



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

André Nel, Corentin Jouault, Guilherme Cunha Ribeiro

► To cite this version:

André Nel, Corentin Jouault, Guilherme Cunha Ribeiro. The third aeschnidiid dragonfly genus and species from the Lower Cretaceous Crato Formation (Odonata, Anisoptera). *Historical Biology*, 2022, 35 (6), pp.865-869. 10.1080/08912963.2022.2067995 . insu-03653388

HAL Id: insu-03653388

<https://insu.hal.science/insu-03653388>

Submitted on 28 Apr 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Historical Biology

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

André Nel^{a,*}, Corentin Jouault^{a,b,c} Guilherme Cunha Ribeiro^{d,*}

^aInstitut de Systématique, Évolution, Biodiversité (ISYEB) Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier 75005 Paris, France; ^bUniv. Rennes, CNRS, Géosciences Rennes, UMR 6118, F-35000, Rennes, France; ^cCNRS, UMR 5554 Institut des Sciences de l'Évolution de Montpellier, Place Eugène Bataillon, 34095, Montpellier, France; ^dCentro de Ciências Naturais e Humanas (CCNH), Universidade Federal do ABC, Avenida dos Estados, 5001 - Bangú, Santo André - SP, 09210-580.

*corresponding authors

ABSTRACT

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

KEYWORDS

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

Introduction

The family Aeschnidiidae is a speciose fossil dragonfly clade currently encompassing 33 genera. Representatives of this family were distributed worldwide between the Late Jurassic and the latest Cretaceous (Fleck and Nel 2003; Nel 2021). Recent studies indicate that the family seems to die out during the Cretaceous-Cenozoic (K-Pg) crisis, and not during the mid-Cretaceous floristic and faunal turnover as previously supposed by Fleck et al. (1999). However, the effect of the K-Pg crisis on insects appears to be soft and poorly quantified (Condamine et al. 2016; Schachat and Labandeira 2021) suggesting that the family may be present during the Paleocene, even if not recorded from Paleocene deposits (e.g., Nel and Jouault, 2022). The Aeschnidiidae were apparently extremely diversified in the Lower Weald Clay (Hauterivian), in the UK, but less diverse in the Lower Cretaceous of Spain (Las Hoyas and Montsec) (e.g., Nel and Martínez-Delclòs 1993; Fleck and Nel 2003). In China, the family is known by a few genera, some of them being very frequent in the Lower Cretaceous of Liaoning (e.g., Huang and Nel 2010). Interestingly, several species are known from the Southern Hemisphere with specimens known from Australia, Brazil, and Colombia (e.g. Martill and Nel 1996; Fleck and Nel 2003; Gómez-Cruz et al. 2011; <https://paleobiodb.org/>). This ‘worldwide’ distribution during the Cretaceous suggests that the family was perhaps present on the Gondwana masses during the Jurassic and not only present in the northern hemisphere, as evidenced by their current fossil record. They were possibly not found due to the scarcity of Gondwanan Jurassic insect assemblages. The family could also have rapidly dispersed from Laurasia to Gondwana during the earliest Cretaceous. The Brazilian Lagerstätte of the Crato Formation is worldwide known for its numerous perfectly preserved fossils of insects and odonatan specimens are not an exception.

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

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

Material and methods

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

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

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

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

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

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

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 Humanos, 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

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

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

Discussion

This fossil has all the characteristics typical of a forewing of a dragonfly belonging to the family Aeshnidiidae, especially the presence of two rows of cells between C and RA distal of the nodus, a strongly transverse discoidal triangle, a special shape of the anal area with a series of 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 (Zalessky 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). *Leptoeschnidium 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). *Leptoeschnidium 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 *Leptoeschnidium 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 lacui*, *Cooperaeschnidium durandi*, and
198 *Linaeschnidium sinensis* also have a well-defined pterostigmal brace and a curvature of RA in

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

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

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

Conclusion

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

Acknowledgments

We thank three anonymous referees for their useful remarks on the first version of the paper. We also thank the Brazilian National Mining Agency (ANM) for collecting permits for GCR. This study was supported by the São Paulo State Research Agency (FAPESP) (grant no. 2020/02844-5 to GCR). This paper was contributed by CJ during his PhD project.

Disclosure statement

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

ORCID

André Nel <http://orcid.org/0000-0002-4241-7651>

Corentin Jouault <http://orcid.org/0000-0002-3680-5172>

Guilherme Cunha Ribeiro <https://orcid.org/0000-0003-3604-2651>

References

- Barling N, Martill DM, and Heads SW. 2020. A geochemical model for the preservation of insects in the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research*, 116 (104608):1–19. <https://doi.org/10.1016/j.cretres.2020.104608>
- Barling N, Martill DM, Heads SW, and Gallien F. 2015. High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research*. 52:605–622. <https://doi.org/10.1016/j.cretres.2014.05.007>.
- Bechly G. 2007. Chapter 11.5 Odonata: damselflies and dragonflies. pp. 184–222. In: Martill D, Bechly G, and Loveridge R. (eds). *The Crato fossil beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge:1–624.

