

Natural history notes of the rare enigmatic ant *Opamyrma hungvuong*: A first glimpse of their preying behavior on centipedes (Hymenoptera: Formicidae: Leptanillinae)

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ABSTRACT. *Opamyrma hungvuong* Yamane, Bui & Eguchi, 2008, represents the earliest branching extant leptanilline lineage, whose biology is largely unknown. Although preliminary and fragmentary, as we were only able to observe them for a short period of time between March 18–23, 2023, we report here the first observations on the biology of the species in captivity, focusing on their preying behavior on centipedes. We captured two colonies (possibly fragments, containing several or many alate and dealate queens and no immatures) and a solitary dealate queen of *O. hungvuong* in Pu Hoat Nature Reserve, Nghe An, Vietnam. We could not confirm whether the two colonies contained mated reproductive queens and whether the solitary dealate queen was mated. We observed their reactions by offering some centipedes and juliform millipedes. Individuals from the colonies ignored juvenile juliform millipedes but readily paralyzed a geophilomorph (*Mecistocephalus* sp.), a lithobiomorph (*Lithobius* sp.), and two juvenile scolopendromorph centipedes (*Scolopocryptops* sp.) by stinging. Not only workers but also alate and dealate queens in the colonies aggressively attacked the centipedes. However, they failed to hunt a linotaeniid geophilomorph centipede (*Strigamia* sp.); the ants were quickly killed probably due to the chemical defense of the centipede. The solitary dealate queen also readily paralyzed a juvenile *Scolopocryptops* by sophisticated hunting behavior. The workers and dealate queens of *O. hungvuong* showed eager (apparently hemolymph) licking behavior on the paralyzed *Mecistocephalus* centipede. Our observations indicate that *O. hungvuong* is well-adapted for preying on certain active centipedes, although their exact prey repertoire and degree of prey specialization remain uncertain. Some other notes on their habitat, ovariole number, venom apparatus, and unique metasomal habitus are provided. We also discuss the functional roles of some female caste morphologies of *O. hungvuong* in their centipede hunting.

Keywords Chilopoda, chemical defense, Leptanillomorpha, predator–prey interaction, subterranean ant, Vietnam

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INTRODUCTION

Opamyrra hungvuong Yamane, Bui & Eguchi, 2008 (Fig. 1A) is a unique ant species solely representing a monotypic genus, which can be found in the mountainous areas of northern-central Vietnam to southern China (Yamane et al. 2008; Chen et al. 2017; Yamada et al. 2020). Recent phylogenetic and phylogenomic studies have strongly supported the placement of *O. hungvuong* as the earliest branching lineage in the hypogaecic subfamily Leptanillinae (Ward & Fisher 2016; Borowiec et al. 2019; Griebenow 2020; Boudinot et al. 2022; Romiguier et al. 2022). Leptanillines and the monotypic neotropical subfamily Martialinae likely form a clade (Leptanillomorpha) sister to all other extant ants (Borowiec et al. 2019; Boudinot et al. 2022; Romiguier et al. 2022). Therefore, knowledge on *Opamyrra* is indispensable for understanding the evolution of leptanillines and even the entire Formicidae.

Our knowledge about *O. hungvuong* had been quite limited until recently. Two workers designated as type series were the only known specimens of the genus since the original description before the rediscovery of a worker and dealate queen by Chen et al. (2017). Yamada et al. (2020) collected two colonies of *O. hungvuong* containing not only workers but also alate queens, males, and larvae, and clarified details of the exoskeleton morphology of the species. However, the biology of *O. hungvuong* remains unknown, except for the subterranean habit. The known biological information on other leptanillines (Masuko 1990; Hsu et al. 2017; Yamamuro 2018; Ito & Yamane 2020; Ito et al. 2022) and the female caste morphologies of *O. hungvuong* suggest that the species may be a specialized predator of certain active soil arthropods such as geophilomorph centipedes (Yamada et al. 2020).

During our recent field survey in Pu Hoat Nature Reserve, Nghe An, Vietnam, on March 18–21, 2023, we found two colonies (possibly fragments, containing several or many alate and dealate queens and no immatures) and one solitary dealate queen of *O. hungvuong*. We captured them alive and observed their behavior in captivity, focusing on their reactions against some live centipedes. However, we were only able to observe them for a short period of time between March

18–23, 2023, and in the absence of immatures. We were also unable to conduct feeding experiments on different prey other than some centipedes and juliform millipedes. These limitations were partly due to our unpreparedness and failure to obtain a quarantine permit to import the live colonies of *O. hungvuong* to our laboratory in Japan; thus, we preserved all individuals in ethanol on the night of March 23. Although preliminary and fragmentary, we here present the first glimpse into the centipede-preying behavior of *O. hungvuong*. Some other notes on their habitat, ovariole number, venom apparatus, and unique metasomal habitus are also provided.

MATERIALS AND METHODS

Terminology

Ant caste terminology has been controversial and inconsistent among researchers. In this paper, the caste concepts and terms are only used in a strict morphological sense (following Peeters & Crozier 1988; Peeters 2019). The term “queen” merely refers to female individuals who are queens (or gynes) in the sense of morphological caste, regardless of the reproductive status of the individuals. The term “ergatoid queen” refers to permanently wingless queens that are morphologically distinct from conspecific workers (Peeters 2012, 2019).

