





https://doi.org/10.11646/zootaxa.5562.1.12 http://zoobank.org/urn:lsid:zoobank.org:pub:14DDD852-231F-4150-AE26-550F867EF7EA

Cretaceous beetles from Jinju Formation: Trachypachidae (Coleoptera: Adephaga)

SOO BIN LEE^{1, 2, 4, *}, GI SOO NAM^{2, 5} & JONG KYUN PARK^{3, 6}

¹Korean Fossil Research Center, 50-2, Hangangro 2Ga, YongsangGu, Seoul, Republic of Korea ²Department of Science Education, Gongju National University of Education, 27 Ungjinro, Gongjusi, Chungcheongnam-do 32553, Republic of Korea

³College of Ecology and Environmental Science, Kyungpook National University, Sangju-si, Gyeongsangbuk-do 37224, Republic of Korea

⁴ dinos20000@naver.com; ⁶ https://orcid.org/0000-0003-2112-3897

⁵ sil@gjue.ac.kr; https://orcid.org/0000-0003-0570-8270

⁶ entopark@knu.ac.kr; ⁶ https://orcid.org/0000-0002-4049-3546

*Corresponding author

Abstract

Here we describe two new species, *Psacodromeus recta* **sp. nov.** and *Necronectulus lazarus* **sp. nov.**, that belong to the family Trachypachidae. Only one species of the genus *Psacodromeus*, *P. minor*, was reported from the Gurvaneren Formation in Mongolia, which is estimated as Early Cretaceous. Other species of the genus *Psacodromeus*, including *P. crassus*, *P. gutta*, *P. ovalis*, and *P. rugosus*, were reported from the Karabastau Formation in Kazakhstan, which is dated to the Late Jurassic. *Necronectulus avus*, which is the only species of the genus *Necronectulus*, was reported from the Tologoi Formation in Kazakhstan, which is dated to the Late Triassic. Therefore, our study has expanded the fossil record of the genera *Psacodromeus* and *Necronectulus* from the Early Cretaceous.

Key words: Trachypachidae, Early Cretaceous, Jinju Formation, South Korea

Introduction

The family Trachypachidae was firstly elected by Thomson in 1857. It is classified into two subfamilies: Trachypachinae (extant taxa) and Eodromeinae (extinct taxa). The primary difference between these subfamilies lies in the shape of the metepisternum, which either extends to the mesocoxal cavities or does not (Ponomarenko 1977; Wang *et al.* 2012). Members of Trachypachidae closely resemble to the family Carabidae but they are distinguished by their smooth, non-pubescent flagellar segments of the antennae and large metacoxae that extend to the lateral margins of the body (Ball 2000). Extent Trachypachidae are diurnal (active during day light) predator or scavenger, mesophilous to xerophilous geophiles and living in coniferous or deciduous forest (Ball 2000).

Extant members of Trachypachidae are distributed across northern Eurasia, North America, and South America while fossil records of the family have been found from Europe to Asia, with the greatest diversity observed during the Mesozoic (Beutel & Arndt 2005; Maddison *et al.* 2009; Wang *et al.* 2012; Kirejtshuk & Ansorge 2023). The earliest fossil record of Trachypachidae, *Petrodromeus asiaticus*, was discovered at the Babii Kamen locality in Siberia, which is dated to the Permian or basal Triassic (Wang *et al.* 2012; Ponomarenko & Volkov 2013; Kirejtshuk & Ansorge 2022). Other studies indicate that the Mesozoic fossil record of Trachypachidae includes 19 genera and 51 species discovered across Europe and Asia (Table 1, Fig. 1).

Here, we describe the first fossil record of the family Trachypachidae from the Jinju Formation, South Korea. Two genera, *Psacodromeus* and *Necronectulus*, are identified in this study. Specimens were collected from two localities: Sacheon-si, Sanam-myeon, Gyeongsangnam-do (KNUL-1114-106, KNUL-1114-109; 35°04′05″N, 128°03′51″E) and Goryeong-gun, Seongsan-myeon, Gyeongsangbuk-do (KNUL-1114-110; 35°44′27″ N, 128°19′57″ E).

94 Accepted by C.-Y. Cai: 19 Dec. 2024; published: 31 Dec. 2024

Licensed under Creative Commons Attribution-N.C. 4.0 International https://creativecommons.org/licenses/by-nc/4.0/

TABLE 1. List of the Mesozoic Trachypachidae fossil record.