248 Carle FL, and Wighton DC. 1990. Chapter 3. Odonata. pp. 51–68. In: Grimaldi DA. (ed.).
 249 Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American
 250 Museum of Natural History. 195:1–191. <http://hdl.handle.net/2246/943>

251 Condamine F, Clapham M, and Kergoat G. 2016. Global patterns of insect diversification:
 252 towards a reconciliation of fossil and molecular evidence?. Science Reports. 6, 19208.
 253 <https://doi.org/10.1038/srep19208>

254 Dias JJ, and Carvalho I. de Souza 2022. The role of microbial mats in the exquisite preservation
 255 of Aptian insect fossils from the Crato Lagerstätte, Brazil. Cretaceous Research, 130
 256 (105068):1–13. <https://doi.org/10.1016/j.cretres.2021.105068>

257 Fabricius JC. 1793. Entomologia systematica emendata et aucta, secundum classes, ordines,
 258 genera, species, adjectis synonymis, locis, observationibus, descriptionibus. C.G. Proft,
 259 Hafniae [= Copenhagen], 2:1–519.

260 Fleck G, and Nel A. 2003. Revision of the Mesozoic family Aeschnidiidae (Odonata:
 261 Anisoptera). Zoologica. 153:1–180.

262 Fleck G, Nel A, and Martínez-Delclòs X. 1999. The oldest record of the Libellulidae from the
 263 Upper Cretaceous of Kazakhstan (Odonata, Anisoptera). Cretaceous Research. 20:655–658.
 264 <https://doi.org/10.1006/cres.1999.0166>

265 Gómez-Cruz AdJ, Moreno-Sánchez M, and Vallejo L. 2011. Fósiles de Insecta (Odonata) del
 266 Aptiano tardío en la Formación Paja. Boletín Científico. Centro de Museos. Museo de His-
 267 toria Natural. Novedades en Historia Natural. 15:222.

268 Heimhofer U, and Hochuli PA., 2010. Early Cretaceous angiosperm pollen from a lowlatitude
 269 succession (Araripe Basin, NE Brazil). Review of Palaeobotany and Palynology. 161:105–
 270 126. <https://doi.org/10.1016/j.revpalbo.2010.03.010>. ISSN 0034-6667

271 Huang D-Y, Baudoin A, and Nel A. 2009. A new aeschnidiid genus from the Early Cretaceous
 272 of China (Odonata: Anisoptera). Cretaceous Research. 30:805–809.
 273 <https://doi.org/10.1016/j.cretres.2008.12.014>
 274 Huang D-Y, and Nel, A. 2010. *Protoliupanshania wangi*, a new genus and species from the
 275 Chinese Early Cretaceous (Odonata: Aeshnoptera: Liupanshaniidae). Zootaxa. 2387:57–62.
 276 <https://doi.org/10.5281/zenodo.193804>
 277 Martill DM, Loveridge R, and Heimhofer U. 2007. Halite pseudomorphs in the Crato formation
 278 (Early Cretaceous, Late Aptian–Early Albian), Araripe Basin, northeast Brazil: further
 279 evidence for hypersalinity. Cretaceous Research, 28:613–620.
 280 <https://doi.org/10.1016/j.cretres.2006.10.003>
 281 Martill DM, Bechly G, and Loveridge R. 2007. The Crato fossil beds of Brazil: Window into
 282 an ancient world. Cambridge University Press, Cambridge:624 pp.
 283 Martill DM, and Nel A. 1996. A new dragonfly from the Crato Formation (Lower Cretaceous,
 284 Aptian) of N.E. Brazil. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte.
 285 1996:279–292.
 286 Mendes M, Bezerra FI, and Adami K. 2020. Ecosystem structure and trophic network in the
 287 Late Early Cretaceous Crato Biome. Pp. 1–19. In: Iannuzzi R, Roßler R, and Kunzmann L.
 288 (eds.). Brazilian paleofloras. Springer, Cham. [https://doi.org/ 10.1007/978-3-319-90913-](https://doi.org/10.1007/978-3-319-90913-4_33-1)
 289 [4_33-1](https://doi.org/10.1007/978-3-319-90913-4_33-1).
 290 Needham JG. 1903. A genealogic study of dragonfly wing venation. Proceedings of the United
 291 States National Museum. 26:703–764. <https://doi.org/10.5479/si.00963801.26-1331.703>
 292 Nel A. 2021. Maastrichtian representatives of the dragonfly family Aeschnidiidae question the
 293 entomofaunal turnover of the early Late Cretaceous. Palaeoentomology. 4:209–212.
 294 <https://doi.org/10.11646/palaeoentomology.4.3.5>

