



Aphaenogaster gamagumayaa sp. nov.: the first troglobiotic ant from Japan (Hymenoptera: Formicidae: Myrmicinae)

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Abstract

Aphaenogaster gamagumayaa sp. nov., a new troglobiotic (true cave-dwelling) ant species, from a limestone cave on the island of Okinawa (Okinawa-jima), Ryukyu Archipelago, Japan is described. This is the first discovery of a troglobiotic ant in Japan and the second verified record worldwide. This species has only been found in a cave area with heavy guano deposits, and some worker ants were observed carrying guano. The evidence for categorizing this new species as troglobiotic is discussed.

Key words: cave-dwelling species, guano, island, limestone cave, Myrmicinae, Okinawa-jima, Ryukyu Archipelago, troglobiotic.

Introduction

Several ant species have been observed in caves, but the only known troglobiotic (true cave-dwelling) species is the ponerine ant *Leptogenys khammouanensis* Roncin & Deharveng, 2003 from Laos (Roncin & Deharveng 2003). The myrmicine ants *Aphaenogaster cavernicola* Donisthorpe, 1938 from India, *A. cardenai* (Espadaler, 1981) from Spain and *A. ceconii* Emery, 1894 from Crete (and its allies) have also been found in caves. However, no detailed biological information is available for *A. cavernicola* aside from its original description, and the latter two species have also been observed outside of caves and thus are not troglobiotic (AntWeb 2017, Tinaut & López 2001, Borowiec & Salata 2014). The formicine ants *Nylanderia myops* (Mann, 1920) from Cuba and *N. pearsei* Wheeler, 1938 from Mexico are also known from caves, and they form a species group characterized by small eyes (Wheeler 1938). However, *N. myops* has also been collected from leaf litter (label data: Antweb, 2018), and part of the type series of *N. pearsei* was collected outside of a cave, "from a big midden pile of a leaf-cutter mound above cave." Therefore, these *Nylanderia* species are not true cave-dwelling species. Recently, we discovered a striking undescribed species of *Aphaenogaster* Mayr, 1853 in a limestone cave on the island of Okinawa (Okinawa-jima), Ryukyu Archipelago, Japan that appears to be a true troglobiotic species, based on morphological and circumstantial evidence. This is not only the first discovery of a troglobiotic ant in Japan but also the second confirmed troglobiotic ant in the entire world. This paper describes this new species and discusses the evidence for categorizing it as troglobiotic.

Material and methods

Specimens were compared using standard methods of morphological observation. Photos were taken using a Canon 8000D photo camera, MP-E65 lens and CombineZP software. The following abbreviations are used for the measurements. HL—head length, measured in straight line from mid-point of anterior clypeal margin to mid-point of occipital margin in full face view; TmL—tempora length, straight line distance measured from posterior margin

of the eye to posteromedian margin of head in lateral view; GL—gena length, straight line distance measured from anterior margin of the eye to anteriormost, medial projection of the clypeal margin in face view; HW—head width, width of head at anterior margin of eyes in full-face view; EL—eye length, measured along maximum diameter of eye; EW—eye width, measured along the maximum width of eye perpendicular to EL; SL—scape length, maximum straight-line length of scape, including basal condyle and neck; PNW—pronotum width, maximum width of pronotum in dorsal view; ML—mesosoma length, measured as diagonal length from anterior end of neck shield to posterior margin of propodeal lobe; SDL—spiracle to declivity length, minimum distance from the center of the propodeal spiracle to propodeal declivity; PSL—propodeal spine length, measured from center of the propodeal spiracle to the top of propodeal spine in lateral view; PH—petiole height, maximum height of petiole in lateral view; PL—petiole length, maximum length of petiole in dorsal view; PW—petiole width, maximum width of petiole in dorsal view; PPH—postpetiole height, maximum height of postpetiole in lateral view; PPL—postpetiole length, maximum length of postpetiole in dorsal view; PPW—postpetiole width, maximum width of postpetiole in dorsal view; HTL—hind tibia length, maximum length of hind tibia. Measurements presented as mean \pm standard deviation (minimum-maximum).

