

Triassic floras of Argentina: biostratigraphy, floristic events and comparison with other areas of Gondwana and Laurasia

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Study of the Triassic floristic record of several stratigraphic units of southern and west-central Argentina has permitted recognition of five Assemblage Biozones and three Stages, defined on the basis of Assemblage Biozone chronology, analysis of main stratigraphic unconformities, and evolution of basin infill. These stages are each characterised by a floristic events: a) appearance of mesophytic elements and coexistence of Palaeozoic and Mesozoic groups (Barrealian); b) maximum diversification of the *Dicroidium* Flora (Cortaderitian); and c) decline of the *Dicroidium* Flora and replacement by morphotypes with strong Jurassic affinity (Florian).

The Triassic geological record of Argentina, notable for the remarkable continuity of fossil floras, has great potential for long-distance correlations. Using floristic events recognised in SW Gondwana, a global chart shows the bio- and chronostratigraphic units, and compares them with Triassic floras described from the Eastern Province of extratropical Gondwana, and Laurasia.

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TRIASSIC continental extension resulted in a series of narrow rifts in west-central Argentina and the Patagonian region (Fig. 1). Each depocenter contains a predominantly continental, clastic fill and records complex interactions between alluvial, fluvial, deltaic and lacustrine depositional systems. The volcanoclastic and sedimentary sequences of most of these basins contain well-preserved fossil plants from numerous stratigraphic levels. This extremely abundant and diverse floristic record is valuable in understanding of the ecology and phytogeography of Triassic plants,

as well as in developing a comprehensive biostratigraphic chart of the Triassic continental successions.

Over the last two decades, most investigations on the Argentinian Triassic have focused on the gross stratigraphy and taxonomy of fossil plants (Stipanovic 2001, Stipanovic & Marsicano 2002). Our studies (Spalletti *et al.* 1999, Morel *et al.* 2001, Spalletti *et al.* 2003, Artabe *et al.* 2003) have provided greater understanding of the development and change of these floras over time in response to variation in depositional systems, tectonism and climate. A biostratigraphic and chronostratigraphic chart

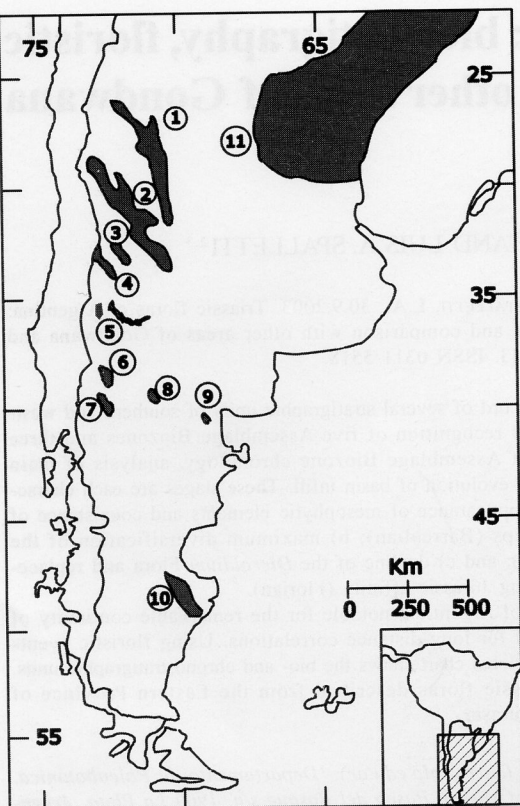


Fig. 1. General map of the main Triassic basins of Argentina. 1, Ischigualasto-Villa Unión-Beazley; 2, Cuyo Basin (*sensu lato*); 3, San Rafael; 4, Malargüe-Atuel; 5, Andacollo-Reyes-Entre Lomas-Neuquén Embayment; 6, Chacaico; 7, Paso Flores; 8, Los Menucos; 9, Eastern sector of North Patagonia; 10, El Tranquilo; 11, Paraná Basin.

based on plant megafossils (Spalletti *et al.* 1999) established correlations between different Triassic depocenters of Argentina. Further, based on analysis of temporal changes in plant megafossils, three floristic events were proposed for the Triassic of western Gondwana by Spalletti *et al.* (2003).

The aim of this paper is firstly to highlight the distinctive character of the Triassic floras of Argentina and, secondly to compare the biostratigraphic, chronostratigraphic and floristic events proposed for SW Gondwana with those of other provinces of Gondwana and Laurasia.

