Cretaceous Research 100 (2019) 138–144

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Short communication

New gomphaeschnid dragonflies (Odonata: Anisoptera: Aeshnoptera) from mid-Cretaceous Burmese amber

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ARTICLE INFO

Article history:
Received 31 January 2019
Received in revised form
11 March 2019
Accepted in revised form 31 March 2019
Available online 5 April 2019

Keywords:
Gomphaeschnidae
Anisoptera
Odonata
Cretaceous
Burmese amber

ABSTRACT

A new true dragonfly, named *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., is described from Cretaceous Burmese amber representing the second gomphaeschnaoidine from this deposit. *Kachinaeshna* Zheng, Nel and Wang, gen. nov. differs from other Gomphaeschnaoidinae in: the absence of an elongate distal paranal cell, directly basal of the anal loop, in the hindwing; a distinct curvature of RP2; and a curve of RP1 at the pterostigmal brace. The gomphaeschnaoidine dragonflies were previously only recorded from the Lower Cretaceous and mainly from the upper Aptian Crato Formation of Brazil. Based on the true dragonfly fossils found in Burmese amber, a possible late Early Cretaceous age is supported for Burmese amber.

1. Introduction

Mid-Cretaceous Burmese amber contains abundant true dragonflies represented by the families Araripegomphidae, Burmaeshnidae, Burmagomphidae, Gomphidae, Gomphaeschnidae, and Paraburmagomphidae (Schädel and Bechly, 2016; Zheng et al., 2016, 2017a, 2018a, b, c; Huang et al., 2017a, b). Among them, Gomphaeschnidae is a member of Aeshnoptera, whose fossil record show a world-wide distribution (Bechly et al., 2001). Gomphaeschnidae comprise two subfamilies Gomphaeschnaoidinae and Gomphaeschninae, with the former containing the tribes Sinojagorini Bechly et al., 2001 and Gomphaeschnaoidini Bechly et al., 2001, and the unplaced species *Anomalaeschna berndschsteri* Bechly et al., 2001. Sinojagorini contain three species of the genus *Sinojagoria* Bechly et al., 2001 described from the Lower Cretaceous Yixian Formation (Barremian–Aptian) of western Liaoning, NE China (Zheng et al., 2017b). *A. berndschsteri* is from the Lower Cretaceous Crato Formation (upper Aptian) of Brazil. The Gomphaeschnaoidini have a high diversity but are all recorded from the Lower Cretaceous and mostly from the Crato Formation (Bechly et al., 2001). A very fragmentary gomphaeschnaoidinin, *Cretagomphaeschnaoides jarzembowskae* Zheng et al., 2016, has been previously described from Burmese amber (Zheng et al., 2016). Here we describe the second gomphaeschnid dragonfly from this amber.

2. Material and methods

The amber containing the dragonflies was collected in the Hukawng Valley (26° 29′ N, 96° 35′ E) of Kachin Province, Myanmar (locality in Zheng et al., 2018d: Supplementary fig. 2b). The age of Burmese amber is considered to be earliest Cenomanian with a U–Pb zircon dating of ca. 98.79 ± 0.62 Ma (Shi et al., 2012) although

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https://doi.org/10.1016/j.cretres.2019.03.027
0195-6671/

this may be too young (Mao et al., 2019). Palynology and an ammonite from the amber-bearing layers indicate a late Albian age (Cruickshank and Ko, 2003), which is also supported by a dragonfly inclusion of a Gondwanan group previously only recorded from the Crato Formation of Brazil (Zheng et al., 2018c). It may be noted that another site yielding an amber biota (Tilin; ca. 72.1 Ma) has been recently reported from central Myanmar and is distinctly younger than Kachin burmite (Zheng et al., 2018d).

The amber pieces containing the dragonflies are yellow and transparent. Photographs were taken using a Zeiss Stereo Discovery V16 microscope system and Zen software. In most instances, incident and transmitted light were used simultaneously. All images are digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using the free software Combine ZP for a better illustration of the 3D structures. The line drawings were prepared from photographs using image-editing software (CorelDraw X7 and Adobe Photoshop CS6). The specimen is housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences. All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:6EF767AE-A5FC-468E-8E71-FEA9E3926C34.

