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A new genus of isophlebioid damsel-dragonflies (Odonata: Isophlebioptera: Campterophlebiidae) from the Middle Jurassic of China

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Abstract

Sinokaratawia prokopi **gen. nov., sp. nov.** is the fifth representative of the Campterophlebiidae from the Chinese Middle Jurassic Jiulongshan Formation, which corresponds to one of the most diverse fauna of isophlebioid damsel-dragonflies. The synapomorphies for the Campterophlebiidae and Isophlebiidae are discussed.

Key words: Insecta, Odonata, Campterophlebiidae, **gen. nov., sp. nov.,** Middle Jurassic, Daohugou fauna, Inner Mongolia, China

Introduction

The Isophlebioptera Bechly, 1996 is an insect clade that flourished during the Triassic, Jurassic and Early Cretaceous in Europe and Central Asia (Fleck & Nel 2002). More than fifty species have been described (Nel *et al*. 1993; Bechly 1997), but many are based mainly on isolated, sometimes fragmentary, fossil wings. This clade was unknown in the Chinese Mesozoic before the works of Fleck and Nel (2002) and Zhang *et al*. (2006) who described several complete isophlebioid specimens of great importance for the morphology and paleobiogeography of this group. Here we describe new well-preserved specimens attributable to a new genus and species, collected from the Daohugou Village, Wuhua Twon, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Middle Jurassic (Aalenian-Bajocian). The Daohugou fauna includes more than one hundred adult or larval Isophlebioptera and Aeshnoptera (dragonflies). The present discovery is the fifth species of this isophlebioid 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 and Kukalová-Peck (1984), as amended by 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, IRi 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, RP radius posterior.

Although a phylogenetic revision of the whole clade Isophlebioptera *sensu* Bechly (1996) is necessary, it should be based on the discovery of new better preserved fossil material for numerous taxa. It is not the subject of the present work. We follow the taxonomic results of the phylogenetic system of Bechly (1996) concerning the Isophlebioidea, with some restrictions concerning some of the synapomorphies he proposed (see discussion below).

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Taxonomic part

Order Odonata Fabricius, 1793

Superfamily Isophlebioidea Handlirsch, 1906

Family Campterophlebiidae Handlirsch, 1920

Genus *Sinokaratawia* gen. nov.

Type species. *Sinokaratawia prokopi* **sp. nov.**

Etymology. Named after the Latin name for China and the genus *Karatawia*.

Diagnosis. Wing characters only. Forewing Ax2 strongly oblique; subdiscoidal cell posteriorly open in male but posteriorly closed or nearly so in female; MP straight, MAa with a smooth bend, distally zigzagged, a constricted area between MAa and MP; a very acute projecting anal angle in male hind wing; a distinct constriction of the area between RP3/4 and IR2; MAa distally zigzagged; no long basal branch of AA parallel to AP; two rows of cells in forewing postdiscoidal area and basal part of area between MP and CuA; CuAa short.

Sinokaratawia prokopi sp. nov.

Figs 1–10

Material. Holotype NIGP 142170 (male), allotype NIGP 142169 (female), paratypes NIGP 142168 (female), and NIGP 142167 (male), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Etymology. Named after the palaeontomologist Dr Jakub Prokop.

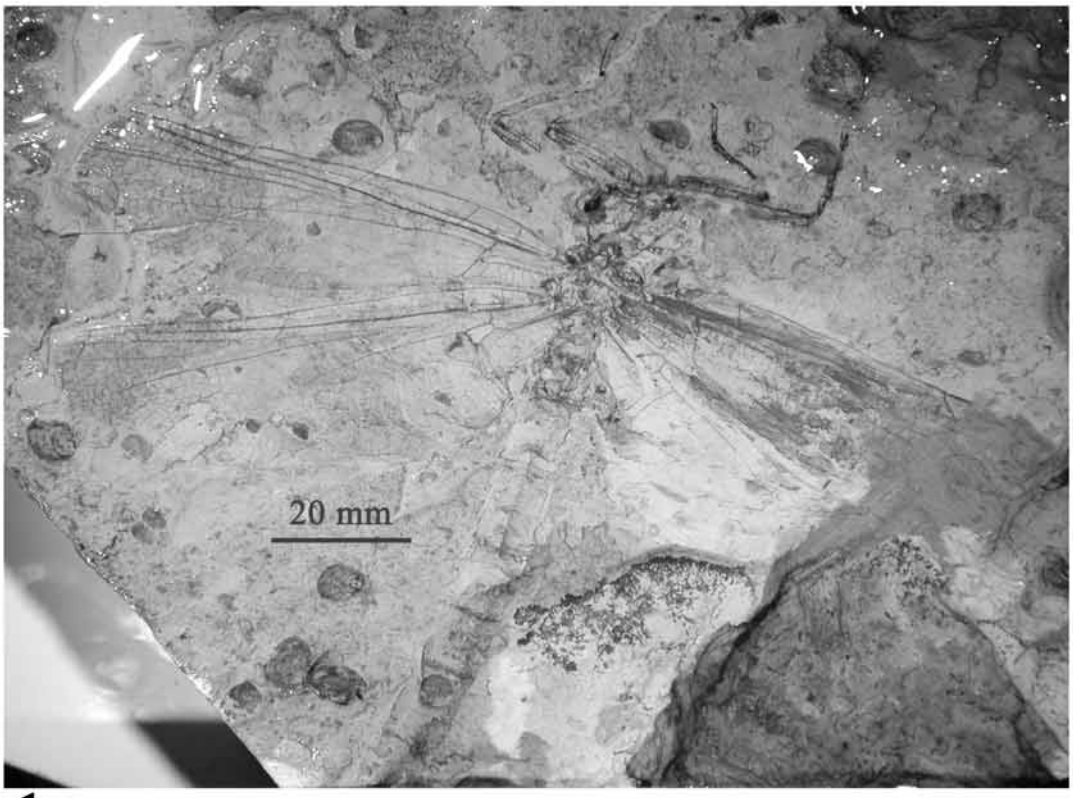
Species diagnosis. As for the genus.

