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Megachile (*Hackeriapis*) *lucifer* (Hymenoptera, Megachilidae), a new megachilid with demon-like horns that visits the Critically Endangered *Marianthus aquilonaris* (Pittosporaceae)

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Abstract

A new species *Megachile* (*Hackeriapis*) *lucifer* (Hymenoptera: Megachilidae) is described from both sexes. *Megachile lucifer* **sp. nov.** is of conservation importance, as it is a visitor to the range-restricted, Critically Endangered flowering plant species *Marianthus aquilonaris* (Pittosporaceae). This new *Megachile* has yet to be collected outside the region in which this rare plant occurs. A diagnostic feature of *Megachile lucifer* is the presence of a large pair of outward and upwardly facing, convex horns on each side of the clypeus, which is deeply recessed and features a medial ridge. These horns are found only in the female, unlike most sex-specific weaponry or ornamentation in animals. Clypeal modifications occur in a number of female megachilids which may be related to nest construction, whilst other clypeal horns are found in *Hackeriapis* females. The description of this new species provides the opportunity for future research into their function, and evolution among this subgenus. DNA barcoding with the CO1 gene confirmed the sexes belonged to the same species and it did not match any previously barcoded species. The species was collected only during mass-flowering of another host, *Eucalyptus livida* (Myrtaceae). The limited known distribution, and short activity season of this species, along with being associated with a Critically Endangered plant species in a region subjected to mining, suggested it may be a species of conservation concern.

Keywords
Australia, DNA barcoding, Megachilidae, new species, pollinators, threatened species

Introduction

Australia is facing a pollination crisis, with related crises relating to a lack of information on the pollinators of plants, and the taxonomic impediment (Pyke et al. 2023). For many critically endangered plants, their visitors are unknown, jeopardising our ability to conserve their populations (Prendergast 2010). The Australian native bee fauna is also threatened by a lack of monitoring, and many regions have not been surveyed, whilst many native bees remain undescribed (Taxonomy Australia 2020).

This is clearly demonstrated by the Australian Megachilidae. A recent revision of the subgenus *Austrochile* (Michener, 1965) resulted in 71 new species being described, as well as synonyms being revealed, and changes to taxonomic placement of species being made (Leijs et al. 2025). *Hackeriapis* was erected by Cockerell in 1922. There are currently 17 described species in Australia (Australian Fauna Directory 2025). An interesting feature of this subgenus is that some of the females have projections on the clypeus (King 1994).

Here, we describe a new species of *Megachile* (*Hackeriapis*) from both sexes, where the female has highly distinctive, prominent horns on the clypeus, which is deeply depressed with a medial ridge. This species was recorded to be a visitor of *Marianthus aquilonaris* N.Gibson & Wege (Pittosporaceae), which occurs only in the Bremer Ranges of Western Australia (Prendergast 2019), and is listed Critically Endangered following IUCN criteria on the Western Australian *Biodiversity Conservation Act* (Department of Biodiversity Conservation and Attractions 2025). By describing this species, we hope to promote greater research into the conservation of this new species, which may be important in turn for the conservation of this range-restricted plant that is threatened with extinction.

Materials and methods

Specimens involved in the description were collected by K.S. Prendergast with an entomological sweep net (bag mesh size 0.9 × 0.3 mm) during a survey conducted from November 2nd – 4th, 2019, to sample pollinators around populations of *Marianthus aquilonaris* (Pittosporaceae) on behalf of Botanica Consulting for Audalia Resources. Prior to these surveys, there had been no insect surveys in the region, nor had the visitors to this critically endangered plant been determined.

Standard melittological terminology is used to describe the morphology (Michener, 2007). The following standard acronyms are used (following Michener (2007) and King (1994): HL head length; HW head width; AOD antennocular distance; IAD interantennal distance; OOD ocellocular distance; OAD ocelloantennal distance; IOD inter-ocellar distance; ITS intertegular span; LID lower interocular distance; UID upper interocular distance; metasomal sterna and terga are denoted S[segment number] and T[segment number], flagellomeres are denoted F, teeth on the mandible are denoted Te, with Te1 being the most basal. Measurements are given in millimetres.

