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Two new species of *Geodiscelis* Michener & Rozen (Hymenoptera: Apoidea: Colletidae) with a phylogenetic analysis and subgeneric classification of the genus

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Abstract

Two new species of the genus *Geodiscelis* are described: *Geodiscelis nazcalinea* Packer & Dumesh, **sp. nov.** from Peru (the first record of the genus from that country) and *G. phisquiri* Packer & Dumesh, **sp. nov.** from northern Chile. The new species are most closely related to *G. longiceps*, but differ primarily in having somewhat less elongate heads and in details of the male terminalia. A key to the five known species of the genus is provided as are the results of a phylogenetic analysis based upon 68 characters, and the genus is formally divided into three subgenera: *Geodiscelis s. str.* Michener and Rozen, *Geodiscelis (Nazcoediscelis)* Packer and Dumesh, subgenus nov. and *Geodiscelis (Thaumoediscelis)* Packer and Dumesh, subgenus nov. The two new species described herein belong to subgenus *Geodiscelis (Nazcoediscelis)*. Figures of the most important characters are provided. *Tiquilia* sp. (Boraginaceae) is the probable floral host of both new species and it is suggested that all species are ground-nesters. Sexual dimorphism in an unusual character is recorded for *G. thaumaskelos* Packer.

Key words: bee, Xeromelissinae, extreme modifications, sexual dimorphism, nectaries, Boraginaceae, Peru, Chile

Introduction

Geodiscelis Michener & Rozen, 1999 was described based upon an Argentinean species with an unusual combination of morphological characteristics (Michener & Rozen, 1999). The type species, *G. megacephala* Michener & Rozen, 1999 has unmodified maxillary palpi, epistomal lobe invading the surface of the clypeus almost reaching the clypeal apex, and a pale banded metasoma. The epistomal lobe characteristic was previously considered to be apomorphic among Xeromelissinae only for *Xeromelissa* Cockerell, 1926 *sensu* Packer (2008) (Toro & Moldenke, 1979), but all species of that genus have modified maxillary palpi, usually with the basal 3 palpomeres distinctly more robust than the apical 3 (Toro & Moldenke, 1979; Packer, 2005, 2008). Phylogenetic analysis suggests that the epistomal lobe and pale integumental metasomal band characters are synapomorphies linking *Geodiscelis* with its sister taxon, *Xeromelissa* (Packer, 2008). The unmodified maxillary palpus is plesiomorphic (Packer, 2008).

Two additional species of *Geodiscelis* have been described, both remarkably divergent from the type species, but in entirely different ways. *Geodiscelis longiceps* Packer, 2005 has an enormously elongate head with the malar space longer than the compound eye (Packer, 2005). *Geodiscelis thaumaskelos* Packer, 2009 has the malar space strongly reduced but possesses remarkably modified hind legs in the male (all other species of the genus have entirely unmodified male hind legs); it also lacks the inner hind tibial spur in both sexes and the females have an almost glabrous second metasomal sternum (Packer, 2009). This last feature is contrary to what had been a defining characteristic of the subfamily Xeromelissinae among non-cleptoparasitic bees: the scopa on S2 is as well, or better, developed than that on the hind leg (Michener 2007, p. 127; Packer & Ratti, 2009). For a genus containing so few species, the morphological diversity found in *Geodiscelis* is extreme.

During a field trip to Peru in 2009, another new species of *Geodiscelis* was discovered and is described herein. More recently, an additional new species was discovered in northern Chile and is also described. We also present

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the results of a phylogenetic analysis that includes all five known species of the genus and define and describe three subgenera to encompass the variation found in *Geodiscelis*.

Material and methods

Male terminalia were cleared in 5% KOH for five hours and then stored in glycerine. Terminology for morphology follows Packer & Genaro (2006) and for surface sculpture Harris (1979). The letters F, T and S followed by a number refer to antennal flagellomeres and metasomal terga and sterna respectively. UOD and LOD indicate the minimum distances between the compound eyes above and below respectively and some features are measured in terms of MOD—the diameter of the median ocellus. Puncture spacing is given in terms of the relative sizes of the interspaces (i) and puncture diameters (d).

Images were taken with a Visionary Digital BK Plus system, using a Canon 5D Mark II camera with a Canon 65mm lens. Image slices were stacked using Helicon Focus and photo-editing was done using Adobe Lightroom and Photoshop.

Relevant collection acronyms are MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; PCYU: Packer Collection at York University, Toronto, Canada and PUCV: Pontificia Univerdidade Católica de Valparaiso, Chile.

For phylogenetic analysis, a morphology-based data matrix of 68 characters was constructed for characters that varied among *Geodiscelis* species as well as between the genus and other Xeromelissinae and among the other genera. Both members of *Xenochilicola* Toro & Moldenke, 1979 that are known from both sexes, both members of *Patagonicola* Packer, 2014 and three members of *Xeromelissa* were also chosen for inclusion. The latter were chosen based upon the results of preliminary phylogenetic analysis of the genus so as to include a member of a relatively early branching clade, *X. nortina* (Toro & Moldenke, 1979) as well as the type species of the genus, *X. wilmattae* Cockerell and, *X. luisa* (Toro & Moldenke, 1979) the type species of the genus *Chilimelissa* Toro & Moldenke, 1979, later synonymized with *Xeromelissa* by Packer (2008). *Chilicola herbsti* (Friese, 1906) was used to root the tree, based upon earlier results (Packer, 2008, 2014).

The data were analysed with TNT (Goloboff *et al*., 2003a) using ratchet, drift and tree fusing until the most parsimonious result(s) had been found 100 times. Successive approximations character weighting (Farris, 1969; Carpenter, 1988) was applied to the resulting tree using the rescaled consistency index as the weighting factor. Group support was estimated using symmetric resampling (Goloboff *et al*., 2003b) and traditional bootstrap approaches with GC and absolute frequency as the measures respectively (see Goloboff *et al*., 2003b). The former calculates the proportion of times the most parsimoniously recovered node was found among the replicates minus the proportion of times the second most commonly found rearrangement for that node was found. Both measures were calculated based upon 1000 iterations and the acronyms GC and BS are used to denote them in the results.

Taxonomy

Geodiscelis nazcalinea Packer and Dumesh new species

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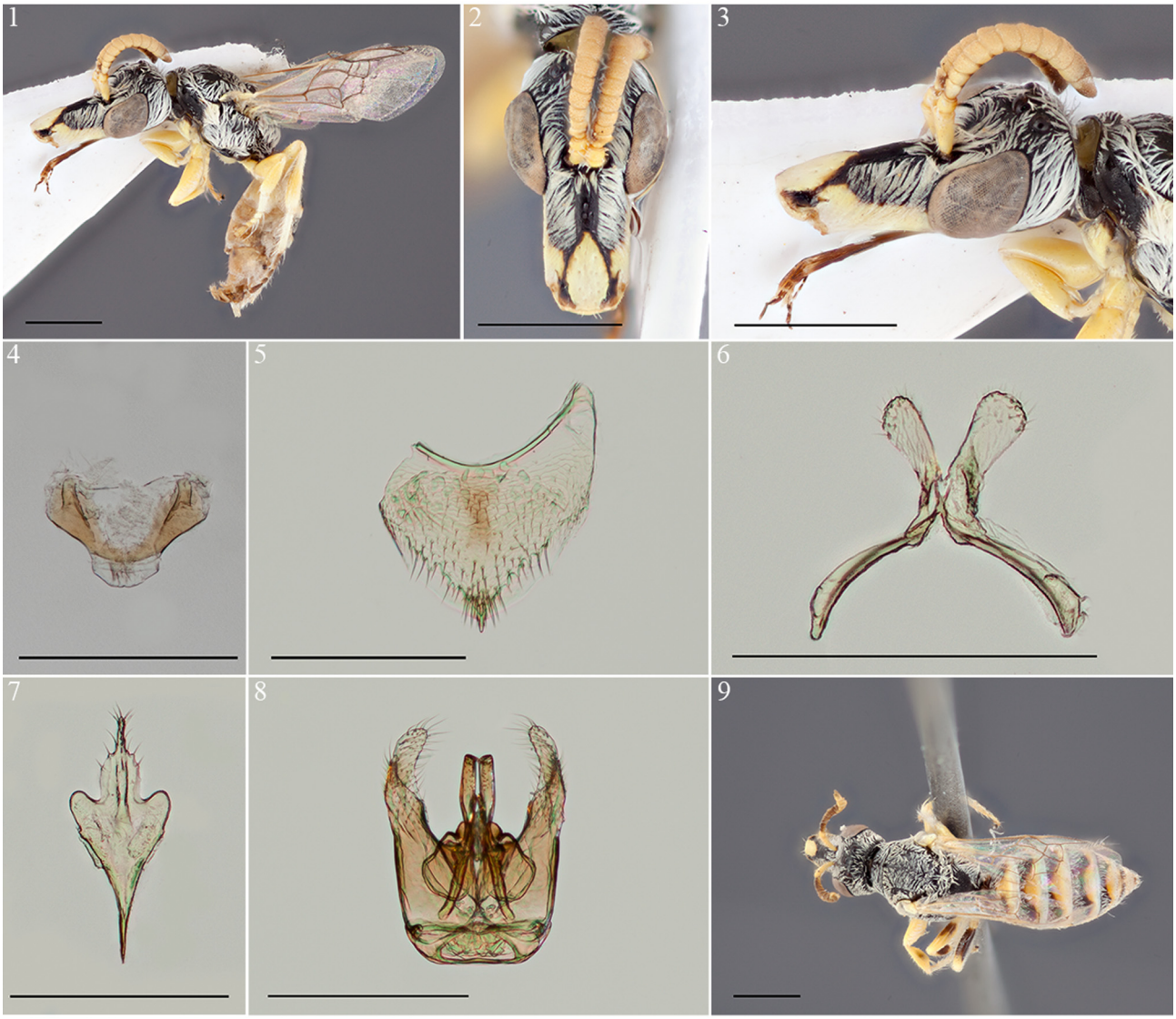
(Figures 1−9 and 18)

