

Halictus (Protohalictus) flaminii, the first *Halictus* described from Indonesia (Hymenoptera: Halictidae)

THOMAS BRAU^{1,2} & DENIS MICHEZ^{1,3}

¹Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Place du parc 20, 7000, Mons, Belgium

² thomas.brau@student.umons.ac.be;  <https://orcid.org/0009-0000-1182-5022>

³ denis.michez@umons.ac.be;  <https://orcid.org/0000-0001-8880-1838>

Abstract

The genus *Halictus* is a widespread and abundant bee group, especially in the Holarctic Region. A new species of *Halictus* from the subgenus *Protohalictus*, *Halictus flaminii* **sp. nov.**, has been discovered out of the genus' currently known range, from Lombok, Indonesia. This study provides a detailed description of the species and highlights its diagnostic features in comparison to closely related members of the subgenus in Asia.

Key words: Anthophila, Apoidea, biodiversity, disjunct range, pollinators, taxonomy

Introduction

The taxonomy of the bee genus *Halictus* Latreille (Halictidae) is controversial, with three hypotheses considered in recent decades: (i) one genus *Halictus* sensu lato with three subgenera (i.e. *Halictus* sensu stricto., *Seladonia* Robertson and *Vestitohalictus* Blüthgen; Ebmer 1988) or multiple subgenera (Michener 2007, Gibbs *et al.* 2012), (ii) three genera, considering *Seladonia* and *Vestitohalictus* as distinct genera (Pesenko, 2004; Pauly & Belval 2017; Rasmont *et al.* 2017); (iii) two genera, considering *Seladonia* as a distinct genus including *Vestitohalictus* (Ghisbain *et al.* 2023). Phylogenetic studies on this group have been conducted to elucidate the relationships between these three taxa (Danforth *et al.* 1999, Gibbs *et al.* 2012). According to the main results, *Seladonia* and *Vestitohalictus* seem to form a monophyletic group, the *Vestitohalictus* species being nested in the clade of the other *Seladonia*, while *Halictus* forms another monophyletic group (but see parsimony analyses supporting only the monophyly of the *Halictus* s.l., Danforth *et al.* 1999). In the present study, *Halictus* and *Seladonia* are considered as distinct genera and *Vestitohalictus* as a subgenus of *Seladonia* (for more details see Ghisbain *et al.* 2023). We also consider *Halictus* divided into 12 subgenera (i.e. *Acalcaripes* Pesenko, *Argalictus* Pesenko, *Halictus*, *Hexataenites* Pesenko, *Lampralictus* Pesenko, *Monilapis* Cockerell, *Nealictus* Pesenko, *Odontalictus* Robertson, *Platyhalictus* Pesenko, *Protohalictus* Pesenko, *Ramalictus* Pesenko and *Tytthalictus* Pesenko), following Pesenko (2004). These subgenera remain a point of contention but at least some of them show well-defined apomorphic characters such as *Hexataenites*, *Monilapis*, *Nealictus*, and *Tytthalictus* (Danforth *et al.* 1999; Ebmer, 2014; Pesenko, 2004). These 12 subgenera encompass fewer than 100 described species (Pesenko, 2004). This genus is almost cosmopolitan, being distributed through Europe, Asia, Africa, North and South America, but absent from Oceania (Pesenko, 2004). Most species occur in temperate areas of Europe, Asia and Africa. Southern Africa, North America and South America are poorer in diversity (Pesenko, 2004). In Southeast Asia, the diversity of the *Halictus* genus remains largely understudied, with minimal research dedicated to this taxon. Furthermore, the scarcity of specimens recorded in this region may indicate a relatively low diversity in the area.

Southeast Asia, recognized as a biodiversity hotspot, encompasses three megadiverse countries: Indonesia, Malaysia, and the Philippines (von Rintelen *et al.* 2017). These three countries predominantly experience tropical climates, with tropical rainforest being the most prevalent ecosystem, alongside less common climates such as tropical monsoon, tropical savanna, and occasionally subtropical with dry winters. The natural landscapes are primarily tropical forests, complemented by extensive artificial habitats shaped by human activities like agriculture

and plantations. The terrain is highly varied, ranging from lowland plateaus to towering mountains. Altitudes span from sea level up to remarkable peaks, including 4,884 metres in Indonesia, 2,954 metres in the Philippines, and 4,100 metres in Malaysia. Despite its rich biodiversity and habitats, the Indomalayan region has comparatively low bee diversity (Hymenoptera: Anthophila). With only 89 bee genera recorded compared to over 120 genera found in the Palearctic region and more than 310 genera in the Neotropical regions. This is primarily due to the greatest bee diversity being located in arid temperate zones (Corlett, 2004; Widhiono *et al.* 2017; Orr *et al.* 2021). *Halictus* follow the same pattern and are known by only a few records in the Indomalayan region (Pesenko 2005).

