Rev. Mus. Argentino Cienc. Nat., n.s.
5(1): 99-112, 2003
Buenos Aires, ISSN 1514-5158

Description, phylogenetic relationships, and biology of *Litocalliopsis adesmiae*, a new genus and species of South American calliopsine bees (Hymenoptera, Andrenidae)

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Abstract: The new genus and species *Litocalliopsis adesmiae* is described from the province of Buenos Aires, Argentina. The phylogenetic relationships of the new genus are discussed, suggesting that it is the sister group of the broadly distributed genus *Calliopsis* Smith. Descriptions and illustrations of the new taxon, and a key to separate *Litocalliopsis* from other calliopsine genera, are presented. A nesting area of the species was studied, and the biological features of the species are described and compared to those of other calliopsines. Such features are adult activity, nest architecture, cell structure, shape and position of provisions, egg placement, mating behavior, and plants visited. These bees collected pollen from the legume *Adesmia bicolor* (Poir.) D.C. The postdefecating larva is also described and illustrated.

Key words: bees, phylogeny, nesting behavior, larval morphology.

The bee tribe Calliopsini is a distinctive group of andrenids restricted to the Americas. It has an amphitropical distribution, with maximum diversity in xeric areas (Ruz, 1991, Michener, 2000). Four of its genera, *Acamptopoeum* Cockerell, *Arhysosage* Brèthes, *Callonychium* Brèthes, and *Spinoliella* Ashmead, are South American, while the large genus *Calliopsis* Smith is represented in both South and North America, with several subgenera particular to each region. According to the phylogeny presented by Ruz (1986, 1991) the tribe originated in the southern hemisphere. In this contribution we describe a new genus and suggest that it is the sister group of *Calliopsis*, reinforcing the idea of a South American origin of the group.

The new genus *Litocalliopsis* shares some features with *Calliopsis*, and it could have been described as another of its subgenera. But *Litocalliopsis* lacks the male sternal characters that Ruz (1991) considered as distinctive of *Calliopsis* in the broad sense that she proposed. The males of *Calliopsis s. l.* have median projections of the distal margins of the fourth and fifth sterna which are unique to this genus. The inclusion of *Litocalliopsis* as a subgenus would have weakened the usefulness of *Calliopsis* in its current sense (Ruz, 1991, Michener, 2000). Furthermore, even though our phylogenetic analysis suggests that *Litocalliopsis* is the sister group of *Calliopsis*, it presents some features, both of adult and larval morphology, that are suggestive of *Acamptopoeum*. In the key to the genera of Calliopsini presented by Ruz (1991), the males of *Litocalliopsis* run to *Calliopsis*, but the females run to *Acamptopoeum*.

Litocalliopsis adesmiae is only known from its type locality in the province of Buenos Aires, Argentina. It was found in the "Francisco J. Muñiz" Reserve, near the locality of Moreno, where a nesting area was discovered. The bees were collecting pollen from *Adesmia bicolor* (Poir.) D.C., a creeping native legume which is highly palatable to cattle. The protected conditions in the Reserve have probably helped in preserving blooming stands of this plant, as well as the population that we found of this rare bee.

MATERIAL AND METHODS

Morphological terminology for adults follows Ruz (1991). The metasomal terga (T) and sterna (S) are identified with Arabic numerals. The formats of the generic and the species descriptions follow those of Ruz (1991) for an easy comparison, although the characters have not been num-

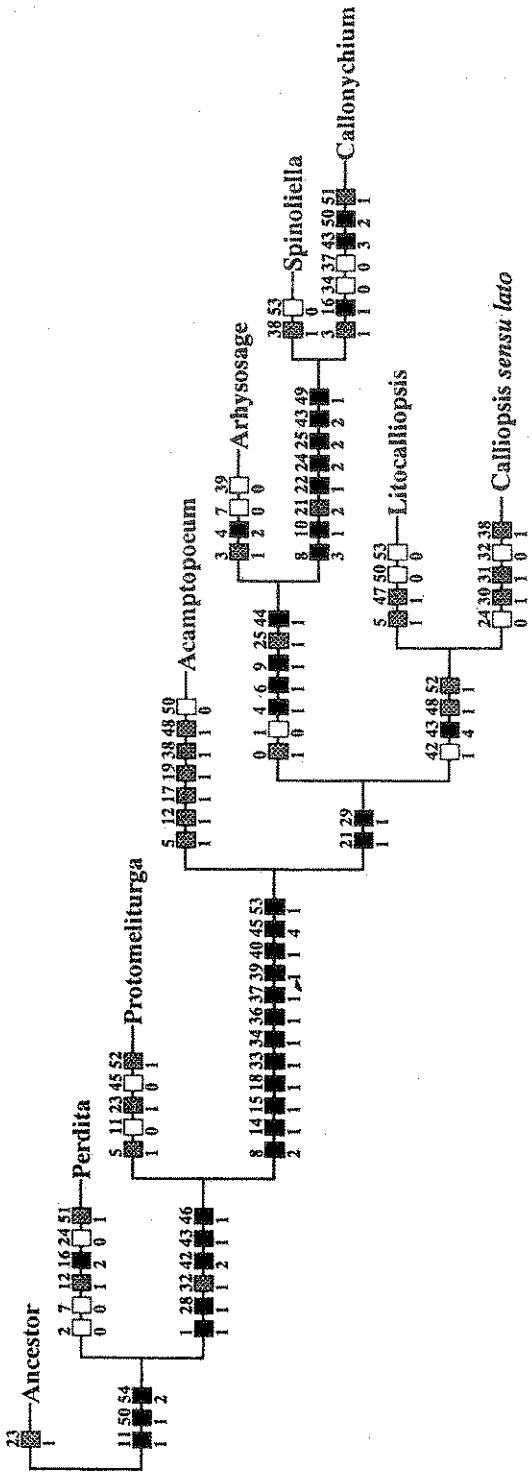


Fig. 1. Cladogram showing relationships among genera of Callopsini. Black squares represent nonhomoplastic changes, gray squares represent homoplastic changes, and white squares represent nonhomoplastic reversals.

bered. Terminology for larval description follows Michener (1953) and Rozen (1966), and for nest features, Rozen (1989).

Type material is deposited in the following collections: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Fundación e Instituto Miguel Lillo, Tucumán, Argentina (FIML); Museo de La Plata, La Plata, Argentina (MLP); Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile (PUCV); University of Kansas, Lawrence, U.S.A. (KU).

RELATIONSHIPS OF *LITOCALLIOPSIS*

The relationships of *Litocalliopsis* were studied taking into account the phylogenetic study of the tribe Calliopsini made by Ruz (1991). Outgroups are the tribes Perditini and Protomeliturgini. The new genus was coded for the 51 characters considered by Ruz (Table 1), and also for three characters that she discussed but did not include (characters 52-54 in the list).

Character 29 (pygidial plate of the male well defined or not) has been re-coded for *Acamptopoeum*, which lacks a pygidial plate. This genus is miscoded in Ruz (1991), probably due to an error, since it is coded correctly in Ruz (1986). Once corrected, her matrix from 1991 gives the same two topologies presented in 1986 for the Calliopsini, which differ in the position of *Acamptopoeum*.

The inclusion of character 52 (length of male first flagellomere) modifies the topology presented by Ruz (1991) regarding the subgenera of *Calliopsis*. The subgenera *Calliopsis (Calliopsis)* and *C. (Perissander)* in our analysis are not sister groups, but *C. (Calliopsis)* first and *C. (Perissander)* second are the sister groups of the next branch. Besides this exception, the analysis results in a topology that is entirely similar to that of Ruz (1991). The relationships among subgenera of *Calliopsis* are not depicted in Fig. 1, since they are beyond the scope of this contribution.

