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Description of *Prenolepis rinpoche* sp. nov. from Nepal, with discussion of Asian *Prenolepis* species biogeography

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ABSTRACT. *Prenolepis rinpoche* sp. nov. is described, imaged, and compared with similar species from South and Southeast Asia. This new species description raises the total number of extant *Prenolepis* species to 20. Distribution maps of all Asian *Prenolepis* species are included. Further justification for this new species description is provided using principal component analysis (PCA) of linear morphometric data collected from 15 *Prenolepis* species. This species is most similar morphologically to *P. darlena* Williams & LaPolla 2016, *P. fisheri* Bharti & Wachkoo 2012, *P. fustinoda* Williams & LaPolla 2016, *P. nepalensis* Williams & LaPolla 2018, and *P. shanialena* Williams & LaPolla 2016. The geographical distributions of these six similar species are concentrated around montane areas of South and Southeast Asia, including The Himalayas in Nepal and northern India. Similar morphology suggests that these six species together form a high elevation clade. A re-evaluation of the literature and distribution records confirms there are presently four species known to Nepal, two of which are likely endemic: *P. nepalensis* and *P. rinpoche*. Most *Prenolepis* species, including *P. rinpoche*, are found at elevations above 1200 meters, suggesting an evolutionary pathway to temperate climate adaptation and winter activity in species such as *P. imparis* Say (1836) in the Nearctic and *P. nitens* Mayr (1853) in the Palearctic.

Keywords	biodiversity, Himalayas, Lasiini, taxonomy, Tibetan Plateau, winter ant
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INTRODUCTION

Prenolepis was originally described by Mayr (1861), but a set of reliable diagnostic morphological synapomorphies for the genus was only discovered six years ago by Williams & LaPolla (2016). Previously, the generic boundaries of *Prenolepis* were poorly understood and definitions of the genus varied over time (Forel 1878, 1893; Ashmead 1905; Wheeler 1970; Agosti 1991; Bolton 2003). The evolutionary relationships of *Prenolepis* and six other Lasiine genera, collectively called the *Prenolepis* genus-group, were clarified using molecular phylogenetics (LaPolla et al. 2010, 2012). With generic boundaries of *Prenolepis* being stabilized with both morphological and molecular data, 13 total *Prenolepis* species were recognized in a global taxonomic revision by Williams & LaPolla (2016), four of which were described as new. Chen & Zhou (2018) contributed four new species from

China, and Williams & LaPolla (2018) updated the fauna with two new species, one synonymy, and one comb. rev. In the present study, I describe and provide images of *P. rinpoche* from Nepal. I also provide updated distribution maps to all 18 Asian/Australasian *Prenolepis* species and discuss their biogeography.

Prenolepis has a disjunct distribution with 20 total extant species: one in North America, one in Europe, 17 across South and Southeast Asia, and one in Papua New Guinea (Williams & LaPolla 2016, 2018; Chen & Zhou 2018). One fossil species, †*P. henschei* Mayr 1868, is known from Baltic amber and other northern European amber deposits (LaPolla & Dlussky 2010). *Prenolepis imparis* in North America and *P. nitens* in southern Europe are among the most collected ants in their respective bioregions, especially in late winter to early spring. Similarly, *Prenolepis* is one of the most collected ant genera from Nepali forests (I. Subedi pers. comm.). However, in most parts of Asia/Australasia, collecting events of *Prenolepis* species are much rarer.

MATERIALS AND METHODS

All three specimens of *P. rinpoche* examined in this study are deposited in the Museum of Comparative Zoology (MCZC), Harvard University, Cambridge, MA, USA.

Measurements and imaging

Measurements of all *P. rinpoche* specimens (n = 3) were recorded to the nearest 0.001 mm using a Mitutoyo IT-012U digital stage micrometer on a Leica S8 APO dissecting microscope. Measurements of all other *Prenolepis* specimens (n = 41) were previously taken by Williams & LaPolla (2016). Images of the *P. rinpoche* holotype were taken at 5x using a Canon EOS 6D Mark II camera with a macro photo MP-E 65mm manual focus lens on a Macropod Pro 3D and Micro Kit System (Macroscopic Solutions, East Hartford, CT, USA). Images were focus stacked using Zerene Stacker. Measurements and indices are defined as:

