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Revision and phylogenetic analysis of *Chilioediscelis* (Hymenoptera: Colletidae) with descriptions of three new species

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Abstract

The southern South American subgenus *Chilioediscelis* Toro and Moldenke is revised. The males and females of three new species, *C. mirzamalae* Willis & Packer, *C. sardonyx* Willis & Packer and *C. penai* Willis & Packer, are described. A key to species, distribution map and results of a phylogenetic analysis of the subgenus are provided. All character states used in phylogenetic analysis are either illustrated or references to figures of them are given.

Key words: *Chilioediscelis*, *Chilicola*, Xeromelissinae, Colletidae, bees, taxonomy, new species, phylogeny, Chile, Argentina

Introduction

The subfamily Xeromelissinae is found in South and Central America as far north as Mexico (Toro and Michener 1975; Michener 1995; 2000; 2002). It consists of five genera including *Chilicola*, the largest genus in the subfamily. *Chilicola* is a genus of small hylaeiform bees which is most species rich in the temperate parts of South America (Michener and Rozen 1999). *Chilicola* females can readily be differentiated from other members of the Xeromelissinae by the sternal corbicula in which posteromedially directed long scopal hairs surround a central bare space that is broader anteriorly than posteriorly (Packer and Genaro 2006). However, the subgenus investigated here is the one exception. Males of the genus can be distinguished from other xeromelissines by the absence of yellow integumental bands on the metasoma and absence of a strongly concave posterior margin to S5.

Chilioediscelis can be separated from all other subgenera of *Chilicola* by their robust and strongly curved hind tibial spurs in conjunction with a hind tarsal claw with a considerably reduced inner tooth in both sexes and by lacking the corbicular structure to the scopa of S2 in the females. In their revision of the Chilean Xeromelissinae, Toro and Moldenke (1979) described the subgenus for three species: *C. andina* Toro and Moldenke, *C. patagonica* Toro and Moldenke and *C. araucana* Toro and Moldenke. *Chilicola araucana* was only known from the male until Packer (2004) described the female. The purpose of this paper is to revise the subgenus *Chilioediscelis* and describe three new species.

Material and methods

Material

Specimens used in this paper were obtained from the following institutions: AMNH, American Museum of Natural History, New York, USA; CASC, California Academy of Sciences, San Francisco, USA; MACN,

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Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina and PBYU, the Packer bee collection at York University, Toronto, Canada.

Descriptions

Descriptions generally follow the format used by Toro and Moldenke (1979). The following abbreviations are used: individual metasomal terga or sterna and antennal flagellomeres are represented by the letter T, S and F respectively followed by the appropriate number; IOC – interocellar distance, OOC – ocellocular distance, UOD – upper interocular distance, LOD – lower interocellar distance, i – interspace, d – puncture diameter (i and d are used together to give a relative measure of puncture density), and OD – median ocellus diameter (used as a relative measure of hair length). Relative size measurements are given as ratios in eyepiece graticule units at the magnification used. This avoids translation into standard units which would result in rather cumbersome numbers being reported. All measurements were made using a Leica MZ 125 microscope fitted with an ocular micrometer.

Phylogenetic analysis

Four taxa from three additional *Chilicola* subgenera were selected as outgroups based on a higher level phylogenetic analysis (Packer, 2008): *C. (Oediscelis) vernalis* Phillipi, *C. (Heteroediscelis) mantagua* Toro and Moldenke, *C. (Chilicola) rubriventris* Spinola and *C. (Chilicola) venticola* Packer. It has been suggested that *Chilioediscelis* evolved from within *Chilicola s. str.* (Michener, 1995). Gibbs and Packer (2006) and Packer (2008) provided evidence that the two subgenera are reciprocally monophyletic (i.e., they are both monophyletic and sister taxa to one another). Two species from the nominate subgenus were included in the analysis, representing the two major clades within *Chilicola s. str.*

All character states used in the phylogenetic analysis are illustrated except those already given in Gibbs and Packer (2006) or Packer (2008). In the appendix, the characters used by Gibbs and Packer (2006) and Packer (2007) are denoted by “G&P” or “P,” respectively, followed by the appropriate figure number.

Since only 10 taxa were included in the phylogenetic analysis, an exhaustive search was possible. The data matrix (Table 1) was analysed using TNT (Goloboff et al., 2000). Characters were treated as unordered and weighted equally. Branch support was investigated using symmetrical resampling (Goloboff et al., 2003). GC support values, which are calculated as the difference in frequency between the group and the second most common arrangement at each particular node, were calculated in TNT using the default 33% reweighting probability and 10,000 replications (Goloboff et al., 2003). GC values range from -100 to 100 and represent the frequency of the group in replications in comparison to the most commonly found alternative grouping. Bootstrap values were calculated using the standard (with replication) option in TNT, again with 10,000 replications. They are provided for comparison only and are not discussed further.

Biology

Little is known of the biology of these bees. Packer (2004) described the nest and brood cells of *C. araucana* from the dried stems of tumble mustard and found females commonly on a moderately large species of *Adesmia* (Fabaceae). Other species have been collected on flowers of *Adesmia*. Brood cells of one species, *C. sardonyx* Willis & Packer, new species, were found between two flat stones along with the allotype female. These observations suggest a wider range of nesting substrate than is known for other subgenera of *Chilicola*.

Along with those species of the nominate subgenus whose floral host associations are known, *Chilioediscelis* seem to forage primarily on species of *Adesmia*. It is possible that the flat face of the type subgenus and the striations commonly found on the lower face of most species of *Chilioediscelis* are different adaptations to pushing into the rather tight flowers of this plant.

TABLE 1. Data matrix used in the phylogenetic analysis.

Character											1	1	1	1	1	1	1	1	1	1	2	2
number	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
O. vernalis	1	1	2	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
H. mantagua	1	1	2	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	0
C. rubriventris	0	0	0	0	?	0	1	1	0	0	1	2	2	1	0	1	0	1	1	0	0	0
C. venticola	1	1	2	1	1	1	1	1	0	1	1	2	2	1	0	0	0	1	1	0	0	0
Ch. araucana	?	1	1	1	1	1	1	1	1	1	2	0	1	0	1	1	1	2	1	1	1	1
Ch. patagonica	0	1	1	1	0	1	1	1	0	1	2	1	3	0	1	0	1	1	1	1	1	1
Ch. andina	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0	2	2	1	1	1	1
Ch. mirzamalae	0	1	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0
Ch. penai	1	1	1	1	0	1	1	1	1	1	3	1	3	0	1	0	0	1	1	1	1	1
Ch. sardonyx	1	1	3	1	0	1	1	1	1	1	3	1	3	0	1	0	2	2	1	1	1	1

(continued).

Character	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4
number	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
O. vernalis	1	0	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0
H. mantagua	0	0	0	2	1	0	0	1	0	0	1	0	0	1	0	0	1	0	3	0	0	1
C. rubriventris	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	1	2	1	1	2
C. venticola	1	0	0	0	1	1	1	0	0	0	1	1	1	4	1	0	0	1	1	1	1	3
Ch. araucana	1	1	0	1	2	1	0	2	1	2	1	1	1	2	1	1	0	1	0	0	2	4
Ch. patagonica	1	?	0	1	2	1	0	0	1	2	1	1	1	2	1	1	0	1	0	0	2	4
Ch. andina	1	1	1	2	2	1	0	2	1	1	1	1	0	2	1	1	1	1	0	0	2	4
Ch. mirzamalae	0	1	0	2	2	1	0	0	1	1	0	1	1	3	1	1	0	1	1	0	2	4
Ch. penai	1	1	0	2	2	1	0	0	1	2	1	1	1	2	1	1	0	1	1	0	2	4
Ch. sardonyx	1	1	0	2	2	1	0	2	1	2	0	1	1	2	1	1	0	1	1	0	2	4

Taxonomy

Chilioediscelis Toro and Moldenke 1979.

Type species *C. andina* Toro and Moldenke, 1979. Original designation.

Diagnosis. Members of the subgenus *Chilioediscelis* are differentiated from all other subgenera of *Chilicola* by the following unique characteristics: absence of an episternal groove below the level of the scrobe, lack of a well developed tooth on the hind pretarsal claw and the lack of true corbicular structure on the scopa on S2 in females.

Description. Smallish bees, body length, 4.9–9.0mm.

Colouration: Black. Male with yellow on labrum, mandible, clypeus, lower paraocular area and on ventral surface of flagellomeres. Tegula sometimes marked with yellow. Legs marked with yellow and/or orange. Female lacking facial markings, but mandible base sometimes marked with yellow or orange, with reduced areas of yellow on legs compared to male and with metasomal terga varying from entirely dark to mostly orange-red.

Surface Sculpture: Microsculpture imbricate. Punctation not foveolate, sparse to dense but not crowded. Lower face and/or frons often with longitudinal striae. Dorsal area of propodeum striate. Metasomal terga with sparse, shallow, obscure punctures.

Pubescence: Long, woolly and whitish throughout. Males without specialised hair patches on metasomal sterna. Females with hairs forming non-corbiculate scopa on S2. Both sexes with long, dense hairs on dorso-lateral portions of propodeum and poorly defined apicolateral hair bands on some metasomal terga.

Structure: Head: Slightly broader than long. Labrum more than 2 X as broad as long. Mandible more than 2.5 X as long as basal depth, subapical tooth not attaining apex. Malar space varying from less than 0.5 X to slightly more than basal depth of mandible. Epistomal suture expanded below anterior tentorial pit, pit not separate from suture; paraocular lobe absent. Frons usually with weak supra-antennal depressions. Vertex weakly rounded, flat or concave. Facial fovea absent. Inner margins of compound eyes emarginate, eyes convergent below. Upper ocular tangent passes through lateral ocelli. Antenna unmodified, scape more than 3 X as long as greatest breadth.

Mesosoma: Approximately 1.5 X as long as greatest depth. Pronotal collar medially short, noticeably less than the diameter of median ocellus to entirely declivous medially. Episternal suture absent below level of scrobe. Scrobal groove weak but entire (except in *C. andina* where it is absent anterior of scrobe). Propodeum subequal in length to scutellum, slightly longer than metanotum. Hind leg of male modified; hind femur somewhat swollen, hind tibia somewhat swollen but lacking preapical concavity. Metatibial spur robust and strongly curved. Hind tarsal claw with reduced inner tooth. Distal stigmal perpendicular crossing second submarginal cell close to base. Both recurrent veins reach Rs+M in second submarginal cell.

Metasoma: Male with S1 either evenly convex or slightly swollen apically, remaining sterna otherwise unmodified. S7 with dorsal and ventral lobes; S8 with apical process narrow at base expanded towards apex; penis valve with two membranous lobes.

Key to species of subgenus *Chilioediscelis* Toro and Moldenke

1 Female..... 2
- Male 7
2 Hypostomal area with a triangular flange (Fig. 4F); tegula dark (Fig. 9D). *C. mirzamalae* Willis & Packer
- Hypostomal area without flange; tegula pale straw (Fig. 10F)..... 3
3 Metasoma entirely brown (Fig. 1B) ..... *C. andina* Toro and Moldenke
- Metasoma mostly red or orange or apical terga red or orange (Fig. 10M)..... 4
4 Metasoma T1-T3 entirely dark brown; T5-T6, and usually T4, mostly orange (Fig. 10K) ..... *C. araucana* Toro & Moldenke
- Metasoma with some red on all terga (Fig. 9J-L)..... 5
5 Dark brown on T2&T3 extending across entire tergum (Fig. 2F) .....*C. patagonica* Toro & Moldenke
- Brown on T1&T2 restricted to sides of terga (Fig. 5B) 6
6 Mandible base entirely orange (Fig. 5E) ..... *C. sardonyx* Willis & Packer
- Mandible base with a yellow spot on the condyle, otherwise black (Fig. 9B)..... *C. penai* Willis & Packer
7 Protibia with yellow only on anterior surface; anterior surface of profemur almost entirely dark (Fig. 9F) 9
- Protibia mostly yellow; anterior surface of profemur mostly yellow (Fig. 9G) 9
8 Metatibia mostly dark with limited yellow (Fig. 9H)..... *C. andina* Toro & Moldenke
- Metatibia with at most a small dark spot medially (Fig. 9I)..... *C. patagonica* Toro & Moldenke
9 Metatibia entirely dark (Fig. 12A); posterolateral margin of pronotal lobe dark (Fig. 4D) .... *C. mirzamalae* Willis & Packer.

