

On the classification of sphecodine bees (Hymenoptera: Halictidae)

BY MICHAEL S. ENGEL

Division of Invertebrate Zoölogy, American Museum of Natural History, Central Park West at
79th Street, New York, New York 10024-5192, U.S.A.

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ABSTRACT

Taxonomic notes are presented for the exclusively cleptoparasitic halictine bee subtribe Sphecodina (Halictinae: Halictini). Keys are presented to the Western and Eastern Hemisphere genera of Sphecondina. In the New World fauna, the genus *Melissocleptis* Gonçalves is considered a subgenus of *Austrosphecodes* Michener *s.l.*, and the following species transferred: *Austrosphecodes* (*Melissocleptis*) *albifacies* (Gibbs), *A. (M.) capriciosus* (Schrottky), *A. (M.) coriae* (Moure & Hurd), *A. (M.) diabolitus* (Gibbs), *A. (M.) genaroi* (Engel), *A. (M.) nigrinus* (Ashmead), *A. (M.) tainoi* (Engel), *A. (M.) variabilis* (Schrottky) comb. n. A key is provided to the subgenera of *Microsphecodes* Eickwort & Stage *s.l.*, with *Trichosphecodes* subgen. n., established for those species with elongate ocular setae. Keys are also presented for the species of *Microsphecodes s.str.* and *Trichosphecodes*, along with the descriptions of the species *Microsphecodes* (*Microsphecodes*) *eickworti* sp. n., *M. (M.) multirugosus* sp. n., *M. (M.) quechua* sp. n., and *M. (Trichosphecodes) trichophthalmus* sp. n. The Brazilian species *Nesosphecodes depressus* Gonçalves is transferred to *Notoclops* gen. n., resulting in the new combination *Notoclops depressus* (Gonçalves) comb. n. A key is presented to New World subgenera of *Sphcodes* Latreille, with the following new or resurrected groups: *Proteraner* Robertson, *Drepanium* Robertson, *Sphcodium* Robertson, *Asphcodium* subgen. n., and *Boreosphcodes* subgen. n. The following new species are described among New World *Sphcodes*: *Sphcodes* (*Asphcodium*) *breviusculatus* sp. n., *S. (Sphcodium) eustaurus* sp. n., *S. (S.) electrum* sp. n., *S. (Sphcodes) zacatuche* sp. n. The genus *Caenosphcodes* gen. n. is proposed for *Sphcodes pseudoredivivus* Astafurova & Proshchalykin and *S. redivivus* Blüthgen, differing from *Sphcodes* by the elongate free part of the marginal cell, in this respect resembling New World *Microsphcodes*. This results in the combinations *Caenosphcodes pseudoredivivus* (Astafurova & Proshchalykin), *C. sauteri* (Meyer), *C. simlaensis* (Blüthgen), and *C. redivivus* (Blüthgen) comb. n. The currently employed characters for subgenera of *Eupetersia* Blüthgen *s.l.* fail to distinguish the groups. Accordingly, the key to subgenera is revised and the species newly organized as to subgenera. *Cephalosphcodes* subgen. n. is established for *Eupetersia macrocephala* Pauly and *E. mandibulata* Blüthgen, *Xanthocleptis* subgen. n. is proposed for *E. reticulata* (Benoist), and *Pollinicleptis* subgen. n. is erected for *E. nathani* Baker, *E. malayensis* (Blüthgen), *E. sabahensis* Pauly, and *E. singaporensis* Pauly. A new species of *Nesoeupetersia*, *E. dnophera* sp. n., is described from Sabah, Malaysia and a tentative key provided to species of the subgenus. *Thrausmus* Buysson and *Callosphcodes* Friese are treated as independent genera, and the latter considered close to *Melittocleptes* gen. n., with *Melittocleptes insularis* (Smith) comb. n. as type species. A key is presented to Old World subgenera of *Sphcodes*, with the following new or resurrected groups: *Proteraneropsis* subgen. n., *Paradrepanium* subgen. n., *Eusphcodes* subgen. n., *Sabulicola* Verhoeff, *Caenocleptes* subgen. n., *Xystoclops* subgen. n., *Callocleptes* subgen. n., and *Nomiocleptes* subgen. n.

Keywords: Apoidea, Halictinae, Sphecodina, cleptoparasite, taxonomy

INTRODUCTION

Bees of the halictine subtribe Sphecodina (Halictinae: Halictini) are obligate cleptoparasites of a diversity of other bees, ranging from various Halictinae (most hosts) to the short-tongued bee subfamilies Colletinae and Neopasiphaeinae

(Colletidae), Andreninae and Panurginae (Andrenidae), and even Dasypodainae (Melittidae) (Michener 1978, 2007; Michener, Breed & Bell 1979). Where most other parasitic Halictidae are specialized derivatives or relatives of various unrelated lineages [e.g., cleptoparasitic species of *Dialictus* Robertson, *Noctoraptor* Engel *et al.* among *Megalopta* Smith, *Temnosoma* Smith, *Echthralictus* Perkins & Cheesman (a synonym under *Homalictus* Cockerell), parasitic *Thrinchostoma* Saussure], the sphecodines are a diverse monophyletic group of parasites, not derived from amongst their hosts. They are also one of the more challenging groups of Halictinae, with many similar-looking species with sometimes broad distributions and a variety of different hosts for a single parasite. Most species are arranged in the genus *Sphecodes* Latreille and, given the challenging mosaic of characters across the lineage, many historical classifications have simply lumped all sphecodines into *Sphecodes* for a lack of clear patterns. Robertson (1903) was one of the first to attempt a supraspecific classification of the group [although Buysson (1900) predated him in proposing other genera, Buysson did not associate his genus with sphecodines and instead considered it allied to *Nomia* Latreille or *Lipotriches* Gerstacker], and it was followed by minor additions from Friese (1909), Bluthgen (1928a, 1928b), and Cockerell (1938), although most authors resorted to a retrograde organization whereby most taxa were simply lumped into a growingly diverse and complex genus *Sphecodes* (e.g., Meyer 1919a, 1919b; Bluthgen 1928a, 1928b; Cockerell 1938; Eickwort & Stage, 1972; Michener 1978, 2007). For the fauna of the Western Hemisphere two distinct clades were isolated from *Sphecodes* proper (Eickwort & Stage 1972; Michener 1978), and these were then joined by two others (Engel 2006b; Gonalves 2021). The far richer fauna of the Eastern Hemisphere, however, has continued to languish with only two lineages recognized – *Eupetersia* Bluthgen and *Sphecodes* – both overlapping in many features and each with currently ill-conceived infrageneric groups employed (Michener 2007). While regional treatments of species are exceptional and significantly aid the identification of species in Europe and much of Asia (e.g., Warncke 1992; Bogusch & Straka 2012; Astafurova, Proshchalykin & Schwarz 2018, 2020; Astafurova & Proshchalykin 2015, 2020), the sphecodines remain a largely intractable group for most melittologists and it has been challenging to identify putatively monophyletic subgroups that would be more manageable for revisionary work.

Building upon earlier treatments of sphecodines (e.g., Engel 2006a, 2006b, 2011, 2013), I present here various notes on the classification of the subtribe that have accumulated over the last 25 years and based on the examination of specimens in many collections throughout the world during that same period, but especially those in the American Museum of Natural History, the University of Kansas Natural History Museum, the Natural History Museum London, the Museum fur Naturkunde Berlin, the United States National Museum of Natural History (Smithsonian), and the California Academy of Sciences. It is hoped that these notes might stimulate more research into the relationships and biology of these remarkable bees. The classification presented herein is therefore merely meant as a first step toward a more robust and comprehensive organization.

MATERIAL AND METHODS

Morphological terminology follows Engel (2001) and Michener (2007), while the format for the descriptions follows the recent account of *Microsphecodes* Eickwort

& Stage by Mahlmann & Engel (2023: refer to that paper for an elaboration on methods), and generally abbreviated descriptions for all but the first species. Type material of the new species is deposited in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (SEMC), with some paratypes in the Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA (AMNH). Nomenclatural acts established herein are registered in ZooBank (www.zoobank.org) with LSID urn:lsid:zoobank.org:pub:7D4F730D-C13E-4679-B0FF-323B061A033F.

SYSTEMATICS

Subtribe Sphecodina Schenck

Sphecodina is one of five subtribes in the Halictini, the others being the diverse lineages Halictina and Gastrohalictina, the latter notable for the weakened distal wing veins, and the much smaller Thrinchostomatina¹ of the Afrotropical and Oriental regions and Mexalictina² of the southern Nearctic to Central America. The classification of the subtribe advocated herein is summarized in Table 1. For ease of use, the accounts that follow are segregated by broad geographic areas.

TABLE 1. CLASSIFICATION OF SPHECODINE BEES (HALICTINAE: HALICTINI: SPHECODINA)

Genus <i>Austrosphecodes</i> Michener <i>s.l.</i>	Genus <i>Caenosphecodes</i> n.
Subgenus <i>Austrosphecodes</i> Michener <i>s.str.</i>	Genus <i>Sphecodes</i> Latreille <i>s.l.</i>
Subgenus <i>Melissocleptis</i> Gonçalves	Subgenus <i>Proteraner</i> Robertson
Genus <i>Notoclops</i> n.	Subgenus <i>Proteraneropsis</i> n.
Genus <i>Microsphecodes</i> Eickwort & Stage <i>s.l.</i>	Subgenus <i>Eusphcodes</i> n.
Subgenus <i>Baeosphcodes</i> Engel	Subgenus <i>Sabulicola</i> Verhoeff
Subgenus <i>Trichosphcodes</i> n.	Subgenus <i>Boreosphcodes</i> n.
Subgenus <i>Microsphecodes</i> Eickwort & Stage <i>s.str.</i>	Subgenus <i>Sphecodes</i> Latreille <i>s.str.</i>
Genus <i>Nesosphcodes</i> Engel	= <i>Sphecodes</i> Mavromoustakis
Genus <i>Ptilocleptis</i> Michener	Subgenus <i>Caenocleptes</i> n.
Genus <i>Eupetersia</i> Blüthgen <i>s.l.</i>	Subgenus <i>Xystoclops</i> n.
Subgenus <i>Xanthocleptis</i> n.	Subgenus <i>Paradrepanium</i> n.
Subgenus <i>Eupetersia</i> Blüthgen <i>s.str.</i>	Subgenus <i>Drepanium</i> Robertson
= <i>Calleupetersia</i> Cockerell	= <i>Dialonia</i> Robertson
Subgenus <i>Cephalosphcodes</i> n.	= <i>Machaeris</i> Robertson
Subgenus <i>Nesoeupetersia</i> Blüthgen	Subgenus <i>Asphcodium</i> n.
Subgenus <i>Pollinicleptis</i> n.	Subgenus <i>Sphecodium</i> Robertson
Genus <i>Thrausmus</i> Buysson	= <i>Stelidium</i> Robertson
Genus <i>Callosphecodes</i> Friese	Subgenus <i>Callocleptes</i> n.
Genus <i>Melittocleptes</i> n.	Subgenus <i>Nomioleptes</i> n.

¹ Although Sakagami (1974) established the name using the incorrect stem, as Thrinchostomini (*nomen imperfectum*; recte Thrinchostomatini), I use the spelling where the name is corrected to the proper genitive derivation, as Thrinchostomatina. It is true that under the ICZN (1999) incorrect spellings of the stem of names proposed after 1999 are to be maintained (Art. 29.4); however, those prior to 1999 are to be maintained only if the form of the name is in prevailing usage (Art. 29.5), otherwise they should be corrected. Given that this name was established prior to 1999 (meaning Art. 29.4 does not apply), and that no 'prevailing usage' can be rightly justified since when the name has been used in the literature (which has been rare) both spellings have appeared (e.g., Pesenko 2004; Engel 2009; Dehon *et al.* 2014, 2017; Herhold *et al.* 2019) (meaning that Art. 29.5 cannot be defended), the name should therefore be corrected. Thrinchostomatina stands.

² **Mexalictina** Engel, *subtribus novum* (genus *typicum*: *Mexalictus* Eickwort, 1978, *hic designatus*); the diagnosis of the subtribe is identical to that of the type genus as outlined by Eickwort (1978) and supplemented by the absence of the facial 'foveae' bordering the compound eye found in Caenohalictini, the strong distal wing venation, metasomal terga I–IV typically without bands of pubescence (rarely present), and the epistomal sulcus acute to slightly obtuse. LSID: urn:lsid:zoobank.org:act:967E213F-9EA6-4A20-9FC0-91EF25D48AA7.

Western Hemisphere Sphecodina

Herein I recommend the recognition of six genera in the Western Hemisphere: *Sphecodes*, *Microsphecodes*, *Austrosphecodes* Michener, *Nesosphecodes* Engel, *Notoclops* gen. n., and *Ptilocleptis* Michener. I believe that there are good reasons to think that the recently established *Melissocleptis* Gonçalves is either synonymous with *Austrosphecodes* or at least best considered as subgeneric given that the distinctions between the two are exceptionally minor and the key to Neotropical sphecodines provided (Gonçalves 2021) contains some errors. By focusing solely on the Neotropical fauna, which may not be monophyletic relative to all Sphecodina and perhaps not even all *Sphecodes* s.l., some challenges were introduced. For example, the key (Gonçalves 2021) assumes that *Sphecodes* have a preoccipital carina (many do not, including within the Neotropical region), that the female scape reaches the median ocellus (in some it does not, notably some Malagasy species, and this character is quite continuous), and that the males have a narrow pygidial plate (in some it is quite broad, easily encompassing that of species placed in *Melissocleptis*, again notably so in some Holarctic and African species as well as others from different regions), and thus will lead to misconceptions regarding character combinations for *Sphecodes*. Furthermore, an elongate mandible was indicated as a feature of *Nesosphecodes* (which is certainly true), in contrast to mandibles that are not elongate in *Melissocleptis* (true), *Austrosphecodes* (true), and *Sphecodes* (actually variable, with several species bearing quite elongate mandibles). By looking more broadly at characters across *Sphecodes* outside of the Neotropical region one finds that *Melissocleptis* falls entirely within the circumscription of *Austrosphecodes* and significantly overlaps subsets of *Sphecodes*, even in the Neotropical fauna. Indeed, if one ignores the length of the female scape, length of the male antenna, and width of the male pygidial plate (all of which are actually variable within *Sphecodes* rather than fixed as the key implies), then the species will run to *Austrosphecodes* in Gonçalves's key (2021), noting, however, that the diagnosis of *Austrosphecodes* also overlaps many groups of *Sphecodes* as defined. This is not to say that the recognition of *Melissocleptis* was misguided. On the contrary, I fully believe the group is a necessary contribution to the subject, although it differs so minorly from *Austrosphecodes* that it seems more informative to treat it as a subgenus therein. Nonetheless, even the distinction of *Austrosphecodes* from *Sphecodes* s.l. remains poor and needs further evaluation.

The points raised above emphasize the heterogeneous and ill-defined nature of *Sphecodes*, which has largely become a wastebasket for all other sphecodines not placed in more properly circumscribed units. The mosaic of characters among sphecodines, particularly those historically and currently placed in *Sphecodes*, is complex. Several studies already have emphasized the need to more carefully explore this wide-ranging and diverse group of cleptoparasitic bees, noting the necessary removal of groups like *Austrosphecodes* from therein (e.g., Habermannová, Bogusch & Straka 2013; Gonçalves 2021). Regardless, when it comes to sphecodines and *Sphecodes* in particular, we still look through a glass darkly. Further clean-up will be needed and the account here is not meant to solve any of these challenges; indeed, it may well introduce new and unexpected hurdles, although it is sincerely hoped that this is not the case. Instead, the intended goal is that by providing some attempt at segregating these groups more finely this will stimulate the following future research: 1) more extensive treatments of sphecodine phylogeny to test the monophyly and relationships of the units; 2) careful surveys in

various regions of the world to improve sampling for most species (particularly Central America, Africa, and Indomalaya); 3) exploration of sphecodine biology; and 4) the ultimate construction of a robust subgeneric system for *Sphecodes* that will ease not only identification of the vast diversity but hopefully stimulate melittologists to tackle species-level revisions of monophyletic subsets over strictly, albeit helpful, faunal summations.

