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Revision of the Cleptoparasitic Bee Tribe Protepeolini, Including Biologies and Immature Stages (Hymenoptera: Apoidea: Apidae)

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CONTENTS

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ABSTRACT

A systematic revision of the tribe Protepeolini is presented. The tribe comprises the single genus *Leiopodus* Smith, of which *Protepeolus* Linsley and Michener is a junior synonym. Five species are recognized: *L. abnormis* (Jörgensen), *L. lacertinus* Smith, *L. nigripes* Friese, *L. singularis* (Linsley and Michener), and *L. trochantericus* Ducke. A cladistic analysis of the five species supports the synonymy of *Protepeolus* since its type species, *L. singularis*, and the phenetically similar *L. abnormis* and *L. trochantericus* form a paraphyletic group with respect to *L. lacertinus*, type species of *Leiopodus*. A key to the species, as well as synonymies, redescriptions, and geographic distributions for the species, are presented.

Biological information concerning *Leiopodus lacertinus* is discussed, including mode of parasitism, egg deposition and anatomy, and such larval activities as locomotion, feeding, defecation, and cocoon spinning. Differences in oocyte shape and size are noted for *L. singularis, L. abnormis*, and *L. trochantericus*. A tabular key to the oocytes/eggs of four of the species is provided.

All known host associations (listed in tabular form) of the species of *Leiopodus* indicate that the genus is restricted to attacking nests of the bee tribe Emphorini.

The first instar of *Leiopodus lacertinus* is characterized. Although it shares many features with first instars of *L. singularis* and thus supports the monophyly of the tribe, these two species are amply distinct at this stage. The mature larvae and pupae of *L. lacertinus* and *L. abnormis* are described and compared with one another and with those of *L. singularis*. Whereas these stages of *L. lacertinus* can be distinguished from those of the other two species, the larvae and pupae of *L. abnormis* and *L. singularis* appear identical, coinciding with the close agreement of adults of these taxa. The immature stages clearly support the synonymy of *Protepeolus* and *Leiopodus*.

RESUMEN

Se presenta una revisión sistemática de la tribu Protepeolini. La tribu comprende un único género, *Leiopodus* Smith, del cual *Protepeolus* Linsley y Michener es un sinónimo posterior. Se reconocen cinco especies: *L. abnormis* (Jörgensen), *L. lacertinus* Smith, *L. nigripes* Friese, *L. singularis* (Linsley y Michener), y *L. trochantericus* Ducke. Un análisis cladístico de las cinco especies apoya la sinonimia de *Protepeolus* pues la especie tipo, *L. singularis*, y las fenéticamente similares *L. abnormis* y *L. trochantericus* forman un grupo parafilético con respecto a *L. lacertinus*, especie tipo de *Leiopodus*. Se presenta una clave para las especies, como así también sinonimias, distribuciones geográficas y redescripciones de las especies.

Se presenta información biológica sobre *Leiopodus lacertinus*, incluyendo modo de parasitismo, oviposición, anatomía del huevo y actividades larvales como locomoción, alimentación, defecación y tejido del capullo. Se señalan diferencias en la forma y tamaño del oocito de *L. singularis*, *L. abnormis*, y *L. trochantericus*. Se presenta una clave en forma de tabla para los oocitos/huevos de cuatro de las especies.

Todas las asociaciones con huéspedes de las especies de *Leiopodus* (presentadas en forma de tabla) indican que éstas sólo atacan nidos de abejas de la tribu Emphorini.

Se caracteriza la larva de primer estadio de *Leiopodus lacertinus*. Aunque ésta comparte muchos rasgos con la de *L. singularis*, apoyando la monofilia de la tribu, ambas especies son ampliamente distintas en este estadio. La larva madura y la pupa de *Leiopodus lacertinus* y *L. abnormis* se describen y comparan entre sí y con las de *L. singularis*. Mientras que estos estadios de *L. lacertinus* se pueden distinguir de aquellos de las otras dos especies, las larvas y pupas de *L. abnormis* y *L. singularis* parecen idénticas, coincidiendo con la estrecha concordancia de los adultos de estos taxa. Los estadios inmaduros claramente apoyan la sinonimia de *Protepeolus* y *Leiopodus*.

INTRODUCTION

This paper revises the Protepeolini, a tribe of New World bees, cleptoparasites of bees of the tribe Emphorini (= Melitomini, Michener, 1986). Although the revision concentrates on adults, information on biology is also presented, and the known larvae and pupae are described.

The tribe Protepeolini comprises the single genus *Leiopodus* Smith, of which *Protepeolus* Linsley and Michener is a junior synonym, as shown by larval and adult morphological characters discussed in the present contribution. In spite of this generic synonymy, the tribal name Protepeolini is valid. Of the five species recognized in this study, one ranges from the southwestern United States to Guatemala, while the other four are South American.

The relationships of the tribe are not well understood. Protepeolines are behaviorally similar to bees in the subfamily Nomadinae, among which they have long been included. Like nomadines, protepeolines enter open host cells that are in the process of being provisioned and hide their eggs by embedding them in the cell wall (Rozen et al., 1978). Females of Protepeolini and Nomadinae have a specialized area of setae on the apex of the fifth tergum, known as the pseudopygidial area, not present in any other bees. In spite of these similarities the two taxa seem not to be closely related. No other adult morphological features link the Protepeolini to the monophyletic subfamily Nomadinae (Roig-Alsina, 1991). Rozen (1991) showed that the suite of parasitic specializations possessed by the first larval instar of Protepeolini is different from that of nomadines and from all other parasitic anthophorids, and hypothesized an independent parasitic origin for the tribe. In a recent study, Roig-Alsina and Michener (1993) found that the Protepeolini do not belong in the Nomadinae, but to the Apinae, a clade including those tribes previously classified in the Apidae and Anthophorinae. The group of extant bees to which the tribe is most closely related is a matter that needs further study.

The first author (AR) was primarily responsible for preparing and drafting the revision section of this paper. The contribution of the second author (JGR) concentrated on the sections pertaining to oocytes, larvae, and pupae. Both authors supplied information about biology.

ACKNOWLEDGMENTS

Abraham Willink, Cátedra de Entomología, Universidad Nacional de Tucumán, Tucumán, Argentina, kindly provided laboratory space and other assistance during the study of the biology and immature stages of *Leiopodus lacertinus*. Institutions from which material was borrowed are identified in the Systematics section.

The National Geographic Society, Washington, D.C., through grant number 3844-88 to JGR, supported the field investigations leading to the recovery of the immature stages of *Leiopodus lacertinus* in Tucumán Province, Argentina.

We thank Charles D. Michener and George C. Eickwort for their careful review of and valuable comments on the manuscript.

BIOLOGICAL OBSERVATIONS AND HOST ASSOCIATIONS

Life history information on *Leiopodus singularis* was reported by Rozen et al. (1978).

Biology of *Leiopodus lacertinus*

This species was studied at two sites in Argentina, one in Tucumán Province and the other in Buenos Aires Province. Because the information gathered from the sites was largely nonoverlapping, it is presented separately for each site, followed by a description of the egg and oocyte.

A nesting site of an unidentified species of *Melitoma* that had been attacked by *Leiopodus lacertinus* was found between Taruca Pampa and Rio del Nio, Tucumán Province, on October 29, 1989. At that time adults were no longer flying, but cells contained immature stages of the host and a larva and two pupae of the cleptoparasite. The following observations were made by JGR from this material.

A single vacated egg chorion of *Leiopodus lacertinus* was embedded in the wall on the

side of the *Melitoma* cell containing the larval cleptoparasite. Although the egg operculum was lost, the rim of the chorion to which it had been attached was level with the cell lining, and the opening (approximately circular) had a diameter of 0.25 mm.

In all three cells containing immatures of *Leiopodus lacertinus*, the larvae had applied feces over the entire cell wall and cap. Most of the feces adhered to the front (closure end) part of the cell where they were at most approximately 1 mm thick at the junction of the convex inner surface of the cell cap and the cell wall. They decreased in thickness toward the cell rear, and at the very rear of the cell most areas were without feces altogether. In the rear of the cell, feces obviously had been applied as elongate, almost certainly moist, flat pellets. The inner surface of the cocoon was uneven because of the presence of these flattened pellets.

Cocoon spinning started only after all feces had been deposited, for no silk was incorporated in the feces. The developing *Leiopodus* was walled off from the feces by a single thin layer of translucent reddish-tan silk that was thicker at the front of the cocoon than at the rear. The cocoon did not display a specialized area, such as a filter or macropyle, at the closure end. The silk was sheetlike although fibrous silk was also discernible particularly toward the cocoon rear and contained small fenestrations also toward the rear. The cocoon adhered to the feces and to the cell wall where there were no feces. In general the cocoon and feces could be more easily separated from the cell wall than could those of the host *Melitoma*. The inner surface of the cocoon glistened because of the sheetlike nature of the silk and the uneven surface of the feces beneath. The internal shape of the cocoon was oval because the thick layer of feces at the front end of the cell obscured the angle created by the junction of the cap with the cell wall. The external shape of the cocoon and feces combined conformed to the internal shape of the cell which was approximately 10 mm long and 7.5 mm in maximum diameter.

The single larva was slightly active when discovered and more active the following day, probably because it was near pupation as revealed in the preserved specimen which showed the pharate pupa. This larva bore on its venter debris of sand and perhaps other matter glued together by water-soluble, transparent, brown material, much as had also been observed in *Leiopodus singularis* (Rozen et al., 1978: figs. 6, 7). Of the 17 cells with live immature bees from the site, 14 cells contained quiescent postdefecating *Melitoma* larvae; 1 cell, a *Leiopodus* larva nearing pupation; and 2 cells, *Leiopodus* pupae. This suggests that the host and parasite emergence may not be closely synchronized. An adult *Leiopodus* emerged between November 10 and 20, 1990.

AR discovered a nesting site of *Melitoma segmentaria* (Fabricius) attacked by *Leiopodus lacertinus* in Martínez, Buenos Aires Province, on the banks of La Plata River. Nests were excavated and cells opened during the period March 15 to 25, 1993. Two cells contained freshly deposited *Leiopodus* eggs. One of these cells had recently been constructed and contained no provisions; the egg was embedded in the wall near the bottom, assuming a vertical orientation of the cell. The other cell, as yet incompletely provisioned, contained two eggs embedded in the lower third of the cell.

Cells from which larval stages of *Leiopodus* were recovered showed eggs inserted in the wall from near the closure to almost the cell bottom. The number of *Leiopodus* eggs per parasitized cell varied from 1 to 11. Of nine cells carefully examined, three had 1 cleptoparasite egg, two had 2 eggs, one had 4, one had 5, one had 6, and one had 11. In the last case, all eggs were in the bottom (rear) third of the cell.

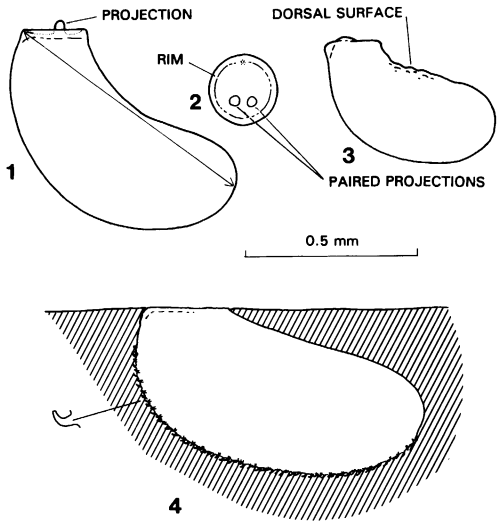
Leiopodus eggs (and cast chorions) were easily discovered because the soil-filled holes where they were hidden appeared as pale, roughly circular areas (diameter 0.6–0.9 mm; N = 5) against a slightly darker tan wall surface. The surface of the fill was smooth except for a slight roughening at the periphery in some cases. It was continuous with the cell wall and hydrofuge when tested with a water droplet, as was the cell lining. In each case the whitish operculum or dark emergence hole was exposed near the perimeter of the pale area. Usually only the operculum could be distinguished, but sometimes part of the chorion adjoining the operculum was evident. In

the case of emergence holes (maximum diameters 0.2–0.25 mm; N = 3), at least the rim of chorion was always evident, and the hole was nearly circular to slightly oblong with its greatest length at right angles to the long axis of the egg. In one oviposition hole, the soil fill dislodged during study, and the egg chorion was visible lying just beneath the cell surface.

The above observations on oviposition indicate that a female of *Leiopodus lacertinus* enters the host cell while it is still open, lays an egg (or possibly more than one) by first gouging a shallow hole in the cell wall large enough to receive the egg, and then oviposits in the pit so the egg's long axis is more or less parallel to the cell wall (fig. 4). She then fills in the excavation with soil. This soil is either mixed with a waterproofing secretion or coated with such a secretion after it has been smoothed and leveled. The egg, thus embedded, is completely covered except for the opercular end which is more or less flush with the cell surface. In the case of two unhatched eggs, there was no visible crack between the smooth surface of the fill and the operculum.