Ants

The two colonies (colony codes: EG20230318-783 and AKY21iii23-312) and the solitary dealate queen (individual code: AKY21iii23-311) of *O. hungvuong* were collected alive by excavating soil in an evergreen forest (Fig. 1B, C) in Pu Hoat Nature Reserve, Nghe An, Vietnam (19.7651–19.7661°N, 104.7930–104.7939°E, 913–955 m alt.). The colony EG20230318-783 was collected on March 18, 2023. The other colony and the solitary dealate queen were collected on March 21, 2023.

The present collection of *O. hungvuong* from Pu Hoat Nature Reserve represents the fifth locality record for the species (Fig. 1D). The external morphology of the newly collected specimens was consistent with previous descriptions of the species (Yamane et al. 2008; Chen et al. 2017; Yamada et al. 2020). Some voucher specimens of the newly collected colony series are or will

be deposited in the following institutions: IEBR, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam; MCZC, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHAH, the Museum of Nature and Human Activities, Hyogo, Japan.

Morphometry

To examine the body sizes and unique characteristics of body proportions of *O. hungvuong* workers and queens, the following morphometric measurements were taken: Head Width (HW), maximum width of cranium in full-face view, excluding compound eyes; Pronotal Width (PW), maximum width of pronotum in dorsal view; Weber's Length of Mesosoma (WL), maximum diagonal distance of mesosoma in lateral view, measured from the angle at which the pronotum meets the cervix to posteroventralmost point of mesosoma; Metasomal Length (MtL), maximum summed metasomal length in lateral view excluding sting apparatus (Fig. 2A); Abdominal Segment IV Width (A4W), maximum width of abdominal segment IV in dorsal view (Fig. 2B); Total Body Length (TL), sum of anteroposterior length of cranium in lateral view, WL, and MtL.

The female castes of *O. hungvuong* appear to have an elongated and laterally flattened metasoma, which may be relevant to their preying behavior. To demonstrate the unique metasomal habitus of *O. hungvuong*, the relative length and lateral flatness of metasoma were compared among *O. hungvuong* and several other leptanillines using morphometric ratios of MtL to WL and A4W respectively. MtL/WL and MtL/A4W ratios were calculated for 15 workers and 10 queens of *O. hungvuong*, respectively. The ratios were also calculated for the following leptanilline species based on images of workers and dealate queens available from AntWeb (<https://www.antweb.org/>) or from the literature: *Anomalomyrma boltoni* Borowiec, Schulz, Alpert & Banas, 2011 (CASENT0217032, worker); *Anomalomyrma helenae* Borowiec, Schulz, Alpert & Banas, 2011 (CASENT0220221, worker); *Anomalomyrma taylori* Bolton, 1990 (CASENT0101976, dealate queen), *Protanilla beijingensis* Man, Ran, Chen & Xu, 2017 (CASENT0842639, worker); *Protanilla*

bicolor Xu 2002 (CASENT0235341, worker); *Protanilla flamma* Baidya & Bagchi, 2020 (CESM-198516, worker); *Protanilla izanagi* Terayama, 2013 (CASENT0842850, worker); *Protanilla jongi* Hsu, Hsu, Hsiao & Lin, 2017 (CASENT0842693, worker); and a dealate queen based on images from Hsu et al. 2017); *Protanilla lini* Terayama, 2009 (CASENT0007002, worker; and a dealate queen based on images from Hsu et al. 2017); *Protanilla rafflesi* Taylor, 1990 (CASENT0102375, worker); *Protanilla wardi* Bharti & Akbar, 2015 (CASENT0221924, worker); *Leptanilla escheri* (Kutter, 1948) (ANTWEB1008003, worker); *Leptanilla japonica* Baroni Urbani, 1977 (CASENT0902775, worker); *Leptanilla kubotai* Baroni Urbani, 1977 (CASENT0902776, worker); *Leptanilla lamellata* Bharti & Kumar, 2012 (ANTWEB1008004, worker); *Leptanilla oceanica* Baroni Urbani, 1977 (CASENT0911452, worker); *Yavnella laventa* Griebenow, Moradmand & Isaia, 2022 (CASENT0842746, worker). In addition, a worker of an undescribed species, *Leptanilla* sp. eg-1 from Sa Pa Area (Lao Cai) of Hoang Lien National Park, Vietnam, was also measured. Ergatoid queens of *Leptanilla* were not examined because there are no available images of them in AntWeb, and also because they are unlikely ever to directly engage in foraging (Masuko 1990; Ito & Yamane 2020).

Captive observations

The two colonies were captured with soil in separate plastic bags and later transferred into simple plaster nests without soil (polystyrene box of 63 mm × 50 mm × 26 mm, with a plaster bottom layer to maintain humidity, without subchambers). The solitary dealate queen was kept in a 5.0 mL Eppendorf tube with wet tissues on the bottom. Feeding experiments and behavioral observations were conducted in the Hanh Dich field station of Pu Hoat Nature Reserve between March 18–22, 2023, and in a laboratory of the Department of Soil Ecology, IBER on March 23, 2023.