Stratigraphic horizon. Middle Jurassic Jiulongshan Formation (ca. 165 Ma).

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

Descriptions.

Holotype NIGP 142170 (male). A body with thorax and abdomen, fore and median legs and all four wings connected. Apices of wings not preserved; forewing hyaline; preserved part of forewing 33.0 mm long, 9.0 mm wide; distance between base and arculus, 5.0 mm, between arculus and nodus, 17.0 mm; petiole short, 0.5 mm long and 2.2 mm wide; 1–2 rows of cells between posterior wing margin and AA; AA parallel to MP + Cu; median and submedian areas free of cross-veins, vein CuP strongly curved between submedian and subdiscoidal areas, opposite arculus; subdiscoidal space free of cross-veins, transverse, short but broad, 1.7 mm long; discoidal space basally opened; RP+MA separated at nearly right angle from RA in arculus, strongly curved; RP separated from MA 0.3 mm distally; distance between base of RP and point of separation between MAa and MAb, 0.7 mm, RP and MA parallel; MAb short, 1.0 mm long, well-aligned with distal free part of CuA; CuA separating from MP 8.6 mm from wing base and directed towards posterior wing margin for 1.4 mm; CuA distally fused with AA; CuA (+AA) divided into a very short CuAb directed towards posterior wing margin and CuAa basally nearly parallel to posterior wing margin and distally delimitating a short but rather broad cubito-anal area, with three posterior branches and 3–4 rows of cells in its broadest part; apex of CuA 7.8 mm basal of nodus level; area between CuA and MP with two rows of large transverse cells; distal of apex of CuA, area between MP and posterior wing margin very long and broad, with 8–12 rows of cells; MP nearly straight and without any curve in its middle; MP reaching posterior wing margin well distal of nodus level, at about 31.5 mm from wing base; MAa slightly curved, nearly parallel with MP, and zigzagged distal of nodus



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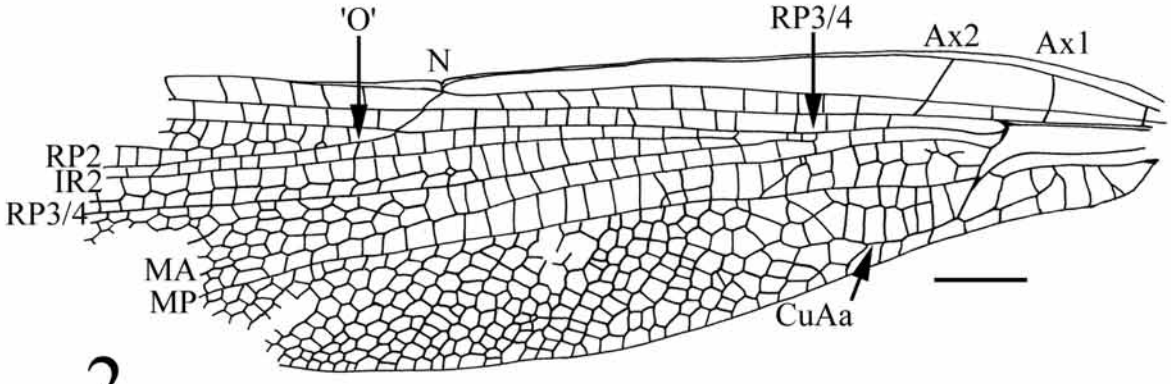

