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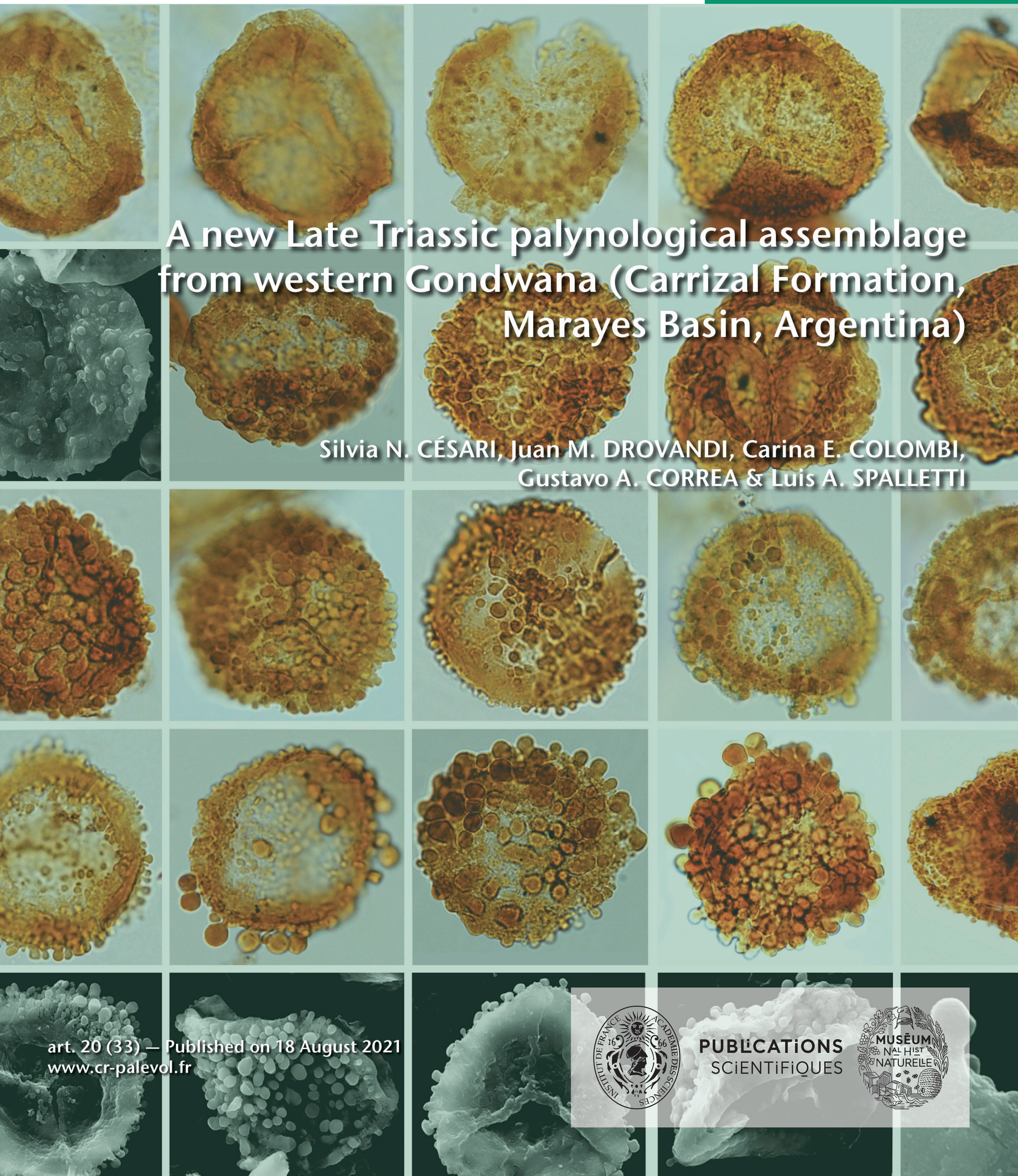

A new Late Triassic palynological assemblage from western Gondwana (Carrizal Formation, Marayes Basin, Argentina)

Silvia N. CÉSARI, Juan M. DROVANDI, Carina E. COLOMBI, Gustavo A. CORREA & Luis A. SPALLETTI

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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., *Retusotriletes 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,
systematics,
Gondwana,
Argentina.

RÉSUMÉ

Nouvel 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 révisées : *Uvaesporites hammenii* (Herbst) Césari, comb. nov., *Retusotriletes wielandii* (Jain) Césari, comb. nov., et *Lundbladispora stellae* (Herbst) Césari, comb. nov. La reconnaissance de *Cadargasporites baculatus* de Jersey & Paten emend. Reiser & Williams, *Craterisporites rotundus* de Jersey, *Enzonalasporites vigens* Leschik, *Leptolepidites argenteaeformis* (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,
palynologie,
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, Umkomansiales (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 Cortaderitian 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 palaeoflora, coinciding with the age proposed by Spalletti *et al.* (1999).

Although those 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 palynofloras 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 neighbourg 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).

