



SHORT NOTE

Description of Putative Courtship Behavior and Morphology of the Male in *Stigmatomma caliginosa* (Hymenoptera: Formicidae)

KAZUMA CHIYODA¹, MAMORU TERAYAMA²

1 - Cooperative Division of Veterinary Sciences, Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo, 183-8509, Japan

2 - Graduate School of Science, Tokyo Metropolitan University, Hachioji, Tokyo, 192-0397, Japan

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Corresponding author

Kazuma Chiyoda 

Cooperative Division of Veterinary Sciences, Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo, 183-8509, Japan.
E-Mail: k.chiyoda.0910@gmail.com

Abstract

The subterranean ant genus *Stigmatomma* exhibits ancestral traits and specialized behaviors, but its mating ecology and male morphology remain largely unexplored. In this study, we describe the behavior and male morphology of *S. caliginosa* for the first time. Laboratory video recordings captured a behavioral sequence in which the male initiated contact with an alate queen via antennation, followed by mounting, body vibration, and antennal boxing directed toward her while strongly curling his gaster. Morphological analysis revealed that the male is relatively large, similar in size to alate queens, and possesses 12-segmented filiform antennae. Although genital insertion was not observed during behavioral observations, the observed sequence of behaviors resembled courtship behavior reported in other ants that engage in intranidal mating. This suggests that the behavior may be related to mating and raises the possibility that *S. caliginosa* also engages in intranidal mating.

The ant genus *Stigmatomma* Roger (Hymenoptera: Formicidae: Amblyoponinae: Amblyoponini) is widely distributed throughout the world except in polar regions and comprises 56 species (AntCat, 2026). Amblyoponini ants, including the genus *Stigmatomma*, retain the ancestral morphological trait of a petiole broadly attached to the gaster, a feature unique within the ant family. Their social behavior has therefore attracted attention as a key to understanding social evolution (Traniello, 1982; Masuko, 1986; Hölldobler & Wilson, 1990; Ito, 1993; Thorne & Traniello, 2003). The genus is also known for a specialized behavior termed 'larval hemolymph feeding' (LHF), in which queens pierce the integument of their larvae and feed on the exuding hemolymph (Masuko, 1986). However, *Stigmatomma* ants are predominantly subterranean and cryptic, making colonies difficult to collect, and ecological knowledge of the genus therefore remains limited (Brown, 1960; Ward & Fisher, 2016; Esteves & Fisher, 2016). Knowledge of male

morphology and mating ecology is particularly scarce. In *S. pallipes*, the best-known species of the genus in North America, males are smaller than queens and workers (Wheeler, 1900). Regarding mating ecology, Wheeler (1900) reported males mating with newly emerged queens within the nest and noted that queens often shed their wings before acquiring deep adult coloration. However, males have also been observed leaving the nest during nuptial flights, suggesting that *S. pallipes* may engage in both mating strategies (Wheeler, 1900; Haskins, 1928; Traniello, 1982). Accumulating detailed knowledge across a wider range of species is therefore essential for clarifying male morphology and mating ecology in the genus *Stigmatomma*, and for revealing evolutionary trends common to the genus as a whole.

Stigmatomma caliginosa (Onoyama, 1999), described from Japan, has been little studied ecologically. This species nests underground at a depth of about 15 cm in evergreen

broad-leaved forests. Records of alate queens collected in emergence traps suggest that it engages in nuptial flights from August to September (Ohkawara & Iwanishi, 2007; Terayama et al., 2014; Terayama, unpublished). However, the male of this species has remained unknown.

We discovered a nest of *S. caliginosa* containing males and alate queens, providing an opportunity to investigate mating behavior and describe male morphology for the first time. In this study, we describe behavior observed in males under laboratory conditions using video recordings and describe male morphology. These findings provide important insights for understanding the reproductive ecology and evolutionary processes of this genus, which remain largely unexplored.