We first provided several live whitish juvenile juliform millipedes (about 3 mm length) to the colony EG20230318-783. These millipedes were found together with the colony from proximate soil. The millipedes were ignored by ants, and they remained intact after a whole day (March 18–19). Then, the colony was provided a

fresh cut piece of a scolopendrid centipede (about 30–40 mm length). Some workers instantly showed apparent interest, tightly grasped the centipede's leg with their mandibles, and tried to pull the cut piece, but they later left it alone. The cut piece was placed for a day (March 19–20). They occasionally showed similar pulling behavior, but feeding behavior was never observed at least when we were watching them.

Upon seeing their strong interest in the cut piece of centipede, we observed their response and behavior by offering various kinds of live centipedes between March 21–23. The centipedes used as prey were collected in the same forest as *O. hungvuong* and morphologically identified to the genus level. One *Mecistocephalus* Newport, 1843 (Geophilomorpha: Mecistocephalidae, about 40 mm length); one *Strigamia* Gray, 1843 (Geophilomorpha: Linotaeniidae, about 25 mm length); two juvenile *Scolopocryptops* Newport, 1844 (Scolopendromorpha: Scolopocryptopidae, about 10 mm length); and one *Lithobius* Leach, 1814 (Lithobiomorpha: Lithobiidae, about 10 mm length), were offered to the colonies (mostly to AKY21iii23-312, except for one of the juvenile *Scolopocryptops* which was offered to EG20230318-783). In addition, we provided one juvenile *Scolopocryptops* sp. (about 10 mm length) to the solitary dealate queen (AKY21iii23-311). Note that some observations on the colony AKY21iii23-312 (= experiments with the *Strigamia* and *Lithobius* centipedes, and the observation of post-hunting behavior against the *Mecistocephalus* centipede mentioned in the Results section) were made after all alate queens were removed and preserved in ethanol.

Some behaviors were video recorded using a Nikon DS-Fi3 microscope digital camera attached to a Nikon SMZ800N stereo microscope. The videos are provided as electronic supplementary material (Videos S1–S3; the same videos are also deposited at <https://doi.org/10.5281/zenodo.8285361>, with unedited source videos). Finally, some queens and workers were dissected to observe reproductive organs and venom apparatus.

RESULTS

Habitat, colony composition, and dissection

The two *O. hungvuong* colonies EG20230318-783 and AKY21iii23-312 were collected by digging soil near the roots of trees on a steep mountain slope covered by a subtropical evergreen forest with rich undergrowth (Fig. 1A–C). Both colonies were found on the same slope (913–955 m alt.) but the collection spots were several tens of meters distant from each other. No evident nest chambers were observed in both colonies; they just spilled out as we dug the soil. During the collection of these colonies, we noticed the emanation of distinctive chemical odors. Their behavior to construct a narrow tunnel in soil along the plastic wall was observed when kept in plastic bags. In addition, the solitary dealate queen (AKY21iii23-311) was found in the soil approximately seven meters away from where the colony AKY21iii23-312 was found. Careful excavation of the soil around the spot where the solitary dealate queen was found did not reveal additional individuals.

Colony EG20230318-783 contained a total of one dealate queen, six alate queens, and 23 workers. Colony AKY21iii23-312 contained 69 dealate and alate queens (at least 44 were alates when counted after ethanol preservation) and 27 workers. The wings of alate queens were relatively easily detached by our disturbance during soil excavation and sifting for collection. Therefore, it was unclear how many were originally dealate before being influenced by our disturbance. Many detached wings were observed during the collection of the second colony and in the sample tube after ethanol preservation. No immatures were collected from either colony. Physogastry was never observed in any of the individuals collected. We may have missed some colony members which might have escaped to deeper soil, and could not confirm the existence of reproductive queens in the two colonies, as explained below.

Two workers and two alate queens from colony EG20230318-783, and seven dealate queens from colony AKY21iii23-312 were dissected and examined for reproductive organs and venom apparatus. The solitary dealate queen (AKY21iii23-311) was undissected, and whether she was mated or not remained unknown. Queens had six (three per ovary; $N = 4$) or seven (three

