

Research Article

Mesozoic Coleopteran Faunas from Argentina: Geological Context, Diversity, Taphonomic Observations, and Comparison with Other Fossil Insect Records

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Received 2 October 2011; Revised 30 November 2011; Accepted 14 December 2011

Academic Editor: Ai-Ping Liang

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The order Coleoptera is the most diversified group of the Class Insecta and is the largest group of the Animal Kingdom. This contribution reviews the Mesozoic insects and especially the coleopteran records from Argentina, based on bibliographical and unpublished materials (86 described species, 526 collected specimens). The material came from different geological units from the late Middle Triassic to the Late Triassic (Bermejo, Cuyo, and Malargüe basins) to the Middle-Late Jurassic and Early Cretaceous (Deseado Massif, Cañadón Asfalto, and San Luís Basin). The coleopteran record is composed of 29 described species with 262 collected specimens (isolated elytra) mainly represented by Triassic species and only four specimens recorded in Jurassic units, all of them currently unpublished. These fossil coleopterans provide fundamental information about the evolution of insects in the Southern Hemisphere and confirm the Triassic Argentinean insect deposits to be among the most important in the world.

1. Introduction

Continental invertebrate communities from the Mesozoic Era are represented principally by two phyla: Arthropoda and Mollusca. Arthropods constitute the most abundant and diverse fossil record in lacustrine sequences of Argentina with “conchostracans”, insects and ostracods as most representative groups. The mollusks, represented by bivalve and occasionally gastropods, have a low diversity and restricted distribution [1].

The recent insects constitute the richest class in terms of species diversity with estimates ranging from 3 to 50 million species [2–5]. There are 1275 families of known insects in the fossil record and 967 presently existing, of which 70% are also known as fossils [6, 7]. The data from insect fami-

lies/genera indicate that the group's growth model follows an exponential curve of evolution, contrary to the occurrence of new orders, which declines [8, 9].

The Coleoptera represents the most diverse order within the Class Insecta, both taxonomically and ecologically. In addition, it is the most speciose group in the Animal Kingdom with the number of described modern species exceeding 350,000, representing about 40% of the known insect fauna [10]. This diversity is probably related to certain features that allow adult living in restricted niches while retaining their ability to fly [10].

The systematics and phylogeny of fossil beetles is a very complex area, with old and new proposals and numerous publications which surprisingly still not clear this question. Most studies use different methodologies and are based

mainly on adult morphology and rarely use immature stages of ontogenetic development. The basis of modern classification of fossil coleopterans was initially established by Crowson [10, 11].

The oldest record of the Coleoptera is from Paleozoic Era: Lower Permian deposits of the Wellington Formation from Oklahoma and Kansas (USA) [12, 13], Obora (Czech Republic) [14, 15], and the Chekarda, Ural region (Russia) [16].

Mesozoic beetles were much more common and diverse than Paleozoic; geological information shows that beetles have had a dominant record among the group of insects since early Jurassic [16]. However, further information still remains elusive as the Mesozoic beetles are less informative, because of isolate elytra, than those of the Paleozoic [11]. The Mesozoic associations consisted mainly of xylophagous forms and larval stages have been found in numerous localities, except in the Upper Cretaceous.

The aim of this paper is to present the record of abundance and diversity of Mesozoic beetles in Argentina. The information comes from a bibliographic compilation and study of materials found in recent paleontological expeditions conducted by our research group. At the same time, we provide information on the geology and age of localities where the material was collected and present a comparison with other Mesozoic groups of insects collected in Argentina and contemporary faunas from southern Hemisphere. Finally, it provides paleobiogeographic information and highlights the importance of beetles in understanding the evolution of the Mesozoic after the Permian Triassic extinction event.

Our analyses are based primarily on elytra in the Upper Triassic localities from Argentina, which provide a significant amount of information for Coleoptera and allow to have a vision of the composition of the assemblages about 252 million years ago. Cretaceous and Jurassic materials are mentioned in passing, and their study is in progress.

2. Previous Coleopteran Records

Contributions involving the study of beetles in Mesozoic continental sediments of Argentina began with Frenguelli [17, 18], who observed small curculionid elytra in shale samples from southwestern Mendoza Province (stratigraphical levels unknown) and other beetle elytra originating from various levels of the Ischigualasto Formation (probably levels of the Los Rastros Formation *sensu* Stipanovic and Bonaparte [19]), San Juan Province. Fossa-Mancini [20] reported the presence of galleries related to burrowing larvae of certain xylophagous beetles in silicified trunks from Upper Cretaceous of Patagonia. Feruglio [21] mentioned fossil beetles represented by silicified incomplete elytra, thorax, and abdomen remains, probably attributable to the Elateridae, from Laguna del Molino locality (Gran Bajo de San Julián) in Santa Cruz Province.

Subsequently, Genise [22] presented a description of different ichnofossils found in fossil trunks and fructifications from the Upper Cretaceous of Rio Negro Province, assigned to the probable activity of beetle and termites larvae. Further, Genise and Hazeldine [23] described insect traces in fossil

wood from La Matilde Formation from the Jurassic Petrified Forest of Jaramillo in Santa Cruz Province, probably assigned to the activity of buprestid larvae. Martins-Neto and Gallego [24] disclosed the remains of beetles consisting of isolated elytra and body parts from the La Matilde Formation of Gran Bajo de San Julián in Santa Cruz Province, assigned mainly to Caraboidea. Gallego et al. [25] reported a second discovery of fossil beetles as *Argentinocupes* and *Argentinosyne* and other insects as blattids and hemipterans in the Bermejo Basin in San Juan Province and the first record from the upper Los Rastros Formation of this basin.