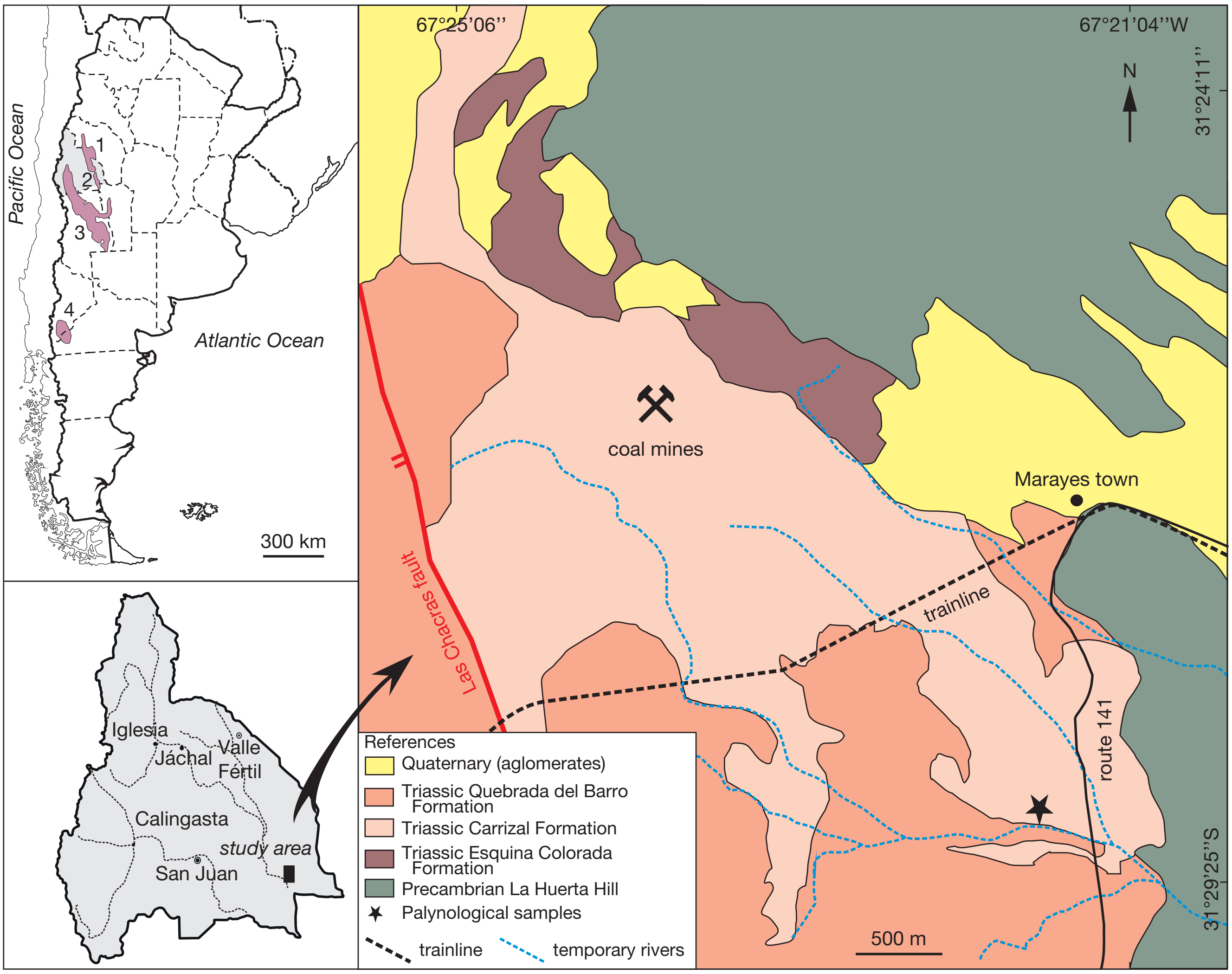

FIG. 1. — Geological map showing the location of the fossiliferous site (**star**). The smaller map of Argentina highlights the location of Triassic basins mentioned in the text; numbers correspond to: **1**, Ischigualasto-Villa Unión Basin; **2**, Marayes- El Carrizal Basin; **3**, Cuyana Basin; **4**, Paso Flores and Comallo depocenters.

At the top of the sequence, the Early Jurassic Balde de Leyes Formation is characterized by a 200 m thick finning 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

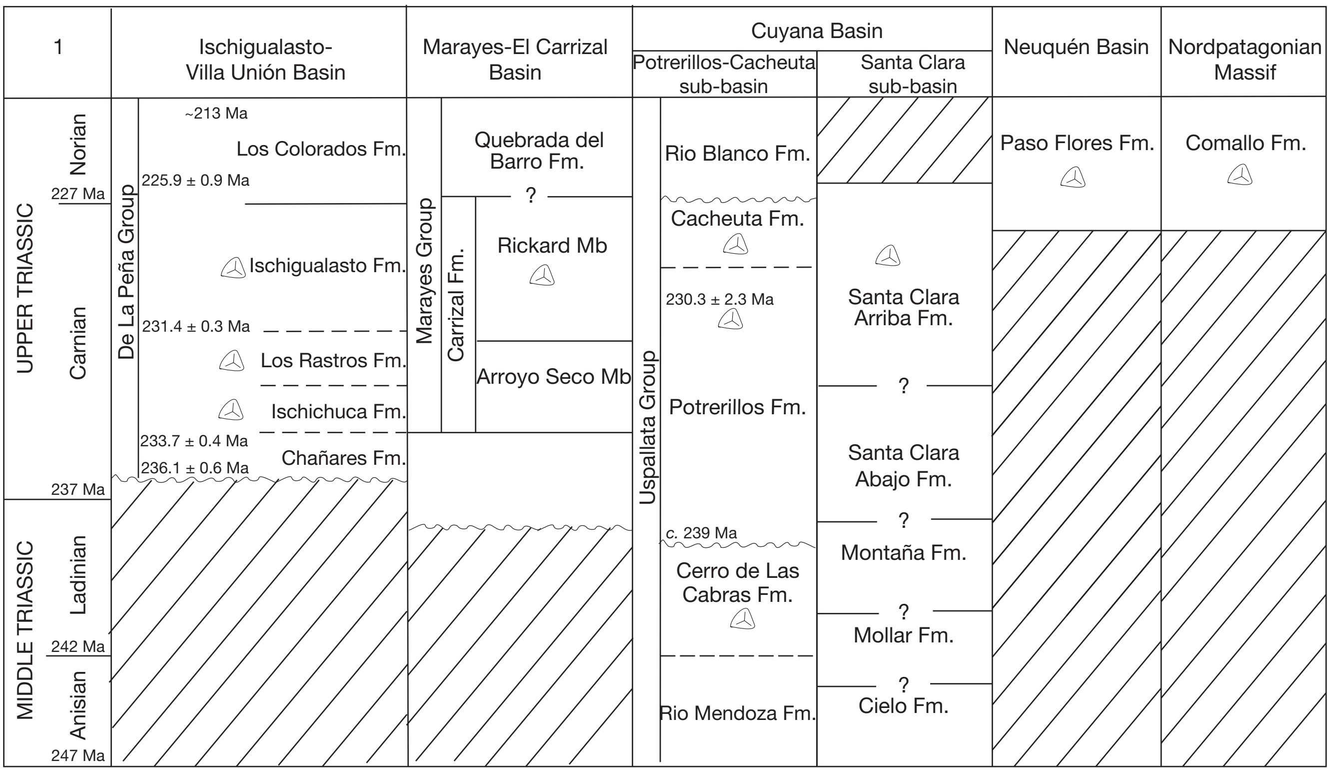

FIG. 2. — Lithostratigraphic scheme of the main Middle-Upper Triassic units and location of the palynological assemblages mentioned in the text. **Dashed lines** indicate transitional contacts, **wavy lines** indicate erosional contacts and the **question mark** uncertainty of age-range delineation. **1**: Chronostratigraphy according to the International Time Scale (Cohen *et al.* 2013). Local datings taken from Kent *et al.* (2014), Marsicano *et al.* (2016), Martinez *et al.* (2011) and Spalletti *et al.* (2008). Additional references in the text.

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 *Protocupressinoxylon* in the southern sector, at the Cerro Gigantillo locality. In this member 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 flood plain. Associated with these levels, in the southern area of the basin, were recovered the palynological assemblages subject of this study.

The paleofloristic assemblage of the Carrizal Formation has been studied by several authors, since Geinitz (1876), Borrello (1946), Bergmann (1948), Frenguelli (1948), Groeber & Stipanicic (1953), Yrigoyen & Stover (1969) and more recently Herbst (1994, 2006), Lutz & Arce (2013), Morel *et al.* (2015) and Correa *et al.* (2019). The paleoflora is represented by a total of nine orders and 57 species comprising 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*, *Cladophlebis kurtzii*, *C. mendozaensis*, *C. mesozoica*, *Cuneumxylon spallettii*, *Dicroidium argenteum*, *D. dubium* var. *tasmaniensis*, *D. lancifolium* var. *lancifolium*, *D. marayaensis*, *D. odontopteroides* var. *moltense*, *D. odontopteroides* var. *remotum*, *D. odontopteroides* var. *obtusifoliun*, *Dicroidium odontopteroides* var. *odontopteroides D. odontopteroides* subespecie *orbiculoides* cf. *Fanerotheca papilioformis*, *Fraxinopsis andium*, *Ginkgophytoxylon lucasii*, *Hepaticites* sp., *Heidiphyllum elongatum*, *J. stelzneriana* var. *stelzneriana*, *J. stelzneriana* var. *serrata*, *J. coriacea*, *Kurtziana cacheutensis*, *Lepidopteris strombergensis*, *Linguifolium tenison woodsii*, *Millerocaulis lutzii*, *Neocalamites* sp., *Pachydermophylum praecordillerae*, *Protophyllocladoxylon* sp., *Sphenobaiera argentinae*, *S. tormbergensis*, *S. sectina*, *Taeniopteris* spp., *Telemachus elongatum*, *X. argentina*, *Y. brackebuschiana*, *Yabeiella mareyesiaca*, *Y. crassa*, *Y. wielandi*, *Xilopteris argentina*, *Zuberia shanni*, and *Zuberia zuberi*.

