

Description of a new species of the ant genus *Leptanilla* (Formicidae: Leptanillinae) with a putative non-dichthadiiform ergatoid queen from Okinawa-jima Island, Japan

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ABSTRACT. The subfamily Leptanillinae represents a basal lineage within Formicidae, and the biology of most of its members remains poorly understood due to their cryptic nature and small body size. Here, we describe *Leptanilla fuminorii* sp. nov., a species from Okinawa-jima Island, Japan. The worker and queen are characterized by a clypeus with a median lobe and a pair of lateral lobes, and postpetiole markedly higher than petiole in lateral view in the worker. Morphologically, *L. fuminorii* sp. nov. closely resembles *L. boltoni* Baroni Urbani, 1977, from Ghana, but differs in its larger size and in the structure of the clypeus and postpetiolar sternite. The colony (type series) found at approximately 15 cm depth in forest soil was composed of 352 workers, 207 larvae, and a single queen. The larvae were actively feeding on a centipede *Strigamia* sp., consistent with the previously reported diet of the genus. Queen-worker dimorphism is remarkably low compared to other species. This discovery enhances our understanding of *Leptanilla* diversity.

Keywords *Leptanilla*, new species, Okinawa, queen-worker dimorphism, taxonomy.

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INTRODUCTION

The subfamilies Martialinae and Leptanillinae constitute the sister group of all other extant Formicidae (Borowiec et al. 2019; Romiguiet et al. 2022). The members of *Leptanilla* Emery, 1870, one of the Leptanillinae genera, are cryptic ants with flat bodies, no eyes, antennae inserted very close to the anterior margin of the head, subtriangular mandibles with three to five teeth, and twelve-segmented antennae (Griebenow 2024). Also, all described queens of this genus

so far are dichthadiiform (Baroni Urbani 1977; López et al. 1994; Ogata et al. 1995; Xu 2002; Ito & Yamane 2020; Griebenow 2024; Griebenow et al. 2025), a specialized wingless queen caste with an extremely hypertrophied gaster that does not resemble workers (Peeters 2012).

This genus has unique habits that are specialized for predators of geophilomorpha centipedes, and the queen and workers feed on hemolymph secreted by the larvae from hemolymph feeding taps (Masuko 1989, 1990; Ito & Yamane 2020; Sasaki et al. 2025). The

subfamily - including *Leptanilla* - diverged from other lineages at an early stage but is thought to have evolved in a derivative manner not seen in other groups, considering that it has a unique habit not found in any of the other lineages (Masuko 1990; Borowiec et al. 2019; Romiguier et al. 2022). Thus, studying this genus is crucial for understanding the early evolutionary history of Formicidae and the extent of morphological and behavioral diversification in basal lineages. Due to their small size and completely cryptic lifestyle, however, getting intact colonies is extremely difficult, and as a result, their biology remains poorly understood.

A colony of *Leptanilla* species was collected from Okinawa-jima Island, Central Ryukyus Islands, Japan. This species features a unique clypeal shape, and a postpetiole higher than the petiole and remarkably low queen-worker dimorphism. In this paper, we describe it as *Leptanilla fuminorii* sp. nov. based on the worker and ergatoid queen. We also report the prey of this new species in the field.

MATERIALS AND METHODS

All specimens were examined under stereomicroscopes (Olympus SZ61, MVX10, Japan; Nikon SMZ1270, Japan), photographed using a digital camera (Sony α 6300, Japan) connected to a stereomicroscope (Nikon SMZ1270, Japan), and then the stacked images were created using Zerene Stacker 1.04 (Zerene Systems, USA). SEM images were taken using a JCM-7000 scanning electron microscope (JEOL, Japan) at 15.0 kV. The software ImageJ 1.53t (National Institutes of Health, USA) was used to measure the specimens.

Measurements (in mm) and indices

HW	Head Width, maximum width of cranium in full-face view.
HL	Head Length, maximum length of head in full-face view from anterior margin of head capsule to cranial vertex.
MaL	Mandible Length, maximum mandible length from its apex to base at anterior clypeal margin.
SL	Scape Length, maximum length of scape excluding bulbous.

