



Rediscovery of the rare ant genus *Bannapone* (Hymenoptera: Formicidae: Amblyoponinae) and description of the worker caste

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Abstract

The genus *Bannapone* was described in 2000 on the basis of a single dealate queen specimen. Since its original collection in Yunnan, China, no other specimen has been reported, making it one of the rarest ant genera in the world. Here we report the collection of two workers of *Bannapone* also from Yunnan province. The description of the worker caste is presented. Furthermore, we found significant differences with the described *B. mulanae* Xu, 2000 which leads us to describe the workers as a new species, *B. scrobiceps* n. sp.. Finally, we briefly discuss the importance of leaf-litter collection methods to collect taxa considered as “rare”.

Key words: Formicidae, Amblyoponinae

Introduction

The subfamily Amblyoponinae includes 116 species spread over 13 genera. Most of the Amblyoponine genera exhibit a pan-tropical distribution (Guénard *et al.* 2011), although a few species are also known to be adapted to cooler habitats of temperate regions. A few fossils have also been described, found in deposits located in more northern regions of Europe and Asia and now outside the distribution range of the subfamily (Figure 1). Many species of this subfamily are known to exhibit a subterranean life and are occasionally collected through leaf litter extraction (Brown 1949, 1960). Amblyoponine colonies are typically small, consisting of only a dozen to a few hundred workers (Gotwald & Levieux 1972, Traniello 1982, Hölldobler & Wilson 1990, Ito 1991, Yoshimura & Fisher 2012). The typical mandibular shape of several genera encountered in this subfamily is an adaptation for their specialized predatory diet of centipedes and insect larvae found in rotten wood or leaf litter (Brown 1960, Gotwald & Levieux 1972, Masuko 1993, Ito 1993). Another unusual feeding characteristic of some Amblyoponinae species is the feeding from larval hemolymph though non-destructive parental cannibalism (Masuko 1986, Ito 2010). This behavior, considered as “primitive” in ants and linked to some of the morphologically primitive characters (e.g. broad attachment of the petiole to the gaster, see Ward 1994) of this subfamily have supported the hypothesis that Amblyoponinae is a basal lineage in ants. Recent molecular phylogenetic work has confirmed this conclusion (Moreau & Bell 2013).

Among the genera that constitute the Amblyoponinae, the genus *Bannapone* is one of the rarest. *Bannapone* was described from a single dealate queen specimen from Mengla county, Yunnan province, China (Xu 2000). This is the only known record for this genus, making it one of the rarest ants in the world. Many species are known from single specimens, but it is unusual for a genus or higher taxon to be so poorly represented (e.g., the subfamily Martialinae, known from a single worker; Rabeling *et al.* 2012). Rareness in ants can be factual or artificial due to incomplete or inadequate sampling (Espadaler & López-Soria 1991). Specifically, ant species that live in microhabitats that are difficult to sample or ants with highly specialized life histories (e.g., social parasites) may be abundant but can be perceived as rare due to inadequate sampling methods. Several subterranean ants that were

thought to be rare are now known to be more common and widespread than thought due to the use of new techniques (Brandão *et al.* 2008, Schmidt *et al.* 2013).

Here we report for the first time the collection of the worker caste of *Bannapone*, collected through leaf-litter extraction in Yunnan province, from a field site about 20km from the type locality of *B. mulanae*. Furthermore, these new specimens belong to a new species that we describe here, adding a second species to the genus.

