

Research article

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Overview of the ant genus *Vollenhovia* (Hymenoptera, Formicidae) in India and Sri Lanka, with an illustrated key and the description of a new species

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Abstract. The ant genus *Vollenhovia* Mayr, 1865 (Myrmicinae, Crematogastrini) mostly occurs in the Australasian and Oriental regions. We revised its diversity in India and Sri Lanka based on qualitative and quantitative morphology, recognizing eleven taxa, including a new species which is described herewith: *V. escherichi* Forel, 1911, *V. gastropunctata* Bharti & Kumar, 2013, *V. karimalaensis* Dhadwal *et al.*, 2023, *V. keralensis* Kripakaran & Sadasivan, 2022, *V. mawrapensis* Dhadwal *et al.*, 2023, *V. oblonga laevithorax* Emery, 1889, *V. penetrans* (Smith, 1857), *V. pfeifferi* Bharti *et al.*, 2023, *V. taylori* Rilta *et al.*, 2023, *V. terayamai* Rilta *et al.*, 2023, and *V. yasmeenae* sp. nov. The subspecies status of *V. oblonga laevithorax* and its relationship with *V. penetrans*, whose type series does not contain workers, still requires to be assessed in the context of a broader revision including the whole Oriental region. The known distribution of the genus in the Indian subcontinent appears to be fragmentary, still requiring extensive sampling efforts. Four species are from the Western Ghats biodiversity hotspot in the southern Indian state of Kerala, one is endemic to the biogeographically related Sri Lanka, three are known from Eastern India near the border with Bangladesh, two are reported from the Andaman and Nicobar Islands, and one is restricted to the Himachal Pradesh in northern India. A comprehensive key of the known *Vollenhovia* species from India and Sri Lanka is provided.

Keywords. Myrmicinae, Crematogastrini, systematics, Oriental, new species.

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Introduction

The ant genus *Vollenhovia* Mayr, 1865 is currently represented by 65 extant valid species, 17 valid subspecies, and three fossil species (Bolton 2023) and is placed within the tribe Crematogastrini Forel, 1893 of the subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835 (Ward *et al.* 2015; Blaimer *et al.* 2018). The genus was placed in several different tribes before Crematogastrini (i.e., Myrmicini, Stenammini, Metaponini, Solenopsidini, and even incertae sedis), and several different genera were synonymized under *Vollenhovia* since the genus was described based on the type species *V. punctatostriata* Mayr, 1865 (Bolton 2023). *Vollenhovia* comprises small- to moderately-sized (2–6 mm) ants mostly distributed in the Oriental and Australasian regions (Janicki *et al.* 2016; Guénard *et al.* 2017), with a few species also reported from the Palearctic region (Bolton 1995; Terayama & Kinomura 1997). These ants are mostly cryptic, arboreal, and lignicolous, and usually inhabit forest habitats, nesting in decayed wood, rotting twigs, dry tree branches, and in spaces under the bark of logs (Radchenko & Dlussky 2013). The widespread *Vollenhovia emeryi* Wheeler, 1906, which successfully colonized parts of Eastern Asia and the United States after being introduced (Wetterer *et al.* 2015), has also been found in urban parks (Iwata *et al.* 2005; Harada *et al.* 2010) and in agricultural fields (Hosoishi *et al.* 2007). Little is still known of the diet of *Vollenhovia* ants, but species may be mostly predatory, feeding on beetle larvae and a variety of other small arthropods (Sadasivan & Kripakaran 2022). The genus is known to include workerless socially parasitic species and is peculiar for queen polymorphism, clonal reproduction, and caste differentiation mechanisms (Ohkawara *et al.* 2006; Ohkawara & Satoh 2015). These ants are an interesting model system to trace the evolution of caste determination (Ohkawara *et al.* 2006; Satoh & Ohkawara 2008). Unlike most ant species, queens and males are produced clonally, while sterile workers arise sexually (Kobayashi *et al.* 2011). This selfish clonal reproduction and the role of certain reproductive manipulators such as *Wolbachia* causing the host's clonal reproduction remain fascinating and still unresolved aspects of their biology (Noh *et al.* 2020).

In the Indian subcontinent, the species of *Vollenhovia* are scattered across different regions, with the genus apparently showing a disjunct distribution (Fig. 1). Four species (*V. karimalaensis* Dhadwal *et al.*, 2023, *V. keralensis* Kripakaran & Sadasivan, 2022, *V. pfeifferi* Bharti *et al.*, 2023 and *V. yasmeenae* sp. nov.) are known from the Western Ghats biodiversity hotspot in the southern state of Kerala, three were recently described near the border with Bangladesh in the East (*V. mawrapensis* Dhadwal *et al.*, 2023, *V. taylori* Rilta *et al.*, 2023, *V. terayamai* Rilta *et al.*, 2023), while *V. gastropunctata* Bharti & Kumar, 2013 is the only species known from the northern state of Himachal Pradesh. Furthermore, two species, *V. oblonga laevithorax* Emery, 1889 and *V. penetrans* (Smith, 1857), are recorded from the Andaman and Nicobar Islands, and one, *V. escherichi* Forel, 1911, is endemic to Sri Lanka.

The Western Ghats of India is a biodiversity hotspot (Mittermeier *et al.* 2004; Kass *et al.* 2022), with several rare ant species reported from the region, particularly in the Silent Valley National Park and Periyar Tiger Reserve in the Idukki District of Kerala (Bharti & Akbar 2013, 2014a, 2014b, 2014c; Bharti *et al.* 2015; Dad *et al.* 2019; Akbar *et al.* 2023a, 2023b). As a result of recent investigations in the region, we present the description of an additional Indian species. Furthermore, we provide a taxonomic overview of the genus *Vollenhovia* from India and Sri Lanka with an illustrated key to their eleven taxa.

Material and methods

New material examined in this study was collected by Shahid A. Akbar during ant inventories carried out in the Western Ghats of India region from 2011 to 2013. The Western Ghats are characterized by a mosaic of vegetation types that include tropical wet evergreen forest, moist deciduous forest, montane stunted evergreen forest (Shola), and grasslands, providing variety in habitat structure (Dad *et al.* 2019).

The specimens were collected by hand picking and Winkler extraction. Morphological analysis was conducted using a Nikon SMZ 1500 stereo zoom microscope. Terminology follows Prebus (2021) for morphological characters and Harris (1979) for surface sculpture. For digital images, an MP Evolution digital camera was used on the same microscope, coupled with Auto-Montage software (Syncroscopy, Division of Synoptics, Ltd). Images were subsequently edited using Adobe Photoshop CS6.

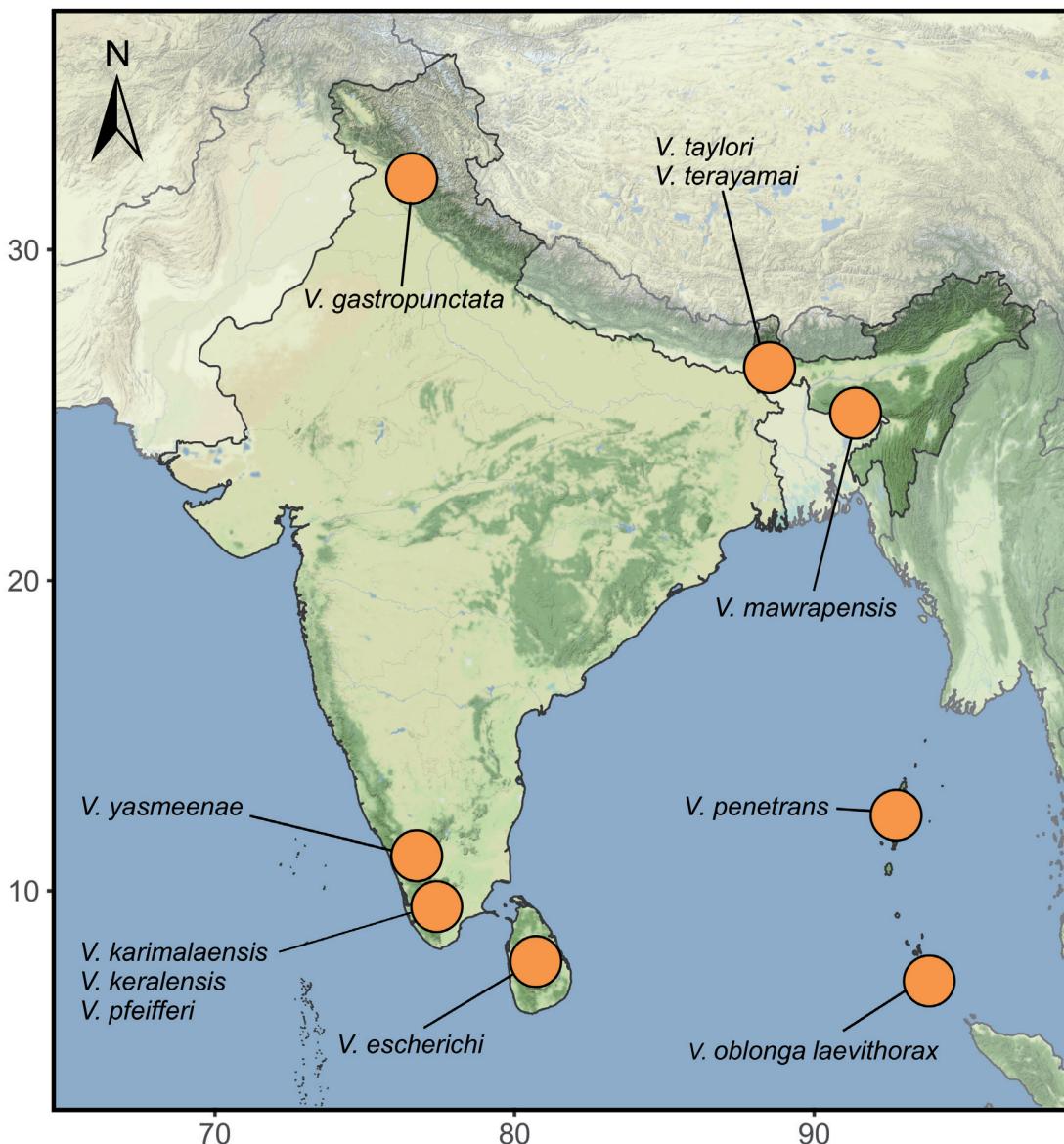


Fig. 1. Distribution map of the species of *Vollenhovia* Mayr, 1865 from India.

Morphometric measurements of the physical specimens were performed with a Nikon SMZ 1500 stereo zoom microscope equipped with an orthogonal pair of micrometers at magnifications ranging from 80 \times to 150 \times .