PrW	Pronotal Width, maximum pronotal width in dorsal view.
ML	Mesosoma Length, diagonal length of mesosoma in profile view from point at which pronotum meets cervical shield to posterior basal angle of metapleuron.
PtW	Petiole Width, maximum petiolar width in dorsal view.
PtL	Petiole Length, maximum petiolar length in dorsal view.
PtH	Petiole Height, maximum petiolar height in profile view.
PptW	Postpetiole Width, maximum postpetiole width in dorsal view.
PptL	Postpetiole Length, maximum postpetiole length in dorsal view.
PptH	Postpetiole Height, maximum postpetiole height in profile view.
TW4	Width of abdominal tergite IV, maximum width of abdominal tergite IV in dorsal view.
GL	Gastral Length, maximum gastral length in profile view, excluding sting.
TL	Total Length, the sum of HL, ML, PtL, PptL, and GL.
CI	Cephalic Index, Head width divided by head length x 100.
SI	Scape Index, Scape length divided by head width x 100.
MaI	Mandibular Index, mandible length divided by head length x 100.
PI	Petiolar Index, petiole width divided by petiole length x 100.
PHI	Petiolar Height Index, petiole width divided by petiole height x 100.
PPI	Postpetiolar Index, postpetiole width divided by postpetiole length x 100.
PPHI	Postpetiolar Height Index, postpetiole width divided by postpetiole height x 100.

Type specimens are deposited in the following institutions/collections.

KU	Entomology Laboratory, Kagawa University, Kagawa prefecture, Japan.
MNHAH	Museum of Nature and Human Activities, Hyogo, Hyogo prefecture, Japan.
SKYC	Yamane Collection, Kitakyushu Museum of Natural History and Human History, Japan.

TAXONOMY

Leptanilla fuminorii sp. nov.

Figs 1A-F, 2, 3A-F, 5, 6

(Japanese name: Yanbaru-mukashi-ari)

<http://zoobank.org/50835C47-E7D6-4C48-965C-927570FE9FD3>

Type materials. Holotype. Worker (MNHAH; B2593483); Oku, Kunigami-son, Kunigami-gun, Okinawa-ken, Japan; 26.828°N, 128.282°E; 5 iv 2025; Hajime Sasaki Leg., colony code: SK25-8;

Paratypes. 56 workers (KU; SK25-8-5 to SK25-8-52, MNHAH; B2593484 to B2593488, SKYC; SK25-8-2 to SK25-8-4) and 1 queen (KU; SK25-8-1); Same date as the holotype.

Non-type materials. The remaining workers and larvae from the same colony are preserved in 70% ethanol and deposited in KU.

Description of holotype worker. Measurements (mm) and indices. HW: 0.31; HL: 0.39; MaL: 0.17; SL: 0.22; PrW: 0.22; ML: 0.57; PtW: 0.13; PtL: 0.16; PtH: 0.15; PptW: 0.14; PptL: 0.12; PptH: 0.18; TW4: 0.34; GL: 0.60; TL: 1.82; CI: 80; SI: 70; MaI: 44; PI: 85; PHI: 86; PPI: 118; PPHI: 77.