Species	Formation	Age	Reference
Apermunda minor	Mal'tseva Fm.	Permian or Triassic	Ponomarenko &Volkov (2013
Coreoeicos dilatatus	Posidonia Shale Fm.	Jurassic (Toarcian)	Bode (1953)
Denudirabus exstrius	Lushangfen Fm.	Cretaceous (Aptian)	Ren (1995)
Dolichorabus longipes	Ichetuy Fm.	Jurassic (Oxfordian)	Ponomarenko (1985)
Dundorabus glabrus	Ulaan-Ereg Fm.	Jurassic (Tithonian)	Ponomarenko (1989)
Eodromeites udensis	Uda Fm.	Jurassic (Oxfordian/Kimmeridgian)	Ponomarenko (1985)
E. minimus	Ichetuy Fm.	Jurassic (Oxfordian)	Ponomarenko (1985)
Eodromeus antiquus	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
E. daohugouensis	Daohugou Fm.	Jurassic (Callovian/Oxfordian)	Wang et al. (2012)
E. dissectus	Zaza Fm.	Cretaceous (Aptian)	Ponomarenko (1977)
E. major	Zaza Fm.	Cretaceous (Aptian)	Ponomarenko (1977)
E. mongolicus	Dzun-Bain Fm.	Cretaceous (Aptian)	Ponomarenko (1989)
E. robustus	Daohugou Fm.	Jurassic (Callovian/Oxfordian)	Wang et al. (2012)
E. sternalis	Tignin Fm.	Cretaceous (Neocomian)	Ponomarenko (1977)
E. sulcatus	Shinekhudag Fm.	Cretaceous (Aptian)	Ponomarenko (1989)
Evertus cornutus	Gurvan-Eren Fm.	Cretaceous (Aptian)	Ponomarenko (1986)
E. notatus	Gurvan-Eren Fm.	Cretaceous (Aptian)	Ponomarenko (1986)
E. pervalimand	Yixian Fm.	Cretaceous (Aptian)	Jia & Ren (2011)
Karadromeus capitatus	Gurvan-Eren Fm.	Cretaceous (Aptian)	Ponomarenko (1986)
K. elongatus	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1977)
K. erensis	Gurvan-Eren Fm.	Cretaceous (Aptian)	Ponomarenko (1986)
K. gobiensis	Mogotuin Fm.	Cretaceous (Aptian)	Ponomarenko (1980)
K. latus	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
K. mongolicus	Shinekhudag Fm.	Cretaceous (Aptian)	Ponomarenko (1977)
K. rostratus	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
Karadromeus. verrucosus	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1989)
Karatoma agilis	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
K. raptor	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1977)
Liassodites obsti	Mecklenburg- Vorpommern	Jurassic (Toarcian)	Kirejtshuk & Ansorge (2022)
Necronectulus avus	Tologoi Fm.	Triassic (Camian/ Norian)	Ponomarenko (1977)
V. lazarus sp. nov.	Jinju Fm.	Cretaceous (Albian)	This study
Novunda angulata	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1977)
V. chifengensis	Daohugou Fm.	Jurassic (Oxfordian)	Wang et al. (2012)
N. cursoria	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1977)
N. microplata	Glushkovo Fm.	Jurassic (Tithonian)	Ponomarenko (1977)
N. pachycephala	Daohugou Fm.	Jurassic (Oxfordian)	Ponomarenko (1989)
Petrodromeus asiaticus	Mal'tseva Fm.	Permian (Changhsingian)	Martynov (1936)
Platycoxa armata	Dzhil Fm.	Jurassic (Hettangian)	Ponomarenko (1977)
^P . jurassica	Tologoi Fm.	Triassic (Norian)	Ponomarenko (1977)
Prosynactus scissus	Posidonia Shale Fm.	Jurassic (Toarcian)	Bode (1953)
P. procerus	Posidonia Shale Fm.	Jurassic (Toarcian)	Bode (1953)
P. gracilis	Posidonia Shale Fm.	Jurassic (Toarcian)	Bode (1953)
Psacodromeus gutta	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
2. crassus	Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
P. minor	Gurvaneren Fm.	Cretaceous (Aptian)	Ponomarenko (1986)
2. minor 2. ovalis	Gurvaneren Fm. Karabastau Fm.	Jurassic (Callovian/Oxfordian)	Ponomarenko (1986) Ponomarenko (1977)
	Karabastau Fm. Karabastau Fm.		
P. rugosus		Jurassic (Callovian/Oxfordian)	Ponomarenko (1977)
P. recta sp. nov.	Jinju Fm. Vivion Fm	Cretaceous (Albian)	This study
Sinodromeus liutiaogouensis	Yixian Fm. Madygen Fm.	Cretaceous (Barremian) Triassic (Ladinian)	Wang <i>et al.</i> (2012) Ponomarenko (1977)



FIGURE 1. Fossil record of Trachypachidae during the Mesozoic. A, Cretaceous. B, Jurassic. C, Triassic. Data source from PaleobioDB website (2024). Skyblue color dots at 'a' indicate the new fossil record on our research.

