

# An alternative host searching strategy found in the subfamily Hybrizontinae (Hymenoptera, Ichneumonidae)

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## Abstract

The present study reports the oviposition behavior of the ant parasitoid wasp, *Ghilaromma orientalis*, on an undescribed ant species from *Lasius fuliginosus* species group in Japan, illustrated by clear photographs. Previously, the oviposition behavior in the subfamily Hybrizontinae had been limited to species hovering on an ant trail and attacking larvae carried by worker ants. In contrast, in *G. orientalis*, whose oviposition behavior had not been reported to date, the wasp hung on the grass growing along the ants' trail by its hind legs with its head down, and when workers with larvae pass by, directed its abdomen toward the larvae with its hind legs remaining on the grass. Our findings suggest that the subfamily Hybrizontinae employs two host-searching strategies—an active strategy previously known and the ambush-type host-searching strategy employed by *G. orientalis*. The ambush-type strategy affords *G. orientalis* the advantage of laying eggs in a narrow environment where wasps cannot fly without being noticed by ants. Moreover, by avoiding detection through ambush tactics, wasps are increasing their chance for attack, as ants continue to transport their larvae. However, the search range of wasps is reduced, which may limit the opportunities for parasitization. Additionally, while *Lasius nipponensis* has been observed as the sole known host of *G. orientalis*, the oviposition behavior has now been observed in an undescribed species of *L. fuliginosus* group, suggesting that *G. orientalis* may have a subgenus-specific host range.

## Keywords

*Ghilaromma orientalis*, host ant, host-searching behavior, oviposition behavior, parasitoid

## Introduction

Parasitoid wasps have developed behaviors to adapt to the ecology of various hosts and overcome the means of avoiding parasitism (Harvey 2005; Fatouros et al. 2008; Johnson 2013). Host searching behavior is a crucial stage for parasitoids, not only for efficient host search, but also for competing with other parasitoids that exploit the same host as a resource. A variety of such behaviors have been reported, including those utilizing chemical or sonic cues (Vet 2001). Parasitoid wasps select their strategies from these options based on their own morphology, the host, and the host's habitat (Tschopp et al. 2013; Yamamoto et al. 2020). In Hymenoptera, various parasitic behaviors have developed, and the host range extends to 19 orders, making it the second most diverse after the one found in Diptera (Eggleton and Belshaw 1992).

Numerous species of hymenopterans are associated with ants, which possess the largest biomass of insects in the world (Schultheiss et al. 2022), through predation, parasitism on the brood and/or adults, cleptoparasitism, parabiosis, mimetism, true symphily, or indirect parasitism through trophobionts and/or social parasites (Kistner 1982; Lachaud et al. 2013). On the other hand, the number of species that parasitize ants is limited, except within the family Eucharitidae, which are ant specialists. This is believed to be due to the social system of ants, which greatly inhibits parasitism by parasitoids (Lachaud and Pérez-Lachaud 2012). Myrmecophilous insects, which share a life history with ants, have evolved unique strategies to exploit sociality (Kistner 1982; Hölldobler and Wilson 1990; Maruyama and Parker 2017). Rove beetles and clown beetles avoid attacks by ants by producing compounds that both appease their hosts and stimulate adoption, and can live in ant nests (Parker 2016; Hölldobler and Kwapich 2019). Ant crickets and the butterfly family Lycaenidae prevent ants from attacking them by altering the components of cuticular hydrocarbons on their body surfaces (Komatsu et al. 2009; Omura et al. 2012).

Parasitoid wasps that challenge ant society are known to have highly specialized morphologies and behaviors that are not deducible from their sister group and their higher classification (Kistner 1982; Lachaud and Pérez-Lachaud 2012). For example, females from the family Eucharitidae oviposit several eggs at random between the spicules on the underside of a leaf (Clausen 1923; Das 1963; Heraty 1994). Once the eggs hatch, the planidial first-instar larvae gain access to the host ant nest by phoretic attachment to foraging ant workers (Das 1963; Heraty 1994; Heraty et al. 2018). Members of the tribe Neoneurini (Braconidae, Euphorinae) are also capable of rapid parasitism of the adults of *Formica* ants because of their high-flying ability and specialized ovipositor that allows them to quickly lay eggs on ant abdomens (Pierre 1893; Donisthorpe 1927; Gómez Durán and van Achterberg 2011). Furthermore, *Smicromorpha* spp. (Chalcididae) approach the nests of weaver ants (*Oecophylla smaragdina* (Fabricius, 1775)) and lay eggs directly on the larvae (Darling 2009).

