

A new titanopteran *Magnatitan jongheoni* n. gen. n. sp. from southwestern Korean Peninsula

Authors: Park, Tae-Yoon S., Kim, Do-Yoon, Nam, Gi-Soo, and Lee, Mirinae

Source: Journal of Paleontology, 96(5) : 1111-1118

Published By: The Paleontological Society

URL: <https://doi.org/10.1017/jpa.2022.30>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A new titanopteran *Magnatitan jongheoni* n. gen. n. sp. from southwestern Korean Peninsula

Tae-Yoon S. Park,^{1,2*} Do-Yoon Kim,^{3*} Gi-Soo Nam,⁴ and Mirinae Lee¹

¹Division of Earth Sciences, Korea Polar Research Institute, Incheon 21990, Republic of Korea <typark@kopri.re.kr>
<mirinae.lee@kopri.re.kr>

²Polar Science, University of Science and Technology, Daejeon 34113, Republic of Korea

³Department of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea <trex97@naver.com>

⁴Gongju National University of Education, Gongju, Chungcheongnam-do, Republic of Korea <nks@hanmail.net>

Abstract.—Titanopterans are spectacular, giant, predatory insects mainly known from the Triassic, but they are known from a few localities in Central Asia (including European Russia) and Australia. The Nampo Group is a nonmarine sequence, located on the southwestern Korean Peninsula, the age of which has remained controversial, due to lack of proper age-constraining fossils. Here, we report a new titanopteran *Magnatitan jongheoni* n. gen. n. sp. from the Amisan Formation, Nampo Group. The division of the radius anterior and radius posterior beyond the distal half of the fossil wing is a characteristic of the family Paratitanidae. This is the first discovery of a titanopteran fossil outside of Central Asia and Australia, suggesting a possible circum-Tethys oceanic distribution. Given the possibly widespread distribution of titanopterans, this group might have played a critical role as giant predatory insects in Triassic terrestrial ecology. Because titanopterans have never been found beyond the Triassic-Jurassic boundary, the occurrence of a titanopteran corroborates the Triassic age of the Nampo Group.

UUID: <http://zoobank.org/10177029-0044-424f-9816-e3fb057cfe85>

Introduction

Titanoptera is an iconic insect group of the Triassic. The prominently large size (wingspan to 400 mm documented for *Gigatitan vulgaris* Sharov, 1968) and the raptorial forelegs equipped with stout spines make them the most impressive predatorial insects of the Triassic (Sharov, 1968; Grimaldi and Engel, 2005). Both sexes seemed to have had a ‘sound apparatus’ in the forewings, which might have produced deep and resonant acoustic signals in Triassic forests (Grimaldi and Engel, 2005; but see Schubnel et al., 2021). Despite the fame, however, their phylogenetic affinity remains unstable. Although titanopterans are often considered closely related to orthopterans, their phylogenetic position has been the subject of debate. Sharov (1968) argued that titanopterans originated from the Permian orthopteran family Tcholmanvissidae Zalesky, 1929, rendering this family paraphyletic. Subsequently, Gorochov (2001, 2007) suggested the Carboniferous protorthopteran family Geraridae Scudder, 1885 as a sister group of Titanoptera. Béthoux (2007) reinvestigated the wing veins and concluded that the order Titanoptera is derived from the Tcholmanvissidae. Recently, Huang et al. (2020), however, questioned the close

relationship between the Tcholmanvissidae and Titanoptera, stating that further investigation is required (but see Béthoux, 2020). The incomplete understanding of the affinity is partly due to the small number of fossils with limited paleogeographic occurrences; to date, all titanopteran fossils have been known only from Central Asia (including European Russia) and Australia (Tillyard, 1925; Riek, 1954; Sharov, 1968).

The Nampo Group in the Chungnam Basin is situated in the southwestern part of the Korean Peninsula and consists of non-marine fluvial, alluvial, and lacustrine successions (Egawa and Lee, 2009; Lee and Chung, 2010). Although it is one of the largest Mesozoic basins in Korea, its depositional age has remained controversial. Paleontological evidence such as plant and choncostracan fossils have suggested Late Triassic to Early Jurassic as the age (Kim and Kimura, 1988; Kim, 1989; Kim and Lee, 2015). In contrast, radiometric dating from a volcanic deposit provided Jurassic ages (172 Ma) for the deposition of the Nampo Group (Koh, 2006; Jeon et al., 2007). Kee et al. (2019) also regarded the Nampo Group as coeval to the Jurassic nonmarine deposits of the small-scale piggyback basins in other parts of the Korean Peninsula. Recently, Park and Noh (2015) and Park et al. (2018a) discovered that the formation process of the volcanics should be distinguished from the deposition of the Nampo Group and suggested that the Nampo Group was deposited during the Late Triassic to Early Jurassic, and

*Corresponding authors.

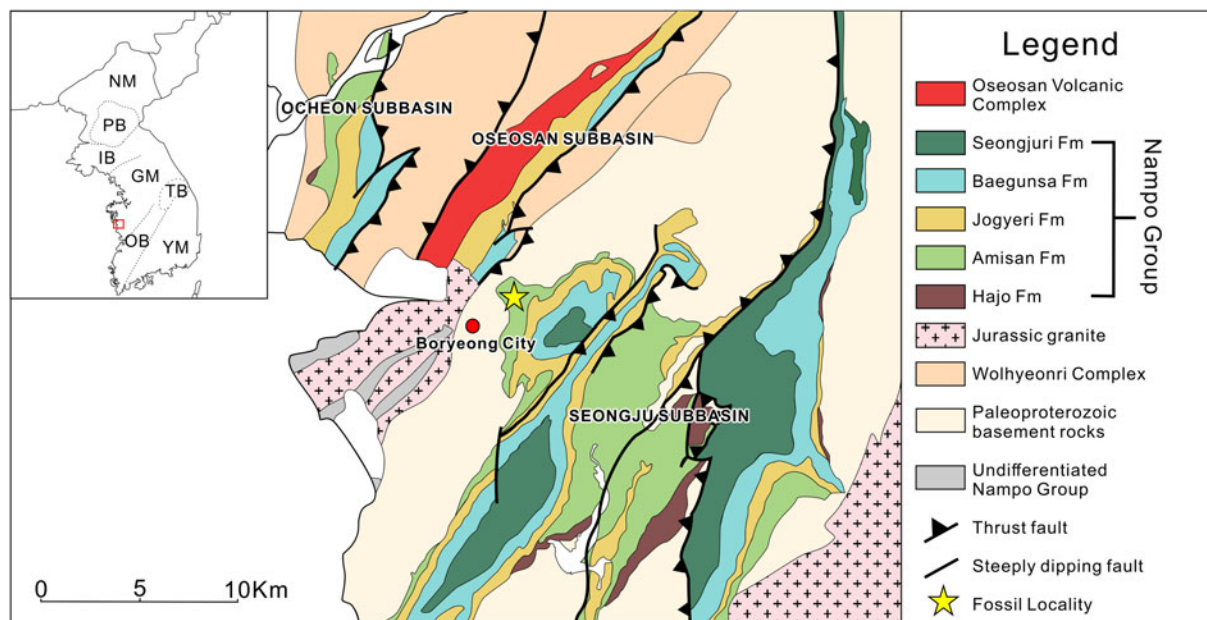


Figure 1. Geological map of the study area with its location on the Korean Peninsula, modified from Egawa and Lee (2009), Kee et al. (2019), and Park et al. (2019). GM = Gyeonggi Massif; IB = Imjingang Belt; NM = Nangrim Massif; OB = Okcheon Basin; PB = Pyeongan Basin; TB = Taebaeksan Basin; YM = Yeongnam Massif; star = fossil locality, Myeongcheon Section.

