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A new Synlestidae damselfly (Insecta: Odonata: Zygoptera) from the early Eocene of Nahuel Huapi Este, Patagonia, Argentina.

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Abstract: A new lestoid genus, *Inacayalestes* **gen. nov.**, based on *Inacayalestes aikunhuapi* **sp. nov.** is described from Nahuel Huapi Este locality (Ypresian), Neuquén province, Patagonia, Argentina. The new genus is assigned to Synlestidae and seems to be related to *Ecchlorolestes* Barnard, 1937 and *Synlestes* Selys, 1868, both genera from Southern Hemisphere, from South Africa and Australia, respectively. The new genus enlarges the record of Lestomorpha in Argentina to three fossil genera: *Promegalestes* Petrulevičius & Nel, 2004, *Austroperilestes* Petrulevičius & Nel, 2005, and *Inacayalestes* **gen. nov.**, whereas two extant genera are present: *Lestes* Leach, 1815 and *Archilestes* Selys, 1862.
Key words: Odonata, Zygoptera, Lestodea, Synlestidae, *Inacayalestes aikunhuapi* **gen. nov.** et **sp. nov.**, Ypresian, Patagonia, Argentina.

Resumen: Un nuevo zigóptero Synlestidae (Insecta: Odonata: Zygoptera) del Eoceno temprano de Nahuel Huapi Este, Patagonia, Argentina. Se describe un nuevo género, *Inacayalestes* **gen. nov.**, basado en *Inacayalestes aikunhuapi* **sp. nov.** de la localidad de Nahuel Huapi Este (Ypresiano), Provincia de Neuquén, Patagonia, Argentina. El nuevo género se asigna a Synlestidae y parece estar relacionado con *Ecchlorolestes* Barnard, 1937 y *Synlestes* Selys, 1868, ambos géneros del Hemisferio Sur, de Sudáfrica y Australia, respectivamente. El nuevo género amplía el registro de Lestomorpha en Argentina a tres géneros fósiles: *Promegalestes* Petrulevičius & Nel, 2004, *Austroperilestes* Petrulevičius & Nel, 2005 e *Inacayalestes* **gen. nov.**, mientras que se registran dos géneros actuales, *Lestes* Leach, 1815 y *Archilestes* Selys, 1862.
Palabras clave: Odonata, Zygoptera, Lestodea, Synlestidae, *Inacayalestes aikunhuapi* **gen. nov.** y **sp. nov.**, Ypresiano, Patagonia, Argentina.

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Introducción

The Lestomorpha Bechly, 1996 (superfamily Lestoidea *sensu* Dijkstra *et al.*, 2013) are present worldwide from the Cretaceous to recent times. Recent Lestomorpha include 208 species in 21 genera (Schorr & Paulson, 2015) in all continents except Antarctica. The number of fossil Lestomorpha represents about the 10% of the extant ones with about 27 species, 13 extinct genera, and 4 extinct families. Most of the fossil species belong to the genus *Lestes* Leach, 1815 (about 10 species) which is concordant to the extant diversity of the genus (85 species).

The specimen studied here represents the third Zygoptera: Euzygoptera Bechly, 1996 fossil from Argentina, being the other two from the Paleocene and Eocene (Petrulevičius & Nel, 2003, 2005). These two fossils and the one studied here coincidently belong to the Lestomorpha. This is quite surprising as this clade is not so well represented in America, with three families, Perilestidae,

Synlestidae, and Lestidae, and five genera (Heckmann, 2008; Dijkstra *et al.*, 2014; DSA, 2015; Paulson, 2015a, b). In Argentina, the only recent Lestomorpha are the derived Lestidae: Lestinae with the genera *Lestes* Leach, 1815 and *Archilestes* Selys, 1862 (Paulson, 2015a). The fossil Lestomorpha are *Promegalestes* Petrulevičius & Nel, 2004, a Lestinoidea of uncertain family from the late Paleocene of the Northwest (Petrulevičius & Nel, 2003), and *Austroperilestes* Petrulevičius & Nel, 2005, belonging to an endemic family, the Austroperilestidae, from the middle Eocene (52 Ma) of Laguna del Hunco, Patagonia (Petrulevičius & Nel, 2005).

