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A new geinitziid forewing reveals biostratigraphic correlation between Daohugou and Shar Teg

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Abstract

The Middle–Late Jurassic insect assemblages of the Asian interior, such as the Daohugou and Shar Teg biotas, provide critical windows into insect evolution. These biotas share similar faunal compositions, yet their similarities are largely limited to the generic level. This lack of species-level evidence has hindered precise stratigraphic correlation. In this study, we describe a complete forewing of a geinitziid fossil from the Haifanggou Formation at the Daohugou locality, Ningcheng, Inner Mongolia. The specimen is identified as *Sinosepididontus shartegicus* Aristov *et al.*, 2009, a species previously known only from a basal wing fragment recovered from the lower Shar Teg sequence in southwestern Mongolia. Based on this well-preserved new material, we provide an emended diagnosis and supplementary description for *S. shartegicus*, offering the first full characterization of its wing venation. The discovery of *S. shartegicus* in the Daohugou biota substantially reinforces the biotic link between the Daohugou and Shar Teg assemblages. Based on regional geological data, we correlate the Shar Teg sequence with the Haifanggou Formation, and we further correlate the overlying Ulan Malgait sequence with the Tiaojishan Formation.

Keywords: Insecta, Polyneoptera, Mesozoic, Yanliao biota, Middle–Late Jurassic

Introduction

In the Middle–Late Jurassic of Asia, there are three major biotas with exceptionally preserved fossils: the Daohugou biota of northeastern China, the Shar Teg biota of Mongolia, and the Karatau biota of Kazakhstan. The Daohugou beds were formed in a lacustrine environment with fine clastic sediments. The fossils were buried rapidly by volcanic ash, creating an exceptional taphonomic setting.

This area has yielded a large number of diverse and well-preserved insect fossils, providing important evidence for studying the evolutionary history, palaeoclimate, and palaeogeography of the Mesozoic (Huang, 2015; Huang *et al.*, 2018). The Shar Teg biota is one of the most diverse among Jurassic *Lagerstätten*, and it plays an important role in connecting the insect palaeofaunas of East Asia, Central Asia, and Europe. The Shar Teg locality consists of two parts: the lower Shar Teg sequence and the upper Ulan Malgait sequence. Insect fossils are found within the Shar Teg sequence (Ponomarenko *et al.*, 2014). The fossil layers of the Karabastau Formation are located in southern Kazakhstan. This area is often called the “Karatau Jurassic Lake”, and it is one of the most famous fossil sites for Jurassic insects. To date, more than 800 species have been described from this locality (Kopylov & Rasnitsyn, 2025).

In the Daohugou biota, the family Geinitziidae is abundantly recorded, with two genera and three species published based on more than a dozen specimens. In this region, the family is typically represented by the genus *Sinosepididontus* (Huang & Nel, 2008; Cui *et al.*, 2012). In contrast, the only geinitziid record from the Shar Teg biota is a fragmentary holotype of *Sinosepididontus shartegicus* and no geinitziid has been reported from the Karatau biota to date (Aristov *et al.*, 2009). Notably, the genus *Sinosepididontus* is found only in Daohugou and Shar Teg, with no known records from other fossil localities globally.

Through a systematic study of geinitziid fossils from the Haifanggou Formation, we identified a nearly complete forewing specimen that is identical to *S. shartegicus*. This discovery represents the first record of the species within the Daohugou biota and fills important morphological gaps in our knowledge of *S. shartegicus*.

Material and methods

The single forewing without counterpart was preserved in greyish tuffaceous shale within the Middle Jurassic Haifanggou Formation near Daohugou Village, Ningcheng County, Inner Mongolia, NE China. This individual co-occurred with abundant conchostracans assigned to *Triglypta haifanggouensis* (Liao *et al.*, 2017), which indicate that the fossil was recovered from the middle–upper sections of the Daohugou Beds.

