



The Triassic insect fauna from the Los Rastros Formation (Bermejo Basin), La Rioja Province (Argentina): their context, taphonomy and paleobiology

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Abstract. In the Bermejo Basin, the Los Rastros Formation bears an abundant insect fauna, mainly with terrestrial adult winged organisms related to the Blattoptera and the Coleoptera orders. The insect remains are found in the black shales of the offshore lacustrine facies and the insect taphonomic features suggest that the specimens were allochthonous to the lake. The individuals appear to have arrived alive to the lake and suffered a rapid fall through the water column thus, preserving them intact, and some of them suffered fragmentation in air transportation and by biological attack during long periods of flotation.

Resumen. LA FAUNA DE INSECTOS TRIÁSICOS DE LA FORMACIÓN LOS RASTROS (CUENCA BERMEJO), PROVINCIA DE LA RIOJA (ARGENTINA): SU CONTEXTO, TAFONOMÍA Y PALEOBIOLÓGÍA. En la Cuenca Bermejo, la Formación Los Rastros es portadora de una abundante fauna de insectos, principalmente organismos adultos terrestres y alados pertenecientes a los órdenes Blattoptera y Coleoptera. Los restos de insectos son encontrados en las pelitas negras de la facies de lago abierto. Las características tafonómicas de los insectos sugieren que los especímenes son alóctonos al lago. Los individuos pudieron llegar vivos al lago y sufrir una rápida caída a través de la columna de agua, preservándose intactos, o sufrieron fragmentación en el transporte aéreo y por ataques biológicos durante largos períodos de flotación.

Key words. Triassic. Insecta. Taphonomy. Los Rastros Formation. Argentina.

Palabras clave. Triásico. Insecta. Tafonomía. Formación Los Rastros. Argentina.

Introduction

Generally, the fossil insect bearing deposits are found in very quiet depositional environments, such as lacustrine systems and transitional environments (Martinell and Martinez-Delclós, 1990). During the biostratinomic stage, exist several processes which can affect the insect remains. In some cases, insects are attracted by physical factors, such as temperature

and moisture, and these factors can promote the presence of these organisms in a specific environment. The wind factor is considered completely external to the organism, and is one of the most important factors in the generation of insect deposits (Martinell and Martinez-Delclós, 1990).

The Los Rastros succession has an abundant insect fauna. Most of the individuals are adult winged organisms and terrestrial representatives belonging to the Blattoptera and the Coleoptera orders. The remains are only associated with the black shales of the offshore lacustrine facies.

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Geological setting

The Bermejo Basin is an extensional basin formed along the western margin of Gondwana during the Late Permian and Early Triassic in the pre-breakup stage of Pangea (Uliana and Biddle, 1988). Basin deposits crop out in the northwest of Argentina along the border between San Juan and La Rioja provinces, and shows a NW-SE orientation. The sedimentary infilling of the Bermejo Basin is dominated by 2.000 to 6.000 m of Triassic alluvial, fluvial and lacustrine deposits (Stipanovic, 2002).