This is the first fossil insect described from the locality Nahuel Huapi Este (Melendi *et al.*, 2003), also called Nahuel Huapi or Pampa de Jones (Melendi *et al.*, 2003; Wilf *et al.*, 2010). The locality is well known because of the micro and macroflora (Melendi *et al.*, 2003; Wilf *et al.*, 2010) and amphibians (Báez, 1996; Báez & Pugener, 2003). Plant record is diverse and interesting with pollen and macrofossils of Podocarpaceae and *Araucaria* but no micro nor macrofossils of Nothofagaceae (Melendi *et al.*, 2003; Wilf *et al.*, 2010), absence which could be related to the temperate climate prevailing in the Ypresian (Wilf *et al.*, 2010). Odonata are already present from the close historical locality of Confluencia (Ypresian?), as nymphs resembling families such as Synlestidae, Libellulidae, and Gomphidae (Petrulevičius, 2012, 2013). In Patagonia, adult Odonata are registered in Laguna del Hunco with the basal Epiproctophora family Frenguelliidae Petrulevičius & Nel, 2003, with two species, *Frenguellia patagonica* Petrulevičius & Nel, 2003 and *Frenguellia iglesiasi* Petrulevičius & Nel, 2013; the basal Aeshnidae *Huncoaeshna corrugata* Petrulevičius & Nel, 2010; and the Austroperilestidae mentioned above. The record of Patagonian Eocene Odonata is fulfilled with endophytic ovipositions in angiosperm leaves in Laguna del Hunco and Río Pichileufú (Petrulevičius, 2013).

Insects were cited but never described nor figured in Nahuel Huapi Este (Wilf *et al.*, 2010). The age of the locality is suggested to be early Eocene by Melendi *et al.* (2003) and an absolute dating by Wilf *et al.* (2010) yielded a 40Ar/39Ar age of 54.24 ± 0.45 Ma. The locality is within Nahuel Huapi National Park, exposed near the northeastern shore of Nahuel Huapi lake, close to San Carlos de Bariloche. The strata consist of tuff and mudstone, siltstone, and sandstone beds, somewhat more than 8 m thick on a single section line in the center of the outcrop (Wilf *et al.*, 2010), representing a volcanic lacustrine environment probably located near a lake margin (Báez & Pugener, 2003; Melendi *et al.*, 2003). Demic fauna is represented by an ontogenetic sequence of tadpoles of the pipid frog *Llankibatrachus truebae* (Báez, 1996; Báez & Pugener, 2003). Most of the macrofossils at the site occur in a blocky, silty mudstone unit of 1 m thickness (Unit 16 in Wilf *et al.*, 2010).

Materials and methods

In this paper, we follow the wing venation nomenclature by Kukalová-Peck (1983), amended by Kukalová-Peck (1991, 2009), and also contributions by Riek & Kukalová-Peck (1984), Nel *et al.* (1993), and Bechly (1996). The higher classification of fossil and extant Odonata is based on the phylogenetic system of Bechly (1996).

The fossil is housed at the Museo Asociación Paleontológica Bariloche (repository prefix MAPBAR), San Carlos de Bariloche, Río Negro, Argentina. The fossil was photographed with a Nikon D5000 digital camera. The new species was drawn with a camera lucida attached to a Wild M5 stereomicroscope.

Systematic Paleontology

Odonata Fabricius, 1793

Euzygoptera Bechly, 1996

Lestodea Bechly, 1996

Synlestidae Tillyard, 1917

***Inacayalestes* gen. nov.**

Type species: *Inacayalestes aikunhuapi* **sp. nov.**

Diagnosis. This genus is known by wing characters: discoidal cell narrow and long; distal angle of discoidal cell acute; Ax2 just distal of the arculus; MP distinctly curved after its origin; postnodal and postsubnodal crossveins aligned; vein "O" slightly oblique; bases of RP3/4 two cells basal to nodus; IR2 aligned with nodus; base of RP2 6 cells distal of subnodus; CuP ending in A (wing margin); AA+CuP bifurcates from AP (wing margin) just basal to arculus; distal side of discoidal cell (MAb) 1.5 times longer than anterior side (MA); sdv long; 1/3 of the posterior margin of the subdiscoidal cell fused to the hind margin.

