J. Insect Biodiversity 77 (1): 060–070
https://www.mapress.com/jib

Article

ISSN 2538-1318 (print edition)
J. Insect Biodiversity
ISSN 2147-7612 (online edition)

https://doi.org/10.12976/jib/2025.77.1.10
http://zoobank.org/urn:lsid:zoobank.org:pub:CE6BBACF-5430-4805-94E8-B0A2F09948E7

Farther East: New Ghilarellinae wasps (Hymenoptera: Sepulcidae) from the Albian of the Republic of Korea extend the geographic range of the subfamily

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Abstract

The study of the invertebrate fauna of the lower Albian Jinju Formation (Republic of Korea) has experienced renewed interest over the past decade, with numerous new extinct species described each year. Among the various insect orders, Hymenoptera are relatively abundant in the assemblage, with many taxa being discovered and formally described on a regular basis. Within this group, Symphyta are particularly well represented, with series of specimens of varying preservation quality being documented. These newly discovered specimens frequently represent new species belonging to genera already known from subcontemporaneous deposits in China, Mongolia, and Russia, supporting the idea of a relatively homogeneous Early Cretaceous Asian entomofauna. Here, we further corroborate this pattern by describing a new species of Ghilarellinae assigned to the Asian genus *Ghilarella*, *Ghilarella jinjuensis* **sp. nov.** In addition, we describe a second species of the previously monotypic genus *Meiaghilarella*, which was formerly known only from Spain. The new species, *Meiaghilarella stanislawlemi* **sp. nov.**, substantially extends the geographic range of the genus during the Albian, from a previously restricted occurrence in Spain to a trans-Laurasian distribution.

Key words: Jinju Formation, Cretaceous, Korean Peninsula, new genus, new species

Introduction

The extinct family Sepulcidae is a lineage of sawfly wasps regarded as closely related to the extant Cephidae, and likely representing a stem lineage within Cephoidea (Rasnitsyn 1968, 1988). Recent molecular phylogenies place Cephidae—and therefore Cephoidea—as the sister group to the Vespina clade (Orussidae + Apocrita), recovering the relationship Cephidae + (Orussidae + Apocrita). Estimates for the origin of Cephidae vary widely: analyses focused on “Symphyta” evolution suggest an Early Jurassic divergence (Wutke *et al.* 2024), whereas broader studies of Hymenoptera evolution infer a Middle Triassic origin (Blaimer *et al.* 2023). In contrast, fossil-based estimates place the origin of the superfamily in the Late Triassic (Jouault *et al.* 2025).

The family Sepulcidae appears to have been notably diverse in deep time, with more than 50 species described so far from deposits ranging from the Early Jurassic to the Late Cretaceous (e.g., Kopylov & Rasnitsyn 2014; Li *et*

 Received: 15 Dec. 2025; Accepted by Yan-Zhe Fu: 26 Dec. 2025; published: 31 Dec. 2025

al. 2023, 2024). Its peak diversity occurred during the Late Jurassic–Early Cretaceous, and its earliest record, *Sogutia liassica* Rasnitsyn, 1977, is from the Lower Jurassic Dzhil Formation (Kyrgyzstan) (Rasnitsyn 1977; Kopylov & Rasnitsyn 2017a). A possible earlier occurrence, an isolated wing fragment attributed to *Sepulenia* sp. Rasnitsyn, 1968, from the Upper Triassic of Langenberg (Germany), has been mentioned, but the specimen was neither formally described nor illustrated (Barth *et al.* 2011). It should also be noted that sepulcid wings can easily be confused with those of Xyelidae: Madygellinae, a group that was widespread during the Triassic (Denisova *et al.* 2024). The family is currently subdivided into five subfamilies: Parapamphiliinae Rasnitsyn, 1968 (12 species); Sepulcinae Rasnitsyn, 1968 (three species); Trematothoracinae Rasnitsyn, 1988 (25 species); Ghilarellinae Rasnitsyn, 1988 (nine species, including two described in this work); and Xyelulinae Rasnitsyn, 1993a (12 species) (e.g., PBDB; Darling & Sharkey 1990; Rasnitsyn 1993; Rasnitsyn & Ansorge 2000; Jattiot *et al.* 2011; Kopylov & Rasnitsyn 2014, 2017a, b; Jouault & Nel 2021; Li *et al.* 2023). As fossiliferous insect deposits continue to be discovered—particularly in regions where Sepulcidae are already known, such as East Asia—the number of potential occurrences of the family has expanded accordingly. With the recovery of numerous insect fossils from the Jinju Formation (e.g., Rosse-Guillevic *et al.* 2023; Boderau *et al.* 2025), a unit contemporaneous or slightly younger than other formations in Russia and China (e.g., the Zaza and Yixian formations), we report here the first records of Sepulcidae—and specifically of Ghilarellinae—from the Republic of Korea.

The subfamily Ghilarellinae includes two genera: *Ghilarella* Rasnitsyn, 1988 (six species) and the monospecific *Meiaghilarella* Rasnitsyn & Martínez-Delclòs, 2000. Members of the subfamily have previously been recorded from Cretaceous deposits in China, Mongolia, Russia, and Spain (Rasnitsyn 1988, 1993b; Rasnitsyn & Martínez-Delclòs 2000; Kopylov & Rasnitsyn 2017b; Li *et al.* 2024).

Here, we report two additional taxa from the Jinju Formation (Republic of Korea): a new species of *Ghilarella* and the second species of the genus *Meiaghilarella*. These findings expand both the diversity of the subfamily and its known geographic range within East Asia.

