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Discovery of the worker caste and descriptions of two new species of *Anomalomyrma* (Hymenoptera: Formicidae: Leptanillinae) with unique abdominal morphology

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Abstract

The hitherto unknown worker caste of *Anomalomyrma* Taylor, 1990 is described for the first time. Two new species, *Anomalomyrma boltoni* **n. sp.** from Cameron Highlands, Peninsular Malaysia and *Anomalomyrma helenae* **n. sp.** from El Nido region of Palawan, Philippines, are described. In workers of both new species abdominal segments II and III (petiole and postpetiole) are rigidly fused together across both tergites and sternites. This is the first report of such fused abdominal morphology in worker Formicidae. Both new species lack a vertical lamella on the mandible, originally considered to be diagnostic for the genus and the main character separating *Anomalomyrma* from *Protanilla* Taylor, 1990. Modified generic diagnoses are proposed for both *Anomalomyrma* and *Protanilla*. Wing venation is described for the first time from an anomalomyrmine alate gyne, and prospects for the future of the nomenclature of the group's genera are discussed. A modified key to the genera of Leptanillinae is given along with a short note on the correct authorship of some leptanilline names.

Key words: ants, taxonomy, systematics, new species, wing venation, Philippines, Malaysia, *Protanilla*

Introduction

The ant subfamily Leptanillinae represents one of the early branches of ant phylogeny, and until the recent discovery of Martialinae (Rabeling *et al.* 2008), the leptanillines were considered to be sister to all other ants under certain molecular phylogenetic analyses (Moreau *et al.* 2006, Brady *et al.* 2006). Brady *et al*. (2006), however, questioned the statistical rigor of this result and suggested alternative rooting of their tree that would result in Amblyoponinae and Leptanillinae emerging within a clade together with Agroecomyrmecinae. A close relationship of amblyoponines and leptanillines is also supported by some shared morphological and behavioral features (Brown *et al*. 1971, Gotwald & Lévieux 1972, Masuko 1986, 1990, Bolton 1990, Ward 1994, Brady *et al*. 2006, Yamane *et al*. 2008).

The Leptanillinae are small to tiny subterranean ants that are infrequently collected, and very little is known of their habits. Masuko (1990) studied the biology of *Leptanilla japonica* and showed that adult queens are incapable of taking food on their own, instead relying on larval haemolymph secreted through specialized abdominal structures. Recent collections of *Leptanilla* in Europe show that there is a high cryptic diversity of these ants in the Mediterranean region (López *et al.* 1994, Scupola & Ballarin 2009). López *et al.* (1994) reported collecting large numbers of *Leptanilla* thanks to a rarely employed method and searching in a habitat seldom explored by ant collectors, i.e., “lavage de terre” method and sandy banks of periodic streams.

The subfamily is presently divided into two tribes, Anomalomyrmini Taylor, 1990 and Leptanillini Emery, 1910. A full list of subfamily, tribe, and generic references can be obtained from Bolton (2003) and the most recent

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catalogue of species has been provided by Bolton *et al.* (2007). The Bolton Synopsis and Catalogue are now updated on the web at Bolton's Catalogue and Synopsis, http://gap.entclub.org/.

In 1990 Bolton published the description of Anomalomyrmini, with two genera: the type genus *Anomalomyrma* Taylor, and *Protanilla* Taylor. *Anomalomyrma taylori* Bolton, 1990, the sole species in the genus was described from a dealate gyne from Borneo and *Protanilla rafflesi* Taylor, 1990 was based on a worker specimen from Peninsular Malaysia. Both species were rather superficially treated and names were attributed to R.W. Taylor as at that time he was preparing an exhaustive taxonomic study of both genera and was to give more detailed accounts later (Bolton 1990). Undescribed species of *Anomalomyrma* and *Protanilla* also appeared in text and figures (under *nomina nuda A. kubotai* and *P. wallacei*) in Hölldobler & Wilson (1990). The above mentioned taxonomic treatment by Taylor never appeared although subsequent authors have contributed new species descriptions for the tribe. From Yunnan, China, Xu & Zhang (2002) described *Protanilla furcomandibula* and Xu (2002) described *P. bicolor* and *P. concolor* (see Appendix). In 2006 Baroni Urbani & de Andrade described a new species from Sri Lanka, *P. schoedli*, reporting the first gyne known in the genus *Protanilla*. Terayama (2009) added one more species, *P. lini* from Taiwan.

Here we describe the worker caste of *Anomalomyrma* and two new species. We note peculiar fusion of abdominal segments II and III, compare worker *Anomalomyrma* with *Protanilla*, and discuss prospects for the tribe's taxonomy.

Material, methods, and measurements

For this study, we compared the few available specimens of *Anomalomyrma*, which are restricted to the holotype of *A. taylori* (not examined, deposited in Muséum d'Histoire Naturelle de la Ville de Genève, Geneve, Switzerland), and the four workers of the two newly described species. Although we did not examine the holotype of *A. taylori* directly, the detailed drawings in Bolton (1990) and color photographs from www.antweb.org (AntWeb 2010; Figs. 11, 12) provide enough data to draw conclusions about the species' morphology. We also discuss an alate gyne specimen from Borneo. Unfortunately, at present only photographs are available for this apparently undescribed species, as the specimen itself cannot be located (Brian Fisher, Stefan Cover, pers. comm.). From *Protanilla* and *Leptanilla* we examined workers of several species and gynes from an additional two species, stored in the private collections of Andreas Schulz (Leverkusen, Germany), Marek Borowiec (Wrocław, Poland) and Philip Ward (Davis, USA), as well as in the California Academy of Sciences collection (San Francisco, USA) and the Natural History Museum collection (London, Great Britain). Some putative males of the Leptanillinae were examined in material from the collection of the Lund Zoological Museum, University of Lund, Sweden. Additionally we analyzed the photographs, descriptions and drawings of workers, males and gynes of additional leptanilline species (Wheeler & Wheeler 1930, Petersen 1968, Kugler 1987, Bolton 1990, Ogata *et al*. 1995, Xu 2002, Xu & Zhang 2002, Imai *et al*. 2003, Baroni Urbani & de Andrade 2006, AntWeb 2010). Most of the taxonomic literature cited here was obtained from the website www.antbase.org (Agosti & Johnson 2010).

