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1 Historical Biology

2

3 The third aeschnidiid dragonfly genus and species from the Lower Cretaceous Crato
4 Formation (Odonata, Anisoptera)

5

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16

17 **ABSTRACT**

18 *Cratoaeschnidium martinsnetoi* gen. et sp. nov., third genus and species of Aeschnidiidae from
19 the Crato Formation (Brazil), is described and illustrated based on one well-preserved forewing.
20 It can be differentiated from the other genera in the family, *inter alia*, because of its discoidal
21 triangle very narrow with only one row of cells; three rows of cells between Mspl and MAa,
22 and between Rspl and IR2; one row of cells between CuAa and MP in basal part; three rows of
23 cells between RP3/4 and MAa. This new genus and species confirms that much can be expected
24 in regard to discovering the Odonata in the Crato Formation.

25

26 **KEYWORDS**

27 Insecta; Aeschnidiidae; Aptian; Early Cretaceous; gen. et sp. nov.; Brazil

28

29 **Introduction**

30 The family Aeschnidiidae is a speciose fossil dragonfly clade currently encompassing 33 genera.

31 Representatives of this family were distributed worldwide between the Late Jurassic and the

32 latest Cretaceous (Fleck and Nel 2003; Nel 2021). Recent studies indicate that the family seems

33 to die out during the Cretaceous-Cenozoic (K-Pg) crisis, and not during the mid-Cretaceous

34 floristic and faunal turnover as previously supposed by Fleck et al. (1999). However, the effect

35 of the K-Pg crisis on insects appears to be soft and poorly quantified (Condamine et al. 2016;

36 Schachat and Labandeira 2021) suggesting that the family may be present during the Paleocene,

37 even if not recorded from Paleocene deposits (e.g., Nel and Jouault, 2022). The Aeschnidiidae

38 were apparently extremely diversified in the Lower Weald Clay (Hauterivian), in the UK, but

39 less diverse in the Lower Cretaceous of Spain (Las Hoyas and Montsec) (e.g., Nel and Martínez-

40 Delclòs 1993; Fleck and Nel 2003). In China, the family is known by a few genera, some of

41 them being very frequent in the Lower Cretaceous of Liaoning (e.g., Huang and Nel 2010).

42 Interestingly, several species are known from the Southern Hemisphere with specimens known

43 from Australia, Brazil, and Colombia (e.g. Martill and Nel 1996; Fleck and Nel 2003; Gómez-

44 Cruz et al. 2011; <https://paleobiodb.org/>). This ‘worldwide’ distribution during the Cretaceous

45 suggests that the family was perhaps present on the Gondwana masses during the Jurassic and

46 not only present in the northern hemisphere, as evidenced by their current fossil record. They

47 were possibly not found due to the scarcity of Gondwanan Jurassic insect assemblages. The

48 family could also have rapidly dispersed from Laurasia to Gondwana during the earliest

49 Cretaceous. The Brazilian Lagerstätte of the Crato Formation is worldwide known for its

50 numerous perfectly preserved fossils of insects and odonatan specimens are not an exception.

51 This rich entomofauna encompasses two aeshnidiid species, viz. *Santanoptera gabbotti*
52 Martill and Nel, 1996 and *Leptaeschnidium araripina* (Carle and Wighton, 1990) (originally in
53 the genus *Wightonia* Carle and Wighton, 1990). The latter genus is known from numerous
54 specimens while the former is known by only one specimen.

55 Here we describe a new genus and species from this formation, superficially looking
56 like *Leptaeschnidium araripina*, but showing a unique combination of characters. This
57 discovery confirms that the odonatan diversity of the Crato Formation is really impressive
58 (Bechly, 2007).

59

60 **Material and methods**

61 The specimen studied herein comes from the Crato Formation, which is one of the stratigraphic
62 units that constitute the Santana Group of the Araripe Basin. From the base to the top, the
63 Santana Group consists of the Barbalha, Crato, Ipubi, and Romualdo formations. The specimen
64 was collected at ‘Pedreira Três Irmão’, one of the many local mining queries near the city of
65 Nova Olinda (State of Ceará, Northeastern Brazil), where the Crato Formation outcrops are
66 explored for the extraction of paving stones.