In the host cell with 11 eggs, three hatched eggs had their opercula still attached, in each case at the most anterior end of the opening. Four hatched eggs no longer had opercula attached (either they had become dislodged during hatching or while the cell was being examined). Two eggs had their opercula unopened, an indication that they had failed to develop or that they may have been killed by a *Leiopodus* first instar (it is unclear, however, how a first instar could pierce the essentially flat and flush operculum with its mandibles). The last two eggs appeared to have lost their opercula, but with each the exit hole was filled with amorphous material that may have been a dead embryo or larva (although a head capsule was not evident).

An egg containing a fully developed first instar with a pigmented head capsule was recovered from another cell and preserved. Obviously about to eclose, the first instar had its head just beneath the operculum and its venter positioned along the ventral side of the chorion. Had it emerged, it would have had to swing the operculum open (assuming that the operculum remained hinged) as illustrated for *Leiopodus singularis* (Rozen et al., 1978: fig. 4).



Figs. 1–4. **1.** *Leiopodus abnormis*, oocyte, side view. **2.** Same, operculum, top view. **3.** *L. trochantericus*, oocyte, side view. **4.** *L. lacertinus*, egg in cell wall, side view, including an enlargement of one of the hooks from the ventral band. Anterior ends of side views to the left. Arrow in figure 1 indicates how lengths of oocytes and eggs are measured. All figures drawn to same scale with camera lucida.

First instars of *Leiopodus lacertinus* (one newly emerged larva measured 1.1 mm long) crawled with the help of the pygopod, as described by Rozen et al. (1978) for *L. singularis*. They moved their heads with a rhythmic up and down movement. As they raised their heads, larvae opened their mandibles, so that when the head was raised at its maximum, the mandibles were fully open. The mandibles were then closed with the downward movement of the head.

Evidence is quite clear that newly emerged first instars crawl onto the provisions, fight with eventual conspecifics, and (contrary to the behavior of *Leiopodus singularis*, Rozen et al., 1978) kill the egg of the host. In four of five parasitized cells, the shrunken egg of *Melitoma* was identified, and in no case were older dead hosts encountered. In one cell with five first instars of the cleptoparasite, one was alive and four were dead, scattered on the food mass. Another cell contained four first instars, apparently all dead. In yet another

cell were discovered one live third instar, one cast skin of a second instar *Leiopodus*, one partly decomposed second instar (in two pieces), four dead first instars, and the partly decomposed *Melitoma* egg identified by its reticulated chorion. It is impossible to determine whether the dead second instar had been attacked by the live larva when the latter was in its first, second, or third stage. Mandibles of second and third instars appear to be sufficiently pointed apically (figs. 11, 12) for them to damage rivals, but the anatomy of the other mouthparts and antenna has changed (see section on Other Instars of *Leiopodus lacertinus*, below), perhaps suggesting that only the first instar is highly specialized for killing hosts and competitors.

Last instars began to defecate well before finishing the provisions. Their feeding movements relative to the food mass and their actions while ingesting food were as in *Leiopodus singularis*. All opened cells that contained quiescent larvae of *Leiopodus* had cocoons. Three larvae, kept in a tray until they finished defecating, also spun cocoons.

Information about eggs was derived from both field sites. As in the other species of *Leiopodus* whose eggs or oocytes have been examined, the egg of *L. lacertinus* consisted of an operculum at the anterior end (fig. 4). The operculum of *L. lacertinus* was nearly flat, bearing no conspicuous swellings or paired tubercles. Its rim was not elevated but was somewhat modified at its most anterior point (hinge). Maximum egg length ranged from 0.83 to 0.95 mm (N = 4) measured as indicated by the arrow in figure 1. One egg had a maximum dorsoventral diameter of 0.38 mm and a horizontal diameter of 0.33 mm. The chorion was grayish white, translucent, and much of it was finely but inconspicuously reticulate. Along the ventral surface it bore a narrow band of hooked projections that pointed anteriorly and that may serve to hold the egg in the ground as the tip of the female metasoma is withdrawn during oviposition. This band was approximately 0.1 mm in width and extended the entire length of the egg (fig. 4).

Two females from the site in Buenos Aires Province, preserved in Kahle's solution, had a total of eight ovarioles (presumably four per ovary) each. For both females, the egg index (egg length divided by distance between outer margins of tegulae; see Alexander and Rozen, 1987, for details and for references) was 0.25, almost as small as that of *Leiopodus trochantericus*, below.[3] Mature oocytes numbered nine in one female. The other female had six clearly mature oocytes and four more that seemed slightly less developed though of the same size as the first six. The four had a distinct opercular rim as did all others, but their chorions were perhaps less differentiated from the egg within. In many of the oocytes the ventral bands of hooks were evident even through the follicular wall.

Biology of *Leiopodus trochantericus*

Two females of this species were collected as they emerged from nests of *Diadasia* sp. 8 km southwest of Ticucho, Tucumán Province, and 40 km west-northwest of Hickmann, Salta Province, both in Argentina. These data as well as numerous collections of this species in association with *Diadasia* leave no doubt that *Diadasia* is the host of this cleptoparasite.

A single female preserved in Kahle's solution from the first locality appeared to have four ovarioles per ovary although the abundant oocytes made observation difficult. Its oocytes (fig. 3) had the same shape as the eggs of *Leiopodus singularis* (Rozen et al., 1978: fig. 3) and *L. lacertinus* and bore a nearly circular operculum at the anterior end. Oocyte length was 0.56 mm. The egg index was 0.24, the smallest index for any known clep-

[3] Some statistics regarding the oocytes of *Leiopodus* may not be comparable to those of other parasitic bees. The length presented here is the greatest distance between the anterior edge of the rim to the rear of the oocyte, but it is uncertain whether the anterior edge of the rim is homologous with the apex of the rounded end of a more normal-shaped bee egg. Also, in this study the mature oocytes are probably comparable to Iwata's (1955) Category A oocytes because of the well-formed chorions and because it was not possible to clearly differentiate Category B oocytes as a distinct class. In Alexander and Rozen (1987), these two categories were lumped, but in Rozen (1992) only Category A was identified.

toparasitic bee recorded to date. The number of mature oocytes was at least 10, but that figure does not include many other oocytes in which the rim of the operculum was visible but the operculum was not fully deposited. The chorion of mature oocytes was nearly transparent, colorless. Its dorsal surface was irregular, as shown in figure 3, but elsewhere the chorion was smooth except for a fine reticulate pattern. The rim projected above the operculum only slightly, and the operculum itself exhibited a vague double mound on its anterior half. The most apical point of the operculum was somewhat different from the rest of the opercular rim, as discussed under *L. abnormis* below.

Biology of *Leiopodus abnormis*

A female of this species, preserved in Kahle's solution at the same time and from the same place as the female of *Leiopodus trochantericus*, discussed above, possessed four ovarioles per ovary and contained a total of eight mature oocytes (opercula fully formed), which were uniform in size and shape. One oocyte was 0.75 mm long, and the egg index was 0.31, which was somewhat greater than that of *L. lacertinus* and *L. trochantericus* but still small compared with most other parasitic bees. The oocyte shape was similar to that of the other species in the genus. The dorsal surface of the chorion was smooth, not irregular as in *L. trochantericus*, and the ventral surface lacked the band of hooks found in *L. lacertinus*. The operculum differed in a number of respects from that of *L. trochantericus* and *L. lacertinus*: the rim was more pronounced and elevated above the disc, and the operculum itself bore a pair of conspicuous projections arising from the posterior half (figs. 1, 2). These projections were not hollow but were solid extensions of the chorion and extended well beyond the rim in lateral view. As was the case with *L. lacertinus* and *L. trochantericus*, the anterior point on the rim of the operculum appeared slightly interrupted and the chorion beneath it slightly thickened internally, but details of this feature could not be determined, although it may have related to the micropyle or the hinging device if the operculum functions as in *L. singularis* (Rozen et al., 1978: 7) and *L. lacertinus*.

Biology of *Leiopodus singularis*

Brief observations were made on the oocytes of a female of this species (1 mi north of Rodeo, Hidalgo Co., N.M., August 28, 1987, J. G. and B. L. Rozen). One oocyte was 0.88 mm long and was identical in shape and other features to eggs from the study of the biology of that species (Rozen et al., 1978). The egg index was 0.30. Although the oocytes and eggs of *L. singularis* possessed a slightly bulging operculum (as diagrammed in Rozen et al.,1978: figs. 1–3), they lacked the paired projections of the oocytes of *L. abnormis*, and the opercular rim was somewhat less pronounced. Whereas differences in mature larvae and pupae of these two species were not detected, egg-oocyte features appear diagnostic.

Host Relationships

So far as we now know, hosts of the Protepeolini are restricted to the Emphorini. *Diadasia, Melitoma,* and *Ptilothrix* serve as hosts. While other host species will undoubtedly be discovered, Rozen et al. (1978) have shown that some emphorine species [(e.g., *Diadasia diminuta* (Cresson)] are not subject to cleptoparasite attack. Table 1 gives the host associations of *Leiopodus* as known to date.

Discussion of Biological Features, with a Key to Species Based on Eggs/Oocytes

Information presented here as well as in Rozen et al. (1978) indicates that the biological attributes of the species of *Leiopodus* are homogeneous with some notable exceptions. Both *L. singularis* and *L. lacertinus* make shallow holes in the cell wall, deposit their eggs in them, and then cover the eggs with soil so that the opercula are flush with the wall. The small size of these eggs as well as their anatomy and shape are similar to the mature oocytes of *L. abnormis* and *L. trochantericus*. The close agreement in oocyte and egg characteristics suggests that egg deposition of all these species is the same. In-

TABLE 1
Host Associations of *Leiopodus*
(Host names are in boldface where immature *Leiopodus* have been collected from host cells, denoting certain host-cleptoparasite associations.)

Leiopodus species	Host species	Reference
lacertinus	***Melitoma segmentaria*** (Fabricius)	present paper
	Melitoma sp.	present paper
	? *Ptilothrix plumata* Smith	Friese, 1908; Strand, 1909[a]
nigripes	*P. fructifera* (Holmberg)	present paper
trochantericus	*Diadasia distincta* (Holmberg)	present paper
abnormis	*D. distincta*	Schrottky, 1920
	D. baraderensis (Holmberg)	present paper
	D. sp.	present paper
singularis	***D. olivacea*** (Cresson)	Rozen et al., 1978
	D. angusticeps Timberlake	Hurd & Linsley, 1963

[a] The records of Friese and Strand refer to material collected in Paraguay by K. Fiebrieg, who observed a nest aggregation (and sent a chunk of earth with nests and bees to Berlin) of *Ptilothrix plumata.* Fiebrieg observed *L. lacertinus* entering nests. The description of the nests (in Strand, 1909) is confusing, because it reminds one of the nest of a *Melitoma,* not of a *Ptilothrix.* On the other hand, AR finds it difficult to believe that Friese (who saw the specimens) might have misidentified a *Melitoma* for *P. plumata,* a species well known to him.

teresting structural differences in the chorions and opercula make possible the identification of the species whose eggs or oocytes are known (see table 2). Eclosion in *L. singularis* and *L. lacertinus* involves the operculum splitting along its perimeter from the rest of the chorion. At least in many cases the operculum remains attached at the most anterior point which then serves as a hinge.

Because the larvae of *L. singularis, L. lacertinus,* and *L. abnormis* have projecting salivary lips, it seems likely that they all are capable of cocoon spinning, although cocoons of only the first two species have been described. Because *L. singularis* is known to be a facultative spinner (only overwintering larvae are found in cocoons), this may also be true for other species in the genus, although all observed mature larvae of *L. lacertinus* spun cocoons.

Although the mode of parasitism of *Leiopodus singularis* (Rozen et al. 1978) is to some degree like that of the Nomadinae, it differs in that the highly modified first instar of *L. singularis* routinely kills the host larva as it is about to molt to the last instar. In sharp contrast to those of *L. singularis*, first instars of *L. lacertinus* kill the host egg, a behavior corresponding closely to that of the nomadines. The mode of parasitism of other species of *Leiopodus* has yet to be observed.

DESCRIPTION OF IMMATURE STAGES

Specimens of immature *Leiopodus* are in the collection of the American Museum of Natural History.

First Instar of *Leiopodus Lacertinus*
Figures 5–10

The following description is modified from that of the first instar of *Leiopodus singularis* (Rozen et al., 1978; Rozen, 1991).

Diagnosis: Although the first instar of this species shares many similarities with that of *Leiopodus singularis*, *L. lacertinus* can be identified because of its much larger antennae, cockscomb arrangement of its labral tubercles, and shorter dorsal body spicules. These and other important distinguishing features are in boldface, below. Features by which first instars of both *L. lacertinus* and *L. singularis* can be separated from those of other hospicidal first-instar apid larvae are in italics.