EL	(Eye Length): In full-face view, maximum anteroposterior length of the compound eye.
EW	(Eye Width): In oblique lateral view, maximum width of the compound eye.
GL	(Gaster Length): In lateral view, maximum length from the anterior most point of the third abdominal segment to the posterior most point of the terminal abdominal segment. Measured only to estimate TL.
HL	(Head Length): In full-face view, length from a line drawn across the posterior margin of the head to a line drawn across the anterior margin of the clypeus.
HLA	(Head Length Anterior): In full-face view, length from a line drawn across the anterior-most points of the compound eyes to a line drawn across the anterior margin of the clypeus.
HLP	(Head Length Posterior): In full-face view, length from a line drawn across the posterior-most points of the compound eyes to a line drawn across the posterior margin of the head.
HW	(Head Width): In full-face view, maximum width of the head between the lateral margins, excluding the compound eyes.
IOD	(Interocular Distance): In full-face view, distance between the medial-most points of the compound eyes.
LHT	(Length of Hind Tibia): Length of the metatibia, excluding the proximomedial part of the articulation with the metafemur.
MW	(Mesonotum Width): In dorsal view, maximum width of the mesonotum.
PDH	(Propodeum Height): In lateral view, height of the propodeum from the base of the metapleuron to the highest point dorsally.
PrW	(Propodeum Width): In dorsal view, maximum width of the propodeum.
PTH	(Petiole Height): In lateral view, maximum height of the petiole.
PTL	(Petiole Length): In lateral view, length of the petiole from the anterior-most point of the peduncle to the posterior margin.
PTW	(Petiole Width): In dorsal view, maximum width of the petiole.
PW	(Pronotum Width): In dorsal view, maximum width of the pronotum.
SL	(Scape Length): In a view perpendicular to the long axis of the scape, maximum length of the scape, excluding the condyle.
TL	(Total Length): HL + WL + GL
TC	(Tooth Count): Number of teeth found on the masticatory margin of one mandible.

WL (Weber's Length): In lateral view, 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
EPI (Eye Position Index): (HLA/HLP) x 100
HTI (Hind Tibia Index): (LHT/HW) x 100
PetHI (Petiole Height Index): (PTH/PTW) x 100
PetLI (Petiole Width Index): (PTL/PTW) x 100
REL (Relative Eye Length Index): (EL/HL) x 100
SI (Scape Index): (SL/HW) x 100

See Electronic Supplementary Material for full locality information and measurements for all specimens used in this study (Table S1).

Principal Component Analysis

All measurements except GL and TL (n = 12) were included in the principal component analysis (PCA). Gaster length was excluded from the PCA because this measurement is highly dependent upon variable flexion, distension, and preservation of abdominal segments. Total length was excluded because it is not an independent measurement from HL and WL. Analysis was performed using the 'prcomp' command in R, and the proportion of variance attributed to each principal component was plotted (Fig. S1) and inspected to ensure that the first two (PC1 and PC2) capture most of the variance. See Table 1 for full summary statistics of PCA.

Table 1. Summary statistics of principal component analysis of 15 *Prenolepis* species, including standard deviation and proportion of variance of PC1-PC17 and correlation coefficients of PC1-PC2.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Std. Dev.	3.66	1.28	0.87	0.68	0.48	0.39	0.31	0.26	0.21
Prop. Var.	0.79	0.10	0.04	0.03	0.01	0.01	0.01	0.00	0.00
Cum. Prop.	0.79	0.89	0.93	0.96	0.97	0.98	0.99	0.99	0.99

	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17
Std. Dev.	0.19	0.18	0.15	0.13	0.11	0.11	0.08	0.07
Prop. Var.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cum. Prop.	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Correlation Coefficients

	HW	EL	EW	SL	HL	WL	PDH	HLP	HLA
PC1	0.89	0.68	0.80	0.85	0.96	0.96	0.91	0.86	0.95
PC2	0.39	-0.62	-0.49	-0.37	0.18	-0.09	-0.10	0.36	0.20

	PW	MW	PrW	PTL	PTH	PTW	LHT	IOD
PC1	0.98	0.95	0.97	0.78	0.81	0.88	0.94	0.88
PC2	0.08	0.04	0.11	-0.46	-0.04	0.27	-0.15	0.41

RESULTS

Systematic Treatment

The three worker specimens examined and described in this study were originally ascribed to *P. shanialena* (Williams & LaPolla 2016: 242), but upon re-examination, they were determined to be a new, undescribed species with multiple key morphological characters: This new species has a quadrate head with a flat posterior margin, the anterior margin of its mesonotum does not rise above the pronotum, and its darker reddish brown head, mesosoma, and abdominal tergites form a strong color contrast with its lighter yellow brown legs and antennae. *Prenolepis shanialena* instead has a round or oval head, the anterior margin of its mesonotum rises as a hump above the pronotum, and its overall color is uniformly light to medium brown with little to no contrast.