Around this region, the most common subgenus of *Halictus* is the subgenus *Protohalictus* (Pesenko, 2005). Adjacent to the Indomalayan region, *Protohalictus* are distributed across India, Central Asia, and East Asia. It is characterised by the granulate or rugulose texture of the sides of the propodeum. Female specimens are characterized by a head that is wider than long and has toothless genae. Male specimens exhibit a distinct feature on sterna IV, which is strongly emarginated. Indian species include *Halictus fimbriatus* Smith, 1853, while *Halictus rubicundus* (Christ, 1791) and *Halictus hedini* Blüthgen, 1934 are found in Central and East Asia (Blüthgen, 1926; Murao & Gibbs, 2019; Pesenko, 2006). Morphological distinctions between *H. rubicundus* and *H. hedini* primarily involve the punctuation on the T1 segment in females. *Halictus hedini* features deeper, more defined punctures compared to the shallower, less distinct punctures of *H. rubicundus* (Murao & Gibbs, 2019; Yeonghyeok *et al.* 2024). We describe here a new species of the subgenus *Protohalictus* recorded 4300 km from the nearest *Halictus* record with confirmed identification, extending significantly the spatial distribution of this genus.

Materials and methods

Acronyms used for museums and private collections

NHMUK—Natural History Museum, London, United Kingdom;

OÖLM—Biodiversitätszentrum Oberösterreich, Linz, Austria;

TBPC—Personal collection of Thomas Brau, Mons, Belgium;

UMONS—Laboratory of Zoology collection, University of Mons, Mons, Belgium

Picture material

The specimen photos were captured using a Keyence VHX-970F digital microscope equipped with a VHX-7020 camera and a VH-Z20R/Z20T zoom lens, ensuring high-resolution stacking for detailed imaging. The photos were refined using GIMP (version 2.10.32) to enhance visibility by adjusting minor imperfections such as brightness and contrast, ensuring that features like punctuation are clearly discernible. The colorimetry has not been modified.

Materials examined

Specimens of the following species were selected to be examined as they are close relatives of the new described species (i.e. from the subgenus *Protohalictus*). Species with * were studied based on pictures. The other species were studied based on pinned specimens.

Halictus (Protohalictus) atripes Morawitz, 1893

Turkey: 1 ♀ Sivas, Zara lake, 39.8836N, 37.2883E, 1436 m, 05.VII.960, OÖLM.

Halictus (Protohalictus) bagirensis Blüthgen, 1936

Iran: 46 ♀ Golestan, 70 km E Minudasht, 37.4333N, 56.65E, 1050 m, 12.VI.2010, leg. M. Halada, OÖLM.

Halictus (Protohalictus) fimbriatus Smith, 1853*

Lectotype: **India:** 1 ♀ Simla, V.1997, NHMUK014030024, NHMUK.

Halictus (Protohalictus) funerarius Morawitz, 1876

Uzbekistan: 1 ♀ Západni Tausan Catkalskij chrebet Su-Kok, 28.V.1976, leg. Dr. P. Stary, OÖLM; 1 ♀ Aktas, 1100–1500 m, 24.V.1974, Leg. K. Denes, OÖLM; 1 ♀ Osh Region, Jangy-Aryk, 700 m, 22.V.1974, leg. K. Warncke, OÖLM.

Halictus (Protohalictus) hedini hebeiensis Pesenko & Wu, 1997

China: 2 ♀ Shaanxi, 35 km NE Yan'an, 36.8N, 110.3E, 17–18.V.1996, leg. J. Halada, OÖLM; 1 ♀ Shaanxi, 50 km W Linfen, 36.02N, 111.07E, 29–30.V.1996, leg. J. Halada, OÖLM.

Halictus (Protohalictus) hedini hedini Blüthgen, 1934

South Korea: 1 ♀ North Gyeongsang Province, Buk-myeon, 37.98N, 127.45E, 31.V.2023, leg. M. Kafka, TBPC.

Halictus (Protohalictus) rubicundus (Christ, 1791)

Belgium: 1 ♀ Namur, Nismes, 50.078N, 3.5569E, 182 m, 11.VIII.2023, leg. T. Brau, TBPC; 3 ♀ Liège, Bassenge, 47.5508N, 5.6728E, 94 m, 11.VII.2016, leg. J. Schoy, UMONS.

France: 9 ♀ Pyrénées-orientales, Eyne, 42.4642N, 2.0902E, 1700 m, 29.VIII.2012, leg. P. Rasmont, UMONS.

Austria: 1 ♀ Irrenedt, 48.3667N, 13.8167E, 392 m, 22.IV.1986, leg. F. Gusenleitner, OÖLM.

