



# **The first Heloridae (Hymenoptera: Proctotrupoidea) from the Albion of the Republic of Korea: inferences about the relict diversity of the family**

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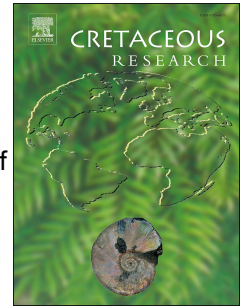


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# The first Heloridae (Hymenoptera: Proctotrupoidea) from the Albian of the Republic of Korea: inferences about the relict diversity of the family

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## ABSTRACT

*Korehelorus jinjuensis* gen. et sp. nov., a new genus and species of the family Heloridae, is described and figured from a specimen preserved in the dark grey shales of the lower Albian Jinju Formation (Republic of Korea). This description further increases the diversity of the family Heloridae in the Mesozoic and provides additional evidence for a rapid decline of the latter in the Cretaceous. To date,

no explanations nor hypotheses have been proposed to explain this particular pattern but we assume and hypothesize that the species and genus diversities of helorid wasps are linked with the diversity of their hypothetical hosts (i.e., Chrysopidae or closely related extinct lineages). We show that the Cretaceous chrysopoid diversity is dominated by the Mesochrysopidae and stem-chrysopid subfamily (Limaiinae), which declined and/or die out through the Cretaceous. We find a peak of diversity for the Heloridae, synchronous with that of the Mesochrysopidae and Limaiinae, leading us to suggest that the decline of these clades in the Cretaceous consequently triggered a decline in the Heloridae.

**Keywords:** Jinju Formation, Cretaceous, Sinuiju Formation, Korean Peninsula, new genus and species

## 1. Introduction

Heloridae is a relict proctotrupoid family wasp with relatively small and usually black extant representatives (6-8 mm – Huber and Sharkey, 1993). Its extant members are represented by only one genus (*Helorus* Latreille, 1802), they are solitary endoparasitoids of Chrysopidae larvae (Huber and Sharkey, 1993), and are mostly found in the Holarctic region – with other species found in the Neotropical, Afrotropical and Indo-Australian ecozones (van Achterberg, 2006). Fossil and extant helorid wasps possess a distinctive wing venation, and the latter is mostly used to identify their genera (Li et al., 2017). They are mostly recognizable by their subtriangular first discal cell (1mcu), and the genus *Helorus* is discernible among living proctotrupoids because of its antennae with 15 antennomeres, a distinct pterostigma, a subtriangular first discal cell (1mcu), veins 1Rs+M present, 1-Rs absent (desclerotised), an elongate first metasomal segment and the metasomal tergites 2–4 fused into a syntergite (Kusigemati, 1987; Masner, 1993). Several fossil genera show a more developed wing venation with the presence of a tubular vein 1-Rs (plesiomorphy).

Interestingly, the family was more speciose in the past than today, as more than ten genera



are known in the fossil record, with its oldest occurrences dated back to the Middle Jurassic (Shih et al., 2011). During or after the Late Cretaceous, the diversity of the family declined to be only represented by one genus after the Cretaceous-Paleogene boundary (<https://paleobiodb.org>). This particular diversity dynamic (i.e., drastic diminution of the generic diversity) is also found in numerous Jurassic or Early Cretaceous wasp families (e.g., Anaxyelidae: Gao et al., 2021; Evanioidea: Jouault et al., 2022a) and is likely the result of drastic environmental changes, leading either to the decline of the stem groups of these lineages and the diversification of their crown groups, or to a faunal turnover due to the diversification of the Angiosperms (e.g., Sinitshenkova, 2003; Jouault et al., 2022b; Wang et al., 2022). If this explanation (i.e., the impact of Angiosperms diversification) is particularly true for lineages feeding on plants (Peris and Condamine, 2023) or parasitizing plant eaters, the decline of Heloridae is difficult to explain, as they parasitize Chrysopidae larvae (fierce predators).

An alternative hypothesis would be to consider that their hosts (i.e., certain lineages of Chrysopidae), which were diverse and speciose during the Jurassic and Cretaceous periods (i.e., Limaiinae), declined in the Cretaceous, driving the decline of the Heloridae. This type of bottom-up effect (i.e., the decline of a food source or host triggers the decline of the predators or parasitoids) is frequent in today's ecosystems and it would not be surprising if similar phenomena had taken place in the deep past (e.g., Ehrlich and Raven, 1994; Singer and Stireman, 2003). We propose to investigate this trophic linkage by describing a new genus of helorid wasp, which further accentuates the disparity between the diversity of the family during the Mesozoic and Cenozoic eras, and by studying variations in the diversity of Chrysopoidea over time.

## 2. Material and methods

### *Specimen origin, examination, and illustration*

The specimen was 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: fig. 1). A detailed columnar section of the Jinju Formation, exposed at the Jeonchon Section, was recently published by Park et al. (2019) with a clear indication of the insect-bearing layers. The most recent detrital zircon analysis shows that the age of the lower boundary of the Jinju Formation is  $112.4 \pm 1.3$  Ma, while the upper boundary is  $108.7 \pm 0.5$  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. (2020: p. 1236-1237). The paleoentomofauna of the Jeonchon section is rich with numerous fossils of Odonata (Anisoptera and Zygoptera), numerous Anaxyelidae, and some Ichneumonidae (G.S.N. pers. obs.). The Hymenoptera diversity is clearly dominated by symphytan lineages but we also recorded a few specimens of Aculeata belonging to non-apoid lineages.

