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Cover: A female Javan Leopard *Panthera pardus melas* in rehabilitation phase at Cikananga Wildlife Center. © Yayasan Cikananga Konservasi Terpadu.

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ARTICLE

First record of *Proceratium* Roger, 1863, *Zasphinctus* Wheeler, 1918, and *Vollenhovia* Mayr, 1865 (Hymenoptera: Formicidae) from the Western Ghats of peninsular India, description of three new species, and implications for Indian biogeography

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Abstract: Three new ant species from the genera *Proceratium* Roger, 1863, *Zasphinctus* Wheeler, 1918, and *Vollenhovia* Mayr, 1865 are described from the Western Ghats of southern India. This is the first report of *Proceratium* and *Zasphinctus* from peninsular India and the first record of *Vollenhovia* from the Western Ghats mountain range proper. *Proceratium gibbosum* sp. nov. is described from Periyar Tiger Reserve in Kerala, being the first record of the *stictum* species group from the Indian subcontinent; it differs from other members of the *stictum* group by the mesonotum bearing a prominent rounded dorsal hump (tumulus) and petiole devoid of ventral tooth. The first record of the genus *Zasphinctus* Wheeler, 1918 from the Indian region is also presented here, with a description of a new species. *Zasphinctus sahyadriensis* sp. nov. differs from all known Afrotropical and Asian *Zasphinctus* by a combination of characters including clypeal area with single median tooth, occipital margin being regular in outline, and head sculpture sparsely punctate. The occurrence of the genus *Vollenhovia* Mayr, 1865 is confirmed from peninsular India, with the description of the female castes of *Vollenhovia keralensis* sp. nov. We provide ecological notes on these new taxa. In addition, separate identification keys based on the worker caste are also presented to Indo-Malayan species of *Proceratium*, Afrotropical-Indomalayan species of *Zasphinctus*, and *Vollenhovia* of the Indian subcontinent. The biogeographical implications of the presence of these three genera are also discussed in relation to plate tectonics of the Indian subcontinent.

Keywords: Agasthyamalais, ant taxonomy, Cretaceous, Dorylinae, Gondwana, Kerala, Myrmicinae, Paleogene, Proceratiinae, Tectonics.

Abbreviations: DSLR—Digital SLR | NCBS—National Centre for Biological Sciences | SEM—Scanning electron microscope | TARG—TNHS Ant Research Group | TNHS—Travancore Nature History Society | ZSI—Zoological Survey of India.

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Author contributions: KS and MK together did the field-work and photography. KS wrote the manuscript and MK gave his suggestions.

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INTRODUCTION

The Western Ghats complex is one of the world's major biodiversity hotspots (Myers et al. 2000). Lying on the western edge of the Indian peninsula, this mountain chain runs for over 1,600 km (8–21^0 N), with a single major break– the Palghat gap (Subramanyam & Nayar 1974). Although the region houses exceptional biodiversity and endemism especially for invertebrates, the speciation and biogeographic processes are not well known (Joshi & Karanth 2013). As per Sheela et al. (2020), there are currently 455 species of ants including 123 endemics in 75 genera in the Western Ghats. Since Bingham (1903), many new species were reported in the region from few isolated studies, including range extensions for some genera. But, there has not been any comprehensive work on ants of the Western Ghats, making it a relatively less explored region (Sheela et al. 2020). We came across three new generic records from the region—*Proceratium* Roger, 1863, *Zasphinctus* Wheeler, 1918, and *Vollenhovia* Mayr, 1865—in studies on ants in southern Western Ghats of the Kerala state, during the last decade.

Ants of the genus *Proceratium* are cryptic, hypogaeic (subterranean) in habits and nest in rotting wood, leaf litter, topsoil, and below stones as far as known (Brown 1974; Urbani & De Andrade 2003; Staab et al. 2018). The genus has a global distribution, and most species are rarely collected due to their cryptobiotic lifestyle (Urbani & De Andrade 2003). Currently, 86 extant and six fossil species are known (Urbani & De Andrade 2003; Bolton 2021). The natural history of this genus remains mostly unknown, with a few fragmentary reports based on observations of a small number of species (Garcia et al. 2015). The genus was recorded for the first time in India with the description of *P. williamsi* Tiwari, 2000, from East Khasi Hills in Meghalaya (Mathew & Tiwari 2000). Up to this study, it was the only known species from the country (AntWeb 2021; Bharti et al. 2016).

Zasphinctus is a genus of subterranean doryline ants with Afrotropical, Indomalayan, and Australasian distribution. Currently, 23 valid species of this genus have been described, with most species found in the Australasian region. The only species recorded from mainland Asia was *Z. siamensis* (Jaitrong, 2016) from Thailand, initially described in the genus *Sphinctomyrmex*. Until now, no species of *Zasphinctus* were reported from the Indian subcontinent (Bharti et al. 2016; Sheela et al. 2020; AntWeb 2021).

Vollenhovia are myrmicine ants belonging to the tribe Crematogastrini Forel 1893 (Ward et al. 2015). These are small to moderate-sized monomorphic ants (Bolton 2003) and some of them are social parasites (Terayama & Kinomura 1997). Globally, currently 59 extant species, 18 subspecies, and three fossil species are recognized (Bolton 2021). The genus is distributed in Australasia, Indomalaya, Malagasy, Oceania, and Palearctic biogeographic regions. It is found in Seychelles in the Malagasy region, but is curiously absent from Madagascar, Reunion, Mauritius, and Africa (Fisher 1996; AntWeb 2021). In 2013, *V. gastropuncta* Bharti & Kumar, 2013 was described from Himachal Pradesh in India thereby extending the range of this genus to the western Himalaya. Even though the presence of the genus *Vollenhovia* is reported from the adjacent Biligiri Rangaswamy Temple Wildlife Sanctuary, to the east of Nilgiris, the taxon was undescribed (Rajan et al. 2006). Presently, there are no confirmed records of *Vollenhovia* from the Western Ghats mountain range proper (Sheela et al. 2020; AntWeb 2021).

We describe here one new species from each of these genera. *Proceratium* is reported here from the tropical evergreen forests of Periyar Tiger Reserve of Kerala, *Zasphinctus* from a mixed evergreen forest of Ponmudi hills from Agasthyamalai, and *Vollenhovia* from the primary evergreen and mixed forests of Periyar and Agasthyamalai. We also provide taxonomic keys based on the worker caste of Indo-Malayan species of *Proceratium* (modified from Urbani & De Andrade (2003)); Afrotropical-Indomalayan species of *Zasphinctus* (modified from Garcia et al. (2017)); and *Vollenhovia* of the Indian subcontinent.

METHODS AND TERMINOLOGY

The two study locations were Ponmudi hills in Agasthyamalai, Thiruvananthapuram District and Periyar Tiger Reserve, Idukki District, both in the Western Ghats of Kerala State of southern India (Image 1). Ants were collected from tray-sifted leaf litter samples and preserved in 1.5 ml plastic vials containing absolute ethanol. Morphological characters were studied and measurements taken with the help of a HEADZ Model HD81 stereomicroscope. Photographs were taken with a Canon 7D Digital SLR and MPE 65 f 2.8 1–5x Lens. Photographs of whole ants and surface sculpturing of parts were obtained using a FEI Quanta 200 scanning electron microscope (SEM). The holotypes were photographed with a DSLR camera and paratypes were subjected to electron microscopy. The morphological terminology follows Garcia et al. (2015)

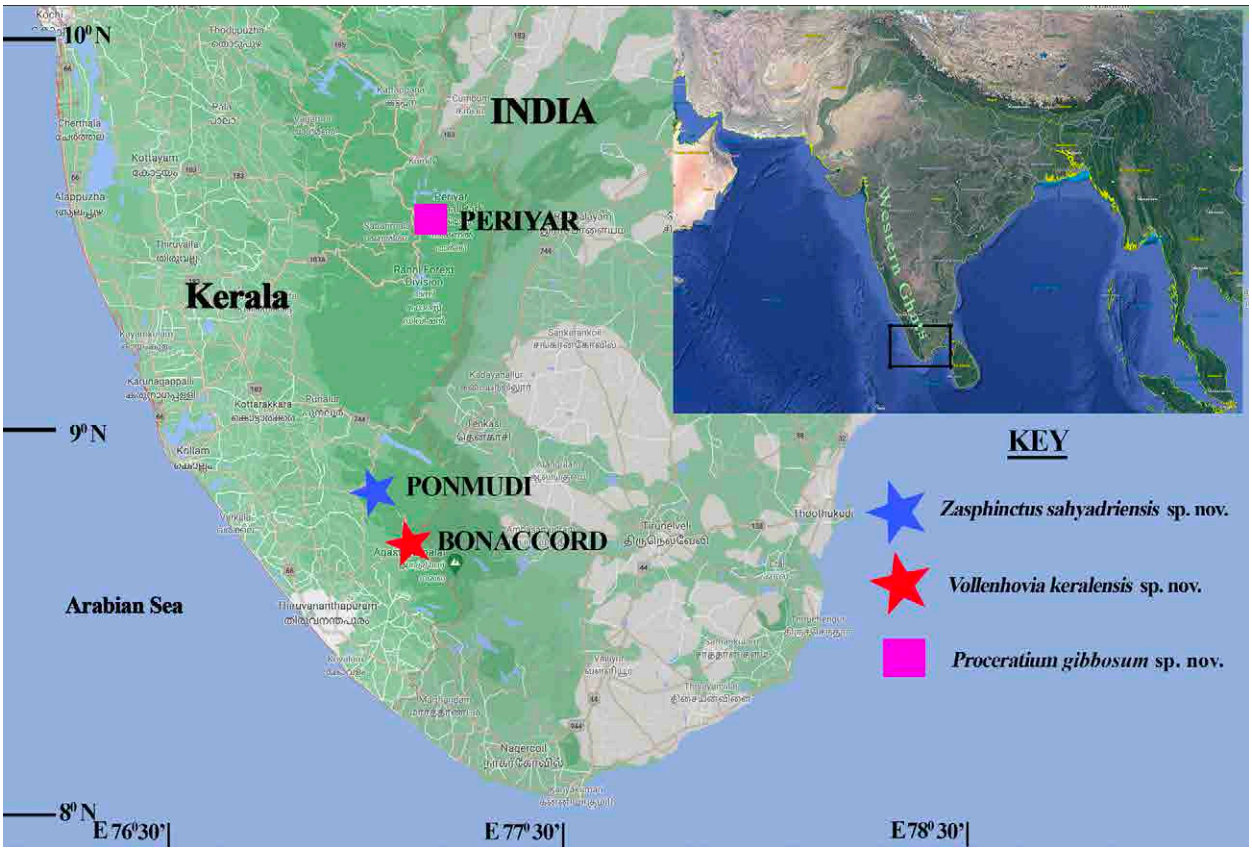

Image 1. Type localities of *Proceratium gibbosum* sp. nov., *Zasphinctus sahyadriensis* sp. nov., and *Vollenhovia keralensis* sp. nov. in southern Western Ghats, India, based on GoogleEarth. © Google 2021.