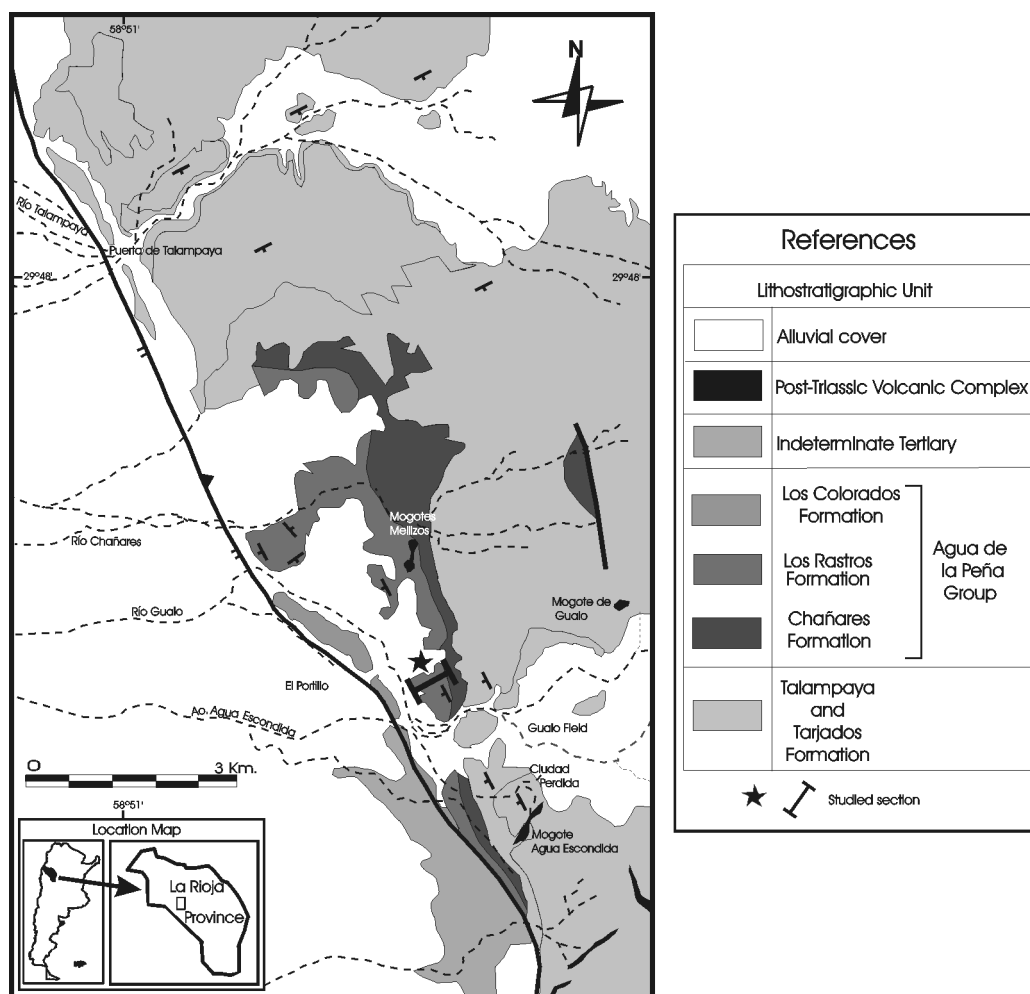


Figure 1. Geologic map of the Río Gualo section in the Bermejo Basin (modified from Mancuso 1999) / *mapa geológico de la sección de Río Gualo en la Cuenca del Bermejo (modificado de Mancuso 1999).*

From a lithostratigraphic point of view, the sedimentary succession has been subdivided, in ascending order, into the Talampaya and Tarjados formations (Romer and Jensen, 1966), and the Agua de la Peña Group, which was divided into four units (Mancuso, 2005 a, 2005b) which are from the base to the top: the Chañares Formation (Romer and Jensen, 1966), the Los Rastros Formation (Frenguelli, 1944; Ortiz, 1968), the Ischigualasto Formation (Frenguelli, 1944; Stipanovic, 1969) and the Los Colorados Formation (Groeber and Stipanovic, 1953; Stipanovic, 1969) (figures 1, 2).

The Chañares Formation is dominated by tuffaceous sandstones and siltstones of fluvial-lacustrine deposits, and by alternation of polymictic clast- and matrix-supported conglomerates belonging to alluvial fan deposits (Rogers *et al.*, 2001; Mancuso, 2005a, 2005b). This succession passes upward into the lacustrine black shales and deltaic sandstones of the Los Rastros Formation (Rogers *et al.*, 2001; Mancuso, 2005a, 2005b). The sandstones, mudstones and tuffs

of the Ischigualasto Formation deposited by a moderate to high-sinuosity river system overlay the Los Rastros succession (Milana and Alcober, 1994). The succession culminates with the red beds of the Los Colorados Formation. Following these, a regional unconformity separates the Triassic succession from the overlying ?Cretaceous Cerro Rajado Formation (Bossi, 1977; Stipanovic and Bonaparte, 1979; López-Gamundi *et al.*, 1989; Caselli *et al.*, 2001).

Facies analysis of the Los Rastros Formation

Based on the field data recovered at the Río Gualo locality (figure 1), several lacustrine-deltaic cycles were defined, which respond to a shallowing-upward sequence (Vail *et al.*, 1991). Each cycle is characterized by a coarsening-upward succession, and consists of *Facies association A* (offshore lacustrine deposits) dominated by claystones with iron mudstones interbedded, and *Facies association B* (deltaic deposits) repre-

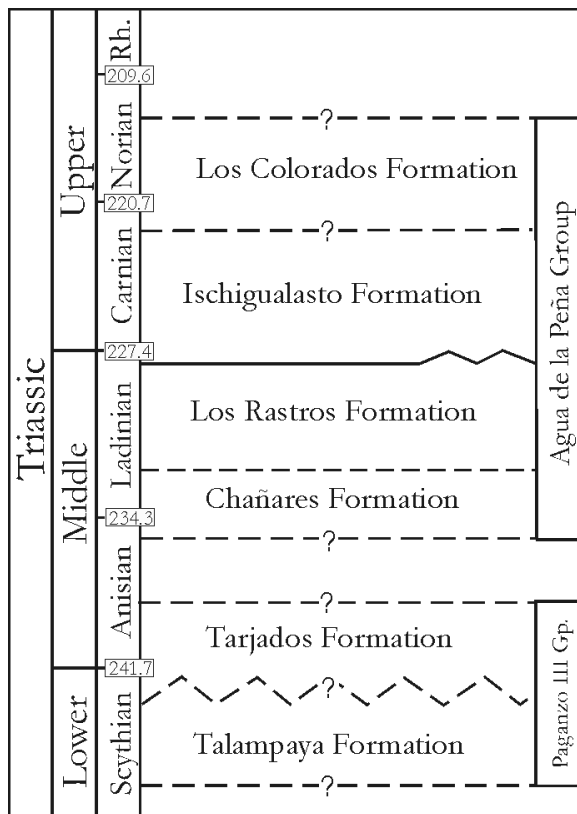


Figure 2. Triassic lithostratigraphy and chronostratigraphy in the Bermejo Basin (modified from Rogers *et al.*, 2001). Limits in my. / litoestratigrafía y cronoestratigrafía triásica en la cuenca Bermejo (modificado de Rogers *et al.*, 2001). Límites en ma.

sented by coarsening-upward siltstones and sandstones with rare organic-rich shales interbedded (figure 3). The individual coarsening-upward cycle ranges, approximately, from 20 to 40 m.

