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REVISION OF THE ANT GENUS *PERISSOMYRMEX*, WITH NOTES ON THE PHYLOGENY OF THE TRIBE MYRMECININI

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ABSTRACT

The ant genus *Perissomyrmex* is one of the four extant genera of the tribe Myrmecinini. The present study revises the genus including a definition of the taxon, a description of a new species from China, discussions on the phylogenetic position in the tribe and biogeography. Our phylogenetic analysis based on morphological characters shows that (1) the tribe Myrmecinini is justified as a monophyletic taxon by the structures of the antennal base and the labrum, (2) the genera *Perissomyrmex* and *Pristomyrmex* are sister groups, sharing the short masticatory margin of the mandible nearly vertical to the long axis of the head and more or less raised structure on the basal margin of the mandibles, and (3) each of the genera is recognized as a monophyletic taxon. Our provisional conclusion of the phylogeny is (*Myrmecina* + (*Acanthomyrmex* + (*Pristomyrmex* + *Perissomyrmex*))).

A key to the four species of *Perissomyrmex* is given. *P. snyderi* from Central America is distinctive in having a subpetiolar process and three other Asian species are distinguishable by the dentition on the anterior clypeal margin and the shape of the ventral margin of the petiole. The disjunct distribution of the genus is also discussed. The discovery of a fourth species from SW China, *Perissomyrmex emarginatus*, **n. sp.**, suggests that the genus is an old temperate ant living in the boundary to northern zoogeographical regions. Judging from the sister group relation to *Pristomyrmex* that occurs in the Old World tropics and from higher species diversity in Asia, *Perissomyrmex* would have originated in Asia. The fossil record of *Ennaemerus* in Baltic Amber suggests that the Proto-*Perissomyrmex* might have Arcto-Tertiary distribution, and the present distribution would be a relic of the old temperate range in Paleogene.

Key words: Hymenoptera, Formicidae, *Perissomyrmex*, new species, phylogeny, biogeography

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INTRODUCTION

The ant genus *Perissomyrmex* is a small, rare taxon including only three known species occurring in the Oriental and Neotropical regions. The ant was first described from a quarantine specimen in the USA and the original locality of the specimen was supposed to be from Guatemala (Smith, 1947). This presumed original locality had been questioned because the genus shows a close affinity to the genus *Pristomyrmex*, found exclusively in the Old World (Bolton, 1981). The discovery of the second species from Bhutan (Baroni Urbani & de Andrade, 1993) encouraged speculation that *Perissomyrmex* might not be native in Central America. However, the rediscovery of *Perissomyrmex* in Mexico and Guatemala (Longino & Hartley, 1994) confirmed the disjunct distribution of the genus, although the relationships of the genus remained unclear.

Perissomyrmex is easily distinguished from the genus Pristomyrmex in having 9-segmented antennae and a small but distinct tooth on the basal margin of the mandible, all of which are apomorphic, while for Pristomyrmex there have been no clear synapomorphies although Baroni Urbani & Andrade (1993) cited the absence of the metanotal groove. Once Perissomyrmex is recognized as a separate genus, Pristomyrmex would become a paraphyletic taxon. This might lead to a case of a possible junior synonym of Perissomyrmex under Pristomyrmex. Practically, since there have been only two known species of the Perissomyrmex until 2000, the generic characters were not clear. Bolton (2003) diagnosed the tribal characters, but the generic relationship among the members of the Myrmecinini to which the Perissomyrmex and Pristomyrmex belong is still unclear.

Thus, to summarize the taxonomic situation concerning *Perissomyrmex*, the following questions exist: (1) the identities of *Perissomyrmex* and *Pristomyrmex*, (2) phylogenetic relationships among the genera of the tribe Myrmecinini, and (3) disjunct distribution of *Perissomyrmex*. We have already given a brief discussion of this matter (Ogata & Okido, 2002), with a report of an undescribed species from China.

Recently Radchenko (2003) described a new species of *Perissomyrmex* from Nepal and India, which is different from our Chinese species. Now the genus includes four species and these allow insights into the taxonomic status of the genus and the tribe. The present study analyzes the phylogeny of the genera of the tribe Myrmecinini based on morphological characters. Finally, we clarify the taxonomic position of *Perissomyrmex* in relation to *Pristomyrmex*, giving a key to the species, redescriptions of three known species and a description of a new species of *Perissomyrmex* from southwestern China. Finally the biogeography of *Perissomyrmex* is discussed.

Measurements and indices

Total Length (TL). The total outstretched length of the individual, from mandibular apex to gastral apex.

Head Length (HL). The length of the head capsule, measured in a straight line from the midpoint of a line connecting the median paired teeth of the anterior clypeal margin to the midpoint of the preoccipital margin, in full-face view.

Head Width (HW). The maximum width of the head excluding eyes in full-face view; in *Perissomyrmex* broadest in the anterior part of head.

Cephalic Index (CI). $HW/HL \times 100$

Scape Length (SL). The maximum straight-line length of the antennal scape, excluding the basal condylar bulb.

Scape Index (SI). $SL/HW \times 100$

Eye Length (EL). The maximum diameter of the eye.

Pronotal Width (PW). The maximum width of the pronotal in dorsal view.

Mesosomal Length (**ML**). The diagonal length of the mesosoma (= alitrunk) in lateral view from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobes or teeth.

Gastral Length (GL). The maximum straight-line length of the gaster in lateral view.

Gastral Width (GW). The maximum width of the gaster.