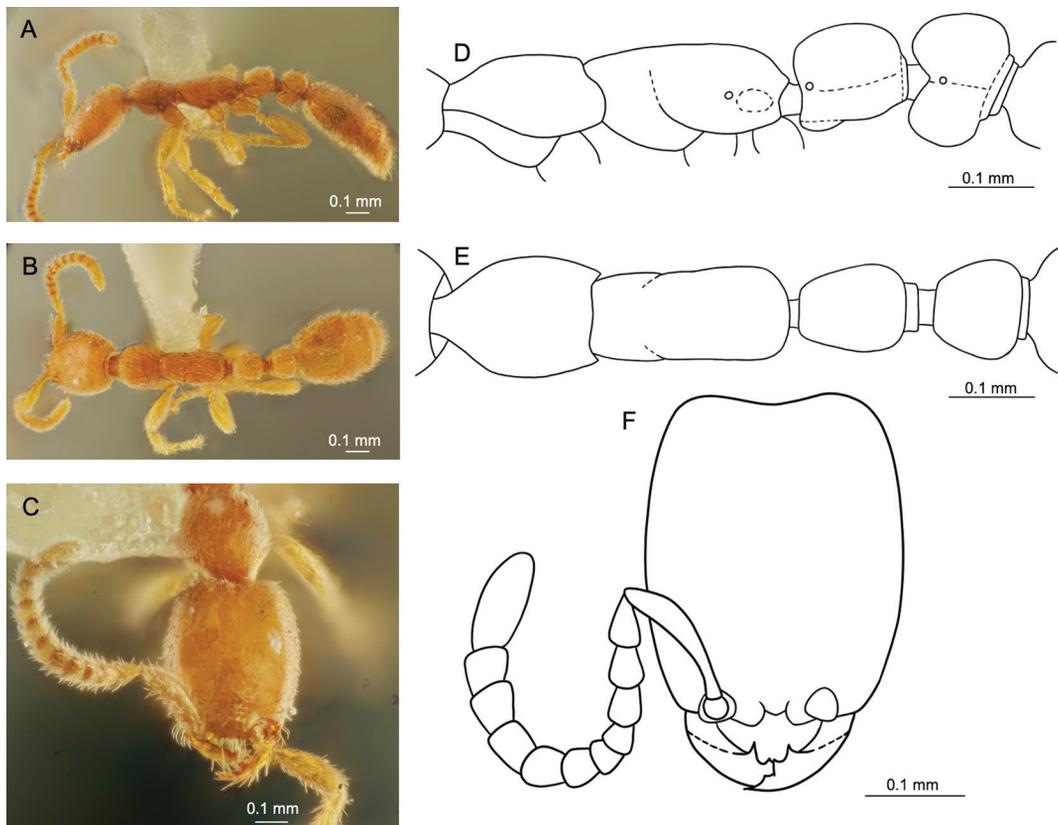


Fig. 1. *Leptanilla fuminorii* sp. nov. holotype worker. (A, D) body in lateral view; (B, E) body in dorsal view; (C, F) head in full-face view. (A-C) images, (D-F) illustrations, drawn by Hajime Sasaki.

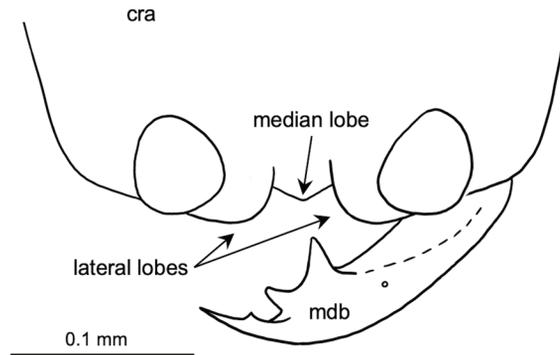


Fig. 2. Clypeus and its surrounding enlarged of *Leptanilla fuminatorii* sp. nov. holotype worker in full-face view. Abbreviations: cra = cranium; mdb = mandible.

