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Alcheringa

The first representative of the odonatan superfamily Triassolestoidea (Odonatoptera: Parazygoptera) from the Upper Triassic of Korean Peninsula

André Nel^{a,*}, Gi-Soo Nam^b, and Corentin Jouault^{a,c,d}

^aInstitut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier, F-75005 Paris, France. [anel@mnhn.fr]; [jouaultc0@gmail.com]

^bGongju National University of Education, Gongju, Chungcheongnam-do 32553, Republic of Korea. [nks33@naver.com]

^cUniv. Rennes, CNRS, Géosciences Rennes, UMR 6118, F-35000, Rennes, France.

^dCNRS, UMR 5554 Institut des Sciences de l'Évolution de Montpellier, Place Eugène Bataillon, F-34095, Montpellier, France.

*Corresponding author

ABSTRACT

Koreatriassothemis elongatus gen. et sp. nov. is the first representative of the odonatan superfamily Triassolestoidea described from the Upper Triassic of the Republic of Korea. Despite close similarities with the genera *Pseudotriassothemis* and *Triassoneura*, exact affinities within Triassolestoidea remain uncertain, thus discoveries of more complete triassolestoid fossils are required to resolve relationships. The identification of *K. elongatus* gen. et sp. nov. shows that Odonatoptera and Triassolestoidea diversity was high during the

Late Triassic and is currently underestimated. A ‘*Samarura*-like’ odonatopteran nymph is also identified from the same Upper Triassic outcrop, and may be referable to *K. elongatus* gen. et sp. nov.

KEY WORDS

Insecta; Odonoptera; Epiproctophora; Isophlebioptera; classification; correspondence between adults and nymphs

THE ODONATAN suborder Epiproctophora (= Epiprocta) —also called damsel-dragonflies— encompasses both the Anisoptera and ‘relic’ family Epiophlebiidae (Beusse 2016). The Epiproctophora are currently divided into two sister clades: Isophlebioptera and Euepiproctophora (the latter containing Anisoptera as a subgroup: Bechly 1996). These insects flourished during the Mesozoic with more than 750 species known to date (<https://paleobiodb.org>). Recent nodedated molecular phylogenies have suggested a Permian or Triassic divergence timeframe for the suborder (Kohli et al. 2021, Suvorov et al. 2022). However, these analyses did not accommodate advances in tip-dating or total-evidence dating techniques (dos Reis et al. 2016, Wright 2019). Such approaches have otherwise been used to clarify the diversification tempo of lineages with well-documented fossil records, but remain little used for insect clades (Ronquist et al. 2012, Veà & Grimaldi 2016, Jouault et al. 2021, Spasojevic et al. 2021). As an example, a total-evidence analysis of the superorder Odonoptera has the potential to resolve placements of fossil taxa and refine divergence estimates; these are still inferred primarily from wing venation morphologies (Bechly 1996, 2016) and have never been tested using a phylogenetic framework.

The most ancient representatives of Isophlebioptera are contained within the superfamily Triassolestoidea, which is known from fossils spanning the Upper Triassic to

Upper Jurassic (Carpenter 1960, Nel et al. 2002). Interestingly, their geologically latest occurrences postdate the early Toarcian oceanic anoxic event, which is associated with dramatically increasing atmospheric CO₂, oceanic anoxia, and global warming that promoted extinctions amongst insect clades, probably because of major changes in flora (e.g., Caswell & Coe 2012, Dmitriev et al. 2018, Mander & McElwain 2019).

Here we describe a new Late Triassic triassolestoid damsel-dragonfly based on a single forewing from the Amisan Formation at Seongju-myeon near Boryeong City in the Republic of Korea. We also report an odonatopteran nymph, an evolutionary stage that is extremely rare as fossils before the Middle Jurassic, and are otherwise represented by only one other occurrence from the Carboniferous—the only example documented from the entire Paleozoic (Kukalova- Peck 2009).

Institutional abbreviations

BCM, Boryeong Coal Museum, Boryeong, Republic of Korea. GNUE, Gongju National University of Education, Gongju, Republic of Korea.

