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Colony structure and life history of *Lioponera daikoku* (Formicidae: Dorylinae)

Naoto Idogawa* and Shigeto Dobata

Laboratory of Insect Ecology, Graduate School of Agriculture,
Kyoto University, Kitashirakawa-oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan.

*Corresponding author: idogawa.naoto.na@alumni.tsukuba.ac.jp

ABSTRACT. We report the colony structure and life history of the basal doryline ant *Lioponera daikoku* in Kyoto Prefecture, Japan. The following characteristics were observed in the field: (1) nests were always in the cavities of dead bamboo stems on the forest floor; (2) the colonies were small, averaging 10 workers with a single dealate queen; (3) each queen had four ovarioles (2 + 2), while workers had two (1 + 1); (4) alate sexuals with normal wings were produced in August, and participated in nuptial flights the next May; (5) brood production showed no indication of synchronization, and immatures at different stages coexisted in the same nests; and (6) the larvae and pupae of *Monomorium* ants were stored in the nests. Although many ant species nested in the bamboo stems at the study site, we suspect that *L. daikoku* is a specialist predator of *Monomorium* ants. We also describe the male of this species.

Keywords: *Cerapachys*, *Ooceraea*, army ants, raider ants, bamboo-dwelling ants

INTRODUCTION

The subfamily Dorylinae Leach, 1815 is a group of monophyletic predatory ants distributed mainly in tropical and subtropical regions (Brady *et al*. 2014, antmaps.org 2018). The subfamily encompasses the so-called army ants and raider ants. Some army ant genera, including *Aenictus*, *Eciton*, and *Dorylus*, possess a peculiar set of traits, often known collectively as army ant syndrome, including a nomadic life history, extreme queen–worker dimorphism, and specialized mass predation (Schneirla 1971; Gotwald 1995). Their social organizations have been studied extensively as a typical example of a superorganism (Camazine *et al*. 2001). Recently, the draft genome sequence of the clonal raider ant *Ooceraea biroi* Forel, 1907 (previously *Cerapachys biroi* in the subfamily Cerapachyinae) was determined (Oxley *et al*. 2014), making this subfamily an emerging model system of integrative biology that covers studies ranging from molecular mechanisms to social organization (Kronauer 2009).

For a deeper understanding of the diversity of this subfamily, comparative studies are essential: detailed information on the species' biology and their phylogenetic relationships should yield insights into the adaptive significance of their peculiar life history and the evolutionary history of their diversification. A recent taxonomic revision (Borowiec 2016) and large-scale molecular phylogenetic studies (Brady *et al*. 2014; Borowiec 2017) have made this possible.

The genus *Lioponera* was originally described by Mayr (1879), but was later downgraded to a subgenus in the genus *Cerapachys* (Brown 1975). Recently, (Borowiec 2016) revived its taxonomic status as a genus in the subfamily Dorylinae based on molecular phylogeny (Brady *et al*. 2014). *Lioponera* is one of the phylogenetically basal groups in the Dorylinae (Borowiec 2017), and all known species are specialist predators of ants (Borowiec 2016). This group is the most species-rich outside of true army ants (Borowiec 2016), which are distributed across the Old World. Here, we report the basic life history information of *L. daikoku* Terayama, 1996, which is one of the northernmost distributed of the Dorylinae species (Terayama 1996; antmaps.org 2018). We report on colony composition, colony size, nesting sites, seasonal production of sexuals, and prey items. We also provide the first description of the male of this species.

MATERIALS AND METHODS

The study site was a thicket consisting mostly of deciduous broad-leaved trees located in the northern suburbs of Kyoto, Japan (35°03'33" N, 135°47'01" E, alt. 90 m). We collected *L. daikoku* and other ant species nesting in the cavities of dead bamboo stems during field studies conducted between 5 May and 27 November 2017. The numbers of each caste (dealate and alate queens, workers, and males) in the nests were counted in the laboratory immediately after sampling. Other species collected were identified using keys from Terayama *et al*. (2014) to clarify the myrmecofauna of the study site, because several studies of *Lioponera* ants suggest that species in this genus are specialist predators of other ants (Wilson 1958; Hölldobler 1982). Between 8 August and 27 November, the diameters of bamboo nest stems were measured using digital Vernier calipers (accuracy 0.1 mm, DT-150; Niigata Seiki) to investigate nest site preference for all ant species collected.