Diagnosis. The combination of maxillary palpus unmodified (Fig. 3), pale subapical integumental bands and basal bands of appressed broad, almost squamose, hairs on the metasomal terga (Fig. 9), and malar space almost as long as the compound eye (Figs. 1−3) separates this species from all other bees except for *G. phisquiri* **sp. nov.** described below. Some other Xeromelissinae have unmodified maxillary palpi and pale integumental bands on the metasomal terga, but they either have the malar space considerably shorter than the compound eye and also lack the basal metasomal bands of appressed hairs (*Xenochilicola diminuta* Toro & Moldenke, 1979), or have a malar space that is considerably longer (*Geodiscelis longiceps*). *Geodiscelis nazcalinea* **sp. nov.** can be differentiated from *G. phisquiri* **sp. nov.** through its darker wing veins, broader metasomal hair bands and details of the terminalia, especially the obtuse subapical medial margin to the gonocoxa (Fig. 8) (right angular in *G. phisquiri* Fig. 15) and in

the orientation of the inner lobe to the gonostylus, which is predominantly vertical (Fig. 8) (primarily horizontal in *G. phisquiri* Fig. 15). *Geodiscelis nazcalinea* is also unique among xeromelissine bees in having a medioapical spine to S6 in the male (Fig. 5); although both *G. longiceps* and *G. phisquiri* have an angulation or slight thickening in the same location (Fig. 12), it is not developed into a distinct spine.



FIGURES 1−9. *Geodiscelis nazcalinea* **sp. nov.** 1−8. Male, 9. Female. 1. Habitus, side view, 2. head, frontal view, 3. head, side view, 4. proctiger, 5. S6, 6. S7, 7. S8, 8. genital capsule, 9 habitus, dorsal view. Scale bar = 1mm for Figs. 1−3 and 9. Scale bar = 0.5mm for Figs. 4−8. Figs. 1–3 are of the holotype, 4–9 are from paratypes.

Description.: Male: *Dimensions:* Body length: 5.0mm, fore wing length: 2.3mm head width: 1.0mm.

Colouration: Black with following parts pale yellow: labrum; mandible (apex dark amber); malar space; clypeus (except for extreme sides); hypostomal area apicad of compound eye; scape, pedicel, F1 (except most of anterior surface brownish); anterior surface of F2-F4; spot on pronotal lobe; mesal 1/3 of tegula; entire foreleg (except for orange smudges on femur dorsobasally and tibia posteroventrally and protarsus white); apical ring on mesocoxa, entire mesotrochanter, mesofemur (except dark brown for basal half of dorsal surface), mesotibia (except for dark brown posteromedial mark), mesotarsomeres 3–5 (basal two white); apical 2/3 of metacoxa; apical 1/3, basal ring and narrow ventral stripe on metafemur; metatibia (except for posteromedial dark brown spot and anteromedial orange mark); apical ~1/2 of metasomal terga (except for narrow translucent marginal zones), margined anteriorly with orange; T2-T4 with small, dark brown, subcircular sublateral maculae; apex of S1, all of S2 and S3-S6 (except for brown marking on disc). Metabasitarsus white, metatarsomeres 2-5 dusky brown. Wing veins brown, paler towards base. Anterior surface of F5-F11 pale orange-brown with more apical flagellomeres increasingly darker; posterior surface of flagellum reddish brown.

Pubescence: White, thickened, dense on lower paraocular area, between antennal socket and compound eye, genal area, pronotum, anterior portion of mesoscutum, posterior margin of scutellum, mesopleuron, metanotum, dorsolateral area of propodeum, declivitous surface of T1, anterior 1/3 of T2-T7.

Sculpture: Microsculpture imbricate, strong on clypeus, weaker on paraocular and frontal areas and weakest on mesoscutum and metasomal terga. Punctures small and shallow; i=2–5d on clypeus, i=1–3d on supraclypeal area; irregularly spaced on malar area, i=0.5–4d apically, i=0.5–1d basally; difficult to discern on frontal area; irregularly shaped on mesoscutum, i=1–2d; i=2–4d on scutellum and metanotum; i~d on setose portions of metasomal terga. Horizontal surface of propodeum weakly rugulose for basal 1/3, otherwise granulose.

Structure: *Head*: Longer than mesosoma (90:75) and 1.5X as long as wide (90:57). Labrum broader than long (16:12), apex rounded. Mandible with subapical tooth small. Malar space more than three times as long as basal depth of mandible (32:9) and 4/5 as long as compound eye (32:40), malar line absent. Clypeus much longer than greatest breadth ignoring portion laterad of epistomal lobe (30:19); epistomal lobe and anterior tentorial pit strongly protruding into clypeus almost attaining apex. Compound eye broad, length to breadth 40:27, in profile its margin coincident with that of genal area ventrally; inner margin weakly concave; eyes converging below, UOD;LOD 32:27; lower ocular tangent near middle of supraclypeal area; upper ocular tangent just below lower margin of median ocellus. Genal and vertexal areas somewhat expanded, genal area half as wide as breadth of compound eye (16:32), ocelloccipital distance greater than diameter of lateral ocellus (~5:4); OOD:IOD 7:13. Scape less than three times as long as greatest width (12:5); pedicel slightly wider than long (6:5); Flagellomeres wider than long (6.5:5) except F11 with width and length subequal.

Mesosoma: Pronotum with collar poorly defined, anterior surface gradually curving to posterodorsal margin; ratio of lengths of scutellum:metanotum:horizontal surface of metapostnotum 13:9:13. Legs unmodified; hind tibial spurs long and narrow, inner spur half as long as metabasitarsus (16:32). Stigma with margin basal to vein R divergent, portion in marginal cell weakly concave.

Metasoma: Flattened, broadest at T3. S6 with apex angulate, bearing a short spine. *Terminalia*: As in figures 6–8. Proctiger well sclerotised but only narrowly so medially. S7 with weakly sclerotised, long, apical lobes, gradually widening towards rounded apex, with a few short, erect setae near apex; basal lobes absent. S8 narrow, more than twice as long as wide (30:12); apical lobe with narrow, almost cylindrical, slightly downturned apical process; lateral lobe posterolaterally directed, spiculum long, gradually narrowing. Gonobase lacking apicoventral process. Gonocoxa with dorsomedial margin forming a right angle at midlength and with obtuse angulation medially at base of gonostylus, concave between these two angulations; with short, broadly based medioventral lobe. Gonostylus weakly differentiated from gonocoxa; membranous subapical gonocoxal lobe elongate, surpassing posterior extremity of gonocoxa, outer margin convex, inner margin concave towards base, vertically oriented.

Female: As in male except for usual secondary sexual characteristics and as follows:

Colouration: Labrum suffused with brown; malar area with yellow reduced, brown attaining hypostomal area at margin of compound eye; legs with dark markings slightly more extensive; wing veins pale yellow-brown; metasomal terga with orange more extensive, covering over half of midlength of T2 and T3; metasomal sterna suffused with orange, lacking brown markings.

Pubescence: Mesotarsal rake of robust setae up to 4MOD in length. Tibial scopa with hairs $\leq$2MOD, a few apical setae robust and up to 3MOD in length. S2 with sparse scopa, hairs <2MOD.

Structure: Prementum 15X longer than greatest width (45:3). Maxillary palpus with 6 palpomeres of approximately equal length and width; labial palpus with 4 palpomeres approximately equal in length. Subapical mandibular tooth small but distinct.

Material Studied. Holotype male and one male paratype: PERU: Departamento Arequipa; Caravelli, Bella Unión, Quebrada Jahuay, 15°24’54”S 74°52’21”W, 198m, 22-24.x.2012, C. Carranza; one paratype female and one paratype male: PERU: Departamento Ica; Pampas de Nazca, South of Nazca Lines World Heritage Site; 14.78875°S 75.02109°W, 564m; pan traps, 12-19.vii.2009, L. Packer and J. Rivera.

The holotype and the male paratype from the same locality are deposited in MUSM where the female paratype will also be deposited pending further study. The second male paratype is at PCYU. The holotype is in good condition.

Etymology. This species is named after the locality where the first specimens were collected, just south of the Nazca Lines in Ica Department, Peru. The specific epithet is somewhat of a double entendre in that the long, narrow body form of the bee could be considered “linear”.

Floral hosts. Unknown, but the pans where the Nazca specimens were collected were set among *Tiquilia* sp. (Boraginaceae) which was almost the only plant in bloom at the locality at the time. This genus is the known host for *G. longiceps* (Packer, 2005). The floral host of the type species of the genus is *Heliotropium* also a member of the Boraginaceae (Michener & Rozen, 1999).

Comment. The two known localities for this species are approximately 80km from one another.

Geodiscelis phisquiri Packer and Dumesh, new species

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(Figures 10−15 and 19)

Diagnosis. The combination of malar space 0.8X as long as the compound eye (Fig. 10), metasoma with yellow bands (Fig. 10) and maxillary palpus unmodified (as in Fig. 3) separates this species from all other colletid bees. It is most similar to *G. longiceps* and *G. nazcalinea*. It can be separated from the former by having a malar space shorter than the length of the compound eye (longer in *G. longiceps*, compare Figs. 19 and 20). See diagnosis of *G. nazcalinea* for differentiation of *G. phisquiri* from that species.