subsequently, the Chungnam Basin further subsided at the Early–Middle Jurassic to accommodate the volcanic deposits (Park et al., 2019; Lee et al., 2021).

This study reports a new titanopteran genus from the Amisan Formation, Nampo Group, Chungnam Basin, Korea, which is the first discovery of a titanopteran fossil outside of Central Asia and Australia, contributing to a better understanding of the morphological diversity and paleogeographic distribution of this group of giant insects. In addition, because titanopteran fossils do not occur above the Triassic, the new discovery is relevant to the debate on the age of the Nampo Group.

Geological setting

The outcrops of the Chungnam Basin are distributed in three closely situated areas, namely (from west to east) the Ocheon, Oseosan, and Seongju areas (Fig. 1), which have even been recognized as isolated sediment fills in subbasins (Egawa and Lee, 2009). The Chungnam Basin includes the Nampo Group and the mid-Jurassic Oseosan Volcanic Complex that unconformably overlies the Nampo Group in the Oseosan area (Park et al., 2018a). The fluvial, alluvial, and lacustrine successions of the Nampo Group of the Chungnam Basin consist of five formations, in ascending order, the Hajo, Amisan, Jogyeri, Baegunsa, and Seongjuri formations (Choi et al., 1987; Yang, 1999; Egawa and Lee, 2009). The Hajo, Jogyeri, and Seongjuri formations are dominated by conglomerate and sandstone facies, whereas the fossiliferous Amisan and the Baegunsa formations comprise coal-bearing shale and sandstone, with a minor amount of conglomerate in the lower part of the Baegunsa Formation (Yang, 1999). The Nampo Group is unconformably overlain by the Early–Middle Jurassic Oseosan Volcanic Complex, which consists of light gray to gray tuff and lapilli tuff, overlain by thick tuffaceous sedimentary rocks of gray to dark

gray shale, sandstone, and conglomerate (Park et al., 2018a). The basement rocks of the Chungnam basin are largely of Neoproterozoic and Paleozoic metamorphic rocks (the Wolhyeonri complex) west of the Oseosan area, whereas Paleoproterozoic granite gneiss is prevalent to the east of the Oseosan area (Kee et al., 2019) (Fig. 1). Various hypotheses have been proposed for the development of the Chungnam Basin, under the view that the Chungnam Basin is part of the Daedong Supergroup, which include development of half-grabens or a pull-apart basin from the late stage of the Triassic Songrim orogeny (Cluzel, 1992), deposition in synorogenic (Songrim orogeny) piggyback basins (Chough et al., 2000), and syntectonic deposition during the early stages of the Jurassic Daebio orogeny (Jeon et al., 2007). Subsequently, Egawa and Lee (2009) considered the ‘subbasins’ of the Chungnam Basin as piggyback basins formed during the Daebio orogeny. Park et al. (2019) and Lee et al. (2021) proposed a postcollisional extensional deformation in the Late Triassic for the basin development based on the assumption that an eastward extension of the Sulu collisional belt runs through this area (Oh, 2006; Kwon et al., 2009).

The Amisan Formation is known to 1,000 m thick and consists of the lower sandstone units, the lower shale unit, the middle sandstone units, the middle shale unit, and the upper sandstone unit (Yang, 1999). Diverse fossils have been documented from the Amisan Formation, including plants (Kim, 1976, 1990, 2001; Kimura and Kim, 1984; Kim et al., 2002; Kim and Roh, 2008), bivalves (Kim et al., 2015), conchostracans (Kim and Lee, 2015), insects (Nam and Kim, 2014; Nam et al., 2017), and fishes (Kim et al., 2020). Of these, plant and conchostracan fossils have been used for age-dating the Amisan Formation. Plate assemblages led Kimura and Kim (1984) to suggest a Late Triassic age, but most of the genera later appeared to have ranges to the Lower Jurassic and even to the Cretaceous (Kim and Kimura, 1988; Kim, 1990, 2009, 2013; Kim et al.,

2002; Lee et al., 2004; Kim and Roh, 2008). Conchostracan species, known from poorly preserved specimens, were also regarded as indicating Triassic age (Kim and Lee, 2015), but the Mesozoic occurrence of the bivalve genus *Margaritifera* Schumacher, 1816, the only known bivalve genus from the Amisan Formation, was then known to be restricted to the post-Triassic (Kim et al., 2015). In addition, Jurassic radiometric ages of the Nampo Group (Koh, 2006; Jeon et al., 2007) questioned the Triassic age derived from the paleontological evidence, calling for more convincing cues (Kim and Lee, 2015).

Materials and methods

A single forewing with well-preserved venation was discovered in the middle shale unit of the Amisan Formation exposed in the Myeongcheon section (36°20' 21"N, 126°37' 34"E; Fig. 1). The sample was photographed submerged in water with a Canon EOS 60D using a Canon EF 100 mm f/2.8 USM macro lens. High-angle lighting was used for the maximal reflective image of the specimen. Images were cropped and enhanced by means of contrast and brightness in Adobe Photoshop CS6. For the relief-enhanced images, raw images for polynomial texture mapping (also known as Reflectance Transforming Imaging) were acquired by a self-crafted system that permits lighting from 50 different directions (see Béthoux et al., 2016; Chen et al., 2021 for previous application of this method on insect fossils), and the same Canon EOS 60D camera setting mentioned above. The specimen was white-coated with magnesium oxide for this process. To enhance surface details of the fossil, 50 images were taken and converted into a PTM format file (see Supplemental Data), which was then run in RTI Viewer software (http://culturalheritageimaging.org/What_We_Offer/Downloads/).

