Article

The ant genus *Stenamma* Westwood (Hymenoptera: Formicidae) redefined, with a description of a new genus *Propodilobus*

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Abstract

The myrmicine ant genus *Stenamma* Westwood is redefined and a new diagnosis of the worker caste is presented. Justified by both morphology and molecular data, two species are removed from *Stenamma* and transferred to the genus *Lordomyrma* Emery: *L. bhutanensis* (Baroni Urbani) **comb. n.** and *L. sinensis* (Ma, Xu, Makio & DuBois) **comb. n.** Based on compelling differences in morphology, a third species originally described in *Stenamma* is transferred to the genus *Propodilobus* **gen. n.**: *P. pingorum* (DuBois) **comb. n.** Molecular results also indicate that *Stenamma*, as newly defined here, is a monophyletic genus that forms a clade with *Aphaenogaster* Mayr and *Messor* Forel. Additional notes on the diversity and distributions of *Stenamma*, *Lordomyrma*, and *Propodilobus* are provided.

Key words: ant taxonomy, molecular phylogenetics, Myrmicinae, *Stenamma*, *Lordomyrma*, *Propodilobus*

Introduction

Stenamma Westwood (1839) comprises an unfamiliar genus of cryptic, cold-adapted myrmicine ants that occur throughout most of the northern hemisphere. Although rarely encountered by the casual observer, *Stenamma* is frequently collected in extracts of sifted leaf litter. Many species are represented by only a few samples and not much is known about their natural history. Despite this paucity of information, taxonomists have described over forty species and produced several significant regional revisions: Smith (1957) and Snelling (1973) revised the species of the Nearctic region; Smith (1962) reviewed the species known from the Neotropics; Arnol'di (1975) revised the species of the former USSR; and DuBois (1998) revised the species of the Palearctic and Oriental regions. DuBois (1998) also included the most thorough diagnosis of the genus to date. Each treatment has contributed greatly to a regional understanding of the genus, yet a more comprehensive, global survey is lacking.

One of the greatest challenges to adequately diagnosing *Stenamma* has been insufficient knowledge about the Neotropical fauna. New survey efforts and a greater appreciation for leaf litter sampling have increased the number of *Stenamma* specimens from this region substantially, and it is now apparent that the genus has undergone an extensive radiation in Mesoamerica, rivaling the Holarctic in diversity of species, morphology, and behavior (pers. obs.). A thorough, species-level revision of the Neotropical taxa is currently in progress. To organize this revision around natural groupings, I am constructing a broad-scale molecular phylogeny of the genus. This effort is intended to clarify the definition of the genus and to elucidate how species from different biogeographic regions are related to one another. Here I present initial findings from this work.

Stenamma specimens from most of the currently recognized species groups were reviewed, including all of the described and many undescribed Neotropical species. What results from this analysis is a new diagnosis of the *Stenamma* worker caste along with the removal of several species from the genus. I transfer *Stenamma bhutanense* Baroni Urbani and *S. sinensis* Ma, Xu, Makio & DuBois to the genus *Lordomyrma* Emery and move *S. pingorum* DuBois to the newly described genus *Propodilobus*. Justification for these transfers based

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on both morphological and molecular (transfers to *Lordomyrma* only) evidence is presented following the synopsis.

Materials and methods

All morphological observations were made with a Leica MZ12.5 stereomicroscope. Color images and measurements were created with a JVC KY-F75U digital camera, a Leica MZ16A stereomicroscope and Syncroscopy Auto-Montage (v5.0) software.

An index used to distinguish *Stenamma* from similar looking myrmicine genera with 12-segmented antennae is the Antennal Club Index (ACI). This is calculated by dividing the length of antennal segments 11 plus 12 by the combined lengths of segments 9–12 and multiplying by 100 (Figure 1). Genera with a 2- or 3-segmented club have higher ACIs than genera with a club containing 4 or more segments.

Where specimen codes are listed, additional data, such as images, collection records, and specimen information can be accessed via AntWeb (http://www.antweb.org).

Molecular methods are described in the section discussing the phylogenetic placement of *Lordomyrma bhutanensis* and *L. sinensis*.
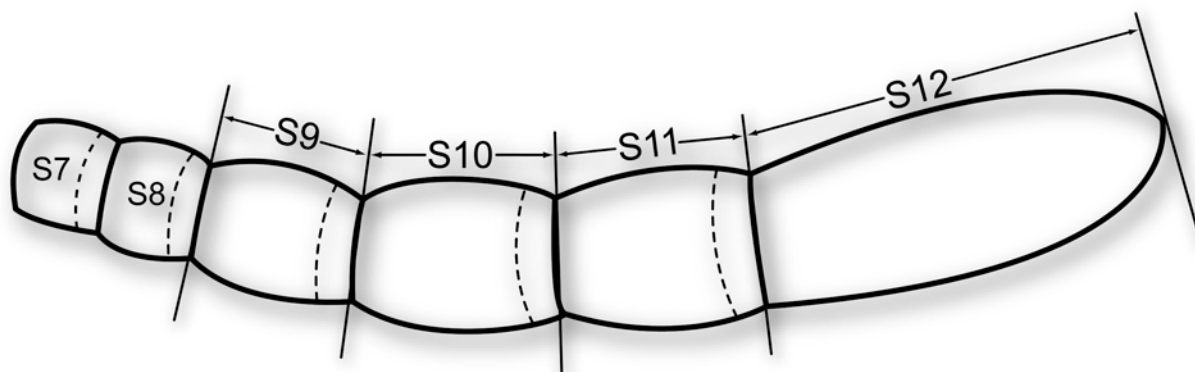
FIGURE 1. Antennal club of a *Stenamma expolitum* worker. The Antennal Club Index (ACI) is calculated by dividing the length of S11 + S12 by the total length of S9 – S12 and multiplying by 100. *Stenamma* species have an ACI between 60 and 70.

Museum abbreviations

ANIC	Australian National Insect Collection, Canberra, Australia
BMNH	The Natural History Museum (= British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A
DBSNU	Department of Biology, Shaanxi Normal University, Shaanxi, China
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
NHMB	Naturhistorisches Museum, Basel, Switzerland
NMNH	National Museum of Natural History, Washington, DC, U.S.A.
UCDC	The Bohart Museum of Entomology, University of California, Davis, California, U.S.A.

Generic synonymy of *Stenamma*

***Stenamma* Westwood**

Stenamma Westwood, 1839: 219. Type-species: *Stenamma westwoodii*, by monotypy.

Asemorhoptrum Mayr, 1861: 76. Type-species: *Myrmica lippula*, by monotypy. [Synonymy with *Stenamma* by André, 1883: 310.]