Material and methods

Three specimens were examined in this study. Photographs were taken using a Sony a7R IV mirrorless camera equipped with an MP-E 65mm f/2.8 $1-5 \times$ Macro lens. Sketches were produced using Adobe Illustrator. All specimens are currently deposited in Kyungpook National University.

The data for the Trachypachidae fossil record shown in Figure 1 were obtained from the PaleobioDB package in RStudio version 2024.9.1.394 (Varela *et al.* 2015; RStudio Team 2024). Global maps in Figure 1 were generated using the ggplot2 and mapspackages (Wickham *et al.* 2016; Becker *et al.* 2024). The Korean peninsula map in Figure 2 was created using the sf, ggplot2, rnaturalearth, rnaturalearthdata, and dplyrpackages in RStudio version 2024.9.1.394 (Wickham 2016; Pebesma 2018; Massicotte *et al.* 2023; Wickham *et al.* 2023; South *et al.* 2024; RStudio Team 2024) and further refined using Adobe Illustrator, Adobe Photoshop and SAI tool software (https://www.systemax.jp/en/sai/). Geological map data were sourced from the Korea Institute of Geoscience and Mineral Resources (KIGAM) database (https://data.kigam.re.kr/mgeo/map/main.do?process=geology_tree).



FIGURE 2. Fossil locality. **A**, Location of Gyeongsangbuk-do Goryonggun seongsanmyeon and Gyeongsangnam-do Sacheonsi Sanammyeon. **B**, Geological map of Gyeongsangbuk-do Goryonggun seongsanmyeon. **C**, Geological map of Gyeongsangnam-do Sacheonsi Sanammyeon.

Geological setting

The Jinju Formation, part of the Sindong Group within the Gyeongsang Supergroup, is distributed across the Gyeongsang Basin (Chang 1975). Its age is estimated to be Albian based on SHRIMP U-Pb analysis (Kang & Paik 2013). The paleoenvironment of the Jinju Formation is interpreted as lacustrine (Um *et al.* 1983; Choi 1985; Paik *et al.* 2019). Its lithology is characterized by alternating layers of gray sandstone and shale, with local occurrences of carbonate deposits, sandstone, and stromatolites (Um *et al.* 1983; Sohn 1989; Chun 1992; Lee & Woo 1996; Lee 1997; Lee & Kong 2004; Paik 2005; Paik *et al.* 2019).

Numerous fossils, including vertebrates, invertebrates, plants, and trace fossils, have been discovered in the Jinju Formation (Yabe 1905; Park & Chang, 1998; Yabumoto & Yang 2000; Lim *et al.* 2001; Yun *et al.* 2001, 2004, 2007; Baek & Yang 2004; Yun & Yang 2004; Kim *et al.* 2005, 2014, 2016, 2017, 2018, 2019a, b, 2020; Kim & Kim 2008; Kim 2009; Yabumoto *et al.* 2006; Park *et al.* 2012, 2019; Choi & Huh 2015; Choi *et al.* 2018, 2021; Paik *et al.* 2019; Lockley *et al.* 2020; Ha *et al.* 2022). Fossil insects from the Jinju Formation encompass a diverse taxa including: Alienoptera, Blattodea, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Neuroptera, Odonata, Orthoptera, and Raphidioptera (Engel *et al.* 2006, 2020; Nam & Kim 2016, 2021; Sohn *et al.* 2019; Khramov & Nam 2020; Sohn & Nam 2021, 2024; Lee *et al.* 2022, 2023, 2024a, b; Jouault & Nam 2023; Rosse-Guillevic *et al.* 2023a,b). Additionally, Lee (2018) described a possible insect cocoon or pupation chamber.

The lithology of the Goryeong-gun, Seongsan-myeon area in Gyeongsangbuk-do consists primarily of sandstone and shale, while the Sacheon-si, Sanam-myeon area in Gyeongsangnam-do is predominantly shale with heat-transformed trace fossils. However, many outcrops in the latter locality have been destroyed due to construction activities (Lee, 2016).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Trachypachidae Thomson, 1857

Subfamily Eodromeinae Ponomarenko, 1977

Genus *Psacodromeus* Ponomarenko, 1977

Psacodromeus recta sp. nov.

Material. Holotype KNUL-1114-106, Paratype KNUL-1114-109

Etymology. The species name recta is derived from the Latin word recta, meaning straight.

Locality and horizon. Sacheon-si, Sanam-myeon, Gyeongsangnam-do, Republic of Korea; Jinju Formation, Early Cretaceous, Albian

Diagnosis. Lateral margin of the pronotum straight; the anterior margin of the pronotum is extremely narrower than the posterior margin.