Later, Morel *et al.* (2015) added the finding of the following species in the Rickard Member: *Baiera cuyana*, *Cordaicarpus* sp., *Equisetites fertilis*, *Ginkgoites matatiensis*, *Heidiphyllum elongatum Kurtiziana brandmayri*, *Neocalamites carrerei*, *Pteruchus rhaetica*, *Rhexoxylon* cf. *piatnitzkyi*, and *Scytophyllum* cf. *S. argentinum.* 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 lenticular 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 (taeniate and non taeniate), polyplicate and colpate pollen together with rare representatives of inaperturate and monosaccate pollen and freshwater algae. The samples are dominated by bisaccate non taeniate pollen, but taeniate 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.

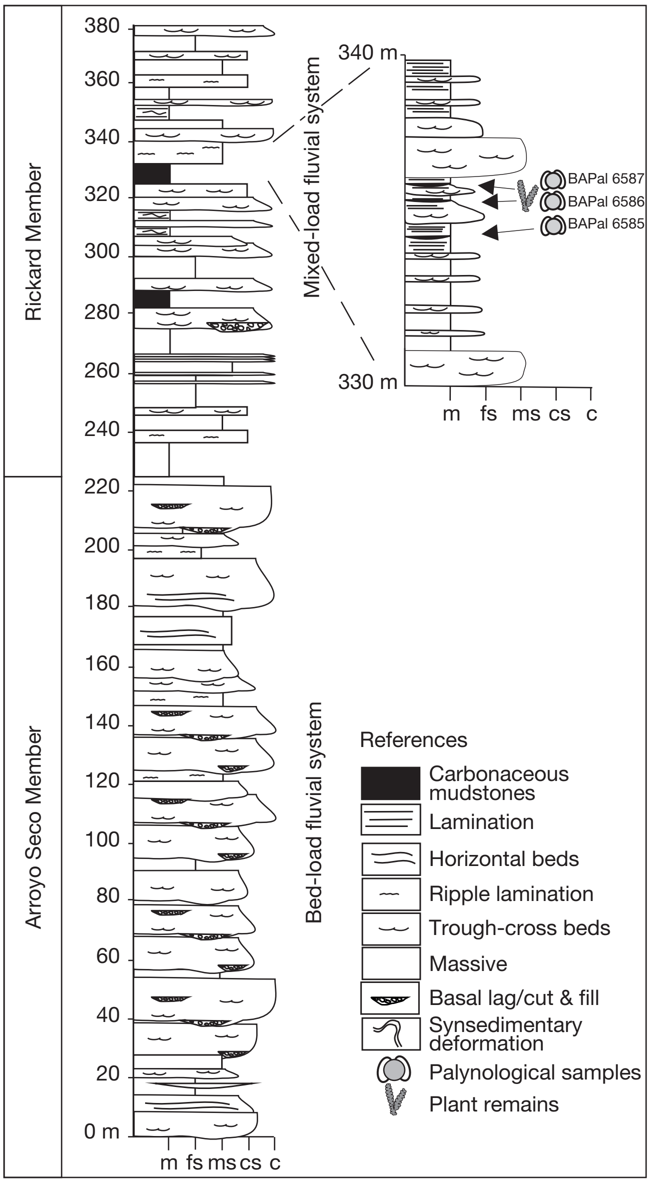

Fig. 3. — Sedimentary log of the Carrizal Formation at the fossiliferous site to the south of the Marayes town. Abbreviations: c, conglomerate; cs, coarse sand; fs, fine sand; m, mud; ms, medium sand.

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)

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

Cingutriletes* 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 argenteaeformis (Bolkhovitina)
Morbey, 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)

Cingulatisporites stellae Herbst, *Ameghiniana* 4: 143; pl. 1; figs 5; 6 (1965).

? *Densoisporites* sp. 1, Zavattieri, *Ameghiniana* 27: pl. III; figs 5; 8; 9 (1990b).

? *Cirratriradites* sp. 1, Zavattieri, *Ameghiniana* 27: pl. IV; figs 2; 4; 7; 9-11 (1990b).

EMENDED DIAGNOSIS. — Spores trilete, triangular to rounded subtriangular, cavate (overall equatorial diameter 30-46 µm). Laesurae straight to sinuous with lips that are 1.5-3 µm in overall width and usually reaching the equatorial margin. Distinct inner body triangular, reaching ¾ of the spore radius. Exoexine scabrate, densely covered distally by small verrucae and grana (0.5-1.5 µm high); in some specimens the exine is thickened equatorially into a narrow rim. Sculpture reduced on proximal surface. Scattered bigger verrucae or gemmae often present on the outer third of the radius.

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 *Secarisporites triangularis* Gutiérrez, Zavattieri & Ezpeleta, who adhered to Foster's reinterpretation of the genus *Secarisporites*, which is considered synonym of *Uvaesporites* Döring (Foster, 1979). The inclusion of the spores from the Carrizal Formation into *Secarisporites* 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 cavate 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 *Secarisporites* Neves.

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

Osmundacidites 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 wielandii 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* Naumova emend. Pashkevich, with the Y-shaped ends of the lesura continuous into a sub-peripheral ring or "curvaturae imperfectae". Zavattieri (1990a) enlarged the diagnosis of *Cacheutasporites*, remarking the presence of curvaturae imperfectae and pefectae 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 specimens, 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 curvaturae 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. *Striatella* 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 *Ischyosporites* 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)

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

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

Uvaesporites verrucosus (de Jersey) Helby *in* de Jersey 1971; Zavattieri & 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 & Colombi, *Palaeogeography, Palaeoclimatology, Palaeoecology* 449: fig. 6.14 (2016).

Emended diagnosis. — Spores radial, trilete. Amb subtriangular or roundly subtriangular. Laesurae reaching the equatorial margin, with narrow 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 *Clavatriletes hammenii* by Herbst (1965) was transferred to *Clavatisporites* 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 predominate 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. Subordinated 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*. *Clavatisporites* 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 elements form a pseudocingulum and the proximal face is laevigate.

