A new Late Triassic palynological assemblage from western Gondwana (Carrizal Formation, Marayes Basin, Argentina)

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ABSTRACT

The Carrizal Formation, exposed in the Marayes-El Carrizal Basin (western Argentina), has been the focus of palaeobotanical studies since the late 1800s. The recent finding of well-preserved palynological assemblages provides the first detailed studies about its palynofloras. In this paper, the 63 taxa identified in the unit are illustrated and discussed, as well as their stratigraphic distribution in equivalent palynological assemblages of Argentina. Some spore species are revised: Uvaesporites hammenii (Herbst) Césari, comb. nov., Retuotritites wielandii (Jain) Césari, comb. nov. and Lundbladispora stellae (Herbst) Césari, comb. nov. The recognition of Cadargasporites baculatus de Jersey & Paten emend. Reiser & Williams, Craterisporites rotundus de Jersey, Enzonalasporites vigens Leschik, Leptolepidites argenteaeformis (Bolkhovitina) Morbey, Protodiploxypinus americus Dunay & Fisher and Rugulatisporites permixtus Playford, among others, appears to be useful for local and intercontinental correlations. A Carnian age is proposed for the palynofloras.

KEY WORDS
Triassic, Carnian, palynology, systematic, Gondwana, Argentina.
RÉSUMÉ
Novel assemblage palynologique du Trias supérieur de l’Ouest du Gondwana (formation Carrizal, bassin de Marayes, Argentine).

La formation de Carrizal, exposée dans le bassin de Marayes-El Carrizal (Ouest de l’Argentine), fait l’objet d’études paléobotaniques depuis la fin du xixe siècle. La découverte récente d’assemblages palynologiques bien conservés fournit les premières études détaillées sur ces palynoflores. Dans cet article, les 63 taxons identifiés dans l’unité sont illustrés et commentés, ainsi que leur répartition stratigraphique dans des assemblages palynologiques équivalents de l’Argentine. Certaines espèces de spores sont révées : Uvaeportites hammenii (Herbst) Césari, comb. nov., Retuviroletes wielandii (Jain) Césari, comb. nov., et Lundbladispora stellae (Herbst) Césari, comb. nov. La reconnaissance de Cadargarportites baculatus de Jersey & Paten emend. Reiser & Williams, Cuaterisporites rotundus de Jersey, Enzonalasporites vigens Leschik, Leptolepidites argenteaformis (Bolkhovitina) Morbey, Protodiploxypinus americus Dunay & Fisher et Rugulatisporites permixtus Playford, entre autres, semble être utile pour les corrélations locales et intercontinentales. Un âge Carnien est proposé pour les palynoflores.

MOTS CLÉS
Trias, Carnien, systématiques, Gondwana, Argentine.

INTRODUCTION

The Argentinian Triassic paleofloras are characterized mainly by 17 orders and a group of incertae sedis genera, all included in four classes (Lycopsida: Sphenopsida; Filicopsida and Gymnospermopsida) known as the “Dicroidium Flora”, comprising a total of about 200 and 36 species (e.g. Artabe et al. 2007). The paleofloristic assemblage of the Carrizal Formation (San Juan Province) has been studied since the late 1800s (Geinitz 1876), and more recently by Lutz & Arce (2013) and Morel et al. (2015). The paleoflora is characterized mainly by Pleuromeiales, Marattiales, Equisetales, Osmundales, Umbkomansiales (Corystospermales), Peltaspermales, Ginkgoales, Coniferales, Cycadales and incertae sedis genera. According to its paleofloristic content, Spalletti et al. (1999) considered a Middle-Late Triassic age (Carnian) for the unit, and by the paleoenvironmental conditions, it was referred to the regional Cortalderitain Stage (Stage 2: lacustrine). Stipanicic & Marsicano (2002) also assigned a Late Triassic (Carnian-Norian) age for the Carrizal Formation. Later, Lutz & Arce (2013) and Morel et al. (2015) revised and compared the paleoflora, coinciding with the age proposed by Spalletti et al. (1999).

Although these macrofloristic assemblages are well-known, the palynological records consist of brief mentions. The first palynological studies were carried out by Yrigoyen & Stover (1969) recognizing an assemblage “M1” recovered from the basal section of the strata assigned by Borrello (1946) to the Quebrada de la Mina Group (or Arroyo Seco Member of the Carrizal Formation). Later, Lutz (2006), in her unpublished thesis, mentioned the presence of palynological assemblages, dominated by pollen, to the south of Marayes locality. The recovering of three palynological assemblages analyzed in this paper improves the correlation of the unit and the knowledge about the composition of the Late Triassic palynoflora in this part of Gondwana, including new reports of the northern Enzonalasporites group.

GEOLOGICAL SETTING

The Marayes-El Carrizal Basin is part of a series of extensional basins developed in the SW of Pangea during the early Mesozoic. This depocenter and the neighbor Ischigualasto-Villa Unión Basin were located at around 48°S drifting toward North during the Late Triassic (Goddéris et al. 2008; Kent et al. 2014). In this paleogeographic context the Marayes-Carrizal Basin would be placed in the austral temperate humid belt.

This basin is in the San Juan Province, at S and SW of La Huerta Hill (Fig. 1) and is characterized by a 2300 m thick sedimentary succession (Bossi 1976). The stratigraphy of this basin changed through time, firstly Borrello (1946) defined four units: Esquina Colorada, Quebrada de la Mina, Carrizal, and Quebrada del Barro groups. Stipanicic (1957, 2002) agreed to Borrello’s stratigraphic division but considered these units as formations, including them into the Marayes Group. Later, Bossi (1976), considered the Quebrada de la Mina Formation into the Carrizal Formation. Recently, Colombi et al. (2015) described a new unit at the top of the succession: the Balde de Leyes Formation, which was included into the Marayes Group.

The basin succession is formed by continental facies (Fig. 2) that can be summarized as follows. The Esquina Colorada Formation is characterized by a conglomerate succession with scarce red sandstones that reach 550 m thick, accumulated by alluvial fan piedmont facies (Bossi 1976). The Carrizal Formation, the focus of this study and later described in detail, is characterized by distinctive gray and light greenish-gray sandstones and abundant mudstones interlayered with carbonized material and quartz conglomerates, reaching 350 m of thickness. These deposits occurred in fluvial systems of high slope at the beginning and low slope at the end (Spalletti et al. 2011). The red beds of the Quebrada del Barro Formation are characterized by a succession of muddy sandstones and conglomerates 700 m thick, interpreted as the medial and distal facies of a distributary fluvial system (Colombi et al. 2015).
At the top of the sequence, the Early Jurassic Balde de Leyes Formation is characterized by a 200 m thick fining in upward siliciclastic succession. In the base is characterized by dark red coarse conglomerates and scarce interlayered red mudstones, while towards the top, this relation is reversed. This succession was also interpreted as a distributary fluvial system, although from proximal to distal facies (Colombi et al. 2015).

The complete sequence shows evidence of seasonality by paleosols (Argillisols and Calcisols), paleoecology and taphonomy of fossil plants, taphonomy of vertebrate assemblages and fluvial architecture (e.g. Colombi et al. 2015; Morel et al. 2015; Correa et al. 2019). However, the sedimentary record suggests a general decrease in humidity from the El Carrizal (where carbonaceous mudstones characterized floodplains) upward to the Balde de Leyes Formation at the top, which is characterized by evaporitic playa lake deposits.

The Carrizal Formation (Figs 2; 3) is characterized by two members (Spalletti et al. 2011). The lower, Arroyo Seco Member, comprises vertical stacked multistory-channel belt conglomerates and minor sandstones, interlayered with rare mudstones bearing plant remains and in situ gymnospermous trunks (Morel et al. 2015). It has been interpreted as deposited in a braided fluvial system dominated by bedload channels (low-accommodation system track, Spalletti et al. 2011).

On the other hand, the upper Rickard Member is composed of lenticular beds of conglomerates and sandstones forming channels encased in floodplain deposits of dark green and gray fine sandstones, mudstones, and carbonaceous shales. This member corresponds to a mixed-load fluvial system showing low sinuosity lenticular channels and well-developed wet poorlydrained floodplain deposits (high-accommodation system track, Spalletti et al. 2011).

THE MACROFLORA

The Carrizal Formation contains fossil plant remains throughout the succession. The Arroyo Seco Member preserves impressions-compressions of fronds and a monotypic Umkomasiaceae (or Corystospermaceae) forest, initially found in the northern...
sector of the basin, at the Sierra de la Huerta area (Spalletti et al. 2011; Morel et al. 2015). This forest was interpreted to have grown on the tops of point bars or emergent islands, which periodically were washed away by the channels, uprooting, and transporting the trees that grew there, as can be seen by the presence of logs in situ and transported.

In the Rickard Member, there are also trunk remains transported in conglomerate-like facies, interpreted as lenticular channels (Spalletti et al. 2011). Correa et al. (2019) described a monotypic assemblage of fossil woods, assigned to *Protocu*pressinoxyylon in the southern sector, at the Cerro Gigantillo locality. In this member, they are also recognized cuticles of large fronds preserved in carbonaceous levels of centimetric thickness. These facies are characterized by horizontally laminated to low angle ripple-cross laminated gray mudstones, corresponding to flooded areas of the floodplain. Associated with these levels, in the southern area of the basin, were recovered mosses to gymnosperms, listed in recent works (Herbst 1994, 2006; Lutz & Arce 2013; Morel et al. 2015). Lutz & Arce (2013) recognized in the El Carrizal Formation the presence of *Carpolithus mackayi, Cladophlebus kurzii, C. mendozaensis, C. mesozaico, Cuneumxylon spalletti, Dicroidium argentum, D. dubium var. taaninemii, D. lancifolium var. lancifolium, D. marayaeensis, D. odontopteroides var. moltense, D. odontopteroides var. remotum, D. odontopteroides var. obtusifolium, Dicroidium odontopteroides var. odontopteroides D. odontopteroides subspecie orbiculoides cf. *F. papilioformis, Fraxinopsis andium, Ginkgophytoxylon lucasi, Hepaticites sp., Heidiphyllum elongatum, J. stelzneriana var. stelzneriana, J. stelzneriana var. serrata, J. coriacea, Kurtziana cacheutensis, Lepidopteris strombergensis, Linguifolium tenison woodsi, Milieroaculis lutzii, Noocalamites sp., Pachydermophylum praecordillerae, Protophylocladoxylon sp., Sphenobaiera argentinae, S. tormbergensis, S. sectina, Taeniopteris spp., Telemanchus elongatum, X. argentina, Y. brackebuschiana, *Yabeiella mariae, Y. crasa, Y. wielandi, Xilopteris argentina, Zuberia shamni, and Zuberia zuberti.

