A NEW DRAGONFLY FROM THE LOWER CRETACEOUS OF BRAZIL

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ABSTRACT. *Procordulagomphus xavieri* is a new genus and species of gomphid dragonfly (subfamily Cordulagomphinae) from the Lower Cretaceous of Araripe (Brazil). It is the sister-genus of another gomphid from Araripe, *Cordulagomphus*.

THE number of fossil dragonflies known from the Lower Cretaceous Araripe basin increases every year. Carle and Wighton (1990) described two Zygoptera (one Pseudostigmatidae and one Protoneuridae) and six Anisoptera (four Gomphidae and two Aeschnidiidae), while Nel and Paicheler (1994, in press) have described another Gomphidae (*Araripegomphus cretacicus* Nel and Paicheler) and a Corduliidae Gomphomacromiinae (*Araripelibellula martinsnetoi* Nel and Paicheler). Recently, the authors have discovered two new gomphid specimens, that could not be assigned to any described genus and species, and are the subject of the present paper.

The specimens are described using the nomenclature for wing venation proposed by Riek and Kukalova-Peck (1984), which was amended by Nel and Martínez-Delclòs (1993), and Nel *et al.* (1993). The only differences that we add to this nomenclature were suggested to us by Bechly and Jarzembowski (pers. comm.), as follows: RP3/4, for RP3–4 *sensu* Riek and Kukalova-Peck (1984); MAa, for MA1; MAb, for MA2; MPa, for MP1; CuAa, for CuA1; CuAb, for CuA2, and AAa, for AA1 *sensu* Nel and Martínez-Delclòs (1993).

SYSTEMATIC PALAEONTOLOGY

Family GOMPHIDAE Selys Longchamps, 1850
Subfamily CORDULAGOMPHINAE Carle and Wighton, 1990
Genus PROCORDULAGOMPHUS gen. nov.

Derivation of name. From *Cordulagomphus* Carle and Wighton, 1990, the sister-group of this new genus.

Type-species. Procordulagomphus xavieri sp. nov.

Diagnosis. Small dragonfly of the Gomphidae, subfamily Cordulagomphinae. Anterior branch MPa of MP joins main branch of MA. Anal triangle lacks cross-vein. Antenodal veins of hind wing fewer and more in line with cross-vein between ScP and RA than in *Cordulagomphus*. RP1 becomes curved at very beginning of pterostigmal brace. Anal loop one-celled. Only three rows of cells in anal and cubito-anal fields. Distal sides (MAb) of discoidal triangles straight. Between RP and MA, before the point of separation of RP3/4, third cross-vein not sigmoid or strongly slanted.

Procordulagomphus xavieri sp. nov.

Text-figures 1–3

1982 'spec. indet., Gomphidae', Schlüter and Hartung, p. 304.

Derivation of name. After our friend Dr Xavier Martínez-Delclòs, in recognition of his numerous studies on fossil insects.

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Types. Female holotype MNHN–LP–R.10406 (Escuillé Collection). Male allotype MNHN–LP–R.10407 (Nel Collection). Specimens stored at the Laboratoire de Paléontologie, Museum national d'Histoire naturelle, Paris.

Type locality and horizon. Nova Olinda, Ceara, Araripe Basin, N.E. Brazil. Crato Formation, Upper Aptian to Lower Albian (Maisey, 1990; Martill, 1993).

Diagnosis. As for genus (this is the only recognized species).

Description of holotype. This is a nearly complete female dragonfly, in which only the legs are missing. The wings are hyaline. The specimen exposes the ventral part of the body.