Material and methods

The isolated triassolestoid damsel-dragonfly forewing with preserved venation (BCM2081) was discovered in the middle shale unit of the Amisan Formation exposed in the Myeongcheon section (36°20'21"N, 126°37'34"E) at Seongjumyeon; the odonatopteran nymphs (GNUE112004, GNUE112005) are from the Dongdae section (36°21'10" N, 126°37'49" E) of the Amisan Formation (see Park et al. 2022). The Amisan Formation is 1000m thick and sequentially comprises the lower sandstone unit, lower shale unit, middle sandstone unit, middle shale unit, and upper sandstone unit (Yang 1999). The Amisan Formation has long been considered as Triassic based on plant fossil content (Kimura & Kim

1984), although more recent studies have suggested a possible extent into the lower Jurassic or Cretaceous (Kim & Kimura 1988, Kim 1990, 2009, 2013, Kim et al. 2002, Lee et al. 2004, Kim & Roh 2008). Invertebrate remains including clam shrimp have otherwise supported a Triassic age (Kim et al. 2015). The bivalve Margaritifera Schumacher, 1816 might also indicate a post- Triassic range (Kim et al. 2015), but phylogenetic assessments of Margaritiferidae support a Triassic origin for the family (Araujo et al. 2017). Radiometric dating of the Nampo Group (which encompasses the Amisan Formation) infers a Jurassic age (contra Koh 2006, Jeon et al. 2007). However, we regard the unit as predominantly Late Triassic based on the presence of the age-diagnostic insect clades Titanoptera and Triadophlebiomorpha (Jouault et al. 2022, Park et al. 2022). Herein, we consider the age of the Amisan Formation to be Late Triassic until clear-cut analyses clarify the age of the formation.

The samples were photographed using a Canon EOS 6D camera with an attached Canon EF 100 mm f/2.8 USM macro lens. Images were cropped and enhanced using Adobe Illustrator and Adobe Photoshop CC2019. The holotype specimen of *Koreatriassothemis elongatus* gen. et sp. nov. is housed in the Boryeong Coal Museum, under the following registration number BCM2081. The fossil nymphs GNUE112004 and GNUE112005 are housed in the Gongju National University of Education.

We follow the wing venation nomenclature of Riek & Kukalová-Peck (1984) and Nel *et al.* (2002), as modified by Jacquelin *et al.* (2018: fig. 3).

Venation abbreviations are as follows: ASn antesubnodal oblique crossvein basad subnodus, between RA and RP; Ax primary antenodal crossvein; C costa; Cr nodal crossvein; CuA cubitus anterior; CuP cubitus posterior; IR intercalary radial vein; MAa anterior branch of media anterior; MAb posterior branch of media anterior; MP media posterior; Pt pterostigma; RA radius anterior; RP radius posterior; ScP subcosta posterior; Sn subnodus.

Systematic paleontology

Class INSECTA Linnaeus, 1758

Superorder ODONATOPTERA Martynov, 1932

Order ODONATA Fabricius, 1793

Suborder EPIPROCTOPHORA Bechly, 1996

Clade ISOPHLEBIOPTERA Bechly, 1996

Clade PARAZYGOPTERA Bechly, 1997

Superfamily Triassolestoidea Tillyard, 1918

Family *incertae sedis*

Genus *Koreatriassothemis* gen. nov.

Type species

Koreatriassothemis elongatus sp. nov.

Etymology

Named after Korea and the genus name *Triassothemis*. Gender neutral.

Diagnosis

Wing venation characters only. Areas between RP3/4 and MAa and between IR2 and RP2 distally widened; areas between MAa and MP, RP3/4 and IR2, and between RP2 and IR1 distally narrowed, apex of ScP smoothly ending into C, without strong curvature; base of IR2 just distad nodus; ASn short; CuA elongate, ending opposite nodus; base of IR2 on RP3/4, well distad base of RP3/4.

Koreatriassothemis elongatus sp. nov.

(Fig. 1)

Etymology

Named after the elongate shape of the wing.

Material

Holotype BCM2081 (a nearly complete wing, with basal part up to discoidal cell missing), housed in collection of the Boryeong Coal Museum, Boryeong, Republic of Korea.

