

# Geological Factors and Evolution of Southwestern Gondwana Triassic Plants

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(Manuscript received May 16, 2002; accepted October 15, 2002)



## Abstract

A synergistic model based on reciprocal influences between biotic and abiotic factors is developed for the Triassic of southwestern Gondwana. Changes in physical environment exerted a strong influence on the characteristics and evolution of plant assemblages. The Permian-Triassic extinction, and the change from palaeophytic to mesophytic floras, is one of the most striking examples of direct influence of physical environment upon plant communities. Pangea coalescence, the distribution of land masses and seas, the spreading of continental climates (megamonsoonal conditions) and the waning polar glaciation determined the expansion of xeromorphic morphotypes that became dominant during the whole Mesozoic. In southwestern Gondwana, the introduction or invasion of immigrant lineages suggests a strong asymmetrical interchange from the Euroamerican realm to the Gondwana realm. In addition, generalised extensional volcanism, development of intracratonic rifts and the palaeolatitudinal location of climatic zones during the early-Middle Triassic favoured extinction of the *Glossopteris* flora and explosive diversification of endemic groups.

From the chronological viewpoint, the Barrealian, Cortaderitian and Florian stages are recognised in the Triassic of southwestern Gondwana. These stages are respectively characterised by: (a) appearance of mesophytic elements, and coexistence of Palaeozoic and Mesozoic groups, (b) maximum diversification of the *Dicroidium* flora, and (c) *Dicroidium* flora decline and replacement by morphotypes with strong Jurassic affinity. These palaeofloristic changes seem to be strongly influenced by tectonic evolution of sedimentary basins, temporal and regional distribution of sedimentary environments, and intra-Triassic palaeoclimatic change.

**Key words:** Triassic, Gondwana, environments, palaeobotany, synergism.

## Introduction

The study of the Triassic is essential in order to understand the evolution of the land Mesozoic ecosystems. During this period great changes occurred in continental positions, in global climate, and therefore in the resulting floras. Taking into account that the study of the particular variables (flora, environment) does not explain by itself the possible causes of the changes and the sense of the system evolution, a model that integrates the cycle of influences between the physical environment and its resident biota (synergism) is proposed.

The Triassic flora of the Gondwana Realm known as "*Dicroidium* Flora" is characterised by an association of endemic groups (taxonomic groups) with a particular

evolutionary history. The characteristics of the plant associations and the modifications in the types of vegetation are closely related to the physical attributes of the environments.

This contribution shows a synergistic model for the Triassic of southwestern Gondwana, in which the association between biotic and abiotic factors is analysed. The change from palaeophytic to mesophytic floras is related to the Pangea coalescence and global climatic change towards megamonsoonal conditions (Parrish, 1993; Scotese et al., 1999). The development of the endemic taxa, the competition with exotic lineages that migrated from low latitudinal regions, the diversification of the Triassic floras, as well as their further decline and

replacement by elements of Jurassic affinity is here associated with the interaction of a number of abiotic factors and events. Tectonics, volcanism and local climatic conditions are dominant. These factors, together with basin dimensions, topographic barriers and the characteristics of the sedimentary facies were essential controls in the generation of various types of soils and in the positioning of the water table, and therefore in the development of plant palaeocommunities.

### Floristic Realms of Pangea in the Upper Palaeozoic and in the Triassic

For the late Palaeozoic, four phytogeographic units of maximum taxonomic range are recognised. Each of these realms, Euroamerican (=Atlantic), Cathaysia, Angara and Gondwana (Fig. 1), is characterised by its respective flora (Archangelsky, 1996; Meyen, 1987; Wnuk, 1996). The Gondwana Realm is subdivided into four provinces. The Palaeoequatorial Province, in the north of South America and Africa, is identified by a great number of Euroamerican taxons (Archangelsky, 1990). The Palaeoantarctic Province, in high latitudes (60° and 90° S), is characterised by pure floras of *Glossopteris* (without equatorial elements *sensu* Archangelsky, 1990). Between 30° and 60° S two provinces are defined: that of the west (Northafroamerican) with mixed panequatorial and subantarctic floras (Archangelsky, 1990, 1996), and that of the east of Gondwana (Australia and neighbour areas) where panequatorial taxons are rare or absent.

During the Triassic, in the North Hemisphere palaeophytogeographic differences are less marked than during the Permian (Fig. 2), and only one realm (Laurasia)

is recognised. According to Meyen (1987) and Dobruskina (1993), the extraequatorial realm of Angara was preserved as an area: Siberian-Canadian, whereas the equatorial realms, Euroamerica and Cathaysia, are synthesized in the European-Sinica area, which in turn is composed of three east-west - oriented provinces (European, Central Asia and East Asia, Fig. 2).

The Triassic Gondwana realm is composed of two areas: the tropical area defined by Onslow microfloras and the extratropical area defined by Ipswich microfloras. The extratropical area is also characterised by "*Dicroidium*" megafloras, which can be identified because a great number of their components show an endemic distribution. These phytogeographic areas were defined for Australasia (De Jersey and Raine, 1990) as provinces, but as they were recognised in South America (Zavattieri and Batten, 1996; Ottone and Azcuy, 1998; Zamuner et al., 2001), it is shown that they have a greater territorial range.

The extratropical area, characterised by Ipswich microfloras, is also defined by "*Dicroidium*" megafloras, which are characterised by a great number of endemic components (Anderson and Anderson, 1993; Zamuner et al., 2001; Artabe et al., 2002). *Corystospermaceae* is the only family that characterises the extratropical Gondwana. Some genus of *Pleuromieaceae*, *Asterothecaceae*, *Voltziaceae*, *Podocarpaceae* (*Cylostrobus*, *Rienitsia*, *Voltziopsis*, *Heidiphyllum*, *Telemachus*, *Rissikia*), pteridosperms *incertae sedis* (*Dejerseya*), Cycadales (*Kurtziana*, *Yabeiella*) and gymnosperms *incertae sedis* as *Linguifolium* are also restricted to Gondwanaland. The endemism is shown by many species of genus that had a very wide geographic distribution; this is the case for *Pleuromeia*, *Phyllothea*, *Equisetites*, *Neocalamites*, *Cladophlebis*, *Asterotheca*, *Chansitheca*, *Gleichenites*,

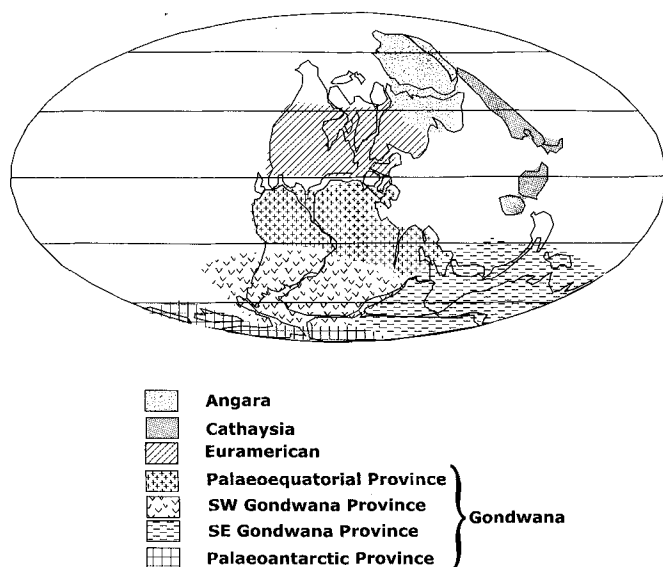


Fig. 1. Distribution of Permian Palaeofloristic Realms.

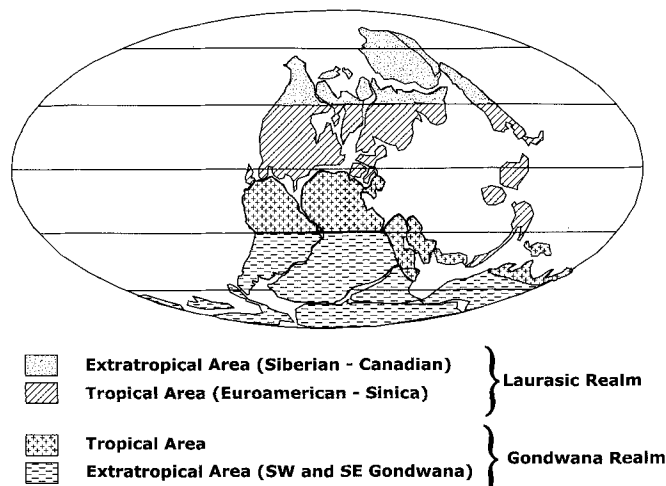


Fig. 2. Distribution of Triassic Palaeofloristic Realms.

