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A new genus of isophlebioid damsel-dragonflies with "calopterygid"-like wing shape from the Middle Jurassic of China (Odonata: Isophlebioidea: Campterophlebiidae)

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Key words. Odonata, Isophlebioidea, Campterophlebiidae, gen. n., sp. n., Middle Jurassic, China, wing shape

Abstract. *Zygokaratawia reni*, a new campterophlebiid genus and species is described from the Middle Jurassic of China. This fossil has a wing shape unique for this clade, i.e. a fore- and hind wing of the same width and very shortly petiolated, and hind wing cubito-anal area nearly as narrow as that of the forewing. This wing shape is convergently similar to that of recent Zygoptera: Calopterygidae, as well as to several other Cenozoic zygopteran clades, suggesting similar styles of flight and habits, i.e. predation on small insects and flight along trees of river banks.

INTRODUCTION

The Isophlebiida Bechly, 1996 [= (Archithemistidae Tillyard, 1917 + (Campterophlebiidae Handlirsch, 1920 + Isophlebiidae Handlirsch, 1906))] is a damsel-dragonfly clade that flourished from the Triassic, through the Jurassic and Early Cretaceous in Europe and Central Asia (Fleck & Nel, 2002). More than fifty species are described (Nel et al., 1993; Bechly, 1996), many of which are based mainly on isolated and sometimes fragmentary fossil wings. This clade was unrecorded from the Chinese Mesozoic before the studies of Fleck & Nel (2002), Zhang et al. (2006) and Nel et al. (2007) all of whom describe several complete specimens of Isophlebiida of great importance for the paleobiogeography and morphology of this group, contrary to the recent opinion of Trueman (2007), who erroneously supposed that the "relevant material" of the so-called Anisozygoptera "consists of wing impressions only, as odonate bodies are morphologically conservative and in any case are rarely preserved". Curiously, Trueman (2007) ignored that prior to Lohmann (1996) and Bechly (1996), Nel et al. (1993) indicated that the Anisozygoptera were not monophyletic. Even more curiously, this author ignored all the recent studies on fossil Odonatoptera made by Nel and his team (Fleck et al., 2003, 2004; Fleck & Nel, 2002, 2003; Nel et al., 2003, among others). Although a phylogenetic revision of the whole clade Isophlebiida is required, based on new and better preserved fossil material of numerous taxa, this is not the subject of the present work. Here we describe a new well-preserved specimen attributable to a new genus and species with a very particular, unique wing shape and venation, collected from Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Middle Jurassic (ca. 165 Ma). Our collection includes more than one hundred specimens of adult or larval Isophlebiida and Aeshnoptera (dragonflies). The present discovery is the sixth species of this damsel-dragonfly clade in this fauna, which becomes one of the most diverse for the Middle Jurassic.

The geology and stratigraphy of the Jiulongshan Formation was extensively studied in Zhang et al. (2006). Wing venation nomenclature used in this paper follows Riek (1976) and Riek & Kukalová-Peck (1984), as amended by Nel et al. (1993) and Bechly (1996), despite the recent paper of Trueman (2007) who said that this nomenclature is unconvincing, but did not justify this comment. Trueman (2007), but not Trueman (1996), apparently ignored the work and arguments of Nel et al. (1993: 35–54, pl. 4) who indicated that the previous wing venation nomenclatures of Fraser (1957), Hamilton (1972), and Carle (1982) were incompatible with the morphology of the Isophlebiidae in which the anal vein (sensu these last authors) is divided into two disconnected segments, but resolved by using the nomenclature of Nel et al. (1993) and Bechly (1996). We use the following standard abbreviations: AA anal vein, AP anal posterior, Ax0 Ax1 Ax2 primary antenodal cross-veins, CuAa distal branch of cubitus anterior, CuAb proximal branch of cubitus anterior, IR1, IR2 intercalary radial veins, MAa distal branch of median anterior, MAp posterior branch of median anterior, MP median posterior, N nodus, O oblique vein, Pt pterostigma, RA radius anterior and RP radius posterior. We follow the taxonomy of Isophlebiida indicated by the phylogenetic system of Bechly (1996), but do not accept all the synapomorphies he proposes (see Discussion below).