Theryella Santschi, 1921: 68. Type-species: *Theryella myops* (provisional junior synonym of *Stenamma punctiventre*), by monotypy. [Synonymy with *Stenamma* by Santschi, 1923: 136.]

Diagnosis of *Stenamma*. A new diagnosis of the *Stenamma* worker caste is presented followed by a short discussion on interspecific variation and how to distinguish *Stenamma* from closely related genera. The classification of Bolton (2003) placed *Stenamma* within the tribe Stenammini, which, as currently defined, is not monophyletic (Brady *et al.* 2006; Moreau *et al.* 2006). *Stenamma* instead is more closely related to the genera *Aphaenogaster* Mayr and *Messor* Forel, suggesting that the older tribal classification of Emery (1921), which included these genera together, should be reconsidered. Some of the characters mentioned here may help to diagnose the group formed by *Stenamma*, *Aphaenogaster*, and *Messor*. Standard images of *Stenamma* representing species from different biogeographic regions are shown in Figures 2–16.

Diagnosis of the *Stenamma* worker caste. With characters of the Myrmicinae as described by Bolton (2003), and the following more specific features:

1. Mandible triangular to elongate triangular; masticatory margin usually with 6–8 teeth or denticles (rarely 9 or 10) which decrease in size irregularly from apex to base; teeth on basal half frequently reduced and poorly defined.

2. Palp formula 4,3.

3. Apex of anterior clypeal margin with a small to prominent notch or concavity, never smoothly convex or with a projecting tooth.

4. Anterior clypeal margin usually lacking a strong isolated median seta.

5. Median portion of clypeus often longitudinally bicarinate and with area between carinae slightly to strongly depressed.

6. Posteromedial margin of clypeus narrowed and prolonged backward between frontal lobes; width not exceeding that of frontal lobes in full-face view.

7. Frontal lobes small and closely approximated, not entirely covering antennal insertions.

8. Antennal scrobes and frontal carinae absent.

9. Torular lobe present and visible in full-face view projecting over condylar bulb.

10. Compound eyes located slightly to distinctly in front of midlength of side of head (excluding mandibles), small to moderate in size, usually with 2–12 ommatidia across greatest diameter.

11. Antenna 12 segmented and terminating in a distinct to indistinct 4-segmented club (ACI 60-70).

12. Posteroventral corners of head lacking grooves.

13. Promesonotum convex in profile, often low domed-convex and very prominent; faint impression or line marking track of former promesonotal suture sometimes present dorsally.

14. Metanotal groove present.

15. Propodeum usually armed with a pair of teeth or short spines (rarely unarmed or with long spines).

16. Propodeal lobes present and prominent, rounded to quadrate in shape, never long and projecting dorsally.

17. Middle and hind tibiae lacking spurs.

18. Pretarsal claws small, simple.

19. Petiole with a long, anterior peduncle and sometimes with an anteroventral process.

20. Postpetiole with short peduncle and low node often slightly longer than broad, never distinctively broader than long.

21. Postpetiolar node always wider than petiolar node.

22. Basigastral striae often present on anterior margin of abdominal tergite 4.

23. Metasternal process present and often well developed.

Comments on worker characters

3. The structure of the clypeus varies greatly among species of *Stenamma* and has been useful for distinguishing species groups in western North America (Snelling 1973) and will likely be useful for distinguishing Neotropical groups (pers. obs.; Figures 2, 5, 8, 11, 14, 17–20). The concavity is easy to observe in all species except for those belonging to the *smithi* group (*S. chiricahua, S. punctatoventre, S. smithi*). In this group, a median lobe projects over the clypeal margin, obscuring the concavity. The best way to observe this character in the *smithi* group is in a ventral view of the head (as in Figure 20).

4. Several species commonly display a short- to medium-sized median seta that is located between two longer setae. It is never stouter or longer than the two surrounding setae. This character has been observed in *S. brevicorne*, *S. debile*, *S. heathi*, *S. owstoni*, *S. sequoiarum,* and *S. smithi*. Additionally, as observed by Bolton (2003), the median seta can be variable among specimens within a nest series.

5. There are many exceptions to this character among Neotropical species. *Stenamma. alas, S. diversum*, and *S. expolitum* completely lack clypeal carinae (Figures 11, 14). Most other Neotropical taxa have only faint carinae and lack a strong median depression.

7. The frontal lobes are expanded laterally in *S. diversum*, covering the torular lobe in full-face view (Figure 14).

11. This character can be difficult to assess when looking at a single specimen with an indistinct club. However, *Stenamma* never has a distinct 2- or 3-segmented antennal club and in all observed specimens, it is possible to see a marked increase in antennal segment length between segments 8 and 9, indicating the beginning of the club. This is captured by the antennal club index (ACI) which is never more than 70, i.e., the last two antennal segments make up no more than 70% of the total length of the last four segments.

15. Only Neotropical species are completely unarmed or have long projecting spines. The former state is exhibited by *S. expolitum* (Figure 12) and *S. alas* and the latter by *S. diversum* (Figure 15).

19. Neotropical species lack a strongly projecting anteroventral petiolar process.

22. Most Holarctic species have short basigastral striae. Neotropical species usually have carinae around the girdling constriction separating the pre- and postsclerites of the third abdominal segment, but never have striae extending further onto the tergites or sternites of the gaster (compare Figures 22 and 24).

23. This character appears to be present only in Holarctic species. Neotropical species have a small raised area, but it is never elongated into a distinct process (compare Figures 21 and 23).

Comments on similarities and differences among *Stenamma, Aphaenogaster*, and *Messor*

Aphaenogaster and *Messor* show greater morphological variation than *Stenamma* and differ from *Stenamma* in characters 5, 6, 10, 11, 17, and 22. The most notable difference is the structure of the clypeus. In both *Aphaenogaster* and *Messor*, the posteromedial portion of the clypeus is broadly inserted between the frontal lobes and when looked at in full-face view is generally much wider than either lobe at the broadest point. Additionally, along the apical margin of the clypeus, *Aphaenogaster* and *Messor* tend to have a row of setae, which are much stouter than the setae observed in *Stenamma*.

Notable similarities among the genera also exist. In most species of all three genera, the frontal lobes do not completely cover the antennal insertions, allowing the torular lobes to be visible in full-face view. *Aphaenogaster* and *Messor* have an ACI that is even lower than *Stenamma* (53–57); however, many species have a distinct to indistinct 4-segmented antennal club. In some species the club is not distinctly broader or longer that the previous segments, but is covered with a denser layer of setae, sometimes giving these segments a noticeably lighter color. Lastly, like *Stenamma,* some species of *Aphaenogaster* and *Messor* have meso- and metasternal processes.

Synonymic list of species

Assignment of species to species groups follows Snelling (1973) for Nearctic species and DuBois (1998) for Palearctic species.