Locality, unit and age

Amisan Formation, Upper Triassic, Myeongcheon Section, Seongju-myeon, Boryeong City, Chungcheongnam-do, Republic of Korea.

Diagnosis

As for the genus (*vide supra*).

Description

Forewing apparently hyaline; preserved part 34.1 mm long, wing 8.0 mm wide; distance from nodus to proximal part of preserved portion of wing 14.1 mm, from nodus to wing apex 18.7 mm, from nodus to pterostigma 10.7 mm; from pterostigma to wing apex 6.7 mm, exact position of nodus unknown but nodus probably about midway between base and apex; pterostigma short and rather broad, 3.8 mm long, 1.0 mm wide, covering one cell and a half; pterostigmal brace, postnodal and postsubnodal crossveins not discernable; no visible antenodal crossveins; nodus well preserved with ScP ending in C smoothly, not making a kink; nodal crossvein Cr perpendicular to ScP and RA subnodus not aligned with nodal Cr and oblique, nodal crossing and subnodus situated well basad apex of ScP; a crossvein 'ASn' basad subnodus; areas between C and RA and between RA and RP very broad distad nodus, of same widths; no visible antefurcal crossvein in space between RP and MA basal of base of RP_{3/4}; base of RP_{3/4} 8.5 mm basad nodus; base of IR₂ on RP_{3/4}, 3.7 mm distally, distinctly basad nodus; CuA elongate, ending on posterior margin of wing just distad level of nodus; cubito-anal area with one-two rows of cells between CuA and posterior margin of wing; area

between MP and CuA as broad as postdiscoidal area, with one row of cells and 1.5 mm wide, area between MP and posterior margin of wing with two-three rows of cells in-between; postdiscoidal area 1.5 mm wide distad discoidal cell, narrowed near posterior wing margin, with one row of cells in this area; area between MAa and RP3/4 greatly widened distally, with one row of cells between them in basal two-third; area between RP3/4 and IR2 very narrow proximally, progressively widened distally and not narrowed close to posterior wing margin, with one-two rows of cells between them; base of RP2 2.5 mm distad level of nodus; area between IR2 and RP2 greatly widened distally, no visible crossvein stronger and more oblique than others between IR2 and RP2, that would correspond to an oblique vein 'O'; base of IR1 3.4 mm distad that of RP2; IR1 strongly approximating RP2 in its basal part; area between RP2 and IR1 progressively widening distally; area between IR1 and RP1 progressively narrowed distally; one row of cells between RP1 and RA and between RA and costal margin; all main veins distally curved.

Nymph of '*Samarura*-type'

(Fig. 2)

Material. Specimen GNUE112004 & GNUE112005 (part and counterpart of a nearly complete nymph), housed in collection of the Gongju National University of Education.

Locality, unit and age

Amisan Formation, Upper Triassic, Dongdae Section, Seongju-myeon, Boryeong City, Chungcheongnam-do, Republic of Korea.

Description

A nearly complete nymph (possible an exuvia as the head seems to be dorsally opened), complete body with gills 16.8 mm long; mask partly preserved below head, apparently of zygopteran-type; wing pads well-developed, 1.9 mm long, but without visible trace of

tracheation; thorax 2.5 mm long; legs thin and elongate, with patterns of coloration on mid and hind femora at least in form of an alternation of hyaline and darkened transverse bands (similar to those of an extant Lestidae); abdomen quite long, 11.6 mm long, 1.8 mm wide; three apical tracheal gills of same shape, broad and rounded, 2.1 mm long, 1.8 mm wide.

Discussion

Affinities of the triassolestoid damsel-dragonfly forewing

BCM2081 represents a forewing because of the narrow cubitoanal area with CuA parallel to posterior wing margin. Its general shape resembles the forewings of Triassic ‘protozygopteran’ and triassolestoidans (= †Cyclothemistidae Bechly, 1996 and †Triassolestidae Tillyard, 1918; Nel et al. 2002, 2012). Missing information from the wing base, particularly the discoidal cell, makes discrimination between these clades problematic. Nevertheless, the nodal crossing and subnodus situated well basad of the apex of the ScP, the very broad areas between C and RA, the RA and RP of the distad nodus being of equal width, and the distally broad area between the MA and RP_{3/4} are features not typically encountered in ‘Protozygoptera’. BCM2081 otherwise possesses both the parazygopteran apomorphy of a RP₂ that arises distal to the subnodus (Bechly 1996) and the triassolestoidan apomorphy of a nodal and subnodal veinlet that are not well aligned (Bechly 1996, 2016). Members of Asiopteridae, the sister group of Triassolestoida, exhibit strongly curved distal ends of the ScP and nodal crossing, together with a well-aligned subnodus that is situated at the apex of the ScP (Pritykina 1968). We, therefore, consider BCM2081 as most probably representing a parazygopteran within the superfamily Triassolestoida.

