

Two new species of the bee genus *Leioproctus* (Hymenoptera: Colletidae) that forage from flowers of bloodroot (genus *Haemodorum*)

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ABSTRACT – Two new species of *Leioproctus* (*L. aureofimbriatus* from eastern New South Wales and *L. haemodori* from south-western Australia) are described. Both species have been found only when visiting *Haemodorum* species that have dull brown to black flowers that do not open. The bee species are closely related to each other, but their relationship with other *Leioproctus* species is unclear. Both have morphological features that would assist in foraging from the flowers, males have similar terminalia and antennae with the apical segment flattened and expanded. This last feature occurs also in the distantly related species *Leioproctus* (*Ceratocolletes*) *antennatus* resulting in occasional misidentifications.

We have not created a new subgenus for these species because of difficulties with separating phylogenetically significant features from adaptive or adventitious ones. The mutualistic association between the bees and flowers has some novel characteristics and warrants further study.

KEYWORDS: floral attraction, oligolecty, mutualism

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INTRODUCTION

The plant genus *Haemodorum* Smith, 1798, is comprised of 29 known species, all but one of which are endemic to Australia, the exception occurring in Papua New Guinea (Macfarlane 1987; Barrett et al. 2015). The majority of species have dull brown to black flowers and the sepals and petals do not spread (Figures 1–3). The only known regular visitors to southern Australian species are two undescribed species of bees that force their way into the flowers to obtain nectar and/or pollen.

Images of the bees have appeared periodically on the internet, always in association with *Haemodorum* flowers. Males have been photographed on flowers in early morning, presumably after roosting overnight (Figure 2) and females have been reported foraging efficiently (J. Whitehead, pers. comm.). Other images demonstrate that the flowers provide both pollen and nectar (Figure 3). To date, neither species has been found visiting flowers other than *Haemodorum* and some of their morphological characteristics are likely to be adaptations for foraging.

The absence of visual signals typically used by flowers to attract insects makes these interactions between bees and *Haemodorum* particularly interesting. The flowers are unlikely to be self-pollinating because they produce both pollen and nectar (Simpson 1990, 1993) and at anthesis the stigma is produced well above the anthers (Figure 1). Yet the dull colours and closed flowers greatly restrict the number of potential pollinators.

The bees are assigned to the genus *Leioproctus* but their relationship to other species in the genus is not immediately obvious. Males have antennal modifications resembling those of the subgenus *Ceratocolletes* and, as a result, have been confused with that taxon, but are otherwise quite distinct.

MATERIALS AND METHODS

In addition to specimens in the Australian Museum and the Western Australian Museum, we have viewed several sets of images of the bees on the image hosting web-site *Flickr*. The locations where these images were captured are plotted, together with collection localities of museum specimens, in our distribution maps.



FIGURE 1 Inflorescence of *Haemodorum planifolium* showing flower heads setting seeds and clusters of immature buds (arrowed). Inset shows interior of flower at anthesis.



FIGURE 2 *Leioproctus aureofimbriatus* sp. nov.: five dew-covered males that have apparently roosted together overnight on flowers of *Haemodorum planifolium* (photo J. Whitehead).

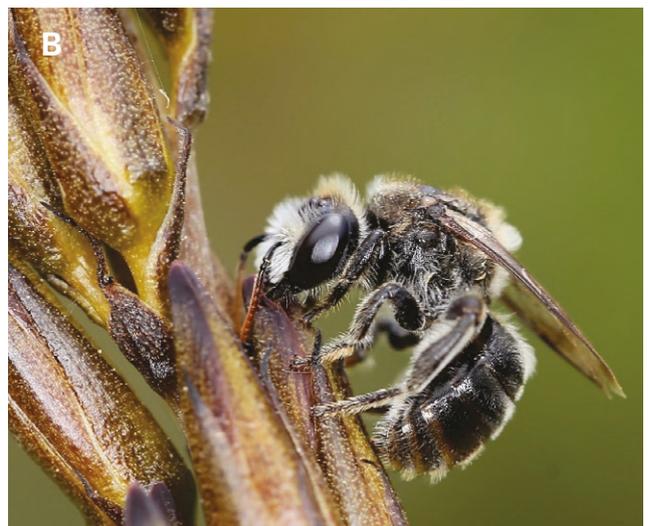
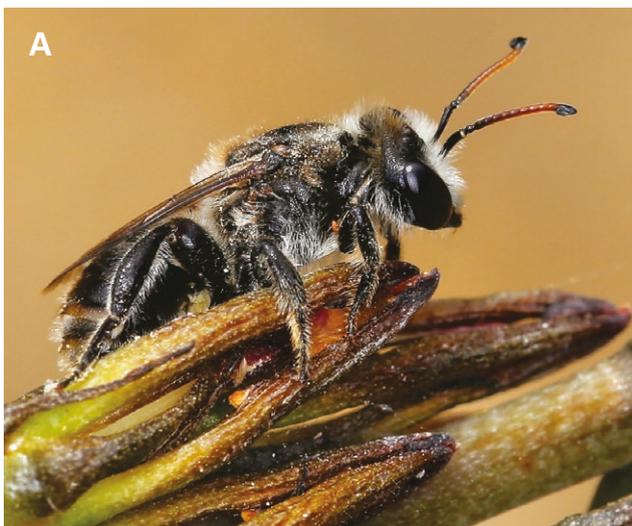


FIGURE 3 *Leioproctus haemodori* sp. nov. on flowers of *Haemodorum*: A) male, in alert position on flowers; B) male, working to open a flower; C) female, collecting pollen from anthers; D) female, probing deeply for nectar (photos: A–B Kerry Stuart; C–D Kate Brown).

