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To cite this article: Diyang Huang, Yanzhe Fu & André Nel (2020) The first Chinese representative of the Jurassic damsel-dragonfly genus *Hypsothemis* (Odonata: Isophlebioidea: Campterophlebiidae), *Alcheringa: An Australasian Journal of Palaeontology*, 44:1, 99-103, DOI: [10.1080/03115518.2019.1665709](https://doi.org/10.1080/03115518.2019.1665709)

To link to this article: <https://doi.org/10.1080/03115518.2019.1665709>



Published online: 07 Oct 2019.



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The first Chinese representative of the Jurassic damsel-dragonfly genus *Hypsothemis* (Odonata: Isophlebioidea: Camptero-phlebiidae)

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HUANG, D., FU, Y. & NEL, A. 4 October 2019. The first Chinese representative of the Jurassic damsel-dragonfly genus *Hypsothemis* (Odonata: Isophlebioidea: Camptero-phlebiidae). *Alcheringa* 44, 99–103. ISSN 0311–5518

A new camptero-phlebiid damsel-dragonfly, *Hypsothemis sinensis* sp. nov., is described from the lowermost Upper Jurassic Haifanggou Formation at the Daohugou locality in the Ningcheng Basin, China. This is the first Chinese representative of this genus, previously known only from the coeval upper Karabastau Formation in Kazakhstan, reflecting strong palaeobiogeographic links between these two entomofaunas.

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Key words: Odonata, Camptero-phlebiidae, Late Jurassic, new taxon.

CAMPTEROPHLEBIIDAE Handlirsch, 1920 is the largest family of the clade Isophlebiida Bechly, 1996 (Fleck & Nel 2002). Eleven genera were recorded from the Lower Jurassic–Lower Cretaceous of northern China, mostly from the Middle Jurassic of Inner Mongolia (Zheng *et al.*, 2018). In this paper, we describe a well-preserved camptero-phlebiid dragonfly attributable to a new species from the Daohugou locality, Ningcheng County, Inner Mongolia, China. This outcrop has yielded hundreds of insect fossils including other camptero-phlebiid damsel-dragonflies. This new species is attributed to *Hypsothemis* Pritykina, 1968, a genus known previously from only one species from the middle–upper Karabastau Formation of the Karatau Range in Kazakhstan.

Material and methods

The damsel-dragonfly described herein was collected from the hill behind Beigou Village (for detailed information, see Huang 2015) at Daohugou, Ningcheng County, Inner Mongolia, NE China. The fossil was collected from a location higher than the conchostracan layers that are supposed to be dated to the earliest Late Jurassic but very close to the Middle–Late Jurassic boundary (Huang *et al.* 2018a,b, Huang 2019). It was

prepared using a sharp knife. The specimen was examined dry and photographed using a Zeiss Discovery V16 microscope system and Nikon 5d2 digital camera. The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996). The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). Wing abbreviations are as follows: AA: anterior anal; AP: posterior anal; Arc: arculus; Ax: primary antenodal cross-vein; C: costa; Cr: nodal cross-vein; CuAa: distal branch of anterior cubitus; CuAb: proximal branch of anterior cubitus; CuP: posterior cubitus; DC: discoidal cell; IR: intercalary radial vein; MAa: anterior branch of anterior median; MAb: posterior branch of anterior median; MP: posterior median; N: nodus; 'O': oblique vein; Pt: pterostigma; RA: anterior radius; RP: posterior radius; Sn: subnodal cross-vein; ScP: posterior subcosta.

Systematic palaeontology

Order ODONATA Fabricius, 1793

Superfamily ISOPHLEBIOIDEA Handlirsch, 1906–1908

Family CAMPTEROPHLEBIIDAE Handlirsch, 1920

Hypsothemis Pritykina, 1968

Type species. Hypsothemis fraseri Pritykina, 1968.

Hypsothemis sinensis sp. nov. (Fig. 1)

Etymology. Named after ‘Sinica’, Latin name for China.

