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The Triassic coleopteran fauna of southern South America: Morphometric variation of elytra, paleobiogeography, and a phylogenetic approach[1]

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ABSTRACT
A review of the southern South American Triassic coleopteran fauna as well as a phylogenetical approach resulting from its analysis is presented. This work provides new tools for the study of fossil coleopteran elytra, based in its morphological aspects, its fossil record in the Middle to Late Triassic levels from southern South America basins, and by the record of speciation episodes in the assemblages. Additionally, an area cladogram and a probable phylogenetic scheme for the coleopteran fauna are provided and suggestions to age insertion and correlation are also presented.

Key words: Triassic, Coleoptera, Paleobiogeography, Phylogeny, South America, Morphometry.

RESUMO
FAUNA DE COLEOPTERA DO TRIÁSSICO DO SUL DA AMÉRICA: VARIAÇÃO MORFOMÉTRICA DOS ÉLITROS, PALEOBIOGEOGRAFIA E INFERÊNCIAS FILOGENÉTICAS. Este trabalho apresenta uma revisão da coleopterofauna sul-americana e, a partir daí, algumas propostas sobre sua evolução e idade. O principal objetivo é fornecer novas ferramentas para o estudo de élitros de coleópteros fósseis, através de seus caracteres morfológicos, do registro em níveis do Triássico Superior do sul da América do Sul, e de seus episódios de especiação. Um cladograma de área e um possível esquema filogenético são apresentados, bem como sugerida a correlação de sua ocorrência nas diferentes bacias.

Palavras-chave: Triássico, Coleóptera, Paleobiogeografia, Filogenia, América do Sul, Morfometria.

INTRODUCTION

The knowledge of the South American Triassic paleoentomofauna increased dramatically in the last few years due to continuous collecting headed by OFG and his team. Apart from the Argentinean Triassic outcrops, Triassic deposits are very poorly known in the South American continent. The contrast to those in other parts of Gondwana of which at least two areas belong to the most fossiliferous ones: the Ipswich Series of Queensland in Australia, and the Molteno Formation of the main Karoo basin in South Africa. The transition from the Permian to the Triassic was in particular dramatic for the insects with several groups became ex-

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tinct, including entire orders as Permothemistida, Megasecoptera, Diaphanopterodea, "Protorthoptera", Protelytroptera, Caloneurodea, Hypoperlida, as well as several families of the most traditional orders, Orthoptera, Hemiptera, and Coleoptera (Zherikhin, 2002).

As stressed in previous papers (Martins-Neto, 2002; Martins-Neto *et al*., 2003), some Triassic groups are conservative in their distribution, occurrence and paleogeographic patterns. Furthermore, they are widely spread and have a relatively short stratigraphic range. In particular, the Permosynidae (Coleoptera), Dysmorphoptilidae (Hemiptera), Polycitellidae (Jurinina) and triassoblattids (Blattida) are, therefore, guided fossils, indeed, from the Middle to the Late Triassic (Gallego and Martins-Neto, 2005, 2006).

The current state of knowledge of the coleopteran family Permosynidae, which is the main focus here, indicates that this family is one of the dominant components in all known Triassic localities of Gondwana, both in the number of species and in the collected specimens. Systematic, as well as an extensive analysis of the morphometric variation, ornamentation types and degree of preservation of the Argentinean Triassic permosynid elytra, was treated by Martins-Neto *et al*. (2006a), the article that is the base of the present discussion.

THE ARGENTINEAN TRIASSIC PALEOENTOMOFAUNA

The knowledge of the South American Triassic paleoentomofauna was summarized by Martins-Neto *et al*. (2003). Recent new finds, newly discovered localities, and the advance in the systematic of the Coleoptera and Blattida (Brauckmann *et al*., 2010; Gallego *et al*., 2005; Martins-Neto and Gallego, 2009; Martins-Neto *et al*., 2005, 2006a, 2006b, 2007, 2008), not included in the previous article, motivates the organizing of a new checklist (Table 1).

The Argentinean Triassic entomofauna confirms the general tendency for the classic Gondwana sites, in having Coleoptera, Hemiptera and Blattida as dominant groups, both in number of species, as well as in the total number of collected specimens (Table 2). It makes those groups crucial for the knowledge of paleoentomofaunas of the entire Triassic System.

Table 1. Summary of South American Triassic paleoentomofauna. (*) Material not considered in the statistical analysis.

Potrerillos Formation - early Late Triassic (Cerro Cacheuta, Mendoza, Cuyana Basin, Argentina)		
Odonatoptera	*Incertae sedis*	*Triassothemis mendozensis* Carpenter, 1960
Coleoptera	Schizocoleidae	*Argentinosyne duraznoensis* Martins-Neto and Gallego, 2008
Plecoptera	Gripopterygidae	*Gondwanoperlidium argentinarum* Pinto and Purper, 1978
		Gondwanoperlidium mendozensis Pinto and Purper, 1978
Miomoptera	*Incertae sedis*	*Miomina mendozina* Martins-Neto and Gallego, 1999
Grylloblattida	Atactophlebiidae	*Triasseuryptilon acostai* (Marquat) Storozhenko, 1997
Orthoptera	Haglidae	*Notopamphagopsis bolivari* Cabrera, 1928
Hemiptera	Dysmorphoptilidae	*Gallegomorphoptila acostai* Martins-Neto and Gallego, 1999
	Chiliocyclidae	*Tipuloidea rhaetica* Wieland, 1925
		Argentinocicada magna Martins-Neto and Gallego, 1999
		Argentinocicada minima Martins-Neto and Gallego, 1999
	Scytinopteridae	*Potrerillia nervosa* Martins-Neto and Gallego, 1999
	Incertae sedis	*Cacheutacicada kurtzae* Martins-Neto e Gallego, 2008
Trichoptera?	*Incertae sedis*	*Tipulidites affinis* Wieland, 1925
Potrerillos Formation - early Late Triassic (Quebrada del Puente, Mendoza, Cuyana Basin, Argentina)		
Blattoptera	Subioblattidae	*Potrerilloblatta stipanici* Martins-Neto and Gallego, 2007
	Delpuenteblattidae	*Delpuenteblatta dangeloi* Martins-Neto and Gallego, 2007
		Lariojablatta neiffi Martins-Neto and Gallego, 2007
	Blattulidae	*Anablatta compacta* Martins-Neto and Gallego, 2007
Coleoptera	Permosynidae	*Delpuentesyne menendezi* Martins-Neto and Gallego, 2007
Los Rastros Formation-early Late Triassic (Los Chañares, Bermejo Basin, Argentina)		
Odonatoptera	*Incertae sedis*	*Frenguelliphlebia labandeirai* Martins-Neto and Gallego, 2003
Miomoptera	*Incertae sedis*	*Miomina riojana* Martins-Neto *et al*., 2006
Glosselytrodea	Policytellidae	*Chanarelytrina nana* Martins-Neto *et al*., 2006
Hemiptera	Scytinopteridae	*Chanarescytina carmonae* Martins-Neto *et al.,* 2006
Blattoptera	Argentinoblattidae	*Condorblatta lutzae* Martins-Neto and Gallego, 2005
Coleoptera	Cupedidae	*Argentinocupes pulcher* Martins-Neto and Gallego, 2006
	Schizocoleidae	*Argentinosyne frenguellii* Martins-Neto and Gallego, 2006
		Argentinosyne bonapartei Martins-Neto and Gallego, 2006
		Argentinosyne losrastrosensis Martins-Neto and Gallego, 2006

