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Redescription of the 'libelluloid' *Mesocordulia boreala* (Odonata: Mesocorduliidae) from the Lower Cretaceous of China

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Abstract

On the basis of a very well-preserved new specimen, we redescribe the Early Cretaceous genus and species *Mesocordulia boreala*, currently attributed to the Cretaceous subfamily Mesocorduliinae of Araripelibellulidae. We refine key characteristics of wing venation, which allow us to exclude this species from the Araripelibellulidae and elevate the Mesocorduliinae to the family rank as Mesocorduliidae. The relationships of this fossil are clarified. As the genus name *Mesocordulia* is preoccupied, we propose a replacement name, *Guocordulia*.

Key words: Insecta, Anisoptera, Araripelibellulidae, morphology, phylogeny

Introduction

The Mesozoic was a crucial period in the evolution of dragonflies, during which the stem groups of modern anisopteran families underwent significant diversification, giving rise to numerous families with distinct wing venation patterns (Nel *et al.* 1998; Bechly *et al.* 2001; Fleck *et al.* 2008; Bechly 2016). It is especially the case for the 'libelluloid' clade with a series of late Jurassic to early Cretaceous families (Fleck *et al.* 2008; Bechly 2016). Among these the Araripelibellulidae Bechly, 1996 is very close to the clade of the extant 'libelluloid' dragonflies (Eurypalpida Bechly, 1996). Thus, it is of great interest to define the process of the changes that have conducted to the diversification of this group of modern families that dominate the diversity of the Anisoptera, with in particular the family Libellulidae.

The Araripelibellulidae have a broad distribution, with taxa found in the Early Cretaceous of Brazil, the UK, Spain, and China (Nel & Paicheler, 1994; Ren & Guo, 1996; Bechly, 1998; Zhang *et al.*, 2006; Fleck *et al.*, 2008; Nel & Pouillon, 2020). Currently, all genera within this family are assigned to the subfamily *Araripelibellulinae*, except for *Mesocordulia boreala* Ren & Guo, 1996, for which Bechly (1996) established the subfamily Mesocorduliinae. However, the type specimen of this species is partially poorly preserved, and some of its characters remain uncertain.

Here, we describe a remarkably well-preserved new specimen of *Mesocordulia boreala*, which refines the diagnosis and description of this taxon and facilitates a more thorough discussion of its phylogenetic position among the 'libelluloid' dragonflies.

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Material and methods

The fossil was collected from the yellow tuffaceous shale of the Lower Cretaceous Yixian Formation at Huangbanjigou, Beipiao City, Liaoning Province, NE China. It was preserved alongside many conchostracan individuals, namely *Eosestheria* sp., one of the major representatives of the Jehol fauna.

The photographs were taken using a Canon EOS 5D Mark II camera with a Canon 100 mm macro lens attached and a Zeiss AxioZoom V16 stereomicroscope. The new specimen is deposited at the Nanjing Institute of Geology and Palaeontology (NIGPAS), Chinese Academy of Sciences, Nanjing, China.

The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters follow the phylogenetic system proposed by Bechly (1996, 2016). Wing venation terminology follows Riek & Kukalová-Peck (1984), as amended by Nel *et al*. (1993) and Bechly (1996).

Abbreviation of venation: Ax1 and Ax2 primary antenodal crossveins; C costa; CuA cubitus anterior; CuP cubitus posterior; IRxx supplementary longitudinal veins between branches of RP; MAa anterior branch of media anterior; MAb posterior branch of media anterior; MP media posterior; Mspl supplementary vein in postdiscoidal area; RA radius anterior; RP radius posterior, Rspl supplementary vein in area between IR2 and RP3/4; PsA anterior branch of AA; ScP subcostal posterior.

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication under urn:lsid:zoobank.org:pub:2E5EF063-9540-4BD8-830E-FAC6306A4000.

Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys-Longchamps (*in* Selys-Longchamps & Hagen, 1854)

Clade Cavilabiata Bechly, 1996

Clade Paneurypalpida Bechly, 1996

Family Mesocorduliidae Bechly, 2003 (stat. nov. for Mesocorduliinae Bechly, 2003)

Type genus. *Guocordulia* **nom. nov.** for *Mesocordulia* Ren & Guo, 1996.