Key to New World genera of Sphecodina

- 1 Inner orbits of compound eyes usually not strongly converging; head distinctly wider than long, as seen in facial 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 metasomal sternum II usually not strongly convex in profile, apparent constriction between sterna I and II weak 2
- Inner orbits of compound 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 metasomal sternum II conspicuously convex in profile, its base strongly depressed, suggesting strong constriction between sterna I and II [Mexico to Bolivia and southeastern Brazil] *Ptilocleptis* Michener
- 2(1) Free part of marginal cell about or less than twice as long as part subtended by submarginal cells; metasomal tergum I usually broader than long; tergum V with margin more setose than that of preceding terga (*i.e.*, pre-pygidial fimbria present) 3
- Free part of marginal cell about or more than three times as long as part subtended by submarginal cells; metasomal tergum I slightly longer than broad; tergum V with apical margin bare, like that of preceding terga (*i.e.*, pre-pygidial fimbria absent) [Mexico to southern Brazil, Greater Antilles] *Microsphecodes* Eickwort & Stage *s.l.*
- 3(2) Anterior margin of mesoscutum in profile gently convex, not sharply differentiated from dorsal surface; head and mesosoma finely punctate; flagellomere II about twice as long as flagellomere I; free part of marginal cell about twice as long as part subtended by submarginal cells; preoccipital ridge rounded 4
- Anterior margin of mesoscutum abruptly declivitous, well differentiated from dorsal surface; head and mesosoma coarsely pitted; flagellomere II less than twice as long as flagellomere I; free part of marginal cell less than twice as long as part subtended by submarginal cells; preoccipital ridge variable, rounded to wholly or partly carinate 5
- 4(3) Flagellomere I broad, distinctly shorter than flagellomere II; clypeus exceptionally broad, apical margin scarcely extending below lower tangent of compound eyes, comparatively straight, lateral thirds scarcely slanting relative to medial third, thus forming a comparatively continuous straight margin between compound eyes; mandible of female longer than compound eye length; forewing with three submarginal cells; basal area of propodeum with fine radiating striae or rugae, without large areolae; metasoma black, concolorous with head and mesosoma [Greater Antilles] *Nesosphecodes* Engel
- Flagellomere I about as long as flagellomere II; clypeus not as broad as above, apical margin well below lower tangent of compound eyes, with lateral thirds sloping and converging apically to medial third, therefore not forming a continuous straight margin (typical of most other sphecodines); mandible of female slightly shorter than compound eye length; forewing typically with two submarginal cells, sometimes three submarginal cells; basal area of propodeum with fine rugae and large paramedial areolae; metasoma with basal terga reddish orange, blending to dark reddish brown and contrasting with head and mesosoma (coloration typical of *Sphecodes*) [Brazil] *Notoclops* gen. n.
- 5(3) Female always with combination of mandible simple, metabasitibial plate absent (neither defined anteriorly nor posteriorly), and usually without spinelike setae on retrodorsal margin of metatibia, or such setae as long as plumose setae; preoccipital ridge carinate; metatarsomere II of male as narrow at base as metatarsomere III; gonocoxite not striate, gonapophyses narrow [Central America to Chile and Argentina] *Austrosphecodes* Michener *s.l.*

- Mandible of female simple or with subapical tooth or angle; spinelike setae on retrodorsal margin of metatibia present or absent; metabasitibial plate typically obsolescent anteriorly and delimited posteriorly or entirely absent; preoccipital ridge variable, typically rounded; metatarsomere II of male broader at base than metatarsomere III; genital capsule variable [Alaska, USA and northern Canada to Central America] *Sphecodes* Latreille *s.l.*

Genus *Austrosphecodes* Michener, *s.l.*

Melissocleptis could render *Austrosphecodes s.str.* paraphyletic as the differences are comparatively minor and similar variation exists within *Sphecodes* where these same traits do not seem to unite natural groups. That does not mean that such characters do not do so within *Austrosphecodes* and so it is best to maintain the two subgenera, particularly as the recognition of *Melissocleptis* significantly aids identification of the Neotropical diversity. Once extensive phylogenetic work across all Sphecodina has been completed these groups can be properly evaluated and the potential need to synonymize *Melissocleptis* determined at that time.

Note that the gender of the name *Melissocleptis* is masculine, rather than feminine as cited by Gonçalves (2021), since Latin *cleptīs* is masculine, as is the Ancient Greek κλέπτῃς, from which it is derived. The same applies to the name *Ptilocleptis*, which was also wrongly cited as feminine (Michener 1978), and perhaps misled Gonçalves to consider his name similarly in gender.

The species once transferred to *Melissocleptis* (Gonçalves 2021) are here placed within a broader *Austrosphecodes*: *Austrosphecodes (Melissocleptis) albifacies* (Gibbs), *A. (M.) capriciosus* (Schrottky), *A. (M.) coriae* (Moure & Hurd), *A. (M.) diabolitus* (Gibbs), *A. (M.) genaroi* (Engel), *A. (M.) nigrinus* (Ashmead), *A. (M.) tainoi* (Engel), and *A. (M.) variabilis* (Schrottky), all comb. n.

Key to subgenera of *Austrosphecodes*

- 1 Scape of female reaching median ocellus; flagellum of male long, as long as mesosoma; pygidial plate of male narrow *Austrosphecodes* Michener *s.str.*
- Scape of female not reaching median ocellus; flagellum of male short, shorter than mesosoma; pygidial plate of male broad *Melissocleptis* Gonçalves

Genus *Microsphecodes* Eickwort & Stage *s.l.*

The genus *Microsphecodes* has been diagnosed in detail by Eickwort & Stage (1972: as a subgenus of *Sphecodes*) and Engel (2013), the latter of which also provided a key to the species of *Baeosphecodes* Engel. Here the organization of the genus is augmented once again to place those species with prominent ocular setae in their own subgenus.

Key to subgenera of *Microsphecodes* (revised from Engel 2013)

- 1 Basal area of propodeum striate-foveolate, posteriorly delimited by distinct, strong carina (Figs 3, 6, 9, 14); pubescence of mesosoma prominent, particularly on pleura [continental] 2
- Basal area of propodeum rugoso-striate, not delimited posteriorly by carina, instead posterior angle rounded; pubescence of mesosoma sparse, particularly on pleura [Caribbean] *Baeosphecodes* Engel

- 2(1) Setae of compound eye absent or scarcely visible [Mexico to southern Brazil] *Microsphecodes* Eickwort & Stage *s.str.*
 – Setae of compound eye prominent, longer than two ommatidial diameters (Fig. 13) [Colombia to Bolivia] *Trichosphecodes* subgen. n.

Subgenus *Microsphecodes* Eickwort & Stage *s.str.*

***Microsphecodes (Microsphecodes) multirugosus* sp. n.**

(Figs 1–3)

Diagnosis: The new species is most similar to *M. stenochorus* Engel from Peru but differs from it in the colour of the mesosoma, the irregular rugosostriae of the basal area of the propodeum, and in the forewing 3Rs distinctly shorter than 4Rs, with r-rs about as long as 3Rs.

Description

♀: Total body length 5.20mm; forewing length 3.90mm. Head broader than long, width 1.42mm, length 1.13mm (as measured from clypeal apex to vertex in facial view). Mandible long, without subapical tooth. Clypeus width 2.8× medial length, width 0.70mm, medial length 0.25mm, with a faint apical depression. Frontal line carinate from lower tangent of antennal toruli to median ocellar diameter from median ocellus. Upper interorbital distance 0.88mm; lower interorbital distance 0.78mm; inner margin of compound eye slightly emarginate above level of antennal toruli. Gena more than one half as wide as compound eye in profile. Intertergular distance 0.78mm. Mesoscutellum without mediolongitudinal depression, uniformly convex. Inner metatibial spur simple, finely serrate. Hind wing with six distal hamuli arranged in a single series.

Integument shiny. Clypeus smooth with shallow punctures separated by less than a puncture width, those centrally larger and closer than those laterally; supraclypeal area smooth with punctures as on clypeus except sparser; remainder of head smooth and densely punctate, although punctures more spaced in ocellular area and sparse on vertex, particularly posterior and between ocelli; gena smooth with minute punctures separated by 1–3× a puncture width; postgena impunctate. Mesoscutum smooth to faintly imbricate with punctures separated by 2–5× a puncture width, sparser medioanteriorly and denser outside of parapsidal lines, separated by 0.5–1× a puncture width; mesoscutellum smooth and almost impunctate over disc, with minute punctures along anterior border separated by about a puncture width; metanotum smooth with shallow, nearly contiguous punctures. Pleura minutely rugulose. Basal area of propodeum rugosostriate, rugae-striae largely radiating from basal margin but interconnecting centrally and therefore without distinct areolae, particularly on either side of midline (Fig. 3), integument between rugae smooth and shining; lateral and posterior surfaces of propodeum rugosostriate-foveolate with irregular rugae (Fig. 3). Metasomal terga smooth, virtually impunctate except sparse minute punctures associated with setal bases.

Mandible orange testaceous, with reddish apex; labiomaxillary complex brown, labrum and clypeus yellowish orange, scape yellow, pedicel brown, flagellum dark brown, remainder of head dark brown to black (Fig. 2). Mesosoma yellowish orange except mesoscutum dark brown to black except yellowish medioanteriorly, above pronotal lobe, and thin margin bordering tegula; tegula semitranslucent yellow. Wing veins brown to dark brown; wing membrane hyaline (Fig. 1). Legs yellowish orange. Metasomal tergum I largely orange testaceous, with brown apically, tergum II largely brown except orange testaceous or orange brown basally, remaining terga brown to dark brown; sterna I–II yellowish orange, sternum III as on basal sterna except apically brown, remaining sterna brown.

Pubescence relatively sparse, fine, generally white except tinged yellowish on clypeus, pronotum, mesoscutellum, legs, and tinged yellowish brown on metasomal apex. Setae generally erect with minute branches, some simple; face with dense, decumbent, short, plumose setae, particularly on lower face (Fig. 2); mesosomal dorsum with scattered, erect, largely simple setae. Metasomal terga I and II almost glabrous, except long lateral setae, remaining terga uniformly and finely setose.

♂: *Latet.*

Material examined

Holotype, ♀, ECUADOR: Sucumbios, Sacha Lodge, 0.5°S, 76.5°W, 270m, 14–24-III-1994, Hibbs, ex: Malaise (SEMC).

Etymology: The specific epithet is a combination of the Latin adjectives *multus* (meaning, ‘many’) and *rūgōsus* (meaning, ‘wrinkled’).

ZooBank LSID: urn:lsid:zoobank.org:act:C51310FB-B0B7-46CB-8DAF-95E3FA41EBF6.



Figs 1–3. — *Microsphecodes (Microsphecodes) multirugosus* sp. n., holotype, ♀, from Sucumbíos, Ecuador: 1, Lateral habitus; 2, Facial view; 3, Basal area of propodeum.

***Microsphecodes (Microsphecodes) eickworti* sp. n.**
(Figs 4–6)

Diagnosis: This species is most similar to *M. truncaticaudus* Michener from neighbouring Colombia but can be distinguished by the distinct and large areolae bordering the midline of the basal area of the propodeum (Fig. 6).



Figs 4–6. — *Microsphecodes (Microsphecodes) eickworti* sp. n., holotype, ♀, from Darien, Panamá: 4, Lateral habitus; 5, Facial view; 6, Basal area of propodeum.

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 4.87mm; forewing length 3.93mm. Head broader than long, width 1.37mm, length 1.07mm (as measured from clypeal apex to vertex in facial view). Mandible long, without subapical tooth. Clypeus width 3× medial length, width 0.67mm, medial length 0.22mm, with a faint apical depression. Frontal line carinate from lower tangent of antennal toruli to about frons midlength. Upper interorbital distance 0.88mm; lower interorbital distance 0.78mm. Gena about one half as wide as compound eye in profile. Intertegular distance 0.87mm. Hind wing with five distal hamuli.

Clypeus smooth with coarse, shallow punctures separated by less than a puncture width; supraclypeal area smooth with punctures as on clypeus except smaller and more well-defined; remainder of head smooth with punctures separated by less than a puncture width, punctures more spaced in ocellocular area and on vertex; gena smooth with minute punctures separated by 0.5–1× a puncture width. Mesoscutum smooth with punctures separated by 1–4× a puncture width, sparser medioanteriorly and smaller and denser along posterior border, scarcely denser outside of parapsidal lines; mesoscutellum smooth and almost impunctate over disc, with minute punctures along midline and along anterior and posterior borders. Pleura smooth with punctures separated by a puncture width or less, particularly anteriorly and dorsally; hypopimeral area longitudinally rugulose. Basal area of propodeum rugosostriate, rugae comparatively weak and incomplete medially, forming large areolae on either side of midline (Fig. 6), integument between rugae smooth and shining; lateral and posterior surfaces of propodeum rugosostriate-foveolate with irregular rugae (Fig. 6).

Mandible yellowish orange, with reddish apex; labiomaxillary complex dark brown, labrum dark brown, scape dark brown, pedicel brown, flagellum lighter brown, remainder of head black (Figs 4, 5). Mesosoma black (Figs 4, 6) except tegula semitranslucent brown. Legs yellowish orange except procoxa dark brown, meso- and metacoxae brown. Metasoma yellowish orange except diffusely brown on disc of tergum I (Fig. 4).

♂: *Latet.*

Material examined

Holotype, ♀, PANAMA: Darien, Cana Biological Station, Serrania de Pirre, 1250m, 7°45'18"N, 77°41'6"W, 7 Jun 1996, J. Ashe, ex: flight intercept trap (SEMC).

Etymology: The specific epithet honours George Campbell Eickwort (1940–1994), former friend and mentor who introduced me to many fascinating lineages of halictines and who described, along with Gerald Irving Stage (1935–2014), the genus *Microsphecodes*. The day before George died we went collecting north of Ithaca, New York and dug nests of *Dialictus* on what can only be described as an idyllic summer day. We laughed, found many sweat bees, and had a grand time. He is missed.

ZooBank LSID: urn:lsid:zoobank.org:act:2841CD1C-AB97-445D-BC79-43DE96B9F95C.

***Microsphecodes (Microsphecodes) quechua* sp. n.**
(Figs 7–9)

Diagnosis: This species is most similar to *M. russeiclypeatus* (Sakagami & Moure) from southeastern Brazil but can be distinguished by the darker coloration of the mesoscutellum (Fig. 9) and the shorter scape (Fig. 8), which in *M. russeiclypeatus* extends to the outer margin of the compound eyes.

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 4.67mm; forewing length 3.87mm. Head broader than long, width 1.45mm, length 1.15mm (as

measured from clypeal apex to vertex in facial view). Mandible long, without subapical tooth. Clypeus width $3.8\times$ medial length, scarcely projecting below lower tangent of compound eyes (Fig. 8), width 0.88mm, medial length 0.23mm, with a faint apical depression. Upper interorbital distance 0.95mm; lower interorbital distance 0.92mm; inner margin of compound eye faintly emarginate above level of antennal toruli. Intertergular distance 0.83mm. Hind wing with five distal hamuli.

Clypeus smooth with minute punctures separated by $1\text{--}2.5\times$ a puncture width; supraclypeal area smooth with punctures as on clypeus except with distinct impunctate patch near border with



Figs 7–9. — *Microsphecodes* (*Microsphecodes*) *quechua* sp. n., holotype, ♀, from Tambopata, Perú: 7, Lateral habitus; 8, Facial view; 9, Basal area of propodeum.

clypeus; remainder of head smooth and densely punctate, although punctures more spaced in ocellular area and sparse on vertex, particularly posterior and between ocelli; gena smooth with minute punctures separated by 1–3× a puncture width; postgena impunctate. Mesoscutum smooth with small punctures sparse centrally, becoming closer laterally and posteriorly where separated by 1–3× a puncture width; mesoscutellum smooth and almost impunctate over disc, with minute punctures in mediolongitudinal strip and along borders where separated by about 1–1.5× a puncture width; basal area of propodeum rugosostriate, rugae-striae radiating from basal margin, with distinct and large areolae on either side of midline (Fig. 9), integument between rugae smooth and shining; lateral and posterior surfaces of propodeum rugosostriate-foveolate.

Mandible orange testaceous, with reddish apex; labrum and clypeus yellowish orange, scape yellowish orange, pedicel brown, flagellum dark reddish brown, remainder of head dark brown to black (Fig. 8). Mesosoma orange to reddish orange except mesoscutum, mesoscutellum, and much of mesepisternum dark reddish brown; tegula semitranslucent yellow. Wing veins brown to dark brown; wing membrane hyaline. Legs yellowish orange. Metasomal tergum I largely orange, remaining terga brown to dark brown except tergum II with orange basally; sterna I–II orange, with apical areas of brown, remaining sterna dark brown.

♂: *Latet*.

Material examined

Holotype, ♀, PERU: Tambopata Prov., 15km NE Pto. Maldonado, 20 June 1989, 200m, J. Ashe, R. Leschen, ex: flight intercept (SEMC).

Etymology: The specific epithet is the name of the indigenous language family spoken by Quechuan peoples. The name is treated as a noun in apposition.

ZooBank LSID: urn:lsid:zoobank.org:act:2FD7B67B-D202-4A0F-9C48-578DA824C9DF.

Key to species of *Microsphcodes s.str.*

(females only; revised from Mahlmann & Engel 2023)

- 1 Head and mesosoma entirely dark brown to black except pronotal lobe sometimes testaceous or ferruginous 2
- Head dark brown or black with clypeus largely to entirely orange, orange red, or testaceous; mesosoma with large areas of orange, orange-red, or testaceous integument, particularly on pronotum, mesoscutellum, and metanotum, such areas sometimes infusate 3
- 2(1) Basal area of propodeum with areolae bordering midline not greatly enlarged relative to neighbouring areolae [Colombia] *M. truncaticaudus* Michener
- Basal area of propodeum with areolae bordering midline greatly enlarged [Panama] *M. eickworti* sp. n.
- 3(1) Basal area of propodeum with areolae on either side of midline distinctly enlarged relative to those between radiating striae (sometimes with incomplete rugae within the enlarged areolae) 4
- Basal area of propodeum with areolae on either side of midline narrow, more similar in size relative to those between radiating striae 7
- 4(3) Mesoscutum reddish brown, dark brown, or black; clypeus exceptionally broad, 3.5× or more as wide as medially long 5
- Mesoscutum orange testaceous (Figs 2, 4); clypeus 3× as wide as long [Amazonian Brazil] *M. amazonophilus* Mahlmann & Engel
- 5(4) Mesoscutellum orange to infusate testaceous 6
- Mesoscutum dark reddish brown [Peru] *M. quechua* sp. n.
- 6(5) Mesoscutellum orange-red; clypeus 3.5–4× as wide as medially long [Costa Rica, Colombia] *M. kathleenae* (Eickwort)
- Mesoscutellum infusate testaceous; clypeus 4.5× as wide as medially long [southeastern Brazil] *M. russeiclypeatus* (Sakagami & Moure)

- 7(3) Basal area of propodeum with striae comparatively regular; mesoscutum laterally, medioanteriorly, and medioposteriorly orange-red, remainder of surface pitch black with thickened H-shaped appearance; pleura with patches of dark brown to black; forewing r-rs shorter than 3Rs, 3Rs and 4Rs about equal [Peru] *M. stenochorus* Engel
- Basal area of propodeum with rugosostriae irregular, particularly medially (Fig. 3); mesoscutum dark brown except yellowish brown medioanteriorly and thinly laterally; pleura entirely yellowish orange; forewing r-rs about as long as 3Rs, 3Rs distinctly shorter than 4Rs [Ecuador] *M. multirugosus* sp. n.

