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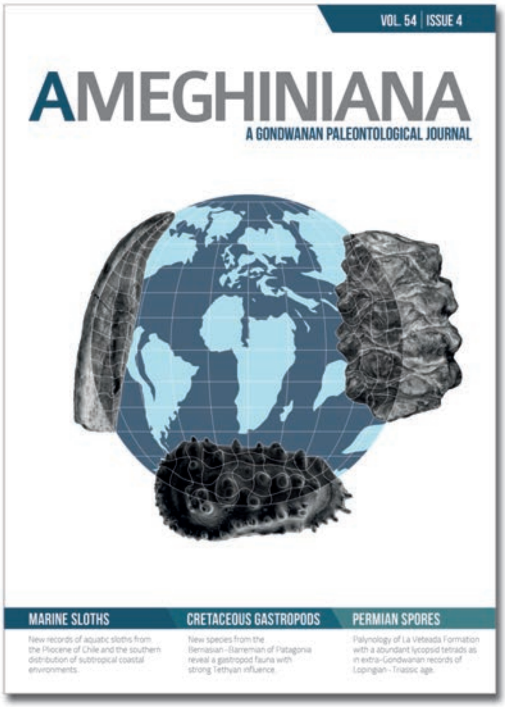

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MARINE SLOTHS
CRETACEOUS GASTROPODS
PERMIAN SPORES

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ARTICLES

PALYNOLOGY OF THE LA VETEADA FORMATION (LOPINGIAN) AT ITS TYPE LOCALITY, FAMATINA RANGE, LA RIOJA PROVINCE, ARGENTINA. SPORES

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Abstract. In this systematic study of palynological assemblages from the upper part of the type section of the La Veteada Formation, 38 species of trilete and monolete spores are described and/or illustrated. Two new species are instituted: *Lundbladispora verrucosa* and *Secarisporites triangularis,* and a new combination *Secarisporites imperialis* (Jansonius) is proposed. Trilete spores comprise a dominant group in the analyzed palynoflora and show a reduced frequency from the base to the top of the section (from 32.2 to 14.5%). Cinguli-cavate spores (derived from herbaceous lycophytes) are dominant and represented by the genera *Densoisporites*, *Lundbladispora* and *Secarisporites.* Smooth and apiculate trilete spores (derived from ferns and sphenopsids) are represented by genera such as *Calamospora*, *Punctatisporites*, *Granulatisporites*, *Brevitriletes*, *Cyclogranisporites* and *Osmundacidites.* This upper section of the La Veteada Formation was deposited in fluvial-hypersaline/brackish lacustrine environments under arid to semiarid climatic conditions. The areas surrounding these water-bodies dominated by evaporites were vegetated mainly by herbaceous lycopsids (Isoetales, Selaginellales, Lycopodiales) and ferns. Pteridophytes (Filicales, Zygopteridales), bryophytes and herbaceous sphenophytes were developed along the river courses and in the surrounding areas of fresh-water bodies (ponds and small lakes) on the flood plain. The presence of *Densoisporites complicatus*, *D. nejburgii, D. playfordii, D. solidus, Leptolepidites jonkeri, Lundbladispora brevicula, L. obsoleta, L. springsurensis, L. wilmotti, Ringosporites fossulatus, Secarisporites bullatus, S. imperialis* and *S. lacunatus* confirm a late Permian (Lopingian) age for the upper La Veteada Formation. The palynofloras contain significant proportions of lycopsid tetrads; as is the case with many extra-Gondwanic strata of Lopingian/Early Triassic age.

Key words. Spores. Upper Permian. La Veteada Formation. Paganzo Basin.

Resumen. PALINOLOGÍA DE LA FORMACIÓN LA VETEADA (LOPINGIANO) EN SU LOCALIDAD TIPO, SIERRA DE FAMATINA, PROVINCIA DE LA RIOJA, ARGENTINA. ESPORAS. Se presenta el estudio sistemático de las asociaciones palinológicas registradas en la sección superior de la Formación La Veteada (Asociación La Veteada). En esta contribución se describen y/o ilustran 38 especies de esporas triletes y monoletes. Se describen dos nuevas especies: *Lundbladispora verrucosa* y *Secarisporites triangularis*, también se propone una nueva combinación para *Secarisporites imperialis* (Jansonius). Las esporas triletes son uno de los grupos dominantes de la microflora analizada reduciendo su frecuencia de base a techo de la sección (de 32,2 a 14,5%). Dominan las esporas cíngulo-cavadas (derivadas de lycofitas/licópsidas herbáceas) representadas por especies de los géneros *Densoisporites, Lundbladispora* y *Secarisporites.* Esporas triletes lisas y apiculadas (derivadas de helechos y esfenópsidas) están representadas por los géneros *Calamospora*, *Punctatisporites*, *Granulatisporites*, *Brevitriletes*, *Cyclogranisporites*, *Osmundacidites*, entre otros. La sección superior de la Formación La Veteada representa ambientes fluvio-lacustres depositados en condiciones climáticas áridas o semiáridas. Las áreas que rodeaban estos cuerpos de agua dominados por evaporitas fueron vegetadas principalmente por licópsidas herbáceas (Isoetales, Selaginellales, Lycopodiales) y helechos. Pteridophytas (Filicales, Zygopteridales), briofitas y esfenofitas herbáceas se desarrollaron a lo largo de los cursos de ríos y en las áreas circundantes de los cuerpos de agua dulce (pantanos y pequeños lagos) en la llanura de inundación. La presencia de *Densoisporites complicatus*, *D. nejburgii, D. playfordii, D. solidus, Leptolepidites jonkeri, Lundbladispora brevicula, L. obsoleta, L. springsurensis, L. wilmotti, Ringosporites fossulatus, Secarisporites bullatus, S. imperialis* y *S. lacunatus* permite confirmar una edad lopingiana para la sección superior de la Formación La Veteada. Microfloras que contienen altas proporciones de lycopsidas en tétrades han sido registradas principalmente en áreas extra-gondwánicas para el período Lopingiano/Triásico Temprano.

Palabras clave. Esporas. Pérmico superior. Formación La Veteada. Cuenca Paganzo.

The continental La Veteada Formation (Dávila *et al.*, 2005) is exposed in scattered outcrops in the Famatina Range (Paganzo Basin) and has been dated as late Guadalupian to late Lopingian (Gutiérrez *et al.*, 2008; Zavattieri *et al.*, 2008). Gutiérrez *et al.* (2011) studied the diverse palynological assemblage from the lowest exposures of the unit in the Sierra de Narváez, Catamarca Province, central-western Argentina. Later, Zavattieri and Gutiérrez (2012), Gutiérrez *et al.* (2014) and Zavattieri *et al.* (2017) reported palynofloras (in part) from the type section of the La Veteada Formation (previously known as La Yesera Formation) exposed at the eastern end (28° 34′ S; 68° 45′ W) of the Famatina Range, north La Rioja Province (Fig. 1.1). The type sedimentary succession encompasses the upper part of the unit, which consists of 180 m of lenticular evaporites and laminate dolomites interbedded with red siltstones, mudstones and sandstones (Dávila *et al.*, 2005). This unit paraconformably overlies the Cisuralian De La Cuesta Formation (Turner, 1964) and is unconformably succeeded by the early Miocene Del Crestón Formation (Turner, 1964). (Figs. 1.1–2).