Later, Morel et al. (2015) added the finding of the following species in the Rickard Member: *Baiera cuyana, Cordiacarpus sp., Equisetites fertilis, Ginkgoites matutinensis, Heidiphyllum elongatum Kurtziana brandmayri, Noocalamites carreri, Perucus rhetaeica, Rhezoxxylon cf. piatrixzyi, and Scytoxyllum cf. *S. argentim. Morel et al. (2015) reported a compositional similarity with the Carnian Potrerillos Formation from the Cuyana Basin. Thus, this unit shares 15 (of the 18) taxa with the Potrerillos Formation (83% of affinity).
MATERIAL AND METHODS

The analyzed outcrops of the Carrizal Formation are located to the south of the Marayes town (Fig. 1). The fossiliferous levels are situated around 330 m above the base of the Carrizal Formation (110 m above the base of the Rickard Member, Fig. 3). The sampled section (10 m thick) consists of lentillar strata, 0.1 to 1 m thick, of massive, ripple laminated, and in minor proportion trough cross-stratified sandstones. The sandstone bodies are interdigitated with thin layers of carbonaceous mudstones bearing abundant fossil plants. The mudstones form lenses of limited lateral continuity (up to 1 m long) and few millimeters to tens of centimeters thick with abundant soft-sediment deformation. The fossiliferous beds are interpreted as minor channels that fed crevasse splays in floodplain areas. During flooding stages, autochthonous riparian vegetation, together with allochthonous transported plant remains, accumulated in floodplains and crevasse splays. Distally, in the floodbasin, a second type of deposits consists in small swamps in which thin levels of coals where deposited. Northwestward, these carbonaceous levels laterally correlate with the thick coal layers, which were economically exploited during the last century (Fig. 1).

Fifteen samples were collected for palynological studies and processed, but only three samples yielded palynomorph assemblages. They were treated with the standard method described in Phipps & Playford (1984); oxidation was not necessary, and the slides were prepared using the mounting media proposed by Noetinger et al. (2017). Sample preparations were analyzed with an Olympus BX53 microscope, and photomicrographs were taken with a Nikon DS-Fi1. All material is housed in the Paleopalynological Collection at the Museo Argentino de Ciencias Naturales B. Rivadavia (BA Pal 6585-6587). Stage coordinates quoted in the Appendix 1 were read on an England Finder slide.

RESULTS

The palynological assemblages contain exclusively terrestrial palynomorphs, including spores, bisaccate pollen (taeniata and non taeniata), polyplicate and colpate pollen together with rare representatives of inaperturate and monosaccate pollen and freshwater algae. The samples are dominated by bisaccate non taeniata pollen, but taeniata specimens are common components, as well as, spores sculptured by verrucae, clavae or baculae. These last specimens usually occur in tetrads indicating their autochthonous origin. Fragments of cuticles are also recognized in the BA Pal 6586 and 6587 samples, recovered from mudstones at the top of abandoned crevasse channels, supporting the scarce transport of the material.

The taxonomic composition is consistent in the three samples; however, slight variations in the relative abundances of some taxa were observed, being the BA Pal 6585 (recovered from a swamp deposit) less diverse than the others. Their tentative paleoecological significance is discussed.

SYSTEMATIC PALYNOLOGY

**Spores**

*Trilete*

*Annulispora* sp.

(Fig. 7A)

**Remarks.** The specimens are 34-38 µm in diameter and the exine is finely microgranulate to punctate on the distal and the proximal equatorial area. They lack the radial distal ridges characteristic of *A. folliculosa* and *A. microannulata* sculptural elements and have a larger internal diameter of the distal annulus.
**Apiculatisporis cf. A. serratus**
Sajjadi & Playford, 2002
(Fig. 4S, T)

**Remarks.** Annulispora serratus Sajjadi & Playford from the Jurassic of Australia is similar by its small size and its zipper-like laesurate margins, where the sculpture is fused.

**Baculatisporites comaumensis**
(Cookson) Potonié, 1956
(Fig. 4N, O)

**Biretisporites sp.**
(Fig. 4C)

**Cadargasporites baculatus**
de Jersey & Paten emend.
Reiser & Williams, 1969
(Fig. 7C)

**Camptotritiles cf. C. warchianus**
Balme, 1970
(Fig. 7D, E)

**Cingutritiles cf. C. cestus**
Stevens, 1981
(Fig. 4AA, BB)

**Clavatisporites conspicuus**
Playford, 1982
(Fig. 4U-Y)

**Remarks.** Specimens ranging from subtriangular amb, with distal short pila and bacula (Fig. 4U-V) to circular spores bearing longer sculptural elements densely arranged, are included in this species (Fig. 4W-Y). The sculpture, with the apices widened in form of "cauliflower", coincides with those illustrated originally by de Jersey & Hamilton (1967) as Clavatisporites cf. C. hammenii and included into C. conspicuus by Playford (in Playford et al. 1982).

**Craterisporites rotundus**
de Jersey, 1970
(Fig. 4BB, CC)

**Foveosporites sp.**
(Fig. 4R)

**Leptolepidites volkheimerii**
Zavattieri, 1986
(Fig. 7F-N)

**Leptolepidites argentaeformis**
(Bolkhovitina)
Morby, 1975
(Fig. 7O, Q-T)

**Remarks.** This species is characterized by the sculpture of big, flat, and rounded verrucae usually fused producing a negative reticulum.

**Lundbladispora punctata**
Césari & Colombi, 2016
(Fig. 4Z)

**Lundbladispora stellae**
(Herbst) Césari, comb. nov.
(Fig. 5A-E)

**Remarks.** Herbst (1965) defined *Cingulatisporites stellae* as: "Trilete cingulate; triangular amb with slightly concave sides, cingulum a bit more rounded than the body. Arms of the lesura, not exactly rights, somewhat thickened, reaching the equator (?). Exine relatively thickened up to 2.5 µm on the sides of the triangle. Cingulum width from 3.1 µm in the apex up to 4.7 µm in the sides of the triangle. Verrucate sculpture (extending to the cingulum?), verrucae of approximately 2 µm diameter. Size of the grain: 28-33 µm diameter (holotype 32 µm)". The specimens illustrated by Herbst (1965, 1970) from the Los Rastros Formation displays an equatorial expansion of the exine more translucent than the central body, which not corresponds to a thickened cingulum. Specimens described by Herbst (1965) as *Cingulatisporites stellae* are coincident with the here illustrated in Figure 5A-E.

Illustrations of several specimens described by Zavattieri (1990b) from the Cerro de las Cabras Formation are considered here probably similar to *L. stellae*, such as *Cirratriradites* sp. 1, *Densoisporites* sp. 1 and *Cirratriradites* sp. cf. *C. splendens* Balme & Hennelly. However, Gutiérrez et al. (2017) included those specimens into *Lundbladispora verrucosa* Gutiérrez, Zavattieri & Ezpeleta, which differs in its inner body close to the equatorial amb, proximal face concave, distal surface convex densely covered by small verrucae usually fused in irregular muri.

Some spores (Fig. 5D), resemble *Secarisporis triangularis* Gutiérrez, Zavattieri & Ezpeleta, who adhered to Foster’s reinterpretation of the genus *Secarisporis*, which is considered synonym of *Uveaeisporites* Döring (Foster, 1979). The inclusion of the spores from the Carrizal Formation into *Secarisporis* it is not followed here, taking into account the distinctive morphology of the Namurian type species *S. lobatus* with the robust regulate sculpture with subordinate verrucae on the equatorial surface, and the distal polar region covered by loosely spaced ridges and warts. The distinctive caviate condition of the species, with the exine, expanded equatorially, and densely sculptured on the distal surface and margin by small ornament differs from the exclusive morphology of *Secarisporis* Neves.

...
Osmundacites fissus (Leschik) Playford, 1965
(Fig. 4D, E)

Osmundacites wellmanii Couper, 1953
(Fig. 4I-J)

Remarks. The similar species O. cacheutensis Jain, may be an extreme variation between O. senectus/O. wellmanii as it was proposed by Rojo & Zavattieri (2005).

Playfordiaspora cancellosa (Playford & Dettmann) Maheshwari & Banerji, 1975
(Fig. 7C)

Retusotriletes wielandii (Jain) Césari, comb. nov.
(Fig. 4A, B)

Cacheutasporites minutus Jain, Palaeontographica Abteilung B 122: 10; pl. 1; fig. 8 (1968).
Cacheutasporites minutus Jain, Palaeontographica Abteilung B 122: 10; pl. 1; fig. 11 (1968).

Remarks. Jain (1968) defined Cacheutasporites in similar terms that Retusotriletes Novumaca emend. Pashkevich, with the Y-shaped ends of the lesura continuous into a sub-Peripheral ring or "curvatures imperfectae". Zavattieri (1990a) enlarged the diagnosis of Cacheutasporites, remarking the presence of curvatures imperfectae and perfectae in the genus and including subcircular to subtriangular spores. The simple morphology of these genera does not justify its separation into different genera, Retusotriletes having priority. Cacheutasporites minutus Jain was defined on eight spmnes, which differ only in its slightly small size (32-37 μm), from the five original specimens assigned to C. wielandii (42-45 μm), so the former it is considered a junior synonym. Klaus (1960) defined R. mesozoicus for including spores ranging from 35 to 55 μm in diameter and pointed out that in some specimens, the curvatures are not so clear, sometimes almost completely smoothed out. Our specimens, approximately 30 μm in diameter, coincide in the lowest range of the species and differ only in their more subtriangular outlines.

Rugulatisporites neuquenensis Volkheimer, 1972
(Fig. 4F, G)

Rugulatisporites permixtus Playford, 1982
(Fig. 4K, L)

cf. Striattella sp.
(Fig. 7Y)

Trilites cf. T. wolfgangii Sajjadi & Playford, 2003
(Fig. 4P, Q)

Remarks. Sajjadi & Playford (2002, 2003) combined the specimens described by Volkheimer (1972) as Ischyospo-
rites sp. A, Ischyosporites sp. B and Ischyosporites sp. C, to Trilites wolfgangii. Ischyosporites variegatus differs in its rounded muri and bigger lumina. The specimens illustrated by de Jersey & Raine (1990) and the originals have a subtriangular amb with concave sides, which differ from the here illustrated.

Uvaesporites hammenii (Herbst) Césari, comb. nov.
(Fig. 5R-DD)

Clavatrilites hammenii Herbst, Ameghiniana 4: pl. 2; figs 14; 15 (1965).

Clavatisspores dubius Herbst, Ameghiniana 4: pl. 1; figs 1; 2 (1965).

Uvaesporites verrucosus (de Jersey) Helby in de Jersey 1971; Zavat-
tieri & Mego, Ameghiniana 45: figs 3.17-18 (2008).

Uvaesporites glomeratus (Döring) Hiltmann 1967; Rojo & Zavattieri, Ameghiniana 42: fig. 3F (2005).

Uvaesporites glomeratus (Döring) Hiltmann 1967; Césari & Co-
lombi, Palaeoecology, Palaeoclimatology, Palaeoecology 449: fig. 6:14 (2016).

EMENDED DIAGNOSIS. — Spores radial, trilette. Amb subtriangular or roundly subtriangular. Laesurae reaching the equatorial margin, with narrox lips. Exine two layered, up to 2.5 μm thick with discrete, densely arranged short clavae, and subordinate rounded bacula and gemmae of variable size (1.5-7 μm long), on the distal surface. Proximal surface depressed, laevigate or with reduce sculpture, with an equatorial thickening or cingulum one-third to one-half of spore radius.

Remarks. This species described as Clavatrilites hammenii by Herbst (1965) was transferred to Clavatisspores Kedves & Simoncsics by de Jersey (1971). Although, Herbst (1965, 1972) originally considered the sculpture covering all the exine, the holotype and the specimens here described possesses the proximal surface laevigate or with reduced sculpture and the laesurae reaching the equatorial margin. The predominant sculptural elements are clavae, according to Punt et al. (2007), that is, club-shaped elements with a basal pillar or column higher than wider and the apex thicker and rounded. Subor-
dinated elements include baculae and gemmae (see Fig. 6).

In the same study Herbst (1965) defined C. dubius, which was distinguished from C. hammenii by its sparse sculpture. The wide range in variation observed in the specimens of the Carrizal Formation suggests the inclusion of C. dubius as a synonym of C. hammenii. Clavatisspores Döring differs by the presence of sculpture in all its single layered exine.