Material and methods

The specimens were collected from the lower part of the Jinju Formation at the Jeongchon section (35°07′45″N, 128°06′02″E), 5.6 km south of the city of Jinju, Republic of Korea (see Park *et al.* 2019). The most recent detrital zircon analysis shows that the age of the lower boundary of the Jinju Formation is 112.4 ± 1.3 Ma, while the upper boundary is 108.7 ± 0.5 Ma; hence, the age of the formation can be considered early Albian (Lee *et al.* 2018). The Jinju Formation is referred to as the latest stage of the famous Jehol Biota by Kopylov *et al.* (2020b: p. 1236–1237). The fossils are preserved as a reflective carbonaceous film on different slabs of dark grey shale. The specimens are housed in the Gongju National University of Education, with registration numbers GNUE218033, and GNUE218046.

The fossils were photographed, under ethanol, with a Canon 6D camera with an attached Canon EF 100 mm lens. Wing venation and cell nomenclature are adapted from Goulet & Huber (1993).

This published work and its included nomenclatural acts are registered in ZooBank (https://www.zoobank.org), with the following LSID: urn:lsid:zoobank.org:pub:CE6BBACF-5430-4805-94E8-B0A2F09948E7.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Suborder Symphyta Gerstaecker, 1867
Superfamily Cephoidea Newman, 1834
Family Sepulcidae Rasnitsyn, 1968
Subfamily Ghilarellinae Rasnitsyn, 1988

Genus *Ghilarella* Rasnitsyn, 1988

Type species. *Ghilarella mercurialis* Rasnitsyn, 1988

Other species. *Ghilarella alexialis* Kopylov & Rasnitsyn, 2017; *Ghilarella elegantula* Li, Wang, Rasnitsyn & Shih, 2024; *Ghilarella jinjuensis* **sp. nov.**; *Ghilarella kopylovi* Li, Wang, Rasnitsyn & Shih, 2024; *Ghilarella masculina* Kopylov & Rasnitsyn, 2017; *Ghilarella nivalis* Rasnitsyn, 1993.

***Ghilarella jinjuensis* sp. nov.**

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(Figs 1–2)

Material. GNUE218033 (holotype, ♀), housed in the collection of the Gongju National University of Education, Gongju, Republic of Korea.

Etymology. Named after the city of Jinju (Republic of Korea) near the type locality.

Locality and horizon. Jinju Formation, Jeongchon section, near the city of Jinju, Republic of Korea; lower Albian, Lower Cretaceous.