Photographs were taken with a digital camera attached to a Zeiss AxioZoom V16 stereomicroscope. Line drawings were made using Adobe Illustrator 2019 software. The venational terminology is based on the nomenclature of Schubnel *et al.* (2020). The sole specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Systematic palaeontology

Order Reculida Handlirsch, 1906

Family Geinitziidae Handlirsch, 1906

Genus *Sinosepididontus* Huang & Nel, 2008

Type species. *Sinosepididontus chifengensis* Huang & Nel, 2008

Included species. *Sinosepididontus chifengensis* Huang & Nel, 2008, *Sinosepididontus shartegicus* Aristov *et al.*, 2009.

Sinosepididontus shartegicus Aristov, Wappler & Rasnitsyn, 2009

2009 *Shurabia shartegica* Aristov, Wappler & Rasnitsyn, p. 423, figs. 1g, 2e.

2012 *Sinosepididontus shartegicus* (Aristov, Wappler & Rasnitsyn); Cui *et al.*, p. 259.

Material. Holotype (PIN, no. 4270/1939) is a fragmentary forewing preserving only the basal portion. New material is an imprint of a complete forewing (NIGP210222).

Diagnosis (revised). Medium-sized geinitziid. RA with three branches; RP with four terminal branches. M forks distal to R fork; MA with four branches; apical parts of PCu and AA curve towards CuP, forming a unique two-celled Y-shaped loop; crossveins simple, forming two regular rows of cells in intercubital and CuA branch areas.

Locality and horizon. Holotype originated from Gobi-Altai Province east of Mount Atas-Bogd, Mongolia; late Middle Jurassic Shar Teg Formation. The new material was collected from the Haifanggou Formation near the

Daohugou Village, Ningcheng County, Inner Mongolia, NE China; Callovian, late Middle Jurassic.

Description. Forewing 17.0 mm long, 6.78 mm wide; costal area broad, about three times wider than subcostal area. ScP strongly developed, with 15 straight anterior branches, terminating at 2/3 wing length. R forks into RA and RP at basal 1/3; RA pectinate with three branches; RP dichotomously branched with four branches. M forking distal to R fork; MP with two branches; crossvein m-cua (so-called ‘m5’) short and oblique, joining CuA proximal to CuA fork. CuA divided into CuA₁ and CuA₂ near level of RP origin; CuA₁ with two branches; CuA₂ smoothly curved; CuP substraight, but slightly distally curved; distal ends of PCu and AA curving towards CuP. Crossveins simple in radial-median area; double rows of cells developed between branches of CuA and in intercubital space; wing spots developed posterior to ScP, prominent along crossveins, gradually fading in posterior areas of M and Cu.

Remarks. This species was originally described as *Shurabia shartegica* by Aristov *et al.* (2009), based on a fragmentary wing base from the Shar Teg locality in Mongolia. It was subsequently transferred to *Sinosepididontus* due to the presence of characteristic two-celled anal loops, establishing the new combination *Sinosepididontus shartegicus* (Cui *et al.*, 2012). However, the complete venation pattern remained poorly known, as the holotype lacked the distal and posterior portions of the wing. The present complete forewing exhibits characters in the basal part (*e.g.*, crossveins and wing spots) identical to those of the holotype. A minor difference is observed in the spacing between R and M, which is slightly closer in the holotype than in our new specimen. This is most likely to be an intraspecific variation. *Sinosepididontus shartegicus* can be distinguished from the type species, *S. chifengensis*, by its branched RA (*vs.* simple) and more numerous branches of MA. Furthermore, while *S. chifengensis* possesses only simple crossveins in the CuA area, *S. shartegicus* displays double rows of crossveins and even develops a specialized triple anal loop. This discovery provides the first complete view of the venation for this species.