***Aphaenogaster gamagumayaa* Naka & Maruyama, sp. nov.**

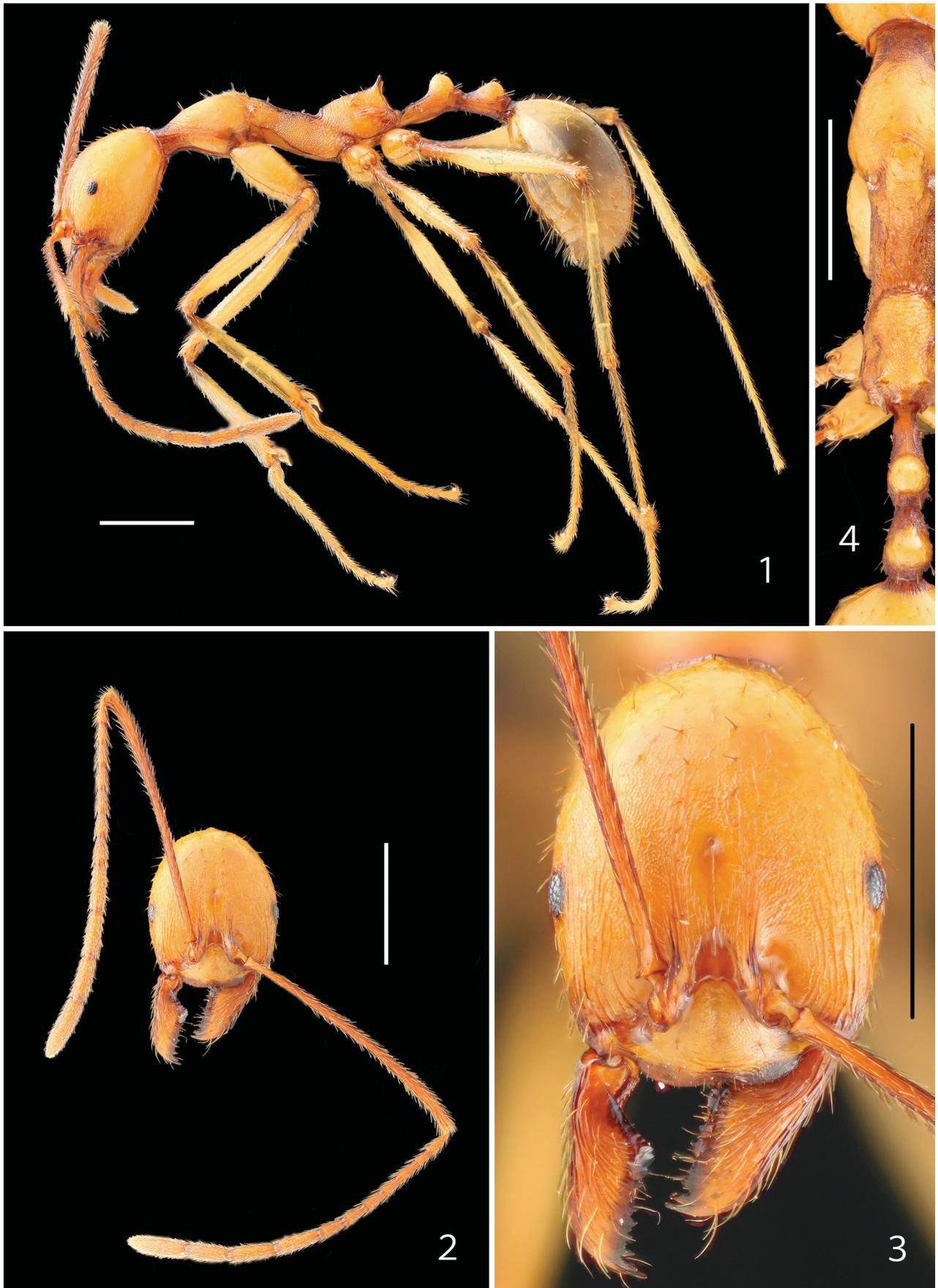
Type series. Holotype, worker, Nakagusuku-son, Okinawa-jima, Japan, 10 IX 2017, T. Naka (The Institute of Tropical Agriculture, Kyushu University = KUM, no MMANT001). Paratypes, 7 workers, the same locality, collected between 31 VIII - 10 IX 2017 (5 in KUM, nos. MMANT002-006; 2 in MCZC = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA, nos. MMANT007,008).

