Two new *Prenolepis* species (Hymenoptera: Formicidae) from Indomalaya and Australasia, with a redescription of *P. dugasi* from Vietnam

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Abstract

*Prenolepis* is a lineage of formicine ants with its center of diversity in the Old World tropics. Three more *Prenolepis* species are added to the Indomalayan and Australasian fauna and another is synonymized, bringing the total number of *Prenolepis* species worldwide to 19. Two new species are described: *P. nepalensis* from Nepal and *P. lakekamu* from Papua New Guinea, the latter being the first in the genus east of Wallace’s Line. Additionally, *P. dugasi* Forel (comb. rev.) from Vietnam is transferred from *Nylanderia* and redescribed. Based on morphology, each of the three species appears to be most closely-related to other species found predominantly in or nearest to their respective bioregions: *P. nepalensis* most resembles *P. darlena*, *P. fisheri*, and *P. fustinoda*; *P. lakekamu* bears strongest resemblance to *P. jacobsoni*, *P. jerdoni*, and *P. subopaca*; and *P. dugasi* most resembles *P. melanogaster*. Descriptions, illustrations and images are provided for all three species. One new synonymy is proposed: *P. angulinoda* Chen & Zhou 2018 = *P. fustinoda* Williams & LaPolla 2016. An updated key for workers of all extant *Prenolepis* species is also included.

Key words: Formicinae, *Prenolepis*, genus-group, new species, Papua New Guinea, Nepal, Vietnam

Introduction

*Prenolepis* was the first described genus in what today is called the *Prenolepis* genus-group. *Prenolepis* was originally described by Mayr (1861) from the type species *Tapinoma nitens* Mayr, 1853 (= *Prenolepis nitens*). Soon after, Motchoulsky (1863) described the genus *Paratrechina*, which was later synonymized with *Prenolepis* by Dalla Torre (1893). *Paratrechina* was later returned to generic status by Emery (1925).

Until recently, taxonomic treatment of *Prenolepis* genus-group ants has relied on uncertain and in many cases poorly delineated morphological characters. Using molecular data, LaPolla et al. (2010a) revised the *Prenolepis* genus-group and proposed several major taxonomic changes, including the elevation of *Nylanderia* and *Paraparatrechina* to generic status. The genus *Prenolepis* was also discovered to be polyphyletic with respect to a lineage from the Greater Antilles, which was soon after described as an entirely new genus, *Zatania* (LaPolla et al. 2012). Since the revision of the generic level taxonomy, species-level revisions and descriptions have been completed for part of *Nylanderia* (LaPolla et al. 2011a; LaPolla et al. 2011b; Kallal & LaPolla 2012), *Paratrechina* (LaPolla et al. 2013; LaPolla & Fisher 2014b), and *Paraparatrechina* (LaPolla et al. 2010b; LaPolla & Fisher 2014a).

A recent taxonomic revision of *Prenolepis* uncovered new morphological characters that are useful for diagnosis of the genus (Williams & LaPolla 2016). As a result, four new *Prenolepis* species were described and three others were transferred from *Prenolepis* to *Paratrechina* and *Nylanderia*. Following the global revision of *Prenolepis* by Williams & LaPolla (2016), four more new species from China have since been described (Chen & Zhou 2018).

Although the majority of *Prenolepis* species diversity resides in Indomalaya, natural history descriptions are severely lacking and most of what is known about the genus comes from studies of *P. imparis* in North America (Wheeler 1930; Talbot 1943; Tschinkel 1987) and *P. nitens* in Europe (Lörinczi 2016). However, as the taxonomy...
improves, natural history is becoming easier to describe and attribute to a species. In comparison to other *Prenolepis* genus-group genera, *Prenolepis* (sensu stricto) collections in Indomalaya and Australasia are relatively rare. One possible explanation for this is that *Prenolepis* species from these regions are arboreal or most active in the evening, and day collecting methods and pitfall traps are unlikely to capture them. Interestingly, Peeters & Yong (2017) discovered that *P. subopaca* nests in the soil but forages in trees in the evening, presumably tapping into a substantial honeydew source in the canopy. Workers coming down from the canopy also exhibit a physogastric state, superficially similar to but physiologically different from the corpulent state caused by hypertrophic fat bodies in callow workers of *P. imparis* (Tschinkel 1987) and *P. nitens* (Lörinczi 2016).