The Order Coleoptera was also treated in the works of Martins-Neto et al. [26–30] and Martins-Neto and Gallego [31], where new Triassic species assigned to Permosynidae, Schizocoleidae, Cupedidae, and Elateridae were described. The material (elytra) was collected in Ischichuca and Los Rastros Formations of the Bermejo Basin in La Rioja Province and Potrerillos and Cacheuta Formations, Cuyo Basin of Mendoza Province. Monferran et al. [32] mention a new locality with a record of Coleoptera: Estancia Fossati, Puesto Almada Member of the Cañadón Asfalto Formation, from Middle to Late Jurassic in age. Brauckmann et al. [33] describe two elytra of Permosynidae (*Ademosyne rosenfeldi* and *Ademosyne llantenesensis*) from the Llantenes Formation of the Malargüe Basin, Mendoza Province.

3. Material and Methods

Triassic specimens from the Cuyo Basin originate from three areas: (a) south of Cerro Cacheuta at the Puesto Miguez, Quebrada del Durazno and Agua de las Avispas localities, in Potrerillos and Cacheuta strata of the Upper Triassic; (b) north of Cerro Bayo at the Quebrada del Cerro de las Cabras locality in Cerro de las Cabras Formation of the Middle Triassic and Quebrada del Puente locality in Potrerillos Formation of the lower Upper Triassic; and (c) southeast of Cerro de los Colorados, Paramillos de Uspallata, in strata of the Cacheuta Formation (Upper Triassic).

In the Malargüe Basin, material was collected from the upper portion of the Llantenes section of the Llantenes Formation (Late Triassic). In the Bermejo Basin, the fossil insects come from Río Gualo, Picos Gemelos, Agua Escondida, Quebrada de Ischichuca Chica, and Chañares localities, belonging to Los Rastros (early Late Triassic) and Ischichuca (late Middle Triassic to early Upper Triassic) Formations, in La Rioja Province.

Jurassic beetles were collected from the La Matilde Formation of Middle to Late Jurassic ages, Laguna del Molino locality (Gran Bajo de San Julián), and from Estancia El Malacara locality (Bahía Laura), from Santa Cruz Province, and the Cañadón Asfalto Formation, of Middle to Late Jurassic age, from the Estancia Fossati locality, Chubut Province.

Cretaceous insects originate from the Anfiteatro de Ticó Formation, of the Baqueró Group, Bajo Grande, in Santa Cruz Province and La Cantera Formation, Gigante Group, in San Luis Province; both are from the Early Cretaceous.

It is important to emphasize that material collected in the Potrerillos-Cacheuta sequences during an expedition occur-

ring in April of 2010 was included in our analyses, as was Jurassic specimens from Chubut Province, collected during a 2009 fieldtrip and material from the Los Rastros Formation. This newly discovered material is important for understanding beetle evolution in Argentina during the Mesozoic because it is so diverse, abundant and well preserved.

The material cited in the literature is deposited in the paleontological collection with the acronyms PULR-I (Invertebrate Paleontological Collection, Universidad Nacional de La Rioja, La Rioja Province), CTES-PZ (Paleozoological Collection of the Universidad Nacional del Nordeste, Corrientes Province), MCNAM (Museo de Ciencias Naturales y Antropológicas “J. C. Moyano”, Mendoza Province), MHIN-UNSL-GEO (Museo de Historia Natural de la Universidad Nacional de San Luis, San Luis Province), MLP (Museo de La Plata, Invertebrate Paleontology, La Plata, Buenos Aires Province), and CORD-PZ (Palaeozoological Collection, Universidad Nacional de Córdoba, Córdoba Province).

4. Mesozoic Insects Record from Argentina

Most information on the Mesozoic insect faunas of Argentina comes from the Triassic Period and, above all, from collections made of the Los Rastros Formation, Bermejo Basin (La Rioja), and Potrerillos Formation, Cuyo Basin (Mendoza). Both provide 90% of the total abundance of insects in Argentina, constituting one of the most important records of continental life developed in Gondwana. In addition, these basins are known for their large extent, exceptional outcrops, well-developed stratigraphy columns, and the wealth of their taphofloras and vertebrate faunas.

In Argentina, knowledge of Mesozoic insects has made remarkable strides in recent years, having as a background the works published by Wieland [34, 35], Tillyard [36], and Cabrera [37] on fossil insects from the Cacheuta and Potrerillos Formations of early Late Triassic age. So far, 86 species in 27 families of 12 orders have been described from 526 samples collected (Figure 1). The fossil insect fauna of Argentina comes from stratigraphic levels of continental sediments assigned to the interval between the upper Middle Triassic to Lower Cretaceous.

4.1. Insects Records and Geological Context (Figure 2)

4.1.1. Triassic. The fossiliferous potential of the Argentina Triassic units is highly significant, based on 510 collected specimens and 81 described species. The insect record comes from Los Rastros and Ischichuca Formations of the Bermejo basin, La Rioja Province; Potrerillos, Cacheuta, and Cerro de las Cabras Formations of the Cuyo Basin, Mendoza Province; and Llantenes Formation of the Malargüe Basin, southern Mendoza Province (Figure 3).

