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A new libelluloid dragonfly from late Paleocene deposits in Argentina (Odonata: Italoansida)

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Abstract. A new genus and species of "libelluloid" dragonfly, *Jujusia maizgorda* gen. n., sp. n., of the clade Italoansida Bechly, 1996, from the late Paleocene, Maíz Gordo Formation, north-western Argentina, is described. Its phylogenetic relationships within the clade Cavilabiata Bechly, 1996 are discussed.

INTRODUCTION

The oldest representatives of the clade Brachystigmata Bechly, 1996 ("libelluloid" dragonflies) are from the Upper Jurassic - Lower Cretaceous (Bechly et al., 1996; Bechly, 1998). The more advanced group Italoansida, comprising the "Corduliidae", Hemicorduliidae, Macrodiplacidae and Libellulidae, is less well documented in the Mesozoic and the Paleocene-Eocene. Thus, the discovery of a fossil wing of a new taxon related to Italoansida, in Paleocene deposits in Argentina gives us a better understanding of the past diversity of this group.

The wing venation nomenclature of Riek & Kukalová-Peck (1984), amended by Kukalová-Peck (1991), Nel et al. (1993) and Bechly (1996) is followed. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996).

TAXONOMIC PART

Odonata Fabricius, 1793
Italoansida Bechly, 1996
Family undetermined
***Genus Jujusia* gen. n.**

Type species. *Jujusia maizgorda* sp. n.

Diagnosis. The characters are from the hindwing. (1) elongated and boot-shaped anal loop ('italian loop' *sensu* Bechly, 1996), with a long toe, a well defined but slightly curved Cuspl, and a long, basally sigmoidally curved CuA, with a strong angle between CuAa and CuAb; (2) Mspl absent; (3) Rspl present, distinctly curved, with one row of cells between it and IR2; (4) RP3/4 and MA strictly parallel up to posterior margin; (5) basal part of postsubnodal area free of cross-veins ("libellulid gap"); (6) 2 primary antenodal brackets Ax1 and Ax2 only slightly stronger than secondary antenodal cross-veins; (7) arculus between Ax1 and Ax2; (8) bridge space free; (9) only one cross-vein beneath pterostigma; (10) RP and MA not basally fused in the arculus but strongly approximated; (11) only 3 cross-veins in the area between RA and RP, between arculus and nodus; (12) no "libellulid oblique vein"; (13) anal area very wide with five rows of cells between anal loop and posterior wing margin.

Etymology. After the Province of Jujuy, North-west Argentina, where the specimen was found.

***Jujusia maizgorda* sp. n.**

(Figs 1–2)

Diagnosis. That of the genus.

Description. Imprint of a hindwing with the extreme apex and base missing; no trace of coloration preserved; length of the preserved part, 21.03 mm; probable length of the wing about 23 mm; width 10 mm; distance from base to arculus, 2.3 mm; from arculus to nodus, 6.55 mm; from nodus to pterostigma, 10.34 mm; pterostigma 1.55 mm long and 0.7 mm wide, covering 3/4 of a cell, with one basal cross-vein below it; costal and posterior sides of pterostigma widened; 5 complete antenodal veins, the three basal veins stronger than the others, and the 2 first basal antenodal cross-veins (primary antenodals) slightly stronger than the third; arculus between the 2 primary antenodal veins, closer to Ax1; RP and MA not fused in arculus but basally strongly approximate; arculus in a very slightly distal position (0.068 mm) relative to proximal side of discoidal triangle; 7 preserved postnodal veins, the first proximal one incomplete between RA and RP1, and the fifth and sixth not aligned with the corresponding cross-veins between RA and RP1; 3 cross-veins between RA and RP between arculus and nodus; oblique vein 'O' 1.3 mm long, 2 cells distal to subnodus; absence of Bqs; hypertriangle and median space free; submedian space only crossed by CuP, basal to Cuspl; discoidal triangle free, triangular, its anterior side slightly convex,

