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# Revision of the Cleptoparasitic Bee Tribe Isepeolini (Hymenoptera: Anthophoridae)<sup>1</sup>

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# ABSTRACT

The tribe Isepeolini is interpreted to comprise the revalidated genus *Melectoides* Taschenberg, with 10 species, and *Isepeolus* Cockerell, with 11 species. The tribe is South American, with maximal diversity in Argentina and Chile. Three species are described as new and several synonyms and new combinations are proposed. A cladistic analysis, keys to the genera and species, descriptions and illustrations are provided.

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# INTRODUCTION

Bees of the tribe Isepeolini are cleptoparasites of bees of the genus *Colletes* Latreille, but they may have a wider host range, as suggested below. The first instar larva has large, sharp mandibles, which it uses to kill the host larva (Michener, 1957) before consuming the provisions stored in the nest. The tribe is endemic to South America. Its maximal diversity is in Argentina and Chile, but one species reaches as far north as Colombia. The purpose of the present paper is to clarify the generic composition of the tribe and to review the species of the two recognized genera.

The tribe is interpreted to comprise Melectoides Taschenberg and Isepeolus Cockerell. The genus Melectoides was properly recognized by Holmberg (1887), Brèthes (1909) and Ducke (1912), but later it disappeared from the literature. Schrottky (1902) mistakenly identified and diagnosed specimens of Leiopodus lacertinus Smith as Melectoides senex Taschenberg, creating a lasting confusion on the identity of Melectoides. Sandhouse (1943) listed Melectoides as a junior synonym of Leiopodus Smith. Taschenberg's genus is revalidated here and its scope broadened to include several species previously treated as Isepeolus.

The genus Isepeolus has been considered a close relative of Leiopodus (Protepeolini). Moreover, the two genera have been confused in the past. Ducke (1907) treated the Isepeolus species known to him as Leiopodus, and Jörgensen (1909) described two species of Leiopodus as Isepeolus. Ducke (1912) clarified the limits of both genera. Linsley and Michener (1939) included Isepeolus in their new tribe Protepeolini. The unusually large arolium of the pretarsus is the most conspicuous feature that supports such a relationship. Later Michener (1944), even though including Protepeolus, Leiopodus and Isepeolus in that tribe, suggested that Isepeolus might belong in a separate tribe, in consideration of its largely bare, papillate wings, long first flagellomere and articulated male gonostylus. Rozen et al. (1978) remarked on the striking divergence of Protepeolus and Isepeolus in larval morphology, dismissed a close relationship between them, and proposed the monotypic tribe Isepeolini. It should be noted that the females of both tribes have modified apical segments of the metasoma, probably related to the process of oviposition, but they are modified in completely different fashions. The Isepeolini have the sixth sternum specialized, bearing a single sclerotized apical point, sometimes bordered by spinelike setae. It is the sixth tergum which is modified in the Protepeolini, with spinelike setae at each side of the spatulate apex, the sixth sternum being unspecialized.

The distinctiveness of the Isepeolini is well supported by both larval and adult morphology, but its phylogenetic relationships remain elusive. Isepeolines have been customarily considered as members of the Nomadinae. Rozen (1966), in his study of Nomadinae larvae, found that Isepeolus was in many respects plesiomorphic and in others quite divergent from nomadines, and suggested that it might represent a basal branch to that group, or even an independent lineage from nonparasitic ancestors. Bohart (1970) also suggested a separate origin. Nevertheless the Isepeolini have been included in the Nomadinae in recent studies (Rozen et al., 1978; Alexander, 1990). Roig-Alsina (1989, 1990) excluded several genera from the Nomadinae, suggesting later in a tribal analysis of the group (1991) that the subfamily is monophyletic in such a restricted sense. He could not find any synapomorphy uniting the Isepeolini (or the Protepeolini) to the re-defined Nomadinae. The tribe was left in an uncertain position, since it may still be the sister group of the Nomadinae, or belong elsewhere in the Anthophoridae. J. G. Rozen, Jr. (in press) is advancing a new hypothesis, based on the analysis of first instar larvae, that suggests a close relationship to the cleptoparasitic tribe Ericrocidini.

Systematic accounts of the Isepeolini consist mainly of species descriptions. Exceptions are the contributions of Grütte (1935), who separated and diagnosed as species groups of *Isepeolus* the two genera here recognized, and of Toro and Rojas (1968), who published a useful key to the Chilean species. The present contribution is the first revision of the group.

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#### MATERIALS AND METHODS

Material studied, including types, was obtained from several collections. I am indebted to the following: American Museum of Natural History, New York, J. G. Rozen, Jr. (AMNH); California Academy of Sciences, San Francisco, W. J. Pulawski (CAS); Central Texas Melittological Institute, Austin, J. L. Neff (CTMI); Florida State Collection of Arthropods, Gainesville, L. A. Stange (FSCA); M. Fritz, Rosario de Lerma, Salta (MF); Instituto Miguel Lillo, Tucumán, A. Willink (IML); Martin Luther Universität, Halle, M. Dorn; Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata, La Plata, R. Ronderos (MLP); Natural History Museum, London, G. R. Else; National Museum of Natural History, Washington, R. J. McGinley (USNM); Naturhistorisches Museum, Bern, H. D. Volkart; Snow Entomological Museum, University of Kansas, Lawrence, C. D. Michener (SEM); Universidad Católica de Valparaíso, H. Toro (ÚCV); Universidade Federal do Paraná, Curitiba, J. S. Moure (UFPR); University of California, Davis, L. S. Kimsey; Utah State University, Logan, T. L. Griswold; Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch; Zoologisk Museum, Copenhagen, B. Petersen. The acronyms are used below to indicate depositories of specimens.

Morphological terminology of Michener (1944, 1965) has been followed, except that metapostnotum is used instead of propodeal triangle (Brothers, 1976). The metasomal terga (T) and sterna (S) are identified with Arabic numerals. Abbreviations used are upper interocular distance (UID), lower interocular distance (LID), ocello-ocular distance (OOL) and distance between posterior ocelli (POL). UID has been measured along the lower tangent of the anterior ocellus. The malar space has been measured at the level of the abductor swelling of the mandible. For easy comparison characters are numbered in the descriptions and are applicable to both genera. The cladograms were obtained with the help of the computer program Hennig86, version 1.5 (Farris, 1988).

#### BIOLOGY

Most of the published information indicates that isepeolines are parasitic in the nests of the genus Colletes. Host relationships are known for four species, and each one has been associated with more than one Colletes, indicating a low host specificity. Claude-Joseph (1926) associated Isepeolus luctuosus (Spinola) with C. cyanescens Haliday, C. araucariae Friese and C. laticeps Friese; Melectoides triseriatus (Friese) with the same three hosts; and I. septemnotatus (Spinola) with C. musculus. Michener (1957) reared I. viperinus (Holmberg) from nests of C. kerri Moure and from other unidentified Colletes; later Oliveira (1966) obtained the same species from nests of C. petropolitanus Dalla Torre. Two specimens of I. septemnotatus collected by P. Herbst in Cautín, Chile (CAS) bear the following labels: "raised from cell of Colletes seminitidus Spinola" and "raised from celi of Colletes musculus," respectively. Other records are those of Janvier (1933) and of Gazulla and Ruiz (1928), who reported a dense aggregation of C. laticeps heavily parasitized by I. luctuosus. Claude-Joseph (1926) mentioned Lonchopria zonalis (Reed) as the host of *I. viperinus* (Holmberg); since viperinus does not occur in Chile, it is uncertain what species he referred to.

The host relationships of isepeolines may be more varied than is suggested by the available data. The large *Melectoides senex* Taschenberg and *M. tucumanus* (Friese) (up to 16 mm long) need a similarly large host, and there is no species of *Colletes* of such a size in Argentina. Indirect evidence suggests *Caupolicana* as the possible host (J. Genise, personal communication).

There is a single record on the parasitic behavior of the adults. Claude-Joseph (1926) stated for *I. luctuosus*, "As soon as the *Colletes* provision the cells, they [*Isepeolus*] frequently visit the colonies and, in the absence of the owners, they lay an egg on the provisions." Claude-Joseph's observations should be taken cautiously, and new field studies are needed. Morphological specialization of female isepeolines suggests that they might hide their eggs in some way in the host cells. Females have a modified sixth sternum which ends in a sharp point and, depending on the group, may bear short or long spinelike setae. The possession of a modified abdominal apex is convergent with nonhomologous modifications in the Protepeolini and the Nomadinae (Roig-Alsina, 1991, and references therein), which are known to hide their eggs, embedding them in the cell walls (Rozen et al., 1978, and references therein). An analogous behavior can be expected for the Isepeolini. Another trend of specialization is seen in the mandibles of both sexes. Mandibles are elongate and sharp in the Melectoides senex group and tridentate in most Isepeolus. The functional meaning of such mandibles is not known; they may well be related to the female parasitic behavior.

Immatures of *I. viperinus* (Holmberg) are known in detail. Michener (1957) discovered and described the first stage larva, as well as the pupa. Oliveira (1966) and Rozen (1966) described the mature larva. A detailed comparison of isepeoline larvae to other parasitic anthophorids is to be found in Rozen et al. (1978) and Rozen (in press). The mature larva spins a cocoon before overwintering.

# CLADISTIC ANALYSIS

The monophyly of the Isepeolini is supported by the broad, apically fimbriate T6 of the female, which lacks any trace of a pygidial plate (character 5, Figs. 15, 16), by the apically sclerotized, pointed S6 of the female (character 6, Figs. 9–14 and 50–61), and by the large spatha of the male genitalia covering almost all the dorsum of the penis (character 11, Figs. 20, 71). The two first features are unique, but an enlarged spatha is present in other groups, although not to the extent seen in the Isepeolini. The Melectini and some Anthophorini have spathae with poorly defined apical margins, covering up to twothirds of the dorsum of the penis.

Striking features of the known larvae also support the distinctiveness of the Isepeolini. The first instar larva has a strongly depressed, prognathous head, with maxillae, labrum and hypopharynx forming a single sclerotized ventral plate (Michener, 1957; Rozen, in press). The presence of lateral body tubercles, the elongate labial and maxillary palpi and the single median labral tubercle of the mature larva are considered apomorphies of the tribe (Rozen, 1966; Rozen et al., 1978).

Primary analysis. A first analysis of the 21 species of Isepeolini was performed using as outgroups other tribes of Anthophoridae. As mentioned above, relationships of Isepeolini are not certain; hence all the tribes were considered to form a polytomy for outgroup comparison. This procedure has the drawback that only a reduced set of available characters, those invariant in the outgroups, can be polarized (characters 1-13 in Table 1). Until a general analysis of the anthophorid tribes is available, this is the alternative of choice. Characters with more than one apomorphic state were coded as nonadditive; all characters were given equal weight. Fourteen most parsimonious trees were obtained (tree length = 18steps. CI = 88, RI = 95). Ten trees resulted from the uncertainty in the position of M. fumipennis due to the lack of information on its male characters, and the apparent sister group relationships suggested are dismissed as artifacts. The four remaining topologies depend on the interpretation of the reduction of the male gonostylus (character 13); one of them is shown in Fig. 1a. Alternatively M. rozeni may be the sister group to all other Melectoides, and M. bellus and kiefferi may be united to the terminal polytomy or may be the sister group to it. The interpretation of character 13 is discussed below.

The analysis suggests that Melectoides and Isepeolus are monophyletic groups, and supports their recognition as distinct genera. Apomorphies of Melectoides are related to specializations of the terminal segments of the female metasoma. The fifth tergum is prolonged apically by a membranous rim bearing upcurved setae (character 4, Figs. 15, 16). The sixth sternum has a series of long spinelike setae bordering the apical point, and the lateral apical margin of the sternum is expanded, membranous, folded and clothed with short hairs (characters 7 and 8, Figs. 9-14). The lateral apical margin of S6 is variable in the outgroups; it can be more or less sclerotized or membranous, but the condition seen in Melectoides is unique. Isepeolus is supported by the presence of a subapical tubercle on the male sixth sternum

TABLE 1. List of apomorphous characters. In the primary analysis (characters coded with numbers) outgroups are other tribes of Anthophoridae; in the secondary analysis (characters coded with letters) each of the two major clades obtained in the primary analysis is used as the outgroup for the other.

1. Mandible with two subapical teeth (Fig. 43) (1). Mandible with one subapical tooth is the plesiomorphic condition in Anthophoridae (Michener and Fraser, 1978).

2. Labrum with arched transverse carina and two lower preapical tubercles (Fig. 44) (1). Tubercles and carinae are common features on the labra of cleptoparasitic bees, but such a labrum is unique for a group of species of *Melectoides*.

3. Claws of all legs of female and of middle and hind legs of male with inner ramus flattened and truncate apically (Figs. 47, 49) (1). An inner flattened ramus occurs in several cleptoparasitic bee groups (Michener, 1944), but in every case it is interpreted as the derived condition.

4. Apical margin of T5 of female prolonged by membranous, usually hyaline rim bordered by upcurved hairs (Figs. 15, 16) (1). No such rim in outgroups.

5. T6 of female without pygidial plate, apex broad and bordered with a fringe of hairs (Figs. 15, 16) (1). Unique feature of Isepeolini. A tapering tip of metasoma is the usual condition in Anthophoridae, and considered plesiomorphic.

6. S6 of female ending in sclerotized apical point (Figs. 9-14, 50-61) (1). Unique feature of Isepeolini.

7. S6 of female with short spinelike setae at each side of sclerotized apical point (Figs. 56-61) (1); spinelike setae long and curved (Figs. 9-14) (2). Absence of spinelike setae is the plesiomorphic condition. Females of several groups of Nomadinae have spinelike setae on S6, but on lateral lobes of the sternum, suggesting that the structures are not homologous.

8. S6 of female with lateral apical margin membranous, much expanded and folded (Figs. 9-14) (1). A simpler margin as in Figures 50-61 approaches the condition in outgroups.

9. S6 of male with subapical tubercle (Figs. 77-79) (1). Sternum without tubercle in outgroups. 10. Gonocoxite of male genital capsule with sub-basal constriction (Figs. 71, 73 and 75) (1). No such constricted capsule in outgroups.

11. Spatha of male genitalia large, extended dorsally as strong sclerotization almost to tip of penis (Figs. 20, 71) (1). Spatha continued by dorsal sclerotization of penis in some other anthophorids (Melectini, some Anthophorini) but never to the extent seen in Isepeolini.