The holotype specimen of the new helorid taxon is preserved as a reflective carbonaceous film on two slabs (part and counterpart) of dark grey shale (Figs. 1A, B). The specimen is housed in the Gongju National University of Education, with registration number GNUE218014. The fossil was photographed with a Canon Eos 6D camera with an attached Canon EF 100 mm lens. Wing venation and cell nomenclature is adapted from Li et al. (2017).

This published work and its included nomenclatural acts are registered in ZooBank (<https://www.zoobank.org/>, last access: XXXXXX), with the following LSID (reference): XXXX.

#### *The fossil record of the family Heloridae, Chrysopidae, and Mesochrysopidae*

We extracted from the Palaeobiology Database (PBDB: <https://paleobiodb.org/>) both clades' diversities. We used the filter (*taxa*) and called the database for all valid species using the option (*Accepted names* and *Show accepted names only*). These functions allow removing outdated names and synonyms from the dataset. The outputs from PBDB indicate that 21 helorid species and 55 chrysopid species are known in the time interval spanning for the Jurassic to the Eocene (Supplementary Material). We then extract the age of all the species of the families Heloridae, Chrysopidae, and Mesochrysopidae to generate a plot of the life span of these lineages. We manually

extract the oldest and youngest ages of these lineages from PBDB and correct the min age of extant lineage to 0. To generate the species diversity plot, we consider that when the dating of a fossil deposit is not clear (e.g., not clearly belonging to one stage: Callovian/Oxfordian), we chose to consider that the species are present in both stages (following the previous example, one occurrence is counted for the Callovian and one for the Oxfordian). We used R (R Core Team, 2022) and the package ggplot2 (Wickham, 2016) to generate the plots. for the Oxfordian).

### 3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Superfamily Proctotrupoidea Latreille, 1802

Family Heloridae Förster, 1856

**Genus *Korehelorus* Rosse-Guillevic, Rasnitsyn, Nam, & Jouault gen. nov.**

Lsid XXXXx

*Type species. Korehelorus jinjuensis* sp. nov.

*Etymology.* The genus name is a combination of the prefix *Kore* referring to Korea (the peninsular region in east Asia) and *Helorus* Latreille, 1802 (type genus of the family). Gender masculine.

*Diagnosis.* Forewing with pterostigma thinner than 2r-rs length; 2r-rs proclival, arising slightly before middle of pterostigma; Rs+M almost touching Cu; 2-Rs+M curved, much longer than 2-Rs; 2-Rs strongly angled with 2-Rs+M; 2-Rs strongly angled with 3-Rs; 1cu-a interstitial. Metasoma with first segment narrow, petiole-like and sub-equal in length with second metasomal segment.

***Korehelorus jinjuensis* Rosse-Guillevic, Rasnitsyn, Nam, & Jouault sp. nov.**

Lsid XXXXx

(Figs. 1–2)

*Holotype*. GNUE218014, part (Fig. 1A) and counterpart (Fig. 1B), housed in the collection of the Gongju National University of Education, Gongju, Republic of Korea.

*Etymology*. The specific epithet refers to the type locality: the Jinju Formation.

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

*Diagnosis*. As for the genus (*vide supra*).

*Description*. Body length 10.25 mm. Head poorly preserved; preserved flagellomeres thick, longer than wide (measured flagellomeres ca. 0.5 mm long).

Mesosoma (as preserved) ca. 3.3 mm long, 1.7 mm wide (poorly preserved), ovoid, shorter than metasoma, wider than head; mesoscutum short; mesopleuron large; propodeum trapezoidal. Legs ill-preserved.

Forewing (Figs. 2A–D) ca. 7 mm long and ca. 2.7 mm wide, broad, subtriangular (basal of anterior margin not preserved) (Fig. 2A); pterostigma elongate and acute apically, width smaller than 2r-rs length; cell 3r thin and long, enclosed by a slightly arched vein 3-Rs (Fig. 2B); absence of Rs+M+Cu section (Fig. 2C); 2r-rs arising slightly before midlength of pterostigma, oblique and about twice as long as pterostigma width; cell 1-2r hexagonal, enclosed by R, 1-Rs, 1-M, 1-Rs+M, 2-Rs+M, 2-Rs, and 2r-rs; M+Cu straight and tubular (Fig. 2D); 1-Rs not preserved; 1-M and 1-Rs+M meeting point located at ~30% of cell 1mcu length; 1-M curved, about half as long as 1-Rs+M; cell 1mcu small and triangular; 1-Cu longer than 1-Rs+M; 2-Rs+M about 1.4× longer than 1-Rs+M; 2-M and 2-Cu distinct, nearly straight, tapering toward wing margin, 2-Cu aligned with 1-Cu; 2-Rs oblique, longer than 2r-rs; 1cu-a straight and aligned with 1-M; 2cu-a slightly proclival, intersecting Cu at level of 2-Rs+M originating point; position of 2-Rs+M furcation point (into 2-Rs and 2-M) located at ca. 66%

of the distance between 1m-cu and 2r-rs.

Metasoma (Fig. 2E) ca. 6.1 mm long, largest width ca. 1.9 mm, partially preserved, elongate, with seven segments visible (distal-most probably missing), in lateral view slightly arched with convex sternites; first segment petiole-like ca. 1.25 mm long and 0.6 mm wide, slightly conical, narrower than second segment, with extremities not constricted; second segment slightly longer than petiole, ca. 1.3 mm long; third segment ca. 0.75 mm long; fourth segment ca. 0.69 mm long; fifth segment ca. 0.64 mm long.