Los Rastros Formation - early Late Triassic (Río Gualo, La Rioja, Bermejo Basin, Argentina)		
Blattoptera	Argentinoblattidae	*Argentinoblatta herbsti* Martins-Neto and Gallego, 2005
		Condorblatta lutzae Martins-Neto and Gallego, 2005
	Mancusoblattidae	*Mancusoblatta pulchella* Martins-Neto and Gallego, 2005
		Hermosablatta crassatella Martins-Neto and Gallego, 2005
		Hermosablatta pectinata Martins-Neto and Gallego, 2005
	Delpuenteblattidae	*Lariojablatta chanarensis* Martins-Neto and Gallego, 2005
	Mesoblattinidae	*Triassoblatta argentina* Martins-Neto and Gallego, 2005
		Samaroblatta gualoensis Martins-Neto and Gallego, 2005
		Samaroblatta corrientesina Martins-Neto and Gallego, 2005
		Pulchellablatta nana Martins-Neto and Gallego, 2005
	Blattulidae	*Argentinoblattula revelata* Martins-Neto and Gallego, 2005
Glosselytrodea	Polycytellidae	*Argentinoglosselytrina pulchella* Martins-Neto and Gallego, 2001
Plecoptera	Gripopterygidae	*Argentinoperlidium rogersi* Martins-Neto and Gallego, 2003
Orthoptera	Haglidae	*Notopamphagopsis*? sp. 1 Martins-Neto and Gallego, 1999
		Notopamphagopsis? sp. 2 Martins-Neto and Gallego, 2003
		Notopamphagopsis? sp. 3 Martins-Neto and Gallego, 2003
Hemiptera	Dysmorphoptilidae	*Gallegomorphoptila acostai* Martins-Neto and Gallego, 1999
		Gallegomorphoptila gigantea Martins-Neto and Gallego, 2001
		Gallegomorphoptila pulcherrima Martins-Neto and Gallego, 2003
		Gallegomorphoptila breviptera Martins-Neto, 2003
	Scytinopteridae	*Australocicada arcucciae* Martins-Neto and Gallego, 2001
		Gualoscytina mayae Martins-Neto and Gallego, 2003
	Stenoviciidae	*Argentinopheloscyta forsterae* Martins-Neto and Gallego, 2003
	Progonomicidae	*Popovigocimex yurii* Martins-Neto and Gallego, 2003
Coleoptera	Permosynidae	*Ademosyne arcucciae* Martins-Neto and Gallego, 2006
		Ademosyne elongatus Martins-Neto and Gallego, 2006
		Ademosyne hexacostata Martins-Neto and Gallego, 2006
		Ademosyne punctuada Martins-Neto and Gallego, 2006
	Schizocoleidae	*Argentinosyne gualoensis* Martins-Neto and Gallego, 2006
		Argentinosyne rugosa Martins-Neto and Gallego, 2006
		Argentinosyne frenguellii Martins-Neto and Gallego, 2006
		Argentinosyne gonaldiae Martins-Neto and Gallego, 2006
		Undescribed species
	Cupedidae	*Argentinocupes pulcher* Martins-Neto and Gallego, 2006
		Argentinocupes abdalai Martins-Neto and Gallego, 2006
	Elateridae?	*Gemelina triangularis* Martins-Neto and Gallego, 2006
		Cardiosyne obesa Martins-Neto and Gallego, 2006
		Cardiosyne elegans Martins-Neto and Gallego, 2006
Cacheuta Formation - early Late Triassic (Uspallata, Mendoza, Cuyana Basin, Argentina)		
Coleoptera	Schizocoleidae	*Argentinosyne rugosa* Martins-Neto and Gallego, 2006
		Argentinosyne gonaldiae Martins-Neto e Gallego, 2006
Ischichuca Formation - late Middle Triassic-early Late Triassic (Ischichuca, La Rioja, Bermejo Basin, Argentina)		
Blattoptera	Mancusoblattidae	*Hermosablatta pygmaea* Martins-Neto and Gallego, 2009
Hemiptera	Prosbolidae	*Lariojaprosbole melchori* Martins-Neto and Gallego, 2001
	Dysmorphoptilidae	*Gallegomorphoptila kotejai* Martins-Neto and Gallego, 2006
Coleoptera	Permosynidae	*Ademosyne punctuada* Martins-Neto and Gallego, 2006
		Ademosyne umutu Martins-Neto and Gallego, 2009
		Ischichucasyne cladocosta Martins-Neto and Gallego, 2009
	Schizocoleidae	*Argentinosyne ischichucaensis* Martins-Neto and Gallego, 2009
		Argentinosyne frenguellii Martins-Neto and Gallego, 2006
	Elateridae?	*Babuskaya elaterata* Martins-Neto and Gallego, 2009
	Cupedidae	*Argentinocupes pulcher* Martins-Neto and Gallego, 2006
		Argentinocupes sara Martins-Neto and Gallego, 2009

Llantenes Formation - Late Triassic (Llantenes, Mendoza, Malargüe Basin, Argentina)*		
Coleoptera	Permosynidae	*Ademosyne rosenfeldi* Brauckmann *et al.*, 2010
		Ademosyne llantenesensis Brauckmann *et al.*, 2010
Mecoptera	Mendozachoristidae	*Mendozachorista volkheimeri* Brauckmann *et al.*, 2010
Rio do Rasto Formation - Late Permian to ?Lower Triassic (Poço Preto, Santa Catarina, Paraná Basin, Brazil)		
Hemiptera	Prosboloidae Prosbolidae	*Prosbolidinella riorastensis* Martins-Neto and Rohn, 1996
Santa Maria Formation - Late Triassic (Passo das Tropas, Rio Grande do Sul, Paraná Basin, Brazil)		
Trichoptera	*Incertae sedis*	*Sanctipaulus mendesi* Pinto, 1956
Blattoptera	Mancusoblattidae	*Triassoblatta cargnini* Pinto and Ornellas, 1974
Coleoptera	Indet.	Undescribed species Pinto and Ornella, 1974
Santa Juana Formation - Late Triassic (Concepción, Chile)		
Hemiptera	Dysmorphoptilidae	*Bandelnielsenia chilena* Martins-Neto and Gallego, 2003
Coleoptera	Permosynidae	*Ischichucasyne santajuanaensis* Martins-Neto and Gallego, 2005
		Ademosyne sp. Martins-Neto and Gallego, 2005

Table 2. Absolute number of species to each order of insects in the main knowing Triassic insect-bearing localities (Ipswich, Australia, and Molteno, South Africa), and the occurrences in Argentine basins.

Insect orders	Australia (Queensland) Ipswich Series	South Africa Molteno Formation	Argentina (see details in Table 3)
Blattoptera	11	10	17
Coleoptera	31	161	23
Ephemeroptera	--	1	--
Grilloblattida	--	2	1
Hemiptera	50	69	16
Hymenoptera	--	2	--
Glosselytrodea	2	2	2
Lepidoptera	--	3	--
Mantodea	--	5	--
Mecoptera	3	15	1
Megaloptera	--	2	--
Meganisoptera	--	8	--
Miomoptera	--	--	2
Neuroptera	5	5	--
Odonatoptera	7	22	2
Orthoptera	3	9	4
“Paraplecoptera”	--	12	--
Phasmatoptera	1	--	--
Plecoptera	--	5	3
Trichoptera	2	1	1
TOTAL	**115**	**324**	**72**

The Argentinean paleoentomofauna exhibits some peculiar traits in its composition, as for example, a relative high number of blattid species (24.3% of all species), contrasting with 3.1 % in Ipswich and 9.6 % in Molteno, although the absolute number of named species is quite the same (10-17 species). On the other hand, the number of hemipteran species in South Africa (43.4 %) is twice as much as in the other areas (22.4% in Argentina, 21.3% in Australia). As for the Coleoptera, although the relatively percentage is practically the same (34.3%, 49.7% and 43.4%, for Argentina, Africa and Australia respectively), the absolute number of species in Africa is almost five times greater. The dominant groups for Africa and Argentina are Coleoptera, Hemiptera and Blattida, while for Australia they are Hemiptera, Coleoptera and Blattida. When comparing the species number of the three localities it is noted that African coleopterans and hemipterans are the most numerous, but for the blattids, Argentina shows the highest diversity.

It might be expected that, due to preservation conditions, the coleopteran elytra should be dominant. However, this seems not to be true for Ipswich, where the number of preserved membranous and coriaceous wings (all groups except Coleoptera) is notably greater than the preserved elytra, and less pronounced in the Argentinean sites.

Another distinctive feature of these three localities is the unexpected presence of groups considered rare to Triassic times, like Mecoptera, Meganisoptera, Lepidoptera, Mantodea, Neuropteroidea, Hymenoptera, and Odonatoptera. In Africa all of them are well represented, except for rare Odonatoptera. Thus, a typical aquatic entomofauna is clearly better represented in Africa.

Glosselytrodea seems to be the most conservative group in phylogenetic sense, with two species represented in each region, although there is no correspondence at a generic level. Another group, Neuroptera, which is well represented in both Africa and Australia, each with five species, is unknown in Argentina until now, apparently without taphonomic reasons. In terms of diversity, at higher taxonomic categories (order and family), the Molteno Formation (Africa) is the most diverse, followed by the Australian records. The less diverse to this group is Argentina.

The southern South American Triassic paleoentomofauna (Table 3) is best documented in the Los Rastros Formation, with 56% of all known taxa, followed by those from the Potrerillos Formation (26.7%) and Ischichuca Formation (14.6%). Those from Brazil and Chile are very poorly known, with just three species each (Martins-Neto *et al.*, 2003). Another distinctive character is the paucity of hemimetabolous insects which are only represented by adults of Odonatoptera, at Potrerillos and Los Rastros Formations, three adults and one unpublished nymph of Plecoptera, and by wing fragments of Trichoptera, one from Potrerillos (Argentina) and the other from Santa Maria Formation in Paraná Basin, South Brazil (Pinto, 1956).

PROBLEMS OF PERMOSYNIDAE SYSTEMATIC

The family Permosynidae Tillyard, 1924 was defined based on Permian beetles from the Belmont Beds, in Australia (Tillyard, 1924) and after detected to the same interval in Europe and Asia (Ponomarenko, 1969, 2003), Africa (Ponomarenko and Mostovski, 2005) and Australia (Tillyard, 1924). In Triassic represents one of the most typical families of coleopterans, widely distributed in Gondwana and Laurasia (Papier *et al.*, 2005; Ponomarenko, 2008; Meller *et al.*, 2011).

The most common morphogenus is *Ademosyne* Handlirsch 1906, with a worldwide distribution in Australia (Handlirsch, 1906; Tillyard, 1916; Dunstan, 1923), South Africa (Riek, 1974, 1976), Germany (Brauckmann and Schlüter, 1993), Austria (Meller *et al.*, 2011), Japan (Fujiyama, 1973), Russia (Rohdendorf, 1961), Mongolia (Ponomarenko, 1969) and South America (Argentina and Chile).

According to Ponomarenko (2003), isolated coleopteran elytra with the presence of 11 longitudinal punctuate striae, short scutellar and submarginal striae, belongs to the genus *Permosyne* Tillyard, rather than to *Ademosyne* Handlirsch. He based it in the fact that the holotype of *Ademosyne* is not represented by isolated elytron, but by a complete beetle with ventral sutures in the body, therefore, it should be treated within a natural classification. Informal families were

Table 3. Triassic insects know from Argentina and other places of southern South America. Abbreviations: LR1=Los Rastros, upper section (Gualo River); LR2=Los Rastros, lower section (Los Chañares); QIC1=Quebrada Ischichuca Chica; USP=Uspallata; QDP=Quebrada del Puente; QDD=Quebrada del Durazno; TS=total number of species; F=Family; G=Genus; S=Species; %/SA=percentage of species in South America. Symbol: (*) occurrence of the same species, Genus or Family in distinct units, like is the case of four species of Coleoptera and one Hemiptera, the Dysmorphoptilidae. Obs: the %/SA, includes the Argentinean species, five of them in more than one formation, three from Brazil and three from Chile.