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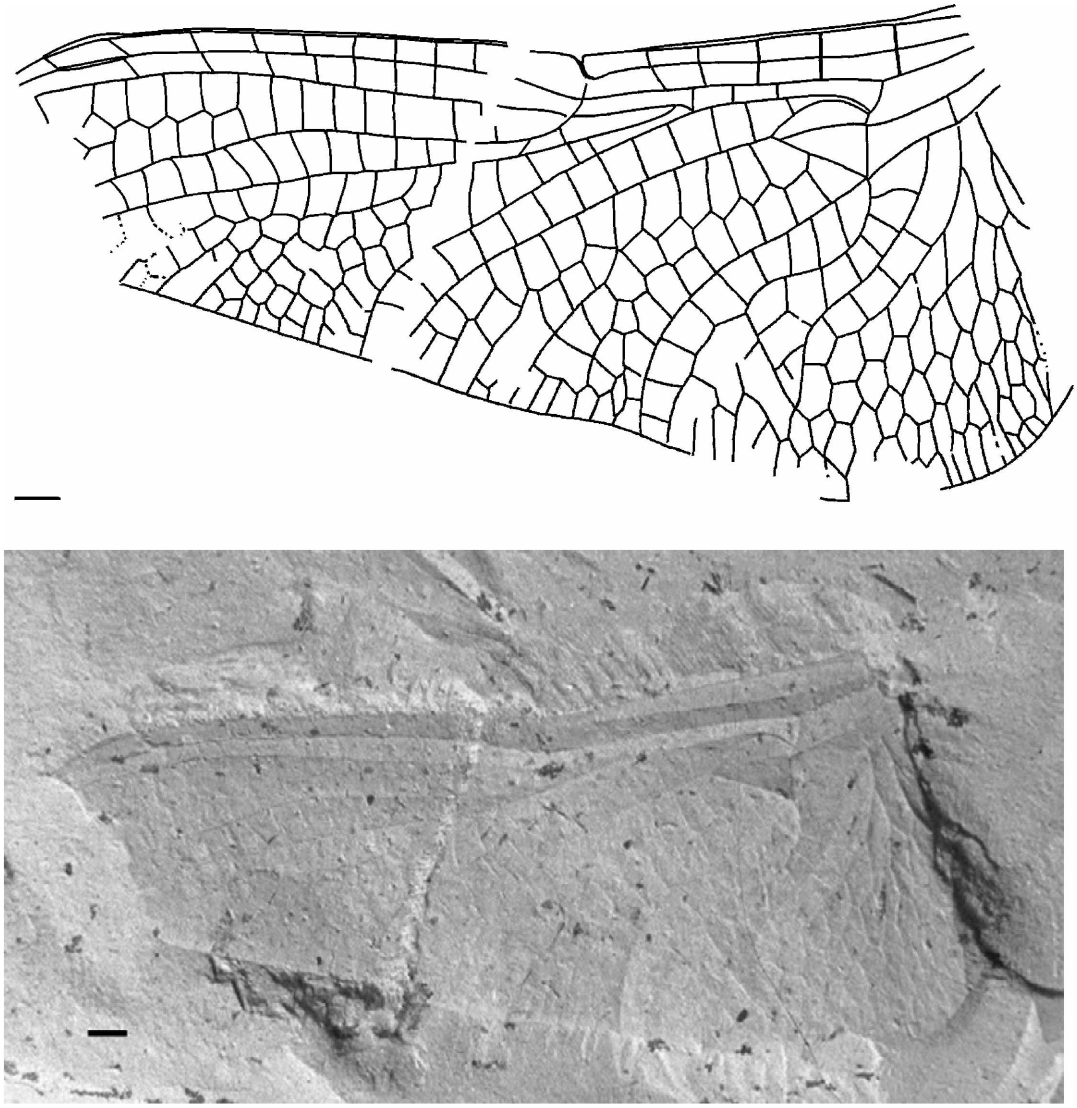

Figs 1–2. *Jujusia maizgorda* gen. n., sp. n.; holotype specimen 29014; late Paleocene; La Mendieta, Province of Jujuy, Argentina. above – reconstruction of the hindwing; below – photograph of the hindwing. Scale = 5 mm.