Further justification for this new species description is provided through analysis of morphometric data: The PCA (Fig. 4) shows that all three specimens of *P. rinpoche* form a distinct cluster in morphospace, well outside the range of *P. shanialena*. Similarly, index plots (Figs. 5 and 6) indicate distinct clustering of these two species. Biogeography also provides support for this new species description: *P. rinpoche* appears to be endemic to Nepal (Fig. 6A), well outside the Southeast Asian range of *P. shanialena* (Fig. 6B).

The PCA (Fig. 4) and index plots from linear morphometrics (Fig. 5) also provide clues about broader systematic treatment of *Prenolepis* species. Of note, hind tibia length (HTI; Fig. 5C) and scape length (SI; Fig. 5G) separate the genus into two major groups: one with relatively longer legs and scapes belonging to lowland tropical species (*P. jacobsoni*, *P. jerdoni*, *P. lakekamu*, *P. naoroji*, and *P. subopaca*) found primarily near coastlines and on islands and one with relatively shorter legs and scapes including all highland or temperate species represented in the plot (*P. darlena, P. dugasi, P. fustinoda, P. imparis, P. mediops, P. melanogaster, P. nitens, P. quinquedenta, P. rinpoche, P. shanialena,* and *P. striata*). In the PCA plot, the temperate species *P. imparis* and *P. nitens* cluster most closely with primarily high elevation species (*P. darlena, P. fustinoda,* and *P. shanialena*) found throughout mainland South and Southeast Asia. See Fig. 6 for full distributions of Asian species.

Description of the new species

Prenolepis rinpoche sp. nov.

http://zoobank.org/0C69DACC-18E2-49FB-BE6B-A69541BFBBF4

(Figs. 1 – 3)

