced over metanotum and propodeum (Fig. 71); 1, produced over metanotum and propodeum (Figs 35, 50).

47. **Mesoscutellar pilosity anteriorly:** 0, bare or nearly so, lacking appressed hairs (Fig. 71), 1, hairs forming two separate distinct patches (Figs 50, 85); 2, hairs forming an uninterrupted fascia (Figs 51, 69).

48. **Posterior margin of mesoscutellum medially:** 0, not emarginate (Fig. 51); 1, emarginate (Fig. 35).

49. **Posterior margin of mesoscutellum:** 0, not produced medially (Fig. 71); 1, produced medially (Figs 35, 42, 50, 51, 69).

50. **Posterior margin of mesoscutellum, median process:** 0, blunt (Fig. 51); 1, tooth-like (Fig. 69); 2, apex of process emarginate (Fig. 35). Not applicable for taxa without a convex posterior margin to the mesoscutellum.

51. **Tooth-like process on mesoscutellum, orientation:** 0, horizontal (Fig. 69); 1, dorsally oriented. Not applicable for taxa without a process.

52. **Tooth-like process on mesoscutellum:** 0, dorsoventrally flattened; 1, not dorsoventrally flattened, thick, robust (Fig. 69). Not applicable for taxa without a tooth.

53. **Mesoscutellum with medial longitudinal ridge, carina, or weakly raised line:** 0, present (Figs 51, 69); 1, absent (Fig. 50).

54. **Mesoscutellum, medial dorsal surface:** 0, indistinctly raised (Rocha-Filho & Packer, 2015: fig. 5C); 1, swollen (Fig. 51); 2, keeled (Fig. 69). Not applicable for taxa with a flat dorsal surface.

55. **Mesoscutellum, length of dorsal raised portion:** 0, weakly present only basally; 1, strong, sharp, but only basally (Fig. 11); 2, strong, complete (Fig. 69). Not applicable for taxa with a flat dorsal surface.

56. **Dorsal and superior surfaces of mesoscutellum:** 0, fully separated by a distinct subcarinate, somewhat sharp, nearly impunctate edge, forming a distinct acute angle (Fig. 50); 1, separated by an indistinct subcarinate edge, forming an obtuse angle, the edge at least sparsely punctate (Fig. 51); 2, surfaces not separated, continuously curving in profile (Fig. 71). In spite of being punctate to some extent in *Coelioxys praetextata*, *C. barbata*, *C. paraguayensis*, and both *Noteriades* species, this character was coded as 0 in these taxa because of the distinct subcarinate edge between dorsal and superior surfaces of the mesoscutellum.

57. **Mesoscutellum medioposteriorly:** 0, slightly to strongly depressed; 1, flat or convex. In *Coelioxys alternata* the subcarinate edge gives the impression that the area anterior to it is depressed; however, it is not the same depressed area as observed in *C. odin* and *Coelioxys reginae* Cockerell, 1905, and thus this species was coded as 1.

58. **Mesoscutellum posteriorly:** 0, with subappressed or appressed hairs (Fig. 50); 1, without subappressed or appressed hairs.

59. **Metanotum towards base:** 0, produced into a tooth-like process; 1, conspicuously expanded, flat (Fig. 11); 2, not produced or expanded (Fig. 50).

60. **Metanotum medially:** 0, lacking appressed or scale-like hairs; 1, with appressed hairs at least medially (Fig. 50); 2, with scale-like hairs at least medially.

61. **Axilla:** 0, poorly defined, posterior margin of mesoscutellum evenly convex (Michener, 2007: fig. 84-9); 1, well defined, margin between axilla and posterior margin of mesoscutellum concave to angularly incised (Figs 6, 7, 50, 51, 69).

62. **Axilla, angle between free apical portion and posterior margin of mesoscutellum:** 0, obtuse (Schwarz, 2001; Abb. 5); 1, acute (Figs 6, 7, 50, 51, 69). Not applicable for taxa with a poorly defined axilla.

63. **Axilla, length of free apical portion in relation to basal potion:** 0, long, free apical portion produced up to or beyond the posterior tangent of the mesoscutellum (Fig. 6); 1, short, not attaining the posterior tangent of the mesoscutellum (Fig. 7). Not applicable for state 0 in previous character.

64. **Axilla, free apical portion length:** 0, longer than or subequal to the basal portion (Figs 51, 69); 1, shorter than the basal portion (Figs 35, 69). Not applicable for state 0 in character 62.

65. **Axillae, orientation:** 0, subparallel with one another (Fig. 85); 1, curved apicomedially (Fig. 83); 2, divergent from one another (Fig. 69). Not applicable for state 0 in character 62.

66. **Free apical portion of axilla and posterior margin of mesoscutellum:** 0, forming a conspicuously broad, rounded area (Fig. 50); 1, not forming a broad, rounded area (Fig. 69). Not applicable for state 0 in character 62.

67. **Axilla, laterally:** 0, not carinate (Fig. 7); 1, with a conspicuously raised carina (Fig. 6).

68. **Forewing colour:** 0, entirely dark, infuscate; 1, subhyaline on the basal third, infuscate or subinfuscate on the apical two-thirds; 2, subhyaline throughout.

69. **Jugal lobe of hindwing:** 0, long, half or more vannal lobe length; 1, short, less than half but more than one-quarter vannal lobe length; 2, very short, less than one-quarter vannal lobe length (Gonzalez *et al.*, 2012).

70. **Length of second submarginal cell on posterior margin:** 0, equal to or longer than first submarginal cell; 1, shorter than first submarginal cell (Gonzalez *et al.*, 2012).

71. **Stigma:** 0, longer than broad, length beyond vein r at least half as long as margin basal to vein r, margin within marginal cell convex or sometimes straight; 1, longer than broad, length beyond vein r less than half as long as margin basal to vein r, margin within marginal cell concave; 2, not longer than broad, almost parallel-sided, margin with marginal cell straight to concave (Gonzalez *et al.*, 2012; modified).

72. **Vein 2m-cu, second recurrent vein:** 0, distinctly diagonal, strongly or gently curved before meeting with 2r-m; 1, straight, or nearly so, for entire length (Gonzalez *et al.*, 2012).

73. **Propodeal triangle with integument sculpture:** 0, largely smooth and shiny; 1, dull, lineolate, imbricate, minutely punctate (Gonzalez *et al.*, 2012).

74. **Propodeal pit:** 0, rounded or elongate; 1, linear (Gonzalez *et al.*, 2012).

75. **Outer surfaces of fore and mid tibiae apically with acute angle and distinct notch anteriorly:** 0, absent; 1, present (Gonzalez *et al.*, 2012: fig. 14).

76. **Fore and middle tibiae, medial spine:** 0, long, at least 2.5× longer than basal breadth; 1, short, at most 2× longer than basal breadth.

77. **Fore and middle tibiae, medial and anterior spines:** 0, parallel with each other and of similar orientation and length; 1, subparallel and of similar shape, but anterior spine longer than medial spine; 2, divergent from one another, with medial spine much longer than anterior spine. Not applicable for taxa without distinct notch on outer surfaces of fore and mid tibiae.

78. **Fore and middle femora:** 0, each with two strong but irregular longitudinal carinae and densely hairy; 1, without two strong irregular carinae and not densely hairy.

79. **Fore coxa:** 0, lacking spine-like process (Fig. 20); 1, process very short, obsolescent, somewhat rounded or flattened; 2, process short, tooth-like, flattened (Fig. 16); 3, process very long, flattened.

80. **Ventral surface of mesepisternum between mid and hind coxa:** 0, bare and deeply emarginate, forming two distinct, parallel, elongate lobes; 1, inconspicuously hairy and deeply emarginate, forming two distinct, divergent lobes; 2, densely hairy, not emarginate or forming lobes.

81. **Hind coxa with ventral carina:** 0, absent; 1, present (Gonzalez *et al.*, 2012).

82. **Hind basitarsus, anterior margin:** 0, straight or weakly serrate; 1, conspicuously serrate.

83. **Hind basitarsus with flattened tooth-like process:** 0, absent; 1, present.

84. **Hind tibia apicomedial spine:** 0, absent; 1, short, inconspicuous, flat, rounded apically; 2, short, conspicuous, acute apically; 3, elongate, cylindrical, subacute apically; 4, very long, more or less flattened, acute apically.

85. **Hind tibia apicomedial spine:** 0, forked; 1, not forked. Not applicable for taxa without medial spine.

86. **Hind tibia: posterior spine:** 0, absent; 1, short, rounded apically; 2, long, acute apically.

87. **Arolia:** 0, present; 1, absent (Gonzalez *et al.*, 2012).

88. **Pretarsal claw:** 0, bifid, inner and outer rami separated by narrow, acute cleft; 1, bifurcate, inner and outer rami separated by broad concavity (Fig. 36); 2, lacking inner ramus (Fig. 82).

89. **Sternal apical fasciae:** 0, absent; 1, present, interrupted medially; 2, complete. In *Coelioxys weinlandi* this character was coded as 2 (although the fascia on S4 is interrupted medially it is complete on the other sterna).

90. **Sterna medially:** 0, carinate or at least with a discrete longitudinal ridge; 1, not carinate or elevated.

91. **S1 basomedially:** 0, conspicuously and acutely produced (Fig. 70); 1, swollen, not acutely produced (Fig. 72); 2, keeled; 3, unmodified, flat.

92. **S5 apical margin:** 0, entire (Rocha-Filho & Packer, 2015: fig. 5D); 1, emarginated, at least weakly (Rocha-Filho & Packer, 2015: fig. 9F).

93. **S5 apex with fringe of hairs:** 0, absent (Rocha-Filho & Packer, 2015: fig. 5D); 1, present (Rocha-Filho & Packer, 2015: fig. 9F).

94. **S5 shape:** 0, not expanded towards apex (Rocha-Filho & Packer, 2015: fig. 5D); 1, greatly expanded towards apex, margins straight, ventral surface convex, apex broad and truncate (Warncke, 1992; Abb. 5); 2, greatly expanded towards apex, margins a bit swollen and shining, ventral surface concave, apex ellipsoid (Fig. 44).

95. **S5 shape towards apex:** 0, greatly elongate, tapering, conspicuously triangular (Rocha-Filho & Packer, 2015: fig. 5D); 1, greatly elongate, elliptical or trapezoidal, not triangular (Fig. 44); 2, elongate, not triangular, elliptical or trapezoidal, more evenly convex; 3, not elongate, rectangular.

96. **S5 apex:** 0, thickened (Fig. 17); 1, not thickened (Fig. 21).

97. **S5 hairs:** 0, absent or with an inconspicuous row of short erect hairs on the lateral margins; 1, erect, thick, forming a distinct row on lateral margins; 2, very long, erect, forming a row on the lateral margins and apex.

98. **T1 concavity, margin:** 0, carinate, carina extended at least to the base of the lateral margins of the tergum (Fig. 42); 1, carinate, carina inconspicuous, not extending to the base of the lateral margins of the tergum, and interrupted medially; 2, not carinate (Fig. 43).

99. **T1 concavity, surface:** 0, densely covered with appressed hairs; 1, not densely covered with appressed hairs (Figs 42, 43).

100. **T1 posterior margin to basal concavity:** 0, elevated; 1, not elevated.

101. **T1 lateral hair bands:** 0, absent; 1, present (Figs 88, 90).

102. **T1 lateral hair bands:** 0, appressed hairs, forming at least narrow longitudinal bands (Fig. 90); 1, bands composed of subappressed or suberect hairs, at least basally. Not applicable for taxa without lateral bands.

103. **T1 medially with discrete longitudinal sulcus:** 0, present; 1, absent.

104. **Fascia on concavity of T1:** 0, absent (sometimes with sparse long, erect hairs not forming a fascia); 1, present and entire, distinct, composed of long or short, suberect hairs (Fig. 43); 2, present but broadly interrupted, distinct, composed of subappressed or appressed hairs (Fig. 42).

105. **T2–T5 apical fasciae composed of appressed or subappressed hairs:** 0, complete (Fig. 84); 1, sparse medially, narrowly interrupted, broader laterally; 2, present only laterally (Fig. 86);

3, lacking fasciae. This character was coded as 2 in *Noteriades chapini* based upon the fasciae of T2–T3 (they are absent on T4–T5).

106. **Apical fascia of T1:** 0, nearly absent, restricted to lateral margins of tergum (Fig. 86); 1, complete. Not applicable for taxa lacking tergal fasciae.

107. **Apical fasciae of T2–T5, hairs:** 0, very thin, long, plumose, suberect; 1, thin, elongate, appressed, feather-like (Fig. 24); 2, elliptical, appressed, scale-like (Fig. 25). Not applicable for taxa lacking tergal fasciae.

108. **T2–T5 with distinct depressed marginal zones:** 0, absent; 1, present (Gonzalez *et al.*, 2012).

109. **Gradulus of T2:** 0, bowed posteriorly; 1, transverse (Fig. 24).

110. **Postgradular groove of T2:** 0, complete (Fig. 24); 1, narrowly interrupted medially; 2, broadly interrupted medially (Figs 25, 84, 86); 3, indistinct.

111. **Postgradular groove of T3:** 0, complete (Fig. 24); 1, narrowly interrupted medially; 2, broadly interrupted medially (Fig. 25); 3, indistinct throughout. Note that although this character appears identical to the previous one other than it being from the succeeding tergum, the distribution of states among taxa differs.

112. **Metasoma shape:** 0, ovoid, cylindrical (Michener, 2007: fig. 84–9); 1, conic, tapering towards apex (Michener, 2007: fig. 84–2).

113. **Metasomal sternal scopa:** 0, absent; 1, present (Gonzalez *et al.*, 2012).

114. **T6 in profile, dorsal surface:** 0, horizontal or subhorizontal; 1, sinuate, mostly vertical (Gonzalez *et al.*, 2012).

115. **T6, lateral margin in dorsal view:** 0, angulate near midlength (Fig. 9); 1, not angulate near midlength (Figs 12, 26).

116. **T6 shape in dorsal view:** 0, gradually tapering towards apex (Figs 12, 26); 1, abruptly tapering subapically, forming a broad apical process (Fig. 17); 2, broad, rounded. *Lithurgopsis apicalis* was considered abruptly tapering because of the pygidial plate.

117. **T6 apex:** 0, never ending in a spine-like process or tooth (Fig. 26); 1, ending in a short, rounded tooth (Figs 12, 46); 2, ending in a long spine-like process (Fig. 9). *Lithurgopsis apicalis* was coded as inapplicable because of the pygidial plate.

118. **T6 subapically:** 0, with long, thick, erect hairs (Figs 9, 46); 1, without long, thick, erect hairs (Figs 12, 26).

119. **T6 apex:** 0, not emarginate (Figs 12, 26); 1, emarginate.

120. **T6 apex shape:** 0, truncate, wide; 1, convex, rounded or trapezoidal, wide; 2, ovoid, tapering towards the apex; 3, subacute, elongate, at most 1.25× longer than broad (Fig. 26); 4, subacute or acute, greatly elongate, at least 1.75× longer than broad (Fig. 12); 5, spinose (Fig. 9). *Lithurgopsis apicalis* was coded as 3 because of the pygidial plate medially.

121. **T6 lateral carinae:** 0, absent (Figs 67, 79); 1, present, not expanded or barely expanded (Fig. 44); 2, present, very expanded with regular margins (Figs 9, 33); 3, present, very expanded with irregular margins. Despite the existence of carinate margins of the pygidial plate in *L. apicalis* this species was coded as 0 for this character as it seems unlikely that these carinae are homologous to the lateral carinae observed in some *Coelioxys* species.

122. **T6 sulci:** 0, absent (Fig. 67); 1, present (Fig. 40).

123. **T6 sulci length:** 0, incomplete, not reaching the apex (Fig. 38); 1, complete, reaching the apex but not uniting (Fig. 40); 2, complete reaching the apex where they fuse. Not applicable for taxa without sulci.

124. **T6 sulci pilosity:** 0, bare or covered with plumose appressed hairs only basally (Fig. 89); 1, conspicuously covered with plumose appressed hairs throughout (Fig. 40). Not applicable for taxa without sulci.

125. **T6 dorsal carina:** 0, absent (Fig. 33); 1, present (Figs 38, 40).

126. **T6 dorsal carina orientation:** 0, longitudinal (Figs 38, 40); 1, transverse. Not applicable for taxa without dorsal carina.

127. **T6 dorsal carina length:** 0, at least two-thirds the length of T6 (Fig. 89); 1, less than two-thirds the length of T6 (Fig. 77). *Coelioxys caudata* was coded as 0, although the carina is not complete at the apex. Not applicable for taxa without a dorsal carina.

128. **T6 dorsal carina apically:** 0, obsolescent, inconspicuously elevated (Fig. 38); 1, conspicuous, elevated and rounded or elevated and flattened (Fig. 67); 2, inconspicuously carinate, carina not sharply elevated (Fig. 65); 3, conspicuously keeled, keel sharply elevated (Fig. 40). In *Coelioxys argentea* Lepeletier, 1841 there is a very short, sharp carina restricted to the apex, and thus it was considered as 0. Not applicable for taxa without a dorsal carina.

129. **T6 dorsal carina laterally:** 0, hairy, even if only inconspicuously (Figs 9, 46); 1, bare (Figs 12, 44). Not applicable for taxa without a dorsal carina.

130. **T6 depressions:** 0, deep, conspicuous (Fig. 46); 1, shallow (Figs 9, 77, 79); 2, absent (Figs 65, 67).

131. **Pregradular area of S6:** 0, not elongate laterally, convexity broader than long (Gonzalez *et al.*, 2012: fig. 18); 1, elongate laterally, convexity longer than broad (Gonzalez *et al.*, 2012: figs 19, 20).

132. **Apodeme of S6:** 0, with distinct disc between marginal ridge and transapodemal ridge (Gonzalez *et al.*, 2012: fig. 18); 1, with disc reduced or absent (Gonzalez *et al.*, 2012: figs 19, 20).

133. **S6 basal margin concavity:** 0, deep, ≤2× wider than deep (Gonzalez *et al.*, 2012: figs 19, 20); 1, shallow, ≥2.1× wider than deep (Gonzalez *et al.*, 2012: fig. 18).

134. **S6 apical margin:** 0, not emarginate; 1, weakly emarginate; 2, strongly emarginate.

135. **S6 medioventrally:** 0, keeled at least apically (Fig. 91); 1, not keeled (Fig. 87).

136. **S6 lateral margins subapically:** 0, gradually tapering (Figs 26, 38); 1, abruptly tapering (Figs 14, 28); 2, broad, rounded, not tapering. *Lithurgopsis apicalis* was coded as 1 because S6 is slightly folded medially.

137. **S6 margin with expanded area attaining dorsal carina:** 0, present (Figs 14, 26, 28, 38); 1, absent (Fig. 12).

138. **S6, expanded lateral area:** 0, serrate only subapically; 1, weakly serrate throughout (Fig. 65); 2, lacking serrations (Figs 26, 28). Not applicable for taxa without expanded area attaining S6 dorsal carina.

139. **S6 marginal pilosity:** 0, at most a few minute hairs, not forming a conspicuous fringe (Figs 26, 28); 1, forming an inconspicuous marginal fringe of sparse, short or sparse, long hairs (Fig. 12); 2, a conspicuous marginal fringe of dense, short hairs (Figs 9, 46); 3, conspicuously fringed with long, thick hairs.

140. **S6 orientation:** 0, horizontal (Fig. 9); 1, slightly flexed downwards (Fig. 17); 2, strongly flexed downwards (Fig. 21).

141. **S6 dorsolateral margin:** 0, with a conspicuous, long hook; 1, with a short hook; 2, with an obsolescent hook; 3, lacking a hook.

142. **S6 shape apically:** 0, broad and rounded; 1, ovoid, gradually tapering (Figs 33, 89); 2, trapezoidal, gradually tapering, apex weakly produced medially (Fig. 87); 3, rounded but abruptly narrowed medially (Figs 9, 14, 28); 4, triangular, gradually tapering towards apex, apex very acute, pointed (Baker, 1975: figs 42A, 42B); 5, elongate and subacute, at most 1.50× longer than broad (Figs 26, 38); 6, greatly elongate, subacute or acute apically, at least 1.75× longer than broad (Fig. 12). *Lithurgopsis apicalis* was coded as 3 because the S6 is slightly folded medially. In *Coelioxys argentea* the apex is not subacute but it is conspicuously folded, so it was coded as 6.

143. **S6 notches:** 0, absent (Figs 9, 12, 28, 46); 1, obtuse, clearly visible in dorsal view (Fig. 14); 2, a weak impression, not interrupting outline in dorsal view (Figs 38, 65); 3, acute, triangular, clearly visible in dorsal view (Figs 26, 67, 77, 79). In *Coelioxys aperta* the subapical region approaches state 3 but the margins of the notch are rounded, and thus this species was coded as 1.

144. **S6 notches and lateral flattened area:** 0, separated by an indistinct triangular area (Fig. 38); 1, separated by a conspicuous triangular area (Fig. 79); 2, separated by a broadly rounded area (Fig. 77). Not applicable for taxa without notches.

145. **Hemitergite 7 (H7), apodemal region:** 0, not at an angle to rest of H7 (Fig. 94A; apodemal region indicated by black arrow); 1, at an angle to rest of H7 (Figs 94B, C; apodemal region indicated by black arrow).

146. **H7, lateral portion of marginal ridge:** 0, strongly developed (Fig. 94A); 1, evanescent (Fig. 94C).

147. **H7, medial portion of marginal ridge:** 0, strongly developed; 1, evanescent (Fig. 94A).

148. **Medial and lateral portions of marginal ridge of H7:** 0, not parallel with each other or convergent posteriorly; 1, parallel or subparallel with each other (Fig. 94A) (Gonzalez *et al.*, 2012; modified).

149. **Apodemal region of H7:** 0, narrow, subacute (Fig. 94A); 1, wider, rounded or quadrate (Fig. 94B).

150. **Lateral process of H7:** 0, long (Fig. 94A; lateral process indicated by red arrow): 1, short or reduced, almost absent or absent (at most as long as in Fig. 94B; lateral process indicated by red arrow).

151. **H7 with strong protrusion on the lamina spicularis, near base of lateral process:** 0, absent; 1, present, but inconspicuous (Fig. 94A); 2, present, distinct (Fig. 94B) (Gonzalez *et al.*, 2012; modified).

152. H7 spiracle: 0, large, more than one-third length of lamina spiracularis (Fig. 94B); 1, moderate in size, more than one-quarter but less than one-third length of lamina spiracularis (Fig. 94C); 2, short, less than one-quarter length of lamina spiracularis (Fig. 94A).

153. **H7 location of entire spiracle:** 0, in the basal two-thirds of H7; 1, at or near the apical third of H7 (Fig. 94A) (Gonzalez *et al.*, 2012).

154. **H7 lateral lamella length:** 0, clearly longer than lamina spiracularis (Fig. 94A); 1, approximately as long as lamina spiracularis; 2, clearly shorter than lamina spiracularis.

155. **H7 lateral lamella, posteriorly:** 0, with a pointed process; 1, entire, without a process (Fig. 94A).

156. **H8, posterior expansion:** 0, narrow, apex acutely pointed (Fig. 94D): 1, tapering, triangular, subacute apically (Fig. 94E); 2, distinctly convex but

not angulate (Fig. 94F); 3, inconspicuously rounded to transverse.

157. **H8 carina:** 0, conspicuous, strong; 1, evanescent (Fig. 94E).

158. **Furcula dorsal arm:** 0, conspicuously flattened laterally on apex (Fig. 94F, apex of dorsal arm indicated by red arrow); 1, not flattened.

159. **Sting shaft compared with gonostylus:** 0, equal to or shorter than 2× gonostylus length; 1, longer than 2× but shorter than 3× gonostylus length; 2, much longer than 3.5× gonostylus length.

160. **Apex of gonostylus, pubescence:** 0, nearly hairless to sparsely covered with short hairs (hairs ≤ maximum gonostylus width in lateral view); 1, densely covered with long plumose hairs (hairs ≥1.2× gonostylar width) (Gonzalez *et al.*, 2012).

161. **Gonostylus apically:** 0, broadened; 1, not broadened.

Male

162. **Pubescence of face:** 0, copious and elongate, erect; 1, copious and short, appressed or subappressed.

163. **Genal surface:** 0, not excavated (Fig. 15); 1, excavated along posterior margin of eye (Figs 39, 41).

164. **Genal pilosity:** 0, suberect or erect (Fig. 15); 1, appressed (Figs 39, 41).

165. **Hypostomal area:** 0, lacking concavity or distinct flat, hairless plate (Fig. 18); 1, concavity present (Fig. 15); 2, with a distinct, flat, hairless plate that is not raised above surrounding surface (Fig. 22); 3, with a distinct, flat, hairless plate that is raised above the surrounding surface. In *Coelioxys alternata*, *C. apacheorum*, and *C. hunteri* the hypostomal concavity is inconspicuous but nonetheless present, and so these were scored as 1.

166. **Hypostomal concavity surface:** 0, shallow (Fig. 39); 1, deep (Fig. 15). Not applicable for taxa without concavity.

167. **Hypostomal concavity length:** 0, less than half eye length (Fig. 15); 1, longer than or equal to half eye length (Rocha-Filho & Packer, 2015: fig. 7E). Not applicable for taxa without concavity.

168. **Posterior margin of hypostomal concavity:** 0, without long or apically curved hairs (Fig. 22); 1, with conspicuous, long hairs that are not curved apically (Fig. 15); 2, with hairs conspicuously curved apically (Rocha-Filho & Packer, 2015: fig. 7E). Not applicable for taxa without concavity.