*Coniopteris*, *Lepidopteris*, *Scytophyllum*, *Pachydermophyllum*, *Saportaea*, *Ginkgoites*, *Baiera* and *Sphenobaiera*.

Within the extratropical area of Gondwana, Artabe et al. (2002) have recognised two provinces (Fig. 2): the southwest province (identified in Brazil, Chile, Argentina and South Africa) and the southeast province (Antarctica and Australasia). The identification of these provinces is based on the phytogeographic distribution of *Asterothecaceae*, *Dipteridaceae*, *Corystospermaceae*, *Peltaspermaceae*, *Zamiaceae*-*Encephalarteae* and *Ginkgoales*.

### Synergistic Model for the Triassic of Pangea

At the end of the Permian and the beginning of the Triassic, great floristic changes occurred. New adaptive types, different from those present in their Palaeozoic ancestors, simultaneously appeared in different plant lineages. The evolutionary process of replacement of different morphotypes occurred in all the Palaeozoic groups. The lycophytes, sphenophytes, pteridophytes, pteridosperms, cycadophytes and coniferophytes produced the *Pleuromeiaceae* (*Pleuromeia*), *Apocalamitaceae* (*Neocalamites*), *Osmundaceae* (*Cladophlebis*), *Peltaspermaceae* (*Lepidopteris*), *Corystospermaceae* (*Zuberia*, *Dicroidium*), *Cycadales* (*Nilssonia*) and *Voltziaceae*, respectively. Both in the Laurasia Realm and the Gondwana Realm, the replacement of palaeophytic elements by mesophytic elements in the plant associations seems to be a gradual process in pantropical areas (Meyen, 1987; Dobruskina, 1993; McLoughlin et al., 1997), but abrupt in extratropical regions (Retallack, 1995, 1997; Retallack et al., 1996, 1998).

The abrupt replacement of plant groups at the Permian-Triassic boundary has been considered as one of the most severe of the geological past (Erwin, 1993; Kemp, 1999; Kerr, 2001), and it has caused 96% of the Permian species to disappear. Parallel to the interpretations on the crisis of the KT boundary, some authors have invoked catastrophic causes, such as the impact of an extraterrestrial bolide, to explain the PT extinction (Becker et al., 2001). Though the PT palaeofloristic change could be related to an event of that type, it is generally attributed to a global heating phenomenon (Kemp, 1999) associated with episodes of intense volcanic activity. In this sense, Frakes et al. (1992) and Scotese et al. (1999) have shown that between the Permian and the Triassic, the passage from globally cold to warm climates is produced (Fig. 3). The Triassic is a period in which greenhouse or hot house conditions prevailed (Retallack and Alonso Zarza, 1998), and therefore it is characterised by the lack of ice in the polar regions and global average

temperatures between 18°C and 22°C (Scotese et al., 1999).

The trend towards the uniformisation of the vegetation, which implies the synthesis of the four Permian floristic realms in two Triassic realms (cf. Figs. 1 and 2), may find a correlation with the mentioned climatic factors. The global climatic conditions that prevailed during the Upper Palaeozoic (Cold House period) does not seem to be very different from the present ones (Fig. 4A), since between the equator and the pole, dry subtropical, moderate warm, moderate cold and polar regions are recognised (Scotese et al., 1999). During the Triassic, instead, the Pangea was characterised by strongly seasonal or megamonsoonal climate (Wing and Sues, 1992; Dubiel et al., 1991; Parrish, 1993; Smith et al., 1994; Scotese et al., 1999). This caused subtropical regions to extend into high latitudes (Fig. 4B),

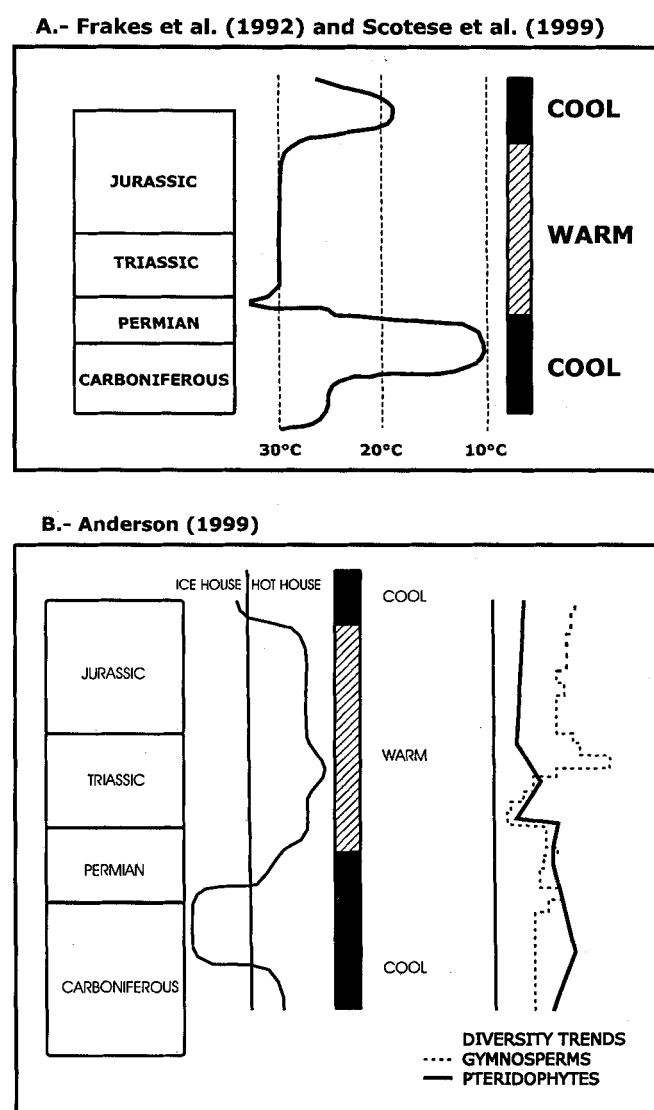


Fig. 3. Global climatic change in the passage from late Palaeozoic to Triassic.

with the resulting disappearance of the cool temperate and polar regions (Ziegler et al., 1993; Retallack and Alonso Zarza, 1998; Scotese et al., 1999).

Therefore, in southwestern Gondwana the continental coalescence and the modification of the climate to megamonsoonal conditions could have been the abiotic determinants in the change from palaeophytic to mesophytic floras. A general synergistic model of the links between biotic and abiotic factors is shown in figure 5. Among the biological components of floristic change, the extinctions, the migrations and the diversification of the endemic groups are recognised (Fig. 5).

#### *Migration, extinction and endemism of the Gondwanan Triassic vegetation*

Between the Permian and Triassic, a major taxonomic change occurred, with the temporal substitution of different groups of pteridosperms, Glossopteridaceae in

the Permian and Corystospermaceae in the Triassic (Fig. 5). Permian Glossopteridales lived in periglacial areas as dominant elements and in subtropical regions as subordinate elements suggesting ecological plasticity (Archangelsky, 1990). Their decline could have been related to the global climatic change that caused the subtropical areas to be extended up to high latitudes and the purely moderate cold areas to disappear. However, the record of *Glossopteris* floras in red beds of the Upper Permian suggests that floristic change cannot be thoroughly attributed to climate, and extinctions could be related with a combination of environmental factors such as fluctuations in sea level and changes in the proportion of atmospheric gases (McLoughlin et al., 1997).

On the other hand, the biological impact that caused the introduction of immigrants in Permian-Triassic extinctions should not be disregarded. Extinction and migration are considered complementary concepts and of mutual influence (Margalef, 1986). Organisms use migration as a strategy to elude environmental change; however, when these variations are too fast to be followed by normal migration and evolutionary processes, they become extinct. As shown by Margalef (1986), extinctions cause the liberation of resources that may be used as a support of new forms (immigrants), whereas the introduction of exotic species may be accompanied by extinction of indigenous organisms (Potts and Behrensmeier, 1992).

By the end of the Permian and the beginning of the Triassic, some species of the equatorial belt preadapted to the new environmental conditions (mesophytic elements) had extended their range of distribution together with the expansion of the subtropical areas towards high latitudes (Fig. 5). This migration pattern seems to be strongly asymmetrical, since several Apocamitaceae, Peltaspermaceae, Cycadales and Voltziales migrated from pantropical areas to Gondwana (Archangelsky, 1990, 1996). On the other hand, the Isoetaceae (= Pleuromeiaceae) reached a cosmopolitan distribution, migrating from extratropical areas (Gondwana or Angara) to low latitudinal areas (Wang Zi-Qiang, 1991; Retallack, 1997).