Etymology. Named after Z.-G. Guo, second author of the genus *Mesocordulia*, and the genus name *Cordulia*. Gender feminine. A genus name *Rencordulia* already exists.

Remarks. The genus name *Mesocordulia* Ren & Guo, 1996, unique genus of the Mesocorduliidae, is preoccupied by the subgenus name *Mesocordulia* May, 1992. Thus, we need to propose a new genus name *Guocordulia* for *Mesocordulia* Ren & Guo, 1996.

Guocordulia boreala (Ren & Guo, 1996), comb. nov. for *Mesocordulia boreala* Ren & Guo, 1996

(Figs 1, 2)

Material. Holotype LB94021 (female), paratype LB94022 (hind wing), Geological Museum of China, Beijing. New specimen: NIGP206353 (complete female in dorsal view).

Diagnosis (new diagnosis for genus and species). Compound eyes well separated; forewing secondary antenodals incomplete; hind wing antenodals complete; five crossveins in forewing antesubnodal area, only one in hind wing; sector of arculus well separated; a well-defined elongated anal loop with ten cells; PsA well defined in fore- and hind wings; six postnodal crossveins; subdiscoidal vein (basal part of CuA that is aligned with the distal side MAb of discoidal triangle) reduced in hind wing; hind wing CuA shortened with only one distinct dichotomic branching into CuAa and CuAb; forewing Ax2 situated distinctly above mid part of discoidal triangle; pterostigmal brace vein shifted distally beneath pterostigma.