for *Proceratium* and Borowiec (2016) for *Zasphinctus*. They use certain terms that are specific to these taxa in their descriptions and identification keys. The terms in Garcia et al. (2015) and Borowiec (2016) are adhered to facilitate comparison to these works. Gyne morphology follows Boudinot (2015). Wilson (1955) was followed for pubescence and pilosity. The terminology for the description of surface sculpturing is based on Harris (1979). The term abdominal segment III is alternately used for the postpetiole and abdominal segment IV for the gastral segment I following Fisher (2005). Abdominal segments 1 to 4 are denoted as AI, AII, AIII and AIV, respectively. We use the term 'calcar of strigil' following Keller (2011). Measurements follow Ward (1988) and Garcia et al. (2015, 2017). All measurements are in millimetres unless otherwise specified. Research permissions granted to us precludes publication of GPS points for places inside protected areas as a publication policy, hence we are unable to provide them.

The following measurements and indices are used:

EL—Eye length: maximum length of eye measured in lateral view | HL—Head length: maximum measurable distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of head, measured in full-face view | HW—Head width: maximum head width directly behind the eyes, measured in full face view | SL—Scape length: maximum length of scape shaft excluding basal condyle | PH—Pronotal Height: the maximum height of the pronotum in profile | PW—Pronotal Width: the maximum width of the pronotum in dorsal view | DML—Dorsal Mesosoma Length: maximum length of mesosomal dorsum from antero-dorsal margin of pronotum to dorsal margin of propodeal declivity | WL—Weber's Length of Mesosoma: the maximum diagonal length of the mesosoma in profile, from the angle at which the pronotum meets the cervix to the posterior basal angle of the metapleuron | HFeL—Metafemur Length: the maximum straight-line length of the metafemur, measured in dorsal view | HTiL—Hind tibia length: maximum length of hind tibia measured on its external face | HBaL—Hind basitarsus length: maximum length of hind basitarsus measured along its external face | PeL—Abdominal Segment II (petiole) Length: the maximum length of abdominal segment II (petiole), measured in dorsal view | PeH—Abdominal Segment II (petiole) Height: the maximum height of the

petiolar tergum in profile view, including laterotergite, excluding petiolar sternum | PeW—Abdominal Segment II (petiole) Width: the maximum width of abdominal segment II (petiole), measured in dorsal view | A3L—Abdominal Segment III Length: the maximum length of abdominal segment III, measured in dorsal view | A3W—Abdominal Segment III Width: the maximum width of abdominal segment III, measured in dorsal view | A3H—Postpetiole Height: Maximum height of postpetiole in profile |

A4L—Abdominal Segment IV Length: the maximum length of abdominal segment IV, measured in dorsal view | A4W—Abdominal Segment IV Width: the maximum width of abdominal segment IV, measured in dorsal view | LS4—Abdominal sternum IV length: maximum length of abdominal sternum IV in lateral view | A5L—Abdominal Segment V Length: the maximum length of abdominal segment V, measured in dorsal view | A5W—Abdominal Segment V Width: the maximum width of abdominal segment V, measured in dorsal view | A6L—Abdominal Segment VI Length: the maximum length of abdominal segment VI, measured in dorsal view | A6W—Abdominal Segment VI Width: the maximum width of abdominal segment VI, measured in dorsal view | WL—Weber's length: diagonal length of mesosoma in lateral view from the anterior-most point of pronotal slope (excluding neck) to posteroventral margin of propodeal lamella or lobe | TL—Total body length: combined length of HL + WL + PeL + A3L + A4L for Proceratiinae and HL + ML + PeL + A3L + GL for Myrmicinae.

Indices

CI—Cephalic index: HW / HL × 100 | OI—Ocular index: EL / HW × 100 | SI—Scape index: SL / HL × 100 | DMI —Dorsal Mesosoma Index: PW / WL × 100 | DMI2 —Dorsal Mesosoma Index 2: DML / WL × 100 | LMI —Lateral Mesosoma Index: PH / WL × 100 | DPe (DPI)—Dorsal petiole index: PeW / PeL × 100 | LPI —Lateral Petiole Index: PeL / PeH × 100 | MFI —Metafemur Index: HFeL / HW × 100 | ASI—Abdominal segment index: A4L /A3L × 100 | IGR—Gastral reflexion index: LS4 / A4L.

RESULTS

Genus *Proceratium* Roger, 1863

Description of worker caste *stictum* species group

Monomorphic hypogaeic ants of tribe Proceratiini with petiole narrowly attached to the first gastral segment; tergite of second gastral segment strongly arched and vaulted with remaining segments directed anteriorly; eyes present even if small; mandible linear to triangular with three or more teeth, not overhung by the clypeus; apical funicular segment moderately enlarged but not strongly bulbous well-developed (Bolton 2003). Medially excavated clypeus protruding anteriorly, vertex in full-face view weakly concave, calcar of strigil with a basal spine, belonging to the *stictum* species group as defined by Urbani & De Andrade (2003).

Proceratium gibbosum

Sadasivan & Kripakaran sp. nov.

(Image 2A–C)

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Material Examined

Holotype: NRC-AA-3758, 23 May 2016, Worker, Vallakadavu, Periyar Tiger Reserve, Idukki District, Kerala State, India, at 900 m, coll. by Kalesh Sadasivan, tray-sifting loose soil under a decaying log, in forest floor of a primary evergreen forest, deposited in the insect collection facility of the NCBS (National Centre for Biological Sciences), Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru, Karnataka 560065, India. Earlier, the holotype was with number TARG-1007, mounted for morphological study and later removed & preserved as wet specimen in absolute alcohol, deposited in the research collections facility at the Travancore Nature History Society (TNHS), Thiruvananthapuram, Kerala.

Measurements: EL 0.05, HW 0.80, HL 0.90, HFeL 0.75, HTiL 0.55, HBaL 0.40, A3L 0.90 A4L 0.45, LS4 0.25 PeL 0.47, PeW 0.34, SL 0.50, WL 1.09, TL 3.91, CI 89, OI 6.25, SI 55.55, DPeI 72.34, ASI 50, IGR 55.56.

Head: In full-face view marginally longer than wide (CI 89). Vertexal margin almost straight with only very shallow concavity. Head wider at midway distance between the level of eyes and the lateral angle of the vertex. Clypeus narrow, not surrounding the antennal insertions and projecting inferiorly only in the area between the anterior margin of the frontal carinae. Anterior clypeal margin notched medially. The frontal carinae are well-separated, running in parallel anteriorly and then diverging posteriorly. The frontal carinae reaches up to midway between the anterior clypeal margin and the level of the eyes (Image 2C). Eyes simple (single ommatidium), located slightly below the mid-length of the head in full-face view. Ocelli absent. Antennal scape distally incrassate and not reaching the vertexal margin. Antennal scape as long as broad, all other segments broader than long. Length of last funicular segment equal to the sum of lengths of 7–11 funicles. Mandibles with three denticles before the apical tooth. Palp formula 4,3.

Image 2. *Proceratium gibbosum* sp. nov. holotype (NRC-AA-3758): A—lateral view | B—dorsal view showing the mesonotal tumulus | C—fronto-oblique view of the head and antennae. © Manoj K.

Mesosoma: In lateral view, slightly convex; mesonotum presenting a visible tumulus. Mesosoma slightly longer than the sum of HL and mandible length. Both the promesonotal suture and metanotal groove shallow and barely discernible. Propodeal margins with a well-defined tooth, lobes expanded into a broad lamella. In dorsal view, pronotal margin angulate, but lacking projections, tooth or spines. The mesonotum bears on its mid-dorsal surface aspect a large tumulus (0.25 mm), occupying almost half of the area on dorsal side of the mesonotum (Images 2B). The propodeum has the tooth directed postero-laterally and the broad propodeal lobes. Propodeal declivity slightly concave, almost flat. The posterolateral aspect of metapleuron with a concavity bearing the opening of the metapleural gland.

Petiole: In dorsal view, slightly longer than broad (PeL 0.47, PeW 0.34). The narrowest part of the petiole is its anterior end (peduncle). The sides of the node are diverging to about the beginning of distal third where it is the widest and the converges slightly towards the posterior end. The anterior margin of the peduncle is thickly marginated. In profile view, a mid-ventral keel extends till the end of the junction of the anterior and middle third of the length of the petiole. No tooth or spine present ventrally (Images 2A,B).

Postpetiole: In lateral view, postpetiole is 2.5 times the length of the petiole. Dorsal profile broadly convex, ventrally the anterior half is slightly concave and distal half is convex in outline (Image 2A). The sides of the tergite are convex and the anterior end is produced as a small blunt triangular extension. In ventral view, the sternite has a mid-carina which is rudimentary. The anterior margin of the sternite extends as a broad triangular extension (Images 2A,B).

Gaster: Constriction between the post petiole (abdominal segment AIII) and first gastral segment (AIV) well defined and deep (Image 2A). Tergite of the AIII twice the length of the post petiole (AII). The tergite of AIII double the length of tergite of AIV. The first gastral segment recurved ventrally to almost a right angle and its curvature is smooth and convex. The distal edge of the AIII was marginated. Remaining gastral segments curved ventrally and telescoped inside the gaster. Sting present, robust (0.2 mm long).

Legs: All tibiae with pectinate spur. Calcar of strigil with a basal spine. Hind basitarsi slightly longer than half the length of the hind tibia.

