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# A New Species of *Hemicotelles* (Hymenoptera: Colletidae) from Peru

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## Abstract

We diagnose, describe and illustrate *Hemicotelles misti* Anaya, Huanca and Packer **n. sp.**, from the slopes of the Misti Volcano in Arequipa Province, Peru. The new species represents a range extension of 1500 km from the nearest confirmed locality for the genus, in Central Chile. We provide a fully illustrated key for the identification of the three species in the genus and add the species to an earlier phylogeny for Colletinae.

Key words: Adesmia, Argentina, Chile, Colletinae, phylogeny, range extension

#### Introduction

The genus Hemicotelles was described by Toro and Cabezas (1977) with Lonchopria ruizii Herbst, 1923 as its type species. They also included a second, newly described, species H. magallanes Toro and Cabezas, 1977, in their new genus. Since its description, Hemicotelles has not always been treated at the level originally designated. For example, Michener (2007) considered it as a subgenus of Mourecotelles, along with Toro and Cabezas (1978) Xanthocotelles and Mourecotelles, both also originally described at the generic level. However, both morphological (Ferrari and Packer 2021) and molecular phylogenies (Kuhlmann et al. 2009; Almeida and Danforth 2009; Ferrari et al. 2020) demonstrate that Hemicotelles is sister to Colletes Latreille with the two in combination being sister to [Mourecotelles+Xanthocotelles]. Further, Hemicotelles readily differs from Colletes in diagnostic features i.e. the metapostnotum lacks a complete transverse carina with the metapostnotal dorsal surface divided into pits by longitudinal carinae or sinuate striae as found in *Colletes* and the second recurrent vein is straight, whereas it is S-shaped in Colletes. Ferrari and Packer (2021) found no single character that was synapomorphic for the genus that was also not homoplasious elsewhere on the tree: the aforementioned differences to Colletes either being plesiomorphies (the straight recurrent vein) or part of a multi-character transformation series (the state of the metapostnotum). However, the nine synapomorphies that exhibited additional changes elsewhere on the phylogeny contributed to the very high statistical support for monophyly of the genus (98 to 99 out of 100 for the two different methods included and the best supported generic grouping in the analysis).

Since its description, *Hemicotelles* has comprised only two species, both from the southern cone of South America, the type species from Central Chile (Coquimbo Province) and *H. magallanes* from two closely approximated localities either side of the Argentina/Chile border in Patagonia: Los Antiguos, Santa Cruz province in Argentina and Chile Chico, Aisén province in Chile. The purpose of this paper is to describe a new species that extends the range of the genus 1500 km further north to southern Peru. We also provide an identification key and add the species to the earlier morphological phylogeny.

## **Materials and Methods**

The first specimens of the new species were collected as part of a hymenopteran pollinators study in the Andean Scrub Ecosystem (MINAM, 2019), Paramo ecoregion (Arroyo and Cavieres, 2013) (also called Southwestern Xeric Puna montane desert scrub (Josse *et al.*, 2011)) of the Alto Selva Alegre district, Arequipa. The study was performed by the lead author at the Pastores sector (3395 masl). Collections were made from May to July, 2023 (i.e. during the dry season), every 14 days; temperatures ranged from 16–23°C and relative humidity was from 12–36%. Sampling occurred from 8:00 to 13:00 hours at ten evenly spaced points along a linear transect of 200 m with ten minutes of sampling per point. Hymenoptera associated with flowering plants were collected manually using a plastic vial (250ml) (Arroyo *et al.*, 1982). Additional samples were obtained from lower down the slope of the volcano in March and April 2024 using entomological nets and spot-netting (Packer and Darla-West, 2020).

Morphology was studied using a Leica S APO and Leica MZ 12.5 stereomicroscopes using standard terminology from earlier papers from the Packer lab (e.g. Mir Sharifi *et al.* 2018; Packer and Graham 2020) informed by the formats of Ferrari *et al.* (2021) and Toro and Cabezas (1977). Surface sculpture was studied using diffused light from Philips 14W LED daylight bulbs following the terminology of Harris (1979) as emended in the two papers cited above. Whole specimen and face shot images were taken with a Visionary Digital imaging system that comprises a Canon EOS 5D Mark II camera, a Tamron SP AF Tele-Converter with 1.4x magnification, a Canon MP-E 65mm macro lens and a P-51 Camlift, version 2.9.7.1. They were amalgamated using Helicon Focus version 5.3 and final images edited and amalgamated into plates using Adobe Photoshop CS 6 extended. Details of the metapostnotum and male genitalia were taken with a Keyence 6000 and processed as above. The distribution map was obtained using SimpleMappr (Shorthouse, 2010) and the large-scale map was taken from Google Earth Pro, version 7.3.6.