The base of the La Veteada Formation is marked by a regionally recognizable silcrete unit (Fig. 1.2). Above this, the formation consists of rhythmically interbedded fine tabular sandstones and red-purple, fine to very fine dark grey laminated siltstones and claystones; gypsum beds are locally present. Deposition evidently occurred under shallow lacustrine conditions in hypersaline semi-perennial lakes with periodic transgressions-regressions on a terrain of low relief. Dávila *et al.* (2005), Ezpeleta (2009) and Zavattieri *et al.* (2017) provided further details.

For this palynological study, all the pelitic levels of the succession were sampled; of these, six samples of carbonaceous silty mudstones yielded abundant and well-preserved palynomorphs (Fig. 1.2). Zavattieri and Gutiérrez (2012), Gutiérrez *et al.* (2014) and Zavattieri *et al.* (2017) reported that the palynoflora of the type section of La Veteada Formation comprises diverse bisaccate and monosaccate (striate and non-striate), plicate and colpate pollen grains, freshwater algae, fungi, and other organic-walled microphytoplankton. Reworked Devonian and Carboniferous acritarchs and miospores occur in minor proportions. The palynological association of the upper La Veteada Formation is regarded as Lopingian in age and it is thus the youngest Permian palynoflora hitherto recorded in Argentina and elsewhere in South America.

This contribution describes and illustrates the diverse spore (land-derived) palynological content of the La Veteada Formation at its type locality. Two new species are described: *Secarisporites triangularis* and *Lundbladispora verrucosa*. *Leptolepidites jonkeri* (Jansonius) Yaroshenko and Golubeva in Yaroshenko *et al.* (1991) is herein described for the first time from western Gondwana, and a new combination of *Secarisporites imperialis* (Jansonius) is proposed. Spore tetrads referable to the lycopsid genera *Densoisporites, Lundbladispora* and *Secarisporites* are as common here as in extra-Gondwanan assemblage areas of Lopingian to Early Triassic age.

MATERIALS AND METHODS

The samples were processed in the Unidad de Paleopalinología, Departamento de Paleontología of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (**IANIGLA**), CCT-CONICET-Mendoza using standard palynological acid maceration techniques (Volkheimer and Melendi, 1976), and organic residues were sieved using a 10 µm mesh and finally mounted on glycerine jelly. Some organic residues were slightly oxidized as required. The slides were studied with an Olympus BX 50 microscope and digital camera of the IANIGLA, and with a Nikon H550S microscope and photograpied DS-U2-Fil-U2 digital camera of the Laboratorio de Paleopalinología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (**MACN**), Buenos Aires. The slides are designated by the abbreviation **MPLP** (Mendoza-Paleopalinoteca-Laboratorio de Paleopalinología, Unidad de Paleopalinología, Departamento de Paleontología, Instituto de Nivología, Glaciología y Ciencias Ambientales, CCT-CONICET, Mendoza, Argentina) and the catalogue numbers 8248 (A–H), 8249 (A–I), 8250 (A–J), 8251 (A–K), 8252 (A–K) and 8253 (A–K). Specimen locations are referred to with England Finder coordinates (**E.F.co.**). For scanning electron microscopy (SEM), residues of samples 8248 and 8251 were mounted on aluminum stubs and coated with gold-palladium. A Phillips XL 30 TMP of MACN was used to examine and photograph selected specimens, which are identified by the number of the stub (**T**) and the photograph (**f**).

Descriptions of new species, taxonomic and morphological discussions of some species, and forms of uncertain assignment are detailed in the Systematic Paleontology section. Specimens with relatively poor preservational conditions that hindered precise taxonomic assignment are

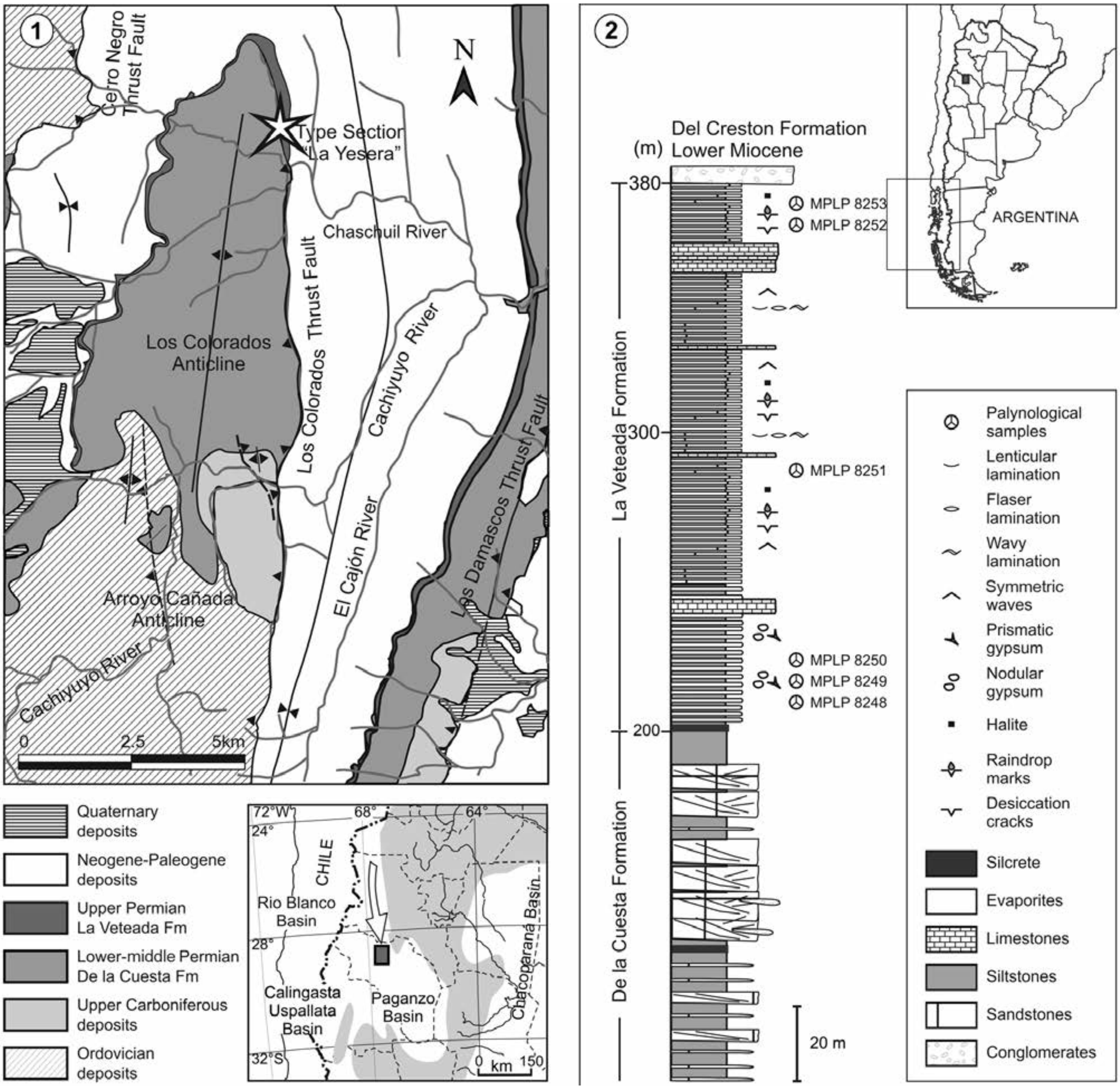

Figure 1.1, geological map of the study area, showing the location of the studied type section profile (star). **2,** stratigraphic type section of the La Veteada Formation at Famatina Range and location of the palynological samples (modified from Dávila *et al.,* 2005).

referred to as "spp". For descriptions, we follow the terminology of Dettmann (1963), Kremp (1965) and Playford and Dettmann (1996).