295 Nel A, and Jouault C. 2021. New grasshoppers (Orthoptera: Elcanidae, Locustopsidae) from
 296 the Lower Cretaceous Crato Formation suggest a biome homogeneity in Central Gondwana.
 297 Historical Biology <https://doi.org/10.1080/08912963.2021.2000602>
 298 Nel A, and Jouault C. 2022. The odonatan insects from the Paleocene of Menat, central France.
 299 Acta Palaeontologica Polonica (in press)
 300 Nel A., and Martínez-Delclòs X. 1993. Essai de révision des Aeschnidioidea (Insecta, Odonata,
 301 Anisoptera). Cahiers de Paléontologie. 1993:7–99.
 302 Pons D, Berthou P-Y, and Campos DA. 1991. Quelques observations sur la palynologie de
 303 l’Aptien supérieur et de l’Albien du bassin d’Araripe (N.E. du Brésil). pp. 241–252. In:
 304 Campos DA, Vianna MSS, Brito PM, and Beurlen G. (eds). Atas do I simposio sobre a Bacia
 305 do Araripe e Bacias Interiores do Nordeste, Crato. Crato: Departamento Nacional da
 306 Produção Mineral.
 307 Ribeiro AC, Ribeiro GC, Varejão FG, Battistola LD, Pessoa EM, Simões MG, Warren LV,
 308 Riccomini C, and Poyato-Ariza FC. 2021. Towards an actualistic view of the Crato
 309 Konservat-Lagerstätte paleoenvironment: a new hypothesis as an Early Cretaceous (Aptian)
 310 equatorial and semi-arid wetland. Earth-Science Reviews. 216:103573.
 311 <https://doi.org/10.1016/j.earscirev.2021.103573>.
 312 Schachat S, and Labandeira CC. 2021. Are insects heading toward their first mass extinction?
 313 Distinguishing turnover from crises in their fossil record. Annals of the Entomological So-
 314 ciety of America. 114:99–118. <https://doi.org/10.1093/aesa/saaa042>
 315 Varejão FG, Warren LV, Simões MG, Buatois LA, Mángano MG, Bahniuk AMR, and Assine
 316 ML. 2021. Mixed siliciclastic-carbonate sedimentation in an evolving epicontinental sea:
 317 aptian record of marginal marine settings in the interior basins of north-eastern Brazil.
 318 Sedimentology. 68:2125–2164. <https://doi.org/10.1111/sed.12846>.

Woodward H. 1884. On the wing of a neuropterous insect from the Cretaceous limestone of Flinders River, north Queensland, Australia. Geological Magazine Decade III. 1:337-339.

Zalessky GM. 1953. Novye mestonakhozhdeniya Melovykh nasekomykh v Povolzh'e, Kazakhstane i Zabaykal'e. Doklady Akademii Nauk SSSR. 89:163–166.

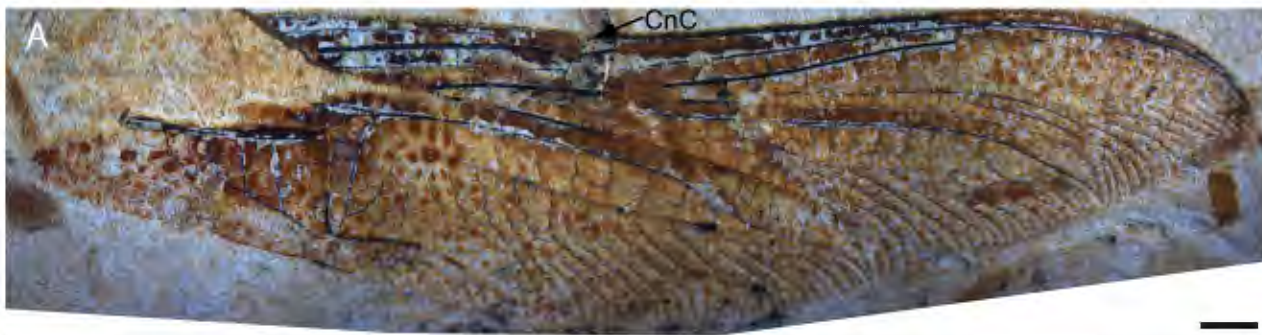
Figures

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

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

A

CnC



B