ARGENTINA																					
INSECT ORDER	**Los Rastros**						**Ischichuca**			**Cacheuta**			**Potrerillos**						**TS**	**TS***	**%/SA**
	LR1			**LR2**			QIC1			USP			QDP			QDD					
	F	G	S	F	G	S	F	G	S	F	G	S	F	G	S	F	G	S			
Odonatoptera																?	2	2	**2**	**2**	**2.78**
Blattoptera	5	8	11	1	1	1	1	1	1				3	4	4				**17**	**17**	**23.61**
Orthoptera	1	1?	3?													1	1	1	**4**	**4**	**5.56**
Grylloblattida																1	1	1	**1**	**1**	**1.39**
Glosselytrodea	1	1	1	1	1	1													**2**	**2**	**2.78**
Miomoptera				1	1	1										1	1	1	**2**	**2**	**2.78**
Plecoptera	1	1	1													1	1	2	**3**	**3**	**4.17**
Hemiptera	4	6	8	1	1	1	2	2	2							3	4	6	**16**	**17***	**22.22**
Coleoptera	2	5	13	2	2	2	1	5	8	1	1	2	1	1	1	1	2	2	**24**	**28***	**33.33**
Trichoptera																1	1	1	**1**	**1**	**1.39**
TS Argentina	**14**	**22**	**37**	**6**	**6**	**6**	**4**	**8**	**11**	**1**	**1**	**2**	**4**	**5**	**5**	**8**	**13**	**15**	**72**	**77**	**100**
% Argentina	**18,6**	**29,3**	**48,0**	**8,0**	**8,0**	**8,0**	**5,3**	**10,6**	**14,6**	**1,3**	**1,3**	**2,7**	**5,3**	**6,6**	**6,7**	**10,6**	**18,6**	**20,0**			

proposed for isolated elytra, like Permosynidae Tillyard for elytra with sulci, and Schizocoleidae Rohdendorf for smooth elytra or elytra without regular rows of punctures. Ponomarenko (1969) has proposed the family Ademosynidae for complete remains. After it, many generic names were proposed for different types of isolated elytra, yet most suggested that Permosynidae (and Ademosynidae) do not belong to archostematan beetles, but rather can be referred to Adephaga and Polyphaga (Ponomarenko, 2003, 2006). Later, the genus *Ademosyne* was also used for isolated elytra again (Riek, 1974, 1976; Brauckmann and Schlüter, 1993; Martins-Neto *et al.*, 2006a).

Recently, Ponomarenko (Meller *et al.*, 2011) analyzed the problematic situation of the genus *Ademosyne*, remembering that it was defined on a complete beetle remain (Handlirsch, 1906; Dunstan, 1923), and divided the genus into *Ademosyne* with punctate striae, and *Ademosynoides* with impunctate striae. Also maintains the early procedure (Ponomarenko, 1969) based on the natural family Ademosynidae, on the genus *Ademosyne,* and uses this name for whole beetle remains. Ponomarenko (Meller *et al.*, 2011) also pointed out that the beetles described as *Ademosyne* by Riek (1974, 1976) from the Upper Triassic of South Africa, and by Brauckmann and Schlüter (1993) from the Middle and Upper Triassic of Germany, do not belong to the genus (*sensu* Dunstan, 1923) and stated that there are no *Ademosyne* species among the beetles described by Papier *et al.* (2005) from the Anisian of north-east France (Vosges). He also mentioned that only *A. punctuada* Martins-Neto and Gallego has elytra with punctate striae among the species described by Gallego *et al.* (2005) and Martins-Neto *et al.* (2006a, 2006b) to the Upper Triassic of Argentina and Chile and remarked that the genus *Ischichucasyne* Martins-Neto and Gallego (Gallego *et al.*, 2005; Martins-Neto and Gallego, 2009) and *Delpuentesyne* Martins-Neto and Gallego (Martins-Neto *et al.*, 2007) clearly differs from the genus *Ademosyne*. Finally, Ponomarenko (Meller *et al.*, 2011) modified his previous conception of *Ademosyne* for complete coleopteran remains by describing the species *Ademosyne polyzetete* Ponomarenko which comprises an isolated punctuate elytron with 11 striae.

Due to this confused systematic panorama, we consider that it is not necessary to modify the taxonomic assignment for the South American material until this situation is clarified. Nevertheless, the Triassic coleopteran elytra described as *Ademosyne* by Martins-Neto *et al.* (2006a, 2006b, 2007, 2008) and Martins-Neto and Gallego (2009), and in the present paper, differ from the diagnosis of *Permosyne* by having 6 to 11 punctuate to smooth longitudinal striae, instead of 11 longitudinal punctuate striae, with a short scutellar and submarginal striae, from Ponomarenko (2003).

The genus *Argentinosyne* was originally assigned by Martins-Neto *et al.* (2006a, 2006b) to the family Permosynidae. However, Martins-Neto *et al.* (2008) and Martins-Neto and Gallego (2009) suggest that this genus would actually belong to the Schizocoleidae Rohdendorf, according to Ponomarenko (2006). This proposal considers that the family Schizocoleidae includes species of isolated elytra with smooth surface (lacking striae) or elytra without regular rows of punctures (as referred to in the diagnosis of *Argentinosyne*).

THE PERMOSYNIDAE FOSSIL RECORD

The alleged cosmopolitism of this group seems to be apparent. Indeed, the group is rather concentrated in Australia which retains about 50% of all known species, and Argentina, which retains 33.33% (Table 4). Furthermore, Australia and Argentina have a high rate of endemic genera. All other localities bearing permosynids have no endemic genera.

Apart from Australia and Argentina, with more than 80% of all described taxa, the permosynids are very poorly represented, by only five species, in other Gondwanan localities, and no more than five species in Laurasia (Austria, Russia, Germany, Mongolia, and Japan). The endemic genera of Gondwana cover a striking account of 88.8%, remaining only two common genera: *Ademosyne* (represented in Austria, Russia and Germany), and *Ademosynoides* (represented in Mongolia and Japan). The absence of this group in Brazil until now (except for the unidentified coleoptera elytra of Pinto and Ornellas, 1974), as well as in other Gondwana localities (e.g. Antarctica, India and Madagascar), is most probably

Table 4. Triassic global record of species related to the permosynid genera.

Genera	ARGENTINA	CHILE	BRAZIL	AFRICA	AUSTRALIA	GERMANY	MONGOLIA	JAPAN
Ademosyne	7	1		3	15	1		
Ademosynoides					3		1	1
Argentinosyne	8							
Ischichucasyne	1	1						
Undescribed species	1							
Platycrossos					3			
Simmondsia					2			
Grammosites					1			
Polysites					2			
TOTAL	**17**	**2**		**3**	**26**	**1**	**1**	**1**
%	**33.33**	**3.92**		**5.88**	**50.98**	**1.96**	**1.96**	**1.96**
% endemics	**33,3**				**44,4**			

caused by less intensive and incomplete collecting.

The regional and local distribution of permosynids in Argentina and Chile is also peculiar (Table 5). The species are notably common in the Los Rastros Formation, more specifically at Gualo (five levels) and Picos Gemelos (one level) localities. The former locality also yields the greater number of endemic taxa (at genus and species level) except for some localities that are notably poor, probably due to a lack of more intensive collecting. Apart from the obvious sampling problems, some new localities as Quebrada del Puente (Potrerillos Formation) and Los Chañares (Los Rastros Formation), although still poor at the present stage of the knowledge of Coleoptera, have revealed a higher degree of endemism in respect to other insect groups, in particular the Blattida and Hemiptera (Martins-Neto *et al.*, 2006a).

Some differences in the taxonomic composition of these localities were observed at least to the low difference in age and depositional paleoenvironment (Artabe *et al.*, 2001; Stipanicic and Marsicano, 2002), between Los Rastros (early Late Triassic, Bermejo Basin, fluvial-lacustrine), Potrerillos (early Late Triassic, Cuyana Basin, fluvial-lacustrine), Cacheuta (lacustrine) and Ischichuca (late Middle Triassic to early Late Triassic, Bermejo Basin, lacustrine) formations (Table 1). There are also some few differences in the assemblages, between Quebrada del Puente, that represent the lower unit of Potrerillos Formation, with black shale of lacustrine deposits, and Quebrada del Durazno, representing the upper unit, with siltstones and swamp deposits of a floodplain environment (Martins-Neto *et al.*, 2007, 2008). But for the sections corresponding to the same geological unit, for example Picos Gemelos, Gualo, Agua Escondida and Quebrada de Ischichuca Chica, no dramatic differences in the taxonomic composition were seen.

The data from Table 5 shows in summary that, (i) a great number of collected specimens came from Gualo River locality, followed by Picos Gemelos (together representing 81% of all collected elytra); (ii) the genus *Ademosyne* represents 70% of all collected specimens; (iii) *Ademosyne arcucciae* represents 76% of all collected *Ademosyne* species, with a rate of 81% at Pico Gemelos, and less than 34% at Gualo River; (iv) *Ademosyne punctuada* and *A. hexacostata* are dominant at Gualo River, where also came from about 87% of the *Argentinosyne* specimens.