Twelve morphometric characters were recorded on each specimen examined. The definition and nomenclature of these characters follows Wagner *et al.* (2017) and Prebus (2021):

CL = Cephalic Length = with the head in full-face view, it is measured as the maximum distance between the occipital margin of the head to the lowermost margin of the clypeus
CW = Cephalic Width = with the head in full-face view, it is the maximum width of the head across the eyes
EL = Eye Length = the longest diameter of the compound eye (including unpigmented marginal ommatidia)
ML = Mesosoma Length = measured in lateral view from caudalmost portion of propodeum to dorsofrontal corner of pronotal slope
PEH = Petiole Height = the longest distance measured from the ventral petiolar profile at node level (perpendicular to the chord length of the petiolar sternum, excluding the subpetiolar process) to the distalmost point of the dorsal profile of the petiolar node
PEL = Petiole Length = diagonal petiolar length in lateral view; measured from the apex of the subpetiolar process to the posterodorsal corner of the caudal cylinder
PEW = Petiole Width = maximum petiole width in dorsal view
PPH = Postpetiole Height = maximum height of the postpetiole in lateral view measured perpendicularly to a line defined by the linear section of the segment border between the postpetiolar tergite and sternite
PPL = Postpetiole Length = the longest distance, perpendicular to the posterior margin of the postpetiole, between the posterior postpetiolar margin and the anterior postpetiolar margin, excluding the helcium
PPW = Postpetiole Width = maximum postpetiole width in dorsal view
PW = Pronotal Width = maximum width of pronotum in dorsal view
SL = Scape Length = maximum scape length excluding the basal neck and the articular condyle

Based on these characters, we computed CS (Cephalic Size) as the arithmetic mean between CL and CW and the Cephalic index as the CL/CW ratio. Furthermore, we divided all other morphometric characters for the CS value to weight them on an indicator of specimen size (Bharti & Kumar 2013; Wagner *et al.* 2017; Schifani *et al.* 2022). All measurements are presented in millimeters as the minimum-maximum range followed by the arithmetic mean in parentheses. All morphometric data produced in this study are provided in the Supp. File 1: Table S1 together with those produced in the recent revision by Dhadwal *et al.* (2023).

Species delimitation is based on the detection of gaps in the patterns of qualitative morphological variation, following the criteria used in previous revisions of *Vollenhovia*.

The following institutions were consulted:

MSNG = Natural History Museum, Genoa, Italy
NHMUK = Natural History Museum, London, UK
OXUM = Oxford University Museum of Natural History, Oxford, UK
PUAC = Punjabi University Patiala Ant Collection, Punjab, India
TNHS = Travancore Nature History Society, Thiruvananthapuram, Kerala, India

The holotype and paratypes of the new species have been deposited in PUAC.

Results

Taxonomic account

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Myrmicinae Lepetier de Saint-Fargeau, 1835
Genus *Vollenhovia* Mayr, 1865

Vollenhovia escherichi Forel, 1911
Fig. 2

Vollenhovia escherichi Forel, 1911: 198. Type locality: Sri Lanka [Ceylon], Peradeniya [Syntype MHNG; worker examined].

Remarks

Long known as an endemic Sri Lankan species, *V. escherichi* is very easily distinguished from the other taxa treated in this study due to its light yellowish-brown coloration as well as its small size. Recently, it was also recorded by Wang *et al.* (2022) from Pulau Ubin, an island off Singapore. Further investigation on the relationships between the Sri Lankan and Singaporean populations seems to be needed to better establish the biogeography of this species.

Distribution

Sri Lanka, Singapore (Dias *et al.* 2020; Wang *et al.* 2022).

Vollenhovia gastropunctata Bharti & Kumar, 2013
Fig. 3

Vollenhovia gastropunctata Bharti & Kumar, 2013: 180. Type locality: India, Himachal Pradesh, Andretta [Holotype PUAC; type series examined].

Worker measurements & indices (2 specimens: holotype & paratype, 1 colony, 1 locality)

CL 0.56–0.56, CW 0.49–0.49, CS 0.52–0.52, EL 0.12–0.12, ML 0.73–0.75, PEH 0.23–0.23, PEL 0.23–0.24, PEW 0.18–0.18, PPH 0.19–0.19, PPL 0.24–0.24, PPW 0.20–0.20, PW 0.36–0.36, SL 0.33–0.33. Indices: CL/CW 1.14–1.14, EL/CS 0.23–0.23, ML/CS 1.39–1.43, PEH/CS 0.44–0.44, PEL/CS 0.44–0.46, PEW/CS 0.34–0.34, PPH/CS 0.36–0.36, PPL/CS 0.46–0.46, PPW/CS 0.38–0.38, PW/CS 0.69–0.69, SL/CS 0.63–0.63.

Remarks

Vollenhovia gastropunctata is the only species of the genus known from the northwest Shivalik region of India (Bharti & Kumar 2013; Bharti *et al.* 2017). It is perhaps entirely arboreal, having been collected near a mango tree in a semi-arid type of environment (Fig. 3D). It can be distinguished by the punctured mandibles with seven teeth, sculptured promesonotum, larger subpetiolar process, indistinct metanotal groove, anteriorly divergent longitudinal carinae on clypeus, concave anterior clypeal margin, and unarmed propodeum (Bharti & Kumar 2013). On the other hand, the punctate sculpture on the gaster its name refers to is a feature shared by many other species in the region.

Distribution

India (Himachal Pradesh) (Bharti & Kumar 2013).

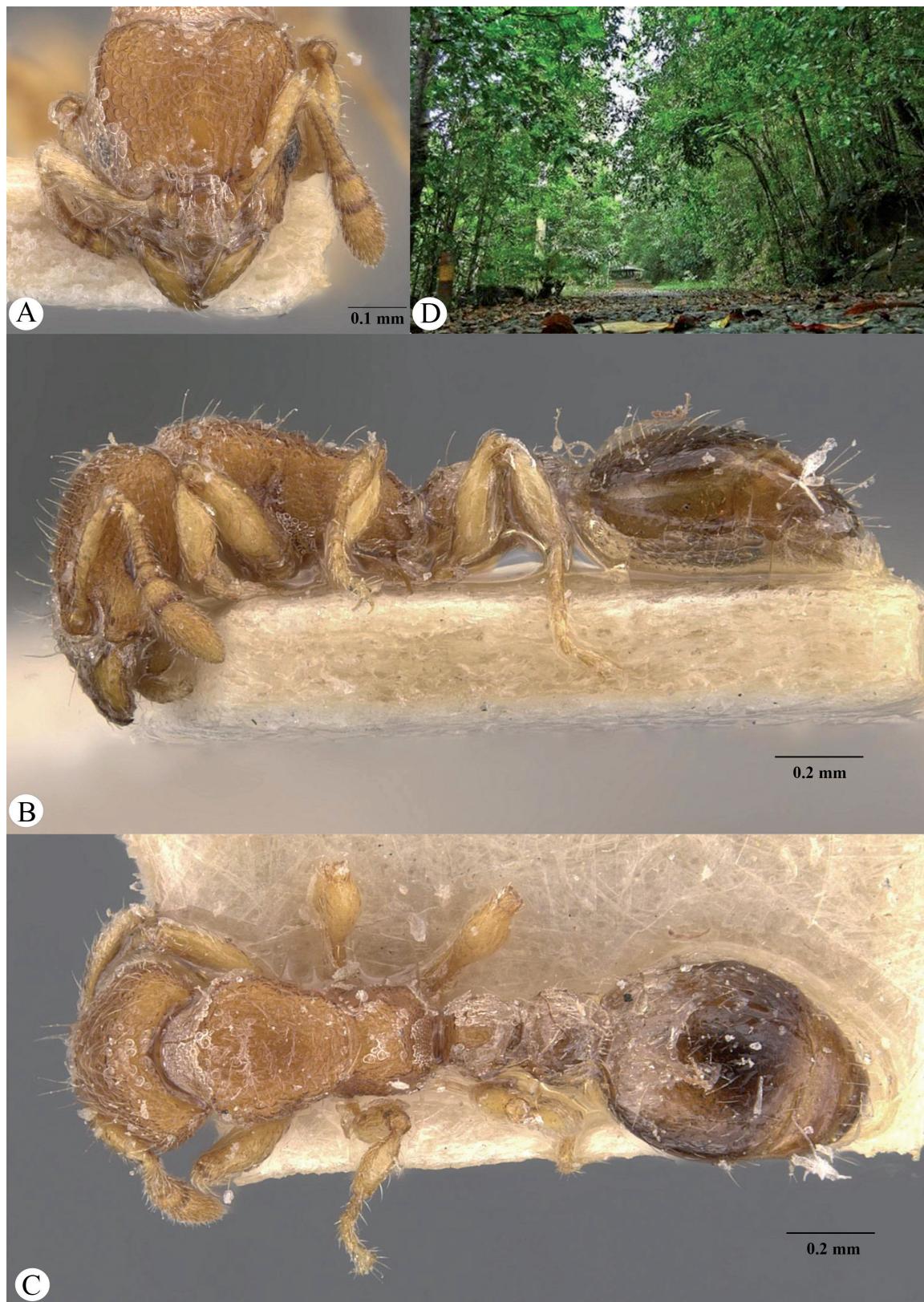


Fig. 2. *Vollenhovia escherichi* Forel, 1911, syntype worker from Sri Lanka (CASENT0908656, photographer: Will Ericson). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Typical forest habitat of Peradeniya, Sri Lanka.