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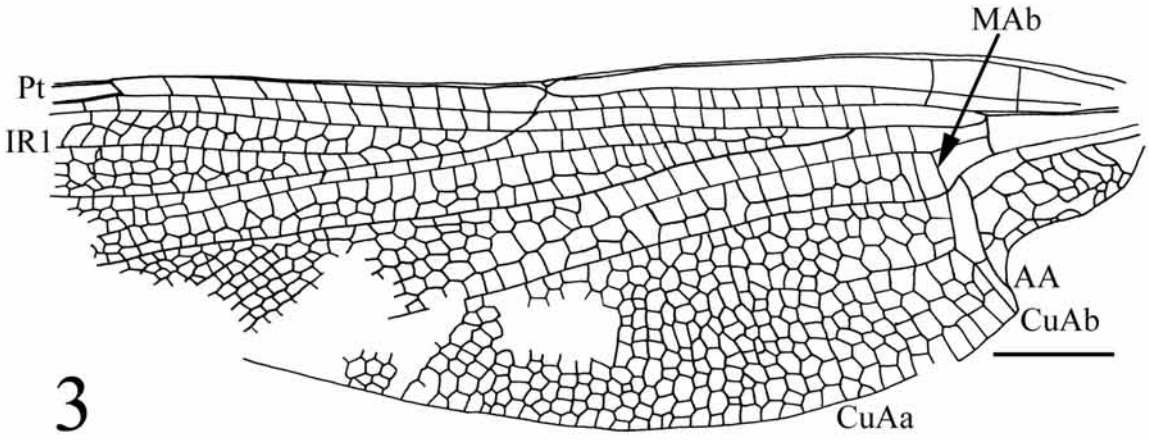

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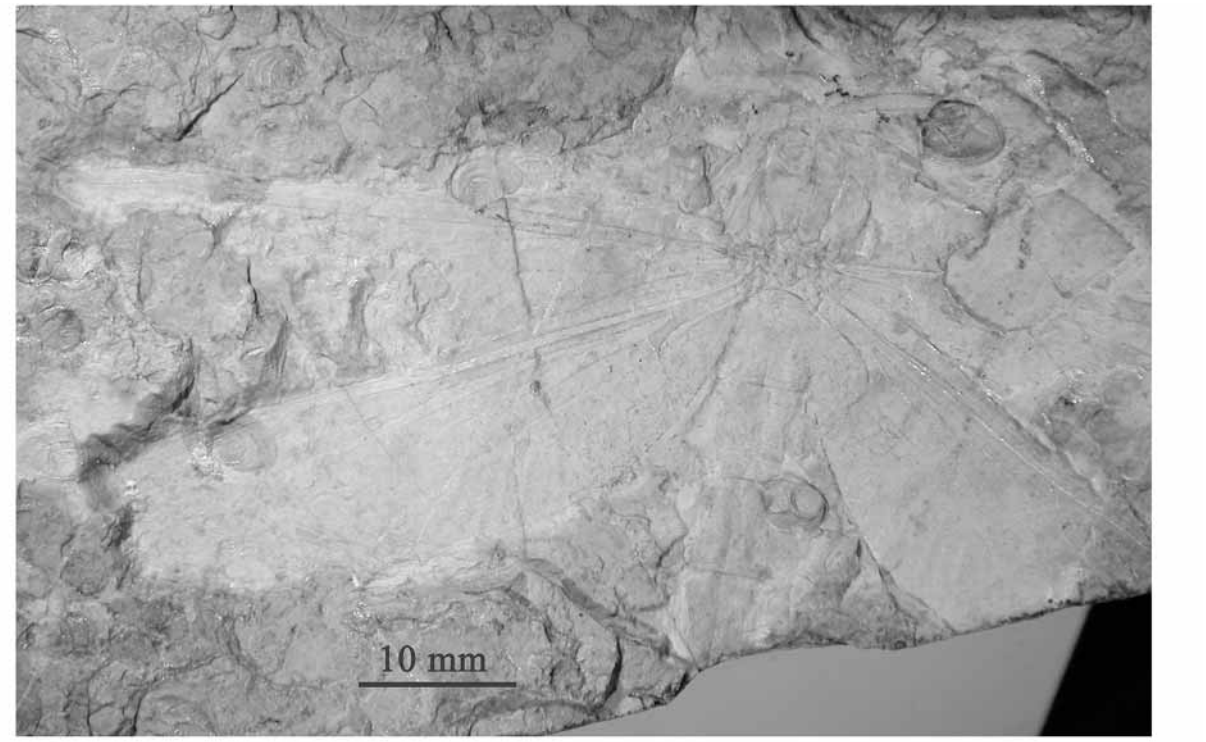
FIGURES 1–3. *Sinokaratawia prokopi* **gen. nov., sp. nov.**, holotype NIGP 142170 (male). 1, photograph (scale bar represents 20 mm). 2, drawing of forewing (scale bar represents 3 mm). 3, drawing of hind wing (scale bar represents 4 mm).