12. Volsella of male genitalia absent (1). Volsella present is plesiomorphic condition for bees in general.

13. Gonostylus of male genitalia short, one-third to one-fourth as long as gonocoxite (1). Gonostylus reduced to small triangular pilose lobe, not fused (Figs. 30, 32) (2). Gonostylus a small lobe fused dorsally to gonocoxite (Fig. 20) (3). (This lobe may not be homologous to the gonostylus of other Isepeolini; if not, then a gonostylus would be absent.) Gonostylus variable in outgroups, but articulate, pilose and well developed is considered plesiomorphic for anthophorids. Gonostyli of most *Isepeolus* (Figs. 71, 73) and *M. rozeni* (Fig. 22) are interpreted as plesiomorphic.

a. Bees over 12.5 mm long (1). All *Isepeolus* and the *triseriatus* group of *Melectoides* range between 6 and 11 mm long.

b. Lateral ocellus separated from posterior margin of head by 1.2 ocellar diameters, or more (1). Vertex narrow, lateral ocellus separated from posterior margin of head by 0.6-1.1 ocellar diameters in *Isepeolus*.

c. Mandible narrow and elongate, approximately 3 times as long as basal width (Fig. 39) (1). Mandible at most 2.5 times as long as basal width in *Isepeolus*.

d. Hypoepimeral area with lower polished band (1). Hypoepimeral area thoroughly punctate or with small polished round spot above scrobe in *Isepeolus*.

e. S5 of female with broad, round apical notch; margin of notch with row of close hairs, basal to which are plumose hairs, longest medially, and at each side a group of stout setae (1). Notch basal to marginal row of hairs with bare, hyaline area that forms a band separating apical row from basal plumose hairs (2). Apex of S5 with notch V-shaped; margins of notch densely hairy and with no further specializations in *Isepeolus*.

f. S6 of female with sclerotized apical point sharp (Figs. 52-61) (1). Apical point spatulate, concave below, in all species of *Melectoides*.

g. S6 of female basal to spinelike setae with "pocket" (Fig. 14, p) (1). No such pocket in Isepeolus.

h. Apex of female metasoma extraordinarily broad, T6 more than half of maximum width of T2 (Fig. 68) (1). T6 approximately one-third as broad as maximum width of T2 in *Melectoides* and most *Isepeolus*.

i. S3 of male without fringe of hairs (1). S3 with well developed fringe of hairs in Melectoides.

j. T7 of male with broad bare basal band (basal one-third to one-half bare) (1). Hairs arising nearby to tergal base, as on other terga, in *Melectoides* and most *Isepeolus*.

k. Gonocoxite of male genitalia without digitiform ventral lobe (1). Gonocoxite with digitiform ventral lobe in all *Isepeolus* (Fig. 71).

(character 9, Figs. 77–79) and by the basal constriction of the gonocoxite (character 10, Figs. 71, 73, 75). The two genera are further characterized phenetically. The most conspicuous differences (shape of the head and sexual dimorphism of the first flagellomere) are given in the key to the genera; a more detailed list is given under each genus heading.

Both genera have species with spinelike setae bordering the sclerotized apical point of the female sixth sternum. The size and position of such setae are constant in each group: all species of Melectoides have setae long, curved, and directed upward; species of the viperinus group of Isepeolus have setae short, straight, and directed laterally. Since no intermediate cases are known that link the two types, the homology of the spinelike setae can be seen as problematic. Besides the nature of the setae, the shape of the sclerotized point is different, being spatulate and concave below in Melectoides, and usually conical in the viperinus group (I. lativalvis has a secondarily reduced apical point). In the analysis the two types were treated as derived states of the same character (homology assumed), but coded to evolve independently (nonadditively) from the plesiomorphic state. The cladogram obtained suggests that the acquisition of stout setae has occurred independently.

Secondary analysis. A second approach was attempted in order to resolve the polytomies seen in Fig. 1a. Characters that show variation in one of the two genera but are constant in the other can therefore be polarized. An additional 11 characters were found (characters a-k in Table 1). Two types of characters are included here, those that vary in the outgroups and therefore could not be polarized in the primary analysis (a, b, c, d, i, j), and those that are exclusive to the Isepeolini, so the observed variation could not be rationalized a priori (e, f, g, h, k). Again multistate characters were coded nonadditively. Two most parsimonious topologies were obtained (tree length = 33steps, CI = 84, RI = 92), differing in the interpretation of character g (female S6) in Melectoides. The new trees show a better resolution (Fig. 1b).

The basal position of *I. octopunctatus* within Isepeolus is reinforced, suggesting that the pointed inner tooth of the claws of both sexes of I. septemnotatus represents a reversed condition (character 3). The claws of the latter species look like those of the pollen-collecting outgroups, and before the analysis I. septemnotatus was a likely candidate as the sister species of all other Isepeolus. It is interesting to note that the fore claws of the males are always bifid, pointed, in the Isepeolini; since this condition has not completely disappeared it is possible to think that the reappearance of pointed claws in the mid and hind legs is due to some developmental rearrangement. Within the I. viperinus group two additional clades are distinguished. I. lativalvis and smithi are united by the broad apex of the female metasoma, and I. vachali and wagenknechti are united by the bare base of the male T7.

The basal ambiguity in Melectoides is resolved, further distinguishing the pair M. senex and tucumanus, and placing it as the sister group to all other Melectoides species. As mentioned above, the two topologies obtained in the secondary analysis differ in the interpretation of character g (basal pocket of female S6). If a reversal is allowed, a loss supports the clade M. niveiventris plus fumipennis; if g arises in parallel, the clade above M. rozeni becomes a trichotomy. The interpretation of characters e and g in Fig. 1b seems problematic. Character e in particular (S5 of female) is a complex feature with a peculiar arrangement of different types of setae, unlikely to have appeared twice de novo. A more satisfying topology would be with M. rozeni as sister taxon of the polytomy that includes M. triseriatus, etc. (Fig. 1c). Characters e and g would arise only once, M. rozeni would have lost the transverse carina of the labrum, and characters 13 and k (reduction of gonostylus, and reduction of ventral lobe of gonocoxite respectively) would arise convergently. This suggested topology is two steps longer, but in it new structures appear once and losses add to the homoplasy. It should be noted that a reduction of the gonostylus also occurs independently in a group of Isepeolus, and reduction of the genitalia in general is a common trend in many groups of bees.



Figure 1. Cladograms showing relationships of species of Isepeolini. a. Primary analysis. b. Secondary analysis. c, alternative interpretation of b; dashed line indicates tentative position for species known only from female, node being supported only by male characters. Bars indicate apomorphies, crosses indicate reversals. Characters numbered according to Table 1.

## KEY TO THE PARASITIC GROUPS OF SOUTH AMERICAN ANTHOPHORIDAE

A key is provided below to facilitate the recognition of the isepeolines among other groups of parasitic Anthophoridae in South America. The key will not work for other areas, since the Melectini and several tribes within the Nomadinae, which add to the variability of the subfamily, are not included. Current knowledge suggests that parasitism may have arisen independently in the seven groups presented below.

1. Metapleura strikingly narrow, meso-metapleural and metapleural-propodeal sutures close
together, appearing as only one suture. Gena bordered posteriorly by strong carina, which
reaches top of eye
-Metapleura broad, meso-metapleural and metapleural-propodeal sutures distinct and well
separated. Never with carina reaching top of eye
2. Forecoxa with ventral carina along inner margin and sometimes also along basal margin.
Neck with round ventral sclerite on cervical membrane. T5 of female with wide polished
apical margin, bordered by long hairs Osirini
-Forecoxa without carina, ventral inner margin rounded. Cervical membrane at most with
faint ventral sclerotization. T5 of female usually hairy to apex of tergum
3. S6 of female apically emarginate forming two projecting lobes or points, or sometimes
truncate; usually bearing spinelike setae. S6 of female concealed, usually only tip of apical
points or margin of truncate apex visible beyond apex of S5. T7 of male with distinct pygidial
plate; lateral margins of plate well defined. Exception is T7 of male Caenoprosopidini with
square apico-lateral angles and raised into central, apically bilobed area; in this case labrum
longer than wide
-S6 of female apically rounded or pointed; when spinelike setae present, S6 with conspicuous
apical sclerotized point. S6 of female visible beyond apex of S5. T7 of male with apex usually
bilobate or bidentate, sometimes apex more or less carinate, but never with pygidial plate
defined basal to it. Labrum usually wider than long, at most as long as wide
4. Basal vein of forewing arising from base of second cubital cell. First flagellomere longer than
second
-Basal vein of forewing arising from apex of first cubital cell. First flagellomere shorter than to
as long as second
5. T6 of female with apex broad, medially emarginate and margin with fringe of hairs longer at
sides. Mandible of male with sparse, long hairs on outer surface Isepeolini
-T6 of female with narrow spatulate apex, bordered by spinelike setae. Mandible of male with
dense brush of hairs on outer surface Protepeolini
6. Midtibial spur with apex bifid or multidentate. Foretibial spur with no prong coming out
from main axis
-Midtibial spur with apex pointed. Main axis of foretibial spur with strong prong at 90 degrees
to velum

#### TRIBE ISEPEOLINI

Diagnosis. Length 6 to 16 mm. Vestiture on head, thorax and propodeum usually long, erect; on metasoma short, appressed, usually forming distinctive patterns of pale and dark maculations. First flagellomere elongate, 1.8 to 5 times as long as second, broadened apically in females (apex twice as broad as base), variable in males. Mandible with one or two subapical teeth. Labrum transverse, with sides bent backward. Maxillary palpus with three to four flattened segments. Stipes with longitudinal ridge on outer surface; stipital comb absent. Gena frequently depressed behind eye. Preoccipital and paraocular carinae absent. Axilla rounded. Metanotum and propodeum steeply slanting to vertical. Claws usually with flat, truncate inner tooth in both sexes, but fore claws of males always bifid. Wings basally largely bare, beyond closed cells papillate. Forewing with three submarginal cells, pterostigma moderate, 2.3-3.4 times as long as wide. Marginal cell shorter than distance from its apex to wing tip (0.65-0.80 : 1); apex separated from wing margin, truncate to pointed. Jugal lobe of hindwing one-third as long as vannal lobe measured from wing base. T5 of female without pseudopygidial area. T6 of female without pygidial plate; apex broad, medially emarginate and margin with fringe of hairs longer at sides. S6 of female with apex sclerotized, forming a point; in some groups such a point bordered by spinelike setae. T7 of male without pygidial plate, but apical margin sclerotized. Male genitalia with gonostylus simple, articulate; volsella present, setose; spatha large, covering almost all dorsum of penis.

Most Isepeolini, with the single exception of

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*M. tucumanus*, have distinctive pale and dark color patterns on the metasoma due to short, dense, appressed hairs that form definite maculae. The pattern of maculation is not described in detail for each species in the present contribution (except for the new ones), since many of the original descriptions include illustrations of the patterns, or they can be easily recognized from the literature. The patterns are quite constant for most species. The extent and shape of the maculae in *I. viperinus* look alike over its entire range of distribution, from Colombia to southern Argentina. Other species that show constancy in pattern over large areas are *M. bellus* (from Salta to Río Negro in Argentina), *M. triseriatus* (from Atacama to Cautín in Chile), *I. septemnotatus* (from Coquimbo in Chile to Río Negro in Argentina) and *I. luctuosus* (from Copiapó in Chile to Chubut in Argentina). In some species the extent of the maculae is variable, mainly geographycally. Four such species are *I. vachali* (Fig. 67), *I. octopunctatus, I. atripilis* and *I. bufoninus;* the last one has wide white maculae on the metasoma of specimens from Buenos Aires, Argentina, but specimens from Paraná, Brasil, have the metasoma almost black. *I. cortesi* also presents latitudinal variation in the color pattern (Toro and Rojas, 1968).

# KEY TO THE GENERA OF ISEPEOLINI

1. Vertex of head between lateral ocellus and eye slightly rounded to flat in frontal view (Figs. 2-6, 8), at most with shallow depression (Fig. 7). First flagellomere of male conspicuously widened apically, as much as that of female (Figs. 33-35). Female S6 with sclerotized apex bordered by long spinelike setae, and lateral apical margin folded down, partially covering such setae (Figs. 9-14). Apex of female T5 prolonged by membranous rim bordered by upcurved hairs (Figs. 15, 16). Male S6 without subapical tubercle

Vertex of head with conspicuous depression near eye (Figs. 62-65). First flagellomere of male slightly widened apically, contrasting with conspicuously apically widened female first flagellomere (Figs. 36-38). Sclerotized apex of female S6 with spinelike setae absent or short, barely visible at low magnification; lateral apical margin not expanded, not folded down (Figs. 50-61). Apex of female T5 without membranous rim. Male S6 with conspicuous subapical tubercle (Figs. 77-79)

#### **GENUS** MELECTOIDES TASCHENBERG

Melectoides Taschenberg, 1883: 75. Type species: Melectoides senex Taschenberg, 1883, by original designation and monotypy.

Diagnosis. Length 7.5-16.0 mm. Head with vertex flat to slightly rounded. Gena behind eye depressed to rounded. Lateral ocellus surrounded by polished area, not wider than ocellar diameter. Inner orbit of eye in females concave to almost straight, of males almost straight to convex. Distance from lateral ocellus to posterior margin of head 0.74-1.40 times ocellar diameter. First flagellomere equally widened apically in males and females. Mandible with one subapical tooth. Hind coxa with upper external margin strongly keeled to carinate. Marginal cell with apex rounded or pointed, not truncate. T5 of female with subapical band of dense hairs and apex of tergum prolonged by membranous rim with upcurved hairs. S6 of female with sclerotized apical point curved, spatulate, concave below; apical point bordered by 4-8 long spinelike setae at each side; lateral apical margin of sternum membranous, enlarged and folded. S3-5 of male with dense apical fringes of hairs. S6 of male densely hairy, without subapical tubercle. S7 and S8 of male with disc reduced. Gonocoxite of male genitalia rounded basally.

The genus *Melectoides* includes two distinctive groups of species. *M. senex* and *tucumanus* are

robust bees with extensive metallic pubescence that much resemble some ericrocidines, in particular those of the genus Mesonychium Lepeletier and Serville. They have several unique features (characters 12, 14, a, c, in Table 1 and Fig. 1). The group can be further distinguished by the eyes of the female slightly converging below (proportion of LID to UID, 0.95-0.98 : 1), the eyes of the male diverging below (proportion of LID to UID, 1.15 : 1), the lateral ocellus of the female separated from the occipital margin by 0.7-0.8 times the diameter of the ocellus, the long first flagellomere of both sexes subequal to sum of flagellomeres 2-4 in the female (1: 0.93-1.02), longer in the male (1:0.78) and the hind coxa with the upper external margin sharply keeled.