67 The geology and paleontology of the Crato Formation were revised in detail by Martill
68 et al. (2007a,b) and Ribeiro et al. (2021). The age of the Crato Formation is considered to be
69 upper Aptian (early Cretaceous) (Pons et al. 1991; Heimhofer and Hochuli 2010; Varejão et al.
70 2021). Dias and Carvalho (2022) recently demonstrated the role of the microbial mats in the
71 preservation of the insects in the Crato Formation.

72 According to Ribeiro et al. (2021), the paleoenvironment of the fossil-rich interval of
73 the formation – the ‘Crato Konservat-Lagerstätte’ or CKL – consisted of a semi-arid seasonal
74 lacustrine wetland with a shallow water body. A diverse aquatic fauna and flora were present
75 as an integral part of this biome, and was succeeded up landward by neighboring mesophytic

76 ecotones, which were periodically flooded. This system was surrounded by outer xeric habitats.
77 Trophic structure analysis detailing the putative food web that took place within the Crato
78 Ecosystem was studied by Mendes et al. (2020).

79 The fossils were preserved with the cuticle being replaced by dark brown iron hydroxide
80 (goethite) (Barling et al., 2015, 2020). The holotype of *Cratoaeschnidium martinsnetoi* gen. et
81 sp. nov. was prepared by removing limestone matrix from around the wing with fine blades and
82 needles. Photographs of the holotype were taken with a digital camera (Nikon DSRi) attached
83 to a Nikon SMZ 1000 stereomicroscope. The holotype (CCNH 445) is housed in the
84 paleontological collection of the Centro de Ciências Naturais e Humanas (CCNH),
85 Universidade Federal do ABC, Santo André, São Paulo Brazil.

86 We follow the wing venation nomenclature adapted to the highly specialized
87 Aeschniidae, from Fleck and Nel (2003: fig. 8). Abbreviations are as follows: AA: analis
88 anterior; AA1: branch of AA posterior closing subdiscoidal area; Ax0, Ax1, Ax2 primary
89 antenodal crossveins; Bcv: basal concave vein; bSd: basal part of subdiscoidal area; cMspl:
90 convex supplementary median vein; CnC: convex nodal crest; dSd: distal part of subdiscoidal
91 area; faab: first anterior aeschnidiid bulla; fpab: first posterior aeschnidiid bulla; IR: intercalary
92 radial vein; ISd: infra-subdiscoidal space; MA: media anterior; MAa: anterior branch of MA;
93 MAb: posterior branch of MA; MP: media posterior; Mspl: supplementary median vein
94 between MAa and MP; N: nodus; 'O' oblique crossvein between RP2 and IR2; pseudo IR1:
95 longitudinal vein between RP1 and RP2 distad pterostigma; RA: radius anterior; RP: radius
96 posterior; Rspl: supplementary radial vein between IR2 and RP3/4; saab: second anterior
97 aeschnidiid bulla; ScP: subcostal posterior; sms: submedian space; spab: second posterior
98 aeschnidiid bulla; Sn: subnodus; t: discoidal triangle.

99 **Zoobank xxxx**

101 **Systematic paleontology**

102 Class: Insecta Linnaeus, 1758

103 Order: Odonata Fabricius, 1793

104 Family: Aeschnidiidae Needham, 1903

105 Genus: *Cratoaeschnidium* gen. nov.

106 **Zoobanks xxxx**

107 Type species. *Cratoaeschnidium martinsnetoi* sp. nov.

108 Etymology. Named after the Crato Formation from which the type species originates, and the
109 genus name *Aeschnidium*.

110 Diagnosis: Forewing characters only. Discoidal triangle very narrow with only one row of cells;
111 no pterostigma; no curvature of RA in its distal part; no pterostigmal brace; vein AA1 not angled;
112 three rows of cells between M_{spl} and MA_a, and between R_{spl} and IR₂; one row of cells between
113 CuA_a and MP in basal part; three rows of cells between RP_{3/4} and MA_a; two well defined and
114 posteriorly closed infrasubdiscoidal spaces.