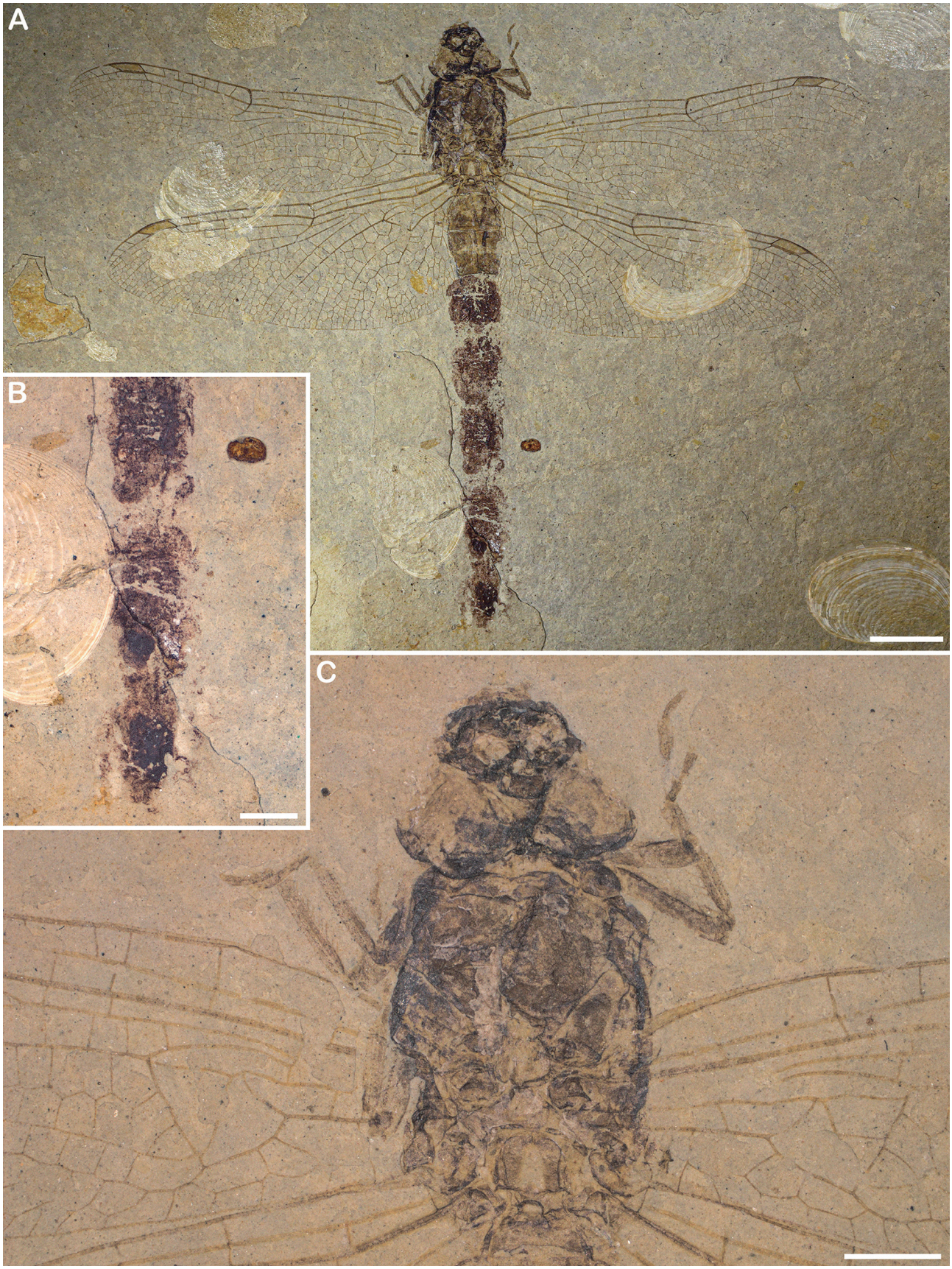

FIGURE 1. *Guocordulia boreala* (Ren & Guo, 1996), **comb. nov.**, new specimen: NIGP206353. Photographs. **A**, Habitus. **B**, Apex of abdomen. **C**, Head and thorax. Scale bars = 5 mm in **A**, 2 mm in **B** and **C**.