We photographed each adult under a digital microscope (VHX-900; Keyence). As indicators of body size, the widths of the head, thorax, and abdomen were measured using ImageJ software (Open Source: http://imagej.nih.gov/ij/). Some queens and workers were dissected under a binocular microscope (SZ40; OLYMPUS) to determine the number of ovarioles. All statistical tests were conducted using R software (ver. 3.3.1; R Development Core Team 2013). Voucher specimens were deposited in the Laboratory of Insect Ecology at Kyoto University and the Ehime University Museum.

RESULTS

Colony composition: Twenty-three colonies of *L. daikoku* were collected between 5 May and 30 September (Table 1). The mean colony size was 12.74 ± 12.60 workers (mean ± SD, n = 23), ranging from 1 (a founding queen) to 44. Of the 23 colonies, 19 (82.6%) had a single queen (monogynous), 3 (13.0%) had multiple queens (polygynous), and 1 (4.3%) had no queen (Table 1). Immatures at different stages coexisted in the colonies. Alates of both sexes were first observed in the two colonies collected on 16 May, and sexuals were continuously collected until 30 September when the last *L. daikoku* colonies were collected. The largest number of sexuals (48) was found in colony 6 (Table 1). The population size of colonies producing sexuals ranged from 5 to 44 workers. No relationship was found between colony size and the number of sexuals produced (Poisson regression, likelihood ratio test, $\chi^2 = 0.279$, df = 1, p = 0.598, n = 9; Fig. 1). Most of these colonies produced a large number of sexuals relative to their colony size (Fig. 1). There were two colonies that had a single gyne (10 & 14) and without these two colonies, a significantly positive relationship was detected between colony size and the number of sexuals produced (Poisson regression, likelihood ratio test, $\chi^2 = 23.985$, df = 1, p < 0.001, n = 7). We could not determine whether these two colonies were irregular. Further collections are required to determine if these colonies are highly unusual or not. The proportion of males to the total number of sexuals ranged from 0 to 0.65, with a mean value of 0.30. Solitary queens (presumably at the founding stage as these colonies did not contain any brood) were found on 27 May, 3 June, and 2 July. These queens also nested in cavities in bamboo stems.

Caste dimorphism: Significant size dimorphism was observed between queens and workers in the following body regions: head width, 0.50 ± 0.02 mm for queens (mean ± SD, n = 43, range 0.45–0.56) and 0.48 ± 0.02 mm for workers (mean ± SD, n = 48, range 0.44–0.51; Welch's t-test, t = −5.38, df = 69.41, p = 0.001); thorax width, 0.45 ± 0.03 mm for queens (mean ± SD, n = 43, range 0.40–0.53), and 0.37 ± 0.02 mm for workers

Table 1. Composition of the *Lioponera daikoku* colonies and *Monomorium* brood found in the nests.

		L. daikoku							***Monomorium* spp.**	
Colony ID	**Date**	**Queen**	**Worker**	**Male**	**Gyne**	**Cocoon**	**Larva**	**Egg**	**Larva**	**Pupa**
1	May 5	1	2	-	-	-	-	-	-	-
2	May 11	1	13	-	-	-	-	-	-	-
3	May 11	1	1	-	-	-	-	-	-	-
4	May 16	1	15	-	-	-	-	-	-	-
5	May 16	1	34	30	16	-	-	-	60	-
6	May 16	1	20	16	32	-	1	1	202	-
7	May 20	1	29	-	-	-	30	4	70	-
8	May 27	1	-	-	-	-	-	-	-	-
9	May 27	1	-	-	-	-	-	-	20	-
10	May 27	1	44	-	1	-	29	-	150	-
11	June 3	1	-	-	-	-	-	-	-	-
12	July 2	1	-	-	-	-	-	-	10	1
13	July 2	3	14	-	-	-	6	7	102	40
14	July 2	2	24	-	1	14	36	29	42	-
15	July 2	1	20	-	-	3	27	13	112	34
16	July 25	5	-	-	-	33	39	35	105	5
17	July 25	1	3	-	-	10	4	6	59	14
18	Aug. 8	1	18	-	23	47	23	10	177	-
19	Aug. 19	-	5	2	3	4	-	-	1	-
20	Sep. 19	1	27	14	31	-	58	5	123	-
21	Sep. 30	1	9	14	17	-	14	-	53	-
22	Sep. 30	1	3	-	-	4	12	2	7	14
23	Sep. 30	1	12	20	15	-	47	4	108	4