The morphological terminology used herein follows that used by Michener (2007) and Harris (1979), including interchangeable use of the words hair and seta. Abbreviations used for measurements are as follows: ASD antennal socket diameter; AOD antennocular distance; FL flagellum length; HL head length; HW head width; IAD interantennal distance; LFW lower face width; MOD diameter of median ocellus; SL scape length; SW scape width; UFW upper face width (maximum width of face above antennae). Metasomal terga are referred to as T1, T2 etc. and sterna as S1, S2 etc.

The following acronyms have been used in this paper:

AMS	Australian Museum (Sydney, New South Wales)
ANIC	Australian National Insect Collection, CSIRO (Canberra, ACT)
WAM	Western Australian Museum (Perth, Western Australia)

SYSTEMATICS

Family Colletidae Lepeletier, 1841

Subfamily Neopasiphaeinae Cockerell, 1930

REMARKS

We use the definition of the subfamily Neopasiphaeinae as circumscribed by Almeida et al. (2012).

Genus *Leioproctus* Smith, 1853

Leioproctus (Leioproctus) aureofimbriatus Batley, sp. nov.

Figures 2, 4–13

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MATERIAL EXAMINED

Holotype

Australia: New South Wales: ♂, Gibraltar Range NP, 29.5345°S, 152.2659°E, 13 December 2021, J. Whitehead (AMS K.593175).

Paratypes

Australia: New South Wales: 1 ♂, Heathcote, 18 November 1970, D.K. McAlpine (AMS K.182777); 1 ♂, Patonga, 24 November 1946 (AMS K.182778); 1 ♂ Bilpin, 5 December 1985, N.W. Rodd (AMS K.182779); 1 ♀, Gibraltar Range NP, 29.5345°S, 152.2659°E, 13 December 2021, J. Whitehead (AMS K.593176); 1 ♀, Yoogali Lookout, 33.7430°S, 150.6358°E, 25 November 2022, M. Batley (ANIC); 1 ♀, Marramarra NP, 33.5631°S, 151.0692°E, 13 December 2022, M. Batley (AMS K.396004); 1 ♂, 1 ♀ 4 km SW Mount Wilson, 33.5409°S, 150.3430°E, 24 December 2022, M. Batley (AMS K.396006, K.396007); 1 ♀, Lithgow, 33.4859°S, 150.1906°E, 9 January 2023, M. Batley (AMS K.396013).

Queensland: 1 ♂, Ballandean, 28.7942°S, 151.8616°E, 3 December 2007, M. Newman (AMS K.395998).

DIAGNOSIS

Distinguishable from all other *Leioproctus*, except *L. haemodori*, in combining the following character states: clypeus and supraclypeal area of both sexes flat; facial foveae very broadly impressed, particularly in female, less so in male; propodeal triangle smooth, shining; fore wing with three submarginal cells; mid tibia of both sexes lacking spur; hind tibia of male with spurs reduced; flagellum of male slender and mostly yellow-brown but apical flagellomere black, expanded into rounded disc; T4–T6 of male clothed in short, highly branched, white setae. Differs from *L. haemodori* in the following combination of characters: female with prepygidial fimbria grey-brown not black; facial fovea strongly impressed; scutum flattened anteromedially; male hind leg unmodified.

DESCRIPTION

Male (Holotype)

Head width 3.6 mm; body length c. 10.8 mm (slightly contracted, another specimen same head width was 11.2 mm long). Relative dimensions: HW 100; HL 74; UFW 66; LFW 56; IAD 20; ASD 6; AOD 14; SL 30; SW 7; FL 76.

Head wider than long; vertex gently convex in anterior view (Figure 4A); inner orbits gently converging ventrally; clypeus flat and supraclypeal area slightly concave; facial fovea broad, weakly impressed; gena about half as wide as eye viewed laterally; malar space absent; scapes exceeding median ocellus; flagella much shorter than head width; flagellomeres 3–9 almost cylindrical, apical flagellomere produced into a posterior flange (Figure 4B); mandible short and broad; scutum with strongly impressed medial and parapsidal lines; metanotum about half as long as scutellum with no evidence of a tubercle; short subhorizontal part of propodeal triangle rounding smoothly onto longer vertical part; hind basitibial plate 0.2 × length of tibia, with strong marginal carina on apical half only; fore tibial calcar with a greatly reduced apical spine; mid tibial spur absent and hind tibia with only one short spur (absent in northern specimens); claws of fore and mid tarsi cleft, that of hind tarsus with strong inner prong much closer to base than in other claws (Figure 5A–B); second submarginal cell of forewing (Figure 8) receiving first recurrent vein near distal end, marginal cell curves away from costa well before apex, stigma yellow brown, narrow, 0.6 times as long as costal margin of marginal cell, jugal lobe of hind wing just reaches cu-v; fore and mid tarsi about half as long as hind tarsus; marginal areas of metasomal terga broad, depressed, postgradular area of T2 weakly depressed.

Colouration: Integument black, except apical margins of metasomal terga T4–T7 brown; flagellum orange-brown, except expanded apical segment black; fore and mid tarsi brown to orange-brown; wings with infuscation near apices (Figure 8).