The Cuyo Basin of central western Argentina is composed of thick sedimentary sequences from the Middle to Late Triassic that constitute the Uspallata Group. These units have a rich and well-known *Dicroidium* flora, as well as a microflora and a fauna as invertebrates, fishes, and tetrapods that are interpreted as dwelling in fluvial-lacustrine systems. Insect collections of coleopterans, blattids, hemipterans,

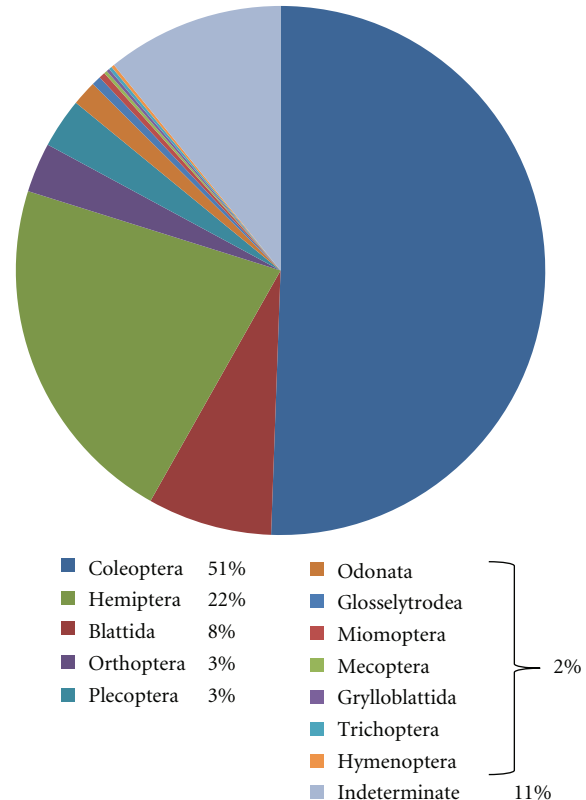


FIGURE 1: Pie-chart showing the abundance of Mesozoic specimens from Argentina, grouped by taxonomic order.

miomopterans, orthopterans, trichopterans, plecopterans, odonatans, and grylloblattids originate from the Cerro de las Cabras Formation (1 specimen), the Potrerillos Formation (21 described species and 229 collected specimens), and the Cacheuta Formation (2 described species and 27 specimens) [29, 30, 39–43].

The Malargüe Basin of southern Mendoza Province includes Choiyoi volcanic and overlain siliciclastic deposits. The insect fauna was collected from the upper section of the Llantenes Formation (Late Triassic) which is built of two coarsening-upward cycles reflecting a deltaic progradation of a fluvial into a lacustrine environment (lower part), succeeded by repeated progradation into a floodplain dominated environment (upper part; with insects, conchostracans, fish, and plants remains). The insect remains includes 2 coleopteran elytra and 1 mecopteran, and these new finds represent the youngest Triassic occurrence from Argentina and South American and the second youngest record from the Southern Hemisphere [33].

The Los Rastros and Ischichuca Formations (Agua de la Peña Group, La Rioja Province) are part of the Bermejo Basin (Ischigualasto-Villa Unión Basin), an extant basin located in northwestern Argentina. The Los Rastros Formation of early Late Triassic age is a lacustrine-deltaic that consists of several sedimentary cycles of black shales, siltstones, and sandstones. The succession is characterized by record of five plants, four invertebrates, and four vertebrates taphofacies [44]. The

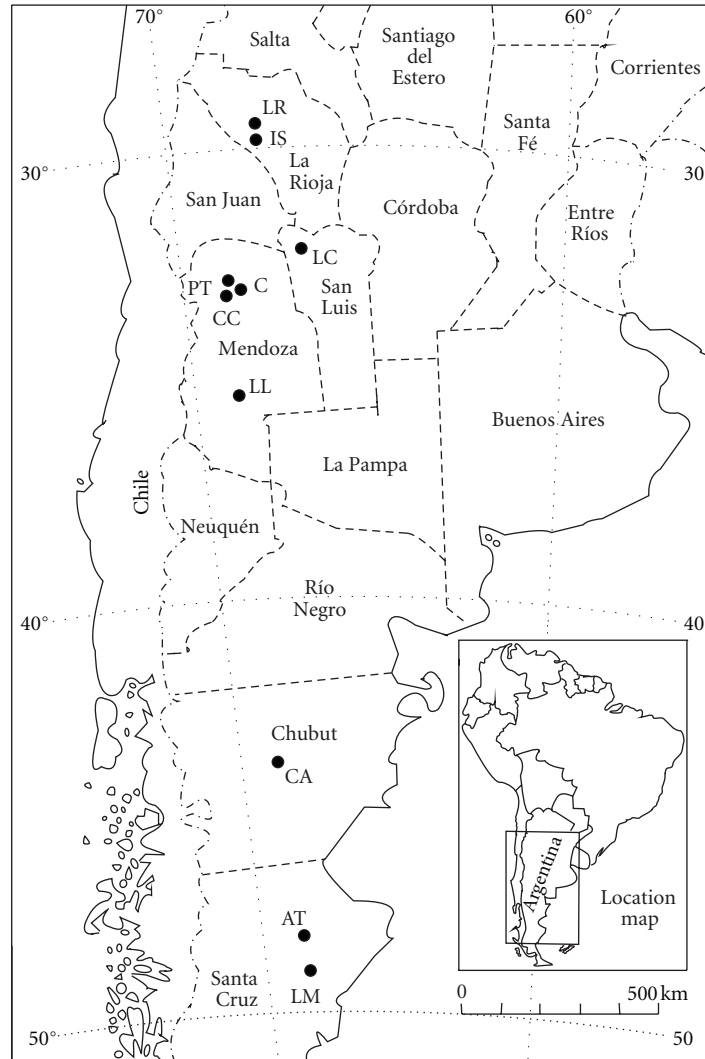


FIGURE 2: Map showing the Mesozoic units and outcrop areas approximately that carried the insect fauna mentioned in the text. AT: Anfiteatro de Ticó; C: Cacheuta; CA: Cañadón Asfalto; CC: Cerro de las Cabras; IS: Ischichuca; LC: La Cantera; LL: Llantenes; LM: La Matilde; LR: Los Rastros; PT: Potrerillos. (modified from Zavattieri [38]).