***Trichosphecodes* subgen. n.**

Type species: Microsphecodes (Trichosphecodes) trichophthalmus sp. n. (*vide infra*).

Diagnosis: Setae of compound eye prominent, longer than two ommatidial diameters (Figs 12, 13); pubescence of mesosoma and metasoma generally sparse although setae of pleura fine and numerous; basal area of propodeum striate-foveolate, with areolae bordering midline enlarged (Fig. 14), posteriorly delimited by distinct, strong carina (Fig. 14).

Etymology: The new subgeneric name is a combination of Ancient Greek *trikhós* [τρίχός, genitive of *thríx* (θρίξ, meaning, 'hair')] and *Sphecodes* Latreille [itself a combination of the genitive of *sphḗx* (σφήξ, meaning, 'wasp') – *sphēkós* (σφηκός) – and the suffix *-ódēs* (–ώδης, meaning, 'like' or 'full of')]. The name refers to the prominent setation of the compound eyes. The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:4949D700-82D9-475B-8ADC-3912FA9DA5F8.

***Microsphecodes (Trichosphecodes) trichophthalmus* sp. n.**
(Figs 10–14)

Diagnosis: The new species is quite similar to *M. trichommus* Michener from Colombia but differs in the short first flagellomere (flagellomeres I and II are similar to each other in *M. trichommus*), the orange clypeus contrasting with the dark brown supraclypeal area (clypeus and supraclypeal area concolorous and dark brown in *M. trichommus*), the fine and minute punctures of the clypeus (punctures coarse and drawn apically in *M. trichommus*), and the mesosoma with extensive areas of orange (almost wholly dark brown to black in *M. trichommus*).

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 5.73mm; forewing length 4.47mm. Head broader than long, width 1.63mm, length 1.28mm (as measured from clypeal apex to vertex in facial view). Mandible long, without subapical tooth. Clypeus width 3.1× medial length, width 0.87mm, medial length 0.28mm, with a faint apical depression. Frontal line carinate from lower tangent of antennal toruli to midpoint to median ocellar diameter. Upper interorbital distance 1.08mm; lower interorbital distance 1.08mm; inner margin of compound eye slightly emarginate above level of antennal toruli. Intertegular distance 0.95mm. Hind wing with six distal hamuli arranged in a single series.

Clypeus smooth with small punctures separated by a puncture width or less (denser in paratype); supraclypeal area smooth with punctures as on clypeus; remainder of head smooth and densely punctate, although punctures more spaced in ocellular area and sparse on vertex, particularly posterior and between ocelli; gena smooth with minute punctures separated by a puncture width; postgena impunctate. Mesoscutum smooth with punctures sparse centrally, denser laterally and posteriorly, around and outside parapsidal lines separated by 0.5–1× a puncture width; mesoscutellum smooth and almost impunctate over disc, with minute punctures

along borders separated by about a puncture width or less; metanotum smooth with shallow, nearly contiguous punctures. Pleura minutely rugulose. Basal area of propodeum rugosostriate, rugae-striae radiating from basal margin with large areolae on either side of midline (Fig. 14), integument between rugae smooth and shining; lateral and posterior surfaces of propodeum rugosostriate-foveolate.

Mandible orange, with reddish apex; labiomaxillary complex brown, labrum and clypeus orange, scape and pedicel yellowish orange, flagellum brown except flagellomere I lighter, remainder of head dark black. Mesosoma largely reddish orange except mesoscutum with



Figs 10–11. — *Microsphecodes* (*Trichosphecodes*) *trichophthalmus* sp. n., holotype, ♀, from Cochabamba, Bolivia: 10, Lateral habitus; 11, Dorsal habitus.



Figs 12–14. — *Microsphecodes (Trichosphecodes) trichophthalmus* sp. n., holotype, ♀, from Cochabamba, Bolivia: 12, Facial view; 13, Expanded detail of ocular setae; 14, Basal area of pronotum, metanotum, and mesoscutellum.

extensive reddish brown as in Fig. 11 and pleura largely reddish brown; tegula semitranslucent yellow. Wing veins brown to dark brown; wing membrane faintly infumate apically, otherwise hyaline. Legs largely yellowish orange except darker on coxae, metatrochanter, metafemur (except apex lighter), and metatibia brownish. Metasomal tergum I largely orange, with brown apically, tergum II largely brown except orange basally, remaining terga dark brown; sterna I–II orange to reddish orange with brown apically, remaining sterna brown.

♂: *Latet.*

Material examined

Holotype, ♀, BOLIVIA: Cochabamba, Cochabamba, 67.5km NE- Est. Biol. Valle del Sajita, Univ. de San Simón, 300m, 17°6'33"S, 64°47'52"W, 9–13 Feb 1999, R. Hanley, ex: flight intercept trap (SEMC).

Paratype, 1♀, BOLIVIA: Cochabamba, Cochabamba, 67.5km NE, Est. Biol. Valle del Sajita, Univ. de San Simón, 300m, 17°6'33"S, 64°47'52"W, 9–13 Feb 1999, F. Genier, ex: flight intercept trap (AMNH).

Etymology: The specific epithet is a combination of the Ancient Greek *τρίχος* (*trikhós*, genitive singular of *θρίξ* / *thrix*, meaning, 'hair') and the noun *ὀφθαλμός* (*ophthalmós*, meaning, 'eye').

ZooBank LSID: urn:lsid:zoobank.org:act:A612ED57-1476-414B-851C-565956DDA96F.

Key to species of *Trichosphecodes* (females only)

- 1 Mesosoma dark brown to black except orange on pronotal lobe and pronotal collar; clypeus dark brown, concolorous with supraclypeal area; clypeus with coarse, shallow punctures typically drawn out apically; flagellomere I nearly as long as flagellomere II [Colombia] *M. trichommus* Michener
- Mesosoma with extensive areas of orange; clypeus orange, contrasting with supraclypeal area and remainder of head; clypeus with distinct, minute punctures; flagellomere I distinctly reduced compared to flagellomere II [Bolivia] *M. trichophthalmus* sp. n.

Notoclops gen. n.

Type species: *Nesosphecodes depressus* Gonçalves, 2021.

Diagnosis: This genus is superficially similar to the Caribbean *Nesosphecodes* but can be easily distinguished by the reddish orange to dark reddish brown metasoma (black in *Nesosphecodes*), apical margin of clypeus extending well below lower tangent of compound eyes and with lateral thirds sloping and converging apically (at or scarcely extending beyond lower tangent of compound eyes and nearly uniformly straight margin between compound eyes in *Nesosphecodes*), flagellomere I and II of nearly equal lengths (flagellomere I much shorter than flagellomere II in *Nesosphecodes*), mandible of female slightly shorter than compound eye length (as long as or longer than compound eye length in *Nesosphecodes*), basal area of propodeum with fine rugae and distinct, large, paramedial areolae (basal area with fine radiating striae or rugae, without areolae in *Nesosphecodes*), and usual presence of only two submarginal cells (always three submarginal cells in *Nesosphecodes*). The transfer of the type species from *Nesosphecodes* results in the following new combination: *Notoclops depressus* (Gonçalves) comb. n.

Etymology: The new genus-group name is a combination of the Ancient Greek νότος (*nótos*, meaning, 'south') and κλώψ (*klōps*, meaning, 'thief'). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:5B622121-C420-4C28-821F-BADB02E4CD98.

Genus *Ptilocleptis* Michener

The genus *Ptilocleptis* Michener includes three species that superficially resemble polybiine wasps (Fig. 15), but are likely highly derived from among *Sphcodes* s.l., although such a phylogenetic placement is currently speculative. The genus has been recorded from central Mexico to eastern Peru and southeastern Brazil. Here a single female is newly recorded from Bolivia, representing the first occurrence of the genus for the country.

Ptilocleptis polybioides Michener
(Figs 15–17)*New record*

1♀, BOLIVIA: Cochabamba, Cochabamba, 67.5km NE, Est. Biol. Valle del Sajita, Univ. de San Simon, 300m, 17°6'33"S, 64°47'52"W, 9–13 Feb 1999, F. Genier, ex: flight intercept trap (SEMC).

Genus *Sphcodes* Latreille s.l.Key to New World subgenera of *Sphcodes*

- 1 Mandible of female simple (e.g., Fig. 23) 2
- Mandible of female with subapical tooth or subapical angle 3
- 2(1) Posterior rim of basal area of propodeum irregularly carinate (Fig. 22); posterior surface of propodeum with zig-zagging carina (margins of areolae) running lateral-obliquely, sometimes running laterally to completely encircle posterior surface (Fig. 22) *Drepanium* Robertson
- Posterior rim of basal area of propodeum rounded and polished, particularly medially (Fig. 21); posterior surface without zig-zagging lateral-oblique carina, posterior surface never encircled by carinae [typically smaller species] *Asphcodium* subgen. n.



Figs 15–17. — *Ptilocleptis polybioides* Michener, ♀, from Cochabamba, Bolivia: 15, Lateral habitus; 16, Facial view; 17, Posterior view of propodeum, metanotum, and mesoscutellum.

- 3(1) Hind wing with 5–6 hamuli 4
- Hind wing with 7–14 hamuli 5
- 4(3) Propodeal posterior surface with ridges bordering pit roughly parallel to weakly divergent in upper third, delimiting a narrow interspace *Boreosphecodes* subgen. n.
- Propodeal posterior surface with ridges bordering pit distinctly diverging upward in upper half to third and exposing large, polished, triangular interspace rounding into rim of basal area *Sphecodium* Robertson

- 5(3) Preoccipital carina present; flagellomere II of male $4\times$ or more than length of flagellomere I *Proteraner* Robertson
 – Preoccipital carina absent; flagellomere II of male $1.20\text{--}2.5\times$ length of flagellomere I ...
 *Sphecodes* Latreille *s.str.*

***Asphecodium* subgen. n.**

Type species: Sphecodes (Asphecodium) brevisulcatus sp. n. (*vide infra*)

Diagnosis: This is one of two groups of New World *Sphecodes* in which the female mandible is simple. Unlike *Drepanium* Robertson, however, this subgenus includes typically smaller, less robust species in which the posterior rim of the basal area of the propodeum is rounded and polished (Fig. 21), smooth to sometimes faintly imbricate, and not delimited by a strong, irregular carina that is contiguous with the areolae or rugae of the basal area, lateral surfaces, and often the posterior surface, as is the case in *Drepanium* (Fig. 22).

Etymology: The new genus-group name is a combination of the Ancient Greek prefix $\alpha\text{--}$ ($a\text{--}$, the alpha privative indicating negation) and *Sphecodium* Robertson (itself a combination of *Sphecodes* and the neuter form of the suffix $\text{--}ius$, which is used to form adjectives from nouns or is often used to Latinize surnames). The gender of the name is neuter.

ZooBank LSID: urn:lsid:zoobank.org:act:C4663756-FD78-43F4-A834-620BBE87A225.

***Sphecodes (Asphecodium) brevisulcatus* sp. n.**
 (Figs 18–21)

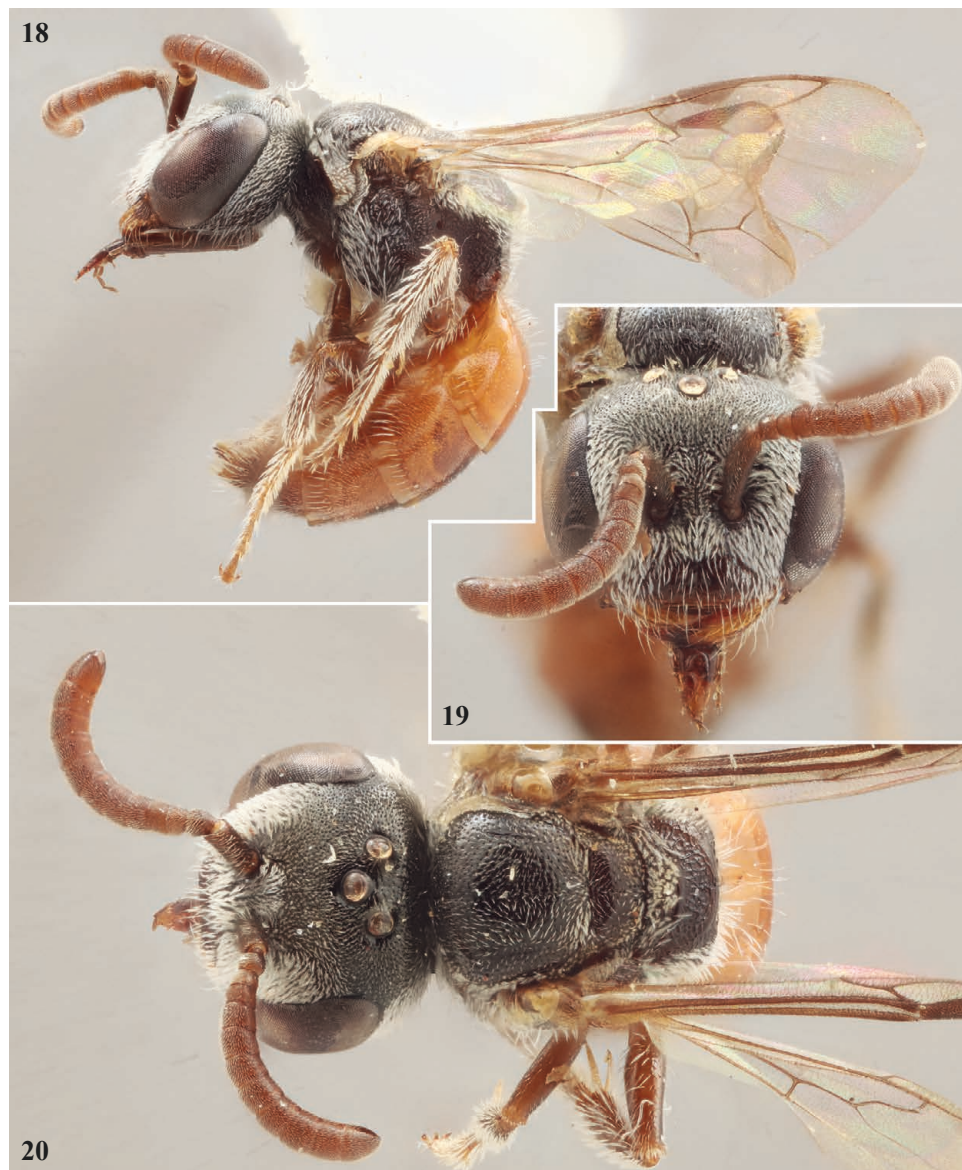
Diagnosis: *Sphecodes brevisulcatus* superficially resembles *S. brachycephalus* Mitchell but can be quickly distinguished by the simple mandible, the uniform density of facial punctures that do not become sparser in ocellocular area, the distinct tuft of erect white setae on the metanotum medially, the dense network of irregular reticulating rugae on the basal area of the propodeum, and the distinct, shallow, mediolongitudinal sulcus traversing the clypeus.

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 4.13mm; forewing length 3.20mm. Head broader than long, width 1.40mm, length 1.10mm (as measured from clypeal apex to vertex in facial view). Mandible long, simple. Clypeus width $2.7\times$ medial length, width 0.72mm, medial length 0.27mm, with a distinctive mediolongitudinal sulcus. Frontal line carinate from just above lower tangent of antennal toruli to mid-distance to median ocellus. Upper interorbital distance 0.95mm; lower interorbital distance 0.80mm; inner margin of compound eye slightly emarginate above level of antennal toruli. Intertegular distance 0.80mm. Mesoscutellum without mediolongitudinal depression, uniformly flattened. Hind wing with five distal hamuli.