The specimen was also gold-coated using a Cressington 108 Auto sputter coater with 10 mA for 80 s. A field-emission electron probe microanalyzer (JEOL JXA-8530F) and a low-vacuum field emission scanning electron microscope (JEOL JSM-7200F-LV) at the Korea Polar Research Institute were used to acquire X-ray elemental maps and surface analysis. X-ray elemental maps for C, N, O, Mg, Al, Si, P, S, Cl, K, Ca, Ti, Mn, Fe, Ni, Cu, Zn, and Ba were obtained using five wavelength dispersive spectrometry (WDS) and 19 energy dispersive spectrometry (EDS), with an acceleration voltage of 20 kV, beam current of 200 nA, beam size of 13 µm, dwell time of 10 ms, and step size of 13 µm. Raw data of X-ray elemental maps were imported and processed for brightness and contrast by ImageJ (Schneider et al., 2012).

General wing venation nomenclature follows that of Béthoux and Nel (2002; see also Desutter-Grandcolas et al., 2017). Interpretation of titanopteran-specific wing venation pattern follows Béthoux (2007). Anatomical abbreviations used in the text are: AA1 = first anal veins; AA2 = second anal veins; CuA = cubitus anterior; CuP = cubitus posterior; CuPa = anterior branch of CuP; CuPaα = anterior branch of CuPa; CuPaα• = first posterior branch of CuPaα; CuPaα* = second posterior branch of CuPaα; CuPaα° = anterior stem of CuPaα; CuPaβ = posterior branch of CuPa; CuPb = posterior branch of CuP; M = media vein; MA = media anterior, MP = media posterior;

R = radius; RA = radius anterior; RP = radius posterior; ScA = subcosta anterior; and ScP = subcosta posterior.

Repository and institutional abbreviation.—The specimen figured in this study is deposited in the Gongju National University of Education (GNUE).

Systematic paleontology

Superorder Archaeorthoptera Béthoux and Nel, 2002

Titanoptera Sharov, 1968

Family Paratitanidae Sharov, 1968

Genus *Magnatitan* new genus

Type species.—*Magnatitan jongheoni* n. gen. n. sp.

Diagnosis.—As for the type species by monotypy.

Etymology.—The generic name is derived from the Latin *magna*, referring to its large size, plus the general name of the group, *titan*.

Remarks.—The two most important synapomorphies of titanopterans are CuPaα• + CuPaβ and CuPb having the same point of origin (Béthoux, 2007), and the presence of strongly developed crossveins between MA and MP, both of which are conspicuous in the new specimen. The family Paratitanidae is characterized by the division of RA and RP near the distal half of the wing, and previously included two genera, *Paratitan* Sharov, 1968 and *Minititan* Gorochoy, 2007 from the Triassic of Kyrgyzstan. The location of the RA and RP division in the forewing justifies the assignment of *Magnatitan* n. gen. into the Paratitanidae. The short length of the stem of M and fusion of CuA and anterior branch of CuPaα° make the new genus *Magnatitan* different from *Minititan*, and *Paratitan* in Paratitanidae. The presence of a single anterior veinlet in RA is distinct from the genus *Paratitan* with three or more anterior veinlets and a simple RA as in the genus *Minititan*.

Magnatitan jongheoni new genus new species

Figure 2

Holotype.—GNUE 112001, an almost complete left forewing.

Diagnosis.—ScP with many strong veinlets, dichotomously ramified distally; RA extending a single anterior veinlet distally; stem of M short; MP with two branches; basal parts of CuPaα• and CuPaα* fused; basal part of CuPaβ fused with CuPb; CuPaβ + CuPb short; area between posterior wing margin widened.

Occurrence.—The middle shale unit of the Amisan Formation, Upper Triassic, Myeongcheon Section, Seongju-myeon, Boryeong City, Chungcheongnam-do, Republic of Korea.

Description.—Forewing large with likely pointed apex, anterior margin anteriorly bowed, posterior margin posteriorly bowed,

