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Systematics of the South American Bee Genus Orphana (Hymenoptera, Apoidea)

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ABSTRACT

The rare Chilean bee genus *Orphana*, formerly regarded as belonging to the Colletidae, is placed in the Andrenidae and a new species is described, *O. wagenknechti*. The relationships of *Orphana* with other andrenids are discussed. As a result of an analysis of anatomical features, it is decided that *Orphana* belongs to the Andreninae. This same analysis shows that the monotypic Chilean andrenid subfamily Euherbstiinae must be regarded as a synonym of the Andreninae.

The purposes of the present paper are to discuss the interfamilial and intrafamilial relationships of the genus *Orphana*, to review the systematics and distribution of the genus, and to describe a new species.

Recently I examined specimens of *Orphana* in some of the Chilean collections. Although Vachal (1909), who described the genus, placed it in the colletid subfamily Diphaglossinae, I immediately recognized that specimens possessed paired subantennal sutures beneath each antennal socket. This fact suggested that the genus might belong to the Andrenidae rather than the Colletidae. A further study of the specimens has shown that the glossa, although very short, is apically acute rather than truncate or bilobed, as it is in the Colletidae. Furthermore, the pre-episternal suture is absent and the jugal lobe of the posterior wing is three-fourths as

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long as the vannal lobe. These features confirm the relationship of *Orphana* to the Andrenidae.¹

I would like to acknowledge the assistance of the following persons who allowed me to examine specimens in their collections: Padre J. S. Moure, Universidade Federal do Paraná, Curitiba, Brazil; Miss Fresia Rojas A., Museo Nacional de Historia Natural, Santiago, Chile; Prof. Haroldo Toro, Universidad Católica, Valparaíso, Chile; and Mr. Rodolfo Wagenknecht Huss, La Serena, Coquimbo, Chile. Dr. Eberhard Königsmann, Institut für Spezielle Zoologie und Zoologisches Museum, Humboldt-Universität, Berlin, kindly lent the types of *Leptoglossa paradoxa*. Drawings were prepared by Miss Liliane Floge, and Mrs. Rose Ismay typed the manuscript.

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The following labels are used to identify the source of the material:

AMNH—the American Museum of Natural History

Moure-Universidade Federal do Paraná, Curitiba, Brazil

Santiago—Museo Nacional de Historia Natural, Santiago, Chile

Toro—private collection of Haroldo Toro, Universidad Católica, Valparaíso, Chile

Wagenknecht—private collection of Rodolfo Wagenknecht Huss, La Serena, Coquimbo, Chile

Berlin—Institute für Spezielle Zoologie und Zoologisches Museum, Humboldt-Universität, Berlin

RELATIONSHIPS TO OTHER ANDRENIDS

The Andrenidae are currently divided into three subfamilies—Andreninae, Euherbstiinae, and Panurginae. Another subfamily, the Oxaeinae, previously placed in the family, was recently accorded family status because of its distinctive larva and other features (Rozen, 1965). The Andreninae contain the essentially Holarctic genus Andrena with approximately 2000 species and the small genus Megandrena from the western United States. The subfamily Euherbstiinae is monotypic, containing only Euherbstia excellens (Friese) (figs. 19–24), and restricted to Chile. Panurginae, although excluded from the Australian region, range over most of the rest of the world; the greatest concentration of genera occurs in the New World. A diverse group, the Panurginae are nonethe-

¹The names Orphana, inquirenda, and paradoxa, which had been applied in the genus, indicate that the taxonomic assignment of the genus was perplexing to previous workers. Friese (1925), although placing Leptoglossa "before" the colletid Caupolicana, went so far as to state that Leptoglossa paradoxa was "remarkable as a transitional link to the genus Andrena."