Discussion

The Shar Teg fossil locality is located in a significant geological exposure near the southeastern end of the Aj Bogd Range in the southwestern Gobi-Altai Province of Mongolia. The stratigraphic section at Shar Teg primarily comprises two sequences, the lower Shar Teg sequence and the upper Ulan Malgait sequence. A layer of caliche occurs between these two sequences. The Shar Teg

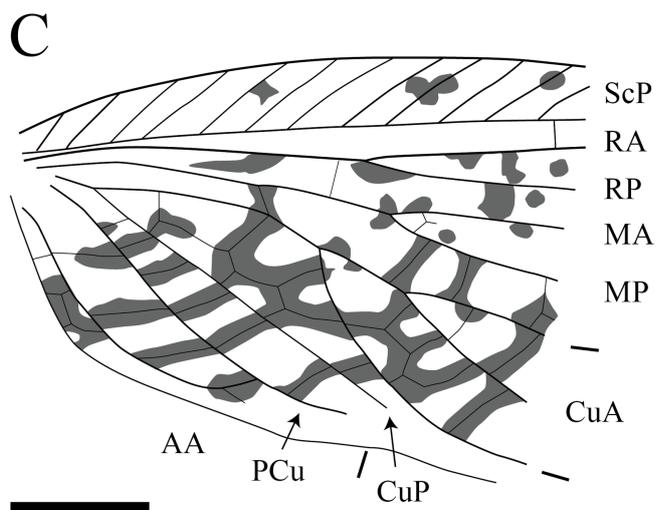
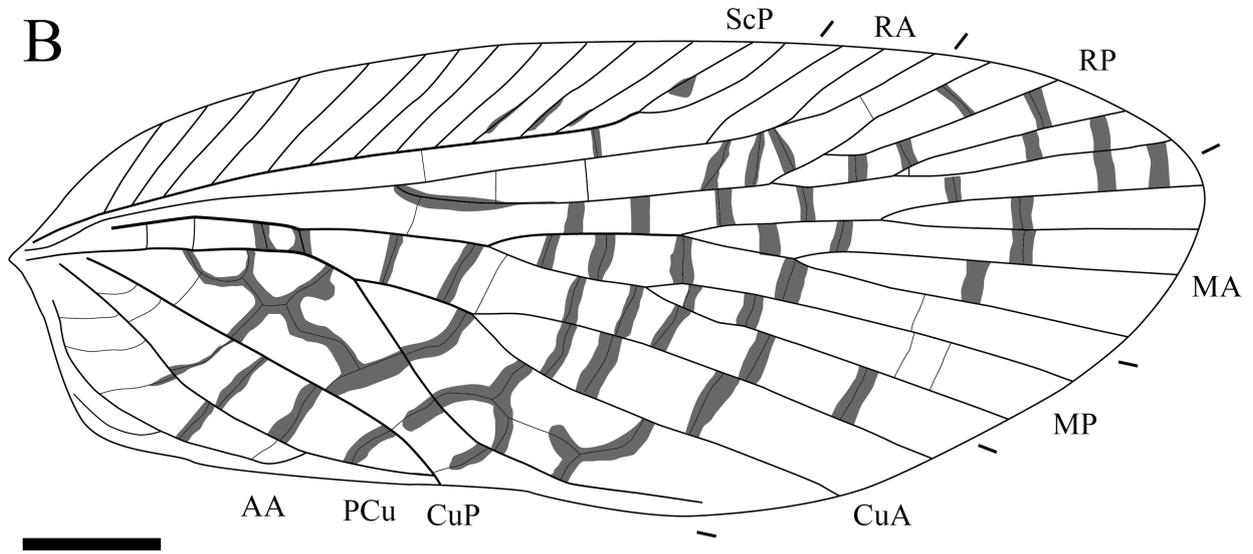


FIGURE 1. Forewing of *Sinosepididontus shartegicus* Aristov *et al.*, 2009. **A**, NIGP210222. **B**, Line drawing of NIGP210222. **C**, Line drawing of holotype PIN, no. 4270/1939. Scale bars = 2 mm.