On 9 August 2025, a colony of *S. caliginosa* was collected in Higashimatsuyama, Saitama Prefecture, Japan (36°00'N, 139°21'E), from soil at a depth of approximately 15 cm. The collected nest contained four alate queens, two males, seven workers, and 13 cocoons. Until the start of observations, the colony was maintained in a plastic case lined with moistened plaster in an incubator at 25 ± 1 °C and was not fed.

To observe mating-related behavior, all individuals from the nest were placed in a transparent plastic case (Styrene square case type 2, $68 \times 39 \times 15$ mm; AS ONE, Japan) lined with a 5 mm layer of plaster on 11 August, two days after collection. Because one of the two males had been lost prior to the observation, only a single male ($n = 1$) was used. The nest was recorded for 300 minutes at 25 ± 1 °C using a video camera (HC-V480MS, Panasonic, Japan) positioned above the case.

After the behavioral observations, the male specimen ($n = 1$) was preserved in 70% ethanol and used for morphological description. The specimen was examined under a stereomicroscope (SZM-41, BaoMic, China) and photographed with an EOS M6 Mark II camera (Canon, Japan) equipped with an M-PLAN APO 5X objective lens (Mitutoyo, Japan) and a DCR-250 conversion lens (Raynox, Japan). Photographs were taken at successive focal planes and stacked using Zerene Stacker (Zerene Systems, Richland, WA, USA), after which backgrounds were cleaned using GIMP 3.0.4 (The GIMP Development Team 2025).

Measurements of the male specimen were taken using a stereomicroscope (SZX16; Olympus, Tokyo, Japan) equipped

with a digital camera (ToupCam; Hangzhou ToupTek Photonics, Hangzhou, China) and image analysis software (ToupView ver. X64; Hangzhou ToupTek Photonics, Hangzhou, China). Measurements were recorded to the nearest 0.01 mm. The abbreviations used for measurements and indices are as follows:

HL (Head length): Maximum length of the head in full-face view, excluding the mandibles (measured from the anterior median margin of the clypeus to the posterior median margin of the head).

HW (Head width): Maximum width of the head in full-face view, measured at the level of the upper margin of the compound eyes.

EL (Eye length): Maximum diameter of the compound eye.

SL (Scape length): Length of the antennal scape, excluding the basal condyle.

WL (Weber's length of mesosoma): Maximum diagonal length of the mesosoma in lateral view, measured from the anterior-most point of the pronotal collar to the posterior-most point of the propodeal lobe.

TL (Total body length): Outstretched length from mandibular apex to metasomal apex.

CI (Cephalic index): $(HW/HL) \times 100$

EI (Eye index): $(EL/HW) \times 100$

SI (Scape index): $(SL/HW) \times 100$

The examined specimen is deposited in the personal collection of M. Terayama.

Approximately four hours into the recording, a sequence of behaviors was observed in which the male approached and mounted an alate queen (Table 1). The male initiated this sequence by intermittently antennating the alate queen from the front (Fig 1a). After antennation, the alate queen turned around to face the same direction as the male (Fig 1b). The male then mounted the alate queen and performed antennal boxing while vibrating his body and strongly curling his gaster ventrally (Fig 1c, d). After several gaster curls, the male dismounted the alate queen (Fig 1e), concluding the behavioral sequence (Fig 1f).

Table 1. Sequence of behavior observed in *Stigmatomma caliginosa* under laboratory conditions. Time is indicated as hh:mm:ss (hours: minutes:seconds).

Time (start)	Duration	Behavioral phase	Description
4:05:39	44 s	Antennation	The male faced an alate queen and began intermittent antennation (Fig 1a).
4:06:23	18 s	Reorientation	The alate queen turned around to face the same direction as the male (Fig 1b).
4:06:41	6 s	Mounting	The male mounted the alate queen.
4:06:47	64 s	Antennal boxing and gaster curling	The male performed antennal boxing against the alate queen, vibrated his body, and repeatedly curled his gaster toward her gaster (Fig 1c, d).
4:07:51	-	Dismounting	The male dismounted the alate queen, ending the sequence (Fig 1e, f).