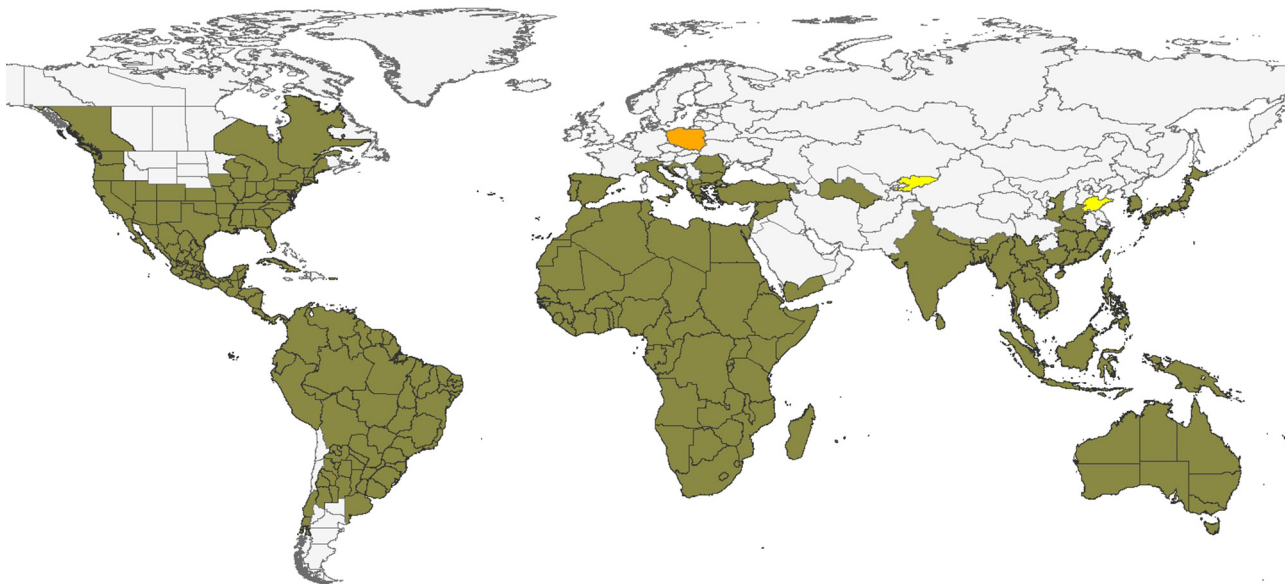


FIGURE 1. Global distribution of the subfamily Amblyoponinae. Regions in green represent the current known distribution. Fossil records are presented in orange (Eocene) and yellow (Miocene).

Materials and methods

Images: Pictures of specimens were obtained with an incorporated digital camera mounted on a Leica M205C dissecting microscope through the Leica Application Suite V4 software. A total of 44 to 63 images were taken and stack together with the Helicon Focus software.

Measurements: Head Width (HW): maximum width of head in full-face view excluding the eyes.

Head Length (HL): maximum length of head from the anterior median clypeal margin to the median posterior margin of the cephalic capsule measured along the midline as a straight line.

Mandible Length (MaL): maximum length of mandible from the anterolateral margin of clypeus at outer side of mandibular insertion to mandibular apex.

Scape Length (SL): maximum measurable length of scape, from the proximal point of scape shaft, not including the condyle, to the distal end of scape.

Total Length (TL): maximum length of specimen measured from the tip of the mandibles to the tip of the abdominal segment VII, not including sting.

Weber's Length of Mesosoma (WL): maximum diagonal distance in lateral view, from base of anterior slope of pronotum to metapleural lobe.

Pronotal Width (PrW): maximum width of the pronotum measured in dorsal view.

Mesonotal Width (MW): maximum width of the mesonotum measured in dorsal view.

Propodeal Width (PdW): maximum width of the propodeum measured in dorsal view.

Petiole Width (PW): maximum width of the node of the petiole (abdominal segment II) in dorsal view.

Petiole Length (PL): maximum length of the petiole (abdominal segment II) in dorsal view, from the anterior margin of the peduncle to the posterior margin of the tergite.

Forecoxa Width (FCoW): maximum width of the front coxa in lateral view.

Forecoxa Length (FCoL): maximum length of the front coxa in lateral view.

3rd Abdominal segment Width (AIIIW): maximum width of the third abdominal tergite in dorsal view.

3rd Abdominal segment Length (AIII L): maximum length of the third abdominal tergite in dorsal view.

4th Abdominal segment Width (AIVW): maximum width of the fourth abdominal tergite in dorsal view.

4th Abdominal segment Length (AIVL): maximum length of the fourth abdominal tergite in dorsal view.

Descriptions of pubescence and sculpture follow terminology defined respectively by Francoeur (1973) and Harris (1979).

Description

Bannapone scrobiceps sp. nov.

Holotype worker. CHINA: Yunnan, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden, Tropical Rain Forest, 21°55'07.1"N, 101°16'20.6"E, 550 m elevation, leaf litter sifting (Winkler extractor method) (B. Guénard coll.), 5 June 2013, CASENT0339957.

Paratype worker. Same data as the holotype, CASENT0340393. Due to the rarity of the *Bannapone* genus, the paratype is preserved in 99% Ethanol and was not mounted. Therefore no measurements were taken from this specimen.

