

A revised genus-level classification for the Neotropical groups of the cleptoparasitic bee tribe Sphecodini Schenck (Hymenoptera, Apidae, Halictinae)

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ABSTRACT

Sphecodini are a clade of obligatory parasitic Halictinae, comprising 332 species and five genera worldwide. Recently, *Sphecodes* Latreille was considered polyphyletic according to the results of a molecular phylogeny. Morphological analysis of Neotropical groups revealed groups of species in *Sphecodes* s.l. that can be recognized at genus level to improve the classification of the tribe. The main objective of this study is to review the generic classification of Sphecodini, with emphasis on Neotropical groups. I propose *Austrosphecodes* Michener as a separate genus from *Sphecodes* s.s. and describe a new genus, *Melissoleptis* gen. nov. for eight known species. Both genera comprise most of the Neotropical species. *Nesosphecodes depressus* sp. nov. is described for Brazil and a revised diagnosis for *Nesosphecodes* Engel is given to accommodate this new species and to include data on male terminalia. A revised key for the genera from the Western Hemisphere is provided.

Introduction

Sphecodini Schenck are a clade of obligatory parasitic halictine bees related to the tribe Halictini (Danforth et al., 2008). Most studied species behave as cleptoparasites but a social parasite of *Dialictus* Robertson (Halictini) was studied by Eickwort and Eickwort (1972). The host range of the tribe includes several bee subfamilies (Michener, 1978). The tribal classification backbone was encompassed by Michener (1978) in his monograph on parasitic halictids and later in his book “Bees of the World” (Michener, 2000, 2007). Currently, the tribe comprises 332 species (compiled from Ascher and Pickering, 2020) distributed in five genera: *Eupetersia* Blüthgen, *Microsphecodes* Eickwort & Stage, *Nesosphecodes* Engel, *Ptilocleptis* Michener and *Sphecodes* Latreille. According to the only phylogeny for the group (Habermannová et al., 2013), *Sphecodes* s.l. is polyphyletic in relation to *Eupetersia* and *Microsphecodes*.

Eupetersia comprise 34 species from Africa and Oriental region distributed in two subgenera (Michener, 2007; Ascher and Pickering, 2020). This genus resembles *Microsphecodes* for the weak body punctuation, but it is related to the Holarctic species of *Sphecodes* according to Habermannová et al. (2013). The most reliable diagnostic

character for the genus is the relative elongation of F1, being subequal to F2 (Pauly, 2012).

The Neotropical *Microsphecodes* was originally described by Eickwort & Stage (1972) as a subgenus of *Sphecodes*. Michener (1978) elevated the group to genus status. Recently, Engel (2013) divided *Microsphecodes* in two subgenera, *Microsphecodes* s.s. and *Baeosphecodes* Engel. *Microsphecodes* s.s. (five species) occurs from Panamá to Brazil and has striate-foveolate metapostnotum and mesosoma with prominent pubescence, while *Baeosphecodes* (five species) occurs in the West Indies and has rugoso-striate metapostnotum and mesosoma with sparse pubescence (Engel, 2013). This genus can be separated from the remaining Sphecodini by the long free portion of the marginal cell and the shape of the first tergum (longer than broad). According to Michener's (1978) compilation its hosts are *Dialictus* and *Habralictus*. According to the results of Habermannová et al. (2013), *Microsphecodes* is nested within *Austrosphecodes*, a subgenus created by Michener (1978) in *Sphecodes* for a group of Neotropical species.

Nesosphecodes comprises three species from the Antilles (Engel, 2006a). The genus is quite similar to *Microsphecodes* and was separated by the longer mandibles, broader clypeus, and shorter length of free portion of marginal cell (Engel, 2006a, 2013). Nothing is known about

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its phylogenetic affinities and host species. Similarly, *Ptilocleptis* also comprises three species from the Neotropical Region (Michener, 1978). This is the most distinctive genus of the tribe due to moderate body punctation and pubescence, head and clypeus shape, transversally carinate pronotum (Michener, 1978, 2007). As for the previous genus, nothing is known about its phylogenetic affinities and host species.

Sphecodes is the largest genus of the tribe with 282 species and has a cosmopolitan distribution (Ascher and Pickering, 2020). This genus is quite variable and hard to diagnose when compared to the other genera, with its monophyly being frequently questioned (Engel, 2006b; Michener, 2007). Also, a total of 10 genus-group names are available for the group according to the synonymic list updated by Michener (2007). Michener (1978) recognized two subgenera, *Austrosphcodes* Michener and *Sphecodes* s.s. *Austrosphcodes* was originally diagnosed from *Sphecodes* s.s. by the lack of subapical tooth in the mandible, lack of conspicuous spinelike setae on hind tibiae, and lack of basitibial plate (Michener, 1978). Moure & Hurd (1987) followed this classification and cataloged 32 species of *Austrosphcodes*. But later, Michener (2000, 2007) opted not to consider the subgenera, a position followed by Moure (2007). Hosts of *Sphecodes* are distributed in several bee subfamilies and tribes according to Michener (1978). Following the phylogeny provided by Habermannová et al. (2013), *Austrosphcodes* is more related to *Microsphcodes* and not with the remaining *Sphecodes*.

The main objective of this study is to provide a revised classification of Sphecodini, with emphasis on Neotropical groups. *Eupetersia* and non-Neotropical groups of *Sphecodes* s.s. are beyond the scope of the present revision. This classification is based on morphological characters from females and males, taking into consideration the polyphyly of *Sphecodes* revealed by molecular data (Habermannová et al., 2013). I recognize *Austrosphcodes* as a separate genus from *Sphecodes* and describe a new genus, *Melissocleptis* gen. nov. A new species of *Nesosphcodes* is described from Brazil and a revised diagnosis for this genus is given to accommodate this new species and to include data on male terminalia. A revised key for the genera from the Western Hemisphere is provided.

Material and methods

Material mentioned here is deposited in the following institutions: Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah (BBSL), British Natural History Museum, London, England, U.K. (NHMUK), Coleção Entomológica Pe. Jesus Santiago Moure, Curitiba, Brazil (DZUP), Museo de La Plata, La Plata, Argentina (MLP), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP), University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, U.S.A. (KUNHM).

The species description was made following Engel (2006a) in order to facilitate the comparison. Structure terminology also follows Engel (2006a) except that here I refer to the basal area of propodeum as the metapostnotum. I use the abbreviations T1, T2, etc., to denote the metasomal terga; S1, S2, etc., to denote metasomal sterna; and F1, F2, etc., to denote the flagellomeres. Generic diagnosis terminology follows Eickwort (1969) and Michener (2007). All measurements are in millimeters. Interspaces among punctures (i) are given in relation to the puncture diameter (pd). Sculpturing terminology follows Harris (1979). For some sculpturing I use two terms to describe transitional patterns, as areolate rugose. For microsculpture, visible only in magnifications above 50x, I use the prefix micro-.

Most examinations were made with an Olympus SZ51 using white LED ring illumination. Measurements were made with Leica Stemi DV4 and a micrometric rule. Photographs were taken with a Nikon D700 with a 105 mm Sigma Macro lens using Helicon Remote for controlling image capture and with a Leica DFC 500 cam coupled with a Leica MZ16

stereomicroscope using the Leica Las 3D Viewer. Illumination followed the system of Kawada and Buffington (2016). Image stacking was made with Helicon Focus (version 6.0.18)—render method based on Method C (Pyramid). Final image adjustments (unsharp mask filtering, level control) were made with GIMP 2.8.16 (©The GIMP Team).