For *A. boltoni* measurements were made using a Nikon SMZ 1500 stereomicroscope with ocular micrometer. Digital color images of *A. boltoni* and an undescribed gyne (Figs. 1, 2, 4, 9–12) were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software and obtained from www.antweb.org (photography: April Nobile and Erin Prado, courtesy of Brian Fisher). The scanning electron micrograph of *A. boltoni* (Fig. 3) waist was prepared using a Zeiss/LEO 1450VP SEM at the California Academy of Sciences. For *A. helenae*, measurements were made using a Zeiss Stemi SR stereomicroscope equipped with an ocular graticule and color photographs (Figs. 5–8) were prepared using a Leica MZ16 stereomicroscope and a Leica DC420 digital camera and processed with Helicon Focus software. All images were cleaned and adjusted using Adobe Photoshop.

Measurements

HW Head capsule width: Maximum head width in full-face view.

HL Head capsule length: Measured in full-face view as a straight line from the anterior most point of median clypeal margin to the mid-point of the posterior margin of the head. Concavity of posterior margin reduces HL.

MaL Mandible length: Maximum length of mandible from the anterolateral margin of clypeus at outer side of mandibular insertion to mandibular apex.

SL Scape length: The maximum length, measured from the proximal point of scape lobe to the distal end of scape in frontal or dorsal view.

ML Mesosoma length: The diagonal length measured in lateral view from the anterior most point of the pronotal slope to the posterior or postero-ventral corner of mesosoma.

PrW Pronotal width: Maximum width of pronotum in dorsal view. In *Anomalomyrma* workers also the widest point of mesosoma.

PW Petiole width: Maximum width of abdominal segment II in dorsal view.

PL Petiole length: Length of abdominal segment II measured in dorsal view, from the anterior corners (tubercles above petiolar spiracles) behind the petiolar peduncle to posterior margin of petiolar posttergite.

AIIIW Third abdominal segment (postpetiole) width: Maximum width in dorsal view.

AIIIL Third abdominal segment (postpetiole) length: Maximum length in dorsal view, measuring only the length of the posttergite, excluding pretergite III (helcium).

AIVW Fourth abdominal tergite width: Maximum width in dorsal view.

AIVL Fourth abdominal tergite length: Maximum length in dorsal view, excluding pretergite.

FCoW Front coxa width: Maximum width in lateral view.

FCoL Front coxa length: Maximum length in lateral view.

CS Head size: The arithmetic mean of HL and HW.

BS Body size: Calculated from the arithmetic mean of HW, HL and ML.

All measurements are given in millimeters.

Descriptions

Characters of the subfamily and the tribe Anomalomyrmini can be found in Bolton (1990, 2003).

Anomalomyrma boltoni n. sp.

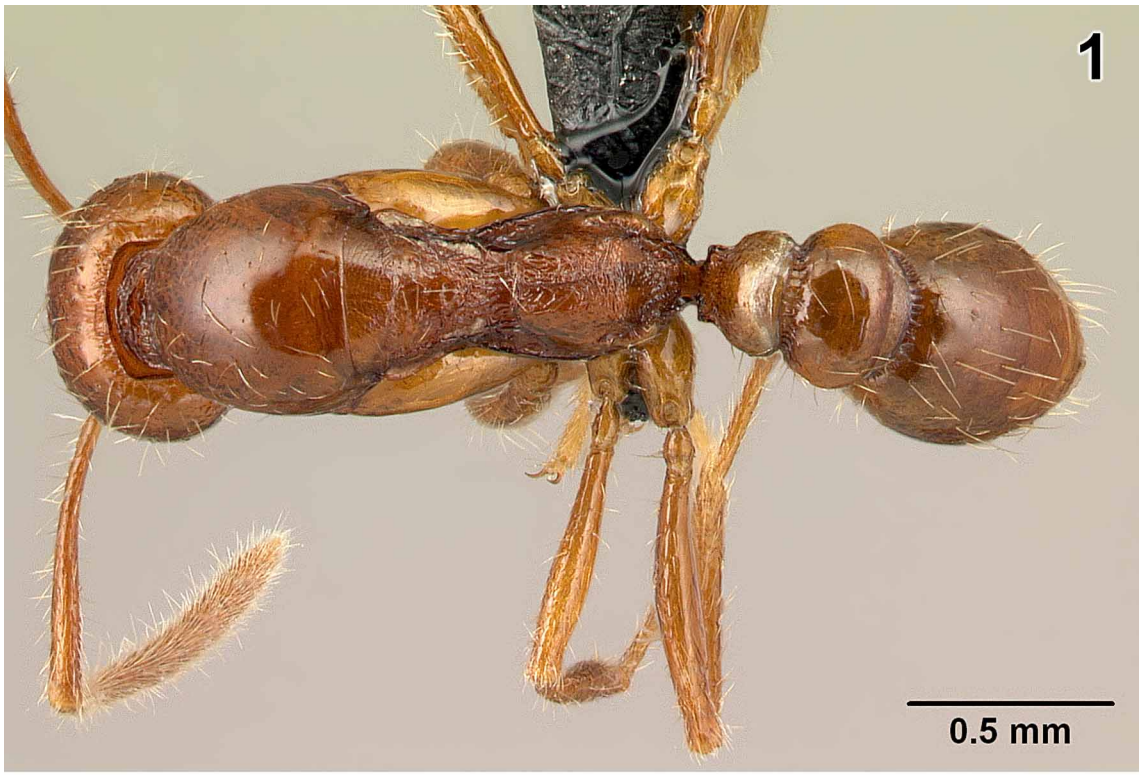
Figs. 1–4.

Holotype worker. MALAYSIA: Perak, Cameron Highlands, Batu [=Mile] 19 village environment, 04°22.2' N 101°20.0' E, 590 m, sifting leaf litter & rotten wood (*P. Baňař*) 30 IV-7 V 2009, CASENT0217035. The specimens were sifted from the trunk of a dead tree at a late stage of decomposition, very close to a stream and extracted using Winkler apparatus. The sifted material was wet.