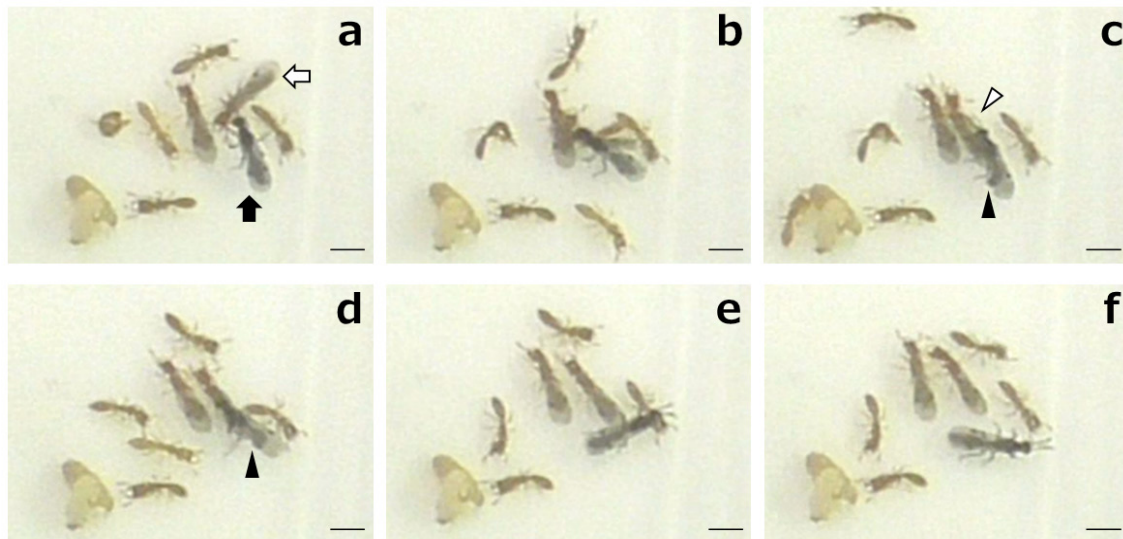


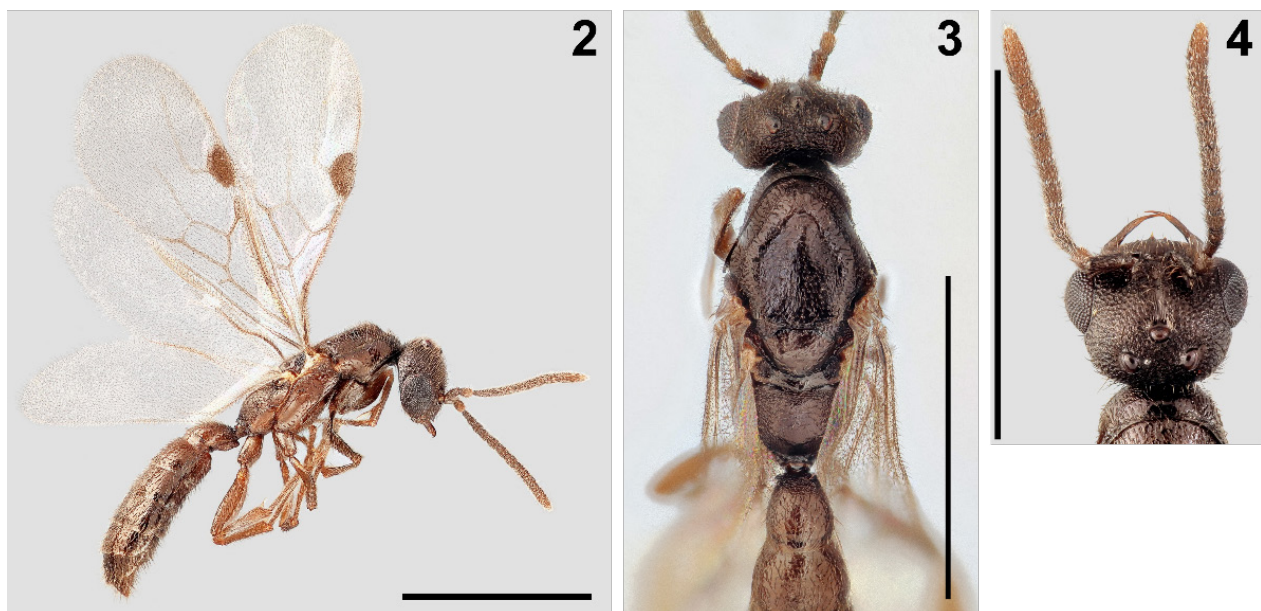
Fig 1. Sequence of behavior observed in *Stigmatomma caliginosa* under laboratory conditions. (a) The male (filled arrow) antennates the alate queen (open arrow) from the front. (b) The alate queen turns around to face the same direction as the male. (c, d) The male mounts the alate queen and performs antennal boxing (open arrowhead) while curling his gaster ventrally (filled arrowhead). (e, f) The male dismounts the alate queen, ending the sequence of behavior. Scale bars: 1 mm.