*Remarks.* The forewing with 2-Rs+M strongly curved and much longer than 2-Rs (the latter being angled at ca.  $105^\circ$  with 2-Rs+M) combined with a particular configuration of the metasoma with the first segment long and petiolar and the second one sub-equal in length with it are unique characters allowing rapid distinction between the new genus and all other genera of the family (Fig. 2E).

#### 4. Discussion

##### *Systematic placement*

Following the dichotomous key provided in Li et al. (2017), our specimen keys out near *Sinohelorus* and *Liaoropronia* because of the following couplets and characters: forewing with pterostigma not much wider than 2r-rs length, first metasomal segment rarely as long and narrow as succeeding segment; first metasomal segment individualized as petiole; metasoma with first segment elongate, narrower than second segment basally; forewing with Rs+M not touching Cu (i.e., 1-Rs+M does not ‘enter’ into Cu to then emerge as 2-Rs+M but rather runs parallel to Cu); 2r-rs starting far distad base of pterostigma, longer than pterostigma width, oblique; 2r-rs starting before middle of pterostigma, longer than pterostigma width; 1cu-a interstitial. However, it cannot be attributed to any of these genera, as it possesses diagnostic characters from both (forewing with 2r-rs oblique [*Sinohelorus*]; forewing with the position of Rs+M forking about 50% [66% in our specimen] distance between 1m-cu and 2r-rs [*Liaoropronia*]) (Shi et al., 2013; Zhang and Zhang, 2001). The new specimen further

differs from all the other fossil and extant helorid genera because of its 2nd metasomal tergum is *circa* of same length than the petiole (Zhang and Zhang, 2001; Shi et al., 2013).

Recently, the genus *Sinujuhelorus* Jon et al. (2019) was described from the Cretaceous of the Korean Peninsula (Democratic People's Republic of Korea: DPRK). The exquisite preservation of the forewing venation of the type specimen of *Sinujuhelorus* allows a rapid distinction with our new specimen. In fact, the long (about twice as long as 2-Rs) and strongly arched 2-Rs+M of *Korehelorus* gen. nov. strongly differs from the comparatively shorter and less arched 2-Rs+M of *Sinujuhelorus* (Jon et al., 2019: fig. 4). The recent descriptions of fossil insects from the DPRK open new perspectives for the study of paleoentomofauna of the Cretaceous in Asia (So and Won 2022; Won and So, 2022), and provide important data for future comparison of the assemblages of fossil insects in the peninsula.

#### *Hypothesis to explain the diversity dynamics of the family Heloridae*

At first, it appears difficult to explain the decline of the family Heloridae through the end of the Mesozoic but their particular biology (endoparasitoids of Chrysopidae larvae: Huber and Sharkey, 1993) lets us assume that their diversity dynamics may be correlated with that of chrysopoid lineages (Fig. 3). If this hypothesis explores correlations between two patterns, it is important to keep in mind that a correlation does not necessarily advocate for causality between two events. Nevertheless, we hope that future descriptions of fossil helorid will strengthen or refine our tentative hypothesis.

The Heloridae fossil record is diverse during the Early Cretaceous (13 valid species) and Jurassic (four valid species) – as for today the family encompasses about 12 extant species (Izadzadeh et al., 2015) – with a maximum diversity during the Early Cretaceous (Fig. 3). Surprisingly, no fossil Heloridae are known from the Late Cretaceous, and the clade is scarce after the K/Pg, with only two species belonging to the extant genus *Helorus* Latreille, 1802 – respectively from the Baltic amber and the Oligocene of the Rott Formation (Fig. 4; Statz, 1938; Muona, 2020).

The extinct Neuroptera family Mesochrysopidae is considered to be closely related to the Chrysopidae (also called green lacewings) or to represent the stem group of modern green lacewings (e.g., Nel et al., 2005; Liu et al., 2016; Engel et al., 2018). Because of their phylogenetic position, it is important to also consider the diversity dynamics of the Mesochrysopidae as a potential driver of the Heloridae diversity. The Mesochrysopidae show a diversity pattern ‘similar’ to that of the Heloridae, with many species documented in Jurassic and Lower Cretaceous deposits (e.g., Panfilov, 1980; Martins-Neto and Vulcano, 1988). However, they are also known from the Late Cretaceous, notably through the discovery of a few species in Kachin amber (e.g., Cao et al., 2021), while the Heloridae are absent from this epoch. Fossil record shows that the Mesochrysopidae declined during the Late Cretaceous, as no occurrence has been recorded after the mid-Cretaceous (Fig. 4). During the time interval spanning from the Jurassic to the Cretaceous, the Chrysopidae are mainly represented by their stem subfamily i.e., the Limaiinae (Fig. 4).

