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ABSTRACT

The hawker dragonfly *Cratoliupanshania magnifica* gen. et sp. nov. is described from the Lower Cretaceous Crato Formation in Brazil, corresponding to the third genus of this Mesozoic family from this formation. This family is otherwise known from the Lower to 'mid'-Cretaceous of China, Central Asia, and France. This new discovery shows that the Odonata from the Crato Formation, although extensively studied, can hold interesting surprises.

Keywords: Insecta; Odonata; Aeshnoptera; gen. et sp. nov., Early Cretaceous.

1. Introduction

The Lower Cretaceous Crato Formation is a well-known Konservat Lagerstätte with a very rich entomofauna. The Odonata are especially very diverse and extensively studied (Bechly,

1998, 2000, 2007, 2010; Nel et al., 1998; Bechly et al., 2001; Bechly & Ueda, 2002) with representatives of all the extant anisopteran main subgroups. One could think that this dragonfly fauna is completely described. Thus it is with some surprise that we discovered in the collection of one of us (C.P.) a very well-preserved wing that does not correspond to any already described taxa. It represents the third genus of the Cretaceous family Liupanshaniidae found in this formation. This family is otherwise known from France, China, and Central Asia.

2. Material and methods

The specimen was examined with a Nikon SMZ 1500 and a Nikon SMZ25. Photographs were taken with a Nikon D800 digital camera mounted on the stereomicroscopes lenses; photographs were processed using the image editing software Adobe Photoshop Element 12. Helicon focus software was used for stacking the different photographs. The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters follow the phylogenetic system proposed by Bechly (1996, 2016) and Bechly et al. (2001) for the Mesozoic Aeshnoptera. Wing venation terminology follows Riek & Kukalová-Peck (1984), as amended by Kukalová-Peck (1991), Nel et al. (1993) and Bechly (1996).

Abbreviation of venation: Ax1 and Ax2 primary antenodal crossveins; C costa; CuA cubitus anterior; CuP cubitus posterior; d discoidal triangle; 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.

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3. Systematic palaeontology

Superorder Odonatoptera Martynov, 1932

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys-Longchamps, 1854, in Selys-Longchamps & Hagen, 1854

Family Liupanshaniidae Bechly et al., 2001

Genus *Cratoliupanshania* gen. nov.

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Type species: *Cratoliupanshania magnifica* sp. nov.

Etymology. Named after the Crato Formation and the genus *Liupanshania*.

Diagnosis. Forewing venation characters. Arculus shifted very close to antenodal Ax1; RP3/4 and MA closely parallel up to wing margin; RP2 and IR2 not converging near hind margin of wing; discoidal triangle nearly equilateral, two-celled; trigonal planate strong at its base and zigzagged distally; no distal accessory oblique vein between RP2 and IR2; Rspl zigzagged with one row of cells between it and IR2; Mspl poorly-defined, zigzagged; only two rows of cells in proximal half of postdiscoidal area up to base of IR2; Ax2 at level of basal side of discoidal triangle; pterostigmal brace very weakly oblique; only one secondary antenodal crossvein of first row between Ax1 and Ax2.

Cratoliupanshania magnifica sp. nov.

Fig. 1

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Material. Holotype MGP-PD 32312 (a nearly complete forewing, coll. Cristian Pella), stored in Museo di Geologia e Paleontologia dell'Università di Padova.

Locality and horizon. Vicinity of Nova Olinda (precise outcrop is unknown), Araripe Basin, Ceara, NE Brazil. Lower Cretaceous, Aptian (ca. 115 Ma), Crato Formation (Martill & Heimhofer, 2007).

Etymology. Named after the wonderful state of preservation of the holotype.

Diagnosis. As for the genus.