Etymology. In honour of Inacayal (1833-1888), Günün a Küne (Puelche) chief (Cacique) of the region of Nahuel Huapi lake; and "lestes", because of usual ending for lestoid damselflies. Inacayal was captured by the Argentinean state army (conducted by General Julio Argentino Roca) during the genocidal campaign "Conquest of the Desert" carried out to break the sovereignty of the indigenous communities in Patagonia. After that, he was "rescued" from the detention camp with part of his family by the Perito Francisco Josué Pascasio Moreno in gratitude for his help in a previous Patagonian expedition. He was installed, as a living and afterwards as a dead specimen, in the Museo de La Plata from 1886 to 1888 where he died by no clear reasons. His skeleton was restituted to Patagonia by a National Law, after claims by several indigenous communities and a National Senator, in 1994. Nevertheless, other claimed remains as his scalp and brain and also from other members of the community are still part of the collection of the museum.

***Inacayalestes aikunhuapi* sp. nov.** (Figs. 1-4)

Diagnosis. As for the genus (see above).

Description. Basal half of a hindwing (?); no color preserved, wing was probably hyaline in the preserved part; length of preserved part, 17 mm; wing 5.4 mm wide three cells distal to RP2 base; wing with long petiole, 4.1 mm preserved part; distance between base and arculus, 4.3 mm, between arculus and nodus, 3.9 mm; between nodus and RP2, 4.7 mm; two primary antenodals aligned with antesubnodals; supplementary antenodal crossveins absent; first primary antenodal brace Ax1 2.5 mm from the (preserved and suspected original) base of the petiole, and 1.7 mm from the second primary antenodal brace Ax2; second primary antenodal brace Ax2 just distal the arculus; RP originates at midpoint of the arculus and basal to arcular brakcet; distance between fork of MA and base of subnodus, 1 mm; vein MAb oblique and long, distal angle of discoidal cell acute; discoidal cell elongate, narrow, 1.6 mm long, 0.3 mm wide, anterior side 0.6 mm, posterior side sigmoidal 1.5 mm, basal side 0.3 mm, distal side 0.7 mm; CuP short and straight, ending at the wing margin, nearer to Ax1 than to Ax2, 0.4 mm distal to Ax1; sdv (part of CuA inmediate to discoidal cell) 0.25 mm long; 1/3 of the posterior margin of the subdiscoidal cell fused to the hind margin; CuP+AA+AP (0.7 mm long) separates from wing margin (AA"+AP), 0.4 mm basal to arcular bracket; MP distally straight; MP distinctly curved after its origin at the distal angle of the discoidal cell; CuA zigzagged in its distal part, reaching posterior wing margin distal (four cells) of the level of base of RP2; one row of cells in cubito-anal area; one row of cells in area between MP and CuA, MA and MP, RP3/4 and MA, IR2 and RP; MA very straight, not zigzagged from the base to three cells distal RP2 base; anterior wing margin depressed at nodus; base of RP3/4 two cells basal to subnodus; base of IR2 opposite to subnodus; subnodus well oblique; base of RP2 6 cells distal of subnodus (4.4 mm); a slightly oblique vein 'O' 3 cells distal base of RP2; postnodal and postsubnodal crossveins aligned (only two preserved).

Etymology. After "áikün", meaning lake in günün a yajütshü language spoken by the günün a küne (Puelche) people; and "huapi" from the Nahuel Huapi lake, aside the locality, and meaning island in Mapudungum language.

Type material. Holotype MAPBAR 4138, Museo de la Asociación Paleontológica Bariloche, Argentina.

Occurrence. From Nahuel Huapi Este locality (also named Pampa de Jones), S41° 02', W71° 12', Parque Nacional Nahuel Huapi (National Protected Area), province of Neuquén, Patagonia Argentina, early Eocene (54 Ma; Wilf *et al.*, 2010).