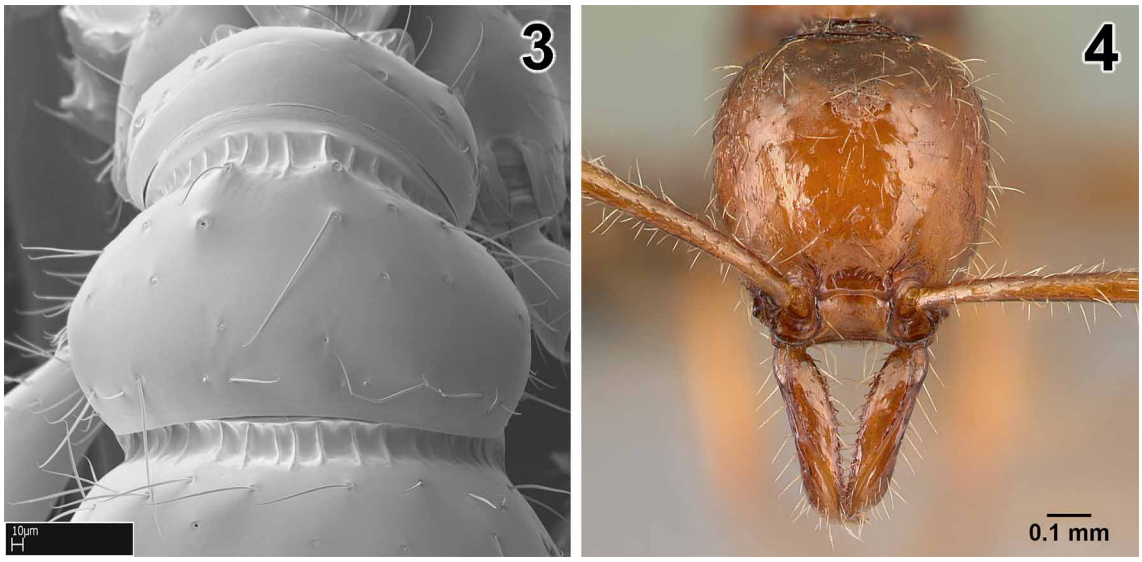
Paratype worker. Same data as the holotype, CASENT0217032. Holotype worker will be deposited at California Academy of Sciences Collection, San Francisco, CA, USA and the paratype will be deposited in Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. After performing measurements and taking color digital images, the paratype was sputter coated with gold in order to examine external abdominal morphology using SEM.

Etymology. This species is dedicated to Barry Bolton.

Description of worker. Measurements and ratios of holotype worker. HW 0.67, HL 0.75, MaL 0.51, SL 0.85, ML 1.30, PrW 0.58, PW 0.32, PL 0.20, AIIIW 0.42, AIIIL 0.22, AIVW 0.55, AIVL 0.51, FCoW 0.41, FCoL 0.67, CS 0.71, BS 0.91, HW/HL 0.89, SL/HW 1.27, PL/PW 0.63, PL/AIIIL 0.91, PW/AIIIW 0.76, AIIIL/AIIIW 0.52, PW/ML: 0.25, AIIIW/ML: 0.32. Measurements and ratios of paratype worker. HW 0.73, HL 0.83, MaL 0.56, SL 0.93, ML 1.52, PrW 0.65, PW 0.36, PL 0.23, AIIIW 0.47, AIVL 0.29, AIVW 0.64, AIVL 0.58, FCoW 0.40, FCoL 0.70, CS 0.78, BS 1.03, HW/HL 0.88, SL/HW 1.27, PL/PW 0.64, PL/AIIIL 0.79, PW/AIIIW 0.77, AIIIL/AIIIW 0.61, PW/ML: 0.24, AIIIW/ML: 0.31. Head longer than wide, with vertex margin straight and posterior corners broadly, evenly rounded. Occipital carina visible in frontal view. Head sides rounded, with tooth-like prominence



FIGURES 1–2. *Anomalomyrma boltoni* **n. sp.**, paratype worker. FIGURE 1. Body in dorsal view; FIGURE 2. Body in lateral view.



FIGURES 3–4. *Anomalomyrma boltoni* **n. sp.**, paratype worker. FIGURE 3. Waist in dorso-posterior view; FIGURE 4. Head in dorsal view.

lateral to antennal sockets and a notch below. Eyes absent. Mandible elongate, sabre- to sickle-like and downcurved, with one row of about 15 cuticular teeth at masticatory margin. In lateral view mandible thin, without vertical lamella on dorsal surface and without any processes on lateroventral margin. Modified peg-like setae absent from ventral surface of mandibles. Dorsolateral surface of mandible with a broad longitudinal groove which runs forward from a laterobasal pit. Surface of labrum with six pairs of very long (almost equal in length to mandibular blade) and two pairs of shorter hairs. Medial part of labrum surface with two small setae modified into peg-like teeth and with irregular row of about eight minute, peg-like teeth basally near articulation with clypeus. Palp formula unknown. Clypeus broad, concave medially with sharply keeled ridges laterally and posteriorly separated from frons by transverse impression; anterior margin shallowly concave. Antennae with 12 segments, not clavate, all segments longer than broad. Scape very long, distinctly longer then head width. Promesonotal connection flexible. In dorsal and lateral views mesosoma constricted at mesonotum, metanotal groove distinct. Deep pits in anepisternal area. Katepisternum bordered on anterior, dorsal and posterior sides by keeled edge. Propodeal dorsum rounded, shorter than declivity. Metapleural gland bulla separated from propodeal spiracle by less than spiracle diameter. Bulla of metapleural gland visible through semi-translucent cuticle, extending below propodeal spiracle. Metapleural trench present below bulla. Forelegs enlarged, coxa and femur broadened, mid- and hind legs much more slender. Middle tibiae without spurs and hind tibiae each with one pectinate spur. Abdominal segment II (petiole) with narrow anterior peduncle and evenly rounded dorsal surface without differentiated posterior surface. Both abdominal segments II and III (petiole and postpetiole) wider than long in dorsal view. Subpetiolar process a blunt tooth in lateral view, in ventral view composed of two cuticular ridges converging anteriorly. Semitranslucent fenestra absent. Abdominal segment III (postpetiole) with sharp anteroventral edge and differentiated anterior surface. Ventral surface short, shallowly concave, dorsal surface long, evenly rounded, without differentiated anterior and posterior faces, broadly attached to segment IV (first gastral). The tergite of abdominal segment II is fused to the tergite of abdominal segment III, and the same is true for the sternites of the two segments. Abdominal segment II with complete tergosternal fusion and without trace of suture.