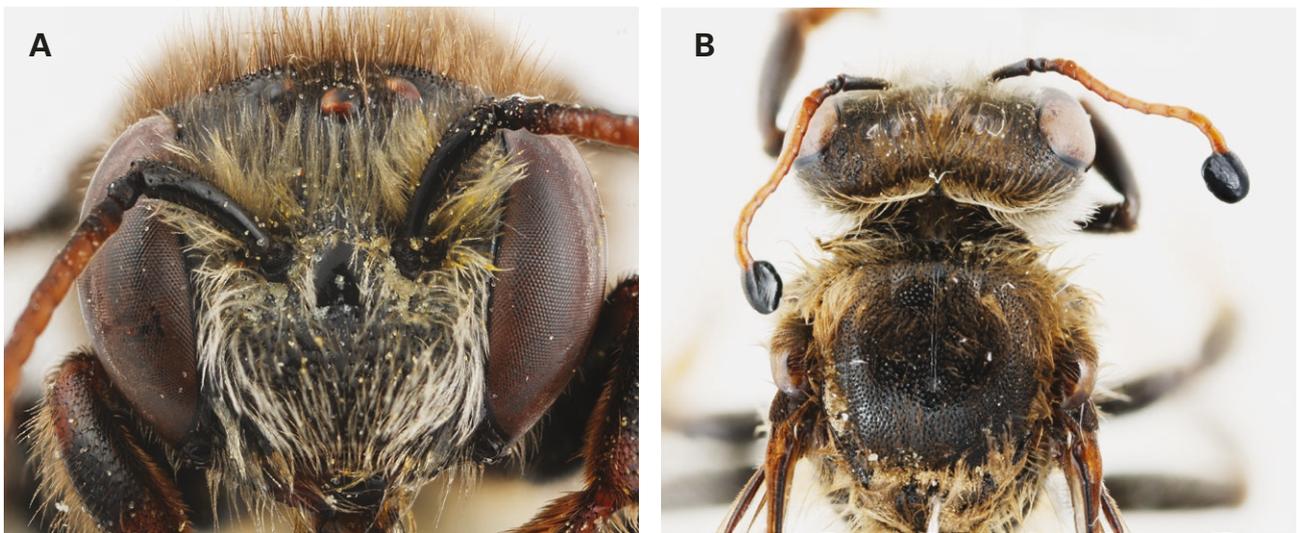


FIGURE 4 *Leioproctus aureofimbriatus* sp. nov. male: A) front view of head; B) dorsal view of head and thorax showing expanded segment of flagellum (AMS K.593175).



FIGURE 5 *Leioproctus aureofimbriatus* sp. nov., tarsal claws: A) male, fore leg; B) male, hind leg; C) female, fore leg; D) female, hind leg. Scale = 100 μ , all figures to same scale.



FIGURE 6 *Leioproctus aureofimbriatus* sp. nov. male metasoma (part): A) posterodorsal view of terga showing short, white, highly branched setae; B) posteroventral view showing fringe on S5.

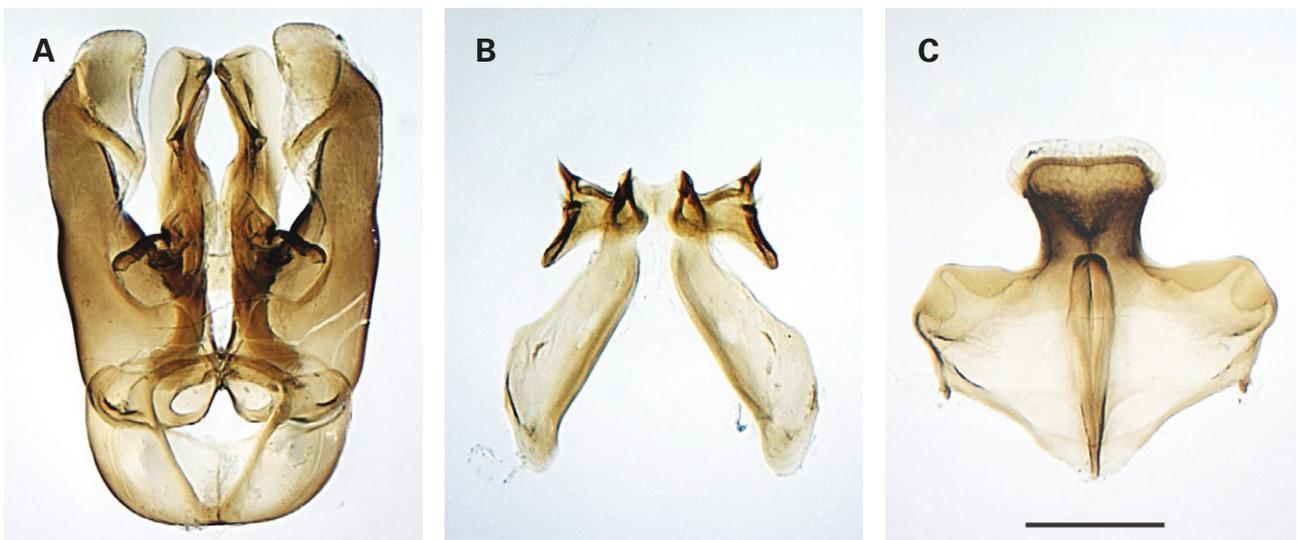


FIGURE 7 *Leioproctus aureofimbriatus* sp. nov. male terminalia: A) genital capsule ventral view; B) S7 ventral view; C) S8, ventral view. Scale = 0.5 mm, all figures to same scale.

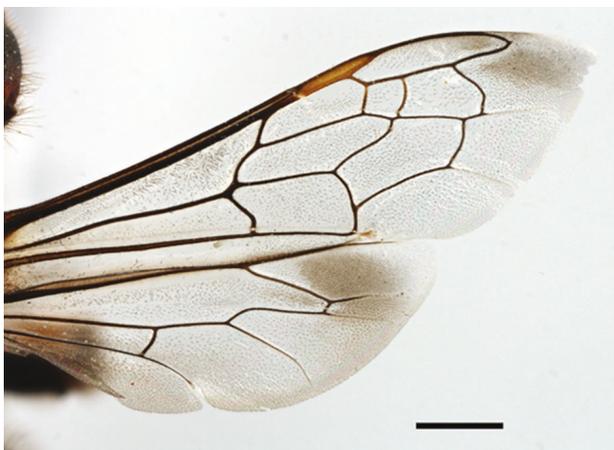


FIGURE 8 *Leioproctus aureofimbriatus* sp. nov. male wings, scale = 1 mm.



FIGURE 9 *Leioproctus aureofimbriatus* sp. nov. female frons, showing impressed fovea.