Description of the male

Head (Fig 3): Head capsule almost as long as wide excluding eyes, with straight posterior margin and convex posterolateral corner in full-face view. Mandible long and slender, nearly 0.5 times as long as head length, with an apical tooth. Anterior margin of clypeus weakly convex, with 3 denticles at midlength; median one larger. Antenna with 12 segments, filiform; scape short, 1.7 times as long as wide and nearly as long as distance from antennal socket to anterior margin of eye; pedicel 1.7 times as long as wide; 3rd to 11th antennomeres each slightly longer than wide; terminal segment 2.0 times as long as wide. Frontal carinae absent. Eye large and prominent with straight inner margin in full-face view. Ocelli well developed, arranged in obtuse triangle.

Mesosoma (Figs 2, 3): Mesonotum almost as wide as head in dorsal view; pronotum and mesoscutum distinctly separated by promesonotal suture; mesoscutum and mesoscutellar-axillar complex separated by scuto-scutellar suture; notauli and parapsidal furrows absent; metanotum short. In lateral view, dorsal margin of pronotum convex; dorsum of mesonotum straight and with weakly angulate anterior margin; propodeal dorsum gently convex.

Metasoma (Fig 2): Petiole longer than height in profile, with gently convex dorsal margin; anterodorsal corner not forming an angle; posterior margin broadly attached to 2nd metasomal segment. Subpetiolar process low, with straight ventral margin and weakly angulate anterior margin. In dorsal view, petiole slightly longer than wide, widest at posterior end. Second



Figs 2-4. *Stigmatomma caliginosa*, male. 2. Body in lateral view; 3. Body in dorsal view; 4. Head in full-face view. Scale bars: 0.5 mm.

metasomal tergum 0.8 times as long as wide, widest at posterior end in dorsal view; 3rd and 4th terga each 0.6 times as long as wide, with parallel sides.

Legs: Hind tibia 0.35 mm long, with two tibial spurs.

Wings: Forewing with a large pterostigma, 0.23 mm long and 1.8 times as long as wide; radial sector (Rs) connected with radius (R1); 2r-rs connected with radial sector (Rs), fully present and reaching the costal margin; 2rs-m present. Hindwing without media (M) and radial sector (Rs).

Color: Body dark brown; mandible, antenna and legs brown; wings hyaline; wing veins and pterostigma brown.

Sculpture: Frons and vertex of head densely punctate. Dorsum of mesosoma microreticulate; posterior half of lateral surface of pronotum, mesopleuron, and anterior half of lateral surface of propodeum largely smooth, the rest of portions microreticulate. Metasoma sparsely punctate with smooth interspaces.