In the fore wing, the subnodus is not in perfect alignment with the nodus. The nodus is normal, with a well-pronounced nodal furrow. IR1 begins under the proximal part of the pterostigma. The pterostigma covers one and a half cells, and a strongly slanted pterostigmal brace is present. RP1 is curved at the very beginning of the pterostigmal brace. The costal margin and RA are thickened where they border the pterostigma. The arculus is angulate with the lower portion perpendicular to MP + CuA. Sectors of the arculus (RP and MA) are well separated (1·05 mm). Neither Rspl nor Mspl are present. Hypertrigonal, median, submedian, subdiscoidal spaces and discoidal triangle are all free, except for the vein CuP in the submedian space between MP + Cu and AA. Discoidal triangle large and quadrangular; the branch MPa joins the main branch of MA 0·15 mm before MA divides into MAa and MAb at the distal angle of the discoidal triangle. The distal side (MAb) of the discoidal triangle is almost straight. The subdiscoidal space is well-defined, almost triangular in shape. AA divides symmetrically into AA0 (*sensu* Nel *et al.* 1993) and AAa branches. AAa meets CuA exactly at the ventral angle of the discoidal triangle. CuA is never free and separates from MP to meet immediately AAa. The anal field is very simple, with only one row of cells. The cubito-anal field has one and two rows of cells. CuA does not produce a ventral branch. Three rows of cells lie between IR1 and RP2, one row each between RP2 and IR2, RP3/4 and MAa, and MP and CuA. RP3/4 and MAa are straight, but RP2 and IR2 curve slightly to the wing margin. There are six antenodal veins, including AX0. The first three antenodal veins (AX1, AX2 and a third vein) are strongly developed, with the corresponding cross-veins between ScP and RA well in line with them. The two distal antenodal veins are less strongly developed, but still have the corresponding cross-veins between ScP and RA well in line with them. The last antenodal vein is incomplete. The arculus is situated between the two first antenodal veins. There are six postnodal veins, with the cross-veins between RA and RP1 not in line with them. The first postnodal vein is slanted and directed proximally. There is no cross-vein under the first postnodal vein after the nodus. There are only two Bqs between RP2 and IR2 under the subnodus. The fork defined by RP3/4 and RP1/2 is symmetrical. Two cross-veins lie between RP and MA and only one between RP and RA before the fork of RP3/4 + RP. There are only three cross-veins between RP and RA, between the arculus and nodus. No supplementary longitudinal vein runs from the distal side (MAb) of the discoidal triangle. Two rows of cells in the postdiscoidal field occur after the discoidal triangle.

Dimensions of fore wing: length 16·6 mm; width at nodus 4·3 mm; base of wing to arculus 2·3 mm; base of wing to nodus 7·5 mm; nodus to apex 9·1 mm; nodus to pterostigma 6·1 mm; pterostigma to apex 2 mm; nodus to arculus 5·2 mm; nodus to RP3/4 2·3 mm; nodus to IR2 1·7 mm; RP2 begins 0·5 mm after subnodus; distance between RA and RP1 just before pterostigmal brace 0·5 mm, just after pterostigmal brace 0·6 mm; an obique vein O is at 1·1 mm from subnodus; pterostigma 1·3 mm long, 0·55 mm wide; distal side of discoidal triangle 1·25 mm long, costal side 1·05 mm long, and proximal side 1·05 mm long; distance between CuA and wing margin 0·6 mm.

The hind wing is almost identical to the fore wing, except for the following points. Only four antenodal veins (the three proximal ones–AX1, AX2 and another vein) are exactly in line with the corresponding cross-veins between ScP and RA. AX2 is the third one. AX2 appears to be a little nearer to the nodus than to AX1. The last antenodal vein is not in line with the corresponding cross-vein between ScP and RA. The arculus is more slightly angulate than in fore-wing. The anal field presents only three rows of cells between AA and the ventral margin. The cubito-anal field also has three rows of nearly regular, hexagonal cells. CuAa has not ventral branch. CuA divides into CuAa and CuAb 0·4 mm from the ventral angle of discoidal triangle. CuAb is well-defined and is directed towards the base of the wing, not towards the ventral wing margin. The one-celled anal loop is well-defined, fully longitudinal, and limited by CuAb and a ventral branch of AA. AA has three short ventral branches. The ventral margin of the wing is rounded at the base. No membranule is present.

Dimensions of hind wing: length 16·5 mm; width at nodus 5·8 mm; base of the wing to arculus 3·0 mm, base of wing to nodus 7·4 mm; nodus to apex 9·1 mm; nodus to pterostigma 5·7 mm; pterostigma to apex 1·7 mm;

TABLE 1. Dimensions of abdomen segments in holotype of *Procordulagomphus xavieri*.