- Metatibia with some yellow (Fig. 5D); posterolateral margin of pronotal lobe yellow (Fig. 5D) 10
10 OOC equal to IOC (Fig. 5C) ..... *C. sardonyx* Willis & Packer
- OOC less than IOC (Fig. 3C) 11
11 Metabasitarsus brown (G&P 11C) ..... *C. araucana* Toro & Moldenke
- Metabasitarsus yellow basally (G&P 11D)..... *C. penai* Willis & Packer

***Chilicola (Chilioediscelis) andina* Toro & Moldenke**

Diagnosis: Males of *C. andina* can be distinguished from other members of the subgenus except *C. patagonica* by the colouration of their legs. The protibia of *C. andina* and *C. patagonica* has yellow only on the anterior surface and the anterior surface of their profemur is almost entirely dark. In all others *Chilioediscelis* the protibia is mostly yellow and the anterior surface of the profemur is mainly yellow. *Chilicola andina* and *C. patagonica* can be differentiated from one another by the colour of their metatibia, which has extensive dark markings in *C. andina* but is yellow with at most a small amount of dark colouration medially in *C. patagonica*. These two species can also be distinguished by the shape of the S7 dorsolateral lobes: *C. andina* is the only species with ventral lobes that are small and narrow (Fig. 1E) while those of *C. patagonica* are larger, broader and more setose (Fig. 2E).

Females of this species can be distinguished from all other females except *C. mirzamalae* by the dark colouration of their metasomal terga (all other species have some orange or red markings on the metasoma). *Chilicola andina* females can easily be distinguished from those of *C. mirzamalae* by the absence of a large hypostomal flange that is present in *C. mirzamalae*. Also, *C. mirzamalae* females have a dark unmaculated pronotal lobe, whereas the pronotal lobe has yellow along the posterolateral margin in *C. andina*.

Description: Male: Length 6.7mm, forewing length 4.1mm, head width 1.8mm, intertegular span 1.5mm.

Colouration: Black with following parts yellow: distal half of labrum (basal half brown), mandible (except apex brown-red), inverted T-shaped mark on clypeus, lower paraocular area to just above dorsal margin of clypeus (maculation running along margin of eye, but absent along dorsolateral margin of the clypeus), anterior spot on tegula, posterolateral margin of pronotal lobe, apical ring on profemur, dorsoapical spot on meso- and metafemur, dorsal surface of protibia, dorsobasal and dorsoapical spot on mesotibia, most of surface of metatibia (brown maculation at midlength on outer surface, inner surface suffused with brown, carina brown), pro- and mesobasitarsus (the latter yellow-brown). The remainder of legs, metasomal terga and wing venation brown. Tegula and apical impressed area of metasomal terga translucent pale straw. Ventral surface of flagellum orange.

Pubescence: Whitish, long and somewhat woolly throughout. Head and thorax with sparse, erect pubescence; (= 3MOD) longest hairs between antennal sockets. Long sparse genal beard (= 4MOD, becoming shorter towards base of mandible). Shorter dense hairs on pronotal lobe (= 1.5 MOD). Mesopleuron with long, sparse hairs (= 3MOD). Dorsolateral portion of propodeum with long, dense hairs (= 3MOD). T1-T6 with poorly defined apical hair bands. Sterna with short sparse hairs, longer on S1 and S2 (= 2MOD).

Surface Sculpture: Clypeus, lower paraocular area and supraclypeal area weakly longitudinally microstriate. Punctures on labrum dense and evenly spaced (i~d). Sparse, irregularly spaced punctures on clypeus (i=1-6d). Punctures on lower paraocular area deeper and more evenly spaced (i=1-3d). Punctures on supraclypeal area more regular (i=1-2d). Upper paraocular area and frons with deep dense elongate punctures (i<d), situated among strong longitudinal striae. Vertex areolate-rugulose. Gena (posteriorly, except close to mandible base) and hypostomal area microstriate with moderately dense shallow punctures (i=1-2d). Thorax with weak, imbricate microsculpture, surface shiny. Mesoscutum and mesopleuron with fine, moderately dense punctation (i=1-3d), slightly sparser on mesoscutum; scutellum densely punctate (i~d). Dorsal area of propodeum

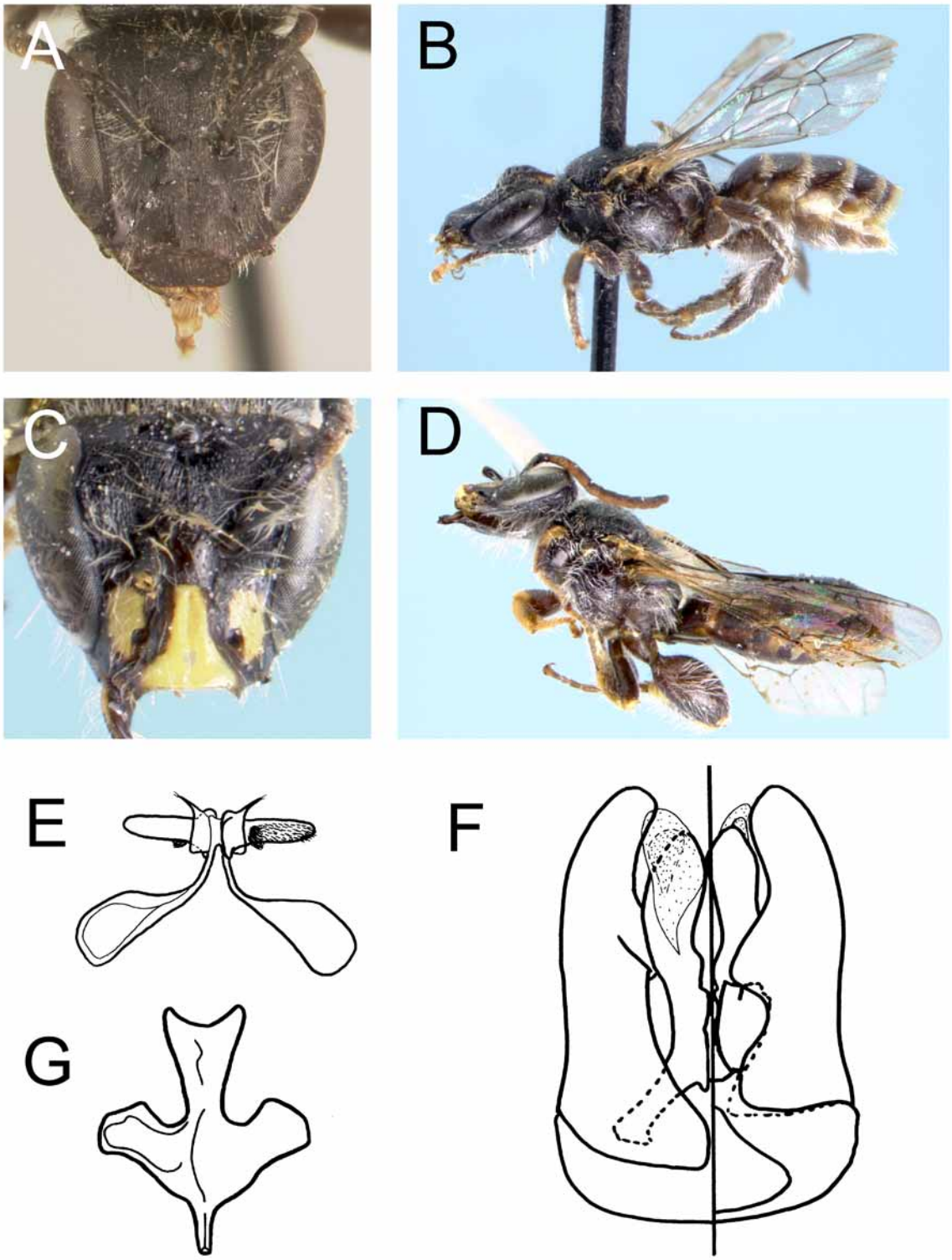

FIGURE 1. *Chilicola andina*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. S7, F. S8, G. genitalia, stippling represents membranous lobes of penis valves. Drawings of terminalia with ventral views to left, dorsal views to right.

with irregular longitudinal striae attaining posterior margin. Metasomal terga with strong microsculpture and dense distinct but fine punctures on anterior terga, sparser and less distinct on more posterior terga (i= 1-2d), punctures on sterna less distinct.

Structure: Head: broader than long (51:43). Labrum short (length to breadth 12:30), concave dorsally, apex weakly convex. Clypeus weakly convex, broader than long (21:16); apical third extending beyond lower ocular tangent; with a strong longitudinal median groove; apex very weakly concave medially. Supraclypeal area somewhat swollen, broader than long (10:9). Subantennal sutures shorter than distance that separates them (6:8), converging below. Frontal line raised and complete from median ocellus to supraclypeal area. Vertex flat in frontal view. Eyes convergent below, UOD:LOD (35:28); OOC less than IOC (7:9). Ratio of lengths of pedicel:F1:F2:F3 (5:6:7:7). Flagellomeres approximately 1.5 X as long as greatest breadth. Malar space 0.67 X the basal depth of mandible (4:6). Gena narrow, ratio of width:eye width (9:13).

Mesosoma: 1.5 X as long as greatest depth (95:63). Pronotal collar short, noticeably less than diameter of median ocellus, entirely declivous medially. Ratio of scutellum:metanotum:propodeum (13:5:8). Scrobal groove absent anterior to scrobe. Metatrochanter with ventral surface forming right angle in lateral view. Metafemur somewhat swollen, length twice maximum depth (35:18), ventral surface concave. Metatibia somewhat swollen, 2.5 X as long as greatest depth (30:12), which is subapical ventral surface flat with a carina extending from basal 0.16 of inner margin, around apex and for apical 0.25 of outer margin. Metabasitarsus 5 X longer than greatest depth (20:4). Ratio of length of stigma to marginal cell on wing margin (16:30). Stigmal margin in marginal cell straight.

Metasoma: T1 somewhat broader than long (42:38). Apical impressed areas of T2-T6 extensive, about 0.33X as long as corresponding tergum. S7 with posterior process of ventral lobe short and narrow, with several apical setae; dorsal lobe broad and laterally oriented. S8 with apical process broadly concave at apex. Genital capsule elongate, broadest towards base of gonocoxites. Penis valve with two membranous lobes of unequal size.

Description: Female: Length 6.4mm, forewing length 4.8mm, head width 2.0 mm, intertegular span 1.5mm.

Colouration: Entirely brown except yellow as follows: spot on mandibular condyle and dorsoapically on profemur, broad longitudinal stripe on dorsal surface of protibia. Ventral surface of flagellum light brown.

Pubescence: As in male except metafemur and metatibia with dense plumose scopal hairs (=2MOD). Sterna with long dense hairs (=3MOD), densest and longest on S2.

Surface Sculpture: As in male except punctures finer and facial striae stronger.

Structure: As in male except: head broader (51:40); labrum longer (length to breadth 8:18); clypeus broader (25:15); supraclypeal area broader (12:10); subantennal sutures not so strongly convergent below; eyes less convergent below, UOD:LOD (35:32); ratio of pedicel:F1:F2:F3 (6:7:5:5), flagellomeres approximately as long as broad.

Mesosoma: As in male except as follows: ratio of scutellum:metanotum:propodeum (15:6:11); hind legs unmodified.

Metasoma: T1 broader (38:46). Apical impressed areas of terga less extensive, less than 0.33 X as long as corresponding tergum.

