The oldest representative of the modern clade Aeshnodea from the Lower Cretaceous Crato Formation, Araripe Basin, NE Brazil (Odonata: Anisoptera)

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ABSTRACT

The hawker dragonfly *Primumaeshna britta* gen. et sp. nov., type genus and species of the new family Primumaeshnidae, is described from the Lower Cretaceous Crato Formation in Brazil, corresponding to the oldest record of the clade Aeshnodea. The previously described representatives of the Aeshnoptera from this formation belonged to extinct families or to the Gomphaeschnidae. Otherwise the oldest Aeshnodea were previously only known from the Cenomanian. This new discovery confirms that the diversification of the modern lineages of hawker dragonflies occurred during the Early Cretaceous.

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 were 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. Among these, the clade Aeshnoptera or stem group of the modern Aeshnidae (hawker dragonflies) are especially diverse. Nevertheless, they all belong to clades with phylogenetic positions more inclusive than the Aeshnodea Bechly, 1996, with representatives of the extant family Gomphaeschnidae. Up to now, the Aeshnodea that comprise all the other extant hawker dragonflies, have a rather reduced Mesozoic record, with only the two 'mid'-Cretaceous families Burmaeshnidae and Enigmaeshnidae. The Aeshnodea are much more diversified during the Cenozoic, especially in the Oligocene and Miocene.

Here we describe the oldest representative of the stem group of the Aeshnodea, in a new family, genus and species from the Crato Formation.

2. Material and methods

The specimen is on a piece of rock 14x11x1 cm. It is stored in the collection of the Musée d'Histoire Naturelle et d'Ethnographie de Colmar, France. It was examined with a Nikon SMZ 1500 and a Nikon SMZ25. Photographs were taken with a Nikon D800 digital camera mounted on the stereomicroscopes; photographs were processed using the image editing software Adobe Photoshop CS. Helicon focus software was used for stacking the different photographs.

For data on the Crato Formation and its fauna and flora and location map of the fossil locality in the vicinity of Nova Olinda, in the Araripe Basin, Ceara, northeastern Brazil, see Martill et al. (2007: figs 2.4-2.6).

The higher classification of fossil and extant Odonatoptera, as well as familial and generic characters follows 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 subcosta posterior.

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3. Systematic palaeontology

Superorder Odonatoptera Martynov, 1932

Order Odonata Fabricius, 1793

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

Clade Aeshnoptera Bechly, 1996

Subclade Aeshnodea Bechly, 1996

Family Primumaeshnidae fam. nov.

urn:lsid:zoobank.org:act:4D566517-7497-45E5-8349-FDCBB140420A

Type genus. *Primumaeshna* gen. nov.

Diagnosis. As for the genus.

Genus *Primumaeshna* gen. nov.

urn:lsid:zoobank.org:act:0AE63E56-3D89-4488-A6FB-A0CACA69F7E7

Type species. *Primumaeshna britta* sp. nov.

Etymology. Named after ‘Primus’, Latin for first, and *Aeshna*. Gender feminine.

Diagnosis. Forewing characters only. RP1 and RP2 basally parallel up to pterostigma, with one row of cells between them; Rspl well-defined, not zigzagged; discoidal triangle strongly longitudinally elongated; subdiscoidal triangle unicellular; PsA strong and curved; no supplementary crossveins in submedian area, discoidal triange and hypertriangle; distal side MAb of discoidal triangle somewhat bent; a strongly curved Mspl; a trigonal planate not aligned with Mspl; MP and CuA closely parallel with only one row of cells between them up to wing margin; distal accessory oblique vein between RP2 and IR2 absent; distal primary antenodal bracket Ax2 shifted distinctly basal of level of distal angle of discoidal triangle; most distal part of antesubnodal area between RA and RP with five crossveins; one row of cells in area between RP3/4 and MAa near posterior margin of wing; undulation of RP3/4 absent; MAa strongly curved; a strongly pronounced double undulation of RP2; RP2 and IR2 distinctly non-parallel; a short longitudinal vein parallel to IR2 corresponding to a rudimentary 'anterior branch' of IR2, but no well-defined fork of IR2.