Specimens were observed with a Leica M205 C stereomicroscope. Measurements and images of key features were made on high-resolution images taken with the same stereomicroscope and using the Passport II imaging system, by Visionary Digital and a camera mounted on the microscope (Canon 7D Mark II), with a 100 mm macro lens, and the Helicon image stacking software. Measurement and scales bars were calibrated (by Visionary Digital) by lens and focal length, and these calibrations uploaded to Photoshop. Description and measurements were made on the female holotype and male paratype.

A subsample of the hind femur from a female paratype, and male allotype, were submitted to BOLD (Barcode of Life Database) for DNA barcoding using the cytochrome c oxidase subunit 1 (CO1) gene. The DNA barcode sequence, and other specimen information associated, can be accessed in BOLD via: as part of the Australasian and Pacific bee fauna Project (MSAPB): http://www.boldsystems.org/index.php/MAS_Management_DataConsole?codes=MSAPB.

See also Suppl. material 2. The sequences were obtained from Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph, Guelph, Ontario, Canada. Standard DNA sequencing protocols were carried out by CCDB (available online at: http://www.ccdb.ca/resources.php), using the PCR primers LepF1/LepR1. The barcoded vouchers are deposited at the Museum of Western Australia. BOLD delineates molecular operational taxonomic units (MOTUs), which are in concordance with species delineations based on traditional methods (Schmidt et al. 2015), to which a Barcode Index Number (BIN) (Ratnasingham and Hebert 2013) is automatically assigned and incorporated into BOLD.

Taxonomy

Family Megachilidae
Subfamily Megachilinae
Genus *Megachile* Latreille, 1802

Subgenus *Hackeriapis* Cockerell, 1922

Remarks. Using Michener (2007)'s Key to the Australian and Papuan Subgenera of *Megachile*, this species is tentatively placed in the subgenus *Hackeriapis* Cockerell, 1922, on the basis that collected females have the following characteristics in common with Michener's description: mandible with four teeth, cutting edges absent, metasoma parallel sided, S1 without apical spine, claws without ventral tooth, metasomal integument black, glossa linear, fulvous pubescence confined to apical part of metasoma, and for the male specimen collected, the terga has deep postgradular grooves; pubescence with a grey appearance, fulvous on metasoma, forming metasomal bands; and posterior margin of T6 with four teeth.

Megachile lucifer **sp. nov.**
https://zoobank.org/B8D8CCFA-CF8B-4B70-B79E-28C85F4156FE

Material examined. Type material: *Holotype*. Australia • 1 ♀, holotype; Western Australia, Lake Johnston; 32.52652E 120.79661S; 4 Nov. 2019; K. S. Prendergast leg.; sweep net *Marianthus aquilonaris*; KSP code233. WAM E112233.

Other material. *Allotype*. Australia • 1 ♂; Western Australia, Lake Johnston; 32.53081E, 120.7925S; 4 Nov. 2019; K. S. Prendergast leg.; yellow pan-trap; KSP code0261. WAM E112061. ***Paratypes***. • 1 ♀ Western Australia, Lake Johnston, 32.5318E, 120.78531S, 2 Nov. 2019, sweep netting (*Eucalyptus livida*); • 1 ♀ 3 Nov. 2019, blue bee bowl; • 2 ♀ 4 Nov. 2019, blue bee bowl; • 7 ♀ 4 Nov. 2019, yellow bee bowl; • 2 ♀ Western Australia, Lake Johnston, 32.53081E, 120.7925S, 3.Nov.2019, sweep netting (*Eucalyptus livida*); • 1 ♀ 4 Nov. 2019, blue bee bowl; • 2 ♀ 4 Nov. 2019, yellow bee bowl; • 1 ♀ 4 Nov. 2019, Western Australia, Lake Johnston, 32.52691E, 120.79694S, sweep netting (*Eucalyptus livida*); K.S. Prendergast leg.

Specimens used by DNA barcoding. BOLD DNA barcode: BOLD:AEJ4534. (WAM E112150); BOLD DNA barcode: BOLD:AEJ4534. (WAM E112061) dx.doi.org/10.5883/DS-MEGMAQ.

All specimens are deposited in the Western Australian Museum. Accession numbers are provided in Suppl. material 1.