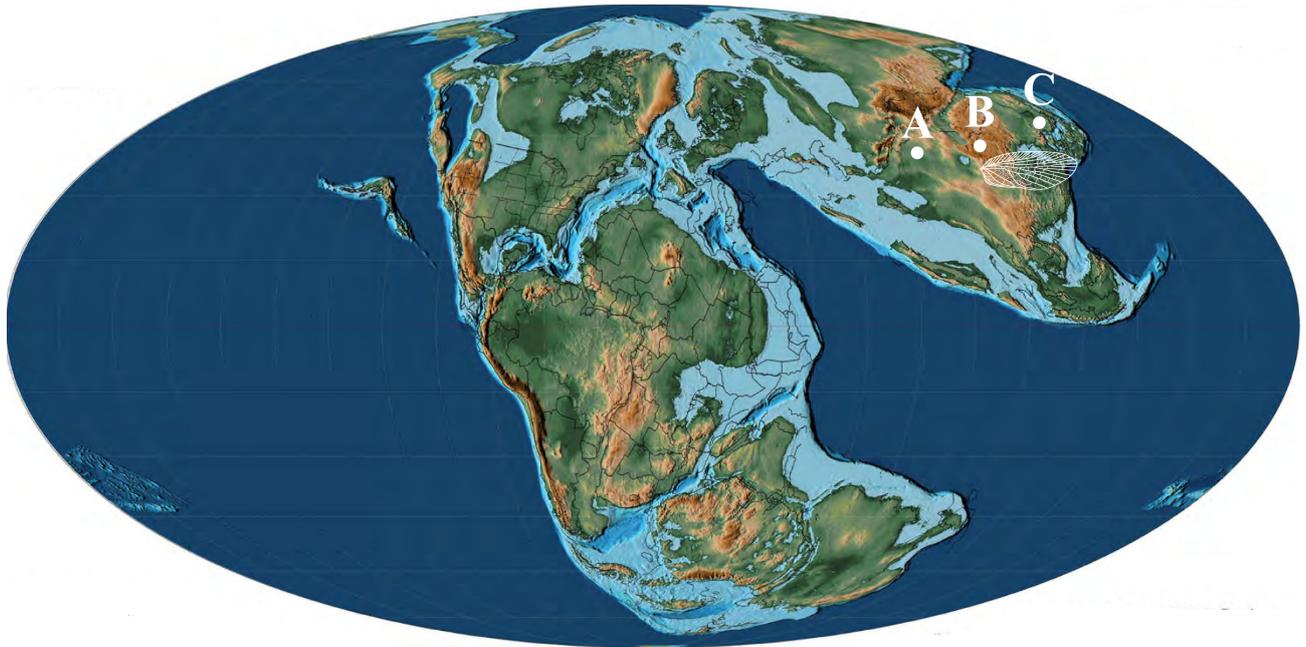


FIGURE 2. Three exceptionally preserved biota from the Middle Jurassic (164.5 Ma): **A**, Karatau; **B**, Shar Teg; **C**, Daohugou. Palaeogeographic base map (164.5 Ma) modified from Scotese (2014).

sequence represents a progressively receding lacustrine deposit characterized by a distinct cyclic structure. The total thickness of the Shar Teg sequence is approximately 250–400 m. Its lithology is primarily composed of grey, green, and yellow sandstones and siltstones, locally interbedded with purple and multicoloured siltstones. The succession contains coal seams. Its lower part bears fossil wood, and the sandstones at the top include intermediate-acidic volcanic lithic fragments (Gubin & Sinitza, 1996). The Shar Teg sequence yields a diverse fossil assemblage, including abundant insects, ostracods, conchostracans, gastropods, bivalves, fishes, labyrinthodonts, turtles, dinosaurs, plants, and charophytes (Sodov, 1993; Vrřanský, 2004). The Ulan Malgait sequence is more widespread than the Shar Teg sequence. It rests unconformably on the caliche. The sequence is a *ca.* 600 m thick red-bed sequence primarily composed of red and multicoloured sandstones and siltstones. The lower part of the sequence consists of alternating beds of sandstone and siltstone. These strata contain a diverse fossil assemblage including mollusks, ostracodes, fishes, turtles, crocodiles, dinosaurs, and plants. The upper part comprises three subdivisions: brown-reddish siltstone at the base, conglomerate in the middle layer, and the crimson and red siltstone with white and pinkish carbonate lime nodules at the top (Ponomarenko *et al.*, 2014).

