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Cretaceous beetles of the Jinju Formation (Coleoptera): An overview of the Jinju Formation, its coleopteran diversity, and past and future research

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Abstract

Several Coleoptera fossils, including Coptoclavidae, Elateridae, Ommatidae, and Staphylinidae, were previously described from the Jinju Formation (Albian), South Korea. However, numerous beetle fossils require further research to fully understand the biodiversity of this important Cretaceous deposit. In this study, we present an overview of the diversity of Coleoptera from the Jinju Formation. Future studies on beetles of the Jinju Formation will be divided into several parts corresponding to the major lineages found in this Albian deposit. In this first part, we introduce the geological context, review previous studies related to Coleoptera fossils from the Jinju Formation, and present specimens that will undergo detailed examination in subsequent papers.

Key words: Insect, Coleoptera, Jinju Formation, Paleoenvironment, Cretaceous, Republic of Korea

Introduction

Beetles (order Coleoptera) are the behemoths of biodiversity, with almost 450,000 described species and thriving in every habitat throughout the world (Grimaldi and Engel, 2005; Ślipiński et al., 2011; Smith and Marcot, 2015; Goczał et al. 2024) and with evolutionary roots extending back to the earliest Permian (Kirejtshuk et al., 2014; Beutel et al. 2024). While molecular analyses estimate the origin of beetles to the Late Carboniferous or possibly earlier (McKenna et al., 2019; Cai et al., 2022), they rose to prominence and diversified ecologically during the Triassic, including the invasion of novel niches such as freshwater environments (Ross et al., 2000; Grimaldi and Engel, 2005; Papier et al., 2005; Kukulová-Peck and Beutel, 2012; Cai et al., 2022; Beutel et al. 2024).

Mesozoic and Cenozoic deposits often encompass diverse coleopteran assemblages, reflective of the considerable proliferation of beetles following the End Permian Extinction Event (e.g., Zhao et al., 2021; Jouault et al., 2022). Such diversity is well reflected in post-Paleozoic deposits in Korea, where numerous sedimentary formations yield specimens of Coleoptera, ranging in age from the Triassic (Nam, 2015) to the Miocene (Lee and Nam, 2021; Lee et al., 2023). Nonetheless, despite the abundance of available material and the diversity of groups discovered, the taxonomic diversity of fossil beetles across Korea remains limited, leaving ample room for novel research and exploration.

Here we introduce a series of studies that will explore the diversity and paleobiological significance of Cretaceous Coleoptera found in outcrops of the Jinju Formation in South Korea. While many specimens were previously studied by Lee (2016), a preliminary examination of the material has highlighted the necessity for a reclassification of most species. This underscores the need for new work on this diversity. Accordingly, we provide a new analysis of both recently collected specimens and those documented by Lee (2016), organizing them into a series of papers addressing particular beetle lineages. Here, we introduce the Jinju Formation, elaborate on the localities from which material has been recovered, provide a brief overview of the diversity preserved, and offer insights into upcoming taxonomic analyses.

Prior research on Jinju Coleoptera

The first fossil beetles reported from the Jinju Formation were of the genus *Coptoclava* Ping, a group attributed to the extinct family Coptoclavidae. However, these specimens were not assigned to a given species. They differ from the well-known *Coptoclava longipoda* Ping in having a different shape to the abdominal outline in adults; however, further study on the classification of these specimens is required to provide a more robust hypothesis of the specific identity and morphological variety (Park et al., 2013).

Subsequent to the aforementioned work, two genera of click beetles (Elateridae) were described as *Megalithomerus magohalmii* Sohn and Nam and *Koreagrypnus jinju* Sohn and Nam (Sohn et al., 2019), followed by a carrion beetle (Staphylinidae: Silphinae), *Cretosaja jinjuensis* Sohn and Nam (Sohn and Nam, 2021), and a reticulated beetle (Archostemata), *Notocupes premeris* Lee et al. (Lee et al., 2022). The latter, *N. premeris*, was a typical member of the genus *Notocupes* Ponomarenko (Li et al., 2023a, 2023b) and added only minor information on the range of morphological variation in the genus as well as extending its known distribution. The two elaterids were originally placed in the the Protagyrypnini (Protagyrypninae). However, the validity of Protagyrypninae remains dubious as the morphological characters originally

proposed to define this putatively extinct subfamily have been questioned by various authors (Muona et al., 2020; Kundrata et al., 2021; Li et al., 2021). Of these, *M. magohalmii* is the largest fossil click beetle currently known, exceeding 40 mm in length (Sohn et al., 2019). *Cretosaja jinjuensis* was identified as a microphorine carrion beetle (Sohn and Nam, 2021), and the authors even proposed that the genus *Cretosaja* Soh and Nam could potentially represent ‘a primitive lineage’ of the extant genus *Ptomascopus* Kraatz. Such an interpretation raises the prospect that the fossil may support the appearance of stridulatory sound production among Staphylinidae, at least as early as the Early Cretaceous, supporting the analysis of Toussaint and Condamine (2016).

Although these findings each hold interest and significance within their respective taxonomic groups, their collective contribution to the broader composition of the coleopteran fauna during that time period is limited. While individually informative, current understanding of the diversity does not allow for in-depth investigation into the paleoecology and paleobiology of beetles within the Early Cretaceous ecosystems of the Korean Peninsula. Thus, future parts of this project will provide taxonomic overviews of particular groups, working to enhance our understanding of beetles from the Jinju Formation. Ultimately, this effort aims to establish a solid foundation for the reconstruction of the coleopteran assemblage and its implications for paleoecology.