Facies assemblage A (offshore lacustrine deposits). This facies assemblage is dominated by dark gray to black carbonaceous claystones (Fl) interbedded with iron mudstones and very fine-grained sandstones (SFm) (figures 3, 4). The tabular beds form a laterally persistent succession with thickness that ranges from 2 to 5 m. The claystones are horizontally laminated, and formed by continuous microlamination with different grain sizes (figure 4). The ironstone beds show up massive or laminated and rarely gradated, and range in thickness from 0.01 to 0.3 m (figure 4).

The fossil remains preserved in claystone facies include plant debris, and sometimes well-preserved plant fragments related to the “*Dicroidium*-type Flora”; conchostracans, insects and, rarely, fish are also recorded (Mancuso, 2003). On the other hand, the ironstone facies contains plant and wood remains, conchostracans, fish, and putative fish locomotion traces (cf. *Undichnia*) and grazing traces (Mancuso, 2003).

The features observed in facies association A suggest that it was deposited in a deep off-shore lacustrine depositional environment. The claystones were deposited by suspension in distal-lake conditions, whereas the ironstones by distal turbiditic currents (Farquharson, 1982; Talbot and Allen, 1996; Mancuso, 2003).

Facies assemblage B (delta deposits). This facies assemblage consists of a coarsening and thickening-upward succession with a thickness of 15 to 30 m. It is dominated by green siltstones, grey claystones, fine to coarse-grained sandstones and rare gravelly sandstones deposited by stream load (figures 3, 4). The facies assemblage begins with an alternation of green siltstones and gray claystones (Fm) with very fine sandstones interbedded, which form like “rhythmic packages” of massive individual beds with a thickness of approximately 0.1 m (figure 4). The thin layers of small ripple cross-laminated fine to medium-grained sandstones interbedded are more abundant and thicker upwards (figure 4). These layers present plant debris. Upward, medium to coarse-grained sandstones prevail. They begin with horizontal lamination (Sh), which passes upwards to planar cross-bedded (Sp) and culminate with trough cross-bedded (St) in the upper coarser material (figure 4). This coarsening and thickening-upward succession shows more abundant and thicker sandstone layers upwards, occasionally interbedded with scarce thin siltstone levels. The individual bed thickness ranges between 0.05 and 3 m. Fossil fish bodies and woody tissues were preserved in the horizontal laminated sandstones, while only fossil woods were found in the planar and trough cross-bedded sandstones (Mancuso, 2003, 2005a).

To the top, the assemblage is dominated by dark gray mudstones and very fine-grained sandstones (FSC) interbedded with planar and trough cross-bedded sandstones (figures 3, 4). They are internally massive, or pass upward from plane to rippled-lamination, and present a significant amount of organic matter, which are represented mainly by carbonized fragments. The important content of organic matter can form coal layers of 0.2 m thickness (figure 4) (Mancuso, 2003, 2005a).

Based on the stratal geometry and the interpretation of depositional mechanisms of the succession, this facies association is interpreted as deltaic mouth-bar deposits (Guirín *et al.*, 1994; Milana, 1998; Rogers *et al.*, 2001; Mancuso, 2003, 2005a). The gradation from suspension deposits through cross-stratified sandstones represents the shallowing upward trend, which evidences the progradation of a mouth-bar of the fluvial system into the lake body (see Farquharson, 1982; Talbot and Allen, 1996; Mancuso, 2003, 2005a).