The analysis was performed with the program NONA (Goloboff, 1993), and the trees were later examined and printed with CLADOS v.1.0 (Nixon, 1991). NONA was run using the following: mult*15 (hold 50); the Bremer suppport was also calculated. Multistate characters were run as additive, following the criterium used by Ruz (1991).

A single tree was obtained (Fig. 1). Its statistics are: tree length 127, CI = 56, RI = 73. *Acamptopoeum* appears as the sister group of the remaining Calliopsini, and the *Arhysosage* group (*Arhysosage, Callonychium,* and *Spinoliella*) as the sister group of *Litocalliopsis* + *Calliopsis s. l.*

The position of *Acamptopoeum* as the basal group is conflicting in the analyses of Ruz (1986, 1991). In these analyses the *Arhysosage* group can be alternatively the basal branch. In our analysis there is no ambiguity regarding the position of *Acamptopoeum* (Fig. 1), but the support for the branch leading to all other Calliopsini (Bremer support = 1) is low, in spite of the low homoplasy of character states 21-1 (keirotrichia of the female forming a longitudinal strip) and 29-1 (pygidial plate of the male well defined).

The *Arhysosage* group is strongly supported (Bremer support = 9). It is a distinctive group, as pointed out by Ruz (1991).

The clade *Litocalliopsis* + *Calliopsis s. l.* is supported by character states 42-1 (gonocoxites connected by membrane), 43-4 (gonostylus absent), 48-1 (penis completely separated from penis valves), and 52-1 (first flagellomere of male about twice as long as second). The first two character states have a low homoplasy, and are invariant within the clade. Character state 48-1 is also invariant within the clade but is shared with only *Acamptopoeum*; this is one of the characters that contributes to the conflicting position of the latter genus. Character state 52-1 has a high homoplasy. The branch is moderately supported (Bremer support = 3).

Calliopsis s. l. is supported by character states 24-0 (scopa of female dense), 30-1 (S4 of male with distal margin medially produced), 31-1 (S5 of male with distal margin medially produced), 32-0 (S1-5 of female with stratum of short scattered hairs), and 38-1 (S6 of female with basal sclerotization free). The Bremer support for the branch is 4. The particular shapes of the male sterna S4 and S5, which are exclusive of the group, are the best support for *Calliopsis s. l.* The absence of a gonostylus, that was considered as diagnostic of *Calliopsis s. l.* by Ruz (1991), is also shared by *Litocalliopsis*.

It should be noted that *Litocalliopsis* shares with *Acamptopoeum* several features. These are the structure of the labrum, the elongate sting of the female, and the fused volsellae of the male (also shared with *Verbenapis*). These characters, together with the free penis valves (character 48-1) mentioned above, suggest that the basal position that we have obtained for *Acamptopoeum* in the cladogram (Fig. 1) may still be challenged by further study.

KEY TO SEPARATE *LITOCALLIOPSIS* FROM OTHER CALLIOPSINI
(Modified from Ruz, 1991)

1. Orbits subparallel or divergent below. Tentorial pit of male at median point of outer subantennal suture, or nearly so. Labrum of female flat or with smooth, rounded, nearly transverse ridge; distal area flat, not inflexed. (*Arhysosage, Callonychium,* and *Spinoliella*, see Ruz, 1991, to separate this genera) ..... *Arhysosage* Group
- Orbits generally convergent below. Tentorial pit of male clearly below median point of outer subantennal suture (Fig. 4). Labrum of female with basal area well excavated; distal area convex, inflexed, protuberant in lateral view. 2
2. Males 3
- Females 5
3. T7 distally with a median smooth area, delimited by hairs, tapered at apex ..... *Acamptopoeum*
- T7 with pygidial plate rounded or truncate at apex (sometimes poorly delimited by ridge or carina laterally) 4
4. S5 with well-developed median projection on distal margin, though sometimes inconspicuous (Figs. 11C, 18E, 20H, in Ruz, 1991). S6, in South American groups, apically deeply emarginate, and with two lateral points ..... *Calliopsis*
- S5 with distal margin simple, without median projection or any other modification. S6 slightly emarginate apically, and with two apical longitudinal ridges united basally forming a U-shaped structure (Figs. 11, 14) ..... *Litocalliopsis*
5. Labrum with basal area usually glabrous; if pilose, also flat (without ridge). Hind tibia with keirotrichia widespread, but absent toward ventral margin, to completely absent between dense apical and basal patches ..... *Calliopsis*
- Labrum with basal area at least laterally pilose (Fig. 9F, G, in Ruz, 1991). Hind tibia with keirotrichia widespread on most of inner surface 6
6. Lower mesial paraocular area rather flattened or slightly convex. Facial fovea oval. T1-4 with posterior marginal bands formed by long hairs with their apices directed apically ..... *Acamptopoeum*
- Lower mesial paraocular area ("cheeks") swollen. Facial fovea elongate, 7.5 times as long as broad (Fig. 3). T1-4 with posterior marginal bands formed by short hairs (0.3 x as long as flagellar diameter), hairs toward sides with their apices directed posterolaterally (Fig. 12) ..... *Litocalliopsis*

Table 1. List of characters (Summarized from Ruz, 1991). Character state numbers corresponding to *Litocalliopsis* are in boldface.