Size measurements are presented in the format N1(N2)N3, where N1 and N3 represent the minimum and maximum values, respectively, and N2 are the mean sizes. **ED/id** ratio refers to Exoexine Diameter (**ED**)/intexine diameter and (**id**) ratio. For statistical analyses, two slides were studied per sample and the total palynomorph genera content was counted and expressed in percentages (Supplementary Online Information 1).

RESULTS

Spores are a major constituent of the upper La Veteada palynoflora (Tab. 1). The following is a comprehensive list of spore species identified in this study.

Trilete Spores

Laevigati. *Calamospora breviradiata* Kosanke, 1950 (Fig. 2.1); *Calamospora tener* (Leschik, 1955) de Jersey, 1962 (Fig. 2.2); *Leiotriletes directus* Balme and Hennelly, 1956 (Fig. 2.9); *L.* sp. cf. *L. adnatus* (Kosanke, 1950) Potonie and Kremp, 1955 (Fig. 2.13); *L.* spp.; *Punctatisporites gretensis* Balme and Hennelly, 1956 (Fig. 2.4); *P. lucidulus* Playford and Helby, 1968 (Fig. 2.5); *P. priscus* Bharadwaj and Salujha, 1964 (Fig. 2.6); *P.* spp.; *Retusotriletes* spp.; *Stereisporites psilatus* (Ross, 1949) Pflug in Thomson and Pflug, 1953 (Fig. 2.8); *S.* sp.

Apiculati. *Anapiculatisporites* spp.; *Brevitriletes cornutus* (Balme and Hennelly, 1956) Backhouse, 1991 (Fig. 2.18–19); *B. levis* (Balme and Hennelly, 1956) Bharadwaj and Srivastava, 1969 (Fig. 2.21); *B.* sp. A (Fig. 2.20); *Brevitriletes* spp.; *Converrucosisporites* sp. A (Fig. 2.14); *Convolutispora* spp.; *Cristatisporites* spp.; *Cyclogranisporites* sp. A Backhouse, 1991 (Fig. 2.3); *C.* spp.; *Dictyotriletes* spp.; *Granulatisporites* spp.; *Grumosisporites* sp. A (Fig. 2.15–16); *Horriditriletes ramosus* (Balme and Hennelly, 1956) Bharadwaj and Salujha, 1964 (Fig. 2.17); *Leptolepidites jonkeri* (Jansonius, 1962) Yaroshenko and Golubeva in Yaroshenko *et al.* (1991) (Fig. 3.1–2); *Lophotriletes lentiginosus* Playford and Dino, 2000 (Fig. 2.10); *Osmundacidites senectus* Balme, 1963 (Fig. 2.11); *O. wellmanii* Couper, 1953 (Fig. 2.12); *Ringosporites fossulatus* (Balme, 1970) Tiwari and Rana, 1981 (Fig. 2.7); *Secarisporites bullatus* Foster, 1979 (Fig. 3.3–5); *S. imperialis* (Jansonius, 1962) nov. comb. (Fig. 3.6–14); *S. lacunatus* (Tiwari, 1965) Backhouse, 1988 (Fig. 3.15–19); *S. triangularis* sp. nov. (Fig. 3.20–29); *Verrucosisporites* spp.

Cingulicavati. *Densoisporites complicatus* Balme, 1970 (Fig. 4.1–4); *D. nejburgii* (Schulz, 1964) Balme, 1970 (Fig. 4.7–9); *D. playfordii* (Balme, 1963) Balme, 1970 (Fig. 4.10–11); *D. solidus* Segroves, 1970 (Fig. 4.5–6); *D.* spp.; *Indotriradites apiculatus* Stephenson and Osterloff, 2002 (Fig. 4.13); *I.* spp.; *Kraeuselisporites punctatus* Jansonius, 1962 (Fig. 4.12); *Lundbladispora brevicula* Balme, 1963 (Fig. 4.14–15); *L.* sp. cf. *L. gracilis* Stephenson and Osterloff, 2002 (Fig. 5.1); *L. obsoleta* Balme, 1970 (Fig. 5.2); *L. riobonitensis* Marques-Toigo and Piccarelli, 1985 (Fig. 5.3–5); *L.* sp. cf. *L. springsurensis* de Jersey, 1979 (Fig. 5.7); *L. verrucosa* sp. nov. (Figs. 5.6, 8–9, 12; 6.1–10, 12–14), *L. wilmotti* Balme emend. Playford, 1965 (Fig. 5.10–11).

Monolete Spores. *Laevigatosporites callosus* Balme, 1970 (Fig. 6.16–17); *L.* sp. cf. *L. vulgaris* (Ibrahim) Ibrahim, 1933 (Fig. 6.11, 15); *L.* spp.

SYSTEMATIC PALEONTOLOGY

Anteturma Sporites Potonié, 1893
Turma Triletes Reinsch emend. Dettmann, 1963
Suprasubturma Acavartitriletes Dettmann, 1963
Subturma Azonotriletes Lüber emend. Dettmann, 1963
Infraturma Apiculati Bennie and Kidston emend.
Potonié, 1956

Genus ***Brevitriletes*** Bharadwaj and Srivastava, 1969

Type species. *Brevitriletes communis* Bharadwaj and Srivastava, 1969 (by original designation).

***Brevitriletes* sp. A**
Figure 2.20

Description. Radial trilete spores, circular amb. Laesurae without lips, straight, extending to the equator of the spore. Proximal face slightly depressed in the contact areas; laevigate exine. Distal face convex. Acuminate ornament and verrucae appear spaced to tightly clustered, 1–3 μm in basal diameter, <2 μm high. Weak curvatural ridge is occasionally present. Exine 1–1.5 μm thick.

Dimensions (27 specimens). Equatorial diameter, 30(38.7)48 μm.