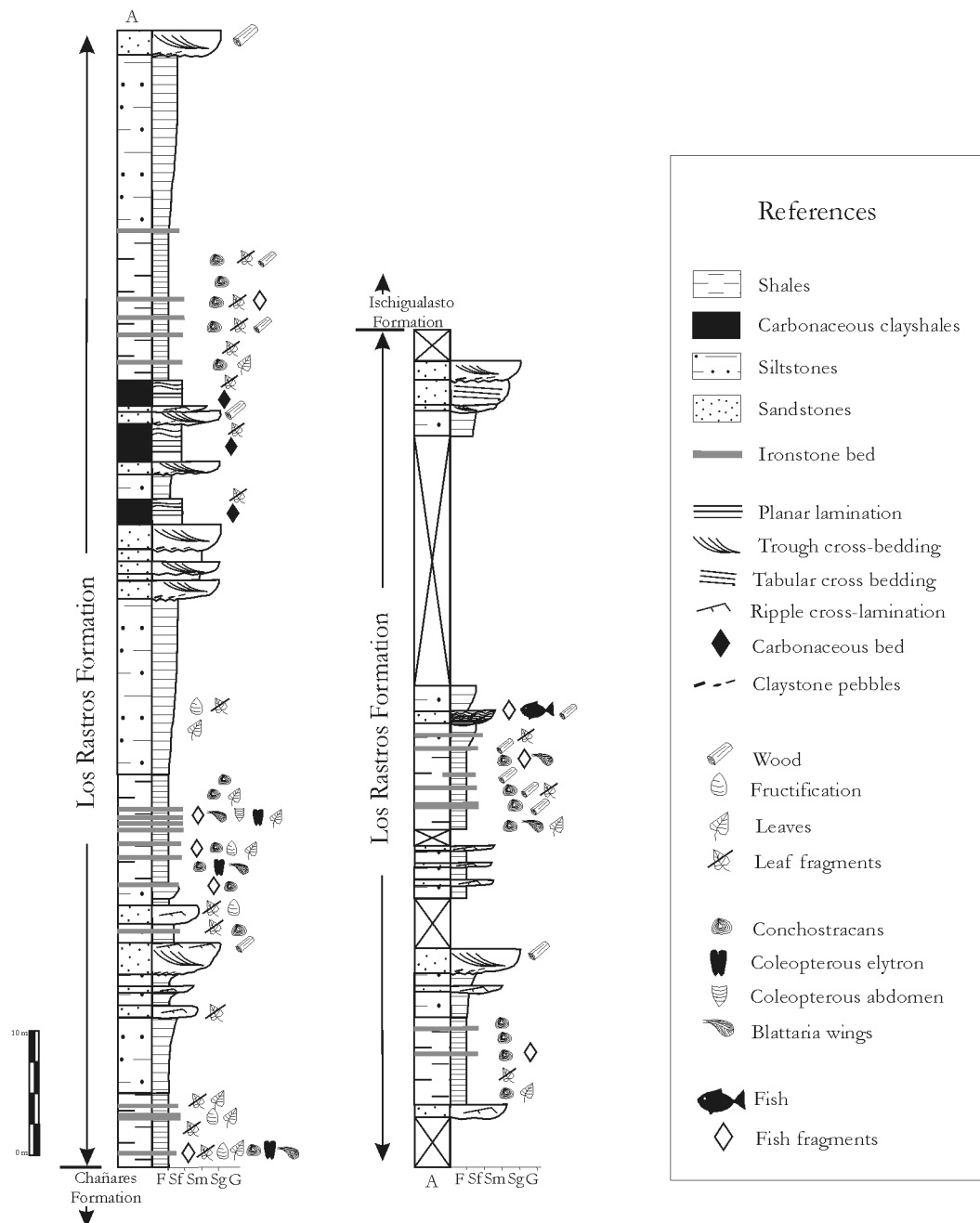


Figure 3. Detailed stratigraphic section of Los Rastos Formation in Río Gualo locality indicating fossiliferous horizons / *sección estratigráfica detallada de la Formación Los Rastos en Río Gualo indicando los horizontes fosilíferos.*

Paleontology of the Los Rastos Formation

At present, the Los Rastos flora record is represented by an abundant macrofloristic assemblage related to the “*Dicroidium*-type Flora” (Frenguelli, 1948; Stipanovic and Bonetti, 1969; Stipanovic and Bonaparte, 1979; Kokogian *et al.*, 1999; Spalletti *et al.*, 1999) and a rich palynological association related to “*Ipswich*-type microflora” (Yrigoyen and Strover, AMEGHINIANA 44 (2), 2007

1970; Zavattieri and Melchor, 1999; Mancuso, 2005a; Ottone *et al.*, 2005). Knowledge about the faunal record of the unit has increased during the last years. The invertebrate remains include different groups of conchostracans (clam shrimps) (Gallego, 1999; Mancuso and Gallego, 2000; Mancuso, 2005a), insects (Gallego, 1997; Gallego and Martins-Neto, 1999; Martins-Neto and Gallego, 1999, 2001; Mancuso and Gallego, 2000; Martins-Neto *et al.*, 2003, 2005, in

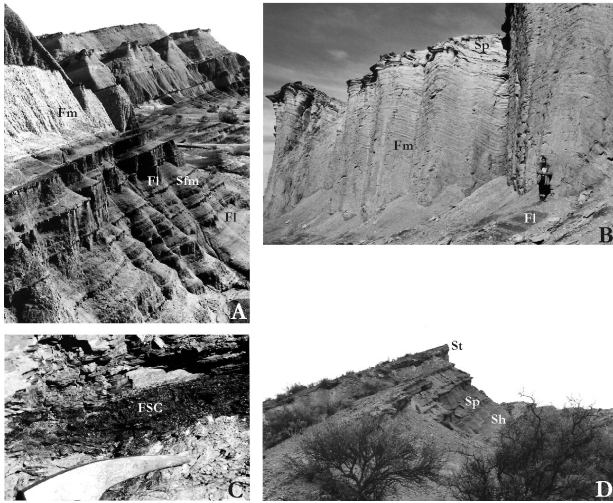


Figure 4. Exposures of the Los Rastos Formation in Río Gualo locality, **A-B**, Facies association **A**, **C-D**, Facies association **B** / fotos de la Formación Los Rastos en Río Gualo, **A-B**, Asociación de facies **A**, **C-D**, Asociación de facies **B**.

press; Mancuso, 2005a) and bivalves (Frenguelli, 1945). The vertebrate fauna is represented by skeletal remains and ichnites. The skeletal remains are dominated by actinopterygian fishes (Cabrera, 1944; Forster *et al.*, 1995; Mancuso, 2003), and a single temnospondyl amphibian (Contreras *et al.*, 1997, Mancuso, 2002). The remaining tetrapod fauna is represented by non-mammalian therapsid, archosaur and possible dinosaur footprints (von Huene, 1931; Arcucci *et al.*, 1995, Marsicano *et al.*, 2004).