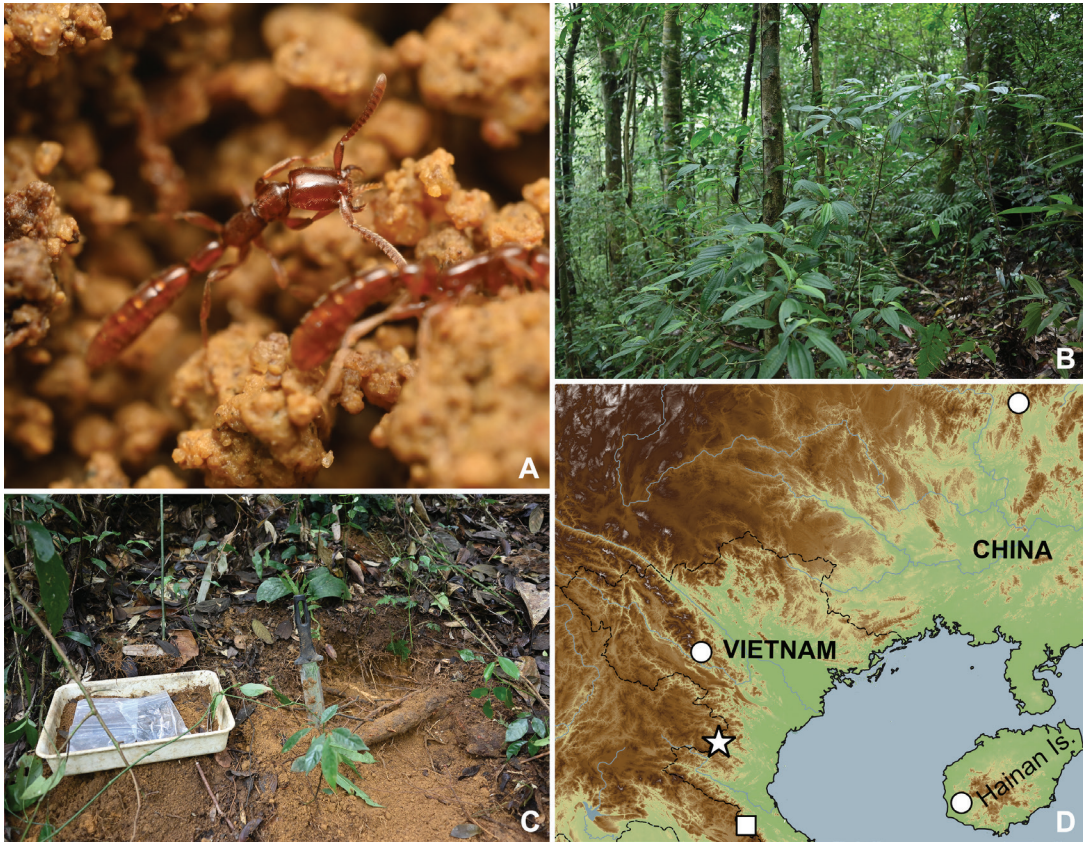


Fig. 1. Habitat and the collecting site of *Opamyra hungvuong*. (A) workers of *O. hungvuong* photographed on excavated soil, colony EG20230318-783; (B) evergreen forest on the mountain slope in Pu Hoat Nature Reserve (Nghe An, Vietnam) where the two colonies and the solitary dealate queen were collected; (C) excavated spot where the colony AKY21iii23-312 was collected; (D) known locality records of *O. hungvuong* (the present new record is indicated by a star; the type locality is indicated by a square).

and four; $N = 1$) ovarioles. None of the dissected queens had the spermatheca filled with sperm, and neither had developing oocytes. The queen ovarioles of the same ovary were tightly attached to each other (Fig. S1A, B). The tight attachment was also present between the paired ovaries apically (except for an alate queen whose ovaries were poorly developed, Fig. S1C). Ovaries were not recognized in the dissected workers; they may lack functional ovaries but the possibility that ovaries were artificially broken and overlooked during dissection could not be fully ruled out. The venom gland was similar in appearance between the castes and had an elongated gourd-form venom reservoir with a central constriction and a pair of long free filaments (Fig. S1A, C, D). The Dufour's gland of the queen was subrounded, opaque whitish, and conspicuously enlarged compared with that of the workers (Fig. S1C, D).

Morphometry

Body size differed distinctly between the two female castes of *O. hungvuong*, with slight within-caste variation. Queen measurements were as follows: HW, 0.69 ± 0.01 mm (mean \pm SD; 0.66–0.71 mm); PW, 0.58 ± 0.01 (0.56–0.60) mm; WL, 1.48 ± 0.02 (1.42–1.51) mm; MtL, 2.97 ± 0.06 (2.86–3.04) mm; TL, 5.33 ± 0.11 (5.14–5.44) mm; A4W, 0.55 ± 0.01 (0.53–0.56) mm ($N = 19$ for HW and PW; $N = 10$ for the others). Worker measurements were as follows: HW, 0.53 ± 0.01 (0.49–0.55) mm; PW, 0.40 ± 0.01 (0.36–0.42) mm; WL, 1.08 ± 0.03 (0.99–1.11) mm; MtL, 2.02 ± 0.07 (1.87–2.14) mm; TL, 3.80 ± 0.11 (3.50–3.96) mm; A4W, 0.38 ± 0.01 (0.34–0.39) mm ($N = 20$ for HW and PW; $N = 15$ for the others).