A second, more numerous group, formed of smaller species of predominantly dark and white pubescence, has been treated in the literature as *Isepeolus*. Despite the similarity to *Isepeolus* in size and color, they share derived structural characters with the *senex* group and should be placed in *Melectoides*. Most species, with the exception of M. *rozeni*, are easily recognized by the arched labral carina. The group is distinguished by the eyes converging below in both sexes (proportion of LID to UID, females 0.75-0.85: 1, males 0.83-0.95: 1), the lateral ocellus of the female separated from the occipital margin by 1.1-1.4 times the diameter of the ocellus, the first flagellomere of the female shorter than the sum of flagellomeres 2-4 (1:1.5-1.8), subequal to shorter in males (1:0.95-1.65) and the hind coxa with the upper external margin mostly rounded, at most with a weak carina. Three subgroups can be recognized, one including *niveiventris* and *fumipennis*, another with *rozeni*, and a third with the remaining species. Their relationships and the supporting characters are discussed in the cladistic analysis.



Figures 2-14. 2-8, heads of *Melectoides* species. 2, 3, *M. politus*, female; 4, *M. politus*, male; 5, *M. senex*, female; 6, *M. senex*, male; 7, *M. niveiventris*, female; 8, *M. fumipennis*, female holotype. 9-14, S6 of *Melectoides* species, lateral and ventral views. 9, 10, *M. tucumanus*; 11, 12, *M. fumipennis*; 13, 14, *M. kiefferi*; p, pocket; m, membranous lateral apical margin. Scale lines 1 mm.

### CLEPTOPARASITIC BEE TRIBE ISEPEOLINI

#### KEY TO THE SPECIES OF MELECTOIDES

1. Large species, 12.5–16.0 mm long. Pubescence of metasoma metallic, bluish or greenish. Mandible elongate 2.85 (males) to 3.25–3.30 (females Fig. 39) times as long as basal
width
-Medium-sized species, 7.5-11.0 mm long. Pubescence of metasoma not metallic, brown to
black with white maculation. Mandible of both sexes $2.0-2.3$ times as long as basal width (Figs. 40, 41)
(Figs. 40, 41)
those on T1-3 narrow, on T4 widest medially, T2-4 with bands also widened on sides of terga:
male with similar pattern, but band on T1 absent, on T5-6 widest medially. Both sexes with
white hairs on face, vertex, scape, pronotal lobe and scutum above tegula 1. senex Taschenberg
-Pubescence of metasoma bluish with no maculations. White hairs absent or restricted to face
around antennal sockets and spot above tegula
5. Labrum at most with two rounded elevations in center of disc separated by median longitudinal depression. Gonostylus of male genitalia as long as gonocovite 5. rozeni (Toro)
—Labrum with strong arched carina and two preapical tubercles (sometimes fused into single
one); usually lateral parts of carina nearly parallel to sides of labrum (Fig. 44). Gonostylus of
male genitalia one-third or less as long as gonocoxite
4. Integument of scutellum and metanotum red. Hairs of mesopleuron below hypoepimeral
area appressed, short, as long as or shorter than diameter of pedicel
Integument of morax black. Trans of mesopleuron below hypoepimeral area usually erect,
5. Wings infuscated. Membranous apical rim of female T5 almost reaching sides of tergum in
dorsal view (Fig. 17); apex of T5 approximately one-fourth as wide as apex of T2. Maxillary
palpus with second segment longer than wide. (Only female known.) 4. fumipennis n. sp.
-Wings hyaline. Membranous apical rim of female T5 restricted to central part of tergum in
dorsal view (Figs. 15, 19); apex of 15 over one-third as wide as apex of 12. Maxillary palpus
6. T1 with continuous apical band of white bairs. T2 with extended white pubescence on sides
and apical margin, leaving central dark area and 2 small black spots; T5–7 of male white; T5
of female mostly white, leaving distinctive apical anchor-shaped dark area. T7 of male with
apex rounded
-T1-2 with lateral white maculae prolonged mesally by narrow, fingerlike lobe separated from



Figures 15-19. 15, Melectoides kiefferi, apex of female metasoma, dorsal view. 16, M. cockerelli, apex of female metasoma, dorsal view. 17, M. fumipennis, female, pattern of metasomal pubescence, dorsal view. 18, M. fumipennis, female, pattern of pubescence of scutum. 19, M. politus, female, pattern of metasomal pubescence, dorsal view.

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apical margin; T5-7 of male with white spots; T5 of female dark or at most with 2 white spots. T7 of male with apex emarginate
7. T1-3 with white hairs covering almost all dorsum, laterally black; T4-5 black
-T1-3 with pale maculation on a dark background; T4-5 usually also maculated
8. Pubescence on pleura, sternal region and face below antennae, white. Parapsidal furrow on
elevated ridge. Metapostnotum, at least at sides, dull, minutely rugose (Chile) 6. triseriatus (Friese)
-Pubescence on lower part of mesopleuron, sternal region and face below antennae, black.
Parapsidal furrow not elevated. Metapostnotum shiny, although with minute roughening in
cockerelli (Argentina)
9. Scutellum evenly rounded, sometimes with median longitudinal furrow indicated on
posterior half; hairs on scutellum sparse, polished integument visible. Hypoepimeral area
polished on lower half. Female T5 with apical hyaline rim laterally not reaching the bending
side of tergum (Fig. 19)
-Scutellum bigibbous, with median longitudinal furrow conspicuous; hairs on scutellum dense,
hiding integument at least posteriorly. Hypoepimeral area polished on lower third. Female T5
with apical hyaline rim laterally reaching the bending side of tergum (Fig. 16) 7. cockerelli (Jörgensen)

#### 1. Melectoides senex Taschenberg

(Figs. 5, 6, 20, 21, 33, 39)

Melectoides senex Taschenberg, 1883: 75. Lectotype female, by present designation, from Paraná (Prov. Entre Ríos, Argentina, March) (Halle, examined). Holmberg, 1887: 18. Dalla Torre, 1896: 318. Schrottky, 1903: 183. Ducke, 1912: 101. Schrottky, 1913: 264.

Melissa senex: Friese, 1912a: 201.

The size, elongate mandible, keeled hind coxa, metallic pubescence of the metasoma, elongate first flagellomere in both sexes and the eyes of the male converging above, distinguish M. senex from most Melectoides except tucumanus. It can be separated from *tucumanus* by the green metallic pubescence of the metasoma with whitish maculae, and the more extended white hairs on the head and thorax, as detailed in the key to species. The sexual dimorphism in the shape of the head is distinctive. The female has a broad face with eyes slightly converging below and a narrow vertex. the lateral ocellus being closer to the posterior margin of the head than in any other Melectoides. The male has eyes converging above and a broad vertex behind the ocelli.

Female lectotype. Length 15 mm; length of forewing 13 mm. (1) Vertex flat in frontal view. (2) Gena depressed behind eye. (3) Eyes slightly converging below, proportion of LID to UID 0.98 : 1; inner orbits concave. (4) Proportion of OOL to POL 1.17 : 1. (5) Lateral ocellus separated from posterior margin of head by 0.77 ocellar diameter. (7) Labrum with short transverse carina on upper third, below slightly concave, preapical tubercles absent, apical margin denticulate. (8) Malar space absent at level of abductor swelling, but anterior articulation of mandible separated from margin of eye by 0.25 times mandibular width. (9) Maxillary palpus with 4 segments, second and third longer than wide. (10) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1: 0.98. (11) Hairs

of mesopleuron black with greenish tinge, erect; hypoepimeral area nearly all punctate, small polished area above scrobe present. (12) Scutellum convex, evenly rounded. (13) Metapostnotum tessellate. (14) Hind coxa with keeled carina on apical three-quarters of upper external margin. (15) Vein cu-v of hindwing as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 dark, laterally not reaching the bending sides of tergum.

*Male.* Length 14 mm; length of forewing 12 mm. (18) Eyes converging above, proportion of LID to UID 1.14–1.15 : 1; inner orbits slightly concave on upper third, convex below. (19) Proportion of OOL to POL 0.70–0.83 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.78. (21) Hind femur not swollen. (22) Apex of T7 rounded. (25) Genitalia as in Figure 20, volsella and gonostylus absent.

Material studied. Besides lectopype, 1 male paralectotype, same locality and date (Mus. Halle) and 1 male, Paraná, Entre Ríos, Argentina, 1919, J. Brèthes (MACN).

#### 2. Melectoides tucumanus (Friese) (Figs. 9, 10)

Melissa tucumana Friese, 1906a: 102. Holotype female, Tucumán, Argentina, Steinbach leg. (not examined). Friese, 1912a: 210, fig. 9. Schrottky, 1913: 265.

Melectoides tucumanus: Ducke, 1912: 101.

This species is closely related to *senex*. It is distinguished by the blue metallic pubescence of the metasoma without white maculations, and the areas of white hairs reduced on head and thorax. The color pattern is quite constant over its distribution range. *M. tucumanus* is considered as different from *senex*, in spite of the close similarity in morphological features, until the variability of *senex* is known and males of *tucumanus* are collected.

Female. Length 12.5-16.0 mm; length of fore-

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wing 10-12 mm. (1, 2, 7, 9, 12-16) As in *M.* senex. (3) Proportion of LID to UID 0.98-1.0:1. (4) Proportion of OOL to POL 1.21-1.28:1. (5) Lateral ocellus separated from posterior margin of head by 0.75-0.80 ocellar diameter. (8) Malar space 0.05 times as long as mandibular width; anterior articulation of mandible separated from margin of eye by 0.25 times mandibular width. (10) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1:0.93-1.02. (11) Hairs of mesopleuron blue, erect.

Male. Unknown.

Material studied. ARGENTINA. Salta: 1 female, Tastil, 3200 m, I-1988, M. Fritz (MF). Catamarca: 2 females, Andalgalá, 17-III-1973 and 12-III-1974, J. L. Neff (CTMI). San Luis: 1 female, Merlo, Duret col. (MF).

#### 3. Melectoides niveiventris (Friese) n. comb. (Figs. 7, 24)

*Epeolus niveiventris* Friese, 1925: 35-36. Holotype female, Baños de Cauquenes, 1900, Herbst leg. (Cauquenes, Maule, Chile) (ZMB, examined).

Isepeolus niveiventris: Grütte, 1935: 501. Toro and Rojas, 1968: 60.

This species is easily recognized by the color pattern: the scutum, scutellum, metanotum and T1-3 are dorsally wholly covered by white pubescence; the face, pleura, legs and T4-6 have black hairs. A similar pattern is seen in *Isepeolus wagenknechti* Toro and Rojas, *Mesonychium gayi* (Spinola), and many other Chilean bees. *M. niveiventris* and *fumipennis* differ from other small *Melectoides* in the *Isepeolus*-like shape of the female S5, medially compressed and densely hairy apically, without round apical notch.

Female. Length 9.8 mm; length of forewing 7 mm. (1) Vertex slightly depressed between lateral ocellus and eye in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.79-0.82 : 1; inner orbits concave. (4) Proportion of OOL to POL 1.04-1.24 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with arched transverse carina and two subapical, central tubercles; apical margin not denticulate. (8) Malar space 0.15 times as long as mandibular width; anterior and posterior mandibular articulations equidistant from margin of eye. (9) Maxillary palpus with three segments, second as long as wide, third minute. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.59-1.64. (11) Hairs of mesopleuron black, erect; hypoepimeral area polished on lower half. (12) Scutellum evenly rounded with weak median longitudinal furrow. (13) Metapostnotum polished. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.65 times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally not

reaching the bending sides of tergum, but wide, 0.8 times as wide as T5 apically.

*Male.* Length 8-9 mm; length of forewing 6.5-7.2 mm. (18) Proportion of LID to UID 0.84-0.91 : 1; inner orbits almost straight, convex below. (19) Proportion of OOL to POL 0.93-1.0 : 1. (20) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1 : 0.95-1.10. (21) Hind femur not swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 24.

Material studied. CHILE. Coquimbo: 1 male, Embalse Laguna, 10–I–1940, Wagenknecht (SEM); 1 male, Laguna Dam, 5–XII–1950, Ross and Michelbacher (CAS); 1 male, Elqui (SEM). Santiago: 1 female, Farellones, 17–II–1980, M. Arroyo (UCV). Maule: 1 female holotype, see data above.

#### 4. Melectoides fumipennis n. sp. (Figs. 8, 11, 12, 17, 18)

This species is known from the female sex only. It is distinguished by the infuscated wings and the extended reddish coloration of the integument. The metasoma is more elongate and narrowed apically than in any other *Melectoides;* the apex of T5 is approximately one-fourth of the apical width of T2. Measurements of the paratype are indicated in parentheses below.

Female. Length 9.5 mm (8.5-11.0); length of forewing 7.3 mm (6.3-7.1). Integument of head black, with apex of clypeus, labrum, mandible and antenna reddish; propodeum black; thorax, legs and metasoma dark reddish, but tegula, pronotal lobe, hypoepimeral area and tarsi light red. Wings infuscated, darkest beyond closed cells. Vestiture. Pubescence of head white, hairs appressed on face and gena, erect on vertex, occipital region and around proboscidial fossa; scape with hairs white on basal half, brown on apex. Thorax, legs and metasoma with short, appressed hairs forming design of brown and white maculae; hairs of mesopleuron shorter than diameter of pedicel. Propodeum laterally with short, appressed brown hairs, along lateral angles and posteriorly with long, erect, white hairs. Hairs white on most of pronotum, except on anterior surface of pronotal lobe, laterally and a transverse band near anterior margin of scutum brown. Scutum with maculae as in Figure 18. Axilla with brown erect hairs that give appearance of elevated axilla; posterior margin with hairs white. Scutellum with hairs white leaving round brown spot on top of each gibbosity. Metanotum and upper half of pleura with hairs white; lower half of mesopleuron and ventral region of thorax with mixed brown and white hairs, except anterior surface of mesopleuron brown and two well-delimited brown spots at level of upper end of midcoxa; in holotype anterior spot connected to anterior surface of mesopleuron and posterior spot continued with lower half of metapleuron, in paratype both spots surrounded by white hairs. Hairs white on anterior surface of coxae, lower surface of fore femur and apex of mid and hind femora and tarsi. Tibiae with irregular pattern of brown and white hairs. Maculae on metasomal terga as in Figure 17. Sterna with intermixed brown and white hairs not forming definite pattern, except lateral apical white spot on S3 and S4. Sculpture. Punctation dense and even; punctures on scutum leaving interspaces a third to a half as wide as diameter of punctures. Morphology. (1) Vertex rounded between lateral ocellus and eye in frontal view. (2) Gena rounded behind eye. (3) Eyes converging below, proportion of LID to UID 0.80(0.72-0.87) : 1; inner orbits concave. (4) Proportion of OOL to POL 0.95(0.93) : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with arched carina and two preapical tubercles; lateral parts of carina parallel to sides of labrum. (8) Malar space 0.05 times as long as mandibular width; anterior and posterior mandibular articulations equidistant from margin of eye. (9) Maxillary palpus with four segments, second and third little longer than wide, fourth minute. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.56(1.60-1.61). (11) Mesopleuron with appressed hairs, shorter than length of pedicel; hypoepimeral area polished on lower half. (12) Scutellum bigibbous, median longitudinal furrow broad posteriorly. (13) Metapostnotum tessellate at sides and above, polished below. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.86 (0.75-0.94) times as long as second abscissa of M+Cu. (16) Membranous apical rim of T5 hyaline, laterally reaching the bending sides of tergum; T5 narrow, 0.28 times as wide as T2 apically.