Results

Key to the Genera of the Sphecodini of the Western Hemisphere (modified from Michener, 2007)

1. Inner orbits of eyes strongly converging below; head little wider than long; clypeus about twice as broad as long; carina across pronotum, between dorsolateral angles, continuous; surface of S2 conspicuously convex in profile, its base strongly depressed, suggesting strong constriction between S1 and S2; body tomentum yellowish, *usually* dense and covering terga ***Ptilocleptis* Michener**
- Inner orbits of eyes usually not strongly converging; head distinctly wider than long, as seen in frontal view; clypeus three or more times as wide as long, rarely only twice as broad as long; carina between dorsolateral pronotal angles incomplete; surface of S2 usually not strongly convex in profile, apparent constriction between S1 and S2 being weak; body tomentum, *when present*, whitish, not dense nor covering terga 2
2. Free part of marginal cell at least three times as long as part subtended by submarginal cells; T1 slightly longer than broad; T5 with apical margin bare, like that of preceding terga ***Microsphcodes* Eickwort & Stage**
- Free part of marginal cell at most twice as long as part subtended by submarginal cells; T1 usually broader than long; T5 with margin hairier than that of preceding terga 3
3. Preoccipital ridge not carinate; anterior margin of mesoscutum in profile gently convex, not sharply differentiated from dorsal surface; head and thorax finely punctate; mandibles elongate; free part of marginal cell about twice as long as part subtended by submarginal cells ***Nesosphcodes* Engel**
- Preoccipital ridge carinate; anterior margin of mesoscutum abruptly declivous, well differentiated from dorsal surface; head and thorax usually coarsely pitted, *except* in small species (less than 6 mm); mandibles not elongate; free part of marginal cell less than twice as long as part subtended by submarginal cells 4
4. Female scape not reaching median ocellus (Fig. 1A). Male flagellum short, shorter than mesosoma length (Fig. 1B); male T7 pygidial plate broad (Fig. 1C) ***Melissocleptis* gen. nov.**
- Female with scape reaching median ocellus (Fig. 1D). Male flagellum long, as long as mesosoma length (Fig. 1E); male T7 pygidial plate narrow (Fig. 1F) 5
5. Female mandible bidentate *or* simple; with *or* without thick, short spinelike setae on posterior margin of hind tibia; hind tibial plate rudimentary (defined at least along posterior margin) *or* absent. Male second hind tarsal segment broader at the base than the third; genital capsule *variable* (North and Central America) ***Sphecodes* Latreille**
- Females always with the following combination: mandible simple; usually without tibial spinelike setae, *or* these setae as long as the plumose ones; hind tibial plate absent (not defined on posterior margin). Male second hind tarsal segment as narrow at the base as the third; gonocoxite not striate, gonapophyses narrow (South and Central America) ***Austrosphcodes* Michener, stat. nov.**

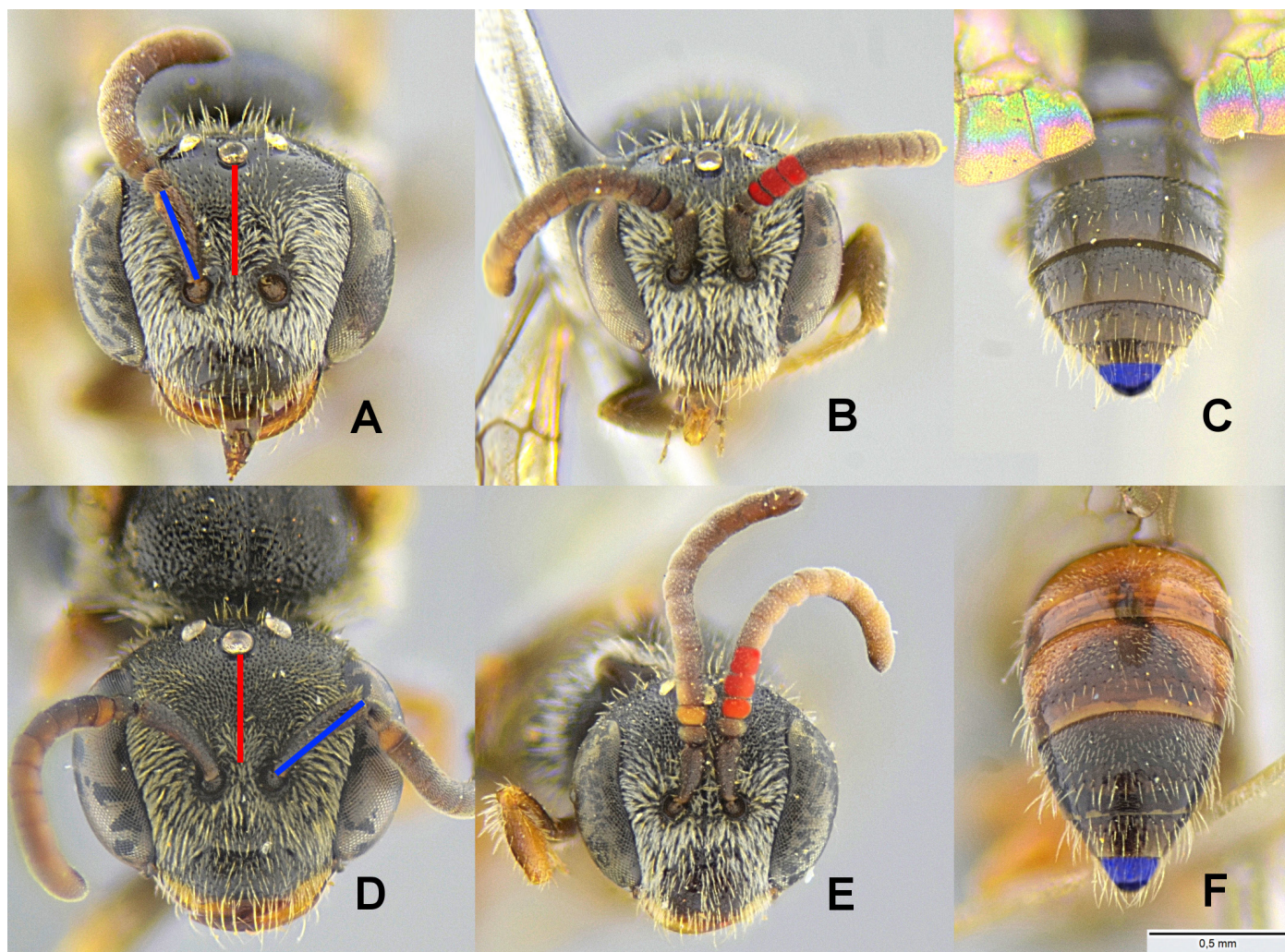


Figure 1 *Melissoleptis* gen. nov. and *Austrosphecodes*. A) *Melissoleptis capriciosus*, female head, colored bars indicating the scape and frons length, B) *M. capriciosus* male head, F1–3 colored; C) *M. capriciosa* male metasoma, pygidial plate indicated in blue; D) *Austrosphecodes brasiliensis*, female head, colored bars indicating the scape and frons length, E) *A. brasiliensis* male head, F1–3 colored; F) *A. brasiliensis* male metasoma, pygidial plate indicated in blue. All images under the same scale.

Taxonomy

Austrosphecodes Michener, stat. nov.

(Figures 1C–E, 2A)

Sphecodes subg. *Austrosphecodes* Michener, 1978. Type species: *Sphecodes chilensis* Spinola, 1851 by original designation.

