

***Leioproctus* bees associated with Western Australian smoke bushes (*Conospermum* spp.) and their adaptations for foraging and concealment (Hymenoptera: Colletidae: Paracolletini)**

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Abstract

Three new south-western Australian species of *Leioproctus*, *L. conospermi*, *L. pappus* and *L. tomentosus*, are described and figured. They form a natural group, designated the *L. conospermi* species-group, assigned to the subgenus *Leioproctus*. Males intermediate in character between those of *L. conospermi* and *L. pappus* and of uncertain status are recorded.

All species are oligolectic on flowers of *Conospermum* spp. (Proteaceae). Modifications of the mouth parts are evidently associated with the explosive pollen release mechanism of the forage plants and the unusually sparse scopa of females is adapted to carry the relatively coarse pollen.

Two of the species, *L. pappus* and *L. tomentosus*, especially the males, are remarkably well adapted for concealment on the inflorescences, being densely clothed in white hair and having white eyes and milky wings.

Introduction

This paper makes known a small group of bees and their interesting association with certain species of the plant genus *Conospermum* Smith in south-western Australia. *Conospermum* is an endemic Australian genus of about 40 species, 29 of which occur in Western Australia (Rye 1987). Some species (those with zygomorphic flowers) are reported to have an unusual, explosive, pollen release mechanism (Carolin 1961, Holm 1978). These authors presumed that insects, probably flies, were responsible for triggering the mechanism, but no records of *Conospermum* pollinators have been published.

An unusual feature of two of the bee species described here is that their males (and to a lesser extent, their females) are conspicuously modified for concealment on the hoary flowers of their forage plants. This is novel and I am unaware of any reports of bee camouflage.

Terminology and Abbreviations

The morphological terminology employed here follows that of Michener (1965).

Relative dimensions quoted in the descriptions are directly comparable between the sexes and between species. All were measured using an eye-piece graticule on a stereomicroscope with the zoom objective set to give a head width reading of 50 eye-piece graticule divisions. By doubling the figure for any given dimension, a percentage of head width is obtained.

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The abbreviations used for relative dimensions are: AOD Antennocular distance; ASD Antennal socket diameter; BMW Basal width of mandible (viewed laterally); FL Flagellum length; HL Head length; HW Head width; IAD Interantennal distance; LID Lower interocular distance (distance between lower ends of compound eyes viewed anteriorly); LPL Labial palpus length; MFW Minimum face width (shortest distance between compound eyes viewed anteriorly); ML Mandible length; MOD Median ocellus diameter; MPL Maxillary palpus length; OOD Ocellocular distance; SL Scape length; SW Scape width; UID Upper interocular distance (distance between summits of compound eyes viewed anteriorly). Other abbreviations: ANIC, Australian National Insect Collection, CSIRO, Canberra; TFH, author's name; UQ, University of Queensland, Brisbane; WAM, Western Australian Museum, Perth.

Systematics

The bees described here key out readily to *Leioproctus* (*Leioproctus* Smith) using Michener's (1965) keys and conform well with his description of this taxon. Michener (l.c.) listed all species-level taxa which were assignable to *Leioproctus s. str.* in the Australian Region and summarised the main morphological variation that occurred amongst them. He made no mention of the kinds of striking characteristics displayed by the smokebush bees, although I am sure he would have done so had the bees then been known. Although *Leioproctus s. str.* is a large group much in need of revision, I am confident that my three species warrant description and naming; they could not be identified using Cockerell's (1934) key to *Paracolletes* Smith (the genus in which most species of *Leioproctus* were originally placed) nor by comparison with all subsequent descriptions of Australian *Leioproctus s. str.* species.

The *Leioproctus conspermi* species-group

Diagnosis

Readily distinguishable from other *Leioproctus s. str.* as follows: prementum bowed ventrally (=posteriorly) in profile, glossa directed anteriorly (Figure 2a); maxillary palpi reduced, shorter than labial palpi, with 3-5 segments (Figures 2a, d-i); hind tibial scopa of female very sparse, setae on outer surface of tibia mostly bifurcate or trifurcate (Figure 3e).

Description

Small bees (body length 5-9 mm); integument predominantly black, non-metallic, smooth, shining; eyes (in life) pale green or white; pubescence predominantly or wholly white; metanotum non-tuberculate; propodeum with sloping dorsal surface about 1.5 X as long as metanotum, rounding evenly onto posterior vertical surface; fore tibial calcar with a very short, simple, apical spine or none (Figures 3l-q); fore basitarsus of female only 2-3 X as long as notch of strigilis (Figure 3a), with coarse vestiture of stiff, simple setae ventrally; hind basitarsus

long, narrow, 5-6 X as long as high in females, 6-8 X in males (Figures 3e, h); inner hind tibial spur of female finely serrate (Figures 3i-k).

Distribution

South-western Australia (except the extreme South-West) from near Shark Bay to 150 km east of Esperance (Figure 5).

Key to species of the *Leioproctus conospermi* species-group

1. Glossa very broad, deeply bifurcate (Figures 2k, l); prementum with few, scattered, simple setae (Figure 2b); male with large frontal concavities (Figure 1c), concavities and lower face covered by short, dense tomentum; female with lower clypeus, labrum and pygidial plate orange-brown. *L. tomentosus*
 Glossa narrower, truncate or slightly bilobed (Figure 2j); prementum with numerous simple setae (Figures 2a, c); male without frontal concavities and facial tomentum, all facial setae long; female with lower clypeus, labrum and pygidial plate black 2
2. Prementum with setae graded in length from much shorter than to about as long as 1st segment of labial palpus (Figure 2c); flagellum of male wholly black, bare posteriorly, middle segments no longer than wide; female with pubescence of 5th and 6th metasomal terga brownish *L. conospermi*
 Prementum with setae of more or less uniform length, much shorter than 1st segment of labial palpus (Figure 2a); flagellum of male largely orange-brown with brush-like vestiture of short erect setae posteriorly (Figure 1e), middle segments about 1.4 X longer than wide; female with pubescence of 5th and 6th metasomal terga white 3
3. Maxillary palpus usually 3-segmented (rarely 4-segmented); fore tibial calcar terminating in a decurved spine (slightly spatulate in male) (Figures 3n, o); male with fore basitarsus slightly curved, attenuated, partially bare at midsection (Figure 3c) *L. pappus*
 Maxillary palpus 4-segmented; fore tibial calcar terminating in an erect tapered spine; male (female unknown) with fore basitarsus straight, not attenuated or bare at midsection Intermediate (*conospermi-pappus*) form

***Leioproctus (Leioproctus) conospermi*, sp. nov.**

Figures 1a, b; 2c-e, j; 3a, b, e, f, i, l, m; 4a-c; 5.