Taxonomic nomenclature

Subgeneric concepts follow Pesenko (2004). Morphological terminology follows Harris (1979), and Michener (2007). The abbreviations used for the female description: A1–12: antennal articles 1–12 including the scape as A1; S1–7: sterna 1–6; T1–7: terga 1–6. The measurements of antennal article length have been normalized to reduce size variation errors caused by intraspecific differences. The width of antennal article A3 (W_{A3}), measured at its midpoint, has been selected as the reference length. The relative length of each antennal article (Lr_A) is calculated using the formula: $Lr_A = L_A / W_{A3}$ where L_A is the actual length of the article. The quantity Lr_A expresses how many times longer the article is compared to W_{A3} . In the species description, “A3 apical width” is also rescaled by W_{A3} such that it is equal to 1. The “relative length of articles” refers to the calculated Lr_A values.

Describing colors can be challenging, as perception may vary from person to person. To ensure accuracy and minimize ambiguity, each color used in the species description is identified by a hexadecimal code (HEX). The color names and their corresponding HEX codes used in this study are as follows: Graphite gray = #4f555b, Black = #171517, Testaceous = #c79961, Ferruginous = #9c4c29, Chamois = #a0785a, Floral white = #ffff0, Dark brown = #48352e, and Orange = #be6e3a. When an anatomical region shows color variation, this is explicitly stated. When a region is described with a single color, it corresponds to the average coloration observed for that area. All color values were determined directly in GIMP using photographs of the specimen.

Results

Morphology and diagnosis

The specimen is assigned to the subgenus *Protohalictus* as it shows that (i) the sides and posterior surface of the mesosoma are densely rugulose, (ii) the head is slightly broader than long (eyes to eyes/apical clypeus part to vertex) and toothless gena and (iii) the hind tibia displays a reddish-yellow coloration. The specimen exhibits morphological similarities to *Halictus rubicundus* and *Halictus hedini hebeiensis*, such as a black body cuticle, brown mesosomal hair, terga with fine white apical hair bands, and orange coloration on the tibiae and posterior tarsi. However, it differs in significant traits, particularly the punctuation of T1, which is deeper and sparser. *Halictus hedini* has dense, deep punctuation on T1 with punctures separated by 0.1–1 puncture diameters and a smooth, shiny underlying surface. *Halictus rubicundus* features shallower punctuation with a similar density but a more structured, less shiny underlying surface. In contrast, the Indonesian specimen has anterior T1 punctures separated by 1–2 puncture diameters, while the rest of T1 shows sparser punctuation, with punctures separated by 1–4 diameters. The underlying surface is slightly imbricate, nearly smooth, and shiny. The T1 punctuation and underlying surface characteristics are key species identifiers within *Protohalictus*, as these traits show minimal intraspecific variation. This extremely sparse punctuation on the Indonesian specimen differs not only from *H. rubicundus* and *H. hedini* but also from species like *H. atripes*, *H. bagirensis*, *H. fimbriatus*, and *H. funerarius*. Additional distinctions include sparse lateral punctuation on the scutellum, in contrast to the uniformly dense scutellar punctuation of *H. rubicundus*.

and *H. hedini*. The scutellum structure more closely resembles *H. bagirensis*, a species native from Middle East to Uzbekistan. Posterior tibiae and tarsi are orange, which differ from the black coloration seen in *H. hedini hedini* and *H. fimbriatus*. The combination of unique morphology and geographic distribution support the conclusion that this Indonesian specimen represents a distinct species within the subgenus *Protohalictus*.

Species description

Halictus (Protohalictus) flaminii sp. nov.

Etymology: The species is dedicated to my colleague and friend Simone Flaminio, an active Italian wild bee specialist and Halictini taxonomist, who found this specimen in the collection of the Biodiversitätszentrum Oberösterreich in Linz.

Type material. Holotype. Indonesia: ♀, Lombok, Kuta, 8.881S, 116.281E, 30 m, 27–31.XII.2019, leg. J. Starkova, OÖLM.

Female. Body length (vertex to T6): 10 mm (Fig. 1a), andreniform.