Museum acronyms associated with this study, taken from Evenhuis (2024), along with the curators responsible, are as follows:

EACSAU—Entomology and Acarology Collection at Universidad Nacional de San Agustin de Arequipa, Peru—Javier Huanca.

MEKRB—Entomology Museum Klaus Raven Buller at Universidad Nacional Agraria La Molina, Lima, Peru—Clorinda Vergara.

PCYU—Packer Collection at York University, Toronto, Canada - Laurence Packer.

We added the new species to the discrete character data matrix from Ferrari and Packer (2021) and used the routine setk to set the concavity function (Santos *et al.*, 2015) for an implied weights analysis using TNT (Goloboff and Catalano, 2016). The resulting tree was read into Asado (Nixon, 2004) for tree visualization and output. Group support was assessed using symmetrical resampling and GC values (Goloboff *et al.*, 2003), where the support value measures the proportion of all iterations in which the same arrangement of taxa at that node was found minus the proportion in which the second most commonly found arrangement occurred.

## **Species Description**

## Hemicotelles misti Anaya, Huanca & Packer

Figs. 1, 4, 6–7, 11, 13–26, 29 & 31

**Diagnosis:** The new species clearly belongs to the genus *Hemicotelles* based upon the structure of the metapostnotum, which has a transverse carina (albeit medially interrupted) without longitudinal carinae or striae that divide the horizontal portion into pits (Fig. 1). *Mourecotelles* and *Xanthocotelles* lack both the transverse carina and the longitudinal surface sculpture (Fig. 2) whereas *Colletes* has both (Fig. 3). The genus has a small subapical mandibular tooth (Fig. 4) rather than a large one as found in *Mourecotelles* and *Xanthocotelles* (Fig. 5) and has a straight second recurrent vein (Fig. 6) and a short horizontal surface to T1 (Fig. 8; see also Figs. 10, 11) rather than the S-shaped vein (Fig.7) and long T1 horizontal surface (Fig. 9) found in *Colletes*.



**FIGURES 1–3.** Metapostnotal characteristics to separate *Hemicotelles* from other Colletinae, all posterodorsal views. Fig. 1—*H. misti* **n. sp.** to show presence of transverse carina (red arrow) and absence of longitudinal striae; Fig. 2—*Mourecotelles mixta* Toro & Cabezas to show absence of transverse carina and absence of longitudinal striae; Fig. 3—*Colletes* sp. to show presence of both transverse carina (red arrow) and longitudinal striae (blue arrows).



**FIGURES 4–9.** Additional characteristics to separate *Hemicotelles* from other Colletinae. Fig. 4—*H. misti* **n.sp.**  $\bigcirc$  mandible to show small subapical tooth; Fig. 5—*M. mixta*  $\bigcirc$  mandible to show large subapical tooth; Fig. 6—*H. misti* **n.sp.**  $\bigcirc$  forewing to show straight second recurrent vein (orange arrow); Fig. 7—*Colletes* sp.,  $\bigcirc$  forewing to show S-shaped second recurrent vein (dark blue arrow); Fig. 8—*H. ruizii* base of  $\bigcirc$  metasoma to show horizontal surface of T1 (pale blue line) shorter than T2 (red line); Fig. 9—*Colletes* sp., base of  $\bigcirc$  metasoma to show horizontal surface of T1 (pale blue line) as long as T2 (red line).

Both sexes of *H. misti* n.sp. can most easily be differentiated from the other two species in the genus by having the metasomal apical hair bands relatively extensive, being approximately  $1.5 \times MOD$  in length submedially on T2 in relatively fresh specimens (Fig. 10). In contrast, *H. ruizii* and *H. magallanes* have the apical tergal bands narrow to medially interrupted (<0.5 × MOD) (Figs. 11 & 12). See also the characteristics in the key below.