Holotype

In WAM (88 974). ♂, 48 km SW Mt Ragged (33°27'S, 123°29'E), Western Australia, 21 Oct. 1982, C.A. Howard & TFH, on flowers of *Conospermum distichum*.

Paratypes

2♂, 1♀ in ANIC; 2♂, 1♀ in UQ; 6♂, 4♀ in WAM. See Specimens Examined.

Diagnosis

Agrees with *L. pappus* and differs from *L. tomentosus* as follows: prementum with numerous simple erect setae; male with long erect facial hair (not short tomentum), slender scapes, no frontal concavities; female with pubescence of metasomal terga 2-4 densest on hind margins, forming distinct bands, clypeus and pygidial plate black.

Readily distinguished from *L. pappus* as follows: prementum with many setae longer than 1st segment of labial palpus (Figure 2c); male with fore basitarsus simple and straight (Figure 3b), fore tibial calcar obtuse apically (Figure 3l); female with pubescence of 5th and 6th metasomal terga brownish.

Description

Male (holotype)

Head width 2.15 mm; body length 7.0 mm. Relative dimensions: HW 50; HL 40; UID 39; LID 28; MFW 24; IAD 6; ASD 4; AOD 6; SL 12; SW 4; FL c. 40; MOD 4.5; OOD 10; LPL 9.5; MPL 7; ML 17.

Head 25% broader than long; inner orbits converging ventrally (Figure 1 a); malar space obsolete; interantennal area elevated to a peak medially; scape slender with slightly concave ventral margin; flagellum simple, middle segments about as long as broad; glossa distinctly bilobed; maxillary palpus 4-segmented, 4th segment incompletely divided (Figure 2d), relative lengths of segments 1-4 are respectively 4, 3.5, 2 and 4% of HW; relative lengths of labial palpus segments 1-4 are respectively 7, 4, 4 and 5% of HW; mandible with posterior tooth scarcely exceeding anterior tooth; pronotum low, inconspicuous; metasoma moderately slender, 1st segment nearly as long as wide; 2nd cubital cell about 1/3 as long as 1st and 1/2 as long as 3rd; fore basitarsus straight (Figure 3b); fore tibial calcar obtuse at apex (Figure 3l); hind legs slender, simple; hind femur uniformly rounded in cross section; hind tibia with straight ventral margin (Figure 3f); hind basitarsus c. 8 X as long as high, straight.

Head, scapes, mandibles, thorax, propodeum and legs with long, erect, white, plumose setae, not dense enough to obscure underlying integument except on clypeus; metasoma with sparse but uniform vestiture of shorter, white, plumose setae, sterna 4 and 5 with weak apical hair fringes; prementum with numerous simple setae as in female (Figure 2c); flagellum posteriorly bare, dull.

Eyes (in life) greenish; integument generally black (black-brown on underside of flagellum and apical margins of metasomal terga); apices of mandibles dark red-brown; wing membranes clear in incident illumination, with dark hairs, veins thin, brown.

Integument mostly shining with ill-defined small punctures; propodeal enclosure dulled by very fine roughening and tessellation, transversely striate at base; metasomal terga 2-4 dulled anteriorly by very fine roughening and tessellation.

Terminalia as in Figures 4a-c.

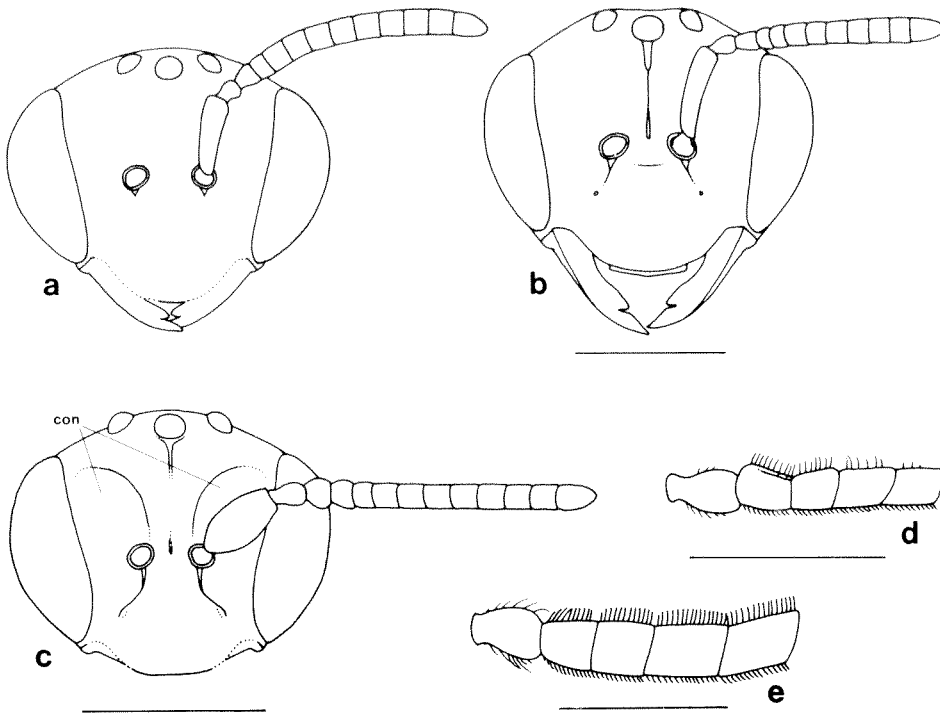


Figure 1 *Leioproctus conospermi* species-group: (a-c) anterior views of head and left antenna of (a, b) *L. conospermi* male and female, respectively, and (c) *L. tomentosus* male (con = concavities of frons); (d, e) dorsal views of left pedicel and first four segments of flagellum of males of *L. tomentosus* and *L. pappus*, respectively, showing setation in profile only. Scale lines: (a-c) 1 mm, (d, e) 0.5 mm.

Female (paratype WAM 88/984)

Head width 2.2 mm; body length 7.2 mm. Relative dimensions: HW 50; HL 39; UID 36; LID 32; MFW 29; IAD 6; ASD 4; AOD 9; SL 15; FL 30; MOD 4; OOD 10; LPL 9; MPL 7; ML 21.