Material Studied: Holotype male: CHILE, **Region IV**: Coquimbo (North of Laguna Dam) 8,000ft, 6.xii.1950, Ross, Michelbacher. Additional male, Santiago, Farellones, 9.i.1980, M. Arroyo. Female from same location as additional male except 20.xii.1980 and collected by F. Squed, from flowers of *Adesmia ascilis*. The holotype is at CASC; the other specimens we have examined are at the AMNH.

***Chilicola (Chilioediscelis) patagonica* Toro and Moldenke**

Diagnosis: Males can be differentiated from all other species except *C. andina* by the colouration of their legs (See diagnosis for *C. andina* on how to separate these two species from all others and each other). Females of the species can be distinguished by their unique metasomal colouration: T1 mostly dark brown, remaining terga red, suffused with brown on sides and across disc of T2. Other species with a mostly red metasoma, *C. penai* and *C. sardonyx*, have brown colouration restricted to the sides on T1 and T2; while those with more reduced red have dark colouration extending across at least T1-T3.

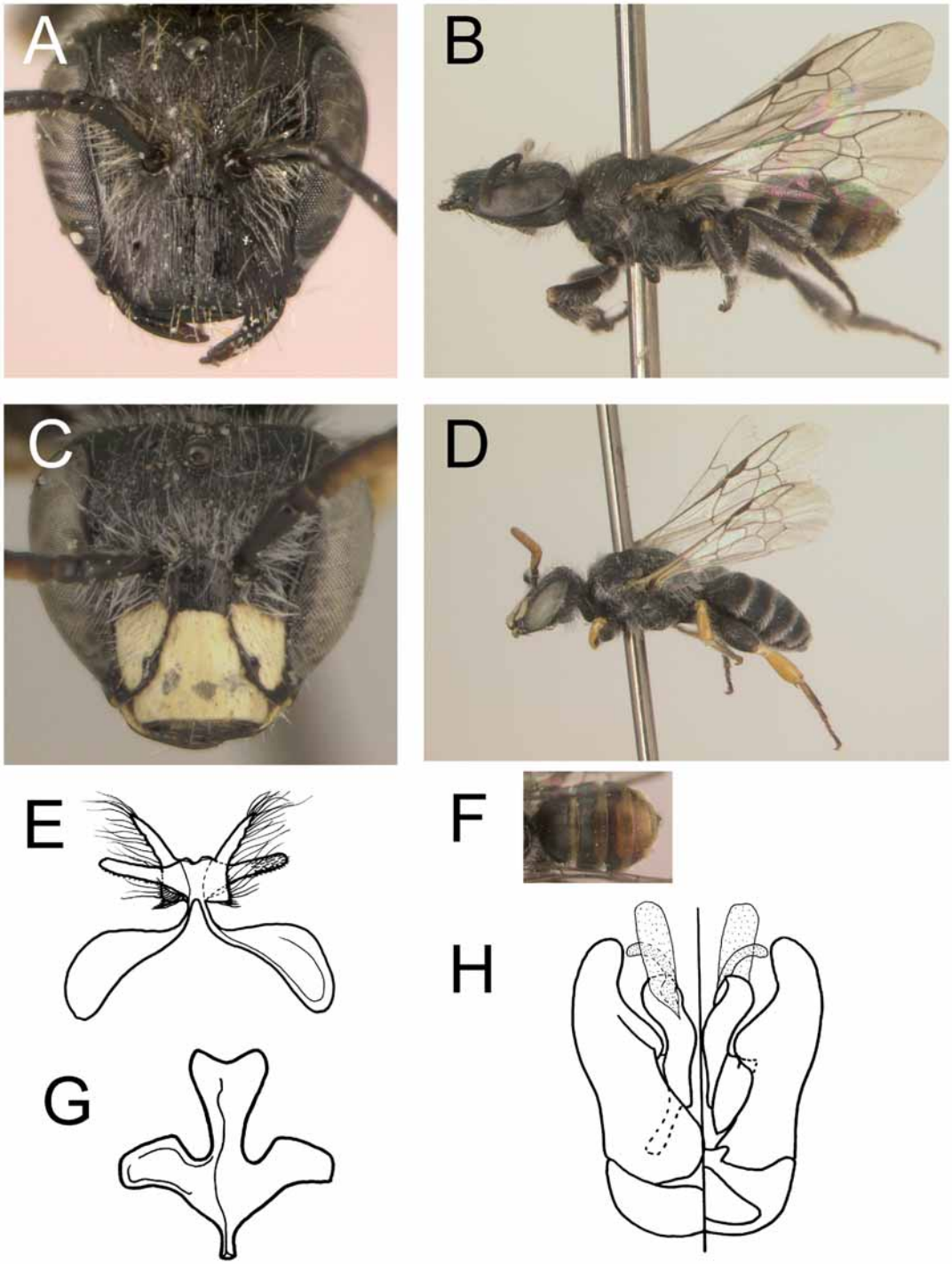

FIGURE 2. *Chilicola patagonica*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. S7, F. metasomal terga of female in dorsal view, G. S8, H. genitalia, stippling represents membranous lobes of penis valves. Drawings of terminalia with ventral views to left, dorsal views to right.

Description: Male: Length 5.4mm, forewing length 4.2mm, head width 1.6mm, intertegular span 1.3mm.

Colouration: As in *C. andina* except yellow as follows, labrum either above or entirely (varies among individuals), clypeus mostly, maculation on lower paraocular area to just above dorsal margin of clypeus (present along dorsolateral margin of the clypeus), dorsoapical spot on all femora, anterior surface of pro- and mesotibia, most of metatibia (at most a small dark spot on outer surface and carina brown), pro- and mesobasitarsus entirely, metabasitarsus basally.

Pubescence: As in *C. andina* except hairs of sterna sparser, not noticeably longer on S1 and S2 (= 2MOD).

Surface Sculpture: As in *C. andina* except as follows, gena striate close to mandible base, punctures on gena and hypostomal area deeper and somewhat denser (i=1-2d); mesoscutum with punctures deeper and slightly sparser (i=1–4d); punctures on mesopleuron denser and deeper (i=1–2d), noticeably sparser above level of scrobe; dorsal area of propodeum reticulate basally and striate apically.

Structure: As in *C. andina* except as follows: *Head*: Labrum not concave dorsally. Apex of clypeus more strongly concave medially in apical view. Frontal line not raised above surface of frons, difficult to detect among striae. Vertex concave in frontal view. Ratio of pedicel:F1:F2:F3 (8:7:6:7). Flagellomeres broad, length only slightly greater than breadth. Malar space shorter, length:basal depth of mandible (3:7). Gena narrower, ratio of width:eye (9:17).

Mesosoma: Ratio of scutellum:metanotum:propodeum (12:5:7). Scrobal groove entire. Ventral surface of metatrochanter acutely angulate in lateral view. Metafemur not so swollen, length to breadth (41:22). Metatibia more swollen length to breadth (45:15). Metabasitarsus shorter, less than 5 times as long as greatest depth (27:6). Ratio of length of stigma to marginal cell on wing margin (15:23). Stigmal margin in marginal cell convex.

Metasoma: S7 with ventral lobe elongate, outer margin irregular and bearing uneven row of long setae; dorsal lobe slightly posteriorly directed, narrower than that of *C. andina*. S8 as in *C. andina* except apicolateral margins of apical lobe more broadly rounded. Genital capsule broadened towards apical 0.33 of gonocoxite. Penis valve with one very large, membranous lobe and one comparatively narrow one.

Description: Female: Length 5.6mm, forewing length 4.2mm, head width 1.6 mm, intertegular span 1.3mm.

Colouration: As in *C. andina* except pro- and mesotibia only yellow basally. T1 mostly dark brown, remaining terga red, suffused with brown on sides and across disc of T2, antecostal areas black, those of T3-T5 visible through previous tergum and appearing as narrow black transverse bands.

Pubescence: As in *C. andina* except: apical hair bands only evident on T1 & T2.

Surface Sculpture: As in male except as follows: punctures finer, punctures on gena and hypostomal area denser (i=d); facial striae stronger; mesoscutum with punctures sparser (i=1–6d); mesopleuron with punctures not noticeably sparser above scrobe than below.

Structure: As in male except as follows: *Head:* Eyes less convergent below, UOD:LOD (36:32). OOC:IOC, (9:11). Scape longer and narrower (15:3); ratio of pedicel:F1:F2:F3 (7:6:4:5). Ratio of widths of gena:eye (7:15).

Mesosoma: As in *C. andina* except: more robust, length to breadth (80:60). Hind leg unmodified. Metabasitarsus 6 times longer than greatest depth (30:5).

Metasoma: As in *C. andina* except: apical impressed areas more extensive, more than 0.33 X as long as corresponding tergum.

Material Studied: Holotype, allotype and one paratype of each sex ARGENTINA, Santa Cruz, Los Antiguos, 21.xi.1966 Irwin & Schlinger. Two males and one female, CHILE, Magallanes, Lag. Azul, xii.1978 W. Sielfeld. Two females ARGENTINA, Santa Cruz, Lago Belgrano, i.1978 E. Maury. One male and one female, ARGENTINA, Santa Cruz, 25km S of Los Antiguos S46.42.654 W071.40.422, 653m, 22.xi.2003 L. Packer. The types and Sielfeld's specimens are at CASC; the remaining material is in PBYU.

***Chilicola (Chilioediscelis) araucana* Toro and Moldenke**

Diagnosis: Males of *C. araucana* can be separated from all other members of the subgenus except *C. patagonica* and *C. penai* by having the metatibia yellow with at most a small dark mark on the external surface. Males of all other species of *Chiloediscelis* have more extensive dark colouration on the hind tibia. Males of *C. araucana* and *C. patagonica* can be differentiated from one another by colour of their protibia and profemur. In *C. araucana* the protibia and profemur are mostly yellow, in *C. patagonica* the protibia is yellow only

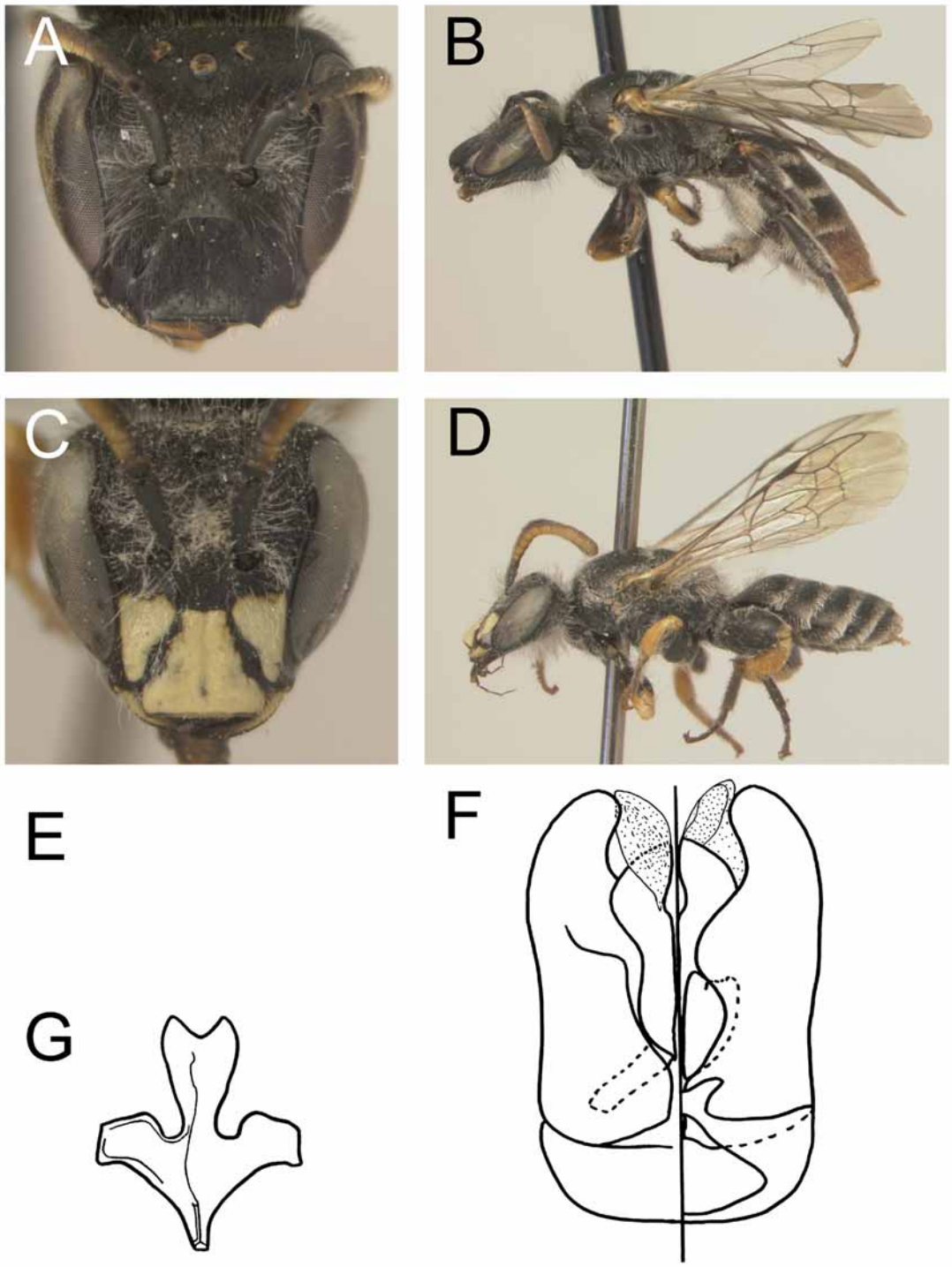

FIGURE 3. *Chilicola araucana*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. S7, F. genitalia, stippling represents membranous lobes of penis valves, G. S8. Drawings of terminalia with ventral views to left, dorsal views to right.