The subfamily Hybrizontinae of Ichneumonidae (=Darwin wasp) represents the third most diverse group of ant parasitoids after Eucharitidae and Neoneurini (Yu et al. 2016). This subfamily is distributed throughout the Holarctic Region and includes 16 extant species of four genera, namely *Ghilaromma*, *Hybrizon*, *Neohybrizon*, and *Ogkosoma* (Yu et al. 2016; Broad et al. 2018; Hisasue and Konishi 2019; Liu et al. 2019). Among these, the oviposition behavior has been reported for three species belonging to three different genera, *Ogkosoma cremieri* (Romand, 1838) and *Neohybrizon mutus* Hisasue & Konishi, 2019 by Komatsu and Konishi (2010), and *Hybrizon buccatus* (de Brébisson, 1825) by Gómez Durán and van Achterberg (2011). In these species, the females hover over an ant trail, and when they come across ant larvae carried by workers, they attack and lay eggs on the ant larvae. However, the oviposition behavior has not been reported for *Ghilaromma*. The host of this genus is suggested to be the *Lasius fuliginosus* species group based on a few observations (Donisthorpe and Wilkinson 1930; Maruyama et al. 2013). In Japan, females of *Ghilaromma orientalis* Tobias, 1988 were observed hovering over the trail of *Lasius nipponensis* Forel, 1912 and hanging on a branch near the trail (Maruyama et al. 2013). Herein, we present our observations on the oviposition behavior of *G. orientalis*, which are reported for the first time. Additionally, we undertake a comparison of host-searching strategies between those previously known and observed in *G. orientalis*, while also discussing their respective advantages and disadvantages. Furthermore, host-range of *G. orientalis* is also discussed.

## Material and method

### Study site

Observations were carried out in the vicinity of a Japanese red pine, *Pinus densiflora* Sieb. & Zucc., in the Hitsujigaoka area of Sapporo, Hokkaido, Japan (43.005222°N, 141.416495°E; Fig. 1), where a nest and trails of *Lasius* ants were discovered.

### Observation

The observed nest featured an entrance situated at the base of the Japanese red pine, with several trails extending to several meters on the trunk of the tree and several tens of meters on the ground. Though the second and third authors visited and observed this nest every September and October from 2008 to 2021, larval transportation was observed only in 2015. On 18 October 2015, we discovered larvae being transported in one of the ant trails on the ground, and several individuals of *G. orientalis* were flying and *O. cremieri* were hovering around the ant trail, and the second author took the photo of hovering *O. cremieri* using a camera and lens, LUMIX DMC-GX7 (Panasonic, Tokyo, Japan) with Panasonic Leica DG Macro-Elmarit 45 mm f/2.8 lens (Panasonic, Tokyo, Japan). The first author observed more than 10 females of *G. orientalis* flying randomly 50–100 cm above the nest and near the trail without hovering at 11:00 a.m. on 18 October, 2015.



**Figure 1.** Observation site in the study area (Hitsujigaoka, Sapporo City, Hokkaido, Japan).

On 19 October 2015, we visited this nest again and continued to observe the behavior of *G. orientalis* around the nest and along the ant trail. On 20 October 2015, the third author observed and captured photos of oviposition using a smartphone, iPhone 4S (Apple, California, U.S.A.). To compare host searching and attacking behaviors, we observed *O. cremieri* at the same nest and at a nest of *L. nipponensis* in the same area.

## Results

Unlike previously known host-searching behavior in Hybrizontinae, the females of *G. orientalis* did not hover over the ant trail. Instead, they were observed hanging upside down from the grass covering the ant trail with their heads and antennae directed towards the trail (Fig. 2). The ambush behavior before the attack sometimes lasted for up to an hour. When a worker ant with ant larvae passed beneath, the female touched the larva with its front legs and stretched its legs and directed its abdomen toward the larva while gripping the grass with its hind legs (Fig. 3). The ants then continued to advance. However, the female *G. orientalis* did not release the grip with its hind legs from the grass but instead moved for some time while maintaining its position (Fig. 4). During this period, the worker ant was not observed to be bothered by the parasitoid wasp. Unfortunately, it is not confirmed whether the eggs were laid or not.