0. Metasoma with yellow markings (1); without yellow markings **(0)** (Character 3 of Ruz, 1991).
1. Metasomal terga with distal hair bands **(1)**; without distal hair bands (0) (Character 5 of Ruz, 1991).
2. Glossa more or less as long as prementum **(1)**; shorter than prementum (0) (Character 6 of Ruz, 1991).
3. Galeal comb absent (1); well-developed **(0)** (Character 13 of Ruz, 1991).
4. Labrum of male with weak transverse ridge (1); labrum flat (2); with ridge (sometimes strong) or carina (delimiting the basal area) **(0)** (Character 15 of Ruz, 1991).
5. Labrum of male with basal area pilose **(1)**; basal area not pilose (0) (Character 16 of Ruz, 1991).
6. Labrum of female with apex not inflexed (1); with apex at least slightly inflexed **(0)** (Character 17 of Ruz, 1991).
7. Mandible of male simple **(1)**; with preapical tooth (0) (Character 18 of Ruz, 1991).
8. Tentorial pit of male at intersection of outer subantennal and epistomal sutures (1); in outer subantennal suture (close to epistomal suture) **(2)**; near middle of outer subantennal suture (3); in epistomal suture (0) (Character 22 of Ruz, 1991).
9. Antennal sockets of male (lower margins) on lower 1/3 or 1/4 of face (1); more or less in the middle of the face **(0)** (Character 23 of Ruz, 1991).
10. Lower paraocular area strongly swollen mesially (1); flattened or slightly convex **(0)** (Character 28 of Ruz, 1991).
11. Pre-episternal groove short, not extending below scrobal level **(1)**; long, extending below scrobal level (0) (Character 39 of Ruz, 1991).
12. Pre-episternal groove curved, meeting scrobe (1); straight, not meeting scrobe **(0)** (Character 40 of Ruz, 1991).
13. Metanotum with lateral patch of short velvety hairs (1); without lateral patch of short velvety hairs **(0)** (Character 42 of Ruz, 1991).
14. Pterostigma with sides parallel or subparallel **(1)**; sides not parallel or subparallel (0) (Character 44 of Ruz, 1991).
15. Pterostigma with margin within marginal cell straight or nearly so **(1)**; clearly convex (0) (Character 45 of Ruz, 1991).
16. Marginal cell shorter than distance between its apex and wing tip (1); much shorter (2); about as long or usually longer **(0)** (Character 46 of Ruz, 1991).
17. Metapostnotum smooth (1); striate or rugose, or at least minutely areolate **(0)** (Character 52 of Ruz, 1991).
18. Femur 2 of female with well-defined basal comb on ventral margin (Fig. 10D, Ruz, 1991) **(1)**; without such a comb (0) (Character 56 of Ruz 1991).
19. Basitarsus 2 of male longer than 3 (1); equal to, or shorter than 3 **(0)** (Character 58 of Ruz, 1991).
20. Tarsus 2 of male with tarsomeres 2-4 widened distally (1); tarsomeres rather narrow **(0)** (Character 60 of Ruz, 1991).
21. Tibia 3 of female on inner surface with keirotrichia forming a longitudinal dorsal or median strip **(1)**; with keirotrichia only at both ends (Fig. 28D, Ruz, 1991) (2); with keirotrichia on most of inner surface (0) (Character 62 of Ruz, 1991).
22. Tibia 3 of female with keirotrichia forming a longitudinal strip (1); keirotrichia on most of the inner surface **(0)** (Character 63 of Ruz, 1991).
23. Tibia 3 of male with dorsal margin evenly carinate (Fig. 4F, Ruz, 1991) or the carina fragmented, forming a series of teeth (1); without such a carina **(0)** (Character 64 of Ruz, 1991).
24. Tibial scopa of moderately abundant hairs **(1)**; of extremely sparse hairs (2); hairs dense (0) (Character 67 of Ruz, 1991).
25. Apex of basitarsus 3 of female with upper distal projection reduced so that apex is oblique (1); apex of basitarsus transverse (2); such a projection well-developed **(0)** (Character 70 of Ruz, 1991).
26. Tarsus 3 of male with tarsomeres 2-4 widened (1); tarsomeres unmodified **(0)** (Character 71 of Ruz, 1991).
27. Tarsus 3 of male with tarsomeres 2-4 asymmetrical (1); symmetrical **(0)** (Character 72 of Ruz, 1991).
28. T1-5 of male with posterior marginal area (at least partially) pilose **(1)**; bare (0) (Character 76 of Ruz, 1991).
29. Pygidial plate of male well defined **(1)**; plate not defined (0) (Character 79 of Ruz, 1991).
30. S4 of male with distal margin slightly produced medially (1); distal margin clearly produced medially (2); concave or almost straight medially **(0)** (Character 81 of Ruz, 1991).
31. S5 of male with distal margin slightly produced medially (1); with a rather small median projection (2); with an elongate median projection (3); concave or almost straight medially **(0)** (Character 84 of Ruz, 1991).
32. S1-5 of female with dense stratum of short, appressed hairs **(1)**; this stratum formed by scattered hairs (0). This character is best seen in S2. The female S1-5 have two strata of hairs: a stratum of long, erect hairs, which is invariable among calliopsines, and a stratum of short, appressed hairs, which can be more or less dense. This character has been reinterpreted from character 85 of Ruz (1991).
33. S5 of female with distal margin convex medially **(1)**; concave or almost straight medially (0) (Character 87 of Ruz, 1991).
34. S5 of female with median sclerotized area between gradulus and basal margin of sternum (Fig. 12A, Ruz, 1991) **(1)**; without such sclerotization (0) (Character 88 of Ruz, 1991).

35. S6 of male with distal, elongate, tapered projection on each side of deep emargination (Fig. 11H, Ruz, 1991) (1); without such a projection **(0)** (Character 89 of Ruz, 1991).
36. S6 of female with two proximal laminar lobes (Fig. 17H, Ruz, 1991) **(1)**; straight (0) (Character 93 of Ruz, 1991).
37. S6 of female with basal spine-shaped longitudinal sclerotization (Fig. 1D, Ruz, 1991) **(1)**; without spine-shaped sclerotization (0) (Character 95 of Ruz, 1991).
38. S6 of female with basal sclerotization free at least at apex (1); such sclerotization usually fused to sternum **(0)** (Character 96 of Ruz, 1991).
39. S6 of female with strong, almost straight ridge on lateral margin (Fig. 1D, Ruz, 1991) **(1)**; such ridge, if present, usually curved (0) (Character 97 of Ruz, 1991).
40. S6 of female with premarginal hairs in well-organized rows forming a continuous or medially interrupted patch or band (Fig. 10H, 12C, Ruz, 1991) **(1)**; such hairs usually organized in a dense patch (0) (Character 99 of Ruz, 1991).
41. S8 of male with a small lateral projection between body and distal projection (Fig. 11F, Ruz, 1991) (1); without such a projection **(0)** (Character 105 of Ruz, 1991).
42. Gonocoxites (ventral view) connected by membrane (Fig. 18A, Ruz, 1991) **(1)**; partially or fully fused to each other (2); completely separated (0) (Character 111 of Ruz, 1991).
43. Gonostylus about 1/2 to 1/3 length of gonocoxite (ventral view) (1); vestigial, about 1/8 length of gonocoxite (2); rudimentary (recognizable only by the presence of few, short hairs at apex of gonocoxite) (3); absent **(4)**; longer than gonocoxite (0) (Character 115 of Ruz, 1991).
44. Volsella rudimentery or absent (1); well-developed **(0)** (Character 118 of Ruz, 1991).
45. Volsellae connected to one another by basal, narrow and weak, membranous bridge (1); by widened membranous area or by slightly sclerotized cuticle (2); partially fused to one another (3); fully fused but line of fusion visible **(4)**; absent or completely fused forming a highly sclerotized plate (?); free (0) (Character 119 of Ruz, 1991).
46. Volsella without denticles **(1)**; with denticles (0) (Character 120 of Ruz, 1991).
47. Penis valves complex **(1)**; simple (0) (Character 123 of Ruz, 1991).
48. Penis completely separated from penis valve **(1)**; partially or fully fused to the penis valve (0) (Character 125 of Ruz, 1991).
49. Penis with internal sclerotization (1); without internal sclerotization **(0)** (Character 126 of Ruz, 1991).
50. Sting short to very short, not reaching (or at least not surpassing) stylus (1); sting rudimentary (2); sting elongate **(0)** (Character 127 of Ruz, 1991).
51. First valvifer elongate (1); more or less triangular **(0)** (Character 129 of Ruz, 1991).
52. Flagellomere 1 of male about twice as long as 2 or less **(1)**; much longer than 2 (2); more or less as long as 2 (0) (Character 26 of Ruz, 1986). The male of *Ceroliopoeum*, which has flagellomere 1 about half as long as 2, has been coded as zero.
53. S6 of female with curved band of hairs on premarginal area (Fig. 51h, in Ruz, 1986) (1); without such a band **(0)** (Character 100 of Ruz, 1986).
54. Gonostylus partially fused to gonocoxite (1); fully fused to gonocoxite (2); fully articulated with the gonocoxite (0); absent **(?)** (Character 116 of Ruz, 1986).

Litocalliopsis, new genus

Type species: *Litocalliopsis adesmiae n. sp.*

Diagnosis. Close to *Calliopsis,* from which it can be distinguished as follows: labrum with basal area partially pilose, S5 of male on distal margin without median projection or any other modification, S6 of male slightly emarginate apically, and sting of female elongate, surpassing stylus. Among the South American Calliopsini it resembles *Acamtopoeum*, from which it can be differentiated by the posterior marginal hair bands of T1-4, the swollen lower mesial paraocular area, the elongate facial fovea, and the presence of a pygidial plate in the male.