169. Hypostomal concavity pilosity: 0, hairy throughout (Rocha-Filho & Packer, 2015: fig. 1F); 1, bare at least on the posterior margin (Rocha-Filho & Packer, 2015: fig. 7E). Not applicable for taxa without concavity.

170. **Fore coxa with spine-like process:** 0, absent; 1, short; 2, long (Gonzalez *et al.*, 2012; modified). This is similar in some ways to character 79 in females, but the state distributions differ between the sexes in numerous taxa.

171. **Forecoxal spine, shape:** 0, thick, swollen, conical to rounded, not elongate; 1, elongate and cylindrical; 2, elongate and flattened. Not applicable for taxa without spine.

172. **Apical fasciae of T2–T5:** 0, complete (Fig. 29); 1, weak or interrupted medially (Figs 66, 68); 2, absent. In *Coelioxys slossoni*, *C. cayennensis*, and *C. cerasiopleura* the fasciae are interrupted on T4–T5, but the character was coded as 0 for these species.

173. **Postgradular area of T2:** 0, punctate area or fovea absent; 1, with a more or less transverse, punctate area only (Figs 29, 66, and 68); 2, with a more or less transverse, punctate area and a fovea (Figs 27, 78, 88, 90); 3, only foveate (Fig. 45).

174. **Postgradular area of T2, punctate area:** 0, punctures of the densely punctate area irregular and smaller than the adjacent punctures on the disc; 1, punctures of the densely punctate areas smaller than the adjacent punctures of the disc and sparse; 2, punctures of the densely punctate area smaller than the punctures of the disc and arranged in a broad, rectangular area posteriorly to the gradulus (Fig. 29); 3, punctures of the densely punctate areas smaller than the adjacent punctures of the disc and arranged in a slender, transverse area; 4, punctures of the densely punctate areas smaller than the punctures of the disc and arranged in a circular to elliptical area (Figs 66, 68); 5, punctures of the same size as those of the adjacent punctures and arranged randomly on the disc in a more or less transverse row (Rocha-Filho & Packer, 2015: fig. 1G). Not applicable for taxa without punctate area or fovea.

175. **Postgradular area of T2, fovea:** 0, shallow, circular, hairy fovea composed of small punctures with small punctures on adjacent disc; 1, a transverse, shallow, hairless fovea composed of small punctures with punctures posteriorly to the fovea or a deep, transverse, hairless fovea not composed of punctures with punctures posteriorly to the fovea (Figs 27, 88); 2, a very slender, deep fovea not composed of punctures but with punctures posteriorly to the fovea (Baker, 1975: fig. 25C); 3, an inconspicuous, minute, circular, hairy fovea with a densely punctate area posteriorly to it (Fig. 78); 4, a small, circular, hairless fovea not surrounded by punctures; 5, an elliptical, small, deep fovea covered with minute hairs and not surrounded by punctures (Fig. 45). Not applicable for taxa without punctate area or fovea.

176. **Foveal or punctate area of T2:** 0, without impunctate area (Fig. 29); 1, with an irregular, small, impunctate area posteriorly to the punctate

area; 2, with a slender, impunctate area at least posteriorly to the punctate area or fovea (Fig. 27); 3, punctate area or fovea surrounded by an impunctate area (Fig. 45); 4, fovea surrounded by an impunctate, elevated area (Fig. 78). Not applicable for taxa without punctate area or fovea.

177. **Postgradular area of T3:** 0, punctate area or fovea absent (Fig. 29); 1, with a more or less transverse, punctate area only (Figs 66, 68); 2, with a more or less transverse, punctate area and a fovea (Fig. 78); 3, only foveate (Fig. 45). This is similar to character 175, but the state distributions differ in numerous taxa.

178. **Postgradular area of T3, punctate areas/foveae:** 0, punctures of the same size as those of the adjacent disc and arranged randomly on the disc in a more or less transverse row (Rocha-Filho & Packer, 2015: fig. 1G); 1, punctures of the punctate areas smaller than, or of the same size, as those on the disc and arranged in a circular to elliptical area (Figs 66, 68); 2, a circular, shallow fovea composed of punctures smaller than the adjacent punctures on the disc and surrounded by punctures forming a more or less elliptical area; 3, a circular, deep, conspicuous fovea composed of punctures smaller than the adjacent punctures of the disc and surrounded by punctures forming a more or less elliptical area (Fig. 80); 4, a small, slender fovea surrounded by an elevated, impunctate area with a depressed, coarsely punctate area posteriorly to the fovea (Fig. 78); 5, a small, circular fovea surrounded by an impunctate area (Fig. 45). Not applicable for taxa without punctate area or fovea.

179. **Gradular grooves of T3–T6:** 0, not fasciate or not conspicuously fasciate, fasciae at most narrow and only on T3 or T4 to T6 (Fig. 66); 1, conspicuously fasciate, fasciae increasing in width from T2 or T3 to T6 (Fig. 68).

180. **Sternal pilosity, at least on S2–S3:** 0, conspicuous, hairs plumose/scale-like medially and covering the surface; 1, disc lacking scale-like/plumose hairs but with long, erect hairs. In *Aspidosmia volkmanni* there are some erect hairs and tufts apicomedially on S2–S3, but the character was coded as 1. In *Coelioxys texana* the sterna are covered with small scale-like hairs but very sparsely so, and thus was scored as 1. In *C. echinata* the sterna are hairy only on S2 and inconspicuously on S3, and thus was scored as 1. *Coelioxys nasuta* is hairy basally and apically below the fasciae on S2–S3, not medially, and thus was scored as 1.

181. **S3 subapicomedially:** 0, flat (Fig. 64); 1, shallowly concave medially and hairy; 2, conspicuously sulcate and hairy, sulcus deep and narrow.

182. **S4 medially:** 0, flat and glabrous (Figs 49, 62, 64); 1, sulcate and hairy. *Coelioxys chilensis* is conspicuously sulcate here but not hairy, so this species was coded as 1.

183. **S4 apicomedially:** 0, flat (Fig. 62); 1, canaliculate (Figs 49, 64).

184. **Apical rim of S4:** 0, flexed ventrally (Fig. 93); 1, on same plane as disc (Figs 49, 64).

185. **Apical rim of S4:** 0, entire (Figs 49, 64); 1, slightly emarginate, width of concavity more than 3× longer than depth; 2, emarginate, width of concavity less than 2× longer than depth; 3, deeply emarginate, arms forming a U-shaped process (Fig. 93).

186. **Apical margin of S4 junction between disc and apical rim:** 0, entire (Fig. 62); 1, somewhat emarginated, but not in a U-shaped process (Fig. 93); 2, deeply emarginate, forming a U-shaped process (Figs 49, 64).

187. **U-shaped emargination of S4:** 0, apical margin produced into two robust, broad arms, broadly separated from one another, the distance between them more than half their length; 1, arms flattened, elongate, and separated from one another, with the distance between them more than half their length (Fig. 64); 2, arms robust, thick, and separated from one another, with the distance between them more than half their length (Fig. 49); 3, arms elongate, sharply elevated, and close to one another, with the distance between them equal to half their length. Not applicable for taxa without U-shaped process.

188. **T5 lateral spines:** 0, absent (Fig. 13); 1, very short, broader than wide (Fig. 61); 2, intermediate in length, at least as long as wide but not reaching the apex of the apical rim (Fig. 63); 3, long, reaching the apex of the apical rim.

189. **T5 lateral spines and surface of tergum:** 0, not separated from the surface of the tergum apically (Rocha-Filho & Packer, 2015: fig. 1H); 1, separated from the surface of the tergum apically (Fig. 63). Not applicable for taxa without lateral spines.

190. **T6 apicodorsal process(es):** 0, absent; 1, forming a transverse irregular crenulate plate (Schwarz, 2001; abb. 27, 35; Michener, 2007: fig. 84-14a); 2, two dorsal process (Figs 13, 19, 23, 61, 63).

191. **Apicodorsal processes of T6, shape:** 0, cylindrical (Michener, 2007: fig. 84-18b); 1, flattened (Figs 13, 19, 23, 61, 63). Not applicable for taxa without apicodorsal processes.

192. **Apicodorsal processes of T6, orientation:** 0, slanting (Fig. 13); 1, horizontal (Figs 61, 63); 2, strongly curved downwards (Michener, 2007: fig. 84-18b). Not applicable for taxa without apicodorsal processes.

193. **T6 laterobasal teeth:** 0, absent (Michener, 2007: fig. 84-6g); 1, very short, flat, almost vestigial (Fig. 13); 2, elongate and flattened (Figs 19, 23); 3,

elongate and cylindrical, acutely pointed (Figs 61, 63). In *Radoszkowskiana gusevi*, *R. tkalcui*, and *Coelioxys ducalis* there is an inconspicuously enlarged area, not forming a tooth, and thus these were scored as 1.

194. **T6 apex of apicodorsal process:** 0, forked (Fig. 23); 1, not forked (Figs 19, 61, 63). Not applicable for taxa without apicodorsal processes.

195. **T6 apex of apicodorsal process:** 0, pointed (Figs 10, 61); 1, rounded (Figs 13, 63); 2, broadly rounded (Baker, 1975: fig. 38H). Not applicable for taxa without apicodorsal processes or with forked apicodorsal processes.

196. **T6 space between apicodorsal processes:** 0, without a tooth (Figs 61, 63); 1, with an obsolescent tooth (Fig. 23); 2, with a conspicuous tooth.

197. **T6 ventral processes:** 0, absent; 1, present, flattened; 2, present, cylindrical (Figs 61, 63). In *Megachile felina* the ventral processes are in a somewhat different position than in *Coelioxys* spp.; nonetheless, it was scored 1 for this character because of the shape of the ventral processes.

198. **T7:** 0, exposed; 1, hidden by T6 (Gonzalez *et al.*, 2012).

199. **T7 with distinct apicolateral lobe:** 0, absent; 1, present (Gonzalez *et al.*, 2012).

200. **T7 mediolaterally:** 0, without distinct lateral convexity; 1, with distinct lateral convexity (Baker, 1975: fig. 19A).

201. **T7 apicomedial tooth-like process:** 0, present, long, narrow, and conspicuous (Fig. 94G); 1, present, short, and wide, or inconspicuous; 2, absent. In *Lithurgopsis apicalis* the pygidial plate bears a short, acute tooth apically, and thus it was coded as 1 for this character. In *Coelioxys decipiens* the tooth is long but broad, not narrow; it was considered as 0.

202. **T7 apex:** 0, rounded (Baker, 1975: fig. 19A); 1, tapering (Baker, 1975: fig. 26A); 2, nearly truncate or slightly produced medially; 3, deeply emarginate. In *Coelioxys mexicana* Cresson, 1878 there is an obsolescent convex process medially, such that it is slightly produced, and it was coded as 2.

203. **Number of fully exposed sterna:** 0, two or three; 1, four; 2, five or six (Gonzalez *et al.*, 2012).

204. **S5 shape:** 0, long, ≥1.25× longer than wide; 1, wide, ≥2× wider than long.

205. **S5 integument:** 0, membranous; 1, lightly sclerotized, clearly not as well sclerotized as the preceding sterna; 2, as strongly sclerotized as the preceding sterna (Gonzalez *et al.*, 2012; modified).

206. **S5 medially:** 0, flat (Fig. 64); 1, depressed medially (Figs 49, 62).

207. **S5 apical margin, medially:** 0, entire; 1, emarginated, with width more than 3× greater than depth (Fig. 62); 2, emarginated, with width less than 2× greater than depth; 3, produced medially.

208. **S5 apical margin, laterally:** 0, deeply notched, incision between outer margin and rest of sternum acute, longer than broad; 1, slightly notched, incision between outer margin and rest of sternum rounded, not longer than broad; 2, not notched.

209. **S5 apical rim:** 0, entire; 1, weakly emarginate, width of concavity more than 3× longer than depth; 2, emarginate, width of concavity less than 2× longer than depth; 3, produced medially.

210. **Postgradular area of S5:** 0, densely, conspicuously covered with plumose hairs; 1, inconspicuously hairy or not densely hairy.

211. **Gradulus of S5:** 0, evanescent; 1, conspicuous, strong (Rocha-Filho & Packer, 2015: fig. 16A–F).

212. **S5 gradulus shape:** 0, largely straight medially or slightly rounded medially; 1, convex; 2, U-shaped, angulate towards base with medial area broadly rounded; 3, V-shaped, angulate towards base (Rocha-Filho & Packer, 2015: fig. 16C, F); 4, V-shaped, deeply angulate towards base, gradulus almost reaching base (Rocha-Filho & Packer, 2015: fig. 16A, B, D, E); 5, W-shaped. Not applicable for taxa coded as 0 in the previous character.

213. **Gradulus of S5:** 0, incomplete, lateral margins evanescent (Rocha-Filho & Packer, 2015: fig. 16A–F); 1, complete. Not applicable for taxa coded as 0 in character 211.

214. **Gradulus and basal margin of S5:** 0, meeting medially; 1, not meeting medially (Rocha-Filho & Packer, 2015: fig. 16A–F). Not applicable for taxa coded as 0 in character 211.

215. **Lateral margins of S6:** 0, angulate (Rocha-Filho & Packer, 2015: fig. 20B); 1, rounded, not angulate (Rocha-Filho & Packer, 2015: fig. 16G–L).

216. **Lateral margins of S6, apically:** 0, acutely pointed, incision between outer margin and rest of sternum acute; 1, bluntly pointed, incision between outer margin and rest of sternum narrowly rounded (Rocha-Filho & Packer, 2015: fig. 20B); 2, incision between outer lobe and rest of sternum broadly rounded; 3, entire apical margin evenly convex (Rocha-Filho & Packer, 2015: fig. 16G–L).

217. **Lateral margins of S6:** 0, heavily sclerotized, contrasting with the medial area (Rocha-Filho & Packer, 2015: figs 16G–L, 20B); 1, heavily or lightly sclerotized or translucent, but not contrasting with the medial area. In all *Radoszkowskiana* species as well as in *Coelioxys acanthura* there is a very small, slender band apically that is more strongly sclerotized, but because of its small size and apical position these taxa were coded as 1 for this character.

218. **S6:** 0, as well sclerotized as the preceding sterna; 1, poorly sclerotized, translucent to membranous (Rocha-Filho & Packer, 2015: figs 16G–L, 20B) (Gonzalez *et al.*, 2012).

219. **S6 shape:** 0, long, ≥1.25× longer than wide (Rocha-Filho & Packer, 2015: figs 16G–L, 20B); 1, wide, ≥1.2× wider than long.

220. **S6 apically:** 0, copiously setose (Rocha-Filho & Packer, 2015: fig. 16G–L); 1, inconspicuously hairy to bare (Rocha-Filho & Packer, 2015: fig. 20B).

221. **S6 hairs:** 0, spatulate (Rocha-Filho & Packer, 2015: fig. 16G–L); 1, lanceolate.

222. **S6 basally:** 0, with thick hairs; 1, lacking thick hairs (Rocha-Filho & Packer, 2015: figs 16G–L, 20B).

223. **S6 basal membranous lip:** 0, folded ventrad (Rocha-Filho & Packer, 2015: figs 16G–L, 20B); 1, not folded ventrad.

224. **S7:** 0, undivided (Fig. 94H); 1, divided into two small sclerites (Baker, 1975: fig. 26D).

225. **S8 apex:** 0, emarginate; 1, convex, but not produced medially (Fig. 94I); 2, produced medially (Schwarz, 2001; abb. 31).

226. **S8 shape:** 0, elongate, ≥2× longer than wide (Rocha-Filho & Packer, 2015: figs 16G–L, 20B); 1, wider, <2× longer than wide (Fig. 94I).

227. **S8 base shape:** 0, triangular, base wide and tapering to subacute apex (Fig. 94I); 1, convex or trapezoidal, base wide and tapering, rounded or trapezoidal apex (Baker, 1975: fig. 39C); 2, elongate, narrowly triangular, tapering to apex (Rocha-Filho & Packer, 2015: figs 16G–L, 20B).

228. **S8 base:** 0, a tip produced (Fig. 94I); 1, lacking a tip (Rocha-Filho & Packer, 2015: figs 16G-L, 20B).

229. **Gonocoxa length:** 0, distinctly longer than penis valve (Fig. 94J); 1, subequal to penis valve in length (Fig. 94K); 2, distinctly shorter than penis valve (Fig. 94L).

230. **Gonocoxa subapically:** 0, strongly compressed laterally; 1, slightly compressed laterally (Fig. 94J); 2, not compressed (Fig. 94L).

231. **Gonocoxa apex, concavity:** 0, absent; 1, present, strongly concave (Schwarz, 2001; abb. 39, 43, 44).

232. **Gonocoxa apically:** 0, rounded (Fig. 94L); 1, more pointed (Fig. 94J).

233. **Gonocoxa apically:** 0, copiously hairy, hairs long and curved (Fig. 94L); 1, less densely hairy, hairs long but not curved; 2, inconspicuously hairy or bare (Fig. 94J).

234. **Gonocoxa and gonobase, junction between them:** 0, approximately right-angular (Fig. 94K); 1, obtuse to broadly concave and not angulate (Fig. 94J).

235. **Gonocoxa:** 0, divergent; 1, parallel or convergent.

236. **Gonocoxa apex with mesal barb:** 0, present (Fig. 94K); 1, absent (Fig. 94J).

237. **Gonocoxa apically:** 0, parallel-sided or narrowing towards apex, not swollen (Fig. 94J); 1, swollen (Fig. 94L).

238. **Penis valve:** 0, gradually tapering towards apex or subparallel; 1, abruptly tapering subapically (Schwarz, 2001; abb. 39, 41).

RESULTS AND DISCUSSION

The phylogenetic analysis using equally weighted characters resulted in 25 most-parsimonious trees (tree length = 2135, consistency index = 0.181, retention index = 0.610), with four collapsed nodes in the consensus tree (Fig. 1). The character weighting in successive approximations stabilized after two iterations, giving the tree shown in Figure 2. Implied weighting produced one tree with a fit of 57.898 (Fig. 3). The strict consensus of the equally most-parsimonious trees in the equal-weights analysis was different from those obtained from the successive and implied weighting analyses regarding the position of Megachilini among the out-groups and ambiguity related to the monophyly of the subgenus *Coelioxys* (*Boreocoelioxys*). Almost all of the decisions regarding *Coelioxys* subgenera (details below) were based upon monophyly for the subgenus in all three trees, or upon monophyly in both weighted results when that decision was not contradicted by the equal-weights result. In the equal-weights consensus tree presented as Figure 1, Michener's classification of the *Coelioxys* subgenera was retained. In contrast, the new classification based upon our phylogenetic analyses was used in both weighted trees (Figs 2, 3). Thus, comparison of Figure 1 with Figures 2 and/or 3 shows the classificatory changes for the taxa used in our analyses. All species currently thought to belong to each of the subgenera as we define them are listed below in the accounts of each subgenus.

MONOPHYLY AND SISTER-GROUP RELATIONSHIPS OF MEGACHILINI

All analyses gave a monophyletic Megachilini (with *Noteriades* included within it), and the weighted

Figure 1. Strict consensus tree of the 25 equally most-parsimonious trees in the equal-weights analysis. Branch support values are displayed below the nodes in the following order: bootstrap, Bremer support, and symmetric resampling values (values in square brackets are negative). When only two values are displayed they refer to bootstrap and symmetric resampling, as the Bremer values could not be estimated, and when only one value is shown it refers to bootstrap. Colours indicate Michener's subgeneric classification.

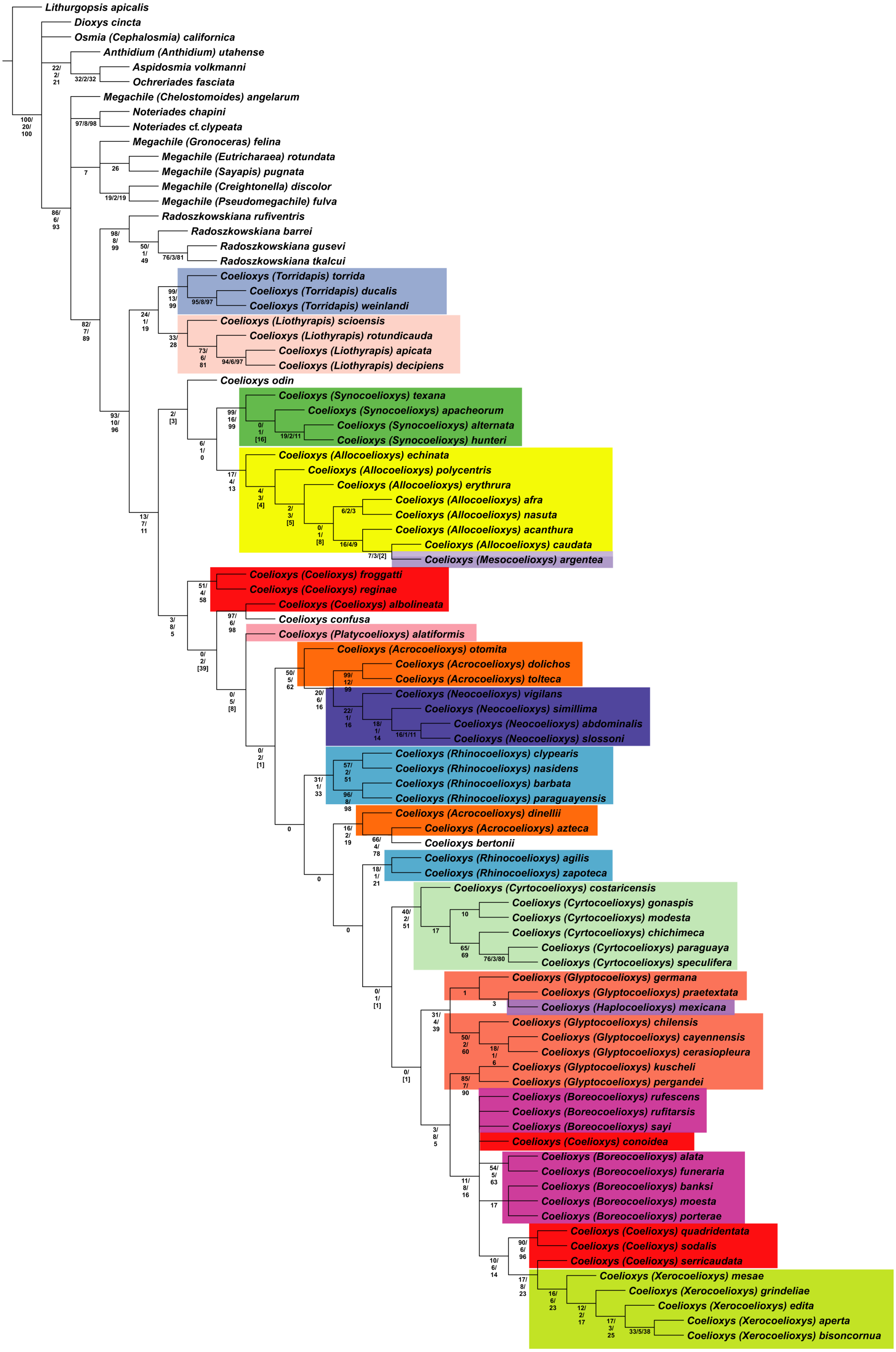

Lithurgopsis apicalis
Dioxys cincta
Osmia (Cephalosmia) californica
Anthidium (Anthidium) utahense
Aspidosmia volkmanni
Ochreriades fasciata
Megachile (Chelostomoides) angelarum
Noteriades chapini
Noteriades cf. clypeata
Megachile (Gronoceras) felina
Megachile (Eutricharaea) rotundata
Megachile (Sayapis) pugnata
Megachile (Creightonella) discolor
Megachile (Pseudomegachile) fulva
Radoszkowskiana rufiventris
Radoszkowskiana barrei
Radoszkowskiana gusevi
Radoszkowskiana tkalcui
Coelioxys (Torridapis) torrida
Coelioxys (Torridapis) ducalis
Coelioxys (Torridapis) weinlandi
Coelioxys (Liothyrapis) scioensis
Coelioxys (Liothyrapis) rotundicauda
Coelioxys (Liothyrapis) apicata
Coelioxys (Liothyrapis) decipiens
Coelioxys odin
Coelioxys (Synocoelioxys) texana
Coelioxys (Synocoelioxys) apacheorum
Coelioxys (Synocoelioxys) alternata
Coelioxys (Synocoelioxys) hunteri
Coelioxys (Allocoelioxys) echinata
Coelioxys (Allocoelioxys) polycentris
Coelioxys (Allocoelioxys) erythrura
Coelioxys (Allocoelioxys) afra
Coelioxys (Allocoelioxys) nasuta
Coelioxys (Allocoelioxys) acanthura
Coelioxys (Allocoelioxys) caudata
Coelioxys (Mesocoelioxys) argentea
Coelioxys (Coelioxys) froggatti
Coelioxys (Coelioxys) reginae
Coelioxys (Coelioxys) albolineata
Coelioxys confusa
Coelioxys (Platycoelioxys) alatiformis
Coelioxys (Acrocoelioxys) otomita
Coelioxys (Acrocoelioxys) dolichos
Coelioxys (Acrocoelioxys) tolteca
Coelioxys (Neocoelioxys) vigilans
Coelioxys (Neocoelioxys) simillima
Coelioxys (Neocoelioxys) abdominalis
Coelioxys (Neocoelioxys) slossoni
Coelioxys (Rhinocoelioxys) clypearis
Coelioxys (Rhinocoelioxys) nasidens
Coelioxys (Rhinocoelioxys) barbata
Coelioxys (Rhinocoelioxys) paraguayensis
Coelioxys (Acrocoelioxys) dinellii
Coelioxys (Acrocoelioxys) azteca
Coelioxys bertonii
Coelioxys (Rhinocoelioxys) agilis
Coelioxys (Rhinocoelioxys) zapoteca
Coelioxys (Cyrtocoelioxys) costaricensis
Coelioxys (Cyrtocoelioxys) gonaspis
Coelioxys (Cyrtocoelioxys) modesta
Coelioxys (Cyrtocoelioxys) chichimeca
Coelioxys (Cyrtocoelioxys) paraguaya
Coelioxys (Cyrtocoelioxys) speculifera
Coelioxys (Glyptocoelioxys) germana
Coelioxys (Glyptocoelioxys) praetextata
Coelioxys (Haplocoelioxys) mexicana
Coelioxys (Glyptocoelioxys) chilensis
Coelioxys (Glyptocoelioxys) cayennensis
Coelioxys (Glyptocoelioxys) cerasiopleura
Coelioxys (Glyptocoelioxys) kuscheli
Coelioxys (Glyptocoelioxys) pergandei
Coelioxys (Boreocoelioxys) rufescens
Coelioxys (Boreocoelioxys) rufitarsis
Coelioxys (Boreocoelioxys) sayi
Coelioxys (Coelioxys) conoidea
Coelioxys (Boreocoelioxys) alata
Coelioxys (Boreocoelioxys) funeraria
Coelioxys (Boreocoelioxys) banksi
Coelioxys (Boreocoelioxys) moesta
Coelioxys (Boreocoelioxys) porterae
Coelioxys (Coelioxys) quadridentata
Coelioxys (Coelioxys) sodalis
Coelioxys (Coelioxys) serricaudata
Coelioxys (Xerocoelioxys) mesae
Coelioxys (Xerocoelioxys) grindeliae
Coelioxys (Xerocoelioxys) edita
Coelioxys (Xerocoelioxys) aperta
Coelioxys (Xerocoelioxys) bisoncornua
22/2/21
32/2/32
100/20/100
97/8/98
26
7
19/2/19
86/6/93
98/8/99
50/1/49
76/3/81
99/13/99
95/8/97
24/1/19
82/7/89
33/28
73/6/81
94/6/97
2/[3]
99/16/99
93/10/96
0/1/[16]
19/2/11
6/1/0
17/4/13
4/3/[4]
2/3/[5]
6/2/3
13/7/11
0/1/[8]
16/4/9
7/3/[2]
51/4/58
97/6/98
3/8/5
0/2/[39]
50/5/62
99/12/99
20/6/16
0/5/[8]
22/1/16
18/1/14
16/1/11
0/2/[1]
57/2/51
31/1/33
96/8/98
0
16/2/19
66/4/78
18/1/21
0
40/2/51
10
17
65/69
76/3/80
0
0/1/[1]
1
3
31/4/39
50/2/60
18/1/6
0/[1]
85/7/90
3/8/5
54/5/63
11/8/16
17
90/6/96
10/6/14
17/8/23
16/6/23
12/2/17
17/3/25
33/5/38

Figure 2. Tree from the successive approximations character weighting analysis. All the resultant taxonomic changes based upon the phylogenetic analyses are shown. Branch support values are shown as in Figure 1. The six new subgenera are highlighted in grey.