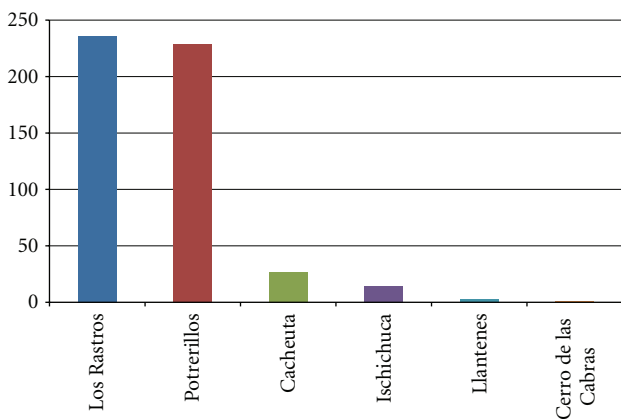


FIGURE 3: Bar graphic showing the abundance of specimens in different Triassic insect localities. (Note: included new undescribed materials).

insect record consists of 44 described insect species and 236 collected specimens and is comprised of coleopteran elytra and wing remains of blattids, plecopterans, miomopterans, orthopterans, glosselytrodeans, and odonatans [26, 27, 42, 45]

The Ischichuca Formation of late Middle Triassic to early Late Triassic age is predominantly composed of shallow and deep lacustrine facies with progradational deltaic successions, that starts to begin as fanglomerates with sandstones and tuffitic intercalations and continue with dark carbonaceous shales alternating with sandstones and pelitic and tuffaceous strata. In particular, insect remains are found in dark brown to olive-green claystones with abundant plant remains from the middle to the basal upper parts of the unit. This interval is interpreted as a shallow, partly saline lake (interpreted from a perennial playa lake association facies, L2 from Melchor [46, 47]) that ranges to a deep freshwater lake (deep freshwater lake association facies, L3 from Melchor [46, 47]).

The fossil insects, consisting of 11 described species and 14 specimens, comprise a blattid wing and coleopteran elytra [31, 41, 48].

4.1.2. Jurassic. The Jurassic insect fauna from Argentina (Table 1) is less well known than the Triassic one and also sparse when compared with other Jurassic localities of the world. This rarity is due to its restricted geographic distribution and low species diversity and is related to the low number of collections and studied localities.

The first contribution probably was made by Frenguelli [18] who mentioned and illustrated the “rare insect remains” of a paleohemipteran wing from the “Estancia El Malacara” from Bahia Laura, in Santa Cruz, Province. In the 1990s one of us (O. F. Gallego) and Rafael Martins-Neto restudied this specimen and concluded that it is probably not an insect. Later, Feruglio [21] reported the presence of silicified coleopteran remains from the Laguna del Molino locality of Gran Bajo de San Julian, in Santa Cruz Province) associated with plant fragments, bones, freshwater mollusks, and conchostracans. These previous contributions of insect reports were summarized by Gallego and Martins-Neto [49], Martins Neto and Gallego [24, 50], Monferran et al. [32, 51, 52], Genise et al. [53], and Gallego et al. [54] who reported new finds of insects from the orders Coleoptera (elytra and body remains), Heteroptera (fragmentary wings), and Trichoptera (wing fragments and larval cases) from both the La Matilde Formation of the Laguna del Molino locality and Cañadón Asfalto Formation of Cerro Cóndor and Estancia Fossati localities. These records are associated also with gastropods, bivalve mollusks, ostracods, conchostracans, plants, and fish remains. Other Jurassic insect records such as the presence of chironomid head capsules and larval cases [55] and mecopterans (Bittacidae) with complete bodies [56] come from Gan Gan locality of the Cañadón Asfalto Formation in Chubut Province.

The Jurassic fossil insect record from Argentina comes from two geological units: the La Matilde Formation (late Middle Jurassic, Santa Cruz Province) and the Cañadón Asfalto Formation of late Middle Jurassic to Late Jurassic age, Chubut Province.

The late Middle Jurassic La Matilde Formation comprises a volcanoclastic sequence that bears silicified woods (ferns and gymnosperms), a taphoflora, invertebrates, and tetrapods. The sediments show a typical continental sequence of a low-energy fluvial system, with lentic water bodies under reduced conditions within a floodplain environment, influenced by intensive volcanism evidenced by pyroclastic deposits [57].

The Cañadón Asfalto Formation of Middle-Late Jurassic age is a thick sedimentary sequence with volcanic intercalations that constitutes one of the most important nonmarine Jurassic records from South America. Two members can be distinguished, the lower one, the Las Chacritas Member, and the upper one, the Puesto Almada Member [58]. The insects were found in the upper member and particularly from the locality “Estancia La Sin Rumbo”, an assemblage of “con-

TABLE 1: Mesozoic insects from Argentina.