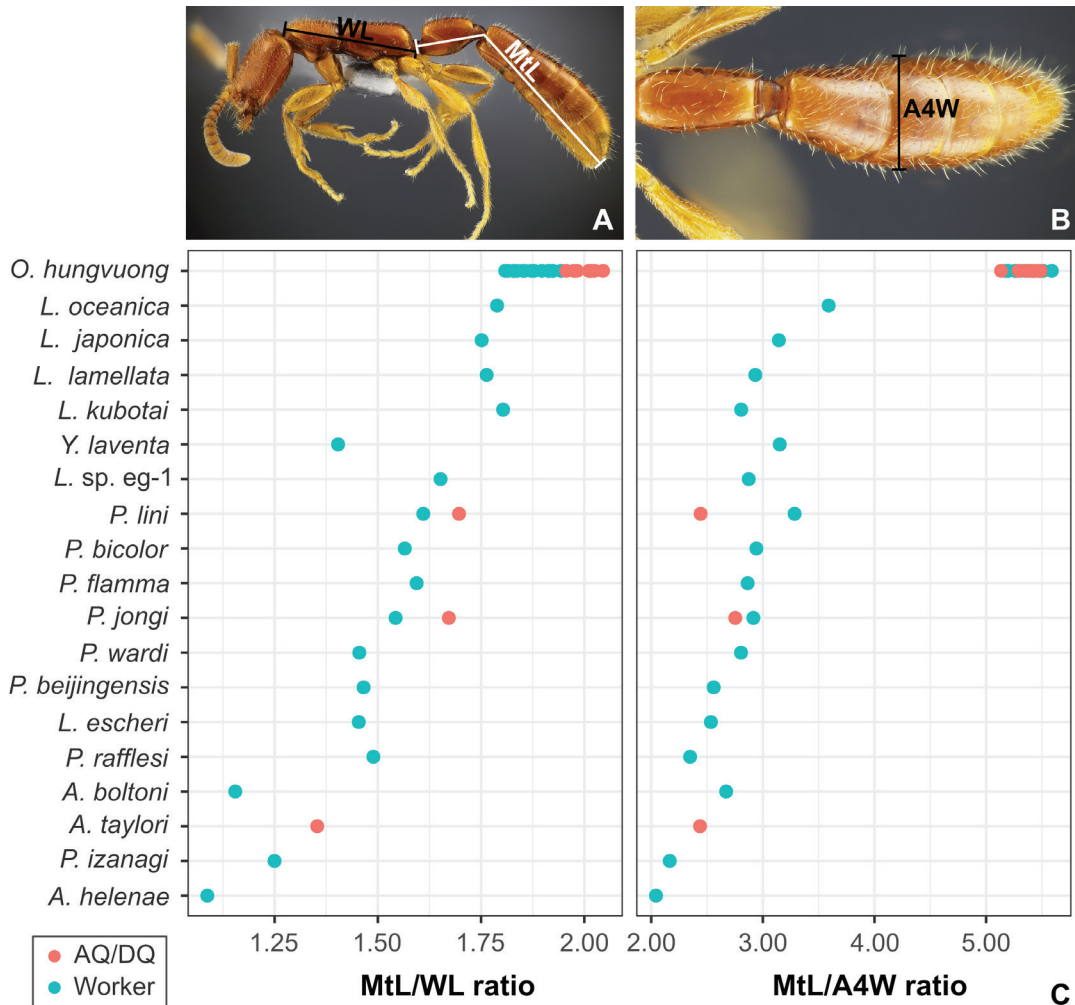


Fig. 2. Morphometric comparison of relative metasomal length and lateral flatness in workers and alate/dealate queens of *Opomyrma hungvuong* and other leptanillines. (A, B) definitions of WL, MtL, and A4W measurements illustrated on the worker of *O. hungvuong* (images are from those used in Yamada et al. 2020); (C) comparison of MtL/WL and MtL/A4W ratios. Abbreviation: AQ/DQ = alate/dealate queen.

Alate/dealate queens of *O. hungvuong* were slightly larger in MtL relative to WL than conspecific workers: MtL/WL ratio was 2.00 ± 0.03 (1.96–2.05) in queens and 1.87 ± 0.04 (1.81–1.94) in workers. MtL/A4W ratio was comparable between the female castes of *O. hungvuong*: 5.38 ± 0.11 (5.13–5.49) in queens and 5.36 ± 0.13 (5.17–5.59) in workers. Workers of *O. hungvuong* had the highest MtL/WL and MtL/A4W ratios among the compared leptanilline species, with 1.00–1.78 times higher MtL/WL and 1.44–2.74 times higher MtL/A4W values than those of the others (Fig. 2A–C). This highlights their unique

body proportion with strong metasomal elongation and lateral flatness. However, some *Leptanilla* species (*L. oceanica*, *L. japonica*, *L. lamellata*, and *L. kubotai*) were close or almost equal to *O. hungvuong* in the former ratio (Fig. 2C). Alate/dealate queens of *O. hungvuong* showed 1.15–1.51 times higher MtL/WL and 1.87–2.25 times higher MtL/A4W values than the dealate queens of *P. lini*, *P. jongi*, and *A. taylori*.



Fig. 3. Scenes of centipede hunting by *Opamyrra hungvuong*. (A, B) attacks against the *Mecistocephalus* geophilomorph centipede; in B, two workers are clinging to the antennae of the centipede by their mandibles and stinging or attempting to sting on the prey's head venter (see also the alate queen connecting to the prey only via sting); (C, D) attacks against the juvenile *Scolopocryptops* scolopendromorph centipede; in C, three workers are grasping the centipede's legs by mandibles and one worker stinging on the prey's body; in D, a worker is attempting to sting the centipede's head while clinging to the prey's antenna.