1.93 mm long, posterior side, 2.06 mm long, basal side, 1.17 mm; postdiscoidal area with two rows of cells distal to discoidal triangle, much wider distally; Mspl absent, but a secondary longitudinal vein between MA and posterior wing margin, with 2 rows of cells between it and MA at its base and 4 distally; Rspl well defined, curved, with one row of cells between it and IR2; cubito-anal area very wide (7.2 mm wide) with 6 rows of cells between AA and posterior wing margin, and probably 2 rows of cells between anal loop and basal wing margin; anal loop well developed, with an elongate toe of 3 cells; a strong angle between CuAa and CuAb (anterior and postero-distal sides of anal loop); Cuspl making an angle of 45°; one row of cells between CuAb and Cuspl, and one row between Cuspl and the posterior branch of AA in the toe of the anal loop; 2 rows of cells between posterior end of toe and posterior wing margin; one row of cells between CuA and MP ; one row of cells between MA and RP3/4, and between IR2 and RP2; IR1 zigzagged, beginning 3 cells basal to pterostigma; base of pseudo-IR1 visible below middle of pterostigma; IR2 nearly straight; RP2 with a double curvature; MA and RP3/4 parallel and bent before reaching posterior wing margin, at nearly a right angle.

Holotype. Specimen n° MLP 29014 (isolated hindwing), stored at the Departamento Científico Paleozoología Invertebrados, Museo de la Plata, La Plata, Argentina.

Type locality. La Mendieta, province of Jujuy, Northwest Argentina, latitude 24° 21' S, longitude 64° 59' W.

Type strata. Green shale facies, Maíz Gordo Formation, late Paleocene (Volkheimer et al., 1984; Marshall et al., 1997; Quattrocchio et al., 1997).

Etymology. After the Maíz Gordo Formation.

Phylogenetic systematics. Following the phylogenetic system proposed by Bechly (1996, 1997) (in part in Fig. 3), *Jujusia* gen. n. shares with the Cavilabiata the reduced hindwing pseudo-anal vein PsA (no subdiscoidal space),

