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Aeshnodea from the Lower Cretaceous Crato Formation,
Araripe Basin, NE Brazil (Odonata: Anisoptera)**

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

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14 ABSTRACT

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

22

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

24

25 **1. Introduction**

26 The Lower Cretaceous Crato Formation is a well-known Konservat Lagerstätte with a very rich
27 entomofauna. The Odonata are especially very diverse and were extensively studied (Bechly,
28 1998, 2000, 2007, 2010; Nel et al., 1998; Bechly et al., 2001; Bechly & Ueda, 2002) with
29 representatives of all the extant anisopteran main subgroups. Among these, the clade
30 Aeshnoptera or stem group of the modern Aeshnidae (hawker dragonflies) are especially
31 diverse. Nevertheless, they all belong to clades with phylogenetic positions more inclusive than
32 the Aeshnodea Bechly, 1996, with representatives of the extant family Gomphaeschnidae. Up
33 to now, the Aeshnodea that comprise all the other extant hawker dragonflies, have a rather
34 reduced Mesozoic record, with only the two ‘mid’-Cretaceous families Burmaeshnidae and
35 Enigmaeshnidae. The Aeshnodea are much more diversified during the Cenozoic, especially in
36 the Oligocene and Miocene.

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

39

40 **2. Material and methods**

41 The specimen is on a piece of rock 14x11x1 cm. It is stored in the collection of the Musée
42 d’Histoire Naturelle et d’Ethnographie de Colmar, France. It was examined with a Nikon SMZ
43 1500 and a Nikon SMZ25. Photographs were taken with a Nikon D800 digital camera mounted
44 on the stereomicroscopes; photographs were processed using the image editing software Adobe
45 Photoshop CS. Helicon focus software was used for stacking the different photographs.

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

49 The higher classification of fossil and extant Odonatoptera, as well as familial and generic
50 characters follows the phylogenetic system proposed by Bechly (1996, 2016) and Bechly et al.

51 (2001) for the Mesozoic Aeshnoptera. Wing venation terminology follows Riek & Kukalová-
52 Peck (1984), as amended by Kukalová-Peck (1991), Nel et al. (1993) and Bechly (1996).
53 Abbreviation of venation: Ax1 and Ax2 primary antenodal crossveins; C costa; CuA cubitus
54 anterior; CuP cubitus posterior; d discoidal triangle; IRxx supplementary longitudinal veins
55 between branches of RP; MAa anterior branch of media anterior; MAb posterior branch of
56 media anterior; MP media posterior; Mspl supplementary vein in postdiscoidal area; RA radius
57 anterior; RP radius posterior, Rspl supplementary vein in area between IR2 and RP3/4; PsA
58 anterior branch of AA; ScP subcosta posterior.

59 [urn:lsid:zoobank.org:pub:E3B64B7C-A817-482E-8AB9-5305CE908AE2](https://zoobank.org/pub/E3B64B7C-A817-482E-8AB9-5305CE908AE2)

60

61 **3. Systematic palaeontology**

62 Superorder Odonatoptera Martynov, 1932

63 Order Odonata Fabricius, 1793

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

65 Clade Aeshnoptera Bechly, 1996

66 Subclade Aeshnodea Bechly, 1996

67 Family Primumaeshnidae fam. nov.

68 [urn:lsid:zoobank.org:act:4D566517-7497-45E5-8349-FDCBB140420A](https://zoobank.org/act:4D566517-7497-45E5-8349-FDCBB140420A)

69 Type genus. *Primumaeshna* gen. nov.

70 Diagnosis. As for the genus.

71

72 Genus *Primumaeshna* gen. nov.

73 [urn:lsid:zoobank.org:act:0AE63E56-3D89-4488-A6FB-A0CACA69F7E7](https://zoobank.org/act:0AE63E56-3D89-4488-A6FB-A0CACA69F7E7)

74 *Type species. Primumaeshna britta* sp. nov.

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

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

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

95

96 *Primumaeshna britta* sp. nov.

97 Fig. 1

98 [urn:lsid:zoobank.org:act:DCE5B395-801D-4A06-9F67-27FA00380595](https://zoobank.org/urn:lsid:zoobank.org:act:DCE5B395-801D-4A06-9F67-27FA00380595)

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

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

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

107 *Diagnosis.* As for the genus.

