

Palynology of the Late Triassic Ischigualasto Formation, Argentina: Paleoecological and paleogeographic implications



Silvia N. Césari^{a,*}, Carina Colombi^b

^a Museo Argentino de Ciencias Naturales “B. Rivadavia”, Av. Ángel Gallardo, 470, Buenos Aires, Argentina

^b Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan 5400, Argentina

ARTICLE INFO

Article history:

Received 18 October 2015

Received in revised form 24 January 2016

Accepted 9 February 2016

Available online 18 February 2016

Keywords:

Carnian

Argentina

Ischigualasto

Palynology

Onslow

ABSTRACT

In this study we describe and compare the palynological assemblages from the Carnian Ischigualasto Formation of westernmost Gondwana to those of eastern Gondwana, which have been referred to the Onslow and Ipswich phytogeographic provinces. The palynofloras studied contain many taxa common to both regions, as well as several species that are widely recorded in European Carnian successions and less frequently recovered in the Carnian of the Southern Hemisphere. For the first time in Argentinean assemblages, we recognize *Anapiculatisporites spiniger*, *Cadargasporites granulatus*, *Cycadopites stonei*, *Ellipsovelatisporites plicatus*, *Enzonalasporites vigens*, *Ovalipollis pseudoalatus*, *O. ovalis*, *Patinasporites densus*, *Quadraeculina anellaeformis*, *Samaropollenites speciosus*, *Staurosaccites quadrididus*, “*Rimaesporites*” *aquilonalis*, *Vallasporites ignacii* and *Zonalasporites cinctus*. The new evidence extends the distribution of the Onslow palynoflora to include Carnian associations formerly assigned to the Ipswich Province. The affinities of Argentinean palynofloras seem to indicate the existence of a similar flora extending from the northern Australian margin (West Timor), through the western Tethys coasts, to westernmost Gondwana during the Carnian. Moreover, the new data reinforce the close relationship between some diagnostic species and humid environmental conditions.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

During the Triassic, Pangea extended from about about 85° N to 90° S and was surrounded by the Panthalassa Ocean. This landmass started to divide at the beginning of the Middle Triassic, resulting in Laurasian in the north (North America, Europe and Asia) and Gondwana in the south (South America, Antarctica, Africa, India and Australia) separated by the shallow Tethys Sea.

In the Southern Hemisphere, two floral provinces have been proposed for the Late Triassic (Dolby and Balme, 1976; Foster et al., 1994). The Onslow palynofloras in northwestern Australia are associated with the parental warm temperate forests recognized along the continental margins. The Ipswich palynofloras in southeastern Australia consist of cool temperate floras.

The Ischigualasto Formation outcropping in westernmost Gondwana is known worldwide for its tetrapod assemblage, which is considered the oldest known occurrence of dinosaurs. The unit is considered Carnian to Norian in age (231.4 to 225.9 Ma, Rogers et al., 1993; Martínez et al., 2011). The palynological record of the Ischigualasto Formation has not been studied in detail; just two brief communications

were published. One sample from the basal section of the Ischigualasto Formation was included in the “M1” palynological association with samples from other stratigraphic units, but lacked a precise list of identified species (Yrigoyen and Stover, 1969). Later, two samples from the middle Ischigualasto Formation were reported (Zavattieri and Milana, 2000). On the basis of abundant Gondwanan genera, an age no older than Norian was proposed for these fossiliferous strata (Zavattieri and Milana, 2000).

Recently, the same swamp deposit of the Ischigualasto Formation that yielded isotopic data (Colombi et al., 2011) on floristic remains (mainly cuticles) has also yielded mixed palynofloras containing southern and European species (Césari and Colombi, 2013). The palynological assemblages suggested a late Carnian–early Norian age for the fossiliferous strata. Here we describe the palynological content of those twenty-three assemblages as well as an additional sample from the site known as “El Hongo” in the Ischigualasto Provincial Park. We analyse the associated plant remains, their affinities with coeval palynofloras, and their palaeoecological and phytogeographical significance.

2. Geological setting

The Ischigualasto–Villa Unión Basin lies in northeastern San Juan and southwestern La Rioja provinces, Argentina (Fig. 1). The basin is part of a series of Triassic basins that developed during the early Mesozoic along

* Corresponding author.

E-mail addresses: scsari@macn.gov.ar (S.N. Césari), ccolombi@unsj.edu.ar (C. Colombi).

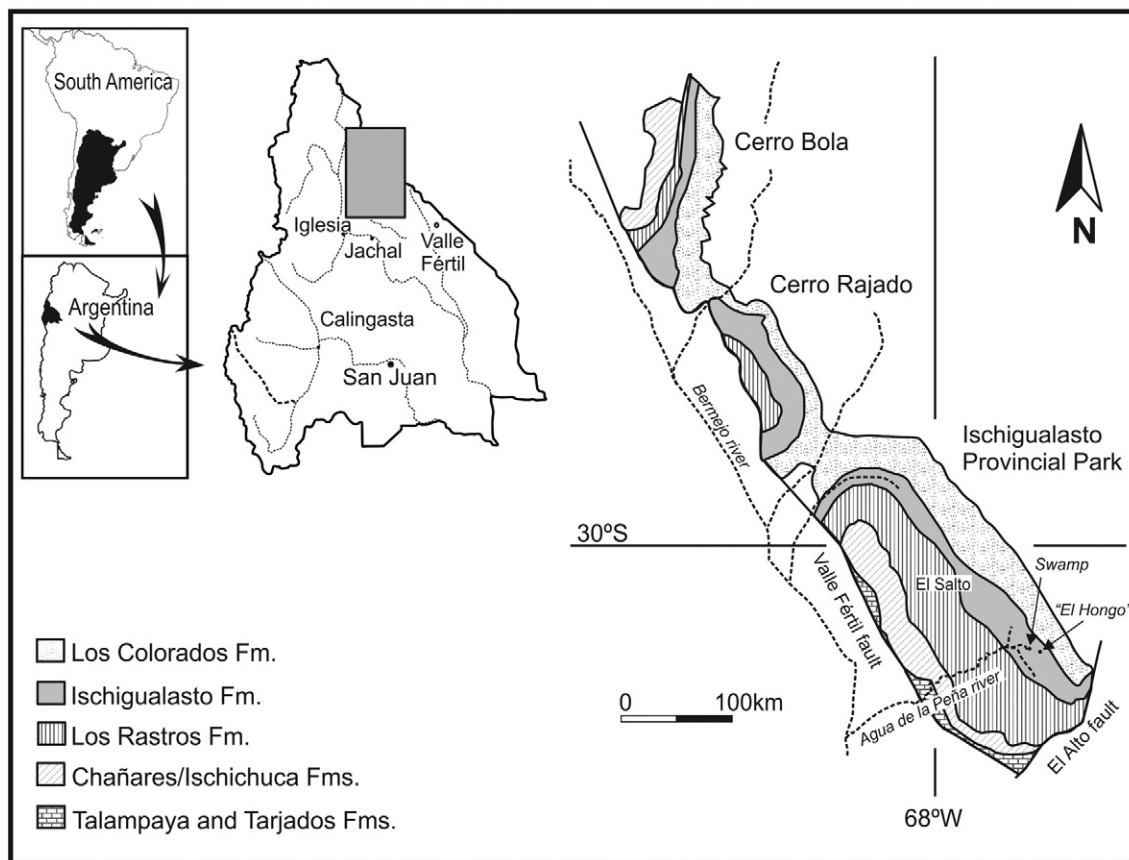


Fig. 1. Location and geological maps of the Ischigualasto area.

the southwestern margin of Pangea ($\sim 40^\circ\text{S}$) parallel to and cratonward of the proto-Andean arc (Uliana and Biddle, 1988; López-Gamundí et al., 1994). The filling of the Ischigualasto-Villa Unión Basin began during the Late Permian and persisted throughout the remainder of the Triassic. Miocene compressional tectonics related to the uplift of the Andes reactivated faults and generated extensive outcrops of Triassic rocks in a homoclinal succession (Milana and Alcober, 1994).

The Ischigualasto Formation is one of the upper units of the succession and is best known for its diverse and exceptionally well-preserved record of Late Triassic vertebrates including early dinosaurs, archosauriforms, crurotarsal archosaurs, therapsids and amphibians. The Los Rastros Formation underlies the Ischigualasto Formation, and is a predominantly lacustrine unit characterized by carbonaceous shale, siltstone, and sandstone arranged in recurrent coarsening-upward packages that represent the deposits of Gilbert-type deltas (Rogers et al., 2001). The Ischigualasto Formation is overlain by terrestrial deposits of the Los Colorados Formation, which consist of fluvial red-beds comprised of siltstone and sandstone (Milana and Alcober, 1994) (Fig. 1). The thickness of the Ischigualasto Formation ranges from 300 m on the margin of the basin, next to El Alto fault, to more than 700 m in the basin depocenter, in the El Salto area. The Ischigualasto Formation can be subdivided into four members (Fig. 2), from base to top: La Peña, Cancha de Bochas, Valle de la Luna, and Quebrada de la Sal (Currie et al., 2009). These members are distinguished by variations in the sedimentary architecture and paleosol development. The formation includes deposits of fluvial channels characterized by massive and trough cross-stratified sandstones and conglomerates intercalated with finer-grained proximal and distal floodplain facies (Fig. 2). Fine-grained sandstones and mudstones with horizontal and ripple lamination are frequently disturbed by paleosol

development, and indicate the proximal floodplain deposits. The distal floodplain facies, in contrast, are formed by massive or finely laminated siltstones and mudstones that are always overprinted by mature paleosol development. In the Valle de la Luna member, the focus of this contribution, the distal floodplain facies also tends to include abandoned channel and swamp deposits, which are characterized by laminated mudstone deposits intercalated with abundant seams of compressed plant cuticles and abundant palynomorphs (Colombi and Parrish, 2008; Currie et al., 2009; Césari and Colombi, 2013).

3. Material and methods

Twenty-three palynological samples from the Ischigualasto Formation were recovered from a swamp deposit 300 m long and 8 m thick (Fig. 3), 350 m above the base of the unit. An additional correlated sample comes from lower strata (330 m above the base) at the site known as “El Hongo”. Sample processing consisted of a preliminary treatment with dilute HCl and subsequent handling with HF for about 48 h. Any mineral matter remaining in the final residue was, when necessary, removed by heavy-liquid separation using ZnCl solution (density 2.0). All of these samples are preserved in the palynological collection of the Palynological Section of the Argentinean Museum of Natural Sciences “B. Rivadavia”, Argentina. Slide numbers with the prefix BA PI refer to the museum catalogue of that repository. Stage coordinates quoted in the Appendix 1 were read on the England Finder. The species identified in the samples are listed below. Details of the illustrated specimens are available in Appendix 1. Comments are confined to significant species or those without prior record in Argentina.

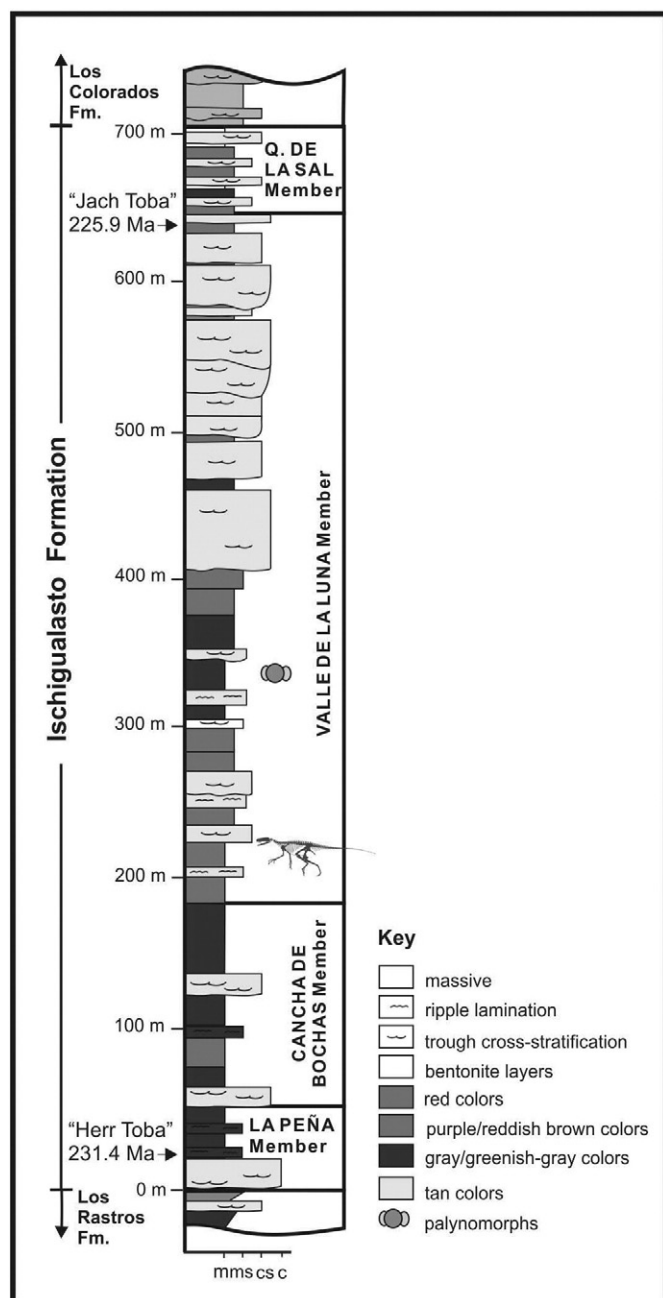


Fig. 2. Simplified log of the Ischigualasto Formation showing the stratigraphic positions of the studied palynological samples, the first dinosaur findings and radiometric dates.

4. Palynological results

4.1. Spores

Anapiculatisporites cooksonae Playford, 1965

Fig. 4. 1–2

Remarks. Although *Anapiculatisporites pristidentatus* Reiser & Williams shows stronger and sparse sculptural elements, some specimens are similar to the described here (e.g., de Jersey, 1970, plate 4, 9; de Jersey, 1971, plate 1, 2). A comparison with the two specimens described as *A. cooksonae* by Rojo and Zavattieri (2005) from Argentina is difficult due to the absence of a well-defined trilete mark in those spores. *Anapiculatisporites sandrae* Ottone has been distinguished by Ottone et al. (1992) by its smaller sculpture.

Anapiculatisporites spiniger (Leschik) Reinhardt/*Carnisporites anteriscus* Morbey 1975

Fig. 4. 3–5, 8–9

Remarks. This is the first mention of this species from the Triassic of western Gondwana. When viewed in the scanning electron microscope (Fig. 4), these specimens show characteristic simple, bifurcate and sometimes tetrafurcate tips of the processes interspersed with low grana or verrucae on the proximal surface. *Anapiculatisporites spiniger* (Leschik) Reinhardt has similar simple and bifurcate tips according to specimens illustrated by Schuurman (1977) and Visscher and van der Zwan (1981). Comparable forms, but exhibiting curvature, have been included in *Carnisporites* Mädlar by Morbey (1975). Among the species described in Morbey (1975), *C. anteriscus* shares more diverse sculpture with the Argentinean specimens. If the presence or absence of curvature is not considered a diagnostic feature, it is likely that the species mentioned are part of a complex (or morphon) that represents variations of the same taxon or very similar taxa. Kavary (1972) defined *Raistrickia alpina* from the Carnian of Austria, to include subcircular, trilete spores with the exine covered with spaced, terminally bifurcated bacula except for the contact area, which is ornamented with top rounded grana. A revision of these specimens will likely show their similarity with *A. spiniger*.

The specimens also resemble *Anapiculatisporites helidonensis* (de Jersey) de Jersey and McKellar (2013), although this species includes spores with exine mainly sculptured equatorially with spinae, about 2 to 5 µm in length with pointed apices (a few apices are bifurcate). Sculptural elements are reduced in size towards distal pole and the proximal exine is smooth (de Jersey and McKellar, 2013).

Anapiculatisporites sandrae Ottone 1992

Fig. 4.6–7

Remarks. Specimens included in this species are characterized by the presence of broadly based coni closely arranged on the distal and equatorial surface and occasional imperfect curvature on proximal area. Original specimens illustrated by Ottone et al. (1992) from the Triassic of Argentina seem to have imperfect curvature, too.

Annulisporea folliculosa (Rogalska) de Jersey, 1959

Fig. 4.10–11

Remarks. This species is interpreted to encompass spores with a distal circumpolar annular crassitude from which arise variable radial ridges.

Aratrisporites parvispinosus Leschik emend. Playford, 1965

Fig. 4.12

Remarks. This species is scarcely represented in the assemblages.