Diagnosis. The female of *Megachile lucifer* is distinguished from all other species of *Hackeriapis* by the presence of a pair of upward and outward projecting triangular horns on the sides of the clypeus, with a deeply impressed clypeus featuring a slightly raised medial ridge. The clypeal horns, each measuring 0.9 mm in length, are almost half as long as the head width in profile (Fig. 1a–c). The male is distinguished from other *Hackeriapis* by the carina of T6 being bilobed, each lobe emarginate.

The presence of clypeal processes suggests that *Megachile lucifer* should be part of King's "Species-group 2" of *Hackeriapis* (*M. patera* King, 1994, *M. bicornis* King, 1994, *M. franki* Friese, 1920, *M. semicandens* Cockerell, 1910, *M. monkmani* Rayment, 1935), however, unlike King's "Species-group 2", the mandible is not deeply emarginate between Te3, Te4, nor is the polished medial plate flat, which according to King's key would place *M. lucifer* with "Species-group 1" (King 1994). The clypeal horns of *M. lucifer* are most similar to *M. bicornis* and *M. patera*, however the horns project more upward, there is a medial ridge in the clypeus, and the metasoma is not completely orange. The male of *M. lucifer* differs from *M. bicornis* in its metasomal colouration, and each lobe of the carina on T6 is emarginate (the male of *M. patera* is unknown).

Description. Female (Fig. 1):

Dimensions**:** Total body length 9.80 mm, HW 3.56 mm, ITS 2.68 mm.

Colouration**:** Non-metallic black; integument of head black; clypeal horns black; mesosoma black; metasoma black; red-brown border on tergites; legs black, final tarsi brown; wings dusky, semi-opaque with wing veins very dark brown; microtrichia especially dark under radial vein of the marginal cell on the forewing; scape, pedicel, F1 dark brown, remainder brown, mandibles black with red Te1 and Te2.

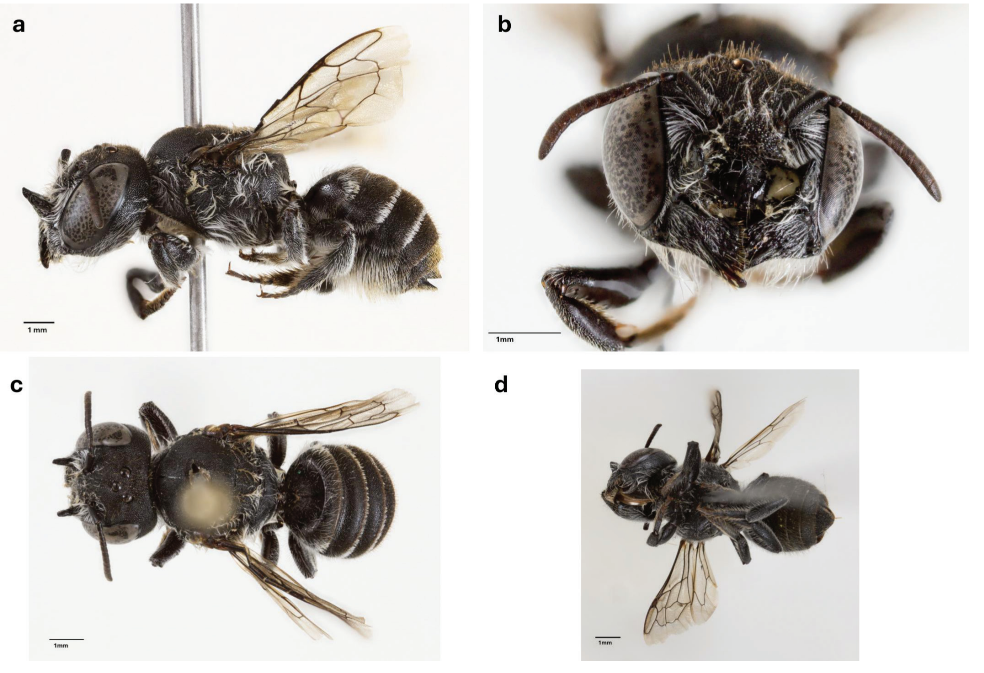

Figure 1. *Megachile lucifer* sp. nov. female, **a** lateral view **b** head, frontal view **c** dorsal view **d** ventral view.