Figure 2. **1,** ***Calamospora breviradiata*****, MPLP** 8248(G) N34/4. **2,** ***Calamospora tener*****, MPLP** 8251(K) V51/3. **3,** ***Cyclogranisporites*** sp. A, **MPLP** 8248(H) V40/0. **4,** ***Punctatisporites gretensis*****, MPLP** 8251(H) E41/3. **5,** ***Punctatisporites lucidulus*****, MPLP** 8248(H) E43/3. **6,** ***Punctatisporites priscus*****, MPLP** 8248(C) P42/0. **7,** ***Ringosporites fossulatus*****, MPLP** 8248(D) Y37/0. **8,** ***Stereisporites psilatus*****, MPLP** 8248(B) N42/2. **9,** ***Leiotriletes directus*****, MPLP** 8252(I) J44/0. **10,** ***Lophotriletes lentiginosus*****, MPLP** 8250(G) V46/0. **11,** ***Osmundacidites senectus*****, MPLP** 8249(H) Z36/0. **12,** ***Osmundacidites wellmanii*****, MPLP** 8250(B) F26/0. **13,** ***Leiotriletes*** sp. cf. ***L. adnatus*****, MPLP** 8248(H) R50/0. **14,** ***Converrocosisporites*** **sp. A, MPLP** 8248(G) E36/0. **15–16,** ***Grumosisporites*** sp. A; **15, MPLP** 8250(G) Q44/4; **16, MPLP** 8251(J) T37/3. **17,** ***Horriditriletes ramosus*****, MPLP** 8249 (H) W39/4. **18–19,** ***Brevitriletes cornutus*****; 18, MPLP** 108; **19, MPLP** 8249(E) H36/0. **20,** ***Brevitriletes*** sp. A, **MPLP** 8251(J) K45/3. **21,** ***Brevitriletes levis*****, MPLP** 8250(I) T49/0. Scale bars= 20 μm.


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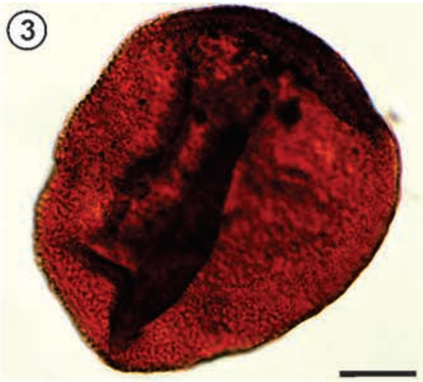
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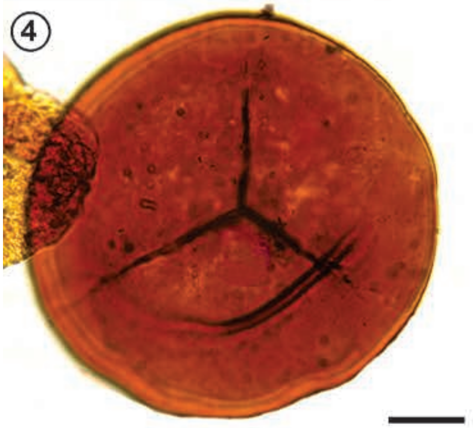
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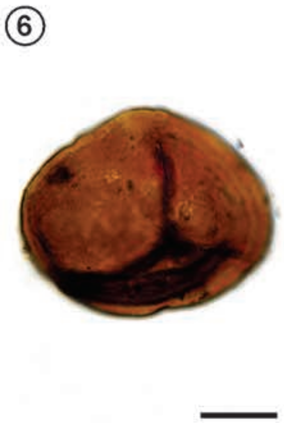
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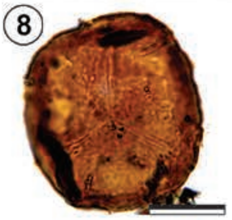
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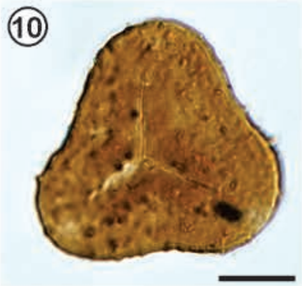
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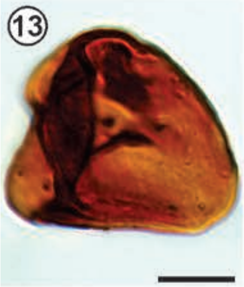
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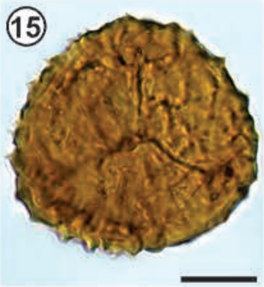
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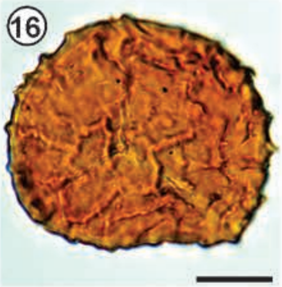
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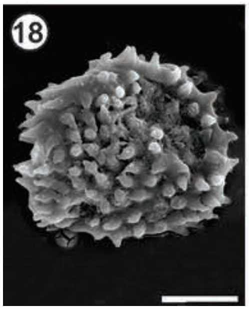
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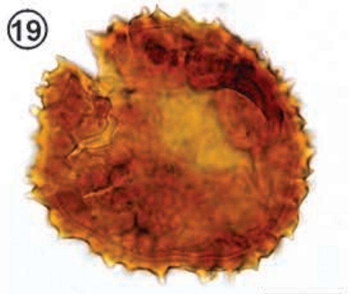
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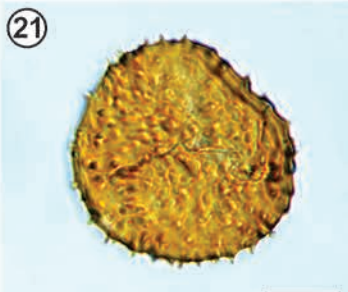
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Remarks. The type of ornamentation and the size of the sculptural elements differentiate *Brevitriletes* sp. A from other described species of the genus *Brevitriletes*.

Genus ***Cyclogranisporites*** Potonié and Kremp, 1954

Type species. *Cyclogranisporites leopoldi* (Kremp) Potonié and Kremp, 1954 (by original designation).

Cyclogranisporites **sp. A** in Backhouse, 1991

Figure 2.3

Remarks. The La Veteada specimens are consistent with the description given by Backhouse (1991, p. 264, pl. III, figs. 14–19) for his *Cyclogranisporites* sp. A regarding the sculpture consisting of small densely arranged rugulae (less than 1 μm apart). However, the trilete mark was not observed because the studied specimens are strongly folded.

Genus ***Leptolepidites*** Couper, 1953

Type species. *Leptolepidites verrucatus* Couper, 1953 (by original designation).

Leptolepidites jonkeri (Jansonius, 1962) Yaroshenko and Golubeva in Yaroshenko *et al.*, 1991

Figure 3.1–2

Description. Trilete spores, circular to subcircular amb. Laesurae simple, two thirds of spore radius. Exine 1–1.5 μm thick. Distal face sculptured with irregular verrucae that fuse between them to form short discontinuous flat rugulae. These elements can be merged in the equatorial region forming a discontinuous thickening on the proximal face and giving the appearance of a cingulum. Verrucae protrude into the outline of the spores giving rise to an irregularly undulating contour. Verrucae of 1(3)6 μm in largest diameter.
Dimensions (6 specimens). Maximun diameter, 35(39)45 μm.