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 Jacquelin et al. (2018). The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system proposed by Bechly (1996). Wing abbreviations are as follows: AA, anal anterior; AL, anal loop; Arc, arculus; Ax, primary antenodal crossvein; Cr, nodal crossvein; CuAa, distal branch of anterior cubitus; CuAb, proximal branch of anterior cubitus; CuP, cubitus posterior; DT, discoidal triangle; HT, hypertriangle; IR, intercalary radial vein; MA, median anterior; MP, median posterior; N, nodus; 'O', oblique vein; PC, paranal cell; RA, radius anterior; RP, radius posterior; ScP, subcosta posterior; SdT, subdiscoidal triangle; Sn, subnodal crossvein. All measurements are given in mm.

3. Systematic palaeontology

Order Odonata Fabricius, 1793.
Suborder Anisoptera Selys Longchamps, 1854.
Clade Aeshnoptera Bechly, 1996.
Family Gomphaeschnidae Tillyard and Fraser, 1940.
Subfamily Gomphaeschnaoidinae Bechly et al., 2001.

Genus ***Kachinaeshna*** Zheng, Nel and Wang, gen. nov.
(urn:lsid:zoobank.org:act:2134F163-EFDD-4C11-8F5C-4AB71133052E).
Type species. *Kachinaeshna zhuoi* Zheng, Nel and Wang, sp. nov.

Diagnosis. Wing venation characters only available. Forewing Ax2 shifted basally to level of basal angle of discoidal triangle; hindwing Ax2 lying well distal of basal side of discoidal triangle; secondary antenodal crossvein between Ax1 and Ax2 well aligned; discoidal triangles two-celled; pterostigma long, covering two or three cells; no curvature of RP1 at pterostigmal brace; no elongate distal paranal cell in hindwing, directly basal of anal loop; RP2 nearly straight; IR1 base opposite to pterostigmal brace; anal loop closed, four- or five-celled.
Etymology. Named after Kachin Province and the genus *Aeshna*.

Kachinaeshna zhuoi Zheng, Nel and Wang, sp. nov.
(urn:lsid:zoobank.org:act:69D910CE-BC12-4837-9839-2637560755AB).
(Figs. 1–5).

Diagnosis. Same as generic diagnosis, monotypic.
Holotype NIGP 170038, a pair of nearly complete forewings, and an incomplete, divided hindwing.
Paratype NIGP 170039, a pair of incomplete forewings and a partly curled hindwing.
Locality and horizon. Hukawng Valley, Kachin Province, Myanmar; lower Cenomanian, lowermost Upper Cretaceous but see discussion.
Etymology. The specific name is after Mr. Zhuo De who helped us collect the specimens.

