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Palaeoenvironmental interpretation of an Upper Triassic deposit in southwestern Gondwana (Argentina) based on an insect fauna, plant assemblage, and their interactions

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ABSTRACT

We present a multidisciplinary study of the Potrerillos Formation at the Quebrada del Durazno locality, Cuyana Basin, central-western Argentina, providing novel information on the Upper Triassic biota and its palaeoenvironmental context. The sedimentological and palaeoecological analysis suggests that the Potrerillos Formation section at the Quebrada del Durazno locality represents deltaic plain deposits with significant development of black carbonaceous shales and coal facies formed in semi-permanent swamps and/or ponds within interdistributary bays with intermittent episodes of flooding, allowing the establishment of an abundant hydro-hygrophytic vegetation and creating environments suitable for the development of a rich fauna of insects, spinicaudatans (='conchostracans') and fishes. The entomofauna is represented by hemipterans, odonatans, mecopterans, orthopterans, grylloblattids, coleopterans, dipterans and miomopterans. The plant fossils are typical of the *Dicroidium* Flora (represented by Corystospermales, Peltaspermales, Cycadales, Gnetales, Ginkgoales and sphenophytes). Plant-insect interactions (hole, marginal and surface feeding, piercing and sucking, and oviposition) are described for the first time from the Triassic of the Cuyana Basin, pointing to the importance of the vegetation as a food and shelter, and also providing a suitable reproduction site for several groups of herbivorous insects.

1. Introduction

The Triassic is considered the 'Dawn of Modern Ecosystems' as it marks one of the greatest transitions in the history of life. The Period includes not only the recovery of ecosystems from the end-Permian extinction, but also the appearance and diversification of many of the principal extant groups of terrestrial and marine fauna (Sues and Fraser, 2010).

Triassic strata in Argentina are extensive and provide some of the best exposed sections of this system in Gondwana. Recent exploration carried out at the Puesto Miguez, Quebrada del Durazno and Agua de las Avispas localities (southern flank of the Cerro Cacheuta, Cuyana Basin, Mendoza Province), where the lower Upper Triassic Potrerillos and Cacheuta formations are exposed, led to the discovery of exquisitely preserved associations of fossil insects, many of which are completely new for the Triassic of Argentina (Lara, 2016; Lara and Lukashevich, 2013; Lara and Aristov, 2016; Lara and Wang, 2016; Lara et al., 2015). In particular, the discovery of several layers bearing insect and plant fossils at the Quebrada del Durazno locality provides an unique opportunity for the study and interpretation of past environments.

In this paper, we present a full palaeoenvironmental and palaeoecological reconstruction of the Triassic Quebrada del Durazno locality (Potrerillos Formation) using the fossil insect, palaeobotanical and sedimentological records, with the ultimate goal of shedding new information on the Upper Triassic biota and environmental development in this part of southwestern Gondwana. Furthermore, we discuss the taphonomic processes at the site based on the preservational state of the fossils and facies interpretation of the host strata. As a novel approach, in this study we present the first plant-insect interactions revealed by the flora, in addition to providing insights about the potential trace-marker based on the insects recorded at this fossil assemblage.

To date, only a few studies have described the fossil insects and plant assemblages from other Gondwanan Triassic deposits, namely the Molteno Formation (Karoo Basin) in South Africa (e.g. Anderson and

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Anderson, 1984, 1993a, 1993b; Cairncross et al., 1995; Anderson et al., 1998); the Perth (western) and the Ipswich and Sydney (eastern) basins in Australia (e.g. Retallack, 1977; Haig et al., 2015); the Chañares and Los Rastros formations (Bermejo or Ischigualasto Villa-Unión Basin), and the Cerro Puntudo Formation (Cuyana Basin) in Argentina (e.g. Mancuso, 2009; Mancuso and Marsicano, 2008; Mancuso and Casselli, 2012; Mancuso et al., 2007, 2014).

2. Geological setting

The elongate NW-SE trending basins on the western margin of southern South America were developed during Triassic times as a consequence of the early breakup of Gondwana by the extensional relaxation that induced rapid subsidence and development of fault-bounded half-graben troughs in west Argentina and Chile (Uliana and Biddle, 1988; López Gamundí, 2010).

The Cuyana Basin (also named 'Cuyo Basin') is the largest Triassic rift basin of central-western Argentina. It extends through Mendoza, San Juan and San Luis provinces (>400 km along a NW-strike) and includes several depocenters, such as the Potrerillos-Cacheuta sub-basin (see Supplementary Information, Fig. S1). This basin has a great economic importance because of its hydrocarbon resources (Chebli et al., 2001; López Gamundí, 2010) and also remarkable in its diverse fossil content (see Stipanicic and Marsicano, 2002, and references therein). Previous studies (i.e., Kokogian and Mancilla, 1989; Kokogian et al., 1993; Barredo, 2012) have given full details of the depositional and tectonic evolution of the sedimentary and volcaniclastic Triassic infilling of the Potrerillos-Cacheuta sub-basin.

The basement of the Cuyana Basin consists of Palaeozoic metasedimentites and magmatic and effusive rocks of the Choiyoi Group (see Supplementary Information, Fig. S2). The whole Triassic succession of the Potrerillos-Cacheuta sub-basin is represented by the Uspallata Group. The complete lithostratigraphic units are well exposed in the Potrerillos area (see Supplementary Information, Fig. S1). The Triassic column starts with reddish conglomerates of alluvial fan facies of the Río Mendoza Formation that laterally interfinger with multicolored mudstones, fine-grained sandstones, and tuffs and stromatolitic limestones of ephemeral-fluvial and playa-lake deposits of the Cerro de Las Cabras Formation. This first sequence of Middle Triassic age is separated by a regional unconformity from the second early Upper Triassic depositional fining-upward succession on a smoother relief composed by the Potrerillos Formation characterized by fluvial conglomerates at the base intercalated with light greenish cross-bedded sandstones, and light tuffaceous sandstones of perennial braided river origin; these fluvial deposits grade to greenish-gray laminated siltstones and sandstones interbedded with black bituminous shales and tuffs, related to high-sinuosity river systems. These facies laterally interfinger and are covered by the widespread lacustrine black shales of the Cacheuta Formation. Finally, the red sandstones, mudstones, and tuffs of the Río Blanco Formation represent the instauration of a fluvial-deltaic system over the lacustrine black shales (Kokogian et al., 1993, 1999).

The Potrerillos Formation is constrained to late Middle Triassic (Late Ladinian) to early Upper Triassic (Carnian) in age. Spalletti et al. (2008) determined U—Pb SHRIMP 239.2 ± 4.5 Ma, 239.7 ± 2.2 ages on tuff beds from the base of the unit at Potrerillos locality. This is also supported by the palynological evidence, ranging in age as a whole from Late Ladinian to Carnian (Zavattieri and Batten, 1996). Zavattieri and Rojo (2005) and Zavattieri and Prámparo (2006) studied palynological assemblages from the uppermost part of the Potrerillos Formation strata outcropping at the south of the Cacheuta Hill, and assigned them to Carnian in age.

3. Materials and methods

The fossils studied herein (insects, plants, spinicaudatans and fish remains) were recovered as impressions from the deltaic cycle of >22 m thick represented in the uppermost strata of the Potrerillos Formation.

The macroflora consists of impression fossils, partially fragmentary, of several leaves, a few isolated seeds and various shoots. For the plant-insect interactions, a total of 56 plant specimens were thoroughly inspected for insect damage with the aid of a magnifying lens under strong unilateral illumination. Plants and plant-insect interactions were photographed with a Canon EOS 40D with an EF 50 mm macro lens and external flash unit. Detailed analysis and illustration of the material were undertaken with the aid of a Nikon SMZ800 stereomicroscope and an attached Nikon DS-Fi1-U2 digital camera. We adhere to the systematic classification proposed by Stewart and Rothwell (1993) and subsequently adopted by Zamuner et al. (2001) for plants, and follow the classification of "damage types" (Labandeira et al., 2007) for the plant-insect interactions.

More than 90 specimens of insect fossils have been collected at the Quebrada del Durazno locality, mostly consisting in impressions of the wings and elytrae, and less frequently, parts and complete bodies. All the material used in this study belongs to Lara (2016), with the exception of nine specimens from previous collections (Wieland, 1925; Cabrera, 1928; Martins-Neto and Gallego, 1999; Martins-Neto et al., 2008). The insects were examined using a Leica M50 stereomicroscope, measured with a caliper and software (LAS EZ, Version 3.2.1), and photographed using a Leica EC3 digital camera.

The specimens included in this paper are housed in the following repositories: Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-CCT-CONICET) and Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano' in Mendoza Province, under denomination IANIGLA-PI and MCNAM-PI (for the insects) and IANIGLA-PB (for the plants); Universidad Nacional del Nordeste in Corrientes Province, PZ-CTES (insects and spinicaudatans); and at the Departamento de Paleontología, Invertebrados, Museo de La Plata (Buenos Aires), MLP (insects).

4. The Quebrada del Durazno section

At the southern end of the Precordillera in Mendoza Province, approximately 35 km to the southwest of Mendoza city, the Triassic units of the Uspallata Group form continuous exposures along the south and west flanks of the Cacheuta Hill (Cerro Cacheuta).

The Potrerillos Formation is partly exposed in this area (lacking approximately the lower third of the unit), and is succeeded by lacustrine black shales of the Cacheuta Formation. Both units, interpreted as fluvio-deltaic-lacustrine cycles, crop out in this area forming several homoclines that dip in a SSE direction with variable inclination (ca. 25°–28°) and thickness (Fig. 1). Morel (1991, 1994), Zavattieri and Prámparo (2006) and Gallego et al. (2011) gave detailed descriptions of the lithology, diverse fossil contents and interpretation of the sedimentary environments of the Potrerillos and Cacheuta formations exposed at the two classical sections on the southern flank of the Cacheuta Hill called "Agua de las Avispas" and "Puesto Miguez" (also known as "Minas de Petróleo" or former "YPF Administration", sensu Jain, 1968, Stipanicic et al., 1996) (Fig. 1).

In this contribution, we provide a thorough characterization of the litho- and biofacies of an intermediate section named "Quebrada del Durazno" (33°04′74″S/69°07′18″ W). Fossils described herein were recovered from the deltaic cycle represented in the uppermost strata of the Potrerillos Formation (Figs. 1, 2).

The studied section is a coarsening-upward sequence >22 m thick (Figs. 2, 3). It begins with massive banks of bentonites as the base of the profile, followed by thick packages of tabular, horizontally laminated and rhythmic dark-gray to gray-brownish carbonaceous shales, and thin coals interbedded with laminated to massive dark-gray claystones and siltstones. These basal packages constitute predominantly swamp/pond deposits of delta plain environments, and host most of the plants, insects, spinicaudatans (='conchostracans') and fish remains (cf.

