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First record of the genus *Paralipsis* Förster, 1863 (Hymenoptera, Braconidae, Aphidiinae) from South Korea, with description of a new species and report of a newly recorded species

Sangjin Kim[1,2*], Seonwoo Yoon[3*], Hyojoong Kim[1]

1 *Animal Systematics Laboratory, Department of Biology, Kunsan National University, Gunsan 54150, Republic of Korea* **2** *Center for Convergent Agrobioengineering, Department of Biology, Kunsan National University, Gunsan 54150, Republic of Korea* **3** *Ulsan Agricultural Technology Center, Ulsan, Republic of Korea*

Corresponding author: Hyojoong Kim (hkim@kunsan.ac.kr)

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Abstract

The genus *Paralipsis* Förster, 1863 is recorded from South Korea for the first time. Two species are treated: *Paralipsis triangulata* Kim & Yoon, **sp. nov.** and *P. eikoae* (Yasumatsu, 1951), the latter newly recorded from South Korea. *Paralipsis triangulata* **sp. nov.** was collected from unidentified root-aphid colonies on the roots of *Miscanthus* sp. (Poaceae) and attended by *Lasius koreanus* Seifert, 1992 (Hymenoptera: Formicidae), whereas *Paralipsis eikoae* (Yasumatsu, 1951) (Hymenoptera: Braconidae) was collected from a nest of *Lasius japonicus* Santschi, 1941 (Hymenoptera: Formicidae), where no aphids were observed. Morphological descriptions, diagnostic characters, high-resolution photographs, and sequence data for seven gene regions (*COI*, *COII*, *ND1*, *Cytb*, *28SD2*, *EF1–alpha*, and *Wingless*) are provided for both species. A *COI* gene tree and species delimitation analyses using ABGD and bPTP are also provided. Laboratory observations and videos revealed repeated antennal contact, riding behavior, grooming by associated ant workers, and trophallaxis in both species, as well as wing-pulling behavior in both species. These findings expand the known diversity and distribution of *Paralipsis* and provide new information on the ant-associated biology of root-aphid parasitoids in East Asia.

Keywords

Natural enemy, parasitoid wasps, root aphids, systematics, taxonomy

* These authors contributed equally.

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Introduction

The genus *Paralipsis* Förster, 1863 (Hymenoptera: Braconidae: Aphidiinae) is a specialized group of endoparasitoid wasps restricted to the Palaearctic region (Davidian 2007; van Achterberg and Ortiz de Zugasti Carrón 2016; Yu et al. 2016; Mitrović et al. 2019). Unlike most aphidiines, which parasitize aphids on above-ground parts of a plant, species of *Paralipsis* are associated with concealed hosts, namely root aphids inhabiting subterranean environments (Takada and Hashimoto 1983; Takada and Hashimoto 1985; van Achterberg and Ortiz de Zugasti Carrón 2016; Mitrović et al. 2019). The genus currently comprises six described species worldwide, of which only one, *Paralipsis eikoae* (Yasumatsu, 1951) (Hymenoptera: Braconidae), has been recorded from the Eastern Palaearctic region (van Achterberg and Ortiz de Zugasti Carrón 2016; Mitrović et al. 2019).

Species of *Paralipsis* are closely associated with ant-attended root aphids and exhibit pronounced myrmecophilous adaptations (Takada and Hashimoto 1985; van Achterberg and Ortiz de Zugasti Carrón 2016). However, the behavioral and chemical mechanisms involved in these associations may differ among species. In *P. eikoae*, mounting and rubbing against ant workers have been suggested to facilitate the acquisition and maintenance of colony-specific chemical cues, and trophallactic interactions with ants are also documented (Takada and Hashimoto 1985; Akino and Yamaoka 1998). In contrast, Völkl et al. (1996) did not observe comparable leg-rubbing behavior in *Paralipsis enervis* (Nees, 1834) (Hymenoptera: Braconidae) and found no evidence that this species actively acquired substances from ants for chemical camouflage. Instead, they suggested that chemical similarity to its host aphids, together with tactile communication with *Lasius niger* (Linnaeus, 1758) (Hymenoptera: Formicidae), may contribute to its integration with the ant. Thus, the mechanisms involved in ant integration should not necessarily be generalized across the genus.

Previous studies have also described aspects of the seasonal biology of *P. eikoae*. Takada and Hashimoto (1983) reported spring emergence from overwintered mummies, prolonged reproductive inactivity in females, and the appearance of mature eggs and parasitized aphids in late summer. Akino and Yamaoka (1998) observed fully winged females outside an ant nest and documented a worker of *Lasius sakagamii* Yamauchi & Hayashida, 1970 (Hymenoptera: Formicidae) carrying a female toward the nest. These reports provide background for examining seasonal occurrence and interactions with associated ants, although comparable life-history information remains limited for other *Paralipsis* species.

In addition, truncated wings have frequently been reported in *Paralipsis*, and this condition has traditionally been attributed to mutilation by aphid-attending ants (Maneval 1940; Starý 1966, 1970). However, subsequent observations have questioned whether ant-mediated mutilation is the sole mechanism responsible for wing loss (Takada and Hashimoto 1985; Völkl et al. 1996; Akino and Yamaoka 1998; van Achterberg and Ortiz de Zugasti Carrón 2016). Similar ant-mediated wing damage has been suggested in other myrmecophilous wasps, such as *Rhadinoscelidia lixa* Hisasue

& Mita, 2020 (Hymenoptera: Chrysididae), whereas direct wing-biting by host ants has recently been observed in *Tetramopria turbinata* Notton, 1994 (Hymenoptera: Diapriidae) (Hisasue and Mita 2020; Kawai et al. 2025). Starý (1970) suggested that wing mutilation in *P. enervis* restricts dispersal and may retain the parasitoid within the nest as a symphile. Takada and Hashimoto (1985) regarded the association between *P. eikoae* and *Lasius niger* (Linnaeus, 1758) as a form of cleptoparasitism because the parasitoid oviposits in aphids tended and protected by ants. Following Seifert (1992), records of *L. niger* from Korea and Japan have generally been regarded as referring to *Lasius japonicus* Santschi, 1941. Therefore, the aphid-attending ant reported as *L. niger* by Takada and Hashimoto (1983, 1985) was most likely *L. japonicus*. However, because this interpretation cannot be confirmed without re-examination of the original ant material, the original name *L. niger* is retained herein.

The genus *Lasius* Fabricius, 1804 (Hymenoptera: Formicidae: Formicinae) currently comprises 17 species in South Korea, seven of which belong to the *Lasius niger* group (Dong et al. 2025). During 14 years of field observations in South Korea, the author, Seonwoo Yoon, observed a diverse assemblage of myrmecophilous insect genera associated with *Lasius* ants, including *Diartiger* Sharp, 1883 (Coleoptera: Staphylinidae), *Batrisus* Aubé, 1833 (Coleoptera: Staphylinidae), *Myrmecophilus* Berthold, 1827 (Orthoptera: Myrmecophilidae), and *Drosicha* Walker, 1858 (Hemiptera: Monophlebidae) (S. Yoon, pers. obs.). These taxa are rarely collected, suggesting that additional unrecorded myrmecophilous species associated with *Lasius* ants may be discovered through further sampling.

In this study, we report the genus *Paralipsis* from South Korea for the first time, based on one newly recorded species and one new species. We provide morphological descriptions with high resolution photographs and molecular data for seven gene regions for both species, and present biological observations, including their associations with *Lasius* ants.

Materials and methods

Field and laboratory work

Samples were collected during April and May of 2024, 2025, and 2026, either by collecting aphid mummies from the roots of *Miscanthus* sp. (Poaceae) (Fig. 1A, B) or by turning over stones and hand-collecting adults found beneath them (Fig. 1C) together with ants. The collected wasps were preserved in 99% ethyl alcohol at room temperature (ca. 20–25 °C) approximately one year and subsequently transferred to 4 °C.

The behavior of ants and parasitoid wasps was documented using a Nikon D7500 digital camera equipped with a Kenko DG extension tube and an AF-S Micro NIKKOR 60 mm f/2.8G ED lens. Illumination was provided by a Godox MF12 strobe light. Videos were recorded using a Vitiny UM08 digital microscope under consistent lighting conditions.

