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New basal Odonoptera (Insecta) from the lower Carboniferous
(Serpukhovian) of Argentina.Julián F. Petrulevičius^{1,2} & Pedro R. Gutiérrez^{1,3}¹ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).² Museo de La Plata, División Paleozoología Invertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata (1900), ARGENTINA. e-mail: levicius@museo.fcnym.unlp.edu.ar³ División Paleobotánica y Paleopalínología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, Ciudad de Buenos Aires (C1405DJR), ARGENTINA. e-mail: pedroraulgutierrez@gmail.com

Abstract: Three new basal species of Odonoptera from the upper Serpukhovian (325-324 Ma) of Guandacol 1 locality, Quebrada de las Libélulas, Guandacol Formation, La Rioja province, central West Argentina, are described. Two known species also from the Serpukhovian, *Eugeropteron lunatum* Riek, 1983 and *Geropteron arcuatum* Riek, 1983, from Cuestita de La Herradura, Malanzán Formation, La Rioja province, are discussed. Several higher taxa are nominated to include these species, resulting in a new classification: 1 Superorder Odonoptera, 1.1 Eugeroptera ord. nov., 1.1.1 Eugeropteridae, 1.1.1.1 *Eugeropteron*, 1.1.1.1.1 *Eugeropteron lunatum*, 1.1.1.1.2 *Tupacsala niunamenos* gen. nov. et sp. nov., 1.2 Palaeodonoptera taxon nov., 1.2.1 Kukaloptera ord. nov., 1.2.1.1 Kirchneralidae fam. nov., 1.2.1.1.1 *Kirchnerala treintamil* gen. nov. et sp. nov., 1.2.2 Plesiodonoptera taxon nov., 1.2.2.1 Argentinoptera ord. nov., 1.2.2.1.1 Argentinidae fam. nov., 1.2.2.1.1.1 *Argentina cristinae* gen. nov. et sp. nov., 1.2.2.2 Apodonoptera taxon nov., 1.2.2.2.1 Orden Geroptera, 1.2.2.2.1.1 Geropteridae fam. nov., 1.2.2.2.1.1.1 *Geropteron*, 1.2.2.2.1.1.1.1 *Geropteron arcuatum*, 1.2.2.2.2 Neodonoptera.

Key words: Eugeroptera ord. nov., *Tupacsala niunamenos* gen. nov. et sp. nov., Kukaloptera ord. nov., Kirchneralidae fam. nov., *Kirchnerala treintamil* gen. nov. et sp. nov., Argentinoptera ord. nov., Argentinidae fam. nov., *Argentina cristinae* gen. nov. et sp. nov., Geropteridae fam. nov.

Resumen: Nuevos Odonoptera (Insecta) basales del Carbonífero inferior (Serpukhoviano) de la Argentina. Nuevos Odonoptera basales del Serpukhoviano superior (325-324 Ma) son descritos de la localidad Guandacol 1, Quebrada de las Libélulas, Formación Guandacol, provincia de La Rioja, centro oeste de la Argentina. Otras dos especies conocidas del Serpukhoviano, *Eugeropteron lunatum* Riek, 1983 y *Geropteron arcuatum* Riek, 1983, de Cuestita de La Herradura, Formación Malanzán, provincia de La Rioja, son discutidas. Varios taxones de orden superior nuevos son nominados para incluir estas especies, resultando en una nueva clasificación: 1 Superorden Odonoptera, 1.1 Eugeroptera ord. nov., 1.1.1 Eugeropteridae, 1.1.1.1 *Eugeropteron*, 1.1.1.1.1 *Eugeropteron lunatum*, 1.1.1.1.2 *Tupacsala niunamenos* gen. nov. et sp. nov., 1.2 Palaeodonoptera taxon nov., 1.2.1 Kukaloptera ord. nov., 1.2.1.1 Kirchneralidae fam. nov., 1.2.1.1.1 *Kirchnerala treintamil* gen. nov. et sp. nov., 1.2.2 Plesiodonoptera taxon nov., 1.2.2.1 Argentinoptera ord. nov., 1.2.2.1.1 Argentinidae fam. nov., 1.2.2.1.1.1 *Argentina cristinae* gen. nov. et sp. nov., 1.2.2.2 Apodonoptera taxon nov., 1.2.2.2.1 Orden Geroptera, 1.2.2.2.1.1 Geropteridae fam. nov., 1.2.2.2.1.1.1 *Geropteron*, 1.2.2.2.1.1.1.1 *Geropteron arcuatum*, 1.2.2.2.2 Neodonoptera.

Palabras clave: Eugeroptera ord. nov., *Tupacsala niunamenos* gen. et sp. nov., Kukaloptera ord. nov., Kirchneralidae fam. nov., *Kirchnerala treintamil* gen. nov. et sp. nov., Argentinoptera ord. nov., Argentinidae fam. nov., *Argentina cristinae* gen. nov. et sp. nov., Geropteridae fam. nov.

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Introduction

Odonatoptera basal to the Neodonatoptera Bechly, 2001 are extremely rare in the fossil record. Only two previous genera were described from the Argentinean locality Cuestita de la Herradura, i.e., *Eugeropteron* Riek, 1983 and *Geropteron* Riek, 1983 (Riek & Kukalová-Peck, 1984). These two insects and *Xenoptera riojaensis* Pinto, 1986 were recovered from the Malanzán Formation (Pinto, 1986), considered a lateral equivalent of Guandacol Formation (Césari & Gutiérrez, 2001) (see below). *Eugeropteron* and *Geropteron* were considered the most basal of the Odonatoptera (Kukalová-Peck, 1991, 2009; Brauckmann *et al.*, 1996; Bechly, 2007). These taxa and those described here are coincidentally treated as basal to Neodonatoptera in the present contribution.

The new species described here were exhumed from the base of the Guandacol Section of the Guandacol Formation with an age of *circa* 325–324 Ma (Césari *et al.*, 2011). Oldest records of winged insects in the world are one undetermined species of Archaeorthoptera from the Paskov Mine (*circa* 324–325 Ma), Czech Republic (Prokop & Nel, 1996), and a species of Palaeodictyoptera from Delitzsch (320–323 Ma), Germany (Brauckmann & Schneider, 1996; Zhang *et al.*, 2013). Concerning oldest Odonatoptera, there are four genera with four species of Neodonatoptera from the German locality Hagen-Vorhalle (320 Ma) (Zessin *et al.*, 2011) and *Erasipteron* Pruvost, 1933 from Horní Suchá (318 Ma), Czech Republic (Zessin, 2008).

One of the specimens described here (see below) is the most complete and prettiest female dragonfly from the Carboniferous, with part of head, thorax with 6 wings and abdomen with ovipositor. The preservation of prothoracic wings is unusual for basal Odonatoptera, being the only other species worldwide *Erasipteroides valentini* Brauckmann, 1985 from the Carboniferous of Germany (Brauckmann *et al.*, 1985; Bechly *et al.*, 2001). The specimen has been part of a research about fly adaptations in Carboniferous insects (Wotton *et al.*, 1998; Vogel, 1998; Wotton & Kukalová-Peck, 2000) and has been discussed and figured in several contributions (Wotton *et al.*, 1998; Gutiérrez *et al.*, 2000; Bechly *et al.*, 2001; Bechly, 2007; Kukalová-Peck, 2008; Staniczek *et al.*, 2011). In this work it is described, named and included in a new classification.

