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**Research article**

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# Descriptions and biological data on three new species of Trigonalyidae (Hymenoptera: Trigonalyoidea) from South Korea

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**Abstract.** Three new species of Trigonalyidae, belonging to three genera, are described and illustrated from South Korea: *Jezonogonalos koreana* sp. nov., *Lycogaster clauseni* sp. nov., and *Orthogonalys inornata* sp. nov. We discuss their possible biology based on collection data, and for *Lycogaster clauseni* on rearing records. We confirm that *Lycogaster clauseni* is a regular parasitoid of Eumeninae larvae.

**Keywords.** *Jezonogonalos koreana*, *Lycogaster clauseni*, *Orthogonalys inornata*, checklist.

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## Introduction

The family Trigonalyidae Cresson, 1887 comprises a group of about 150 usually rare parasitoid or hyperparasitoid wasp species, distinguished from all other families of Apocrita Gerstaecker, 1867 by a characteristic combination of morphological traits and a uniquely complex biology (Clausen1929,1940; Carmean & Kimsey 1998; Yamane 2014).

As far is as known, all species of Trigonalyidae lay several thousand minute eggs along the edges of plant leaves. Successful hatching requires ingestion of these eggs by a phytophagous host larva (the primary host, typically Lepidoptera Linnaeus, 1758 or symphytan Hymenoptera Linnaeus, 1758). For the wasp's development to be completed, in most cases the primary host has to be consumed by a secondary host. In most cases, the secondary host is the larva of an internal parasitoid wasp or fly developing within the primary host. However, in a few genera Trigonalyidae emerge from the brood cells of social Vespidae Latreille, 1802, after the parasitized primary host has been provisioned as food. This unlikely chain of events explains the very large number of eggs that has to be laid, and the usually very low density of adults in the wild.

To date, the Korean fauna of Trygonalyidae comprises eight species within two genera, *Taeniogonalos* Schulz, 1906, and *Bareogonalos* Schulz, 1907 (Teranishi 1929; Carmean & Kimsey 1998; Lelej 2003; Kim *et al.* 2020; Lee *et al.* 2024; Kim & Tripotin 2024).

In this study, we describe and illustrate three new species from Korea, belonging to three different genera: *Jezonogonalos koreana* sp. nov., *Lycogaster clauseni* sp. nov., and *Orthogonalys inornata* sp. nov. These are the first records of these genera in Korea, significantly augmenting the known distribution of Trigonalyidae in the Far East. Generic diagnoses are refined, incorporating characteristics observed in the species described here, and checklists of extant species of the three genera are provided. Biological data for the three new species are also presented and discussed.

## Material and methods

### Morphological terms, photography and measurements

The terminology for body structures primarily follows Carmean & Kimsey (1998).

Stacked images were taken with a Leica DMS 1000a digital camera, and measurements were made using its integrated image analyzer. Measurements of body parts were taken at their maximal dimensions. Frontal head length was measured along the midline, from the median dorsal margin of the head to the level of the posterolateral margin of the malar space. Distance between supra-antennal elevations was measured as the distance between the apices of the two supra-antennal elevations, easily measured in dorsal view of the head. Eye width and genal width were measured at the mid-length of the head in lateral view. Posterior head in descriptions refers to the area behind the eye, including vertex and gena; dorsal length of posterior head was measured as the distance between eye and occipital carina.

### Institutional abbreviations

DHU = Private collection of Jeong-Kyu Kim in Dongnam Health University, Suwon, South Korea
NIBR = National Institute of Biological Resources, Incheon, South Korea
PTC = Pierre Tripotin, private collection, Gongju, South Korea

### Other abbreviations

MT = Malaise trap

## Results

### *Taxonomy*

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Trigonalyoidea Cresson, 1887
Family Trigonalyidae Cresson, 1887

Genus ***Jezonogonalos*** Tsuneki, 1991

*Jezonogonalos* Tsuneki, 1991: 32. Type species: *Jezonogonalos marujamae* Tsuneki, 1991, by original designation.

*Pseudogonalos* – Lelej 1995: 12 (synonymized *Jezonogonalos* with *Pseudogonalos* Schulz, 1906).
*Jezonogonalos* – Carmean & Kimsey 1998: 70. — Tsuneki 2003: 4. — Chen *et al.* 2014 (resurrection from Lelej 1995); 2020: 84. — Tan et al. 2017: 27. — Zhang et al. 2022: 105.

**Diagnosis**

**Both sexes**

Body length 6.2–12.0 mm. Antenna with 23–27 segments; flagellomeres filiform, medial articles much longer than broad and scarcely thickened. Head in frontal view rounded and broad, but dorsal margin scarcely convex with more or less flattened broad median part (sometimes vertex with a weak median longitudinal depression, thus dorsal margin of head in frontal view slightly notched). Supra-antennal elevation well-developed, in dorsal view triangular to semicircular. Mandibular condyli close to eyes, mandibles sub-laterally attached to head in frontal view. Malar space shorter than antennal pedicel. Occipital carina broadened dorsally and invariably narrow laterally. Maxillary palps with 6 long and slender segments. Last segment of labial palp widened distally, forming an elongate asymmetrical triangle in shape. Metanotal disk, except anterior marginal portion, largely smooth and shiny. Anterior propodeal furrow well-developed with inner longitudinal keels, distinctly broadened in its median part. Propodeal foramen reverse V-shaped, but foramen carina semicircular. Fore trochanter subparallel-sided and distinctly longer than hind trochanter; hind trochantellus sub-posteriorly with vertical groove, forming posterior triangular compartment, seemingly two-segmented. Metasomal tergum I in dorsal view usually much broader than long (more distinct in female; but almost as long in male of *J. jiangliae* Chen, Archterberg, He & Xu, 2014), anteriorly with large hemi-spherical depression. Wings hyaline but usually with darkened spot covering pterostigma and anterior part of marginal cell below pterostigma, or often also expanding to posterior portion of submarginal cell I, entire submarginal cell II, and entire submarginal cell III. Metasomal sterna simple, without armature.

**Females**

Metasoma straight distally, sometimes with posterior two segments obliquely downward-directed. Posterior margin of metasomal sternum VI not forming distinct awl. Ventral margin of metasomal sternum II in lateral view weakly convex.

**Males**

Flagellomeres 12–18 with rounded or elliptical tyloids. Metasoma straight distally. Paramere tongue-shaped, length-to-width ratio variable. Aedeagus laterally flattened.

**Taxonomic remarks**

This genus was established by Tsuneki (1991), who based his description of *Jezonogonalos marujamae* Tsuneki, 1991 from Japan on a single old and poorly preserved specimen. Lelej (1995) contested this validity and included *J. marujamae* in the genus *Pseudogonalos* Schulz, 1906. However, Chen *et al.* (2014) re-instated *Jezonogonalos* Tsuneki, 1991, included in the genus two species (*J. laeviceps* (Tsuneki, 1991) and *J. satoi* (Tsuneki, 1991)) initially described by Tsuneki from Taiwan under the genus *Taiwanogonalos* Tsuneki, 1991, and described a number of new species from China. Other new Chinese species have recently been added (Tan *et al.* 2017; Chen *et al.* 2020; Zhang *et al.* 2022), bringing the number of *Jezonogonalos* species to 11. We agree with Chen *et al* (2014) on the validity of this genus.

**Included species and distribution**

Among the Trigonalyidae, the genus *Jezonogonalos* has been notable for its limited distribution, having been recorded only from Japan, continental China and Taiwan. The distribution of the genus is extended to Korea by a new species described in the present study. With 12 species described (Tsuneki 1991; Carmean & Kimsey 1998; Chen *et al.* 2014, 2020; Tan *et al.* 2017; Zhang *et al.* 2022; this study), the genus appears to be well diversified in continental China: *Jezonogonalos eburnalva* Zhang & Chen, 2022 (China: Yunnan); *J. elliptifera* Chen, Achterberg, He & Xu, 2014 (China: Sichuan); *J. jiangliae* (China: Tibet: Ranwu-Chayu); *J. koreana* sp. nov. (South Korea: Gyeonggi-do, Gangwon-do, Chungcheongnam-do, Chungcheongbuk-do, Daejeon Metropolitan City, Jeollabuk-do, Jeollanam-do, Gyeongsangnam-do);

*J. laeviceps* (Taiwan); *J. luteata* Chen, Achterberg, He & Xu, 2014 (China: Sichuan); *J. mandibularis* Tan & Achterberg, 2017 (China: Shaanxi); *J. marujamae* (Japan); *J. nigrata* Chen, Achterberg, He & Xu, 2014 (China: Sichuan); *J. nyingchinensis* Chen & Achterberg, 2020 (China: Tibet); *J. shaanxiensis* Tan & Achterberg, 2017 (China: Shaanxi); *J. satoi* (Taiwan).

***Jezonogonalos koreana*** sp. nov.
urn:lsid:zoobank.org:act:44CEDE53-2C06-4AEE-9F5B-5B3E15CFB59A
Figs 1–2

### Diagnosis

Both sexes of this new species can be distinguished from the other *Jezonogonalos* by the following combination of structural and color characters: broadened dorsal occipital carina with a pair of fovea-like depressions medially; arcuate, layered striae on the area above the propodeal foramen carina (Fig. 1G); elongated metasomal sternum III, measuring slightly more than half as long as metasomal sternum II (Fig. 1J); weakly fuscous, small spot on the fore wing, restricted to the pterostigma, anterior portion of the marginal cell, submarginal cell II and submarginal cell III (Fig. 1E); extensive pale yellow facial markings, covering supra-antennal elevation, larger lateral parts of the clypeus (paired large rounded spots), proximal portion of the mandible, inner orbits and the malar space (Fig. 2C).

### Etymology

The specific epithet is an adjective derived from its origin, Korea.

### Type material

#### Holotype

SOUTH KOREA – **Chungcheongnam-do** • ♀; Changdong 2-gu, Daedeok-gu; 19 Jun.–24 Jul. 2007; P. Tripotin leg.; MT set on tombs and gardens on small forested hills; NIBR.

