

# First Coenagrionid Damselfly (Odonata: Zygoptera) from the Late Palaeocene of Northwestern Argentina<sup>1</sup>

Julián F. Petrulevičius<sup>2</sup>

**Abstract:** A new Coenagrionid zygopteran, *Marado marado* n. gen. and n. sp., is described from the late Palaeocene of Maiz Gordo Formation, Jujuy province, Northwest Argentina. The new genus is characterised by wing characters such as the subnodus aligned with the base of IR<sub>2</sub>; postnodal crossveins aligned with rows of crossveins below forming several pseudo-transverse veins; only two primary antenodal crossveins Ax<sub>1</sub> and Ax<sub>2</sub> retained; distal discoidal vein MAb very oblique, so that the anterior side of the discoidal cell is much shorter than the posterior one; very short petiole; RP<sub>2</sub> nearly three cells distal to subnodus; and a RP<sub>3+4</sub> two cells (and with one crossvein to MA) basal to subnodus. This is the first fossil for South America of the well represented family Coenagrionidae.

**Key Words:** Coenagrionidae, *Marado marado* n. gen. n. sp., late Palaeocene, Northwest Argentina.

## Introduction

Coenagrionidae is a highly diverse family of damselflies with 129 genera and about 1300 species (Paulson et al. 2021). This is the classical view of the family, also shared by Bridges (1994) and coincidentally by Bechly (2007). In an attempt to redefine the damselfly families through a molecular phylogeny, Dijkstra et al. (2014) reformulated the Coenagrionidae defining a core group with *Coenagrion* and the subfamilies Agriocnemidinae, Ischnurinae and Pseudagrioninae and a remaining group including the Protoneurinae, Pseudostigmatinae and Teinobasinae (Dijkstra et al. 2014). These “remaining coenagrionids” form a less resolved monophyletic sister group of the core coenagrionids (Dijkstra et al. 2014). One important point is that Argiinae is considered polyphyletic, being *Argia* the only remaining genus in Coenagrionidae for the latter authors. The genus *Argia* is distributed from Central Argentina to Southern Canada (Garrison et al. 2010) with about 130 sp (Paulson et al. 2021). The remaining Argiinae, *Mesocnemis*, *Onychargia*, *Palaiargia* and relatives are considered Platycnemididae (Dijkstra et al. 2014). With this hypothesis the coenagrionid type of discoidal cell (with the MAb very oblique, resulting in an anterior side much shorter than the posterior one) became convergent to that of Platycnemididae. The

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<sup>2</sup> CONICET - Consejo Nacional de Investigaciones Científicas y Técnicas and División Paleozoología Invertebrados, FCNyM - Facultad de Ciencias Naturales y Museo, UNLP - Universidad Nacional de La Plata. Paseo del Bosque s/n, La Plata (1900), Argentina. Email: [levicius@fcnym.unlp.edu.ar](mailto:levicius@fcnym.unlp.edu.ar).

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Argiinae, for Dijkstra et al. (2014), is also weakly retained as the sister group of the core coenagrionids. With this hypothesis, the only character known in the wing venation for the Argiinae is a very short petiole ending well basal to Ax1. The combination of characters defining the former Argiinae (i.e., basal part of CuA not aligned with crossveins between AA and posterior wing margin; venation at wing apex not especially dense; wings narrow; wings stalked well before level of AA so that distance between end of petiole and origination of CuP longer than CuP) are present in the genera now placed into the Platycnemididae *sensu* Dijkstra et al. 2014.

Coenagrionids are quite common in the fossil record mainly represented by isolated wings. This renders difficult their study because, for example, in recent genera highly diverse such as *Argia*, the taxonomy is based principally in colour patterns of the body and male genitalia (see Garrison et al. 2010; Zheng et al. 2018). Coenagrionids were absent up to now in the fossil record of South America, but represented in Central America by extant genera from the Miocene Mexican amber by undetermined *Argia*, *Neoerythromma* and *Nehalennia* (Ross et al. 2016; Zheng et al. 2018), from the Dominican amber by *Diceratobasis worki* (Poinar, 1996) and from North America by several species, many of them described in the nineteenth century and beginnings of twentieth and attribution doubtfully to recent genera (Scudder 1890, 1892; Cockerell 1907, 1908a, 1908b). Other Cenozoic records of Coenagrionids come from European deposits like Baltic amber, upper Eocene of the Isle of Wight (UK) and Oligocene and Miocene of Germany and France (Nel and Fleck 2014, Nel and Paicheler 1993, Nel and Papazian 1990, Zheng et al. 2018).