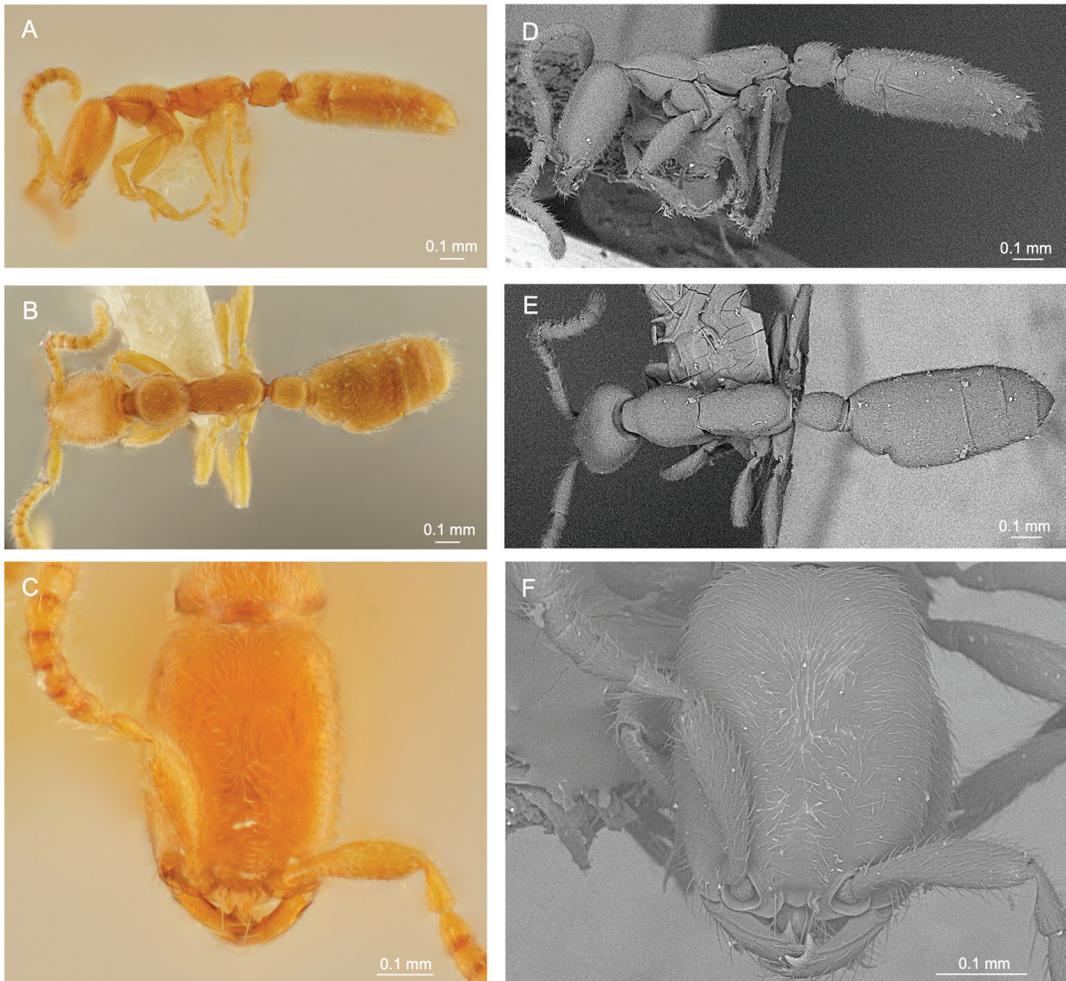


Fig. 3. *Leptanilla fuminatorii* sp. nov. paratype queen. (A, D) body in lateral view; (B, E) body in dorsal view; (C, F) head in full-face view. (A-C) images, (D-F) electron microscope images.

Head in full-face view, weakly convex laterally, with posterior margin weakly concave and posterolateral corner round. Clypeus posteriorly not demarcated from frons; its anterior area composed of short median lobe and pair of larger and rounded lateral lobes; anterior margin of lateral lobe clearly extending beyond anterior margin of antennal socket. Mandibles with 4 teeth including apical tooth; basal tooth sharp, weakly recurved. Antennae 12-segmented; apex of scape reaching 1/2 length of head measured from antennal socket to cranial apex; pedicel subequal in length to first flagellomere; apical flagellomere more than 2x as long as preapical flagellomere. Head in lateral view with dorsal and ventral margins shallowly convex. Occipital carina recognized throughout, encircling posterior edge of head, but not sharp in dorsal area where it is partly dark-pigmented. Median sulcus complete on ventral face of head, posteriorly connected with occipital carina.

Mesosoma in lateral view moderately constricted at promesonotal suture. Pronotum weakly convex dorsally. Dorsum of mesonotum and propodeum straight; metanotal groove indistinct; propodeum with posterodorsal corner rounded without clear differentiation between dorsum and declivity; declivity steeply sloping and very short. Mesopleuron demarcated from metapleuron but not from mesonotum. Metapleuron and lateral face of propodeum completely fused, both without differentiation from dorsum. Propodeal spiracle circular, located at mid-height of propodeal side. Metapleural gland bulla large and roughly elliptical, located just behind spiracle. Petiole almost as long as high; its node with dorsal margin moderately convex, ventral margin weakly convex, anterodorsal and posterodorsal corners rounded and anterior slope steep; spiracle located at anteroventral corner of node; sternite transverse with dorsal and ventral margins nearly parallel; subpetiolar process low and lamellate. Postpetiole higher than long and higher and shorter than petiole, strongly constricted at level of spiracle with anterodorsal corner roundly produced, posterodorsal corner rounded; sternite large, moderately inclined anteriorly with ventral margin strongly convex and rounded. Gaster elongate, slightly longer than mesosoma; first segment longest, occupying 1/2 of entire length of gaster; apex with sting.