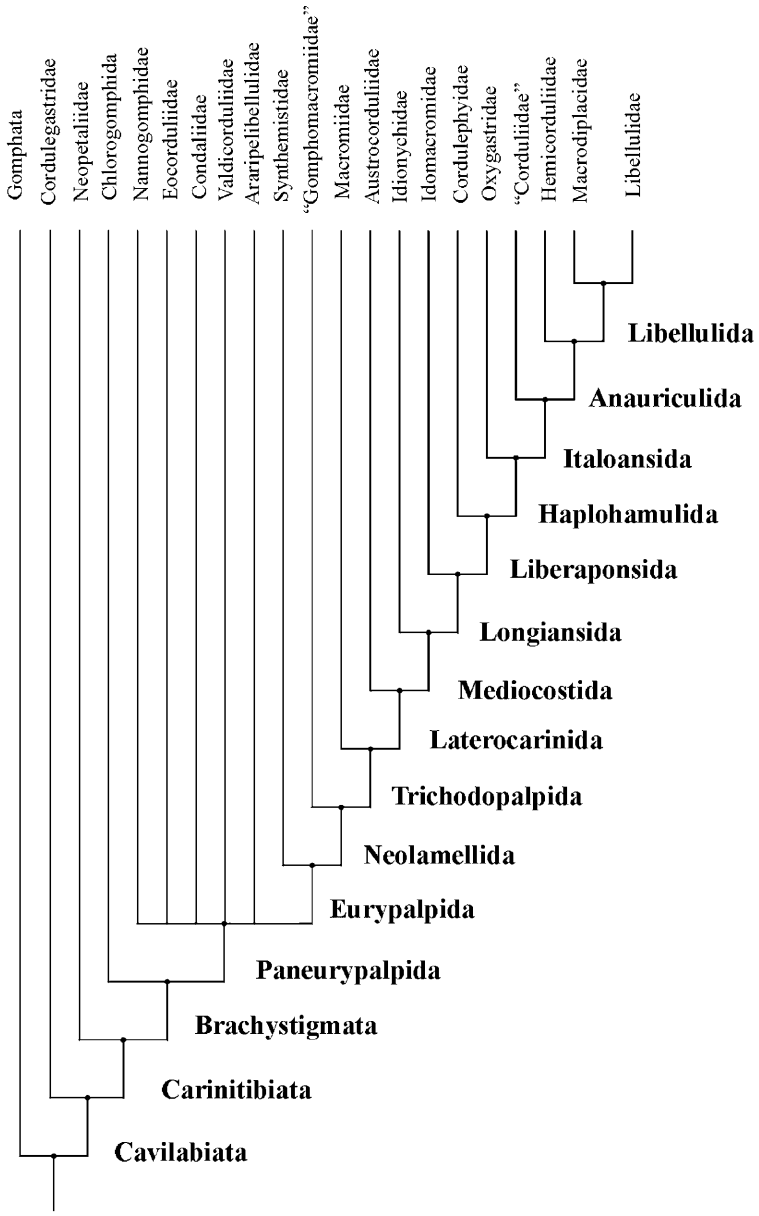

Fig. 3. Phylogenetic tree of Cavilabiata (after Bechly, 1996). Family group names are used in sense of Bechly (1996). The clade Italoansida shares with *Jujusia* gen. n. the following synapomorphies: hindwing discoidal triangle recessed to the level of the arculus; elongated and boot-shaped anal loop that nearly reaches the hind margin of the wing with its "toe", with a straight (non-zigzagged) and forked midrib (Cuspl). *Jujusia* appears not to fall into the families Corduliidae, Hemicorduliidae, Macrodiplacidae, and Libellulidae; but its relationships are still unknown because of the poor preservation of the extreme base of the wing.

the 'cordulegastrid gap' in the antesubnodal space, the basal CuA greatly prolonged proximally to its branching and a wide and long anal loop. It lacks the basal furcation of IR2 characteristic of the Cordulegastrida, the very elongated and enlarged anal loop, and the reduction in the number of branches of CuA (only two distal branches) of the Carinitibiata Bechly, 1996.

Within this clade, *Jujusia* gen. n. does not fall in the Neopetaliidae because of its short and zigzagged IR1. It has nearly all the synapomorphies of Brachystigmata Bechly, 1996 (i.e. (1) sectors of arculus strongly approximate; (2) posterior part of arculus distinctly shorter than anterior part; (3) oblique pterostigmal brace reduced; (4) short pterostigma covering one complete cell; (5) the "gaff" (= basal CuA basal of its branching) strongly prolonged in the hindwing; (6) CuA with only 2 posterior branches; (7) anal loop very large; (8) RP3/4 and MA strictly parallel up to posterior margin.

Within Brachystigmata, *Jujusia* gen. n. does not fall in the Chlorogomphida because it has only one row of cells between MP and CuA; that the basal part of CuA is not straight but curved and the terminal branch of CuA not secondarily branched on CuAb also exclude it from the Araripephlebiidae Bechly, 1998. Within the Paneurypalpida, the Mesozoic families Nannogomphidae, Eocorduliidae, Condaliidae, Valdicorduliidae, and Araripelibellulidae can be excluded because of their distinctly shorter, less foot-shaped anal loop. Also, the Eocorduliidae Bechly, 1996 are excluded because they have more than one row of cells in the distal half of the area between

RP3/4 and MA. The Valdicorduliidae and Araripellibellulidae are excluded because of their well-defined subdiscoidal triangle.