Cadargasporites baculatus (de Jersey & Paten) Reiser and Williams, 1969

Fig. 4.13–15

Remarks. This species was previously recorded in the Los Rastros Formation of Argentina by Ottone et al. (2005). The Argentinean specimens at SEM are very similar to the illustrated by Filatoff (1975) from the Jurassic of Australia.

Cadargasporites granulatus de Jersey and Paten, 1964

Fig. 4.16

Remarks. This is the first record of the Australian species in Argentina.

Cadargasporites reticulatus de Jersey and Paten, 1964

Fig. 4.17–21

Remarks. Using the SEM, thin and long membranes were observed along the proximal contact area, as suggested by Bai et al. (1983) and



Fig. 3. View of the swamp deposits of the Valle de la Luna Member.

Reiser and Williams (1969) in *Cadargasporites baculatus*. The specimens from the Ischigualasto Formation are closely comparable with the Australian species. *C. reticulatus* was originally described from the Jurassic, but was also recognized in the Upper Triassic. Helby et al. (1987) noted the first appearance of this species in the *Craterisporites rotundus* and *Samarisporites speciosus* Biozones of Australia. The only previous records in Argentina were found in the Paso Flores Formation (Zavattieri and Mego, 2008). Tripathi and Raychowdhuri (2005) and Vijaya et al. (2009) recognized the species in the Late Triassic of India.

Cadargasporites senectus de Jersey and Hamilton, 1967
Fig. 4.22–23

Calamospora spp.

Remarks. Circular to subcircular trilete spores with smooth exine are also components of the assemblages. These spores without significant biostratigraphic relevance are only referred to generic rank.

cf. *Carnisporites megaspiniger* Morbey 1975
Fig. 4.24

Remarks. Some specimens identified in the assemblages show similar sculpture to *C. megaspiniger* Morbey but apparently they lack curvature and occasional coni on the proximal surface.

Cingutritiles cf. *C. cestus* Stevens, 1981
Fig. 4.25–27

Remarks. Specimens (30–40 µm diameter) from the Ischigualasto Formation are closely similar to those illustrated by de Jersey and Raine (1990). However, Argentinean spores differ in having an inner body and a variation in the width of the cingulum, which may be weakly concentrically striated.

Cingutritiles sp.
Figs. 4.28–30, 5.1

Description. Spore trilete, amb subcircular to subtriangular with convex sides and broadly rounded angles (ca. 40 µm diameter). Laesurae slightly sinuous, length spore radius confined by cingulum's inner margin and usually open in a subtriangular area. Exine smooth and thin on the proximal surface. Equatorial thickening of variable width (2–4 µm)

and usually undulate with rounded projections. A distinctive narrow subequatorial furrow of thin exine separates the cingulum of the distal smooth and thickened surface.

Comparisons. These spores are provisionally assigned to *Cingutritiles* Pierce, until the recognition of more specimens permits the definition a new taxon. Related taxa like *Murospora* Sommers were interpreted by Pocock (1961) as spores whose bodies are completely enclosed by a thick outer structure or “patella”. *Cingulatisporites* Thomson was also revised by Pocock (1961) and was characterized by single layered spores with an equatorial narrow cingulum (exinal thickening only at the equator). *Rogalskaisporites* Danzé-Corsin & Laveine differs from the Argentinean specimens in that the former have radial striae or foveolae between the distal crassitude and the cingulum. Although some Australian Triassic species with distal polar crassitudes and thickened lateral sides have been referred to *Stereisporites* Pflug the genus was not originally defined as cingulate.

The specimens differ from *Cingutritiles cestus* by the presence of a subequatorial narrow furrow and the undulate cingulum.

Clavatisporites conspicuus Playford 1982
Fig. 5.2–4

Remarks. *Clavatisporites conspicuus* Playford differs from *Clavatisporites hammenii* Herbst (1965, 1972) in its exine densely sculptured predominantly with pila and subordinate bacula and verrucae up to 5 µm in length, usually with the apices widened in form of “cauliflower”. de Jersey and Hamilton (1967) illustrated in detail the sculpture of specimens included by Playford (in Playford et al., 1982) in *C. conspicuus*, which is identical to the present in the Argentinean spores. This species has been identified in the Comallo Formation, Argentinean Patagonia, by Zavattieri et al. (1994).

Clavatisporites hammenii Herbst, 1965
Fig. 5.9

Remarks. The characteristic clavae with a short base and bigger rounded apices of *C. hammenii* (Herbst, 1965, 1970) allowed Playford to distinguish similar Australian specimens, including them in *C. conspicuus* Playford (Playford et al., 1982). Backhouse and Balme (2002) noted that *C. hammenii* more closely resembles *Uvaeisporites verrucosus* (de Jersey) Helby than *C. conspicuus*.

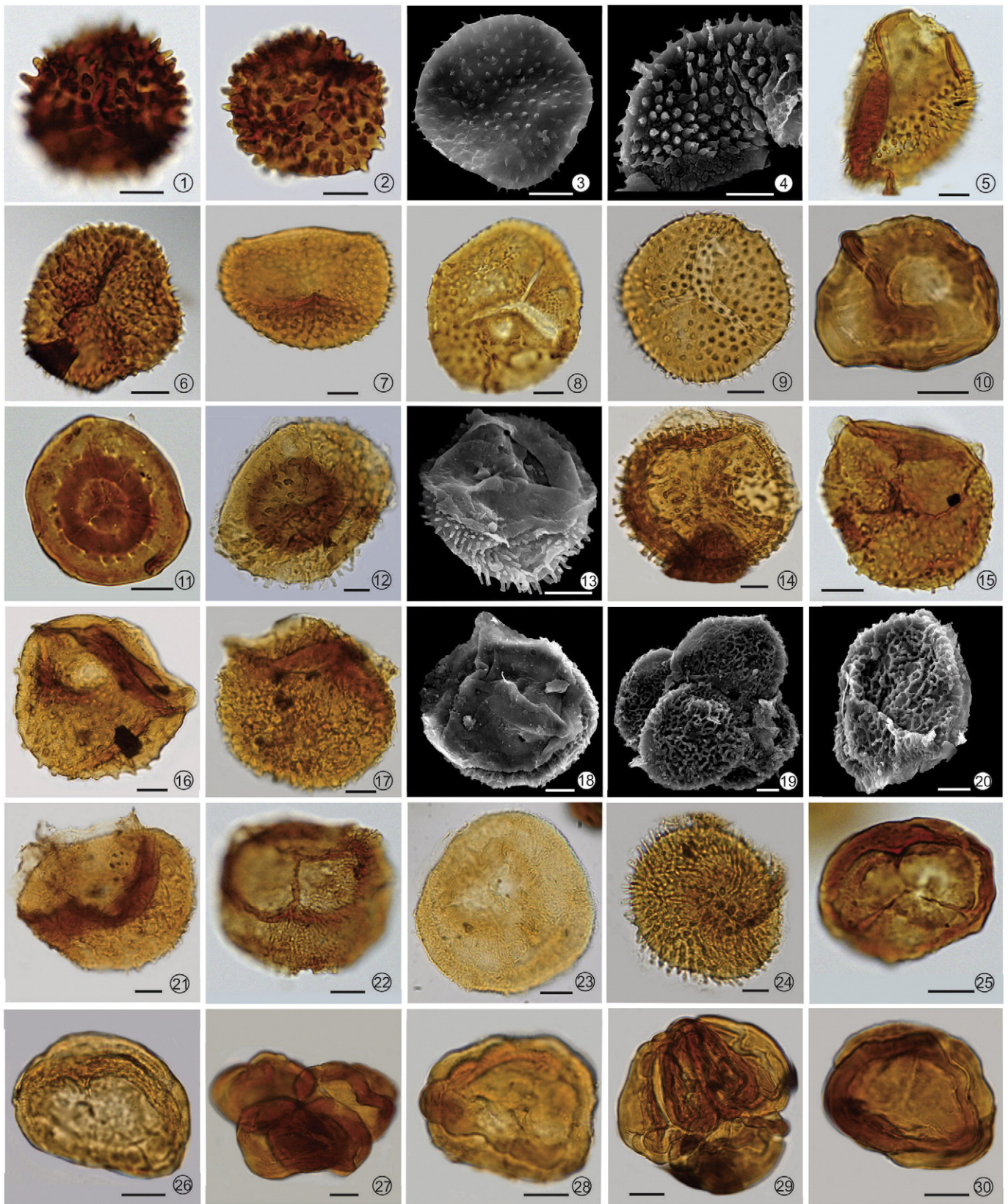


Fig. 4. 1–2. *Anapiculatisporites cooksonae* Playford; 3–5, 8–9 *Anapiculatisporites spiniger* (Leschik) Reinhardt/*Carnisporites anteriscus* Morbey; 6–7. *Anapiculatisporites sandrae* Ottone; 10–11. *Annulispora folliculosa* (Rogalska) de Jersey; 12. *Aratrisporites parvispinosus* Leschik emend. Playford; 13–15. *Cadargasporites baculatus* (de Jersey & Paten) Reiser & Williams; 16. *Cadargasporites granulatus* de Jersey and Paten, 1964; 17–21. *Cadargasporites reticulatus* de Jersey & Paten; 22–23. *Cadargasporites senectus* de Jersey & Hamilton; 24. cf. *Carnisporites megaspinigifer* Morbey; 25–27. *Cingutritiles* cf. *C. cestus* Stevens; 28–30. *Cingutritiles* sp. Scale = 10 μ m.

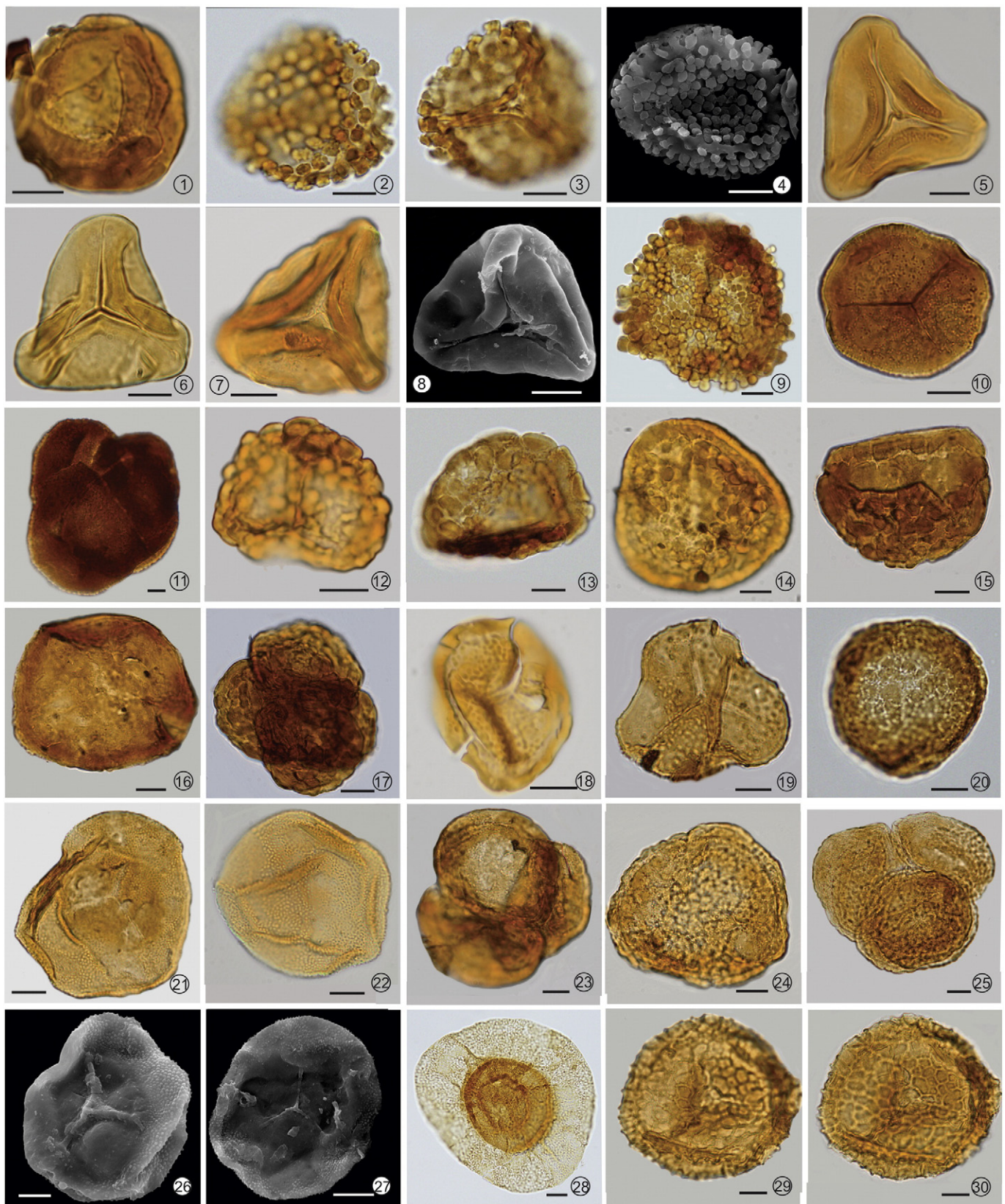


Fig. 5. 1. *Cingutritiles* sp.; 2–4. *Clavatisporites conspicuus* Playford; 5–8. *Dictyophyllidites mortoni* (de Jersey) Playford & Dettmann/*D. harrisii* Couper; 9. *Clavatisporites hammenii* Herbst; 10. *Foveosporites mimosae* De Jersey & Hamilton; 11, 16. *Lundbladispota* sp.; 12–13. *Leptolepidites argenteaeformis* (Bolchovitina) Morbey (= *Uvaesporites argenteaeformis* Schulz); 14–15, 17. *Leptolepidites* cf. *L. crassibalteus* Filatoff; 18. *Limatulasporites fossulatus/limatulus* complex Foster et al.; 19. *Lophotritiles bauhiniae* de Jersey & Hamilton; 20, 23–25. *Lundbladispota punctata* sp. nov.; 21–22, 26–27. *Osmundacidites* sp. Balme; 28. *Playfordiaspora cancellosa* (Playford & Dettmann) Maheshwari & Banerji; 29–30. *Retitritiles* sp. Scale = 10 μ m.

Dictyophyllidites mortoni (de Jersey) Playford & Dettmann 1965/
D. harrisii Couper, 1953

Fig. 5.5–8

Remarks. These species have a widespread distribution in Late Triassic and Jurassic palynological assemblages. There is a range of variation between spores with more or less prominent kytome. Both types of spores were found in situ in *Phlebopteris smithii* sporangia (Litwin, 1985).

Foveosporites mimosae de Jersey and Hamilton, 1967

Fig. 5.10

Remarks. This species from the middle Triassic of Australia includes spores with a thick and pitted exine; pits are small and sometimes coalescent. Zavattieri and Rojo (2005) described the species in the Argentinean Potrerillos Formation. *F. moretonensis* de Jersey differs in its smaller size and pits reduced on the proximal face.

Leptolepidites argenteaeformis (Bolchovitina) Morbey 1975
(= *Uvaesporites argenteaeformis* Schulz, 1967)

Fig. 5.12–13

Remarks. Morbey (1975) characterized this species by low and broad verrucae on the distal face and equatorial area. Schulz (1967) combined the species with *Uvaesporites* but we prefer to follow Morbey's proposal, which considers the presence of low and wide verrucae and discards spore size as a generic characteristic. Helby emended the genus *Uvaesporites* (in de Jersey, 1971), which bear a predominately gemmate sculpture. Some Argentinean specimens resemble *Camerosporites secatus* in the shape of the equatorial verrucae (Fig. 5.13).

Leptolepidites cf. *L. crassibalteus* Filatoff, 1975

Fig. 5.14–15, 17

Remarks. Although the specimens from the Ischigualasto Formation (35–50 µm diameter) are slightly bigger than the originally described by Filatoff (1975) and possess smaller verrucae densely distributed, they coincide in the sculpture not protruding usually at the equator.

Limatulasporites fossulatus/limatulus complex Foster et al., 1994

Fig. 5.18

Remarks. The Triassic species *Limatulasporites fossulatus* (Balme) Helby & Foster and *Limatulasporites limatulus* (Playford) Helby & Foster have a wide record in Australia and differ only in size (Balme, 1970). Playford (in Playford et al., 1982) and de Jersey and Raine (1990) considered the possibility that *L. fossulatus* may be equivalent to *limatulus*. Sajjadi and Playford (2002) considered *Limatulasporites* a junior synonym of *Nevesisporites* following an unpublished emendation of McKellar.

Lophotriteles bauhiniae de Jersey and Hamilton, 1967

Fig. 5.19

Lundbladispota punctata sp. nov.

Fig. 5.20, 23–25

Holotype. BAPI 6415(A) C23/3, Fig. 5.25

Stratigraphic horizon. Valle de Luna Member, Ischigualasto Formation.