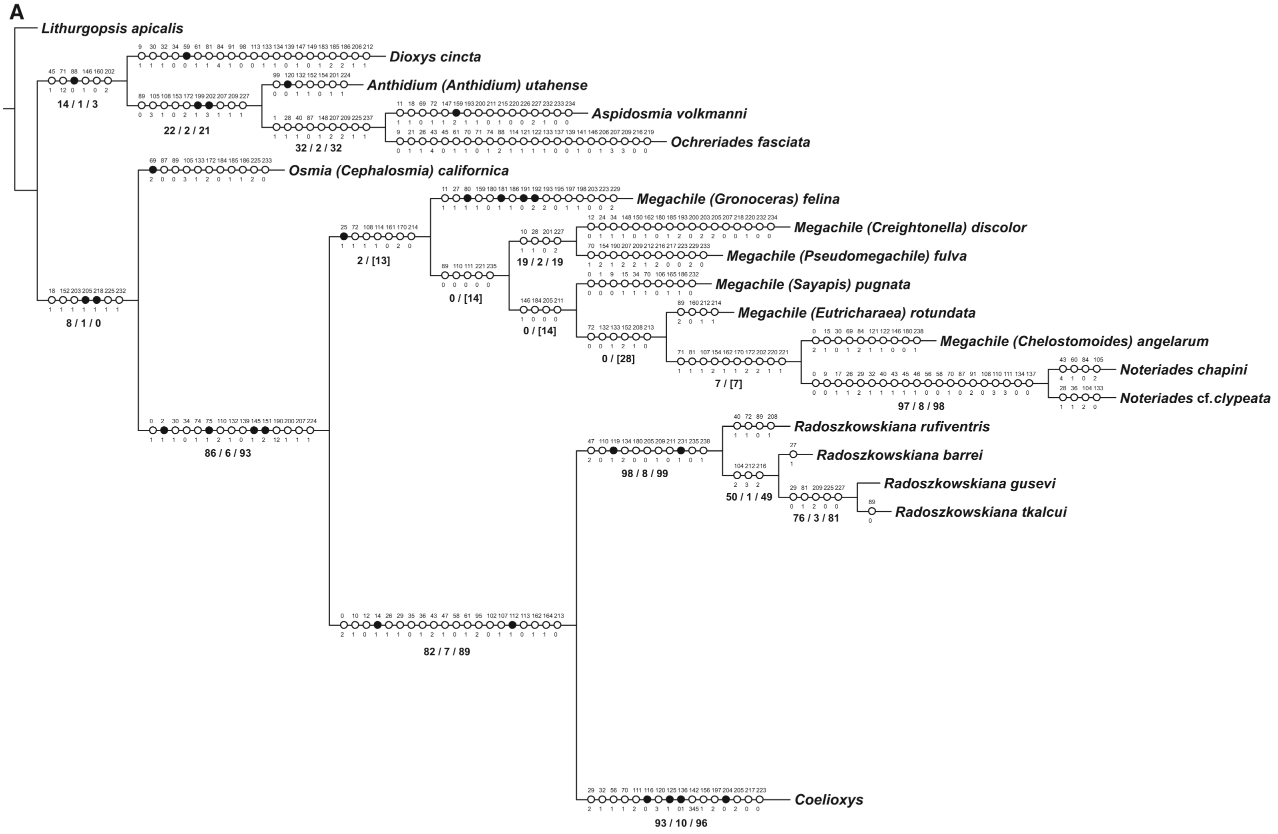


Figure 3. Tree from the implied weighting analysis with all character state changes mapped upon it. All taxonomic changes resulting from the phylogenetic analyses are shown. Black circles indicate unique character state changes; white circles indicate homoplastic changes; character numbers are placed above each change; the changed character state is shown below. Branch support values are shown as in Figure 1. A: *Coelioxys* (*Rhinocoelioxys*) + remaining subgenera.

results were also consistent in the arrangement of the out-group taxa: (*Dioxys* (*Anthidium* (*Aspidosmia* + *Ochreriades*))), with *Osmia* as sister to the Megachilini. In contrast, the equal-weights analysis had *Dioxys* and *Osmia* forming a polytomy along with (*Anthidium* (*Aspidosmia* + *Ochreriades*)) and the Megachilini. Different sister-group relationships for the Megachilini have been found in previous phylogenetic studies of Megachilidae (Praz *et al.*, 2008; Litman *et al.*, 2011, 2013; Gonzalez *et al.*, 2012); however, because our study was aimed at resolving relationships within and between *Radoszkowskiana* and *Coelioxys*, we make no further comment on the relevance of our results to higher level phylogeny within the subfamily.

The monophyly of Megachilini was supported by the following three characters: the presence of a distinct mesal process on the upper half of the antennal socket (2-1; Gonzalez *et al.*, 2012: fig. 5); the outer surfaces of fore- and midtibiae apically with acute angle and distinct notch anteriorly (75-1; Gonzalez *et al.*, 2012: fig. 14), and the S7 in males divided into two small sclerites (224-1; Baker, 1975: fig. 26D). All these characters were listed by Gonzalez *et al.* (2012) as synapomorphies of Megachilini. A list of some least-homoplasious synapomorphies for the nodes is presented in Tables S1 and S2.

RELATIONSHIPS WITHIN THE MEGACHILINI

As also reported by Praz *et al.* (2008), Litman *et al.* (2011), and Gonzalez *et al.* (2012), *Noteriades* was nested within Megachilini. In the successive and implied weighting analyses we found that *Noteriades* was nested within *Megachile*, whereas in the equal-weights consensus tree it formed a polytomy with two groups within *Megachile*. The discrepancy between our three trees arises from the genus *Megachile*, as the clade (*Coelioxys* + *Radoszkowskiana*) arises from a polytomy with three other groups within Megachilini but in both weighted analyses this clade is the sister group of (*Megachile* + *Noteriades*). The molecular phylogenetic study of Litman *et al.* (2011) also showed the clade (*Coelioxys* +

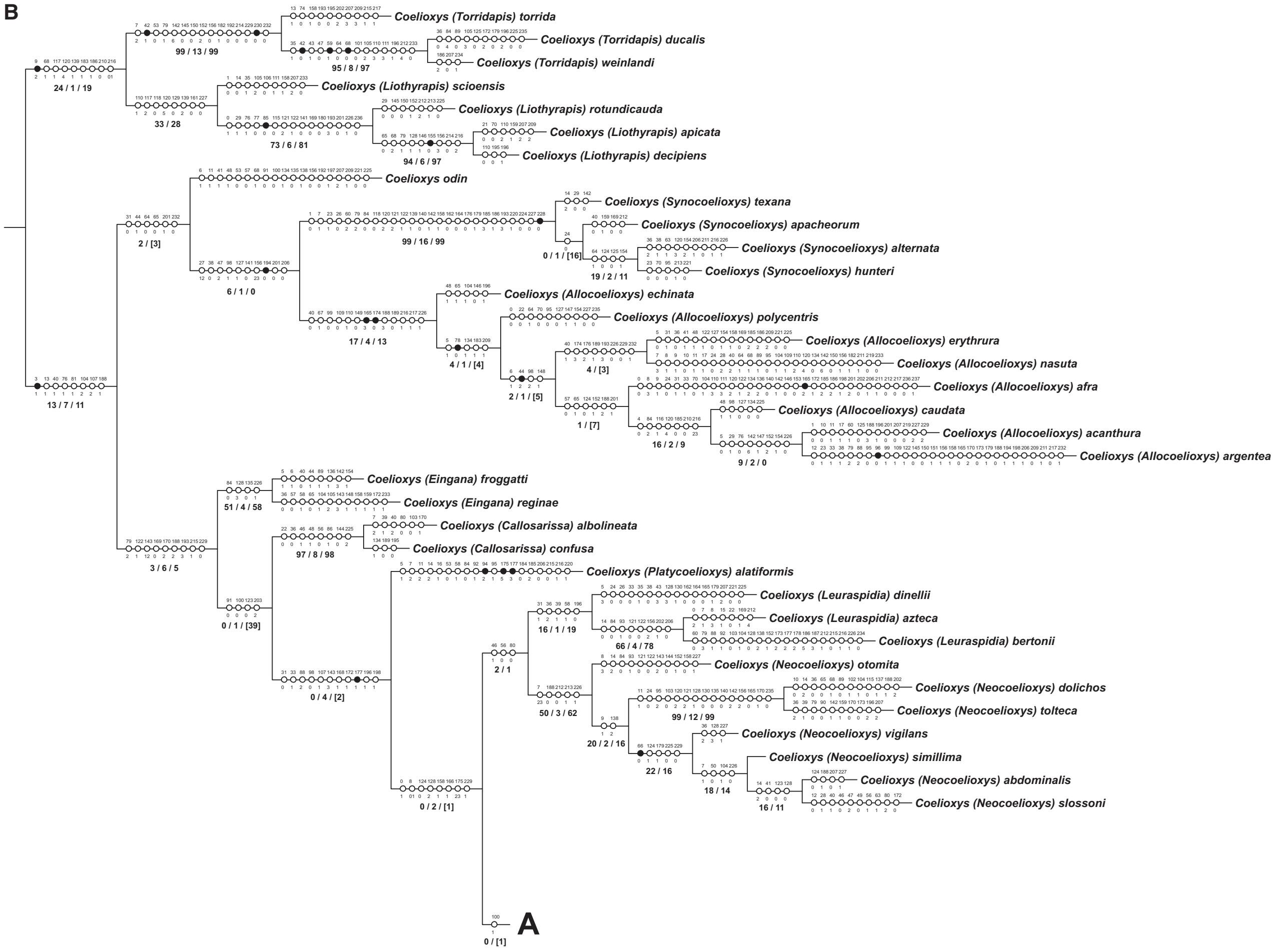


Figure 3. Continued.

Radoszkowskiana) arising from *Megachile*, thus rendering latter paraphyletic.

The position of *Radoszkowskiana* as sister group of *Coelioxys* was observed in all of our analyses, and was also reported by Litman *et al.* (2011). This clade was supported by the following synapomorphies: clypeus with sparse, thin, erect, long hairs throughout the disc (14-1; Fig. 81) and female metasoma conical (112-1; Michener, 2007: fig. 84-2).

MONOPHYLY OF *RADOSZKOWSKIANA* AND RELATIONSHIPS AMONG ITS SPECIES

The monophyly of the genus *Radoszkowskiana* is supported by some homoplasious character state changes as well as two unique, unreversed synapomorphies (Fig. 3): T6 apex in females emarginate (119-1) and apex of the gonocoxa in males strongly concave (231-1; Schwarz, 2001; abb. 39, 43, 44). Only one species, *R. rufiventris*, has been used in previous phylogenetic analyses (Litman *et al.*, 2011, 2013; Gonzalez *et al.*, 2012), and thus the relationships among the four species of *Radoszkowskiana* remained unknown. The following result was obtained in all of our analyses: (*R. rufiventris* (*R. barrei* (*R. gusevi* + *R. tkalcui*))). The clade (*R. barrei* (*R. gusevi* + *R. tkalcui*)) is supported by the following synapomorphies that arise elsewhere on the tree in other genera: fascia on concavity of T1 present and composed of subappressed or appressed hairs (104-2; Fig. 42); S5 gradulus V-shaped, angulate towards base (212-3; Rocha-Filho & Packer, 2015: fig. 16C, F); and outer margins of S6 apically broadly rounded, with incision between outer lobe and rest of sternum broadly rounded (216-2). The clade formed by the two species described by Schwarz (2001), *R. gusevi* + *R. tkalcui*, is supported by five homoplasious character state changes (see Table S1), of which the hind coxa of females with ventral carina present (81-1) and male S8 apex emarginate (225-0) are the least homoplasious. Both species seem to be poorly represented in collections

Figure 3. Continued.

and few specimens are known: from Syria for *R. gusevi* and from Turkey for *R. tkalcui* (Schwarz, 2001). On the other hand, *R. barrei* and *R. rufiventris* are more widely distributed in the Palaearctic region, with records of the former species ranging from Turkey to India, whereas *R. rufiventris* occurs in Northern Africa, from Algeria to Egypt (Schwarz, 2001; Ascher & Pickering, 2015) (Tables S1 and S2).

MONOPHYLY OF *COELIOXYS* AND RELATIONSHIPS AMONG SUBGENERA

The monophyly of *Coelioxys* is supported by the following unique, unreversed synapomorphies: T6 in females gradually tapering towards apex (116-0; Figs 12, 26); and in males S5 long, ≥1.25× longer than wide (204-0). Two more characters have unique changes that help define the genus, but are reversed in one or more subtaxa within it: T6 dorsal carina present (125-1; Figs 38, 40) and S6 gradually tapering towards apex (136-0; Figs 26, 38), both are characters of females.

In all analyses the subgenera *Coelioxys* (*Torridapis*) Pasteels, 1977 and *Coelioxys* (*Liothyrapis*) Cockerell, 1911, , i.e. a clade comprising species of the genus with glabrous compound eyes, were a monophyletic sister group to all other *Coelioxys* subgenera combined. The monophyly of (*C.* (*Torridapis*) + *C.* (*Liothyrapis*)) is supported by: supraclypeal area elevated medially, forming a sharp keel at least apically (9-2; Fig. 54). The monophyly of the clade comprising all remaining subgenera is supported by: compound eye hairy (3-1; Fig. 5). Michener (2007) highlighted how different *C.* (*Torridapis*) and *C.* (*Liothyrapis*) were from the rest of the genus because of their hairless eyes, and also mentioned that Pasteels (1982) placed both in a separate genus, *Liothyrapis*. As *Coelioxys* is supported by two unique, unreversed synapomorphies and lack of eye hairs is plesiomorphic, we regard these two groups with hairless eyes as subgenera. Furthermore, we do not unite these into a single subgenus because of the relatively large differences between them. Also, it should be noted that one species, *Coelioxys* (*Allocoelioxys*) *madagascariensis* Benoist, 1955, exhibits a reversal to glabrous compound eyes, despite clearly being a member of *C.* (*Allocoelioxys*) based upon the characters of that subgenus (see next paragraph). This species thus comes out in a separate place from its consubgeners in the key.

Another result found in all analyses was the clade formed by *C. odin* + (*C.* (*Synocoelioxys*) + *C.* (*Allocoelioxys*)), which is supported by four homoplasious character state changes, the least homoplasious of which are: the pubescence of body composed of both scale-like and fine hairs (44-1) and male T7 with medial tooth reduced (201-1). The position of the subgenus *Coelioxys* (*Mesocoelioxys*) Ruszkowski, 1986 nested within *C.* (*Allocoelioxys*) was found in all the analyses, and the clade formed by those two subgenera is supported by: axilla laterally carinate, carina conspicuously elevated (67-1; Fig. 6). Because *C.* (*M.*) *argentea*, the only species in its subgenus, is nested within *C.* (*Allocoelioxys*), it renders the latter paraphyletic. Consequently, we place *C.* (*Mesocoelioxys*) in synonymy with *C.* (*Allocoelioxys*) syn. nov. Michener (2007: 549) had already noted some similarities between *C.* (*Mesocoelioxys*) and *C.* (*Allocoelioxys*).

The *Coelioxys* species from Australia, previously assigned to *Coelioxys* (*Coelioxys s.s.*) Latreille, 1809; (Michener, 1965), form two successive sister groups to all other *Coelioxys* subgenera not yet discussed in the analyses. Furthermore, in all tree topologies, both groups are separated from the type species of *C.* (*Coelioxys s.s.*) by numerous other subgenera. Consequently, and given the high support and presence of some unreversed synapomorphies found in each of the two branches of Australian taxa, *C. reginae* + *Coelioxys froggatti* Cockerell, 1911 are placed in one new subgenus *Coelioxys* (*Eingana*) subgen. nov. and *Coelioxys albolineata* Cockerell, 1905 + *C. confusa* are placed in a second *Coelioxys* (*Callosarissa*) subgen. nov. described below (see comments in the section on Taxonomic implications).

The monotypic *Coelioxys* (*Platycoelioxys*) Mitchell, 1973 is the sister group of all the remaining subgenera according to all analyses. *Coelioxys* (*Platycoelioxys*) *alatiformis* Friese, 1921 possesses the following autapomorphies: S5 in females greatly expanded towards apex, margins straight, ventral surface concave, apex broad and truncate (94-2; Fig. 44); postgradular area of T2 with an elliptical, small, deep fovea covered with minute hairs and not surrounded by punctures (175-5; Fig. 45); and postgradular area of T3 with a small, circular fovea surrounded by an impunctate area without punctures (178-5; Fig. 45).

In all analyses, the species of *C.* (*Neocoelioxys*) came nested within most species currently assigned to *C.* (*Acrocoelioxys*), including its type species. The type species of *C.* (*Acrocoelioxys*), *Coelioxys* (*Acrocoelioxys*) *otomita* Cresson, 1878 is the sister species of a clade containing two other *C.* (*Acrocoelioxys*) species and all of our exemplars of *C.* (*Neocoelioxys*). Consequently, we synonymize *C.* (*Acrocoelioxys*) under *C.* (*Neocoelioxys*) syn. nov., as the latter has priority in Mitchell's (1973) revision. The placement of two *C.* (*Acrocoelioxys*) species (*Coelioxys azteca* Cresson, 1878 and *Coelioxys dinellii* Holmberg, 1916) along with the *incertae sedis* species *C. bertonii* varied among analyses. Nonetheless, they form a well-supported monophyletic group separate from all other named subgenera in all three results, and consequently a new subgenus *Coelioxys* (*Leuraspidia*) subgen. nov. is described for them. This clade is supported by: mesoscutum conspicuously swollen medially (39-1; Fig. 58) and S5 in females with erect thick hairs forming a distinct row on the lateral margins (97-1).

All analyses failed to support the monophyly of *C.* (*Rhinocoelioxys*), with it either forming two successive sister groups to the subgenera yet to be discussed or, in the equal-weights analysis, forming, along with *C.* (*Leuraspidia*), three successive sister groups to the remainder. Given the synapomorphies for both groups (see also Supporting Information, Table S2), the name *C.* (*Rhinocoelioxys*) will be applied to the branch formed by the type species, *Coelioxys zapoteca* Cresson, 1878 along with *Coelioxys agilis* Smith, 1879. Thus, a new subgenus [*C.* (*Austrocleptria*) subgen. nov.] is required for the branch composed of ((*Coelioxys nasidens* Friese, 1922 + *Coelioxys clypearis* Friese, 1922) + (*Coelioxys barbata* Schwarz & Michener, 1954 + *Coelioxys paraguayensis* Schrottky, 1907)) (see Taxonomic implications).

The subgenus *Coelioxys* (*Cyrtocoelioxys*) Mitchell, 1973 was monophyletic in all analyses, and is supported by: the hind basitarsus with a flattened tooth-like process (83-1) and the hind tibia apically with an elongate, cylindrical, subacute medial spine (84-3).

A newly delineated *Coelioxys* (*Glyptocoelioxys*) Mitchell, 1973 includes *Coelioxys* (*Dasycoelioxys*) *chilensis* Reed, 1892, *Coelioxys* (*Haplocoelioxys*) Mitchell, 1973, and *C.* (*Glyptocoelioxys*), based upon the following synapomorphies: postgradular area of T2 with an inconspicuous, minute, circular fovea with a densely punctate area posteriorly to it (175-3; Fig. 78) and postgradular area of T3 with a small, circular fovea surrounded by an impunctate area without punctures (178-4; Fig. 78). As *C.* (*Haplocoelioxys*) syn. nov. renders *C.* (*Glyptocoelioxys*) paraphyletic, it is synonymized under *C.* (*Glyptocoelioxys*) syn. nov. While page priority in Mitchell (1973) would suggest that *C.* (*Haplocoelioxys*) should take priority, this is not a requisite under article 24.2.2. of the International Code of Zoological Nomenclature, and as *C.* (*Haplocoelioxys*) is monotypic, but *C.* (*Glyptocoelioxys*) contains 27 species, we chose the latter subgenus to minimize the number of changes in subgeneric assignments [see remarks in the *C.* (*Glyptocoelioxys*) section].

We also transfer *C. chilensis*, assigned to the subgenus *C.* (*Dasycoelioxys*) by Mitchell (1973; as

Coelioxys brevicaudata Friese, 1905), to *C*. (*Glyptocoelioxys*). This is unsurprising as this species does not possess the diagnostic features that Mitchell (1973) cited for *C*. (*Dasycoelioxys*). He differentiated *C*. (*Dasycoelioxys*) from those species of *C*. (*Glyptocoelioxys*) because of their dense and erect pubescence on the head and mesosoma and the form of the female S6, which is slender and elongate with lateral notches minute or absent. These characters are not observed in *C*. *chilensis*; hence this species was originally incorrectly assigned to *C*. (*Dasycoelioxys*) and is now transferred to *C*. (*Glyptocoelioxys*).

The subgenus *C*. (*Dasycoelioxys*), synonymized under *C*. (*Glyptocoelioxys*) by Michener (2007), came out as a monophyletic group (once *C*. *chilensis* is removed from it, see above) with high support (Figs 1–3) in all analyses. It is sister to all subgenera other than those already discussed. Its status is therefore revalidated herein.

A clade composed of *C*. (*Coelioxys s.s.*) + *Coelioxys* (*Xerocoelioxys*) Mitchell, 1973, was found in all trees. Both subgenera received high support (Fig. 3) in the implied weighting analysis. The sister-group relationship of the two subgenera is supported by the gradulus of T2 bowed posteriorly (109-0). The subgenus *C*. (*Coelioxys s.s.*) is supported by the outer margin of pronotal lobe distinctly rounded, not carinate (34-1; Fig. 30), and *C*. (*Xerocoelioxys*) is supported by the T6 apex in females ovoid, tapering towards the apex (120-2; Fig. 14).

Species of *Coelioxys* (*Boreocoelioxys*) Mitchell, 1973 + *Coelioxys conoidea* (Illiger, 1806) came as the sister group of the clade *C*. (*Coelioxys s.s.*) + *C*. (*Xerocoelioxys*) in all weighted analyses. In the consensus tree from the equal-weights analysis these two subgenera arise from a polytomy containing nine species previously placed in two subgenera. The subgenus *C*. (*Boreocoelioxys*) came as paraphyletic in the successive weighting tree with *Coelioxys rufitarsis* Smith, 1854, the type species of this subgenus, as the sister group of *C*. *conoidea* and the clade *C*. (*Coelioxys s.s.*) + *C*. (*Xerocoelioxys*).

