

A new, large Permian Parelmoidae (Insecta, Megasecopteromorpha, Diaphanopteroidea) found in Shanxi Province (China)

Zi Q. XU, Nan YANG, Nozomu OYAMA,
Yanqi XU, Liyang DONG, Dong REN &
Olivier BÉTHOUX



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A new, large Permian Parelmoidea (Insecta, Megasecopteromorpha, Diaphanopteroidea) found in Shanxi Province (China)

Zi Q. XU
Nan YANG

College of Life Sciences, Capital Normal University,
105 Xisanhuanbeilu, Haidian District, Beijing (China)
15797685694@163.com
yangnan0504@qq.com

(these authors contributed equally to this work and should be considered co-first authors)

Nozomu OYAMA

Centre de recherche en paléontologie – Paris (CR2P), CNRS, MNHN,
Sorbonne Université, Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
and The Kyushu University Museum, 6-10-1 Hakozaki, Higashi-ku, Fukuoka 812-8581 (Japan)
oyama@g.fpu.ac.jp

Yanqi XU

Geological Survey of Jiangsu Province, 700 Zhujiang Road, Nanjing City, Jiangsu (China)
170215950@qq.com

Liyang DONG

Shanxi Natural History Museum, 17 North, West Binhe Road, Taiyuan city, Shanxi (China)
ryuunang_919@yeah.net

Dong REN

College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District,
Beijing, China
rendong@mail.cnu.edu.cn (corresponding author)

Olivier BÉTHOUX

Centre de recherche en paléontologie – Paris (CR2P), CNRS, MNHN,
Sorbonne Université, Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
olivier.bethoux@mnhn.fr

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ABSTRACT

The insect family Parelmoidea Rohdendorf, 1962 belongs to the extinct order Diaphanopteroidea Handlirsch, 1919, itself belonging to the larger taxon Megasecopteromorpha Béthoux *in* Yang,

KEY WORDS

Permian,
Cisuralian,
Palaeoptera,
China,
fossil insect,
wing venation,
vein translocation,
new genus,
new species.

MOTS CLÉS

Permien,
Cisuralien,
Palaeoptera,
Chine,
Insecte fossile,
nervation alaire,
translocation de nervure,
genre nouveau,
espèce nouvelle.

Ren & Béthoux, 2020. Although generally rare, representatives of this family are a typical component of Permian environments, particularly in the Cisuralian, with occurrence in renowned localities such as Obora, Elmo & Midco, and Chekarda. Here we describe a new Parelmoidea, *Grandelmoa jingqii* n. gen., n. sp., known from a well-preserved, isolated wing discovered from a new locality, named ‘Zhiyu’ (Shanxi Formation; Shanxi Province, China). The peculiar wing venation pattern of this new taxon is best explained by a translocation (as it is, of MP branches onto CuA), a phenomenon yet rarely documented among palaeopteran taxa. The new species occurs to be, by a small amount, the largest Permian Diaphanopteroidea known to date.

RÉSUMÉ

Un nouveau Parelmoidea (Insecta, Megasecopteromorpha, Diaphanopteroidea) du Permien, de grande taille, découvert dans la province du Shanxi (Chine).

La famille d’insectes Parelmoidea Rohdendorf, 1962 appartient à l’ordre éteint des Diaphanopteroidea Handlirsch, 1919, lui-même appartenant au plus grand taxon Megasecopteromorpha Béthoux *in* Yang, Ren & Béthoux, 2020. Bien que généralement rares, les représentants de cette famille sont une composante typique des environnements permien, particulièrement durant le Cisuralien, avec une occurrence dans des localités célèbres comme Obora, Elmo & Midco, et Chekarda. Nous décrivons ici un nouveau Parelmoidea, *Grandelmoa jingqii* n. gen., n. sp., connu par une aile isolée, bien conservée, découverte dans une nouvelle localité dénommée ‘Zhiyu’ (Formation Shanxi ; Province du Shanxi, Chine). La meilleure explication du patron de nervation alaire particulier du nouveau taxon implique une translocation (dans ce cas, d’une branche de MP sur CuA), un phénomène encore rarement documenté parmi les taxons de paléoptères. La nouvelle espèce est, de peu, le plus grand Diaphanopteroidea permien connu à ce jour.