Segment Number	Length (mm)	Width (mm)
10	0·5	1·0
9	0·6	1·5
8	1·4	1·8
7	2·8	3·2
6	3·2	1·6
5	3·5	1·6
4	3·5	1·7
3	3·2	1·8
2	2·0	1·8

TABLE 2. Dimensions of abdomen segments in allotype of *Procordulagomphus xavieri*.

Segment Number	Length (mm)	Width (mm)
10	0·4	1·3
9	1·5	1·5
8	2·0	1·6
7	2·6	1·7
6	2·6	1·1
5	3·2	1·1
4	3·5	1·2
3	3·2	1·2
2	2·0	1·5

nodus to arculus 4·3 mm; nodus to RP3/4 2·2 mm; nodus to IR2 1·6 mm; AX1 to AX2 2·9 mm; AX2 to nodus 2·5 mm; pterostigma 1·8 mm long, 0·7 mm wide; distal side of discoidal triangle 1·8 mm long, costal side 1·7 mm long, proximal side 1·05 mm long; anal loop 1·5 mm long, 0·7 mm wide; AA to ventral margin 2·1 mm; CuA to wing margin 1·9 mm.

The head is 1·8 mm long and 3·5 mm wide, poorly preserved, and visible in section. No detail of dorsal structures can be seen. The eyes seem to be widely separated.

The thorax is 6·2 mm long and 3·5 mm wide, and also preserved in section.

The abdomen is 21·5 mm long and almost complete, although only a part of its internal cuticle is visible. Segment dimensions are given in Table 1. No segments are widened.

The female genital structures are partly preserved at the apex of the abdomen, visible from below. Metagonocoxae extend from middle of segment nine to apex of segment ten. All the ventral surface of segment eight is destroyed.

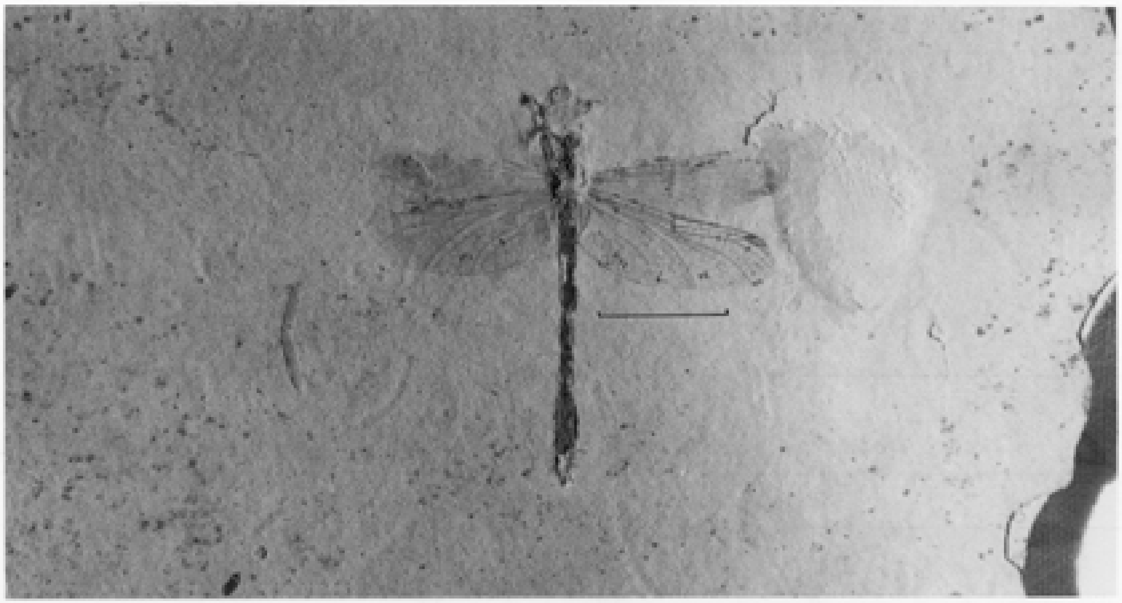
Description of allotype. This is also a nearly complete dragonfly, this time a male, with only the legs, the head and the distal portions of three wings missing. The wings are hyaline. The specimen exposes the ventral part of the body.