In dorsal view, pronotum broader than the rest of mesosoma, with lateral margins moderately convex and humeral corners indistinct. Promesonotal suture distinct, laterally curved posteriad. Mesonotum faintly demarcated laterally from metanotum + propodeum, shorter than broad, with lateral margins almost parallel. Metanotal groove indistinct. Propodeum longer than broad, slightly widened posteriad, with posterolateral corners broadly rounded. Petiolar node longer than broad, nearly rectangular but moderately widened posteriad; its anterior corners roundly angulate, posterior corners broadly rounded. Postpetiole node broader than long, nearly trapezoid, widened posteriad, lateral margins moderately convex, posterior corners broadly rounded. Gaster elongate and roughly elliptical. Abdominal segment IV (gastral segment I) largest; segment V slightly longer than VI; segment VII shortest.

Body surface smooth and shiny. Scapes with abundant subdecumbent hairs and dense decumbent pubescence. Body color brownish yellow, antennae and legs yellow.

Description of paratype workers. Measurements (mm) and indices (n = 15). HW: 0.27-0.33; HL: 0.34-0.41; MaL: 0.14-0.17; SL: 0.19-0.23; PrW: 0.19-0.23; ML: 0.47-0.60; PtW: 0.11-0.15; PtL: 0.13-0.17; PtH: 0.12-0.16; PptW: 0.13-0.15; PptL: 0.11-0.14; PptH: 0.15-0.20; TW4: 0.25-0.33; GL: 0.53-0.67; TL: 1.57-1.97; CI: 76-84; SI: 68-79; MaI: 37-46; PI: 75-105; PHI: 81-112; PPI: 107-135; PPHI: 71-84.

Structure, sculpture, and pilosity as in holotype worker, but body size weakly variable and body color yellow to brownish yellow.

Description of paratype queen. Measurements (mm) and indices. HW: 0.29; HL: 0.38; MaL: 0.16; SL: 0.21; PrW: 0.21; ML: 0.54; PtW: 0.12; PtL: 0.13; PtH: 0.15; TW4: 0.30; GL: 0.70; TL: 1.75; CI: 78; SI: 72; MaI: 43; PI: 93; PHI: 83.

The morphological features of the queen are almost the same as those of the worker, except for the clypeus, petiole and gaster. Head in full-face view, weakly convex laterally, with posterior margin weakly concave. Eyes completely missing. Clypeus similar to that of worker, but anterior margin of median lobe rounded, without angled apex. Mandibles short with 4 teeth including apical one. Antennae 12-segmented; apex of

scape reaching 1/2 length of head; pedicel length subequal to basal segment length of flagellum, apical flagellomere 2x as long as preapical flagellomere.

Mesosoma in lateral view, moderately constricted at promesonotal suture. Pronotum in lateral view weakly convex; in dorsal view broader than the rest of mesosoma, with lateral margins moderately convex; humeral corners indistinct. Metanotal groove indistinct. Propodeum in lateral view with posterodorsal corners broadly rounded, in dorsal view longer than broad with lateral margins weakly convex and narrowing posteriorly; posterolateral corners broadly rounded. Propodeal spiracle circular and located at mid-height of propodeal side. Metapleural gland bulla large and roughly elliptical.

Waist one-segmented. Petiolar node in lateral view nearly rectangular, with dorsal margin moderately convex, ventral margin weakly convex, anterodorsal corner indistinct, posterodorsal corner broadly rounded; subpetiolar process lamellate,

weakly convex in anteroventral portion; in dorsal view nearly rectangular, with lateral margins weakly convex, widened posteriorly. With gaster in dorsal view, abdominal segment III (gastral segment I) narrower and shorter than segment IV, with indistinct anterolateral corners; segment IV largest, subequal in length to V and VI combined; segment V subequal in length to VI; segment VII shortest.