Preservation and taphonomy

The insect remains include blattopteran and hemipteran wings, and coleopteran elytra and fragmented bodies (figure 5). This material is preserved as hard parts, for example elytra, and/or impressions with partial or total loss of the original material, mainly through recent weathering.

Most of the insect remains are constituted by disarticulated wings and elytra, and, only in some cases, the articulated elytra and nearly complete coleopteran bodies were found (figures 5.A-F). Thus, the state of articulation of the remains observed in this assemblage is mainly isolated and dispersed, and sometimes articulated.

With regard to postmortem modification, only few fractures were observed in blattopteran wings (figures 5.A, 5.B), mainly related to recent surface exposure and collection. The rest of the insect material does not show evidence of postmortem modification (e.g. abrasion, cracking, breakage).

The insect remains have been found in the laminated black shale of the offshore-lacustrine facies, and show an arrangement pattern in space parallel to the bedding (figure 5). The material has been reported to be, in some cases, preserved in several successive levels, and without preferential orientation.

The association shows a moderate to low abundance of remains. Thus, the biofabric is characterized by a moderate to low density of accumulation, a dispersed packing, and a good sorting in size and shape.

In the insect-bearing facies, plant debris, conchostacans and isolated fish scales (figures 6 A-C) are also preserved. Only in seldom cases, these remains have been reported to be directly associated with insect material.

All collected insect specimens are winged organisms with terrestrial habit (Gallego, 1997; Gallego and Martins-Neto, 1999; Martins-Neto and Gallego, 1999, 2001; Martins-Neto *et al.*, 2003, 2005, in press). Thus, they are considered allochthonous to the lacustrine sub-environment depositional site where they were found.

Paleobiology and paleoecology

The Los Rastos insect assemblage includes different orders: Blattoptera (cockroaches), Coleoptera (beetles), Hemiptera (planthoppers), Ensifera (crickets), Glosselytrodea, Odonatoptera (dragonflies), Miomoptera, and Plecoptera (stoneflies) (Martins-Neto *et al.*, 2003, 2005, in press).

Blattoptera is the most conspicuous order among the described species. The extant nymph and adult of this order are terrestrial omnivores. They are primarily nocturnal, unspecialized scavengers in the leaf litter, feeding largely on decomposing plant material (figure 6). The abundance and diversity of the Los Rastos blattopterans was probably due to the large *Dicroidium* forests and the *Taeniopteris* and *Baiera* thickets around or next to the Los Rastos lake area, which provided many ecotopes where the blattopterans could survive, consuming litter. They had a major role in the mechanical reduction of litter (see also Martins-Neto *et al.*, 2005).

The coleopteran assemblage is mainly composed by members of the suborder Archostemata (Proto-coleoptera *sensu* Crowson, 1975). This primitive group (presence of the crossveins ornamentation) includes the Permosynidae and Cupedidae families, which are closely related phylogenetically, and known from the Lower Permian. The Permosynidae vanished in the Jurassic. The life habit of the fossil and extant forms probably are the same, and the recent cupedids are characterized by living in different habitats such as closed forest, open forest, rotting wood and woodland (figure 6). Many of the cupedid