Material and Methods

Fossils examined in this research are deposited in the Kyungpook National University in Sangju-si, South Korea and Gongju National University of Education in Gongju-si, South Korea. The fossils were photographed with a Sony α 7R IV mirrorless camera equipped with a Canon EF 100mm f/2.8L Macro IS USM lens *plus* the Kenko extension tube set or a Canon MP-E 65mm f/2.8 1-5X Macro lens.

Geological setting

The Jinju Formation is one of several sedimentary formations in the Gyeongsang Basin of South Korea (Kang and Paik, 2013). Its age has been estimated to be of Albian age (Lee et al., 2010, 2018; Chae et al., 2020). The lithology is mostly formed of dark gray to black shale, with some localities of sandstone (Park et al., 2013). Sedimentological investigations have unveiled the paleoenvironment of Jinju Formation, interpreting it as freshwater and perennial lake (Paik et al., 2023). Traces of lacustrine environment such as ripple marks, turbidites, and stromatolites are also present in the Jinju Formation (Um et al., 1983; Paik et al., 2019; Paik et al., 2023). While sedimentary analysis previously implied a shift from humid to more arid climate within the Jinju Formation (Paik et al., 2023), isotopic study of the plant remains revealed alternation between humid and subhumid periods (Hong et al., 2020).

Considerable work has been undertaken recently on the paleontology of the formation, particularly on pollens or macrofossils of plants (Yi et al., 1994; Kim, 2009), vertebrate footprints (Kim and Lockley, 2016; Kim et al., 2018ab; Kim et al., 2019a,b,c; Kim et al., 2020; Kang et al., 2021), fishes (Lee et al., 2001), ostracods (Choi, 2016; Choi et al., 2018; Choi et al., 2021), spiders (Selden et al., 2012; Park et al., 2019), isopods (Park et al., 2012; Park et al., 2019), and other trace fossils (Kim et al., 2000; Kim and Kim, 2003; Kim et al., 2005; Kim et al., 2008; Lee, 2017).

Numerous insect lineages have been described from the Jinju Formation, including a termite, caddisfly cases, dragonflies, earwigs, lacewings, long-proboscid flies, orthopterans, and snakeflies (Engel et al., 2002; Engel et al., 2006; Paik, 2005; Nam and Kim, 2016; Khramov and Nam, 2020; Khramov et al., 2020; Kim et al., 2021; Jouault and Nam, 2022). Notably, Lee (2018) reported the potential discovery of an insect cocoon or pupation chamber within the sandstone bed of the Jinju Formation. The nature of the fossil record in the Jinju Formation is contingent upon the distinct localities and sedimentological settings (Um et al., 1983; Sohn, 1989; Choi, 1999; Paik et al., 2019; Paik et al., 2023).

Despite the numerous fossil records of beetles in the formation, a comprehensive systematic study has not been published to date. The beetle fossils from Jinju Formation scrutinized for this series of studies were discovered at the following localities. Localities 1–4 are located in Sacheon-si, Gyeongsangnam-do (1: Yonghyeon-myeon; 2: Sanam-myeon; 3, 4: Chukdong-myeon); locality 5 is in Jeongchon-myeon, Jinju-si, Gyeongsangnam-do; localities 6 and 7 are located in Seongsan-myeon, Goryeong-gun, Gyeongsangbuk-do (6:

Gisan-ri, 7: Deukseong-ri); locality 8 is in Habin-myeon, Dalseong-gun, Daegu-gwangyeoksi; and localities 9 and 10 are located in Gunwi-gun, Gyeongsangbuk-do (9: Ubo-myeon, 10: Gwanghyeon-ri, Gunwi-eup) (Fig. 1).

Figure 1

Results

Checklist of Coleoptera from Jinju Formation

Order Coleoptera Linnaeus, 1758

Suborder Adephaga Clairville, 1806

Superfamily Caraboidea Latreille, 1802

Family ? Carabidae Latreille, 1802

Family ? Trachypachidae Thomson, 1857

Suborder Archostemata Kolbe, 1908

Family Ommatidae Sharp and Muir, 1912

Suborder Polyphaga Emery 1886

Series Elateriformia Crowson 1960

Superfamily Buprestoidea Leach, 1815

Family Buprestidae Leach, 1815

Superfamily Elateroidea Leach, 1815

Family Elateridae Leach, 1815

Family Eucnemidae, Eschscholtz, 1829

Series Staphyliniformia Lameere 1900

Superfamily Hydrophiloidea Latreille, 1802

Superfamily Scarabaeoidea Latreille, 1802

Family Geotrupidae Latreille, 1802

Family Scarabaeidae Latreille, 1802

Superfamily Staphylinoidea Latreille, 1802

Family Staphylinidae Latreille, 1802

Series Cucujiformia Lameere 1938

Superfamily Tenebrionoidea Latreille, 1802

Family ? Ripiphoridae Gemminger, 1870

Family ? Tenebrionidae Latreille, 1802

Superfamily Nitiduloidea Latreille, 1802

Family ? Nitidulidae Latreille, 1802

Superfamily Curculionoidea Latreille, 1802

Family Caridae Thompson, 1992

Family Cimberididae de Gozis, 1882

Superfamily Chrysomeloidea Latreille, 1802

Family ? Cerambycidae Latreille, 1802

Family ? Chrysomelidae Latreille, 1802

We confirmed 17 family taxa in this initial research, including: Buprestidae, probable Carabidae, probable Cerambycidae, probable Chrysomelidae, Cimberididae, Caridae, Elateridae, Eucnemidae, Geotrupidae, Hydrophiloidea (genus *Laetopsia* Fikáček et al. and genus *Cretotaenia* Ponomarenko), probable Nitidulidae, Ommatidae, probable Ripiphoridae, Scarabaeidae, Staphylinidae, probable Tenebrionidae, and probable Trachypachidae, with 81 specimens of uncertain taxonomic placement (Table 1, Figs. 2, 3). A total of 52 specimens of the genus *Laetopsia* were identified, showing a much higher number compared with all other taxa, while Cimberididae, Eucnemidae, Ripiphoridae, and Tenebrionidae were each represented by a single specimen.