RESULTS

Morphometric variations in Permosynidae elytra

As demonstrated in Martins-Neto *et al.* (2006a), between the morphometric parameters shown by the permosynid elytra, the most useful to distinguish species is the length/width ratio, due to its independence on the size variability (Figures 2; 3A-B). No species has a

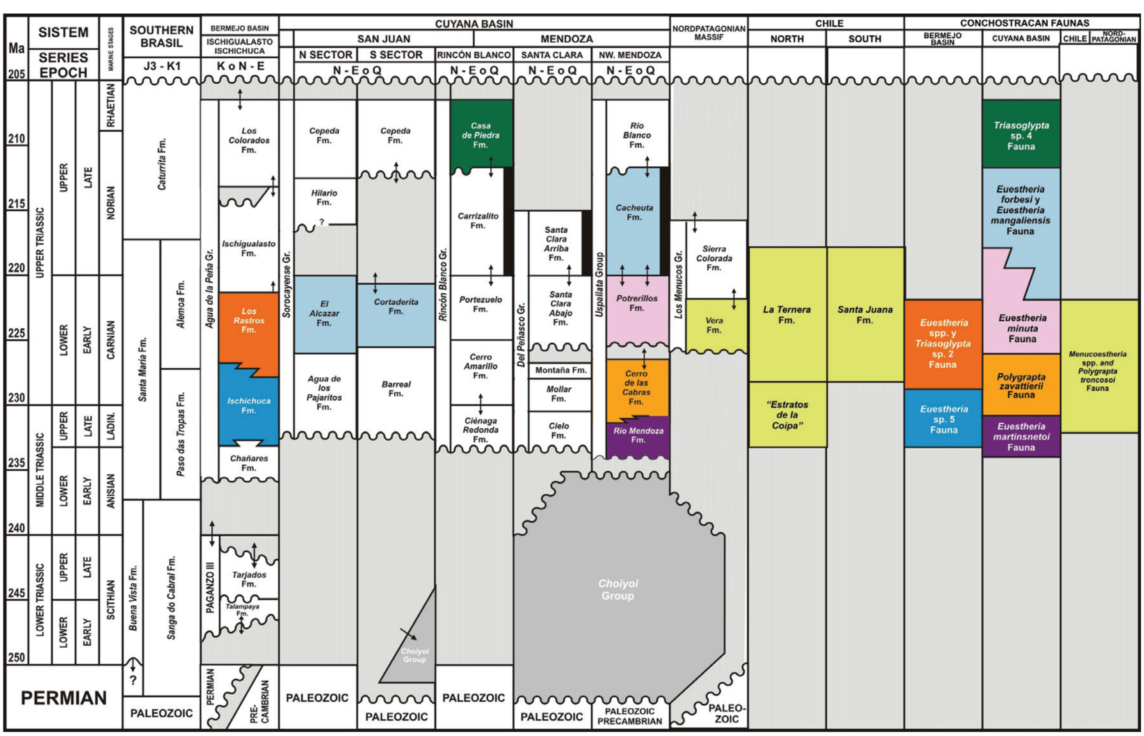

Figure 1. The general geochronologic and stratigraphic chart of the Triassic in southern South America, including the conchostracan fauna distribution and focusing the Argentinean units with insect-conchostracan record, based in Gallego and Martins-Neto (2006). Stratigraphic chart modified from Stipanicic and Marsicano (2002).

Table 5. Triassic species of Coleoptera in Argentina and Chile, geological units and outcrops associated. Abbreviations: PG=Picos Gemelos; G=Gualo River; AE=Aguas Escondida; LC=Los Chañares; QIC=Quebrada de Ischichuca Chica; QIC2=Quebrada de Ischichuca Chica; USP=Uspallata; QDP=Quebrada del Puente, QDD=Quebrada del Durazno; BB=Bíobío River (Chile); te=total number of specimens.

TAXA/ FORMATIONS	**Los Rastros**							**Cacheuta**	**Ischichuca**	**Potrerillos**		**Santa Juana**	**%T**
	PG	G	AE	QIC	LC	te	%	USP	QIC2	QDP	QDD	BB	
1.*Ademosyne arcucciae*	54	29	11	2	0	96	**78,0**	0	0	0	0	0	76.2
2. *Ademosyne elongatus*	2	1	0	0	0	3	**2,4**	0	0	0	0	0	2.3
3. *Ademosyne hexacostata*	3	14	0	0	0	17	**13,8**	0	0	0	0	1	14.3
4. *Ademosyne punctuada*	2	4	1	0	0	7	**5,8**	0	1	0	0	0	6.2
5. *Ademosyne umutu*	0	0	0	0	0	0		0	1	0	0	0	
Total number of specimens	61	48	12	2	0	123		0	2	0	0	1	126
% specimens	49,6	39	9,7	1,7	0	66,8							68.5
6. *Argentinosyne gualoensis*	0	10	0	0	0	10	**33,4**	0	0	0	0	0	28.6
7. *Argentinosyne rugosa*	0	3	0	0	0	3	**1,0**	1	0	0	0	0	11.4
8. *Argentinosyne losrastrosensis*	2	6	0	0	0	8	**26,6**	0	0	0	0	0	22.8
9. *Argentinosyne frenguellii*	0	5	0	0	1	6	**20,0**	0	1	0	0	0	20.0
10. *Argentinosyne gonaldiae*	0	2	0	0	0	2	**0,66**	1	0	0	0	0	8.6
11. *Argentinosyne duraznoensis*	0	0	0	0	0	0		0	0	0	1	0	2.8
12. *Argentinosyne ischichucaensis*	0	0	0	0	0	0		0	1	0	0	0	2.8
13. *Argentinosyne bonapartei*	0	0	0	0	1	1	**0,34**	0	0	0	0	0	2.8
Total number of specimens	**2**	**26**	**0**	**0**	**2**	***30***		2	2	0	1	0	35
% of locality	6,6	86,8			**6,6**	***16,3***							19,0
14. *Ischichucasyne cladocosta*	0	0	0	0	0	0		0	1	0	0	0	50
15. *Ischichucasyne santajuanensis*	0	0	0	0	0	0		0	0	0	0	1	50
Total number of specimens	0	0	0	0	0	0		0	1	0	0	1	2
% of locality						0							1,1
16. *Delpuentesyne menendezi*	0	0	0	0	0	0		0	0	1	0	0	1
Total number of specimens	0	0	0	0	0	0		0	0	1	0	0	**1**
% of locality													0.5
17. Undescribed species	0	0	0	0	0	0		0	0	0	2	0	2
Total number of specimens	0	0	0	0	0	0		0	0	0	2	0	2
% of locality													1.1
18. *Cardiosyne obesa*	1	5	0	0	0	6	**60.0**	0	0	0	0	0	**60**
19. *Cardiosyne elegans*	1	3	0	0	0	4	**40.0**	0	0	0	0	0	40
Total number of specimens	2	8	0	0	0	10		0	0	0	0	0	10
% of locality	20.0	80.0				5.4							5,4
20. *Argentinocupes pulcher*	0	1	0	0	1	2	**66,7**	0	1	0	0	0	1.63
21. *Argentinocupes abdalai*	0	1	0	0	0	1	**33.3**	0	0	0	0	0	0.5
22. *Argentinocupes sara*	0	0	0	0	0	0		0	1	0	0	0	0.5
Total number of specimens	0	2	0	0	1	3		0	2	0	0	0	5
% of locality		66.7			33.3	1.63							2,8
23. *Gemelina triangularis*	1	0	0	1	0	2	**100**	0	0	0	0	0	**2**
Total number of specimens	1	0	0	1	0	2		0	0	0	0	0	2
% of locality	50			50		100							1.1
24. *Babuskaya elaterata*	0	0	0	0	0	0	-	0	1	0	0	0	**1**
Total number of specimens	0	0	0	0	0	0		0	1	0	0	0	1
TOTAL GENERAL	66	84	12	3	3	168		2	8	1	3	2	184
% TOTAL	35,8	45,6	6,5	1,7	1,7	91,3		1,0	4,3	0,5	1,7	1,0	

coincident L/W parameter, even within the same genus (Figures 2; 3C-D). The second useful character is the ornamentation of the elytra, at least for the South American specimens, particularly to a preliminary taxonomic identification.