Maíz Gordo formation is a lacustrine sequence that crops out in Jujuy and Salta provinces and could be considered a concentration Lagerstätten *sensu* Seilacher *et al.* (1985) with a collected insect fauna of about 19000 specimens (Petrulevičius 2001) from end members of cyclical sedimentary facies (Petrulevičius 2002). It includes a quite well described fauna of Odonata with 10 species placed in extinct families, such as the endemic Latibasaliidae (Petrulevičius and Nel 2004a), the Palaeomacromiidae (Petrulevičius and Nel 2002a; Petrulevičius et al. 1999), which are also present in the Eocene of Monte Bolca (Petrulevičius and Nel 2007), two other italoansids (Petrulevičius and Nel 2002b, 2003), a Neophyinae (Petrulevičius and Nel 2009), a Lestinoidea (Petrulevičius and Nel 2004b), and an Argiolestidae (Petrulevičius 2020).

## Methods

In this work, I follow the wing venation nomenclature of Kukulová-Peck (1983), amended by Kukulová-Peck (1991, 2008), also contributions by Riek and Kukulová-Peck (1984), Nel et al. (1993), Bechly (1996), and Petrulevičius and Gutiérrez (2016). The higher classification of fossil and extant Odonata is based on the phylogenetic system of Bechly (1996, 2007).

The wing of the new species was drawn and photographed in detail using a camera lucida and a Leica digital camera (DMC5400), attached to a Leica M205C stereomicroscope.

**Institutional abbreviations:** The specimen was collected in the final part of twentieth century and was housed at the División Paleozoología Invertebrados, Museo de La Plata, La Plata, Argentina (acronym MLP).

**Morphological abbreviations:** AA, anterior anal; Arc, arcus; Ax0, Ax1, Ax2, three primary antenodal braces; Cr, crossvein; CuA, anterior cubitus; CuP, posterior cubitus; DC, discoidal cell; IR2, intercalary radial vein; MAb, anterior media b; MP, posterior media; N, nodus; RA, anterior radius; RP, posterior radius; ScP, posterior subcosta; SdC, subdiscoidal cell; Sn, subnodus.

### Systematic Palaeontology

**Odonata Fabricius, 1793**  
**Euzygota Bechly, 1996**  
**Coenagrionidae Kirby, 1890**

**Genus *Marado* n. gen.**

**Type species:** *Marado marado* n. sp.

**Etymology:** “Marado” is a contraction from Maradona. In honour of Diego Armando Maradona, the best world football player ever.

**Diagnosis:** (1) number of hexagonal and pentagonal cells greatly reduced; (2) only two primary antenodal crossveins Ax1 and Ax2 retained; (3) no antesubnodal and antefurcal crossveins; (4) postnodal and postsubnodal crossveins aligned; (5) terminal kink of CP at nodus and nodal membrane sclerotisation suppressed; (6) distal discoidal vein MAb very oblique, so that the anterior side of the discoidal cell is much shorter than the posterior one; (7) very short petiole; (8) four cells between discoidal cell and subnodus; (9) RP2 nearly three cells distal to subnodus; (10) RP3+4 displaced basal (two cells, and with one crossvein to MA) to subnodus.

**Characters:** 1 is a synapomorphy of Coenagrionomorpha Bechly (2007); 2-4 are synapomorphies of Coenagrionida *sensu* Bechly (2007); 5 is a synapomorphy of Coenagrionodea *sensu* Bechly (2007); 6 is a synapomorphy of Coenagrionidae *sensu* Bechly (2007); 7 is present in Argiinae (presumed synapomorphy of the subfamily). The combination of characters 8 to 10 is unique.

***Marado marado* n. sp.**

Figures 1-2

**Type data: Holotype:** MLP 18833. **Type locality and Age:** El Garabatal, latitude 24° 20' S, longitude 64° 28' W, Maíz Gordo Formation, green shales, Late Palaeocene (Volkheimer et al. 1984; Quattrocchio et al. 1997), province of Jujuy, Argentina.

**Etymology:** “Maradóoo maradóoo” is the voice of the people, the popular song on the stands of the football stadiums cheering the idol as in the Estadio Azteca in Mexico City (Figure 3). Diego was always on the people side from where he came (Maradona 2006). After his physical disappearance, Maradona will be alive forever in the people’s memory.