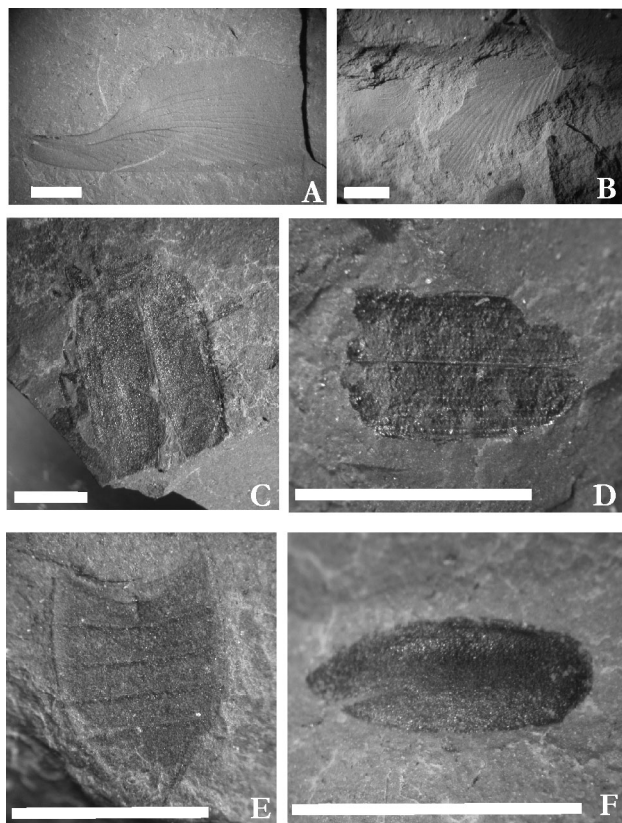


Figure 5. Insect remains exhumed of the Los Rastros Formation, A-B, blattopteran wings, C, nearly complete coleopteran bodies, D, articulated coleopteran elytra, E, coleopteran abdomen, F, coleopteran elytra. / restos de insectos exhumados de la Formación Los Rastros, A-B, alas de blattaria, C, cuerpo de coleóptero casi completo, D, élitros de coleóptero articulados, E, abdomen de coleóptero, F, élitro de coleóptero. Scale bar 3 mm. / Escala gráfica 3 mm.

species are endemic, known only in limited areas (Neboiss, 1960, 1984). Like the Ommatidae they may be found in rainforests as well as in arid grazing or open woodland. Adults are poor fliers (Atkins, 1958). The structure of adult mouthparts suggests pollen-feeding habits; this is supported by the presence of pollen grains in the gut of one species and observations of another species frequenting flowers (Crowson, 1962). All known larvae feed in dead wood, which may be firm and dry, but has been attacked by wood-rotting fungi (figure 6). The other coleopterans belong to the Polyphaga suborder and the Elateridae family (represented up today), which are common and abundant throughout the world (Lawrence, 1982). The biology of this family varies considerably with the larvae being found in a variety of habitats. Larval stages can be found under the bark of trees, in rotten wood or in the soil. Larvae of different genera can live adjacent to termite nests and feed upon their inhabitants, the soil, where they prey upon other coleopteran larvae, or partially rotten wood, feeding upon cerambycid coleopteran larvae. However, the natural habitat of the larval stage of

numerous elaterid species is either grassland or pasture (Calder, 1996).

The Hemiptera order is represented by Cercopidea (froghoppers, planthoppers), Dymorphoptilidae and Scytinopteridae families (Martins-Neto *et al.*, 2003). In general extant forms of the hemipterans have jumping adults and underground scavenger nymphs. They consume leaves and roots of great variety of non herbaceous plants (figure 6). The other hemipteran represented in the Los Rastros is a small group: the Coleorrhyncha. Today, it is only present in the southern hemisphere, living in caves, leaf-litter of the southern beech-tree forest or feeding on wet mosses (Bryophyta), on them (figure 6).

The Ensifera (crickets), are one of the less common insect orders represented in the Los Rastros fossil biota, together with the Miomoptera, Plecoptera and Odonoptera (Martins-Neto *et al.*, 2003). These Triassic ensiferans belong to the Haglidae family, which had a great diversity from the late Permian to the early Cretaceous (Sharov, 1968; Storozhenko, 1997) but only five relict species survive today. Most of the available biological information on the family is from haglines. The recent hagline genera inhabit coniferous taiga zones (Morris and Gwynne, 1978; Storozhenko, 1980), and emerge in spring being only active at night when the insects move into low bushes or coniferous trees to mate and to feed on vegetation (staminate cones and leaf-galls of sagebrush are known food items). During daylight, adults and nymphs retreat into shallow burrows, often under stones. Oviposition behavior is unknown, but as female haglines have lost the sword-like ovipositor characteristic of most Ensifera, they probably lay eggs in burrows; the few ensiferans that show maternal care of eggs or young have a reduced or absent ovipositor (Gwynne, 1995).

Living Tettigoniidae, the closest related group to the Haglidae, are characterized by living in vegetated areas with trees and bush, and they are represented by both carnivorous and omnivorous forms. The species of *Notopamphagopsis* (Haglidae) was one of the unique sound producers among the insect fossil biota, and its sound probably was strong if we consider wing span reported from other species of this genus (fore wing length 36 mm in *N. bolivari* Cabrera from the Potrerillos Formation, Mendoza province).

The aquatic component of the Los Rastros fossil biota is very scarce, but Wilson (1988) suggests that under-representation of aquatic groups is common in the lacustrine fossil record. In the Los Rastros succession the only indirect evidence of this fact, up to date, is the record of adult forms of the orders Miomoptera, Plecoptera and Odonoptera. Their nymph stages have aquatic habits, and are active predators. Immature stoneflies are aquatic nymphs