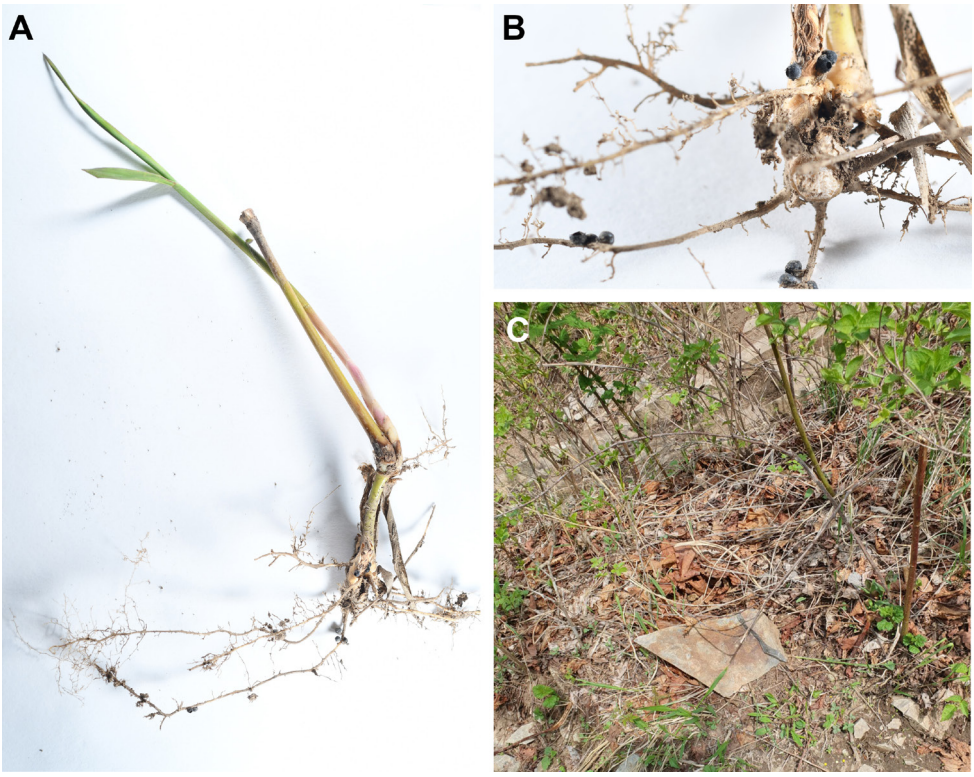

Figure 1. Mummies and habitat of *Paralipsis triangulata* Kim & Yoon, sp. nov. **A** *Miscanthus* sp. bearing aphid mummies **B** mummies on the subterranean basal parts of *Miscanthus* sp. **C** Habitat of *P. triangulata* sp. nov.

Parasitoid wasp and ant colonies were maintained for observation in polypropylene insect breeding dishes (external diameter 100.00 mm, height 40.00 mm; internal diameter 91.35 mm, height 38.50 mm) with a 40.00 mm ventilation hole covered with mesh (SPL Life Sciences). Colonies were provided with honey water as a food source. Humidity within the containers was maintained by adding a layer of soil.

Taxonomy

The morphological and molecular identification of *Paralipsis* species was based on Mitrović et al. (2019). Specimens were initially sorted into morphologically similar groups using stereomicroscopes (Olympus SZX16, Leica M205C), after which individual specimens were labelled and subjected to DNA extraction. Following DNA extraction, voucher specimens were prepared as dried-mounted and slide mounted specimens.

Morphological examination and photography were conducted using the same stereomicroscopes (Olympus SZX16, Leica M205C). Multiple images of slide and dried mounted were taken at various focal heights using Mosaic V2.3 (Tucsen Software) and VXH-7100 (Keyence). The image stacking process was carried out using VXH-X1 Ver

3.3.19.528 (Keyence) and Helicon Focus 7 (Helicon Soft) (Berkovitch et al. 2009). After stacking, illustrations were generated using Adobe Photoshop CS6.

Morphological terminology, including terminology for surface sculpture, follows Wharton et al. (1997), whereas terminology for wing venation follows Mitrović et al. (2019). Generic identification and the concept of *Paralipsis* follow Davidian (2007) and van Achterberg and Ortiz de Zugasti Carrón (2016). Species identification and morphological descriptions were based on Mitrović et al. (2019) and van Achterberg and Ortiz de Zugasti Carrón (2016), including the identification keys provided therein.

In the morphological descriptions, F1, F2, F3, etc. refer to the first, second, third, and subsequent antennal flagellomeres, respectively.

Korean vernacular names are provided for the genus and species treated in this study. Newly proposed Korean names are indicated by "신칭" (sinching), meaning "new Korean name". The names were coined based on taxonomically or biologically informative characteristics, including host associations, diagnostic morphology, and the Korean vernacular names of known aphid hosts. The newly proposed Korean generic name "뿌리진디벌속" for *Paralipsis* refers to the root aphids that are known hosts of species of this genus. For *Paralipsis triangulata* sp. nov., the Korean name "삼각뿌리진디벌" reflects the meaning of the specific epithet *triangulata*, which refers to the distinct triangular lamellate projection on the outer basal margin of the fore femur. For *P. eikoae*, the Korean name "동글밑뿌리진디벌" incorporates "동글밑", derived from "배나무동글밑진딧물", the Korean vernacular name of its known aphid host, *Sappaphis piri* Matsumura, 1918 (Hemiptera: Aphididae).

The holotype of the new species is deposited in the NIBR (National Institute of Biological Resources, Incheon) collection. Paratypes and other specimens are deposited in the KSNU (Kunsan National University, Gunsan 54150, Republic of Korea).

Molecular analysis

Total genomic DNA was extracted using a LaboPass Tissue Kit (COSMOgenetech, Korea) following the manufacturer's protocol with slight modifications. To preserve the morphological integrity of the specimens, we adapted the "freezing method" described by Yaakop et al. (2013). Our modification involved extending the incubation period from 30 minutes to 2 hours at 56 °C with 200 µl of TL buffer and 20 µl of proteinase K. This adjustment allowed for effective DNA extraction while minimizing damage to the specimens' structure. Each sample underwent individual genomic DNA extraction to ensure sample-specific results.

For molecular identification and barcoding, we targeted three partial regions of nuclear genes (*28SD2*, *EF1–alpha*, and *Wingless*) and four partial regions of mitochondrial genes (*COI*, *COII*, *Cytb*, *NAD1*). The primer sets, PCR mixture composition, and thermal cycling conditions followed Kim et al. (2025) without modification. These regions were amplified using the primers with AccuPower PCR PreMix (Bioneer Corp., Daejeon, Korea). The PCR products were visualised by electrophoresis on agarose gel. When bands were observed, the samples were sent to Macrogen (Daejeon, Korea) for purification and sequencing analysis. All sequences generated in this study were deposited in GenBank (Accession numbers provided in Table 1).

Table 1. Analysis sample list using *COI* from GenBank.

No	Species	NCBI accession number
1	*Paralipsis eikoae*	PZ412705 (this study)
2	*P. eikoae*	PZ412706 (this study)
3	*P. triangulata* sp. nov.	PZ412707 (this study)
4	*P. triangulata* sp. nov.	PZ412708 (this study)
5	*P. enervis*	MH475319
6	*P. enervis*	MH475320
7	*P. enervis*	MH475322
8	*P. enervis*	MH475323
9	*P. enervis*	MH475327
10	*P. enervis*	MH475329
11	*P. enervis*	MH475331
12	*P. tibiator*	MH475328
13	*P. tibiator*	MH475330
14	*P. rugosa*	MH475325
15	*P. brachycaudi*	MH475321
16	*P. brachycaudi*	MH475324
17	*P. brachycaudi*	MH475326
18	*Pauesia cinaravora*	PZ094471
19	*P. unilachni*	PZ094478

Sequence alignment was performed using MAFFT version 7 (Katoh et al. 2019), with default settings. We checked for frameshifts to avoid pseudogenes. Although seven gene regions were sequenced for the Korean specimens, only *COI* was used for interspecific comparisons because comparable sequences were available for other *Paralipsis* species in GenBank. Sequence divergences were calculated using the 'p-distance' model with 1,000 bootstrap replications and pairwise deletion for data gaps in MEGA version 7.0 (Kumar et al. 2016).

For the Bayesian inference analysis, substitution models were selected for each *COI* codon position (1st, 2nd, and 3rd) using IQ-TREE under the Bayesian information criterion (BIC), and the resulting models were imported into BEAUti/BEAST 2. (Bouckaert et al. 2014). We used Relaxed Clock Log Normal model (Drummond et al. 2006), with site options based on ModelFinder results (HKY+F+I; TN+F+I; HKY+F+G4). The speciation model used a Yule model because the dataset consists exclusively of extant species. The MCMC was run for 100 million generations and assessed using Tracer (Rambaut et al. 2018) and DensiTree (Bouckaert 2010). Subsequently, the summarized tree was generated in TreeAnnotator as a maximum clade credibility (MCC) tree, using a posterior probability limit of 1.0 and 10% burn-in.