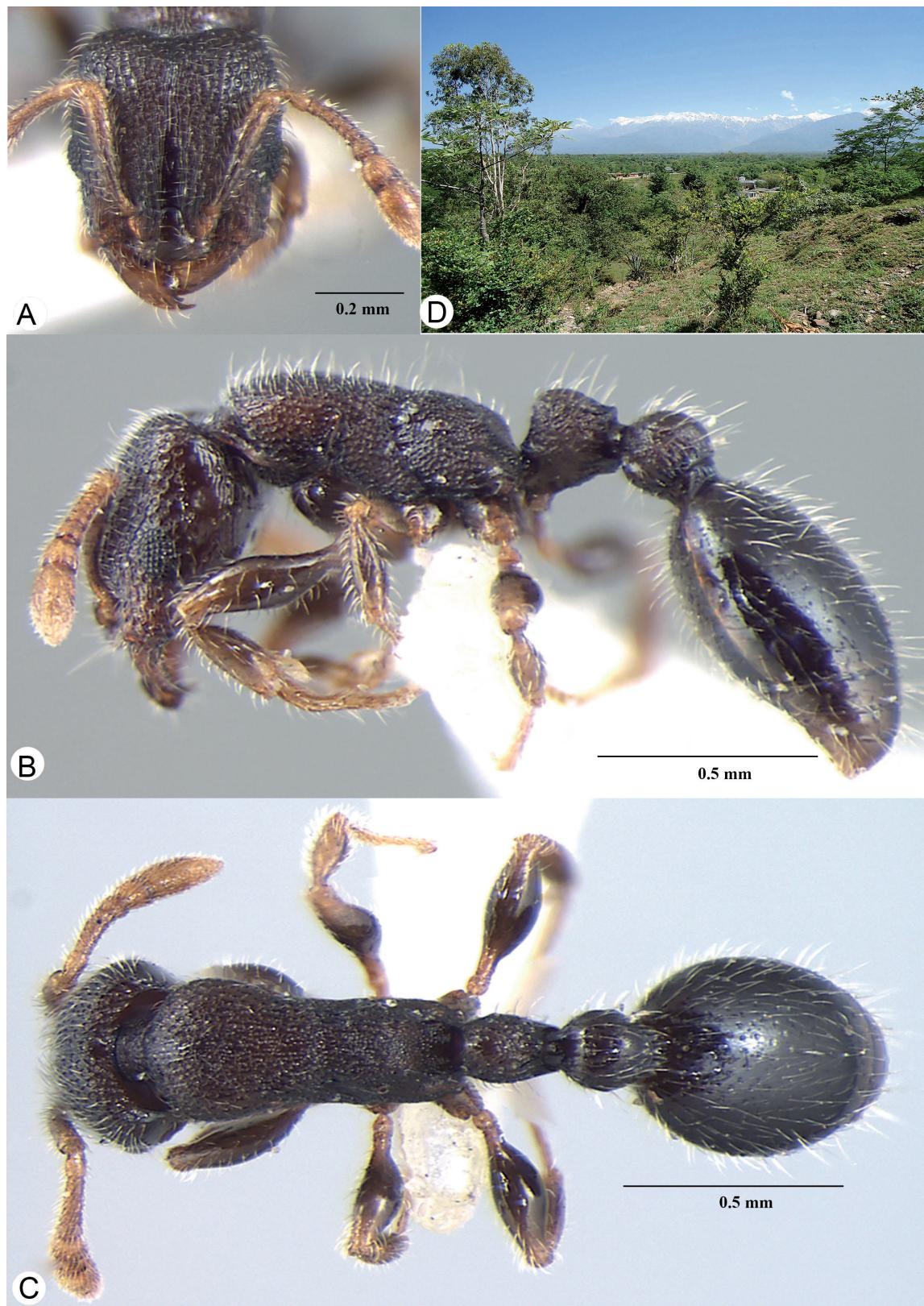


Fig. 3. *Vollenhovia gastropunctata* Bharti & Kumar, 2013, holotype worker from India (PUAC0045, photographer: Rakesh Kumar). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Type locality of the species.

Vollenhovia karimalaensis Dhadwal, Rilta & Bharti, 2023
Fig. 4

Vollenhovia karimalensis Dhadwal, Rilta & Bharti, 2023: 2. Type locality: India, Kerala, Parambikulam Tiger Reserve, Karimala [Holotype: PUAC, type series examined].

Worker measurements & indices (3 specimens, 1 colony, 1 locality)

CL 0.76–0.82, CW 0.69–0.78, CS 0.72–0.80, EL 0.12–0.14, ML 0.99–1.12, PEH 0.26–0.30, PEL 0.30–0.33, PEW 0.24–0.26, PPH 0.24–0.28, PPL 0.30–0.45, PPW 0.27–0.32, PW 0.50–0.58, SL 0.45–0.48. Indices: CL/CW 1.05–1.11, EL/CS 0.16–0.18, ML/CS 1.36–1.40, PEH/CS 0.36–0.37, PEL/CS 0.41–0.42, PEW/CS 0.31–0.33, PPH/CS 0.33–0.35, PPL/CS 0.39–0.56, PPW/CS 0.35–0.40, PW/CS 0.69–0.72, SL/CS 0.60–0.63.

Remarks

Vollenhovia karimalaensis is a recently described taxon that appears most similar to *V. keralensis*, the two species being both known from the Western Ghats and having similar features including the convex anterior clypeal margin with a median tooth. According to Dhadwal *et al.* (2023), its distinction from *V. keralensis* can be based on the head distinctly longer than broad (shorter in *V. keralensis*), the mandibles having seven teeth instead of eight, the different shape of the subpetiolar process, and the whole body being finely punctate instead of foveate.

Distribution

India (Kerala) (Dhadwal *et al.* 2023).

Vollenhovia keralensis Kripakaran & Sadasivan, 2022
Fig. 5

Vollenhovia keralensis Kripakaran & Sadasivan in Sadasivan & Kripakaran, 2022: 21381. Type locality: India, Kerala, Trivandrum Bonaccord, Peppara Wildlife Sanctuary [Holotype TNHS; images of holotype worker examined in Sadasivan & Kripakaran 2022].

Material examined

INDIA • 8 workers; Kerala, Periyar Tiger Reserve; 9°48' N, 77°24' E; alt. 1005 m; 17 Oct. 2011; hand picking; S.A. Akbar leg.; PUAC0026 to PUAC0033; 4 workers; Periyar Tiger Reserve, Manalar; 9°35' N, 77°18' E; alt. 1630 m; 27 Oct. 2011; hand picking; leg. S.A. Akbar leg.; PUAC0034 to PUAC0037.

Worker measurements & indices (12 specimens, 2 colonies, 2 localities)

CL 0.65–0.70 (0.67), CW 0.56–0.58 (0.57), CS 0.60–0.63 (0.62), EL 0.13–0.15 (0.14), ML 0.80–0.92 (0.85), PEH 0.35–0.37 (0.36), PEL 0.22–0.26 (0.24), PEW 0.23–0.24 (0.24), PPH 0.21–0.22 (0.21), PPL 0.23–0.27 (0.24), PPW 0.24–0.25 (0.24), PW 0.42–0.51 (0.47), SL 0.38–0.40 (0.39) mm. Indices: CL/CW 1.12–1.25 (1.17), EL/CS 0.21–0.24 (0.22), ML/CS 1.30–1.47 (1.38), PEH/CS 0.56–0.60 (0.58), PEL/CS 0.36–0.43 (0.39), PEW/CS 0.37–0.40 (0.38), PPH/CS 0.34–0.37 (0.35), PPL/CS 0.37–0.44 (0.39), PPW/CS 0.38–0.42 (0.39), PW/CS 0.68–0.82 (0.76), SL/CS 0.60–0.65 (0.63).

Remarks

This species from the Western Ghats closely resembles *V. karimalaensis* from the same region but can be separated based on the number of mandible teeth, the sculpture, and the petiole shape (see Remarks under *V. karimalaensis*). It is one of the few species of the genus of which all three castes have been described (Sadasivan & Kripakaran 2022). We were able to collect specimens from two new localities

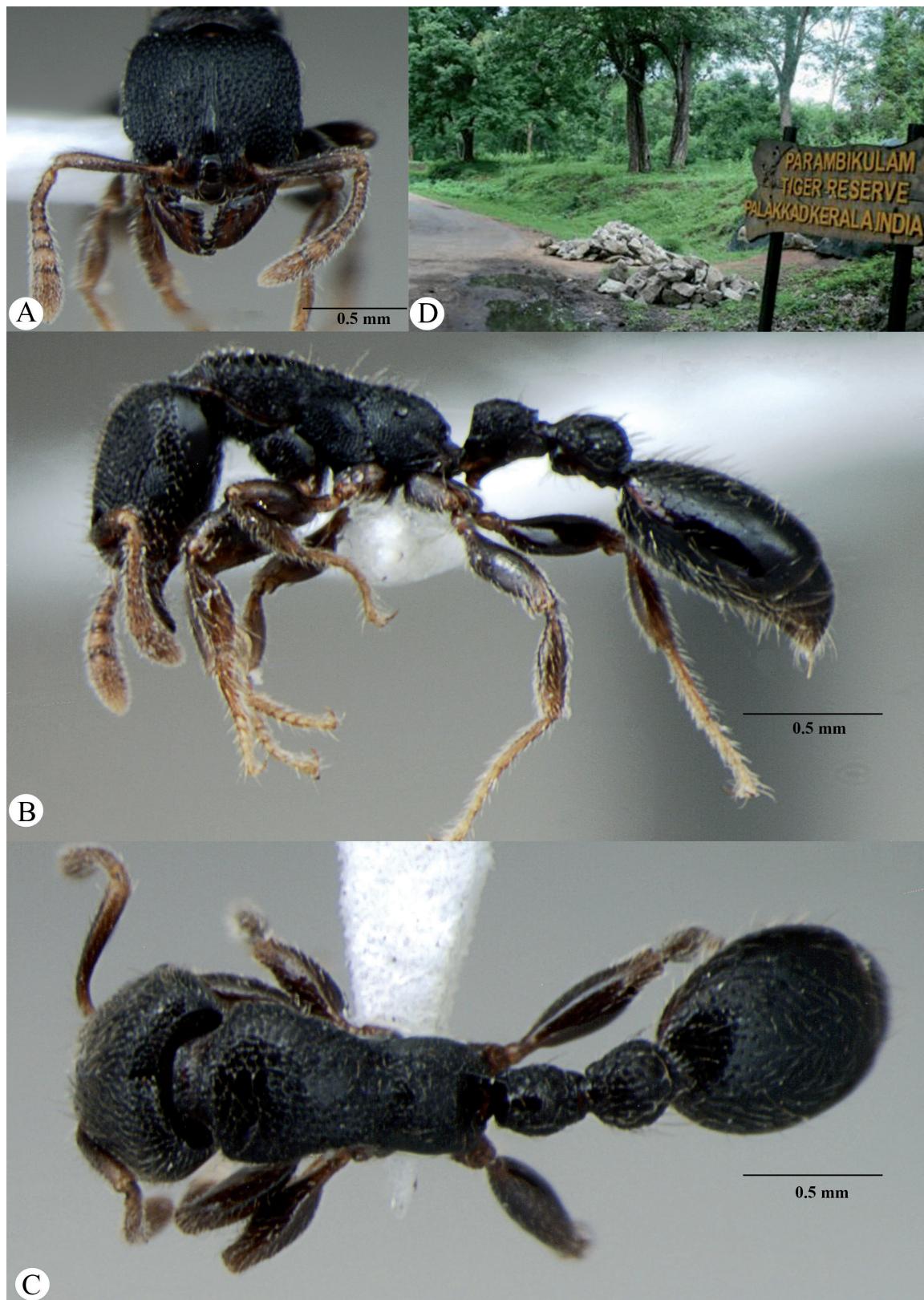


Fig. 4. *Vollenhovia karimalaensis* Dhadwal, Rilta & Bharti, 2023, holotype worker from India (PUAC T701, photographer: Himender Bharti). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Type locality.