Sculpture and Pilosity: Head, mesosoma, petiole and AIII irregularly foveolate with sparse tiny nodules. The irregular edges of the foveolae gives a scabrous appearance to the surface. Area of the mesonotal tumulus finely granular. AIV almost scabrous in appearance. Legs covered in dense but shallow foveolae, giving them a reticular appearance. Body is covered in four types of hairs:

1) Very short decumbent hairs on the antennal funicles;

2) Short sub-decumbent hairs, which are denser on the legs and the mesonotal tumulus;

3) Long sub-erect hairs throughout the whole body;

4) Short appressed hairs on the apical antennal funicle.

Short hairs on the mesonotal tumulus irregular, disposed with the tips pointing to the centre of the tumulus.

Color: Live specimens dark brown. Petiole, the mesonotal tumulus and the propodeum darker. The pronotum, postpetiole and head slightly paler. Legs and antennae dark orange brown. Hairs pale amber brown.

Additional Material Examined

Paratype workers (n = 3) (Images 3–5): NRC-AA-3759, 28 March 2021, Worker, Vallakadavu, Periyar Tiger Reserve, Idukky District, Kerala State, India, at 930 m, coll. Kalesh Sadasivan, tray-sifting leaflitter, in forest floor of a primary evergreen forest, deposited in the insect collection facility of the NCBS (National Centre for Biological Sciences), Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru, Karnataka 560065, India. Earlier, paratype number TARG-1008, preserved in absolute alcohol and currently deposited in the research collections facility at the TNHS, Trivandrum, Kerala.

Two other paratype workers, same data as paratype above. One paratype (TARG-1009) and (TARG-1010) both in absolute alcohol, to be deposited in the insect collection of Zoological Survey of India (ZSI), Kozhikode, Kerala.

Measurements: EL 0.05–0.06, HW 0.70–0.80, HL 0.80–0.90, HFeL 0.80–0.90, HTiL 0.50–0.60, HBaL 0.35–0.45, A3L 0.90–1.00, A4L 0.45–0.50, LS4 0.20–0.30, PeL 0.47–0.50, PeW 0.34–0.40, SL 0.50–0.70, WL 1.09–1.30, TL 3.71–4.20, CI 87.5–89, OI 6.20–7.50, SI 55.55–77.78, DPeI 72–80, ASI 50.00, IGR 44.40-60.

Variation in workers. No variation except subtle differences in body measurements as given above.

Gyne: Unknown

Male: Unknown

Etymology: The specific epithet *gibbosum* (from Latin 'gibbosus', meaning protruding or humpbacked) is a singular neuter adjective in the nominative case and refers to the hump-like protuberance on the mesonotum, characteristic of the species.

Ecological Notes: This species nests in the forest floor

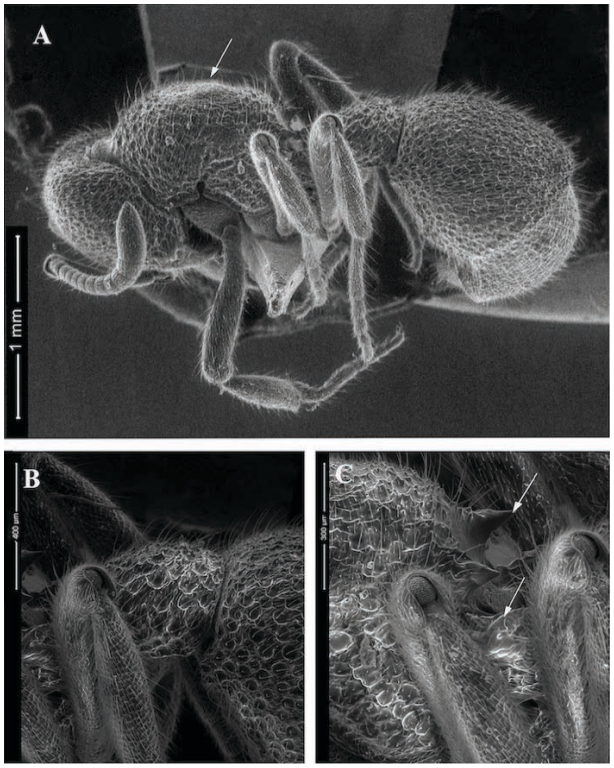

Image 3. *Proceratium gibbosum* sp. nov. Scanning electron images of a paratype from TARG collection of the same colony as the holotype: A—dorsolateral view of a paratype with tumulus (white arrow) | B—close-up of dorsolateral view of petiolar node showing surface sculpture | C—closeup of the propodeal spines and lobe (white arrows).

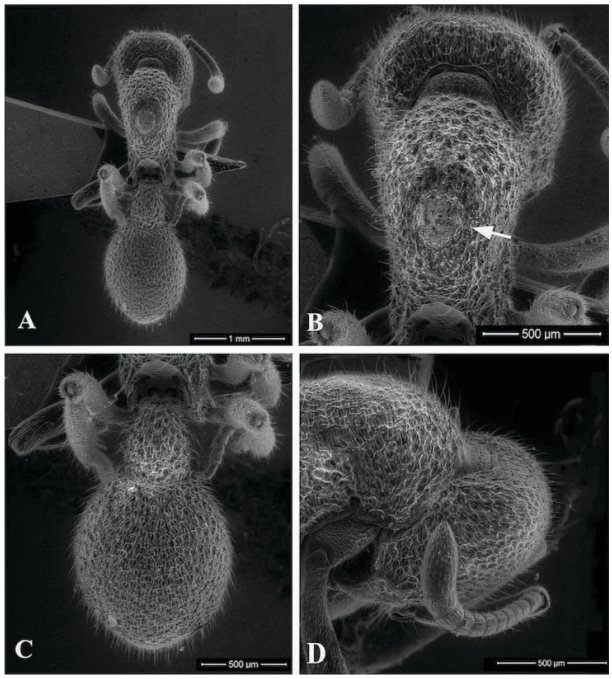

Image 4. *Proceratium gibbosum* sp. nov. Scanning electron images of a paratype from TARG collection of the same colony as the holotype: A—dorsal view of a paratype | B—closeup of the mesonotal tumulus (white arrow) | C—close-up of gaster and petiole | D—close-up of latero-oblique view of head and pronotum showing the sculpture.

and the colonies are probably small. This new species can be found in wet evergreen and secondary tropical rainforests, nesting in the interphase of soil and leaf litter or in the debris along sheltered edges of decaying logs on floor (Image 6). Workers are solitary foragers and move at a slow pace. They feign dead when disturbed, camouflaging against the soil (Image 5D). In captivity, the workers readily accepted spider eggs as food (Image 5E) and built a nest chamber with spider silk and soil. Workers were slow in movement, looked generally uncoordinated and were averse to light. Other species that were found in the same microhabitat of *P. gibbosum* were *Tyrannomyrmex alii* Sadasivan & Kripakaran, 2017, *Protanilla* sp., *Discothyrea* sp., and *Recurvidris* sp. So far, this new species is restricted to the mid-elevation tropical evergreen jungles of the Periyar Tiger Reserve, in Kerala.

Diagnosis and Remarks

The new taxon is characterised by a clypeus, protruding anteriorly, surrounding the antennal sockets and medially excavated (distinctly and broadly notched), vertex in full-face view weakly concave; calcar of strigil

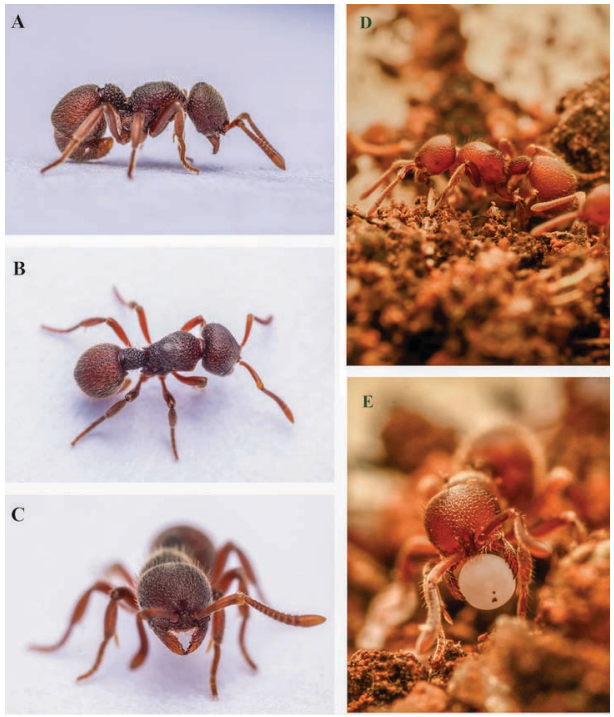

Image 5. *Proceratium gibbosum* sp. nov. Images of a live paratype from TARG collection of the same colony as the holotype: A—lateral view | B—dorsal view | C—close-up of head with antennae and mandibles | D—foraging workers in soil | E—foraging worker with spider egg. © A–C Kiran. M.R. | D–E © Manoj. K.

Image 6. *Proceratium gibbosum* sp. nov. Image showing the habitat of type locality at Periyar Tiger Reserve, Western Ghats, Kerala. © Raghuram, E.

with a basal spine; hence of the *stictum* species group (Urbani & De Andrade 2003). According to Staab et al. (2018), the *stictum* species group is exclusively tropical with taxa in Africa, Madagascar, the Mascarene Islands of southeastern Asia, Indochina, Australia, and Mesoamerica. There are four known species of the *stictum* species group from the oriental region. The species *P. deelemani* Perrault, 1981 is distributed in Borneo, Brunei Darussalam, Malaysia (Sabah & Sarawak), Thailand, and Singapore; *P. foveolatum* Baroni Urbani and de Andrade, 2003 is reported from Borneo, Brunei Darussalam, Indonesia and Malaysia; *P. stictum* Brown, 1958 is found in Queensland, Australia; and, *P. shohei* Staab, Xu & Hita Garcia, 2018 was described from a tropical forest of Yunnan Province in China. Thus, this is the first record of a taxon of the *stictum* species group for India.

Proceratium gibbosum differs from the other members of the *stictum* species group by the following character combination: mesonotum with a small rounded dorsal hump, and petiole lacking ventral projections. *Proceratium gibbosum* also presents a pedunculate petiole with its dorsal margin convex in profile; all tibiae with pectinate spur, calcar of strigil with a basal spine; eyes composed of a single large convex ommatidium; propodeum unarmed but angulate, convex in profile, propodeum with a robust spine on each side, propodeal lobes broad lamellaceous expansions; head, mesosoma, petiole and postpetiole irregularly foveolate; first gastral tergite convex in profile; antennal funicles wider than long; total length <4.8 mm; propodeum with a robust spine on each side, the propodeal lobes with broad lamellaceous expansions.