Body surface smooth and shiny. Body color brownish yellow, antennae and legs yellow.

Remarks. *Leptanilla fuminorii* sp. nov. is easily distinguished from all other Japanese congeners by the following combination of characteristics in both the worker and queen castes: 1) median lobe of clypeus not reaching the level of anterior margin of antennal sockets, its anterior margin apically angled (in the queen rather rounded); 2) lateral lobes of clypeus distinctly surpassing anterior margin of antennal sockets; 3) postpetiole in lateral view distinctly higher than petiole (worker).

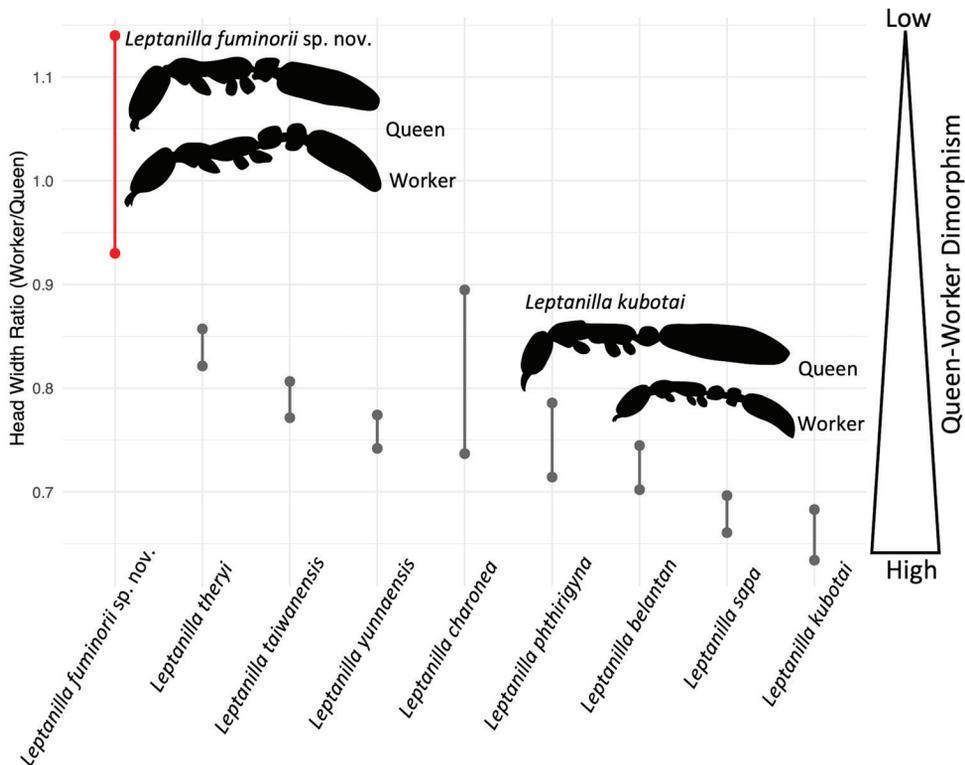


Fig. 4. Ratio of the queen to worker head width in *Leptanilla fuminorii* sp. nov. (red) compared to known *Leptanilla* species (gray). Minimum and maximum values are shown. The data for each plot is presented in Table 1. The silhouettes of workers and queens of *Leptanilla fuminorii* sp. nov. and *Leptanilla kubotai* are drawn on the same scale.

Leptanilla fuminorii sp. nov. is morphologically similar to *L. boltoni* Baroni Urbani, 1977, as the worker castes of both species possess mandibles with four teeth, a median lobe of clypeus that does not surpass the antennal sockets in full-face view, and a postpetiole that is distinctly higher than the petiole in lateral view. The new species is distinguished from *L. boltoni*, however, by its greater total body length (1.57-1.97 mm, versus 1.1-1.2 mm in *L. boltoni*). Furthermore, the anterior margin of the lateral lobes of the clypeus extends clearly beyond the anterior margin of the antennal socket, whereas in *L. boltoni*, the raised margin of the anterior margin of the antennal socket projects slightly beyond the anterior margin of the clypeus. Finally, the postpetiole sternite of the new species has its anterior margin moderately inclined and its ventral margin strongly convex and rounded. In *L. boltoni*, its anterior margin is abruptly interrupted at a right angle, and its posterior margin descends obliquely.