The holotype will be deposited at the Smithsonian National Museum of Natural History, Washington, DC, USA; a preserved paratype will be stored in the research collection of EPE, Okinawa Institute of Science and Technology Graduate University, Okinawa, Japan.

Diagnosis. Specimens of *B. scrobiceps* represent the first workers known from this genus. Although *B. mulanae* is known from a single dealate queen, we believe that the workers described here represent a new species. The specimen of *B. mulanae* was not examined directly but the original description and drawings in Xu (2000) and photographs available on Antweb.org were used to compare specimens. The main differences we identified are summarized in Table 1. Among those, the absence of developed frontal carinae in *B. mulanae* represents the most important characteristic. Other morphological characters in *B. scrobiceps*, such as the presence of well-developed clypeal conical setae, a clear separation of the frontal lobes, the shape of the scape, the presence of metapleural lobes, and the distinctive shape of the petiolar process further distinguish this species from the type specimen of *B. mulanae*. Finally, it should also be noted that the workers of *B. scrobiceps* are much larger than the queen of *B. mulanae*. The diagnosis presented here is susceptible to change with the description of the worker caste of *B. mulanae*.

TABLE 1. Main morphological differences observed between the specimens of *Bannapone mulanae* and *B. scrobiceps*.

<i>Bannapone scrobiceps</i> sp. nov (worker)	<i>Bannapone mulanae</i> (queen) Xu 2000
Presence of five distinct clypeal conical setae	Absence of distinct clypeal conical setae (if present, then much more reduced)
Frontal lobes distinctly separated	Frontal lobes closely approximated
Scape of antenna thin and elbowed distally	Scape of antenna thick and not elbowed
Frontal carinae extending to the posterior margin of the cephalic capsule	Frontal carinae extending by no more than one length of the antennal socket area.
Metapleural lobes present	Metapleural lobes absent
Subpetiolar process well developed and spoon-shaped	Subpetiolar process narrow and cuneiform
Small size (3.3mm), HW= 0.64mm	Very small size (2.1mm), HW= 0.32mm

Description. *Holotype worker:* HL 0.62 mm, HW: 0.64 mm, MaL: 0.54 mm, SL: 0.34 mm, TL: 3.30 mm, WL: 0.79 mm, PrW: 0.37 mm; MW: 0.22 mm; PdW: 0.28 mm; PW: 0.29 mm, PL: 0.18 mm, FCoW: 0.15 mm, FCoL: 0.28 mm; AIIIW: 0.41 mm; AIII L: 0.21 mm; AIVW: 0.50 mm; AIVL: 0.22 mm.

Head: Head in full face view square-shaped (mandibles excluded), slightly wider than long and inflated on its anteromedian portion. Posterolateral corners round. Posterior margin flat with weak median emargination. Frontal lobes separated and elevated forming a deep impression of the posterior clypeal margin. Frontal lobe obscuring the

inner lateral side of antennal socket. Clypeus with anterior margin slightly convex, dentate, bearing five distinct teat-like setae. The middle seta is larger than the two pairs of lateral setae. Anterolateral corner of head, near mandibular insertion, angular and lacking teeth. Eyes absent. Antennal scrobe well defined and moderately impressed, reaching almost to the posterior head margin. At about two third of the head length, the antennal scrobe depression bends at an angle of about 120 degrees. Frontal carina very long, reaching almost to the posterior margin of head, very well defined and elevated. The distance separating the frontal carinae increases along the antero-posterior axis of the head. Surface between the frontal carinae distinctively raised and forming a heart-shaped region on the posterior part of the head. Mandible elongate, narrow and sickle-like, bearing 3 teeth on the masticatory margin. Apical tooth acute and very long, followed by two blunt teeth; with the median tooth less than 1/4 the length of the apical tooth; and the basal tooth less than half length of the median tooth. Irregular striate sculpture present on mandibles. Palps not visible on examined specimens; if present, then extremely reduced. Palp formula unknown. Antenna 11-segmented. Scape reaches almost two thirds of the head length. Scape narrows medially and widens apically, with apical fifth part weakly elbowed. Funiculus incrassate apically but not forming a distinct club. Apical antennal segment longer than combined length of preceding three segments.



FIGURE 2. *Bannapone scrobiceps* sp. n., head of holotype worker (Yunnan, CASENT0339957).



FIGURE 3. *Bannapone scrobiceps* sp. n., profile of holotype worker (Yunnan, CASENT0339957).