Order	Triassic	Jurassic	Cretaceous	Mesozoic insects
Coleoptera	262	4		266
Hemiptera	104	4	6	114
Blattida	39		1	40
Orthoptera	16			16
Plecoptera	16			16
Odonata	7		1	8
Glosselytrodea	3			3
Miomoptera	2			2
Mecoptera	1			1
Grylloblattidae	1			1
Trichoptera	1			1
Hymenoptera	1			1
Indeterminate	57			57
Total	510	8	8	526

chostracans”, ostracods, bivalves, and caddisfly cases. This assemblage occurs in the upper part of a volcanoclastic lacustrine sequence consisting of yellowish tuffs and tuffites providing evidence of dry climatic conditions. The assemblage recorded from the Estancia Fossati locality came from three levels consisting of shales, limestones, and tuffs, associated with invertebrates such as bivalve mollusks, insect larval cases, ostracods, conchostracans), and fish scales. The Estancia Fossati faunas represent low-energy shallow freshwater environments within associated plant communities [54, 59].

4.1.3. Cretaceous. The poorly known Cretaceous insect fauna from Argentina is reflected by only 5 described species and only 8 collected specimens (Table 1). These records are based on two Early Cretaceous localities: (a) the Anfiteatro de Ticó Formation, Bajo Grande locality, from Santa Cruz Province, and (b) the La Cantera Formation, Gigante Group of San Luis Province.

The Anfiteatro de Ticó Formation of the Baqueró Group is composed by siliciclastic and volcanoclastic deposits [60] and the insect fauna consisting of the species *Blattulopsis popovi* (Blattida) [61] and *Argentinopetala archangelskyi* (Odonata) [62].

The La Cantera Formation of the Gigante Group exhibits greenish to gray limonite and arcillite with intercalated red sandstones and shales in the upper part [63]. The La Cantera assemblage is composed of a large, diverse association of ostracods, insects (hemipterans, orthopterans, coleopterans and caddisfly larval cases), palynomorphs, plants (leaves and sphenopsid reproductive organs), and fish fragments [64]. The paleontological content of this deposit suggests a lakeshore environment, attributable to fish taxonomic diversity and the poor state of terrestrial insect preservation [65]. Insect remains comprise of *Canteronecta irajae* (Naucoroidea) [66], *Rhomboidella popovi* (Corixidae) [67] and

Notonecta mazoniae (Notonectidae) [65]. Also are recorded the poorly preserved orders Coleoptera, Orthoptera, and Trichoptera.

5. Mesozoic Coleopterans from Argentina

The analysis of Coleoptera used information obtained from previous publications [21, 26–33, 39, 44]. Information was also obtained from observation of new unpublished material collected in the 2010 expedition to the Potrerillos Formation of Mendoza Province (Figures 4(f)–4(r)), Los Rastros Formation of La Rioja Province, and Jurassic specimens from Cañadón Asfalto Formation of Chubut Province.

Coleoptera is the most abundant and exhibits the greatest speciosity among Mesozoic insect fauna in Argentina. Until now, 262 specimens have been collected, covering about 50% of the total abundance, and 29 species have been described, including the permosynids *Ademosyne umutu*, *A. llantenesensis*, *A. rosenfeldi*, *A. arcucciae* (Figure 4(c)), *A. punctuata* (Figure 4(d)), *A. elongatus*, *A. hexacostata*, *Ademosyne* sp. 1, *Ischichucasyne cladocosta*, and *Delpuentesyne menendezii*; the schizocoleids *Argentiniosyne ischichucaensis*, *A. duraznoensis*, *A. bonapartei*, *A. frengüelli* (Figure 4(b)), *A. rugosa*, *A. gualoensis*, *A. gonaldiae*, and *A. losrastrosensis*, Gen. et sp. indet. 1 and 2; the elaterids *Babuskaya elaterata*, *Gemelina triangularis*, *Cardiosyne obesa*, *C. elegans*; the cupedids *Argentinocupes sara*, *A. pulcher* (Figure 4(a)), and *A. abdalai* (Figure 4(e)); and two specimens Gen. et sp. indet. 1 tentatively assigned to the Permosynidae family and other specimen (Gen. et sp. indet. 1) of uncertain position.

From an analyses of the information about Triassic beetles, the best represented groups are families Permosynidae (135 specimens) and Schizocoleidae (40 specimens); the genera *Ademosyne* (129 specimens) and *Argentiniosyne* (39 specimens); and the species *Ademosyne arcucciae* (96 specimens, Figure 4(c)) and *Ademosyne hexacostata* (17 specimens). Ninety-eight percent of the specimens collected are from Triassic continental sedimentary rocks, from Los Rastros Formation (69% of total abundance), Potrerillos Formation (17%), Cacheuta Formation (9%), Ischichuca Formation (4%), and Llantenes and Cerro de las Cabras Formations (2%).

The beetles preserved in the various localities appear as complete impressions, body part impressions (abdomens, thoraces), and as elytra moulds that can be complete or fragmentary, articulated or disarticulated, smooth or striated, with or without ornamentation.

Two analyses were performed. The first considered the state of preservation, namely, if the specimen was complete/incomplete, and its degree of articulation/disarticulation. For these measurements, there were used 262 elytra distributed in the different formations as shown in Table 2.

The beetle fauna consists mainly in complete and disarticulated elytra (211 samples; Figures 4(a), 4(d), 4(f)–4(l), 4(n)–4(r)), followed by incomplete and disarticulated elytra (41 samples), complete and articulated elytra (8 samples; Figures 4(b), 4(c), 4(e), 4(m)), and last incomplete and articulated elytra (2 samples) (Figure 5).