Description. Body lengths ranging from 6.3 mm (KNUL-1114-109) to 9 mm (KNUL-1114-106) and widths from 3.5 mm (KNUL-1114-106) to 5 mm (KNUL-1114-109). Head narrowed anteriorly, with a rounded basal edge; anterior edge of labrum rounded; maxillary palp with three segments, third one slightly wider than others; antennae long, with 11 antennomeres.

Pronotum wider posteriorly, with lateral outer margins straight; posterior margin concave, but the middle partly protruding, pronotum with an overall tetragonal shape; prosternum almost straight posteriorly and contiguous with procoxae; prosternal process short and contiguous with mesoventrite, mesoventrite large, resembling an inverted triangle, with anterior margin pulled posteriorly in middle and posterior margin slightly pulled anteriorly in middle; metepisternum anteriorly large and extremely narrowed posteriorly; metepimeron roughly square-shaped, with posterior part slightly wider than anterior one; epipleuron thick; elytra oval and narrowed posteriorly; no striae or punctures on elytra; prolegs preserved with procoxae and profemora in KNUL-1114-106; profemora poorly preserved in KNUL-1114-109; procoxa polygonal, profemur slightly narrower distally, but with a straight overall outer margin; midleg preserved in KNUL-1114-106, including mesocoxa, mesofemur, and a part of mesotibia;

mesocoxa rounded to polygonal and larger than procoxa; mesofemur wide distally, with widest part at middle; mesofemora poorly preserved in KNUL-1114-109; hindlegs preserved in both KNUL-1114-106 and KNUL-1114-109; metacoxal plate elongated laterally and meeting epipleuron; metacoxae large and polygonal; metafemur widest anteriorly and slightly narrowed distally; metatibia almost straight, widest at distal end; metatarsus with five segments.



FIGURE 3. Psacodromeus recta sp. nov. (KNUL-1114-106).

Remarks. The overall morphology of KNUL-1114-106 and KNUL-1114-109 are showing the features of the family Trachypachidae including: 1) head narrower than prothorax; 2) Antennae inserted between eyes and base of mandibles; 3) antenna filiform and formed with 11 antennomeres; metacoxae extended laterally, meeting with lateral margins of body (Ball, 2000).

The overall body shape of KNUL-1114-106 and KNUL-1114-109 is teardrop-shaped. The head is narrowed anteriorly, with a triangular shape. The anterior edge of the pronotum is rounded and sharp. These features are diagnostic for the genus *Psacodromeus* (Ponomarenko, 1977). Most species of *Psacodromeus* (*P. crassus, P. gutta*,

P. ovalis, and *P. rugosus*) have been discovered from the Jurassic of Kazakhstan (Ponomarenko, 1977). Only *P. minor* has been discovered from the Gurvaneren Formation in Mongolia, which is dated as Early Cretaceous, Aptian (Ponomarenko, 1986). *P. recta* **sp. nov.** is differ from the *P. minor* that 1) lateral margin of the pronotum is straight (rounded in P. minor) and 2) width of anterior margin of pronotum noticeably narrower than the posterior margin (slightly narrower in *P. minor*).



FIGURE 4. Psacodromeus recta sp. nov. (KNUL-1114-109).

Genus Necronectulus Ponomarenko, 1977

Necronectulus lazarus sp. nov.

Material. Holotype KNUL-1114-110

Etymology. The species name *lazarus* is derived from the term "Lazarus taxon", which refers to a taxon that was initially considered to have disappeared from a particular period but later reappeared in the fossil record.

Locality and horizon. Goryeong-gun, Seongsan-myeon, Gyeongsangbuk-do, Republic of Korea; Jinju Formation, Early Cretaceous, Albian.



FIGURE 5. Necronectulus lazarus sp. nov. (KNUL-1114-110).

Diagnosis. Large scutellum; 9 longitudinal striae grooved on the elytron.

Description. Overall body oval shape, with greatest width at posterior part of pronotum extending to anterior margin of elytra. Total body length 7.5 mm, width 4.5 mm. Head wider than long, and extremely narrowed anteriorly; frons wider than long; width of frons and clypeus almost equal from posterior to anterior parts; labrum rounded anteriorly; maxillary palp with three segments; compound eyes large; antennae long, with 11 antennomeres; lateral margin of pronotum slightly rounded, with both anterior and posterior margins straight; anterior corners sharp; a longitudinal groove running medially from pronotum to frons; anterior margin of elytra straight, elytra formed with nine longitudinally grooved striae; epipleuron thick; scutellum large, triangular in shape; adephagus protruded and rounded posteriorly. Ventral part of body poorly preserved, but several traces evident; precoxae contiguous with each other, and profemur wider distally; metacoxal plate extending laterally to meet epipleuron.