Tergosternal fusion of abdominal segment III was not determined through dissections due to scarcity of material. The suture runs the length of the segment. Abdominal segments III and IV with deep girdling constrictions between pre- and postsclerites. Abdominal segments IV–VII (gaster) oval in dorsal view, gastral shoulders not surrounding abdominal segment III, and no notch between tergite and sternite IV in lateral view. Mandibles smooth with small punctures (ca. 0.01 mm). Head with similar punctation and strip of irregular roughness of cuticle in middle of frons, posterior portion of head capsule with roughness and small tubercles. Pronotum mostly smooth with scattered small punctures, only pronotal flange and margins with irregular roughness, meso- and metanotum also very irregularly sculptured. Propodeum with the same type of roughness, except sides, where smooth. Body pilosity of suberect to erect hairs on all surfaces. Color orange brown to reddish brown, appendages lighter.

***Anomalomyrma helenae* n. sp.**
Figs. 5–8.

Holotype worker. PHILIPPINES: Palawan, El Nido Region, Bulalacao Waterfall, 11°13'41" N 119°28'00" E, 200–450 m, seasonal dry primary forest on steep slope near the waterfall (*A. Schulz*) 25 XI 2009, CASENT0220220. The ants were sifted from leaf litter on wet forest floor and extracted with a Winkler apparatus.

Paratype worker. Same data as holotype, CASENT0220221.

Holotype will be deposited in Staatliches Museum für Naturkunde Karlsruhe, Germany and the paratype will be deposited in California Academy of Sciences Collection, San Francisco, CA, USA.

Etymology. This species is dedicated to Helene Faulhaber for her understanding.

Description of worker. Measurements and ratios of holotype worker. HW 0.67, HL 0.75, MaL 0.51, SL 0.86, ML 1.36, PrW 0.61, PW 0.39, PL 0.26, AIIIW 0.48, AIIIL 0.30, AIVW 0.68, AIVL 0.71, FCoW 0.32, FCoL 0.66, CS 0.71, BS 0.93, HW/HL 0.89, SL/HW 1.27, PL/PW 0.66, PL/AIIIL 0.84, PW/AIIIW 0.80, AIIIL/AIIIW 0.63, PW/ML: 0.29, AIIIW/ML: 0.3. Measurements and ratios of paratype worker. HW 0.70, HL 0.79, MaL 0.52, SL 0.88, ML 1.39, PrW 0.65, PW 0.41, PL 0.32, AIIIW 0.55, AIIIL 0.33, AIVW 0.68, AIVL 0.65, FCoL 0.66, FCoW 0.32, CS 0.75, BS 0.95, HW/HL 0.89, SL/HW 1.26, PL/PW 0.79, PL/AIIIL 0.97, PW/AIIIW 0.74, AIIIL/AIIIW 0.60, PW/ML: 0.29, AIIIW/ML: 0.39. Head longer than broad, vertex margin medially slightly concave, posterior corners more abruptly rounded. Occipital carina visible in frontal view. Head sides evenly and slightly convex, with tooth-like prominence lateral of antennal sockets, with a notch below. Eyes absent. Mandible elongate, sabre- to sickle-like and downcurved, only with marginal basal margin. Masticatory margin with one row of about 20 irregular, very small, cuticular saw-blade like teeth. Mandible with an obvious dorsolateral groove, framed by ridges, with a conspicuous basal pit arising laterally on the mandible and close to mandibular insertions. In lateral view the mandibles are thin and strongly bent backwards, apically each mandible with one thick, very long hair. Labrum with 10–12 very long (nearly equally long as mandible blade) hairs. Labrum armed with seven peg-like teeth, from which the two submedian are longer than the others. Palp formula 4,2 or 4,1 (uncertain *in situ* count). Clypeus broad, in lateral view raised convexly over the remaining surface of head. In dorsal full face view anterior margin of clypeus evenly concave, posteriorly separated from frons by transverse impression. Antennae with 12 segments, not clavate, all segments longer than broad. Scape very long, distinctly longer then head width. Neck of pronotum with an oval median depression. Pronotum high and bulky. Promesonotal connection flexible. In lateral view mesosoma with a deep and wide metanotal groove, in dorsal view between mesonotum and propodeum distinctly constricted. Katepisternum bordered by a keeled edge. Propodeum delimited from thorax by a scrobiculate-fossulate groove, visible in lateral and dorsal views. In lateral view propodeum with dorsal surface flat, declivitous and dorsal faces meeting at obtuse angle. In dorsal view the propodeum is distinctly narrower than pronotum, and the base of it is broader than the upper part. Propodeal spiracle and metapleural gland bulla separated by about twice the spiracle diameter. Bulla of metapleural gland visible though semi-translucent cuticle. Metapleural trench present below bulla. Forelegs enlarged, coxa and femur broadened, mid- and hind legs much more slender. Middle tibiae without spurs and hind tibiae each with one pectinate spur. Abdominal segments II (petiole) with narrow anterior peduncle and evenly rounded dorsal surface, without differentiated posterior surface. Both abdominal segments II and III (postpetiole) distinctly broader than long. Subpetiolar process with a large lobe-like extension, and a small anterior-basal semi-translucent fenestra, in ventral view broad, tapering distally. Abdominal segment II with complete tergosternal fusion and without trace of suture. Abdominal segment III in dorsal view broad, nearly oval, broadly attached to segment II and IV (first gastral), separated from surrounding segments by scrobiculate constrictions between pre- and postsclerites. In lateral view abdominal segment III distinctly higher than long; dorsal surface flat, outline slightly convex; attached to segment II by an immobile joint. Ventral outline of segment III with a visible articulatory surface with segment IV and capable of relative movement. Tergite and sternite of abdominal segment III separated by a visible suture; the tergosternal fusion was not determined. Gaster oval in dorsal view, gastral shoulders not surrounding abdominal segment III, and no notch between tergite and sternite IV in lateral view. Mandibles smooth with very few, isolated foveolae. Head capsule devoid of sculpture except tiny punctures at the base of hairs, surface shiny. Pronotal neck roughly reticulate/rugulate, propleuron reticulate. Pronotum, mesonotum, and surface of propodeum, generally without any sculpture, surfaces glossy. Articulatory surface between pronotum and mesonotum strigulate, the distinct groove between mesonotum, katepisternum and propodeum is scrobulate. Propodeal declivity with very shallow reticulate sculpture. Abdominal segments II, III

and IV–VII (gaster) without sculpture. Body pilosity of suberect to erect hairs on all surfaces. Color mainly brown to dark brown with antennae, legs (except foreleg coxae), parts of pronotum and mesonotum testaceous.