The analysis of Triassic palaeocommunities (Artabe et al., 2001), have shown that corystosperms were the most characteristic endemic elements of the Gondwanan floras, and some of the pantropical invaders, such as other Pteridosperms like the Peltaspermaceae, had relatively little impact on these indigenous forms. It appears that Corystospermaceae had an adaptative advantage that Peltaspermaceae invaders lacked (Petriella, 1985; Artabe and Brea, 2002). In spite of the anomalous structure (liana-like) of Corystospermaceae

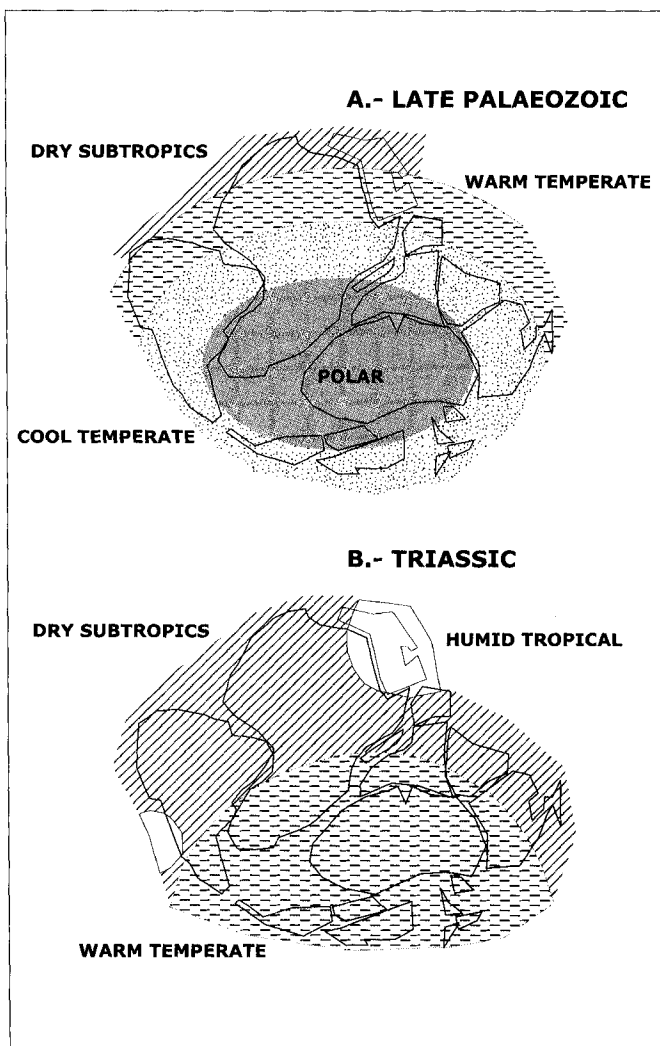


Fig. 4. Gondwana palaeoclimates.

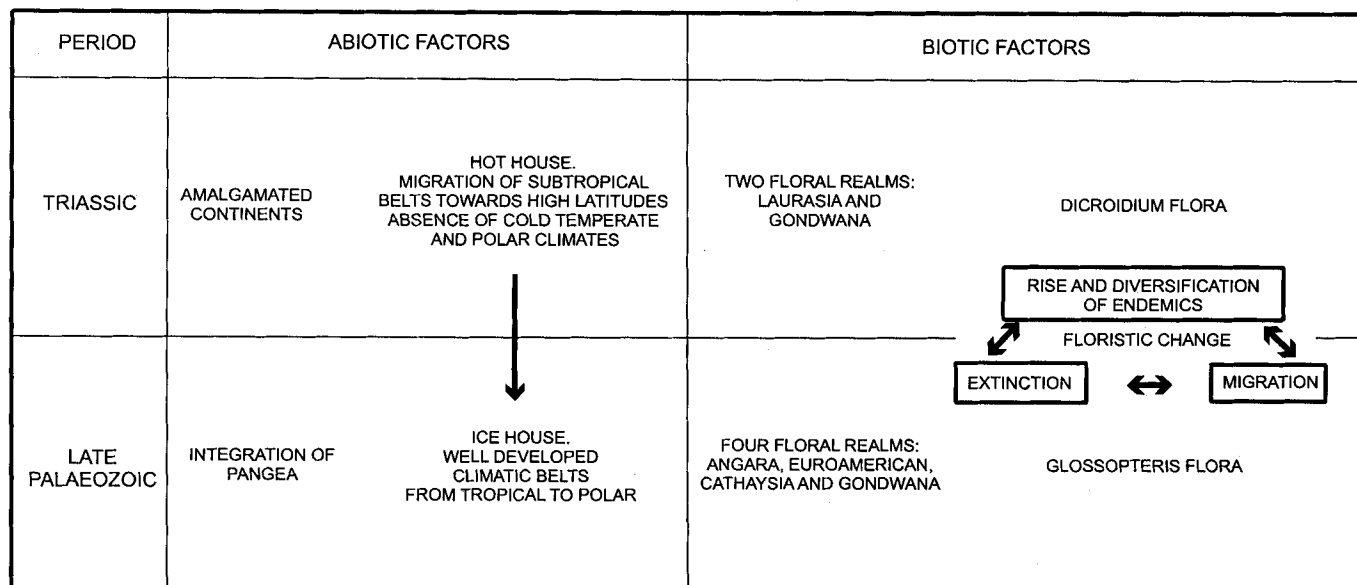


Fig. 5. Global change across the Palaeozoic-Mesozoic boundary.

stems, they typically attain moderate (28 m) to very large size (59 m) (Artabe et al., 2001; Artabe and Brea, 2002). As stature is the major factor controlling canopy position, the deduced height of corystosperms suggests that the Triassic forested landscape was dominated by corystosperms and by coniferophytes, and in the understorey other corystosperms, peltasperms, cycadophytes, and ferns developed. Corystosperms constituted the biggest emergent or second arboreous stratum of the *in situ* mixed forest (Spalletti et al., 1999). Other groups, instead, encouraged by a minimum competition, behaved like pioneer elements. In this sense, Retallack (1997) pointed out that the cosmopolitan distribution of Pleuromeiaceae during the early Triassic was due to their pioneer capacity to colonise oligotrophic environments.

### Triassic Basins and Palaeofloristic Record of Southwest Gondwana

Triassic floras of Argentina are identified in several, mostly continental, sedimentary basins. The most important outcrops of these sedimentary successions are located in the west-central region of Argentina and Chile (Fig. 6) and in Patagonia (Deseado and North Patagonian Massifs, Fig. 6). These depocentres are narrow and elongated depressions floored by a thick continental crust. The substrate of these Triassic basins is composed of rocks of different types and ages: metamorphic and plutonic rocks of the Pampean and Patagonian crystalline basement, and Cambrian-Ordovician, Silurian-Devonian and Upper Palaeozoic sediments. In west-central Argentina and in the North Patagonian area, the Triassic

deposits succeed a volcano-pyroclastic magmatism known as the Choiyoi Group, which is composed of two main associations (Llambías and Sato, 1995; Llambías et al., 1993): Lower Permian intermediate magmatic arc rocks, and Upper Permian–Lower Triassic acidic intraplate volcanics developed under extensional and postcollisional tectonic conditions.

The Triassic sediments of the Patagonian region are identified in the Deseado Massif (El Tranquilo Basin) and in a series of isolated depocentres, as Los Menucos, placed in the North Patagonian Massif (Fig. 6). In west-central Argentina, the Ischigualasto-Villa Unión, Cuyo, San Rafael, Atuel-Malargüe Paso Flores and Chacaico basins are recognized, among the most important ones (Fig. 6). These narrow and elongate depressions are markedly asymmetric half-grabens and may be considered as passive rift systems (Spalletti, 2001b). During the synrift stage they were dominated by tectonic subsidence, high accommodation space and a strongly asymmetric depositional architecture. During the postrift, slow and protracted subsidence due to thermal contraction occurred and the isolated depocentres amalgamated. The sedimentary infill of the Triassic basins is mainly composed of alluvial, fluvial and lacustrine siliciclastic and volcanoclastic deposits, associated with pyroclastic deposits and lava flows. Only the westernmost (Atuel and Chilean) depocentres consist of continental and marine siliciclastic rocks.