Materials and methods

In this work, we follow the wing venation nomenclature of Kukalová-Peck (1983), amended by Kukalová-Peck (1991, 2009), and contributions by Riek & Kukalová-Peck (1984), Nel *et al.* (1993), and Bechly (1996). Abbreviations of the wing venation used in the text and figure are: CP (Costa Posterior), ScA (Subcosta Anterior), ScP (Subcosta Posterior), RA (Radial Anterior), RP (Radial Posterior), MA (Media Anterior), MP (Media Posterior), CuA (Cubital Anterior), CuP (Cubital Posterior), CuAc (Cubital Anterior crossing), CuPc (Cubital Posterior crossing), AA (Anal Anterior), AP (Anal Posterior). Crossveins are in lower case letter.

We use the groundplan method of phylogenetic Systematics *sensu* Hennig (1968, 1981) and Kukalová-Peck (2009). In this sense, the groundplan plesiomorphies and synapomorphies could be retained by basal and successive intermediate taxa and could be not visible in the crown group. As example of typical groundplan character of Odonatoptera, the presence of “prothoracic winglets obliquely directed anteriorly with venation and articulated” is a synapomorphy of Odonatoptera only preserved in the most basal taxa: Argentinoptera *ord. nov.* and Eomeganisoptera, and supposedly present in Geroptera and Kukaloptera *ord. nov.*

The protowing evolutionary model of wing articulation was proposed by Kukalová-Peck (1983, 1998, 2008) after an extensive study of extinct and extant insects (Kukalová-Peck *et al.*, 2009). The higher phylogenetical classification of basal Odonatoptera proposed here adds new taxa and new characters and discusses with some coincidence with the phylogenetic system of Bechly (1996, 2007).

Specimens are deposited in two institutions of Argentina. The Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina, under the acronym MACN-In, and the Museo de La Plata, División Paleozoología Invertebrados, La Plata, Argentina, under the acronym MLP.

Age and strata. Specimens described and studied here come from two localities and formations 200 km distant, in La Rioja Province, Argentina. The new species described come from the base of Guandacol Formation in the Paganzo Basin (Gutiérrez *et al.*, 2000). They were collected by one of us (P.G.) in Guandacol 1 locality, Quebrada de las Libélulas (South East from Quebrada Las Blanquitas), Cerro Guandacol. Guandacol Formation strata are deposited in the interval between 325 and 318.79 Ma (Gulbranson *et al.*, 2010; Césari *et al.*, 2011). The insects were found in the very base of the formation and could be restricted to 325-324 Ma, which corresponds to the upper Serpukhovian *sensu* Cohen *et al.* (2013; updated 2016).

The remaining species (Riek & Kukalová-Peck, 1984) were exhumed from Cuestita de la Herradura locality from the Malanzán Formation. The Malanzán Formation lacks absolute datation until now, though in previous literature, based on flora and microflora, it is considered to be a lateral equivalent of Guandacol Formation (Césari & Gutiérrez, 2001). The discovery in the last fieldtrip of a specimen of Megasecoptera: Xenopteraidae assignable to *Xenoptera* in Guandacol Formation (Petrulevičius & Gutiérrez, in prep.) is coincident with this equivalence.

New classification of basal Odonatoptera (see below)

1 Superorder Odonatoptera Lameere, 1900

Included taxa: Egeroptera **ord. nov.** and Palaeodonatoptera **taxon nov.**

1.1 Egeroptera **ord. nov.**

Included taxa: Egeropteridae Riek, 1983 with *Egeropteron* Riek, 1983: *Egeropteron lunatum* Riek, 1983 and *Tupacsala niunamenos* **gen. nov. et sp. nov.**

1.2 Palaeodonatoptera **taxon nov.**

Included taxa: Kukaloptera **ord. nov.** and Plesiodonatoptera **taxon nov.**

1.2.1 Kukaloptera **ord. nov.**

Included taxa: Kirchneralidae **fam. nov.** with *Kirchnerala treintamil* **gen. nov. et sp. nov.**

1.2.2 Plesiodonatoptera **taxon nov.**

Included taxa: Argentinoptera **ord. nov.** and Apodonatoptera **taxon nov.**

1.2.2.1 Argentinoptera **ord. nov.**

Included taxa: Argentinidae **fam. nov.** with *Argentinala cristinae* **gen. nov. et sp. nov.**

1.2.2.2 Apodonatoptera **taxon nov.**

Included taxa: *Geroptera* Brodsky, 1994 and Neodonatoptera Bechly, 1996

1.2.2.2.1 Order *Geroptera* Brodsky, 1994

Included taxa: *Geropteridae* **fam. nov.** with *Geropteron arcuatum* Riek, 1983

1.2.2.2.2 Neodonatoptera Bechly, 1996

Systematic Paleontology

Hydropalaeoptera Rohdendorf, 1968 *sensu* Kukalová-Peck, 2009 (= Eupalaeoptera Bechly, 2003)

Palaeoptera Martynov, 1923

1. Superorder Odonatoptera Lameere, 1900

1.1. Eugeoptera ord. nov.

Included taxa: Eugeopteridae Riek, 1983 with *Eugeopteron* Riek, 1983 including only *Eugeopteron lunatum* Riek, 1983, and *Tupacsala niunamenos* gen. nov. et sp. nov.

Phylogenetic definition: Eugeoptera ord. nov. shall include all the Odonatoptera more closely related to *Eugeopteron lunatum* Riek, 1983 than to any of the type species of the other type genera of the Odonatoptera group taxa (stem-based definition).

Diagnosis: Characters from mesothoracic and metathoracic wing venation (see below). (1) wings with relatively undeveloped anal field (more marked in forethoracic wing); (2) MP unbranched; (3) CuP with a kink at the point of contact with AA; (4) archaediectyon reduced; (5) presence of a subcostal brace; (6) Presence of an anal brace in fore- and hindwings; (7) presence of a cubital cell; (8) ScP short (up to RP1 and RP2 bifurcation) in hindwings; (9) free ScA(+) relatively short, forked into a ScA1+2 branch fused with the anterior margin, and a strong crossvein like branch ScA3+4; (10) subcostal brace formed by ScA+ScA fork+scp-ra+ra-rp; (11) ScA3+4+scp-ra+ra-rp aligned; (12) MP linked by a crossvein to CuA in hindwings; (13) MP bending anteriorly before and in the connection (via crossvein) with CuA; (14) RA bending to wing margin and running adjacent at the level of RP1-RP2 bifurcation (no place to pterostigma); (15) cubital cell in (forewings ? and) hindwings formed by five elements: CuA, CuA crossing, CuP crossing, CuP, cua-cup; (16) AA1+2 not fused with CuP in fore- and hindwings; (17) anal brace composed of five venal elements: AA, AA1+2, cup-aa1+2 crossvein, kink in CuP, cua-cup crossvein; (18) pectination of AA1+2 in mesothoracic wing; (19) RP+MA elevated basally to convex level.

Phylogenetic systematic: Eugeoptera ord. nov. retains nearly all the synapomorphies of the stem group of the Odonatoptera (Characters: 1-7). Character 8 is a synapomorphy of the new order (convergent to Eomeganisoptera, Bechly, 2007). Characters 9-18 are groundplan symplesiomorphies of Odonatoptera. Character 19 seems to be a synapomorphy for Hydropalaeoptera (see Remarks of Neodonatoptera). Kukalová-Peck (2016) considered the RP elevated basally to convex level a synapomorphy for Palaeoptera.

Etymology: Named after the family Eugeopteridae Riek, 1983.

Remarks: *Eugeopteron* and *Tupacsala* gen. nov. remain the only genera of Eugeopteridae. *Geropteron* placed by Riek & Kukalová-Peck (1983) in Eugeopteridae Riek, 1983 is transferred to *Geropteridae* fam. nov. and maintained in the Order *Geroptera* Brodsky, 1994 (see below).