Discussion. This wing is strongly similar to that of a lestid damselfly, by autapomorphies and simplesiomorphies as the presence of an oblique vein "*O*". The wing seems to be a hindwing because the discoidal cell is not so vertical as in forewings of Synlestidae like *Synlestes* Selys, 1868 and *Ecchlorolestes* Barnard, 1937. In the forewing of these genera and even in *Phylolestes* Christiansen, 1947, the distance from the basal part of the discoidal cell to the wing margin is longer than in its apical part and in the hindwing are equal as in the studied specimen. After Bechly (1996), the Eulestiformia (= Lestinoidea *sensu* Fraser, 1957) are characterized by "MP distinctly curved after its origin at the distal angle of the discoidal cell." Thus *Inacayalestes* **gen. nov.** would fall into this group. The group is composed by the Chorismagrionidae Tillyard & Fraser, 1938 and the Lestida Bechly, 1996. The Chorismagrionidae could be excluded because have the origin of IR2 shifted several cells distal of the midfork. The Lestida are characterized by the basal closure of discoidal cell in forewings, character not surely preserved in the new genus as it is unknown if it is represented by a posterior or anterior wing. Lestida *sensu* Bechly, 1996 is composed by the Perilestidae *sensu* Bechly (1996) composed by *Perilestes* Hagen in Selys, 1862, *Perissolestes* Kennedy, 1941, and *Nubiolestes* Fraser, 1945, and the Lestodea Bechly, 1996. The Perilestidae could be excluded because they have the apex of discoidal cell close or ending in the hind margin of the wing and IR2 distinctly shortened and arising close to the origin of RP2 or even on RP2. The new genus has the autapomorphy of Lestodea, the arculus shifted basally beneath the ax2. The Lestodea are composed by Synlestidae (considered here *sensu* Bechly, 1996), *Austroperilestes* Petrulevičius & Nel, 2005, Eolestidae Greenwalt & Bechly, 2014, Priscalestidae Wappler & Petrulevičius, 2007, Lestinoidea Bechly, 1996, and unassigned genera as *Lithagrion* Scudder, 1890, *Promegalestes* Petrulevičius & Nel, 2004, and *Lutetialestes* Greenwalt & Bechly, 2014. Lestinoidea (Megalestidae + Lestidae), Priscalestidae, Austroperilestidae, Eolestidae, and the genera *Promegalestes* and *Lutetialestes* could be excluded because they have the midfork recessed basally to a position of 20-26% of wing length, therefore the subnodus is located between the bases of RP2 and IR2 that are widely separated (Bechly, 1996). *Lithagrion hyalinum* Scudder, 1890 and *L. umbratum* Scudder, 1890, possibly related to Synlestidae (Greenwalt & Bechly, 2014), could be excluded because of their wider wings with two rows of cells from CuP to posterior wing margin. The new genus seems to be related to some genera of Synlestidae *sensu* Bechly (1996), i.e., *Synlestes*, *Episynlestes*, *Euchlorolestes*, *Chlorolestes*, and *Ecchlorolestes*. The Synlestidae *sensu* Bechly (1996) are composed by the genera listed by Bridges (1994) for Synlestinae, i.e., *Chlorolestes* Selys, 1862, *Euchlorolestes* Kennedy, 1920, *Ecchlorolestes* Barnard, 1937, *Episynlestes* Kennedy, 1920, *Phylolestes* Christiansen, 1948, *Sinolestes* Needham, 1930, and *Synlestes* Selys, 1868. Excepting the genus *Phylolestes*, the Synlestidae have a synapomorphy that is the posterior margin of the subdiscoidal cell mostly fused to the hind margin. The new genus has the posterior margin of the subdiscoidal cell in part (one third) fused to the hind margin what could be plesiomorphic. This character is absent in the genus *Phylolestes*, which is accepted to be of enigmatic position (Dijkstra *et al.*, 2014). Other genus considered to belong to Synlestidae by Bechly (1996), *Sinolestes*, has a different arrangement of IR2, originating several cells distal to subnodus. In the latter years Synlestidae is anew considered in a wider sense (Schorr & Paulson, 2014) based in Tillyard & Fraser (1938) and including *Megalestes* Selys, 1862, *Nubiolestes*, and *Chorismagrion* Morton, 1914. Then, Dijkstra *et al.* (2014) found that

the family in this sense is paraphyletic, what seems reasonable and coincident with the morphological analysis made by Bechly (1996, 2007) considering the three latter genera in three different families.

In conclusion, *Inacayalestes* **gen. nov.** could be considered a Synlestidae in the sense of Bechly (1996) by sharing principally the fusion of the posterior margin of the subdiscoidal cell to the hind margin. *Phylolestes* is the unique in having the subdiscoidal cell unfused to the hind margin. The new genus shares with *Ecchlorolestes* and *Synlestes* the arrangement of the basis of RP3/4 and IR2, the discoidal cell long and narrow with distal side longer than anterior side and the posterior side sigmoid. *Inacayalestes* **gen. nov.** differs from all genera by the bifurcation of CuP+AA' from AA"+AP basal to the arcular bracket instead of being distal to MAb arising. Other character that differentiates the new genus from all of these genera except *Euchlorolestes* is the sdv long and developed.