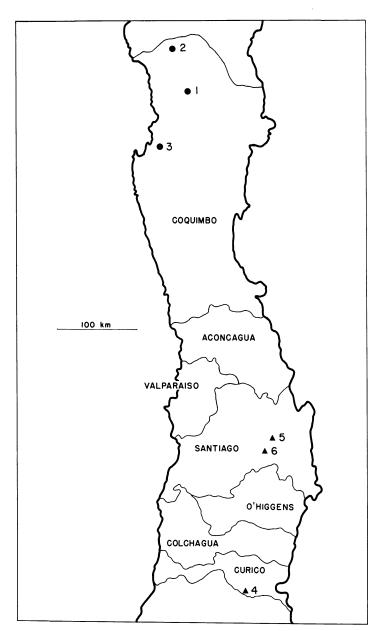


Fig. 1. Map of central provinces of Chile showing distribution of Orphana. Circles represent Orphana wagenknechti; triangles, O. inquirenda.

less monophyletic and can be recognized by the fact that the males lack a gonobase in almost all cases. Because *Orphana* possesses a complete although thin gonobase and because of a number of other features, it is obviously not closely related to the Panurginae. Therefore, in the following analysis of the relationships of *Orphana* to the andrenids, the genus is compared with only three elements, namely: *Andrena*, *Megandrena*, and *Euherbstia*.

Metasomal sternum VII of male Orphana (figs. 5, 12) is a moderately short plate with a long median process that is not lobed apically. This sternum is relatively longer in Euherbstia (fig. 20) but the median process is only faintly expressed. In Andrena (Mitchell, 1960) the plate itself is somewhat similar to that of Orphana although the median process, at least in most Andrena, is shorter and apically bifurcate. Sternum VII is much shorter in Megandrena (fig. 18) than in Andrena and Euherbstia, and, unlike that of the other three genera, the median process has a pair of lateral extensions so that the shape of the sternum is reminiscent of that of some of the Panurginae and Colletidea.

Metasomal sternum VIII of the male is similar in Andrena (Mitchell, 1960), Megandrena, Euherbstia (fig. 21), and Orphana (figs. 6, 13) except that the median apical process is shorter in Euherbstia than in the other genera.

The gonobases of the male genitalia of Andrena (Rozen, 1951; Mitchell, 1960) and Euherbstia (figs. 22, 23) agree in that the dorsal surface is very long and curved, whereas in Megandrena (Rozen, 1951) and Orphana (figs. 7, 8, 14, 15) it is very short.

In most species of Andrena (Mitchell, 1960) each gonoforcep is bilobed although in some the dorsal lobe is not expressed. Of the two species of Megandrena examined, one had the gonoforcep bilobed and the other lacked the dorsal lobe. In Euherbstia (figs. 22, 23) the gonoforcep is simple, as is the case in Orphana (figs. 7, 8, 14, 15). (The apical bifurcation of the gonoforcep in Orphana apparently is not a homologue of the more basal division of the structure found in Andrena and Megandrena.)

Orphana is unique compared with the other genera because the penis valve (figs. 8, 15) is divided into a dorsal and ventral arm. Megandrena exhibits a complicated middorsal projection of the penis valves, which seems to have a less pronounced counterpart in Euherbstia (fig. 23). Orphana (figs. 8, 15) and Andrena (Rozen, 1951) lack such projections.

Males of Andrena and Euherbstia (fig. 24) are without distinct pygidial plates but such plates are defined although narrow in Megandrena, and defined, broad but wrinkled in Orphana (fig. 17).

Facial foveae with dense short hairs are characteristic of Andrena and

Megandrena but absent in Euherbstia. Although the foveae of Orphana may be indicated by a slight modification of the integumental sculpturing, they are not impressed and do not possess dense short hairs.

The subantennal areas of Andrena and Megandrena are usually trapezoidal, with the subantennal sutures running essentially parallel. However, in those species of Andrena in which the antennal sockets are very close to the epistomal suture, the inner subantennal suture runs diagonally toward the lower part of the outer subantennal suture. As a consequence, the subantennal areas are triangular. This condition is found in Euherbstia where the antennal sockets are also very close to the epistomal suture. In Orphana the shape of the subantennal area is difficult to analyze because of the extreme shortness of the inner subantennal suture.

The apex of the marginal cell on the forewing in *Orphana* (fig. 10), *Euherbstia*, and *Megandrena* is slightly bent away from the costal margin; in *Andrena* the apex of the cell is normally on the costal margin.