Holotype. NIGP170590 (imprints of fragments of legs, a complete abdomen, and two hind wings, one nearly complete, the base of the second hidden under the first).

Diagnosis. Hindwing venation characters only. Two rows of cells between CuAa and posterior wing margin; 10 cells in anal area.

Description. Abdomen 61.6 mm long, 4.0 mm wide, with a strong, curved and rather long ovipositor, surpassing apex of abdomen by 5.3 mm; hindwings without any trace of coloration, probably hyaline, 63.5 mm long, 10.6 mm wide (at nodus level); distance between base and arculus 7.1 mm, between arculus and nodus 24.1 mm, between nodus and pterostigma 19.2 mm, between pterostigma and apex 8.2 mm; wing not petiolate, anal area 6.7 mm long, 2.5 mm wide; two rows of large irregular cells between AA and AP; no anal angle (congruent with female specimen); a long basal posterior branch of AA parallel with AP and delimiting a long and narrow cell; main branch of AA distally bent strongly towards posterior wing margin and nearly parallel with MP + CuA and distally with CuA, distally reaching CuAb; median area free of cross-veins; submedian area free; a curved vein CuP separating submedian and subdiscoidal areas; subdiscoidal space transverse, free of cross-veins, 1.2 mm long, 2.6 mm wide; discoidal cell closed basally, 1.8 mm long, 1.4 mm wide, free of cross-veins, length of proximal side 0.67 mm, of distal side MAb 1.4 mm; RP + MA separated at right angle from RA, strongly curved; RP separated from MA just distal of arculus; MA very strong basally, divided into MAa and MAb 1.9 mm distally; MAb well aligned with distal free part of CuA; CuA separating from MP 9.1 mm from wing base and directed towards posterior wing margin for 1.7 mm; CuA divided distally into CuAa and CuAb, CuAb 1.0 mm long, meeting main branch of AA and posteriorly closing subdiscoidal area; CuAa basally more or less parallel to posterior wing margin with two rows of cells between them; CuAa strongly curved distally, short; area between CuAa and MP with 2–4 rows of large cells, 2.3 mm wide; 13–14 rows of cells in area between MP and posterior wing margin; MP nearly straight, reaching posterior margin well distal of nodus level; MAa nearly straight, parallel with MP, with one

row of cells in postdiscoidal area, 1.3 mm wide, this area being distinctly narrower near posterior wing margin; primary antenodal cross-veins very strong, Ax1 1.2 mm basal of arculus and Ax2 2.9 mm distal of arculus; Ax2 and Ax1 of distinct and converging obliquity; no secondary antenodal cross-vein of first row between C and ScP; seven preserved secondary antenodal cross-veins of second row between ScP and RA and seven in area between RA and RP, between arculus and nodus; base of RP3/4 14.1 mm basal to nodus, closer to arculus than to nodus; base of IR2 close to that of RP3/4, 1.2 mm distally; *ca* 18 postnodal cross-veins of first row between C and RA; *ca* 19 preserved postnodal cross-veins of second row between RA and RP1, not aligned with those of first row; no pterostigmal brace; two cross-veins in distal part below pterostigma; pterostigma long and narrow, basally recessed at two-third of distance between nodus and apex, sclerotized, 5.9 mm long, 0.8 mm wide, covering four cells; vein C distinctly widened along pterostigma; area between C and RA distal of pterostigma long; RP2 aligned with subnodus; 11 cross-veins in Bqr space between RP, RP2, IR2 and oblique cross-vein ‘O’; one oblique vein ‘O’ two cells and 1.2 mm distal of base of RP2; RP2 nearly straight; base of IR1 six cells and 5.9 mm distal of base of RP2; IR1 basally zigzagged but regularly curved distally, more or less parallel to RP1; area between MA and RP3/4 strongly widened distally with 12 rows of cells along posterior wing margin; area between RP3/4 and IR2 with one row of cells basally but broadened distally, and further distally constricted again; area between IR2 and RP2 with one row of cells and distally with 3–4 rows of cells near posterior wing margin; area between RP2 and IR1 progressively widened, with 2–3 zigzagged intercalary longitudinal veins and about five rows of cells between them; area between IR1 and RP1 not widened distally, with seven rows of cells between them and one or two weak longitudinal intercalary veins.

