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Colony composition and queen behavior in three allopatric forms of *Stictoponera binghamii* in Vietnam, Thailand and Peninsular Malaysia (Hymenoptera: Formicidae)

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ABSTRACT. *Stictoponera* (Formicidae: Ectatomminae) shows a wide range of reproductive structures and therefore represents a good model organism for studying the evolutionary process of diversifying reproductive strategies. In this paper, the colony composition, reproductive and behavioral characteristics of three allopatric forms of *Stictoponera binghamii* ("TH" from Thailand, "VN" from Vietnam, and "MA" from Malaysia) are described. Based on the examination of 14 colonies, the average colony size is small, ranging from 24 to 44 workers. Colonies of all three forms were monogynous, each containing one mated dealate queen with four (2-2) ovarioles. In contrast, important variation was observed in workers of the different forms of *S. binghamii: "*TH" and *"*MA" had four (2-2) and two (1-1) ovarioles, respectively, while *"*VN" had either two or four ovarioles. Queen behavior was observed for more than 100 hours across nine colonies of the three forms and revealed that all forms exhibited larval hemolymph feeding. Workers under queenright conditions laid trophic eggs, some of which were eaten by the queens. Under orphaned conditions, workers of *S. binghamii* "TH" laid reproductive eggs that developed into males, indicating that worker ovaries are functional for producing reproductive eggs.

Keywords	Larval hemolymph feeding, ovary, trophic egg, worker reproduction
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INTRODUCTION

Recently, the phylogenetic relationships of ants in the subfamily Ectatomminae were revised, resulting in the division of the genus *Gnamptogenys* into five distinct genera (Camacho et al. 2022). Most Asian species previously assigned to *Gnamptogenys* have been transferred to the genus *Stictoponera*, which currently contains 43 species restricted to the Oriental tropics and Australian realms (Bolton 2026), and is considered a monophyletic group (Camacho et al. 2022). This genus shows a wide range of reproductive structures: some species reproduce by gamergates (mated and egg-laying workers) with alate queens and/or ergatoid queens, while other species have alate queens without gamergates (Gobin et al. 1998a; Tanigawa et al. 2002; Ito et al. 2021). Therefore, *Stictoponera* represents a good model organism for studying the evolutionary processes driving the diversification of reproductive strategies. Furthermore, the genus has the potential to be used as an indicator of environmental conditions, as at least some species display a distinct preference for specific habitats, such as primary forests (Lattke 2004). For example, in the Lambir Hills forest, Yamane et al. (2021) reported 11 species of "*Gnamptogenys*" (mostly *Stictoponera*), whereas the Bogor Botanical Gardens, a green island surrounded by urban areas, had only one species of *Stictoponera* (Ito et al. 2001). However, the natural history of most species remains unknown; to date, only two species, *S. menadensis* (Mayr, 1887) and *S. bicolor* (Emery, 1889) have been studied (Gobin et al. 1998a, b; Aikawa et al. 2002; Tanigawa et al. 2002; Allard et al. 2010; Ito et al. 2021). This paper reports the colony composition, queen behavior, and worker reproduction of three allopatric forms of *S. binghamii* (Forel, 1900). To compare colony size and ovariole number among *Stictoponera* species, we also present new data from six species collected in Indonesia and Malaysia, along with published information on *S. menadensis* and the related genus *Holcoponera,* one of the four ectatommine genera occurring in the Oriental tropics besides *Stictoponera*.

MATERIALS and METHODS

Ants: Lattke (2004) revised the taxonomy of Asian *Stictoponera*, treating a series of samples collected from India to Papua New Guinea as *S. binghamii*, a species originally described from Myanmar. He further noted that *S. binghamii* comprises two distinct forms: a larger form distributed from Malaysia to New Guinea, and a smaller form found between Thailand and India. The latter closely aligns with the type specimen of *S. binghamii* (Lattke 2004).