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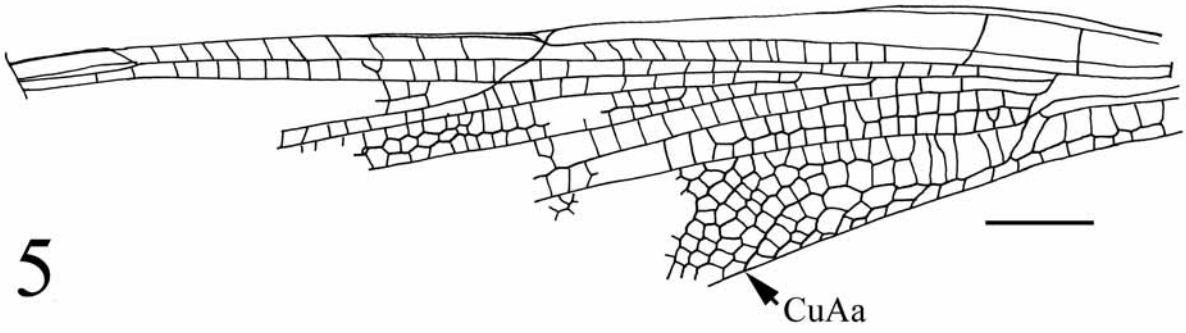

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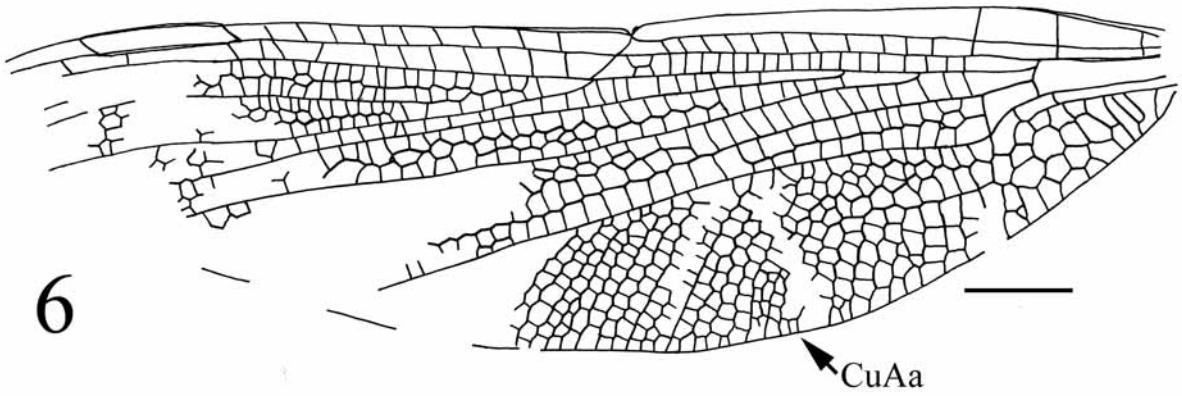

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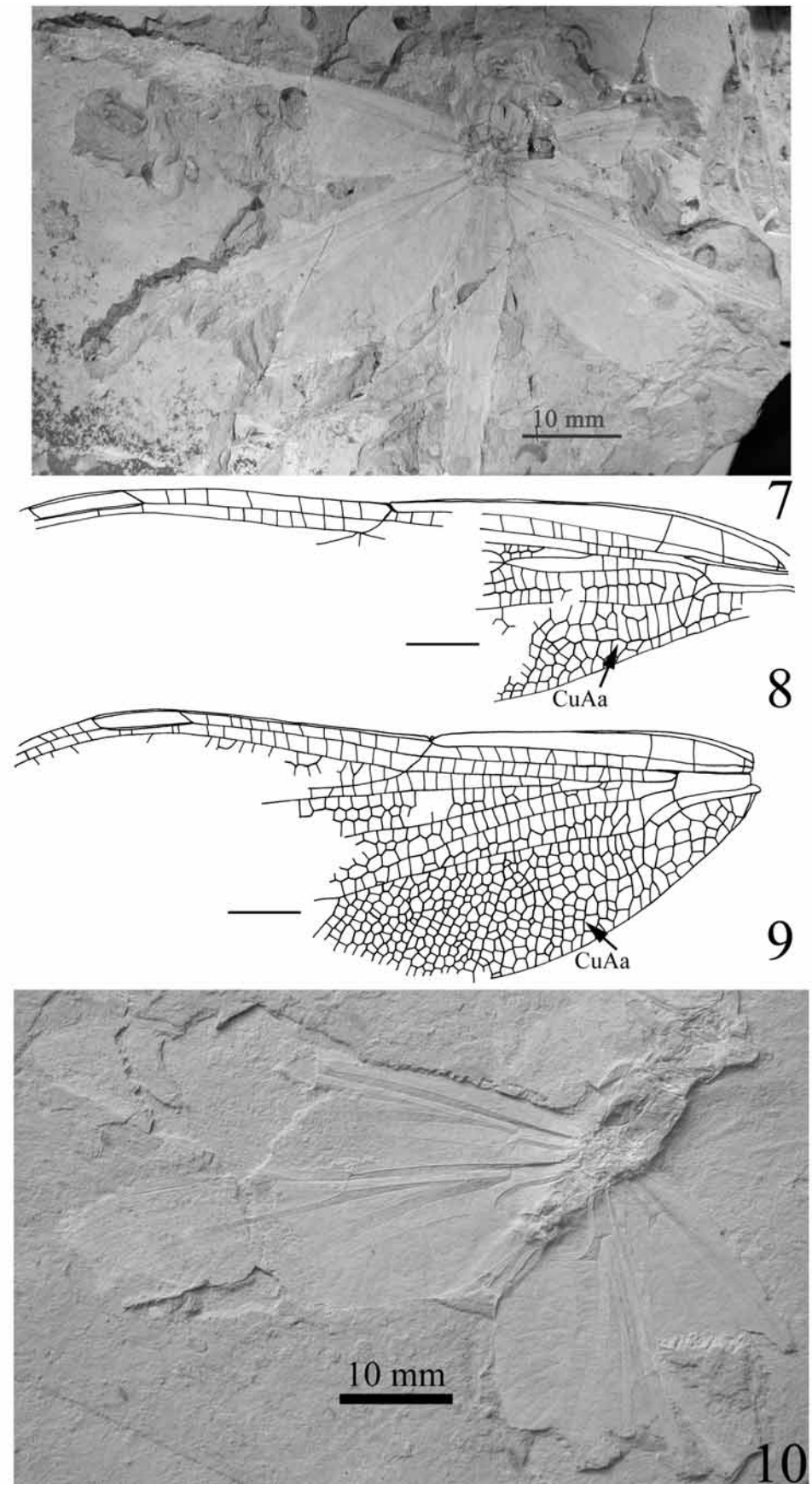
FIGURES 4–6. *Sinokaratawia prokopi* **gen. nov., sp. nov.**, allotype NIGP 142169 (female). 4, photograph (scale bar represents 10 mm). 5, drawing of forewing (scale bar represents 4 mm). 6, drawing of hind wing (scale bar represents 4 mm).