Figure 2

Figure 3

Table 1

Discussion

Future research plan on Jinju Coleoptera

While the above accounts have offered valuable insights into their individual lineages, the actual diversity of the fauna within the Jinju Formation is considerably richer than what has been documented. In fact, there exists at least 215 specimens of fossil Coleoptera from the Jinju Formation that require further examination. These specimens encompass a relatively wide spectrum of families, representing three of the four extant suborders and several series and superfamilies (Cai et al., 2022). In addition, many of these clades comprise groups of diverse ecologies, ranging from aquatic beetles (e.g., Hydrophiloidea) to prominent terrestrial herbivores (Curculionidae, Chrysomelidae, Cerambycidae). There is therefore a sufficient sampling of families to build an initial view of the coleopteran assemblage in the Jinju Formation and its potential contributions to the paleoecology of the biota at that time. Only five families were described during previous research (see ‘Prior research on Jinju Coleoptera’ part). We have acquired at least 17 taxa from the Jinju Formation. Nonetheless, the classification of a number of taxa is currently uncertain (e.g., ? Chrysomelidae, ? Trachypachidae). Our aim is to provide detailed taxonomic accounts of these taxa and lineages, ultimately permitting a thorough evaluation of the coleopteran fauna and its

paleoecology within the Jinju Formation environment.

There are several early Cretaceous faunas with abundant beetles. The Yixian Formation in China currently encompasses 36 family lineages of beetles, including: Armatopodidae, Cupedidae, Ommatidae, Schizophoridae, Hydroscaphidae, Carabidae, Dytiscidae, Hydrophilloidea (including Helophoridae, Hydrophilidae, genus *Laetopsia*), Staphylinidae, Geotrupidae, Glaphyridae, Glaresidae, Hybosoridae, Lithoscarabaeidae, Lucanidae, Ochodaeidae, Pleocomidae, Scarabaeidae, Septiventeridae, Dascillidae, Buprestidae, Schizopodidae, Eulichadidae, Heteroceridae, Cerophytidae, Elateridae, Eucnemidae, Trogossitidae, Cleroidea, Parandrexidae, Mordellidae, Tenebrionidae, Cerambycidae, Brentidae, and Nemonychidae (Ren et al., 2019), while the Crato Formation in Brazil embodies 12 family lineages including Anthrididae, Attelabidae, Belidae, Brentidae, ? Cantharidae, Curculionidae, Eccoptarthridae, Lymexylidae, Nemonychidae, Passalidae, Pyrochroidae, Scarabaeidae, and Ulyanidae (Vulcano and Pereira, 1987; Grimaldi, 1990; Zherikhin and Gratshev, 2004; Menon, 2006; Santos et al., 2011; Wolf-Schwenninger, 2011; Dos Santos et al., 2021; Háva, 2022). In our future research we will compare the fauna of the Jinju Formation with those mentioned above, and reconstruct the paleoecology and paleogeographical distribution of beetles during the Early Cretaceous.

Conclusion

Here we introduce an interdisciplinary, international collaborative research program centered on the fossil beetles (Coleoptera) of the Early Cretaceous (Albian) Jinju Formation in South Korea. This first part provides a brief introduction of the outcrop localities where Coleoptera were found, elaborates on the geological setting of the formation, and gives a brief history of prior studies undertaken on specific groups within this larger fauna, namely isolated work on Ommatidae, Elateridae, Staphylinidae, and the aedeophagan genus *Coptoclava*. We provided a comprehensive list of the new taxa from several localities from the Jinju Formation, underscoring their significance in elucidating the ecological dynamics of the region at that time. Our additional research will provide descriptions of those taxa and reconstruct the paleoecology of the Jinju Formation, with comparisons to the comparable Yixian and Crato Formations in order to analyze the paleogeographical distribution of beetles during the Early Cretaceous.

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Reference

- Beutel, R.G., Xu, C., Jarzembowski, E., Kundrata, R., Boudinot, B.E., McKenna, D.D., Goczał, J. (2024) The evolutionary history of Coleoptera (Insecta) in the late Palaeozoic and the Mesozoic. *Systematic Entomology*, in press, doi: 10.1111/syen.12623.
- Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J. F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M. K., Newton, A. F., Leschen, R. A. B., Gimmel, M. L., Lü, L., Engel, M. S., Bouchard, P., Huang, D., Pisani, D., Donoghue, P. C. J., 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science* 9(3), 211771.
- Chae, Y. U., Lim, J. D., Kim, C. B., Kim, K. S., Ha, S., Lim, H. S., 2020. Detrital zircon U-Pb ages of the uppermost Jinju Formation in the Natural Monument No. 534 ‘Tracksite of Pterosaurs, Birds, and Dinosaurs in Hotandong, Jinju’, Korea. *Journal of the Korean Earth Science Society* 41, 367–380.