(mean ± SD, n = 48, range 0.34–0.41; Welch's t-test, t = −15.77, df = 63.40, p = 0.001); and abdomen width, 0.57 ± 0.03 mm for queens (mean ± SD, n = 43, range 0.52–0.66) and 0.52 ± 0.02 for workers (mean ± SD, n = 48, range 0.46–0.56; Welch's t-test, t = −8.95, df = 68.36, p = 0.001). In addition, there was a marked queen-worker difference in the adult thorax structure (Fig. 2A & B): the queen's thorax had clear boundaries (i.e., sutures) between the pronotum, mesonotum, and metanotum (Fig. 3A & C), and normal wings were initially attached to the latter two segments. The worker's dorsal thoracic sclerites were fused completely (Fig. 3B & D). Female castes also differed in the number of ovarioles: queens (n = 43) had four (2 + 2), whereas all but one (n = 48) worker had two (1 + 1); one "worker", as determined by external morphology, had four ovarioles (2 + 2).

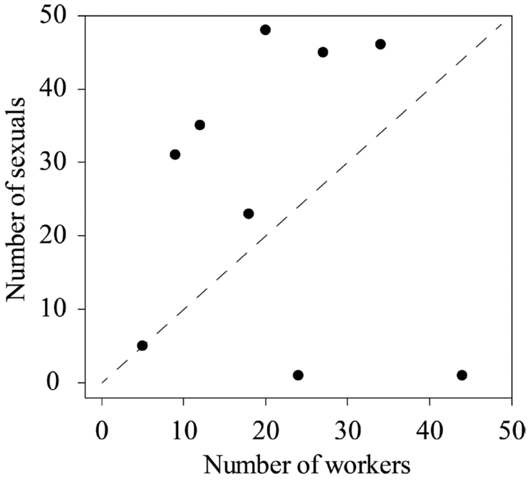

Fig. 1. Relationship between colony size and the number of sexuals. Most colonies had a larger number of sexuals compared to the number of workers (i.e., above the dashed line).

Nesting and food habits: Six ant species were found inside bamboo cavities at the study site: *Monomorium triviale* Wheeler, 1906 (32 nests), *Camponotus yamaokai* Terayama & Satoh, 1990 (22 nests), *Temnothorax* spp. (20 nests), *Crematogaster teranishii* Santschi, 1930 (9 nests), *Dolichoderus sibiricus* Emery, 1889 (3 nests) and *M. intrudens* Smith, 1874 (1 nest), together with six *L. daikoku* colonies. The first three species occupied the majority of nests (74/87 = 85%). The diameters of nest stems of *Ca. yamaokai* were significantly larger (Tukey–Kramer test, $p \leq 0.0046$) than for the other species (including *L. daikoku*), which showed no significant difference among them ($p \geq 0.252$; Fig. 4). Throughout the field study, larvae and pupae of unidentified species of *Monomorium* were found in the nests of *L. daikoku* (Table 1 and Fig. 5). These immatures likely belonged to *M. intrudens* and *M. triviale* because these *Monomorium* occur at the study site. Feeding experiments conducted in the laboratory revealed that the workers of *L. daikoku* stung the larvae of *M. intrudens* and *M. triviale* and carried them back to their nests (Fig. 6), while they did not do this when provided with larvae of *Ca. yamaokai* and *Temnothorax* spp.