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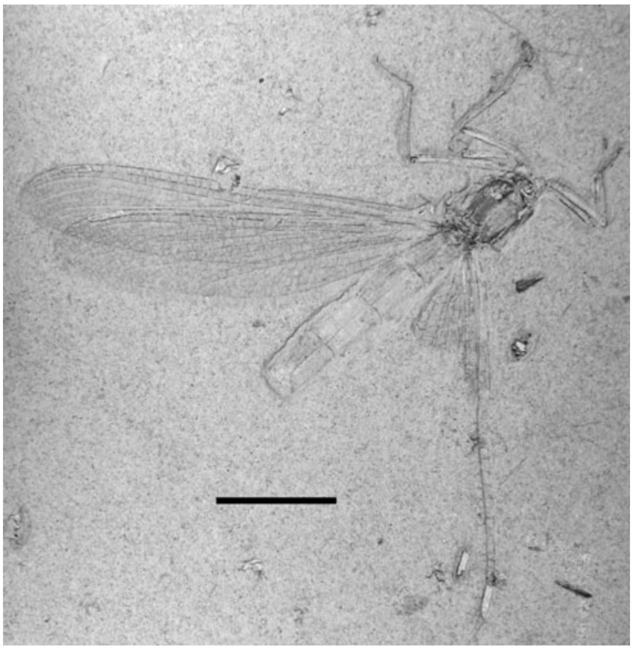

Fig. 1. *Zygokaratawia reni* gen. n., sp. n., holotype NIGP 148158, photograph of general habitus (scale bar represents 10 mm).

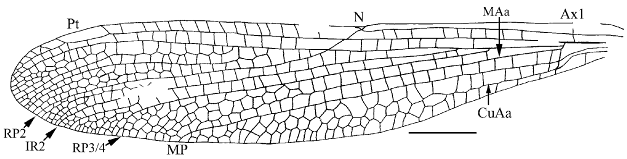

Fig. 2. *Zygokaratawia reni* gen. n., sp. n., holotype NIGP 148158, drawing of forewing (scale bar represents 4 mm).

SYSTEMATICS

Order Odonata Fabricius, 1793

Suborder Isophlebioptera Bechly, 1996

Superfamily Isophlebioidea Handlirsch, 1906

Family Campterophlebiidae Handlirsch, 1920

Genus *Zygokaratawia* gen. n.

Type species. *Zygokaratawia reni* gen. n., sp. n. by present designation.

Diagnosis. Wing characters only. Hind wing subdiscoidal space small and posteriorly closed; cubito-anal and anal areas very narrow in both fore and hind wings (no “anal triangle”); 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; a distinct constriction in the area between RP3/4 and IR2 in the hind wing, but not in the forewing; pterostigma not basally recessed.

Etymology. So named because its wing shape, similar to that of Zygoptera: Calopterygidae and the genus *Karatawia*.

***Zygokaratawia reni* sp. n.**

(Figs 1–4)

Diagnosis. That of the genus.

Description. A body with a thorax, five basal abdominal segments, fore, median and hind legs (partly missing) and all four wings connected. Only the left wings and the bases of right wings are exposed to keep a part of the wings in their original conditions for future works.

Thorax 7.0 mm long, 5.0 mm wide; abdomen 3.0 mm, with no secondary genital structure on segment 2 (indicating that this is a female); legs slender, middle legs shorter than fore legs, hind legs distinctly the longest, all legs uniform in shape; fore coxa longer than mid and hind coxae, fore femora 5.4 mm long, tibia 5.0 mm, first tarsomere 0.5 mm, second 1.1 mm, third 1.1 mm; middle femora 4.1 mm, tibia 4.1 mm; hind femora 7.7 mm, tibia 6.7 mm, first tarsomere 0.7 mm, second 1.7 mm, third 1.6 mm, hind tarsal claws 0,7 mm; tibia armed with two rows of inner spines, with length of spines increasing distally, outer side of tibia armed with a row of small spines, all tarsi three-segmented, first tarsomere short and oblique apically, second and third tarsomeres elongate and of same length, armed with a row of inner spines; tarsal claws moderately large, with base large, and apical part thin and sharp at apex.