Additionally, *H. misti* n. sp. has the bright fulvous mesosomal pubescence also found in *H. ruizii*, (Figs. 13-16), although this may not be useful in old specimens as the colours fade and the most worn specimen approaches the paler colouration of relatively fresh exemplars of *H. magallanes*.



**FIGURES 10–12.** Metasoma of  $\bigcirc$  of *Hemicotelles* species to show more extensive tergal hair bands in *H. misti* **n.sp**, including the presence of a distinct band on T4 (blue line), than in either of the other two species. Fig. 10—*H. misti* **n.sp**., Fig. 11—*H. magallanes* Toro & Cabezas, Fig. 12—*H. ruizii* (Herbst).

**Description.** Holotype. *Dimensions (mm)*. Approximate body length 13; head width 4.2; head length 3.5; intertegular distance 3.8; forewing length 9.0.

*Colouration.* Integument black except: brown on clypeal lip, all claws, tarsomeres 3-5, tegula; tibial spurs pale; stigma and wing veins blackish; metasomal tergal apical impressed areas narrowly orange-brown.

*Structure.* Labrum median tubercle swollen with weak vertical medial depression. Clypeus with weak medial subapical convexity. Mandibular preapical tooth narrowly rounded. Malar area 1.5× longer than basal depth of mandible, subequal to width of and less than half as long as compound eye. Inner margins of compound eyes slightly divergent below: UOD:LOD 2.6mm:2.8mm. F1 more than twice as long as its apical width: 0.56mm:0.26mm and more than twice as long as F2 0.26mm. Facial fovea poorly demarcated medially, most easily recognised by absence of punctures. Frontal line carinate below, a broader ridge above, the two parts separated by a narrowly oval pit. Dorsolateral margin of pronotum broadly rounded. Metapostnotum transverse carina broadly interrupted medially, curved anteriorly towards sides without additional gap. Tibial spurs ciliate. Hind basitarsus 2.5× longer than broad: 1.1mm:0.45mm. Tarsal claws toothed. T6 with remnant of pygidial plate, apicomedially truncate with small smooth elevated triangular area, narrowly extended anteriorly as a weak longitudinal ridge. S6 in ventral view with truncate apex, posterolateral margin glabrous, straight, weakly sclerotized.

**Pubescence.** Clypeus with scattered short hairs on disc and dense long ( $\sim 3 \times MOD$ ) hairs along lateral margins. Face covered with long ( $\sim 4 \times MOD$ ), erect, short-branched, pale-yellow hairs with black hairs intermixed on paraocular area; interantennal and vertexal areas hairs plumose, pale orange, some with apical half black, except some entirely black on ocellocular area; gena with short appressed and long erect white hairs ( $<6 \times MOD$ ); mandible with long yellow setae. Mesosomal dorsum and hypoepimeral area hairs shorter ( $\sim 3 \times MOD$ ), dense, plumose, orange, some with black tips, rest of lateral and ventral surface of mesosoma hairs pale cream ( $\leq 4 \times MOD$ ). Legs with short and long ( $\leq 5 \times MOD$ ) pale-cream simple hairs; femoral scopal hairs dense and straight anteriorly, sinuate posteroventrally, ventral tibial scopa hairs upcurved  $\leq 3 \times MOD$ ; hind basitarsus with pale-cream hairs, long dorsally ( $\leq 5 \times MOD$ ). T1–T2 with sparse erect somewhat plumose cream long ( $\sim 2 \times MOD$ ) hairs with short pale hairs

intermixed; T3 hairs suberect pale brown,  $\leq 2 \times MOD$ ; T4–T6 suberect hairs black, longer towards sides ( $\leq \times 2MOD$ ); marginal hair bands appressed, whitish,  $\sim 1.5 \times MOD$ , shorter on T4 ( $\sim 1 \times MOD$ ) and T5 (0.7× MOD). S1–S5 hairs suberect, plumose intermixed with pale-yellow setae, longest ( $\leq 4 \times MOD$ ) apically on T1–T2.



FIGURES 13 & 14. Hemicotelles misti n. sp. 2 paratype. Fig. 13—lateral habitus, Fig. 14—face.