In last analysis, the phylogenetic relationships of the four genera—Andrena, Megandrena, Euherbstia, and Orphana—cannot be determined on the basis of features discussed above. This is owing in part to the impossibility of discovering which features are primitive and which are derived, and in part to the mosaic sharing of characters. The only conclusion that can be drawn is that the four genera are approximately equally distinct.

Padre Moure (1950) created a separate subfamily for *Euherbstia*, the Euherbstiinae, on the basis of the absence of facial foveae, nonbilobed gonoforceps, the triangular subantennal areas, and the tip of the marginal cell being slightly bent away from the costal margin of the forewing. If *Euherbstia* is to be recognized as a separate subfamily, then each of the other genera must be accorded similar rank. Such an arrangement seems unnecessarily cumbersome and therefore I regard *Euherbstia*, as well as *Orphana* and *Megandrena*, as a member of the subfamily Andreninae.¹

ORPHANA VACHAL

Orphana Vachal, 1909, p. 38 (type: O. inquirenda, monobasic).

Leptoglossa Friese, 1925, p. 9 (type: L. paradoxa, monobasic).

Ptoleglossa Friese, 1930, p. 127 (Leptoglossa preoccupied; replacement name);

Hedicke, 1933, p. 46 (= Orphana).

DIAGNOSIS: Members of Orphana are moderately large bees which can be distinguished from Andrena, Megandrena, and Euherbstia by the longi-

¹ Dr. Wallace E. LaBerge (in litt.), who is an authority on Andrena and who kindly examined specimens of Orphana that I sent him, stated that these specimens "do not show anything by which I would exclude them from the Andreninae."

tudinal median ridge on the clypeus of both males and females. Males are also immediately recognizable on the basis of their sternal plates and genitalia, especially the divided penis valves (see above discussion on the relationships of *Orphana* to the other genera). Females lack pubescent facial foveae and thereby can be separated from those of *Andrena* and *Megandrena*. Their nonmetallic integument and robust body form contrast sharply with the submetallic integument and more slender body of *Euherbstia*.

Remarks: This genus, restricted to Chile, is known only from a few specimens.

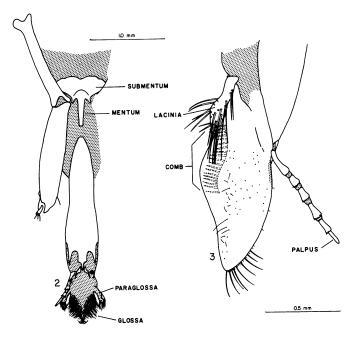
Orphana wagenknechti, new species

Figures 2-10

Diagnosis: Orphana wagenknechti and inquirenda, although structurally similar, are easy to separate because of the color of the setae and of the integument of the legs. The legs of male O. wagenknechti are brown to black and bear brown setae on the tibiae and tarsi. In contrast, those of O. inquirenda are reddish and have reddish setae on the tibiae and tarsi. The mesosoma, metasoma, and legs of the female of O. wagenknechti appear at first to be completely black or very dark gray although the dorsal mesosomal setae on the allotype are pale yellowish at their bases. The mesosoma of the female of O. inquirenda is covered with dense, pale yellow hairs, the metasoma is black except for sparse, pale hairs at the base, and the legs are reddish, somewhat like those of the male. The differences in the genitalia and sternal plates of the males of the two species are apparently diagnostic, as are the differences in shape and size of the pygidial plate of the female.

DESCRIPTION OF HOLOTYPE, MALE: Body length 11.0 mm.; length of forewing from costal sclerite to tip 8.0 mm.