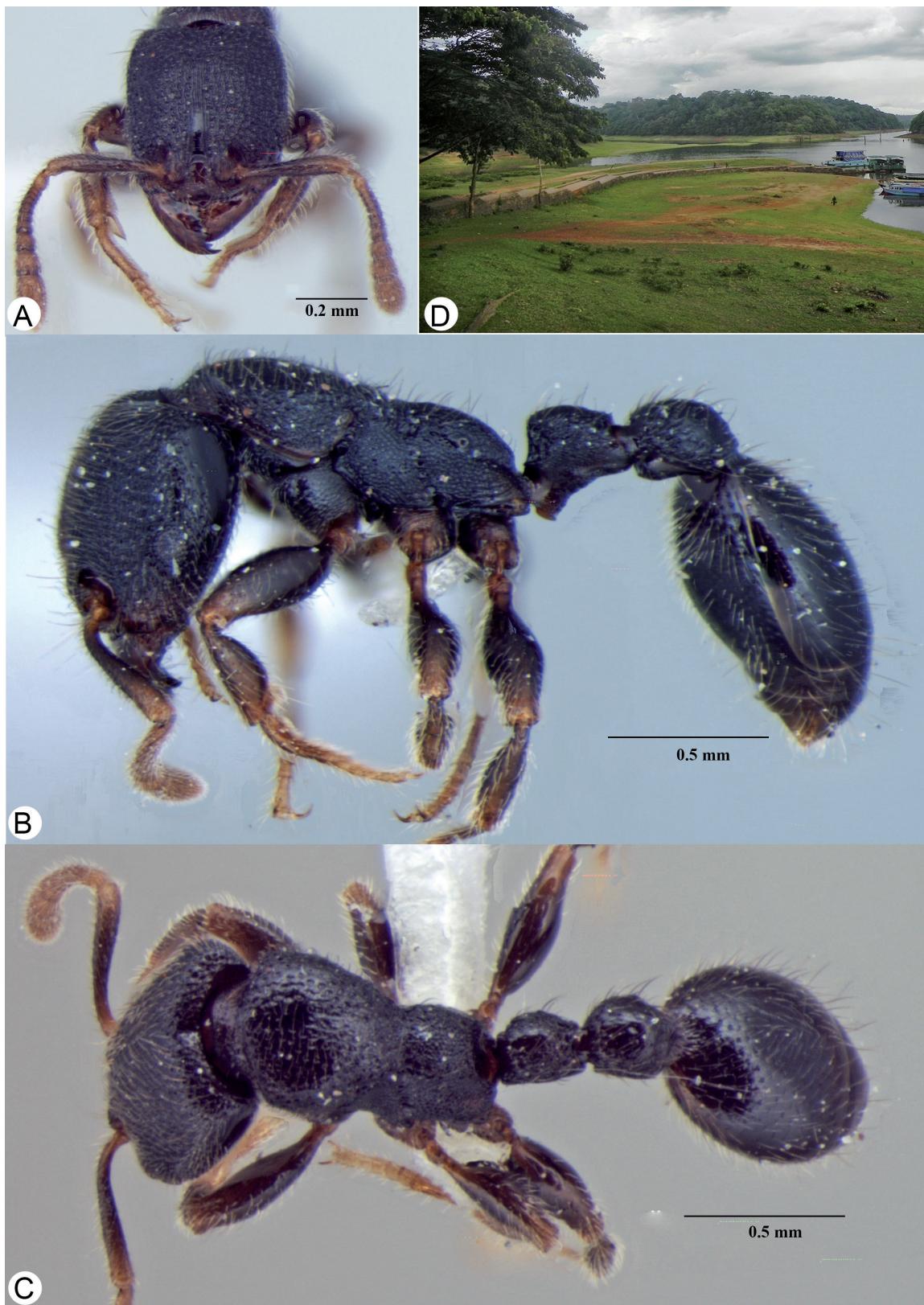


Fig. 5. *Vollenhovia keralensis* Kripakaran & Sadasivan, 2022, worker from India (PUAC0026, photographer: Shahid Ali Akbar). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Type locality.

in the Periyar Tiger Reserve under the bark of a log; the general vegetation and overview of one of the collecting sites are shown in Fig. 5D.

Distribution

India (Kerala) (Sadasivan & Kripakaran 2022).

Vollenhovia mawrapensis Dhadwal, Rilta & Bharti, 2023
Fig. 6

Vollenhovia mawrapensis Dhadwal, Rilta & Bharti, 2023: 3. Type locality: India, Meghalaya, Mawrap [Holotype: PUAC, type series examined].

Worker measurements & indices (3 specimens, 1 colony, 1 locality)

CL 0.44–0.48, CW 0.40–0.44, CS 0.42–0.46, EL 0.11–0.12, ML 0.56–0.60, PEH 0.19–0.20, PEL 0.15–0.17, PEW 0.14–0.16, PPH 0.15–0.18, PPL 0.14–0.16, PPW 0.16–0.19, PW 0.32–0.34, SL 0.28–0.30. Indices: CL/CW 1.09–1.12, EL/CS 0.24–0.26, ML/CS 1.22–1.33, PEH/CS 0.43–0.45, PEL/CS 0.33–0.37, PEW/CS 0.33–0.35, PPH/CS 0.36–0.39, PPL/CS 0.30–0.35, PPW/CS 0.38–0.42, PW/CS 0.69–0.76, SL/CS 0.65–0.67.

Remarks

This species is the only one so far known from the Meghalaya region of Eastern India. According to Dhadwal *et al.* (2023), it is most similar to the Eastern Indian *V. taylori*, which is also similarly very small; however, it can be distinguished by having a shorter head (CL/CW: 1.09–1.12), mandibles with seven teeth instead of six, an elongate and rectangular subpetiolar process, mesopleuron and metapleuron transversely striate instead of coarsely punctate, petiole and postpetiole reticulate rugose instead of finely punctate, the dorsal surface of first gastral tergite more densely punctate and remaining gastral tergites with piligerous punctures instead of smooth and shiny, and the body less pilose, covered with fewer erect and suberect short hairs.

Distribution

India (Meghalaya) (Dhadwal *et al.* 2023).

Vollenhovia oblonga laevithorax Emery, 1889
Fig. 7

Vollenhovia laevithorax Emery, 1889: 501. Type locality: Myanmar, Tenasserim [Syntypes: MSNG; Images of CASENT 0904539 syntype worker examined].

Vollenhovia levithorax – Dalla Torre 1893: 61 (misspelling).

Vollenhovia oblonga laevithorax – Emery 1897: 560; subspecies of *Vollenhovia oblonga* (Smith, 1860).

Vollenhovia oblonga leviuscula var. *rufescens* – Emery 1901: 567 (misspelled as *leviuscula*).

Remarks

Vollenhovia oblonga laevithorax Emery, 1889 is considered a relatively larger subspecies compared to the nominal *V. oblonga oblonga* (Smith, 1860), having the mesosoma smooth and shiny with a few delicate, scattered punctures anteriorly, and with the mandibles having six teeth. This subspecies forms part of the *oblonga* complex which contains six other subspecies including the nominal *V. oblonga oblonga*, *V. oblonga alluaudi* Emery, 1894, *V. oblonga bandarensis* Forel, 1913, *V. oblonga dispar* Forel, 1910, *V. oblonga pedestris* (Smith, 1861), and *V. oblonga rufescens* Emery, 1894. The *oblonga* complex



Fig. 6. *Vollenhovia mawrapensis* Dhadwal, Rilta & Bharti, 2023, holotype worker from India (PUAC T710, photographer: Himender Bharti). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Forest trail to Mawrap, Meghalaya.

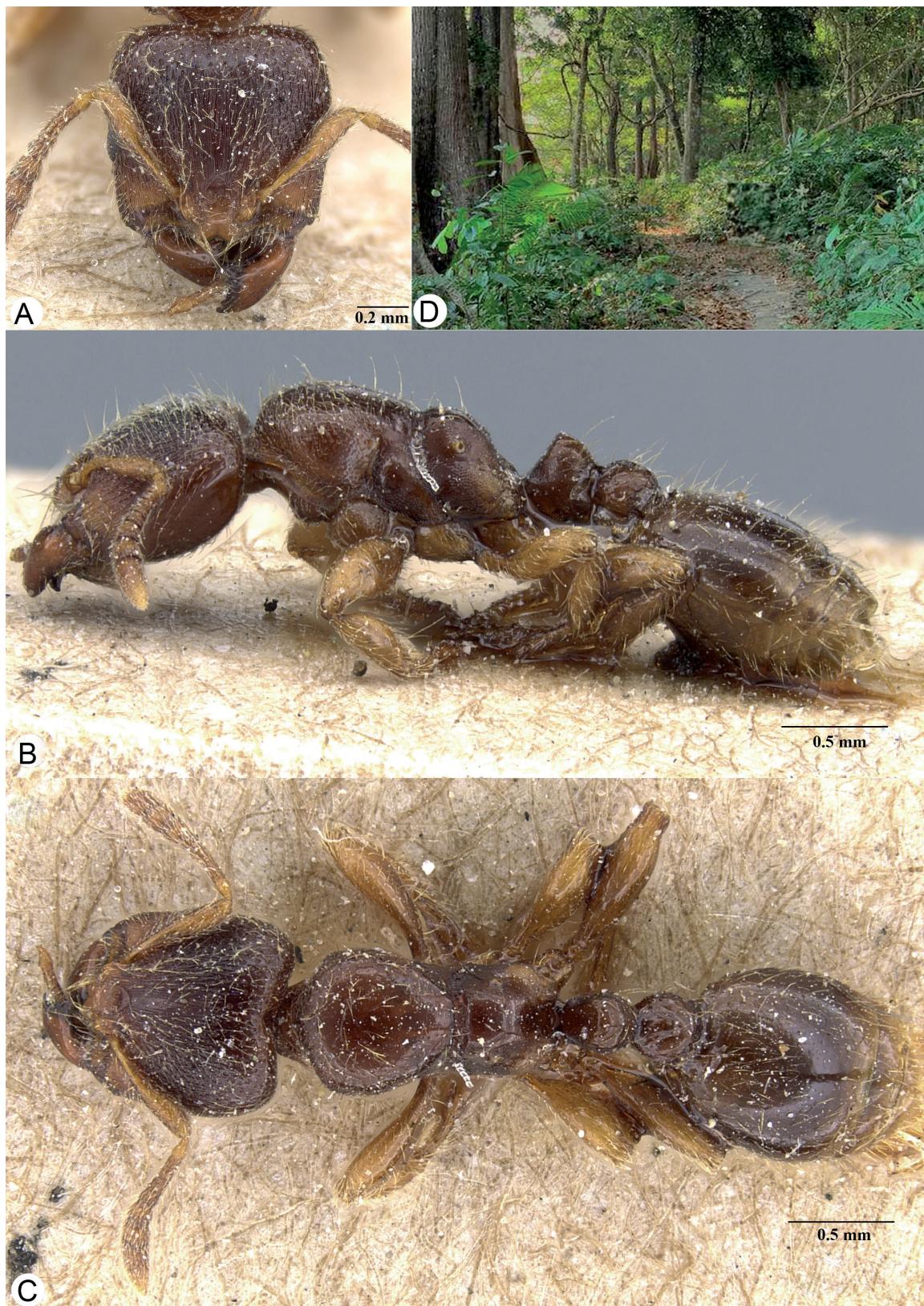


Fig. 7. *Vollenhovia oblonga laevithorax* Emery, 1889. Syntype worker from Myanmar (CASENT0904539, photographer: Zach Lieberman). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Forest trail on Andaman Islands, collection site.

is morphologically diverse and has a vast geographical range, being recorded from Pakistan to the Marshall Islands, the Solomon Islands, and New Caledonia (Wheeler 1927; Wilson 1959; Clouse 2007). Some of the subspecies exhibit characters suggesting that they may merit being raised to species status, with arguments for and against such changes already present in the literature, but the issue has never been resolved (see Bolton 2023).