Differential diagnosis. The general appearance of *A. helenae* is similar to that of *A. boltoni*, but they are distinguishable by the characters in Table 1.

FIGURES 5–6. *Anomalomyrma helenae* **n. sp.**, holotype worker. FIGURE 5. Body in dorsal view; FIGURE 6. Body in lateral view.

FIGURES 7–8. *Anomalomyrma helenae* **n. sp.**, holotype worker. FIGURE 7. Waist in dorsal view; FIGURE 8. Head in dorsal view.

TABLE 1. Characters differentiating *A. boltoni* and *A.helenae*.

A. boltoni	*A.helenae*
Labrum only with very small peg like teeth of about the same length	Labrum with two distinctly larger teeth, and five well developed small teeth
Propodeal spiracle not far from metapleural gland bulla, separated by less than the spiracle diameter	Propodeal spiracle distant to metapleural gland bulla, separated by about twice the spiracle diameter
Propodeum convex, declivitous face less steeply sloping	Propodeum with dorsal face relatively flat and declivitous face more steeply sloping
Subpetiolar process in lateral view developed as a relatively smaller blunt tooth, lacking fenestra	Subpetiolar process in lateral view large and lobate, with visible fenestra
Abdominal segment II (petiole) and III (postpetiole) narrower (PW/ML 0.25; AIIIW/ML 0.32)	Abdominal segment II (petiole) and III (postpetiole) broader (PW/ML 0.29; AIIIW/ML 0.37)
Head surface with visible sculpture	Head without any sculpture
Mesonotum and propodeum with more than 50% of surface irregularly reticulate to rugose, mesopleuron sculptured	Mesonotum and propodeum without distinct sculpture, shiny, mesopleuron smooth
Color orange brown to reddish brown	Color testaceous to dark brown

Unfortunately, *A. taylori* (Figs. 11, 12) was described only from a gyne, and we are unable to compare our new species in the same caste. Nevertheless, we found some characters that should apply for both worker and reproductive female castes. The gyne of *A. taylori* and the undescribed gyne from the collection of the Museum of Comparative Zoology, Harvard University (see Discussion: Wing venation of the Anomalomyrmini) are very similar in sculpturing and color. They differ, however, in labrum and mandible armament, mesosoma height and robustness, and especially the complete fusion of petiole and abdominal sternite III (postpetiolar) in *A. taylori*. In the undescribed gyne both segments are clearly constricted. The characters separating *A. taylori* from the undescribed gyne are also useful to distinguish *A. taylori* from *A. boltoni* and *A.helenae*. Given the extreme abdominal morphology of *A. taylori*, we are confident that our two new species are not *A. taylori*. *Anomalomyrma boltoni* differs from both gynes also by the stronger sculpture, the different propodeum morphology, and the mandibular and labral armament. Characters distinguishing *A. helenae* from the undescribed gyne are a little less obvious. There are differences in the dimensions of the mesosoma, distinct color differences and, most obviously, differences in mandible

shape. The mandibles are relatively narrow in *A. helenae* and broader in the undescribed gyne. Also, the two collections come from relatively distant localities (SW Borneo and Palawan). It is possible, however, that in the future the undescribed gyne will be shown to belong to one of our new species.

Discussion

Unique abdominal morphology. Among ants, the degree of tergosternal fusion of the abdominal sclerites of segments II (petiole), III (postpetiole) and IV (first gastral) are relevant diagnostic characters at the subfamily level, and have proved useful in ant classifications (Gotwald 1969, Ward 1994, Bolton 2003). However, the longitudinal fusion of adjacent segments of the abdomen is extremely rare and hitherto reported only in the holotype of *A. taylori*. In 1990, Bolton described *A. taylori* from a dealate gyne and noted the bizarre arrangement of abdominal segments II and III, namely fusion of sternites of both, which are in turn fused laterally to the tergites. In the two new species described here the fusion of both tergites and sternites of segments II and III occurs, but to a lesser degree than in *A. taylori*. Since the new species are known from two specimens each, no attempt at dissection was made. However, efforts at manipulation that normally would result in relative movement of the segments, carried out on a relaxed specimen, proved ineffective. While in alcohol, specimens of *A. boltoni* were gently grabbed by the petiole with tweezers and the remainder of abdomen was prodded with a pin. This resulted in visible movement of segment IV relative to segment III (postpetiole) but no observable mobility between petiole and postpetiole. Investigation with SEM showed a line of junction between the petiole and helcium (presclerite of segment III) which is very thin and markedly different from the junction of segments III and IV (Fig. 3). A girdling constriction is still visible in both tergal and sternal portions, unlike in the *A. taylori* gyne, where the constriction is obliterated and both sternites II and III form a completely fused plate, without a groove (Figs. 11, 12). The unusual morphology of the abdomen in the gyne of *A. taylori* led Bolton (1990) to suggest that such a structure arose as a modification towards dichthadiigyny or was simply teratological. Since no workers of *Anomalomyrma taylori* have been reported so far, there is no way to know if the peculiarly built waist of *A. taylori* is unique to the gynes or also shared by workers. After the discovery of the workers of the new species described here it seems probable that the abdomen structure in *Anomalomyrma taylori* is not teratological. However, the alate gyne of the undescribed *Anomalomyrma* from Borneo seems much closer in general habitus to *A. boltoni* and *A.helenae* than to the gyne of *A. taylori*. The waist condition in the Borneo gyne seems to be similar to the workers described here.