Head as in Figure 1b; interantennal area elevated to a peak medially; mandible obliquely truncate at apex; glossa distinctly bilobed (Figure 2j); maxillary palpus apparently 4-segmented (Figure 2e), relative lengths of segments 1-4 are respectively 4, 3, 3 and 3% of HW; relative lengths of labial palpus segments 1-4 are respectively 7, 4, 3 and 4% of HW; fore tarsi relatively short, basitarsus only 2.25 X as long as high, flattened, notch of strigilis occupying about $\frac{2}{5}$ of ventral margin (Figure 3a), anterior surface with coarse simple bristles; fore tibial calcar with straight acute apical spine (Figure 3m); hind basitarsus slender, straight, *c.* 5 X as long as high and 0.58 X as long as hind tibia (Figure 3e); inner hind tibial spur finely serrate (Figure 3i); pygidial plate truncate, slightly emarginate, margined by raised,

rim-like carina and with longitudinal median ridge; 1st cubital cell 3.5 X as long as 2nd, the 3rd 2.5 X as long. Integument of head and body black; eyes greenish in life; appendages black to dark brown; apices of mandibles dark red-brown; hind margins of metasomal terga translucent; wings clear (not milky in incident illumination), with dark setae and normally thin, brown veins.

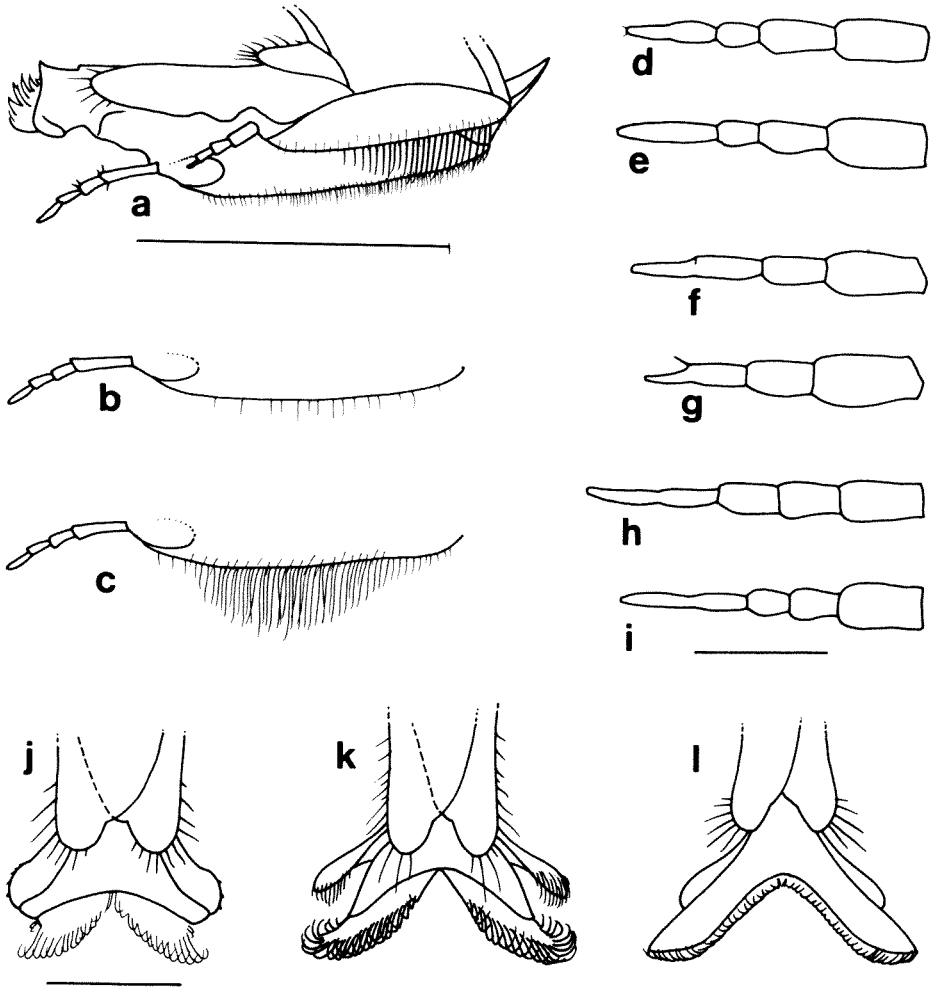


Figure 2 Details of mouth parts of *Leioproctus conspermi* species-group: (a) proboscis of *L. pappus* female in profile; (b, c) profiles of prementum of *L. tomentosus* and *L. conspermi* females, respectively, showing setation (not to same scale); (d-i) maxillary palpi of male (above) and female (below) of (d, e) *L. conspermi*, (f, g) *L. pappus*, and (h, i) *L. tomentosus*; (j-l) anterior views of apex of proboscis of (j) *L. conspermi* female and (k, l) *L. tomentosus* female and male, respectively. Scale lines: (a) 1 mm, (d-l) 0.25 mm.

Integument mostly shiny with close to very sparse setigerous punctures; scutum and scutellum almost glossy; propodeal enclosure dull, transversely striate basally, minutely roughened elsewhere; 1st metasomal tergum glossy, others dulled by minute tessellation.

Head, thorax, propodeum (except enclosure), legs proximally and 1st metasomal tergum with sparse to moderately dense, erect, white, plumose setae not obscuring integument; 2nd-4th metasomal terga with mostly sparse, short, simple setae, with adpressed, plumose setae on hind margins; 5th and 6th terga with long, brown, plumose setae; 5th sternum with regular apical fringe of white setae; prementum with numerous erect, simple setae, grading from very short posteriorly to long in middle, longest setae exceeding length of 1st segment of labial palpus (Figure 2c).

Variation

Head widths vary from 1.9-2.3 mm in males and 2.1-2.4 mm in females. In some specimens the division of the 4th segment of the maxillary palpus is more pronounced or even complete so that the palpus is 5-segmented, sometimes only on one side. Such specimens occur more frequently in the north-western part of the range. A male from near Eneabba is unique in having the fore tibial calcar like that of the female.

Distribution

South-western Australia from south of Dongara to 150 km east of Esperance (Figure 5).

Etymology

The specific epithet is derived from the generic name of the forage plants.

Specimens Examined

The holotype and the following. Western Australia: 10♂, 6♀, paratypes (WAM 87/1435-6, 88/975-88) same data as for holotype (ANIC, UQ, WAM); 9♂, 5♀, Badgingarra National Park (30°24'S, 115°27'E), 1-3 Oct. 1980, TFH, on flowers of *Conospermum triplinervium* (WAM); 25♂, 9 and 14 km WSW and 16 km NW of Eneabba (29°49'S, 115°16'E), 8-12 Sept. 1987, TFH, on flowers of *Conospermum incurvum* (17♂) and *C. triplinervium* (8♂), (WAM); 1♂, 1♀, paratypes (WAM 88/989-90), 3 km W of Mt Ragged (33°27'S, 123°29'E), 22 Oct. 1982, C.A. Howard & TFH, on flowers of *Conospermum distichum* (WAM); 2♂, 3♀, Tutanning Reserve, 18-25 km E of Pingelly, 30 Oct.-3 Nov. 1980, TFH, on flowers of *Conospermum stoechadis* (WAM); 11♂, Watheroo National Park (30°12'S, 115°50'E), 3-5 Oct. 1980, TFH, on flowers of *Conospermum triplinervium* (WAM).