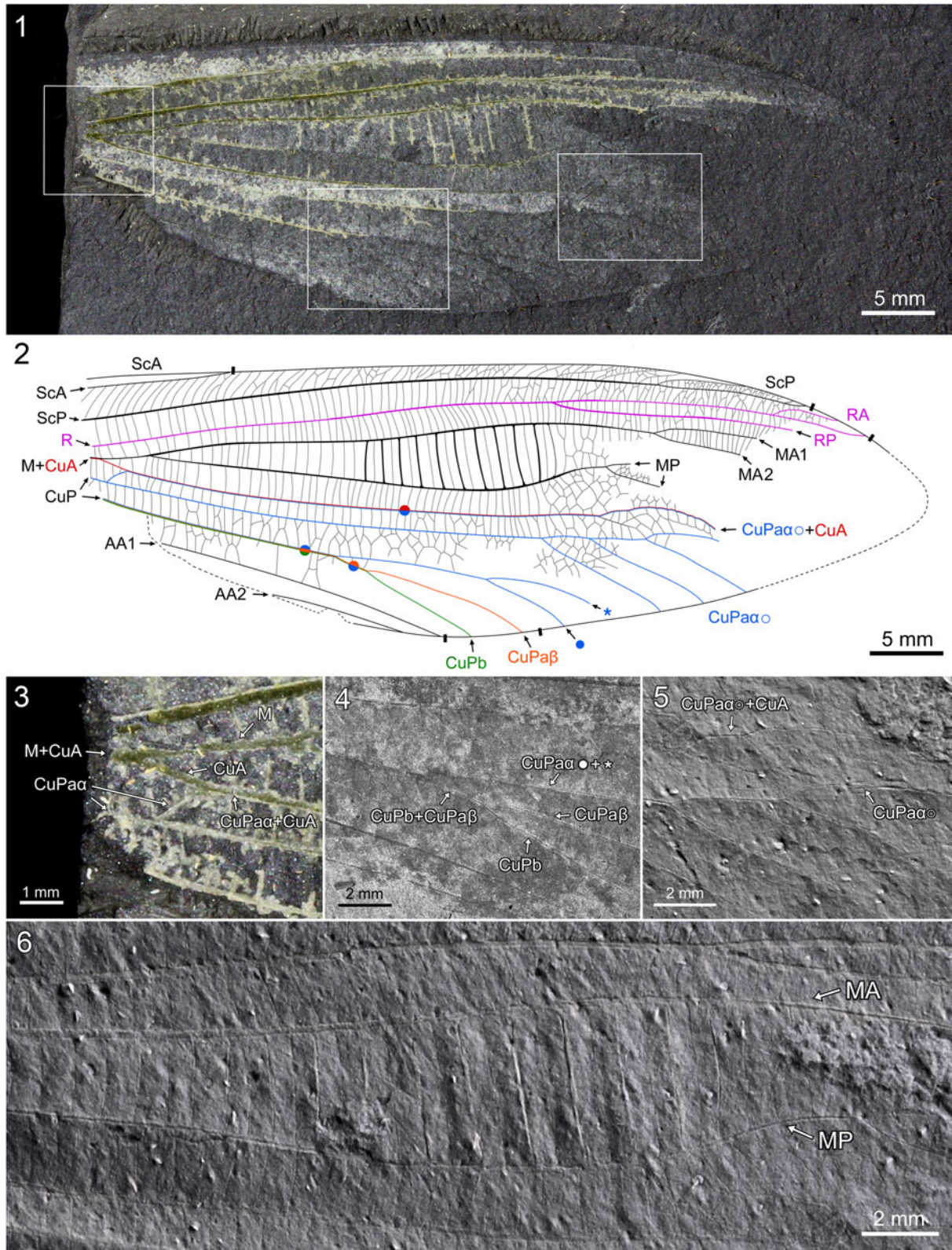


Figure 2. Holotype of *Magnatitan jongheoni* n. gen. n. sp., GNUE 112001: (1) overview of the specimen (rectangles, left to right, represent details shown in 1.3, 1.4, and 1.5, respectively); (2) interpretive drawing; (3) magnified image of the proximal part of the forewing; (4) wavelength dispersive spectrometry (WDS) silicon map, showing details around the division of CuPb; (5) PTM image showing CuA + CuPa α° and CuPa α° , and the cross-veins between; (6) PTM image, showing the distinctive cross-veins developed between MA and MP. AA1 = first anal veins; AA2 = second anal veins; CuA = cubitus anterior (in red); CuP = cubitus posterior; CuPa α = anterior branch of CuPa (in blue); CuPa α° = first posterior branch of CuPa α ; CuPa α° = anterior stem of CuPa α ; CuPa β = posterior branch of CuPa (in orange); CuP β = posterior branch of CuP (in green); M = media vein; MA = media anterior (with its branches MA1 and MA2); MP = media posterior; R = radius (in pink); RA = radius anterior; RP = radius posterior; ScA = subcosta anterior; ScP = subcosta posterior; * (= CuPa α°) = second posterior branch of CuPa α ; • (= CuPa α°) = first posterior branch of CuPa α . Large colored dots indicate fusion of veins.

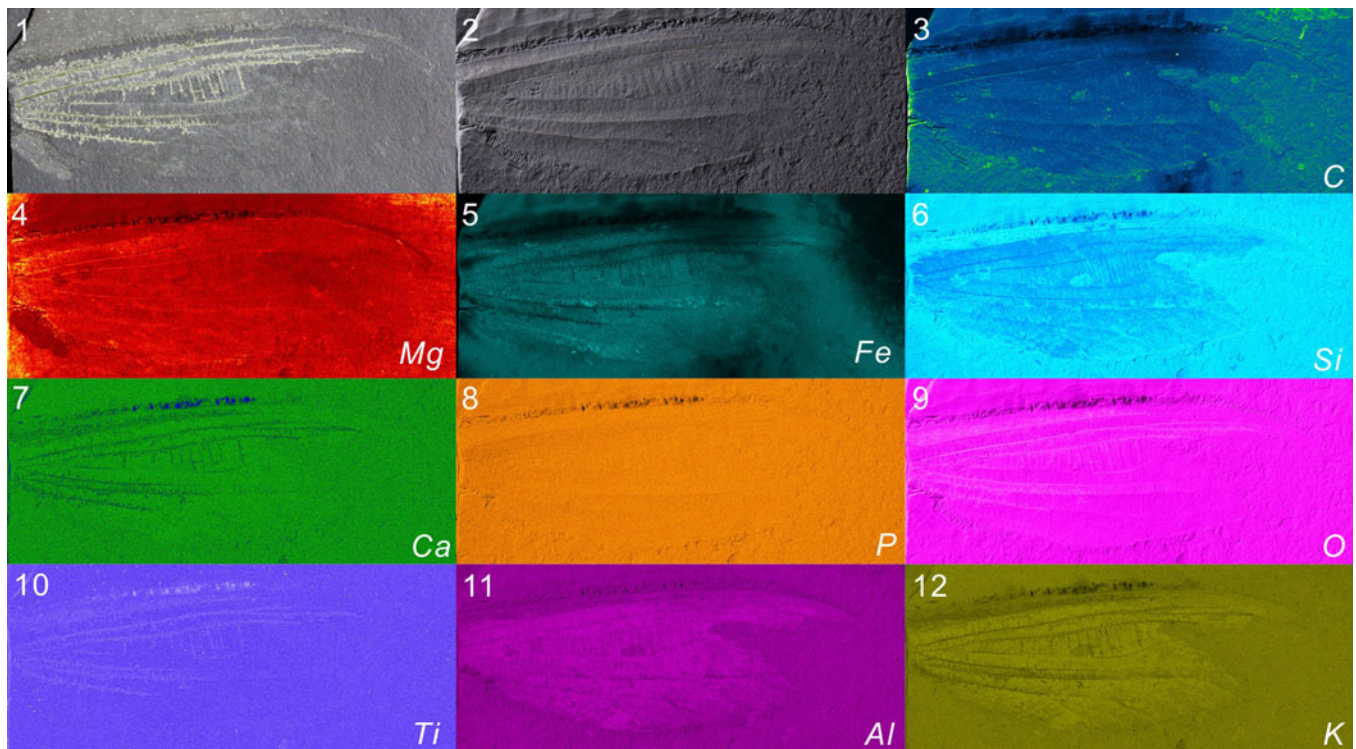


Figure 3. Wavelength dispersive spectrometer (WDS) and energy dispersive spectrometer (EDS) images of the wing of *Magnatitan jongheoni* n. gen. n. sp. from the Amisan Formation: (1) normal image of the holotype, submerged in water; (2) PTM image; (3–6) WDS elemental maps of carbon (C), magnesium (Mg), iron (Fe), and silicon (Si), respectively; (7–12) EDS elemental maps of calcium (Ca), phosphorus (P), oxygen (O), titanium (Ti), aluminum (Al), and potassium (K), respectively.

preserved length 57.3 mm, width 19.0 mm; distal part of ScA preserved, weak; area between ScA and anterior margin narrow; ScP long, strong, anteriorly pectinate with many branches and dichotomously ramified distally; R convex; RA and RP divided near distal half of wing; RA with single, weak anterior veinlet; split of M and CuA preserved, stem of M 3.8 mm long; M gently twisted, MA1-MA2 split located distally with respect to RA-RP split; MP concave, with fork located between RA-RP split and MA1-MA2 split; area between MA and MP wide with dense, sturdy crossveins; CuA separated from M, free part of basal CuA short; basal part of $\text{CuPa}\alpha^\circ$ divided into two branches; anterior branch of $\text{CuPa}\alpha^\circ$ weak, fused with CuA like a crossvein; CuA + $\text{CuPa}\alpha^\circ$ long, gently concave; posterior branch of $\text{CuPa}\alpha^\circ$ posteriorly pectinated; fused $\text{CuPa}\alpha^\bullet + \text{CuPa}\alpha^* + \text{CuP}$ long; basal parts of $\text{CuPa}\alpha^\bullet$ and $\text{CuPa}\alpha^*$ fused, $\text{CuPa}\alpha^\bullet + \text{CuPa}\alpha^*$ separated near widest area between MA and MP; basal part of $\text{CuPa}\beta$ fused with CuPb , $\text{CuPa}\beta + \text{CuPb}$ short; preserved AA1 and AA2 long without branches; crossveins dense, long, simple, forming network near wing margins and in broad intervenal areas.