One of the notable characters of Odonatoptera basal to Neodonatoptera is the R stem separated into RA and RP from the very base. The separated closely parallel RA and RP is only present (partially preserved) somewhere else in *Bojophlebia prokopi* (Kukalová-Peck, 1985; Sroka *et al.*, 2014). In the Odonatoptera basal to Neodonatoptera these veins are not only independent but not parallel; basally RA bends anteriorly and RP bends posteriorly and between them they could have even one crossvein, character that is unique (autapomorphy) from these basal forms (Figs. 1-2). Other unique character from Odonatoptera basal to Neodonatoptera is that free RP is convex (+) in the base, getting concave (-) just after the emergence of the MA (Figs. 1-2, 5-6) (see Remarks in Neodonatoptera). RP

was considered concave by Riek in Riek & Kukalová-Peck (1984: text and fig. 1) and Kukalová-Peck (1991: fig. 6.15A) but rectified to convex in Kukalová-Peck (2009: see fig. 7) and considered an autapomorphy of Palaeoptera by Kukalová-Peck (2016).

1.1.1. Eugeopteridae Riek, 1983

Type genus: *Eugeopteron* Riek, 1983.

1.1.1.1. *Eugeopteron* Riek, 1983

Type species: *Eugeopteron lunatum* Riek, 1983.

1.1.1.1.1. *Eugeopteron lunatum* Riek, 1983

Type material: Holotype specimen MLP 12886. Cuestita de La Herradura locality, province of La Rioja, Northwest Argentina, at paleolatitude $\approx 60^\circ$. Malanzán Formation, La Divisoria Member, Serpukhovian (circa 325-324 (?) Ma) (Césari *et al.*, 2011; Césari & Gutiérrez, 2001).

Remarks: The specimen was named by Riek in Riek & Kukalová-Peck (1983). In the description and analysis of the species in the cited paper, and in Kukalová-Peck (1991), the RP was considered concave in all its length. In a more recent paper, Kukalová-Peck (2008) noted the convexity of RP(+) before the arising of MA. So, both RA and RP are convex. After the arising of MA, RP becomes concave. See below our consideration that while RP is convex, MA is fused to it. In present contribution we interpret the cup-aa1+2 as a crossvein as in Kukalová-Peck (2009) and contrary to Riek & Kukalová-Peck (1983), where they interpret it as AA1.

1.1.1.1.2 *Tupacsala* gen. nov.

Type species: *Tupacsala niunamenos* sp. nov.

Diagnosis: Characters from metathoracic wing venation (see below). (1) CuP kink; (2) Cubital cell; (3) MP single; (4) anal brace; (5) CuA is not fused with CuP in the hindwings; (6) Crossvein between CuP and AA long; (7) Cubital cell oblique; (8) CuA with four branches; (9) and MA bifurcated well basal to RP bifurcation.

Etymology: Dedicated to the memory of José Gabriel Condorcanqui Noguera, "Túpac" Amaru II (1738-1781) and to Milagro Amalia Ángela "Sala" (1963-). Túpac Amaru in 1780-1781 initiated a revolt against Spanish State and its rules. He was tortured (forced to witness the execution of the sentences imposed on his family), executed and quartered to be exposed (Cline, 2015). Milagro Sala (1963-) is a prominent Argentine social leader, Secretary of the "Organización Barrial Túpac Amaru" and Parliamentary of the Parlasur imprisoned with other members of the organization since January 16, 2016.

1.1.1.1.2.1 *Tupacsala niunamenos* sp. nov. (Figs. 1-2)

Previous references to *Tupacsala niunamenos* gen. et sp. nov.:

2000: Eugeopteridae [Gutiérrez *et al.* (2000)]

Type material: Holotype specimen MACN-In 2678C. Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, province of La Rioja, Northwest Argentina, at paleolatitude $\approx 60^\circ$. Lowermost part of Guandacol Formation (Gutiérrez *et al.*, 2000), Serpukhovian (circa 325-324 Ma) (Césari *et al.*, 2011).

Diagnosis: That of the genus by monotypy.

Description: A basal fragment of a metathoracic wing. Only the counterpart (reverse) is known. Venation three-dimensionally preserved. Wide anal area and development of anal veins indicate a hindwing.

Metathoracic wing fragment; length of the fragment 19.9 mm; width of the fragment 12.9 mm. RA shortly preserved well distal to discoidal cell; RP shortly preserved diverging from RA. MA bifurcated well basal to RP bifurcation. MP single. Cubital cell partially preserved, less vertical and narrower than *Argentina*. Cubital cell with four partially preserved elements: CuA crossing curved, CuP crossing slightly curved, CuP (0.6 mm long) (nearly straight and longer than cua-cup), and cua-cup quite long (0.3 mm) (similar than *Eugeropteron*). CuP kink strong. CuA with three veins. CuP bifurcated basal to CuA. AA1+2 connected to CuP via a long crossvein. AA not fused with CuP connected by cup-aa (1.1 mm long). AA1+2 with three or four branches. AA3 sinuous. AP long and single.

Etymology: Dedicated to "Ni Una Menos" (No one less), a collective against gender violence. It is a collective campaign that arose from the need to say "enough femicides", because in Argentina every 30 hours a woman is killed just by being a woman.

Discussion: We decided to describe and name this fragmentary specimen due to the rarity of preserved winged insects from lower Carboniferous worldwide and to highlight the diversity of these strange stem dragonflies. Although it is not evident at first sight, fortunately it preserves some interesting characters to place it within basal Odonoptera. The specimen is an Odonoptera because has 1) a CuP kink, 2) a cubital cell, 3) a MP single, and 4) an anal brace. It is an Odonoptera basal to Apodonoptera **taxon nov.** because the CuA is not fused with the CuP in the hindwings. The crossvein between CuP and AA is long and the cubital cell is oblique contrary to *Argentinoptera ord. nov.* which have a short crossvein and a vertical cubital cell. The new species seems to fit better with *Eugeroptera ord. nov.* because of the oblique cubital cell. *Eugeroptera ord. nov.* has both forewing and hindwing cubital cells oblique and quite broad like the new species and unlike *Kukaloptera ord. nov.* having it horizontal and narrower. In spite of the fragmentary condition of the wing that makes difficult the comparison with *Kukaloptera ord. nov.* we place the new species provisionally in *Eugeroptera ord. nov.*: *Eugeropteridae*. Differences with *Eugeropteron* are the MA bifurcated well basal to RP bifurcation and a CuA with four branches. These differences allows us to erect a new genus *Tupacsala gen. nov.*

1.2. Palaeodonoptera taxon nov.

Included taxa: *Kukaloptera ord. nov.* and *Plesiodonoptera taxon nov.*

Synapomorphies: Fusion of MP with CuA in forewings. This character is tentative as only *Kirchnerala gen. nov.* and *Argentina gen. nov.* preserve this part of the forewing among the most basal Odonoptera. *Eugeropteron* lacks the antero-basal part of the forewing.

1.2.1. Kukaloptera ord. nov.

Included family: *Kirchneralidae fam. nov.*

Phylogenetic definition: *Kukaloptera ord. nov.* shall include all the Odonoptera more closely related to *Kirchnerala treintamil gen. et sp. nov.* than to any of the type species of the other type genera of the *Palaeodonoptera taxon nov.* group taxa (stem-based definition).

Etymology: In honour of the most influential paleoentomologist Jarmila Kukalová-Peck. Kukalová-Peck's theories about monophyly of Arthropoda based on fossil and recent species are foundational of modern view of these animals. Her theories include the homology of the multiramous Arthropoda limb and detailed morphologies of specialization in head, thorax and abdomen. One of her outstanding results is the comprehension of the limb origin of the insect wing and the homology of wing articulation and venation.