Interestingly, we found that the diversity of the family Heloridae is maximal when the Mesochrysopidae and Limaiinae were abundant i.e., through the Early Cretaceous (Fig. 3). When the Mesochrysopidae declined, and slightly before, much of the diversity of fossil Heloridae disappears (Fig. 3). It is likely that Mesozoic Heloridae were associated with Mesochrysopidae and Limaiinae in the same way as they are today with the Chrysopidae (i.e., endoparasitoids). Thus, the decline of their hosts has most probably reduced their ecological niche, and ultimately lead to the disappearance of Mesozoic taxa. The fact that they did not go completely extinct suggests that at least some of their representatives were maybe associated with lineages lasting longer than the Mesochrysopidae (e.g., Limaiinae), and managed to adapt or switch hosts. This phenomenon is not uncommon in Hymenoptera as ancestral state reconstruction on other clades suggests that some lineages have switched food sources through time – sometimes switching once to later come back to their original food source – and managed to adapt and diversify, taking advantage of environmental changes (e.g., Nyman et al., 2019; Blaimer et al., 2023). From an ecological perspective, it will be interesting to study the diversity dynamics of plants on which the aphids feed (i.e., prey of Chrysopoidea) and search for a potential

link between changes in plant assemblages and in parasitoid lineages. We expect that the diversity dynamics of plants have affected the diversity of aphids, which have then affected the diversity dynamics of Chrysopidae to ultimately shape the diversity dynamics of their parasitoids.

## 5. Conclusion

The Jinju Formation provides novel insights into the insect paleodiversity of East Asia in the Early Cretaceous, and the ongoing description of its paleoentomofauna will allow for documenting of numerous lineages. This process is essential to better understand the diversity dynamics of extant insect families during the Cretaceous. The fossil insect assemblage of the Jinju Formation is to be compared with that of the Sinuiju Formation (DPRK) to draw up a general overview of the paleoentomofauna present on the Korean Peninsula during the Early Cretaceous. The description of *Korehelorus jinjuensis* gen. et sp. nov. increases the diversity of helorid wasps documented from the Lower Cretaceous of the Korean Peninsula, and helps to better understand the variability of the forewing venation of fossil Heloridae. We propose a hypothesis to explain the diversity dynamics of the family Heloridae, linking the diversity of Chrysopoidea lineages through time with that of their parasitoids. If we found a good correlation between the diversity of these two lineages, additional studies should be conducted to better understand this process and its stem.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

## References

- van Achterberg, C., 2006. European species of the genus *Helorus* Latreille (Hymenoptera: Heloridae), with description of a new species from Sulawesi (Indonesia). *Zoologische Medelingen* 80, 1–12.
- Blaimer, B., Santos, B.F., Cruaud, A., Gates, M.W., Kula, R.R., Mikó, I., Rasplus, J.-Y., Smith, D.R., Talamas, E.J., Brady, S.G., Buffington, M.L., 2023. Key innovations and the diversification of Hymenoptera. *Nature Communications* 14, 1212. <https://doi.org/10.1038/s41467-023-36868-4>
- Cao, L.-R., Wang, B., Liu, X.-Y., 2021. A new genus and species of Mesochrysopidae (Neuroptera) from the mid-Cretaceous Burmese amber. *Palaeoentomology* 4, 77–84. <https://doi.org/10.11646/PALAEOENTOMOLOGY.4.1.12>
- Cohen, K.M., Harper, D.A.T., Gibbard, P.L., 2022. ICS International chronostratigraphic chart 2022/02. International Commission on Stratigraphy, IUGS. <https://stratigraphy.org>
- Ehrlich, P.R., Raven, P.H., 1994. Butterflies and plants: a study in coevolution. *Evolution* 18, 586–608. <https://doi.org/10.2307/2406212>
- Engel, M.S., Winterton, S.L., Breitkreuz, L.C.V., 2018. Phylogeny and Evolution of Neuropterida: Where Have Wings of Lace Taken Us? *Annual Review of Entomology* 63, 531–551. <https://doi.org/10.1146/annurev-ento-020117-043127>
- Gao, J., Engel, M.S., Shih, C., Ren, D., Gao, T., 2021. A new genus of anaxyelid wood wasps from the mid-Cretaceous and the phylogeny of Anaxyelidae (Hymenoptera). *Journal of Hymenoptera Research* 86, 151–169. <https://doi.org/10.3897/jhr.86.73161>

- Huber, J.T., Sharkey, M.J., 1993. Structure (Chapter 3). In: Goulet, H., Huber, J.T. (Eds.), *Hymenoptera of the World: An Identification Guide to Families*. Research Branch Agriculture Canada Publication, Ottawa, 13–59.
- Izadzadeh, M., Talebi, A.A., van Achterberg, C., Rakhshani, E., 2015. First record of the family Heloridae (Hymenoptera: Proctotrupoidea) from Iran, with description of a new species. *Zootaxa* 3946, 577–582. <https://doi.org/10.11646/zootaxa.3946.4.6>
- Jon, S.H., Won, C.G., So, K.S., Nam, T.Y., 2019. New Mesozoic insect fossils from the Democratic People's Republic of Korea. *Cretaceous Research* 99, 240–245. <https://doi.org/10.1016/j.cretres.2019.02.019>
- Jouault, C., Maréchal, A., Condamine, F.L., Wang, B., Nel, A., Legendre, F., Perrichot, V., 2022a. Including fossils in phylogeny: a glimpse into the evolution of the superfamily Evanioidea (Hymenoptera: Apocrita) under tip-dating and the fossilized birth–death process. *Zoological Journal of the Linnean Society* 194, 1396–1423. <https://doi.org/10.1093/zoolinnean/zlab034>
- Jouault, C., Nel, A., Legendre, F., Condamine, F.L., 2022b. Estimating the drivers of diversification of stoneflies through time and the limits of their fossil record. *Insect Systematics and Diversity* 6, 1–14. <https://doi.org/10.1093/isd/ixac017>
- Kopylov, D.S., Rasnitsyn, A.P., Aristov, D.S., Bashkuev, A.S., Bazhenova, N.V., Dmitriev, V.Y., Gorochoy, A.V., Ignatov, M.S., Ivanov, V.D., Khramov, A.V., Legalov, A.A., Lukashevich, E.D., Mamontov, Y.S., Melnitsky, S.I., Ogłaza, B., Ponomarenko, A.G., Prokin, A.A., Ryzhkova, O.V., Shmakov, A.S., Sinitshenkova, N.D., Solodovnikov, A.Yu., Strelnikova, O.D., Sukacheva, I.D., Uliakhin, A.V., Vasilenko, D.V., Wegierek, P., Yan, E.V., Zmarzły, M. 2020. The Khasurty Fossil Insect Lagerstätte. *Paleontological Journal* 54, 1221–1394. <https://doi.org/10.1134/S0031030120110027>
- Kusigemati, K., 1987. The Heloridae (Hymenoptera: Proctotrupoidea) of Japan. *Kontyû* 55, 477–485.