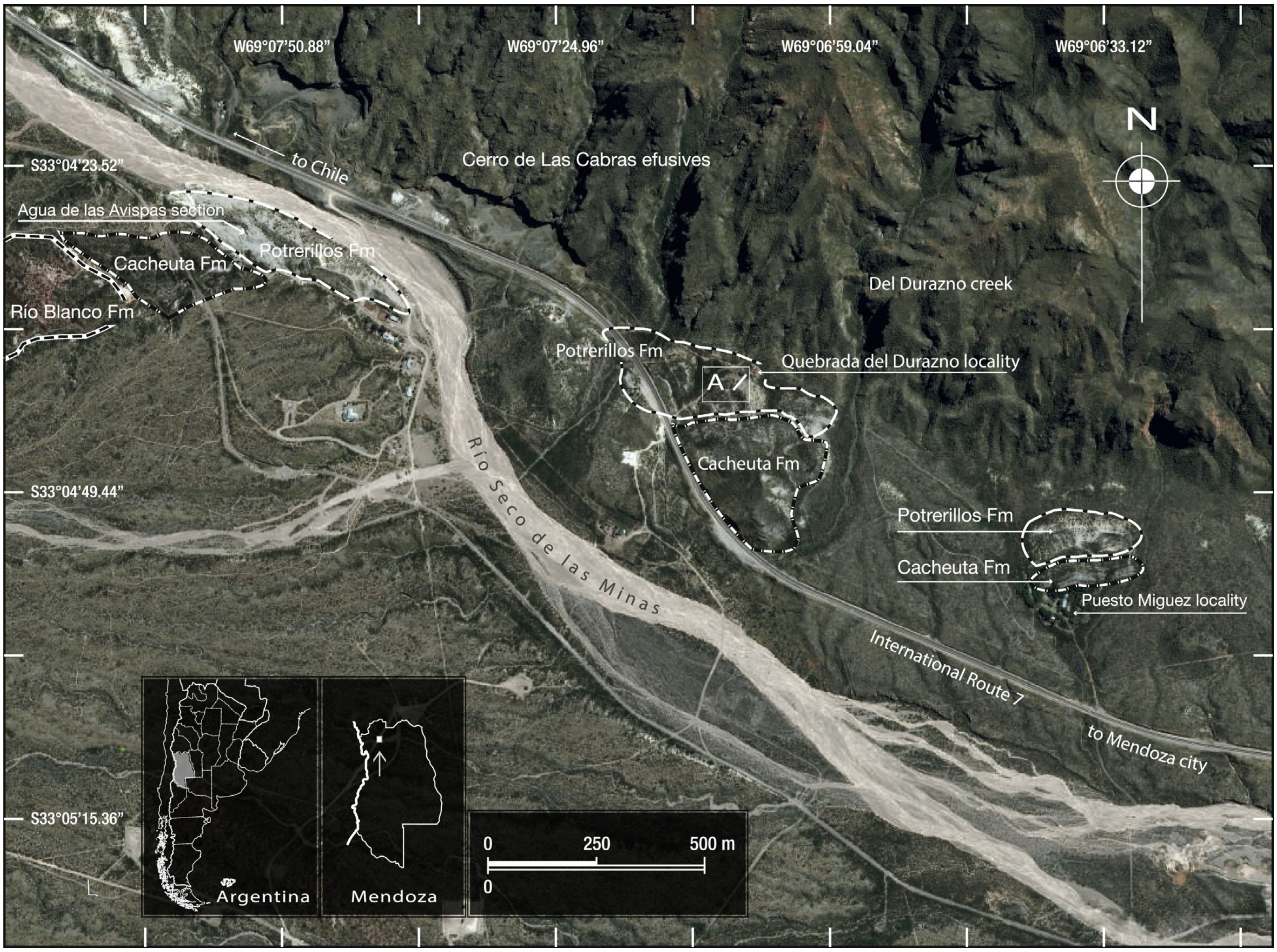


Fig. 1. Aerial view of the southern flank of the Cerro Cacheuta, Mendoza Province (Argentina) showing the mentioned outcropping stratigraphic units. The studied section of the Potrerillos Formation (Carnian) at the Quebrada del Durazno locality is indicated with "A".

Neochallaia sp. López-Arbarello pers. comm., 2017) (Figs. 2, 3, 4). Towards the top of the sequence, there are tuffaceous sandstones, laminated mudstones and sporadic immature palaeosols, and thin carbonaceous mudstones that are interpreted as stream distributary fills, overbank sediments and interdistributary bay deposits of a delta plain (Figs. 2, 3, 4). The studied section is capped by planar to- cross-laminated coarse-grained sandstones, culminating with clast-supported conglomerates and cross-bedded coarse-grained sandstones representing the prograding mouth bars of the delta front (Figs. 2, 3, 4). This uppermost deltaic cycle at the top of the Potrerillos sequence interdigitates upwards and southwards into the lacustrine black bituminous shales of the Cacheuta Formation, which characterize the maximum flooding event.

4.1. Facies associations

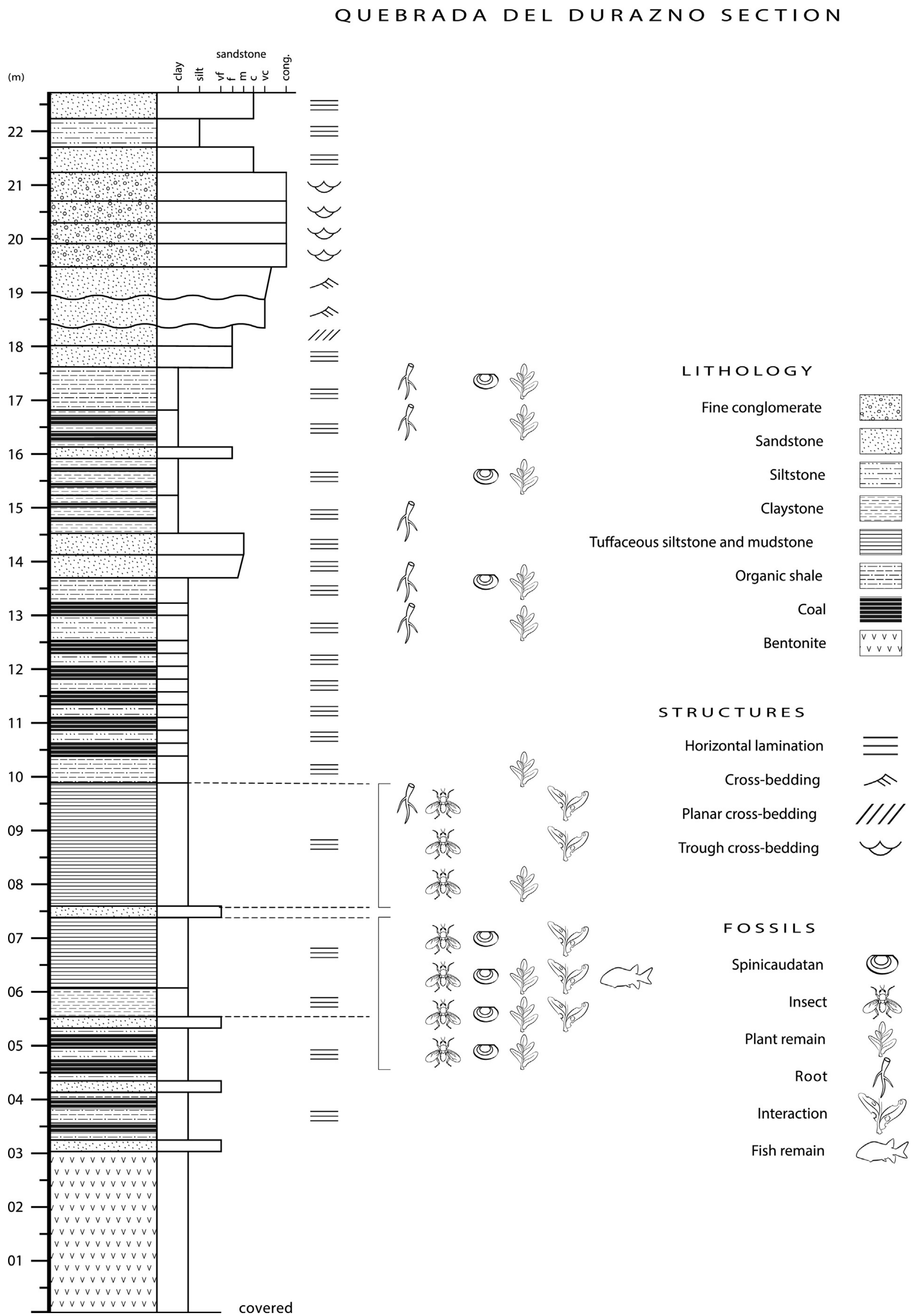
Three facies associations were recognized in the Quebrada del Durazno section (Tables 1 and 2). These form one of the above-mentioned deltaic cycles.

4.1.1. Coal swamps within delta plain facies association

"Carbonaceous dark shales and coals" (FA-A1; Tables 1, 2 and Fig. 3A, C): Dominated by finely (rhythmic) horizontally (micro) laminated dark-gray to black carbonaceous claystones to brownish carbonaceous siltstones with intercalations of coals, interbedded with massive or parallel finely laminated very fine grained tabular sandstones (Sm-Sl); in the basal part of the package, massive gray bentonitic layers are interbedded regularly. The package of dark carbonaceous claystones and siltstones includes plant fragments and abundant spinicaudatans and insects.

"Massive to finely laminated mudstones and very fine sandstones" (FA-A2; Tables 1, 2 and Fig. 3B): Consists of massive gray- to dark-gray claystones and siltstones (Fm) interbedded with very fine grained sandstones (Sl), commonly intercalated with A1. The strata are mainly massive or laminated without visible gradation. They form tabular beds that range in average thickness from 2 to 10 cm. Well-preserved plant fragments and insect remains, abundant large, commonly articulated spinicaudatans (*Euestheria forbesi*) and fish remains are found in these beds.

This facies association is interpreted to represent deposits of coal swamps, waterlogged and/or poorly drained areas within the lower delta plain. The formation of coal suggests locally abundant organic matter (plant remains) and reducing conditions at the bottom of small lakes or swamps indicated by the presence of scarce pyrite and small iron nodules at the base of the profile. Rhythmic coal beds and carbonaceous mudstones suggest suspension settling but frequent gentle clastic influx into the swamp to maintain a constant critical water level. Abundance of articulated spinicaudatans and fish remains point to quiet and stable water conditions. The common presence of insects and identifiable plant remains with damage features suggests well-developed riparian vegetation supporting a diverse insect fauna in the vicinity of the depositional setting.


QUEBRADA DEL DURAZNO SECTION
(m)
sandstone
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01
covered
LITHOLOGY
Fine conglomerate
Sandstone
Siltstone
Claystone
Tuffaceous siltstone and mudstone
Organic shale
Coal
Bentonite
STRUCTURES
Horizontal lamination
Cross-bedding
Planar cross-bedding
Trough cross-bedding
FOSSILS
Spinicaudatan
Insect
Plant remain
Root
Interaction
Fish remain

4.1.2. Delta plain facies association

"Finely laminated mudstones and fine-grained sandstones" (FA-B1; Tables 1, 2 and Fig. 3G): This facies association consists of whitish gray- to gray-yellowish (dark-gray when fresh) very fine grained parallel-laminated sandstones (Sl) and laminated whitish-gray tuffaceous siltstones (Fl) interbedded with dark-gray carbonaceous claystones and siltstones (Fm) bearing plant remains and few spinicaudatans. This package is tabular to slightly lenticular or laterally wedged with erosive bases. Thin massive to laminar fine grained tuffaceous sandstones are more common towards the upper part of the package (Sl). This facies is interpreted to represent flood deposits and sedimentation from weak traction currents as overbank deposits that formed swamps or ponds where the vegetation developed abundantly and diverse arthropods lived within the delta plain.

"Carbonaceous mudstones and fine-grained sandstones" (FA-B2; Tables 1, 2 and Fig. 3D): This facies is dominantly represented by an alternation of brownish-gray finely laminated siltstones and claystones (Fl) interbedded with thin levels of massive fine-grained sandstones (Sl). Bed thickness decreases upwards where massive brownish-gray mudstones (Fm) with fine roots mainly preserved in the plane of stratification. Towards the top, they are succeeded by gray- to brownish-gray strongly weathered finely laminated siltstones (shales) (Fl) bearing abundant carbonaceous well-preserved plant remains that locally form thin coal layers. This facies is interpreted as low delta plain deposits with incipient palaeosol development having marked paludal features. The facies associations B1 and B2 alternate and repeat throughout the basal and middle part of the studied section.

4.1.3. Delta front facies association

"Fine- to medium-grained sandstones and siltstones" (FA-C1; Tables 1, 2 and Fig. 3E, F): Characterized by an alternation of gray to dark-yellowish (ochre) massive, fine- to medium-grained sandstones (Sm), mainly flat bedded and having erosive bases interbedded with gray- to dark-gray finely laminated siltstones (Fl). Medium- to coarse-grained, planar cross-bedded sandstones become more common towards the top of the package (Sp). The composition and architecture of this package suggest deposition in channels that probably migrated laterally and interdigitated with finer sediments within the delta plain (interdistributary bay). The tabular laminated packages of fine- to medium-grained sandstones are interpreted as crevasse-splay deposits (Fig. 3E).