Features separating *Anomalomyrma* from *Protanilla*. In his 1990 treatment Bolton had only one worker of *Protanilla* and one gyne of *Anomalomyrma* and thus was not able to do direct comparisons within castes. When differentiating the two genera, he considered the presence of a peculiar lamella arising vertically from the mandible of *A. taylori* as the major character differentiating *Anomalomyrma* from *Protanilla*. He mentioned workers of another assumed *Anomalomyrma* known from Japan (discussed below). Since Bolton's 1990 paper there appeared a few contributions to the knowledge of *Protanilla*, summarized in the introduction. In descriptions of species from China, Xu (2002) and Xu & Zhang (2002) introduced three new species, of which one, *P. furcomandibula*, possesses peculiar broadening of the mandibular blade with the lateroventral margin forming two teeth. We were unable to examine this species or Japanese *Anomalomyrma* and we draw our knowledge from Xu & Zhang (2002) and Imai *et al*. (2003) that, in addition to a written account, provide figures of both species. The Japanese "*Anomalomyrma*" apparently possesses the peculiar mandibular structure similar to the one described in *A. taylori* (SEMs of the Japanese species also appear in Hölldobler & Wilson 1990). However, the structure of the waist in the Japanese species is very different from that found in *A. taylori* and both species described here. Rather it conforms to the structure typical for hitherto described *Protanilla*: abdominal segment III (postpetiole) is narrowly attached to segment II (petiole) and the nodes of both have differentiated posterior surfaces, absent in the gyne of *A. taylori* and in the workers described here. Moreover, from the SEM illustrations in Hölldobler & Wilson (1990: 592) it is evident that the mandibular armament of this species is formed mostly by modified, peg-like setae and not cuticular teeth, as is the case with *A. taylori* (Bolton 1990) and the two species described in this study. On the other hand, *A. boltoni* and *A.helenae* do not possess the erect mandibular lamella, present in *A. taylori* and the undescribed species from Japan that was considered a major trait separating *Anomalomyrma* from *Protanilla* (Bolton 1990, 1994, Imai *et al*. 2003). We regard abnormal abdominal morphology a putative synapomorphy of *Anomalomyrma* and a better character for diagnosing the two genera, hence we suggest a modification of the definition of both and transfer the

undescribed Japanese species to *Protanilla.* Since mandibular morphology is frequently connected to foraging strategies (Wheeler 1910), we consider it probable that in this rarely collected tribe the mandibles may be subject to frequent modifications and thus of less relevance for phylogeny and resulting classifications than abdominal morphology, which is quite stable in ants, at least at the generic level (Gotwald 1969, Bolton 2003, Perrault 2004). Additionally, in *Protanilla furcomandibula* another peculiar modification of the mandible was described, and it seems that the undescribed *Anomalomyrma* gyne from Borneo represents a somewhat intermediate stage of mandibular modification between the narrow mandibles of *A. boltoni* and *A.helenae* and that of *A. taylori*, equipped with a conspicuous lamella (Fig. 10). Thus, in our opinion, *Anomalomyrma* and *Protanilla* should be diagnosed by the structure of the waist, rather than the presence of a mandibular lamella. There are other characters that seem to be relevant, and all are summarized in Table 2.

TABLE 2. Characters differentiating *Anomalomyrma* and *Protanilla*. Character states in italics are considered putative synapomorphies.

Anomalomyrma	*Protanilla*
Mandibles with a very distinct dorsolateral groove framed by two ridges and with a conspicuous basal pit	Mandibles with or without inconspicuous dorsolateral groove which is not framed by two ridges, basal pit very small or absent
Mandibles relatively elongate, without a distinct basal margin	Mandibles more triangular and shorter, with differentiated basal margin
In workers, mandibles with very small saw-blade like cuticular teeth, without peg-like teeth	*In workers and gynes, mandibles with peg-like teeth (modified setae),* with cuticular armament, if present*, arranged in only one row of small teeth on the masticatory margin
Clypeal disc concave	Clypeal disc flattened
In workers, the scape is very long, distinctly longer than head width (SL/HW 1.26–1.27)	In workers, the scape is more or less as long as head width (SL/HW <1.1)
In lateral view petiole depressed with approximately triangular appearance	In lateral view petiole rectangular, node like
Mesosoma of worker with pro-mesonotal region arched, pronotum robust with spiracle well below midheight	Mesosoma of worker with pro-mesonotal region more or less flattened**, pronotum more slender with spiracle at about midheight
Nodes of abdominal segment II (petiole) and III (postpetiole) without differentiated posterior faces	Nodes of abdominal segment II (petiole) and III (postpetiole) with clearly differentiated posterior faces
Abdominal segment II widely fused with abdominal segment III and immobile	Abdominal segment II and III not fused and mobile
Abdominal segment III distinctly broader than long, also distinctly broader than segment II	Abdominal segment III about as broad as long, or longer, not distinctly broader than segment II

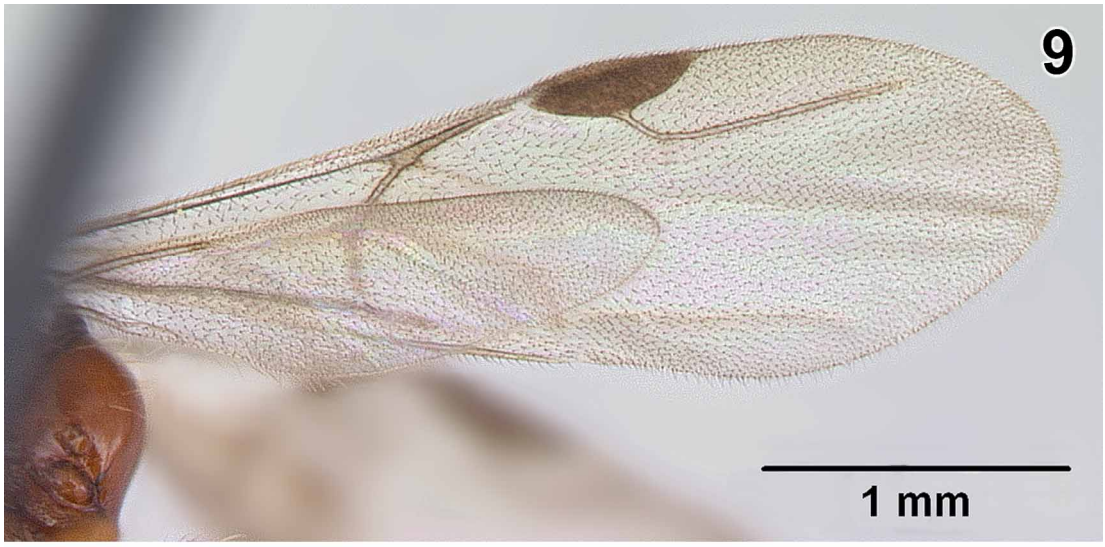
* The cuticular teeth have so far been observed only in the "*Anomalomyrma*" species from Japan.
** Judging from description and figures in Xu & Zhang (2002), *P. furcomandibula* has the promesonotal region slightly more bulky and convex, the lateral surface of mandible has a more visible groove, and exceptionally abdominal segment III (postpetiole) is more broadly attached to the segment IV (first gastral), which makes this species partially intermediate between *Anomalomyrma* and hitherto known *Protanilla* species.