The antenodal veins on the fore wing are not well-preserved and the distal parts of wings are missing. The wing is identical to the holotype fore wing except for being smaller.

Dimensions of fore wing: length of preserved part 14·0 mm; width at nodus 4·3 mm; base of wing to arculus 2·5 mm; base of wing to nodus 7·7 mm; nodus to arculus 5·1 mm; nodus to RP3/4 2·3 mm; nodus to IR2 1·6 mm; distal length of discoidal triangle 1·3 mm, costal length 1·0 mm, proximal length 1·0 mm.

The hind wing is identical to that of the holotype, except for its smaller dimensions and the sexual dimorphism structures of the wing base.

The anal loop is also identical to that of the holotype. AA produces only three short ventral branches: one limiting the anal loop, and two proximal branches which rapidly fuse into a straight vein defining the anal



TEXT-FIG. 1. *Procordulagomphus xavieri* gen. et sp. nov. MNHN-LP-R.10407; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). Scale bar represents 10 mm.

triangle. The ventral wing margin is well angulated. The anal triangle is free of veins; the vein that should in fact be in the anal triangle is fused at its base to the vein that forms the distal side of anal triangle.

Dimensions of hind wing: length 15·6 mm; width at nodus 5·5 mm; base of the wing to arculus 3·0 mm; base of wing to nodus 7·3 mm; nodus to apex 8·3 mm; nodus to pterostigma 5·5 mm; pterostigma to apex 1·8 mm; nodus to arculus 4·4 mm; nodus to RP3/4 2·4 mm; nodus to IR2 1·7 mm; pterostigma 1·7 mm long, 0·6 mm wide; distal length of discoidal triangle 1·7 mm, costal length 1·4 mm, proximal length 1·0 mm; anal loop 1·45 mm long, 0·8 mm wide; anal triangle 2·0 mm long, 1·0 mm wide.

The thorax is nearly 5·0 mm long and 3·2 mm wide, and preserved in section.

The abdomen is 22·4 mm long and almost complete, although only a part of its internal cuticle is visible. Segment dimensions are shown in Table 2.

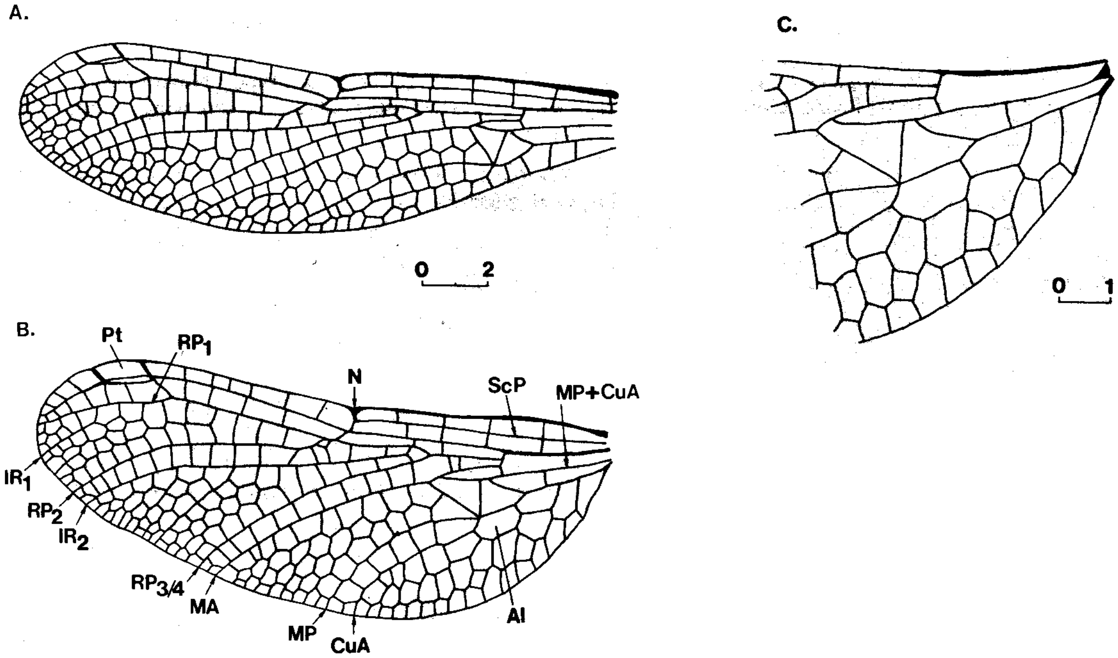
The secondary genital organs are apparently of Neanisopteran type (*sensu* Pfau 1991), and are partly in segment two and partly in segment three. However, the visible structures are almost impossible to interpret. No lateral oreillet is visible.