All sequences for analysis were processed using two efficient tools to define each species. First, ABGD (Automatic Barcode Gap Discovery) analysis was performed to automatically separate sequences into hypothetical molecular species by contrasting

inter- and intra-specific distances (Puillandre et al. 2012) (https://itaxotools.org/download.html#hyperlinkMol). The Kimura K80 model was used with two relative gap widths (X = 1 and 1.5) in standard settings. Then, PTP (Poisson Tree Processes) analysis was conducted on the Exelixis Lab webserver (https://species.h-its.org/), using the maximum likelihood solution under standard settings (Zhang et al. 2013).

The 658 bp *COI* fragment was sequenced for *Paralipsis* species and deposited in GenBank. For comparative analysis, 15 *COI* sequences representing four additional *Paralipsis* species were retrieved from GenBank and combined with two Korean sequences generated in this study, resulting in 17 ingroup sequences representing six *Paralipsis* species. Two *Pauesia* Quilis, 1931 sequences were used as outgroups (Table 1).

Results

Key to species of the genus *Paralipsis* based on females

This key is modified from Mitrović et al. (2019) and van Achterberg and Ortiz de Zugasti Carrón (2016) to include the new described species.

1 Propodeum and scutellum with strong and deep rugosities (Fig. 2F, G); F1 less than 2.0 times as long as middle width (Fig. 2C); longitudinal placodes start at F4 (Fig. 2C) **2**

– Propodeum and scutellum with smooth with short carina (Fig. 4F) or moderate expressed rugosities; F1 2.0 or more times as long as middle width (Fig. 4C); longitudinal placodes not start at F4 (Fig. 4B) **3**

2 Maxillary palp one segmented; vein 2-1A of forewing sclerotized; pterostigma length less than 2.0 times as long as width; (Antennae 15–segmented)... .....***Paralipsis rugosa*** **Tomanović & Starý, 2019**

– Maxillary palps two segmented; vein 2-1A of forewing faintly pigmented but unsclerotized; pterostigma length 2.5 or more times as long as width (Fig. 2K); (antennae 16–segmented (Fig. 2B))..... ***P. triangulata*** **Kim & Yoon, sp. nov.**

3 Vein 2-1A of forewing completely absent (Fig. 4J) **4**

– Vein 2-1A of forewing present, either distinctly sclerotized or faintly pigmented and not sclerotized (Fig. 2K) **5**

4 Antennae 16–17-segmented; Propodeum smooth with two short carinae at the base; longitudinal placodes start at F3 ..... ***P. eikoae*** **(Yasumatsu, 1951)**

– Antennae 15-segmented; Propodeum smooth and shiny; longitudinal placodes start at F4 ..... ***P. tibiator*** **van Achterberg & Ortiz de Zugasti, 2016**

5 Vein 2-1A of forewing faintly pigmented but not sclerotized, petiole length 1.1 times as long as maximum width at level of spiracles..... .....***P. planus*** **van Achterberg, 2016**

– Vein 2-1A of forewing distinctly sclerotized, petiole length more than 1.3 times as long as maximum width at level of spiracles..... **6**

6 Maxillary palps two segmented; propodeum rugosities in the central parts which indicate for the presence of a central areola; petiole length less than 1.5 times as long as maximum width at level of spiracles....***P. enervis*** **(Nees, 1834)**

– Maxillary palp one segmented; propodeum smooth, sometimes with rugosities but not areolated; petiole length 1.5 or more times as long as maximum width at level of spiracles..... ***P. brachycaudi*** **Tomanović & Starý, 2019**

Systematic accounts (description based on females)

Genus *Paralipsis* Förster, 1863

Myrmecobosca Maneval, 1940: 9–14.

Korean name. 뿌리진디벌속 (신칭).

Type species. *Aphidius enervis* Nees, 1834

Paralipsis triangulata Kim & Yoon, sp. nov.

https://zoobank.org/05F379BD-E5C5-4B75-988E-7975899B3528

Figs 2A–O, 3A–H, Suppl. materials 1–7

Korean name. 삼각뿌리진디벌 (신칭).

Diagnosis. The new species shares with *P. rugosa* Tomanović & Starý, 2019 having the rugose propodeum (Fig. 2F, G) and scutellum (Fig. 2E). However, it clearly differs in having F1 length equal to F2 (Fig. 2C), pterostigma length/width ratio over than 2.5 (Fig. 2K), vein 2-1A of the forewing faintly pigmented and unsclerotized, the presence of a distinct triangular lamellate projection on the outer basal margin of the fore femur (Fig. 3B), and the presence of a distinct blunt subapical process in lateral view of fore basitarsus (Fig. 2N) in *P. triangulata* sp. nov. In contrast, *P. rugosa* having F1 length longer than F2, pterostigma length/width ratio less than 2.0, vein 2-1A sclerotized, and lacks such a projection on the fore femur and fore basitarsus.

Description. Female from South Korea. Length of body in lateral view 2.5 mm (Figs 2A, 3A). Length of antennae 1.8 mm (Fig. 2B).

Head. Width of head 1.3× middle length in dorsal view; posterior of antenna socket depressed; head 1.1× wider than mesosoma at tegulae, with sparse erected setae; eye 0.6× as long as temple in dorsal view (Fig. 2D, H). Eyes small and oval, sparsely setose. Face moderately pubescent; width 2.5–2.7× as wide as height; tentorial index (tentorio-ocular line/intertentorial line) = 0.6–0.7; clypeus oval with four long setae; malar space 0.6–0.7× as long as longitudinal eye diameter (Fig. 2D). Antenna 16–segmented; F1 1.0× as long as F2; F1 and F2 1.7× and 1.8× as long as their middle width, respectively; 2.3× and 2.1× as long as their basal width, respectively; penultimate flagellomere 1.8× as long as their middle width; F1–3 without longitudinal placodes, start with F4 (Fig. 2B, C). Maxillary palp with two palpomeres, labial palp with one palpomere.