The Yanliao biota is widely distributed across North China and is divided into early and late assemblages. The early assemblage is preserved in the Middle Jurassic Haifanggou Formation, represented by the

Daohugou biota. The late assemblage is preserved in the lower to middle parts of the Upper Jurassic Tiaojishan Formation, represented by the Linglongta biota. A regional angular unconformity separates these two successions at approximately 161 Ma (Huang, 2015, 2019). The Haifanggou Formation consists of a suite of lacustrine deposits. The lower parts contain a polymictic conglomerate containing volcanic rocks, followed by grey and yellow tuffaceous mudstones, shales, and siltstones. The upper part comprises multicoloured clastic rocks, including conglomerates, with intermediate-acidic volcanic rocks. Petrified wood occurs in the lower parts, and occasional coal streaks are interbedded within the strata. The early assemblage of the Yanliao biota, represented by the Daohugou biota, yields abundant fossils including insects, arachnids, conchostracans, bivalves, amphibians, reptiles, mammals, and plants (Huang *et al.*, 2018). Fish and ostracod fossils occur occasionally in adjacent regions. In correlated strata of the western regions, volcanic components decrease, transitioning into yellow-green clastic deposits also with a polymictic conglomerate at the base. The Tiaojishan Formation is more widely distributed than the Haifanggou Formation. It consists primarily of intermediate-acidic volcanic rocks, transitioning upward into intermediate-basic volcanic rocks. The lower and middle parts contain clastic interbeds, with abundant petrified wood occurring in the lower sections. Sedimentary interbeds yield diverse fossils including insects, conchostracans, ostracodes, bivalves, gastropods, fishes, amphibians, reptiles, mammals, plants,

and charophytes (Duan *et al.*, 2009; Huang *et al.*, 2018). The lower Tiaojishan Formation typically comprises multicoloured beds, grading into red beds in the upper part.

Correlated strata in the Junggar Basin of Xinjiang are referred to as the Toutunhe Formation, with the base dated to younger than 161.2 Ma (Fang *et al.*, 2015). This formation unconformably overlies the underlying Xishanyao Formation in some areas. In the Turpan-Hami Basin, the equivalent sequence includes the lower Sanjianfang and the upper Qiketai formations. This stratigraphic succession in northern Xinjiang consists of red-and-green multicoloured clastic rocks in the lower part and well-developed red beds in the upper part (Deng *et al.*, 2010).

The geochronological age of the Shar Teg sequence remains controversial. Some scholars propose a Middle Jurassic age based on the floral assemblages such as the fern *Klukia* (Sodov, 1993). In contrast, specific groups like cockroaches exhibit more advanced evolutionary traits, showing a combination of Late Jurassic and Early Cretaceous characteristics (Vršanský, 2004). However, the insect fauna as a whole suggests that the Shar Teg sequence should be dated to the Late Jurassic, likely within the first half (Ponomarenko *et al.*, 2014). This temporal uncertainty underscores the importance of regional correlations.

The Daohugou and Shar Teg biotas exhibit a remarkably similar fossil aspect. Both assemblages share floral elements such as *Coniopteris* and *Phoenicopsis* (Sodov, 1993; Huang, 2019). Although ostracods have not been recorded in the Daohugou biota, the Shar Teg sequence and its equivalent strata in China contain an abundance of the diagnostic ostracod *Darwinula sarytirmensis* Sharapova (Mandelstam, 1947; Sharapova, 1947; Huang, 2019). In terms of insect fauna, both biotas share widespread caddisfly cases (Huang *et al.*, 2009; Wu & Huang, 2010). The neuropteran family Grammolingiidae, a typical component of the Daohugou biota, has also been recorded in Shar Teg (Ren, 2002; Khramov, 2010). Similarly, the dipteran genus *Archizelmira* and the geinitziid genus *Sinosepididontus* are represented by closely allied species in both localities (Huang, 2015).