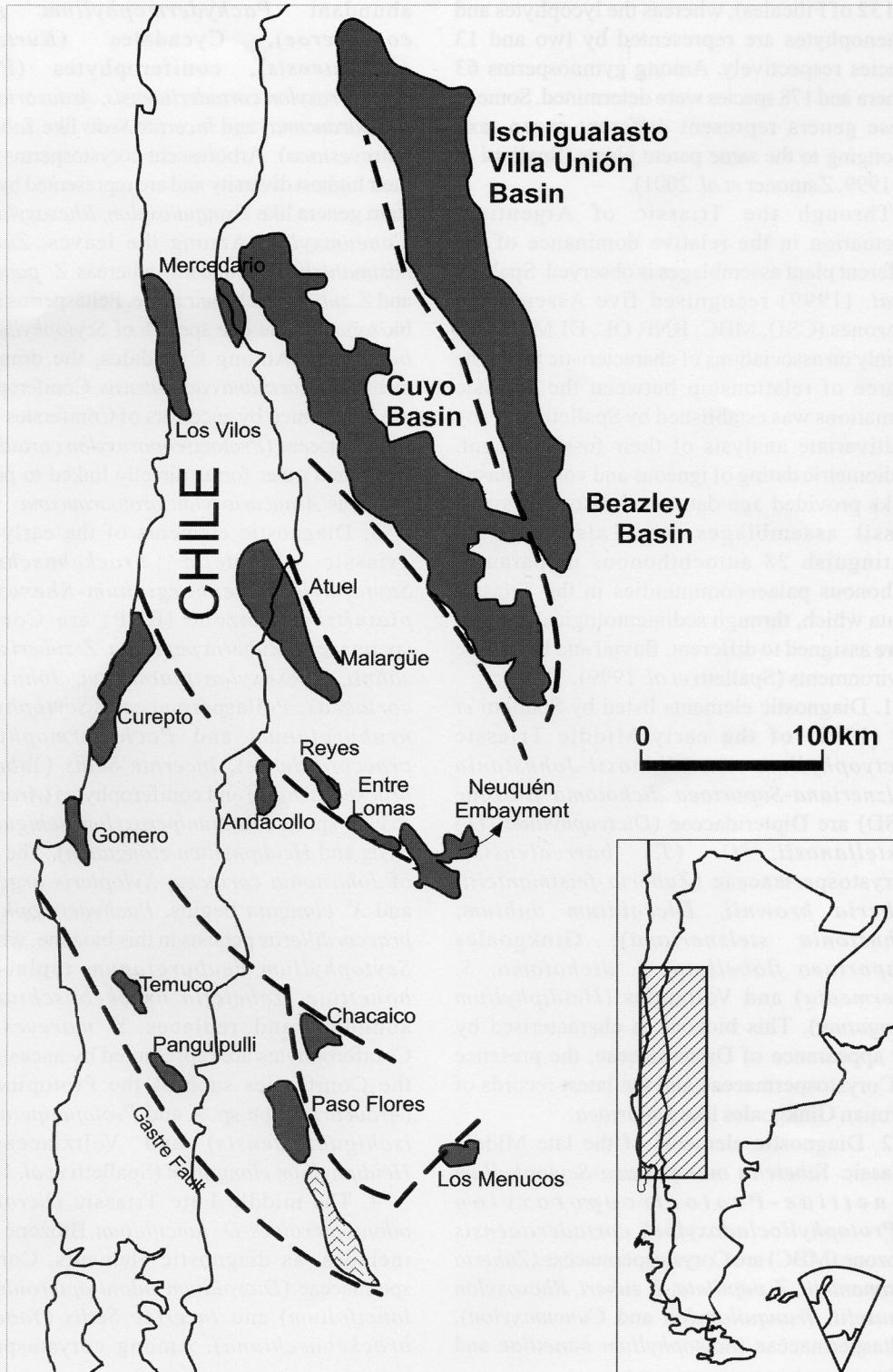
Floristic global correlation requires analysis of plant distribution in time and space, and

palaeophytogeography must be linked with biostratigraphy. The Triassic Gondwana realm is composed of the tropical and the extratropical areas. The extratropical area, defined by 'Dicroidium' megafloras, has two provinces: the SW province (identified in Brazil, Chile, Argentina and South Africa) and the SE province (Antarctica and Australasia) (Artabe *et al.* 2003). Whereas the biostratigraphy and chronostratigraphy proposed by Spalletti *et al.* (1999) and Anderson & Anderson (1985, 1993a) were used for the SW province, and that established by Retallack (1977) and Retallack *et al.* (1993) was used for the SE province. In the Northern Hemisphere, only one realm (Laurasia) is recognised, with two areas: Siberian-Canadian and the European-Sinic, which in turn is composed of three east-west oriented provinces (European, Central Asia and East Asia: Meyen 1987, Dobruskina 1993). North America may constitute another province in this area, as suggested by Artabe *et al.* (2003). The stages of development of floras recognised by Dobruskina (1993, 1995) are used to assign temporal value to the Laurasian megaflora assemblages.