All measurements are expressed in millimeters.

Abbreviations of museums

BMNH The Natural History Museum, London, U.K.

NMB Naturhistorisches Museum, Basel, Switzerland

KU Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan

UCD University of California, Davis, California, U.S.A.

PHYLOGENY AND TAXONOMIC POSITION OF PERISSOMYRMEX

The tribe Myrmecinini and its monophyly

Presently the tribe Myrmecinini comprises 4 extant genera: *Myrmecina, Acanthomyrmex, Pristomyrmex* and *Perissomyrmex* (Bolton, 2003). When Ashmead (1905) established the tribe, it included two genera: *Myrmecina* and *Podomyrma*. Emery (1922) considered the tribe to include 10 genera, divided into two subgroups: subtribe Myrmecinini including *Myrmecina, Acanthomyrmex, Pristomyrmex* and *Dacryon*; subtribe Podomyrmini including *Podomyrma, Lordomyrma, Atopomyrmex, Dilobocondyla, Atopula* and *Terataner*. Although Wheeler (1922) did not recognize the subdivisions and did not include the genus *Atopula*, his concept of the tribe was almost identical to Emery's. Later *Perissomyrmex* was described and assigned to the tribe (Smith, 1947), *Dacryon* was synonymized with *Podomyrma* (Brown, 1973; Taylor & Brown, 1985), and the latest concept of the tribe treats the subtribe Podomyrmini *sensu* Emery as an independent tribe (Dlussky & Fedoseeva, 1987: *Lordomyrma* was removed to the tribe Pheidolini) or placed under the tribe Formicoxenini (Bolton 1994: *Lordomyrma* was removed to the tribe Stenammini). In any case *Podomyrma* and related genera are removed from the Myrmecinini and the tribe is presently diagnosed as follows (Bolton, 2003):

- (1) Anterior margin of labrum angled abruptly downward preapically so that margin appears very thick in anterior view
- (2) Labrum mediodorsally, at line of down curvature (apparent anterior margin), with a transverse cuticular raised ridge, or series of 2 3 small teeth, or both of these.
- (3) Antennal sockets relatively close to anterior margin of head (except in major workers of *Acanthomyrmex*).
- (4) Median portion of clypeus broad, broadly inserted between antennal sockets, the latter relatively widely separated.
- (5) Lateral portion of clypeus usually raised into a ridge in front of toruli.
- (6) Stridulum present on pretergite of abdominal segment IV.
- (7) Antennae with 9, 11, or 12 segments, with a 3-segmented club (12-13 segments in male).

Among the characters listed above, Bolton considered the first two to be synapomorphies but the phylogenetic relationship among the genera of the tribe has been left unchallenged.

The characters and the phylogenetic relationships among the genera

Taxonomic and biogeographic overview of the members of tribe Myrmecinini is as follows. *Myrmecina* includes 35 described species, but there are almost as many undescribed species in the Oriental and Australopapuan faunas, so we are estimating 60-70 species in the genus.

Acanthomyrmex is a relatively small genus including 16 described species from the Oriental and Indo-Australian regions. *Pristomyrmex* contains 52 species from the Afrotropical, Oriental, Australian and the Pacific regions (Wang, 2003). *Perissomyrmex* comprises three known and one new species described in this paper, showing disjunct distribution in Central America and Himalayan region.

We have examined the morphology of above genera and found the following characters as useful for constructing the phylogeny:

- 1) **Frontal lobe:** In most of the genera of the subfamily Myrmicinae, the frontal lobe covering antennal insertion is developed, as in *Myrmecina* (Fig. 1), but in the genera *Acanthomyrmex*, *Pristomyrmex*, and *Perissomyrmex*, the structure is reduced, so that the toruli are exposed (as in Fig. 2). The character is a synapomorphy of those three genera.
- 2) Genal carina: The genus *Myrmecina* has unique carinae originated from mandibular insertion, running parallel in the genal region, and connecting to the preoccipital carina (Fig. 3). This structure would be a reinforcement of the head capsule. A similar structure is also observed in *Vombisidris*, but since the position is different, this would be homoplasous. In any case, the genal carina of *Myrmecina* is an autapomorphy of the genus.
- 3) Antennomere count: The number of antennal segments in worker and queen varies in genera: 12 in *Myrmecina* and *Acanthomyrmex*, 11 in *Pristomyrmex*, and 9 in *Perissomyrmex*. Bolton (2003) showed the count 11 to 12 in *Myrmecina*, possibly the result of a miscount of *Myrmecina cacabau* (see Brown, 1971), in which Taylor (1980) found the 3rd antennal segment to be distinctly small and hairless. We have confirmed that this is true of all the species of the genus *Myrmecina* and unique to the genus (Fig. 4). The reduction in size of the 3rd antennal segment would be a synapomorphy of the genus. Judging from this situation, the reduction of the antennomere count in *Pristomyrmex* would be a loss of the original 3rd antennal segment. And if the further trait on the reduction in size of an antennal segment were observed in *Pristomyrmex*, we could conclude a successive reduction of antennomere count in *Perissomyrmex*. But there is no such structure in *Pristomyrmex*, so we suppose the reduction occurred independently in *Pristomyrmex* and *Perissomyrmex*.
- 4) Antennal scape base: Moffett (1986) showed that the basal end of the antennal scape in *Acanthomyrmex*, *Pristomyrmex* and *Myrmecina* has a characteristic structure which forms a flange encircled by a groove (as in Fig. 5). We found the same structure in *Perissomyrmex*. The situation in Myrmecinini is unique and thus the flange is a synapomorphy of the tribe. The structure might be correlated with the reduction of the frontal lobe, since the flange sometimes develops to form a lamella covering the antennal insertion.
- 5) Labrum: The labrum of the tribe is also unique in having a ridge or teeth on the dorsal surface. In most cases the labrum is a simple flap-like structure covering the labio-maxillary complex. But in the tribe Myrmecinini as Bolton (2003) described, the anterior portion is sharply bent inward forming angled preapical margin. Along with transverse preapical margin a ridge or teeth are developed (Figs. 6). The presence of dorsal teeth on the labrum in *Myrmecina* and *Pristomyrmex* was pointed out by Ogata (1991), and the transverse ridge in *Perissomyrmex* by Longino & Hartley (1994) ('ledge'). In *Acanthomyrmex*, the portion bears transverse ridge. The structure suggests a peculiar function, that is, they use the labrum not only for a cover of labio-maxillary complex but also for grasping or fixing an object with mandibles.
- 6) Mandible: The mandible of ants is typically subtriangular in shape, with basal shaft, basal margin, masticatory margin and outer margin in dorsal view. The terminology of the