Etymology.—The species name honors the collector of the specimen, Professor Jongheon Kim (Kongju National University) who has made significant paleontological contributions from the Nampo Group over the last 30 years.

Remarks.—Huang et al. (2020) argued that a divided CuPb is present in some members of Archaeorthoptera, Panorthoptera, and Titanoptera, and considered this feature in those groups as the result of convergent evolution, questioning the close

relationship between the Titanoptera and the orthopteran family Tcholmanvissiidae. In contrast, Béthoux (2007, 2020) reinterpreted the wing vein homology of those groups and proposed that the divided CuPb was not present in titanopterans, reinstating the close relationship of the Titanoptera and the Tcholmanvissiidae. Following the most recent interpretation by Béthoux (2020), we interpret that $\text{CuPa}\beta$ is fused into CuPb . In line with this, $\text{CuPa}\alpha^\bullet$ and $\text{CuPa}\alpha^*$ also fuse with each other, as also appears in a species of *Tcholmanvissiella* Gorochoff, 1987 (see Béthoux, 2007, 2020).

In recent paleontological research using WDS analyses on fossiliferous shale, various body structures (e.g., brains in Cambrian stem-arthropod fossils [Park et al., 2018b] and wing venations and a subgenital plate in Cretaceous elcanid orthopteran fossils [Kim et al., 2021]) were highlighted in the carbon elemental maps by different carbon concentrations, indicating that the fossils were preserved as thin carbonaceous film on dark shale. The mineralogy of the new titanopteran fossil from the Amisan Formation in this study, however, seems different from those in the previous studies. Carbon distribution on the fossil surface is scarce (Fig. 3.3) and there is less silicon (Fig. 3.6) compared to the matrix. Instead, aluminum and potassium are enriched on the fossil surface (Fig. 3.11, 3.12).

Along the thick wing veins, dendrite-like overgrowth textures are present (Fig. 3.1). Qualitative point analysis by EDS equipped at the low-vacuum field emission scanning electron microscope, however, has shown that the total EDS spectra of the wing membrane area, the wing veins, and the dendrite-like textures are comparable to each other. Similar results have been acquired from a XRD microstructural analysis applied to the wing and the rock



Figure 4. Artistic reconstruction of *Magnatitan jongheoni* n. gen. n. sp., preying upon a small amphibian (artwork by Do-Yoon Kim).

matrix. In the elemental maps, a slight amount of magnesium and oxygen is present along the thick veins (Fig. 3.4, 3.9), whereas traces of titanium are recognized along the dendrite-like overgrowth (Fig. 3.10). There are prominent absences of iron, calcium, and potassium along the dendrite-like overgrowth (Fig. 3.5, 3.7, 3.12). At present, however, the mineralogy of the fossil is not clearly identified, requiring further research.

Discussion

First documentation of a titanopteran in East Asia.—Compared to the large number of plant fossils (> 20 species reported), only a small number of invertebrate fossils have been documented from the Nampo Group, i.e., a single species of bivalve (Kim et al., 2015), four species of conchostracans (Kim and Lee, 2015), and two species of insects (Nam and Kim, 2014; Nam et al., 2017). The occurrence of the titanopteran fossil from the

Amisan Formation, therefore, adds an important component to the Late Triassic ecology of the Nampo Group. Given its large size, *Magnatitan jongheoni* n. gen. n. sp. must have played an important role in the food web as a daunting predator on insects, invertebrates, and possibly small tetrapods, e.g., amphibians (Fig. 4). Previously, the occurrences of titanopterans have been restricted to Central Asia (Triassic Madygen Formation of Kyrgyzstan), Australia (Middle Triassic of New South Wales), and possibly European Russia (Permian of Vologda and Orenburg regions—Deinotitanidae, assigned to Titanoptera with some reservations; Gorochov in Aristov et al., 2013). A recent report documented a fragmentary titanopteran forewing from the Carboniferous of France (Schubnel et al., 2021), but given the much earlier age and incomplete preservation of the fossil, further investigation is required. In Permo-Triassic paleogeography, Central Asia (including European Russia) was located north of the Tethys Ocean, Australia was located south of the ocean, and the two areas were connected by regions spreading along the western margin of the Tethys Ocean, e.g., northern Africa, Arabia, and India (Scotese, 2021). This implies that titanopterans might have also inhabited those regions along the western margin of the Tethys Ocean (Fig. 5). By the Late Triassic, the East Asian plates, including the Sino-Korean, South China, and Indochina cratons were accreted to form a large continental crust, located east of the Tethys Ocean (Scotese, 2021) (Fig. 5). Accordingly, the new discovery of titanopteran fossil from Korea could suggest a circum-Tethys Ocean distribution of titanopterans, at least in the Late Triassic. The possible widespread distribution of titanopterans implies a critical role played by this giant insect predator in Triassic terrestrial ecology. Future investigations on the Triassic nonmarine deposits in the circum-Tethys Ocean regions could lead to new discoveries of titanopterans.