Forewing hyaline; 35.5 mm long, 6.9 mm wide; distance between base and arculus 3.3 mm, arculus and nodus 11.7 mm, nodus and pterostigma 14.4 mm, pterostigma and apex 3.7 mm; a short petiole 1.0 mm long, 1.5 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, in a distal position just basal of arculus; subdiscoidal space free of cross-veins, transverse; discoidal space basally opened; RP+MA separated at nearly a right angle from RA in arculus, strongly curved; RP separated from MA 0.2 mm distally; distance between base of RP and point of separation between MAa and MAb 0.2 mm, RP and MA well parallel; MAb rather short, 0.7 mm long, well aligned with distal free part of CuA; CuA separates from MP 4.0 mm from wing base and directed towards posterior wing margin for 0.4 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; apex of CuA 1.8 mm basal of 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, at about 26.2 mm from wing base; MAa more or less parallel with MP, nearly straight in basal half but zigzags distal of subnodus level and vanishes apically; postdiscoidal area with one row of cells, 0.7 mm wide near discoidal cell and 0.3 mm at apex of MA; Ax0 not preserved; Ax1 0.5 mm basal of arculus, nearly perpendicular to ScP and R+MA, Ax2 probably distal of arculus but not preserved; no secondary antenodal cross-veins between C and ScP; nine visible secon-

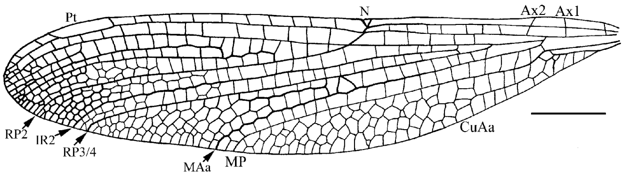

Fig. 3. *Zygokaratawia reni* gen. n., sp. n., holotype NIGP 148158, drawing of hind wing (scale bar represents 4 mm).

dary antenodal cross-veins between ScP and RA distal of Ax2; 16(–17?) postnodal cross-veins between C and RA and 12(–13?) postsubnodal cross-veins between RA and RP1 basal of pterostigma; seven preserved cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 4.1 mm distal of arculus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 1.8 mm distally; no visible antefurcal cross-vein in space between RP and MA basal of midfork (base of RP3/4); subnodus oblique and well aligned with nodal cross-vein Cr; RP2 aligned with subnodus; Bqr space between RP, RP2, IR2 and first oblique vein "O" long and narrow, with one row of cells and six cross-veins; first oblique vein "O" two cells distal of RP2 base; RP2 nearly straight in its preserved part; base of IR1 four cells distal of base of RP2; IR1 zigzags basally but nearly straight distally, more or less parallel to RP1; area between MA and RP3/4 much widens distally, with several long intercalary longitudinal veins; area between RP3/4 and IR2 widened distally with a intercalary longitudinal vein zigzagging between them; area between IR2 and RP2 narrow, with a intercalary longitudinal vein zigzagging between them; pterostigma 3.0 mm long, 0.6 mm wide, covering two cells; pterostigmal brace neither aligned with basal side of pterostigma or strongly oblique.

Hind wing hyaline; distinctly shorter than forewing, 32.1 mm long, 7.2 mm wide, widest part at level of nodus; distance between base and arculus 3.9 mm, arculus and nodus 9.2 mm, nodus and pterostigma 12.9 mm, pterostigma and apex 3.3 mm; a very short petiole, 1.2 mm long, 1.4 mm wide; anal area very narrow, 3.6 mm long, 0.9 mm wide, nearly triangular in shape, with one row of irregular cells between AA and AP; no anal angle (female specimen); no membranule; AA distally strongly bent towards posterior wing margin and nearly parallel with MP+CuA, distally fused with CuAb; median and submedian areas free; curved vein CuP just basal of arculus; subdiscoidal area transverse, posteriorly closed, short and broad, with one cross-vein, 1.7 mm long, 0.7 mm wide; discoidal cell basally closed, 1.0 mm long, 0.7 mm wide, free of cross-veins, length of proximal side, 0.3 mm; RP+MA separates at approximately a right angle from RA and strongly curved in arculus; RP separated from MA 0.2 mm distally; just distal of arculus base, MA basally strong and divided into MAa and MAb 0.2 mm distally; MAb short, 0.7 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, separates from MP 4.8 mm from wing base and extends towards posterior wing margin for 0.7 mm; CuA distally