Male morphology: Twelve specimens were examined to obtain the following measurements: Total body length, 2.94 ± 0.17 mm (range: 2.63–

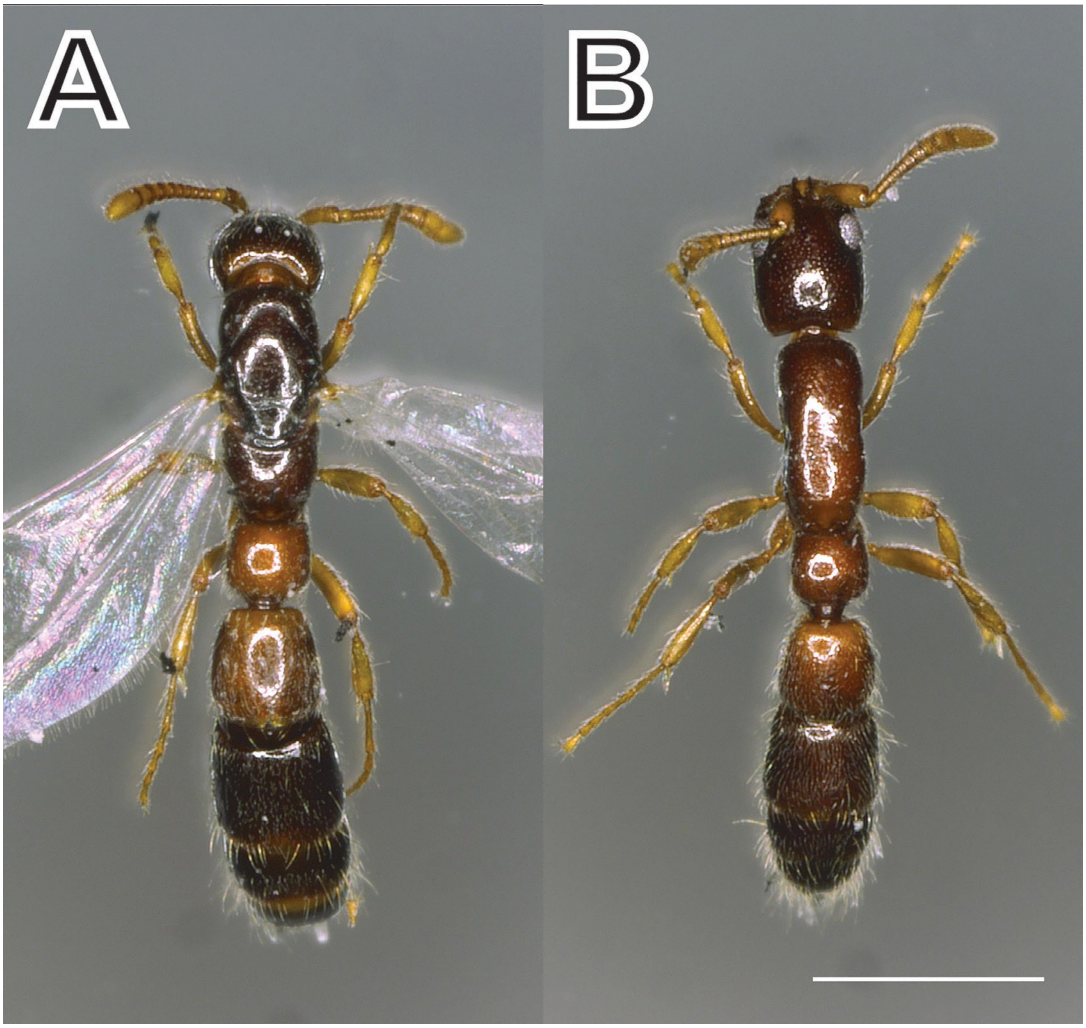

Fig. 2. Dorsal view of *L. daikoku* female castes: A gyne, B worker. Scale bar: 1.0 mm.