"Coarse tuffaceous sandstones and gravelly sandstones" (FA-C2; Tables 1, 2 and Fig. 3H): Packages of coarse- to very coarse tuffaceous and arkosic sandstones (Sp), with some small lenses of fine gravel (SGp), planar cross-laminated and bedded, amalgamated, lenticular beds (in wedge-sets) (St), interpreted as distributary channels within the delta front, capped by progradating mouth bars (C3).

"Conglomerates" (FA-C3; Tables 1, 2 and Fig. 3I): Packages of lenticular banks (1 to 2 m thick on average) of fine- to medium-grained polymictic clast-supported conglomerates with a coarse sandy matrix. Each bank has planar- to trough cross-bedding (Gp-Gt). The clasts are sub-angular to sub-rounded, range from fine pebbles to small cobbles (2 cm average), and they are composed mainly of basalts, vein quartz, and acid to intermediate volcanic rocks. These conglomeratic banks have erosive bases, and they are amalgamated laterally by inclined surfaces indicating lateral accretion. Between the conglomerate banks, especially towards the top, gravelly and coarse sandstones with planar and trough cross-bedding become predominant. This upward-coarsening sequence is consistent with the prograding distributary mouth bar of delta front (high energy) deposits.

5. Insect fauna

In recent years, the southern flank of the Cerro Cacheuta in the Cuyana Basin (Mendoza, Argentina) has yielded several hundred insect specimens, becoming the most important Triassic insect site in South America and one of richest in the Southern Hemisphere (Lara, 2016). The first described Triassic insects from Argentina, *Tipuloidea rhaetica* Wieland, 1925 (Hemiptera) and *Tipulidites affinis* Wieland, 1925 (Mecoptera), both initially described as dipterans (Wieland, 1925; Lara and Lukashevich, 2013) come from this basin. To date, >123 specimens, 10 orders and 21 species have been collected and described from the Puesto Miguez, Quebrada del Durazno, and Agua de las Avispas localities, Potrerillos-Cacheuta section (lower Upper Triassic) (Lara, 2016).

The fossil insects from the Quebrada del Durazno locality (Cerro Cacheuta, Cuyana Basin) examined in this study are assigned to eight orders, eight families and 13 species, based on >90 collected specimens (Table 3) (Figs. 5, 6) (Lara, 2016; Lara and Aristov, 2016). Fossil insects come from five beds in the uppermost part of the Potrerillos Formation, where there is also a rich representation of plant remains of the well-known *Dicroidium* Flora, spinicaudatan carapaces and fish remains (Figs. 2, 7).

5.1. Terrestrial entomological association (allochthonous or para-autochthonous elements)

The terrestrial insect component is constituted by sclerotized forewings of hemipterans (Scytinopteridae, Eoscarterellidae, Protopsyllidiidae, Dysmorphoptilidae, Chiliocyclidae), followed in abundance by membranous forewings of odonatans, mecopterans (Permochoristidae), orthopterans (Haglidae), dipterans (Hennigmatidae), grylloblattids (Geiniziidae), miomopterans and elytra of coleopterans (Figs. 5, 6) (Martins-Neto et al., 2008; Lara, 2016; Lara and Lukashevich, 2013; Lara and Aristov, 2016; Lara and Wang, 2016; Lara et al., 2015). Scytinopterids (Hemiptera) are common elements in Triassic entomological associations, owing to the coriaceous nature of their tegminous forewings. The modified 'knob' mechanism for the forewing fixation on the mesopleuron acquired by this group is interpreted as an adaptation for subelytral air storage, possibly in relation to an amphibious habit (Shcherbakov, 2000; Shcherbakov and Popov, 2002). The existence of numerous and well-preserved forewings of hemipterans (Scytinopteridae) in this locality supports the idea of a waterside habitat life for scytinopteroids (Shcherbakov and Popov, 2002).

The recorded insect orders inhabited either open or closed humid forests, associated with herbaceous-shrub by vegetation growing close to water bodies on the delta plains (Rentz and Ingrisch, 2009; Cui, 2012) (Fig. 8). According to Labandeira (2006), detritivory was the principal dietary guild of mecopterans, herbivory for hemipterans, dipterans, beetles, orthopterans and miomopterans, and a predatory behaviour is interpreted for grylloblattids (ground diurnal predators, Cui, 2012) and odonatans (probably active aerial ambushed predators of others flying insects as modern odonatans). The abundant presence of phytophagous and detritivorous groups of insects supports the existence of a rich flora at the Quebrada del Durazno locality.

Certain forewings recorded at the Quebrada del Durazno locality (Hemiptera, Mecoptera, Grylloblattida, Orthoptera and Mecoptera, Fig. 5B, E, G, H, L) show color patterns that may indicate camouflage adaptations against predators (Lara and Aristov, 2016; Lara and Wang, 2016). Futhermore, *Miomina mendocina* (Miomoptera, Fig. 5) presents a similar venation pattern to *Dicroidium odontopteroides* leaves, suggesting

Fig. 2. Sedimentologic profile of the Potrerillos Formation outcrops (Carnian) at the Quebrada del Durazno locality, south of the Cerro Cacheuta, Mendoza Province (Argentina) showing fossiliferous levels.

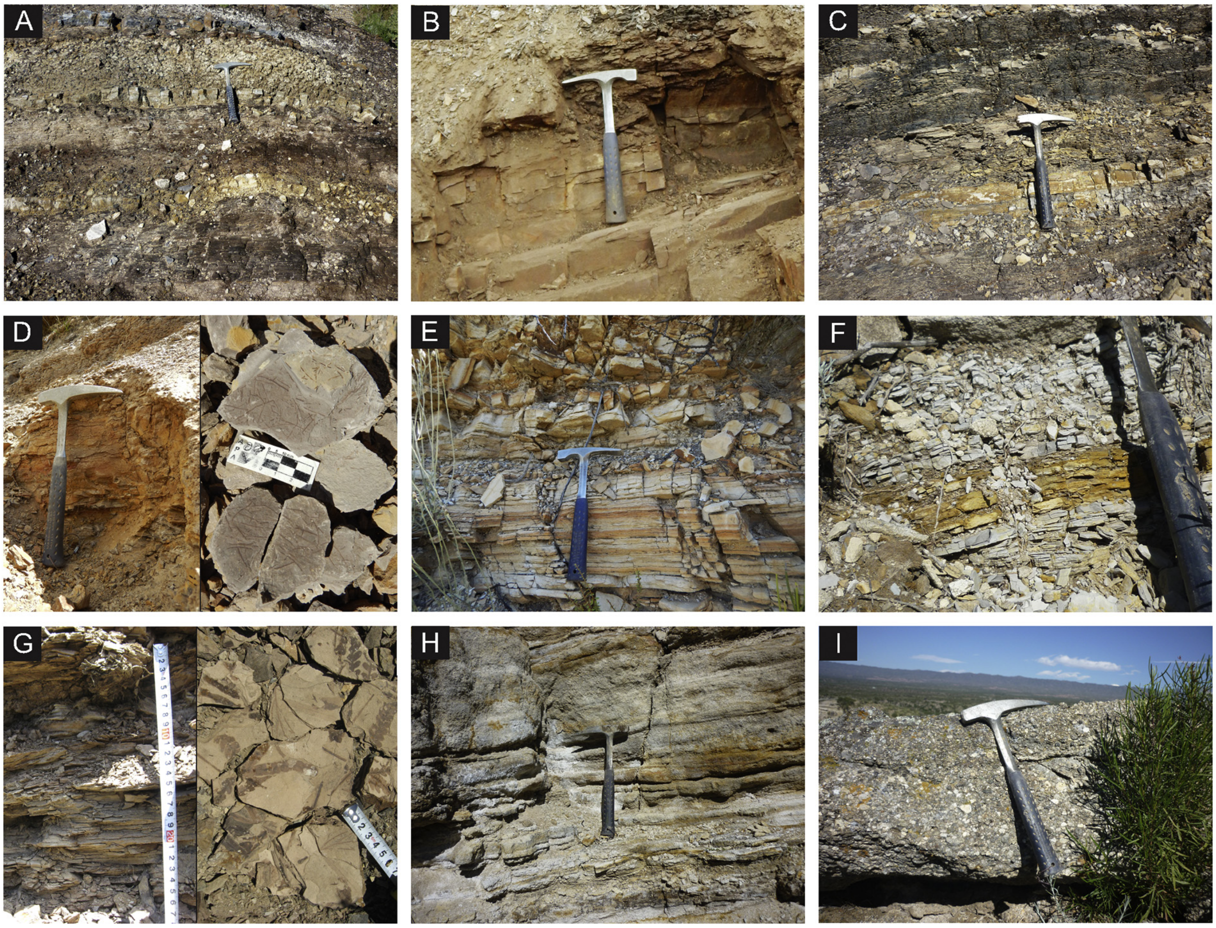

Fig. 3. Main lithologies and sedimentary structures of the recognized facies associations at the Quebrada del Durazno section (see Tables 1 and 2). A. Facies association A1 at the base of the profile showing alternating finely (rhythmic) horizontally (micro) laminated dark-gray to black carbonaceous claystones and carbonaceous siltstones with intercalations of coal levels, interbedded with massive very fine-grained tabular sandstones and massive gray bentonitic levels. B. Facies association A2, showing massive tuffaceous light-gray to dark-gray claystones and tuffaceous very fine-grained sandstones in tabular beds, bearing diverse fossil remains (see Table 2). C. Facies association A1 mainly dominated by finely (rhythmic) horizontally (micro) laminated dark-gray to black carbonaceous claystones dominated by coal levels. D. Facies association B2, massive to finely laminated brownish-gray to brown-yellowish mudstones upwards interbedded with thin (micro) laminated carbonaceous siltstones showing details of the fine roots. E–F. Facies association C1, showing light gray to light brownish parallel laminated fine sandstones interbedded with light gray siltstones that form tabular to lenticular packages. G. Facies association B1, parallel brownish-gray to brown-yellowish mudstones in tabular packages with abundant carbonaceous plants as shows in detail. H. Facies association C2, showing medium to coarse tuffaceous sandstones, small lenses of fine gravel, planar cross-laminated and amalgamated tabular to lenticular packages; I. Facies association C3, clast-supported polymictic conglomerate with coarse sandy matrix showing sub-angular to sub-rounded clasts, ranging from fine pebbles to small cobbles (2 cm average), mainly composed of basalts, quartz veins, and acid to intermediate volcanic rocks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 4. General view of the Potrerillos Formation (Carnian) at the Quebrada del Durazno section, Mendoza Province (Argentina) showing the fossil levels.

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Table 1
Lithofacies recognized at the Quebrada del Durazno locality (Upper Triassic), Cuyana Basin, Mendoza Province (Argentina).

Codes	Main descriptive characteristics of lithofacies	Depositional processes
Flc	Thin, black to brown coalified to highly carbonaceous laminae of coal (coal shale)	Waterlogged, poorly drained
Fm	Massive siltstones and claystones	Suspension settling of clay/silt-particles
Fl	Finely laminated siltstones and claystones	Suspension settling of clay/silt-particles
Sl	Fine to very fine-grained laminated-to cross-laminated sandstones	Laminar flow
Sm	Medium- to coarse-grained sandstones, massive, flat bedded sandstones, poorly sorted	Plane-bed flow or (high) laminar flow
Sp	Planar-cross-bedded sandstones, medium- to coarse-grained, moderately to poorly sorted	Bed-load traction deposits
St	Trough-cross-bedded sandstones, coarse-to very coarse-grained, commonly contain scattered granule grains	Bed-load traction deposits
SGp	Pebbly sandstones, planar-cross-bedded; coarse- to very coarse-grained, poorly sorted, arkosic. Wedge sets	Bed-load traction deposits
Gp/Gt	Moderately well-sorted, clast-supported, planar-cross-bedded grading to trough-cross-bedded clast-supported conglomerates with coarse matrix. Cobble to pebble clasts subangular to subrounded	Highly (hyperconcentrated) flow regime

Note: Lithofacies codes, description (cf. Miall 1984, 1996 with modifications) and depositional processes.

Table 3
Triassic insects described at the Quebrada del Durazno locality (Upper Triassic), Cuyana Basin, Mendoza Province (Argentina).