#### Male. Unknown.

Material studied. Holotype female, Cebollar, La Rioja, Argentina, 14-XI-1944 (MLP). Paratype female, Los Tigres, Santiago del Estero, Argentina, 11-16-I-1970, R. Golbach (IML); paratype female, between El Cadillal and Ticucho, Tucumán, Argentina, 27-X-1989, J.G. Rozen and A. Roig-A. (AMNH).

#### 5. Melectoides rozeni (Toro) n. comb. (Figs. 22, 23)

Isepeolus rozeni Toro, 1971: 262-265, fig. 4. Holotype female, 41.5 km S Copiapó, Atacama (Chile), 19 Oct. 1969, Rozen and Peña leg. (AMNH, examined).

This species resembles *niveiventris* in the slightly depressed lateral areas of the vertex and the continuous bands of white pubescence on the metasoma, but those bands do not cover the entire terga and are also present on T5 (Toro, 1971, fig. 4); the face above the clypeus has white hairs. It can be distinguished from *niveiventris* and all other *Melectoides* of similar size by the labrum without transverse carina but with two rounded elevations at each side of a central longitudinal depression. The female S5 has a round apical notch with specialized setae, relating *rozeni* to *triseriatus* and close species, but the male genitalia have plesiomorphic features that render the placement of this species in the analyses conflicting. The gonostylus is long, well developed, and the gonocoxite has a digitiform lobe much as in all *Isepeolus*. Also the T7 of the male has the disc less reduced than in other *Melectoides*.

Female. Length 10 mm; length of forewing 6.3 mm. (1) Vertex between lateral ocellus and eye slightly depressed in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.78 : 1; inner orbits almost straight. (4) Proportion of OOL to POL 1.04 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. (7) Labrum medially elevated at each side of central longitudinal depression; apical margin not denticulate. (8) As in niveiventris. (9) Maxillary palpus with 3 segments, second longer than wide, third as long as wide, apically emarginate. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.57. (11) Hairs of mesopleuron erect, white on upper half; hypoepimeral area polished on lower fourth. (12) Scutellum evenly rounded, with weak median longitudinal furrow. (13) Metapostnotum minutely rugose. (14) Hind coxa with weak carina on apical third of upper external margin. (15) Vein cu-v of hindwing 0.65 times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally not reaching the bending sides of tergum.

*Male.* Length 8 mm; length of forewing 7.2 mm. (18) Proportion of LID to UID 0.83 : 1; inner orbits convex. (19) Proportion of OOL to POL 0.88 : 1. (20) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.64. (21) Hind femur not swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 22.

Material studied. Besides holotype, 1 male, Coquimbana, 25 km from Freirina, Atacama, Chile, 19-20-X-1957, L. Peña (SEM).

#### 6. Melectoides triseriatus (Friese) (Figs. 25, 26, 34, 41, 44)

*Epeolus triseriatus* Friese, 1908: 82-83. Lectotype female, by present designation, from Concepción, Chile, XII-1903, Herbst leg. (Berlin, examined). Schrottky, 1913: 265.

*Isepeolus triseriatus:* Claude-Joseph, 1926: 268. Gazulla and Ruiz, 1928: 302. Janvier, 1933: 325. Grütte, 1935: 501. Toro and Rojas, 1968: 60.

Melectoides triseriatus: Alexander, 1990: 144.

The name *triseriatus* has been consistently applied to a Chilean species by several authors, as shown in the synonymy, and is fixed in this sense in the present revision. To my knowledge this species does not occur in Argentina and the



Figures 20-32. Genitalia of males of *Melectoides;* ventral left, dorsal right; g, gonostylus; s, spatha; sparser stippling indicates partially sclerotized ventral surface of penis. 20, *M. senex;* 22, *M. rozeni;* 24, *M. niveiventris;* 25, *M. triseriatus;* 27, *M. cockerelli;* 28, *M. politus;* 30, *M. bellus;* 32, *M. kiefferi.* S7 and S8 of males of *Melectoides.* 21, *M. senex;* 23, *M. rozeni;* 26, *M. triseriatus;* 29, *M. politus;* 31, *M. bellus.* Scale lines 0.1 mm.

specimen from Tucumán included by Friese in the original description was probably *M. bellus* (Jörgensen) or *M. kiefferi* (Jörgensen).

This species is recognized by its dense punctation, the punctures with almost no interspaces; the pubescence is correspondingly dense. The parapsidal furrow is situated on an elevated ridge, the metapostnotum is usually rugose with polished areas reduced or absent and the hypoepimeral area is also sculptured, tessellate.

Female. Length 9.0-10.2 mm; length of forewing 6.5-7.0 mm. (1) Vertex rounded between lateral ocellus and eye in frontal view. (2) Gena rounded behind eye. (3) Eyes convergent below, proportion of LID to UID 0.73-0.79 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 1.09-1.21 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with strong, arched carina and two middle, close preapical tubercles, lateral parts of carina nearly parallel to sides of labrum; apical margin not denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 4 segments, second and third longer than wide, fourth minute. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1:1.54-1.76. (11) Mesopleuron with dense, erect hairs, white on upper two-thirds, below with variable pattern of white and dark hairs; hypoepimeral area without hairs on lower half, but integument tessellate. (12) Scutellum slightly bigibbous, with median longitudinal furrow forming behind a wide triangular depression. (13) Metapostnotum minutely rugose, sometimes polished below. (14) Hind coxa with carina on apical half of upper external margin. (15) Vein cu-v of hindwing 0.75 times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally not reaching the bending sides of tergum. (17) S6 of female basal to spinelike setae with pocket (as in Fig. 14, p).

Male. Length 7.8-10.0 mm; length of forewing 6.5-7.5 mm. (18) Proportion of LID to UID 0.84-0.91 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.93-1.0 : 1. (20) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.21-1.32. (21) Hind femur usually swollen. (22) Apex of T7 truncate, with lateral angles sometimes curved up; usually short median carina present ending at moderate apical projection. (25) Genitalia, Figure 25.

Material studied. CHILE. Atacama: 1 male, 20 km N Vallenar, 29-IX-1957, L. Peña (SEM). Coquimbo: 1 male, Portezuelo Tres Cruces, 30-31-X-1957, L. Peña (SEM); 1 female and 4 males, Fray Jorge, 15 km SW Pachingo, 20-X-1966, Schlinger and Irwin (CAS). Valparaíso: 1 male, Rio Marga-Marga, Los Perales, 13-X-1966, Irwin and Schlinger (CAS); 1 female, Lilenes, 7-XI-1965, De la Hoz (Logan). Santiago: 1 male, El Canelo (SEM); 2 females, El Canelo, 14-XI, Ramírez (MLP); 1 male, Cajón del Maipo, 21-XI-1965, Dazarola (Logan); 2 males, Pérez Caldera, XII-1988, M. Fritz (MF). Cautín: 1 female, Temuco, P. Herbst (CAS).

# 7. Melectoides cockerelli (Jörgensen) n. comb. (Figs. 16, 27)

- Isepeolus cockerelli Jörgensen, 1912a: 144-145, fig. C. Lectotype male, by present designation, from Chacras de Coria (Prov. Mendoza, Argentina), 21-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.
- Isepeolus bruneri Cockerell, 1917: 479-480. Holotype female, Carcarana (Carcarañá, Prov. Santa Fe, Argentina) (USNM, type number 23159, examined). New synonym.

This species is similar to *kiefferi* in pattern of maculation, but the integument is black. It differs from *kiefferi* and all other species in the group that have the S5 of the female with a large, round apical notch, by the wide apical rim of T5, that reaches the sides of the tergum.

Female. Length 8.5-9.5 mm; length of forewing 6.2-6.8 mm. (1) Vertex between lateral ocellus and eye flat in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.79-0.83 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 1.0-1.08 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.2 ocellar diameters. (7, 8) As in triseriatus. (9) Maxillary palpus with at least 3 segments, second and third as long as wide, in some specimens a fourth minute segment distinguishable. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.55-1.79. (11) Hairs of mesopleuron black, erect; hypoepimeral area polished on lower third to lower half. (12) Scutellum bigibbous. (13) Metapostnotum polished. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.75 times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally reaching the bending sides of tergum. (17) As in triseriatus.

Male. Length 8.0-9.5 mm; length of forewing 7.0-7.3 mm. (18) Proportion of LID to UID 0.89-0.9 : 1; inner orbits almost straight. (19) Proportion of OOL to POL 0.81-0.93 : 1. (20) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.16-1.28. (21) Hind femur swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 27.

Material studied. ARGENTINA. Santa Fe: 1 female, holotype of *I. bruneri* Cockerell, data above. Mendoza: 1 male, lectotype of *I. cockerelli* Jörgensen, data above; 3 females paralectotypes, Mendoza, 17-X-1908 and 1-XI-1908, P. Jörgensen (MLP); 1 male, Mendoza, C.S. Reed (MACN). Neuquén: 1 male, Confluencia Traful, 20-XII-1964, A.J. Giai (SEM); 1 male, Aluminé, Rinconada, XI-1965, M. Gentili (MF).

#### 8. Melectoides politus n. sp. (Figs. 2-4, 19, 28, 29, 40)

This species is recognized by the sparse punctation and polished integument, the punctures being particularly sparse on the scutum, scutellum, metanotum and lower half of mesopleuron. Also characteristic are the low, evenly rounded scutellum and the sinuous apex and membranous rim of the female T5. Measurements of the female paratypes are indicated in parentheses.

Female. Length 8.5 mm (8.0-8.5); length of forewing 6.5 mm (6.3-6.6). Integument black; mandible, pedicel, pronotal lobe, tegula and tarsi dark reddish brown. Wings hyaline, weakly infuscated, with pterostigma and veins dark brown. Vestiture. Hairs long, erect, on head, thorax and propodeum, those on mesopleuron over 1.5 as long as diameter of pedicel. With black and white intermixed hairs on face below antennal sockets, around proboscidial fossa, occipital region, sides of pronotum, ventral half of pleura, ventral region of thorax and coxae. Hairs white on upper half of face, gena, vertex, pronotal lobe, upper half of mesopleuron, propodeum, below fore femur and apex of mid and hind femora and basitarsi. Fore and mid tibiae with irregular pattern of black and white hairs; hind tibia mostly black; tarsi with intermixed black and white hairs. Metasoma with short, appressed hairs forming white and black maculae as in Figure 19. Sterna mostly black, except S1 with some intermixed white hairs and \$2 with narrow white apical band. Sculpture. Integument polished and punctation sparse; punctures on scutum leaving interspaces 2-5 times as wide as diameter of punctures. Morphology. (1, 2, 7, 15-17) As in triseriatus. (3) Eyes converging below, proportion of LID to UID 0.85 : 1 (0.79-0.87 : 1); inner orbits slightly concave. (4) Proportion of OOL to POL 0.91 : 1 (0.82-1.0 : 1). (5) Lateral ocellus separated from posterior margin of head by 1.1 ocellar diameters. (8) Malar space 0.15 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 3 segments, second flattened, roundish, third not always clearly distinguishable. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.79 (1.70-1.89). (11) Hairs of mesopleuron erect, white on upper half; hypoepimeral area polished on lower two-thirds. (12) Scutellum flat, evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum polished. (14) Hind coxa angulose on upper external margin, but no carina.

Male. Length 8.0-9.5 mm; length of forewing 7.0-7.5 mm. Color and vestiture similar to female, but hairs black on lower half of face, most of pleura and propodeum; T3-6 with apical white spots, T7 black. (18) Proportion of LID to UID 0.90-0.95 : 1; inner orbits almost straight. (19) Proportion of OOL to POL 0.79-0.94 : 1. (20) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.05-1.19. (21) Hind femur swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 28.

Material studied. Holotype female from Quebrada Horcones, 2900 m, Departamento Las Heras, Mendoza, Argentina, 10-I-1985, A. Roig-Alsina (MACN); 5 females and 4 males, paratypes, same data as holotype (MACN, SEM).

#### 9. Melectoides bellus (Jörgensen) n. comb. (Figs. 30, 31)

Epeolus triseriatus: Jörgensen, 1909: 225 (misidentification).

Isepeolus bellus Jörgensen, 1912a: 149-150, fig. G. Holotype female, Chacras de Coria (Prov. Mendoza, Argentina), 5-XII-1907, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

This species can be distinguished by the extensive short, appressed, white pubescence and red scutellum and metanotum. The female T5 has a characteristic median anchor-shaped dark spot. This species is related to *kiefferi*, as indicated by the reduced male gonostylus and the rounded second segment of the maxillary palpus.

*Female.* Length 8.2-10.5 mm; length of forewing 5.8-7.5 mm. (1, 2, 7, 9, 13-17) As in *politus.* (3) Eyes convergent below, proportion of LID to UID 0.73-0.78 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 0.83-0.95 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.1-1.3 ocellar diameters. (8) Malar space almost absent; anterior and posterior articulations of mandible equidistant from margin of flagellomeres 2-4, proportion 1 : 1.50-1.71. (11) Mesopleuron with appressed hairs, as long as diameter of pedicel, hairs white on upper half. (12) Scutellum bigibbous.

*Male.* Length 9.5-10.5 mm; length of forewing 7.8-8.3 mm. (18) Proportion of LID to UID 0.84-0.86 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.76-0.77 : 1. (20) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.32-1.59. (21) Hind femur swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 30.

Material studied. ARGENTINA. Salta: 1 male, Cafayate, I-1983, M. Fritz (MF); 1 female, Río Las Conchas, 35 km Cafayate, 3-III-1978, A. Willink (IML). Santiago del Estero: 1 female, 37-47 km SE Añatuya, 20-XI-1979, C. and M. Vardy (London). Catamarca: 1 female, Joyango-Coipes, on flowers of Verbesina encelioides, 2-XII-1972, J.L. Neff (CTMI). La Rioja: 1 male and 1 female, Cebollar, 14-XI-1944, A. Ogloblin (MLP); 1 female, Chepes, 24-XI-1944, A. Ogloblin (MLP); 1 male, La Rioja (MACN). Mendoza: 1 female, holotype, see data above. Río Negro: 6 females, Río Colorado, 1321-II-1946, Hayward and Willink (MLP, SEM); 1 female, Choele Choel, 15-XII-1989, M. Fritz (MF).