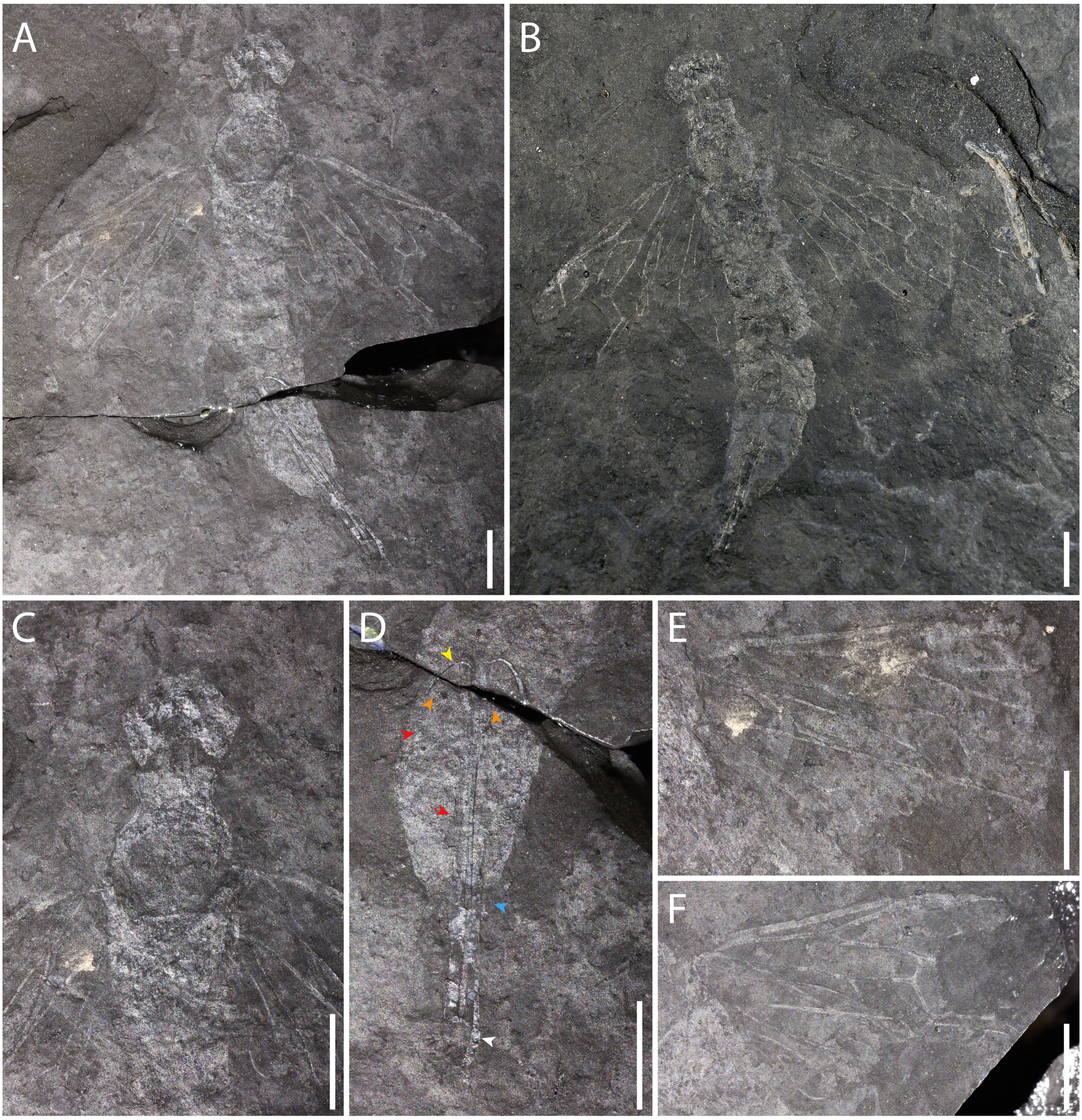

Figure 1. *Ghilarella jinjuensis* **sp. nov.**, holotype GNUE218033. **A,** Part. **B,** Counter part. **C,** Detailed view of head and mesosoma. **D,** Detailed view of metasomal apex (arrows pointing to structures as highlighted in the description). **E,** Detailed view of left forewing, mirrored. **F,** Detailed view of right forewing. Scale bars = 2 mm.

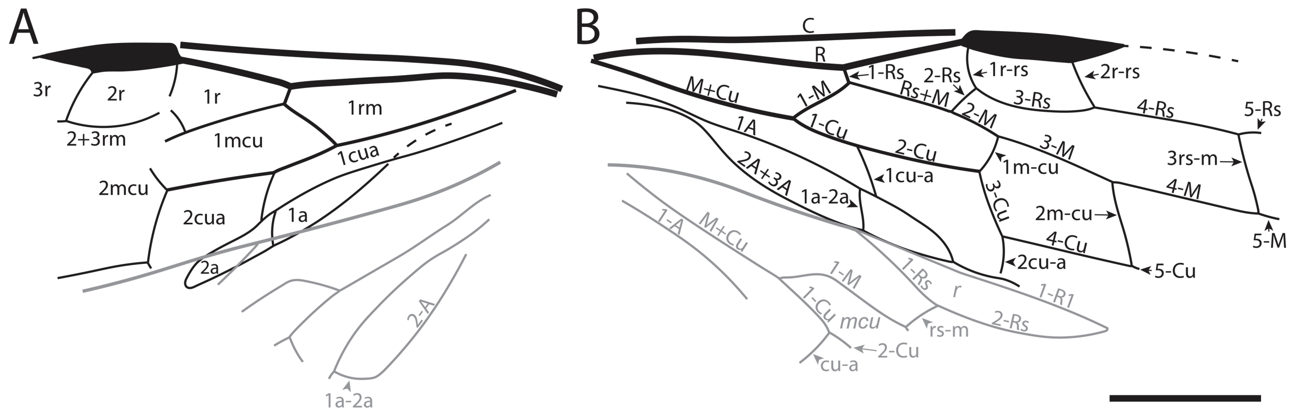

Figure 2. *Ghilarella jinjuensis* **sp. nov.**, holotype GNUE218033. Line drawings wing names of cells and veins labelled: **A,** Left fore- (in black) and hind (in grey) wings. **B,** Right fore- (in black) and hind (in grey) wings. Scale bar = 2 mm.

Diagnosis. Medium size species (body length about 16.7 mm). Forewing lacking colouration patterns (*vs*. with colour pattern in *G. alexialis*, *G. elegantula*, *G. masculina*, *G. mercurialis*, *G. nivalis*); 2r-rs originating from distal half of pterostigma (*vs*. near its mid-length in *G. alexialis*, *G. elegantula*); crossvein 3rs-m located close to cell 3r apex (*vs*. near its middle in *G. nivalis*); 4-Rs longer than 5-Rs (*vs.* as long as in *G. nivalis*); crossvein 1cu-a reaching 1-A distinctly distad 1a-2a crossvein (*vs*. before 1a-2a crossvein in *G. alexialis*, and opposite in *G. nivalis*). Hindwing with rs-m long, slightly shorter than cu-a (*vs*. about half the length of cu-a in *G. masculina*, *G. mercurialis,* and *G. elegantula*; the state of this character is unknown for remaining species of *Ghilarella*). Ovipositor sheaths (total length about 7.2 mm) more than 2× as long as cells 1r and 2r combined (*vs.* less than 1.5× as long as in *G. mercurialis* and *G. kopylovi*).

Description. Female. Body thin, long, and apparently tubular. No distinct colour pattern.

Head (probably preserved in dorso-ventral view) rounded, wider than long (about 1.45 mm long, 2.5 mm wide), slightly narrower than mesosoma but wider than pronotum; eyes narrow, elongate (about 1.2 mm long), about half head length; ocelli not visible (preservation); mandibles small, relatively short, slightly sickle-shaped, with marginal teeth; antennae thin, filiform, moderately long (about 6 mm long), flagellum preserved incompletely (with at least five flagellomeres, likely more but poorly preserved), preserved ones longer than wide cylindrical; occiput strongly concave.

Mesosoma about 4.9 mm long and 3 mm wide (measured between tegulae); pronotum trapezoidal, without visible medial line or furrow, at least 1.75× as wide as long, anterior margin slightly concave, posterior margin concave, sides concave; propleura extending anteriorly to from a neck-like structure; mesoscutum large, with anterior margin broadly convex, notauli not clearly discernible; mesoscutellum somewhat triangular; metascutum with metascutellum small, rounded quadrangular, transverse; cenchrus large and oval. Legs slender and poorly preserved; fore and mid legs present but hardly discernible. Hind leg: femur ≥ 2.0 mm; tibia about 1.3 mm, widening distally; tarsus about 1.0 mm long.