A series of transitional forms (Fig. 5S-V), interpreted here as different development stages of the outer layer, lead from immature spores (Fig. 5R), which may be referred to U. verrucosus or U. hammenii, to mature perispores (Fig. 5W, X).

Similar spores have been described under different names such as Uvaesporites verrucosus and U. glomeratus in Argentina. According to the original diagnosis (Döring 1965) and later emendation of Hiltmann (1967), Uvaesporites is characterized by having coarse, ± spherical, verrucate, grape-shaped elements on its distal face, often fused at their bases; basally coalescent sculptural ele-
ments form a pseudocingulum and the proximal face is laevigate.
Fig. 4. — A, B, *Retusotrilites wielandii* (Jain) Césari, comb. nov.; C, *Biretisporites* sp.; D, E, *Osmundacitites fissus* (Leschik) Playford, 1965; F, H, *Rugulatisporites neuquenensis* Volkheimer, 1972; I, J, *Osmundacitites wellmani* Couper, 1953; K, L, *Rugulatisporites permixtus* Playford, 1982; M, *Verrucosisporites varians* Volkheimer, 1972; N, O, *Baculatisporites comauensis* (Cookson) Potonié, 1956; P, Q, *Trilites* cf. *T. wolfgangii* Sajjadi & Playford, 2003; R, *Foveosporites* sp.; S, T, *Apiculatisporites* cf. *A. serratus* Sajjadi & Playford, 2002; U–Y, *Clavatisporites conspicuus* Playford, 1982; Z, *Lundbladispora punctata* Césari & Colombi, 2016; AA, BB, *Cingutriletes* cf. *C. cestus* Stevens, 1981; CC, DD, *Craterisporites rotundus* de Jersey, 1970. Scale bars: 10 µm.
Fig. 5. — **A-E**, Lundbladispora stellae (Herbst) Césari, comb. nov.; **F-P**, Uvaesporites verrucosus (de Jersey) Helby in de Jersey, 1971, specimens illustrating intra-specific variation in sculpture; **Q-DD**, Uvaesporites hammenii (Herbst) Césari, comb. nov., specimens illustrating intra-specific variation in sculpture. Scale bars: A-CC, 10 µm; DD, 5 µm.
Helby, *in de Jersey* (1971), proposed a new emended diagnosis which differs little of the original, including cavate spores, with a thickened equatorial exoexine, distal diverse sculptural elements, although gemmae usually predominate.

The proposal of Foster (1979) to consider *Secarisporites*

A synonym of *Uvaesporites* it is not accepted here following de Jersey & Raine (1990) and taking into account the distinctive morphology of the Namurian type species *S. lobatus* with the robust lobate-rugulate sculpture protruding on the equatorial surface, and the distal polar region covered by loosely spaced ridges and warts.

*Uvaesporites glomeratus* differs in its sculptural elements ranging from grape-shaped, kidney-shaped, irregularly convolute, and similar, which are bigger and fused at the equatorial margin (Döring 1965). The Australian species *U. verrucosus* (*de Jersey*) Helby includes spores sculptured by gema, pila, grana, and verrucae.

Zavattieri & Mego (2008: figs 3.17-18) illustrated as *U. verrucosus* (*de Jersey*) Helby a specimen from the lower section of the Paso Flores Formation, closely similar to those described here with small clavae. Rojo & Zavattieri (2005: fig. 3F) illustrated a specimen, from the Cacheuta Formation, assigned to *U. glomeratus*, which is very similar in sculpture to *U. hammenii*. Zavattieri (1990a: pl. VI; figs 8-9) described from the Cerro de Las Cabras Formation specimens of *U. hammenii*, including clavae and baculae in the sculpture.

The specimen illustrated as *Clavatriletes hammenii* by Benavente *et al.* (2018), from Santa Clara Arriba Formation, possesses apparently a mainly baculate sculpture. These authors also figured as *U. verrucosus* a specimen with sculptural elements comparable to the here described for *U. hammenii*.

Specimens ascribed to the species by *de Jersey* & Hamilton (1967) and *de Jersey* (1971), have been transferred to *Clavatriletes conspicua* by Playford *et al.* (1982). The specimen illustrated by Vijaya *et al.* (2012) as *C. hammenii* is doubtful.

*Uvaesporites imperialis* (Jansonius) Utting, 1994

(Fig. 7P, U-X)

Remarks. These rounded triangular spores, cavate, proximally laevigate, and distally ornamented by low and wide verrucae, reniform and rounded elements that may be fused, are coincident with those originally illustrated by Utting (1994) from Early Triassic assemblages. Gutiérrez *et al.* (2017) transferred the species to *Secarisporites*, but this concept is not followed here according to the reasons presented above for *U. hammenii*. Rojo & Zavattieri (2005), assigned spores to *Antulpisporites* sp. A McKellar, which seems to possess a distinctive inner body like the here described; however, those authors interpreted the presence of a subequatorial distal ring. The specimens illustrated by McKellar (1974) were reported as *Dejeresyysporites verrucosus* (Pocock) McKellar by Sajjadi & Playford (2002) and characterized by a smooth equatorial cingulum. McKellar has not published the formal diagnosis of *Dejeresyysporites*, and the validation of the genus remains incomplete.

*Uvaesporites verrucosus* (de Jersey) Helby

*in de Jersey*, 1971

(Fig. 5F-R)

**Remarks.** A continuous variation appears to exist, from specimens with cingularizate appearance and discrete low verrucae and grana of variable size (Fig. 5F-J) to cingulate spores with more densely packed verrucate, short baculate projections and gemmae (Fig. 5K-Q). The specimen illustrated in Figure 5H shows the inner body. As it was mentioned above, the specimen illustrated in Figure 5R is a transitional form to *U. hammenii* and like the original spores figured by *de Jersey* (1964, 1971) characterizing *U. verrucosus*. *Herbst* (1972) described as *Verrucosisporites riojanus*, specimens from the Los Rastros Formation, which are considered here conspecific with *U. verrucosus*, a widely distributed species in Middle Triassic to Middle Jurassic assemblages from Australia and New Zealand (e.g. *de Jersey* & Raine 1990). Bomfleur *et al.* (2014) illustrated as *Uvaesporites verrucosus* (*de Jersey*) Helby, a specimen showing bigger verrucae, which resemble the sculpture of *Leptolepidites argenteaformis*.

**Verrucosisporites varians**

*Volkheimer*, 1972

(Fig. 4M)

**Pollen**

**Bisaccate**

**Remarks.** *De Jersey* (1970) was one of the first authors that pointed out the dominance of *Alisporites*-like bisaccate pollen grains in the southern Triassic palynofloras and their little stratigraphic value. This pollen, usually related to *Pteruchus*-like sporophylls, possesses a broad variability. *De Jersey* (1970) noted that specific and even generic differentiation is difficult and depends on preservation too. Moreover, the existence of abnormal morphotypes of living and fossil gymnosperm pollen has been reported by several authors (Srivastava 1961; Wilson 1965; Lindström *et al.* 1997; Foster & Afonin 2005 among others). As was pointed out by Foster & Afonin (2005), the unrecognition of these abnormalities increases the diversity of the assemblages.
Alisporites australis de Jersey, 1962  
(Fig. 8A-C)

Alisporites sulcatus Jain, 1968  
(Fig. 8D)

Ashmoripollis sp.  
(Fig. 8M)

Remarks. The Australian species Ashmoripollis reducta Helby differs in its usually bigger size (41-71um) and sacci shorter than the corpus height.

Chordasporites australiensis de Jersey, 1962  
(Fig. 8E)

Falcisporites nuthalensis  
Balme, 1970  
(Fig. 8F, G)

Falcisporites cf. F. zapfei (Potonié & Klaus)  
Leschik, 1956  
(Fig. 8H)

Indusiisporites sp.  
(Fig. 8I)

Klausipollenites staplinii  
Jansonius, 1962  
(Fig. 8J)

Platysaccus praevius  
Goubin, 1965  
(Fig. 8S)

Platysaccus queenslandi  
de Jersey, 1962  
(Fig. 8K, L)

Protodiploxypinus americus  
Dunay & Fisher, 1979  
(Fig. 8N)

Remarks. Dunay & Fisher (1979) had already indicated that the taxonomic status of the genera Protodiploxypinus, Minutosaccus, and Podosporites is not clearly resolved. Scheuring (1970) emended Protodiploxypinus and considered Minutosaccus Mädler a junior synonym of Protodiploxypinus Samoilovich. Zavattieri & Volkheimer (1992) pointed out that both genera include specimens with and without a distal sulcus. Minutosaccus acutus Mädler, like P. americus, possesses a distal sulcus, but its holotype differs in its diploxilonoid aspect with more expanded and subcircular sacci.

The specimens described by Zavattieri (1991: figs 5; 6) from the Cerro de Las Cabras Formation possess sacci of the same height as the corpus.

“Rimaesporites” aquilonalis Goubin, 1965  
(Fig. 8Q, R)

Remarks. A discussion about the validity of this and other related genera was presented by Césari & Colombi (2016). As it was pointed out, Vesicaspora fuscus Morbey is closely similar to specimens described as Cedripites, Brachysaccus, Rimaesporites, and Sulcatisporites species. Although Vesicaspora may not be an adequate repository of these pollen grains due to its debatable monosaccate or bisaccate structure, it is valuable the intra-specific size and outline variation recorded in V. fuscus, which can be applied when this type of pollen is classified.

Scheuringipollenites maximus (Hart) Tiwari, 1973  
(Fig. 8U)

Sulcosaccispora lata de Jersey & Hamilton, 1967  
(Fig. 8O, P)

Remarks. De Jersey (1968) considered S. lata a junior synonym of Caytoniidites alaticorniformis Malyavkina, but this Siberian species was included in Vitreisporites signatus Leschik by Balme (1970).

Triadispora cf. T. aurea Scheuring, 1970  
(Fig. 8V)

Remarks. The specimens described by Zavattieri (1991: pl. II; figs 3; 6) as Falcisporites cf. stabilis Balme, are similar to the here described but differ in lacking a trilete mark.

Triadispora sp.  
(Fig. 8W, X)

Monosaccate

Callialasporites sp.  
(Fig. 9A, B)

Remarks. Zavattieri (1991) assigned, with doubts, to Callialasporites specimens from the Cerro de Las Cabras Formation. The specimens from the Carrizal Formation possess a barely visible trilete mark (Fig. 9B) and lack granulate exine.