mandible and dentition is sometimes inconsistent. For example, in Perissomyrmex, Smith (1947) used "superior border" in describing the basal margin, Baroni Urbani & de Andrade (1993) interpreted the tooth on the basal margin as "basal tooth". Here we use the names of teeth only on the masticatory margin. In the genera Pristomyrmex and Perissomyrmex, the mandibles are sometimes referred to as elongate (e.g. Smith, 1947). This is due to the extension of the basal margin of the mandible and the masticatory margin becomes short and somewhat vertical to the long axis of the head. Figs. 7 and 8, where the left mandible is removed, show contrasting examples of the angle of masticatory margin in Acanthomyrmex and Pristomyrmex. In Acanthomyrmex (Fig. 7), like in most of the genera of Myrmicinae, the masticatory margin inclines from dorsal point that fits for anterior margin of the clypeus to ventral point, so that the masticatory margin is elongate, while in Pristomyrmex (Fig. 8) and Perissomyrmex the axis of the masticatory margin turns outward, which probably correlates with elongate basal shaft and basal margin. Although the elongation of the basal shaft of mandible is also observed in Myrmecina, the vertical masticatory margin is distinct and would be a synapomorphy of Pristomyrmex and Perissomyrmex. In both genera, the basal margin has a protuberance in the middle; broadly produced and sometimes weak in *Pristomyrmex* (Wang, 2003) but forming a distinct tooth in Perissomyrmex.

- 7) **Mesopleuron:** Anterior free margin of lower part of mesopleuron sometimes expands to form a lamella partly covering the procoxa. This situation is observed in *Myrmecina* and *Pristomyrmex* (Fig. 9). The expansion of the mesopleuron would be an apomorphy, but not a synapomorphy in both genera, because the situation occurs in many genera of different tribes such as *Hylomyrma, Mayriella, Paedalgus, Tetramorium*. In his terminology of Bolton (1994), the mesopleuron was divided into upper anepisternum and lower katepisternum by a transverse groove. But this usage is not correct, because the groove is a secondary structure and not homologous with the paracoxal suture which separates the anepisternum from the katepisternum (Matsuda, 1970). The mesopleural part of ants is largely occupied by the anepisternum.
- 8) Spines on mesosoma: Spines are often developed on the pronotum in most *Pristomyrmex* species, all the *Acanthomyrmex* species and some *Myrmecina*. It is unclear whether this structure in the different genera is homologous or not. One of the unique characters of *Myrmecina* is paired metanotal teeth in front of the base of the propodeal spines, although not clearly developed in all the species.
- **9) Metanotal groove**: The 'propodeal suture' mentioned by Baroni Urbani & de Andrade (1993) is synonymous with the metanotal groove. They inferred that the loss of the suture would be an autapomorphy of *Pristomyrmex*. We confirmed their statement, but the loss also occurs in *Myrmecina* which would be a homoplasy.
- **10) Tibial spur on middle and hind legs**: Smith (1947) mentioned that the absence of spurs on the middle and hind legs of *Perissomyrmex* is one of the characters to distinguish it from *Pristomyrmex*. But actually *Pristomyrmex* has no spurs and only *Acanthomyrmex* has long and distinct spurs in the tribe Myrmecinini. The absence of the tibial spurs on middle and hind legs is found in many genera of Myrmicinae.
- 11) Petiole: The petiole of *Myrmecina* is unique in shape. Most of the keys say "sessile" for describing the form (e.g. Bolton, 1994), but it would be interpreted that the node is depressed because the anterior oblique face corresponds to peduncle of the petiole (Fig. 11). This characteristic shape of the petiole is an autapomorphy of *Myrmecina*. In *Acanthomyrmex* the petiolar node is consistently bispinose, which is an independant synapomorphy of the genus.

12) First gastral tergum: *Acanthomyrmex* has a unique ventral margin of the 1st gastral tergum, forming a M-shaped line (Fig. 12), which is due to a characteristic constriction of the anterior part of the 1st tergum. This is a synapomorphy of the genus.

Those characters discussed above are summarized in Table 1. Based on these, applying a classical Hennigian algorithm, the provisional phylogenetic relationships among four genera are shown in Fig. 13. Now it is clear that the genera *Perissomyrmex* and *Pristomyrmex* are each a monophyletic taxon justified by synapomorphies, and they together form a sister group within the tribe Myrmecinini.