FIGURES 7–10. *Sinokaratawia prokopi* **gen. nov., sp. nov.**, 7–9, paratype NIGP 142168 (female). 7, photograph (scale bar represents 10 mm). 8, drawing of forewing (scale bar represents 4 mm). 9, drawing of hind wing (scale bar represents 4 mm). 10, paratype NIGP 142167 (male), photograph (scale bar represents 10 mm).

level; postdiscoidal area with 1–2 rows of cells and a distinct constriction opposite nodus level, narrower near posterior wing margin, 1.2 mm wide near discoidal cell and 0.7 mm wide near posterior wing margin; Ax0 visible near wing base; two strong primary antenodal cross-veins, Ax1 1.2 mm basal of arculus and Ax2 2.8 mm distal of arculus; Ax2 oblique and Ax1 nearly perpendicular to ScP and R+MA; no secondary antenodal cross-veins between C and ScP; 12 secondary antenodal cross-veins between ScP and RA distal of Ax2; six preserved postnodal cross-veins between C and RA and seven preserved postsubnodal cross-veins between RA and RP1 basal of pterostigma; about 15 cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 5.7 mm distal of arculus, closer to arculus than to nodus; base of IR2 distal 2.4 mm of RP3/4 base; two antefurcal cross-veins present 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 about 12 cross-veins; first oblique vein 'O' two cells distal of RP2 base; RP2 nearly straight in its preserved part; base of IR1 three cells distal of base of RP2; IR1 basally zigzagged but distally nearly straight, nearly parallel to RP1; area between MA and RP3/4 strongly widened distally, with several long intercalary longitudinal veins; area between RP3/4 and IR2 distally widened with a zigzagged intercalary longitudinal vein between them; area between IR2 and RP2 narrow, with one row of cells.