*Sculpture.* Clypeus disc irregularly longitudinally ridged, superficially punctate, dorsolaterally smooth with large distinct punctures, lateral slopes with dense small hair–bearing punctures; medial linear longitudinal depression narrow, densely punctate, restricted to most of upper  $\frac{1}{2}$ . Supraclypeal area densely punctate (i<d). Frontal and paraocular areas moderately coarsely and densely punctate (i=0.5–1.0d). Malar area with patches of imbricate microsculpture, larger punctures longitudinally effaced, small round punctures scattered towards base, 1–6d apically. Vertexal area punctures variable in size and spacing, with large impunctate area laterad of lateral ocellus. Mesoscutum and scutellum irregularly punctate i=1–7d, metanotal punctures dense (i<d). Mesepisternum punctures dense (i=1–2d), interspaces imbricate, lower half of hypoepimeral area impunctate. Metepisternum and lateral surface of propodeum imbricate, punctures obscure. Metapostnotum mostly smooth and shiny, with few weak transverse rugulae medially in addition to transverse carina. Metasomal terga punctures smaller and sparser towards base (i<4d basally, mostly <2d apically on T1; mostly i<2d on T5 and T6), T1–T4 weakly imbricate, T5–T6 coarsely imbricate; sterna imbricate, moderately densely punctate (i<2d).

Male Allotype. *Dimensions (mm)*. Approximate body length 10.5; head width 3.5; head length 3.1; intertegular distance 3.3; forewing length 8.1.



FIGURES 15 & 16. Hemicotelles misti n.sp. & paratype. Fig. 15—lateral habitus; Fig. 16—face.

As in female except for usual secondary sexual characteristics of apical metasomal segments, scopa, antenna and as follows:

*Structure.* Labrum median tubercle less pronounced, vertical medial depression absent. Malar area 2× longer than basal depth of mandible (1.1mm:0.55mm), less than width of compound eye (0.7mm) and more than half as long as compound eye (1.8mm). Inner margins of compound eyes less divergent below: UOD:LOD 2.45mm:2.55mm. F1 1.5× longer than its apical width: 0.3mm:0.45mm and slightly longer than F2 0.4mm. Frontal line strongly ridged above, indistinct below. Hind basitarsus 3× longer than broad: 1.3mm:0.4mm. Tarsal claws lacking teeth. Apical margin of T7 narrowly truncate, lacking any remnant of pygidial area. S6 in ventral view with truncate apex, posterolateral margin glabrous, straight, weakly sclerotized. Terminalia (of a paratype) as in Figs. 17–19.



**FIGURES 17–19.** Terminalia of paratype ♂ of *H. misti* **n. sp.** Fig. 17.— S7; Fig. 18—S8 and genital capsule lateral view; Fig. 19—genital capsule dorsal view.

**Pubescence.** Clypeal hairs on lateral and dorsal margins decumbent, long (~4MOD) largely overlying clypeal surface. T1–T2 erect hairs denser and longer (~3× MOD), laterally oriented erect hairs on sides of T4–T7 mostly pale. S3 apical hairs forming suberect fringe, S4–S5 apical fringe of subappressed apically oriented hairs, S6 appressed hairs posteromedially oriented on disc, posteriorly oriented apically.

*Sculpture.* Supraclypeal area irregularly punctate, some punctures crowded, others separated by 2d. Frontal and paraocular areas moderately finely but densely punctate (i=0.5-1.0d). Malar area mostly imbricate, punctures of irregular size and spacing. Mesoscutum and scutellum somewhat less irregularly punctate i=1-5d, except scutellum impunctate anteriorly. Metapostnotum with weak median carina on horizontal surface, transverse carina narrowly interrupted medially and submedially. Metasomal terga lacking imbrication, punctures relatively sparse (i<4d on basal terga) becoming denser and larger on more apical terga.

**Variation**. In females, the extent of the median depression on the labral tubercle varies from being clearly visible in dorsal view such that the tubercle is clearly bigibbous to being absent above such that the tubercle is entirely convex in dorsal view. Either side of the tubercle there may be some weak longitudinal fluting. The details of the metapostnotal transverse carina varies: the medial interruption varies in width and the lateralmost parts may be interrupted or entire, irregularly curved or abruptly curved anteriorly or almost right angularly bent before attaining the anterior margin (Figs. 20–22).