Diagnosis: Characters from mesothoracic and metathoracic wing venation (see below). (1) anterior articular plate (AAP), with an "h" shaped basalare (B-C), a large bi-lobed fulcalare (F-C) narrowly separated from the axalare (AX-C) by a deeply incised groove-like suture; (2) wings with relatively undeveloped anal field (more marked in mesothoracic wing); (3) MP unbranched; (4) CuP with a kink at the point of contact with AA; (5) archaedyon reduced; (6) presence of a subcostal brace; (7) presence of an anal brace in forewings; (8) presence of a cubital cell; (9) reduction of pectination of AA1+2 and AA3+4 pectinated in forewing; (10) cubital cell long, straight and horizontal in forewings; (11) MP shortly fussed to CuA in forewings; (12) ScA3+4+scp-ra+ra-rp aligned; (13) MP bending anteriorly before and in the connection with CuA; (14) RA bending to wing margin and running adjacent at the level of RP1-RP2 bifurcation (no place to pterostigma).

Phylogenetic systematic: Eugeoptera ord. nov. retains nearly all the synapomorphies of the stem group of the Odonoptera (Characters 1-8). Character 9-10 are synapomorphies of the new order. Character 11 is a synapomorphy of Palaeodonoptera taxon nov. Characters 12-14 are groundplan symplesiomorphies of Odonoptera.

1.2.1.1. Kirchneralidae fam. nov.

Type genus: *Kirchnerala* gen. nov.

Diagnosis: That of the order by monotypy.

1.2.1.1.1 *Kirchnerala* gen. nov.

Type species: *Kirchnerala treintamil* sp. nov.

Diagnosis: That of the order by monotypy.

Etymology: In honour of Argentinean President (2003-2007) Néstor Kirchner, who passed away on October 27th, 2010 and the Latin "ala" meaning wing. On July 16th, 2003 he agreed to a public meeting requested by two designed delegates of CONICET External Postdoctoral Fellows in the Argentinean Embassy in Paris. In relation to our concerns, he explained us the promissory future plans of the government for the scientific system in our country. After our return to Argentina in 2004, his sayings were corroborated year by year and continued in the same way by the next (twice) President of the country, Cristina Fernández de Kirchner. At the end of the meeting he proposed to Gabriel Moron and one of us (JFP) to visit him when returned; a pending issue that will never be carried out.

1.2.1.1.1.1 *Kirchnerala treintamil* sp. nov. (Figs. 3-4)

Previous references of *Kirchnerala treintamil* gen. et sp. nov.:

2000: Eugeopteridae [Gutiérrez et al. (2000)]

2009: *Eugeopteron* sp., the right forewing of a complete adult dragonfly (Wootton & Kukalová-Peck 2000, fig. 10); fig. 7A [Kukalová-Peck (2009)]

2009: *Eugeopteron lunatum*; fig. 3 [Kukalová-Peck et al. (2009)]

Type material: Holotype MACN-In 2678D, housed in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina. Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, province of La Rioja, Northwest Argentina, at paleolatitude $\approx 60^\circ$. Lower part of Guandacol Formation (Gutiérrez et al., 2000), Serpukhovian (circa 325-324 Ma) (Gulbranson et al., 2010; Césari et al., 2011).

Description: The mesothoracic wing of an adult dragonfly, with part of tergum preserved and bearing two axillary plates. Only the part (obverse) is known. Venation and articulation three-dimensionally preserved. Narrow anal area indicates a forewing.

Wing: mesothoracic wing fragment, preserved length 29.2 mm; probable total length 34.6 mm; maximum width 11.9 mm. The wing is about 2.9 times as long as broad. Anterior margin (PC) slightly falcate. Curved posterior margin bent slightly concavely between AP and AA and strongly convexly after that. CP- short and single, joining CA+ close to base. ScA+ forming a prominent recurrent subcostal brace (ScA+ScA fork+scp-ra). ScA+ relatively short, forked into a ScA1+2 branch fused with the anterior margin well before 1/12 of wing length, and a strong crossvein like branch ScA3+4, curved and ending on ScP(-). Several crossveins not aligned between wing margin to ScP (≈ 8), ScP to RA (≈ 18) and RA to RP (≈ 10). ScP ending on wing margin (?) up to RP1 and RP2 bifurcation. RA(+) separated from RP(+) from the very base. RA and RP arched and divergent (0.4 mm) in the middle of the segment from the base to MA emergence. Strong crossvein like veins aligned ScA3+4, scp-ra, and ra-rp. RA bending to wing margin at the level of RP1-RP2 bifurcation. RP convex up to MA emergence (at the level of distal half of cubital cell), distally concave. RP(-) forked beyond mid-wing into RP1+2 and RP3+4. RP1+2 bifurcated into RP1 and RP2. IR2 between RP1+2 and RP3+4. MA forked distal of mid-wing in three branches. MP \pm bending anteriorly (MP concavely curved) before and in the connection with CuA. MP shortly fused with CuA. MP single. Cu- bending to anterior and forked into CuA and CuP forming a cubital cell. Cubital cell (horizontal) long (4.4 mm) and narrow (0.6 mm) with five elements: CuA (curved and short) (1.2 mm), CuA crossing (curved and long) (3.4 mm), CuP crossing (curved and long) (3.4 mm), CuP (slightly bended anteriorly and short) (0.85 mm), cua-cup (very short) (0.07 mm). CuP kink strong. CuA with three branches and connected via a bifurcated (Y like) crossvein to CuP. CuP not fused with AA connected by a long crossvein (cup-aa1+2). AA1+2 not pectinated with four branches. AA3+4 pectinated with three branches sinuous at the base. Ap- long and single. Jugal area scalloped. Anal brace composed of five veinal elements: AA, AA1+2, cup+aa1+2, kink in CuP, cua-cup.

Mesothoracic wing articulation: Anterior articular plate (AAP) partially preserved formed by precostal and costal pteralia, with an "h" shaped basalare (B-C), a large bi-lobed (?) costal fulcalare (F-C) narrowly separated from the costal axalare (AX-C) by a deeply incised groove-like suture. Subcostal pteralia row free with well developed axalare (A-Sc) and fulcalare (F-Sc) and not so noticeable basivenale (B-Sc) and proxalare (PR-Sc). Posterior articular plate (PAP) formed by radial, medial and cubital pteralia. A deep groove posterior to cubital pteralia coinciding with the arising of Cu. Anal and jugal veins arising obliquely from the posterior articular plate and from the posterior side.

Diagnosis: That of the order by monotypy.

Etymology: Dedicated to the 30,000, in Spanish "treinta mil" (*presentes, ahora y siempre!*), detained-disappeared by the Argentinean Military-Civil-Ecclesiastic Dictatorship 1976-1983. *Mil* is also a linguistic morph in Kakan (Diaguita) language (Nardi, 1979) from La Rioja province whose meaning has unfortunately disappeared (Nardi, 1979) as well as its speaking (Fabre, 2005).

Discussion: The specimen could be included into Odonatoptera because of the: (1) anterior articular plate (AAP), with an "h" shaped basalare (B-C), a large bi-lobed fulcalare (F-C) narrowly separated from the axalare (AX-C) by a deeply incised groove-like suture; (2) wings with relatively undeveloped anal field (more marked in mesothoracic wing); (3) MP unbranched; (4) CuP with a kink at the point of contact with AA; (5) archaediectyon reduced; (6) presence of a subcostal brace; (7) presence of an anal brace in forewings; (8) presence of a cubital cell. It could be included in Palaeodonatoptera **taxon nov.** because of the MP shortly fused to CuA in forewings. It could be excluded from the more derived Plesiodonatoptera **taxon nov.** because of the absence of (1) CuA-CuP fused in forewings; (2) loss of the crossvein between RA and RP; and (3) fusion of CuP with AA1+2 in forewings. It also could not be included in the derived Apodonatoptera **taxon nov.** because of the absence of (1) RA parallel one cell distant to anterior wing margin (place to pterostigma); (2) CuA-CuP fused in hindwings and; (3) AA1+2 fused with CuP in hindwings. The new genus and species has two autapomorphies, i.e., (1) reduction of pectination of AA1+2 and AA3+4 pectinated in forewing and (2) the cubital cell long, straight and horizontal in forewings.