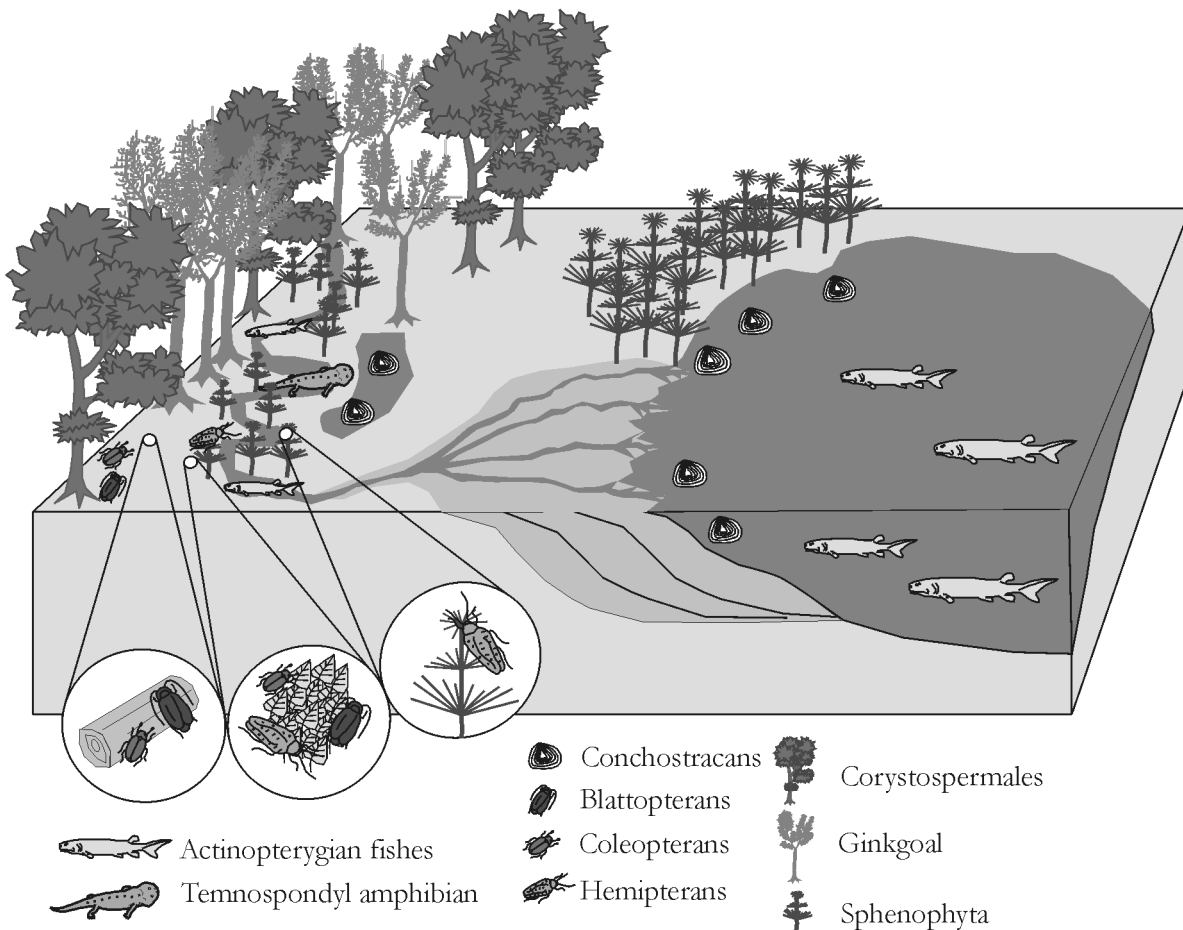


Figure 6. Paleobiological reconstruction of the Los Rastros biota taken from Mancuso, 2005a. It shows the different habitats and diet that the blattopterans, coleopterans and hemipterans may have developed. Organisms and environment are out of scale / *reconstrucción paleobiológica de la biota de Los Rastros tomado de Mancuso, 2005a. Se muestran los diferentes hábitats y dietas que los blattópteros, coleópteros y hemípteros pudieron desarrollar. Organismos y ambiente fuera de escala.*

(naiads) that usually live under stones in fast-moving, well-aerated water. Most species are herbivorous, feeding on algae and other submerged vegetation, but two families are predators on mayfly nymphs (Ephemeroptera) and on other small aquatic insects. Adult stoneflies emerge from their streams and can generally be found on the banks next to their previous habitat. They are not active fliers and usually remain near the ground where they feed on algae or lichens. In many species, the adults are short-lived and do not have functional mouthparts. Stoneflies are most abundant in cool climates with a few exceptions in the southern hemisphere living on damp soil; stonefly nymphs dwell in aquatic habitats. The preferred habitat is in rocky streams with a noticeable current at least. Some species can live in damp sandy areas. The usual habitat in running water contains rocky, stony, or gravelly substrata with more diversity in cooler, swifter water. Some studies have shown a correlation between certain species and certain habitats. For instance, Perlidae and Perlodidae are usual-

ly encountered under large stones, while Chloroperlidae tend to appear in gravel and Pteronarcyidae are frequently found in leaf packs. Extant members of the Gripopteriidae (Plecoptera) have aquatic nymphs, with both predator and herbivorous habits (Richard and Davies, 1984).

Discussion

Biostratigraphic processes are very important as control on insect preservation, and are mainly responsible for the disarticulation and fragmentation of organisms. Particularly in the aquatic setting, the floating time of insects in the surface is uneven, and is also an important control on preservation (Martinell and Martínez-Delclós, 1990; Martínez-Delclós and Martinell, 1993; Martínez-Delclós *et al.*, 2004). One of the main variables is whether the insect arrives to the water dead or alive. The insects that die in aerial or terrestrial conditions, and are later intro-

duced into water, float for a longer time. In contrast, live insects fall to the bottom in relatively short time. This is caused by the increase of their weight, due to water penetrating into the body when the individuals try to escape from surface tension (Martinell and Martinez-Delclós, 1990; Martinez-Delclós and Martinell, 1993; Martinez-Delclós *et al.*, 2004).