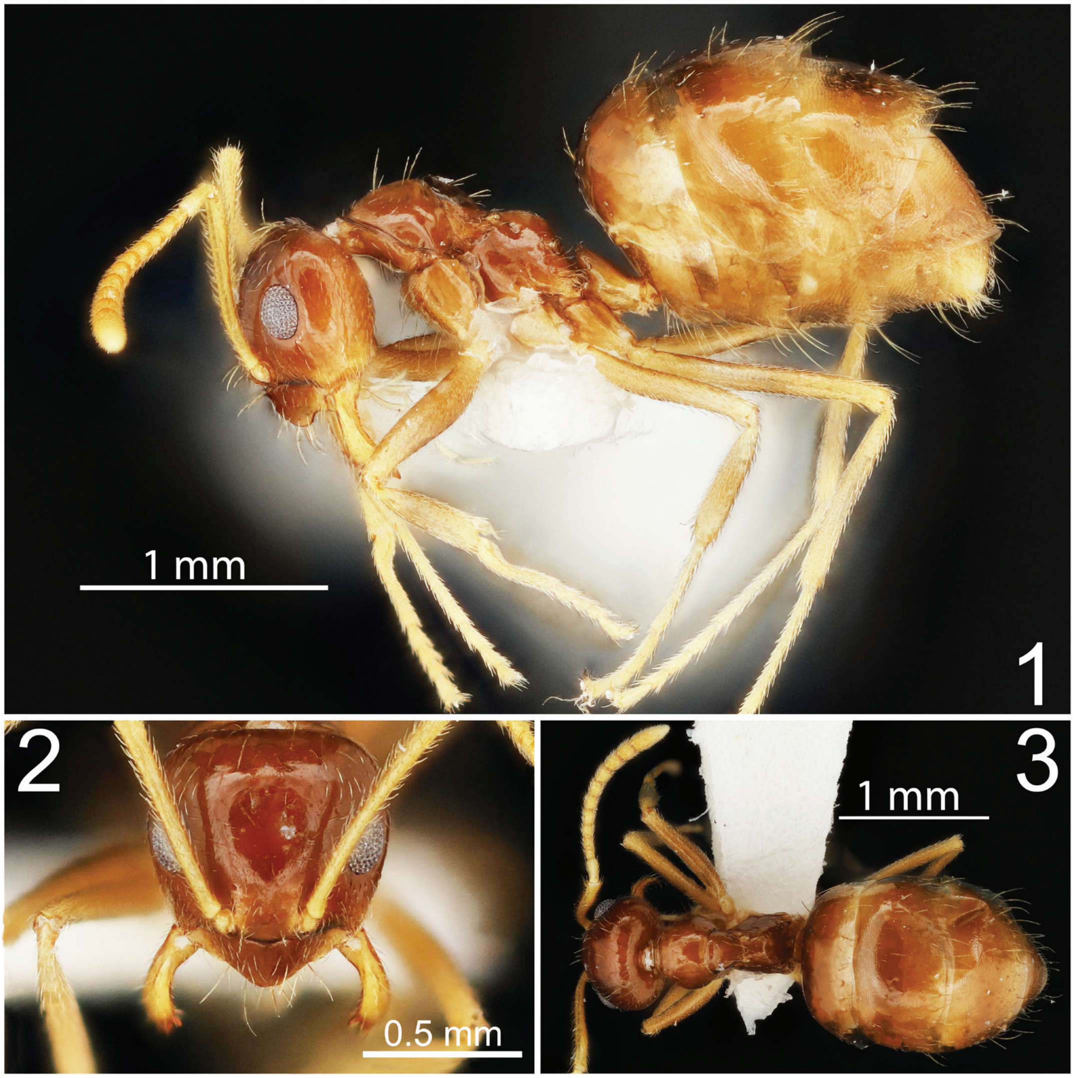
Material examined

Type material. ***Holotype worker*:** Nepal, Gandaki Province, Mustang District, 20 km SSW Jomsom, 28.6167 N, 83.6333 E, 2300 m, 4 Dec 1988, Phil S. Ward #9645 (deposited in MCZC). ***Paratypes*:** 2 workers with same locality information as holotype (deposited in MCZC).

Similar species: *P. darlena, P. fisheri, P. fustinoda, P. nepalensis,* and *P. shanialena*

Description: Light to medium brown in overall color; most of mesosoma, head, and abdominal tergites distinctly darker and reddish, which strongly contrasts with lighter yellow brown antennae and legs; cuticle of most of body smooth and shiny, except for light reticulation on gaster and light mesopleural striations; abundant decumbent setae and pubescence on scapes and legs, except for lateral surfaces of coxae, which lack hair entirely; long, erect setae on pronotum, mesonotum, gaster, and anterior surface of procoxae; macrosetae toward posterior margin of head mostly decumbent, and macrosetae between torulae and near anterior margin of clypeus mostly erect; pubescence mostly concentrated on gena and clypeus, with little to no pubescence found elsewhere on head; sparse patches of pubescence on pronotum and propodeum; no pubescence on mesopleuron or lateral surfaces of propodeum; sparse pubescence scattered across entire surface of gaster; head about as long as broad and quadrate, with flat posterior margin and distinct posterolateral corners; compound eyes large and widely set, but do not surpass lateral margins of head in full-face view; torulae overlap with posterior margin of clypeus; clypeus smooth, shining, and strongly medially carinate with prominent anterolateral lobes on anterior margin; antennae 12-segmented; mandibles subtriangular with 6 teeth on masticatory margin; ectal surface of mandibles smooth and shiny; in profile view, anterior margin of mesonotum does not rise above pronotum; dorsal face of propodeum lightly rounded; dorsal apex of petiole scale is sharply angled and forward-inclined.

Measurements and indices (n = 3): EL: 0.19-0.20; EW: 0.16-0.17; HL: 0.73; HLA: 0.32-0.33; HLP: 0.20; HW: 0.65-0.67; IOD: 0.40-0.43; LHT: 0.82-0.85; MW: 0.25-0.25; PDH: 0.24-0.25; PrW: 0.34-0.36; PTH: 0.23-0.24; PTL: 0.26-0.27; PTW: 0.20-0.23; PW: 0.43; SL: 0.82-0.85; TL: 2.96-3.15; WL: 0.90-0.94; CI: 90-92; EPI: 163-168; HTI: 126; PetHI: 105-113; PetLI: 118-131; REL: 118-131; SI: 126



Figs. 1-3. *Prenolepis rinpoche* holotype worker (MCZENT00532864). Lateral, full-face, and dorsal view of the body.