Derivatio nominis. After *punctum*: elongate or rounded perforation lower than 1 µm.

Diagnosis. Spores radial, trilete, cavate with convexly subtriangular amb. A faint equatorial thickening may develop. Lesurae usually indistinct and the exine finely sculptured distal and equatorially by small pits fused in narrow sinuous grooves, which separate irregular and flattened verruca-like elements usually 1 µm high, with crenulate outlines. Proximal surface smooth or with reduced sculpture. Inner body, smooth and thin, usually visible. Diameter (based on 20 measured specimens): 40–58 µm.

Remarks. The specimens occur commonly in tetrads and are distinguished from other species by the conspicuous sculpture. Provisionally

are assigned to *Lundbladispota*, a morphotaxon characterized by the same general features of our material.

Guttatisporites guttatus Visscher is similar in its sculpture of irregularly shaped, low verruca-like elements with narrow pits between the elements forming a negative reticulum, but differs in its bigger size and lacking inner body.

Lundbladispota sp.

Fig. 5.11, 16

Remarks. Rare specimens with a finely textured exoxine characteristic of *Lundbladispota* Balme emend. Playford are recognized in tetrads or isolated spores.

Osmundacidites sp.

Fig. 5.21–22, 26–27

Remarks. The genus *Osmundacidites* was defined by Couper (1953) for including subcircular-circular anisopolar spores with grana reduced in proximal surface. The specimens from the Ischigualasto Formation are 35–50 µm in diameter and sculptured by small grana and short bacula lower than 1 µm in height, absent in the contact area (Figs. 26, 27). Zavattieri (1986) described similar spores from the Triassic of Argentina, with sculpture lower than 1 µm that were referred to *O. cf. senectus* Balme; however, Balme (1963) described grana 1–2 µm high in the Australian species that are present in the contact area. *O. diazii* Volkheimer is also characterized by sculpture under 1 µm, but differs in that the sculpture is not reduced at the proximal pole. *Osmundacidites araucanus* Volkheimer has higher sculpture, which is reduced in the proximal pole.

Considering the probable range of intraspecific variation among these spores with granulate sculpture, we consider superfluous define a new species for the moment.

Playfordiaspora cancellosa (Playford & Dettmann) Maheshwari and Banerji, 1975

Fig. 5.28

Remarks. Until the type specimens of *Endosporites velatus* Leschik and *Endosporites hexareticulatus* Klaus have been revised, we accept the validity of *Playfordiaspora cancellosa* (= *Guthoerlisporites cancellosus*).

Retitriteles sp.

Fig. 5.29–30

Remarks. *Retitriteles rosewoodensis* (de Jersey) McKellar and *Retitriteles austroclavatidites* (Cookson) Döring et al. differ from the Argentinean specimens in their larger lumina and distinctive lips. *Limboisporites antiquus* (de Jersey) de Jersey & Raine is distinguished by its proximal face psilate and distal surface and zona foveolate.

Retusotriteles herbstii sp. nov.

Fig. 6.1–5

Holotype. BAPI 6413 D31/2, Fig. 6.5

Stratigraphic horizon. Valle de Luna Member, Ischigualasto Formation.

Derivatio nominis. In honour of Rafael Herbst an outstanding Argentinean paleobotanist, who pioneered the research on Triassic Argentinean palynofloras.

Diagnosis. Spores radial trilete, amb circular to subcircular. Lesura straight, length approximately 0.5 or less of spore radius, flanked by narrow lips and encircled within the contact area, which is clearly delimited by perfect curvaturae with margins usually raised and faintly granulate. Exine laevigate to finely scabrate. Diameter (based on 20 measured specimens): 40–55 µm.

Remarks. Herbst (1972) described two specimens from the Los Rastros Formation (Triassic, Argentina) as *Stereisporites* sp., which are characterized by a short trilete mark encircled by a narrow annular

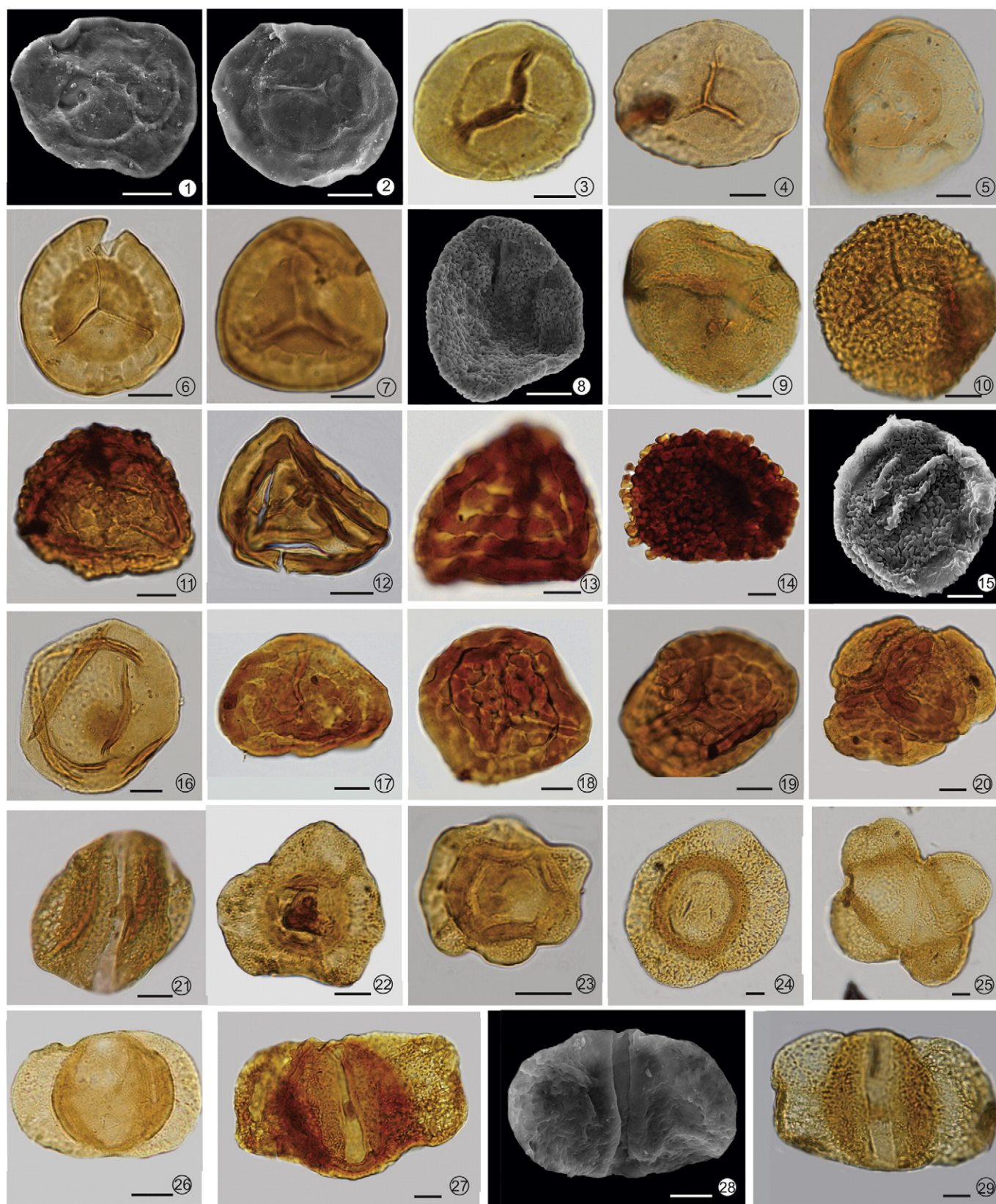


Fig. 6. 1–5. *Retusotriletes herbstii* sp. nov.; 6–7. *Rogalskaisporites cicatricosus* Rogalska ex Danze-Corsin & Laveine; 8–9. *Rugulatisporites* cf. *R. neuquenensis* Volkheimer; 10, 15. *Rugulatisporites permixtus* Playford; 11. *Uvaesporites verrucosus* (de Jersey) Helby in de Jersey; 12–13. *Striatella seebergensis* Mädlér; 14. *Uvaesporites glomeratus* (Döring) Hiltmann; 16. *Araucariacites australis* Cookson; 17–20. *Taurocusporites* sp. A Morbey; 21. *Alisporites sulcatus* Jain; 22–25. Abnormal pollen grains; 26. *Alisporites parvus* de Jersey; 27–29. *Alisporites australis* de Jersey; Scale = 10 μ m.

thickness or rim. Abundant specimens from the Ischigualasto Formation allow us to define a new species that include those illustrated by [Herbst \(1972, plate 1, fig. 12\)](#). It is likely that the specimens described by [Zavattieri \(1986\)](#) as *Calamospora* sp. 1, could be included in the new species. Although it is questionable that the distance between curvature and equator could be a diagnostic characteristic, all of the *Retusotriletes mesozoicus* Klaus (*Carnisporites hercynicus* Mädlér) specimens differ in having trilete rays that almost reach the equator, delineating a distinctive curvature. *Retusotriletes diversiformis* (Balme and Hennelly) Balme and Playford differs in its trilete rays usually longer than half the radius and the presence of a subtriangular area at the proximal pole (not always coinciding with the curvature). *Aulisporites* (Leschik) Klaus resembles the Argentinean species but has a two-layered exine and a very short trilete mark. The globose shape of the new species and the characteristic short trilete mark encircled into a sub-circular area are characteristics shared with *Cadargasporites*, which differ in that the remainder of the exine is sculptured. It is possible that *Retusotriletes herbstii* represents an immature stage or laevigate form of *Cadargasporites* spores.

Rogalskaisporites cicatricosus Rogalska ex Danzé-Corsin and Laveine, 1963 (= *Stereisporites perforatus* Leschik, 1955)
Fig. 6.6–7

Remarks. This species includes small trilete cingulate spores with a distal crassitude and radially arranged striae or foveolae that were referred to *Annulispora* de Jersey, *Stereisporites* Thomson & Pflug or *Rogalskaisporites* Danzé-Corsin & Laveine. The description of *R. cicatricosus* by [Rogalska \(1954\)](#) was succeeded by the description of very similar spores as *Stereisporites perforatus* by [Leschik \(1955\)](#). [Playford and Dettmann \(1965\)](#) and [de Jersey \(1970\)](#) consider *Sporites cicatricosus* Rogalska taxonomically invalid and a synonym of *Stereisporites perforatus* Leschik. [Morbey \(1975\)](#), in contrast, considered the species illustrated by [Rogalska \(1954\)](#) valid and, in view of the presence of a circumpolar annular crassitude, proposed the combination *Annulispora cicatricosa* which distinguished from *S. perforatus*. At the same time, [Filatoff \(1975\)](#) interpreted the presence of a non-annular distal crassitude and proposed combination *Rogalskaisporites cicatricosus* Rogalska ex Danzé-Corsin & Laveine, this criterion was followed by [de Jersey and Raine \(1990\)](#).

[Sajjadi and Playford \(2002\)](#) included in *Annulispora canalicula* (Filatoff) McKellar specimens described as *Annulispora cicatricosus* by [Morbey \(1975\)](#) that resemble the here illustrated.

[Zavattieri \(1986\)](#); [Rojo and Zavattieri \(2005\)](#) and [Zavattieri and Mego \(2008\)](#) have illustrated this species in the Triassic of Argentina.

Rugulatisporites cf. *R. neuquenensis* Volkheimer, 1972
Fig. 6.8–9

Remarks. [Volkheimer \(1972\)](#) originally recognized this species as Jurassic circular to subcircular trilete spores (46–63 µm) with sculpture of muri approximately 1 µm high, formed by the fusion of verrucae. [Azcuy and Longobucco \(1983\)](#) and [Zavattieri \(1986\)](#) also recorded the species in Triassic assemblages of Argentina. The specimens from Ischigualasto have muri up to 2 µm in height and are similar to those illustrated by [Filatoff \(1975\)](#) as *R. cf. neuquenensis*. *R. permixtus* Playford in [Playford et al. \(1982\)](#), from the Middle Triassic of Australia, closely resembles the specimens described here but has muri up to 1.3 µm high and 2.5 µm wide, and subordinate grana and verrucae. *R. stonecrofti* de Jersey & Hamilton from the Middle Triassic of Australia possesses a laevigate proximal face and smaller size. *R. nelsonensis* Raine in [de Jersey and Raine \(1990\)](#) from the Triassic of New Zealand is larger.

Rugulatisporites permixtus Playford 1982
Fig. 6.10, 15

Striatella seebergensis Mädlér, 1964
Fig. 6.12–13

Remarks. This species originally described by [Mädlér \(1964\)](#) from the Upper Triassic of Germany has a wide distribution in Australia and other Gondwanan continents.

Uvaesporites glomeratus (Döring) Hiltmann, 1967
Fig. 6.14

Remarks. The specimens bear the characteristic sculpture of gemmae that densely cover the distal and equatorial area.

Uvaesporites verrucosus (de Jersey) Helby in [de Jersey, 1971](#)
Fig. 6.11

Remarks. *Uvaesporites* Döring includes subcircular, cingulate, distally rugulo-verrucate spores. This species encompass spores sculptured equatorially and distally with, gemmae, pila, coni and bacula.

Taurocusporites sp. A [Morbey, 1975](#)
Fig. 6.18–20

Remarks. Specimens from the Ischigualasto Formation are very similar to those illustrated and described by [Morbey \(1975\)](#) as a new species of *Taurocusporites* (Stover) Playford & Dettmann, differing only in the absence of papillae in the former. The width of the labra and presence of curvaturae is variable in the Argentinean spores.

4.2. Pollen

Araucariacites australis Cookson, 1947.
Fig. 6.16

Abnormal pollen grains
Fig. 6.22–25

Remarks. Rare specimens with diverse structure, ranging from monosaccate to tetrasaccate, are considered abnormal morphotypes of gymnosperm pollen. [Foster and Afonin \(2005\)](#) recognized similar variation of abnormal pollen in assemblages from the Permian–Triassic boundary. These authors described the abnormal specimens as variations of *Alisporites* and *Klausipollenites* genera.

Alisporites australis de Jersey, 1962
Fig. 6.27–29

Remarks. Bisaccate pollen is the most abundant group in the assemblages and displays wide variations that may represent intraspecific gradation. Several taxa have been distinguished but further precision would not be relevant to the biostratigraphic goals of this study due to their uncertain taxonomy.

Alisporites, according to [Jansonius's \(1971\)](#) re-examination of Daugherty's type material is regarded as a repository for non-taeniate, distally sulcate species ([Foster, 1979](#)). *Falcisporites* Leschik emend. Klaus is also distally sulcate and can be distinguished from *Alisporites* by its longitudinally elongated corpus. [Foster \(1979\)](#) noted a considerable overlap between the measurements of *Alisporites australis* and *Falcisporites stabilis* and suggested at least 20 measurable specimens are necessary for a confident specific assignment. [De Jersey and McKellar \(2013\)](#) reinforced the concept that *Alisporites australis* exhibits a narrow, well-defined, parallel-sided distal cleft ('sulcus' or 'colpus'). *Falcisporites*, in contrast, has a broad, thinner distal area (leptoma) with broadened, rounded extremities.