In southwestern Gondwana, the Triassic floras are characterised by the diversification of the gymnosperm groups (Anderson et al., 1999) (Fig. 3), which developed mesophytic or meso-xeromorphic adaptive features

(Wing and Sues, 1992). Based on the morpho-anatomical traits observed in roots, stems and leaves Petriella (1985) suggests that *Corystospermaceae* are meso-xeromorphic plants that exhibit adaptations to seasonal climate. Like extant plants living in arid regions, the included phloem and the parenchyma associated (polyxyly) developed in Gondwanaland *Corystospermaceae* stems may be an important adaptative strategy to avoid water stress (Artabe and Brea, 2002). *Corystospermaceae* can be used as palaeoclimatic indicators because their cycadophytic habit (Norstog and Nicholls, 1997) suggests subtropical dry and warm areas without frosts or with occasional frosts (Artabe et al., 2001).

In the Middle Triassic and Lower late Triassic, the corystosperms (*Cuneumxylon*, *Tranquiloxyton*, *Rhexoxylon*) constituted mainly evergreen mixed seasonal subtropical forests (with Ginkgoales, Voltziales and incertae sedis conifers). They also developed sclerophyllous subtropical forests where the arboreal stratum was exclusively composed of corystosperms. The Equisetales (sphenophytes) constituted monospecific thickets of canes both in fluvial and lacustrine environments (Spalletti et al., 1999; Artabe et al., 2001).

During the late Triassic, in the depocentres located close to the proto-Pacific margin, deciduous forests with an arboreal stratum integrated by coniferophytes, ginkgophytes and *Linguifolium* are identified (Spalletti et al., 1999; Artabe et al., 2001). As will be discussed later, these communities could have developed under seasonal and subtropical oceanic climates, the latter influenced by wet currents from the proto-Pacific, with rains during the whole year.

The palaeogeographic distribution of Dipteridaceae and Marattiales suggests that one of the controlling factors on the Triassic floras was climate. In Laurasia, the northern China floras are characterised by Marattiales and those from southern China are mainly composed of Dipteridaceae. In the southern hemisphere, an equivalent and specular distribution has been found, because Marattiales are dominant in high palaeolatitudes (Herbst, 1988; Webb, 1983, 2001; Barale et al., 1995; Morel et al., 2000), whilst Dipteridaceae are typical of lower palaeolatitudes (Herbst, 1993, 2000; Webb, 1982; Spalletti et al., 1999). This palaeogeographic distribution is congruent with the distribution of extant forms, being Marattiales indicative of humid warm-temperate climate (Webb, 2001) and Dipteridaceae of strong seasonal subtropical conditions (Cantrill, 1995). The Triassic floras with Dipteridaceae are restricted to basins of the continental interior of west-central Argentina and the north of Patagonia, and would support the development of megamonsoonal climates. Instead, the floras with

Marattiales, recorded to a palaeolatitude of about 60°S in the Patagonia (El Tranquilo basin), were probably controlled by a moderate warm climate with rains during the whole year.

### Analysis of the Abiotic Factors for the Triassic of Southwest Gondwana

In the previous pages, the influence of the global climate on the development of Pangea floras in general, and on the southwestern of Gondwana in particular, has been shown. However, floristic changes are strongly dependant upon the soil characteristics and the variations of the substratum humidity, especially the changes in the position of the water table (Clea, 1991).

In figure 7, we have tried to synthesize the abiotic factors that have finally determined the soil development and

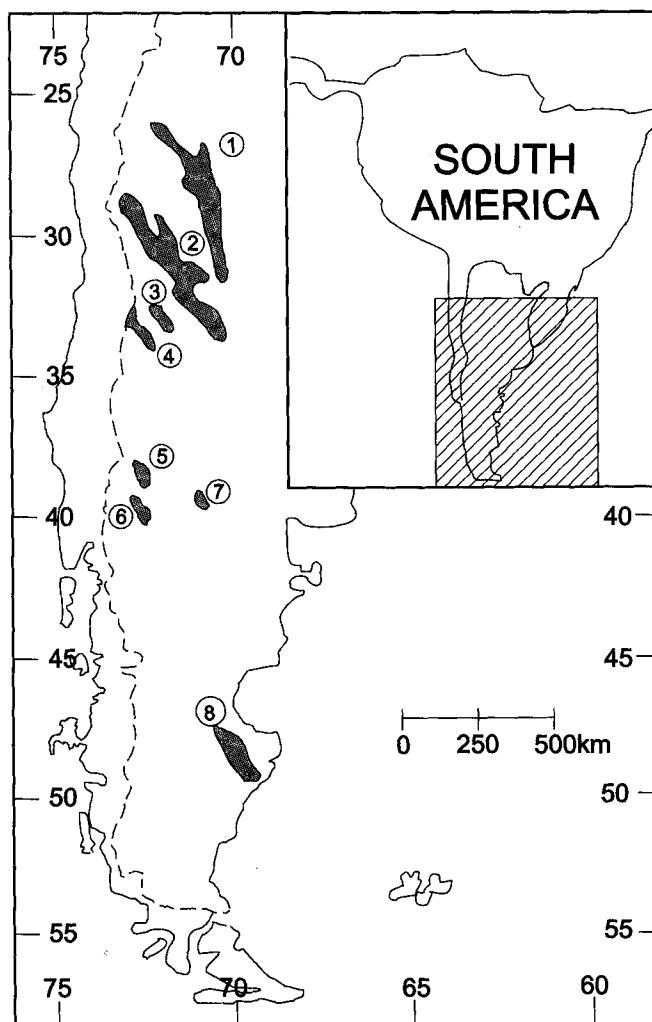


Fig. 6. Location of the main Triassic Basins of Argentina. 1–Ischigualasto-Villa Unión, 2–Cuyo (*sensu lato*), 3–San Rafael, 4–Atuel - Malargüe, 5–Chacaico, 6–Paso Flores, 7–Los Menucos, 8–El Tranquilo.

the location of the water table in the Triassic basins of Argentina. Independently from global controls, such as the continental displacements and connections, and climatic changes, tectonics has played an essential role (cf. Kerp, 1996). Tectonics determines the rhythm and intensity of base level oscillations as well as the subsidence rate in sedimentary basins. During the synrift, base level oscillation was intense and subsidence rate was high, affecting the development of regional soils and producing systematic variations in the position of the water table. Tectonics also had direct influence on the dimensions of the basins and the depositional slopes (Fig. 7). From facies analysis, Spalletti (1994a, 1997, 2001a, 2001b) demonstrated that in the synrift stage, the Triassic depocentres of southwestern Gondwana occupied reduced areas and the slopes were quite steep. The flora had to support different conditions, compared to the periods in which the sedimentary basins were regionally integrated and had gentle depositional slopes. Under these abiotic constraints, plant communities became ruderal, tolerant and poorly diversified. However, it should be taken into account that the levels with fossil plants are better preserved when processes of quick sedimentation or sedimentary aggradation and burial under the water table occur (Dubiel et al., 1991).

Another aspect in which tectonics plays an essential role is that connected with volcanism. Axelrod (1981) pointed out that volcanism may cause a strong decrease of temperature, but Kemp (1999) has suggested that the heating process and the greenhouse effect in the Triassic would be related to the intensification of the volcanic phenomena. Simms and Ruffell (1990) pointed out that,

independently from temperature, volcanism might cause an increase in environmental humidity. For southwestern Gondwana, the Triassic was a period in which the intensification of the volcanic processes, especially the explosive type, caused important effects, among which the presence of very peculiar (pyroclastic and volcanoclastic) facies, the instantaneous destruction of regional soil profiles and the generation of reliefs that could alter rainfall patterns must be mentioned. Axelrod (1981), in turn, has pointed out that the generalized processes of volcanic ash fall may directly influence the biota, to the extent of causing extinction phenomena.

The tectonic rise connected with the phenomenon of generalised extension occurred during the Triassic in a great part of southwestern Gondwana, generated important topographic reliefs, particularly along the active margins of grabens and/or halfgrabens (cf. Spalletti, 2001b; Franzese and Spalletti, 2001). This favoured, on one side, the presence of climatic barriers, and on the other side, a strong control over the characteristics and distribution of the depositional systems and the resulting sedimentary facies, which finally influenced soil development and the surficial and subsurficial humidity conditions of the substrate where plant palaeocommunities settled (Fig. 7).