on the anterior surface and the profemur is mostly dark. *Chilioediscelis araucana* can be distinguished from *C. penai* by the colouration of the metabasitarsus. In *C. araucana*, the metabasitarsus is brown, in *C. penai* it is yellow basally. The female has a unique metasomal colouration, T1-T3 are dark brown and contrast markedly with the orange of T4-T6. Other *Chilioediscelis* (indeed, other *Chilicola*) with a red or orange marked metasoma have extensive amounts of red on at least T2 and T3, in addition to the more apical terga.

Description: Male: length 6.8mm, forewing length 4.6mm, head width 1.8 mm, intertegular span 1.3mm.

Colouration: As in *C. andina* except yellow as follows, labrum below or entirely (varies among individuals); clypeus mostly; maculation on lower paraocular area to just above dorsal margin of clypeus (present along dorsolateral margin of the clypeus); spot on scape; pro- and mesobasitarsus entirely, pro- and mesotibia entirely, metatibia at most with a small dark spot and carina brown, pro- and mesofemora apically, metafemur with a dorsoapical spot.

Pubescence: As in *C. andina*.

Surface Sculpture: As in *C. andina* except as follows, punctures on labrum sparser and unevenly spaced (i=1–2d); punctures on lower paraocular area not noticeably deeper than those on clypeus; punctures on supraclypeal area sparser (i=1–3d); striae on gena extend close to mandible base; mesoscutum and mesopleuron with punctures denser (i=1–2d), not noticeably sparser on mesoscutum or above level of scrobe.

Structure: As in *C. andina* except as follows: *Head:* Labrum wider (12:35), not concave dorsally. Clypeus more strongly concave medially in apical view. Supraclypeal area broader (12:10). Vertex concave in frontal view. Eyes not as convergent below, UOD:LOD (37:32). OOC:IOC (9:11). Ratio of pedicel:F1:F2:F3 (6:7:7:7), flagellomeres only slightly longer than broad. Gena narrower (6:17);

Mesosoma: Ratio of scutellum:metanotum:propodeum (16:7:10). Scrobal groove entire. Ventral surface of metatrochanter acutely angulate in lateral view. Metafemur broader (47:23). Metatibia broader (40:15). Ratio of length of stigma to marginal cell on wing margin (18:33). Stigmal margin very weakly convex in marginal cell;

Metasoma: S7 as in *C. andina* except ventral lobe longer and dorsal lobe broader. S8 with apical lobe strongly convex laterally. Genital capsule elongate, parallel-sided.

Description: Female: Length 6.6mm, forewing length 4.2mm, head width 1.8 mm, intertegular span 1.3mm.

Colouration: As in *C. andina* except as follows, most of the anterior surface of the protibia and base of mesotibia yellow; T4 apically and T5 and T6 entirely orange.

Pubescence: As in *C. andina*.

Surface Sculpture: As in male except as follows, punctures finer, slightly sparser on lower paraocular area and mesopleuron (i=1–4d); more regular on supraclypeal area (i=1–2d); facial striae stronger.

Structure: As in male except as follows: *Head*: Clypeus longer (27:18); eyes not as convergent below UOD:LOD (36:32); scape narrower (length:breadth 16:4), ratio of pedicel:F1:F2:F3 (5:5:4:4), flagellomeres about as broad as long; subantennal sutures not as strongly convergent below; gena not so narrow (10:15);

Mesosoma: Metafemur shorter and narrower (35:11). Metatibia less swollen (40:10). Metabastitarsus 6 X longer than greatest depth (30:5).

Metasoma: Apical impressed areas less extensive, less than 0.33 X as long as corresponding tergum.

Material Studied: Holotype male, ARGENTINA, Rio Negro (S.C. de Bariloche) 2.xii.1964 A.Giai. Additional female, ARGENTINA, Rio Negro (S.C. de Bariloche), Valle Challhuasco, 11.i.2001 C. Morales & C. Quintero. Additional female, ARGENTINA, Santa Cruz, 0.5km E. of Los Antiguos, S46.33.500 W071.35.507, 237m, pan traps, 17–19.xi.03, L. Packer. Additional male, same data except 35km E. of Los Antiguos, S46.36.118 W071.11.845, 234m, 17–23.xi.03. Packer (2004) listed additional material of this species at PBYU. The type is at the AMNH; the second specimen from Bariloche is at MACN.

***Chilicola (Chilioediscelis) mirzamalae* Willis and Packer new species**

Diagnosis: *C. mirzamalae* females possess a triangular flange on their hypostoma, a trait that does not appear in any other species of the subgenus. *Chilicola mirzamalae* males can be distinguished by the entirely dark metatibia (all other species have at least some yellow) and by the punctation of their mesopleuron: *C. mirzamalae* males have punctures equally dense above and below the scrobe, in all other species the punctures are sparser above. Lastly, the tegula of *C. mirzamalae* females is entirely dark. In the other species the tegula is pale straw.

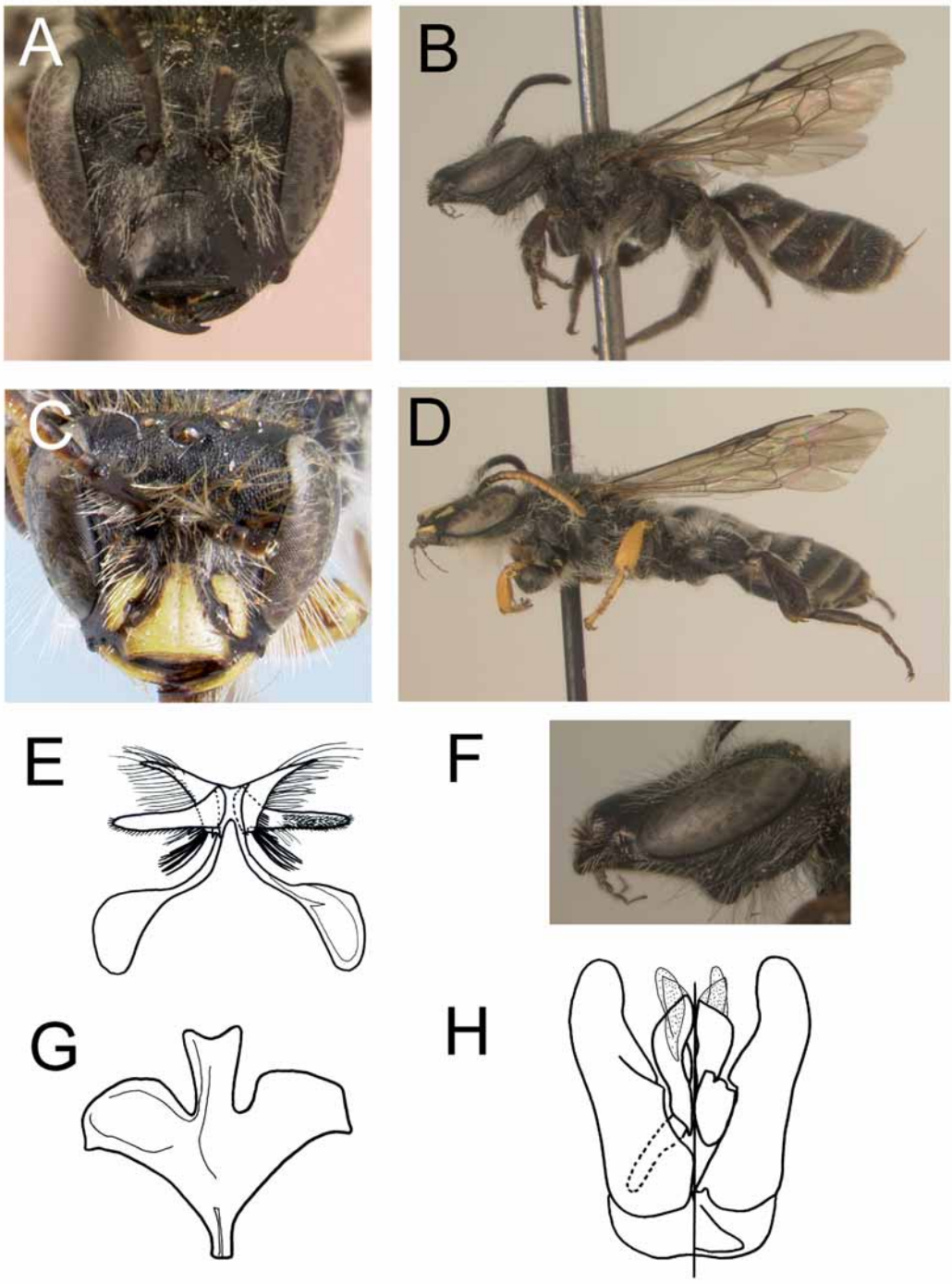

FIGURE 4. *Chilicola mirzamalae*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. S7, F. hypostomal flange of female, G. S8 H. genitalia, stippling represents membranous lobes of penis valves. Drawings of terminalia with ventral views to left, dorsal views to right.

Pubescence: As in *C. andina*.

Surface Sculpture: As in *C. andina* except as follows, labrum with sparser and more uneven punctures (i=1–2d); clypeus impunctate; mesoscutum densely and regularly punctate (i~d); mesopleuron more evenly punctate (i=1–2d).

Structure: As in *C. andina* except as follows: *Head*: Labrum not concave dorsally. Frontal line not raised indetectable amongst striae. Ratio of pedicel:F1:F2:F3 (5:6:6:8). Flagellomeres slightly longer than broad. Malar space slightly more than two-thirds the basal depth of mandible (5:6). Gena narrower, ratio of width:eye (11:19);

Mesosoma: Pronotal collar short, noticeably less than diameter of median ocellus, present medially. Ratio of scutellum:metanotum:propodeum (18:8:11). Scrobal groove entire. Ventral surface of metatrochanter acutely angulate in lateral view. Carina of metatibia incomplete. Metabasitarsus 6 times as long as deep (36:6). Ratio of length of stigma to marginal cell on wing margin (20:42). Stigma convex in marginal cell;

Metasoma: S1 slightly swollen apically. S7 with ventral lobe elongate, broadly triangular, with long setae on outer margin; dorsal lobe elongate, parallel-sided, with small concave process at base anteriorly and very long robust setae arising from basal ridge, basal portion of lobe glabrous. S8 with apical lobe weakly concave, lateral lobe very large. Genital capsule broadest at apical third.