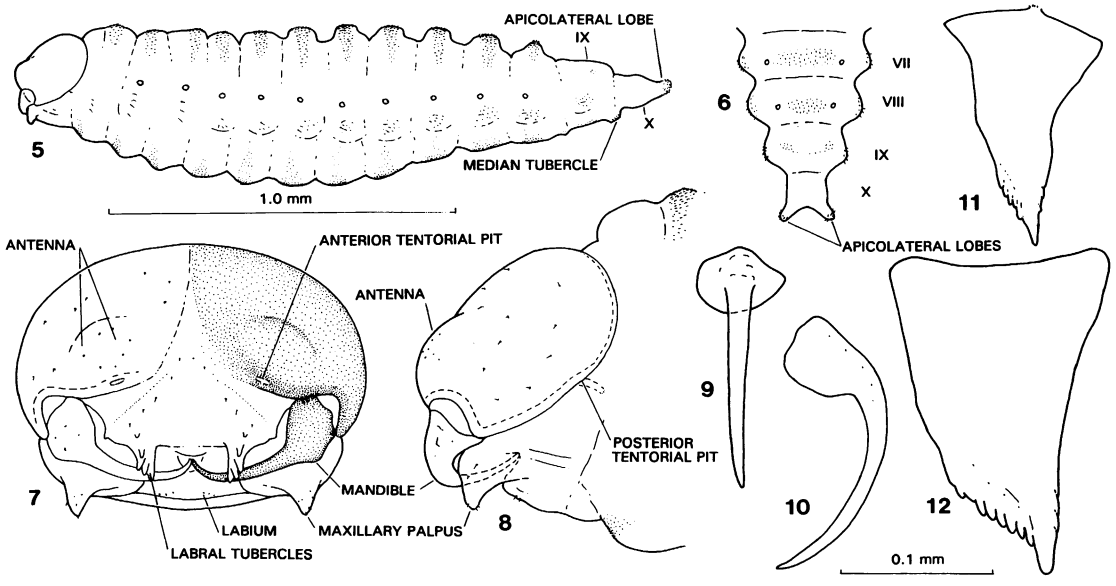
Total length: 1.1, 1.7 mm (N = 2).

Head (figs. 7, 8): *Head more or less hypognathous, about as in Leiopodus singularis,* and **wide as seen in frontal view (fig. 7), much wider than that of *L. singularis;*** in lateral view, head capsule not appearing as shallow as that of *L. singularis*; *foramen approximately as*

TABLE 2
Tabular Key to Species of *Leiopodus*, Based on Eggs/Oocytes
(Eggs and oocytes of *Leiopodus nigripes* are unknown.)

Characteristic	*lacertinus* (fig. 4)	*trochantericus* (fig. 3)	*abnormis* (figs. 1, 2)	*singularis* (Rozen et al., 1978: fig. 3)
Dorsal surface of chorion	smooth	irregular	smooth	smooth
Ventral surface of chorion	with band of hooks	smooth	smooth	smooth
Operculum	flat	with vague paired mounds on anterior half	with distinct paired tubercles on posterior half	slightly bulging

wide as head capsule. Parietals and mandibles darkly pigmented but frontoclypeal area and labrum scarcely pigmented; *pigmentation and sclerotization of head capsule not extending below hypostomal ridge, i.e., labiomaxillary region entirely membranous.* Head-capsule sensilla setiform. Tentorium weakly developed, perhaps with anterior arms absent; posterior arms thin but pigmented laterally; anterior tentorial pits conspicuous. Postoccipital ridge (posterior thickening of head capsule) well developed, defining posterior margin of head capsule; *this ridge in lateral view curving to meet hypostomal ridge so that these two ridges together appearing to be more strongly curved than those of L. singularis (Rozen, 1991: fig. 13) but not angulate as in some other groups of cleptoparasites;* hypostomal ridge well developed; *external hypostomal groove not troughlike (as it is in Nomadinae, Ericrocis, and Melectini);* pleurostomal ridge well developed; epistomal ridge laterad of anterior tentorial pit well developed, absent mesad of pit; pale median ecdysial line present. Parietal band absent. **Each antenna a pronounced swelling, much larger than that**



Figs. 5–12. *Leiopodus lacertinus.* **5.** First instar, entire larva (partly fed), lateral view. **6.** Same, apex of abdomen, dorsal view. **7, 8.** Same, head, frontal and side views. **9, 10.** Same, right mandible, outer and ventral views, in maximum relief. **11.** Second instar, right mandible, outer view. **12.** Third instar, right mandible, outer view.

Scales refer to figures 5, 6 and figures 9–12, respectively.

of *L. singularis;* *antenna fused with parietal (i.e., antennal papilla not distinct from parietal);* sensilla six or seven, widely scattered over antenna, not setiform as are other head sensilla. Anatomy of frontoclypeal area incompletely understood as is also case for mature larva (see description, below) and for first instar of *L. singularis*. Labrum distinct (not fused with frontoclypeal area), nearly unsclerotized, much broader than that of *L. singularis*; **each side bearing linear series of tubercles, apical four of which branch from one another (like a cockscomb); these two series of tubercles widely separated from each other, in contrast to apical labral tubercles of *L. singularis* which are close together (Rozen, 1991: fig. 12); labral surface between two series broadly sulcate longitudinally, curving toward buccal cavity so that apical margin of labrum not sharply defined medially.**

Mandible fanglike; base (figs. 9, 10) broad, but not as broad as that of Leiopodus singularis; apical part very elongate, slender, circular in cross section, strongly curved; in repose (figs. 7, 8), mandibular apices resting in pocket where salivary gland and buccal cavity open (see Remarks) as is case with L. singularis. Maxilla distinct from labium, with adoral lobe finely spiculate; lobe less pronounced than that of *L. singularis*; **maxillary palpus** large, **downturned apically, its apex not appressed to maxilla as is case with *L. singularis*** (see Remarks); labial palpus not evident except for sensilla. *Hypopharyngeal area not defined because of proximity of salivary opening to mouth and because of median cuplike arrangement of integument to receive mandibular apices.*

BODY: Form (figs. 5, 6) straight, without tubercles except for pair of lateral swellings below spiracles on most body segments and for small median spiculate tubercle ventrally between abdominal segments IX and X; *abdominal segment X (figs. 5, 6) with pair of apicolateral lobes* bearing anteriorly directed, sharp spicules. Thoracic segments dorsally divided into cephalic and caudal annulets; division of abdominal segments not clear. *Integument with scattered setae particularly noticeable on sides of body segments;* thoracic segments and abdominal segments I–VIII each with band of spicules; **these spicules moderately long but distinctly shorter than those of *Leiopodus singularis;*** abdominal segment IX (figs. 5, 6) with a few spicules dorsally; lateral swellings of abdominal segments bearing spicules that become denser toward posterior end of abdomen; thoracic segments and abdominal segments I–IX spiculate ventrally, these spicules tending to be smaller than dorsal ones. All spiracles present, normal in position, subequal in size. Anus not evident.

MATERIAL STUDIED: Thirteen first instars (many found dead in cells) or cast skins of first instars, Martínez, Buenos Aires Province, on the banks of La Plata River, March 15–25, 1993 (A. Roig-Alsina) from nests of *Melitoma segmentaria*.

REMARKS: The large downturned maxillary palpus of this species explains the anatomy of the peculiar padlike palpus of *L. singularis*. In the latter species, the palpus is bent backward and appressed to the maxilla so that its apex is pointed posteriorly. The ventral, padlike surface of the palpus is derived from the palpal surface that is dorsal on other bee larvae.

The unique shape and resting position of the mandibles of *Leiopodus lacertinus* and *L. singularis* lead to speculation as to the adaptive function of the mandibles and the pocket into which their apices fit. Although Rozen et al. (1978) and Rozen (1991) thought that the apices fit into the buccal cavity, examination of first instars of *L. lacertinus* and reexamination of larvae of *L. singularis* indicate that in both species the apices seem to rest in a cavity which holds the openings of the pharynx and the salivary duct which is well developed. When at rest, could the mandibular tips be bathed in saliva? Could the saliva be a venom, enabling the larva to kill the host egg or larva (which in the case of *L. singularis* is many times larger than the cleptoparasite—Rozen et al., 1978) as well as conspecific competitors? Or could the saliva serve as a lubricant, assisting the thin mandibular apex in piercing deeply into the body of the opponent? These questions remain unanswered.

Information concerning the first instar of *Leiopodus lacertinus* sheds no further light on possible relationships of the Protepeolini with other parasitic apids than did the first instar of *L. singularis* (Rozen, 1991). Al-

though the first instars of the two differ in a number of ways as indicated above, such shared features as the shape of the mandibles, the resting position of their apices, similar frontoclypeal region, dense body spiculation, multituberculate labrum, and modified maxillary palpus are strong synapomorphies, indicating their relationship.

Other Instars of *Leiopodus lacertinus*

At the time the first instars were collected, a dead second instar, a cast skin of a second instar, and two live third instars were also found. The following shows that second instars differ from the first in a number of ways: Head more normal in width. Antenna no longer an enlarged swelling but now a small, apparently somewhat dorsoventrally flattened, downward projecting papilla separated from parietal by distinct ring (disc); papilla about as long as basal diameter; diameter of ring about one-third distance between ring and anterior mandibular articulation (about as in mature larva); antennal sensilla closely grouped because of small size of papilla. Labral tubercles much smaller, well separated from one another; labrum normal in width (similar to that of mature larva) with surface no longer sulcate but moderately convex. Mandible (fig. 11) no longer fanglike, tapering more or less evenly to acute apex. Maxillary palpus moderate in size, now forward projecting; labial palpus not evident except for sensilla. Salivary opening well separated from mouth by convex area, no longer forming cuplike depression. Anatomy of body unknown.

The third instar is quite similar to the second, differing in structure as follows: Antennae now somewhat more pronounced. Labral tubercles scarcely evident, apical ones appearing as slight swellings. Mandible (fig. 12) stouter at base but remaining sharp pointed apically. Maxillary palpus reduced in size relative to head size. Labial palpus still not evident. Salivary opening apical on labiohypopharyngeal lobe. Abdominal segment X small, attached dorsally to IX; apicolateral lobes no longer evident.

Hence the anatomy of the head of both the second and third instar more closely resembles that of the mature larva than the first instar. This would seem to suggest that only the first instar is hospicidal although the mandibles remain sharp pointed and possibly effective for defense or attack.

Mature Larvae

Leiopodus lacertinus

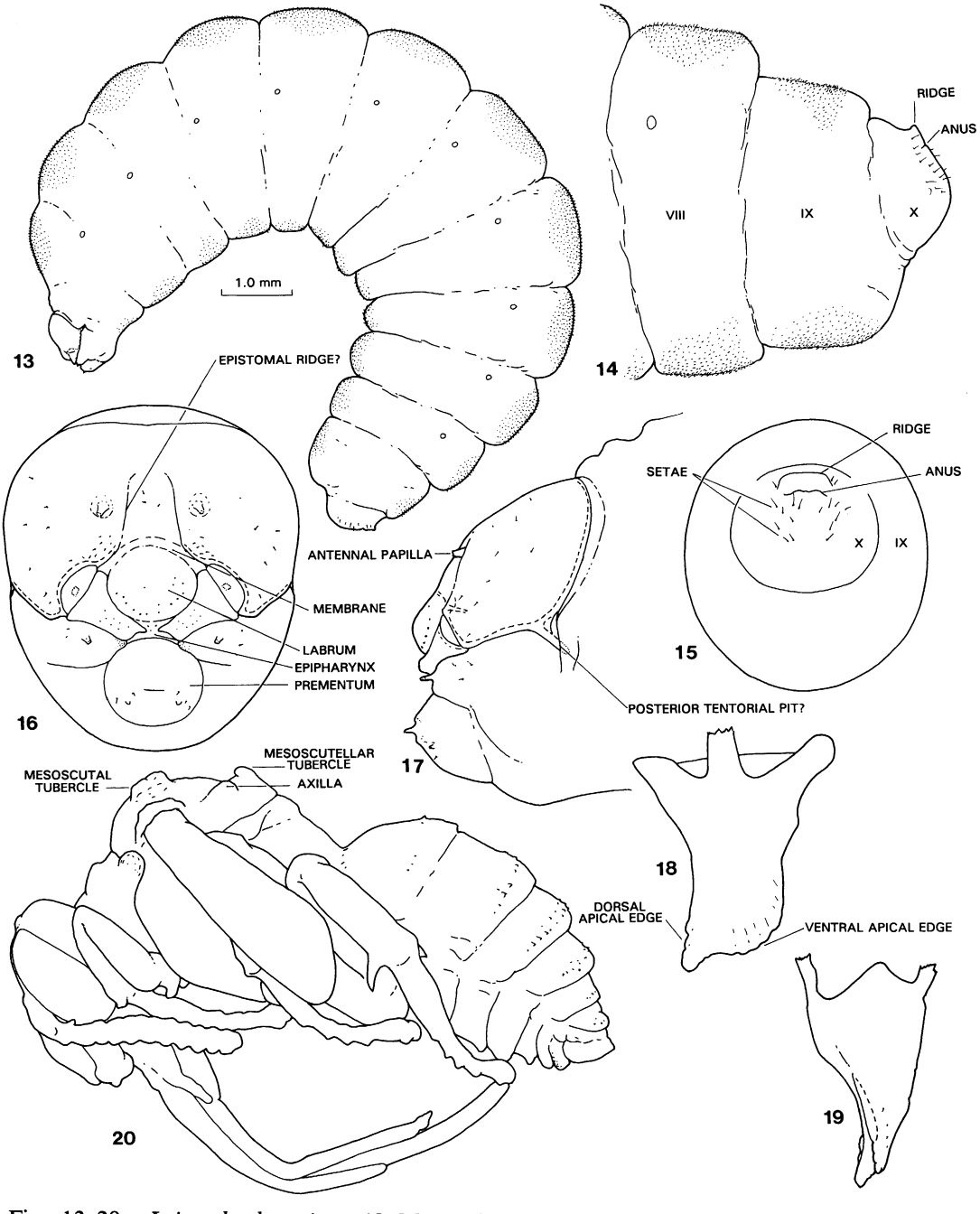
Figures 13–19

Diagnosis: The larva of this species can most easily be distinguished from larvae of *Leiopodus singularis* and *L. abnormis* because it possesses ventral body spicules that are as long as the dorsal ones and because the dorsal spicules are simple. By contrast, the ventral spicules of the other two species are much shorter than the dorsal ones and most dorsal spicules are transverse (Rozen et al., 1978: fig. 25). Other less obvious larval features by which this species can be separated from the other two are printed in boldface below. There is no certain way to differentiate the mature larva of *L. singularis* from that of *L. abnormis*.