In the present study, we add two *Prenolepis* species to the Indomalayan fauna, one to the Australasian fauna, and propose one synonymy to bring the total number of species known in the genus worldwide to 19. Two new *Prenolepis* species are described: *P. nepalensis* from Nepal and *P. lakekamu* from Papua New Guinea. Also included is a redescription and transfer of *P. dugasi* from *Nylanderia*. The synonymy of *P. angulinoda* with the senior *P. fustinoda* is proposed.

**Materials and methods**

**Sources of material.** Specimens examined for this study are deposited in the following institutions:

MHNG  Muséum d’Histoire Naturelle, Geneva, Switzerland
USNM  National Museum of Natural History, Washington D.C., U.S.A.

**Measurements and imaging.** All measurements were taken using a Leica S8 APO dissecting microscope with a Mitutoyo IT-012U digital stage micrometer, recorded to the nearest 0.001 mm, and rounded to two decimal places for presentation. For each species, the total number of specimens measured is designated as *n* in parentheses. Minimum and maximum measurements and indices are provided. Imaging includes dorsal, full-face, and lateral views of workers of each species. For the *P. lakekamu* holotype, digital color images were created using a Q-imaging digital camera and Syncroscopy Auto-Montage software. High-quality images of the *P. nepalensis* holotype and the *P. dugasi* lectotype were already available from www.AntWeb.org and were therefore downloaded for this study. Measurements and indices, some of which are modified from LaPolla (2009) and Williams & LaPolla (2016), are defined as:

- **CMC** (Cephalic Macrosetal Count): Total number of erect macrosetae found posterior to the midline of the head.
- **EL** (Eye Length): In full-face view, the maximum anteroposterior length of the compound eye.
- **HL** (Head Length): In full-face view, the length from a line drawn across the posterior margin of the head to a line drawn across the anteriormost point of the clypeal margin.
- **HW** (Head Width): In full-face view, the maximum width of the head between the lateral margins, excluding the compound eyes.
- **MMC** (Mesonotal Macrosetal Count): On the mesonotum, the number of erect macrosetae found to one side of the sagittal plane.
- **PMC** (Pronotal Macrosetal Count): On the pronotum, the number of erect macrosetae found to one side of the sagittal plane.
- **PrMC** (Propodeal Macrosetal Count): On the propodeum, the number of erect macrosetae found to one side of the sagittal plane.
- **SL** (Scape Length): Excluding the condyle, the maximum length of the first antennal segment.
- **TL** (Total Length): HL + WL + GL (Gaster Length)
- **WL** (Weber’s Length): In lateral view, the maximum length from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.
- **CI** (Cephalic Index): (HW/HL) x 100
- **REL** (Relative Eye Length Index): (EL/HL) x 100
- **REL2** (EL/HW) x 100
- **SI** (Scape Index): (SL/HW) x 100
Results

Systematic Treatment

The following combination of morphological characters place the three species treated here in the genus *Prenolepis*: (1) the mesonotum is curved and depressed immediately posterior to the pronotum, resulting in a constriction of the mesosoma; (2) mesonotal and metanotal sutures are shallow or incomplete; (3) longitudinal rugae extend from the mesonotum to the mesopleuron; and (4) eyes are placed far posterior to the midline of the head. See Williams & LaPolla (2016) for a complete discussion of these characters and others found in *Prenolepis* species.

Synopsis of Species

*Prenolepis angularis* Zhou, 2001
*Prenolepis cyclopia* Chen & Zhou, 2018
*Prenolepis darlena* Williams & LaPolla, 2016
*Prenolepis dugasi* Forel, 1911, **comb. rev.**
*Prenolepis fisheri* Bharti & Wachkoo, 2012
*Prenolepis fustinoda* Williams & LaPolla, 2016
= *Prenolepis angulinoda* Chen & Zhou, 2018, **syn. nov.**
*Prenolepis imparis* (Suy, 1836)
*Prenolepis jacobsoni* Crawley, 1923
*Prenolepis jerdoni* Emery, 1893
*Prenolepis lakekamu, sp. nov.*
*Prenolepis mediops* Williams & LaPolla, 2016
*Prenolepis melanogaster* Emery, 1893
*Prenolepis naorogi* Forel, 1902
*Prenolepis nepalensis, sp. nov.*
*Prenolepis nitens* (Mayr, 1853)
*Prenolepis quinquedenta* Chen & Zhou, 2018
*Prenolepis shanialena* Williams & LaPolla, 2016
*Prenolepis striata* Chen & Zhou, 2018
*Prenolepis subopaca* (Emery, 1900)

Updated key to the worker caste of extant *Prenolepis* species

This key is modified from Williams & LaPolla (2016) and includes the species from Chen & Zhou (2018).