Diagnosis. This species is distinguished from the other East Asian species by having the most elongate body, the longest antennae and legs, and the most reduced eyes. Among the Japanese species, it is most similar to *A. irrigua* Watanabe & Yamane, 1999 described from Ryukyu Archipelago. It differs from *A. irrigua* in lighter color, smaller eyes (EL 0.19 x TmL vs. 0.38 x TmL), basal margin of mandible with weaker serration, and scapes more elongate and slim (SL 2.28 x HW vs. 1.53 x HW).

Measurements. Workers (n = 6). HL, 1.499 \pm 0.047 (1.439–1.566); HW, 1.118 \pm 0.030 (1.073–1.152); TmL, 0.790 \pm 0.038 (0.743–0.843); GL, 0.808 \pm 0.027 (0.778–0.856); SL, 2.429 \pm 0.053 (2.350–2.509); EL, 0.143 \pm 0.006 (0.134–0.149); EW, 0.119 \pm 0.005 (0.114–0.128); ML, 2.563 \pm 0.074 (2.463–2.659); PSL, 0.363 \pm 0.017 (0.348–0.388); SDL, 0.252 \pm 0.010 (0.242–0.270); HTL, 2.121 \pm 0.047 (2.046–2.176); PL, 0.753 \pm 0.026 (0.702–0.769); PPL, 0.480 \pm 0.017 (0.465–0.513); PH, 0.389 \pm 0.008 (0.380–0.399); PPH, 0.356 \pm 0.034 (0.330–0.423); PNW, 0.748 \pm 0.022 (0.713–0.775); PW, 0.271 \pm 0.009 (0.260–0.283); PPW, 0.327 \pm 0.007 (0.317–0.338).

Description. Body (Figs. 1–4) almost entirely yellowish. Head and mesosoma yellow, but mandibles and antennae darker, and base of head and anterior area of prothorax brown; legs light yellow but bases of femora, tibiae and tarsi darker. Gaster light yellow, but basal constriction brown, and posterior 1/2 slightly darker.

Head (Figs. 2, 3) oval, without basal constriction or neck. Anterior margin of clypeus with weak transverse wrinkles and shallowly concave. Eyes very small, 0.19 times as long as length of tempora. Scapes elongate and slim, 2.28 times as long as width of head, at base 1.7 times as wide as at apex, gradually widened, straight, only apex slightly bent down with slight preapical constriction. Surface of scape shiny, uniformly covered with short and sparse adherent setae. Scape straight, only apex slightly bent down with shallow preapical constriction. Funicle elongate and thin, 1.38 times as long as scape, first funicular segment elongate, 3.17 times as long as wide at apex, 1.74 times as long as second segment, relative lengths of segments, 100:57:68:75:76:76:92:150:145:143:213, apical segment 3.1 times as wide as first segment. Pronotum (Figs. 1, 4) elongate, 1.37 times as long as wide, regularly convex in profile. Propodeum (Figs. 1, 4) almost as long as wide, propodeal spines short, needle-like, obliquely directed upwards. Petiole (Fig. 1, 4) elongate with long peduncle, its anterior face deeply concave, node globular and strongly convex. Ventral margin of petiole with low, short carina around middle. In dorsal view, petiole gently widened posteriorly before petiolar node. Postpetiole (Figs. 1, 4) short, 0.68 times as long as petiole, in profile regularly rounded, its node slightly lower than petiole. In dorsal view postpetiole 1.5 times as long as wide with regularly rounded sides.