Discussion

Hypsothemis sinensis sp. nov. has the synapomorphies of Campterophlebiidae: CuAa shortened in hind wing, correlated with a distally more strongly expanded area between MP and CuAa and with development of numerous convex parallel ‘secondary branches’ of MP; pterostigmata elongated and recessed basally; hind wing subdiscoidal space enlarged and transversely elongated, correlated with a very long and straight gaff (=basal CuA before its branching); space between MAa and MP constricted distally by an opposite curvature of these two veins [but Nel *et al.* (2009) noticed that this character is ambiguous and variable among Campterophlebiidae]; a distinct distal constriction of the area between the veins RP3/4 and IR2.

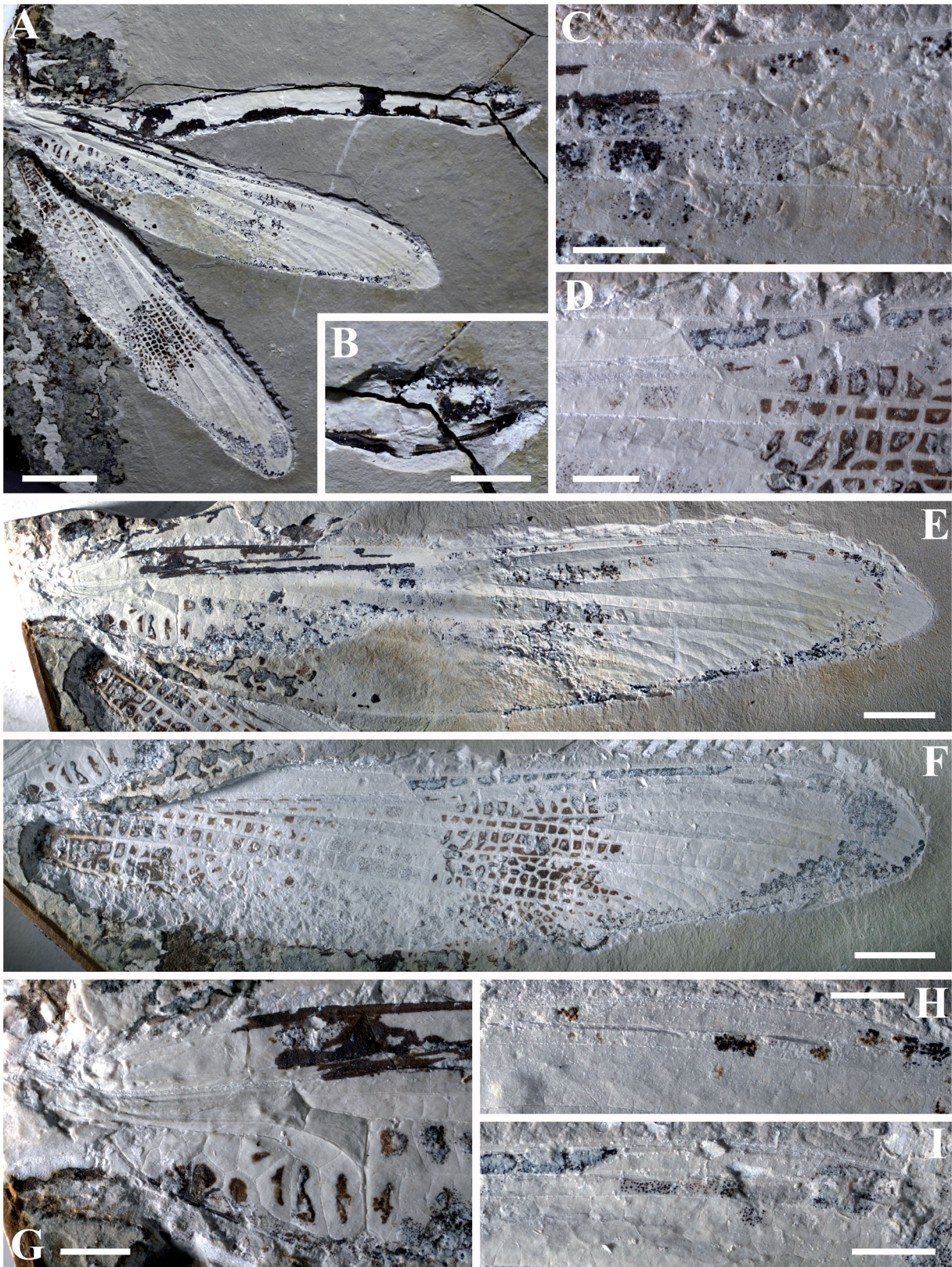


Fig. 1. *Hypsothemis sinensis* sp. nov., holotype NIGP170590. A, General habitus; B, Apex of abdomen with ovipositor; C, Nodus of first wing; D, Nodus of second wing; E, First hind wing; F, Second hind wing; G, Base of first wing; H, Pterostigma of first wing; I, Pterostigma of second wing. Scale bars = 10 mm (A); 5 mm (B, E, F); 2 mm (C, D, G, H, I).