Diagnosis. Females have coarse punctation overall (differently from *Eupetersia*, *Microsphecodes* and *Nesosphecodes*) and sparse body tomentum (differently from *Ptilocleptis*). The yellow markings are missing (differently from *Microsphecodes*) and the metasoma frequently has reddish color. Their clypeus is flattened with a longitudinal medial sulcus (differently from *Ptilocleptis*). Scape is long, reaching mid ocellus (differently from *Melissoleptis* gen. nov.), and the eyes are subparallel (differently from *Ptilocleptis*). Mandibles are simple (differently from most *Sphecodes*) and hypostomal ridge is not raised (differently from *Ptilocleptis*). F2 is not elongate in relation to F1 (differently from *Eupetersia*). The preoccipital ridge is carinate (differently from *Nesosphecodes*). The pronotal transverse carina is incomplete and the lateral ridge present (differently from *Ptilocleptis*). Mesoscutum anterior surface is abruptly delimited (differently from *Nesosphecodes* and some *Microsphecodes*). The free part of marginal cell is short (differently from *Microsphecodes* and *Nesosphecodes*). Spinelike setae and hind

basitibial plate are not developed (differently from most *Sphecodes*). The T1 width is broader than long, T5 is fimbriate (differently from *Microsphecodes*) and S2 is not convex (differently from *Ptilocleptis*). Males have long flagellum, usually as long as mesosoma; their T7 pygidial plate is narrow (differently from *Melissoleptis* gen. nov., *Ptilocleptis* and *Nesosphecodes*). The spicule of S7 is absent (differently from *Ptilocleptis* and *Nesosphecodes*) and the gonocoxites lack striae (differently from *Sphecodes*, *Melissoleptis* gen. nov. and *Nesosphecodes*). The gonapophyses are narrow and the ventral prong is absent (differently from *Melissoleptis* gen. nov.). The gonostyli have distinct lobes (differently from *Melissoleptis* gen. nov., *Ptilocleptis* and *Nesosphecodes*) and the internal setose patch is absent (differently from most *Sphecodes*, *Melissoleptis* gen. nov., *Eupetersia* and *Nesosphecodes*).

Comments. For additional comments to separate *Austrosphecodes* from *Sphecodes* see Michener (1978). The body size is variable among species, some of them quite small, with about 6 mm and resembling the species of *Melissoleptis* gen. nov. I did not examine the type species, *Sphecodes chilensis*, but follow the interpretation of Michener (1978) and unpublished notes of the type made by Moure that this species has the characteristics to diagnose the group.

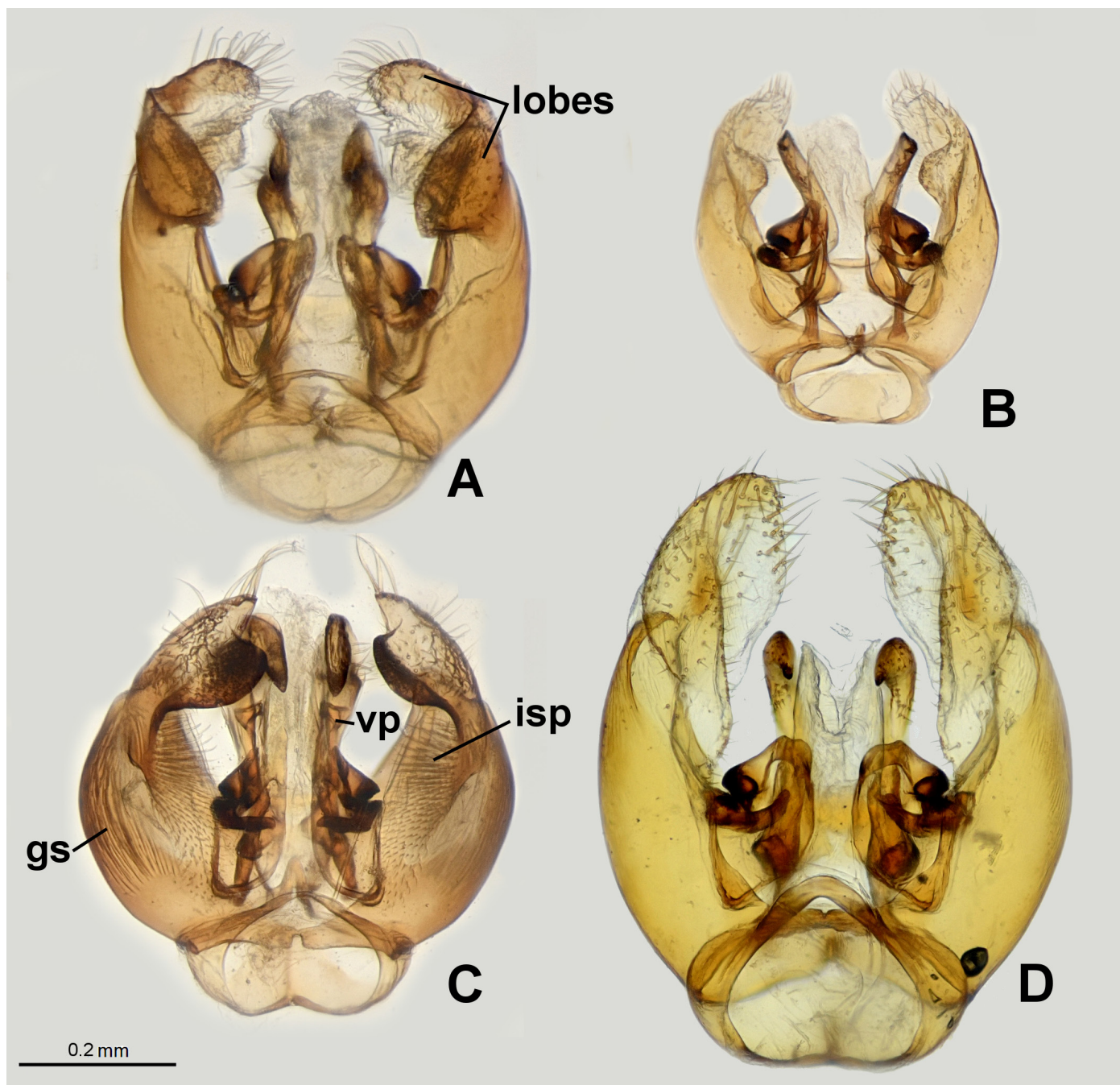


Figure 2 Sphecodini male genital capsule. A) *Austrosphecodes* sp., B) *Microsphecodes* sp., C) *Melissoleptis capriciosa*, D) *Ptilocleptis tomentosa*. Abbreviations: gs = gonocoxite striations, isp = gonostylus internal setose patch, vp = ventral prong. All images under the same scale.