Alisporites parvus de Jersey, 1962
Fig. 6.26

Alisporites sulcatus Jain, 1968
Fig. 6.21

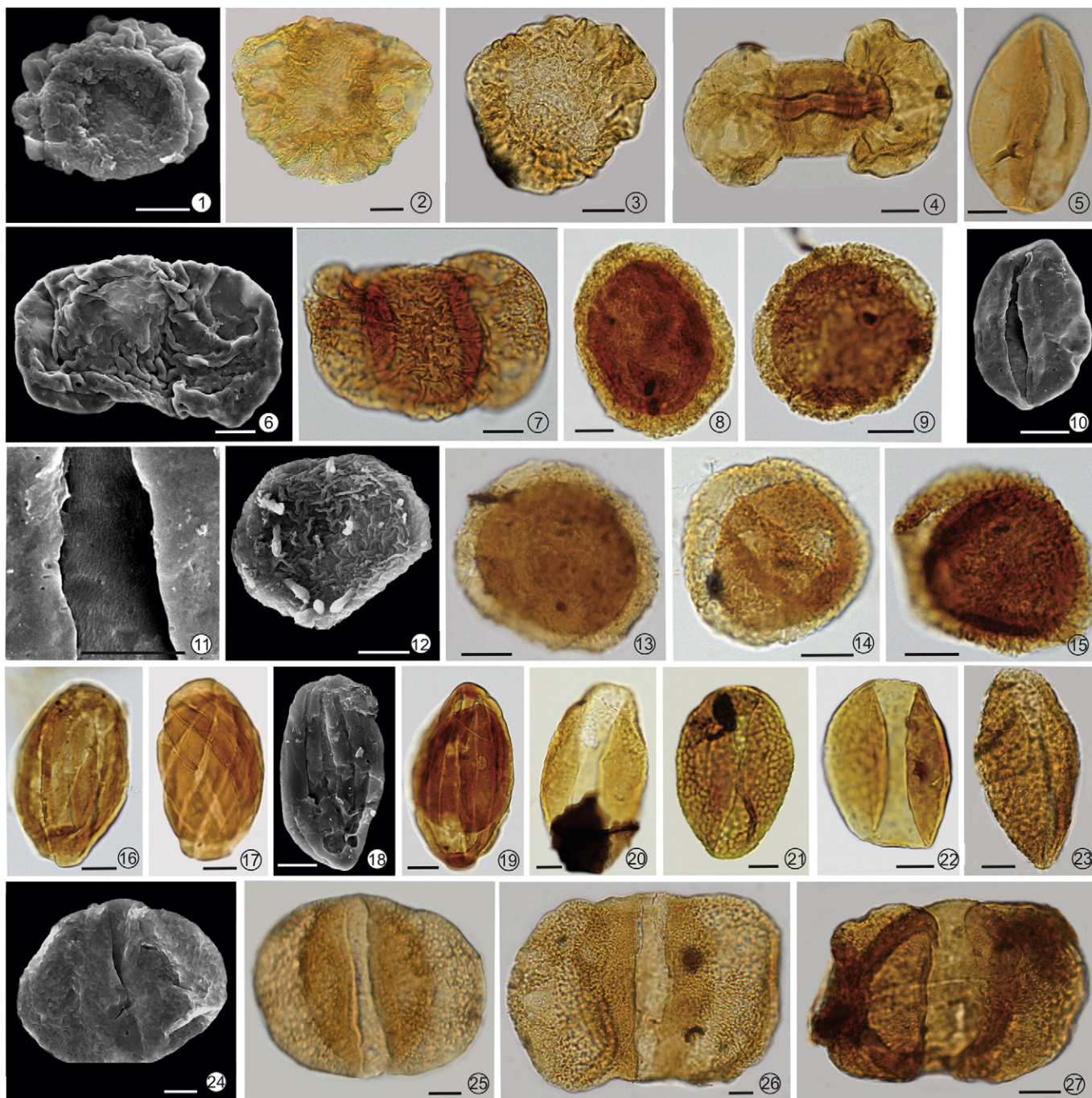


Fig. 7. 1–3. *cf. Callialasporites dampieri* (Balme) Dev; 4. *Chordasporites singulichorda* Klaus; 5, 10–11. *Cycadopites* sp.; 6–7. *Ellipsovelatisporites plicatus* Klaus; 8–9, 12, 13–15. *Enzonalsporites vigens* Leschik; 16–17. *Equisetosporites cf. E. tortuosus* (Mädler) de Jersey; 18–19. *Equisetosporites steevesi* (Jansonius) de Jersey; 20–22. *Cycadopites stonei* Helby, 22. colpus exine on distal surface smooth; 23. *Cycadopites granulatus* (de Jersey) de Jersey; 24–25. *Falcisporites cf. F. zapfei* (Potonié & Klaus) Leschik; 26. *Falcisporites nuthallensis* Balme; 27. *Lueckisporites cf. L. singhii* Balme; 28. *Lunatisporites noviaulensis* (Leschik) Foster; 29–32. *Minutosaccus crenulatus* Dolby in Dolby and Balme. Scale = 10 µm, = 5 µm in Fig. 11.

cf. Callialasporites dampieri (Balme 1957) Dev, 1961
Fig. 7.1–3

Remarks. A few specimens are similar to the monosaccate genus *Callialasporites*, which is characterized by the saccus strongly folded at the equator and the exoexine over the central body convolute to rugulate. Although the genus is best known from the Jurassic, some specimens have been recognized in Late Triassic assemblages (Zavattieri, 1991; Tripathi and Ray, 2006; Goswami et al., 2010).

Chordasporites singulichorda Klaus, 1960
Fig. 7.4

Cycadopites sp.
Fig. 7.5, 10–11

Remarks. Rounded-oval specimens with smooth surface when observed at SEM show the exine of the sulcus finely rugulate (Fig. 7.11).

Cycadopites granulatus (de Jersey) de Jersey, 1964
Fig. 7.23

Cycadopites stonei Helby, 1987

Fig. 7.20–22

Remarks. *Cycadopites stonei* Helby is common in the Late Triassic from Western Australia. The relation length/width and the sculpture of low and rounded elements decreasing in size towards the long-axis extremities where the colpus expanded are the main features that distinguish this species from *Granamegamonocolpites cacheutensis* Jain, *Granamegamonocolpites campbellii* de Jersey & McKellar and *Cycadopites andrewsii* Cornet & Traverse. Argentinean specimens coincide in the distal smooth exine and very low sculptural elements larger in the central proximal area.

Ellipsovelatisporites plicatus Klaus, 1960

Fig. 7.6–7

Remarks. According to Scheuring (1970) *E. rugosus* differs from *E. plicatus* by its bigger proportions and subcircular corpus, as well as by a distinctive distal sulcus and the sculpture more prominent on the corpus.

Enzonasporites vogens Leschik, 1955

Fig. 7.8–9, 12, 13–15

Remarks. This species described by Leschik (1955) and Scheuring (1970) from Carnian to Rhaetian assemblages of Switzerland was later identified by Dolby and Balme (1976) in the Carnarvon Basin of Australia. The type specimen of *E. vogens* (Leschik, 1955, pl. 5, fig. 24) that was re-illustrated by Scheuring (1970, pl. 27, figs. 220–224) possesses in optical section a central body surrounded by the rugulate exine forming a narrow and light zone at the equator.

Equisetosporites cf. *E. tortuosus* Mädlar, 1964.

Fig. 7.16–17

Remarks. De Jersey (1971) illustrated similar specimens that were provisionally assigned to *E. tortuosus* on the basis of the smaller size of the Australian material. Although smaller, the specimen described by Zavattieri (1991) as *Equisetosporites* sp. 2, are similar to those illustrated here.

Equisetosporites steevesi (Jansonius) de Jersey, 1968

Fig. 7.18–19

Remarks. According to Zavattieri and Rojo (2005) *E. cacheutensis* Jain could be considered to be a junior synonym of *E. steevesi* (Jansonius) de Jersey because they share the same morphologic characteristics, but these authors maintain both species. Although the exine of the *E. steevesi* was described as single layered by Jansonius (1962); de Jersey (1968) suggested this difference is preservational; therefore the former name is used.

Falcisporites nuthallensis Balme, 1970

Fig. 7.26

Falcisporites cf. *F. zapfei* (Potonié & Klaus) Leschik, 1956

Fig. 7.24–25

Remarks. The specimens from the Valle de la Luna Member are similar to those illustrated by Klaus (1963) as *Falcisporites zapfei*, and coincide with the interpretation of the species presented by de Jersey and McKellar (2013).

Lueckisporites cf. *L. singhii* Balme, 1970

Fig. 7.27

Remarks. Rare specimens of this taeniate bisaccate pollen are similar to *L. singhii* Balme but differ in their narrower cappula and the cappa divided in two by a narrow cleft.

Lunatisporites noviaulensis (Leschik) Foster, 1979

Minutosaccus sp.

Remarks. Rare specimens of small bisaccate pollen were recognized in the assemblages. Some of them have been assigned to *M. crenulatus* Dolby & Balme by Césari and Colombi (2013) but a reexamination casts doubts on the presence of this Norian Australian species.

Ovalipollis pseudoalatus (Thiergart) Schuurman, 1976

Fig. 8.1–2

Remarks. This species was originally reported from Lower Jurassic strata but it is a common element in most assemblages from the Late Triassic of Europe. Schuurman (1976) placed all the later, validated species into synonymy with *O. pseudoalatus*. Dolby and Balme (1976) reported the genus in Australia from the *S. speciosus* and *S. quadrifidus* Zones.

Ovalipollis ovalis Krutzsch emend. Scheuring, 1978

Fig. 8.3

Remarks. This species identified by Dolby and Balme (1976) in the late Triassic of the Carnarvon Basin (Australia), is characterized by its large size (total breadth greater than 100 µm). Although in the same year Schuurman (1976) considered *O. ovalis* a synonym junior of *O. pseudoalatus*, the species *ovalis* was emended by Scheuring (1978) and considered valid by many authors.

Patinasporites densus Leschik, 1955

Fig. 8.4, 7–9

Remarks. The Argentinean specimens are similar to those illustrated by Leschik (1955) and Scheuring (1970). Under optical and scanning electron microscopes the exine is distinctively rugulate (Fig. 5.9) forming at the equator a wide zone usually denser than the central body. Dolby and Balme (1976) included this species in the genus *Enzonasporites* and characterized it as possessing a thicker exine than *E. vogens*.

Platysaccus queenslandi de Jersey, 1962

Fig. 8.12–13

Partitisporites spp.

Fig. 8.5–6, 10–11, 14

Remarks. Rare subcircular specimens of 40–46 µm in diameter with a subequatorial furrow that divides the pollen in two parts, grading from specimens with exine sculptured by low verrucae to almost smooth and, are referred to *Partitisporites* Leschik. Van der Eem (1983) defined the *Partitisporites novimundanus* morphon including the species *Partitisporites novimundanus* Leschik, "*Paracirculina*" *verrucosa* Praehauser-Enzenberg and *Praecirculina granifer* (Leschik) Klaus. All the components have a subequatorial furrow, sexine ornamented, small trilete mark and a sexinal thinning at the distal pole. These characteristics are variable through of transitional specimens of this complex. The specimens from Ischigualasto Formation are similar to those illustrated by Van der Eem (1983) but insufficient in number to characterize individual species with precision.

Pteruchipollenites sp.

Fig. 8.15–16

Protohaploxylinus samoilovichii (Jansonius) Hart, 1964

Fig. 8.17

Quadraeculina anellaformis Maljavkina, 1949

Fig. 8.18

Remarks. Although represented by few specimens, this distinctive protosaccate pollen (Batten and Dutta, 1997) of the Late Triassic–Middle Jurassic assemblages from northwestern Europe is identified for the first time in the Late Triassic of Argentina.

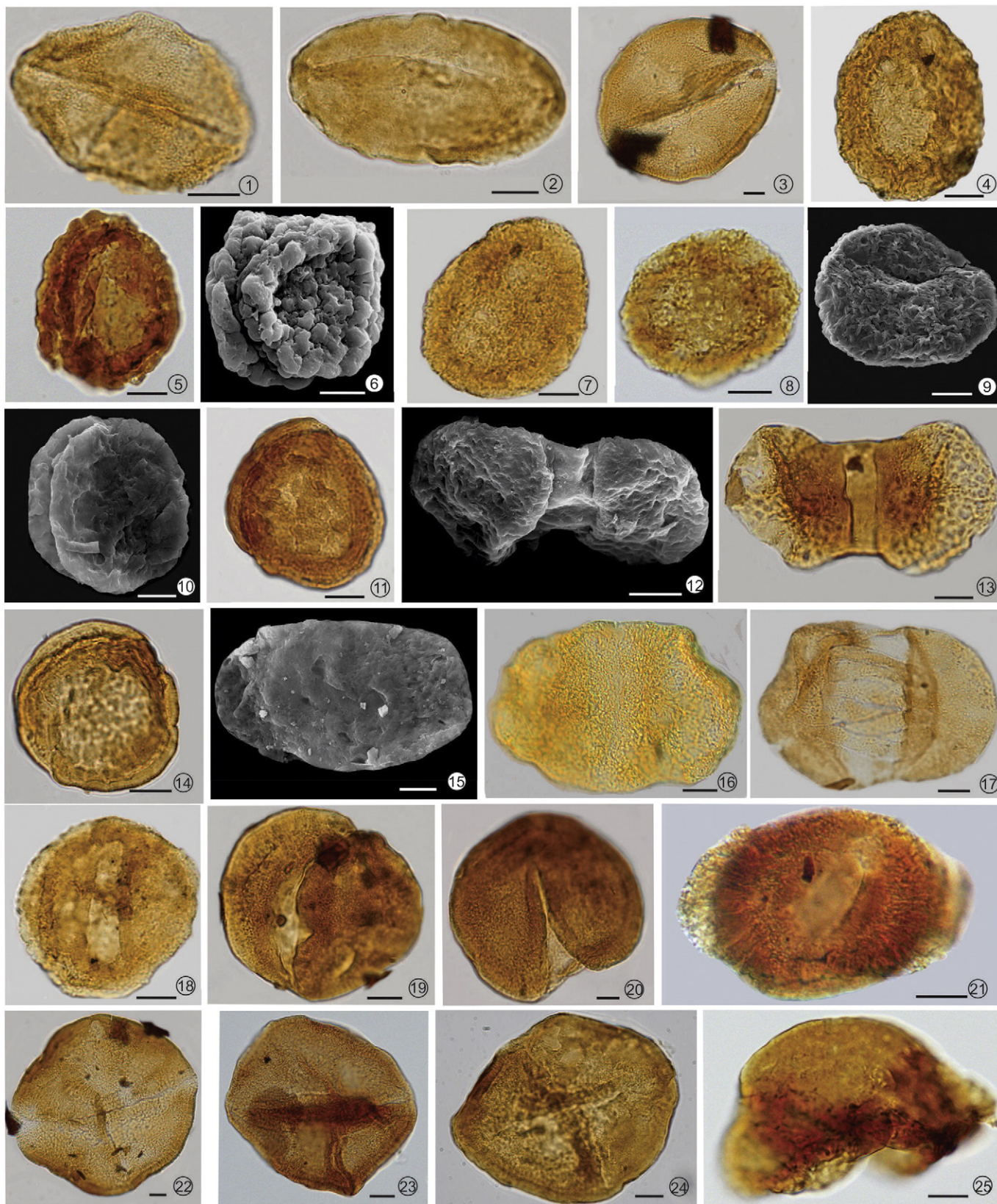


Fig. 8. 1–2. *Ovalipollis pseudoalatus* (Thiergart) Schuurman; 3. *Ovalipollis ovalis* Krutzsch; 4, 7–9. *Patinasporites densus* Leschik; 12–13. *Platysaccus queenslandi* de Jersey; 5–6, 10–11, 14. *Partitisporites* sp.; 15–16. *Pteruchipollenites* sp.; 17. *Protophaploxypinus samoilovichii* (Jansonius) Hart; 18. *Quadraeculina anellaformis* Maljavkina; 19–20 “*Rimaesporites*” *aquilonalis* Goubin; 21, 25. *Samaropollenites speciosus* Goubin; 22–24. *Staurosaccites quadridus* Dolby. Scale = 10 μ m.

“*Rimaesporites*” *aquilonalis* Goubin, 1965 (= *Vesicaspora fuscus* (Pautsch) Morbey, 1975)
Fig. 8.19–20

Remarks. Several species of this type of pollen have been included in the literature into different genera: *Rimaesporites* Leschik, *Lorisporites* Leschik, *Saeptasporites* Leschik, *Cedripites* Wodehouse,

Vesicaspora (Schemel) Wilson & Venkatachala, and *Brachysaccus* Mädlér. Scheuring (1974) revised the holotype of *Rimaesporites potoniei*, type species of the genus originally described by Leschik (1955). As a result of this revision, Scheuring (1974) advised against use of the genus because the holotype is embedded in lateral view and secondarily folded. Furthermore, according to Scheuring, the features of the proximal hemisphere are indistinguishable. Jain (1968) emended the genus *Lorisporites* Leschik and considered *Rimaesporites* and *Saeptasporites* as junior synonyms. Jain (1968), following Bharadwaj and Singh (1964), proposed that the three genera are based on different specimens of the same species compressed in different planes during preservation.

Similar specimens from the Argentinean Triassic Potrerillos Formation were described by Zavattieri and Volkheimer (1992) as *Cedripites* cf. *priscus* Balme. These authors considered that the specimens referred to cf. *R. aquilonalis* by Dolby and Balme (1976) differ in their greater size (75–156 µm) and larger sacci. Ottone et al. (1992) described *Cedripites* sp. from the Argentinean Rancho de Lata Formation, which closely resembles the specimens described in Dolby and Balme (1976) as well as *Cedripites priscus* Balme, from the Upper Permian of Pakistan (Balme, 1970). However, Ottone et al. (1992) suggested the possibility that all of these forms constitute a single morphospecies of *Cedripites*-type pollen grains. *Cedripites tectus* Ottone and Rodríguez Amenábar (2001) from the middle–late Triassic of Argentina differs from *R. aquilonalis* in its longitudinally oval outline, subrhomboidal corpus and narrower cappula. The use of the genus *Cedripites*, which is based on a single specimen from the Eocene of the United States, seems unsuitable for the Triassic pollen.