Females of *O. cremieri* were observed to stop hovering when the wind blew and to rest on a tree trunk nearby. In addition, worker ants were observed to rise their body and open their mandibles wide toward the hovering *O. cremieri* (Fig. 5); some individuals were even caught by ant workers.



**Figure 2.** Female of *Ghilaromma orientalis* Tobias, 1988 hanging from the grass above the ant trail with her head facing the trail.



**Figure 3.** Female *Ghilaromma orientalis* Tobias, 1988 using her front legs to contact an ant larva and directing her abdomen towards it, while maintaining a firm grip on the grass with her hind legs.



**Figure 4.** Female *Ghilaromma orientalis* Tobias, 1988 maintaining a firm grip on the grass with her hind legs while adjusting her body position to oviposition onto a larva being carried away by an ant.



**Figure 5.** Workers of *Lasius nipponensis* Forel, 1912 with their mandibles open, alerted to the hovering *Ogcosoma cremieri* (Romand, 1838).

The ants that were collected and identified as being parasitized by *G. orientalis* were not *L. nipponensis*, which was previously thought to be the only host species. They were an undescribed species close to *Lasius fuji* (*Lasius* sp. B in the study of Terayama et al. 2014). This species is distributed only in Hokkaido and is larger than *L. nipponensis* (Terayama et al. 2014).

## Discussion

The reported oviposition behavior of the ant parasitoid wasp, *Ghilaromma orientalis*, on an ant species from the *Lasius fuliginosus* species group in Japan, provides valuable insights into the host-searching strategies of the subfamily Hybrizontinae. Previous studies have shown that the three species of Hybrizontinae employ an “active type” host-searching strategy by hovering over ant trails (Kawai 1972; Komatsu and Konishi 2010; Gómez Durán and van Achterberg 2011). This strategy has the advantage of covering a wider search area and enable the movement of parasitoid to areas where the ants carrying larvae are located. However, this strategy has the drawback that hovering of parasitoid wasps over an ant trail alerts the ants and prevents larva-carrying ants from exiting the nest entrance or covered area. Similar observations have been made for *Hybrizon buccatus*, suggesting that hovering species may lose parasitism opportunities because they alarm ants (K. Takasuka pers. comm.). During our observations, the ants opened their mandibles to threaten hovering *Ogkosoma cremieri*, which then occasionally failed to fly or were captured by worker ants. These findings suggest that the parasitism efficiency of *O. cremieri* is declining when the workers detect the wasps. Additionally, *O. cremieri* became stationary on a nearby trunk when the wind blew, indicating that wind can disrupt the host-searching behavior of parasitoids while hovering. On the other hand, the host-searching strategy observed in *G. orientalis* can be described as “ambush type”. The advantage of this strategy is considered to lie not only in conserving the energy expended in sustaining hovering but also in avoiding alerting ants. The flight behavior observed in this species suggests that *G. orientalis* flies over the ant colony without hovering not to lay eggs on the larvae but to search for suitable sites to ambush the worker ants transporting larvae. Consequently, the “ambush type” is less likely to attract physical attention from ants than the “active type” and can successfully parasitize in grassy environments. Nevertheless, the “ambush type” has a limitation of a narrow search area. As ant larvae are not always conveniently transported by workers close to the wasp, narrowing the search area directly leads to a decrease in parasitic opportunities.

Parasitoid wasps that utilize hosts with similar biology, but employ different host-searching strategies, are also observed in some Darwin wasps from the *Poly-sphincta* genus-group (Pimplinae: Ephialtini), which are parasitoids of adult and subadult spiders. *Hymenoepimecis argyraphaga* Gauld, 2000 hovers to approach and attack its host (Eberhard 2000). On the other hand, non-hovering parasitoid wasps,