Included species. The 29 valid names transferred to *Austrosphecodes* follows the subgeneric assignment of Moure & Hurd (1987) cross-referenced with Moure's Bee Catalog (Moure, 2007): *Austrosphecodes andinus* (Schrottky, 1906), *A. arequipae* (Meyer, 1925), *A. argentinus* (Schrottky, 1906), *A. bogotensis* (Meyer, 1922), *A. bonaerensis* (Holmberg, 1886), *A. brasiliensis* (Schrottky, 1910), *A. bruchi* (Schrottky, 1906), *A. chilensis* (Spinola, 1851), *A. convergens* (Michener, 1978), *A. cordillerensis* (Jorgensen, 1912), *A. friesei* (Herbst, 1908), *A. granulosus* (Sichel, 1865), *A. inornatus* (Schrottky, 1902), *A. joergenseni* (Meyer, 1920), *A. laetus* (Meyer, 1922), *A. lunaris* (Vachal, 1904), *A. melanopus* (Schrottky, 1906), *A. mendocinus* (Joergensen, 1912), *A. minarum* (Schrottky, 1910), *A. paraguayensis* (Schrottky, 1906), *A. patagonicus*

(Schrottky, 1906), *A. pallitarsis* (Vachal, 1909), *A. peruensis* (Meyer, 1925), *A. rufiscapis* (Vachal, 1909), *A. rugulosus* (Sichel, 1865), *A. vachali* (Meyer, 1925), *A. costaricensis* (Friese, 1916), *A. equator* (Vachal, 1904), *A. mutillaeformis* (Schrottky, 1906). The later three species have less than 6 mm and the possibility that they belong in *Melissoleptis* gen. nov. should be further investigated. Additional 11 Neotropical species (Moure, 2007) placed in *Sphecodes* s.s. according to Moure & Hurd (1987) should also be checked for correct generic placement.

Distribution. Chile to Mexico.

Melissoleptis gen. nov.

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(Figures 1A–C, 2C)

Type species: *Sphcodes coriae* Moure & Hurd, 1987.

Diagnosis. Females have moderate punctation overall (differently from most genera) and body tomentum sparse (differently from *Ptilocleptis*). Bees are mostly black and the yellow markings are missing (differently from *Microsphcodes*) and the metasoma frequently has reddish color. Their clypeus is flattened with a longitudinal medial sulcus (differently from *Ptilocleptis*). Scape is short, not reaching the mid ocellus (differently from all genera) and eyes subparallel (differently from *Ptilocleptis*). Mandibles are simple (differently from most *Sphcodes*) and hypostomal lamella is not raised (differently from *Ptilocleptis*). F2 is not elongate in relation to F1 (differently from *Eupetersia* and most *Nesosphcodes*). The preoccipital ridge is weakly carinate (differently from *Nesosphcodes*). The pronotal transverse carina is incomplete and the lateral ridge present (differently from *Ptilocleptis*). Mesoscutum anterior surface is abruptly delimited (differently from *Nesosphcodes* and some *Microsphcodes*). The free part of marginal cell is short (differently from *Microsphcodes* and *Nesosphcodes*). Spinellike setae on posterior margin of hind tibia are as long as nearby plumose setae (differently from most *Sphcodes* that have thick and short spinellike setae). Hind basitibial plate is not defined along posterior margin (differently from most *Sphcodes*). The T1 is broader than long, T5 is fimbriate (differently from *Microsphcodes*) and S2 is not convex (differently from *Ptilocleptis*). Males have short flagellum, shorter than mesosoma length, the T7 pygidial plate broad (similarly to *Ptilocleptis*). The spicule of S7 is absent (differently from *Ptilocleptis* and *Nesosphcodes*) and the gonocoxite is striate (similarly to some *Sphcodes* and *Nesosphcodes*). Gonapophyses are wide and the ventral prong is present (similarly to a few *Sphcodes* species). The gonostyli have reduced lobes (similarly to *Ptilocleptis* and *Nesosphcodes*) and the internal setose patch is present (similarly to most *Sphcodes*, *Eupetersia* and *Nesosphcodes*).

Description. Body punctation moderate except for rugose mesepisternum and propodeum, tomentum sparse, yellow markings absent, metasomal color varying from reddish to dark brown. Clypeus wide, longitudinal clypeal sulcus present. Scape short (not reaching mid ocellus). Eyes subparallel. Mandible simple. Hypostomal lamella short in height. Mouthparts with four subequal labial palpomeres and six maxillary palpomeres. F2 not elongate in relation to F1. Preoccipital ridge carinate. Pronotal transverse carina incomplete, lateral ridge present. Mesoscutum anterior surface abrupt. Free part of marginal cell short, usually with three submarginal cells. Tibial spinellike setae absent, hind basitibial plate absent. T1 broader than long. T5 fimbriate. S2 not convex. Male similar to female in general body features. T7 pygidial plate broad. Spicule of S7 absent. Gonocoxite striae present. Gonapophysis not narrow, ventral prong present. Gonostylus reduced to one lobe, internal setose patch present.

Etymology. Derived from the Greek, *melissa*, bee, and *kleptis*, thief, meaning robber bee. The name is feminine.

Comments. Species in this genus have small body size, rarely reaching 6 mm, with metapostnotum usually carinate, being similar to the smallest *Austrosphcodes* as *A. brasiliensis*. I include eight described species in this genus but probably more described and undescribed species are waiting to be added. It is interesting to note that the latest species described as *Sphcodes* from the West Indies belong to *Melissoleptis* gen. nov. (Engel, 2006b; Gibbs, 2016).

Distribution. Known records of the genus are from Argentina, Brazil, Chile (undetermined species), Costa Rica (identified as *Sphcodes costaricensis* Friese by Michener), Cuba, Dominica and Saint Vincent (Antilles), but probably the genus has a broader distribution in the Neotropical Region.

Melissoleptis albifacies (Gibbs, 2016), new combination

Sphcodes albifacies Gibbs, 2016. Holotype male (BBSL), from Dominica, St. Paul Parish, Springfield Estate.

Comments. According to the original description and associated images this species should be placed in *Melissoleptis* gen. nov. Genital capsule is typical of the new genus.

Distribution. Dominica.

Melissoleptis capriciosa (Schrottky, 1906), new combination

Sphcodes capriciosus Schrottky, 1906, syntype whereabouts unknown <M>, from Paraguay, Itapúa, Encarnación.

Comments. The females of this species lack a carina separating the posterior surface of the propodeum from its latero-dorsal surfaces and their frons is depressed above the supraclypeal area (also in males). Those characters are shared with other undetermined species from Argentina and Chile.

Distribution. Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, São Paulo, Santa Catarina), Paraguay.

Melissoleptis coriae (Moure & Hurd, 1987), new combination

Sphcodes (Austrosphcodes) coriae Moure & Hurd, 1987, new name for *Halictus meridionalis* Jörgensen, 1912, male lectotype (MLP), examined.

Comments. This species can be separated from other *Melissoleptis* gen. nov. from South America by the denser punctation on the mesoscutum, especially along its anterior margin where it is crowded. The species was redescribed by Gonçalves (2017).

Distribution. Argentina.

Melissoleptis diabolina (Gibbs, 2016), new combination

Sphcodes diabolinus Gibbs, 2016. Holotype male (BBSL), from Dominica, St. Paul Parish, Springfield Estate.

Comments. According to the original description and associated images this species should be placed in *Melissoleptis* gen. nov. Genital capsule as illustrated by Gibbs (2016) is typical of the new genus.

Distribution. Dominica.

Melissoleptis nigrita (Ashmead, 1900), new combination

Sphcodes nigritus Ashmead, 1900, holotype BMNH 17A.589 <M>, from Lesser Antilles, Saint Vincent. Examined through photographs.

Comments. Based on the images available in BMNH database, the type specimen has size, color and metapostnotum patterns of *Melissoleptis* gen. nov. This record is important to indicate that most Neotropical lineages of Sphecodini are distributed into the Antilles.

Distribution. Saint Vincent.

Melissoleptis genaroi (Engel, 2006), new combination

Sphcodes (Austrosphcodes) genaroi Engel, 2006, holotype SEMK <F> from Cuba, Pinar de Río, El Veral. Examined through photographs.

Comments. According to the original description and associated images this species should be placed in *Melissoleptis* gen. nov. Genital capsule is also typical of the new genus.