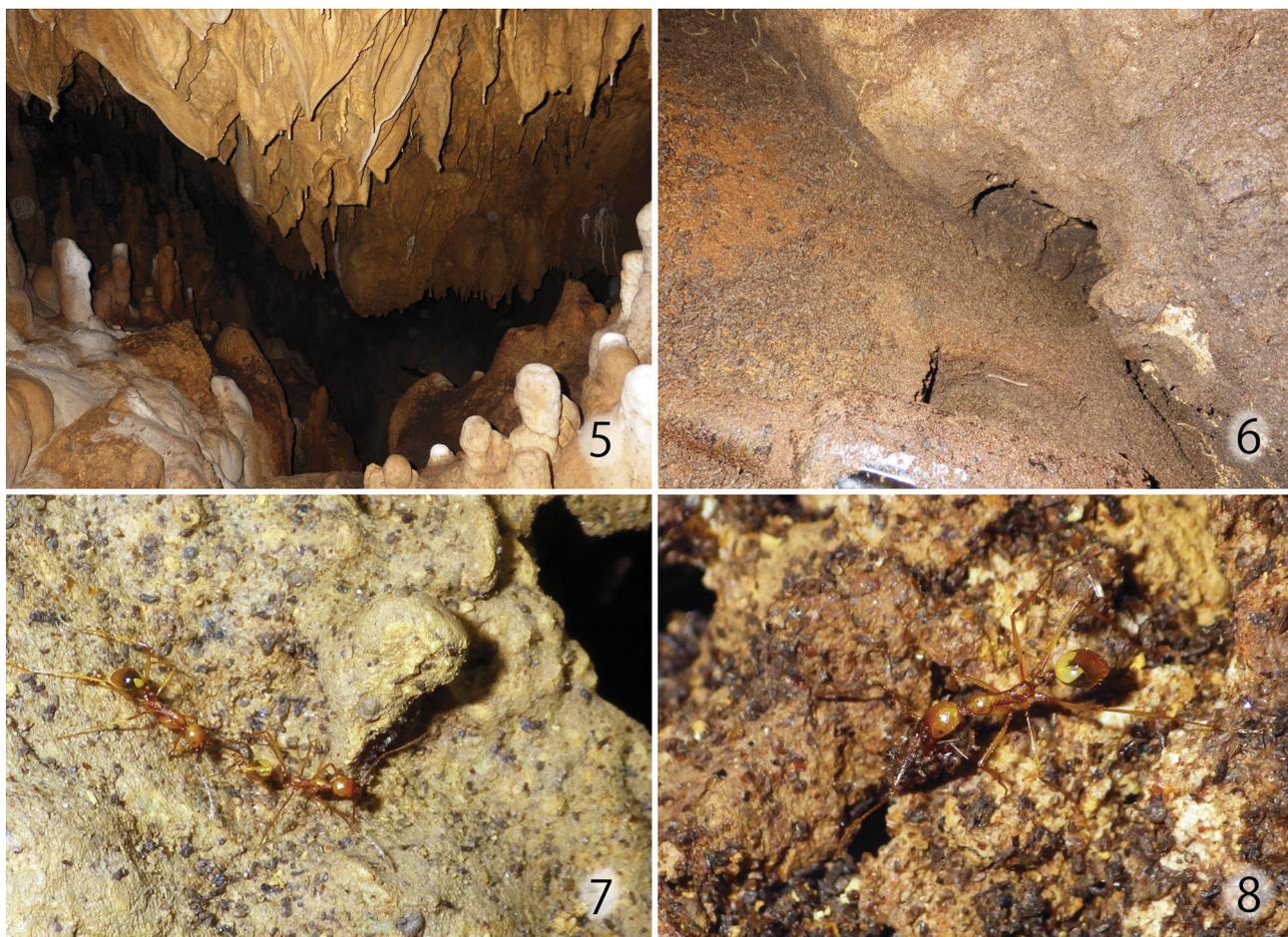


FIGURES 1–4. holotype worker of *Aphaenogaster gamagumayaa* sp. nov. 1) whole body in lateral view; 2) head; 3) head capsule; 4) mesosoma and fore segments of abdomen. Scales= 1.0 mm.