INTRODUCTION

The insect order Diaphanopteroidea Handlirsch, 1906, known from Pennsylvanian and Permian strata, is particular among the extinct Rostroptera Kukalová-Peck *in* Wootton & Kukalová-Peck, 2000 (also referred to as Palaeodictyoptera Grimaldi & Engel, 2005, as in Prokop & Engel [2019]; and see Yang *et al.* 2020) for its ability to hold wings backward, along the abdomen, at rest (Carpenter 1992; Rohdendorf 1962), a trait regarded as a convergence with neopteran insects. The family Parelmoidea Rohdendorf, 1962, the most diverse diaphanopteroidean family, has been recovered from many renowned Permian localities, in particular from the Cisuralian, such as Obora, Elmo & Midco, and Chekarda, but also from the new, Shuiquan Gully locality, Shanxi Formation (Shanxi Province, China; Yang *et al.* 2024). Here, we describe a new isolated wing discovered from a new locality also belonging to the Shanxi Formation, near the Zhiyu Village. The new specimen, belonging to a new genus and species within Parelmoidea, is also the largest representative of this family.

MATERIAL AND METHODS

GEOLOGICAL SETTING

The new material (specimen CNU-DIA-SS-2024001) was collected from a new locality, namely ‘Zhiyu locality’ (Fig. 1), located near the Zhiyu Village, Shuocheng District, Shuozhou

City, Shanxi Province, North China (Fig. 1B). This locality belongs to the Shanxi Fm, composed of deposits of continental-oceanic interaction facies, with the main lithologies being sandstone, mudstone and thin coal seams, including coal seams No. 3 and 4-1 as identified by Kong *et al.* (1996) for the Shuocheng District section (coal seam No. 3, see p. 79, within a set of layers numbered ‘51’; coal seam No. 4-1, see p. 80, layer numbered ‘48’), bordered by the Taiyuan Formation and the Xiashihezi Formation (Fig. 1C; and see Yang *et al.* 2024), all part of the North China Block (NCB). More specifically, the new locality is part of the lower Shanxi Fm. The fossiliferous layer is a grayish, fine-grained siltstone layer (about 0.7 m) situated between a greyish-white layer of coarse-grained sandstone and the coal beds 4. Besides the recovered insect material, it contains few plant fragments (Kong *et al.* 1996).

The North China Block (NCB) is a series of deposits of continental – oceanic interaction facies, which were not simultaneous deposited throughout the area, and therefore the age of the Shanxi Formation on the NCB varies among different studies. Currently, the most accurate age range for the Shanxi Fm in the northern part of the NCB is 298.18 ± 0.32 to 295.346 ± 0.080 Ma, obtained for the Baode County using U-Pb data (Wu *et al.* 2021; Shen *et al.* 2022). This point provides a reliable inference on the age of the Zhiyu locality, because it is located in its vicinity. Moreover, the fossil locality is located along a line of sections of very similar age (points 1 to 8 in Shen *et al.* 2022). We can therefore regard the Zhiyu locality as early to middle Asselian.