The numerous characters italicized below distinguish mature larvae of *Leiopodus lacertinus, L. singularis,* and *L. abnormis* as a group from those of other bees.

Head (figs. 16, 17): Integument of head capsule with scattered sensilla many of which are clearly setiform at higher magnifications. Sclerotized integument moderately pigmented; following areas darker: internal head ridges, posterior arms of tentorium (internal extension of hypostomal ridge) (but not rest of tentorium), two vertical lines mesad of antennae, antennae, mandibles, maxillary palpi, and salivary lips.

Head size (fig. 13) small by comparison with body; **head capsule much wider than long as seen in frontal view but not as wide as head capsules of *Leiopodus singularis* (Rozen et al., 1978: fig. 30) and *L. abnormis,*** *anteriorly-posteriorly shallow in lateral view.* Tentorium very thin but perhaps complete; *posterior arms of tentorium (i.e., posterior extension of hypostomal ridge; see Remarks) well developed, pigmented; posterior thickening of head capsule (i.e., postoccipital ridge, but see Remarks) well defined by pigmented internal ridge; sclerotization of head capsule extending*



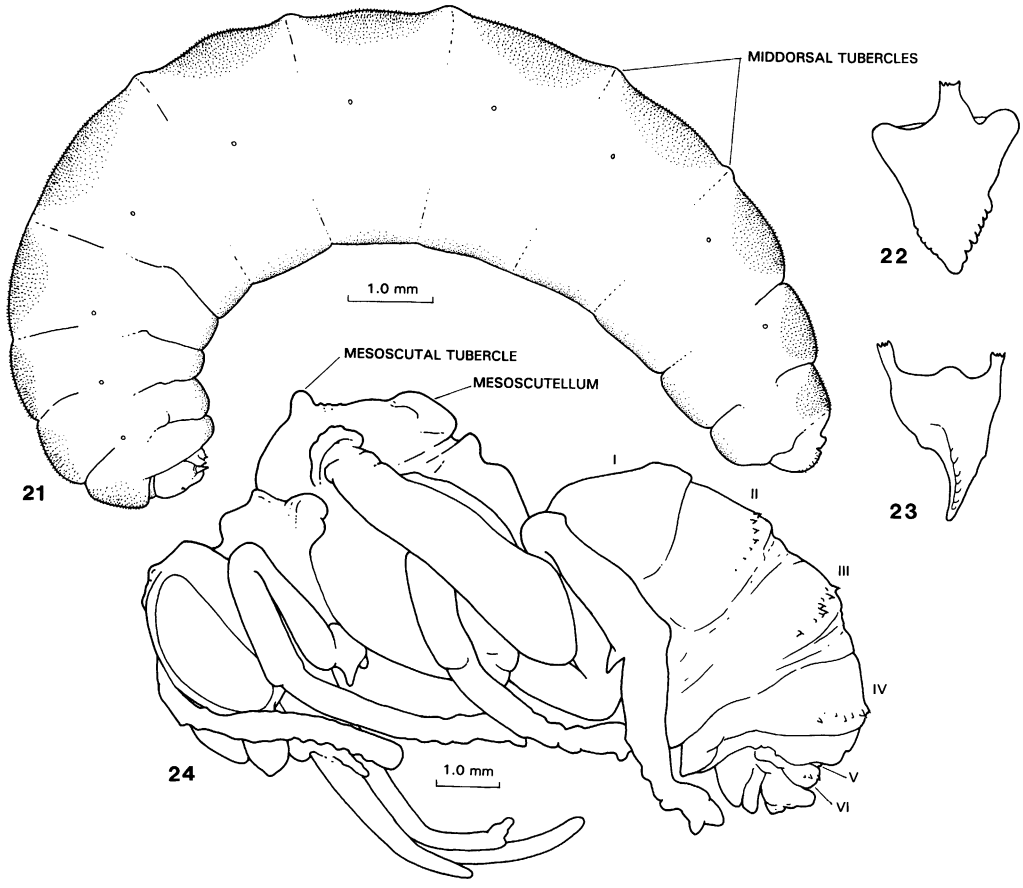
Figs. 13–20. *Leiopodus lacertinus*. **13.** Mature larva, lateral view. **14.** Apex of abdomen of mature larva, lateral view. **15.** Same, posterior view. **16, 17.** Head of mature larva, frontal and lateral views. **18, 19.** Right mandible, inner and ventral views. **20.** Pupa, lateral view. Scale refers to figures 13, 20.

posteriorly to thickening; posterior ridge bending forward only slightly above as seen in dorsal view; distinct median longitudinal thickening of head capsule absent. Parietal bands not defined. Antenna not borne on prominence; antennal disc not certainly defined because antennal papilla appearing to arise from membranous area which may or may not be disc; **antennal papilla** moderately long, considerably longer than basal diameter, **somewhat more robust than papillae of L. singularis and L. abnormis,** bearing five or more sensilla. Vertex evenly rounded and without projections or tubercles; *anatomy of frontoclypeal areas uncertain: either clypeus greatly shortened, fusing with frons above and separated from labrum by upward arching membranous area; or, alternatively, clypeus extending dorsally well above level of antennae, and pigmented nearly parallel vertical lines mesad of antenna actually mesal extension of epistomal ridge.* Frontoclypeal area not projecting as seen in lateral view (fig. 17). *Labrum with outer surface curved but not strongly projecting as seen in lateral view, bearing numerous conspicuous sensilla;* labral sclerite not evident; *labral tubercles absent, apex rounded; epipharynx large swollen area beneath curved anterior boundary of labrum and behind closed mandibles (superficially epipharynx appearing to be hypopharynx but clearly identifiable because of entrance of alimentary tract immediately below it).*

Mandible (figs. 18, 19) short, not reaching midline of head, adorally-orally flattened, broadly expanded apically, shallowly scoop shaped; outer surface without seta-bearing tubercle but with number of conspicuous sensilla; dorsal apical edge with faint crenulations (modified teeth); ventral apical edge with more distinct crenulations; cusp not evident; **dorsal apical edge of mandible tending to be straighter and ventral apical edge more extended (and therefore more scooplike) than comparable edges in *L. singularis* and *L. abnormis,* as seen in adoral or aboral view (fig. 18).** *Labiomaxillary region large in relation to head capsule, as seen in lateral view (fig. 17),* moderately projecting; maxilla moderately fused to labium at base. Maxillary apex produced mesially into pointed process bearing sharp spicules; cardo and stipes not sclerotized; articulating arm of stipes not evident although area pigmented; **maxilla not sclerotized immediately below hypostomal ridge as in *L. singularis* (Rozen et al., 1978: fig. 31) and perhaps *L. abnormis;*** palpus moderately elongate, somewhat smaller than antennal papilla; galea absent. Labium divided into prementum and postmentum; premental sclerite faintly pigmented; **prementum circular as seen from front (fig. 16);** labial palpus small, much smaller than maxillary palpus, considerably lower than salivary opening. Salivary lips projecting but moderately narrow, much narrower than distance between labial palpi. *Hypopharyngeal area not produced, not differentiated from dorsal surface of labium; hypopharyngeal groove absent.*

BODY: Integument with obvious pigmented setae on abdominal segment X; scattered short unpigmented setae, similar in length to dorsal spicules, on other body segments; *integumental spiculation conspicuous dorsally and ventrally on most segments, as illustrated (figs. 13, 14);* **dorsal body spicules sharp pointed, not transverse; ventral body spicules large, same length as dorsal ones,** *usually more or less decumbent, those of segments of thorax and abdominal segments I–V tending to be directed posteriorly,* body without spines or sclerotized areas. Body form moderately robust; *body segments not divided into cephalic and caudal annulets;* body tubercles absent except low, eversible middorsal tubercles between most body segments, apparently particularly noticeable on predefecating larvae (as in fig. 21); abdominal segment IX not produced but small segment X attached dorsally to IX as seen in lateral view; anus a downward curved transverse slit borne dorsally on segment X; *perianal area bearing distinct transverse ridge above anus.* **Spiracles moderately large; atrium somewhat larger compared to subatrium, than atria of *L. singularis* and *L. abnormis;*** spiracles uniform in size, not borne on tubercles; atrium globular, projecting slightly above body wall, with distinct but faint rim; *atrial wall with concentric rows (as seen from exterior) of small denticles;* peritreme present; primary tracheal opening with collar; subatrium moderate in length, consisting of about 10 chambers. Sex characters of larva unknown (described larva a female as revealed by pharate pupa).

MATERIAL STUDIED: One postdefecating



Figs. 21–24. *Leiopodus abnormis*. **21.** Mature, predefecating larva, lateral view. **22, 23.** Right mandible, inner and ventral views. **24.** Pupa, lateral view. Scales refer to figures 21 and 24, respectively.

larva, between Taruca Pampa and Rio del Nio, Tucumán Province, Argentina, October 29, 1989 (J. G. Rozen, A. Roig-Alsina) from cell of *Melitoma* sp.; two cast larval skins, same data. Three postdefecating larvae and one predefecating larva, Martínez, Buenos Aires Province, on the banks of La Plata River, March 15–25, 1993 (A. Roig-Alsina) from nests of *Melitoma segmentaria*.

REMARKS: The posterior tentorial arm referred to above as appearing like the posterior extension of the hypostomal ridge is a unique synapomorphy of the larvae of *Leiopodus*. Pigmented and continuous with the pigmented hypostomal ridge, it contrasts sharply with the pale thin tentorial bridge which branches at nearly right angles from it. Because it is internal, it is considered anatomically as part of the tentorium, but its true homologies are unclear. It may indeed be an internal extension of the hypostomal ridge in which case the position of the true posterior tentorial pit is in doubt (is the true pit located where the ridge enters the postcephalic region as labeled, or is it the point of attachment of the posterior point on the extension to the tentorial ridge?).

This unsettled matter leads to further complications. The posterior thickening of the head capsule of almost all bee larvae demarks the posterior boundary of the head capsule. The posterior tentorial pit lies in the most ventral point of this thickening on each side of the head. Thus the thickening is correctly termed the postoccipital ridge (Snodgrass, 1935). However, with *Leiopodus*, the conspicuous, darkly pigmented ridge that dorsally arches the head capsule as does the post-

occipital ridge of other bee larvae may not have the posterior tentorial pits at its ventral extremities. Furthermore there is a posterior extension of the head sclerotization beyond the ridge. This could mean that the ridge in *Leiopodus* is secondary, the true postoccipital ridge having been lost and functionally replaced by a more anterior one. It seems likely a better understanding of the functioning of the peculiar anterior-posterior flattening of the head capsule of all the larval instars may shed light on this matter.

Leiopodus abnormis
Figures 21–23

DIAGNOSIS: See Diagnosis of *Leiopodus lacertinus* for features by which these two species can be distinguished. The larvae of *L. singularis* and *L. abnormis* seem identical.

HEAD: As described for *Leiopodus lacertinus* except for following: Head capsule very wide, wider than that of *Leiopodus lacertinus*, about as in *L. singularis* (Rozen et al., 1978: fig. 30). Antennal papilla smaller and more tapering than that of *L. lacertinus*, about as in *L. singularis* (ibid.: figs. 30, 31).

Dorsal apical edge of mandible (fig. 22) tending to be curved and ventral apical edge more oblique; consequently apex of mandible generally more pointed. Maxilla not sclerotized immediately below hypostomal ridge as in *Leiopodus singularis* (Rozen et al., 1978: fig. 31). Prementum subtriangular as seen from front, as in *L. singularis* (Rozen et al., 1978: fig. 30.)