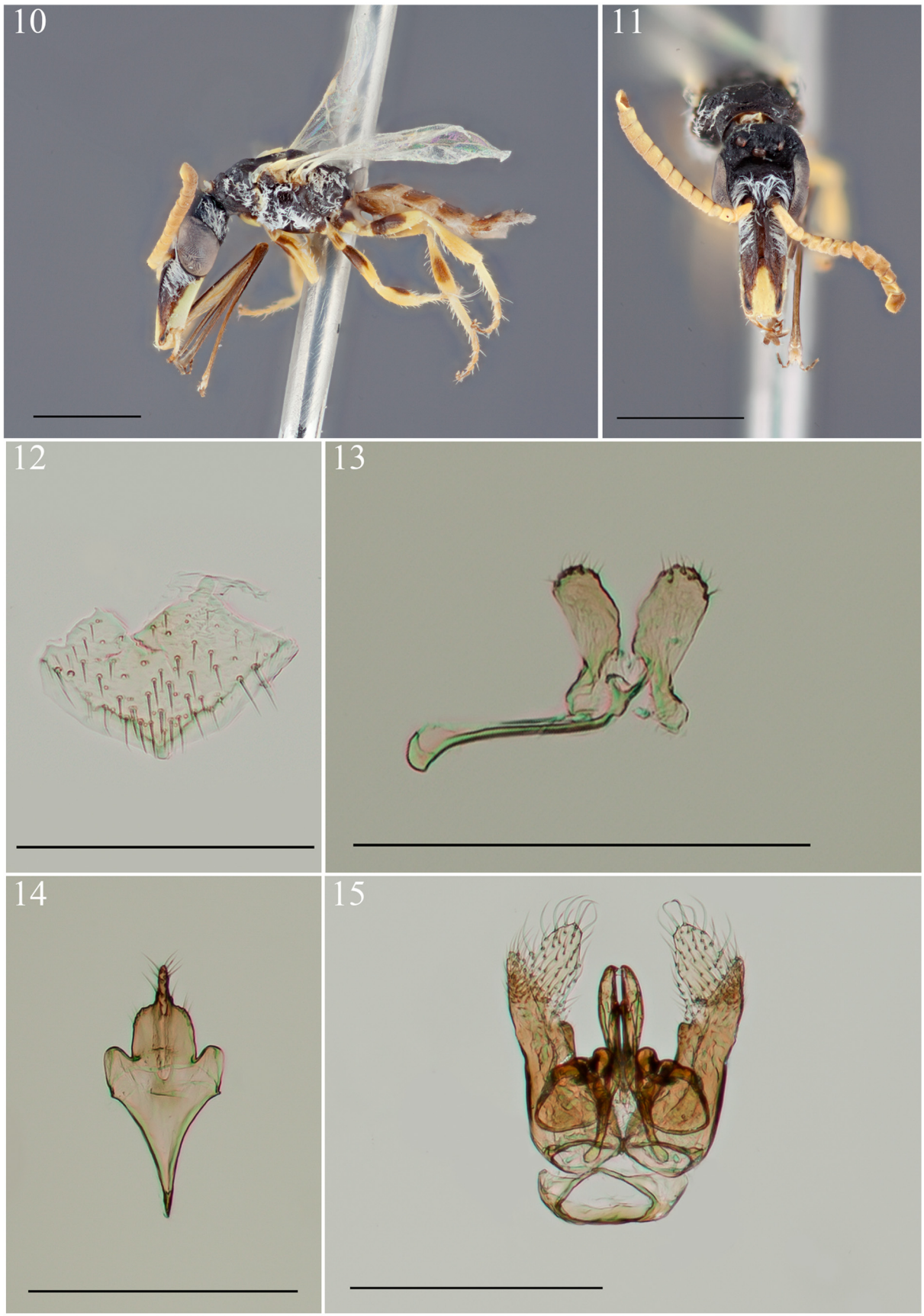
Description. Male: *Dimensions:* Body length 4.2mm, wing length 2.5mm, head width 0.7mm.

Colouration: Black with following parts pale yellow: labrum; mandible (apex amber); malar space (except narrowly dark brown adjacent to compound eye); clypeus (except for lateral and dorsal margins dark brown); hypostomal area apicad of compound eye for entire length laterad, for apical half mesad; antenna (except gradually darkening to yellow brown apically and for narrow dark bands on apices of posterior surfaces of F1-F10); narrow posterior band on pronotal lobe; mesal 1/3 of tegula; foreleg (except base of procoxa dark brown, orange-brown smudges on dorsal surface of protrochanter and on profemur dorsobasally and small ventral mark at midlength of protibia ventrally); midleg as foreleg (except dark markings darker and somewhat more extensive especially on mesocoxa, and mesopretarsus brown); apical 2/3 of metacoxa; apical ¼ of metafemur dorsally and apical 2/3 ventrally; metatibia (except for large posteroventral dark brown mark); metabasitarsus (metatarsomeres 2–4 orange, metapretarsus dark brown); wing veins pale yellow; apical ~1/3 of metasomal terga (except for narrow translucent marginal zones), margined anteriorly with pale brown forming irregularly undulate anterior margin; T2-T4 with small, dark brown, subcircular lateral maculae; metasomal sterna pale yellowish-brown except S1 largely darker brown.

Pubescence: White, thickened, dense on lower paraocular area, between antennal socket and compound eye, above antennal socket for somewhat more than a socket diameter, genal area, mesopleuron, dorsolateral area of propodeum, declivitous surface of T1, anterior <1/3 of T2-T7.

Sculpture: Surface somewhat shiny, shallowly imbricate. Punctures small and shallow; i=2–5d on clypeus; supraclypeal area with very few punctures; malar space irregularly punctate, i~0.5–1d apically, i=1–5d basally; frontal area punctures i=1–2d towards side, sparsely punctate medially and towards antennal sockets; punctures irregularly shaped on mesoscutum, i=1–2d; less irregular on scutellum and metanotum, i=1–2d; i~d on setose portions of metasomal terga. Horizontal surface of propodeum with few weak rugae basally, coarsely imbricate throughout.

Structure: *Head*: Longer than mesosoma (73:59) and more than 1.5X as long as wide (73:40). Labrum broader than long (11.5:9), apex rounded. Mandible with subapical tooth small. Malar space four times as long as basal depth of mandible (24:6) and 4/5 as long as compound eye (24:30), malar line absent. Clypeus almost twice as long as greatest breadth ignoring portion laterad of epistomal lobe (22:12); epistomal lobe strongly protruding into clypeus, almost attaining apex. Compound eye broad, length to breadth 30:20, in profile coincident with genal area ventrally; inner margin weakly concave; eyes converging below, UOD;LOD 23:19; lower ocular tangent near middle of supraclypeal area; upper ocular tangent just below lower margin of median ocellus. Genal area somewhat expanded, half as wide as breadth of compound eye (11:20). Ocelloccipital distance greater than diameter of lateral ocellus (~5:4); OOD:IOD 7:12. Scape twice as long as greatest width (11:5); pedicel as wide as long (5.5:5.5); F1 and F2 slightly wider than long (~5.5:5) (remaining flagellomeres distorted due to method of capture in only specimen available).



FIGURES 10−15. *Geodiscelis phisquiri* **sp. nov.**, male holotype. 10. Habitus, side view, 11. head, frontal view, 12. S6, 13. S7, 14. S8, 15. genital capsule. Scale bar = 1mm for Figs. 10, 11 and 15. Scale bar = 0.5mm for Figs. 12−14.

Mesosoma: Pronotum with collar poorly defined, anterior surface gradually curving to posterodorsal margin; ratio of scutellum:metanotum:horizontal portion of metapostnotum 10:6:9. Legs unmodified; hind tibial spurs long and narrow, inner spur approximately half as long as metabasitarsus (11:20). Stigma with margin basal to vein R divergent, portion in marginal cell straight.

Metasoma: Flattened, broadest at T3. S6 with apex obtusely angulate but lacking a spine.

Terminalia: As in figures 13–15 Proctiger well sclerotised but only narrowly so medially. S7 apical lobes moderately well sclerotised, somewhat rectangular, with few short, erect setae at apex; basal lobes absent. S8 narrow, more than twice as long as wide (18:7); apical process with narrow, laterally somewhat compressed, slightly downturned apical lobe; lateral lobe posteriorly directed, separated from apical lobe by narrow, angulate concavity; spiculum long, gradually narrowing. Gonobase lacking apicoventral process. Gonocoxa with dorsomedial margin forming an obtuse angle at midlength,right angular medially at base of gonostylus; small, obtusely rounded membranous medioventral lobe present. Gonostylus weakly differentiated from gonocoxa; membranous subapical gonocoxal lobe large, horizontally oriented, surpassing posterior extremity of gonocoxa, inner and outer margins convex, apex rounded.

Female: Unknown.

Material Studied. Holotype: CHILE, Region I, West of Chusmiza, 54km marker Hwy 15-CH, -19.79347 -69.32174, 2591m, 25.ix.-29.x.2013, L. Packer and S. Monckton, pan trap.

Etymology the specific epithet is the Aymara word for "fifth", referring to the fact that this is the fifth species described in the genus.