Description. Length 6.3-10.2 mm. Integument dull. Yellow marks restricted to lower half of face and to tarsi and parts of tibiae in male, and to clypeus, subantennal area, and bases of fore and middle tibiae in female. Metasoma with no yellow marks. Pubescence long on head, thorax and legs, shorter on metasoma. Punctation in general fine, similar to that of *Acamptopoeum*. Head broader than long, broader than thorax. Glossa as long as prementum. Segment 1 of labial palp nearly three times as long as segments 2-4 together. Post-palpal part of galea as long as prepalpal part. Galeal comb with approximately 30 bristles. Labrum twice as long as broad; basal part pilose; distal margin of basal part distinct in female, carinate in male; apical part of labrum inflexed. Mandible simple in both sexes. Clypeus 2.3 times broader than long. Inner subantennal suture angulose. Subantennal area broader than inner suture length. Tentorial pit on outer

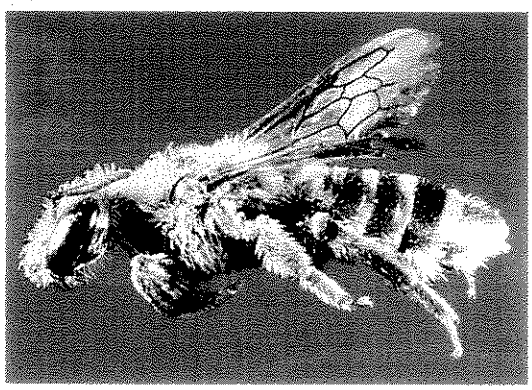
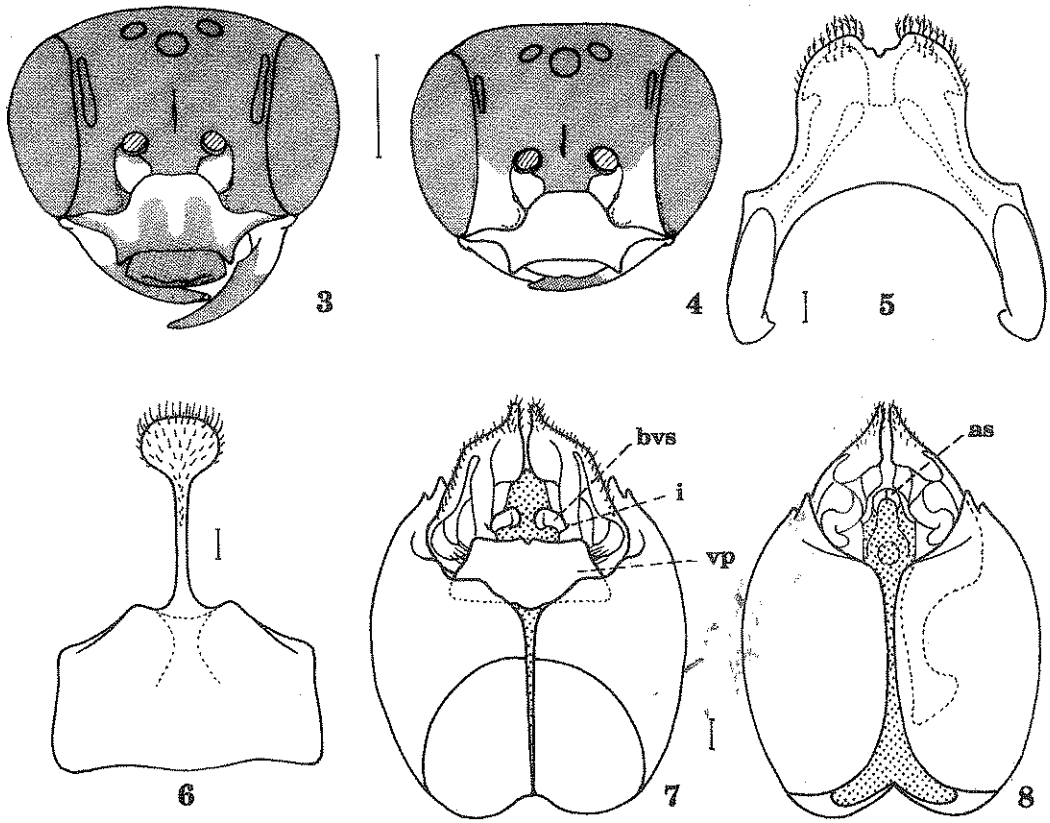


Fig. 2. *Litocalliopsis adesmiae sp. n.*, habitus of female.

subantennal suture, close to epistomal suture. Antennal sockets in middle of face. Antenna of male unmodified; first flagellomere longer than second. Lower mesial paraocular area swollen. Facial fovea elongate. Orbits convergent below. Lateral ocelli at dorsal orbital tangent. Vertex convex. Gena of male (lateral view) narrower than eye (half as broad on middle point of eye), wider dorsally than ventrally. Pronotum with dorsal preapical ridge rounded. Metanotum laterally with hairs long, sparse. Anterior surface of mesepisternum convex not reduced. Preepisternal groove short, straight, not reaching scrobe. Pterostigma longer and wider than prestigma, sides subparallel, margin within marginal cell slightly convex. Marginal cell obliquely truncate at apex, as long as distance from its apex to wing tip. Two submarginal cells. Submarginal cell 1 as long as second (maximum length measured). First recurrent vein far from first transverse cubital. Forewing with cu-v 1.3 times longer than second abscissa of M+Cu. Hind wing with cu-v 0.2 as long as second abscissa of M+Cu. Dorsal surface of metapostnotum as long as metanotum; metapostnotum glabrous, integument microreticulate. Basitarsus and tarsomeres 2-4 unmodified. Middle tibial spur of female about as long as basitarsus 2, with fine teeth, that of male rather longer than half basitarsal length. Basitarsus 1 longer than 2 and 3; tarsomeres 2-4 unmodified. Femur 2 of female with well-defined basal comb on ventral margin. Tibia 3 of female over twice as long as basitarsus 3; with keirotrichia on inner surface not interrupted but lacking on ventral margin. Tibia 3 of male with dorsal margin not carinate. Tibial scopa moderately dense, on outer surface with simple hairs, except some finely branched hairs near base. Hind tibial spurs with fine teeth, apex straight. Basitibial plate of male well defined. Tarsus 3 unmodified; apex of basitarsus 3 of female with upper distal projection. Claws bifurcate, in female inner ramus shorter than outer. Metasoma in male somewhat wider than thorax. T2-5 of male with gradulus posterolaterally not surpassing anterior half of tergum. T1-5 of male and T1-4 of female with pilose posterior marginal bands, formed by short (0.3 x as long as flagellar diameter), dense, decumbent hairs which toward the sides have their apices directed posterolaterally. T1-6 of male and T1-T5 of female with translucent posterior marginal bands. Lateral fovea of T2 inconspicuous. Pygidial plate of male present, carinate apically and also briefly carinate laterally, with upper surface pilose. T7 of female squared. T8 of male, figure 13. S1-5 of female with stratum of short, appressed, rather dense hairs. S4-5 of male with apical margin straight medially. S5 of female with distal margin convex medially; with median sclerotized area between gradulus and basal margin of sternum. S6 of male with two apical longitudinal ridges united basally forming U-shaped structure which encloses less sclerotized, concave area; U shaped elevation densely pilose and remainder of sternum glabrous (Figs. 11, 14). S6 of female with basal sclerotization long and acute, fused to sternum; with two proximal laminar lobes; duplication strongly sclerotized; lateral ridge straight; distal margin staight laterally and convex medially. S6 with dense, lateral, preapical patch of hairs. S7 and S8 of male as in figures (Figs. 5-6). Gonoxites globose, not fused ventrally, ending apically in double spiniform projection. Gonostylus not distinguishable. Volsellae well developed, without denticles, fused to each other forming ventral plate, but line of fusion distinguishable with transmitted light. Penis valves complex, with several lobes, not fused to each other (Figs. 9a-d). Penis separated from penis valves, with basiventral sclerotized areas (Fig. 7, **bvs**) which rest on indentation of penis valves (Figs. 7, 9-10, **i**), and with apical sclerotization (Fig. 8, **as**); penis dorsally with a small membranous hemispherical lobe; endophallus absent. Sting elongate, surpassing stylus; first valvifer triangular.