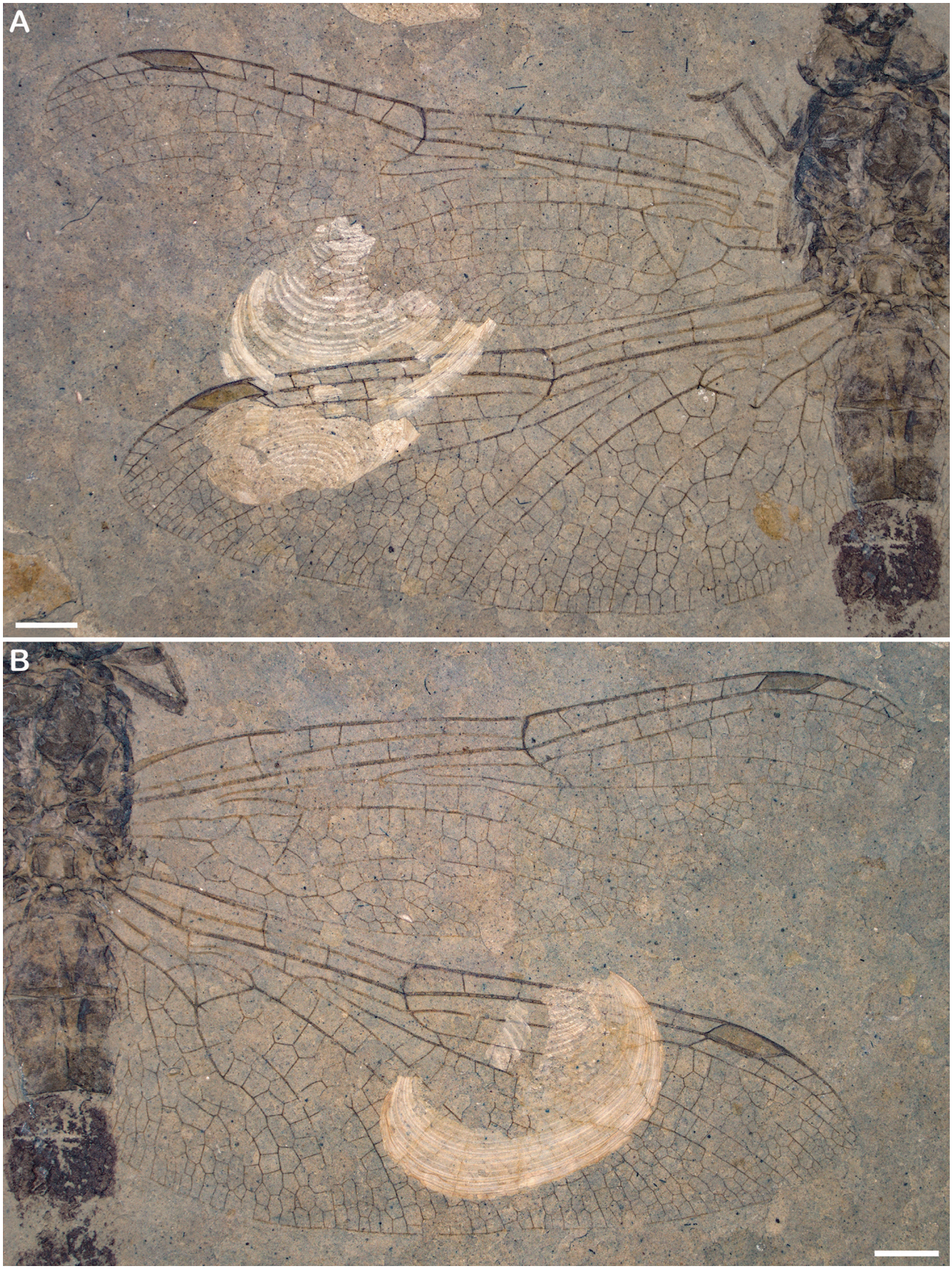

FIGURE 2. *Guocordulia boreala* (Ren & Guo, 1996), **comb. nov.**, new specimen: NIGP206353. Photographs. **A**, Right wings. **B**, Left wings. Scale bars = 2 mm.

Locality and horizon. Huangbanjigou, Beibiao City, West Liaoning, NE China; Lower Cretaceous Yixian Formation (ca. 125 Ma, lower Barremian).

Description. Specimen NIGP206353. Head 5.0 mm long, 3.5 mm wide, compound eyes large, 0.5 mm apart; ocelli disposed in triangle; thorax robust, 8.5 mm long, 5.2 mm wide; legs rather short and robust with strong spines, very similar to those of an extant Corduliidae; fore-, mid-, hind legs uniform, metafemur distinctly larger than mesofemur, the latter distinctly larger than fore femur, inner edge bearing two longitudinal ridges covered with spines; tibiae distinctly longer than femora, metatibiae distinctly larger than mesotibiae, mesotibiae slightly larger than foretibiae, all tibiae armed with several rows of longitudinal spines, inner edges bearing a row of long spines, ca. 8; tarsi with three tarsomeres, first tarsomere very short, second long, widened apically, third tarsomere elongate, longer than first and second tarsomeres together; paired claws small. Abdomen 29.3 mm long, 3.7 mm wide, with transverse hyaline band on segments I and II; segment II without secondary genital organs (female), cerci small, no ovipositor visible. Wing hyalines. Forewing (Fig. 2) 24.0 mm long, width opposite nodus 6.4 mm, distance from base to arculus 2.9 mm, from base to nodus 12.7 mm; from nodus to pterostigma 6.9 mm; from nodus to wing apex 8.9 mm; nodus nearer to apex than base of wing; pterostigma short, strong and covering one cell, about 1.6 mm long, 0.5 mm wide and with proximal and distal sides rather strongly divergent; pterostigmal brace distinctly oblique, slightly distal to basal side of pterostigma; Ax1 and Ax2 stronger than secondaries, 2.3 mm apart, four secondaries of first row not aligned with the three of second row; six postnodal crossveins; two proximal postnodal crossveins incomplete; arculus in a proximal position, only 0.9 mm distal of first antenodal crossvein and 0.5 mm basal of discoidal triangle; MA and RP clearly separated at their bases in arculus; free isosceles discoidal triangle, with anterior side straight; anterior side 1.6 mm long, proximal side 1.8 mm, distal side 1.8 mm; hypertriangle and median space free, MA arcuate at base; submedian space crossed by CuP; submedian and subdiscoidal spaces clearly separated by a strong oblique vein PsA; subdiscoidal space free; anal area not very broad, with two rows of cells; CuA not very long, with four posterior branches and reaching posterior wing margin slightly basal to level of nodus; three rows of cells in cubito-anal area; postdiscoidal area narrow, with two rows of cells distal of triangle, not widened near posterior wing margin, with four rows of small cells; no Bq crossvein and no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; five antesubnodal crossvein in space between RA and RP; no distinct Rspl; base of RP2 opposite subnodus; oblique crossvein 'O' 0.8 mm, one cell distal of subnodus; area between IR2 and RP2 slightly narrowed distally, these veins converging near posterior wing margin; area between RP2 and RP1 narrow, with four rows of cells at most and a short but distinct vein IR1, no sigmoidal crossvein in proximal part of area between RP2 and RP1; no Mspl; MA and RP3/4 undulate, more or less parallel and directed obliquely to posterior wing margin.