FIGURE 10 *Leiproctus aureofimbriatus* sp. nov. female inner hind tibial spur.



FIGURE 11 *Leiproctus aureofimbriatus* sp. nov. female head, front view.



FIGURE 12 *Leiproctus aureofimbriatus* sp. nov. female, dorsal view showing metasomal hair bands and flattened scutum, scale = 2 mm.

Sculpture: Surface polished, though very weak imbrication is present in some areas. Pitting of clypeus moderately large, dense, pits occasionally contiguous; supraclypeal area not pitted; pitting of paraclypeal areas and frons similar to that of clypeus; scutum and scutellum have strong, mid-sized pitting with interspaces roughly equal to pit diameter; propodeal triangle highly polished with weak, very fine transverse rugae; metasomal terga with strong, small pitting, interspaces about half pit diameter; metasomal sterna have sparse, weak, small pitting.

Pubescence: Facial hair white, plumose, length $2 \times$ MOD, dense in lower paraocular areas and on lower frons, open to sparse on clypeus; ventral margin of mandible with subapical plume of white hair $\sim 3 \times$ MOD; vertex with erect, pale brown, weakly plumose hair $2 \times$ MOD; genae with open, white, plumose hair $\sim 2 \times$ MOD; hair on scutum, scutellum and metanotum golden brown, plumose, erect $1.5 \times$ MOD, longer on anterior part of scutum, on scutellum and metanotum; hair on sides of mesosoma paler becoming white ventrally $3 \times$ MOD. All basitarsi with moderately long fringes of gold hair on both anterior and posterior margins. Metasoma with sparse hair except T1 and T2 with erect, open, weakly plumose, off-white hair $1 \times$ MOD and T4–T6 with similar dark brown hair openly interspersed with very short, branched, stiffly erect, white setae (Figure 6A); S5 with a dense, gold fringe $2 \times$ MOD laterally, $1 \times$ MOD medially (Figure 6B).

Terminalia: See Figure 7. When retracted posterior head of S8 fits snugly into cup formed by the rear end of gonoforceps.

Female (AMS K.593176)

Head width 3.8 mm; body length c. 12.5 mm. (slightly distended). Relative dimensions: HW 100; HL 72; UFW 66; LFW 57; IAD 18; ASD 6; AOD 16; SL 30; SW 6; FL 50.

As for male except facial fovea strongly impressed (Figure 9), infuscations of wings weak, flagellum not modified, and hind basitibial plate convex, without a peripheral carina, densely covered with adpressed dark setae. Width of mandible near apex, including preapical tooth, almost as great as basal width of mandible. All claws with a strong basal inner tooth (Figure 5C–D). Pygidial plate acarinate, with rounded apex and a broad, smoothly convex medial elevation. Inner hind tibial spur yellow-brown with a strongly curved apex and 8–10 oblique, closely-spaced teeth about as long as width of shaft (Figure 10), outer spur slender, noticeably shorter than inner spur.

Colouration: Integument black, except mandible dark red apically preceded by an area of amber colour, flagellum ventrally orange-brown, tegula, all tarsi and parts of tibiae dark brown, wings with only faintly infuscated areas.

Sculpture: As for male.

Pubescence: As for male but facial hair less dense (Figure 11), hair on clypeus simple, pale brown, scutal hair dark brown. Hair of hind tibial scopa close, plumose, anterior margin golden brown becoming dark brown on posterior half, hind femoral scopa plumose, mostly golden brown. Metasomal terga T2–T4 with white apical hair bands, interrupted medially on T2–T3 (Figure 12); prepygidial fimbria grey-brown; metasomal sterna S2–S5 with close, white, apical fringes, apical half of S6 with adpressed, pale brown, plumose hair.

Variation: The length of the expanded apical flagellomere of males is greater than the length of the two preceding flagellomeres combined for the two male

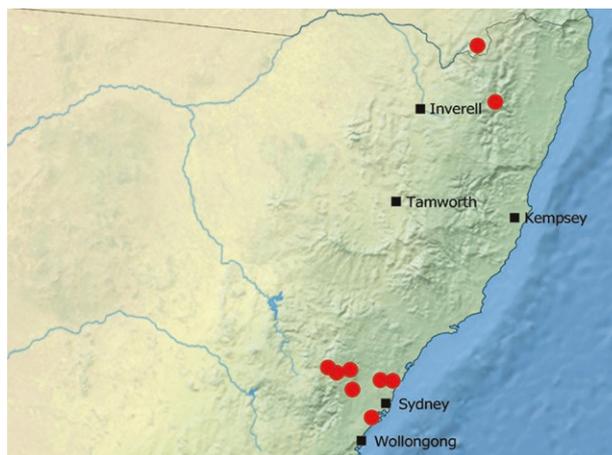


FIGURE 13 Known distribution of *Leioproctus aureofimbriatus* sp. nov. in eastern Australia (circles).

specimens from northern New South Wales, while its is slightly less than the length of the preceding flagellomeres in specimens from the Sydney region. The northern specimens also lack hind tibial spurs, while males from further south have a small residual spur. No difference could be detected in the terminalia or any other feature of males from the two areas.

The dorsum of the male flagellum is sometimes infuscated or uniformly brown.

DISTRIBUTION

Eastern coast and ranges of New South Wales from the Sydney region to the Queensland border (Figure 13).

Floral records

This species has been collected only from flowers of *Haemodorum planifolium*. There were no flower visiting records associated with AMS K.182777–182779.

ETYMOLOGY

The specific epithet is a Latin adjective meaning with a golden fringe, referring to fringes on the fore basitarsus and S5 of the male.

Leioproctus (Leioproctus) haemodori Houston, sp. nov.

Figures 3, 14–22

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MATERIAL EXAMINED

Holotype

Australia: Western Australia: ♂, Greenmount National Park, Padbury Road, Darlington, $31^{\circ}54'33''$ S, $116^{\circ}34'3''$ E, 13 November 2016, T.F. Houston 1499-3 and J. and F. Hort, on flowers of *Haemodorum* (WAM E114807).