Head (Fig. 1b, d): Graphite gray to black, 1.2 times wider than long, testaceous minutely barbed hairs (Fig. 1b). Mandible black to hyaline-ferrugineous at the apex, bidentate, rounded. Labrum black to hyaline-ferrugineous at terminal edge, semi elliptical, testaceous simple hairs at edge of labrum, twice as long as wide, protuberance of the labrum forming a simple carina. Labral process black, semi-elliptical, central protuberance triangle shaped, edge of labral process carinate. Clypeus graphite gray to black, 1.5 times wider than long, dense punctation, punctures separated by 0.1–3 puncture diameters, underlying surface smooth and glossy (Fig. 1b). Supraclypeal region graphite gray to black, slightly domed, dense punctation, punctation separated by 0.1–1.5 punctation diameters, underlying surface slightly imbricate and glossy (Fig. 1a, b). Malar area black, short, equal to 3 times the eye rim width. Gena graphite gray to black, large, equal to the width of the eye, shallow punctation, punctation separated by 0.5 punctation diameter, underlying surface strongly rugose and matte (Fig. 1a, b). Vertex short, equal to 2.3 times the diameter of a lateral ocelli, dense punctation, punctation separated by 0.1 punctation diameter, underlying surface strongly rugose and matte (Fig. 1b). Antenna black, flagellum filiform, A3 apical width = 1; relative length of articles: A3 = 1.0; A4 = 0.66; A5 = 0.8; A6 = 1.06 (Fig. 1d).

Mesosoma (Fig. 1c,e,f,g; 2g): Pronotum graphite gray to black, strigulate. Scutum graphite gray to black, sparse testaceous plumose hairs, dense punctation, punctures separated by 0.5–1 puncture diameters, underlying surface slightly imbricate and glossy except for the sides of the propodeum which are reticulate-rugulose up to the parapsidal line (Fig. 1c). Scutellum graphite gray to black, sparse testaceous plumose hairs, sparse punctation, punctures separated by 1–3 puncture diameters except border and middle of the scutellum which have dense punctation, punctures separated by <1 puncture diameter, underlying surface smooth and glossy (Fig. 2g). Metanotum graphite gray to black, sparse testaceous plumose hairs, rugose with few shallow punctures (Fig. 1f). Mesepisternum graphite gray to black, strongly rugose with dense shallow punctation, punctures separated by <1 puncture diameter (Fig. 1e). Metepisternum graphite gray to black, strigulate (Fig. 1e). Propodeal enclosure black, almost triangular, rugulose (Fig. 1f). Propodeum side graphite gray to black, sparse testaceous plumose hairs, rugulose with dense shallow punctation to granulate at dorsal part of propodeum without punctation, punctures separated by 0.1 puncture diameter (Fig. 1f). Tegula black to hyaline-testaceous at external edge, sparse punctation, punctures separated by 1–4 puncture diameters, underlying surface slightly coriaceous (Fig. 1c). Wings slightly smoked, venation black to dark brown (Fig. 1a). Anterior leg graphite gray to black except tarsus orange, testaceous simple hairs. Mid leg graphite gray to black except tarsus and basitarsus orange, testaceous simple hairs. Hind leg black to light orange; coxa and femur graphite gray to black, tibia to tarsus light orange with one black elliptical spot on anterior surface of basitarsus (Fig. 1g). Hind leg scopa with testaceous long branched plumose hair (Fig. 1g). Pilosity of femur simple and testaceous (Fig. 1g). Pilosity of tibia and tarsus yellow-golden (Fig. 1g). Inner hind spur orange, finely toothed.

Metasoma (Fig. 1g, h; 2a): Metasoma graphite gray to black, elliptical (Fig. 1h). Posterior part of T1–4 terminated by interrupted floral white hair band. T1 graphite gray to black, sparse punctation, punctures separated by 1–4 puncture diameters, disc of the terga less punctuated, underlying surface slightly imbricate almost smooth and shiny, coriaceous on the marginal zone (Fig. 2a). T2 graphite gray to black, dense punctation, punctures separated



FIGURE 1. Holotype female *Halictus flaminii* sp. nov. holotype. **a)** Lateral habitus. **b)** Head, front view. **c)** Scutum. **d)** Antenna. **e)** Mesosoma, side view. **f)** Propodeum. **g)** Hind leg. **h)** Metasoma, dorsal view.



FIGURE 2. Comparative of species morphologically related to *Halictus flaminii*. **a)** T1 of *H. flaminii*. **b)** T1 of *H. hedini*. **c)** T1 of *H. rubicundus*. **d)** Scutellum of *H. flaminii*. **e)** Scutellum of *H. hedini*. **f)** Scutellum of *H. rubicundus*. **g)** Scutellum of *H. bagirensis*.

by 0.1–1 puncture diameter, underlying surface smooth and glossy (Fig. 2a). T3 and T4 with the same structure as T2 (Fig. 1h). T5 graphite gray to black, shallow punctation, punctures separated by 1 puncture diameter, underlying surface imbricate and glossy, fimbria chamoisee (Fig. 1h). T6 graphite gray to black (Fig. 1h).