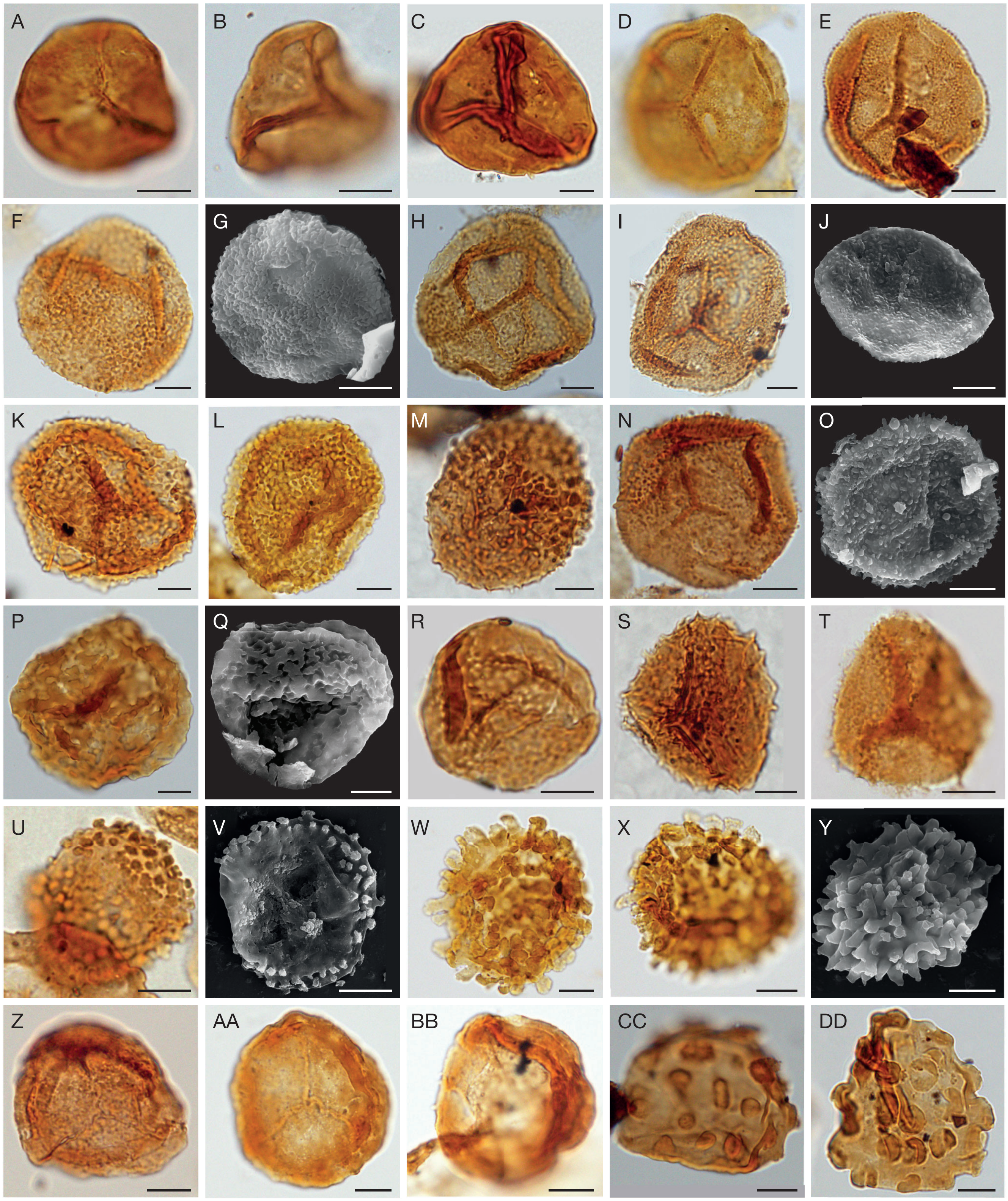

FIG. 4. — **A**, **B**, *Retusotriletes wielandii* (Jain) Césari, comb. nov.; **C**, *Biretisporites* sp.; **D**, **E**, *Osmundacidites fissus* (Leschik) Playford, 1965; **F**, **H**, *Rugulatisporites neuquenensis* Volkheimer, 1972; **I**, **J**, *Osmundacidites wellmanii* Couper, 1953; **K**, **L**, *Rugulatisporites permixtus* Playford, 1982; **M**, *Verrucosisporites varians* Volkheimer, 1972; **N**, **O**, *Baculatisporites comaumensis* (Cookson) Potonié, 1956; **P**, **Q**, *Trilites* cf. *T. wolfgangii* Sajjadi & Playford, 2003; **R**. *Foveosporites* sp.; **S**, **T**, *Apiculatisporis* 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.

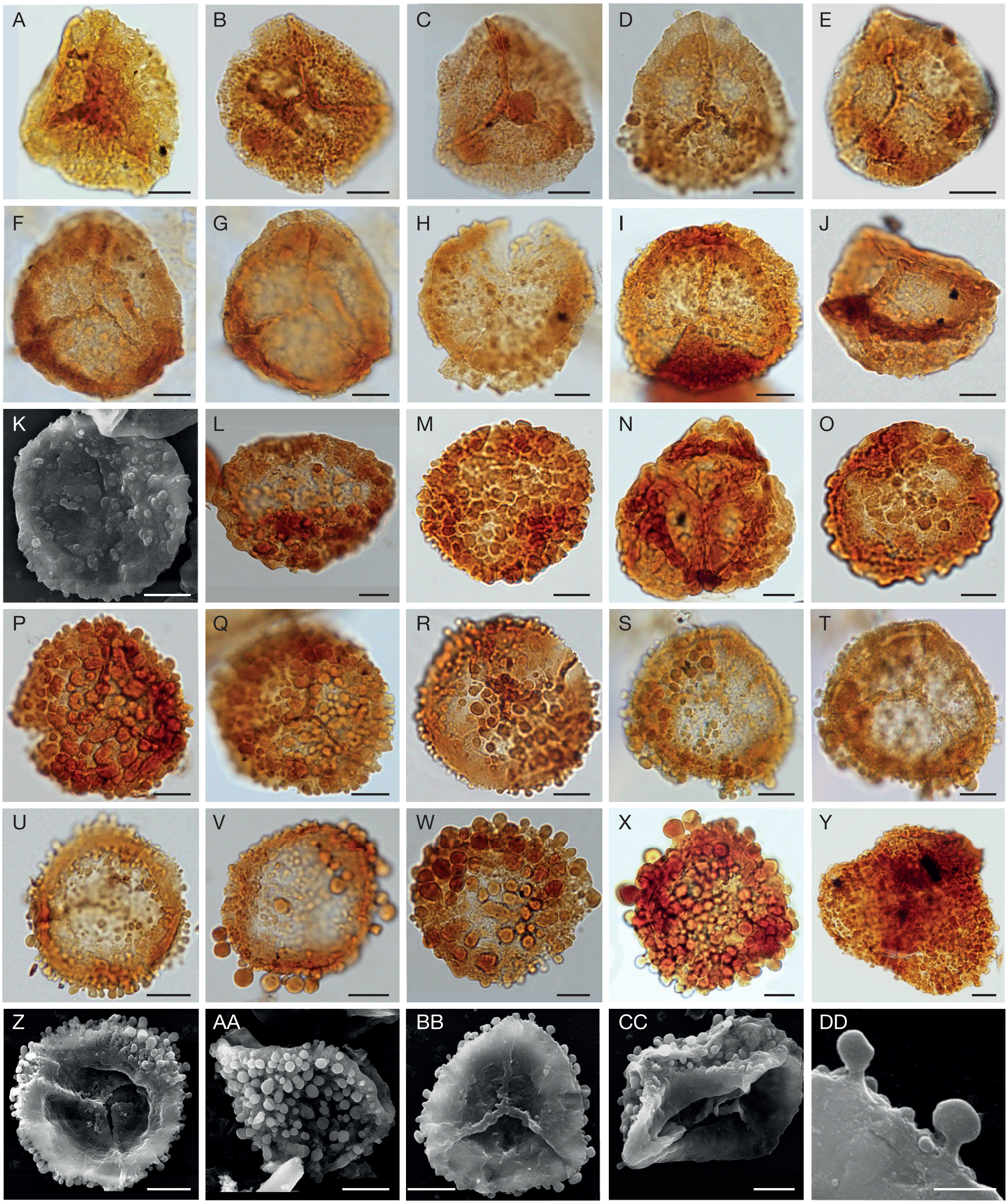

FIG. 5. — **A-E**, *Lundbladispora stellae* (Herbst) Césari, comb. nov.; **F-P**, *Uvaesporites verrucosus* (de Jersey) Helby in de Jersey, 1971, specimens illustrating intra-specific variation in sculpture; **Q-DD**, *Uvaesporites hammenii* (Herbst) Césari, comb. nov., specimens illustrating intra-specific variation in sculpture. Scale bars: A-CC, 10 µm; DD, 5 µm.