Perissomyrmex M. R. Smith

Perissomyrmex M. R. Smith 1947: 281. Type-species: Perissomyrmex snyderi, by original designation.

DIAGNOSIS

Worker and Female

Monomorphic or polymorphic terrestrial myrmicine ants with the following combination of characters:

- 1. Head almost as broad as long in minor worker, or slightly broader in major worker, divergent anteriorly.
- 2. Eyes protruding, situated at about the midlength of the side of head, or slightly posteriorly.
- 3. Clypeus with a few paired teeth on the anterior margin; lateral portions reduced to a thin raised strip in front of the antennal insertions.
- **4**. Frontal lobe absent; frontal carina poorly developed.
- 5. Antennal toruli exposed.
- **6.** Antennae 9-segmented, scape extending over posterior border of head, apical 3 segments forming a club.
- Mandibles with long basal margin and short masticatory margin; basal margin with a distinct tooth; masticatory margin with one basal and two apical teeth separated by a diastema.
- 8. Labrum with transverse ridge at the preapical portion.
- **9**. Palp formula 4,2.
- 10. Pronotum unarmed, promesonotal suture weakly impressed.
- 11. Lower part of mesopleuron not expanding to cover on procoxa.
- **12**. Metanotal groove deeply impressed.
- 13. Propodeal spiracle rounded situated in the middle of lateral surface of propodeum.
- 14. Propodeal spine long and acute.
- 15. Propodeal lobe low and obtuse angled.
- 16. Petiole pedunculate with lateral projection, petiolar node rounded.
- 17. Postpetiole with rounded node.

Male Unknown.

Of the four species of the genus, *P. snyderi* is easily diagnosed by the presence of a subpetiolar process in the workers, the dentition of the anterior margin of the clypeus and the coarse and irregular sculpturation on the head. This does not mean that the three Asian species comprise a monophyletic group. Because the loss of the subpetiolar process is frequently

observed in *Myrmecina* and *Pristomyrmex*, we do not confirm the polarity of the character state of the dentition and the sculpture. There is no strong evidence, however, that Central American *snyderi* has a close relationship with any of the Asian species. The detailed phylogeny of the four species is not clear.

The polymorphism of the genus was reported by Longino & Hartley (1994) in *P. snyderi* from Mexico. While no Asian species are known to be polymorphic, it is possible. Because the available materials were mostly from litter extractions, whole colony composition has not been clear.

It should be noted that the individuals of the *Perissomyrmex* are highly variable in the morphology. In particular, projected structures, such as teeth on the mandibles, propodeal spines, lateral projections on the petiolar peduncle, are varying due to wearing down or polymorphism.

Perissomyrmex species

emarginatus n. sp. monticola de Andrade nepalensis Radchenko snyderi Smith, M.R.

KEY TO PERISSOMYRMEX SPECIES (workers)

1.	Subpetiolar process small but distinct (Fig. 17d); median paired teeth of anterior margin of clypeus distinct but base not forming differentiated tubercle so that outline of anterior clypeal margin is evenly convex (Fig. 16g, h); body almost blackish; Central America
	Subpetiolar process absent (Fig. 17a-c); median paired teeth on anterior clypeal margin strongly protuberant so that there is a distinct median projection (Fig. 16a-f); body color brownish; Asia
2.	Lateral paired teeth on anterior clypeal margin close to median pair, bases fused (Figs.16a-c); median notch of anterior margin of clypeus inverted U-shape (Fig. 16a); SW China
	Lateral paired teeth on anterior clypeal margin well isolated from median paired teeth (Figs. 16d-f); median notch of anterior margin of clypeus inverted V-shape
3	Ventral margin of propodeum mostly straight, curved in front of the area below spiracle (Fig. 17b); gaster reddish brown, contrasting with blackish mesosoma; Bhutan
	Ventral margin of propodeum curved behind the area below the spiracle (Fig. 17c);
	gaster concolorous with mesosoma, but lighter; Nepal & NE India

SPECIES ACCOUNTS

Perissomyrmex emarginatus new species Figures 14, 16a-c, 17a

DESCRIPTION

Worker: Holotype measurements (mm): TL 3.73, HL 0.86, HW 0.90, , SL 0.78, EL 0.10, PW 0.57, ML 0.98, GL 1.07, GW 0.86. Indices: CI 104.65, SI 86.67.

Paratype measurements (4 workers, 3 measured): TL 3.97-4.14, HL 0.86-0.96, HW 0.92-0.94, SL 0.74-0.78, PW 0.57-0.59, ML 0.90-1.11, GL 1.07-1.39, GW 0.86-0.90). Indices: CI 95.74-106.98, SI 82.22-86.67.

Head subrectangular, with slightly concave posterior border and rounded posterior corners; sides slightly diverging anteriorly. Eyes situated in the midlength of sides, comprising 15-18 ommatidia. Anterior margin of clypeus with four teeth; median paired teeth large and distinct, lateral paired teeth smaller and lower; the median paired ones separated by median notch, the lateral tooth located just in front of antennal insertion, and the median and lateral ones closely situated each other, sometimes fused at the base in each side; median notch distinct and deep, inverted U-shape, the bottom of notch reaching or exceeding level of anterior margin of lateral edge in front of antennal insertion. Frontal lobes almost reduced, frontal carina low, diverging posteriorly, reaching the level of eyes. Antennal toruli exposed, antennal insertion forming deep hollow forming distinct anterior edge. Mandible elongate with long basal margin and short masticatory margin; basal margin with one small but distinct tooth in the midlength; masticatory margin equipped with one apical and one subapical teeth followed by a diastema and one basal tooth. Antennae 9 segmented, scape exceeding posterior corner of head by its width; apical three segments forming club but obscure. Labrum with transverse preapical ridge; two small projections present on the dorsal surface in the middle.