Wing venation of the Anomalomyrmini. The Borneo gyne at the Museum of Comparative Zoology has the following label data:

INDONESIA: Borneo, West Kalimantan, Gunung Palung National Park, Cabang Panti Research Station, 100 m, 1°15' S 110°5' E (*D.C. Darling & U. Rosichon*) 15 VII-1 VIII 1991, primary rainforest GP-11 Sandstone-closed canopy. Fine Malaise traps (pans) IIS 910120*.15121f (MCZ), CASENT0178553.

This is the only known alate female specimen of Anomalomyrmini. Unfortunately, the specimen is no longer available for direct examination, as it could not be located despite efforts. Therefore, we based our account on photographs (Figs. 9, 10). The wing venation of the female is relatively simple (Fig. 9). The forewing (nomenclature

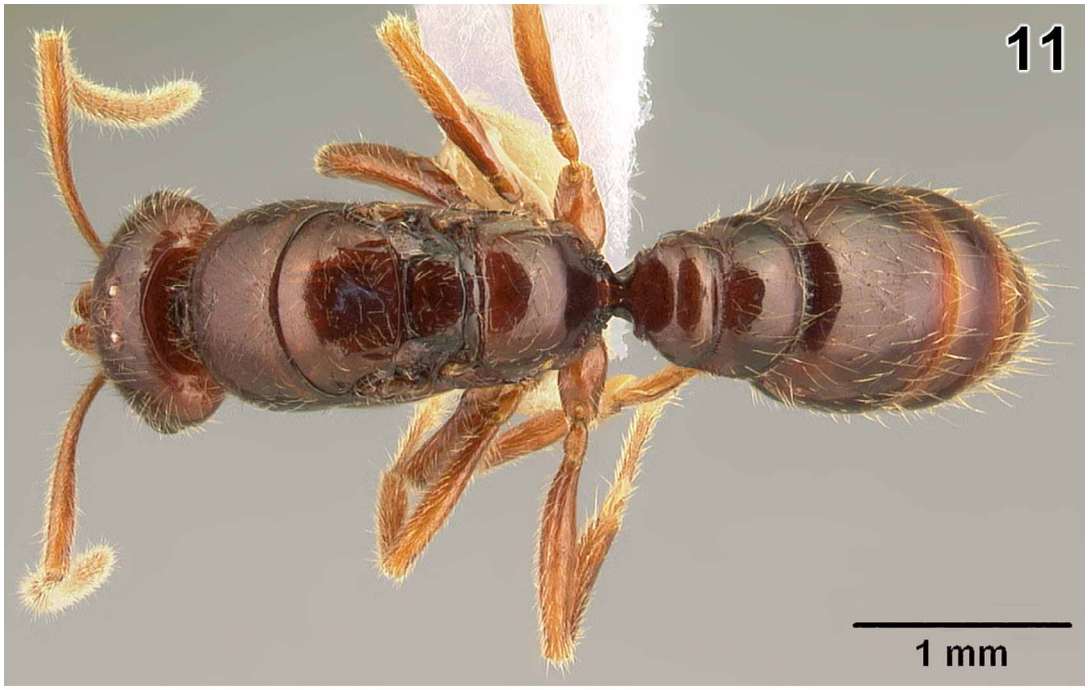
after Bolton, in preparation) has Sc+R visible. Proximal to the pterostigma there is a node which appears to mark the split of R+Sc into R1+Sc and Rs. Rs·f1 seems to be contracted so that it forms most or all of this node. The "stigmal vein" (2r-rs & Rs·f4&5) is conspicuous, not reaching the wing margin. The strong vein descending from the node appears to be M·f1 and the spectral line that extends distally from the node toward the wing margin apparently corresponds to fused Rs+M & M·f2-4. Below this the forewing is too obscured by the hindwing to be sure of the venation. The hindwing seems to possess only short tubular Sc+R and a A·f1 stub.