We collected *Stictoponera* colonies from the following locations: Tay Yen Tu Nature Reserve in northern Vietnam (seven colonies, March 2017), Doi Chiang Dao, northern Thailand (one colony, August 2014), Trang in southern Thailand (four colonies, November 2014) and Ulu Gombak, Peninsular Malaysia (two colonies, March 2012). The morphology of individuals from Vietnamese and Malaysian colonies aligns with the smaller and larger forms of *S. binghamii* sensu Lattke (2004), respectively. While the individuals from Thai colonies from both sites show no distinct morphological variations and are morphologically more similar to individuals from Vietnamese colonies than the Malaysian colonies, Thai specimens differ from Vietnamese specimens in their abdominal traits: the Vietnamese colonies possess a reddish abdomen with relatively longer setae, whereas the Thai colonies have a dark bluish abdomen with shorter setae. The images of the syntype worker of *S. binghamii* provided in AntWeb (CASENT0907195) closely resemble the workers from Vietnamese colonies. Therefore, in the present paper, we tentatively distinguish these three allopatric forms as "TH" (Thai form), "VN" (Vietnamese form), and "MA" (Malaysian form), and use these abbreviations hereafter. Voucher specimens will be deposited in the Department of Biological Science, University of Malaya; Forest Research Institute Malaysia; Institute of Ecology and Biological Resources, Vietnam; and the Thailand Natural History Museum.

Colony collection: Colonies of "MA" and "TH" nested in dead wood fallen on the forest floor, while those of "VN" nested in the soil. All colony members were collected by using an aspirator, and colony composition was assessed immediately after sampling. All colonies were kept in the laboratory for observation, and some queens and workers were subsequently dissected to check for their reproductive condition under a binocular microscope. The spermatheca of a few queens and workers of "TH" were removed from the ovaries under a dissecting microscope and put on a glass slide in a droplet of water. A cover glass was put on the spermatheca, and the reservoir diameter was measured under a light microscope. The head width of queens and workers of the three forms was measured under a binocular microscope.

Laboratory observation: Each colony was kept in the laboratory within an artificial nest (9.5 x 6.2 x 2.8 cm) containing a small nest chamber (3.6 x 3.6 x 1.4 cm). The floors of both the chamber and the foraging arena were lined with plaster of Paris to maintain high humidity. Small cockroaches, *Blatta lateralis* (Walker, 1868), termites, *Reticulitermes speratus* (Kolbe, 1885), and mealworms, *Tenebrio molitor* L., 1758, were given as prey. Queen behavior was observed under a binocular microscope for four "TH", three "VN" and one "MA" colonies. Observations were typically conducted in 30-minute sessions, replicated 9 (4 hours 30 min) to 39 times (19 hours 30min) per colony over a period of one to two weeks. In total, queen behavior was observed for 114.5 hours. For one colony of "TH" (FI14-132), observations were conducted 20 times (10 hours, FI14-132a in Table 2) when the colony contained 7-10 workers, and 28 times (14 hours, FI14-132b in Table 2) after the worker number increased to 22.

To assess the egg laying ability of workers under orphaned conditions, four subcolonies, each consisting of ten workers, were established from four "TH" colonies, and kept in the artificial nests described above. Brood and male production were monitored once or twice per week.

To compare colony size and ovariole numbers among *Stictoponera* species, we included data from seven species of *Stictoponera* and one species of *Holcoponera* collected in Indonesia (Sumatra and Java) and Malaysia (Ulu Gombak) between 1990 and 2011. The collection localities are shown in Table 3. The collection methods and subsequent procedure are identical to those used in the present study.