Description: Female: Length 8.4mm, forewing length 4.9mm, head width 2.2 mm, intertegular span 1.7mm.

Colouration: Black to dark brown with yellow spot on protibia basally and often on the base of the mandible. Ventral surface of flagellum light brown.

Pubescence: As in *C. andina*.

Surface Sculpture: As in male except punctures finer and facial striae stronger.

Structure: As in male except as follows: *Head*: Clypeus broader (34:22). Subantennal sutures less strongly convergent below. Compound eyes only slightly convergent below (46:43). Scape almost 6 X as long as broad (23:4). Ratio of pedicel:F1:F2:F3 (6:5:5:4). Flagellomeres about as long as broad. Gena narrower (15:21);

Mesosoma: Hind leg unmodified. Metabasitarsus less than 3 X longer than greatest depth (23:8);

Metasoma: S1 not swollen apically. Apical impressed areas less extensive, less than 0.33 X as long as corresponding tergum.

Material Studied: Holotype male, allotype female and one female paratype: CHILE, **Region VIII**: Shangrila, Las Trancas, Chillán area, SE Recinto, 1600m, 19–22.i.1979, L. Peña. One male paratype with data as in holotype except collected on xii.1983. Two paratype females with data same as holotype male except 1500m, 13–17.xii.1983 for one and 1200m, i.1984 for the other. Additional paratype females: CHILE, **Region IX**: Malleco, La Raices, Lonquimay area, 1600m, 13–20.ii.1980, L.Pena, one female and ARGENTINA, Rìo Negro, San Carlos de Bariloche, 2.xii.1964, A.J.Giai, one female. Four additional paratype males and two paratype females with same data as holotype except 78 km E of Chillán, S36.54.5 W71.29, 12.xii.03, F.D. Parker, one male collected in net, all others collected in pan traps. All material except one male and one female paratype (PBYU) are in the AMNH.

Etymology: This species is for the senior author's good friend Nancy Mirza. The species name is a reference to both her unique jaw structure and the flange found on the hypostomal area of the female bee; *malae* is latin for jawbones or cheeks.

Chilicola (Chilioediscelis) sardonyx Willis and Packer new species

Diagnosis: Males of *C. sardonyx* can be differentiated from all other *Chilioediscelis* by the ratio of OOC to IOC. In all other OOC is less than IOC, in *C. sardonyx* OOC is equal to IOC.

Females of *C. sardonyx* can be distinguished from all others by the coloration of its mandible base, which is entirely orange; other species have at most a small yellow spot.

Description: Male: Length 6.2mm, forewing length 3.8mm, head width 1.6 mm, intertegular span 1.2mm.

Colouration: As in *C. andina* except yellow as follows, labrum, lower paraocular area maculations extend to dorsolateral margin of clypeus, profemur and mesotibia anteriorly, pro- and metatibia mostly, pro- and mesobasitarsi entirely, metabasitarsi entirely.

Pubescence: As in *C. andina*.

Surface Sculpture: As in *C. andina* except as follows, gena striate close to mandible base; mesoscutum with punctures sparser (i=1–4d); mesopleuron with punctures denser (i=1–2d), noticeably sparser above level of scrobe.

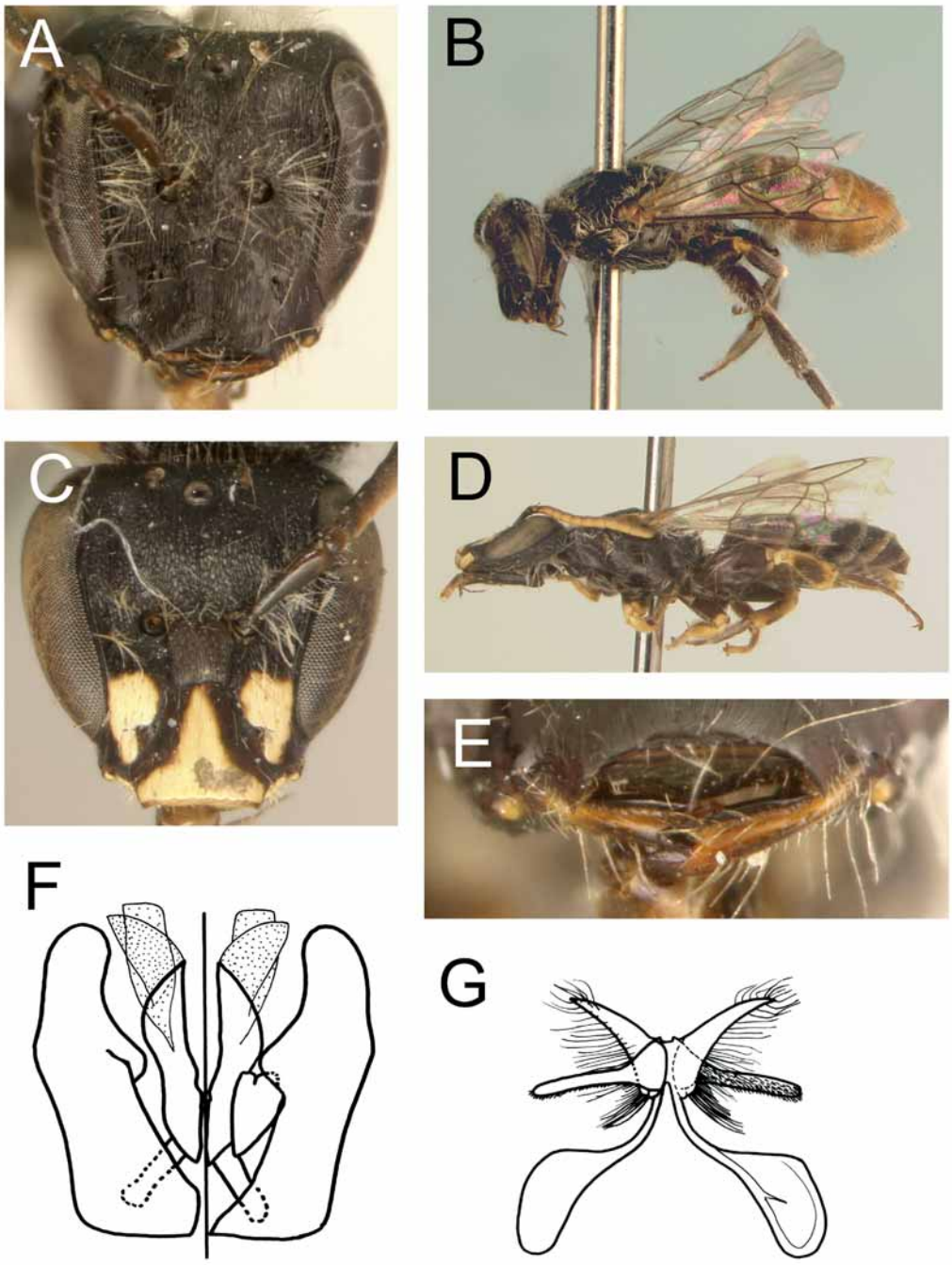

FIGURE 5. *Chilicola sardonyx*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. apical view of head of female to show colour of mandible, F. genitalia, stippling represents membranous lobes of penis valves. G. S7. Drawings of terminalia with ventral views to left, dorsal views to right.

Structure: As in *C. andina* except as follows: *Head*: Labrum not concave dorsally. Subantennal sutures separated more widely, length:distance that separates them, 6:10. Frontal line raised, and extending about 0.5–0.75X the length between median ocellus and supraclypeal area. Vertex concave in frontal view. OOC equal to IOC (9:9). Ratio of pedicel:F1:F2:F3 (4.5:4.5:4:4). Flagellomeres slightly longer than broad. Malar space shorter, length:basal depth of mandible (3:7). Gena narrower, (6:15);

Mesosoma: Pronotal collar short, noticeably less than diameter of median ocellus, present medially. Ratio of scutellum:metanotum:propodeum (14:5:8). Scrobal groove entire. Ventral surface of metatrochanter acutely angulate in lateral view. Metafemur and metatibia less swollen, length to breadth (36:20) and (32:14) respectively. Stigmal margin convex in marginal cell;

Metasoma: S1 slightly swollen apically. Apical impressed areas less extensive, less than 0.33 X as long as corresponding tergum. S7 as in *C. mirzamalae* but ventral lobe broader and short setae of dorsal lobe extending to base. S8 lost in only male known. Genital capsule broadened towards apical one third, convex laterally just before gonostylus. Penis valve with both membranous lobes long and broad. Gonobase and S8 lost in sole male specimen.

Description: Female: Length 6.4mm, forewing length 4.1mm, head width 1.7 mm, intertegular span 1.2mm.

Colouration: As in *C. andina* female except protibia and profemur brown, mesofemur yellow apically and meso- and metatibiae yellow basally; T1 dark, rest of metasomal terga orange except suffused with brown on sides of T2 and T3.

Pubescence: As in *C. andina* except apical hair bands only evident on T1-T3

Surface Sculpture: As in male except punctures finer and facial striae stronger.

Structure: As in male except as follows: *Head*: Clypeus broader (25:18). Eyes less convergent below, UOD:LOD (33:31). Ratio of pedicel:F1:F2:F3 (4.5:5:5:5). Flagellomeres about as long as broad;

Mesosoma: Hind leg unmodified;

Metasoma: S1 not swollen apically. Apical impressed areas more extensive, more than 0.33 X as long as corresponding tergum.

Material Examined: Holotype male: ARGENTINA, Mendoza, Horcones, 2900m, 10.i.1985, A.Roig. Allotype female: same data except 3000m and collected on 9.i.1985. Both specimens are at MACN.

Etymology: This specific epithet is a reference to where the allotype was found, at a nest between two flat stones: *sardonyx* is the latin word for “precious stone”.

Chilicola (Chilioediscelis) penai Willis and Packer new species

Diagnosis: Males can be differentiated from all other species except *C. araucana* and *C. patagonica* by the colouration of their legs (See diagnosis for *C. araucana* on how to separate these three species from all others and each other).

Females are unique in the combination of mandible with yellow spot at base and metasomal terga mostly orange, with brown markings laterally on T1 and T2.

Description: Male: Length 7.0mm, forewing length 3.5mm, head width 1.8 mm, intertegular span 1.3mm.

Colouration: As in *C. andina* except yellow as follows, labrum entirely, clypeus mostly (brown along lateral margins), lower paraocular area maculation present along dorsolateral margin of clypeus, anterior surface of profemur, pro- and mesotibia mostly, metatibia almost entirely with at most small dark spot, probasistarsus entirely.

Pubescence: As in *C. andina*.

Surface Sculpture: As in *C. andina* except as follows, striae on gena extending to close to mandible base; mesoscutum and mesopleuron with punctures denser (i=1–2d), noticeably sparser above level of scrobe.

