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Terrestrial Arthropod Reviews 6 (2013) 53–60

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Palaeoenvironmental and palaeoecological implications from body fossils and ovipositions of Odonata from the Eocene of Patagonia, Argentina

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Received on January 12, 2013. Accepted on March 17, 2013.
Final version received on March 31, 2013

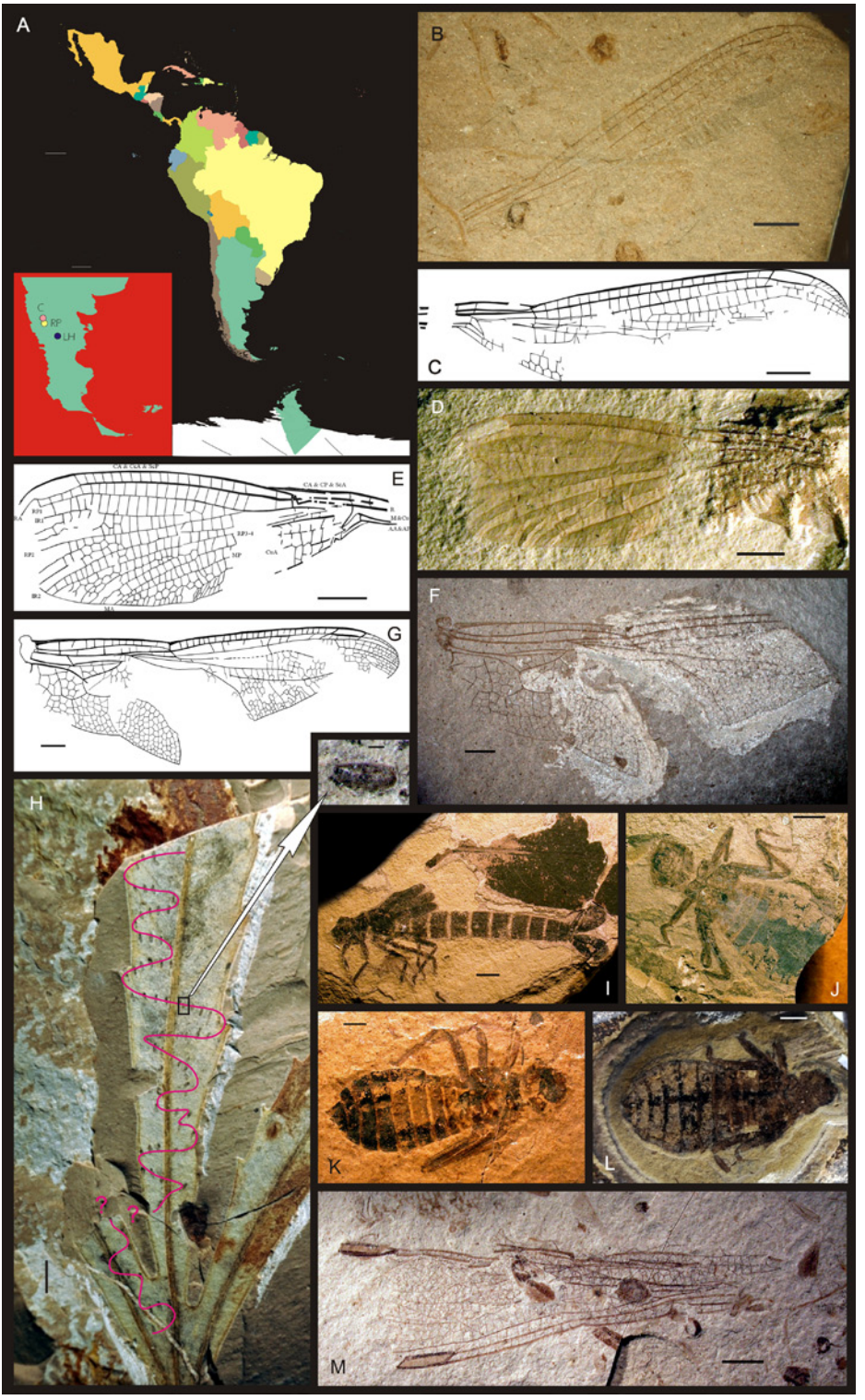
Summary
Odonata are beginning to be well recorded in the Eocene of Patagonia, Argentina. They are represented by body fossils and traces in three localities. Oviposition scars are recorded in Río Pichileufú (Lutetian: 47.7 Ma; Río Negro province) and Laguna del Hunco (Ypresian: 52.2 Ma; Chubut province), nymphs in Confluencia (Ypresian?; Río Negro), and adults (wings) in Laguna del Hunco. The absence of different stages in given localities could depend on different factors, such as as environmental, taphonomical and/or sampling bias. Laguna del Hunco is well sampled and the absence of nymphs seems to depend on taphonomical factors since there are other preimaginal aquatic inhabitants of the lake, such as Trichoptera nymph cases. Confluencia has not been well sampled and adults could be absent due to a sampling bias. The nymphs of Confluencia indicate a water body with low energy flux. Ovipositions in Laguna del Hunco and Río Pichileufú are made on terrestrial leaves of bushes and trees and have three different morphologies. Leaves are interpreted to be alive when oviposition was done as they show tissue reactions associated to the injuries. Wrinkled wings at Laguna del Hunco are interpreted to be signals of predation probably by birds or mammals.