#### 10. Melectoides kiefferi (Jörgensen) n. comb. (Figs. 13-15, 32, 35)

Isepeolus kiefferi Jörgensen, 1912a: 148-149, fig. F. Lectotype female, by present designation, from Mendoza (Argentina), 26-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

*M. kiefferi* can be recognized by its short, appressed pubescence and by its red, bigibbous scutellum and red metanotum. These characters are shared with *bellus*, from which it is distinguished by the reduced white vestiture and the emarginate apex of the male T7.

*Female.* Length 9.5-10.5 mm; length of forewing 7.2-7.5 mm. (1, 2, 7, 9, 13, 15-17) As in *politus.* (3) Eyes convergent below, proportion of LID to UID 0.75-0.78 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 0.95-1.09 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. (8) As in *bellus.* (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.50-1.59. (11) Mesopleuron with appressed, short hairs, as long as diameter of pedicel; usually with a white band below hypoepimeral area, which is polished on lower third. (12) Scutellum bigibbous. (14) Hind coxa with weak carina on apical 0.4 of upper external margin.

*Male.* Length 10.0-10.7 mm; length of forewing 7.3-9.0 mm. (18) Proportion of LID to UID 0.90-0.91 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.8 : 1. (20) First flagellomere shorter to longer than sum of flagellomeres 2-4, proportion 1 : 0.95-1.13. (21) Hind femur swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 32.

Material studied. ARGENTINA. Catamarca: 2 females, Punta Balasto, 30 km Santa María, 24-XI-1966, A. Willink (IML). La Rioja: 1 male, Patquía, IX-1945, A. Breyer (MACN). Mendoza: 1 female lectotype, see data above. Neuquén: 1 male, 16 km E Picún Leufú, 5-XII-1987, A. Willink (IML). Río Negro: 1 female, Choele Choel, 22-23-XI-1946 (MLP). Chubut: 1 male, San Jorge (MACN).

#### **GENUS** ISEPEOLUS COCKERELL

- Isepeolus Cockerell, 1907: 64. Type species: Isepeolus albopictus Cockerell, 1907 (= Epeolus viperinus Holmberg, 1886), by monotypy.
- Palinepeolus Holmberg, 1909: 77. Type species: Epeolus viperinus Holmberg, 1886, by original designation. New synonym.
- Calospiloma Brethes, 1909: 68. Type species: Epeolus viperinus Holmberg, 1886, by original designation. Synonymy with Isepeolus by Jörgensen, 1912a: 142.

Diagnosis. Length, 6.0–10.5 mm. Head with vertex raised behind ocelli and depressed between lateral ocellus and eye. Gena depressed behind eye. Punctation of vertex variable, dense to sparse with large polished areas. Inner orbit of eye in females concave, converging below, that of males

usually sinuous, viz. concave on upper half and convex below. Distance from lateral ocellus to posterior margin of head usually 0.7-1.0 times ocellar diameter. First flagellomere of male slightly widened apically, that of female broadly widened apically. Mandible usually with two subapical teeth (one in octopunctatus). Hindcoxa with upper external margin angulate to carinate on apical one-third to one-half. Marginal cell with apex truncate. T5 of female with narrow apical band of dense dark hairs that usually leaves middle triangular area of pale, silky hairs; no membranous rim continuing apex of tergum. Apex of S5 of female densely hairy, medially compressed, with V-shaped notch whose sides frequently are close together forming vertical slit in upturned apical zone. S6 of female with sclerotized apical point sharp, frequently keeled ventrally; lateral apical margin of sternum not folded. S3-4 of male without apical fringes of hairs, or if present, fringes conspicuously weaker than that on S5. S6 of male with subapical tubercle. Gonocoxite of male genitalia with basal constriction.

Three groups of species can be recognized in Isepeolus. One of the groups is not supported by synapomorphies; the similarity among its species is most probably due to plesiomorphy. This group includes I. octopunctatus, septemnotatus and bufoninus. The three species have long black vestiture with a bluish tinge on the head and the thorax; their integument has dense punctation, leaving almost no polished areas around ocelli; the males have eyes with nearly parallel inner orbits, and the subapical tubercle of the male S6 is conical or compressed longitudinally. A second group is formed by I. cortesi and atripilis. In this group the vein cu-v of the hindwing is 0.7-1.0 times as long as the second abscissa of vein M + Cu, the subapical tubercle of the male S6 is transverse, bilobed, and the males have genitalia with reduced gonostyli. The head of the male is narrow, as wide as the pronotal width (measured at the pronotal lobes); species of the other two groups usually have the head wider than the pronotum. The group comes out from a polytomy in the cladograms (Figs. 1a, b), but if a conical subapical tubercle on the male S6 is taken as plesiomorphic for Isepeolus in the context of those topologies, then the transverse tubercle of cortesi and atripilis would unite them to the next group. The viperinus group includes the remaining six species. It is characterized by the presence of short spinelike setae on the female S6 and the transverse, pointed or rounded subapical tubercle of the male S6. Most species in the group have wide polished areas on the vertex and the anterior margin of the scutum.

# CLEPTOPARASITIC BEE TRIBE ISEPEOLINI

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Figures 33-49. 33-38, pedicel and flagellomeres 1-4 of Isepeolini; female left, male right. 33, Melectoides senex; 34, M. triseriatus; 35, M. kiefferi; 36, Isepeolus octopunctatus; 37, I. bufoninus; 38, I. viperinus. 39-43, mandibles of females. 39, M. senex; 40, M. politus; 41, M. triseriatus; 42, I. octopunctatus; 43, I. viperinus. 44-46, labra of females, front and lateral views. 44, M. triseriatus; 45, I. vachali; 46, I. octopunctatus. 47-49, outer claw of female hind leg. 47, I. atripilis; 48, I. septemnotatus; 49, I. octopunctatus.

# Key to the Species of Isepeolus

#### Females

1. Metasoma with white maculation as follows: T1 with apical central band, T2 almost wholly
covered except at sides, T3-4 with central white spots and black laterally
-Pattern of white maculation on metasoma different, disc of T2 never wholly covered, and
maculation on all terga more expanded laterally than mesally, leaving central dark areas 2
2. T5 broad (Fig. 68), its apical width more than half (0.55-0.65) of apical width of T2 3
-T5 (Figs. 67, 69) with apical width less than half (0.3-0.4) of apical width of T2 4
3. Apex of S6 rounded (Fig. 56). First flagellomere shorter than the sum of flagellomeres 2-4
(1:1.24-1.30). T4 with white maculae confluent, usually forming continuous band; T5
dorsally with white spots
-Apex of S6 pointed (as in Fig. 58). First flagellomere subequal to the sum of flagellomeres 2-4
(1:1.00-1.04). T4 with white maculation forming 4 separate spots (sometimes only 2); T5
dorsally dark9. smithi Jörgensen
4. Pleura with hairs black, sometimes with a bluish tinge, at most with a tuft of white hairs
covering spiracular entrance
-Pleura with hairs white at least on upper half, no conspicuous bluish tinge
5. Punctation on vertex leaving wide polished areas, those between lateral ocellus and eye
wider than ocellar diameter. Scutellum bigibbous. S6 with short spinelike setae bordering
apical point (seen as serration at low magnification)
-Punctation between and around ocelli dense, almost no polished areas, or such areas less than
three-fourths diameter of lateral ocellus. Scutellum usually evenly rounded, sometimes
median longitudinal furrow distinct on posterior half. S6 without spinelike setae 6
6. Flagellum black. T2 with white spot at each side and T4 with two apical central spots that
can be confluent. Inner tooth of claws narrowly rounded apically (Fig. 48)
-Flagellum reddish. Pattern of white maculation on metasoma different. Inner tooth of claws
truncate apically (Figs. 47, 49)



Figures 50-61. S6 of Isepeolus females, lateral and ventral views. 50, 51, I. octopunctatus; 52, 53, I. septemnotatus; 54, I. atripilis; 55, I. cortesi; 56, 57, I. lativalvis; 58-60, I. viperinus, with detail of apical point of sternum; 61, I. wagenknechti. Scale lines 1 mm.

7. Outer ramus of claws elongate, more than twice as long as truncate inner ramus (Fig. 49). Mandible bidentate (Fig. 42).
—Outer ramus of claws less than twice as long as inner ramus. Mandible tridentate (Fig. 43).
8. Hind wing with vein cu-v and second abscissa of vein M + Cu of similar length. Labrum with blunt transverse elevation on apical third. First flagellomere subequal to sum of flagellomeres 2-4 (1 : 0.93-1.04). S3-4 thoroughly dark.
—Hind wing with vein cu-v nearly half as long as second abscissa of vein M + Cu. Labrum flat to slightly concave. First flagellomere shorter than sum of flagellomeres 2-4 (1 : 1.29-1.35). Apex of S3-4 laterally with white hairs .

# Cleptoparasitic Bee Tribe Isepeolini

<ul> <li>9. Integument of scutellum and metanotum red. Pubescence on terga, other than pale maculations, usually reddish brown.</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black.</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black.</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black.</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black.</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black .</li> <li>Integument of scutellum and metanotum black spot; each side of researce in the term of science and soles and the macula, median ones rectangular, lateral ones sometimes connected to basal white band; T2 with white macula at each side not encircling black spot, even though a notch present (Specimens from northern Argentina may have vaguely formed black spots on T2, but in areas of sympatry with <i>luctuosus</i> maculation is distinctive; specimens from southern Argentina run to couplet 5.)</li> <li>Males</li> </ul>
Males
<ol> <li>Integument of scutellum and metanotum red. Pubescence on terga, other than pale maculation, usually reddish brown</li></ol>
<ul> <li>(Figs. 77-79)</li></ul>
<ul> <li>4. Outer ramus of claws elongate, more than twice as long as truncate inner ramus (Fig. 49). Mandible bidentate. First flagellomere much longer than sum of flagellomeres 2-4 (1:0.57-0.61).</li> <li>—Outer ramus of claws less than twice as long as inner ramus. Mandible tridentate. First flagellomere longer than sum of flagellomeres 2-4 (1:0.69-0.86).</li> <li>5. Subapical tubercle of S6 in caudal view bilobed (Fig. 77), without posterior longitudinal carina. Triangular polished area contiguous with lateral ocellus at most three-fourths of</li> </ul>
<ul> <li>ocellar diameter</li> <li>Subapical tubercle of S6 pointed, rounded, or sometimes briefly truncate, usually with posterior longitudinal carina. Triangular polished area contiguous with lateral ocellus extended laterally, as wide as ocellar diameter or wider</li> <li>Mesopleuron with hairs black, at most a tuft of white hairs covering entrance of spiracle. T4-6 black.</li> <li>Mesopleuron with white hairs on upper half. T4-6 usually with white spots</li> </ul>
<ul> <li>7. Face below antennal sockets and pleura with hairs black. Metasoma with white maculation usually restricted to T1-2, if present on T3-5, then white hairs on T1-2 forming complete bands across those terga</li></ul>
spot

- 9. Subapical tubercle of S6 a strong transverse elevation almost reaching sides of sternum (Fig. 79). T7 thoroughly covered by hairs, without bare basal band (Chile and southern Argentina)
- -Subapical tubercle of S6 smaller (Fig. 78), separated from sides of sternum. T7 with wide bare basal band (tergum needs to be pulled off to observe this band) (central and northern Argentina to Peru; specimens from southern Argentina run to couplet 11) ..... 11. vachali Jörgensen (part)

- 10. First flagellomere broadened on apical fifth, second flagellomere shorter than its basal width. Apical fringe of S4 with dense, short hairs barely surpassing margin of sternum. T7 usually with hairs white. Subapical tubercle of S6 with some scattered long hairs on posterior surface
- -First flagellomere broadened at very tip, second flagellomere as long as or longer than its basal width. Apical fringe of S4 with long hairs, surpassing margin of sternum. T7 with hairs





Figures 62-69. 62-66, heads of Isepeolus species. 62, I. atripilis, female; 63, I. atripilis, male; 64, I. bufoninus, male; 65, 66, I. bufoninus, female. 67-69, pattern of metasomal pubescence of Isepeolus species, dorsal view. 67, I. vachali, a, female from Río Negro, Argentina, b, female from Catamarca, Argentina, c, female from Moquegua, Perú, d, male from Río Negro, Argentina, e, male from Catamarca, Argentina; 68, I. smithi, female; 69, I. atripilis, female. Scale lines 1 mm.

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11. Lateral border of clypeus weakly lamellated and such lamella not continued above level of anterior mandibular articulation. Outer surface of mandible with basal patch of hairs white with brown spot, dense. T7 thoroughly covered by hairs, without bare basal band

-Lateral border of clypeus conspicuously lamellated, lamella continued above level of anterior mandibular articulation. Outer surface of mandible with basal patch of hairs whitish, thin. T7 with broad bare basal band (tergum needs to be pulled off to observe band)

..... 11. vachali Jörgensen (part)

#### 1. Isepeolus octopunctatus (Jörgensen) (Figs. 37, 42, 46, 49, 50, 51)

*Epeolus octopunctatus* Jörgensen, 1909: 226. Holotype female, from Chacras de Coria (Prov. Mendoza, Argentina), 11 Nov., Jörgensen leg. (location of type?). Schrottky, 1913: 265.

Isepeolus octopunctatus: Cockerell, 1910: 144. Jörgensen, 1912a: 142-143. Jörgensen, 1912b: 316.

It was not possible to locate the holotype of this species. Jörgensen's original description fits equally well the species described below as I. atripilis, but his redescription (1912a) includes an additional character that narrows the possibilities to the present interpretation. The strong blue shine of the body hairs, mentioned by Jörgensen (1912a), readily distinguishes octopunctatus from atripilis. The present treatment of the species is also supported by a specimen identified by Jörgensen as octopunctatus in the Museo de La Plata. The pattern of maculation of the metasoma varies in both species and overlaps to a large extent; I have studied specimens of both species with eight spots on T1-2. The bidentate mandible and the long outer rami of the claws differentiate octopunctatus from atripilis and all other species of Isepeolus.