#### Paratypes

SOUTH KOREA – **Gyeonggi-do** • 1 ♀; Yeogi-san, Suwon-si; 29 Jun. 1994; D.S. Gu leg.; DHU. – **Gangwon-do** • 2 ♀♀; along Hongcheon river, Magok-ri, Nam-myeon, Chuncheon-si; P. Tripotin; 70 m a.s.l.; 12 Jun.–11 Jul. 2004; MT at sunlit in clearing in a planted resinous forest; DHU • 1 ♀; same data as for preceding; PTC • 1 ♀; Nodong valley, Nodong-ri, Yongpyeong-myeon, Pyeongchang-gun; 37°42.08′ N, 128°28.89′ E; 26 Aug.–1 Oct. 2006; P. Tripotin leg.; 3 MTs in shaded forest area; PTC • 1 ♂; near Dongdaesa, Mt Odaesan; 37°44.31′ N, 128°35.71′ E; 800 m a.s.l.; 1 Oct.–11 Nov. 2006; P. Tripotin leg.; MT in old Korean fir forest; PTC. – **Chungcheongnam-do** • 1 ♂; near Boseoksa, Geumsan-gun; 15 Jun. 1998; P. Tripotin leg.; PTC • 1 ♂; same data as for preceding; 20–27 Jun. 1999; P. Tripotin leg.; MT on forest path; PTC • 2 ♂♂; same data as for preceding; 27–30 Jun. 1999; P. Tripotin leg.; MT under canopy; PTC • 1 ♂; same data as for preceding; 7–10 Jul. 1999; P. Tripotin leg.; DHU • 1 ♂; near Poyeonsa, Seokdong-ri, Nami-myeon, Geumsan-gun; 6–24 Jun. 2005; P. Tripotin leg.; MT in forested area; PTC. – **Chungcheongbuk-do** • 1 ♂; Yangji-ri, Cheongsong-myeon, Okcheon-gun; 36°18.92′ N, 127°41.99′ E; 26 May–12 Jun. 2021; P. Tripotin leg.; MT in clearing at edge of forest; DHU • 2 ♂♂; same data as for preceding; 19 Jun.–1 Jul. 2021; P. Tripotin leg.; PTC • 1 ♂; Hapgeum-ri, Dongi-myeon, Okcheon-gun; 36°18.28′ N, 127°58.97′ E; 6–19 Jun. 2021; P. Tripotin leg.; MT in deciduous forest along brooklet; DHU • 1 ♀, 5 ♂♂; same data as for preceding; 19 Jun.–1 Jul. 2021; P. Tripotin leg.; PTC • 1 ♂; Giotong-ri, Okcheon-up, Okcheon-gun; 36°19.85′ N, 127°35.71′ E; 20–24 Jun. 2021; P. Tripotin leg.; MT in clearing in deciduous forest; DHU • 1 ♂; same data as for preceding; 24 –29 Jun. 2021; P. Tripotin leg.; PTC. – **Daejeon Metropolitan City** • 2 ♂♂; Wa-dong; 36° 24.02′ N, 127°25.98′ E; 28 May–19 Jun.; 2006; P. Tripotin leg.; MT on wild *Rosa* L. patch; PTC • 3 ♀♀; Changdong 2-gu, Daedeok-gu; 25 Sep.–17 Nov. 2021; P. Tripotin leg.; MT on tombs and gardens; PTC. – **Jeollabuk-do** • 4 ♂♂; Bukjangri, Jeoksang-myeon, Muju-gun; 35˚98.15′ N, 127°69.01′ E; 12 Jun.–2 Jul. 2022; P. Tripotin leg.; MT on small terrace in deciduous forest; DHU • 1 ♀; same data as for preceding; 35˚09.87′ N, 127˚68.0937′ E; 250 m a.s.l.; 21 Jun.–2 Jul. 2022; P. Tripotin leg.; MT in deciduous forest on *Rubus* L.; PTC • 2 ♂♂; same data as for preceding; 35.96194 N, 127.69717 E; 515 m a.s.l.; 12 Jun.–2 Jul. 2022; P. Tripotin leg.; MT on rivulet in deciduous forest; PTC • 3 ♂♂; same data as for proceding; 2 Jul.–22 Aug. 2022; P. Tripotin leg.; DHU. – **Jeollanam-do** • 1 ♀; Oryang-ri, Sadeung-myeon, Geoje-si; 34˚5251 N, 128˚3031 E; Jun. 20–6 Jul. 2004; O.-C. Kwon leg.; DHU. – **Gyeongsangnam-do** • 1 ♀; Munsu-sa, Songjeon-li, Hamyang-gun; 400 m a.s.l.; 6–27 Jun. 2004; P. Tripotin leg.; MT in sunlit area of forest; PTC.

### Description

**Female** [holotype characteristics in square brackets]
MEASUREMENTS. Body length 7.8–10.3 [10.3] mm, fore wing length 6.3–8.2 [8.2] mm (Fig. 1A–B).

HEAD (Fig. 1C–D). In frontal view dorsal margin more or less flattened with slight median notch due to a slight longitudinal depression on vertex, appearing more or less transverse, approximately 1.3 × as broad as long. Dorsal length of posterior head 0.7–0.8 [0.8] × as long as dorsal length of eye. Genal width 1.3 × as long as eye width. Antenna with 23–24 [23] segments. Supra-antennal elevation moderately developed, in dorsal view nearly semicircular and approximately 1.5 × as broad as long; distance between supra-antennal elevation 0.29–0.40 [0.29] × as long as distance between eyes at level of supra-antennal elevation. Median length of malar space 0.5 × as long as anterior ocellus diameter. Occipital carina directed toward middle of hypostomal carina, terminates far from it, leaving considerable gap; broadened dorsally, median length approximately one-third of anterior ocellus diameter, medially with pair of deep fovea-like depressions partitioned by strong longitudinal keel. Frons above supra-antennal elevation sparsely to moderately punctate, punctures irregularly spaced by 1–3 puncture diameter; area between supra-antennal elevations smooth, shiny; lower frontal area lateral to toruli, except near eyes, smooth and shiny; supra-antennal elevation densely punctate except posterior rim. Ocellar region, gena, vertex and occiput largely smooth with sparse, fine punctures being much smaller than those on frons. Clypeus with sparse, fine punctures. Supraclypeal area densely punctate except marginally. Mandible densely punctate in proximal vertical face and moderately punctate in remaining face.

MESOSOMA (Fig. 1F–H). Median lobe of mesonotum not strongly elevated, with anterior portion slightly higher than lateral lobes. Notauli broad and deep, with transverse inner keels over their entire length. Scutellar disk with shallow median longitudinal impression. Median length of anterior propodeal furrow about 0.8 × as long as anterior ocellus diameter. Propodeal foramen approximately 1.4 × as broad as long, foramen carina approximately 1.8 × as broad as long; tip of foramen almost touching foramen carina. Propleuron, lower half of pronotal side, almost entire posterior inclined face of mesopleuron, upper three-quarters of metapleuron shiny, with sparse and tiny punctures. Upper half of pronotal side densely punctate. Anterior two-thirds of mesopleuron punctate-reticulate. Lower quarter of metapleuron densely, longitudinally carinate. Mesoscutum coarsely sculptured, its lateral lobes more or less irregularly punctate-reticulate, anterior vertical face of median lobe largely smooth, almost entire dorsum of median lobe transversely ridged and partially irregularly reticulate. Anterior horizontal face of scutellar disk punctate-reticulate, posterior declivity densely punctate; scutellar trough with three to four longitudinal carinae [four carinae, innermost one shorter than others]. Metanotal disk smooth; metanotal trough posteriorly with three short longitudinal carinae. Anterior one-third of propodeal dorsum with fine rugae, except anterolateral smooth areas; posterior declivity arcuately striate. Propodeal sides irregularly reticulate.

METASOMA (Fig. 1I–J). Tergum I flat, in dorsal view 0.62–0.70 [0.65] × as long as broad posteriorly, with hemi-spherical depression in anterior half; bottom of depression with dense radial ridges originating from articulation; posterior flat area with very fine, sparse punctures. Terga II–VI sparsely to moderately

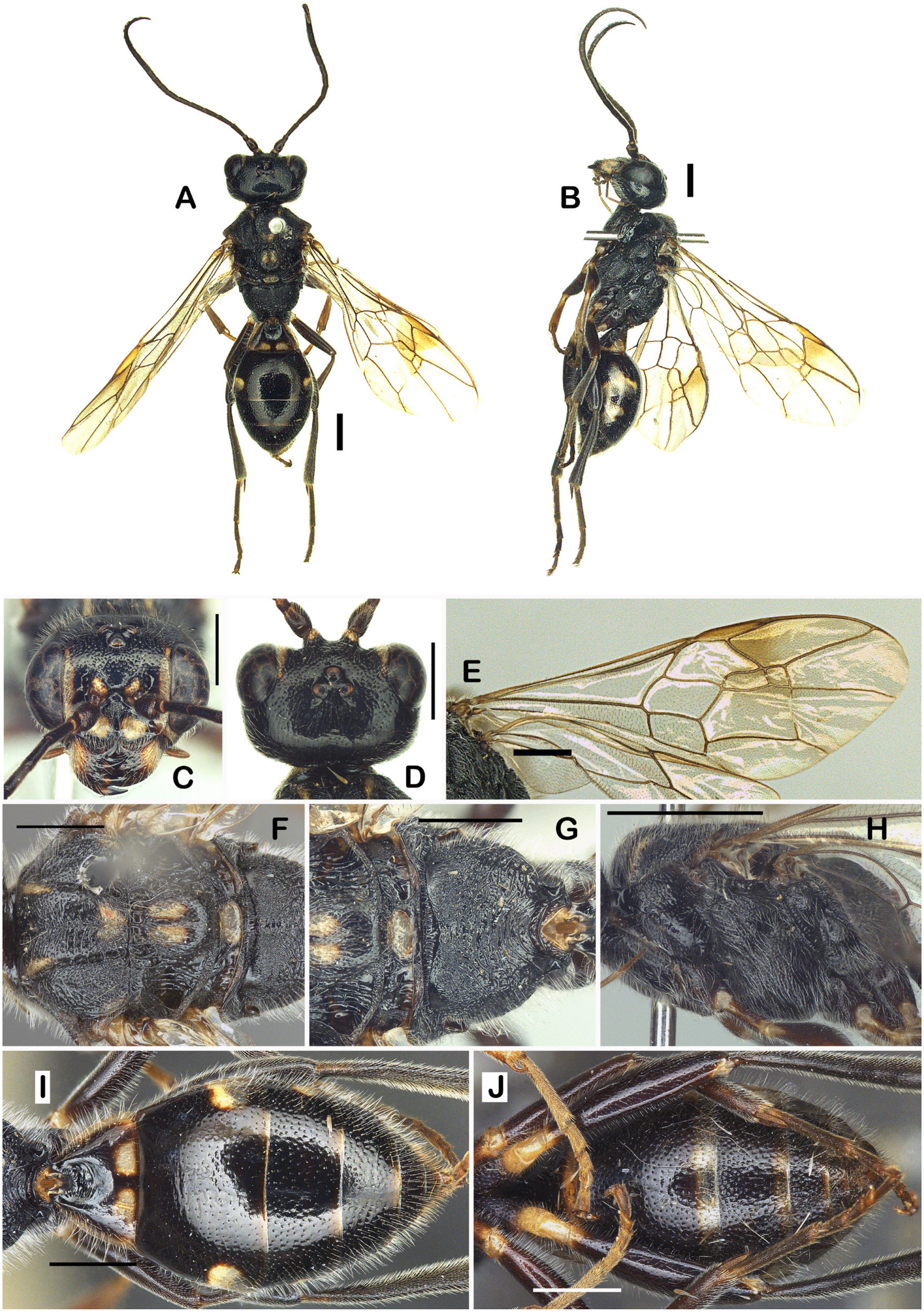


**Fig. 1.** *Jezonogonalos koreana* sp. nov., holotype, ♀ (NIBR). **A**. Whole body, dorsal view. **B**. Whole body, lateral view. **C**. Head, frontal view. **D**. Head, dorsal view. **E**. Wing. **F**. Mesosoma, dorsal view. **G**. Posterior part of mesosoma, dorsal view. **H**. Mesosoma, lateral view. **I.** Metasoma, dorsal view. **J**. Metasoma, ventral view. Scale bars = 1 mm.

punctate except posteriorly, punctures finer than those on sterna. Sternum I moderately punctate, with sparser punctures in large posteromedian portion. Sterna II–VI densely punctate, with sparser punctures in posteromedian portions of sterna II–III.

Setae. Almost entire body covered with suberect to erect whitish setae.