Nearctic Species
brevicorne **group**
    brevicorne (Mayr, 1886)
        = *neoarcticum* Mayr, 1886
    chiricahua Snelling, 1973
    punctatoventre Snelling, 1973
    smithi Cole, 1966
        = *knowltoni* Gregg, 1972
diecki **group**
    diecki Emery, 1895
        = *diecki impressum* Buren, 1944
    snellingi Bolton, 1995
        = occidentale Smith, 1957 (homonym)
    sequoiarum Wheeler, 1917
    californicum Snelling, 1973
    dyscheres Snelling, 1973
heathi **group**
    heathi Wheeler, 1915
    exasperatum Snelling, 1973
huachucanum **group**
    huachucanum Smith, 1957
wheelerorum **group**
    wheelerorum Snelling, 1973
Currently unassigned
    schmittii Wheeler, 1903
    impar Forel, 1901
    meridionale Smith, 1957
    foveolocephalum Smith, 1930
        = *carolinense* Smith, 1951

Neotropical species
Currently unassigned
    alas Longino, 2005
    expolitum Smith, 1962
    diversum Mann, 1922
    felixi Mann, 1922
    manni Wheeler, 1941
    schmidti Menozzi, 1931

Palearctic Species
owstoni **group**
    kurilense Arnol'di, 1975
    nipponense Yasumatsu & Murakami, 1960
    ussuriense Arnol'di, 1975

    gurkhalis DuBois, 1998
    koreanense Lyu, DuBois, & Cho, 2002
    owstoni Wheeler, 1906
punctiventre **group**
    punctiventre Emery, 1908
        = *myops* Santschi, 1921
westwoodii **group**
    debile (Foerster, 1850)
        = *minkii* (Foerster, 1850)
        = *westwoodii polonicum* Begdon, 1932
        = *golosojevi* Karavaiev, 1926
        = *ucrainicum* Arnol'di, 1928
    georgii Arnol'di, 1975
    hissarianum Arnol'di, 1975
    kashmirense Urbani, 1977
    jeriorum DuBois, 1998
    lippulum (Nylander, 1849)
        = *hirtulum* Emery, 1898
        = *caucasicum* Arnol'di, 1975
    msilanum Forel, 1901
        = *africanum* Santschi, 1939
        = *africanum submuticum* Santschi, 1939
    petiolatum Emery, 1897
    picetojuglandeti Arnol'di, 1975
    sardoum Emery, 1915
    sogdianum Arnol'di, 1975
    striatulum Emery, 1895
        = *tscherkessicum* Arnol'di, 1928
    westwoodii Westwood, 1839
    orousseti Casevitz-Weulersse, 1990

Species *incertae sedis*
    berendti (Mayr, 1868) [fossil]
    westwoodii asiaticum Ruzsky, 1905

Summary of *Stenamma* distribution and diversity

As defined here, *Stenamma* includes 45 extant, described species. Seventeen are Nearctic, 22 are Palearctic, and 6 are Neotropical. *Stenamma* has been collected from North America south through Central America to northern South America (Colombia and Ecuador), Europe, northern Africa (Morocco and Algeria), temperate Asia, and Japan. No species are known to occur in the Indo-Australian region.

***Lordomyrma bhutanensis* (Urbani, 1977) & *L. sinensis* (Ma, Xu, Makio, DuBois, 2007): Generic transfer and justification**

Generic synopsis of *Lordomyrma*

FIGURES 2–16. Full-face, profile, and dorsal images of several *Stenamma* species, representing the Palearctic, Nearctic, and Neotropical regions. Figures 2–4: *S. debile* CASENT0605171 (Bavaria, Germany). Figures 4–6: *S. nipponense* CASENT0605172 (Hokkaido, Japan). Figures 8–9: *S. dyscheres* CASENT0171182 (CA, USA). Figures 11–13: *S. expolitum* CASENT0600043 (Heredia Prov., Costa Rica). Figures 14–16: *S. diversum* CASENT0605173 (Izabal, Guatemala).
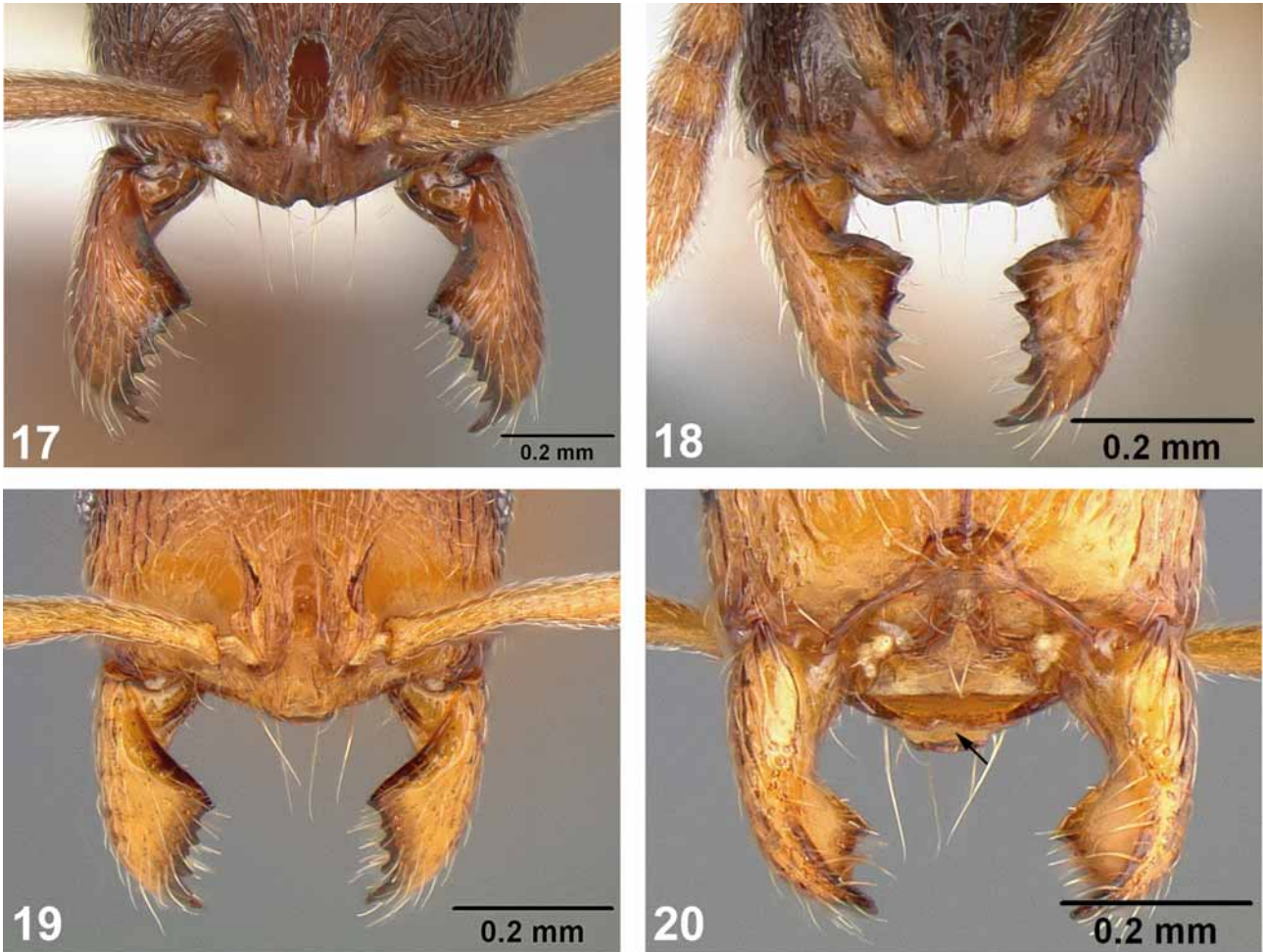
FIGURES 17–20. Several examples of clypeal structure in Nearctic *Stenamma*. Figure 17: *S. diecki* CASENT0126091 (NS, Canada). Figure 18: *S. huachucanum* CASENT0126215 (AZ, USA). Figures 19–20: Dorsal and ventral images of *S. punctatoventre* CASENT0126072 (CA, USA).