Interestingly, queen-worker dimorphism is low in *Leptanilla fuminorii* sp. nov. compared to other known species (Fig. 4; Table 1). All the previously known species in this genus possess dichthadiiform queens, characterized by large

body size, extreme abdominal hypertrophy, and clear morphological divergence from workers (Baroni Urbani 1977; López et al. 1994; Ogata et al. 1995; Xu 2002; Terayama & Kinomura 2015; Ito & Yamane 2020; Griebenow 2024; Griebenow et al. 2025). The discovery of an ergatoid queen having a similar body size to workers in the new species overturns the current understanding of queen differentiation in this genus. It is considered that this deviation reflects either a maintenance of ancestral queen morphology or a secondary reduction in queen-worker dimorphism driven by shifts in colony growing strategies. This finding is essential for understanding the evolution of queen morphology in this genus and raises new questions about the phylogenetic and ecological mechanisms underlying queen differentiation in this cryptic, subterranean genus.

Male. Unknown.

Etymology. The specific name is dedicated to Dr. Fuminori Ito, the first author's mentor, for his invaluable guidance and contribution to myrmecology.

Table 1. Head widths of workers and queens in *Leptanilla* species. The sample size (number of measured individuals) is shown in parentheses if provided in the references. For *L. kubotai*, data for the worker are from Baroni Urbani (1977) and for the queen from Terayama & Kinomura (2015).

Species	Head width (min-max)			References
	Worker/ Queen ratio	Worker (mm)	Queen (mm)	
<i>L. fuminorii</i> sp. nov.	0.93-1.14	0.27-0.33 (16)	0.29 (1)	Present study
<i>L. charonea</i>	0.74-0.89	0.14-0.17 (33)	0.19 (1)	López et al. (1994)
<i>L. theryi</i>	0.82-0.86	0.23-0.24	0.28	Baroni Urbani (1977)
<i>L. taiwanensis</i>	0.77-0.81	0.24-0.25 (5)	0.31 (1)	Ogata et al. (1995)
<i>L. phthirigyna</i>	0.71-0.79	0.20-0.22	0.28 (1)	Griebenow et al. (2025)
<i>L. yunnaensis</i>	0.74-0.77	0.23-0.24 (6)	0.31 (1)	Xu (2002)
<i>L. belantan</i>	0.70-0.74	0.33-0.35 (6)	0.47 (1)	Griebenow (2024)
<i>L. sapa</i>	0.66-0.70	0.39-0.39 (13)	0.56 (1)	Griebenow et al. (2025)
<i>L. kubotai</i>	0.63-0.68	0.26-0.28	0.41 (1)	Baroni Urbani (1977) Terayama & Kinomura (2015)



Fig. 5. Centipede *Strigamia* sp. being hunted by *Leptanilla fuminatorii* sp. nov. on 5 April 2025. Arrows indicate *L. fuminatorii* sp. nov. workers participating in the hunt.