such as *Zatypota albicoxa* (Walker, 1874) and *Brachyzapus nikkoensis* (Uchida, 1928) hide from their web-spinning spider hosts until they have the opportunity to parasitize (Iwata 1942; Takasuka et al. 2009). Furthermore, parasitoid wasps such as *Hymenoepimecis veranii* Loffredo & Penteado-Dias, 2009 have also been observed to ambush host spiders from hidden locations (Gonzaga and Sobczak 2007; Kloss et al. 2022). In the case of the *Polysphincta*-group, the exploratory strategy of hovering is generally restricted to parasitizing spiders that form vertical circular webs. However, the ambush strategy allows them to attack a more diverse range of environmental hosts, and if they fail to do so, they can hide from spiders that will fight back. Taking into account these behaviors, the ambush type without hovering that *G. orientalis* engages in may have the advantage of increasing the wasp's probability of survival and allowing it to take advantage of environments that the active type cannot invade.

According to Komatsu and Konishi (2010), *N. mutus* and *O. cremieri* occur intensively in August and October, and females of *G. orientalis* are collected from July to October. The timing of occurrences for *N. mutus* and *O. cremieri* corresponded with the time when oviposition behavior was observed, while for *G. orientalis*, oviposition behavior was observed only in October within their occurrence period. Further investigation is required to comprehend the activities of female *G. orientalis* before October, when they commence oviposition behavior. It is possible that the ambush strategy employed by *G. orientalis*, which does not entail hovering, is linked to the prolonged seasonal occurrence of this species, unlike other species.

The host of *Ghilaromma* is suggested to be the *Lasius fuliginosus* species group. A European species, *G. fuliginosi* (Donisthorpe & Wilkinson, 1930), has been observed hovering over *Lasius fuliginosus* (Latreille, 1798) ants (Donisthorpe and Wilkinson 1930). Another species, *G. orientalis*, has been suggested to be a parasitoid of *L. fuji* Radchenko, 2005 *sensu lato* (Watanabe 1984). Later, Maruyama et al. (2013) suggested that this species is a specialist parasitoid of *L. nipponensis*, because it was only observed around the nests of *L. nipponensis*. However, the present observations confirm that this species is also a parasitoid of other species of the *Lasius fuliginosus* species group (*Lasius* sp. B of Terayama et al. 2014). Some members of this species group are known to transport their larvae outside the nest (Komatsu and Konishi 2010; Holý et al. 2017). Therefore, it is plausible that *G. orientalis* may use not only a single ant species, but multiple *L. fuliginosus*-group species that have a habit of transporting larvae outside the nest.

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## References

- Broad GR, Shaw MR, Fitton MG (2018) Ichneumonid wasps (Hymenoptera: Ichneumonidae): their classification and biology. *Handbooks for the Identification of British Insects* 7(12): 1–418.
- Clausen CP (1923) The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. *Annals of the Entomological Society of America* 16: 195–217. <https://doi.org/10.1093/aesa/16.3.195>
- Darling DC (2009) A new species of *Smicromorpha* (Hymenoptera, Chalcididae) from Vietnam, with notes on the host association of the genus. *ZooKeys* 20: 155–163. <https://doi.org/10.3897/zookeys.20.195>
- Das GM (1963) Preliminary studies on the biology of *Orasema assectator* Kerrich (Hymenoptera: Eucharitidae) parasitic on *Pheidole* and causing damage to leaves of tea in Assam. *Bulletin of Entomological Research* 54: 393–398. <https://doi.org/10.1017/S0007485300048884>
- Donisthorpe HSJK (1927) The guests of British ants. Their habits and life-histories. George Routledge & Sons, Ltd., London, 244 pp.
- Donisthorpe HSJK, Wilkinson DS (1930) Notes on the genus *Paxylomma* (Hymenoptera, Braconidae) with the description of a new species taken in Britain. *Transactions of the Royal Entomological Society of London* 78: 87–93. <https://doi.org/10.1111/j.1365-2311.1930.tb01203.x>
- Eberhard WG (2000) The natural history and behavior of *Hymenoepimecis argyraphaga* (Hymenoptera: Ichneumonidae) a parasitoid of *Plesiometa argyra* (Araneae: Tetragnathidae). *Journal of Hymenoptera Research* 9: 220–240.
- Eggleton P, Belshaw R (1992) Insect parasitoids: an evolutionary overview. *Philosophical Transactions of the Royal Society B, Biological Sciences* 337(1279): 1–20. <https://doi.org/10.1098/rstb.1992.0079>
- Fatouros NE, Dicke M, Mumm R, Meiners T, Hilker M (2008) Foraging behavior of egg parasitoids exploiting chemical information. *Behavioral Ecology* 19: 677–689. <https://doi.org/10.1093/beheco/arn011>
- Gómez Durán JM, van Achterberg C (2011) Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species. *ZooKeys* 125: 59–106. <https://doi.org/10.3897/zookeys.125.1754>
- Gonzaga MO, Sobczak JF (2007) Parasitoid-induced mortality of *Araneus omnicolor* (Araneae, Araneidae) by *Hymenoepimecis* sp. (Hymenoptera, Ichneumonidae) in southeastern Brazil. *Naturwissenschaften* 94: 223–227. <https://doi.org/10.1007/s00114-006-0177-z>
- Harvey JA (2005) Factors affecting the evolution of development strategies in parasitoid wasps: the importance of functional constraints and incorporating complexity. *Entomologia Experimentalis et Applicata* 117: 1–13. <https://doi.org/10.1111/j.1570-7458.2005.00348.x>
- Heraty JM (1994) Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). *Life Sciences Contributions, Royal Ontario Museum* 157: 1–174. <https://doi.org/10.5962/bhl.title.53489>