1. In profile view, dorsal face of propodeum flattened and much longer than the rounded posterior face, giving propodeum an elongate appearance (Fig 10); scale of petiole flattened, forming a right angle at its anterodorsal point. 
   - In profile view, dorsal face of propodeum about as long as posterior face and propodeum does not appear elongate (Fig 13); scale of petiole either rounded or pointed and does not form a right angle at its anterodorsal point. 
   - P. lakekamu
2. In profile view, petiole narrow and elongate with rounded dorsal apex of the scale. 
   - In profile view, petiole short and broad and forward-inclined with sharply-angled dorsal apex of the scale. 
   - P. jacobsoni
3. Ocelli absent; compound eyes surpassing lateral margins of head in full-face view (Fig 2); scapes with appressed setae. 
   - Three small ocelli present; compound eyes not surpassing lateral margins of head in full-face view (Figs 1 and 3); scapes with erect setae. 
   - P. lakekamu
4. Small (TL < 2.70mm), robust with short legs, antennae, and mesosoma; body light to medium brown; in profile view, posterodorsal part of propodeum obtusely angled; petiolar scale low in profile with weakly sinuate anterodorsal outline. 
   - Medium to large (TL > 2.70mm), gracile with elongate legs, antennae, and mesosoma; body uniformly dark brown to black; posterodorsal part of propodeum in profile view roundly produced, much higher than pronotum; petiolar scale high in profile with roughly subtriangular anterodorsal outline. 
   - P. jacobsoni
5. Overall cuticle shiny and smooth to lightly reticulate; pubescence completely absent on dorsal surface of pronotum, propo-
deum, and gaster .......................... P. jerdoni
- Overall cuticle dull and finely reticulate; thick patches of pubescence present on dorsal surface of pronotum, propodeum, and gaster .......................... P. subopaca
6. Body uniformly dark brown to black; head roughly subtriangular in shape; cuticle of head lightly reticulate; ectal surface of mandibles with light longitudinal striations; in profile view, ventral surface of petiole almost straight ...................... P. fisheri
- Head and mesosoma light brown in overall color; ectal surface of mandibles smooth and shiny; in profile view, ventral surface of petiole is curved upward toward anterior articulation with metanotum .......................... 7
7. Body light brown with little to no difference in color among head, mesosoma, and gaster; head roughly square in full-face view; cuticle of head lightly reticulate; in profile view, dorsal outline of petiolar scale roughly subtriangular in shape ........................................ 7
- Head and mesosoma light brown and gaster distinctly dark brown to black; head roughly subtriangular in full-face view; cuticle of head finely rugoreticulate, giving dull appearance; in profile view, petiole club-shaped with dorsal outline of petiolar scale rounded. .......................... P. fustinoda
8. In full-face view, compound eyes strongly convex, surpassing lateral margins of head .......................... P. naoroji
- In full-face view, compound eyes subcircular and not surpassing lateral margins of head .......................... 9
9. Body medium to dark brown with dark brown to gaster; cuticle of propodeum finely rugoreticulate .......................... 10
- Color variable; cuticle of propodeum smooth and shiny .......................... 11
10. Cuticle of head smooth and shiny .......................... P. cyclopia
- Cuticle of head finely rugoreticulate, giving dull appearance .......................... P. striata
11. Three small ocelli present; head subtriangular in shape with straight posterior margin (Figs 1 and 3) .......................... 12
- Ocelli absent; head shape and posterior margin variable, but not subtriangular .......................... 13
12. Body light to medium brown; torulae do not overlap with posterior border of clypeus (Fig 1); clypeal tooth with single seta extending from its point found medially on anterior border of clypeus; erect macrosetae on dorsum of head; abundant suberect setae on scapes and legs; no appressed pubescence on scapes and legs; in profile view, mesonotum is continuous with pronotum (Fig 4) .......................... P. dugasi
- Body medium to dark brown; torulae overlap with posterior border of clypeus (Fig 3); no medial clypeal tooth on anterior border of clypeus; no erect macrosetae on dorsum of head, scapes, and legs; scapes and legs are covered in appressed pubescence; in profile view, mesonotum humped anteriorly and discontinuous with pronotum (Fig 6) .......................... P. nepalesis
13. Large (TL > 4.25mm); in profile view, propodeum with rounded dorsal face; head and mesosoma yellow-brown, and gaster dark brown to black .......................... P. melanogaster
- Small to medium (TL < 4.25mm); in profile view, propodeum with flat to softly rounded dorsal face, posterodorsally obtusely angled .......................... 14
14. Body dark brown, with faint blue cuticular iridescence .......................... P. angularis
- Body light to dark brown, without faint blue cuticular iridescence .......................... 15
15. Compound eyes round in shape, medium-sized (distinctly smaller than those of other Prenolepis species); interocellar distance relatively long .......................... P. mediops
- Compound eyes oval in shape, relatively large; interocellar distance relatively short .......................... 16
16. Ectal surface of mandibles smooth and shiny, without longitudinal striations; in profile view, mesonotum humped anteriorly and discontinuous with pronotum .......................... P. shanialena
- Ectal surface of mandibles with shallow to deep longitudinal striations; in profile view, mesonotum continuous with pronotum .......................... 17
17. Ectal surface of mandibles with shallow longitudinal striations; mandibles with 5 teeth on masticatory margin; distributed in China (Hunan) .......................... P. quinquecincta
- Ectal surface of mandibles with deep longitudinal striations; mandibles with 5-7 teeth on masticatory margin; distributed in Europe or North America .......................... 18
18. In profile view, mesosoma more robust at mesonotal constriction; distributed across southeastern Europe, the Balkan Peninsula, Turkey, and east to Georgia .......................... P. nitens
- In profile view, mesosoma slender at mesonotal constriction; distributed across North America, from southern Canada to Mexico .......................... P. imparis