BODY: As described for *Leiopodus lacertinus* except for following: Dorsal body spicules mostly transverse, minute lamellae with serrate edges, like those of *L. singularis* (Rozen et al., 1978: fig. 25). Spiracular atria smaller relative to size of subatrium than that of *L. lacertinus*.

MATERIAL STUDIED: One postdefecating and two predefecating larvae, 12 km north Tigre, Buenos Aires Province, Argentina, January 18, 1990 (A. Roig-Alsina, L. Moffatt) in nests of *Diadasia baraderensis*.

REMARKS: The close agreement in larval structures of this species and *Leiopodus singularis* parallels the situation with respect to adult characters.

Leiopodus singularis
(Linsley and Michener)

The mature larva of this species was described by Rozen et al. (1978). It seems indistinguishable from the mature larva of *Leiopodus abnormis*, described above. Differences in mandibular shape seem to be the result of differential wear, for older larvae exhibit teeth that are less distinct than teeth on younger specimens, as pointed out in Rozen et al.(1978). Although the description of *L. singularis* did not refer to middorsal body tubercles, these intersegmental protrusions are evident on predefecating larvae in the collection of the American Museum of Natural History. They are also found on predefecating larvae of *L. lacertinus*.

PUPAE

Leiopodus lacertinus
Figure 20

DIAGNOSIS: Although this pupa agrees in most respects to pupae of *Leiopodus singularis* (Rozen et al., 1978) and *L. abnormis*, it can immediately be recognized because of its paired low mesoscutellar tubercles (absent in the other two species) and varicose (as opposed to evenly rounded) paired mesoscutal tubercles. An even more obvious diagnostic feature related to adult anatomy is its elongated labium and maxilla that nearly reach the abdominal apex (fig. 20), in contrast to the much shorter mouth parts of *L. singularis* (Rozen et al., 1978: fig. 34) and *L. abnormis*. The following description addresses features characteristic of pupae but not of adult-related structures, such as mouthpart length.

HEAD: Integument without setae or spicules; certain areas, especially center of mandibular swelling and palpi, evenly, finely granulate. Frons and vertex without tubercles except for scarcely noticeable swellings on vertex near ocelli; clypeus and labrum without tubercles; genal tubercles absent; antenna with only usual small tubercles but pedicel with small inner apical tubercle.

MESOSOMA: Integument without setae or spicules but some areas, especially on legs, evenly, finely granulate. Lateral angle of pronotum not produced; lateral lobe of pronotum strongly produced but rounded; mes-

episternum without tubercles; mesoscutum with paired tubercles as in *Leiopodus singularis* and *L. abnormis* but these tubercles apically varicose unlike those of *L. singularis* and *L. abnormis*; unlike in other two species, scutellum bearing distinct paired tubercles which are slightly varicose apically; axilla faintly produced; metanotum with low transverse swellings laterally; propodeum without tubercles. Tegula lacking tubercle but dorsal surface somewhat varicose; wings without tubercles or varicose areas. Forelegs with coxa having low inner apical projections; trochanter with small but distinct, rounded apical tubercles; apex of tibia with apical projection. Mid-leg without special features except inner apex of trochanter with small tubercle (near tibial spine) (not visible in illustration) and apex of tibia with apical projection. Hind legs without special features except apex of tibia somewhat swollen.

METASOMA: Integument nonspiculate, setae absent. Tergum I with several small apical pigmented tubercles on each side; terga II–VI (male) and II–V (female) each with apical row of small apically pigmented tubercles; on apical metasomal segments these tubercles best developed dorsolaterally rather than medially; sternum II with median rounded apical tubercle; other sterna without tubercles; terminal spine absent.

MATERIAL STUDIED: One male pupa, one female pupa, collected between Taruca Pampa and Rio del Nio, Tucumán Province, Argentina, October 29, 1989, (J. G. Rozen, A. Roig-Alsina) from cells of *Melitoma*.

Leiopodus abnormis
Figure 24

DIAGNOSIS: For diagnostic characters to separate the pupa of this species from that of *Leiopodus lacertinus*, see Diagnosis of the latter. There are no features by which the pupae of *L. abnormis* and *L. singularis* can be separated at this time.

HEAD: As described for *Leiopodus lacertinus*.

MESOSOMA: As described for *Leiopodus lacertinus* except for following: paired mesoscutal tubercles apically rounded; mesoscutellum without paired tubercles, each side a low generalized swelling.

METASOMA: As described for *Leiopodus lacertinus* except: Sternum II without median apical tubercle.

MATERIAL STUDIED: One male and one female pupa, same data as for larva of this species.

Leiopodus singularis
(Linsley and Michener)

The pupa of this species, described originally by Rozen et al. (1978), does not differ from the pupal description of *Leiopodus abnormis*. Apparent differences, such as in the silhouette of the mesoscutum and mesoscutellum in the illustration of *L. singularis* (Rozen et al. 1978: fig. 34) and figure 24, are due to artifacts in the preservation of the pupa of *L. singularis*.

SYSTEMATICS AND DESCRIPTIONS OF ADULTS

MATERIAL AND METHODS

Material studied, including types, was obtained from various collections. We are indebted to the curators responsible for their care. Acronyms and localities in parentheses indicate depositories of specimens. American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco, W. J. Pulawski (CAS); Cornell University Insect Collection, Ithaca, N.Y., G. C. Eickwort (CU); Central Texas Melittological Institute, Austin, J. L. Neff (CTMI); M. Fritz, Rosario de Lerma, Salta (Fritz); Instituto Miguel Lillo, Tucumán, A. Willink (IML); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata, La Plata, R. Ronderos (MLP); National Museum of Natural History, Washington, R. J. McGinley (NMNH); Natural History Museum, London, G. R. Else (London); Naturhistorisches Museum, Bern, Ch. Huber (Bern); Programa Cooperativo Sobre la Apifauna Mexicana, W. E. LaBerge (PCAM); R. B. Roberts Collection, Rutgers University, New Brunswick (RBR); Snow Entomological Museum, University of Kansas, Lawrence, C. D. Michener (SEM); Universidade Federal do Paraná, Curitiba, J. S. Moure (UFPR); University of California, Davis, L. S. Kimsey (Davis); Utah State University, Logan, T. L.

Griswold (Logan); Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch (Berlin).

Redescriptions of adults include only those morphological characters that have been found useful in distinguishing species; for details of color and vestiture the reader is referred to previous descriptions, mentioned under the synonymy of each species. Metasomal terga (T) and sterna (S) are identified with Arabic numerals.

Tribe Protepeolini

Characterization Based on Adults

Bees 5.5–13 mm long. Vestiture on head and metasoma short, appressed, on latter forming distinct patterns of pale and dark maculations, vestiture of thorax variable, erect or appressed. Mandibles bidentate, those of male with distinct brush along outer surface. Maxillary palpus with 3 to 5 segments. Stipes with longitudinal ridge on outer surface; stipital comb absent. Labium with small, dark, ovate sclerite at each side of subligular process. First flagellomere elongate, as long as following three flagellomeres. Head without ridges or carinae, vertex rounded. Axilla rounded. Metanotum slanting to nearly vertical; metapostnotum with broad basal area at an angle with more slanting posterior surface. Hind coxa enormous. Hind femur of female keeled ventrally, that of male swollen and also keeled ventrally. Claws with flat, truncate inner tooth in both sexes, except foreclaws of male bifid. Forewing with three submarginal cells; pterostigma moderate in size, approximately 2–2.5 times as long as wide. Jugal lobe of hind wing 0.30–0.35 times as long as vannal lobe measured from wing base. T5 of female with pseudopygidial area. T6 of female with apical, sclerotized, flattened projection probably homologous to pygidial plate, and row of spinelike setae at each side of projection. S6 of female not specialized. T6 of male with apical lateral angles thickened, lobate. T7 of male without pygidial plate, slightly to deeply emarginate. Male genitalia with gonocoxites and penis valves fused, forming single structure.

Characterization Based on Larvae and Pupae

Larval anatomy of the Protepeolini is distinctive. Anatomical features italicized in the description of *Leiopodus lacertinus* (above) are shared by the known larvae of *Leiopodus* and characterize the tribe. Pupal anatomy in the tribe, to the extent known, is quite uniform. However, so little is known about pupae of long-tongued bees that features distinguishing this tribe cannot be identified at present.

Larvae and pupae are described in a separate section of this paper.

Genus *Leiopodus* Smith

Leiopodus Smith, 1854: 252. Type species *Leiopodus lacertinus* Smith, 1854, by monotypy.

Protepeolus Linsley and Michener, 1937: 75. Type species *Protepeolus singularis* Linsley and Michener, 1937, by original designation.

Relationships Among Species

An analysis of the five species of *Leiopodus* was made using as outgroups all of the other tribes of Apinae. All tribes were considered to form a polytomy for outgroup comparison. Nine characters were polarized, listed in table 3. There is a single most parsimonious solution, obtained with the help of computer program Hennig86, version 1.5 (Farris, 1988). The default settings of the program were used. The cladogram in figure 25 supports the proposed synonymy of *Leiopodus* and *Protepeolus*. The phenetically more similar *L. singularis* (type species of *Protepeolus*), *L. abnormis*, and *L. trochantericus* do not form a clade. Although *L. lacertinus* (type species of *Leiopodus*) is quite distinct due to the pro-

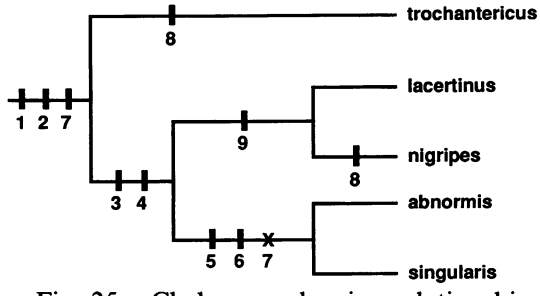


Fig. 25. Cladogram showing relationships among species of *Leiopodus*.

truding clypeus, the elongate proboscis, and the elongate, tapering female metasoma, it is shown as a derived species within the group.

A further character that may support the clade formed by *Leiopodus lacertinus, L. nigripes, L. abnormis,* and *L. singularis* is the extensive sclerotization of the dorsal surface of the penis in these species. In *L. trochantericus* there is little sclerotization of the penis dorsum, a condition probably plesiomorphic, but variation of this feature in the outgroups precluded certain polarization of the character.

TABLE 3
List of Apomorphies Based on Adult Morphology
(Outgroups are other tribes of Apinae. Apomorphies are coded 1.)

1. Female T6 with apical flattened process (probably homologous to pygidial plate) and row of spinelike setae at each side of process (figs. 26–28) (1). Unique character of Protepeolini.
2. Penis valves fused to dorsal bridge of gonocoxites (figs. 33–35), thus genital capsule forming a single sclerotized structure (1). Unique feature among bees.
3. Maxillary palpus with 4 segments (1). Plesiomorphic condition is 6 segments (*L. trochantericus* with 5, coded 0).
4. Dorsal margin of gonocoxite without distinct lobe (1). Dorsal lobe of gonocoxite present (fig. 33) is usual condition in apid bees.
5. Female T5 with crescent-shaped, membranous, hyaline, hairless area, apical to pseudopygidial area (1). Unique feature of *L. abnormis* and *L. singularis*.
6. Male S8 fused laterally to T8, forming a sclerotized ring (1). S8 and T8 connected by membranes is plesiomorphic condition.
7. T6 of male with apical lateral angles thickened, lobate (1). No such tergum in outgroups.
8. Mid-trochanter of male with spine on center of outer surface (1). Mid-trochanter rounded in outgroups.
9. Proboscis long, reaching beyond forecoxae in resting position (1). An exceedingly long proboscis occurs in certain taxa of a few outgroup tribes, but is interpreted as independently derived. This character is part of a more complex set of features: the clypeus is more protruding than in other species, the labrum is longer, and the malar area is larger. Since these features are understood as correlates of mouthparts elongation (Michener, 1944), they are not coded separately.