RESULTS

Colony composition: Colony composition is shown in Table 1. Colony size across the three forms was consistently small, with 20 and 28 workers in "MA", 49.8 ± 25 in "TH", and 30.0 ± 16.7 in "VN". Colonies contained one or two dealate queens across all forms; however, each colony possessed only a single mated, egg-laying queen. The size dimorphism between queens and workers was inconspicuous across all forms, with the head width of the queens being almost identical to that of the largest workers (Fig 1). The size distribution of workers was unimodal in all forms (head width, Shapiro-Wilk test, $W = 0.95$, $P = 0.28$ in "MA"; $W = 0.97$, $P = 0.45$ in "TH"; $W = 0.961$, $P = 0.28$ in "VN"). The number of ovarioles in queens was four (2-2) in all three forms. "TH" workers also possessed four ovarioles (2-2), whereas "MA" workers had two (1-1), and "VN" workers exhibited variation from two to four. Workers of all forms possessed a small spermatheca. In "VN", the spermatheca size in workers (0.12 mm ± 0.008SD, n = 3) was significantly smaller than that in queens (0.19 mm ± 0.006, n = 3, Welch two-sample t-test, $t = 74.7$, $df = 4$, $p < 0.0001$). The epithelium in the hilar region of the worker spermathecae was thin, indicating that the worker spermatheca in this form is non-functional. Similarly, in "MA" and "TH", worker spermathecae were remarkably smaller than those of queens, although their sizes were not measured. The cocoon tip of the three forms was not cut. Eggs were elongate, measuring 0.81 mm ± 0.013SD in length and 0.29 mm ± 0.008SD in width (N = 5) in "TH", and 0.81 mm ± 0.02SD in length and 0.31 mm ± 0.001SD in width (N = 3) in "VN". The egg shape of "MA" was similar to these two forms but their sizes were not measured.

Queen behavior: Dealate queens of all three forms were usually inactive inside the nest chambers. They typically remained on or near the brood piles located in the innermost part of the chambers, only occasionally walking within the chambers. Aggressive behavior against workers was rarely observed in any colony.

Table 1. Colony composition of three forms of *Stictoponera binghamii*. Localities of each colony were as follows: FI12-36 and FI12-44: Ulu Gombak, Peninsular Malaysia; FI14-70: Doi Chiang Dao, northern Thailand; FI14-123,131,132,144: Trang, southern Thailand, All colonies of S. "VN": Tay Yen Tu Nature Reserve, northern Vietnam. Colonies are arranged according to the number of workers.

Colony code	The number of individuals						
	Dealated queens	Workers	Alate queens	Males	Cocoons	Larvae	Eggs
S. binghamii "MA"							
FI12-36	1	20	0	0	15	12	8
FI12-44	2	28	0	0	15	30	25
S. binghamii "TH"							
FI14-132	2	28	0	0	22	12	20
FI14-70	2	37	0	0	24	10	10
FI14-144	2	38	0	0	0	6	5
FI14-131	1	55	2	0	9	10	3
FI14-126	1	91	0	4	0	25	3
S. binghamii "VN"							
FI17-35	1	13	0	0	0	13	5
FI17-43	1	22	0	0	0	25	5
FI17-14	1	23	0	0	0	6	12
FI17-13	1	25	0	0	0	5	0
FI17-44	1	28	0	0	0	15	0
FI17-58	1	30	0	0	0	NC	0
FI17-15	1	69	0	0	0	12	0

NC: not counted

Egg-laying by the queens was observed once in "TH" and four times in "MA". In both forms, the queen bent her abdomen ventrally underneath the thorax and extruded an egg from the abdominal tip. The newly emerged egg was then picked up by the queen using her mandibles and placed onto an egg pile.

All nine queens across the three forms exhibited larval hemolymph feeding (LHF) (Table 2, Fig. 2). They bit the dorsal region of the larval body with their mandibles and licked the exuding hemolymph. Since bite locations on *S. binghamii* larvae varied, no distinct, clear wounds remained. The larvae subjected to LHF did not die in the three forms. The frequency of LHF by queens varied among colonies, ranging from 0.05 to 0.25 times per 30 min. in "TH", 0.03 to 0.1 times per 30min in "VN", and 0.15 times per 30 min. in "MA". A feeding bout of LHF lasted on average 14 min. (2 min. 15 sec. to 21 min. 55 sec., N = 3) in "MA", 7 min. 42 sec. (36 sec. to 18 min. 40 sec., N = 19) in "TH", and 6 min. 30 sec. (4 min. 30 sec. to 8 min. 40 sec., N = 3) in "VN" (Fig. 2). The frequency of LHF tended to be higher in "TH" colonies with a larger number of larvae than in those with fewer larvae (Fig. 3). Feeding on insect prey was observed only thrice in queens of "TH" (two times in FI14-144, and once in FI14-131), but 18 times in a queen of "VN" (FI17-13). Queens in "MA" and the remaining "VN" colonies never exhibited prey feeding. In addition, queens across all three forms were observed feeding on trophic eggs laid by workers.