Promesonotum raised, but the dorsal surface somewhat depressed; promesonotal suture weakly impressed. Anteroventral free margin of mesopleuron carinated but not forming expansion covering procoxa. Metanotal groove complete, deeply impressed. Dorsal outline of propodeum slightly raised. Spiracle circular and large, situated on lateral surface of propodeum in the middle. Propodeal spine straight, long and acute, directed backward and upward. Propodeal lobe low and rounded.

Petiole with anterior declivity, rounded tip and posterior face; ventral margin weakly sinuate but no subpetiolar process; anterior peduncle with distinct paired lateral projections in dorsal view, situated anterodorsal to the spiracle in lateral view. Postpetiole, in profile, with raised dorsal outline, anterior face convex, posterior face nearly vertical and in frontal view the crest rounded but pointed. Ventral margin to 1st gastral segment not sinuate.

Head, mandible and mesosoma costate, lower part of mesopleuron and posterior part of propodeal spiracle unsculptured. Petiole mostly unsculptured. Anterior face of postpetiole smooth and shining, the rest finely punctate. Body dark yellowish brown, the appendages lighter.

Queen. TL 4.63-4.92, HL 1.07-1.19, HW 1.11-1.23, CI 103.36-110.81, SL 0.78-0.90, SI 68.91-73.17, PW 0.82-0.90, ML 1.31-1.39, GL 1.35-1.48, GW 1.11-1.19 (5 measured).

Similar to the worker, but the head wider than long with three ocelli. The dentition on mandibles and anterior clypeal margin basically same as in worker but tending to be worn down, so that the teeth are often low and obscure; the median portion of anterior clypeal margin produced with less distinct median notch and four teeth which are sometimes fused together. Mesosoma robust short and high, mesonotum thick, mesoscutellum overhanging metanotum, metanotum more of less convex in profile, propodeal spine robust directed backward. Petiole basically as in worker, but the ventral surface with distinct paired longitudinal keel originated

from posterior end of the petiole running anteriorly and convergent at anterior 1/4 of petiole, lateral surface with longitudinal ridge from the portion above the spiracle to posterior end, and lateral projection more distinct. Apex of postpetiolar node pointed. Sculpture more distinct than that of worker. Coloration same as worker.

TYPE MATERIAL

Holotype, Worker, Lianwangpo, Mt. Emeishan, Emeishan Shi, Sichuan Prov., **CHINA**, 2310m alt., 4.x.1996 (*S. Nomura & Zhao*) (KU No. 3149). **Paratypes** (All from **CHINA**): 4 workers, 2 queens, same as holotype; 2 queens, Mt. Jiudingshan, Chapingshan Mts., Mao Xian, Sichuan Prov., 3670 m alt., 22.ix.1996 (*S. Nomura & Zhao*); 1 queen, Leidongping, Mt. Emeishan, Emeishan Shi, Sichuan Prov., 2310-2350 m alt., 4.x.1996 (*S. Nomura & Zhao*).

Remarks

All the material was collected by Berlese funnel. Collecting site of Mt Emeishan is a road side of mixed coniferous forest, Dabei site is more like evergreen forest, and Mt Jiudingshan site is somewhat shrubby. The altitudinal range of collecting sites is from 2300 m to 3700 m elevation. The lateral projections of the petiolar peduncle are sometimes asymmetrically developed.

In the worker caste, *P. emarginatus* is distinguished from two other Asian species in having the deeper median notch on the anterior clypeal margin. The bottom of the notch reaches or even exceeds the level of anterior ridges in front of antennal insertions. The body of *P. emarginatus* has more sculptured surface and the color is more brownish than the two other Asian species. The propodeal spines, if they are fully developed, are also different from those of *P. monticola* and *P. nepalensis*, being straight without upper curve. In the queen the median notch is shallower than that of the nonspecific workers, so that the depth and the shape cannot be used in separating species. Although we did not observe the queen of *P. nepalensis*, the dentition of the anterior clypeal margin is still useful; the 4 teeth are arranged closer together forming a blunt median projection in *P. emarginatus*, while the lateral paired teeth are small and separate from the median pair in *P. monticola*.

Perissomyrmex monticola de Andrade Figures 16d,e, 17b

Perissomyrmex monticola de Andrade, in Baroni Urbani & de Andrade 1993: 90. Holotype worker. **Bhutan**.

Diagnosis

Worker, measurements (mm): TL 4.6, HL 1.12, HW 1.08, SL 0.92, PW 0.64, AL 1.24, GL 1.35, GW 0.96. Indices: CI 96.4, , SI 85.2,

Four teeth of anterior margin of clypeus well isolated; median paired teeth large and distinct; lateral paired teeth small and their tip not reaching the level of the bottom of median notch; median notch converted V shape; the bottom of notch not reaching the level of anterior margin of lateral ridge in front of antennal insertion; distance between a median teeth closer than that between a median tooth and a lateral tooth; position of lateral tooth just below in the middle of toruli. Promesonotum forming single raised convex. Propodeal spines long and acute, directing backward and curved upward. Propodeal lobe low and rounded. Following the restriction on anterior articulator portion to mesosoma, sides of petiole almost parallel in dorsal view.