Hind wing (Fig. 13) 23.5 mm long, 8.8 mm wide; width opposite nodus 8.0 mm; distance from base to arculus 2.7 mm, from base to nodus 9.6 mm, from nodus to pterostigma 9.3 mm, from nodus to apex 14.3 mm; nodus in a proximal position between base and apex; pterostigma 2.4 mm long, 0.7 mm wide, short, covering one cell and with proximal and distal sides divergent; pterostigmal brace distinctly oblique, slightly distal to basal side of pterostigma; three antenodal crossveins, all of same strength; five postnodal crossveins with the three proximal incomplete; arculus in a proximal position, just distal of first antenodal crossvein and nearly opposite discoidal triangle; MA and RP clearly separated at their bases in arculus; free isosceles discoidal triangle, with anterior side slightly curved; length of anterior side 2.0 mm, of proximal side 1.2 mm, of distal side 1.9 mm; hypertriangle and median space free; MA strongly arcuate at base; submedian space crossed by CuP, a free subdiscoidal space and a distinct oblique vein PsA; anal area wide, with eight rows of cells between AA and posterior wing margin; AA with three perpendicular branches directed towards posterior wing margin, no anal triangle; no anal angle distal branch of AA provides the basal side for a long and narrow ten-cells anal loop, 5.0 mm long, 1.3 mm wide, with a ill-defined zigzagged midrib; subdiscoidal vein (basal part of CuA that is aligned with the distal side MAb of the discoidal triangle) strongly reduced; gaff of CuA elongated and slightly curved; CuAa distally zigzagged, not very long, with no well-defined posterior branches, and reaching posterior wing margin well basal of nodus level; six rows of cells in cubito-anal area; postdiscoidal area narrow, distinctly broader near posterior wing margin, with two rows of cells in proximal part and 12 rows of cells along posterior wing margin; Mspl rudimentary; MA and RP3/4 not undulating, parallel and obliquely reaching posterior wing margin; no Bq crossvein; no crossvein in proximal part of area between RP3/4 and IR2, basal of nodus; only one antesubnodal crossvein in space between RA and RP; no distinct vein Rspl; base of RP2 opposite subnodus; oblique crossvein 'O' 0.9 mm distal of subnodus; area between IR2 and RP2 slightly narrowed distally; IR2 and RP2 directed obliquely to posterior wing margin; area between RP2 and RP1 with 3–4 rows of cells; a short IR1, no sigmoidal crossvein in proximal part of area between RP2 and RP1.

Discussion

The fossil belongs to *Mesocordulia boreala* because it has exactly the same hind wing venation, especially the same anal loop and structures of the anal area, presence of a vein PsA, only one complete secondary antenodal crossvein distal of Ax2, etc. Also Ren & Guo (1996: fig. 8) proposed a reconstruction of the forewing that fits exactly with the venation of the new specimen in the preserved parts (the main part of the wing), except in one important point: they figured three complete secondary antenodal crossveins distal of Ax2 in the right wing and two complete on the left wing plus two in dotted lines. In the new specimen there are four secondary antenodal crossveins of first row between C and ScP and three of second row between ScP and RA, furthermore these are not aligned. Unfortunately, in their photograph (Ren & Guo 1996: fig. 7), it is not possible to determine the precise shape of the forewing antenodal crossveins. The dimensions of the new fossil align closely with those of the holotype of *Mesocordulia boreala*. Therefore, we consider that the new fossil belongs to this species.