Clypeus smooth, flat, with coarse, shallow punctures separated by $0.5\text{--}4\times$ a puncture width, particularly sparse on either side of midline, with distinct mediolongitudinal sulcus traversing from base to apex; supraclypeal area smooth with small, distinct punctures separated by much less than a puncture width; remainder of face smooth and punctured as on supraclypeal area, punctures not becoming more spaced in ocellocular area, punctures similar on vertex although slightly weaker and slightly more spaced, particularly between ocelli; gena smooth with punctures as on vertex except puncture smaller and separated by $1\text{--}2\times$ a puncture width; postgena impunctate. Mesoscutum smooth with punctures separated by a puncture width, slightly denser along borders; mesoscutellum smooth and sparsely impunctate over disc, with punctures separated by less than

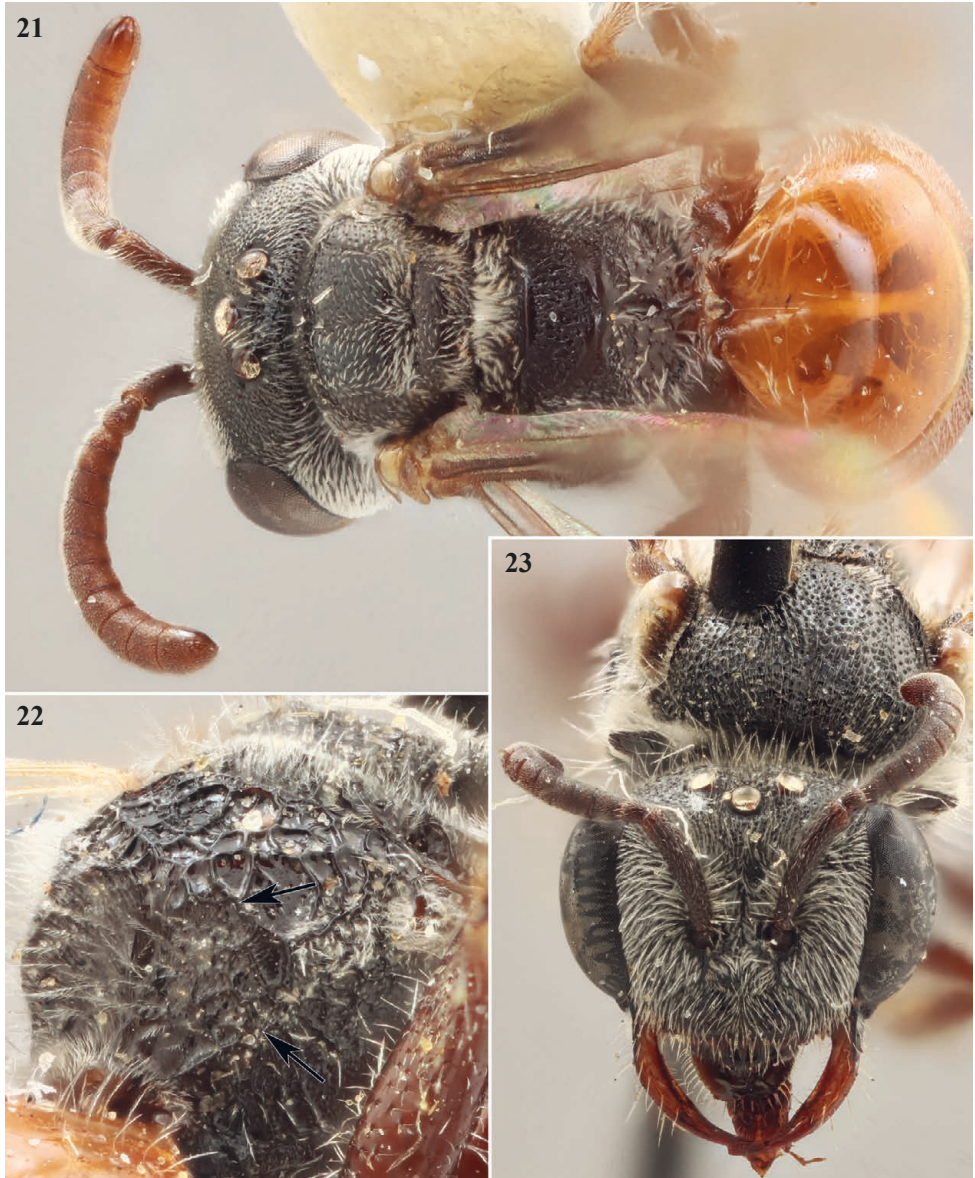
a puncture width along borders and along midline; metanotum smooth with shallow, nearly contiguous punctures. Pleura minutely ruguloso-punctate. Basal area of propodeum with network of irregular reticulating rugae (Figs 20, 21), integument between rugae smooth and shining, posterior border rounded and polished; posterior surface largely smooth with irregular setigerous punctures; lateral surface irregularly and finely rugoso-foveolate (Fig. 18). Metasomal terga smooth, tergum I impunctate, remaining terga with minute punctures separated by a puncture width or less but becoming gradually sparser apically until impunctate in broad apical margins of



Figs 18–20. — *Sphecodes (Asphecodium) brevisulcatus* sp. n., holotype, ♀, from Humboldt County, California, USA: 18, Lateral habitus; 19, Facial view; 20, Dorsal view of head and mesosoma.

each tergum; sterna faintly and finely imbricate and largely impunctate except some setigerous punctures.

Mandible yellowish orange, with reddish apex; labrum yellowish orange except dark brown on basal area; labiomaxillary complex brown, clypeus dark brown except apical margin slightly lighter, scape and pedicel brown, flagellum brown, slightly lighter than scape, remainder of head black. Mesosoma black except pronotal lobe brown; tegula semitranslucent yellow. Wing veins



Figs 21–23. — Details of Western Hemisphere *Sphecoides* Latreille: 21, *Sphecoides* (*Asphecodium*) *brevisulcatus* sp. n., holotype, ♀, from Humboldt County, California, USA; 22, Oblique posterior view of ♀ propodeum of *S. (Drepanium) confertus* Say (arrows indicate irregular carinae on posterior surface margins); 23, Facial view of ♀ of *S. (Drepanium) confertus*.

brown; wing membrane hyaline to slightly parchment coloured. Legs brown except yellowish to yellowish brown on tarsi and at femoral-tibial articulations. Metasoma reddish orange, slightly more brownish on apical two segments.

Pubescence white except slightly tinged yellow on apical metasomal segments; metanotum with distinct tuft of erect white setae medially (Fig. 21).

♂: *Latet*.

Material examined

Holotype, ♀, CALIFORNIA: Humboldt Co., 2 mi S Redwood Valley, VII-7-75 [7 July 1975, no collector indicated] (SEMC).

Paratype, 1♀, CALIFORNIA: San Mateo Co., 4.V.17 [4 May 1917], F. Muir, W.M. Giffard (AMNH).

Etymology: The specific epithet is a combination of the Latin adjective *brevis*, meaning, 'short', 'low', 'shallow', or 'brief', and *sulcātus*, meaning, 'sulcate' or 'ploughed', and referring to the mediolongitudinal sulcus of the clypeus.

ZooBank LSID: urn:lsid:zoobank.org:act:6AB676A9-6F2C-47B8-B1A3-A29DC EED908E.

***Boreosphecodes* subgen. n.**

Type species: *Sphecodes asclepiadis* Cockerell, 1898.

Diagnosis: This subgenus is quite similar to *Sphecodium* in a broad sense as construed herein, but differs in the roughly parallel-sided ridges, sometimes slightly diverging above, on either side of the propodeal pit, thereby creating a narrow interspace rather than the strongly diverging ridges of *Sphecodium*, which results in a large, polished, triangular interspace in the upper half to third and blending into the rounded posterior rim of the basal area. As in most groups of *Sphecodes* the mandible of the female has a small subapical tooth and the preoccipital area is rounded, while the hind wing has a reduced number of hamuli (5–6 hamuli).

Etymology: The new genus-group name is a combination of the Ancient Greek *Bopéās* (*Boréās*, personification of the north wind) and *Sphecodes* (for derivation of *Sphecodes* refer to etymology of *Trichosphecodes*, *supra*). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:302FC64D-24A3-4DA9-B86D-52DA 1949B039.

Subgenus *Sphecodium* Robertson

***Sphecodes (Sphecodium) eustauros* sp. n.** (Figs 24–28)

Diagnosis: *Sphecodes eustauros* is distinctive among Mexican *Sphecodium* for the combination of its wholly dark coloration, fine punctation of the head and mesosomal dorsum (in this respect superficially resembling species of *Microsphecodes*), the radiating striae that reach the polished posterior rim of the basal area of the propodeum, and metasomal punctation.

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 6.07mm; forewing length 4.43mm. Head broader than long, width 1.63mm, length 1.23mm (as measured from clypeal apex to vertex in facial view). Mandible long, with small subapical tooth. Clypeus width 2.7× medial length, width 0.75mm, medial length 0.28mm, comparatively flat.

Frontal line carinate from just above lower tangent of antennal toruli to median ocellar diameter from median ocellus. Upper interorbital distance 1.03mm; lower interorbital distance 0.88mm; inner margin of compound eye slightly emarginate well above level of antennal toruli. Intertegular distance 1.07mm. Mesoscutellum without mediolongitudinal depression, gently convex. Hind wing with five distal hamuli.

Clypeus smooth with shallow, coarse punctures separated by less than a puncture width; supraclypeal area smooth with small distinct punctures separated by less than a puncture width;



Figs 24–28. — *Sphecodes (Sphecodium) eustauros* sp. n., holotype, ♀, from Veracruz, Mexico: 24, Lateral habitus; 25, Facial view; 26, Dorsal view of metasoma; 27, Anterior of mesoscutum; 28, Basal area of propodeum.

remainder of head smooth and densely punctate, punctures nearly contiguous to contiguous on frons, punctures in ocellular area becoming separated by a puncture width, or slightly more toward lateral ocellus, vertex without distinct punctures, surface weakly wrinkled; gena smooth with faint, minute punctures separated by a puncture width or less posteriorly, anteriorly bordering compound eye surface minutely and weakly wrinkled; postgena impunctate. Mesoscutum smooth with comparatively shallow punctures separated by less than a puncture width (Fig. 27), centrally punctures more distinct and sparser, central disc with punctures separated by 1–4× a puncture width; mesoscutellum as on anterior of mesoscutum except punctures sparser in small paramedial patches; metanotum with coarse, shallow, nearly contiguous punctures. Pleura minutely rugulose except hypoepimeral area smooth with shallow punctures separated by a puncture width or slightly more. Basal area of propodeum with strong radiating striae, such ridges extending to polished posterior rim, integument between striae smooth and shining (Fig. 28); lateral and posterior surfaces of propodeum rugosostriate-foveolate with irregular rugae, albeit weaker on posterior surface. Metasomal terga largely smooth, tergum I impunctate, tergum II virtually impunctate except sparse, minute, setigerous punctures, remaining terga with more prevalent minute punctures albeit still sparse, all terga with broad impunctate apical margins (Fig. 26); sterna largely finely imbricate with scattered setigerous punctures.

Mandible brown, with reddish apex; labiomaxillary complex brown, labrum dark brown; scape and pedicel dark brown, flagellum dark brown, slightly lighter ventrally, remainder of head black (Fig. 25). Mesosoma black except pronotal lobe dark brown; tegula semitranslucent brown. Wing veins brown to dark brown; wing membrane faintly infumate. Legs dark brown. Metasoma dark brown.

Pubescence white except prepygidial fimbria fuscous (Fig. 26).

♂: *Latet*.

Material examined

Holotype, ♀, MEXICO: Veracruz, 8km S Carrizal, 5 Nov 1991, R. Ayala, 140m, hot spring resort along river (SEMC).

Etymology: The specific epithet is a combination of the Ancient Greek prefix *eu-* (*eu-*, meaning, ‘good’, ‘well’, ‘genuine’, or ‘true’) and the noun *σταυρός* (*staurós*, meaning, ‘crucifix’). The name is a play on the name of Veracruz.

ZooBank LSID: urn:lsid:zoobank.org:act:35947E84-A0C3-4F09-8302-D58BFD868D47.

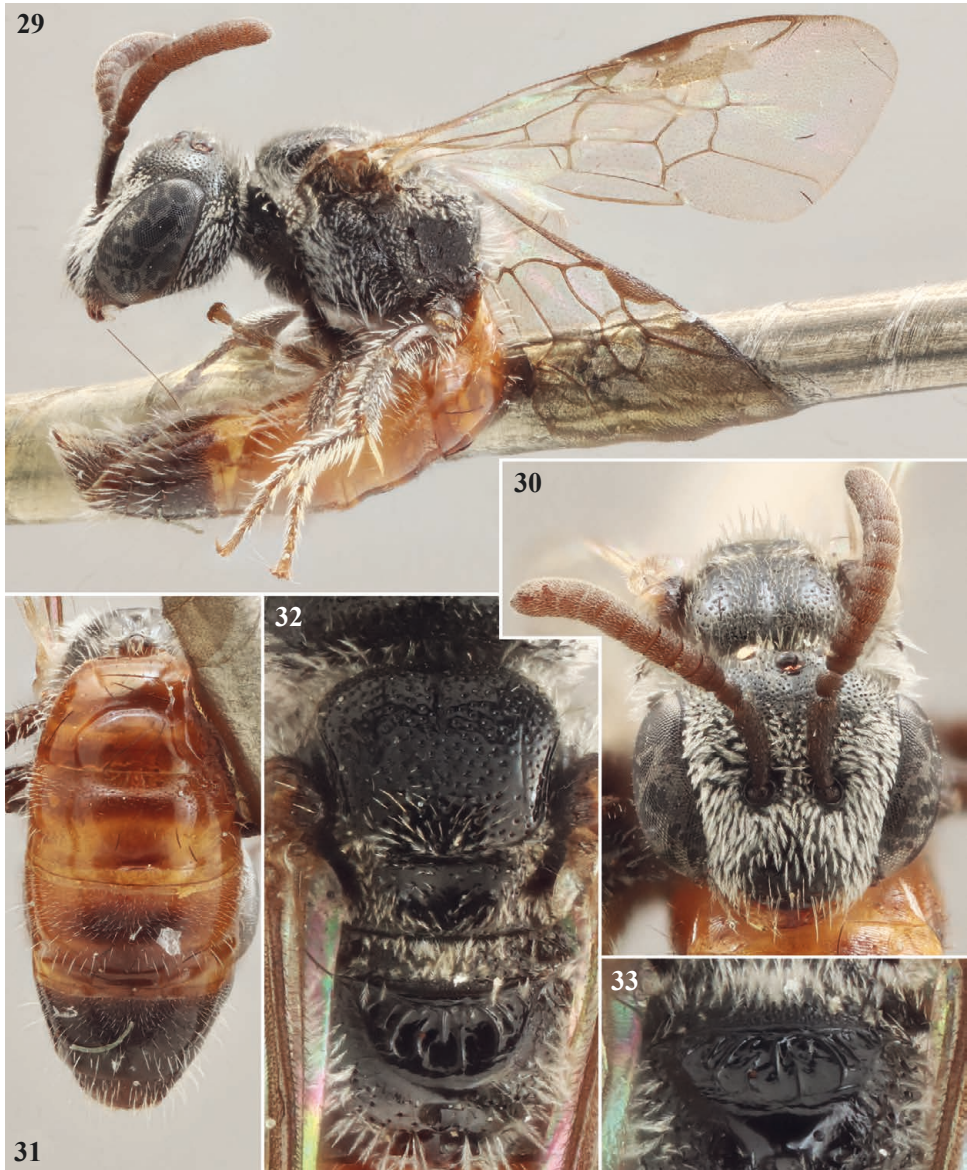
Sphecodes (Sphecodium) electrum sp. n. (Figs 29–33)

Diagnosis: This is among the smallest species of *Sphecodes* in western North America, with a body length less than 4.00mm. It is distinctive for the combination of its small size, the mesosomal and mesoscutellar punctation (Fig. 32), the weakly bigibbous mesoscutellum, distinctive sculpturing of the basal area of the propodeum (Fig. 32), absence of reticulate-foveolate sculpturing on the posterior surface of the propodeum, and metasomal punctation (*vide infra*).

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 3.87mm; forewing length 2.53mm. Head broader than long, width 1.13mm, length 0.92mm (as measured from clypeal apex to vertex in facial view). Mandible long, with small subapical tooth. Clypeus width 2.4× medial length, width 0.53mm, medial length 0.22mm. Frontal line carinate from just above lower tangent of antennal toruli to midlength of frons to median ocellus. Upper interorbital distance 0.77mm; lower interorbital distance 0.62mm; inner margin of compound eye slightly emarginate above level of antennal toruli. Intertegular distance 0.53mm. Mesoscutellum with weak mediolongitudinal depression, thus slightly bigibbous. Hind wing with five distal hamuli.

Clypeus smooth with coarse, shallow punctures separated by a puncture width or less basally and laterally, otherwise noticeably sparser in apical half; supraclypeal area punctured as on basal area of clypeus; remainder of head smooth with small punctures separated by a puncture width or less, including ocellular space; vertex weakly and finely wrinkled transversely and nearly impunctate; gena with minute punctures separated by a puncture width or slightly more; postgena imbricate and impunctate. Mesoscutum smooth with punctures coarser than those of face, separated by about a puncture width (Fig. 32), sparser posteriorly and around posterior of



Figs 29–33. — *Sphecodes (Sphecodium) electrum* sp. n., holotype, ♀, from Chiapas, Mexico: 29, Lateral habitus; 30, Facial view; 31, Dorsal view of metasoma; 32, Dorsal view of mesosoma; 33, Posterior view of propodeum.

parapsidal lines; mesoscutellum as on mesoscutum except punctures much sparser, particularly on paramedial elevations of weakly bigibbous surface (Fig. 32); metanotum smooth with shallow, nearly contiguous punctures. Pleura longitudinally rugosostriate. Basal area of propodeum with few prominent radiating arched striae, such striae ending just before polished posterior rim, with some weak, interconnecting rugae between or incomplete striae, thus surface appearing as large medial areolae, diminishing in size laterally (Figs 32, 33); lateral surface coarsely imbricate; posterior surface largely smooth, with scattered, shallow, setigerous punctures. Metasomal terga smooth, virtually impunctate except tergum II onward with sparse, minute, shallow, punctures associated with setal bases becoming absent in broad impunctate apical margins (Fig. 31); tergum I impunctate; tergum II with minute punctures sparse; remaining terga with punctures more abundant but still quite sparse; terga IV–VI finely and faintly imbricate; tergum VI with coarse, shallow, setigerous punctures separated by a about a puncture width.

Mandible orange, with reddish apex; labiomaxillary complex and labrum dark brown; head black; scape, pedicel, and basal flagellomeres dark brown, remainder of flagellum brown (Fig. 30). Mesosoma black except pronotal lobe dark brown; tegula semitranslucent brown. Wing veins brown to dark brown along anterior wing margin; wing membrane hyaline (Fig. 29). Legs dark brown except tarsi lighter. Metasomal segments I–III largely reddish orange except blending to dark brown centrally on disc of tergum III; tergum IV basally reddish orange, remainder dark brown; tergum V dark brown; tergum VI light brown on pregradular area, remainder dark brown; sterna I–III reddish orange; sternum IV reddish orange basally, remainder dark brown; sterna V and VI dark brown.

Pubescence white except slightly tinged yellow on apical metasomal segments; metanotum with distinct tuft of erect white setae medially (Fig. 32).

♂: *Latet*.

Material examined

Holotype, ♀, MEXICO: Chiapas, 18km S Palenque, Cascadas de Misolhá, 25-IV-1993 [25 April 1993], G. Eickwort (SEMC).

Etymology: The specific epithet is the Latin noun *ēlectrum*, meaning, ‘amber’, and refers to the both the colour of the metasoma and the fact that Chiapas is famous for its extensive outcrops of Miocene amber.