**FIGURES 20–22.** Variation in the metapostnotal carinae of *H. misti* **n. sp.,** all figures oblique dorso-lateral views of left half of metapostnotum. Fig. 20—Carina laterally complete as in both holotype and allotype; Fig. 21—Carina narrowly interrupted (red arrow); Fig. 22—Carina broadly interrupted (blue line).



**FIGURE 23**. Distribution map showing localities for *Hemicotelles misti* n. sp. (left) and for the genus as a whole (right). Red - *H. misti*, **n. sp**., yellow - *H. ruizii*, blue - *H. magallanes*. On the left, Arequipa is at the bottom left and the Misti Volcano towards the top.



FIGURES 24 & 25. Localities for *H. mist* n. sp, Fig. 24—holotype locality, Fig. 25— one of the paratype localities. Bushes of the host plant, *Adesmia verrucosa* are visible in both.



**FIGURES 26–33.** Key characters for the differentiation of *Hemicotelles* species. Fig. 26—*H. misti* **n. sp.** metasoma dorsal view to show extensive apical hair bands and complete band on T4 (red arrow). Fig. 27—*H. magallanes* and Fig. 28—*H. ruizii* to show narrow apical hair bands and interrupted band on T4 (red arrows). Fig. 29—*H. misti* **n. sp.**, oblique lateral view of base of metasoma to show extensive long plumose hairs towards side of T2 (yellow arrows); Fig. 30—*H. magallanes* oblique lateral view of base of antenna to show lack of long plumose hairs towards side of T2 (orange arrows); Fig. 31—*H. misti* **n. sp.**, base of antenna to show F1 (yellow line) longer than F2 (red line); Fig. 32—*H. ruizii* base of antenna to show F1 (yellow line).



**FIGURES 34–37.** Key characteristics for the separation of *H. ruizii* and *H. magallanes*. Fig. 34—*H. ruizii*  $\bigcirc$  lower face to show extensive macrosculpture on clypeus; Fig. 35—*H. magallanes*  $\bigcirc$  lower face to show extensive areas lacking macrosculpture (red arrows); Fig. 36—*H. ruizi*  $\bigcirc$  metasoma dorsal view to show dark hairs especially on T4 Fig. 37—*H. magallanes*  $\bigcirc$  metasoma dorsal view to show pale hairs on T4–T5.

**Material Studied**. *Holotype*  $\bigcirc$ : PERU, Arequipa, Alto Selva Alegre, Pastores Sector -16.331, -71.447, ca 3500 masl, 28.v.2023, L. Anaya ex. *Adesmia verrucosa* Meyen (Fabaceae). (EAC-001-2023-4). Allotype  $\bigcirc$ : same data except 09.vii.2023, L. Anaya ex. *Adesmia verrucosa* (EAC-004-2023-1). Paratypes:  $3\bigcirc$ : same data except ca 3470 masl, 28.v.2023, L. Anaya ex. *A. verrucosa, Grindellia tarapacana* Phil. (Asteraceae) and *Oxalis megalorrhiza* Jacq. (Oxalidaceae) (EAC-001-2023-1 to 3);  $3\bigcirc$ : same data except 3484 masl, 11.vi.2023, L. Anaya ex. *A. verrucosa* (EAC-002-2023-1 to 3);  $1\bigcirc$  and  $1\bigcirc$  same data except 25.vi.2023 (EAC-003-2023 1-3);  $1\bigcirc$ : same data except 3440 masl, 09.vii.2023, L. Anaya ex. *A. verrucosa* (EAC-004-2023-1);  $1\bigcirc$ : PERU, Arequipa, Alto Selva Alegre, -16.34053, -71.47056, ca 3120 masl, 26.iii.2024, L. Anaya, ex. *A. verrucosa* (EAC-001-2024-1);  $1\bigcirc$ , same data except 13..iv.2024, L. Packer (EAC-003-2024-8);  $1\bigcirc$  and  $1\bigcirc$ : PERU, Arequipa, Chiguata -16.38678, -71.34508, 3520 masl, 13.iv.2024, L. Packer, ex. *A. verrucosa* (EAC-002-2024-1 & 2),  $4\bigcirc$  and  $3\bigcirc$ : PERU, Arequipa, Alto Selva Alegre, -16.34053, -71.47056, 3130 masl, 13.iv.2024, L. Packer ex *A. verrucosa* (EAC-002-2024-1 to 7).