Female. Length 7.5-10.0 mm; length of forewing 6-8 mm. (3) Proportion of LID to UID 0.81-0.84 : 1. (4) Proportion of OOL to POL 0.85-0.95 : 1. (5) Lateral ocellus separated from posterior margin of head by 0.65-0.70 ocellar diameter. (6) Punctures between and around ocelli dense, leaving no interspaces; narrow polished area around lateral ocellus less than onequarter of ocellar diameter. (7) Labrum flat to medially weakly elevated on each side of median line; apex denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) Maxillary palpus with three segments, second as long as wide. (10) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.83-0.97. (11) Mesopleuron with hairs erect, black with blue tinge, sometimes with white tuft covering spiracular entrance; hypoepimeral area thoroughly punctate. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum rugose, with upper areolate band narrow, less than one-quarter of width of metanotum. (15) Vein cu-v of hindwing 0.52-0.57 times as long as second abscissa of M+Cu. (17) S6 with apex

briefly concave ventrally, keeled basal to concavity; spinelike setae absent.

*Male.* Length 7-10 mm; length of forewing 7-8 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.9 : 1. (19) Proportion of OOL to POL 0.65-0.69 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.57-0.61. (22) Apex of T7 triangular, narrowly rounded. (23) S3 with fringe of hairs present, weaker than that of S4. (24) S6 with subapical tubercle conical. (25) Genitalia similar to those of *septemnotatus*.

Material studied. ARGENTINA. Salta: 4 males, Cafayate, 19-X-1948, J. Núñez (MLP). Tucumán: 3 females, Amaicha, 19-XI-1966, L. Stange (IML); 1 female, Amaicha del Valle, 28-X-1973, J.L. Neff, on flowers of Prosopis chilensis (CTMI). Catamarca: 3 females, Santa María, 19-X-1948, J. Núñez (MLP). San Juan: 1 male, Carpintería, A. Martínez (MF). Mendoza: 1 female, Mendoza, 14-III-1908, P. Jörgensen (MLP). Buenos Aires: 2 females, Felipe Sola, XI-1942, A. Martínez (MLP). Río Negro: 1 female, Lamarque, X-1957, M. Fritz (UFPR). Santa Cruz: 1 female, 5.6 km E Los Antiguos, 360 m, 23-XI-1966, Schlinger and Irwin (CAS).

#### 2. Isepeolus bufoninus (Holmberg) (Figs. 37, 64-66)

Epeolus bufoninus Holmberg, 1886b: 283-284. Syntypes, females from Las Conchas, Buenos Aires (Argentina), Feb. 1879, M.O. Cesar and E.L. Holmberg (lost). Dalla Torre, 1896: 328. Schrottky, 1903: 183.
Palinepeolus bufoninus: Holmberg, 1909: 78.
Isepeolus bufoninus: Schrottky, 1913: 264.

Holmberg's detailed description permits recognition of this species in spite of the loss of the types. This species resembles octopunctatus in the strong punctation of the head and thorax and the conical subapical tubercle of the male S6, but the scape is shorter in both sexes (see proportions below), the mandible is tridentate, the outer ramus of the claws is less than twice as long as the inner ramus and the apices of S3-4 are clothed laterally with white hairs. Specimens from Argentina have broad white maculae on the metasoma, the lateral macula of the male T2 enclosing a black spot; specimens from Brazil have reduced white areas, the lateral macula of the male T2 being notched, not enclosing a black spot, and the lateral maculae of the female terga being reduced to narrow apical stripes.

Female. Length 8.0-9.5 mm; length of forewing 6.2-7.0 mm. (3) Proportion of LID to UID 0.81-0.83: 1. (4) Proportion of OOL to POL 0.89-0.9: 1. (6) As in octopunctatus. (7) Labrum with disc flat, apex denticulate. (8) Malar space 0.13 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 3 segments, second as long as wide. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.29-1.35. (11, 12) As in octopunctatus, but median longitudinal furrow of scutellum distinct on posterior half. (13) Metapostnotum rugose, with strongly areolate upper band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.52-0.58 times as long as second abscissa of M + Cu. (17) S6 with apex pointed and ventrally keeled; spinelike setae absent.

*Male.* Length 7.5–9.5 mm; length of forewing 7–8 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.95–1.0 : 1. (19) Proportion of OOL to POL 0.62–0.71 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.69–0.86. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle conical. (25) Genitalia similar to those of *septemnotatus*, but gonostylus short, 0.35 times as long as gonocoxite.

Material studied. ARGENTINA. Buenos Aires: 1 female, Tigre, 3-XI-1937, A. Ogloblin (MLP); 1 male, Pacheco, 22-X-1925, Muhn (MACN). Entre Rios: 1 male, Pronunciamiento, I-1964, J. Foerster (UFPR). BRAZIL. Paraná: 2 females and 2 males, Curitiba, XII-1951, V-1953 and XI-1953, J.S. Moure (UFPR, SEM); 1 male Guarapuava, 1120 m, 8-IX-1955, C.D. Michener (SEM); 1 female, Guarapuava, 7-IX-1955, Michener and Moure (UFPR); 1 male, S. José dos Pinhais, 14-IX-1955, R. Lange (UFPR).

#### 3. Isepeolus septemnotatus (Spinola) (Figs. 48, 52, 53, 71, 72)

- Melecta septemnotata Spinola, 1851: 186-187. Type male from Araucanía, Illapel, Chile (not examined). Reed, 1892: 228. Dalla Torre, 1896: 318. Ducke, 1912: 102.
- *Epeoloides septemnotatus:* Friese, 1906b: 172. Friese, 1908: 88-89. Friese, 1912b: 364. Herbst, 1917: 269. Claude-Joseph, 1926: 268. Janvier, 1933: 326.
- Isepeolus septemnotatus Grütte, 1935: 501. Toro and Rojas, 1968: 60.

I have not seen type material of this species, but its identity is clear. The pattern of maculation of the metasoma described by Spinola is diagnostic for the species. He also mentioned that the claws are bifid, *I. septemnotatus* being the only species in the tribe with such claws. The subapical tubercle of the male S6 is also characteristic for the species (see 24 below).

*Female.* Length 8.0-9.5 mm; length of forewing 6.2-7.0 mm. (3) Proportion of LID to UID 0.85-0.88 : 1. (4) Proportion of OOL to POL

0.76-0.9.0 : 1. (6) As in octopunctatus. (7) Labrum with median transverse carina somewhat arched down at sides, surface below carina concave; apex feebly denticulate. (8) As in octopunctatus. (9) Maxillary palpus with 4 segments, second three times as long as wide. (10) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1:0.97-1.0. (11) Mesopleuron with hairs erect, black with blue tinge; hypoepimeral area thoroughly punctate. (12) Scutellum evenly rounded, median longitudinal furrow distinct on posterior half. (13) Metapostnotum rugose, with upper band strongly areolate, half as wide as metanotum. (15) Vein cu-v of hindwing 0.53-0.55 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, ventrally with longitudinal keel; spinelike setae absent.

Male. Length 7.5-9.5 mm; length of forewing 6.5-7.5 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.94-1.0 : 1. (19) Proportion of OOL to POL 0.63-0.67 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.61-0.67. (22) Apex of T7 rounded. (23) S3-4 without fringes of hairs. (24) S6 with subapical tubercle compressed longitudinally, posteriorly carinate; hairs dense, those surrounding carina directed caudally. (25) Genitalia, Figure 71.

Material studied. CHILE. Coquimbo: 3 females, Hacienda Illapel, 600-900 m, 19-X-1966, Schlinger, Irwin and Peña (CAS). Valparaíso: 1 male, Marga Marga, 21-IX-1923, P. Herbst (CAS); 1 female and 2 males, Valparaíso, 18-IX-1914, P. Herbst (CAS). Aconcagua: 1 male, Río Blanco, Piscicultura, XI-1963, Peña (UFPR). Santiago: 1 female, El Manzano, 23-XII-1968, J. Valencia (MF). Talca: 3 fe-males, El Radal, 1100 m, 23-30-X-1957, L. Peña (SEM). Linares: 4 females and 2 males, Romehual, Cord. Parral, XI-1960, L. Peña (UFPR). Valdivia: 1 female, Santo Domingo, 18-XI-1984, E. Krahmer (MF). Cautin: 1 female, Lago Budi, 1923, P. Herbst, "aus Zelle von Colletes musculus Friese gezüchtet" (CAS); 1 male, Temuco, 1923, P. Herbst, "aus Zelle von Colletes seminitidus Spin. gezüchtet" (CAS). ARGENTINA. Río Negro: 1 female, Isla Victoria, 19-XII-1944, on flowers of Fragaria (MLP); 1 male, El Bolsón, 20-I-1964, A. Kovacs (UCV); 1 male, Bariloche, XI-1975, R.M. Bohart (Davis).

#### 4. Isepeolus cortesi Toro and Rojas (Fig. 55)

Isepeolus cortesi Toro and Rojas, 1968: 58-60, figs. 1-5. Holotype male from El Salto, Valparaíso, Chile, Oct. 1967, H. Toro and E. de la Hoz (H. Toro collection, not examined).

This species is closely related to *atripilis*, from which it is readily differentiated by the more extended white pubescence on the scutum, the pleura and the metasomal terga. Females of *cortesi* can be distinguished by the lack of spinelike setae on the apex of S6 and the white hairs on the upper half of the mesopleuron. The males are characterized by the bilobate subapical tubercle of S6 and the reduced gonostylus. This is the smallest species in the genus; some males are scarcely 6 mm long.

Female. Length 6.5-7.5 mm; length of forewing 5.2-5.7 mm. (3) Proportion of LID to UID 0.72-0.75 : 1. (4) Proportion of OOL to POL 0.85-0.95 : 1. (6) Punctures between and around ocelli dense, leaving no interspaces to interspaces one-quarter as wide as diameter of punctures; polished triangular area between lateral ocellus and eye less than ocellar diameter. (7) Labrum transversely elevated on apical third, but without carina; apex feebly denticulate. (8) As in octopunctatus. (9) Maxillary palpus with 3 segments, second as long as wide. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.08-1.12. (11) Mesopleuron with hairs white on upper half; hypoepimeral area punctate, with small polished area above scrobe. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous, sometimes hairs give it bigibbous (13) Metapostnotum tessellate, appearance. sometimes polished on lower fourth. (15) Vein cu-v of hindwing 0.70-0.82 times as long as second abscissa of M+Cu. (17) S6 with apex pointed, ventrally keeled; spinelike setae absent, but some stiff setae present.

Male. Length 6-8 mm; length of forewing 5.8-6.5 mm. (18) Eyes convergent below, proportion of LID to UID 0.83-0.84 : 1. (19) Proportion of OOL to POL 0.71-0.73 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.58-0.61. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle bilobed. (25) Genitalia, figure 4 in Toro and Rojas (1968).

Material studied. CHILE. Coquimbo: 1 male, Fray Jorge, 10-X-1977, De la Hoz (UCV). Valparaíso: 1 female paratype, El Salto, 17-X-1967, De la Hoz (UCV); 1 female, Peñuelas, 7-XII-1967, H. Toro (UCV). Curicó: 1 female, 6 km E Los Queñes, 4-I-1967, M.E. Irwin (CAS). ARGENTINA. Neuquén: 1 male, Paso Coihue, 5-I-1964, A. Giai (SEM); 1 female, Laguna Blanca, 23-XII-1965, A. Giai (SEM). Río Negro: 1 female, 30 km E Bariloche, 16-XI-1964, A. Giai (SEM).

#### 5. Isepeolus atripilis n. sp. (Figs. 47, 54, 62, 63, 69, 75-77)

This species is related to *cortesi* as indicated by the reduced male gonostylus, the hindwing with a short second abscissa of vein M + Cu and the bilobate subapical tubercle of the male S6. The female may be confused with dark specimens of *vachali*, from which it is distinguished by the evenly rounded scutellum and the hindwing venation. It may also be confused with *octopunctatus*, as noted under the latter species. Measurements in parentheses below correspond to the holotype; for other variable characters the holotype condition is indicated by italics.

Female. Length 7-10 (8.7) mm; length of forewing 5.5-7.5 (7) mm. Integument black, apex of mandible, distotarsi and sometimes tegula reddish brown; pedicel and flagellum reddish. Wings hvaline, weakly infuscated beyond closed cells; veins and pterostigma dark brown to black. Vestiture black, some specimens completely so, but others with the following parts white: some hairs above antennal sockets, vertex, pronotal lobes, scutum on anterior and posterior margins and above tegula, scutellum along median line, metanotum at sides, spot on tegula, a tuft on mesopleuron covering spiracular entrance, 4 apical spots on T1 and T2, central ones sometimes missing, sometimes 2 apical median spots on T4 (Fig. 69), and apices of femora and tibiae. *Sculpture*. Punctation dense and even, on mesopleuron leaving no interspaces, on scutum leaving interspaces half as wide as to as wide as diameter of punctures. Morphology. (3) Proportion of LID to UID 0.71-0.76(0.76) : 1. (4) Proportion of OOL to POL 0.83-0.93(0.88): 1. (6) Punctation between and around ocelli dense, almost no interspaces among punctures; polished triangular area between lateral ocellus and eye narrower than ocellar diameter. (7) Labrum with weak transverse elevation on apical third; apex feebly denticulate. (8) Malar space 0.13 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) Maxillary palpus with 3 or sometimes a fourth minute segment, second as long as wide. (10) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1: 0.93-1.04(1.04). (11) Mesopleuron with hairs black, sometimes white hairs covering spiracular entrance; hypoepimeral area punctate, with small polished area above scrobe. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum tessellate, polished on lower fourth. (15) Vein cu-v of hindwing 0.75-1.00 times as long as second abscissa of M+Cu. (17) S6 with apex pointed, ventrally keeled; spinelike setae absent, but a few stiff setae bordering point.

Male. Length 7.5-8.5 mm; length of forewing 6.5-7.5 mm. (18) Eyes converging below, proportion of LID to UID 0.85-0.87 : 1. (19) Proportion of OOL to POL 0.70-0.72 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.64-0.67. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle bilobed. (25) Genitalia, Figure 75.