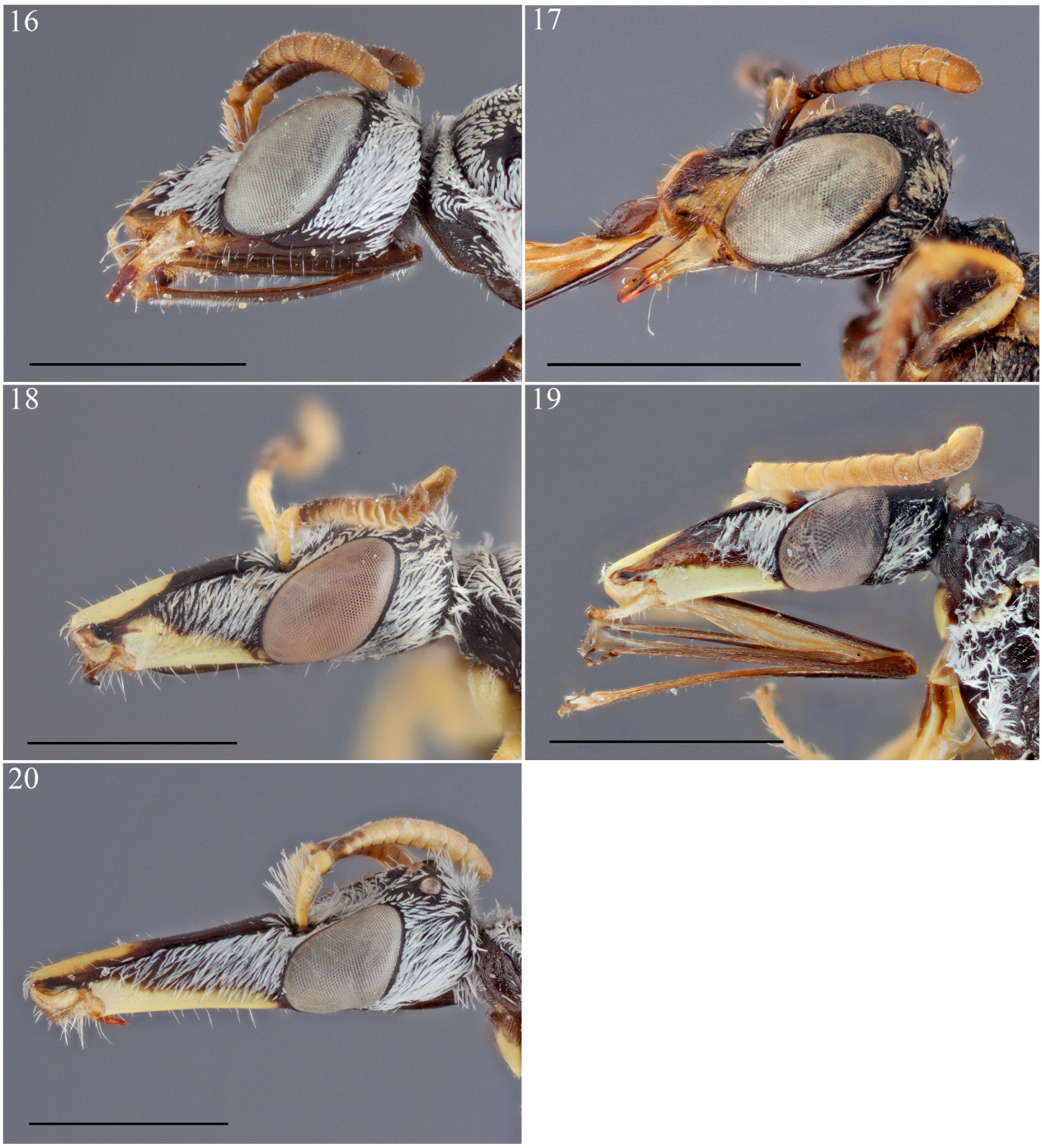
Comments. As is sometimes the case with small bees collected from pan traps that have been left out in the desert for a long period (in this instance 34 days), the only specimen of this species available is in bad condition. In particular, the frontal area is somewhat caved in, the flagellomeres are distorted and the metasoma somewhat crushed. However, it is worth noting that the thin exoskeleton of these bees often results in some distortion even with specimens collected directly from flowers and pinned later the same day. The sole specimen is clearly distinct at the species level based upon colouration and genitalic characters. Additional searching and trapping at the type locality up to the end of November 2013 failed to reveal any additional specimens.

New locality data for *Geodiscelis longiceps*

Since the description of this species (Packer, 2005), hundreds of additional specimens have been collected at the type locality, not all of which have been processed and labelled as of yet. Almost all were collected in pan traps. Here, we note an additional locality 500m higher up along the same road as the type locality: CHILE, Region II, -20.29873 -69.14114, 3004m, 06.ii.-0.iv.2013, Spencer Monckton and James Postlethwaite, pan traps, 2 males and 18 females (PCYU, PUCV).

Key to the Subgenera and Species of *Geodiscelis*

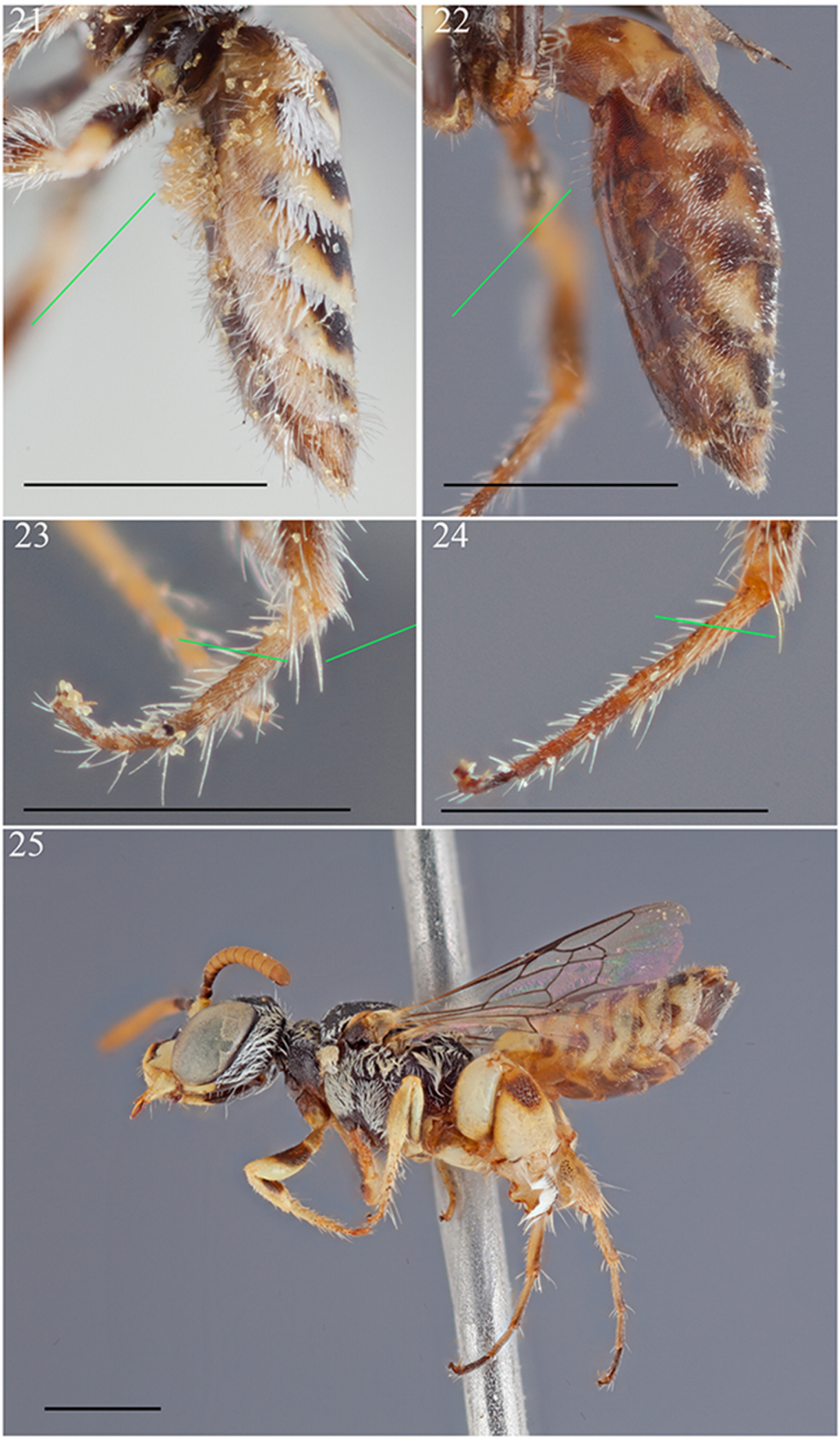
1. Malar space at most only slightly longer than wide (Figs. 16 and 17) 2
- Malar space at least 3 times longer than wide (Figs. 18–20) . . . . . .(subgenus *Nazcoediscelis)* ...3



FIGURES 16–20. Head, side view of males of *Geodiscelis megacephala*, *G. thaumaskelos*, *G. nazcalinea* **sp. nov.**, *G. phisquiri* **sp. nov.** and *G. longiceps* respectively. Scale bar = 1mm.

2. Female with well-developed scopa on S2 (Fig. 21) and two hind tibial spurs (Fig. 23); male with hind legs unmodified (as in Figs. 1 and 10); metasoma of both sexes with distinct basal bands of thick, almost squamose, pubescence (Fig. 21) . . . . . *G.* (*Geodiscelis*) *megacephala* Michener & Rozen, 1999

- Female S2 almost glabrous (Fig. 22) and with only one hind tibial spur (Fig. 24); male with metafemur, metatibia and metabasitarsus considerably swollen (Fig. 25); metasoma in both sexes lacking distinct pubescent bands (Figs. 22 and 27).. . . . . *G.* (*Thaumoediscelis*) *thaumaskelos* Packer, 2009



FIGURES 21–25. *Geodiscelis* 21 and 22: metasoma side views to show development of sternal scopa in *G. megacephala* and it reduced nature in *G. thaumaskelos*. 23 and 24. Apex of metatibiae to show metatibial spurs, two in Fig. 23 of *G. megacephala* and one in Fig. 24 of *G. thaumaskelos*. 25. *G. thaumaskelos* male side view to show enormously enlarged metafemur, metatibia and metabasitarsus. Scale bar = 1mm.