Comparative notes

Prenolepis rinpoche most strongly resembles five other high elevation species found in South and Southeast Asia: *P. darlena, P. fisheri, P. fustinoda, P. nepalensis,* and *P. shanialena*. This new species is similar to *P. darlena, P. fisheri, P fustinoda,* and *P. nepalensis* in the proportions of the head in full-face view: The heads of these species are broad and subtriangular to quadrate, with widely set eyes. However, unlike these other four, *P. rinpoche* has a much more pronounced medial clypeal keel, decumbent (as opposed to erect) scape macrosetae, and almost entirely lacks sculpturing on the head and mesosoma. The four other species also have an elongated petiole with a rounded apex of the scale, whereas *P. rinpoche* has a petiole more comparable to what is found in most other *Prenolepis* species: It is subtriangular and not elongate (Fig. 5D), with a forward inclined, pointed apex of the scale. See 'Systematic treatment' section (above) for detailed comparison with *P. shanialena*.

Queen: Unknown.

Male: Unknown.

Etymology: The species epithet refers to Guru Rinpoche (‘Precious Guru’) and is an honorific to the legendary figure Padmasambhava, a tantric Buddhist Vajra master who is known and revered throughout Nepal.

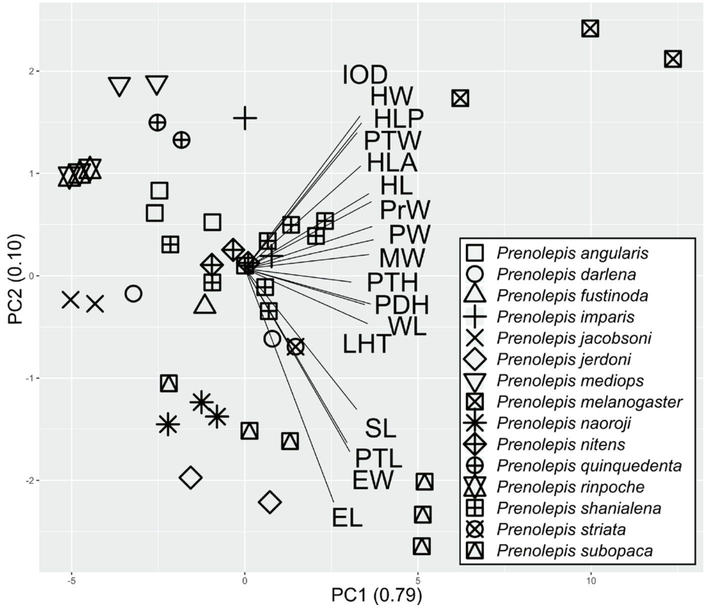


Fig. 4. Principal component analysis of 15 *Prenolepis* species, with loading vectors of all 17 linear measurements used in the analysis. Numbers on the axes in parentheses indicate the proportion of variance that is attributed to the two highest scoring principal components (PC1 and PC2). See Table 1 for summary statistics of PCA.