The other *Proceratium* species from India are *Proceratium bhutanense* de Andrade, 2003, described from Phuntsholing in Bhutan, Darjeeling in West Bengal, Kumaon in Uttar Pradesh (Uttarakhand), and Khasi Hills in Meghalaya (Urbani & De Andrade 2003). Bharti and Wachkoo (2014) found *P. bhutanense* to be conspecific with *P. williamsi* Tiwari, 2000 and hence is now treated as the junior synonym of the latter. The species *P. williamsi* belongs to the *itoi* species group with the fourth abdominal segment sternite protruding over the third abdominal sternite (Urbani & De Andrade 2003).

According to the identification key from Urbani & De Andrade (2003), the closest known species in the *stictum* species group seems to be *P. deelemani*. However, *P. deelemani* lacks the distinct small rounded dorsal hump present on the new species. In addition, the petiole of the new species lacks any ventral projections, while in *P. deelemani* it has a distinct ventral tooth. To *P. stictum*, the new species differs in the cephalic sculpture, deeply impressed on *P. gibbosum* and shallow on the former. Additionally, the frontal carinae of the new species diverge posteriorly, where in *P. stictum* they are not as divergent. Anteriorly, the frontal carinae are closer to each other in *P. gibbosum,* while they are farther away in *P. deelemani*. The frontal carinae run to a level almost midway between the anterior clypeal margin and the level of the eyes, but they extend only one third the same distance in *P. deelemani* (the frontal carinae are shorter in *P. deelemani*). The species is differentiated from *P. foveolatum* by the first gastral tergite being angulate on dorsum, while it is round on the curvature in *P. gibbosum.* The new species is diagnosed from *P. shohei* by the head being widest midway between the eyes and vertex, while the head is widest at the level of eyes in *P. shohei.* The petiolar node is relatively compressed dorsoventrally in *P. shohei,* while *P. gibbosum* has a pedunculate petiole, convex in profile.

Modified part of the key to Indo-Malayan species of *Proceratium* Roger, 1863 based on the worker caste, from Urbani & De Andrade (2003) with placement of the known species from India.

1) Petiole with peduncle, convex or subconvex in profile; anterior clypeal border strongly protruding anteriorly or at least medially triangular 2
- Petiole without peduncle, rectangular in profile; anterior clypeal border straight or weakly concave, never protruding anteriorly ..... (Continued to couplet number '6' in Baroni Urbani & De Andrade 2003)

2) Propodeal angle with a developed spine; propodeal lobes with a broad lamellaceous tooth...3
- Propodeal angle at most with a small tip, without a true spine; propodeal lobes without broad lamellaceous tooth, at most with a lamella over the whole declivitous face 5

3) First gastral tergite angulate on the dorsum (Malaysia).....*P. foveolatum* De Andrade, 2003
- First gastral tergite round on the dorsal curvature 4

4) Mesonotum without any dorsal tumulus; petiole with a mid-ventral tooth (Borneo, Brunei, Malaysia, Thailand and Singapore) ..... *P. deelemani* Perrault, 1981
- Mesonotum with a rounded dorsal tumulus; petiole lacking ventral projections (Western Ghats, India) ..... ***P. gibbosum* sp. nov.**

5) Frontal carinae fused; clypeus strongly protruding anteriorly; mesosoma, petiole, postpetiole and gaster foveolate (Malaysia) ..... *P. microsculptum* De Andrade, 2003
- Frontal carinae not touching each other; clypeus reduced, a triangular tooth like projection between the antennal sockets; mesosoma, petiole and postpetiole granulate, gaster punctat 6

6) Body without long erect hairs; lateral propodeal margin at most with a narrow lamella; hairs on mesobasitarsi shorter than 1/2 the mesobasitarsal length (Himalayas from Uttarakhand to Meghalaya in Northeast India, Bhutan) ..... *P. williamsi* Tiwari, 2000
- Body with long erect hairs; lateral propodeal margin with a broad lamella; mesobasitarsi with hairs 1/2 the mesobasitarsal length (Malaysia) ..... *P. malesianum* de Andrade, 2003

Genus *Zasphinctus* Wheeler, 1918

Description of Worker Caste

Antennae with 12 segments, pygidium armed with numerous peg-like or spiniform setae, much thicker than surrounding fine hairs; waist with abdominal segment III at least weakly differentiated from segment IV; the latter with a constriction between its pre- and post-sclerites; mid- and meta-tibiae with a single spur; tarsal claws of hind legs simple; mesosoma and gaster not conspicuously dorso-laterally marginate pore plate of metatibial gland not in a depression; in lateral view pronoto-mesopleural suture fused, never as a curved slit in the cuticular surface, and approaching dorsolateral margins of promesonotum; circumference of helcium smaller relative to abdominal segment II (petiole) and placed at about mid-height, resulting in pronounced posterior face to abdominal segment II and conspicuous anterior face of abdominal segment III; opening of metapleural gland conspicuous elongate and trench-like and its diameter larger than that of the propodeal spiracle; and constrictions present at anterior end of abdominal segments V and VI (Borowiec 2016).

Zasphinctus sahyadriensis
Kripakaran & Sadasivan sp. nov.
(Image 7A–C)
urn:lsid:zoobank.org:act:423E5FC4-315A-44E1-9C14-C66B2D02268F

Material Examined

Holotype: NRC-AA-3760, 15 October 2015, Worker, Ponmudi, Agasthyamalai, Thiruvananthapuram District, Kerala State, India, at 600 m, coll. Manoj Kripakaran, collected under a small rock, in the forest floor of a mixed evergreen forest, deposited in the insect collection facility of the NCBS (National Centre for Biological Sciences), Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru, Karnataka 560065, India. Earlier, the holotype was with number TARG-1011, mounted for study and preserved as wet specimen in absolute alcohol, deposited in the research collections facility at the TNHS, Thiruvananthapuram, Kerala.

Measurements: HL 0.70, HW 0.40, SL 0.32, PH 0.40, PW 0.50, DML 0.90, WL 1.00, HFeL 0.42, PeL 0.32, PeH 0.23, PeW 0.50, A3L 0.35, A3W 0.43, A4L 0.30, A4W 0.58, A5L 0.30, A5W 0.59, A6L 0.30, A6W 0.60, CI 57.14, SI 45.71, DMI 50, DMI2 90, LMI 40, MFI 105, LPI 139, DPI 156, DA3I 123, DA4I 193, DA5I 197, DA6I 200.

Head: Antennae with 12 segments and relatively short (SI 44–56), scapes reaching half of the height of the head in full-face view. Apical antennal segment is conspicuous, longer than two preceding segments

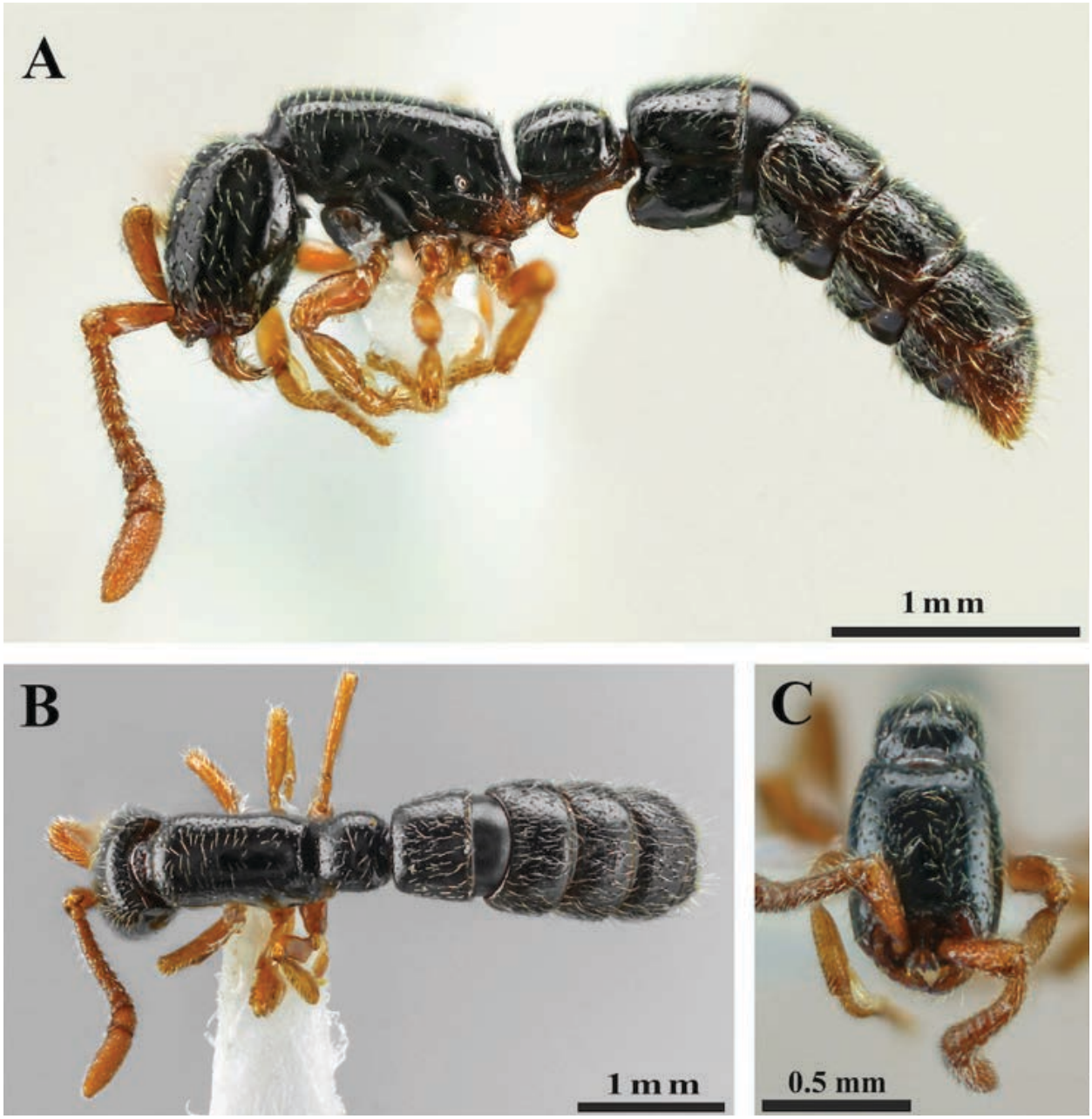

Image 7. *Zasphinctus sahyadriensis* sp. nov. holotype (NRC-AA-3760): A—lateral view | B—dorsal view | C—full-face front view. © Kalesh Sadasivan.

combined. Head distinctly longer than broad (CI 56–59). Parafrontal ridges present and well-developed but somewhat irregular. Torulo-posttorular complex vertical reaching only below half of the height of the parafrontal ridges. Antennal scrobes absent. Median clypeal area with a single short but conspicuous tooth (Image 7C). Palp formula 3,3 (visible palpomeres). Mandibles elongate triangular and curved; masticatory margin almost plain, basal region with inconspicuous denticles. Eyes and ocelli absent. Vertex concave. Head capsule with a well-differentiated vertexal margin with prominent lateral angles.