In the implied weighting analysis *C*. (*Boreocoelioxys*) was not supported (bootstrap, 0; symmetric, –5; Bremer, 2). Considering this outcome and given that the clade formed by *Coelioxys funeraria* Smith, 1854 + *Coelioxys alata* Förster, 1853 had high branch support (bootstrap, 54; symmetric, 63; Bremer, 5), the subgenus *C*. (*Paracoelioxys*) stat. res., previously synonymized under *C*. (*Coelioxys s.s.*), is now raised to encompass those species. *Coelioxys* (*Paracoelioxys*) is supported by the mandible in females angled medially on outer surface (21-2; Fig. 81). Hence, the subgenus *C*. (*Boreocoelioxys*) is now understood to comprise only the New World species previously assigned to it, and it is supported by the postgradular grooves of T2 complete (110-0; Fig. 24), and in males the hypostomal concavity at least half as long as the compound eye (167-1; Rocha-Filho & Packer, 2015: fig. 7E). The other two Palaearctic species nested in the clade containing *C*. (*Paracoelioxys*) and *C*. (*Boreocoelioxys*), *Coelioxys rufescens* Lepeletier & Serville, 1825 and *C*. *conoidea* (Fig. 3), are assigned to new subgenera *Coelioxys* (*Rozeniana*) subgen. nov. and *Coelioxys* (*Melissoctonia*) subgen. nov., respectively (see the following section). The clade composed of *C*. *conoidea* + (*C*. *rufescens* + (*C*. (*Paracoelioxys*) + *C*. (*Boreocoelioxys*)) is supported by the postgradular area of T2 in males with a more or less transverse, punctate area and a fovea (173-2; Figs 27, 88, 90). The clade formed by *C*. *rufescens* + (*C*. (*Paracoelioxys*) + *C*. (*Boreocoelioxys*)) is supported by the T1 lateral bands in females composed of subappressed or suberect hairs, at least basally (102-1; one reversal in *C*. *funeraria*), and by the fovea on the postgradular area of T2 in males transverse, shallow, and composed of small punctures, with punctures posteriorly to the fovea, or a deep, transverse fovea not composed of punctures, with punctures posteriorly to the fovea (175-1; Figs 27, 88; one reversal in *C*. *funeraria*).

TAXONOMIC IMPLICATIONS

Considering the result of the phylogenetic analyses, six new subgenera of *Coelioxys* are described herein and three are synonymized with other subgenera, making a total of 20 subgenera currently recognized. Twenty-one species are transferred among subgenera (Fig. 3).

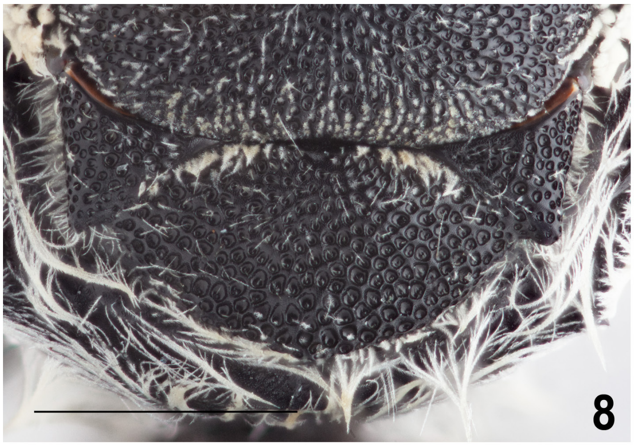
In all three phylogenetic trees, the African species *C*. *odin* is the sister taxon to (*C*. (*Allocoelioxys*) + *C*. (*Synocoelioxys*)). This suggests that we should describe a subgenus for it; however, we are not doing so at this time for several reasons. First, there are numerous additional species that may be related to it, especially from the poorly known Indomalayan and Afrotropical regions. According to Pasteels (1977) these include additional species groups (*aurifrons* and *caffra* species groups) from the Afrotropical region that are related to *C*. *odin*, and we have not been able to study confirmed material of these taxa. Secondly, we have not studied type material of this species, but have identified our specimens using Pasteels' (1968) identification key. Hence *C*. *odin* is regarded herein as *incertae sedis*, as it also treated in Ascher & Pickering (2015). We also emphasize that the key presented herein is provisional for the Afrotropical and Indomalayan zoogeographic regions, where the faunas are poorly known. A key to the 20 *Coelioxys* subgenera is provided below.

KEY TO THE *COELIOXYS* SUBGENERA [MODIFIED FROM MITCHELL (1973) AND MICHENER (2007)]

1. Eyes bare (Fig. 4)……………………………………………………………………2
   Eyes hairy (Fig. 5)………………………………………………………………4
2. Lateral margins of axilla elevated, sharply carinate, from Madagascar (Fig. 6)……………………………… *Coelioxys* (*Allocoelioxys*)

Figures 4 and 5. Female. Frontal view of head (for compound eye): 4, *Coelioxys weinlandi*; 5, *Coelioxys zapoteca*. Scale bars: 1.5 mm.

Figures 6 and 7. Female. Dorsal view of mesoscutellum (for lateral margin of axilla): 6, *Coelioxys madagascariensis*; 7, *Coelioxys verticalis*. Scale bars: 1.5 mm.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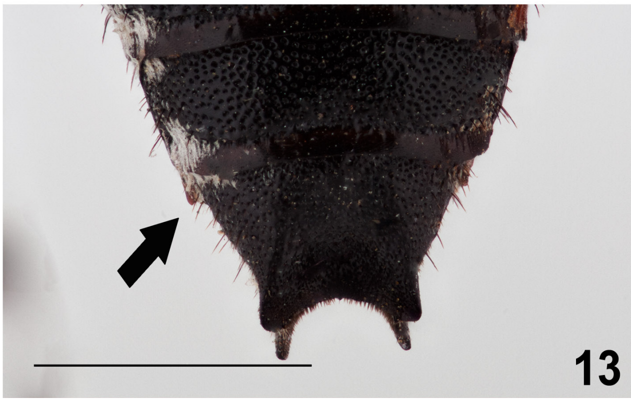
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[in part: *Coelioxys* (*Allocoelioxys*) *madagascariensis* (Benoist, 1955)]

Lateral margins of axilla neither elevated nor carinate, not from Madagascar (Fig. 7)…3

3. Axilla short, free apical portion not produced beyond the posterior margin of the mesoscutellum and not curved apically (Fig. 8). Mesoscutellum flat, lacking dorsal medial carina (Fig. 8). Female: T6 subapically with long, erect, thick hairs, with apex ending in a long spine-like process (Fig. 8); S6 broad and rounded apically, abruptly constricted near midlength and bluntly pointed, its lateral margins with a dense fringe of long, curved, dark hairs (Fig. 9). Male: hypostomal concavity present (as in Fig. 15); T6 basally with long, acute lateral teeth (Fig. 10); S4 medially flat, neither sulcate nor hairy (predominantly Afrotropical but also Palaearctic and Indomalayan)………… ……………. *Coelioxys* (*Liothyrapis*) Cockerell, 1911.

Axilla long, free apical portion produced beyond the posterior margin of the mesoscutellum and curved mesad apically (Fig. 11). Mesoscutellum with a dorsal median carina at least anteriorly (Fig. 11). Female: T6 lacking long, erect, thick hairs, its apex ending in an inconspicuous, short, spine-like process (Fig. 12); T6 and S6 gradually tapering, considerably elongate (Fig. 12); S6 subacute apically, its lateral margins with an inconspicuous fringe composed of short brownish hairs (Fig. 12). Male: hypostomal area lacking concavity (as in Fig. 18); T6 never with long, acute teeth basally, sometimes with short, flattened teeth (Fig. 13); S4 medially sulcate and hairy (Afrotropical, Indomalayan, Palaearctic and Australasian)……………… ……………………… *Coelioxys* (*Torridapis*) Pasteels, 1977

4. Lateral margins of axilla elevated, sharply carinate (Fig. 6)……………………………………5

Lateral margins of axilla neither elevated nor carinate (Fig. 7)…………………………………7

5. Pilosity on vertex composed of long suberect hairs (as in Fig. 52). Female: S6 abruptly constricted near midlength, with lateral margins angled subapically, notches obtuse, clearly visible in dorsal view (Fig. 14). Male: hypostomal concavity present, conspicuous; gena covered with suberect hairs (Fig. 15) (Nearctic)…………

Figures 14 and 15. *Coelioxys edita*: 14, female, dorsal view of T6 and S6; 15, male, lateral view of head (for gena pilosity). Scale bars: 1.5 mm.

Figures 8–13. 8, 9, female, *Coelioxys apicata*: 8, dorsal view of mesoscutellum; 9, dorsal view of T6 and S6. 10, male, *Coelioxys decipiens*: dorsal view of T6 (for lateral tooth of T6). 11, female, *Coelioxys ducalis*: dorsal view of mesoscutellum. 12, 13, *Coelioxys weinlandi*: 12, female, dorsal view of T6 and S6; 13, male, dorsal view of T6 (for lateral tooth of T6). Scale bars: 1.5 mm.


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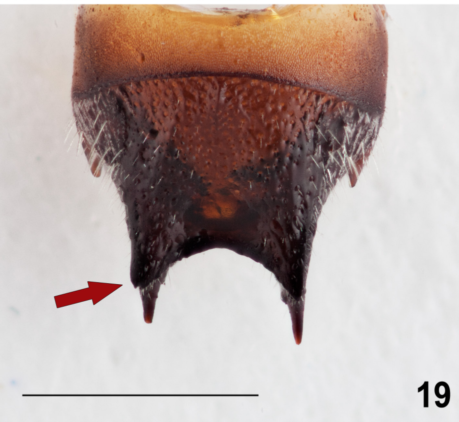
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…………………………………… *Coelioxys* (*Xerocoelioxys*) [in part: *Coelioxys* (*Xerocoelioxys*) *edita* Cresson, 1872]

Pilosity on vertex composed of appressed plumose hairs or scale-like hairs mixed with long suberect hairs (as in Fig. 32). Female: S6 ovoid, elongate or greatly elongate apically, never abruptly constricted near midlength; lateral margins of S6 never angled nor notched subapically. Male: hypostomal area either lacking concavity or with a smooth, elliptical plate that is usually produced; gena covered with appressed hairs (as in Fig. 22) (predominantly Palaearctic and Afrotropical but also Indomalayan and Australasian)……………………………………………………………………………6

6. Female: fore coxa with a flattened, spine-like process (Fig. 16); T6 constricted medially and forming an elongate, cylindrical, conspicuous upwardly oriented process with a rounded apex (Fig. 17); S5 apex truncate and thickened (Fig. 17). Male: hypostomal area unmodified, lacking concavity or a smooth plate (Fig. 18); T5 lacking lateral tooth-like processes; T6 apicodorsal processes not forked (Fig. 19) (Afrotropical and Palaearctic)…………………………………………………………………………………………… *Coelioxys* (*Allocoelioxys*) *argentea* group *sensu* Pasteels (1968, 1977)

Female: fore coxa lacking spine-like process (Fig. 20); T6 variable, if constricted medially then never forming a cylindrical, conspicuous dorsally oriented process (Fig. 21); S5 apex either ovoid or triangular, never thickened (Fig. 21). Male: hypostomal area with a smooth, elliptical plate (Fig. 22); T5 with lateral tooth-like processes; T6 apicodorsal processes forked (Fig. 23) (predominantly Palaearctic and Afrotropical, but also Indomalayan and Australasian)…………………………………… *Coelioxys* (*Allocoelioxys*) Tkalců, 1974 (in part).

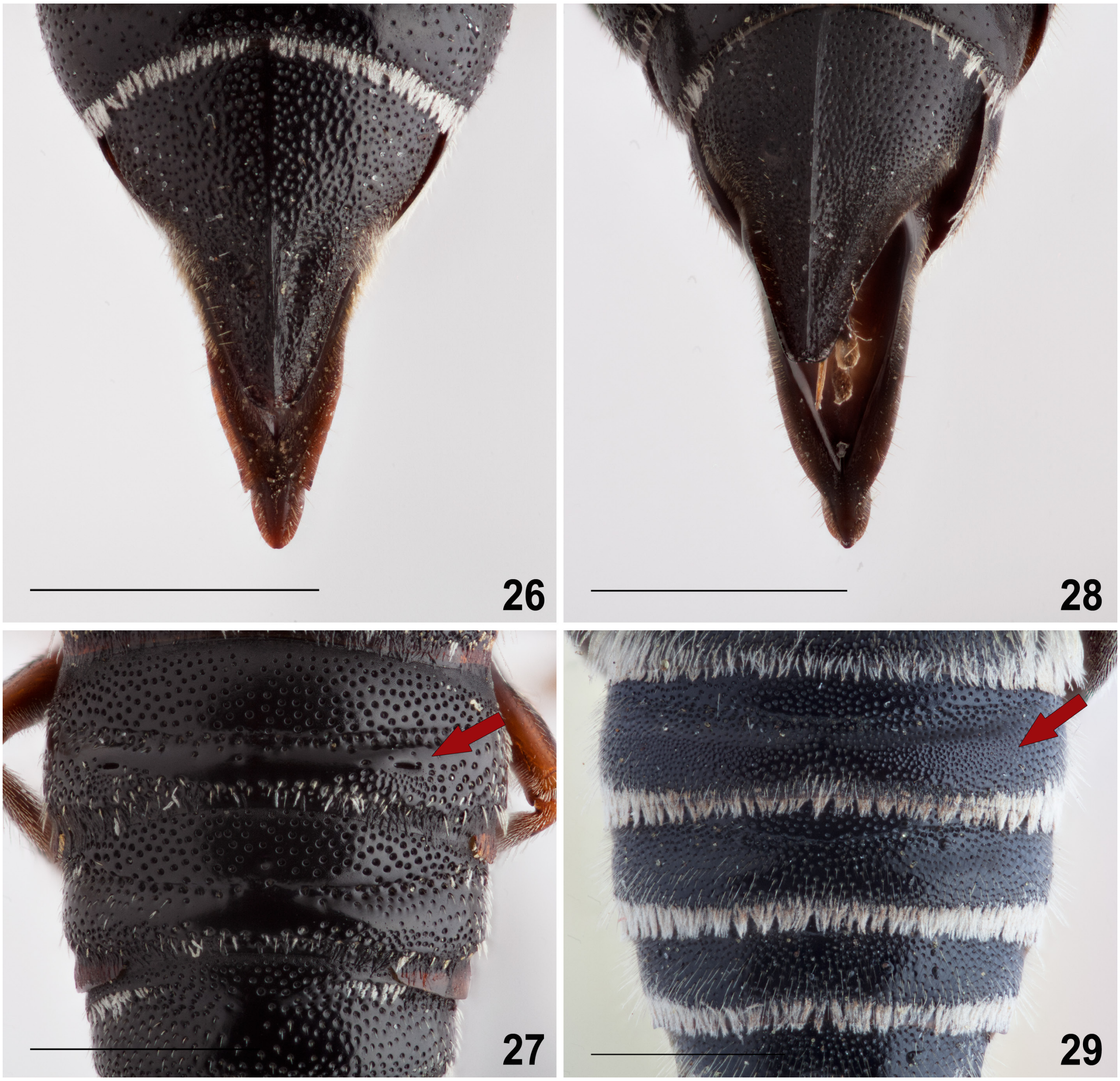
7. Postgradular grooves of T2 and often of T3 complete, uninterrupted medially (Fig. 24)……8

Postgradular grooves of both T2 and T3 interrupted medially (Fig. 25)………………10

8. Female: S6 gradually tapering towards apex and conspicuously notched subapically, notches acute (Fig. 26). Male: postgradular area of T2 with sublateral, elliptical, slender fovea on each side (Fig. 27) (Nearctic)…………………………………………… *Coelioxys* (*Boreocoelioxys*) Mitchell, 1973

Figures 24 and 25. Female, dorsal view of T2–T3 (for postgradular grooves): 24, *Coelioxys rufitarsis*; 25, *Coelioxys apacheorum*. Scale bars: 1.5 mm.

Figures 16–23. 16–19, *Coelioxys argentea*. 16, 17, female: 16, frontal view of fore coxa (spine-like process indicated by black arrow); 17, lateral view of T6, S6, and S5 (indicated by black arrow). 18, 19, male: 18, lateral view of head (hypostomal area indicated by black arrow); 19, dorsal view of T6 (dorsal process indicated by red arrow). 20, female, *Coelioxys erythrura*: frontal view of fore coxa (lack of a spine-like process indicated by black arrow). 21, female, *Coelioxys brevis*: lateral view of T6, S6, and S5. 22, male, *Coelioxys afra*: lateral view of head (hypostomal area indicated by black arrow). 23, male, *Coelioxys echinata*, dorsal view of T6 (dorsal process indicated by red arrow). Scale bars: 1.5 mm.



Figures 26–29. 26, female, *Coelioxys porterae*: dorsal view of T6 and S6. 27, male, *Coelioxys sayi*: dorsal view of T2 (fovea indicated by red arrow). 28, female, *Coelioxys quadridentata*, dorsal view of T6 and S6. 29, male, *Coelioxys sodalis*: dorsal view of T2 (punctate area indicated by red arrow). Scale bars: 1.5 mm.

Female: S6 constricted near midlength, sometimes abruptly so, but lacking subapical notches (Fig. 28) or with obtuse notches (Fig. 14). Male: postgradular area of T2 never foveate, but sometimes with sublateral, transverse, densely punctate area on each side (Fig. 29)……………………………………………………………………9

9. Pronotal lobe inconspicuously carinate, its outer margin distinctly rounded (albeit often obscured by long hairs; Fig. 30). Mesosomal pilosity long, composed of suberect, elongate, thin hairs, lacking appressed hairs that if present would form spots on the mesoscutum (Holarctic)……………………………………………………*Coelioxys* (*Coelioxys s.s.*) Latreille, 1809

Pronotal lobe either distinctly lamellate (Fig. 31) or carinate throughout without forming lamella (as in Fig. 75), albeit sometimes obscured by long hairs. Mesosomal pilosity short, composed of subappressed or appressed hairs forming

Figures 30 and 31. Female, frontal view of pronotal lobe (outer margin indicated by red arrow): 30, *Coelioxys sodalis*; 31, *Coelioxys grindeliae*. Scale bars: 1.5 mm.

Figures 32–34. 32, 33, female. 32, *Coelioxys texana*: dorsal view of mid ocellus. 33, *Coelioxys alternata*: dorsal view of T6 and S6. 34, male, *Coelioxys alternata*: dorsal view of T6 (dorsal process indicated by red arrow). Scale bars: 1.5 mm.

Figures 35–37. 35, 36, female. 35, *Coelioxys albolineata*: dorsal view of mesoscutellum (for axilla length). 36, *Coelioxys froggatti*: lateral view of pretarsal claws (inner rami indicated by black arrows). 37, male, *Coelioxys reginae*: lateral view of head (for genal excavation). Scale bars: 1.5 mm.

marginal lines or spots on the mesoscutum (predominantly Nearctic but also from Neotropical Mexico)…………………………………………….
……………………………………………*Coelioxys* (*Xerocoelioxys*) Mitchell, 1973 (in part).

10. Median ocellus surrounded by a swollen, dull, nearly impunctate area (Fig. 32). Female: lateral margins of T6 apex with long thick hairs forming an inconspicuous fringe (Fig. 33); S6 rounded or elliptical, not notched (Fig. 33). Male: T6 apicodorsal processes forked, each arm flattened, pointed, and irregular, almost forming a crenulate plate (Fig. 34); T7 exposed, with a long tooth-like process medially; S7 undivided, bilobed (predominantly Nearctic but also from Cuba and Mexico)……………………………………………

Figures 38–41. 38, female, *Coelioxys confusa*: dorsal view of T6 and S6. 39, male, *Coelioxys albolineata*: lateral view of head (for posterior margin of genal excavation). 40, female, *Coelioxys reginae*: dorsal view of T6 and S6. 41, male, *Coelioxys froggatti*: lateral view of head (for posterior margin of genal excavation). Scale bars: 1.5 mm.

……………………………..*Coelioxys* (*Synocoelioxys*) Mitchell, 1973

Median ocellus generally not surrounded by a swollen area (Fig. 54), but *if so* then T6 in females with notches subapically (Fig. 26) and T6 apicodorsal processes in males not forked (Fig. 61). Male: T7 hidden by T6 but if exposed never with a median tooth-like process; S7 divided into two small sclerites……………………………………………………………11

11. Axilla short, free apical portion shorter than basal portion (Fig. 35). Female: pretarsal claw bifurcate, inner and outer rami separated by broad concavity (Fig. 36). Male: gena deeply excavated along posterior margin of eye, excavated area densely covered with appressed, plumose white hairs (Fig. 37) (Australasian and Indomalayan)……………………………………12

Axilla long or short, but *if* short *then* pretarsal claws in females never bifurcate (Fig. 82). Gena in males never excavated (Fig. 15)……………………………………………………13

12. Posterior margin of mesoscutellum obtusely produced medially, apex of convexity conspicuously emarginate and posterodorsally oriented. Mesoscutellum sparsely punctate, interspaces greater than puncture diameters. Female: T6 dorsal carina inconspicuously elevated, not sharp (Fig. 38); S6 narrow, elongate, much longer than broad, lateral notches indistinct (Fig. 38). Male: genal excavation linear, anterior and posterior margins nearly parallel, more than 4× longer than broad (Fig. 39); T6 apicodorsal processes long, triangular, acute apically (predominantly Australasian but also Indomalayan)…………………………… *Coelioxys* (*Callosarissa*) Rocha-Filho subgen. nov.

Posterior margin of mesoscutellum rounded, neither produced medially nor emarginate. Mesoscutellum densely to coarsely punctate, interspaces between punctures much shorter than puncture diameter. Female: T6 dorsal carina conspicuously elevated subapically, sharp (Fig. 40); S6 triangular, not conspicuously elongate, subapical notches distinct (Fig. 40). Male: genal excavation convex posteriorly, not linear, posterior margin distinctly curved, less than 3.5× longer than greatest breadth (Fig. 41); T6 apicodorsal processes elongate or short and broad, but always rounded apically (Australia)……………………………………*Coelioxys* (*Eingana*) Rocha-Filho subgen. nov.

13. Concavity of T1 distinctly carinate (although it may be necessary to move the specimen around to make sure the carina is detectable; Fig. 42)…………………………………………………………14

Concavity of T1 lacking marginal carina (Fig. 43)………………………………………………22

14. Female: clypeus with two submedian ridges separating three shallow pits; S5 greatly expanded towards apex, spatulate, hiding all but the apex of S6 (Fig. 44); S6 elongate, notched apically, with three minute tubercles at tip (Fig. 44). Male: postgradular areas of both T2 and T3 foveate, lacking punctures posteriorly to the fovea, fovea on T2 elliptical, covered with minute whitish hairs, fovea on T3 smaller, circular (Fig. 45) (Neotropical)……………………*Coelioxys* (*Platycoelioxys*) Mitchell, 1973

Figures 42 and 43. 42, male, *Coelioxys costaricensis*: dorsal view of T1 (for marginal carina). 43, female, *Coelioxys cerasiopleura*: dorsal view of T1 (for lack of marginal carina). Scale bars: 1.5 mm.

Figures 44 and 45. *Coelioxys alatiformis*: 44, female, dorsal view of T6, S6 and S5 (indicated by black arrow); 45, male, dorsal view of T2–T3 (foveae indicated by red arrows). Scale bars: 1.5 mm.

Female: clypeus without two submedian ridges separating three shallow pits; S5 not expanded towards apexm but *if so* (*C. alata*) then fan-shaped, never spatulate, margins straight, ventral surface convex, apex broad and truncate; S6 elongate, lacking notches (Fig. 46) or notched apically (Figs 57, 60), but never with three minute tubercles at tip. Male: postgradular area of T2 usually not foveate, but *if* so *then* fovea never elliptical and covered with minute whitish hairs, fovea either punctate, transverse and hairless (Fig. 90), or inconspicuous, minute, circular with

Figures 46 and 47. 46, female, *Coelioxys sanguinicollis*: dorsal view of T6 and S6. 47, male, *Coelioxys chichimeca*: dorsal view of T2–T3 (fovea on T3 indicated by red arrow). Scale bars: 1.5 mm.

a densely punctate area posterior to the fovea (Fig. 78); postgradular area of T3 not foveate, but *if so* then fovea always with punctures posteriorly to the fovea (Figs 78, 80)……………………………………………………………15

15. Female: T6 ending in a short, rounded spine-like process (long in *Coelioxys gonaspis* Cockerell, 1924, which agrees with all following characteristics), subapical area covered with long, thick erect hairs apically (Fig. 46); S6 constricted near midlength or gradually tapering, but ending in a spine-like process, its lateral margins either covered with an inconspicuous short fringe or with a dense fringe composed of long, suberect, dark hairs (Fig. 46). Male: postgradular area of T2 never foveate (Fig. 47),

Figures 48 and 49. *Coelioxys mexicana*: 48, female, frontal view of head (for clypeus); 49, male, ventral view of S4 (U-shaped process indicated by blue arrow). Scale bars: 1.5 mm.

Figures 50 and 51. Female, dorsal view of mesoscutellum (for posterior margin): 50, *Coelioxys simillima*; 51, *Coelioxys zapoteca*. Scale bars: 1.5 mm.