Remark. *Primumaeshna* gen. nov. is characterized by having a mixt of synapomorphies of the Aeshnodea and plesiomorphic characters that forbid to consider it as belonging to the crow group of this clade. It has not the apomorphies of the other Mesozoic families of the stem group of the Aeshnodea, but we could not find any autapomorphy that could characterize it. Possibly, its unknown hind wing could show some in the future, but we prefer to erect a new family for this oldest known Aeshnodea.

Primumaeshna britta sp. nov.

Fig. 1

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Material. Holotype MHNE.2020.11.1 (thorax and head in ventral view, with legs and the two forewings attached), stored at the Musée d'Histoire Naturelle et d'Ethnographie de Colmar, France.

Etymology. Named after Britta Sennlaub, owner of the holotype, who allowed us to study it, and donated it.

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

Diagnosis. As for the genus.

Description. Head 7.0 mm wide, with large eyes; thorax 9.1 mm long, 6.7 mm wide; fore femur 3.7 mm long, tibia 3.7 mm long, tarsus 1.8 mm long; mid femur 5.3 mm long, tibia 4.6 mm long, tarsus 3.2 mm long; one hind leg poor preserved; forewing apparently hyaline (Fig. 1); pterostigma sclerotized, brown; wing 43.7 mm long, width at nodus 10.2 mm; distance from base to arculus 4.7 mm; distance from arculus to nodus 17.0 mm; from nodus to pterostigma 14.2 mm; pterostigma rather short (length 3.7 mm; width 0.9 mm), covering two cells, and braced by a strongly oblique crossvein aligned with its basal side; pterostigma not in a basal position; nine postnodal crossveins, not aligned with eight corresponding postsubnodal crossveins; 'Bqs-area ('bridge space') between RP and IR2 basal of the subnodus not narrowed, with two crossveins; 11 secondary antenodal crossveins of first row between costal margin and ScP, distal of Ax2; primary antenodal crossveins Ax1 and Ax2 stronger than secondary antenodals, 4.2 mm apart, with two secondaries in-between; Ax1 basal to arculus; Ax2 slightly distal to basal side of discoidal triangle; ca. nine antesubnodal crossveins between arculus and subnodus basal to base of RP3/4 and five distal, without any gap basal of subnodus; RP and MA distinctly separated at angled arculus; base of RP2 aligned with subnodus; nodus of normal anisopteran-type; only one oblique vein 'O' one cell distal of subnodus; IR2 originating 3.7 mm

and RP3/4 (midfork) 5.2 mm basal of subnodus; a curved, not-zigzagged Rspl, with one row of cells between it and IR2; no 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 in their basal parts, strongly diverging distally, with four rows of cells in broader part, and with three rows of cells near posterior margin of wing; RP2 strongly undulated on a level two cells basal to pterostigma; pseudo-IR1 very weak; RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between, but below pterostigma they become strongly divergent with three or more rows of cells in-between; RP3/4 and MA parallel up to level of nodus, MAa undulating in its distal part, while RP3/4 remaining straight and abruptly curved near posterior marging of wing, with a single row of cells in-between up to curvature of MAa and again one row near hind margin of wing; strong curved Mspl with two row of cells between it and MAa; postdiscoidal area distinctly widened distally (width near discoidal triangle 2.7 mm; width at posterior margin of wing 8.8 mm) with two rows of cells immediately distal of discoidal triangle and up to level of base of RP3/4; hypertriangle with one crossvein (length 6.3 mm; max. width 0.75 mm); discoidal triangle very long and rather narrow, divided into two cells; length of anterior side 5.2 mm; of basal side 2.0 mm; of distal side MAb 5.2 mm; MAb slightly curved, 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 unicellular subdiscoidal triangle, max. 1.8 mm long and basally 1.8 mm wide; PsA curved; a single row of cells in area between MP and CuA; MP reaching posterior margin of wing on a level with nodus; CuA reaching posterior margin of wing somewhat basal of level of nodus; five-six weak posterior branches of CuA; maximum width of cubito-anal area 2.7 mm with maximum four rows of

cells between CuA and posterior margin of wing; anal area max. 2.2 mm wide (below PsA) with two rows of large cells between AA and posterior margin of wing.