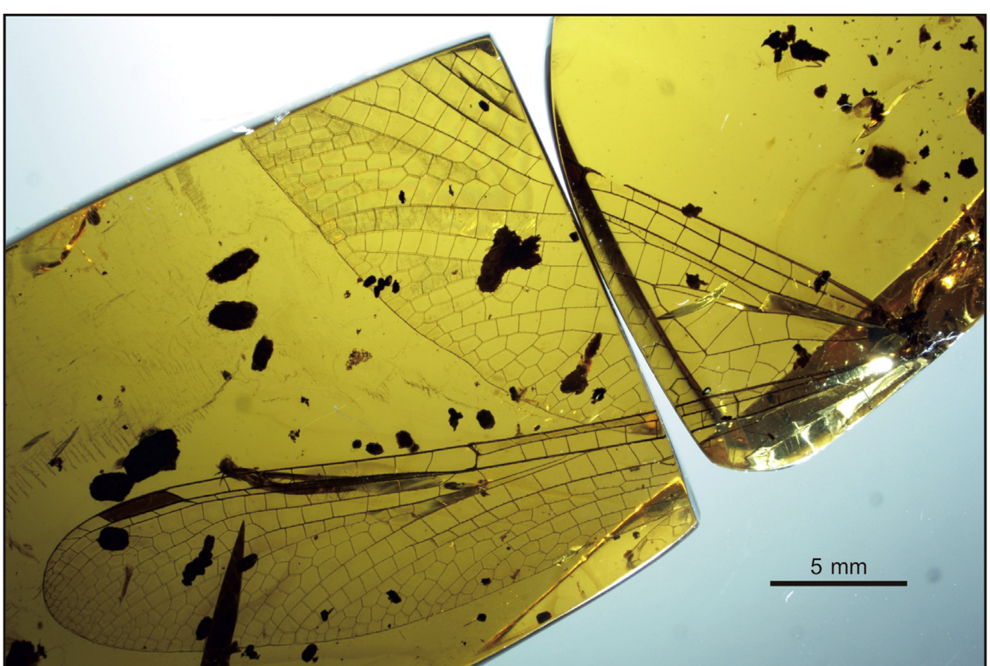

Fig. 1. *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., holotype (NIGP 170038), photograph of general habitus.

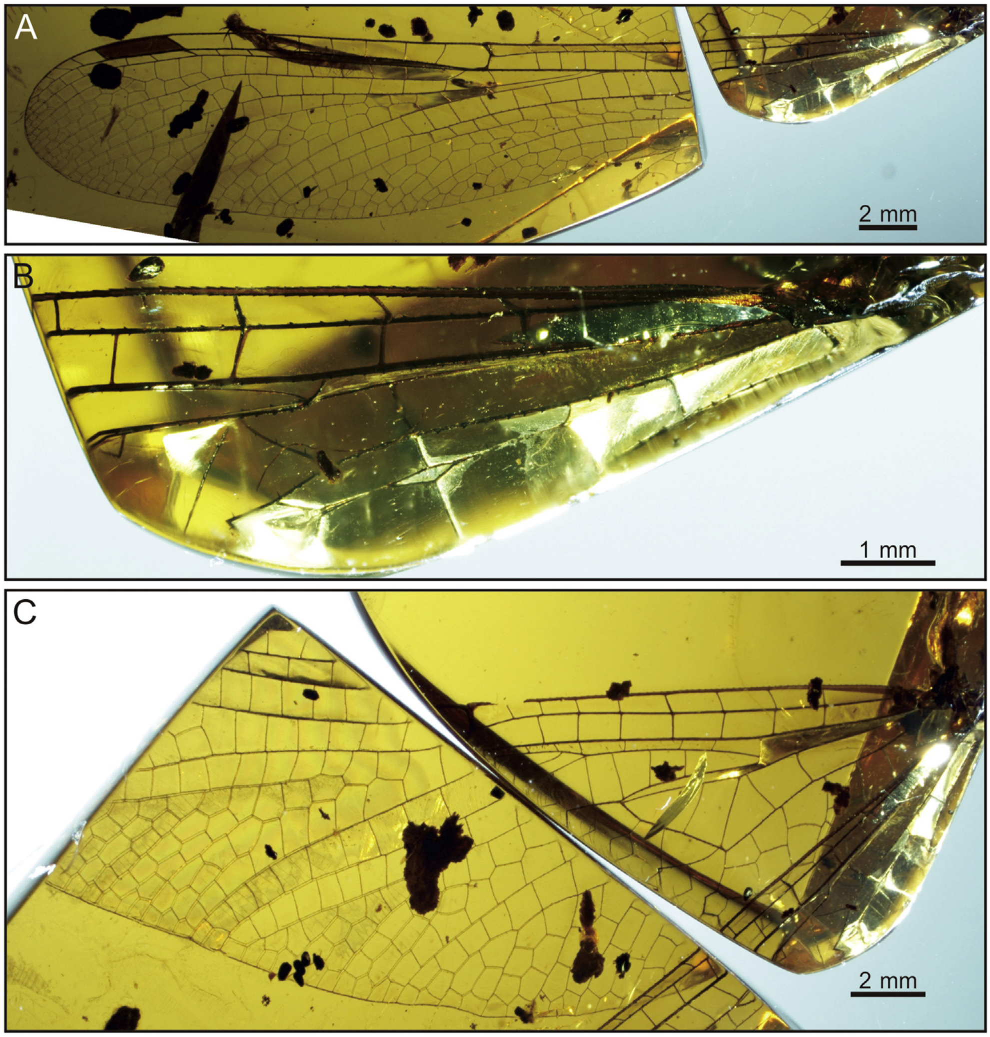

Fig. 2. *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., holotype (NIGP 170038), photograph of forewing (A), forewing base (B); hindwing (C).