Figures 52–54. Female. 52, *Coelioxys menthae*, dorsal view of mid ocellus. 53, 54, frontal view of head (for supraclypeal area): 53, *Coelioxys tolteca*; 54, *Coelioxys bertonii*. Scale bars: 1.5 mm.

postgradular area of T3 with a circular, deep fovea composed of small punctures; fovea surrounded by punctures forming a transverse area and with an impunctate area anterior to the fovea (Fig. 47, fovea indicated by red arrow), except in *Coelioxys costaricensis* Cockerell, 1914, in which the fovea is absent but which agrees with all preceding characters (predominantly Neotropical but also Nearctic)………………… ………...……...….. *Coelioxys* (*Cyrtocoelioxys*) Mitchell, 1973

Female: T6 never ending in a short, rounded spine-like process, subapical area lacking long, thick erect hairs apically (Figs 65, 77, 79); S6 gradually tapering towards apex, never constricted near midlength and ending in a spine-like process, its lateral margins not covered with a fringe composed of long, suberect, dark hairs (Figs 65, 77, 79). Male: postgradular area of T2 foveate (Fig. 78) or lacking fovea (Fig. 68), postgradular area of T3 not foveate (Figs 66, 88) or foveate (Fig. 78, 80), *if foveate* then fovea minute, circular, shallow, with a densely punctate area posterior to it (Fig. 78), or fovea circular, deep, composed of small punctures and completely surrounded by punctures, lacking impunctate areas (Fig. 80)……………… ……………………… ……………………………………………...16

16. Postgradular grooves of T2 and T3 narrowly interrupted medially. Posterior margin of mesoscutellum rounded, not produced medially. Mesoscutellum keeled dorsomedially. Female: clypeus flattened apically (Fig. 48). Male: hypostomal area lacking concavity; S4 apical margin deeply emarginate, forming a U-shaped process, its arms thick, robust (Fig. 49) (Nearctic and Neotropical)………….. *Coelioxys* (*Glyptocoelioxys*) [in part *Coelioxys* (*Glyptocoelioxys*) *mexicana* Cresson, 1878]

Postgradular grooves of T2 and T3 broadly interrupted medially. Mesoscutellum usually triangular with its posterior margin produced medially, but *if* rounded and not produced medially *then* mesoscutellum never keeled dorsomedially. Female: clypeus flat (Fig. 54), swollen or produced medially (Fig. 5), never flattened apically, but *if so* then basal concavity of T1 never carinate. Male: hypostomal area usually with a concavity, but *if* concavity is absent *then* S4 apical margin either entire (as in Fig. 62) or deeply emarginate, forming a U-shaped process, its arms flattened, elongate (as in Fig. 64)……… ………...….. …………………………………17

17. Mesoscutum and mesoscutellum sparsely punctate, interspaces between punctures much larger than diameter of adjacent punctures (Fig. 50). Dorsal and posterior surfaces of mesoscutellum forming a sharp, acute angle that is nearly impunctate (Fig. 50). Mesoscutellum produced over metanotum…...…………………………….. ……..……………………………………...18

Mesoscutum and mesoscutellum moderately densely punctate, interspaces between punctures subequal to or larger than puncture diameter (Fig. 51). Dorsal and posterior surfaces of mesoscutellum forming an angle of at least 90°, edge

Figures 55–60. Female. 55–57, *Coelioxys otomita*: 55, lateral view of mesosoma (anterior margin of mesoscutum indicated by black arrow); 56, lateral view of T6 and S6 (dorsal surface of T6 indicated by black arrow); 57, dorsal view of T6 and S6 (S6 notch indicated by black arrow). 58, *Coelioxys dinellii*: lateral view of mesosoma (anterior margin of mesoscutum indicated by black arrow). 59, *Coelioxys azteca*: lateral view of T6 and S6 (dorsal surface of T6 indicated by black arrow). 60, *Coelioxys dinellii*: dorsal view of T6 and S6 (S6 notch indicated by black arrow). Scale bars: 1.5 mm.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Figures 61–64. Male. 61, *Coelioxys abdominalis*: dorsal view of T5–T6 (lateral tooth of T5 indicated by black arrow). 62, *Coelioxys menthae*: ventral view of S4 (apical margin indicated by black arrow). 63, 64, *Coelioxys azteca*: 63, dorsal view of T5–T6 (lateral tooth of T5 indicated by black arrow); 64, ventral view of S4 (U-shaped process indicated by black arrow). Scale bars: 1.5 mm.

at least somewhat punctate (Fig. 51). Mesoscutellum not produced over metanotum…………………………………………………………20

18. Median ocellus surrounded by a conspicuous impunctate, swollen area (Figs 52, 53). Supraclypeal area elevated medially, forming a rounded ridge (Fig. 53) (predominantly Neotropical but also Nearctic)…………………………………………………*Coelioxys* (*Neocoelioxys*) Mitchell, 1973 (in part).

Median ocellus never surrounded by a conspicuously impunctate, swollen area, subocellar area punctate, flat or inconspicuously elevated (Fig. 54). Supraclypeal area not elevated medially, never forming a rounded ridge (Fig. 54)……………………………………………19

19. Median area of mesoscutum not swollen (Fig. 55). Female: T6 bisinuate in profile (Fig. 56); S6 notches obsolete, weakly impressed, not interrupting outline of sternum in dorsal view (Fig. 57). Male: T5 lacking lateral teeth (as in Fig. 13); S4 apical margin entire (as in Fig. 62); gradulus of S5 straight and complete (requires dissection) (Neotropical)………………………………………………………… *Coelioxys* (*Neocoelioxys*) *otomita* Cresson, 1878

Median area of mesoscutum conspicuously swollen (Fig. 58). Female: T6 convex, never bisinuate in profile (Fig. 59); S6 notches acute, triangular, clearly visible in dorsal view (Fig. 60). Male: T5 with conspicuous lateral teeth (Fig. 63); S4 apical margin deeply emarginate, forming a U-shaped process (Fig. 64); gradulus of S5 semicircular or V-shaped, incomplete, its lateral margins evanescent (requires dissection) (predominantly Neotropical but also Nearctic) ……………………………………… *Coelioxys* (*Leuraspidia*) Rocha-Filho subgen. nov.

20. Median ocellus surrounded by a conspicuous impunctate, swollen area (Figs 52, 53). Supraclypeal area elevated medially, forming a rounded ridge (Figs 52, 53). Male: T5 lacking or with very short, vestigial lateral teeth (Fig. 61); S4 apical margin entire (Fig. 62); gradulus of S5 straight and complete (requires dissection) (Nearctic and Neotropical)…………………………………………………………………… *Coelioxys* (*Neocoelioxys*) (in part) (*Coelioxys slossoni* Viereck, 1902, *Coelioxys menthae* Cockerell, 1897, *Coelioxys rufipes* Guérin-Méneville, 1844, *Coelioxys turbinata* Krombein, 1953, and an undescribed species from the Bahamas)

Median ocellus not surrounded by a conspicuously swollen area, subocellar area punctate, flat or inconspicuously elevated (Fig. 5). Supraclypeal area not elevated medially, never forming a rounded ridge (Fig. 5). Male: T5 with conspicuous lateral teeth (Fig. 63); S4 apical margin deeply emarginate, forming a U-shaped process (Fig. 64); gradulus of S5 convex or V-shaped, never straight, and incomplete, its lateral margins evanescent………………………………………………………………21

21. Posterior margin of mesoscutellum obtusely produced medially into a blunt edge (Fig. 51), without a protuberant median process. Mesoscutellum with a distinct longitudinal median ridge (Fig. 51). Axilla long, free apical portion longer or subequal to basal portion (Fig. 51). Ocular hairs long (~0.12 mm; Fig. 5). Female: S6 lateral notches obsolete, weakly impressed, not interrupting outline in dorsal view (Fig. 65). Male: postgradular areas of T2 and T3 with a transverse, punctate area either formed by punctures that may be fused or by few smaller punctures basally and larger punctures apicolaterally (Fig. 66) (Neotropical)…………………………………*Coelioxys* (*Rhinocoelioxys*) Mitchell, 1973.

Posterior margin of mesoscutellum either produced medially into a protuberant median process (Rocha-Filho & Packer, 2015: figs 3I, 9D) or rounded (Rocha-Filho & Packer, 2015: figs 5C, 7F), never obtusely produced medially into a blunt edge. Mesoscutellum lacking a distinct longitudinal median ridge (Rocha-Filho & Packer, 2015: figs 3I, 5C). Axilla short, free apical portion shorter than basal portion (Rocha-Filho & Packer, 2015: figs 3I, 5C). Ocular hairs short (0.07–0.08 mm). Female: S6 lateral notches acute, triangular, clearly visible in dorsal view (Fig. 67). Male: postgradular areas of T2 and T3 with a conspicuous, elliptical, transverse, punctate area formed by punctures of the same size (Fig. 68) (Neotropical)……………………………………………………………………………… *Coelioxys* (*Austrocleptria*) Rocha-Filho subgen. nov.

22. Mesoscutellum triangular, its posterior margin protuberant, produced medially (Fig. 69). S1 basomedially with a conspicuous pointed process (Fig. 70). Male: postgradular area of T3 with a fovea anterior to a transverse punctate area (except *Coelioxys chilensis* Reed, 1892, in which the postgradular area lacks a fovea and a transverse punctate area)……………………………………………………………23

Mesoscutellum rounded, not produced medially (Fig. 71). S1 basomedially swollen, lacking a conspicuous pointed produced area (Fig. 72). Male: postgradular area of T3 unmodified, without fovea or punctate area…………………………

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23. Pronotal tubercle emarginate, forming two distinct lobes, its carina conspicuously elevated, lamellate (Fig. 73). Pubescence of mesosoma short; on mesoscutum predominantly forming spots of appressed hairs (Fig. 73). Female: eye distinctly convex ventrally (Fig. 74, posterior margin of eye indicated by black arrow); T6 with lateral carina (Fig. 77); S6 elongate, at most 2× longer than broad, lateral notches broader, at least 2.5× broader than long, (Fig. 77). Male: face densely covered with decumbent hairs; Postgradular areas of T2 and T3 with a small fovea surrounded by an elevated, transverse impunctate area with a depressed, transverse densely punctate area posteriorly, the fovea on T2 minute, circular, and on T3 slender, transverse (Fig. 78; postgradular areas of T2 and T3 unmodified in *C. chilensis*); apical rim of S4 flat, not flexed ventrally (as in Fig. 64) (Neotropical). . . . . *Coelioxys* (*Glyptocoelioxys*) Mitchell, 1973 (in part).

Pronotal tubercle straight, not forming distinct lobes, its carina neither elevated nor lamellate (Fig. 75). Pubescence of mesosoma long, dense, in some cases forming spots of appressed hairs (Fig. 75). Female: eye surface not convex ventrally (Fig. 76); T6 lacking lateral carina (Fig. 79); S6 greatly narrower and elongate, at least 2.5× longer than broad, strongly flexed downwards, lateral notches narrower, at least 2.5× longer than broad (Fig. 79) or absent. Male: face densely covered with long, erect or suberect hairs; Postgradular area of T2 with a broad, rectangular, densely punctate area; postgradular area of T3 with a circular, deep, conspicuous fovea surrounded by punctures forming a larger elliptical area (Fig. 80); apical rim of S4 flexed ventrally (as in Fig. 93) (Neotropical). . . . .*Coelioxys* (*Dasycoelioxys*) Mitchell, 1973

24. Axilla very short, free apical portion much shorter than basal portion and not produced beyond posterior margin of mesoscutellum (Fig. 71). Apical fasciae on T2–T5 sparse medially or narrowly interrupted. Female: mandible outer surface angled; S6 apex elongate, longer than broad, notches narrowly acute (Fig. 81). Male: gonocoxa subapically not compressed (Holarctic). . . . .*Coelioxys* (*Paracoelioxys*) Gribodo, 1884

Axilla long, free apical portion longer or subequal to basal portion, and produced beyond posterior margin of mesoscutellum (Fig. 83). Apical fasciae on T1–T5 complete, but if interrupted then broadly so, and bands thick and subtriangular. Female: mandible outer surface curved medially, never angled (Fig. 82); S6 either lanceolate and not notched (Fig. 89) or elongate and notched (Fig. 87) (if notched then S6 apex short, triangular, broader than long, notches not acute). Male: gonocoxa subapically compressed laterally (Palaearctic). 25

25. Mesoscutellum anteriorly either with sparse, erect, long hairs or with a tiny, transverse line of subappressed hairs, never forming separated spots (Fig. 83). Axilla conspicuously curved inwards apically, convergent (Fig. 83). Apical fasciae of T1–T5 and S2–S5 complete (Fig. 84). Female: T6 dorsal carina short, roughly one-third tergal length, weak half basally; fascia on apical margin of S5 complete, composed of yellowish hairs; S6 elongate and conspicuously notched, notches not acute (Fig. 87); S6 ventral surface not keeled (Fig. 87). Male: hypostomal concavity deep and nearly bare, anterior margin with a longitudinal inconspicuous line of hairs; postgradular area of T2 with a very slender, shallow, punctate fovea, with impunctate margin only found posteriorly to the fovea (Fig. 88); S4 apical margin entire and apical rim weakly emarginate (Fig. 92). . . . .*Coelioxys* (*Rozeniana*) Rocha-Filho subgen. nov.

Mesoscutellum anteriorly with two small, separated, sublateral spots of subappressed hairs (Fig. 85). Axilla not curved apically, subparallel with one another (Fig. 85). Apical fasciae of T1–T5 broadly interrupted medially, forming broad, subtriangular lateral bands (Fig. 86). Apical fasciae of S2–S5 interrupted medially. Female: T6 dorsal carina nearly complete, more than two-thirds tergal length (Fig. 89); fascia on apical margin of S5 interrupted medially, composed of white hairs; S6 broad, lanceolate, lacking lateral notches (Fig. 89); S6 ventral surface keeled apically (Fig. 91). Male: hypostomal concavity shallow, densely hairy on anterior margin; postgradular area of T2 with a transverse, deep fovea composed of small punctures, with a narrow impunctate margin entirely surrounding the fovea (Fig. 90); S4 apical margin slightly emarginate and apical rim conspicuously emarginate, forming two slightly elevated arms (Fig. 93). . . . .***Coelioxys* (*Melissoctonia*)** Rocha-Filho **subgen. nov**.

Diagnoses and comments are given for all subgenera. The list of species provided for each of them was based on online databases (Moure *et al.*, 2012; Ascher & Pickering, 2015) and the study of type material by the first author for most Australasian and Neotropical species (species denoted with an asterisk). Other designations were made based on species descriptions and associated images. Given the large size and taxonomic complexity of the genus, all subgeneric assignments not based upon study of type material should be considered tentative.

Coelioxys (Allocoelioxys) Tkalců, 1974

= *Coelioxita* Pasteels, 1977
= *Coelioxula* Pasteels, 1982
= *Coelioxys* (*Intercoelioxys*) Ruszkowski, 1986
= *Coelioxys* (*Lepidocoelioxys*) Ruszkowski, 1986
= *Coelioxys* (*Mesocoelioxys*) Ruszkowski, 1986 syn. nov.
= *Coelioxys* (*Tropidocoelioxys*) Gupta, 1991
= *Coelioxys* (*Argcoelioxys*) Warncke, 1992 syn. nov.
= *Coelioxys* (*Orientocoelioxys*) Gupta, 1992
= *Coelioxys* (*Nigrocoelioxys*) Gupta, 1993

Type species: *Coelioxys afra* Lepeletier, 1841.

Diagnosis: The most obvious diagnostic characteristic of this subgenus is the conspicuously carinate and elevated lateral margins of the axilla (Fig. 6) in both sexes, a feature otherwise only observed in one other *Coelioxys* species: the Nearctic *C.* (*Xerocoelioxys*) *edita*. The T6 apicodorsal processes in males are forked (Fig. 23) in most species (exceptions are *Coelioxys bifoliata* Pasteels, 1968, *Coelioxys madagascariensis* Benoist, 1955, and the *argentea* group *sensu* Pasteels (1968, 1977) (i.e. *C. argentea*, *Coelioxys caeruleipennis* Friese, 1904, *Coelioxys incarinata* Friese, 1904, and *Coelioxys scutellotuberculata* Pasteels, 1968). *Coelioxys* (*Synocoelioxys*) spp. also have forked T6 apicodorsal processes but in that subgenus the processes are flattened, acute, and of unequal length, almost forming an irregular crenulate plate (Fig. 34), whereas in *C.* (*Allocoelioxys*) males the apicodorsal processes are weakly convex, approximately equal in length, rounded apically, and distinct, not forming a crenulate plate (Fig. 23).

Comments: This is one of the most diverse subgenera within *Coelioxys*, with at least 75 species assigned to it (Ascher & Pickering, 2015). This subgenus is largely represented in the Afrotropical and Palaearctic regions, but some species are Indomalayan; at least one, *Coelioxys smithii* Dalla Torre, 1896, occurs in the Australasian region and one, *C. coturnix*, has been introduced to the United States from the Palaearctic region (Ascher & Pickering, 2015). Both these species exhibit the characteristics of the subgenus outlined above.

List of species: *Coelioxys acanthopyga* Alfken, 1940, *Coelioxys acanthura* (Illiger, 1806), *C. afra*, *Coelioxys angulata* Smith, 1870, *C. argentea*, *Coelioxys artemis* Schwarz, 2001, *Coelioxys bifoliata* Pasteels, 1968, *Coelioxys bifoveolata* Pasteels, 1968, *Coelioxys binghami* Pasteels, 1968, *Coelioxys brevis* Eversmann, 1852, *Coelioxys bulbosa* Pasteels, 1985, *C. caeruleipennis*, *Coelioxys capitata* Smith, 1854, *Coelioxys carinicauda* Pasteels, 1968, *Coelioxys castanea* Morawitz, 1886, *Coelioxys caudata* Spinola, 1838, *Coelioxys coloratula* Cockerell, 1939, *Coelioxys congoensis* Friese, 1922, *Coelioxys conspersa* Morawitz, 1874, *Coelioxys cothura* Cockerell, 1918, *C. coturnix*, *Coelioxys cuneata* Smith, 1875, *Coelioxys desmieri* Pasteels, 1968, *Coelioxys difformis* Friese, 1904, *Coelioxys echinata* Förster, 1853, *Coelioxys elegantula* Alfken, 1934, *Coelioxys elongatula* Alfken, 1938, *Coelioxys elsei* Schwarz, 2001, *Coelioxys emarginata* Förster, 1853, *Coelioxys emarginatella* Pasteels, 1982, *Coelioxys erythrura* Spinola, 1838, *Coelioxys florea* Wu, 2006, *Coelioxys formosicola* Strand, 1913, *Coelioxys foveolata* Smith, 1854, *Coelioxys fuscipennis* Smith, 1854, *Coelioxys genoconcavitus* Gupta, 1991, *Coelioxys haemorrhoa* Förster, 1853, *C. incarinata*, *Coelioxys indica* Friese, 1925, *Coelioxys iranica* Warncke, 1992, *Coelioxys kasachstana* Warncke, 1992, *Coelioxys khasiana* Cameron, 1904, *Coelioxys lata* Cameron, 1908, *Coelioxys lucidicauda* Cockerell, 1939, *Coelioxys luzonica* Cockerell, 1914, *C. madagascariensis*, *Coelioxys mielbergi* Morawitz, 1880, *Coelioxys nasuta* Friese, 1904, *Coelioxys nitidicauda* Pasteels, 1968, *Coelioxys obtusa* Pérez, 1884, *Coelioxys octodenticulata* Friese, 1935, *Coelioxys perseus* Nurse, 1904, *Coelioxys polycentris* Förster, 1853, *Coelioxys pruinosa* Smith, 1854, *Coelioxys quadrifasciata* Gupta, 1992, *Coelioxys radoszkowskyi* Popov, 1946, *Coelioxys rajasthaniensis* Gupta, 1992, *Coelioxys recusata* Schulz, 1906, *Coelioxys rubella* Pasteels, 1968, *Coelioxys rufispina* Walker, 1871, *C. scutellotuberculata*, *Coelioxys semenowi* Morawitz, 1894, *Coelioxys sexmaculata* Cameron, 1897, *C. smithii*, *Coelioxys sogdiana* Morawitz, 1875, *Coelioxys somalica* Friese, 1922, *Coelioxys somalina* Magretti, 1895, *Coelioxys spativentris* Friese, 1935, *Coelioxys spilaspis* Cockerell, 1932, *Coelioxys squamigera* Friese, 1935, *Coelioxys squamosa* Friese, 1922, *Coelioxys squamosissima* Pasteels, 1968, *Coelioxys squamosoides* Pasteels, 1968, *Coelioxys squamosula* Popov, 1946, *Coelioxys subelongata* Wu, 1992, *Coelioxys sudanensis* Cockerell, 1933, *Coelioxys unicula* Cockerell, 1939, and *Coelioxys warnckei* Schwarz & Gusenleitner, 2003.

COELIOXYS (BOREOCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys rufitarsis Smith, 1854.

Diagnosis: Species in this subgenus are characterized by the combination of long, dense pubescence on head and mesosoma never accompanied by short, scale-like hairs, and with postgradular grooves of T2 and T3 complete (Fig. 24). This combination is also observed in all species of *C.* (*Coelioxys s.s.*). In *C.* (*Boreocoelioxys*) females, however, the S6 is elongate, gradually tapering towards the apex and conspicuously notched subapically [Fig. 26; constricted subapically and never notched in both *C.* (*Coelioxys s.s.*) (Fig. 28) and *C.* (*Xerocoelioxys*) females (Fig. 14)]. In *C.* (*Boreocoelioxys*) males the postgradular grooves of T2 have a sublateral, slender fovea on each side (Fig. 27), whereas in males of *C.* (*Coelioxys s.s.*) and *C.* (*Xerocoelioxys*) spp. the postgradular area of T2 is never foveate, but instead with sublateral, slender, densely punctate area on each side (Fig. 29), or unmodified.

Comments: This subgenus has been regarded as mainly Holarctic (Michener, 2007), but as such it is very weakly supported (see Results and Discussion and Fig. 1). In contrast, the New World clade is well supported. In light of this, *C.* (*Boreocoelioxys*) is now defined as comprising only the New World species, among which the Nearctic species and *Coelioxys oaxacana* Baker, 1975 were revised and keyed by Baker (1975). There are two additional species from the Neotropics: *Coelioxys sannicolarensis* Genaro, 2001 and *Coelioxys schmidti* Friese, 1917. The following species are being transferred to other subgenera according to the phylogenetic results: *C. alata*, *C. funeraria*, and *C. rufescens*. The other species from the Palaeartic region that were previously assigned to *C.* (*Boreocoelioxys*) (Ascher & Pickering, 2015) may belong to *C.* (*Paracoelioxys*) or to the new subgenus described herein to encompass *C. rufescens*; however, it is important to highlight that a revision of those species is necessary in order to establish an accurate classification for this fauna.

List of species: Coelioxys banksi Crawford, 1914, *Coelioxys insita* Cresson, 1872, *Coelioxys moesta* Cresson, 1864, *Coelioxys novomexicana* Cockerell, 1909, *C. oaxacana*, *C. octodentata*, *Coelioxys porterae* Cockerell, 1900, *Coelioxys pratti* Crawford, 1914, *C. rufitarsis*, *Coelioxys salinaria* Cockerell, 1925, *C. sannicolarensis**, *C. sayi*, and *C. schmidti**. The Neotropical species *Coelioxys auripes* Friese, 1921 also seems to belong to this subgenus given the complete postgradular grooves of T2 and T3.

COELIOXYS (COELIOXYS S.S.) LATREILLE, 1809

Type species: Coelioxys quadridentata (Linnaeus, 1758).

Diagnosis: Coelioxys (*Coelioxys s.s.*) spp. is diagnosable through one unique characteristic found in no other species in the genus: the shape of the pronotal lobe, which is conspicuously rounded on its outer margin and weakly carinate on its inner margin (Fig. 30).

Comments: Mitchell (1973) established this subgenus based only on North American and European species. Michener (2007), on the other hand, considered it as cosmopolitan. Thirteen species previously assigned to *C.* (*Coelioxys s.s.*), such as *Coelioxys serricaudata* Baker, 1975 and the Australasian species (Michener, 1965; Baker, 1975), do not belong to the clade that contains the type species of the subgenus (see also Rocha-Filho, 2016 for the Australian species), *C. quadridentata*. As understood here, *C.* (*Coelioxys s.s.*) comprises only its type species and the Nearctic species *Coelioxys sodalis* Cresson, 1878.

List of species: Coelioxys quadridentata and *C. sodalis*.

COELIOXYS (CYRTOCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys costaricensis Cockerell, 1914.

Diagnosis: The most distinctive characteristic of *C.* (*Cyrtocoelioxys*) spp. is the shape of S6 in females: constricted near midlength, always ending in a spine-like process and with its lateral margins always bearing a fringe, which in most of the species is conspicuous, dense, and formed by long, brown hairs (Fig. 46). Additionally, the T6 in females ends

Figures 65–68. 65, female, *Coelioxys agilis*: dorsal view of T6 and S6 (S6 notch indicated by black arrow). 66, male, *Coelioxys zapoteca*. Dorsal view of T2–T3 (punctate areas indicated by red arrows). 67, female, *Coelioxys barbata*: dorsal view of T6 and S6 (S6 notch indicated by black arrow). 68, male, *Coelioxys clypearis*: dorsal view of T2–T3 (punctate areas indicated by black arrows). Scale bars: 1.5 mm.


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Figures 69–72. Female. 69, *Coelioxys cayennensis*: dorsal view of mesoscutellum (for posterior margin). 70, *Coelioxys praetextata*: lateral view of S1 (basomedial area indicated by black arrow). 71, *Coelioxys alata*: dorsal view of mesoscutellum (for posterior margin). 72, *Coelioxys funeraria*: lateral view of S1 (basomedial area indicated by black arrow). Scale bars: 1.5 mm.