Remarks. The present discovery of a new genus of the Lestinoidea clade is of great importance for the reconstruction of the biogeographic and phylogenetic history of this group. The suggested related genera are *Ecchlorolestes* and *Synlestes* both from the Southern Hemisphere, from South Africa and Australia, respectively. The other genera of Synlestidae are present in South Africa (*Chlorolestes*, *Euchlorolestes*), Asia (*Sinolestes*), and Central America (*Phylolestes*). This discovery in the early Eocene could be related to older southern land connections in the Cretaceous, so it is suspected further findings in the Cretaceous.

The growing knowledge of Lestinoidea by body fossils does not include for the moment the record of endophytic ovipositions. Ovipositions attributed to other groups are recorded from the Eocene of Patagonia (Sarzetti *et al.*, 2009; Petrulevičius, 2013); the typical lestoid scars are absent but awaited.

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Fig. 1.- *Inacayalestes aikunhuapi* **gen. nov.** et **sp. nov.** from the Nahuel Huapi Este locality (early Eocene; 54 Ma); Neuquén Province, Patagonia, Argentina. MAPBAR 4138, holotype. Scale bar = 2 mm.

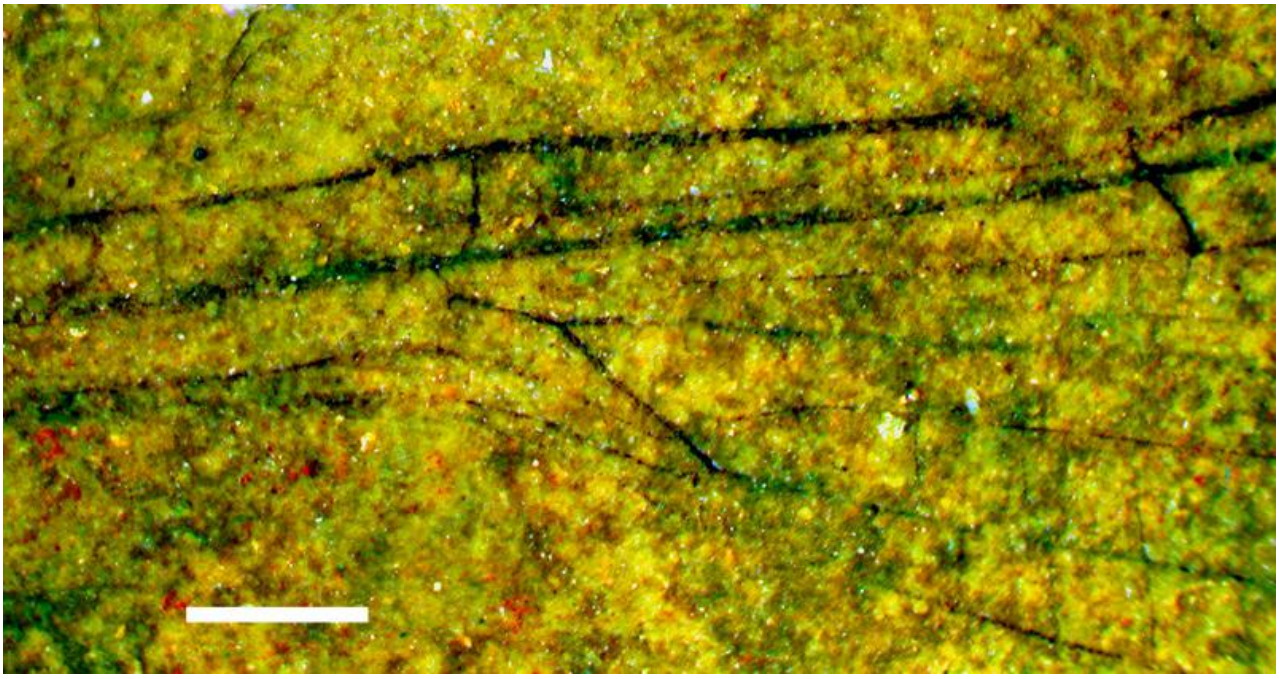

Fig. 2.- Detail of the wing base of *Inacayalestes aikunhuapi* **gen. nov.** et **sp. nov.** Holotype. Scale bar = 1 mm.