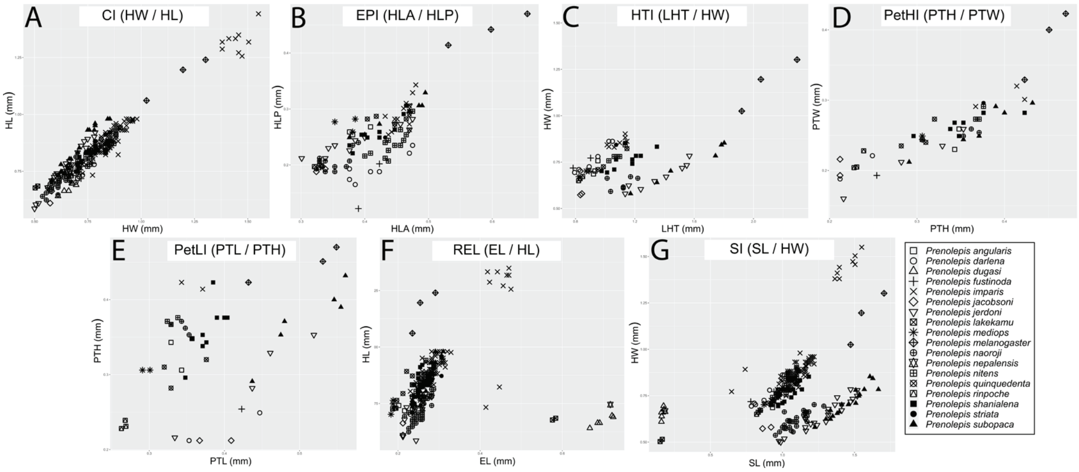


Fig. 5. Bivariate plots of measurement indices: (A) Cephalic Index (HW / HL), (B) Eye Position Index (HLA / HLP), (C) Hind Tibia Index (LHT / HW), and (D) Petiole Height Index (PTH / PTW), (E) Petiole Length Index (PTL / PTH), (F) Relative Eye Length (EL / HL), and (G) Scape Index (SL / HW).

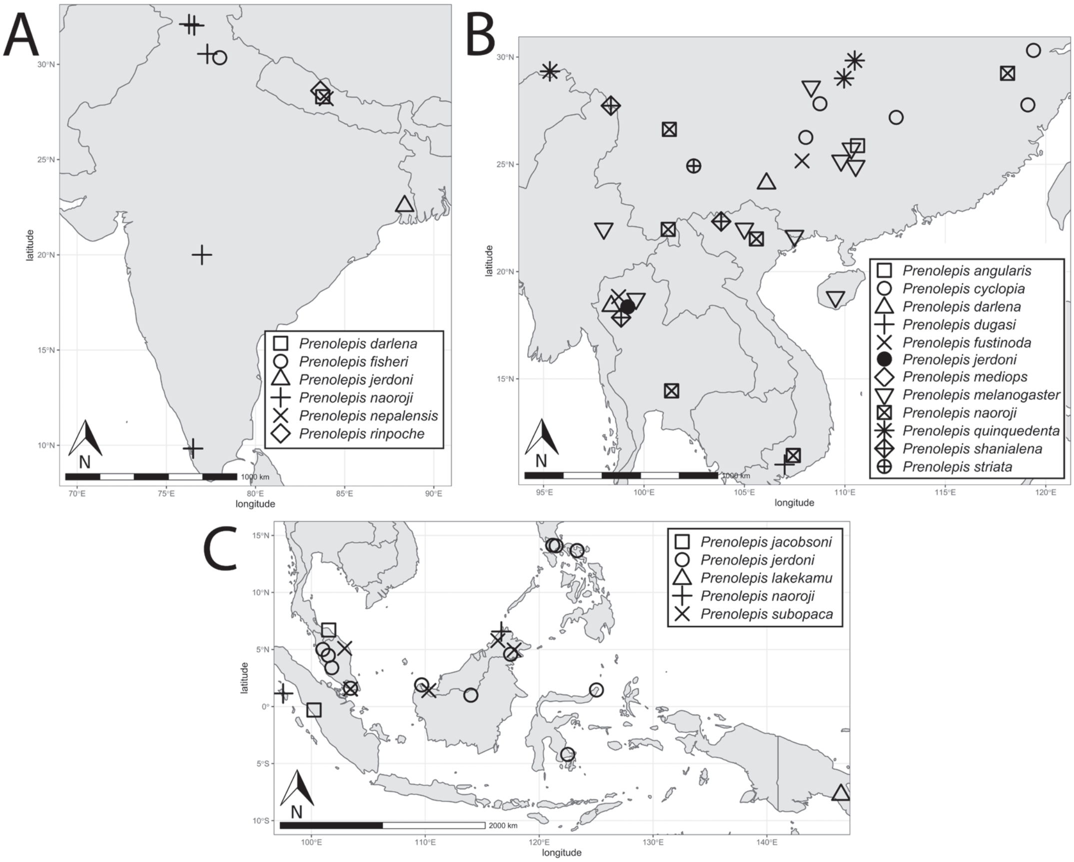


Fig. 6. Maps of *Prenolepis* species distributions: (A) species found in Nepal and India, (B) species found in mainland Southeast Asia, and (C) species found in insular Southeast Asia and Papua New Guinea. Distribution data were used from various publications (Khachonpisitsak et al. 2020; Subedi et al. 2020; Wang et al. 2022; Williams & LaPolla 2018, 2016) and can be found in Table S1.