Head: Integumental color black except for yellow clypeus and for paraocular areas which are yellow below line extending one-quarter of way down inner orbit to subantennal area. Setae long, pale yellowish, those on vertex tending to be brownish at tips. Vertex scarcely produced above level of upper margins of compound eye and finely, irregularly punctured; facial fovea apparently missing; frontal ridge thin but well defined, reaching median ocellus; malar area very short. Subantennal area very short so that length along outer subantennal suture less than diameter of antennal socket; length along inner subantennal suture about half of diameter of antennal socket; shape of area not determined because of difficulty in ascertaining direction of inner suture. Clypeus slightly produced and gently curved, with distinctive, median, longitu-



Figs. 2, 3. Orphana wagenknechti, new species, mouth parts. 2. Labium and basal part of maxilla, ventral view. 3. Apex of maxilla, lateral view.

dinal ridge extending from epistomal suture to lower margin; punctures coarse but shallow. Inner orbits subparallel; compound eyes with scattered short setae. Antennae missing, but presumably like those of male from Tongoycillo and those of *O. inquirenda*. Labrum dark brown, very short, approximately four times wider than median length, with deep, transverse, median groove from which arises brush of short hairs; mandible apically simple, with conspicuous yellow maculation at base; other mouth parts as described for female.

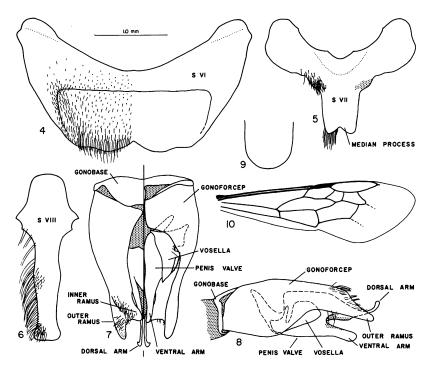
Mesosoma: Integumental background color black or very dark brown. Setae, except for those of legs, pale yellowish, with some slightly brownish at tips; setae abundant and long, obscuring much of integument on dorsum; setae of metanotum somewhat longer than those on preceding sclerites. Mesoscutum finely and rather evenly punctured; pre-episternal suture absent; scrobal suture weak, scarcely visible. Metanotum and propodeum vertical; propodeal triangle shiny but microscopically sculptured, impunctate. Tegula shiny, medium brown, translucent. Forewing (as in fig. 10) with pterostigma narrow, about as wide as prestigma and with length about four times width; apex of pterostigma ending shortly

beyond insertion of vein r; marginal cell of moderate length, distinctly longer than distance from its apex to apex of wing; tip of marginal cell slightly bent back from wing margin; three submarginal cells present; first and third subequal in length; middle one somewhat shorter; hind wing with jugal lobe three-quarters length of vannal lobe; wing membrane moderately pilose, nonpapillate, and not infuscated. Integumental color of legs brown; setae on coxae, trochanters, and femora long and pale yellow; setae on apical segments shorter and medium brown; claws bidentate; arolium moderately small; basitibial plate of hind leg distinct, well elevated, and somewhat concave.

Metasoma: Integumental background color very dark brown, almost black. Setae of tergum I long, pale, like those of mesosoma; setae of terga II to V sparse, very dark brown, and short; setae of terga VI and VII long, brown; sternum I with setae pale and moderate in length; setae of other sterna brown, those of marginal fringes very long but moderately sparse. Metasoma moderately robust; anterior surface of tergum I concave; pygidial plate (as in O. inquirenda, fig. 17) elevated and distinct but with sides and surface somewhat wrinkled; sternum VI (fig. 4) slightly notched medially; sternum VII as in figure 5; sternum VIII (fig. 6) elongate. Gonobase (figs. 7, 8) short (i.e., not as in Andrena [Rozen, 1951, fig. 1a] and Euherbstia [fig. 23] where gonobase is long and curved, especially dorsally, as seen in lateral view); gonoforcep (figs. 7, 8) not divided into dorsal and ventral lobes as are gonoforceps of Megandrena and Andrena; each gonoforcep bifurcate apically, with outer ramus perhaps representing gonostylus; inner ramus (best seen in fig. 7) moderately well developed compared with that of O. inquirenda but outer ramus shorter than that of O. inquirenda; volsellae elongate, heavily sclerotized, and strongly spiculate dorsally; each penis valve divided apically into two arms, with ventral one being thick; dorsal arm curving upward at apex and very thin, thinner than that of O. inquirenda; penis valves fused dorsally at base and without median dorsal projection that is found in Megandrena and, to a lesser extent, in Euherbstia (fig. 23).