- Heraty JM, Burks RA, Mbanyana N, van Noort S (2018) Morphology and life history of an ant parasitoid, *Psilocharis afra* (Hymenoptera: Eucharitidae). *Zootaxa* 4482(3): 491–510. <https://doi.org/10.11646/zootaxa.4482.3.3>
- Hölldobler B, Kwapich CL (2019) Behavior and exocrine glands in the myrmecophilous beetle *Dinarda dentata* (Gravenhorst, 1806) (Coleoptera: Staphylinidae: Aleocharinae). *PloS ONE* 14(1): e0210524. <https://doi.org/10.1371/journal.pone.0210524>
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Massachusetts, xii + 732 pp. <https://doi.org/10.1007/978-3-662-10306-7>
- Hisasue Y, Konishi K (2019) A new genus of the subfamily Hybrizontinae (Hymenoptera: Ichneumonidae) from Japan. *Zootaxa* 4664(2): 241–250. <https://doi.org/10.11646/zootaxa.4664.2.6>
- Holý K, Bezděčková K, Bezděčka P (2017) Occurrence of *Ogkosoma cremieri* Romand (Ichneumonidae: Hybrizontinae) in the Czech Republic with notes on adult behavior. *Acta Musei Moraviae, Scientiae biologicae (Brno)* 102(2): 139–143.
- Iwata K (1942) Biology of some Japanese *Polysphincta*. *Mushi* 14(2): 98–102.
- Johnson NF (2013) Hymenoptera. In: Levin SA (Ed.) *Encyclopedia of Biodiversity*, 2<sup>nd</sup> edn. Academic Press, Waltham, MA, 177–184. <https://doi.org/10.1016/B978-0-12-384719-5.00163-5>
- Kawai M (1972) Observations of oviposition behavior in *Paxylomma buccatum*. *Kontyû*, Tokyo 40(1): 53–54. [In Japanese]
- Kistner DH (1982) The social insects' bestiary. In: Hermann HR (Ed.) *Social Insects*. Vol. 3. Academic Press, New York, 1–244. <https://doi.org/10.1016/B978-0-12-342203-3.50008-4>
- Kloss TG, de Pádua DG, de Almeida SDS, Pentead-Dias AM, Mendes-Pereira T, Sobczak JF, Lacerda FG, Gonzaga MO (2022) A new Darwin wasp (Hymenoptera: Ichneumonidae) and new records of behavioral manipulation of the host spider *Leucauge volupis* (Araneae: Tetragnathidae). *Neotropical Entomology* 51(6): 821–829. <https://doi.org/10.1007/s13744-022-00991-6>
- Komatsu T, Maruyama M, Itino T (2009) Behavioral differences between two ant cricket species in Nansei Islands: host-specialist versus host-generalist. *Insectes Sociaux* 56: 389–396. <https://doi.org/10.1007/s00040-009-0036-y>
- Komatsu T, Konishi K (2010) Parasitic behaviors of two ant parasitoid wasps (Ichneumonidae: Hybrizontinae). *Sociobiology* 56(3): 575–584.
- Lachaud J-P, Pérez-Lachaud G (2012) Diversity of species and behavior of hymenopteran parasitoids of ants: a review. *Psyche* 2012: 134746. [24 pp.] <https://doi.org/10.1155/2012/134746>
- Lachaud J-P, Lenoir A, Hughes DP [Eds] (2013) *Ants and Their Parasites 2013*. *Psyche Special Issue*. Hindawi Publishing Corporation, New York. <https://doi.org/10.1155/2013/264279>
- Liu J-X, van Achterberg C, Zheng B-Y, Yang Q-M (2019) *Hybrizon* Fallén (Hymenoptera, Ichneumonidae, Hybrizontinae) in China. *Journal of Hymenoptera Research* 72: 11–26. <https://doi.org/10.3897/jhr.72.39333>
- Maruyama M, Komatsu T, Kudo S, Shimada T, Kinomura K (2013) *The guests of Japanese ants*. Tokai University Press, Minamiyana, 208 pp.
- Maruyama M, Parker J (2017) Deep-time convergence in rove beetle symbionts of army ants. *Current Biology* 27(6): 920–926. <https://doi.org/10.1016/j.cub.2017.02.030>