Distribution and habitat

Prenolepis rinpoche is known from one locality southwest of Jomsom, Nepal and was collected in temperate forest in the Kali Gandaki Gorge, between the peaks of Dhaulagiri and Annapurna.

DISCUSSION

Clarificatory notes on Nepali species

A recent checklist of ants (Subedi et al. 2020) recognizes six total *Prenolepis* species in Nepal. However, a re-evaluation of locality records for specimens examined by Williams & LaPolla (2016) and Williams & LaPolla (2018) and listed in Table S1 confirms that four total species should now be recognized in the country: *P. darlena, P. naoroji, P. nepalensis,* and *P. rinpoche*. Three species previously recognized as present in Nepal should now be excluded from the checklist: *P. fisheri, P. fustinoda,* and *P. shanialena*. The only specimen identified in Nepal as *P. fisheri* (CASENT0281462) is now the type specimen of *P. nepalensis*. *Prenolepis fustinoda* was misattributed to Nepal (Williams & LaPolla 2018) due to similarity with *P. darlena*, and no records of *P. fustinoda* currently exist in the country. All three *P. rinpoche* specimens were the only ones in Nepal previously identified as *P. shanialena*, and since these specimens are now the type series of *P. rinpoche*, *P. shanialena* should no longer be included.

Along with *P. rinpoche*, two other *Prenolepis* species have been described from type specimens collected in Nepal: *P. darlena* (Williams & LaPolla 2016) and *P. nepalensis* (Williams & LaPolla 2018). *Prenolepis rinpoche* and *P. nepalensis* are not known elsewhere and may be considered endemic.

Biogeography of *Prenolepis*

Prenolepis rinpoche most resembles five other *Prenolepis* species (*P. darlena, P. fisheri, P. fustinoda, P. nepalensis,* and *P. shanialena*) found in Asian highlands, including the Himalayas, suggesting that these six species together belong to a clade of primarily montane *Prenolepis* species. Given that *Prenolepis* appears to be most biodiverse in montane areas across South and Southeast Asia, this could suggest an evolutionary pathway to cold weather adaptation in the North American species *P. imparis,* the southern European species *P. nitens*, and the northern European fossil species, †*P. henschei*. These three species are nearly morphologically identical, and both *P. imparis* and *P. nitens* are among the first ants in their ranges to begin foraging in the late winter to early spring seasons when they are most active, and sometimes they are observed foraging at temperatures near freezing (Tschinkel 1987; Lőrinczi 2016; Talbot 1943; Wheeler 1930). In contrast to these two species, few natural history observations of Asian/Australasian *Prenolepis* species exist in the literature, but 13 of the 18 species found in these regions are collected at elevations above 1200 meters (Table S1) and hint at an evolutionary pathway from tropical to temperate climates and cold weather adaptation.

The discovery of another species in The Himalayas inspires investigation of the role of high elevation in shaping *Prenolepis* biodiversity. Temperate biomes formed and expanded relatively recently in geological time, much later than the Paleocene-Eocene Thermal Maximum (PETM; ~55 mya) and during a global cooling period in the Eocene (Eldrett et al. 2009; Fine & Ree 2006; Zachos et al. 2008). However, most temperate and cold-adapted lineages evolved much later—during and after the Eocene-Oligocene transition (~34 mya)—and the Qinghai-Tibetan Plateau and Himalayas are regarded as a 'one-way' biogeographical transition area from Southeast Asia into the Palearctic (Päckert et al. 2020; Favre et al. 2016). Mainland South and Southeast Asia—especially in high elevation areas—is the major center of biodiversity and the probable geographical origin of *Prenolepis*, which first arose in the early Eocene (~48 mya; Blaimer et al. 2015). In the Holarctic, *P. imparis* diverged from *P. nitens* in the late Miocene (~8.2 mya; Tonione et al. 2022). If montane lineages of Southeast Asian *Prenolepis* species are more closely related to temperate species than to tropical lowland species and predate the Eocene-Oligocene transition, this would implicate the role of elevation in the transition to cold weather adaptation and niche shift into temperate zones. High *Prenolepis* biodiversity at high altitudes suggests that montane climates may have shaped early cold weather adaptation in this lineage, but this hypothesis should be more fully tested using phylogenomic data and a genus-wide reconstruction of biogeographical history.

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