Orders	Species	References
Orthoptera	*Notopamphagopsis bolivari*	Cabrera, 1928
	Notopamphagopsis? sp.1	Martins-Neto et al., 2008
Hemiptera	*Gallegomorphoptila acostai*	Martins-Neto et al., 2003, Martins-Neto and Gallego, 2006
	Argentinocicada magna	Martins-Neto and Gallego, 1999
	Argentinocicada minima	
	Potrerillia nervosa	
	Cacheutacicada kurtzae	Martins-Neto et al., 2008
	Duraznoscarta ramosa	Lara and Wang, 2016
Miomoptera	*Miomina mendocina*	Martins-Neto and Gallego, 1999
Coleoptera	*Argentinosyne duraznoensis*	Martins-Neto et al., 2008
Diptera	*Trihennigma zavattierii*	Lara and Lukashevich, 2013
Mecoptera	*Argentinopanorpa miguezi*	Lara et al., 2015
Grylloblattida	*Permoshurabia argentina*	Lara and Aristov, 2016

mimicry was a common antipredatory resource among these groups of insects.

5.2. Aquatic entomological association (autochthonous elements)

The aquatic insect component at the Quebrada del Durazno is less abundant than the terrestrial one, comprising autochthonous elements represented only by nymphs of odonatans (probably active predators) and schizocoleid coleopterans (Figs. 5, 6). The rarity and low diversity of aquatic insects at this Triassic site could be related to a collection bias, poor preservation of the material and/or to the under-representation of aquatic groups in the lacustrine fossil record (see Wilson, 1988).

6. Fossil plants

The plant macrofossil abundance and richness of the Potrerillos Formation is reflected in many published studies (Jain and Delevoryas, 1967; Zamuner et al., 2001; Artabe et al., 2007; Morel et al., 2010, 2011; among others). At least 62 species of pteridosperms, sphenophytes, cycadophytes, ginkgophytes, ferns, and conifers are described from the many localities at which this formation is exposed. At the Quebrada del Durazno locality, the macroflora consists of

Table 2
Summary of the Quebrada del Durazno sedimentary facies associations (Upper Triassic, Cuyana Basin, Argentina) and corresponding depositional environment interpretation.

Facies associations (codes)	Lithology	Sedimentary structures	Geometry	Fossil content	Interpretation depositional setting
A1 (Flc, Fl)	Dark-gray to black carbonaceous claystones to gray-brownish coal shales and finely laminated dark-gray mudstones, interbedded with bentonitic beds at the base (Figs. 5A, C)	Horizontal micro-lamination and rhythmic	Tabular	Highly carbonized to coalified plant debris. Plants, insects, spinicaudatans	Peat/coal swamps/ponds, waterlogged, poorly drained, lower delta plain
A2 (Fm, Fl, Sl)	Dark-gray to light-gray mudstones and thin siltstones interbedded with very fine-grained sandstones (Fig. 5B)	Horizontal lamination to massive	Tabular	Plants, insects, fish remains and abundant spinicaudatans	Ponds/swamps; shallow embayment by growth of deltaic deposits (deltaic flooding pulses), lower delta plain
B1 (Fl, Sl)	Dark-gray to light brownish carbonaceous claystones and siltstones interbedded with very fine to fine-grained sandstones (Fig. 5G)	Horizontal lamination	Tabular	Carbonaceous plant debris and spinicaudatans	Over-bank deposits (or crevasse-splays) within delta plain, includes swampy or pond deposits
B2 (Fm, Fl, Sl)	Brownish-gray to brown-yellowish mudstones, upwards interbedded with thin (micro) laminated carbonaceous siltstones (Fig. 5D)	Finely laminated	Tabular	Fine roots and carbonaceous weathered plant remains	Soils overlain by marsh bodies. Lower delta plain within interdistributary bay
C1 (Fl, Sl, Sm, Sp)	Light-gray to light brownish tuffaceous fine- to medium-grained sandstones interbedded with siltstones, upwards medium- to coarse-grained sandstones (Figs. 5E, F)	Planar laminated	Tabular to lenticular	–	Crevasse-splays deposits within interdistributary bay
C2 (Sm, Sp, St, SGp)	Light gray tuffaceous medium- to coarse-grained sandstones to very coarse grained to pebbly sandstones at the top of the package (Fig. 5H)	Planar cross-laminated, occasionally trough cross-bedded	Lenticular, wedge sets	–	Distributary channels within delta front with progradation to mouth bars
C3 (Gp, Gt)	Moderately well sorted, clast-supported conglomerates with coarse sand matrix. Cobble to pebble clasts sub-angular to sub-rounded (Fig. 5I)	Planar cross-bedded grading to trough cross-bedded	Tabular wedge sets	–	Prograding distributary mouth bars. Delta front shallowing-upward trend

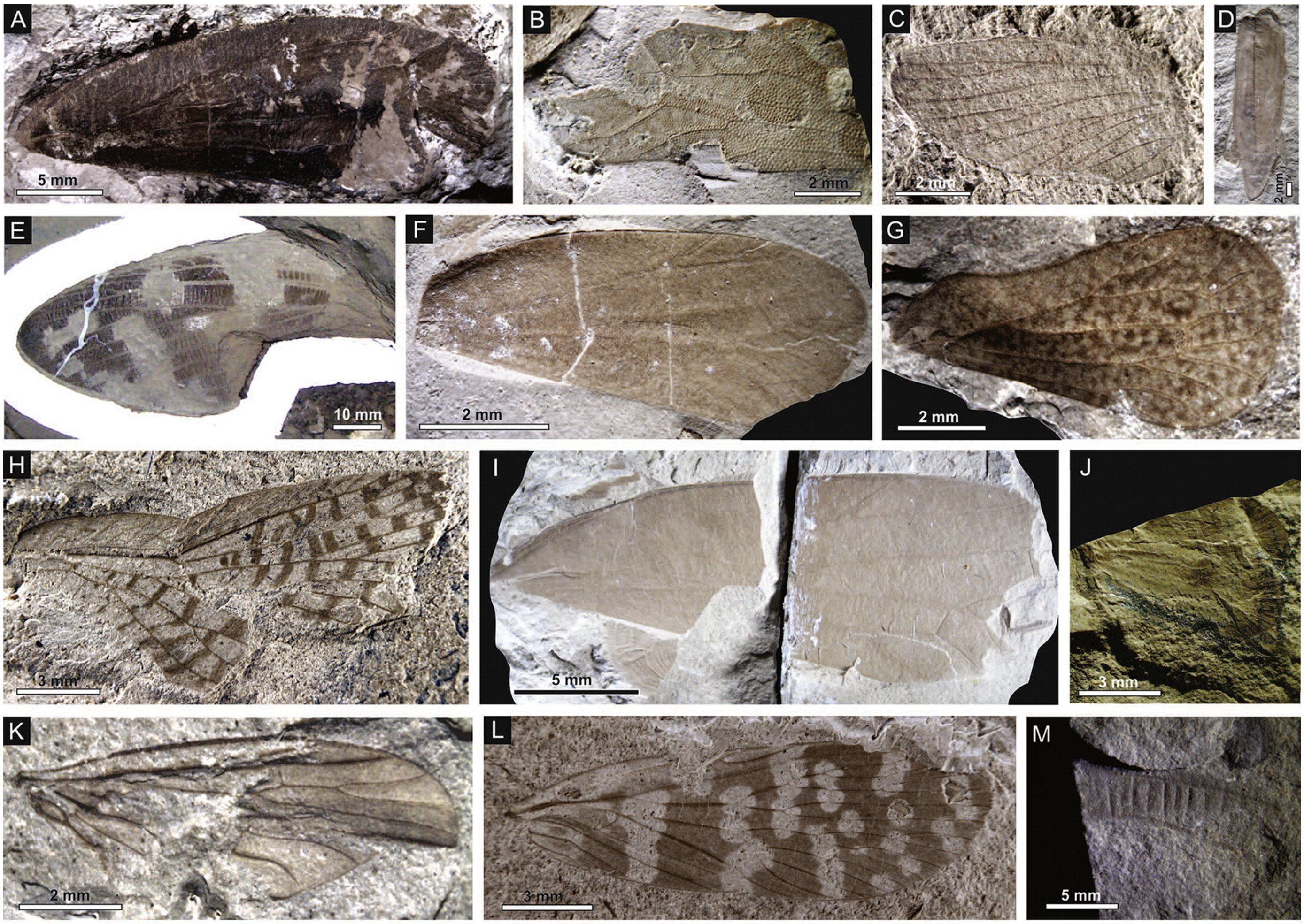

Fig. 5. Fossil insects described at the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina). A-*Argentinocicada magna* Martins-Neto and Gallego; PZ-CTES-5729. B-*Gallegomorphoptila acostai* Martins-Neto and Gallego, Martins-Neto et al.; PZ-CTES-5772. C-*Miomina mendocina* Martins-Neto and Gallego; PZ-CTES-5731. D-*Argentinosyne duraznoensis* Martins-Neto et al.; MCNAM-PI 24304. *E-Notopamphagopsis bolivari* Cabrera; MLP 4354. F-*Argentinocicada minima* Martins-Neto and Gallego; PZ-CTES-5733. G-*Duraznoscarta ramosa* Lara and Wang; IANIGLA-PI 3028. H-*Permoshurabia argentina* Lara and Aristov; IANIGLA-PI 1029. I-*Cacheutacicada kurtzae* Martins-Neto et al.; MCNAM-PI 24305. J-*Potrerillia nervosa* Martins-Neto and Gallego; PZ-CTES-5728. K-*Trihennigma zavattierii* Lara and Lukashevich; MCNAM-PI 24607. L-*Argentinopanorpa miguezi* Lara et al.; MCNAM-PI 24608. M- *Notopamphagopsis?* sp.1 Martins-Neto et al.; CTES-PZ 7390.

impression fossils related to Sphenopsida (Equisetales) and Gymnospermopsida (Corystospermales, Peltaspermales, Cycadales, Gnetales and Ginkgoales) (Fig. 9, Table 4). The specimens recovered are partially fragmentary suggesting at least a short distance transport before the material was buried; however, the fine-grained sediments in which they were deposited allowed the preservation of epidermal tissues in exquisite detail in some specimens (Fig. 10), revealing trichomes, stomata and cell patterns, aiding their identification.

Dicroidium floras were dominant throughout most of the Triassic of Gondwana, with corystosperms and peltasperms playing a leading role, alongside cycadeoids, gnetaleans, ginkgos, conifers, ferns and sphenophytes. Their widespread Southern Hemisphere distribution, however, did not necessarily imply homogeneity. In fact, some authors have recognized several types of vegetational assemblages in these floras, ranging from a monospecific or low-diversity to a moderately or even highly diverse composition (Retallack, 1977; Anderson and Anderson, 1983; Wing and Sues, 1992).

Previous studies based on floras recovered from the Potrerillos Formation strata at the Cerro Cacheuta (Morel, 1994, Morel et al., 2010, 2011; Table 4) have interpreted three "palaeo-communities", based on fossil associations to lithofacies and palaeoenvironments (see Artabe et al., 2001). In this manner, one palaeo-community was interpreted to represent herbaceous and shrubby vegetation growing in periodically flooded lowlands, with dominance of sphenophytes (*Equisetites*), gnetaleans (*Yabeiella*) and pteridosperms (*Johnstonia*, *Xylopteris*) ("Palaeo-community 13" sensu Artabe et al., 2001); another palaeo-community constituted a deciduous forest dominated by conifers (*Heidiphyllum*) and ginkgoaleans (*Baiera*, *Ginkgoites*), with an understorey of ferns and shrubby pteridosperms (*Pachydermophyllum*) growing in bars and deposits associated to the distributary channels ("Palaeo-community 14" sensu Artabe et al., 2001); and a third palaeo-community was composed mostly of seed ferns (*Dicroidium*, *Johnstonia*, *Pachydermophyllum*) and gnetaleans (*Yabeiella*), with secondary elements, such as ferns (*Cladophlebis*) and conifers (*Heidiphyllum*), developing at interdistributary deltaic plains experiencing sporadic flooding events ("Palaeo-community 15" sensu Artabe et al., 2001).