Etymology. The name is formed by *lito*, simple, and the generic name *Calliopsis*, referring to the simple form of the male metasomal sterna.

Comments. The pattern of pubescence of *Litocalliopsis* is similar to that of *Calliopsis*, shorter and less dense than in *Acamptopoeum*. The pubescence of the apical bands of the metasomal terga in both sexes is formed by short hairs with their apices directed postero-laterally

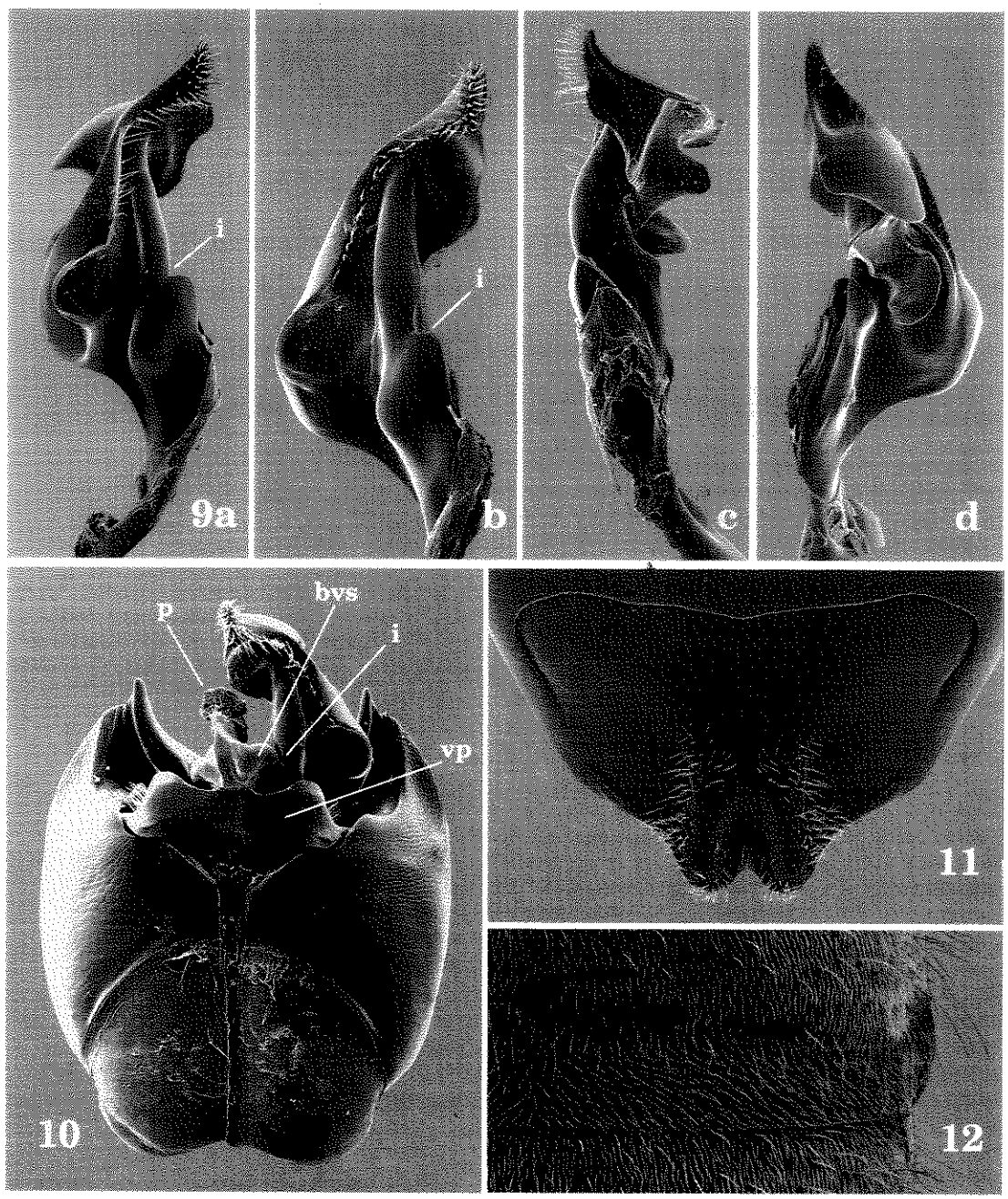


Figs. 3-8. *Litocalliopsis adesmiae sp. n.* 3, head of female. 4, head of male. 5, S7 of male, ventral view. 6, S8 of male, ventral view. 7, genital capsule of male, ventral view; bvs, basiventral sclerotization of penis; i, indentation of penis valve; vp volsellar plate. 8, genital capsule of male, dorsal view; as, apical sclerotization of penis. Scale lines, Figs. 3-4 = 1 mm, Figs. 5-8 = 0.1 mm.

(Fig. 12). This peculiar pilosity is not seen in the outgroups. A similar pattern is present in males of *Calliopsis* (*Calliopsima*). This character was not coded because we did not have enough material of Nearctic *Calliopsis* to check the distribution of the character.

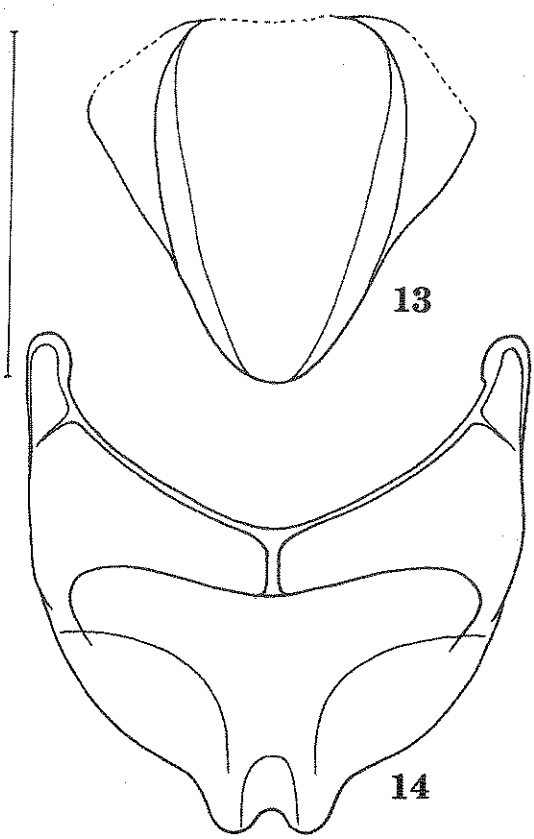
***Litocalliopsis adesmiae*, new species**
(Figs. 2-14)