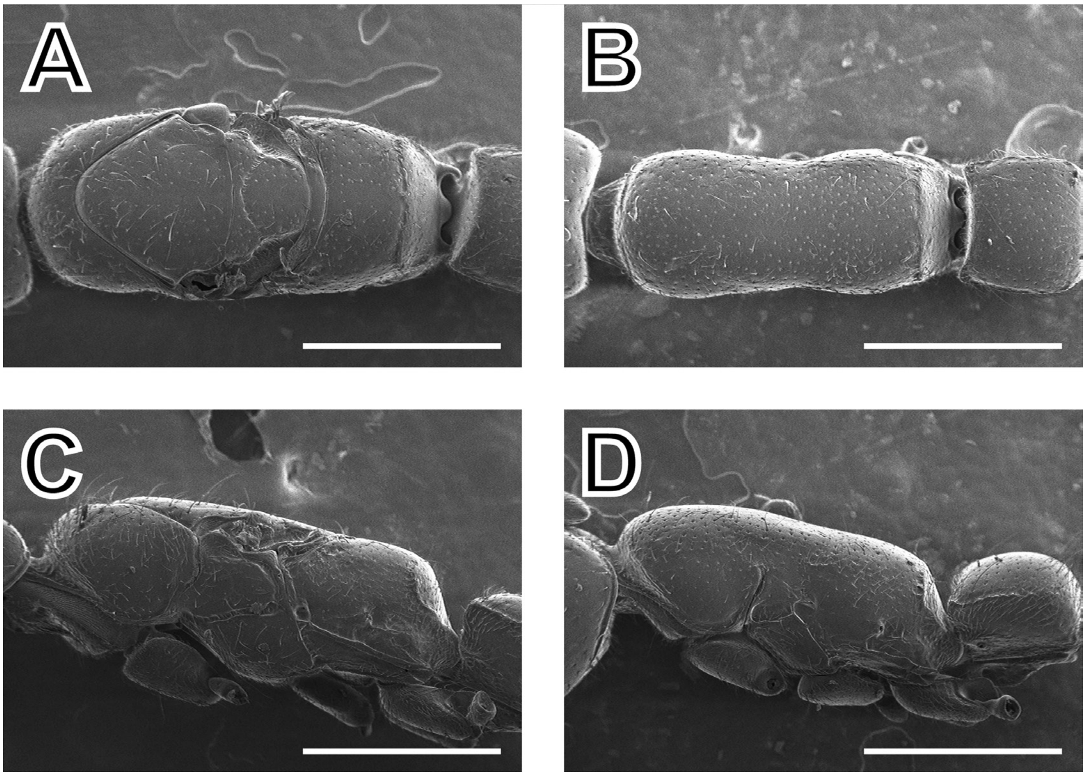

Fig. 3. Thorax structures of *L. daikoku* female castes: A dorsal view of gyne (wings removed to show thorax), B dorsal view of worker, C lateral view of gyne, D lateral view of worker. Scale bar: 0.5 mm.

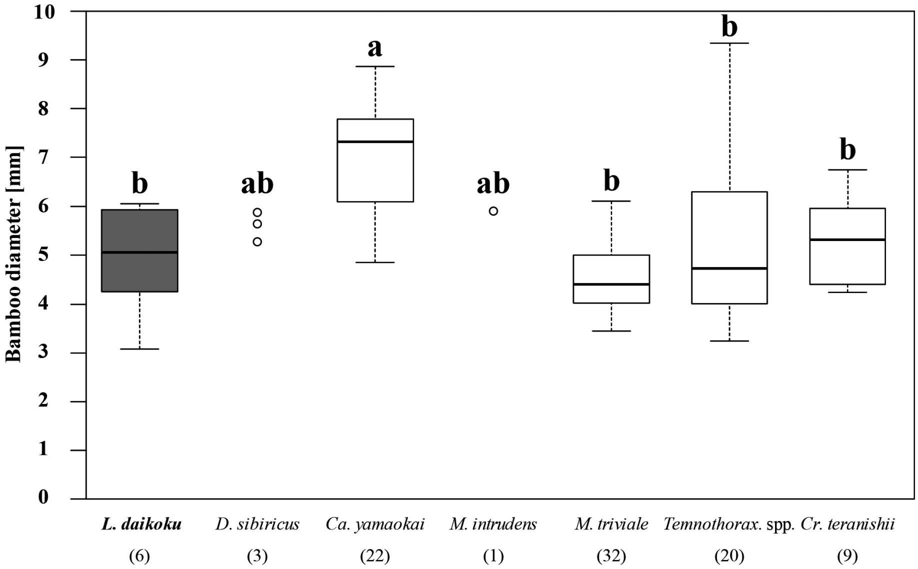

Fig. 4. Box plot illustrating the diameters of bamboo stems containing nests of the seven ant species. Each box shows upper and lower quartiles along with maximum and minimum (whiskers), and median (thick line). The numbers in parentheses under the species name indicate the total numbers of measured nest stem. Different letters indicate significant differences (Tukey–Kramer test, $p < 0.05$).