Remarks: The drawing of fig. 7A of Kukalová-Peck (2009) corresponds to *Kirchnerala treintamil* **gen. et sp. nov.** She referred erroneously to it as "*Egeropteron* sp., the right forewing of a complete adult dragonfly (Wootton & Kukalová-Peck 2000, fig. 10)". Her mention is erroneous since the complete adult dragonfly of Wootton & Kukalová-Peck (2000: fig. 10) corresponds to the species described below as *Argentalina cristinae* **gen. nov. et sp. nov.**

1.2.2. Plesiodonoptera taxon nov.

Included taxa: Argentinoptera **ord. nov.** and Apodonoptera **taxon nov.**

Synapomorphies: CuA-CuP fused in forewings. Loss of the crossvein between RA and RP. Fusion of CuP with AA1+2 in forewings.

1.2.2.1 Argentinoptera ord. nov.

Included family: Argentalidae **fam. nov.**

Phylogenetic definition: Argentinoptera **ord. nov.** shall include all the Odonoptera more closely related to *Argentalina cristinae* **gen. et sp. nov.** than to any of the type species of the other type genera of the Plesiodonoptera **taxon nov.** group taxa (stem-based definition).

Phylogenetic systematic: Egeroptera **ord. nov.** retains nearly all the synapomorphies of the stem group of the Odonoptera (Characters 1-7). Character 8 is a synapomorphy of the new order (convergent to Eomeganisoptera, Bechly, 2007). Characters 9-18 are groundplan symplesiomorphies of Odonoptera.

Diagnosis: Characters from female with 6 wings and body (see below). (1) anterior articular plate (AAP), with an "h" shaped basialare (B-C), a large bi-lobed fulcalare (F-C) narrowly separated from the axalare (AX-C) by a deeply incised groove-like suture; (2) MP unbranched; (3) CuP with a kink at the point of contact with AA; (4) archaediectyon reduced; (5) presence of a subcostal brace; (6) presence of an anal brace in fore- and hind wings; (7) presence of a cubital cell; (8) prothoracic winglets obliquely directed anteriorly with venation and articulated; (9) abdomen elongated and slender; (10) MP shortly fused to CuA in forewings; (11) CuA-CuP fused in forewings; (12) CuP-AA fusion in forewings; (13) loss of crossvein between RA-RP; (14) MP touching punctually CuA in hindwings (shortening of Crossvein (?)); (15) abdominal segment 10 somewhat longer than 9; (16) segments 9 and 10 modified with a rounded genitalia; (17) short and sickle like ovipositor; (18) sharp and sickle valve 1, valve 2 string along with valve 1 and valve 3 curved and sheathing laterally V1 and V2; (19) ScP long (distal to RP1 and RP2 bifurcation) not reaching the anterior wing margin and disappearing before the apex; (20) MP going anteriorly before and in the connection with CuA; (21) RA bending to wing margin and running adjacent at the level of RP1-RP2 bifurcation (no place to pterostigma).

Phylogenetic systematic: Argentinoptera **ord. nov.** retains nearly all the synapomorphies of the Odonoptera (Characters: 1-9). Character 10 is a synapomorphy of Palaeodonoptera **taxon nov.** Characters 11-13 are synapomorphies of Plesiodonoptera **taxon nov.** Characters 14-18 are synapomorphies of the new order. Characters 19-21 are groundplan plesiomorphies of Odonoptera.

Etymology: Named after the family Argentalidae **fam. nov.**

Remarks: Even if MP changes its direction at the fusion with CuA, it is still bending posteriorly, unlike in Neodonoptera whose MP strongly bends anteriorly (synapomorphy).

1.2.2.1.1 Argentalidae fam. nov.

Type genus: *Argentalina* **gen. nov.**

Diagnosis: That of the order by monotypy.

1.2.2.1.1.1 *Argentina* gen. nov.

Type species: *Argentina cristinae* sp. nov.

Diagnosis: That of the order by monotypy.

Etymology: Named after the country, República "Argentina", and the Latin "ala" meaning wing.

1.2.2.1.1.1.1 *Argentina cristinae* sp. nov. (Figs. 5-6)

Previous references to *Argentina cristinae* gen. et sp. nov.:

- 1998: Undescribed eugeropterid from Rioja, Argentina (Carboniferous, Namurian/Westphalian); fig. 2(A) [Wootton *et al.* (1998)]
- 1998: 320-million-year-old dragonfly from Argentina; fig. Ancient aviator [Vogel (1998)]
- 2000: Undescribed geropteryid from Westphalian of Rioja, Argentina [Wootton & Kukalová-Peck (2000)]
- 2000: Eugeropteridae gen. et sp. indet., winged specimen; fig. 3 [Gutiérrez *et al.* (2000)]
- 2001: Undescribed Eugeropteridae gen. et spec. nov., Upper Carboniferous of Argentina (reconstruction drawing by J. Kukalová-Peck) [Bechly *et al.* (2001)]
- 2005: Reconstruction of *Eugeropterum* (Eugeropteridae). Although superficially resembling a palaeodictyopteran, eugeropterids were early odonatopterans and perhaps stem-group relatives of odonates; fig. 6.24 [Grimaldi & Engel (2005)]
- 2007: Recently discovered and still undescribed specimen (Kukalová-Peck pers. comm., and pers. observ. on a cast of the referring specimen) [Bechly (2007)]
- 2008: Carboniferous dragonfly with three pairs of wings; fig. 16 [Kukalová-Peck (2008)]
- 2011: Eugeropteridae gen. et sp. n., cast of undescribed fossil specimen from the Upper Carboniferous of La Rioja (Argentina) in coll. Javier Muzón (ILPLA); fig. 49 [Staniczek *et al.* (2011)]
- 2013: "Rekonstrukce zástupce skupiny †Geroptera, jejich prothorakální křídélka byla namířena směrem dopředu (převzato z Wootton a Kukalová-Peck, 2000 upraveno Grimaldi a Engel, 2005)"; fig. 3 [Pecharová (2013)]
- 2016: The most primitive known fossil dragonflies Eugeropteridae had a short ovipositor [Prokop *et al.* (2016)]
- 2016: Reconstruction of *Eugeropterum* (Eugeropteridae); fig. 1 [Hallam (2016)]

Type material: Holotype female specimen MACN-In 2678A/B. Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, La Rioja province, Northwest Argentina, at paleolatitude $\approx 60^\circ$. Lower part of Guandacol Formation (Gutiérrez *et al.*, 2000), lower Serpukhovian (circa 325-324 Ma) (Césari *et al.*, 2011).

Description: Part and counter-part of a complete female specimen with 6 wings. Head partially preserved with one rounded and conic eye (?). Thorax with six wings, prothoracic ones smaller with venation and apparent articulation, mesothoracic quite slender without an anal region developed and metathoracic ones wider with a developed anal field. Mesothorax and wing in dorsal view with preserved articular plates. Wing span (mesothoracic wings) ≈ 93.7 mm.

Wings: Prothoracic wing with quadrangular/subtriangular shape directed upwards (4.6 mm long, 3 mm wide). Six major longitudinal convex veins. Four veins originating from anterobasal part of the wing. First and second vein slightly combed posteriorly and ending in the margin. Third and fourth veins slightly combed anteriorly. Fifth vein well curved and well separated from the fourth. Sixth vein short and strongly curved.