Mesosoma: Mesosoma in lateral view the profile is almost straight (LMI 40–44). Sides are rounded and not marginate (Images 7A).

In dorsal view, slightly more than twice as long as broad (DMI2 88–93). Promesonotal suture completely fused. Pronotomesopleural suture absent. Mesometapleural groove not impressed. Transverse groove dividing mesopleuron absent. Pleural endophragmal pit concavity

present. Mesosoma dorsolaterally immarginate. Metanotal depression or groove on mesosoma absent. Propodeal spiracle situated low below mid-height on the sclerite. Propodeal declivity almost vertical with an angle of 110 degrees to the dorsum. Propodeal declivity with distinct dorsolateral and lateral edge or margin, and declivity is nearly semi-circular in posterior view. Metapleural gland without bulla visible through the cuticle. Propodeal lobes developed.

Metasoma: Abdominal segment II (petiole) sessile, without peduncle. Petiolar node well-developed. In profile, petiolar tergum 1.4 times longer than high (LPI 136–139). Petiole anterodorsally marginate but blunt, dorsolaterally well rounded, and laterally above spiracle weakly marginate. Subpetiolar process well-developed with strongly anteroventrally projecting "eagle beak" shaped with tip hooked posteriorly (Image 7A) The subpetiolar process without fenestra. Prora on the anterior aspect of the ventral part of abdominal segment III is simple and heart shaped. Spiracle openings of abdominal segments IV–VI circular. Abdominal segment III anterodorsally emarginate and dorsolaterally emarginate. Abdominal segment III distinctly longer than succeeding segment IV, in both dorsal and ventral views. Girdling constrictions of segments IV, V, VI present and distinct. Abdominal tergite IV not folding over sternite, and anterior portions of sternite and tergite equally well visible in lateral view. Pygidium large, with weakly impressed and hypopygium moderately concave proximally, with the posterior end bossed on its midline bearing the ventral part of the tiny sting.

Legs: Pro-, tibia, meso-, and metatibiae with single pectinate spur. Tarsal claws simple. Metafemur moderately long (MFI 105-112).

Sculpture and Pilosity: The head, mandibles, mesosoma, legs and metasoma are generally smooth and shiny, with sparse piligerous punctae and a much lesser number of glabrous punctae. Sculpture on ventral margin of antennal scape, propodeal declivity and helcium imbricate to reticular. Most of body with numerous short to moderately long, decumbent to suberect setae. Few erect hairs present around the pygidium and hypopygium. Pygidium near the sting and the lateral margins armed with short and stout, tubiform to conical setae. Long semierect filiform setae present around the pygidium and hypopygium. The area between vertexal margin and occipital margin unsculptured.

Color: Mainly black, appendages and subpetiolar process amber brown. Mandibles dark amber brown. Hairs pale yellowish and translucent (Image 7).

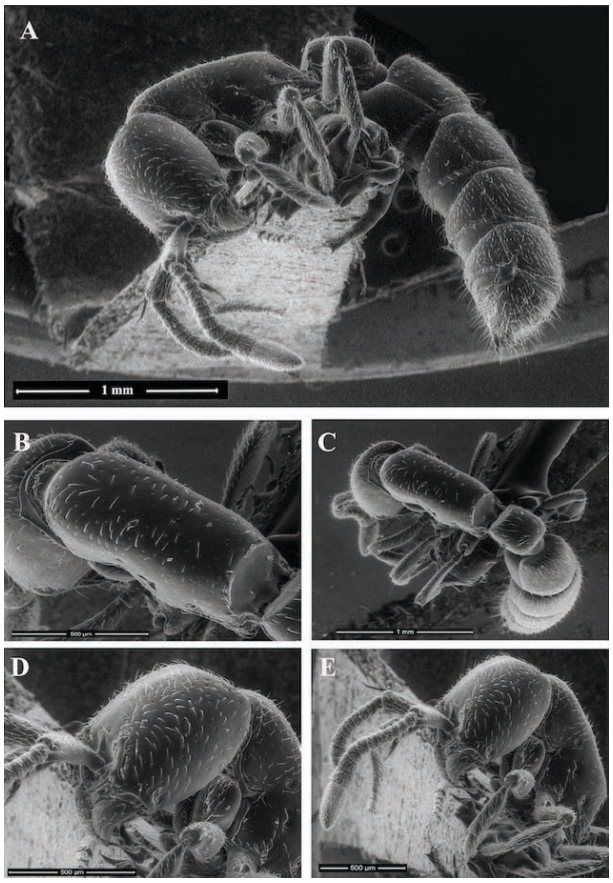

Image 8. *Zasphinctus sahyadriensis* sp. nov. Scanning electron images of a paratype from TARG collection of the same colony as the holotype: A—lateral-ventral view | B—dorsolateral view | C—closeup of mesosoma showing the rounded lateral borders and absence of any prominent sutures | D—close-up of sculpture and pilosity of head | E—lateral-oblique view of head.

Additional Material Examined

Paratype workers (n = 3) (Images 8,9): NRC-AA-3761, Worker with the same collection data as holotype above. Earlier, the paratype was with number TARG-1012, wet specimen in absolute alcohol, currently deposited in the research collections facility at the TNHS, Trivandrum, Kerala.

Two other paratype workers both with the same collection data as paratype above. Of them one worker (TARG-1013), wet specimen in absolute alcohol, will be deposited in the insect collection of ZSI, Kozhikode, Kerala and the other worker (TARG-1014), wet specimen in absolute alcohol, will be retained as voucher specimen in collection facility of TNHS, Thiruvananthapuram, Kerala.

Measurements: HL 0.68–0.72, HW 0.38–0.42, SL 0.31–0.32, PH 0.40–44, PW 0.49–0.54, DML 0.88–0.93, WL 0.98–1.10, HFeL 0.40–0.45, PeL 0.30–0.34, PeH 0.22–0.25, PeW 0.48–0.54, A3L 0.32–0.38, A3W 0.42–0.45,

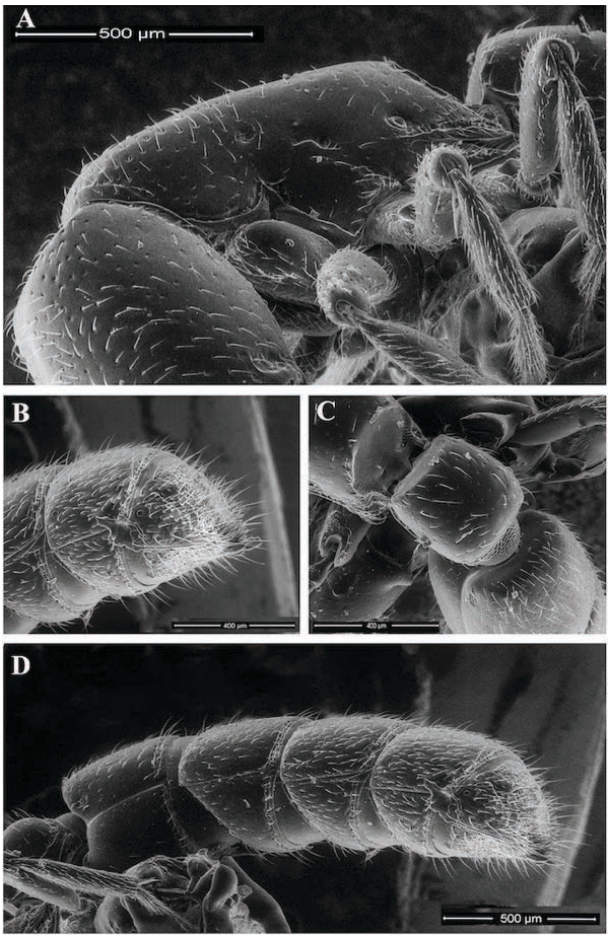

Image 9. *Zasphinctus sahyadriensis* sp. nov. Scanning electron images of a paratype from TARG collection of the same colony as the holotype: A—close-up of latero-oblique view of mesosoma | B—close-up of pygidium | C—dorso-oblique view of petiolar node | D—lateroventral view of metasoma.

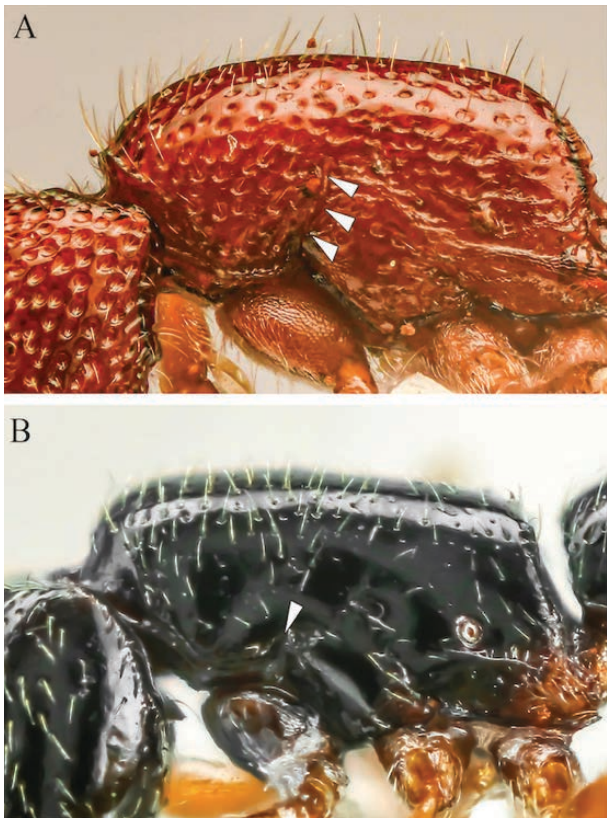

Image 10. Pronotomesopleural sutures *Eusphinctus* and *Zasphinctus* from Agasthyamalai. Kerala, Western Ghats (white arrows): A—*Eusphinctus* with pronotomesopleural suture as a long deep cut in the cuticle | B—*Zasphinctus* with short and rudimentary pronotomesopleural sutures. © Kalesh Sadasivan & Manoj K.