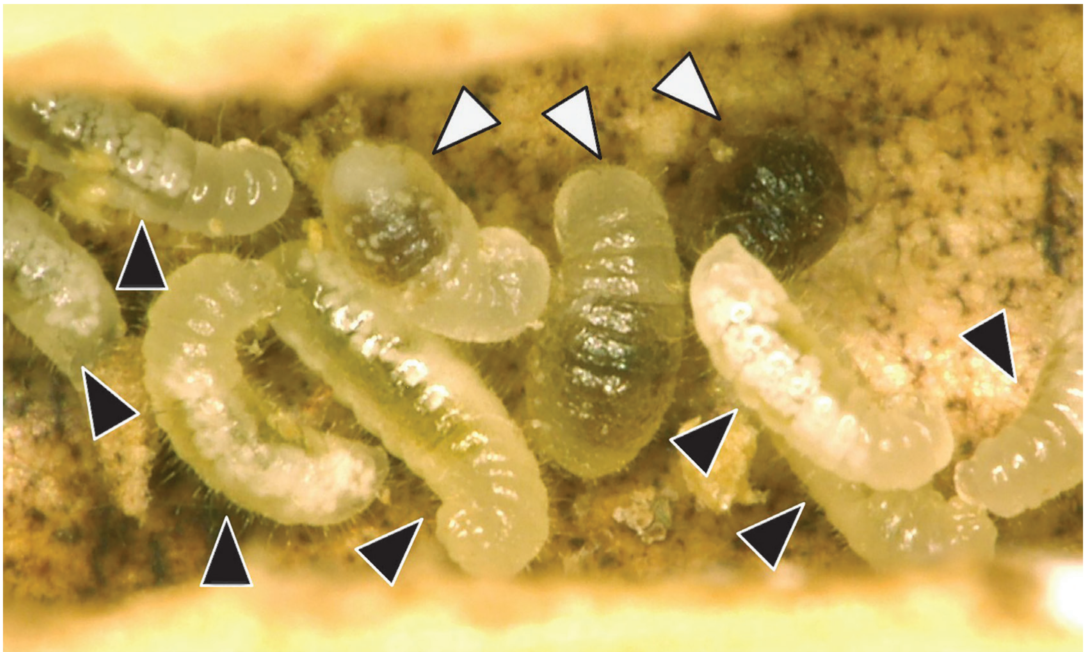

Fig. 5. Larvae (white arrowheads) of *Monomorium* found among a *L. daikoku* larvae (black arrowheads) inside a field collected nest. Because they disappeared in a few weeks, it was suspected that they were consumed by adults or larvae of *L. daikoku*.

Fig. 6. Foraging behavior of *L. daikoku* workers in the laboratory. They bit and stung the *Monomorium triviale* larvae that were fed experimentally.

3.26). Head (Fig. 7A): head width across eyes, 5.01 ± 0.01 mm (range: 0.49–0.53); head length, 0.56 ± 0.02mm (range: 0.54–0.58); eye width, 0.19 ± 0.01 mm (range: 0.16–0.22); eye length, 0.25 ± 0.02 mm (range: 0.21–0.29); and scape length, 0.20 ± 0.01 mm (range: 0.18–0.21). Mesosoma (alitrunk) and abdomen (Fig. 7B and C): mesosoma width in dorsal view, 0.55 ± 0.02 mm (range: 0.52–0.58); mesosoma length, 1.04 ± 0.05 mm (range: 0.94–1.10); mesosoma height, 0.47 ± 0.02 mm (range: 0.44–0.51); petiole width in dorsal view, 0.32 ± 0.02 mm (range: 0.28–0.35); and petiole length, 0.27 ± 0.03 mm (range: 0.23–0.33); petiole height, 0.28 ± 0.02 mm (range: 0.26–0.34). Right wings (Fig. 7D and E): forewing width, 0.67 ± 0.02 mm (range: 0.63–0.69); forewing length, 2.23 ± 0.05 mm (range: 2.13–2.35); hindwing width, 0.40 ± 0.01 mm (range: 0.38–0.42); and hindwing length, 1.75 ± 0.06 mm (range: 1.60–1.83).