Leioproctus (Leioproctus) pappus, sp. nov.

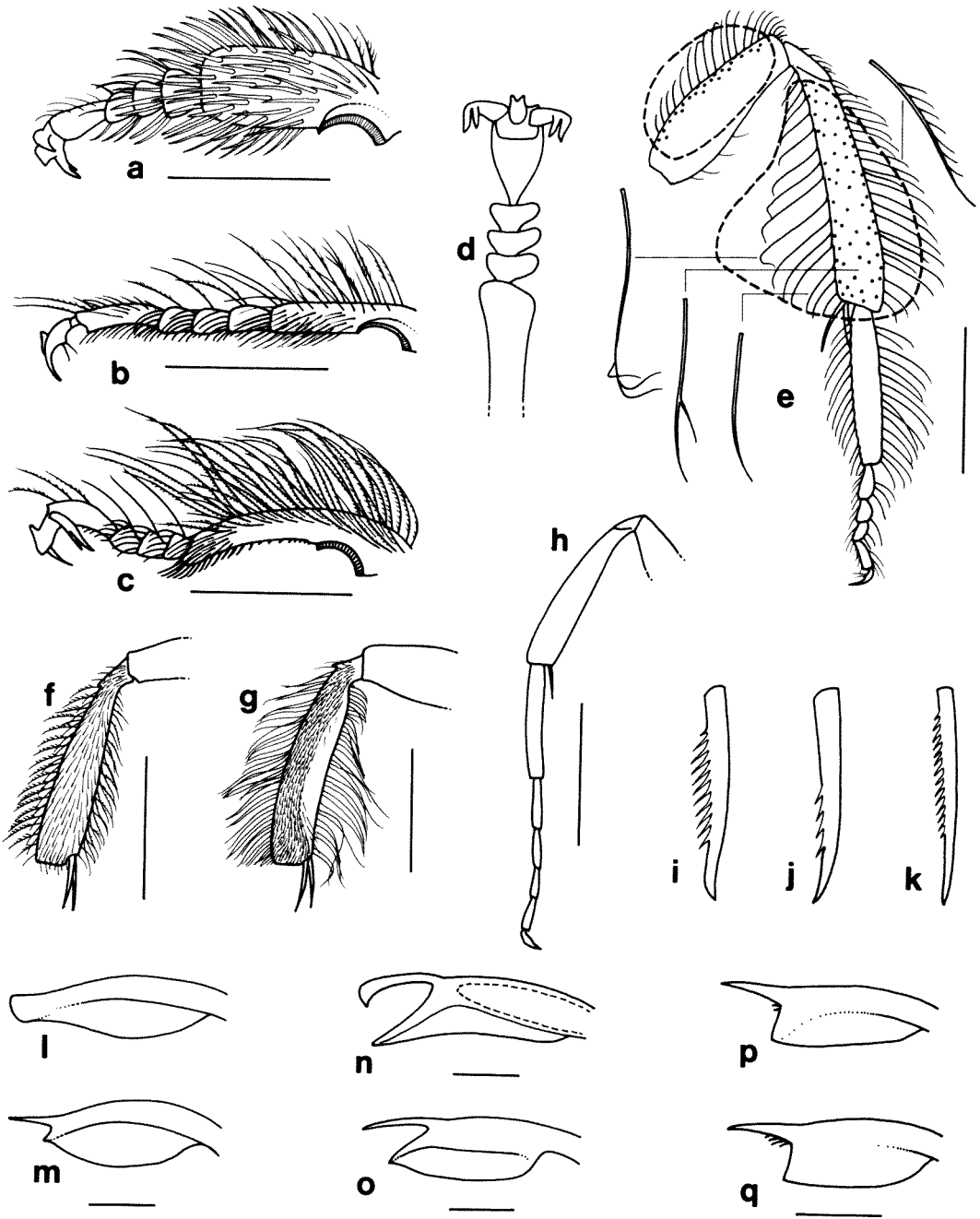
Figures 1 e; 2 a, f, g; 3 c, d, g, j, n, o; 4 d, g; 5; 6 a, b.

Holotype

In WAM (88/991). ♂, Boorabbin Rock (31°12'S, 120°17'E), Western Australia, 4-9 October 1981, TFH, on flowers of *Conospermum stoechadis*.

Paratypes

11♂, 2♀ in ANIC; 2♂, 1♀ in UQ; 37♂, 5♀ in WAM. See Specimens Examined.



Diagnosis

Readily distinguishable from *L. tomentosus* as noted in Diagnosis of *L. conospermi*. Distinguishable from *conospermi* as follows: prementum with setae uniformly shorter than 1st segment of labial palpus (Figure 2a); male with fore basitarsus attenuated at middle and arcuate (Figure 3c, d), fore tibial calcar with spatulate apical spine and velum produced acutely (Figure 3n); female with pubescence of 5th and 6th metasomal terga white.

Description

Male (holotype)

Head width 2.5 mm; body length 7.8 mm. Relative dimensions: HW 50; HL 37; UID 38; LID 34; MFW 30; IAD 7.5; ASD 4; AOD 8.5; SL 13.5; SW 3.5; FL c. 45; MOD 4.5; OOD 11; LPL 9; MPL 6; ML 20; MSL c. 2.

Differs from *conospermi* as noted in Diagnosis and in the following additional features: head relatively broader; malar space present; glossa weakly bilobed; maxillary palpus 3-segmented, 3rd and 4th segments fused (Figure 2f) relative lengths of segments 1-3 are respectively 4, 2.5 and 5% of HW; relative lengths of labial palpus segments 1-4 are respectively 6, 3.5, 3 and 5% of HW; mandible with posterior tooth greatly exceeding anterior tooth; middle segments of flagellum 1.4 X longer than wide; fore basitarsus slightly curved, constricted in middle, widest distally, concave ventral surface bare, with finely serrated ridge proximally (Figures 3c, d); fore tibial calcar with somewhat spatulate apical spine (Figure 3n); hind femur with distinctly flattened ventral surface; ventral margin of hind tibia with distinct convexity proximally (Figure 3g); hind basitarsus c. 6 X as long as high, slightly arcuate.

Eyes (in life) white; flagella yellow-brown ventrally; wing membranes milky in incident illumination, with colourless hairs, veins thick, black.