Forewing long (at least 10 mm long) and narrow (about 3.3 mm wide), *ca.* 3× as long as wide; pterostigma fully sclerotised; C nearly straight, slightly thickened; Sc absent; R strongly thickened; costal space conspicuously narrowed basally, widest at origin of 1-Rs; 1-Rs 0.2× as long as 1-M; 1r-rs long, arched; distance between 1r-rs and 2r-rs about 2.35× length of 1r-rs; 2r-rs slightly curved, inclined apicad, arising from distal third of pterostigma; cell 2r narrow, about twice as long as wide, with subparallel sides; 3-Rs broadly curved, subparallel to pterostigma; 4-Rs longer than Rs+M; M+Cu nearly straight, fork located before origin of 1-Rs; 1-M slightly shorter than 1-Cu, strongly inclined; Rs+M long, nearly straight, more than three times length of 2-Rs; cell 1mcu subrectangular, at least 2.35× longer than wide; 2-M, 3-M, and 4-M nearly aligned, each longer than preceding vein; 2rs-m absent; 3rs-m located well distad mid-length of cell 3r, inclined, nearly straight; cell 2+3rm extremely elongate, nearly 4× longer than wide; 2-Cu about as long as 3-M; 1m-cu situated approximately at pterostigmal mid-length; 2m-cu aligned near pterostigmal apex, parallel to and about as long as 3rs-m; cell 2mcu pentagonal, longer than wide; 1cu-a subvertical, slightly anteriad of mid-length of cell 1mcu, reaching 1A distad 1a-2a; 1a-2a slightly inclined; 2A+3A with pronounced median arch before M+Cu fork. Hind wing with cell r 7× as long as wide; 2-Rs about 1.6× length of 1-Rs; M+Cu long, nearly straight, fork located before origin of 1-Rs and well before cu-a; base of 1-M sharply bent; 2-M present as short stub (likely longer but incompletely preserved); rs-m present, long, located distad cu-a; m-cu not preserved; 2-Cu partially preserved; cu-a likely joining 1A slightly distad vein 1a-2a.

Abdomen about 12.5 mm long, maximal width similar to mesosoma width (about 3 mm), widest at level of ovipositor base, subparallel-sided; nine(?) segments visible; first tergite medially split. Ovipositor: valvifer 1 extremely faint (orange arrow in Fig. 1D), small, subhemicircular (outlined as faint line in carbonaceous film); valvula 1 anterior branch not clearly visible, posterior branch distinct, strongly arched, about 1 mm long (yellow arrow in Fig. 1D); stylet long, about 6.5 mm; valvifer 2 large (red arrow in Fig. 1D), visible as faint line from apex of valvula 1 anterior branch to mid-length of valvula 1 stylet, medially lobe-like, distally narrowing into branch-like structure (dotted arrow in Fig. 1D); valvula 3 visible distally, base indiscernible (white arrow in Fig. 1D). Ovipositor straight, sword-shaped, about. 6.5 mm long; sheaths nearly straight, elongate, narrowly rounded apically, projecting well beyond abdomen. Cerci slightly protruding from apex of abdomen, about 0.4 mm long (blue arrow in Fig. 1D).

***Ghilarella kopylovi* Li, Wang, Rasnitsyn and Shih, 2024** (corrections and additions to Li *et al.* 2024)

Material. PIN 5026/677 (holotype, ♀), housed in the collection of Paleontological Institute, Russian Academy of Sciences, Moscow. Khasurty, Lower Cretaceous, Buryatia, Russia. Specimens PIN 5340/55 (♀) and PIN 5340/2532 (sex unknown), from the same locality.

Remarks. In the original description of *Ghilarella kopylovi* (Li *et al.* 2024), the holotype is mistakenly listed as PIN 5340/55. However, based on the diagnostic characters provided, it is clear that the description pertains to specimen PIN 5026/677. Specimen PIN 5340/55 appears to belong to the same species but is too incomplete to serve as a base for the published description of the holotype. Most of the diagnostic characters used in the original description are missing from PIN 5340/55, making it evident that PIN 5026/677 was actually the specimen described. In this case, it is clearly a typographical error in the designation of the holotype, and there is no need to designate a neotype or lectotype. A corrigendum correcting the error should suffice.

Specimens PIN 5340/55 and PIN 5340/2532 most likely belong to the same species. However, both are highly fragmentary, and reliable species-level identification is difficult. We retain their identification as *Ghilarella* **sp. cf.** *kopylovi*. Including such fragmentary specimens in the type series is not justified.

Genus *Meiaghilarella* Rasnitsyn & Martínez-Delclòs, 2000

Type species. *Meiaghilarella cretacica* Rasnitsyn & Martínez-Delclòs, 2000

Other species. *Meiaghilarella stanislawlemi* **sp. nov.**

***Meiaghilarella stanislawlemi* sp. nov.**

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(Figs 3–4)

Material. GNUE218046 (holotype, ♀), housed in the collection of the Gongju National University of Education, Gongju, Republic of Korea.

Etymology. The species name honors Stanislaw Lem, inventor of the term '*Sepulka*', later referred to as *Sepulca* Rasnitsyn, 1968; and is to be treated as a noun in the genitive case.

Locality and horizon. Jinju Formation, Jeongchon section, near the city of Jinju, Republic of Korea; lower Albian, Lower Cretaceous.

Diagnosis. Forewing with 2r-rs long (*vs*. extremely short in *M. cretacica*); 1m-cu reaching M before cell 2r end (*vs*. distad cell 2r); 3rs-m sigmoidal (*vs*. evenly arched), origin along Rs distinctly distad pterostigma (*vs*. immediately after pterostigma).