Lordomyra Emery

Lordomyrma Emery, 1897: 591. Type-species *Lordomyrma furcifera*, by subsequent designation of Wheeler, 1911: 166.
Prodicroaspis Emery, 1914: 414. Type-species: *Prodicroaspis sarasini*, by monotypy. [Synonymy with *Lordomyrma* by Bolton, 1994: 106.]
Promeranoplus Emery, 1914: 412. Type-species: *Promeranoplus rouxi*, by monotypy. [Synonymy with *Lordomyrma* by Bolton, 1994: 106.]

Taxonomic changes

Lordomyrma bhutanensis (Baroni Urbani) comb. n.
(Figures 25–27)

Stenamma bhutanense Baroni Urbani, 1977: 420–422, Figs. 2, 4. Holotype worker and paratype workers, BHUTAN: Dechhi Paka, 5 km West of Pelela, 3300m, 19–20 June 1972, NHMB Bhutan Expedition. [Holotype and paratype workers in NHMB examined.]
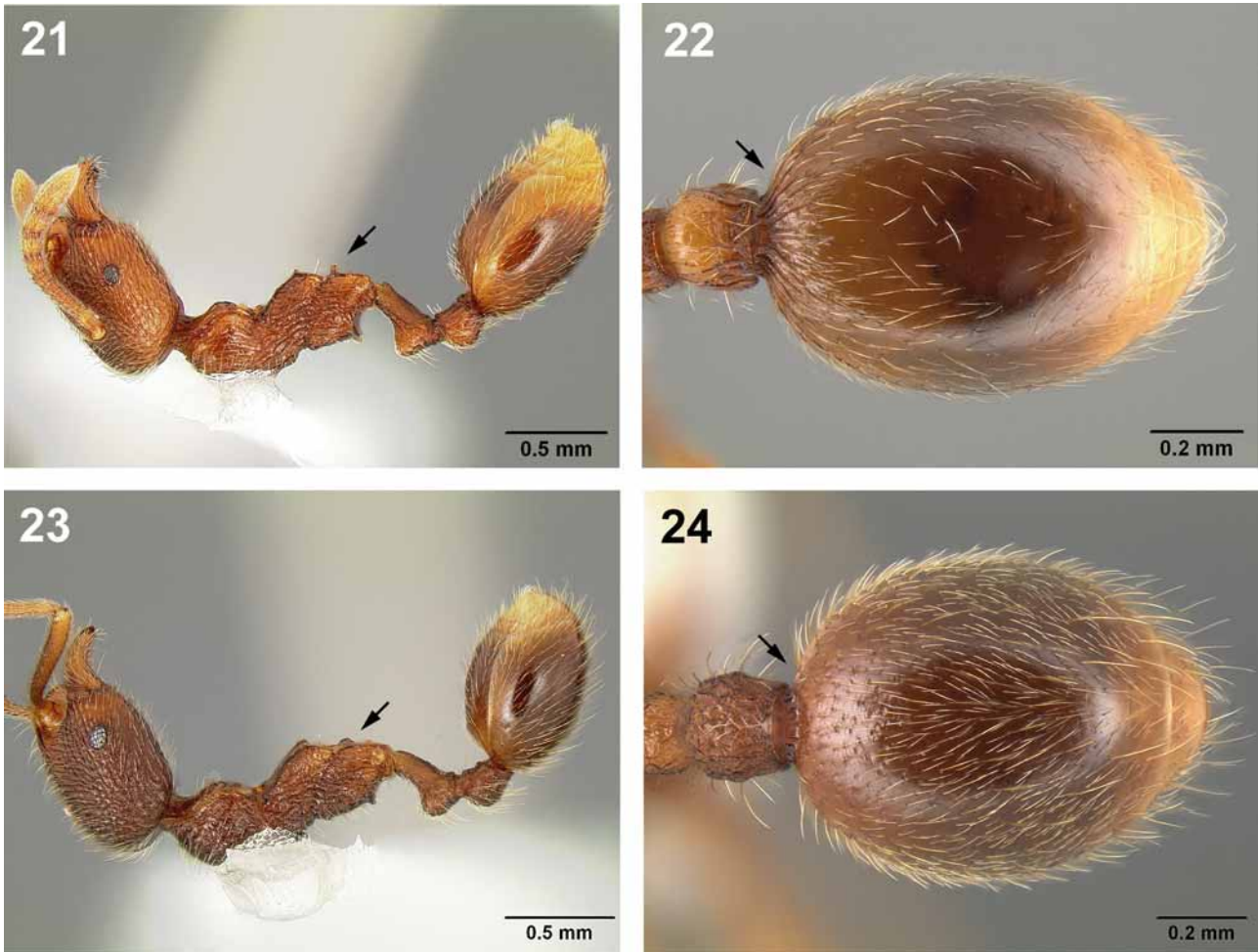
FIGURES 21–24. Comparison of the metasternum and dorsum of the basigaster between a Nearctic and Neotropical *Stenamma* species. Figures 21–22: *S. dyscheres* CASENT0126073 (CA, USA). Figures 23–24: *S. manni* CASENT0126029 (Jalisco, Mexico).

Lordomyrma sinensis (Ma, Xu, Makio, and DuBois) comb. n.