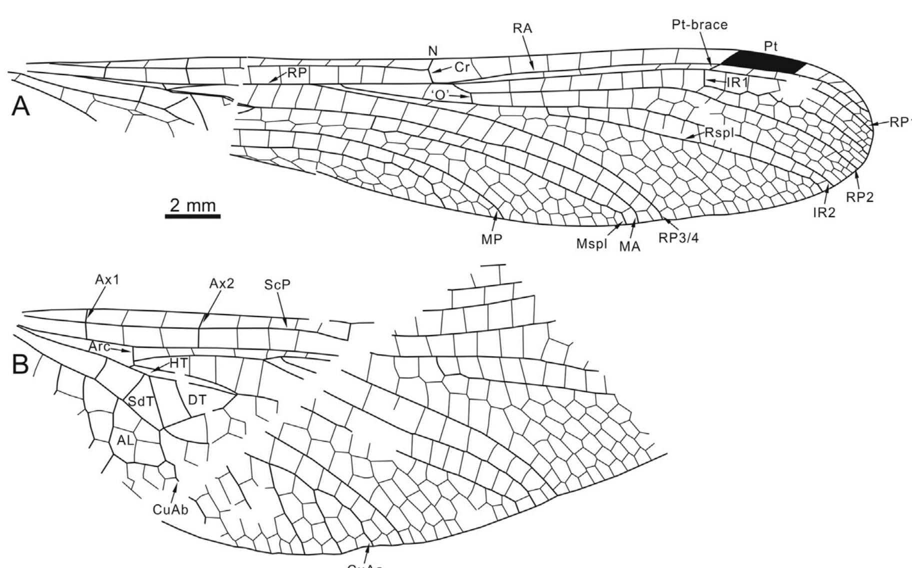

Fig. 3. *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., holotype (NIGP 170038), line drawing showing wing venation of forewing (A); hindwing (B).