3. Malar space longer than compound eye (Fig. 20). . . . . *G.* (*Nazcoediscelis) longiceps* Packer, 2005
- Malar space shorter than compound eye (Figs. 18 and 19). 4
4. F1 dark except narrowly ventrally (Fig. 2); wing veins mostly brown (Fig. 1); male S6 with apicomedian spine (Fig. 5). . . . . *G.* (*Nazcoediscelis*) *nazcalinea* Packer & Dumesh, **sp. nov.**.
- F1 (Fig. 11) and wing veins (Fig. 10) yellow; male S6 apicomedially obtusely angulate, not spinose (Fig. 12). . . . . *G. phisquiri* Packer & Dumesh, **sp. nov.**

Phylogeny

The characters and their states are enumerated in appendix 1 and the data matrix is shown in table 1. One most parsimonious tree was obtained with 156 steps, CI =71 and RI = 80 (Fig. 26). It shows the expected relationship among genera: *Xenochilicola* (*Patagonicola* (*Geodiscelis* + *Xeromelissa*)) and was stable to successive approximations character weighting wherein the weights stabilized after a single iteration. Monophyly of *Patagonicola* and *Xeromelissa* and the sister relationship of *Geodiscelis* + *Xeromelissa* were all strongly supported (≥82 in all cases for both GC and BS). *Geodiscelis* itself was less strongly supported (GC=35, BS=55) but within *Geodiscelis*, the grouping of *G. megacephala* with the long headed species and the monophyly of the subgenus *Nazcoediscelis* were both very strongly supported (≥98 for both measures of support).

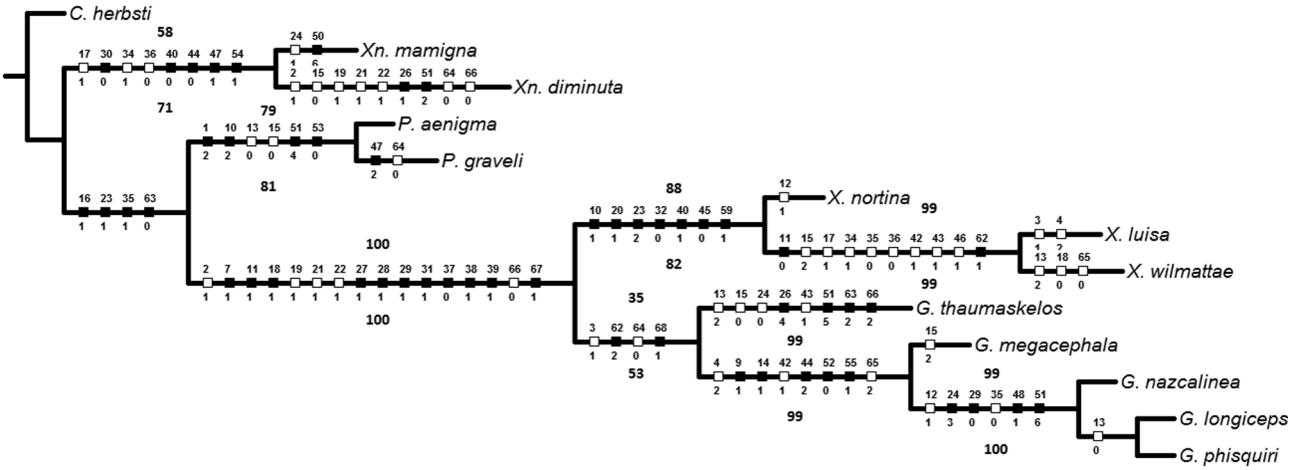
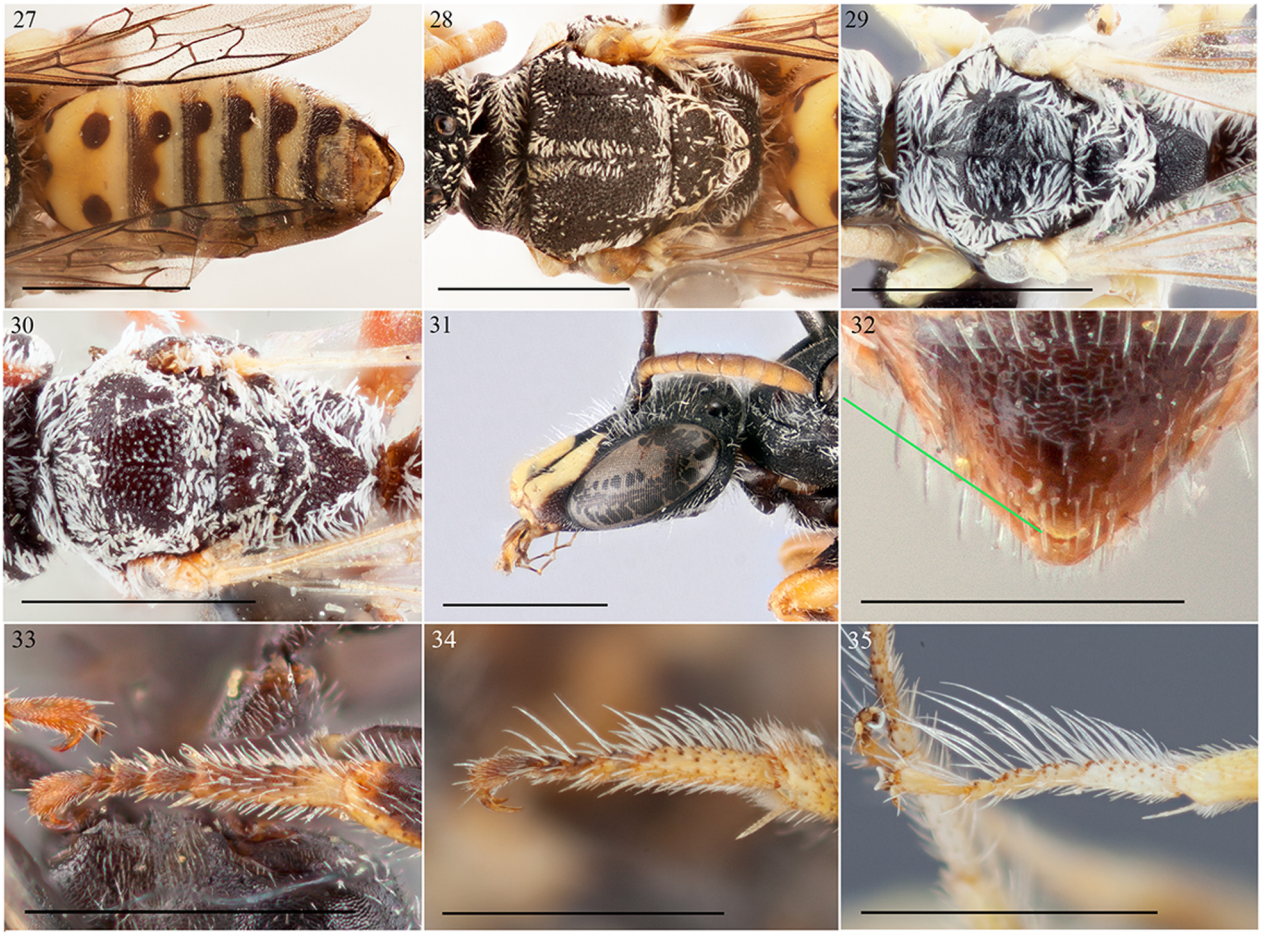


FIGURE 26. Phylogeny for xeromelissine genera related to *Geodiscelis* and for the species of *Geodiscelis*. Filled in squares represent unique synapomorphies, open squares indicate homoplasious apomorphies. Small numbers above and below the squares indicate the character number and state, respectively, as given in the appendix. Large numbers above and below the internodes are GC values and BS percentages respectively, see text for further explanation.

Unique synapomorphies supporting the monophyly of *Geodiscelis* are (plesiomorphic states in brackets): pubescence on head and mesosoma largely made up of somewhat squamose pubescence (Figs. 28–30) (hairs generally finer although often somewhat woolly, as in Fig. 31), mesotrochanteral comb absent (present), mesotarsal rake present and strong (Fig. 35) (absent or weak, Figs. 33 and 34) and metatibial spur fine and long, approximately half as long as metabasitarsus or longer (Fig. 23) (robust, shorter than 0.5X length of metabasitarsus). Monophyly of *Geodiscelis* minus *G. thaumaskelos* is supported by metasomal terga with basal hair bands of appressed squamose pubescence (Fig. 21) (no basal hair bands, Figs. 22 and 27); horizontal surface of metapostnotum subequal in length to scutellum (Figs. 29 and 30) (shorter, Fig. 28); proctiger with sclerotization extending towards, or attaining, midline (Fig. 4) (sclerotized portions well separated); S7 apicodorsal lobe simple in structure and flat (Figs. 6 and 13) (digitiform or more complex in shape); gonobase apicoventral margin lacking process (Fig. 15) (process present) and gonocoxa with inner dorsal angulation near base of gonostylus (Figs. 8 and 15) (angle absent). The long headed clade is supported by male proctiger sclerotized to midline (Fig. 4) (at least narrowly separated medially); male S6 apicomedially angulate to spinose (Figs. 5 and 12) (rounded, Fig. 32); S8 with apical process of apical lobe elongate, gradually narrowing to apex (Figs. 7 and 14) and, unsurprisingly, the malar area at least three times longer than basal width in both sexes (Figs. 18 –20) (at most subequal to basal width, Figs. 16 and 17).