Ecology and habitat

Halictus flaminii was discovered on Lombok Island, Indonesia. The island's climatic zones are primarily divided into tropical savannah (Aw) in the southern parts and tropical monsoon (Am) in the northern regions (Fig. 3b). Surrounding islands share these predominant climates (Fig. 3b). The specimen was collected within a region

characterized by a tropical savanna climate (Aw) (Fig. 3b), in a garden located in an open area featuring significant vegetation cover (Fig. 4). This climate is highly atypical for species of the genus *Halictus*, particularly those in the subgenus *Protohalictus*, which are generally associated with temperate, continental, or arid climates (Fig. 3a). The ecology of *Halictus* species remains poorly understood; however, they are known to nest in the ground, requiring open areas suitable for burrowing (Pesenko *et al.* 2000). While such habitats can support *Halictus* nests, they are also ideal for most *Protohalictus* species, which typically prefer open environments such as plains, grasslands, or steppes. In tropical regions, where vegetation is denser and soils are often covered with organic matter, local disturbed open habitats may provide a more suitable environment for *Protohalictus*. Additionally, managed environments like gardens can serve as refuges for *Halictus*, as they create openings in the landscape conducive to nesting.

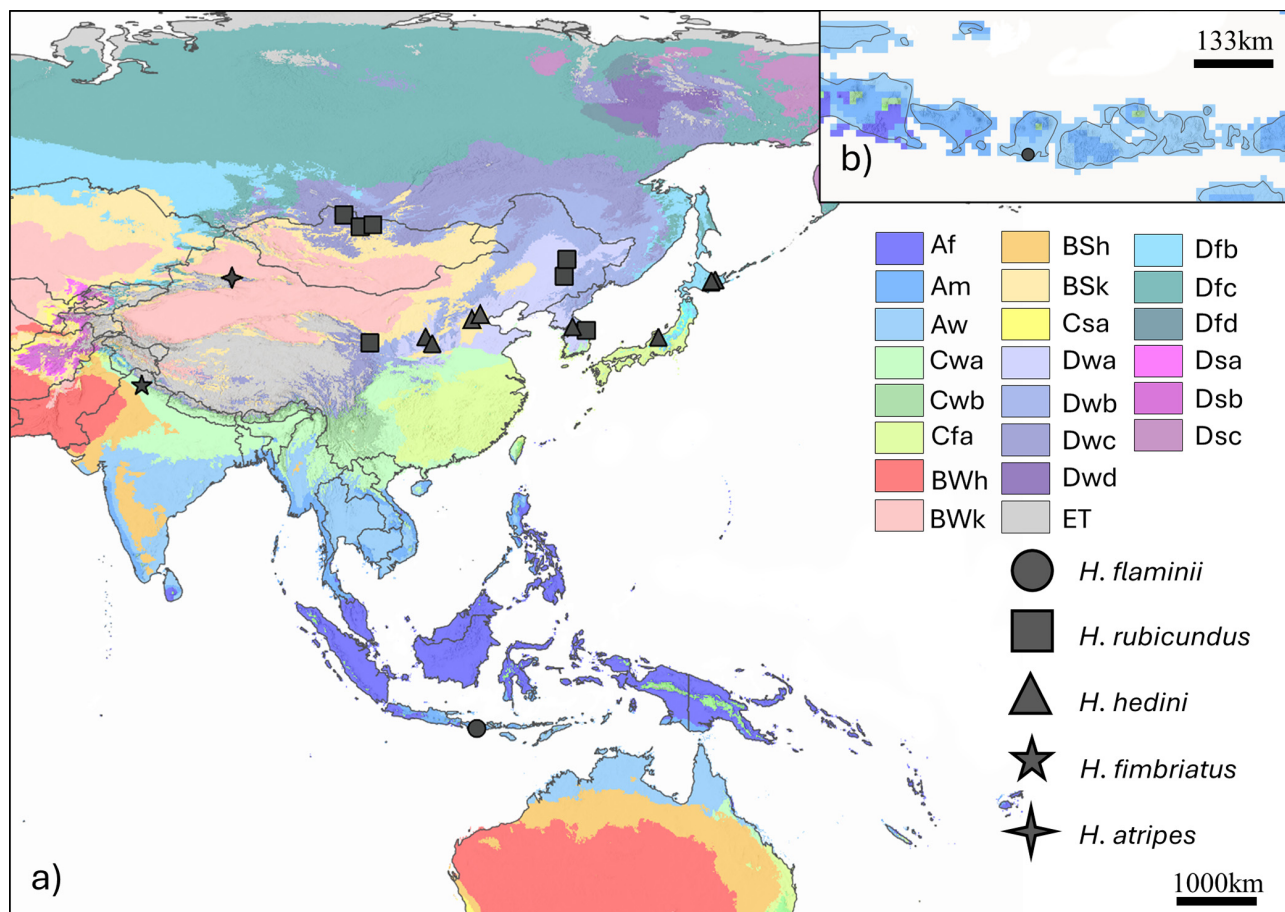


FIGURE 3. Distribution map of species morphologically closest to *Halictus flaminii* superimposed on climate distribution according to Köppen-Geiger classification, the color opacity has been reduced by 50% to enhance the map's readability and improve clarity. A = tropical, B = dry, C = mild temperate, D = snow, E = Polar, f = fully humid, m = monsoon, s = dry summer, w = dry winter, W = desert, S = steppe, T = tundra, F = frost, h = hot arid, k = cold arid, a = hot summer, b = warm summer, c = cool summer, d = cold summer. **a)** Map of Asia. **b)** Zoom on islands surrounding *H. flaminii* locality.