The holotype, allotype and three paratypes (EAC-002-2023, EAC-001-2024) are deposited at MEKRB, six paratypes (EAC-001-2023-1 to 3 and EAC-002-2023-1 to 3) are deposited at EACSAU and nine paratypes (EAC-002-2024-1 & 2, EAC-003-2024-1 to 7) at PCYU.

**Etymology**: the species is named after the volcano, the slopes of which were where the first specimens were collected. The species name is to be considered as a noun in apposition. The material from 2024 was collected from somewhat lower down.

## **Identification Key**

- (Fig. 35, red arrows); both sexes with hairs of T4 mostly whitish to pale brown (Fig. 37) .... *H. magallanes* Toro & Cabezas

## **Phylogenetic Results**

The 174 morphological characters assessed in the phylogenetic analysis were the same as the discrete characters used in Ferrari and Packer (2021); we did not include the twelve continuous characters from the earlier study. The appendix provides the states found in the new species and is formatted to be considered as an augmented description.

Setk yielded a k value of 12.63 and implied weighting resulted in one most parsimonious tree, with a fit of 37.86 and with the same generic level pattern for Colletinae as found earlier (Ferrari and Packer, 2021) i.e. ([*Hemicotelles+Colletes*] [*Mourecotelles+Xanthocotelles*]). Colletinae was found to have almost maximum support (GC=99), and both pairs of genera as well as each genus separately received strong support (GC ranging from 91 to 99) including *Hemicotelles* with a GC value of 95 (Fig. 38). *Hemicotelles magallanes* was found to be the sister species to the two other species in the genus, albeit with a low support value of 42.



**FIGURE 38.** Phylogeny for genera of Colletinae and species of *Hemicotelles*. Small numbers above internodes are the character numbers (see Appendix 1) and below internodes are the character-state that is changed to along that node. Filled in circles are unique synapomorphies, open circles are character state changes that occur elsewhere on the full tree of 62 taxa. Large numbers above internodes are GC values indicating the level of support for the group.

### Discussion

As currently understood, *Hemicotelles* has a doubly disjunct distribution (Fig. 23), being known from either side of the border between Chile and Argentina in Patagonia, the southern Atacama Desert in Chile, and southern Peru. Extensive collections throughout most of Chile by personnel from the Packer laboratory make it seem unlikely that there are additional populations or species of the genus in northern Chile. Samples made by the same group, along with local entomologists, suggest it is unlikely that the genus occurs in the area around Santiago and to the south in Central Chile. Thus, the disjunct distribution of the genus is likely real. The new species extends the confirmed range for the genus considerably as its localities are approximately 1500 km distant from the nearest previously known locality for the genus in central Chile.

Along with most specimens of *Mourecotelles* and *Xanthocotelles* that we have collected on or around flowers, *H. misti* n. sp. was collected primarily associated with flowers of *Adesmia* species, in this case, *A. verrucosa*. This genus would seem to be a common host of Colletinae that occur within its range as multiple species of these genera, as well as *Colletes*, have also been found on *Adesmia* (Ferrari 2017, 2019; Toro and Cabezas, 1977, 1978). The possibility that *Adesmia* is an ancestral host for Colletinae may be worthy of consideration as the crown age of this colletid subfamily has been dated to approximately 40 million years ago (Ferrari *et al.*, 2020), more or less coincident with the stem age for *Adesmia* (Iganci *et al.*, 2013). Furthermore, the geographic range of the more early-diverging branches within the phylogeny of the genus suggests that it originated somewhere in the Andean region from southern Peru to Patagonia (Iganci *et al.*, 2013).

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## APPENDIX 1. Character states coded for *H. misti* n. sp.

Character numbers are given before the close bracket symbol, and the state number is given in square brackets. A character number followed by [-] indicates that that character is inapplicable to *H. misti* n. sp.. See Ferrari and Packer (2021) supplementary appendix S1 and S2 for the full description of characters and their states and for images of (most of) the same respectively. The text is worded such that the list of characters also serves as an additional species description.