Further peculiar characteristics of the Argentinean assemblages can be extracted from the morphometric graphics of the Figure 3C-D: (i) all the species of the genera *Ademosyne* and *Argentinosyne* exhibit the same similar pattern when dimensions are plotted (length, width and length/width ratio) attesting that the length/width ratio is quite constant in each species (white line in the graphics); (ii) the course of the length graph is the same for all species of *Ademosyne* and *Argentinosyne*, beginning with a peak, followed by a rather constant decline, from the larger specimens to the smaller ones. This tendency does not depend neither on the locality nor the species. When all specimens of the same species and from all localities are plotted, it produces an up and down effect, more conspicuous in the most abundant samples (e.g. Picos Gemelos and Gualo), but also observed in small samples; (iii) the course of the width graph has the same behavior as that one of the length, following quite parallel to it. The up and down effect observed is probably due to a certain stimulus (ecological ones?) and the peaks could be caused by an optimal time (more adequate climatic conditions and food supply), followed by a suppression of it. It is possible to

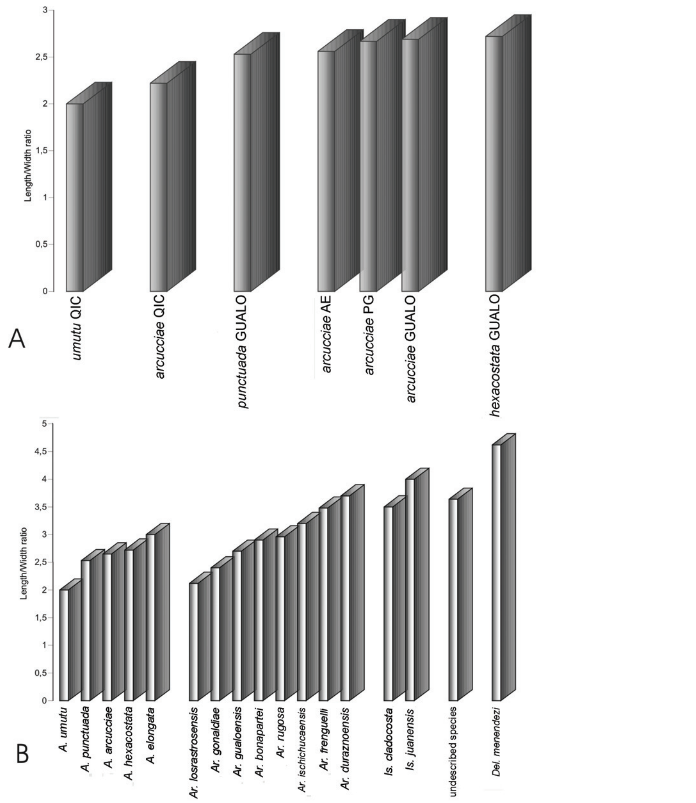

Figure 2. Morphometric variation of the length/width ratio to the known South American Triassic Coleoptera taxa (Martins-Neto *et al.*, 2006a). **A**. *Ademosyne* species and respective localities; **B**. to all known species.

recognize these peaks in the distribution of *Ademosyne* and *Argentinosyne* species without restriction to a particular locality and probably could represent a predictable pattern.

The dispersion graphics also exhibit similar patterns for those species (Figure 3A-B). When the localities are satisfactorily sampled the length/width values clearly reveal a set of plots concentrated at the lower L/W ratio, and few plots totally apart from the main set (great L/W rates). On a first look it seems to constitute a linear equation, obviously more conspicuous at poorly sampled areas. The possible tendency/regression type equation for the best sampled species (*Ademosyne arcucciae*) is summarized in Table 6. A rather linear or more rigorously, polynomial tendency, can be observed, respectively to *Ademosyne* and *Argentinosyne* species. One more time this tendency is virtually the same for all species, independent from the locality or sampling. The graphics in Figure 4, based on same data, are more conspicuous in showing this general tendency, using the size categories, against number of specimens. It shows that all species of *Ademosyne* have virtually the same distribution when size categories were used.

For the genus *Argentinosyne,* however, the pattern is somewhat different and shows species with big and small sizes, when compared with the values found to *Ademosyne* (Figure 5). But when plotted all species of the same genus together, the graphic is virtually the same (Figure 3A-B). The tendency curves (white lines) can be expressed by a polynomial curve (black line) tending to a linear one (Table 7).

The distribution of size for all specimens and from all localities of *Ademosyne arcucciae* is presented in Figure 4A. Despite of minor sampling at some localities, the tendency of distribution is also locality-independent. Show a minimal size length of about 1-1.5 mm, regularly increasing to a maximum at 2-2.5 mm class, and after it decreases to a stable point of 3-3.5 mm (coincident with the median value of the length ratio). A second peak is observed at the size category 4-4.5 mm, followed by a regular decrease until the last size category (6-6.5 mm). Very few specimens show a larger size, with lengths of more than 9 mm. The diagram of distribution also shows the occurrence, at a local and regional scale, of a disturbance, expressed by the U shape of the curve. This event could represent a speciation process, better visualized in *Argentinosyne gualoensis* and the dominant species, *Argentinosyne frenguellii*, both from Gualo (Figure 5). When compared with *Ademosyne* both species exhibit the same pattern (Figure 4). This could be caused by the rise of another (or two) taxa within the population.

The comparison between the graphics (Figures 3, 4 and 5), allows to observe a clearly transition from *Argentinosyne gualoensis* to *Argentinosyne frenguellii*, and let expect the rise of a third taxon. This can be the case for the peaks in the distribution of the species of the genus *Ademosyne* (Figure 3C), where the possible peak represents the beginning of a speciation event. It can be due to a rupture in the genetic flow between specimen, which vary from 1-2 mm, and those with 9 mm or more, but can still be expected that it can also occur between forms with 5-6 mm and those above 9 mm of elytra.

Area cladogram for South American Permosynidae and its implication on stratigraphy

The distribution of the southern South America Triassic insect orders shows that the best sampling coming from the Los Rastros and Ischichuca formations, where is also found a great degree of endemism (at Gualo River and Quebrada de Ischichuca Chica, Table 4 and 8). Yet, the coleopteran fauna reveals a notable correspondence at specific level, with the sampled geological unit.

In previous works (Martins-Neto *et al.*, 2003; Gallego and Martins-Neto, 2005, 2006) the stratigraphic affinity of

Table 6. Possible equations for tendency curves, in the distribution of the Argentine species *Ademosyne arcucciae*. The Quebrada de Ischichuca Chica locality was not quoted due to that only two specimens have been collected. Sampling data from Martins-Neto *et al*. (2006a).

Locality	collected specimens	Equation	Formula	R^2
Picos Gemelos	54	Linear	Y = 0,3208X + 0,178	0,8387
		Logarithmic	Y = 1,1288Ln(X) – 0,337	0,8025
		Polynomial	$Y = -0{,}063X^2 + 0{,}3765X + 0{,}0721$	0,8412
		Potency	Y = 0,4241(X to potency 0,8922)	0,8383
		Exponential	Y = 0,5312(e to potency 0,2368X)	0,7644
Gualo	29	Linear	Y = 0,2672X + 0,351	0,6923
		Logarithmic	Y = 0,9548Ln(X) + 0,1538	0,7594
		Polynomial	$Y = -0{,}0618X^2 + 0{,}7428X – 0{,}4543$	0,7594
		Potency	Y = 0,4757(X to potency 0,7952)	0,7513
		Exponential	Y = 0,5661(e to potency 0,2196X)	0,6855
Agua Escondida	11	Linear	Y = 0,2734X + 0,4715	0,7427
		Logarithmic	Y = 1,2311Ln(X) – 0,0301	0,7694
		Polynomial	$Y = -0{,}0208X^2 + 0{,}4999X + 0{,}0236$	0,7694
		Potency	Y = 0,4709(X to potency 0,8593)	0,7229
		Exponential	Y = 0,7215(e to potency 0,1754X)	0,5897

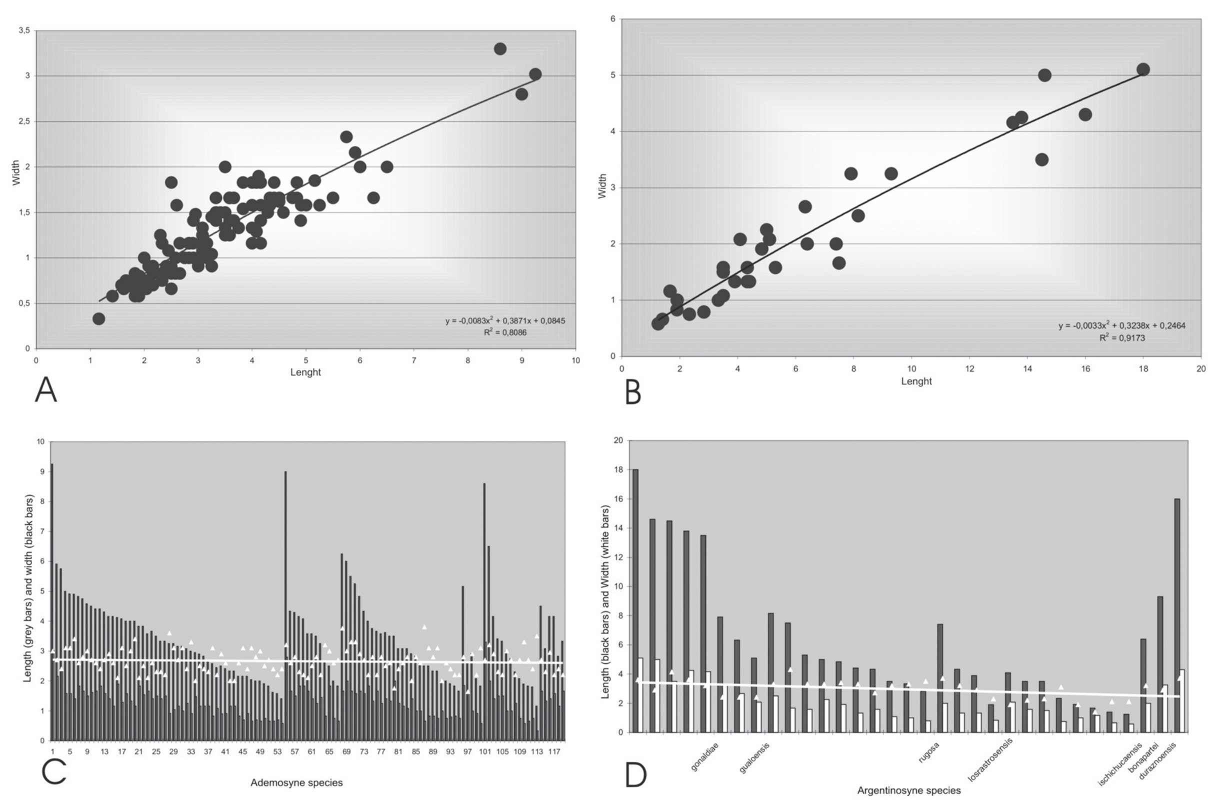

Figure 3. Dispersion graph (L/W) to the morphometric variation of the South American Triassic Coleoptera taxa (Martins-Neto *et al*., 2006a). **A**. *Ademosyne* species; **B**. *Argentinosyne* species and the respective tendency curves (polynomial), by three dimensional graph (length, width, length/width, and locality); **C**. *Ademosyne* species (length, grey bars, width, black bars; **D**. *Argentinosyne* species (length, black bars, width, white bars).