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Subgenus *Sphecodes* Latreille *s.str.*

***Sphecodes (Sphecodes) zacatuche* sp. n.**
(Figs 34–36)

Diagnosis: The is a rather robust higher elevation species distinctive for its wholly black integument; broad head, with the interocular distance greater than the compound eye length; distinctively raised frontal carina in upper portion of frons; abundant semi-translucent spinelike setae on the retrodorsal margin of the metatibia; prepygidial fimbria composed of fuscous setae with whitish tips; basal area of propodeum rugosostriate, with rugae-striae radiating from basal margin and with some interconnecting rugae, particularly apically where the interconnecting rugae form an apical row of areolae delimiting the carinate apical rim; and the characteristic sculpturing of the metasomal terga (*vide infra*).

Description

As described for *M. multirugosus* (*vide supra*), except as follows: ♀: Total body length 11.58mm; forewing length 8.74mm. Head much broader than long, width 3.03mm, length 2.23mm (as measured from clypeal apex to vertex in facial view). Mandible long, with small subapical tooth. Clypeus width 2.7× medial length, width 1.67mm, medial length 0.63mm.

Frontal line carinate from just above lower tangent of antennal toruli to median ocellar diameter from median ocellus, carina particularly raised in upper portion on frons. Upper interorbital distance 1.93mm; lower interorbital distance 1.83mm; inner margin of compound eye slightly emarginate well above level of antennal toruli. Intertegular distance 2.13mm. Mesoscutellum without mediolongitudinal depression, comparatively flat. Hind wing with eight distal hamuli.

Clypeus smooth with coarse, shallow punctures separated by less than a puncture width, nearly contiguous in many places; supraclypeal area deep, nearly contiguous punctures; remainder of



Figs 34–36. — *Sphecodes (Sphecodes) zacatuche* sp. n., holotype, ♀, from Milpa Alta, Mexico: 34, Dorsal view of mesosoma; 35, Facial view; 36, Lateral habitus.

face finely rugoso-punctate, resulting in the appearance of contiguous irregular punctures, ocellular space with punctures near compound eye distinct, rugosopunctate pattern blending gradually to vertex with weak transverse rugae and less distinct punctures; gena as on frons except anteriorly toward compound eye with puncture more distinct; postgena imbricate and impunctate. Mesoscutum smooth (where evident) with deep, coarse punctures contiguous to nearly contiguous, slightly more spaced around parapsidal lines and in posterior fifth; mesoscutellum smooth with punctures as on mesoscutum except sparser on posterior half of disc; metanotum coarsely rugoso-punctate. Pleura coarsely rugoso-punctate. Basal area of propodeum rugosostriate, with rugae-striae largely radiating from basal margin but with some interconnecting rugae, particularly apically where interconnecting rugae form an apical row of areolae delimiting carinate apical rim of basal area; lateral and posterior surfaces coarsely rugulose, except anteriorly finer on lateral surface. Metasomal terga smooth, with minute, shallow punctures, punctures sparser on more basal terga, but punctures of all terga becoming sparser apically to broad impunctate apical margins, punctures of terga II–VI noticeably smaller basally; tergum I with punctures separated by a puncture width or more; tergum II with punctures separated by a puncture width or less; remaining terga with punctures denser basally and becoming of two sizes apically, particularly on tergum IV; tergum V finely imbricate with minute, distinct punctures basally, blending to larger, shallow, coarse punctures in at least apical two-thirds; sterna imbricate with scattered, shallow, setigerous punctures.

Integument wholly dark brown to black (Figs 34–36); wing membranes lightly infumate, veins brown to dark brown.

Pubescence white except metasomal apex with setae fuscous or fuscous with whitish tips.

♂: *Latet*.

Material examined

Holotype, ♀, MEXICO: D.F., 6km SW Milpa Alta, 12 Nov 1991, Ayala, 2600m, wooded area after cactus gardens (SEMC).

Paratype: 1♀, MEXICO: Mexico, 13km SW Milpa Alta, 2700m, 28 Oct 1991, T. Griswold, ex: *Simsia amplexicaulis* [(Cav.) Pers., Asteraceae: Asteroideae: Heliantheae: Helianthinae] (AMNH).

Etymology: The specific epithet is taken from the Spanish name, Zacatuche, for the endangered Volcano rabbit, *Romerolagus diazi* (Ferrari-Pérez) (Lagomorpha), the second-smallest species of Leporidae and endemic to the Milpa Alta – the same area to which this cuckoo bee is confined. The name is treated as a noun in apposition.

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Eastern Hemisphere Sphecodina

In the Eastern Hemisphere fauna I currently advocate the recognition of six genera: *Sphecodes* s.l., *Eupetersia* s.l., *Callosphecodes* Friese, *Thrausmus* Buysson, *Caenosphecodes* gen. n. (for *Sphecodes pseudoredivivus* Astafurova & Proshchalykin and relatives), and *Melittocleptes* gen. n. (for *S. insularis* Smith). The two species of *Callosphecodes* were figured and their shared features briefly summarized by Rasmussen & Michener (2011). *Callosphecodes*, *Thrausmus*, and *Melittocleptes* all have a prominent preoccipital carina, thinly lamellate laterally in the latter two genera, and a strong hypostomal carina that is developed into a prominent tooth posteriorly, particularly so in *Thrausmus*. Each of these groups are remarkably distinctive, even more so than *Eupetersia*, and there is no clear affinity at this time to any subgroup of *Sphecodes* s.l. Accordingly, I believe it is worthy to classify each as a genus. Should phylogenetic studies indicate their derivation from among *Sphecodes*, then they can easily be demoted as subgenera. It seems that

Melittocleptes may be closely related to *Callosphécodes*, in which case they could be united as subgenera of a single group, but as this relationship remains speculative I have erred on the side of treating each as distinct.

Key to Old World genera of Sphecodina

- 1 Free part of marginal cell less than $2\times$ as long as part subtended by submarginal cells, submarginal cells extending well beyond tangent of pterostigmal apex (*i.e.*, juncture of 2rs-m and Rs distad tangent of pterostigmal apex) 2
- Free part of marginal cell about $2.25\text{--}3\times$ as long as part subtended by submarginal cells, submarginal cells not extending beyond tangent of pterostigmal apex (*i.e.*, juncture of 2rs-m and Rs at or before tangent of pterostigmal apex) [Indomalaya] .. *Caenosphécodes* gen. n.



Figs 37–38. — *Thrausmus grandidieri* Buysson, ♀, from Madagascar: 37, Lateral habitus; 38, Dorsal habitus.

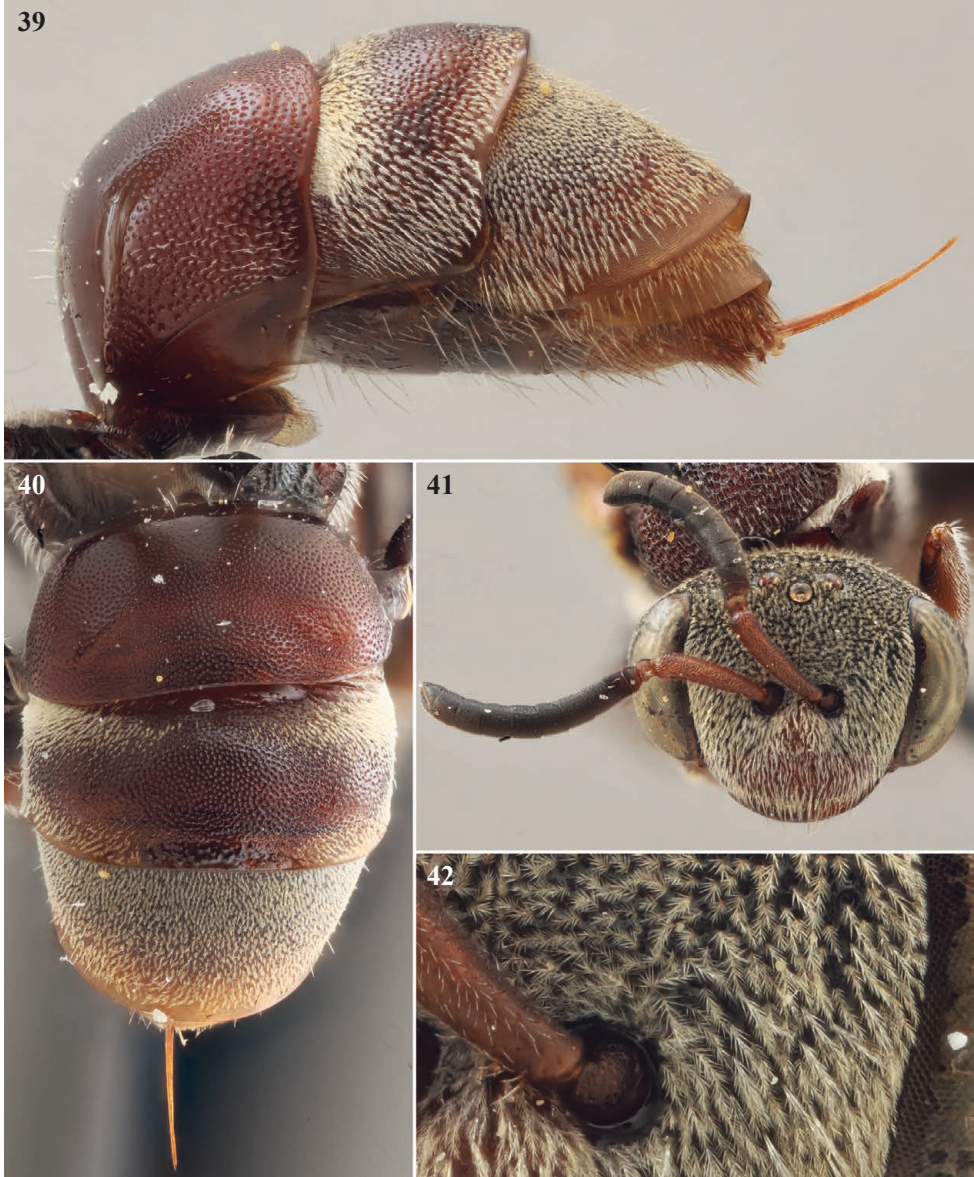
- 2(1) Hypostomal carina projected as a thick tooth posteriorly; preoccipital carina strong, sometimes even thinly lamellate laterally (*i.e.*, *Thrausmus* Buysson and *Melittocleptes* gen. n.); mandible of female strongly bidentate 3
- Hypostomal carina not projected posteriorly as a tooth; preoccipital carina typically absent, sometimes present laterally and often comparatively weak; mandible of female simple or with subapical tooth/subapical angle 5
- 3(2) Apical margin of metasomal tergum II unmodified (Figs 48, 57); head, aside from face, without dense covering of plumose setae, integument not obscured except on face below upper frons (some species with dense setation more restricted to face at level of toruli and below) (Figs 44, 58); metasomal terga without dense covering of short, plumose setae, setae sparse, largely simple, and typically suberect to erect (Figs 48, 57, 61); basal area of propodeum more rounded trapezoidal, lateral margins slightly converging posteriorly, irregularly areolate owing to rugulose to rugosostriate ridges (Figs 49, 54, 60); metabasitibial plate well-defined and raised; tergum III about as long as or shorter than tergum II (*e.g.*, Figs 43, 48, 57), sometimes slightly longer than tergum II 4
- Apical margin of metasomal tergum II with prominent lateral concavities (Fig. 39); head with dense, decumbent, plumose setation largely obscuring integument (Figs 41, 42); metasomal terga III and IV covered with abundant, short, decumbent, plumose setae, such setae basally, laterally, and to a lesser degree apically on tergum II (Figs 37, 39, 40); basal area of propodeum broadly rectangular, with strong striae radiating from basal margin (Fig. 38); metabasitibial plate not raised and ill-defined; tergum III distinctly elongate, noticeably longer than tergum II and obscuring most of tergum IV (Figs 37, 39) [Madagascar] *Thrausmus* Buysson
- 4(3) Integument of head and mesosoma black, with metasoma largely reddish except apex dark brown to black (Figs 57, 61); wing membranes hyaline; flagellomere I of female 0.75× length of flagellomere II [Sulawesi] *Melittocleptes* gen. n.
- Integument of body black with deep metallic blue, purple, or greenish tint; wing membranes strongly infusate; flagellomere I of female about as long as flagellomere II [Papua New Guinea (New Britain), Australia (Queensland)] *Callosphcodes* Friese
- 5(2) Flagellomeres I and II of male both distinctly broader than long; gonocoxa of male not striate, with dorsolateral depression margined by and usually traversed by flanges or ridges; body with moderate to fine punctation, rarely coarsely pitted as is usual in *Sphecodes*; mandible of female simple; horizontal surface of propodeum distinctly longer than mesoscutellum [Africa, southern Asia] *Eupetersia* Blüthgen *s.l.*
- Flagellomere II of male usually longer than broad, unlike flagellomere I; gonocoxa of male usually striate, without depression; body and especially propodeum usually coarsely pitted; mandible of female nearly always with preapical tooth (except in some subgenera such as *Drepanium* Robertson); horizontal surface of propodeum shorter than or about as long as mesoscutellum [Africa, Eurasia (inclusive of Malesia), Papuasia, Australia] ... *Sphecodes* Latreille *s.l.*

Caenosphecodes gen. n.

Type species: Sphecodes pseudoredivivus Astafurova & Proshchalykin in Astafurova, Proshchalykin & Schwarz 2020.

Diagnosis: This genus is the Old World equivalent of *Microsphecodes* as both have the submarginal cells compressed and not extending beyond the tangent of the pterostigmal apex, rather fine punctation, and the mesoscutum low and rounding gently to the pronotal margin. In addition, the areolae on basal area of the propodeum, on either side of the midline, are enlarged and resemble those of *Microsphecodes*. However, unlike *Microsphecodes* the prepygidial fimbria is present. The genus is certainly closely allied to *Eupetersia* and resembles that group in most respects aside from the contracted forewing venation. Indeed, it could just as easily be treated as a subgenus under *Eupetersia* (there is considerable

resemblance to *Pollinicleptis*) were it not for the length of the basal area of the propodeum relative to the mesoscutellum. Until such time, I treat it here as a genus. The transfer of the type species from *Sphecodes* results in the following new combination: *Caenosphecodes pseudoredivivus* (Astafurova & Proshchalykin) comb. n. The genus also includes *C. sauteri* (Meyer) and, at least tentatively, *C. redivivus* (Blüthgen) comb. n. It is possible that *S. simlaensis* Blüthgen also belongs here and so it is tentatively included: *C. simlaensis* (Blüthgen) comb. n.



Figs 39–42. — *Thrausmus grandidieri* Buysson, ♀, from Madagascar: 39, Lateral view of metasoma; 40, Dorsal view of metasoma; 41, Facial view; 42, Detail of facial setae.

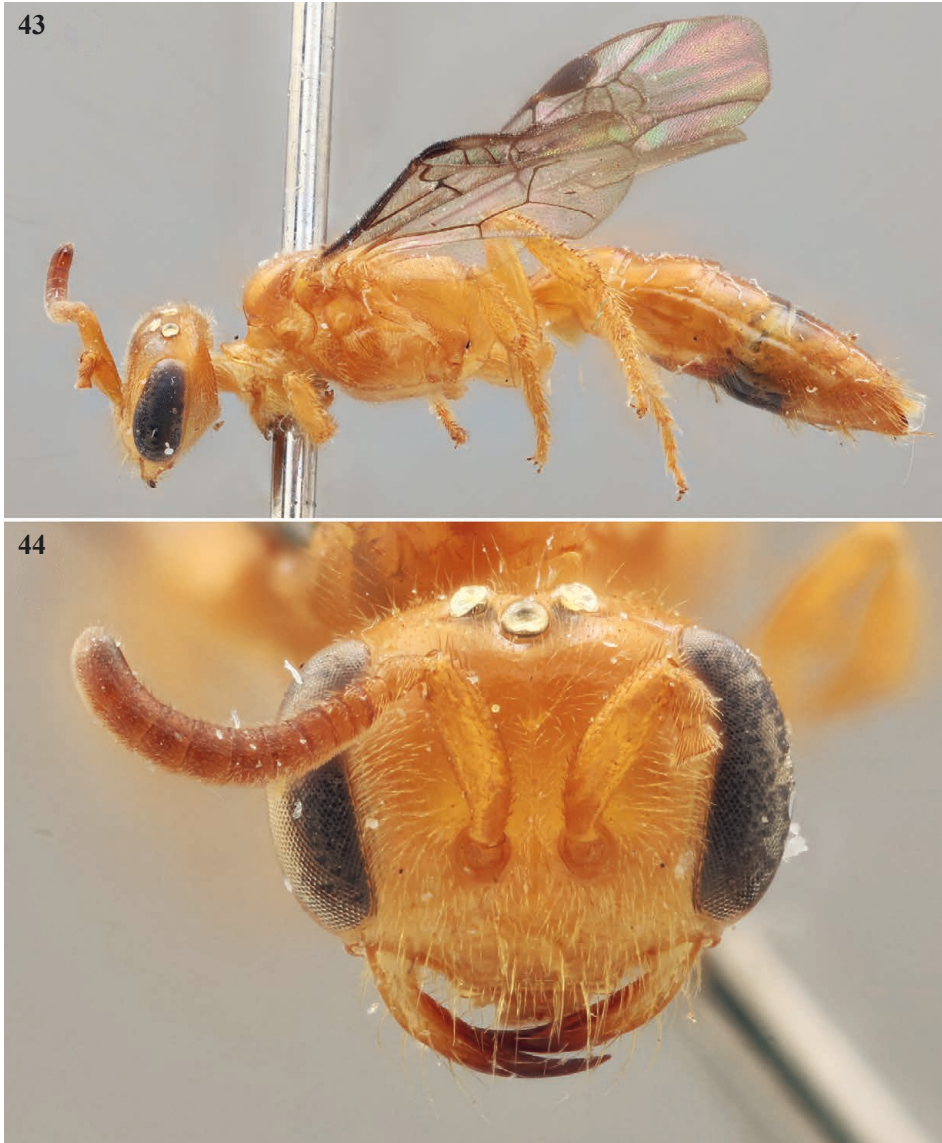
Etymology: The new genus-group name is a combination of the Ancient Greek adjective *καινός* (*kainós*, meaning, 'novel' or 'new') and *Sphecodes* (for derivation of *Sphecodes* refer to etymology of *Trichosphecodes*, *supra*). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:B842038B-5E1F-4E37-837F-CA0F03117701.