Description. Wing apparently hyaline, although darker in anterior third and near base (Fig. 1); pterostigma sclerotized, brown; wing 45.0 mm long, width at nodus 9.7 mm; distance from base to arculus 5.2 mm; from arculus to nodus 19.1 mm; from nodus to pterostigma 12.4 mm; pterostigma rather short (length 3.9 mm; width 1.0 mm), covering three cells and a half, and braced by a weakly oblique crossvein aligned with its basal side; pterostigma not in a basal position; 10 postnodal crossveins, not aligned with nine corresponding postsubnodal crossveins; 'Bqs-area ('bridge space') between RP and IR2 basal of the subnodus not narrowed; 17 secondary antenodal crossveins of first row between costal margin and ScP, distal of Ax2, some of them being well aligned with antenodal crossveins of second row; primary antenodal crossveins Ax1 and Ax2 stronger than secondary antenodals, 3.0 mm apart, with only one secondary in-between; Ax1 opposite arculus; Ax2 at level of basal side of discoidal triangle; basal brace Ax0 visible; ca. 10 antesubnodal crossveins between arculus and subnodus without any clear gap basal of subnodus; RP and MA distinctly separated at angled arculus; three bridge-crossveins Bqs basal of subnodus; base of RP2 aligned with subnodus; nodus of normal anisopteran-type; only one oblique vein 'O' three cells distal of subnodus; IR2 originating 3.7 mm and RP3/4 (midfork) 5.0 mm basal of subnodus; a weak zigzagged Rspl, not curved, with one row of cells between it and IR2; a strong and convex secondary longitudinal vein looking like a posterior branch of IR2 four cells basal of base of Rspl; RP2 and IR2 parallel with only a single row of cells in-between, except two rows of cells near hind margin of wing; RP2 distinctly undulated on a level four cells basal to

pterostigma; pseudo-IR1 very weak; RP1 and RP2 closely parallel up to two cells basal to pterostigma with only a single row of cells in-between, but below pterostigma they become strongly divergent with two or more rows of cells in-between; RP3/4 and MA parallel and undulated with a single row of cells in-between up to hind margin of wing; a weak and zigzagged Mspl with one row of cells between it and MAa; postdiscoidal area distinctly widened distally (width near discoidal triangle 2.5 mm; width at hind margin of wing 6.5 mm) with two rows of cells immediately distal of discoidal triangle and up to level of base of IR2; hypertriangle free of crossveins (length 5.9 mm; max. width 0.7 mm); discoidal triangle nearly equilateral, large, and divided into two cells; length of anterior side 3.0 mm; of basal side 2.5 mm; of distal side MAb 3.2 mm; MAb nearly straight, with a distinct convex secondary vein (trigonal planate) originating on it, distally vanishing in postdiscoidal area; median space free of crossveins; submedian space traversed by CuP-crossing; AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined two-celled subdiscoidal triangle, max. 2.7 mm long and basally 1.7 mm wide; PsA curved and ending slightly basal to basal angle of discoidal triangle; a single row of cells in area between MP and CuA; MP reaching hind margin of wing on a level with nodus; CuA reaching hind margin of wing somewhat basal of level of nodus; three-four weak posterior branches of CuA; maximum width of cubito-anal area 2.5 mm with maximum four rows of cells between CuA and hind margin of wing; anal area max. 2.2 mm wide (below PsA) with two rows of large cells between AA and hind margin of wing.

4. Discussion

Cratoliupanshania gen. nov. lacks the ‘Bqs-area (‘bridge space’) between RP and IR2 basal of the subnodus narrowed’, apomorphy of the Petalurodea Bechly, 1996. On the contrary, it has the following synapomorphies of the Aeshnoptera Bechly, 1996, after Bechly (1996):

‘RP1 and RP2 basally parallel up to the pterostigma, thus area between these two veins basally distinctly narrowed with only one row of cells between them in the ground plan (convergent to many Gomphides-Lindeniidae like the genus *Cacoides*; reversed in several subclades)’; ‘a weakly defined (zigzagged) Rspl’; ‘RP3/4 and MA more or less undulating’. *Cratoliupanshania* gen. nov. also has a weak trigonal planate and a RP2 undulating as in many Aeshnoptera.

Cratoliupanshania gen. nov. shows some similarities with the Araripephebiidae Bechly, 1998 in the shape of the discoidal triangle, and of the main longitudinal veins, but the narrow area between RP1 and RP2 is very long, with 13 cells between subnodus and the point where the area is broadened, typical of the Aeshnoptera, while it is only eight cells long in *Araripephlebia* Bechly, 1998 (Bechly, 1998).