Description. Female holotype. Length 9.3 mm (paratypes, 7.8-9.8 mm); length of forewing 5.1 (paratypes, 5.0-5.3 mm). *Coloration.* Black, except yellowish brown underside of antennal flagellum, translucent tegula, brownish tarsi, translucent apical margins of T2-5, and yellow following parts: basal half of mandible, clypeus laterally, basally and on a median stripe (Fig. 3), subantennal area on lower ¾, small spot on swollen paraocular area close to clypeus (this area black in some paratypes), small spot on apex of femur 1 (lacking in some paratypes), and roundish spot on base of tibiae 1-2. *Vestiture* greyish white; long and erect on head and thorax. Scape with erect hairs 2.3 x as long as flagellar diameter; hairs on clypeus and paraocular areas longer than on scape, those on clypeus with a golden shine. Scutum with two strata of hairs, one of short (as long as flagellar diameter), plumose hairs, denser on antero-lateral angles and lateral margins, and another of long hairs (2.6 x as long as flagellar diameter), with short barbs. Mesopleuron with hairs 3.3 x as long as flagellar diameter. Metapostnotum glabrous. Vestiture rather sparse on legs. Metasomal terga 1-4 mostly with short (0.3 x as long as flagellar diameter), appressed hairs (but some erect scattered hairs present), apically forming distinct hair bands; hairs of bands with their apices directed latero-posteriorly; base of T1 and other terga laterally with erect, longer hairs (1.6 x as



Figs. 9-12. *Litocalliopsis adesmiae sp. n.* 9a-d, left penis valve. a, external-ventral view; b, ventral view; c, internal view; d, dorsal view; i, indentation of penis valve. 10, genital capsule (left penis valve removed), ventral view; p, penis; bvs, basiventral sclerotization of penis; i, indentation of penis valve; vp, volsellar plate. 11, S6 of male, ventral view. 12, T3 of female, right half, detail of apical hair band.

long as flagellar diameter); T5 with long, erect hairs basally and dense, golden brown apical fimbria; T6 with long golden brown hairs laterally. S1-5 with stratum of short, appressed hairs rather dense, and long (2 x as long as flagellar diameter), erect, scattered hairs. *Sculpture.* Labrum punctured, except smooth central part of basal area. Clypeus with punctures separated by 1-1.5 times



Figs. 13-14. *Litocalliopsis adesmiae sp. n.* 13, T8 of male. 14, S6 of male.

their diameter; apical margin smooth, and also smooth median longitudinal upper area which coincides with yellow stripe. Face with punctation finer than on clypeus, denser on upper part and sparser near clypeus, swollen lower paraocular area smooth. Punctures on scutum and mesopleuron separated by 1-1.5 times their diameter, denser and finer on metanotum. Metapostnotum microreticulate. Metasoma with fine, dense punctation. *Morphology.* Head broader than long (1.33:1); inner orbits slightly sinuose, converging below up to level of antennal sockets and then diverging inferiorly; proportion of lower to upper interocular distance 0.98:1. Labrum broader than long (1.8:1); basal area apically with bilobate carina, median smooth area somewhat concave with a basal pit. Clypeus broader than long (2.45:1). Proportion of interantennal to antennocular distance, 1.4:1. Inner subantennal suture angulate, shorter than outer (0.9:1), longer than maximum width of subantennal area (2.2:2). Facial fovea much longer that broad (7.5:1), as long as 0.3 times eye length. Alveolo-ocelar distance about four times longer than distance between alveolus and epistomal suture. Alveolus diameter similar to that of median ocellus (7:7). Proportion of lengths of scape, pedicel and first three flagellomeres 5:1.2:1.1:0.8:1; first flagellomere 1.1 times as long as apical width. Pygidial plate triangular, with rounded apex and carinate margins.

Male. Length 6.2-8.4 mm; length of forewing 4.2-4.8 mm. *Coloration*. Similar to that of female, with yellow parts as follows: labrum except dark median basal spot and dark basal lateral corner (in some specimens labrum completely yellow), basal 2/3 of mandible, clypeus except paramedian small black spot and brown apical margin, lower part of paraocular area extending laterally close to eye up to level of antennal socket, subantennal area on lower ¾ (in some specimens subantennal area completely yellow), femora on dorsal apex, foretibia on dorsal and inner surfaces, middle tibia on base and apex, hind tibia on longitudinal dorsal band extending to inner and outer surfaces basally and to outer surface apically, all tarsi. *Vestiture* and *sculpture* similar to those of female. *Morphology*. Proportion of lengths of scape, pedicel and first three flagellomeres 4.2:0.85:0.85:0.8:1; first flagellomere 0.85 times as long as apical width. S6-S8 and genital capsule, Figs. 5-8, 9-11 and 14.

Etymology. The specific name refers to the plant from which the bee collected pollen.

Material studied. Type material: all from Argentina, province of Buenos Aires, Partido de Moreno, La Reja, "Francisco J. Muñiz" Reserve. Holotype female, 22-XI-2002 A. Roig Alsina and L. Compagnucci coll. (deposited in: MACN) *Paratypes:* 11 males and 5 females, same data as holotype; 3 males and 7 females, 28-XI-2002 A. Roig Alsina and L. Compagnucci coll.; 2 males and 4 females, 10-XII-2002 A. Roig Alsina and L. Compagnucci coll.; 2 males, 6-I-2002 A. Roig Alsina Coll. Paratypes deposited in the following collections: FIML, KU, MACN, MLP, and PUCV.

BIOLOGY

Nesting area

The study was carried out in the "Francisco Javier Muñiz" Reserve, in Partido de Moreno, province of Buenos Aires, approximately 50 km west of Buenos Aires city. The place is near the headwaters of the Reconquista River. It is a wetland, with flooded areas.

The nesting area was located on a small tongue of elevated terrain of approximately 40 m^2 between an artificial channel and a lowland, dry at this time. The surface of the soil was about one

meter above the water level. These conditions kept the soil moist, even on the surface. The soil was a sandy loam, fragile to excavate, of fairly homogeneous texture, and with scattered pieces of calcareous concretions.

The vegetation of the nesting area was sparse, denser on the edges of the area and with patches of bare flat ground in the center, where the nests were aggregated.

Activity

The area was monitored between November 6, 2002, and January 13, 2003. An additional visit to the area was made on February 26, 2003. *Litocalliopsis adesmiae* was sighted for the first time on November 22, and the nesting area was located the same day. Numerous males were patrolling the area and a few females were observed entering the nests with pollen loads. The nests were covered by conspicuous tumuli of loose soil. Digging activity was also evident due to movements of the tumuli and apparition on the surface of wet particles of soil.

Five nests excavated on November 28 were very short, and only three of them had completed cells, suggesting that the nesting season was just beginning. While excavating these nests we came across two cells each containing an adult male, apparently ready to emerge. Another cell contained a pupa. We believe that these cells corresponded to nests from the previous season.

The bees were active during the month of December. On January 6 we no longer observed nesting females. Two males collected while they were patrolling the area had tattered wings. On January 13 we observed no bees. On Februay 26 no activity was recorded, suggesting that the species may be univoltine. At this time the plants of *Adesmia* were no longer in bloom.

Nests

The entrance of each nests was covered by a tumulus of loose soil of approximately 4 cm in diameter. The entrance was in some cases under the middle of the tumulus, but in others it was displaced. There was one entrance to each nest. The tumulus hid the entrance, and the bees, even with full pollen loads, "dived" in the tumulus to enter the nest. Many nest entrances were found uncovered after a rain on December 10, and remained so in subsequent days.