Triassic biostratigraphy of Argentina

The Triassic Argentine megaflora characterizing continental environments is composed of the classes: Lycopsidea (Isoetales: Pleuromeiaceae), Sphenopsida (Equisetales: Apocalamitaceae, Phyllotheceae and Equisetaceae), Filicopsida (Marattiales: Marattiaceae and Asterothecaceae; Filicales: Gleicheniaceae, Osmundaceae, Dipteridaceae and Dicksoniaceae), and Gymnospermopsida as Glossopteridales (or *Gontriglossa sensu* Anderson & Anderson, 1985), Corytospermales, Peltaspermales, Cycadales, Bennettitales, Ginkgoales, Voltziales, Coniferales (Cheirolepidiaceae, Protopinaceae and Araucariaceae), Taxales (Taxaceae) and genera of uncertain systematic affinities such as *Linguifolium*. Pteridophytes are represented by 24 genera. The most diverse group is the filicophytes with 42 species (10 of Marattiales

Fig. 2. Triassic basins of west-central Argentina and northern Patagonia. [see page 233].



and 32 of Filicales), whereas the lycophytes and sphenophytes are represented by two and 13 species respectively. Among gymnosperms 63 genera and 178 species were determined. Some of these genera represent different organ taxa belonging to the same parent plants (Spalletti *et al.* 1999, Zamuner *et al.* 2001).

Through the Triassic of Argentina, fluctuation in the relative dominance of the different plant assemblages is observed. Spalletti *et al.* (1999) recognised five Assemblage Biozones (CSD, MBC, BNP, OL, DLM), based mainly on associations of characteristic taxa. The degree of relationship between the Triassic formations was established by Spalletti *et al.* by multivariate analysis of their fossil content. Radiometric dating of igneous and volcanoclastic rocks provided age data on floristic biozones. Fossil assemblages were also used to distinguish 28 autochthonous or parautochthonous palaeocommunities in the Triassic strata which, through sedimentological studies, were assigned to different, fluvial and lacustrine environments (Spalletti *et al.* 1999).

1. Diagnostic elements listed by Spalletti *et al.* (1999) of the early Middle Triassic *Dictyophyllum castellanosii*-*Johnstonia stelzneriana*-*Saportaea dichotoma* Biozone (CSD) are Dipteridaceae (*Dictyophyllum* (*D.*) *castellanosii*, *D.* (*T.*) *barrealensis*), Corystospermaceae (*Zuberia feistmantelii*, *Zuberia brownii*, *Dicroidium dubium*, *Johnstonia stelzneriana*), Ginkgoales (*Saportaea flabellata*, *S. dichotoma*, *S. intermedia*) and Voltziales (*Heidiphyllum elongatum*). This biozone is characterised by the appearance of Dipteridaceae, the presence of Corystospermaceae and the latest records of Permian Ginkgoales like *Saportaea*.

2. Diagnostic elements of the late Middle Triassic *Yabeiella mareyesiacae*-*Scytophyllum bonettiae*-*Protocircoporoxydon* (= *Protophyllocladoxydon*) *cortaderitaensis* Biozone (MBC) are Corystospermaceae (*Zuberia feistmantelii*, *Z. papillata*, *Z. zuberi*, *Rhexoxylon krausellii*, *Tranquiloxydon* and *Cuneumxydon*), Peltaspermaeae (*Scytophyllum bonettiae* and

abundant *Pachydermophyllum praecordillerae*), Cycadales (*Kurtziana cacheutensis*), coniferophytes (*Protocircoporoxydon cortaderitaensis*, *Araucarioxydon protoaraucana*) and *Incertae Sedis* like *Yabeiella mareyesiacae*). Arborescent corystosperms reach their highest diversity and are represented by three stem genera like *Tranquiloxydon*, *Rhexoxylon* and *Cuneumxydon*. Among the leaves, *Zuberia feistmantelii* is abundant, whereas *Z. papillata* and *Z. zuberi* reach their acme. Peltasperms in this biozone include one species of *Scytophyllum* (*S. bonettiae*). Among Cycadales, the dominant element is *Kurtziana cacheutensis*. Coniferophytes are represented by ancestors of Coniferales as the Protopinaceae (*Protocircoporoxydon cortaderitaensis*) and other forms directly linked to present forms as *Araucarioxydon protoaraucana*.

3. Diagnostic elements of the early Late Triassic *Yabeiella brackebuschiana*-*Scytophyllum neuburgianum*-*Rhexoxylon piatnitzkyi* Biozone (BNP) are Corystospermaceae (*Zuberia papillata*, *Z. zuberi* and *Z. sahnii*, *Rhexoxylon piatnitzkyi*, *Johnstonia coriacea*), Peltaspermaeae (*Scytophyllum neuburgianum* and *Pachydermophyllum praecordillerae*), *Incertae Sedis* (*Yabeiella brackebuschiana*) and coniferophytes (*Araucarioxydon* sp. A, *Protojuniperoxydon ischigualastensis* and *Heidiphyllum elongatum*). The acme of *Johnstonia coriacea*, *Xylopteris argentina* and *X. elongata* begins. *Pachydermophyllum praecordillerae* persists in this biozone, whereas *Scytophyllum neuburgianum* replaces *S. bonettiae*. *Yabeiella brackebuschiana* is abundant and replaces *Y. mareyesiacae*. Coniferophytes are represented by ancestors of the Coniferales such as the Protopinaceae (*Araucarioxydon* sp. A and *Protojuniperoxydon ischigualastensis*) and Voltziaceae as *Heidiphyllum elongatum* (Spalletti *et al.* 1999).