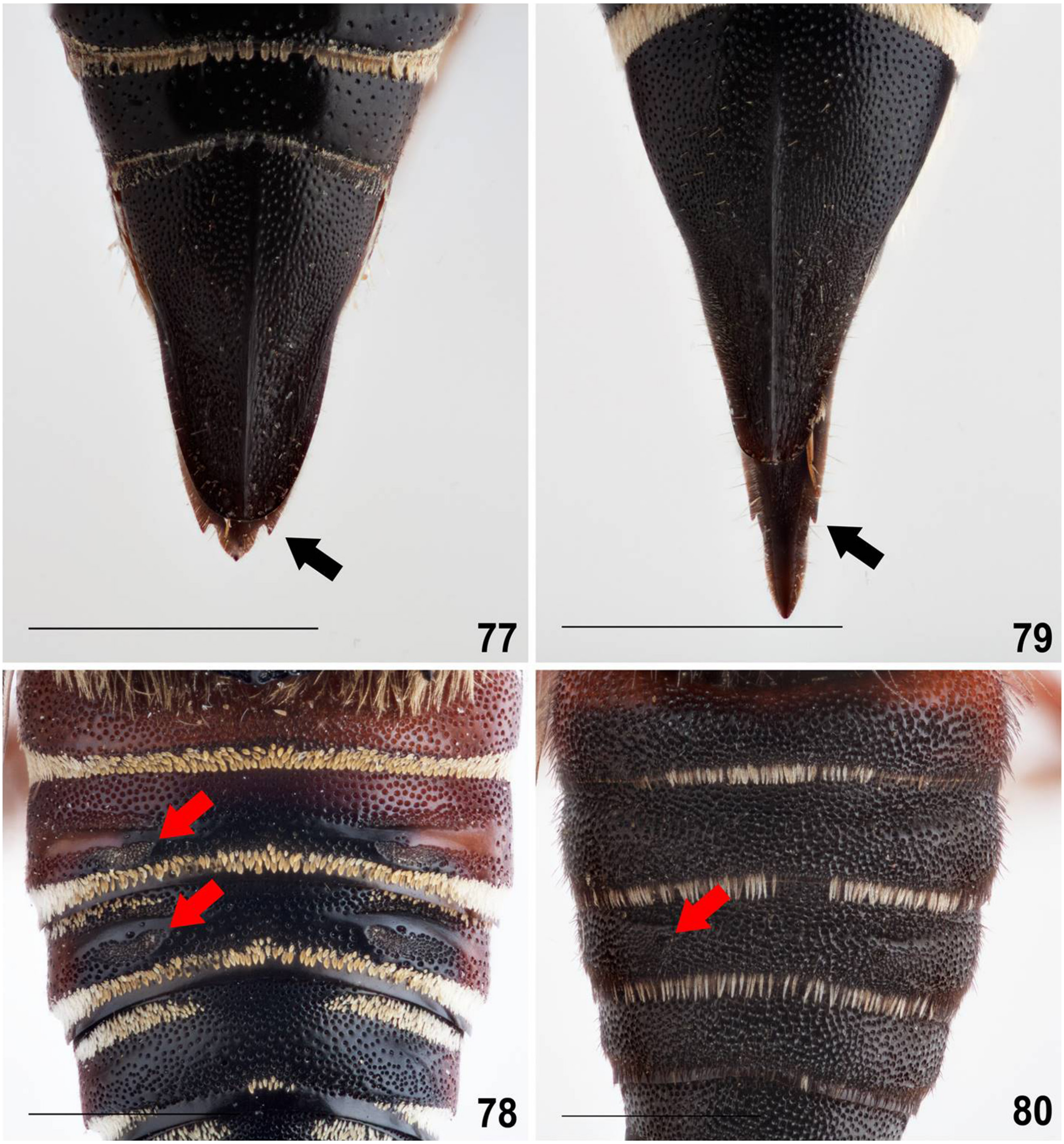
in a short spine-like process, its dorsal carina is strong, and separates two elliptical depressions on either side, and the subapical area is covered with tomentum and scattered long, erect, dark hairs (Fig. 46). These characteristics are similar to those found in females of the Old World subgenus *C.* (*Liothyrapis*), but in those the spine-like process of T6 is always elongate and conspicuous (Fig. 9) and their compound eyes are bare (Fig. 4). In males (among the species in which holotypes have been studied), except in *C. costaricensis*, the postgradular area of T3 bears a circular fovea composed of small punctures, it is hairy and surrounded by punctures forming a transverse area (Fig. 47). This characteristic is also observed in males of *C.* (*Dasycoelioxys*) (Fig. 80), but they can be differentiated by the lack of a carina on the basal concavity of T1 (Fig. 43).

Comments: This is the most speciose subgenus in the Neotropics, with more than 60 species names assigned to it (Moure *et al.*, 2012; Ascher & Pickering, 2015). An updated list with the description of three new species, two synonyms, and

Figures 73–76. Female. 73, *Coelioxys cayennensis*: frontal view of pronotal lobe (outer margin indicated by black arrow). 74, *Coelioxys cerasiopleura*: lateral view of head (posterior margin of compound eye indicated by black arrow). 75, 76, *Coelioxys pergandei*: 75, frontal view of pronotal lobe (outer margin indicated by black arrow); 76, lateral view of head (posterior margin of compound eye indicated by black arrow). Scale bars: 1.5 mm.

also a key to the Mexican species are provided by Rocha-Filho (2015). A few species, denoted in the following list with a section sign symbol (§), occur in the Nearctic region (Baker, 1975; Ascher & Pickering, 2015).

List of species: Coelioxys abnormis Holmberg, 1887, *Coelioxys acanthosara* Rocha-Filho, 2015*, *Coelioxys alayoi* Genaro, 2001*, *Coelioxys alisal* Toro & Fritz, 1993*, *Coelioxys ambrosettii* Holmberg, 1918, *Coelioxys angelica* Cockerell, 1905§, *Coelioxys balasto* Toro & Fritz, 1993*, *Coelioxys brachyvalva* Friese, 1921*, *Coelioxys burgdorfi* Cockerell, 1931*, *Coelioxys chichimeca* Cresson, 1878*, *Coelioxys cisnerosi* Cockerell, 1949*, *Coelioxys cochleariformis* Friese, 1921*, *Coelioxys coloboptyche* Holmberg, 1887, *Coelioxys columbica* Friese, 1921*, *C. costaricensis**, *Coelioxys danielperezi* Genaro, 2009*, *Coelioxys deani* Cockerell, 1909§, *Coelioxys digitata* Friese, 1921*, *Coelioxys dobzhanskyi* Moure, 1951, *Coelioxys duckei* Friese, 1921*, *Coelioxys fimbriata* Friese, 1921*, *Coelioxys floridana* Cresson, 1878*§, *Coelioxys fossulata* Friese, 1921*, *Coelioxys giacomellii* Holmberg 1916, *Coelioxys gilensis* Cockerell, 1898§, *Coelioxys gonaspis* Cockerell, 1924§, *Coelioxys hirtiventris* Popov, 1946*, *Coelioxys*



Figures 77–80. 77, female, *Coelioxys praetextata*: dorsal view of T6 and S6 (S6 notch indicated by black arrow). 78, *Coelioxys cayennensis*: dorsal view of T2–T3 (punctate areas and foveae indicated by red arrows). 79, *Coelioxys pergandei*: dorsal view of T6 and S6 (S6 notch indicated by black arrow). 80, *Coelioxys kuscheli*: dorsal view of T2–T3 (fovea indicated by red arrow). Scale bars: 1.5 mm.

humahuakae Holmberg, 1909, *Coelioxys issororensis* Cockerell, 1923*, *Coelioxys jordiana* Rocha-Filho, 2015*, *Coelioxys lactea* Rocha-Filho, 2015*, *Coelioxys leopoldensis* Friese, 1921*, *Coelioxys leopoldinae* Friese, 1921*, *Coelioxys litoralis* Holmberg, 1888, *Coelioxys macaria* Holmberg, 1916, *Coelioxys marginata* Friese, 1921*, *Coelioxys modesta* Smith, 1854§, *Coelioxys nigrofimbriata* Cockerell, 1919*, *Coelioxys noa* Toro & Fritz, 1993*, *Coelioxys obscuriventris* Friese, 1921*, *Coelioxys obtusivalva* Friese, 1921*, *Coelioxys obtusiventris* Crawford, 1914§, *Coelioxys paradoxa* Friese, 1921*, *Coelioxys*

Figures 81 and 82. Female, frontal view of head (outer surface of mandible indicated by black arrows): 81, *Coelioxys funeraria*; 82, *Coelioxys conoidea*. Scale bars: 1.5 mm.

paranensis Schrottky, 1920, *Coelioxys paraguaya* Moure, 1943*, *Coelioxys pauloensis* Friese, 1921*, *Coelioxys pedregalensis* Holmberg, 1916, *Coelioxys pilivalva* Friese, 1921*, *Coelioxys puncticollis* Friese, 1921*, *Coelioxys quaerens* Holmberg, 1903*, *Coelioxys quechua* Toro & Fritz, 1993, *Coelioxys rhadia* Holmberg, 1916, *Coelioxys rugicollis* Friese, 1921*, *Coelioxys rugulosa* Friese, 1908*, *Coelioxys saltensis* Toro & Fritz, 1993*, *Coelioxys sanguinicollis* Friese, 1921*§, *Coelioxys sanguinosa* Cockerell, 1912*, *Coelioxys schulzi* Holmberg, 1909, *Coelioxys scitula* Cresson, 1872*§, *Coelioxys spatulata* Friese, 1921*, *Coelioxys speculifera* Cockerell, 1931*§, *Coelioxys spinosa* Dewitz, 1881, *Coelioxys subspinosa* Friese, 1921*, *Coelioxys subtropicalis* Holmberg, 1887, *Coelioxys surinamensis* Friese, 1921*, *Coelioxys tabayensis* Schrottky, 1920, *Coelioxys tastil* Toro & Fritz, 1993*, *Coelioxys tiburonensis* Cockerell, 1924§, *Coelioxys trancas* Toro & Fritz, 1993*, *Coelioxys tridentata* (Fabricius, 1775), *Coelioxys triangula* Friese, 1906*, *Coelioxys unidentata* Friese, 1922*, and *Coelioxys zonula* Smith, 1854*.

Coelioxys (Dasycoelioxys) Mitchell, 1973

Type species: Coelioxys pergandei Schletterer, 1890.

Diagnosis: Species of this subgenus as well as all *C.* (*Glyptocoelioxys*) spp. other than *C. mexicana* are unique among all species in the genus by lacking a carina on the basal concavity of T1 (Fig. 43). *Coelioxys* (*Dasycoelioxys*) spp. can be differentiated from *C.* (*Glyptocoelioxys*) by the pronotal tubercle, which in is never lamellate or conspicuously emarginated in *C.* (*Dasycoelioxys*) spp., forming two distinct lobes (Fig. 75), as in *C.* (*Glyptocoelioxys*) spp. (Fig. 73). Also, the pubescence of the head and mesosoma in species of *C.* (*Glyptocoelioxys*) is short and subappressed, forming spots of appressed hairs on the mesoscutum, whereas in species of *C.* (*Dasycoelioxys*) the pilosity is predominantly long and dense, although sometimes there are additional spots of appressed hairs also. The following combination also separates species of *C.* (*Dasycoelioxys*) from *C.* (*Glyptocoelioxys*). Female: eye surface not convex ventrally (Fig. 76); T6 lacking lateral carinae (Fig. 79); S6 greatly narrower and elongate, at least 2.5× longer than broad, strongly flexed downwards, lateral notches narrower, at least 2.5× longer than broad (Fig. 79) or absent. Male: face densely covered with long, erect or suberect hairs; postgradular area of T2 with a broad, rectangular, densely punctate area (Fig. 80); postgradular area of T3 with a circular, deep, conspicuous fovea surrounded by punctures forming an elliptical area (Fig. 80), and apical rim of S4 flexed ventrally (as in Fig. 93).

Comments: Given the similarity with species of *C.* (*Glyptocoelioxys*), Michener (2007) synonymized *C.* (*Dasycoelioxys*) under *C.* (*Glyptocoelioxys*). In all phylogenetic results, *C.* (*Glyptocoelioxys*) came out as a separate clade from *C.* (*Dasycoelioxys*); hence the latter name is resurrected. This subgenus is exclusively Neotropical, with 27 species listed by Moure *et al.* (2012) occurring mostly in Chile and

Figures 83–86. Female. 83, 84, *Coelioxys rufescens*: 83, dorsal view of mesoscutellum (for pilosity on anterior margin of mesoscutellum); 84, dorsal view of terga (for apical tergal fasciae). 85, 86, *Coelioxys conoidea*: 85, dorsal view of mesoscutellum (for pilosity on anterior margin of mesoscutellum); 86, dorsal view of terga (for apical tergal fasciae). Scale bars: 1.5 mm.

Argentina. Toro & Fritz (1991) keyed some of the species of this subgenus.

List of species: Coelioxys bicingulata Holmberg, 1918*, *Coelioxys wagenknechti* Moure, 1951, *Coelioxys bruneri* Cockerell, 1918*, *Coelioxys cameghinoi* Holmberg, 1903, *Coelioxys elizabeth* Toro & Fritz, 1991*, *Coelioxys frieseana* Holmberg, 1916, *Coelioxys genisei* Toro & Fritz, 1991*, *Coelioxys hickeni* Holmberg, 1918*, *Coelioxys hubrichiana* Holmberg, 1918*, *Coelioxys inconspicua* Holmberg, 1884, *Coelioxys insolita* Holmberg, 1903, *Coelioxys kuscheli* Moure, 1951, *Coelioxys ljuba* Toro & Fritz, 1991*, *Coelioxys lyprura* Moure, 1951, *Coelioxys mapuche* Toro & Fritz, 1991*, *Coelioxys melanopus* Schulz, 1906, *Coelioxys miranda* Vachal, 1904*, *Coelioxys occidentalis* Holmberg, 1916, *Coelioxys oriplanes* Moure, 1951, *Coelioxys palmaris* Fritz & Toro, 1990, *C. pergandei*, *Coelioxys pomona* Toro & Fritz, 1991*, *Coelioxys remissa* Holmberg, 1888*, *Coelioxys roigi* Fritz & Toro, 1990*, *Coelioxys rosarina* Holmberg, 1918*, *Coelioxys ruizi* Moure, 1951, *Coelioxys ruzi* Toro & Fritz, 1991*, *Coelioxys strigata* Vachal, 1904*, *Coelioxys tehuelche* Holmberg, 1916, *Coelioxys tenax* Holmberg, 1888, *Coelioxys tucumana* Holmberg, 1903, *C. wagenknechti*, and *Coelioxys weyrauchi* Moure, 1951.

Figures 87–90. 87, 88, *Coelioxys rufescens*: 87, female, ventral view of S6 (S6 notch indicated by black arrow); 88, male, dorsal view of T2 (fovea indicated by black arrow). 89, 90, *Coelioxys conoidea*: 89, female, dorsal view of T6 and S6; 90, male, dorsal view of T2 (fovea indicated by black arrow). Scale bars: 1.5 mm.

COELIOXYS (GLYPTOCOELIOXYS) MITCHELL, 1973: 92

= *Coelioxys* (*Haplocoelioxys*) Mitchell, 1973: 85 syn. nov.

Type species: Coelioxys cayennensis Spinola, 1841.

Diagnosis: Species of this subgenus are characterized by the compound eye convex ventrally (Fig. 74), S6 distinctly notched subapically in females (Fig. 77), and in males the postgradular areas of T2 and T3 with a small fovea surrounded by an impunctate area with a depressed punctate area posteriorly to the fovea (Fig. 78; except in

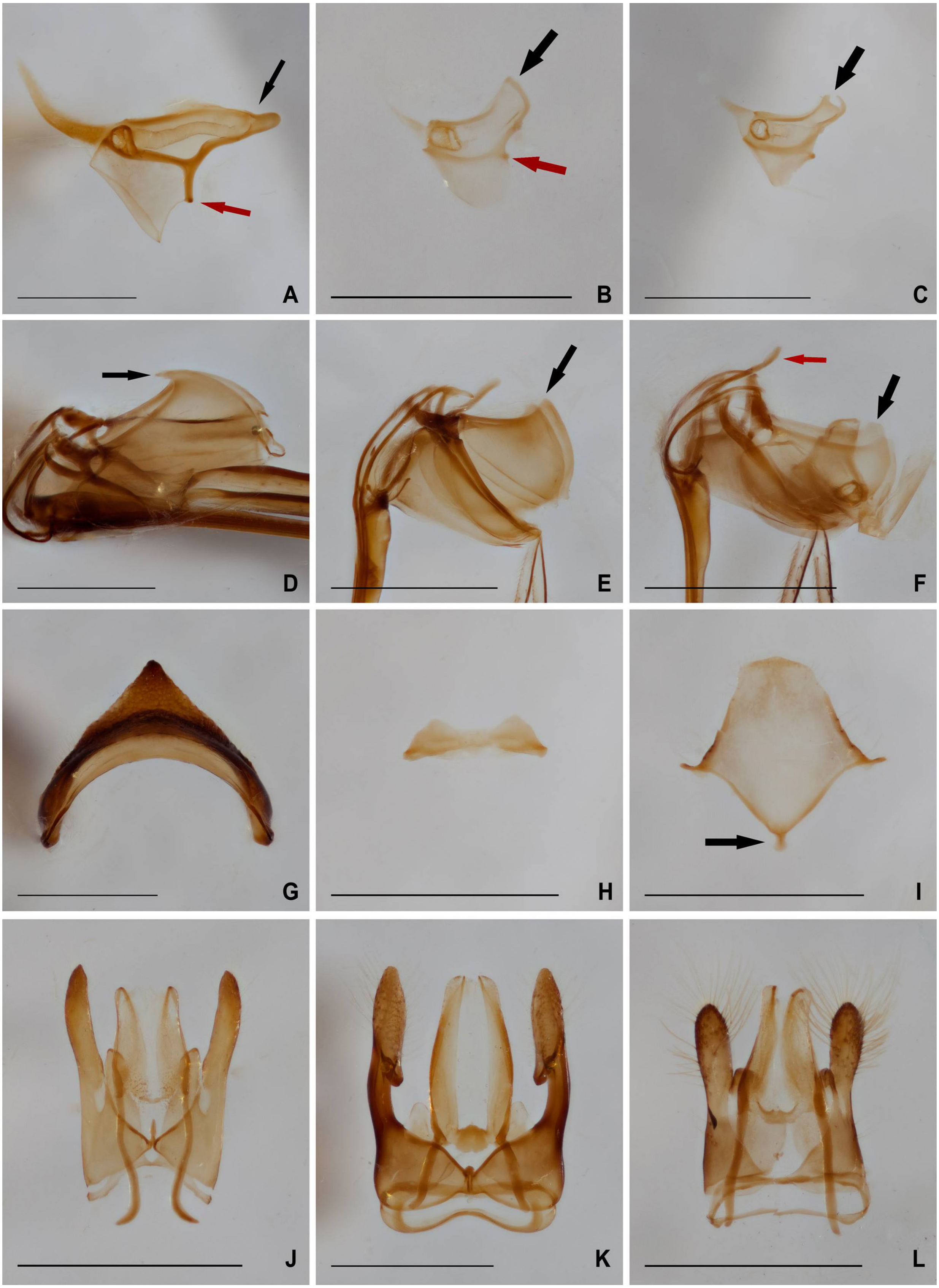
Figures 91–93. 91, female, *Coelioxys conoidea*: ventral view of S6 (S6 ventral keel indicated by black arrow). 92, 93, male: 92, *Coelioxys rufescens*, ventral view of S4 (apical margin indicated by red arrow); 93, *Coelioxys conoidea*, ventral view of S4 (apical rim indicated by black arrow). Scale bars: 1.5 mm.

C. chilensis males). Another important characteristic, observed in all except the type species *C. mexicana*, is the lack of a marginal carina on the basal concavity of T1 (Fig. 43), a characteristic otherwise shared with *C.* (*Dasycoelioxys*) spp. In spite of the resemblance to the latter subgenus, *C.* (*Glyptocoelioxys*) spp. can be differentiated from those of *C.* (*Dasycoelioxys*) by the following combination of characteristics (see also the diagnosis of the latter subgenus above). Pronotal tubercle emarginate, forming two lobes, with carina conspicuously lamellate (Fig. 73); pubescence of head and mesosoma short, predominantly forming spots of appressed hairs on mesoscutum. Female: eye outline distinctly convex ventrally (Fig. 74); T6 with lateral carinae (Fig. 77); S6 elongate, at most 2× longer than broad, lateral notches broader, at least 2.5× broader than long (Fig. 77). Male: face densely covered with decumbent hairs; postgradular areas of T2 and T3 with a small fovea surrounded by an elevated, transverse impunctate area with a depressed, transverse densely punctate area below, the fovea on T2 minute, circular, and on T2 slender (Fig. 78) (postgradular areas of T2–T3 unmodified in *C. chilensis*), and apical rim of S4 flat, not flexed ventrally (as in Fig. 64).

Comments: Prior to this study, the name *C.* (*Haplocoelioxys*) had been applied only to *C. mexicana* (Mitchell, 1973; Michener, 2007; Moure *et al.*, 2012; Ascher & Pickering, 2015). Considering the phylogenetic results (Figs 1–3) *C.* (*Haplocoelioxys*) is merged with *C.* (*Glyptocoelioxys*). In spite of page priority for *C.* (*Haplocoelioxys*), the name *C.* (*Glyptocoelioxys*) is preferred here based upon article 24.2.2 of the International Code of Zoological Nomenclature that states '…the precedence of the names or acts is fixed by the First Reviser unless Article 24.1 applies'. Given that the first revision concerning this matter is carried out herein, we decided to synonymize *C.* (*Haplocoelioxys*) under *C.* (*Glyptocoelioxys*) because the former is monotypic, hence only one subgeneric reassignment is required rather than 27. Species of this subgenus are primarily Neotropical, with only *Coelioxys germana* Cresson, 1878 recorded elsewhere, in the eastern Nearctic region.

List of species: Coelioxys acutivalva Friese, 1921*, *Coelioxys adani* Cockerell, 1949*, *Coelioxys amazonica* Schrottky, 1902, *Coelioxys beroni* Schrottky, 1902, *Coelioxys brasiliensis* Friese, 1921*, *Coelioxys bucephala* Friese, 1921*, *Coelioxys cearensis* Friese, 1921*, *C. cayennensis**, *Coelioxys cerasiopleura* Holmberg, 1903, *Coelioxys chilensis* Reed, 1892, *Coelioxys concolor* Friese, 1921*, *Coelioxys epaenete* Holmberg, 1916, *C. germana**, *Coelioxys ignava* Smith, 1879*, *Coelioxys labiosa* Moure, 1951, *Coelioxys laticeps* Friese, 1921*, *Coelioxys lativalva* Holmberg, 1903, *C. mexicana**, *Coelioxys nitidicollis* Friese, 1921*, *Coelioxys opacicollis* Friese, 1921*, *Coelioxys pampeana*

Figure 94. A–F, female. A–C, dorsal view of hemitergite 7 (apodemal region indicated by black arrow, lateral process indicated by red arrow): A, *Coelioxys ducalis*; B, *Coelioxys alatiformis*; C, *Coelioxys caudata*. D–F, lateral view of hemitergite 8 (postero expansion indicated by black arrow): D, *Coelioxys torrida*; E, *Coelioxys nasuta*; F, *Coelioxys porterae* (apex of dorsal arm of furcula indicated by red arrow). G–L, male: G, dorsal view of T7 of *Coelioxys bisoncornua*; H, dorsal view of S7 of *Coelioxys apacheorum*; I, dorsal view of S8 of *Coelioxys alternata* (tip producing on apex indicated by black arrow). J–L, genitalia: J, *Coelioxys abdominalis*; K, *Coelioxys apicata*; L, *Coelioxys sodalis*. Scale bars: 1 mm.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Holmberg, 1887, *Coelioxys praetextata* Haliday, 1836*, *Coelioxys quadriceps* Friese, 1921*, *Coelioxys ruficollis* Friese, 1921*, *Coelioxys scutellaris* Schrottky, 1902, *Coelioxys totonaca* Cresson, 1878*, *Coelioxys triodonta* Cockerell, 1914*, and *Coelioxys vituperabilis* Holmberg, 1903.

COELIOXYS (LIOTHYRAPIS) COCKERELL, 1911

= *Coelioxys* (*Hemicoelioxys*) Pasteels, 1968.

Type species: *Coelioxys apicata* Smith, 1854.

Diagnosis: Species of the subgenera *C.* (*Liothyrapis*) and *C.* (*Torridapis*), as well as *C.* (*Allocoelioxys*) *madagascariensis* are the only ones within *Coelioxys* with bare eyes (Fig. 4). The species *C. madagascariensis* is differentiated from *C.* (*Liothyrapis*) spp. by the sharply carinate lateral margins of the axilla (Fig. 6). The most easily observed characteristics that separate *C.* (*Liothyrapis*) spp. from *C.* (*Torridapis*) are [alternative conditions in *C.* (*Torridapis*) are given in parentheses]: axilla short, free apical portion not produced beyond posterior margin of mesoscutellum (Figs 7, 8) (long, free apical portion produced beyond posterior margin of mesoscutellum; Fig. 11); T6 in females ending in a long spine-like process, with some long, erect hairs subapically (Fig. 9) (T6 ends in a very short, obsolescent spine-like process and lacks long, erect hairs subapically; Fig. 12), and S6 in females broad and constricted medially, bearing a dense fringe marginally (Fig. 9) (S6 very elongate, never constricted medially and lacking a dense fringe on lateral margins; Fig. 12).

