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Full description of *Cordulagomphus primaerensis* from Santana Formation (Lower Cretaceous of Brazil) (Odonata: Aeshnoptera: Proterogomphidae)

JULIAN F. PETRULEVIČIUS[1]*, RAFAEL G. MARTINS-NETO[2], DANY AZAR[3], EDOUARD MAKHOUL[4] & ANDRÉ NEL[5]

[1]*Museo de La Plata, División Paleozoología Invertebrados, Paseo del Bosque s/n, 1900 La Plata, and CONICET, Argentina. E-mail: levicius@museo.fcnym.unlp.edu.ar*
[2]*Universidade Federal do Ceará (UFC), Campus Cariri/FUNCAP/Sociedade Brasileira de Paleoartropodologia—SBPr. Av. Tenente Raimundo Rocha, s/n, Cidade Universitária, 63000-000, Juazeiro do Norte, CE, Brazil. (Deceased in August 6, 2010)*
[3]*Lebanese University, Faculty of Sciences II, Department of Biology, Fanar—Matn - P. O. box 26110217 Lebanon. E-mail: azar@mnhn.fr*
[4]*Saint-Joseph University, P.O. box 165507, Beirut, Lebanon*
[5]*CNRS UMR 7205, Muséum National d'Histoire Naturelle, CP 50, Entomologie, 45 rue Buffon, F-75005, Paris, France. E-mail: anel@mnhn.fr*
** Corresponding author.*

Abstract

Thanks to the discovery of a new specimen, we discuss and confirm the differences proposed by Petrulevičius and Martins-Neto, 2007 (in Bechly, 2007) between *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007 and its close relative *Cordulagomphus* (*Procordulagomphus*) *michaeli* Bechly, 2007.

Key words: Insecta, Lower Cretaceous, Crato Member, Brazil, taxonomy

Introduction

Although known by one species from the English Wealdian (Vernoux et al. 2010), the Lower Cretaceous Cordulagomphinae were very diverse in the Santana Formation of Aptian age, Brazil) (Martill et al. 2007; Bechly 2010). They share some synapomorphies with the Proterogomphinae from the Upper Jurassic of Solnhofen, Germany. Both subfamilies are included into the Mesozoic family Proterogomphidae (Bechly 1998; Bechly et al. 1998). Petrulevicius and Martins-Neto in Bechly (2007: 213) provided a diagnosis, comments and drawing of *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007. After the discovery by E.M. and D.A. of a new specimen (Figs. 3-4) that we attribute to this species, we consider useful to give a full description, diagnosis, figures, and a new discussion on the affinities of this species.

Material and methods

The holotypes of the described species of Odonata from the Santana formation are stored in different institutions foreign to Brazil. The holotype described herein is the first one stored in a Brazilian repository, following the recommendations of Petrulevičius et al. (2001) based on Brazilian law of protection of its fossiliferous heritage. In this study we follow the wing venation nomenclature of Riek and Kukalová-Peck (1984), emended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1996). The higher classification of fossil and extant Aeshnoptera is based on the work of Bechly et al. (2001).

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Systematic palaeontology

ODONATA Fabricius, 1793
ANISOPTERA Selys in Selys and Hagen, 1854
PROTEROGOMPHIDAE Bechly et al., 1998
Genus *Cordulagomphus* Carle and Wighton, 1990
Subgenus *Procordulagomphus* Nel and Escuillé, 1994

Type-species. *Cordulagomphus* (*Procordulagomphus*) *xavieri* Nel and Escuillé, 1994.