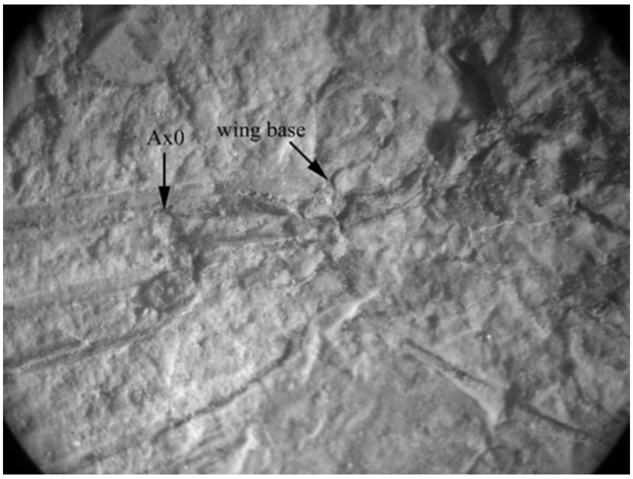

Fig. 4. *Zygokaratawia reni* gen. n., sp. n., holotype NIGP 148158, photograph of the articular structures at the base of the forewing.

divided into CuAa and CuAb, CuAb short, 0.2 mm long, extends towards basal wing margin and meets main branch of AA; CuAa basally more or less parallel to posterior wing margin with only one row of cells between them; CuAa short, shorter than in forewings, ending on posterior wing margin about 11.5 mm from its base; area between CuAa and MP with one row of cells, 1.0 mm wide; distal of the 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, 20.9 mm from wing base; MAa parallel with MP, nearly straight in its basal part and zigzagging distal of level of nodus, postdiscoidal area 0.9 mm wide, narrower near posterior wing margin, with one row of cells; Ax1 1.0 mm basal of arculus, nearly perpendicular to ScP; Ax2 0.9 mm distal of arculus, oblique; no secondary antenodal cross-veins between C and ScP, but seven secondary antenodal cross-veins between ScP and RA distal of Ax2; five cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 2.7 mm distal of arculus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 1.7 mm distally; no antefurcal cross-vein in space between RP and MA basal of midfork (base of RP3/4); nodal structures identical to those of forewing; ten postnodal cross-veins between C and RA; nine postsubnodal cross-veins between RA and RP1 not aligned with postnodals; pterostigmal brace rudimentary, not aligned with basal side of pterostigma; three cross-veins below pterostigma; pterostigma sclerotized, 3.3 mm long, 0.7 mm wide; RP2 aligned with subnodus; seven cross-veins in Bqr space between RP, RP2, IR2 and first oblique vein "O"; oblique vein "O" 2.7 mm and three cells distal of base of RP2; RP2 nearly straight; base of IR1 four cells distal of base of RP2; IR1 basally 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 basally one row of cells 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 widens, with two zigzagging intercalary longitudinal veins and three rows of cells between them; area between IR1 and RP1 not distally widen, with 2–3 rows of cells between them.

Material. Holotype NIGP 148158 (imprint), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Etymology. Named after our colleague Dr. Ren Dong.

Stratigraphic horizon. Middle Jurassic Jiulongshan Formation (ca. 165 Ma); Inner Mongolia, NE China.