In the second analysis, elytra ornamentation was observed, used in describing the following specimens: 187 specimens from Bermejo Basin and 8 from Malargüe and Cuyo Basins. Accordingly, the ornamented elytra may be smooth (46 specimens; Figures 4(b), 4(f), 4(g), 4(k), 4(l), 4(m), 4(o), 4(q) and 4(r)) or striated (149 specimens; Figures 4(a), 4(c)–4(e), 4(h), 4(i), 4(n), 4(p)). In the case of striated elytra, costae may be smooth (91%; Figure 4(c)), punctuate (6%; Figure 4(d)), or granular (3%). The number of costae can vary between 6 and 11. Elytra also can have ornamentation (173 specimens) or lack it (22 specimens). Lastly, the ornamentation can be granular (93%; Figure 4(c)), rough (5%), with rows of cells (1%, Figure 4(a)), or striated (1%).

5.1. Jurassic and Cretaceous Coleopterans. Knowledge of beetles and of insects in general from Jurassic and Cretaceous sediments in Argentina is poorly developed. This absence of data highlights the importance of exploring for new fossil insect localities. In general, beetles are only referenced in works that treat other insect groups. By contrast, information generated for the Jurassic and the Cretaceous of Argentina will allow its characterization and comparison with other continental faunas from the Southern Hemisphere (South America, Antarctica, and Australia), currently which are better known. Therefore, owing to the scarce information about the Jurassic and Cretaceous specimens, the present study has considered only examination of Triassic material.

6. Comments on Other Insect Orders from Argentina (Figure 6)

Hemiptera is the second most common order in the Mesozoic from Argentina with 114 specimens collected (22%) and 19 described species from various assemblages. The material is preserved as impressions of wings (fore or hind, complete or fragmentary, with or without a clavus) and occasionally complete bodies of insects, most attributable to the families Dymorphoptilidae (9 specimens) and Scytinopteridae (7 specimens); the genus *Gallegomorphoptila* (9 specimens); and the specie *Gallegomorphoptila acostai* (5 specimens). For the rest of the Mesozoic, there are only three recorded Cretaceous species: *Canteronecta irajae* (Naucoroidea) [66], *Rhomboidella popovi* (Corixidae) [67], and *Notonecta mazoniae* (Notonectidae) [65].

The Blattida (cockroaches) includes 40 specimens (7%) and 18 species, preserved as disarticulated tegmina (complete or fragmentary, with missing or not the clavus). The assemblage is dominated by the families Mancusoblattidae and Mesoblattinidae (10 specimens) and by the genus *Hermosablatta* (9 specimens). The species *Samaroblatta corrientesina*, *S. gualoensis*, *Hermosablatta crassatella*, *H. pectinata*, *Lariojablatta neiffi*, and *Condorblatta lutzae* are the most abundant taxa. The *Blattulopsis popovi* species occurs in the Lower Cretaceous of Santa Cruz Province [61].

The rest of the orders, Plecoptera and Orthoptera with 16 specimens, Odonata with 8 specimens, Glosselytrodea with

Triassic coleopterans from Argentina



FIGURE 4: Examples of fossil insects collected from Triassic insects localities, Western Argentina, illustrating the stage of preservation seen in the localities. (a) *Argentinocupes pulcher*, complete desarticulated elytron. (b) *Argentinosyne frengüelli*, complete articulated elytron. (c) *Ademosyne arcucciae*, complete articulated elytron and thoracic and abdominal elements. (d) *Ademosyne punctuada*, complete desarticulated elytron. (e) *Argentinocupes abdalai*, complete articulated elytron (Martins-Neto et al., [27]); (f)–(r) Indet. material: complete articulated elytron (m) and complete desarticulated elytron ((f)–(l), (n)–(r)). Ornamentation of elytra: smooth ((b), (f), (g), (k), (l), (m), (o), (q), (r)) and striate ((a), (c)–(e), (h), (i), (n), (p)). Scale bar: 1mm.

TABLE 2: State of preservation of the Triassic beetles.

Elytron	Formation					
	Los Rastros	Ischichuca	Potreriillos	Cacheuta	Llantenes	Cerro de las Cabras
Articulated complete	5	0	3	0	0	0
Articulated incomplete	2	0	0	0	0	0
Disarticulated complete	140	5	41	24	1	0
Disarticulated incomplete	33	5	0	1	1	1
Total	180	10	44	25	2	1

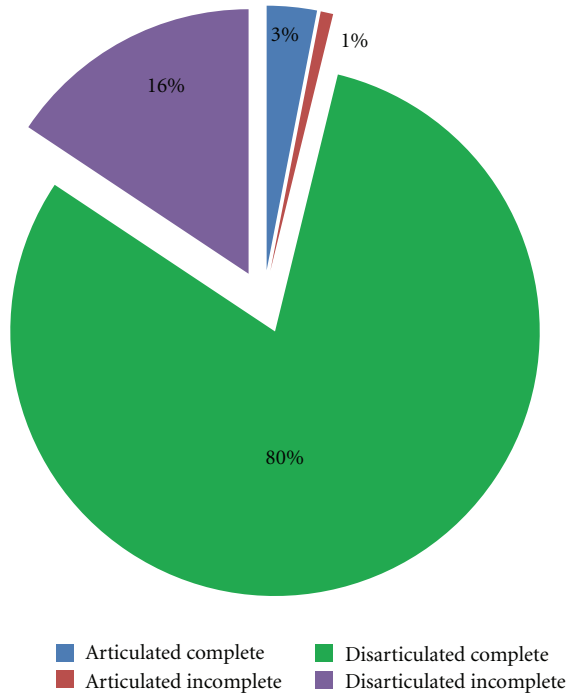


FIGURE 5: Pie-chart showing the relative percentage of specimens from beetle locality collection, grouped by element type.