The most common elements we recovered from the Quebrada del Durazno locality (Fig. 9) are the corystosperms (i.e., several *Dicroidium*, *Johnstonia* and *Xylopteris* species) (Fig. 9C–I), followed by the gnetaleans

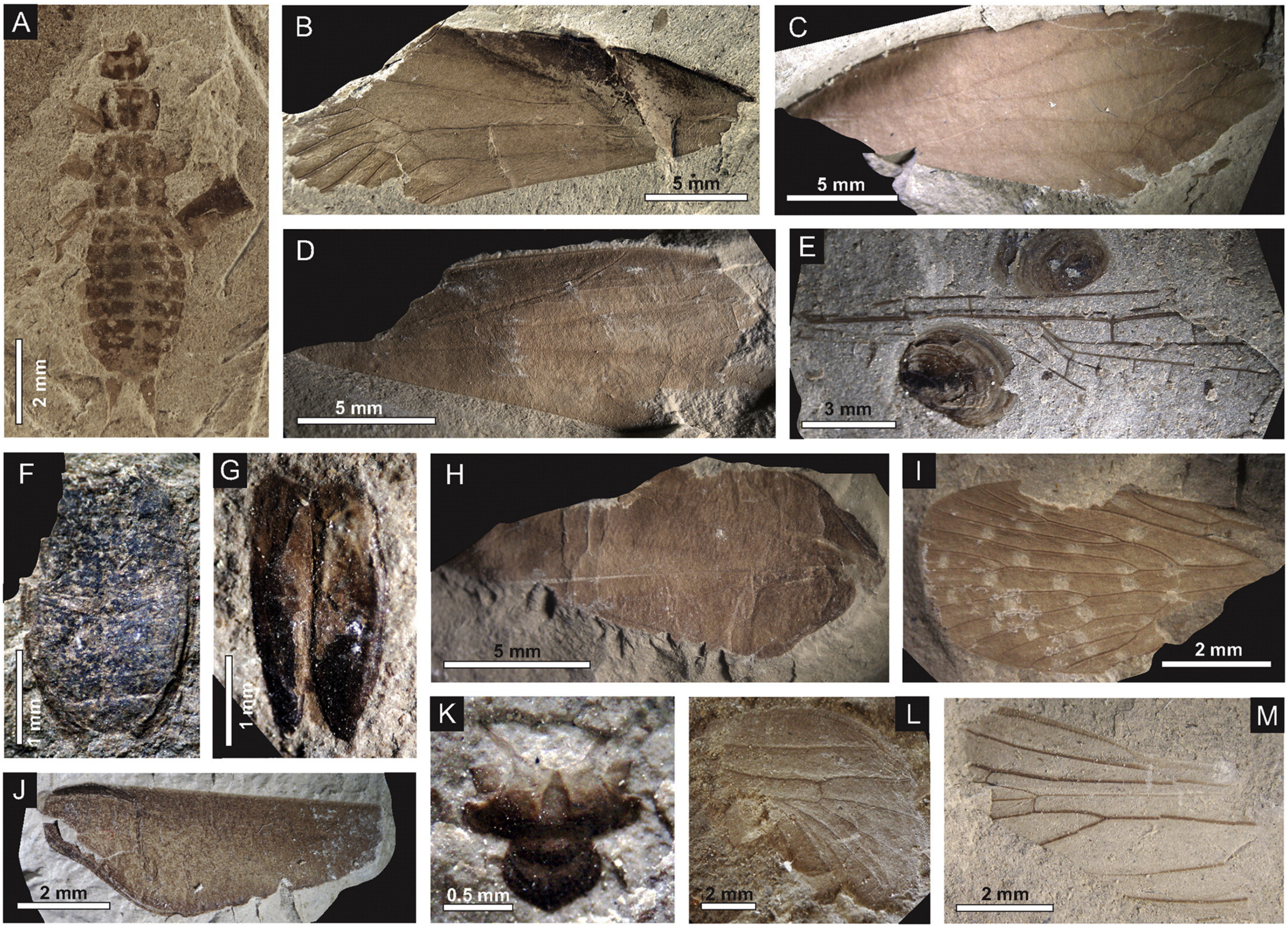

Fig. 6. Fossil insects described at the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina) (Lara et al., 2012; Lara, 2016). A-Odonata nymph, IANIGLA-PI-1017. B-Scytinopteridae sp. 1 forewing, IANIGLA-PI 1030. C-Scytinopteridae sp. 2 forewing, IANIGLA-PI 1039. D-Scytinopteridae sp. 3 forewing, IANIGLA-PI 1071. E-Odonata forewing, IANIGLA-PI-1016. F-Coleoptera body, IANIGLA-PI 1048. G-Coleoptera elytrae, IANIGLA-PI 1046. H–Scytinopteridae sp. 4 complete forewing, IANIGLA-PI 1080. I-Mecoptera forewing, IANIGLA-PI 1060. J-Scytinopteridae clava, IANIGLA-PI 1105. K-Odonata nymphs head, IANIGLA-PI 1102. L-Diptera forewing, IANIGLA-PI 1081. M-Hemiptera hindwing, IANIGLA-PI 1653.

(*Yabeiella*, *Fraxinopsis*) (Fig. 9L–P), and to a lesser degree, but also present, cycads (*Kurtziana*) (Fig. 9J–K), peltasperms (*Pachydermophyllum*) (Fig. 9H), sphenophytes (*Neocalamites*, *Equisetites*) (Fig. 9A, B) and ginkgoales (*Baiera cuyana*) (Fig. 9Q). Taking into account the sedimentary facies in which the fossils are found (Table 2), the plant assemblage at the Quebrada del Durazno would correspond to the "palaeo-community 15" sensu Artabe et al. (2001).

7. Plant-insect interactions

The first evidence of Triassic insect herbivory from Argentina was documented on a flora recorded in the Cañadón Largo and Laguna Colorada formations (Upper Triassic), El Tranquilo Group, Santa Cruz Province (Adami-Rodrigues et al., 2008 and Gnaedinger et al., 2012). In this work, we describe the first records of plant-insect interactions

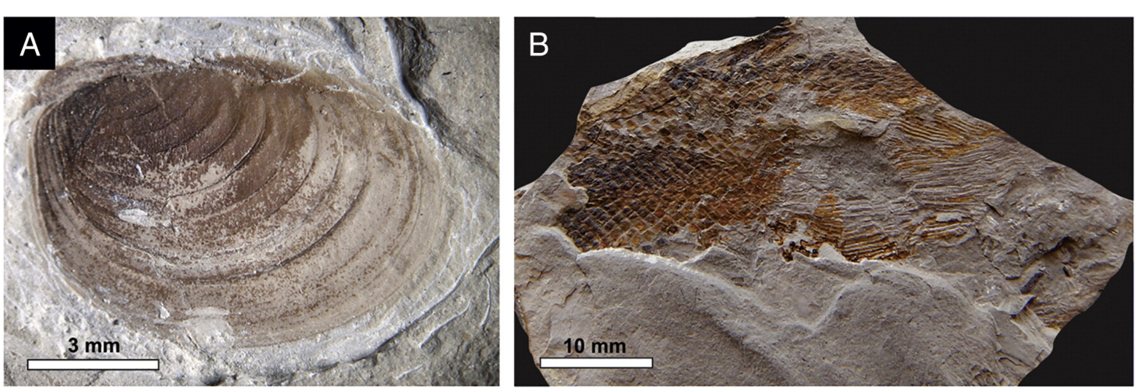

Fig. 7. Fauna associated at the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina). A-*Euestheria forbesi* (Gallego, 1992; Tassi, 2016). B-cf. *Neochallaia* sp. (López-Arbarello pers. comm., 2017).

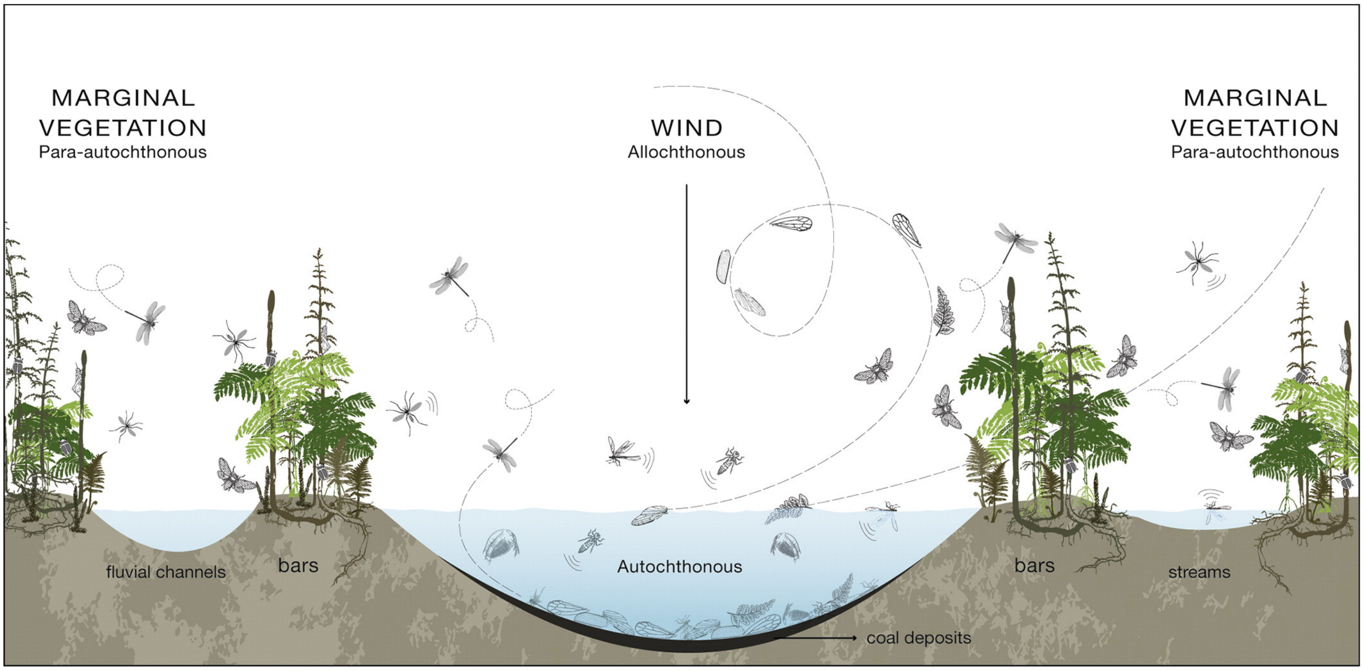

Fig. 8. Reconstruction of the possible insects' pathways up to depositional site (e.g., swamp and/or pond sub-environments in the distributary bay) at the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina).

for the Upper Triassic Potrerillos Formation and for the Cuyana Basin. This new evidence demonstrates an expanded array of herbivory and ovipositional relationships between these two groups.

Almost every fossil was affected post-depositionally by the activity of fungi, which if overlooked, could be mistaken as damage (e.g., galls). In order to correctly ascertain damage produced by insects, we looked for necrotic tissue, easily identifiable as a darker rim around the wound, the presence of patterns (e.g., aligned holes), or evidence of morphological structures suggestive of chewing, piercing or sucking (e.g., veinal stringers and contiguous excisions). Herbivory traces were found in 11 specimens (19.6%), mostly on fronds, whereas oviposition was exclusively located on stems.

7.1. Damage types (DTs)

Plant specimens affected by herbivory revealed external foliage damage, including traces by hole, surface and marginal feeding, piercing and sucking, and oviposition (Fig. 11). We identified and qualitatively described a total of seven damage types (Table 5).