Structure: As in *C. andina* except as follows: *Head*: Labrum shorter (length to breadth 11:33), not concave dorsally. Vertex concave. OOC:IOC (9:10). Ratio of pedicel:F1:F2:F3 (5:5:6:6). Flagellomeres slightly longer than broad. Malar space shorter, length:basal depth of mandible (4:7);

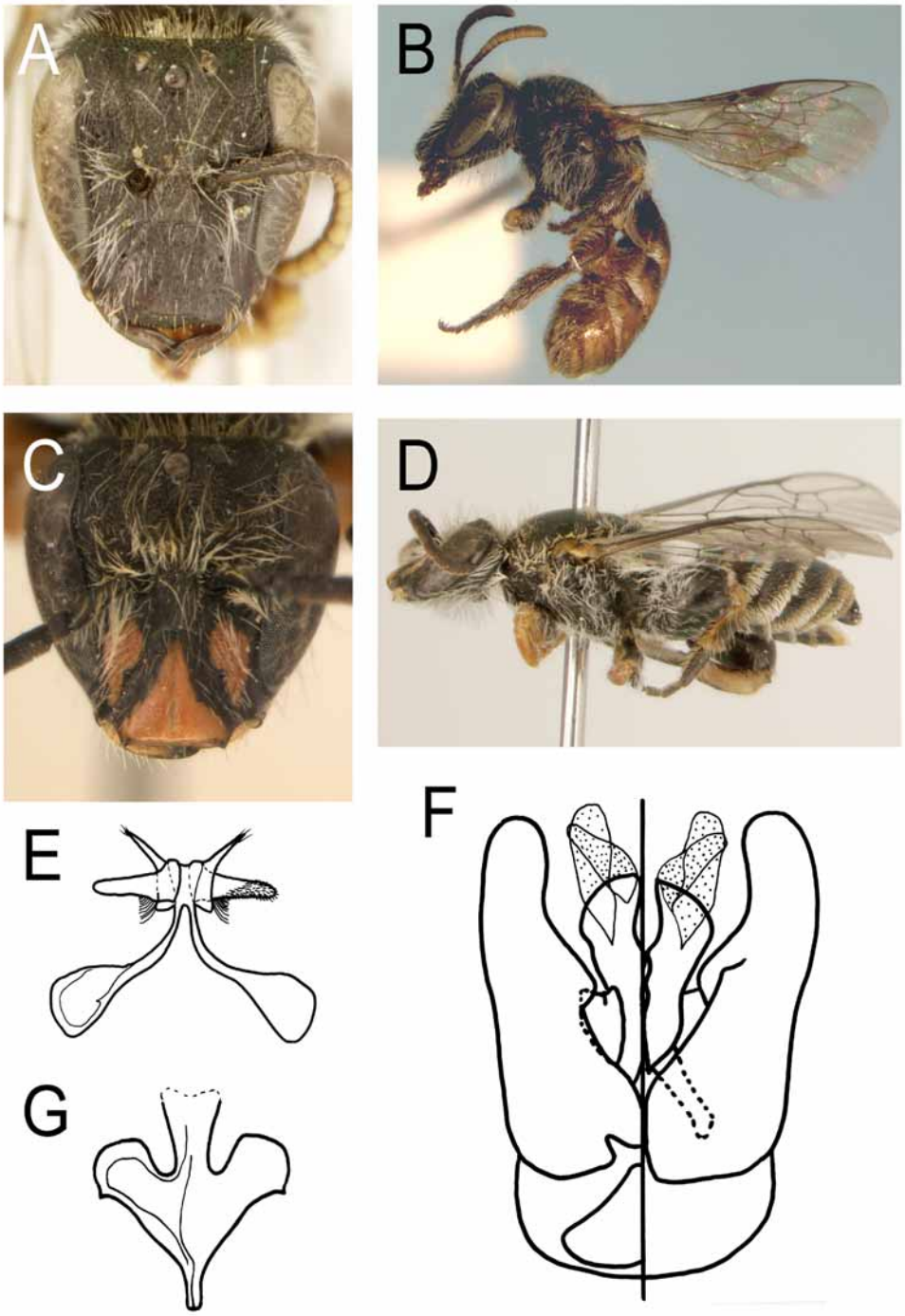

FIGURE 6. *Chilicola penai*. A. head of female, frontal view, B. female, lateral view, C. head of male, frontal view, D. male, lateral view, E. S7, F. genitalia, stippling represents membranous lobes of penis valves, G. S8. Drawings of terminalia with ventral views to left, dorsal views to right.

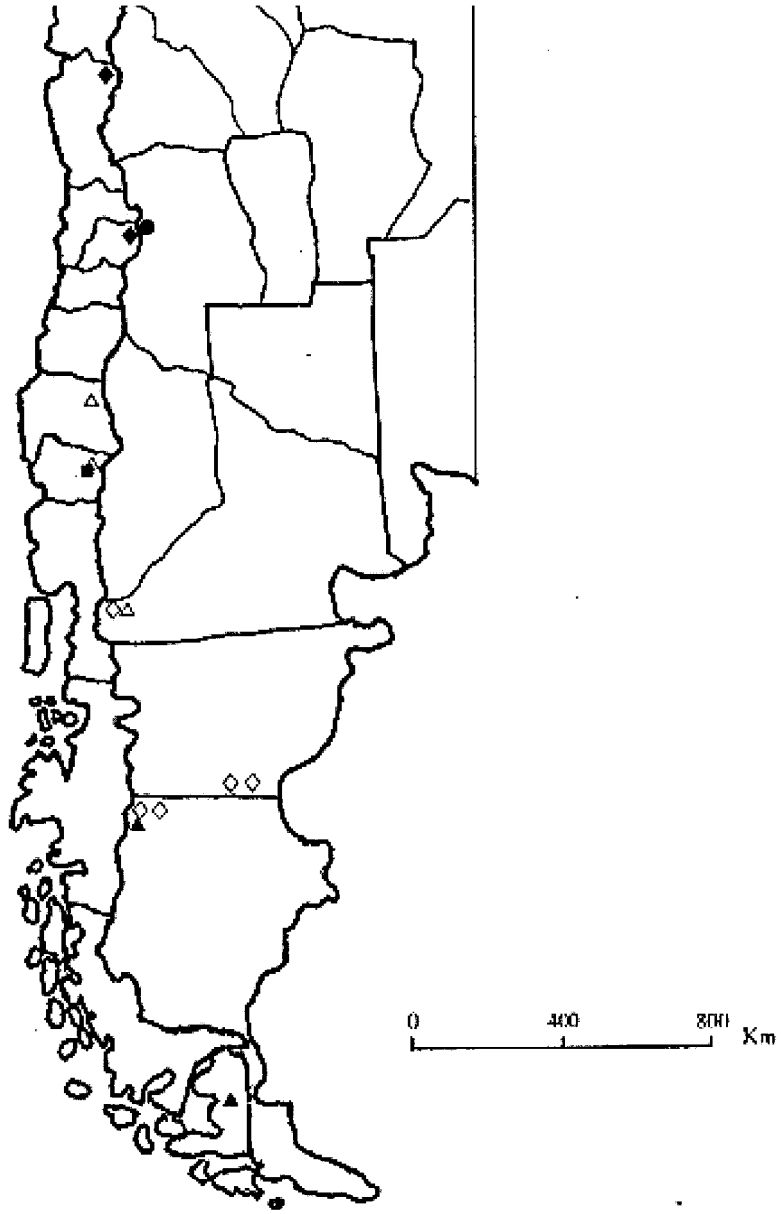

FIGURE 7. Map of Chile and Argentina (except the far north of both countries and north–eastern Argentina) showing localities mentioned in text. ♦ *C. andina,* ◇ *C. araucana,* ▲*C. patagonica,* △ *C. mirzamalae,* ● *C. sardonyx,* ■ *C. penai.* The location for *C. patagonica* in Tierra del Fuego is approximate.

Mesosoma: Ratio of scutellum:metanotum:propodeum (13:7:9). Scrobal groove entire. Ventral surface of metatrochanter acutely angulate in lateral view. Metafemur and metatibia less swollen, length to breadth, (45:21) and (34:10), respectively;

Metasoma: S1 slightly swollen apically. Apical impressed areas less extensive, less than 0.33 X as long as corresponding tergum. S7 with apical process of ventral lobe somewhat longer than in *C. andina*, dorsal lobe with short setae occupying much smaller portion of dorsal surface, robust seta-bearing ridge parallel to long axis of lobe. S8 with apical process weakly concave but (damaged in sole specimen), lateral lobe large. Genital capsule broadest at apical third. Membranous lobes of penis valve moderately long and moderately broad.

Description: Female: Length 6.0mm, forewing length 3.0mm, head width 1.7 mm, intertegular span 1.3mm.

Colouration: As in *C. andina* with the following exceptions, pro- and mesotibia brown; T1 dark, rest of metasomal terga orange except suffused with brown on sides of T2-T4 and on T6.

Pubescence: As in *C. andina*.

Surface Sculpture: As in male except punctures finer and frons only weakly striate.

Structure: As in male except as follows: *Head*: Clypeus broader (25:18). Eyes less convergent below (35:33). Ratio of pedicel:F1:F2:F3 (6:5:4:4);

Mesosoma: Ratio of scutellum:metanotum:propodeum (13:6:8). Hind leg unmodified;

Metasoma: S1 not swollen apically. Apical impressed areas of terga more extensive, more than 0.33 X as long as corresponding tergum.

Material examined: Holotype male and allotype female: CHILE, **Region VIII**: Termas de Chillan, S36.54.441 W071.24.668, 5396 ft., 12–27.xii.2007, L. Packer, pan trap. One paratype male: CHILE, **Region VIII**: Shangrila, Las Trancas, Chillán area, SE Recinto, xii.1983, L. Peña. One paratype female as previous except 1600m, 14.xii.1983; additional paratype female same data as previous except 19.xii.1983 and with no altitude given. One additional paratype male same data as holotype except 06–24.i.2007, A-I. Gravel, vane trap. The Packer and Gravel material including the holotype and allotype are at PBYU; Peña's material is at the AMNH.

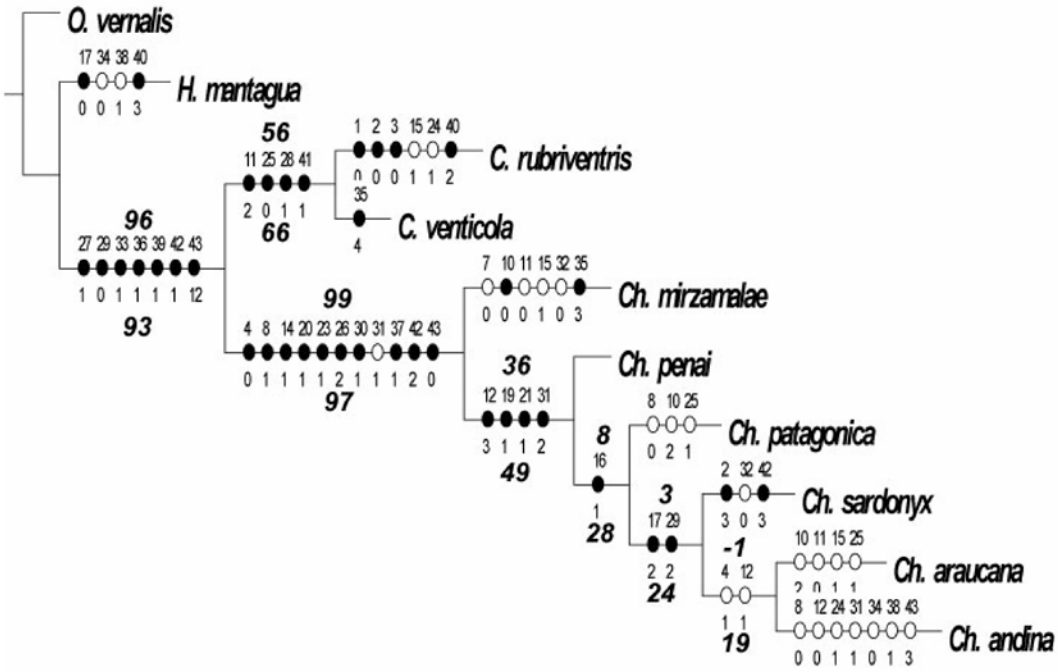

Figure 8

FIGURE 8. Single most parsimonious tree obtained for *Chilioediscelis* with character state changes mapped onto it. Open circles represent homoplasious changes, solid in circles are non–homoplasious changes. Length :103, CI : 69, RI :65. Numbers above internodes are GC values, below nodes bottstrap support.

Etymology: This species is named for the collector of the earlier specimens, the late Luis Peña, one of Chile's most renowned entomologists.

Phylogenetic analysis

An exhaustive search with NONA (Goloboff, 1999) produced a single most parsimonious tree (Fig. 8; length: 108 steps, consistency index (ci): 0.58, retention index (ri): 0.61). The tree was stable to successive approximations character weighting. The monophyly of *Chilioediscelis* is strongly supported in this analysis (GC=99) as is its sister group status to subgenus *Chilicola s. str.* (GC=96); monophyly of *Chilicola* is reasonably well supported (GC=56). Within *Chilioediscelis* none of the nodes are extremely well supported, the group (*C. penai* (*C. patagonica* (*C. sardonyx* (*C. araucana* + *C. andina*)))) received a GC value of 36.