Material studied. Holotype female, Paso Córdoba, Río Negro, Argentina, 24-I-1975, A. Willink and G. Claps (IML). Paratypes. ARGEN-TINA. **Tucumán:** 1 male, road Tafí-Amaicha km 90, 17-XII-1973, L. Stange, on flowers of Adesmia inflexa (IML). **Catamarca:** 2 females, La Ciénaga, 26-XI-1975, R.M. Bohart (Davis); 1 female, Cuesta Mina Capillitas, 2300 m, 17-XI-1972, J.L. Neff, on flowers of Glandularia microphylla (CTMI); 1 female, El Desmonte,

7-XI-1989, J.G. Rozen and A. Roig A. (AMNH). Mendoza: 1 female, Punta de Vacas, 9-I-1980, E. Domínguez (IML); 1 female, Puente del Inca, 2700 m, 26-I-1973, A. Willink (IML); 1 male, Quebrada Horcones, 2900 m, 10-I-1985, A. Roig A. (MACN). Buenos Aires: 1 male, Patagones, J.M. Viana (MACN). Neuquén: 2 females, Confluencia Traful, 20-XII-1964, A. Giai (SEM). Río Negro: 1 female and 1 male, same data as holotype (IML); 3 males, Río Colorado, 13-21-II-1946, Hayward and Willink (MLP); 1 female and 1 male, Luis Beltrán, XI-1987, M. Fritz (MF). Santa Cruz: 1 female, Lago Argentino, 13-I-1953, A. Willink (IML). CHILE. Magallanes: 1 female, 4 km W Laguna Amarga, 8-XII-1966, Irwin and Schlinger (CAS).

#### 6. Iseopeolus viperinus (Holmberg) (Figs. 38, 43, 58-60, 70, 73, 74)

- Epeolus viperinus Holmberg, 1886a: 155-156. Holotype female, from Tandil (Prov. Buenos Aires, Argentina), I-29-1883 (MACN, examined). Holmberg, 1886b: 282-283. Dalla Torre, 1896: 333. Schrottky, 1903: 183.
- Leiopodus depressiventris Ducke, 1907: 88. Lectotype female, by present designation, from Barbacena, Minas Gerais (Brazil), 23-XI-1905, A. Ducke (Bern, examined). Ducke, 1908a: 102-103. Ducke, 1908c: 79. New synonym.
- Isepeolus albopictus Cockerell, 1907: 65. Holotype male from Carcarañá, Argentina (USNM, type number 55258, examined). New synonym.
- Calospiloma viperinum: Brèthes, 1909: 68.
- Palinepeolus viperinus: Holmberg, 1909: 78.
- Epeolus depressiventris: Ducke, 1910: 104.
- Isepeolus depressiventris: Ducke, 1912: 100. Grütte, 1935: 501.
- Isepeolus viperinus: Jörgensen, 1912b: 316. Schrottky, 1913: 264. Grütte, 1935: 501. Michener, 1957: 141–146. Rozen, 1966: 10–12. Oliveira, 1966: 163–176. Rozen et al., 1978: 10–16. Alexander, 1990: 144.

The holotype of *I. viperinus* lacks the abdomen and bears the following two labels: "I-29" and "*Epeolus viperinus*, Tandil."

This is the only *Isepeolus* species that has the integument of the scutellum and the metanotum red. Some specimens may also have the pronotum, the scutum and the pleura red in a variable extent. The pattern of maculation is fairly constant; specimens from Colombia look almost identical to specimens from the type locality in Argentina. The subapical tubercle of the male S6 is usually transverse and glabrous posteriorly, but specimens from southern Argentina (Río Negro and Chubut) have the tubercle conical and thoroughly hairy, much as in *octopunctatus*. The hind femur of the male seems to follow an allometric pattern, being conspicuously swollen in large specimens.

*Female.* Length 6.5–10.0 mm; length of forewing 5.0–7.5 mm. (3) Proportion of LID to UID



Figure 70. Distribution of Isepeolus viperinus.

0.80-0.85 : 1. (4) Proportion of OOL to POL 0.87-0.89: 1. (6) Punctures sparse, between and around ocelli mostly polished; sometimes between front ocellus and vertex with longitudinal rugose area with no definite punctures; polished triangular area between lateral ocellus and eye wider than ocellar diameter. (7) Labrum medially elevated, with 2 conspicuous denticles, below denticles concave; apical margin denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible twice as far from eye margin as posterior articulation. (9) Maxillary palpus with 3 poorly defined segments, second and third forming an ovoid structure. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.24-1.30. (11) Mesopleuron with hairs white on upper half, but in front of hypoepimeral area a distinctive brown spot; hypoepimeral area with small polished area above scrobe. (12) Scutellum bigibbous. (13) Metapostnotum rugose, sometimes polished on lower fourth or less. (15) Vein cu-v of hindwing 0.48-0.58 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, no ventral keel; with short spinelike setae bordering point.

*Male.* Length 6.5–10.0 mm; length of forewing 5.5–8.0 mm. (18) Eyes converging below, proportion of LID to UID 0.87–0.89 : 1. (19) Proportion of OOL to POL 0.81–1.13 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.66–0.73. (22) Apex of T7 emarginate. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, triangular to almost conical. (25) Genitalia, Figure 73.

Material studied (Fig. 70). COLOMBIA. Valle: 1 female, Cali, 8-I-1972, C.D. Michener (SEM); 1 female, Mun. Candelaria, 1010 m, Lago San Luis, 4-6-IV-1975, R. Wilkerson (Gainesville). BRAZIL. 38 specimens from the states of Ceará, Bahia, Minas Gerais, São Paulo, Paraná and Santa Catarina (collection dates August to March). ARGENTINA. 304 specimens from the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Santiago del Estero, Córdoba, San Juan, Mendoza, San Luis, Entre Ríos, Santa Fe, Buenos Aires, La Pampa, Río Negro, Neuquén and Chubut (collection dates September to April).



Figures 71-79. 71-76, Genitalia (ventral left, dorsal right), S7 and S8 of *Isepeolus* males; g, gonostylus; s, spatha; d, digitiform ventral lobe; sparser stippling indicates partially sclerotized ventral surface of penis. 71, 72, *I. septemnotatus;* 73, 74, *I. viperinus;* 75, 76, *I. atripilis.* 77-79, Apex of male metasoma, ventral view showing subapical tubercle of S6. 77, *I. atripilis;* 78, *I. vachali;* 79, *I. luctuosus.* Scale lines 0.1 mm.

#### 7. Isepeolus luctuosus (Spinola) (Figs. 79, 80)

Epeolus luctuosus Spinola, 1851: 189–190. Types: male and female, from Provincias del Norte, Coquimbo, Chile (not examined). Smith, 1854: 258. Reed, 1892: 229. Dalla Torre, 1896: 329. Herbst, 1917: 269. Gazulla and Ruiz, 1928: 301, 302. Ruiz, 1936: 168.

Leiopodus luctuosus: Ducke, 1908b: 39.

Calospiloma luctuosum: Brèthes, 1909: 68.

*Isepeolus luctuosus:* Cockerell, 1910: 144. Ducke, 1912: 100. Schrottky, 1913: 264. Claude-Joseph, 1926: 267. Janvier, 1933: 325. Grütte, 1935: 501. Toro and Rojas, 1968: 60. Alexander, 1990: 139, 144, fig. 9a, b.

I have not seen types of *I. luctuosus*, but Spinola's original description leaves no doubt about its identity. He describes in detail the pattern of coloration, which cannot be confused with that of any other Chilean species. The lateral white maculae on T1-2 encircling central black spots are particularly distinctive.

Female. Length 7.5-10.0 mm; length of forewing 6.0-7.5 mm. (3) Proportion of LID to UID 0.70-0.76: 1. (4) Proportion of OOL to POL 1.05-1.17:1. (6) Punctation between and around ocelli variable, from extensively polished to moderately punctate; triangular polished area between lateral ocellus and eye as wide as or wider than ocellar diameter. (7-9) As in viperinus. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1:1.31-1.39. (11) Mesopleuron with hairs white on upper half; hypoepimeral area with small polished area above scrobe. (12) Scutellum bigibbous. (13) Metapostnotum as in viperinus, but with upper areolate band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.53-0.56 times as long as second abscissa of M + Cu. (17) As in viperinus.

Male. Length 6.2-9.5 mm; length of forewing 5.4-8.0 mm. (18) Eyes converging below, proportion of LID to UID 0.83-0.90 : 1. (19) Proportion of OOL to POL 0.79-0.84 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.71-0.87. (22) Apex of T7 rounded. (23) S3 without fringe of hairs, fringe on S4 weak. (24) S6 with subapical tubercle as strong transverse elevation almost reaching margin of sternum; tubercle posteriorly usually carinate. (25) As in *viperinus*.

Material studied (Fig. 80). CHILE. 93 specimens from the provinces of Copiapó, Coquimbo, Valparaíso, Santiago, Ñuble, Curicó, Malleco, Concepción and Llanquihue (collection dates October to February). ARGENTINA. 22 specimens from the provinces of Neuquén, Río Negro and Chubut (collection dates January to April).

#### 8. Isepeolus lativalvis (Friese) (Figs. 56, 57)

*Epeolus lativalvis* Friese, 1908: 83. Lectotype female, by present designation, from Concepción, Chile, 27-XII-1907, Herbst leg. (Berlin, examined). Schrottky, 1913: 264. Isepeolus lativalvis: Grütte, 1935: 501. Toro and Rojas, 1968: 60.

Friese based *lativalvis* on specimens from Tucumán (Argentina) and Concepción (Chile). A female from the latter locality is selected as the lectotype, following current usage of the name. A syntype specimen from Tucumán (the printed label is overwritten "Mendoza") in the Berlin collection, labeled *lativalvis* by Friese, corresponds to *Melectoides cockerelli* (Jörgensen). *I. lativalvis* as presently delimited occurs in Chile and southern Argentina.

This species together with *smithi* is easily recognized by the broad, rounded apex of the female abdomen. It is distinguished from *smithi* and all other *Isepeolus* by the female S6 which is apically rounded, with a blunt median point.

Female. Length 7.5-8.5 mm; length of forewing 5.5-6.0 mm. (3) Proportion of LID to UID 0.75-0.77: 1. (4) Proportion of OOL to POL 0.94-0.95 : 1. (6, 7) As in luctuosus, but median denticles of labrum usually weak. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) As in luctuosus. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.24-1.30. (11, 12) As in luctuosus. (13) As in luctuosus, but upper areolate band narrow. (15) Vein cu-v of hindwing 0.5-0.6 times as long as second abscissa of M + Cu. (16) Apical width of T5 more than half of apical width of T2. (17) S6 with apex rounded, no ventral keel; short spinelike setae bordering apex present.

Male. Length 6.8-8.0 mm; length of forewing 5.5-6.3 mm. (18) Eyes converging below, proportion of LID to UID 0.87 : 1. (19) Proportion of OOL to POL 0.72-0.75 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.62-0.69. (22) Apex of T7 emarginate. (23) S3 and S4 without fringes of hairs. (24) S6 with subapical tubercle triangular, transverse, usually posteriorly carinate. (25) As in *viperinus*.

Material studied. CHILE. Santiago: 2 males, Santiago, F. Ruiz (ZMC). Nuble: 1 female and 1 male, 5.6 km N Cobequecura, 29-I-1976, L. Stange (IML). Curicó: 1 female, 15-I-1924, P. Herbst (CAS). Malleco: 1 female, Vegas Blancas, 21-XII-1985, A. Roig-A. (MACN). Bio Bio: 1 female, Los Angeles, I-1953, M. Fritz (MLP). Cautin: 1 female and 3 males, 20 km E Temuco, 7-I-1951, Ross and Michelbacher (CAS). Llanquihue: 1 female, Lepihue, 21-I-1951, Ross and Michelbacher (CAS). Ar-GENTINA. Neuquén: 1 male, Hua Hum, Parque Nac. Lanín, 12-I-1950, Schajovskoi (MLP); 1 male, San Martín de Los Andes, 5-XII-1980, M. Gentili (MACN); 4 males, Catán Lil, 15-I-1954, M. Senkute (SEM). Río Negro: 1 male, Bariloche, M. Fritz (MF); 1 male, El Bolsón, II-1955, J. Foerster (SEM).

#### 9. Isepeolus smithi Jörgensen

(Fig. 68)

Isepeolus smithi Jörgensen, 1912a: 146-147, fig. D. Lectotype male, by present designation, from Mendoza (Argentina), 28-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

This species is closely allied to *lativalvis*, from which it is distinguished by the sharp pointed apex of the female S6. The male is distinguished by the margin of the clypeus not continuing as a carina above the level of the anterior mandibular articulation, and the mandible with a dense basal patch of hairs, which is white with a characteristic brown spot.

Female. Length 7.5-8.5 mm; length of forewing 6.0-6.5 mm. (3) Proportion of LID to UID 0.74-0.75: 1. (4) Proportion of OOL to POL 1.06-1.12 : 1. (6) Punctures sparse, area between and around ocelli mostly polished; polished triangular area between lateral ocellus and eye subequal to ocellar diameter. (7-9) As in lativalvis. (10) First flagellomere subequal to sum of flagellomeres 2-4, proportion 1:1.00-1.04. (11) Mesopleuron with variable amount of white hairs, wholly black to white on upper half leaving a dark spot anterior to hypoepimeral area; hypoepimeral area with small polished area above scrobe. (12) Scutellum slightly bigibbous, median longitudinal furrow weak. (13) As in lativalvis. (15) Vein cu-v of hindwing 0.50-0.62 times as long as second abscissa of M + Cu. (16) T6 distinctively wide, as in lativalvis. (17) S6 with apex pointed, sharp, ventral keel present; spinelike setae present.

Male. Length 6.8-7.5 mm; length of forewing 5.8-6.3 mm. (18) Eyes converging below, proportion of LID to UID 0.84-0.88 : 1. (19) Proportion of OOL to POL 0.91-0.97 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.68-0.69. (22) Apex of T7 emarginate. (23) S3 without fringe of hairs, present on S4. (24) As in *lativalvis*. (25) As in *viperinus*. Material studied. ARGENTINA. **Tucumán:** 1 fe-

Material studied. ARGENTINA. Tucumán: 1 female, Alto del Tío, Tafí-Amaicha road, 2700 m, 6-III-1968, A. Willink (IML). Catamarca: 1 female, Cuesta Mina Capillitas, 17-XII-1972, J.L. Neff (CTMI). Mendoza: 1 female, Villavicencio, 20-XI-1941 (MLP); 3 males, Uspallata, 6-XII-1979, A. Roig-A. (MACN); 3 males, Uspallata, 6-XII-1979, C. and M. Vardy (London). Buenos Aires: 1 female and 6 males, Patagones, M.J. Viana (MACN, SEM). Neuquén: 1 female, Mariano Moreno, 750 m, 16-XII-1966, Irwin and Schlinger (CAS). Río Negro: 1 male, Río Colorado, 13-21-II-1946, Hayward and Willink (MLP); 1 female, Luis Beltrán, XI-1987, M. Fritz (MF). Chubut: 3 males, 13 km N Puerto Madryn, 14-XII-1966, Irwin and Schlinger (CAS).

#### 10. Isepeolus wagenknechti Toro and Rojas (Fig. 61)

Isepeolus wagenknechti Toro and Rojas, 1968: 55-58.