Wings (Fig. 1E). Hyaline but weakly fuscous on pterostigma, anterior quarter of marginal cell, submarginal cell II, and submarginal cell III. Submarginal cell II not petiolate proximally, anteriorly receiving 1m-cu (only in one paratype submarginal cell II shortly petiolate proximally and im-cu received by submarginal cell I), much longer than submarginal cell III (2.1–3.4 [2.5] × as long as submarginal cell III), and almost as high as submarginal cell III.

Color. Body largely black, with pale yellow to bright yellow markings and parts as follows: pair of large rounded clypeal spots, proximal half of mandible, inner orbits, supra-antennal elevation except semitransparent brownish posterior rim, pronotal collar, anterior one-third of lateral margins of median

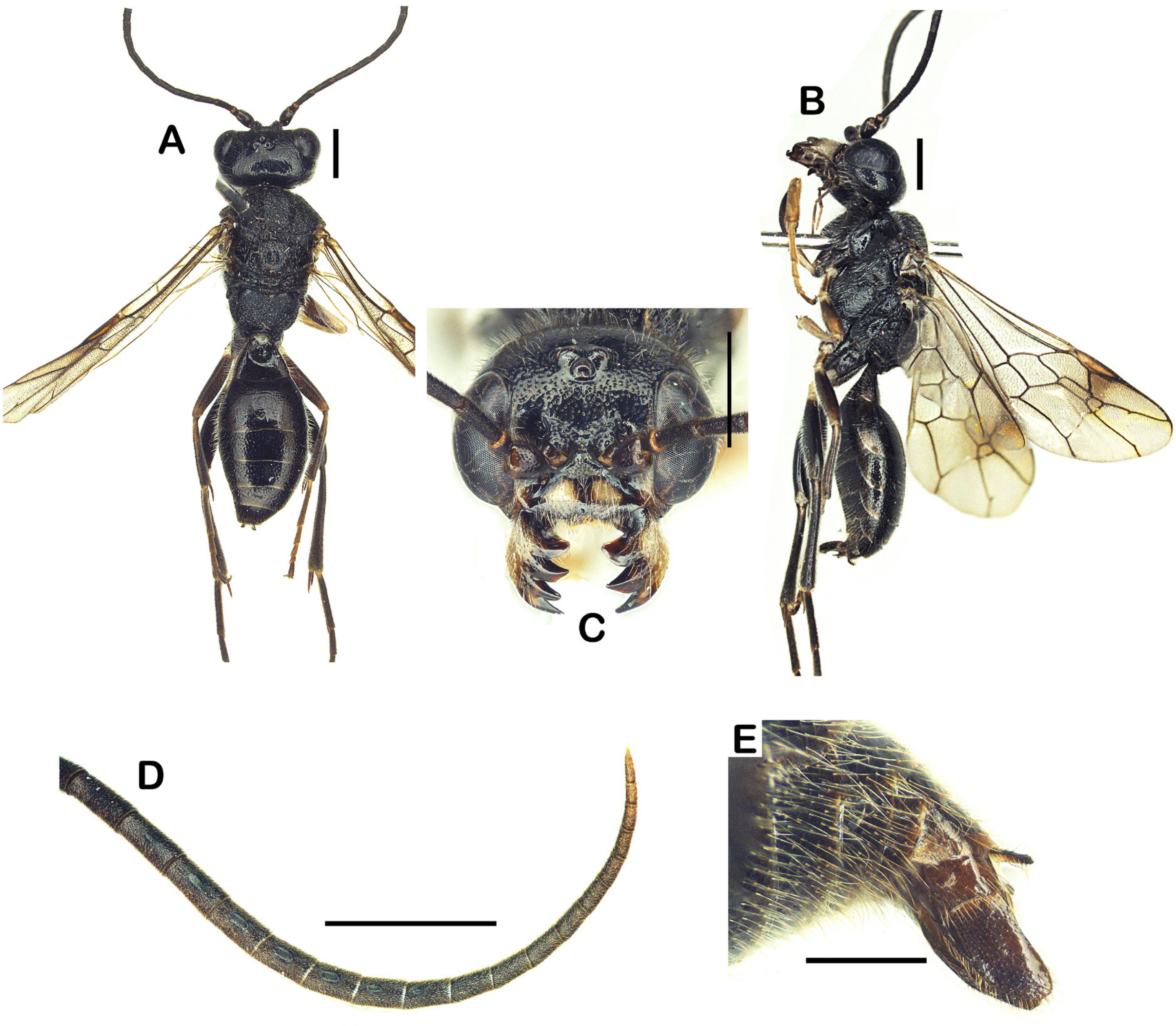


**Fig. 2.** *Jezonogonalos koreana* sp. nov., paratype, ♂ (DHU). **A**. Whole body, dorsal view. **B**. Whole body, lateral view. **C**. Head, frontal view. **D**. Antennal flagellomeres with tyloids. **E**. Posterior metasomal segments with exposed paramere, lateral view.. Scale bars: A–D = 1 mm; E = 0.5 mm.

lobe of mesoscutum, posterolateral margins of mesoscutum (lacking in one paratype), posteromedian cordate spot on mesoscutum (lacking or oval in some paratypes), pair of long elliptical spots in scutellar disk, almost entire metanotal disk, pair of posterior spots on metasomal tergum I (lacking in one paratype), posterior band on metasomal sternum I, spots on mid lateral margins of metasomal terga I–III, trochanter and trochantellus of hind leg. Posterior half of mandible ferruginous. Trochanters, trochantelli and femur of fore and mid legs largely chestnut to reddish brown. Tibia and tarsomeres of foreleg brownish yellow. Posterior margins of metasomal sterna II–III semi-transparent brownish to ferruginous.

**Male**

As in female, but differs in the following details. Body length 9.4–9.8 mm, fore wing length 7.4–8.1 mm (Fig. 2A–B). Antenna with 22–26 segments; flagellomeres 8–14 with oval-shaped tyloids, those in flagellomere 8 and 14 much smaller (Fig. 2D). Metasomal tergum I in dorsal view 0.66–0.76 × as long as broad posteriorly. Submarginal cell II 1.9–3.0 × as long as submarginal cell III, not petiolate proximally, anteriorly receiving 1m-cu (Fig. 2D). Body with more reduced yellow markings (Fig. 2A–C): supra-antennal elevation, inner orbit, mesoscutum, scutellum, metanotum and metasoma without markings. Paramere in lateral view 1.9 × as long as broad (Fig. 2E).

### Biology

No host record or association is available for any species of the genus *Jezonogonalos*. In Korea, about 40 specimens of this species have been caught in Malaise traps set in various forested areas, usually in the company of several other species of *Taeniogonalos*. Specimens were collected in open, deciduous or mixed forests with a rich undergrowth. Adults were flying close to the ground vegetation usually in mid-shaded places, but also sometimes in sun-exposed situations. The males of this species were locally quite abundant in the traps, the females much scarcer (ratio 1:3), possibly an artifact due to the oviposition of females higher on the vegetation. The species was on the wing from early June to mid July, with another, much reduced generation in late fall (October).

Our series of specimens collected at various locations shows a relatively large and uniform body size, an unusual feature within Trigonalyidae. This may indicate a more restricted range of potential hosts, as previously suggested for *Taeniogonalos subtruncata* Schulz, 1906 in Korea (Kim & Tripotin 2024).

According to Chinese records, the genus *Jezonogonalos* seems to occur mostly in elevated, mountainous areas, usually around 1500 m a.s.l. and up to 2500 m a.s.l. in Tibet. This may be an artifact due to collecting efforts focused mainly on large protected natural areas that are usually mountain ranges. However, in South Korea *J. koreana* occurs in forested areas from lowland (Daejeon, 200 m a.s.l.) to mid elevated mountainous areas (Mt Odaesan, 900 m a.s.l.).

### Distribution

South Korea.

## Genus ***Lycogaster*** Shuckard, 1841

*Lycogaster* Shuckard, 1841: 121. Type species: *Lycogaster pullatus* Shuckard, 1841, by original designation.

*Lycogaster* – Weinstein & Austin 1991: 414. — Carmean & Kimsey 1998: 61. — Chen *et al.* 2014: 45.

**Diagnosis**

**Both sexes**

Body length 4.6–15.0 mm. Antenna with 22–24 segments. Head frontally rounded. Flagellomeres usually spindle-shaped (medial articles more or less thickened), but sometimes nearly filiform. Supra-antennal elevation not distinctly elevated, obtuse triangle in dorsal view, broader than long, with smooth posterior lamellate rim. Vertex strongly swollen, in frontal view its dorsal margin convex, highly raised above posterior ocelli. Mandibular condyli close to eyes, mandibles sub-laterally attached to head in frontal view. Malar space shorter than antennal pedicel. Genal carina meeting lateral edge of mandibular base in Asian species and hypostomal carina in New World species (Carmean & Kimsey, 1998). Maxillary palps with 6 segments very long and slender. Last segment of labial palp widened distally, elongate asymmetrical triangle in shape. Metanotal disk, except anterior marginal portion, smooth and shiny. Anterior propodeal furrow well-developed with inner longitudinal keels, more or less broadened in its median part. Propodeal foramen carina reverse V-shaped. Fore trochanter subparallel-sided and distinctly longer than hind trochanter; hind trochantellus sub-posteriorly with vertical groove, forming posterior triangular compartment, seemingly two-segmented. Metasomal tergum I much broader than long (more distinct in females), anteriorly with large hemi-spherical depression. Wings weakly fuscous, without distinct darkened spot.

**Females**

Posterior metasomal segments curved backward to metasomal sternum II. Metasomal sternum II sub-posteromedially with ledged armature with paired triangular teeth, or paired semi-circular lobes (flap-like in Chen *at al*. 2014), or semi-circular lobe; armature short, not projected over metasomal sternum III. Metasomal sternum III anteriorly with a narrow lamelliform transverse ledge. Metasomal sterna IV–V anteriorly with very short to evanescent ledges. In ventral view posterior margin of metasomal sternum V inverted trapezoidal, its posterolateral edges triangularly toothed. In ventral view posterior margin of metasomal sternum VI lengthwise funnel-shaped, forming awl (Fig. 3J; also refer to Yamane & Yamane, 1975: fig. 16).

**Males**

Antennal flagellomeres without tyloids. Posterior segments of metasoma obliquely downward-directed. Metasomal sternum II with armature or without. Metasomal sterna III–V anteriorly with flap-like to carina-like ledges. Parameres elongate, rounded, strap-like (Fig. 4D); aedeagus laterally flattened.