The males of *Lioponera* are characterized by (1) antennae with 13 segments, (2) the absence of a costal vein on the forewing, and (3) the presence of a free stigmal vein on the forewing (Borowiec, 2016). All of these characteristics were shared with the males of *L. daikoku*. As in other *Lioponera* species, *L. daikoku* also had edentate mandibles, a single spur on the middle tibia, and a large brown pterostigma on the forewing. Most of the body was black, while the mandibles, antennae, and legs were yellowish brown. The veins on the wings were very pale. Although the male of *L. daikoku* resembles that of *L. longitarsus*, the type species of this genus, the former is characterized by a V-shaped groove (=notaulus) on the mesoscutum, and black body color.

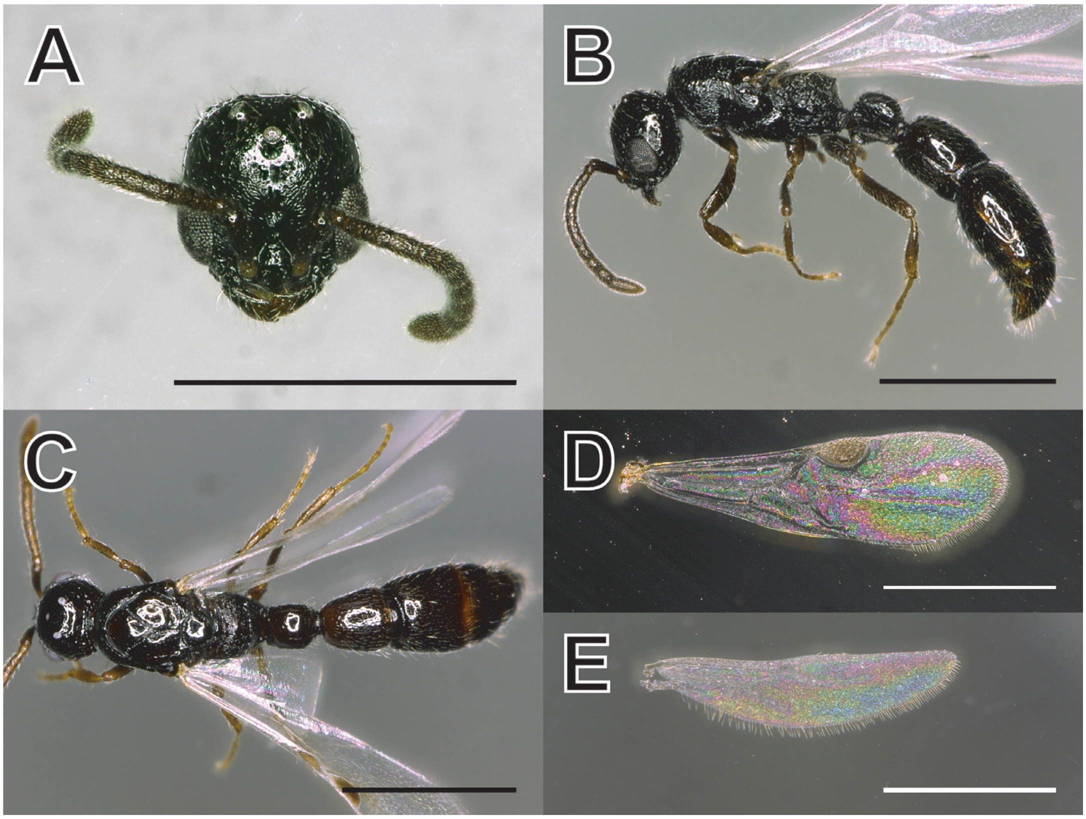

Fig. 7. External morphology of a male *L. daikoku*: A head in full-face view, B lateral view, C dorsal view, D right forewing, E right hindwing. Scale bar: 1.0 mm.