3, Miomoptera with 2 specimens, and Mecoptera, Grylloblattida, Trichoptera, and Hymenoptera, all with one specimen each, constitute 9% of the total abundance of the material collected. Each one is represented by a handful of impressions of fore wings and complete or fragmentary bodies of nymphs such as head and abdominal sclerites.

The label “indeterminate” record (57 specimens, 11%) includes the complete, incomplete or poorly preserved elements, in which we were unable to be confidently assigned to any particular order or alternatively it is under study. They are represented by impressions of wings (complete or fragmentary), some elements associated with abdominal sclerites and partial bodies.

7. Paleoecology and Taphonomy

Given the aforementioned information on the Mesozoic insect fauna of Argentina, the material recovered includes disarticulated and fragmentary specimens (evidence of

postmortem transportation) approximately 97.5% of which comprises mostly impressions of wings of hemipterans and blattids, elytra of beetles, and other isolated body parts (thoraces, abdomens, appendages) of the Orthoptera, Mecoptera, Grylloblattida, Plecoptera, Trichoptera, Miomoptera, Odonoptera, Hymenoptera, and Glosselytrodea, in addition to head capsules and dwelling tubes of chironomid and caddisfly cases.

From an ecologic perspective, the analysis of this fauna shows that most groups have a subaerial or terrestrial habit as adults, and some are represented by immature (often aquatic forms), such as the Plecoptera, Grylloblattida, Hemiptera, and Odonata. This implies that the fossil record is biased by the absence of other autochthonous aquatic forms, the causes of which required future inquiry.

8. Final Considerations

Fossil beetles are one of the most interesting objects in paleontological and stratigraphical research, but they remain poorly understood, as they are difficult to study [68]. The great diversity and abundance that occurs in the fossil record is probably correlated with the composition of the elytra and its shape preservation, appearing as elytra moulds that can be articulated or disarticulated.

In South America, the previous literature reviews and the analyses of unpublished material indicate the relevance of Triassic and Tertiary beetle records. Nevertheless, the group is poorly studied and the intensity of collections is low. Therefore, it requires much more skilled work.

The record (Table 3) is restricted to continental sediments from Brazil, Argentina, Chile, and Peru. In Brazil, 17 species were discovered and come from Early to Middle Permian ages of Irati Formation [69, 70] and from Middle to Late Triassic ages of the Santa María Formation [71] of the Paraná Basin, from the Early Cretaceous age of Santana Formation in Araripe Basin [72–75], from the Oligocene age of Tremembé Formation in Taubate Basin and Fonseca Formation in Fonseca Basin [76–78]. In Argentina the order is restricted to Late Triassic age with twenty nine species described [25–31, 33] from Los Rastros and Ischichuca Formations in La Rioja Province, the Cortaderita Formation in San Juan Province, the Potrerillos, Cacheuta, Cerro de las Cabras, and Llantenes Formation in Mendoza Province; Middle to Late Jurassic ages of the La Matilde Formation in Santa Cruz Province and the Cañadón Asfalto Formation in Chubut Province [21, 24, 32]; Middle to Late Eocene