Captive observations

Centipede hunting by colonies: individuals from colony AKY21iii23-312 readily and successfully paralyzed all the centipedes by stinging within a few minutes of providing the live centipedes, except for the case of the *Strigamia* sp. (see below and Discussion). Individuals from colony EG20230318-783 readily hunted the juvenile *Scolopocryptops* centipede likewise. Not only workers but also alate and dealate queens in the colonies aggressively attacked the prey (Fig. 3A–

D, Video S1). They grasped the prey's appendages (legs or antennae) tightly using mandibles, thereby restraining the movement of active prey and clinging to it for stinging. Their sting remained sticking into the prey body for a while after successful sting penetration; ants that attached to the prey only via their sting were often observed. Ants also clung to the prey's heads by grasping the base of the antennae and stung the head venter (Fig. 3B, D; see 01:25 of Video S1). Their stinging actions were swift: it took only about a second from the start of the bending of the metasoma to



Fig. 4. Finishing scenes of solitary centipede hunting by the dealate queen of *Opamyrrma hungvuong* (prey: juvenile *Scolopocryptops*), in order of time sequence (A–C); the dealate queen grasped the centipede’s antennal base by mandibles (A) and then stung the head venter while continuously holding the prey’s antenna (B, C).

the sting reaching to the prey (e.g., see stinging action of the dealate queen at 00:26 of Video S1; although the stinging attempt appears to have failed). They sometimes swung the metasoma laterally (obliquely) for stinging by inclining and twisting their body while clinging to the prey’s appendages (Figs. 3D, 4B; Video S1).

When the *Strigamia* centipede was provided to colony AKY21iii23-312, the ants immediately began to chase and attack the centipede, as they did to the other centipedes. However, the ants died quickly while grasping or stinging the centipede (Video S2). The centipede appeared to produce sticky secretions. We removed the centipede from the plaster nest after about 4 min. The centipede was still active even after the battle, dragging ant corpses who had died while grasping or stinging on the centipede (see the end of Video S2). The centipede killed two dealate queens and eight workers.

Solitary centipede hunting by dealate queen: the solitary dealate queen (AKY21iii23-311) successfully paralyzed the juvenile *Scolopocryptops* centipede within a few minutes after their first encounter; the prey was approximately twice greater in body length (excluding appendages) than the queen. The queen started wrestling with the centipede immediately when they encountered and then stung the body of the prey. The posterior body of the centipede appeared to be partly paralyzed by the first stinging. The queen then turned to the front of the prey, grasped the base of an antenna, and stung the head venter multiple times (including apparently unsuccessful attempts) to finish the prey

off (Fig. 4A–C). After the stinging on the head, the prey became completely immobile. Afterward, the queen showed a behavior to move the prey, but she died one day later. Neither feeding on the prey nor egg-laying was observed.

Licking behavior on paralyzed *Mecistocephalus* geophilomorph centipede: after providing the *Mecistocephalus* geophilomorph centipede, the colony AKY21iii23-312 was kept together with the paralyzed prey for two days to observe their subsequent behavior against the prey (all alate queens in the colony were preserved in ethanol prior to this observation). The centipede was almost immobile right after being hunted, but later appeared to recover and frequently moved during the two days (but almost could not walk). Ants often pulled the prey’s antenna (see Video S3), but additional stinging was never observed. After one day, we observed that workers and dealate queens frequently licked the prey’s body, mostly on pleural membranes (Fig. 5A, B; Video S3). Dealate queens licking on the leg and around the mouthparts of the prey were also observed (Fig. 5C; Video S3). Conspicuous wound melanizations were observed on several areas of the prey’s pleural membranes (Fig. 5D, E), suggesting that the ants licking on pleural membranes were likely feeding on hemolymph oozing from the wounds, which might have resulted from stinging (whether they performed biting on prey’s body during and after hunting remained unknown). The same explanation may also apply to the individuals who licked around the mouthparts. The centipede’s second maxilla was broken and



Fig. 5. Licking behavior of *Opamyrra hungvuong* workers and dealate queens on the paralyzed *Mecistocephalus* geophilomorph centipede. (A) workers and dealate queens licking on the pleural membranes of the centipede (black arrows); (B) worker licking on the prey's pleural membrane in lateral view; (C) dealate queen licking the prey's leg; (D, E) wound melanizations on the prey's pleural membranes (indicated by red circles; E is a zoom-in view of the area indicated by the non-broken circle in D).

melanized. Although ants were observed stinging around the centipede mouthparts during hunting (Fig. 3B), no other conspicuous melanization was found around the centipede's mouthparts. It was uncertain whether the licked leg had any wounds. Some legs of the centipedes lacked the pretarsus when observed after ethanol preservation, but the licked leg appeared to have an intact pretarsus based on the recorded video (Video S3).

DISCUSSION

The available information on feeding biology and preying behavior of leptanillines has been limited to a few species belonging to the genera *Leptanilla* Emery, 1870, and *Protanilla* Taylor, 1990. *Leptanilla* are specialized predators of certain geophilomorph

centipedes (Masuko 1989, 1990, 2008; Ogata et al. 1995; Terayama & Kinomura 2015; Ito & Yamane 2020). Colonies of *Leptanilla* spp. are sometimes found containing a dead centipede being eaten by their larvae (Ogata et al. 1995; Eguchi et al. 2014). Predation on geophilomorphs has also been observed in captive colonies of *P. lini* and *P. jongi* (Hsu et al. 2017; Yamamuro 2018). Hsu et al. (2017) reported that colonies of the two species from Taiwan accepted only certain groups of centipedes and preferred geophilomorphs. Yamamuro (2018) reported that a colony of *P. lini* from Amami-Oshima Island, Japan, accepted geophilomorph, lithobiomorph, and scolopendromorph centipedes, and cockroaches as prey. Ito et al. (2022) reported that a captive colony of *Protanilla* sp. accepted only japygids (Hexapoda: Diplura) as prey.