Table 7. Polynomial tendency curves to the distribution of *Ademosyne* and *Argentinosyne* species in Argentina. Some localities were not quoted by the species rarity (one or two specimens). Sampling data from Martins-Neto *et al.* (2006a).

Species	Locality	colected specimens	Formula	R^2
	Picos Gemelos	54	$Y = -0,0655X^2 + 1,5475X - 4,1135$	0,3914
	Gualo	29	$Y = -0,0372X^2 + 0,876X - 2,3602$	0,4218
Ademosyne arcucciae	Agua Escondida	11	$Y = -0,0157X^2 + 0,368X - 1,064$	0,27
	Quebrada Ischichuca Chica	2		
	all	96	$Y = -0,1216X^2 + 2,871X - 7,7069$	0,4536
Argentinosyne gualoensis	Gualo	10	$Y = -0,0134X^2 + 0,2613X - 0,3426$	0,2827
	Picos Gemelos	2		
Ademosyne punctuada	Gualo	4	$Y = -0,0038X^2 + 0,080X - 0,2105$	0,116
	Agua Escondida	1		0,06
Ademosyne hexacostata	Picos Gemelos	3	$Y = -0,001X^2 + 0,0455X - 0,1723$	0,1612
	Gualo	14	$Y = -0,0043X^2 + 0,1557X - 0,3168$	0,1687
Argentinosyne rugosa	Gualo	3	$Y = -0,0106X^2 + 0,3118X + 0,2761$	1
	Uspalatta	1		

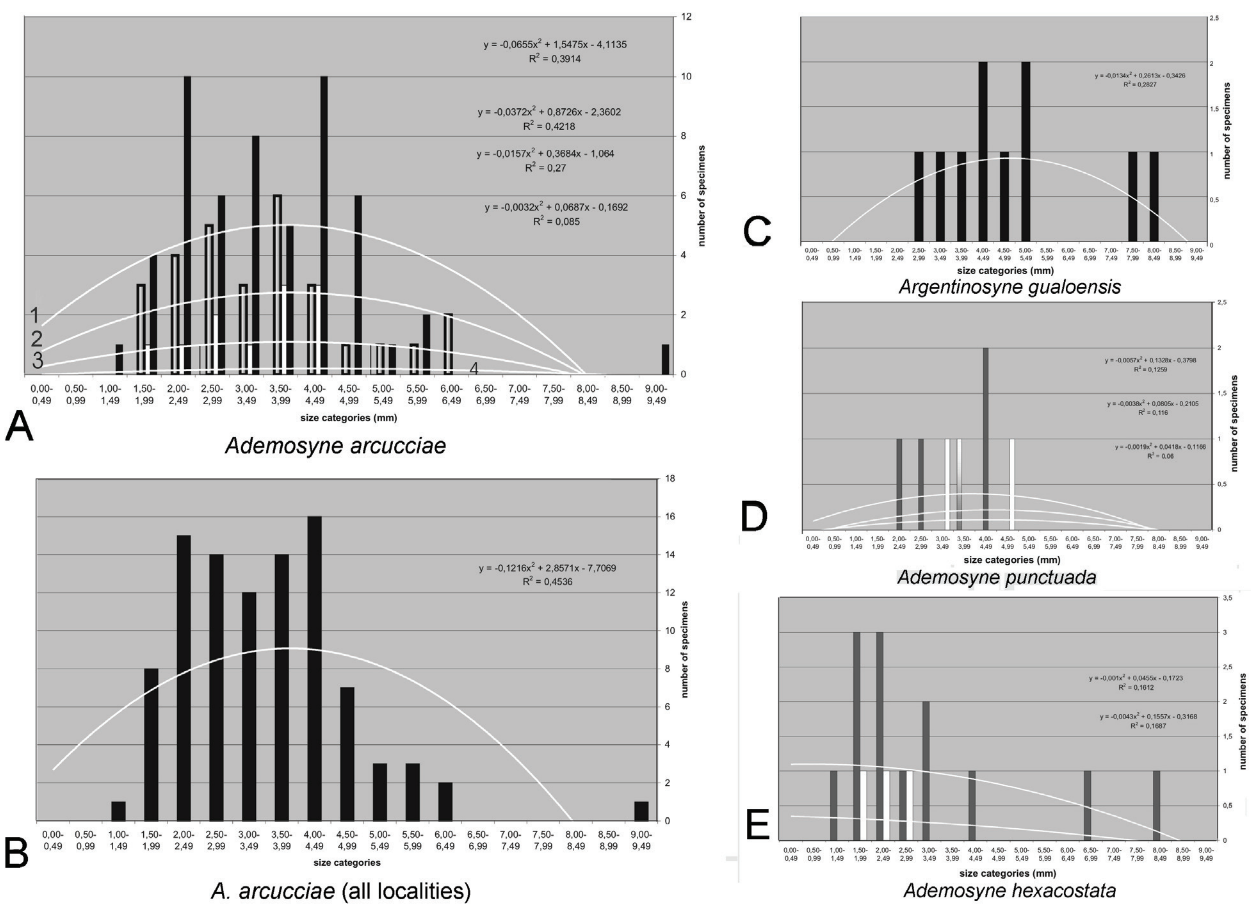

Figure 4. Morphometric variation of the length, by size categories, of the South American Triassic Coleoptera taxa, and the respective tendency curves (polynomial). **A**. *A. arcucciae* at Picos Gemelos (black bar, curve 1), Gualo (grey bar, curve 2), Agua Escondida (white bar, curve 3), and Quebrada de Ischichuca Chica (curve 4); **B**. *A. arcuccie* for all localities; **C**. *A. gualoensis,* all localities; D. variation of the length, by size categories in *A. punctuada;* **E**. the same as D, to *A. hexacostata*.

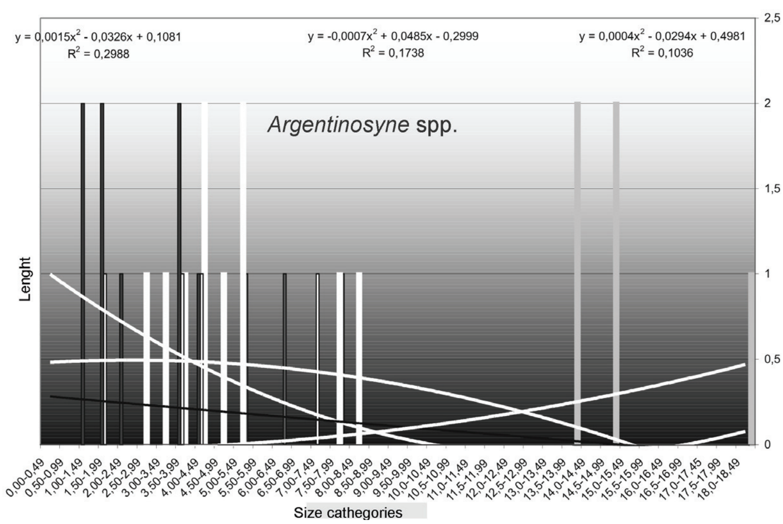

Figure 5. Morphometric variation of the length, by size categories, from *Argentinosyne* species and the respective tendency curves (polynomial). Picos Gemelos (black bar), Gualo (grey bar), Agua Escondida (white bar).

those faunas were discussed and points to the comparative high antiquity of the assemblages coming from Potrerillos Formation, with Los Rastros and Ischichuca formations presenting partially coeval faunas. The last units also show high indices of similarity in the Coleoptera fauna, contrary to those indices obtained with the Potrerillos Formation. Similar condition occurs with the palinological data, but is not found until now when the biostratigraphic analysis of paleobotanical records or sedimentological information is taken into account (Spalletti *et al.,* 1999; Morel *et al.*, 2001).

Between the Los Rastros and Ischichuca Formations the correspondence in terms of insect content is remarkable, and also, yet in a lesser degree, between Ischichuca and Santa Juana formations. It confirms the distance between those units and the "older" Potrerillos Formation faunas, which were proposed to have the same age (Figure 1).

Those propositions are also tentatively supported by conchostracan faunas, with the presence of ancestral forms of the Euestheriidae (*Euestheria,* with five species in Potrerillos Formation, and four in Los Rastros/Ischichuca Formations) and more advanced species of the Loxomegaglyptidae (*Triasoglypta,* with two species in the Los Rastros/Ischichuca Formations). The more ancient age to Potrerillos Formation assemblage is also suggested by the presence of a Paleozoic form of Pemphilimnadiopseidae (*Challaolimnadiopsis*). And a younger to Santa Juana Formation is informed by the presence of a derived (from the euestheriid-eosestheriid stock) Eosestheriidae, the genus *Menucoestheria* (Gallego, 1999, 2001a, 2001b; Shen *et al.*, 2001).

A flow model to coleopteran species between the sampled localities is suggested in Figure 6, based on data of Table 5. The area diagram exhibits a reasonable coherency and points towards Gualo and Quebrada de Ischichuca Chica, as representing a possible pool of the species. When replacing the localities by the occurring taxa, we obtain a cladogram (Figure 7A), and when transforming the localities in taxa, with the presence or absence of the permosynid species at each locality as characters, we can obtain an area matrix (Table 9) and, consequently, an area cladogram (Figure 7B).