- Choi, B. D., Huh, M., 2016. *Mongolocypris kohi* sp. nov.: A new Early Cretaceous non-marine ostracod species from the Jinju Formation, South Korea. *Cretaceous research* 57, 239–247.
- Choi, B. D., Wang, Y. Q., Huh, M., 2018. Cypridea species (Crustacea, Ostracoda) from the Lower Cretaceous Jinju Formation of the Gyeongsang Basin, South Korea. *Palaeoworld* 27(3), 382–391.
- Choi, B. D., Jia, B., Huh, M., Jung, J., Wang, Y., 2021. Taxonomy, biostratigraphic and paleoecological aspects of non-marine ostracod fauna from the Jinju Formation (Albian) of the Gyeongsang Basin, South Korea. *Cretaceous Research* 127, 104944.
- Choi, H. I., 1999. Upper Mesozoic. In: Geological Society of Korea (ed.), *Geology of Korea*. Sigma Press, 233–273 (in Korean).
- Dos Santos, M. F. A., Mattos, I., Mermudes, J. R. M., Scheffler, S. M., & Reyes-Castillo, P. (2021). A new passalid fossil (Insecta: Coleoptera) from the Santana Formation (Crato member, Lower Cretaceous), Araripe Basin, NE Brazil: Paleocological and paleobiogeographic implications. *Cretaceous Research*, 118, 104664.
- Goczał, J., Beutel, R.G., Gimmel, M.L., Kundrata, R. (2024) When a key innovation becomes redundant: patterns, drivers and consequences of elytral reduction in Coleoptera. *Systematic Entomology* 49(2), 193–220.
- Grimaldi, D. 1990. Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History* 195: 5–191
- Grimaldi, D., Engel, M. S. (Eds.), 2005. *Evolution of the Insects*. Cambridge University Press, Cambridge, The Natural History Museum, London.
- Ha, S., Kim, K. S., Lim, H. S., Lockley, M. G., Yoo, J. S., Lim, J. D., 2022. Diminutive pterosaur tracks and trackways (*Pteraichnus gracilis* ichnosp. nov.) from the Lower Cretaceous Jinju Formation, Gyeongsang Basin, Korea. *Cretaceous research* 131, 105080.
- Háva, J. (2022) The oldest fossil record of Cetoniinae (Coleoptera: Scarabaeidae) from the Lower Cretaceous Crato Formation of Brazil. *Euroasian Entomological Journal*, 21(3), 164–165.
- Jouault, C., Nam, G. S., 2022. A new primitive termite from the lower Cretaceous (Albian) Jinju Formation of Korea. *Historical Biology* 1-6 DOI: 10.1080/08912963.2022.2098490.
- Jouault, C., Nel, A., Perrichot, V. et al. Multiple drivers and lineage-specific insect extinctions during the Permo-Triassic. *Nat Commun* 13, 7512 (2022). <https://doi.org/10.1038/s41467-022-35284-4>
- Hong, S. K., Yi, S., Shinn, Y. J., 2020. Middle Albian climate fluctuation recorded in the carbon isotope composition of terrestrial plant matter. *Journal of Asian Earth Sciences* 196, 104363.
- Kang, H. C., Paik, I. S., 2013. Review on the geological ages of the formations in the Gyeongsang Basin, Korea. *Journal of Geological Society of Korea* 49(1), 17–29.
- Kang, S. H., Buckley, L. G., Mccrea, R. T., Kim, K. S., Lockley, M. G., Lim, J. D., Lim, H. S., Kim, C. B., 2021. First report of bird tracks (*Ignotornis seoungjoseoi* ichnosp. nov.) from the Jinju Formation (Lower Cretaceous), Sacheon City, Korea. *Cretaceous Research* 127, 104899.
- Kim, J. Y., Kim, K. S., Pickerill, R. K., 2000. Trace fossil *Protovirgularia* McCoy, 1850 from the nonmarine Cretaceous Jinju Formation of the Sacheon area, Korea. *Journal of the Korean Earth Science Society* 21(6), 695–702.
- Kim, J. Y., Pickerill, R. K., 2003. Cretaceous nonmarine trace fossils from the Hasandong and Jinju Formations of the Namhae Area, Kyongsangnamdo, southeast Korea. *Ichnos* 9(1-2), 41–60.
- Kim, J. Y., Keighley, D. G., Pickerill, R. K., Hwang, W., Kim, K. S., 2005. Trace fossils from marginal lacustrine deposits of the Cretaceous Jinju Formation, southern coast of Korea. *Palaeogeography, Palaeoclimatology,*

Palaeoecology 218(1-2), 105–124.

Kim, J. Y., Lockley, M., 2016. First report of turtle tracks from the Lower Cretaceous of Korea. *Cretaceous Research* 64, 1–6.

Kim, K. S., Kim, J. Y., 2008. *Lockeia gigantus* ichnosp. nov. in the lacustrine deposits of the Early Cretaceous Jinju Formation, southern coast of Korea. *Journal of the Korean Earth Science Society* 29(1), 13–28.

Kim, J. H., 2009. New occurrence of *Cupressinocladus* sp. from the Lower Cretaceous Jinju Formation, Shindong Group, Korea. *Journal of the Korean Earth Science Society* 30(5), 605–610.

Kim, K. S., Lim, J. D., Lockley, M. G., Xing, L., Ha, S. J., Kim, C. B., Paik, I. S., Ahn, J. H., Mun, S. C., 2018a. First reports of a distinctive theropod track assemblage from the Jinju Formation (Lower Cretaceous) of Korea provides strong correlations with China. *Cretaceous Research* 81, 26–35.