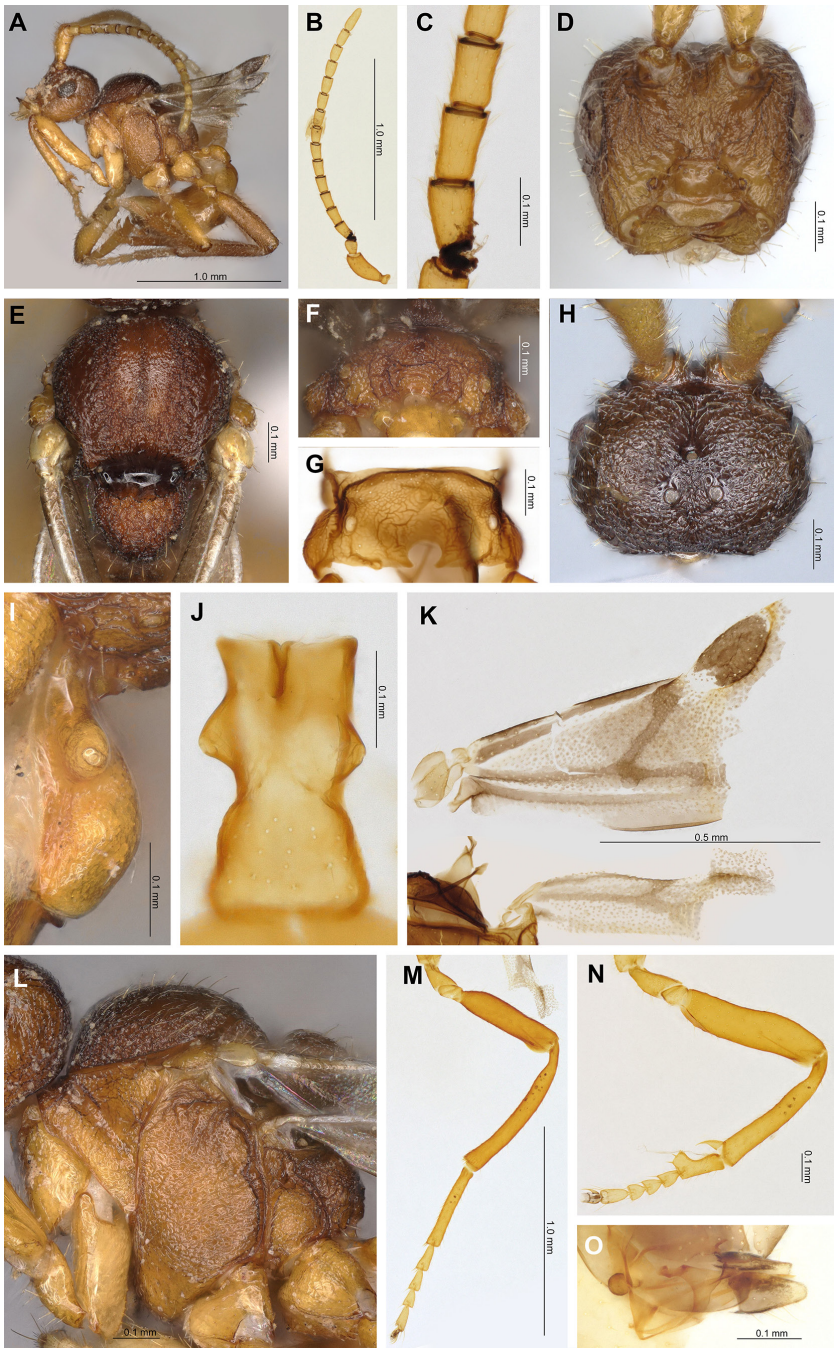

Figure 2. *Paralipsis triangulata* Kim & Yoon, sp. nov.: **A** habitus, dried mounted **B** antenna, slide mounted **C** F1–3, slide mounted **D** head, dried mounted **E** mesoscutum, dried mounted **F** propodeum, dried mounted **G** propodeum, slide mounted **H** dorsal view of head, dried mounted **I** lateral view of petiole, dried mounted **J** dorsal view of petiole, slide mounted **K** wings, slide mounted **L** lateral view of mesosoma, dried mounted **M** hind leg, slide mounted **N** fore leg, slide mounted **O** ovipositor sheath, slide mounted.

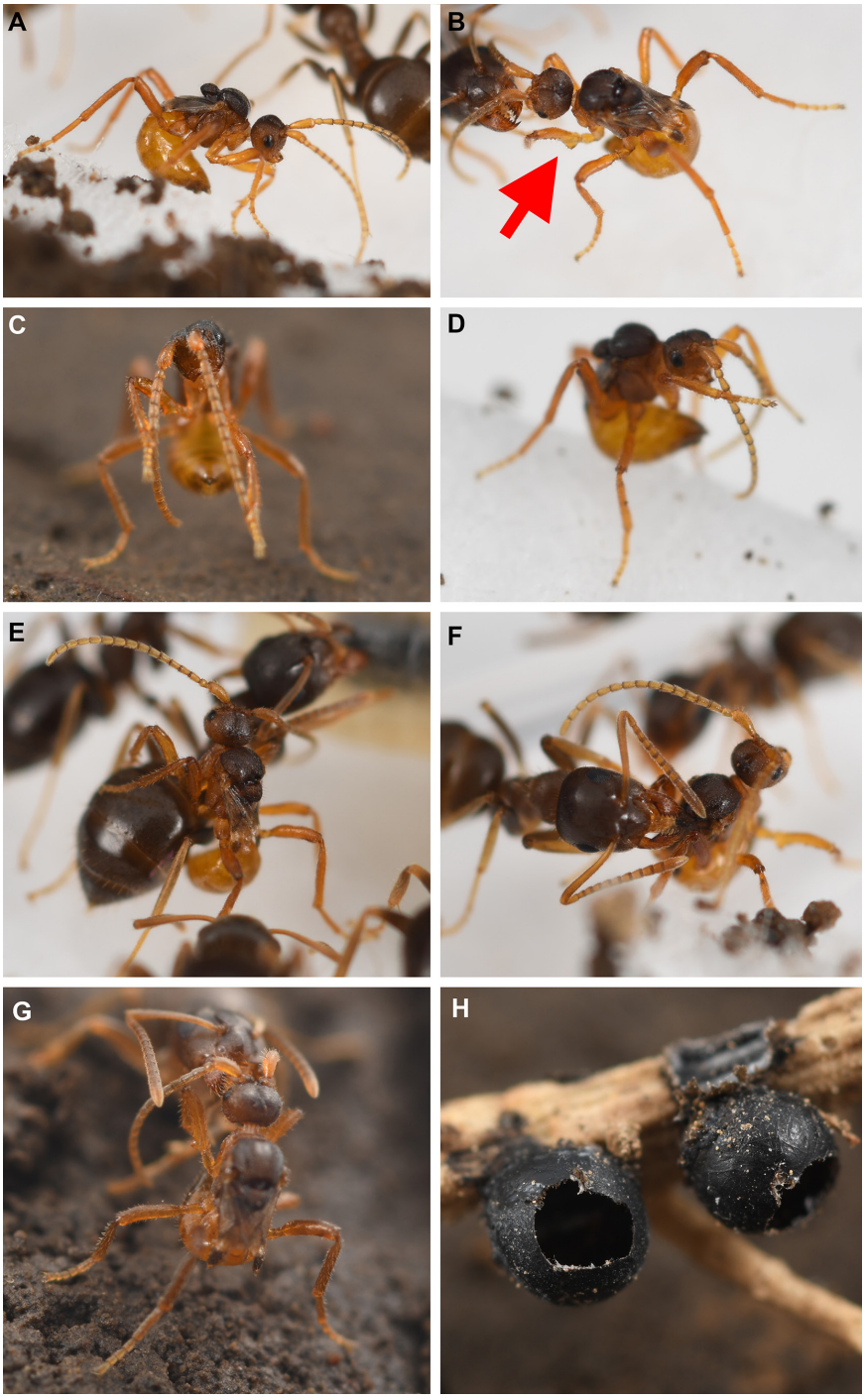

Figure 3. Biological characters of *Paralipsis triangulata* sp. nov. **A** alive habitus **B** triangular lamellate projection on the outer basal margin of the fore femur **C** cleaning the antennae **D** cleaning the antennae **E** riding **F** grooming **G** trophallaxis **H** mummies.

***Mesosoma*.** Pronotum without pronope and subpronope (Fig. 2E); present pronotal sulcus, almost reach to mesopleuron (Fig. 2L). Mesopleuron finely rugulose–reticulate, with dense shallow impressions throughout (Fig. 2L). Mesoscutum surface slight rugose, smooth area on dorsal and lateral lobes in each side (total four area); without notauli, covered with numerous long setae (Fig. 2E). Scutellum nearly circular, protuberant; bearing numerous long setae, without scutellar sulcus carina (Fig. 2E). Propodeum with coarse subconcentric rugae; interspaces shallowly impressed and irregularly reticulate (Fig. 2F, G).

***Forewing*.** Pterostigma (= Stigma) with colorless area in both anterior and posterior side; 2.5–3.1× as long as wide. Vein R1 (= metacarpus) absence. Vein 2-1A present, not sclerotized. (Fig. 2K).

***Leg*.** Legs sparsely semi erected setose. Fore femur 4.0–4.4× as long as maximum width. Fore tibia 6.5–7.0× as long as maximum width with one tibial spur (Fig. 2N). Fore femur length equal to fore tibia. Fore tarsus 3.0–3.3× as long as fore basitarsus (= 1st tarsomere); fore basitarsus straight, with a distinct blunt subapical process in lateral view; with a single row of densely comb–shaped setae; second fourth segments of fore tarsomeres length equal to width, claws acute (Fig. 2N). Middle femur 4.6–5.0× as long as maximum width. Middle tibia 8.1× as long as maximum width with two tibial spurs. Middle femur length 0.8× as long as middle tibia. Middle tarsus 3.0–3.3× as long as middle basitarsus. Hind femur 4.1× as long as maximum width (Fig. 2M). Hind tibia 8.0–8.1× as long as maximum width. Hind femur 0.7× as long as hind tibia. Hind tarsus 2.2× as long as hind basitarsus (Fig. 2M).

***Metasoma*.** Petiole with prominent spiracular tubercles, 1.6× as long as maximum width at level of spiracles and 2.7× as long as width at level of posterior spiracles (Fig. 2I, J). Ovipositor sheath short, straight, and slight broad in apex, 1.5–1.9× as long as maximum width; with long hairs (Fig. 2O).

Color. Antenna light brown. Head light brown and dark brown dorsally; face, clypeus and mouthparts light brown. Mesosoma light brown with brown; mesoscutum brown in dorsal and light brown in lateral view. Both anterior and posterior of pterostigma with colorless area in forewing. Metasoma light brown. Legs light brown with dark apices.

Distribution. South Korea.

Biology. Unknown root aphid on *Miscanthus* sp., associated with colonies of *Lasius koreanus* Seifert, 1992. The parasitized aphids formed black mummies attached to the root and basal subterranean parts of *Miscanthus* sp.

Etymology. The specific name *triangulata* sp. nov. refers to the distinct triangular lamellate projection on the outer basal margin of the fore femur.