In the study area, *V. oblonga laevithorax* has only been reported once from the Andaman and Nicobar Islands (Forel 1903). Mohanraj *et al.* (2010) carried out a comprehensive survey of ants on these islands (Fig. 5D) but could not find it again. The recent Pakistani record of *V. oblonga laevithorax* by Khudadad *et al.* (2021) is about 2000 km distant from any other record of *V. oblonga* (the closest region being Myanmar), which may be explained by insufficient sampling in northern India but also raises the possibility of a further separate taxon. Furthermore, it should be noted that at least the worker caste of *V. oblonga laevithorax* shows an overall similarity with species belonging to the *V. penetrans* complex from Southeastern Asia (Wang *et al.* 2022), which raises some doubts over the supposed co-occurrence of *V. oblonga laevithorax* and *V. penetrans* on the Andaman and Nicobar Islands (see Remarks under *V. penetrans*). However, *V. oblonga laevithorax* is very different from any other species of the region due to a combination of very extensive smooth areas (e.g., covering the whole promesonotum) and the deep metanotal impression.

Distribution

Borneo, India (Andaman and Nicobar Islands), Indonesia, Myanmar, Pakistan (Emery 1889, 1900; Wheeler 1919; Mohanraj *et al.* 2010; Khudadad *et al.* 2021).

Vollenhovia penetrans (Smith, 1857)

Fig. 8

Atta penetrans Smith, 1857: 77. Type locality: Malaysia, Borneo, Sarawak [Holotype OXUM; images of CASENT 0901383 holotype queen examined].

Aphaenogaster penetrans – Emery 1893: 104; first combination in *Aphaenogaster*.
Vollenhovia penetrans – Donisthorpe, 1932: 450; first combination in *Vollenhovia*.

Remarks

The only mention of *V. penetrans* in the region is that of an AntWeb specimen (CASENT0280819) verified by Bolton in 1976 (Bharti *et al.* 2016). This Indian specimen was collected from the Andaman Islands by G. Rogers and housed at NHMUK and agrees well with the holotype (Smith 1857). The species is unfortunately only known from the queen caste, which is characterized by a finely longitudinally striate head and mesosomal dorsum with oblong punctures. *Vollenhovia* taxonomy is almost entirely based on the worker caste, which makes the current lack of information on *V. penetrans* workers problematic. The worker caste is known in *V. brevicornis* (Emery, 1893) and *V. pertinax* (Smith, 1861) from Southeastern Asia, two species that are considered extremely similar to *V. penetrans* to the point of being considered potential synonyms (Wang *et al.* 2022). As mentioned before, known workers from the *V. penetrans* complex resemble *V. oblonga laevithorax* among the taxa treated in this study, while they differ from all the others by having a largely smooth area with sparse punctuation near the posterior margin of the head and an almost entirely smooth dorsal surface of the mesosoma and metasoma. It is therefore unclear whether *V. penetrans* and *V. oblonga laevithorax* records from the Andaman and Nicobar Islands may refer to a single species.

Distribution

Borneo, India (Andaman and Nicobar Islands), Indonesia, Malaysia (Smith 1857; Wang *et al.* 2022).

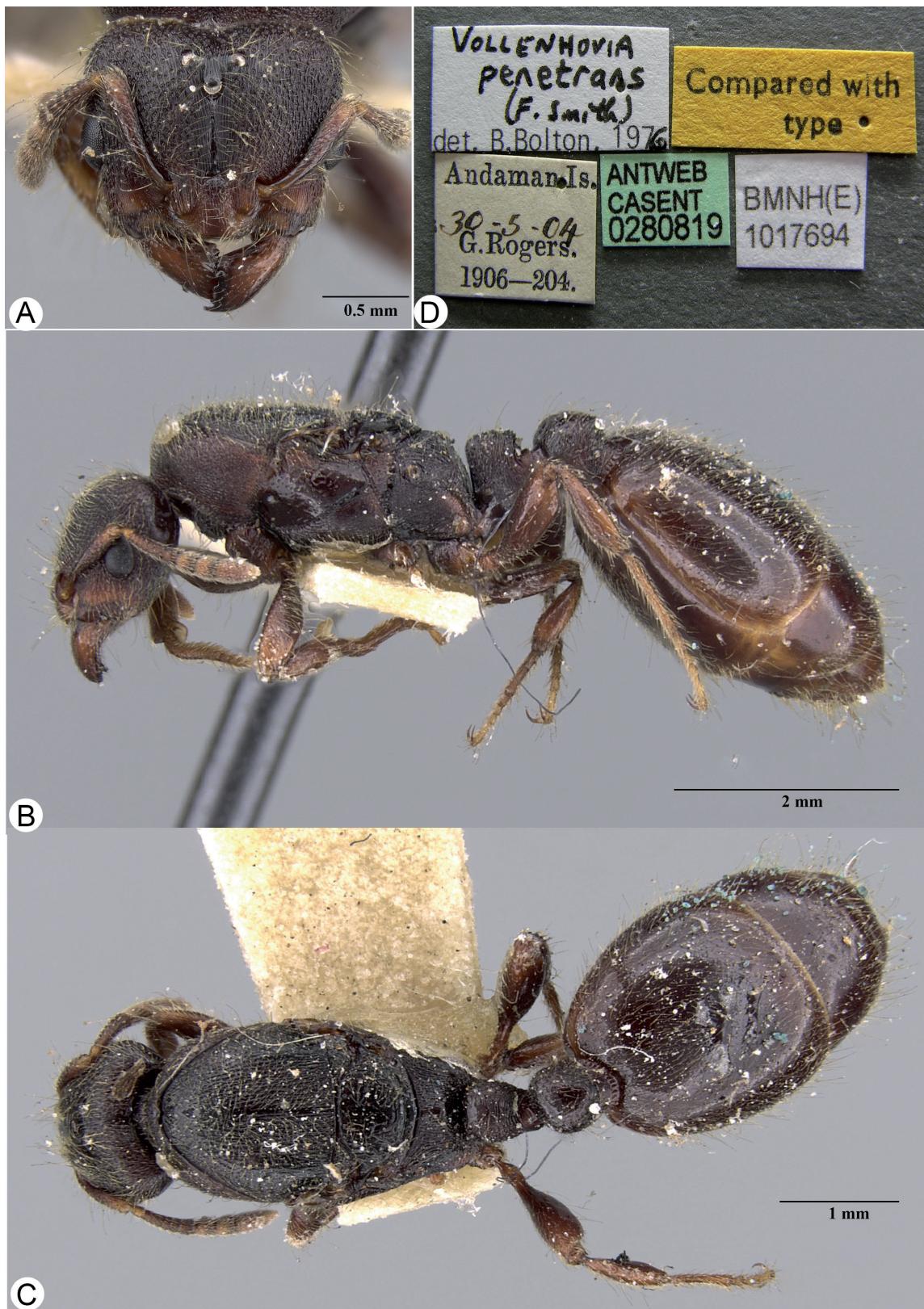


Fig. 8. *Vollenhovia penetrans* (Smith, 1857). Dealate queen from India (CASENT0280819, photographer: Shannon Hartman). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Data labels of the Indian specimen.

Vollenhovia pfeifferi Bharti, Dhadwal & Rilta, 2023
Fig. 9

Vollenhovia pfeifferi Bharti, Dhadwal & Rilta in Dhadwal *et al.*, 2023: 4. Type locality: Kerala, Parambikulam Tiger Reserve, Karimala [Holotype: PUAC, type series examined in Dhadwal *et al.* 2023].

Material examined

INDIA • 8 workers; Kerala, Periyar Tiger Reserve; 9°46' N, 77°14' E; alt. 1005 m; 10 Oct. 2011; hand picking; S.A. Akbar leg.; PUAC0018 to PUAC0025.

Worker measurements & indices (11 specimens, 2 colonies, 2 localities)

CL 0.56–0.70, CW 0.51–0.55, CS 0.53–0.62, EL 0.09–0.13, ML 0.60–0.76, PEH 0.22–0.33, PEL 0.16–0.22, PEW 0.18–0.21, PPH 0.19–0.24, PPL 0.16–0.23, PPW 0.21–0.25, PW 0.37–0.43, SL 0.34–0.40. Indices: CL/CW 1.10–1.30, EL/CS 0.16–0.22, ML/CS 1.00–1.36, PEH/CS 0.39–0.63, PEL/CS 0.27–0.39, PEW/CS 0.31–0.37, PPH/CS 0.32–0.43, PPL/CS 0.27–0.41, PPW/CS 0.35–0.45, PW/CS 0.64–0.78, SL/CS 0.61–0.72.

Remarks

Due to its dentiform propodeal spines, *Vollenhovia pfeifferi* appears unique among its congeners in the region and thus is easily recognizable (Dhadwal *et al.* 2023). We report a second locality for this recently described taxon of the Western Ghats, based on samples collected in the Periyar Tiger Reserve.

Distribution

India (Kerala) (Dhadwal *et al.* 2023).

Vollenhovia taylori Rilta, Dhadwal & Bharti, 2023
Fig. 10

Vollenhovia taylori Rilta, Dhadwal & Bharti in Dhadwal *et al.*, 2023: 5. Type locality: West Bengal, Chapramari Wild Life Sanctuary [Holotype: PUAC, holotype examined in Dhadwal *et al.* 2023].

Worker measurements & indices (1 specimen, 1 colony, 1 locality)

CL 0.50, CW 0.42, CS 0.46, EL 0.10, ML 0.54, PEH 0.22, PEL 0.20, PEW 0.16, PPH 0.18, PPL 0.14, PPW 0.2, PW 0.34, SL 0.30. Indices: CL/CW 1.19, EL/CS 0.22, ML/CS 1.17, PEH/CS 0.48, PEL/CS 0.44, PEW/CS 0.35, PPH/CS 0.39, PPL/CS 0.30, PPW/CS 0.43, PW/CS 0.74, SL/CS 0.65.