Suprasubturma LAMINATITRILETES Smith and Butterwort, 1967
Subturma ZONOLAMINATITRILETES Smith and Butterwort, 1967
Infraturma TUBERCULORNATI Smith and Butterwort, 1967

Genus ***Grumosporites*** Smith and Butterwort, 1967

Type species. *Grumosisporites verrucosus* (Butterworth and Williams) Smith and Butterwort, 1967 (by original designation).

Grumosisporites **sp. A**

Figure 2.15–16

Description. Radial trilete spores, subcircular to rounded triangular amb. Laesurae straight, simple or with narrow and low lips, reaching to 3/4–4/5 of the radius length. Exine separated into two layers; exoexine ornamented with irregular low ridges and verrucae; on the spore outline, elements of ornamentation are projected into acuminate, conical and/or spine-like forms; in plant view, the sculptural elements can be fused forming an irregular and opened reticulum.
Dimensions (6 specimens). Maximum diameter, 42(47.5)53 μm.

Infraturma PSEUDOCINGULATI Neves, 1961

Genus ***Secarisporites*** Neves, 1961 *sensu* Foster, 1979

Type species. *Secarisporites lobatus* Neves 1961 (by original designation).
Discussion. We adhere to Foster's criteria (1979, p. 58) reinterpreting the genus *Secarisporites* Neves, 1961 according to the following diagnostic features: 1, spores totally or partially cavate; 2, extension of the sculpture (verrucae and/or pilae) over the equator simulating an ornamented zone ("flange-like zone"); 3, thin proximal face, laevigate or with small ornamentations; 4, apparently cingulate. In this sense, Backhouse (1991, p. 68) described *Secarisporites lacunatus* for those forms that included Foster's (1979) interpretation and emphasized the presence of a thin cingulum formed by the fusion of the bases of the large verrucae that are projected in the equator.

Secarisporites bullatus Foster, 1979

Figure 3.3–5

Remarks. Foster (1979, p. 59, pl. 17, figs. 1–2) characterized this species as having diverse sculptural elements (grana, baculae, verrucae and pilae) developed comprehensively and projecting equatorially. The La Veteada specimens are also sculptured with clavae and gemmae, and are predominantly verrucate.
Dimensions (17 specimens). Exoexine maximum diameter

(ED), 35–48 μm; intexine maximum diameter (id), 26–39 μm; ED/id ratio, 1.2–1.4. Sculptural elements in equatorial view: basal diameter 1.4(1.6–2.3)3.5 μm x height 1.5(1.9–2.5)3.5 μm; in distal view: 1.5(2.3–2.6)3.7 x 1(1.6–2.4)3 μm; ratio major/minor diameter of the discrete elements 1(1.1–2.4)3.

Secarisporites imperialis (Jansonius, 1962) nov. comb.

Figure 3.6–14

1962 *Lycospora imperialis* Jansonius, p. 46, pl. 11, figs. 15–16.
1994 *Uvaesporites imperialis* (Jansonius), Utting, p. 39–40, pl. 10, figs. 1–3.

Description. Radial trilete spores, cavate, with equatorial extension of the exoexine. Intexine contracted forming an inner body of rounded subtriangular to triangular outline. Smooth proximal face having a simple trilete mark which can be bordered by lips of 1–2 μm in width and extending up to the outer border of the inner body. Distal face irregularly covered by verrucae up to 4 μm in maximum diameter; variable in shape, from spherical and globular (uvate or gem-like) to polygonal, low, sometimes with a flat top. They appear to be concentrated from the edge of the inner body giving rise to a thin continuous thickening parallel to the equator of the spores; on the marginal equatorial outline, verrucae give a crenate aspect.

Dimensions (66 specimens). Exoexine maximum diameter (ED), 35(40)45 μm; intexine maximum diameter (id), 27(32–34)40 μm; ED/id ratio, 1.2–1.4. Sculptural elements: in lateral view, 1(1.5–2.5)3.5 μm basal diameter and 0.5(1–1.6)2 μm high; ratio basal diameter/high, (1–2.1)3; polygonal verrucae in plain view of 1(1.2–3)4 x 0.6(1–2)3 μm; spherical-globular verrucae, 0.9–3 x 0.8–2.8 μm in diameter.

Discussion. Originally, Jansonius (1962) characterized this species with the exine divided into two layers; the "flange" or equatorial extension has crenate margins. The distal face has verrucae distributed in concentric disposition parallel to the equator of the spores; fused verrucae are also disposed along the entire base of the flange forming an annular thickening. These features give a cingulo-zonate aspect to the spores. Some authors included these spores in the genus *Lycospora* Jansonius, 1962. Bek (2012, tab. 8) excluded it from the genus *Lycospora*.

Meanwhile, Utting (1994) combined this species with the genus *Uvaesporites* Döring, 1965 on the basis of its distal ornamentation characterized by globular, "uvate" or grape-shaped and reniform elements. Besides, these elements can merge forming an equatorial thickening of the exine (flange) but it does not constitute neither a cingulum nor a cingulate-zone. According to the diagnosis of the genus *Uvaesporites* and Hiltman's emendation (1967), the fusion of the sculpture (and consequent thickening of the exine) occurs on the equatorial margin but is not concentric sub-equatorially as described or interpreted by Jansonius (1962) and as observed in the La Veteada specimens.

Secarisporites lacunatus (Tiwari, 1965) Backhouse, 1988

Figure 3.15–19

Dimensions (190 specimens). Exoexine maximum diameter (ED), 35(40–45)50 μm; intexine maximum diameter (id), 25(30–38)43 μm; ED/id ratio, 1.1(1.2–1.3)1.4. Sculptural elements; in lateral view, 1(1.6–2.6)6 μm; in basal width, 1–(2)3 μm in height; in plan view, diameter warts, 1(1.2–2.7)5 x 0.8(1–2.4)4 μm. Ratio major/minor diameter of sculptural elements 1(1.1–1.5)2.

Secarisporites triangularis sp. nov.

Figure 3.20–29

Derivation of name. Referred to the triangular amb of the central body.