**Included species and distribution**

The genus *Lycogaster* Shuckard, 1841 is widely distributed across the eastern Palaearctic (Palaearctic China, Korea), Oriental (southern China, Myanmar, Laos, Thailand, Indonesia), Nearctic and middle Neotropical (USA, Mexico, Costa Rica) regions, but has a limited number of species. Nine species, including a new species in the present study have been described to date (Shuckard 1841; Cameron 1897; Magretti 1897; Chen 1949; Carmean & Kimsey 1998; Chen *et al.* 2014, 2020; Smith & Tripotin 2015; Tan *et al.* 2017; Zhang *et al.* 2022): *Lycogaster angustula* Chen, Achterberg, He & Xu, 2014 (China: Zhejiang); *L. apicipennis* (Cameron, 1897) (Costa Rica; Mexico); *L. clauseni* sp. nov. (South Korea: Incheon Metropolitan City, Gyeonggi-do, Chungcheongnam-do, Daejeon Metropolitan City, Chungcheongbuk-do, Jeollabuk-do, Gyeongsangbuk-do, Gyeongsangnam-do); *L. flavonigrata* Chen, Achterberg, He & Xu, 2014 (China: Fujiang, Jiangxi, Yunnan; Indonesia; Laos; Thailand); *L. nigralva* Chen, Achterberg, He & Xu, 2014 (China: Sichuan); *L. pullata* Shuckard, 1841 (USA, Canada); *L. rufiventris* (Magretti, 1897) (Myanmar; Thailand); *L. umbonata* Chen & Achterberg, 2022 (China: Yunan); *L. violaceipennis* Chen, 1949 (China: Zhejiang, Sichuan).

***Lycogaster clauseni*** sp. nov.
urn:lsid:zoobank.org:act:5A27BFA6-6A11-4E94-A6C5-C53D61648985
Figs 3–4

**Diagnosis**

This species closely resembles *L. angustula* known from China, particularly in the shape of the armature on metasomal sternum II (Fig. 3K) and coloration in females. However, both sexes of this species can be readily distinguished from *L. angustula* by the densely punctate mesoscutum and metasoma (Fig. 3G–J), which are almost smooth and shiny in *L. angustula*. Additionally, the paired sub-posterior teeth on metasomal sternum II shown in females are straight distally in this species, whereas their tips are ventrally bent in *L. angustula* (Dr H.-Y. Chen 2024, pers. com.).

**Etymology**

It is an honor to dedicate this species to Curtis P. Clausen, the senior American entomologist (28 Mar. 1893–28 Feb. 1976) and author of the famous reference book "Entomophagous Insects", who first discovered and described the unique biology of the Trigonalyidae. We are delighted to bring here some new informations on the fascinating biology of this family.

**Type material**

**Holotype**

SOUTH KOREA – **Chungcheongnam-do** • ♀; Songnae-ri, Maseo-myeon, Seocheon-gun; 36º01′47.19″ N, 126º43′35.77″ E; 9–17 Jun. 2017; O.C. Kwon leg.; MT; NIBR.

**Paratypes**

SOUTH KOREA **– Incheon Metropolitan City** • 1 ♀; Giljeon-dong, Yangdo-myeon, Ganghwa-gun; 37º40′12.65″ N, 128º28′1.70″ E; 27 Jun.–11 Jul. 2018; S. Yang leg.; MT; DHU. – **Gyeonggi-do** • 1 ♀; Seodun-dong, Suwon-si; 4 Sep. 2001; H.S. Lee leg.; DHU • 1 ♀; Osammi-dong, Osan-si; 6 Sep. 2011; J.K. Kim leg.; DHU. – **Chungcheongnam-do** • 1 ♀; Changdae-ri, Geumsan-gun; 17 Jun. 1996; P. Tripotin leg.; PTC • 1 ♂; Pohyeonsa, Seokdong, Nami-myeon, Keumsan-gun; 36º03.494′ N, 127º27.225′ E; 8–24 Jun. 2005; P. Tripotin leg.; MT; PTC • 2 ♂♂; same data as for preceding; 21–31 Aug. 2005; P. Tripotin leg.; MT; PTC • 7 ♀♀, 1 ♂; Songnae-ri, Maseo-myeon, Seocheon-gun; 36º01′47.19″ N, 126º43′35.77″ E; 22 May–5 Jun. 2017; O.C. Kwon leg.; MT; DHU • 6 ♀♀, 7 ♂♂; same data as for preceding; 16 Jun.–5 Jul. 2017; O.C. Kwon leg.; MT; DHU • 1 ♀, 1 ♂; same data as for preceding; 15 Jul.–1 Aug. 2017; O.C. Kwon leg.; MT; DHU • 4 ♀♀, 1 ♂; same data as for preceding; 14–27 Jun. 2018; O.C. Kwon leg.; MT; DHU • 1 ♂; same data as for preceding; 8–21 Aug. 2018; O.C. Kwon leg.; MT; DHU • 1 ♀, 2 ♂♂; same data as for preceding; 10–27 May 2019; O.C. Kwon leg.; MT; DHU • 12 ♂♂; same data as for preceding; 27 May–2 Jun. 2019; O.C. Kwon leg.; MT; DHU • 3 ♀♀, 8 ♂♂; same data as for preceding; 2–9 Jun. 2019; O.C. Kwon leg.; MT; DHU • 5 ♀♀, 8 ♂♂; same data as for preceding; 9–17 Jun. 2019; O.C. Kwon leg.; MT; DHU • 2 ♂♂; same data as for preceding; 17–23 Jun. 2019; O.C. Kwon leg.; MT; DHU • 1 ♀, 1 ♂; same data as for preceding; 23 Jun.–1 Jul. 2019; O.C. Kwon leg.; MT; DHU • 2 ♀♀; same data as for preceding; 8–15 Jun. 2020; O.C. Kwon leg.; MT; DHU • 1 ♀; same data as for preceding; 15–22 Jun. 2020; O.C. Kwon leg.; MT; DHU • 4 ♀♀; same data as for preceding; 22–29 Jun. 2020; O.C. Kwon leg.; MT; DHU • 1 ♀; same data as for proceding; 20–27 Jul. 2020; O.C. Kwon leg.; MT; DHU. – **Daejeon Metropolitan City** • 1 ♀; Jangdong-2-gu; 22 May 1995; P. Tripotin leg.; PTC • 1 ♀; same data as for preceding; 14 Jul. 1996; P. Tripotin leg.; PTC • 2 ♂♂; Changdong-2-gu, Daedeok-gu; 20 May –19 Jun. 2007; P. Tripotin leg.; MT; PTC • 2 ♀♀, 3 ♂♂; same data as for preceding; 19 Jun.–24 Jul. 2007; P. Tripotin leg.; MT; PTC. – **Chungcheongbuk-do** • 1 ♀; Seongnae-ri, Geumseong-myeon, Jecheon-si; 10 Jun. 1992; P. Tripotin leg.; PTC. – **Chungcheongnam-do** • 1 ♀; Bosoksa, Geumsan-gun; 13–15 Jun. 1999, P. Tripotin leg.; PTC. – **Gyeongsangbuk-do** • 1 ♀;

Heuibangyegok, Mt Sobaeksan, Yeongju-si; 14 Jul. 1997; D.K. Chung leg.; DHU. – **Jeollabuk-do** • 1 ♂; Mileuksan, Geumma-myeon, Iksan-si; 36º01′12″ N, 127º01′52″ E; 20 Jul.–9 Aug. 2004; P. Tripotin leg.; MT; PTC • 2 ♀♀; same data as for preceding; 10 Jun.–1 Jul. 2006; P. Tripotin leg.; MT; PTC. – **Gyeongsannam-do** • 1 ♀, 1 ♂; Munsusa, Mt Jirisan, Songjeon-ri, Hamyang-gun; 35º24.739′ N, 127º43.818′ E; 19 Jun.–9 Jul. 2005; P. Tripotin leg.; MT; PTC • 1 ♀; same data as for preceding; 5 Sep.–4 Oct. 2005; P. Tripotin leg.; MT; PTC.

### Description

**Female** [holotype characteristics in square brackets]

Measurements. Body length 4.6–11.4 [7.2] mm, fore wing length 3.4–8.5 [5.3] mm.

Head (Fig. 3B–C, F). In frontal view dorsal margin very convex, appearing rounded, 1.3–1.4 [1.4] × as broad as long. Posterior head strongly swollen and enlarged, dorsal length of posterior head 1.3–1.7 [1.4] × as long as dorsal length of eye, genal width 1.7 × as long as eye width. Antenna with 22–24 [23] segments. Occipital carina narrow throughout, reaching lateral edge of mandibular base. Supra-antennal elevation in dorsal view low obtuse triangular; distance between supra-antennal elevations 0.42–0.46 [0.43] × as long as distance between eyes at level of supra-antennal elevation; area between supra-antennal elevations medially with very tiny tubercle. Median length of malar space 0.61–0.67 (0.67) × as long as anterior ocellus diameter. Frons densely punctate to partially punctate-reticulate laterally; moderately punctate sublaterally, punctures spaced by 1–2 puncture diameter; impunctate and shiny mesally. Vertex, gena, ocellar region, area between supra-antennal elevations, supraclypeal area, clypeus, and mandible largely smooth, just with sparse, fine punctures that are much smaller than those on frons.

Mesosoma (Fig. 3F–G). Median lobe of mesoscutum much elevated, distinctly higher than lateral lobes. Notauli broad and deep, with inner transverse keels over their entire length. Scutellar disk with shallow median longitudinal impression. Propodeal foramen carina reverse V-like with apex arcuate, 1.25 × as broad as long. Propleuron, pronotum except for anterior vertical face and dorsum of pronotal collar, mesoscutum except for areas surrounding parapsidal lines and notauli, and mespisternum except for smooth lower portion of epimeron densely punctate, punctures stronger and larger than those on lower frons and almost contiguous. Large median portion of scutellum smooth and shiny; remaining marginal portion densely punctate, punctuation similar to mesoscutum. Metanotum smooth and shiny except densely punctate anterior and lateral marginal portions. Metapleuron largely smooth. Anterior propodeal dorsum, except anterolateral smooth areas, matte with oblique longitudinal striae; remainder dorsum areolate with median longitudinal area shiny and smooth; posterior declivity above foramen carina shiny and weakly areolate. Anterior three-quarters of propodeal side areolate; posterior quarter shiny with several longitudinal carinae.

Metasoma (Fig. 3H–K). Tergum I much broader than long, in dorsal view 0.43–0.59 [0.48] × as long as broad posteriorly, with hemi-spherical depression in its anterior three-quarters to almost entire dorsum [almost entire dorsum]; bottom of depression irregularly sculptured. Posterior margin of tergum II broadly and weakly concave medially; posterior margins of terga III–IV scarcely concave. Sternum II higher than tergum II in lateral view, posteromedially with pair of small, long, triangular, ledged protuberances more or less spinous (Fig. 3K); sternum III anteriorly with lamellate ledge, crescent-shaped medially, and narrow, sharp, carina-like laterally. Sub-posterolateral portions of terga V–VI more or less strongly bulging. Posterior flat part of tergum I moderately punctate except for smooth posterior rims; terga II–VI and entire sterna moderately to densely punctate, but punctures not contiguous.

Setae. Almost entire body covered with dense, suberect to erect whitish setae, except areas with fine punctures as in upper gena and occiput. Coxae, trochanters, trochantelli, femora ventrally with erect whitish setae; remainder legs with shorter appressed setae.