Remarks

This Eastern Indian species was unfortunately described from a single specimen (Dhadwal *et al.* 2023), and the discovery of further material appears crucial to define its intraspecific variation. However, the holotype specimen of *V. taylori* bears some unique characteristics, including the relatively enlarged nodes (PEW/CS: 0.35; PPW/CS: 0.43) and coarse sculpture and large punctuations over the dorsal surface of the body. The most similar taxon is *V. mawrapensis*, the two being both from Eastern India and very small in size, but *V. mawrapensis* is distinguishable based on the number of mandibular teeth, head shape, sculpture and pilosity (see Remarks under *V. mawrapensis*).

Vollenhovia terayamai Rilta, Dhadwal & Bharti, 2023
Fig. 11

Vollenhovia terayamai Rilta, Dhadwal & Bharti in Dhadwal *et al.*, 2023: 5. Type locality: West Bengal, Chapramari Wild Life Sanctuary [Holotype: PUAC, type series examined in Dhadwal *et al.* 2023].

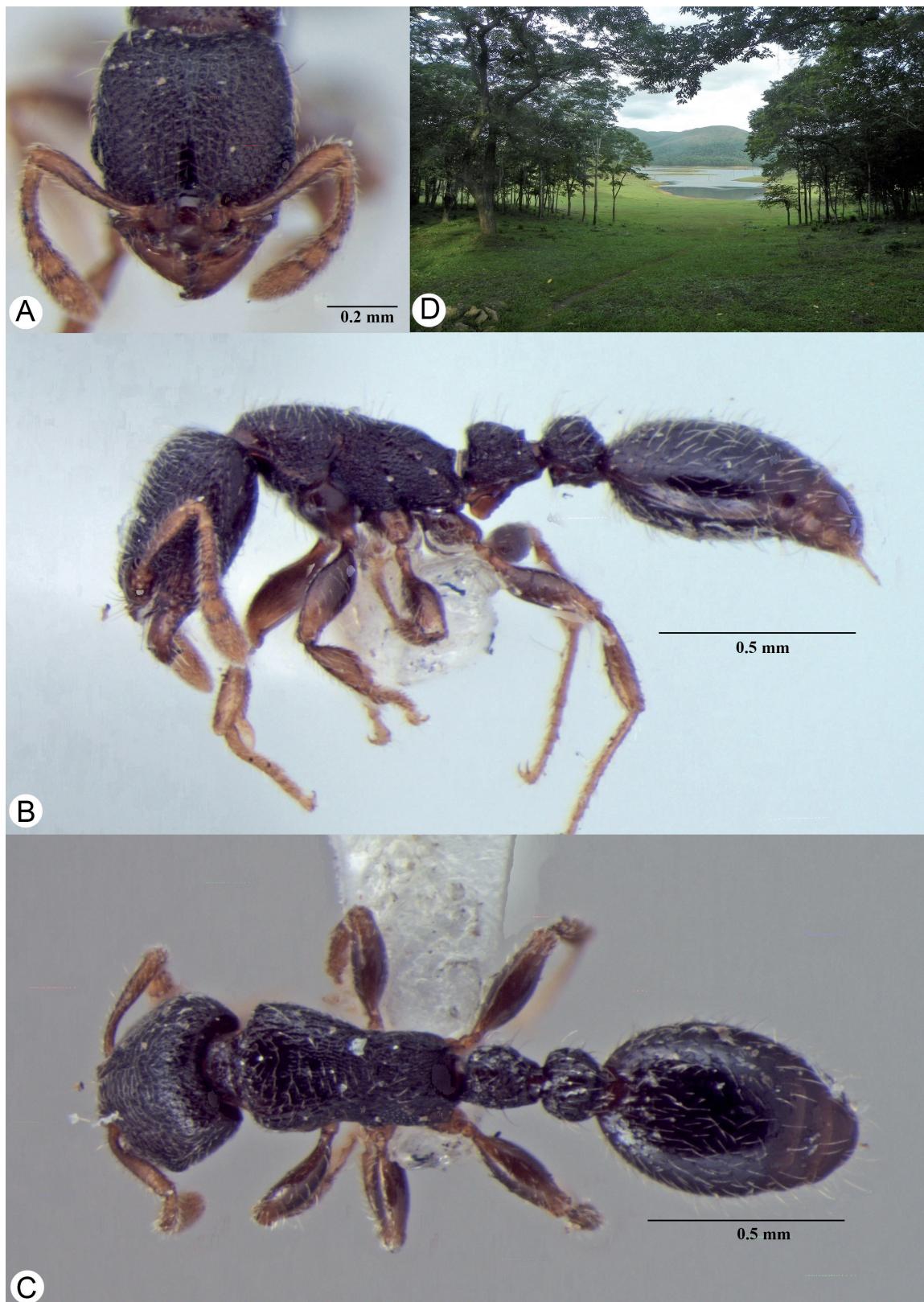


Fig. 9. *Vollenhovia pfeifferi* Bharti, Dhadwal & Rilta, 2023, worker from India (PUAC0018, photographer: Shahid Ali Akbar). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Periyar Tiger Reserve, Kerala, collection site.

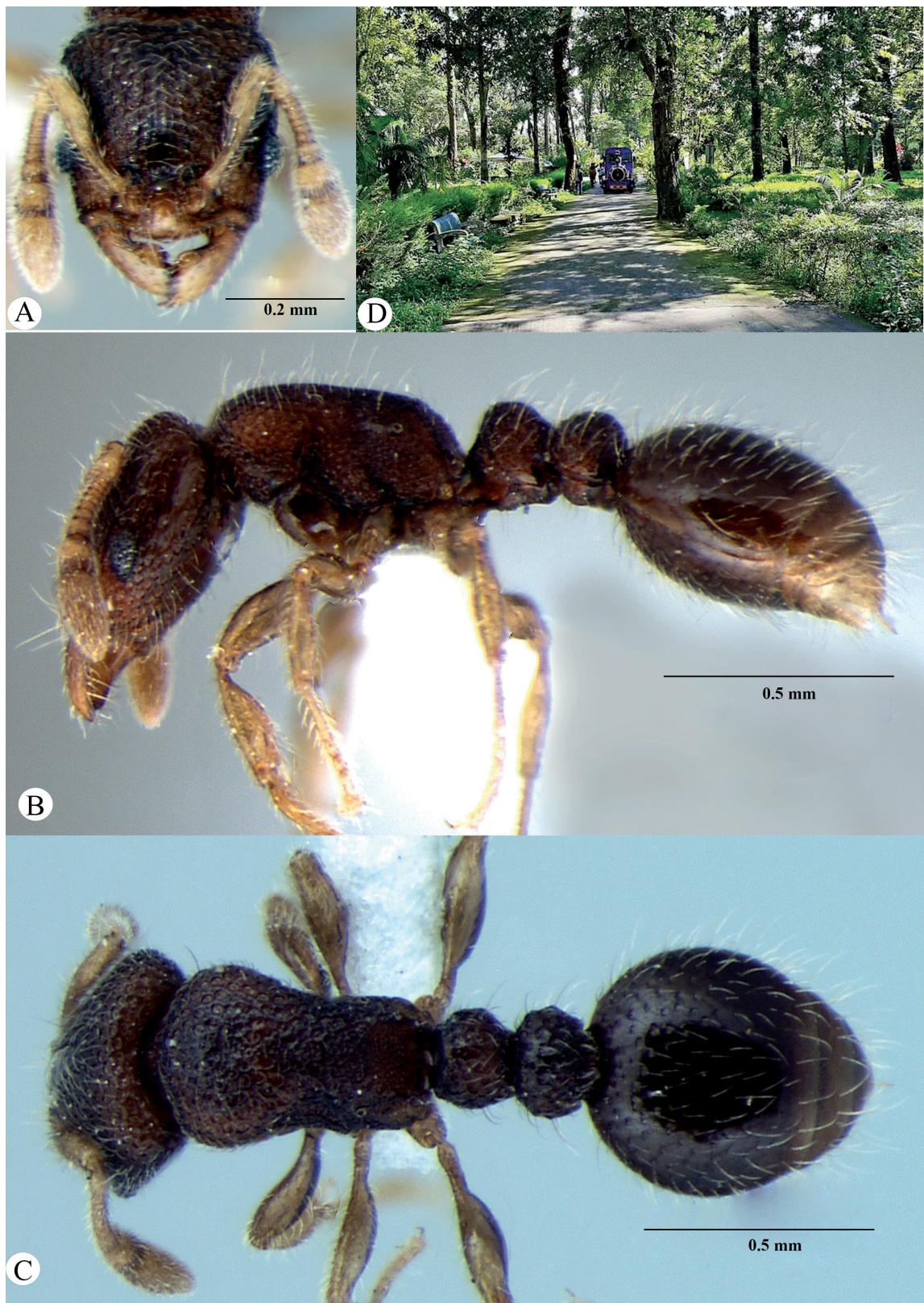


Fig. 10. *Vollenhovia taylori* Rilta, Dhadwal & Bharti, 2023, holotype worker from India (PUAC T728, photographer: Himender Bharti). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Type locality.



Fig. 11. *Vollenhovia terayamai* Rilta, Dhadwal & Bharti, 2023, holotype worker from India (PUAC T731, photographer: Himender Bharti). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Entrance to Chapramari Wild Life Sanctuary, West Bengal.

Worker measurements & indices (2 specimens, 1 colony, 1 locality)

CL 0.54–0.58, CW 0.46–0.50, CS 0.50–0.54, EL 0.12–0.14, ML 0.66–0.68, PEH 0.28–0.30, PEL 0.24–0.26, PEW 0.16–0.18, PPH 0.28–0.30, PPL 0.18–0.20, PPW 0.20–0.22, PW 0.36–0.40, SL 0.35–0.36. Indices: CL/CW 1.16–1.17, EL/CS 0.24–0.26, ML/CS 1.26–1.32, PEH/CS 0.55–0.56, PEL/CS 0.48–0.48, PEW/CS 0.32–0.33, PPH/CS 0.55–0.56, PPL/CS 0.36–0.37, PPW/CS 0.40–0.41, PW/CS 0.72–0.74, SL/CS 0.67–0.71.

Remarks

This last Eastern Indian species was unfortunately described based on two specimens only (Dhadwal *et al.* 2023) so the discovery of further material once again appears crucial to appreciate its intraspecific variation. *Vollenhovia terayamai* differs from the other Eastern Indian taxa by having a wide smooth band in the front and on the promesonotum, as well as a largely smooth postpetiole dorsum, in addition to larger body size. It shares some affinities with *V. yasmeenae* sp. nov. but differs by having a broad smooth median band on the head and a finer punctate sculpture on the sides of the petiole.