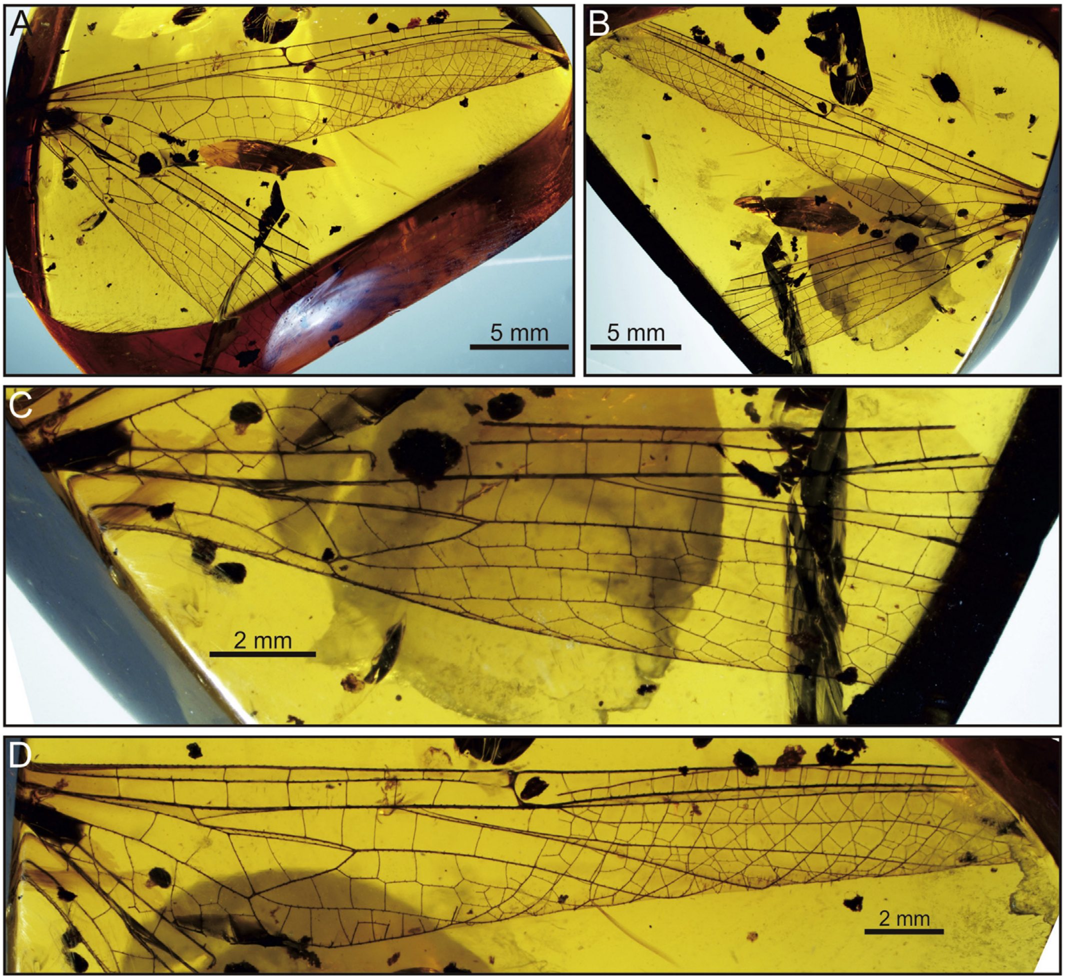

Fig. 4. *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., paratype (NIGP 170039), photograph of habitus (A–B), forewing (C); hindwing (D).

Description. Forewing hyaline (Figs. 1, 2A–B, 3A), 31.1 mm long and 5.3 mm wide at level of N; length from Arc to N 9.7 mm; from N to Pt 10.5 mm, from Pt to wing apex 5.2 mm; Pt rather long, 2.5 mm long and 0.64 mm wide, covering two and a half cells, braced by an oblique and straight crossvein; seven postnodal crossveins between N and Pt, not aligned with corresponding postsubnodal crossveins between RA and RP1; primary antenodal crossveins well defined, Ax1 2.1 mm basal of Arc, and Ax2 1.0 mm distal of Arc at level of basal angle of DT; a single aligned secondary antenodal crossvein present between Ax1 and Ax2; six non-aligned secondary antenodal crossveins present between Ax2 and N; antefurcal crossveins not visible; ScP fusing with costal margin at N, of

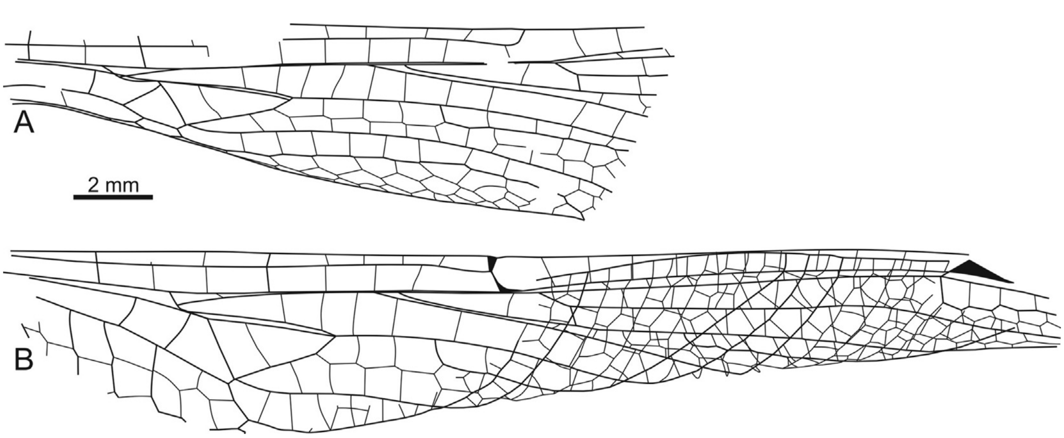

Fig. 5. *Kachinaeshna zhuoi* Zheng, Nel and Wang, gen. et sp. nov., paratype (NIGP 170039), line drawing of forewing (A); hindwing (B).