Pubescence much more abundant and longer than in *L. conospermi*, obscuring more of integument and imparting a hoary appearance (Figure 6a); flagellum shiny with brush-like vestiture of short, erect setae most developed posteriorly (Figure 1e); malar areas densely pubescent; hind tibia and basitarsus posteriorly with extremely dense simple spatulate setae obscuring integument; femur ventrally and large postero-ventral area of hind tibia bare; 4th and 5th metasomal sterna with

◀ **Figure 3** Details of legs of *Leioproctus conospermi* species-group: (a, b) inner views of fore tarsus of *L. conospermi* female and male, respectively; (c) same of *L. pappus* male; (d) ventral view of fore tarsus of *L. pappus* male (except base, setation omitted); (e) outer view of hind leg (except base) of *L. conospermi* female showing scopa (setation shown in profile only; dots represent insertions of setae on anterior surfaces of femur and tibia; heavy broken lines indicate extent of a full pollen load); (f, g) inner views of hind tibia of males of *L. conospermi* and *L. pappus*, respectively; (h) anterior view of hind tibia and tarsus of *L. tomentosus* male; (i-k) inner hind tibial spurs of females of *L. conospermi*, *L. pappus* and *L. tomentosus*, respectively; (l-q) calcar of fore tibia (male above, female below) of (l, m) *L. conospermi*, (n, o) *L. pappus* and (p, q) *L. tomentosus*, respectively. Scale lines: (a-c) 0.5 mm, (e-h) 1.0 mm, (l-q) 0.1 mm.

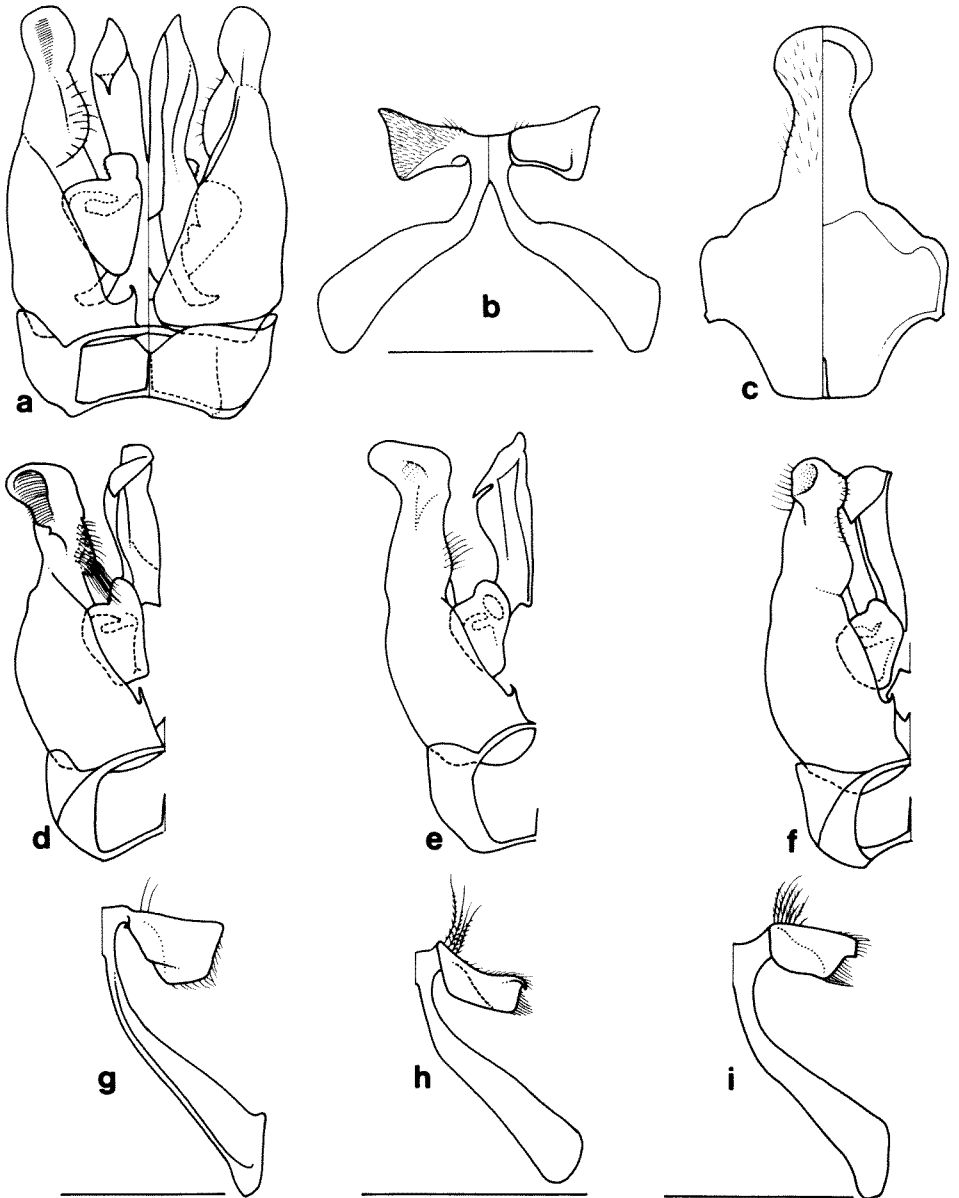


Figure 4 Details of male terminalia of *Leioproctus conospermi* species-group: (a-c) genital capsule, 7th and 8th metasomal sternites of *L. conospermi* (ventral view on left, dorsal on right); (d-f) half ventral views of genital capsule and (g-i) half dorsal views of 7th metasomal sternite of (d, g) *L. pappus*, (e, h) *L. tomentosus* and (f, i) intermediate (*conospermi*-*pappus*) form. Scale lines: 0.5 mm.

quite distinct apical fringes; prementum with numerous erect, simple setae, uniformly shorter than 1st segment of maxillary palpus.

Terminalia as in Figures 4d, g.

Female (paratype WAM 88/1014)

Head width 2.75 mm; body length 9 mm. Relative dimensions: HW 50; HL 37; UID 36; LID 33; IAD 7.5; ASD 4; AOD 9; SL 14; SW 3.5; FL *c.* 30; MOD 4; OOD 10; ML 23; MSL 0.5; BMW 14; LPL 6.6; MPL 5.

Differs from female of *conospermi* as noted in Diagnosis and in the following additional features: interantennal area convex but not peaked; malar area almost obsolete; glossa less bilobed, apical annular area folded medially but scarcely emarginate; maxillary palpus 3-segmented through fusion of 3rd and 4th segments (Figure 2g), relative lengths of segments 1-3 are respectively 4, 2 and 4% of HW; relative lengths of labial palpus segments 1-4 are respectively 5, 3, 2 and 3.5% of HW; fore basitarsus 3.5 X as long as high; fore tibial calcar with decurved apical spine (Figure 3 o); hind basitarsus 6 X as long as high with irregular, knobbly margins because of setal insertions; inner hind tibial spur with only 3-4 subapical serrations (Figure 3j); pygidial plate flat, granular; 1st and 3rd cubital cells approximately equal in length, 1.5 X as long as 2nd.