This last character is less pronounced than in the majority of campterophlebiid genera (*Campterophlebia* Bode, 1905, *Karatawia* Martynov, 1925, *Oreophlebia* Pritykina, 1970, *Sarytashia* Pritykina, 1970, *Olonkia* Pritykina, 1985, *Bathmophlebia* Pritykina, 1970, *Xanthohypsa* Pritykina, 1970, *Oshinia* Pritykina, 1985, *Sibirioneura* Pritykina, 1985, *Bellabrunetia* Fleck & Nel, 2002, *Amnifleckia* Zhang *et al.*, 2006, *Parabrunetia* Zhang *et al.*, 2006 and *Zygokaratawia* Nel *et al.*, 2008) (Fleck & Nel 2002, Zhang *et al.* 2006, Nel *et al.* 1993, 2008).

This constriction is less pronounced in *Sinokaratawia* Nel *et al.*, 2007 and *Sinitsia* Nel *et al.*, 2009 (Nel *et al.* 2007, 2009), as in *Hypsothemis sinensis*. Unfortunately, this structure is unknown for several taxa currently included in Campterophlebiidae.

Hypsothemis sinensis differs from *Sinitsia* and *Hsiufua* Zhang & Wang, 2013 in the more distal position of the pterostigma between the nodus and wing apex and a less pronounced constriction of the area between RP3/4 and IR2, even if they have very similar anal and cubito-anal areas (Zhang *et al.* 2013). *Hypsothemis sinensis* differs from *Sinokaratawia* in the presence of only one row of cells in the postdiscoidal area, a narrower area between MP and the posterior wing margin, and a distinctly narrower anal area (Nel *et al.* 2007, Zhang *et al.* 2006).