Remarks. Morphological features such as: head narrower than prothorax; Antennae inserted between the eyes and base of the mandible; Filiform shape antennae formed with 11 antennomeres; metacoxae extended laterally

and meet with the lateral margins of body are features of the family Trachypachidae (Ball 2000). The overall body shape of KNUL-1114-110 is oval, with the head being transverse and wider than long. The length of the head is greater than that of the pronotum. The pronotum tapers roundly anteriorly, with both the posterior margin of the pronotum and the anterior margin of the elytra being straight. The antennae are short and slender. These features are characteristic of the genus *Necronectulus* (Ponomarenko 1977).

Discussion

Ponomarenko (1977) described genera of the family Trachypachidae including: *Sogdodromeus*, *Platycoxa*, *Unda*, *Psacodromeus*, *Karatoma*, *Karadromeus*, *Eodromeus* and *Necronectulus*. Our study presents the first fossil record of the genera *Psacodromeus* and *Necronectulus* from the Korean Peninsula, specifically from the Early Cretaceous. Fossil records of the genus *Psacodromeus* have been found in Kazakhstan and Mongolia. However, the fossil records from the Kazakhstan are estimated to be the Jurassic (Ponomarenko 1977). The only known *Psacodromeus* species from the Early Cretaceous is *P. minor*, which is the species from the Gurvaneren Formation in Mongolia (Ponomarenko, 1982). Thus, our findings describe a new species of the genus *Psacodromeus* from the Early Cretaceous.

Ponomarenko (1977) initially proposed the genus *Necronectulus* into the *incertae sedis* within the suborder Adephaga. However, Lin (1986) and Kirejtshuk & Ansorge (2023) proposed this genus within the family Trachypachidae because of the morphological features. We support their classification on the genus *Necronectulus* contains the features of the family Trachypachidae such as filiform antennae formed with 11antennomeres and metacoxae extended laterally to the lateral part of the body and classify the genus *Necronectulus* into the family Trachypachidae (see fig. 51 from Ponomarenko 1977; Ball 2000). Only one species, *N. avus* was discovered in the Tologoi Formation of Kazakhstan, which is estimated to be the Late Triassic (Ponomarenko 1977). Therefore, we present the first fossil record of the genus *Necronectulus* from the Early Cretaceous, and this means that this genus had survived from the Late Triassic to the Early Cretaceous.

Ponomarenko (1977) describe that *N. avus* contains no trace of striae on the elytra, but only shallow punctures which are not forming the regular rows. However, *N. lazarus* **sp. nov.** contains 9 striae on the elytron which is different from the *N. avus*. This could suggests that this genus had evolved the striae from the shallow punctures through the Mesozoic. Further studies about the is required to resolve this.

Conclusion

Here we describe two new species in the genera *Psacodromeus* and *Necronectulus* of the family Trachypachidae from the Jinju Formation, South Korea. The genus *Psacodromeus* were described from the Karabastau Formation in Kazahstan and Gurvaneren Formation in Mongolia. Only one species, *P. minor* was discovered from the Gurvaneren Formation which is the Early Cretaceous. However, *P. recta* **sp. nov.** shows the different morphological features on the pronotum, comparable to *P. minor*. We extend the distribution of the genus *Psacodromeus* during the Early Cretaceous. Previously, *Necronectulus avus*, the sole species of the genus *Necronectulus*, was described from the Tologoi Formation in Kazakhstan (Late Triassic). Our research introduces a new species, *N. lazarus* **sp. nov.**, representing the first fossil record of the genus *Necronectulus* from the Early Cretaceous. While *N. avus* exhibits no traces of striae but displays shallow punctures forming irregular rows on the elytra, *N. lazarus* **sp. nov.** has nine striae on the elytra. This could suggests that the genus *Necronectulus* may have evolved striae from shallow punctures over the Mesozoic. Further studies are necessary to clarify this evolutionary transition.

Acknowledgement

We thank to Dr André Nel from the Museum National d'Histoire Naturelle, Dr Chenyang Cai from the Nanjing Institute of Geology and Palaeontology, CAS and Do Yoon Kim from the Seoul National University for assistance and advice on the manuscript. We also thank to anonymous reviewers and editors for their effort and helpful suggestion.