Genus *Eupetersia* Blüthgen *s.l.*

A further challenge among sphecodines is the circumscription of *Eupetersia*, and particularly its two subgenera (Michener 2007). Most characters would indicate that *Eupetersia* is nothing more than a subtly different group of *Sphecodes*, and even Benoist (1962) suggested that they were not sufficiently distinct. Indeed, it is tempting to treat *Eupetersia* within *Sphecodes* if it were not for the preliminary results of Habermannová, Bogusch, P. & Straka (2013), which suggested it is a group sister to all other *Sphecodes*. One might therefore argue it should be an early diverging subgenus therein, but maintaining current usage, as it does not seem to render *Sphecodes* paraphyletic, seems a more stable option for the classification. Nonetheless, the organization of the species into the subgenera *Eupetersia* and *Nesoeupetersia* Blüthgen seems problematic (Michener 1978, 2007). For example, there are several species that fully intermingle the characters purported to segregate these two groups, thereby obviating their distinctions as currently circumscribed. Currently, *Eupetersia s.str.* purportedly comprises those species with dense mesoscutal punctation, a bigibbous mesoscutellum, and both 1m-cu and 2m-cu meeting the third submarginal cell (or 1m-cu confluent with 1rs-m), while *Nesoeupetersia* encompasses those species with a more scattered mesoscutal punctation, a gently convex to relatively flat mesoscutellum (not bigibbous), and 1m-cu entering the second submarginal cell. Yet, in the Malagasy species *Eupetersia atra* Pauly & Brooks the mesoscutum is punctured as in *Nesoeupetersia*, while the mesoscutellum is faintly bigibbous and 1m-cu is confluent as in *Eupetersia s.str.* The same is basically true for *E. nathani* Baker (Fig. 52), although 1m-cu enters the second submarginal cell. Conversely, *E. angavokely* Pauly & Brooks has a denser mesoscutal punctation and distinctly bigibbous mesoscutellum as in *Eupetersia s.str.*, with 1m-cu entering the second submarginal cell as in *Nesoeupetersia*. There is a pattern for some species to have the hypoepimeral area polished and rather smooth compared with the remainder of the mesepisternum (typical in most *Nesoeupetersia*), while the hypoepimeral area may be coarsely sculptured as on the rest of the mesepisternum, which is more common in *Eupetersia s.str.* But again, this intermingles, with a putative species of *Nesoeupetersia*, *E. emini* Blüthgen, combining the typical features of *Nesoeupetersia* with the coarsely sculptured hypoepimeral area. Other species also intermingle the subgeneric traits in similar fashion. The concavity of the anterior margin of the pronotal collar also intergrades across the species (*e.g.*, Figs 54–56). And, then there is a species like *E. constricta* (Benoist) (Fig. 48), which lacks a preoccipital carina and even obviates one of the distinctions between *Eupetersia s.l.* and *Sphecodes*. The point of this summation is that the character complexes across *Eupetersia s.l.* are fraught with challenges. The subgenera as currently circumscribed do not hold and their characters intermix. If one ignores the steady transition among the species from the flatter mesoscutella, to the convex, to the weakly bigibbous, and ultimately to the prominently bigibbous,

as well as the position of 1m-cu, then the mesoscutal sculpturing does appear to segregate the bees into nice groups, which could be natural, although they do not correspond in composition to the subgenera as currently populated. Furthermore, one species, *E. reticulata* (Benoist) (Figs 43–47), does not belong to any of the groups and is here treated as a distinct lineage in its own right and may be worthy of generic rank in the future. The arrangement of species to subgenera in the new system for *Eupetersia* s.l. is provided in Appendix I while a new species is presented in Appendix II.



Figs 43–44. — *Eupetersia* (*Xanthocleptis*) *reticulata* (Benoist), ♀, from Madagascar: 43, Lateral habitus; 44, Facial view.

Key to subgenera of *Eupetersia*

- 1 Flagellomere II of female distinctly shorter than flagellomere III, more similar to flagellomere I; antenna of female not compact, length of flagellum twice or more length of scape and extending back well over mesoscutum, at least to posterior third of mesoscutum if not further; antennal toruli slightly below facial midlength, with subantennal sulcus as long as or longer than torular diameter; pronotal lateral ridge carinate (sometimes weakly so) to rounded, but if rounded then dorsal surface with abundant, minute, white (sometimes tinged yellowish), plumose setae; metatibia with or without spine-like setae on retrodorsal edge; integument variable, typically head and mesosoma largely black with either partly or wholly reddish to orange metasoma, but also at times metallic blue, blue-green, with or without reddish legs contrasting 2
- Flagellomere II of female similar to flagellomere III, with entire flagellum comparatively compact (Fig. 44); antenna of female compact, length of flagellum only slightly longer than length of scape, distinctly less than twice length of scape; antennal toruli low on face, near clypeus, with subantennal sulcus shorter than torular diameter (Fig. 44); pronotal lateral ridge wholly rounded with scant plumose pubescence dorsally; metatibia with spine-like setae on retrodorsal edge (Fig. 45); integument wholly yellow to reddish yellow (Figs 43–47) [Madagascar] *Xanthocleptis* subgen. n.
- 2(1) Basal area of propodeum rugulose to rugosostriate, without large, paired areolae on either side of midline (Figs 49, 51, 54, 55); metatibia with or without spine-like setae on retrodorsal edge 3
- Basal area of propodeum with large, paired areolae on either side of midline (Figs 53, 56), otherwise with irregular striae and rugae; metatibia without spine-like setae on retrodorsal edge [Indomalaya] *Pollinicleptis* subgen. n.
- 3(2) Mesoscutum with smaller and finer punctures, punctures separated by 2× puncture width or more 4
- Mesoscutum densely and coarsely punctate, punctures contiguous or separated by a puncture width or more frequently less (Fig. 55), or if more widely spaced, then integument metallic blue with green and purple highlights [sub-Saharan Africa, Madagascar] *Eupetersia* Blüthgen s.str.
- 4(3) Mandible shorter than compound eye length; interocular distance shorter than or subequal to compound eye length [Indian Ocean islands (Madagascar, Seychelles), Southeast Asia (Thailand), Borneo (Sabah)] *Nesoeupetersia* Blüthgen
- Mandible as long as or longer than compound eye; interocular distance greater than compound eye length [tropical Africa] *Cephalosphecodes* subgen. n.

Xanthocleptis subgen. n.

Type species: Nomia reticulata Benoist, 1962.

Diagnosis: This is the most distinctive group of *Eupetersia*, and the species could easily be recognized as a separate genus but any further decision on its classification should await resolution of its relationship to other African *Eupetersia* or *Sphecodes*. The group is easily diagnosed by the following combination of characters (Figs 43–47): integument wholly yellow to reddish yellow, with sparse minute punctures, otherwise smooth; mandible slightly shorter than compound eye; antennal toruli low on face, near clypeus, with subantennal sulcus shorter than torular diameter; antenna of female compact, length of flagellum only slightly longer than length of scape, distinctly less than twice length of scape; flagellomere II of female similar to flagellomere III; pronotal lateral ridge wholly rounded with scant plumose pubescence dorsally; metatibia with spine-like setae on retrodorsal edge; basal area of propodeum with fine rugulae radiating from base to apex.

Etymology: The new genus-group name is a combination of the Ancient Greek adjective ξανθός (*xanthós*, meaning, 'yellow') and the noun κλέπτης (*kléptēs*, meaning, 'thief', which in Latin is *cleptīs*). The gender of the name is masculine.

ZooBank *LSID:* urn:lsid:zoobank.org:act:2D402C59-9448-4099-B519-5E09DE254592.

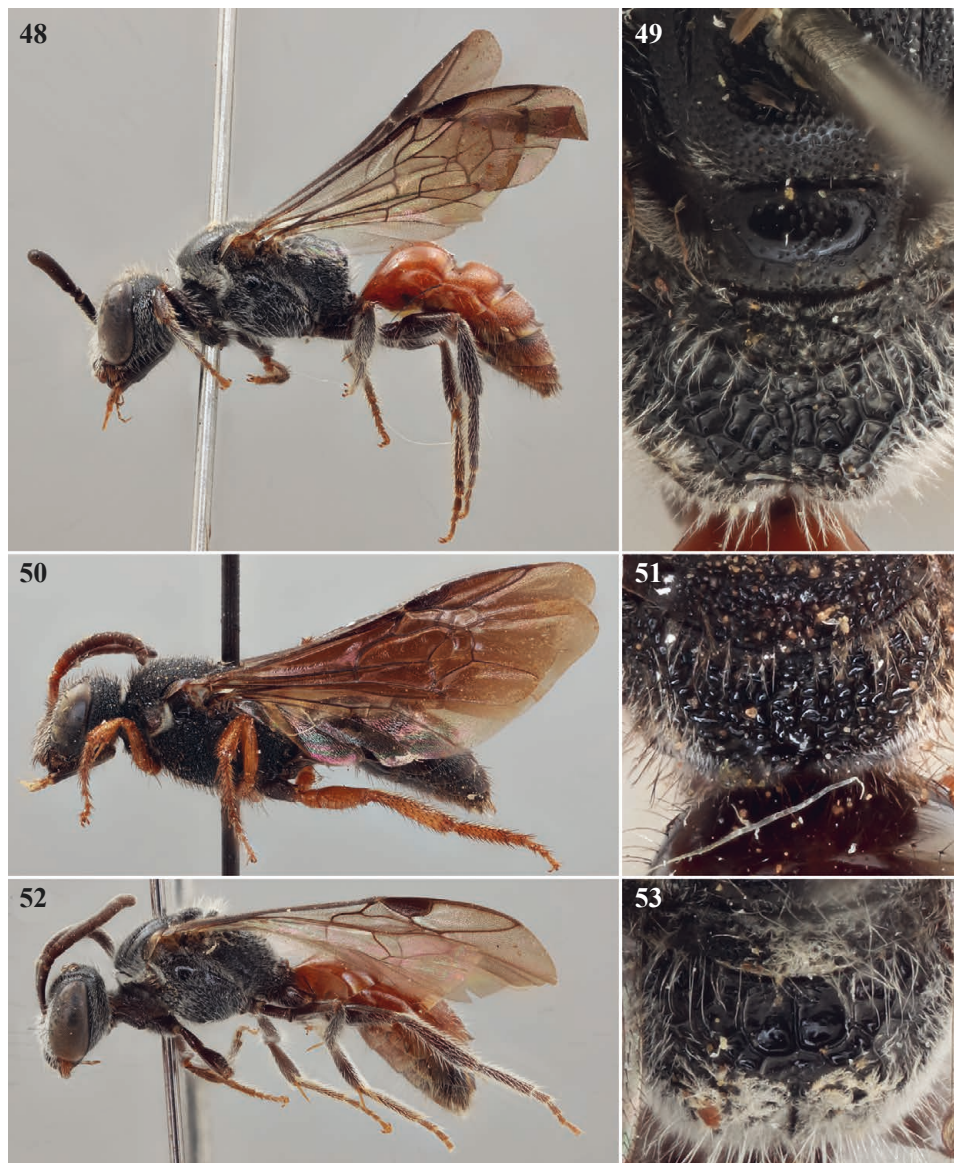


Figs 45–47. — *Eupetersia* (*Xanthocleptis*) *reticulata* (Benoist), ♀, from Madagascar: 45, Detail of spinelike setae on retrodorsal margin of metatibia; 46, Dorsal habitus; 47, Dorsal view of head and mesosoma.

***Pollinicleptis* subgen. n.**

Type species: Eupetersia nathani Baker, 1974.

Diagnosis: This subgenus can be distinguished by the following combination of characters: mandible of female shorter than compound eye; antennal toruli slightly below facial midlength, with subantennal sulcus as long as or longer than torular



Figs 48–53. — Species of *Eupetersia* Blüthgen: 48, Lateral habitus of *Eupetersia* (*Eupetersia*) *constricta* (Benoist); 49, Basal area of propodeum of *E. (E.) constricta*; 50, Lateral habitus of *E. (E.) guillarmodi* Michener; 51, Basal area of propodeum of *E. (E.) guillarmodi*; 52, Lateral habitus of *E. (Pollinicleptis) nathani* Baker (holotype); 53, Basal area of propodeum of *E. (P.) nathani*.

diameter; antenna of female not compact, length of flagellum twice or more length of scape and extending back well over mesoscutum; flagellomere II of female distinctly shorter than flagellomere III, more similar to flagellomere I; pronotal lateral ridge carinate (sometimes weakly so) to rounded; metatibia without spine-like setae on retrodorsal edge; basal area of propodeum with large, paired areolae on either side of midline.

Etymology: The new genus-group name is a combination of the Latin noun *pollen* (meaning, 'finest dust', 'milledust', and, of course, today referring to floral pollen; genitive *pollinis*) and the noun *cleptīs* (meaning, 'thief'). The gender of the name is masculine.

ZooBank *LSID*: urn:lsid:zoobank.org:act:0B668745-468E-4698-8DEA-BE4D6A39CD95.

Cephalosphecodes subgen. n.

Type species: *Eupetersia macrocephala* Pauly, 1981.

Diagnosis: This subgenus can be distinguished by the following combination of characters: integument black with brown to dark orange on metasoma; head considerably broadened; mandible elongate, as long as or longer than compound eye; interocular distance greater than compound eye length; antennal toruli slightly below facial midlength, with subantennal sulcus as long as or longer than torular diameter; antenna of female not compact, length of flagellum twice or more length of scape and extending back well over mesoscutum; flagellomere II of female distinctly shorter than flagellomere III, more similar to flagellomere I; pronotal lateral ridge carinate or at least strongly angulate; mesoscutum with smaller and finer punctures, punctures separated by 2× puncture width or more; metatibia without spine-like setae on retrodorsal edge; basal area of propodeum rugulose to rugosostriate (without large areolae on either side of midline).



Figs 54–56. — Species of *Eupetersia* Blüthgen, dorsal view of mesosoma: 54, *Eupetersia (Eupetersia) constricta* (Benoist); 55, *E. (E.) guillarmodi* Michener; 56, *E. (Pollinicleptis) nathani* Baker (holotype).

Etymology: The new genus-group name is a combination of the Ancient Greek κεφαλή (*kephalḗ*, meaning, 'head') and *Sphecodes* (for derivation of *Sphecodes* refer to etymology of *Trichosphecodes*, *supra*). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:CF65A0AF-FC41-448F-BD0F-D5099C3445EA.



Figs 57–58. — *Melittocleptes insularis* (Smith), ♀ (compared with holotype), from Central Sulawesi, Indonesia: 57, Lateral habitus; 58, Facial view.

***Melittocleptes* gen. n.**

Type species: Sphecodes insularis Smith, 1858.

Diagnosis: As in *Thrausmus* and *Callosphecodes*, the hypostomal carina is strong and is developed at its posterior-end into a thick tooth, the preoccipital carina is strong and thinly lamellate laterally (as in *Thrausmus*), the mandible of the female is strongly bidentate, and metasomal segment II is depressed basally forming weak constrictions between the first and second terga and sterna. Like *Callosphecodes* the



Figs 59–61. — *Melittocleptes insularis* (Smith), ♀ (compared with holotype), from Central Sulawesi, Indonesia: 59, Dorsal view of mesosoma; 60, Basal area of propodeum; 61, Dorsal view of metasoma.

metabasitibial plate is raised and comparatively well-defined and the face below the upper frons is densely covered in white pubescence, but the integument of the head and mesosoma is black and the metasoma is largely reddish except apically dark brown to black (Figs 57–61) (versus wholly black with dark metallic blue, purple, or greenish tint in *Callosphcodes*) and the wings are hyaline (rather than infuscate). In addition, the first flagellomere of the female is compact and only about half as long as the second flagellomere (flagellomeres nearly equal in *Callosphcodes*). Both genera have the vertex elevated, raised to a peak above the level of the ocelli (Fig. 58), but lacking a keel or transverse ridge that sometimes occurs in *Sphcodes*, and the pronotal lateral angles are projected and slightly acute, forming a distinct and sharp angled point. The transfer of the type species from *Sphcodes* results in the following new combination: *Melittocleptes insularis* (Smith) comb. n.

Etymology: The new genus-group name is a combination of the Ancient Greek μέλιττα (*mélitta*, meaning, ‘bee’) and κλέπτῃς (*kléptēs*, meaning, ‘thief’). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:5DEE7DFD-4213-4483-AD3A-4B72B9E44148.

Genus *Sphcodes* Latreille *s.l.*

Key to Old World subgenera of *Sphcodes*

- 1 Mandible of female simple 2
- Mandible of female with subapical tooth or subapical angle 4
- 2(1) Preoccipital carina absent 3
- Preoccipital carina present [Indonesia (Java, Lesser Sunda Islands)] ... *Paradrepanium* subgen. n.
- 3(2) Retrodorsal margin of female metatibia with spine-like setae [Holarctic, northern Africa] . . . *Drepanium* Robertson
- Retrodorsal margin of female metatibia without spine-like setae [Europe, northern Africa] *Xystoclops* subgen. n.
- 4(1) Hind wing with 7–14 hamuli 5
- Hind wing with 5–6 hamuli 10
- 5(4) Preoccipital carina present laterally 6
- Preoccipital carina absent 8
- 6(5) Vertex without transverse ridge or keel 7
- Vertex with transverse ridge or keel *Eusphcodes* subgen. n.
- 7(6) Tegula unmodified, ovoid; retrodorsal margin of female metatibia with spinelike setae . . . *Proteraneropsis* subgen. n.
- Tegula expanded, anterior and anterolateral margins explanate; retrodorsal margin of female metatibia without spinelike setae [Madagascar] *Nomiocleptes* subgen. n.
- 8(5) Lateral ridges on either side of propodeal pit roughly parallel along length, sometimes slightly diverging above but generally forming narrow space to margin with dorsal surface 9
- Lateral ridges on either side of propodeal pit distinctly diverging dorsally, forming large triangular polished surface between in upper half to third *Sabulicola* Verhoeff
- 9(8) Retrodorsal margin of female metatibia without spinelike setae; basal area of propodeum about as long as metanotum [Africa] *Callocleptes* subgen. n.
- Retrodorsal margin of female metatibia with spinelike setae; basal area of propodeum about as long as or slightly shorter than mesoscutellum [Eurasia, northern Africa] *Sphcodes* Latreille *s.str.*

- 10(4) Hypoepimeral area polished and largely smooth, sculpturing noticeably differing from remainder of mesepisternum [Eurasia] ***Caenocleptes*** subgen. n.
 – Hypoepimeral area coarsely sculptured, sculpturing similar to remainder of mesepisternum [Holarctic, Africa, Indomalaya] *Sphecodium* Robertson

Proteraneropsis subgen. n.