DESCRIPTION OF FEMALE: Body length 13.0 to 15.0 mm.; that of allotype 13.0 mm.; length of forewing from costal sclerite to tip 8.0 to 10.0 mm.; that of allotype 8.5 mm.

Head: Integumental color black to very dark brown except for clypeus which is dark brown; yellow markings completely absent. Setae long, medium brown to moderately light brown; if moderately light brown, tips of setae tending to be dark brown. Vertex as described for male; facial fovea not impressed and without short setae characteristic of *Andrena*; area where fovea would be found dull due to microscopic sculpturing;



Figs. 4-10. Orphana wagenknechti, new species. 4. Metasomal sternum VI of male, ventral view. 5. Metasomal sternum VII of male, ventral view. 6. Metasomal sternum VIII of male, ventral view. 7. Genital capsule of male, dorsal (left) and ventral views. 8. Genital capsule of male, lateral view. 9. Pygidial plate of female, caudal view. 10. Right forewing. Scale refers to figures 4-8.

frontal ridge and malar area as described for male. Subantennal area as described for male. Clypeus as described for male except for color. Inner orbits and setae on compound eyes as described for male. First flagellar segment long, about equal in length to following three segments together; middle flagellar segments slightly longer than wide. Labrum, except for color, as described for male; mandible reddish brown, apically simple; postpalpal portion of galea (fig. 3) short; prepalpal portion (fig. 3) extremely short; most of inner comb of 19 teeth apicad of insertion of palpus; maxillary palpus six-segmented; submentum (fig. 2) a trapezoidal plate; mentum fused with submentum, poorly sclerotized; glossa (fig. 2) very short, apically acute; paraglossa about half length of glossa; labial palpus four-segmented; first and fourth segments subequal; each middle segment somewhat shorter than either first or fourth segment; first segment bowing outward at middle (fig. 2).

Mesosoma: Integumental background color black to very dark brown. Setae, except for those of legs, brown on some specimens but on allotype pale at base and becoming brown toward tips; setae on all specimens sufficiently dark to give impression that bee is all black to very dark brownish gray; length of setae similar to those of male. Mesoscutal punctation, pre-episternal suture, scrobal suture, metanotum, propodeum, tegula, and wings as described for male. Integumental color of legs brown to dark brown; setae on coxae, trochanters, and femora tending to be concolorous with setae of mesosoma; setae golden on inner surface of fore basitarsus; setae brown on outer surface of fore basitarsus, on fore tibia, and on tibiae and tarsi of middle and hind legs; basitibial plate large, subcircular, flat to slightly convex, bearing numerous very short setae; claws with inner tooth considerably shorter than outer tooth; arolium moderately small as in male. Extent of scopa not certainly known because no specimen carrying pollen when collected; setae on lateral face of propodeum moderately long; setae on hind trochanter long but neither extremely long nor curved apically as is often the case in Andrena; scopal setae on hind tibia and basitarsus long, nonplumose.

Metasoma: Integumental background color black to very dark redbrown. Setae of tergum I essentially concolorous with setae of mesosoma; setae on other terga very dark brown to black; fimbria of tergum V dense. Metasoma moderately robust; anterior surface of tergum I concave; pygidial plate convex, with apex (fig. 9) broadly rounded, with maximum width more than 0.7 mm., distinctly larger than that of O. inquirenda.

Type Material: Holotype (male), allotype, Condoriaco, La Viñita (fig. 1–1), Coquimbo Province, Chile, December 10, 1963 (R. Wagenknecht); one female paratype, same data, except October 21, 1957 (collection Wagenknecht); two female paratypes, Pajonales (fig. 1–2), Coquimbo Province, October 20, 1957 (collected by R. Wagenknecht but not so labeled; collection Toro, AMNH). The holotype is in the collection of Rodolfo Wagenknecht Huss, La Serena, Coquimbo, Chile; the allotype is in the Museo Nacional de Historia Natural, Santiago, Chile.