Kim, K. S., Lim, J. D., Lockley, M. G., Xing, L., Kim, D. H., Pinuela, L., Romilio, A., Yoo, J. S., Kim, J. H., Ahn, J., 2018b. Smallest known raptor tracks suggest microraptorine activity in lakeshore setting. *Scientific Reports* 8(1), 1–10.

Kim, K. S., Lockley, M. G., Lim, J. D., Kim, D. H., 2019a. The oldest known anuran (frog) trackways from the Jinju Formation, Lower Cretaceous, Korea. *Cretaceous Research* 96, 142–148.

Kim, K. S., Lockley, M. G., Lim, J. D., Xing, L., 2019b. Exquisitely-preserved, high-definition skin traces in diminutive theropod tracks from the Cretaceous of Korea. *Scientific Reports* 9(1), 1–10.

Kim, K. S., Lim, J. D., Lockley, M. G., Hee, K. D., Pinuela, L., Yoo, J. S., 2019c. Largest Cretaceous lizard track assemblage, new morphotypes and longest trackways comprise diverse components of an exceptional Korean Konservat-Lagerstätten ichnofauna. *Scientific Reports* 9(1), 1–12.

Kim, K. S., Lockley, M. G., Lim, J. D., Bae, S. M., Romilio, A., 2020. Trackway evidence for large bipedal crocodylomorphs from the Cretaceous of Korea. *Scientific Reports* 10(1), 1–13.

Kim, D. Y., Lee, M., Nam, G. S., Park, T. Y. S., 2021. The first orthopteran fossils from the Lower Cretaceous (Albian) Jinju Formation of Korea: Ethological implications for elcanids. *Cretaceous Research* 125, 104843.

Khramov, A. V., Nam, G. S., 2020. The first record of lacewings (Insecta: Neuroptera: Mesochrysopidae) from the Lower Cretaceous of South Korea. *Paleontological Journal* 54, 613–616.

Khramov, A. V., Nam, G. S., Vasilenko, D. V., 2020. First long-proboscid flies (Diptera: Zhangsolvidae) from the Lower Cretaceous of South Korea. *Alcheringa* 44(1), 160–168.

Kirejtshuk, A. G., Poschmann, M., Prokop, J., Garrouste, R., Nel, A., 2014. Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tsherkardocoleidae). *Journal of Systematic Palaeontology* 12(5), 575–600.

Kukalová-Peck, Beutel, R. G., 2012. Is the Carboniferous *Adiphlebia lacoana* really the "oldest beetle"? Critical reassessment and description of a new Permian beetle family. *European Journal of Entomology* 109(4), 633–645

Kundrata, R., Packova, G., Prosvirov, A. S., Hoffmannova, J., 2021. The fossil record of Elateridae (Coleoptera: Elateroidea): Described species, current problems and future prospects. *Insects*, 12(4), 286.

Lee, D. C., 2017. *Radialimbricatus*, a new ichnogenus from the lacustrine sandstone facies of the Lower Cretaceous Jinju Formation, South Korea. *Alcheringa* 41(3), 350–364.

Lee, D. C., 2018. Probable insect cocoon or pupation chamber in a channel-fill sandstone bed of the Lower Cretaceous Jinju Formation, South Korea. *Lethaia* 51(3), 433–443.

Lee, S. S., 2016. Systematic classification of the Cretaceous Coleoptera fossils from the Jinju Formation of

- Sindong Group in Gyeongsang Basin, Korea (Unpubl. Master thesis). Kyungpook National University, 89 pp.
- Lee, S. B., Nam, G. S., 2021. A new species of fossil *Calosoma* (Coleoptera: Carabidae) from the Geumgwangdong Formation (Early Miocene), South Korea. *Zootaxa* 5072(1), 1–11.
- Lee, S. B., Nam, G. S., Li, Y. D., 2022. A new species of *Notocupes* (Coleoptera: Archostemata) from the Lower Cretaceous (Albian) Jinju Formation in South Korea. *Cretaceous Research* 140, 105357.
- Lee, S. B., Nel, A., Nam, G. S., 2023. The first fossil *Scarites* (Coleoptera: Carabidae) from the Duho Formation (middle Miocene), Korean Peninsula. *Palaeoworld*, <https://doi.org/10.1016/j.palwor.2023.05.002>
- Lee, T. H., Park, K. H., Chun, J. H., Yi, K., 2010. SHRIMP U-Pb zircon ages of the Jinju Formation and Silla conglomerate, Gyeongsang Basin. *Journal of the Petrological Society of Korea* 19, 89–101.
- Lee, T. H., Park, K. H., 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.
- Lee, Y. N., Yu, K. M., Wood, C. B., 2001. A review of vertebrate faunas from the Gyeongsang Supergroup (Cretaceous) in South Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165(3-4), 357–373.
- Li, Y. D., Kundrata, R., Huang, D. Y., Cai, C. Y., 2021. Notes on the Morphology and Systematic Position of *Archaeolus* Lin, 1986, from the Jurassic of South China (Coleoptera: Elateroidea). *Insects* 12(10), 876.
- Li, Y. D., Tihelka, E., Yamamoto, S., Newton, A. F., Xia, F. Y., Liu, Y., Huang, D. Y., Cai, C. Y., 2023a. Mesozoic *Notocupes* revealed as the sister group of Cupedidae (Coleoptera: Archostemata). *Frontiers in Ecology and Evolution*, 11, 1015627.
- Li, Y. D., Tihelka, E., Newton, A. F., Huang, D. Y., Cai, C. Y. 2023b. New species of *Notocupes* (Coleoptera: Archostemata) from the Middle Jurassic Daohugou beds, with discussion on the generic circumscription. *Palaeoentomology*, 6(4), 398-415.
- McKenna, D. D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D. J., Donath, A., Escalona, H. E., Friedrich, F., Ietsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P. J., Niehuis, O., Peters, R. S., Podsiadlowski, L., Pohl, H., Scully, E. D., Yan, E. V., Zhou, X., Ślipiński, A., Beutel, R. G., 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences*, 116(49), 24729–24737.
- Muona, J., Chang, H., Ren, D., 2020. The clicking Elateroidea from Chinese Mesozoic deposits (Insecta, Coleoptera). *Insects*, 11(12), 875.
- Menon, F. (2006). *Studies on the Palaeoentomology of the Cretaceous Crato Formation of Brazil*. The University of Manchester (United Kingdom).
- Nam, K. S., 2015. Mesozoic fossil insect fauna from the Amisan Formation in Boryeong area, Korea and its geological implication (Unpubl. PhD thesis). Kongju National University, 135pp.
- Nam, K. S., Kim, J. H., 2016. Reconstruction and paleoecological implications of dragonfly *Hemeroscopus baissicus* Pritykina, 1977 (Hemeroscopidae) from the Lower Cretaceous Jinju Formation in the Jinju Area, Korea. *Journal of the Geological Society of Korea* 52(2), 105–112.
- Paik, I. S., 2005. The oldest record of microbial-caddisfly bioherms from the Early Cretaceous Jinju Formation, Korea: occurrence and palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 218(3-4), 301–315.
- Paik, I. S., Kim, H. J., Kim, S. Y., Lee, J. E., So, Y. H., Lee, H. i., 2019. Fossil-bearing deposits in the Jinju Formation at Jinju: Occurrences, paleoenvironments and stratigraphic implications. *Journal of the Geological Society of Korea* 55(5), 513–530.
- Paik, I. S., Kim, H. J., Park, J. G., Kim, Y. S., 2023. Lacustrine deposits of the Miryang Sub-basin in the southern Gyeongsang Basin, Korea: Occurrences, stratigraphic changes, and paleoenvironmental implications. *Journal of*