Triassophlebia stigmatica Tillyard, 1922 may be related to Triassolestoida but differs from BCM2081 in possessing a ‘bridge’ between the IR₁ and RP₂ veins (Nel et al. 2002). BCM2081 also lacks the cyclothemistid synapomorphy of a postdiscoidal without distal

narrowing, and a weakly expanded space between RP3/4 and MA which is evident in triasolestids; these characters are otherwise visible in the cyclothemistines *Cyclothemis* Pritykina, 1980, *Shurabiola* Pritykina, 1980, and *Sogjutella* Pritykina, 1980 (Pritykina 1980). Bechly (1997, 2016) also included *Pseudotriassothemis nipponensis* (Fujiyama, 1991) (= type species), *Pseudotriassothemis okafujii* (Fujiyama, 1991), and *Pseudotriassothemis minensis* (Fujiyama, 1991) in a separate subfamily, Pseudotriassothemistinae Bechly, 1997, within Cyclothemistidae.

The two putative synapomorphies of the Cyclothemistidae are unknown in *Pseudotriassothemis okafujii* because the distal parts of the veins MA, RP3/4, IR2 and RP2 are not preserved in the type specimen. *Pseudotriassothemis minensis* has a strongly broadened distal half of the postdiscoidal area in hind wing, synapomorphy of the Cyclothemistidae. The situation is more ambiguous for *Pseudotriassothemis nipponensis* because the veins MA and MP are nearly parallel up to posterior wing margin, and the area between RP3/4 and MA is strongly broadened, unlike the situation in the Cyclothemistinae. Thus, the inclusion of *Pseudotriassothemis* in the Cyclothemistidae is questionable, also because its apical part of ScP is not making a strong curvature when entering into C. This last character also separates the new fossil from the Cyclothemistinae.

The putative synapomorphies of Cyclothemistidae are unknown in *P. okafujii* because the distal parts of the veins MA, RP3/4, IR2 and RP2 are not preserved in the type specimen. On the other hand, *P. minensis* has a very broad distal half of the postdiscoidal area in the hind wing, which represents a cyclothemistid synapomorphy. The condition in *P. nipponensis* is ambiguous because the MA and MP veins are sub-parallel with the posterior wing margin, and the area between RP3/4 and MA is very broad, unlike the typical condition in Cyclothemistinae. The inclusion of the *Pseudotriassothemis* lineage within Cyclothemistidae

is therefore questionable. The lack of a strongly curved apical part of the ScP where it enters into C also serves to distinguish BCM2081 from cyclothemistines.

Amongst Triasolestidae, BCM2081 shares a subnodus base in the RP3/4 and IR2 with *Mesophlebia* Tillyard, 1916 and *Progonophlebia* Tillyard, 1925; however, these taxa differ in the vein ScP ending at C without making a strong curvature (Tillyard & Dunstan 1916, 1925, Nel et al. 1993, 2002). Both Triasolestini Tillyard, 1918 and Triasothemistini Fujiyama, 1991 (including the Late Triassic genera *Triasothemis* Carpenter, 1960 and *Italophlebia* Whalley, 1986) share the presence of a basal subnodus in the distinctly oblique crossvein 'ASn' that is obliquely slanted towards the apex between RA and RP. While this is visible in BCM2081, Fujiyama (1991) did not illustrate this morphology in *P. okafujii* and *P. nipponensis*, although it is visible in *P. minensis*.