Discussion

Although this new species is known from a single specimen, its classification as a distinct species is well-supported due to the diagnostic morphological characters that set it apart from other members of the subgenus *Protohalictus*. The punctuation pattern on T1 remains a particularly reliable feature for species identification within this subgenus, especially for those closely related to *Halictus rubicundus*, such as *Halictus hedini* (Murao & Gibbs, 2019; Yeonghyeok *et al.* 2024). Notably, the density and definition of punctuation on the scutum, scutellum, and T1 are highly consistent and stable at the intraspecific level across most *Halictus* groups and is used in most cases as a character to distinguish species (Blüthgen, 1926; Ebmer, 1975; Murao & Gibbs, 2019; Pesenko, 2004; Pesenko, 2005; Yeonghyeok *et al.* 2024).



FIGURE 4. Habitat of *Halictus flaminii*. **a)** Similar habitats to the specimen's sampling site (photo by Hen San Bunardy). **b)** Example of vegetation cover at the sampling site (photo by Hen San Bunardy). **c)** Type of landscape from which the specimen was sampled (photo by Lily Heise).

Moreover, the geographical origin of this specimen further supports its status as a separate species. This Indonesian species is geographically isolated from other members of the *Protohalictus* subgenus, occurring in a tropical savanna climate that contrasts markedly with the habitats of its relatives (Pesenko, 2005). The Indomalayan region is already recognized for its high levels of endemism, and the discovery of this species emphasizes the region's distinctiveness (Astafurova *et al.* 2020; Myers *et al.* 2000; Sloan *et al.* 2014; Sing *et al.* 2016). The high level of endemism in this region may result from speciation and divergence driven by vicariance events, particularly the rising sea levels during the Oligocene, around 25 million years ago, which fragmented many territories (De Bruyn *et al.* 2015; Dusfour *et al.* 2007). Additionally, the region's tectonic complexity and climate evolution likely amplified vicariance effects. Climatic shifts, such as the expansion of rainforest at the expense of savanna and grassland habitats, may have further shaped evolutionary trajectories. Savanna and grassland environments, which are optimal for *Halictus* species, were virtually replaced by tropical habitats, potentially imposing significant evolutionary constraints on the *Protohalictus* species present.

This pattern, in which a tropical species or group of species is described within a clade primarily composed of species from arid or temperate regions, is not uncommon in bees. For example, the subgenus *Megachile* (*Pseudomegachile*) Friese comprises mostly species found in temperate or arid climates. However, some species, such as *Megachile opposita* Smith, also occur in tropical monsoon (Am) and tropical savanna (Aw) zones of Indonesia (Praz, 2017; Gonzalez & Engel, 2012). Similarly, certain widely distributed groups like the genus *Bombus* Latreille, primarily inhabiting temperate and colder environments, include a few tropical species found at the periphery of the genus' distribution (Ghisbain *et al.* 2025). These include *Bombus* (*Melanobombus*) *rufipes* Lepeletier, *Bombus* (*Megabombus*) *senex* Vollenhoven, and *Bombus* (*Pyrobombus*) *flavescens* Smith, all of which are also found in Indonesia in mountainous areas (Thanoosing *et al.* 2023).

This finding underscores how little is currently known about Indonesia's bee fauna in general and Halictidae in particular. It highlights the need for further research into bee diversity in this area. Enhanced understanding of pollinator biodiversity could provide critical insights into the ecological dynamics of Indonesia and help address broader conservation and ecological challenges in the region.

Acknowledgements

We sincerely thank Simone Flaminio for his dedicated work on the Halictidae and her unwavering passion for taxonomy. Our gratitude extends to the entire staff at the Biodiversitätszentrum Oberösterreich in Linz for their invaluable assistance during my stay and their meticulous efforts in maintaining the entomological collection, which significantly contributed to the progress of this research. We would also like to extend our warmest thanks to the following photographers for sharing their wonderful pictures: Hen San Bunardy and Lily Heise. We sincerely thank also Sarah Lescot for requesting the right to use the photos.