FIGURES 27–35. Figures illustrating phylogenetic character states (in brackets), see appendix 1 for details. 27. *Geodiscelis thaumaskelos* male metasoma (8-1 and 9-1), 28. *G. thaumaskelos* mesoscutum to show surface sculpture (14-0, 15-0), 29. *G. nazcalinea* **sp. nov.** mesoscutum to show surface sculpture (14-1, 15-1), 30. *G. megacephala* mesoscutum to show surface sculpture (15-2), 31. *Patagonicola aenigma* head side view to show long compound eye (31-0), 32. *G. megacephala* S6 to show absence of apical angulation or spine (48-0), 33. *Patagonicola aenigma* mesotarsus to show absence of rake (62-0); 34. *Xeromelissa wilmattae* mesotarsus to show weakly developed rake (62-1); 35. *G. longiceps* to show strongly developed mesotarsal rake (62-2). Scale bar = 1mm for Figs. 27–31, 33–35. Scale bar = 0.5mm for Fig. 32.

TABLE 1. Phylogenetic data matrix for specimens used in analysis.

.

	1111111111222222222233333333334444444444555555555566666666
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678
Chilicola herbsti	00000000002010100000000?0002101102110022001100014311000000000110100
Xenochilicola diminuta	11021100002010001010110211002001012010002000101005212100040100102000
Xn. mamigna	10020100002010101000000110002001012010002000101006012100050000112100
Patagonicola aenigma	20010000022000010000001213002101101110020001100005410000040000010100
P. graveli	20011000022000010000001213002101101110020001102005410000040100001100
Geodiscelis longiceps	01121110101101110110111302110111000101123102120103 60?012020112002011
G. nazcalinea	01121110101111110110111302110111000 10___2102120103 60?01202011200_0_1
G. phisquiri	01121110101101110110111302110111000 10___2_0212010360?0120201_____
G. thaumaskelos	11111111001020010110110?5111111001101121011100001513002100112201011
G. megacephala	01121110101011210110111202111111001101123102110003 00?012020112002011
Xeromelissa nortina	01011111011110110111112202111110001101112001000022712001131100011010
X. luisa	11121111010010211111112112111110010001113111010030112001111111011010
X. wilmattae	11011111010020211011112 0?2111110010001113111010030112001111111010010

Discussion

The two new species described herein do not add considerably to the morphological variability found among *Geodiscelis* species because neither are as extremely modified as *G. longiceps*, the species to which they are most closely related. Within the genus, only *G. thaumaskelos* has remarkably enlarged hindlegs in the male, it is also the only species with the female metasomal scopa almost entirely absent and metasoma with basal bands of appressed, almost squamose pubescence absent.

Geodiscelis megacephala was the first xeromelissine found to nest in the ground (Michener & Rozen, 1999). Subsequently, Packer (2004) found *Xeromelissa australis* (Toro & Moldenke, 1979) nesting in loose sand. *Geodiscelis longiceps* was also found associated with loose sand and, although nests were not located, the strong brushes of hairs on the pro- and mesotarsi were considered as "tarsal rakes" for movement of sand.

Packer (2009) noted this broad morphological variability within the genus but declined to suggest a subgeneric level classification which would have required three monotypic subgenera. With the discovery of two additional species that clearly form a monophyletic group with one of the extreme forms, such reticence may no longer be warranted. The results of the phylogenetic analysis as well as some of the diagnostic features for the different groupings also seem to support the view that subgeneric level differentiation might usefully be applied to these bees. Consequently, we divide *Geodiscelis* into three subgenera. In the descriptions of these subgenera below, only characters that vary within the genus are considered.

Subgenus *Geodiscelis* Michener & Rozen

Type species. *Geodiscelis megacephala* Michener & Rozen, 1999. By original designation.

Diagnosis. The combination of pale metasomal markings present, maxillary palpus with all 6 palpomeres similarly robust, length of malar space subequal to basal depth of mandible and malar line lacking is diagnostic among Xeromelissinae for the only known species in this subgenus. Some *Xeromelissa* species are similar in all but the palpal character, *Xenochilicola diminuta* is similar except in possessing a malar line. Other xeromelissines except *Xeromelissa and Xn. diminuta* lack the pale metasomal banding. Other subgenera of *Geodiscelis* either have a linear malar space or one that is more than three times as long as the basal width of the mandible.

Description. Lower paraocular area black. Male protibia entirely or almost entirely yellow. Metasomal terga with pale subapical integumental bands, basal bands of appressed squamose pubescence present, minute silvery hairs absent. Clypeus and lower paraocular area shiny, lacking distinct imbricate microsculpture. Frontal area with interspaces similar to puncture diameters. Mesoscutum shiny, microsculpture absent; punctures transversely effaced. Galeal comb teeth absent. Mandible with small preapical tooth. Malar space present but short. Anterior tentorial pit elongate, almost attaining apex of clypeus. Supraclypeal area strongly curved in profile. Metasternum between metacoxae very narrow, at least 1.5X as long as maximum width, which is $\leq$1MOD. First abscissa of M+Cu of hind wing shorter than 2nd abscissa. Male hindleg unmodified, narrow; both sexes with two metatibial spurs. Horizontal surface of metapostnotum subequal in length to scutellum. Sclerotized portion of proctiger narrowly interrupted medially. Male S6 with apex rounded. S7 apicodorsal lobe simple, flat. S8 apical process narrow, elongate, broadened towards apex; posterior margin of lateral lobe transverse. Gonobase with apicoventral rim lacking a median process. Gonoforceps with subapical medial angulation. Gonostylus short, narrow; retrorse lobe considerably elongate, narrowing to apex. Female sternal scopa well developed.

Included species. *Geodiscelis megacephala* Michener and Rozen 2000.

Comment. As currently understood, this subgenus is restricted to semi-arid regions of western Argentina and visits *Heliotropium* flowers (Michener & Rozen, 2000).

Geodiscelis (Thaumoediscelis) Packer and Dumesh, new subgenus

urn:lsid:zoobank.org:act:50D34864-9C61-491D-9713-5C53CE4468F2

Type species. *Geodiscelis thaumaskelos* Packer, 2009. Here designated.

Diagnosis. This is the only xeromelissine with a single metatibial spur. This character works for both sexes but

the male has a truncate process where the outer metatibial spur would be, this process is immovably fused to the tibia. Each sex has additional diagnostic characteristics: the male hind leg is enormously modified and the metabasitarsus in particular is uniquely modified, being as wide as it is long, deeply concave on the anterior surface and trilobed—no other bee known to us has such an unusually modified metabasitarsus; the female S2 is almost glabrous, which is unique among the xeromelissines.

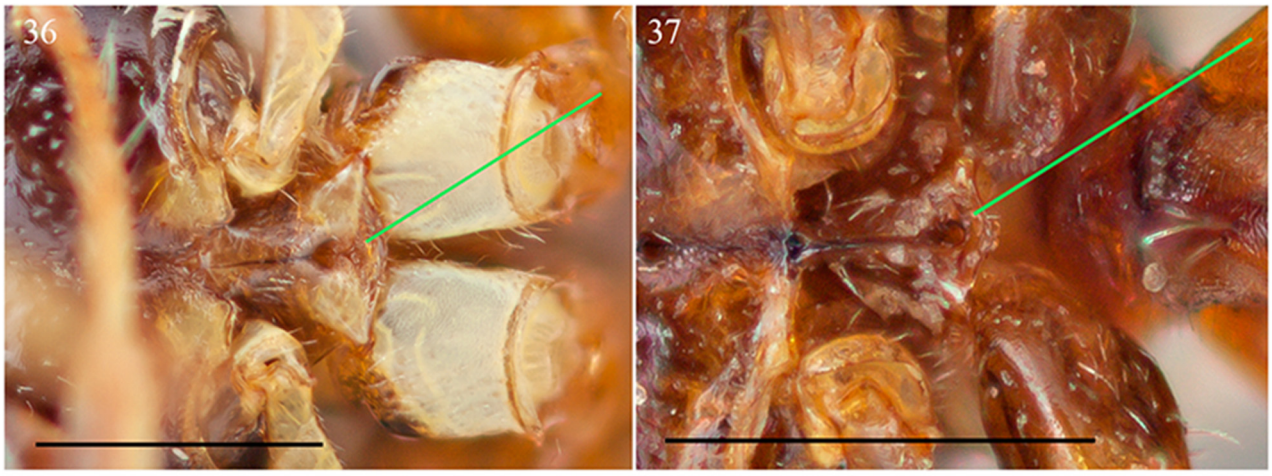
Description. Both sexes with extensive yellow on lower paraocular area. Male protibia black basally. Metasomal terga mostly pale, dark areas mostly maroon; lacking basal bands of appressed squamose pubescence, minute silvery hairs present. Clypeus and lower paraocular area shiny, lacking distinct imbricate microsculpture. Frontal area and mesoscutum with punctures crowded, dull. Galeal comb with a few teeth. Mandible with well developed subapical tooth. Malar space absent. Anterior tentorial pit elongate, almost attaining apex of clypeus. Supraclypeal area strongly concave in profile. Metasternum between metacoxae broad, as wide as long (both measurements >2MOD) widening posteriorly in male, narrower in female (L:B 1.2:1 both <1.5MOD). First abscissa of M+Cu of hind wing subequal in length to 2nd. Male hindleg considerably modified, femur and tibia strongly swollen, basitarsus with complex structure. Both sexes lacking inner metatibial spur; male with robust process where inner metatibial spur might be expected but this immovably fused to tibia. Horizontal surface of metapostnotum shorter than scutellum, longer than metanotum. Sclerotized portion of proctiger, widely separated, not extending mesad. Male S6 with apex rounded. S7 apicodorsal lobe narrowly extended posteriorly, margin with row of hairs, bearing hair tuft anteriorly. S8 apical process narrowly oval; posterior margin of lateral lobe transverse with posteriorly oriented convexity laterad. Gonobase with apicoventral rim with large median process broadening from base to apex. Gonoforceps without subapical medial angulation. Gonostylus moderately long, broad, curved posteromesad; retrorse lobe large, broad. Female sternal scopa considerably reduced, S2 almost glabrous.