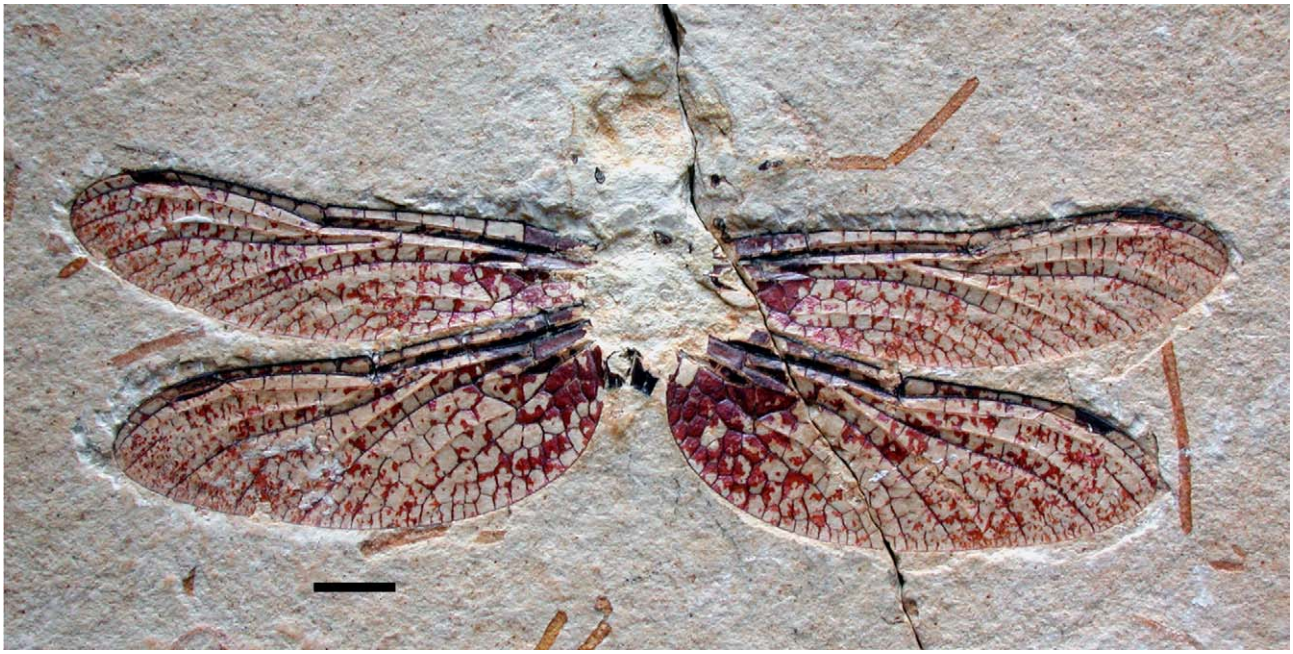

FIGURE 1. Photograph of *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007, holotype UFC-0110i. Scale bar 3 mm.

Cordulagomphus (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007
(Figs 1–4)

Etymology. Refers to the fact that was the first species of Odonata deposited in a Brazilian repository.

Material. Holotype specimen UFC-0110i, housed at the Instituto de Paleontologia e Geologia do Cariri, Universidade Federal do Cariri, Crato, Ceará State, Brazil (previously deposited under GMN-T165 at the Sociedad Brasileira de Paleoartropodologia; Ribeirão Preto, São Paulo, Brazil; Bechly, 2007). The new specimen is temporarily housed in the collection of E. Makhoul with the number BI-1 and will be deposited with the number UFC-0111i.

Type locality and horizon. Pedra Branca, northeast Brazil, Santana Formation, Crato Member, Lower Cretaceous (Upper Aptian).

Diagnosis. Presence of an accessory cubito-anal crossvein in the forewing; distal antefurcal crossvein very oblique; 5–6 postnodal crossveins and 4–6 postsubnodals; base of pseudo-IR1 below mid-distal part of pterostigma in forewing; high number of simple cells in area between RP3/4 and IR2; presence of two rows of cells between RP3/4 and MA only one cell distal of nodus level.

Descriptions. Holotype (Figs. 1–2). Counterpart of four wings preserved of a female specimen; wings purple coloured but probably hyaline in the living insect.