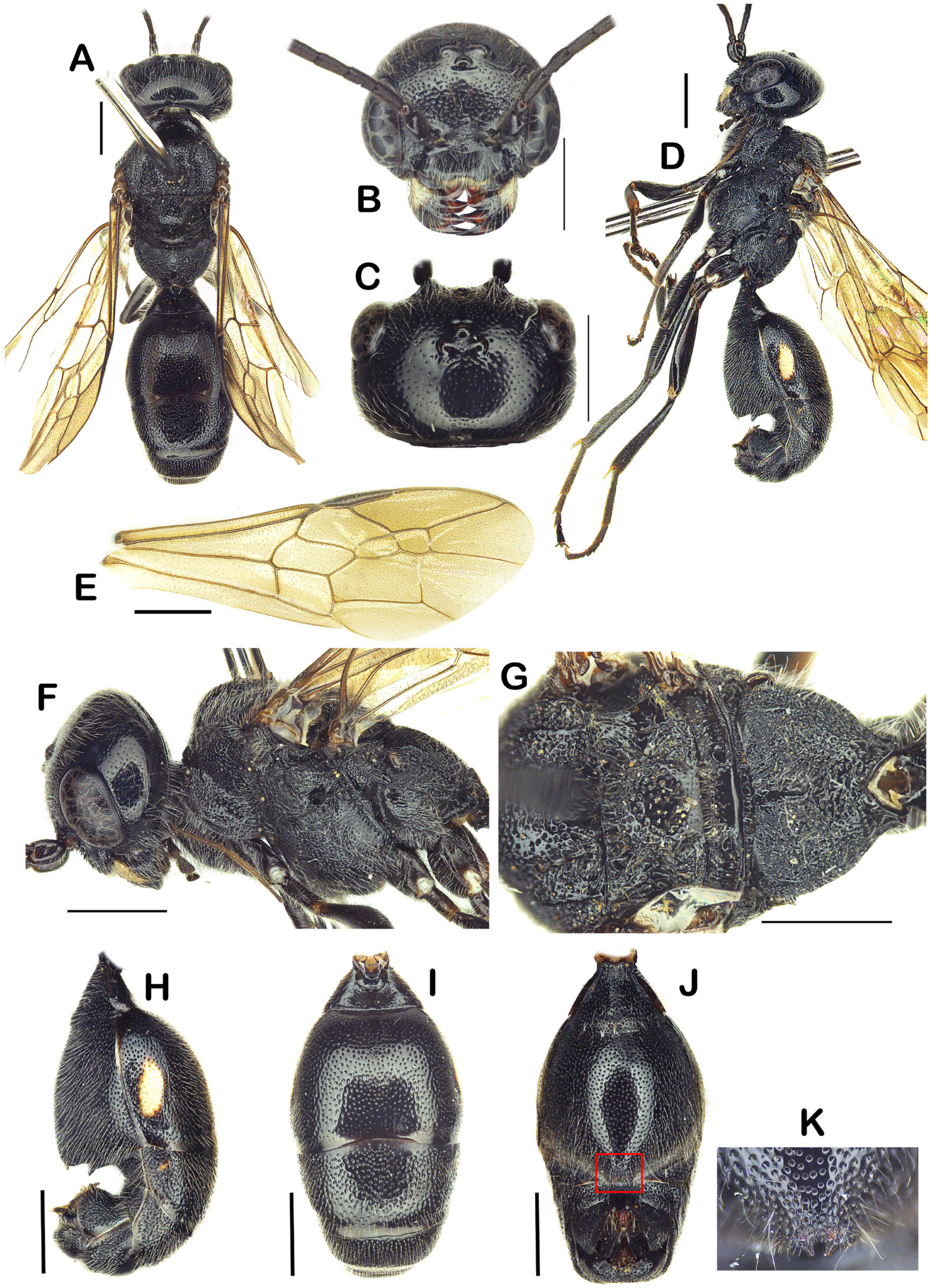


**Fig. 3.** *Lycogaster clauseni* sp. nov., holotype, ♀ (NIBR). **A**. Whole body, dorsal view. **B**. Head, frontal view. **C**. Head, dorsal view. **D**. Whole body, lateral view. **E**. Forewing. **F**. Head and mesosoma, lateral view. **G**. Mesosoma, dorsoposterior view. **H**. Metasoma, lateral view. **I**. Metasoma, dorsal view. **J**. Metasoma with a red square box indicating posteromedian part, ventral view. **K**. Posteromedian part of metasomal sternum II, with paired median spinous protuberances. Scale bars = 1 mm.

Wings (Fig. 3E). Almost entire wings very weakly fuscous; medial, submedial, first submarginal, discal, and subdiscal cells less fuscous. Submarginal cell II not petiolate proximally, anteriorly receiving 1m-cu, longer and slenderer than submarginal cell III, 1.2–1.4 [1.4] × as long as and 0.69–0.74 [0.73] × as high as submarginal cell III.

Color. Body almost entirely black. Proximal triangular marking on mandible and lateral long oval spot on metasomal tergum II creamy-yellow. Teeth of mandible, tegula, posteromedian teeth of metasomal sternum II, inner face of fore tibia, and posterior tip of T6 ferruginous [marking in posteromedian teeth of metasomal sternum II reduced as in Fig. 3K].

**Male**

As in female, but differs in following details. Body length 3.6–8.3 mm, fore wing length 3.5–6.2 mm. Antennae with 22–23 segments. Vertex less swollen than in female. Metasomal sternum II without armature, less swollen, slightly lower than metasomal tergum II in lateral view (Fig. 4A). Metasomal

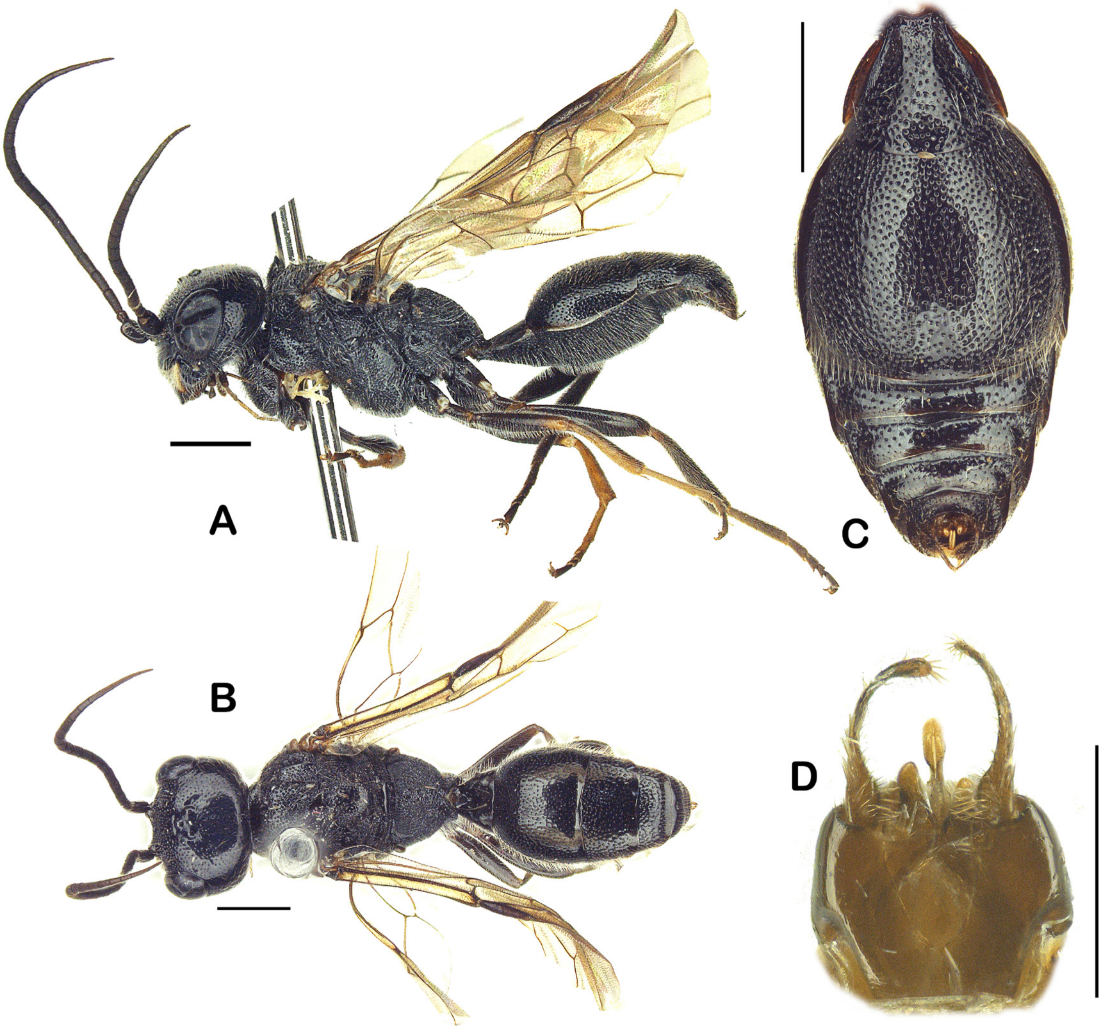


**Fig. 4.** *Lycogaster clauseni* sp. nov., paratype, ♂ (DHU). **A**. Whole body, lateral view. **B**. Whole body, dorsal view. **C**. Metasoma, ventral view. **D**. Genitalia extracted, ventral view. Scale bars: A–C = 1 mm; D = 0.5 mm.

sterna III–V anteriorly with very short ledges across sternal width (Fig. 4C). Metasomal terga V–VI not bulging sub-posteriorly. Posterior margins of metasomal sterna IV–V slightly concave, sternum VI more deeply concave but still much less semi-circular. Metasomal sterna III–VI much more sparsely punctate than other metasomal sterna (Fig. 4C).

Antennal flagellomeres ventrally chestnut colored; lateral spot on metasomal tergum II absent; fore tarsus, inner face of mid tibia, and mid tarsus yellowish brown (Fig. 4A–B). Genitalia as in Fig. 4D: paramere rounded strap-like with sparse setae; aedeagus extends far beyond digitus, with tip long elliptical in dorsal view.

### Biology

One of the authors (PT) has observed oviposition in natural conditions (Daejeon, Jangdong-2-gu, 14 Jul. 1996, small clearing on low hills) which follows the general pattern for the family. The microtype eggs were laid in mid shade along the edges of leaves of low deciduous plants or shrubs, with no apparent selection of the plant. On another occasion, a caged female laid plenty of eggs on leaves of different plants, including a low-growing Fabaceae Lindl. The eggs, rice-grain shaped and about 0.15 mm in length, are not inserted, but simply stuck on the underside of the leaf, at a constant distance of the edge (about 0.8 mm). As is usual for Trigonalyidae, the female lived only for a few days.

The species is encountered from mid May to the end of September, with staggered periods of emergence, and probably at least two generations a year.

In North America, *Lycogaster pullata* has been reared as a hyperparasitoid of Ichneumonidae Latreille, 1802 (including *Enicospilus* Stephens, 1835) in larvae of different families of moths (Saturniidae Boisduval, 1837, Erebidae Leach, 1815 (Arctiinae Leach, 1815), and Notodontidae Stephens, 1828, see Carmean & Kimsey 1998). Two other North American records (Cooper, 1954; Parker & Bohart, 1966) mentioned the emergence of *Lycogaster* from Eumeninae nests. However, Chen *et al.* (2014) were sceptical, writing: "The record from Eumeninae nests probably concerns prey caterpillars that have been infested with both Ichneumonidae and Trigonalyidae".

PT has collected Eumeninae nests intensively in Korea, and has obtained this species and observed the consumption of the larva of Eumeninae on a number of occasions, including: a very large female (12 mm) obtained from a larva of *Oreumenes decoratus* Smith, 1852 (Changdong-2-gu, Daejeon, adult emerged on 29 Apr. 1998); a very small female (5.5 mm) obtained from the larva of a minute, unidentified *Eumenes* sp. (Wadong, Changdong-2-gu, Daejeon, emerged on 16 May 1996); a small female (7 mm) obtained from the larva of *Eumenes rubronotatus* Perez, 1905 (Changdong-2-gu, Daejeon, nest collected on 4 Feb. 1996, emerged on Apr. 1996).