Vollenhovia yasmeenae sp. nov.

urn:lsid:zoobank.org:act:B34A100E-9543-45E4-BFAF-86D662F0BE33

Fig. 12

Diagnosis

Among the species of the region, *V. yasmeenae* sp. nov. can be separated based on some unique qualitative morphological features. It can be immediately distinguished from *V. escherichi* by its dark brown to blackish pigmentation as opposed to pale yellow, and from *V. oblonga laevithorax* by its sculptured as opposed to smooth mesosoma, and from *V. pfeifferi* by the absence of dentiform propodeal spines. Unlike *V. keralensis* and *V. karimalaensis*, its anterior clypeal margin is emarginate and has no median tooth, while the presence of a smooth area on the dorsum of the mesosoma separates it from *V. gastropunctata*, *V. mawrapensis*, and *V. taylori*. Finally, it differs from *V. terayamai* in having a much reduced smooth median area on the head and lacking the fine punctate sculpture on the sides of the petiole that characterizes the latter. The dorsal promesonotal sculpture appears relatively well-distinct and with a clear longitudinal orientation.

Etymology

The specific epithet is a Latinized noun in genitive, derived from the first name of Jammu and Kashmir's first female Director of Colleges, Dr Yasmeen Ashai, for her service to higher education in the region.

Type material

Holotype

INDIA • worker; Kerala, Silent Valley National Park; 11°09' N, 76°44' E; alt. 900 m; 25 Sep. 2011; Winkler extraction method; S.A. Akbar leg.; PUAC0038.

Paratypes

INDIA • 3 workers; same collection data as for holotype: PUAC0039 to PUAC0041 • 3 workers; Kerala, Silent Valley National Park, near Badriya Juma Masjid, Mukkali; 11°06' N, 76°53' E; alt. 700 m; 20 Dec. 2013; Winkler extraction method; S.A. Akbar leg.; PUAC0042 to PUAC0044.

Worker measurements & indices (7 specimens, 2 colonies, 2 localities)

CL 0.61–0.65 (0.63), CW 0.54–0.57 (0.55), CS 0.57–0.6 (0.59), EL 0.14–0.16 (0.15), ML 0.80–0.82 (0.81), PEH 0.34–0.36 (0.35), PEL 0.16–0.19 (0.18), PEW 0.19–0.20 (0.19), PPH 0.20–0.23 (0.22), PPL 0.17–0.19 (0.18), PPW 0.23–0.24 (0.24), PW 0.38–0.41 (0.39), SL 0.38–0.39 (0.38). Indices: CL/

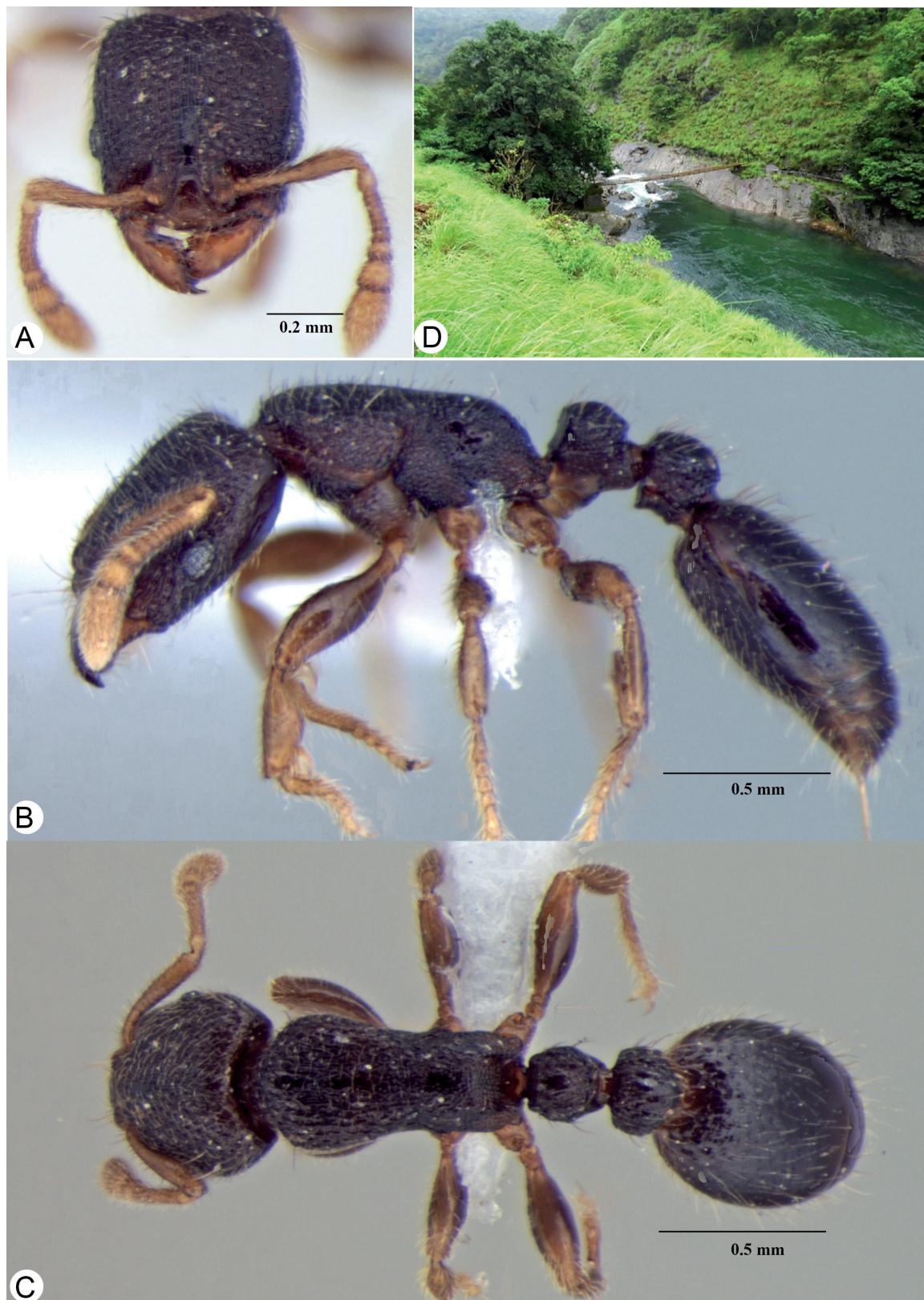


Fig. 12. *Vollenhovia yasmeenae* sp. nov., holotype worker from India (PUAC0038, photographer: Shahid Ali Akbar). **A.** Head, full face view. **B.** Habitus, lateral view. **C.** Habitus, dorsal view. **D.** Type locality of the new species.

CW 1.09–1.21 (1.14), EL/CS 0.23–0.27 (0.25), ML/CS 1.34–1.39 (1.37), PEH/CS 0.57–0.61 (0.59), PEL/CS 0.28–0.32 (0.30), PEW/CS 0.32–0.35 (0.33), PPH/CS 0.35–0.39 (0.37), PPL/CS 0.28–0.32 (0.30), PPW/CS 0.39–0.42 (0.40), PW/CS 0.64–0.71 (0.67), SL/CS 0.63–0.66 (0.65).

Description

Head in full-face view, subrectangular or subquadrate (CL/CW 1.09–1.21), posterior margin with a median concavity; posterolateral corner of head roundly convex, lateral margin broadly convex; clypeus emarginate; anterior clypeal margin laminate; mandible broad, masticatory margin consisting of 5–6 well-defined teeth, apical tooth strongly falcate; antenna 12-segmented; antennal scape short reaches about two-thirds the head length (SL/CS 0.63–0.66); eye prominent, protruding, placed well below mid-line of head (EL/CS 0.23–0.27).

In lateral view, dorsal outline of mesosoma flat; mesopleuron demarcated from lateral face of pronotum and propodeum by distinct sutures; posterior face of propodeum rounded and smooth; viewed dorsally, pronotal humeri rounded and smooth, and wider than the rest of the mesosoma; posterior propodeal margin convex; promesonotal suture absent; metanotal groove visible as a slight disruption in the surface sculpture, mesonotum and propodeum completely fused and lateral margins converging evenly to the propodeal declivity, no propodeal spines.

Petiole in lateral view, subquadrate with longer anterior face and shorter posterior face, dorsum concave; subpetiolar process well developed, subquadrate in shape (almost as long and as high, 0.09 mm); postpetiole dorsally rounded, much wider than long; sub-postpetiolar process pointed, peg-like, leaning anteriorly; gaster elliptical.

Surface sculpture throughout the body punctate-reticulate; punctures on head coarse; middle area of the head with a small smooth and unsculptured band in the middle of the head with few longitudinal striations running posteriorly, almost reaching the posterior margin; mandible smooth and shiny, with a few punctures present along masticatory margin; clypeus colliculate; mesosoma punctate-reticulate with longitudinally striations on dorsum; propodeal declivity colliculate; petiole and postpetiole sides minutely colliculate, dorsum mostly smooth with few punctures; gaster mostly smooth and shiny with fine punctures on first segment.

Whole body covered with abundant long, sub-erect, whitish pilosity.

Body black, appendages ferruginous to dark brownish.

Distribution

India (Kerala).

Ecology

Specimens were collected from the Silent Valley National Park (Fig. 12D), a primary tropical rainforest in Kerala, using the Winkler extraction method. Leaf litter samples of approximately 2 cm thickness were taken near tree trunks at two different locations in the National Park, one in the buffer zone (Mukkali) and one in the core region (Sairandhri). The species appears to be locally rare and may have a restricted distribution, although further research extending to other areas is required.

Remarks

Vollenhovia yasmeenae sp. nov. is the fourth species of the genus to be described from the Western Ghats region, further stressing its importance as a biodiversity hotspot for ants.