The results are expressive and very close to a possible phylogeny of South American permosynids, indicating a speciation event that seems to be close of a vicariance one, at least in a local and/or regional scale (Figure 8A). At a specific level, for *Argentinosyne*, the area cladogram indicates that the left branch seems to be exclusive to the genus, and that it is probably the ancestor of *Ademosyne* (Figure 8B).

The global area cladogram from *Argentinosyne* is indicating a close relation between LR1+(ISCH+SJ), and that the upper part of the Los Rastros Formation is closely related to the Ischichuca + Santa Juana Formations (Figure 8C), and that the probable vicariance events were repeated several times. The historic event attested by the right branch is quite different, showing to be older and that *Argentinosyne* species 9 were probably ancestors of many other species from the genus in South America. In this case, the area cladogram suggests that the localities exposing levels of Potrerillos Formation could represent the ancestral area. It also indicates that the area relations could be [(LR1+CACH)+(ISCH+SJ))+LR2)+POTR], where LR, corresponds to Los Rastros, ISCH, to Ischichuca, CACH to Cacheuta and POTR, to Potrerillos formations.

The area cladogram of other genus is expressed in Figure 8D.

Toward a phylogenetical approach

The proposed area cladogram seems to be coherent with the herein used systematic and the phylogeny of the South American permosynids. The main problem is to choose when working with isolated elytra which are the best characters to consider. Some parameters like ornamentation, length/width rates, presence or absence of a conspicuous lateral border, and the number of costae, seems to be the more useful.

The first dichotomy is the presence/absence of costae. This dichotomy divides the cladogram into two initial branches: *Argentinosyne* (without costae) and the other genera (with costae). The number of costae reveals a series of transformations from the character "presence of costae" (Figure 7), passing into the first step from 6-11 costae, after dividing in a branch with 6-9 and from there, to 7-8 and 6. In the other branch,

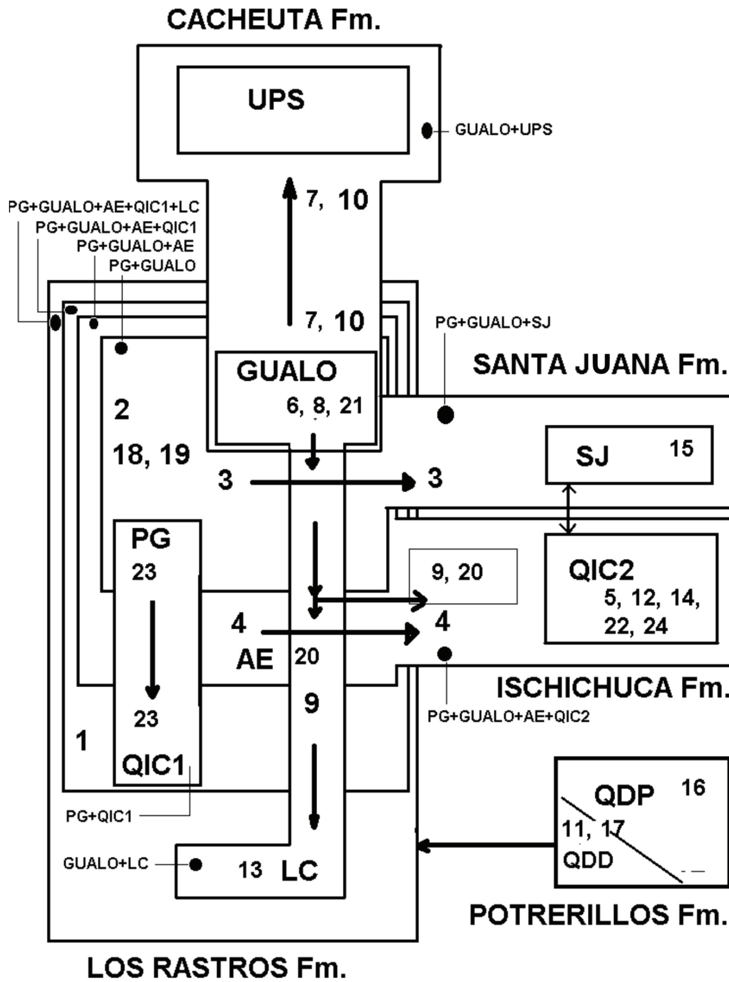

Figure 6. Area distribution of the South American Coleoptera species (the numbers 1 to 24 refers to the known species, see Table 5).

Table 8. Triassic genera of insect knowing in Argentine basins and its outcrops. To abbreviations see Table 5 and CON=Concepción, Chile. Symbol: *same species.

Insect order	Formation	Los Rastros					Cacheuta	Potrerillos		Ischichuca	Santa Joana
	Place	PG	GR	AE	QIC1	LC	USP	QDD	QDP	QIC2	CON
COLEOPTERA	*Ademosyne*	x	x	x	x					x	x
	Ischichucasyne									x	x
	Argentinosyne		x			x	x	x		x	
	Duraznosyne							x			
	Delpuentesyne								x		
	Argentinocupes		x			x	x			x	
	Gemelina	x			x						
	Babuskaya									x	
BLATTOPTERA	*Condorblatta*		x			x					
	Lariojablatta					x				x	
	Hermosablatta		x							x	
MIOMOPTERA	*Miomina*					x		x			
HEMIPTERA	*Gallegomorphoptila*		x*					x*		x	
Total	**12**	**2**	**6**	**1**	**2**	**5**	**2**	**4**	**1**	**8**	**2**
% Total		**16,6**	**50,0**	**8,3**	**16,6**	**41,6**	**16,6**	**33,3**	**8,3**	**66,6**	**16,6**

Table 9. Matrix area of coleopteran species (numbers 1 to 24 and abbreviations as in Table 5).

places/ species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
PG	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
GUA	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0
AE	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
QIC1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
LC	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
USP	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
QIC2	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1
QDP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
QDD	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
SJ	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

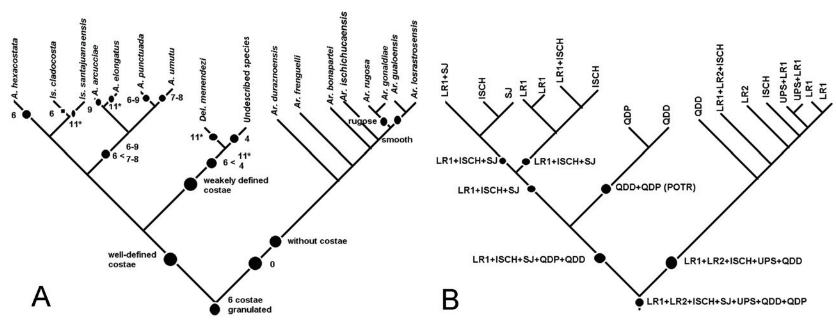

Figure 7. A. Phylogenetic cladogram (numbers indicate number of costae, and asterisks, the character occurring in more than one taxon independently); **B.** area cladogram. Abbreviations: PG=Picos Gemelos; AE=Agua Escondida; QIC1=Quebrada de Ischichuca Chica; QDD=Quebrada del Durazno; QDP=Quebrada del Puente; LR1= upper unit of the Los Rastros Formation ; LR2=lower unit of the Los Rastros Formation; CACH=Cacheuta Formation; ISCH=Ischichuca Formation; POTR=Potrerillos Formation.

the steps are from 6-11 to 6, 11 and 9, respectively. This arrangement defines reasonably well the South American permosynid species and it is the first step toward a definitive phylogeny of the group. The *Argentinosyne* branch is also coherent with the graphs of Figure 3 and can be reasonably subdivided by the ornamentation traits: granular, rugose and entirely smooth (Figure 8 and Table 10).

Predicting new taxa

The area cladogram and the possible phylogeny of the southern South American Triassic coleopterans are coherent with an allopatric speciation and a vicariance event as discussed above and represented by [(((LR1+CACH)+(ISCH+SJ))+LR2)+POTR)]. If it is true, several taxa can be predicted. Two crucial localities are important to confirm and test our hypothesis, Uspallata (Cacheuta Formation) and Bío-Bío River (Santa Juana Formation), both until now very poorly sampled, but which potentially yield several predictable taxa (Table 11). These possible and coherent future findings will be crucial for the consistency and robustness of the proposed cladograms and a useful tool for stratigraphical correlations. Recent findings at the Cerro de la Cabras (Cerro Bayo), Potrerillos (Quebrada del Puente and Puesto Miguez), Cacheuta (Puesto Miguez), Cortaderita (Quebrada La Cortaderita) and Llantenes formations, will allow us to confirm this hypothesis. Some preliminary results attest this possibility (Lara *et al.*, 2010).

The phylogeny proposed for the Family Dyrmorphoptilidae based on data from Martins-Neto and Gallego (2006) clearly shows a similar pattern of distribution and area cladogram (Figure 9A) within the Coleoptera. Adding other known Argentinean Triassic insect taxa the consistency of the area cladogram is maintained (Figure 9B). So the current stage of knowledge reveals a picture markedly distinct from that proposed by Morel *et al.* (2001), at least in the position and age of both Cacheuta and Potrerillos formations, suggested to be younger than Los Rastros-Ischichuca. The coleopteran fauna indicates, at least in part, that the insect fauna of the upper unit of Los Rastros Formation, Ischichuca, Cacheuta and Santa Juana Formations could be preserved in a similar time interval (Figure 10).