Reference

- Baca, S.M., Gustafson, G.T., Alexander, A.M., Gough, H.M. & Toussaint, E.F. (2021) Integrative phylogenomics reveals a Permian origin of Adephaga beetles. *Systematic Entomology*, 46 (4), 968–990. https://doi.org/10.1111/syen.12506
- Baek, K.S. & Yang, S.Y. (2004) Cockroaches from the Early Cretaceous of Korea (Blattaria: Mesoblattinidae). *Journal of the Paleontological Society of Korea*, 20 (2), 71–98. [in Korean with English abstract].
- Ball, G.E. (2000) 9. Trachypachidae Thomson, C. G., 1857. In: Arnett, R.H. Jr. & Thomas, M.C. (Eds). American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, Florida, pp. 144–146.
- Becker, R.A., Wilks, A.R., Brownrigg, R., Minka, T.P. & Deckmyn, A. (2024) Maps: Draw geographical maps. R package version 3.4.2.1. Available from: https://CRAN.R-project.org/package=maps (accessed 7 Nov. 2024).
- Beutel, R.G. & Arndt, E. (2005) 7.7. Trachypachidae. In: Beutel, R.G. & Leschen, R.A.B. (Eds), Handbook of Zoology, Vol. IV Arthropoda: Insecta. Part 38. Coleoptera, Vol. 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga (partim). Walter De Gruyter, Berlin, Germany, pp. 116–119. https://doi.org/10.1515/9783110904550
- Cai, C.Y., 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.Y., Pisani, D. & Donoghue, P.C.J. (2022) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science*, 9 (3), 211771. https://doi.org/10.1098/rsos.211771
- Chang, K.H. (1975) Cretaceous stratigraphy of Southeast Korea. Journal of the Geological Society of Korea, 11, 1-23.
- 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. https://doi.org/10.1016/j.cretres.2015.09.008
- 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. https://doi.org/10.1016/j.palwor.2018.03.005
- 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.

https://doi.org/10.1016/j.cretres.2021.104944

- Engel, M.S., Lim, J.D., Baek, K.S. & Martin, L.D. (2002) An earwig from the Lower Cretaceous of Korea (Dermaptera: Forficulina). *Journal of the Kansas Entomological Society*, 75 (2), 86–90.
- Engel, M.S., Lim, J.D. & Baek, K.S. (2006) Fossil snakeflies from the Early Cretaceous of southern Korea (Raphidioptera: Mesoraphidiidae). Neues Jahrbuch für Geologie und Paläontologie-Monatshefte, 2006 (4), 249–256. https://doi.org/10.1127/njgpm/2006/2006/249
- Jouault, C. & Nam, G.S. (2023) A new primitive termite from the lower cretaceous (Albian) Jinju Formation of Korea. *Historical Biology*, 35 (9), 1522–1527.

https://doi.org/10.1080/08912963.2022.2098490

- 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. https://doi.org/10.1016/j.cretres.2021.105080
- 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.
- https://doi.org/10.1016/j.jseaes.2020.104363
- Kang, H.C. & Paik, I.S. (2013) Review on the geological ages of the formations in the Gyeongsang Basin, Korea. *Journal of the Geological Society of Korea*, 49 (1), 17–29. [in Korean with English abstract].
- 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. https://doi.org/10.1134/S003103012005007X
- 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, 105–124.

https://doi.org/10.1016/j.palaeo.2004.12.008

- 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. https://doi.org/10.5467/JKESS.2008.29.1.013
- Kim, H.M., Chang, M.M., Wu, F. & Kim, Y.H. (2014) A new ichthyodectiform (Pisces, Teleostei) from the Lower Cretaceous of South Korea and its paleobiogeographic implication. *Cretaceous Research*, 47, 117–130. https://doi.org/10.1016/j.cretres.2013.11.007

Kim, J.H., Nam, K.S., Lee, S.B. & Jeon, Y.S. (2016) Fossil Plants from the Early Cretaceous Hasandong Formation of Chilgok

Area, Korea. *Journal of the Korean Earth Science Society*, 37 (5), 295–308. https://doi.org/10.5467/JKESS.2016.37.5.295

- 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. (2017) 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. https://doi.org/10.1016/j.cretres.2017.08.005
- Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Kim, D.H., Piuela, L., Romilio, A., Yoo, J.S., Kim, J.H. & Ahn, J. (2018) Smallest known raptor tracks suggest microraptorine activity in lakeshore setting. *Scientific Reports*, 8 (1), 1–10. https://doi.org/10.1038/s41598-018-35289-4
- Kim, K.S., Lockley, M.G., Lim, J.D. & Xing, L. (2019a) Exquisitely-preserved, high-definition skin traces in diminutive theropod tracks from the Cretaceous of Korea. *Scientific Reports*, 9 (1), 2039. https://doi.org/10.1038/s41598-019-38633-4
- Kim, K.S., Lockley, M.G., Lim, J.D. & Kim, D.H. (2019b) The oldest known anuran (frog) trackways from the Jinju Formation, Lower Cretaceous, Korea. *Cretaceous Research*, 96, 142–148. https://doi.org/10.1016/j.cretres.2018.12.008
- 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), 8680. https://doi.org/10.1038/s41598-020-66008-7
- 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. https://doi.org/10.1016/j.cretres.2021.104843
- Kirejtshuk, A.G. & Ansorge, J. (2023) An extraordinarily preserved new genus and species of Trachypachidae (Coleoptera, Adephaga) from the Early Jurassic of Germany and a review of fossil trachypachid genera. *Historical Biology*, 35 (6), 958–975.