Type species: Sphecodes spinulosus Hagens, 1875.

Diagnosis: As the name suggests, this subgenus is superficially similar to *Proteraner*, largely owing to the lateral preoccipital carina, the larger number of hamuli, the absence of ridge on the vertex, the subapical tooth of the female mandible, and the spinelike setae of the retrodorsal margin of the female metatibia, but can be most readily distinguished by the shorter flagellomeres of males, in which flagellomere II is elongate, but does not reach to 4× or more the length of flagellomere I (as is the case in *Proteraner*).

Etymology: The new subgeneric name is a combination of *Proteraner* Robertson [itself a combination of the adjective *próteros* (πρότερος, meaning, ‘before’ or ‘former’) and the noun *anér* (ἄνθρωπος, meaning, ‘adult male’); Robertson (1903) was apparently referring to the early appearance of males in the Spring in the type species] and ὄψις (*opsis*, meaning, ‘sight’ or ‘countenance’ or ‘appearing like’). The gender of the name is feminine.

ZooBank LSID: urn:lsid:zoobank.org:act:186CAD98-CF35-42EE-8D23-B11E745AC4A8.

Paradrepanium subgen. n.

Type species: Sphecodes brunneipes Friese, 1914.

Diagnosis: This subgenus is similar to *Drepanium* as both have the female mandible simple, but unlike that group the preoccipital carina is present (wholly absent in *Drepanium*). In addition, there is a smaller number of hamuli on the hind wing (six or seven hamuli) and a weakly elevated vertex.

Etymology: The new subgeneric name is a combination of Ancient Greek παρά (*pará*, meaning, ‘near’ or ‘beside’) and *Drepanium* Robertson [itself formed of Ancient Greek δρεπάνη (*drepanē*, meaning, ‘sickle’ or ‘scythe’) and the Latin suffix *-ium* (neuter of *-ius*, adjective-forming suffix)]. The gender of the name is neuter.

ZooBank LSID: urn:lsid:zoobank.org:act:60F41D74-544C-4E80-9D08-1A3BE8E25CE7.

Xystoclops subgen. n.

Type species: Sphecodes hirtellus Blüthgen, 1923.

Diagnosis: *Xystoclops* is quite similar to *Drepanium* (e.g., simple female mandible and lack of a preoccipital carina) but can be distinguished by the absence of spinelike setae on the retrodorsal margin of the female metatibia.

Etymology: The new subgeneric name is a combination of Ancient Greek ξυστός (*xustós*, meaning, ‘scraped’, ‘cropped’, or ‘shaved’)] and κλώψ (*klōps*, meaning, ‘thief’). The name refers to the absence of the metatibial spine-like setae. The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:60C78AA3-CC78-4456-BAD5-229474B19979.

Eusphecodes subgen. n.

Type species: Sphecodes olivieri Lepeletier de Saint Fargeau & Audinet-Serville, 1828.

Diagnosis: *Eusphecodes* includes those species with a subapical tooth or subapical angle and a larger number of distal hamuli on the hind wing. The preoccipital carina is present laterally, and most importantly, there is a characteristic transverse ridge or keel on the vertex.

Etymology: The new subgeneric name is a combination of Ancient Greek prefix εὖ– (*eu*–, meaning, ‘good’, ‘well’, ‘genuine’, or ‘true’) and *Sphecodes* Latreille (for derivation of *Sphecodes* refer to etymology of *Trichosphecodes*, *supra*). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:F73F27C8-5326-47BC-94ED-848744C44E1F.

Caenocleptes subgen. n.

Type species: Sphecodes niger Hagens, 1874.

Diagnosis: *Caenocleptes* encompasses a group of Eurasian species similar to *Sphecodium*, with the hind wing bearing a smaller number of distal hamuli and the female mandible with a subapical tooth or subapical angle. Unlike Old World *Sphecodium*, the hypoepimeral area is polished and largely smooth, the sculpturing differing noticeably from that of the remainder of the mesepisternum.

Etymology: The new subgeneric name is a combination of the Ancient Greek adjective καινός (*kainós*, meaning, ‘novel’ or ‘new’) and κλέπτης (*kléptēs*, meaning, ‘thief’). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:216E4404-D0EF-458C-9AD4-836E6888A67A.

Callocleptes subgen. n.

Type species: Sphecodes rufichelis Strand, 1911 [1912].

Diagnosis: *Callocleptes* is an African subgenus similar to *Sphecodes s.str.*, but differs in that the basal area of the propodeum is about as long as the metanotum (versus about as long as the mesoscutellum), combined with an absence of spinelike setae on the retrodorsal margin of the female metatibia.

Etymology: The new subgeneric name is a combination of Ancient Greek κάλλος (*kállōs*, meaning, ‘noble’ or ‘beauty’) and κλέπτης (*kléptēs*, meaning, ‘thief’). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:1A1109FA-22FF-4496-810B-9A97A880287D.

Nomioleptes subgen. n.

Type species: Nomia rudiusscula Benoist, 1963 [1964].

Diagnosis: This subgenus is immediately distinctive for the explanate anterior and apicolateral margins of the tegula, superficially resembling the enlarged tegulae of

some nomiines (and perhaps partially leading Benoist to place his species in *Nomia*). In addition, the retrodorsal margin of the female metatibia lacks spinelike setae, the female mandible has a subapical tooth, the preoccipital carina is present laterally at least weakly so, the vertex lacks a distinct ridge, and the hind wing has a larger number of distal hamuli.

Etymology: The new subgeneric name is a combination of Ancient Greek *Νομία* (*Nomia*, an Arcadian nymph and a reference to the genus *Nomia* Latreille) and *κλέπτης* (*kléptēs*, meaning, ‘thief’). The gender of the name is masculine.

ZooBank LSID: urn:lsid:zoobank.org:act:5679A99D-59A5-4B32-AA08-14C286AAE1C7.

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APPENDIX I

Checklist of species of Sphecodina

The following list summarizes currently valid species of Sphecodina (as of 24 July 2023), arranged by their placement to genus and subgenus. Synonyms are not indicated. Type species are indicated by an asterisk (*). Species of *Sphecodes* Latreille are not arranged as to subgenus given that I have yet to examine definitively identified material of perhaps 35% of the diversity and existing descriptions are inadequate for evaluating the placement of those species.

Genus *Austrosphecodes* Michener s.l.
subgenus *Austrosphecodes* Michener s.str.

A. andinus (Schrottky)
A. arequipae (Meyer)
A. argentinus (Schrottky)
A. asmodeus Gonçalves & Pereira
A. balrog Gonçalves & Pereira
A. bogotensis (Meyer)
A. bonaerensis (Holmberg)
A. brasiliensis (Schrottky)
A. bruchi (Schrottky)
A. cerberus Gonçalves & Pereira
A. chilensis (Spinola)*
A. convergens (Michener)
A. cordillerensis (Jørgensen)
A. costaricensis (Friese)
A. equator (Vachal)
A. friesei (Herbst)
A. gorgon Gonçalves & Pereira
A. granulosus (Sichel)
A. krampus Gonçalves & Pereira
A. inornatus (Schrottky)
A. joergenseni (Meyer)
A. jurupari Gonçalves & Pereira
A. laetus (Meyer)
A. lucifer Gonçalves & Pereira

A. lunaris (Vachal)
A. melanopus (Schrottky)
A. mendocinus (Jørgensen)
A. minarum (Schrottky)
A. mutillaeformis (Schrottky)
A. orcus Gonçalves & Pereira
A. pallitarsis (Vachal)
A. paraguayensis (Schrottky)
A. patagonicus (Schrottky)
A. peruensis (Meyer)
A. rufiscapis (Vachal)
A. rugulosus (Sichel)
A. tartarus Gonçalves & Pereira
A. vachali (Meyer)

subgenus *Melissoleptis* Gonçalves

A. albifacies (Gibbs)
A. capriciosus (Schrottky)
A. coriae (Moure & Hurd)*
A. diabolitus (Gibbs)
A. genaroi (Engel)
A. nigrinus (Ashmead)
A. tainoi (Engel)
A. variabilis (Schrottky)

Genus *Caenosphecodes* Engel

C. pseudoredivivus
 (Astafurova & Proshchalykin)*

-
- C. redivivus* (Blüthgen)?
C. sauteri (Meyer)
C. simlaensis (Blüthgen)?
Genus Callosphécodes Friese
C. manskii (Rayment)
C. ralunensis (Friese)*
Subgenus Eupetersia Blüthgen s.l.
subgenus Cephalosphécodes Engel
E. macrocephala Pauly*
E. mandibulata Benoist
subgenus Eupetersia Blüthgen s.str.
E. angavokely Pauly & Brooks
E. arnoldi Blüthgen
E. atra Pauly & Brooks
E. atrocoerulea Pauly & Brooks
E. avontuurensis Kuhlmann
E. bequaerti (Meyer)
E. clypeata Blüthgen
E. coerulea Blüthgen
E. constricta (Benoist)
E. emini Blüthgen
E. guillarmodi Michener
E. lasurea (Friese)
E. lettowvorbecki Blüthgen
E. neavei Blüthgen*
E. paradoxa Blüthgen
E. plumosa Pauly
E. robusta Benoist
E. ruficauda Pauly
E. ruficrus Blüthgen
E. rufipes Pauly
E. sakalava Blüthgen
E. seyrigi Blüthgen
E. similis Benoist
E. subcoerulea Pauly
E. violacea Pauly
E. wissmanni Blüthgen
subgenus Nesoeupetersia Blüthgen
E. dnophera Engel
E. picea Blüthgen
E. scotti (Cockerell)*
E. yanegai Pauly
subgenus Pollinicleptis Engel
E. malayensis (Blüthgen)
E. nathani Baker*
E. sabahensis Pauly
E. singaporensis Pauly
subgenus Xanthocleptis Engel
E. reticulata (Benoist)*
Genus Melittocleptes Engel
M. insularis (Smith)*
Genus Microsphécodes Eickwort & Stage s.l.
subgenus Baeosphécodes Engel
M. dominicanus (Stage)*
M. kittensis Engel
M. solitarius (Ashmead)
M. thoracicus (Ashmead)
M. xaymacensis Engel
subgenus Microsphécodes Eickwort & Stage s.str.
M. amazonophilus Mählmann & Engel
M. eickworti Engel
M. kathleenae (Eickwort)*
M. multirugosus Engel
M. quechua Engel
M. russeichypeatus (Sakagami & Moure)
M. stenochorus Engel
M. truncaticaudus Michener
subgenus Trichosphécodes Engel
M. trichomus Michener
M. trichophthalmus Engel*
Genus Nesosphécodes Engel
N. anthracinus Engel*
N. halictophagus Engel
N. cubicola Engel
Genus Notoclops Engel
N. depressus (Gonçalves)*
Genus Ptilocleptis Michener
P. eickworti (Michener)
P. polybioides Michener
P. tomentosus Michener*
Genus Sphecodes Latreille s.l.
S. abessinicus Friese
S. aeneiceps Friese
S. albifrons Smith
S. albilabris (Fabricius)
S. albociliatus Meyer
S. algoensis Blüthgen
S. almoransii Gupta & Saini
S. alternatus Smith
S. anaticus Warncke
S. anonymus Blüthgen
S. antennariae Robertson
S. arnoldi Blüthgen
S. aroniae Mitchell
S. arroyanus Cockerell
S. arvensiformis Cockerell
S. asclepiadis Cockerell
S. aspericollis Sichel
S. assamensis Blüthgen
S. atlanticus Warncke
S. atlantis Mitchell
S. atlassa Warncke
S. atriapicatus Strand
S. autumnalis Mitchell
S. bakeri Cockerell
S. banksii Lovell
S. barbatus Blüthgen
S. basalis Sichel
S. binghami Blüthgen
S. biroi Friese
S. bischoffi Blüthgen
S. bluethgeni Astafurova & Proshchalykin
S. borealis Cockerell
S. brachycephalus Mitchell
S. braunsi Blüthgen
S. brevisulcatus Engel
S. brunneipes Friese
S. californicus Meyer
S. cameronii (Bingham)
S. capensis Cameron
S. carolinus Mitchell
S. castaneae Mitchell
S. centralis Cockerell
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<i>S. chaprensis</i> Blüthgen	<i>S. ignitus</i> Cockerell
<i>S. chinensis</i> Meyer	<i>S. ikudomei</i> Mitai & Tadauchi
<i>S. clematidis</i> Robertson	<i>S. illinoensis</i> (Robertson)
<i>S. clypeatus</i> Friese	<i>S. ilyadadaria</i> Astafurova
<i>S. columbiae</i> Cockerell	<i>S. intermedius</i> Blüthgen
<i>S. confertus</i> Say	<i>S. invidus</i> (Cameron)
<i>S. confusus</i> Blüthgen	<i>S. iridescent</i> Cockerell
<i>S. congoensis</i> (Benoit)	<i>S. iridipennis</i> Smith
<i>S. connexus</i> Blüthgen	<i>S. ituriensis</i> Blüthgen
<i>S. cordovensis</i> Cockerell	<i>S. javanicus</i> Friese
<i>S. coronus</i> Mitchell	<i>S. johnsonii</i> Lovell
<i>S. crassanus</i> Warncke	<i>S. kershawi</i> Perkins
<i>S. crassicornis</i> Smith	<i>S. kincaidii</i> Cockerell
<i>S. crassus</i> Thomson	<i>S. kozlovi</i> Astafurova & Proshchalykin
<i>S. crawfordi</i> Mitchell	<i>S. lasimensis</i> Blüthgen
<i>S. cressonii</i> (Robertson)	<i>S. laticaudatus</i> Tsuneki
<i>S. cristatus</i> Hagens	<i>S. laticeps</i> Meyer
<i>S. croaticus</i> Meyer	<i>S. lautipennis</i> Cockerell
<i>S. dathei</i> Schwarz	<i>S. levicinctus</i> Cockerell
<i>S. davisii</i> Robertson	<i>S. levis</i> Lovell & Cockerell
<i>S. dichrous</i> Smith	<i>S. libericus</i> Cockerell
<i>S. dilutus</i> Cockerell	<i>S. longuloides</i> Blüthgen
<i>S. direptus</i> Cockerell	<i>S. longulus</i> Hagens
<i>S. discoverlifei</i> Astafurova & Proshchalykin	<i>S. luteiventris</i> Friese
<i>S. dissimilandus</i> (Cameron)	<i>S. luzonicus</i> Blüthgen
<i>S. distinctus</i> Meyer	<i>S. macswaini</i> Michener
<i>S. duplex</i> Blüthgen	<i>S. magnipunctatus</i> (Cockerell)
<i>S. dusmeti</i> Blüthgen	<i>S. majalis</i> Pérez
<i>S. dutti</i> Blüthgen	<i>S. manchurianus</i> Strand & Yasumatsu
<i>S. ebmeri</i> Astafurova & Proshchalykin	<i>S. mandibularis</i> Cresson
<i>S. electrum</i> Engel	<i>S. manni</i> Cockerell
<i>S. engeli</i> Astafurova & Proshchalykin	<i>S. marginatus</i> Hagens
<i>S. ephippius</i> (Linnaeus)	<i>S. mariyammanus</i> Tsuneki
<i>S. eritrinus</i> Friese	<i>S. matheranensis</i> Blüthgen
<i>S. eugnathus</i> Blüthgen	<i>S. metanotiaes</i> Sichel
<i>S. eustauros</i> Engel	<i>S. metathoracicus</i> Sichel
<i>S. eustictus</i> Cockerell	<i>S. mexicanorum</i> Cockerell
<i>S. exaltus</i> Mitchell	<i>S. millsii</i> Cockerell
<i>S. fattigi</i> Mitchell	<i>S. miniatus</i> Hagens
<i>S. ferruginatus</i> Hagens	<i>S. minor</i> Robertson
<i>S. fimbriatus</i> Blüthgen	<i>S. monilicornis</i> (Kirby)
<i>S. formosanus</i> Cockerell	<i>S. montanus</i> Smith
<i>S. fortior</i> Cockerell	<i>S. murotai</i> Tsuneki
<i>S. fragariae</i> Cockerell	<i>S. nagasei</i> Mitai & Tadauchi
<i>S. fuelleborni</i> Blüthgen	<i>S. nambui</i> Tsuneki
<i>S. fulvicornis</i> Blüthgen	<i>S. natalensis</i> Friese
<i>S. fumipennis</i> Smith	<i>S. niger</i> Hagens
<i>S. galeritus</i> Blüthgen	<i>S. nigeriae</i> Blüthgen
<i>S. galerus</i> Lovell & Cockerell	<i>S. nigricans</i> Timberlake
<i>S. geoffrellus</i> (Kirby)	<i>S. nigricorpus</i> Mitchell
<i>S. gibbus</i> (Linnaeus)*	<i>S. nippon</i> Meyer
<i>S. grahami</i> Cockerell	<i>S. nipponicus</i> Yasumatsu & Hirashima
<i>S. guineensis</i> Vachal	<i>S. nitidissimus</i> Cockerell
<i>S. hagensi</i> Ritsema	<i>S. nomioidis</i> Pesenko
<i>S. hakkariensis</i> Warncke	<i>S. nyassanus</i> Strand
<i>S. haladai</i> Warncke	<i>S. okuyetsu</i> Tsuneki
<i>S. hemirhodurus</i> Cockerell	<i>S. olivieri</i> Lepeletier & Audinet-Serville
<i>S. heraclei</i> Robertson	<i>S. oneili</i> Cameron
<i>S. hirtellus</i> Blüthgen	<i>S. paraplesius</i> Lovell
<i>S. howardi</i> Cockerell	<i>S. patruelis</i> Cockerell
<i>S. hyalinatus</i> Hagens	<i>S. pectosensis</i> Cockerell
<i>S. hydrangeae</i> Mitchell	<i>S. pectoralis</i> Morawitz