Distribution. Cuba.

Melissoleptis tainoi (Engel, 2006), new combination

Sphcodes (Austrosphcodes) tainoi Engel, 2006, holotype SEMK <F> from Cuba, Ciudad de La Habana, Marianao. Examined through photographs.

Comments. According to the original description and associated images this species should be placed in *Melissoleptis* gen. nov. Genital capsule is also typical of the new genus.

Distribution. Cuba.

Melissocleptis variabilis (Schrottky, 1906), new combination

Sphecodes variabilis Schrottky, 1906, syntype whereabouts unknown <M>, from Paraguai, Itapúa, Encarnación.

Comments. The females of this species have a sinuous carina contouring the posterior surface propodeum, giving it a somewhat stylized heart-shape, and their frons is not depressed above the supraclypeal area (also in males). *Microsphecodes coriae* also shares this condition, but its mesoscutum is more densely punctured. An undescribed species from northern Brazil (Belém, Pará) also has these features.

Distribution. Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, São Paulo, Santa Catarina), Paraguay.

Nesosphecodes Engel, 2006

Nesosphecodes Engel, 2006. Type species: *Nesosphecodes anthracinus* Engel, 2006 by original designation.

Diagnosis. Females have a fine punctation overall (differently from *Austrosphcodes*, *Melissocleptis* gen. nov. *Sphecodes*, and *Ptilocleptis*) and body tomentum sparse (differently from *Ptilocleptis*). The yellow markings are missing (differently from *Microsphecodes*) and the metasoma is rarely reddish brown. Their clypeus is flattened with a longitudinal medial sulcus (differently from *Ptilocleptis*). Scape is long, reaching mid ocellus (differently from *Melissocleptis* gen. nov.) and eyes subparallel (differently from *Ptilocleptis*). Mandibles are simple (differently from most *Sphecodes*) and the hypostomal lamella is not raised (differently from *Ptilocleptis*). F2 can be elongate in relation to F1, similarly to *Eupetersia*. The preoccipital ridge is rounded (differently from *Austrosphcodes*, *Eupetersia*, *Melissocleptis* gen. nov., some *Microsphecodes* and *Ptilocleptis*). The pronotal transverse carina is incomplete and the lateral ridge is absent (differently from most other genera). Mesoscutum anterior surface is gently convex (differently from most genera, similar to some *Microsphecodes*). The free part of marginal cell is about two times the portion in contact with the submarginal cells (similar to *Eupetersia*). Tibial spines and hind basitibial plate are absent (differently from most *Sphecodes*). The T1 is broader than long, T5 is fimbriate (differently from *Microsphecodes*) and S2 is not convex (differently from *Ptilocleptis*). Males have the T7 pygidial plate very weakly developed (differently from all genera). The spicule of S7 is developed (similarly to *Ptilocleptis*) and the gonocoxite is striate (similarly to some *Sphecodes*, and *Melissocleptis* gen. nov.). Gonapophyses are narrow and the ventral prong is present (similarly to *Melissocleptis* gen. nov.). The gonostyli have distinct lobes (similarly to *Ptilocleptis*) and the internal setose patch is present (similar to most *Sphecodes*, *Eupetersia* and *Melissocleptis* gen. nov.).

Comments. A revised diagnosis is necessary to accommodate the new species from Brazil, especially because it does not have an elongate F2 and its clypeus and mandibles are not as wide as those from the previously known species. These characteristics should be considered as distinctive of the Caribbean species. Engel (2006a) did not give information about terminalia and the male diagnosis is based only on the new species. The new species add a substantiation range extension to *Nesosphecodes*, but this can purely be seen as absence of records of the group, since other Neotropical Sphecodini, *Austrosphcodes*, *Microsphecodes*, and *Melissocleptis* gen. nov. have broad distributions.

Nesosphecodes depressus sp. nov.

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Diagnosis. Females can be separated from other species for the clypeus shape, produced apically (not produced in other species), the F2 as long as F1 (longer than F1 in other species), the depression on parocular area near antennal alveoli, and the orange colored terga.

Specimens, including males, have two or rarely three submarginal cells, while other species have three submarginal cells.

Description. Female. Total body length 5 mm; forewing length 3 mm. Head about as long as wide (width 1.5 mm, length 1.2 mm as measured from clypeal apex to vertex in frontal view). Clypeus apex broadly rounded with oblique lateral margins. Frontal line carinate from just below antennal toruli to half of distance to median ocellus, becoming an impressed line from that point onward. Mandibular base meeting lower border of compound eye. Upper and lower interorbital distances nearly equal but compound eyes slightly converging ventrally; inner margin of compound eye relatively straight. Parocular area depressed near torulus. Gena narrower than compound eye in profile. Scape length 0.6 mm; F1 as long as F2; distal flagellomere with inner apical half glabrous. Intertegular distance 1.0 mm. Basal vein distad cu-a by two times vein width; 1rs-m distad 1m-cu by vein width; 2rs-m distad 2m-cu by ten times vein width; first and second submarginal cells fused due to the absence of 2nd abscissa of Rs (weakly indicated in one paratype); anterior border of third submarginal cell nearly one-half length of posterior border; hind wing with distal hamuli arranged 3-2. Pygidial plate large and broadly rounded at its apex, margins (lateral and apical) lamellate. Clypeus weakly imbricate with weak punctures separated by a puncture width; remainder of head with minute punctures, i= 1-2 pd, integument between punctures microreticulate and shining, punctures weaker on vertex; postgena microreticulate and impunctate. Pronotum with minute punctures, i=1-3 pd, punctures of anteriolateral borders closer to each other, integument between punctures microreticulate. Mesoscutum with minute punctures, i=1-4 pd (Fig. 3), those of lateral and posterior borders with i =1-2 pd, integument between punctures smooth and shining; tegula translucent, smooth except inner border imbricate and minutely punctured; mesoscutellum nodulose, sculptured as on mesoscutum except that i=1-4 pd over entire surface. Metanotum areolate, integument in between smooth and shining. Anterior surface of mesepisternum rugulose; mesepisternum rugulose anteriorly and almost polished posteriorly; metepisternum rugulose, upper fourth carinate. Metapostnotum with lateral straight and two depressed central areolae, integument between striae smooth and shining; lateral and posterior surfaces of propodeum areolate except for broad, smooth basal triangle just above propodeal pit on posterior surface. Metasomal terga and sterna very sparsely and faintly punctulate.

Mandible dark reddish brown; labrum and mouthparts dark brown; remainder of head and mesosoma black and shining. Metasoma reddish brown, lighter on first two segments. Legs brown. Wing veins brown; wing membrane hyaline except on costal cell, yellowish.