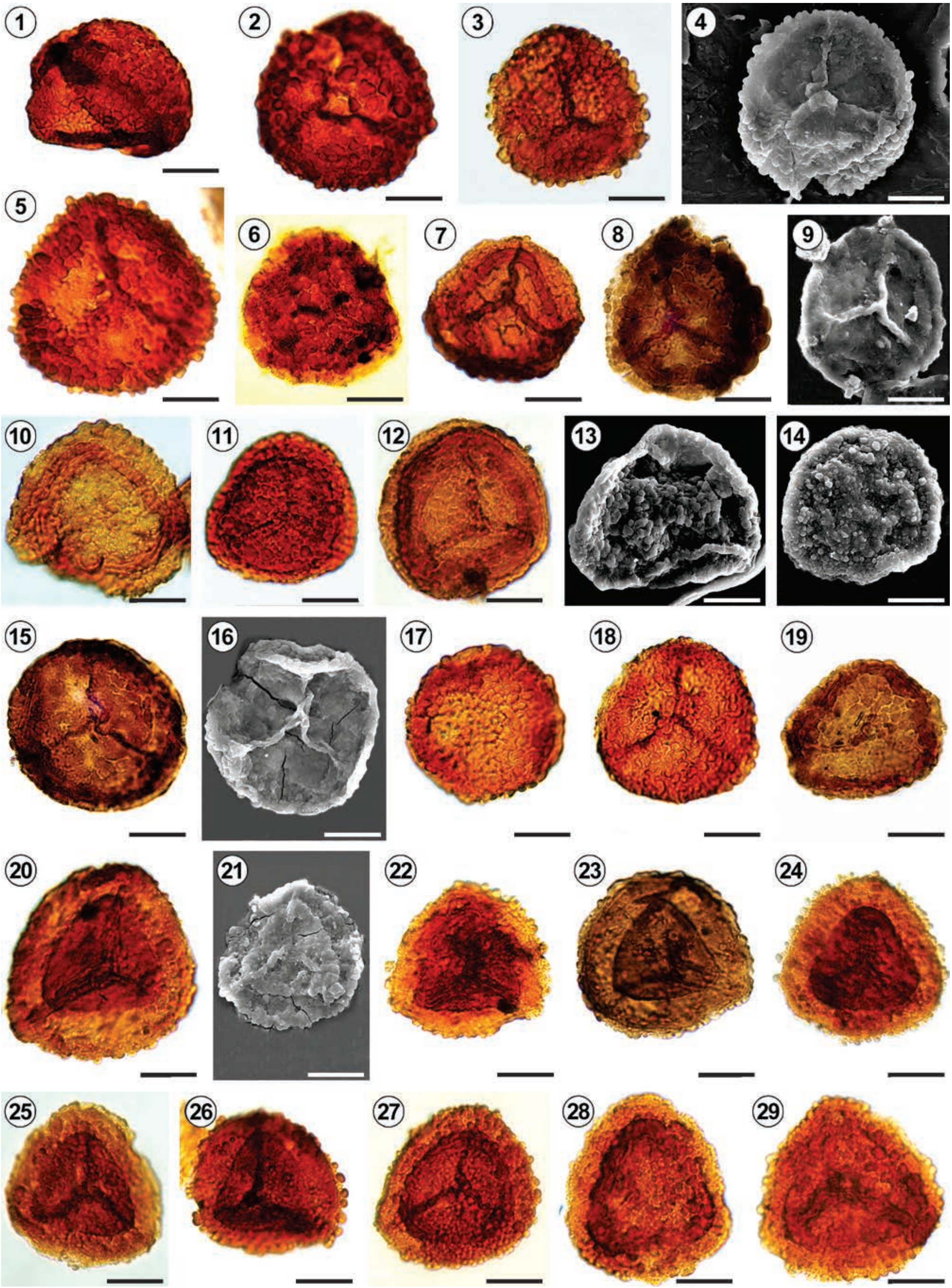
Diagnosis. Radial trilete spores, cavate, rounded subtriangular amb, with equatorial extension of the exoexine in the distal face. Intexine contracted forming an inner body of triangular outline, usually straight to slightly convex sides. Wall of the intexine thick, clearly visible. Exoexine slightly thickened towards the marginal equatorial zone. Proximal face smooth; trilete mark accompanied by low lips whose rays can reach the contour of the spores. Distal face and margin densely and irregularly covered by small verrucae (in general less than 2 μm in width), mainly spherical to globular in shape and polygonal in less proportion.

Holotype. MPLP 8250(H) M49/1 (Fig. 3.20).

Paratypes. MPLP 8250(G) O39/2 (Fig. 6.23), MPLP 8250(I) H40/3 (Fig. 6.24), MPLP MEB 8249(T6) 0271 (Fig. 6.21).

Geographic provenance. La Yesera locality, Paganzo Basin, Famatina Range, La Rioja Province, Argentina.

Stratigraphic provenance. Upper section and type locality of the La Veteada Formation, Lopingian.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Description. Radial trilete spores, cavate, rounded sub-triangular amb, with equatorial extension of the exoexine in the distal face. Intexine contracted forming a triangular inner body with straight to slightly convex sides. Wall of the intexine 1–1.2 µm in thickness. Exoexine slightly thicker towards the equatorial margin. Proximal face laevigate/smooth; trilete mark bordered by low lips 1–1.5 µm wide, rays reaching near the equatorial margin of the spores. Distal face and zone irregularly covered by small verrucae of 1–2 x 0.7–1.6 µm in size, mainly spherical to globular in shape and rarely polygonal.

Discussion. *Secarisporites triangularis* sp. nov. is distinguished from *S. bullatus*, *S. lacunatus* and *S. imperialis* by its clearly cavate condition, its intexine (central body) triangular in shape and its high ratio between intexine/exoexine. Furthermore, *S. imperialis* is distinguished from *S. triangularis* sp. nov. by a distal equatorial ring formed by the fusion/merge of the verrucae.

Dimensions (66 specimens). Exoexine maximum diameter, 35(38–40)45 µm; intexine maximum diameter, 20(24–29)32 µm; ED/id ratio, 1.3(1.4–1.6)1.8. Lips, (1–1.5)2.5 µm wide. Sculptural elements: in lateral view, 1(1.5–2.2)3 µm in basal diameter x 0.5(1–1.8)3 µm high; in plant view, verrucae, (1–2)3 wide x 0.5(0.7–1.6)2.5 µm high. Major/minor diameter ratio of verrucae, (1–1.5)2.2.

Infraturma CINGULICAVATI Smith and Butterwort, 1967

Genus ***Densoisporites*** Weyland and Krieger, 1953 emend. Dettmann, 1963

Type species. *Densoisporites velatus* Weyland and Krieger, 1953 emend. Krasnova in Samoilovitch and Mtchedlishvili, 1961 (by original designation; monotypy).

Densoisporites complicatus Balme, 1970

Figure 4.1–4

Remarks. La Veteada specimens exhibit the amb and internal body subtriangular in outline, spongy exoexine (intragranular), proximal face with fine radial folds (0.7–1.5 µm wide) extending from the proximal pole, and reaching up to 2 µm of the equatorial outline; trilete mark with thin and low lips, which thicken towards the outline where they reach the inner edge of the cingulum.

Dimensions (113 specimens). Exoexine maximum diameter, 32(38–40)50 µm; intexine maximum diameter, 22(28–32)40 µm; ED/id ratio, (1.2–1.5)1.7; cingulum thickness, 1(1.5–2.5)3.5 µm; total width of the lips, 1(1.5–2)3 µm.

Densoisporites nejburgii (Schulz, 1964) Balme, 1970

Figure 4.7–9

Remarks. The La Veteada specimens show circular to strongly rounded subtriangular amb; the intexine has concentric marginal folds (width from 1.2 to 3 µm, generally between 1.5–2.3 µm) that form the smaller eccentric inner body than the exoexine and having typically spongy structure. The trilete mark shows narrow and elevated lips (width, 0.8(1)1.7 µm; 1.4(2)3 µm high).