The specimen discovered in this study is identical to the holotype of *S. shartegicus* from the Shar Teg biota (Aristov, 2009). This discovery highlights a remarkable faunal similarity between the two biotas during the Middle Jurassic. The two-celled anal loop observed in this complete forewing represents an extremely rare character among Jurassic insects, further confirming the taxonomic identity. To date, the genus *Sinosepididontus* is exclusively restricted to the Daohugou and Shar Teg biotas, with no records from the contemporaneous Karatau biota or any

other global localities. This discovery not only fills the critical morphological gaps of *S. shartegicus* but also provides robust evidence for the direct stratigraphic correlation between the Haifanggou Formation and the Shar Teg sequence. Our findings strengthen the biotic links across the Asian continent, offering a new benchmark for understanding Jurassic terrestrial ecosystems.

In summary, regarding lithostratigraphic correlation, we propose the Middle Jurassic Haifanggou Formation roughly corresponds to the Shar Teg sequence, and that the Late Jurassic Tiaojishan Formation correlates with the Ulan Malgait sequence. A subtle angular unconformity separates these two units.

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References

- Aristov, D.S., Wappler, T. & Rasnitsyn, A.P. (2009) New and little-known grylloblattids of the family Geinitziidae (Insecta: Grylloblattida) from the Triassic and Jurassic of Europe, Asia, and South Africa. *Paleontological Journal*, 43, 418–424. <https://doi.org/10.1134/S0031030109040091>
- Cui, Y.Y., Storozhenko, S.Yu. & Ren, D. (2012) New and little-known species of Geinitziidae (Insecta: Grylloblattida) from the Middle Jurassic of China, with notes on taxonomy, habitus and habitat of these insects. *Alcheringa*, 36, 251–261. <https://doi.org/10.1080/03115518.2012.628806>
- Deng, S.H., Lu, Y.Z., Fan, R., Pan, Y.H., Cheng, X.S., Fu, G.B., Wang, Q.F., Pan, H.Z., Shen, Y.B., Wang, Y.Q., Zhang, H.C., Jia, C.K., Duan, W.Z. & Fang, L.H. (2010) *The Jurassic system in northern Xinjiang*. China University of Science and Technology Press, Hefei, 219 pp.
- Duan, Y., Zheng, S.L., Hu, D.Y., Zhang, L.J. & Wang, W.L. (2009) Preliminary report on Middle Jurassic strata and fossils from Linglongta area, Jianchang, Liaoning. *Global Geology*, 28, 143–147. [In Chinese with English abstract]
- Fang, Y.N., Wu, C.D., Guo, Z.J., Hou, K.J., Dong, L.H., Wang, L. & Li, L. (2015) Provenance of the southern Junggar Basin in the Jurassic: Evidence from detrital zircon geochronology and depositional environments. *Sedimentary Geology*, 315, 47–63. <https://doi.org/10.1016/j.sedgeo.2014.10.014>
- Gubin, Y.M. & Sinitza, S.M. (1996) Shar–Teg: a Unique Mesozoic Locality of Asia. *Museum of Northern Arizona Bulletin*, 60, 311–318.