4. Discussion

Primumaeshna gen. nov. falls in the Aeshnoptera: Aeshnomorpha because of the following putative synapomorphies (Bechly et al., 2001): RP1 and RP2 basally parallel up to the pterostigma, with area between these two veins basally distinctly narrowed with only one row of cells between them; Rspl well-defined; MA undulating; forewing discoidal triangle longitudinal elongate; hypertriangle divided by one crossvein; RP2 strongly undulating.

Primumaeshna gen. nov. has none of the synapomorphies of the Austropetaliida Bechly, 2001, viz. no series of five to eight reddish costal spots; its pterostigmata are not shortened; its pterostigmal brace vein is aligned with its basal side; its IR1 is short; its insertions of CuP-crossing and PsA on anal vein AA are very far to each other; and its basal true lestine oblique vein is present.

On the other side, *Primumaeshna* gen. nov. has not two of the putative synapomorphies of the Panaeshnida Bechly, 2001, sister group of the Austropetaliida, viz. hypertriangles divided by several parallel crossveins; submedian space divided by one or more accessory cubito-anal crossveins between CuP-crossing and PsA; and discoidal triangles divided into more than two cells. But these characters are reversed in some Gomphaeschnidae Tillyard & Fraser, 1940. Its Rspl is not zigzagged, supporting its attribution to the Panaeshnida.

The well-developed Mspl with three rows of cells between it and MAa excludes affinities with the Progobiaeshnidae Bechly et al., 2001 and Cymatophlebioidea Handlirsch, 1906. This last group is also excluded because of the absence of a convex oblique and undulating secondary vein anastomosing between IR2 and RP3/4 directly basal of origin of Rspl, and absence of crossvein in submedian area except CuP and PsA.

Primumaeshna gen. nov. falls in the Paneuaeshnida Bechly et al., 2001 because of: RP2 and IR2 not parallel; RP2 distinctly undulating; RP3/4 and MA closely parallel up to wing margin in both pairs of wings.

Primumaeshna gen. nov. shares with the Paracymatophlebiidae Bechly et al., 2001 the absence of the second oblique crossvein between IR2 and RP2, but it strongly differs from this family in the better-defined and longer Mspl and presence of only one row of cells between RP1 and RP2 up to pterostigma. On the contrary, it shares with the Euaeshnida Bechly, 1996 the synapomorphies: RP2 and IR2 distinctly non-parallel; forewing discoidal triangle quite elongate; forewing subdiscoidal triangle unicellular; distal side MAb of discoidal triangles somewhat bent. Affinities with the Eumorbaeschnidae Bechly et al., 2001 are excluded because the postdiscoidal area is quite broadened distally; Ax2 is distal to basal side of discoidal triangle; while it shares with the Neoaeshnida Bechly, 1996 the following synapomorphies: Mspl not zigzagged; a trigonal planate; MP and CuA are closely parallel with only one row of cells between them up to wing margin; distal accessory oblique vein between RP2 and IR2 absent; distal primary antenodal bracket Ax2 shifted distinctly basal of level of distal angle of discoidal triangle in forewing.

Affinities with the Gomphaeschnidae are excluded because the most distal part of antesubnodal area between RA and RP contains five crossveins, instead of being free or with few crossveins. But this gomphaeschnid 'cordulegastrid gap' is also not present in the Cenozoic †*Alloaeschna quadrata* Wighton & Wilson, 1986, which differs from *Primumaeshna* gen. nov. in the shape of Rspl and Mspl, among other characters. *Paramorbaeschna araripensis* Bechly et al., 2001 has two such crossveins in the most distal part of antesubnodal area between RA and RP. It also differs from *Primumaeshna* gen. nov. in the less undulate vein RP2, discernable by the presence of two rows of cells between RP1 and RP2 and of three rows of cells between RP2 and IR2 at the level of this curvature, instead of respectively three rows and two rows in

Primumaeshna gen. nov. Also the area between RP3/4 and MAa contains two rows of cells up to posterior margin of wing in *Paramorbaeschna*, instead of only one in *Primumaeshna* gen. nov.