It is distinguished from *Densoisporites playfordii* (Balme) Balme, 1970 by its subcircular amb, its laesurae with developed lips and its smaller spores (see Balme, 1970).

Dimensions (130 specimens). Exoexine maximum diameter (ED), 35(40)45 µm; intexine maximum diameter (id), 26(30–36)40 µm; ED/id ratio, 1.1(1.2–1.3)1.5; cingulum thickness, 1(1.2–2)3 µm.

Densoisporites playfordii (Balme, 1963) Balme, 1970

Figure 4.10–11

Remarks. The specimens from La Veteada show simple laesurae; rarely present thin elevated lips; the intexine

Figure 3. 1–2, *Leptolepidites jonkeri*; 1, MPLP 8249(I) E45/0; **2, MPLP** 8250(H) J44/1. **3–5, *Secarisporites bullatus*; 3, MPLP** 8252(I) G47/0; **4, MPLP** MEB 8249(T7) 0331; **5, MPLP** 8250(G) F34/3. **6–14, *Secarisporites imperialis*** (Jansonius) nov. comb.; **6, MPLP** 8248(B) S41/3; **7, MPLP** 8251(H) D46/0; **8, MPLP** 8250(B) B24/4; **9, MPLP** MEB 8253(T1) 0072; **10, MPLP** 8252(I) T46/0; **11, MPLP** 8251(J) K44/1; **12, MPLP** 8251(J) K54/0; **13, MPLP** MEB 8249(T7) 0320; **14, MPLP** MEB 8249(T6) 0265. **15–19, *Secarisporites lacunatus*; 15, MPLP** 8250(B) L27/3; **16, MPLP** MEB 8249(T6) 0251; **17, MPLP** 8250(H) L53/0; **18, MPLP** 8252(I) J49/3; **19, MPLP** 8249(E) W31/1. **20–29, *Secarisporites triangularis*** sp. nov., **20,** Holotype, **MPLP** 8250(H) M49/1; **21,** Paratype, **MPLP** MEB 8249(T6); **22, MPLP** 8250(G) G36/0; **23,** Paratype, **MPLP** 8250(G) O39/2; **24,** Paratype, **MPLP** 8250(I) H40/3; **25, MPLP** 8248(H) M43/1; **26, MPLP** 8249(G) G41/3; **27, MPLP** 8249(G) L52/0; **28, MPLP** 8251(J) S49/1; **29, MPLP** 8251(K) U43/3. Scale bars= 20 µm.

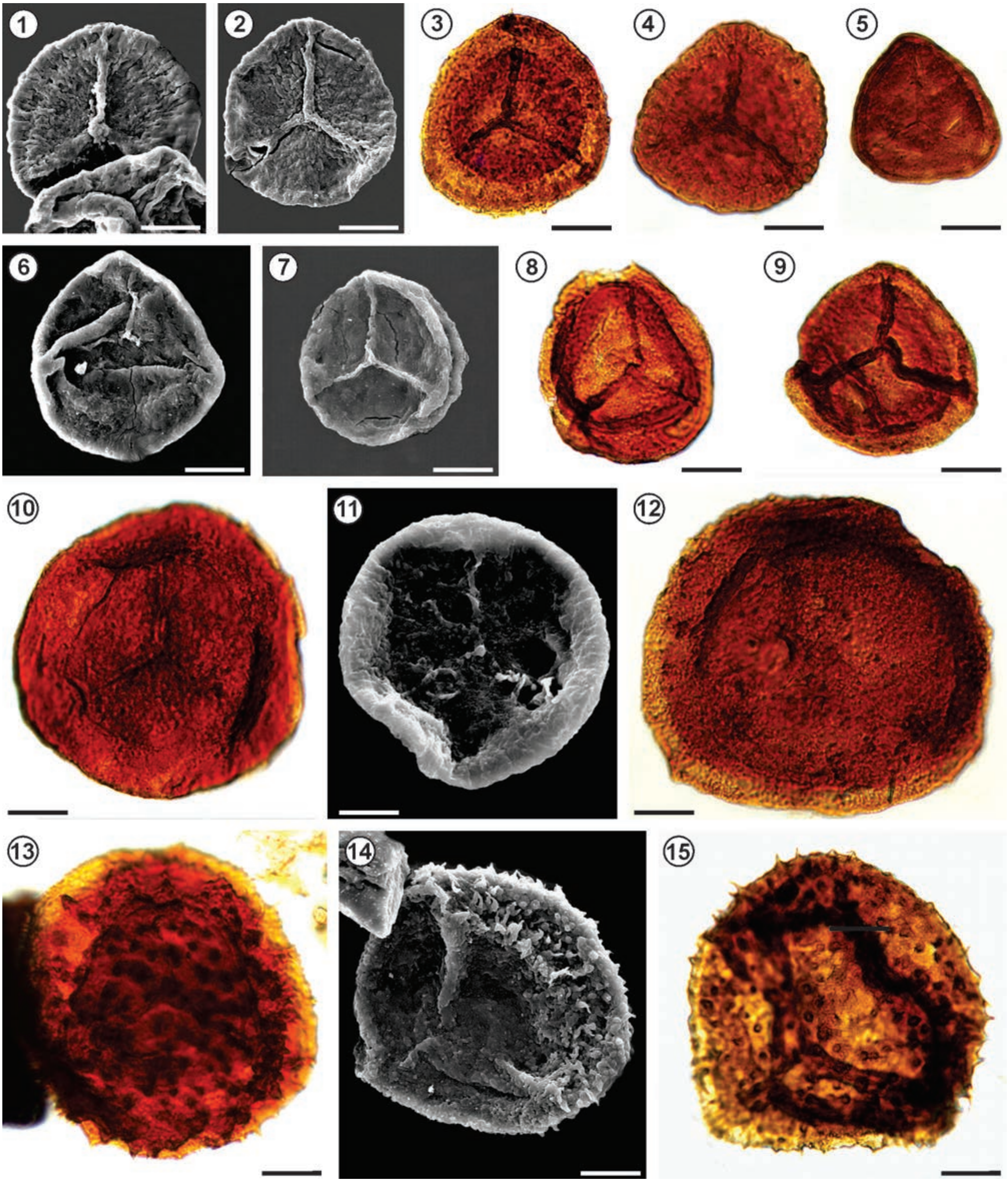

Figure 4. 1–4, ***Densoisporites complicatus*****; 1, MPLP** MEB 8249(T5) 0169; **2, MPLP** MEB 8249(T7) 0398; **3, MPLP** 8250(H) F47/3; **4, MPLP** 8249(F) N46/1. **5–6,** ***Densoisporites solidus*****; 5, MPLP** 8251(H) T45/1; **6, MPLP** MEB 8249(T7) 0306. **7–9,** ***Densoisporites nejburgii*****; 7, MPLP** MEB 8249(T6) 0243; **8, MPLP** 8250(H) N49/0; **9, MPLP** 8250(I) P49/4. **10–11,** ***Densoisporites playfordii;*** **10, MPLP** 8250(H) O47/0; **11, MPLP** MEB 8249(T5) 0201. **12,** ***Kraeuselisporites punctatus*****, MPLP** 8251(H) M37/0. **13,** ***Indotriradites apiculatus*****, MPLP** 8248(H) J45/1. **14–15,** ***Lundbladispora brevicula*****; 14, MPLP** MEB 8249(T6) 0269; **15, MPLP** 8248(C) L31/4. Scale bars= 20 μm.

appears frequently folded forming an inner body smaller than the exoexine, whereas the exoexine is finely scabrate –microreticulate– exhibiting a cingulum of 2–5 µm wide.
Dimensions (35 specimens). Exoexine maximum diameter (ED), (40–60)70 µm; intexine maximum diameter (id), 30–52 µm; ED/id ratio, 1.1(1.2–1.3)1.5; thickness of the cingulum, 2(2.3–3)5 µm.