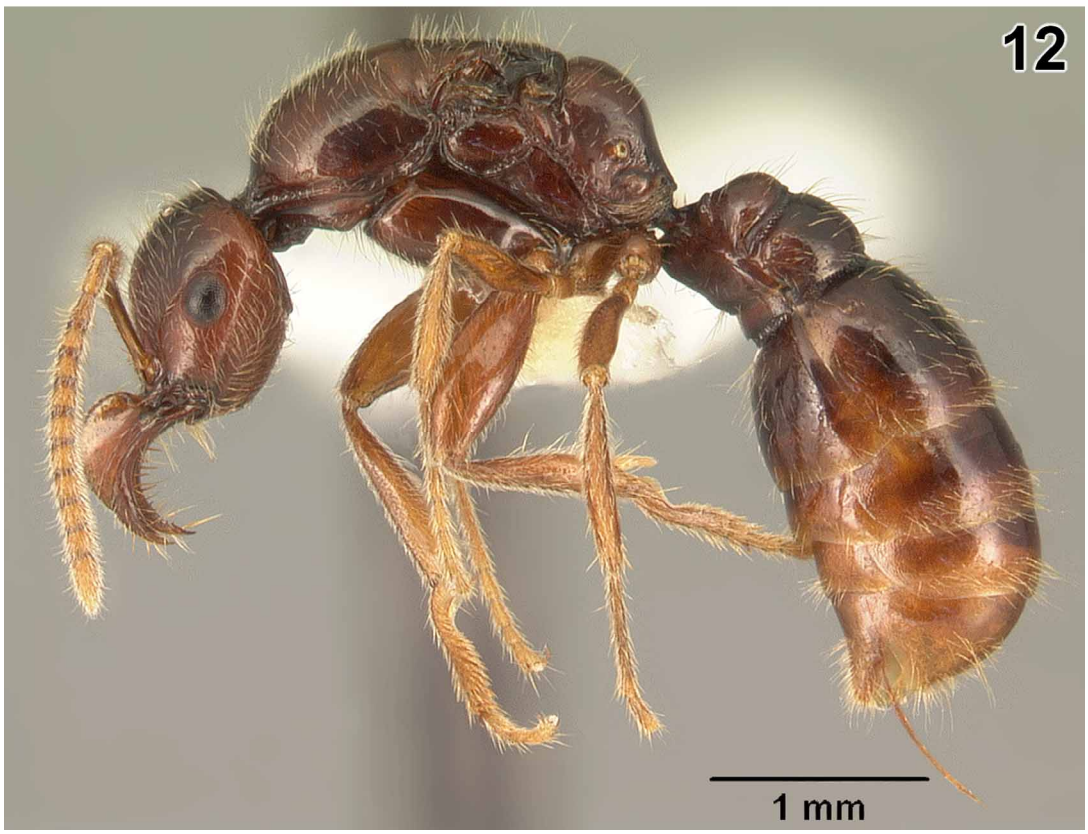


FIGURES 9–10. *Anomalomyrma* sp., alate gyne. FIGURE 9. Wings; FIGURE 10. Body in lateral view.

The relatively simple venation is markedly different from the complete venation described for the Amblyoponinae (Brown 1960). Among the venation patterns described for the Leptanillinae, the venation bears some resemblance to that of the male-based taxon from the Philippines, *Noonilla copiosa* Petersen, 1968. Some significant differences can be seen, most notably the lack of Cu, narrow and pale pterostigma, and complete lack of hind wing veins in *Noonilla*. This genus was originally placed in the Leptanillinae, although later it was considered to be

subfamily *incertae sedis* (Ogata *et al*. 1995). The venation is similar to a California Academy of Sciences male specimen, tentatively identified as *Protanilla* th02 (CASENT0128922), making it a good candidate for the male caste of *Anomalomyrma*. Based on molecular data, however, this male clusters within a clade of other worker-based morphospecies of *Protanilla* (Philip Ward, pers. comm.). It may be noted that the habitus of this specimen does not correspond clearly to any of the male-based leptanilline genera hitherto described. The diversity of leptanilline male-based morphospecies and their highly divergent morphologies among Borneo material alone (Marek Borowiec, unpublished) makes any statement about their affinities highly speculative.





FIGURES 11–12. *Anomalomyrma taylori* Bolton, 1990, holotype gyne. FIGURE 11. Body in dorsal view; FIGURE 12. Boby in lateral view.

Future of anomalomyrmine names. In addition to the uncertain differentiation of *Anomalomyrma* and *Protanilla*, there are three senior generic names available for unassociated male specimens in the subfamily: *Phaulomyrma* Wheeler & Wheeler, 1930, *Yavnella* Kugler, 1987, and *Noonilla* Petersen, 1968. There is also another enigmatic taxon, *Scyphodon* Brues, 1925, currently considered family *incertae sedis* (Ogata et al. 1995), but at times recognized as a leptanilline (Petersen, 1968). Thus, the names of worker-based taxa are likely to change in the future. It seems most probable that eventually *Anomalomyrma* and/or *Protanilla* will need to be sunk into synonymy with *Scyphodon*, *Phaulomyrma*, *Yavnella* or *Noonilla*, once worker-associated males are collected or sufficient fresh material enables comparison of DNA sequence data for both castes (cf. Ward 2007). At present, however, the possibility that the worker-based and male-based taxa of the Leptanillinae represent distinct lineages cannot be excluded.

Key to the genera of the subfamily Leptanillinae based on workers, slightly modified from Bolton (1994)

1. Mandible with 3–5 cuticular teeth, all located on distal half of masticatory margin. Maxillary palp with 1 segment. Metanotal groove vestigial to absent. Bulla of metapleural gland rounded, located behind level of propodeal spiracle. Metapleural trench absent. Clypeus very narrow in front of antennal insertions, the latter very close to the anterior margin of head (Old World tropics and temperate regions). . . . . *Leptanilla*
- Mandible with more than 5 peg-like or cuticular saw-like teeth located along full length of masticatory margin. Maxillary palp with 4 segments (when known). Metanotal groove present, strong, and impressed. Bulla of metapleural gland elongate and narrow, running longitudinally below the propodeal spiracle. Metapleural trench present. Clypeus relatively broad in front of antennal insertions, the latter well back from the anterior margin of the head . . . . . 2.
2. Mandible with peg-like teeth, sometimes with an additional row of saw-like cuticular teeth along masticatory margin. Petiole with well differentiated posterior face (Southern Palaearctic, Indo-Malayan) . . . . . *Protanilla*
- Mandible without peg-like teeth, only saw-like cuticular teeth along masticatory margin. Petiole without differentiated posterior face (Indo-Malayan) . . . . . *Anomalomyrma*

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APPENDIX. The authorship of Chinese *Leptanilla yunnanensis*, *Protanilla bicolor* and *P. concolor.*

In the catalogue of Bolton *et al.* (2007) the names *Leptanilla yunnanensis*, *Protanilla bicolor* and *P. concolor* are attributed to Xu & Zhang, 2002, who provided a key to differentiate the leptanilline species found in China, and not to Xu, 2002, who formally described the three species. This stems from the publication dates available for the two papers, with the Xu & Zhang paper predating the formal descriptions, according to imprint. However, the latest edition of the International Code of Zoological Nomenclature (1999) provides regulations (Articles 16.1, 16.4) that do not allow considering the Xu & Zhang treatment as a publication of valid new names. According to article 16.4, each name published after 1999 must be accompanied by explicit type designation along with information on the place of deposition. Additionally, article 16.1 states that each new name published after 1999 must be explicitly indicated as intentionally new. The Xu & Zhang paper of 2002 does not meet the above mentioned requirements, and therefore the correct authorship of *Leptanilla yunnanensis*, *Protanilla bicolor* and *P. concolor* is Xu, 2002.