Paratypes

Australia: Western Australia: 1 ♂, 2 ♀, 9 km NNE of Eurardy HS on NW Coastal Hwy, 27°30'S, 114°43'E, 25 October 1996, T.F. Houston 915-13, on flowers of *Haemodorum venosum* (WAM E8453–8455); 1 ♀, Flynn Drive, Neerabup, 30 km N of Perth, 11 November 1995, T.F. Houston (WAM E8456); 3 ♂, 3 ♀, Vermin Fence, 6 km S of Great Eastern Highway, Koorarawalyee, 31°19'30"S, 120°00'34"E, 21 October 2012, T.F. Houston 1405-10, on flowers of *Haemodorum (discolor?)* (WAM E114801–114806); Gooseberry Hill National Park, 19 km E of Perth, T.F. Houston 664-1, 804-2, 807-1, 810-3 and 814-2, on flowers of *Haemodorum simulans*: 1 ♀, 7 November 1987 (WAM E8447); ♂, 26 November 1992 (WAM E8448); 2 ♂, 4 December 1992 (WAM E8449–50); 1 ♂, 13 December 1992 (WAM E8451); 1 ♂, 22 December 1992 (WAM E8452); 2 ♂, Midland, A.M. Douglas (WAM E8457–8458); 1 ♂, Dundas Road, [Kewdale], 31°58'43"S, 115°59'16"E, L. Lach, Acc # 0275, Sample 10.207 (WAM E114808); 0.5 km E of Forrestdale Lake, 25 km SSE of Perth, T.F. Houston 662-7 and 663-1, on flowers of *Haemodorum spicatum*: 1 ♂, 28 October 1987 (WAM E8442); 1 ♂, 3 ♀, 6 November 1987 (WAM E8443–8446).

DIAGNOSIS

Shares most of the diagnostic character states of *L. aureofimbriatus* except as follows: scutum not flattened anteromedially; female lacking hair bands and with prepygidial fimbria black; facial foveae only weakly impressed; hind leg of male modified (trochanter with stout ventral spine, tibia distinctly bent mesad).

DESCRIPTION

Male (Holotype)

Head width 3.62 mm; body length c. 10.3 mm. Relative dimensions: HW 100; HL 74; UFW 64; LFW 54; IAD 17; ASD 8; AOD 13; SL 33; SW 6; FL c. 65.

Body form moderately robust; head broader than long; vertex gently convex in anterior view and distinctly higher than ocelli (Figure 14A); inner orbits gently converging ventrally; lower face (including supraclypeal area and clypeus) flattened; facial foveae slightly defined apically by a weak edge; gena about half as wide as eye viewed laterally; malar space absent; scapes long and slender, exceeding median ocellus; flagella much shorter than head width; flagellomeres 3–9 cylindrical, apical flagellomere produced into a flange posteriorly (Figure 14B); metanotum ordinary, lacking a protuberance; propodeum with short, gently sloping basal surface rounding onto longer vertical surface; propodeal pit broadly V-shaped; metasomal terga gently convex with distinct post-gradular grooves and weakly defined hind margins; fore tibial calcar lacking a prominent apical spine (Figure 16C); mid tibia lacking apical spur; hind trochanters each produced posteriorly into a stout spine (Figure 16A); hind femur swollen; hind tibia bent mesad (Figure 16B), outer convex surface coarsely wrinkled, apical spurs vestigial;

all basitarsi flattened, more or less straight and at least as long as rest of tarsus; tarsal claws bifid (Figure 18A–B); arolia present.

Colouration: Integument black except as follows: flagellomeres 2–10 pale yellow-brown; metasomal T4–T6 brown; wings hyaline except for some patches of light infuscation apically (Figure 15).

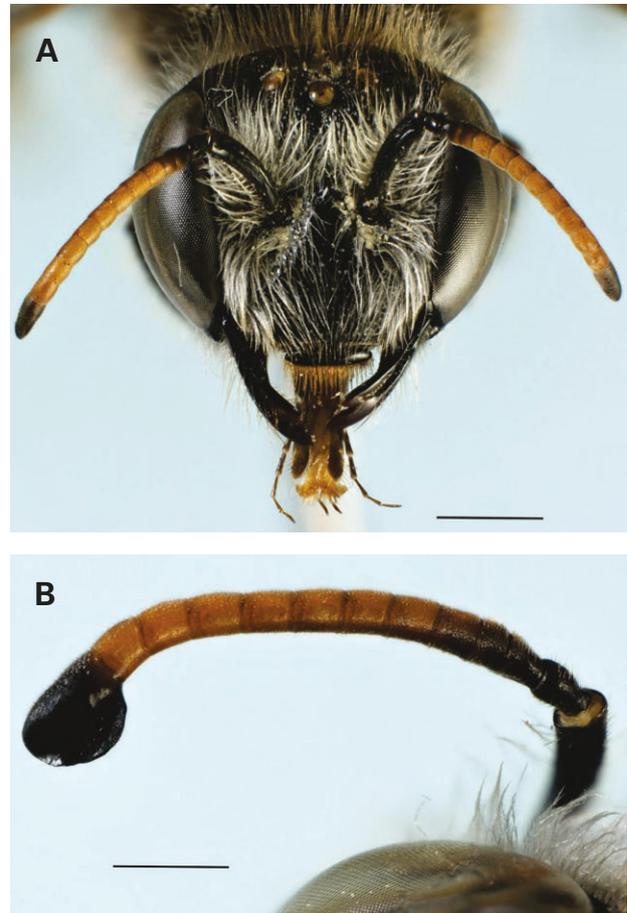


FIGURE 14 *Leioproctus haemodori* sp. nov. male: A) head, anterior view, scale = 1 mm; B) antenna, dorsal view, scale = 0.5 mm.