Obviously, the conjunction of global, secular and local climatic phenomena is essential in all that is connected with the extinctions, migrations and evolution of the Triassic flora in the southwestern Gondwana. From the geological point of view, there are two main aspects that can be used for palaeoclimatic interpretation: the

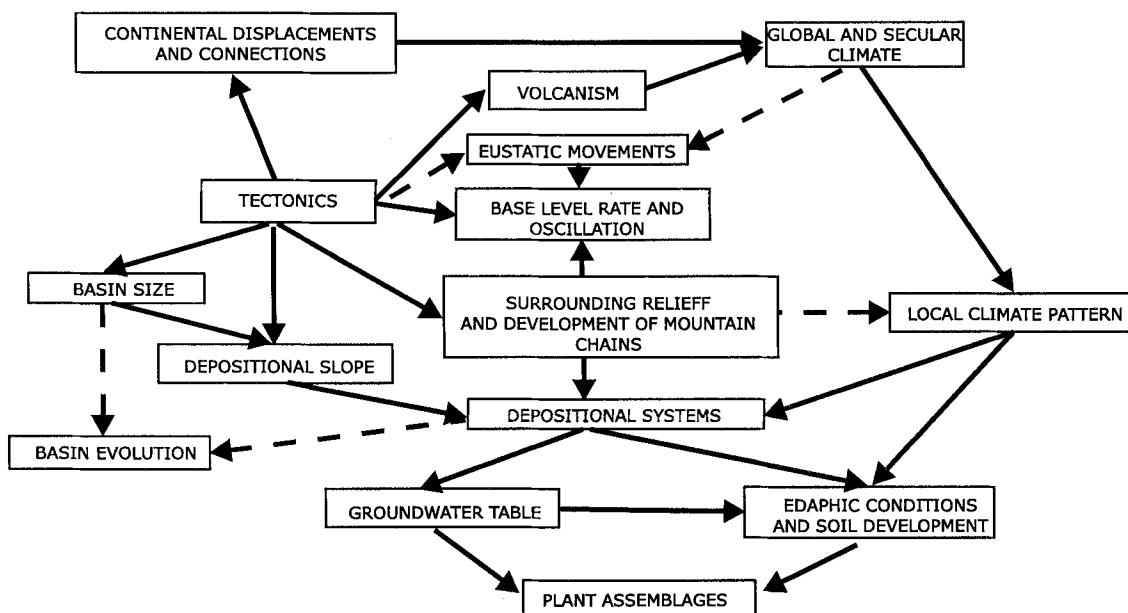


Fig. 7. Major abiotic factors affecting biotic changes and ecosystems structure through time in southwestern Gondwana.

depositional systems and the palaeosols (cf. Dubiel et al., 1991; Dubiel, 1994; Dubiel and Smoot, 1994; Tanner, 2000; Kessler et al., 2001). A summary of the features that can be taken into account for the interpretation of cold, arid, semiarid, moderate humid and humid conditions is shown in table 1. As regards palaeosols, the modified classification criterion by Mack et al. (1993) has been followed since in our case we also recognise mollisols (cf. Retallack, 1988) and aridisols.

The importance of the climatic indicators for the Triassic in southwestern Gondwana basins is also seen in table 1. Thus the clear predominance of depositional systems and palaeosols that suggest semiarid conditions, followed by those that indicate arid and moderate humid

palaeo-climates can be seen. In addition, no cold or humid warm climate indicators have been found in these Triassic basins.

### Evolution of the Gondwanan Triassic Flora in Relation with the Variations in Abiotic Factors

As previously indicated, during the Triassic southwestern Gondwana was part of the Pangea and seems to have been controlled by a megamonsoonal climatic regime. However, within this period, three floristic events are recognised which seem to be quite related to abiotic changes. The synergistic model was prepared based on

Table 1. Palaeoclimatic indicators for the Triassic of southwestern Gondwana: (a) depositional systems, (b) palaeosols.

<b>(a) Triassic Basins. Palaeoclimates and Depositional Systems</b>				
Cold (Arid or Humid) (*)	Arid (**)	Semiarid (***)	Humid Temperate - Warm (**)	
Glacial systems. Tillite	Proximal alluvial systems, debris-flow dominated	Alluvial fan systems (Fanglomerate and hyperconcentrated-flow deposits)	Alluvial fan systems. Coarse-grained facies formed in braided networks.	
Glaciofluvial associations.	Wadi-ephemeral fluvial systems. Poorly developed soils.	Fluvial systems. Flood plains and interfluves with well developed soils.	Fluvial systems (different patterns). Flood-plains characterised by well developed palaeosols and paludal facies	
Holomictic glaciolacustrine systems (varves, turbidites).	Playa and playa-lake systems (altering meromictic and holomictic conditions).	Partially closed lacustrine systems (usually meromictic).	Open lacustrine systems (holomictic and meromictic regime)	
Loessite and associated depositis	Aeolian systems. Fluvial-aeolian interactions.	Loessite and associated deposits		
	Diverse evaporite associations			
Glaciomarine associations	Marginal sabkha systems			

<b>(b) Triassic basins. Palaeoclimates and Palaeosols</b>				
Cold (Arid or Humid) (*)	Arid (**)	Semiarid (***)	Humid	
			Temperate (**)	Warm (*)
Tundra Azonal soils	Algal mats. Azonal soils Hardgrounds: gypcrete, calcrete	Calcrete (nodular horizons)	Silicrete Karstic features	Laterite (ferricrete) Bauxite (aluminocrete)
Inceptisols (poorly developed soils: cryosols). Entisols (lack horizons).	Entisols (lack horizons) Inceptisols (poorly developed horizons) Aridisols (crusts of carbonates or soluble salts).	Vertisols (high clay content) Subordinated mollisols (classic soils, Mollic horizon). Ustic (limited water storage) and xeric (mediterranean-type) regime.	Mollisols (classic soils, mollic horizon). Subordinated vertisols. Udic (cation removal) and aquic (saturated, poorly oxygenated) regime. Inceptisols (gley-type).	Oxisols (high degree of weathering and leaching).

(\*\*): common features. (\*\*): less-common features. (\*): absent (not identified).



the guidelines given by Potts and Behrensmeier (1992) and is briefly explained in figures 8 (abiotic) and 9 (biotic).

#### *Permian - Triassic transition and characteristics of the Barrealian*

In southwest Gondwana, the passage from the Permian to the Triassic is marked by two main factors: the presence of a strongly arid phase and important volcanic activity (Fig. 8) (Spalletti, 2001b). These climatic conditions have been interpreted for the Upper Palaeozoic sedimentary record by López Gamundí et al. (1992) and they could have remained during the early Triassic times. Between the Upper Permian and the Triassic (280–240 Ma) the Choiyoi plutonic, volcanic and volcanoclastic episode occurred in the west and central regions of Argentina and in the north of Patagonia (Llambías et al., 1993; Llambías and Sato, 1990, 1995). This episode of magmatism is the result of intracontinental extension and seems to be associated with a period of lack of subduction in the protopacific margin of Gondwana (Ramos and Kay, 1991; Llambías et al., 1993). The main expression of the Choiyoi magmatism is the generation of an extensive rhyolitic-ignimbritic plateau.

Contemporarily with the Choiyoi magmatism, the generation of a system of extensional basins both within the plateau area and towards the oceanic margin and towards the foreland occurred (Franzese and Spalletti, 2001). As can be seen in figure 10, along the proto-Pacific margin short-lived narrow depocentres were formed due to transcurrence (Charrier, 1979), whereas towards the east there appears an important system of rift basins (Cuyo, Beazley, Ischigualasto basins) with continental clastic fill that is typical of the first stages of the Barrealian Stage (Spalletti et al., 1999). During this early stage of development, the basins constituted isolated depocentres (Fig. 10) controlled by a strong tectonic subsidence and accompanied by volcanic relief associated with the Choiyoi activity. Isolation, topographic barriers and the generalised situation of aridity (Fig. 8), favoured the development of volcanoclastic depositional systems (Ramos and Kay, 1991; Milana and Alcober, 1995; Spalletti et al., 1999; Spalletti, 2001b), which are typical of dry environments (alluvial fans, wadi, ephemeral fluvial systems, playas; cf. Kokogíán et al., 1993), with poorly developed palaeosols, such as entisols, inceptisols and aridisols (Table 1). This group of abiotic factors resulted in stress conditions that influenced the development of floras in these early to Middle Triassic basins (Fig. 9).