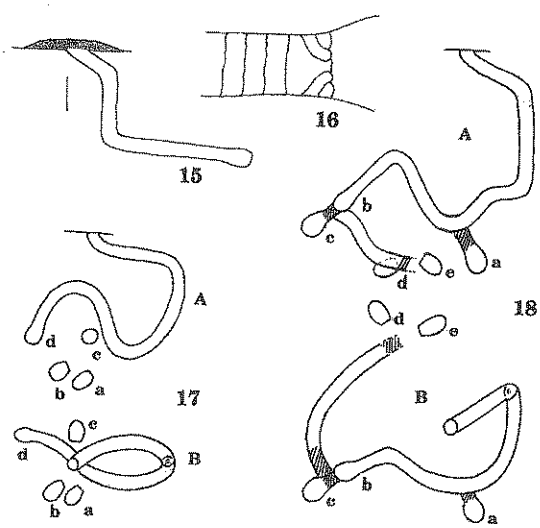
Each nest was occupied by a single female. The nests consisted of a main unbranched tunnel to which the cells were connected by short laterals. The tunnel began with a slanting, shallow sector which varied between 1.5 cm and 16 cm in length (n=8); this sector was present in all the nests excavated, and it was not filled with soil. After this sector, the tunnel descended perpendicular to the soil surface to a depth of 2.5-4.5 cm. From this point on, the tunnel continued in an irregular, sometimes tortuous manner. The tunnel did not surpass 7 cm in depth in any case. In some nests the tunnel was observed to go up, in one case approaching the surface (Fig. 17). These changes in direction were not associated with any apparent obstacle in the soil. The diameter of the tunnel is aproximately 4 mm.

The nests in an early stage of construction excavated on November 28 (n=5) had a short main tunnel (Fig. 15), suggesting a progressive construction of the nests. However, we did not find a clear sequence in more developed nests excavated on December 10. For example, in one nest (Fig. 17), a cell with a pollen mass and egg (a) was found, anteceding two cells with developing larvae (b and c). In another nest (Fig. 18) it is possible to interpret cell construction as folows: e (large larva) → d (medium-sized larva) → c (small larva) → a (pollen mass with egg) → b (open cell with small pollen mass). Cells a, b and c have been constructed regressively with respect to cells e and d, but cell b has been constructed progressively with respect to cell a. A third nest, with four cells, was clearly progressive with an open cell at the bottom. According to these observations, *L. adesmiae* would not always follow a definite order of cell construction.

Most cells were found between 5 to 7 cm in depth and were arranged singly, but two cells were found at 3.5 cm. The short laterals leading to closed cells were filled with soil. The cells slanted to rear from 30° to 45° from the horizontal. The cell length was 8.6-9.8 mm (mean 9.0, n=4) and the maximum diameter was 5.8-6.0 mm (mean 5.9, n=3); the neck of the cell was narrower (3.4 mm) than the tunnel. The neck is distinguished from the inner part of the cell because it is less smoothed.

The inner surface of the cell was waterproof. A drop of water remained on the inner surface of the cell for 15 minutes, without being absorbed; to the contrary, drops of water on the neck or the tunnel were absorbed immediately. Even though the cell was waterproof we did not detect any conspicuous lining, except for a waxy shine.

The closed cells presented a plug which seen from the inside was fairly irregular. A first cord of material can be distinguished against the neck, and in some cases a second cord. The center of the closure (seen from the inside) was completely irregular; there was no spiral. A longitudinal section of a plug (Fig. 16) showed that after the first and second cords were applied the material was



Figs. 15-18. *Litocalliopsis adesmiae sp. n.* 15, nest in an early stage of construction. 16, diagram of cell closure. 17-18, diagrams of nest architecture; A, side view; B, top view.

pressed against the closure in several successive layers; from this point on the lateral was filled with loose soil.

Provisioning

The pollen masses were spherical, 3.0-3.4 mm in diameter. The orange masses, very homogeneous in color and texture, were located on the rear end of the cell floor, but not touching the bottom. Even tiny masses of pollen in open cells, obviously the outcome of a first collecting trip, were shaped as spheres. In one case a pyriform mass was found (length 2 mm, maximum diameter 1.8 mm, minimum diameter 1.6 mm), probably due to the addition of a smaller load to a previous one. Pollen masses with eggs preserved in alcohol have a thin, whitish coating, which could not be detected on dry-preserved masses. A pollen mass recovered from a cell was analyzed, its contents being 99.5% pollen of *Adesmia*, and 0.5% pollen of other plants, mainly composites and monocots.

Development

The white, elongate, curved egg (length 2 mm, width 0.5 mm) rested on top of the mass touching the pollen only with its tips. One end of the egg was rounded, but the other end was somewhat pointed. The egg was oriented along the longitudinal axis of the cell.

An egg on its pollen mass was brought to the laboratory and a day later the larva hatched. The larva consumed most of the provisions and on the sixth day it began to defecate. The seventh day the larva ate no more (a tiny pollen mass was left over) and continued defecation. On the eighth day the larva had changed to a yellowish color and the body tubercles became conspicuous; it was fixed. Two young larvae were brought to the laboratory inside their fairly complete cells, where they completed feeding and defecation. These larvae applied their feces against the upper half of the bottom and the rear ceiling of the cell as a roughly circular patch.

Visited plants

In the surroundings of the nesting area the bees were observed visiting flowers of *Lotus corniculatus* L. and *Centaurium pulchellum* (Sw.) Druce. The bees were observed collecting pollen from flowers of *Adesmia bicolor* (Poir.) D.C., on a dense patch of this plant, some 20 m from the nesting area.

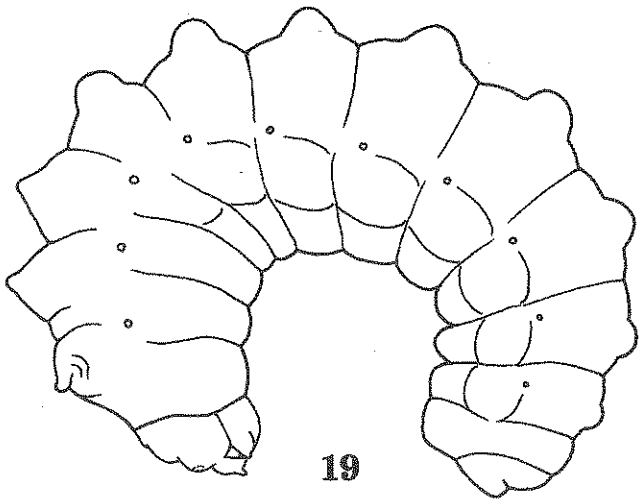
Mating behavior

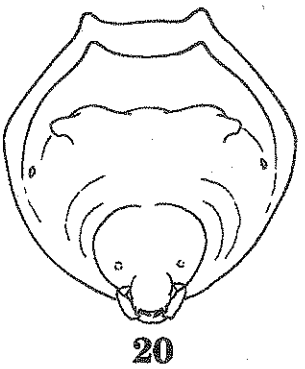
These bees have the ability to fly *in copula*. Copulation was observed on the flowers, in flight, and on the floor in the nesting area. A pair *in copula* was observed landing close to a nest entrance. The female had a full pollen load. The pair remained *in copula* for 3 min. 20 sec. until the male took off and then the female entered the nest.