Keywords
Fossil Odonata; palaeoenvironment; palaeoecology; body fossils; ovipositions; Laguna del Hunco; Río Pichileufú; Confluencia; Eocene; Patagonia; Argentina

Introduction

Odonata are quite well recorded in the Eocene of Patagonia. They are represented by body fossils and/or traces in three different localities (Fig. 1 A). Oviposition scars are recorded in Río Pichileufú (Lutetian: 47.7 Ma; Río Negro province) and Laguna del Hunco (Ypresian: 52.2 Ma; Chubut province), nymphs in Confluencia (Ypresian?;

DOI 10.1163/18749836-06021057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Río Negro), and adults (wings) in Laguna del Hunco. The absence of some (different) stages in the different localities could depend on factors as quality of water, taphonomical and sample bias. Laguna del Hunco and Río Pichileufú are well sampled and the absences seem to depend on taphonomical factors. On the contrary, Confluencia (inaccessible outcrop) is not well sampled and the absences could depend on bias of sampling.

Odonata, as hemimetabolous insects, have in general aquatic nymphs and terrestrial adults, even though some rare groups have terrestrial nymphs. This is the case of the petalurids that deposit eggs in very wet grounds and nymphs live in muddy burrows (Winstanley, 1981). In general the record of adults does not imply necessarily that nymphs inhabit the lake and the absence of these latter could be due to environmental or taphonomical factors. The presence of preimaginal stages is interesting as their morphology could bring data about energy flux, palaeoenvironment and palaeoecology of water bodies (Pritykina, 1965). The record of Odonata indicates in general aquatic and terrestrial surrounding environments with preys that could sustain the complete cycle of these predators.

The record of oviposition traces is also interesting as these imply that adults choose the water body as the place to develop their offspring. We have to take into account that this choice is complex and influences the reproductive success of the species.

Methods

Materials

Laguna del Hunco specimens are curated at Museo Paleontológico Egidio Feruglio (repository prefix MPEF-PI for palaeoinvertebrates and MPEF-IC for ichnofossils), in Trelew, Chubut, and División Paleozoología Invertebrados of the Museo de La Plata (repository prefix MLP), in La Plata, Buenos Aires, Argentina. The Río Pichileufú and Confluencia specimens are housed at Museo Asociación Paleontológica Bariloche (repository prefix MAPBAR), San Carlos de Bariloche, Río Negro, Argentina.

Localities

There are three Eocene localities with Odonata in Patagonia (Fig. 1 A). Palaeontological, stratigraphical and age available data of the localities are unequal. Laguna del Hunco

Figure 1. (A) Map showing the sampled localities, LH: Laguna del Hunco, RP: Río Pichileufú and C: Confluencia. (B.) Photo of holotype of *Austroperilestes hunco* Petrulevičius and Nel, 2005, MPEF-PI 997. (C) Drawing of the same. (D) Photo of hindwing of *Frenguellia patagonica* Petrulevičius and Nel, 2003, holotype specimen MLP 6431. (E) Drawing of the same. (F) Photo of holotype of *Huncoaeshna corrugata* Petrulevičius and Nel, 2010, MPEF-PI 1002. (G) Drawing of the same. (H) Ovipositions of Odonata in LH (*Paleoovoidus arcuatus* isp.) showing the zigzag pattern on a leaf of *Lomatia* (Proteaceae), MPEF-IC 931; details of an individual scar. (I-L) Photos of four types of nymphs from Confluencia: (I) Type 1, MAPBAR 1491; (J) Type 2, MAPBAR 1501; (K) Type 3, MAPBAR 1505; (L) Type 4 MAPBAR 2699; (M) Photo of an Odonata indet. from LH showing wrinkled wings, MPEF-PI 983. Scale bars = 3 mm, except for Fig. 1H (= 4 mm) and its detail (= 0.2 mm). This figure is published in color in the online version.

and Río Pichileufú are the best known (Petrulevičius, 1999; Wilf et al., 2003, Wilf, 2011). Confluencia is the least known and unavailable at the present time (Petrulevičius, 1999).