ETYMOLOGY: This species is named in honor of Rodolfo Wagenknecht Huss who has contributed greatly to our understanding of the bees of Chile.

REMARKS: In addition to the material listed above, a single male, labeled Tongoycillo (fig. 1-3), Coquimbo Province, Chile, October 27, 1962 (R. Wagenknecht) may belong to this species. However, setae on the metasomal tergum II and the first three metasomal sterna are pale

yellow like the setae of the mesosoma. Further, the outer ramus of each gonoforcep is slightly more elongate than that of the holotype and the median processes of sterna VII and VIII are somewhat thinner. It is impossible to assess the significance of such differences without a series of specimens to examine, and, consequently, the specimen in the collection of Wagenknecht is tentatively labeled as O. wagenknecht. The antennae of this specimen are similar to those of the females except that the basal flagellar segment is somewhat shorter than the next three segments together.

On the basis of the few specimens available, this species (fig. 1) seems to have a more northerly distribution than does O. inquirenda. Wagen-knecht has collected other specimens, presumably of this species, from other localities in Coquimbo Province. However, since I have not examined them, they are not included either on the map or in the type series.

Wagenknecht reports (in litt.) that a number of females have been taken on the flowers of Adesmia cinerea, but none of the specimens before me was carrying pollen when collected. Consequently, the pollen source of this species is uncertain.

Orphana inquirenda Vachal

Figures 11-17

Orphana inquirenda VACHAL, 1909, p. 38.

Leptoglossa paradoxa Friese, 1925, p. 10; Hedicke, 1933, p. 44 (= Orphana inquirenda).

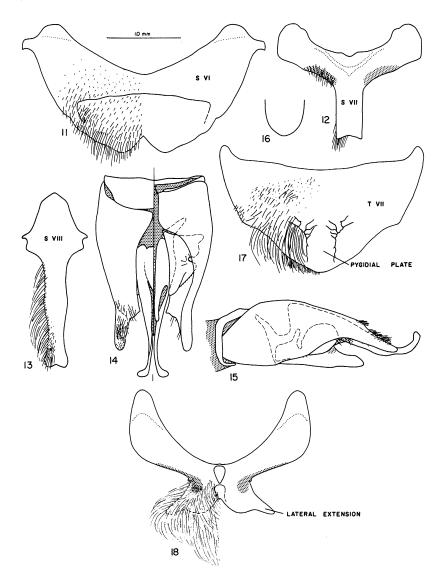
DIAGNOSIS: See O. wagenknechti.

DESCRIPTION OF MALE: Body length 10.0 to 13.0 mm.; length of forewing from costal sclerite to tip 7.5 to 8.0 mm.

Head: As described for male of *O. wagenknechti* except for following: Antennae with basal flagellar segment somewhat shorter than combined length of three following segments; mid-flagellar segments slightly longer than wide; mouth parts as described for female of *O. wagenknechti*.

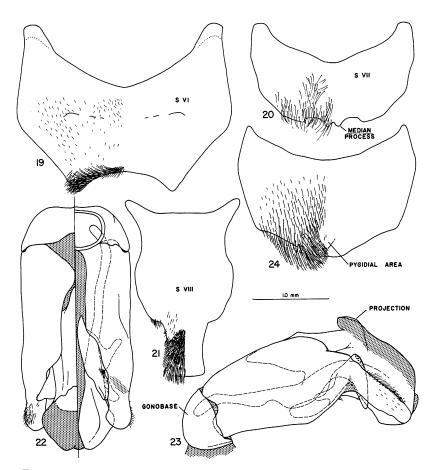
Mesosoma: As described for male of *O. wagenknechti* except for following: Tegula reddish brown to brown; integumental color of legs reddish; setae on apical segments of legs reddish gold.