Bechly (2016) distinguished Triasolestini from Triasothemistini on the basis of differing positions in the primary antenodal cross-veins versus the arculus; a character state that is unfortunately not preserved in BCM2081. Nevertheless, the arrangements between RP3/4 and MA, IR2 and RP3/4, and between RP2 and IR2 in BCM2081 are identical to those of *Triasothemis* and *Italophlebia* (Carpenter 1960; Whalley 1986; Bechly 1997; Barth et al. 2013). BCM2081 otherwise contrasts in the apical shape of ScP being less curved. *Triasolestodes* Pritykina, 1981 and *Sogdopterites* Nel et al. 2002, the type species of which, *Sogdopterites legibile* (Pritykina, 1980), is represented only by a hind wing, also have a distinctly curved apex on the ScP (Pritykina 1980: fig. 122). The base of IR2 is also distad the nodus, unlike BCM2081. The genus *Sogdopterites* further differs from BCM 2081 in the absence of the ASn (Pritykina 1980). *Triasolestes epiophlebioides* Tillyard, 1918 (the type genus and species of Triasolestidae) is based on an incomplete wing that does not preserve the nodal structures. However, it also differs BCM2081 in the vein CuA being strongly posteriorly curved and ending opposite the base of RP3/4 (Tillyard 1918).

Triassoneura Riek, 1976 shares a ScP extending obliquely into C and an IR2 that closely approximates the base of RP3/4 with both BCM2081 and *Pseudotriassothemis*; yet the CuA vein is strongly posteriorly curved and terminates opposite the base of RP3/4 (Riek 1976). This character state is also present in *P. minensis* but not *P. nipponensis*, or probably *P. okafujii* (see Fujiyama 1991).

In summary, BCM2081 shares several key character states (the ScP smoothly entering into C, which is unknown in *Triassolestes*, the base of IR2 being positioned closely and even entering into the RP3/4, and a short and weakly oblique ASn vein) with *Pseudotriassothemis* and *Triassoneura*, which brings into question the inclusion of *Pseudotriassothemis* in the Cyclothemistidae, and *Triassoneura* in the Triassolestidae.

The distally broad postdiscoidal area is not visible in *Pseudotriassothemis*, except in *P. minensis*, and this feature may be homoplastic since it is also present in Selenothemistidae Handlirsch, 1939 amongst isophlebiopterans. The ScP smoothly entering into C could be plesiomorphic because it is present elsewhere in several examples of ‘Protozygoptera’ (Nel et al., 2012). BCM2081 differs from *P. okafujii* in the base of IR2 being well distad of RP3/4, inferring a common origination point. Nonetheless, it does share a similar arrangement of the IR1, RP2, IR2 and RP3/4 veins with *P. nipponensis*, but can be distinguished by the RP2 being closer to the nodus, and the postdiscoidal area becoming narrow at the wing margin rather than having a continuous width from the base. Thus, while BCM2081, *Pseudotriassothemis* and *Triassoneura* could represent a distinct clade, or perhaps even a new family, we consider it premature to modify the existing higher-level taxonomies at this stage.

Affinities of the odonatopteran nymph

GNUE112004/GNUE112005 is only the second recorded odonatopteran nymph (*Samarura* sp.) documented from the Triassic, the other example being recovered from Carnian deposits

of the Brassall Subgroup at Brassall Quarry near Ipswich in Queensland, Australia (Rozefelds 1985). The elongated body shape is of ‘zygopteran-type’, with three expanded gills at the apex of the abdomen resembling the ‘*Samarura*-type’, which is characterized by broad leaf-like caudal gills (Nel & Paicheler 1994). ‘*Samarura*-type’ nymphs have been reported from Upper Triassic and Lower Cretaceous strata (Qin et al. 2019), with Pritykina (1985) offhandedly attributing Jurassic and Cretaceous forms to the isophlebiopteran clades Karatawiidae (or Campterothlebiidae) and Isophlebiidae. Nel & Paicheler (1994) described similar nymphs from Oligocene sequences, which postdate isophlebiopteran occurrences. We, therefore, suggest that the ‘*Samarura*-type’ gill morphology could have evolved convergently or constitute a symplesiomorphy within Odonata. Nymphs of the extant leptomorph zygopteran genera *Synlestes* Selys, 1869 (Synlestidae) and *Chorismagrion* Morton, 1914 (Chorismagrionidae) also possess broadly rounded gills (Fraser 1956). Fossil synlestids are known from the Lower Cretaceous (Huang et al. 2022), and Garrouste & Nel (2015) established the isophlebiopteran family Pseudostenolestidae based on adult specimens from the Middle Eocene of Messel in Germany. Consequently, a stratigraphical range extension of isophlebiopterans into the Oligocene may potentially be plausible.