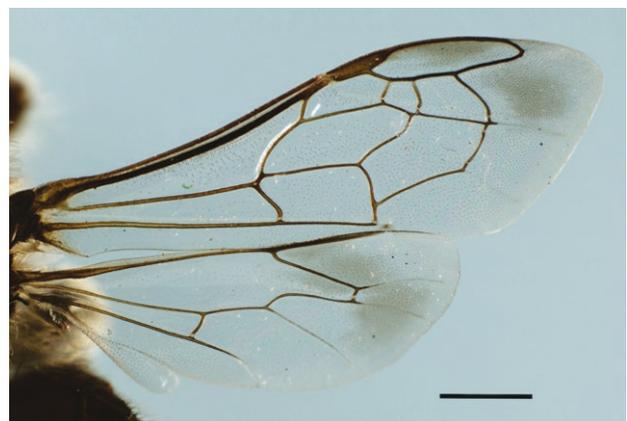


FIGURE 15 *Leioproctus haemodori* sp. nov. male wings, scale = 1 mm.



FIGURE 16 *Leioproctus haemodori* sp. nov. leg features: A) bases of hind legs of male, dorsal view, showing stout spine on each trochanter, scale = 1 mm; B) middle section of hind leg of male (posterior view) showing bent tibia, scale = 1 mm; C–D) antenna cleaners of male and female, respectively, scale = 0.1 mm.



FIGURE 17 *Leioproctus haemodori* sp. nov. male: A) metasoma, lateral view, showing much denser pubescence of T4–T6 compared with that of T1–T3, scale = 1 mm; B) apex of metasoma, ventral view, showing dense, medially emarginate fringe of S5 (arrowed), scale = 0.5 mm.



FIGURE 18 *Leioproctus haemodori* sp. nov. tarsal claws: A) male, fore; B) male, hind; C) female, fore; D) female, hind. Scale bar = 0.1 mm, all to same scale.



FIGURE 19 *Leioproctus haemodori* sp. nov. male terminalia: A) genital capsule, ventral view; B) S7, dorsal view; C) S8, dorsal view. Scale = 0.5 mm, all to same scale.



FIGURE 20 *Leioproctus haemodori* sp. nov. female head, anterior view, scale = 1 mm.

Sculpture: Integument of face and mesosoma generally shining with minute to medium sized pitting, coarsest on clypeus, finest and densest on vertex; supraclypeal area not pitted medially; propodeal triangle smooth and lacking sculpture except for a few carinae at lateral extremities; metasomal terga dulled by close, fine pitting.

Pubescence: Generally sparse and not obscuring integument; long, white, plumose setae cover much of face (but sparser and less plumose on lower medial area), genae, mesosoma ventrally and laterally and basal parts of legs; dorsal areas of head and mesothorax with erect, light brown, plumose setae; T1 and T2 with erect, short, white setae; T3 with similar but brown setae; T4–T6 with mixture of erect, weakly plumose, brown setae and short, white, highly branched setae (Figure 17A); sterna largely bare but with erect, sparse, simple setae more apically; S5 with dense, beige, apical fringe that is broadly emarginate medially (Figure 17B).

Terminalia: See Figure 19.

Female (WAM E8444)

Head width 3.7 mm; body length c. 10.5 mm. Relative dimensions: HW 100; HL 73; UFW 66; LFW 55; IAD 16; ASD 8; AOD 16; SL 30; SW 5; FL 45.

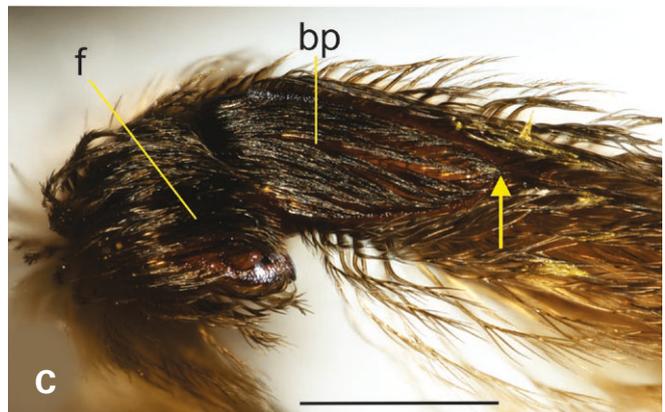
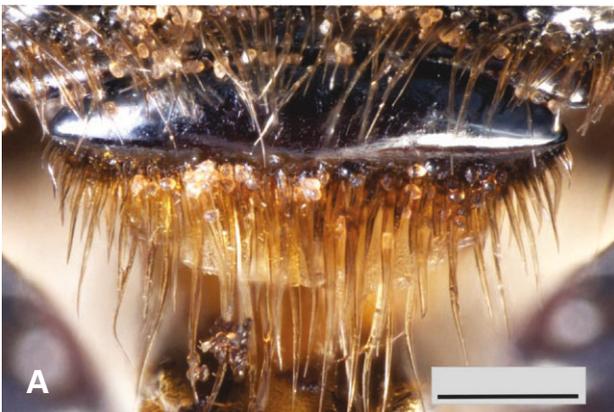


FIGURE 21 *Leioproctus haemodori* sp. nov. female: A) labrum, scale = 0.25 mm; B) hind tibia and tarsus (lateral view), scale = 0.5 mm; C) apex of hind femur (f) and base of hind tibia showing hair-covered basitibial plate (bp) that tapers to apex (arrowed), scale = 1 mm; D) apex of metasoma (posterior view) showing medially convex pygidial plate, scale = 0.5 mm.