Primumaeshna gen. nov. shares with the Aeshnodea, sister group of the Gomphaeschnidae, the undulation of RP3/4 completely absent (still slightly present in the Gomphaeschnidae), the forewing discoidal triangle strongly longitudinal elongated, and the absence of the second second (distal) lestine oblique vein (Bechly & Rasmussen, 2019). But *Primumaeshna* gen. nov. has not the undulation of RP2 modified to a simple curvature beneath pterostigma, nor the PsA reduced to an oblique cubito-anal crossvein similar to the others crossveins in the submedian space, other synapomorphies of the Aeshnodea (= Allopetaliidae + Euaeshnodea after Bechly, 2016) (= Aeshnidae sensu Dijkstra et al., 2013 or Bechly & Rasmussen, 2019). Thus *Primumaeshna* gen. nov. cannot be attributed to the crown group of Aeshnodea, but to its stem group. The exact structure of the submedian space and vein PsA is unknown in the Mesozoic genus *Baissaeshna* Pritykina, 1977, currently attributed to the Allopetaliidae. Thus the reduction of the PsA to a simple oblique crossvein remains unknown in this genus. Nevertheless *Primumaeshna* gen. nov. differs from *Baissaeshna* in the very strongly double curve of RP2, instead of having only one pronounced curve and being straight in its distal part below the pterostigma, in having a strong curve of MAa, and in the trigonal planate not prolonged by Mspl in forewing (Bechly et al., 2001: text-figs 129-130).

This stem group is currently known in the Mesozoic by the 'mid'-Cretaceous families Burmaeshnidae Huang et al., 2017 (*Burmaeshna* Huang et al., 2017, *Cretaeshna* Zheng et al., 2016, *Angustaeshna* Huang et al., 2017, and *Proaeschna* Wei et al., 2019, all from Burmese amber) and Enigmaeshnidae Nel et al., 2008 (*Enigmaeshna* Nel et al., 2008). *Primumaeshna* gen. nov. differs from the Burmaeshnidae in the absence of a well-defined fork of IR2, and the strongly curved Mspl. *Primumaeshna* gen. nov. has only a short longitudinal vein parallel to

IR2 that corresponds to a rudimentary 'anterior branch' of IR2. *Primumaeshna* gen. nov. differs from the Enigmaeshnidae in the absence of supplementary crossveins in submedian area, discoidal triange and hypertriangle.

Primumaeshna gen. nov. shares with the

5. Conclusion

Primumaeshna gen. nov. is the oldest record of the clade Aeshnodea, the most diverse group of extant hawker dragonflies. It confirms that this group diversified during the early Cretaceous, a conclusion supported by the presence of two other aeshnodean families in the Cenomanian and by the molecular dating (Letsch et al., 2016). These last authors considered that the representatives of the Aeshnodea probably lived in lotic waters. Nevertheless, the abundance and diversity of the hawker dragonflies in the Crato paleolake could suggest that these taxa were living in the lake or close to it, and were possibly adapted to lentic environments. This paleolake is considered as brackish, but the abundance and diversity of the ephemeropteran and anisopteran nymphs strongly suggest that they could develop in the lake or at its margin (Martill et al., 2007). But the qualification of lentic vs. lotic for these ancient periods possibly did not correspond to the modern ones, because the quality of water in the Jurassic and early Cretaceous lakes was probably different from that of the late Cretaceous and younger ones, after the 'mid'-Cretaceous floristic 'revolution' and the diversification of the aquatic macrophytes (Du & Wang, 2016).

CRediT authorship contribution statement

Jean-Marc Pouillon: Writing, illustrating. **André Nel:** Writing – original draft, Formal analysis, Conceptualization.

Acknowledgements

We sincerely thank two anonymous referees and the editor for their useful remarks on the first version of the paper. We also thank Mr. Markus Sennlaub who allowed us to study the holotype specimen.

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Fig. 1. *Primumaeshna britta* gen. et sp. nov., holotype MHNE.2020. MHNE.2020.11.1. Photograph of habitus; CuAa cubitus anterior, CuP cubitus posterior, d discoidal triangle, h hypertriangle, IR2 intercalary radial vein 2, MAa median anterior, MP median posterior, Mspl supplementary median vein, PsA pseudo-anal vein, Pt pterostigma, RP2 & RP3/4 branches of Radius posterior, Rspl supplementary radial vein. Scale bar represents 3 mm.


Pt
N
Ax2
x
RP2
IR2
n
d
Rspl
RP3/4
MAa
Mspl
MP
CuAa
PsA
CuP