Included species. *Geodiscelis thaumaskelos* Packer 2009.

Etymology. The subgeneric name is a combination of the specific epithet—*thaumaskelos* and *Oediscelis*, a genus-group name within the Xeromelissinae that means “swollen thighs”: a descriptor that applies only to this species within the genus.

Comments. This subgenus is known only from an arid valley in western Argentina and contains the southernmost species in the genus.

An interesting observation not previously made concerning this taxon is sexual dimorphism in the form of the metasternum. In the male it is considerably broadened posteriorly and almost on the same plane as the mesopleuron immediately in front of it (Fig. 36). In the female, it is much narrower, not considerably expanded posteriorly, and recessed dorsad (Fig. 37). The metasternum of the female is most similar to that of related species and genera and the unusual modification of the male is undoubtedly an autapomorphy associated with the extreme modifications of the hind legs.



FIGURES 36–37. *Geodiscelis thaumaskelos* mesosomal venter to show sexual dimorphism in metasternum. 36. Male; 37. Female. Scale bar = 0.5mm. Note that the magnification differs between the two images.

***Geodiscelis (Nazcoediscelis)* Packer and Dumesh, new subgenus**
urn:lsid:zoobank.org:act:0249B978-22A9-4919-95D9-A54EE618DE33

Type species. *Geodiscelis nazcalinea* Packer & Dumesh **sp. nov.** Here designated.

Diagnosis. The combination of metasoma with pale subapical transverse bands, maxillary palpus with all 6 palpomeres similarly robust and malar space at least 3X as long as the basal depth of the mandible is sufficient to identify any colletid bee as belonging to this subgenus. Additionally, the males have S6 obtusely angulate or with a spine apicomedially.

Description. Lower paraocular area black. Male protibia entirely or almost entirely yellow. Metasomal terga with pale subapical integumental bands, basal bands of appressed squamose pubescence present, minute silvery hairs absent. Clypeus and lower paraocular area dull due to imbricate microsculpture. Frontal area with interspaces equal to or greater than puncture diameters. Mesoscutum somewhat shiny, microsculpture imbricate; punctures transversely effaced. Galeal comb teeth absent. Mandible with subapical tooth small to absent. Malar space enormous, at least three time as long as basal depth of mandible. Anterior tentorial pit elongate, almost attaining apex of clypeus. Supraclypeal area mostly flat. Metasternum between metacoxae very narrow, width subequal to MOD. First abscissa of M+Cu of hind wing shorter than 2nd abscissa. Male hindleg unmodified, narrow; both sexes with two metatibial spurs. Horizontal surface of metapostnotum subequal in length to scutellum. Sclerotized portion of proctiger undivided medially. Male S6 with apex angulate or spinose. S7 apicodorsal lobe simple, flat. S8 apical process narrowing to apex; posterior margin of lateral lobe narrowly concave, posterior convexity laterad. Gonobase with apicoventral rim lacking a median process. Gonoforceps with subapical medial angulation. Gonostylus short, narrow; retrorse lobe broad, rounded. Female sternal scopa well developed.

Included species. *Geodiscelis longiceps* Packer, 2005, *G. nazcalinea* Packer & Dumesh, **sp. nov.** and *G. phisquiri* Packer & Dumesh **sp. nov.**

Etymology. The name is derived from that of the type species, which was first found very near to the famous Nazca lines in Peru, combined with *Oediscelis*.

Comments. This subgenus is known only from west of the peaks of the Andes mountains and occurs from the coastal plains of Peru to moderate altitude on the western slopes of the mountains in Chile. The enormously elongate head is undoubtedly related to the need to obtain nectar from Boraginaceae with deep nectaries. Similarly elongate heads are known in a few species of *Xeromelissa* where additional mouthpart elongation arises primarily through lengthening of the maxillary palpus. In contrast, the maxillary palpi of *Geodiscelis (Nazcoediscelis)* are unmodified, as is the case in all xeromelissine genera except *Xeromelissa* (although they are elongate in some species of *Chilicola* (*Hylaeosoma*)); *Geodiscelis (Nazcoediscelis)* have the cardines, stipites and prementum all extremely elongate.

While three subgenera may seem excessive for a genus containing only 5 species at present, the enormous diversity found within these few species would seem to justify recognizing them at this rank. It is perhaps worth noting that there are 170 monotypic subgenera, and almost 100 monotypic genera, among the bees (Ascher & Pickering, 2013).

All *Geodiscelis* species have been found associated with flowers of *Heliotropium* or *Tiquilia*, both members of the Boraginaceae. There are numerous species in this group of plants in the region encompassed by known records of *Geodiscelis* and additional searching among their flowers will undoubtedly result in the discovery of more undescribed bees.

Following more exhaustive searches for these interesting little bees and the discovery of more species, a formal biogeographic analysis might be of interest. Currently, the two short headed subgenera are from Argentina whereas species of the long headed subgenus are from west of the Andes.

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APPENDIX 1.

Characters 1−59 were scored from males, 60−68 were scored from females although due to a lack of sexual dimorphism, *G. phisquiri* **sp. nov.** was scored for some of them despite being known only from the male on the basis of a lack of sexual dimorphism in the same characters for the other included species.

1 Paraocular area colour: 0 dark (Fig. 2); 1 with yellow that does not attain lower margin of antennal socket (Fig. 17); 2 yellow attaining lower margin of antennal socket (Fig. 31).

2 Malar area colour: 0 dark (Fig. 31); 1 with yellow (Figs. 2 and 11).

3 Profemur colour: 0 with some yellow (Packer, 2014, Fig. 7); 1 all yellow, or yellow except dorsobasally (Figs. 1 and 10).

4 Protibia colour: 0 anterior surface yellow; 1 more than anterior surface yellow but with some dark areas (Fig. 10); 2 all yellow (Fig. 1).
5 Metasoma with pale integumental transverse subapical bands: 0 absent (Packer, 2014, Fig. 7); 1 present (as in Fig. 9).
6 Pubescence on paraocular area and anteriorly on mesoscutum: 0 erect to subappressed (Packer, 2014, Fig. 8); 1 mostly appressed (Figs. 2 and 9).
7 Metanotal pubescence density: 0 normal, underlying surface readily visible (Packer, 2014, Fig. 6); 1 dense mostly hiding underlying surface (as in Fig. 9).
8 Tergal surface with silvery hairs: 0 absent (Fig. 9); 1 present (as in Fig. 22).
9 Tergal basal hair bands: 0 absent (as in Fig. 22); 1 present (as in Fig. 9).
10 Tergal apicolateral hair patches: 0 absent (Fig. 22); 1 present on T1 (Packer, 2014, Fig. 27); 2 present on T1-T3 (Packer, 2014, Fig. 7).
11 Labral punctures (apicomedian puncture patch excepted): 0 none; 1 sparse, most interspaces several times diameter of adjacent punctures; 2 dense, most interspaces punctures subequal to diameter of adjacent punctures (as in Gibbs & Packer, 2006, Fig. 9A).
12 Clypeus and paraocular area: 0 not imbricate, shiny (Packer, 2014, Fig. 2); 1 imbricate, at least somewhat dull (Fig. 2).
13 Frontal area punctures: 0 i>d; 1 i~d; 2 crowded.
14 Mesoscutal punctures effaced: 0 no (Figs. 28 and 30); 1 yes (Fig. 29).
15 Mesoscutal microsculpture: 0 strong, surface dull (Fig. 28); 1 moderate, surface shiny despite presence of distinct microsculpture (Fig. 29); 2 absent, surface glassy (Fig. 30).
16 Metasomal tergal punctures: 0 distinct; 1 obscure and shallow.
17 T1 puncture density subapically: 0 sparse, interspaces clearly greater than puncture diameter; 1 dense, with space between punctures subequal to their diameters.
18 Labrum shape: 0 transverse, twice as wide as long (as in Gibbs & Packer, 2006, Fig. 9A); 1 more elongate, at most 1.5X as wide as long (as in Toro & Moldenke, 1979, Fig. 343).
19 Labrum, apical margin: 0 straight (as in Toro & Moldenke, 1979, Fig. 286); 1 convex (as in Toro & Moldenke 1979, Fig. 343).
20 Maxillary palpomeres 1–3 distinctly more robust than 4–6: 0 no (Packer, 2014, Fig. 26); 1 yes (Packer, 2014, Fig. 22).
21 Lacinia, length: 0 short, at most ~3X as long as wide; 1 much more than 3X as long as wide.
22 Prementum in cross section: 0 broad, at least twice as wide as deep subapically; 1 narrow, not much wider than deep subapically.
23 Clypeus, apically around labrum: 0 obtuse; 1 right angular; 2 curved around labrum.
24 Malar space: 0 absent (Fig. 17); 1 shorter than basal depth of mandible; 2 longer than but at most 1.5X as long as depth of mandible (Fig. 16); 3 enormous, at least three times longer than depth of mandible (Figs. 18–21).
25 Malar line: 0 absent (Figs. 18–21); 1 present (as in Michener, 2007, Fig. 46-3g). This character was scored as inapplicable for taxa with the malar space absent.
26 Anterior tentorial pit: 0 small, round; 1 comma-shaped (as in Packer, 2008, Fig. 2); 2 extremely elongate (Fig. 2); 3 at the end of a side branch to the epistomal suture (Packer, 2014, Fig. 23); 4 long and deep (Packer, 2009, Fig. 9). The pit is on, or adjacent to, the epistomal suture unless stated otherwise.
27 Epistomal lobe produced as a narrow lobe that is recurved laterally setting off a lateral clypeal flange: 0 no (Packer, 2014, Fig. 1); 1 yes (Fig. 2).
28 Face strongly produced: 0 no (Fig. 31); 1 yes (Figs. 16–20).
29 Supraclypeal area profile: 0 flat except depressed towards frontal area above (Fig. 3); 1 convex throughout (Fig. 18); 2 flat throughout (Fig. 20).
30 Inner eye margins: 0 strongly convergent below, not concave (Packer & Genaro, 2005, Figs. 1–3); 1 not strongly convergent below, concave (Fig. 2).
31 Eye shape in lateral view: 0 elongate, length more than twice maximum width (Fig. 31); 1 short, length less than twice maximum width (Figs. 16–20).
32 Ratio of ocellocular distance to diameter of lateral ocellus: 0 ~1:1 (Packer & Genaro, 2007, Fig. 5C); 1 clearly >1:1 (Packer & Genaro, 2007, Fig. 16C).
33 Hypostomal carina in profile: 0 straight; 1 convex (Packer, 2014, Fig. 48).
34 Number of flagellomeres that are very short (approximately 3 times wider than long): 0 none or one (as in Fig. 3); 1 two or more (Michener, 2007, Fig. 46-5).
35 Anterior surface of pronotal collar, orientation medially: 0 strongly posterodorsal (Figs. 18–20); 1 weakly posterodorsal (Fig. 16); 2 vertical .
36 Pronotal collar: 0 absent, posterior margin of pronotum sharp (Packer, 2014, Fig. 31); 1 with distinct horizontal surface (Fig. 16).
37 Posterolateral portion of propleuron with incision to receive pronotum: 0 no; 1 yes.
38 Prosternum shape: 0 cruciform; 1 diamond. This character, and the two following ones, could not be scored for the two new species described herein because of a shortage of material for destructive dissection.
39 Procoxal articulatory lobe: 0 short and broad (Packer, 2008, Fig. 4E); 1 long and narrow (Packer, 2008, Fig. 4D).
40 Mesophragma shape: 0 short (Packer, 2008, Fig. 4G); 1 long, broad; 2 long, narrow (Packer, 2008, Fig. 4J).