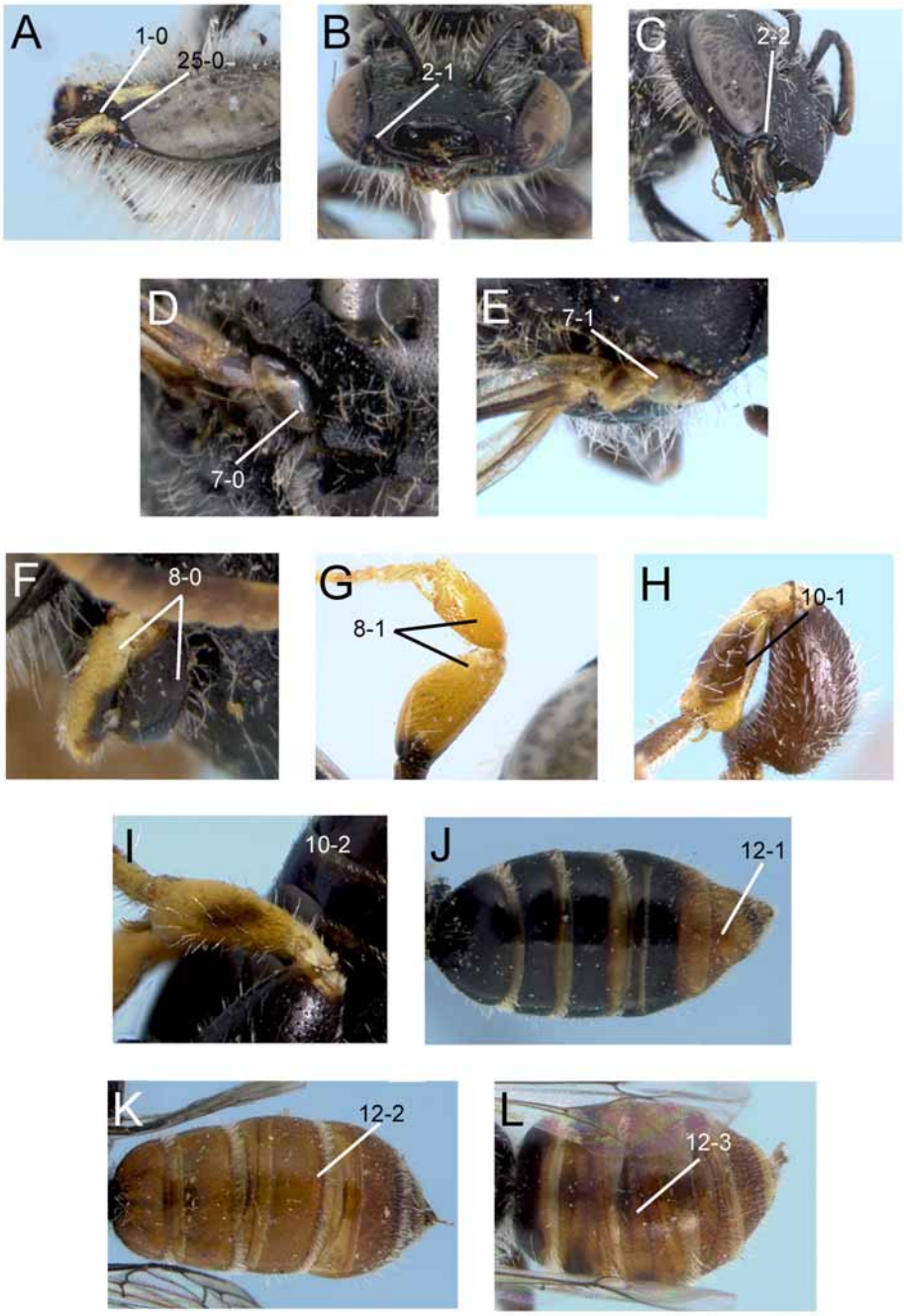

FIGURE 9. Morphological structures included as character states in the phylogenetic analysis (refer to Appendix for complete list of characters). A. mandible of male *C. (Chilicola) rubriventris*, B. mandible of female *C. patagonica*, C. mandible of female *C. (Oediscelis) vernalis*, D. tegula of female *C. mirzamalae*, E. tegula of female *C. andina*, F. protibia and profemur of male *C. patagonica*, G. protibia and profemur of male *C. araucana*, H. metatibia of male *C. andina*, I. metatibia of male *C. patagonica*, J. metasoma of female *C. araucana*, K. metasoma of female *C. (Chilicola) rubriventris*, L. metasoma of female *C. penai*.

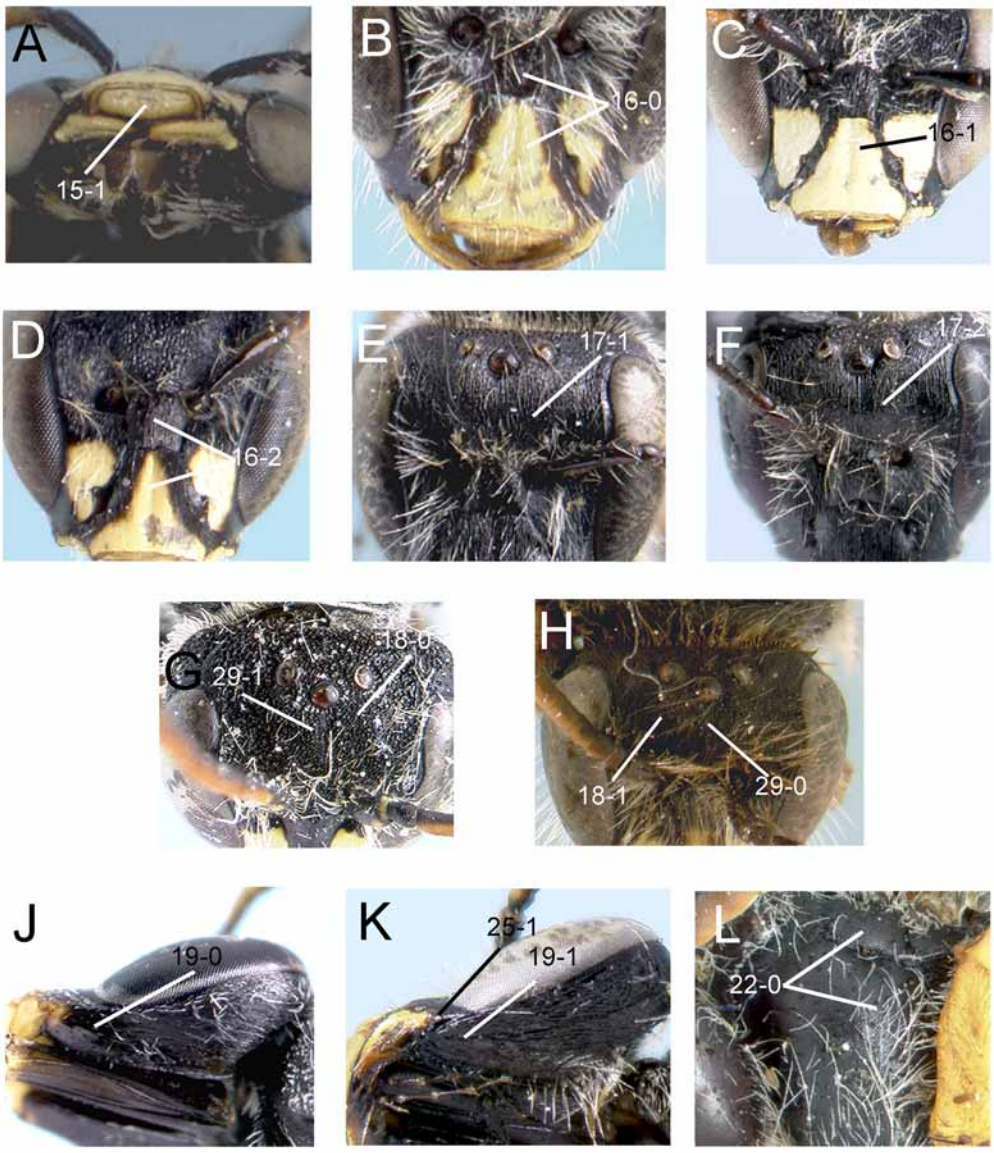

FIGURE 10. Morphological structures included as character states in the phylogenetic analysis (refer to Appendix for complete list of characters). A. labrum of male *C. araucana*, B. clypeus and supraclypeal area of male *C. penai*, C. clypeus and supraclypeal area of male *C. araucana*, D. clypeus and supraclypeal area of male *C. sardonyx*, E. frons of female *C. penai*, F. frons of female *C. sardonyx*, G. frons of male *C. (Oediscelis) vernalis*, H. frons of male *C. penai*, I. gena of male *C. aenigma*, J. gena of male *C. araucana*, K. mesopleuron of male *C. mirzamalae*.

Discussion

As previously mentioned, it has been suggested that *Chilioediscelis* is a possible specialist on the legume genus *Adesmia*, which possess quite flat, tight flowers. Assuming that *Chiolioediscelis* is indeed a specialist on this group, it is possible that the longitudinal striations found on the lower face in many species is an adaptation for reducing friction as the bees push open the flowers. Both *Chilicola* and *Chilioediscelis* also possesses a strongly curved hind-tibial spur, a structure that in other groups has been suggested to aid bees in gaining a firm grip on the flowers while they push their heads through the constricted lumen to the nectary (Houston, 2000; Almeida, 2006).

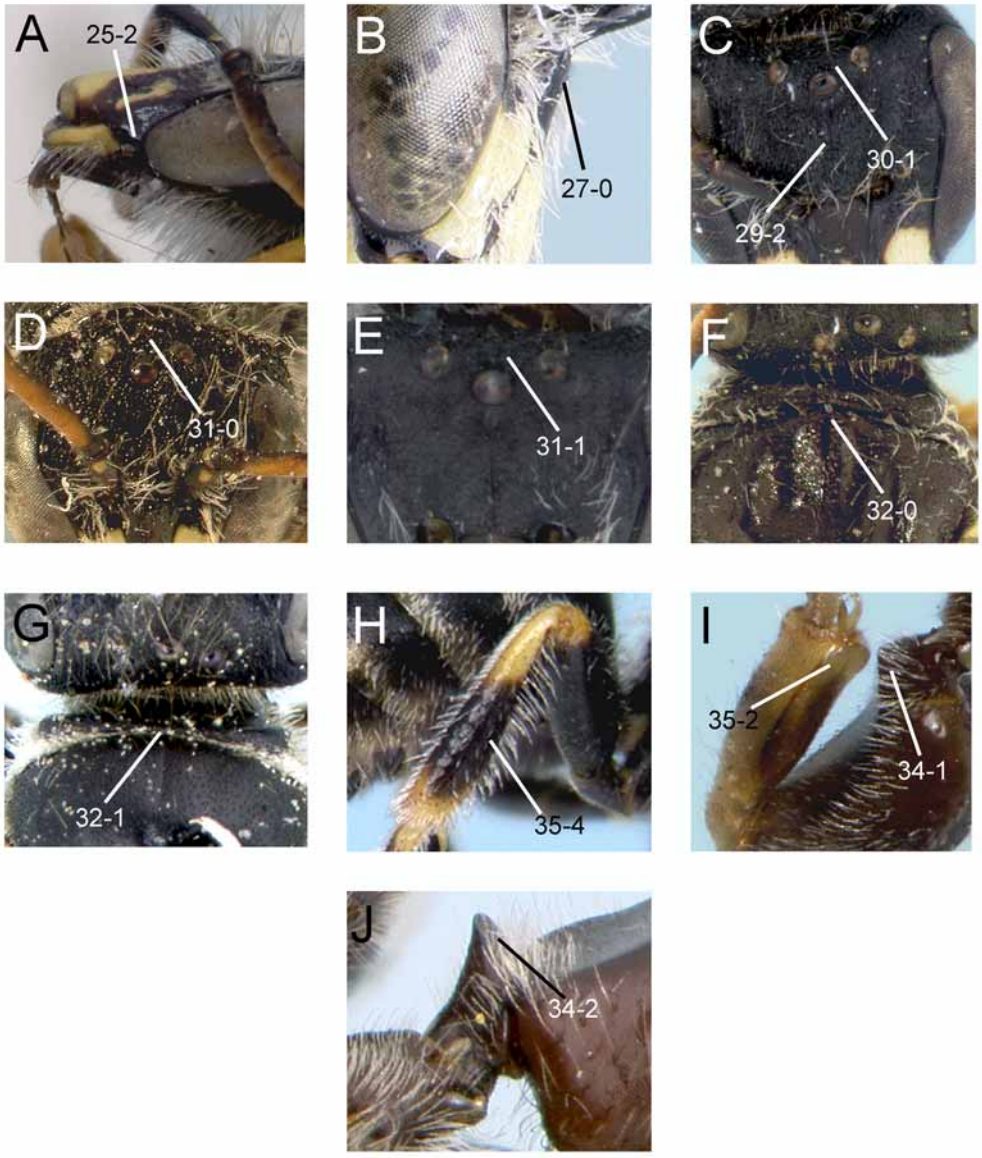

FIGURE 11. Morphological structures included as character states in the phylogenetic analysis (refer to Appendix for complete list of characters). A. malar space of male *C. mirzamalae*, B. supraclypeal area of *C. (Oediscelis) vernalis*, C. frontal line and vertex of male *C. sardonyx*, D. vertex of male *C. (Oediscelis) vernalis*, E. vertex of *C. andina*, F. pronotal collar of female *C. sardonyx*, G. pronotal collar of female *C. araucana*, H. hind leg of male *C. aenigma*, I. hind leg of male *C. andina*, J. hind trochanter of male *C. mirzamalae*.