We can therefore confirm here without doubt that *Lycogaster clauseni* sp. nov. is found regularly in Eumeninae cells, and that the secondary (ultimate) host is the larva of the potter wasp.

The larva of *Lycogaster* emerges ventrally from the larva of Eumeninae during what is probably stage 4 (length about 3 mm), and then feeds externally until pupation. The feeding seems to rely on suction made possible by a sealing of the host's body fluids around the emergence hole. If broken, this fragile connection can not be reconstructed and the larva of *Lycogaster* will invariably die.

The young *Lycogaster* larva emerges from his host about 10 days after the beginning of the prepupal stage in the non-parasitized larvae of Eumeninae found in the same nest or locality. This stage is well marked in the larvae of Eumeninae by the appearance of a constriction between what will become the meso- and the metasoma in the future wasp. In parasitized hosts this constriction never occurs.

It is very likely that the emergence of the minute larva of *Lycogaster* is induced by a stimulus occurring in the eumemine host itself when it breaks its dormancy. Whatever the precise mechanism (hormonal signal, reactivation of the host's metabolism?), the dates of emergence of the parasitoid and its host (when not parasitized) are synchronized. The development of the larva of *Lycogaster* is rapid after it has begun to feed externally (about a month), and close to or only a few days longer than the host's normal pupal stage. Both host and parasitoid will emerge almost simultaneously. No cocoon is spun.

As seen above, the size of the imago (very variable, from 4 to 12 mm) depends on the size of the secondary host larva. This species is remarkable for its ability to achieve development on minute hosts. In the case of very large hosts, like some larvae of *Oreumenes decoratus*, the host is not consumed completely.

**Distribution**

South Korea.

**Remarks**

Two smaller female specimens (approximately 4.6 mm in body length) and three male specimens (approximately 3.6 mm) among the paratypes have an entirely shiny head with very sparse, tiny, or even evanescent punctures. The markings on the metasomal tergum II are also absent in these female specimens. Since no other features differ from those of the larger specimens, we consider them conspecific. The largest female specimen examined is more strongly punctate, with the frons almost punctate-reticulate.

Genus ***Orthogonalys*** Schulz, 1905

*Orthogonalys* Schulz, 1905: 76. Type species: *Orthogonalys boliviana* Schulz, 1905, by original designation.
*Satogonalos* Teranishi, 1931: 10. Type species: *Satogonalos debilis* (Teranishi, 1929), by original designation. Synonymized by Tsuneki 1991.

*Orthogonalos* – Schulz 1907: 8. — Marshakov 1981: 104. — Tsuneki 1991: 19. — Weinstein & Austin 1991: 421. Unjustified emendation.
*Orthogonalys* – Weinstein & Austin 1991: 421. — Carmean & Kimsey 1998: 52. — Chen et al. 2014: 60; 2020: 90. — Tan et al. 2017: 36.
*Satogonalos* – Weinstein & Austin 1991: 424. — Lelej 1995: 12.

**Diagnosis**

**Both sexes**

Body relatively slender, elongate, 3.5–14.1 mm long. Head rounded and broad in frontal view, but dorsal margin scarcely convex (appearing flat); sometimes vertex with a weak median longitudinal depression, thus dorsal margin slightly notched in frontal view. Antenna with 21–32 segments; flagellomeres filiform, often sub-posterior articles brightly colored (antennae banded). Supra-antennal elevation usually strongly produced, in dorsal view long semi-elliptic, as long as broad or longer than broad (except in *Orthogonalys formosana* Teranish, 1931 where it is low and triangular). Occipital carina invariably narrow laterally, slightly broadened medially, often with weak longitudinal inner keels. Mandibular condyli close to eyes, mandible sub-laterally attached to head in frontal view. Malar space almost as long as antennal pedicel. Maxillary palps with 6 segments very long and slender. Last segment of labial palp widened distally, long, asymmetrical triangle in shape. Anterior propodeal furrow very shallow and broad, sometimes slightly narrowed laterally, with inner longitudinal carinae. Propodeal foramen reversed U-shaped; foramen carina obtuse triangle (apex not pointed) to broad and low-semicircle. Fore trochanter subparallel-sided and distinctly longer than hind trochanter; hind trochantellus sub-posteriorly with vertical groove, posteriorly forming triangular compartment, seemingly two-segmented. Metasoma much less sclerotized than head and mesosoma. Metasomal tergum I almost entirely flat, without large anterior depression, at most with small depression surrounding articulation. Metasomal sterna simple, without armature; sternum II scarcely swollen. Wings hyaline, fore wing without dark spot.

**Females**

Metasoma more-or-less flattened ventrally, usually straight distally, at most posterior segments obliquely downward-directed. Metasomal sternum VI not forming awl.

**Males**

Antennae without tyloids. Paramere tongue-shaped; its length-to-width ratio variable. Aedeagus laterally flattened.

**Included species and distribution**

The genus *Orthogonalys* Schulz, 1905 has a very broad distribution, covering the Afrotropical (Ethiopia, Tanzania, Madagascar), eastern Palaearctic (Palaearctic China, Russian Far East, Korea, Japan), Oriental (India, Vietnam, Taiwan), and Neotropical (northeastern America) regions. Nineteen species including a new species in the present study have been described to date, including a remarkable diversification of six closely related species (five endemics) in Madagascar (Cresson 1867; Schulz 1905; Teranishi 1929, 1931; Bischoff 1933, 1951; Benoit 1951; Tsuneki 1991; Carmean & Kimsey 1998; Smith & Tripotin 2012; Chen *et al.* 2014, 2020; Tan *et al.* 2017; Zhang *et al.* 2022): *Orthogonalys albomaculata* Bischoff, 1951 (India); *O. boliviana* Schulz, 1905 (South America); *O. brevis* Smith & Tripotin, 2012 (Madagascar); *O. centrimaculata* Bischoff, 1951 (Vietnam); *O. cheni* Chen, Achterberg, He & Xu, 2014 (China: Zhejiang, Hubei, Sichuan); *O. inornata* sp. nov. (South Korea: Gangwon-do, Chungcheongnam-do, Daejeon Metropolitan City, Jeollabuk-do, Gyeongsannam-do); *O. clypeata* Chen, Achterberg, He & Xu, 2014 (China: Ningxia, Shaanxi, Sichuan, Guizhou, Yunnan); *O. elongata* Teranishi, 1929 (China: Henan, Sichuan, Tibet; Russian Far East; Japan: Hokkaido, Honshu, Shikoku); *O. formosana* Teranishi, 1931 (Taiwan); *O. fukuiensis* Tsuneki, 1991 (Japan: Honshu); *O. gigantea* Benoit, 1951 (Madagascar); *O. hagoromonis* Teranishi, 1929 (Russian Far East; Japan: Hokkaido, Honshu, Kyushu); *O. hova* Bischoff, 1933 (Madagascar); *O. maculata* Bischoff, 1933 (Madagscar); *O. paraclypeata* Tan & Achterberg, 2017 (China: Shaanxi); *O. parahova* Smith & Tripotin, 2012 (Madagascar); *O. pulchella* (Cresson, 1867) (northeastern America); *O. robusta* Chen, Achterberg, He & Xu, 2014 (China: Shaanxi, Guangxi); *O. seyrigi* Bischoff, 1933 (Tanzania; Madagascar).

***Orthogonalys inornata*** sp. nov.
urn:lsid:zoobank.org:act:169D8EE0-EDE9-4B71-A75C-3815C05A1D1E
Figs 5–6

**Diagnosis**

Both sexes of this species are easily distinguished from all other *Orthogonalys* by the completely black coloration except for distinctive yellow marks on mandibles and reddish-brown marks on some parts of the legs (Figs 5A–C, 6A–C). A well-developed supra-antennal elevation and a densely punctate head (particulary on supra-antennal elevation, clypeus, frons, mandible) and mesosoma (mesoscutum, scutellum) are also diagnostic.

### Etymology

The specific epithet is named after the Latin adjective *'inornata'*, meaning 'lacking decoration' ('inornate'), the species being remarkable for the absence of the bright markings usually encountered in this genus.

### Type material

#### Holotype

SOUTH KOREA – **Jeollanam-do** • ♀; Piagol valley, Mt Jirisan, Jikjeok, Toji-myeon, Gurye-gun; 35˚16.39′ N, 127˚33.91′ E; 1–15 Jun. 2003; C. Young leg.; MT on shade clearing in forest; NIBR.