Holotype female from Quebrada Honda, Coquimbo, Chile, 10 Nov. 1957, R. Wagenknecht (H. Toro collection, not examined). Toro, 1971: 261–262, figs. 1–3.

This species has a color pattern that makes it easily distinguishable from related forms in which the female S6 bears short spinelike setae and the male S6 has a transverse subapical tubercle. The color pattern of I wagenknechti much resembles that of Melectoides niveiventris. The vestiture is deep black, except for most of the dorsum of the body, which has white hairs; the metasomal T1-2 have broad white uninterrupted bands and T3-4 have median white spots.

Female. Length 9-10 mm; length of forewing 6.8-7.2 mm. (3) Proportion of LID to UID 0.74-0.76 : 1. (4) Proportion of OOL to POL 0.80-0.81 : 1. (6) Punctures between and around ocelli dense; polished triangular area between lateral ocellus and eye subequal to ocellar diameter. (7) As in viperinus. (9) Maxillary palpus with second segment longer than wide, distinct from third; a fourth minute segment may be present in some specimens. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1:1.11-1.18. (11) Mesopleuron with hairs black; hypoepimeral area punctate. (12) Scutellum bigibbous. (13) Metapostnotum rugose, with upper areolate band as wide as half of metanotum. (15) Vein cu-v of hindwing 0.45-0.52 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, ventral keel present; short spinelike setae present.

Male. Length 7.5-8.0 mm; length of forewing 6.0-6.6 mm. (18) Eyes converging below, proportion of LID to UID 0.84-0.87 : 1. (19) Proportion of OOL to POL 0.68-0.71 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.74-0.80. (22) T7 with bare basal band present, apex rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, low, medially elevated and with longitudinal carina posteriorly. (25) Genitalia, figure 3 in Toro (1971).

Material studied. CHILE. Atacama: 4 males, 20 km SE Caldera, 16-X-1957, L. Peña (SEM). Coquimbo: 1 female, Quebrada Los Choros, 12-X-1977, L. Ruz (UCV); 1 female, Loros Bajos, La Serena, 9-XI-1961, R. Wagenknecht (UCV).

#### 11. Isepeolus vachali Jörgensen (Figs. 45, 67, 78, 80)

- Isepeolus vachali Jörgensen, 1912a: 143-144, fig. B. Lectotype female, by present designation, from Chacras de Coria, Mendoza (Argentina), 17-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.
- Isepeolus viecki Jörgensen, 1912a: 147-148, fig. E. Lectotype female, by present designation, from Mendoza (Argentina), 17-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316. New synonym.
- Isepeolus vierecki Cockerell, 1917: 479 (emendation).

**Figure 80.** Distributions of *Isepeolus luctuosus* (open circles) and *I. vachali* (dots).

This species shows considerable variation in the color pattern. The vestiture is extensively white in specimens from Perú to central Argentina, while specimens from southern Argentina (Neuquén, Río Negro and Chubut) have white vestiture reduced. Southern specimens are less variable in size, averaging 8-10 mm in length; elsewhere the size range is broader, probably due to exploitation of more than one host. Small pale specimens, common in northern Argentina, look quite different from the mostly black, large specimens from the south. I have not found any morphological features suggesting that this is not a single species. Populations from Mendoza are particularly variable, and most intermediates in color and size can be found. This species is related to *wagenknechti* by the male T7 which has a broad bare basal band.

Female. Length 6.5-10.5 mm; length of forewing 5-8 mm. (3) Proportion of LID to UID 0.71-0.81: 1. (4) Proportion of OOL to POL 1.03-1.21: 1. (6, 7-9) As in viperinus, but sometimes median denticles of labrum forming single strong projection. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1: 1.18-1.35. (11) Mesopleuron with variable amount of white hairs; hypoepimeral area as in viperinus. (12, 13) As in viperinus, but upper areolate band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.46-0.57 times as long as second abscissa of M + Cu. (17) As in viperinus.

Male. Length 6.5-10.0 mm; length of forewing 6.0-8.7 mm. (18) Eyes converging below, proportion of LID to UID 0.84-0.9 : 1. (19) Proportion of OOL to POL 0.71-0.79 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.63-0.71. (22) T7 with basal bare band present, apex emarginate. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, triangular, usually with posterior longitudinal carina. (25) As in *viperinus*.

Material studied (Fig. 80). PERU. Arequipa: 1 female, Yura, 12-X-1983, A. Roig-A. (MACN). Moquegua: 2 females, Carumas, IV-1961, Zevallos (IML). CHILE. Antofagasta: 1 female, Chiu Chiu, 24-I-1972, Sielfeld (SEM). BOLIVIA. Cochabamba: 1 female, Cochabamba, 26-IX-1972, G. E. Bohart (Logan). Oruro: 1 male, Poopo, 15-IX-1965, J.C. Ballard (Logan). AR-GENTINA. 319 specimens from the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Mendoza, La Pampa, Buenos Aires, Neuquén, Río Negro, Chubut and Santa Cruz (collection dates October to April).

#### LITERATURE CITED

- Alexander, B. 1990. A cladistic analysis of the nomadine bees (Hymenoptera: Apoidea). Syst. Entomol. 15: 121-152.
- Bohart, G. E. 1970. The Evolution of Parasitism among Bees. Utah State University, Logan. 33 pp.
- Brèthes, J. 1909. Himenópteros nuevos de las Repúblicas del Plata y del Brasil. An. Mus. Nac. Buenos Aires 19: 49-69.
- Brothers, D. J. 1976. Modifications of the metapostnotum and the origin of the 'propodeal triangle' in Hymenoptera Aculeata. Syst. Entomol. 1: 177-182.
- Claude-Joseph, F. 1926. Recherches biologiques

sur les Hyménoptères du Chili (Meliferes). Ann. Sci. Nat., Zool., ser. 10, 9: 113-268.

- Cockerell, T. D. A. 1907. Descriptions and records of bees. XV. Ann. Mag. Nat. Hist. (7)20: 59-68.
- Cockerell, T. D. A. 1910. Some Neotropical bees. Psyche 17:142-144.
- Cockerell, T. D. A. 1917. Descriptions and records of bees. 75. Ann. Mag. Nat. Hist. (8)19: 473-481.
- Dalla Torre, C. G. de. 1896. Catalogus Hymenopterorum..., X. Lipsiae. viii+643 pp.
- Ducke, A. 1907. Contribution à la connaissance



de la faune hyménoptérologique du Nord-Est du Brésil. Revue d'Ent. 26: 73-96.

- Ducke, A. 1908a. Zur Kenntnis der Schmarotzer Bienen Brasiliens. (Hym). Zeitschr. Hym. Dipt. 1908: 99-104.
- Ducke, A. 1908b. Contributions à la connaissance des Hyménoptères des deux Ameriques. Rev. d'Ent. 27: 28-55.
- Ducke, A. 1908c. Contribution à la connaissance de la faune hyménoptérologique du Nord-Est du Brésil. II Hyménoptères récoltés dans l'Etat de Ceara en 1908. Revue d'Ent. 27: 57-87.
- Ducke, A. 1910. Contribution à la connaissance de la faune hyménoptérologique du Nord-Est du Brésil. III Hyménoptères récoltés dans l'Etat de Ceara en 1909 et supplements aux deux listes anterieures. Revue d'Ent. 28: 78-109.
- Ducke, A. 1912. Die Natürlichen Bienengenera Südamerikas. Zool. Jahrb., Abt. Syst. 34(1): 51-116.
- Farris, J. S. 1988. Hennig86, version 1.5.
- Friese, H. 1906a. Resultate einer Reise des Herrn A. C. Jensen-Haarup in die Gegend von Mendoza (Argentina). Flora og Fauna 3. Hefte: 89-102.
- Friese, H. 1906b. Neue Bienenarten aus Chile und Argentina. Zeitschr. Hym. Dipt. 6: 169-176.
- Friese, H. 1908. Die Apidae (Blumenwespen) von Argentina nach der Reisenergebnissen der Herren A.C. Jensen-Haarup und P. Jörgensen in den Jahren 1904–1907. Flora og Fauna 1908: 1–111.
- Friese, H. 1912a. Neue und wenig bekannte Bienenarten der neotropischen Region. Arch. Naturg. A6: 198-226.
- Friese, H. 1912b. Zur Bienenfauna des südlichen Argentinien (Hym.) II. Deutsche Entomol. Zeitschr. 1912: 362-367.
- Friese, H. 1925. Neue Formen von Schmarotzerbienen, besonders aus dem paläarktischen Gebiet. Konowia 4(1-2): 27-42.
- Gazulla, P., and F. Ruiz. 1928. Los insectos de la hacienda de "Las Mercedes." Rev. chilena Hist. Nat. 32: 288-305.
- Grütte, E. 1935. Zur Abstammung der Kuckucksbienen (Hymenopt., Apid.). Archiv. Naturg., N.F., 4(4): 449–534.
- Herbst, P. 1917. Durchsicht der von Spinola in der von Claude Gay 1851 herausgegebenen Historia física y política de Chile, Zoologia, Vol.IV beschriebenen Apidae, nebst einigen einleitenden Bemerkungen. Deutsch. Ent. Zeitschr. 1917: 257-294.
- Holmberg, E. L. 1886a. Viajes a las Sierras del Tandil y de la Tinta, Himenópteros. Actas Acad. Ciencias Córdoba 5: 137-184.
- Holmberg, E. L. 1886b. Sobre ápidos nómadas de la República Argentina. An. Soc. Cientif. Argentina 22: 272-286.
- Holmberg, E. L. 1887. Sobre ápidos nómadas de la República Argentina. An. Soc. Cientif. Argentina 23: 17-33.

- Holmberg, E. L. 1909. *Palinepeolus* Holmb., nom. nov. . . . Apuntes de Hist. Nat. 1: 77-78.
- Janvier, H. 1933. Etude biologique de quelques hyménoptères du Chili. Ann. Sci. Nat., Zool., ser. 10, 16: 209-356.
- Jörgensen, P. 1909. Beobachtungen über Blumenbesuch, Biologie, Verbreitung usw. der Bienen von Mendoza (Hym.). Deutsch. Ent. Zeitschr. 1909: 211-227.
- Jörgensen, P. 1912a. Revision der Apiden der Provinz Mendoza, Republica Argentina (Hym.). Zool. Jahrb., Abt. Syst. 32(2): 89-162.
- Jörgensen, P. 1912b. Los crisídidos y los himenópteros aculeados de la provincia de Mendoza. An. Mus. Nac. Buenos Aires 22: 267-338.
- Linsley, E. G., and C. D. Michener. 1939. A revision of the North American Nomadidae (Hymenoptera). Trans. Am. Entomol. Soc. 65: 265-305.
- Michener, C. D. 1944. Comparative external morphology, phylogeny and a classification of the bees. Bull. Amer. Mus. Nat. Hist. 82: 151-326.
- Michener, C. D. 1957. Notes on the biology of a parasitic bee, *Isepeolus viperinus* (Hymenoptera, Anthophorinae). Entomol. News 68: 141-146.
- Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific Regions. Bull. Am. Mus. Nat. Hist. 130: 1-362, 15 pl.
- Michener, C. D., and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. Univ. Kansas Sci. Bull. 51(14): 463-482.
- Oliveira, B. L. de. 1966. Descriçao de estadios imaturos de *Isepeolus viperinus* (Holmberg) e confrontaçoes com outras larvas de Anthophoridae parasitas conhecidas (Hymenoptera-Apoidea). Bol. Univ. Federal Paraná, Zool. 2(11): 163-176.
- Reed, E. C. 1892. Revisión de las abejas chilenas descritas en la obra de Gay. Actas Soc. Cient. Chile 2: 223-240.
- Roig-Alsina, A. 1989. The tribe Osirini, its scope, classification and revisions of the genera *Parepeolus* and *Osirinus* (Hymenoptera, Apoidea, Anthophoridae). Univ. Kansas Sci. Bull. 54: 1-23.
- Roig-Alsina, A. 1990. Coelioxoides Cresson, a parasitic genus of Tetrapediini (Hymenoptera: Apoidea). J. Kansas Entomol. Soc. 63: 279-287.
- Roig-Alsina, A. 1991. Cladistic analysis of the Nomadinae s. str. with description of a new genus (Hymenoptera: Anthophoridae). J. Kansas Entomol. Soc. 64: 23-37.
- Rozen, J. G., Jr. 1966. The larvae of the Anthophoridae (Hymenoptera, Apoidea). Part 2. The Nomadinae. Am. Mus. Novitates 2244: 1-38.
- Rozen, J. G., Jr. In press. Evolution of cleptoparasitism in anthophorid bees as revealed by

their mode of parasitism and first instars. Am. Mus. Novitates.

- Rozen, J. G., Jr., K. R. Eickwort, and G. C. Eickwort. 1978. The bionomics and immature stages of the cleptoparasitic bee genus *Protepeolus*. Am. Mus. Novitates 2640: 1–24.
- Ruiz, F. 1936. Himenópteros de la provincia de Coquimbo. Rev. chilena Hist. Nat. 40: 159-169.
- Sandhouse, G. A. 1943. The type species of the genera and subgenera of bees. Proc. U. S. Nat. Mus. 92: 519-619.
- Schrottky, C. 1902. Ensaio sobre as abelhas solitarias do Brasil. Rev. Mus. Paulista 5: 330-613, pls. 12-14.
- Schrottky, C. 1903. Enumération des Hyménoptères connus jusq'ici de la R. Argentine, de l'Uruguay et du Paraguay. An. Soc. Cientif. Argentina 55: 176-186.

- Schrottky, C. 1913. La distribución geográfica de los himenópteros argentinos. An. Soc. Cientif. Argentina 75: 225-286.
- Smith, F. 1854. Catalogue of hymenopterous insects in the collection of the British Museum. Part II Apidae. London. pp. 199-465, pls. 7-12.
- Spinola, M. 1851. Himenópteros, in C. Gay, Historia física y política de Chile, 6: 153-569.
- Taschenberg, E. 1883. Die Gattungen der Bienen (Anthophila). Berliner Ent. Zeitschr. 27: 37-100.
- Toro, H., and F. Rojas. 1968. Dos nuevas especies de *Isepeolus* con clave de las especies chilenas. Rev. chilena Entomol. 6: 55-60.
- Toro, H. 1971. Una nueva especie de *Isepeolus* (Hym. Anthophoridae) de Chile. An. Mus. Hist. Nat. Valparaíso 4: 261-265.



Roig-Alsina, A. 1991. "Revision of the cleptoparasitic bee tribe Isepeolini (Hymenoptera: Anthophoridae)." *The University of Kansas science bulletin* 54, 257–288.

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