***Pubescence*:** Long white pubescence on face around antennal sockets covering paraocular area and gena, along underside of mandibles, sides of thorax, and metanotum; dense white hairs on base of mandibles; very sparse fine gold hairs short on scutum, short thick gold hairs along cutting edge of mandibles; short white hairs along legs; posterior hairbands on terga present on T1-4, colour of hair bands white; T1 with thick, dense lateral patch; hairbands on T1 and T4 very short and sparse, hairbands on T2-3 complete and about one-fifth of tergite width; T5–T6 pubescence on orange-gold; sparse long white hairs on T1; metasomal scopae cream.

***Sculpture*:** Head, mesoscutum, and scutellum with large, deep, close punctures; antennal scape with fine, shallow punctures; propodeal triangle with small, shallow punctures (Fig. 1c); terga with minute, shallow, close punctures.

***Structure head*:** face wider than long (1.6×); distinct pair of horns on clypeus, triangular in shape, projecting out and slightly up, with pointed tips rounded at the apex, convex on ocular side, inner face deeply concave medially, clypeus has medial vertical ridge with a small protuberance at the base of the clypeus, strongly depressed, hollowed out and concave on each side of the central ridge and horns (Fig. 1b); supraclypeal area slightly elevated and concave; malar space present; mandibles relatively large, with blunt edges, four teeth (three above the notch in along the preapical margin), distance from Te4 to Te3, is greater than from Te3 to Te2, and length of teeth decreases from Te1 to Te4, preapical margin almost vertical (Fig. 1b); gena ca. 0.4× as wide as compound eye viewed laterally; scape not attaining median ocellus; scape 0.75 mm long, with apex approx. 1.5× broader than base, last five flagellomeres longer than wide, F3-5 equal, pedicel and F1-2 longer than wide; final flagellomere wedge-shaped such that it tapers apically, total length of flagellum (pedicel and flagellomeres) 2.09 mm.

***Head measurements*:** HL 2.1 mm; gena width 0.86 mm; clypeus length 0.59 mm; UID 2.5 mm; LID 2.53 mm; IAD 0.92 mm; OOD 0.63 mm; IOD 0.65 mm; AOD 0.67 mm; OAD distance 0.53 mm; malar space 0.08 mm; mandible base length 0.67 mm; mandible length 1.5 mm; UID: LID 0.99; clypeus: HL 0.28.

***Mesosoma*:** Propodeal triangle slightly convex, carina weak, almost vertical.

***Mesosoma measurements*:** overall mesosoma length 3.54 mm; pronotal collar absent; mesoscutum length 2.28 mm; scutellum length 0.73 mm; mesoscutum length:ITS 1.32; scutellum:mesoscutum 0.32.

***Legs*:** tarsal claws simple, no basal claw; hind tibial spurs with small, dense serrations.

***Metasoma*:** overall metasoma length 3.54 mm; metasoma longer than mesosoma (metasoma:mesosoma 1.33); T1 width 3.1 mm, anterior face concave, with surface highly declivous; metasoma broadest at T3; T1-4 slightly convex.

Male (Fig. 2):

***Dimensions*:** Body length 8.9 mm, HW 2.87 mm, ITS 2.6 mm.

***Colouration*:** similar to female, except T5-T7 orange, slight brown apical border laterally on T5.

***Pubescence*:** Pubescence on face much thicker than female, hairs cover entire head including clypeus; beard of hairs on genae longer (Fig. 2b). Preapical hair bands incomplete.

***Sculpture*:** similar to female, except polished impunctate apical bands on T1-5.

***Structure – head*:** horns absent, clypeus slightly concave, covered in dense long white hairs, mandibles tridentate. Scape 0.55 mm long, similar in structure to female with final flagellomere wedge-shaped such that it tapers apically, total length of flagellum (pedicel and flagellomeres) 2.01 mm.

***Head measurements*:** HL 1.77 mm; gena width 0.7 mm; clypeus length 0.50 mm; UID 1.58 mm; LID 1.74 mm; IAD 0.78 mm; OOD 0.68 mm; IOD 0.56 mm; AOD 0.47 mm; OAD distance 0.53 mm; malar space 0.13 mm; mandible base length 0.51 mm; mandible length 0.86 mm; UID:LID 0.91; clypeus:HL 0.28.