Jujusia gen. n. has the main hindwing venational synapomorphies of the Eurypalpida: pterostigma very short, covering only one cell; hindwing PsA completely absent; basal part of CuA, aligned with MAb and reduced in hindwing; CuA with only one dichotomous branching; oblique vein "O" less than 2 cells distal of subnodus; sectors of arculus diverging from one point; antenodal cross-veins well aligned; Ax1 and Ax2 with no secondary cross-vein between them; lack of cross-veins in basal part of postsubnodal interspace ("libellulid gap"); anal loop with, at least, 8 cells.

Within this clade, the Synthemistidae can be excluded because of its foot-shaped anal loop and median space free of cross-veins. It shares with the Neolamellida the secondary antenodal cross-veins nearly as strong as the 2 primary antenodal cross-veins in hindwing. All the venational synapomorphies of the Gomphomacromiidae (*sensu* Carle, 1995) proposed by Bechly (1996) are also shared by the clades Liberaponsida and Laterocarinida. Nevertheless, *Jujusia* gen. n. has its hindwing discoidal triangle exactly aligned with the arculus and lacks a PsA. Both these characters are absent in the Gomphomacromiidae but present in the Liberaponsida.

Jujusia gen. n. has a strong Rspl more or less parallel to IR2, a synapomorphy of the Trichodopalpida. Within this clade, the Macromiidae can be excluded because of its undulate RP3/4 and MA and its "cordulegastrid" and "libellulid" gaps, which are shortened. The discoidal triangle aligned with the arculus is a synapomorphy of the Laterocarinida. All the venational synapomorphies of the Austrocorduliidae are present in Liberaponsida (due to convergences, Bechly, 1996). Fortunately, the Austrocorduliidae lack midrib (Cuspl) in the anal loop, unlike *Jujusia* gen. n. and the clade Mediocostida. *Austrocordulia* Tillyard, 1908 has no hindwing Rspl. The Idionychidae *sensu* Bechly (1996) are excluded because their 2 primary antenodal brackets Ax1 and Ax2 are very indistinct or even indistinguishable from the secondaries (Fraser, 1957) and their sectors of arculus are stalked, with a long fusion (Fraser, 1957). Also, the hindwing arculus of *Jujusia* gen. n. is between the 2 basal antenodals, and its anal loop has a strong toe, unlike *Idionyx* Hagen, 1867. *Jujusia* gen. n. has the 2 synapomorphies of the clade Longiansida Bechly, 1996, i.e. anal loop and Cuspl distinctly elongated (with the tip pointing to the wing apex in the groundplan), correlated with a strongly elongated and sigmoidal "gaff".

The Idomacromiidae are excluded because their RP3/4 and MA undulate in both pairs of wings, their elongated anal loop has an unique shape, with secondarily 2 rows of cells in the basal part anterior of the midrib, their discoidal triangle is not aligned with the arculus, and at least their hindwing cubital cell (between CuP-crossing and pseudo-anal cross-vein PsA) is divided by several accessory cubito-anal cross-veins.

Jujusia gen. n. has the synapomorphies of the clade Liberaponsida, i.e. there is no secondary antenodal present between the 2 primary antenodal brackets Ax1 and Ax2, therefore the arculus is situated between the first 2 antenodal cross-veins; bridge-space free; no cubito-anal cross-vein retained, except for CuP; hypertriangle free. Within this clade, the Cordulephyidae can be excluded because of their highly specialized nearly quadrangular discoidal triangle. *Cordulephya* Selys, 1870 has a very reduced cubito-anal area, without anal loop, and *Neophya* Selys, 1881 has no toe in its long anal loop (Martins, 1906). Within the Haplohamulida (sister group of the Cordulephyidae, after Bechly, 1996), the Oxygastridae Bechly, 1996 are excluded because of their anal loop lacks a defined toe and their vein PsA is well-defined. The sister group of this family, the clade Italoansida shares with *Jujusia* gen. n. the following synapomorphies: hindwing discoidal triangle recessed to the level of the arculus; elongated and boot-shaped anal loop that nearly reaches the hind margin of the wing with its "toe", with a straight (non-zigzagged) and forked midrib (Cuspl). The unique synapomorphy of the Italoansida not present in *Jujusia* gen. n. is a well-defined Mspl. Nevertheless, this vein is also not very well defined in some Corduliidae (*sensu* Bechly, 1996) (*Cordulia shurtleffi* Scudder, 1966; see Martins, 1906). Bechly (1996) characterized the wing venation of the Corduliidae by the presence of only one cross-vein below the pterostigma, but noted that this character is also present in some Anauriculida. It is present in many Libellulidae, and also Hemicorduliidae and Macrodiplacidae. Thus, this homoplastic character, present in *Jujusia* gen. n., is not sufficient to include it in Corduliidae.