**Diagnosis:** As in the genus.

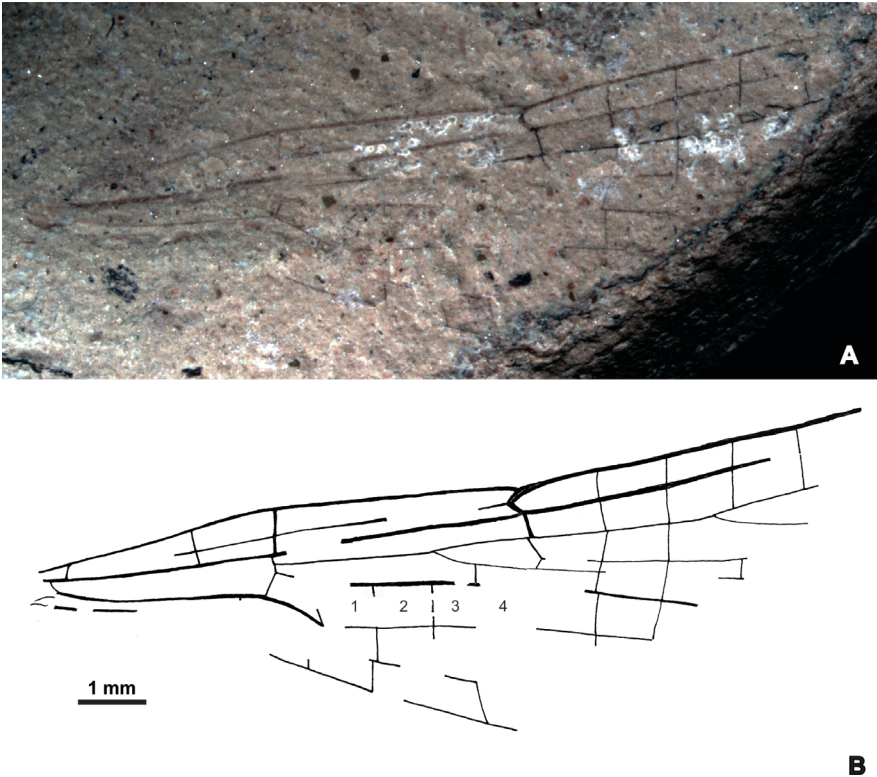


Figure 1. Habitus of *Marado marado* n. gen. n. sp., holotype MLP 18833 from El Garabatal (Jujuy, Argentina); late Palaeocene. Photograph (A), camera lucida drawing with the number of cells between discoidal cell and subnodus (B).