<i>S. pellucidus</i> Smith	<i>S. scrobiculatus</i> Pauly & Brooks
<i>S. perlustrans</i> Cockerell	<i>S. semicoloratus</i> (Cockerell)
<i>S. perplexus</i> Nurse	<i>S. senegalensis</i> Sichel
<i>S. persimilis</i> Lovell & Cockerell	<i>S. setiger</i> Blüthgen
<i>S. pesenkoi</i> Astafurova & Proshchalykin	<i>S. shawi</i> Lovell
<i>S. pieli</i> Cockerell	<i>S. shillongensis</i> Blüthgen
<i>S. pilosulus</i> Smith	<i>S. sibuyanensis</i> Cockerell
<i>S. pimpinellae</i> Robertson	<i>S. sikkimensis</i> Blüthgen
<i>S. pinguiculus</i> Pérez	<i>S. simillimus</i> Smith
<i>S. politulus</i> Cockerell	<i>S. smilacinae</i> Robertson
<i>S. profugus</i> Cockerell	<i>S. solidaginis</i> Cockerell
<i>S. propinquus</i> Blüthgen	<i>S. solonis</i> Graenicher
<i>S. prosphorus</i> Lovell & Cockerell	<i>S. sophiae</i> Cockerell
<i>S. prostygius</i> Mitchell	<i>S. spinulosus</i> Hagens
<i>S. pseudocrassus</i> Blüthgen	<i>S. strandi</i> Meyer
<i>S. pseudofasciatus</i> Blüthgen	<i>S. stygius</i> Robertson
<i>S. pulsatillae</i> Cockerell	<i>S. subconfertus</i> Sichel
<i>S. punctatus</i> Sichel	<i>S. sulcatulus</i> Cockerell
<i>S. puncticeps</i> Thomson	<i>S. sulcifera</i> Tsuneki
<i>S. puncticollis</i> Sichel	<i>S. tadschicus</i> Blüthgen
<i>S. punctiscutum</i> Eardley & Urban	<i>S. takaensis</i> Blüthgen
<i>S. pusillus</i> Cockerell	<i>S. tanoi</i> Tsuneki
<i>S. pycnanthemii</i> Robertson	<i>S. tantalus</i> Nurse
<i>S. quadrimaculatus</i> Blüthgen	<i>S. tertius</i> Blüthgen
<i>S. quettensis</i> Blüthgen	<i>S. togoanus</i> Strand
<i>S. ranunculi</i> Robertson	<i>S. townesi</i> Mitchell
<i>S. reticulatus</i> Thomson	<i>S. trjapitzini</i> Astafurova & Proshchalykin
<i>S. rhois</i> (Cockerell)	<i>S. trentonensis</i> Cockerell
<i>S. rohweri</i> Cockerell	<i>S. tristellus</i> Cockerell
<i>S. rotundiceps</i> Cockerell	<i>S. tuckeri</i> Fries
<i>S. rubicundus</i> Hagens	<i>S. turanicus</i> Astafurova & Proshchalykin
<i>S. rubripes</i> Spinola	<i>S. turneri</i> Cockerell
<i>S. rudiusculus</i> (Benoist)	<i>S. ugandae</i> Blüthgen
<i>S. rufichelis</i> Strand	<i>S. uttaricus</i> Astafurova & Proshchalykin
<i>S. ruficrus</i> (Erichson)	<i>S. veganus</i> Cockerell
<i>S. rufiventris</i> (Panzer)	<i>S. villosulus</i> Schwarz
<i>S. rufoantennatus</i> Benoit	<i>S. vumbuensis</i> Blüthgen
<i>S. samarensis</i> Blüthgen	<i>S. washingtoni</i> Cockerell
<i>S. sandykachis</i> Astafurova & Proshchalykin	<i>S. wheeleri</i> Mitchell
<i>S. saxicolus</i> Warncke	<i>S. woodi</i> Cockerell
<i>S. scabricollis</i> Wesmael	<i>S. zacatuche</i> Engel
<i>S. schenckii</i> Hagens	<i>S. zangherii</i> Noskiewicz
<i>S. schoanus</i> Blüthgen	Genus <i>Thrausmus</i> Buysson
<i>S. schwarzi</i> Astafurova & Proshchalykin	<i>T. grandidieri</i> (Buysson)*

APPENDIX II

A new Malaysian species of *Eupetersia*

While this paper was in review a distinctive new species of *Eupetersia* came to my attention. Rather than follow this work with another small taxonomic paper on a genus treated herein I have appended a brief description and set of figures for this species.



Fig. 62. — *Eupetersia (Nesoeupetersia) dnophera* sp. n., holotype, ♂, from Sabah, Malaysia, lateral habitus.

Genus *Eupetersia* Blüthgen s.l.

Subgenus *Nesoeupetersia* Blüthgen

***Eupetersia (Nesoeupetersia) dnophera* sp. n.**

(Figs 62–70)

Diagnosis: This a comparatively large species noteworthy for its deep black coloration (lacking the broader areas of orange on the mesosoma found in species such as *E. yanegai* and *E. scotti*, as well as the yellow legs of the latter), strongly bigibbous (almost bituberculate) mesoscutellum, and unique terminalia (Figs 67–70).

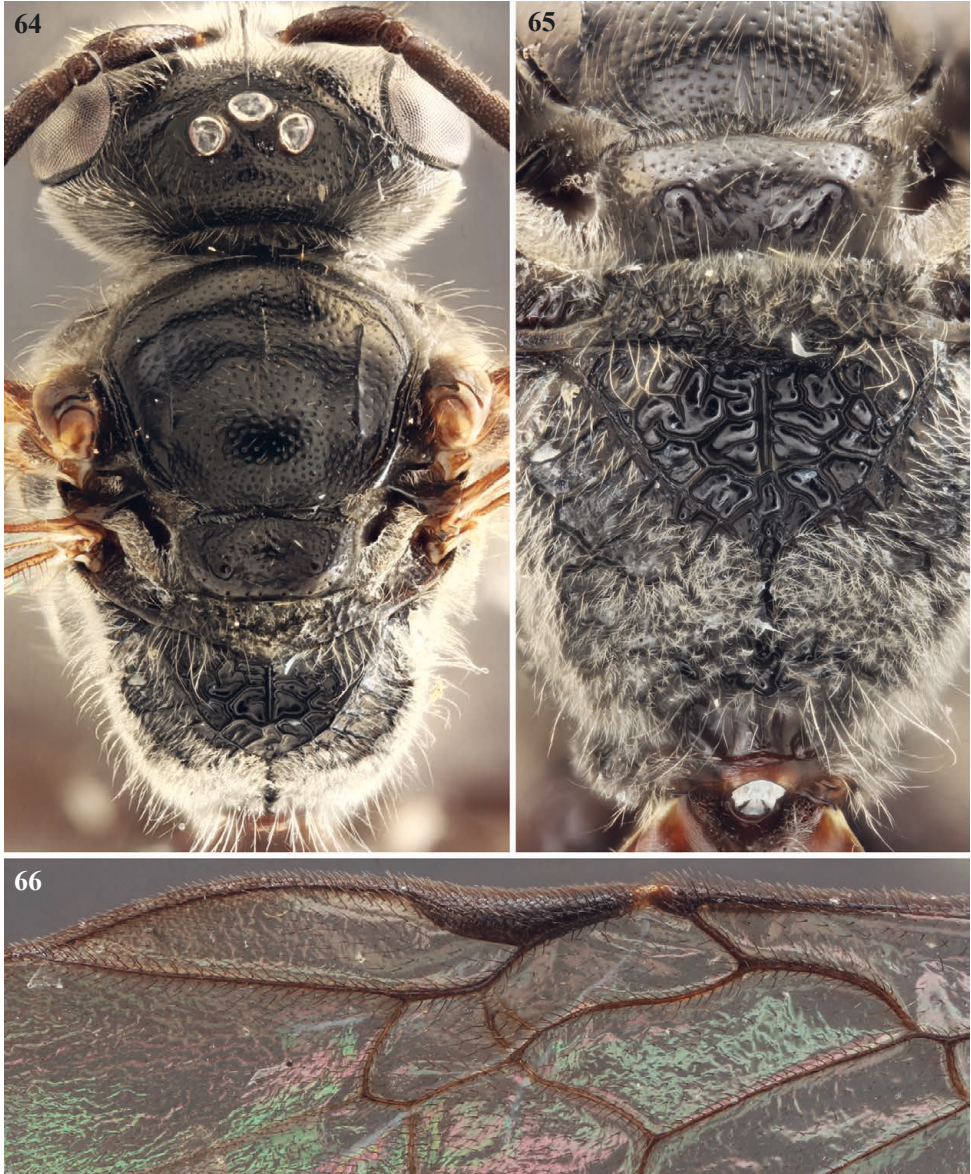
Description

♂: Total body length 7.37mm, forewing length 6.00mm. Head broader than long, width (maximum width across compound eyes) 2.02mm, length (as measured from clypeal apex to peak of vertex in facial view) 1.52mm; upper interorbital distance 1.25mm, lower interorbital distance 1.04mm. Mandible simple, long but shorter than compound eye length. Malar space linear.

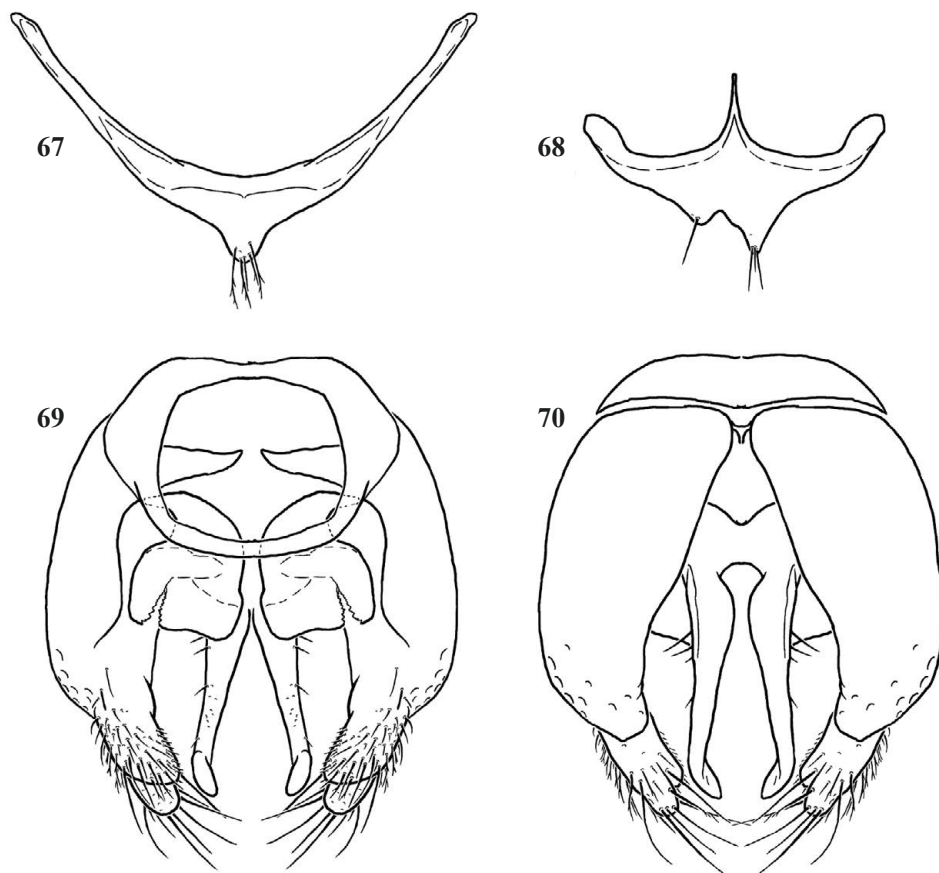


Fig. 63. — *Eupetersia (Nesoeupetersia) dnophera* sp. n., holotype, ♂, facial view.

Epistomal sulcus broadly obtuse. Frontal line strongly carinate from elevated peak at lower tangent of antennal toruli to point on upper frons where sparser punctation begins, slightly more than one median ocellar diameter in front of median ocellus. Scape slightly longer than torulocellar distance, length 0.69mm. Intertergular distance 1.31mm. Mesoscutellum deep depression, surface therefore bigibbous, paramedial elevations pronounced. Hind wing with five distal hamuli arranged 2-1-2. Terminalia as in Figs 67–70.



Figs 64–66. — *Eupetersia (Nesoeupetersia) dnophera* sp. n., holotype, ♂: 64, Dorsal view of head and mesosoma; 65, Dorsal-posterior oblique view of propodeum, metanotum, and mesoscutellum; 66, Apical-anterior forewing venation of left wing (note the anteriorly merged 2Rs and 1Rs-m).



Figs 67–70. — *Eupetersia* (*Nesoeupetersia*) *dnophera* sp. n., holotype, ♂, terminalia: 67, Metasomal sternum VII; 68, Sternum VIII; 69, Genital capsule, ventral view; 70, Genital capsule, dorsal view.

Clypeus with irregular-sized, shallow punctures separated by less than a puncture width, integument between punctures smooth and shining; supraclypeal area with small, deep, nearly contiguous punctures; face with distinct punctures separated by less than a puncture width, integument between punctures smooth and shining, punctures slightly more spaced in lower paraocular area and in area bordering ocelli, ocellocular area with punctures noticeably sparser than face, separated by 2–3× a puncture width; vertex with punctures as on face except on average slightly more spaced; gena with small punctures separated by 1–2× a puncture width, integument between punctures smooth and shining; postgena smooth with scattered setigerous punctures. Mesoscutum with small punctures separated by 1–2× a puncture width, punctures slightly more spaced anteriorly and outside of parapsidal lines, integument between punctures smooth and shining; mesoscutellum with punctures similar to mesoscutum except slightly denser, punctures separated by 0.5–1.5× a puncture width; metanotum rugulose; mesepisternum coarsely rugoso-areolate posteriorly extending into widely separated longitudinal striae and elongate areolae; hypoepimeral area with minute punctures separated by about a puncture width, integument between punctures smooth and shining; metepisternum rugoso-areolate; basal area of propodeum coarsely, irregularly rugoso-areolate, lateral and posterior surfaces coarsely rugoso-areolate. Metasomal terga smooth, terga I and II virtually impunctate aside from sparse setigerous punctures laterally, remaining terga with sparsely scattered setigerous punctures; sterna with

small, distinct punctures intermixed with larger, shallow punctures, puncture separated by 0.5–2× a puncture width, sparser on sternum II.

Head and mesosoma black except mandible, labiomaxillary complex, and antenna dark brown and tegula semi-translucent brown except lighter laterally and posteriorly; legs dark brown; wing veins dark brown, membranes hyaline clear; metasoma dark brown.

Pubescence bright white except that of wings fuscous; pattern of pubescence typical for genus.

♀: *Latet*.

Material examined

Holotype, ♂, MALAYSIA: Sabah (Borneo), Penampang Dist., Crocker Range, Kipandi Butterfly Park, 720m, 5°52'20"N, 116°14'53"E, 14–24.X.2011 [14–24 October 2011], Malaise, M. Hauser & S.D. Gaimari (AMNH).

Etymology: The specific epithet is the Ancient Greek adjective *δνοφερᾶ* (*dnopherā*), meaning, ‘murky’, ‘gloomy’, or ‘dark’, and is a reference to the coloration of the species.

ZooBank: urn:lsid:zoobank.org:act:45767C0B-846C-47BB-A2E5-162C39E7F44C

Remarks: The left forewing of the holotype has an aberrant formation of the second submarginal cell whereby 2Rs and 1rs-m are partly fused in their anterior third (Fig. 66). The result of this partial fusion is a narrow, triangular second submarginal cell separated from 3Rs (*i.e.*, there is no margin of the second submarginal cell anteriorly along what would be 3Rs). In the right forewing 2Rs and 1rs-m are wholly independent of each other and there is therefore an anterior border to the second submarginal cell along 3Rs.

Similarly, metasomal sternum VIII is asymmetrical (Fig. 68). When first dissected it was believed to be damaged but upon clearing and closer inspection it was clear that the sternum was complete and that one of the protrusions of the apical margin is significantly reduced relative to the other, although both bear distinct setae at their apices, indicating that the sternum developed this way. Whether this asymmetry is unique to this particular male, is variable within the species, or is fixed across all males remains to be discovered.

Key to Species of *Nesoeupetersia* (*sensu* herein)

- 1 Legs dark brown to black 2
- Legs wholly yellow to brownish yellow [Seychelles] *E. scotti* (Cockerell)
- 2(1) Pronotum, mesoscutum, and mesoscutellum black 3
- Pronotum, mesoscutum, and mesoscutellum orange [Thailand] *E. yanegai* Pauly
- 3(2) Mesoscutellum gently convex, not bigibbous; metasoma with yellowish pubescence [Madagascar] *E. picea* Blüthgen
- Mesoscutellum distinctly bigibbous; metasoma with bright white pubescence [Malaysia: Sabah] *E. dnophera* sp. n.