Forewings. Measurements from left wing; length 19.3 mm; width at nodus 5.1 mm; distance from base to arculus 2.5 mm, from arculus to nodus 7.6 mm, from nodus to pterostigma 5 mm, from pterostigma to wing apex 1.8 mm, from nodus to RP2 0.3 mm, from nodus to IR2 2.2 mm, from nodus to RP3/4 3.0 mm; pterostigma 2 mm

long and 0.7 mm wide, covering two cells in right and one and 3/4 cells in left wing; anterior side of pterostigma more oblique than distal side; costal and posterior sides distinctly thickened; pterostigma braced; nodus and nodal crossvein aligned; subnodal crossvein oblique; IR1 originating from RP1 just below distal end of perostigma; two rows of cells between IR1 and RP1; three rows of cells between IR1 and RP2; RP1 and RP2 basally slightly divergent, with one row of cells until middle length of pterostigma; RP1 curved at level of pterostigmal brace; RP2 aligned with subnodus; one row of cells between RP2 and IR2, in distal part in left wing two rows by two cells; RP2 and IR2 gently curved and reaching posterior wing margin obliquely; seven antenodal crossveins; six antesubnodal crossveins; first and third antenodal and antesubnodal crossveins aligned and stronger than others (Ax1 and Ax2); other antenodal and antesubnodal crossveins not aligned; distal antesubnodal crossvein absent; arculus between Ax1 and Ax2, closer (1 mm) to Ax1; five postnodal crossveins; three postsubnodal crossveins in left wing and four in right wing; basal postnodal crossvein strongly oblique; distal postsubnodal crossvein absent; one bridge crossvein (Bqs) basal to subnodus between RP2 and IR2; oblique vein "O" between RP2 and IR2; kink of RP2 at oblique vein; fork of RP1/2 and RP3/4 symmetrical; three crossveins between RA and RP in right wing between arculus and nodus and four in left wing; four crossveins in right wing between RP and MA and three in left wing; two rows of cells in postdiscoidal area after discoidal cell, four in distal part; Mspl and Rspl absent; eight rows of cells between IR2 and RP3/4; area between RP3/4 and MA somewhat distally widened (five cells before wing margin) with three rows of cells between them (four rows at wing margin); discoidal triangle large and quadrangular; anterior side (1.2 mm long) ends 0.16 mm basal to MA fork; distal side (1.6 mm long) with a distinct angle; basal side 1.2 mm long; hypertriangle free, 1.7 mm long and 0.3 wide with a curved anterior side; median space free; submedian space with one crossvein distal to CuP; unicellular subdiscoidal triangle (pentagonal) with its anterior side 0.9 mm long, posterior side 1.4 mm long; one or two rows of cells in anal area; CuP 1.1 mm basal to arculus; MP gently curved and ending slightly distal to level of nodus; CuA zigzagged and parallel to MP; two rows of cells between CuA and posterior wing margin; arculus slightly angled and bases of RP and MA distinctly separated at arculus.

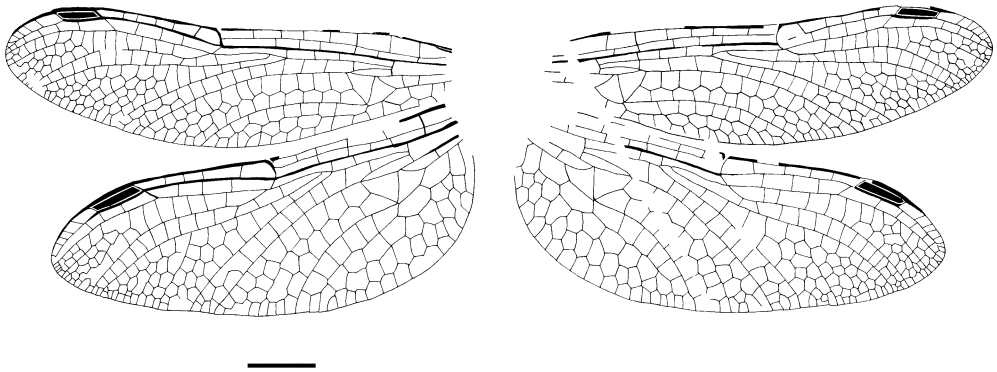

FIGURE 2. Interpretation of the venation of *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007, holotype UFC-0110i. Scale bar 3 mm.