Hind wing hyaline, probable slightly shorter than forewing; preserved part 34.0 mm long, 11.2 mm wide at nodus level; distance between base and arculus 5.0 mm, between arculus and nodus 13.6 mm, between nodus and pterostigma 13.2 mm, between pterostigma and apex unknown; petiole short, about 0.3 mm long and 15.0 mm wide; anal area 6.6 mm long and 2.6 mm wide, nearly triangular in shape, with about four rows of irregular cells between AA and AP, some being very small and others very large; anal angle strong (male specimen); no membranule; AA distally strongly bent towards posterior wing margin and nearly parallel with MP+CuA and distally with CuA, distally separated from CuAb; median and submedian areas free of cross-veins; subdiscoidal area transverse and reaching posterior wing margin, long and broad, with one row of cross-veins, 4.2 mm long and 0.8 mm wide; discoidal cell basally closed, 1.9 mm long and 1.3 mm wide, free of cross-vein, length of proximal side, 0.5 mm; RP+MA separated at right angle from RA and strongly curved in arculus; RP separated from MA 0.1 mm distally; just distal of arculus base, MA basally strong and divided into MAa and MAb 2.2 mm distally; MAb short, 1.3 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 separating from MP 6.6 mm from wing base and directed towards posterior wing margin for 1.8 mm; CuA distally divided into CuAa and CuAb, CuAb long, 2.7 mm, directed towards posterior wing margin and not meeting main branch of AA, basally nearly parallel to posterior wing margin with 3–6 rows of cells between them; CuAa distally strongly curved, shorter than in forewings, ending on posterior margin about 7.5 mm from its base; area between CuAa and MP with 3–4 rows of cells, 2.3 mm wide; distal of end of CuAa, about 12 rows of cells in area between MP and posterior wing margin; MP nearly straight, reaching posterior margin well distal of nodus level, about 29.0 mm from wing base; MAa nearly straight, parallel with MP and zigzagged distal of nodus level, postdiscoidal area 1.5 mm wide, narrower near posterior wing margin, with 1–2 rows of cells, Ax1 0.9 mm basal of arculus and Ax2 2.0 mm distal of arculus, distance between Ax1 and Ax2 smaller than on forewings; Ax2 and Ax1 nearly parallel; no secondary antenodal cross-vein between C and ScP but 14 secondary antenodal cross-veins between ScP and RA distal of Ax2; 14 cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 4.2 mm distal of arculus, closer to arculus than to nodus; base of IR2 2.0 mm distal of RP3/4 base; three antefurcal cross-veins present in space between RP and MA basal of midfork (base of RP3/4); nodal structures identical to those of forewing; 11 postnodal cross-veins between C and RA; 13 postsubnodal cross-veins between RA and RP1 not aligned with postnodals; no pterostigmal brace; at least two cross-veins below pterostigma; pterostigma sclerotized, long and very narrow, 0.6 mm wide, probably basally recessed; C strongly widened along pterostigma; RP2 aligned with subnodus; 15 cross-veins in Bqr space between RP, RP2, IR2 and first oblique vein 'O'; oblique vein 'O' four cells 2.5 mm distal of base of RP2; RP2 nearly

straight; base of IR1 two cells distal of base of RP2; IR1 as in forewing; area between MA and RP3/4 strongly widened distally, with more than 12 rows of cells along posterior wing margin; area between RP3/4 and IR2 with one row of cells basally, distally greatly broadened; area between IR2 and RP2 with one row of cells and distally with 2–3 rows of cells near posterior wing margin; area between RP2 and IR1 progressively widened, with two zigzagged intercalary longitudinal veins and 4–5 rows of cells between them; area between IR1 and RP1 not distally widened with 2–3 rows of cells between them.

Allotype NIGP 142169 (female). A body with the thorax and five abdominal segments, with the fore and median legs and all four wings connected; apices of wings not preserved. Main differences with NIGP 142170 are as follows: forewing slightly longer, preserved part 46.0 mm long, 11.0 mm wide; distance between base and arculus 5.0 mm, between arculus and nodus 20.0 mm, petiole not preserved; subdiscoidal space 2.1 mm long; CuA separating from MP 6.5 mm from wing base; cubito-anal area slightly narrower than that of NIGP 142170; apex of CuA 11.0 mm basal of nodus level; Ax1 0.9 mm basal of arculus and Ax2 3.6 mm distal of arculus; 13 secondary antenodal cross-veins between ScP and RA distal of Ax2; 10 postnodal cross-veins between C and RA and 15 postsubnodal cross-veins between RA and RP1; about 14 cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 6.9 mm distal of arculus, closer to arculus than to nodus; base of IR2 2.9 mm distal to RP3/4 base; three antefurcal cross-veins present in space between RP and MA basal of midfork (base of RP3/4); Bqr space with 13 cross-veins; first oblique vein 'O' three cells distal of RP2 base.

Hind wing preserved part 46.0 mm long, 13.1 mm wide at nodus level; distance between base and arculus 5.5 mm, between arculus and nodus 16.1 mm, between nodus and pterostigma 15.5 mm, between pterostigma and apex about 75.5; anal area 7.5 mm long and 3.5 mm wide, nearly triangular in shape, no anal angle (female specimen); subdiscoidal area transverse but apparently posteriorly closed and not reaching posterior wing margin, long and broad, with one row of cross-veins, 0.8 mm wide, distance between anterior angle of subdiscoidal space and posterior wing margin 4.8 mm; discoidal cell 2.3 mm long and 1.5 mm wide, length of proximal side 0.6 mm; distal free part of CuA separating from MP 7.5 mm from wing base and directed towards posterior wing margin for 1.8 mm; CuAb more strongly directed towards main branch of AA than in NIGP 142170, with a distinct constriction of subdiscoidal space between them; Ax2 2.5 mm distal of arculus, 12 secondary antenodal cross-veins between ScP and RA distal of Ax2; 20 cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 4.5 mm distal of arculus, base of IR2 2.9 mm distally; two antefurcal cross-veins present in space between RP and MA basal of midfork (base of RP3/4); 10 postnodal cross-veins between C and RA; 10 postsubnodal cross-veins between RA and RP1 not aligned with postnodals; no pterostigmal brace; at least four cross-veins below pterostigma; pterostigma sclerotized, long and very narrow, 6.3 mm long, 0.6 mm wide, basally recessed; RP2 aligned with subnodus; 12 cross-veins in Bqr space.