A4L 0.30–0.32, A4W 0.56–0.59, A5L 0.28–0.32, A5W 0.56–0.60, A6L 0.28–0.32, A6W 0.58–0.61, CI 55.88–58.33, SI 44.44–55.56, DMI 49–54, DMI2 88–93, LMI 40–44, MFI 105–107, LPI 136–139, DPI 156–160, DA3I 118–131, DA4I 184–193, DA5I 188–200, DA6I 191–207.

Variation in workers: No variation except in the subtle differences in body measurements indicated above.

Gyne. Unknown

Male. Unknown

Etymology. The epithet '*sahyadriensis*' is masculine and derived from the Sanskrit and regional Malayalam language word '*Sahyadri*', denoting the Western Ghats.

Ecological Notes. The species was found in a tropical evergreen forest floor. Five workers were collected from a subterranean tunnel under a small rock, near the buttress of a tree (Image 11). The workers were moving in the narrow tunnel which happened to get opened when the rock was removed. The movement was army ant-like, fast, irregular, and the ants were averse to light. In captivity, workers accepted brood of a *Pheidole* species as food. The species is restricted to Ponmudi hills in Agasthyamalai region of southern Western Ghats in Kerala state of southern India as far as is known.

Diagnosis and Remarks

Following Borowiec (2016), the genus *Sphinctomyrmex* now refers to species from the Neotropics, with the Old World taxa now placed in *Zasphinctus* Wheeler, 1918 and *Eusphinctus* Emery, 1893. *Zasphinctus* is easily differentiated from *Eusphinctus* by pronotomesopleural suture being present as a deep cut in the cuticle in the latter (Image 10) (Borowiec 2016). *Zasphinctus* can be distinguished from other doryline lineages with pronounced abdominal constrictions by highly-positioned propodeal spiracles, propodeal lobes present, pygidium large and armed with modified setae, and pronotomesopleural suture fused (Borowiec 2016). *Zasphinctus* is a moderately speciose lineage of

Image 11. *Zasphinctus sahyadriensis* sp. nov. Image of habitat at the type locality in Agasthyamalais. © Raghuram, E.

specialized ant predators, most prominently distributed in Australia (AntWeb 2021). Workers are of variable size, color, and sculpturation, but always possessing conspicuous girdling constrictions between abdominal segments IV, V, and VI. The eyes are absent in most species.

This is the first confirmed report of the occurrence of *Zasphinctus* for the Indian Subcontinent. The new species seems to be a subterranean predatory in the mid-elevation of mixed evergreen forests (600 m) of Western Ghats (Image 11). *Zasphinctus sahyadriensis* is easily differentiated from the sympatric *Eusphinctus furcatus* Emery, 1893, occurring in the same habitat. Although superficially similar, *Z. sahyadriensis* has 12-segmented antennae, a shallow pronotomesopleural suture, smaller size (TL 3.04–3.33), and shiny black color, while *E. furcatus* has 11-segmented antennae, a deep pronotomesopleural suture, larger size (TL 6.85–6.90 mm), and dark brown integument coloration. Additionally, *E. furcatus* was recorded above 900 m, while the highest elevation for *Z. sahyadriensis* was 700 m.

Analysis of AntWeb (2021) images revealed morphological similarities between *Zasphinctus sahyadriensis* and other shiny black Afrotropical species (*Z. sarowiwai* Hita Garcia, 2017, *Z. obamai* Hita Garcia, 2017, and *Z. wilsoni* Hita Garcia, 2017). The presence of the conspicuous tooth in the median clypeal area distinguishes the new species from *Z. obamai* and *Z. wilsoni* Hita Garcia. From *Z. sarowiwai,* the new species is diagnosed by the irregular occipital margin of the former. With the sole Asian species *Z. siamensis*, the new taxon Z. *sahyadriensis* shares the median clypeal tooth and the regular occipital margins; but the new species is easily distinguished by the black integumental coloration (brown on *Z. siamensis*) and the sparsely punctate head sculpture (densely foveolate on *Z. siamensis*).

Key to Afrotropical-Indomalayan species of *Zasphinctus* Wheeler, 1918 based on worker caste (modified from Hita Garcia et al. **2017).**

Note: *Z. rufiventris* (Santschi, 1915) and *Z. chariensis* (Santschi, 1915) are known from males only.

1) With head in full-face view, median clypeal area with conspicuous tooth 2
- With head in full-face view, median clypeal area without a conspicuous tooth 4

2) Occipital margin regular (Image 8B) 3
- Occipital margin irregular .... *Z. sarowiwai* Hita Garcia, 2017

3) Sculpture of head sparsely punctate (Image 8D) ..... ***Z. sahyadriensis* sp. nov.**
- Sculpture of head densely foveolate .... *Z. siamensis* (Jaitrong, 2016)

4) With head in full-face view, parafrontal ridges with irregularly shaped dorsal outline petiolar tergum in profile relatively lower, 1.2 times longer than high (LPI 117–123) .... *Z. obamai* Hita Garcia, 2017
- With head in full-face view, parafrontal ridges with regularly shaped dorsal outline; petiolar tergum in profile relatively higher, 1.1 times longer than high (LPI 112) .... *Z. wilsoni* Hita Garcia, 2017

Genus *Vollenhovia* Mayr, 1865

Description of worker caste

Based on Bolton (2003), Eguchi et al. (2011) and Ward et al. (2015), monomorphic myrmicine ants of tribe Crematogastrini Forel, 1893; head in full-face view subrectangular; frontal carina and antennal scrobe absent; median portion of clypeus raised, laterally margined with a slight to conspicuous longitudinal carina; anteromedian portion often forming a transverse strip; an isolated median seta absent; posteromedian portion relatively narrowly inserted between frontal lobes; lateral portion of clypeus never modified into a distinct ridge or wall in front of antennal insertion; mandible triangular; masticatory margin with six or more teeth; antennae 12-segmented, with 3-segmented club; eye present; mesosoma in lateral view long and low; promesonotum in lateral view usually not domed; promesonotal suture absent dorsally; metanotal groove weakly to slightly impressed dorsally; posterodorsal portion of propodeum with rounded corners; propodeal lobe present as low lamella; petiole nodiform; anterior peduncle short and obscure; posterodorsal margin of petiole produced posterodorsad as a rim which is distinctly higher than the dorsal outline of helcium of petiole; subpetiolar process developed as a large lamella; gastral shoulder absent.

***Vollenhovia keralensis* Kripakaran & Sadasivan sp. nov.**

(Images 12A–C)

urn:lsid:zoobank.org:act:3D7B8E5C-DD40-4396-83E3-30E6944DC46C

Material Examined

Holotype: NRC-AA-3762, 23 March 2011, Worker, Bonaccord, Peppara Wildlife Sanctuary, Trivandrum District, Kerala State, India, at 900 m, coll. Manoj Kripakaran, from under the bark of a dead and fallen tree in a primary evergreen forest, deposited in the insect collection facility of the NCBS (National Centre for Biological Sciences), Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru, Karnataka 560065, India. Earlier, the holotype was with number TARG-1015, mounted for study and preserved in absolute ethanol, currently deposited in the research collections facility at the TNHS, Thiruvananthapuram, Kerala.

Measurements: HL 0.86, HW 0.81, SL 0.51, EL 0.14, Clypeal groove 0.36, DML 1.01, PW 0.52, PeL 0.31, PeW 0.23, PeH 0.30, A3L 0.30, A3W 0.27, A3H including the ventral tubercle 0.24, GL 1.14, Subpetiolar process H 0.10, TL 3.62, CI 94.19, SI 62.96.

Head: Head length and width almost equal, subquadrate (CI 94.19), vertexal margin with mild depression medially (Image 12C); mandibles with eight teeth: a well-developed basal tooth, and masticatory margin of mandibles with large apical and pre-apical teeth followed by six teeth, gradually decreasing in size towards the base of the mandible; anteroclypeal margin convex, with a single median tooth; antennae 12-segmented with inconspicuous three-segmented club; eyes large, placed just below the middle of side margin of head (Images 12A). Lateral head margin weakly convex.

Mesosoma: Pronotum slightly convex in lateral view, mesonotum flat and sloping toward propodeal declivity, promesonotal suture indistinct; metanotal groove distinct and impressed (Images 12A–B); propodeal dorsum convex, posterodorsal corners rounded and unarmed, propodeal lobes developed.

Petiole: In lateral view, the dorsal margin convex, node longer than wide, posterodorsal margin angulate; subpetiolar process well-developed, its free lower edge rounded; on ventral view it diverges in the middle-third and then gently slopes to merge with the petiole at the junction of middle and distal third of the ventral margin of petiole. Subpetiolar process lamellar wall distinctly longer than high.

Postpetiole: in lateral view, slightly longer than high, dorsal margin convex; in dorsal view, almost spherical; in profile; a well-developed rounded process present on its ventrum almost occupying the anterior half.

Gaster: In profile, elliptical, dorsoventrally flat. Sting present, small (Images 12A).