***Mesosoma*:** overall mesosoma length 3.50 mm; pronotal collar absent; mesoscutum length 2.04 mm; scutellum length 0.79 mm; mesoscutum length:ITS 1.34; scutellum:mesoscutum 0.39.

***Structure – legs*:** tarsal claws with basal tooth (Fig. 2a). Hind-tibial spurs similar to female. Forelegs not modified.

***Structure metasoma*:** metasoma longer than mesosoma, less so than female (metasoma:mesosoma 1.29); broadest at second segment, overall metasoma length 3.54 mm; metasoma longer than mesosoma (metasoma:mesosoma 1.33); T1 width 3.02 mm; T1-4 slightly convex; carina of T6 bilobed, each lobe emarginate (Fig. 2b, d).

Etymology. The name “lucifer” alludes to the projections on the female clypeus, reminiscent of devil-like horns. It is proposed as a noun in apposition.

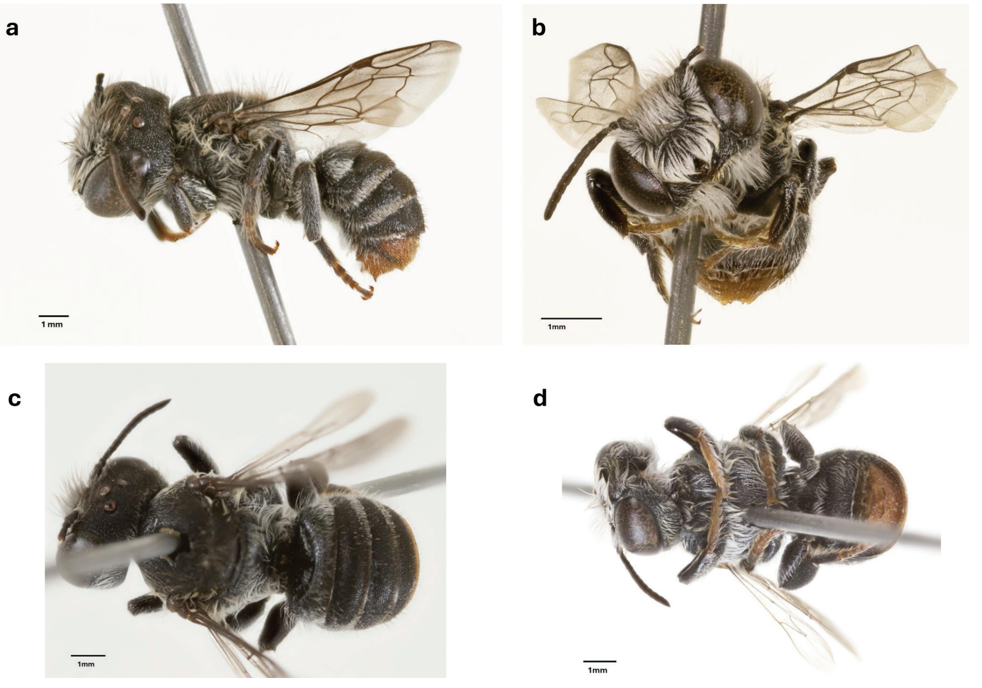

Figure 2. *Megachile lucifer* sp. nov. male, **a** lateral view **b** head, frontal view **c** dorsal view **d** ventral view.

Distribution. Bremer Ranges region around Lake Johnston, Coolgardie bioregion of inland southeast Western Australia (Fig. 3).

Type-locality. Australia, Western Australia: Bremer Ranges, Lake Johnston; 32.52652E, 120.79661S; habitat type is open woodland with sparse understory on skeletal sandy-loam over laterite, collected with an entomological sweep net, foraging on *Marianthus aquilonaris*, 4 Nov. 2019, K. Prendergast.

Ecology. Months collected: Nov 2- 4 2019. Surveys in the region conducted earlier in October in 2022 and 2024 failed to collect this species.

Floral visitation: 1 ♀ *Marianthus aquilonaris* (Fig. 4a), 3 ♀ *Eucalyptus livida* Brooker & Hopper (Fig. 4b).