Pubescence white except when indicated. Face with long, short branched setae on lower half with very few subappressed, highly-branched setae, shorter setae noticeably more dense on lower half of face and clypeus but not obscuring integument; upper half of face and vertex with less numerous, short, simple setae; some setae on vertex slightly fuscous. Setae on gena like those of vertex. Postgena almost glabrous except for few scattered long setae. Pronotum covered in long plumose setae, not obscuring integumental surface, such setae sparse anterior to pronotal lobe. Mesoscutum and mesoscutellum with scattered, short, simple setae, those on mesoscutellum more confined to posterior border where longer with more branches; tegula with minute setae on apical and inner borders. Metanotum with similar setae as to those on mesoscutellum except denser. Anterior surface of mesepisternum covered with long, plumose setae, largely obscuring integumental surface; mesepisternum with long, plumose setae becoming longer, more branched and more numerous ventrally; metepisternum with short, plumose setae dense on lower third and anterior border, sparse on posterior median border. Lateral and posterior surfaces of

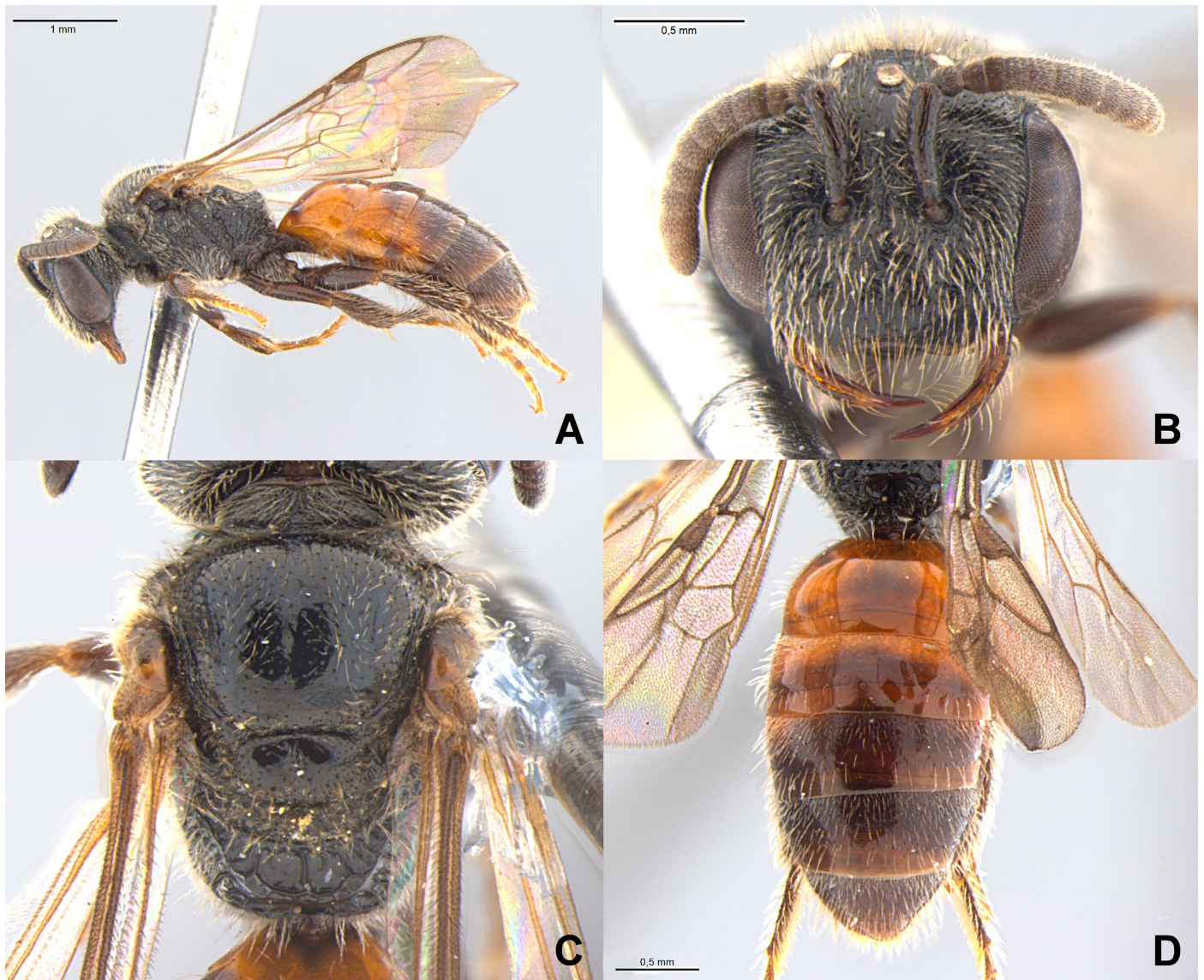


Figure 3 *Nesosphecodes depressus* sp. nov. Female Holotype. A) habitus, B) head in frontal view, C) mesosoma in dorsal view, D) metasoma in dorsal view. B and C under the same scale.

propodeum densely covered in long, plumose setae that do not obscure integumental surface. Metasomal T1 with simple, yellowish short setae on lateral borders; T2 with yellowish, minute, simple setae scattered on basal two-thirds, such setae longer laterally and denser and longer on marginal areas; T3–5 with similar setae as to those on T2 except longer and denser; T6 with setae with more branches and denser; sterna with scattered simple setae, also yellowish, short to long in length, longer setae generally scattered in apical halves; S6 densely clothed with long branched setae.

Male. As described for the female except total body length 4.8 mm; forewing length 3 mm. Head about as long as wide (width 1.33 mm, length 1.15 mm as measured from clypeal apex to vertex in frontal aspect). Scape length 0.3 mm. Intertegular distance 0.83 mm. On forewing 2nd abscissa of Rs present or absent Punctures of head denser than on female. Body pubescence shorter, unbranched on terga. Hidden terga and genital capsule as Fig 5.

Type material. Holotype female (DZUP): "INCT-HYMPAR\ BR: SP: São Luiz Paraitinga\ PESM Núcleo Santa Virgínia\ 23°19'23.6"S

45°05'21.8"O\ 22.iii.2010 Malaise ponto 5\ N.W. Perioto e eq. cols". Paratypes (one female and two males deposited in DZUP and one female and one male deposited in MZSP): "INCT-HYMPAR\ BR: SP: Ribeirão Grande\ Pq. Est. Intervalles\ 24°16'23.6"S 45°25'21.8"O\ 21(2).iv.2010 Malaise ponto 5\ N.W. Perioto e eq. cols"; one male (DZUP) "DZUP 548731" "Brasil, Paraná, Curitiba,\ UFPR, C. J. Botânico,\ -25.443472, -49.236524,\ 24.IV.2018, L. Graf".

Etymology. The specific epithet refers to the depression on parocular area, from Latin.

Discussion

The monophyly of *Sphecodes* s.l. was not recovered by the molecular phylogenetic analysis of Habermannová et al. (2013), who found the following topological relationships: ((*Austrosphecodes* in part+ (*Austrosphecodes* in part+ *Microsphecodes*))(*Sphecodes* s.s. + *Eupetersia*). This finding indicates the necessity to propose a new classification for the group. A first decision is to consider the