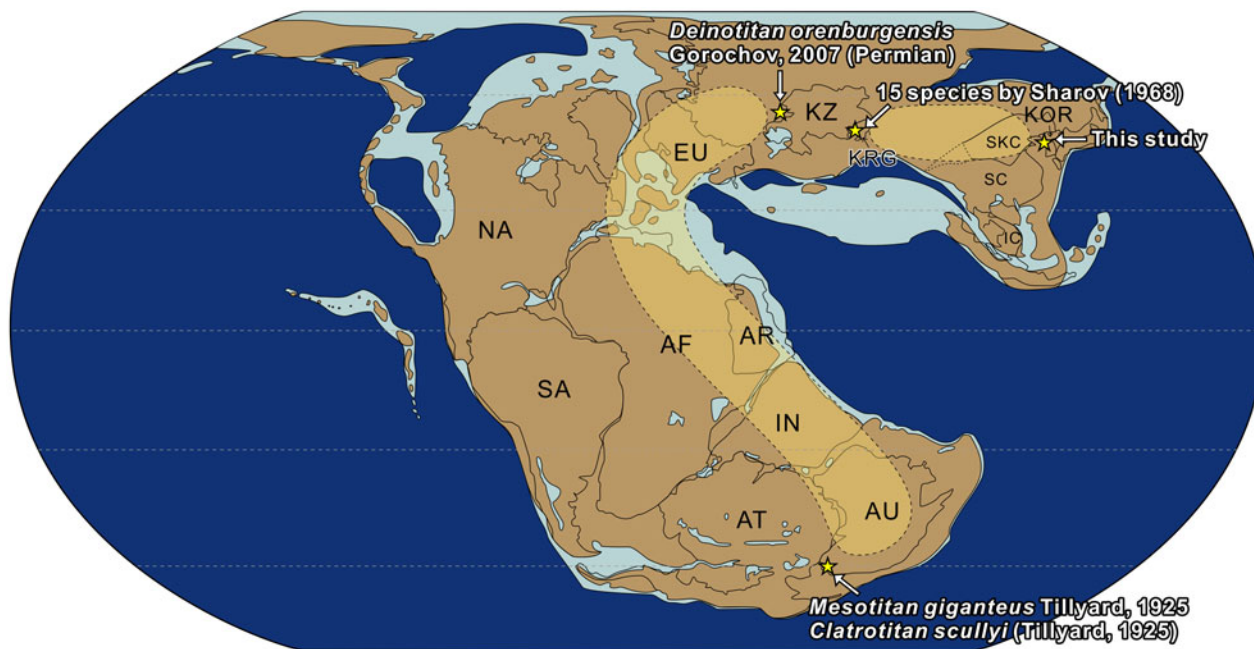


Figure 5. A paleogeographic map of the Late Triassic with the occurrences of titanopterans (stars) and the inferred areas with possible distributions (marked by dotted lines) (modified from Scotese, 2021). AF = Africa; AR = Arabia; AT = Antarctica; AU = Australia; EU = Europe; IC = Indochina; IN = India; KOR = Korea; KRG = Kyrgyzstan; KZ = Kazakhstan; NA = North America; SA = South America; SC = South China; SKC = Sino-Korean (North China) Craton.

Triassic age of the Nampo Group.—Titanopterans are known as predatory insects of the Triassic (Grimaldi and Engel, 2005), although an occurrence from the upper Permian has been documented (Gorochov, 2007). The occurrence of a titanopteran, therefore, corroborates a Triassic age for the Amisan Formation. Previously, the family Paratitanidae to which the newly described genus belongs, included two genera, *Paratitan* and *Minititan* from the Middle–Upper Triassic Madygen Formation. The worldwide ‘coal accumulation gap’ interval is known in the Lower–Middle Triassic (Retallack et al., 1996; Dai et al., 2020; Shao et al., 2020), the cause of which is still debated (see Dai et al., 2020). The frequent occurrences of coal-bearing layers in the Amisan and Baegunsa formations, therefore, constrains the age of these formations as post-Middle Triassic. Overall, the new discovery finally confirms a Late Triassic age for the Amisan Formation proposed previously by Kimura and Kim (1984) and Kim and Lee (2015). In this regard, occurrences of the plant fossil genera *Lobatannularia* Kawasaki, 1927 and *Sphenophyllum* Brongniart, 1828 from the Baegunsa Formation, which overlies the Amisan and the Jogyeri formations, could suggest that the Upper Triassic spans to the Baegunsa Formation. Kim and Lee (2015) and Kim and Kimura (1988) even regarded the two genera as relic components from the Late Paleozoic Cathaysian flora of East Asia. If so, the uppermost unit of the Nampo Group, the Seongjuri Formation, remains the only unit with the possibility of stretching into the Lower Jurassic. The youngest detrital zircon data from the Seongjuri Formation shows a range from 197–175 Ma (Lee et al., 2021), supporting this possibility.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q573n5tkz>.