During floating time on the water surface, insects may undergo several processes. The main process, in the aquatic setting, is the biologic activity produced by possible predators such as other insects, fishes or amphibians. They eat most of the insect and result in an important taphonomic filter (Martinell and Martinez-Delclós, 1990; Martinez-Delclós and Martinell, 1993; Martinez-Delclós *et al.*, 2004). The predators may also produce insect disarticulation and/or fragmentation. The predator attack may be random or selective, thus the soft tissues, as the abdomen, are selected, whereas other tissues, like wings, are deposited. These attacks produce fragments with different floating potential (Martinell and Martinez-Delclós, 1990; Martinez-Delclós and Martinell, 1993; Martinez-Delclós *et al.*, 2004). The decomposition is the other process that affects the insect body on the water surface and any biological or physical disturbance promotes fragmentation and rapid decay.

The floating time depends on several factors. The relation between volume and surface of the insect body is one of these factors. For example, the rough outside organisms show void floating time whereas, the organisms with big wing surface can experience complete decomposition processes on the water surface (Martinell and Martinez-Delclós, 1990; Martinez-Delclós and Martinell, 1993; Martinez-Delclós *et al.*, 2004). During the decay process, the water infiltrated the soft tissue producing the increase of insect weight and the fall through the water column. However, there are external factors that produce the fall of the remains, such as rain, waves produced by wind, and variation of surface tension. Moreover, push from other organisms may produce selective fall, as observed by Martinell and Martinez-Delclós (1990) where the shocks produced by crustaceans cause some body parts to fall and leave the rest of the body afloat.

The fall of an insect carcass, in a quiet environment, is usually slow and vertical; during the fall the same processes as described above may affect them. So, the biological attacks may both occur on water surface or during the fall through the oxygenated zone. Besides, the insects may also suffer the normal degradation of the soft tissues during their fall in the oxygenated zone. (Martinell and Martinez-Delclós, 1990; Martinez-Delclós and Martinell, 1993; Martinez-Delclós *et al.*, 2004).

Wilson (1980, 1988) observed that the insect taxa AMEGHINIANA 44 (2), 2007

with weak flying ability (Coleoptera, Hemiptera Fulgoroidea, Hemiptera, Heteroptera, etc.) are relatively more common at near-shore facies, whereas insect taxa with strong flying ability (Diptera, Hymenoptera) are more common in off-shore associations.

Generally, the insect-bearing sediments show evidence of anoxic conditions such as absence of benthonic organisms, invertebrate trails and bioturbation. Therefore, insect disarticulation and/or fragmentation presumably occurred during the arrival to the water, floating, or sinking through the oxygenated zone. In contrast, the presence of partially or totally articulated insects suggests that they probably arrived alive to the water and suffered a relatively rapid fall. Thus, the insect remains were safeguarded from attacks and degradation on the water surface and in the oxygenated zone. Finally, there are no biologic and/or physical disturbing agents in the bottom.

The Los Rastros insects are mainly adult, terrestrial and winged, and they are considered allochthonous to the lake. Thus, they may stem from the paleoshoreline of the lake or from more distant sectors into the affluent system. The insect record includes from almost complete individuals to isolated wings, and its taphonomic features allow to characterize several possible pathways. The disarticulated insect remains represented by isolated wings (blattopteran and hemipteran wings and coleopteran elytra) can be produced by three possible pathways. The first pathway is that the insect remains arrived already disarticulated to the lake; the second is that the insects are selectively attacked and only wings are preserved; and the third is that the individuals suffered the normal decay on the water surface and/or during sinking through the oxygenated zone. Another pathway is denoted by the articulated remains represented by almost complete individuals (coleopteran elytra and bodies), which suggests that some living organisms arrived to the lake and suffered a relatively rapid fall, and housed in the anoxic bottom, where they were saved from biological attacks and decay.

Conclusions

The insect assemblage from the Los Rastros Formation bears the same composition as the other known classic Triassic Gondwana deposits, specially constituted by isolated wings of Hemiptera, Coleoptera and Blattoptera. They suggest a global taphonomic pattern and fossilization process, with a complex of anoxic and calm lakes and streams associated to a low diversity pattern, after the Permian-Triassic transition. The whole insect assemblage is es-

entially allochthonous, and the remarkable amount of isolated wings of different types and thickness, suggests different taphonomic histories. The thick elytra of the coleopteran specimens suffer less fragmentation like (in a minor scale) the fragmentation of the coreaceous wings of the cercopoid-like *Dysmorphoptilidae*. The presence of articulated elytra indicates that specimens arrived alive to the lake, suffered a relatively rapid fall through the water column, and were housed in the anoxic bottom, which preserved them intact. The blattopteran wings, together with the more fragile wings of other insect groups, are more liable to undergo fragmentation during transport and long periods of flotation on the water surface, as well as during the fall through the water column by the attack of other organisms, like conchostracans and small fishes.

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