Paratype NIGP 142168 (female). A body with the thorax and seven abdominal segments, with the fore and median legs and all four wings connected; apices of wings not preserved. Main differences with the specimens NIGP 142170 and NIGP 142169 are as follows: forewing slightly longer, preserved part 44.3 mm long, 11.5 mm wide; distance between base and arculus 5.1 mm, between arculus and nodus 18.0 mm, petiole not preserved; subdiscoidal space 1.7 mm long; cubito-anal area slightly narrower than that of NIGP 142170; area between CuA and MP with 1–2 rows of large transverse cells; Ax1 0.8 mm basal of arculus and Ax2 3.0 mm distal of arculus; 11 visible secondary antenodal cross-veins between ScP and RA distal of Ax2; eight visible postnodal cross-veins between C and RA and eight visible postsubnodal cross-veins between RA and RP1; more than eight cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 6.4 mm distal of arculus, closer to arculus than to nodus; structure of base of IR2 aberrant; pterostigma 6.6 mm long, 0.8 mm wide.

Hind wing preserved part 42.2 mm long, 14.0 mm wide; distance between base and arculus 4.3 mm, between arculus and nodus 13.8 mm, between nodus and pterostigma 13.4 mm, pterostigma 5.6 mm long, 0.9

mm wide; anal area 6.4 mm long and 3.3 mm wide, nearly triangular in shape, no anal angle (female specimen); subdiscoidal area transverse but apparently posteriorly closed and not reaching posterior wing margin, long and broad, with one row of cross-veins, 0.8 mm wide, distance between anterior angle of subdiscoidal space and posterior wing margin 4.4 mm; discoidal cell 2.0 mm long and 1.4 mm wide, length of proximal side, 0.6 mm; distal free part of CuA directed towards posterior wing margin for 1.8 mm; CuAb more strongly directed towards main branch of AA than in NIGP 142170, with a distinct constriction of subdiscoidal space between them; Ax2 1.9 mm distal of arculus, 11 secondary antenodal cross-veins between ScP and RA distal of Ax2; 18 cross-veins in area between RA and RP, between arculus and nodus; base of RP3/4 4.1 mm distal of arculus, base of IR2 2.3 mm distally; three antefurcal cross-veins present in space between RP and MA basal of midfork; 12 postnodal cross-veins between C and RA; 12 postsubnodal cross-veins between RA and RP1 not aligned with postnodals; no pterostigmal brace; at least four cross-veins below pterostigma; 15 cross-veins in Bqr space.

Paratype NIGP 142167 (male). A body with the thorax and three abdominal segments, with the fore and median legs and all four wings connected; apices of wings not preserved, except for the left wings. The wing venation is nearly identical to that of specimen NIGP 142170. Forewing 50.0 mm long, 11.0 mm wide; distance from base to arculus 5.5 mm; from arculus to nodus 18.0 mm, from nodus to pterostigma 14.5 mm; from pterostigma to wing apex 8.0 mm; pterostigma 5.0 mm long, covering three or four cells. Hind wing 46.0 mm long, 13.0 mm wide; distance from base to arculus 5.2 mm; from arculus to nodus 14.5 mm, from nodus to pterostigma 14.5 mm; from pterostigma to wing apex 7.5 mm; pterostigma 5.9 mm long, covering four cells.

Discussion. The four fossils described here belong to the same species because of their similar wing venation. Their main differences are attributable to sexual dimorphism or intraspecific variations. *Sinokaratawia* **gen. nov.** has all the synapomorphies of the Isophlebioidea (= Campterophlebiidae and Isophlebiidae) (see Bechly, 1996).

Bechly (1996) proposed the following potential synapomorphies for the Isophlebiidae:

(1) ‘forewing primary antenodal cross-veins Ax1 and Ax2 hypertrophied and of distinct and converging obliquity’. This character is related to the strong obliquity of Ax1, present in *Isophlebia* Hagen, 1866 and *Anisophlebia* Handlirsch, 1908. If Ax1 and Ax2 are convergent in *Sinokaratawia* forewing, this is due to the strongly oblique Ax2, thus this is not homologous to the situation in Isophlebiidae.