Key to Species of *Leiopodus*, Based on Adults

1. Proboscis in resting position with apex reaching beyond forecoxae; labial palpus twice as long as eye. Scutellum black 2

   Proboscis in resting position with apex barely reaching bases of forecoxae; labial palpus subequal to length of eye. Scutellum red 3

2. Legs light red. Clypeus above level of tentorial pits with punctures, although sometimes sparse. Mid-trochanter of male rounded; hind basitarsus without upper tooth .... *lacertinus* Smith

   Legs dark reddish brown to black. Upper part of clypeus above level of tentorial pits polished, without punctures. Mid-trochanter of male with spine on outer surface; hind basitarsus with tooth in the middle of upper margin ..... *nigripes* Friese

3. T1 and T2 with basal and apical pale bands enclosing central dark areas, apical bands sometimes interrupted. Apex of female T5 with hairs of pseudopygidial area reaching apical margin of tergum. Middle trochanter of male with conspicuous spine on center of outer surface. T6 of male lobate laterally; T7 deeply emarginate and lobate (fig. 29) .... *trochantericus* Ducke

   T1 and T2 with basal but no apical pale bands. Apex of female T5 with hairs of pseudopygidial area surrounding hairless, membranous, hyaline, crescent-shaped apical area. Middle trochanter of male without spine. T6 of male not lobate; T7 weakly emarginate apically (fig. 31) 4

4. Pale band of female T1 with posterior margin slightly curved at each side of median line forming inverted V, sometimes broken medially, then mesal portions of margin convergent. Pale band of female T2 occupying basal ⅓ to ½ of tergum. Male with hairs of mesopleuron above signum mostly appressed, no longer than 1.5 times flagellar width. South America .... *abnormis* (Jörgensen)

   Pale band of female T1 with posterior margin forming an abrupt angle at each side of median line; mesal portions of margin parallel, leaving median dark stripe. Pale band of female T2 occupying basal ½ to ⅔ of tergum. Male with hairs of mesopleuron above signum erect, over twice as long as flagellar width. North and Central America .... *singularis* (Linsley and Michener)

Leiopodus lacertinus Smith

Leiopodus lacertinus Smith, 1854: 252, Pl. 8, fig. 2, pl. 9, figs. 14–16. Types female and male, South America (London, not examined). Taschenberg, 1883: 69. Holmberg, 1886: 281. Dalla Torre, 1896: 334. Schrottky, 1902: 513; 1903: 183. Cockerell, 1905: 316. Ducke, 1907: 88; 1908a: 101–102; 1908b: 39. Friese, 1908: 90. Strand, 1909: 232, 234. Ducke, 1910a: 104. Ducke, 1910b: 366; 1912: 100. Friese, 1923: 6.

Epeolus vagans Smith, 1879: 103. Type female, Ega, Brazil (London, not examined). Dalla Torre, 1896: 331. Schrottky, 1902: 513. Cockerell, 1905: 314. Synonymy by Ducke, 1910a: 104.

Melectoides senex: Schrottky, 1902: 489 (misidentification).

This species, together with *Leiopodus nigripes*, is readily recognized by the following: long proboscis, protruding clypeus, elongate, fusiform metasoma, whitish pale pubescence, black scutellum, and pseudopygidial area of female with setae apically curved, broadened, and flattened forming shiny surface. It is distinguished from *L. nigripes* by the entirely punctate clypeus, pale red legs, and male mid-trochanter and hind basitarsus without toothlike projections.

The specimen studied from Zulia, Venezuela, differs from others in its exceedingly long proboscis, the labial palpus being 2.78 times as long as the eye, while other specimens of *Leiopodus lacertinus* have the labial palpus approximately twice as long as the eye (2.03–2.30:1). In other respects it is in agreement with the other specimens.

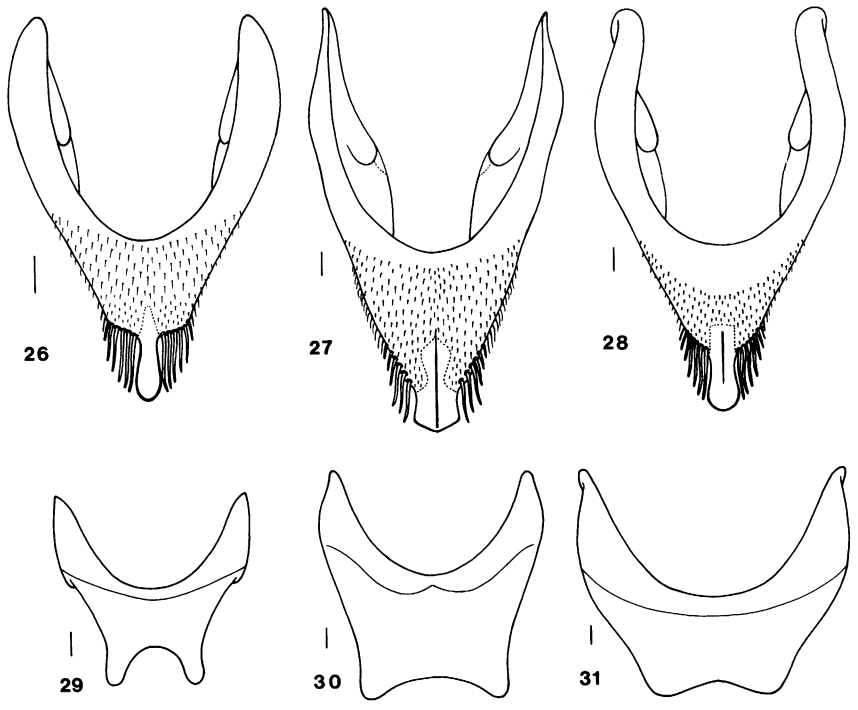
AR has not seen type material, but Smith's description and drawings allow identification of the species with certainty.

FEMALE: Length 7.5–11.0 mm; length of forewing 5.7–8.0 mm. Clypeal protuberance 0.59–0.68 times maximum width of eye in lateral view. Clypeus above level of tentorial pits with punctures and hairs, although sometimes sparse. Labrum rectangular, 0.55–0.65 times as long as broad, apical margin irregularly denticulate. Maxillary palpus with 4 segments, palpus 0.25 times as long as eye. Second segment of labial palpus longer than first, the two together over twice as long as eye length (proportion 2.03–2.78:1). Second flagellomere as long as to slightly longer than apical width. Lower portion of metapleuron with close punctures, interspaces smaller than diameter of punctures; propodeum below spiracle without punctures, tessellate or sometimes more or less polished. Metapostnotum in lateral view strongly convex, its broad base slanting, almost in the same plane as posterior part of scutellum and metanotum. Marginal cell on costal margin 0.95–1.03 times as long as distance from its apex to apex of wing. Second recurrent vein meeting second submarginal cell near its apical 0.15–0.25. Metasomal T1 in dorsal view 0.55–0.65 times as long as wide; T2 with sides converging apically in dorsal view, length from gradulus to apex of tergum approximately 0.5 times apical width. Middle triangular area of S1 basally with erect hairs, longer than diameter of flagellum, distally bare. Pseudopygidial area with hairs stiff, curved, broadened and flattened apically, forming shiny surface; hairs reach emarginate apical margin of tergum. T6, figure 27.

MALE: Length 8.3–12.5 mm; length of forewing 6.2–8.5 mm. Antenna with 11 flagellomeres. Mid-trochanter without spine on middle of outer surface. Hind femur moderately swollen, its maximum width 0.43–0.45 times its length; hind femur keeled below, hind trochanter rounded. Hind basitarsus broadest near basal third, upper margin without tooth. Apex of T6 slightly emarginate, lateral angles thickened, slightly lobate. T7 emarginate, with lateral angles lobate, apically upcurved (fig. 30). T8 and S8 articulated by membranes, as usual. Genitalia, figure 34.

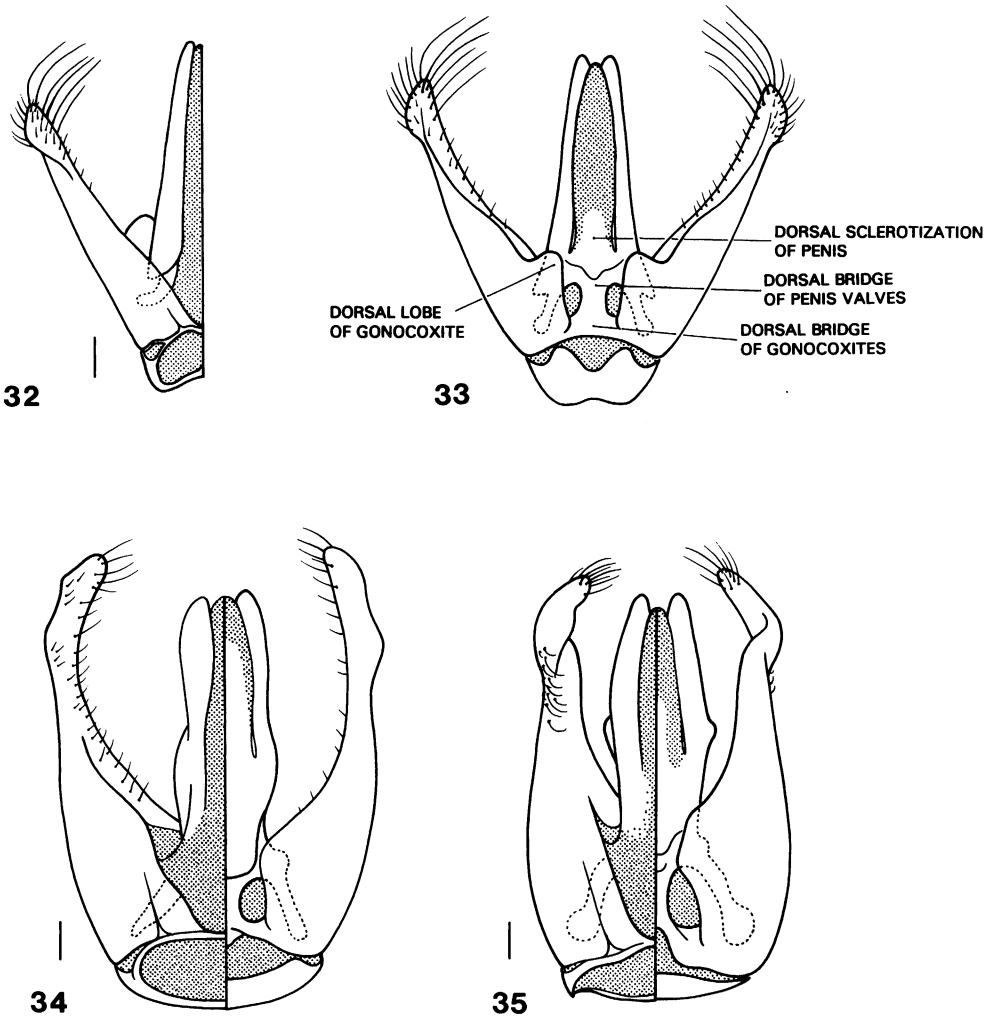
DISTRIBUTION: Panama, Colombia, and Venezuela to central Argentina (fig. 36).

MATERIAL STUDIED: **Panama**. Santa Rosa: 1 male, 27-XII-1930, A. L. Brody (CU). **Venezuela**. Zulia: 1 female, Carrasquero, 29–30-V-1976, A. S. Menke and D. Vincent (NMNH). Carabobo: 1 male, San Esteban, 1–20-XII-1929, P. J. Arduze (CU). Guárico: 1 male, Estación Biol. de los Llanos, Calabozo, 23-VI-1987, N. Ramirez (CU). **Colombia**. Meta: 1 female, Restrepo, 18-VI-1974, L. Stange (IML); 1 female, 10 km S Puerto López, 21-XI-1971, R. B. Roberts (RBR). **Ecuador**. El Oro: 1 female, 15 mi S Santa Rosa, 23-I-1955, Schlinger and Ross (CAS); 1 female, San Pedro, 8-IV-65, L. E. Peña (AMNH). **Peru**. Cuzco: 4 females, 68 km W Cuzco, Rio Apurimac, 2400 m, 23-IV-1983, C. and M. Vardy (London). **Brazil**. Pará: 1



Figs. 26–28. Female T6. **26.** *Leiopodus trochantericus*. **27.** *L. lacertinus*. **28.** *L. abnormis*.
Figs. 29–31. Male T7. **29.** *L. trochantericus*. **30.** *L. lacertinus*. **31.** *L. abnormis*. Scale lines 0.1 mm.