Type material. ***Holotype*:** South Korea • ♀; Mt. Goheon, Daehyeon–ri, Sannae–myeon, Gyeongju–si, Gyeongsangbuk–do from *Lasius* (*Lasius*) *koreanus*. colony; 28.IV.2025; leg. S. Yoon; Dried mounted; specimen code: YPC003118. ***Paratypes*:** South Korea • 4♀; same collection data as holotype; • 2♀ slide mounted specimen except one specimen's head (Ap26009); GenBank (Ap26009, YPC003120): *COI*, PZ412707; *28SD2*, PZ411506; *COII*, PZ416387; *Cytb*, PZ420655; *NAD1*, PZ420657; *Wingless*, PZ447458; GenBank (Ap26010, YPC003121): *COI*, PZ412708; *28SD2*, PZ411507;

COII, PZ416388; *EF1–alpha*, PZ447456; *NAD1*, PZ420658; *Wingless*, PZ447459; • 2♀ alcohol preserved; specimen code: YPC003117, YPC003119.

Additional material examined. South Korea • 4♀; same collection location as holotype; 28.IV.2024; • ♀ alcohol preserved; specimen code: YPC2293; 25. IV.2026; • ♀ alcohol preserved; specimen code: YPC3475; • 2♀ alcohol preserved; specimen code: YPC3476_1, YPC3476_2; these specimens are not included in the type series.

Biological notes. All specimens of *Paralipsis triangulata* sp. nov. were collected from unidentified root-aphid colonies on *Miscanthus* sp. (Fig. 1A, B, C) attended by *Lasius koreanus*. Individuals were usually found living together with aphid-attending ants and moved freely within the colony, and no aggressive behavior by the ant workers was observed. Aphid mummies, presumed belonging to the host root aphid, were found on the roots and basal subterranean parts of *Miscanthus* sp. (Fig. 1A, B). On 28 April 2025, one adult that had failed to emerge from a mummy was observed. The mummy was tough and difficult to tear apart, and the emergence hole was nearly circular with an irregularly torn margin (Fig. 3H).

Adults were periodically observed licking the fore tibial spur (=calcar) with their mouthparts and then repeatedly used it to clean the antennae. During the behavior, the wasp hooked the base of antennae with the fore tibial spur and pushed it distally, cleaning the antenna with the dense comb of setae on the basitarsus (= 1st tarsomere) (Fig. 3C, D, Suppl. material 1). In addition, when approached by ant workers, individuals frequently waved their antennae and made contact with the ants.

Under laboratory conditions, a characteristic riding behavior was repeatedly observed. *P. triangulata* sp. nov. approached stationary workers and mounted the dorsal surface of the ant with the fore legs held flexed in a mantis-like posture, positioning its body between the legs of the ant worker. During riding (Fig. 3E, Suppl. material 2), the fore legs grasped the petiole and fore coxa of the aphid-attending ant, while the middle tibia repeatedly moved in a sawing motion, scraping the surface of the aphid-attending ant's gaster toward the parasitoid's body. The ridden ant generally stopped moving and lowered its body posture, apparently accepting the behavior. This posture was similar to that observed when workers receive grooming from nestmates. Riding behavior lasted for up to six minutes when uninterrupted. After riding, parasitoids were occasionally observed rubbing the middle and forelegs against each other, although this behavior was not consistently observed in all individuals.

After repeated riding events, aphid-attending ants were frequently observed grooming the body of *P. triangulata* sp. nov. (Fig. 3F, Suppl. materials 3, 4). Trophallaxis between ants and *Paralipsis* was also commonly observed, especially after honey water was provided. Ant workers often opened their mandibles and appeared to wait for trophallaxis when encountering *P. triangulata* sp. nov. (Fig. 3G, Suppl. materials 5, 6). Parasitoids actively solicited trophallaxis by rapidly tapping the mandibles of the aphid-attending ants with their antennae and fore legs.

The wings of all collected individuals were damaged, and the wing margins were irregular and ragged. During laboratory observation, individuals were observed pulling the damaged wings posteriorly with the apical parts of the hind tibiae. The apical parts

of the hind tibiae reached approximately the regions corresponding to the damaged wing margins (Suppl. material 7). However, neither ant-mediated wing removal nor direct self-removal of wing tissue by the parasitoids was observed. Therefore, the mechanism responsible for the wing damage could not be determined from the present observations.

On 9 May 2026, an experiment was conducted to examine acceptance among different ant colonies. One adult *Paralipsis* was introduced into a different colony of *Lasius koreanus*, which contained one adult *Paralipsis* and was located approximately 300 m from the original collection site. After investigation, the ant workers surrounded the introduced individual and repeatedly bit and pulled its legs and antennae. Although the parasitoid repeatedly contacted workers with its antennae, riding behavior was not observed. After approximately three hours, the individual was found dead, with its antennae and legs severed. When a worker of *Lasius koreanus* from the same colony as the introduced *Paralipsis* was introduced together, they were also killed in the same manner.

Remarks. *Paralipsis triangulata* sp. nov. possesses a distinct triangular lamellate projection on the outer basal margin of the fore femur. This structure was not observed in *P. eikoae*. Considering that this projection is positioned near the base of the ant worker's gaster during riding behavior (Suppl. material 2), it may function to stabilize the body of the parasitoid on the ant. However, these proposed functions have not been directly tested, and further behavioral investigation is needed.

***Paralipsis eikoae* (Yasumatsu, 1951)**
Figs 4A–N, 5A–D, Suppl. materials 8–10

Myrmecobosca eikoae Yasumatsu, 1951: 171–174.

Korean name. 동글밑뿌리진디벌 (신칭).

Diagnosis. *Paralipsis eikoae* is characterized by the following combination of characters: antenna with 16–17 segments (Fig. 4B); F1 approximately 1.1× as long as F2 (Fig. 4C); longitudinal placodes absent on F1 and F2 and beginning on F3; maxillary palp with two palpomeres and labial palp with one palpomere (Fig. 4D); notauli very shallowly impressed (Fig. 4E); forewing venation strongly reduced, with R1 and 2-1A absent; pterostigma approximately 2.3–2.4× as long as wide (Fig. 4J); propodeum with two short divergent carinae at the base (Fig. 4F); petiole approximately 1.7–1.9× as long as its maximum width at the level of the spiracles (Fig. 4H, I); ovipositor sheath relatively short and broad, bearing long setae (Fig. 4N) (Takada 1976).

Morphology of Korean specimens. In addition to the characters described by Takada (1976), the following morphological measurements and character states were observed in the Korean specimens.

Head. Width of head 1.5× middle length in dorsal view; head 1.1–1.2× wider than mesosoma at tegulae (Fig. 4D, G). Tentorial index 0.6–0.7; malar space 0.8–0.9× as long as longitudinal eye diameter (Fig. 4D). F1 and F2 2.0× and 1.7× as long as their middle width, respectively; F2 2.4× as long as its basal width (Fig. 4B, C).