Enzonalasporites vigens Leschik, 1955  
(Fig. 9H)

Remarks. The specimen illustrated by Benavente et al. (2018) as Perinopollenites sp., from the Santa Clara Arriba Formation is apparently similar to the European species. A future detailed description will enable precise generic assignation.
Variapollenites sp.
(Fig. 9C, D)

Remarks. The genus Accinitisporites was defined by Leschik (1955) as a body surrounded by a saccus with polygonal lumina, but the revision made by Scheuring (1974) pointed out the invalidity of the genus. These criteria were followed by most authors, although several Argentinian specimens were referred to the genus. The specimens illustrated by Jain (1968) as A. circumdatus (Leschik) Jain show the variation from monosaccate radial to bisaccate with bilateral insertion of the saccus. Ottone et al. (1992) defined Variapollenites to replace Accinitisporites and defined three new species; the distinctive trilete lesurae with thick folds distinguished the specimens from the Carrizal Formation.
Fig. 8. — A–C, Alisporites australis de Jersey, 1962; D, Alisporites sulcatus Jain, 1968; E, Chordasporites australiensis de Jersey, 1962; F, G, Falcisporites nuthalis Bârnie, 1970; H, Falcisporites cf. F. zapfei (Potonié & Klaus) Leschik, 1956; I, Indusisporites sp.; J, Klausipollenites staplini Jansonius, 1962; K, L, Platysaccus queenslandi de Jersey, 1962; M, Ashmoripollis sp.; N, Protodiploxypinus americus Dunay & Fisher, 1979; O, P, Sulcosaccispora lata de Jersey & Hamilton, 1967; Q, R, "Rimaesporites" aquilonalis Goubin, 1965; S, Platysaccus praevius Goubin, 1965; T, Tetrasaccus sp.; U, Scheuringipollenites maximus (Hart) Tiwari, 1973; V, Triadispora cf. T. aurea Scheuring, 1970; W, X, Triadispora sp. Scale bars: 10 µm.
Bisaccate taeniate

*Illinites* sp.
(Fig. 9E)

**Remarks.** Only one specimen may be assigned to this genus, mainly representative of late Paleozoic assemblages. The possibility of representing an aberrant form of *Striatoabieites* is probable.

*Protohaploxypinus microcorpus* (Schaarschmidt)
Clarke, 1965
(Fig. 9J)

*Striatoabieites aytugii* Visscher emend.
Scheuring, 1970 (Fig. 9F, G)

**Possible aberrant forms**

*Tetrasaccus* sp.
(Fig. 8U)

Polylicate

*Equisetosporites stevesi* (Jansonius)
de Jersey, 1968
(Fig. 9N, T)

*Steevesipollenites* cf. *S. claviger*
de Jersey & Raine, 1990
(Fig. 9Y)

Colpate

**Remarks.** Triassic monocolpate (or monosulcate) pollen from Argentina has been assigned to *Cycadopites* and *Monosulcites* genera. Cornet & Traverse (1975) and Sajjadi & Playford (2002), among others, have considered *Monosulcites* Cookson ex Couper a junior synonym of *Cycadopites* Wodehouse ex Wilson & Webster. Moreover, Ottone et al. (2005), analyzed extant pollen grains of *Ginkgo biloba* Linnaeus (recovered in situ from a microsporangiate organ), which show different outlines and sulcus shapes. Those authors proposed that in the absence of wall ultrastructure analysis, the genera *Bharadwajapollenites* Jain, *Monosulcites* Cookson ex Couper, *Megamonoporites* Jain, and *Sulcatopites* Jain 1968 among others should be considered synonym of *Cycadopites*. We agree with this proposal, but the original generic assignment is mentioned between parenthesis for comparative purposes.

*Cycadopites (Monosulcites) elegans* Jain, 1968
(Fig. 9M)

*Cycadopites granulatus* (de Jersey) de Jersey, 1964
(Fig. 9O)

*Cycadopites magnus* Herbst, 1965
(Fig. 9I)

*Granamegamonocolpites blancae* Herbst, 1965
(Fig. 9P)

*Granamegamonocolpites cacheutensis* Jain, 1968
(Fig. 9Q)

*Psilomonoporites cacheutensis* Jain, 1968
(Fig. 9R)

**Punctamonoaperturites bharadwajii** Jain, 1968
(Fig. 9T, WW)

**Inaperturate pollen**

*Inaperturopollenites reidii* de Jersey, 1959
(Fig. 9U)

**Freshwater algae**

*cf. Lecaniella multigonata* Yi, 1994
(Fig. 9X)

**Remarks.** Yi (1997) described the species *L. multigonata* from Upper Cretaceous assemblages of Korea, which has a similar size to the specimens recognized here. The species is comparable with *Lecaniella* forma 9 described originally by Head (1992), although the Pliocene specimens may be smaller. Specimens described as *Peroaletes khuffensis* Stephenson & Filatoff from the late Permian of Saudi Arabia, are similar to the here recognized. However, *Peroaletes* was defined to include two-layered alete miospores, with the outer layer forming many folds on all surfaces.

*Pilasporites* cf. *P. calculus* Balme & Hennelly, 1968
(Fig. 9V)

**AGE**

A palynostratigraphic scheme has not been established for the Triassic of Argentina to date. The palynological assemblages nevertheless suggest a Carnian age for the Carrizal Formation,
especially by the co-occurrence of Cadargasporites baculatus, Craterisporites rotundus, Enzonalasporites vigens, Leptolepidites argenteaformis, Protodiploxypinus americus, Rugulatisporites permixtus, and “Rimaesporites” aquilonalis as diagnostic species. The apparent absence of the cheirolepidiaceous pollen Classopollis (or Corollina) in the Carrizal Formation suggests an age not younger than early Norian because of this taxon first appears in late Norian Argentinian sequences (Zavattieri & Batten 1996). However, Cheirolepidiaceae woods (Classopollis pollen producers) have recently been identified in the Carrizal Formation (Correa et al. 2019).

Craterisporites rotundus is a persistent element of Ipswich assemblages from the Late Triassic of south-eastern Australia, although Helby et al. (1987) mentioned its presence also in the Onslow Microflora of western Australia. De Jersey & Raine (1990) suggested that paleoecological factors other
than paleolatitudinal locations controlled this species. The first appearances of *C. rotundus* occur in the *Samaropollenites speciosus* Oppel Zone in Western Australia (Helby et al. 1987) and the eponymous Oppel Zone in Eastern and southern Australia, New Zealand and parts of India and China. Mantle et al. (2010) considered a latest Ladinian age for the base of Price’s APT4 (Craterisporites rotundus Zone), which extends to the middle Norian. A recent CA-IDTIMS dating of the Brisbane Tuff of the Clarence-Mortonon Basin (Queensland) (assigned to the Craterisporites rotundus Biozone) provides a date of 227.08 ± 0.10 Ma for the youngest zircons, which is about 6 Myr older than the previous calibration of the base of APT4 of Price (1997). However, Smith et al. (2018) considered this result with caution because the dated grains may be detrital in origin and thereby provide only a maximum age for the Brisbane Tuff.

Peng et al. (2018) defined the middle to upper Norian Craterisporites rotundus Taxon-range Zone in the Southern Xizang Province (Tibet) which was situated in the southern mid-latitudes at the northern margin of the Indian Plate China, as a part of Gondwana. This important biostratigraphic species probably is also present in the Lower Carnian deposits of the Dolomites (van der Eem 1983); however, it was described as Bocciaspora blackstonensis (de Jersey) Van der Eem. De Jersey & Raine (1990) discarded the similarity of the European specimens with Pustulatisporites blackstonensis and suggested that they resemble more closely Craterisporites rotundus de Jersey.

Similar palynological assemblages were recognized in the Falla Formation, Antarctica (Farabee et al. 1989, 1990), which contain Craterisporites rotundus, Striatella seebergensis (Asertospora gyrata in Farabee et al. 1989, 1990), Cadargasporites sp., Polycingulatisporites crenulatus and Uvaesporites verrucosus. Besides, Upper Triassic assemblages from the Prince Charles Mountains McLoughlin et al. (1997) also comprise the distinct taxa Craterisporites rotundus, Ashmoriopollis reducta, Enzonadaspores vigenis, Minutosaccus crenulatus, Samaropollenites speciosus, Ceratospores helidonensis and Polycingulatisporites crenulatus.

Three Argentinian assemblages contain specimens of *C. rotundus*: Santa Clara Arriba, Paso Flores and Comallo formations (Figs 2; 10). The preliminary palynological content of the deltaic-lacustrine deposits of the Santa Clara Arriba Formation was reported by Zavattieri & Batten (1996) and Benavente et al. (2018). A Carnian-early Norian age was assigned to this unit, proposing that it was deposited before the Paso Flores (late Carnian to early Norian) and Comallo formations (Fig. 2). These last units provided palynological associations (Zavattieri et al. 1994; Zavattieri & Mego 2008) characterized by the presence of Classpollis simplex, an abundant species in Rhaetian-Jurassic palynofloras.

Enzonadaspores vigenis characterizes the latest Ladinian-early Norian interval of Northern Hemisphere and the Onslow Microflora in Southern areas. The first report of this species in Argentinian palynofloras corresponds to the Ischigualasto Formation (Césari & Colombi 2013). According to Helby et al. (1987) Enzonadaspores vigenis and Craterisporites rotundus occur together in Late Triassic assemblages of western Australia referred to the *Samaropollenites speciosus* Zone. The co-occurrence of these species in the Carrizal Formation signify close similarity between the western Australian palynofloras and the here described.

Cadargasporites baculatus is a diagnostic species of Carnian-Jurassic assemblages in Australia; in Argentina it has been recorded in samples from the Ischigualasto Formation (Césari & Colombi 2013), Los Rastos Formation (Ottone et al. 2005) and specimens reported as *C. cf. C. baculatus* were recognized in Los Rastos (Ottone et al. 2005) and Ischichuca Formations (Zavattieri & Melchor 1999). This species was also identified in assemblages from the lower section of the Paso Flores and the Santa Clara formations, which contain Craterisporites rotundus too.

Bisaccate pollen referred here to “Rimaesporites” aquilonalis comprises several species which have been included in the literature into different genera: Lorispores Leschik, Saetaesporites Leschik, Cedripites Wodehouse, Vesicaspora (Schemel) Wilson & Venkatachala, and Brachysaccus Mädlar. Following the discussion presented by Césari & Colombi (2013), the original nomination of Dolby & Balme (1976) is maintained, while recognizing their very probable synonymy with the northern species Vesicaspora fuscus (Pautsch) Morbey. According to Backhouse et al. (2002), it is a common species in the *S. speciosus* Zone and rare throughout the *M. crenulatus* and *A. reducta* Zones.

**COMPARISONS**

Several palynological associations have been referred to the Late Triassic in Argentina (Figs 2; 10). These palynofloras come from the upper section of the Potrerillos Formation, basal strata of the Cacheuta Formation and the Santa Clara Arriba Formation (Mendoza province), Rancho de Lata, Ischichuca, Los Rastos and Ischigualasto formations (San Juan province), Paso Flores and Comallo formations (Patagonia). Stratigraphic location of these units is shown in Figure 2. Distribution of selected species, which characterize the Carnian assemblages of the Potrerillos, Santa Clara Arriba, Los Rastos, Ischigualasto, Paso Flores, Comallo and Carrizal formations, are presented in Figure 10. The palynological assemblage from the Rancho de Lata Formation is not included because approximately 50% of the taxa are assigned to generic level or are new species (Ottone et al. 1992). In the same way, the species from the Ischichuca Formation (Zavattieri & Melchor 1999) were only listed without illustrations, and many were assigned with uncertainty. The palynoflora of the Cacheuta Formation, although less diverse, is characterized by species also present in the underlying uppermost Potrerillos Formation and considered by Zavattieri & Rojo (2005) without a chronological difference. The Chañares Formation (overlaid by the Ischichuca, Los Rastos and Ischigualasto formations) has been referred to the late Ladinian-early Carnian. Palynomorphs are only known from scarce specimens (including Ovalipollis and Ellipsovelatisporites), recovered from one coprolite (the
A new Late Triassic palynological assemblage

**Fig. 10.** — Distribution of selected species in the Carnian assemblages from Argentina. Colors: Orange shading indicates the typical Carnian species in Onslow or mixed palynofloras; blue shading the presence of *Craterisporites rotundus* de Jersey, 1970; green shading the presence of *Classopollis* specimens.

Other two samples contain almost exclusively plant debris, which also contain late Permian species (Perez Loinaze *et al.* 2018). Marsicano *et al.* (2016) reported maximum depositional ages of 236 and 234 Ma for the base of the Chañares Formation (Fig. 2).