- Lee, T., Park, K., Yi, K., 2018. Nature and evolution of the Cretaceous basins in the eastern margin of Eurasia: a case study of the Gyeongsang Basin, SE Korea. *Journal of Asian Earth Sciences* 166, 19–31. <https://doi.org/10.1016/j.jseaes.2018.07.004>.
- Li, L., Shi, C., Ren, D., 2017. New fossil helorid wasps (Hymenoptera, Proctotrupoidea) from the Early Cretaceous of China. *Alcheringa: An Australasian Journal of Palaeontology* 41, 474–486. <https://doi.org/10.1080/03115518.2017.1282980>
- Liu, X., Zhang, W., Winterton, S.L., Breitkreuz, L.C.V., Engel, M.S., 2016. Early Morphological Specialization for Insect-Spider Associations in Mesozoic Lacewings. *Current Biology* 26, 1590–1594. <https://doi.org/10.1016/j.cub.2016.04.039>
- Masner, L., 1993. Superfamily Proctotrupoidea (Chapter 13). In: Goulet, H., Huber, J.T. (Eds.), *Hymenoptera of the World: An Identification Guide to Families*. Research Branch Agriculture Canada Publication, Ottawa, 537–557.
- Muona, J., 2020. *Helorus arturi* sp. nov. (Hymenoptera, Proctotrupoidea, Heloridae) from Baltic amber. *Palaeoentomology* 3, 347–351. <https://doi.org/10.11646/PALAEOENTOMOLOGY.3.4.4>
- Martins-Neto, R.G., Vulcano, M.A., 1988. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. I - Família Chrysopidae. *Anais da Academia Brasileira de Ciências* 60, 189–201.
- Nel, A., Delcos, X., Hutin, A., 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société Entomologique de France (N.S.)* 41, 29–68. <https://doi.org/10.1080/00379271.2005.10697440>
- Nyman, T., Onstein, R.E., Silvestro, D., Wutke, S., Taeger, A., Wahlberg, N., Blank, S.M., Malm, T., 2019. The early wasp plucks the flower: disparate extant diversity of sawfly superfamilies (Hymenoptera: “Symphyta”) may reflect asynchronous switching to angiosperm

- hosts. *Biological Journal of the Linnean Society* 128, 1–19. <https://doi.org/10.1093/bi-olinnean/blz071>
- Panfilov, D.V., 1980. New representatives of the Neuropterans (Neuroptera) from the Jurassic of the Karatau region. *Fossil insects of the Mesozoic* 82–111.
- Park, T.-Y.S., Nam, K.-S., Selden, P.A., 2019. A diverse new spider (Araneae) fauna from the Jinju Formation, Cretaceous (Albian) of Korea. *Journal of Systematic Palaeontology* 17, 1271–1297. <https://doi.org/10.1080/14772019.2018.1525441>
- Peris, D., Condamine, F.L., 2023. The dual role of the angiosperm radiation on insect diversification. *bioRxiv*, 2023.02.07.527317. <https://doi.org/10.1101/2023.02.07.527317>
- R Core Team, 2022. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Shi, X., Zhao, Y., Shih, C., Ren, D., 2013. New fossil helorid wasps (Insecta, Hymenoptera, Proctotrupeoidea) from the Jehol Biota, China. *Cretaceous Research* 41, 136–142. <https://doi.org/10.1016/j.cretres.2012.12.001>
- Shih C., Feng H., Ren, D., 2011. New fossil Heloridae and Mesoserphidae wasps (Insecta, Hymenoptera, Proctotrupeoidea) from the Middle Jurassic of China. *Annals of the Entomological Society of America* 104, 1334–1348. <https://doi.org/10.1603/AN10194>
- Singer, M.S., Stireman, J.O., 2003. Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* 100, 554–562. <https://www.jstor.org/stable/25681930>
- Sinitshenkova, N.D., 2003. Main ecological events in aquatic insects history. *Acta zoologica cracoviensia* 46, 381–392.
- So, K.-S., Won, C.-G., 2022. A new fossil lacewing (Ithonidae) from the Lower Cretaceous (Barremian-Aptian) Sinuiju Formation, Democratic People's Republic of Korea. *Cretaceous Research* 138, 105288. <https://doi.org/10.1016/j.cretres.2022.105288>