Acknowledgments

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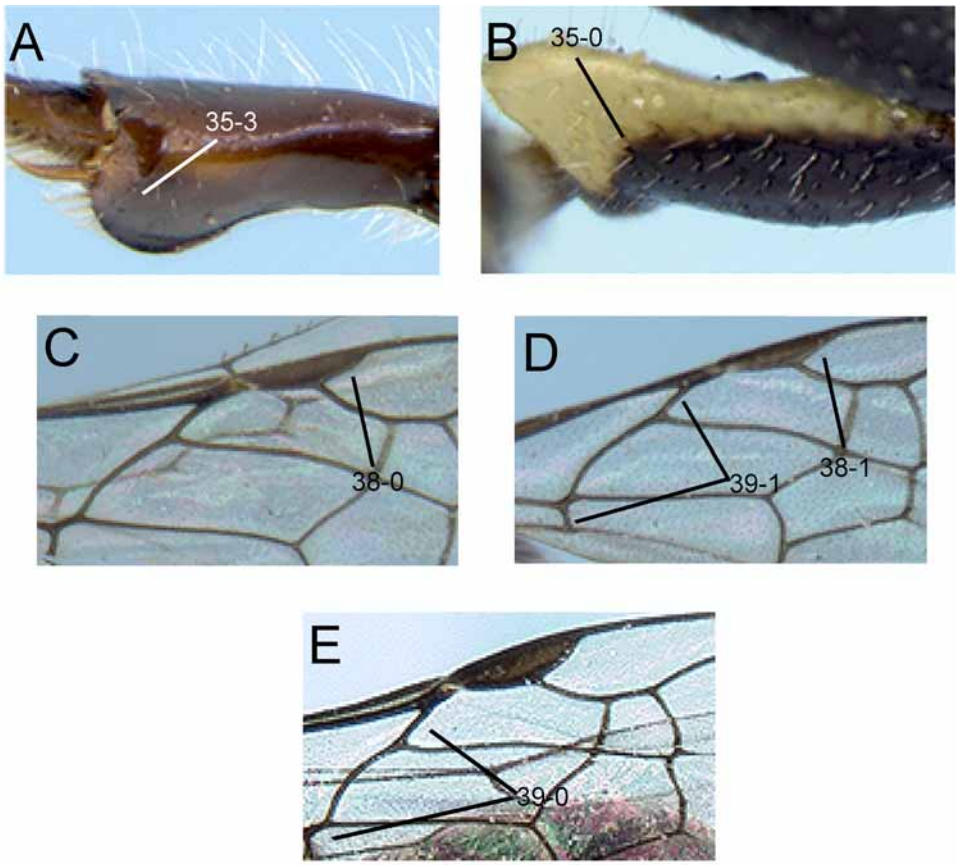

FIGURE 12. Morphological structures included as character states in the phylogenetic analysis (refer to Appendix for complete list of characters). A. hind tibia of male *C. mirzamalae*, B. hind leg of male *C. (Oediscelis) vernalis*, C. wing of male *C. sardonyx*, D. wing of male *C. andina*, E. wing of male *C. (Oediscelis) vernalis.*

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Appendix

Characters used in the phylogenetic analysis (Figs. 10–13). Additional figures published in Gibbs & Packer (2006) and Packer (2008) are indicated as (G&P Fig#) and (P Fig#), respectively.

0) Male, colour of labrum: (0) dark with yellow above (G&P, Fig. 9B); (1) all yellow (G&P, Fig. 9C).
1) Male, colour of mandible: (0) dark with yellow basal spot (Fig. 9A); (1) more or less all yellow (G&P, Fig. 9B).
2) Female, mandible base: (0) black (G&P, Fig. 9D); (1) dark with a yellow spot (Fig. 9B); (2) half yellow (Fig. 9C); (3) more or less all orange at base (Fig. 5E).
3) Male, colour of clypeus: (0) mostly black with a little yellow (G&P, Fig. 9A); (1) mostly yellow (G&P, Fig. 9H).
4) Male, yellow dot on apex of scape: (0) absent (G&P, Fig. 9I); (1) present (G&P, Fig. 9J).
5) Male and female, colour of pronotal lobe: (0) entirely black (G&P, Fig. 10A); (1) black with yellow posterior margin (G&P, Fig. 10B).
6) Male, colour of tegula: (0) dark without a pale spot (G&P, Fig. 10C); (1) pale straw with a pale spot (G&P, Fig. 10D).
7) Female, colour of tegula: (0) dark (Fig. 9D); (1) pale straw (Fig. 9E).
8) Male, yellow on protibia & profemur: (0) protibia anterior surface only, profemur almost entirely dark (Fig. 9F); (1) most of protibia and profemur (Fig. 9G).
9) Male, colour of mesotibia: (0) black with yellow base and apex (G&P, Fig. 10H); (1) black with anterior surface yellow (G&P, Fig. 10I).
10) Male, colour of metatibia: (0) dark (G&P, Fig. 11A); (1) mostly dark with limited yellow (Fig. 9H); (2) yellow with at most a small dark spot (Fig. 9I).
11) Male, colour of metabasitarsus: (0) brown (G&P, Fig. 11C); (1) mostly brown with yellow base (G&P, Fig. 11D); (2) mostly yellow (G&P, Fig. 11E).
12) Female, colour of metasoma: dark (G&P, Fig. 11F); (1) T4-T6 orange (Fig. 9J); (2) all orange (Fig. 9K); (3) T1 dark, rest mostly orange (Fig 9L).
13) Male, S2 specialized hair patch: (0) absent (G&P, Fig. 12G); (1) present (G&P, Fig. 12H).
14) Female, S2 pubescence: (0) corbiculate (G&P, Fig. 12I); (1) not corbiculate (G&P, Fig. 12J).
15) Male, punctation on labrum: (0) dense and even (G&P, Fig. 9B); (1) sparser and irregular (Fig. 10A).
16) Male, striae on lower face: (0) not striate (Fig. 10B); (1) striate only on clypeus (Fig.10C); (2) clypeus and supraclypeal area striate (Fig. 10D).
17) Female, striae on frons: (0) absent (G&P, Fig. 13C); (1) weakly striate (Fig. 10E); (2) strongly striate (Fig. 9E).
18) Male, punctation on frons: (0) crowded (Fig. 10G); (1) dense (Fig. 10H).
19) Male, striae on gena: (0) not approaching mandible base (Fig 10I); (1) extending to close to mandible base (Fig. 10J).
20) Female, longitudinal striae on gena: (0) absent (G&P, Fig. 13A); (1) present (G&P, Fig. 13B).
21) Male, punctation on mesoscutum: (0) dense (G&P, Fig. 13E); (1) uneven or sparse (G&P, Fig. 13F).
22) Male, punctation above versus below scrobe: (0) equally dense (Fig. 10K); (1) sparser above (G&P, Fig. 13G).
23) Male, sculpture of dorsal area of propodeum: (0) reticulate (G&P, Fig. 13I); (1) striate (G&P, Fig. 13J).
24) Male, dorsal margin of labrum: (0) flat (G&P, Fig. 9A); (1) concave (G&P, Fig. 9B).
25) Male and female, malar space: (0) absent (Fig. 9A); (1) short (Fig. 3C & 11K); (2) intermediate (Fig. 11A).
26) Male and female, median groove on clypeus: (0) absent (G&P, Fig.14C); (1) short, less than half the length of clypeus (G&P, Fig.14D); (2) long, entire length of clypeus (G&P, Fig.14E).
27) Male, supraclypeal area in profile: (0) angulate (Fig. 11B); (1) weakly curved (G&P, Fig. 14H).
28) Male and female, face in lateral view: (0) not concave (G&P, Fig.14H); (1) concave (G&P, Fig.14I).
29) Male, frontal line: (0) not raised (Fig. 10H); (1) raised for ½ to ¾ length from supraclypeal area to median ocellus (Fig. 10G); (2) raised for entire length (Fig. 11C).
30) Male, upper ocular tangent: (0) below lateral ocelli (G&P, Fig.14J); (1) through lateral ocelli (Fig. 11C).
31) Male, vertex: (0) rounded (Fig. 11D); (1) flat (Fig. 11E); (2) concave (G&P, Fig.14K).
32) Male and female, pronotal collar: (0) present medially (Fig. 11F); (1) declivous medially (Fig. 11G).
33) Male and female, episternal suture below level of scrobe: (0) present (G&P, Fig. 13H); (1) absent (G&P, Fig. 13G).
34) Male, hind trochanter in lateral view: (0) right angular (Fig. 11I); (1) acute angular (Fig. 11J).
35) Male, modification of hind tibia: (0) greatly expanded sinuate, laterally compressed (Fig. 12B); (1) deeply excavate subapically (G&P, Fig. 1E); (2) flat ventrally with carina surrounding inner apex (Fig. 11I); (3) as in (2) but carina

incomplete (Fig. 12A); (4) almost quadrate (G&P, Fig. 6F).

36) *Male and female, metatibial spurs*: (0) unsclerotised and straight (G&P, Fig. 15E); (1) sclerotised and strongly curved (G&P, Fig. 15F).

37) *Female, inner tooth of hind claw*: (0) well developed (G&P, Fig. 15G); (1) very small (G&P, Fig. 15H).

38) *Male and female, stigma in marginal cell*: (0) convex (Fig. 12C); (1) straight or weakly concave (Fig. 12D).

39) *Male, basal vein length before Cu versus length of Rs*: (0) more than half as long (Fig. 12E); (1) only half as long (Fig. 12D).

40) *Male, S1*: (0) evenly convex (P 3R); (1) slightly swollen apically (G&P 15I); (2) long pointed process (G&P 15J); (3) long truncate process (P 3T).

41) *Female, S6 apical spine*: (0) absent (G&P, Fig. 15K); (1) present (G&P, Fig. 15L).

42) *Male, shape of S7 dorsal lobe*: (0) narrow and recurved apically (G&P 16A); (1) curved posteriorly (G&P 1G); (2) elongate almost parallel-sided (Fig. 1E).

43) *Male, shape of S7 ventral lobe*: (0) short and bluntly rounded (G&P 16A); (1) short and narrow; (2) broad, apex concave (G&P 1G); (3) curved posteromedially (G&P 6G); (4) curved posterolaterally (Fig. 1E).