the Geological Society of Korea 59(1), 131–157.

Papier, F., Nel, A., Grauvogel-Stamm, L., Gall, J.-C., 2005. La diversité des Coleoptera (Insecta) du Trias dans le nord-est de la France. *Geodiversitas*, 27 (2), 181–199.

Park, T. Y., Wilson, G. D., Lee, D. C., Choi, D. K., 2012. Occurrence of the isopod *Archaeoniscus coreaensis* new species from the Lower Cretaceous Jinju Formation, Korea. *Journal of Paleontology* 86(4), 626–640.

Park, T. Y. S., Kim, Y. H., Nam, K. S., 2013. Preliminary research on the aquatic Coleopteran, *Coptoclava* from the Early Cretaceous Jinju Formation. *Journal of the Geological Society of Korea* 49(6), 617–624.

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(15), 1271–1297.

Ping, C., 1928. Study of the Cretaceous fossil insects of China. *Paleontologica Sinica B*, 13(1), 1–56.

Ponomarenko, A. G., 1977. Suborder Adephaga, Polyphaga Incertae Sedis, Infraorder Staphyliniformia, In: Zherikhin, V. V., (Ed.), *Mesozoic Coleoptera. Infraorder Elateriformia. Series of Superfamilies of Cucujiformia. Family Attelabidae, Family Curculionidae. Remarks on the phyletic links and ecology of Baisian Rhynchophora*. Trudy Paleontologicheskogo Institut, Akademia Nauk, 17–90.

Selden, P. A., Nam, K. S., Kim, S. H., Kim, H. J., 2012. A fossil spider from the Cretaceous of Korea. *Journal of Paleontology* 86(1), 1–6.

Ren, D., Shih, C., Gao, T., Wang, Y., & Yao, Y. (Eds.). (2019). *Rhythms of insect evolution: evidence from the Jurassic and Cretaceous in northern China*. John Wiley & Sons.

Ross, A. J., Jarzembowski, E. A., Brooks, S. J., 2000. The Cretaceous and Cenozoic record of insects (Hexapoda) with regard to global change. In: S. J. Culver and P. F. Rawson (Ed.), *Biotic Response to Global Change: The Last 145 Million Years*, Cambridge University Press, Cambridge, The Natural History Museum, London, 288–302.

Santos, M. F. D. A., Mermudes, J. R. M., & Fonseca, V. M. M. D. (2011). A specimen of Curculioninae (Curculionidae, Coleoptera) from the Lower Cretaceous, Araripe Basin, north-eastern Brazil. *Palaeontology*, 54(4), 807–814.

Ślipiński, S., Leschen, R., Laweence, J., 2011. Order Coleoptera Linnaeus, 1758. In: Zhang, Z. Q. (ed.), *Animal biodiversity: an outline of higher level classification and survey of taxonomic richness*, *zootaxa* 3148, 203–208.

Sohn, J.D., 1989, *Sedimentology of the Jinju and Iljik formations of the Cretaceous Gyeongsang Supergroup in the Gunwi area, Gyeongsangbuk-do, Korea* (Unpubl. PhD thesis). Seoul National University, 110 p (in Korean with English abstract).

Smith, D. M., Marcot, J. D., 2015. The fossil record and macroevolutionary history of the beetles. *Proceedings of the Royal Society B: Biological Sciences* 282(1805), 20150060.