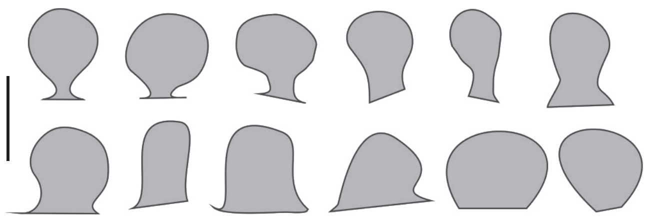

FIG. 6. — Diagrammatic lateral view of the higher sculptural elements characteristic of *Uvaesporites hammenii* (Herbst) Césari, comb. nov. Scale bar: 5 µm.

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 gemma, 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 *Clavatisporites conspicuus* 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 *Antulsporites* 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 *Dejerseysporites verrucosus* (Pocock) McKellar by Sajjadi & Playford (2002) and characterized by a smooth equatorial cingulum. McKellar has not published the formal diagnosis of *Dejerseysporites*, and the validation of the genus remains incomplete.

Uvaesporites verrucosus (de Jersey) Helby
in de Jersey, 1971
(Fig. 5F-R)

Verrucosisporites riojanus Herbst, *Ameghiniana* 9: pl. I; figs 8-11 (1972).

Remarks. A continuous variation appears to exist, from specimens with cingulizonate 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 be not 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 alaticonformis* 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.

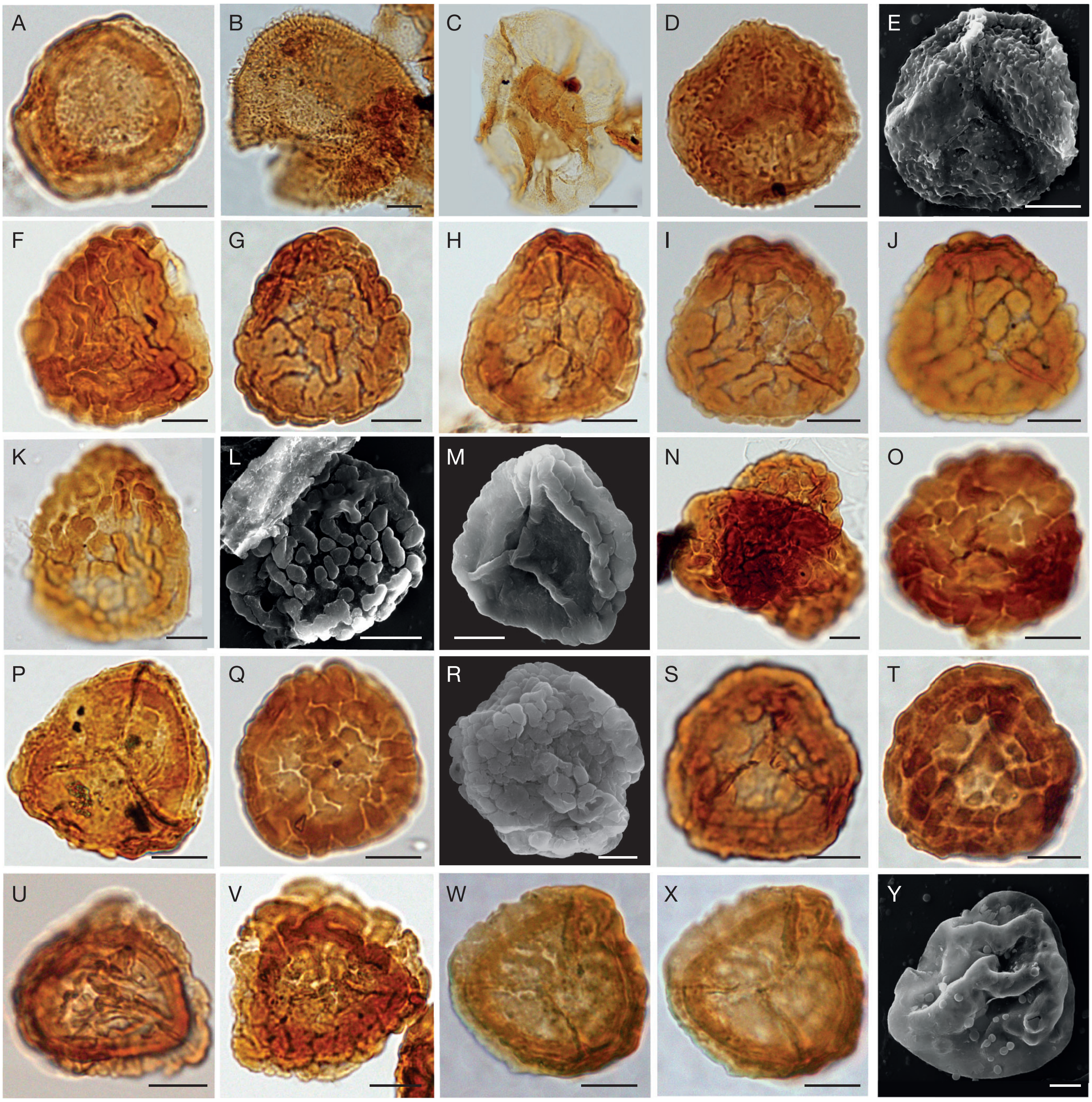

FIG. 7. — **A**, *Annulispora* sp.; **B**, *Cadargasporites baculatus* de Jersey & Paten emend. Reiser & Williams, 1969; **C**, *Playfordiaspora cancellosa* (Playford & Dettmann) Maheshwari & Banerji, 1975; **D**, **E**, *Camptotriletes* cf. *C. warchianus* Balme, 1970; **F**-**N**, *Leptolepidites volkheimerii* Zavattieri, 1986; **O**, **Q**-**T**, *L. argenteaeformis* (Bolkhovitina) Morbey, 1975; **P**, **U**-**X**, *Uvaesporites imperialis* (Jansonius) Utting, 1994; **Y**, cf. *Striatella* sp. Scale bars: 10 µm.

Variapollenites sp.
(Fig. 9C, D)

Remarks. The genus *Accintisporites* 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 *Accinctisporites* and defined three new species; the distinctive trilete lesurae with thick folds distinguished the specimens from the Carrizal Formation.