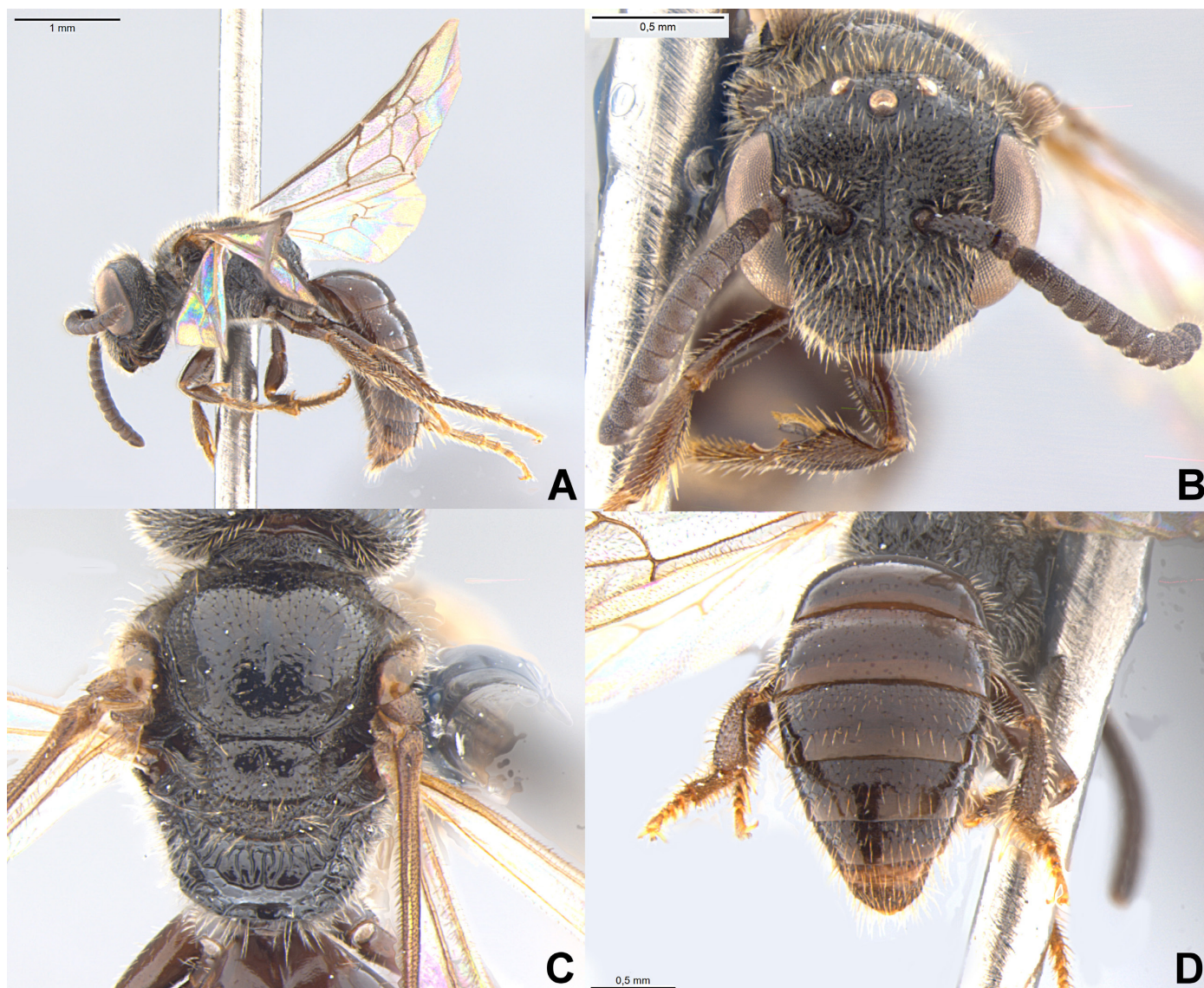


Figure 4 *Nesosphecodes depressus* sp. nov. Male Paratype. A) habitus, B) head in frontal view, C) mesosoma in dorsal view, D) metasoma in dorsal view. B and C under the same scale.

Neotropical group *Austrosphecodes* at generic status to make *Sphecodes* s.s. monophyletic. Both groups were recognized by former authors (Michener, 1978, Moure and Hurd, 1987) but later Michener (2000, 2007) opted to synonymize all genus-group names under *Sphecodes*, a position followed by subsequent authors. Habermannová et al. (2013) did not include all lineages of *Sphecodes* and its monophyly should be examined further, especially to investigate the possibility to subdivide the genus: there are 09 genus-group names available for it excluding *Austrosphecodes* (Michener, 2007); only three names were included on the available phylogeny. I did not have the opportunity to study material from these groups and cannot make statements about them. The second decision is to recognize two separate genera for the 32 species allocated under *Austrosphecodes* by the catalog of Moure and Hurd (1987). Habermannová et al. (2013) found that *Austrosphecodes* is paraphyletic with respect to *Microsphecodes* and I have presented here morphological evidence for recognizing two distinct groups in *Austrosphecodes* sensu Michener (1978). However, it is important to highlight that I did not examine the vouchers from Habermannová et al. (2013) study (after repeated image requests), so it is not possible to infer properly what lineages correspond to the genera circumscribed here.

Following this decision, the first group, representing *Austrosphecodes* proper, includes most Neotropical species and is characterized by the female scape reaching mid ocellus (Fig. 1D) and by features of male genital capsule (gonobase outer surface not striate, inner surface without internal setose patch, gonapophysis without ventral prong, gonostylus strongly divided into lobes, Fig. 2A). The second group, *Melissoleptis* gen. nov., is characterized by the female scape not reaching mid ocellus (Fig. 1A) and features of male genital capsule (gonobase outer surface striate, inner surface with internal setose patch, gonapophysis with ventral prong, gonostylus weakly divided into lobes, Fig. 2C). Despite other features mentioned in the diagnoses, species of *Austrosphecodes* vary in size and are similar to *Sphecodes* in body color and sculpturing while the species of *Melissoleptis* gen. nov. are small, having no more than 6 mm in body length, and being more similar to *Nesosphecodes*.

The features of the male genital capsule seem to provide important characters for phylogenetic analysis of the group. Some features were already mentioned by Michener (1978) but not properly explored by subsequent authors. The genital capsule of *Austrosphecodes* (Fig. 2A) is very similar to that of *Microsphecodes* (Fig. 2B), suggesting a close relationship. On the other hand, the genital capsule of *Melissoleptis*