1. Laguna del Hunco (LH)

The locality was dated by Wilf et al. (2003, 2005a) and recalibrated by Wilf (2012) yielding an age of 52. 2 ± 0.22 Ma. LH is well sampled giving a nice diversity of insects, plants, vertebrates, and ichnotaxa (Fidalgo and Smith, 1987; Wilf et al., 2003, 2005a, b, 2009; Wilf, 2012; Petrulevičius and Nel, 2003, 2005, 2007, 2013; Zamaloa et al., 2006; González et al., 2007; Sarzetti et al., 2008, 2009; Petrulevičius, 2009 ; Petrulevičius et al., 2010; Azpelicueta and Cione, 2011; Gandolfo et al., 2011; Gómez et al., 2011). Odonata are recorded by oviposition traces (Sarzetti et al., 2009) and adults (papers by Petrulevičius cited above). Body fossils are represented by adults of Austroperilestidae (Zygoptera) (Petrulevičius and Nel, 2005) (Fig. 1 B, C), Frenguelliidae (a basal lineage of Epiproctophora) (Petrulevičius and Nel, 2003) Fig. 1 D, E) and Aeshnidae (Anisoptera) (Petrulevičius and Nel, 2010) Fig. 1 F, G). Specimens are wings nearly complete but generally wrinkled (Fig. 1 B-G; Petrulevičius and Nel, 2010).

Oviposition scars of the ichnogenus *Paleoovoidus* Vasilenko, 2005 have three basic morphologies belonging to three ichnospecies *P. rectus* Vasilenko, 2005, *P. bifurcatum* Sarzetti et al., 2009 and *P. arcuatum* Sarzetti et al., 2009 (Fig. 1 H). They are made on terrestrial leaves of bushes and trees. Sarzetti et al. (2009) tentatively attributed *P. rectus* and *P. bifurcatum* to Lestidae and *P. arcuatum* to Coenagrionidae. Other potential candidate producers could be also the extinct families Frenguelliidae and Austroperilestidae present in LH (Sarzetti et al., 2009; Petrulevičius et al., 2011). Frenguelliidae could be a candidate for *P. arcuatus* because of the similarities with the ovipositions of modern Epiophlebiidae (*Epiophlebia*) (Petrulevičius et al., 2011) (for ovipositions of *Epiophlebia* see Shimura, 2005).

2. Confluencia

The locality is unavailable since 1985, after the construction of a road and a dam. Confluencia shares with Río Pichileufú the ant genus *Archimyrmex* (Dlusky and Perfilieva, 2003).

The Odonata recorded in the locality are only nymphs of Zygoptera and Anisoptera with four morphological types. The first type (Fig. 1 I) could be attributed to "type 1, subtype 1" of Pritykina (1965) and resembles the nymphs of Synlestidae (Zygoptera) like *Episynlestes* with long body and broad terminal gills with leaf shape. The second and third types could be attributed to "type 5" of Pritykina (1965) and resemble the nymphs of Libellulidae (Anisoptera) with short and wide body, and oblong abdomen, short legs with setae in the second type (Fig. 1 J) and without setae in the third type (Fig. 1 K). The fourth type could be attributed to "type 6, subtype 1" of Pritykina (1965) and resembles the nymphs of Gomphidae (Anisoptera) like *Agriogomphus* (Ramírez, 2010) with short, wide and depressed body, short and depressed legs without setae and oblong abdomen (Fig. 1 L).

3. Río Pichileufú (RP)

The locality was recently dated (Wilf et al., 2005a) and recalibrated by Wilf (2011) yielding an age of 47.7 ± 0.10 Ma. RP is quite well sampled giving a nice diversity of insects, plants and ichnotaxa (Wilf et al., 2003, 2005a, b, 2009; Petrulevičius, 2008; Zamaloa et al., 2006; González et al., 2007; Sarzetti et al., 2009; Barreda et al., 2010 ; Gandolfo et al., 2011). Odonata are recorded only by ovipositions (Sarzetti et al., 2009).