Female:

- 0) mandible with one subapical tooth [0] that is:
- 1) narrow [0],
- 2) angle between apical and preapical mandibular teeth obtuse [0],
- 3) labrum medial modification present [1] and
- 4) tuberculate [2] and
- 5) with a medial longitudinal sulcus [1],

6) clypeal apical margin broadly concave [1] (note that states 1 and 2 were reversed in the text of the earlier paper but were correct on the figure (S8)),

- 7) clypeal subapical depression present [1] and
- 8) narrowly transverse [0],

9) clypeus with longitudinal striation present [1] (note that these are broader and relatively indistinct in comparison to most taxa scored as state 1 originally) and

- 10) striae not attaining dorsal <sup>1</sup>/<sub>4</sub> of clypeal length [0],
- 11) clypeal disc in profile flat [0],
- 12) clypeus mediolongitudinally depressed [1] and
- 13) raised above level of paraocular area [1] and
- 14) raised abruptly [1],
- 15) supraclypeal area depressed in relation to upper margin of clypeus [0] and
- 16)medially densely punctate i=0.5-1d [1],
- 17) subantennal suture curved towards antennal socket [0],
- 18) frontal line below carinate [0],
- 19) facial fovea lacking appressed short hairs [0],
- 20) vertexal area flat in posterodorsal view [0] and
- 21) angularly separated from occipital surface [0],
- 22) genal area tomentum above present [1],
- 23) mesoscutal pubescence with branches distinctly separated [0],
- 24) mesosomal pubescence ventrally sparse, not obscuring underlying integument [0],
- 25) lateral surface of propodeum with tomentose hairs [1] and
- 26) these hairs dense [1],
- 27) front coxa with short apicomedial process [1]
- 28) hind femur with scopa present [1],
- 29) hind tibial spurs ciliate [0],
- 30) hind basitarsus dorsal surface flat [0],
- 31) hind tarsal claws lacking subapical tooth [0],
- 32) T1 lacking tomentum on horizontal surface [0],
- 33) T2 lacking tomentum on pregradular area [0],
- 34) T2-T5 discs lacking tomentum [0],
- 35) T5 prepygidial fimbria absent [0],
- 36) T6 remnant of pygidial plate present [1] and
- 37) indicated by a longitudinal ridge [1],
- 38) T6 marginal zone forming a lip [1] and
- 39) broadly truncate [2],
- 40) S2 pubescence dense but not forming distinct scopa [1],
- 41) S5 specialized area absent [0],

42) S6 longer than broad [1] and 43) with lateral ridge absent [1] and 44) with weakly sclerotized area [1] that is 45) medial and longitudinal [0] and 46) lacking yellowish markings [0], 47) [-], 48) S6 lacking oblique raised posterolateral area [0] and 49) with posterolateral margin convex [0] and 50) posteromedial longitudinal ridge absent [0] and 51) with apical margin entire [0], 52 [-], Male: 53) glossa bilobed [1], 54) premental fovea absent [0], 55) mandible dark basally [0] and 56) with apical tooth lower margin gently curved distally [0] and 57) apical tooth much longer [1] and 58) slightly narrower than subapical tooth [0], 59) labrum impunctate [0], 60) face lacking pale markings [0], 61) clypeus punctation of disc sparse [0], 62) paraocular area with black hairs [1] that 63) form a stripe [1], 64) eye hairs minute [0], 65) flagellum blackish ventrally [0], 66) frontal line carinate above [1], 67) facial fovea present [1] and 68) relatively narrow and deep (at least laterally) [2], 69) area lateral to lateral ocellus with smooth impunctate area [1] that is 70) relatively narrow [0], 71) pronotal lateral angle rounded [0], 72) mesoscutal pubescence long and dense [1] but 73) lacking black hairs (though some are black-tipped) [0], 74) [-], 75) tegula dark brown [0], 76) scutellum flat [0], and 77) with dark orange hairs [3] and 78) lacking posterolateral hook-like process [0], 79) hypoepimeral area with impunctate band below [1], 80) mesepisternum punctures fine [1] and 81) with imbricate interspaces [1], 82) metepisternum imbricate on upper protuberance [1] but 83) lacking a pale transverse lamella [0] and 84) with oblique striae below protuberance [1] that are 85) relatively strong [1], 86) metapostnotum with subhorizontal surface [1] that 87) lacks longitudinal carinae [0] but 88) which has a transverse carina [1] that is 89) broadly interrupted medially [0], 90) lateral surface of propodeum punctures fine [1] and 91) interspaces imbricate [0], 92) forewing hyaline [0] with