(2) ‘AA not reaching CuA in both pairs of wings, so that the subdiscoidal cell is posteriorly opened’. This character is less important than Bechly supposed because it is present in the male hind wings of the campterophlebiid genera *Pteropteron* Pritykina, 1970 and *Amnifleckia* Zhang *et al*., 2006 (Zhang *et al*. 2006), while the female hind wing in the closely related genus *Bellabrunetia* Fleck and Nel, 2002 has its subdiscoidal cell is posteriorly closed (Fleck and Nel 2002). This character is also present in the male hind wing of *Sinokaratawia* but the subdiscoidal cell is posteriorly closed or nearly so in the female hind wing of the same species. Thus this character is of little use in separating Campterophlebiidae and Isophlebiidae.

(3) ‘basal closure of discoidal cell in forewings, correlated with a shifting of distal side (MAb) of discoidal cell distinctly distal of arculus’. The forewings of several Campterophlebiidae are unknown. The forewing discoidal cell of *Sinokaratawia* is not of this type but of campterophlebiid type.

(4) ‘distal side (MAb) of discoidal cell and gaff (basal of CuA, before its furcation) orientated in one transverse axis’. This character is present in *Sinokaratawia* but also in some campterophlebiid genera.

(5) ‘gaff further prolonged, so that basal area between MP and CuA twice as wide as basal area between MA and MP’. In the Campterophlebiidae and *Sinokaratawia*, the basal area between MP and CuA is less than twice as wide as the basal area between MA and MP.

(6) ‘very large size, correlated with an extremely strong thorax and abdomen’. This is not the case for *Sinokaratawia*.

Bechly (1996) proposed two other putative synapomorphies for Isophlebiidae: (1) ‘CuAa strongly bent at bifurcation of gaff and running more or less parallel to MP for some distance’. *Sinokaratawia* has this charac-

ter, but it is also present in some Campterophlebiidae (*Bathmophlebia* Pritykina, 1970, *Campterophlebia* Bode, 1905, *Hypsomelana* Pritykina, 1968, *Oreophlebia* Pritykina, 1970 [Pritykina 1970; Nel *et al*. 1993]); (2) 'RP3/4 not parallel to IR2'. This character is erroneous, as already noted by Fleck and Nel (2002). Thus, these characters are not sufficient to characterize Isophlebiidae. In conclusion, *Sinokaratawia* shares no synapomorphy with the Isophlebiidae.

Bechly (1996) proposed the following potential synapomorphy for Campterophlebiidae: 'space between MAa and MP distally constricted by an opposite curvature of these two veins'. This character is very ambiguous because it is present in some Campterophlebiidae (hind wings of *Campterophlebia* and *Oreophlebia*) but in the hind wings of *Xanthohypsa* Pritykina, 1970 and *Oshinia* Pritykina, 1985, MP is straight and MAa curved, unlike the curved MP and straight MAa in hind wing of *Bathmophlebia*. The definition and homology of this character need improvement. *Sinokaratawia* has MP straight, MAa with a smooth bend, and a constriction of the area between MAa and MP. Bechly (1996) also characterized Campterophlebiidae by presence of a very acute or even hook-like projecting anal angle in male hind wing, which is present in *Sinokaratawia*.

All Campterophlebiidae with veins RP3/4 and IR2 preserved have a distinct constriction of the area between these veins, present in *Sinokaratawia* (*Campterophlebia*, *Karatawia* Martynov, 1925, *Oreophlebia*, *Sarytashia* Pritykina, 1970, *Olonkia* Pritykina, 1985, *Bathmophlebia*, *Xanthohypsa*, *Oshinia*, *Sibirioneura* Pritykina, 1985, *Bellabrunetia*, *Amnifleckia*, and *Parabrunetia* Zhang et al., 2006). This character is unique to this group of taxa and probably represents a synapomorphy not listed by Bechly (1996). It is absent in *Isophlebia*, *Anisophlebia* and *Hypsosagulia*. This structure is unknown for several taxa currently included in the Campterophlebiidae.

The wing venation of *Sinokaratawia* is very similar to the recently described genera *Bellabrunetia*, *Amnifleckia*, and *Parabrunetia*, from which it differs in its MAa distally zigzagged. The same character excludes the genus *Sarytashia*. *Sinokaratawia* differs from the two rather enigmatic genera *Xeta* Pritykina, 2006 and *Sinitsia* Pritykina, 2006 in the same character and in the absence of long basal branch of AA parallel to AP (Pritykina 2006). *Sinokaratawia* differs from *Pternopteron* in its hind wing cubito-anal area broader and male anal angle less developed. The same second character excludes the genus *Oreophlebia*. *Sinokaratawia* differs from *Karatawia* and *Melanohypsa* Pritykina, 1968 in the presence of two rows of cells in its forewing postdiscoidal area and basal part of area between MP and CuA. The poorly known genus *Adelophlebia* Pritykina, 1980 is based on a forewing base. It differs from *Sinokaratawia* in its CuAa longer and better defined in its distal part. All other described genera differ from *Sinokaratawia* in their anal and cubito-anal area of both male and female (Nel and Paicheler 1993).

Acknowledgements

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