Furthermore, the elongated body shape of the Carboniferous meganisopteran nymph *Dragonympha srokai* Kukalova-Peck, 2009 might indicate that the ‘zygopteran-type’ morphology is plesiomorphic. Unfortunately, though, the abdominal apex is unknown in *D. srokai* (Kukalova-Peck, 2009), and no other odonatopteran nymph fossils have been recognized from before the Upper Triassic (Rozefelds 1985). It is thus currently impossible to determine the polarity of this character state amongst odonatopteran nymphs, or whether it has undergone convergent acquisition in multiple phylogenetically distant lineages.

The Triassic isophlebiopteran *Triassolestes epiophlebioides* was identified from the Carnian section of the Ipswich Coal Measures in Queensland, Australia, which are coeval

with the ‘*Samarura*-type’ nymph described by Rozefelds (1985). Similarly, the stratigraphical proximity of GNUE112004/ GNUE112005 to BCM2081 as a possible imago could indicate the referral of the nymph to Isophlebioptera. However, the indistinct tracheal pattern in the wing pads renders any attribution of GNUE112004/GNUE112005 as tentative.

Conclusion

We describe the forewing of a new triassolestoid damsel-dragonfly from an undifferentiated Upper Triassic strata of the Amisan Formation in the Myeongcheon Section at Seongju-myeon, near Boryeong City in the Republic of Korea.

The specimen is designated as the holotype of a new genus and species, *Koreatriassothemis elongatus* gen. et sp. nov., which shows close affinity with other the Triassic genera *Pseudotriassothemis* and *Triassoneura*.

In addition, a new fossil odonatopteran nymph from the Dongdae Section of the Amisan Formation at Seongju-myeon is morphologically compatible with the ‘*Samarura*-type’ and might be attributable to Isophlebioptera.

These discoveries show that current knowledge of Late Triassic odonatans is incomplete and that further field exploration could elucidate the early stages of diversification within this order.

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Disclosure statement

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.

ORCID

Corentin Jouault: <https://orcid.org/0000-0002-3680-5172>

André Nel: <https://orcid.org/0000-0002-4241-7651>

References

- ARAÚJO, R., SCHNEIDER, S., ROE, K.J., ERPENBECK, D. & MACHORDOM, A., 2017. The origin and phylogeny of Margaritiferidae (Bivalvia, Unionoida): a synthesis of molecular and fossil data. *Zoologica Scripta* 46, 289–307.
- BECHLY, G., 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. *Petalura Special Volume* 2, 1–402.
- BECHLY, G., 2016. Phylogenetic systematics of Odonata. - homepage on Internet site: <https://bechly.lima-city.de/phylosys.htm>
- BÜSSE, S., 2016. Morphological re-examination of *Epiophlebia laidlawi* (Insecta: Odonata) including remarks on taxonomy. *International Journal of Odonatology* 19, 221–238.
- CARPENTER, F.M., 1960. A Triassic Odonate from Argentina. *Psyche* 67, 71–75.
- CASWELL, B.A. & COE, A.L., 2012. A high-resolution shallow marine record of the Toarcian (Early Jurassic) Oceanic Anoxic Event from the East Midlands Shelf, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* 365-366, 124–135.
- DMITRIEV, V.Y., ARISTOV, D.S., BASHKUEV, A.S., VASILENKO, V., VŘSANSKÝ, P., GOROCHOV, A.V., LUKASHEVITCH, E.D., MOSTOVSKI, M.B., PONOMARENKO, A.G.,