108 *Description.* Head 7.0 mm wide, with large eyes; thorax 9.1 mm long, 6.7 mm wide; fore femur
109 3.7 mm long, tibia 3.7 mm long, tarsus 1.8 mm long; mid femur 5.3 mm long, tibia 4.6 mm
110 long, tarsus 3.2 mm long; one hind leg poor preserved; forewing apparently hyaline (Fig. 1);
111 pterostigma sclerotized, brown; wing 43.7 mm long, width at nodus 10.2 mm; distance from
112 base to arculus 4.7 mm; distance from arculus to nodus 17.0 mm; from nodus to pterostigma
113 14.2 mm; pterostigma rather short (length 3.7 mm; width 0.9 mm), covering two cells, and
114 braced by a strongly oblique crossvein aligned with its basal side; pterostigma not in a basal
115 position; nine postnodal crossveins, not aligned with eight corresponding postsubnodal
116 crossveins; 'Bqs-area ('bridge space') between RP and IR2 basal of the subnodus not narrowed,
117 with two crossveins; 11 secondary antenodal crossveins of first row between costal margin and
118 ScP, distal of Ax2; primary antenodal crossveins Ax1 and Ax2 stronger than secondary
119 antenodals, 4.2 mm apart, with two secondaries in-between; Ax1 basal to arculus; Ax2 slightly
120 distal to basal side of discoidal triangle; ca. nine antesubnodal crossveins between arculus and
121 subnodus basal to base of RP3/4 and five distal, without any gap basal of subnodus; RP and
122 MA distinctly separated at angled arculus; base of RP2 aligned with subnodus; nodus of normal
123 anisopteran-type; only one oblique vein 'O' one cell distal of subnodus; IR2 originating 3.7 mm

124 and RP3/4 (midfork) 5.2 mm basal of subnodus; a curved, not-zigzagged Rspl, with one row of
125 cells between it and IR2; no convex secondary longitudinal vein looking like a posterior branch
126 of IR2 four cells basal of base of Rspl; RP2 and IR2 parallel with only a single row of cells in-
127 between in their basal parts, strongly diverging distally, with four rows of cells in broader part,
128 and with three rows of cells near posterior margin of wing; RP2 strongly undulated on a level
129 two cells basal to pterostigma; pseudo-IR1 very weak; RP1 and RP2 closely parallel up to
130 pterostigma with only a single row of cells in-between, but below pterostigma they become
131 strongly divergent with three or more rows of cells in-between; RP3/4 and MA parallel up to
132 level of nodus, MAa undulating in its distal part, while RP3/4 remaining straight and abruptly
133 curved near posterior margin of wing, with a single row of cells in-between up to curvature of
134 MAa and again one row near hind margin of wing; strong curved Mspl with two row of cells
135 between it and MAa; postdiscoidal area distinctly widened distally (width near discoidal
136 triangle 2.7 mm; width at posterior margin of wing 8.8 mm) with two rows of cells immediately
137 distal of discoidal triangle and up to level of base of RP3/4; hypertriangle with one crossvein
138 (length 6.3 mm; max. width 0.75 mm); discoidal triangle very long and rather narrow, divided
139 into two cells; length of anterior side 5.2 mm; of basal side 2.0 mm; of distal side MAb 5.2 mm;
140 MAb slightly curved, with a distinct convex secondary vein (trigonal planate) originating on it,
141 distally vanishing in postdiscoidal area; median space free of crossveins; submedian space
142 traversed by CuP-crossing; AA divided into a strong and oblique secondary anterior branch
143 PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal
144 triangle, max. 1.8 mm long and basally 1.8 mm wide; PsA curved; a single row of cells in area
145 between MP and CuA; MP reaching posterior margin of wing on a level with nodus; CuA
146 reaching posterior margin of wing somewhat basal of level of nodus; five-six weak posterior
147 branches of CuA; maximum width of cubito-anal area 2.7 mm with maximum four rows of

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

150

151 **4. Discussion**

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

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

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

168 The well-developed Mspl with three rows of cells between it and MAa excludes
169 affinities with the Progobiaeshnidae Bechly et al., 2001 and Cymatophlebioidea Handlirsch,
170 1906. This last group is also excluded because of the absence of a convex oblique and
171 undulating secondary vein anastomosing between IR2 and RP3/4 directly basal of origin of
172 Rspl, and absence of crossvein in submedian area except CuP and PsA.

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

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

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

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

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

217 This stem group is currently known in the Mesozoic by the ‘mid’-Cretaceous families
218 Burmaeshnidae Huang et al., 2017 (*Burmaeshna* Huang et al., 2017, *Cretaeshna* Zheng et al.,
219 2016, *Angustaeshna* Huang et al., 2017, and *Proaeschna* Wei et al., 2019, all from Burmese
220 amber) and Enigmaeshnidae Nel et al., 2008 (*Enigmaeshna* Nel et al., 2008). *Primumaeshna*
221 gen. nov. differs from the Burmaeshnidae in the absence of a well-defined fork of IR2, and the
222 strongly curved Mspl. *Primumaeshna* gen. nov. has only a short longitudinal vein parallel to

223 IR2 that corresponds to a rudimentary ‘anterior branch’ of IR2. *Primumaeshna* gen. nov. differs
224 from the Enigmaeshnidae in the absence of supplementary crossveins in submedian area,
225 discoidal triangle and hypertriangle.

226 *Primumaeshna* gen. nov. shares with the

227

228 **5. Conclusion**

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

243

244 CRediT authorship contribution statement

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

247

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252

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

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