Petrophlebia Tillyard, 1925 has a small, not transverse subdiscoidal space, unlike *Hypsothemis sinensis* and the other Isophlebioidea (Kelly & Nel 2018). It probably does not belong to this clade. *Olonkia* Pritykina, 1985 (based on a forewing fragment) has its veins RP + MA, MA, Mab, and CuA very well aligned, and two rows of cells in the postdiscoidal area, unlike *Hypsothemis sinensis*. *Hypsophlebia dubia* Pritykina, 1985 (based on a hind wing fragment) has a longer CuAa and a broader and shorter subdiscoidal space than *Hypsothemis sinensis*. *Hypsophlebia scalaris* Pritykina, 1970 and *Hypsomelana sepulta* Pritykina, 1968 have long and zigzagged CuAa in the hind wing, unlike *H. sinensis*. *Gampsophlebia* Pritykina, 1980 has a very short hind wing subdiscoidal space, unlike *H. sinensis* (Pritykina 1980). *Melanohypsa* Pritykina, 1968, *Parafleckium* Li *et al.*, 2012 and *Dorsettia* Whalley, 1985 have a hind wing subdiscoidal space that is posteriorly opened, unlike *H. sinensis* (Whalley 1985, Li *et al.* 2012, Zheng *et al.* 2016). *Sogdophlebia* Pritykina, 1970 has a hind wing subdiscoidal space that is not transverse and an oblique basal free part of CuA, unlike *H. sinensis*. Note that the Chinese species ‘*Sogdophlebia*’ *xinjiangica* Zhou, 1993 is a very strange fossil that should be revised. Nevertheless, it strongly differs from *Hypsothemis sinensis* in the very broad postdiscoidal area (Zhou 1993). *Pteropteron* Pritykina, 1970, *Qibinlina* Nel *et al.*, 2009, *Lateophlebia* Kelly & Nel 2018 and *Pritykinia* Nel *et al.*, 2009 have posteriorly opened subdiscoidal

spaces (Nel *et al.* 1993, 2009, Kelly & Nel 2018). *Jufengi* Zheng *et al.*, 2017 has a relatively narrow area between MP and CuAa, as wide as the postdiscoidal area, unlike *Hypsothemis sinensis* (Zheng *et al.* 2017).

Hypsothemis sinensis differs from *Sogdophlebia singularis* Pritykina, 1970, *Sagulia ansinervis* Pritykina, 1970, and *Honghea* Zheng *et al.*, 2018 in the anal area. *Zygokaratawia* Nel *et al.*, 2008, *Ctenogampsophlebia* Petrulėvičius *et al.*, 2011, and *Parazygokaratawia* Huang *et al.*, 2018a have much narrower wings (Petrulėvičius *et al.* 2011, Huang *et al.* 2018a).

Hypsothemis sinensis shares with *Hypsothemis fraseri* Pritykina, 1968, *Sogdophlebia singularis*, *Sagulia ansinervis*, *Campterophlebia* and *Sinitsia* the presence of a long basal posterior branch of AA, that is long and parallel to AP in the hind wing.

Hypsothemis sinensis has an anal area and a subdiscoidal space very similar to those of *Hypsothemis* Pritykina, 1968. *Hypsothemis* is a poorly known genus based on the basal part of a female hind wing. Apparently, *Hypsothemis sinensis* differs from *Hypsothemis fraseri* Pritykina, 1968 by the presence of two rows of cells between CuAa and the posterior wing margin, instead of only one in *H. fraseri* (Pritykina 1968). *Hypsothemis sinensis* also has more cells (10 vs eight) in the anal area compared with *H. fraseri*. These differences support only a difference at species level. Thus, we provisionally consider that *Hypsothemis sinensis* belongs to *Hypsothemis*, but only the discovery of a more complete specimen of *H. fraseri* will enable definitive comparison between these two taxa.

Conclusion

The presence of a long, curved ovipositor was known previously for a few other Isophlebioidea. Its discovery in this fossil suggests that it is a widespread character in this clade. This structure could be linked to oviposition in mud, similar to the extant Cordulegastridae. Three other Mesozoic clades have similar long ovipositors, viz., Aeschnidiidae, Steleopteridae and Tarsophlebiidae (Nel *et al.*, 1993, Fleck and Nel, 2003, Fleck *et al.* 2004). It is possibly an adaptation to a specialized lifestyle or to particular environments that no longer exist. *Hypsothemis fraseri* is from the early Late Jurassic of Karatau, whereas *Hypsothemis sinensis* is only slightly older, from the earliest Late Jurassic. This discovery shows that this genus was rather widespread in Central Asia at these times.

Acknowledgements

We sincerely thank one anonymous referee for the very useful comments on the first version of the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Key Research and Development Program of China [Grant No. 2016YFC0600406], the Strategic Priority Research Program of the Chinese Academy of Sciences [XDB26000000 and XDB18000000], and the National Natural Science Foundation of China [41688103].

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