- Handlirsch, A. (1906) *Die fossilen Insekten und die Phylogenie der rezenten Formen, parts I-IV*. Ein Handbuch für Palaontologen und Zoologen, 640 pp.
- Huang, D.Y. (2015) Yanliao biota and Yanshan Movement. *Acta Palaeontologica Sinica*, 54, 501–546. [In Chinese with English abstract]
- Huang, D.Y. (2019) Jurassic integrative stratigraphy and timescale of China. *Science China Earth Sciences*, 62, 223–255. <https://doi.org/10.1007/s11430-017-9268-7>
- Huang, D.Y., Cai, C.Y., Fu, Y.Z. & Su, Y.T. (2018) The middle-late Jurassic Yanliao entomofauna. *Palaeoentomology*, 1, 3–31. <https://doi.org/10.11646/palaeoentomology.1.1.2>
- Huang, D.Y. & Nel, A. (2008) New ‘Grylloblattida’ related to the genus *Prosepididontus* Handlirsch, 1920 in the Middle Jurassic of China (Insecta: Geinitziidae). *Alcheringa*, 32, 395–403. <https://doi.org/10.1080/03115510802417893>
- Huang, D.Y., Wu, H. & Dong, F.B. (2009) Discovery and preliminary study of fossil caddis case in China. *Acta Palaeontologica Sinica*, 48 (4), 646–653. [In Chinese with English abstract]
- Khramov, A.V. (2010) A new lacewing (Insecta: Neuroptera: Grammolingiidae) from the Upper Jurassic of Mongolia. *Paleontological Journal*, 44 (2), 188–191.
- Kopylov, D.S. & Rasnitsyn, A.P. (2025) Anaxyelidae of Karatau: 100 Years After. *Insects*, 16, 943. <https://doi.org/10.3390/insects16090943>
- Liao, H.Y., Shen, Y.B. & Huang, D.Y. (2017) Conchostracans of the Middle–Late Jurassic Daohugou and Linglongta beds in NE China. *Palaeoworld*, 26, 317–330. <https://doi.org/10.1016/j.palwor.2016.11.001>
- Mandel'shtam, M.I. (1947) Ostracoda from the middle Jurassic of the Mangyshlak Peninsula. In: *Mikrofauna neftyanykh mestorozhdenii Kavkaza, Embyi Tsentral'noi Azii* (Microfauna of oil deposits of the Caucasus, Emba, and Central Asia). Gostoptekhizdat, Leningrad, pp. 239–256. [In Russian]
- Ponomarenko, A.G., Aristov, D.S., Bashkuev, A.S., Gubin, Y.M., Khramov, A.V., Lukashovich, E.D., Popov, Y.A., Pritykina, L.N., Sinitshenkova, N.D., Shcherbakov, D.E., Sukatsheva, I.D., Vassilenko, D.V., Vladimirova, E.V. & Yan, E.V. (2014) Upper Jurassic Lagerstätte Shar Teg, southwestern Mongolia. *Paleontological Journal*, 48 (14), 1573–1682. <https://doi.org/10.1134/S0031030114140160>
- Ren, D. (2002) A new lacewing family (Neuroptera) from the Middle Jurassic of Inner Mongolia, China. *Insect Science*, 9, 53–67. <https://doi.org/10.1111/j.1744-7917.2002.tb00172.x>
- Schubnel, T., Desutter-Grandcolas, L., Legendre, F., Prokop, J., Mazurier, A., Garrouste, R., Grandcolas, P. & Nel, A. (2020) To be or not to be: postcubital vein in insects revealed by microtomography. *Systematic Entomology*, 45, 327–336. <https://doi.org/10.1111/syen.12399>
- Scotese, C.R. (2014) *Atlas of Jurassic paleogeographic maps, PALEOMAP atlas for arcGIS. Vol. 4. The Jurassic and Triassic, maps 32–42*. PALEOMAP Project, Evanston, Illinois, 11 pp.
- Sharapova, E.G. (1947) Order Ostracoda. In: Krymgorols, G.Ya. (Ed.), *Atlas rukovodyashchikh form iskopaemykh faun SSSR* (Atlas of index forms of the fossil fauna of the USSR). Vol. 8. *Nizhnii i srednii otdely yurskoi sistemy* (Lower and Middle series of the Jurassic system). Gosgeolizdat, Moscow–Leningrad, pp. 208–216. [In Russian]
- Sodov, Z. (1993) Jurassic floras with Siberian affinities in southwestern Mongolia. *Acta Palaeontologica Polonica*, 38 (1-2), 115–124.
- Vršanský, P. (2004) Transitional Jurassic/Cretaceous cockroach assemblage (Insecta, Blattaria) from the Shar-Teg in Mongolia. *Geologica Carpathica*, 55 (6), 457–468.
- Wu, H. & Huang, D.Y. (2010) Diversity of Jurassic caddis cases (Insecta, Trichoptera). *Earth Science Frontiers*, 17 (Special Issue), 156–158.