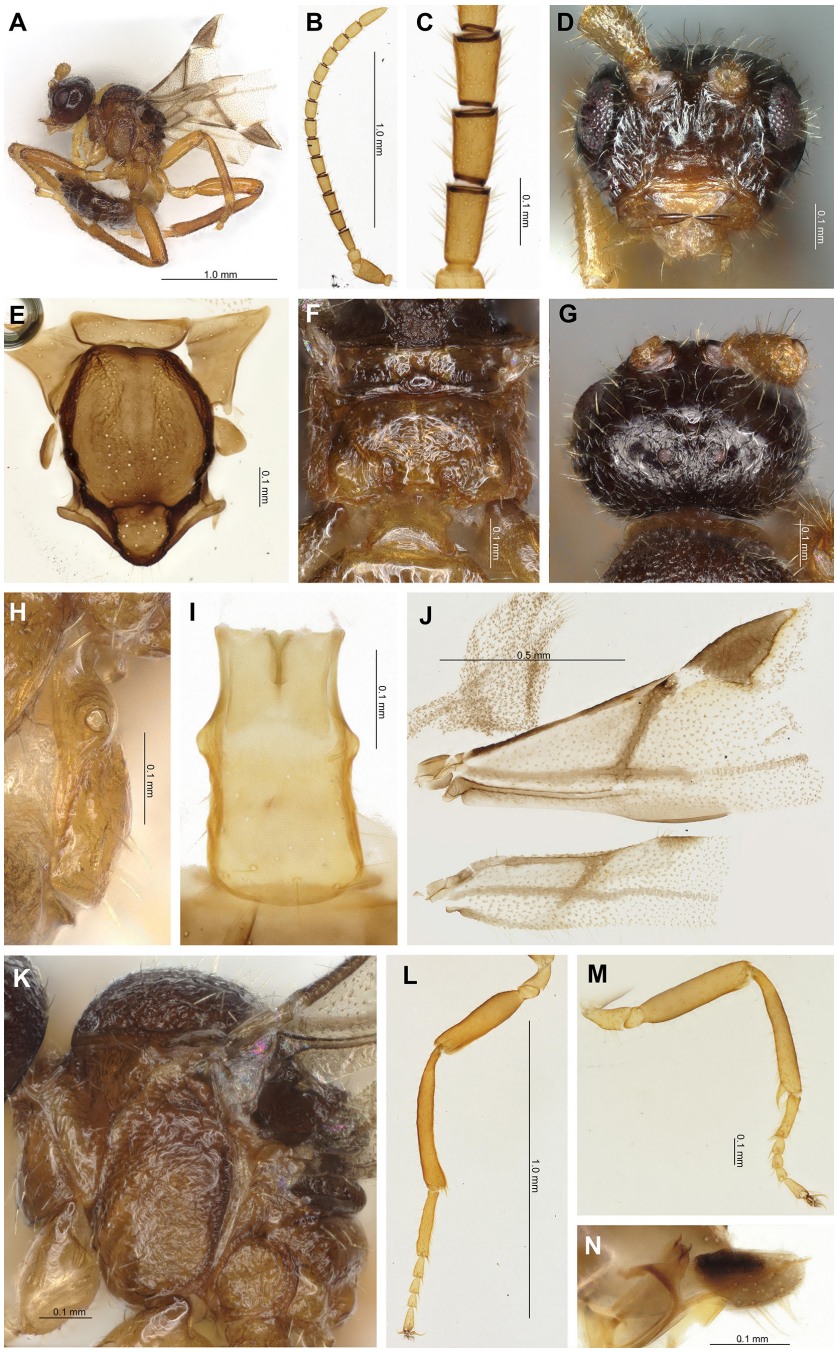

Figure 4. *Paralipsis eikoae*. **A** habitus, dried mounted **B** antenna, slide mounted **C** F1–3, slide mounted **D** head, dried mounted **E** mesoscutum, slide mounted **F** propodeum, dried mounted **G** dorsal view of head, dried mounted **H** lateral view of petiole, dried mounted **I** dorsal view of petiole, slide mounted **J** wings, slide mounted **K** lateral view of mesosoma, dried mounted **L** hind leg, slide mounted **M** fore leg, slide mounted **N** ovipositor sheath, slide mounted.

Mesosoma. Pronotum without pronope and subpronope; without pronotal sulcus (Fig. 4E). Mesopleuron finely rugulose–reticulate, with dense shallow impressions throughout (Fig. 4K). Scutellum nearly circular, protuberant; bearing numerous long setae, without scutellar sulcus carina (Fig. 4E).

Forewing. Pterostigma with colorless area in anteriorly (Fig. 4J).

Leg. Legs sparsely semi erected setose. Fore femur 4.2× as long as maximum width. Fore tibia 7.0× as long as maximum width with one tibial spur. Fore femur length subequal (0.9×) to fore tibia. Fore tarsus 3.1× as long as fore basitarsus; fore basitarsus with a single row of densely comb–shaped setae; second to fourth fore tarsomeres length equal to width, claws acute (Fig. 4M). Middle femur 3.8× as long as maximum width. Middle tibia 7.7× as long as maximum width with two tibial spurs. Middle femur length subequal (0.9×) to middle tibia. Middle tarsus 3.2× as long as middle basitarsus. Hind femur 3.7× as long as maximum width. Hind tibia 7.6× as long as maximum width. Hind femur 0.7× as long as hind tibia. Hind tarsus 2.3× as long as hind basitarsus (Fig. 4L).

Metasoma. Petiole 2.1× as long as width at level of posterior spiracles (Fig. 4H, I). Ovipositor sheath 1.9× as long as maximum width (Fig. 4N).

Comparison with previous description of Takada (1976). The antenna is shorter in the Korean specimens (1.8 mm; Fig. 4A) than in the material examined by Takada (2.0–2.2 mm). The eye is 0.7× as long as the temple in dorsal view in the Korean specimens (Fig. 4G), whereas Takada reported the temple to be approximately 0.59–0.63× as long as the eye. The face is 2.7–2.9× as wide as high in the Korean specimens (Fig. 4D), largely overlapping the range of 2.3–2.8× reported by Takada. F1 is slightly shorter relative to its basal width in the Korean specimens (2.3×; Fig. 4C) than in Takada's material (2.5–2.8×). Despite these differences, the principal diagnostic characters of the Korean specimens agree with those reported by Takada (1976).

Distribution. Japan, Russia, South Korea (this study).

Biology. Parasitoids of *Sappaphis piri* Matsumura, 1918 [Host plant: *Artemisia princeps* Pamp. (Asteraceae)] associated with colonies of *Lasius niger* (Takada and Hashimoto 1983); collected from nests of *Lasius japonicus* Santschi, 1941, with no aphids observed (this study).

Specimen examined. South Korea • 3 ♀; San14–4, Wonho–ri, Iljik–myeon, Andong–si, Gyeongsangbuk–do from *Lasius* (*Lasius*) *japonicus* colony; 05.V.2025; leg. S. Yoon; • 1♀ dried mounted; GenBank (Ap26008, YPC003131): *COI*, PZ412706; *28SD2*, PZ411505; *COII*, PZ416386; *Cytb*, PZ420654; *Wingless*, PZ447457; • 1♀ slide mounted; GenBank (Ap26007, YPC003129): *COI*, PZ412705; *28SD2*, PZ411504; *COII*, PZ416385; *EF1–alpha*, PZ447455; • 1♀ alcohol preserved; specimen code: YPC003160.

Biological notes. *Paralipsis eikoae* was collected from within nests of *Lasius japonicus*, but root-aphid colonies were not observed at the time of collection. The specimen (YPC003129) collected on 5 May 2025 retained intact wings at the time of collection. During laboratory observations, the female was repeatedly observed pulling its wings posteriorly using the apical parts of the hind tibiae (Suppl. material 8). Direct removal or detachment of the wings was not observed. However, at a later observation, part of

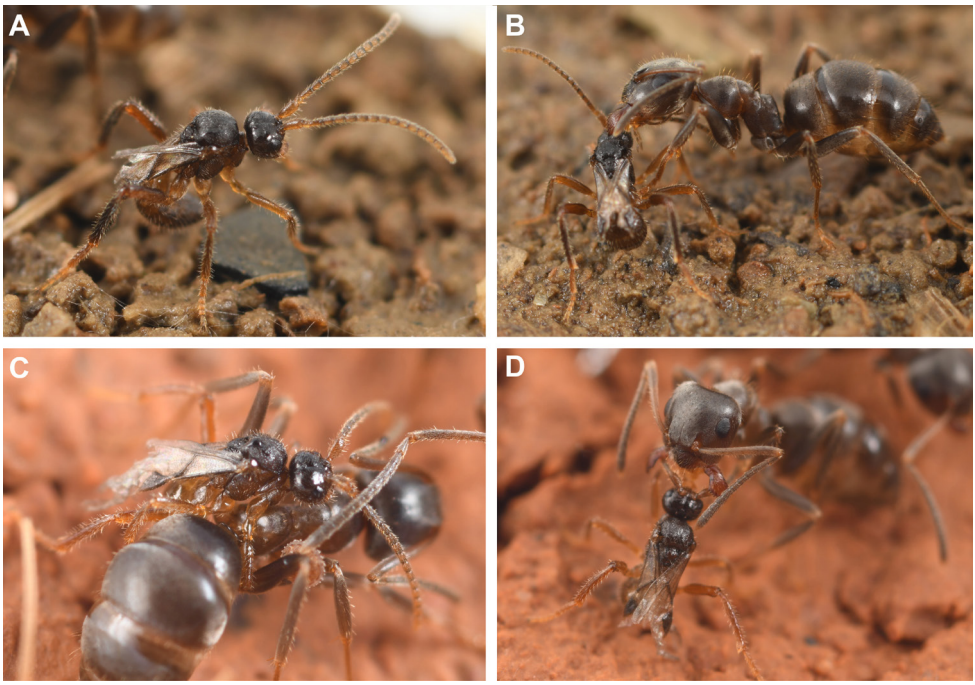

Figure 5. Biological characters of *Paralipsis eikoae*. **A** alive habitus **B** grooming **C** riding **D** trophallaxis.

the posterior margin of the forewing was found to be missing. Although wing removal by aphid-attending ants was not observed, it remains unclear whether the repeated pulling behavior contributed to the observed wing loss.