Mandible (Fig. 3) elongate, with outer edge straight, dorsal surface with distinct striation, inner margin with 7 or 8 small teeth. Lateral portion of clypeus (Fig. 3) with 2–3 thin oblique rugae, central part without sculpture, shiny. Frontal carinae short, not extending to line connecting anterior margin of eyes, subparallel; interantennal area deeply impressed, smooth and shiny, frontal triangle shiny, with a few, shallow longitudinal wrinkles. Anterior portion of frons with thin longitudinal rugae, mesal area between eyes glabrous and shiny, posterior portion around vertex without rugae but with distinct microreticulation (Fig. 3). Pronotum (Figs. 1, 4) with microreticulation, but with smooth areas postero-laterally, with 8 short setae. Top of mesonotum (Figs. 1, 4) covered with strong longitudinal rugae; mesopleuron with distinct granulate sculpture, matte. Propodeum (Figs. 1, 4) with slightly granulate sculpture, below spiracles with two short, thin, longitudinal rugae with distinct transverse wrinkles, and dorsal surface of both mesonotum and propodeum appears slightly matte. Entire petiole and postpetiole covered with fine microreticulation, without rugae, appearing slightly matte, covered with several sparse setae. Gaster (Fig. 1) smooth, shiny, without microreticulation except in basal area, tergites with sparse, suberect setae much shorter than propodeal spines. Legs (Fig. 1) very long, hind femora 1.13 times as long as mesosoma, hind tibiae 0.77 times as long as hind femora, hind tarsi 1.19 times as long as hind femora. Surface of legs shiny, fore tarsi only on ventral surface covered with very short, appressed pubescence; femora and mid- and hind tibiae completely without pubescence.

Queens and males are unknown.

Etymology. The specific epithet is a Ryukyuan dialect “gamagumayaa” (= cave-dwelling hermit), referring to the habitat of the new species.



FIGURES 5–8. habitat photos of *Aphaenogaster gamagumayaa* sp. nov. 5) guano hall where the type series found; 6) the nest entrance; 7) two workers walking together; 8) worker carrying a guano ball.

Biological notes. The type series of *Aphaenogaster gamagumayaa* is based on workers probably from a single nest, collected in a limestone cave on the island of Okinawa. All specimens were found in a guano hall (Fig. 5), an area of approximately 25 m² (2–3 m in height), approximately 20 m from the cave entrance. The hall is completely

dark, and during the study period (August to October 2017), it was consistently cooler ($< 25^{\circ}\text{C}$ during the day) than the exterior of the cave ($28\text{--}32^{\circ}\text{C}$). The cave contains no pools or streams but is generally wet, and the substrate is clay soil.

The ants were moving around an approximately 4-m^2 area in which there were many small holes (Fig. 6) and cracks in the cave floor. Ants were observed entering these holes. Although one of the authors, TN, did not dig into the holes, they were surmised to be associated with a core part of the nest. TN observed a maximum of 12 individual workers, most likely nest mates; no aggression was seen between them. Most of them were solitary foragers and observed on the cave floor or on the lower part of the cave wall. However, on one occasion two ants were observed walking together (Fig. 7) for some time. On two occasions ants were seen carrying balls of guano into a hole (Fig. 8). Another individual was observed carrying a small white object that did not appear to be guano. Upon perceiving human movement, the ants stopped moving and hid. While motionless, they waved their antennae, most likely to assess the situation. Gaster bending behavior, which is often observed in other *Aphaenogaster* species (Terayama *et al.* 2014), has not been observed in *A. gamagumayaa*.

Discussion

There are four pieces of morphological and circumstantial evidence to support our view that *Aphaenogaster gamagumayaa* is a troglotrophic species: 1) this species has only been found inside a cave; 2) it has several characteristics that are unique to cave insects; 3) ants were concentrated in an area of the cave with a high abundance of guano; 4) this cave is located on Okinawa, which harbors many endemic troglotrophic species.

1) The first specimens of *A. gamagumayaa* were found in a cave situated in a small evergreen forest in Okinawa. TN performed six searches of the area outside the cave (three during the day and three at night; 24 h in total). These searches were focused especially on the forest floor, crevices in and under rocks, and an old cemetery, all of which are generally suitable habitats for *Aphaenogaster* species. Also several other Okinawa forests were surveyed on multiple occasions to confirm the presence/absence of *A. gamagumayaa*. However, no *A. gamagumayaa* specimens were found in any of these searches. The ant fauna of Japan, including Okinawa, has been well investigated (e.g., Japanese Ant Database Group 2008), and *A. gamagumayaa* is a large and conspicuous species. It seems likely that if its habitat is not restricted to cave interiors, it would have been discovered prior to this study.