41 Metasternum at mesocoxae: 0 wider than long posteriorly (Packer, 2014, Fig. 47); 1 approximately as wide as long (Fig. 36); 2 slightly narrower than long (Packer, 2014, Fig. 50); 3 at least 1.5X longer than wide (as in Packer, 2008, Fig. 7N).
42 M+Cu length of 2nd abscissa relative to that of 1st: 0 subequal (as in Michener, 2007, Fig. 46-2a); 1 2nd longer (as in Michener, 2007, Fig. 46-2b).
43 Metafemur and metatibia form: 0 narrow (Fig. 10); 1 noticeably swollen (Fig. 25).
44 Horizontal surface of metapostnotum length: 0 subequal in length or shorter than metanotum (Packer, 2014, Fig. 6); 1 longer than metanotum but clearly shorter than scutellum (Packer, 2014, Fig. 5); 2 approximately as long as scutellum (as in Fig. 9).
45 Metapostnotum-propodeum profile: 0 gradually curved; 1 strongly curved at apex of horizontal surface of metapostnotum (Fig. 1).
46 Proctiger, separation of two sclerotized sides: 0 widely separated, no transverse portion (Packer, 2005, Fig. 8); 1 narrowly separated, with transverse portion incomplete (Packer, 2005, Fig. 7); 2 entire (Fig. 4).
47 S4: 0 unmodified, lacking spines or processes (Fig. 1); 1 with two lobate processes (Packer, 2014, Fig. 18); 2 with two spines (Packer, 2014, Fig. 15).
48 S6 apex: 0 rounded (Fig. 32); 1 angulate or with apical spine (Figs. 5 and 12).
49 S7 ventral lobes: 0 absent to minute (Packer, 2014, Fig. 16); 1 present, laterally oriented, acutely triangular (as in Packer, 2008, Fig 10G); 2 present, rectangular (Toro & Moldenke 1979, Fig. 345); 3 present, long, apex rounded (Toro & Moldenke, 1979, Fig. 299).
50 S7 apicodorsal lobe: 0 digitiform, with short hairs (Toro & Moldenke, 1979, Fig. 299); 1 narrowly pointed, with long hairs apically and basally (Packer, 2009, Fig. 6); 2 conical, short, glabrous (Toro & Moldenke, 1979, Fig. 345); 3 flat, elongate, broad, glabrous or almost so (Figs. 6 and 13); 4 flat, moderately short, rounded, with long hairs (Toro & Moldenke, 1979, Fig. 186); 5 short, blunt, somewhat dorsally oriented, glabrous (Packer, 2014, Fig. 16); 6 flat, broad, auricular, membranous, with very short hairs ventrally (Genaro & Packer, 2005, Fig. 10).
51 S8 apical process: 0 elongate, narrow, broadened at apex (Michener & Rozen, 1999, Fig. 8); 1 abruptly narrowing subapically to an elongate, narrow rod (Toro & Moldenke, 1979, Fig. 292); 2 short, narrowly rounded (Genaro & Packer, 2005, Fig. 16); 3 broad, flat, parallel sided to truncate apex (Toro & Moldenke, 1979, Fig. 187); 4 very short, not extending posterior to lateral lobes (Packer, 2014, Fig. 17); 5 abruptly narrowed to elongate oval apex (Packer, 2009, Fig. 7); 6 gradually narrowed (Figs. 7 and 14); 7 short, broadly rounded (Toro & Moldenke, 1979, Fig. 342). The apical lobe extends beyond the lateral lobes unless stated otherwise.
52 Gonobase, apicoventral rim process: 0 absent (Fig. 15); 1 present (Packer, 2009, Fig. 8).
53 Gonobase, apicoventral rim process: 0 very broad, appearing as two separate lobes (Packer, 2014, Fig. 19); 1 broad but not appearing as two lobes (Toro & Moldenke, 1979, Fig. 184); 2 narrow (Packer, 2014, Fig. 51); 3 broadest at apex (Packer, 2009, Fig. 8). The sides of the process are subparallel or apically narrowing unless stated otherwise.
54 Gonobase anterior margin; 0 not deeply concave (Fig. 8); 1 deeply concave (Packer, 2014, Fig. 51).
55 Gonocoxa posteromedially: 0 not angulate (Packer, 2009, Fig. 8); 1 angulate (Figs. 8 and 15). This is least developed in *G. nazcalinea* where the angle is obtuse (Fig. 8), in the other taxa possessing state 1 it is approximately right angular (Fig. 15).
56 Gonocoxa with apicomedial lobe: 0 absent (Genaro & Packer, 2005, Fig. 17); 1 present, small (Toro & Moldenke, 1979, Fig. 291); 2 present, large (Figs. 8 and 15).
57 Gonostylus, demarcation from gonocoxa: 0 indistinct (Figs. 8 and 15); 1 distinct (Packer, 2009, Fig. 8).
58 Gonostylus form: 0 short and round, posteriorly oriented (Packer, 2009, Fig. 8); 1 narrow, short, posteromedially oriented (Toro & Moldenke, 1979, Fig. 291); 2 short, narrowing to apex, posteriorly oriented (Figs. 8 and 15); 3 moderately long, parallel-sided, posteriorly oriented (Toro & Moldenke, 1979, Fig. 344); 4 somewhat triangular with rounded apex, moderate length, posteriorly oriented (Packer, 2014, Figs. 19 & 51); 5 somewhat triangular, short, posteromedially oriented.
59 Volsella, cuspis: 0 mostly not covered ventrally by gonocoxa (Fig. 8); 1 mostly covered by gonocoxa (Toro & Moldenke, 1979, Fig. 291).
60 Clypeus colour: 0 entirely dark (Packer, 2014, Fig. 10); 1 pale marked (Figs. 16–20).
61 Protarsal rake: 0 absent; 1 present.
62 Mesotarsal rake: 0 absent (Fig. 33); 1 present with one long hair per tarsomere (Fig. 34); 2 present with more than one long hair per tarsomere (Fig. 35).
63 Scopa on S2: 0 entire (Fig. 21); 1 corbiculate (Packer, 2014, Fig. 52); 2 reduced to a few hairs (Fig. 22).
64 Frontal line below: 0 not strongly carinate; 1strongly carinate.
65 Galeal comb teeth: 0 >10; 1 1–9; 2 0.
66 Premental fovea: 0 narrow, substantially shorter than prementum; 1 broad, extending almost to base of prementum (Packer, 2008, Fig. 8C); 2 broad but short, with specialized capitate hairs. The fovea lacks specialized capitate hairs unless stated otherwise.
67 Scape, length: 0 long, more than 3X as long as greatest width; 1 short, less than 3X as long as greatest width.
68 Metatibial spurs: 0 robust, clearly wider than adjacent hairs, less than half length of basitarsus (Packer, 2014, Figs. 42 and 44): 1 fine, not markedly more robust than adjacent hairs, at least half as long as basitarsus (Fig. 23).