Metasomal terga 2-4 closely pitted but little less shining than 1st.

Hind margins of metasomal terga 1-4 with distinct, complete bands of adpressed white pubescence; 5th tergum with long white hair; setae of prementum no more than 1.5 as long as 1st segment of labial palpus; stipes with fringe of long, simple setae on ventral margin (Figure 2a).

Variation

Slight. The Watheroo female has 4-segmented maxillary palpi while some other specimens have the 3rd (terminal) segment partially divided.

Distribution

South-western Australia from near Perth to Geraldton with an outlying population between Southern Cross and Coolgardie (Figure 5).

Etymology

The specific epithet is Latin for 'plant down' and is used as a noun in apposition.

Specimens Examined

The holotype and the following paratypes. Western Australia: 21♂, 4♀ (WAM 88/992-1016), same data as for holotype (WAM); 10♂ (WAM 87/1430-1, 88/1026-33), Badgingarra National Park (30°24'S, 115°27'E), 1-3 Oct. 1980, TFH, on flowers of *Conospermum stoechadis* (WAM); 1♂ (WAM 88/1025), East Yuna Nature Reserve, 34 km WNW of Mullewa, 23-24 Sept. 1983, C. & TFH, on flowers of *Conospermum stoechadis*, (WAM); 11♂, 2♀, 9 km NNE of Geraldton, 19 Sept. 1972, N. McFarland, on flowers of *Conospermum stoechadis*, (ANIC); 7♂, 1♀ (WAM 88/1017-24), 10 km NE of Muchea (31°35'S, 115°58'E), 11 Oct. 1980, C.A. Howard & TFH, on flowers of *Conospermum stoechadis*, (WAM); 1♀ (WAM 87/1432), Watheroo National Park (30°12'S, 115°50'E), 3-5 Oct. 1980, TFH, on flowers of *Conospermum triplinervium*, (WAM).

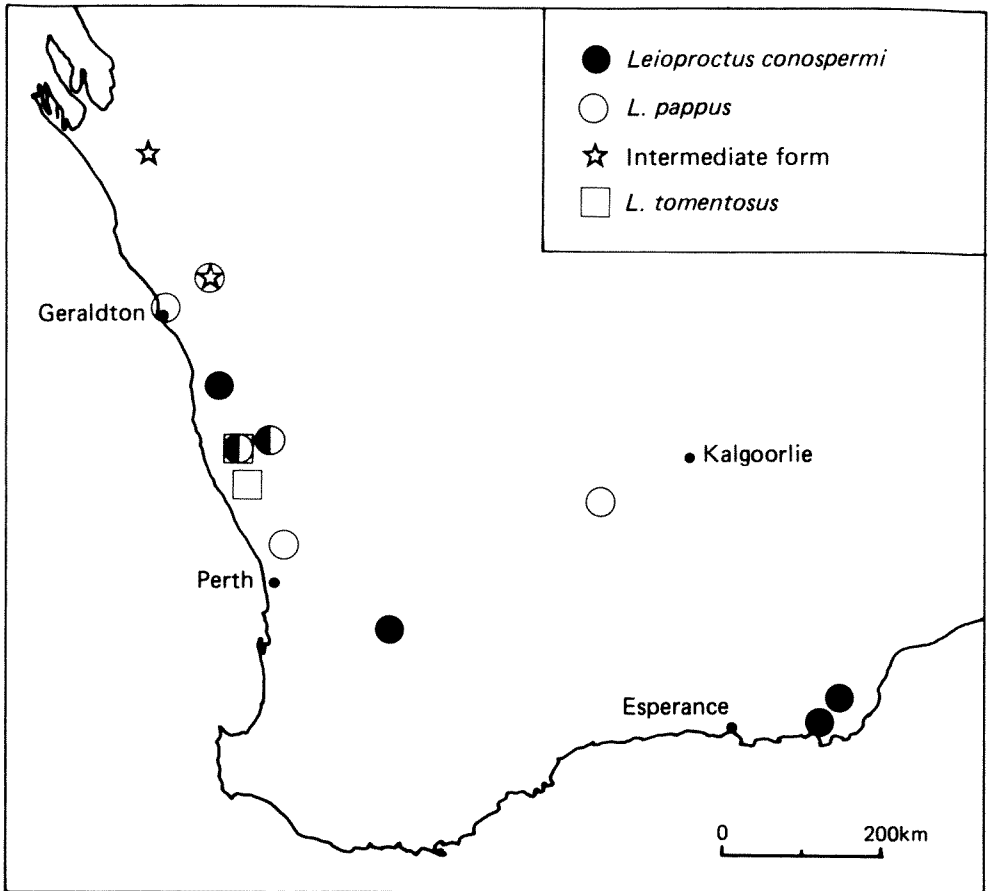


Figure 5 Collection localities for members of the *Leioproctus conospermi* species-group in south-western Australia. Localities where more than one species have been collected are represented by composite symbols.

***Leioproctus (Leioproctus) tomentosus*, sp. nov.**

Figures 1 c, d; 2 b, h, i, k, l; 3 h, k, p, q; 4 e, h; 5.

Holotype

In WAM (88/959), ♂, 8.4 km NNW of Cataby (30°44'S, 115°32'E), Western Australia, 8 Jan. 1983, C.A. Howard & TFH, on flowers of *Conospermum crassinervium*.

Paratypes

1♂, 1♀ in ANIC; 6♂, 3♀ in WAM. See Specimens Examined.

Diagnosis

Readily distinguished as follows: prementum sparsely setose (Figure 2b); metasomal terga 2-4 with adpressed pubescence uniformly distributed, not forming distinct apical

bands; male with tomentose frontal concavities and expanded scapes (Figure 1c); female with ventral margin of clypeus, labrum, mandibles and pygidial plate orange-brown.

Description

Male (holotype)

Head width 1.75 mm; body length 5.2 mm. Relative dimensions: HW 50; HL 40; UID 37; LID 30; MFW 25; IAD 5; ASD 4; AOD 8; SL 13; SW 7; FL c. 45; MOD 4.75; AOD 8.5; LPL 11; MPL 8; ML 17.5; MSL 1.