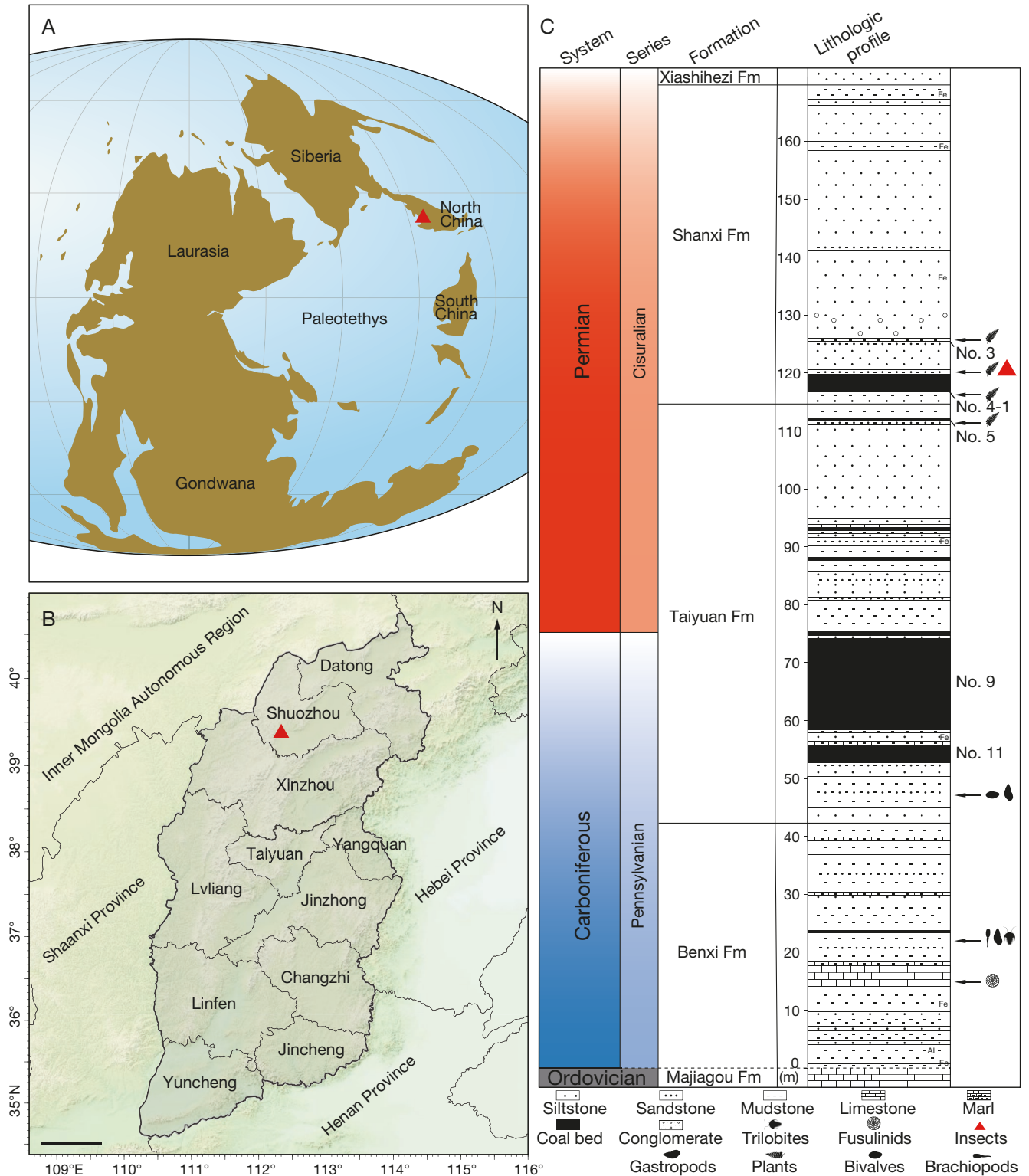


FIG. 1. — Geographic and stratigraphic information on the Zhiyu locality (red triangle): **A**, **B**, location of the collecting site; **A**, palaeogeographic map of Cisuralian; **B**, map of Shaanxi Province, China; **C**, chronological and stratigraphic framework of Pennsylvanian and Cisuralian strata according to Kong *et al.* (1996; including coal seams numbering), Shen *et al.* (2020), Shen *et al.* (2022) and Sun *et al.* (2022). Scale bar: 100 km (**B**). Palaeogeographic map of Cisuralian, redrawn by A. Lethiers (CR2P, Paris), from reconstruction by R. Blakey. All Chinese maps data source, Tianditu (<http://www.tianditu.gov.cn>, 2024/05/08). Silhouettes in **C** are from PhyloPic, unaltered, courtesy of Jagged Fang, Ben Moon, Felix Vaux, Katie S. Collins, T. Michael Keesey, and Ferran Sayol (CC BY 3.0).

DOCUMENTATION OF FOSSIL MATERIAL

The new specimen was collected from a locality near Zhiyu village, Shuozhou City, Shanxi Province, China (Kong *et al.* 1996; Shen *et al.* 2020; Shen *et al.* 2022). It is housed at the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), Beijing, China, and bears the specimen number CNU-DIA-SS-2024001.

The specimen was photographed using a Canon EOS 5D Mark IV digital camera (Canon, Tokyo, Japan) coupled with a Canon MP-E 65 mm macro lens, under both dry and ethanol conditions. Original photographs were optimized using Adobe Photoshop CS6. In addition, Reflectance Transformation Imaging (RTI) files of the complete wing and of the wing base were generated for each side of the specimen, and are accessible from an online Dryad repository (Xu *et al.* 2025). These files were generated using a Fly Dome automated light dome, ~30 cm diameter and equipped with 54 LEDs arranged in three rows (Fly Dome, Paris, France), driving a Canon EOS 5DS digital camera, itself coupled to a Canon MP-E 65 mm macro lens. Original photographs were then optimized using Adobe Photoshop CS6 prior to RTI processing, itself achieved using the RTI builder software (Cultural Heritage Imaging). In details, the entire set of photographs was used to compute RTI files of complete wing, but only 42 photographs were used to compute RTI files of the wing base, for the Canon MP-E 65 mm macro lens, once deployed, prevented light from LEDs of the upper ring from reaching the specimen surface.

The photograph reproduced on Fig. 2 was generated by combining a RTI snapshot under a setting with a low-angle of incidence (of the side 'b' of the specimen -its negative imprint) and photographs taken under dry conditions under zenithal light (both sides) ('RTI-dry-dry' composite).

TERMINOLOGY

We follow standard wing venation terminology and abbreviations, as follows:

AA	Analís anterior;
AP	Analís posterior;
Cu	Cubitus;
CuA	Cubitus anterior;
cua-cup	first cross-vein in the area between CuA and CuP;
CuP	Cubitus posterior;
M	Media;
MA	Media anterior;
MP	Media posterior;
R	Radius;
RA	Radius anterior;
RP	Radius posterior;
rp-ma	first cross-vein to connect RP and MA;
ScP	Subcosta posterior.

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
 ROSTROPALAEOPTERA
 Kukalová-Peck *in* Wootton & Kukalová-Peck, 2000
 MEGASECOPTEROMORPHA
 Béthoux *in* Yang *et al.*, 2020

Order DIAPHANOPTERODEA Handlirsch, 1906

Family PARELMOIDAE Rohdendorf, 1962

TYPE GENUS. — *Parelmoo* Carpenter, 1947.

INCLUDED GENERA. — *Diapha* Kukalová-Peck, 1974; *Elmodiapha* Kukalová-Peck, 1974; *Paradiapha* Kukalová-Peck, 1974; *Permelmoa* Prokop & Nel, 2011; *Permiodiapha* Kukalová-Peck, 1974; *Permuralia* Sinichenkova & Kukalová-Peck, 1997; *Protodiapha* Kukalová-Peck, 1974; *Pseudelmoa* Carpenter, 1947; *Stenodiapha* Kukalová-Peck, 1974; *Sinoelmoa* Yang, Cui, Xu & Béthoux, *in* Yang *et al.* (2024); and *Grandelmoa* n. gen.

Genus *Grandelmoa*

Xu, Yang, Oyama, Ren & Béthoux, n. gen.

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TYPE SPECIES. — *Grandelmoa jingqii* Xu, Yang, Oyama, Ren & Béthoux, n. sp.

DIAGNOSIS. — By monotypy, same as for the type species. Gender feminine.

ETYMOLOGY. — The genus name derives from the Latin '*grandis*', referring to the large size of the type species, as the largest individual in the family Parelmoidea, and the genus *Elmoa* Tillyard, 1937.

Grandelmoa jingqii

Xu, Yang, Oyama, Ren & Béthoux, n. gen., n. sp.

(Fig. 2)

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TYPE MATERIAL. — Holotype (by monotypy): China • North China, Shanxi Province, Shuozhou City, Shuocheng District, Zhiyu Village, Zhiyu locality; 39°24'11"N, 112°21'46"E; 26.III.2023; Jingqi Zhang leg.; CNU-DIA-SS-2024001.

DIAGNOSIS. — ScP long, ending beyond the second fork of RP; MA/MP split distal of the RA/RP split, itself located in a very basal position; cua-cup cross-vein located distally (distal to the RA/RP split) and basal to MA/MP split; CuP forked; anal area well-developed, with 10 terminal branches; two gradate rows of cross-veins, sub-parallel to the posterior wing margin.

ETYMOLOGY. — Named after Jingqi Zhang, the collector of type specimen. The specific epithet is to be treated as a noun in genitive case.

TYPE LOCALITY AND STRATIGRAPHY. — Zhiyu locality, between coal seam layers no. 3 and 4-1 (following numbering by Kong *et al.* 1996); Shanxi Formation; Permian, Cisuralian, Asselian (Kong *et al.* 1996; Shen *et al.* 2020; Shen *et al.* 2022).

MEASUREMENTS. — Wing length 22.7 mm, width 7.6 mm.

DESCRIPTION

Positive and negative imprints of a complete right wing, possibly a forewing; veins elevation sharply contrasted in the basal half, and attenuated more distally; near wing base, ScP long, ending on RA beyond the second RP fork; stem of R+M convex, with a conspicuous inflexion opposite the point of

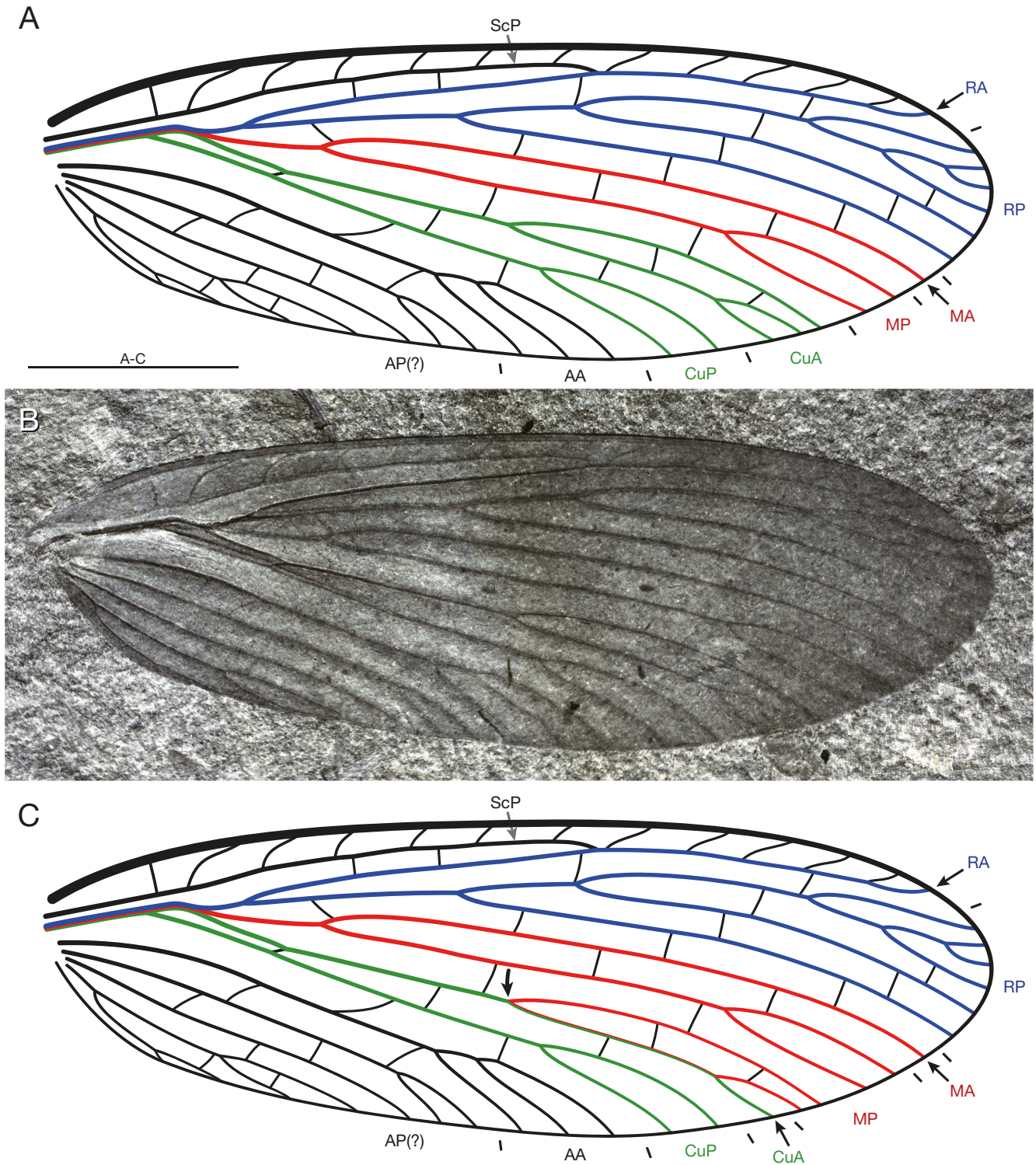


FIG. 2. — *Grandelmoa jingqii* n. gen., n. sp., holotype, specimen CNU-DIA-SS-2024001: **A**, drawing under the 'branched CuA' interpretation; **B**, photograph ('RTI-dry-dry' composite); **C**, drawing under the 'translocated MP branch' interpretation (large black arrow indicating translocation). Scale bar: 5 mm.

separation of R and M (located about 4.0 mm distal from wing base); RA convex, simple and strong, almost parallel to anterior wing margin; RP with 6 terminal branches, with the two first posterior ones simple; MA/MP split located behind the RA/RP split; MA diverging somewhat obliquely (i.e. M and MP are aligned); rp-ma cross-vein long and oblique,

located just distal of the MA/MP split; MA simple; MP forked distally, with 4 branches, 2 of them successively arising from CuA (under the 'translocated MP branch' interpretation; see Fig. 2C and Remarks section); short Cu stem, distinct from (R+)M, distinguishable; CuA diverging obliquely from Cu, then running close and parallel to R+M stem for some

distance, suddenly diverging posteriorly, very close to the R/M split; CuA simple (under the ‘translocated MP branch’ interpretation; see Fig. 2C and Remarks section); CuP forked distally (distal to first point of emergence of MP branches translocated onto CuA); CuA–CuP area narrow until the first cross-vein occurring in this area, which is short and strong, located slightly distal to RA/RP split and basal to MA/MP split; anal area very well-developed, with a total of ten terminal branches (AA with 3 terminal branches; AP(?) with 7 terminal branches); 12 oblique, sigmoidal veinlets evenly dispersed in the area between anterior margin and ScP/RA; two gradate rows of cross-veins paralleled with each other.

REMARKS

A seemingly branched CuA is present in the new specimen (‘branched CuA’ interpretation; see Fig. 2A). However, a branched CuA is extremely rare in Megasecopteromorpha. Based on our literature search, the only known cases are two isolated wings belonging to the Parelmoidea species *Stenodiapha moravica* Kukalová-Peck, 1974 (see original description). However, a translocation of a branch of MP onto CuA, coupled with a pectinate fusion, is an alternative, plausible interpretation. Vein translocation has been documented in many different taxa of Neoptera, and in particular in orthopterans (Béthoux 2007, 2012) and grylloblattodeans (Cui *et al.* 2015). Translocation can also lead to a ‘pectinate fusion’, and one of the best examples is the organisation of the radial system in dictyopterans (Guo *et al.* 2013). Such transformation is also known in Hemerobiidae Leach, 1815 (neuropterans; among others, see Carpenter [1940], Aspöck *et al.* [1980]) and some orthopterans (Béthoux 2012). Such transformations are apparently less common among palaeopteran taxa, but it can be considered established in Spilapteridae Brongniart, 1893 (Rostropalaeoptera; Liu *et al.* 2015; Sinitshenkova 2025). Bearing this in mind, a translocation of a posterior branch of MP, with a partial fusion of its posterior branch with CuA, is a plausible explanation for the morphology observed in the specimen CNU-DIA-SS-2024001 (‘translocated MP branch’ interpretation; Fig. 2C). Moreover, in known Parelmoidea, MP usually has two or three branches, and rarely four. Under the ‘branched CuA’ interpretation (Fig. 2A), the specimen would then have a two-branched MP, which is incongruous, given its large size (relative to other Parelmoidea), very generally implying a relatively higher number of vein branches. Conversely, if the first two anterior branches of the seemingly branched CuA are assigned to MP (assuming translocation and pectinate fusion), the latter vein then has a total of four branches, more consistent with its size. It must be noted that veins elevation in this area of the wing is homogeneous, and therefore does not provide insights on the nature of the corresponding veins. In summary, the ‘translocated MP branch’ interpretation provides a plausible answer to the peculiar configuration observed in the specimen CNU-DIA-SS-2024001. It remains unclear whether a translocation of a MP branch is an unusual or a usual feature of the corresponding species.

DISCUSSION

SYSTEMATIC PLACEMENT

According to Yang *et al.* (2024; and references therein), the combination of the character states ‘long fusion of Cu/CuA with R+M (or, CuA running very close to R+M for some distance)’ and ‘occurrence of a very short and strong cua-cup cross-vein’ allows assigning the species to which the new specimen belongs to the families Parelmoidea or Elmoidae Tillyard, 1937, within Diaphanopteroidea. Then, two main character states allow distinguishing it from the Elmoidae, namely ‘long ScP, ending on RA beyond the wing mid-length’ and ‘a very well-developed anal area’.

Characters relevant to the placement of the species to which the new specimen belongs are summarized in Table 1, showing that it displays a unique combination of traits. Among them, the position of cua-cup cross-vein is worthy of attention. It is located between the RA/RP split and the MA/MP split in the new specimen, a state shared only with *Sinoelmoa* (Yang *et al.* 2024; Shuiquan Gully locality; China; Cisuralian, Asselian), and *Protodiapha* (Kukalová-Peck 1974; Obora; Czech Republic; Cisuralian, Sakmarian). However, the wing lengths of species belonging to these genera are much smaller than in the new specimen. The new specimen further differs from *Sinoelmoa* by several traits (Table 1), including the presence of clear veinlets in the area between ScP and the anterior wing margin, ScP remaining strong distally (as opposed to ‘vanishing’), and the presence of a rp-ma cross-vein (instead of a fusion of RP and MA). As for *Protodiapha*, the new specimen also differs from this genus by well distant RP and MA, and the lack of dark spots on the wing membrane, among other traits (see Table 1).

Another relevant trait is the development of the anal area, which is large in many genera of Parelmoidea. However, this area is even more extensively developed in the new specimen. In this trait, it compares, to some extent, with *Pseudelmoa* (Elmo & Midco; USA; Cisuralian, Artinskian). Nevertheless, the larger size implies that the new material belongs to another taxon. Another prominent trait is the position of the RA/RP split. It is located basally in the genera *Parelmoa* and *Pseudelmoa*, but it is even more basal in the new specimen. Finally, as mentioned above, it is not unlikely that a translocation of a branch of MP onto CuA is a usual feature of the species to which belongs the new specimen, in which case it would compose a very unique trait. In summary, it is legitimate to erect a new genus and species for the new material.