Table 2. Feeding behavior of queens in three forms of *Stictoponera binghamii*. Frequencies of each behavior are shown. Time spent (seconds) is shown in parenthesis. * time spent was not measured.

	S.b. "MA"	*S. binghamii*"TH"					
	FI12-36	FI14-70	FI14-144	FI14-126	FI14-131	FI14-132a	FI14-132b
Hour of observation	19h 30m	10 h	10 h	10 h	10 h	10 h	14h
Frequency of feeding on							
insect prey	0	0	2 (257)	0	1 (5)	0	0
trophic eggs	1 (949)	1*	0	0	0	0	1 (750)
larval hemolymph	6 (4807)	2 (943)	1 (197)	5 (730)	1 (20)	4 (2117)	5 (2240)

	S. binghamii "VN"		
	FI17-13	FI17-44	FI17-58
Hour of observation	11 h	15.5 h	4.5 h
Frequency of feeding on			
insect prey	18 (5065)	0	0
trophic eggs	2 (880)	1(580)	0
larval hemolymph	1 (520)	1 (270)	1 (380)

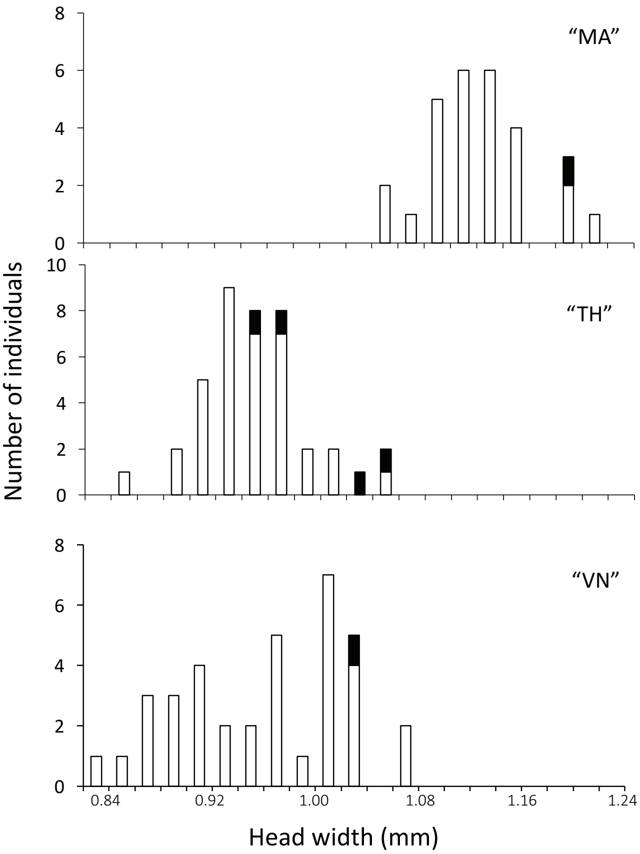

Fig. 1. Head width distribution of queens and workers in three forms of *Stictoponera binghamii*.

Table 3. Colony composition of *Stictoponera* and *Holcoponera* species in the Oriental tropics. Localities of colonies are as follow: a; Sitiung, Sumatra, b; Ulu Gombak, Peninsular Malaysia, c; Ujung Kulong, West Java, d; Sungaidareh, West Sumatra, e; Gunung Gede, West Java, f; Gunung Halimun, West Java, g; Kebun Raya Bogor, West Java. – not examined. Colonies are arranged according to the number of workers. *Ito et al. (2021), **Ito and Gobin (2008), *** Two colonies reproduced by one queen while the remaining 33 colonies reproduced by one to 14 gamergates.