115

116 *Cratoaeschnidium martinsnetoi* sp. nov.

117 **Figures 1-2**

118 **Zoobank xxxx**

119 Etymology. Named after Dr Rafael Martins-Neto, who extensively studied the entomofauna of
120 the Crato Formation. The species epithet is to be treated as a noun in a genitive case.

121 Type material. Holotype specimen CCNH 445, a nearly complete forewing, with only costo-
122 basal part missing, stored at the paleontological collection of Centro de Ciências Naturais e
123 Humans, Universidade Federal do ABC, Santo André, São Paulo, Brazil.

124 Age and outcrop. Lower Cretaceous, late Aptian, Crato Formation, Araripe Basin, Brazil.

125 Diagnosis: As for the genus; six cells in discoidal triangle; distal part of subdiscoidal area
126 divided into 12 small cells.

127 Description. Forewing in main part hyaline, but with darkened zones (costal part, discoidal and
128 subdiscoidal zone) and spots in postdiscoidal area; wing ca. 44.0 mm long, 10.2 mm wide;
129 distance from base to nodus ca. 20.7 mm, from arculus to nodus ca. 11.0 mm; from nodus to
130 wing apex 23.2 mm; submedian space with crossveins; hypertriangle elongate, with numerous
131 crossveins; discoidal triangle transverse and narrow, more or less perpendicular to wing axis,
132 4.4 mm long, 1.8 mm wide, divided into six cells disposed in one row; distal margin of discoidal
133 triangle (MAb) distinctly curved, 4.4 mm long; basal margin (MP+CuA) curved, 3.6 mm long;
134 costal margin 1.9 mm long; PsA vein reaching MP+CuA, just basal of discoidal triangle; distal
135 part of subdiscoidal area transverse, broad, nearly quadrate, 1.8 mm long, 3.5 mm wide, divided
136 into 12 small cells; basal part of subdiscoidal area transverse, 1.2 mm long, 2.5 mm wide, four
137 visible strong posterior convex branches of AA, viz. AA1 to AA4; two well defined and
138 posteriorly closed infrasubdiscoidal spaces; AA1 nearly straight; anal area broad; base of MP
139 at posterior angle of discoidal triangle; free part of CuA directed towards wing base and aligned
140 with AA; CuAa with four posterior distal branches; cubital area narrow; postdiscoidal area
141 broad, with seven rows of cells just distal of MAb, distally greatly widened; no clear 'cMspl';
142 an irregular veinlet between posterior part of MAb and base of Mspl; base of concave Mspl
143 three cells distal of MAb); Mspl weakly curved; three rows of cells between MA and Mspl;
144 three 'MA-Mspl veinlets'; no 'first anterior and posterior aeshnidiid bullae'; base of IR2 close
145 to that of RP3/4; numerous crossveins in area between RA and RP, between arculus and nodus;
146 few Bq crossveins; oblique crossveins 'O' hardly visible, if present; area between MA and
147 RP3/4 with one row of cells basally and three rows in broadest part, RP3/4 and MA convergent
148 near posterior wing margin; RP3/4 with a strong posterior curve near its distal end; a weak
149 'MA-RP3/4 veinlet'; two weak 'RP2-IR2 veinlets'; one row of cells in area between IR2 and

150 RP2 basally, and two rows in widest part; RP2 and IR2 strongly convergent near posterior wing
151 margin; RP2 with a strong posterior curve near its distal end; three rows of cells between R_{spl}
152 and IR2; second 'aeshnidiid bullae' not discernable; ScP straight, clearly crossing through
153 nodus and reaching costal margin 5.8 mm distad nodus; distal end of ScP straight; presence of
154 bent of vein CP between C and ScP and of oblique 'CnC vein' between ScP and C, well
155 separated from nodus (opened nodal 'V'); Ax0, Ax1 and Ax2 not preserved; ca. 20 antenodals
156 preserved in distal part of area between C and ScP; no postnodal supra-ScP; no zigzagged
157 longitudinal vein between ScP and RA; nodal Cr curved, well aligned with subnodus; base of
158 RP2 aligned with subnodus; no secondary zigzagged longitudinal vein between RA and RP1,
159 between subnodus and wing apex, postnodal and postsubnodal crossveins very numerous, not
160 aligned together; pterostigma and pterostigmal brace totally absent, no curvature of RA
161 suggesting a pterostigma; primary IR1 present; presence of basal concave supplementary vein
162 between RP1 and RP2; no clear pseudo-IR1; presence of numerous cells and secondary
163 longitudinal veins making a kind of 'fan' in area between RP1 and RP2.