As tectonic subsidence was replaced by a more generalised thermal subsidence and the Triassic depocentres began to enlarge and integrate (final stage of the Barrealian Stage, Spalletti et al., 1999), more

favorable situations for the diversification and the preservation of the plant palaeocommunities appeared, and the first floristic Triassic event is defined (Figs. 8 and 9). Still under effects of the latest Choiyoi volcanic activity low gradient deposits began to prevail, which could retain more effectively the soil humidity even in dry subtropical climatic conditions. In San Rafael, a typical depocentre of the continental interior, a pure association of "*Pleuromeia*" was developed (Spalletti, 1994a; Spalletti et al., 1999). According to Retallack et al. (1996) and Retallack (1997), this plant palaeocommunity could have developed in a subhumid environment with evidence of seasonal and progressive desiccations (Spalletti, 1994a), and which probably took advantage of localised increments of humidity due to volcanic activity (cf. Simms and Ruffell, 1990). The "*Pleuromeia*" behaved like pioneer plants and constituted a dominant group among the poorly diversified early Triassic floras (cf. Retallack, 1997). In the Upper Barrealian, fine-grained facies accumulated in the synrift stage of the Barreal and Ischigualasto basins. These deposits favoured the development of inceptisols and vertisols, upon which transitional floras evolved. These palaeocommunities are characterised primitive Dipteridaceae, Corystospermaceae, Ginkgoales and Voltziaceae (Spalletti et al., 1999). The environments were colonised by seasonal subtropical forests (Fig. 9); those of fluvial influence (point bars and flood plains) were formed by corystosperms and Ginkgoales, with a herbaceous stratum of ferns, whereas along lacustrine margins, associations of corystosperms and coniferophytes, and in the understorey other corystosperms developed (Artabe et al., 2001).

#### *Characteristics of the Cortaderitian*

In the Middle Triassic and at the beginning of the late Triassic, the decrease of the volcanic activity was produced (Fig. 8). Isolated activity in the Cuyo and Ischigualasto basins and the development of a new ignimbritic plateau in the North Patagonian area occurred (Los Menucos magmatism, Rapela et al., 1996). The Cuyo, Beazley and Ischigualasto basins are now characterised by a postrift phase dominated by thermal subsidence and expansion of the area occupied by continental sedimentation (Fig. 10). In Patagonia, the opening of Los Menucos and El Tranquilo depocentres with synrift sedimentation and an important contribution of volcanoclastics occurred.

In this phase, which according to Spalletti et al. (1999) belongs to the Cortaderitian Stage (Fig. 8), the sedimentologic and palaeopedologic indicators suggest semiarid conditions (see Table 1). These conditions are similar to those described for other Triassic basins

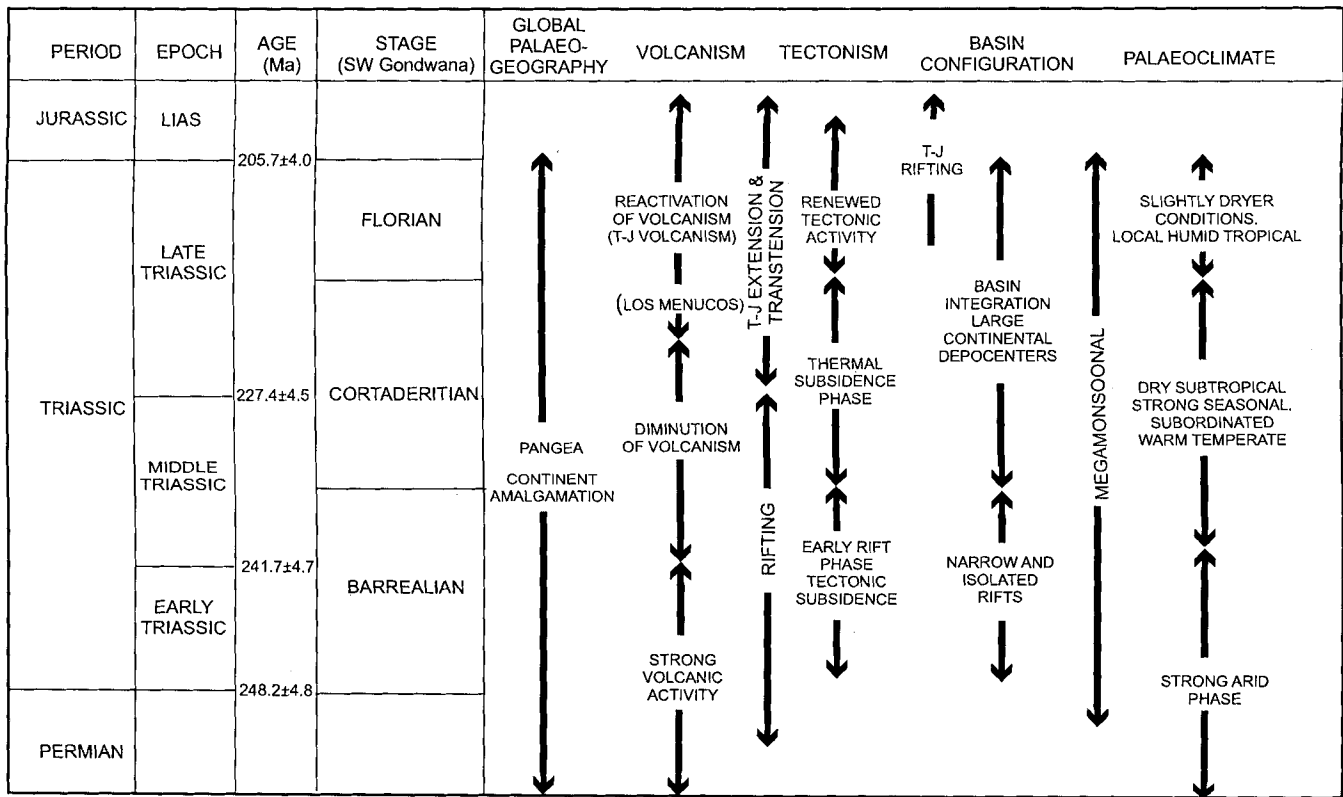


Fig. 8. Synergistic model for the Triassic of southwestern Gondwana. Abiotic factors and events.

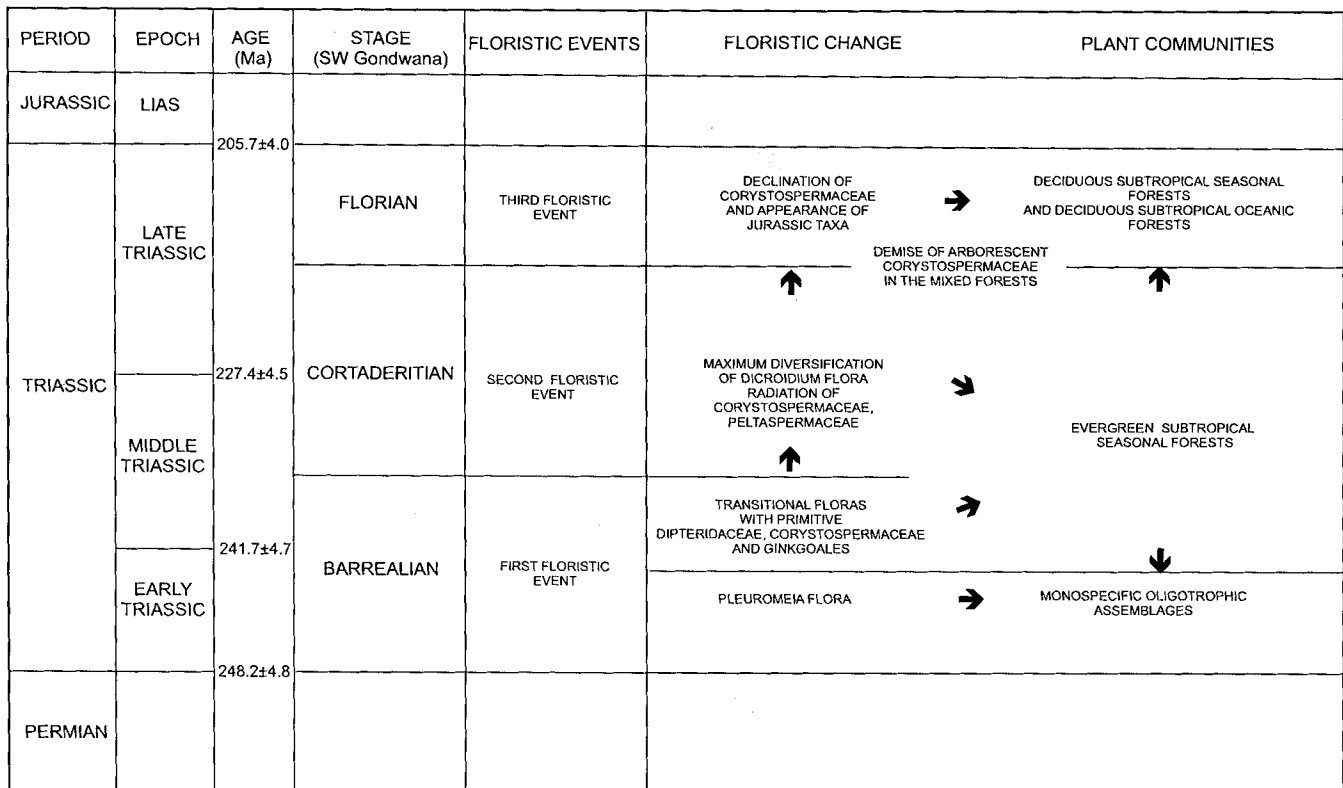


Fig. 9. Synergistic model for the Triassic of southwestern Gondwana. Biotic factors and events.