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

Discussion. *Zygokaratawia* gen. n. has all the synapomorphies of the Isophlebiida sensu Bechly (1996). Within this clade, the hind wing subdiscoidal space of *Zygokaratawia* is nearly of the same size as in the Archithemistidae, distinctly smaller than that of the Isophlebioidea Handlirsch, 1906 (= Campterophlebiidae + Isophlebiidae). But this rather small subdiscoidal space is certainly correlated with the very strong narrowing of the cubito-anal and anal areas in *Zygokaratawia*, unlike in the Archithemistidae. In *Zygokaratawia* and the Isophlebioidea the CuA has a long basal part before it branches; which is correlated with the broad area between MP and CuA, which is as broad as the postdiscoidal area. But the hind wing "anal triangle" of *Zygokaratawia* is not hypertrophied and subdivided into numerous cells, unlike in the other Isophlebioidea.

Nel et al. (2007) discussed the synapomorphies of the Isophlebiidae proposed by Bechly (1996). The first character is the strong obliquity of Ax1, which is not present in *Zygokaratawia*, the second the posterior separation between AA and CuAb. Nel et al. (2007) noted the latter is present in some campterophlebiid genera. Nevertheless, it is absent in *Zygokaratawia*, but this may be due to the very narrow anal and cubito-anal areas. The third character is the "basal closure of discoidal cell in forewings", which is not present in *Zygokaratawia*. The fourth is the relatively broad area between MP and CuA (twice as wide as basal area between MA and MP), also not present in *Zygokaratawia*. In conclusion, *Zygokaratawia* has none of the significant synapomorphies of the Isophlebiidae.

On the contrary, *Zygokaratawia* has the following potential synapomorphy of the Campterophlebiidae (Bechly, 1996): "space between MAa and MP distally constricted by an opposite curvature of these two veins". Nel et al. (2007) proposed a further potential synapomorphy of the Campterophlebiidae (although undescribed for several taxa currently included in this family), i.e. "a distinct constriction of the area between veins RP3/4 and IR2", present in the hind wing of *Zygokaratawia*, but not the forewing. Thus, we tentatively attribute *Zygokaratawia* to the Campterophlebiidae.

Zygokaratawia strongly differs from all or nearly all Isophlebioidea in the very narrow fore- and hind wing cubito-anal and anal areas (Nel et al., 1993, 2007; Pritykina, 2006). But information on these structures is lacking for some genera. *Adelophlebia* Pritykina, 1980 is based only on a forewing base. The forewing of *Zygokaratawia* is rather similar to that of *Karatawia*, with an important difference in that the CuA is longer and better defined distally. *Sarytashia* Pritykina, 1970 is based on the apical half of a wing. It differs from *Zygokaratawia* in that its pterostigma is distinctly basally recessed.

Zygokaratawia is important for any assessment of the morphological disparity of the Isophlebioidea. Contrary to all the other representatives of this clade (in which the wing bases are known), its hind wing anal and cubito-anal areas are very narrow. Thus, the general shape of its wings is not of the type encountered in the Epiproctophora (= former "Anisozygoptera" + Anisoptera, minus the Tarsophlebiidae), in which the hind wings are distinctly broader than the forewings, but very similar in shape to those of some Zygoptera, viz. the recent Calopterygidae and the Cenozoic Latibasaliidae, Frengueliidae, Sieblosiidae and Dysagrioninae (fore and hind wings with very short petioles and with cubito-anal areas of similar widths and shapes) (Petrulevičius & Nel, 2003, 2004, 2007; Nel et al., 2005). This similarity with the Calopterygidae may indicate that *Zygokaratawia* had similar flight habits and habitats, i.e. a predator of small insects along river banks overhung by trees. Unfortunately, the articular structures at the base of the wing (articular sclerites) of *Zygokaratawia* are not very well-preserved, although clearly small, as in recent Calopterygidae and unlike the larger ones in Isophlebiidae (Fig. 4). The Calopterygidae are still unrecorded from the Jurassic. The epiproctophoran adults of the *Zygokaratawia*-type could have occupied ecological niches similar to those of recent Calopterygidae. They are unrecorded in the Cretaceous and were probably replaced by Zygoptera (of the sieblosiid, dysagrionine, or latibasaliid lineages, etc.) with similar wing shapes.

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