Comments: This subgenus is mostly Afrotropical, with some species in the Indomalayan region and others in the Palaearctic. Additionally, one species, *C. apicata*, has been introduced into Puerto Rico (Genaro & Franz, 2008). There are at least 24 species assigned to *C.* (*Liothyrapis*) (Ascher & Pickering, 2015). The Afrotropical fauna was revised by Pasteels (1968).

List of species: *Coelioxys aberrans* Morawitz, 1894, *Coelioxys albociliata* Pasteels, 1968, *C. apicata*, *Coelioxys bruneipes* Pasteels, 1968, *Coelioxys calabarensis* Pasteels, 1968, *Coelioxys cavigena* Pasteels, 1968, *Coelioxys cherenensis* Friese, 1913, *Coelioxys chionospila* Cockerell, 1935, *Coelioxys circumscripta* Schulz, 1906, *C. decipiens*, *Coelioxys dormitans* Cockerell, 1919, *Coelioxys elongativentris* (Pasteels, 1977), *Coelioxys gracillima* (Pasteels, 1977), *Coelioxys heterozona* Cockerell, 1939, *Coelioxys integra* Pasteels, 1968, *Coelioxys junodi* Friese, 1904, *Coelioxys lativentris* Friese, 1909, *Coelioxys luangwana* Cockerell, 1939, *Coelioxys neavei* Vachal, 1910, *Coelioxys reticulata* Pasteels, 1968, *Coelioxys rotundicauda* Cockerell, 1935, *Coelioxys rotundiscutum* (Pasteels, 1977), *Coelioxys scioensis* Gribodo, 1879, *Coelioxys umbripennis* Friese, 1922, and *Coelioxys verticalis* Smith, 1854.

COELIOXYS (*NEOCOELIOXYS*) MITCHELL, 1973: 64

= *Coelioxys* (*Acrocoelioxys*) Mitchell, 1973: 71 syn. nov.

= *Coelioxys* (*Melanocoelioxys*) Mitchell, 1973: 78 syn. nov.

Type species: *Coelioxys simillima* Smith, 1854.

Diagnosis: Most species of *C.* (*Neocoelioxys*) can be diagnosed through the combination of supraclypeal area elevated medially, forming a rounded ridge in both sexes (Fig. 53) (not elevated; Fig. 54), and T5 lacking lateral spines in males (Fig. 61). Nevertheless, *C. otomita* does not possess the former characteristic, and *C. dolichos* and *C. abdominalis* do not possess the second; however, all three can be correctly assigned using the key. Both these characteristics also show parallelisms elsewhere within *Coelioxys*, but only in Old World species that are very different morphologically, with the sole exception of *C. bisoncornua* from North America, but this species has the postgradular grooves of both T2 and T3 complete (Fig. 24), whereas they are broadly interrupted medially (Fig. 25) in all *C.* (*Neocoelioxys*) spp.

Comments: As the type species of both *C.* (*Acrocoelioxys*) and *C.* (*Melanocoelioxys*) were nested among *C.* (*Neocoelioxys*) spp., the latter is regarded as a valid subgenus with which the other two are now synonymized. Species of this subgenus are mostly Neotropical, with several species distributed in the Caribbean, and a few: *Coelioxys dolichos* Fox, 1890, *Coelioxys menthae* Cockerell, 1897, and *Coelioxys slossoni* Viereck, 1902 found in the Nearctic. In both Moure *et al.* (2012) and Ascher & Pickering (2015) databases, many species are listed as *C.* (*Acrocoelioxys*), but three are assigned herein to *C.* (*Leuraspidia*), and *Coelioxys praetextata* Haliday, 1836 is regarded as belonging to *C.* (*Glyptocoelioxys*), based upon the results of the phylogenetic analyses.

List of species: *Coelioxys abdominalis* Guérin-Méneville, 1844*, *Coelioxys aculeata* Schrottky, 1902, *Coelioxys albifrons* Friese, 1916*, *Coelioxys bipustulata* Friese, 1921*, *Coelioxys brachypyga*

Friese, 1921*, *C. dolichos**, *Coelioxys eximia* Friese, 1921*, *Coelioxys foxii* Viereck, 1902*, *Coelioxys laevicollis* Friese, 1921*, *Coelioxys laevigata* Smith, 1854*, *Coelioxys laevis* Friese, 1921*, *C. menthae**, *C. otomita**, *Coelioxys popovi* Strand, 1934*, *Coelioxys producta* Cresson, 1865*, *C. rufipes**, *C. simillima**, *C. slossoni**, *Coelioxys spinipyga* Strand, 1910*, *Coelioxys tolteca* Cresson, 1878*, *Coelioxys trispinosa* Friese, 1921*, *Coelioxys turbinata* Krombein, 1953*, and *Coelioxys vigilans* Smith, 1879*.

COELIOXYS (PARACOELIOXYS) GRIBODO, 1884

= *Coelioxys* (*Schizocoelioxys*) Mitchell, 1973 syn. nov.

Type species: Coelioxys alata Förster, 1853.

Diagnosis: This subgenus can be differentiated from all the other subgenera based upon the mandible that is angled dorsally on the outer surface in females (Fig. 81). *Coelioxys* (*Paracoelioxys*) spp. are similar to species of *C.* (*Boreocoelioxys*), but can be distinguished by the postgradular grooves of T2–T3, which are broadly interrupted medially in the former (Fig. 25) and complete in the latter (Fig. 24). They can also be differentiated from species of both of the new subgenera described herein, *C.* (*Melissoctonia*) subgen. nov. and *C.* (*Rozeniana*) subgen. nov., as well as from all other subgenera, by the following combination of characteristics. Axilla very short, free apical portion much shorter than basal portion, and not produced beyond posterior margin of mesoscutellum (Fig. 71); apical fascia on T1 nearly absent, restricted to the lateral margins of tergum; apical fasciae on T2–T5 reduced medially or slightly interrupted. Female: mandible angled (Fig. 81); S6 apex elongate, longer than broad, notches acute, narrow (Fig. 26). Male: postgradular area of T2 with sublateral, elliptical, slender fovea on each side (Fig. 88) (Baker, 1975: fig. 25B) and gonocoxa subapically not compressed (Fig. 94L) (Baker, 1975: fig. 19F).

Comments: This subgenus had previously been regarded as a synonym of *C.* (*Coelioxys s.s.*) (see comments on that subgenus above), whereas *C.* (*Schizocoelioxys*) was synonymized under *C.* (*Boreocoelioxys*) by Michener (2007). The subgenus *C.* (*Paracoelioxys*) is resurrected here based on the phylogenetic results (see Results and Discussion). Whereas *C.* (*P.*) *alata* is Palaearctic, *C. funeraria* is restricted to North America (Ascher & Pickering, 2015).

List of species: C. alata and *C. funeraria*. Some other Palaearctic species, *Coelioxys hosoba* Nagase, 2003, *Coelioxys hiroba* Nagase, 2003, *Coelioxys inermis* (Kirby, 1802), *Coelioxys mandibularis* Nylander, 1848, and *Coelioxys elongata* (Lepeletier, 1841), might also belong to this subgenus as they share the modified mandible in the female.

COELIOXYS (PLATYCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys alatiformis Friese, 1921.

Diagnosis: This monotypic subgenus can be distinguished from all other *Coelioxys* subgenera by the shape of S5 in females, which is spatulate and greatly expanded towards the apex, its margins somewhat swollen and shining, and ventral surface convex (Fig. 44), and by the postgradular areas of T2–T3 in males that are foveate in a manner not found in other subgenera (Fig. 45): on T2, the fovea is elliptical and covered with minute whitish hairs, whereas in T3 it is smaller and circular (Fig. 45). In females from other subgenera the S5 is elongate towards apex, never spatulate nor greatly expanded, except in *C.* (*Paracoelioxys*) *alata*, in which the S5 margins are greatly expanded but straight, never swollen, as in *C. alatiformis* (Fig. 44); the ventral surface of S5 is concave and the apex is broad and truncate, in contrast to the convex surface and ellipsoid apex in *C. alatiformis*. The fovea on the postgradular area of T2 of males from other subgenera is never elliptical, hairy and deep, but slender as in *C. conoidea* (Fig. 90), *C. rufescens*, *C.* (*Paracoelioxys*) (Fig. 88), and *C.* (*Boreocoelioxys*) (Fig. 27); minute and circular, as in *C.* (*Glyptocoelioxys*) (Fig. 78), except *C. chilensis* [see Discussion of *C.* (*Glyptocoelioxys*)], and circular and bare, as in *C. reginae*, *C. albolineata*, and *C. confusa*.

Comments: This subgenus comprises only one species, *C. alatiformis*, which ranges from Mexico to Argentina (Rocha-Filho & Packer, 2015).

*List of species: Coelioxys alatiformis**.

COELIOXYS (RHINOCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys zapoteca Cresson, 1878.

Diagnosis: The following characteristics combined (four for either sex) separate species of *C.* (*Rhinocoelioxys*) from all the other subgenera. Mesoscutellum with a distinct longitudinal median ridge (Fig. 51); posterior margin of mesoscutellum obtusely produced medially into a blunt edge

(Fig. 51); axilla long, free apical portion longer or subequal to basal portion (Fig. 51); ocular hairs long (~0.12 mm) (Fig. 5). Female: S6 lateral notches obsolete, a weak impression, not interrupting outline in dorsal view (Fig. 65). Male: postgradular areas of T2 and T3 with a transverse, punctate area either formed by punctures that may be fused or by few smaller punctures basally and larger punctures apicolaterally (Fig. 66).

Comments: The phylogenetic results indicate that *C.* (*Rhinocoelioxys*) as previously defined is polyphyletic. The type species *C. zapoteca* as well as *C. agilis* and *Coelioxys platygnatha* Rocha-Filho & Packer, 2015 are in a different clade from the other four species that were included by Rocha-Filho & Packer (2015), which are now transferred to *C.* (*Austrocleptria*) subgen. nov. (see below). The three species are Neotropical. Rocha-Filho & Packer (2015) revised and keyed the species of this subgenus [as well as those of *C.* (*Austrocleptria*) subgen. nov.].

*List of species: Coelioxys agilis**, *C. platygnatha**, and *C. zapoteca**.

COELIOXYS (SYNOCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys texana Cresson, 1872.

Diagnosis: This is the only *Coelioxys* subgenus and perhaps the only members of the Megachilini in which the male S7 is bilobed (Fig. 94H) rather than divided into two small sclerites (Baker, 1975: fig. 26D). Some characteristics such as the scale-like pubescence in parts of the body (Fig. 32), the inner ramus of pretarsal claws in females acute (Fig. 36), and apicodorsal processes of T6 in males forked (Fig. 34) are shared only with species of the Old World subgenus *C.* (*Allocoelioxys*). Species belonging to *C.* (*Synocoelioxys*) are characterized by the following combination of characteristics that separates them from all other subgenera. Median ocellus surrounded by a swollen and nearly impunctate area (Fig. 32). Female: lateral margins of T6 apex with long thick hairs forming an inconspicuous fringe (Fig. 33); S6 rounded or elliptical, not notched and straight (Fig. 33), not flexed downwards. Male: T6 apicodorsal processes forked, with processes flattened, pointed, and irregular, almost forming a crenulate plate (Fig. 34), and T7 exposed, with a long median tooth-like process medially (Baker, 1975: fig. 13A).

Comments: Species of *C.* (*Synocoelioxys*) are primarily Nearctic; five of them were revised and keyed by Baker (1975); another two, *Coelioxys toltecoides* Cockerell, 1923 from Mexico and *Coelioxys tegularis* Cresson, 1869 from Cuba, are also assigned to the subgenus (Ascher & Pickering, 2015).

List of species: Coelioxys alternata Say, 1837, *Coelioxys apacheorum* Cockerell, 1900, *Coelioxys erysimi* Cockerell, 1912, *Coelioxys hunteri* Crawford, 1914, *C. tegularis**, *C. texana*, and *C. toltecoides*.

COELIOXYS (TORRIDAPIS) PASTEELS, 1977

Type species: Coelioxys torrida Smith, 1854.

Diagnosis: With *C.* (*Liothyrapis*) and the species *C.* (*A.*) *madagascariensis*, this Old World subgenus is the only one within *Coelioxys* in which the compound eyes are bare (Fig. 4). Species of *C.* (*Torridapis*) can be distinguished from *C. madagascariensis* by the lateral margins of axilla neither elevated nor carinate (Fig. 11) (conspicuously elevated and carinate in the latter; Fig. 6). They can be separated from those of *C.* (*Liothyrapis*) by the following list of characteristics. Axilla long, free apical portion produced beyond the posterior margin of mesoscutellum, and curved apically (Fig. 11); mesoscutellum with a dorsal median carina at least basally (Fig. 11). Female: T6 lacking long, erect, thick hairs, with apex ending in an inconspicuous, short, spine-like process (Fig. 12); T6 and S6 gradually tapering, greatly elongate, S6 folded, subacute apically, its lateral margins with an inconspicuous fringe composed of short brownish hairs (Fig. 12). Male: hypostomal area lacking concavity; T6 basally lacking, or with short, flattened lateral expanded areas, never with long, acute teeth (Fig. 13); S4 medially sulcate, hairy, and S6 long, ≥1.2× longer than broad.

Comments: Ten species are classified in this subgenus (Ascher & Pickering, 2015), with a new one described by Rocha-Filho (2016); the four Afrotropical species were revised by Pasteels (1968) and classified as *Liothyrapis*, the other species come from Indomalayan or Palaearctic regions, Mauritius or Madagascar.

List of species: Coelioxys analis Friese, 1911, *Coelioxys basalis* Smith, 1875, *Coelioxys ducalis* Smith, 1854, *Coelioxys fenestrata* Smith, 1873, *Coelioxys julia* Rocha-Filho, 2016*, *Coelioxys* *kosemponis* Strand, 1913, *Coelioxys maculata* Friese, 1913, *Coelioxys maculoides* Pasteels, 1968, *C. torrida*, *Coelioxys torridula* Pasteels, 1968, and *Coelioxys weinlandi* Schulz, 1904.

COELIOXYS (XEROCOELIOXYS) MITCHELL, 1973

Type species: Coelioxys edita Cresson, 1872.

Diagnosis: Species in this subgenus are very similar to *C.* (*Coelioxys s.s.*) spp., but can be differentiated by the pronotal lobe distinctly lamellate (Fig. 31) or carinate throughout, whereas in species of *C.* (*Coelioxys s.s.*) the pronotal lobe is conspicuously rounded on its outer margin and weakly carinate on its inner margin (Fig. 30). Another difference between species of these two subgenera is in the mesosomal pilosity, which is short, composed of subappressed or appressed hairs, forming marginal lines or spots on the mesoscutum in *C.* (*Xerocoelioxys*) spp. (Fig. 31), contrasting with the long and dense pubescence in species of *C.* (*Coelioxys s.s.*) (Fig. 30). The following combination of characteristics together with the two preceding ones separate species of *C.* (*Xerocoelioxys*) from all other subgenera. Mesoscutum coarsely and densely punctate, no interspaces linear to shorter than puncture diameter (as in Figs 83, 85); postgradular grooves of T2–T3 complete, uninterrupted medially (Fig. 24), and gradulus of T2 bowed posteriorly.

Comments: Baker (1975) revised and keyed ten species in this subgenus. As a result of our phylogenies, *C. serricaudata*, previously placed in *C.* (*Coelioxys s.s.*), is now regarded as belonging to *C.* (*Xerocoelioxys*). Also, considering the diagnostic characteristics of this subgenus, the other three North American species assigned by Baker (1975) to *C.* (*Coelioxys s.s.*), *Coelioxys hirsutissima* Cockerell, 1912, *Coelioxys immaculata* Cockerell, 1912, and *Coelioxys mitchelli* Baker, 1975, should be classified as *C.* (*Xerocoelioxys*). This subgenus is predominantly Nearctic but with some species reaching the Neotropical region of Mexico.

List of species: Coelioxys aperta Cresson, 1878, *Coelioxys bisoncornua* Hill, 1936, *Coelioxys boharti* Mitchell, 1962, *C. edita*, *Coelioxys galactiae* Mitchell, 1962, *Coelioxys grindeliae* Cockerell, 1900, *C. hirsutissima*, *C. immaculata*, *Coelioxys mesae* Cockerell, 1921, *C. mitchelli*, *Coelioxys nodis* Baker, 1975, *Coelioxys piercei* Crawford, 1914, *C. serricaudata*, *C. soror*, and *Coelioxys soledadensis* Cockerell, 1909.

Six new subgenera are described as follows.

COELIOXYS (AUSTROCLEPTRIA) ROCHA-FILHO **SUBGEN. NOV.**

http://zoobank.org/urn:lsid:zoobank.org:
act:0F9870B7-254E-45E3-8C21-7045E431BFEF

Type species: Coelioxys barbata Schwarz & Michener, 1954.

Diagnosis: The following combination of characteristics for either sex distinguishes the new subgenus from all other subgenera (alternative conditions in parentheses): for both sexes, axilla short, with free apical portion shorter than the basal portion (Rocha-Filho & Packer, 2015: figs 3I, 5C, 9D) (free apical portion longer than basal portion); S6 lateral notches in females acute (Fig. 67) [obsolete notches in *C.* (*Callosarissa*) and *C.* (*Rhinocoelioxys*) (Figs 38, 65), notches absent in *C.* (*Liothyrapis*) (Fig. 9), *C.* (*Torridapis*) (Fig. 12), *C.* (*Allocoelioxys*) (Figs 17, 21), *C.* (*Synocoelioxys*) (Fig. 33), *C.* (*Cyrtocoelioxys*) (Fig. 46), *C.* (*Coelioxys s.s.*) (Fig. 28), *C.* (*Melissoctonia*) (Fig. 89), and *C.* (*Xerocoelioxys*), except *C.* (*X.*) *aperta*, *C. bisoncornua*, and *C. edita* (Fig. 14), in which notches are present but obtuse], and apical margin of S4 in males deeply emarginate, forming a U-shaped process with arms flattened, elongate, and separated from one another, and with the distance between them more than half their length (Rocha-Filho & Packer, 2015: figs 3L, 5I, 7I, 9L) [apical margin produced into two robust, broad arms in *C.* (*T.*) *weinlandi*, *C.* (*A.*) *erythrura*, and *C.* (*A.*) *afra*; U-shaped process with arms robust, thick and separated from one another, and with the distance between them more than half their length in *C.* (*G.*) *germana* and *C.* (*G.*) *mexicana* (Fig. 49); U-shaped process arms elongate, sharply elevated, and close to one another, and with the distance between them equal to half their length in *C.* (*L.*) *bertonii*, *C.* (*Cy.*) *gonaspis*, and *C.* (*D.*) *kuscheli*; all other subgenera lack such processes].

Description: Supraclypeal area not elevated or keeled (Fig. 54); ocular hairs short (0.07–0.08 mm; Rocha-Filho & Packer, 2015: fig. 3B); area around mid ocellus flat, not swollen or carinate (as in Fig. 54) or swollen only anteriorly in *C. barbata* (Rocha-Filho & Packer, 2015: fig. 3G); pronotal tubercle lamellate and emarginate, forming two distinct lobes (Rocha-Filho & Packer, 2015: fig. 7B); mesoscutum densely punctate, interspace between punctures subequal to or larger than puncture diameter (Fig. 51); mesoscutellum pilosity anteriorly with hairs forming an uninterrupted line (Figs 51, 69); posterior margin of mesoscutellum medially either produced into a flat tooth-like process (Rocha-Filho & Packer, 2015: figs 3I, 9D) or rounded, not produced (Rocha-Filho & Packer, 2015: figs 5C, 7F); axilla short, its free apical portion shorter than basal portion (Rocha-Filho & Packer, 2015: fig. 5C); basal concavity of T1 carinate (Rocha-Filho & Packer, 2015: fig. 7G); postgradular grooves of T2–T3 broadly interrupted medially (Rocha-Filho & Packer, 2015: fig. 7G). Female: clypeus apically either emarginate (Rocha-Filho & Packer, 2015: figs 5B, 7B) or with a tuberculate process (Rocha-Filho & Packer, 2015: figs 3B, 9B, 9C); pretarsal claw lacking inner ramus (as in Fig. 82); apical fasciae of T2–T5 complete (as in Fig. 84); T6 dorsal carina apically either conspicuous, elevated, and rounded (Fig. 67) or inconspicuously keeled, keel not sharply elevated (Fig. 65); S6 lateral notches acute, distinctly separated from marginal area (Fig. 67). Male: gena surface not excavated (as in Fig. 15); hypostomal concavity deep, bare at least on posterior margin (Rocha-Filho & Packer, 2015: fig. 7E); postgradular areas of T2 and T3 with a conspicuous, elliptical, transverse, punctate area, formed by punctures of the same size (Fig. 68); apical fasciae of T2–T5 broadly interrupted medially (Fig. 68); T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (as in Fig. 63); apical margin of S4 deeply emarginate, forming a U-shaped process, arms flattened, elongate, and separate from one another, and with the distance between them more than half their length emarginate (Rocha-Filho & Packer, 2015: figs 3L, 5I, 7I, 9L).

Comments: Prior to this phylogenetic study the species within this subgenus were regarded as belonging to *C.* (*Rhinocoelioxys*), as described in Rocha-Filho & Packer (2015). Species within this subgenus are restricted to the Neotropical region.

Etymology: From the Latin word *auster* (= 'south') and Greek word *κλέπτης* (*kleptes* = 'thief'), 'Thief from the South', referring to the subgeneric distributional range (through most of South America) in combination with their cleptoparasitic behaviour.

*List of species: C. barbata**, *C. clypearis**, *C. nasidens**, and *C. paraguayensis*.

***COELIOXYS* (*CALLOSARISSA*) ROCHA-FILHO SUBGEN. NOV.**

http://zoobank.org/urn:lsid:zoobank.org:act:326AC07E-CA54-4799-BA8A-711649B3A044

Type species: *Coelioxys albolineata* Cockerell, 1905.

Diagnosis: The following combination of characteristics for either males or females distinguishes *C.* (*Callosarissa*) subgen. nov. from species of all subgenera [alternative condition(s) in parentheses]. For both sexes, mesoscutellum sparsely punctate, interspaces between punctures larger than puncture diameter (Fig. 35) [coarsely punctate (Figs 6, 7, 83, 85), densely punctate, interspaces linear to subequal to puncture diameter]; axilla short, free apical portion shorter than basal portion (Fig. 35) (free apical portion longer than basal portion; Fig. 69). Female: pretarsal claw bifurcate (pretarsal claw lacking inner ramus); S6 notches obsolete, not interrupting outline in dorsal view (Fig. 38) [notches absent (Fig. 28), obtuse (Fig. 14), or acute (Fig. 40)]. Male: gena deeply excavated along posterior margin of eye (Fig. 39) (not excavated; Fig. 15), excavation linear, anterior and posterior margins nearly parallel (Fig. 39) [enlarged posteriorly, not linear in *C.* (*Eingana*) subgen. nov., the only other subgenus with an excavation (Fig. 41)]. Males of this subgenus as well as those of *C.* (*Eingana*) subgen. nov. are the only *Coelioxys* in which the gena is both deeply excavated and densely hairy along the posterior margin of the compound eye.

Description: Supraclypeal area not elevated or keeled (Fig. 54); ocular hairs long (~0.12 mm; as in Fig. 5); area around mid ocellus swollen only posteriorly (Rocha-Filho & Packer, 2015: fig. 19B); pronotal tubercle lamellate and nearly straight, not forming distinct lobes (Fig. 31); mesoscutum and mesoscutellum sparsely punctate, interspaces between punctures larger than puncture diameter (Fig. 35), or densely punctate, interspaces between punctures subequal to or larger than puncture diameter (as in Fig. 51); mesoscutellum anteriorly with hairs forming two separate distinct patches (Fig. 35); posterior margin of mesoscutellum obtusely produced medially, convexity conspicuously emarginate medially and upwardly oriented (Fig. 35); axilla short, free apical portion shorter than basal portion (Fig. 35); concavity of T1 lacking marginal carina; postgradular grooves of T2–T3 broadly interrupted medially (as in Fig. 86); apical fasciae of T2–T5 complete (as in Figs 29, 84). Female: clypeus with surface flat or nearly so (as in Fig. 54); pretarsal claw bifurcate, inner and outer rami separated by broad concavity (Fig. 36); T6 dorsal carina inconspicuously elevated, not sharp (Fig. 38); S6 narrow, elongate, much longer than broad, lateral notches obsolete, a weak impression, not interrupting outline in dorsal view (Fig. 38). Male: gena deeply excavated along posterior margin of eye, excavated area densely covered with appressed, plumose white hairs (Fig. 39); genal excavation linear, anterior and posterior margins nearly parallel, more than 4× longer than broad (Fig. 39); hypostomal concavity shallow and hairy throughout (Fig. 39); postgradular area of T2 with a small, circular fovea, not hairy, not surrounded by punctures but by an impunctate area; postgradular area of T3 without fovea or punctate area; T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (as in Fig. 63); apical margin of S4 entire (as in Fig. 62).

Comments: Species within this subgenus are primarily Australasian but *C. confusa* is Indomalayan. Rocha-Filho (2016) provides a revision of the Australian fauna with two synonyms concerning the species of this new subgenus.

Etymology: From the Greek words *καλός* (*kalos* = 'beautiful') + *σάρισα* (*sarissa*/*sarisa* = 'long pike'), for the elongate and narrowed S6 shape in females.

*List of species: Coelioxys albolineata**, *Coelioxys confusa**, and *Coelioxys dispersa* Cockerell, 1911*. *Coelioxys peregrinata* Cockerell, 1911* from the Solomon Islands is likely to be a member of this subgenus, but the mesoscutellum is coarsely and densely punctate and not emarginate medially on posterior margin.