Stenamma sinensis Ma, Xu, Makio, and DuBois, 2007: 371–377, Figs. 1–4. Holotype worker and paratype workers, CHINA: Mt. Qinling, Shaanxi, 33º39`N 107º48`E, 1580–1641m, 7–18 September 2005 and 1–13 August 2006, Li-Bin Ma. [Holotype and partype workers in DBSNU not examined.]

Justification for transfer of species to *Lordomyrma*

Morphological analysis

The holotype and several paratype specimens of *Lordomyrma bhutanensis* from the NHMB were examined. Additional material recently collected from Nepal and Yunnan Province, China was borrowed from MCZC and CASC, respectively. These latter specimens were sorted into two morphospecies and identified as *L.* cf. *bhutanensis* 1 and *L.* cf. *bhutanensis* 2 (Figures 28–33). Careful examination revealed several morphological characters distinguishing these species from *Stenamma*: (1) Antenna with a 3-segmented club of which the last two segments display the largest increases in length relative to preceding segments (ACI 73-77; compare Figures 34 and 37); (2) apex of anterior clypeal margin with a small projecting tooth (compare Figures 35 and 38; note, this character was not discerned in the types of *L. bhutanensis* because the mandibles were closed in all specimens); (3) posteromedial margin of clypeus as wide or wider than frontal lobes in full-

face view (compare Figures 35, 38); (3) postpetiolar node broader than long (Figures 27, 30, 33); (4) sting robust and often exposed and projecting dorsally in pinned specimens (compare Figures 36 and 39). Although specimens of *L. sinensis* were not examined, the characters mentioned above were confirmed by reviewing the species description and accompanying figures (Ma *et al.* 2007).

FIGURES 25–33. Full-face, profile, and dorsal images of several *Lordomyrma* taxa. Figures 25–27: *L. bhutanensis* holotype CASENT0171178 (Bhutan). Figures 28–30: *L.* cf. *bhutanensis* 1 CASENT0097951 (Yunnan Prov., China). Figures 31–33: *L.* cf. *bhutanensis* 2 CASENT0171179 (Yunnan Prov., China).

To adequately delimit species in this group, a more detailed analysis of regional variation will be necessary. From the specimens examined here, I find it difficult to comfortably define species boundaries. Surprisingly, Ma *et al.* (2007) did not directly compare *L. sinensis* to *L. bhutanensis*, but instead stated that it would most likely be confused with other species within the *Stenamma owstoni* species group, the group to which both *L. sinensis* and *L. bhutanensis* were assigned. I examined three additional members of this species group, *S. koreanensis*, *S. owstoni*, and *S. nipponense* (Figures 5–7), and determined that these have the attributes of true *Stenamma*. It is likely that this confusion was caused by a poor understanding of which characters are most important in diagnosing *Stenamma*. For example, Ma *et al.* (2007) were the first to notice the presence of a median clypeal tooth. However, they incorrectly used this trait as a species diagnosing rather than a genus diagnosing character.

Phylogenetic methods

The DNA from one specimen each of *L.* cf. *bhutanensis* 1 and *L.* cf. *bhutanensis* 2 was non-destructively extracted. Both specimens were collected from sifted leaf litter in forest, Shibali, Yunnan Province, China at

2,475 m. Shortly after extraction, I obtained fragments of four nuclear genes from both taxa: 28S rDNA, abdominal-A (abdA), elongation factor 1-alpha F2 copy (EF1αF2), and long-wavelength rhodopsin (LW Rh). DNA extraction, amplification, and sequencing were performed as in Brady *et al.* (2006). All newly generated sequences have been uploaded into GenBank (see Table 1 for specimen codes and GenBank accession numbers). Preliminary phylogenetic analyses were then performed using both a comprehensive *Stenamma* data set, which included over 30 species representing all regions where *Stenamma* is found (Branstetter unpubl.), and a large myrmicine data set containing 63 myrmicine genera and several outgroups (Ward pers. com.) Both data sets revealed that *L.* cf. *bhutanensis* 1 and *L.* cf. *bhutanensis* 2 fall outside of the genus *Stenamma* and the myrmicine data showed consistent association between *L.* cf. *bhutanensis* and the genus *Lordomyrma*.

Following these initial results, a more rigorous analysis was performed. The above gene fragments were obtained from four additional *Stenamma* species (*Stenamma expolitum*, *S. felixi* , *S. meridionale*, *S. striatulum*), *Cyphoidris exalta* Bolton (Ward pers. com.), *Lordomyrma desupra* Sarnat (Ward pers. com.), and *L. epinotalis* Mann (Lucky and Sarnat pers. com.). *Cyphoidris exalta* was included in these analyses because it has been hypothesized to be the sister group to *Lordomyrma* (Bolton 1981; Taylor 2009). These sequences were then incorporated into the 162-taxon Ant Tree of Life data set of Brady *et al.* (2006). This data matrix was culled to include the majority of myrmicine species and several outgroups for a final 63-taxon data matrix. Sequence alignment was performed using default settings in the program ClustalX v1.83.1 (Jeanmougin *et al.* 1998) and manually edited with MacClade v4.08 (Maddison & Maddison 2005). An intron in LW Rh and hypervariable regions of 28S were excluded from all analyses. The final data matrix included 2326 base pairs, with 646 parsimony informative sites, and 826 variable sites.

TABLE 1. Countries of origin, specimen codes, voucher types, voucher depositions, and GenBank accession numbers for taxa with new DNA sequences. The voucher type indicates whether the DNA voucher specimen is the same individual, is from the same nest-series, or is from the same collection series. Complete collection and specimen data are available from AntWeb (http://www.antweb.org).

Taxon	Country	Specimen Code	Voucher Type	Deposited	LW Rh	EF1aF2	abdA	28s
Cyphoidris exalta	Central African Republic	CASENT0405993	same series	CASC	GQ411015	GQ410981	GQ410990	GQ410999
Lordomyrma cf. *bhutanensis* 1	China	CASENT0065792	same individual	UCDC	GQ411009	GQ410987	GQ410996	GQ411005
L. cf. *bhutanensis* 2	China	CASENT0065793	same individual	UCDC	GQ411008	GQ410984	GQ410993	GQ411002
L. desupra	Fiji	CASENT0106145	same nest-series	UCDC	GQ411016	GQ410982	GQ410991	GQ411000
L. epinotalis	Solomon Islands	CASENT0171169	same individual	NMNH	GQ411014	GQ410983	GQ410992	GQ411001
Stenamma expolitum	Costa Rica	CASENT0600047	same individual	UCDC	GQ411011	GQ410985	GQ410994	GQ411003
S. felixi	Costa Rica	CASENT0600053	same individual	UCDC	GQ411010	GQ410986	GQ410995	GQ411004
S. meridionale	U.S.A.	JTLC000006624	same individual	UCDC	GQ411012	GQ410988	GQ410997	GQ411006
S. striatulum	Switzerland	CASENT0605174	same series	UCDC	GQ411013	GQ410989	GQ410998	GQ411007