- Omura H, Watanabe M, Honda K (2012) Cuticular hydrocarbon profiles of *Lycaeides subso-lanus* larvae and their attendant ants. *Lepidoptera Science* 63(4): 186–190. [https://doi.org/10.18984/lepid.63.4\\_186](https://doi.org/10.18984/lepid.63.4_186)
- Parker J (2016) Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News* 22: 65–108. [https://doi.org/10.25849/myrmecol.news\\_022:065](https://doi.org/10.25849/myrmecol.news_022:065)
- Pierre A (1893) Un parasite des Fourmis *Elasmosoma berolinense* Ruthe. *Revue scientifique du Bourbonnais et du centre de la France* 6: 112–114.
- Schmid-Hempel P (1998) Parasites in Social Insects. *Monographs in Behavior and Ecology*. Princeton University Press, Princeton, New Jersey, 392 pp.
- Schultheiss P, Nooten SS, Wang R, Wong MK, Brassard F, Guénard B (2022) The abundance, biomass, and distribution of ants on Earth. *Proceedings of the National Academy of Sciences* 119(40): e2201550119. <https://doi.org/10.1073/pnas.2201550119>
- Takasuka K, Matsumoto R, Ohbayashi N (2009) Oviposition behavior of *Zatypota albicoxa* (Hymenoptera, Ichneumonidae), an ectoparasitoid of *Achaearanea tepidariorum* (Araneae, Theridiidae). *Entomological Science* 12: 232–237. <https://doi.org/10.1111/j.1479-8298.2009.00338.x>
- Terayama M, Kubota S, Eguchi K (2014) *Encyclopedia of Japanese Ants*. Tokyo, Asakura-shoten, 278 pp. [In Japanese]
- Tschopp A, Riedel M, Kropf C, Nentwig W, Klopstein S (2013) The evolution of host associations in the parasitic wasp genus *Ichneumon* (Hymenoptera: Ichneumonidae): convergent adaptations to host pupation sites. *BMC Evolutionary Biology* 13: 74. <https://doi.org/10.1186/1471-2148-13-74>
- Vet LEM (2001) Parasitoid searching efficiency links behaviour to population processes. *Applied Entomology and Zoology* 36(4): 399–408. <https://doi.org/10.1303/aez.2001.399>
- Watanabe C (1984) Notes on Paxylommatinae, with review of Japanese species (Hymenoptera, Braconidae). *Kontyû, Tokyo* 52(4): 553–556.
- Yamamoto T, Hasegawa H, Nakase Y, Komatsu T, Itino T (2020) Cryptic diversity in the aphid-parasitizing wasp *Protaphidius nawaii* (Hymenoptera: Braconidae): discovery of two attendant-ant-specific mtDNA lineages. *Zoological Science* 37: 117–121. <https://doi.org/10.2108/zs190093>
- Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015. Database on flash-drive, Nepean, Ontario, Canada. <http://www.taxapad.com> [accessed 3 September 2017]