Hindwings. Measurements from left wing; length 18.5 mm; width 6.8 mm; distance from wing base to arculus 2.6 mm, from arculus to nodus 6 mm, from base to nodus 8.6 mm, from nodus to pterostigma 5.4 mm, from pterostigma to wing apex 2.1 mm, from nodus to RP2 0.4 mm, from nodus to IR2 2.0 mm, from nodus to RP3/4 2.5 mm; pterostigma 2.4 mm long and 0.74 mm wide, covering two cells; basal side of pterostigma more oblique than distal one; anterior and posterior sides distinctly thickened; pterostigma brace more oblique than in fore wing; nodus and nodal crossvein aligned; subnodal crossvein less oblique than in fore wing; IR1 originating from RP1 just below distal end of pterostigma; two rows of cells between IR1 and RP1; three rows of cells between IR1 and RP2; RP1 and RP2 basally slightly divergent, with one row of cells until middle length of pterostigma; RP1 curved at level of pterostigma brace; RP2 not aligned with subnodus (0.1 mm one displaced distally); one row of cells between RP2 and IR2, in distal part in left wing two rows by three cells (ending with three rows), in right wing only two rows in distal cell; RP2 and IR2 gently curved and reaching posterior wing margin obliquely; five antenodal crossveins; five antesubnodal crossveins; first and third antenodal and antesubnodal aligned and stronger than others (Ax1 and Ax2); anteapical antenodal and antesubnodal crossveins nearly aligned; distal antesubnodal

crossvein absent; arculus between Ax1 and Ax2, closer (0.8 mm) to Ax1; four postnodal crossveins; three postsubnodal crossveins; one bridge crossvein (Bqs) basal to subnodus (left wing not preserved (?)) between RP2 and IR2; oblique vein "O" between RP2 and IR2, 1.8 mm from subnodus; kink of RP2 at oblique vein (slightly developed in left wing); fork of RP1/2 and RP3/4 symmetrical; two crossveins between RA and RP between arculus and nodus; two crossveins in right wing between RP and MA and one (?) in left wing; two rows of cells in postdiscoidal area after discoidal cell, four in distal part; Mspl and Rspl absent; seven rows of cells between IR2 and RP3/4; area between RP3/4 and MA somewhat distally widened (four cells before distal margin) with two rows of cells between them (three rows at wing margin); discoidal triangle large; anterior side 1.6 mm long; distal side (1.8 mm long) with a distinct angle; basal side 1.3 mm long; hypertriangle free, 2.3 mm long and 0.45 wide with a curved anterior side; median and submedian space free; unicellular subdiscoidal triangle (pentagonal) with its anterior side 1.1 mm long, posterior side 1.9 mm long; three to four rows of cells in anal area; CuP 1.1 mm basal to arculus; MP gently curved and ending at level of nodus; CuA zigzagged and parallel to MP; three rows of cells between CuA and posterior wing margin; arculus slightly angled and bases of RP and MA distinctly separated at arculus; CuAb strongly angular to CuAa; CuAb and a posterior branch of AA enclose a well-defined unicellular anal loop, longitudinal, 1.7 mm long and 0.8 mm wide; AA with three posterior branches; postero-basal margin rounded.

FIGURE 3. Photograph of *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007, new specimen. Scale bar 3 mm.

New specimen (Figs. 3–4). Forewing length 19.0 mm; width at nodus 5.0 mm; distance from base to nodus ca. 10.0 mm (nodus situated at about 52% of wing length); distance from nodus to pterostigma 5.1 mm, from base to arculus ca. 3.2 mm; Ax1 and Ax2 not preserved; distal of Ax2 at least five secondary antenodal crossveins between costal margin and ScP and three of them between ScP and RA; four antesubnodal crossveins with a distinct gap directly distal of arculus and a long "cordulegastrid gap" directly basal of subnodus; six postnodal crossveins and six postsubnodal crossveins between nodus and pterostigma, non-aligned; no "libellulid gap" of postsubnodal crossveins directly distal of subnodus; pterostigma 2.1 mm long and max. 0.60 mm wide; pterostigma distinctly braced and covering about one and two-third cells; arculus partly destroyed; hypertriangle only partly preserved but probably free; discoidal triangle transverse and free; length of basal side of discoidal triangle 1.3 mm; length of its costal side 1.1 mm, of its distal side 1.6 mm; MAb relatively straight (weakly angled); a distinct pseudo-anal vein PsA delimiting an unicellular subdiscoidal triangle; median space free; submedian space with CuP-crossing