Phylogenetic analyses employed Bayesian and maximum likelihood (ML) methods and were run through the Cyberinfrastructure for Phylogenetic Research (CIPRES) computer cluster at the San Diego Super Computer Center (http://www.phylo.org/). Four partitioning schemes were employed: single partition, partitioning by gene, partitioning by codon position (positions 1+2 versus 3) with 28S forming its own partition, and partitioning by gene and codon position. This resulted in a one-, four-, three-, and seven-partition model, respectively. The model of sequence evolution for each partition was selected using the AIC with MrModeltest v2 (Nylander 2004b; Posada & Crandall 1998). This resulted in the model GTR+I+G being selected for all partitions except LW Rh (HKY+I+G) and EF1αF2 codon positions 1+2 (SYM+I+G). Bayesian analyses were conducted using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) under each of the four partitioning schemes mentioned above. For each analysis, two independent MCMC runs were performed for 5 million generations, distributed across four chains with the default heating parameter. Convergence between runs was assessed using the average standard deviation of split frequencies and by plotting likelihood

values across generations using Tracer v1.4.1 (Rambaut & Drummond 2007). A burn-in value of 500,000 generations was established and only the post-burn-in generations from both runs were included in the results. Bayes factor comparisons (Nylander 2004a) showed that the best partitioning scheme was by gene and codon position. Maximum Likelihood inference was implemented in the rapid bootstrapping program RAxML (Stamatakis *et al.* 2008). First, single gene analyses were performed to look for aberrant results. Next, the combined data set, partitioned by gene and codon position, was analyzed and RAxML was set to find the highest scoring ML tree and to perform 1000 ML bootstrap replicates. The GTR+CAT model of DNA sequence evolution was applied to all partitions in RAxML.
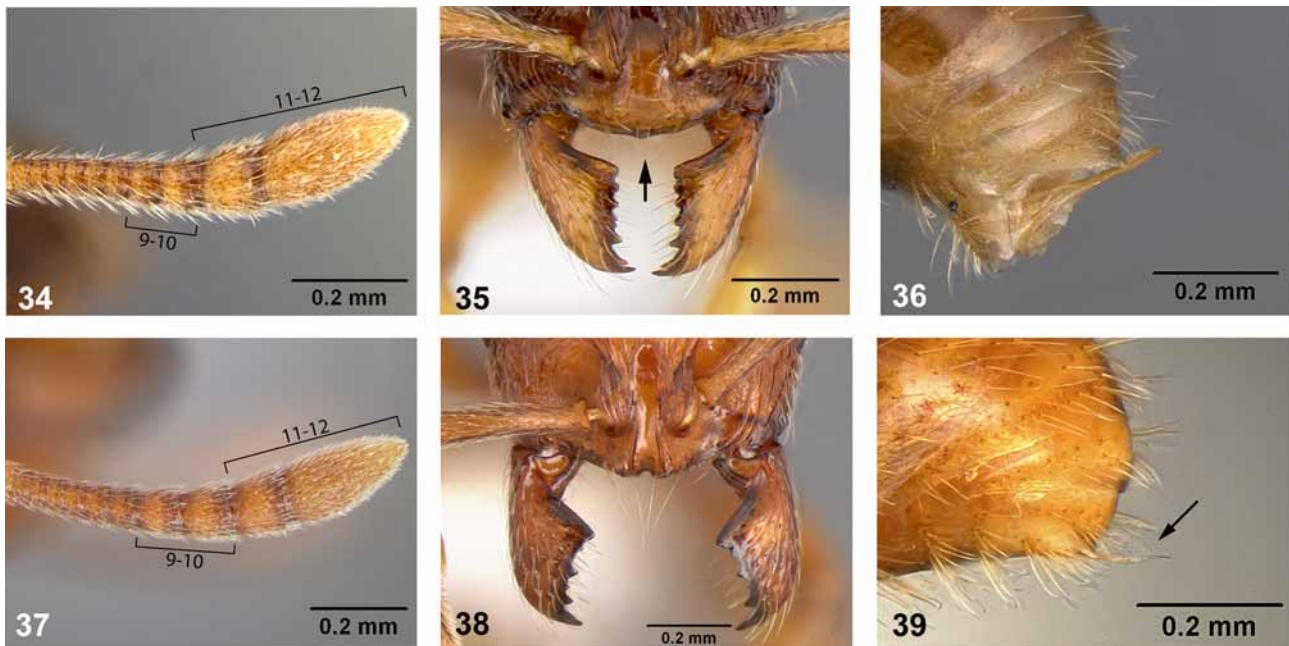
FIGURES 34–39. Comparison of the antennal club, anterior clypeal margin, and sting shaft between *Lordomyrma* and *Stenamma*. Figures 34–35: *L.* cf. *bhutanensis* 2 CASENT0171183 (Yunnan Prov., China). Figure 36: *L. bhutanensis* paratype CASENT0126076 (Bhutan). Figures 37–38: *S. dyscheres* CASENT0126075 (CA, USA). Figure 39: *S. dyscheres* CASENT0126074 (CA, USA).

Phylogenetic results and discussion

All phylogenetic analyses of the combined data set resulted in *L.* cf. *bhutanensis* 1 and *L.* cf. *bhutanensis* 2 being nested within the genus *Lordomyrma* with maximum support: Bayesian posterior probability (PP) of 1.00 and a ML bootsrap of 100 (Figure 40). Single-gene analyses resulted in slightly different topologies, but in all cases *L.* cf. *bhutanensis* 1 and 2 grouped with *Lordomyrma*.

The true *Stenamma* species were found to be monophyletic and formed a well-supported clade with the genera *Messor* and *Aphaenogaster*. As in Brady *et al.* (2006), the genera *Messor* and *Aphaenogaster* were not monophyletic; instead, species grouped according to whether they were from the Old World or New World. Relationships among *Stenamma*, *Messor*, and *Aphaenogaster* are unclear. The tree presented here shows *Stenamma* as sister to *Messor* plus *Aphaenogaster*, but support is low (0.52 PP). Several other analyses recovered *Messor andrei* and *Aphaenogster albisetosa* as sister to *Stenamma*. Future work, incorporating more candidate taxa, is needed to identify the sister group to *Stenamma*.

Within *Stenamma,* the two Neotropical species *S. expolitum* and *S. felixi* were found to be sister to the Holarctic species *S. dyscheres*, *S. meridionale,* and *S. striatulum*. However, support for the European species *S. striatulum* being sister to the North American species is low (PP of 0.57, ML boostrap of 47). These findings are consistent with results from a larger *Stenamma* data set (Branstetter in prep.).