The present study supports the hypothesis that *O. hungvuong*, likewise with some of the other leptanillines, is a specialized predator of certain centipedes. The *O. hungvuong* colonies ignored juvenile juliform millipedes (mentioned under Materials and Methods) but readily hunted a geophilomorph (*Mecistocephalus* sp.), a lithobiomorph (*Lithobius* sp.), and juvenile scolopendromorph centipedes (*Scolopocryptops* sp.). The solitary dealate queen also readily paralyzed a juvenile *Scolopocryptops* through sophisticated hunting behavior. However, the exact prey repertoire and degree of prey specialization of *O. hungvuong* remain uncertain, as we could not perform feeding experiments for different prey other than the centipedes and millipedes and observe the consumption of the prey (except for the adult licking behavior). Nevertheless, their effective hunting behavior and the successful paralyzation of active centipedes within a few minutes (except the *Strigamia* sp.) indicate that *O. hungvuong* is well adapted for preying on certain centipedes. Given the leptanilline phylogeny, centipede-preying may be the ancestral habit for the subfamily.

Although based on a single observation, the dealate queen of *O. hungvuong* was shown to be highly capable of hunting a small centipede alone. In Leptanillinae, besides *O. hungvuong*, alate queens are known in some *Protanilla* and *Anomalomyrma* Taylor, 1990 (Bolton 1990; Baroni Urbani & de Andrade 2006; Borowiec et al. 2011; Chen et al. 2017; Hsu et al. 2017; Man et al. 2017; Yamada et al. 2020). Based on their slender mesosomal morphology with large relative prothorax size (see Keller et al. 2014), it can be speculated that the alate queens of leptanilline species initiate a new colony by a non-claustral independent colony foundation, which requires solitary foraging by a foundress (non-claustral ICF: Cronin et al. 2013) and is most likely the ancestral strategy in ants. However, no observations of solitary foraging by dealate queens have so far been made in Leptanillinae. Therefore, the present study provides the first, albeit incomplete, behavioral evidence for non-claustral ICF in the subfamily. In *Leptanilla*, it is likely that all species have morphologically specialized permanently flightless ergatoid queens, and are thought to establish new colonies obligately through dependent colony

foundation (DCF: Cronin et al. 2013) i.e., colony fission (Masuko 1990; López et al. 1994; Ogata et al. 1995; Terayama & Kinomura 2015; Ito & Yamane 2020). Less specialized ergatoid queens are reported in an undescribed *Protanilla* species (Ito et al. 2022), suggesting ergatoid queens have evolved multiple times in leptanillines.

The strong aggressiveness of the alate and dealate queens against the prey observed in the *O. hungvuong* colonies and their relatively easy wing detachment by our disturbance are noteworthy. The latter phenomenon was already suggested by our previous collection of a colony containing alate queens (Yamada et al. 2020). These observations suggest the possibility that virgin queens of *O. hungvuong* in a colony may conditionally serve as, or become, non-reproductive helpers, and may participate in foraging in nature. Considering the larger body size, the participation of virgin queens can be potentially advantageous in foraging. In the present study, we could not confirm whether the two colonies contained mated reproductive queens and whether the solitary dealate queen was mated. Future detailed studies on the colony structure, the queen behavior and reproduction of *O. hungvuong* are critical to understanding the evolution of the specialized life histories and queen phenotypes within the subfamily.

It might be worth mentioning that the *O. hungvuong* colonies which contained alate queens (two in the present study and one in Yamada et al. 2020; the latter also contained two males) have so far been collected in March in northern-central and northern Vietnam. The period March–April roughly corresponds to the end of the dry season in the regions (Nguyen et al. 2000), possibly suggesting that the reproductive phenology of *O. hungvuong* may be associated with the transition to the rainy season.

Functional implications of *O. hungvuong* morphologies for centipede hunting

Our observations provide some insights into how the female caste morphologies of *O. hungvuong* may function to facilitate their effective hunting of centipedes (see Yamada et al. 2020 for the morphological descriptions). One of their morphological features of particular interest is the labral chaetae. Their labrum, which completely conceals the maxillolabial complex when the

mouthparts are fully closed, bears numerous stout traction chaetae (often called “peg-like setae”) on its proximofrontal surface. Labral traction chaetae are also found in some other ants, including *Protanilla*, *Anomalomyrma*, the apomyrmine genus *Apomyrma* Brown, Gotwald & Levieux, 1971, some amblyoponines, and some extinct stem-group ants, and have been thought to function as a structure to enhance the gripping of active prey (Brown 1960; Yoshimura & Fisher 2014; Barden & Grimaldi 2016; Cao et al. 2020; Richter et al. 2021, 2022).