DISCUSSION

The colony size (number of workers) of Dorylinae colonies varies markedly among species, ranging from 9.1 in *Syscia humicola* (Masuko 2006) and 150–600 in *Ooceraea biroi* (Tsuji and Yamauchi 1995), both belonging to the former Cerapachyinae, to > 20 million in some *Dorylus* army ants (e.g., Vosseler 1905, Raignier & Boven 1955). The small colony size of *L. daikoku* of about 10 on average is the smallest among previous single-nest records of colony size of *Lioponera* species (ranging from a few dozen to several hundred, Clark 1924; Wilson 1958), and is of interest regarding the basal status of this species in the Dolyrinae. Monogyny was the dominant social structure of *L. daikoku*. However, three of 23 colonies had more than one dealate queen, whose reproductive status was unknown. One of them, collected on 25 July 2017 (Colony 16), had five dealate queens and many brood, despite the lack of workers (Table 1). Although these queens were not dissected, this hints at pleometrotic colony foundation. Clark (1924) and Hölldobler (1982) reported polygynous nests in other species of *Lioponera*, suggesting the existence of within- and between-species diversity of social structure. Synchronization of brood production was not observed in *L. daikoku*, indicating that this species is non-phasic (see also Ito *et al.* 2018). Gotwald (1988) postulated that the phasic lifestyle of army ants and clonal raider ants evolved secondarily from non-phasic ancestors. The updated phylogeny (Borowiec 2017) and studies of the life cycles of *Lioponera* (reviewed in Borowiec 2016) support this hypothesis. Our study suggests that the mating flight occurs in May, and involves alate sexuals that emerged the previous August. Solitary dealate queens were found in the field, suggesting that *L. daikoku* employs independent colony founding. As some *Lioponera* species have ergatoid queens and reproduce by colony fission (Borowiec 2016), and a comparative study of the mode of colony founding in this genus would be of interest.

Our field and laboratory observations strongly suggest that *L. daikoku* is a specialist predator of ant brood, especially of *Monomorium*. Although *Lioponera* are specialist ant hunters, the developmental stage of their prey varies among species. Hölldobler (1982) and Brown (1975) observed *Lioponera* workers preying on both adult and immature *Pheidole* sp. We observed in the laboratory that adult workers of *Monomorium* were stung and killed by *L. daikoku* but were not consumed, suggesting that *L. daikoku* preys exclusively on brood. At the study site, *Monomorium* is the only genus with an adult body size smaller than *L. daikoku* (data not shown), which might explain the preference for *Monomorium*. There were two *Monomorium* species at the study site, and we postulate that *M. triviale* is the dominant prey of *L. daikoku* due to its relative abundance and smaller colony size. We did not observe the foraging behavior of *L. daikoku* in the field. T. Satoh (pers. comm.) observed several *L. daikoku* workers in a queue on a tree branch, seemingly engaged in group foraging. Some studies of other *Lioponera* species reported group foraging (reviewed in Borowiec 2016). Interestingly, the number of fresh brood items in the nests of *L. daikoku* seemed to far exceed the capacity of the workers to carry them (Table 1). In Thailand, R .Mizuno (pers. comm.) observed that a colony of *Cerapachys* sp. moved into the abandoned nests of prey ant species, possibly to predate on the remaining brood. The foraging behaviors of *L. daikoku* and other basal doryline species deserve further study.

Finally, we found a low degree of dimorphism between queens and workers, and monomorphism among workers in *L. daikoku*, which is also the case in the basal Dorylinae groups. A female with the external morphology of a worker and the same number of ovarioles as a queen can be classified as an intercaste (Peeters 1991, Molet *et al*. 2012); this has been reported in *Lioponera clarki* Crawley, 1922 (Clark 1924) and might reflect the low degree of queen–worker dimorphism.

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