Triassic insects from Argentina

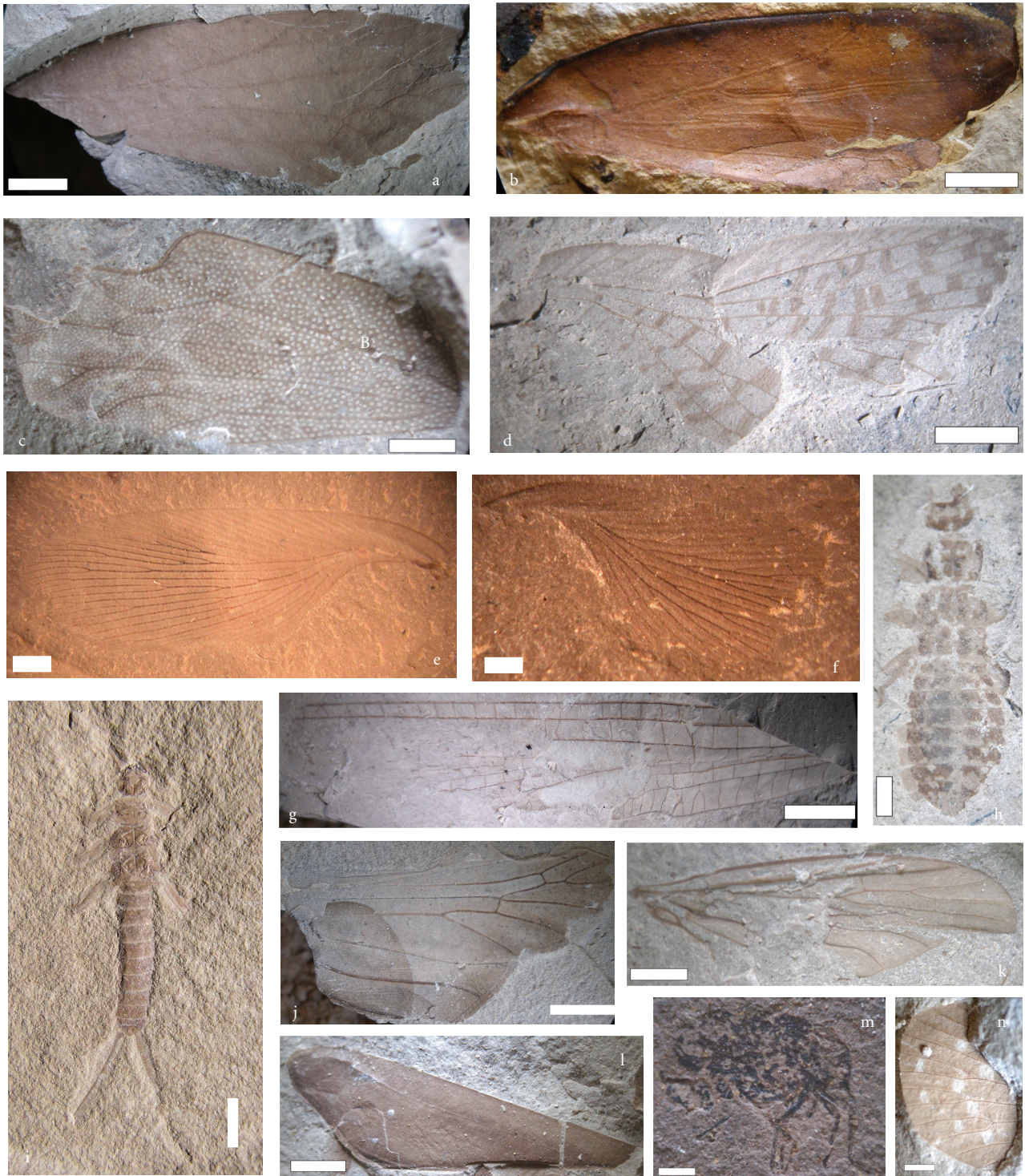


FIGURE 6: Examples of fossil insects collected from Triassic insects localities, Western Argentina, illustrating its diversity and the stage of preservation (impression) seen in the localities. (a), band (c): Hemiptera. (d): Orthoptera. (e): *Mancusoblatta pulchella* and (f): *Heramosablatta crassatella* (Blattida), Martins-Neto et al., [45]. (g) and (h): Odonata adult and nymph, respectively. (i): *Platyperla marquati* (nymph), Gallego et al., [54]. (j), (k), (m), and (n): indet. material. l: Hemiptera clavus. Scale bar: 1 mm (except (a), (b), (c), and (i): 2 mm).

TABLE 3: Main stratigraphic units and beetle localities in South America.

Erathern Era	System Period	Series Epod	Argentina			Brazil	Chile	Perú	
Cenozoic	Quaternary	Holocene							
		Pleistocene						Talara	
	Neogene	Pliocene							
		Miocene	Palo Pintado Formation						
	Paleogene	Oligocene				Tremembé and Fonseca Formation			
		Eocene		Lumbrera Formation	Ventana Formation				
		Paleocene	Maíz Gordo Formation						
	Mesozoic	Cretaceous	Upper					Dorothea Formation	
			Lower				Santana Formation		
		Jurassic	Upper		Cañadón Asfalto Formation				
Middle			La Matilde Formation						
Lower									
Triassic		Upper		Cacheuta Formation	Llantenes Formation				
				Potrerillos Formation		Cortaderita Formation	Santa Juana Formation		
			Los Rastros Formation	Cerro de las Cabras Formation			Santa María Formation		
		Middle	Ischichuca Formation						
Lower									
Paleozoic	Permian	Upper							
		Middle							
		Lower				Irati Formation			

ages from the Lumbreira Formation (Grupo Salta) in Salta Province [79]; Late Paleocene to Early Eocene age from the Maíz Gordo Formation in Jujuy Province with thirty one species [80–84]; Eocene to Early Oligocene age from the Ventana Formation in Neuquén Province [85]; and Late Miocene age from the Palo Pintado Formation in Salta Province [86]. In Chile the material just comes from Santa Juana Formation of Late Triassic age with one species [87] and Dorothea Formation of Upper Cretaceous [88]. In Peru the specimens come from the Pleistocene tar-seeps of Talara in Piura Province [89].

The Mesozoic localities in Argentina, typically from the Triassic Period, have proven to be rich in fossil insect material; recent findings of insects in the strata of the Cuyo Basin have increased the number of taxa represented to currently 510 specimens. This makes Argentina one of the most important paleoentomologic regions not only in South America but also generally in the Southern Hemisphere, such as the Triassic sequences already known from Australia and South Africa.

All the knowledge provides invaluable information about the composition of the Mesozoic biota, essential for understanding biological processes that different groups of organisms experienced after the great Permian extinction event about 252 million years ago. In addition, time series of taxa within lineages could provide data for understanding beetles evolution.

Acknowledgments

The authors would like to especially thank Ana María Zavattieri for her friendship, field-work support, and contributions to the knowledge of the Triassic Biota. Also thanks go to their friend and brother Rafael Gioia Martins-Neto for being greatly responsible for the present knowledge of Triassic insect faunas from South America. They also acknowledge Tom De Vries and Carsten Braukmann and Finnegan Marsh (as journal reviewer) for all suggested improvements to this paper. This contribution was partially supported by the Consejo Nacional de Investigaciones Científicas y Técnicas, Secretaría General de Ciencia y Técnica, Universidad Nacional del Nordeste, and by the Agencia Nacional de Promoción Científica y Tecnológica (Grants PI-64/04 and PI-075/07 and PI-2010/F022; PIP-CONICET 5581; PICTO-UNNE 0226/07 to O. F. Gallego and PIP-CONICET- 5760 and 112-201001-00034 to Nora Cabaleri).

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