female, Ilha Malandeua, Maracaná, II-1955, Damasceno (UFPR). Maranhao: 2 males, Imperatriz, 20-II-1962, F. M. Oliveira (UFPR). Bahia: 1 female and 1 male, Jequié, 15-XI-1964, C. Elias (UFPR); 2 females and 2 males, Ilheus, 16-VII-1965, S. Laroca (UFPR). Minas Gerais: 1 male, P. de Caldas, XI-1961, C. Elias (UFPR); 8 males, Araxá, 29-II-1965, C. Elias (UFPR, AMNH); 6 females and 2 males, Passos, XII-1963, C. Elias (UFPR, AMNH); 1 male, Varginha, IV-1955, F. M. Oliveira (UFPR); 2 males, Virginha, II-1972 (AMNH); 1 male, Jacui, 27-XI-1962, C. Elias (UFPR, AMNH). Espiritu Santo: 2 male and 1 female, Santa Teresa, 5-II-1964, C. Elias (UFPR); 2 males, Itaguazu, 14-V-1964, C. Elias (UFPR); 1 male, Fundao, 19-I-1966, C. Elias (UFPR); 1 male, Itarana, 12-II-1966, C. Elias (UFPR); 2 males, Domingos Martins, 28-II-1966, C. Elias (UFPR). Rio de Janeiro: 1 male, Floresta da Tijuca, Distrito Federal, 14-V-1953, C. Seabra (UFPR); 1 male, S. Bento, Caxias, XI-1955, P. A. Teles (UFPR); 2 males, 6 females, Silva Jardim, III-1974, F. M. Oliveira (AMNH); São Gonçalo, XI-1955, R. Arle (AMNH). São Paulo: 1 male, Campinas, 5-XI-1972, R. M. Bohart (Logan); 1 male, Mogi-Guaçu, 23-I-1974, J. G. Rozen, F. C. Thompson, J. S. Moure (AMNH); 2 males, Guarulhos, XII-1952, P. A. Blumer (UFPR); 2 females and 1 male, Rio Claro, XI-1943, P. Fiamenghi (UFPR). Paraná: 1 male, Paranaguá, 18-I-1976, R. M. Bohart (Davis). Santa Catarina: 1 female, Nova Teutonia, 1-II-1955, F. Plaumann (Logan). Rio Grande do Sul: 1 female, Esteio, XII-1952, R. Laperriere (UFPR). **Argentina**. Misiones: 1 male and 12 females, Loreto, A. Ogloblin (MLP). Formosa: 1 female, Clorinda, III-1947, I. Morel (IML). Salta: 9 females, El Alisal, I-1990, M. Fritz (Fritz, MACN). Tucumán: 1 female, Los Nogales, II-1947, R. Golbach (IML); 1 female, Horco Molle, 5-I-1966, L. Stange (IML); 1 female, Tucumán, 20-I-1968, Weyrauch (IML); 1 female, between Taruca Pampa and Rio del Nio, 28, 1989, J. G. Rozen and A. Roig-Alsina (AMNH). Santiago del Estero: 1 male, Las Termas, 11-X-1972, G. E. Bohart (Logan). Córdoba: 1 male, El Sauce, Calamu-



Figs. 32–35. Male genitalia. **32, 33.** *Leiopodus trochantericus*, ventral and dorsal views. **34.** *L. lacertinus*, ventral and dorsal views. **35.** *L. abnormis*, ventral and dorsal views. Scale lines 0.1 mm.

chita, XII-1938, M. J. Viana (MACN); 2 females, Valle Hermoso, II-1943, M. J. Viana (MACN). Corrientes: 1 male, Ituzaingó, III-1982, M. Fritz (Fritz). Entre Ríos: 1 male, Salto Grande, II-1978, M. Fritz (Fritz). Buenos Aires: 1 male, San Fernando, 5-I-1952 (MLP); 4 females, Martínez, 16-II-1985, L. Moffatt (MACN); 1 male, La Plata, III-1985, A. Abrahamovich (Fritz).

Leiopodus nigripes Friese

Leiopodus lacertinus nigripes Friese, 1908: 91. Holotype male, from São Paulo, Brazil, 1897, Ihering (Mus. Berlin, examined). Ducke, 1910a: 104.

This species is closely allied to *Leiopodus lacertinus*, from which it is distinguished by the impunctate upper area of the clypeus, the dark legs, the male mid-trochanter with a sharp tooth on the outer surface, and the male hind basitarsus with a tooth near the middle of the upper margin.

Leiopodus nigripes is morphologically quite similar to *L. lacertinus*, but the constancy of the observed differences over a broad geographic range suggests that it is a different species. The male genitalia are similar to those of *L. lacertinus*, except for the slenderer gonostyli, and no illustration is provided.

Fig. 36. Distributions of *Leiopodus lacertinus* (dots) and *L. nigripes* (open circles).

The large size of the specimens and the circumstantial association with *Ptilothrix fructifera* (see material studied), suggest a host other than *Melitoma*.

FEMALE: Length 10.5–12.5 mm; length of forewing 8.0–8.5 mm. Clypeal protuberance 0.72–0.76 times maximum width of eye in lateral view. Clypeus above level of and around tentorial pits without punctures, polished. Labrum rectangular, 0.60–0.62 times as long as broad, apical margin irregularly denticulate, medially slightly emarginate. Maxillary palpus with 4 segments, palpus 0.25 times as long as eye. Second segment of labial palpus longer than first, the two together 2.21–2.30 times as long as eye length. Second flagellomere as long as to slightly longer than apical width. Metapleuron, metapostnotum, and propodeum as in *Leiopodus lacertinus*. Marginal cell on costal margin 0.90–1.15 times as long as distance from its apex to apex of wing. Second recurrent vein meeting second submarginal cell near its apical fifth. Metasomal T1, T2, S1, and pseudopygidial area as in *L. lacertinus*. T6 similar to *L. lacertinus*, but sclerotized apical projection longer, narrower, and parallel sided.

MALE: Length 11.0–13.5 mm (holotype 11.3); length of forewing 9.2–9.8 mm (holotype 9.2). Antenna with 11 flagellomeres. Middle trochanter with strong spine on middle of outer surface. Hind femur swollen, its maximum width 0.47–0.55 times its length; hind femur keeled below, hind trochanter rounded. Hind basitarsus broadest near middle, with distinct tooth on upper margin. Apex of T6 slightly emarginate, lateral angles thickened, slightly lobate. T7 broadly emarginate (medially notched in holotype) with lateral angles lobate, apically upcurved. T8, S8, and genitalia as in *Leiopodus lacertinus*, but gonostyli slenderer.

DISTRIBUTION: Colombia, Brazil (fig. 36).

MATERIAL STUDIED: **Colombia**. Guajira: 1 male, Nazaret. 1976, J. Bird (AMNH). **Brazil**. São Paulo: 1 male, holotype (see above); 1 female, Botucatu, X-1956, Bockermann (UFPR). Goiás: 1 male, Ihla do Bananal, Santa Isabel do Moro, VI-1961, M. Alvarenga (SEM). Paraná: 1 male and 1 female, Vila Velha, 21-II-1965, "junto as ninho de *Ptilothrix fructifera*," Mitchell and Moure (UFPR).

Leiopodus trochantericus Ducke

Leiopodus trochantericus Ducke, 1907: 87. Lectotype male, by present designation, from Codó, Maranhao, Brazil, 21 June 1907, A. Ducke (Bern, examined). Ducke, 1908c: 79; 1912: 100.

Isepeolus analis Jörgensen, 1912a: 150, fig. H. Lectotype male, by present designation, from Chacras de Coria, Mendoza, Argentina, 28-X-1908, P. Jörgensen (Mus. La Plata, examined). Jörgensen, 1912b: 316. NEW SYNONYMY.

This species can be distinguished by the combination of the following features: the scutellum is red, the metasomal terga have basal and apical pale bands, the maxillary palpus has 5 segments, the female pseudopygidial area is formed by pointed setae which reach the apical margin of the tergum, the male antenna has only 10 flagellomeres, the male mid-trochanter has a strong spine on the outer surface, and the male T7 is deeply emarginate and lobate.

FEMALE: Length 6–8.5 mm; length of forewing 4.5–6.2 mm. Clypeal protuberance 0.4–0.5 times maximum width of eye in lateral view. Clypeus entirely punctate and hairy. Labrum transverse, twice as broad as long,

lateral angles rounded, apical margin with sharp denticle at each side of deep median emargination. Maxillary palpus with 5 segments, palpus 0.3 times as long as eye. Second segment of labial palpus shorter than first (proportion 0.6–0.65:1), the two together slightly longer than eye length (proportion 1.1:1). Antennal segments short, second flagellomere shorter than its apical width (0.60–0.77:1). Lower portion of metapleuron polished, with few punctures separated by interspaces wider than diameter of punctures; propodeum below spiracle with punctures sparse or no punctures at all. Metapostnotum in lateral view slightly convex, its broad base slanting, almost in the same plane as posterior part of scutellum and metanotum. Marginal cell on costal margin 0.79–0.93 times as long as distance from its apex to apex of wing. Second recurrent vein meeting second submarginal cell near its apical ⅙ to interstitial with second transverse cubital vein. Metasomal T1 in dorsal view approximately half (0.45–0.51) as long as wide; T2 with sides parallel, in dorsal view length from gradulus to apex of tergum 0.4 times apical width. Middle triangular area of S1 with hairs erect, longer than diameter of flagellum. Pseudopygidial area formed by erect, stiff setae, which reach emarginate apical margin of tergum. T6, figure 26.

MALE: Length 5.8–8.2 mm; length of forewing 4.3–6.5 mm. Antenna with 10 flagellomeres. Middle trochanter with conspicuous spine on middle of outer surface. Hind femur swollen, its maximum width 0.55–0.68 times its length; hind femur and trochanter bluntly keeled below. Hind basitarsus without tooth on upper margin. T2–T5 with lateral subapical rounded elevations, enhanced by color pattern. Apex of T6 slightly emarginate, lateral angles thickened, lobate, upcurved. T7 deeply emarginate, with lateral angles lobate, apically upcurved (fig. 29). T8 and S8 articulated by membranes, as usual. Genitalia, figures 32, 33.

DISTRIBUTION: Northern Brazil to central Argentina (fig. 37).

MATERIAL STUDIED: **Brazil**. Maranhao: 1 male, Codó, lectotype of *L. trochantericus* (data as above). Ceará: 1 female, Aurora, VI-1956, A. Soares (UFPR). Paraíba: 2 females, São João do Cariri, 2-XI-1955, C. Gonçalves

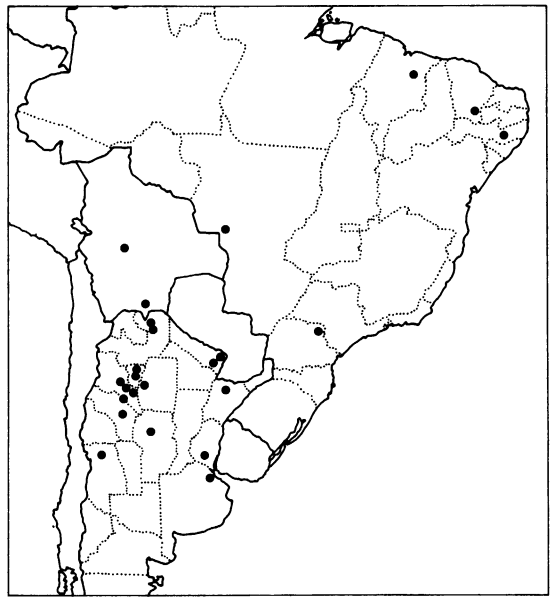


Fig. 37. Distribution of *Leiopodus trochantericus*.

(SEM). Mato Grosso: 1 male, Caceres, 19-X-1961, F. Oliveira (UFPR). Paraná: 1 female, Jacarezinho, 18-II-1961, M. Laroca (UFPR). **Bolivia**. Cochabamba: 1 female, Cochabamba, 2600 m (MLP). Tarija: 1 male, Tarija, 20-III-1968, J. C. Ballard (Logan). **Argentina**. Salta: 3 females and 1 male, 40 km WNW Hickmann, 12–14-XI-1989, J. G. Rozen and A. Roig-Alsina (AMNH); 2 females, Tartagal, 11-VII-1944, R. Golbach (IML); 1 male, Tablillas, 15-II-1945, A. Martínez (MLP); 1 male, Orán, II-1945, A. Martínez (MLP). Tucumán: 9 males, Tapia, 21-XI-1989, J. G. Rozen and A. Roig-Alsina (AMNH); 5 females, 8 km SW Ticucho, 24-III-1990, J. G. Rozen and A. Roig-Alsina (AMNH); 1 female, Horco Molle, 17-X-1972, J. L. Neff (CTMI); 2 males and 12 females, 11 km N El Cadillal, 11 and 18-XII-1983, R. B. Roberts (RBR, SEM). Santiago del Estero: 1 female, Termas de Rio Hondo, 24-IV-1951, A. Ogloblin (MLP); 1 male, Tapeo, 22-IV-1951, A. Ogloblin (MLP). Formosa: 5 males and 4 females, Gran Guardia, 20-X-1952, J. Foerster (MLP); 1 male, Clorinda, III-1947, I. Morel (IML). Catamarca: 1 male, San Fernando, J. G. Rozen and A. Roig-Alsina (AMNH); 1 male and 2 females, 30 km ESE Mazán, 9-II-1984, R. B. Roberts (RBR, SEM); 3 males

and 2 females, Andalgalá, 29-X-1973, J. L. Neff (CTMI); 2 males, Belén, 1-XI-1972, G. E. Bohart (Logan); 1 male Campo Pocara, 11-XI-1951, J. Foerster (SEM); 3 females, Las Viñas, 9-XI-1942, A. Ogloblin (MLP). La Rioja: 1 male, La Rioja (SEM); 1 male and 1 female, La Rioja (MACN). Mendoza: 1 male, Chacras de Coria, lectotype of *L. analis* (data as above). Córdoba: 1 male, Córdoba, Giacomelli (MACN). Corrientes: 2 females, Palmar Grande, 11-II-1949 (MACN). Entre Ríos: 1 female, Tuyuparé, 26-II-1911, J. Brèthes (MACN). Buenos Aires: 1 female, Tigre, 21-X-1948, A. Ogloblin (MLP); 5 males and 4 females, Canal San Fernando, 25-XII-1945, A. Ogloblin (MLP); 1 female, Otamendi, 1-II-1990, L. Moffatt (entering nest of *D. distincta* (Holmberg)) (MACN).