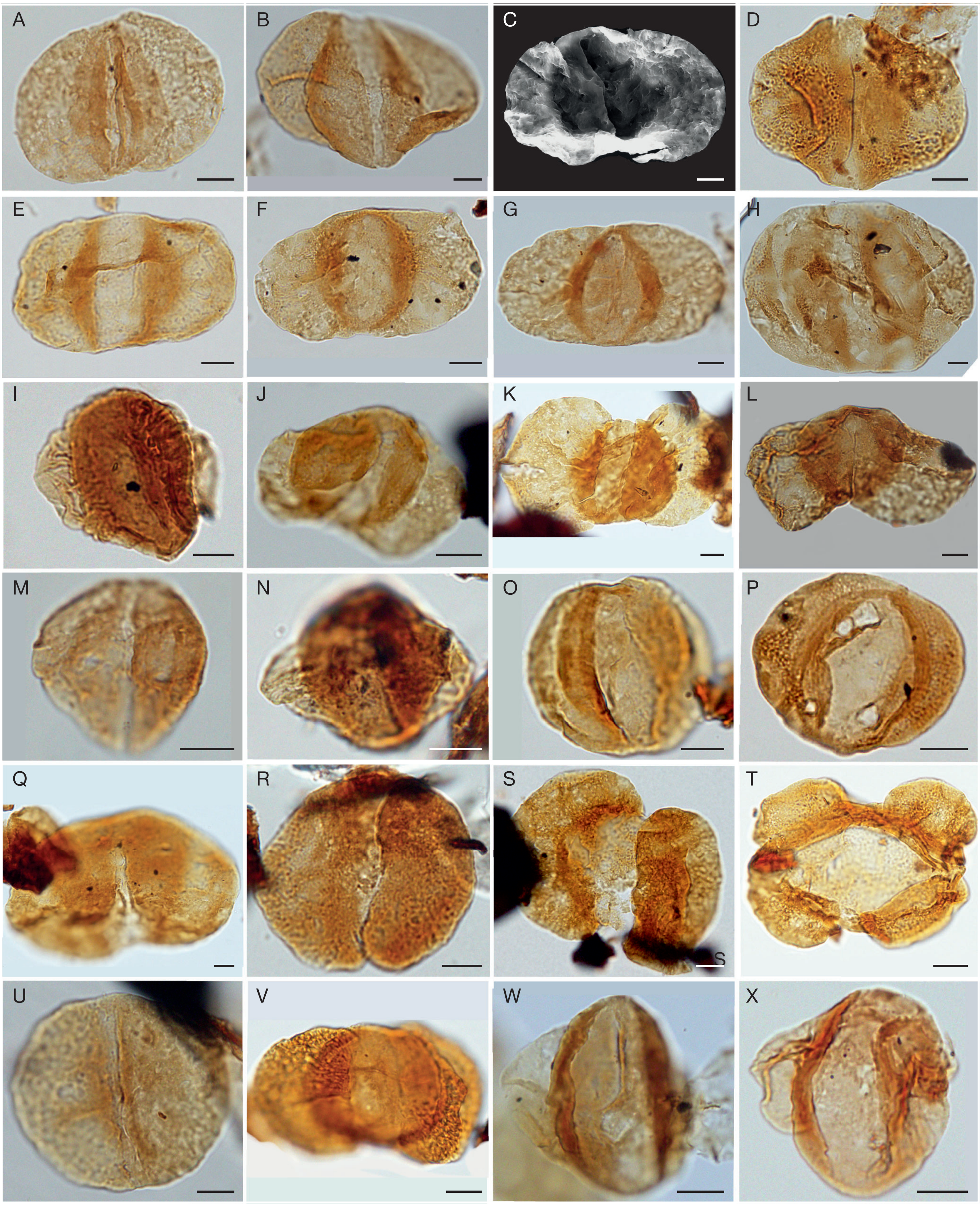

FIG. 8. — **A**-**C**, *Alisporites australis* de Jersey, 1962; **D**, *Alisporites sulcatus* Jain, 1968; **E**, *Chordasporites australiensis* de Jersey, 1962; **F**, **G**, *Falcisporites nuthalensis* Balme, 1970; **H**, *Falcisporites* cf. *F. zapfei* (Potonié & Klaus) Leschik, 1956; **I**, *Indusiisporites* sp.; **J**, *Klausipollenites staplinii* 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)

Polyplicate

Equisetosporites steevesi (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 (Megamonoporites) argentinus Jain, 1968
(Fig. 9K)

Cycadopites (Monosulcites) balmei Jain, 1968
(Fig. 9L)

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)

Remarks. Jain (1968) defined the species for subcircular grains with aperture V-shaped, club shaped, irregular in outline. We consider that specimens like Fig. 9W may be included in the range of variation of the taxon.