4 The middle Late Triassic *Dicroidium odontopteroides*-*D. lancifolium* Biozone (OL) includes, as diagnostic elements, Corystospermaceae (*Dicroidium odontopteroides*, *D. lancifolium*) and *Incertae Sedis* (*Yabeiella brackebuschiana*). Among corystosperms,

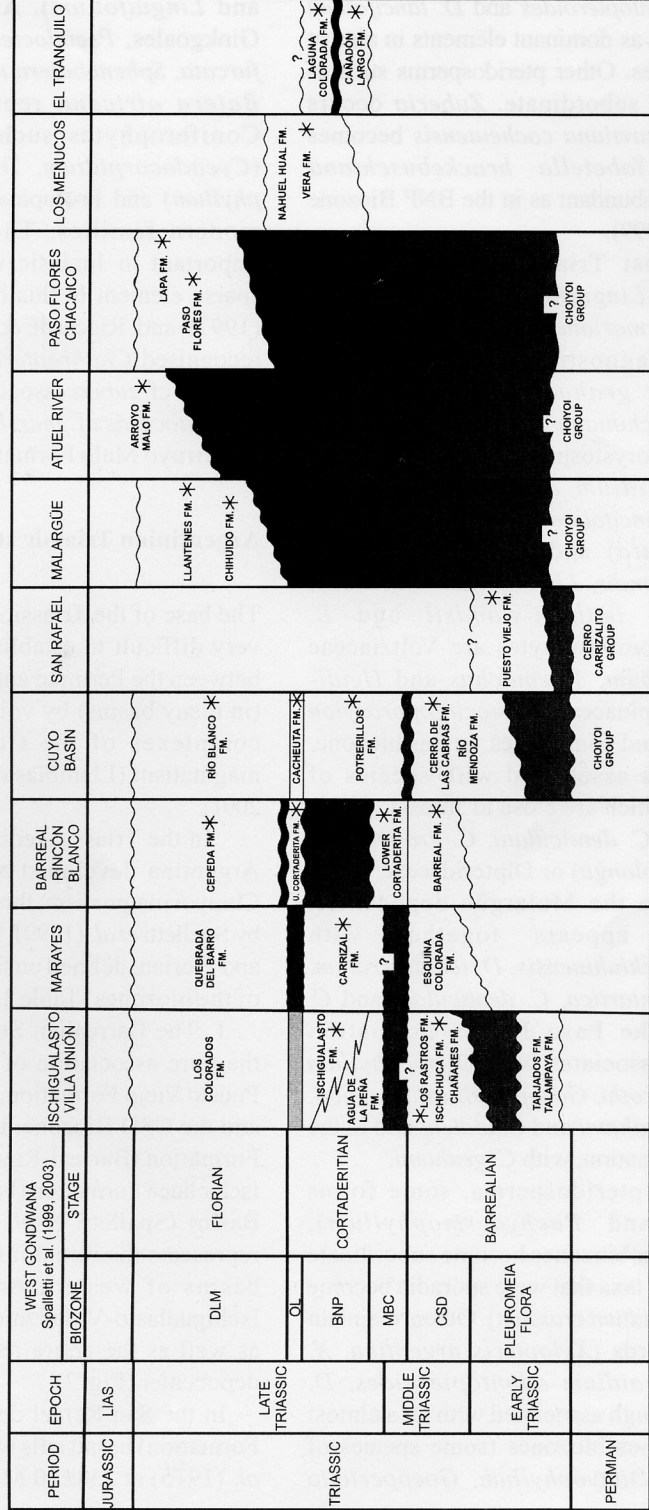


Table 1 Biostratigraphic and chronostratigraphic chart of Argentina showing the correlation of Triassic formations (adapted from Spalletti *et al.* 1999).

Dicroidium odontopteroides and *D. lancifolium* reach their acme as dominant elements in almost pure communities. Other pteridosperms such as *Johnstonia* are subordinate. *Zuberia* occurs occasionally. *Kurtzia cacheutensis* becomes subordinate; *Yabeiella brackebuschiana* continues to be abundant as in the BNP Biozone (Spalletti *et al.* 1999).

5 The latest Triassic *Dictyophyllum tenuiserratum*-*Linguifolium arctum*-*Protocircoporoxydon marianaensis* Biozone (DLM) contains as diagnostic elements Filicales (*Cladophlebis grahami*, *C. denticulata*, *Dictyophyllum chihuiensis*, *D. tenuiserratum* and *D. rothi*), Corystospermaceae (*Rhexoxylon brunoi*, *Dicroidium crassum*, *D. odontopteroides*, *D. lancifolium*, *Xylopteris argentina* and *X. elongata*) and *Incertae Sedis* as *Scleropteris grandis*, *Linguifolium arctum*, *L. lilleanum*, *L. tenison-woodsii* and *L. steinmannii*. Coniferophytes are Voltziaceae (*Cycadocarpidium*, *Telemachus* and *Heidiophyllum*), Protopinaceae (*Protocircoporoxydon marianaensis*) and Ginkgoales. In this biozone, *Linguifolium* is associated with species of *Cladophlebis* which are close to Jurassic forms (*C. antarctica*, *C. denticulata*, *C. grahami*, *C. indica* and *C. oblonga*) or Dipteridaceae. More specifically, in the Malargüe depocenter, *Linguifolium* appears together with *Dictyophyllum chihuiensis*, *D. tenuiserratum*, *Cladophlebis antarctica*, *C. denticulata* and *C. oblonga*. In the Paso Flores Formation *Linguifolium* associates with *Dictyophyllum tenuifolium*, *D. rothi*, *Goeppertella stipanicicii*, *Cladophlebis grahami* and *C. indica*, and in the Río Blanco Formation, with *C. grahami*.