- Statz, G., 1938. Neue Funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. *Decheniana* 98A, 71–144.
- Wang, B., Xu, C., Jarzembowski, E.A., 2022. Ecological radiations of insects in the Mesozoic. *Trends in Ecology & Evolution* 37, 529–540. <https://doi.org/10.1016/j.tree.2022.02.007>
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. <https://ggplot2.tidyverse.org>.
- Won, C.-G., So, K.-S., 2022. Two new wasps (Insecta: Hymenoptera) from the Lower Cretaceous Sinuiju Formation of Ryonsang-dong, North Phyongan Province, Democratic People's Republic of Korea. *Cretaceous Research* 131, 105086. <https://doi.org/10.1016/j.cretres.2021.105086>
- Zhang, H.-C., Zhang, J.-F., 2001. Proctotrupoid wasps (Insecta, Hymenoptera) from the Yixian Formation of western Liaoning Province. *Acta Micropalaeontologica Sinica* 18, 11–28.

#### Figure caption

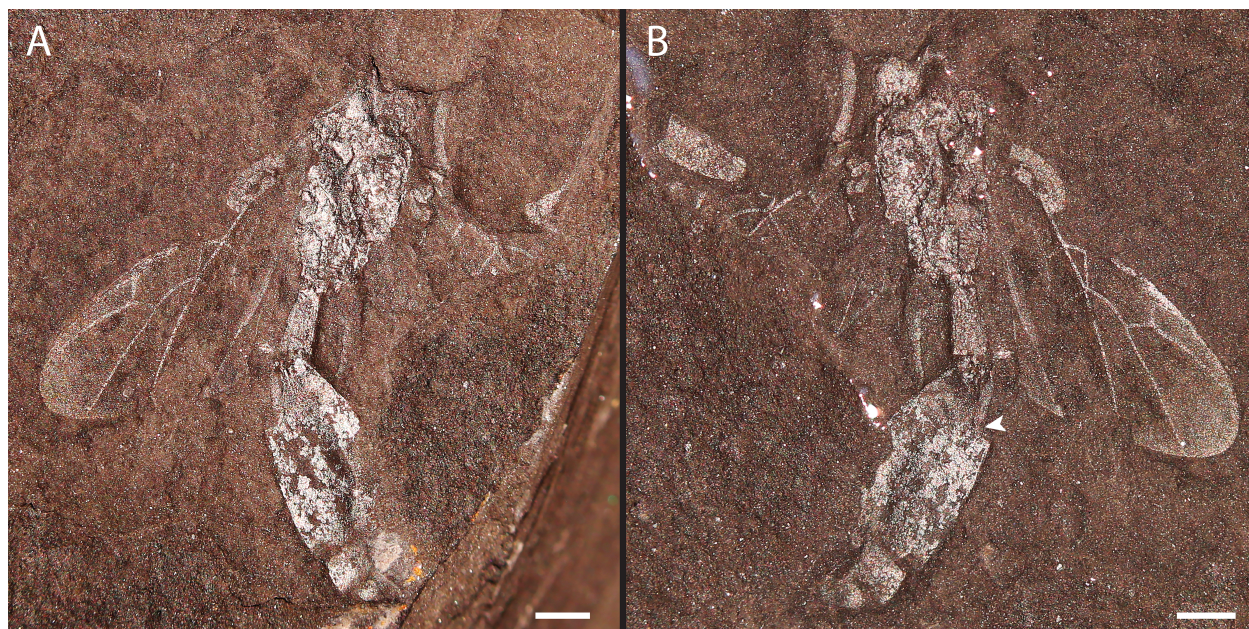
Figure 1. *Korehelorus jinjuensis* gen. et sp. nov., holotype GNUE218014. (A), Part; (B), Counterpart (the arrow points to the boundary between the second and the third segment of the abdomen). Scale bars equal 1 mm.