normal anisopteran-type; antesubnodal area hardly visible; DT two-celled, elongate, with length of anterior side 1.1 mm, of basal side 1.7 mm, of distal side Mab (slightly bent) 1.5 mm; HT poorly visible (because of restricted viewing angle), but apparently free and 3.3 mm long; RP2 aligned with Sn; only a single oblique vein 'O', one cell distal of Sn; a long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2; two convex secondary veins visible in area between Rspl and RP3/4; IR2 weakly curved; RP2 and IR2 divergent somewhat basal of Pt with two or three rows of cells in widened area in-between; RP2 weakly curved but not undulating; RP1 and RP2 only slightly divergent basally with only a single row of cells in-between, but divergent basal of Pt with six cells along wing margin; IR1 well-defined and long, nearly straight and closely parallel to RP1 with only a single row of cells in-between; RP3/4 and MA parallel and gently curved with only one row of cells in-between, except for two rows of cells along posterior wing margin; Mspl long, straight, and parallel to MA with a single row of cells in-between; post-discoidal area basally with two rows of cells, but distally much widened; MP ending on wing margin distal of nodus; CuA ending on wing margin just below N; cubito-anal area with two or three rows of cells; posterior branches of CuA weak.

Hindwing hyaline (Figs 2C, 3B), partly preserved; RP1 and RP2 only slightly diverging basally with only a single row of cells in-between; Rspl long and straight, parallel to IR2 with only a single row of cells between it and IR2. RP3/4 and MA parallel and gently curved with a single row of cells in-between; Mspl long and straight, parallel to MA with only a single row of cells between it and MA; basal part of postdiscoidal area with three rows of cells. Ax1 2.7 mm distal of wing base; Ax2 1.8 mm distal of basal side of DT; two secondary antenodal crossveins between Ax1 and Ax2; four secondary antenodal crossveins distal of Ax2 somewhat aligned; median space free; submedian space crossed by CuP; PsA weakly oblique; SdT one-celled; DT two-celled, shorter than in forewing, with length of anterior side 3.2 mm, of basal side 1.9 mm, of distal sideMAb (weakly angled) 2.9 mm; HT free, 4 mm long. Anal area with three or four rows of cells; anal loop four-celled, posteriorly closed; cubital area with four rows of cells between CuA and posterior wing margin.

Paratype (Figs 4A–B) with partly preserved fore- (Figs 4C, 5A) and hindwing (Figs 4D, 5B), providing additional hindwing characters: Pt basally preserved, strongly braced by an oblique vein; ten postnodal crossveins between N and Pt, not aligned with corresponding postsubnodal crossveins; base of RP2 aligned with Sn. Only a single oblique vein 'O', one cell distal of Sn; a long and straight Rspl, parallel to IR2 with only a single row of cells between it and IR2; IR2 gently curved. RP2 and IR2 begin to diverge somewhat basal of Pt with 2 or 3 rows of cells in widened area in-between; RP2 weakly curved but not undulating; RP2 and RP1 only slightly diverging basally with a single row of cells in-between, but two cells basal of Pt; IR1 slightly zigzagged, parallel to RP1; RP3/4 and MA parallel and gently curved with only a single row of cells in-between, except for a short area with two rows of cells near posterior margin of wing. Mspl long and straight, and parallel to MA with a single row of cells in-between; postdiscoidal area with two rows of cells distal of DT, distally widened; Ax1 1.8 mm basal of Arc; Ax2 2.5 mm distal of Arc; two secondary antenodal crossveins between Ax1 and Ax2; four secondary antenodal crossveins distal of Ax2, not well aligned; median space free; submedian space crossed by CuP. PsA weakly oblique; SdT one-celled; DT two-celled, shorter than in forewing, with length of anterior side 3.2 mm, of basal side 1.7 mm, and of distal side MAb (weakly angled) 2.8 mm; hypertriangle free, 3.2 mm long; anal loop five-celled, posteriorly closed.