The Anauriculida (= Hemicorduliidae + Libellulida), sister group of the Corduliidae *sensu* Bechly, 1996, appear to be excluded because they have a strongly curved Mspl distally "rejoining" vein MA and a Rspl distally "rejoining" vein IR2 (Bechly, 1996). If both these veins are more or less curved in all Anauriculida, they will not "rejoin" MA and IR2 in all of them. In *Hemicordulia* Selys, 1870, the forewing Mspl is curved but that of hindwing is nearly straight and does not "rejoin" MA. Furthermore, the "corduliid" *Aeschnosoma* Selys, 1870 has a well defined Mspl and Rspl, curved and "rejoining" MA and IR2.

The absence of an oblique second cross-vein between RP1 and RP2 ("libellulid oblique vein") excludes the Libellulida = (Macrodiplacidae + Libellulidae). Note that the Libellulidae: Tetrathemistinae *Palaeothemis tillyardi* Fraser, 1923 has no "libellulid oblique vein" and that this vein is only weakly oblique in *Libellula depressa* Linneaus, 1758. Thus, this character is subject to homoplasies within the Libellulidae. Furthermore, *Jujusia* gen. n. has a more developed anal toe and a cubito-anal area distinctly broader and larger than those of the Corduliidae, and as broad and large as in modern Macrodiplacidae + Libellulidae.

Because of the poor preservation of the extreme base of the wing of *Jujusia* gen. n., it is not certain if it had an

anal triangle, as in Corduliidae and Hemicorduliidae, or an anal angle, as in Corduliidae and unlike Macrodiplacidae + Libellulidae.

On basis of its hindwing venation, *Jujusia* gen. n. belongs in the Italoansida.

Comparison with the Palaeomacromiidae Petrulevičius, Nel & Muzón, 1999

Palaeomacromiidae is a fossil family known only from forewings from the same locality and horizon as *Jujusia* gen. n. This family is based on *Palaeomacromia multicellulata* Petrulevicius, Nel & Muzón, 1999. Recently, Petrulevicius & Nel (in press) described a new genus with two new species. This group is characterized by the presence of a Mspl and a curved Rspl, numerous cells in discoidal triangle and subdiscoidal space, and more than 5 rows of cells in the postdiscoidal space (Petrulevicius et al., 1999; Petrulevicius & Nel, in press). It is difficult to compare fore- and hindwings of Anisoptera. *Jujusia* gen. n. has clearly fewer rows of cells in its postdiscoidal area than the Palaeomacromiidae (2 rows instead of more than 5) and no Mspl. Thus, it is probably not a Palaeomacromiidae.

CONCLUSIONS

The 3 known species of Palaeomacromiidae and *Jujusia* gen. n. belong in Italoansida and are not closely related to any of the modern families within this clade. This indicates that the late Paleocene was probably a crucial period for the diversification of the "libelluloid" dragonflies, especially now that the Libellulidae are known from the Turonian (Fleck, Nel & Martínez-Delclòs, 1999), and that there was a great diversity of anisopteroids in Northwest Argentina during the period when these geological strata were deposited.

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