7.2. Potential trace-markers

The assignation of a specific insect group to a particular damage type is speculative in most cases because even today, with few exceptions, similar feeding traces are not specially distinctive or diagnostic among extant mandibulate leaf-feeding insects (Ash, 1997; Labandeira et al., 2007). Therefore, the abundant fossil insects recorded at the Quebrada del Durazno locality allow us to only tentatively associate the damage described to the various insect orders found at the site. Probably the most obvious candidates for external foliage feeding (hole and marginal feeding, surface feeding) are the orthopterans, which are extensive foliage feeders today, and the coleopterans. Potentially, the piercing and sucking types were produced by hemipterans with their relatively unspecialized piercing mouth apparatuses (Scott et al., 1992). Labandeira (2006) mentioned the orthopteroids, hemipteroids and basal holometabolans as dominant arthropods of the Herbivore Expansion Phase 3 (Middle Triassic to Recent, 245 Ma.); all of these are documented at the Quebrada del Durazno locality. The oviposition traces are associated possibly with hemipterans (oviposition in living plant tissues is secondary in orthopterans and represents a later acquisition sensu Vasilenko and Rasnitsyn, 2007) because both this type of damage and the insect order have been recorded in abundance. However, although the record of odonatans (nymphs and imago) at this locality is still relatively poor (probably owing to a collection/taphonomic bias) we cannot discard this group as the potential oviposition producer. The density, shape and disposition of the scars documented at the Quebrada del Durazno locality resemble the oval and elongate endophytic Odonata-like oviposition described from the Triassic of Germany (Grauvogel-Stamm and Kelber, 1996). Vasilenko and Rasnitsyn (2007) mentioned that the former odonatans oviposition scars had the same elongate oval structure and were sporadically organized in a zigzag arrangement (differing from the aligned display of the scars in our material); therefore, these marks clearly need further detailed studies.

The interactions recorded at the Quebrada del Durazno locality share the same basic damage categories with coeval floras elsewhere in Gondwana. External feeding and oviposition traces occur in a wide variety of gymnosperms and seed ferns from the Triassic of South Africa (Scott et al., 2004), Australia (McLoughlin, 2011) and Chile (Gnaedinger et al., 2014). Contrarily to other gondwanan localities, our flora did not show conclusive evidence of more specialized type of damages, such as leaf mining or galling (Rozefelds and Sobbe, 1987; Scott et al., 2004; Labandeira and Anderson, 2005; McLoughlin, 2011; Ghosh et al., 2014). Randomly scattered circular marks with a thick dark rim and carbonaceous residue in the middle are present in numerous specimens (Figs. 9D–E, H, K, 11I–J), showing some resemblance with the galls described in *Dicroidium* species from Australia and India (McLoughlin, 2011; Ghosh et al., 2014). However, the lack of an elevated or depressed surface and the uncertain existence of an exit hole question their assignation to any type of gall and point to post-burial fungal activity. Regardless their current absence in our material, we believe future work at this locality will reveal the presence of more specialized type of damages, including both leaf mines and galls.

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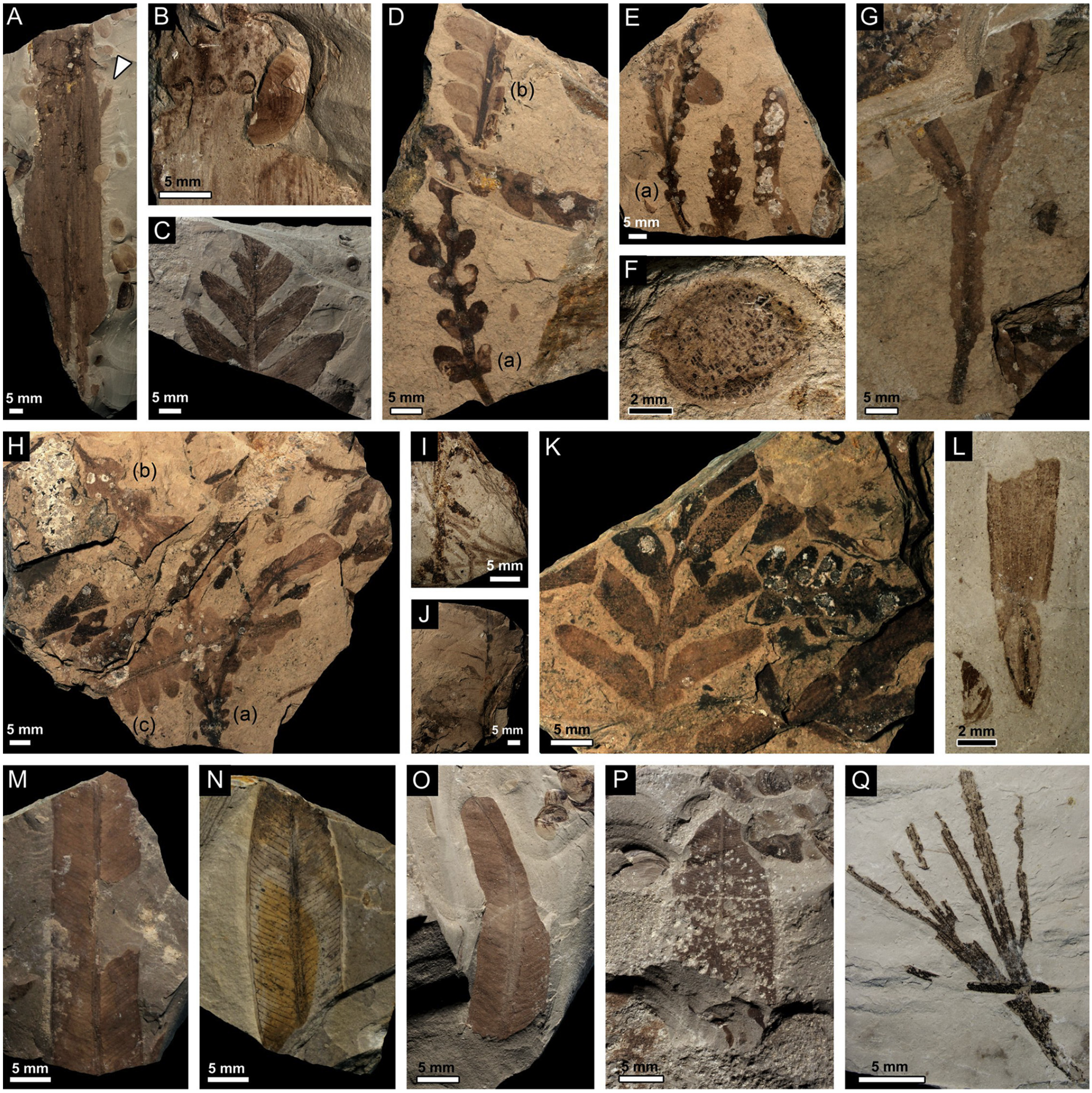

Fig. 9. Plant remains from the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina). A - Potential *Neocalamites* stem with a lateral branch (arrow); IANIGLA-PB 63. B - Another sphenophyte remain showing the vascular bundles; IANIGLA-PB 69. C - *Dicroidium lancifolium* (Morris) Gothan; IANIGLA-PB 64. D - (a) *Dicroidium argenteum* (Retallack) Gnaedinger, and (b) *Dicroidium crassum* (Menéndez) Petriella; IANIGLA-PB 79A. E - *Dicroidium odontopteroides* (Morris) Gothan; IANIGLA-PB 79B. F - *Feruglioa samaroides* Frengüelli; IANIGLA-PB 18. G - *Johnstonia coriacea* (Johnston) Walkom; IANIGLA-PB 78. H - (a, b) *Johnstonia stelzneriana* (Geinitz) Frengüelli, and (c) *Pachydermophyllum praecordillerae* (Frengüelli) Retallack; IANIGLA-PB 73. I - *Xylopteris* cf. *X. elongata* (Carruthers) Frengüelli; IANIGLA-PB 89. J - *Kurtziana brandmayri* Frengüelli; IANIGLA-PB 78. K - (?) *Kurtziana paipotensis* Herbst & Gnaedinger; IANIGLA-PB 86. L - *Fraxinopsis minor* Wieland; IANIGLA-PB 68. M - *Yabeiella wielandii* Oishi; IANIGLA-PB 66. N - *Yabeiella brackebuschiana* (Kurtz) Oishi; IANIGLA-PB 67. O - *Yabeiella spathulata* Oishi; IANIGLA-PB 63. P - (?) *Yabeiella mareyesiaca* (Geinitz) Oishi; IANIGLA-PB 63. Q - *Baiera cuyana* Frengüelli; IANIGLA-PB 70.

8. Discussion

8.1. Palaeoenvironment and palaeogeography

The insect fauna described for the uppermost section of the Potrerillos Formation at the Quebrada del Durazno locality occurs in association with a typical and diverse *Dicroidium* Flora. The palaeogeographic position of the Triassic basins from Argentina explains the presence of a marked floristic provincialism with a similar eco-environment and climate patterns throughout southern Gondwana. The Cuyana Basin was located at palaeolatitudes of ca. 45°–48° S for the early Upper Triassic according to the palaeogeographical reconstruction based on the palaeomagnetic pole of Torsvik et al. (2012) (Iglesia Llanos pers. comm., 2017). The *Dicroidium* Flora occupied middle to high palaeolatitudes (>30°) in the extratropical belt of Gondwana (Artabe et al., 2003). It progressed under temperate/warm and humid conditions, by maximal development of the megamonsoon in the Late Triassic (Parrish, 1993; Colombi and Parrish, 2008; Preto et al., 2010). The insects would be thus adapted to strongly seasonal conditions.

Sedimentary facies analysis of the studied sequences supports the existence of deltaic environments with the development of stable water bodies or swamps and/or pond sub-environments within

Table 4
Palaeofloristic record of the Potrerillos Formation at the Cerro Cacheuta.

Order	Species	Potrerillos formation		
		Quebrada del Durazno	Agua de las Avispas	Puesto Miguez
Equisetales	*Equisetites fertilis* (Frengüelli) Frengüelli	–	–	X
	Neocalamites carrerei (Zeiller) Halle	–	–	X
	Neocalamites suberosus (Artabe & Zamuner) Bomfleur et al.	–	–	X
	Sphenopsid indet.	X	–	–
Filicales	*Asterotheca truempyi* Frengüelli	–	–	X
	Cladophlebis copiosa Frengüelli	–	–	X
	C. kurtzii Frengüelli	–	–	X
	C. mendozaensis (Geinitz) Frengüelli	–	X	X
	C. mesozoica (Kurtz) Frengüelli	–	–	X
	Coniopteris harringtoni Frengüelli	–	–	X
Corystospermales	*Dicroidium argenteum* (Retallack) Gnaedinger & Herbst	X	–	X
	D. lancifolium (Morris) Gothan	X	–	–
	D. odontopteroides (Morris) Gothan	X	X	X
	D. crassum (Menéndez) Petriella	X	–	–
	Johnstonia coriacea (Johnston) Walkom	X	X	X
	J. stelzneriana (Geinitz) Frengüelli	X	X	X
	Xylopteris argentina (Kurtz) Frengüelli	–	–	X
	X. elongata (Carruthers) Frengüelli	X	–	X
	Feruglioa samaroides Frengüelli	X	–	
Petriellales	*Rochipteris* sp.	–	–	X
Peltaspermales	*Scytophyllum argentinum* (Frengüelli) Morel et al.	–	–	X
	Pachydermophyllum dubium (Burges) Retallack	–	X	–
	P. pinnatum (Walkom) Retallack	–	–	X
	P. praecordillerae (Frengüelli) Retallack	X	X	X
Cycadales	*Kurtziana brandmayri* Frengüelli	X	–	X
	K. paipotensis Herbst & Gnaedinger	?	–	
	Pseudoctenis spectabilis Harris	–	–	X
Gnetales	*Gontriglossa* sp.	–	–	X
	Yabeiella brackebuschiana (Kurtz) Oishi	X	–	X
	Y. mareyesiaca (Geinitz) Oishi	?	–	–
	Y. spathulata Oishi	X	–	X
	Y. wielandii Oishi	X	–	X
	Fraxinopsis andium (Frengüelli) Anderson & Anderson	–	–	X
	F. major Wieland	–	–	X
	F. minor Wieland	X	–	X
Ginkgoales	*Baiera cuyana* Frengüelli	X	–	X
	B. rollerii Frengüelli	–	–	X
	Ginkgoidium bifidum Frengüelli	–	–	X
	Sphenobaiera argentinae (Kurtz) Frengüelli	–	–	X
Voltziales	*Heidiphyllum elongatum* (Morris) Retallack	–	X	X
	Telemachus elongatus Anderson		X	–
	T. lignosus Retallack	–	–	X
	Cordaicarpus sp.	–	–	X

Note: Plant macrofossil taxa recovered from the three sections at the Cerro Cacheuta: Quebrada del Durazno (this work), Agua de las Avispas and Puesto Miguez (Morel et al., 2011).