164 Remark: The coloration on wings or bodies of fossil insects from the Crato Formation is often
165 well preserved (Nel and Jouault, 2021) allowing species delineation in some cases. However,
166 it is impossible to ensure that the color pattern recorded in the present specimen is that of the
167 original wing or results from taphonomic processes.

168

169 **Discussion**

170 This fossil has all the characteristics typical of a forewing of a dragonfly belonging to the family
171 Aeshnidiidae, especially the presence of two rows of cells between C and RA distal of the
172 nodus, a strongly transverse discoidal triangle, a special shape of the anal area with a series of
173 large areas limited by branches of AA (Fleck and Nel 2003).

174 Because of the configuration of the discoidal triangle recorded in the new fossil, we
175 restrain our comparison with genera possessing a very narrow discoidal triangle with only one
176 (at most two) row(s) of cells (Fleck and Nel 2003; Huang et al. 2009; Nel 2021). Therefore, the
177 new fossil differs from the genus *Aeschnidiella* because of the presence of only one row of cells
178 between CuAa and MP, and crossveins between IR2 and RP2 perpendicular to these veins,
179 instead of being oblique (Zalesky 1953). It differs from *Aeschnidiopsis* owing to the presence
180 of one row of cells between IR2 and RP2 in their basal parts, and two rows of cells between
181 IR2 and RP3/4 below subnodus, vs. three to four (Woodward 1884). Note that the pterostigmal
182 zone is unknown in these two genera. *Gigantoeschnidium* has no pterostigma and no
183 pterostigmal brace, as in the new fossil, but it also has much more rows of cells between Mspl
184 and MAa and between Rspl and IR2 than the new fossil (Nel and Martínez-Delclòs 1993).
185 *Iberoeschnidium* has a widened pterostigmal zone with a curve of RA and RP1, unlike the
186 new fossil (Nel and Martínez-Delclòs 1993). *Leptaeschnidium araripina* (from the Crato Fm.)
187 and *Lleidoeschnidium maculatum* have a weak but distinctly oblique pterostigmal brace, and
188 a curvature of RA in the pterostigmal zone, unlike the new fossil (Carle and Wighton 1990;
189 Fleck and Nel 2003). *Leptaeschnidium latum* (based on a hind wing) seems to have no defined
190 pterostigmal brace and curvature of RA in the pterostigmal zone, but it has much more rows of
191 cells between RP3/4 and MAa and between RP1 and RP2 (Fleck and Nel 2003).
192 *Leptaeschnidium araripina*, *Lleidoeschnidium valloryi*, *Lleidoeschnidium maculatum*, and
193 *Coramaeschnidium minimum* have distinctly narrower basal and distal parts of the subdiscoidal
194 area, with a vein AA1a angled between these two parts of the subdiscoidal area, vs. straight in
195 the new fossil (Fleck and Nel 2003; Nel and Martínez-Delclòs 1993). *Nannoeschnidium*
196 *pumilio* has also a distinct angle in the course of AA1. *Angloeschnidium toyei*,
197 *Angloeschnidium montreuili*, *Angloeschnidium lacaii*, *Cooperaeschnidium durandi*, and
198 *Linaeschnidium sinensis* also have a well-defined pterostigmal brace and a curvature of RA in

199 the pterostigmal zone (Fleck and Nel 2003; Huang et al. 2009). *Delcloeschnidium magnum*
200 and *Jarzebowskiacschnidium polandi* have much more rows of cells between all main veins
201 (Fleck and Nel 2003). The latter genus can also be differentiated from our specimen owing to
202 its oblique pterostigma brace. *Diastatopsaeschnidium reneeheiko* shares with the new fossil a
203 vein AA1 without angle, but it has a pterostigmal brace and a curvature of RA in the
204 pterostigmal zone and basal part of the subdiscoidal area distinctly larger (Fleck and Nel 2003).
205 Similarly, affinities with *Kessleraeschnidium simonae* are excluded (Fleck and Nel 2003).