https://doi.org/10.1080/08912963.2022.2071709

- 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. https://doi.org/10.1111/let.12257
- 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. https://doi.org/10.1016/j.cretres.2022.105357
- Lee, S.B., Nam, G.S., Park, J.K., Lee, B.H. & Li, Y.D. (2023) Cretaceous beetles of the Jinju Formation (Coleoptera): Archostemata. *Palaeoentomology*, 6 (5), 496–506.
- Lee, S.B., Li, Y.D., Cai, C., Engel, M.S., Nam, G.S., Park, J.K., Nel, A., Jenkins, J.S., Jouault, C., Legalov, A. & Kundrata, R. (2024a) Cretaceous beetles of the Jinju Formation (Coleoptera): An overview of the Jinju Formation, its coleopteran diversity, and past and future research. *Journal of Asia-Pacific Entomology*, 27 (2), 102236. https://doi.org/10.1016/j.aspen.2024.102236
- Lee, S.B., Cai, C.Y., Engel, M.S., Nam, G.S. & Park, J.K. (2024b) Cretaceous beetles of the Jinju Formation (Coleoptera: Hydrophiloidea). *Palaeoentomology*, 7 (3), 443–452.

https://doi.org/10.11646/palaeoentomology.7.3.14

Lim, J.D., Martin, L.D. & Baek, K.S. (2001) The first discovery of a brachiosaurid from the Asian continent. *Naturwissenschaften*, 88, 82–84.

https://doi.org/10.1007/s001140000201

Lin, Q.B. (1986) Early Mesozoic fossil insect from the south China. Science Press, Beijing, 112 pp.

Lockley, M.G., Lim, J.D., Park, H.D., Romilio, A., Yoo, J.S., Choi, J.W., Kim, K.S., Choi, Y., Kang, S.H., Kim, D.H. & Kim, T.H. (2020) First reports of Crocodylopodus from Asia: implications for the paleoecology of the Lower Cretaceous. *Cretaceous Research*, 111 (2), 104441.

https://doi.org/10.1016/j.cretres.2020.104441

Maddison, D.R., Moore, W., Baker, M.D., Ellis, T.M., Ober, K.A., Cannone, J.J. & Gutell, R.R. (2009) Monophly of terrestrial adephagan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). *Zoologica Scripta*, 38 (1), 43–62.

https://doi.org/10.1111/j.1463-6409.2008.00359.x

- Massicotte, P., South, A. & Hufkens, K. (2023) rnaturalearth: World Map Data from Natural Earth. R package version 1.0.1, Available from: https://CRAN.R-project.org/package=rnaturalearth (accessed 7 Nov. 2024).
- Nam, K.S. & Kim, J.H. (2016) Reconstruction and paleoecogical 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. [in Korean with English abstract]. https://doi.org/10.14770/jgsk.2016.52.2.105
- Park, S.O. & Chang, K.H. (1998) Some Cretaceous conchostracans of Kyongsang Basin. *Journal of the Paleontological Society* of Korea, 14, 179–199.

Park, T.Y., Wilson, G.D., Lee, D.C. & Choi, D.K. (2012) Occurrence of the isopod Archaeoniscus coreaensis new species fom

theower Cretaceous Jinju Formation, Korea. *Journal of Paleontology*, 86 (4), 626–640. https://doi.org/10.1666/11-131R.1

- 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. https://doi.org/10.1080/14772019.2018.1525441
- 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. [in Korean with English abstract].

https://doi.org/10.14770/jgsk.2019.55.5.513

- 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. [in Korean with English abstract]. https://doi.org/10.14770/jgsk.2023.003
- Pebesma, E. (2018) Simple Features for R: Standardized Support for Spatial Vector Data. The *R Journal*, 10 (1), 439–446. https://doi.org/10.32614/RJ-2018-009
- Ponomarenko, A.G. (1977) Suborder Adephaga. In: Arnoldi L.V., Zherikhin V.V., Nikritin L.M. & Ponomarenko, A.G. (Eds), Mezozoiskie zhestkokryiye. Nauka Publishers, Moscow, pp. 17–104. [in Russian].
- Ponomarenko, A.G. (1986) Insects of the Early Cretaceous ecosystems of the West Mongolia. Descriptions of fossil Scarabaeida (=Coleoptera). Sovmestnaya Sovetsko-Mongolskaya Paleontologichekaya Ekspeditsia, 28, 84–105.
- Ponomarenko, A.G. & Volkov, A.N. (2013) Ademosynoides asiaticus Martynov, 1936, the earliest known member of an extant beetle family (Insecta, Coleoptera, Trachypachidae). Paleontological Journal, 47, 601–606. https://doi.org/10.1134/S0031030113060063
- Rosse-Guillevic, S., Kopylov, D., Rasnitsyn, A., Nam, G.S., Kwon, S.H. & Jouault, C. (2023a) Blurring the limits of anaxyelid subfamilies: a new genus and species (Hymenoptera: Anaxyelidae) from the Albian of the Republic of Korea. *Palaeoentomology*, 6 (4), 424–434.