Conservation status. To date, the species has only been collected in the Bremer Ranges. Viewing the WA Museum entomology collection additional specimens were not found, nor have other specimens been collected by K.S. Prendergast in surveys across Canarvon, Eighty Mile Beach, Purnululu, Geradlton, across the Swan Coastal Plain or the Jarrah Forest region. No other specimens were found in the OZBOL BOLD database. The Bremer Ranges region is at risk from a number of threatening processes, including gold mining, inappropriate fire regimes, and climate change (Prendergast 2019; Pick 2020; Prendergast 2021). One of the host plants, *Marianthus aquilonaris*, is Critically Endangered under the Western Australian Biodiversity Conservation Act, as its extent of occurrence is less than 100 km2, its area of occupancy

Figure 3. Map of Australia showing sites where specimens of *Megachile lucifer* sp. nov. has been collected (see also Supplementary Information. Map produced via MyMaps Google.

being less than 10 km, and suffers from fragmentation (Hopley and Byrne 2019; Prendergast 2019; Pick 2020; Prendergast 2021). The region where the species has been collected is not currently under any conservation protection.

Under the IUCN Red List criteria, criteria A, C and E cannot be assessed as there is no ongoing monitoring; however, based on criteria B: Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both, it may be considered to be Critically Endangered (IUCN 2012). However, further surveys in areas with *Eucalyptus livida*, another host plant, are required to determine if it occurs in other locations within the Coolgardie region where *E. livida* occurs.

DNA barcoding (See also Suppl. material 2). The specimens barcoded were both assigned the BIN BOLD:AEJ4534.

The associated Genbank accession numbers are:

BankIt2979786 gnl|uoguelph|OZBOL2716-21.COI-5P PV919132 BankIt2979786 gnl|uoguelph|OZBOL2721-21.COI-5P PV919133.

No other specimens in BOLD matched the BIN BOLD:AEJ4534 assigned to these specimens. The association of the sexes was confirmed, with only 0.3% distance between the two specimens in this BIN. The distance to the nearest neighbour of *M. lucifer* is 7.1%, and thus exceeds the cut off of a minimum of 2% distance to be considered a distinct species. The nearest neighbour in BOLD has the BIN BOLD:AEC5722, and is not assigned to a species of *Megachile*. This species is in turn the nearest neighbour (6.1%) to an undescribed *Megachile*, BIN BOLD:AGD4390.

Figure 4. Images of the two host plant species of *Megachile lucifer* sp. nov., **a** *Marianthus aquilonaris* and **b** *Eucalyptus livida*.

Discussion

Megachile lucifer is distinctive in the clypeal horns in the female. As the clypeal modifications occur only in the female, rather than the male, it cannot be related to male-male competition (e.g. (Alcock and Houston 1996; Fraberger and Ayasse 2007)). Horn-like clypeal modifications also occur in a number *Centris* Fabricius, 1804, (Velez and Vivallo 2012), *Osmia* Pranzer, 1806 (MacIvor et al. 2022), and *Megachile* Latreille, 1802 (Snelling 1990; King 1994), solely in the female. These cases of independent evolution would suggest they have some adaptive function. It may be that these assist with accessing floral resources (as hypothesised for (Prendergast 2022b)); defending off competitors for floral resources (Tobias et al. 2012); or defending off competing females over nest sites as has been observed in other *Megachile* species (e.g. *Megachile erythropyga* Smith, 1853, Prendergast, pers. obs., 2019; *Megachile* (*Schizomegachile*) *monstrosa* Smith, 1868 (bee.babette_performer 2025)). In another megachilid, *Osmia cornuta* (Latreille, 1805), females use the horn to fight natural enemies (bees and kleptoparasitic flies), mainly while they are in their nests (Monzón, personal communication, in (Velez and Vivallo 2012)). In *O. cornifrons* Radoszkowski, 1887, the facial horns are used to polish partitions between cells made of mud (Lee et al. 2016). It has also been suggested that modifications of the clypeus of female *Hackeriapis* may be related to resin, pebble, or sand collection for cell closures (Gonzalez 2008). Further research observing females on flowers or at nests may help elucidate these proposed functions of the clypeal horns.

A full revision of *Megachile* (*Hackeriapis*) involving molecular phylogenetic work will also help determine whether the clypeal horns evolved once in a common ancestor of species that possess it, with subsequent modifications to lead to the unique horn structures in the different species that possess them or whether the horns convergently (independently) evolved in different lineages.