Among the pteridosperms, some forms (*Johnstonia* and *Pachydermophyllum*), abundant in older biozones become subordinate and, conversely, taxa that were sporadic become abundant (*Dicroidium crassum*). Others maintain consistent records (*Xylopteris argentina*, *X. elongata*, *Dicroidium odontopteroides*, *D. lancifolium*) though associated with taxa almost absent in previous biozones (some species of *Cladophlebis*, *Dictyophyllum*, *Goeppertella*

and *Linguifolium*). Among Cycadales and Ginkgoales, *Pseudocercospora carteriana*, *Baiera furcata*, *Sphenobaiera robusta*, *S. taeniata* and *Baiera africana* represent this biozone. Coniferophytes such as the Voltziaceae (*Cycadocarpidium*, *Telemachus* and *Heidiophyllum*) and Protopinaceae are precursors of modern families. The Cheirolepidiaceae, important in Jurassic woodlands, appears as sparse element in this biozone. Riccardi *et al.* (1997) and Riccardi & Iglesia Llanos (1999) recognised *Clathropteris* cf. *meniscioides* and *Zuberia* cf. *zuberi* associated with the ammonoid *Choristoceras* cf. *marshi* in marine deposits of the Arroyo Malo Formation.

Argentinian Triassic stages

The base of the Triassic System in Argentina is very difficult to establish because the passage between the Permian and the Triassic is masked (in many basins) by volcanics and plutonics or complexes of the Gondwana or Choiyoi magmatism (Llambías *et al.* 1993, Morel *et al.* 2001).

In the Triassic sedimentary successions of Argentina developed after the climax of the Choiyoi magmatism, three Stages were proposed by Spalletti *et al.* (1999): Barrealian, Cortaderitian and Florian, defined on the stratigraphic position of the biozones (Table 1).

1. The Barrealian Stage is characterised by the pure association of Pleuromeiaceae in the Puesto Viejo Formation, San Rafael depocenter, and the CSD Biozone, identified in the Barreal Formation (Barreal-Rincón Blanco rift) and the Ischichuca Formation (Ischigualasto-Villa Unión Basin) (Spalletti *et al.* 1999). The Barrealian represents the initial infill of the large Triassic basins of western Argentina, such as the Ischigualasto-Villa Unión and the Cuyo basins, as well as the entire record of the San Rafael depocenter (Fig. 2).

In the San Rafael depocenter (Puesto Viejo Formation) basalt sills were dated by Valencio *et al.* (1975) at 238 ± 10 Ma and 232 ± 4 Ma. In the

Cuyo Basin, the upper sector of the Río Mendoza Formation was dated at 243 ± 4.7 Ma (Ávila 2003), and in the Cerro de las Cabras Formation (Cuyo Basin) two basaltic sills were dated in 235 ± 5 Ma (Ramos & Kay 1991). Analysis of all data suggests that the Barrealian is Early to early Middle Triassic (Spalletti *et al.* 1999).

2. The Cortaderitian Stage includes the MBC, BNP and OL Biozones; the '*Dicroidium* Flora' reaches its maximum diversity. The MBC Biozone was identified in the Cuyo Basin (Potrerillos Formation) and in the Barreal-Rincón Blanco rift (lower Cortaderita Formation). The BNP Biozone is recorded in the Ischigualasto-Villa Unión Basin (Ischigualasto Formation), Cuyo Basin (Potrerillos Formation), Los Menucos (Vera Formation) and in southern Patagonia (El Tranquilo Group). The flora of the OL Biozone occurs in the Cacheuta and upper Cortaderita Formations (Cuyo and Barreal-Rincón Blanco basins, respectively; Fig. 2).

In the Ischigualasto-Villa Unión Basin, a bentonitic tuff located 20 m above the base of the Ischigualasto Formation (BNP) was dated by Rogers *et al.* (1993) at 228.5 ± 0.3 Ma (Middle Triassic – Late Triassic boundary). In the Los Menucos depocenter, Rapela *et al.* (1996) defined an isochron of 222 ± 2 Ma (early Late Triassic). The data suggest that the Cortaderian is late Middle to middle Late Triassic (Spalletti *et al.* 1999).

The lower boundary of the stage is represented by conspicuous discontinuities in the Ischigualasto-Villa Unión Basin and the Cuyo Basin but, in other areas, the sedimentary record is continuous, as the gradual passage between the Barrealian and Cortaderitian Stages in the Barreal-Calingasta depocenter (Table 1).