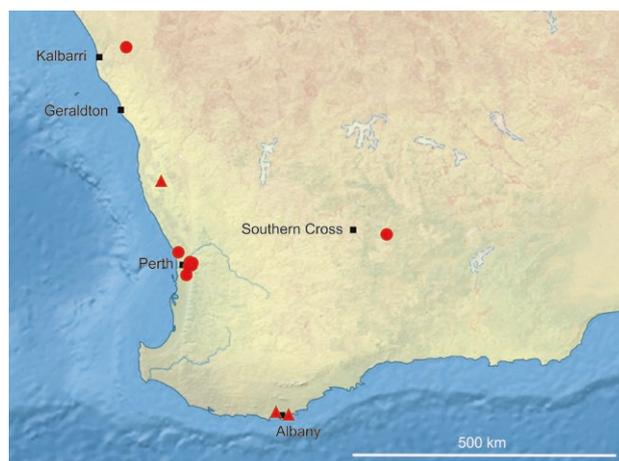


FIGURE 22 Known distribution of *Leioproctus haemodori* sp. nov. in south-western Australia: circles = specimen records (WAM); triangles = photographic records.

Generally similar to male, except as follows: facial foveae moderately impressed, quadrate; flagella unmodified (Figure 20); labrum (Figure 21A) about a quarter as long as wide, elevated basal zone smooth, lacking tubercle and carina, ventral margin transverse, reflexed to extremely short setose apical flange; basitibial plate completely defined by carina, acute apically, obscured by adpressed short setae (Figure 21C); hind basitarsus laterally compressed, one third as high as long (Figure 21B); inner hind tibial spur finely pectinate as in *L. aureofimbriatus*; pygidial plate (Figure 21D) smooth, convex medially and tapering to rounded apex; tarsal claws with teeth diverging more widely than in male (Figure 18C–D).

Colouration: As in male, except as follows: wings completely hyaline, lacking infuscation.

Sculpture: As in male, but clypeus with coarse open pitting.

Pubescence: Much as in male, except as follows: T4–T6 lacking tomentum, like T2 and T3, mostly covered with short, simple, brown to black, recumbent setae; hind leg with scopa developed on trochanter, anterior surface of femur, outer surface of tibia and basitarsus (basally only) and consisting of long, dense, highly divided setae, those of tibia grading from light brown ventrally to dark brown dorsally (Figure 21B); pygidial and prepygidial fimbriae well-developed, composed of dense, dark brown to black, plumose setae (Figure 21D).

DISTRIBUTION

South-western Australia north as far as Kalbarri, south to Albany and east to Boorabbin (Figure 22).

Floral records

This species has been collected only from flowers of *Haemodorum*, including the species *H. discolor*, *H. laxum*, *H. simulans*, *H. spicatum* and *H. venosum*.

Photographic records

Junction of Brand Hwy and Marchagee Track, 30.2297°S, 115.4269°E, October 2015, on flowers of *H. spicatum*, Mark Brundrett; Downs Road Nature Reserve, 34.95°S, 117.76°E, c. 14 km WNW of Albany, on flowers of *H. spicatum*, Kate Brown; Gull Rock National Park, 35.004°S, 118.018°E, just E of Albany, on flowers of *H. spicatum*, Kate Brown.

ETYMOLOGY

The specific epithet is in the genitive singular and alludes to the close association of the bee with the plant genus *Haemodorum*.

BEHAVIOURAL OBSERVATIONS

Males of *L. haemodori* were collected by TH either while flying about the forage flowers or perched on them. Males frequently remained stationary for several minutes, sitting in an alert pose (Figure 3A). On one occasion, TH observed a cluster of flowers of *H. simulans*, receiving persistent attention from one male (or possibly two or more males arriving at different times). Every few minutes, a male would fly up to the flower cluster, hover while facing it, alight for some time, then depart. A week later, at the same plant, similar behaviour was observed. However, as well as perching on the flowers, the male occasionally landed on and ran down the flower stem for 20–30 cm before flying off. One male was netted and, after 1.5 hrs, was replaced by another.

Males of *L. aureofimbriatus* were seen only occasionally as they paused their flight very briefly near flowers, but females were observed foraging by MB at four sites during the summer of 2022–23. They were tolerant of the human observer and continued to push into flowers methodically. At all four sites there were periods of 30–60 minutes when no bees could be seen interspersed with periods of systematic foraging by one or two females.

Adding to our personal observations, some extra information on behaviour of the bees has been gleaned from photographs taken by others: evidently, males of at least *L. aureofimbriatus* roost overnight in groups on flowers of *Haemodorum* (Figure 2); males as well as females prise open flowers to take nectar and/or pollen (Figure 3B–D); both sexes of *L. haemodori*, have been photographed (by K. Brown) regurgitating crop contents onto their mouthparts (presumably thickening nectar) while perched on flowers of *Haemodorum*.

Finally, samples of pollen taken from the heavily laden scopae of three females of *L. haemodori* from widely separated localities were uniformly of one morphotype matching the illustration of a pollen grain of *H. spicatum* provided by Simpson (1990, Figure 77).

DISCUSSION

The two species described herein, particularly their males, bear a striking resemblance to *Leioproctus* (*Ceratocolletes*) *antennatus* (Smith, 1879). Indeed, Michener (1965) incorrectly associated the male of

L. haemodori with the female of *L. (C.) andreniformis* (Cockerell, 1915) when establishing the subgenus *Ceratocolletes* and included the leg modifications of the male in his description of the subgenus. Maynard (1993), in revising the subgenus, synonymised *L. andreniformis* with *L. antennatus* and noted Michener's error. A male specimen of *L. haemodori* in the WAM bears one of Michener's identification labels on which he had written '*Leioproctus andrenoides* Ckll male?' As the specific epithet 'andrenoides' was not listed in Michener's 1965 treatise, it was almost certainly an error for *L. andreniformis*. Failing to heed Maynard's correction, Michener (2000, 2007) continued to include strong modifications of the hind legs of males as characteristics of *Ceratocolletes*.