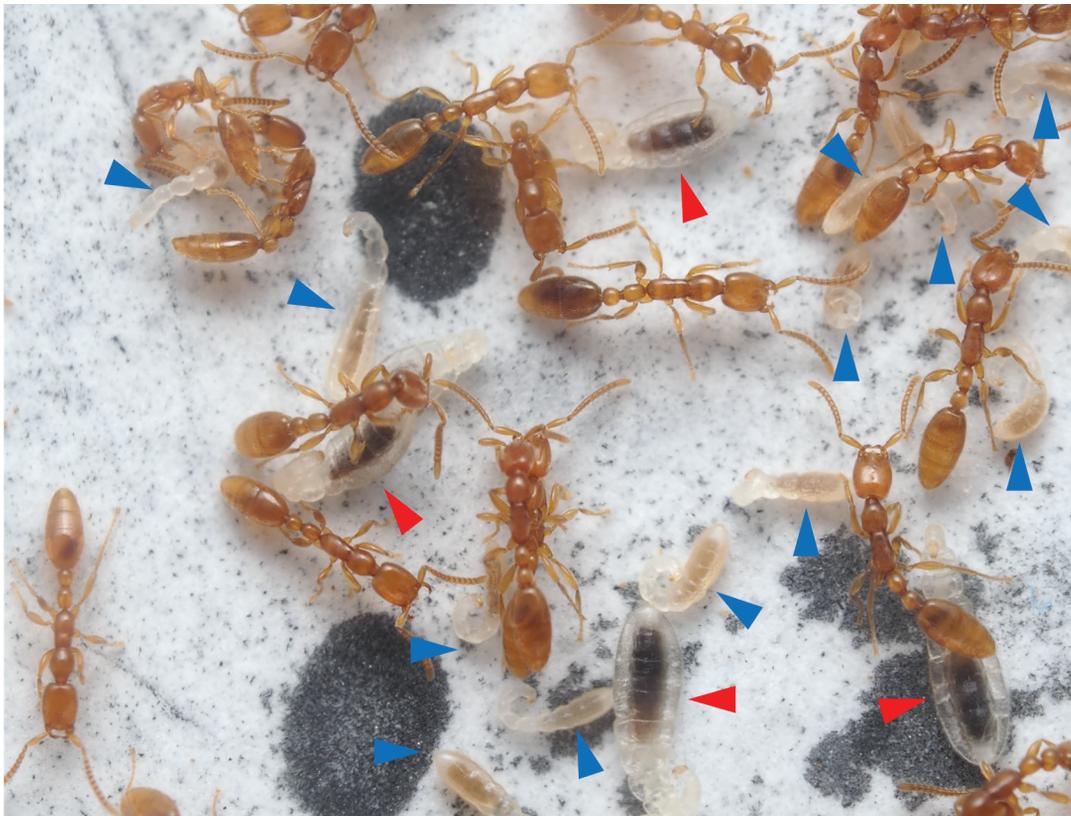


Fig. 6. The photo shows the two larval stages included in the *Leptanilla fuminatorii* sp. nov. colony. Red arrows indicate larger larvae, and blue arrows indicate smaller larvae. The photo was taken on 6 April 2025 (one day after the collection). Photo by Riou Mizuno.

Biological notes. A nest containing a queen, 352 workers, and 207 larvae was found in the soil at a depth of about 15 cm on a slope along a stream in a broad-leaf forest. At that time, workers were hunting a prey centipede *Strigamia* sp. that was caring nymphs (Fig. 5). An immature centipede was just being eaten by the larvae of the new species when we found it. Feeding on geophilomorpha centipedes has also been reported for other *Leptanilla* spp., e.g., *L. clypeata* (Ito & Yamane 2020), *L. japonica* (Masuko 1990), and *L. kubotai* (Terayama & Kinomura 2015; Sasaki et al. 2025).

Dissection of five workers confirmed their sterility, as they lacked ovarioles. On the other hand, the abdomen of the queen could not be dissected; since the specimen was very tiny and nearly indistinguishable from the workers, it was inadvertently preserved in ethanol along with the workers. While the external morphology suggests it is an ergatoid queen, we cannot strictly rule out the possibility that the queen specimen described here is not a true queen but a queen-worker “intercaste”, a phenomenon known from several other ant species (Peeters 2012). However, whether it is a true queen or an intermediate phenotype between true queens and workers, this specimen represents a previously unreported phenotype in *Leptanilla*. Future investigations utilizing non-destructive techniques, such as micro-CT scanning or the acquisition of additional samples, are required to definitively verify its reproductive status and further elucidate the colony structure of this species.

The colony included two larval stages (Fig. 6). In *L. clypeata*, *L. japonica*, and *L. kubotai*, the colonies observed contained a single growth stage of larvae due to strictly synchronized brood production (Masuko 1990; Ito & Yamane 2020; Sasaki et al. 2025). In particular, *L. japonica* is known to exhibit a cycle where the queen’s egg-laying is tightly synchronized with larval development (Masuko 1990). However, the coexistence of two larval stages in *L. fuminorii* sp. nov. suggests that the reproductive cycle of this species may not be as strictly synchronized as that of *L. japonica*, or that brood production occurs in overlapping batches. This observation implies potential interspecific diversity in colony reproductive strategies within the genus.

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