3. The Florian Stage is defined by the DLM Biozone, identified in the Cuyo Basin (Río Blanco Formation), Ischigualasto-Villa Unión Basin (Los Colorados Formation), Paso Flores – Chacaico Basin (Paso Flores and Lapa Formations), and Malargüe-Atuel depocenters (Chihuido, Llantenes and Arroyo Malo Formations). The Florian Stage has not been recognised in Patagonia. It shows particular geological and

biostratigraphic features. The basins of west-central Argentina record the passage from the early postrift phase to the late postrift and/or transtensional-filling phase. The sedimentary record is characterised by the conspicuous development of fluvial-dominated red-beds and a marked reactivation of explosive volcanism revealed by frequent pyroclastic-fall deposits (Fig. 2). Analysis suggests the Florian is latest Triassic (Spalletti *et al.* 1999) (Table 1).

Triassic floristic events of southwestern Gondwana

In the Early Triassic, adaptive types, different from their Palaeozoic ancestors, simultaneously appeared in different plant lineages. In pantropical areas of the Laurasia and the Gondwana Realms, replacement of palaeophytic elements by mesophytic elements in the plant associations seems to be gradual (Meyen 1987, Dobruskina 1993, McLoughlin *et al.* 1997), and floras of both palaeophytic and mesophytic groups occurred in Permian and Triassic deposits. In extratropical regions the palaeophytic '*Glossopteris* Flora' was suddenly replaced by the '*Dicroidium* Flora', which persisted until the Late Triassic (Retallack 1995, 1997; Retallack *et al.* 1996, 1998).

In southwestern extratropical Gondwana three major floristic events have been distinguished by Spalletti *et al.* (2003). The first event (Table 2) involved the appearance of the mesophytic '*Dicroidium* Flora', which first occurred in southwest Gondwana occurs in the upper part of the Barrealian Stage (CSD Biozone), characterised by corystosperms. Some relict Palaeozoic plants persist as subordinate components of this flora, though the main palaeophytic representatives were extinct. In Argentina, the low diversity Early Triassic lycopsid flora of the Puesto Viejo Formation (Morel & Artabe 1994, Spalletti 1994, Spalletti *et al.* 1999) was succeeded by the early Middle Triassic '*Dicroidium* Flora' of the CSD Biozone. The monospecific *Pleuromeia sensu lato* assemblage characterised the lower part of the

Barrealian Stage. Further evidence from palynology and vertebrate palaeontology support the Early Triassic age of the lycopsid assemblage (Ottone & García 1991). This biozone is dominated by Dipteridaceae (*Dictyophyllum castellanosii*, *D. barrealensis*), Corystospermales (*Zuberia feistmantelii*, *Zuberia brownii*, *Dicroidium dubium*, *Johnstonia stelzneriana*), Ginkgoales (*Saportaea flabellata*, *S. dichotoma*, *S. intermedia*) and Voltziales (*Heidiphyllum elongatum*).

The first appearance of Dipteridaceae in SW Gondwana is Middle Triassic (Zamuner *et al.* 2001, Artabe *et al.* in press). Although evolutionary radiation of Triassic Dipteridaceae is not well known, Herbst (1992) considered *Dictyophyllum castellanosii*, present in CSD Biozone, the prototype from which other species and genera radiated. The corystosperms in this biozone were considered ancestral in the leaf lineages by Retallack (1977). During the early Middle Triassic, the Permian *Saportaea* survived with three species (Spalletti *et al.* 1999, Zamuner *et al.* 2001, Artabe *et al.* 2003).

The second floristic event (Table 2) is characterised by the maximum diversification of the 'Dicroidium Flora' (Anderson & Anderson 1993b, Anderson *et al.* 1999, Spalletti *et al.* 1999, Zamuner *et al.* 2001), with adaptative radiation of Corystospermaceae, Peltaspermaceae and Cycadales. It corresponds to the Cortaderitian stage, which contains the MBC, BNP and OL biozones. Corystosperms dominate most floristic assemblages in which Peltaspermales, such as *Scytophyllum* and *Yabeiella* appear. During the late Middle Triassic-early Late Triassic the greatest biodiversity of corystosperm stems is recorded (three genera and five species). Artabe & Brea (2003) suggest that the corystosperm stele evolved along two principal lineages (rhoxoxyloid and cuneumxyloid) from a polyxylic precursor (Artabe & Brea 2003). The rhoxoxyloid line is characterised by *Rhexoxylon*, the southwestern Gondwanaland species of which seem to fit into a developmental series: *R. sp.* (*R. krauseli*?) and *R. piatnitzkyi* occurred during the Cortaderitian, and *R. brunoi* during the Florian (third floristic event). The series

shows an increase of the anomalous vascular tissue development with formation of successive cycles of medullar bundles inside the trunk and the progressive acquisition of bigger stems by an increase in the amount of centrifugal secondary conducting tissues (Artabe & Brea 2003). *Cuneumxylon* and *Tranquiloxydon* characterise the cuneumxyloid line of the second floristic event; these taxa only show anomalous vasculature in the form of centrifugal secondary xylem because they do not produce centripetal xylem or perimedullar bundles (Artabe & Brea 2003).