Description. Female. Body long and apparently tubular. No distinct colour pattern (except on the forewings).

Head (probably preserved in dorso-ventral view) rounded, wider than long (about 1.3 mm long, 1.85 mm wide), narrower than mesosoma; eyes round, *ca.* 0.75 mm long and 0.44 mm wide, occupying more than half head length; ocelli not visible (preservation); mandibles thin, small, relatively short, sickle-shaped; antennae poorly preserved, thin, filiform, moderately long (measurable part about 2.5 mm long), preserved flagellomeres longer than wide cylindrical; occiput slightly concave.

Mesosoma about 4.5 mm long and 2.1 mm wide (measured between tegulae); pronotum trapezoidal, without visible medial line or furrow, wider than long, anterior margin slightly concave, posterior margin concave, sides concave; propleura not strongly projected anteriorly (*i.e.*, not forming a long neck-like structure); mesoscutum large, with anterior margin broadly convex, notauli not clearly discernible; mesoscutellum somewhat triangular. Legs slender and moderately well-preserved. Fore leg with tibia folded against femur (measurable part about 1.5 mm long). Midlegs with femur about 1.8 mm long, tibia about 1.65 mm long, tarsus 2.3 mm long. Hind leg with femur stout, widening medially, about 1.3 mm long; tibia about 1.5 mm long, slightly widening towards apex; tarsus not discernible.

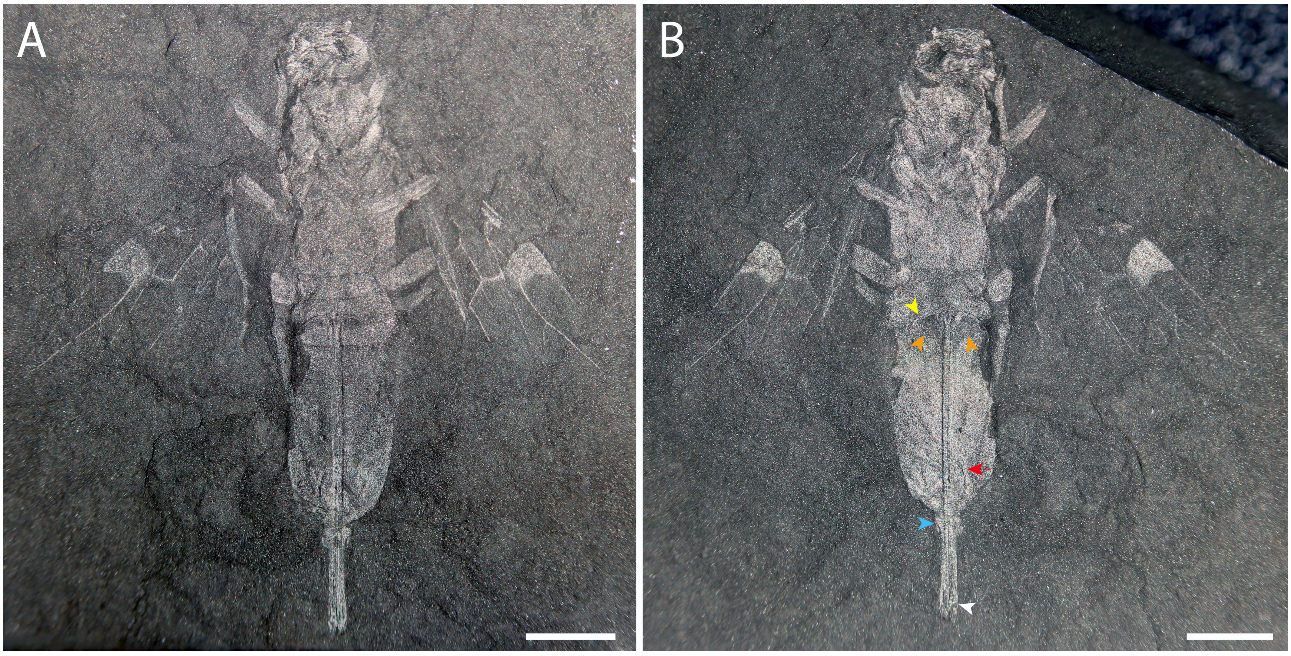

Figure 3. *Meiaghilarella stanislawlemi* **sp. nov.**, holotype GNUE218046. **A,** Part. **B,** Counter part (arrows pointing to structures as highlighted in the description). Scale bars = 2 mm.