The character 'forewing secondary antenodals complete vs. incomplete' is crucial for the family attribution of *Mesocordulia* Ren & Guo, 1996 because it is currently attributed to the Mesozoic family Araripelibellulidae Bechly, 1996, in its own subfamily Mesocorduliinae. Bechly (1996, 2016) proposed the following diagnosis for the Araripelibellulidae: 'no secondary antenodal crossveins between ax1 and ax2, and only two or three secondary antenodal crossveins distal of ax2; all antenodal crossveins strictly aligned (but the two primaries ax1 and ax2 are still stronger than the secondaries); only one or two antesubnodal crossveins; forewing with only about four postnodal crossveins; anterior side of hindwing hypertriangle very strongly curved, and posterior side at least slightly curved, too; postdiscoidal area very narrow in the forewing (distal part even narrower than basal part); anal loop very elongate'.

The new specimen of *Mesocordulia boreala* exhibits several distinguishing features: the forewing antenodal crossveins are not strictly aligned, it possesses five antesubnodal crossveins in the forewing instead of two, and six postnodal crossveins instead of four or fewer. Additionally, it has a distinct hind wing vein PsA, unlike the taxa in Araripelibellulinae. Consequently, this specimen cannot be placed within that family.

Nevertheless, the new specimen of *Mesocordulia boreala* has some important characters of the Paneurypalpida (= Araripelibellulidae + Eurypalpida Bechly, 1996), viz. 'the subdiscoidal vein (basal part of CuA that is aligned with the distal side MAb of the discoidal triangle) is reduced in the hindwings; the hindwing CuA is further shortened with only one distinct dichotomic branching into CuAa and CuAb; RP3/4 and MA secondarily not undulating, at least in the hindwing; antenodal crossveins more or less aligned, at least the hindwings with more than two aligned and bracket-like antenodal crossveins' (Bechly 2016). It shares with the Eurypalpida some synapomorphies: arculus strictly straight in both pairs of wings, pterostigmal brace vein shifted distally beneath pterostigma, forewing pseudo-anal vein PsA hypertrophied, area between RP2 and IR2 not distinctly widened distally, and anal loop elongate and at least eight cells large. Nevertheless, it cannot be assigned to the Eurypalpida sensu stricto (Synthemistidae, Gomphomacromiidae, Pseudocorduliidae, Macromiidae, and other extant 'libelluloid' families), as these have the sectors of arculus approximate, diverging from one point or even shortly fused basally vs. dictinctly separated in *Mesocordulia boreala*, Ax2 situated distinctly basal of the discoidal triangle in forewings vs. situated above mid part of triangle.

The head structure of Araripelibellulinae is largely unknown, except for *Sopholibellula* Zhang, Ren, Zhou & Pang, 2006, in which the compound eyes are dorsally contiguous for a length of about 6 mm (Zhang *et al.*, 2006). In the other representatives of this group, the head remains unknown. In contrast, the compound eyes of Eurypalpida are medio-dorsally contiguous. The head of the holotype of *Mesocordulia boreala* is poorly preserved, offering no information on its structure. However, the new specimen clearly has well-separated compound eyes, suggesting a more basal position for *Mesocordulia*.

Conclusion

Mesocordulia could belong to the stem group of the Eurypalpida, as it shares some synapomorphies with this clade. However, but its head morphology would rather suggest a position in the Paneurypalpida, more basal than the Araripelibellulidae *sensu stricto* (Araripelibellulinae). Further investigation into the head morphology of *Araripelibellula* Nel & Paicheler, 1994, and other representatives of Araripelibellulinae is needed to confirm

whether they possess contiguous eyes, as seen in *Sopholibellula*. At this stage, the subfamily Mesocorduliinae should be elevated to the new family Mesocorduliidae, though no known synapomorphy currently supports this monospecific group. The discovery of the male of *Mesocordulia boreala* may provide additional information to help more definitively define this group.

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