Worker-based key to the species of *Vollenhovia* Mayr, 1865 from India and Sri Lanka

1. Light colored, yellowish-brown with coarse alveolate head sculpture (Fig. 13A–B); small species (CW < 0.4 mm), only known from Sri Lanka (Fig. 13A) *V. escherichi* Forel, 1911
- Dark brown to black (Fig. 13C–D), India 2
2. Anterior clypeal margin convex, forming a single median tooth (Fig. 13E) 3
 - Anterior clypeal margin emarginate with no median tooth (Fig. 13F) 4
3. Body generally foveolate; mandible with 8 teeth; subpetiolar process lamellar wall distinctly longer than high (Fig. 13G–I) *V. keralensis* Kripakaran & Sadasivan, 2022
 - Body generally punctate; mandible with 7 teeth; subpetiolar process elongate and sickle-shaped (Fig. 13H–J) *V. karimalaensis* Dhadwal *et al.*, 2023
4. Mesosoma smooth and shiny, with few delicate, scattered punctures anteriorly, very evident metanotal depression (Fig. 13K) *V. oblonga laevithorax* Emery, 1889 or a member of the *V. penetrans* complex sensu Wang *et al.* (2022)
 - Mesosoma strongly sculptured throughout (Fig. 13L) 5
5. Propodeal spines dentiform; declivity carinate (Fig. 13M) *V. pfeifferi* Bharti *et al.*, 2023
 - No propodeal spines; declivity smoothly rounded (Fig. 13N) 6
6. Mesosoma dorsum with a smooth and shiny central area (Fig. 14A) 7
 - Mesosoma dorsum dorsally entirely sculptured, with no central smooth region (Fig. 14B) 8
7. Head with a broad smooth median band (Fig. 14C), postpetiole narrower and dorsally smooth, Eastern India (Fig. 14E) *V. terayamai* Rilta *et al.*, 2023
 - Entirely sculptured (Fig. 14D), postpetiole wider and dorsally sculptured, Western Ghats (Fig. 14F) *V. yasmeenae* sp. nov.
8. Body size small (CL: 0.44–0.50; CW: 0.40–0.44; ML: 0.54–0.60) 9
 - Body size larger (CL: 0.56; CW: 0.49; ML: 0.73–0.75)
 - *V. gastropunctata* Bharti & Kumar, 2013
9. Mandible with 7 teeth, mesosoma dorsum more finely and densely sculptured, mesopleuron transversely striate (Fig. 14G–H) *V. mawrapensis* Dhadwal *et al.*, 2023
 - Mandible with 6 teeth, head, and mesosoma characterized by a coarse punctate sculpture, mesopleuron coarsely punctate (Fig. 14I–J) *V. taylori* Rilta *et al.*, 2023

Fig. 13 (see next page). Characters used in the identification key. **A–B**. Yellowish-brown (syntype worker of *V. escherichi* Forel, 1911 from Sri Lanka: CASENT0908656, photographer: Will Ericson). **C–D**. Dark brown to black (worker of *V. keralensis* Kripakaran & Sadasivan, 2022). **E**. Convex anterior clypeal margin with a single median tooth (worker of *V. keralensis*). **F**. Emarginate anterior clypeal margin with no median tooth (holotype worker of *V. gastropunctata* Bharti & Kumar, 2013). **G, I**. Generally foveolate body with mandible having 8 teeth (worker of *V. keralensis*). **H, J**. Generally punctate body with mandible having 7 teeth (H. Worker of *V. piroskae* Forel, 1912; CASENT0159915, photographer: Michele Esposito. J. Holotype worker of *V. karimalaensis*). **K**. Mesosoma smooth and shiny (syntype worker of *V. oblonga laevithorax*, CASENT0904539). **L**. Mesosoma strongly sculptured throughout (holotype worker of *V. taylori*). **M**. Declivity carinate, dentiform (worker of *V. pfeifferi*). **N**. No propodeal spines; declivity smoothly rounded (holotype worker of *V. yasmeenae* sp. nov.).

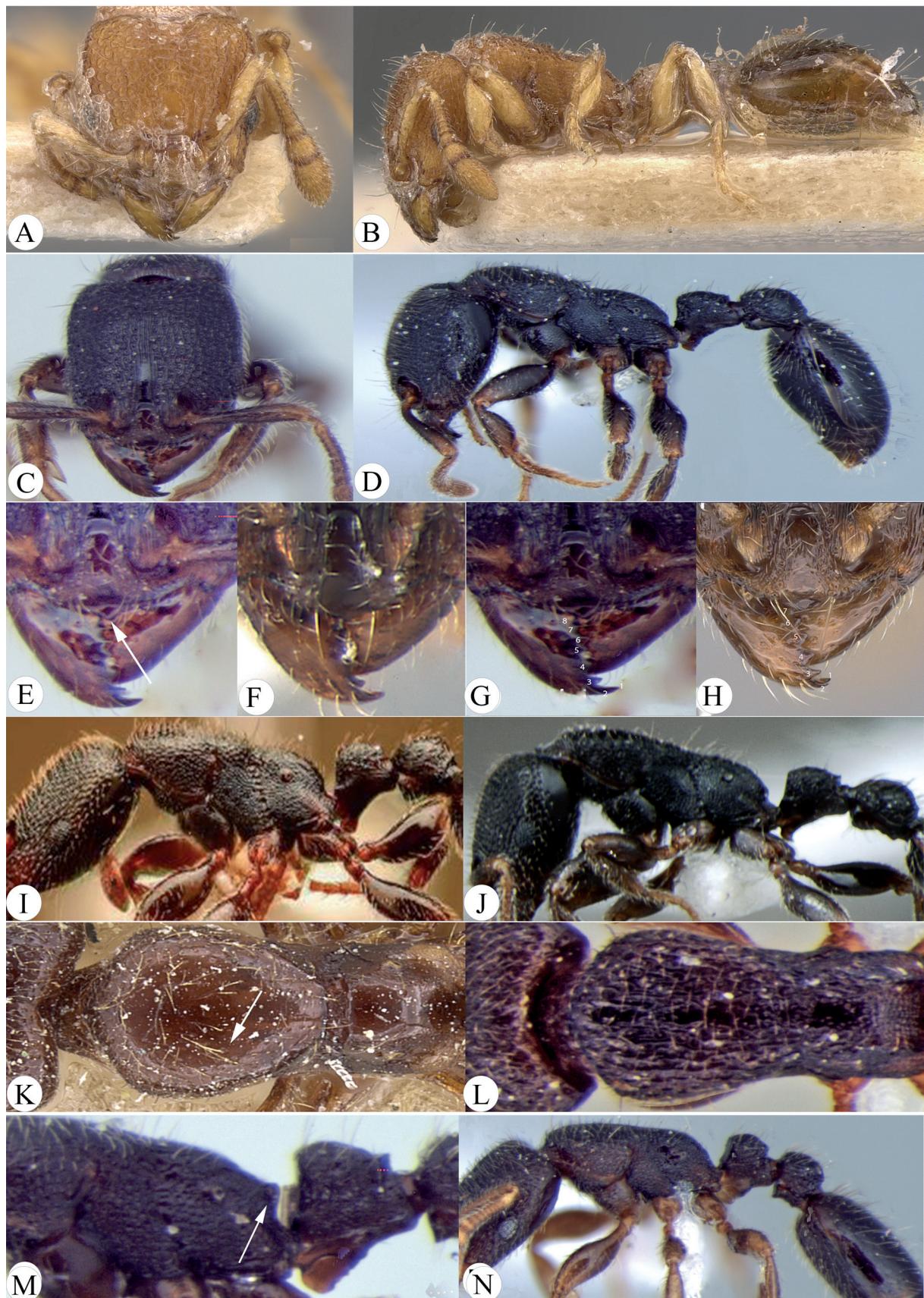




Fig. 14. Characters used in the identification key. **A.** Mesosoma dorsum with a smooth and shiny central area (holotype worker of *V. terayamai*). **B.** Mesosoma dorsum dorsally entirely sculptured (holotype worker of *V. taylori*). **C, E.** Head with broad median smooth band with postpetiole narrower and dorsally smooth (holotype worker of *V. terayamai*). **D, F.** Head entirely sculptured with wider postpetiole, dorsally sculptured (holotype worker of *V. yasmeenae* sp. nov.). **G–H.** Mandible with 7 teeth, mesopleuron transversely striate (holotype worker of *V. mawrapensis*). **I–J.** Mandible with 6 teeth, mesopleuron coarsely punctuate (holotype worker of *V. taylori*).

Discussion

Up to half of the species of *Vollenhovia* are restricted to small ranges in Southeastern Asia. Only one species, *V. emeryi*, originally from Southeastern Asia has established itself in the New World and is now spreading in its exotic range (Wetterer *et al.* 2015), while the presence of *V. piroskae* Forel, 1912 in the Seychelles may be anthropogenic (Guénard *et al.* 2017). As the genus is absent from the Afrotropical

and Malagasy regions, Sadasivan & Kripakaran (2022) suggested a possible westward dispersal of the genus from the Australasian and Oceania bioregions aided by cyclones of the Bay of Bengal and the equatorial currents of the Indian Ocean, with dispersal via rafting being facilitated by nesting in tree branches and trunks. However, no phylogenetic and phylogeographic reconstruction of the history of the genus has yet been attempted.

The taxonomy of Asian species has been treated in various regional works before this study, focusing on mainland China (Wu & Wang 1995), Japan (Terayama & Kinomura 1997), Taiwan (Terayama 1999, 2009), Singapore (Wang *et al.* 2021), and India (Bharti & Kumar 2013; Sadasivan & Kripakaran 2022; Dhadwal *et al.* 2023). However, a revision conducted at a broader geographic scale still appears necessary to assess the taxonomy of certain species, such as those from the *oblonga* and *penetrans* complexes mentioned in this study.

Species known from the Western Ghats and the biogeographically related Sri Lanka all credibly appear to be endemic to that region (e.g., Pathirana 1980; Briggs 2003; Bossuyt 2004; Sudasinghe *et al.* 2021). Interestingly, *V. gastropunctata*, currently considered to be an Indian endemic, is known from Himachal Pradesh State that borders the Pakistani province of Mansehra, which is the only area known to be inhabited by *Vollenhovia* in the country and the westernmost distribution region of the genus at the global scale (Khudadad *et al.* 2021). The species recently described from near the Bangladesh borders may likely occur inside Bangladesh as well, where the genus *Vollenhovia* has never been recorded yet. Finally, the two species recorded from the Andaman and Nicobar Islands are at the westernmost limit of their distribution, which extends throughout large parts of Southeastern Asia and even Oceania in the case of *V. oblonga*. However, given their problematic taxonomy, it is on the one hand possible that the queen-based record of *V. penetrans* and the worker-based record of *V. oblonga laevithorax* from the islands refer to a single species, and on the other hand that the current concepts of *V. oblonga* and *V. penetrans* consist of multiple distinct species.

Despite inhabiting areas with differing environments, the known habitats of the Indian and Sri Lankan species accord well with previous accounts of the genus from other regions, inhabiting forest habitats and nesting in rotting twigs, wood fragments, and logs, and in spaces under the bark of logs (Eguchi *et al.* 2011). The cryptic nesting habits of species of *Vollenhovia* presently represent one of the most challenging aspects of their study. Insufficient sampling across vast regions of India, paired with the difficulty of detecting colonies of *Vollenhovia* during field surveys, still likely prevents a full understanding of the true diversity of the genus in the region and could contribute to the disjunct distributional pattern observed in the country. It also hinders a full understanding of the intraspecific variation of the species of the region since most species are currently known from the type series. Much more awaits to be uncovered on the biology, behavior, and systematics of this unique but poorly studied ant genus in India.

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Supplementary material

Supp. file 1. Morphometric data of species of *Vollenhovia* Mayr, 1865 from India.

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