Mesothoracic wings: right wing almost complete, 44.5 mm long; left wing nearly complete; maximum width of right wing 12.3 mm, left one 12.5 mm. The wing is about 3.6 times as long as broad. Anterior margin slightly falcate. Curved posterior margin bent slightly concavely between AP and AA and strongly convexly after that. CP- long running well separate and parallel to the wing margin, joining ScA basal to CA+ arrival. ScA+ forming a rather weak subcostal brace in right wing (ScA+ScA fork+scp-ra). ScA+ relatively short, forked into a ScA1+2 (reaching CP well before 1/12 of wing length) and an

oblique crossvein like branch ScA_{3+4} that ends on ScP^- . In left wing there are not ScP_{3+4} and $scp-ra$ preserved. Several crossveins between wing margin to ScP (≈ 7 on left, ≈ 8 on right), between ScP to RA (≈ 11) and RA to RP (≈ 15). Crossveins from wing margin to ScP and ScP to RA not aligned. ScP long, noticeably curved and sinuous at the base, ending on the wing margin at the height of IR_2 . $RA+$ separated from $RP+$ from the very base. RA and RP arched and divergent (0.3 mm) in the middle of the segment from the base to MA emergence (6.2 mm distant wing base). Absence of crossvein between $RA-RP$. Crossvein $scp-ra$ aligned to ScA_{3+4} (preserved in right wing). RA bending to wing margin at the level of RP_1-RP_2 bifurcation running adjacent to wing margin (no space for pterostigma). RA bifurcates at the wing apex (right wing). RP convex up to MA emergence (at the level of distal half of cubital cell), distally concave. RP^- forked beyond mid-wing into RP_{1+2} and RP_{3+4} . RP_{1+2} bifurcated into RP_1 and RP_2 . RP_1 bifurcated. IR_1 between RP_1 and RP_2 , $1/3$ longer than RP_1 bifurcation. IR_{2+} between RP_2 and RP_{3+4} . MA forked distal of mid-wing in three branches. MP_{\pm} bending anteriorly before and in the connection with CuA . Free MP 3.8 mm long. MP single fused shortly with CuA for about 1 mm. Cu^- bending to anterior and forked into CuA and CuP forming a cubital cell. Cubital cell (horizontal) (4.2 mm long and 0.8 mm wide) developed and broad with six elements: CuA (curved and short) (0.3 mm), $CuA+MP$ (0.96 mm), CuA crossing (curved and long) (2.9 mm), CuP crossing (curved and long) (2.7 mm), $CuP+AA_1$ (0.8 mm in rightwing, 1.1 in leftwing), CuP (nearly straight and short) (1.0 mm in rightwing, 0.5 in leftwing). CuP kink strong. CuA fused with CuP shortly after cubital cell (0.3 mm long in right wing, 0.5 mm long in left wing). CuA with three terminal branches. CuP slightly falcate and single. $CuP+AA_1$ fused just to the middle of posterior side of cubital cell. AA_1 with five branches, AA_2 and AA_3 single, AA_4 with two branches. AP^- single. JA and JP short. Anal brace composed of five veinal elements: AA , AA_1 , $CuP+AA_1$, CuP , $CuA+Cup$.

Metathoracic wings basally broad, left wing complete, 42 mm long; right wing basal third preserved; maximum width of left wing 14.8 mm. The wing is about 2.8 times as long as broad. Anterior margin slightly falcate. Posterior margin strongly convex from base to CuA , distal part nearly straight. $ScA+$ forming a prominent recurrent subcostal brace ($ScA+ScA$ fork+ $scp-ra$) in leftwing. $ScA+$ relatively short, forked into a ScA_{1+2} (only visible in leftwing) ending in costal margin well before $1/12$ of wing length, and crossvein like branch ScA_{3+4} (only visible in leftwing), ending on ScP^- . About five crossveins between wing margin to ScP in leftwing (not aligned with that of ScP to RA), ≈ 15 crossveins from ScP to RA and ≈ 13 crossveins from RA to RP . ScP noticeably curved at the base ending on wing margin at the height of IR_2 . $RA+$ separated from $RP+$ from the very base. RA and RP arched and divergent (0.4 mm) in the middle of the segment from the base to MA emergence. Absence of crossvein between $RA-RP$. Crossvein $scp-ra$ aligned to ScA_{3+4} (preserved in right wing). RA bending to wing margin just basal to the level of RP_1-RP_2 bifurcation running adjacent to wing margin. RA single. RP convex up to MA emergence (at the level of distal half of cubital cell) (6.2 mm from the base), distally concave. RP^- forked beyond mid-wing into RP_{1+2} and RP_{3+4} . RP_{1+2} bifurcated into RP_1 and RP_2 . RP_1 trifurcated. IR_1 between RP_1 and RP_2 , equal to RP_1 bifurcation. IR_{2+} between RP_2 and RP_{3+4} . MA forked distal of mid-wing in three branches. MP_{\pm} bending anteriorly (MP concavely curved) before and in the connection with CuA (4.1 mm from wing base). MP connected to CuA by an extremely short crossvein. Cu^- bending anteriorly and forked into CuA and CuP forming a cubital cell. Cubital cell (vertical) developed, shorter and broader than forewing with five elements: CuA (straight and short) (0.9 mm in both wings), CuA crossing (curved and long) (3.7 mm in both wings), CuP crossing (curved and long) (2.7 mm in both wings), CuP (1.5 mm in rightwing, 1.2 mm in leftwing), and $cua-cup$ (0.2 mm in rightwing, 0.6 mm in leftwing). CuP kink. CuA connected with CuP by a crossvein. Cubito-anal area very broad. CuA with three terminal branches. CuP with two short terminal branches. CuP connected to AA_{1+2} by a short in right wing (long in left wing) $cua-aa_{1+2}$ crossvein. AA_{1+2} with four branches, AA_{3+4} with three branches. AP^- single. JA and JP single. Anal brace composed of five veinal elements: AA , AA_{1+2} , $cup+aa_{1+2}$, CuP , $cua+cup$.

Prothoracic wing articulation: Not well preserved but seems to have two parts, an anterior and a posterior one.

Mesothoracic wing articulation: Anterior articular plate (AAP), with an "h" shaped basalare (B-C), a uni(?)-lobed fulcalare (F-C) narrowly separated from the axalare (AX-C) by a deeply incised groove-like suture. Subcostal pteralia row free well developed. Posterior articular plate (PAP) formed by radial, medial, and cubital pteralia. A deep groove posterior to cubital pteralia coinciding with the arising of Cu vein. Anal and jugal veins arising obliquely at the middle height of the posterior articular plate.

Metathoracic wing articulation: Anterior articular plate (AAP), with an wide triangle shaped basalare (B-C), a uni(?)-lobed fulcalare (F-C) with a long nose like structure, axalare (AX-C) oblong touching the B-C and separated from the F-C by a deeply incised groove-like suture.

In forewings and hindwings, axialare of AAP connected by an arched and fine rib. Axialare of PAP connected by an arched fine double rib.

No apparent division between pro- meso- and metathorax.

Abdomen: elongated and slender with 10 segments preserved. Female terminalia with segments VIII-X modified and principally segments IX-X by a rounded genitalia. Segment X plate like slightly longer than IX. Short and sickle like ovipositor between segments IX and X. Sharp and sickle valve 1, valve 2 string along with valve 1 and valve 3 curved (at some distance from V1 and V2) and sheathing laterally V1 and V2.