Colony code	**The number of individuals**						
	Dealate queens	**Workers**	**Alate queens**	**Males**	**Cocoons**	**Larvae**	**Eggs**
S. coxalis							
FI11-52[b]	1	20	0	0	0	12	0
FI03-57[b]	1	28	0	0	52	40	27
FI92MG-259[b]	1	31	2	3	10	24	12
FI96-133[a]	1	55	0	0	-	-	-
FI00-94[b]	1	55	2	6	-	-	-
FI97-181[c]	1	120	0	0	-	-	-
Average ±SD		51.5 ± 37.4					
S. laevior							
FI98-380[f]	2	24	0	0	4	5	10
FI92-119[d]	1	33	1	2	-	-	-
FI91-28[e]	1	48	0	0	-	-	-
Average ±SD		35.5 ± 9.9					
S. menadensis[b]							
Average ±SD (35 colonies)*	1***	161 ± 225					
S. paso							
FI99-147[b]	1	1	0	0	-	-	-
FI92MG-706[b]	1	7	0	0	-	-	-
FI92MG-23[b]	1	19	0	0	7	3	27
FI98-X[b]	3	66	2	0	-	-	-
Average ±SD		23.3 ± 25.5					
S. sp. 4 of FI (nr. *coxalis*)							
FI09-108[b]	1	2	0	0	0	0	0
FI92MG-243[b]	1	3	0	0	4	0	0
FI11-30[b]	2	10	0	0	4	2	2
FI99-86[b]	1	11	2	3	10	0	8
FI11-29[b]	1	24	0	1	10	4	2
Average ±SD		10 ± 7.9					
S. sp. (*binghamii* gp)							
FI99-119[b]	1	7	0	0	0	6	7
S. sp. 17 of FI							
FI11-58[b]	1	36	0	3	24	13	5
H. cribrata[g]							
Average ±SD (6 colonies)**	1	27 ± 14	1.5	0.2			

-: not counted

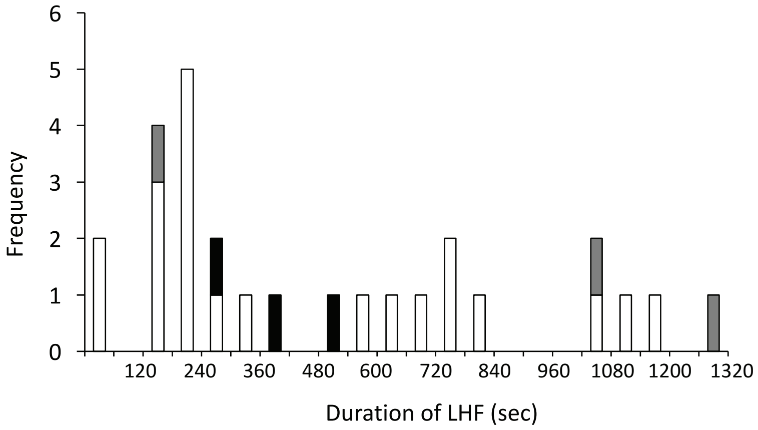

Fig. 2. Duration of LHF by queens of three forms of *Stictoponera binghamii* black: “VN”, gray: “MA”, white: “TH”.

Fig. 3. Relationship between the number of larvae and the frequency of LHF in *Stictoponera binghamii* “TH”..

Table 4. Ovariole numbers per individual in the Oriental *Stictoponera* and *Holcoponera* species

Species	**Alate or Dealated queens**	**Workers**
S. coxalis	4	2
S. laevior	6, 4	2
S. menadensis[a]	7	6-12
S. paso	4	2
S. sp. 4 of FI (nr. *coxalis*)	4	2
S. sp. *(binghamii* gp)	4	2
S. sp. 17 of FI	4	2
H. cribrata[b]	2	2

[a]Ito et al (2021), [b]Ito and Gobin (2008)

Trophic eggs laid by workers: Workers laid trophic eggs across all three forms, although the frequency was remarkably low. In "TH", worker oviposition was observed only twice: once during 10 hours in FI14-70 (37 workers) and once during 10 hours in FI14-132 (22 workers). These two eggs were smaller than the reproductive eggs laid by queens, and both were eaten by the queens. In FI14-132, the egg-laying worker held her egg between the mandibles; the queen then approached the worker and licked the egg while it was still being held by the worker. This behavior continued for 12 min. 30 sec., then the egg was completely consumed by the queen. In FI14-70, the queen retrieved the egg directly from the worker and began feeding on it, though the duration was not recorded. In "VN", three trophic eggs were laid by workers in two colonies during a total of 26.5 hours of observation. All three eggs were eaten by queens, who spent 4 min. 40 sec. to 10 min. to completely consume them. In "MA", trophic egg laying by workers was observed thrice during 19 h 50 min. of observation. Of these three eggs, one was eaten by the queen; in this instance, the queen antennated the worker while she was in the egg-laying posture. Following oviposition, the queen picked up the egg from the worker and consumed it over a duration of 15 min. 48 sec. The queen also picked up one of the remaining two eggs but subsequently dropped it onto the body of a nestmate worker, making no further attempt to feed on it. For the other trophic egg laid by the worker, the queen did not show any interest.