93) three submarginal cells [1] and 94) a straight second recurrent vein [0], 95) tibiae dark [0], 96) including anterior surface of front tibia [0], 97) hind tibia with ventral spine absent [0] and 98) with basitibial plate absent [0] and 99) lacking anteroventral distal process [0], 100) hind tibial spurs pale brown [1], 101) hind basitarsus lacking anterior concavity [0], 102) hind tarsomere 2 lacking posterodistal process that extends beyond the insertion of tarsomere 3 [0], 103) [-], 104) T1 upper margin of vertical surface concave [1] and 105) horizontal surface short in relation to that of T2 [0] and 106) with branched hairs [1] that are 107) pale yellow [1] and surface with 108) minute punctures [0] that are 109) moderately sparse towards the sides [1], 110) T1 premarginal line poorly indicated [0] and 111) marginal zone with band of tomentum [1] that is 112) interrupted medially [0], 113) T1-T5 lacking metallic colouration [0], 114) T2-T4 premarginal line poorly indicated [0], 115) T3-T5 marginal zones with tomentum [3], 116) S7 disc anterior margin deeply bisected [1], 117) [-], 118) S7 with apicolateral lobes [1], 119) and only one pair of them [0] which are 120) enormously enlarged [3] and with 121) a short neck [0] that 122) lacks an anteromedial lobelet [0] 123) S7 apicolateral lobe as long as broad [1], 124) [-], 125) S7 apicolateral lobe without additional anterolateral lobe [0] but 126) with glabrous apicomedial area present [1] and 127) lacking medial fold [0] and 128) lacking membranous anterolateral extension [0] and with 129) lateral margin straight anteriorly [0] and 130) ventral rounded protrusion absent [0] and 131) posterior margin concave [0], 132) S8 with spiculum [1] that is 133) longer than basal width [1] that is 134) weakly recurved [0], 135) S8 greatest width anterior to midlength [0] and 136) posterior margin of lateral lobe strongly sclerotized [1] and 137) distal process laterally compressed [1] and 138) lacking subapical lobe [0] but with 139) weakly sclerotized rounded area present [1] and 140) marginally located [0], 141) S8 apical lobe convex throughout [0] and 142) with a laterobasal shoulder [1] and 143) in profile at angle of  $\sim$ 45° from disc [1], 144) gonobase foramen wider than long [0] with

145) relatively straight posterior margin [2] that is

- 146) somewhat swollen laterally [1],
- 147) gonocoxa anteroventral bridge very long [2] and
- 148) ventromedial separation narrow [1] and
- 149) dorsomedial margin open [0] and
- 150) posteroventral process absent [0] but
- 151) transverse cleft present [1] but
- 152) lacking lateral swelling [0] and
- 153) lacking strong sclerotization near base of gonostylus [0],
- 154) [-],
- 155) [-],
- 156) gonocoxa without deep sulcus separating its apex from gonostylus [0],
- 157) volsella, shape of digitus [2] and
- 158) cuspis subequal to digitus [1],
- 159) digitus convex apically [0] and
- 160) narrowly separated from cuspis [0],
- 161) gonostylus distinctly separated from gonocoxa [1],
- 162) relatively short [1],
- 163) narrowly rounded in profile [2] and
- 164) approximately as wide at base as the apex of the gonocoxa [1],
- 165) penis valve lacking semicircular concavity on inner margin [0] but with
- 166) medial lobe present [1] but
- 167) tiny [0],
- 168) dorsal wing of penis valve somewhat angulate [1] and
- 169) medial spine present [1],
- 170) penis valve ventral wing present [1] and
- 171) entire [0],
- 172) penis valve not narrowing to a point in dorsal view [0] and
- 173) apex somewhat swollen [1]