Posterior face of postpetiolar node declined. Head capsule and mesosoma heavily striate. Mandibles very lightly striate. Mesopleural area, propodeum smooth and shining, petiole smooth and shining.

Body bicolored, with dark brown head and mesosoma and reddish gaster, antennae and legs yellowish.

Queen: TL 5.32, HL 1.20, HW 1.20; CI 100, SL 1.00, SI 75, PW 0.84, AL 1.52, GW 1.20, GL 1.56.

Dentition of anterior margin of clypeus and mandible as in worker, but robust and lower. Mesoscutellum overhanging metanotum, metanotum less convex in profile. Petiole as in worker but with low ventral keel and more distinct lateral projection.

Remarks

Seemingly *P. monticola* is distinct in having a bicolored body with blackish head and mesosoma and reddish gaster. The species is similar to *P. nepalensis* in having an inverted V shaped median notch on the anterior clypeal margin. The notch in *P. monticola* and *P. nepalensis* is shallower than in *P. emarginatus*. The bottom of the notch in both species does not reach the level of anterior ridges in front of the antennal insertions. The teeth arrangement of the anterior clypeal margin is similar to that of *P. nepalensis* as well, showing that the lateral paired teeth are more spaced to the median paired teeth. The shape of the propodeal spines, upward curved profile, also show the similarity in *P. monticola* and *P. nepalensis*. According to the key provided by Radochenko (2003) the species is distinct in having abundant short standing hairs on the antenna and legs, but the character is somewhat delicate and *P. emarginatus* also shows the same pilosity. It seems that the ventral profile of the petiole is more reliable.

Among the three Asian species, the sculpture of *P. monticola* is the most distinct, and the unsculptured areas on the mesopleuron and propodeum are broadest. The species is known only from the type locality.

Specimens examined: 1 worker, 1 queen, Nobding 41 km O, Wangdi Ph. 2800 m, Bhutan (NMB).

Perissomyrmex nepalensis Radchenko (Figs. 16f, 17c)

Perissomyrmex nepalensis Radchenko 2003:12. Holotype worker. Nepal.

Diagnosis

Worker, measurements (mm): TL 3.74-4.38, HL 0.90-1.10, HW 0.92-1.10, SL 0.8-0.9, PW 0.56-0.64, ML 1.00-1.10, GL 1.02-1.30, GW 0.80-0.96. Indices: CI 100-102, SI 82-87.

Four teeth on anterior margin of clypeus well isolated; median paired teeth large and distinct, lateral paired teeth small and spaced from the median teeth; median notch converted V shape; the bottom of notch not reaching anterior margin of lateral ridge in front of antennal insertion. Promesonotum raised but less convex. Propodeal spine directed backward and curved upward. Ventral margin of petiole nearly straight. Subpetiolar process absent. Costulation on head and pronotum low and spaced, unsculptured area on mesosoma and propodeum wider. Body color light reddish brown, antennae and legs yellowish.

Specimens examined: 2 workers, W. Bengal, Darjeering, Tiger Hill, 2450 m, 28.viii.1997, **India** (BMNH).

Remarks

The dorsal outline of the promesonotal area varies in the size of workers. In minor worker the area is less raised but in major worker weakly convex in profile. *P. nepalensis* is distinguishable from *P. monticola* by the ventral profile of the petiole: nearly straight in the

former, but widely convex in the latter. Sculpturation of *P. nepalensis* is weaker and more spaced than that of *P. montiocola*. Radchenko (2003) noticed the standing hairs on the antennae and legs in distinguishing *P. nepalensis* from *P. monticola*; short and abundant in the former, long and sparse in the latter.

The species was found in Himalayan region (Nepal and northeastern India) at the altitudinal range of 2450 to 3000m, collected by pitfall traps (Radochenko, 2003).

Perissomyrmex snyderi Smith, M.R. Figures 16g, h, 17d

Perissomyrmex snyderi Smith, M.R. 1947:282. Holotype worker. Guatemala.

Diagnosis.

Worker, TL 3.74-4.94, HL 0.88-1.24, HW 0.88-1.34, CI 100-108, SL 0.82-0.94, SI 73-93, PW 0.56-0.72, ML 0.98-1.20, GL 1.00-1.40, GW 0.80-1.06.

Polymorphic. Labrum with lamellate flange developed at basal part of curvature. Anterior clypeal margin with 3 pairs of projection, the shape and size varying to reduce or fused; basically, the median pair broad and robust, inner lateral pair smaller; outer lateral pair smallest, sometimes reduced or lost; the median notch roundly concave; in some case the median paired teeth fused without median notch in major worker. Propodeal spine straight or slightly curved upward. Subpetiolar process present anteriorly; ventral margin of petiole almost straight in profile; anterior portion of petiole diverging toward midlength of petiole in dorsal view. Sculpture on head and mesosoma irregularly costate. Body color blackish.

Specimens examined: 9 workers (including 1 major), 4 km N Union Juarez, Volcan Tacann, Lower slopes 1950 m, Chiapas, Mexico (4 in UCD, 5 in BMNH).