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,

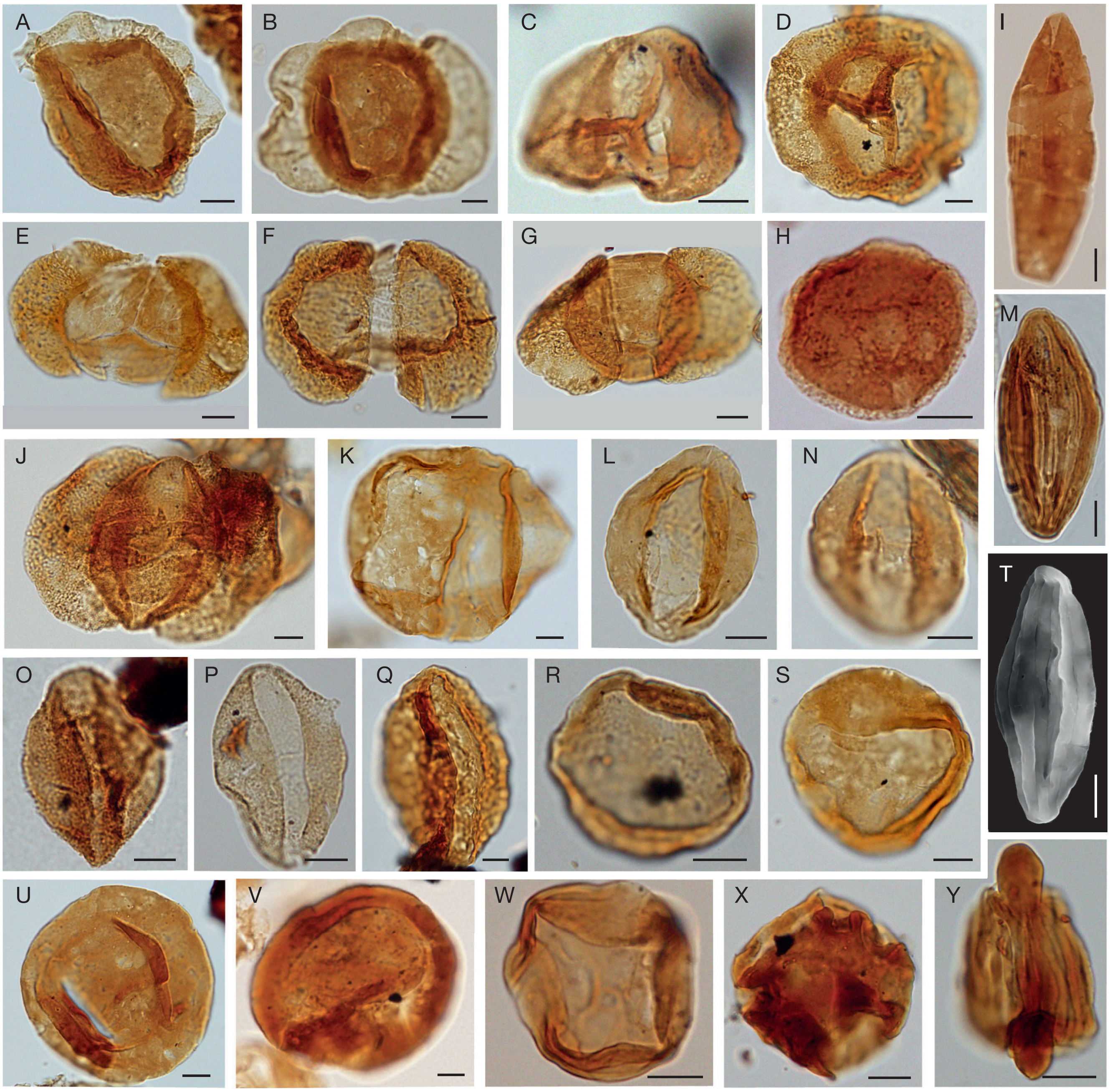

Fig. 9. — **A**, **B**, *Callialasporites* sp.; **C**, **D**, *Variapollenites* sp.; **E**, *Illinites* sp.; **F**, **G**, *Striatoabieites aytugii* Visscher emend. Scheuring, 1970; **H**, *Enzonalasporites vigens* Leschik, 1955; **I**, *Cycadopites magnus* Herbst, 1965; **J**, *Protohaploxypinus microcorpus* (Schaarschmidt) Clarke, 1965; **K**, *Cycadopites (Megamonoporites) argentinus* Jain, 1968; **L**, *Cycadopites (Monosulcites) balmei* Jain, 1968; **M**, *Cycadopites (Monosulcites) elegans* Jain, 1968; **N**, **T**, *Equisetosporites steevesi* (Jansonius) de Jersey, 1968; **O**, *Cycadopites granulatus* (de Jersey) de Jersey, 1964; **P**, *Granamegamonocolpites blancae* Herbst, 1965; **Q**, *Granamegamonocolpites cacheutensis* Jain, 1968; **R**, *Psilomonoporites cacheutensis* Jain, 1968; **S**, *Punctamonoaperturites bharadwajii* Jain, 1968; **U**, *Inaperturopollenites reidii* de Jersey, 1959; **V**, *Pilasporites cf. P. calculus* Balme & Hennelly, 1956; **W**, *Punctamonoaperturites bharadwajii* Jain, 1968; **X**, cf. *Lecaniella multigonata* Yi, 1994; **Y**, *Steevesipollenites* cf. *S. claviger* de Jersey & Raine, 1990. Scale bars: 10 µm.

especially by the co-occurrence of *Cadargasporites baculatus*, *Craterisporites rotundus*, *Enzonalasporites vigens*, *Leptolepidites argenteaeformis*, *Protodiploxypinus americus*, *Rugulatisporites permixtus*, and *“Rimaesporites” aquilonalis* as diagnostic species. The apparent absence of the cheirolepidiacean 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-Moreton 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* (*Asseretospora 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*, *Ashmoripollis reducta*, *Enzonalasporites vigens*, *Minutosaccus crenulatus*, *Samaropollenites speciosus*, *Ceratosporites 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 *Classopollis simplex*, an abundant species in Rhaetian-Jurassic palynofloras.

Enzonalasporites vigens 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) *Enzonalasporites vigens* 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 Rastros Formation (Ottone *et al.* 2005) and specimens reported as *C.* cf. *C. baculatus* were recognized in Los Rastros (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: *Lorisporites* Leschik, *Saeptasporites* Leschik, *Cedripites* Wodehouse, *Vesicaspora* (Schemel) Wilson & Venkatachala, and *Brachysaccus* Mädler. 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 Rastros 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 Rastros, 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 Rastros 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