Synonymy

Prenolepis fustinoda Williams & LaPolla, 2016
= Prenolepis angulinoda Chen & Zhou, 2018, syn. nov.

Notes: The recently described Prenolepis angulinoda bears remarkable resemblance to Prenolepis fustinoda from Nepal. The holotypes for both have the same characteristic shape of the petiole and mesosoma in profile and an identical overall color pattern with a light brown head and mesosoma, and a dark brown to black gaster. The tarsi, trochanters, and intersegmental leg joints in both are also pale yellow and much lighter than the femora and tibiae, which are medium to dark brown in color. Furthermore, the measurements of P. angulinoda provided by Chen &
Zhou (2018) fall within range of those recorded for *P. fustinoda* (Williams & LaPolla 2016). This synonymy expands the native range of *P. fustinoda* to also include the Guizhou province of China.

![Figures 1–3. Illustrations of head shapes in full-face view for all three species. 1, *P. dugasi*; 2, *P. lakekamu*; 3, *P. nepalensis.*](image)

![Figures 4–6. Illustrations of mesosoma shapes in profile view for all three species. 4, *P. dugasi*; 5, *P. lakekamu*; 6, *P. nepalensis.*](image)

**Species Descriptions**

*Prenolepis dugasi* Forel, 1911, comb. rev.

Figs. 7–9 (worker)


**Worker diagnosis:** A clypeal tooth with a single seta extending from its point found medially on the anterior border of the clypeus (Fig 1). This species also has three small ocelli on the head.

**Compare with:** *P. melanogaster.*

**Worker. Measurements (n=5):** CMC: 12–17; EL: 0.16–0.18; HL: 0.67–0.72; HW: 0.61–0.70; MMC: 2–3; PMC: 4–5; PrMC: 2–3; SL: 0.64–0.70; TL: 2.53–2.80; WL: 0.80–0.91; CI: 91–96; REL: 23–25; REL2: 24–26; SI: 99–105.
Light to medium brown, with gaster (and sometimes head) darker than mesosoma; overall cuticle smooth and shiny; decumbent setae on head; long, erect macrosetae on head, mesosoma, and gaster; abundant suberect setae on scapes and legs; head about as long as broad and subtriangular in shape with indistinct posterolateral corners and a straight posterior margin; three small ocelli present; compound eyes moderately large and convex, but do not surpass lateral margins of head in full-face view; torulae do not touch posterior border of clypeus; anterior border of clypeus without prominent anterolateral lobes (Fig 1); single clypeal tooth with an erect seta projecting from its point, located medially on anterior border of clypeus; mandibles with 5 teeth on masticatory margin; ectal surface of mandibles smooth and shiny; in profile view, pronotum is rounded and continuous with mesonotum, which flatly declines posteriorly at a shallow angle before abruptly deepening at mesosomal constriction; propodeum is obtusely angled with flat dorsal and posterior faces; dorsal apex of petiole scale is sharply angled and forward-inclined (Fig 4).