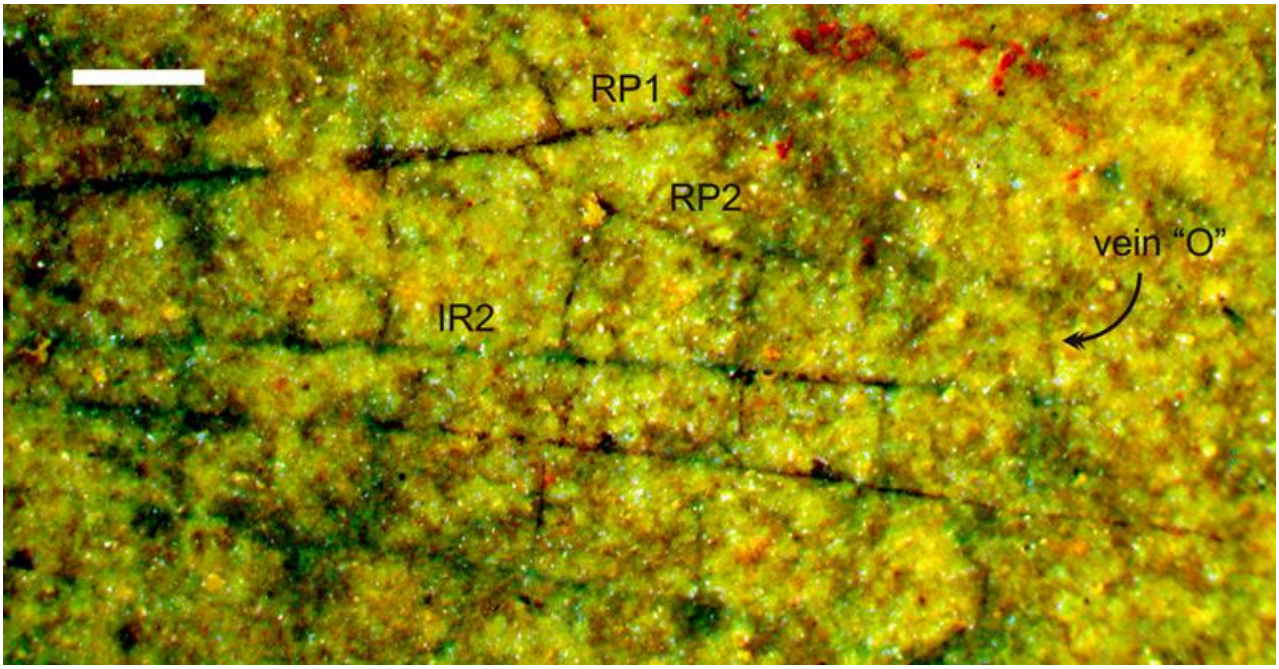

Fig. 3.- Detail of the oblique vein "O" of *Inacayalestes aikunhuapi* **gen. nov.** et **sp. nov.** Holotype. Scale bar = 0.5 mm.

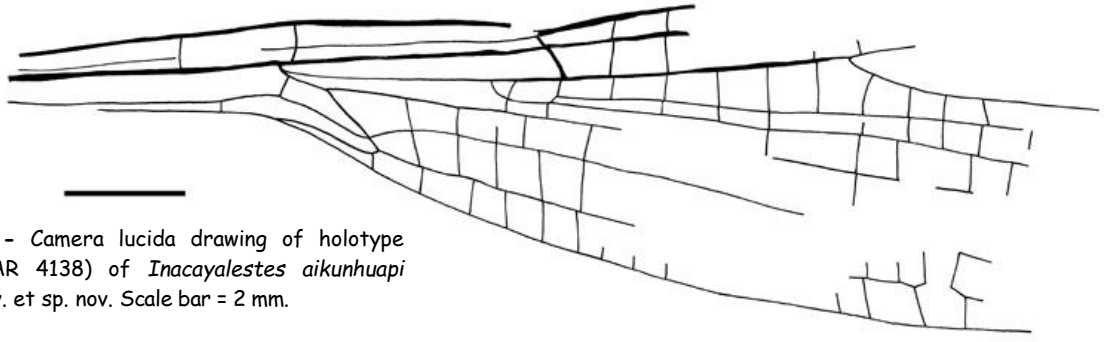

Fig. 4.- Camera lucida drawing of holotype (MAPBAR 4138) of *Inacayalestes aikunhuapi* gen. nov. et sp. nov. Scale bar = 2 mm.