FIGURE 4. *Bannapone scrobiceps* sp. n., dorsum of holotype worker (Yunnan, CASENT0339957).

Mesosoma. In lateral view, dorsum of mesosoma convex and continuous with a distinctly impressed groove posterior to the promesonotal suture. In dorsal view, mesonotum constricted. Pronotum wider than propodeum. Metanotal groove weakly impressed on the dorsum of mesosoma. In lateral view, propodeal declivity separated in

two parts. The superior part of the propodeal declivity slightly concave and presenting a moderate slope, while posterior part of the propodeal declivity steeply sloping and concave. Propodeum unarmed. Propodeal spiracle circular and distinct, located at about two thirds of the superior part of the propodeum. Metapleural lobes large and rounded. Orifice of metapleural gland inconspicuous.

Coxa, femur and tibia of the forelegs much larger than those of the middle and hind legs. Single tibial spur present on fore and hind legs, absent on middle legs. Spurs are pectinate and without simple spur.

Metasoma. Petiole broad, thick, convex and low. Petiolar node longer than tall with anterior face straight and dorsal face slightly convex. In dorsal view petiole much broader than long. Subpetiolar process well developed and spoon-shaped without translucent fenestra. Petiole broadly attached to abdominal segment III. Abdominal segment III smaller than abdominal segment IV. Metasoma ending with a long and up-curved sting.

Sculpture: Head rugulose. Side of pronotum with shallow aerolae. Dorsal surface of pronotum transitioning from a densely striate sculpture anteriorly to a sparser striate-punctulate sculpture posteriorly. Mesonotum and propodeum aerolate-rugulose in dorsal view. Propodeal pleurae with fine and sparse strigulations, with a general shiny appearance. Coxae smooth and shiny. Petiole with fine punctations. Abdominal segments without obvious sculpture but with a shiny appearance in both lateral and dorsal views.

Pubescence: Fine white long suberect hairs present on most of the body to a density ranging from sparse on the head and pronotum to very sparse on the mesonotum and propodeum. The rather long hairs gives an impression of dense pubescence. Hairs on head and pronotum mostly oriented anteriorly; hairs on abdominal segments III to VII oriented posteriorly. Petiole with very sparse pubescence. A few fine and longer erect hairs present on most parts of the body. A few erect hairs present on the scape.

Coloration. Mesosoma, metasoma and legs light yellow, head darker orange-brown.

Etymology. The species name refers to the particular antennal scrobes observed on the head of the workers and derived from the latin “scrobis” (= trench) and “ceps” (= headed). The species epithet is an adjective that is invariant for gender.

Biology. The two specimens were collected from a single site located at 550 meters elevation, consisting of secondary forest habitat with thick leaf litter cover and abundant decomposing woody material on the forest floor. The ants were collected from leaf litter using Winkler extraction. The peculiar morphology of the mandibles suggests a specialized predatory diet, like many other members of the Amblyoponinae (Gotwald and Levieux 1972, Ito 1993, Masuko 1993), but no direct observations have been made. Nothing else is currently known about the ecology of this species.

Discussion

In the original description of *Bannapone*, Xu (2000) used several morphological characteristics for establishing the taxonomic status of the genus. Here, we review and modify those characteristics based on the newly described worker caste and species.

The evolutionary placement of *Bannapone* within the subfamily Amblyoponinae will remain uncertain until molecular phylogenetic studies are available. However, *Bannapone* has morphological similarities with the pantropical genus *Prionopelta* and the Afrotropical genus *Concoctio*. *Concoctio* was described by Brown (1974) and differentiated by its reduced number of teeth on the mandibles. Mandibles of *Prionopelta* and *Bannapone* possess 3 teeth, while *Concoctio* possess only 2 teeth, contrasting with the mandibles of other Amblyoponinae genera that possess more than 3 teeth. Molecular phylogenies have supported a clade composed of the genera *Concoctio* and *Prionopelta* (Saux *et al.* 2004, Moreau *et al.* 2006, Brady *et al.* 2006). At this point, there are no molecular data for *Bannapone*, but based on morphological affinities with *Prionopelta*, it seems likely that *Bannapone* might belong to the *Concoctio* + *Prionopelta* clade.