On the other hand, Morbey (1975) referred this type of pollen to *Vesicaspora* (Schemel) Wilson & Venkatachala including in synonymy *Sulcatisporites* (Leschik) Mädlér and *Brachysaccus* Mädlér. *V. fuscus* (Pautsch) Morbey was described with wide intraspecific variation in the shape of the ca. 100 specimens measured, ranging from oval, circular or quadrangular. *Brachysaccus* was interpreted by Potonié (1970) and de Jersey (1972) as monosulcate pollen with an endoreticulate exine.

The presence or absence of a cleft in the type specimens of *R. aquilonalis* is not considered a characteristic sufficient to discard the use of this Gondwanan species. Thus, in order to highlight the similarities between palynofloras, the original nomination of Dolby and Balme (1976) is maintained, while recognizing their very probable synonymy with the northern species *Vesicaspora fuscus* (Pautsch) Morbey.

R. aquilonalis, originally described by Goubin (1965) from the Middle Triassic of Madagascar, was later recognized in Australia by Dolby and Balme (1976). According to Backhouse et al. (2002) it is a common component in the *S. speciosus* Zone and a rare species throughout the *M. crenulatus* Zone and the *A. reducta* Zone.

Samaropollenites speciosus Goubin, 1965

Fig. 8.21, 25

Remarks. Although few specimens have been identified in the assemblages, they are identical to those illustrated by Dolby and Balme (1976). Originally described from the Late Triassic of Madagascar (Goubin, 1965), Dolby and Balme (1976) selected this species in the identification of the homonymous biozone in Australia.

Staurosaccites quadrifidus Dolby in Dolby and Balme, 1976

Fig. 8.22–24

Remarks. Some specimens closely similar to *S. quadrifidus* have been identified, which may be included in the *Staurosaccites quadrifidus*/*Ovalipollis pseudoalatus* complex proposed by Brugman et al. (1994) that contains intermediate forms between the two species. This is the first mention of the species in Argentinean assemblages.

Steevesipollenites claviger de Jersey and Raine, 1990

Fig. 9.2–3

Remarks. According to Australian records this species characterizes the Carnian assemblages (de Jersey, 1970, 1974) and has been also recognized in the Late Triassic from Argentina (Zavattieri and Rojo, 2005) and New Zealand (de Jersey and Raine, 1990).

Striatoabieites aytugii Visscher emend. Scheuring, 1970

Fig. 9.9–14

Remarks. Visscher (1966) described the species with a central transversely oval body bearing 10–14 taeniae and slightly, to strongly diploxylonoid sacci that are widely separated and distally inclined. Scheuring (1970) emended this species to include larger specimens with 6–12 taeniae and remarked upon the presence of distal leptoma (cappula). The specimens studied here, like the holotype, show a steep, narrow, medial furrow dividing the taeniae in two sets. Rare specimens have a subcircular central body as illustrated by Visscher (1966, plate 14, fig. 4). In the Triassic of Argentina, Zavattieri (1991) recognized the species in the Las Cabras Formation. Zavattieri and Volkheimer (1992) described as *S. cf. S. aytugii* specimens that display minor differences in the exine of the taeniae compared to the original species. *S. rarus* (Bharadwaj and Saluja) Balme, 1970 is distinguished by its more diploxylonoid sacci and a fewer taeniae. *Striatoabieites multistriatus* is a similar Permian form that has 10–23 taeniae, more reduced sacci and, usually, a haploxylonoid amb.

Triadispora plicata Klaus, 1964

Fig. 9.1

Remarks. Zavattieri (1991) referred some specimens from the Triassic of Argentina to *Triadispora* cf. *plicata*.

Vallasporites ignacii Leschik, 1955

Fig. 9.4–8

Remarks. According to Scheuring (1970) this species is distinguished from *Patinasporites densus* by the thickness and sculpture of the exine. This author remarked the usual presence of secondary deformation of the exine that leaves open the question of whether a clearly defined trilete mark exists. A possible trilete mark is visible in the Argentinean specimens when observed by optical and scanning microscopes. The rugulate exine as seen by SEM is similar to the illustrations by Achilles and Schlatter (1986).

Zonalasporites cinctus Leschik, 1955

Fig. 9.8

Remarks. Scheuring (1970) distinguished *Zonalasporites cinctus* Leschik from the *Enzonalasporites*/*Patinasporites* complex by the presence of a trilete lesurae. This is the first record of this Late Triassic species in Argentina.

4.3. Algae

Botryococcus cf. *B. braunii* Kützing, 1849

Remarks. Algal colonies of *Botryococcus* cf. *B. braunii* Kützing are usual components of the assemblages.

5. Age and comparisons

The Ischigualasto Formation is one of very few continental Triassic successions that yield reliable radioisotopic ages. Dated horizons occur near the bottom and top of the formation, placing it between ~231.4 and ~225.9 Ma (Rogers et al., 1993; Martínez et al., 2011), corresponding to the Carnian–Norian interval and with a ~5 Ma depositional interval. Recently, Kent et al. (2014) constrained the deposition of the Los Colorados Formation to the Norian, thereby restricting the majority of the Ischigualasto Formation to the Carnian. The stratigraphic range of

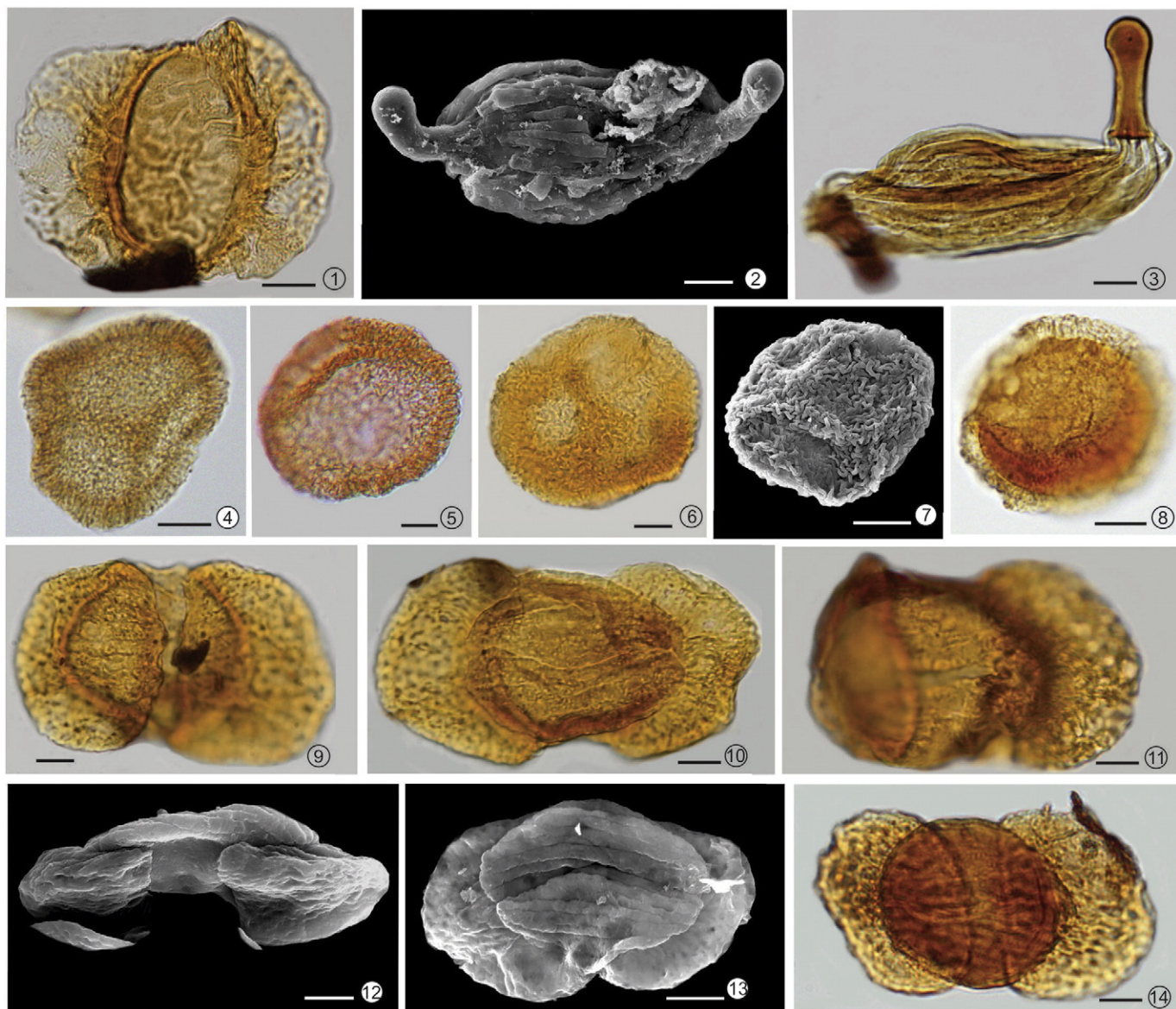


Fig. 9. 1. *Triadispora plicata* Klaus; 2–3. *Steevesipollenites claviger* de Jersey & Raine; 4–7. *Vallasporites ignacii* Leschik; 8. *Zonalasporites cinctus* Leschik; 9–14. *Striatoabieites aytugii* Visscher emend. Scheuring. Scale = 10 μm .

the diagnostic species recognized in the palynological assemblages described here supports the inferred Carnian age for the Ischigualasto Formation and suggests that the Valle de la Luna Member may reach the earliest Norian (Table 1).

Triassic palynofloras from the Southern Hemisphere were formerly studied in detail mainly in Australia where Dolby and Balme (1976) defined a warm temperate Onslow Microflora (Western Australia) and a cool temperate Ipswich Microflora (eastern Australia). The Onslow Microflora is distinguished by a greater number of species shared with the European Tethyan region and more diverse pollen grains. Foster et al. (1994) selected *Aulisporites*, *Camerosporites*, *Minutosaccus*, *Infernopollenites*, *Ovalipollis*, *Staurosaccites*, *Samaropollenites* and *Enzonalasporites* as the most characteristic northern taxa of the Onslow Microflora. De Jersey and Raine (1990) suggested that the distribution of several species in the New Zealand–Australian area was controlled by paleoecological factors. The Onslow Microflora was interpreted as derived from low-latitude, warm-temperate plant associations and a few cosmopolitan species seemingly uncontrolled by paleolatitude. On the other hand, Van der Eem (1983) considered the presence of Gondwanan species in Late Triassic European assemblages the consequence of

dispersal of their parent plants from southern areas during a humid climatic phase.

5.1. Australian, East Indian and East African assemblages

Helby et al. (1987) proposed the *Falcisporites* Superzone, encompassing palynofloras ranging from the Late Permian to latest Triassic. This zone occurs throughout Australia, but varying degrees of provinciality in the Middle to Late Triassic sequences are identified on the basis of distinctive Tethyan elements in the palynofloral associations. Therefore, the *Staurosaccites quadrifidus* Oppel Zone (late Anisian to Ladinian) occurs extensively in Western Australia but is restricted in Eastern Australia. This zone is characterized by the occurrence of *Enzonalasporites vogens* and *Aulisporites astigosus* among other species. In Western Australia, the succeeding *Samaropollenites speciosus* Oppel Zone of Carnian age is dominated in some samples by *Enzonalasporites vogens* and/or *Samaropollenites speciosus*. The first appearances of *Craterisporites rotundus*, *Semiretisporis denmeadi* and *Cadargasporites reticulatus* are identified in this biozone. In the same region, the Norian *Minutosaccus crenulatus* Oppel Zone is distinguished at the base by a

Table 1
Stratigraphic ranges of selected species.

	Ladinian	Carnian	Norian	Rhaetian
<i>Annulispora folliculosa</i>	—			
<i>Cadargasporites reticulatus</i>				
<i>Cadargasporites baculatus</i>				
<i>Cadargasporites granulatus</i>				
<i>Chordasporites singulichorda</i>				
<i>Cycadopites stonei</i>				
<i>Ellipsovelatisporites plicatus</i>	—			
<i>Enzonalsporites vigens</i>	—			
<i>Ovalipollis pseudoalatus</i>	—			
<i>Patinasporites densus</i>				
<i>Quadraeculina anellaeformis</i>				
<i>Rogalskiasporites cicatricosus</i>				
<i>Samaropollenites speciosus</i>		—		
<i>Staurosaccites quadrifidus</i>				
<i>Steevesipollenites claviger</i>				
<i>Vallasporites ignacii</i>				
<i>Striatoabieites aytugii</i>				

marked decline in the dominance of *E. vigens*, *S. speciosus* and other Tethyan forms, and an increase in *F. australis*. Finally, the appearance of *Corollina* spp. characterizes the Rhaetian *Ashmoripollis reducta* Opeel Zone.

Carnian eastern Australian assemblages are included in the *Craterisporites rotundus* Opeel Zone and are distinguished by the first occurrences of the eponymous species, *Cadargasporites reticulatus* and *Semiretisporis denmeadi*. The succeeding Norian *Polycingulatisporites crenulatus* Opeel Zone is characterized at the top by the presence of *Ceratopores helidonensis* and an increase of *Corollina torosa*.

The Carnian Assemblage A from East India, defined by Tripathi and Raychowdhuri (2005) has been correlated with the *Rimaesporites potoniei* Palynozone of South Rewa (Maheshwari et al., 1978) and the *Rimaesporites potoniei/Samaropollenites speciosus* Assemblage zone of the Krishna-Godavari Basin (Prasad, 1997).

Hankel (1987) recognized the *Staurosaccites quadrifidus* Microflora, *Samaropollenites speciosus* and *Minutosaccus crenulatus* Microflora of Carnian–early Norian age in the Luwegu Basin (East Africa). These palynofloras were correlated with those defined by Dolby and Balme (1976) in Western Australia.

The distribution of selected late Carnian–early Norian diagnostic species using a combination of cluster analysis and detrended correspondence analysis (DCA) suggests a close relationship between the palynofloras of the Ischigualasto Formation and the Onslow palynofloras from Australia, India and East Africa (Césari and Colombi, 2013). The diagnostic species shared with these Onslow palynofloras include: *Ellipsovelatisporites*, *Enzonalsporites complex*, *Ovalipollis pseudoalatus*, *Samaropollenites speciosus*, and *Staurosaccites quadrifidus*.

5.2. Argentinean assemblages

The Triassic palynological record of Argentina extends from the Lower to Upper Triassic, including the assemblages from Puesto Viejo, Las Cabras, Potrerillos, Cacheuta, Santa Clara, Ischichuca, Los Rastros, Cerro Puntudo, Chihuido, Comallo, El Tranquilo, Paso Flores and Rancho de Lata formations (see references in Zavattieri and Batten, 1996; Zavattieri and Mego, 2008). Traditionally, these palynofloras have been referred to the Ipswich phytogeographic province based on the absence of Tethyan species.

Among the Late Triassic palynofloras, Zavattieri and Rojo (2005) analysed the palynological content of the upper section of the Potrerillos Formation and basal levels of the Cacheuta Formation in Mendoza Province. The palynological assemblages were referred to the early Late Triassic (Carnian) and were also correlated with the southern and southeastern Australian assemblages included in the Ipswich Microflora. A Carnian age was also proposed for the Los Rastros Formation

(Zavattieri and Batten, 1996) and later studies by Ottone et al. (2005) referred the palynofloras to the Late Triassic without further precision. Zavattieri (1990) considered palynofloras from the Las Cabras Formation to be distinguished by the presence of several northern species in low proportion, and to be late Anisian–early Carnian in age.

Zavattieri and Mego (2008) described two well-preserved assemblages from the type locality of the Paso Flores Formation, in the Estancia Paso Flores area (northern Patagonia). The palynofloral assemblages were correlated compositionally and chronostratigraphically with the *Craterisporites rotundus* Opeel Zone of eastern Australian continental sequences. Zavattieri and Mego (2008) proposed a Late Triassic (late Carnian–early Norian) age for these assemblages. The previously recorded palynoflora from the Comallo Formation, in the Comallo area, northern Rio Negro Province, North Patagonian Massif (Zavattieri et al., 1994) was considered equivalent in age.

All of the above mentioned palynological assemblages are characterized by the apparent absence of the typical Tethyan species that distinguish the Onslow Microflora. However, given that few samples (relative to the sampled thicknesses) from these palynofloras were studied, the possibility that those species may be present in low numbers, hampering their identifications, cannot be ruled out.

5.3. Northern assemblages

Cirilli (2010) reviewed the Carnian palynological assemblages from the Northern Hemisphere. These palynofloras were characterized by an important increase in species of the Circumpollid genera, such as *Camerosporites secatus*, *Duplicisporites granulatus*, *Paracirculina scurrilis*, *Praecirculina granifer*, and the monosaccate pollen *Patinasporites densus*. In the European region, the Carnian is distinguished by the occurrence of *Ovalipollis pseudoalatus*, *Camerosporites secatus*, *Duplicisporites granulatus*, *Ellipsovelatisporites plicatus*, *Enzonalsporites vigens*, *Infernopollenites* spp. and *Triadispora* spp.