- POPOV, YU.A., RASNITSYN, A.P., SINITSHENKOVA, N.D., SUKATSHEVA, I.D., TARASENKOVA, M.M., KHRAMOV, A.V. & SHMAKOV, A.S., 2018. Insect diversity from the Carboniferous to Recent. *Paleontological Journal* 52, 610–619.
- DOS REIS, M., DONOGHUE, P.C.J. & YANG, Z., 2016. Bayesian molecular clock dating of species divergences in the genomics era. *Nature Reviews Genetics* 17, 71–80.
- FRASER, F.C., 1956. The nymphs of *Synlestes tropicus* Tillyard, *Chorismagrion risi* Morton, *Oristicta filicicola* Tillyard and *Lestoidea conjuncta* Tillyard with description of the female of the latter and further notes on the male. *Australian Zoologist* 12, 284–292.
- GARROUSTE, R. & NEL, A., 2015. New Eocene damselflies and first Cenozoic damselfly-dragonfly of the isophlebiopteran lineage (Insecta: Odonata). *Zootaxa* 4028, 354–366.
- HUANG, D., FU, Y., LIAN, X., GAO, J. & NEL, A. 2021. The oldest malachite damselfly (Odonata: Synlestidae) from the Lower Cretaceous of China. *Cretaceous Research* 129, 105023.
- JACQUELIN, L., DESUTTER-GRANDCOLAS, L., CHINTAUAN-MARQUIER, I., BOISTEL, R., ZHENG, DARAN, PROKOP, J. & NEL, A., 2018. New insights on basivenal sclerites using 3D tools and homology of wing veins in Odonatoptera (Insecta). *Scientific Reports* 8 (238), 1–7.
- JEON, H., CHO, M., KIM, H., HORIE, K. & 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* 115, 525–539.
- JOUAULT, C., LEGENDRE, F., GRANDCOLAS, P. & NEL, A., 2021. Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth-death process. *Systematic Entomology* 46, 592–610.
- JOUAULT, C., NAM, G.-S. & NEL, A., 2022. *Koreaphlebia* gen. nov. (Odonatoptera: Triadophlebiomorpha): new evidence of a Triassic age for the Amisan Formation in Korea. *Historical Biology* (in press) <https://doi.org/10.1080/08912963.2022.2102492>

- KIM, J.-H., 1990. Three new *Equisetites* species found from the Upper Triassic Amisan Formation, Nampo Group, Korea. *Journal of Paleontological Society of Korea* 6, 91–99.
- 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* 30, 1–9.
- KIM, J.-H., 2013. *Weltrichia* sp. from the Late Triassic Amisan Formation of Nampo Group, Korea. *Journal of the Korean Earth Science Society* 34, 402–406.
- KIM, J.-H., KIM, Y.-S., LEE, B.-J., KIM, J.-M. & 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* 23, 30–37.
- KIM, J.-H. & KIMURA, T., 1988. *Lobatannularia nampoensis* Kawasaki from the Upper Triassic Baegunsa Formation, Nampo Group, Korea. *Proceedings of the Japan Academy, series B* 64, 221–224.
- KIMURA, T. & 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 series B* 60, 337–340.
- KIM, J.-H., LEE, C.-K. & CHOI, D.-Y., 2015. *Margaritifera* cf. *isfarensis* (Chernishev) from the Amisan Formation, Nampo Group, Korea. *Journal of the Geological Society of Korea* 51, 357–362.
- KIM, J.-H. & 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* 29, 466–473.
- 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, 228–259.
- KOHLI, M., LETSCH, H., GREVE, C., BÉTHOUX, O., DEREGNAUCOURT, I., LIU, SHANLIN ZHOU, XIN, DONATH, A., MAYER, C., PODSIADLOWSKI, L., MACHIDA, R., NIEHUIS, O., RUST, J., WAPPLER, T., YU, XIN, MISOF, B. & WARE, J., 2021. Evolutionary history and divergence times of Odonata (dragonflies and damselflies) revealed through transcriptomics. *IScience* 24, 103324.
- KUKALOVÁ-PECK, J. 2009. Carboniferous protodonatoid dragonfly nymphs and the synapomorphies of Odonoptera and Ephemeroptera (Insecta: Palaeoptera). *Palaeodiversity* 2, 169–198.
- LEE, W.-K., KIM, Y.-S., KIM, C.-Y., KIM, H.-S. & 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* 25, 32–38.
- MANDER, L., MCELWAIN, J.C., 2019. Toarcian land vegetation loss. *Nature Geosciences* 12, 405–406.
- NEL, A., MARIE, V. & SCHMEIBNER, S., 2002. Revision of the Lower Mesozoic dragonfly family Triasolestidae Tillyard, 1918 (Odonata: Epiproctophora). *Annales de Paléontologie* 88, 189–214.
- NEL, A. & PAICHELER, J.-C. 1994. Les Lestoidea (Odonata, Zygoptera) fossiles: un inventaire critique. *Annales de Paléontologie* 80, 1–59.
- PARK, T., KIM, D., NAM, G. & LEE, M., 2022. A new titanopteran *Magnatitan jongheoni* n. gen. n. sp. from southwestern Korean Peninsula. *Journal of Paleontology*, 1–8.
<https://doi.org/10.1017/jpa.2022.30>