Sohn, J. C., Nam, G. S., Choi, S. W., Ren, D., 2019. New fossils of Elateridae (Insecta, Coleoptera) from Early Cretaceous Jinju Formation (South Korea) with their implications to evolutionary diversity of extinct Protagrypninae. *PLoS One* 14(12), e0225502.

Sohn, J. C., Nam, G. S., 2021. New fossil genus and species of carrion beetle (Coleoptera, Silphidae) from the Lower Cretaceous Jinju Formation, South Korea. *Journal of Asia-Pacific Entomology* 24(3), 584–587.

Toussaint, E. F. A., Condamine, F. L. 2016. To what extent do new fossil discoveries change our understanding of clade evolution? A cautionary tale from burying beetles (Coleoptera: *Nicrophorus*). *Biological Journal of the Linnean Society* 117 (4), 686–704.

Um, S. H., Choi, H. I., Son, J. D., Oh, J. H., Kwak, Y. H., Shin, S. C., Yun, S. H., 1983. Geological and

geochemical studies on the Gyeongsang Supergroup in the Gyeongsang basin. Korea Institute of Energy and Resources Bulletin 36, 124.

Vulcano, M. A., & Pereira, F. S. (1987). Entomofauna fóssil da Chapada do Araripe, Ceará, Brasil—Cretaceimelittomoides cearensis gen. nov. sp. nov. (Coleoptera: Pyrochroidae). In *Proceedings of the Congresso Brasileiro de Paleontologia* (p. 27).

Wolf-Schwenninger, K. (2011). The oldest fossil record of Lymexylidae (Insecta: Coleoptera) from the Lower Cretaceous Crato formation of Brazil. *Insect Systematics & Evolution*, 42(2), 205-212.

Yi, M. S., Cho, B. H., Chi, J. M., 1994. Palynomorphs from the Jinju Formation in the Euisong area, Korea. *Journal of the Paleontological Society of Korea* 10, 41–56.

Zhao, X. et al. Early evolution of beetles regulated by the end- Permian deforestation. *eLife* 10, e72692 (2021).

Zherikhin, V. V., & Gratshev, V. G. (2004). Fossil curculionoid beetles (Coleoptera, Curculionoidea) from the Lower Cretaceous of northeastern Brazil. *Paleontological journal*, 38(5), 528-537.

Figure Captions

Figure 1 Localities where specimens involved in our studies were discovered. The stars indicate the location of fossil sites.

Figure 2 Representative fossil aquatic beetles. a: *Laetopsia* Fikáček, Prokin, Angus, Ponomarenko, Yue, Ren, & Prokop (KNUL-1114-02), b: *Cretotaenia pallida* Ponomarenko (KNUL-1141-13) from the Jinju Formation. Scale bars = 5 mm.

Figure 3 Representative fossil beetles (Coleoptera) from the Jinju Formation. a: probable Carabidae (KNUL-1113-11), b: Staphylinidae (KNUL-1114-101), c: Geotrupidae (KNUL-1114-90), d: Buprestidae (KNUL-1114-66), e: Elateridae (KNUL-1114-89), f: Cimberididae (KNUL-1114-79), g: probable Cerambycidae (KNUL-1114-64), h: probable Rhiphoridae (KNUL-1114-96), i: probable Tenebrionidae (KNUL-1114-105). Scale bars = 1 mm (h), 5mm (a, i), 10mm (b, c, d, e, f, g).