Acknowledgments

We are grateful to O. Béthoux and an anonymous reviewer for constructive comments that significantly improved the manuscript. Y. Oh helped us in the field. E. Shim helped by drawing the figures. This project was financially supported by the KOPRI project (PE22060). The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Aristov, D.S., Bashkuev, A.S., Golubev, V.K., Gorochov, A.V., Karasev, E.V., Kopylov, D.S., Ponomarenko, A.G., Rasnitsyn, A.P., Rasnitsyn, D.A., Sinitshenkova, N.D., Sukatsheva, I.D., and Vassilenko, D.V., 2013, Fossil insects of the middle and upper Permian of European Russia: *Paleontological Journal*, v. 47, p. 641–832.
- Béthoux, O., 2007, Cladotypic taxonomy applied: Titanopterans are orthopterans: *Arthropod Systematics and Phylogeny*, v. 65, p. 135–156.
- Béthoux, O., 2020, The nesting of titanopteran insects within tcholanvisiids reassured and the earliest caeliferan identified: A reply to Huang et al. (2020): *Journal of Systematic Palaeontology*, v. 18, p. 1657–1668, <https://doi.org/10.1080/14772019.2020.1797912>.
- Béthoux, O., and Nel, A., 2002, Venation pattern and revision of Orthoptera sensu nov. and sister groups: Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov.: *Zootaxa*, v. 96, p. 1–88, <https://doi.org/10.11646/zootaxa.96.1.1>.
- Béthoux, O., Llamasi, A., and Toussaint, S., 2016, Reinvestigation of *Protelytoron permianum* (Insecta; early Permian; USA) as an example for applying reflectance transformation imaging to insect imprint fossils: *Fossil Record*, v. 20, p. 1–7, <https://doi.org/10.5194/fr-20-1-2016>.
- Brongniart, A.T., 1828, *Prodrome d’une Histoire des Végétaux Fossils*: Paris, F.G. Levrault, 223 p.
- Chen, L., Gu, J., Yang, Q., Ren, D., Blanke, A., and Béthoux, O., 2021, Ovipositor and mouthparts in a fossil insect support a novel ecological role for early orthopterans in 300 million years old forests: *eLife Sciences*, v. 10, p. e71006, <https://doi.org/10.7554/eLife.71006>.
- Choi, H., Kim, D., and Seo, H., 1987, [Stratigraphy, depositional environment and basin evolution of the daedong strata in the chungnam coalfield: KR-87-(B)-3]: Daejeon, Korea Institute of Energy and Resources, 97 p. (in Korean with English abstract)
- Chough, S., Kwon, S.-T., Ree, J.-H., and Choi, D.K., 2000, Tectonic and sedimentary evolution of the Korean peninsula: A review and new view: *Earth-Science Reviews*, v. 52, p. 175–235, [https://doi.org/10.1016/S0012-8252\(00\)00029-5](https://doi.org/10.1016/S0012-8252(00)00029-5).
- Cluzel, D., 1992, Formation and tectonic evolution of early Mesozoic intramontane basins in the Ogcheon belt (South Korea): A reappraisal of the Jurassic ‘Daebio orogeny’: *Journal of Southeast Asian Earth Sciences*, v. 7, p. 223–235, [https://doi.org/10.1016/0743-9547\(92\)90002-S](https://doi.org/10.1016/0743-9547(92)90002-S).
- Dai, S., Bechtel, A., Eble, C.F., Flores, R.M., French, D., Graham, I.T., Hood, M.M., Hower, J.C., Korasidis, V.A., and Moore, T.A., 2020, Recognition of peat depositional environments in coal: A review: *International Journal of Coal Geology*, v. 219, p. 103383, <https://doi.org/10.1016/j.coal.2019.103383>.
- Desutter-Grandcolas, L., Jacquelin, L., Hugel, S., Boistel, R., Garrouste, R., Henrotay, M., Warren, B.H., Chintauan-Marquier, I.C., Nel, P., and Grandcolas, P., 2017, 3-D imaging reveals four extraordinary cases of convergent evolution of acoustic communication in crickets and allies (Insecta): *Scientific Reports*, v. 7, p. 7099, <https://doi.org/10.1038/s41598-017-06840-6>.
- Egawa, K., and Lee, Y.I., 2009, Jurassic synorogenic basin filling in western Korea: Sedimentary response to inception of the western circum-Pacific orogeny: *Basin Research*, v. 21, p. 407–431, <https://doi.org/10.1111/j.1365-2117.2009.00408.x>.
- Gorochov, A.V., 1987, Permian Orthoptera of the infraorder Oedischiiidea (Ensifera): *Paleontological Journal*, v. 21, p. 72–85.
- Gorochov, A., 2001, On the higher classification of the Polyneoptera: *Acta Geologica Leopoldensia*, v. 24, p. 11–56.
- Gorochov, A., 2007, The first representative of the suborder Mesotitanina from the Paleozoic and notes on the system and evolution of the order Titanoptera (Insecta: Polyneoptera): *Paleontological Journal*, v. 41, p. 621–625, <https://doi.org/10.1134/S0031030107060056>.
- Grimaldi, D., and Engel, M.S., 2005, *Evolution of the Insects*: New York, Cambridge University Press, 755 p.
- Huang, D., Schubnel, T., and Nel, A., 2020, A new middle Permian orthopteran family questions the position of the order Titanoptera (Archaeorthoptera: Orthoptera): *Journal of Systematic Palaeontology*, v. 18, p. 1217–1222, <https://doi.org/10.1080/14772019.2020.1733112>.
- Jeon, H., Cho, M., Kim, H., Horie, K., and Hidaka, H., 2007, Early Archean to Middle Jurassic evolution of the Korean Peninsula and its correlation with Chinese cratons: SHRIMP U-Pb zircon age constraints: *The Journal of Geology*, v. 115, p. 525–539, <https://doi.org/10.1086/519776>.
- Kawasaki, S., 1927, The flora of the Heian System, Part 1, Equisetales and Sphenophyales: *Bulletin on the Geological Survey of Chosen (Korea)*, v. 6, no. 1, p. 1–30.
- Kee, W.-S., Kim, S.W., Kim, H., Hong, P.S., Kwon, C.W., Lee, H.-J., Cho, D.-L., Koh, H.J., Song, K., Byun, U.H., Jang, Y., and Lee, B., 2019, Geologic map of Korea: Korea Institute of Geoscience and Mineral Resources, scale 1:1,000,000.
- Kim, B., 1976, Geological and paleontological studies of Chungnam Coalfield: *Journal of the Geological Society of Korea*, v. 12, p. 124–143.
- Kim, D.-Y., Lee, M., Nam, G.-S., and Park, T.-Y.S., 2021, The first orthopteran fossils from the Lower Cretaceous (Albian) Jinju Formation of Korea: Ethological implications for elcanids: *Cretaceous Research*, v. 125, p. 104843, <https://doi.org/10.1016/j.cretres.2021.104843>.
- Kim, J.-H., 1989, *Sphenophyllum* sp. (Sphenophyllales) newly found from Upper Triassic Baegunsa Formation, Nampo Group, Korea: *Bulletin of the National Science Museum, ser. C*, v. 15, p. 93–96.
- Kim, J.-H., 1990, Three new *Equisetites* species found from the Upper Triassic Amisan Formation, Nampo Group, Korea: *Journal of Paleontological Society of Korea*, v. 6, p. 91–99.
- Kim, J.-H., 2001, New fossil plants from the Nampo Group (lower Mesozoic), Korea: *Geosciences Journal*, v. 5, p. 173–180, <https://doi.org/10.1007/BF02910423>.