The *Camerosporites secatus* phase defined by Visscher and Krystyn (1978) has been recorded in diverse palaeofloristic areas: the Alpine Triassic of Europe, southern Albania, Israel, Africa, Tunisia, United States, Arctic Canada, Australia and Timor (Cirilli, 2010). The first appearance of *Patinasporites densus* and *Vallasporites ignacii* marks the base of the Carnian. The top of the *Camerosporites secatus* phase is defined by the first occurrence of *Paracirculina quadruplicis* and *Samaropollenites speciosus*.

In particular, the Circum-Mediterranean palynofloras (Central Tunisia, north-western Sicily, southern Albania, north-western Libya and southern Israel) and the Onslow microfloras have been considered two distinct units (Dolby and Balme, 1976; Visscher and Van der Zwan, 1981; Foster et al., 1994). However, Buratti and Cirilli (2007) analysed the similarities between the assemblages from Timor and the Circum-Mediterranean and discarded the concept of two distinct Circum-Mediterranean and Onslow microfloras. They likely reflect a homogeneous parent flora that grew under warm climatic conditions.

Litwin et al. (1991) proposed three biozones for the Late Triassic North American palynofloras of the Chinle Formation. The Carnian Zone 1 is marked by abundant *Brodispora striata*, *Equisetospores chinleanus*, *Lagenella martini*, *Minutosaccus crenulatus*, *Samaropollenites speciosus* and the LAD of *Lunatisporites* aff. *L. noviaulensis*. Zone 2 has close similarities to European palynofloras and was referred to the Tuvanian. The last appearance of *Brodispora striata*, *Camerosporites secatus*, *Equisetospores chinleanus* and *Lagenella martini* along with the first occurrence of *Camerozonosporites rudis*, *Enzonalsporites vigens*, *Heliosaccus dimorphus*, *Ovalipollis ovalis* and *Pseudoenzonalsporites summus*, among other species, characterize Zone 2. The subsequent Zone 3 was considered early Norian in age and distinguished by the presence *Camerosporites verrucosus* and *Kyrtomispores* spp. However, new precise radioisotopic age constrains and detailed palynological analysis, suggest that the Chinle Formation palynomorphs are likely Norian to Rhaetian in age (Lindström et al., 2016).

The Norian palynofloras from the Middle East show affinity with the Gondwanan palynofloras (e.g. Eastern Australia and New Zealand) while the European assemblages share taxa with the Boreal realm (Cirilli, 2010). Key Austrian sections that documented the Norian–Rhaetian boundary are characterized by lower assemblages containing typical Carnian species such as *Ellipsovelatisporites rugosus*, *Enzonalasporites vigens*, *Partitisporites* spp., *Patinasporites toralis*, *Triadispora* spp. and *Vallasporites ignacii*. According to Cirilli (2010) some species such as *Enzonalasporites vigens*, *Patinasporites densus* and *Vallasporites ignacii* disappear during the latest Norian in Europe.

The following species are common to the northern assemblages and the material studied here: *Anapiculatisporites spiniger*, *Chordasporites singulichorda*, *Ellipsovelatisporites plicatus*, *Enzonalasporites vigens*, *Lueckisporites* cf. *L. singhii*, *Ovalipollis pseudoalatus*, *O. ovalis*, *Patinasporites densus*, *Samaropollenites speciosus*, *Striatoabieites aytugii*, *Triadispora plicata*, *Vallasporites ignacii* and *Zonalasporites cinctus*.

6. Associated plant assemblages

Spalletti et al. (2003) performed a valuable synthesis of worldwide Triassic phytogeography. Laurasia, the only realm recognized in the North Hemisphere, was divided into an extraequatorial area (Siberian-Canadian) and a tropical area composed of the European, Central Asia and East Asia provinces (Meyen, 1987; Dobruskina, 1993). The European-Sinica area is defined by the presence of Peltaspermeaceae together with Bennettitales, Caytoniales, Czekanowskiales, Ginkgoales, Cycadales, Marattiales, ferns, sphenophytes, Voltziaceae, and possibly Pinaceae and Podocarpaceae. During the middle–late Triassic, the laurasic Peltaspermeaceae were significant components of the flora and in both areas the *Dellephyllum* (= *Scytophyllum*) and the *Lepidopteris* Floras characterize the Ladinian-Carnian and Norian-Rhaetian respectively.

According to Spalletti et al. (2003) North America may be a distinct province within Laurasia. Although it shares many genera with Eurasia (*Selaginellites*, *Neocalamites*, *Equisetites*, *Todites*, *Phlebopteris*, *Clathropteris*, *Pseudoctenis*, *Zamites*, *Otozamites*, *Brachyphyllum*, *Voltzia*) it differs in having endemic taxa like *Dinophyton*, *Marcouia*, and *Eoginkgoites*, and in the significant absence of Peltaspermeaceae, Ginkgoales and Czekanowskiales.

The Gondwana realm included two areas: the tropical area characterized by the Onslow palynofloras and the extratropical area distinguished by the Ipswich palynofloras and “*Dicroidium*” macrofloras

Table 2
List of plant species from the Ischigualasto Formation corresponding to different families of the class Sphenopsida, Filicopsida and Gymnospermopsida.

SPECIES	FAMILY/ORDER	CLASS
<i>Neocalamites carrerei</i> (Seiller) Halle	Apocalamitaceae	Sphenopsida
<i>Cladophlebis mendozaensis</i> (Geinitz) Frenguelli	Osmundaceae	Filicopsida
<i>Dicroidium lancifolium</i> (Morris) Gothan <i>Dicroidium odontopteroides</i> (Morris) Gothan <i>Zuberia papillata</i> (Townrow) Artabe <i>Zuberia zuberi</i> (Szajnocha) Frenguelli <i>Johnstonia coriacea</i> (Johnston) Walkom <i>Johnstonia stelzneriana</i> (Geinitz) Frenguelli <i>Xylopteris argentina</i> (Kurtz) Frenguelli <i>Xylopteris elongata</i> (Carruthers) Frenguelli <i>Rhexoxylon piatnitzkyi</i> Archangelsky & Brett emend. Brett	Corystospermaceae	Gymnospermopsida
<i>Lepidopteris stomburgensis</i> (Seward) Townrow <i>Scytophyllum neuburgianum</i> Dobruskina	Peltaspermeaceae	
<i>Micheliltoa waltonii</i> Archangelsky & Brett	Zamiaceae	
<i>Yabeiella</i> sp. <i>Yabeiella brackebuschiana</i> <i>Yabeiella mareysiacae</i>	Gnetales	
<i>Pterophyllum</i> sp.	Cycadeoidales	
<i>Taeniopteris</i> sp.	Cycadal?	
<i>Ginkgoites</i> sp.	Ginkgoales	
<i>Heidiphyllum elongatum</i> (Morris) Retallack	Voltziaceae	
<i>Araucarioxylon</i> sp.	Araucariaceae	
<i>Protouniperioxylon ischigualastensis</i> Bonetti	Protopinaceae	

(De Jersey and Raine, 1990). According to Artabe et al. (2003) the floras from the Tropical Area of Gondwana extended to the Tethys margins under the influence of a humid and warm climate and are characterized by floras with *Dicroidium* and *Glossopteris* species. The presence of some Indian floras composed of Glossopteridales associated with Peltaspermeaceae and Corystospermaceae (Pal, 1984; Maheshwari, 1991; Pal and Ghosh, 1997), may be the consequence of warmer and more humid paleoclimatic conditions than in the Gondwana Extratropical area. Indian assemblages were characterized by the absence of *Pachydermophyllum*, *Linguifolium*, *Asterothecaceae* and *Dipteridaceae* as well as the presence of Peltaspermeaceae different from that found in the extratropical area.

The floras from both areas share Corystospermaceae (*Dicroidium*, *Johnstonia* and *Xylopteris*), several Peltaspermeaceae, Voltziaceae (*Heidiphyllum elongatum*) and the genera *Cylostrobus*, *Pleuromeia* and *Yabeiella*. The assemblages from the Extratropical Area are distinguished by the genera: *Rienitsia*, *Dejerseya*, *Kurtziana*, *Voltziopsis* and *Linguifolium* together with 35 endemic species (Artabe et al., 2003). Endemism is also represented by species of many genera with worldwide geographic distribution (*Pleuromeia*, *Phyllothea*, *Equisetites*, *Neocalamites*, *Cladophlebis*, *Asterotheca*, *Chansithea*, *Gleichenites Coniopteris*, *Lepidopteris*, *Scytophyllum*, *Pachydermophyllum*, *Saportaea*, *Ginkgoites*, *Baiera* and *Sphenobaiera*.

Based on the phytogeographic distribution of some families, Artabe et al. (2003) recognized two provinces: the southwest province (identified in Brazil, Chile, Argentina and South Africa) and the south-east province (Antarctica and Australasia).

The paleofloristic assemblages of the Ischigualasto Formation have been included in the BNP Biozone (*Yabeiella brackebuschiana*/*Scytophyllum neuburgianum*/*Rhexoxylon piatnitzkyi*) also recognized in the Cuyo Basin (Potrerillos Formation), Los Menucos (Vera Formation) and in southern Patagonia (El Tranquilo Group) by Spalletti et al. (1999). This biozone is part of the Cortaderitian Stage when the ‘*Dicroidium* Flora’ reaches its maximum diversity (Anderson et al., 1999, Spalletti et al., 1999, Zamuner et al., 2001), with the adaptative radiation of Corystospermaceae, Peltaspermeaceae and Cycadales. With 131 species, the BNP possesses the greatest Triassic biodiversity, after which 80 taxa were extinguished, representing an extinction event during the Cortaderitian stage, with the disappearance of 61.53% of the taxa (Artabe et al., 2007). Corystosperms dominate most floristic assemblages in which Peltaspermales, such as *Scytophyllum* and *Yabeiella* appear. The greatest biodiversity of corystosperm stems is recorded during the late Middle Triassic–early Late Triassic (three genera and five species). The Cortaderitian flora is closely correlated to the Laurasian ‘*Scytophyllum* Flora’. According to Spalletti et al. (2003) the diversification of the flora coincides with a megamonsoonal seasonal climatic regime (dry subtropical) under which evergreen forests of Corystospermaceae and Peltaspermeaceae flourished.

In particular, twenty-three species have been recognized in the Ischigualasto Formation and their botanical affinities are given in Table 2.

7. Paleoecological implications

The qualitative composition of the palynological assemblages is relatively uniform; this is consistent with the spacing between samples. Representatives of the *Enzonalasporites* complex, *Ovalipollis* spp. and *Striatoabieites aytugii* are present in all the samples albeit the first two in low proportions. *Samaropollenites speciosus* is a rare component, as are *Quadraeculina anellaeformis*, *Cycadopites stonei*, *Limatulasporites limatulus* and *Partitisporites* spp., which are identified by few specimens.

The paleobotanical affinities of the main genera identified in the palynofloras of the Ischigualasto Formation and their possible environmental conditions are summarized in Table 3. Corystospermaceae, represented by the abundant bisaccate pollen (*Alisporites*), are considered meso-xeromorphic plants that exhibited adaptations to seasonal

climate based on the morphology and anatomical features of roots, stems and leaves (Artabe et al., 2001). Whiteside et al. (2015) considered that *Alisporites* is more abundant in the more humid subenvironments within the Norian-Rhaetian Chinle Formation, which was deposited under semiarid climatic conditions.

The climate during the deposition of the Ischigualasto Formation has been reconstructed based on a variety of observations (i.e., fluvial architecture; paleosols; plant and vertebrate taphonomy), but all methods deliver similar conclusions (Tabor et al., 2006; Colombi and Parrish, 2008; Currie et al., 2009; Colombi et al., 2011, 2012). The evidence suggests an overall seasonal paleoclimate with respect to rainfall. In the basal La Peña Member, paleoclimatic inference is complicated due to the facies transition from lacustrine (Los Rastros Formation) to fluvial depositional systems. In the Cancha de Bochas Member, an arid to semi-arid climate is suggested by the presence of calcic paleosols (Tabor et al., 2006), desiccation cracks, the absence of fossil plant remains other than roots in the margin of the river beds (Colombi and Parrish, 2008), and a dominant calcite permineralization of vertebrates (Colombi et al., 2012). In the Valle de la Luna Member, a change in paleoclimate, reflecting an increase in humidity (rainfall), is indicated by the shift from calcic paleosols to argillic paleosols (Tabor et al., 2006), an increase in aggradation rate; the preservation of abundant fossil plant remains, including mummified cuticles, petrified tree trunks, and palynomorphs (Colombi and Parrish, 2008; Césari and Colombi, 2013), and a suite of hematite, barite and silica permineralization of vertebrates. Finally, a potential return to xeric conditions in the Quebrada de la Sal Member is suggested by the absence of fossilized plant remains (Colombi and Parrish, 2008), a change in fluvial architecture and the presence of desiccation cracks.

A study of the isotopic ratios (^{13}C vs. ^{12}C) and the ratio of carbon and nitrogen (C/N) applied to the paleoflora of the Ischigualasto Formation was carried out by Colombi et al. (2011). The analysis of the isotopic values of 97 samples, mainly cuticles, documents minor variation in $\delta^{13}\text{C}$ characteristic of differences in levels of local water-stress and of floral composition variations. Discarding minor

variations, the mean carbon isotope ratio was -25.4% , within a range from -27.4 to -23.7% , according to the average values obtained from C3 plants. This value is enriched by about 3 ‰ with respect to the Middle Triassic plants.

Colombi et al. (2011) analysed the same swamp deposit palynologically studied in the current study (Fig. 4). Many samples contain abundant *Xylopteris*, *Johnstonia* and *Dicroidium* cuticles, together with stems of *Neocalamites* and millimetric conchostracans (Tassi, pers. comm.). The shallowest section (1.5 m thickness) shows a $\delta^{13}\text{C}$ average of -24.3% . The deepest section (~ 7 m thickness), a $\delta^{13}\text{C}$ average of -25.2% and in the middle deep sections (2.5 m and 2.8 m thickness) $\delta^{13}\text{C}$ averages of -24.5% and -25.2% , respectively. The gradual increase in $\delta^{13}\text{C}$ is almost 1‰ in less than 100 m of lateral extension, from the deepest section to the marginal area, which may be the result of water stress produced by seasonal drought in the margins. Under seasonal climatic conditions like those interpreted for the Ischigualasto Formation (Tabor et al., 2006; Colombi and Parrish, 2008; Currie et al., 2009), it is possible that plants would be affected by water stress. A relationship between the abundance of *Alisporites*-like pollen and average $\delta^{13}\text{C}$ is recognized in the swamp subenvironment of the Ischigualasto Formation. The deepest sample contains the lowest proportion of bisaccate *Alisporites*-like pollen (12.6%) and taeniate (5.6%) pollen, while smooth spores and inaperturates predominate. In contrast, the uppermost and shallow samples include up to 85% bisaccate and *Enzonalasporites* complex pollen and 10.3% taeniate bisaccates. Palynofloras preserved at the central part and middle depths of the swamp possess approximately 40% bisaccate pollen and 30% taeniate pollen. At the same depth but in the marginal area, samples maintain the proportion of bisaccate pollen, decrease the presence of taeniate pollen (10%) and increase the proportion of monosulcate pollen (10%).

Finally, the low proportion of C/N (46.1) obtained by Colombi et al. (2011) in the paleoflora preserved in the swamp of the Ischigualasto Formation suggests anaerobic conditions during decay and/or high bacterial activity.

8. Paleogeographic implications

Césari and Colombi (2013) proposed a new scenario for the late Triassic phytogeography, extending the presence of characteristic species of the Onslow Microflora and the Tethys area into westernmost Gondwana (Fig. 10). Traditionally, the Argentinean palynofloras have been considered representative of the Ipswich Microflora because of the absence of these northern species. However, Zavattieri and Batten (1996) considered the presence, although scarce, of some species originally described in Northern Hemisphere in Argentinean palynofloras suggestive of more cosmopolitan flora than previously supposed.

Although the palynofloras from the Valle de la Luna Member are usually dominated by bisaccate pollen and the proportion of key Tethyan and Onslow species is low, their presence relativizes the strong provincialism previously proposed for the Southern Hemisphere. Césari and Colombi (2013) selected late Carnian–early Norian diagnostic species from published records from Australia (Onslow and Ipswich assemblages), East India, East Africa, Europe, Circum-Mediterranean area, Timor, United States and those presented here. We analysed the distribution of these species using a combination of cluster analysis and detrended correspondence analysis (DCA) that revealed three distinct associations or groups. The palynofloras from the Ischigualasto Formation group with Onslow, East African and East Indian assemblages. Despite the presence of shared species, these assemblages are clearly separate from the Euramerican assemblages, which are represented by a well-defined group that includes the Circum-Mediterranean area, Europe and United States and Timor. Likewise, the Ipswich palynofloras are clearly separated from the other two clusters in the DCA results.