Notes: Although this species most closely resembles *P. melanogaster*, the latter is still quite distinct and confusion between the two is very unlikely. *Prenolepis dugasi* is much smaller in comparison, does not have the distinct body color pattern seen in *P. melanogaster* (yellow-brown head and mesosoma with dark brown to black gaster), has suberect rather than erect setae on the scapes, and fewer erect macrosetae overall across the head, mesosoma, and gaster. Additionally, *P. melanogaster* has a head that is broader than long, with scapes that are about a third longer than the head width. *Prenolepis dugasi* has a head that is about as long as it is broad, and the scapes are about as long as the head is wide. *Prenolepis dugasi* also has three small ocelli, while *P. melanogaster* does not have any ocelli at all.

*Prenolepis lakekamu*, sp. nov.
Figs. 10–12 (worker)

Holotype worker, PNG: Gulf Province, Ivimka Res. Station, Lakekamu Basin; 7°44’S, 146°30’E; elev. 120 m; 24.xi.1999; S.L. Heydon (USNMENT01126705) (USNM). 1 paratype worker, same locality as holotype (USNMENT01126706) (USNM).
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Worker diagnosis: Gracile mesosoma with an obtuse angle forming where the pronotum and mesonotum meet, and a sharp decline in the mesonotum just posterior to the pronotum, followed by an upward deflection that flattens out anterior to the metanotum (Fig 2). The dorsal face of the propodeum is distinctly flat and much longer than the rounded posterior face, giving the propodeum an elongate profile. The petiole is low in profile and has a distinct shape, with a flattened scale and a right angle formed at its anterodorsal point, and a weakly sinuate anteroventral outline (Fig 5).

Compare with: P. jacobsoni, P. jerdoni, P. subopaca

Worker. Measurements (n=2): CMC: 14; EL: 0.15–0.17; HL: 0.58; HW: 0.50–0.52; MMC: 1; PMC: 1–2; PrMC: 1–2; SL: 0.68–0.69; TL: 2.38–2.45 WL: 0.83–0.87; CI: 87–88; REL: 26–28; REL2: 30–32; SI: 133–135.

Yellow mesosoma, legs, and antennae with medium to dark brown head and gaster; entire cuticle smooth and shiny; very long, erect macrosetae on head, mesosoma, and gaster; abundant suberect to erect setae on scapes and legs; head slightly longer than broad and round in shape with indistinct posterolateral corners and convex posterior margin; no ocelli present; compound eyes moderately large and convex, slightly surpassing lateral margins of head in full-face view; torulae do not touch posterior border of clypeus; clypeus strongly medially convex with prominent anterolateral lobes (Fig 2); mandibles with 5 teeth on masticatory margin; ectal surface of mandibles smooth and shiny; in profile view, mesosoma is gracile; pronotum is mostly flat and inclines posteriorly; an obtuse angle forms where pronotum and mesonotum meet, and mesonotum sharply declines with an upward deflection posteriorly that flattens just anterior to metanotum; propodeum is posteriorly rounded; dorsal face of propodeum is flat and longer than posterior face; petiole scale low in profile; anterodorsal surface of petiole forms a right angle and does not rise high above as an apex, but instead is flat anteriorly and gradually declines at about a 20 degree angle posteriorly; ventral surface of petiole is entirely rounded with a weakly sinuate anteroventral outline (Fig 5).