2) In general, *Aphaenogaster* ants are slender, with elongated bodies, antennae and legs. The body of *A. gamagumayaa* is especially slender and is characterized by extremely elongated antennae and legs. It also has reduced eyes, and a less pigmented body than other *Aphaenogaster* species. Loss of wings, reduction of eyes, elongation of antennae and legs, and loss of pigmentation are commonly observed in troglotrophic arthropods (Vandel 1964, Christiansen 1965, Culver 1982, Marques & Gnaspini 2001; Juan *et al.* 2010). It is unclear whether *A. gamagumayaa* displays any wing loss/reduction in the queen and male, as during the course of the study only workers were found. However, its other characteristics are typical of troglotrophic arthropods. The only previously known troglotrophic ant, *L. khammouanensis*, shares similar characteristics (Roncin & Deharveng 2003).

3) Cave environments are generally nutritionally poor. The unique morphologies and life histories of many troglotrophic arthropods can be explained as adaptations to this oligotrophic habitat (Deharveng & Bedos 2000). *Leptogenys khammouanensis* is regarded as a troglotrophic species because of its habitat in the deep parts of caves, and of the typical morphology of troglotrophic arthropods. However, as Wilson (1962) stated, caves do not usually provide suitable habitats for ants because of the difficulty of sustaining a colony in such an oligotrophic environment. This difficulty has led to a paucity of troglotrophic species among ants. Although caves are generally characterized by an oligotrophic environment, areas with high densities of guano deposits (so-called guano halls) are an important exception. Guano deposits represent an important source of nutrients derived from the outside environment and are carried into the cave by cave-dwelling bats. *Aphaenogaster gamagumayaa* was found only in a part of a cave where guano is deposited by two bat species (*Rhinolophus pumilus* Andersen, 1905 and *Miniopterus fuscus* Bonhote, 1902). TN observed workers entering and leaving small holes or crevices in rocks on the cave wall and floor; some of them were carrying small balls of guano. They apparently nested under the cave floor and may have adapted to feed on guano (*Leptogenys khammouanensis*, which was not found in guano halls, may possess different adaptations to cave habitats).

4) Okinawa, the type locality of *A. gamagumayaa*, is located in a subtropical region of the Ryukyu Archipelago. Much of the land on Okinawa and its neighboring islands is formed from uplifted coral reef (Machida *et al* 2001), and limestone caves are common in the region. These caves harbor many endemic Okinawan troglolithic or troglophilous animals (Machida *et al* 2001), such as the bat *R. perditus* Andersen, 1918, the shrimp *Macrobrachium miyakoense* Komai & Fujita, 2005, the crab *Orcovita miruku* Naruse & Tamura, 2006 and the millipede *Epanerchodus subterraneus* Verhoeff, 1938. The cave-dwelling spider *Coelotes troglocaecus* Shimojana & Nishihira, 2000 and several species of assimineid snails are found only on Okinawa (Maeda *et al.* 2017). Okinawa may harbor many more troglolithic species that have yet to be identified. Fifteen species of *Aphaenogaster* ants have been identified in the Ryukyu Archipelago (Terayama *et al.* 2014). Many of these are endemic to one or a few islands and have obviously speciated by island or small island chain. This suggests that *Aphaenogaster* ants may have a low migratory ability and are relatively prone to allopatric speciation. Some *Aphaenogaster* species (for example *A. irrigua*) prefer dark, wet habitats such as the area around mountain streams. *Aphaenogaster gamagumayaa* evolved as a troglolithic ant on Okinawa (and possibly its adjacent islands) as a result of various factors, namely the geologic features of the region, traits of the taxon, basic habitat features of *Aphaenogaster* ants and presence of guano in the cave.