Pilosity: Dorsum of head covered with abundant short erect or suberect setae; antenna entirely covered with short suberect setae; eye with short erect setae. Mesosoma and petiole covered with pubescences. Second to terminal metasomal segments covered with relatively long pilosities on both dorsal and ventral surfaces. Legs entirely covered with pubescences.

Measurements (mm) and indices: HL 0.43, HW 0.40, EL 0.23, SL 0.11, WL 0.91, TL 2.32, CI 92.2, EI 57.5, SI 27.5.

Remarks. This species possesses the generic characters for males of the genus *Stigmatomma* in the subfamily Amblyoponinae as follows: frontal carinae absent; pterostigma well-developed; radial sector fully present and reaching the costal margin; 2r-rs connected with radial sector posterior to pterostigma; 2rs-m present; two tibial spurs present on hind leg. However, it is separated from the other congeners by the 12-segmented antennae (13-segmented in the others (Yoshimura & Fisher, 2012; Ramamonjisoa et al., 2024)).

The male's behavior toward the alate queen, including frequent antennation, mounting, antennal boxing, and gaster curling, closely resembles the initial phase of mating behavior described in other ants that engage in intranidal mating, such as *Diacamma* and *Cardiocondyla* (Hölldobler & Wilson, 1990; Yamauchi et al., 1996; Monnin & Peeters, 1998; Mercier et al., 2007), and is particularly similar to the courtship sequence reported in *Cardiocondyla* (Mercier et al., 2007). These similarities indicate that the behavior observed in this study represents putative courtship. The possibility of intranidal mating in the genus *Stigmatomma* has previously been suggested by observations in *S. pallipes* (Wheeler, 1900) and collection records of polygynous colonies of *S. silvestrii* (Terayama et al., 2014; Masuko, 2017). Together with these reports, our observation raises the possibility that intranidal mating also occurs in *S. caliginosa*.

The male of *S. caliginosa* was distinctly larger than workers and was equal to or slightly larger than alate queens. We propose two non-exclusive hypotheses to explain this trait. First, this may reflect an ancestral condition. Sexual size dimorphism is generally less pronounced in social wasps,

the ancestors of ants, than in most ants (Hughes et al., 2008; Boomsma et al., 2005). The large male size in *S. caliginosa* may similarly reflect a primitive, weakly dimorphic state, consistent with other ancestral traits retained in this genus. Second, the large male size may reflect an adaptation to a female-calling nuptial flight system, in which queens release pheromones and males actively search for them (Hölldobler & Bartz, 1985); under this system, males are required to maintain high flight ability and well-developed sensory organs, which would reduce the size difference between alate queens and males. This system is considered advantageous for subterranean-nesting ants such as *Stigmatomma* (Peeters & Ito, 2001), and indeed, a female-calling type of nuptial flight, in which alate queens disperse only short distances and are located by flying males, has been reported in *S. pallipes* (Traniello, 1982). Notably, alate queens of *S. caliginosa* have also been confirmed to leave the nest by emergence traps (Terayama, unpublished). This raises the possibility that this species, like *S. pallipes*, also engages in a female-calling type of nuptial flight, which may explain the large male body size.

This study provides important insights into mating behavior and male morphology in the genus *Stigmatomma*, which has remained insufficiently understood. The genus is known to represent a lineage that retains primitive morphology while having evolved highly specialized behaviors, such as larval hemolymph feeding (LHF) (Traniello, 1982; Masuko, 1986; Hölldobler & Wilson, 1990; Ito, 1993; Thome & Traniello, 2003), although this view has been based mainly on workers and queens. The findings obtained here on male morphology and behavior in *S. caliginosa* extend this picture to males and may provide a foundation for future studies on the early evolution of the Formicidae and adaptation to subterranean environments.

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Authors' Contributions

K.C.: investigation, writing-original draft.

M.T.: investigation, formal analysis, writing-review & editing.

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