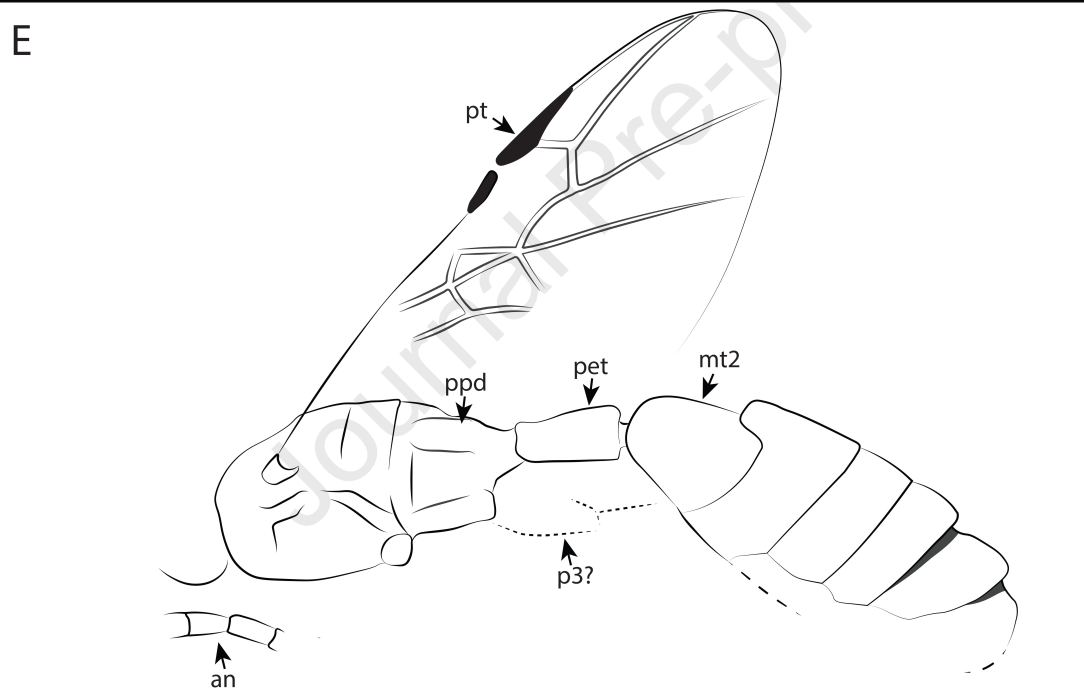
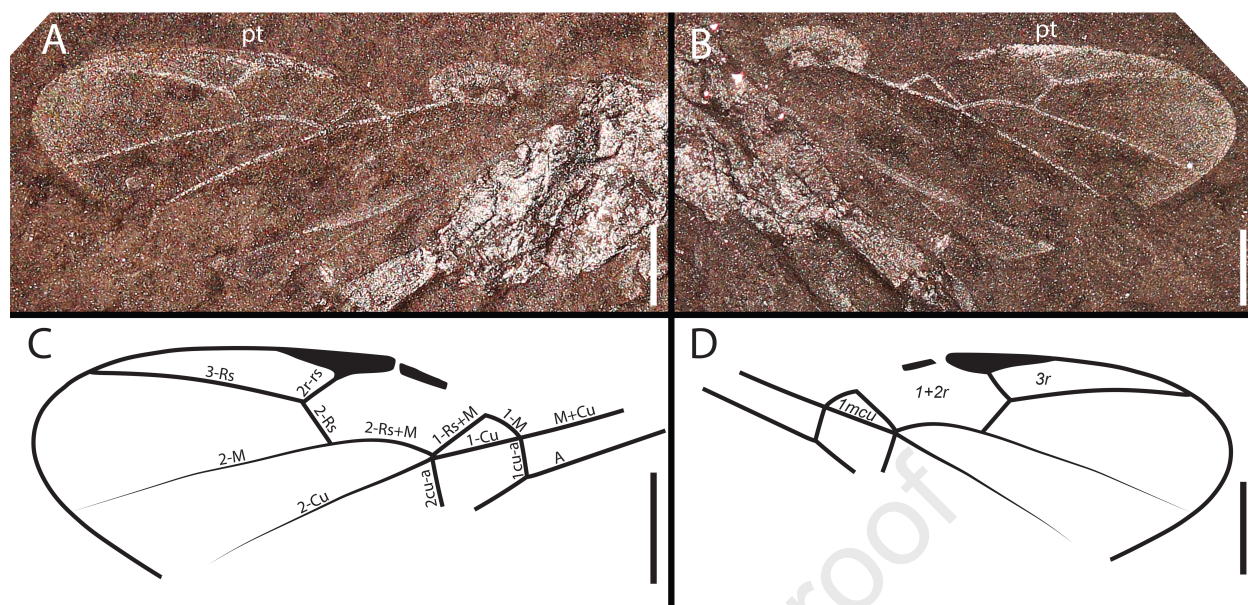
Figure 2. *Korehelorus jinjuensis* gen. et sp. nov., holotype GNUE218014. (A), Detailed view of the wing in part; (B), Detailed view of the wing in counterpart; (C), Interpretative line drawing of the wing venation with names of veins labelled; (D), Interpretative line drawing of the wing venation with names of cells labelled, (E) Interpretative line drawing of counterpart. Abbreviations: an, antenna; first pet, petiole (first segment of the metasoma); mt2, second segment of the metasoma; p3?, putative hind leg; ppd, propodeum; pt, pterostigma; Scale bars: 1 mm (A, B, C, D); 2 mm (E).

Figure 3: Diversity of Heloridae and Chrysopidae through time. (A) Heloridae species. (B) Chrysopidae species. K/Pg: Cretaceous-Paleogene boundary. Data compiled from Palaeobiology Database (PBDB: <https://paleobiodb.org/>; last access the 25/03/2023). Insect silhouettes from <http://phylopic.org/>. Heloridae (by CJ), Chrysopidae licence at <https://creativecommons.org/publicdomain/zero/1.0/>.