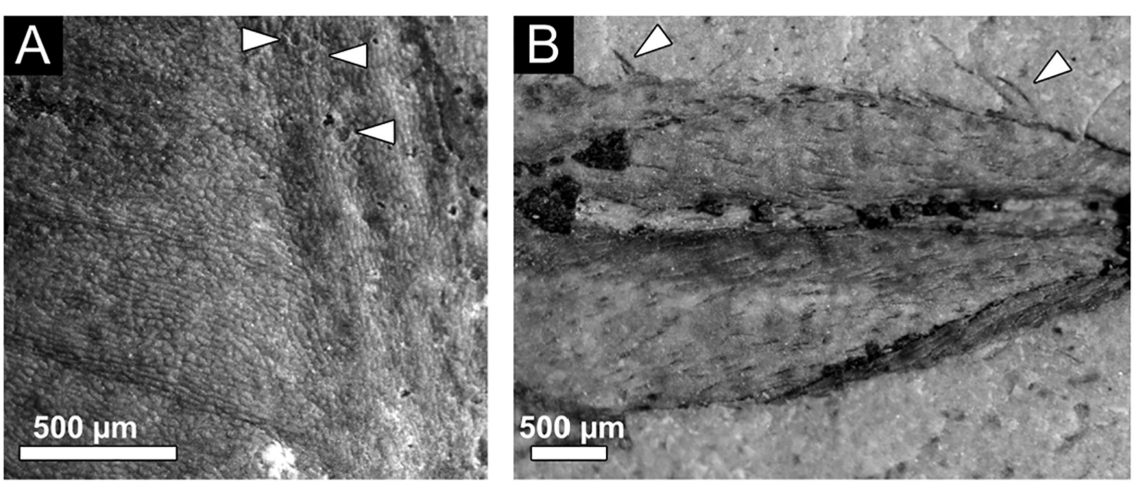

Fig. 10. Magnified photographs showing the exquisite preservation in some of the fossil plant remains from the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina). A - Detail of epidermal tissues and potential stomata (arrows) in *Yabeiella spathulata*; IANIGLA-PB 63. B - Detail of hairs (arrows) and central keel in *Fraxinopsis minor*; IANIGLA-PB 68.

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Fig. 11. Plant-insect interactions from the Quebrada del Durazno locality (Potrerillos Formation, Carnian), Mendoza Province (Argentina). A, B - Hole feeding (DT50) on *Yabeiella wielandi*, observe the veinal string left (arrows), suggesting preferential consumption of tissue by the insect. C - Hole feeding (DT 03) on *Johnstonia* sp. D - Surface feeding (DT31) on indeterminate leaf fragment, observe the clear reaction tissue (arrows) and the abrasion of the surface tissue. E–G, I–K - Margin feeding (DT12) on *Kurtziana brandmayri*, *D. argenteum* and *D. odontopteroides* leaves, arrows point to well-defined reaction tissue. H - Margin feeding (DT15) on *Johnstonia stelzneriana*, observe the deep incision on one side of the leaf (arrow). L, M - Piercing and sucking (DT 46) on indeterminate leaf, observe small punctures randomly arranged on leaf (arrows). N, O - Oviposition (DT 100), with ovoidal scars aligned parallel along an indeterminate sphenophytes stem.

interdistributary plains with intermittent episodes of flooding, allowing the establishment of hydro-hygrophytic vegetation and creating the suitable conditions for the development of a rich insect-fauna (Fig. 12). Martin (2008) mentioned that this palaeoenvironmental type, also observed in Mintaja locality (Lower Jurassic, Australia), could explain the relatively few aquatic organisms seen in the fossil assemblage of the Quebrada del Durazno locality. Additionally, the co-occurrence of perennial and ephemeral streams at the Quebrada del Durazno locality is consistent with those observed in regions with abundant, highly seasonal, rainfall (DeLuca and Eriksson, 1989) and these conditions probably resulted from optimal development of the megamonsoonal climate during the Late Triassic (Colombi and Parrish, 2008).

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Table 5
Plant-insect interactions recorded at the Quebrada del Durazno locality (Upper Triassic), Cuyana Basin, Mendoza Province (Argentina).

Damage types (DTs)	Description	Plant host
DT 50 – Hole feeding traces. (Fig. 11A, B)	Four oval holes ranging from 1.66 to 1.93 mm long and 0.75 to 0.93 mm wide, with a clear, dark reaction-tissue rim, are aligned adjacent on one side of the primary vein of a *Yabeiella wielandi* Oishi leaf. The secondary venation is left untouched, suggesting preferential consumption of tissue by the insect.	*Yabeiella wielandi* Oishi (IANIGLA-PB 63)
DT 03 – Hole feeding traces. (Fig. 11C)	There are at least 5 small, polylobate perforations (1–2 mm in diameter) with a weak reaction rim randomly displayed on a fragment of *Johnstonia* sp. leaf.	*Johnstonia* sp. (IANIGLA-PB 75)
DT 31 – Surface feeding traces. (Fig. 11D)	Small circular removal of surface tissue with a thin but distinctive reaction rim on a pinnule of an indeterminate plant specimen.	Indeterminate (IANIGLA-PB 89)
DT 12 – Margin feeding traces. (Fig. 11E–G, I–K)	Several plant specimens present marginal excisions of varying length (2–7 mm) and degrees (but always <180° of arc), indicated by a dark reaction tissue along the borders.	*Kurtziana brandmayri* Frengüelli (IANIGLA-PB 76, 78, 87); *Dicroidium argenteum* (Retallack) Gnaedinger (IANIGLA-PB 79); *Dicroidium odontopteroides* (Morris) Gothan (IANIGLA-PB 75)
DT 15 – Margin feeding traces. (Fig. 11H)	A deep excision reaches the principal vein on one side of the leaf. It presents a narrow marginal opening, but expands both towards the apex and the base of the leaf, leaving an excision 3 mm long and almost 2 mm wide. There is a conspicuous reaction rim, indicating the damage was produced by herbivory.	*Johnstonia stelzneriana* (Geinitz) Frengüelli (IANIGLA-PB 73)
DT 46 – Piercing and sucking traces. (Fig. 11L–M)	Small circular punctures, 0.3–0.5 mm in diameter, randomly scattered on the surface of the leaf and midvein. Contrary to what is expected for a Triassic flora, piercing and sucking has been difficult to record, most probably due to the somewhat carbonaceous preservation of these fossils which precluded its recognition.	Indeterminate (IANIGLA-PB 92)
DT 100 – Oviposition traces. (Fig. 11N–O)	This interaction is assigned to DT 100 based on the presence of multiple ovoidal scars, 1 mm long and 0.4 mm wide, aligned parallel along the stem, being the only difference with Labandeira et al. (2007) description in that the scars are not on a leaf.	Indeterminate sphenophyte stems (IANIGLA-PB 93)

Insects are good indicators of environmental changes and fluctuations in biodiversity; thus, fossil insects can be used to reconstruct past environmental conditions, primarily because many of the fossil groups are still represented nowadays (Cairncross et al., 1995; Żyła et al., 2013). Odonatan nymphs recorded at the Quebrada del Durazno locality indicate the presence of small freshwater bodies (also supported by the record of plant and fish remains (Fig. 7B), and the many well-preserved 'conchostracans' (Fig. 7A)) with abundant vegetation growing nearby, used as a resource by the adult females for oviposition and early stages of development by the recently hatched insects. Also, the great amount of complete and well-preserved forewings is suggestive of low-energy environments. This contrasts with the nearby locality of Puesto Miguez (also in the south of the Cerro Cacheuta area), where sedimentological information, the presence of plecopteran nymphs and fossil fish remains indicate well-oxygenated permanent freshwater bodies in the floodplains of the fluvio-deltaic environments that characterize that section of the Potrerillos Formation (Gallego et al., 2011; Lara, 2016; Lara et al., 2012; Zavattieri pers. comm., 2015). Last, the numerous hemipterans recorded at the Quebrada del Durazno locality support temperate/warm and humid conditions during the early Late Triassic in the area, similar to the modern hemipteran-climate relationship and in accordance with the global climatic trends of the time.

8.2. Taphonomic analysis

8.2.1. Palaeontomofauna

Taphonomic studies are an essential prerequisite for the reconstruction of fossil insect assemblages, in order to interpret the sedimentary and environmental conditions where the insects lived and died, and to understand the interactions between insects and other organisms (Martínez-Delclòs et al., 2004).

At the moment, the Quebrada del Durazno insect assemblage (Figs. 5, 6) comprises eight orders, eight families and 14 species described from >90 collected specimens that have been found in massive to finely laminated silt-claystone (black shales) and coaly levels of the upper section of the Potrerillos Formation (early Upper Triassic), together with plant fossils, abundant well-preserved spinicaudatans (Fig. 7A) and fish remains (Fig. 7B). The insect parts are spatially arranged parallel to the bedding plane (Figs. 5, 6).

Insects are usually disarticulated, although in a few cases they were found articulated. They mainly consist of impressions of the wings, elytrae (are the most flexible of insect element increasing their preservation potential), and less frequently, parts of the body or complete bodies. The state of preservation observed at the Quebrada del Durazno locality is similar to that in other known classic Gondwana assemblages from the Upper Triassic, i.e., Los Rastros Formation (Argentina) (Mancuso et al., 2007), Molteno Formation (South Africa) (Cairncross et al., 1995) and the Ipswich Series (eastern Australia) (Jell, 2004).

The entomological association at the Quebrada del Durazno locality is dominated by impressions of hemipterans sclerotized forewings (57 specimens) and, in descending order, membranous forewings and nymphs of odonatans (seven specimens), beetle elytrae (four specimens), membranous forewings of Mecoptera (four specimens), Orthoptera (four specimens), Diptera (two specimens), Grylloblattida (one specimen), Miomoptera (one specimen) and few specimens (12) of uncertain taxonomic position (Figs. 5, 6, Table 3). Part of this material is still under study (Lara, 2016). The various insect body parts in the assemblage were preserved in lateral and dorso-ventral views, with mostly isolated and dispersed remains, and few articulated ones (Figs. 5, 6). We observed fractures in hemipteran's wings (mainly without clavus) and damage in a forewing, probably related to sedimentary transport or biological activity, whereas other wing fragments can be associated to post-burial sediment fracturing and/or negligent human collection.

As we mentioned above, the sclerotized forewings of hemipterans (mainly Scitynopteridae with about 35 specimens) are the most frequent, including complete wings (38 specimens), incomplete wings (11 specimens), forewing + clavus (two specimens), and clavus (six specimens) (Fig. 6). This prevalence of hemipterans is essentially due to the robust and flexible nature of the forewing in this order, increasing their preservational potential. Moreover, the excellent preservation that the abundant forewings of scytinopterids show suggests this group of insects was associated with the vegetation growing in the delta plain. The wings did not suffer transport; the insects probably fell into the water bodies and then were attacked by predators or their soft-tissues were quickly degraded by bacteria and fungi while the body was still