We repeatedly observed workers and queens of *O. hungvuong* grasping an appendage (leg or antenna) of active centipedes by tightening it between their labrum and sublinear mandibles, thereby restraining prey movement and clinging to prey for stinging (Figs 3, 4; Video S1). This observation supports the possibility that the labral chaetae of *O. hungvuong* is likely an adaptation to facilitate their firm grasping of a prey’s appendage. Moreover, clinging to the prey’s antenna can facilitate their successful stinging on the head of the active centipede, which allows the injection of venom into or around the prey’s brain (head ganglia). Indeed, individuals performing antennal clinging appeared to aim to sting the head venter of centipedes around mouthparts, where some soft membranous parts are present at the borders of the mouthpart sclerites (Figs 3B, 4). Unlike *Protanilla* spp. (Hsu et al. 2017; Richter et al. 2021), the mandibular movement of *O. hungvuong* is not trap-jaw-like (see Video S1).

We repeatedly observed the sting of workers and queens of *O. hungvuong* sticking into the prey body for a while, and individuals connected to the prey only via sting during their hunting (e.g., the alate queen in Fig. 3B; see also Videos S1, S2). This sting sticking is probably because of their strongly developed apical barbs on the lancets of gonapophysis VIII. Yamada et al. (2020) described the distinct apical barbs on lancets and stylet (sting) of *O. hungvuong* workers and queens; in particular, their lancet barbs are conspicuously large. This feature likely facilitates their successful venom injection into active centipedes. Large lancet and stylet barbs are also reported in *Protanilla* and *Leptanilla* (Kugler 1992). Yamamuro (2018) observed a similar sting sticking into prey in *P. lini*.

Our morphometric comparison demonstrated that the female castes of *O. hungvuong* have a distinctly elongated and laterally flattened metasoma among the leptanillines (Fig. 2). The elongated metasoma of *O. hungvuong* likely facilitates successful stinging by increasing the reach of the sting, and may also enhance their stinging while simultaneously grasping the prey’s appendage. In the solitary hunting of the juvenile *Scolopocryptops* by the dealate queen, we observed that she finished off the centipede by stinging the prey’s head venter while continuously grasping the antenna. This stinging sequence and posture would be less easy if their metasoma were shorter. During their hunting of the Lithobiomorph centipede (*Lithobius* sp.), we also repeatedly observed their swift stinging actions while restraining the movement of the prey by grasping the legs: they suddenly and rapidly attempt to sting by directing their long metasoma anteriad while grasping and pulling the appendages of the prey (see Video S1). The lateral flatness of gastral segments in *O. hungvuong* is extreme compared with other leptanillines (Fig. 2C). We sometimes observed their lateral (oblique) swinging of the metasoma when performing stinging (Figs. 3D, 4B; Video S1). These morphological and behavioral features may be relevant to their relatively large body sizes (among leptanillines) and centipede hunting in a narrow subterranean spaces. Future comparative studies of their hunting behavior with those of the other leptanillines with similar body sizes (some *Protanilla*, and *Anomalomyrma*) may help in understanding the functional significance of the unique metasomal habitus of *O. hungvuong*.

Lack of adaptation against the chemical defense of *Strigamia* geophilomorph centipede

Geophilomorph centipedes of the genus *Strigamia* are reported to be cyanogenic at least in some North American species (Jones et al. 1976). We observed that the *Strigamia* sp. produced sticky secretions as reported in Jones et al. (1976) and immediately killed *O. hungvuong* attackers. The lethality implies that the Vietnamese *Strigamia* centipedes also likely produce hydrogen cyanide as a defensive chemical. The aggressive response by *O. hungvuong* against the *Strigamia* sp. (Video S2) and their failure of hunting indicate that the ants recognize the *Strigamia* centipede as a

potential prey but are not adapted to preying on such chemically defended species. The chemical defenses of geophilomorph centipedes are poorly known despite the presence of segmental clusters of defensive sternal glandular pores in a majority of geophilomorph species (Turcato et al. 1995; Edgecombe & Giribet 2007; Vujisić et al. 2013). Geophilomorpha is basally split into two major clades, Placodesmata and Adesmata (Edgecombe & Giribet 2007; Bonato et al. 2014). The former contains only Mecistocephalidae, which lacks the sternal glandular pores, whereas the latter contains all the other geophilomorph groups, which are characterized by the presence of sternal glandular pores (Edgecombe et al. 2010). Some species in the Adesmata genera including *Strigamia* are reported to be cyanogenic (Jones et al. 1976; Vujisić et al. 2013). Predator–prey interactions between centipede-preying ants (mostly leptanillines and amblyoponines) and chemically defended Adesmata centipedes are poorly understood. Masuko (1990) reported that the captive colonies of *L. japonica*, preyed mostly on the mecistocephalid centipede *Arrup holstii* (Pocock, 1895, formerly known as *Prolamnonyx holstii*), but they rejected a chopped body of a *Strigamia* centipede. In addition, Masuko (1993) reported that the amblyoponine ant *Stigmatomma silvestrii* Wheeler, 1928 (formerly *Amblyopone silvestrii*) mostly preys on mecistocephalids under natural conditions in field, but they always failed to hunt *Strigamia* centipedes (*Scolioplanes* Bergsøe & Meinert, 1866 is currently a junior synonym of *Strigamia*) under laboratory feeding experiments. These observations indicate that the chemically defended Adesmata centipedes, at least cyanogenic groups such as *Strigamia*, may be difficult prey for most centipede-preying ants. However, the feeding biology of centipede-preying ants has been studied only in a few species. Whether there are any ant species adapted to preying on the chemically defended groups of Adesmata is an interesting topic for future exploration.

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