https://doi.org/10.11646/palaeoentomology.6.4.13

Rosse-Guillevic, S., Rasnitsyn, A.P., Nam, G.S. & Jouault, C. (2023b) The first Heloridae (Hymenoptera: Proctotrupoidea) from the Albian of the Republic of Korea: inferences about the relict diversity of the family. *Cretaceous Research*, 151, 105564.

https://doi.org/10.1016/j.cretres.2023.105564

- RStudio Team. (2024) RStudio: Integrated Development Environment for R (Version 2024.9.1.394). Posit Software, PBC. Available from: https://posit.co/ (accessed 7 Nov. 2024).
- 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.

https://doi.org/10.1371/journal.pone.0225502

- 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. https://doi.org/10.1016/j.aspen.2021.05.003
- Sohn, J.C. & Nam, G.S. (2024) New fossil genus and species of Yuripopovinidae (Insecta: Heteroptera, Coreoidea) from the Lower Cretaceous Jinju Formation, South Korea, with insights into the evolution of exaggerated antennae in the family. *Cretaceous Research*, 158, 105847.

https://doi.org/10.1016/j.cretres.2024.105847

- South, A., Michael, S. & Massicotte, P. (2024) rnaturalearthdata: World Vector Map Data from Natural Earth Used in 'rnaturalearth'. R package version 1.0.0, Available from: https://CRAN.R-project.org/package=rnaturalearthdata (accessed 7 Nov. 2024).
- Varela, S., González-Hernández, J., Sgarbi, L.F., Marshall, C., Uhen, M.D., Peters, S. & McClennen, M. (2015) paleobioDB: an R package for downloading, visualizing and processing data from the Paleobiology Database. *Ecography*, 38 (4), 419– 425.

https://doi.org/10.1111/ecog.01154

Wang, B., Zhang, H. & Ponomarenko, A.G. (2012) Mesozoic Trachypachidae (Insecta: Coleoptera) from China. Palaeontology, 55 (2), 341–353.

https://doi.org/10.1111/j.1475-4983.2012.01128.x

- Wickham, H. (2016) ggplot2: Elegant graphics for data analysis. SpringerVerlag. Retrieved from: https://ggplot2.tidyverse.org (accessed 7 Nov. 2024).
- Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023) dplyr: A Grammar of Data Manipulation_. R package version 1.1.4, Available from: https://CRAN.R-project.org/package=dplyr (accessed 7 Nov. 2024).
- Yabe, H. (1905) Mesozoic plants from Korea. *Journal of the College of Science, Imperial University of Tokyo, Japan*, 20, 1–59, pls. 1–4.
- Yabumoto, Y. & Yang, S.Y. (2000) The first record of the Early Cretaceous freshwater fish, *Wakinoichthys aokii*, from Korea. *Bulletin of the Kitakyushu Museum of Natural History*, 19, 105–110.

- Yabumoto, Y., Yang, S.Y. & Kim, T.W. (2006) Early Cretaceous freshwater fishes from Japan and Korea. *Journal of the Paleontological Society of Korea*, 22, 119–132.
- Yun, C.S. & Yang, S.Y. (2004) Three bivalve fossils from the Dongmyeong Formation of Gisan, Goryeong in Korea. *Journal of the Paleontological Society of Korea*, 20 (2), 173–181.
- Yun, C.S., Lim, J.D. & Yang, S.Y. (2004) The first crocodyliform (Archosauria:Crocodylomorpha) from the Early Cretaceous of Korea. *Current Science*, 86, 1200–1201.
- Yun, C.S., Baek, K.S. & Jeong, Y.H. (2007) Cretaceous reptilian teeth from the Gyeongsang Basin. Journal of the Paleontological Society of Korea, 23, 27–47. [in Korean with English abstract].
- Yun, C.S. & Yang, S.Y. (2001) First discovery of big pterosaur teeth in Korea. *Journal of the Paleontological Society of Korea*, 17 (2), 69–76. [in Korean with English abstract].