In the third floristic event (Table 2) substantial changes in plant composition occurred (Florian stage; DLM Biozone). In general, Corystospermaceae, Peltaspermaceae and Ginkgoales decline and some taxa appear which became dominant during the Jurassic (Anderson & Anderson 1993b, Anderson *et al.* 1999, Spalletti *et al.* 1999, Zamuner *et al.* 2001), such as *Goeppertella* (*G. stipanicicii*), *Dictyophyllum* (*D. rothi*), *Marattia* (*M. münsteri*), *Cladophlebis* (*C. antarctica*, *C. denticulata*, *C. grahami*, *C. indica* and *C. oblonga*), *Scleropteris* (*S. grandis*) and *Solenites* (*S. vimineus*) together with the first record of Cheirolepidiaceae.

Global Chart of Triassic Correlation

Biostratigraphic and chronostratigraphic patterns as well as floristic events recognised in southwestern Gondwana (Spalletti *et al.* 1999, Spalletti *et al.* 2003) and the broad zonal plant distribution which distinguished the Laurasia Realm (Meyen 1987; Dobruskina 1993, 1995) are essential for establishing interregional correlations based on the Triassic megafloras. The resulting correlation chart (Table 2) shows that the Triassic floras developed following a synchronous global pattern determined by significant floral changes, such as appearance of mesophytic elements, maximum radiation of pteridosperms and appearance of taxa that become dominant during the Jurassic (Meyen 1987, Dobruskina 1993, Spalletti *et al.* 2003). The global chart also shows there is a good agreement between the floras and floristic events

PERIOD	EPOCH	IUGS (2000) STAGE	AGE (Ma)	LAURASIA Dobruskina (1993)	WEST GONDWANA			EAST GONDWANA Retallack (1993)
					BIOZONE	STAGE	Spalletti et al. (1999, 2003) FLORISTIC EVENTS	Anderson & Anderson (1985, 1993a, 1993b)
JURASSIC	LIAS		203±3					
		RHAETIAN						
		NORIAN						
	LATE TRIASSIC		220	Lepidopteris Flora	DLM	FLORIAN	THIRD FLORISTIC EVENT DECLINE OF CORYSTOSPERMACEAE AND APPEARANCE OF JURASSIC TAXA	Yabeiella
					OL			
		CARNIAN		Scytophyllum Flora	BNP MBC	CORTADERITIAN	SECOND FLORISTIC EVENT MAXIMUM DIVERSIFICATION OF DICROIDIUM FLORA. RADIATION OF CORYSTOSPERMACEAE, PALTASPERMACEAE	
TRIASSIC	MIDDLE TRIASSIC	LADINIAN	230±6 233±5					Dicroidium odontopteroides Dicroidium zuberi Thinnfeldia callipteroides
		ANISIAN						
	EARLY TRIASSIC		240.7±5	Konvunchana Pleuromeia Floras Veltzia	CSD Pleuromeia Flora	BARREALIAN	FIRST FLORISTIC EVENT FLORAS WITH PRIMITIVE DIPTERIDACEAE, CORYSTOSPERMACEAE AND GINKGOALES PLEUROMEIA FLORA	
		SCYTHIAN	251±3.6					
PERMIAN								

Table 2. Global chart of Triassic correlation.

of Argentina, South Africa and Laurasia, but less coincidence with Australasia (Table 2).

The good correlation between western Gondwana and Laurasia is related to the common record of groups of plants that behaved as dominant in the same stratigraphic intervals. Pleuromeiaceae, Dipteridaceae and Peltaspermaeae characterise these two phytogeographic regions, and have been successfully employed in the respective biostratigraphic schemes (Meyen 1987, Dobruskina 1993, 1995; Spalletti *et al.* 1999, 2003; Artabe *et al.* 2003).

The Barrealian floras (Early Triassic to early Middle Triassic: Scythian- Anisian) correlate with the Korvunchana, *Pleuromeia* and the 'Voltzia Flora' of Laurasia. Thus the first floristic event proposed for Argentina is synchronous with the last phase of Palaeophytic Floras evolution defined for Laurasia by Meyen (1987) and Dobruskina (1993) (Table 2). This event involves mixed floras composed of palaeophytic and mesophytic elements. In the European-Sinian and Siberian floristic areas the '*Pleuromeia* Flora' (*Pleuromeia-Densoiosporites* and allied genera) is recognised. In the European-Sinian Area this event is represented by the *Voltzia* Flora, (*Voltzia*, *Aethophyllum*, *Yuccites*, *Schizoneura*, *Echinostachys*, *Equisetites*, *Equisetostachys*, *Neuropteridium*, *Crematopteris* and cycadophytes). The Siberian region is also characterised by the flora assigned to the Permian-Triassic boundary by Meyen (1987) and to the Early Triassic by Dobruskina (1993) and Mogutcheva (1996). This flora is composed of ferns (Osmundales, Marattiales, Matoniaceae), peltasperms (*Lepidopteris*, *Scytrophyllum*, *Madygenopteris*, *Tatarina*, *Peltaspermum*, *Taeniopteris*, *Sphenophyllum* and *Yavorskyia*). In the European-Sinian Area the *Pleuromeia* and *Voltzia* Floras disappeared in the early Middle Triassic (Anisian).