Figure 1

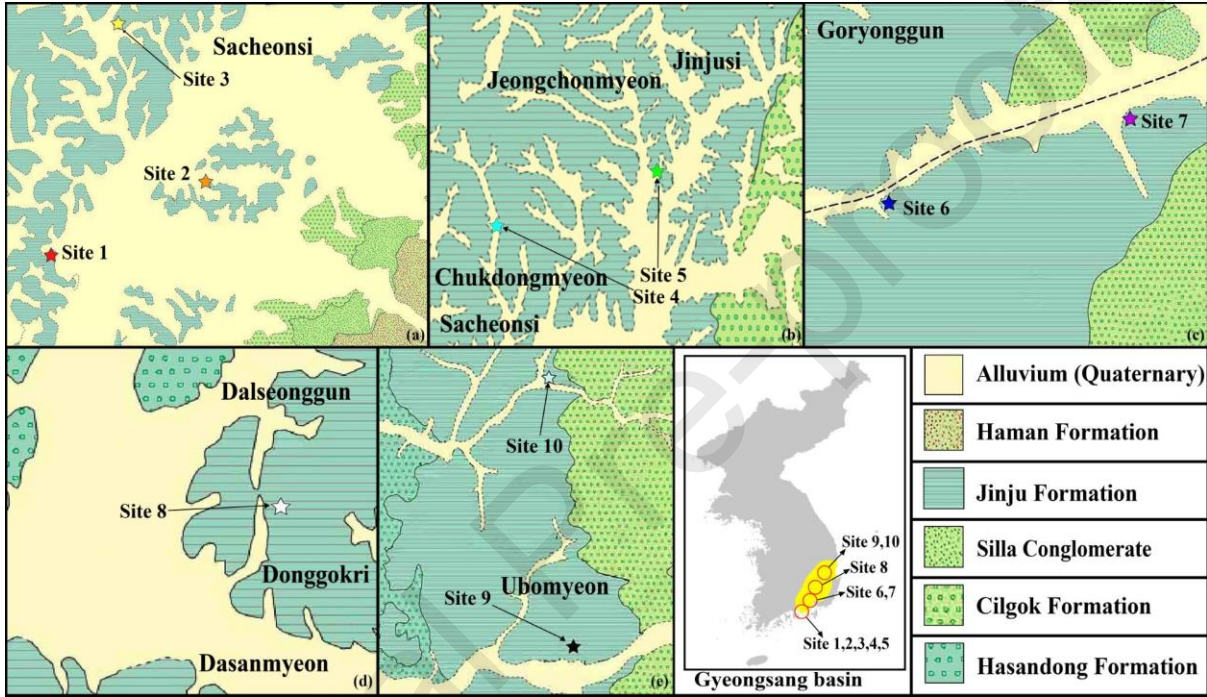


Figure 2

Journal Pre-proofs

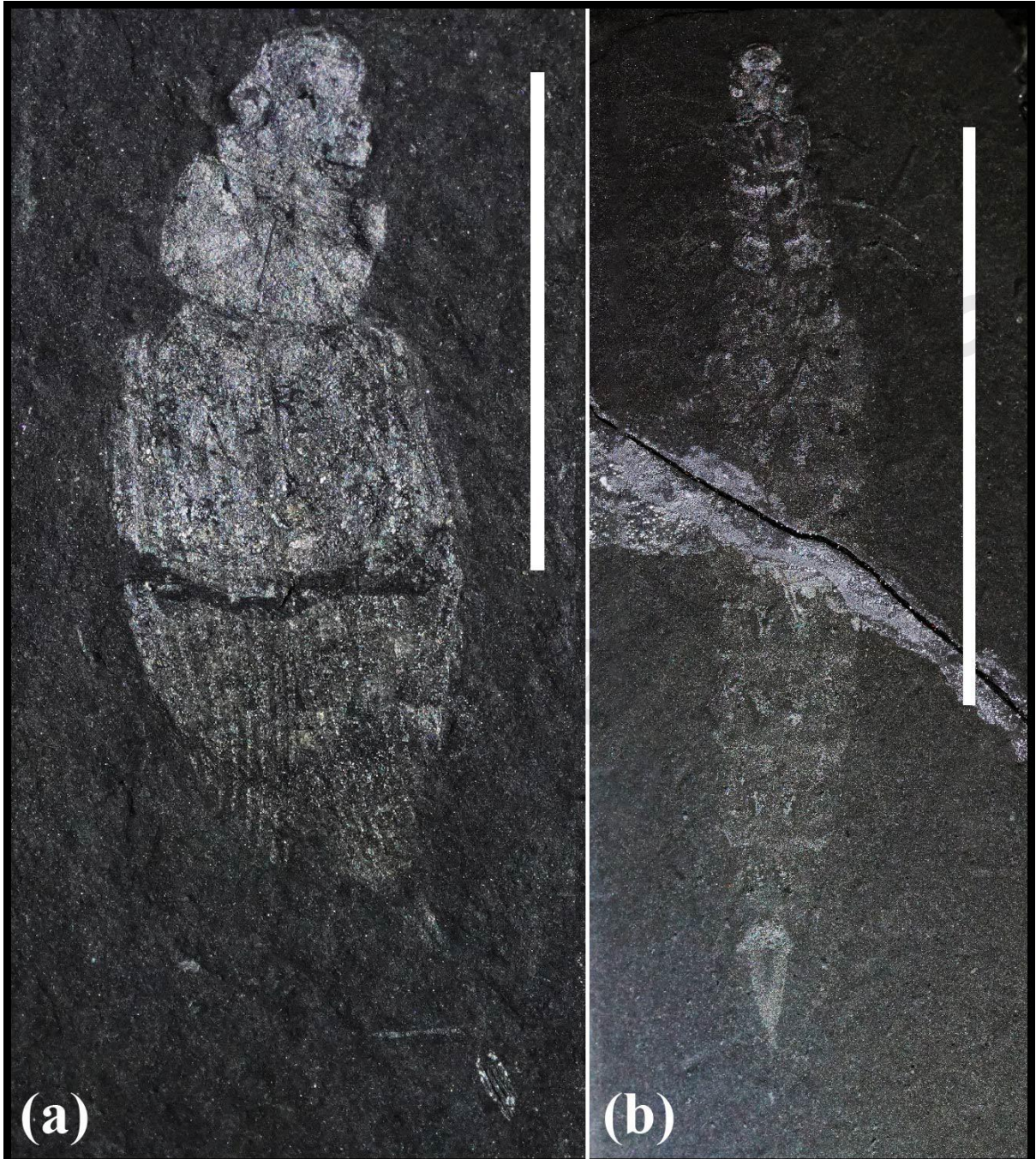


Figure 3



Table caption

Table 1. A summary of coleopteran fossils in our collection.

Journal Pre-proofs

Table. 1

Coleoptera Fossil specimen	Locality Site	Specimen number
Buprestidae	2	5
probable Carabidae	1, 2, 5, 6, 8, 10	12
Caridae	2, 3, 4, 5, 7, 8, 10	5
probable Cerambycidae	2, 4	3
probable Chrysomelidae	2, 6, 10	13
Cimberididae	2	1
Elateridae	5, 8	2

Eucnemidae	5	1
Geotrupidae	2, 4	3
Hydrophiloidea	3, 7, 9, 10	65
probable Nitidulidae	3,4	2
Ommatidae	2, 5	6
probable Ripiphoridae	1	1
Scarabaeidae	2, 6	6
Staphylinidae	2, 3, 5	4
probable Tenebrionidae	7, 8	1
probable Trachypachidae	4,7	3
<i>Incertae sedis</i>	1, 2, 3, 4, 5, 6, 8, 10	81