Leiopodus abnormis (Jörgensen), NEW COMBINATION

Isepeolus abnormis Jörgensen, 1912a: 150–151. Holotype female, La Paz, Mendoza, Argentina, 29-I-1908, P. Jörgensen (MLP, examined). Jörgensen, 1912b: 316. Ducke, 1912: 100.

Leiopodus bifasciatus Schrottky, 1920: 215. Holotype female from Alberdi, Santa Fe, Argentina (lost?). NEW SYNONYMY.

Protepeolus abnormis: Eickwort and Linsley, 1978: 20.

Leiopodus abnormis can be distinguished from the other species, except *L. singularis*, by the absence of pale apical bands on the metasomal terga, the hyaline, hairless, crescent-shaped apical area of the female T5, the T6 of the male not lobate laterally, and the T7 of the male weakly emarginate apically. For differences from *L. singularis*, see comments under that species.

The size variation of this species is striking. The smallest specimens measured 5.5 mm in length, while the largest almost doubled that size. This suggests that more than one host is exploited by *L. abnormis*.

FEMALE: Length 5.5–10 mm; length of forewing 4.5–7.6 mm. Clypeal protuberance 0.3–0.4 times maximum width of eye in lateral view. Clypeus entirely punctate and hairy. Labrum transverse, twice as broad as long, center of disc tuberculate at each side of median line, apex denticulate, in some specimens weakly emarginate medially. Maxillary palpus with 4 segments, palpus 0.15 times as long as eye. Second segment of labial palpus shorter than first (proportion 0.5–0.55:1), the two together slightly longer than eye length (proportion 1.1:1). Second flagellomere shorter than its apical width (proportion 0.70–2D0.85:1). Lower portion of metapleuron and propodeum below spiracle evenly, densely punctate. Metapostnotum in lateral view convex, its base less slanting than metanotum. Marginal cell on costal margin 0.55–0.61 times as long as distance from its apex to apex of wing. Second recurrent vein usually meeting second transverse cubital vein, sometimes basal to it by 1 or 2 vein widths. Metasomal T1 in dorsal view 0.59–0.62 times as long as apical width. T2 with sides parallel, in dorsal view length from gradulus to apex of tergum 0.47–0.5 times apical width. Middle triangular area of S1 with hairs appressed, shorter than diameter of flagellum. Pseudopygidial area formed by erect, stiff hairs, surrounding crescent-shaped, hairless, hyaline membranous area, which is anteriorly margined by a low carina. T6, figure 28.

MALE: Length 5.5–9.5 mm; length of forewing 5–9 mm. Antenna with 11 flagellomeres. Middle trochanter without spine on middle of outer surface. Hind femur moderately swollen, its maximum width 0.43–0.45 times its length; hind femur keeled below, but trochanter rounded. Apex of T6 not emarginate, simple; apex of T7 slightly emarginate, depressed medially. T8 and S8 fused, forming sclerotized ring. Genitalia, figure 35.

DISTRIBUTION: Northern Brazil to central Argentina (fig. 38).

MATERIAL STUDIED: **Brazil**. Rio Grande do Norte: 1 male, Ceará Mirim, X-1940, D. Alves (UFPR). **Bolivia**. Santa Cruz: 1 male, Santa Cruz, 8-II-1971, M. Fritz (UFPR). **Argentina**. Jujuy: 1 female, El Piquete, 28-XI-1951 (MLP). Salta: 2 females, 40 km WNW Hickmann, 12–14-XI-1989, J. G. Rozen and A. Roig-Alsina (AMNH); 3 males and 5 females, Sumalao, II-1989, M. Fritz (Fritz, MACN); 3 males, Coronel Moldes, I-1989, M. Fritz (Fritz); 1 female, Urundel, 22-XI-1942, A. Ogloblin (MLP); 1 male, Urundel, 21-II-1971, M. Fritz (UFPR); 10 females, La Viña, II-1985, XI-1985 and I-1986, M. Fritz (Fritz, MACN); 1 male, Embarcación, 5-XII-1954, A. Ogloblin (MLP); 1 female, Cande-

laria, 20-I-1986, J. L. Neff (CTMI); 2 females, Chicoana, III-1989, M. Fritz (Fritz). Chaco: 1 female, Resistencia, 5-XI-1945, A. Ogloblin (MLP); 1 female, Fuerte Esperanza, XII-1978, M. Fritz (Fritz). Santiago del Estero: 2 females, Termas de Río Hondo, 2-VI-1974, L. Stange (IML); 6 females, Termas de Río Hondo, 13-XII-1983, R. B. Roberts (RBR); 1 female, Suncho Corral, 28-XII-1975, L. Stange (IML); 3 males, Icaño, Wagner (MLP); 1 male, Quirós, 28-XI-1941 (MLP). Tucumán: 4 females and 1 male, 8 km SW Ticucho, 24-III-1990, J. G. Rozen and A. Roig-Alsina (AMNH); 31 females and 4 males, 11 km N Cadillal, 3-4 and 25-III-1990, J. G. Rozen and A. Roig-Alsina (AMNH); 1 female, Tapia, 10-XII-1971, D. J. Brothers (SEM); 3 males and 2 females, Tapia, 4-I-1976, L. Stange (IML); 1 female, Tapia, IX-1959, Hurd and Moure (UFPR); 1 female, Choromoro, 12-XI-1942, A. Ogloblin (MLP); 1 female, Horco Molle, 29-X-1972, J. L. Neff (CTMI); 1 female, Cadillal, 4-XII-1975, R. M. Bohart (Davis); 7 males and 86 females, 11 km N Cadillal, 11 and 18-XI-1983, 9-XII-1983 and 28-IV-1984, R. B. Roberts (RBR, SEM). Catamarca: 8 males and 1 female, Andalgalá, 19-XI-1944, A. Ogloblin (MLP); 1 male, Andalgalá, 27-X-1973, J. L. Neff (CTMI); 1 male and 2 females, Santa María, 16-I-1986, J. L. Neff (CTMI); 1 female, Las Viñas, 9-XI-1942, A. Ogloblin (MLP); 4 females, Santa María, 19-III-1974, L. Stange (IML); 1 female, Belén, 30-X-1972, L. Stange (IML). La Rioja: 16 males and 3 females, La Rioja, 26-XI-1941, A. Ogloblin (MLP); 1 male, Estación Amado, 19-I-1935, J. Cáceres (SEM); 3 males, Villa Unión, 12-XII-1971, Porter and Stange (IML); 1 male, Villa Castelli, 14-XII-1971, Stange and Porter (IML). Mendoza: 1 female holotype, data as above (MLP); 2 females, 10 km W Carrizal, 6-I-1990, A. Roig-Alsina (MACN). Córdoba: 4 males, Bialet Massé, 11-I-1976, A. Willink (IML); 1 male, Valle Hermoso, XII-1942, M. J. Viana (MACN); 1 female, Salsacate, I-1979, G. Williner (MACN); 2 males Córdoba, Giacomelli (MACN). Santa Fe: 3 females, Vera, 16-XI-1945, A. Ogloblin (MLP); 4 females, Guadalupe, 8-XI-1945 (MLP); 3 males and 1 female, Piquete, 9-I-1929, Bridarolli (MACN); 2 males, Rosario, 10-XII-1945, A. Ogloblin (MLP). Buenos Aires: 1 male, Reconquista, 21-XI-1945, A. Ogloblin (MLP); 1 male and 4 females, 12 km NW Tigre, 15-I-1990, A. Roig-Alsina (MACN). Río Negro: 1 male, Río Colorado, III-1958, A. Ogloblin (MLP).

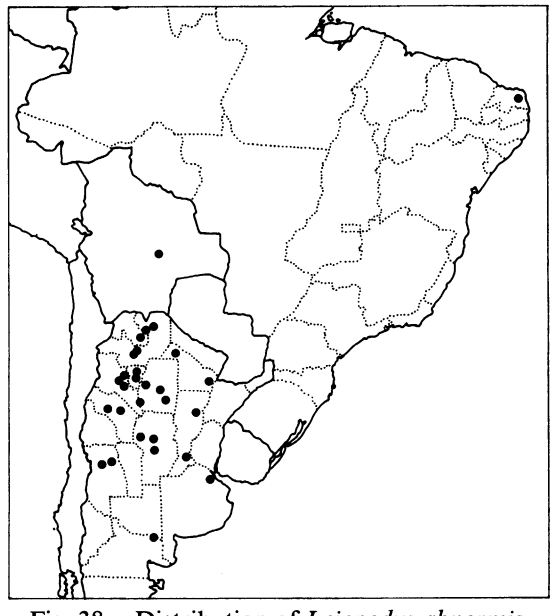


Fig. 38. Distribution of *Leiopodus abnormis*.

Leiopodus singularis (Linsley and Michener), NEW COMBINATION

Protepeolus singularis Linsley and Michener, 1937: 76–77. Holotype female, Albuquerque, New Mexico, 1–3-IX-1935, C. D. Michener (California Academy of Sciences, not examined). Rozen, Eickwort, and Eickwort, 1978: 24 pp. Eickwort and Linsley, 1978: 14–19.

Protepeolus integer Linsley, 1939: 4–5. Holotype male, Douglas, Arizona, 18-VIII-1935, W. Jones (California Academy of Sciences, not examined). Synonymy by Eickwort and Linsley, 1978: 15.

This species is closely allied to *Leiopodus abnormis* from which it is distinguished by the pattern of pubescence and the length of the vestiture, as mentioned in the key to the species. The extent of the pale pubescence is larger and the vestiture is longer in *L. singularis* than in *L. abnormis*. The northernmost record of *L. abnormis* is in the state of Rio Grande do Norte in Brazil, and the southernmost record of *L. singularis* is in

Guatemala. In both cases they are hosted by species of *Diadasia*, which thrive in xeric and mesic habitats in North and South America. The two forms are morphologically quite close, and they may represent disjunct populations of a single species. Since the male genitalia are similar in the two species, no illustration for *L. singularis* is presented.

Eickwort and Linsley (1978) found a 3-segmented maxillary palpus in all the North American specimens they studied, although the length of the palpi varied considerably. AR found that the character is not constant, since at least some Mexican specimens have 4 segments (San Luis Potosí, SEM). This reduction in the number of segments represents, at least as a trend, an apomorphy in respect to *L. abnormis*, since specimens of the latter consistently have a 4-segmented maxillary palpus.

FEMALE: Length 7.0–9.8 mm; length of forewing 5.5–8.0 mm. Clypeus, labrum, and proboscis as in *Leiopodus abnormis*. Maxillary palpus usually with 3 segments of variable length, but some specimens with 4 segments. Second flagellomere shorter than its apical width (proportion 0.78–0.90:1). Metapleuron, propodeum, and metapostnotum as in *L. abnormis*. Marginal cell on costal margin 0.59–0.66 times as long as distance from its apex to apex of wing. Second recurrent vein meeting second transverse cubital vein, or nearly so. Metasomal T1 and T2 as in *L. abnormis*. Middle triangular area of S1 with hairs appressed, at least in part as long as diameter of flagellum. Pseudopygidial area of T5 and T6 as in *L. abnormis*.

MALE: Length 7.5–10.0 mm; length of forewing 6.6–8.5 mm. All features as in *Leiopodus abnormis*, but vestiture on thorax and legs longer and metasomal bands of pale pubescence broader.

DISTRIBUTION: Southwestern U.S.A. to Guatemala.

MATERIAL STUDIED: **U.S.A.** Specimens examined by Eickwort and Linsley (1978) from the United States are not listed here; temporal and geographic distributions are presented in their paper (ibid. 1978: fig. 14). **México.** Chihuahua: 1 female, Catarinas, 26-VII-1947 (AMNH); 42 mi SW Camargo, 15-VII-1947 (AMNH); 1 female, Coyame, 28-VIII-1991, R. L. Minckley (ex: *Dyssodia aurea*) (PCAM); 1 female Guadalupe, 20-VIII-1991, J. G. Rozen, N. Pember (PCAM); 1 female, 31 km W Ojinaga, 28-VIII-1991, R. L. Minckley (PCAM). Sonora: 1 female, 28 mi S Navojoa, 3-X-1972, Villegas and Kane (Davis). Durango: 1 female, Nombre de Dios, 1-VIII-1951, P. D. Hurd (NMNH). San Luis Potosí: 1 female, San Juan Rio, 30-VII-1947 (SEM). Veracruz: 2 males, 8 km S Carrigal, 5-XI-1991, R. Ayala, Noguera (140 m, along river) (PCAM). Additional Mexican localities are mapped in Eickwort and Linsley (1978: fig. 14). **Guatemala.** 2 males, San Gerónimo, Champion colls. (UFPR).

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