When encountering ant workers, *P. eikoae* exhibited riding behavior by mounting the dorsal surface of the ant. During riding (Fig. 5C, Suppl. material 9), the body of the parasitoid was positioned in close contact either between the legs of the ant worker or between the associated ant's gaster and hind leg. One foreleg grasped either the ant petiole or one of the legs, whereas the opposite foreleg was used to hook either the ant fore coxa or the mid leg. The *P. eikoae* repeatedly scraped the surface of the associated ant's gaster toward its own body with the mid tibia in a sawing motion while the antennae contacted those of the ant. Riding behavior was observed repeatedly and was frequently followed by trophallaxis with associated ant workers.

After repeated riding behavior, aphid-attending ants were observed grooming the body of *P. eikoae* (Fig. 5B). Trophallaxis was observed more frequently after honey water was provided. *P. eikoae* actively solicited trophallaxis by repeatedly tapping the mandibles of aphid-attending ant workers with its antennae and fore legs (Fig. 5D, Suppl. material 10). The parasitoid was also observed periodically in an antenna-cleaning behavior. During the behavior, the wasp hooked the base of antennae with the fore

tibial spur (=calcar) and pushed it distally, cleaning the antenna with the dense comb of setae on the basitarsus (= 1st tarsomere).

A myrmecophilous cricket (*Myrmecophilus* sp.) collected from the same colony was observed licking the hind legs of *P. eikoae* during or immediately after riding behavior. Because Myrmecophilus crickets are known to acquire host-ant cuticular hydrocarbons through direct physical contact, and *P. eikoae* can acquire ant cuticular hydrocarbons through mounting and rubbing against workers, this licking behavior may be related to ant-derived cuticular hydrocarbons present on the parasitoid (Akino et al. 1996; Akino and Yamaoka 1998). However, this is possibility was not chemically tested in the present study.

Genetic relationships of the species in the genus *Paralipsis*

A gene tree was constructed using 19 sequences from eight species, including two outgroup species. Two strongly supported ingroup clades were recovered: the first was further divided into two subclades, *P. enervis* + *P. brachycaudi* and *P. tibiator* + *P. triangulata* sp. nov., whereas the second comprised *P. eikoae* and *P. rugosa* (Fig. 6). In the first clade, *P. enervis* was sister to *P. brachycaudi*, whereas *P. tibiator* was sister to *P. triangulata* sp. nov. In the second clade, *P. eikoae* was recovered as sister to *P. rugosa.*

Genetic distance analysis revealed mean intraspecific distances among species ranged from 0.000 to 0.027 (average 0.012), while interspecific distances spanned from 0.042 to 0.089 (average 0.065) (Table 2). The interspecific genetic distances between *P. triangulata* sp. nov. and *P. tibiator* ranged from 0.040 to 0.044 (average 0.042). The pairwise interspecific genetic distances between *P. eikoae* and *P. rugosa* were identical, with a value of 0.069.

The ABGD and bPTP analyses produced largely congruent clustering patterns, although minor discrepancies were observed in two clades. The ABGD analysis delimited all examined species as distinct species, whereas the bPTP analysis further split *P. brachycaudi* and *P. tibiator* into two groups, respectively.

Table 2. Calculated genetic distances based on *COI* sequences among *Paralipsis* species included in the analysis, with values in parentheses indicating intraspecific genetic distances.

	***Paralipsis eikoae* (n = 2)**	***P. triangulata* sp. nov. (n = 2)**	***P. enervis* (n = 7)**	***P. tibiator* (n = 2)**	***P. rugosa***	***P. brachycaudi* (n = 3)**
Paralipsis eikoae (n = 2)	(0.000)					
P. triangulata sp. nov. (n = 2)	0.067	(0.000)				
P. enervis (n = 7)	0.064	0.049	(0.011)			
P. tibiator (n = 2)	0.065	0.042	0.045	(0.023)		
P. rugosa	0.069	0.067	0.068	0.066	–	
P. brachycaudi (n = 3)	0.087	0.076	0.056	0.066	0.089	(0.027)

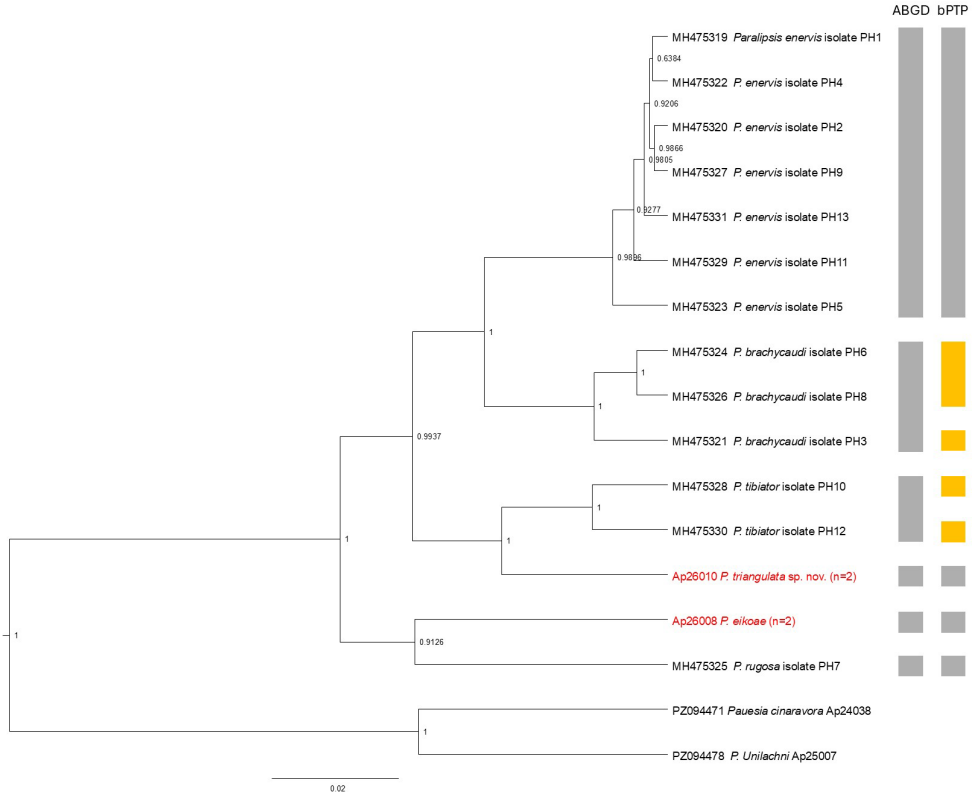

Figure 6. Gene tree of six *Paralipsis* species estimated by Bayesian method using their *COI* DNA barcode data. *Pauesia* spp. were used as outgroup. Scale bar indicates the expected rate of a nucleotide substitution.

Discussion

Mitrović et al. (2019) documented morphological differences among *Paralipsis* species, including strong rugosities of the propodeum and scutellum in *P. rugosa* and an elongated ovipositor sheath and petiole in *P. brachycaudi*. These differences provide useful characters for species discrimination. Mitrović et al. (2019) considered the elongated ovipositor sheath and petiole in *P. brachycaudi* as apomorphic characters, strong rugosities of the propodeum and scutellum *in P. rugosa* as autapomorphic characters, and possession of very short flagellomeres in *P. enervis*, *P. rugosa* and *P. tibiator* as plesiomorphic characters. However, their interpretation as ancestral or derived states requires independent evidence of character polarity. Accordingly, the present study uses morphological characters for diagnosis and comparison without inferring their evolutionary direction from the *COI* gene tree.

The ABGD and bPTP analyses produced largely congruent species-delimitation results but differed in the treatment of *P. brachycaudi* and *P. tibiator*. Whereas ABGD recovered groups corresponding to all species identified on morphological grounds, bPTP further split *P. brachycaudi* and *P. tibiator* into two groups each. The intraspecific

genetic distances within *P. brachycaudi* ranged from 0.018 to 0.035 (average 0.027), whereas the pairwise intraspecific distance within *P. tibiator* was 0.023. These values indicate relatively high mitochondrial divergence within both species. However, they were still lower than the observed interspecific distances among the examined species, and the bPTP subdivisions alone do not establish the presence of additional species.

The conflicting ABGD and bPTP delimitations of *P. brachycaudi* and *P. tibiator* indicate that the present *COI*-based analyses do not conclusively determine whether the subdivisions represent intraspecific variation or unrecognized species diversity. Mitrović et al. (2019) also reported substantial variation within *Paralipsis COI* lineages. The subdivisions recovered by bPTP are therefore treated here as provisional molecular groups requiring further investigation. Broader geographic sampling, morphological reassessment, and independent nuclear markers are needed to evaluate their taxonomic significance. The present *COI* gene tree is used for molecular comparisons and is not interpreted as a species phylogeny or as evidence of character evolution.