The Potrerillos Formation (Fig. 2) is represented mainly by fluvial to deltaic deposits in its uppermost part, while the overlying Cachetea Formation corresponds to a lacustrine system. The palynoﬂoras recovered from both units were considered by Zavattieri & Rojo (2005) as “facies
controlled”, considering that the compositional variations reflect environmental changes. U-Pb SHRIMP ages determined on zircon grains from tuff levels between the middle-upper sections of the Potrerillos Formation at Bayo Hill (Fig. 2), provided an age of 230.3 ± 2.3 Ma (Spalletti et al. 2008), suggesting a Carnian age for the palynofloras described by Zavattieri (1986, 1987), Rojo & Zavattieri (2005) and Zavattieri & Rojo (2005).

Herbst (1965, 1970, 1972) provided the first description of the palynofloras from the Los Rastros Formation; however, many of the species have been subsequently reassigned to other taxa. Later, Ottone et al. (2005) reported assemblages recovered from lacustrine-deltaic cycles with a predominance of lacustrine sedimentation in La Rioja Province. They were characterized by the presence of Cadargasporites baculatus, C. cuyanensis, Aratrisporites spp. and Plaesiodictyon mosellanum, although only few taxa were illustrated or described. The same unit was analyzed in the Agua de la Peña creek (San Juan Province) by Ottone & Mancuso (2006). The palynofloras come from deltaic-lacustrine deposits with the presence of Plaesiodictyon mosellanum and Botryococcus, which are the only taxa described or illustrated together with a new bisaccate pollen.

The overlying Ischigualasto Formation (Fig. 2) contains abundant palynological associations in a swamp deposit of distal floodplain facies of the Valle de La Luna Member. The assemblages are distinguished (Fig. 10) by the presence of several European Carnian species such as Enzonadalasporites, Patinasporites, Ovalipollis, Vallasporites, among others (Césari & Colombi 2013, 2016). Compared to the lacustrine-deltaic Los Rastros’s palynofloras, Aratrisporites spp. are rare hygrophytic elements in these assemblages, and taeniate pollen is more abundant. Césari & Colombi (2016) proposed a late Carnian-early Norian age for the Ischigualasto assemblages.

The lower section of the Paso Flores Formation provided palynological assemblages analyzed by Zavattieri & Mego (2008), characterized by the occurrence of Craterisporites rotundus and Classopolis pollen, which led them to propose a late Carnian-early Norian age for the succession. These species are also recognized in the Comallo Formation (Zavattieri et al. 1994), which was considered Carnian-early Norian in age.

Figure 10 represents the distribution of diagnostic species such as Craterisporites rotundus, Classopolis-like pollen, Rogalikaspores cicastricus, Cadargasporites spp. some plicate species, among others, which characterize Carnian-early Norian assemblages in Gondwana, as well as several typically Carnian northern species (Enzonadalasporites group).

Although Craterisporites rotundus is a rare component of the assemblages from the Carrizal Formation, its presence relates this unit with the Paso Flores and Comallo formations, which in turn can be distinguished by the presence of Classopolis-like pollen. It should be considered that the absence of Classopolis in the Carrizal Formation may be circumstantial since Cheirolepidiaceae (Classopolis pollen producers) have recently been identified in the unit (Correa et al. 2019).

Although cluster analysis does not discriminate the appearance of key age diagnostic species, such as Craterisporites rotundus and Classopolis-like pollen, its application has provided a possible grouping of the assemblages (Fig. 11). Cluster analysis of Raup-Crick similarity coefficients resolves two main groups. This result should be considered with caution because the palynological content of the Los Rastros Formation is known mainly by lists taxa without illustrations or descriptions that confirm assignments. A dissimilarity exists between the palynofloras from the Ischigualasto and the Carrizal formations assemblages with the tight pair Los Rastros/Potrerillos formations, probably due to the exclusive presence of several northern species in the first units. The Comallo, Paso Flores, and Santa Clara Arriba assemblages constitute a distinctive cluster (the first two contain Classopolis-like pollen). A similarity is shown between the Carrizal Formation assemblages with those from the Ischigualasto, Los Rastros and Potrerillos formations, despite the apparent absence of Craterisporites rotundus in the last units. Almost all these southern palynofloras are dominated by pollen grains, whose overrepresentation prevents the identification of species rare in the assemblages, but with biostratigraphic value. Therefore, the exhaustive analysis of many palynological slides is required to confirm the presence or absence of key taxa.

PALEEOECOLOGICAL IMPLICATIONS

Differences in composition between the Carnian palynological assemblages from western Argentina may be the result of variations in the vegetation according to local paleoenvironmental conditions. In this sense, the palynofloras from the lacustrine and lacustrine-deltaic deposits of the uppermost section of the Potrerillos Formation, lower section of the Cacheuta Formation, Los Rastros, and Ischichuca formations share similar composition. All of them contain hygrophytic spores like Aratrisporites spp. and abundant algae, like Botryococcus sp. and Plaesiodictyon mosellanum Wille. This last species is otherwise a component of assemblages from the Onslow Subprovince, Europe, and the United States. On the contrary, the assemblages recovered from fluvial deposits of the Ischigualasto and Carrizal Formations contain more abundant xerophytic components as bisaccate taeniate pollen and representatives of the conifer Enzonadalasporites group. Coincidentally, these associations appear thus grouped in the cluster analysis (Fig. 11).

The palynological assemblages from the fluvial Carrizal Formation were analyzed following the proposal of Abbink et al. (2004). Several miospores have been identified in situ, allowing knowledge of their parental plants and thus their paleoecological preferences. Considering that information, Abbink et al. (2004) introduced the term sporomorph ecogroup (SEG) to characterize the types of spores and pollen that reflect the composition of different communities. Abbink et al. (2004) defined six sporomorph ecogroups (SEG) for the Jurassic-Early Cretaceous of NW Europe, of which three are related to terrestrial conditions: A) Upland SEG, represent vegetation never submerged by water; B) Lowland SEG,
comprises communities on plains and/or freshwater swamps, where a mix of drier and wetter taxa may be present; C) River SEG, represents riverbank communities, which support periodic submersion and erosion. Those authors tentatively assigned Uvaesporites (Sellaginellaceae) to the River SEG, and Leptolepidites (lycopod) to the Lowland or River SEG. Fern spores (Osmundacites, Baculatisporites, Ischyosporites) may be characteristic of the Lowland or River SEGs. Cycadopites/ Monosulcites (Cycadales, Bennettitales, Ginkgoales) pollen is included in the Lowland SEG. The xerophytic elements of the upland SEG are represented by monosaccate and bisaccate pollen. Among the bisaccate pollen, Alisporites-like grains were found in conifer cones and Corystospermales (Kustatscher et al. 2010). These SEGs can be tentatively applied to the palynological assemblages of the Carrizal Formation:

1) Sample BA Pal 6585 from the Carrizal Formation, collected from a carbonaceous layer, contains non taeniate bisaccate (Alisporites) pollen accompanied by abundant tetrads and dispersed spores of Uvaesporites and Leptolepidites, together with Osmundacites, rare specimens of Foveoporites, smooth spores and colpate pollen. The taxonomic composition of this assemblage suggests assignment a Lowland SEG community in a swamp environment, which is consistent with the lithofacies evidence.

2) Samples BA Pal 6586 and 6587, associated with macro-floristic remains in abandoned channels are characterized by well-preserved profuse cuticle remains and bisaccate pollen (taeniate and non taeniate), Leptolepidites and Uvaesporites (as tetrads and dispersed spores), but diversity is higher with representation of Lundbladispora, Clavatisporites, Baculatisporites, Annulatispora, Playfordiaspora, taeniate, monocolpate, plicate and inaperturate pollen. The drought tolerant Volztialean conifer pollen Enzonalasporites (Pacyna et al. 2017) is identified, in low proportion, in this assemblage probably due to its dispersal from parent plants growing in surrounding upland areas. The high species diversity and tetrads would be attributed to the closer proximity of the source area and the absence of prolonged sorting. This composition may be representative of a River SEG community.

PALEOGEOGRAPHIC IMPLICATIONS

Traditionally, the Triassic palynological assemblages from Argentina were correlated to the Ipswich palynofloras derived from cool temperate floras in southeastern Australia. All the Argentinian palynofloras were characterized by the apparent absence of the typical Tethyan species that distinguish the Onslow Microflora of southwestern Australia. Césari & Colombi (2013, 2016), however, identified in the Ischigualasto Formation typical Tethyan species that characterize the Onslow Microflora. The relatively low proportion of productive samples in the stratigraphic units and the overrepresentation of bisaccate pollen may be the reason that hampers the identifications of those species, which occur in a low ratio (Césari & Colombi 2016).

A new phytogeographic scenario was proposed by Césari & Colombi (2013) extending the diagnostic species of the Onslow Microflora and the Tethys area into westernmost Gondwana. The current knowledge about the distribution of some Carnian Tethyan species (Cirilli 2010; Césari & Colombi 2013) suggests constraining the terms Onslow and Ipswich Microfloras (or Subprovinces according to Kustatscher et al. 2018) to Australia and the surrounding area. This new phytogeography supports the idea of a rather homogenous Circum-Mediterranean palynoprovince as suggested earlier by Visscher & Van der Zwan (1981) and Buratti & Cirilli (2007), discarding a strong difference with the Onslow Microflora. Van der Eem (1983) explained the presence of Gondwanan species in Late Triassic European assemblages as the result of dispersal from southern areas during a humid climatic interval. Similar idea of floristic interchange between Laurussia and Onslow Subprovince, and the existence of a warmer climate, was postulated by Kustatscher et al. (2018) to explain the differences with the Ipswich Subprovince.

Recently, Peng et al. (2018) also identified for the first time in China the occurrences of taxa typical of the Onslow Microflora indicating that this palynofloristic province extended to southern Xizang, which was part of the Tethyan margin of northern Gondwana during the Triassic. The finding of the Onslow’s species Enzonalasporites vigens in the Carrizal Formation reinforces the assumption that the composition of several westernmost Gondwanan palynofloras is latitudinally controlled, and they integrate a wide floral belt, probably together with the Circum-Mediterranean assemblages, which in turn contain some Gondwanan species.
CONCLUSIONS

Three well-preserved palynological assemblages were recovered from fluvial deposits at the Rickard Member of the Carrizal Formation. The close similarity obtained by cluster analysis, with the Ischigualasto Formation coincides with similar paleoenvironmental conditions in both sequences. On the other hand, Carrizal’s assemblages are similar to those from the lacustrine-deltaic Potrerillos Formation, reinforcing the previous proposal of Spalletti et al. (1999) and Morel et al. (2015) of 83% of macrofossilistic affinity. In the same way, the Los Rastros Formation shares 66% of plant species with the Carrizal Formation.

The recognition of diagnostic late Triassic species, especially the presence of Craterisporites rotundus, which characterize the Craterisporites rotundus Oppel Zone in Eastern Australia, allows to consider a Carnian age for the palynological assemblages. The rare specimens identified in the assemblages may be interpreted as its first occurrence or may be the result of paleoecological conditions. This species is also recognized in the Paso Flores and Comalito formations, but in these units occurs associated with Claspolis pollen.

The presence of the Tethyan Enzonalasporites vagens results its second record in Argentinian palynofloras, and its association with Craterisporites rotundus is also recognized in Late Triassic assemblages of western Australia referred to the Samaropol-lentites speciosus Zone (Helby, 1987) and some Lower Carnian Circum-Mediterranean palynofloras. This new westernmost Gondwanic palynoflora reinforces the idea that some characteristic species of the Circum-Mediterranean area and Western Australia were cosmopolitan during the Carnian.