Despite the general resemblance of our two new species to members of subgenus *Ceratocolletes*, we are confident that they do not belong to that taxon, primarily because the male S7 has a single pair of apical lobes while that of *Ceratocolletes* males has four. Other distinguishing features are as follows (corresponding features of *Ceratocolletes* in parentheses): clypeus flat (raised medially); metasomal terga not depressed behind post-gradular grooves and with weakly depressed hind margins (terga transversely furrowed behind graduli; with strongly depressed hind margins); fore coxae unmodified (with medial processes); inner hind tibial spur of female finely pectinate (coarsely pectinate). Additionally, the two known species of *Ceratocolletes* specialise in flowers of Fabaceae (Maynard 1993; Houston 2000), not *Haemodorum*.

In Western Australia there are three unnamed species of *Leioproctus* that are monoleptic on flowers of *Conostylis*, another genus of Haemodoraceae, but one in which the flowers are largely bright yellow and open widely. These *Leioproctus* species are smaller in size and do not possess any morphological features that would suggest they are close relatives of the *Haemodorum* bees.

We are not able to name the nearest known relatives of the *Haemodorum* bees. Several of the distinctive features of the new species, like the flat clypeus, may well be associated with the bees' preference for *Haemodorum* flowers, while the expanded apical segment of the male flagellum is a feature that appears randomly in several bee genera. Other features like strong pitting with polished interspaces, impressed facial fovea of females, almost vertical propodeal triangle and a narrow, parallel-sided pterostigma are shared by several subgenera including *Charicolletes*, *Goniocolletes*, *Odontocolletes* and *Protomorpha*, but each of those groups have distinctive male terminalia and all except *Goniocolletes* have a distinct metanotal tubercle.

The current estimation is that radiation of *Haemodorum* species began c. 15 mya (Hopper et al. 2009) and that non-opening species were present 10 mya, so the relationship with bees was presumably established by then. The subgenera *Protomorpha* and

Goniocolletes are believed to have diverged less than 20 mya (Almeida et al. 2019), yet the morphological links between them or to their nearest relatives are not obvious, so it is unsurprising that the ancestors of the *Haemodorum* bees are not clear.

We have chosen to assign the two new species to the nominate subgenus *Leioproctus*. While their floral preference might eventually prove to be the basis for subgeneric grouping, it is preferable to avoid the creation of new (sub)generic names until the complex phylogeny of *Leioproctus* (Almeida and Danforth 2009) is clarified, especially when close relatives cannot be identified.

The species of *Haemodorum* are unusually distributed, occurring in both south-western and south-eastern Australia (except South Australia and Victoria) and northern Australia. Furthermore only 7 of 29 known species have anthers that are exerted at maturity, so the majority strongly restrict the variety of potential pollinators. The currently known ranges of *L. haemodori* and *L. aureofimbriatus* (Figures 13 and 22) correspond broadly to the distribution of *Haemodorum* species in south-western and south-eastern Australia (Macfarlane 1987; AVH 2023) and *L. haemodori* has been found to visit more than one species within its range. No northern Australian bees are known to be *Haemodorum* specialists. The most abundant bloodroot species in the region, *H. coccineum* R.Br., has bright red flowers with exerted anthers at maturity and they are visited by a variety of nectar-seeking insects including bees, wasps and butterflies (S. Hopper pers. comm. 2022).

Observations of *L. aureofimbriatus* at four sites indicate that flowering of *Haemodorum planifolium* is not restricted to the immediate post-fire period. Two of the sites were burnt in wildfires in December 2019 and two were subjected to hazard reduction burning in September and October 2021 followed by observations in the summer of 2022–23. Bees were present at all four sites. The bee population was relatively small, with only a few females observed at any one time. There were extended periods where none were seen, presumably because females were depositing pollen into the nests.

Small bee numbers, together with an extended flowering period, with each plant bearing clusters of flowers of different ages (Figure 1), may be important contributors to the viability of the interaction between the plant and its pollinator. Although flowering of *Haemodorum* species is reported to be stimulated by fire (Baird 1977; Lamont and Downes 2011), these observations demonstrate that the number of flowers of *Haemodorum planifolium* present in the third year after fire were sufficient to support bee populations.

No two mutualistic interactions are exactly the same (Dufay and Anstett 2003; Cook and Rasplus 2003). While details of the interaction between *Haemodorum* bees and their host flowers remain to be explored, it appears that it will have some interesting features. From what is presently known, it is possible that the flowers have evolved a set of characteristics resulting

in a high degree of pollinator fidelity through exclusion of other visitors. Other plant groups limit visitors, but not to the extent shown by *Haemodorum*. Flowers of *Persoonia* Sm. have stiff tepals that bees must force apart limiting the number of visiting species, but their colour means they still attract bees of many species (Batley 2019). Dull brown and green flowers frequently use odour to attract pollinators, so the colour probably reduces visits by insects not attracted to the scent.

The combination of a physical barrier and cryptic colour in *Haemodorum* species seems to have been very effective at selecting pollinators. It remains possible that other bees visit these flowers, but none has been seen so far. *Apis mellifera* was observed inspecting *Haemodorum planifolium* (pers. obs. MB) but appeared to be unable to enter the flowers. The only other visitors observed were bombyliid flies, *Australiphthiria hilaris* (Walker, 1852), that perched on or near the flower heads.

The extended flowering period of *Haemodorum* may also be a significant factor in the mutualism. Individual plants have pannicles that reach maturity sequentially over quite a long period. With limited competition, the bees would be able to forage continuously from moderately small plant populations.

The mutualistic interactions that have attracted most attention are those that allow exploration of ideas about coevolution (Dufaÿ and Anstett 2003; Cook and Rasplus 2003). This is not one of those cases, as *L. haemodori* has been found visiting four different *Haemodorum* species. While this could result in hybridisation, we have no evidence about the frequency of such events.

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