206 *Santanoptera gabbotti*, second described Aeschnidiidae from the Crato Fm., strongly
207 differs from the new fossil in having a very broad discoidal triangle and much more rows of
208 cells between all main veins (Martill and Nel 1996).

209 As aforementioned, the new fossil does not fit with any described genus and species of
210 Aeschnidiidae. We erect a new genus and species to accommodate this new fossil, which is the
211 third aeschnidiid from the Crato Fm.

212

213 **Conclusion**

214 *Cratoaeschnidium martinsnetoi* gen. et sp. nov. is the third genus and species of the family
215 Aeschnidiidae from the Lower Cretaceous Crato Fm. of Brazil. *Cratoaeschnidium* gen. nov.
216 resembles the Early Cretaceous genera *Leptaeschnidium* and *Lleidoaeschnidium*, and shares
217 with the early Cretaceous clade (*Lleidoaeschnidium*, *Angloaeschnidium*, *Leptaeschnidium*,
218 *Kessleraeschnidium*, *Iberoaeschnidium*, *Aeschnidiopsis*, *Aegyptidium*, *Santanoptera*,
219 *Diastatopsaeschnidium*) the putative synapomorphy ‘presence of basal concave supplementary
220 vein between RP1 and RP2’. Even if this clade seems to be stable after Fleck and Nel (2003:
221 fig.147-148), a new phylogenetic analysis of the Aeschnidiidae, including the newly described
222 taxa, is necessary to clarify the relationships within the family.

223

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229

230 **Disclosure statement**

231 No potential conflict of interest was reported by the author(s).

232

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237

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324 Figures

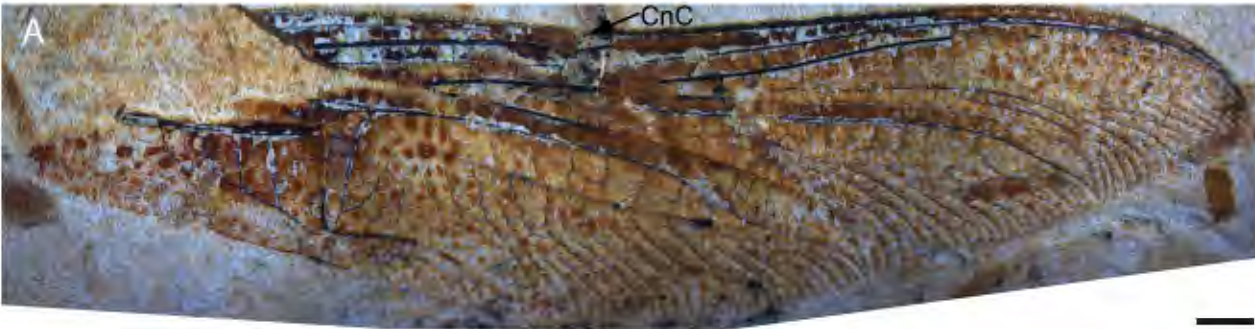
325 **Figure 1.** *Cratoaeschnidium martinsnetoi* gen. et sp. nov., holotype CCNH 445, forewing. (A)
326 Composite image; (B) Composite image of forewing made in Photoshop using ‘photomerge’
327 function; scale bars = 2 mm.

328 **Figure 2.** *Cratoaeschnidium martinsnetoi* gen. et sp. nov., holotype CCNH 445, forewing.
329 Photographs. (A) Detail of basal portion of wing; (B) Detail of mid-portion of wing; (C)
330 Detail of distal portion of wing; scale bars = 2 mm.

331

A

CnC



B