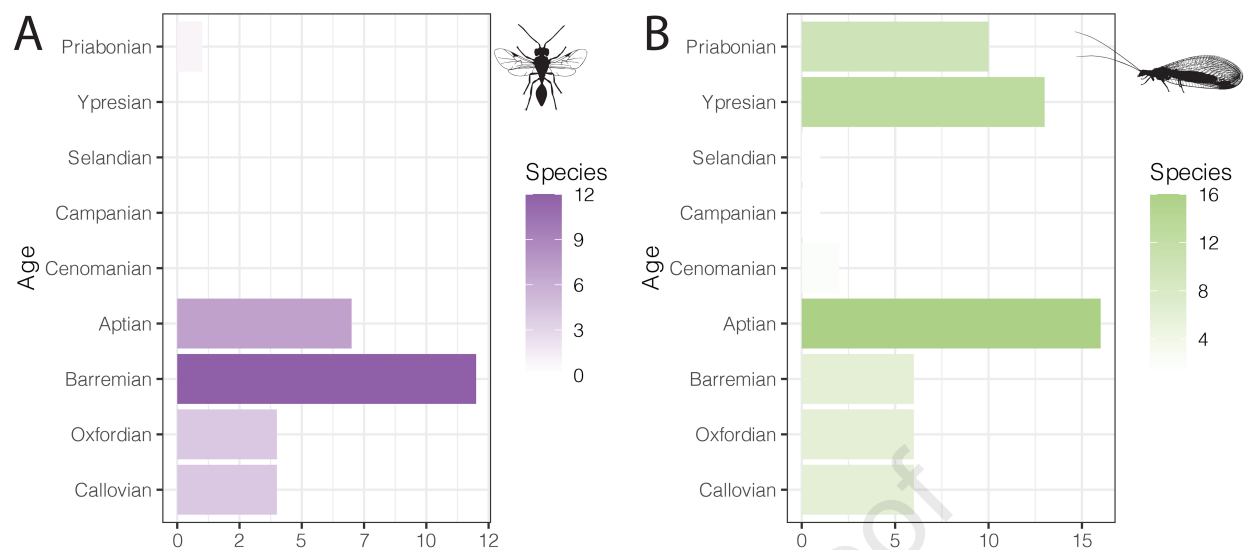
Figure 4: Life span of Mesochrysopidae, Chrysopidae, and Heloridae lineages (K/Pg: Cretaceous-Paleogene boundary). Colors for geological time scale follow Cohen et al. (2022). Data compiled from Palaeobiology Database (PBDB: <https://paleobiodb.org/>; last access the 25/03/2023).

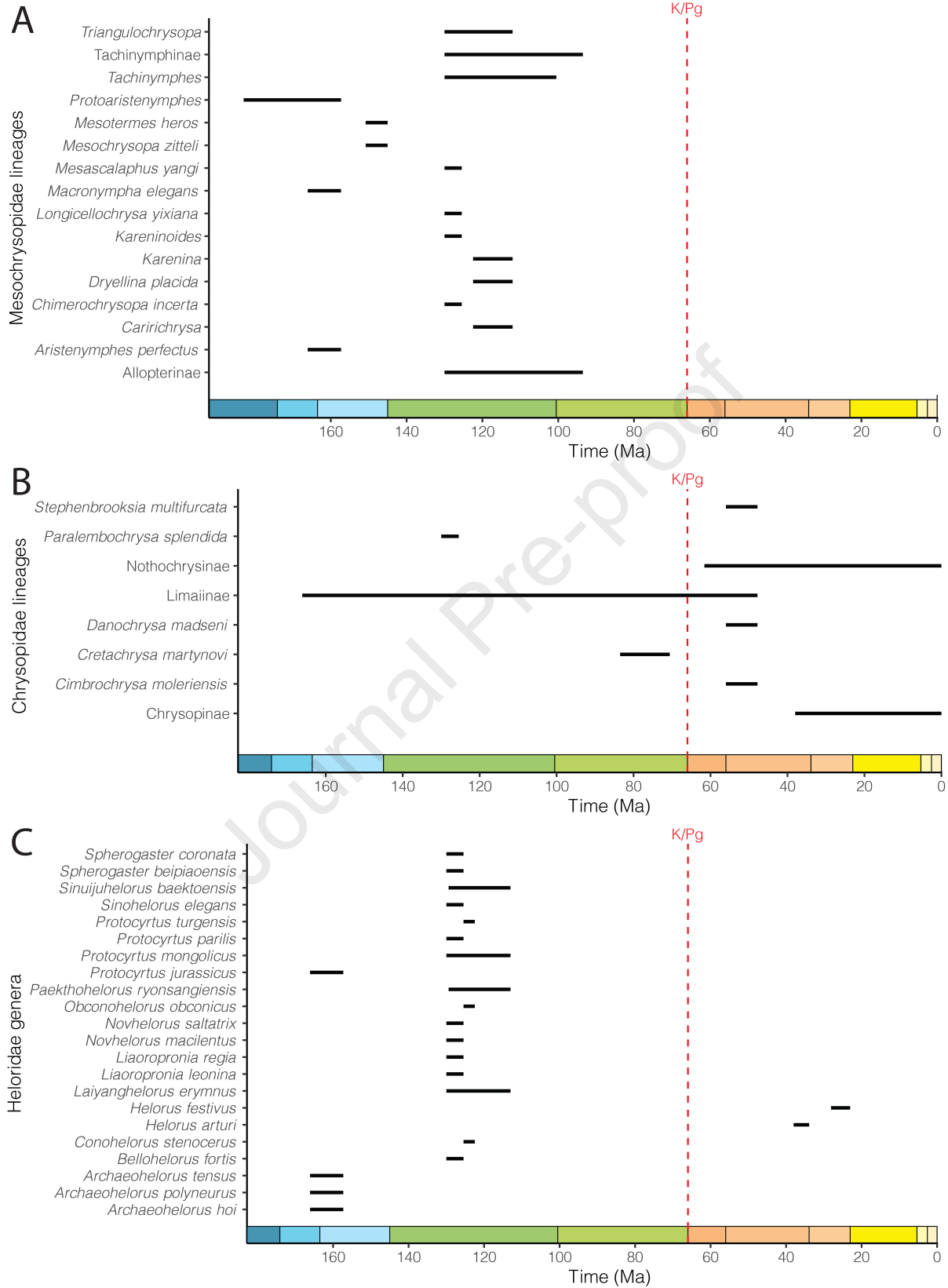












All the authors equally contributed to the manuscript.

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### Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: