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Original article

# New damsel-dragonflies with “calopterygid”-like wing shape from the Middle Jurassic of China (Odonata: Isophlebioidea: Campterochlebiidae)<sup>☆</sup>



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## ABSTRACT

The new damsel-dragonflies *Zygokaratawia incompleta* nov. sp. and *Parazygokaratawia azari* nov. gen., nov. sp., closely related to the campterochlebiid genus *Zygokaratawia*, are described from the Middle Jurassic locality of the Daohugou and Chentaizi villages, respectively (Ningcheng County, Inner Mongolia, NE China). *Parazygokaratawia* nov. gen. and *Zygokaratawia* share a narrowly reduced cubito-anal area, unique synapomorphy in the Isophlebioptera. Campterochlebiids with this character are only known from the Daohugou biota.

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## 1. Introduction

The insect order Odonata is divided into two main clades: Zygoptera (damselflies) and Epiproctophora, a clade that comprises several extinct clades as well as the living Epiophlebiidae (damsel-dragonflies) and the Anisoptera (true dragonflies) (Bechly, 1996). The Isophlebioidea is one of the most diverse clades of Mesozoic damsel-dragonflies. Their oldest-known representatives are found in Late Triassic–Early Jurassic strata and the youngest in the Late Cretaceous. The family Campterochlebiidae is the largest family of this clade (Nel et al., 1993; Bechly, 1996). Ten campterochlebiid genera are currently known from the Middle Jurassic–Lower Cretaceous of north China (Zheng et al., 2016, 2017). Among them, one of the most curious is the genus *Zygokaratawia* Nel et al., 2008, characterized by very narrow hindwings with narrow cubito-anal area. This particular wing shape is looking like that of a modern Calopterygoidea. Here, we describe two new taxa with similar wing shapes from the same

locality of Daohugou (Ningcheng County, Inner Mongolia, NE China).

## 2. Material and methods

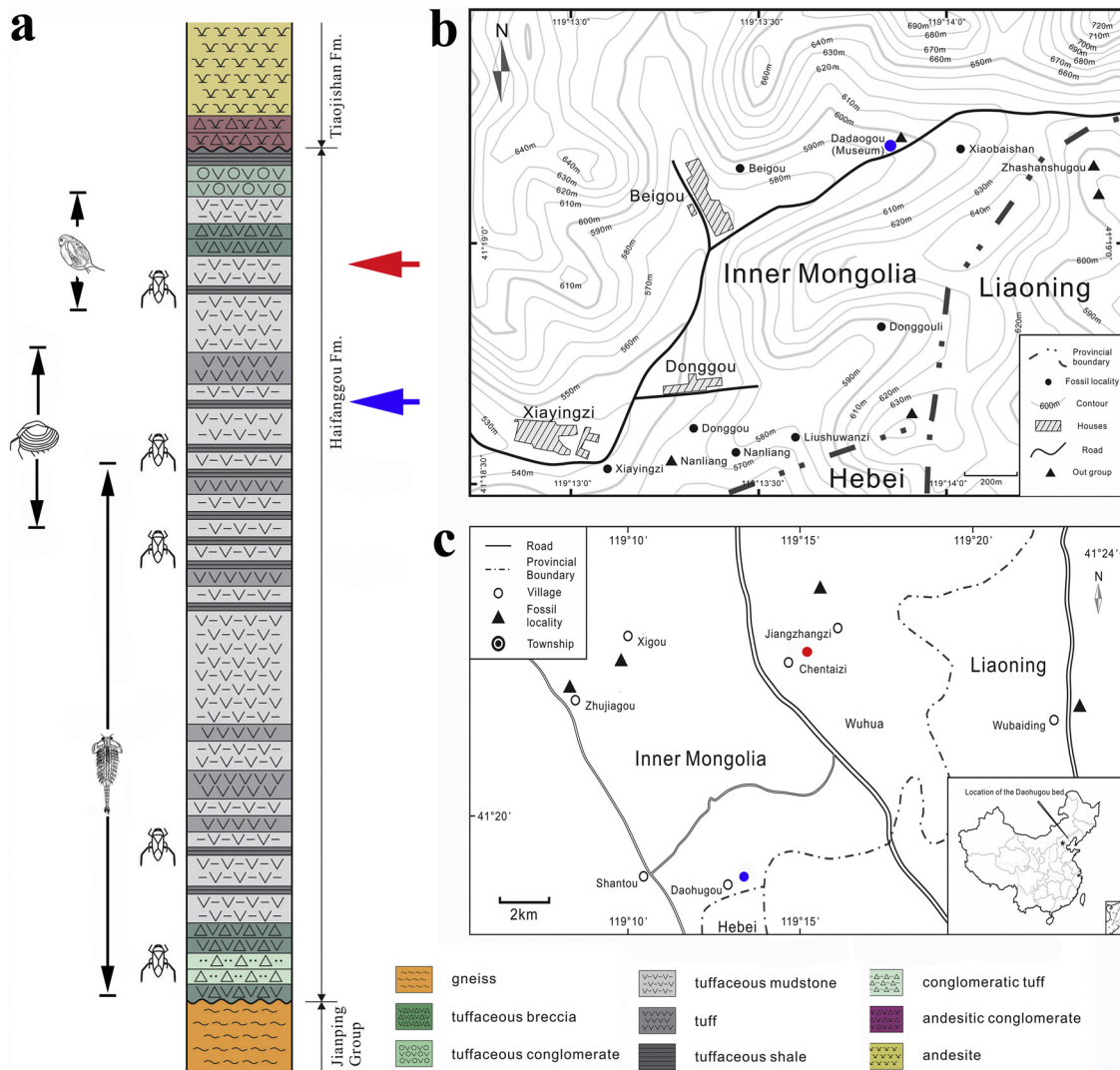
The type specimens were prepared with a steel needle under microscope. Photographs were taken using a Nikon 5d2 camera. The type specimen of *Zygokaratawia incompleta* nov. sp. is preserved in a whitish tuffaceous shale associated with lots of conchostracans of the genus *Euestheria*, indicating that it comes from the Dadaogou Layer near the Daohugou Village where the outcrops are now covered by the Museum. It comes from an upper layer of the Daohugou beds. The type specimen of *Parazygokaratawia azari* nov. gen., nov. sp., is preserved in a grayish tuffaceous shale associated with lots of cladocerans, indicating that it comes from the topmost layers of the Daohugou beds near the Chengtaizi Village (Fig. 1).

The nomenclature of the odonatan wing venation used in this paper is based on the interpretations of Riek and Kukalová-Peck (1984), modified by Nel et al. (1993) and Bechly (1996). The higher classification of fossil Odonatoptera, as well as family and generic characters followed in the present work, are based on the phylogenetic system proposed by Bechly (1996). Wing abbrevia-

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**Fig. 1.** Log and map of the fossil localities. **a:** Daohugou beds as divided by fossil Branchiopoda; blue arrow: layer with *Zygozaratawia incompleta* nov. sp.; red arrow: layer with *Parazygozaratawia azari* nov. gen., nov. sp.; **b:** map showing the fossil localities near Daohugou village; blue spot: location for *Zygozaratawia incompleta* nov. sp.; **c:** map of the Daohugou fossil bed outcrops; blue spot: layer with *Zygozaratawia incompleta* nov. sp.; red spot: layer with *Parazygozaratawia azari* nov. gen., nov. sp.

tions are as follows: AA, analis anterior; AP, analis posterior; Arc, arculus; Ax, primary antenodal crossvein; CuA, cubitus anterior; CuP, cubitus posterior; d, discoidal cell; IRx, intercalary radial veins; MA, median anterior; MP, median posterior; N, nodus; Pt, pterostigma; RA, radius anterior; RP, radius posterior.

### 3. Systematic palaeontology

Order Odonata Fabricius, 1793

Superfamily Isophlebioidea Handlirsch, 1906

Family Campteropteroidea Handlirsch, 1920

**Remark:** The list of campteropteroideid genera is available on the internet site Fossilworks ([http://fossilworks.org/bridge.pl?a=taxonInfo&taxon\\_no=176742](http://fossilworks.org/bridge.pl?a=taxonInfo&taxon_no=176742)).

Genus *Zygozaratawia* Nel et al., 2008

**Type species:** *Zygozaratawia reni* Nel et al., 2008.

**Other species:** *Zygozaratawia incompleta* nov. sp.

*Zygozaratawia incompleta* nov. sp.

Fig. 2

**Derivation of the name:** named after the incomplete state of preservation of the type, as only hindwings are preserved.

**Holotype:** Specimen NIGP167276 (a thorax with two hindwings and the two-third of the abdomen attached), stored at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

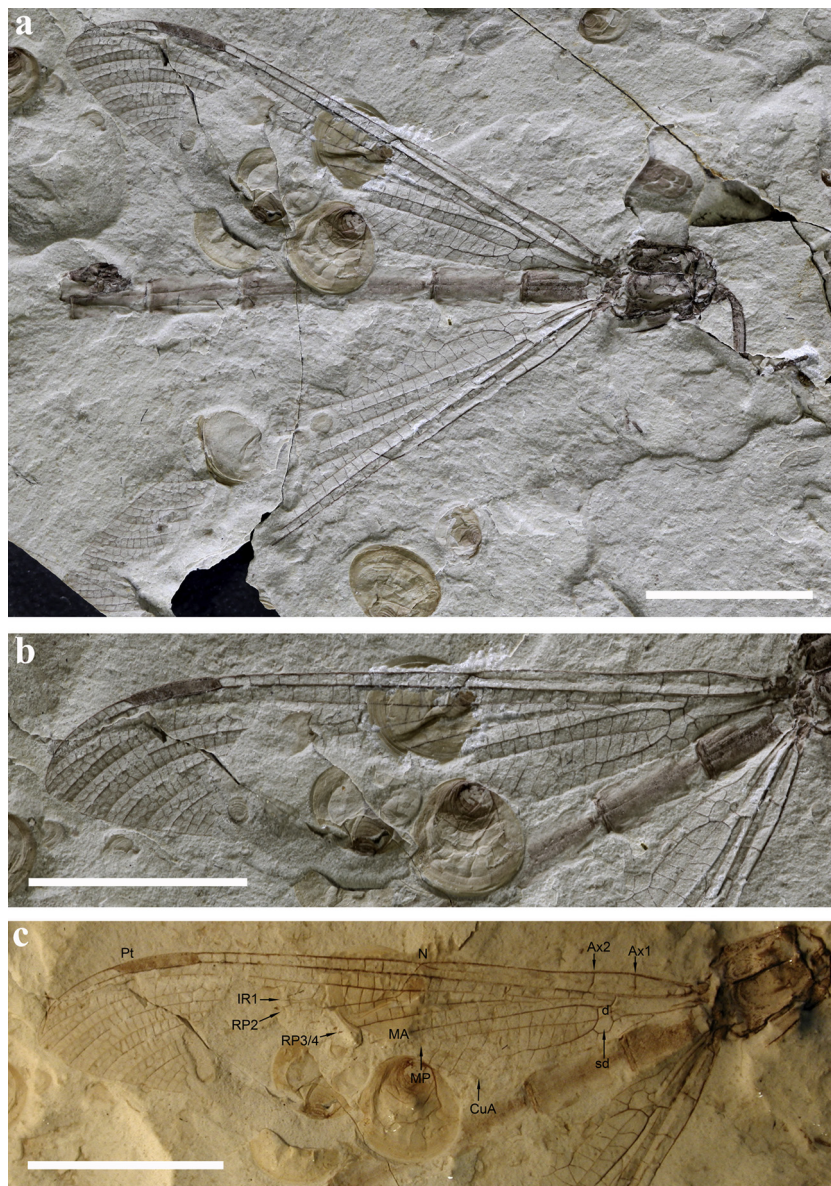
**Type locality:** Near the Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, NE China.

**Type horizon:** Lowest Upper Jurassic, Haifanggou Formation (ca. 162–163 Ma); Inner Mongolia, NE China.

**Diagnosis:** Hindwing pterostigma strongly basally recessed, with ten cells between C and RA distal of pterostigma; 12 post-nodals; 12 crossveins in antesubnodal area; a strongly oblique crossvein between MAa and base of RP3/4; 10 crossveins in Bq space.

**Description:** Thorax large, 4.4 mm wide, 5.2 mm long, but compressed. Hindwing hyaline, 33.3 mm long, 7.5 mm wide, widest part at level of nodus; distance between base and arculus 4.4 mm, arculus and nodus 10.0 mm, nodus and pterostigma 11.2 mm, pterostigma and apex 5.3 mm; a rather long petiole, 2.4 mm long, 1.4 mm wide; anal area very narrow, 3.1 mm long, 0.7 mm wide, nearly triangular in shape, with one row of irregular cells between AA and AP; no anal angle but AP weakly curved (female specimen); no membranule; AA distally strongly bent towards posterior wing margin and nearly parallel with MP+CuA,





**Fig. 2.** *Zygokaratawia incompleta* nov. sp., holotype, NIGP167276. **a:** complete habitus; **b:** right hindwing, dry. **c:** right hindwing, under alcohol. Scale bars: 1 cm.

distally fused with CuAb; median and submedian areas free; curved vein CuP just basal to Ax1; subdiscoidal area transverse, posteriorly closed, short and broad, with one crossvein, 1.4 mm long, 0.9 mm wide; discoidal cell basally closed, 0.7 mm long, 0.5 mm wide, free of crossveins, length of proximal side 0.4 mm; RP+MA separates at approximately a right angle from RA and strongly curved in arculus; RP separated from MA 0.3 mm distally; MA basally strong and divided into MAa and MAb 0.7 mm distally; MAb short, 0.8 mm long, aligned with distal free part of CuA; MP+CuA separated into MP and CuA at distal end of MAb; distal free part of CuA strong, separating from MP 5.4 mm from wing base and extends towards posterior wing margin for 0.5 mm; CuA distally divided into CuAa and CuAb, CuAb short, 0.4 mm long, extending towards basal wing margin and meeting main branch of AA; CuAa basally more or less parallel to posterior wing margin with only one row of cells between them; CuAa short, ending on posterior wing margin about 6.7 mm from its base, well before nodus level; area between CuAa and MP with one row of cells, 1.4 mm wide; distal of end of CuAa, area between MP and posterior wing margin very long and broad; MP nearly straight, reaching posterior margin well distal of nodus level, ca. 22.0 mm from wing

base; MAa parallel with MP, nearly straight in its basal part, postdiscoidal area 0.9 mm wide, with one row of cells; Ax1 0.35 mm basal of arculus, nearly perpendicular to ScP; Ax2 2.1 mm distal of arculus, oblique; no secondary antenodal crossveins between C and ScP, but seven secondary antenodal crossveins between ScP and RA distal of Ax2; 12 crossveins in area between RA and RP, between arculus and nodus; base of RP3/4 0.35 mm distal of arculus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 1.5 mm distally; no antefurcal crossvein in space between RP and MA basal to midfork (base of RP3/4), except for a very oblique crossvein between MAa and base of RP3/4; 12 postnodal crossveins between C and RA; 11 postsubnodal crossveins between RA and RP1 not aligned with postnodals; pterostigmal brace rudimentary, not oblique and not well-aligned with basal side of pterostigma; four crossveins below pterostigma; pterostigma sclerotized, 4.4 mm long, 0.65 mm wide; pterostigma rather basally recessed with 10 cells between C and RA distal of it; RP2 aligned with subnodus; 10 crossveins in Bqr space between RP, RP2, IR2 and first oblique vein "O"; oblique vein "O" 2.3 mm and four cells distal of base of RP2; RP2 nearly straight; base of IR1 five cells distal of base of RP2; IR1 basally weakly zigzagging but distally

nearly straight, more or less parallel to RP1; area between MA and RP3/4 much wider distally, with 17 rows of cells along posterior wing margin; area between RP3/4 and IR2 as broad basally as distally, with one row of cells basally and two distally; area between IR2 and RP2 with one row of cells and distally seven rows near posterior wing margin; area between RP2 and IR1 progressively widened, with one zigzagging intercalary longitudinal vein and 2–3 rows of cells between them; area between IR1 and RP1 not distally widened, with 3–4 rows of cells between them.

Abdomen with only seven basal segments preserved, 2.1 mm wide, no secondary male genital apparatus on second segment.

**Remarks:** *Zygokaratawia incompleta* nov. sp. has hindwings very similar to those of the campterophlebiid *Zygokaratawia reni* Nel et al., 2008, also from the same outcrop (Nel et al., 2008). The differences between the two fossils are as follows: pterostigma more basally recessed in *Z. incompleta* nov. sp. than in *Z. reni*, with ten cells between C and RA distally in *Z. incompleta* nov. sp. against only four in *Z. reni*; 12 postnodals for *Z. incompleta* nov. sp. instead of ten for *Z. reni*; 12 crossveins in antesubnodal area in *Z. incompleta* nov. sp. instead of five in *Z. reni*; a strongly oblique crossvein between MAa and base of RP3/4 in *Z. incompleta* nov. sp., absent in *Z. reni*; 10 crossveins in Bqr space of *Z. incompleta* nov. sp. instead of five in *Z. reni*.

Among the campterophlebiids with a venation relatively similar to that of *Zygokaratawia*, *Z. incompleta* nov. sp. differs from *Sarytashia Pritykina*, 1970 in RP2 without a pronounced distal curve and different shape of secondary veins between IR1 and RP1. *Adelophlebia Pritykina*, 1980 is known by the forewing base but it differs from *Z. incompleta* nov. sp. in the presence of two rows of cells in the postdiscoidal area (Pritykina, 1970, 1980; Nel et al., 1993). *Zygokaratawia incompleta* nov. sp. differs from *Ctenogamp-sophlebia Petrulevičius* et al., 2011 in the shorter discoidal cell, presence of well-defined longitudinal secondary vein between IR1 and RP1, longer pterostigma, and broader area between CuAa and MP (Petrulevičius et al., 2011). For the comparison with *Parazygokaratawia* nov. gen., see below.

Genus *Parazygokaratawia* nov. gen.

**Derivation of the name:** A combination of ‘para’ and the genus name *Zygokaratawia*, indicating the strong similarity between these two genera.

**Type and only known species:** *Parazygokaratawia azari* nov. gen., nov. sp.

**Diagnosis:** Fig venation characters only. Hindwing subdiscoidal space small and posteriorly closed; cubito-anal and anal areas very narrow in both forewings and hindwings; a long basal part to CuA before its branches; area between MP and CuA as broad as postdiscoidal area, which is distally constricted; MP straight; MAa zigzags and becomes much weakened distally; CuAa short; pterostigma not basally recessed; area between RP3/4 and IR2 widened along posterior wing margin; base of RP2 not aligned with subnodus; IR1 basally straight; only one row of cells between IR1 and RP1 between its base and pterostigma; Ax2 perpendicular to ScP in hindwing.

*Parazygokaratawia azari* nov. gen., nov. sp.

Figs. 3–4

**Derivation of the name:** Named after our colleague and friend, Prof. Dany Azar.

**Holotype:** Specimen NIGP167528 (imprint), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

**Type locality:** Near the Chentaizi Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, NE China.

**Type horizon:** Lowest Upper Jurassic, Haifanggou Formation (ca. 161–162 Ma); Ningcheng County, Inner Mongolia, NE China.

**Diagnosis:** As for the genus. Six secondary antenodal crossveins between ScP and RA distal of Ax2; in forewing 10 postnodal

crossveins between C and RA not aligned with 10 postsubnodal crossveins between RA and RP1 basal of pterostigma.

**Description:** a fragment of thorax, with two forewings and one hindwing connected.

Forewing hyaline; 30.8 mm long, 6.0 mm wide; distance between base and arculus 4.0 mm, arculus and nodus 10.0 mm, nodus and pterostigma 12.4 mm, pterostigma and apex 3.2 mm; a short petiole 1.6 mm long, 1.0 mm wide; one row of cells between posterior wing margin and AA; AA parallel to MP+Cu; median and submedian areas free; a curved strong vein CuP between submedian and subdiscoidal areas, lying well basal of arculus; subdiscoidal space free of crossveins, rather transverse; discoidal space basally opened; RP + MA separated at nearly a right angle from RA in arculus, strongly curved; RP separated from MA 0.1 mm distally; RP and MA well parallel; MAb rather short, ca. 0.6 mm long, well aligned with distal free part of CuA; CuA separated from MP ca. 5.0 mm from wing base and directed towards posterior wing margin for 0.2 mm; distal free part of CuA strong, CuA distally fused with AA; CuA divided into a very short CuAb directed towards posterior wing margin and CuAa basally more or less parallel to posterior wing margin and distally delimitating a short and narrow cubito-anal area, with 1–2 posterior branches and 1–2 rows of cells at its broadest part; apex of CuA 1.5 mm basal to nodus level; area between CuA and MP with one row of cells; distal of apex of CuA, area between MP and posterior wing margin very long and broad; MP nearly straight, reaching posterior wing margin well distal of nodus level; MAa more or less parallel to MP, nearly straight in basal half but slightly zigzags distal of subnodus level; postdiscoidal area with one row of cells, 1.0 mm wide near discoidal cell and 0.8 mm at apex of MAa; Ax0 well-preserved very close to wing base; Ax1 0.6 mm basal of arculus, nearly perpendicular to ScP and R + MA, Ax2 well distal of arculus, also perpendicular to ScP and RA, 2.6 mm distal of Ax1; no secondary antenodal crossveins between C and ScP; six visible secondary antenodal crossveins between ScP and RA distal of Ax2; 10 post-nodal crossveins between C and RA not aligned with 10 post-subnodal crossveins between RA and RP1 basal to pterostigma; seven preserved crossveins in area between RA and RP, between arculus and nodus; base of RP3/4 3.0 mm distal of arculus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 0.5 mm distally; no visible antefurcal crossvein in space between RP and MA basal to midfork (base of RP3/4); subnodus oblique and well aligned with nodal crossvein Cr; RP2 three cells distal of subnodus; Bqr space between RP, RP2, IR2 and oblique vein “O” long and narrow, with one row of cells and six crossveins; oblique vein “O” nearly perpendicular to RP2 and IR2, one cell distal of RP2 base; RP2 nearly straight in its preserved part; base of IR1 four cells distal of base of RP2; IR1 basally straight and distally curved, more or less parallel to RP1, with one row of cells between them until the apex of pterostigma; area between MA and RP3/4 much widened distally, with several long intercalary longitudinal veins; area between RP3/4 and IR2 widened distally with an intercalary longitudinal vein zigzagging between them; area between IR2 and RP2 very narrow, without any intercalary longitudinal vein between them; pterostigma 2.0 mm long, 0.6 mm wide, covering two cells; pterostigmal brace neither aligned with basal side of pterostigma nor strongly oblique.

Hindwing hyaline; distinctly shorter than forewing, 26.0 mm long, 5.6 mm wide, widest part at nodus level; distance between base and arculus ca. 2.5 mm (arculus not preserved), between arculus and nodus ca. 7.9 mm, nodus and pterostigma 10.3 mm, pterostigma and apex 3.2 mm; a very short petiole, 0.8 mm long, 0.5 mm wide; anal area not visible, but probably very narrow and triangular in shape, with one row of irregular cells between AA and AP; no anal angle (female specimen); no membranule; AA distally bent towards posterior wing margin and nearly parallel to



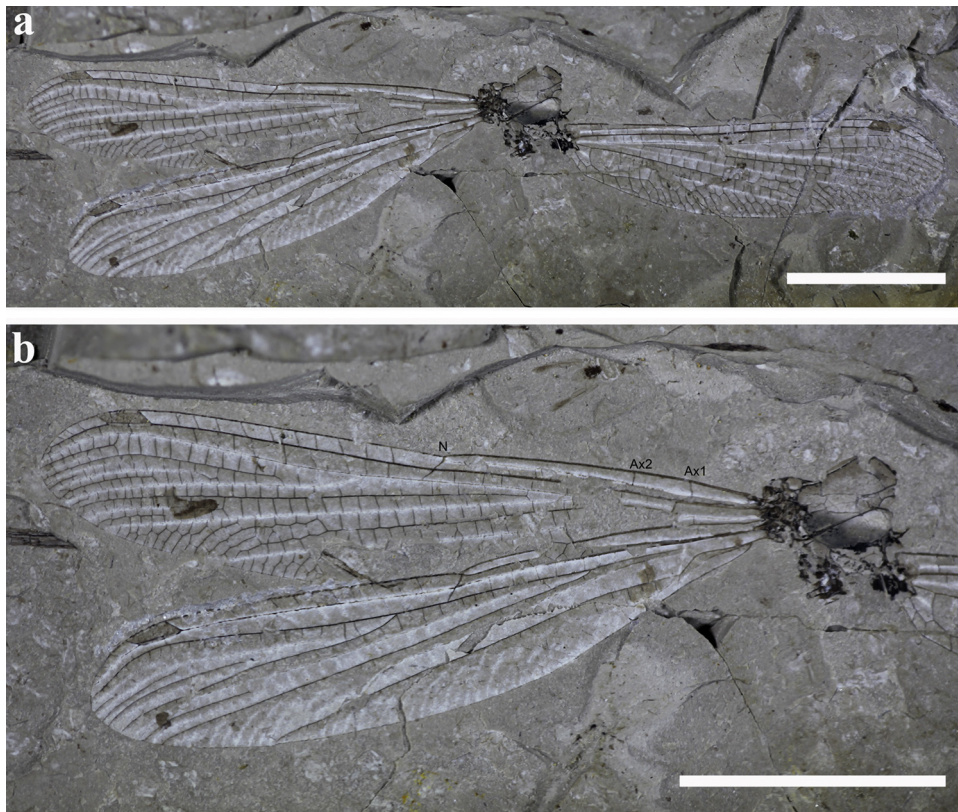


Fig. 3. *Parazygokaratawia azari* nov. gen., nov. sp., holotype, NIGP167528. a: complete habitus. b: Left and right forewings, dry. Scale bars: 1 cm.

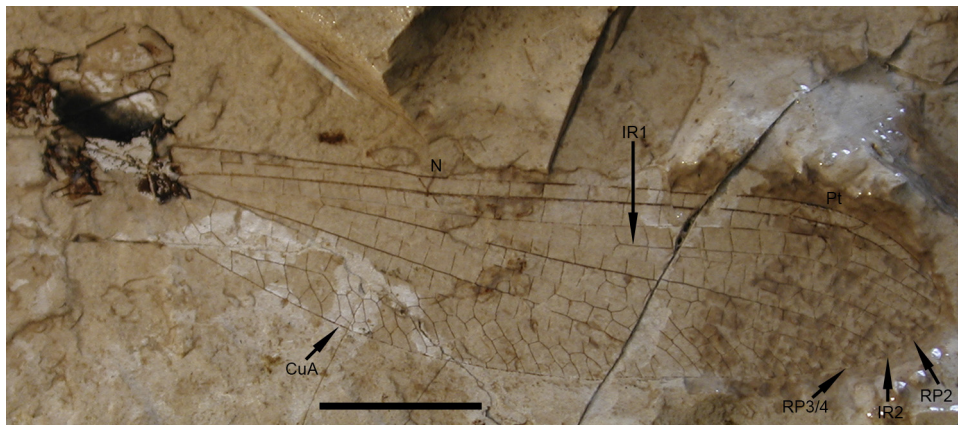


Fig. 4. *Parazygokaratawia azari* nov. gen., nov. sp., holotype, NIGP167528. Hindwing. Scale bar: 5 mm.

MP + CuA, distally fused with CuAb; median and submedian areas and vein CuP not visible; subdiscoidal area rather transverse, posteriorly closed, short and broad, with one basal crossvein, 1.2 mm long, 0.6 mm wide; discoidal cell basally closed, 1.0 mm long, 0.6 mm wide, free of crossveins, length of proximal side, ca. 1.1 mm distal of arculus; MA divided into MAa and Mab, Mab short, 0.6 mm long, aligned with distal free part of CuA; MP + CuA separated into MP and CuA at distal end of MAB; distal free part of CuA strong, separated from MP 4.4 mm from wing base and extended towards posterior wing margin for 0.5 mm; CuA distally divided into CuAa and CuAb, CuAb short, 0.4 mm long, extends towards basal wing margin and meets main branch of AA; CuAa basally more or less parallel to posterior wing margin with 1–2 rows of cells between them; CuAa short, ending on posterior wing margin about 5.3 mm from its base; area between CuAa and MP

with one row of cells, 0.5 mm wide; distal of end of CuAa, area between MP and posterior wing margin very long and broad; MP nearly straight, reaching posterior margin well distal of nodus level, 16.0 mm from wing base; MAa parallel to MP, nearly straight in its basal part and weakly zigzagging distal of nodus level, postdiscoidal area 0.5 mm wide, narrower near posterior wing margin, with one row of cells; Ax1 not visible; Ax2 1.3 mm distal of arculus, nearly perpendicular to ScP; no secondary antenodal crossveins between C and ScP, but five secondary antenodal crossveins between ScP and RA distal of Ax2; eight crossveins in area between RA and RP, between arculus and nodus; base of RP3/4 2.1 mm distal of arculus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 0.6 mm distally; no visible antefurcal crossvein in space between RP and MA basal of midfork (base of RP3/4); nodal structures identical to those of forewing; nine

postnodal crossveins between C and RA; eight postsubnodal crossveins between RA and RP1 not aligned with postnodals; pterostigmal brace rudimentary, not aligned with basal side of pterostigma; one crossvein below pterostigma; pterostigma sclerotized, 2.4 mm long, 0.5 mm wide; RP2 one cell distal of subnodus; four crossveins in Bqr space between RP, RP2, IR2 and oblique vein “O”; oblique vein “O” 2.4 mm and four cells distal of base of RP2; RP2 nearly straight; base of IR1 four cells distal of base of RP2; IR1 basally straight and distally curved, more or less parallel to RP1; area between MA and RP3/4 much wider distally, with 15 rows of cells along posterior wing margin; area between RP3/4 and IR2 slightly broader distally than basally, with one row of cells basally and four distally; area between IR2 and RP2 with one row of cells and distally six rows near posterior wing margin; area between RP2 and IR1 progressively widens, with two zigzagging intercalary longitudinal veins and four rows of cells between them; area between IR1 and RP1 not distally widen, with 2–3 rows of cells between them.

**Remarks:** *Parazygokaratawia* nov. gen. has nearly all the characters listed in the diagnosis of *Zygokaratawia*, i.e.: hindwing subdiscoidal space small and posteriorly closed; cubito-anal and anal areas very narrow in both fore- and hindwings (synapomorphy); a long basal part to CuA before it branches; area between MP and CuA as broad as postdiscoidal area, which is distally constricted; MP straight; MAa zigzags and becomes much weakened distally; CuAa short; pterostigma not basally recessed (Nel et al., 2008). Thus, it is probably closely related to this genus in the family Karatawiidae, with which it also shares the putative synapomorphy ‘space between MAa and MP distally constricted by an opposite curvature of these two veins’.

*Parazygokaratawia* nov. gen. and *Zygokaratawia* differ from all or nearly all Isophlebioidea in the very narrow fore- and hindwing cubito-anal and anal areas (Nel et al., 1993, 2007; Pritykina, 2006; etc.). Nevertheless, information on these structures is lacking for some genera. *Adelophlebia* Pritykina, 1980 is based only on a forewing base; it differs from *Parazygokaratawia* nov. gen. and *Zygokaratawia* in the presence of two rows of cells between CuAa and MP (Pritykina, 1980). The forewings of *Parazygokaratawia* nov. gen. and *Zygokaratawia* are rather similar to that of *Karatawia* Martynov, 1925, with an important difference in that the CuA is longer and better defined distally and also the hindwings of *Karatawia* have distinctly broader cubito-anal areas (Li et al., 2012). *Sarytashia* Pritykina, 1970 is based on the apical half of a wing. It differs from *Parazygokaratawia* nov. gen. and *Zygokaratawia* in that its pterostigma is distinctly basally recessed (Pritykina, 1970).

Nevertheless, *Parazygokaratawia* nov. gen. has no distinct constriction in the area between RP3/4 and IR2 in all wings, unlike *Zygokaratawia*. On the contrary, the area between these veins is rather widened along posterior wing margin in *Parazygokaratawia* nov. gen. *Parazygokaratawia* nov. gen. also differs from *Zygokaratawia* in the base of RP2 not aligned with subnodus, IR1 basally straight, only one row of cells between IR1 and RP1 between its base and pterostigma, Ax2 perpendicular to ScP in hindwing, and different number of antenodal, postnodal and antesubnodal crossveins. This set of characters is sufficient for an attribution to a different, new genus.

#### 4. Conclusion

*Parazygokaratawia* nov. gen. comes from a higher layer of the same paleolake than the two known *Zygokaratawia* species. Maybe it corresponds to a rather rapid local evolution within the same lineage, but this is delicate to show without a complete fossil record through all the strata of this outcrop. These two new

discoveries show that the Campterothlebiidae with narrow wings are more diverse than previously supposed, even if they remain restricted to the Haifanggou Formation, in a palaeoenvironment corresponding to a high mountain lake (Huang, 2015).

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