and a supplementary crossvein; anal area max. 1.1 mm wide with one to two rows of cells (including a large elongate cell beneath cubital cell); cubito-anal area max. 1.6 mm wide with two rows of cells (seven double cells); CuA without visible posterior branches; MP ending on level of nodus; basal part of postdiscoidal area with only two rows of cells; postdiscoidal area widened distally (width near discoidal triangle 1.3 mm; width at hind margin 1.5 mm) with eight cells between MA and MP at hind margin; no Mspl; RP3/4 and MA relatively straight and diverging distally, with only one row of cells between them up to one cell distal to nodus, and four cells at hind margin; distal antefurcal crossvein rather oblique; first branching of RP 2.7 mm basal of subnodus; IR2 originating on RP1/2; seven cells in portion of area between IR2 and RP3/4 with only one row of cells; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 1.0 mm and one and a half cells distal of subnodus; two bridge crossveins between RP2 and IR2 basal of subnodus; RP2 and IR2 nearly parallel with only one row of cells between them up to hind margin; no Rspl; only one row of cells between RP1 and RP2 up to pterostigma (with six cells in this portion of wing); pseudo-IR1 originating on RP1 beneath distal third of pterostigma; up to five rows of cells at margin between pseudo-IR1 and RP1 and six rows of cells between pseudo-IR1 and RP2 near hind margin; one-two rows of cells between C and RA distal of pterostigma.

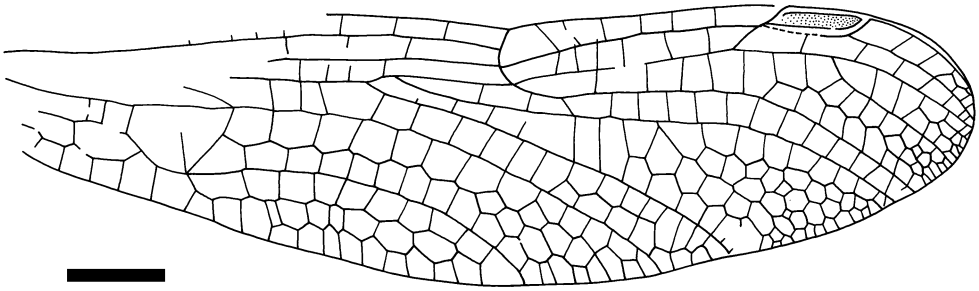

FIGURE 4. Interpretation of the venation of *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevičius and Martins-Neto, 2007, new specimen. Scale bar 2 mm.

Discussion. The new specimen clearly corresponds to Cordulagomphidae, close to the two species *Cordulagomphus* (*Procordulagomphus*) *primaerensis* Petrulevicius and Martins-Neto, 2007 (in Bechly, 2007: 213) and *Cordulagomphus* (*Procordulagomphus*) *michaeli* Bechly, 2007, because of the presence of four rows of cells between MA and RP3/4 along posterior wing margin and the presence of a relatively low number of cells in distal half of wing.

P. primaerensis and *P. michaeli* are very close species that differ in very few points: distal antefurcal crossvein more oblique in the former than in the later; *P. michaeli* has 4–5 postnodal crossveins and 3–4 postsubnodals while *P. primaerensis* has respectively five and four (six and six in our fossil). The new specimen shares with *P. primaerensis* but not with *P. michaeli* the following characters: base of pseudo-IR1 below mid-distal part of pterostigma in forewing; high number of simple cells in area between RP3/4 and IR2 (3–5 in the holotype, six in the new specimen, while 3–4 in *P. michaeli*); presence of two rows of cells between RP3/4 and MA only one cell distal of nodus level in the new specimen, while it is two cells in the holotype and three cells in *P. michaeli*. A further important character shared by our fossil and *P. primaerensis* is the presence of an accessory cubito-anal crossvein in the forewing. Bechly (in Martill et al., 2007) indicated that this character is "probably not a diagnostic character, but an individual aberration." The presence of the same structure in the new specimen and the type of *P. primaerensis* strongly supports the hypothesis that it is not an aberration but a good diagnostic character.

Nevertheless the new specimen differs from both the type of *P. primaerensis* and *P. michaeli* in the presence of five rows of cells between RP1 and IR1 along wing margin instead of 2–3 rows. But this character is not significant to separate the new specimen from *P. primaerensis*.

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