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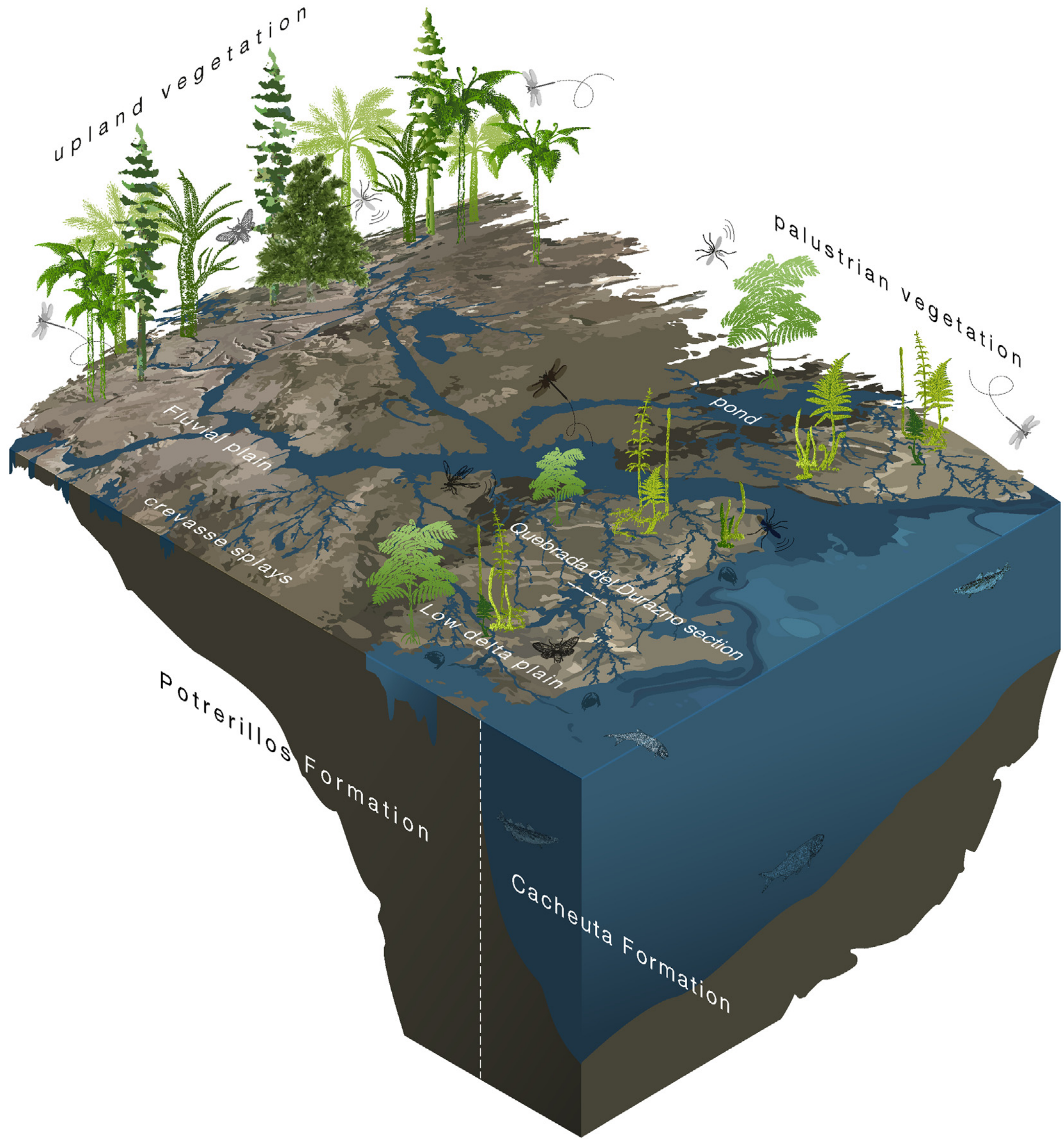

Fig. 12. Palaeoenvironmental interpretation of the Quebrada del Durazno section (Potrerillos Formation, Carnian), Mendoza Province (Argentina).

floating or while sinking through the oxygenated zone. This led to a fossil record represented mainly by complete disarticulated forewings (without clavus) (Figs. 5, 6) and, in lesser proportion, fragmentary forewings (possibly related to external factors and/or collection bias).

With the exception of the impression of a complete nymph and the isolated head of an odonatan (autochthonous element to the depositional sub-environment where they were found), all specimens are represent by adult winged organisms of terrestrial habitats (allochthonous or para-autochthonous element). The abundance of adult-stage insects is probably due to the high degree of sclerotization of their forewings.

The various groups recorded and their preservation stages suggest several fossilization pathways and the development of different sub-environments in the upper section of the Potrerillos Formation during early Upper Triassic (Lara, 2016; Lara and Aristov, 2016). We hypothesize that the insects arrived to the depositional site (e.g., swamp and/or pond sub-environments in the lower delta plain) either alive or dead by three possible pathways: (a) associated and transported by streams of the delta plain and then, by episodes of flooding, reaching the depositional environment, (b) transported by the wind, or (c) deposited in situ right after falling into the water body (Fig. 8). In this last case, the insects with a larger wingspan (i.e., odonatans) together the smaller insects, cannot break the water's surface tension, thus their parts tend to decompose, disarticulate and fragment before burial (Martínez-Delclòs et al., 2004). Occurrence of well-preserved odonatan nymphs suggests that the specimens suffered a fast fall through the oxygenated zone, reaching the bottom, and thus were protected from biological attacks and degradation.

The numerous wing fragments (Figs. 6E, L, M) recorded at the Quebrada del Durazno locality are indicative of the long transport distances they suffered by fluvial channels or streams before they were deposited in the interdistributary bays. Zherikhin (2002) and Martínez-Delclòs et al. (2004) proposed that the high abundance of disarticulated wings observed is very common in these types of associations because the adult terrestrial insects have to pass through different taphonomic filters before achieving burial. Beattie and Avery (2012) mentioned that in Talbragar Fossil Fish Bed, Gulgong (New South Wales, Australia, Jurassic) the articulated nature of the fossil insects is interpreted to have resulted from a sudden but low-energy burial event.

After analyzing the state of preservation of the insect fossils of the Potrerillos Formation (Upper Triassic) at Quebrada del Durazno locality we can observe that the Triassic Gondwana deposits have an identical composition (but in different position within assemblage) with a bias towards strongly sclerotized elements and taxa consisting mainly by hemipteran and blattodean forewings, and disarticulated elytra,

although other body parts have been preserved too. Unusually, to date, we have not recorded cockroaches at the Quebrada del Durazno locality (the order has just been recorded at the Quebrada del Puente locality, Potrerillos Formation, Cerro Bayo, Mendoza Province; Martins-Neto et al., 2007). Their absence could be related to different depositional environments, collection and taphonomic bias, or competition for the same resources with other group that ended in the decrease of blattids (Lara and Aristov, 2016). Vršanský et al. (2002) mentioned that the temporary cockroach decline in the Permian was related with diversity explosion of grylloblattids which occupied similar niches. In some entomological assemblages we can observed that both orders have been recorded but in different proportions (mainly blattids) (Mancuso et al., 2007) maybe correlated to the presence/absence purpose by Vršanský et al. (2002).

8.2.2. Spinicaudatans

The 'clam shrimps' (Order Spinicaudata), with a long geological history extending back to the Devonian, are seemingly inconspicuous small branchiopod crustaceans and are easily recognizable by a short, laterally compressed body enclosed in a carapace of two lateral valves (lightly-mineralized chitin) (Kozur and Weems, 2010; Li and Matsuoka, 2012). The main habitats in which fossil forms are found include small, quiet, temporary freshwater pools world-wide (based partly on the nature of the sediments and other fossils associated as insects, crustaceans, fishes, carbonized leaves and wood) (Webb, 1979) but also, floodplain pools, coastal floodplains and lakes, ponds, tundra, and caves (Monferran et al., 2013; Astrop et al., 2015).

The spinicaudantan records at the Quebrada del Durazno locality were initially reported by Gallego (1992, 1999) and Tassi (2016, unpublished) who described several specimens belonging to *Euestheria forbesi* (Eustheriidae). We found several levels with abundant and well-preserved spinicaudatans (Fig. 7A) (associated with fossil insects, plant and fish remains) that support the occurrence of freshwater bodies at this locality.

8.2.3. Fishes

The material recorded in this locality includes postcranial remains (Fig. 7B) and abundant isolated scales that are compatible with actinopterygians, and in particular, to cf. *Neochallaia* sp. (López-Arbarello pers. comm., 2017). At the moment, several diverse and well preserved fish assemblages have been reported from the Cuyana Basin in Mendoza Province (Stipanicic and Marsicano, 2002, and references therein; Gallego et al., 2004; López-Arbarello, 2004; López-Arbarello and Zavattieri, 2008; López-Arbarello et al., 2010). Preliminarily, the presence of fish remains at the Quebrada del Durazno could suggests the occurrence of freshwater bodies and quiet backwater environment. The record of fish remains points to a fast burial event, impeding the action of bacteria or other organisms that could disintegrate the body, however, a more detailed study by fish specialist is certainly needed.

8.2.4. Fossil plants

Although some of the plants are fragmentary, we consider the plant assemblage at the Quebrada del Durazno locality to be autochthonous to para-autochthonous. If any, transportation distance to the final depositional locality must have been short, indicating the flora grew at or nearby the site (Fig. 12). This is further evidenced by the fine preservational detail of the specimens and mostly, the insect-herbivory observed in some of the vegetative remains, which can be directly related to the insect groups found in close association. The sphenophytes (stems with oviposition), corystosperms (*Johnstonia* and *Dicroidium*), cycadales (*Kurtziana*) and gnetaleans (*Yabeiella*) acted both as shelter and a food resource for the invertebrate fauna at the Quebrada del Durazno locality, indicating a richly interacting biota at the site.

The fossil plants identified in this study were recovered from two main beds, assignable to facies A2 and B1 (Table 1). Plants in facies A2 were found in association with abundant insects, spinicaudatans, and fish remains. The macroflora in this facies reveals exquisite detail of delicate structures, such as trichomes and epidermal tissues (Fig. 10), provided by their preservation in the finely laminated to massive, dark-gray mudstones. The plants in facies A2 were growing right at the depositional site, as inferred from the insect damage that can be attributed to the insect's groups recovered from the same level.

The facies B1 bed from which the rest of the plants derive is almost completely devoided of invertebrates, with few spinicaudatans and a total absence of insect remains, the latter only evidenced by the damage on some of the leaves. Also, the fossils recovered from facies B1, characterized by yellowish mudstones to fine-grained sandstones, were profusely affected by post-depositional fungus, pointing to the slightly coarser lithology that allowed humidity and permeability. The plant assemblage from this level is represented by abundant pteridosperms (*Dicroidium*, *Johnstonia*, *Xylopteris*, *Pachydermophyllum*), Cycadales (*Kurtziana*) and Gnetales (*Yabeiella*), whereas no sphenophytes were found, potentially indicating its development as an upland flora that suffered a short-distance transport before burial.

Last, even though no plant remains were described from these levels, the thick coal strata here assigned to facies A1 are of major interest, since these reveal dense vegetation at the Quebrada del Durazno locality during the Triassic. The banded peat and/or coal formation indicates the partial decomposition of vegetable matter under water-logged and oxygen-deficient conditions. The peat and/or coal layers suggest deposition of semi-carbonized plant remains in water-saturated environments, such as bogs, ponds or swamps where high moisture and waterlogged conditions were persistent. The structure of the plant matter is commonly observed in some levels depending on the degree of organic matter degradation. The clearly "banded" coal/peat feature is interpreted as alternating bands of semi-carbonized plant debris and sapropelic matter where eventual influx of water in the depositional site occurred, establishing a constant water level.

9. Conclusions

Results obtained from this integrative study can be summarized as follows:

- The uppermost levels of the Potrerillos Formation at the studied section are interpreted as semi-permanent swamp/lacustrine bodies within a delta plain environment, that were affected by occasional flooding from distributary channels/streams allowing the development of incipient palaeosols. These are associated with coarsening-upward sequences interpreted as mouth bar deposits, with evidence of deltaic progradation within the Cacheuta lake as base level. The absence of desiccation cracks indicates that these deposits never dried out, and the presence of incipient palaeosols supports a shallowing submerged substrate that was probable exposed episodically but with relative high water content.
- The insect records comprise fragmentary and in some cases articulated specimens as impressions of wings, part of bodies and complete bodies attributable mainly to hemipterans, and in lesser proportion odonatans, mecopterans, miomopterans, grylloblattids, dipterans, beetles and orthopterans.
- The plant association is represented by a typical *Dicroidium* Flora comprising several species of the Corystospermales, Peltaspermales, Cycadales, Gnetales, Ginkgoales and sphenophytes.
- The plant-insect interactions (hole, marginal and surface feeding, piercing and sucking, and oviposition) are qualitatively described for the first time for the Potrerillos Formation (Carnian), Cuyana Basin (Mendoza). These new records of plant-insect interactions demonstrate that Upper Triassic plants in central-western Argentina provided both food and shelter for several types of herbivorous insects.
- This complete study evidences the development in the Cuyana Basin of a megamonsoonal climate supported by abundant records of plants and insects. This section constitutes an important example of the type

of environments developed during Triassic times in this part of Gondwana.

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