Ovipositions of the ichnogenus *Paleoovoidus* Vasilenko, 2005 belong to only one morphological type, attributable to the same ichnospecies present in LH, *P. arcuatum*. Scars are also made on terrestrial leaves of trees.

Discussion

Palaeoenvironment

The record of body fossil and traces of Odonata could give in general an idea of the complexity of the ecological relationships in past environments. Not only the predatory aquatic nymphs and terrestrial adults but also the ovipositions, either inside, on the surface or well above the water, could bring a nice amount of independent data for palaeoenvironmental and palaeoecological reconstructions of the concerned site.

Oviposition scars are recorded in RP and LH. Both places share not only one ichnospecies but the place of oviposition, terrestrial leaves of trees. The leaves are interpreted to be alive (in both localities) when the oviposition was done, as they show tissue reactions in the margin of the injuries (see figures 5 and 6 of Sarzetti et al., 2009). This fact implies a low flux of energy well over the water and in the surrounding margins of the water body as shows a specimen from LH with 63 (+13 ?) scars (Fig. 1 H) continuously made by a female on a leaf attached to a branch next to the water. The deposition rate of an odonate depositing eggs endophytically is from 5 (Martens, 2001) to 20-30 eggs per minute (Robert, 1958) (the latter with doubts raised by Martens, 2001), so for our specimen we have at least some minutes of a calm environment surrounding the lake.

The nymphs in Confluencia share a morphology related to environments of low flux of energy and the fourth nymph could be related also to a medium flux. The first, second and third nymphs could be related to stagnant waters, and the second, third and fourth also to running waters (Pritykina, 1965). The first nymph could be related to submerged plants and the fourth one to a leafy bottom. No conclusions can be extracted from the absence of adults in Confluencia because it is not a well sampled locality, so it could depend on a sampling or taphonomical bias.

The absence of nymphs in LH seems to be due to a taphonomical rather than a sampling bias because, first, the locality is well sampled (see for plants in Wilf et al., 2003, 2005a, b) and also because of the presence of demic trichoptera larvae cases (Genise and Petrulevičius, 2005). The cases give an idea of a low flux energy environment for LH as they are made by detritus, fragments of insects and plant blades.

Palaeoecology

The presence of endophytic ovipositions in LH and RP establishes some basic facts for the autoecology of the producers and synecology of the lakes and their surroundings. To reach the endophytic oviposition, the tracemaker has to choose the site fulfilling at least three steps (Martens, 2001), i.e., selection of a landing site, choice of the insertion site, and deposition of the eggs. These steps imply three evolutionary aspects, i.e., placing the offspring in the best place, minimisation of the predation risk and minimisation of the time of oviposition to have more time to forage (Martens, 2001). Oviposition scars like LH and RP and others in the fossil record made well over the water on small branches or leaves are not so common in recent Odonata (see Robert, 1958; Corbet, 1962; De Block and Stoks, 2007). As signalled above, leaves with ovipositions are interpreted to be alive when oviposition was done as they show tissue reactions in the margin of the injuries. After oviposition and egg development, the larva has to get out the scar and plunge into the lake. The predation risk in the lake should have been important as there are many recorded specimens of an anuran (frogs) and a catfish in LH (Azpelicueta and Cione, 2011).

In LH the odonatan wings of damselflies, "damseldragonflies" and dragonflies are preserved wrinkled (Fig. 1 B-G, M) and also in some cases fragmented, sharing this attribute with some specimens of Orthoptera. Wrinkled wings are interpreted to be signals of predation probably by birds or mammals that could manipulate their preys with legs or hands eating the bodies and throwing away the crumpled wings (Petrulevičius et al., 2010).

Acknowledgements

I thank the CONICET (National Research Council of Argentina), the ANPCyT (National Agency of Scientific and Technological Promotion of Argentina) and the NSF (National Science Foundation of United States of America) for the support through the grants: PIP CONICET 6393 (completed), PIP CONICET 0377, NSF DEB-0345750 (completed), DEB-0919071/DEB-0918932, and FONCyT PICT-2012-1555. Thanks are also due to Norma Brugni and Pose (deceased, November 5, 2012) from the APB (Asociación Paleontológica Bariloche) as well as to Eduardo "Dudu" Ruigómez and Rubén Cúneo from the MEF (Museo Egidio Feruglio) for loaning the specimens for study, and María Celina Digiani for valuable help and discussion.

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