Color, Sculpture and Pilosity: Blackish-brown head and body, gaster shiny blackish-brown. Mandible, antennae and legs brownish (Images 12A–C). Whole body foveolate except the median polished area on the anterior part of mesosoma, dorsolateral aspect of vertex, inferior half of propodeal declivity, the anterior aspect and anterior half of the mid-dorsum of the petiole. Gaster finely punctate, mostly by piligerous punctae, more abundantly on the anterior half of the tergite and across the sternite of the first gastral segment. The distal margin of the tergum and sternum of the first gastral segment reticulate. Surface of the other gastral segments finely reticular on both sides. Body is covered in sparse semierect hairs, brownish white and seen on entire head, body and gaster including petiole and postpetiole. Hairs are absent on the lateral aspect of the mesonotum and propodeum. Few long hairs on the lateral margin of the clypeus, a pair of such hairs on each side much longer and prominent. Distal aspect of gaster near the sting bears some long erect hairs. About 15 vertical rows of piligerous foveolae between the anterior

Image 12. *Vollenhovia keralensis* sp. nov. holotype NRC-AA-3762: A—lateral view | B—dorsal view | C—full-face view. © Manoj K.

margin of the eyes and the midline of the head in full-face view. Opening of metapleural gland guarded by two stout filiform hairs, directed anterodorsally.

Additional Material Examined

Paratype workers (n = 3) (Images 13–15): NRC-AA-3763, 28 March 2021, Worker, Vallakadavu, Periyar Tiger Reserve, Idukky District, Kerala State, India, at 935 m, coll. Kalesh Sadasivan under the bark of a dead and fallen tree in a primary evergreen forest, deposited in the insect collection facility of the NCBS (National Centre for Biological Sciences), Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru, Karnataka 560065, India. Earlier the paratype was with number TARG-1016, in absolute ethanol, currently deposited in the research collections facility at the TNHS, Thiruvananthapuram, Kerala.

Two other paratype workers both with same data as paratype above. TARG-1017 and TARG-1018 to be deposited in the insect collection of the ZSI, Kozhikode, Kerala.

Measurements: HL 0.84–0.86 , HW 0.79–0.81, SL 0.49–0.51, EL 0.14, Clypeal groove 0.35– 0.36, DML 1.00–1.02, PW 0.51–0.53, PeL 0.29–0.31, PeW 0.22–0.24, PeH 0.30 –0.31, A3L 0.28–0.30, A3W 0.27, A3H including the ventral tubercle 0.23–0.25, GL 1.12– 1.016, Subpetiolar

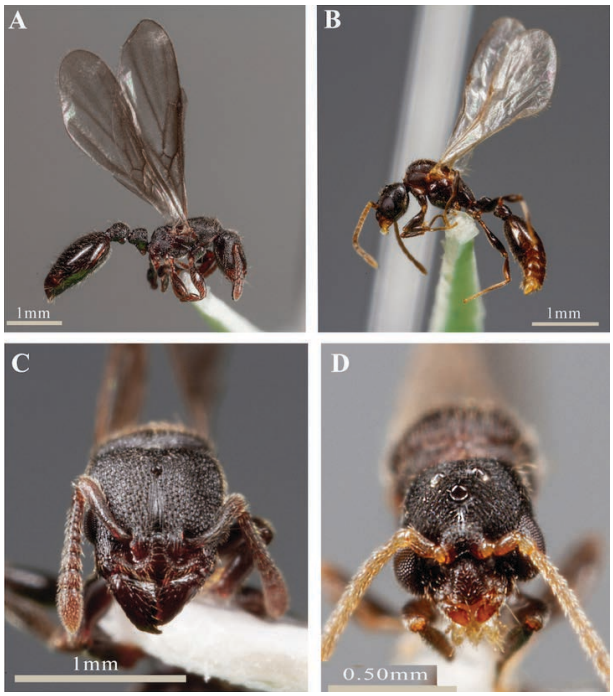

Image 13. *Vollenhovia keralensis* sp. nov. gyne and male: A—lateral view of gyne | B—lateral view of male | C—full-face view of gyne | D—full-face view of male. © Kalesh Sadasivan.

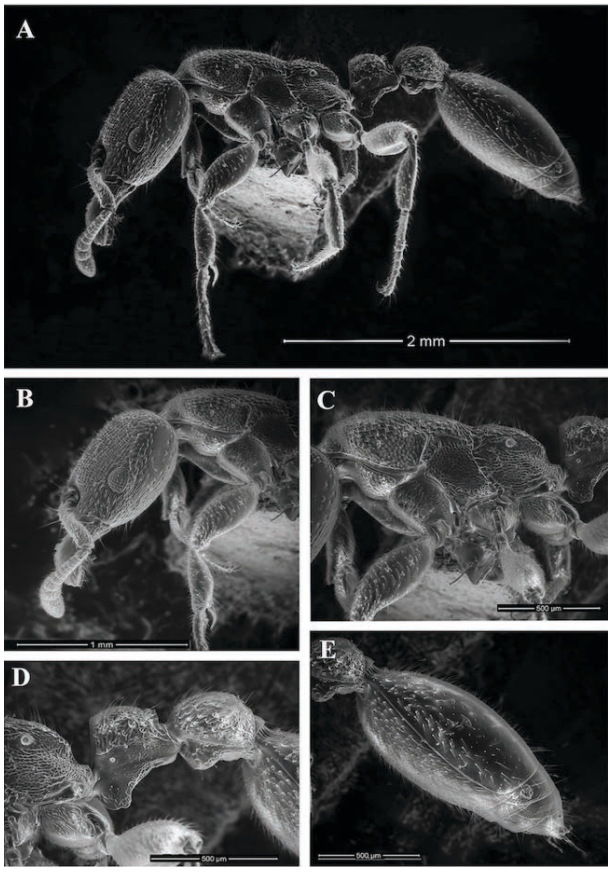

Image 14. *Vollenhovia keralensis* sp. nov. Scanning electron images of a paratype from TARG collection of the same colony as the holotype: A—lateral view | B—head lateral view | C—lateral view of mesosoma | D—lateral close-up view of petiole and postpetiole | E—lateral view of gaster.

process: H 0.08–0.12. TL 3.53–3.65, CI 94.04–94.18, SI 62.03–62.96.

Variation in workers: Some variation was noted in the body measurements (see above) and surface sculpture. The shiny mid-dorsal area on mesosoma was variable amongst the workers of the same colony. The variation ranged from the polished surface extending across the whole dorsum of mesosoma to the propodeum (Image 15A), to highly reduced to the anterior portion of the pronotum (Image 12B).

Gyne (Images 13A,C, 15D,F)

Measurements (n = 1). HL 0.94, HW 0.90, SL 0.54, Clypeus groove: 0.53, EL 0.21, DML 1.52, PW 0.78, PeL 0.38, PeW 0.32, PeH 0.45 (including the subpetiolar process), A3L 0.46, A3W 0.38, A3H 0.32, GL 1.52, Subpetiolar process H 0.20, TL 4.81, CI 95.74, SI 60.00.

Head blackish-brown, shaped similar to the worker, mandible with eight teeth, antennae 12-segmented. Antennal club not distinct from rest of the antennae. Ocelli present. Mesosoma blackish brown, shaped as in the worker except for the wing sockets. On lateral view, mesoscutum almost flat at the same level as the rest of the thorax. Parapsidal lines running longitudinally extending to almost half of the mesoscutum (Image 15f). Promesonotal and mesometanotal sutures distinct. Inferior half of the anepisternum and the superior higher portion of the katepisternum smooth (Image 15D). Mesoscutellum gently sloping towards the metanotum. Petiole and postpetiole same as worker, with well-developed subpetiolar process. Gaster shiny black, otherwise same as worker. Sculpture of head, mesosoma and first gastral tergite punctate, other gastral tergites finely reticulate. Body covered in sparse semierect hairs, brownish white in color throughout the entire body, including petiole and postpetiole (Images 15D,F).

Male (Images 13B,D)

Measurements (n = 1). HL 0.61, HW 0.65, SL 0.12, EL 0.22, Clypeal groove: 0.16, DML 1.20, PW 0.65, PeL 0.30, PeW 0.21, PeH 0.18, A3L 0.26, A3W 0.23, A3H 0.22 including tubercle, GL 1.10, TL 3.47, CI 1.06, SI 17.98.

Smaller than conspecific female castes. Head blackish-brown, wider than long, eyes large and occupying the lower half of the lateral head margin. Three large ocelli present. Mandibles highly reduced, masticatory margin toothless. Antennae 12-segmented, scape short, almost

equal to other segments of the antennae (Images 13B,D). Frontal margins subparallel, extending from the lower median ocelli downwards. Vertexal margin straight. In lateral view, mesosomal dorsum convex. Propodeal declivity less pronounced than in the workers. Subpetiolar process absent. Postpetiole lacking ventral tubercles. Body shiny (especially gaster) and generally finely punctate. Pilosity sparse, whole body covered by semierect whitish hairs and longer brownish hairs (Image 13B).

Etymology: The specific epithet *keralensis* is feminine, and refers to the state of Kerala, in southern India, where the species was discovered.

Ecological Notes: The species is currently only known from Agasthyamalais and Periyar Tiger Reserve in the southern Western Ghats of Peninsular India. This species was collected in tropical evergreen forests and mixed forests, ranging from 500–1,200 m. In the west coast tropical evergreen forest, habitat was characterized by *Myristica* (Myristicaceae) swamp forests and southern sub-tropical hill forests in the southern Western Ghats. Ants were observed moving on fallen tree trunks in shaded regions (Image 16A). On further investigation, the colonies were located inside crevices and under the bark of dead tree trunks. Upon disturbance, workers would disappear into tiny holes and crevices in the dead wood. One full colony was found at 800 m in Agasthyamalai had 52 workers, 20 males, 10 alate gynes, larvae and pupae in various stages of development. Occasionally, solitary gynes were observed under tree bark. No evidence of parasitic behaviour was noticed during our observation, although this needs detailed investigation. Workers were observed preying on beetle larvae and small arthropods nesting on tree bark, dead wood, and bracket fungi (Image 16B).