Etymology: In honour of Argentinean (twice) President (2007-2015) Cristina Fernández de Kirchner. She elevated the Secretary of Science to Ministry rank, creating in 2007 the *Ministerio de Ciencia, Tecnología e Innovación Productiva* (Ministry of Science, Technology and Productive Innovation). Within the Ministry, the CONICET experienced a quali-quantitative leap in all fields: infrastructure, number of workers, projects, organization and production.

Remarks: The metathoracic AAP in *Argentina* **gen. nov.** is quite similar in shape to that interpreted by Kukalová-Peck (2009) for the forewing of *Alanympa richardsoni* Kukalová-Peck, 2009 (Kukalová-Peck, 2009: fig. 6).

Discussion: The specimen could be included into Odonatoptera because of the: (1) anterior articular plate (AAP), with an "h" shaped basalare (B-C), a large bi-lobed fulcalare (F-C) narrowly separated from the axalare (AX-C) by a deeply incised groove-like suture; (2) MP unbranched; (3) CuP with a kink at the point of contact with AA; (4) archaediptyon reduced; (5) Presence of a subcostal brace; (6) presence of an anal brace in fore- and hindwings; (7) presence of a cubital cell; (8) prothoracic winglets obliquely directed anteriorly with venation and articulated; and (9) abdomen elongated and slender. The specimen could be included into Palaeodonatoptera **taxon nov.** because of the MP shortly fused to CuA in forewings. It could be included into Plesiodonatoptera **taxon nov.** by the presence of (1) CuA-CuP fused in forewings; (2) CuP-AA fusion in forewings; and (3) loss of crossvein between RA-RP. It could not be included in Apodonatoptera **taxon nov.** because it lacks the (1) RA parallel one cell distant to anterior wing margin (place to pterostigma); and the (2) CuA-CuP fused in hindwings; AA1+2 fused with CuP in hindwings. The new genus and species has five autapomorphies, i.e., (1) MP touching punctually CuA in hindwings (shortening of Crossvein (?)); (2) abdominal segment 10 somewhat longer than 9; (3) segments 9 and 10 modified with a rounded genitalia; (4) short and sickle like ovipositor; (5) sharp and sickle valve 1, valve 2 string along with valve 1 and valve 3 curved and sheathing laterally V1 and V2.

1.2.2.2. Apodonatoptera taxon nov.

Included taxa: Geroptera and Neodonatoptera **taxon nov.**

Synapomorphies: RA parallel one cell distant to anterior wing margin (place to pterostigma); CuA-CuP fused in hindwings; AA1+2 fused with CuP in hindwings.

1.2.2.2.1. Order Geroptera Brodsky, 1994

Included family: Geropteridae **fam. nov.**

Phylogenetic definition: *Geroptera* Brodsky, 1994 shall include all the Odonatoptera more closely related to *Geropteron arcuatum* Riek, 1983 than to any of the type species of the other type genera of the Apodonatoptera **taxon nov.** group taxa (stem-based definition).

Rediagnosis: Characters from metathoracic wing. (1) wings with relatively undeveloped anal field (more marked in mesothoracic wing); (2) MP unbranched; (3) CuP with a kink at the point of contact with AA; (4) archaediectyon reduced; (5) presence of a subcostal brace; (6) presence of an anal brace; (7) presence of a cubital cell; (8) CuA-CuP fused; (9) AA1+2 fused with CuP; (10) RA parallel one cell distant to anterior wing margin (place to pterostigma); (11) ScP long reaching the RA in the distal fourth of the wing and related to two crossveins from RA to the wing margin (pseudopterostigma); (12) cubital cell in hindwing formed by five elements: CuA, CuA crossing, CuP crossing, CuP+AA1+2, CuP; (13) MP linked by a crossvein to CuA; (14) MP bending anteriorly before and in the connection (via crossvein) with CuA.

Phylogenetic systematic: The Order *Geroptera* retains nearly all the synapomorphies present in the hindwings of the stem group of the Odonatoptera (Characters 1-7). Characters 8-10 are synapomorphies of the Apodonatoptera **taxon nov.** Characters 11-12 are synapomorphies of the order. Characters 13-14 are groundplan symplesiomorphies of Odonatoptera.

1.2.2.2.1.1 *Geropteridae* fam. nov.

Type genus: *Geropteron* Riek, 1983

Diagnosis: That of the order by monotypy.

Remarks: The holotype specimen MLP 12885 was collected by Sergio Archangelsky from the Malanzán Formation, La Divisoria Member, Malanzán, Cuestita de la Herradura locality, La Rioja, Argentina.

Geropteron Riek, 1983

Type species: *Geropteron arcuatum* Riek, 1983

1.1.1.1. *Geropteron arcuatum* Riek, 1983

Type material: Holotype specimen MLP 12885. Cuestita de La Herradura locality, La Rioja province, Northwest Argentina, at paleolatitude $\approx 60^\circ$. Malanzán Formation, Serpukhovian (circa 325-324 (?) Ma) (Césari et al., 2011; Césari & Gutiérrez, 2001).

Remarks: As *Eugeropteron*, *Geropteron arcuatum* was named by Riek in Riek & Kukalová-Peck (1983). For Riek & Kukalová-Peck (1983) the RP was concave (-) in all its length. See below for the consideration that while RP is convex, MA is fused to it (same situation as for *Eugeropteron* in Riek & Kukalová-Peck (1983) work).

1.2.2.2.2.1 *Neodonatoptera* Bechly, 1996

Included taxa: *Eomeganisoptera* Rohdendorf, 1962 and *Euodonatoptera* Bechly, Brauckmann, Zessin & Gröning, 2001.

Synapomorphies: Wing venation characters: wings very slender and elongate [from Bechly (2007)]; RA and RP basally strictly parallel and very close together (but only fused to a long double-barrel radial stem in *Nodialata*) [from Bechly (2007)]; MP and Cu are at least shortly fused [from Riek & Kukalová-Peck (1984), Brauckmann & Zessin (1989) and Bechly (1994)]; the longitudinal wing veins MP and CuA are not straight but undulating or even kinked [from Bechly (2007)]; AA2 of hindwings secondarily supplied with several pectinate posterior branches (reversed in some †"Erasipteridae" and *Nodialata*) [from Bechly (2007)]; MP bending posteriorly (captured) at the fusion with CuA [proposed here].

Remarks: The character "base of MA lost its connection with the medial stem and secondarily fused with RP" proposed by Bechly (2007) for Neodonoptera (and also considered by Riek & Kukalová-Peck (1984), Brauckmann & Zessin (1989) and Bechly (1994) is actually a synapomorphy of Hydropalaeoptera. We have to note that Sroka *et al.* (2014) discussed twice about this matter. In the Phylogenetic affinities of *Bojophlebia prokopi* [page 13] they stated that the "MA attached to RP without anterior connection of MA to MP" is an "autapomorphy [of *Bojophlebia*], convergent with Ephemera and higher Odonoptera". In page 18 (Sroka *et al.*, 2014), they stated a synapomorphy of Hydropalaeoptera: "MA approximated or fused to RP". These two sentences are ambiguous and our new interpretation tries to clarify the matter. In this sense we could note that the free RP is convex before the arising of MA and after that becomes concave in all Odonoptera basal to Neodonoptera. In *Bojophlebia* it could be the case, but Sroka *et al.* (2014) do not point the convexity / concavity of veins in their new interpretation of the taxon. In Kukalová-Peck's interpretation of *Bojophlebia* (Riek & Kukalová-Peck, 1984; Kukalová-Peck, 1985) it is stated that the RP is concave from the very base before MA arising. We have to note that this interpretation coincides with their erroneous interpretation of the concavity of the RP for *Egeropteron* and *Geropteron* (Riek & Kukalová-Peck, 1984). The only possibility is the re-study of *Bojophlebia* to clear up our thoughts. Our interpretation is that RP is convex while it is fused with MA in basal Odonoptera, and when MA arises it becomes concave. The fusion of RP with MA is visible in the crown group of Odonata in the anterior part of the arculus (Kukalová-Peck, 1991: figs. 6.15 I-J).