SIZE ASPECT

A general trend of size reduction has been documented for the Megasecoptera (Nel *et al.* 2023) and likely affected the entire Rostropalaeoptera, including Diaphanopteroidea. It is therefore significant to unravel a large-sized Diaphanopteroidea from Permian strata. To date, the largest known Permian member of this order is *Eumartynovia raaschi* Carpenter, 1947 (family Martynoviidae Tillyard, 1932; Elmo & Midco locality), with a wing length of 22.5 mm. Therefore, with a wing length

TABLE 1. — Characters (and their states) relevant for the Parelmoidea systematics at the genus level and for the placement of the new taxon (framed). Taxon authorships are indicated p. 708.

	Wing length (mm)	Coloration	Position of cua-cup	Well-developed veinlets in the area between ScP and the anterior margin	Ending of ScP	Relation of RP and MA
<i>Diapha</i>	14–18.7	×	basal to the RA/RP split and MA/MP split	✓	reaching RA beyond wing mid-length	fusion
<i>Elmodiapha</i>	18.4–21.4	×	variable	✓	reaching RA beyond wing mid-length	no fusion, long rp-ma
<i>Grandelmoa</i> n. gen.	22.7	×	between the RA/RP split and the MA/MP split	✓	remaining strong distally, reaching anterior margin	no fusion, long rp-ma
<i>Paradiapha</i>	13.4	×	basal to the RA/RP split and MA/MP split	✓	reaching RA beyond wing mid-length	fusion
<i>Parelmoo</i>	12.3–16.1	×	basal to the RA/RP split and MA/MP split	✓	reaching RA beyond wing mid-length	no fusion, long rp-ma
<i>Permelmoa</i>	12.7	×	between the RA/RP split and the MA/MP split	×	remaining strong distally, reaching anterior margin	no fusion, long rp-ma
<i>Permodiapha</i>	12.9–16.3	dark spots on wing membrane, variable	basal to the RA/RP split and MA/MP split	✓	reaching RA beyond wing mid-length	fusion
<i>Permuralia</i>	13.5–18.0	×	basal to the MA/MP split and RA/RP split	✓	reaching RA beyond wing mid-length	fusion
<i>Protodiapha</i>	13.5	dark spots on wing membrane, variable	variable	✓	reaching RA beyond wing mid-length	no fusion, short rp-ma
<i>Pseudelmoa</i>	19.6	×	opposite the RA/RP split and basal to the MA/MP split	✓	reaching RA beyond wing mid-length	no fusion, long rp-ma
<i>Sinoelmoa</i>	18.2 (estimated)	dark area between RA and the anterior margin	between the RA/RP split and the MA/MP split	×	vanishing between RA and anterior margin	RP briefly touching MA
<i>Stenodiapha</i>	15.5–20.2	×	variable	✓	reaching RA beyond wing mid-length	fusion

of 22.7 mm, *Grandelmoa jingqii* n. gen., n. sp. is the largest known Permian Diaphanopteroidea (and also the largest Parelmoidea; with *Elmodiapha ovata* Kukalová-Peck, 1974, from Obora, being the second largest, with a wing length of 21.4 mm). This discovery, made in a new locality, shows that our documentation of this insect group remains largely incomplete.

Data archival statement

A Dryad dataset including four RTI files of the new material is available at <https://doi.org/10.5061/dryad.2bvq83c09>

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Competing interests

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: DR and OB; Investigation: ZX, NY, YX, NO, LD and OB; Resources: DR; Writing – original draft preparation: NY and OB; writing – review and editing: ZX, NY, NO, DR and OB; visualization: ZX, NY and OB; supervision: DR; project administration: DR; funding acquisition: DR All authors have read and agreed to the published version of the manuscript.

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