As expected, the Myrmicinae were found to be monophyletic and sister to the Formicinae, or the Ectatomminae plus the Heteroponerinae. Contrary to the hypothesis of Bolton (1981), and Taylor (2009), and consistent with the results of Lucky and Sarnat (pers. com), *Cyphoidris* did not group closely with *Lordomyra*.

FIGURE 40. Bayesian consensus tree based on four genes showing placement of *Lordomyrma* cf. *bhutanensis* 1 and 2 within the Myrmicinae. Support values above branches represent Bayesian posterior probabilities multiplied by 100. *Stenamma* species, indicated in blue text, form a well-supported clade and are closely related to the genera *Aphaenogaster* and *Messor*. *Lordomyrma* cf. *bhutanensis* 1 and 2, indicated in red text, are nested within the genus *Lordomyrma* and are not closely related to *Stenamma*.

Comments on the systematics of *Lordomyrma*

The genus *Lordomyrma* represents a large radiation of ants in the Australian and Oriental regions and currently contains twenty-seven named species (including the species transferred here) with many more waiting to be described (Sarnat 2006; Taylor 2009). Taylor (2009) states that the genus is the product of several "separate congeneric evolutionary radiations" that have occurred in SE Asia and Japan, Australia, lowland New Guinea and the Solomon Islands, New Caledonia, and Fiji. Consequently, the genus is morphologically diverse and difficult to define. Currently, except for the key couplets in Bolton (1994), a global diagnosis of *Lordomyrma* does not exist.

Sarnat (2006) provided a diagnosis of the species known from the Fiji Islands and Taylor (2009) lists several important characters for the entire genus, but states the need for these to be reassessed. Compared to most species of *Lordoymyra*, *L. bhutanensis* and *L. sinensis* are morphologically aberrant, exemplifying the need to better diagnose the genus. In reference to the characters listed by Sarnat (2006) and Taylor (2009), *L. bhutanensis* and *L. sinensis* differ in several important ways: (1) frontal carinae and scrobes absent; (2) ventrolateral margin of the head not delineated by a short carina; (3) propodeal spines short; and (4) petiolar peduncle of moderate length. The presence of a small tooth projecting from the apex of the anterior clypeal margin of *L. bhutanensis* and *L. sinensis* may be a useful character for future researchers attempting to characterize the genus. This character was observed in several *Lordomyrma* species, including *L. epinotalis*. Additionally, it is worth noting that like *Stenamma*, *L. bhutanensis* and *L. sinensis* have a 4,3 palp formula.

Lordomyrma bhutanensis and *L. sinensis* represent the first named species of *Lordomyrma* known from mainland Asia (Taylor 2009). Other undescribed species are reported, but none of these are known to occur in the Himalayan Mountains. It is not surprising that *L. bhutanensis* and *L. sinensis* were described as species of *Stenamma*. Morphologically they look very similar to *Stenamma* and they have been collected in the same type of habitat. Interestingly, *Lordomyrma* and *Stenamma* share some similarities in natural history (Sarnat 2006). Both genera are commonly collected in leaf litter samples, form small, inconspicuous nests of no more than a few hundred workers, and have slow-moving, timid workers of moderate size. Much more needs to be learned about these two genera, but it is possible that they have converged on a similar biology and in a few cases a similar morphology. Most of the localities where *Lordomyrma* is found lack *Stenamma*. The only recorded areas of overlap are the Himalayan Mountains and Japan. Thus, an intriguing idea is that *Lordomyrma* may represent the ecological equivalent of *Stenamma* in the Indo-Australian region.

Propodilobus New Genus: Diagnosis and justification

Propodilobus gen. n.
(Figures 41–44)

Type species: *Stenamma pingorum* DuBois (replacement name for *Stenamma orientale*, junior homonym).
   Gender: Masculine
   Etymology: The name is descriptive of the prominent propodeal lobes found on the type specimen. It is a combination of propodeum, which is the first abdominal segment in apocritan Hymenoptera, and *lobus*, L., meaning lobe.
   Diagnosis of worker. With characters of the Myrmicinae as described by Bolton (2003), and the following more specific features:

   1. Mandibles elongate triangular with 6 teeth which decrease in size irregularly from apex to base; teeth on basal half reduced and poorly defined.
   2. Palp formula 3,2.
   3. Apex of anterior clypeal margin smoothly convex.
   4. Anterior clypeal margin lacking a strong isolated median seta.
   5. Median portion of clypeus lacking longitudinal carinae.
   6. Posteromedial margin of clypeus narrowed and prolonged backward between frontal lobes.
   7. Frontal lobes small and closely approximated, not entirely covering antennal insertions.
   8. Antennal scrobes and frontal carinae absent.
   9. Antenna 12 segmented and terminating in a distinct 3-segmented club (ACI 74-75).
   10. Promesonotum convex and prominent in profile.
   11. Metanotal groove present.
   12. Propodeum armed with a pair of well-developed spines.

13. Propodeal lobes present and elongate, bluntly triangular in shape and directed posterodorsally; space between lobes and propodeal spines distinctly U-shaped.

14. Middle and hind tibiae lacking spurs.

15. Pretarsal claws small, simple.

16. Petiole with a long, anterior peduncle; anteroventral process lacking.

17. Postpetiole broader than long.

Discussion. *Propodilobus* can be distinguished from *Stenamma* by the reduced palp formula (3,2 versus 4,3), smoothly convex anterior clypeal margin, distinct 3-segmented antennal club (ACI 74-75 versus 60-70), and elongate propodeal lobes. In addition, the postpetiole is broader than long and the scape and funiculus of *Propodilobus* have a more robust appearance than in *Stenamma*.

Propodilobus may be confused with *Lordomyrma* since *Lordomyrma* is morphologically diverse and currently lacks an adequate diagnosis. It is possible that when a more comprehensive morphological review of *Lordomyrma* is undertaken or the phylogenetic position of *Propodilobus* is tested with molecular data, *Propodilobus* will be synonymized under *Lordomyrma* or a related genus. Despite this, from the diagnoses listed in Sarnat (2006) and Taylor (2009), *Propodilobus* can be distinguished from *Lordomyrma* by its lack of longitudinal carinae on the clypeus, lack of scrobes and frontal carinae, the presence of an elongate petiolar peduncle, and the presence of elongate propodeal lobes.

Describing a new genus from a few specimens of one species should generally be avoided. However, no currently described genera have the above combination of characters and in an effort to create a monophyletic *Stenamma*, I believe that this action is defensible. In addition, by erecting a new genus, there might be greater interest in discovering new material for future systematics studies.

Distribution. As reported in DuBois (1998), *P. pingorum* is known only from two localities on the island of Borneo in Sarawak, Malaysia. These are the type locality (listed below) and Fourth Division, Gunong Mulu National Park (Feb 1978, N.M. Collins, BMNH).