Two main genital organs ('cerci' *sensu* Aguesse 1968) are visible, 0·9 mm long, but the supra-anal laminae are not preserved.

Discussion. These two specimens, although of different sex, have nearly identical wing structures. The only visible differences (i.e. presence of an anal angle on male hind wing, the female hind wing being basally rounded) reflect sexual dimorphism similar to that found in present-day Gomphidae, and which appeared in early 'Anisozygoptera' and the Anisoptera (Nel *et al.* 1993).

The species is attributed to the Cordulagomphinae as it has all of the wing characteristics of that subfamily, as defined by Carle and Wighton (1990): antenodal veins AX1 and AX2 are present; first postnodal vein slanted with anterior end directed proximally; pterostigmal brace present and strongly slanted; pterostigma short and convex posteriorly; median space free; arculus strongly angulated in fore-wing, more slightly in hind-wing; sectors of arculus widely separated; only three cross-veins between MA and RP before separation of RP3/4; discoidal triangle, hypertrigonal, median, submedian spaces free; anal loop present, longitudinal and well-defined by CuAb and a branch of AA; CuAb directed towards wing base; anal and cubito-anal fields without strong pectinate branches of AA and CuA; anal triangle present in male; membranule vestigial or absent; and female metagonocoxae well developed.

The fossils are very similar in general appearance to the fossil genus *Cordulagomphus* (Text-figs 4–5), also from the Araripe deposits. Of the characters used to distinguish them from



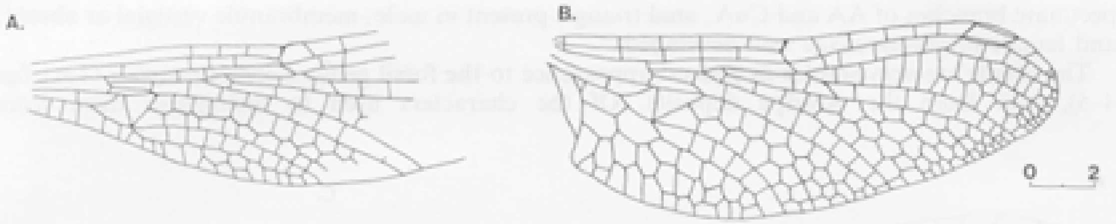
TEXT-FIG. 2. *Procordulagomphus xavieri* gen. et sp. nov. MNHN-LP-R.10406 (holotype). Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). A, fore wing; B, hind wing; C, closeup of base of hind wing. A1, Anal loop; N, Nodus; Pt, Pterostigma. Scale bars in mm.

Cordulagomphus, the following are regarded as apomorphies of *Procordulagomphus*: the anterior branch MPa of MP joins the main branch of MA and not the distal angle of the discoidal triangle; the anal triangle is free of cross-veins; the antenodal veins of the hind wing are fewer and more in line with the cross-veins between ScP and RA; and RP1 is curved from the very beginning of the pterostigmal brace. The following are plesiomorphies of *Procordulagomphus*: the anal loop is one-celled; the anal and cubito-anal fields have only three rows of cells; the distal sides (MAb) of the four discoidal triangles are straight; and the third cross-vein between RP and MA, before the point of separation of RP3/4, is neither sigmoid nor strongly slanted. As the two genera are well-characterized by these characters, *Procordulagomphus* is interprete as a sister-genus of *Cordulagomphus*.