Remarks

The species shows great variation in worker caste body size, the shape of spines and the teeth on the anterior clypeal margin, but the subpetiolar process is consistently present, which is unique among the four *Perissomyrmex* species. In addition, *P. snyderi* is also unique in having coarser and more irregular sculptures on the head and mesosoma and dark color of the body. The degree of the protuberance of the anterior clypeal margin is less distinct than that in Asian species, even though variation exists.

The rediscovered individuals were collected from Berlese samples of a cloud forest floor of 1700 to 2000 m altitude in Chiapas, Mexico (Longino & Hartley, 1995).

Biogeography of Perissomyrmex

Perissomyrmex has a unique biogeographic pattern showing a disjunct Oriental-Neotropical distribution (Fig. 15). According to Bolton's census data (1994) there are no genera showing such disjunct distribution in ants. Seemingly the genus is a tropical element, but the actual distribution records are restricted to higher elevation at moderate northern latitude; 1700 to 2000 m in Central America and over 2000 m in Asia. The species of Asia are never found in the tropical mountains nor in lowlands of temperate zones. The distribution range of the genus in Asia is shown in Fig. 18 with altitude and latitude forest zones. Their habitat includes Lauro-Fagaceae forest, evergreen forest, temperate conifer & deciduous forest. The genus cannot be a tropical element but might be a relic of an old temperate taxon.

Baroni Urbani & de Andrade (1993) and Radchenko (2003) supposed the origin of the genera in Asia. This is supported by the present study as follows: (1) the sister group of *Perissomyrmex* is *Pristomyrmex*, distributed in the Old World Tropics; (2) a clade of *Perissomyrmex* + *Pristomyrmex* is closely related to *Acanthomyrmex*, also distributed in tropical

Asia (Fig. 18), and (3) species diversity of *Perissomyrmex* is highest in Asia. Considering the present ecological distribution of *Perissomyrmex*, the speciation of the ancestor of *Perissomyrmex* + *Pristomyrmex* might have occurred in temperate-tropical regions.

Longino & Hartley (1994) discussed the origin of the disjunct distribution and mentioned that *P. snyderi* is not an accidental introduction to Central America but a relic of widely distributed taxon. If their hypothesis is correct, the Asian and Central American species would be different monophyletic species groups. Morphologically, the Asian species share several characters, e.g. the loss of the subpetiolar process, the distinct protuberance of the median portion of the anterior clypeal margin, and more or less parallel sculpturation on the head. But because of the difficulties of their polarities as mentioned above, we have not confirmed monophyly.

The evidence of vicariance might be in fossil records. There are two more extinct genera of the tribe Myrmecinini: *Stiphromyrmex* Wheeler and *Ennaemerus* Mayr of the Baltic Amber inclusions. Among them, the genus *Ennaemerus* has a 9 segmented antenna, as in *Perissomyrmex*. It should be noted that when Wheeler (1915) referred to the resemblance of *Ennaemerus* to *Pristomyrmex*, *Perissomyrmex* was not discovered yet. If the tribal assignment of them is correct, *Ennaemerus* would be a close relative of *Perissomyrmex*. And the 'Proto-*Perissomyrmex*' (*Ennaemerus* + *Perissomyrmex*) mights have a wide range of distribution. For reference of this pattern, *Myrmecina*, the early derivative of the tribe, shows wide range of distribution (Fig. 19). The difference is that *Myrmecina* would be basically a tropical origin, while *Perissomyrmex* is a temperate one.

Tiffney (1985) suggested that there are five major periods of migration between eastern Asia and eastern North America: pre-Tertiary, Early Eocene, Late Eocene-Oligocene, Miocene and Late Tertiary-Quaternary. Recent molecular analysis of Magnoliaceae (Azuma *et al.*, 2001) showed that tropical disjunction occurred during the middle to late Eocene and that the temperate disjunction occurred in the Oligocene. General resemblance of the distribution pattern of that plant might be referential in considering the disjunction of *Perissomyrmex*. Since geological time of the Baltic Amber is thought to be the Late Eocene (e.g. Dlussky, 1999; Bolton, 2003), the 'Proto-*Perissomyrmex*' (*Ennaemerus* + *Perissomyrmex*) might have Arcto-Tertiary distribution, expanding their distribution from Eurasia to North America during one of the three possibilities of Tiffney's five periods of migrations: Late Eocene-Oligocene, Miocene and Late Tertiary-Quaternary. The present distribution would be a relic of the old temperate range in Paleogene. Molecular analysis would be needed to estimate the detailed phylogeny and diverging time of disjunction.

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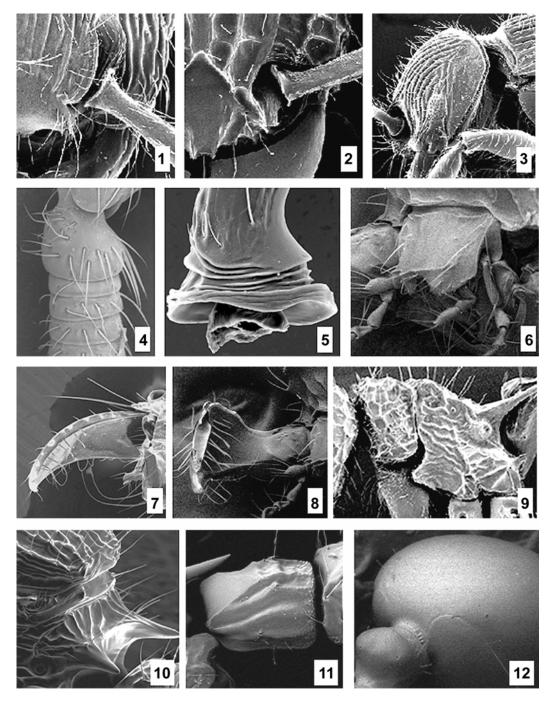
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Figures **1-12**. Characters of Myrmecinini: antennal insertion of *Myrmecina* (1), *Pristomyrmex* (2); genal carina of *Myrmecina* (3); base of funiculus of *Myrmecina* (4), base of scape of *Myrmecina* (5); labrum of *Pristomyrmex* (6); masticatory margin of *Acanthomyrmex* (7), *Pristomyrmex* (8); mesosoma of *Pristomyrmex* (9); propodeal spine of *Myrmecina* queen (10); petiole of *Myrmecina* (11); 1st gastral tergum of *Acanthomyrmex* (12).