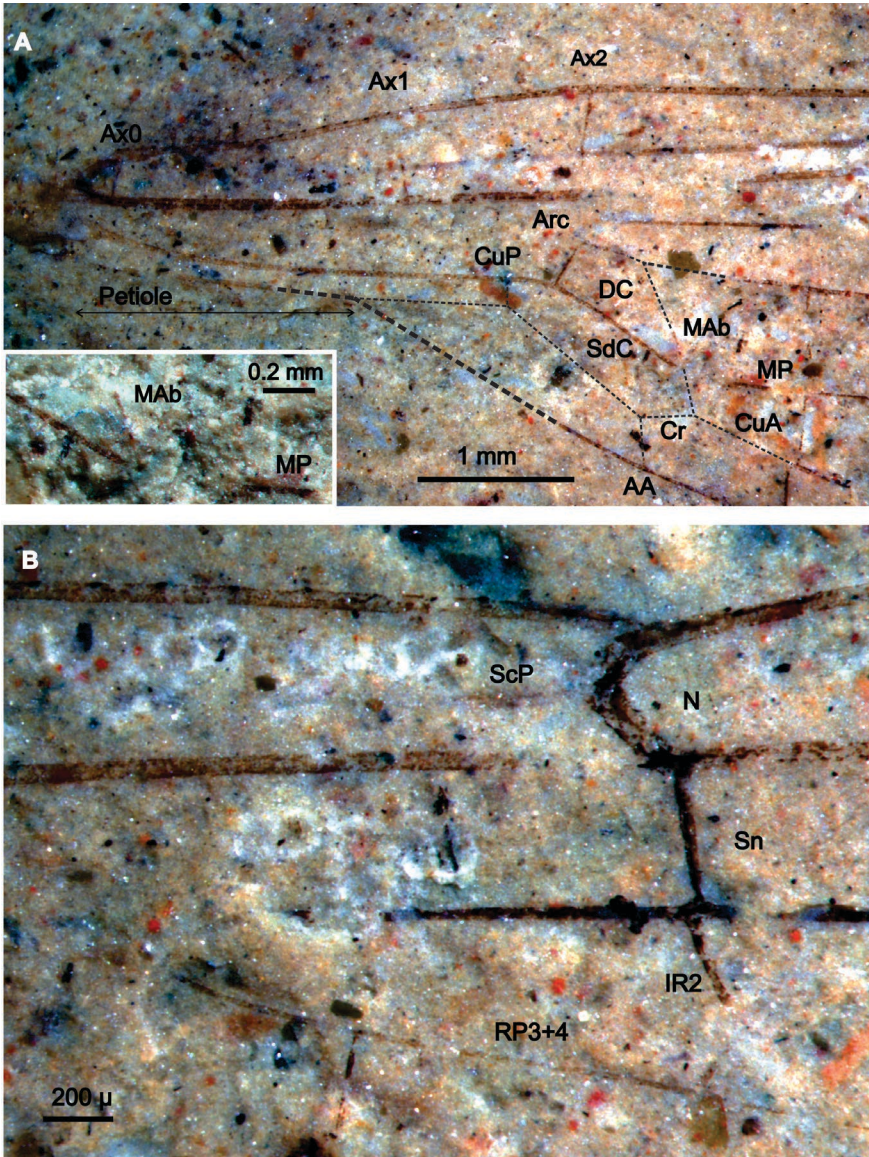


Figure 2. Photographs of the wing of *Marado marado* n. gen. n. sp., holotype MLP 18833 from El Garabatal (Jujuy, Argentina); late Palaeocene. Basal part with interpretation (in dotted lines) of petiole length and discoidal cell (DC) shape; detail of this latter showing the acute distal angle defined by the posterior side cell and the MAb (A), middle part with nodus (N) and subnodus (Sn) (B).

**Description:** Wing hyaline, preserved length 12.7 mm; max. preserved width 3.5 mm; distance from base to arculus 3.4 mm; distance from arculus to nodus 3.6 mm; distance from base to nodus 6.8 mm; Ax0 close to wing base, Ax1 and Ax2 well defined; Ax0 1.8 mm basal to Ax1, Ax2 1.2 mm distal to Ax1; costal margin with spinules distant  $\approx 1.35$  from each other; no secondary antesubnodal and antenodal crossveins; four cells between discoidal cell and subnodus; crossveins between MA and wing margin aligned; 4 preserved postnodal crossveins aligned with the rows of crossveins below, forming pseudo-transverse-veins; Ax2 slightly basal to the arculus; posterior part of arculus (basal discoidal crossvein) forming a quadrangular discoidal cell basally closed, trapezoidal, free of crossveins, with an acute distal angle (Fig. 2A, detail), anterior side (preserved 0.28 mm, estimated 0.4mm) much shorter than distal side MAb (estimated 0.8mm), basal side 0.32 mm long, posterior side 1 mm; posterior margin of discoidal cell aligned with MP; AA preserved last millimeter before wing margin; crossvein inferred between CuA and AA; subdiscoidal cell inferred wide; origin of RP3/4 1.47 mm (two cells) basal to subnodus with one crossvein to MA; one row of cells between CuA and wing margin (in the preserved part); subnodus almost transverse; IR2 aligned with subnodus; one crossvein between RP3/4 and IR2; RP2 2.7 mm, two and 3/4 cells distal to subnodus.

### Discussion

First, a few words about the preservation of the specimen because the preserved fragment of the wing includes many fragmentary veins, some of which are involved in characters useful for the systematic affiliation of the specimen. In this sense, it is important to establish whether the veins are in their original position or if they are displaced; and/or the presence of a possible shape deformation of the wing. The veins are considered to be in their original position and only fragmented by the split of the rock, of which we have the part but no counterpart (Figure 2A, detail). The original position of the veins is verified by the preserved vein fragments, which match each other if we reconstruct the missing parts (Figure 2A). With respect to a possible shape deformation of the wing, it can be dismissed because the general appearance of the wing morphology matches with that of other genera of Euzygoptera.