More accurate characterization and correlation will be achieved by an extensive taxonomic study of additional samples from the Carrizal Formation and coeval stratigraphic units of Argentina.

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REFERENCES

ABBINK O. A., VAN KONIJNENBURG-VAN CITTERT J. H. A. & VISSCHER H. 2004. — A sporomorph ecogroup model for the Northwest European Jurassic-Lower Cretaceous: concepts and framework. *Netherlands Journal Geosciences* 83: 17-31. [https://doi.org/10.1017/S00167764060020436](https://doi.org/10.1017/S00167764060020436)

ARTABE A. E., MOREL E. M. & SPALETTI L. A. 2001. — Paleoecología de las floras tríasicas argentinas, in ARTABE A. E., MOREL E. M. & ZAMUNER A. B. (eds), *El Sistema Triásico en la Argentina*. Fundación Museo de La Plata ‘Francisco Pascasio Moreno’, La Plata: 199-225.

ARTABE A. E., MOREL E. M. & GANUZA D. G. 2007. — Las floras tríasicas de la Argentina. *Publicación Especial Asociación Paleontológica Argentina* 11: 75-86.

BACKHOUSE J., BALME B. E., HELBY R., MARSHALL N. G. & MORGAN R. 2002. — Palynological zonation and correlation of the latest Triassic Northern Carnarvon Basin, in KEPP M. & MOSS S. J. (eds), *The Sedimentary Basins of Western Australia 3. Proceedings of the Petroleum Exploration Society of Australia Symposium*: 179-201.

BALME B. E. 1970. — Palynology of Permian and Triassic Strata in the Salt Range and Surghar Range, West Pakistan, in KUMMEL B. & TIECHERT C. (eds), *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*. Department of Geology-University of Kansas, *Special Publication* 4: 305-453.

BENAVENTE C. A., ZAVATTIERI A. M., MANCUSO A. C., ARAZUZA F. & GIERLOWSKI-KORDESCH E. H. 2018. — Paleolimnology of the Santa Clara Arriba paleolake (Triassic Cuyana rift basin): integrating sedimentology and palynology. *Journal of Paleolimnology* 59: 5-20. [https://doi.org/10.1007/s10933-016-9916-0](https://doi.org/10.1007/s10933-016-9916-0)

BERGMANN F. A. J. 1948. — Contribución al conocimiento de los yacimientos de carbón de Marayes, provincia de San Juan. *Revista Minera Geología y Mineralogía* 19: 3-99.

BOMFLEUR B., SCHÖNER R., SCHNEIDER J. W., VIERECK L., KERP H. & MCKELLAR J. L. 2014. — From the Transantarctic Basin to the Ferrar Large Igneous Province – New palynostratigraphic age constraints for Triassic-Jurassic sedimentation and magmatism in East Antarctica. *Review of Palaeobotany and Palynology* 207: 18-37. [https://doi.org/10.1016/j.revpalbo.2014.04.002](https://doi.org/10.1016/j.revpalbo.2014.04.002)

BORRELLO A. V. 1946. — El perfil de la quebrada de Carrizal (Sierra de la Huerta - San Juan). *Revista de la Asociación Geológica Argentina* 1: 167-176.

BOSSI G. 1976. — Geología de la Cuenca de Marayes-El Carrizal (provincia de San Juan, República Argentina), *Actas 6º Congreso Geológico Argentino, Bahía Blanca, Argentina* 1: 23-38.

BURATTI N. & CIRILLI S. 2007. — Microfossil provincialism in the Upper Triassic Circum-Mediterranean area and palaeogeographic implication. *Geobios* 40: 133-142. [https://doi.org/10.1016/j.ge bios.2006.06.003](https://doi.org/10.1016/j.gebios.2006.06.003)

CÈSARI S. N. & COLOMBI C. E. 2013. — A new Late Triassic phytoecographical scenario in westernmost Gondwana. *Nature Communication* 4 (1889). [https://doi.org/10.1038/ncomms2917](https://doi.org/10.1038/ncomms2917)

CÈSARI S. N. & COLOMBI C. E. 2016. — Palynology of the Late Triassic Ischigualasto Formation, Argentina: Paleoecological and paleogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 449: 365-384. [https://doi.org/10.1016/j.palaeo.2016.02.023](https://doi.org/10.1016/j.palaeo.2016.02.023)

CIRILLI S. 2010. — Upper Triassic-lowermost Jurassic palynology and palynostratigraphy: a review. *Geological Society, London, Special Publications* 334: 285-314. [https://doi.org/10.1144/SP334.12](https://doi.org/10.1144/SP334.12)

CLARKE R. F. A. 1965. — British Permian saccate and monosaccate mioospores. *Palaeontology* 8: 322-354.

COHEN K. M., FINNEY S. C., GIBBARD P. L. & FAN J. X. 2013. — The ICS international chronostratigraphic chart. *Episodes* 36 (3): 199-204.

COLOMBI C. E., SANTI MALNIS P., CORREA G. A., MARTÍNEZ R. N., FERNÁNDEZ E., ABELIN D. & DROVANDI J. 2015. — La Formación Balde de Leyes (nov. Nom.), una nueva unidad estratigráfica de la cuenca tríáica de Marayes-El Carrizal. *Revista de la Asociación Geológica Argentina* 72: 445-455. [https://doi.org/10.1016/j.palaeco.2017.06.001](https://doi.org/10.1016/j.palaeco.2017.06.001)

CORREA G., BODNAR J., COLOMBI J., SANTI MALNIS P., PRADERIO A., MARTÍNEZ R., APALDETTI C., FERNÁNDEZ E., ABELIN D. & ALCOBER O. 2019. — Systematics and taphonomy of fossil woods from a new locality in the Upper Triassic Carrizal Formation of the El Gigantillo area (Marayes-El Carrizal Basin), San Juan,
Argentina. Journal of South American Earth Science 90: 94-106. https://doi.org/10.1016/j.james.2018.11.027

Couper R. A. 1953. — Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geological Survey Palaeontological Bulletin 22: 1-77.

De Jersey N. J. 1959. — Jurassic spores and pollen grains from the Rosewood Coalfield. Queensland Government Mining Journal 30: 346-366.

De Jersey N. J. 1962. — Triassic spores and pollen grains from the Ipswich Coalfield. Geological Survey of Queensland Publication 307: 1-18.

De Jersey N. J. 1964. — Triassic spores and pollen grains from the Bundamba Group. Geological Survey of Queensland Publication 321: 1-27.

De Jersey N. J. 1968. — Triassic spores and pollen grains from the Clematis Sandstone. Geological Survey of Queensland Publication 338, Palaeontological Paper 14: 1-44.

De Jersey N. J. 1970. — Triassic miospores from the Blackstone Formation, Aberdare Conglomerate and Raceview Formation. Geological Survey of Queensland Publication 348, Palaeontological Paper 25: 1-41.

De Jersey N. J. 1971. — Early Jurassic miospores from the Helidon Sandstone. Geological Survey of Queensland Publication 351, Palaeontological Paper 25: 1-49.

De Jersey N. J. 1972. — Triassic microspores from the Esk Group. Geological Survey of Queensland Publication 357, Palaeontological Paper 32: 1-40.

De Jersey N. J. & Hamilton M. 1967. — Triassic spores and pollen grains from the Moosalummer Formation. Geological Survey of Queensland Publication 336, Palaeontological Paper 10: 1-61.

De Jersey N. J. & Raine J. J. 1990. — Triassic and earliest Jurassic miospores from the Murihilku Supergroup, New Zealand. New Zealand Geological Survey Palaeontological Bulletin 62: 1-164.

Dolby J. H. & Balme B. E. 1976. — Triassic palynology of the Carnarvon Basin, Western Australia. Review of Palaeobotany and Palynology 22: 105-168. https://doi.org/10.1016/0034-6667(76)90053-1

Döring H. 1973. — Die sporenpaläontologische Gliederung des Wealden in Westmecklenburg (Struktur Werle). Geologie 47: 1-118.

Dunay R. L. & Fisher M. J. 1979. — Palynology of the Dockum Group (Upper Triassic), Texas, U.S.A. Review of Palaeobotany and Palynology 28: 61-92. https://doi.org/10.1016/0034-6667(79)90025-3

Farabee M. J., Taylor T. N. & Taylor E. L. 1989. — Pollen and spore assemblages from the Falla Formation (Upper Triassic), Central Transantarctic Mountains, Antarctica. Review of Palaeobotany and Palynology 61: 101-138. https://doi.org/10.1016/0034-6667(89)90065-1

Farabee M. J., Taylor E. L. & Taylor T. N. 1990. — Correlation of Permian and Triassic palynomorph assemblages from the central Transantarctic Mountains, Antarctica. Review of Palaeobotany and Palynology 65: 257-265. https://doi.org/10.1016/0034-6667(90)90075-T

Freguelli J. 1948. — Estratigrafía y edad del llamado Rético en la Argentina. Anales de la Sociedad Argentina de Estudios Geográficos 8: 159-309.

Foster C. B. 1975. — Permian plant microfossils from the Blair Athol Coal Measures, Central Queensland, Australia. Palaeontographica Abteilung B 154: 121-171.

Foster C. B. 1979. — Permian plant microfossils of the Blair Athol Coal Measures, Baralaba Coal Measures, and basal Rewan Formation of Queensland. Geological Survey of Queensland Publication 372, Palaeontological Paper 45: 1-244. https://doi.org/10.14264/uqpl.2015.37

Foster C. B. & Afonin S. A. 2005. — Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian–Triassic boundary. Journal of the Geological Society 162: 653-659. https://doi.org/10.1144/0016-764904-047

Geinitz H. B. 1876. — Über Rhätische Tier-und Pflanzenreste in den Argentinischen Provinzen La Rioja, San Juan und Mendoza. Palaeontographica Supplement 3: 1-14.

Godders Y., Donnadieu Y., De Vargas C., Pierrehumbert R. T., Dromart G. & Van de Schootbrugge B. 2008. — Causal link between the rise of nanoplankton calcification and a tectonically-driven massive decrease in Late Triassic atmospheric CO2? Earth Planetary Science Letters 267: 247-255. https://doi.org/10.1016/j.epsl.2007.11.051

Goubin N. 1965. — Description et répartition des principaux pollenites Permien, Triasiques et Jurassicques des sondages du bassin de Morondava (Madagascar). Revue de l’Institut Français du Pétrole 20: 1415-1461.

Groebber P. F. C. & Stipanovic N. P. 1953. — Triásico, in Groebber P. F. C. (ed.) Mesoáxico, Geografía de la República Argentina. Sociedad Argentina Estudios Geográficos 2, Buenos Aires: 13-141.

Gutiérrez P. R., Zavattieri A. M. & Ezpeleta M. 2017. — Palynology of the La Yeteada Formation (Lopingian) at its type locality, Famatina Range, the Rioja Province, Argentina. Spores. Ameghiniana 54: 441-465. https://doi.org/10.5710/AMGH.20.02.2017.3054

Healy M. J. 1992. — Zygosporae of the Zygnemataceae (Division Chlorophyta) and other freshwater algal spores from the uppermost Pliocene St. Erth Beds of Cornwall, southwestern England. Micropaleontology 38: 237-260. https://doi.org/10.2307/1485790

Helby R., Morgan R. & Partridge A. D. 1987. — A palynological zonation of the Australian Mesozoic, in Jell P. A. (ed.), Studies in Australian Mesozoic Palynology. Memoirs of the Association of Australasian Palynologists 4: 1-94.