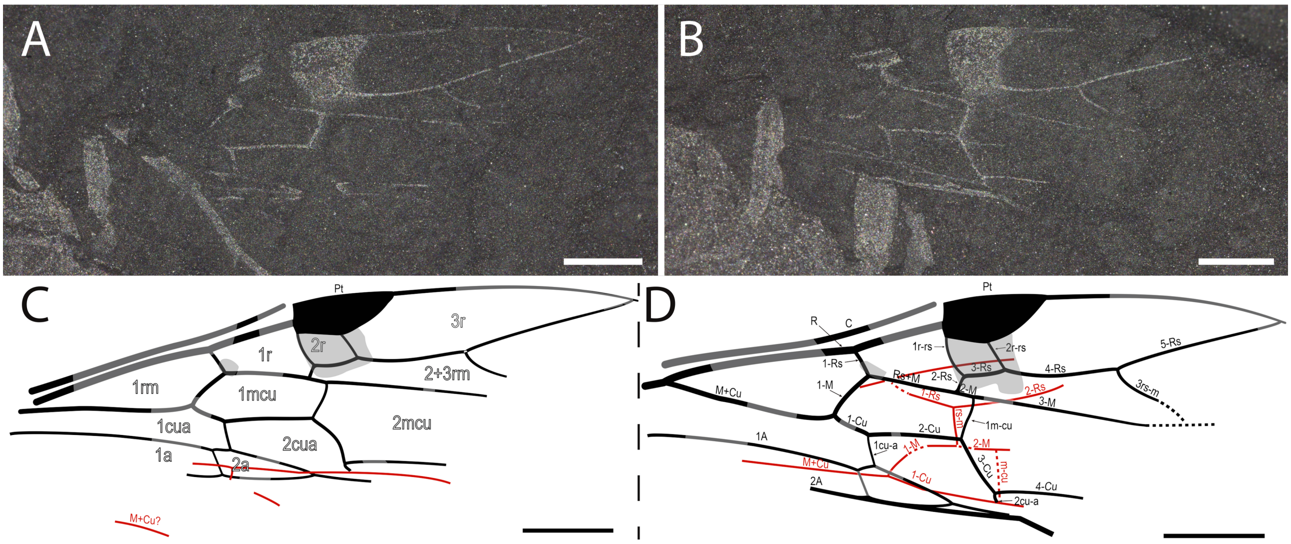

Figure 4. *Meiaghilarella stanislawlemi* **sp. nov.**, holotype GNUE218046. **A,** Left wings. **B,** Right wings. **C,** Drawing of left wings (black: forewing, and red: hind wing) with names of cell labeled. **D,** Drawing of right wings (black: forewing, and red: hind wing) with names of cell labeled. Scale bars = 1 mm.

Forewing long (about 7.7 mm long) and narrow (about 2.3 mm wide), more than 3× as long as wide; coloured spot present and encompassing pterositgma 1r-rs, 2r-rs, and slightly extending along 2-Rs; pterostigma fully sclerotised; C slightly arched; Sc absent; R strongly thickened; costal space conspicuously narrowed basally, widest at origin of 1-Rs; 1-Rs moderately long, about twice as long as 2-Rs and 0.5x as long as 1-M; 1r-rs long, strongly arched; distance between 1r-rs and 2r-rs shorter than length of 1r-rs; 2r-rs straight to slightly curved, inclined apicad, arising from pterostigma before its midlength; cell 2r narrow, longer than wide, with subparallel sides; 3-Rs curved; 4-Rs slightly longer than Rs+M; M+Cu nearly straight, fork located before origin of 1-Rs; 1-M about 1.3× longer than 1-Cu, strongly inclined; Rs+M long, nearly straight, about as long as 2-Cu (ca 1.1 mm); cell 1mcu subrectangular, at least 2.5× longer than wide; 2-M, 3-M, and 4-M nearly aligned; 2rs-m absent; 3rs-m located slightly before mid-length of cell 3r, strongly inclined, sinusoidal; cell 2+3rm extremely elongate, 4.5× longer than wide; 2-Cu nearly straight; 1m-cu reaching M before cell 2r end, and before middle of pterostigma; 2m-cu not preserved (likely present and reaching M before 3rs-m); cell 2mcu longer than wide; 1cu-a slightly inclined, located distinctly anteriad middle of cell 1mcu, reaching 1A distad 1a-2a; 1a-2a slightly inclined; 2A+3A incompletely preserved. Hind wing with cell r long and narrow, much longer than wide; cell mcu subtrapezoidal about twice as long as wide; 1-Rs base incompletely preserved; 2-Rs long distal part not preserved; M+Cu long, nearly straight, fork virtually located at level of 1-Rs origin; 1-M sharply bent; 2-M neatly straight (incompletely preserved); rs-m long, about as long as cell r width; m-cu faint, located distally to rs-m; 2-Cu partially preserved.

Abdomen about 5.5 mm long (excluding ovipositor), maximal width about 2.5 mm, slightly tapering toward apex; 6 segments visible, others too poorly preserved. Ovipositor: base extending extremely close to hind coxa; valvifer 1 extremely faint (orange arrow in Fig. 3B), small, subhemicircular (outlined as faint line in carbonaceous film); valvula 1 anterior branch not clearly visible, posterior branch distinct, strongly arched, about 1 mm long (yellow arrow in Fig. 3B); stylet long, about 6.3 mm; valvifer 2 not clearly visible except distal branch-like structure (dotted arrow in Fig. 3B); valvula 3 visible distally, base indiscernible (white arrow in Fig. 3B). Ovipositor straight, sword-shaped, about 7.1 mm long; sheaths nearly straight, elongate, narrowly rounded apically, projecting well beyond abdomen. Cerci slightly protruding from apex of abdomen, about 0.5 mm long (blue arrow in Fig. 3B).

Remark. This species represents the first described female of the genus, as the type species was based on a male specimen.