Metasoma: As described for male of *O. wagenknechti* except for following: Marginal setae of tergum II pale yellow, similar in color to, though shorter than, setae of tergum I; on some specimens marginal setae of terga III and IV moderately pale; long setae of terga VI and VII, and to some extent V, reddish gold, concolorous with setae on tibiae and tarsi; long setae on most sterna tending to be pale yellow; sterna VI to



Figs. 11–17. Orphana inquirenda Vachal. 11. Metasomal sternum VI of male, ventral view. 12. Metasomal sternum VII of male, ventral view. 13. Metasomal sternum VIII of male, ventral view. 14. Genital capsule of male, ventral (left) and dorsal views. 15. Genital capsule of male, lateral view. 16. Pygidial plate of female, caudal view. 17. Metasomal tergum VII of male, dorsal view, showing pygidial plate.

Fig. 18. Megandrena enceliae (Cockerell), metasomal sternum VII, ventral view. Scale refers to figures 11-15, 17, 18.



Figs. 19–24. Euherbstia excellens (Friese), male. 19. Metasomal sternum VI, ventral view. 20. Metasomal sternum VII, ventral view. 21. Metasomal sternum VIII, ventral view. 22. Genital capsule, dorsal (left) and ventral views. 23. Genital capsule, lateral view. 24. Metasomal tergum VII, dorsal view, showing pygidial plate. Scale refers to figures 19–24.

VIII as in figures 11-13, respectively; inner ramus of gonoforcep (fig. 14) shorter than that of O. wagenknechti; outer ramus much longer than that of O. wagenknechti; apex of volsella, as seen in ventral view (fig. 14), not quite so acute as that of O. wagenknechti; dorsal arm of penis valve, as seen in lateral view (fig. 15), thicker at apex than that of O. wagenknechti.

DESCRIPTION OF FEMALE: Body length 13.0 to 14.0 mm.; length of forewing from costal sclerite to tip 8.0 to 8.5 mm.

Head: As described for female of O. wagenknechti except for following:

Setae pale yellow, with tips of those on vertex and scape brown; maxillae and labium not visible on specimens examined but almost certainly like those of male and of *O. wagenknechti*, as indicated in description of *Leptoglossa paradoxa* (Friese, 1925).

Mesosoma: As described for female of *O. wagenknechti* except for following: Setae, except for those of legs, pale yellow with tips often darkening to brown; integumental color of legs reddish brown; setae on coxae, trochanters, and femora pale yellow; setae on tibiae and tarsi somewhat more reddish; hence coloration of legs similar to that of male; basal tibial plate slightly concave.

Metasoma: As described for female of O. wagenknechti except for following: Setae of terga II, III, and IV pale yellow to brownish; fimbria of tergum V reddish, similar in color to setae on hind tibia and tarsus; pygidial plate (fig. 16) 0.6 mm. at maximum width, smaller than that of O. wagenknechti and with apex more acutely rounded than that of O. wagenknechti.

Material Studied: Two males, one female, El Coigual (fig. 1-4), Curico Province, Chile, October/November 1955 (L. Peña; Moure); one male, one female, El Canelo (fig. 1-5), Santiago Province, Chile, January 1956 (L. Peña; Moure); one male, Peñalolen (fig. 1-6), Santiago Province, December 8, 1952 (Santiago), one male, labeled "type" of Leptoglossa paradoxa, Nord-Chile, 191 (P. Herbst; Berlin); one female, same data, but without type label (Berlin).

REMARKS: The two specimens from "Nord-Chile" are those upon which Friese (1925) based the description of *Leptoglossa paradoxa*. These specimens seem essentially identical to the others listed above except the setae tend to be somewhat paler on the metasomal terga. In consequence, the marginal hair bands of terga III and IV are more conspicuous than they are on the other specimens. The mouth parts from both specimens had been removed and were apparently lost. Although the male alone bears the type label, the description of the female appears first.

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RESUMEN

El raro género chileno de abejas, *Orphana*, que anteriormente se consideraba como perteneciente a las Colletidae, se coloca en las Andrenidae. Se describe una nueva especie, *O. wagenknechti*, de la provincia de Coquimbo. Se discuten las relaciones entre *Orphana* y las Andrenidae restantes. Como resultado de un analisis de caracteres anatómicos, se decide que *Orphana* pertenece a las Andreninae. Este mismo analisis demuestra que la subfamilia monotípica chilena Euherbstiinae tiene que ser considerada como sinónimo de Andreninae.

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