The genus *Bannapone* is distinguished from all other Amblyoponinae genera by the strongly falcate, 3-toothed mandibles. In particular, *Bannapone* is easily distinguished by the mandibular shape composed of three distinct and long teeth (especially the apical tooth) versus the triangular shape of *Concoctio*. The genus *Prionopelta* also has three mandibular teeth, but the mandible is subtriangular, with the teeth clustered near the apex (Xu 2000). Furthermore, the mandible length relative to the head is much larger in *Bannapone* than in *Prionopelta* or *Concoctio*. The mandible length is over 85% of head length in *B. scrobiceps*, and over 79% in *B. mulanae*. In

contrast, mandibles are proportionately much shorter in *Prionopelta* and *Concoctio*. It should also be noted that the eyes are absent in the worker caste of *B. scrobiceps*, but present, while sometimes reduced in *Concoctio* and *Prionopelta*. The 11-segmented antennae are confirmed within *B. scrobiceps*, which is distinct from the 9-segmented antennae of *Concoctio*, but variation occurs within other Amblyoponinae genera such as *Prionopelta*, in which antennal segments vary from 8 to 12 (Xu 2000), and this morphological trait could be more labile in *Bannapone* as well. Xu (2000) also differentiates *Bannapone* from *Prionopelta* based on abdominal segments III and IV being as large as the other segments, occupying less than half of the length of the gaster, and with indistinct constriction between them. The discovery of *B. scrobiceps* confirms this. The length of abdominal segments III and IV combined represent less than half of the total length of the gaster. However, it should be noted that the visibility of the abdominal segments V and VI can vary substantially due to the preservation of the specimen examined. As a consequence, this character should be considered cautiously. Finally, the constriction between abdominal segments III and IV in *B. scrobiceps*, while slightly more apparent than in *B. mulanae*, is still less constricted than observed in *Prionopelta* species.

Other morphological differences between *Bannapone* and *Prionopelta* discussed by Xu (2000) need to be modified or complemented after the discovery of *B. scrobiceps*. A distinction between *Bannapone* and *Prionopelta* noted by Xu (2000) is the “very narrow” clypeus in *Bannapone*. In *B. scrobiceps* the clypeal area is more developed than in *B. mulanae*, and its size seems comparable to certain *Prionopelta* species such as *P. descarpentriensi* Santschi from Madagascar. As a result clypeus size should not be retained as a characteristic to separate these two genera. Xu (2000) also reports the frontal lobes as “closely approximated”, however in *B. scrobiceps*, the frontal lobes are widely separated and thus this morphological criterion should not be retained. The antennae were also described with the presence of a “gradually incrassate strong club” (Xu 2000). However, in *B. scrobiceps*, the antennae are incrassate but do not form a strong club and as such the presence of an antennal club is not characteristic of the genus. Contrary to the original description of *Bannapone* (Xu 2000), we observed well-developed metapleural lobes. Finally, the subpetiolar process of *B. scrobiceps* is more developed than in *B. mulanae* and as a consequence this trait no longer differentiates *Bannapone* and *Prionopelta*. Finally, Xu (2000) characterized the genus *Bannapone* as extremely small. The worker of *B. scrobiceps* is larger than the queen of *B. mulanae* (3.3mm vs. 2.1mm). The new specimens confirm the relatively small size of the genus within Formicidae, but relative to several other genera found in the same area (e.g. *Carebara*, *Leptanilla*, *Prionopelta*), *Bannapone* should not be characterized as extremely small. Furthermore, it seems possible that more variation could exist. For example, the queen caste of *B. scrobiceps*, still unknown, is probably larger than the worker caste, as is typical for many ant species (but see exceptions in Molet *et al.* 2007, Kikuchi *et al.* 2008).

To summarize, diagnosis of *Bannapone* should be based on the peculiar shape of the mandibles formed of three teeth on the masticatory margin with the apical tooth very long and followed by 2 blunt finger-like basal teeth. *Bannapone* is also distinct from *Prionopelta* by the high ratio of the mandible length relative to head length (> 0.75), the indistinct constriction between the abdominal segments III and IV, and with the limitations presented above, by the presence of the abdominal segments III and IV as large as the other segments, which combined length represents less than half of the total length of the gaster.