- Kim, J.-H., 2009, Species diversity and leaf form of ginkgoaleans from the Mesozoic and Cenozoic strata in Korea: Journal of the Korean Earth Science Society, v. 30, p. 1–9, <https://doi.org/10.5467/JKESS.2009.30.1.001>.
- Kim, J.-H., 2013, *Weltrichia* sp. from the Late Triassic Amisan Formation of Nampo Group, Korea: Journal of the Korean Earth Science Society, v. 34, p. 402–406, <https://doi.org/10.5467/JKESS.2013.34.5.402>.
- Kim, J.-H., and Kimura, T., 1988, *Lobatannularia nampoensis* Kawasaki from the Upper Triassic Baegunsa Formation, Nampo Group, Korea: Proceedings of the Japan Academy, ser. B, v. 64, p. 221–224.
- Kim, J.-H., and Lee, G.-H., 2015, Fossil Conchostraca from the Amisan Formation of the Nampo Group, Korea: Journal of the Korean Earth Science Society, v. 36, p. 181–189, <https://doi.org/10.5467/JKESS.2015.36.2.181>.
- Kim, J.-H., Kim, H.-S., Lee, B.-J., Kim, J.-M., and Lee, H.-K., 2002, A new species of *Leptostrobus* from the Upper Triassic Amisan Formation of the Nampo Group in Korea: Journal of the Korean Earth Science Society, v. 23, p. 30–37.
- Kim, J.-H., and Roh, H.-S., 2008, Organ fossils of *Neocalamites carrerei* from the Amisan Formation of the Nampo Group, Korea: Journal of the Korean Earth Science Society, v. 29, p. 466–473, <https://doi.org/10.5467/JKESS.2008.29.6.466>.
- Kim, J.-H., Lee, C.-K., and Choi, D.-Y., 2015, *Margaritifera* cf. *isfarensis* (Chernishev) from the Amisan Formation, Nampo Group, Korea: Journal of the Geological Society of Korea, v. 51, p. 357–362.
- Kim, S.-H., Lee, Y.-N., Park, J.-Y., Lee, S., and Lee, H.-J., 2020, The first record of redfieldiiform fish (Actinopterygii) from the Upper Triassic of Korea: Implications for paleobiology and paleobiogeography of Redfieldiiformes: Gondwana Research, v. 80, p. 275–284, <https://doi.org/10.1016/j.gr.2019.11.008>.
- Kimura, T., and Kim, B.-K., 1984, Geological age of the Daedong flora in the Korean Peninsula and its phytogeographical significance in Asia: Proceedings of the Japan Academy, ser. B, v. 60, p. 337–340.
- Koh, H., 2006, Tectonic implication of the Mungyeong-Jeongseon tectonic line, the Yeongweol Nappe and the Bansong Group in the Ogcheon belt, in Kee, W.-S. ed., Mesozoic Crustal Evolution of Northeast Asia: Daejeon, Korean Institute of Geoscience and Mineral Resources, p. 228–259.
- Kwon, S., Sajeev, K., Mitra, G., Park, Y., Kim, S.W., and Ryu, I.-C., 2009, Evidence for Permo-Triassic collision in Far East Asia: The Korean collisional orogen: Earth and Planetary Science Letters, v. 279, p. 340–349, <https://doi.org/10.1016/j.epsl.2009.01.016>.
- Lee, H., Park, S.-I., Choi, T., and Sim, M.S., 2021, Post-collisional denudation of an orogenic belt traced from geochronological and bulk-rock geochemical records of the western Korean Peninsula: International Geology Review, v. 63, p. 87–108, <https://doi.org/10.1080/00206814.2019.1706649>.
- Lee, S.-W., and Chung, G.-S., 2010, Facies analysis of the early Mesozoic Hajo Formation in the Chungnam Basin, Boryeong, Korea: Journal of the Korean Earth Science Society, v. 31, p. 18–35, <https://doi.org/10.5467/JKESS.2010.31.1.018>.
- Lee, W.-K., Kim, Y.-S., Kim, C.-Y., Kim, H.-S., and Kim, J.-H., 2004, A revision of Mesozoic Equisetales *Annuriopsis bunkeiensis* Kimura et Kim from the Amisan Formation of Nampo Group, Korea: Journal of the Korean Earth Science Society, v. 25, p. 32–38.
- Nam, K.S., and Kim, J.-H., 2014, Occurrence of the fossil *Mesopsyche dobrokhotovae* in the Late Triassic Amisan Formation, Nampo Group, Korea and its geological implication: Journal of the Korean Earth Science Society, v. 35, p. 161–167, <https://doi.org/10.5467/JKESS.2014.35.3.161>.
- Nam, K.S., Wang, Y., Ren, D., Kim, J.H., and Szewo, J., 2017, An extraordinary palaeontinid from the Triassic of Korea and its significance: Scientific Reports, v. 7, p. 40691.
- Oh, C.W., 2006, A new concept on tectonic correlation between Korea, China and Japan: Histories from the late Proterozoic to Cretaceous: Gondwana Research, v. 9, p. 47–61, <https://doi.org/10.1016/j.gr.2005.06.001>.
- Park, S.-I., and Noh, J., 2015, Jangsan fault: Evidence of structural inversion of the Chungnam Basin: Journal of the Geological Society of Korea, v. 51, p. 451–469, <https://doi.org/10.14770/jgsk.2015.51.5.451>.
- Park, S.-I., Kwon, S., Kim, S.W., Hong, P.S., and Santosh, M., 2018a, A Mesozoic orogenic cycle from post-collision to subduction in the southwestern Korean Peninsula: New structural, geochemical, and chronological evidence: Journal of Asian Earth Sciences, v. 157, p. 166–186, <https://doi.org/10.1016/j.jseaes.2017.08.009>.
- Park, S.-I., Noh, J., Cheong, H.J., Kwon, S., Song, Y., Kim, S.W., and Santosh, M., 2019, Inversion of two-phase extensional basin systems during subduction of the Paleo-Pacific Plate in the SW Korean Peninsula: Implication for the Mesozoic ‘Laramide-style’ orogeny along East Asian continental margin: Geoscience Frontiers, v. 10, p. 909–925, <https://doi.org/10.1016/j.gsf.2018.11.008>.
- Park, T.-Y.S., Kihm, J.-H., Woo, J., Park, C., Lee, W.Y., Smith, M.P., Harper, D.A., Young, F., Nielsen, A.T., and Vinther, J., 2018b, Brain and eyes of *Kerygmachela* reveal protocerebral ancestry of the panarthropod head: Nature Communications, v. 9, 1019, <https://doi.org/10.1038/s41467-018-03464-w>.
- Retallack, G.J., Veevers, J.J., and Morante, R., 1996, Global coal gap between Permian-Triassic extinction and Middle Triassic recovery of peat-forming plants: Geological Society of America Bulletin, v. 108, p. 195–207.
- Riek, E., 1954, Further triassic insects from Brookvale, NSW (orders Orthoptera Saltatoria, Protorthoptera, Perlaria): Records of the Australian Museum, v. 23, p. 162–168.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: Nature Methods, v. 9, p. 671–675, <https://doi.org/10.1038/nmeth.2089>.
- Schubnel, T., Legendre, F., Roques, P., Garrouste, R., Cornette, R., Perreau, M., Perreau, N., Desutter-Grandcolas, L., and Nel, A., 2021, Sound vs. light: Wing-based communication in Carboniferous insects: Communications Biology, v. 4, p. 794, <https://doi.org/10.1038/s42003-021-02281-0>.
- Schumacher, C.F., 1816, Afhandling over conchyliologiske Systemer, og om nogle toskallede Conchylier: Oversigt Over det Kongelige Danske Videnskabskabernes Selskabs Vorhandling, Copenhagen, v. 7, p. 1813–1815.
- Scotese, C.R., 2021, An atlas of Phanerozoic paleogeographic maps: The seas come in and the seas go out: Annual Review of Earth and Planetary Sciences, v. 49, p. 679–728, <https://doi.org/10.1146/annurev-earth-081320-064052>.
- Scudder, S.H., 1885, Palaeodictyoptera, or the affinities and classification of Paleozoic Hexapoda: Memoires of the Boston Society of Natural History, v. 3, p. 153–187.
- Shao, L., Wang, X., Wang, D., Li, M., Wang, S., Li, Y., Shao, K., Zhang, C., Gao, C., and Dong, D., 2020, Sequence stratigraphy, paleogeography, and coal accumulation regularity of major coal-accumulating periods in China: International Journal of Coal Science & Technology, v. 7, p. 240–262, <https://doi.org/10.1007/s40789-020-00341-0>.
- Sharov, A., 1968, Phylogeny of Orthoptera insects: Transactions of the Paleontological Institute, Academy of Science of the USSR, v. 118, p. 3–208.
- Tillyard, R., 1925, A new fossil insect wing from Triassic beds near Deewhy: Proceedings of the Linnean Society of New South Wales, v. 50, p. 374–377.
- Yang, S., 1999, The lower Mesozoic strata, in Kim, J.-H., ed., Geology of Korea: Seoul, Sigma Press, p. 206–226.
- Zalessky, M., 1929, O novykh nacekomykh iz permiskikh otlozhenij bassejnov rek Kamy, Vyatki i Beloj: Trudy Obshchestva Estestvoispytatelej pri Kazanskom Universitet, v. 52, p. 1–30.

Accepted: 25 March 2022