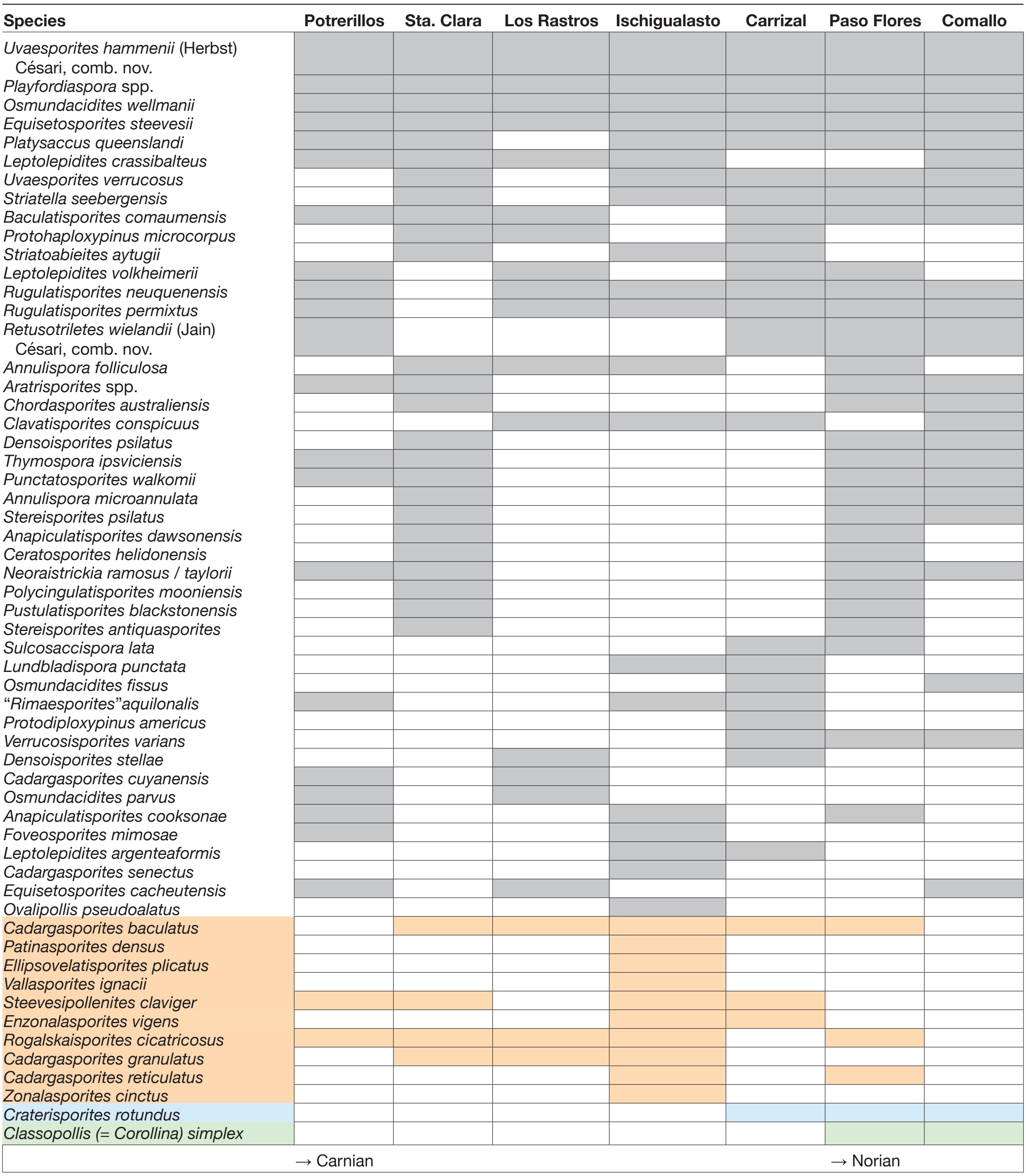

Fig. 10. — Distribution of selected species in the Carnian assemblages from Argentina. Colors: **Orange shading** indicates the typical Carnian species in Onslow or mixed palynofloras; **blue shading** the presence of *Craterisporites rotundus* de Jersey, 1970; **green shading** the presence of *Classopollis* 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 Cacheuta 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 *Enzonalasporites*, *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 *Classopollis* 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*, *Classopollis*-like pollen, *Rogalskaisporites cicatricosus*, *Cadargasporites* spp. some plicate species, among others, which characterize Carnian-early Norian assemblages in Gondwana, as well as several typically Carnian northern species (*Enzonalasporites* 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 *Classopollis*-like pollen. It should be considered that the absence of *Classopollis* in the Carrizal Formation may be circumstantial since Cheirolepidiaceae (*Classopollis* 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 *Classopollis*-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 *Classopollis*-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.

PALEOECOLOGICAL IMPLICATIONS

Differences in composition between the Carnian palynological assemblages from western Argentina may be the result of variances 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 *Enzonalasporites* 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* (lycopsid) to the Lowland or River SEG. Fern spores (*Osmundacidites*, *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 situ* 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 *Osmundacidites*, rare specimens of *Foveosporites*, 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 macrofloristic 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*, *Annulispora*, *Playfordiaspora*, taeniate, monocolpate, plicate and inaperturate pollen. The drought tolerant Voltzialean 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 northwestern Australia. Césari & Colombi (2013, 2016), however, identified in the Ischigualasto Formation typical Thetyan 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.

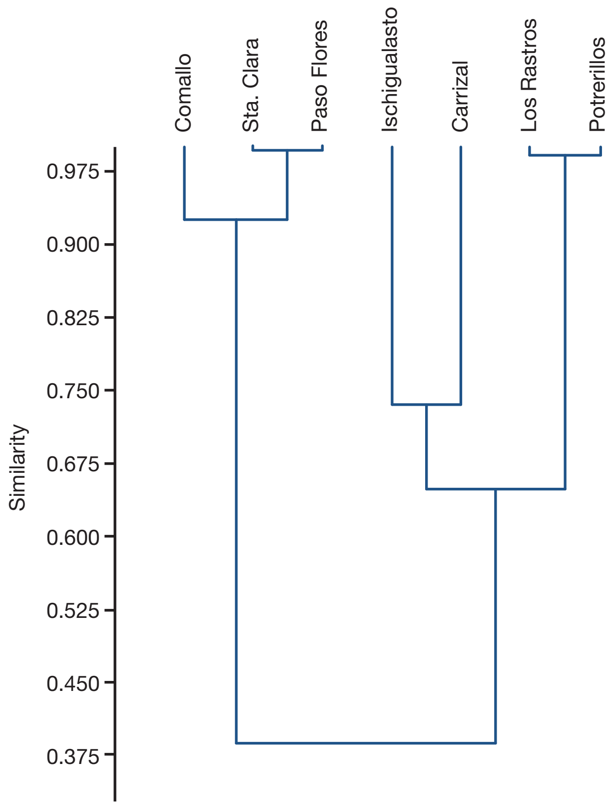

Fig. 11. — Cluster analysis of selected Carnian palynological assemblages from Argentina.

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 the those from the lacustrine-deltaic Potrerillos Formation, reinforcing the previous proposal of Spalletti *et al.* (1999) and Morel *et al.* (2015) of 83% of macroflorisitic 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 Comallo formations, but in these units occurs associated with *Classopollis* pollen.

The presence of the Tethyan *Enzonalasporites vigens* 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 *Samaropollenites 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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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) B26/0	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) L43/3	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) Y33/1	F. BA Pal 6587(4) R45/4	E. BA Pal 6586(1) O57/0	F. BA Pal 6586(6) M23/0
F. BA Pal 6586(3) R48/4	F-G. BA Pal 6586(6) H35/0	G. BA Pal 6587(3) V51/0	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	H. BA Pal 6587(2) L48/4	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	I-J. BA Pal 6587 (1) D61/2	H. 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	K. BA Pal 6585(2) V51/4	I. BA Pal 6587(1) G56/1	J. BA Pal 6586(1) L45/0
L. BA Pal 6586(1) T33/2	L. BA Pal 6586(4) B46/0	M. BA Pal 6587(4) V47/3	J. BA Pal 6587(1) T38/3	K. BA Pal 6586(3) P46/4
LL. BA Pal 6587(3) Q53/4	LL. BA Pal 6586(4) D26/0	N. BA Pal 6587(1) R33/0	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	O. BA Pal 6587(5) L28/2	L. BA Pal 6586(1) V32/0	M. BA Pal 6586(3) C42/3
O. BA Pal 6586(1) O66/3	N. BA Pal 6586(5) G40/0	P. BA Pal 6587(3) B36/2	LL. BA Pal 6586(4) V41/3	N. BA Pal 6586(5) E36/1
Q. BA Pal 6585(2) R63/3	O. BA Pal 6586(3) Y59/4	R-S. BA Pal 6587(3) V51/0	M. BA Pal 6587(3) S64/3	O. BA Pal 6586(3) R33/3
R. BA Pal 6587(3) T45/3	P. BA Pal 6586(2) J39/0	T. BA Pal 6587(1) H52/2	N. BA Pal 6587(4) Z31/2	P. BA Pal 6587(5) Z37/1
S. BA Pal 6587(3) B43/0	Q. BA Pal 6586(6) Q30/4	U. BA Pal 6587(2) M38/1	O. BA Pal 6587(3) W31/4	Q. BA Pal 6586(7) K31/4
T. BA Pal 6587(1) Y38/4	R-S. BA Pal 6586(2) S54/0	V-W. BA Pal 6587(3) T60/4	P. BA Pal 6586(5) O44/1	R. BA Pal 6585(2) P35/3
V. BA Pal 6586(1) S57/4	T. BA Pal 6586(6) L54/0		Q. BA Pal 6587(4) W40/3	S. BA Pal 6586(6) X51/3
W. BA Pal 6586(3) L53/0	U. BA Pal 6586(4)V51/0		R. BA Pal 6586(2) M57/4	T. BA Pal 6586(1) W33/4
Y. BA Pal 6587(1) H61/1	V. BA Pal 6586(6) U27/2		T. BA Pal 6586(5) N60/0	U. BA Pal 6586(6) F33/2
Z. BA Pal 6586(1) V43/1	W. BA Pal 6586(2) T65/3		U. BA Pal 6587(1) X54/4	V. BA Pal 6586(7) E28/4
AA. BA Pal 6586(4) Y41/2	X. BA Pal 6587(4) V47/3		V. BA Pal 6587(1) G60/4	W. BA Pal 6586(1) O52/0
BB. BA Pal 6586(2) L38/0			W. BA Pal 6586(1) F68/3	X. BA Pal 6587(1) V58/4
CC. BA Pal 6586(3) V30/4				