4. Discussion

The above two fossil dragonflies belong to the same species because of nearly identical wing venations. *Kachinaeshna* can be attributed to the Aeshnoptera sensu Bechly (1996) in having RP1 and RP2 basally parallel up to the pterostigma, with area between them basally distinctly narrowed with only one row of cells, and a well-developed Rspl. Within Aeshnoptera, *Kachinaeshna* has the arculus lying far from Ax1, excluding any affinities between it and Mesuropetaloidea sensu Bechly (1996). *Kachinaeshna* can be attributed to the Aeshnomorpha Bechly et al., 2001 (Austropetaliida Bechly et al., 2001 and Panaeshnida Bechly et al., 2001) based on the following synapomorphies: forewing discoidal triangle longitudinally elongate, therefore discoidal triangles of both pairs of wings of similar shape; RP2 at least slightly undulating; Rspl well-defined; 'gaff' prolonged.

The Austropetaliida Bechly et al., 2001 have many costal spots, the pterostigmal brace not aligned with the basal side of the pterostigma, a long IR1, CuA and PsA closing upon each other, and the basal lestine crossvein 'O' reduced, greatly differing from *Kachinaeshna*. The attribution of *Kachinaeshna* to Panaeshnida Bechly et al., 2001 (Progobiaeshnidae Bechly et al., 2001 and Aeshnida Bechly, 1996) is supported by the character 'Rspl very well-defined (not zigzagged) in both pairs of wings'. *Kachinaeshna* does not belong to Progobiaeshnidae because the pterostigmal braces have the same obliquity as the basal side of the pterostigma, the anal loop is rather small, and only one row of cells is present between IR2 and Rspl. The attribution of *Kachinaeshna* to Aeshnida and its subdivision Panaeuaeshnida Bechly, 1996 (Paracymatophlebiidae Bechly et al., 2001, and Euaeshnida Bechly, 1996) is supported in it having a well-defined Mspl parallel to MAa, an undulating RP2, and RP3/4 and MA closely parallel to the wing margin. The Paracymatophlebiidae are excluded from comparision because there is only one row of cells in the area between RP1 and RP2, RP3/4 and MA are not undulating, and the anal loop is closed posteriorly. The attribution to the Euaeshnida (Eumorbaeschnidae Bechly et al., 2001 and Neoaeshnida Bechly, 1996) is supported by the veins RP2 and IR2 being more distinctly non-parallel, the forewing discoidal triangle more elongate than that of the hindwing, the forewing subdiscoidal triangle unicellular, and MAb somewhat angled. It, however, does not belong to Eumorbaeschnidae because the forewing MP and MAa are not distally convergent, and RP2 is not strongly undulating. *Kachinaeshna* belongs to Neoaeshnida on the following characters: a well-defined straight Mspl; trigonal planate present in both wing pairs correlated with an angled MAb; only one oblique vein 'O' present; and Ax2 shifted distinctly basal of the level of the distal angle of the discoidal triangle in the forewings.

The Neoaeshnida consists of two groups: Gomphaeschnidae sensu Bechly, 1996 and Aeshnodea Bechly, 1996. *Kachinaeshna* lacks the curvature of RP3/4 and MA present in the Aeshnodea. However, *Kachinaeshna* has the synapomorphies of the Gomphaeschnidae, viz. the most distal part of the antesubnodal area between RA and RP is free of antesubnodal crossveins, there are no accessory cubito-anal crossveins in the submedian space between CuP and PsA, the discoidal triangles are only divided into two cells by a single crossvein, and the hypertriangles are unicellular. This family consists of two subfamilies: Gomphaeschnaoidinae Bechly et al., 2001 and Gomphaeschninae sensu Bechly, 2001. Bechly et al. (2001) and Bechly (1996) did not propose any clear synapomorphy for the Gomphaeschninae. Within the latter subfamily, *Gomphaeschna* Selys Longchamps, 1871 and *Oligoaeschna* Selys Longchamps, 1889 show an undulation of RP2 and of MAa, unlike *Kachinaeshna* (Martin, 1908). The same occurs in *Linaeschna* Martin, 1909 in which the discoidal triangles are divided into many cells (von Ellenrieder, 2002). *Anglogomphaeschna* Nel and Fleck, 2014 has the discoidal triangles divided into many cells (Nel and Fleck, 2014). *Kachinaeshna* shows more similarities with the fossil genera *Cretalloaeschna* Jarzembowski and Nel, 1996 and *Alloaeschna* Wighton and Wilson, 1986. These two genera, however, have a forewing Ax2 well distal to the level of the basal angle of the discoidal triangle, unlike *Kachinaeshna* (Wighton and Wilson, 1986; Jarzembowski and Nel, 1996).