The following characteristics are additional to those noted in the Diagnosis. Face rather flat except for large concavities in upper paraocular areas; malar space almost obsolete; middle segments of flagellum about 1.2 X longer than broad, proximal two segments slightly enlarged and compressed (Figures 1c, d); glossa very broad, deeply bifid (Figure 2l); maxillary palpi 4-segmented, terminal segment somewhat constricted at middle (Figure 2h), relative lengths of segments 1-4 are respectively 5, 3, 3 and 6% of HW; relative lengths of labial palpus segments 1-4 are respectively 8, 5, 6 and 6% of HW; basitibial plate weakly developed; fore basitarsus strongly depressed, broadest distally but not curved; fore tibial calcar with acute apical spine (Figure 3p); hind legs relatively very long, tarsus (excluding claws) 1.5 X as long as tibia, basitarsus c. 7 X as long as high, slightly curved (Figure 3h); 2nd cubital cell about 1/3 as long as 1st, 1/2 as long as 3rd.

Eyes (in life) white; flagellum (except segments 1 and 2) light brown anteroventrally; wing membranes milky in incident illumination, veins thin, brown, very pale near wing bases.

Antennae dull; propodeal enclosure glossy with only one or two transverse striae.

Lower face and paraocular depressions covered by short, dense, white tomentum; remainder of head, body and legs with moderately dense, moderately long, white pubescence producing hoary appearance; 3rd and 4th metasomal sterna with complete, regular, apical fringes; 5th sternum with medially interrupted fringe; stipes fringed ventrally by single row of short to moderately long setae (at most as long as 1st segment of labial palpus); flagellum with brush-like vestiture of short setae only on proximal three segments posteriorly (Figure 1d).

Terminalia as in Figures 4e, h.

Female (paratype WAM 88/960)

Head width 1.85 mm, body length c. 6 mm. Relative dimensions: HW 50; HL 41; UID 35; LID 30; IAD 6; ASD 4; AOD 8; SL 15; SW 3.5; FL c. 32; ML 18; MOD 4; OOD 8; LPL 11; MPL 6; MSL 0.5.

The following characteristics are additional to those noted in the Diagnosis. Lower face fairly flat, interantennal area only slightly convex; mandible with posterior tooth rounded (worn?); scape with sinuate ventral margin; 1st segment of flagellum 1.4 X longer than wide viewed anteriorly, somewhat compressed; glossa very broad, deeply bifid (Figure 2k); maxillary palpus apparently 4-segmented with incomplete separation of 4th and 5th segments (Figure 2i), relative lengths of segments 1-4 are respectively 5, 3,

2 and 5% of HW; relative lengths of segments 1-4 of labial palpus are respectively 8, 5, 5 and 7% of HW; fore basitarsus *c.* 3 X as long as high, notch of strigilis about half its length; fore tibial calcar with acute apical spine and a few cilia (Figure 3q); hind basitarsus *c.* 6 X as long as high with irregular margins; inner hind tibial spur finely serrate (Figure 3k); pygidial plate smooth, flat, rather triangular but with rounded apex, margins carinate but not raised and rim-like; 2nd cubital cell 1/3 as long as 1st, 1/2 as long as 3rd.

Body mostly black; eyes (in life) white; wings milky in incident illumination with colourless hairs, brown veins becoming whitish near wing bases.

Propodeal enclosure glossy; metasomal terga shiny (largely obscured by pubescence); pygidial plate smooth and weakly shining, with sparse granulation basally.

Pubescence wholly white; face with more or less adpressed plumose setae; 1st metasomal tergum with adpressed plumose setae; longer erect setae occur on terga 1 anteriorly, 2-4 laterally and 5 generally; stipes with weak fringe of long setae on ventral margin.

Distribution

Known only from the coastal plain of Western Australia 140-180 km north of Perth (Figure 5).

Etymology

The specific epithet is Latin, meaning 'densely covered with matted wool or hair'.

Specimens Examined

The holotype and the following paratypes. Western Australia: 3♀ (WAM 87/1429, 88/960, 961), same data as for holotype (WAM); 7♂, 1♀ (WAM 87/1426-8, 88/962-6), Badgingarra National Park (30°24'S, 115°27'E), 27-28 Dec. 1982, C.A. Howard & TFH, on flowers of *Conospermum crassinervium* (ANIC, WAM).

Intermediate Form (near *L. conospermi*, *L. pappus*)

Figures 4 f, i; 5.

Seven males whose collection data are given below are consistent in having character states intermediate between those of *L. conospermi* and *L. pappus*. The available data are insufficient to show whether these males represent a hybrid population or a distinct fourth species. They were collected just prior to and during the known flight season of the above-mentioned species and at flowers of a shared forage plant species. Their two collection localities are the most northerly for the species-group (Figure 5) and only *pappus* is also known from one of them (East Yuna). The nearest known *conospermi* locality is 170 km to the south. However, collecting in these northern areas has not been intensive and *conospermi* and *pappus* may yet be found there.

The males are distinguished as follows: generally similar to male of *L. pappus* but with the following *conospermi*-like features — fore basitarsus straight and parallel-sided; hind femur not flattened ventrally; hind tibia with no convexity on ventral

margin proximally; maxillary palpus with 4 segments, 4th appearing partly divided; eyes (in life) greenish. Pubescence not as dense as that of *pappus* but longer and denser than that of *conospermi*; wings milky in incident illumination but veins not as thick as those of *pappus*; fore tibial calcar terminating in a short acute apical spine (relatively much shorter than that of *pappus* female, Figure 3a); genital capsule and 7th metasomal sternite as shown in Figures 4f, i.

Specimens Examined

Western Australia: 4♂ (WAM 88/967-70), East Yuna Nature Reserve, 34 km WNW of Mullewa, 23-24 Sept. 1983, C. & TFH, on flowers of *Conospermum stoechadis* (WAM); 3♀ (WAM 88/971-3), 13 km S of Wannoo (26°49'S, 114°37'E), 24-28 Aug. 1984, TFH & B.P. Hanich, on flowers of *Conospermum stoechadis* (WAM).

Observations

Concealment

The *Conospermum* species frequented by the *Leioproctus conospermi* species-group are amongst those known as 'smoke bushes'. Their flowers, and in some cases whole inflorescences, are covered by dense white pubescence (Figure 6c) and the allusion is that the swaying, often amassed, hoary inflorescences resemble wisps or plumes of smoke.

Both sexes of *L. conospermi* are conspicuous when settled on the inflorescences of their forage plants because of their sparsely setose black bodies. However, males of *L. pappus* and *L. tomentosus* are virtually invisible while settled. Their concealment is assisted by the following adaptive features: dense white pilosity obscuring almost the whole of the black integument of the head, body and legs, whitish compound eyes and milky wing membranes (under incident illumination; the wings are clear and colourless in transmitted light) (Figure 6a). The bare antennal flagella closely resemble the dark, glabrous, acuminate apices of floral bracts.

Males of the *conospermi* group have been observed patrolling the forage plants, hovering slowly amongst the inflorescences and perched on them, either feeding on nectar or sitting alert. My impression is that males of *pappus* spend proportionately more time alighted on inflorescences than do *conospermi* males and this may account for their superior adaptations for concealment. However, further observations are required to ascertain if there are such species differences in male behaviour.