Both *Procordulagomphus* and *Cordulagomphus* are clearly quite different from *Araripegomphus cretacicus* Nel and Paicheler from the same deposits at Araripe, most obviously in being much smaller. According to Nel and Paicheler (1994), *Araripegomphus* does not belong to Cordulagomphinae.

CONCLUSIONS

With the discovery of *Procordulagomphus*, there are now three genera and four species of Gomphidae known from the Araripe palaeolake, where they were obviously well represented. The Cordulagomphinae would appear to have been one of the more diverse groups of dragonflies



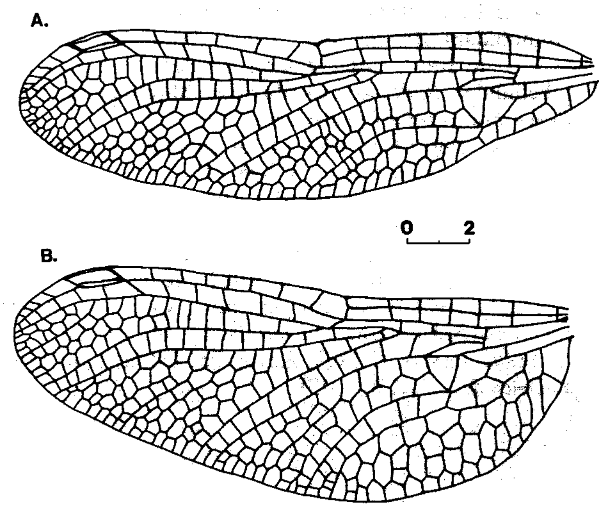
TEXT-FIG. 3. *Procordulagomphus xavieri* gen. et sp nov. MNHN-LP-R.10407 (allotype). Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian). A, fore wing; B, hind wing. Scale bar in mm.

TEXT-FIG. 4. *Cordulagomphus fenestratus* Carle and Wighton, 1990. MNHN-LP-R.10408, female; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian); Scale bar represents 10 mm.

present there, although further evidence of fossil dragonflies from Araripe may require this view to be revised. For instance, the very recent discovery of a new Libelluloidea (Jarzembowski and Nel, work in progress) shows that other taxa are to be found in Araripe's deposits.

Carle and Wighton (1990) suggested that the gomphids of the fossil subfamily Cordulagomphinae may have been adapted to a low-energy environment. This contrast with the present-day gomphids, which tend to be associated with rivers and running water. The habitats of the Cordulagomphinae larvae remain uncertain, even if we now know that the adult stages of those dragonflies were common and diverse in the Araripe palaeolake. Perhaps the Cordulagomphinae larvae lived in streams near the palaeolake and the adults invaded the lake for hunting.

The relationship of the Cordulagomphinae to the other gomphid subfamilies remains unclear (Nel and Paicheler 1994). This is not helped by our knowledge of Mesozoic Gomphidae still



TEXT-FIG. 5. *Cordulagomphus fenestratus* Carle and Wighton, 1990. MNHN-LP-R.10408, female; Nova Olinda, Ceara, Araripe Basin, northeast Brazil; Crato Formation (Upper Aptian to Lower Albian); Scale bar represents 10 mm.

being so poor, with many genera and species needing revision, even including apparently well-known taxa like *Nannogomphus bavaricus* Handlirsch, 1906 (Nel and Martínez-Delclòs, in press; Jarzembowski and Nel, work in progress). Nevertheless, the Brazilian Cordulagomphinae demonstrate that the Gomphidae were already widespread and diverse during the Early Cretaceous. A fascinating and unresolved question is how one of the more diverse and widespread Mesozoic dragonfly families, the Aeschnidiidae, with taxa known from throughout the Early Cretaceous biosphere, became extinct during the middle Cretaceous, while the Gomphidae and other modern Anisopteran groups remained undisturbed. Contingent disappearance could be a convenient answer but it still had to be demonstrated. Further studies on Mesozoic dragonflies are clearly necessary before we are able to answer that problem.

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