The arculus shifted very close to the first primary antenodal Ax1 and the RP3/4 and MA closely parallel up to the wing margin are putative synapomorphies of the †Mesuropetaloidea Bechly, 1996 present in *Cratoliupanshania* gen. nov. *Cratoliupanshania* gen. nov. lacks the two synapomorphies of the †Mesuropetalidae Bechly, 1996, viz. ‘RP2 and IR2 very closely parallel, even converging near the hind margin of wing’ and ‘forewing discoidal triangle very transverse’. The main synapomorphies of the †Liupanshaniidae Bechly et al., 2001 concern the hind wing discoidal triangle, unknown in this fossil. Nevertheless, it has a forewing discoidal triangle nearly identical to those in this family, even if it is divided into two cells, instead of three or four cells cells in †*Araripeliupanshania* Bechly et al., 2001, †*Paramesuropetala* Bechly et al., 2001, and *Libanoliupanshania* Azar et al., 2019, and unicellular in †*Protoliupanshania* Huang & Nel, 2010. The trigonal planate is present in *Cratoliupanshania* gen. nov. (see Lin et al., 2002), but only strong at its base and zigzagged distally, unlike in †*Araripeliupanshania* and †*Paramesuropetala*, but †*Libanoliupanshania* has a weaker trigonal planate than *Cratoliupanshania* gen. nov. Lastly *Cratoliupanshania*

gen. nov. lacks the distal accessory oblique vein between RP2 and IR2, as in the †Liupanshaniidae.

†*Paraliupanshania*, †*Paramesuropetala*, and †*Libanoliupanshania* have better defined Rspl than *Cratoliupanshania* gen. nov.; while †*Galloliupanshania*, †*Guyuanaeschnidia*, †*Araripeliupanshania*, and †*Liupanshania* have also a weak Rspl. The poorly-defined, zigzagged Mspl of *Cratoliupanshania* gen. nov. is a symplesiomorphy that excludes it from the clade (†*Paraliupanshania*+†*Guyuanaeschnidia*).

Cratoliupanshania gen. nov. differs from †*Paramesuropetala*, †*Protoliupanshania*, and †*Libanoliupanshania* in the presence of only two rows of cells in the proximal half of the postdiscoidal area instead of three or four. †*Liupanshania* Hong, 1982, †*Paraliupanshania* Bechly, et al., 2001, †*Galloliupanshania* Nel et al., 2015 and †*Guyuanaeschnidia* Lin, 1982 are based on hind wings, hardly comparable to a forewing (Bechly et al., 2001; Lin et al., 2002; Nel et al., 2015). Nevertheless they also have three rows of cells in postdiscoidal area, thus they had probably three or more rows of cells in that of their forewings, as in the other Liupanshaniidae. Only †*Araripeliupanshania* has two rows of cells in the postdiscoidal areas of fore- and hindwings, as in *Cratoliupanshania* gen. nov. But *Cratoliupanshania* gen. nov. has only two rows of cells in this area up to base of IR2 while it is basal to base of RP3/4 in †*Araripeliupanshania*. Also, Ax2 is opposite the basal side of the discoidal triangle in *Cratoliupanshania* gen. nov., while it is at the level of the middle of the triangle in †*Araripeliupanshania*. The pterostigmal brace of *Cratoliupanshania* gen. nov. is very weakly oblique while it is strongly oblique in †*Araripeliupanshania*. The curvature of vein RP3/4 is more pronounced in *Cratoliupanshania* gen. nov. than in †*Araripeliupanshania*. Lastly there are three secondary antenodal crossveins of first row between Ax1 and Ax2 in †*Araripeliupanshania*, contra one in *Cratoliupanshania* gen. nov.

5. Conclusion

Cratoliupanshania gen. nov. is the third liupanshaniid genus from the Crato Formation, confirming the important diversity of this family during the Early Cretaceous. It also confirms that the diversity of the fauna of Odonata was very high in this paleobiota. It would be very interesting to find nymphs of this family. They could be accurately attributed on the basis of the tracheation of the wing pads. They could give some information of the life habits of these dragonflies, in order to better understand the possible causes of their extinction during the Late Cretaceous.

CRediT authorship contribution statement

Cristian Pella: Writing, illustrating. **André Nel:** Writing – original draft, Formal analysis, Conceptualization.

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Fig. 1. *Cratoliupanshania magnifica* gen. et sp. nov., holotype MGP-PD 32312. Photograph of forewing. Scale bar represents 10 mm.


Ax1
Ax2
N
Pt
d
RP2
IR2
CuP
PsA
MAa
RP3/4
CuA
MP