Propodilobus pingorum **(DuBois) comb. n.**
(Figures 41–44)

Stenamma pingorum DuBois, 2000: 40. Holotype worker and paratype workers, MALAYSIA: Sarawak, First Division, Semengoh Forest Reserve, 19 km SW Kuching (1.33ºN, 110.20ºW) (2 km S 10th mile Bazaar, on Kuching-Penrissen Road), 28–31 May 1968, R.W. Taylor, RWT-68.196, leaf mould berlesate in rainforest [Holotype and paratype workers in ANIC examined.] [Replacement name for *Stenamma orientale* DuBois, 1998: 308–310, Figs 41–43, 210–213 (Junior primary homonym of *Messor orientalis* (Emery 1898: 143))].

Conclusions

Like many other ant genera in the Myrmicinae, *Stenamma* has been a problematic genus lacking an adequate morphological diagnosis. Nevertheless, the combination of new collecting techniques, a global perspective, and the use of sequence data, has made it possible to redefine *Stenamma* with confidence. This new understanding will aid efforts to study the biogeographic history of the genus and to revise the largely unstudied Neotropical fauna.

In contrast to *Stenamma*, it is clear that *Lordomyrma* is not a well-defined genus and is in need of a global analysis similar to the one presented here. The molecular work by Lucky and Sarnat (in press) and the on-going morphological studies of Taylor (2009), offer a strong foundation for the re-examination of generic boundaries. A clearly defined *Lordomyrma* is critical to putting the aberrant morphological characters of the *Stenamma*-like taxa *L. bhutanensis* and *L. sinensis* into a more satisfying context than can be presented here.

The genus *Propodilobus* is defined, but its placement within the Myrmicinae is not yet known. It is imperative that more specimens of *Propodilobus* be collected in order to increase our knowledge of the groups morphological diversity, to provide material for molecular studies, and to confirm the group's proposed generic status.

This is not the first study to show that there are taxonomic problems within the Myrmicinae. Others have suggested or shown that a substantial number of genera and tribes within the subfamily are non-monophyletic (Brady *et al.* 2006; Moreau *et al.* 2006; Ward 2007). Most important in terms of classifying *Stenamma* will be to diagnose the group that contains *Aphaenogaster, Messor,* and *Stenamma*. This will likely require a molecular phylogenetic analysis that includes additional genera currently classified as Pheidolini. Establishing new generic limits should proceed in a manner similar to that adopted here. The combination of molecular data and a global analysis of morphology will reveal which characters are most useful in diagnosing natural groupings. It will also help to reveal interesting cases of convergent evolution within the ants.
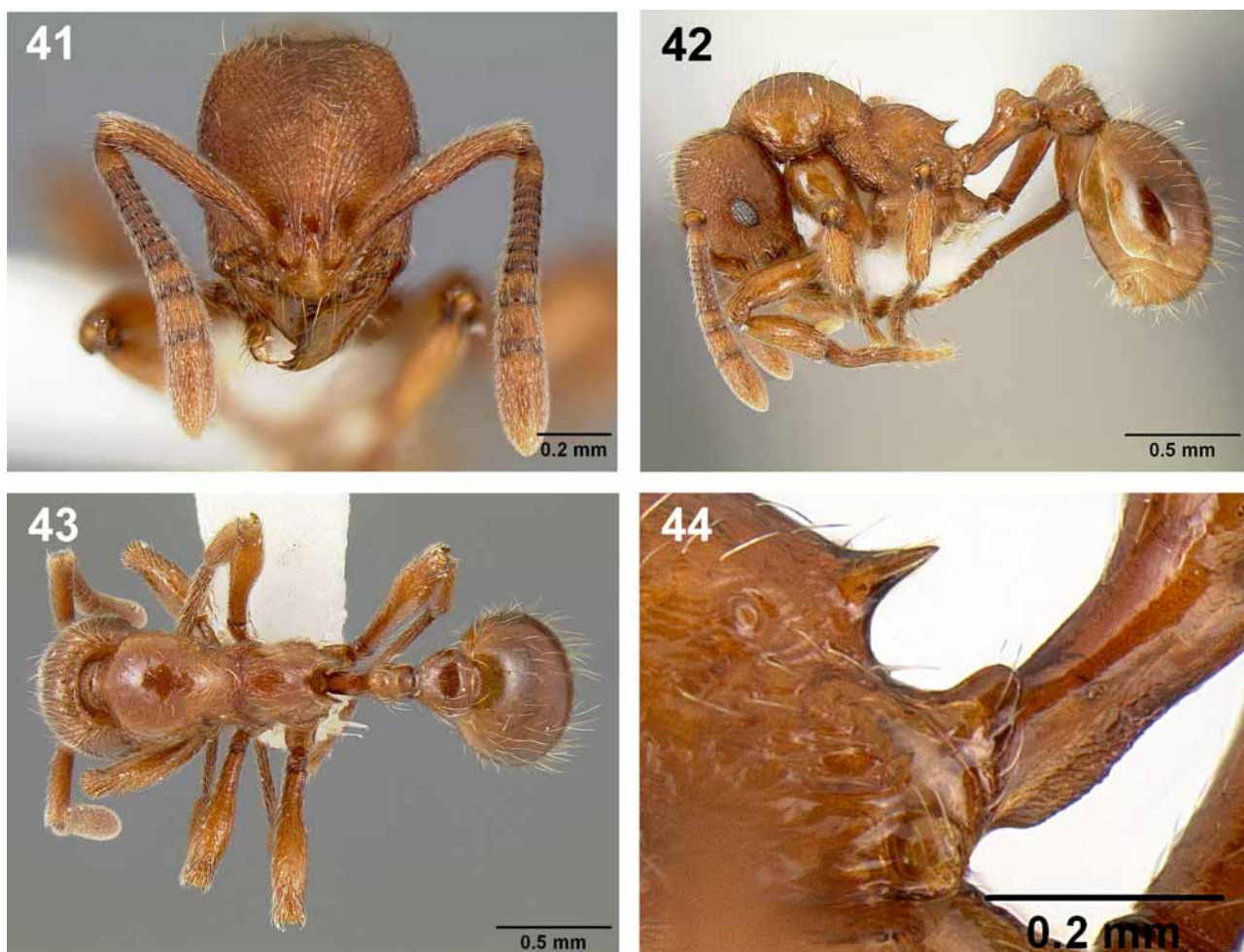
FIGURES 41–44. Images of *Propodilobus pingorum* CASENT0171177 (Sarawak, Malaysia). Figures 41–43: Full-face, profile, and dorsal views, respectively. Figure 44: Close-up of the elongate propodeal lobe in profile.

Acknowledgements

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