References

- Ascher, J.S. & Pickering, J. (2024) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from: http://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed 10 December 2024)
- Astafurova, Y.V., Proshchalykin, M.Y. & Schwarz, M. (2020) New and little-known species of the genus *Sphecodes* Latreille (Hymenoptera, Halictidae) from Southeast Asia. *ZooKeys*, 937, 31–88.
<https://doi.org/10.3897/zookeys.937.51708>
- Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A. & Wood, E.F. (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, 5 (1), 180214.
<https://doi.org/10.1038/sdata.2018.214>
- Blüthgen, P. (1926) Beiträge zur Kenntnis der indo-malayischen *Halictus* und *Thrinchostoma*-Arten (Hym. Apidae. Halictinae). *Zoologische Jahrbücher*, 51 (4/6), 375–698.
<https://doi.org/10.1002/mmnd.192619260411>
- Blüthgen, P. (1936) Neue paläarktische Binden-*Halictus* (Hym. Apidae). *Mitteilungen aus dem Zoologischen Museum in Berlin*, 21 (2), 270–313.
- Brooks, R.W. (1988) Systematics and phylogeny of the anthophorine bees (Hymenoptera: Anthophoridae; Anthophorini). *The University of Kansas Science Bulletin*, 53 (9), 436–575.
- Corlett, R.T. (2004) Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biological Reviews*, 79 (3), 497–532.
<https://doi.org/10.1017/S1464793103006341>
- Danforth, B.N., Sauquet, H. & Packer, L. (1999) Phylogeny of the Bee Genus *Halictus* (Hymenoptera: Halictidae) Based on Parsimony and Likelihood Analyses of Nuclear EF-1 α Sequence Data. *Molecular Phylogenetics and Evolution*, 13 (3), 605–618.
<https://doi.org/10.1006/mpev.1999.0670>
- Dusfour, I., Michaux, J.R., Harbach, R.E. & Manguin, S. (2007) Speciation and phylogeography of the Southeast Asian *Anopheles sundaicus* complex. *Infection Genetics and Evolution*, 7 (4), 484–493.
<https://doi.org/10.1016/j.meegid.2007.02.003>
- De Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Carvalho, G.R., Cannon, C.H., Van Den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L., Maiorano, L., Shoup, R. & Von Rintelen, T. (2014) Borneo and Indochina are Major Evolutionary Hotspots for Southeast Asian Biodiversity. *Systematic Biology*, 63 (6), 879–901.
<https://doi.org/10.1093/sysbio/syu047>
- Ebmer, A.W. (1975) Neue Westpaläarktische Halictidae (Halictinae, Apoidea). teil III. *Linzer Biologische Beiträge*, 7 (1), 41–118.
- Ebmer, A.W. (1988) Kritische Liste der nicht-parasitischen Halictidae Österreichs mit Berücksichtigung aller mitteleuropäischen Arten (Insecta: Hymenoptera: Apoidea: Halictidae). *Linzer Biologische Beiträge*, 20 (2), 527–711.
- Ebmer, A.W. (2014) Die nicht-parasitischen Halictidae der Insel Zypern im Vergleich zu Kreta mit einer Monographie der *Lasioglossum bimaculatum*-Artengruppe und einer Übersicht der *Halictus nicosiae*-Untergruppe (Insecta: Hymenoptera: Apoidea: Halictidae). *Linzer Biologische Beiträge*, 46/1, 291–413.
- Gibbs, J., Brady, S.G., Kanda, K. & Danforth, B.N. (2012) Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). *Molecular Phylogenetics and Evolution*, 65 (3), 926–939.
<https://doi.org/10.1016/J.YMPEV.2012.08.013>
- Ghisbain, G., Rosa, P., Bogusch, P., Flaminio, S., Divelec, R.L., Dorchin, A., Kasparek, M., Kuhlmann, M., Litman, J., Mignot,