- PRITYKINA, L.N., 1980. [New fossil Odonata from the Mesozoic of Central Asia]. pp. 119–131. In: DOLIN, V.G., PANFILOV, D.V., PONOMARENKO, A.G. & PRITYKINA, L.N. (eds). [Mesozoic fossil insects.] Naukova Dumka, Kiev, 1–134. [In Russian.]
- QIN, Z., XI, D., SHI, Z., XU, Y., WEI, F., YU, Z., WU, B. & WAN, X. 2019. Lagerstätte fossils from the Lower Cretaceous Yixian Formation of the Pingquan Basin, North China: stratigraphical correlation and palaeoenvironmental implications. *Lethaia* 52, 335–349.
- RIEK, E.F., 1976. A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum* 22, 791–820.
- RIEK, E.F. & KUKALOVÁ-PECK, J., 1984. A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. *Canadian Journal of Zoology* 62, 1150–1166.
- RONQUIST, F., KLOPFSTEIN, S., VILHELMSSEN, L., SCHULMEISTER, S., MURRAY, D.L. & RASNITSYN, A.P., 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology* 61, 973–999.
- SPASOJEVIC, T., BROAD, G.R., SAAKSJARVI, I.E., SCHWARZ, M., ITO, M., KORENKO, S. & KLOPFSTEIN, S., 2020. Mind the outgroup and bare branches in total-evidence dating: a case study of pimpliform Darwin wasps (Hymenoptera, Ichneumonidae). *Systematic Biology* 70, 322–339.
- SUVOROV, A., SCORNAVACCA, C. & FUJIMOTO, M.S., 2022. Deep ancestral introgression shapes evolutionary history of dragonflies and damselflies. *Systematic Biology* 71, 526–546.
- TILLYARD, R.J., 1918. Mesozoic insects from Queensland. 3. Odonata and Protodonata. *Proceedings of the Linnean Society of New South Wales* 43, 417–435.
- TILLYARD, R.J., 1925. The British Liassic dragonflies. *British Museum (Natural History), Fossil Insects, London*, 1, 1–39.

- TILLYARD, R.J. & DUNSTAN, B., 1916. Mesozoic and Tertiary insects of Queensland and New South Wales. Descriptions of the fossil insects and stratigraphical features. *Publications of the Geological Survey of Queensland* 253, 1–63.
- VEA, I.M. & GRIMALDI, D.A., 2016. Putting scales into evolutionary time: the divergence of major scale insect lineages (Hemiptera) predates the radiation of modern angiosperm hosts. *Scientific Reports* 6, 23487.
- WRIGHT, A.M., 2019. A systematist's guide to estimating Bayesian phylogenies from morphological data. *Insect Systematics and Diversity* 3, 1–14.
- YANG, S., 1999. The lower Mesozoic strata. In: KIM, J.-H. (ed.). *Geology of Korea*: Seoul, Sigma Press, 206–226.

Figure 1. *Koreatriassothemis elongatus* gen. et sp. nov., holotype BCM2081. Photographs. **A**, complete forewing; **B**, basal part, arrowhead base of IR2; **C**, apical part. Scale bars = 2 mm.

Figure 2. Nymph of 'Samarura-type'. Photographs. **A**, specimen GNUE112004 (part); **B**, GNUE112005 (counterpart). Scale bars = 2 mm.