COELIOXYS (*EINGANA*) ROCHA-FILHO SUBGEN. NOV.

http://zoobank.org/urn:lsid:zoobank.org:act:76F4C6C8-757A-4891-A29E-415976C0429B

Type species: Coelioxys reginae Cockerell, 1905.

Diagnosis: Species of *C.* (*Eingana*) subgen. nov. are distinguished from all other *Coelioxys* subgenera by the following combination of characteristics as appropriate for each sex (alternative possibilities). For both sexes: mesoscutellum densely to coarsely punctate, interspaces between punctures much shorter than puncture diameter (as in Figs 83, 85) (sparsely punctate, interspaces between punctures larger than puncture diameter; Fig. 35); axilla short, free apical portion shorter than basal portion (Fig. 35) (free apical portion longer than basal portion; Fig. 69). Female: pretarsal claw bifurcate (Fig. 36) (pretarsal claw lacking inner ramus); S6 notches either obtuse (as in Fig. 14) or acute (Fig. 40), clearly visible in dorsal view [notches absent (Fig. 28), obsolete (Fig. 38), not interrupting outline in dorsal view]. Male: gena deeply excavated along posterior margin of eye (Fig. 37) (not excavated; Fig. 15) and genal excavation distinctly convex posteriorly, not linear (Fig. 41) [excavation linear, anterior and posterior margins nearly parallel in *C.* (*Callosarissa*) subgen. nov.; Fig. 39]. As in males of *C.* (*Callosarissa*) subgen. nov. the gena along the posterior margin of the compound eye is deeply excavated and densely covered with appressed, white, plumose hairs.

Description: Supraclypeal area not elevated or keeled (Fig. 54); ocular hairs long (~0.12 mm; as in Fig. 5), or short (0.07–0.08 mm) in *C. froggatti*; area around mid ocellus swollen only posteriorly (Rocha-Filho & Packer, 2015: fig. 19B); pronotal tubercle lamellate and nearly straight, not forming distinct lobes (Fig. 31); mesoscutellum densely to coarsely punctate, interspaces between punctures much shorter than puncture diameter (as in Figs 83, 85) in *C. reginae*, and coarsely and densely punctate, interspaces linear to shorter than puncture diameter (as in Fig. 83) in *C. froggatti*; mesoscutellum pilosity anteriorly with hairs forming two separate distinct patches (Fig. 35); posterior margin of mesoscutellum rounded, neither produced medially nor emarginate (Fig. 71); axilla short, free apical portion shorter than basal portion (Fig. 35); concavity of T1 lacking marginal carina; postgradular grooves of T2–T3 broadly interrupted medially (as in Fig. 86); apical fasciae of T2–T5 complete in *C. froggatti* (as in Fig. 29), or broadly interrupted medially in *C. reginae* (as in Fig. 86). Female: clypeus surface flat or nearly so (as in Fig. 54); pretarsal claw bifurcate, inner and outer rami separated by broad concavity (Fig. 36); T6 dorsal carina sharp, conspicuously elevated subapically (Fig. 40); S6 triangular, broader, not conspicuously elongate, subapical notches either acute, conspicuous (Fig. 40), or obtuse (as in Fig. 14). Male: gena deeply excavated along posterior margin of eye, excavated area densely covered with appressed, plumose white hairs (Fig. 37); genal excavation convex posteriorly, not linear, posterior margin distinctly curved, less than 3.5× longer than broad (Fig. 41); hypostomal concavity shallow and hairy throughout (Figs 37, 41); postgradular area of T2 lacking fovea or punctate area in *C. froggatti*, but with a small, circular, glabrous fovea, surrounded by an impunctate area in *C. reginae*; postgradular area of T3 without fovea or punctate area in both species; T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (as in Fig. 63); apical margin of S4 entire (as in Fig. 62).

Comments: This subgenus is known only from Australia, its species were treated by Rocha-Filho (2016).

Etymology: According to Australian Aboriginal mythology, *Eingana* is a snake creator-Goddess, mother of humanity, water, and all non-human animals. This name was chosen because this is an Australian endemic subgenus.

*List of species: Coelioxys froggatti**, *C. reginae**, and *Coelioxys tasmaniana* Rocha-Filho, 2016*.

***Coelioxys* (*Leuraspidia*) Rocha-Filho**
subgen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:
1BE5277F-F633-403A-9FA4-577705CEFB61

Type species: Coelioxys azteca Cresson, 1878.

Diagnosis: The following combination of characteristics for either males or females separates species of this subgenus from all other *Coelioxys* subgenera. For both sexes: median ocellus not surrounded by swollen area (Fig. 54) (median ocellus surrounded by a conspicuous impunctate, swollen area; Figs 52, 53); medial area of mesoscutum conspicuously swollen (Fig. 58) (not swollen; Fig. 55); dorsal and superior surfaces of mesoscutellum fully separated by a distinct, somewhat sharp, nearly impunctate edge, forming a distinct acute angle (Fig. 50) [surfaces separated by an indistinct subcarinate edge (Fig. 51) or surfaces gradually curving into each other]; S6 notches in females acute, clearly visible in dorsal view (Fig. 60) [notches absent (Fig. 28), obsolete (Fig. 57), or obtuse (Fig. 14)], and T5 in males with conspicuous lateral tooth (Fig. 63) (lateral tooth absent or indistinct; Fig. 61).

Description: Supraclypeal area not elevated or keeled (Fig. 54); ocular hairs long (~0.12 mm), very long (~0.17 mm or longer) in *C. dinellii* (Fig. 58); subocellar area punctate, flat or inconspicuously elevated, median ocellus not surrounded by swollen area (Fig. 54); supraclypeal area unmodified, not forming a rounded ridge (Fig. 54); carina of pronotal tubercle lamellate and emarginate, forming two distinct lobes (as in Figs 31, 73), or sharply carinate but not forming a lamella, straight, not forming lobes in *C. dinellii* (as in Fig. 75); mesoscutellum sparsely punctate, interspaces between punctures larger than puncture diameters; mesoscutellum produced over metanotum and propodeum, its posterior margin produced medially into a flat, tooth-like process upwardly oriented; mesoscutellum pilosity anteriorly with hairs forming two separated distinct patches (as in Figs 50, 85); axilla long, free apical portion longer than basal portion (as in Fig. 69), not curved apically, nearly parallel with one another; concavity of T1 carinate (as in Fig. 42); postgradular grooves of T2–T3 broadly interrupted medially (as in Fig. 25). Female: clypeus surface flat or nearly so (Fig. 54); pretarsal claw lacking inner ramus (as in Fig. 82) or bifurcate with inner and outer rami separated by broad concavity (as in Fig. 36) in *C. bertonii*; T6 dorsal carina apically obsolescent, inconspicuously elevated (as in Fig. 38) in *C. bertonii*; inconspicuously keeled, keel not sharply elevated (as in Fig. 65) in *C. azteca*, and conspicuously keeled, keel sharply elevated (as in Fig. 40) in *C. dinellii*; S6 elongate and subacute, strongly flexed downwards, conspicuously notched subapically (Fig. 60). Male: gena not excavated (as in Fig. 15); hypostomal area lacking concavity in *C. dinellii* (as in Fig. 18); concavity present and deep in *C. azteca* and *C. bertonii*, bare at least on the posterior margin (Rocha-Filho & Packer, 2015: fig. 13G) in *C. azteca* and hairy throughout (as in Figs 37, 41) in *C. bertonii*; postgradular areas of T2–T3 with punctate areas composed of punctures smaller than those of the disc, and arranged in a circular to elliptical area (as in Figs 66, 68) in *C. azteca* and *C. dinellii*; in *C. bertonii*, postgradular area of T2 with a shallow, hairy fovea composed of small punctures with small punctures adjacent and postgradular area of T3 with a circular, shallow fovea composed of punctures smaller than the adjacent punctures of the disc, and surrounded by punctures forming a more or less elliptical area; apical fasciae of T2–T5 broadly interrupted medially (as in Fig. 68); T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (Fig. 63); S4 apical margin deeply emarginate, forming a U-shaped process (Fig. 64).

Comments: Species of this subgenus are primarily Neotropical, with some records of the type species, *C. azteca*, from the Nearctic areas of Mexico (Ascher & Pickering, 2015).

Etymology: From Greek words *λευρός* (*leuros* = 'smooth') + *ασπίδα* (*aspida* = 'shield') because of the polished, smooth mesoscutum and mesoscutellum of the species in this subgenus.

*List of species: Coelioxys azteca**, *C. bertonii*, and *C. dinellii*. The following species are likely to belong to this subgenus: *Coelioxys aculeaticeps* Friese, 1921*, *Coelioxys bequaertiana* Cockerell, 1931*, *Coelioxys bifida* Friese, 1904*, *Coelioxys buchwaldi* Friese, 1921*, *Coelioxys buehleri* Schrottky, 1909, *Coelioxys haematura* Cockerell, 1914*, *Coelioxys longiventris* Friese, 1921*, *Coelioxys pygidialis* Schrottky, 1902, *Coelioxys rufa* Friese, 1921*, *Coelioxys rufopicta* Smith, 1854*, *Coelioxys tepaneca* Cresson, 1878*, and *Coelioxys wilmattae* Cockerell, 1949*.

COELIOXYS (*MELISSOCTONIA*) ROCHA-FILHO SUBGEN. NOV.

http://zoobank.org/urn:lsid:zoobank.org:act:
ED5F46F1-D00D-4103-A5DC-796333552952

Type species: *Coelioxys conoidea* (Illiger, 1806).

Diagnosis: The species in this subgenus can be distinguished from the other species within *Coelioxys* by the following combination of characteristics for either males or females. For both sexes: pronotal tubercle sharply carinate, discrete, not forming a lamella (Fig. 75) [pronotal tubercle rounded on outer margin (Fig. 30) or lamellate throughout (Fig. 73)]; axilla long, free apical portion longer than basal portion (Fig. 85) (free apical portion shorter than basal portion; Fig. 35); postgradular grooves of T2–T3 broadly interrupted medially (Fig. 86) [grooves complete (Fig. 24) or slightly interrupted medially]; apical fasciae of S2–S5 interrupted medially; mandible in females conspicuously curved medially on outer surface (Fig. 82) (slender, not curved or angled; Fig. 81); S6 in females lacking lateral notches (Fig. 89) (notches present; Figs 26, 87), and in males S4 apical margin slightly emarginate and apical rim conspicuously emarginate, forming two slightly elevated arms (Fig. 93) [apical margin entire (Fig. 92) or deeply emarginate, forming a U-shaped process (Figs 49, 64)].

Description: Supraclypeal area not elevated or keeled (as in Fig. 54); ocular hairs very long (~0.17 mm or longer; as in Fig. 58); area around mid ocellus flat, not swollen or carinate (as in Fig. 54); pronotal tubercle sharply carinate, discrete, not forming lamella, and nearly straight, not forming distinct lobes (Fig. 75); mesoscutum coarsely and densely punctate, no interspaces between punctures or shorter than puncture diameter (Fig. 85); posterior margin of mesoscutellum rounded, neither produced medially nor emarginate (Fig. 85); mesoscutellum basally with two small, separated, sublateral spots of subappressed hairs (Fig. 85); axilla long, free apical portion longer than basal portion, not curved apically, nearly parallel with one another (Fig. 85); concavity of T1 lacking marginal carina; postgradular grooves of T2–T3 broadly interrupted medially (Fig. 86); apical fasciae of T1–T5 broadly interrupted medially, composed only of thick, subtriangular lateral bands (Fig. 86); apical fasciae of S2–S5 interrupted medially. Female: clypeus surface flat or nearly so (as in Fig. 54); pretarsal claw lacking inner ramus (Fig. 82); T6 dorsal carina nearly complete, reaching more than two-thirds the T6 length, conspicuously elevated, sharp, and separating two elliptical, shallow depressions apically (Fig. 89); S6 broad, lanceolate, lacking lateral notches (Fig. 89). Male: gena surface not excavated (as in Fig. 15); hypostomal concavity shallow, conspicuously hairy on anterior margin; postgradular area of T2 with a transverse, deep fovea composed of small punctures, with a narrow impunctate margin entirely surrounding the fovea (Fig. 90), postgradular area of T3 lacking fovea or punctate area; T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (as in Fig. 63); S4 apical margin slightly emarginate and apical rim conspicuously emarginate, forming two slightly elevated arms.

Comments: This subgenus is only represented in the Palaearctic region.

Etymology: From the Greek words *μέλισσα* (*melissa* = 'bee') + *κτόνος* (*ktonos* = 'killer'), literally 'bee killer', because of the hospicidal behaviour displayed by *Coelioxys* larvae.

List of species: *Coelioxys conoidea*.

COELIOXYS (*ROZENIANA*) ROCHA-FILHO SUBGEN. NOV.

http://zoobank.org/urn:lsid:zoobank.org:act:
F11EBF9B-481D-46BE-8018-A76A81BC6AC2

Type species: *Coelioxys rufescens* Lepeletier & Serville, 1825.

Diagnosis: Species within this new subgenus can be separated from all others by the following combination of characteristics for either males or females. Mesoscutellum basally lacking spots of subappressed hairs (Fig. 83) (with two separate spots; Fig. 85); axilla conspicuously curved apically, convergent (Fig. 83) [nearly parallel (Fig. 85) or divergent from one another (Fig. 69)]; postgradular grooves of T2–T3 broadly interrupted medially (Fig. 84) [grooves complete (Fig. 24) or slightly interrupted medially]; apical fasciae of S2–S5 complete; mandible shape dorsally in females conspicuously curved medially on outer surface (Fig. 82) (slender, not curved or angled; Fig. 81); S6 in females conspicuously notched, notches broad and clearly visible from dorsal view (Fig. 87) [notches absent (Fig. 28), obsolete (Fig. 38), or acute (Fig. 26)], and in males S4 apical margin entire and apical rim slightly emarginate (Fig. 92) [apical margin emarginate (Fig. 93) or deeply emarginated, forming a U-shaped process (Figs 49, 64)].

Description: Supraclypeal area not elevated or keeled (as in Fig. 54); ocular hairs very long (~0.17 mm or longer) (as in Fig. 58); area around mid ocellus flat, not swollen or carinate (as in Fig. 54); pronotal tubercle sharply carinate, discrete, not forming a conspicuously elevated lamella and nearly straight, not forming distinct lobes (Fig. 75); mesoscutum coarsely and densely punctate, no interspaces between punctures or shorter than puncture diameter (Fig. 83); posterior margin of mesoscutellum rounded, neither produced medially nor emarginate (Fig. 83); mesoscutellum basally lacking spots of subappressed hairs (Fig. 83); axilla long, free apical portion longer than basal portion, conspicuously curved apically, convergent (Fig. 83); concavity of T1 lacking marginal carina; postgradular grooves of T2–T3 broadly interrupted medially (Fig. 84); apical fasciae of T1–T5 complete (Fig. 84). Female: clypeus surface flat or nearly so (as in Fig. 54); pretarsal claw lacking inner ramus (as in Fig. 82); T6 dorsal carina incomplete, reaching about one-third T6 length, evanescent half basally, inconspicuously elevated apically, rounded, not sharp, and separating two elliptical, obsolescent depressions; S6 elongate and conspicuously notched, lateral notches broad, not acute (Fig. 87). Male: gena surface not excavated (as in Fig. 15); hypostomal concavity deep and nearly bare, anterior margin with an inconspicuous line of hairs; postgradular area of T2 with a very slender, shallow, punctate fovea with impunctate margin only found posteriorly to the fovea (Fig. 88), postgradular area of T3 lacking fovea or punctate area; T5 lateral spines short, at most as long as wide, not reaching the apex of apical rim (as in Fig. 63); S4 apical margin entire and apical rim slightly emarginate.

Comments: Species in this subgenus are restricted to the Palaearctic region.

Etymology: This subgenus is named in honour of Dr Jerome G. Rozen Jr, Curator of the American Museum of Natural History, for his lifetime of work on cleptoparasitic bees and the nesting biology and description of immature stages of bees.

List of species: Coelioxys rufescens. The Palaearctic species *Coelioxys aurolimbata* Förster, 1853, *Coelioxys mongolica* Friese, 1925, *Coelioxys torquata* Warncke, 1992, and *Coelioxys tricarinata* Morawitz, 1875 are likely to belong to this subgenus.

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REFERENCES

Alfken JD. 1928. Eine neue Kegelbienen aus Tunis. *Konowia* **7:** 193–196.

Ascher JS, Pickering J. 2015. *Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila)*. Available via http://www.discoverlife.org/mp/20q?guide=Apoidea_species [Accessed 10 March 2015]

Augusto SC, Garófalo CA. 2004. Nesting biology and social structure of *Euglossa* (*Euglossa*) *townsendi* Cockerell (Hymenoptera, Apidae, Euglossini). *Insectes Sociaux* **51:** 400–409.

Baker JR. 1971. Development and sexual dimorphism of larvae of the bee genus *Coelioxys*. *Journal of the Kansas Entomological Society* **44:** 225–235.

Baker JR. 1975. Taxonomy of five Neartic subgenera of *Coelioxys* (Hymenoptera: Megachilidae). *The University of Kansas Science Bulletin* **50:** 649–730.

Bremer K. 1994. Branch support and tree stability. *Cladistics* **10:** 295–304.

Cockerell TDA. 1911. Bees in the collection of the United States National Museum, 2. *Proceedings of the United States National Museum* **40:** 241–264.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

Genaro JA, Franz NM. 2008. The bees of Greater Puerto Rico (Hymenoptera: Apoidea: Anthophila). *Insecta Mundi* **40:** 1–24.

Goloboff PA. 1993. Estimating character weights during tree search. *Cladistics* **9:** 83–91.

Goloboff PA, Farris JS. 2001. Methods for quick consensus estimation. *Cladistics* **17:** S26–S34.

Goloboff PA, Farris JS, Källersjö M, Oxleman B, Ramirez MJ, Szumik CA. 2003. Improvements to resampling measures of group support. *Cladistics* **19:** 324–332.

Goloboff PA, Carpenter JM, Salvador Arias J, Miranda Esquivel DR. 2008a. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* **24:** 1–16.

Goloboff PA, Farris JS, Nixon JS. 2008b. TNT, a free program for phylogenetic analysis. *Cladistics* **24:** 774–786.

Gonzalez VH, Griswold T, Praz CJ, Danforth BN. 2012. Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. *Systematic Entomology* **37:** 261–286.

Gribodo G. 1884. Sopra alcune specie nuove o poco conosciute di Imenotteri Antofili. *Bollettino della Società Entomologica Italiana* **16:** 269–274.

Gupta RK. 1991. A new subgenus of *Coelioxys* Latreille (Hymenoptera: Apoidea: Megachilidae) from India. *Journal of the Bombay Natural History Society* **88:** 425–428.

Gupta RK. 1992. On a new subgenus *Orientocoelioxys* and a new species of genus *Coelioxys* Latr. from India. *Reichenbachia* **29:** 73–76.

Gupta RK. 1993. *Taxonomic studies on the Megachilidae of North-Western India*. New Delhi: Indian Council of Agricultural Research.

Holmberg EL. 1916. Las especies argentinas de *Coelioxys*. *Anales del Museo Nacional de Historia Natural de Buenos Aires* **28:** 541–591.

Latreille PA. 1809. *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias doisposita, iconibus exemplurisque plurimis explicata*, Vol. 4. Paris: Koenig.

Litman JR, Danforth BN, Eardley CD, Praz CJ. 2011. Why do leafcutter bees cut leaves? New insights into the early evolution of bees. *Proceedings of the Royal Society, Series B, Biological Sciences* **278:** 3593–3600.

Litman JR, Praz CJ, Danforth BN, Griswold TL, Cardinal S. 2013. Origins, evolution, and diversification of cleptoparasitic lineages in long-tongued bees. *Evolution* **67:** 2982–2998.

Michener CD. 1965. A classification of the bees of the Australian and South Pacific regions. *Bulletin of the American Museum of Natural History* **130:** 1–362.

Michener CD. 2007. *The bees of the world*, 2nd edn. Baltimore: The John Hopkins University Press.

Mitchell TB. 1973. *A subgeneric revision of the genus Coelioxys of the Western Hemisphere (Hymenoptera: Megachilidae)*. Raleigh: Department of Entomology, North Carolina State University.

Moure JS, Melo GAR, Dalmolin A. 2007. Megachilini Latreille, 1802. In: M JS, U D, M GAR, eds. *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*. Curitiba: Sociedade Brasileira de Entomologia, 917–1001.

Moure JS, Melo GAR, Dalmolin A. 2012. Megachilini Latreille, 1802. In: Moure JS, Urban D, Melo GAR, eds. *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*, online version. Available via http://www.moure.cria.org.br/catalogue [Accessed 10 March 2012]

Nixon KC. 2002. *WinClada ver. 1.00.08*. Ithaca, NY: Published by the author.

Pasteels JJ. 1968. Révision des Megachilidae (Hymenoptera Apoidea) de L'Afrique Noire. II. Le Genre Coelioxys. *Annales Sciences Zoologiques, Musée Royal de L'Afrique Centrale, Tervuren, Serie In-8* **167:** 1–139.

Pasteels JJ. 1977. Les Megachilini parasites (*Coelioxys* s. l.) d'Afrique noire. *Revue de Zoologie Africaine* **91:** 161–197.

Pasteels JJ. 1982. Les *Coelioxys* Latreille (Hymenoptera, Apoidea) du groupe *afra* Lepeletier d'Europe et du procheorient. *Bulletin et Annales de la Société Royale Belge d'Entomologie* **118:** 109–120.

Praz CJ, Müller A, Danforth BN, Griswold TL, Widmer A, Dorn S. 2008. Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). *Molecular Phylogenetics and Evolution* **49:** 185–197.

Rocha-Filho LC. 2015. A contribution to the taxonomy of the cleptoparasitic bee subgenus *Cyrtocoelioxys* Mitchell of *Coelioxys* Latreille (Hymenoptera: Megachilidae). *Annales Zoologici* **65:** 687–703.

Rocha-Filho LC. 2016. A revision of the cleptoparasitic bee genus *Coelioxys* (Hymenoptera: Megachilidae) from Australia. *European Journal of Entomology* **113:** 9–28.

Rocha-Filho LC, Packer L. 2015. Revision of the Neotropical subgenera *Coelioxys* (*Platycoelioxys*) Mitchell and *C.* (*Rhinocoelioxys*) Mitchell (Hymenoptera; Megachilidae) with the description of one new species. *Zootaxa* **3941:** 151–203.

Rozen JG, Kamel SM. 2007. Investigations on the biologies and immature stages of the cleptoparasitic bee genera *Radoszkowskiana* and *Coelioxys* and their hosts in the genus *Megachile* (Hymenoptera: Apoidea: Megachilidae: Megachilini). *American Museum Novitates* **3573:** 1–43.

Rozen JG, Kamel SM. 2008. Hospicidal behavior of the cleptoparasitic bee *Coelioxys* (*Allocoelioxys*) *coturnix*, including descriptions of its larval instars (Hymenoptera, Megachilidae). *American Museum Novitates* **3636:** 1–15.

Ruszkowski A, Biliński M, Gosek J. 1986. Rośliny pokarmowe I gospodarze pasozyticzych pszczól miesiarkowatych (*Coelioxys* Latr., *Stelis* Pz., *Dioxys* Lep. et Serv., *Dioxoides* Pop. oraz *Paradioxys* Mocs.). *Pszczelnicze Zeszyty Naukowe* **30:** 111–131.

Scheuchl E. 1996. *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band II: Megachilidae, Melittidae*. Velden: Eigenverlag Erwin Scheuchl.

Schwarz N. 2001. Revision der Gattung *Radoszkowskiana* Popov 1955 und ein Beitrag zur Kenntnis der Gattung *Coelioxys* Latreille 1809 (Hymenoptera: Apidae: Megachilinae). *Linzer Biologische Beiträge* **33:** 1267–1286.

Tkalců B. 1974. Ergebnisse der Albanien-Expedition 1961 des "Deutschen Entomologischen Institutes", Hymenoptera: Apoidea V (Megachilidae). *Beiträge zur Entomologie* **24:** 323–348.

Toro H, Fritz M. 1991. Contribución al conocimiento de *Dasycoelioxys* Mitchell (Hymenoptera, Apoidea, Megachilidae). *Acta Entomologica Chilena* **16:** 69–80.

Vinson SB, Frankie G, Rao A. 2011. Field behavior of parasitic *Coelioxys chichimeca* (Hymenoptera: Megachilidae) toward the host bee *Centris bicornuta* (Hymenoptera: Apidae). *Apidologie* **42:** 117–127.

Voith J. 1997. *Coelioxys mandibularis* Nyl. as a cuckoo bee of *Osmia villosa* (Schck.) (Hymenoptera, Apiformes, Megachilidae). *Nachrichtenblatt der Bayerischen Entomologen* **46:** 20–25.

Warncke K. 1992. Die westpaläarktischen Arten der Bienengattung *Coelioxys* Latr. *Bericht der Naturforschenden Gesellschaft Augsburg* **53:** 31–77.

Westrich P. 1990. *Die Wildbienen Baden-Württembergs. Band. 1, 2*. Stuttgart: Eugen Ulmer Verlag.

SUPPORTING INFORMATION

Additional supporting Information may be found online in the supporting information tab for this article:

Table S1. List of important synapomorphies for the nodes. Female characters (0–161); Male characters (162–238).

Table S2. Character matrix used in the phylogenetic analyses of the genera *Coelioxys* and *Radoszkowskiana*.