Discussion

Systematic placement

The two specimens are assigned to Ghilarellinae based on several diagnostic forewing features: a conspicuously narrowed basal costal area, absence of veins 2rs-m and Sc, a short 1-Rs, a straight M+Cu, and a large cell 1mcu (Kopylov & Rasnitsyn 2016; Li *et al.* 2024). Specimen GNUE218033 is further placed in the genus *Ghilarella* due to its combination of characters, including a long, narrow pterostigma, rather short 1-Rs, a large cell 2r, the position of 2r-rs distal to the mid-length of the pterostigma, cell 2mcu rather short, and 3rs-m not significantly inclined, situated closer to the apex than to the base of cell 3r (Li *et al.* 2024). The genus *Ghilarella* currently encompasses six species. Following the *Identification Key for Species of the Genus Ghilarella* proposed by Kopylov & Rasnitsyn (2017b), specimen GNUE218033 would key out close to the species *G. masculina* or *G. mercurialis* because of the following couplets: 1) 1a-2a extends from A_1 more proximally or opposite 1cu-a. Forewing is longer than 9 mm; and 2) 1a-2a extends from A_1 more proximally than 1cu-a. 4+5-Rs is longer than 6-Rs. No spot is present at the base of the forewing between R and M+Cu. Forewing is shorter than 16 mm. Unfortunately, the hind wing of specimen GNUE218033 is poorly preserved, complicating further comparisons using the key for the position of 1a-2a relative to cu-a. Following the *Identification Key for Species of the Genus Ghilarella* proposed by Li *et al.* (2024), the specimen would key out close to *G. kopylovi* because of its forewing lacking a color pattern, and its 2-M aligned with Rs+M, but would differ from the latter, at least, because of its ovipositor sheaths longer than cell 1r (*vs.* shorter than cell 1r in *G. kopylovi*) (see Kopylov & Rasnitsyn 2017b: pl. 9 fig. 5).

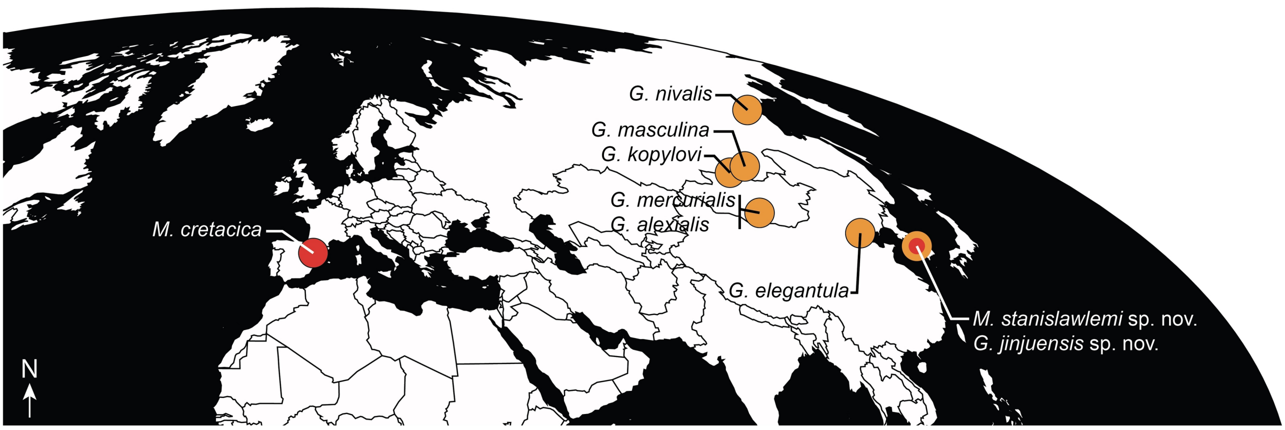

Figure 5. Map of the distribution of Ghilarellinae (*Meiaghilarella* in red, and *Ghilarella* in orange) modified from PBDB.

Ghilarella jinjuensis **sp. nov.** can be readily distinguished from *G. alexialis* by the absence of a forewing colour pattern below the pterostigma (present along 1r-rs and between 2-M and 3-Rs in *G. alexialis*), by the origin of 2r-rs in the distal half of the pterostigma (*vs.* near its midpoint), and by crossvein 1cu-a reaching vein 1-A distinctly distal to the 1a–2a crossvein (*vs.* proximal) (Kopylov & Rasnitsyn 2017b: fig. 1). It differs from *G. elegantula* in its much smaller body (*ca.* 16.7 mm *vs*. 29 mm) and forewings (10 mm *vs*. over 20 mm), the absence of forewing colouration (present in *G. elegantula*), and the distal origin of 2r-rs on the pterostigma (Li *et al.* 2024: fig. 3).

The new species is superficially similar to *G. kopylovi* in lacking forewing colouration, having 2r-rs arising from the distal third of the pterostigma, and possessing 1cu-a reaching 1-A distal to 1a–2a. However, it differs markedly in ovipositor sheath length, which is extremely short in *G. kopylovi* (approximately equal to the combined lengths of cells 1r and 2r) but much longer in *G. jinjuensis* **sp. nov.** (exceeding the combined lengths of these cells) (Kopylov & Rasnitsyn 2017b: pl. 9, fig. 5).

Ghilarella jinjuensis **sp. nov.** is further distinguished from *G. masculina* by the absence of forewing colouration (present in *G. masculina*) and by a relatively long hind-wing rs-m crossvein, only slightly shorter than cu-a (*vs*. about half the length of cu-a in *G. masculina*) (Kopylov & Rasnitsyn 2017b: fig. 2). *G. mercurialis*, the most extensively documented species of the genus, exhibits variable forewing colouration, with most specimens displaying a transverse stripe at the base of the pterostigma (Rasnitsyn 1988; Kopylov & Rasnitsyn 2017b). In contrast, the new species lacks such colouration and differs in hindwing venation, with 3rs-m slightly shorter than cu-a (*vs*. approximately half the length in *G. mercurialis*) (Rasnitsyn 1988: pl. 1, fig. 3). Although the exact junction of cu-a with 1-A cannot be confidently located, it is likely positioned distal to 1a–2a (note that this character is variable in the type series of *G. mercurialis*).

Finally, *G. jinjuensis* **sp. nov.** can be separated from *G. nivalis* by the absence of forewing colouration (present in *G. nivalis*) and by the position of crossvein 3rs-m near the apex of cell 3r (*vs*. near the middle) (Rasnitsyn 1993a: fig. 13).