Worker reproduction in orphan colonies: A representative example of brood development in the orphan colony of "TH" is as follows. Eggs were first detected 14 days after orphaning, and the first larva hatched two weeks after the onset of oviposition. At the time the first larva emerged, the colony contained 22 eggs. Male cocoons were observed 57 days after orphaning, and subsequently, males emerged. All four orphan colonies produced between a few and approximately 10 males over the course of one year.

DISCUSSION

The colony characteristics of the three *S. binghamii* forms were similar, exhibiting monogyny with a single dealate queen and a small colony size. Besides these three forms, at least five other Oriental *Stictoponera* species (*S. coxalis* (Roger, 1860), *S. laevior* (Forel, 1905), *S. paso* (Lattke, 2004), and two unidentified species) are also monogynous with dealate queens, and maintain small colony size (Table 3). Although their reproductive structure remains unknown, the colony sizes of *S. macretes* (Wilson, 1959) and *S. palamala* (Mezger and Pfeiffer, 2010) are also small, with 40 and 6 workers, respectively. In contrast, *S. menadensis* and *S. bicolor* reproduce through both gamergates (mated and egg-laying workers) and queens (Gobin et al. 1998a; Tanigawa et al. 2002; Ito et al. 2021). The average colony size of the former species is ca. 200 workers, with a maximum of 1000 (Gobin et al. 1998a; Ito et al. 2021). Although detailed information has not been published for *S. bicolor,* a maximum colony size of 450 workers was reported (Gobin et. al. 2006). Except for these two species reproducing by both queens and gamergates, monogynous reproduction by a single dealate queen and small colony size appear to be common characteristics among the Oriental Ectatomminae.

Removal of the larval meconium from the cocoon tip has been observed in *H. cribrata*, where the cocoon tip is invariably cut (Ito & Gobin 2008). Although this behavior is sporadically known in some species belonging to the subfamilies Amblyoponinae, Ponerinae, Ectatomminae, and Formicinae (Ito & Billen 1998; Gotoh et al. 2023), it was not observed in the three forms of *S. binghamii*. Beside *H. cribrata*, such meconium removal has not been detected in any of the ten Oriental *Stictoponera* species studied to date: the three forms of *S. binghamii*, S. *bicolor, S. coxalis, S. gastrodeia* (Lattke, 2004)*, S. laevior, S. menadensis, S. paso, S. posteropsis* and two unidentified species (Ito, pers. obs.).

The number of ovarioles of the three *S. binghamii* forms examined in this paper is typical for Oriental *Stictoponera*. In at least five other *Stictoponera* species (*S. coxalis, S. laevior, S. paso,* and two unidentified species), queens possess four (2-2) ovarioles, whereas workers have 2 (1-1) ovarioles, as observed in "MA" (Table 4) . Thus, dimorphism in ovariole numbers between queens and workers is a common trait in this genus. In this respect, "TH" and "VN" — where both castes possess four ovarioles (2-2) — are exceptional within the genus. In aculeate Hymenoptera, six (3-3) and eight (4-4) are the basic numbers of ovarioles (Iwata 1955), and several ponerine ant species retain these numbers in both queens and workers (Ito & Ohkawara 1994; Peeters & Ito 2015). Within the subfamily Ectatomminae, excluding *Stictoponera,* ovariole numbers in female castes has been documented in only a few species of *Ectatomma, Holcoponera,* and *Rhytidoponera*. For instance, only two ovarioles (1-1) were found in both queens and workers of *H. cribrata* (Ito & Gobin 2008). In contrast, queens possess 12 to 20 ovarioles, whereas workers have two or four in *Ectatomma tuberculatum* (Olivier, 1792), *E. vizottoi* Almeida Filho, 1987 and *Rhytidoponera purpurea* (Emery, 1887) (Peeters 1987; Hora et al. 2001; Vieira et al. 2012). Consequently, low ovariole numbers in queens appears to be a remarkable characteristic shared among Oriental Ectatomminae species.