Aphaenogaster gamagumayaa is the only known troglolithic ant in Japan and the second confirmed record of a troglolithic ant in the world. Ants are well studied as an animal group, and the present discovery is a very unusual case in ant evolution. As mentioned above, caves are abundant on Okinawa and its adjacent islands, and many of these caves remain uninvestigated; further investigation of other caves may reveal additional troglolithic *Aphaenogaster* species.

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References

- Antweb (2018) Available from: <https://www.antweb.org/browse.do?genus=nylanderia&species=myops&rank=species&project=allantwebants> (accessed 20 May 2018)
- Borowiec, L. & Salata, S. (2014) Review of Mediterranean members of the *Aphaenogaster cecconii* group (Hymenoptera: Formicidae), with description of four new species. *Zootaxa*, 3861 (1), 40–60.
<https://doi.org/10.11646/zootaxa.3861.1.2>
- Christiansen, K.A. (1965) Behavior and form in the evolution of cave Collembola. *Evolution*, 19, 529–537.
<https://doi.org/10.1111/j.1558-5646.1965.tb03328.x>
- Culver, D. (1982) *Cave life, evolution and ecology*. Harvard University Press, Cambridge, 189 pp.
<https://doi.org/10.4159/harvard.9780674330214>
- Deharveng, L. & Bedos, A. (2000) The cave fauna of southeast Asia. Origin, evolution and ecology. *In*: Wilkens, H., Culver, D.C. & Humphreys, W.F. (Eds.), *Ecosystems of the world. Vol 30. Subterranean ecosystems*. Elsevier, Amsterdam, pp. 603–632.
- Japanese Ant Database Group (2008) Japanese Ant Database 2008. Available from: <http://ant.miyakyo-u.ac.jp/J/index.html> (accessed 4 July 2018)
- Juan, C., Guzik, M.T., Jaume, D. & Cooper, S.J. (2010) Evolution in caves: Darwin's 'wrecks of ancient life' in the molecular era. *Molecular Ecology*, 19, 3865–3880.
<https://doi.org/10.1111/j.1365-294X.2010.04759.x>
- Machida, H. & Kawana, T., Nagaoka, S., Ota, Y. & Moriwaki, H. (2001) *Japanese Geology. Vol. 7. Kyushu and Nansei Islands*. Tokyo University Press, Tokyo, 355, pp.
- Maeda, K. & Tamura, H., Fujita, Y., Nakamura, Y., Sasaki, T., Kameda, Y. & Fukuda, H. (2017) *Threatened wildlife in Okinawa. Animals. Department of Environmental Affairs Okinawa Prefectural Government. 3rd Edition*. Red Data, Okinawa, pp.100 + 303 + 309 + 402 + 419 + 500.
- Marques, A.C. & Gnaschini, P. (2001) The problem of characters susceptible to parallel evolution in phylogenetic reconstructions: suggestion of a practical method and its application to cave animals. *Cladistics*, 17, 371–381.
<https://doi.org/10.1111/j.1096-0031.2001.tb00131.x>

- Roncin, E. & Deharveng, L. (2003) *Leptogenys khammouanensis* sp. nov. (Hymenoptera: Formicidae). A possible troglobitic species of Laos, with a discussion on cave ants. *Zoological Science, Tokyo*, 20, 919–924.
<https://doi.org/10.2108/zsj.20.919>
- Terayama, M., Kubota, S. & Eguchi, K. (2014) *Encyclopedia of Japanese Ants*. Gakken, Tokyo, 278 pp. [in Japanese]
- Tinaut, A. & López, F. (2001) Ants and caves: sociability and ecological constraints (Hymenoptera, Formicidae). *Sociobiology*, 37, 651–659.
- Vandel, A. (1964) *Biospéologie. La biologie des animaux cavernicoles*. Gauthier Villars, Paris.
- Wheeler, W. M. (1938) Ants from the caves of Yucatan, pp. 251-255. In: Pearse, A. S., *Fauna of the caves of Yucatan*. *Carnegie Institution of Washington Publication*, 491, 10150304.
- Wilson, EO. (1962) The trinidad cave ant *Erebomyrma* (= *Spelaeomyrmex*) *urichi* (Wheeler), with a comment on cavernicolous ants in general. *Psyche*, 69, 62–72.
<https://doi.org/10.1155/1962/54863>