#### Paratypes

SOUTH KOREA – **Gangwon-do** • 1 ♂; Nodong valley, Nodong-li, Yongpyeong-myeon, Pyeongchang-gun; 37°42.08′ N, 127°28.89′ E; 900 m a.s.l.; 5–14 Jun. 2006; P. Tripotin leg.; MT on shade area in larch-planted forest with small bamboo undergrowth; DHU • 1 ♀, 4 ♂♂; same data as for preceding; 14–23 Jun. 2006; P. Tripotin leg.; MT; PTC • 2 ♀♀, 5 ♂♂; same data as for preceding; DHU • 5 ♀♀, 2 ♂♂; same data as for preceding; 23 May–3 Aug. 2006; P. Tierre leg.; MT; PTC • 1 ♀; near Dongdaesa, Mt Odaesan; 37°44.31′ N, 128°35.71′ E; 800 m a.s.l.; 15 May–3 Jun. 2006; P. Tripotin leg.; 4 MTs in old Korean fir forest; DHU • 2 ♀♀, 3 ♂♂; same data as for preceding; 3–21 Jun. 2006; P. Tripotin leg.; MT; PTC • 2 ♀♀, 3 ♂♂; same data as for preceding; DHU • 2 ♀♀, 4 ♂♂; same data as for preceding; 21 Jun.–2 Jul. 2006; P. Tripotin leg.; MT; DHU • 1 ♀, 4 ♂♂; Balsan-ri, Nam-myeon, Chuncheon-si; 37°43.29′ N, 127°37.73′ E; 300 m a.s.l.; 17 May–6 Jun. 2006; P. Tripotin leg.; MT in shaded forest area with sparse low plants on soil; PTC • 1 ♀, 3 ♂♂; same data as for preceding; DHU • 1 ♂; same data as for preceding; 6–24 Jun. 2006; P. Tripotin leg.; MT; PTC. – **Chungcheongnam-do** • 1 ♂; near Pohyeonsa, Seokdong-ri, Nami-myeon, Geumsan-gun; 36°03.494′ N, 127°27.225′ E; 27 Apr.–14 May 2005; P. Tripotin leg.; MT in forested area; PTC • 4 ♂♂; same data as for preceding; 14 May–1 Jun. 2005; P. Tripotin leg.; MT; PTC • 2 ♀♀; same data as for preceding; 1–8 Jun. 2005; P. Tripotin leg.; MT; PTC • 1 ♂; Boseoksa, Seongguk-ri, Nami-myeon, Geumsan-gun; 36°03.073′ N, 127°28.688′ E; 2–7 Jul. 2005; P. Tripotin leg.; MT across forest trail; PTC • 1 ♂; same data as for preceding; 5–9 Jun. 1998; P. Tripotin leg.; MT; PTC • 1 ♀, 2 ♂♂; same data as for preceding; 21–25 May 1999; P. Tripotin leg.; MT; PTC • 1 ♀; same data as for preceding; 4–10 Jun. 1999; P. Tripotin leg.; MT; PTC • 1 ♀; same data as for preceding; 10–13 Jun. 1999; P. Tripotin leg.; MT; PTC • 1 ♂; same data as for preceding; 13–18 Jun. 1999; P. Tripotin leg.; MT; PTC • 1 ♂; same data as for preceding; 28–31 Jun. 1999; P. Tripotin leg.; MT; PTC. – **Daejeon Metropolitan City** • 1 ♂; Daedeok-gu; 36°24.02′ N, 127°25.98′ E; 6–28 May 2006; P. Tripotin leg.; MT along forest on wild *Rosa* L. patch; PTC • 1 ♀; same data as for preceding; 28 May–19 Jun. 2006; P. Tripotin leg.; MT; PTC • 1 ♂; same data as for preceding; 24 Apr.–20 May 2007; P. Tripotin leg.; 3 MTs on tombs and gardens on small forested hills; PTC • 2 ♀♀, 1 ♂; same data as for preceding; 20 May–19 Jun. 2007; P. Tripotin leg.; MT; PTC. – **Jeollabuk-do** • 1 ♀, 1 ♂; Geomok-ri, Jeoksang-myeon, Muju-gun; 35°96.194′ N, 127°69.717′ E; 515 m a.s.l., 15–26 May 2022; P. Tripotin leg.; MT near rivulet in deciduous forest; PTC • 2 ♀♀; same data as for preceding; 26 May–12 Jun. 2022; P. Tripotin leg.; MT; PTC • 2 ♀♀; same data as for preceding; 12 Jun.–2 Jul. 2022; P. Tripotin leg.; MT; PTC • 1 ♀; same data as for preceding; 35°98.147′ N, 127°68.937′ E; 250 m a.s.l.; 26 May–12 Jun. 2022; P. Tripotin leg.; MT in deciduous forest on *Rubus*; PTC • 1 ♀; Mileuk-san, Iksan-si; 10 Jun.–1 Jul. 2006; C. Young leg.; MT in forest; PTC. – **Gyeongsangnam-do** • 1 ♀, 2 ♂♂; Mt Jirisan, Samjeong-ri, Macheon-myeon, Hamyang-gun; 35˚20.55′ N, 127˚38.21′ E; 16–31 May 2003; P. Tripotin leg.; MT in shade forest edge along big clearing; PTC • 1 ♂; same data as for preceding; DHU • 2 ♀♀, 2 ♂♂; same data as for preceding; 1–15 Jun. 2003; P. Tripotin leg.; MT; PTC • 1 ♂; same data as for preceding; 22 Jun.– 6 Jul. 2003; P. Tripotin leg.; MT; DHU • 1 ♂; same data as for preceding; 11–18 May 2003; P. Tripotin leg.; MT near small mountain stream; PTC • 3 ♂♂; Munsusa, Mt Jirisan, Seongjeon-ri, Hamyang-gun; 35°24.739′ N, 127°43.818′ E; 400 m a.s.l.; 5 May–4 Jun. 2005; P. Tripotin leg.; MT near

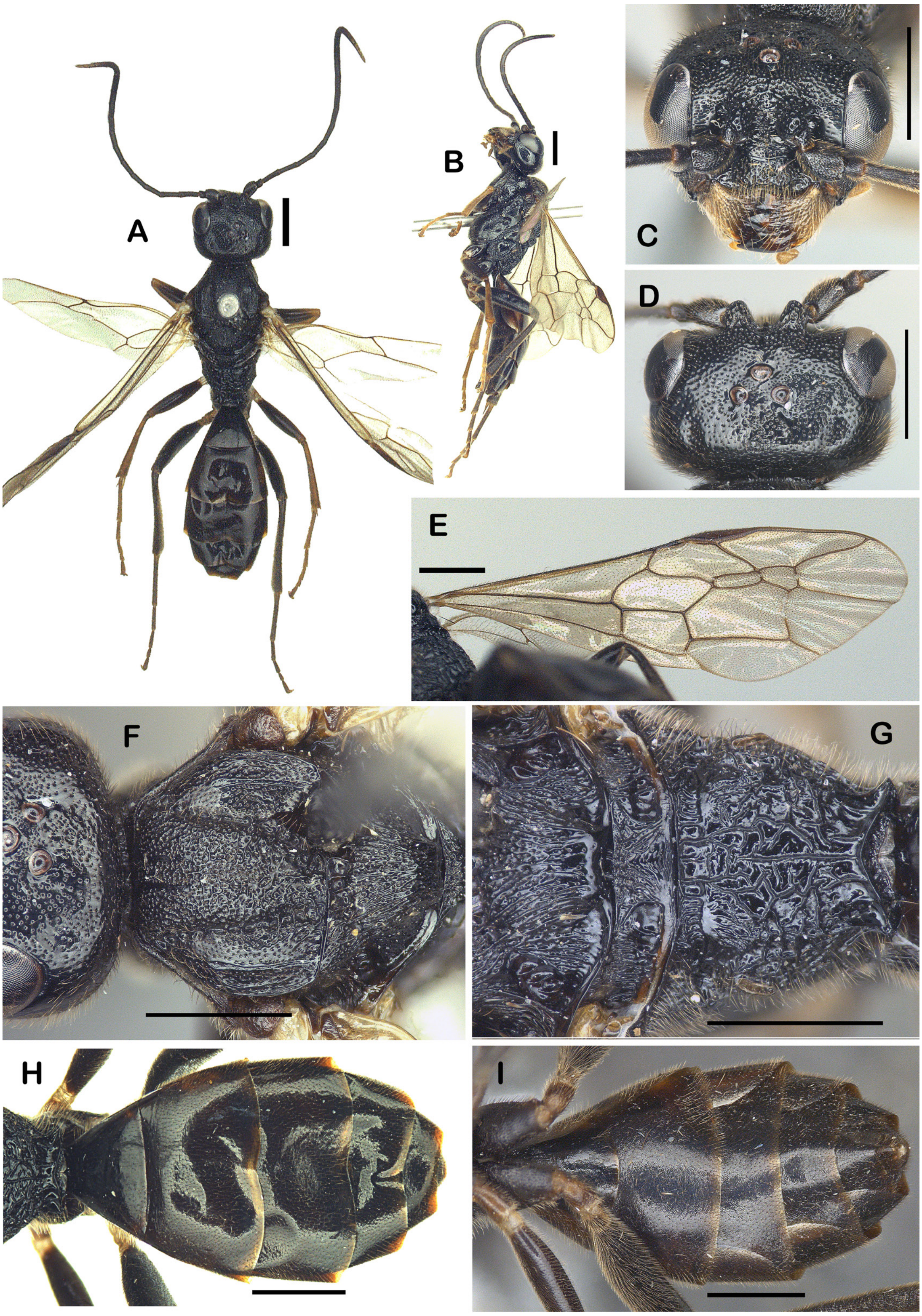


**Fig. 5.** *Orthogonalys inornata* sp. nov., holotype, ♀ (NIBR). **A**. Whole body, dorsal view. **B**. Whole body, lateral view. **C**. Head, frontal view. **D**. Head, dorsal view. **E**. Forewing. **F**. Posterior part of head and mesosoma excluding propodeum, dorsal view. **G**. Posterior part of mesosoma including scutellum, metanotum and propodeum, dorsal view. **H**. Metasoma, dorsal view. **I**. Metasoma, ventral view. Scale bars = 1 mm.

mountain stream in forested area; PTC • 2 ♀♀, 1 ♂; same data as for for preceding; 4–19 Jun. 2005; P. Tripotin leg.; MT; PTC.

### Description

**Female** [holotype characteristics in square brackets]

MEASUREMENTS. Body length 7.8–10.3 [10.2] mm, fore wing length 6.3–8.2 [8.1] mm.

HEAD (Fig. 5C–D). In frontal view 1.4 × as broad as long, with dorsal margin weakly rounded. Dorsal length of posterior head 0.9 × as long as dorsal length of eye, genal width 1.1 × as long as eye width. Antenna with 23–24 [24] segments. Supra-antennal elevation in dorsal view strongly and more or less divergently produced, asymmetrical semi-elliptic, sclerotized throughout, without posterior lamella; distance between supra-antennal elevations 0.33 × as long as distance between eyes at level of supra-antennal elevation; area between supra-antennal elevations with median tiny but distinct triangular tubercle. Median length of malar space almost as long as anterior ocellus diameter. Occipital carina meets hypostomal carina near inner edge of mandible, slightly broadened dorsally with weak longitudinal inner keels. Frons except inner orbits and depressions lateral to toruli, supra-antennal elevations, supraclypeal area, clypeus, and mandible except for teeth densely punctate to punctate-reticulate. Ocellar region and vertex sparsely punctate, punctures spaced by 1–2 puncture diameter and much smaller than those on frons; outer orbit broadly smooth, remainder gena sparsely punctate.

MESOSOMA (Fig. 5F–G). Median lobe of mesonotum highly elevated, much higher than lateral lobes. Notauli broad and deep, with transverse inner keels over their entire length. Anterior propodeal furrow shallow, not distinctly furrowed; very broad throughout, slightly narrower than anterior ocellus diameter, with pair of submedial longitudinal carinae extending to propodeal dorsum and weak shorter inner longitudinal carinae laterally. Propodeal foramen carina obtuse triangular with apex arcuate, about 4.1 × as broad as long, distant from foramen (Fig. 5G). Propleuron, pronotal side, almost entire posterior inclined face of mesopleuron, metapleuron, and areas lateral to scutellar and metanotal disks smooth and shiny, at most with sparse, tiny punctures. Median lobe of mesoscutum irregularly punctate-reticulate; lateral lobes densely punctate except smooth linear area surrounding parapsidal lines. Upper one-third of ventral mesopleuron longitudinally carinate, densely punctate in lower two-thirds. Dorsum of scutellar disk densely, longitudinally carinate; lateral vertical face irregularly reticulate; posterior declivity smooth and shiny. Metanotal disk with oblique fine striae medially and transverse striae posteriorly; metanotal trough with dense longitudinal carinae. Propodeal dorsum and side strongly areolate-rugulose.

METASOMA (Fig. 5H–I). Tergum I in dorsal view 0.83–0.87 [0.87] × as long as broad posteriorly; in lateral view slightly convex. Tergum I almost smooth anteriorly, minutely punctate posteriorly; terga II–VI and entire sterna weakly coriaceous with sparse, fine punctures.

SETAE. Entire body covered with short, suberect to erect, brownish yellow setae.

WINGS (Fig. 5E). Entirely hyalin. Submarginal cell II not petiolate to very shortly petiolate proximally [not petiolate], anteriorly receiving 1m-cu; longer and slenderer than submarginal cell III, 1.5–1.7 [1.6] × as long as and 0.46 × as high as submarginal cell III.

COLOR. Almost entire body black (Fig. 5A–B). Mandible except teeth yellow (Fig. 5C). Trochantelli of all legs, fore femur posteriorly, fore and mid tibiae, fore and mid tarsomeres yellowish brown (Fig. 5B).