Herbst R. 1965. — Algunos esporomorforos del Triásico de Argentina. Ameghiniana 4: 141-155.

Herbst R. 1970. — Estudio palinológico de la Cuenca Ischigualasto-Villa Unión, (Triásico), provincias de San Juan-La Rioja. I. Introducción. II. Monoaperturados. Ameghiniana 7: 83-97.

Herbst R. 1972. — Estudio palinológico de la Cuenca Ischigualasto-Villa Unión (Triásico), provs. San Juan-La Rioja. III. Esporas tríctes. Ameghiniana 9: 280-288.

Herbst R. 1994. — A new genus of Thamnopteridoid ferns (Osmundaceae, Filicales) from the Upper Triassic Carnial Formation of Marayes, province of San Juan, Argentina. Acta GeológicaLeoddenia 17: 93-107.

Herbst R. 2006. — Millerocaulis (Erasmus) ex tidwell (Osmundales, Filicales) de la Formación Carnial (Triásico Superior) de Marayes, provincia de San Juan, Argentina. Revista del Museo Argentino de Ciencias Naturales, n. s. 7: 185-93.

Hiltmann W. 1967. — Über die Sporenfahrung des kernprofils der bohrung contern FG 11 (unterer Lias, Luxemburg). Publications Service géologique de Luxembourg 17: 137-206.

Jain R. K. 1968. — Middle Triassic pollen grains and spores from Minas de Petroleo beds of the Cacheuta Formation (Upper Gondwana), Argentina. Palaeontographica Abteilung B 122: 1-47.

Jansonius J. 1962. — Palynology of Permian and Triassic sediments, Peace River Area, Western Canada. Palaeontographica Abteilung B 110: 35-98.

Kent D. V., Santi Malnis P., Colombi C. E., Alcobre O. A. & Martínez R. N. 2014. — Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetochronology of the Los Colorados Formation (Argentina). Proceedings of the National Academy of Sciences of the United States of America 111(22): 7958-7963. https://doi.org/10.1073/pnas.1402369111

Klaus W. 1960. — Sporen der karnischen stufe der ostalpinen Trias. Jahrbuch der Geologischen Bundesanstalt 5: 107-183.

Kustatscher E., van Konijnenburg-van Cittert J. H. & Rochi G. 2010. — Macroforas and palynomorphs as possible proxies for palaeoclimatic and palaeoeological studies: A case study from the Pelsonian (Middle Triassic) of Cúllwiesenkopf/ Monte Prà della Vacca (Olang Dolomites, N-Italy). Palaeographia, Palaeoclimatology, Palaeoecology 290: 71-80. https://doi.org/10.1016/j.palaeo.2009.07.001
Leschik, L. (ed.). Unpublished PhD thesis, Facultad de Ciencias Exactas y Naturales, Argentina. Unpublished thesis, Facultad de Ciencias Exactas y Agrimensura, Universidad Nacional del Nordeste, Corrientes, 169 p.

Lutz A. I. & Arcé F. E. 2013. — Paleoflora de la Formación Carrizal (Triásico Superior) de la cuenca de Manzay-El Carrizal, provincia de San Juan, Argentina. Unpublished PhD thesis, Facultad de Ciencias Exactas y Agrimensura, Universidad Nacional del Nordeste, Corrientes, 169 p.

Lutz A. I. &Arcé F. E. 2013. — Paleoflora de la Formación Carrizal (Triásico Medio-Superior), provincia de San Juan, Argentina. Revista Mexicana de Ciencias Geológicas 30: 453-462.

Meheshwari H. K. & Banerji J. 1975. — Lower Triassic palynomorphs from the Maitur Formation, West Bengal. Palaeontographica Abteilung B 152: 149-190.

Mantle D. J., Kelman A. P., Nicol R. S. & Laurie J. R. 2010. — Australian Biozoonation Chart. Geoscience Australia, Canberra. https://d28rgr98ar0flks.cloudfront.net/70371/Australian_Biozonation_Chart_2010_Part1.pdf

Marsicano C. A., Irims R. B., Mancuso A. C., Mundil R. & Chemale F. 2016. — The precise temporal calibration of dinosaur origins. Proceedings of the National Academy of Sciences 113: 509-513. https://doi.org/10.1073/pnas.1512541112

Martinez R. N., Sereno P. C., Alcover O. A., Colombe C. E., Renne P. R.,Montané L. P. & Currie B. S. 2011. — A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. Science 331(6041): 206-210.

McKellar J. L. 1974. — Jurassic miospores from the upper Evergreen Formation, Hutton Sandstone and basal Injune Creek Group, northeastern Surat Basin. Geological Survey of Queensland Publication 361. Palaeontological Paper 35: 1-89.

McCoughlin S., Lindstrom S. & Drinnan A. N. 1997. — Gondwanan floristic and sedimentological trends during the Permain–Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. Antarctic Science 9: 281-298. https://doi.org/10.1017/S0954102097000370

Morley S. J. 1975. — The palynostratigraphy of the Rhaetian stage. Upper Triassic, in the Kendelbachgraben, Austria. Palaeontographica Abteilung B 152: 1-75.

Morel E. M., Artabe A. E., Ganaiza D. G., Bodnar J., Correa G. & Spalletti L. A. 2015. — El Triásico de la Formación Carrizal en el depocentro de Marayes (San Juan, Argentina): paleobotánica, tafonomía y bioestratigrafía. Revista de la Asociación Geológica Argentina 72: 456-469.

Noetinger S., Pujana R. R., Burrieza A. & Burrieza H. P. 2017. — Use of UV-curable acrylates gels as mounting media for palynological samples. Revista del Museo Argentino de Ciencias Naturales n.s. 19: 19-23.

Ottone E. & Mancuso A. 2006. — Algas Chlorococcales como indicadores paleoambientales: nuevos datos de la Formación Los Rastro, Triásico del centro-oeste de Argentina. Revista del Museo Argentino de Ciencias Naturales n.s. 8: 209-220.

Ottone E. G., Alveares P. P. & Benoff S. V. 1992. — Late Triassic plant microfossils from the Rancho de Lata Formation, Main Cordilleria, Argentina. Micropaleontology 38: 261-278. https://doi.org/10.2307/1485791

Ottone E. G., Mancuso A. C. & Resano M. 2005. — Miospores and chlorococcal algae from the Los Rastros Formation, Middle to Upper Triassic of central–western Argentina. Ameghiniana 42: 347-362.

Pacyna G., Barbacka M., Zdebska D., Zaja J., Fijalkowska-Mader A., Borka K. & Sulje T. 2017. — A new conifer from the Upper Triassic of southern Poland linking the advanced volvaline type of ovuliferous scale with Bouchryphium-Pagiophyllum-like leaves. Review of Palaeobotany and Palynology 245: 28-54. https://doi.org/10.1016/j.revpalbo.2017.05.015

Penc J., Li J., Slater S. M., Li W., Zhu H. & Vajda V. 2018. — Triassic palynostratigraphy and palynoflora of provinces: evidence from southern Xizang (Tibet), China. Alcheringa 42: 67-86. https://doi.org/10.1080/03115518.2017.1370726

Perez Linares V. S., Vera E. I., Fiorelli L. E. & Desio J. B. 2018. — Palaeobotany and palynology of conoplitic from the Late Triassic Chañales Formation of Argentina: implications for vegetation provinces and the diet of dicynodonts. Palaeoecography, Palaeoclimatology, Palaeoecology 502: 31-51. https://doi.org/10.1017/j.palaeo.2018.04.003

Phipp S. & Playford G. 1984. — Laboratory Techniques for Extraction of Palynomorphs from Sediments. Papers Department of Geology, University of Queensland 11: 1-33.

Playford G. 1965. — Plant microfossils from Triassic sediments near Poatina, Tasmania. Journal of the Geological Society of Australia 12: 173-210. https://doi.org/10.1080/011671661508279592

Playford G., Rigby J. F. & Archibald D. C. 1982. — A Middle Triassic flora from Moolayemmer Formation, Bowen Basin, Queensland. Geological Survey of Queensland, Publication 380: 1-52.

Potion N. 1956. — Synopsis derGattungen der Sporae dispersae, Teil 1: Sportes. Geologisches Jahrbuch 23: 1-103.

Price P. L. 1997. — Permian to Jurassic palynostratigraphic nomenclature of the Bowen and Surat basins, in Green P. M. (ed.), The Surat and Bowen Basins, southeast Queensland, Queensland Department of Mines and Energy, Brisbane: 137-178.

Punt W., Hoen P. P., Blackmore S., Neilson S. & Le Thomas A. 2007. — Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143: 1-81. https://doi.org/10.1016/j.revpalbo.2006.06.008

Reisser R. F. & Williams A. J. 1969. — Palynology of the Lower Jurassic sediments of the Northern Surat Basin. Geological Survey of Queensland Publication 399. Palaeontological Paper 15: 1-24.

Rojo L. D. & Zavattieri A. M. 2005. — Estudio microflorístico de las formaciones Potrerillos y Cacheuta (Triásico) en el sur del cerro Cacheuta, Mendoza, Argentina. Parte 1. Ameghiniana 42: 3-20.

Sajjadi F. & Playford G. 2002. — Systematic and stratigraphic palynology of Late Jurassic–earliest Cretaceous strata of the Eromanga Basin, Queensland, Australia. Palaeontographica Abteilung B 261: 1-165.

Sajjadi F. & Playford G. 2003. — New epipods for two Upper Jurassic miospore species from the Eromanga Basin, Queensland. Alcheringa 27: 171. https://doi.org/10.1080/0315510308619556

Scheuring B. W. 1970. — Palynologische und palynostratigraphischen Untersuchungen des Keupers im bohltunnel (Solothrurn Jura), Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 88: 1-119.

Scheuring B. W. 1974. — On the type material of Accinctisporites Leschik, Saccinctisporites Leschik, Rimaesporites Leschik and Subnispores Bhadrawaj, Review of Palaeobotany and Palynology 17: 205-216. https://doi.org/10.1016/0034-6667(74)90101-8

Smith T., Nicolli R., Laurie J., Crowley J., McKellar J., Campbell H., Raine I., Mantle D. & Morry A. 2018. — Recalibrating Australian Triassic palynostratigraphy to the International Geologic Time Scale Using High Resolution CA-IDTMS Dating. ASEG Extended Abstracts 2018: 1-11. https://doi.org/10.1017/ASEG2018abP010

Spalletti L. A., Artabe A. E., Morel E. M. & Brea M. 1999. — Biozonalización paleoflorística y cronoestratigrafía del Triásico Argentino. Ameghiniana 36: 419-451.
A new Late Triassic palynological assemblage

Spalletti L. A., Fanning M. & Rapela C. W. 2008. — Dating the Triassic continental rift in the southern Andes: the Potrerillos Formation, Cuyo basin, Argentina. Geologica Acta 6: 267-283. https://doi.org/10.1344/105.00000256

Spalletti L., Morel E., Artabe A., Gauza D. & Bodnar J. 2011. — Sedimentología de la Formación Caratral (Triádico) en el Depocentro Marayes-El Caratral, provincia de San Juan, República Argentina. Latin American Journal of Sedimentary Basin Analysis 18: 89-104.

Srivastava S. K. 1961. — Morphology of normal and some abnormal pollen grains of Pinus roxburghii Sarg. Grana Paleontologica 3: 130-132.