developed under the main stage of megamonsoonal or dry subtropical regime, characterised by a marked seasonality (Dubiel and Smoot, 1994; Dubiel et al., 1991; Dubiel, 1994; Dubiel and Hasiotis, 1994; Tanner, 2000). Under these circumstances, well developed proximal to distal fluvial systems and partially closed meromictic lacustrine systems prevailed (Gibling et al., 1998; Spalletti, 1997; Tanner, 2000), and ample interfluves were dominated by loessic deposits (Spalletti, 2001a). Fluvial, flood plain and loessic deposits show evidence of regional ustic and xeric palaeosols, such as the vertisols and mollisols described respectively by Mack et al. (1993) and Retallack (1988, 1999).

The vegetal palaeocommunities developed preferentially near lentic and lotic water bodies, where the influence of water tables, in a general dry subtropical framework, was much more effective. It is then quite possible that the flora has occupied galleries along fluvial margins (levees of fertile land, crevasses and crevasse-splays of flood plains), deltaic distributary systems and the coastal areas of the perennial lakes.

During the Cortaderitian, a second floristic event is recorded (Fig. 9), characterised by maximum diversification of the "*Dicroidium Flora*" (Anderson et al., 1999; Spalletti et al., 1999; Zamuner et al., 2001), with adaptative radiation of *Corystospermaceae*, *Peltaspermaceae* and *Cycadales*. In the Lower Cortaderitian (Upper Middle Triassic), the mainly evergreen seasonal subtropical forests integrated by *corystosperms* (*Corystospermaceae*) and *coniferophytes* (*Voltziaceae* and *Protopinaceae*) characterise the fluvial systems and lacustrine margins. In the fluvial areas, the seed ferns constitute the emergents of these forests, whereas in the lacustrine margins the *coniferophytes* are the trees of greater dimensions. Around the lakes, *sclerophyllous* subtropical forests where the arboreous stratum was exclusively formed by *corystosperms* occasionally developed (Artabe et al., 2001). The *Equisetales* (*sphenophytes*) formed monospecific cane thickets both in fluvial and shallow lacustrine environments.

For the Middle Cortaderitian (Lower late Triassic) there are no floristic records related to lacustrine environments. In the fluvial systems and in the deltaic subaerial plains there appear different types of forests (seasonal subtropical evergreen, subtropical *eclerophiles* and the first deciduous forests) in which a process of decline of arboreous *corystosperms* is seen. In the mainly evergreen forests, the *coniferophytes* are bigger than the *corystosperms*, whereas the deciduous forests appear entirely formed by *coniferophytes*.

Towards the end of the Cortaderitian (Middle late Triassic), the vegetation developed in fluvial and lacustrine systems corresponds to herbaceous shrub-like palaeocommunities dominated by *corystosperms*.

### *Characteristics of the Florian*

In the Upper late Triassic significant changes occur in abiotic factors, which in turn are followed by concomitant variations in the floristic associations. The Florian Stage (Spalletti et al., 1999) shows a reactivation of the tectonic activity with new extensional episodes (Fig. 8). The basins, which in the Cortaderitian experimented great expansion, are reactivated with new synrift stages or with transtensional stages (Milana and Alcober, 1995; Spalletti et al., 1999). The sedimentation is characterised by widespread and thick successions of red beds with fluvial domination accompanied with recession of the lacustrine systems. Frequent pyroclastic fall deposits evidence the reactivation of explosive volcanism (Fig. 8).

To the west, very close to the proto-Pacific margin, new rifting processes occurred (Figs. 8 and 10, cf. Franzese and Spalletti, 2001). New extensional, narrow and isolated rifts are formed, and renewed bimodal and extensional volcanism produced abundant lava flows, pyroclastic fall- and flow-deposits, and volcaniclastic deposits. In the more eastern halfgrabens the sedimentation was clearly continental, whereas the western ones are formed by siliciclastic continental and marine deposits. In this case, the geographical base level was determined by the position of the sea level.

Although the general megamonsoonal characteristics persist in the basins located towards the interior of Gondwana, some conditions suggest a relative increase of environmental dryness (Fig. 8). In this sense, Spalletti et al. (1995) described red beds of the Cuyo Basin and plant associations restricted to well-drained, occasionally flooded, levees of high sinuosity fluvial channels. This palaeocommunity seems to be developed under climatic conditions of strong seasonality characterised by a long and important dry season. In the Barreal and Ischigualasto Basins, the deposits of ephemeral fluvial systems show evidence of poorly evolved inceptisols and vertic protosols that confirm the progressive environmental desiccation of the Florian continental interior.

In the framework of the megamonsoonal characteristics, climate changes to more arid conditions (Dubiel, 1994; Olsen, 1997) or more humid conditions (Parrish, 1993) have been established. Tanner (2000) has suggested that these processes can be interpreted as secular climatic variations, since due to the latitudinal drift of the Pangea, a region can progressively locate itself in different climatic belts. Palaeogeographical reconstructions based on palaeomagnetic information (Lawver et al., 1999) suggest that southwestern Gondwana was in a relatively high and stable palaeolatitudinal position during the late Permian and the early Triassic. A relative shift occurred later, and in

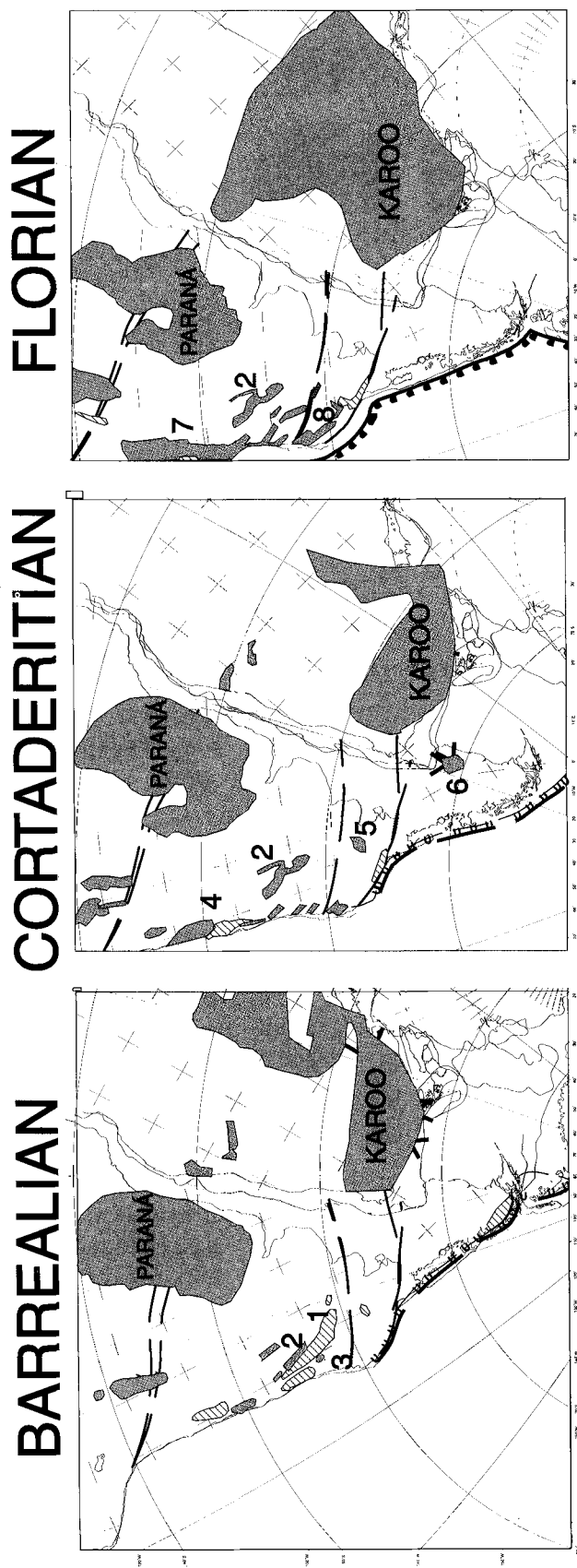


Fig. 10. Development of the main sedimentary basins of southwestern Gondwana for the Barrealian, Cortaderitian and Florian Stages. Base map from Lawver et al. (1999). 1–Choiyoi Volcanism, 2–Cuyo, Alvear, Ischigualasto and Beazley basins, 3–San Rafael Depocentre, 4–Central Chile Basins, 5–Los Menudos Depocentre, 6–El Tranquilo rift, 7–Integrated basins of Central Chile, 8–Triassic–Jurassic rift precursors of the Neuquén Basin (Malargüe - Atuel, Sierra de Reyes, Chacaico, Paso Flores, Puesto Kauffman, among others).

the late Triassic southern Gondwana was displaced in the order of 10° towards the Equator. This could have been the cause of the climatic change towards drier conditions, detected in the interior basins of southwestern Gondwana between the Cortaderitian and the Florian stages.