**Male**

As in female, but differs in following details: body length 9.4–9.8 mm, fore wing length 7.4–8.1 mm. Antenna with 22–24 segments. Metasoma much slenderer (Fig. 6A, D). Metasomal tergum I in dorsal view almost as long as broad posteriorly (Fig. 6D). Submarginal cell II not petiolate proximally, 1.5 ×

as long as and 0.5 × as high as submarginal cell III; 1m-cu joining at junction of submarginal cell I and submarginal cell II. Paramere tongue shaped, 1.5 × as long as broad (Fig. 6E).

### Biology

This species prefers more shady, humid and cool habitats than the other Korean Trigonalyidae. It is abundantly collected from mid-May to the beginning of July at medium elevations (around 800 m a.s.l.) in forests but is also present in smaller densities at lower elevations in suitable habitats.

Surprisingly, despite efforts, one of the authors (PT) has never observed any specimen alive, all our 120 specimens having been collected in Malaise traps. The phenology shows a single generation per year (mostly from mid-May to the end of June): it is remarkable that no specimen has ever been found after mid-July in the numerous Malaise traps set in the same locations.

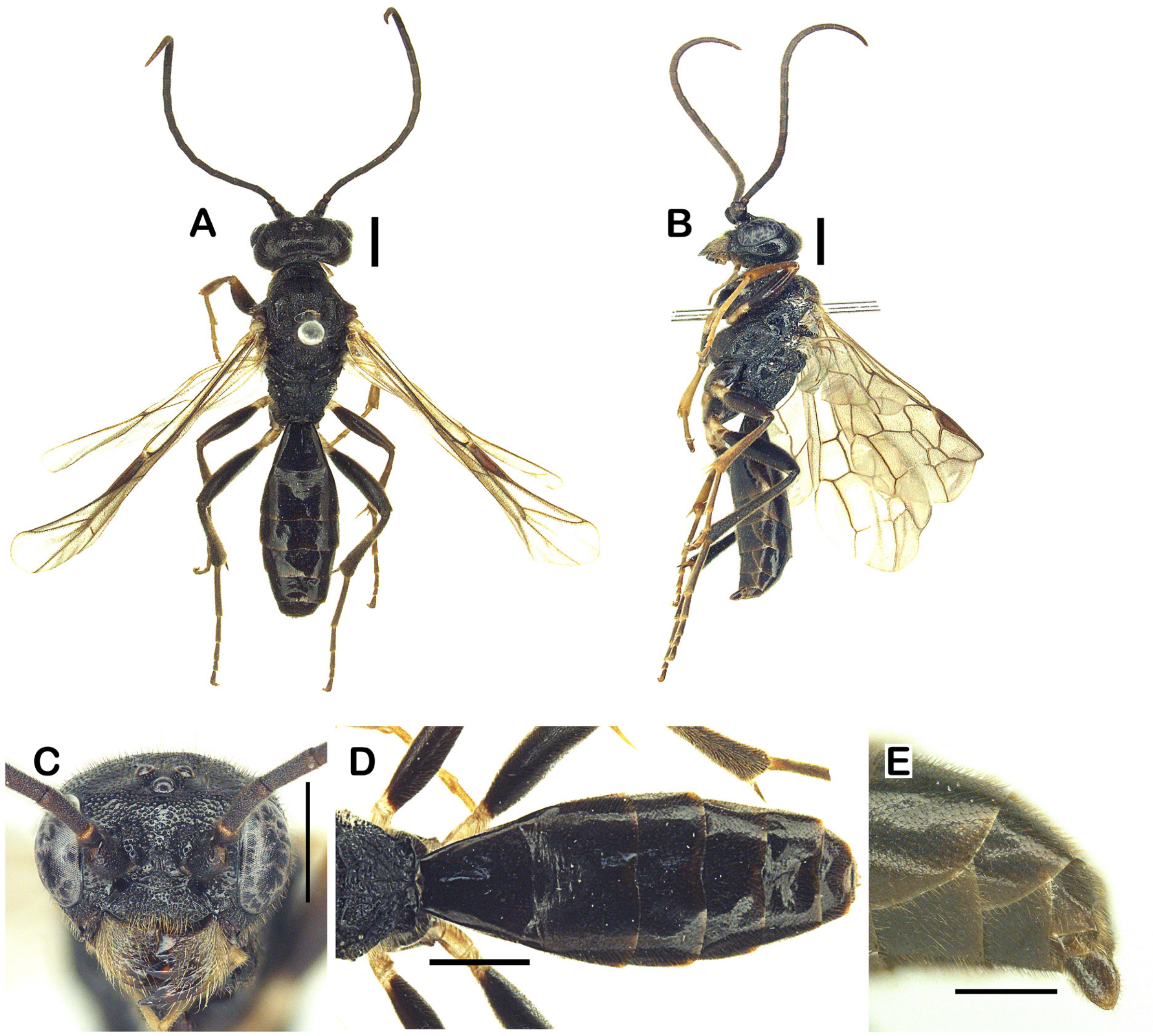


**Fig. 6.** *Orthogonalys inornata* sp. nov., paratype, ♂ (DHU). **A**. Whole body, dorsal view. **B**. Whole body, lateral view. **C**. Head, frontal view. **D**. Propodeum and metasoma, dorsal view. **E**. Posterior metasomal segments with exposed paramere, lateral view.. Scale bars: A–D = 1 mm; E = 0.5 mm.

Adults are constant in size, with only a few specimens smaller than the norm, and no minute specimens. This points toward a biology departing from the usual generalist biology of most Trigonalyidae, including other *Orthogonalys* species whose hosts are known, like *O. pulchella* from North America, recorded as a hyperparasitoid of Tachinidae Robineau-Desvoidy, 1830 in caterpillars (Carmean & Kimsey 1998; Murphy *et al.* 2009).

**Distribution**

South Korea.

## Discussion

### On the biology of *Lycogaster* Shuckard, 1841

One of the authors (PT), who has observed the larval development of *Lycogaster clauseni* sp. nov. on several occasions, has no doubt that this species is a regular parasitoid of a variety of genera and species of Eumeninae which prey on the larvae of Lepidoptera (and possibly also sawflies).

The life cycle of *L. clauseni* sp. nov. is thus different from what has been observed for two other species of Trigonalyidae (*Taeniogonalos formosana* (Bischoff, 1913) and *T. sauteri* (Bischoff, 1933)) also obtained from similar nests of Eumeninae (Kim & Tripotin 2024). In both cases, the parasitoid is introduced in the cell through an infected prey. But, as far as we know, both species of *Taeniogonalos* emerged from pupae of Diptera Linnaeus, 1758 (in our case Sarcophagidae Macquart, 1834) which consumed the prey, but without attacking the larvae of Eumeninae itself.

*Lycogaster clauseni* sp. nov. seems to have developed at least two adaptations for this peculiar range of hosts: the ability for the freshly emerged adult to escape the hard mud nest (no dead specimen of this species has ever been found in the hundreds of mud nests collected, while dead specimens of *T. formosana* are found quite regularly), and a better resistance to dehydration and direct sun exposure than most other Trigonalyidae, thus allowing this species to follow its Eumeninae hosts in more open and dry habitats than usual for Trigonalyidae.

PT has in his collection an unidentified specimen of *Lycogaster* from Indonesia, and the mud nest from which it emerged (Indonesia, Sumba, Isucam; 320 m a.s.l.; 10°01.197′ S, 120°3.385′ E; 19 Jun. 2010; Claire Villemant rec./leg.). The nest is a single large, spherical mud cell installed on a twig, in the manner done occasionally by *Oreumenes decoratus* in Korea (n.b., this monotypic genus not being present in Indonesia, the potter wasp is probably a *Delta* sp.).

Evidence shows that the emerged imago of *Lycogaster* is responsible for the consumption of the eumemine larva: 1) no trace of parasitism by Diptera (remains of pupa) or an ichneumonid or braconid (ovoid silk cocoon) has been detected, the walls of the cell being simply covered as usual with the typical rough silk spun by the mature larva; 2) the emerged larva of *Lycogaster* is large (11 mm, similar to the large specimen of *Lycogaster clauseni* sp. nov. obtained from a larva of *Oromenes decoratus*). If a second parasitoid was involved, the specimen of *Lycogaster* would have been smaller.

As a result, we can state that at least two species of *Lycogaster* are parasitoids of the larvae of Emeninae, or three if we take into account the two previous records for *Lycogaster pullata* in North America (Cooper, 1954; Parker & Bohart, 1966).

It seems reasonable to consider that more species of the genus would follow the same biological pattern. We hypothesize that the emergence of *Lycogaster* from the larvae of Eumeninae may be a specialization of the genus in general. Besides the general pattern of parasitism for the family (obligate hyperparasitism on parasitized phytophagous larvae, encountered in *Taeniogonalos*, *Orthogonalys*, etc.), and the derived genera which attack the social Vespidae (*Bareogonalos*, *Bakeronymus* Rohwer, 1922, *Seminota* Spinola, 1840, etc.), the larvae of *Lycogaster* would occupy a somewhat intermediate position, having developed a focus on solitary Vespidae as secondary hosts. Nevertheless, this specialization is probably not exclusive, as suggested by the emergence records of larvae of *Lycogaster pullata* on Ichneumonidae in North America (see Carmean & Kimsey 1998).

**On the biology of *Orthogonalys inornata* sp. nov.**

This species departs from the other species of *Orthogonalys* for which we have access to sufficient series (*O. hagoromonis* and *O. elongata* from Japan, and *O. pulchella* from the USA) by the strict emergence in spring in a single generation, and by the regularity in size. It also researches particularly shaded habitats, where it is often unusually abundant for a Trigonalyidae.

We hypothesize that the mechanism of correlation between the dates of emergence of the parasitoid and his host, as described above for *Lycogaster*, is also acting here. What other mechanism would explain the strict univoltinism of *Orthogonalys inornata*?

If true, *Orthogonalys inornata* sp. nov. would therefore focus, as primary host, on the phytophagous larvae of a peculiar species, or more likely a group of species, that emerges in spring and is strictly univoltine. This host larva must also be of sufficient size (at least 15 mm), favor particularly shaded habitats, and be reasonably abundant.

The specialization has to be strict. If not, the many eggs likely to be ingested by other phytophagous larvae would produce specimens emerging all over the year, as observed in other species of Trigonalyidae.

PT suspects that specimens of *O. inornata* sp. nov. may target the larvae of some large symphytans (Tenthredininae Latreille, 1802 like *Tenthredo* Linnaeus, 1758 and others, always on the wing in spring in the same habitats).

Furthermore, the remarkable regularity of size and the unusual abundance of specimens suggests that this species may be a simple parasitoid which directly consumes the phytophagous larva after having been ingested during the micro type egg stage. Again, if not, the result of parasitism would be series of specimens with a larger range of sizes (according to the size of secondary host), as encountered in the other species of *Orthogonalys*.

At present, among the Trigonalyidae family, only *Taeniogonalos venatoria* (Riek, 1962) from Australia is known to be a simple parasitoid (Weinstein & Austin 1991), in a genus where all the other species whose biology is recorded are hyperparasitoids. Surprisingly, this species also has a range of hosts restricted to sawflies (in this case, of the family Pergidae Rohwer, 1911, practically the only sawflies present in Australia) (Weinstein & Austin 1991).

More field work on this intriguing species, i.e., the systematic rearing of sawfly larvae in an area where *O. inornata* is also abundant, is needed to test this hypothesis.

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