Table 1. Characters in the tribe Myrmecinini

#	Apomorphic Characters
1	Preapical portion of labrum sharply bent inward
2	Transverse ridge or teeth on anterodorsal part of labrum
3	Basal fringe at antennal scape
4	Ventral carina on the head
5	Reduction of 3rd antennal segment
6	Reduction of petiolar node
7	Loss of frontal lobe
8	M-shaped ventral margin of 1st gastral tergum
9	Petiolar node bispinose
10	Short masticatory margin of mandible nearly vertical to long axis of
10	head
11	Protuberance on basal margin of mandible in the midway
12	11-segmented antenna
13	Expansion of mesopleuron partly covering procoxa
14	Loss of metanotal groove
15	9-segmented antenna
16	Distinct tooth on basal margin of mandible
17	Lateral projection on petiolar peduncle

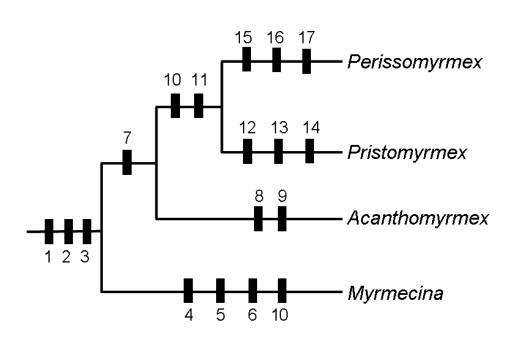


Figure 13. Phylogenetic relationships of the genera of the tribe Myrmecinini. Numbers on each clade show synapomorphies listed in Table 1.



Fig. 14. Perissomyrmex emarginatus n. sp.

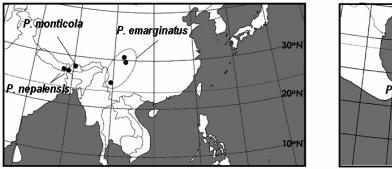




Figure 15. Distribution of Perissomyrmex

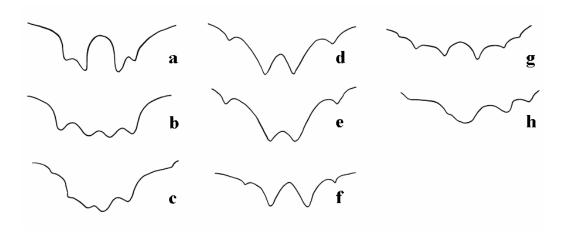


Figure 16. Anterior clypeal margin of *Perissomyrmex* spp., worker of *P. emarginatus* (a), female of *P. emarginatus* (b-c), worker of *P. monticola* (d), female of *P. monticola* (e), worker of *P. nepalensis* (f), minor worker of *P. snyderi*(g), major worker of *P. snyderi* (h).

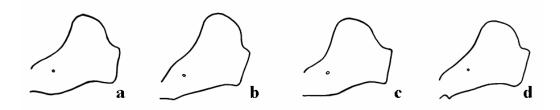


Figure 17. Petiole of *Perissomyrmex* workers in profile, *P. emarginatus* (a), *P. monticola* (b), *P. nepalensis* (c), *P. snyderi* (d).

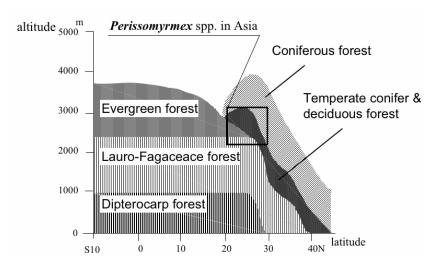


Figure 18. Distribution range of *Perissomyrmex* spp. in Asian forest zones (altitudinal and latitudinal vegetation in SE & E Asia after Ohsawa, 1990).

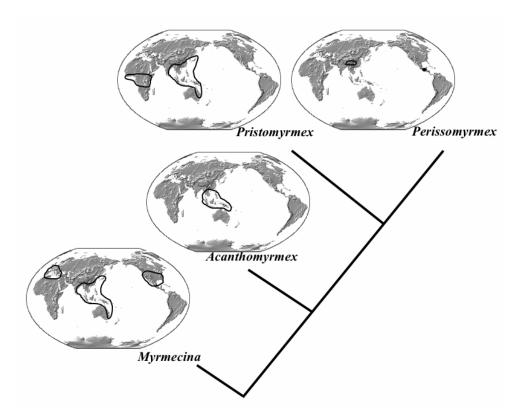


Figure 19. Distribution of the genera of the tribe Myrmecinini.