The discovery of two individuals, representing a new species in one of the rarest ant genera in the world, represents an important discovery for the study of the Amblyoponinae and ants more generally. However, it is impossible to establish whether the rarity of *Bannapone* reflects only its distribution and abundance, or whether it is indicative of a life history trait that could prevent more frequent collection (crypsis and subterranean habit). The Xishuangbanna prefecture where the *B. scrobiceps* were collected has been surveyed in several ant studies (Xu *et al.* 1998, 1999, Xu 1998, 1999, 2002, Zhang *et al.* 2000, Yang *et al.* 2001, Meng & Gao 2007) and no less than 262 species are known for this region (Xu 2002), while 406 species have been reported from Yunnan province (Guénard & Dunn 2012). In this context, this geographic area cannot be considered unexplored. We speculate this may be due the collection techniques used in our sampling (Winkler extraction) that specifically targeted hypogaecic leaf litter species. The collection of this extremely rare genus through Winkler extraction, combined with other recent discoveries of putatively rare subterranean taxa (Brandão *et al.* 2008, Schmidt *et al.* 2013) should encourage myrmecologists to integrate leaf litter extraction and other collection methods that target subterranean ants, especially in parts of the world where those techniques have not been traditionally used.

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References

- Antweb (2002–2013) AntWeb v5.1.24. Available from: <http://www.antweb.org> (Accessed 10 July 2013)
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 18172–18177.
<http://dx.doi.org/10.1073/pnas.0605858103>
- Brandão, C.R.F., Feitosa, R.M., Schmidt, F.A. & De Castro Solar, R.R. (2008) Rediscovery of the putatively extinct ant species *Simopelta minima* (Brandão) (Hymenoptera: Formicidae), with a discussion on rarity and conservation status of ant species. *Revista Brasileira de Entomologia*, 52, 480–483.
<http://dx.doi.org/10.1590/s0085-56262008000300026>
- Brown, W.L. Jr. (1949) A new American *Amblyopone*, with notes on the genus (Hymenoptera: Formicidae). *Psyche*, 56, 81–88.
<http://dx.doi.org/10.1155/1949/67378>
- Brown, W.L. Jr. (1960) Contribution toward a reclassification of the Formicidae, III: Tribe Amblyoponini (Hymenoptera). *Bulletin of the Museum of Comparative Zoology Harvard*, 122, 144–230.
- Brown, W.L. Jr. (1974) *Concoctio* genus nov. *Pilot Register of Zoology Card*, 29, 1.
- Espadaler, X. & López-Soria, L. (1991) Rareness of certain Mediterranean ant species: fact or artifact? *Insectes Sociaux*, 38, 365–377.
<http://dx.doi.org/10.1007/bf01241872>
- Francoeur, A. (1973) Révision taxonomique des espèces néarctiques du groupe *fusca*, genre *Formica* (Formicidae, Hymenoptera). *Mémoires de la Société Entomologique du Québec*, 3, 1–316.
- Gotwald, W.H. Jr. & Levieux, J. (1972) Taxonomy and biology of a new West African ant belonging to the genus *Amblyopone* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, 65, 383–396.
- Guénard, B., Weiser, M.D. & Dunn, R.R. (2011) Ant Genera of the World. Available from: http://www.antmacroecology.org/ant_genera/index.html (Accessed 2 July 2013)
- Guénard, B. & Dunn, R.R. (2012) A checklist of the ants of China. *Zootaxa*, 3358, 1–77.
- Harris, R.A. (1979) A glossary of surface sculpturing. *California Department of Food and Agriculture. Laboratory Services, Entomology. Occasional Papers*, 28, 1–31.
- Hölldobler, B. & Wilson, E.O. (1990) The ants. Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.
- Ito, F. (1991) Preliminary report on queenless reproduction in a primitive ponerine ant *Amblyopone* sp. (*reclinata* group) in West Java, Indonesia. *Psyche*, 98, 319–322.
<http://dx.doi.org/10.1155/1991/81216>
- Ito, F. (1993) Observation of group recruitment to prey in a primitive ponerine ant, *Amblyopone* sp. (*reclinata* group) (Hymenoptera: Formicidae). *Insectes Sociaux*, 40, 163–167.
<http://dx.doi.org/10.1007/bf01240704>
- Ito, F. (2010) Notes on the biology of the Oriental amblyoponine ant *Myopopone castanea*: queen-worker dimorphism, worker polymorphism and larval hemolymph feeding by workers (Hymenoptera: Formicidae). *Entomological Science*, 13, 199–204.
<http://dx.doi.org/10.1111/j.1479-8298.2010.00384.x>
- Kikuchi, T., Miuazaki, S., Ohnishi, S., Takahashi, J., Nakajima, Y. & Tsuji, K. (2008) Small queens and big headed workers in a monomorphic ponerine ant. *Naturwissenschaften*, 95, 963–968.
<http://dx.doi.org/10.1007/s00114-008-0414-8>
- Masuko, K. (1986) Larval hemolymph feeding: a nondestructive parental cannibalism in the primitive ant *Amblyopone silvestrii* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 19, 249–255.
<http://dx.doi.org/10.1007/bf00300639>
- Masuko, K. (1993) Predation of centipedes by the primitive ant *Amblyopone silvestrii*. *Bulletin of the Association for Natural Sciences, Senshu University*, 24, 35–43.
- Meng, L.Z. & Gao, X.X. (2007) Species diversity of rat and ant at different habitats and sites in Xishuangbanna. *Chinese Journal of Ecology*, 26, 802–809.
- Molet M., Peeters, C. & Fisher, B. (2007) Winged queens replaced by reproductives smaller than workers in *Myrmium* ants. *Naturwissenschaften*, 94, 280–287.
<http://dx.doi.org/10.1007/s00114-006-0190-2>