The second specimen is assigned to Ghilarellinae based on the diagnostic characters outlined in the Introduction, but it differs from *Ghilarella* in several forewing features: an inflated pterostigma; a comparatively long 1-Rs; a small cell 2r; 2r-rs originating before the midlength of the pterostigma; elongated cell 2mcu, a strongly inclined 3rs-m positioned closer to the base than to the apex of cell 3r. This combination of characters closely matches the diagnosis of *Meiaghilarella*, a genus previously known only from Spain and currently monospecific (Rasnitsyn & Martínez-Delclòs 2000).

The new specimen is larger than the type species, *Meiaghilarella cretacica*, with a forewing exceeding 7 mm in length (*ca*. 5.7 mm in the type species). It further differs in possessing a relatively long 2r-rs (*vs*. extremely short in *M. cretacica*), 1m-cu reaching M before the end of cell 2r (*vs*. distad of cell 2r), and a sigmoidal 3rs-m (*vs*. evenly arched), originating along Rs distinctly distal to the pterostigma (*vs*. immediately after it) (Rasnitsyn & Martínez-Delclòs 2000). The specimen is clearly a female, as indicated by the presence of an exceptionally long ovipositor, whose base lies unusually close to the hind coxae—a position atypical for Cephoidea, in which the ovipositor is generally located more distally on the abdomen.

An eastward expansion of the subfamily distribution

The genus *Ghilarella* was previously known from China, Mongolia, and Russia; the description of *G. jinjuensis* **sp. nov.** represents the first record of the genus from the Korean Peninsula, thereby extending its known geographic range in Asia (Fig. 5). The discovery of a new *Ghilarella* species in Korea is not unexpected, given that many taxa from the Jinju Formation belong to genera already documented in contemporaneous deposits of China, Mongolia, and Russia. Recent discoveries and taxonomic work increasingly reinforce this pattern, suggesting a broad homogeneity of palaeoentomofaunal assemblages across the region (e.g., Engel *et al.* 2006; Kopylov *et al.* 2020b; Lee *et al.* 2023, 2024a,b; Vršanský *et al.* 2025).

By contrast, the discovery of *Meiaghilarella* in the Jinju Formation is more remarkable. This genus was originally described from the La Cabrua outcrop of the La Pedrera de Rubies Formation, a locality regarded as a "Baissin-type" deposit (see Rasnitsyn *et al.* 1998). Such deposits are typically dominated by Baissidae, Proctotrupidae, Ichneumonoidea, and extinct lineages of Apoidea (referred to as 'archaic' Sphecidae), whereas Ephialtitidae, Cleistogastrinae (Megalyridae), and Mesoserphidae are rare, and Praeaulacinae and Armaniinae are absent. Similar assemblage structures characterize the Weald Clay and Crato formations, as well as the Bon Tsagaan locality in Mongolia (Rasnitsyn & Martínez-Delclòs 2000).

The affinities between the Jinju Formation and these deposits are further supported by non-hymenopteran assemblages—particularly Neuroptera and Orthoptera—as well as by hymenopteran taxa that were once considered endemic to specific localities (e.g., *Araripeneura* Martins-Neto & Vulcano 1989 in the Crato Formation or *Cretosphecium* Pulawski & Rasnitsyn 2000 in Bon Tsagaan) but have since been discovered in the Jinju Formation (Kim *et al.* 2021; Jouault *et al.* 2024; Khramov & Nam 2024).

Taken together, these observations indicate a relatively broad homogeneity in palaeoenvironmental conditions among these formations, facilitating the development of similar insect faunas. Consequently, future discoveries from the Jinju Formation are likely to include additional taxa, or even genera, already known from these comparable deposits, thereby filling biogeographic gap. Such findings may include lineages expected to be present at that time, such as Ephialtitidae, and possibly Praeaulacidae, although the latter remain less likely given the Baissin-type nature of the Formation.

Finally, the description of *Meiaghilarella stanislawlemi* **sp. nov.** from the Jinju Formation may reflect several alternative biogeographic scenarios. The genus may have been broadly distributed, potentially extending into the Western Hemisphere or even the Southern Hemisphere, with its apparent absence from these regions simply resulting from the scarcity of suitable fossil deposits of comparable age—particularly those preserving large-bodied insects as compression fossils, with few exceptions such as the Crato Formation. Alternatively, the known occurrences may represent the western and eastern margins of a wider Eurasian distribution. A third, and perhaps more plausible, explanation is a broader distribution restricted to thermophilous latitudes, with the Spanish and Korean records marking its northernmost limits. Although these hypotheses cannot currently be tested, they are proposed to stimulate future investigations of fossil deposits that may allow their evaluation.

Conclusion

Ghilarella jinjuensis **sp. nov.** and *Meiaghilarella stanislawlemi* **sp. nov.** are described from the Lower Cretaceous (Albian) Jinju Formation of the Republic of Korea. These new taxa increase the known insect diversity of the formation and underscore the richness of its palaeoentomofauna. Both species, and particularly the new *Meiaghilarella*, significantly extend the known geographic ranges of their respective genera; in the latter case, from a previously Spain-restricted distribution to both sides of Laurasia.

These findings further support a broader pattern observed in the Jinju palaeoentomofauna, namely its strong similarity to contemporaneous assemblages from China, Mongolia, and Russia, and more generally to "Baissin-type" deposits. Moreover, these fossils represent the first records of the subfamily Ghilarellinae and the family Sepulcidae from the Republic of Korea, highlighting the importance of continued study of the Jinju Formation to better understand both the ecosystem it preserves and its broader palaeobiogeographic significance.

Acknowledgements

We thank the two anonymous reviewers for their constructive comments, which greatly improved the manuscript.

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