On the contrary, in the rifts resulting from the Triassic-Jurassic extension and located in the western margin of the megacontinent, subtropical humid conditions occurred due to the influence of maritime circulation systems, and the penetration of air masses from the west. The sedimentologic evidences obtained from the study of the Malargüe depocentre (Spalletti and Morel, 1992; Spalletti, 1997) support this palaeoclimatic interpretation, given the existence of fluvial volcanoclastic hyperconcentrated deposits and debris-flow deposits related to conditions of high discharge and steep slopes associated with volcanic reliefs, meromictic lacustrine associations of moderate humid climate showing frequent progradations of deltaic lobes. The fine-grained subaerial deposits formed in interfan areas, fluvial flood plains and deltaic interdistributary plains show the development of palaeosols with strong evidence of illuviation (udic to aquic) to gley type that suggest seasonal humid to subhumid conditions (Dubiel and Hasiotis, 1994; Tanner, 2000).

The rift basins of the terminal Triassic located somewhat farther from the proto-Pacific continental margin (for example, Paso Flores, Puesto Kauffman) are characterised by proximal fluvial facies associations (alluvial fans and braided systems) in which depositional cycles determined by significant changes in the discharge that could have been related to climatic oscillations (Spalletti, 1994b). The vegetation is restricted to areas dominated by the accumulation of fine-grained sediments (silty sandstones and mudstones) typical of distal flood plains and interfluves, where the development of palaeoverisols was favoured.

There also appear various holo and meromictic lacustrine systems (Ganuza et al., 1995; Franzese and Spalletti, 2001) with significant variations in the positioning of the coastal lines, probably related to the mentioned climatic oscillations.

During the Florian, the third floristic event (Fig. 9) characterised by a substantial change in plant composition occurred. In general, the decline of the *Corystospermaceae* and the differentiation of great number of taxons that persist during the Jurassic are observed (Spalletti et al., 1999). The floristic change of the Upper late Triassic is correlated with the modification of the palaeocommunities. Thus, the Florian shows the development of deciduous forests where the *corystosperms* disappear from the arboreous stratum (Artabe et al., 2001). The fluvial areas supported seasonal deciduous forests with arboreous vegetation of *voltzials* and *ginkgoals*, whereas the *corystosperms* are

only present in the understorey. The margins of the lacustrine systems located in subtropical regions with marine influence are characterised by deciduous forests with clear predominance of *Liguifolium* (Artabe et al., 2001).

Artabe and Brea (2002) showed that the redundancy of the vascular system in *corystosperms* is related to habitat. Like in extant plants growing in arid regions, the included phloem and the parenchyma associated of *Corystospermaceae* may be an important adaptive strategy to avoid water stress. Therefore, the causes for the *corystosperms* to disappear as constitutive elements of the arboreous stratum could be related to a change towards more humid climatic conditions. In this sense, Simms and Ruffell (1990) related the plant and vertebrate extinctions that occurred in the Carnian/Norian transition with the presence of a humid lapse and a quick return to the dominantly dry general conditions that prevailed during the whole Triassic.

## Summary and Conclusions

1. The development, characteristics and extension of the floristic realms during the Upper Palaeozoic and the beginning of the Mesozoic show a close relationship with the global tectonic and the global climatic conditions.

2. The continental accretion and the climatic change, with the passage from cold house (with various and well-defined climatic belts) to warm house (with elimination of climatic belts, especially moderate cold and polar, and the extension of subtropical regions to high latitudes) determined a uniformization of the vegetation. This is why the passage is from four floristic realms in the Permian to two floristic realms in the Triassic.

3. In the Gondwanan extratropical floras, a west-east differentiation is observed, like in those of the northern hemisphere. Two provinces are recognised on the basis of the differential distribution of *Dipteridaceae*, *Peltaspermaceae*, *Asterothecaceae* and *Cycadales*.

4. In southwestern Gondwana the establishment of a strongly seasonal climate of megamonsoonal nature was one of the main causes in the floristic change, which results from the extinction (mainly of the *Glossopteridales*), the migration of exotic elements from equatorial areas (like the *Peltaspermaceae*) and the diversification of endemic groups (like the *Corystospermaceae*).

5. The development of different types of soils and the location of the water table have exerted a direct influence on Triassic plant palaeocommunities of southwestern Gondwana. Soils and water table have been, in turn, controlled by tectonism, by volcanic processes and by climatic changes. In this work, the palaeoclimatic

interpretations are based on the combined analysis of depositional systems and palaeosols, these being attributes that allowed to suggest the predominance of semiarid conditions and, in decreasing order of importance, arid and moderate humid palaeoclimates.

6. In close relation with abiotic changes, three floristic events are recognised for the Triassic of Argentina.

7. At the beginning of the Triassic and due to an important extensional episode, an intense explosive volcanic activity (Choiyoi event) and the opening of rift basins with strong tectonic subsidence and continental clastic fill occurred. The conditions of generalized aridity and volcanic activity could have negatively influenced the development of plant communities. The first of the floristic events occurred in the Barrealian. A pure association of *Pleuromeia sensu lato* is the oldest Triassic floristic record of southwestern Gondwana. Then, the expansion and integration of basins began, the depositional slopes decreased and the accumulation of fine-grained facies allowed the formation of inceptisols and vertisols. As a result, the first seasonal subtropical forests composed of transitional floras with primitive Dipteridaceae, Corystospermaceae and Ginkgoales developed.

8. The second floristic event is determined by the maximum diversification of the *Dicroidium* flora and the radiation of the Corystospermaceae and Peltaspermaceae, which constituted seasonal subtropical evergreen forests. This floristic event occurred during the Cortaderitian and coincided with the decrease of the volcanic activity, the predominance of the thermal subsidence in extensional basins characterised by fluvial, interfluvial, lacustrine, and deltaic facies. The southwestern Gondwana corystosperms show adaptative features – such as pith, primary xylem and successive rings of secondary xylem and phloem – that strongly indicate arid conditions. Palaeoverisols and palaeomollisols also suggest a limited water supply. All these features are in accordance with a dry subtropical or megamonsoonal climatic regime.

9. The third floristic event shows the decline of the Corystospermaceae, the presence of taxons with Jurassic affinity and the formation of palaeocommunities of seasonal subtropical deciduous and subtropical forests with oceanic influence. Contemporarily, the tectonic activity is renewed with new extensional episodes. Isolated halfgrabens are opened and the explosive volcanism is reinstalled. The sedimentation is dominated by alluvial and fluvio-lacustrine facies, and the basins closest to the western margin of Gondwana also received a certain marine influence. The palaeoclimatic indicators of the depocentres located to the continent interior suggest an increase of environmental dryness possibly due to the migration of southwestern Gondwana to lower

latitudes, whereas those, which were located to the western margin of the continent, aimed at a subtropical humid climate.

## Acknowledgments

This work has been financed by Project PIP-CONICET 0912/98: El Triásico-Jurásico del Centro-Oeste de la República Argentina, Geología, Sedimentología, Paleobotánica y Bioestratigrafía). The authors want to express their acknowledgment to their colleagues, Daniel Ganuza, Sergio Matheos, Mariana Brea and Alba Zamuner, for their co-operation in the fieldwork, as well as for the important exchange of opinions and ideas during the long years that the investigations on sedimentology and palaeobotany of the Argentine Triassic demanded. Víctor Ramos and an anonymous reader are thanked for their efforts in reviewing the early version of this manuscript.

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