The biological observations reported here provide additional insight into the ant-associated biology of *Paralipsis*. Species of *Paralipsis* are known as endoparasitoids of root aphids and have close associations with ants attending root-aphid colonies (Starý 1966; Takada and Hashimoto 1985; van Achterberg and Ortiz de Zugasti Carrón 2016). In the present study, *P. triangulata* sp. nov. was collected from colonies of *Lasius koreanus*, whereas *P. eikoae* was collected from colonies of *L. japonicus*. The presence of presumed root-aphid mummies at the collection site of *P. triangulata* sp. nov. supports its association with root aphids, although the aphid host was not identified.

The behaviors observed in the present study resemble those previously reported for *P. eikoae*. Both *P. triangulata* sp. nov. and *P. eikoae* repeatedly mounted ant workers and scraped the surface of the ant gaster with the middle tibiae. Riding was frequently followed by grooming by associated ants and trophallaxis. Takada and Hashimoto (1985) described comparable riding and rubbing behavior in *P. eikoae*, and Akino and Yamaoka (1998) reported similarities between the cuticular hydrocarbon profiles of accepted females and resident ant workers. The riding and scraping observed in *P. triangulata* sp. nov. therefore resemble behaviors previously associated with the acquisition or maintenance of colony-specific chemical cues in *P. eikoae*. However, behavioral similarity alone does not demonstrate a shared chemical function, and hydrocarbon transfer was not tested in the present study. Trophallaxis was observed in both species examined here and has also been reported in *P. eikoae* and *P. enervis* (Takada and Hashimoto 1985; Völkl et al. 1996; Akino and Yamaoka 1998). Völkl et al. (1996) found that access to food regurgitated by ant workers increased adult survival in *P. enervis*. Our observations document similar food-receiving interactions in *P. triangulata* sp. nov., although their effects on survival or reproduction were not examined.

The cross-colony transfer experiment with *P. triangulata* sp. nov. also suggests the involvement of colony-specific recognition. The introduced parasitoid was attacked and killed by workers of a foreign *L. koreanus* colony. A worker from the parasitoid's source colony was also attacked when introduced into the same recipient colony. This observation was based on a single trial and should therefore be interpreted cautiously.

Nevertheless, it suggests that successful integration of *P. triangulata* sp. nov. may depend on colony-specific recognition cues rather than on ant species identity alone. A similar colony-specific pattern has been reported in *P. eikoae*, in which females from foreign colonies were initially attacked but could subsequently be accepted after riding and rubbing behavior (Takada and Hashimoto 1985). Whether *P. triangulata* sp. nov. can similarly acquire recognition cues from a foreign colony remains unknown.

Wing damage was already present in spring-collected females. All examined females of *P. triangulata* sp. nov. were collected in late April and already showed wing damage, whereas one female of *P. eikoae* collected in early May retained intact wings at the time of collection. However, the mechanism responsible for this change remains unresolved. Wing mutilation in *Paralipsis* has traditionally been attributed to aphid-attending ants. Maneval (1940) inferred ant-mediated damage from the symmetrical truncation and irregular margins of the wings of *P. enervis*. Starý (1966, 1970) subsequently described the wings as being mutilated by ants, although direct observation of the wing-cutting behavior was not reported. Völkl et al. (1996), however, did not observe wing mutilation by *Lasius niger* during experimental interactions with *P. enervis*. Instead, they frequently observed that the wings were lost through abrasion when parasitoids were maintained with plants and hosts in wet soil. Takada and Hashimoto (1985) also indicated uncertainty regarding the truncated wings of *P. eikoae*. Akino and Yamaoka (1998) also noted that when and how *P. eikoae* sheds its wings remained unknown. van Achterberg and Ortiz de Zugasti Carrón (2016) likewise regarded ant-mediated mutilation as only a possible explanation.

The present observations document wing-pulling behavior performed by the parasitoids themselves. One female of *P. eikoae* retained intact wings when collected and was subsequently observed repeatedly pulling its wings posteriorly with the apical parts of the hind tibiae. Although the actual loss of wing tissue was not observed, part of the posterior margin of the forewing was found to be missing at a later observation. In contrast, all examined individuals of *P. triangulata* sp. nov. already had damaged wings when collected. These individuals were subsequently observed pulling their damaged wings with the hind tibiae, which reached approximately the damaged regions, but the process that initially caused the damage was not observed. Thus, wing-pulling was directly observed in both species, but its contribution to wing damage remains unconfirmed. Neither ant-mediated removal nor self-removal of wing tissue was directly observed.

Taken together, the available evidence suggests that wing reduction in *P. eikoae* may occur during or shortly after entry into an ant-attended root-aphid colony and before reproductive activity begins (Takada and Hashimoto 1983; Akino and Yamaoka 1998). Fully winged and sexually immature females have been observed outside ant nests, whereas females residing within ant-attended root-aphid colonies are typically wing-reduced and remain reproductively inactive until later in the season (Takada and Hashimoto 1983; Akino and Yamaoka 1998). Males are known in several *Paralipsis* species, including *P. enervis*, *P. tibiator*, and *P. eikoae* (van Achterberg and Ortiz de Zugasti Carrón 2016; Mitrović et al. 2019). However, all specimens examined in the present study were female, and mating was not observed. The timing of mating within the proposed sequence remains unknown. The proposed sequence therefore concerns the female life history and is not intended to imply exclusively parthenogenetic repro-

duction. Based on these previous observations, a possible sequence for females is that fully winged females emerge from overwintered mummies, disperse, enter a suitable ant-attended root-aphid colony, undergo colony integration and wing reduction, and subsequently enter a resident phase before reproductive maturation and oviposition later in the season. The occurrence of wing-damaged *P. triangulata* sp. nov. in late April, together with its riding, rubbing-like contact, grooming, and trophallactic interactions with ants, suggests that this species may undergo a comparable transition. However, neither the timing of colony entry nor wing loss was directly observed in the present study, and reproductive diapause, seasonal ovarian development, timing of oviposition, and overwintering biology remain unknown in *P. triangulata* sp. nov. Therefore, whether the two species share the same annual life cycle requires direct seasonal observations.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Author contributions

Data curation: SK. Formal analysis: SK. Investigation: SY. Writing - original draft: SK, SY. Writing - review and editing: SK, SY, HK.

Author ORCIDs

S. Kim https://orcid.org/0000-0001-8395-8019
S. Yoon https://orcid.org/0009-0007-7370-1317
H. Kim https://orcid.org/0000-0002-1706-2991

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Video S1. Antennal cleaning behavior of *Paralipsis triangulata* sp. nov.
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: An adult female clean antenna using the fore tibial spur and the comb-like setae of the fore basitarsus.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl1

Supplementary material 2

Video S2. Riding behavior of *P. triangulata* sp. nov. on a worker of *Lasius koreanus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid mounts the dorsal surface of the ant and repeatedly scrapes the ant's gaster with the middle tibia.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl2

Supplementary material 3

Video S3. Grooming of *P. triangulata* sp. nov. by workers of *L. koreanus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: Aphid-attending ant workers groom the body of the parasitoid.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl3

Supplementary material 4

Video S4. Short grooming of *P. triangulata* sp. nov. by a worker *L. koreanus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: An aphid-attending ant worker grooms the body of the parasitoid for a short time.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl4

Supplementary material 5

Video S5. Trophallaxis between *P. triangulata* sp. nov. and a worker of *L. koreanus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid receives liquid food from a host-ant worker.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl5

Supplementary material 6

Video S6. Solicitation of trophallaxis by *P. triangulata* sp. nov. and antennal cleaning behavior
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid solicits trophallaxis by rapidly tapping the mandibles of a *L. koreanus* worker with its antennae and fore legs. Subsequently, the parasitoid clean antenna.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl6

Supplementary material 7

Video S7. Wing-pulling behavior of *P. triangulata* sp. nov.
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid, whose already damaged at the time of collection, pulls its wings posteriorly using the apical parts of the hind tibiae. The hind tibiae reach approximately the damaged regions of the wings.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl7

Supplementary material 8

Video S8. Wing-pulling behavior of *P. eikoae*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid repeatedly pulls its wings posteriorly using the apical parts of the hind tibiae.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl8

Supplementary material 9

Video S9. Riding behavior of *P. eikoae* on a worker of *L. japonicus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid mounts the host-ant worker and scrapes the surface of the ant's gaster with the middle tibia.
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Link: https://doi.org/10.3897/jhr.99.208537.suppl9

Supplementary material 10

Video S10. Trophallaxis between *P. eikoae* and a worker of *L. japonicus*
Authors: Sangjin Kim, Seonwoo Yoon, Hyojoong Kim
Data type: mp4
Explanation note: The parasitoid solicits and receives liquid food from a host-ant worker.
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