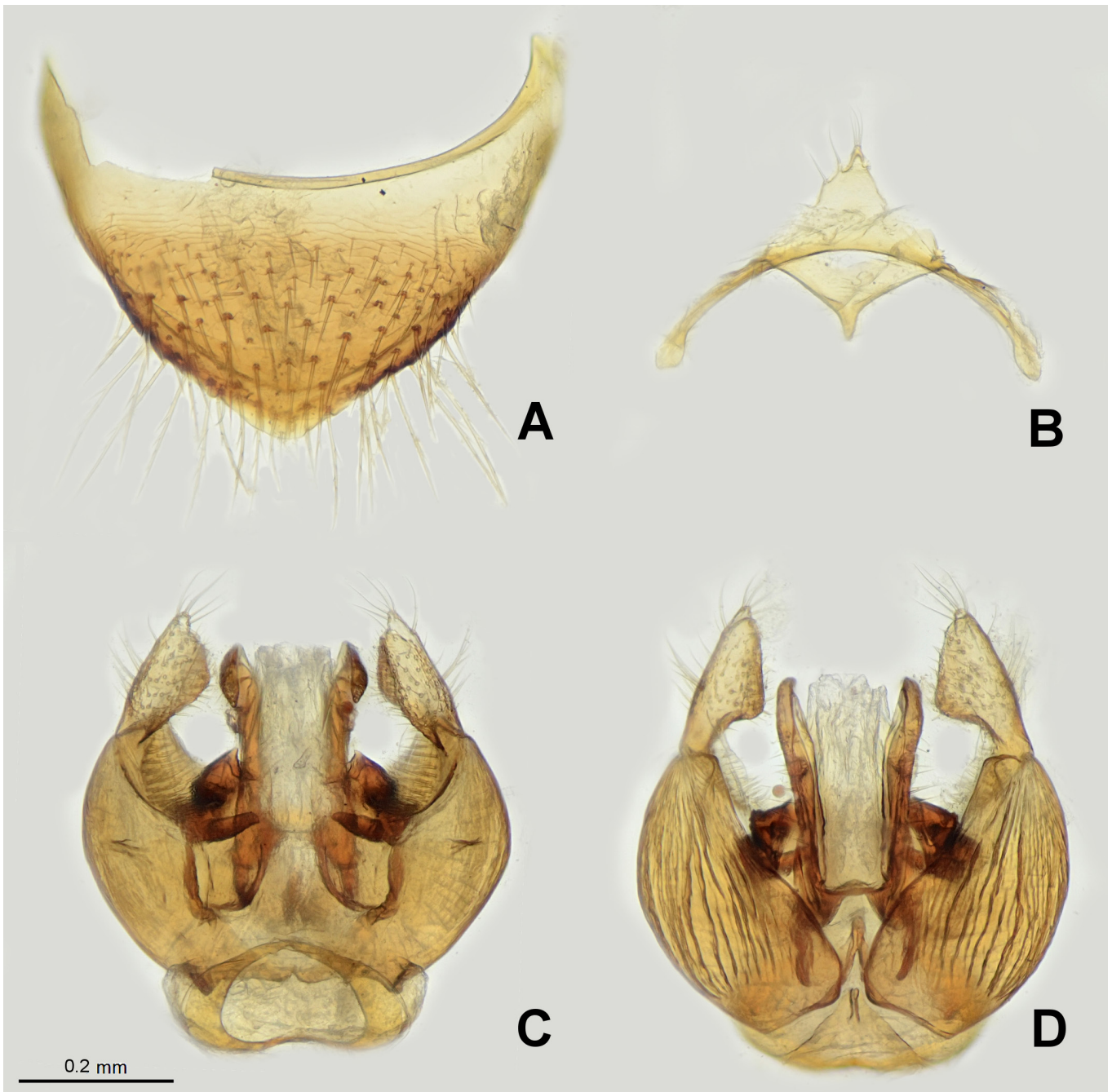


Figure 5 *Nesosphecodes depressus* sp. nov. Male Paratype. A) T6, B) S7 and S8, C) genital capsule, ventral view, D) genital capsule, dorsal view. All images under the same scale.

Table 1

Revised classification of Sphecodini. *Eupetersia* subgeneric classification follows Michener (1978), *Microsphecodes* subgeneric classification follows Engel (2013). Species number follows Ascher & Pickering (2020) with additions and modifications based on this study.

SPHECODINI	Species Number	Distribution
<i>Austrosphcodes</i> Michener, 1978	29	Neotropical
<i>Eupetersia</i> Blüthgen, 1928		
<i>Eupetersia</i> s.s.	24	African
<i>Nesoeupetersia</i> Blüthgen, 1936	10	African and Oriental
<i>Melissocleptis</i> gen. nov.	8	Neotropical
<i>Microsphecodes</i> Eickwort & Stage, 1972		
<i>Microsphecodes</i> s.s.	5	Continental Neotropical
<i>Baeosphecodes</i> Engel, 2013	5	West Indies
<i>Nesosphecodes</i> Engel	4	Neotropical
<i>Ptilocleptis</i> Michener, 1978	3	Neotropical
<i>Sphcodes</i> Latreille, 1804	245	All continents except Australia

gen. nov. (Fig. 2C) has some attributes shared with *Nesosphecodes* (Fig. 5C,D), such as the ventral prong of the gonapophyses. According to these findings it is plausible that these four Neotropical genera form a clade. The most intriguing open question is about the phylogenetic relationships of *Ptilocleptis*. This genus has a long list of particular features for both sexes (Michener, 1978, 2007) and could be sister to all remaining Sphecodini (as suggested by Michener, 2007) or more closely related to the remaining Neotropical genera. Table 1 summarizes the proposed classification of the tribe, currently composed by seven genera and 333 species, which should be tested under a phylogenetic perspective to validate the herein decisions.

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Conflicts of interest

The author declares no conflicts of interest

References

- Ascher, J. S., Pickering, J., 2020. Discover Life Bee Species Guide and World Checklist (Hymenoptera: Apoidea: Anthophila). Available in: <http://www.discoverlife.org/> (accessed 18 March 2020).
- Danforth, B. N., Eardley, C., Packer, L., Walker, K., Pauly, A., Randrianambinintsoa, F. J., 2008. Phylogeny of Halictidae with an emphasis on d endemic African Halictinae. *Apidologie (Celle)* 29, 86-101.
- Eickwort, G. C., 1969. A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: halictidae). *Univ. Kans. Sci. Bull.* 48, 325-524.
- Eickwort, G. C., Eickwort, K. R., 1972. Aspects of the Biology of Costa Rican Halictine Bees, III. *Sphecodes kathleena*, a Social Cleptoparasite of *Dialictus umbripennis* (Hymenoptera: halictidae). *J. Kans. Entomol. Soc.* 45 (4), 529-541.
- Eickwort, G. C., Stage, G. I., 1972. A new subgenus of neotropical *Sphecodes* cleptoparasitic upon *Dialictus* (Hymenoptera: Halictidae, Halictinae). *J. Kans. Entomol. Soc.* 45 (4), 500-515.
- Engel, M. S., 2006a. A new genus of cleptoparasitic bees from the West Indies (Hymenoptera: halictidae). *Acta Zool. Cracovi.* 49B (1-2), 1-8.
- Engel, M. S., 2006b. The *Sphecodes* of Cuba (Hymenoptera: halictidae). *Acta Zool. Cracovi.* 49B (1-2), 73-78.
- Engel, M. S., 2013. A new species of *Microsphecodes* from Peru, with notes on the classification of the genus (Hymenoptera: halictidae). *J. Melittology* 24, 1-9.
- Gibbs, J., 2016. Bees of the family Halictidae Thomson, 1869 from Dominica, Lesser Antilles (Hymenoptera: apoidea). *Eur. J. Taxon.* 180, 1-50.
- Gonçalves, R. B., 2017. Redescription of types of *Sphecodes* (*Austrosphecodes*) (Hymenoptera: Halictinae) from Argentina and Brazil. *Zootaxa* 4269 (4), 513-530.
- Habermannová, J., Bogusch, P., Straka, J., 2013. Flexible Host Choice and Common Host Switches in the Evolution of Generalist and Specialist Cuckoo Bees (Anthophila: sphecodes). *PLoS One* 8 (5), e64537. <https://doi.org/10.1371/journal.pone.0064537>.
- Harris, R. A., 1979. Glossary of surface sculpturing. *Occ. Pap. Entomol.* 28, 1-31.
- Kawada, R., Buffington, M. L., 2016. A scalable and modular dome illumination system for scientific microphotography on a budget. *PLoS One* 11, e0153426.
- Michener, C. D., 1978. The parasitic groups of Halictidae (Hymenoptera, Apoidea). *Univ. Kans. Sci. Bull.* 51, 291-339.
- Michener, C. D., 2000. The bees of the world, 1st ed. Johns Hopkins University Press, Baltimore, Maryland, 913 pp.
- Michener, C. D., 2007. The bees of the world. 2nd ed. Johns Hopkins University Press, Baltimore, Maryland, 953 pp.
- Moure, J. S., 2007. Halictini. In: Moure, J.S., Urban, D., Melo, G.A.R. (Org.), Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical Region, Sociedade Brasileira de Entomologia, Curitiba, xiv+1058 pp.
- Moure, J. S., Hurd P. D. Jr., 1987. An annotated catalog of the halictid bees of the Western Hemisphere (Hymenoptera: Halictidae), Smithsonian Institution Press, Washington, 405 pp.
- Pauly, A., 2012. Three new species of *Eupetersia* Blüthgen, 1928 (Hymenoptera, Halictidae) from the Oriental Region. *Eur. J. Taxon.* 14, 1-12.