The Cortaderitian Floras show a close correlation with the '*Scytrophyllum* Flora' of Laurasia. They represent the second floristic event (Spalletti *et al.* 2003) and the development of the first Mesophytic evolutionary stage (Meyen 1987, Dobruskina 1993, Mogutcheva

1996), occurred between the late Middle Triassic and early Late Triassic (Ladinian–Carnian). These floras are characterised by Peltaspermiales, Cycadales, Bennettitales, Czekanowskiales, Voltziales and Dipteridaceae, which became dominant during the next event.

Floriant floras, representing the latest Triassic (third) floristic event correlate with the '*Lepidopteris* Flora' of Laurasia, assigned by Dobruskina (1993, 1995) to the second (Norian-Rhaetian) stage of Mesophytic Floras evolution (Table 2). According to Meyen (1987) these Floras are characterised by Peltaspermaceae (*Lepidopteris*), associated with Bennettitales (*Pterophyllum*, *Anomozamites*, *Wielandiella*), Cycadales (*Ctenis*, *Pseudoctenis*, *Nilssonina*), conifers (*Cycadocarpidium*, *Elatocladus*), ginkgoales (*Ginkgoites*, *Baiera*, *Sphenobaiera*) and Czekanowskiales (*Czekanowskia*, *Hartzia*, *Phoenicopsis*). Marattiales (*Marattiopsis*, *Danaeopsis*), Osmundales (*Todites*), Dipteridaceae (*Dictyophyllum*, *Clathropteris*) and Matoniaceae (*Phlebopteris*), which persist during the Jurassic, are the outstanding components of this floristic event.

A significant agreement is recognised between the South-American and South African regions of western Gondwana, especially for the Middle and lower Late Triassic (Table 2), although the good sequence of Triassic plants in Argentina allowed recognition of a more complete stratigraphic scheme than that established for South Africa by Anderson & Anderson (1985, 1993a). In Argentina the '*Pleuromeia* Flora' and the CSD Biozone (Barrealian Stage) correlate with the 'Burgersdorp Flora' defined in South Africa by Anderson & Anderson (1985, 1993a). The second floristic event is represented in Argentina by the MBC, BNP and OL Biozones (Cortaderitian Stage) and in South Africa by the Molteno Flora (Anderson & Anderson 1985, 1993a).

In the Extratropical area of the Gondwana Realm, two provinces (Southwestern and Southeastern) are recognised from the phytogeographic distribution of distinctive suites of taxa (Spalletti *et al.* 2003, Artabe *et al.* 2003). The Southwestern Gondwana province experienced mostly a dry

subtropical climate, whereas the Southeastern province developed under warm temperate and humid conditions. These provinces are defined on the basis of heterogeneous and disjunctive distribution of species as well as variation in biodiversity of some groups of plants (Retallack 1977, 1979, 1980a, 1980b, 1981, 1997; Webb 1982, Artabe *et al.* 2003). Therefore, the higher degree of uncertainty in correlation between east and west Gondwana could be explained by phytogeographic reasons, since the Triassic floras of the regions developed under quite different palaeoclimatic conditions. As shown in Table 2, the three floristic events recognised in other areas of Gondwana and Laurasia cannot be defined from the biostratigraphic scheme proposed by Retallack (1977) and Retallack *et al.* (1993) for Australasia. According to the new (IUGS 2000) stratigraphic chart, the *Thinnfeldia callipteroides*, *Dicroidium zuberi* and *Dicroidium odontopteroides* Oppel Zones are Early and Middle Triassic. Thus, the maximum diversification of the *Dicroidium* Flora in Australasia occurred before the second floristic event defined for areas under dry subtropical palaeoclimatic conditions (western Gondwana and Laurasia).

Conclusions

Five Assemblage Biozones are recognised for the Triassic of Argentina. Based on biozone chronology, analysis of stratigraphic unconformities and evolution of basin infill the Barrealian, Cortaderitian and Florian stages are defined. The stages represent three floristic events: a) appearance of mesophytic elements, and coexistence of Palaeozoic and Mesozoic groups (Barrealian); b) maximum diversification of the *Dicroidium* Flora (Cortaderitian); and c) decline of the *Dicroidium* Flora and replacement by morphotypes with strong Jurassic affinity (Florian).

These three floristic events can be, respectively, correlated (see Table 2) with the last phase of Palaeophytic Floras evolution, the first phase of Mesophytic Floras evolution and the second phase of Mesophytic Floras

evolution defined for Laurasia by Meyen (1987) and Dobruskina (1993, 1995). Therefore, a significant degree of correlation is defined for the floras of Laurasia and Argentina.

The Barrealian (first event) and Cortaderitian (second event) Floras from Argentina may be related with the Bursgersdorp and Molteno Floras respectively from South Africa.

Early diversification and provincialism of the *Dicroidium* Flora in Australasia, developed under warm temperate climatic conditions, with less certain correlation with the Triassic floras defined for the dry subtropical regions of western Gondwana.

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