It should be noted that many Australian subgenera of *Megachile* require revisions. The last taxonomic treatment of *Hackeriapis* was by King (1994), over three decades ago.

As there are many other putative *Hackeriapis* to be described (Prendergast, pers. obs.), it is premature to revise King's dichotomous key.

The known host range of *M. lucifer* is currently limited to two species. Further records may reveal further hosts. There is variation among *Hackeriapis* in their degree of dietary specialization and host preferences. There has only been one other record of a *Hackeriapis* on Pittosporaceae (*Bursaria spinosa* Cavanilles, 1797) (King 1994). It is unclear whether the specimen collected from *Marianthus aquilonaris* was foraging for pollen or nectar. For example, *M. oblonga* (Smith, 1879) appears to be polylectic, whereas *M. canifrons* (Smith, 1853) and *M. tosticauda* (Cockerell, 1912) are oligolectic on Fabaceae and Myrtaceae, respectively (Fernandes et al. 2022; Williamson et al. 2025). It may be that like *M. tosticauda*, *M. lucifer* is oligolectic on Myrtaceae. Indeed, many other *Hackeriapis* species have been collected from Myrtaceae in Australia (King 1994). During the surveys in which *M. lucifer* was collected, *E. livida* was flowering profusely, attracting thousands of insects. During subsequent surveys in 2021 and 2024 conducted in October however, *Eucalyptus livida* was not in flower, and *M. lucifer* was not observed. Disruptions to the flowering of *E. livida* for example due to climate change may post a threat by causing mismatches between flowering phenology and emergence *M. lucifer* (Settele et al. 2016; Prendergast 2022a).

Nests have not been located, but presumably like other *Megachile* (*Hackeriapis*) species it nests in pre-made cavities in wood and uses resin to seal the nests (Williamson et al. 2025). It therefore will be vulnerable to loss of nest sites due to destruction of trees for mining activities, or fire (Prendergast and Wilson 2025).

Although there is no formal conservation status of *M. lucifer*, some recommendations can be made based on information regarding its currently known distribution, phenology, habitat, and resource associations. Surveys should be undertaken to survey for nesting locations, but in the absence of this information, trees with small (approx. 4 mm diameter holes, based on preferences of similarly-sized *Megachile* (Prendergast 2023)) should be protected as these offer suitable nesting substrates.

Being associated with the Critically Endangered *Marianthus aquilonaris*, the area in and around where these species occur should be formally protected and gazetted as conservation land that cannot be cleared. Further surveys in the surrounding region during November should be undertaken, and if *M. lucifer* occurs, these areas likewise should not be cleared (e.g. for haul roads to access mining).

Further research should also explore the role of this new *Megachile* species in the pollination of *Marianthus aquilonaris* (e.g. (Figueroa et al. 2017)). Ongoing monitoring is also required to detect any population trends in this new species.

Conclusion

Australian native bees are suffering from a crisis in lack of conservation, attention, and taxonomy, whilst Australian flowers are suffering from a pollination crisis whereby their pollinators are unknown, undescribed, and not included in recovery plans. Without a scientific name, conserving indigenous pollinators and their pollination services for endangered flora is a challenge. Describing and naming this new megachilid, *Megachile lucifer*, will enable it to receive conservation attention, as well as help to preserve the critically endangered *Marianthus aquilonaris.*

By highlighting the unusual clypeus of the female, we hope to inspire further research on the possible function of this structure, and related clypeal modifications in female *Hackeriapis.* DNA barcoding of this species and its description will aid in further investigations into the systematics of Australian megachilid native bees.

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Supplementary material 1

Collection details of specimens of *Megachile lucifer* sp. nov.

Authors: Kit S. Prendergast, Joshua W. Campbell

Data type: xlsx

Explanation note: Holotype is highlighted in yellow; allotype in orange; specimens used for DNA barcoding are in bold.

Link: https://doi.org/10.3897/jhr.98.166350.suppl1

Supplementary material 2

***Megachile lucifer* sp. nov. CO1-5P sequences from DNA barcoding (BOLD:AEJ4534), and Genbank Flatfile**

Authors: Kit S. Prendergast, Joshua W. Campbell

Data type: pdf

Link: https://doi.org/10.3897/jhr.98.166350.suppl2