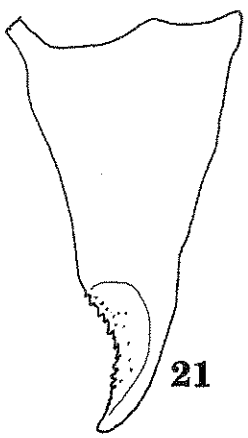
Comments

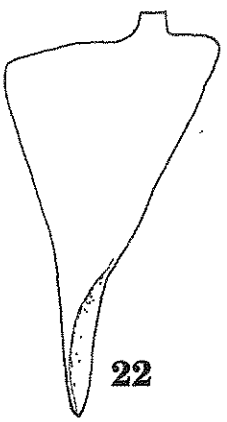
Biological features of *Litocalliopsis adesmiae* are similar to those described for species of *Acamptopoeum* (Rozen & Yanega, 1999) and *Calliopsis* (Danforth, 1990; Rozen, 1958, 1967, 1970; Shinn, 1967). Rozen (1989) presented a list of biological features in panurgine bees and discussed their possible phylogenetic significance. He mentioned seven characters as possible synapomorphies of the calliopsines. Of these, six are also shared by *Litocalliopsis*: the nests are shallow, the entrance of the nests is hidden by a tumulus, the cells present an inconspicuous lining, the early loads of provisions, as well as the completed provisions are shaped as spheres, and the completed provisions are covered with a coating. A further character, the main tunnel filled with soil during nest construction and provisioning (at least the first stretch), is not present in *L. adesmiae*. In this species the tunnel remains open below the tumulus and the first sector of the tunnel is shallow, slightly slanting, not vertical as in other calliopsines.

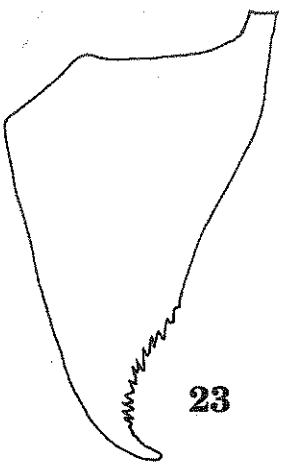
Another observed difference between *L. adesmiae* and other calliopsines is the orientation of the cells, which in the latter bees is usually horizontal to subhorizontal, while in the former the orientation varied from 30° to 45°.

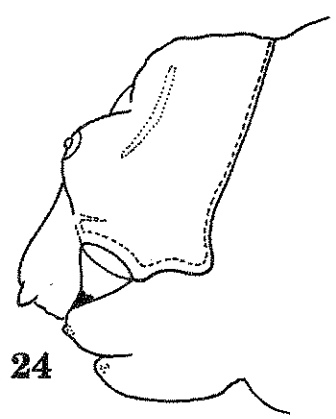


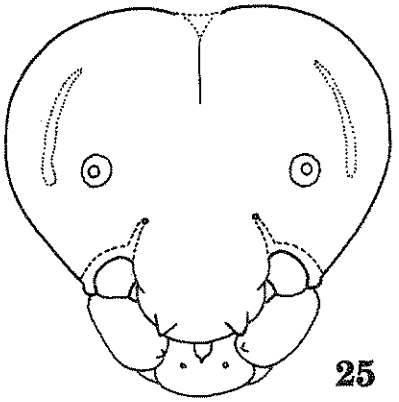












Figs. 19-25. *Litocalliopsis adesmiae sp. n.*, postdefecating larva. 19, lateral view of larva. 20, head and thorax, frontal view. 21, right mandible, ventral view. 22, right mandible, inner view. 23, right mandible, dorsal view. 24, cephalic capsule, lateral view. 25, cephalic capsule, frontal view.

The nests of *L. adesmiae* are extremely irregular, in some cases even with ascending sectors of the main tunnel, and the order of cell construction does not always follow a clear sequence.

DESCRIPTION OF THE LARVA

Six larvae were recovered while digging the nests. The postdefecating larva is described below. The predefecating larva has a more robust body form with intrasegmental lines scarcely evident and the dorsal paired tubercles much less marked, although distinguishable.

Postdefecating larva
(Figs. 19-25)

Head. Integument with scattered setae. Head capsule faintly pigmented and apex of mandible strongly pigmented. Head in frontal view with distinct, moderate prominences: a rounded one bearing the antennal papilla and another rounded prominence between vertex and antenna; face between these prominences and clypeus forming a pentagonal area which is also somewhat swollen. Tentorium complete; sclerotization of anterior tentorial arm tapering toward connection with posterior arm; posterior tentorial bridge strong, well developed, dorsal arm of tentorium present. Epistomal ridge present below anterior tentorial pit, thin (absent between pits); pleurostomal and hypostomal ridges well developed, thick. Postoccipital ridge thin, incomplete, disappearing on top of head, distance between upper extremes of postoccipital ridge twice as broad as diameter of antennal disc. Parietal band distinct, long. Antennal disc and papilla small, scarcely elevated. Labrum with moderate conical tubercle on each side. Epipharynx distinctly spiculate. Mandible with attenuate, pointed apex; inner margin apically concave and bearing numerous, moderate denticles in a single row, ventral surface next to this row with a shallow concavity bearing minute denticles. Maxilla in lateral view scarcely projecting beyond labial apex; maxillary palpus small, smaller than labral tubercle; dorsal surface of maxilla and palpus spiculate; apex of maxilla, close to palpus, with microscopic sensillae. Labium recessed; labial palpus small, smaller than maxillary palpus; salivary opening V-shaped, extending upwards to hypopharyngeal groove, which is distinct.

Body. Larva pale yellow. Body with distinct, large dorsal paired tubercles, three on thorax and 7 on abdomen. Prothoracic tubercles with conical apices directed laterally and slightly directed anteriorly; meso and metathoracic tubercles conical, pointing dorsally; thoracic tubercles pigmented, especially toward their apices; abdominal tubercles dome-shaped, similar in size except smaller last pair. Pro and mesothoracic tubercles separated by deep furrow. Pleural region of abdominal segments 1-8 with distinct swellings. Body cuticle with microscopic spicules, scattered on sides and denser on dorsal and ventral surfaces; area surrounding cephalic capsule with granules instead of spicules. A few microscopic setiform sensillae present on thoracic tubercles apically and on tenth abdominal segment apically. Spiracles simple, small; peritreme present, atrium not projecting above body surface and without spines.

Comments

Larvae of *L. adesmiae* are morphologically similar to those of species of *Calliopsis s. l.* (Michener, 1953; Rozen, 1958, 1966, 1970) and *Acamptopoeum* (Rozen & Yanega, 1999). They are distinguished by the conspicuous, large dorsal paired tubercles, which are conical on the thorax but hemispherical on the abdomen. The thoracic tubercles also differ from the abdominal ones because they are pigmented and have microscopic setiform sensillae. The prothoracic dorsal tubercles are directed laterally and somewhat anteriorly, reminding a similar condition present in *Acamptopoeum* (Rozen & Yanega, 1999); these tubercles usually point upwards in species of *Calliopsis*.

An interesting feature of *L. adesmiae* is the incomplete postoccipital ridge, which is absent on the top of the head. This characteristic was present in all the specimens examined. A similar condition was found by Rozen & Yanega (1999) in the larva of *Acamptopoeum prinii* Holmberg. These authors suggest that the preoccipital ridge may have faded in their specimen due to approaching ecdysis, but it may represent the normal condition. This point merits further study.

ACKNOWLEDGEMENTS

We thank the director of the "Francisco Javier Muñiz" Reserve, Eduardo Schreiber, as well as the personnel of the Reserve for allowing this study. We thank Diego Medán and Roberto Gómez Cadret for the identification of the plants, Marta Caccavari for her help with the pollen analysis, Charles D. Michener and Luisa Ruz for their comments on the manuscript, and Fabián Tricarico and Angel Fusaro for their help with the photography. This study was aided by grant PIP 596-98 from CONICET.

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Recibido: 30-III-2003
Aceptado: 1-VI-2003