Stevens J. 1981. — Palynology of the Callide Basin, east-central Queensland. Papers Department of Geology, University of Queens land 9 (4): 1-42.

Stipanici P. N. 1957. — El Sistema Triádico en la Argentina. 20º Congreso Geológico Internacional, México, Sección 2: 73-112.

Stipanici P. N. 2002. — Cuadro geocronológico y de correlación de las principales formaciones triádicas argentinas, in Stipanici P. N. & Marsigano C. A. (eds), Léxico Estratigráfico de la Argentina: Triádico. Asociación Geológica Argentina, Serie “B”(Didáctica y Complementaria) Buenos Aires 8: 340-343.

Stipanici P. N. & Marsigano C. A. 2002. — Léxico Estratigráfico de la Argentina: Triádico. Asociación Geológica Argentina, Serie “B”(Didáctica y Complementaria), Buenos Aires, 379p.

Vijaya, Tripathi A., Roy A. & Mitra S. 2012. — Palynostratigraphy and age correlation of subsurface strata within the sub-basins in Singrauli Gondwana Basin, India. Journal of Earth System Science 121: 1071-1092. https://doi.org/10.1007/s12040-012-0213-7

Visscher H. & Van der Zwan C. J. 1981. — Palynology of the Circum-Mediterranean-Triassic: Phytogeographical and Palaeoclimatological Implications. Geologische Rundschau 70: 625-634. https://doi.org/10.1007/BF01822140

Utting J. 1994. — Palynostratigraphy of Permian and Lower Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago. Bulletin of the Geological Survey of Canada 478: 1-107.

Van der Eem J. G. L. A. 1983. — Aspects of Middle and Late Triassic palynology. 6. Palynological investigations in the Ladinian and Lower Karnian of the western Dolomites, Italy. Review of Palaeobotany and Palynology 39: 189-300. https://doi.org/10.1016/0034-6667(83)90016-7

Whiteside J. H., Lindstrom S., Irmis R. B., Glasspool I. J. J., Schaller M. F., Dunlavey M., Nesbitt S. J., Smith N. D. & Turner A. H. 2015. — Extreme ecosystem instability suppressed tropical dinosaur dominance for 30 million years. Proceedings of the National Academy of Sciences 112 (26): 7909-7913. https://doi.org/10.1073/pnas.1505252112

Volkheimer W. 1972. — Estudio palinológico de un carbón caloviano de Neusquen y consideraciones sobre los paleoclimas jurásicos de la Argentina. Revista del Museo de La Plata 6, Paleontología: 101-157.

Wilson L. R. 1965. — Tetrapedal forms in pollen of Pinus flexilis James. Journal of Palynology 1: 106-110. Yi S. 1997. — Zygnematacean zygosporos and other freshwater algae from the Upper Cretaceous of the Yellow Sea Basin, southwest coast of Korea. Cretaceous Research 18: 515-544. https://doi.org/10.1006/cre.1996.0072

Yrigoyen M. R., & Stover L. E. 1969. — La palinología como elemento de correlación del Triádico en la Cuenca Cuyana. 4º Jornadas Geológicas Argentinas, Restiennes 2, Mendoza: 427-447.

Zavattieri A. M. 1986. — Estudio palinológico de la Formación Potrerillos (Triádico) en su localidad tipo, Cuenca Cuyana, Provincia de Mendoza, Argentina. II: Granos de polen. Aspectos estadísticos. Correlación palinoestratigráfica. Revista Española de Micropaleontología 19: 173-213.

Zavattieri A. M. 1990a. — Palinología de la Formación Las Cabras (Triádico), en su localidad tipo, Cuenca Cuyana (provincia de Mendoza, Argentina). Parte I. Esporas triletes. Ameghiniana 28: 107-129.

Zavattieri A. M. 1990b. — Palinología de la Formación Las Cabras (Triádico), en su localidad tipo, Cuenca Cuyana (provincia de Mendoza, Argentina). Parte 2. Esporas triletes y monoletes. Ameghiniana 28: 207-224.

Zavattieri A. M. 1991. — Granos de polen de la Formación Las Cabras (Triádico), en su localidad tipo, provincia de Mendoza, Argentina. Parte 2. Ameghiniana 28: 205-224. https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/2020

Zavattieri A. M. & Volkheimer W. 1992. — Granos de polen sacados (Saccites) de la Formación Potrerillos (Triádico) en la localidad de Divisadero Largo, provincia de Mendoza, Argentina. Ameghiniana 29: 27-44.

Zavattieri A. M. & Batten D. J. 1996. — Miospores from Argentinian Triassic deposits and their potential for intercontinental correlation, in Jansonius J. & McGregor D. C. (eds), Palynology: Principles and Applications vol. 2. American Association of Stratigraphic Palynologists Foundation, Utah: 767-778.

Zavattieri A. M. & Melchor R. N. 1999. — Estudio palinológico preliminar de la Formación Ischichuca (Triádico), en su localidad tipo (quebrada de Ischichuca Chica), provincia de La Rioja, Argentina. Publicación Especial Asociación Paleontológica Argentina 6: 33-38.

Zavattieri A. M. & Rojo L. D. 2005. — Estudio microflorístico de las Formaciones Potrerillos y Cacheuta (Triádico) en el sur del cerro Cacheuta, Mendoza, Argentina. Parte 2. Ameghiniana 42: 513-534. https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/920

Zavattieri A. M. & Mego N. 2008. — Palynological record of the Paso Flores Formation (Late Triassic) on the southeastern side of the Limay River, Patagonia, Argentina. Ameghiniana 45: 483-502.

Zavattieri A. M., Volkheimer W. & Rosenfield U. 1994. — Palynology and facies of the Late Triassic of Comallo (Northern Patagonia, Argentina). Zeitschrift für Geologie und Paläontologie, Teil 1:133-154.

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**APPENDIX**

**APPENDIX 1** — List of specimens illustrated and the England Finder coordinates.

| Figure 3 | Figure 4 | Figure 6 | Figure 8 | Figure 7 |
|----------|----------|----------|----------|----------|
| A. BA Pal 6586(4) T32/2 | A. BA Pal 6586(3) P38/3 | A. BA Pal 6587(5) V57/4 | A. BA Pal 6587(2) M46/2 | A. BA Pal 6586(4) P31/4 |
| B. BA Pal 6586 (1)C66/2 | B. BA Pal 6586(2) W44/0 | B. BA Pal 6587(3) D37/3 | B. BA Pal 6586(3) L52/3 | B. BA Pal 6586(3) J32/1 |
| C. BA Pal 6586(5) B28/0 | C. BA Pal 6586(4) A49/2 | C. BA Pal 6586(1) V64/4 | C. BA Pal 6587(5) Y49/4 | D. BA Pal 6586(5) U63/4 |
| D. BA Pal 6586(1) K65/1 | D. BA Pal 6586(6) E43/0 | D. BA Pal 6587(2) L43/8 | D. BA Pal 6587(4) J52/0 | E. BA Pal 6586(1) Y33/3 |
| E. BA Pal 6586(5) W53/3 | E. BA Pal 6586(2) V33/1 | E. BA Pal 6587(4) R45/4 | E. BA Pal 6586(1) Q57/0 | F. BA Pal 6586(6) M23/0 |
| F. BA Pal 6586(3) R48/4 | F-G. BA Pal 6586(6) H35/0 | F. BA Pal 6586(1) Q31/0 | F. BA Pal 6586(1) Q31/0 | G. BA Pal 6586(4) S54/2 |
| H. BA Pal 6586(6) K55/2 | H. BA Pal 6586(1) D40/1 | G. BA Pal 6586(3) V51/0 | G. BA Pal 6586(3) V52/0 | H. BA Pal 6587(3) C31/4 |
| I. BA Pal 6586(3) V31/4 | I. BA Pal 6586 (4) L41/3 | H. BA Pal 6587(1) F45/1 | I. BA Pal 6587(1) F45/1 | I. BA Pal 6587(5) G38/0 |
| K. BA Pal 6586(2) Y47/3 | J. BA Pal 6586(6) B55/0 | I. BA Pal 6587(1) G56/1 | J. BA Pal 6586(1) L45/0 | J. BA Pal 6586(1) Y33/3 |
| L. BA Pal 6586(1) T33/2 | L. BA Pal 6586(4) B46/0 | J. BA Pal 6587(1) T39/3 | J. BA Pal 6586(1) T39/3 | K. BA Pal 6586(3) P46/4 |
| LL. BA Pal 6587(3) O53/4 | L. BA Pal 6586(4) D26/0 | K. BA Pal 6586(1) Q47/0 | K. BA Pal 6586(1) Q47/0 | L. BA Pal 6586(6) Q30/4 |
| M. BA Pal 6586(4) R25/2 | M. BA Pal 6587(2) Q58/3 | L. BA Pal 6586(1) V30/0 | L. BA Pal 6586(1) V30/0 | M. BA Pal 6586(6) C42/3 |
| O. BA Pal 6586(1) O66/3 | N. BA Pal 6586(5) G40/0 | O. BA Pal 6587(5) L28/2 | O. BA Pal 6587(5) L28/2 | M. BA Pal 6586(6) G40/0 |
| Q. BA Pal 6586(2) R65/3 | O. BA Pal 6586(3) Y59/4 | O. BA Pal 6587(5) B36/2 | O. BA Pal 6587(5) B36/2 | O. BA Pal 6586(6) G40/0 |
| R. BA Pal 6587(3) T45/3 | R-S. BA Pal 6586(3) V51/0 | R-S. BA Pal 6586(3) V51/0 | R-S. BA Pal 6586(3) V51/0 | R-S. BA Pal 6586(3) V51/0 |
| S. BA Pal 6587(3) B43/0 | S. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 |
| T. BA Pal 6587(1) Y38/4 | T. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 | S. BA Pal 6586(2) J39/0 |
| V. BA Pal 6586(1) S57/4 | V. BA Pal 6586(1) T33/2 | V. BA Pal 6586(1) T33/2 | V. BA Pal 6586(1) T33/2 | V. BA Pal 6586(1) T33/2 |
| W. BA Pal 6586(3) L53/0 | W. BA Pal 6586(1) L54/0 | W. BA Pal 6586(1) L54/0 | W. BA Pal 6586(1) L54/0 | W. BA Pal 6586(1) L54/0 |
| Y. BA Pal 6586(1) H61/1 | Y. BA Pal 6586(1) H61/1 | Y. BA Pal 6586(1) H61/1 | Y. BA Pal 6586(1) H61/1 | Y. BA Pal 6586(1) H61/1 |
| Z. BA Pal 6586(1) V38/0 | Z. BA Pal 6586(1) V38/0 | Z. BA Pal 6586(1) V38/0 | Z. BA Pal 6586(1) V38/0 | Z. BA Pal 6586(1) V38/0 |
| AA. BA Pal 6586(4) Y41/2 | AA. BA Pal 6586(4) Y41/2 | AA. BA Pal 6586(4) Y41/2 | AA. BA Pal 6586(4) Y41/2 | AA. BA Pal 6586(4) Y41/2 |
| BB. BA Pal 6586(2) L38/0 | BB. BA Pal 6586(2) L38/0 | BB. BA Pal 6586(2) L38/0 | BB. BA Pal 6586(2) L38/0 | BB. BA Pal 6586(2) L38/0 |
| CC. BA Pal 6586(3) V30/4 | CC. BA Pal 6586(3) V30/4 | CC. BA Pal 6586(3) V30/4 | CC. BA Pal 6586(3) V30/4 | CC. BA Pal 6586(3) V30/4 |