Etymology: The specific epithet is named after the Lakekamu Basin, where the type series was collected.
**Notes:** This species most strongly resembles the three species found mostly across maritime Indomalaya (P. jacobsoni, P. jerdoni, and P. subopaca) but is instead known only from Papua New Guinea, east of Wallace’s Line. It is also most readily distinguished morphologically from these other three species by its distinct color pattern—having a yellow mesosoma and medium to dark brown head and gaster—and its flattened, more elongate propodeum. The above three species and P. lakekamu each have a petiole shape distinct among them and unlike those of all other Prenolepis species. The petiole of P. lakekamu has a weakly sinuate anterodorsal outline that most strongly resembles what is seen in P. jacobsoni, but P. lakekamu lacks the diagnostic prominent anterodorsal process seen in P. jacobsoni and instead has a gently rounded ventral surface. The color pattern seen in P. lakekamu is similar to that of P. melanogaster, but P. melanogaster is much larger (TL > 4.5 mm), has a head that is slightly broader than long with eyes spaced far apart, and far more numerous erect macrosetae all across the head, mesosoma, and gaster.

*Prenolepis nepalensis*, sp. nov.
Figs. 13–15 (worker)

Holotype worker, NEPAL: 4 km SSW Pokhara; 28°12'N, 83°58'E; elev. 900 m; *Schima-Castanopsis* forest; low vegetation; 10.xii.1988; P.S. Ward 9670-7 (ANTWEB CASENT0281462) (USNM).

**Worker diagnosis:** Posterolateral borders of the clypeus are shallow, making the cuticle of the clypeus appear continuous with that of the gena (Fig 3). Three small ocelli present. Mesosoma is robust and compact. Pronotum is rounded and discontinuous with the mesonotum, which forms a dorsal hump anteriorly (Fig 6). Petiole is forward-inclined, subtriangular, and not elongate (Fig 6). A distinct sparsity of long macrosetae on the head and mesosoma. Scapes and legs with an abundance of smaller, decumbent setae and pubescence.

**FIGURES 13–15.** *Prenolepis nepalensis* holotype worker ANETWEB CASENT0281462. Lateral, full-face, and dorsal view of the body. Images were downloaded from www.AntWeb.org and were taken by Zach Lieberman.
Compare with: *P. darlena*, *P. fisheri*, *P. fustinoda*

**Worker.** Measurements (n=1): CMC: 2; EL: 0.19; HL: 0.72; HW: 0.67; MMC: 0; PMC: 2; PrMC: 2; SL: 0.75; TL: 2.86; WL: 0.92; CI: 93; REL: 26; REL2: 28; SI: 112.

Uniformly medium to dark brown head, mesosoma, gaster, legs, and antennae; entire cuticle smooth and shiny, with some light reticulation on head and gaster; sparse erect macrosetae on head and mesosoma; longer erect macrosetae on gaster; no erect macrosetae on scapes or legs, except for long, erect hairs on lateral margins of procoxae; decumbent setae and sparse pubescence cover entire head, mesosoma, and gaster; scapes and legs covered in dense pubescence; head about as broad as long and subtriangular in shape, with indistinct posterolateral corners; three small ocelli present; eyes moderately large and convex, but do not surpass lateral margins of head in full-face view; torulae overlap with posterior border of clypeus; clypeus without prominent anterolateral lobes; posterolateral borders of clypeus also relatively shallow, so that cuticle of clypeus and gena appears continuous (Fig 3); mandibles with 5 teeth on masticatory margin; ectal surface of mandibles smooth and shiny; in profile view, mesosoma is overall robust and compact; pronotum is rounded and discontinuous with mesonotum, which is also rounded and abruptly rises above pronotum, and declines posteriorly (Fig 6); metathoracic spiracles abruptly rise above the mesonotum at the point of mesosomal constriction; propodeum is slightly rounded with a flattened dorsif face; dorsal apex of petiole scale is low in profile and forward-inclined (Fig 6).

**Etymology:** The specific epithet is named after the country of Nepal, where the holotype was collected.

**Notes:** This species most strongly resembles the other three that are known from Nepal and nearby regions (*P. darlena*, *P. fisheri*, and *P. fustinoda*) but can most readily be distinguished by its lack of long, erect macrosetae and distinct body shape. Of these four species, *P. nepalensis* is the only one to have: (1) relatively shallow posterolateral clypeal borders, making the cuticle of the clypeus and gena appear continuous (Fig 3); (2) a sparse layer of pubescence or decumbent hairs across the mesosoma, rather than an abundance of erect macrosetae; (3) scapes that are densely covered in pubescence and lack erect macrosetae; (4) a distinctly more robust and compact mesosoma, with the mesonotum rounded and rising above the pronotum; and (5) a forward-inclined triangular petiole that is relatively short in length.

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