The current knowledge about the distribution of some Carnian Tethyan species (Cirilli, 2010; Césari and Colombi, 2013) would suggest constraining the use of the terms Onslow and Ipswich Microfloras to

Table 3

Botanical affinity and environmental interpretation of main genera recognized in the Valle de la Luna Member.

Genera	Botanical affinity	Environmental interpretation
<i>Alisporites</i>	Conifers, Corytospermales	Xerophytic
<i>Aratrisporites</i>	Lycophytes	Hygrophytic
<i>Araucariacites</i>	Conifers	Xerophytic
<i>Calamospora</i>	Sphenophytes	Hygrophytic
<i>Cadargasporites</i>	Hepatycan	Hygrophytic
<i>Chordasporites</i>	Conifers	Xerophytic
<i>Cycadopites</i>	Cycadophytes, Peltaspermales	Hygrophytic
<i>Dictyophyllidites</i>	Filicales	Hygrophytic
<i>Equisetosporites</i>	Gnetales?	Xerophytic
<i>Falcisporites</i>	Peltaspermales, conifers	Xerophytic
<i>Foveosporites</i>	Lycophytes	Hygrophytic
<i>Lophotrilletes</i>	Filicales	Hygrophytic
<i>Lueckisporites</i>	Conifers	Xerophytic
<i>Lunatisporites</i>	Conifers, Peltaspermales	Xerophytic
<i>Lundbladispota</i>	Lycophytes	Hygrophytic
<i>Osmundacidites</i>	Filicales	Hygrophytic
<i>Ovalipollis</i>	Conifers	Xerophytic
<i>Patinasporites</i>	Conifers	Xerophytic
<i>Platysaccus</i>	Corytospermales	Xerophytic
<i>Protohaploxylinus</i>	Gymnosperms	Xerophytic
<i>Retitrilletes</i>	Bryophytes	Hygrophytic
<i>Retusotrilletes</i>	Lycophytes	Hygrophytic
<i>Rimaesporites</i>	Conifers	Xerophytic
<i>Striatella</i>	Ferns	Hygrophytic
<i>Striatoabieites</i>	Conifers	Xerophytic
<i>Triadispora</i>	Conifers	Xerophytic
<i>Uvaesporites</i>	Lycophytes	Hygrophytic
<i>Botryococcus</i>	Algae	Freshwater

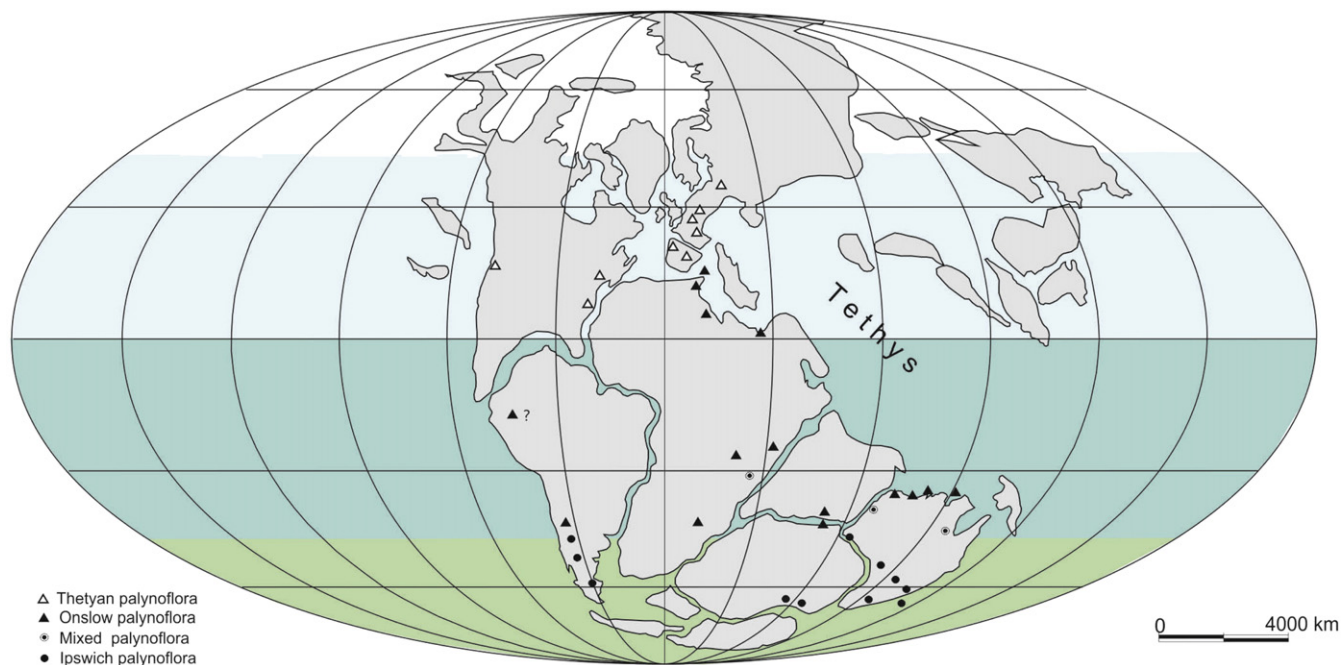


Fig. 10. Distribution of the Ipswich, Onslow, Thetyan and “Mixed” palynofloras. Modified from Dolby and Balme (1976); Foster et al. (1994); Zavattieri and Batten (1996) and Césari and Colombi (2013).

Australia and the surrounding area in future studies. These types of palynological assemblages distinguish assemblages preserved in the continental environments of the eastern region (Ipswich) from those recovered in marine-related deposits of the western region (Onslow).

The suggested relationship between marine environments and key northern species is not confirmed in the Argentinean continental deposits of the Ischigualasto Formation. Therefore, only the paleolatitudinal position, the existence of local humid conditions or simply the age of the palynofloras seem to explain the presence of these key species in assemblages containing abundant Gondwanan species. Paleolatitudinal position seems to be the most feasible factor controlling the distribution of the southernmost palynofloras that are exclusively composed of Gondwanan species and those “mixed” assemblages of the Circum-Mediterranean, Onslow and western Argentina (Césari and Colombi, 2013). Humid conditions are also linked to the presence of some species of these “mixed” palynofloras; these humid conditions characterize an event of wide geographic extension well into the Carnian interval. Coincidentally, the Valle de la Luna Member, which bearing the samples studied, is thought to have been deposited under a humid climatic pulse (Tabor et al., 2006; Colombi and Parrish, 2008). Therefore, some characteristic species of the Circum-Mediterranean area and Western Australia were cosmopolitan during the Carnian.

This type of palynoflora was probably constrained to a paleolatitudinal belt ranging from 30° to 40° S where a characteristic flora flourished during more humid conditions under a wider semiarid-arid context.

9. Conclusions

The recognition of characteristic Gondwanan palynological species together with diagnostic Carnian European species in the Valle de la Luna Member of the Ischigualasto Formation expands the distribution of the Onslow-type palynofloras.

The Valle de la Luna Member was likely deposited under more humid conditions than the rest of the Ischigualasto Formation. A swamp deposit from this Member provided the majority of the samples used in this study and an additional assemblage was recovered from the site known as “El Hongo” in the Provincial Park. All the palynofloras contain the diagnostic “Onslow” species: *Samaropollenites speciosus*, “*Rimaesporites*” *aquilonalis*, *Enzonalasporites vicens*, *Patinasporites*

densus, *Vallatisporites ignacii*, *Ovalipollis pseudoalatus* and *Cycadopites stonci*. Moreover, other Tethyan taxa are found with abundant bisaccate pollen and typical Gondwanan species. The palaeogeographic distribution of these mixed palynofloras suggests the existence of a latitudinal floral belt (30° to 40° S) from Timor (through the Circum-Mediterranean area) to western Argentina, where characteristic flora flourished during more humid conditions. The composition of the macroflora, dominated by *Corystospermales* and participation of *Peltaspermales*, has been also considered product of its paleolatitudinal position.

The stratigraphic ranges of the species support previous radiometric dating that indicates a Carnian–early Norian age for the parent flora.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.02.023>.

Acknowledgements

We are grateful to John Backhouse and J. Ian Raine for providing copies of their papers and to Guido Roghi for helpful information about *Aulisporites*. Also thanks to Kristina Curry Rogers for her revision of the English grammar, and an anonymous reviewer by the valuable suggestions.

References

- Achilles, H., Schlatter, R., 1986. Palynostratigraphische Untersuchungen im “Rhät-bonebed” von Hallau (Kt. Schaffhausen) mit einem Beitrag zur ammonitenfauna im basalen Lias. *Eclogae Geol. Helv.* 79, 149–179.
- Anderson, J.M., Anderson, H.M., Archangelsky, S., Bamford, H., Chandra, S., Dettmann, M., Hill, R., McLoughin, S., Rosler, O., 1999. Patterns of Gondwana plant colonization and diversification. *J. Afr. Earth Sci.* 28, 145–167.
- Artabe, A.E., Morel, E.M., Spalletti, L.A., 2001. In: Artabe, A.E., Morel, E.M., Zamuner, A.B. (Eds.), *Paleoecología de las floras triásicas argentinas*. In: *El Sistema Triásico en la Argentina*. Fundación Museo de La Plata “Francisco Pascasio Moreno” La Plata, pp. 199–225.
- Artabe, A.E., Morel, E.M., Spalletti, L.A., 2003. Caracterización de las provincias fitogeográficas Triásicas del Gondwana extratropical. *Ameghiniana* 40, 387–405.
- Artabe, A.E., Morel, E.M., Ganuza, D.G., 2007. Las floras triásicas de la Argentina. *Asociación Paleontológica Argentina. Publ. Especial* 11 pp. 75–86.
- Azcuy, C.L., Longobucco, M.I., 1983. Palinología de las Formaciones Potrerillos y Cacheuta, provincia de Mendoza, Argentina. *Ameghiniana* 20, 297–316.
- Backhouse, J., Balme, B.E., 2002. Late Triassic palynology of the Northern Carnarvon Basin. Minerals and Energy Research Institute of Western Australia Report No. 226 (168 pp.).