Females of *pappus* and *tomentosus* are modified for concealment in the same ways as their males but less effectively. Their pilosity is sparser, exposing more of the black integument, especially in *pappus* (Figure 6b). This is puzzling as one might expect females to spend more time than males on flowers and consequently to be more vulnerable to predators. Predation pressure is assumed to have been responsible for the evolution of camouflage, not only in the bees, but in other arthropods associated with smokebush inflorescences (e.g. argid sawfly larvae, the cryptorrhynchine weevil *Aonychus lineatus* Pascoe, unidentified bombyliid flies and thomisid spiders).

While I am unaware of any literature reports of camouflage amongst the Apoidea, I can cite the following additional examples of camouflage amongst Australian colletid

bees: certain wholly white, yellow, or pastel green euryglossines (e.g. *Brachyhesma* species, *Euryglossa* (*Callohesma*) *megachlora* Exley) which forage at similarly coloured flowers of *Eucalyptus*, and an unnamed species of *Hylaeus* (*Pseudhylaeus*) with a predominantly white integument, oligolectic on white or yellow flowers of *Dicrasyllis*.

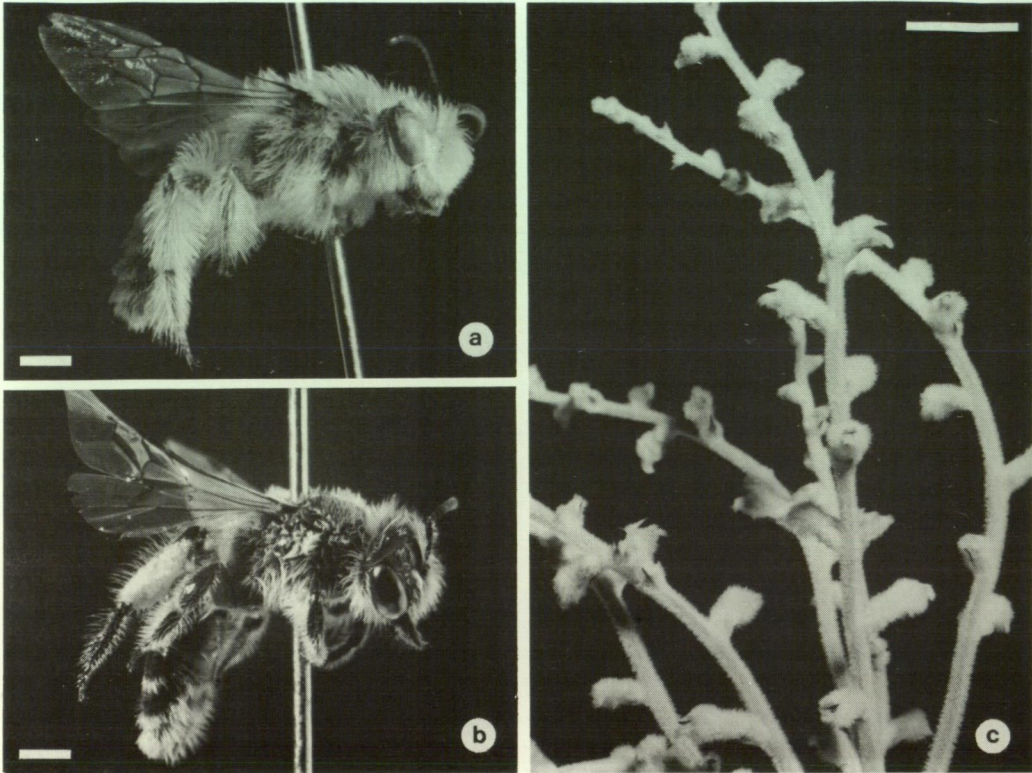


Figure 6 (a, b) pinned specimens of *L. pappus* male and female, respectively (female carries a partial pollen load on hind tibia); (c) inflorescences of *Conospermum stoechadis*. Scale lines: (a, b) 1 mm, (c) 1 cm.

Foraging

Conospermum species are not popular forage plants for bees other than the *L. conospermi* species-group. Only occasional specimens of small halictids (*Lasioglossum* and *Homalictus*) have been collected on smokebush. Bombyliid and syrphid flies and argid sawflies are the only other potential pollinators observed at flowers.

Bees of the *conospermi* group are not always evident or abundant at smokebush blossoms, even in ideal conditions, but occasionally are so numerous that hundreds can be collected by several minutes' sweeping with a net. They obtain both pollen and nectar from *Conospermum* flowers and are not known to visit flowers of other genera.

L. tomentosus is recorded only from *C. crassinervium* Meissner (the only summer flowering smokebush), *L. pappus* only from *C. stoechadis* Endl. and *C. triplinervium* R. Br., and *L. conospermi* from *C. distichum* Benth., *C. incurvum* Lindley, *C. stoechadis* and *C. triplinervium*. All of these *Conospermum* species have zygomorphic flowers. The flowers are quite small, the slender calyx tubes measuring about 6-8 mm in length (about the length of the bees).

Foraging bees insert their proboscis into the opening of the calyx while standing on the outside of the tube (or on adjacent flowers). If the flower has not been visited previously, the bee's proboscis triggers the pollen-release mechanism described by Carolin (1961) and Holm (1978): tactile stimulation of two staminodia within the calyx causes the style to snap from one side of the tube to the other, dabbing an adhesive on the insect; then the fertile anthers explode casting pollen into the lumen of the tube and onto the insect. These reactions occur instantaneously with a tiny audible 'click' and the style falls with such force that it has been known to trap fatally small ants and syrphid flies (Holm 1978, G. Keighery personal communication). *Leioproctus* visitors are clearly untroubled by this explosive mechanism. The reduction of the maxillary palpi in the *L. conospermi* group is perhaps associated with the battering the proboscis receives during feeding.

Almost all specimens of the bees examined had *Conospermum* pollen grains adhering to the prementum and stipites, and sometimes also to the genae, proboscival fossa and adjacent interscleritic membranes. The vestiture of simple erect setae on the prementum and stipites apparently serves to increase the capacity of those structures to hold pollen. It may also serve as a brush, enabling females to extract pollen from the calyx tubes, but I have no observational data to support this suggestion.

Conospermum pollen is comparatively coarse, the grains having a greatest diameter of 80-90 μ , and probably the very sparse scopa of *conospermi* group females is adapted to carry it. Females carry pollen in two distinct clumps on the outer (or anterior) surface of the hind leg, one on the femur and a much larger one on the tibia. The tibial pollen mass of a fully laden female extends well beyond the extremities of the scopal setae (Figure 3e) and must be bound by some adhesive.

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