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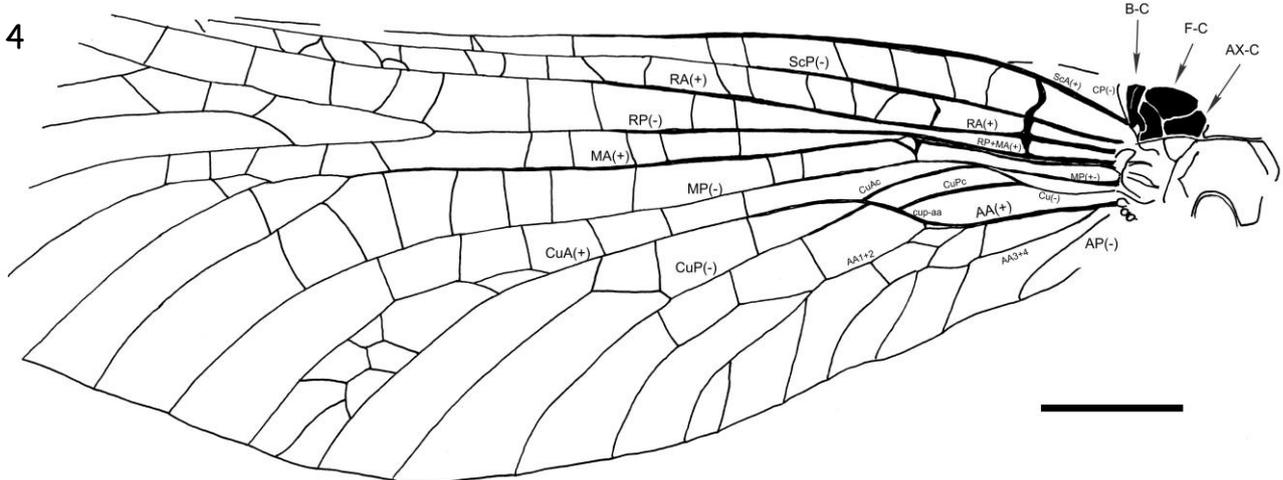
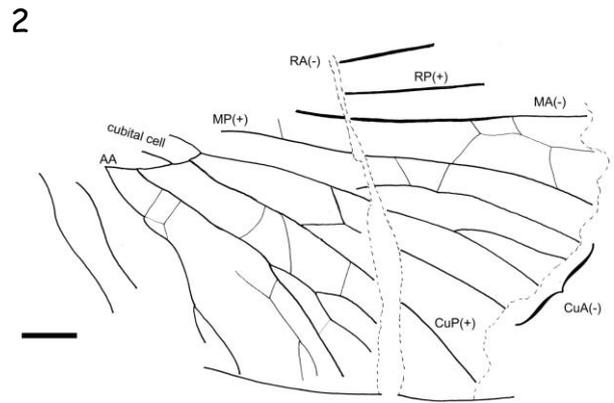


Fig. 1.- Photograph of *Tupacsala niuamenos* gen. nov. et sp. nov. from Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, province of La Rioja, Northwest Argentina. Lowermost part of Guandacol Formation (circa 325-324 Ma). Holotype specimen MACN-In 2678C. Scale bar = 2 mm.

Fig. 2.- Camera lucida drawing of Holotype (MACN-In 2678C) of *Tupacsala niuamenos* gen. nov. et sp. nov. Scale bar = 2 mm.

Fig. 3.- Photograph of *Kirchnerala treintamil* gen. nov. et sp. nov. from Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, province of La Rioja, Northwest Argentina. Lowermost part of Guandacol Formation (circa 325-324 Ma). Holotype specimen MACN-In 2678D. Scale bar = 3 mm.

Fig. 4.- Camera lucida drawing of Holotype (MACN-In 2678D) of *Kirchnerala treintamil* gen. nov. et sp. nov. Scale bar = 3 mm.

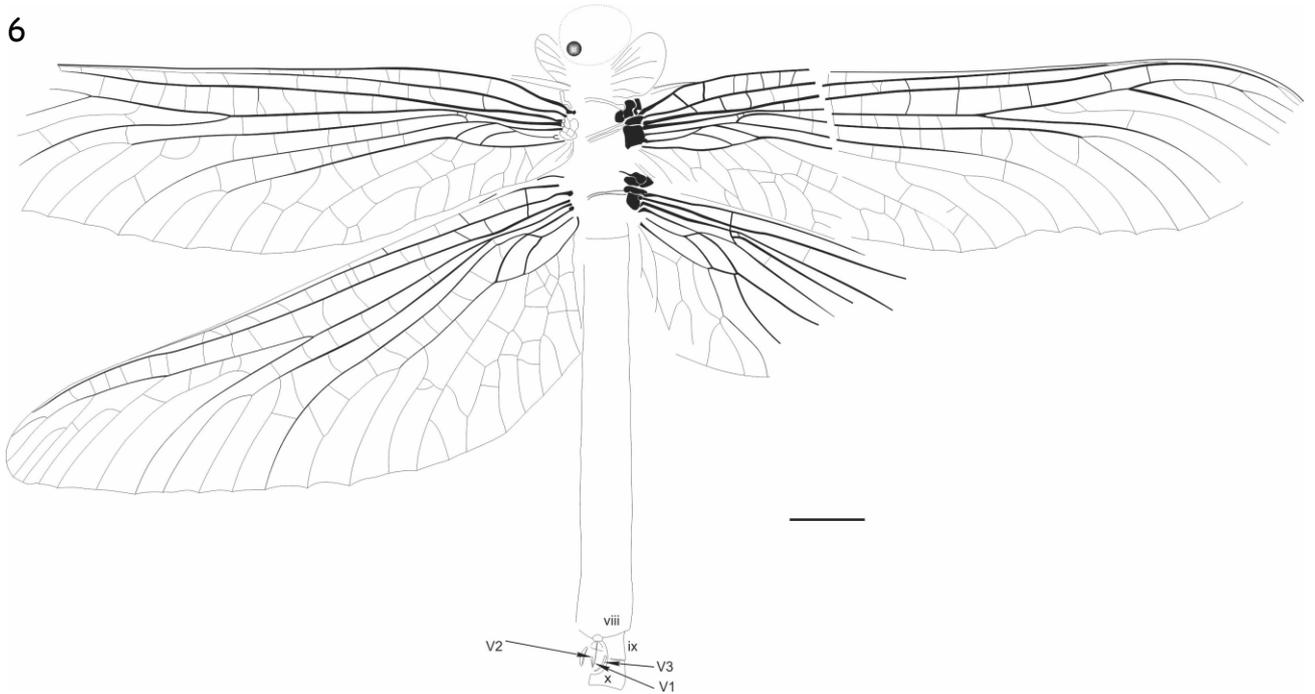


Fig. 5.- Photograph of *Argentina cristinae* gen. nov. et sp. nov. from Guandacol 1 locality, Quebrada de las Libélulas, Cerro Guandacol, province of La Rioja, Northwest Argentina. Lowermost part of Guandacol Formation (circa 325-324 Ma). Holotype specimen MACN-In 2678B. Scale bar = 5 mm.

Fig. 6.- Composite camera lucida drawing of Holotype (MACN-In 2678A-B) of *Argentina cristinae* gen. nov. et sp. nov. Scale bar = 5 mm.