- 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: Keep, M., Moss, S.J. (Eds.), *The Sedimentary Basins of Western Australia* 3, pp. 179–201 (Proceedings of the Petroleum Exploration Society of Australia Symposium).
- Bai, Y., Lu, M., Chen, L., Long, R., 1983. Mesozoic spores and pollen. Chengdu Institute of Geology and Mineral Resources ed. Microfossil volume, Paleontological Atlas of Southwest China Beijing Geological Publishing House, pp. 520–649.
- Balme, B.E., 1963. Plants fossils from the Lower Triassic of Western Australia. *Palaeontology* 6, 12–40.
- Balme, B.E., 1970. Palynology of Permian and Triassic Strata in the Salt Range and Surghar Range, West Pakistan. In: Kummel, B., Teichert, C. (Eds.), *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*. Department Of Geology-University of Kansas, Special Publication 4, pp. 305–453.
- Batten, D.J., Dutta, R.J., 1997. Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships. *Rev. Palaeobot. Palynol.* 99, 25–54.
- Bharadwaj, D.C., Singh, H.P., 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. *Palaeobotanist* 12, 28–44.
- Brugman, W.A., Van Bergen, P.F., Kerp, J.H.F., 1994. A quantitative approach to Triassic palynology, the Lettenkeuper of the Germanic Basin as an example. Sedimentation of organic particles. Cambridge Univ. Press, Cambridge, pp. 409–429.
- Buratti, N., Cirilli, S., 2007. Microfloristic provincialism in the Upper Triassic Circum-Mediterranean area and palaeogeographic implication. *Geobios* 40, 133–142.
- Césari, S.N., Colombi, C.E., 2013. A new Late Triassic phytogeographical scenario in westernmost Gondwana. *Nat. Commun.* 4 (1889). <http://dx.doi.org/10.1038/ncomms2917>.
- Cirilli, S., 2010. Upper Triassic lowermost Jurassic palynology and palynostratigraphy: a review. *Geol. Soc.* 334, 285–314.
- Colombi, C.E., Parrish, J.T., 2008. Late Triassic environmental evolution in Southwestern Pangea. Plant taphonomy of the Ischigualasto Formation. *Palaios* 23, 778–795.
- Colombi, C.E., Fernández, E., Currie, B.S., Alcober, O.A., Martínez, R., Correa, G., 2012. Large-diameter burrows of the Triassic Ischigualasto Basin, NW Argentina: paleoecological and paleoenvironmental implications. *PLoS ONE* 7 (12), e50662. <http://dx.doi.org/10.1371/journal.pone.0050662>.
- Colombi, C.E., Montañez, I.P., Parrish, J.T., 2011. Registro de la relación isotópica de carbono en la paleoflora de la Formación Ischigualasto (Triásico Superior), noroeste argentino: implicaciones paleoatmosféricas. *Revista Brasileira de Paleontología* 14 pp. 39–50.
- Cookson, I.C., 1947. Plant microfossils from the lignites of Kerguelen Archipelago. Antarctic Research Expedition 1929–1931. Reports Series A 2 pp. 127–142.
- Couper, R.A., 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. New Zealand Geological Survey, Paleontological Bulletin 22 (77 pp.).
- Currie, B.S., Colombi, C.E., Tabor, N.A., Shipman, T.C., Montañez, I.P., 2009. Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina. *J. S. Am. Earth Sci.* 27, 74–87.
- Danzé-Corsin, J., Laveine, J.P., 1963. Étude palynologique d'une argile provenant de la limite Lias-Dogger, dans un sondage à Boulogne-sur-mer. *Ann. Soc. Géol. Nord* 83 (1), 79–90.
- de Jersey, N.J., 1959. Jurassic spores and pollen grains from the Rosewood Coalfield. Queensland Gov. Min. J. 60, 346–366.
- de Jersey, N.J., 1964. Triassic spores and pollen grains from the Bundamba Group. *Geol. Surv. Queensland Publ.* 321.
- de Jersey, N.J., 1962. Triassic spores and pollen grains from the Ipswich Coalfield. *Geol. Surv. Queensland Publ.* 307, 1–18.
- de Jersey, N.J., 1968. Triassic spores and pollen grains from the Clematis Sandstone. *Geol. Surv. Queensland, Publ.* 338, *Palaeont. Paper* 14 pp. 1–44.
- de Jersey, N.J., 1970. Triassic miospores from the Blackstone Formation, Aberdare Conglomerate and Raceview Formation. *Geol. Surv. Queensland, Publ.* 348, *Palaeont. Paper* 25 pp. 1–41.
- de Jersey, N.J., 1971. Early Jurassic miospores from the Helidon Sandstone. *Geol. Surv. Queensland, Publ.* 351, *Palaeont. Paper* 25 pp. 1–49.
- de Jersey, N.J., 1972. Triassic microspores from the Esk Group. *Geol. Surv. Qld., Publ.* 357, *Paleontol. Pap.* 32, 1–40.
- de Jersey, N.J., 1974. Palynology and age of the Callide Coal Measures. Queensland Gov. Min. J. 75, 249–252.
- de Jersey, N.J., Hamilton, M., 1967. Triassic spores and pollen grains from the Moolayember Formation. *Geol. Surv. Queensland Publ.* 136, *Palaeont. Paper* 10.
- de Jersey, N.J., McKellar, J.L., 2013. The palynology of the Triassic–Jurassic transition in Southeastern Queensland, Australia, and correlation with New Zealand. *Palynology* 37, 77–114.
- de Jersey, N.J., Paten, R.J., 1964. Jurassic spores and pollen grains from the Surat Basin. *Geol. Surv. Queensland Publ.* 322, 1–18.
- de Jersey, N.J., Raine, J.L., 1990. Triassic and earliest Jurassic miospores from the Murihiku Supergroup, New Zealand. *N. Z. Geol. Surv. Paleontol. Bull.* 62 (164 pp.).
- Dev, S., 1961. The fossil flora of the Jabalpur Series - 3. Spores and pollen grains. *Palaeobotanist* 8 (1–2), 43–56.
- Dobruskina, I., 1993. Relationships of floral and faunal evolution during the transition from the Paleozoic to the Mesozoic. In: Lucas, S.G., Morales, M. (Eds.), *The nonmarine Triassic*. New Mex. Mus. Nat. Hist. Sci. Bull. v. 3, pp. 107–112.
- Dolby, J.H., Balme, B.E., 1976. Triassic palynology of the Carnarvon Basin, Western Australia. *Rev. Palaeobot. Palynol.* 22, 105–168.
- Filatoff, J., 1975. Jurassic palynology of the Perth Basin. *Palaeontogr. Abt. B* 154, 1–113.
- Foster, C.B., 1979. Permian plant microfossils of the Blair Athol Coal Measures, Baralaba Coal Measures, and basal Rewan Formation of Queensland. *Geol. Surv. Queensland, Publ.* 372, *Palaeont. Paper* 45 244p.
- Foster, C.B., Afonin, S.A., 2005. Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian–Triassic boundary. *J. Geol. Soc.* 162 (4), 653–659.
- Foster, C.B., Balme, B.E., Helby, R., 1994. First record of tethyan palynomorphs from the Late Triassic of East Antarctica. *J. Aust. Geol. Geophys.* 15, 239–246.
- Goswami, S., Das, M., Guru, B.C., 2010. Palaeoenvironment in the Mahanadi Basin: inferences from Mesozoic plant and ichno fossils diversity. *The Ecoscan* 4 (1), 7–14.
- Goubin, N., 1965. Description et répartition des principaux pollenites Permiens, Triasiques et Jurassiques des sondages du bassin de Morondava (Madagascar). *Rev. l'Inst. Français Pétrol.* 20(10) pp. 1415–1461.
- Hankel, O., 1987. Lithostratigraphic subdivision of the Karoo rocks of the Luwegu Basin (Tanzania) and their biostratigraphic classification based on microfloras, macrofloras, fossil woods and vertebrates. *Geol. Rundsch.* 76, 539–565.
- Hart, G.F., 1964. A review of the classification and distribution of the Permian miospore: *Disaccitii Striatiti*. *Comptes Rendus 5e. Congrès International de Stratigraphie et Géologie Carbonifère*, Paris, pp. 1171–1199.
- Helby, R., 1987. Three Late Triassic palynomorphs from Northwestern Australia. *Mem. Assoc. Australas. Palaeontol.* 4, 95–100.
- 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 Palaeontologists* 4, pp. 1–94.
- Herbst, R., 1965. Algunos esporomorfos 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 triletes. *Ameghiniana* 9, 280–288.
- Hiltmann, W., 1967. Über die Sporenführung des kernprofils der bohrung contern FG 11 (unterer Lias, Luxemburg). *Publ. Serv. Géol. 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 B* 122, 1–47.
- Jansonius, J., 1962. Palynology of Permian and Triassic sediments, Peace River Area, Western Canada. *Palaeontogr. Abt. B* 110, 35–98.
- Jansonius, J., 1971. Emended diagnosis of *Alisporites* Daugherty 1941. *Pollen Spores* 13, 349–357.
- Kavary, E., 1972. Significant Upper Triassic microspores from Bleiberg, (Austria). *Jahrb. Geol. Bundesanst.* 19, 87–105.
- Kent, D.V., Malnis, P.S., Colombi, C.E., Alcober, 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). *Proc. Natl. Acad. Sci.* 111 (22), 7958–7963.
- Klaus, W., 1960. Sporen der karnischen stufe der ostalpinen Trias. *Jahrb. Geol. Bundesanstalt (Wien), Sonderband* 5 pp. 107–183.
- Klaus, W., 1963. Sporen aus dem südalpinen Perm. *Jahrb. Geol. Bundesanst., Wien* 106, 229–363.
- Klaus, W., 1964. Zur sporenstratigraphische einstufigung von gipsführenden schichten in bohrungen. *Erdoel-Zeitschrift* 4 pp. 119–132.
- Kützing, F.T., 1849. *Species Algarum*. Brockhaus, Leipzig (922 pp.).
- Leschik, G., 1955. Die Keuperflora von neuwelt bei Basel. II. die iso- und mikrosporen. *Schweiz. Paläontol. Abh.* 72, 5–70.
- Leschik, G., 1956. Sporen aus dem Salzton des Zechsteins von neuhof bei Fulda. *Palaeontographica B* 100, 122–142.
- Lindström, S., Irmis, R.B., Whiteside, J.H., Smith, N.D., Nesbitt, S.J., Turner, A.H., 2016. Palynology of the upper Chinle Formation in Northern New Mexico, USA: implications for biostratigraphy and terrestrial ecosystem change during the Late Triassic (Norian–Rhaetian). *Rev. Palaeobot. Palynol.* 225, 106–131.
- Litwin, R.J., 1985. Fertile organs and in situ spores of ferns from the Late Triassic Chinle Formation of Arizona and New Mexico, with discussion of the associated dispersed spores. *Rev. Palaeobot. Palynol.* 44 (1), 101–146.
- Litwin, R.J., Traverse, A., Ash, S.R., 1991. Preliminary palynological zonation of the Chinle Formation, Southwestern USA, and its correlation to the Newark Supergroup (Eastern USA). *Rev. Palaeobot. Palynol.* 68 (3), 269–287.
- López-Gamundi, O.R., Espejo, I.S., Conaghan, P.J., Powell, C.McA., 1994. Southern South America. In: *Veevers, J.J., Powell, C.McA. (Eds.), Permian – Triassic Pangean basins and fold belts along the Panthalassan margin of Gondwanaland*. *Geol. Soc. Amer., Mem.* 184, pp. 281–329.
- Mädler, K., 1964. Die geologische verbreitung von sporen und pollen in der deutschen Trias. *Beihfte zum Geologischen Jahrbuch* 65 pp. 1–147.
- Maheshwari, H.K., 1991. Provincialism in Gondwana Floras. *Palaeobotanist* 46, 101–127.
- Maheshwari, H.K., Banerji, J., 1975. Lower Triassic palynomorphs from the Maitur Formation, West Bengal. *Palaeontographica B* 152, 149–190.
- Maheshwari, H.K., Kumaran, K.P.N., Bose, M.N., 1978. The age of the Tiki Formation with remarks on the miofloral succession in the Triassic Gondwanas of India. *Palaeobot.* 25, 254–265.
- Maljalkina, V.S., 1949. Identification of spores and pollen of the Jurassic and Cretaceous. *Trudy Vsesouznyni Neftyanoi Nauchno-Issledovatel'skii Geologicheskii Institut* 33 pp. 1–137.
- Martínez, R.N., Sereno, P.C., Alcober, O.A., Colombi, C.E., Renne, P.R., Montañez, I.P., Currie, B.S., 2011. A basal dinosaur from the dawn of the dinosaur era in southwestern Pangea. *Science* 331, 206–210.
- Meyen, S.V., 1987. *Fundamentals of Palaeobotany*. Chapman and Hall, London, p. 432.
- Milana, J.P., Alcober, O., 1994. Modelo tectosedimentario de la cuenca triásica de Ischigualasto (San Juan, Argentina). *Rev. Asoc. Geol. Argent.* 49 (3–4), 217–235.
- Morby, S.J., 1975. The palynostratigraphy of the Rhaetian stage, Upper Triassic, in the Kendelbachgraben, Austria. *Palaeontographica B* 152, 1–75.

- Ottone, E.G., Rodríguez Amenábar, C.R., 2001. A new disaccate pollen grain from the Triassic of Argentina. *Ameghiniana* 38, 157–161.
- Ottone, E.G., Alvarez, P.P., Benoit, S.V., 1992. Late Triassic plant microfossils from the Rancho de Lata Formation, Main Cordillera, Argentina. *Micropaleontology* 261–278.
- Ottone, E.G., Mancuso, A.C., Resano, M., 2005. Miospores and chlorococcalean algae from the Los Rastros Formation, Middle to Upper Triassic of central–Western Argentina. *Ameghiniana* 42, 347–362.
- Pal, P.K., 1984. Triassic plant megafossil from the Tiki Formation, South Rewa, Gondwana Basin, India. *Palaeobotanist* 32 (3), 253–309.
- Pal, P.K., Ghosh, A.K., 1997. Megafloral zonation of Permian–Triassic sequence in the Kamthi Formation, Talcher Coalfield, Orissa. *Palaeobotanist* 46 (1–2), 81–87.
- Playford, G., 1965. Plant microfossils from Triassic sediments near Poatina, Tasmania. *J. Geol. Soc. Aust.* 12 (2), 173–210.
- Playford, G., Dettmann, M.E., 1965. Rhaeto-Liassic microfossils from the Leigh Creek Coal Measures, South Australia. *Senckenb. Lethaea* 46, 127–181.
- Playford, G., Rigby, J.F., Archibald, D.C., 1982. A Middle Triassic flora from Moolayember Formation, Bowen Basin, Queensland. *Geol. Surv. Queensland, Publ.* 380 pp. 1–52.
- Pocock, S.A., 1961. The microspore genus *Cingulatisporites* Thomson, 1953. *J. Paleontol.* 1234–1236.
- Potonié, R., 1970. Synopsis der Gattungen der Sporae dispersae. V. Teil: Nachträge zu allen Gruppen (Turmae). *Beih. Geol. Jahrb.* 87 (222 pp.).
- Prasad, B., 1997. Palynology of the subsurface Triassic sediments of Krishna-Godavari Basin, India. *Palaeontogr. Abt.* 242 (4–6), 1–94 (8).
- Reiser, R.F., Williams, A.J., 1969. Palynology of the Lower Jurassic sediments of the Northern Surat Basin. *Geol. Surv. of Queensland, Pub.* 399. *Palaeontol. Pap.* 15 pp. 1–24.
- Rogalska, M., 1954. Spore and pollen analysis of the Liassic coal of Blanowice in Upper Silesia. *Biuletyn Instytut Geologicznego Warszawa* 89 pp. 1–46.
- Rogers, R.R., Arcucci, A.B., Abdala, F., Sereno, P.C., Forster, C.A., May, C.L., 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), Northwestern Argentina: spectacular preservation in volcanogenic concretions. *Palaios* 16 (5), 461–481.
- Rogers, R.R., Swisher, C.C., Sereno, P.C., Monetta, A.M., Foster, C.A., Martínez, R.N., 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar dating of dinosaur origins. *Science* 260, 794–797.
- 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 (1), 3–20.
- Sajjadi, F., Playford, G., 2002. Systematic and stratigraphic palynology of Late Jurassic–earliest Cretaceous strata of the Eromanga Basin, Queensland, Australia. *Palaeontogr. Abt. B* 261, 1–165.
- Scheuring, B.W., 1970. Palynologische und palynostratigraphische untersuchungen des Keupers im bolchentunnel (Solothurner Jura). *Schweiz. Paläontol. Abh.* 88, 1–119.
- Scheuring, B.W., 1974. On the type material of *Accinctisporites* Leschik, *Succinctisporites* Leschik, *Rimaesporites* Leschik and *Sahnisporites* Bharadwaj. *Rev. Palaeobot. Palynol.* 17, 205–216.
- Scheuring, B.W., 1978. Mikrofloren aus den Meridenkalkendes Mte. San Giorgio (Kanton Tessin). *Schweiz. Paläontol. Abh.* 100, 1–205.
- Schulz, E., 1967. Sporenpaläontologische untersuchungen rätoliassischer schichten im zentralteil des germanischen beckens. *Paläontol. Abh. B* 2 (3), 427–633.
- Schuurman, W.M., 1976. Aspects of Late Triassic palynology. 1. On the morphology, taxonomy and stratigraphical/geographical distribution of the form genus *Ovalipollis*. *Rev. Palaeobot. Palynol.* 21 (4), 241–266.
- Schuurman, W.M., 1977. Aspects of Late Triassic palynology. 2. Palynology of the “Gres et Schiste aAvicula contorta” and “Argiles de Levallois” (Rhaetian) of northeastern France and southern Luxemburg. *Rev. Palaeobot. Palynology* 23 (3), 159–253.
- Spalletti, L.A., Artabe, A.E., Morel, E.M., 2003. Geological factors and evolution of Southwestern Gondwana Triassic plants. *Gondwana Res.* 6, 119–134.
- Spalletti, L.A., Artabe, A., Morel, E., Brea, M., 1999. Biozonación paleoflorística y cronoestratigrafía del Triásico Argentino. *Ameghiniana* 36, 419–451.
- Stevens, J., 1981. Palynology of the Callide Basin, east-central Queensland. University of Queensland, Department of Geology Paper 9(4).
- Tabor, N.J., Montañez, I.P., Kelso, K.A., Currie, B., Shipman, T., Colombi, C.E., 2006. A Late Triassic soil catena: landscape and climate controls on paleosol morphology and chemistry across the Carnian-Age Ischigualasto-Villa Union Basin, Northwestern Argentina. *Geol. Soc. Am. Bull.* 416, 17–42.
- Tripathi, A., Ray, A., 2006. Palynostratigraphy of the Dubrajpur Formation (Early Triassic to Early Cretaceous) of the Rajmahal Basin, India. *Palynology* 30 (1), 133–149.
- Tripathi, A., Raychowdhuri, A.K., 2005. Triassic palynoflora from the Mahuli-Mahersop Area, Singrauli Coal-field (Southern Extension), Sarguja District, Chhattisgarh, India. *J. Paleontol. Soc. India* 50, 77–99.
- Uliana, M.A., Biddle, K.T., 1988. Mesozoic–Cenozoic paleogeographic and geodynamic evolution of southern South America. *Rev. Bras. Geosc.* 18, 172–190.
- 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. *Rev. Palaeobot. Palynol.* 39, 189–300.
- Vijaya, Prasad, G.V.R., Singh, K., 2009. Late Triassic palynoflora from the Pranhita-Godavari Valley, India: evidence from vertebrate coprolites. *Alcheringa* 33 (2), 91–111.
- Visscher, H., 1966. Palaeobotany of the Mesophytic III. *Acta Bot. Neerlandica* 15 (2), 316–375.
- Visscher, H., Krystyn, L., 1978. Aspects of Late Triassic palynology. 4. A palynological assemblage from ammonoid-controlled Late Karnian (Tuvalian) sediments of Sicily. *Rev. Palaeobot. Palynol.* 26 (1), 93–112.
- Visscher, H., Van der Zwan, C.J., 1981. Palynology of the circum-Mediterranean Triassic: phytogeographical and palaeoclimatological implications. *Geol. Rundsch.* 70 (2), 625–634.
- Volkheimer, W., 1972. Estudio palinológico de un carbón caloviano de Neuquén y consideraciones sobre los paleoclimas jurásicos de la Argentina. *Rev. Mus. La Plata* 6, Paleont. 49 pp. 101–157.
- Whiteside, J.H., Lindström, S., Irmis, R.B., Glasspool, I.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. *Proc. Natl. Acad. Sci.* 112 (26), 7909–7913.
- Yrigoyen, M.R., Stover, L.E., 1969. La palinología como elemento de correlación del Triásico en la Cuenca Cuyana. *Actas IV Jornadas Geológicas Argentinas* 3 pp. 427–447.
- Zamuner, A.B., Zavattieri, A.M., Artabe, A.M., Morel, E.M., 2001. Paleobotánica. 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, pp. 143–184.
- Zavattieri, A.M., 1990. Stratigraphic and palaeoecologic evaluation of the palynofloras of the Triassic Las Cabras Formation at the type locality, Mendoza, Argentina. *Neues Jahrb. Geol. Paläontol. Abh.* 181, 117–142.
- 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, pp. 767–778.
- 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., Rojo, L.D., 2005. Estudio microflorístico de las Formaciones Potrerillos y Cacheuta (Triásico) en el sur del cerro Cacheuta, Mendoza, Argentina. *parte 2. Ameghiniana* 42, 513–534.
- Zavattieri, A.M., Volkheimer, W., 1992. Granos de polen sacados (Saccites) de la Formación Potrerillos (Triásico) en la localidad de Divisadero Largo, provincia de Mendoza, Argentina. *Ameghiniana* 29, 27–44.
- Zavattieri, A.M., 1986. Estudio palinológico de la Formación Potrerillos (Triásico) en su localidad tipo, Cuenca Cuyana (provincia de Mendoza, Argentina). *Parte I. Esporas triletes y monoletes*. *Rev. Esp. Micropaleontol.* 28, 247–294.
- Zavattieri, A.M., 1991. Granos de polen de la Formación Las Cabras (Triásico), en su localidad tipo, provincia de Mendoza, Argentina. *Parte 2. Ameghiniana* 28, 205–224.
- Zavattieri, A.M., Milana, J.P., 2000. Zonación palinológica informal para la Formación Ischigualasto (Neotriásico) en la provincia de San Juan, Argentina. 9 Simposio Argentino de Paleobotánica y Palinología, Tucumán, Abstracts, p. 119.
- Zavattieri, A.M., Volkheimer, W., Rosenfeld, U., 1994. Palynology and facies of the Late Triassic of Comallo (Northern Patagonia, Argentina). *Zentralbl. Geol. Palaeontol. Teil* 1 133–154.