- M., Müller, A., Praz, C., Radchenko, V.G., Rasmont, P., Risch, S., Roberts, S.P., Smit, J., Wood, T.J., Michez, D. & Reverté, S. (2023) The new annotated checklist of the wild bees of Europe (Hymenoptera : Anthophila). *Zootaxa*, 5327 (1), 1–147.
<https://doi.org/10.11646/zootaxa.5327.1.1>
- Ghisbain, G., Chittka, L. & Michez, D. (2025) Bumblebees. *Current Biology*, 35 (6), R206–R211.
<https://doi.org/10.1016/j.cub.2025.01.041>
- Gonzalez, V.H. & Engel, M.S. (2012) African and Southeast Asian *Chalicodoma* (Hymenoptera : Megachilidae) : New Subgenus, New Species, and Notes on the Composition of *Pseudomegachile* and *Largella*. *Annales Zoologici*, 62 (4), 599–617.
<https://doi.org/10.3161/000345412x659669>
- Klein, A.M., Cunningham, S.A., Bos, M. & Steffan-Dewenter, I. (2008) Advances in pollination ecology from tropical plantation crops. *Ecology*, 89 (4), 935–943.
<https://doi.org/10.1890/07-0088.1>
- Michener, C.D. (2007) *The Bees of the World*. 2nd Edition. Johns Hopkins University Press, Baltimore, Maryland, 953 pp.
- Murao, R. & Gibbs, J. (2019) *Halictus hedini hedini* (Hymenoptera: Halictidae) newly recorded from Japan, revealed by DNA barcoding and morphology. *Journal of Melittology*, 84, 1–8.
<https://doi.org/10.17161/jom.v0i84.7565>
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
<https://doi.org/10.1038/35002501>
- Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.D. & Ascher, J.S. (2021) Global Patterns and Drivers of Bee Distribution. *Current Biology*, 31 (3), e4, 451–458.
<https://doi.org/10.1016/j.cub.2020.10.053>
- Pauly, A. & Belval, S. (2017) Atlas des Halictidae de France (Hymenoptera: Apoidea). *Belgian Journal of Entomology*, 53, 1–34.
- Pesenko, Y.A., Banaszak, J., Cierzniak, T. & Radchenko, V.G. (2000) *Bees of the Family Halictidae (excluding Sphecodes) of Poland: Taxonomy, Ecology, Bionomics*. University of Bydgoszcz, Bydgoszcz, 348 pp.
<https://doi.org/10.13140/RG.2.1.3185.5447>
- Pesenko, Y.A. (2004) The phylogeny and classification of the tribe Halictini with special reference to the *Halictus* genus-group (Hymenoptera: Halictidae). *Zoosystematica Rossica*, 13 (1), 83–113.
<https://doi.org/10.31610/zsr/2004.13.1.83>
- Pesenko, Y.A. (2005) Contributions to the halictid fauna of the Eastern Palaearctic Region: Genus *Halictus* Latreille (Hymenoptera: Halictidae, Halictinae). *Far Eastern Entomologist*, 150, 1–12.
<https://doi.org/10.31610/zsr/2006.15.1.133>
- Pesenko, Y.A. & Wu, Y. (1997) Chinese bees of the genus *Halictus* s. str. with descriptions of a new species and a new subspecies (Hymenoptera: Halictidae). *Acta Entomologica Sinica*, 40 (2), 202–206.
- Praz, C.J. (2017) Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae). *Journal of Hymenoptera Research*, 55, 1–54.
<https://doi.org/10.3897/jhr.55.11255>
- Sing, K.W., Wang, W.Z., Wan, T., Lee, P.S., Li, Z.X., Chen, X., Wang, Y.Y. & Wilson, J.J. (2016) Diversity and human perceptions of bees (Hymenoptera: Apoidea) in Southeast Asian megacities. *Genome*, 59 (10), 827–839.
<https://doi.org/10.1139/gen-2015-0159>
- Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L.A. & Laurance, W.F. (2014) Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation*, 177, 12–24.
<https://doi.org/10.1016/j.biocon.2014.05.027>
- Thanoosing, C., Orr, M.C., Warrit, N., Vogler, A.P. & Williams, P.H. (2023) A taxonomic re-assessment of the widespread oriental bumblebee *Bombus flavescens* (Hymenoptera, Apidae). *Journal of Hymenoptera Research*, 96, 507–541.
<https://doi.org/10.3897/jhr.96.104715>
- Von Rintelen, K., Arida, E. & Häuser, C. (2017) A review of biodiversity-related issues and challenges in megadiverse Indonesia and other Southeast Asian countries. *Research Ideas and Outcomes*, 3, e20860.
<https://doi.org/10.3897/rio.3.e20860>
- Widhiono, I., Sudiana, E. & Yani, E. (2017) Contribution of Plantation Forest on Wild Bees (Hymenoptera: Apoidea) Pollinators Conservation in Mount Slamet, Central Java, Indonesia. *Biosaintifika Journal of Biology & Biology Education*, 9 (3), 437–443.
<https://doi.org/10.15294/biosaintifika.v9i3.10652>
- Williams, N.M., Crone, E.E., T'ai, H.R., Minckley, R.L., Packer, L. & Potts, S.G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143 (10), 2280–2291.
<https://doi.org/10.1016/j.biocon.2010.03.024>
- Yeonghyeok, Y., Hyojoong, K. & Heungsik, L. (2024) A New Record of Bee *Halictus hedini hedini* (Hymenoptera: Halictidae) from South Korea. *Korean Journal of Applied Entomology*, 63 (1), 63–66.
<https://doi.org/10.5656/KSAE.2024.02.0.005>