In summary, some taxa of Triassic insects seem to be particularly useful for local and regional correlations (Gallego and Martins-Neto, 2005, 2006). This is the case of *Ademosyne*, with wide distribution in Gondwana, *Ischichucasyne, Argentinosyne* and *Argentinocupes* (Coleoptera), *Gallegomorphoptila* (Hemiptera), Polycitellidae (Glosselytrodea) and Scytinopteromorpha (Hemiptera). In this context, two poorly sampled localities at Gualo, Agua Escondida and Quebrada de Ischichuca Chica are interesting to test the local distribution of taxa restricted to the Los Rastros Formation. Seemingly some taxa endemic to Gualo River site and to Gualo and Picos Gemelos could be confirmed in respect to this condition by new collects. Clarify the local and regional distribution of the permosynids will be an important step toward a global analysis of the group.

Table 10. Summary of the taxonomic traits in South American permosynids. Abbreviations: NC = number of costae; OR = ornamentation pattern; NS = number of collected specimens.

species	Length/Width ratio	NC	OR	NS	Main character
Ademosyne arcucciae	2.65 +/- 0.43	9	granulated	98	
Ademosyne hexacostata	2.72 +/- 0.33	6	granulated	16	
Ademosyne punctuada	2.53 +/- 0.34	6-9	granulated	7	Punctate costae
Ademosyne elongatus	3.00	11	granulated	3	
Ademosyne umutuae	2.00	7-8	irregular	1	Granules of irregular size
average	2,58 +/- 0.36				6-9 well-defined costae
Argentinosyne gualoensis	3.26 +/- 0.21		smooth	10	
Argentinosyne rugosa	2.96 +/- 0.70		rugose	4	
Argentinosyne frenguelli	3.48 +/- 0.46		granulated	5	
Argentinosyne gonaldiae	2.40		rugose	3	
Argentinosyne duraznoensis	3.70		smooth	1	
Argentinosyne ischichucaensis	3.2		granulated	1	
Argentinosyne bonapartei	2.9		granulated	1	
Argentinosyne losrastrosensis	2.12 +/- 0.40		granulated	8	
average	3.02 +/- 0,24				Without costae
Delpuentesyne menendezi	4.62 +/- 0.53	11	granulated	2	Weak costae/ weakly defined
Undescribed species	3.64 +/- 0.14	4	granulated	2	Lateral border constricted/ costae weakly defined
Ischichucasyne cladocosta	3.50	9-11	striated	1	Dichotomous costae
Ischichucasyne santajuanensis	4,00	6	granulated	1	Dichotomous costae
average	3.75				Dichotomous costae
TOTAL				**164**	

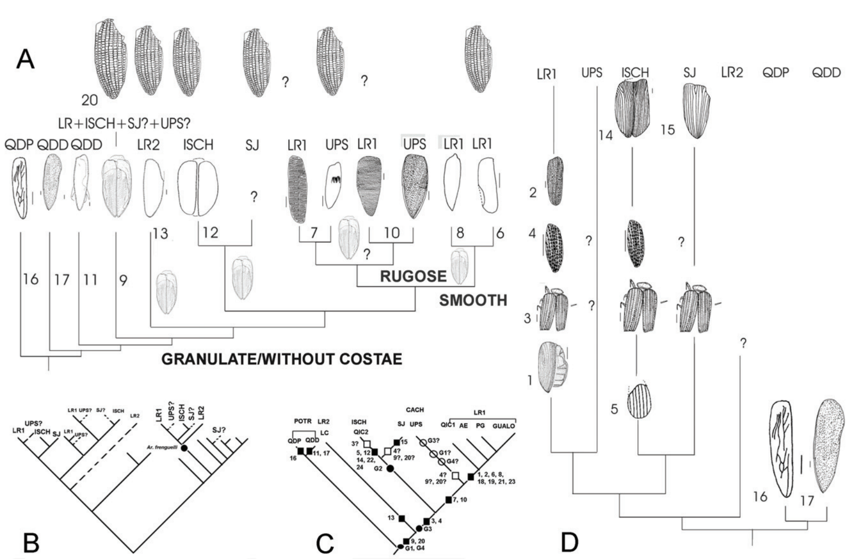

Figure 8. A. Possible phylogeny of South American permosynids showing that predictable taxa is coherent with the area cladogram; **B**. area cladogram to *Argentinosyne* demonstrating a left branch exclusive to the genus and the probable origin of *Ademosyne* at right; **C**. cladogram to the relations between *Ademosyne* (G1), *Argentinosyne* (G2), *Ischichucasyne* (G3), *Argentinocupes* (G4). **D**. the area cladrogram to other genus. Abbreviations as for the Figure 7. Scale bars ~1 mm.

FINAL COMMENTS

The morphometric analysis, and the biogeography and phylogenetical approach herein presented to the southern South American Triassic Coleopterofauna reveal that:

(a) its systematic propositions is in accordance and consistent with the area cladogram and phylogenetical tree obtained;

(b) the pattern of paleogeographic distribution of the coleopteran fauna supports an allopatric speciation and events of vicariance;

(c) an ecological and/or climatic disturbance, at least in a local or regional scale, had occurred, being probably responsible for the morphometric variation and speciation rate;

(d) phylogenetically, *Argentinosyne* seems to be the ancestral of *Ademosyne,* which has a worldwide Gondwanic distribution;

Table 11. Distribution and predictability of selected South American Triassic coleopteran taxa (those restricted to a single locality was ignored). Dark grey squares: confirmed presence; light grey squares: predicted taxa coherent with the area cladogram. To abbreviations and numbers see Table 5.

(■ = dark grey square; □ = light grey square)

TAXA/ FORMATION	Upper Los Rastros				Cacheuta	Ischichuca	Santa Juana	Lower Los Rastros
	PG	G	AE	QIC	USP	QIC2	BB	LC
2. *Ademosyne elongatus*	■	■						
8. *A. losrastroensis*	■	■						
18. *Cardiosyne obesa*	■	■						
19. *Cardiosyne elegans*	■	■						
1. *Ademosyne arcucciae*	■	■	■	■				
23. *Gemelina triangularis*	■	□	□	■				
7. *Argentinosyne rugosa*	□	■	□	□	■			
10. *Argentinosyne gonaldiae*	□	■	□	□	■			
4. *Ademosyne punctuada*	■	■	■	□	□	■		
3. *Ademosyne hexacostata*	■	■	□	□	□	□	■	
9. *Argentinosyne frenguelli*	□	■	□	□	□	■	□	■
20. *Argentinocupes pulcher*	□	■	□	□	□	■	□	■

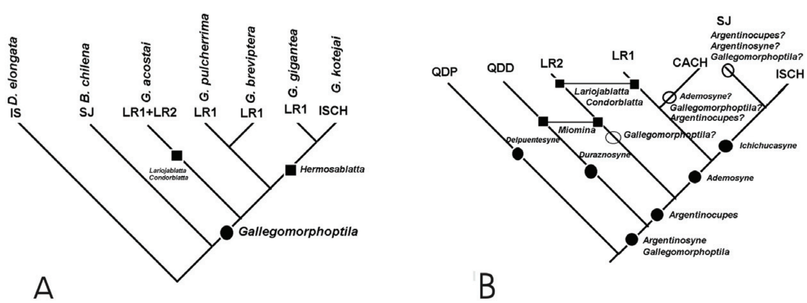

Figure 9. A. area cladogram for Hemiptera: Dysmorphoptilidae (data from Martins-Neto *et al.,* 2005); **B.** area cladogram for some selected South American insect taxa.

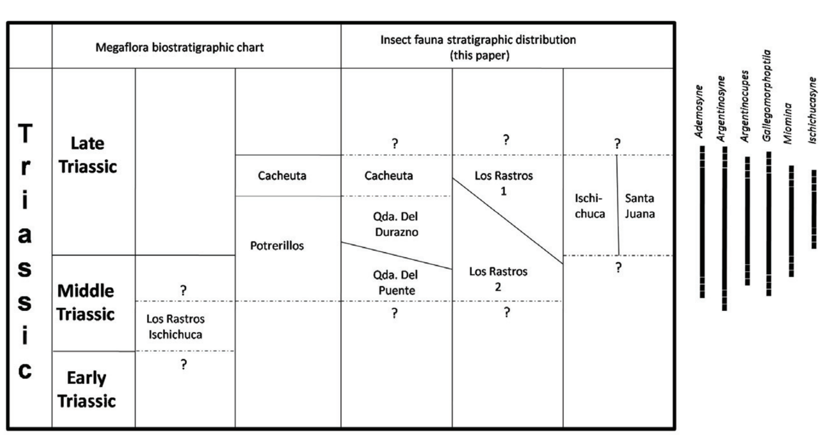

Figure 10. Biostratigraphic correlation to the Triassic levels in Argentina based in the paleobotanical record (from Artabe *et al.,* 2001), in accordance with the here proposed area cladogram to Coleoptera.

(e) several taxa are apparently endemic to South America (especially Argentina);
(f) several new taxa are predictable, in accordance with both the area and phylogenetical cladograms;
(g) the higher degree of faunal correlations is established with the Australian ones, and lesser with the more close areas (Brazil and South Africa);
(h) the insect fauna from the lower part of the Los Rastros Formation (Los Chañares) and that from all Potrerillos Formation seems to be the oldest knowing;
(i) the insect faunas of the upper unit of the Los Rastros Formation (Gualo River) seems to have the same age as those from Cacheuta (Uspallata), Ischichuca (Quebrada de Ischichuca Chica), and Santa Juana formations (Bío-Bío River, Chile).

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