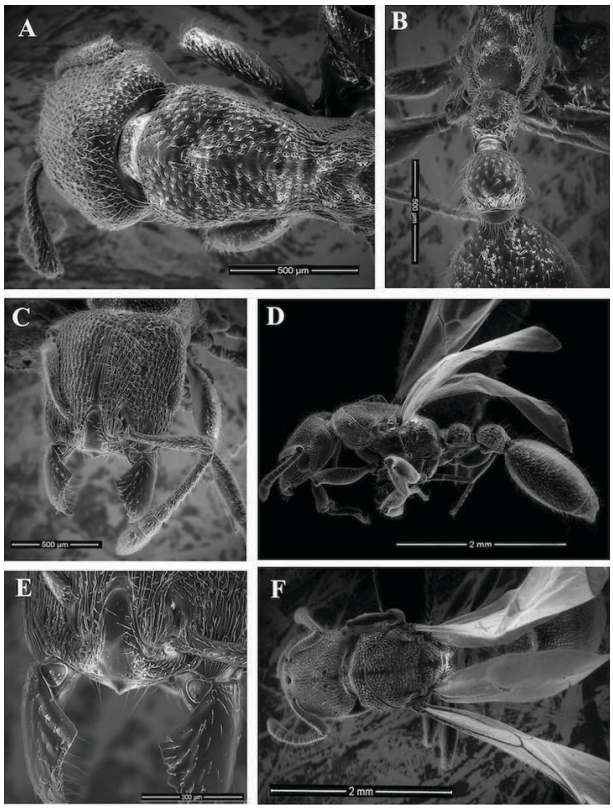

Image 15. *Vollenhovia keralensis* sp. nov. Scanning electron images of paratype worker (A–C &E) and gyne (D&F) in TARG collection: A—dorsal close-up of head and cervix and mesosoma | B— dorsum of petiole and postpetiole | C—head in latero-frontal | D—dorsolateral view of gyne | E—view close-up of clypeus, highlighting anteromedial tooth | F—dorso-oblique view of mesosoma of gyne.

Diagnosis and Remarks

Based on descriptive and morphometric data on workers of *Vollenhovia* from Forel (1911, 1912), Bharti & Kumar (2013), and images of other related species from the AntWeb (2021) (see key below), we found that the workers of *Vollenhovia keralensis* can be distinguished from other *Vollenhovia* species reported for the Indian subcontinent and adjoining Indian Ocean Islands by the following combination of characters: body size (TL 3.53–3.65 mm); convex anterior clypeal margin with a single median tooth; masticatory margin of mandibles with eight teeth, increasing in size from base to apex, and a well-developed subpetiolar process. From *V. oblonga* subspecies (*V. oblonga alluaudi* Emery, 1894 from Seychelles and Andaman and Nicobar Islands, as well as *V. oblonga levithorax* Emery 1889 from Tenasserim hills of Indo-Malaysia), the new species is easily differentiated by having a single median tooth on the clypeal margin, feature absent on *V. oblonga* and its subspecies. *Vollenhovia keralensis* can be differentiated from *V. penetrans* (Smith, 1857) – only known from alate gynes (AntWeb 2021) – based on the petiole length (subequal in the former), and petiole height (higher than long). *Vollenhovia escherichi* Forel, 1911 from Sri Lanka can be easily differentiated from the new species based on its size (TL ≤2.1 mm) as per Forel (1911), and pale yellowish-brown integumental coloration. With *V. piroskae* Forel, 1912 (from Seychelles), *V. keralensis* shares the clypeus with a single median tooth, but the former can be distinguished by its smaller size (TL 2.2–2.4 mm) and mandible with 6–7 teeth while *V. keralensis* is larger (TL 3.53–3.65 mm) and worker having eight teeth on the mandible. *V. keralensis* is distinguished from the Himalayan *V. gastropunctata* by the workers of the former having masticatory margin with a large apical and preapical teeth and followed by five teeth of equal

Image 16. *Vollenhovia keralensis* sp. nov.: A—habitat at the type locality | B—foraging worker, searching bracket-fungus for beetle larva in a dead wood on forest floor. © Kalesh Sadasivan.

size, and body length (≤2.55 mm in *V. gastropunctata*). Additionally, the anterior margin of clypeus is convex with a single median tooth in *V. keralensis* which is concave in *V. gastropunctata*.

Key to *Vollenhovia* species of Indian subcontinent based on the worker caste

1) Comparatively small species (TL ≤2.1 mm); Head small HW less than 0.4 mm; color pale yellowish-brown ..... *V. escherichi* Forel, 1911
- Comparatively larger species (TL >2.1 mm); HW more than 0.5 mm; color dark brown to black 2

2) Anterior clypeal margin convex with a single median tooth 3
- Anterior clypeal margin concave with no such median tooth 4

3) Size smaller (TL <2.50 mm); mandible with 7 teeth or less..... *V. piroskae* Forel, 1912
- Size larger (TL >3.50 mm); mandible with 8 teeth ..... ***V. keralensis* sp. nov.**

4) Mandible with 6 teeth or less ..... *V. oblonga* (Smith, 1860) and its subspecies
- Mandible with 7 teeth .... *V. gastropunctata* Bharti & Kumar, 2013

DISCUSSION

The report of the three new generic records from the Western Ghats region of peninsular India presents interesting observations on ant biogeography of the Indian region.

The new *Proceratium* species is a hypogaeic denizen of wet tropical rainforests at mid-elevation (900–1,200 m). The nearest record of the genus *Proceratium* in the Indo-Malayan region is Meghalaya in India and Bhutan, and in the Afrotropical region from Mauritius, Madagascar and mainland Africa. The discovery of the new species of *Proceratium* in peninsular India provides support to vicariant speciation of its ancestors from Gondwana into mainland Africa, Malagasy region and Indian subcontinent. There are similar examples of such evolutionarily intriguing distributions of Gondwanan hypogaeic lifeforms between Africa, Malagasy, and Kerala state in Western Ghats. The fossorial amphibian *Nasikabatrachus sahyadriensis* Biju & Bossuyt, 2003 from the family Nasikabatrachidae in Kerala is related to Sooglossidae, an amphibian family found only in the Seychelles archipelago (Zachariah et al. 2012). Other examples are found in subterranean freshwater cave fishes of the genus *Horaglanis* Menon, 1950 (Clariidae) which are related to *Uegitglanis* Gianferrari, 1923 (Uegitglanididae) from Somalia (Menon 1951; Silas 2010), and decapod crustaceans of the genus *Eurindicus* De Grave, Arjun & Raghavan, 2018 (Euryrhynchidae) which are related to three west African species (De Grave et al. 2018).

The nearest distribution range of *Zasphinctus* is mainland Africa on the west and Thailand on the east. The absence of the genus from middle east Asia (AntWeb, 2021), Madagascar (Fisher 1996), Mauritius, Reunion, and Seychelles is interesting, although may also be due to collection bias or regional extinction. Most species of *Zasphinctus* are recorded from the Australasian region (AntWeb 2021), with one species recorded from Thailand (Jaitrong 2016). The known distribution of *Zasphinctus* aligns with the tectonics of the region, as Africa and India were in close contact after the Indian plate separated from Madagascar-

Seychelles about 65 mya (Briggs 2003), while the Indian plate had already come into contact with the Eurasian plate (55–65 mya). During the northward migration of India, its land mass maintained close contact with mainland Africa. Since the epicentre of speciation of *Zasphinctus* seems to be the Australasian region, the ancestor of this genus might have reached Africa via the Indian plate. This highlights the fact that the depiction of India as a completely isolated island in the Cretaceous is erroneous (Briggs 2003) and the question raised by Fisher (1996) with respect to the absence of a significant number of endemic taxa in India. Thus, *Zasphinctus*, is a good myrmecological example of east to west faunal dispersal to Africa through India in the late Cretaceous.

The known representatives of genus *Vollenhovia* from the Indian region were from the Himalayas, Burma, rest of the Indo-Malayan region in southeastern Asia, and the associated islands in the Bay of Bengal. The subspecies *V. oblonga levithorax* Emery 1889 is known from the Tenasserim hills of Indo-Malaysia (Bingham, 1903), and *V. oblonga alluaudi* Emery, 1894 is reported from the nearby Andaman & Nicobar Islands. For the Andaman & Nicobar Islands, there are also records of *V. penetrans* (Smith, 1857) as per Bharti (2016) and AntWeb (2021). Sri Lanka has one endemic species – *Vollenhovia escherichi* Forel, 1911, with the remaining members of this genus distributed in the Southeast Asian region and Australasia and further into the Americas (AntWeb 2021). The genus is currently thought to be absent in mainland Africa, Mauritius, and Reunion. Interestingly, the Seychelles Islands in the Malagasy bioregion has two taxa, *V. oblonga* Emery, 1894 (subspecies *alluaudi*) and *V. piroskae* Forel, 1912. Both these species are represented in the Australasian, Oceania, and Andamans in Malayan bioregions, but curiously absent from peninsular India as far as known, even though the latter is closer to the Malagasy region. This presents an interesting mode of distribution as explained below. The ancestors of *Vollenhovia* must have reached the Indian peninsula after its separation from mainland Africa in the Paleogene. By this time, Africa and Seychelles were probably completely separated from the northward-moving Indian plate (Briggs 2003). It may seem plausible that the colonisation of Seychelles might be a recent event for *V. piroskae*, but the other taxon probably colonized much earlier and had sufficient time to evolve as subspecies (*V. o. alluaudi),* and hence are not recent introductions. This biogeographical scenario can probably be a result of a dispersal event from Australasian and Oceania bioregions across the Indian Ocean, rather than by vicariance from Gondwana, as evidenced by their absence in mainland Africa. The mode of arboreal life and lignicolous nesting in dead logs might offer a clue for the survival of colonies and queens along dispersal across the open seas (Brown 1973; Fisher 1996). The dispersal events could be initiated by cyclones of Bay of Bengal and fuelled by the oceanic currents, an example of the latter is the south equatorial current of the Indian Ocean, that run between the Indo-Malayan region and Seychelles (Tomczak & Stuart 2003).

In conclusion, the new distribution records of the three genus add interesting observations on biogeographic origins of ants for the Indian region. The genus *Proceratium* is a good candidate for a vicariance model of speciation from Gondwana into the Indian plate. *Zasphinctus* adds to the body of evidence of linking Africa to mainland Asia by the Indian plate during late Cretaceous. Finally, *Vollenhovia* is a good example of east-to-west faunal dispersal from Malayan bioregion to Western Ghats of India in the Paleogene, in similarity to other ant genera with an Indomalayan distribution like *Tyrannomyrmex* Fernández, 2003 and *Indomyrma* Brown, 1986 (Zryanin 2012). The addition of these new taxa to the building body of molecular phylogenies could provide interesting avenues for future biogeographic analyses.

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