Kachinaeshna is, however, attributable to the Gomphaeschnaoidinae (comprising Sinojagorini Bechly et al., 2001, Gomphaeschnaoidini Bechly et al., 2001, and *Anomalaeschna berndschsteri* Bechly et al., 2001) in having a single secondary antenodal crossvein between Ax1 and Ax2, and the forewing Ax2 shifted basally to the level of the basal angle of the discoidal triangle. Any affinities of *Kachinaeshna* with *Anomalaeschna* Bechly et al., 2001 are excluded because the later has the pterostigma covering only one cell. Also, *Sinojagoria* Bechly et al., 2001 has many cells, a longer and more basally originating IR1, and a broader anal loop, differing from *Kachinaeshna* (Bechly et al., 2001; Zheng et al., 2017b). The Gomphaeschnaoidini, moreover, have an elongate distal paranal cell in the hindwing directly basal of the anal loop, a distinct curvature of RP2, and a curve of RP1 at the pterostigmal brace, not shared with *Kachinaeshna*. The Burmese amber genus *Cretagomphaeschnaoides* Zheng et al., 2016 has a three-celled forewing discoidal triangle, unlike *Kachinaeshna* (Zheng et al., 2016). In conclusion, *Kachinaeshna* cannot be placed in any known subgroups of Gomphaeschnaoidinae. We therefore propose a new genus and species.

Kachinaeshna shares, however, many characters with the enigmatic Eocene Baltic amber genus *Elektrogomphaeschna* Pinkert et al., 2017. The main differences between it and *Elektrogomphaeschna* are as follows: pterostigma distinctly longer in *Kachinaeshna*; secondary antenodal crossveins between Ax1 and Ax2 well aligned, Ax2 opposite basal angle of forewing discoidal triangle and base of IR1 opposite pterostigmal brace instead of well basal in *Elektrogomphaeschna* (Pinkert et al., 2017). In addition, the Lower Cretaceous genera *Sophoaeschna* Zhang et al., 2008 and *Falsisophoaeschna* Zhang et al., 2008 differ from *Kachinaeshna* in the Ax2 of the hindwing being situated at the level of the basal side of the discoidal triangle (Zhang et al., 2008).

5. Conclusions

Kachinaeshna zhuoi Zheng, Nel and Wang, gen. et sp. nov. is the second true dragonfly belonging to the family Gomphaeschnidae known from Burmese amber. All Gomphaeschnaoidinae, to which it also belongs, were previously only known from the Lower Cretaceous, mostly from the Upper Aptian Crato Formation of Brazil. In Burmese amber, another araripegomphid dragonfly, *Araripegomphus shai* Zheng et al., 2018, belongs to a genus and family also previously only recorded from the Crato Formation (Zheng et al., 2018c). These Gondwanan dragonflies support a possible Late Early Cretaceous age for Burmese amber. The burmagomphida dragonfly, however, firstly recorded in Burmese amber (Zheng et al., 2018a), has also been discovered in the Eocene lake deposits of Aegentina (Petrulevičius, 2017), indicating a long extension.

Acknowledgements

We offer our sincere gratitude to editors and anonymous reviewers for their very useful comments on the earlier version of the manuscript. This research was supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000) and the National Natural Science Foundation of China (41572010, 41622201, 41688103), the Second Tibetan Plateau Scientific Expedition program (XDA20070300), and is a Leverhulme Emeritus Fellowship contribution for EAJ.

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