The specimen can be included into Coenagrioniformia Bechly, 1996 by the subnodus aligned with the base of IR2, at least somewhat strengthened and dorsally united with the subnodus by the common sclerotization (interradial bracket); the number of hexagonal and pentagonal cells greatly reduced; the postnodal crossveins aligned with rows of crossveins below forming several pseudo-transverse veins (reversed within Platystictinae); and all intercalary veins (except IR1 and IR2) suppressed. The specimen lacks the following synapomorphies of Platystictidae: nodus in very basal position (at about 22% of wing length); CuP-crossing recessed in a very basal position; subdiscoidal cell traversed by three cross veins delimiting a pseudo-subdiscoidal cell; and CuA

completely fused with hind margin, thus only retained as subdiscoidal vein. The specimen can be included into the Coenagrionida *sensu* Bechly (2007) by sharing only one row of cells present between CuA and hind wing margin; only two primary antenodal crossveins Ax1 and Ax2 retained; no antesubnodal and antefurcal crossveins; and postnodal and postsubnodal crossveins somewhat aligned. The clade Coenagrionida *sensu* Bechly (2007) consists of Pseudostigmatoidea Kirby, 1890 and Coenagrionodea Bechly 1996. Pseudostigmatoidea could be excluded because they have wings very long and slender; nodus in an extremely basal position (16-23 % of wing length); a very high number of postnodal crossveins; and the discoidal cell at least somewhat elongated. The specimen shares with the Coenagrionodea the terminal kink of CP at nodus and the nodal membrane sclerotization completely suppressed. Within Coenagrionodea, the specimen shares with Coenagrionidae *sensu* Bechly (2007) the unique synapomorphy of these latter, i.e., distal discoidal vein MAb very oblique, so that the anterior side of the discoidal cell is much shorter than the posterior side. Then, the specimen is considered a Coenagrionidae also by sharing the reduction of the postnodal crossveins and their strict alignment.

Among Coenagrionidae, the generic composition of the Argiinae *sensu* Bechly (2007) coincides with that of Bridges (1994); whereas Argiinae *sensu* Dijkstra et al. (2014) is restricted to *Argia*. So, the characters of Argiinae are those of *Argia*, including the short petiole and a crossvein between CuA and AA. Looking close to the petiole, *Argia* has the shortest one, in contrast with the remainder genera of the Argiinae *sensu* Bechly (2007). Then, a very short petiole could be the derived character of the subfamily. The new species shares with *Argia* the wings very shortly petiolated and the crossvein between CuA and AA, but the latter character is shared with several genera of the family including the former Argiinae. The new species differs from all the genera of Coenagrionidae in having a RP3/4 two cells basal to subnodus with one crossvein to MA (Figure 2B). This feature seems to be a plesiomorphy shared with the Burmacoenagrionidae from the Cretaceous of Myanmar (Zheng et al. 2017). Is interesting that some species of *Argia* have a RP3+4 one cell basal to the subnodus but without a crossvein to MA.

Another interesting character, evidenced by the reviewer AN, is the subnodus nearly perpendicular to RA and RP. This character is uncommon in recent Coenagrionids but present in some species like *Coenagrion interrogatum* (Sélys, 1876), *Oxyagrion rubidium* (Rambur, 1842), and *Argia funcki* (Sélys, 1854) This character is also present in the Eocene fossil genera *Eopodagrion* from USA (Cockerell 1920) and *Furagrion* from Germany (Petrulevičius et al. 2008). The new species differs from the two latter and from other megapodagrionids in the shorter petiole and in the MAb oblique and larger than the basal side of the discoidal cell (Figure 2A, detail).

### Concluding Remarks

The specimen is treated as a new genus and species *Marado marado* n. gen. n. sp. based on a unique combination of characters with respect to the genera of Coenagrionidae, such as four cells between discoidal cell and subnodus; RP2 nearly three cells distal from subnodus; and a RP3/4 two cells basal to subnodus with one crossvein to MA. The new genus could be included into Coenagrionidae: Argiinae by the presence of a very short petiole. Bechly (2007) commented a possible basal position of the Argiinae as a sister group of all remaining Coenagrionodea based on the morphology of the larval mask. This hypothesis is interesting considering the suspected plesiomorphic condition of the RP3/4 two cells basal to subnodus with one crossvein to MA present in *Marado* n. gen. The Argiinae with the only genus *Argia* have an American distribution. The discovery of a new genus in the Palaeocene of Northwest Argentina provides the first South American fossil coenagrionid and gives a new clue to the biogeographic and phylogenetic history of the family.

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Figure 3. Intervened photo from the football match Argentina versus England (2-1) played on 22 June 1986 in the quarterfinals of the 1986 FIFA World Cup. Maradona and his ball flying through several English player six seconds before scoring his second goal, the goal of the century. Note the shadows, Maradona’s one has eight appendages: two legs, two arms, and four wings. I am deeply saddened by the unexpected passing of Hugo Maradona, youngest brother of Diego, at the age of 52 on December 28, 2021. At age 11, Hugo was the “mastermind” of Diego’s Goal of the Century (Maradona 2000).