- Moreau, C., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of Angiosperms. *Science*, 312, 101–104.
<http://dx.doi.org/10.1126/science.1124891>
- Moreau, C.S. & Bell, C.D. (2013) Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*. [in press]
<http://dx.doi.org/10.1111/evo.12105>
- Rabeling, C., Brown, J.M. & Verhaagh, M. (2008) Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 14913–14917.
<http://dx.doi.org/10.1073/pnas.0806187105>
- Saux, C., Fisher, B.L. & Spicer, G.S. (2004) Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). *Molecular Phylogenetics and Evolution*, 33, 457–468.
<http://dx.doi.org/10.1016/j.ympev.2004.06.017>
- Schmidt, F.A., Feitosa, R.M., de Moraes Rezende, F. & Silva de Jesus, R. (2013) News on the enigmatic ant genus *Anillidris* (Hymenoptera: Formicidae: Dolichoderinae: Leptomyrmecini). *Myrmecological News*, 19, 25–30.
- Traniello, J.F.A. (1982) Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche*, 89, 65–80.
<http://dx.doi.org/10.1155/1982/79349>
- Ward, P.S. (1994) *Adetomyrma*, an enigmatic new ant genus from Madagascar (Hymenoptera: Formicidae), and its implications for ant phylogeny. *Systematic Entomology*, 19, 159–175.
<http://dx.doi.org/10.1111/j.1365-3113.1994.tb00585.x>
- Xu, Z. (1998) A report of forty-one ant species newly recorded in China from Xishuangbanna District of Yunnan Province (Hymenoptera: Formicidae). *Abstract of Chinese Academic Periodicals*, 4, 1119–1121.
- Xu, Z. (1999) An analysis on the ant fauna of the tropical rain forest in Xishuangbanna of China. *Zoological Research*, 20, 379–384.
- Xu, Z.-H. (2000) Two new genera of ant subfamilies Dorylinae and Ponerinae (Hymenoptera: Formicidae) from Yunnan, China. *Zoological Research*, 21, 297–302.
- Xu, Z.-H. (2002) *A study on the biodiversity of Formicidae ants of Xishuangbanna Nature Reserve*. Yunnan Science and Technology Press, 181 pp.
- Xu, Z., Liu, T.Y., He, Y.F. & Zeng, G. (1998) A comparative study on the ant communities in primeval and secondary forests of four vegetation subtypes in Xishuangbanna of China. *Zoological Research*, 20, 360–364.
- Xu, Z., Zeng, G., Liu, T.Y. & He, Y.F. (1999) A study on communities of Formicidae ants in different subtypes of vegetation in Xishuangbanna District of China. *Zoological Research*, 20, 118–125.
- Yang, X.D., She, Y.P., Zhang, Z.H., Cao, M. & Deng, X.B. (2001) Studies on structure and diversity of ant groups in the fragmentary tropical rainforests of Holy Hills of Dai nationality in Xishuangbanna, China. *Acta Ecologica Sinica*, 21, 1321–1328.
- Yoshimura, M. & Fisher, B.L. (2012) A revision of the Malagasy endemic genus *Adetomyrma* (Hymenoptera: Formicidae: Amblyoponinae). *Zootaxa*, 3341, 1–31.
- Zhang, Z.Y., Cao, M., Yang, X.D., Deng, X.B. & She, Y.P. (2000) A study on species diversity of ant in fragments of seasonal rain forest of Xishuangbanna, China. *Zoological Research*, 21, 70–75.