Queen behavior in the three forms of *S. binghamii* is similar to that of *H. cribrata,* with larval hemolymph serving as the primary nutritional source for queens. In "TH", the frequency of LHF was lower in colonies with fewer larvae, suggesting that queens may modulate their feeding behavior according to colony condition. Such a shift in feeding mode has also been reported in *Stigmatomma silvestrii* Wheeler, 1928, where queens in founding colonies rarely exhibit LHF (Masuko 1986). Although queens of the three forms studied here can feed on worker-laid trophic eggs, this does not appear to be a major nutritional source due to the extremely low frequency of worker oviposition. Furthermore, the trophic eggs in these three forms do not seem to be highly specialized, as evidenced by the prolonged time queens required to consume them. Although recorded only a few times for each form, queens spent approximately 4 to 16 min. consuming a single trophic egg. Comparable data have been reported in the myrmicine ant *Aphaenogaster rugulosa* Watanabe & Yamane, 1999 and the ponerine ant *Odontomachus simillimus* Smith, 1858, where queens spent 5 min. 30 sec. and 7 min. 10 sec. eating one trophic egg, respectively (Aupanun et al. 2022a, b). In contrast, Hölldobler and Wilson (1983) reported that *Oecophylla longinoda* (Latreille, 1802) queens consumed five trophic eggs within 20 min. Similarly, in *Technomyrmex brunneus* Forel, 1895 where both workers and queens lay highly specialized trophic eggs, queens spent only a few seconds eating a single trophic egg (Yamauchi et al. 1991). Compared to *O. longinoda* and *T. brunneus,* the trophic eggs laid by workers in the three forms of *S. binghamii* appear to be less specialized for efficient consumption, despite being markedly smaller than reproductive eggs.

In addition to the two *Stictoponera* species (*S. bicolor, S. menadensis)* previously documented and *H. cribrata*, we here report larval hemolymph feeding (LHF) in three *S. binghamii* forms. Furthermore, *S. coxalis* has also been observed to engage in LHF (Ito, personal observation in 2002). These findings suggest that LHF is widespread within the genus *Stictoponera*. As discussed by Ito and Gobin (2008) for *H. cribrata*, the biological characteristics of *Stictoponera* and *Holcoponera* contrast sharply with those of other LHF-performing species studied to date. Masuko (1986) reported the occurrence of LHF across three subfamilies, Amblyoponinae, Leptanilline and Proceratiinae, and discussed that LHF serves as a nutritive adaptation in ant species characterized by specialized predation, an absence of trophic eggs and a lack of stomodeal trophallaxis. Although *Stictoponera* species studied by us lack stomodeal trophallaxis, they are generalist predators and their workers retain the capacity to lay trophic eggs. The behavioral characteristics of LHF in *Stictoponera* also differ from those in the other three subfamilies: as noted above, queens of all studied *Stictoponera* species did not restrict their biting to specific sites on the larval body. These biological and behavioral differences indicate that LHF in *Stictoponera* may not function as a strictly nutritional adaptation, unlike in previously reported subfamilies. The adaptive significance of this behavior in *Stictoponera* remains an open question for future investigation.

As observed in *H. cribrata* and *S. menadensis* (Gobin et al. 1998b; Ito & Gobin 2008), "TH" workers laid reproductive eggs under orphaned conditions; however, the fate of the eggs differed markedly from that in the former two species. In *H. cribrata*, eggs in the orphaned colony failed to hatch for up to three months. Similarly, in *S. menadensis,* eggs laid by virgin workers rarely hatched. The underlying reasons for the low hatching success of worker-laid reproductive eggs under orphaned conditions in these two species remain unknown. In contrast, viable males were readily reared in the orphaned colonies of "TH". Recently, the diversity of worker egg-laying ability and its underlying mechanisms have been documented in ants (Khila & Abouheif 2008). Comparative studies of worker egg-laying activity and related phenomena in *Stictoponera* will provide deeper insight into the evolution of worker reproduction.

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