Densoisporites solidus Segroves, 1970
Figure 4.5–6

Remarks. This species is characterized by its sponge-like exoexine but the cingulum has solid non-structured aspect forming a conspicuous irregular peripheral zone (Segroves, 1970).
Dimensions (29 specimens). Exoexine maximum diameter, 35–55 µm; intexine maximum diameter, 30–42 µm; ED/id ratio, 1.1(1.2)1.4; thickness of the cingulum, 1.2(1.3–2)3 µm; lips, (0.6–1)2 µm in total width, 1(2)2.5 µm in height.

Genus ***Lundbladispora*** Balme emend. Playford, 1965

Type species. *Lundbladispora wilmotti* Balme, 1963 (by original designation).

Lundbladispora brevicula Balme, 1963
Figure 4.14–15

Remarks. *Lundbladispora wilmotti* Balme emend. Playford, 1965 is similar to this species and it is thus difficult to distinguish them. In this work, we follow the criteria of Playford (1965), who considered that the most obvious distinction between both species is the presence of a prominent lipped laesura and longer trilete rays in *L. brevicula*.
Dimensions (51 specimens). Exoexine maximum diameter, 55(65–75)85 µm; intexine maximum diameter, 45–75 µm; ED/id ratio, (1.1–1.3)1.5; thickness of the cingulum, 1.5(2.5–3.5)5 µm; lips, 1.1–4 µm wide, 2–6 µm high. Sculptural elements: spinae of 0.6(1–1.5)2 µm in basal width, 2.7–5 µm high; coni and bulbous elements, 1(1.2–2)3 µm in basal width, 1(1.5–3)4.5 high.

Lundbladispora **sp. cf.** ***L. gracilis*** Stephenson and Osterloff, 2002
Figure 5.1

Remarks. In this material, some specimens show granulae and/or coni elements sparsely disposed.
Dimensions (9 specimens). Exoexine maximum diameter, 40–75 µm; intexine maximum diameter, 35–70 µm; ED/id ratio, 1.1–1.3; thickness of the cingulum, 3–9 µm. Sculptural elements: spinae, coni and granulae, 1–2 µm in basal width and 1–3 µm in hight.

Lundbladispora obsoleta Balme, 1970
Figure 5.2

Dimensions (9 specimens). Exoexine maximum diameter (ED), 52–80 µm; intexine maximum diameter (id), 44–64 µm; ED/id ratio, 1.2–1.3; thickness of the cingulum, 2.5–5 µm. Sculpture: bulbous elements, 1.7–3 µm in basal width and 2–5 µm in hight; coni, 1.7–4 µm in basal width and 2.4–6 µm in hight.

Lundbladispora riobonitensis Marques-Toigo and Piccarelli, 1985
Figure 5.3–5

Dimensions (55 specimens). Exoexine maximum diameter (ED), 60(65–80)100 µm; intexine maximum diameter (id), 43(55–68)80 µm; ED/id ratio, (1.1–1.3)1.4; cingulum thickness, 2(3–4)5 µm.

Lundbladispora **sp. cf.** ***L. springsurensis*** de Jersey, 1979
Figure 5.7

Remarks. We establish compare rather than assign to species because the trilete mark does not show conspicuous lips.
Dimensions (8 specimens). Exoexine maximum diameter (ED), 55–81 µm; intexine maximum diameter (id), 53–67 µm; ED/id ratio, 1.2–1.3; cingulum thickness, 3 µm. Sculptural elements: spinae and some coni, 1(1.5–2)3 µm in basal width, 1.6(3)8 µm high.

Lundbladispora verrucosa sp. nov.
Figures 5.6, 8–9, 12; 6.1–10, 12–14

1979 *Lundbladispora?* sp. A, Foster, p. 54, pl. 13, fig. 8.
1990a *Densoisporites* sp. 1, Zavattieri, p. 219, pl. 3, figs. 5, 8–9
1990a *Cirratriradites* sp. 1, Zavattieri, p. 214, 216, pl. 4, figs. 2, 4, 7, 9–11.

1990a *Cirratriradites* sp. cf. *C. splendens* Balme and Hennelly, 1956, Zavattieri, p. 214, pl. 3, fig. 7, pl. 4, figs. 6, 12.

Derivation of name. Referred to the dominating verrucose sculpture of the distal face.

Diagnosis. Radial trilete spores, cingulate-cavate, anisopolar; sub-triangular to sub-rounded amb. Intexine forming an inner body close to the equatorial amb of the spores and showing occasional foldings and/or thickenings on the margin of the body giving the aspect of a peripheral intexinal ring. Smooth proximal face, usually concave; trilete mark bordered by elevated lips slightly thickened and straight to slightly sinuous reaching the outer edge of the intexine. Distal face convex and carrying verrucae of variable shapes and sizes, tightly arranged, usually joint together forming irregular muri separated by thin spaces (fosules) of irregular design. The sculpture also includes granules (generally between the verrucae) and, occasionally, gemmate elements.

Holotype. MPLP 8251(I) R51/3 (Fig. 5.8).

Paratypes. MPLP 8248(F) E44/3 (Fig. 5.9), MPLP 8249(G) H54/3 (Fig. 5.12), MPLP MEB 8249(T6) 0232 (Fig. 6.8), MPLP MEB 8253(T3) 0126 (Fig. 6.10), MPLP MEB 8249(T6) 0259 (Fig. 6.14).

Geographic provenance. La Yesera locality, Paganzo Basin, Famatina Range, La Rioja Province.

Stratigraphic provenance. Upper section and type locality of the La Veteada Formation, Lopingian.

Dimensions (215 specimens)**.** Exoexine maximum diameter, 30(35–45)55 µm; intexine maximum diameter, 21(30–39)44 µm; ED/id ratio, 1.1(1.2–1.3)1.5; cingulum thickness, 2–4 µm. Lips, 0.7(1–2)3 µm wide x 2.2–3.5 µm high. Sculptural elements: in lateral view, 1(1.2–2.6)5 µm basal diameter x 0,5(0,7–1,7)2,5 µm high; in plain view, verrucae, 1(1.2–2.8)5 x 0.5(0.8–1.8)3 µm, granulae, 0.6(1–2.2)3 µm in diameter.

Comparisons. The most similar species to *Lundbladispora verrucosa* sp. nov. is *Lundbladispora warti* Tiwari and Rana, 1981. However, the latter is larger (84–87 µm in diameter) and has coarser ornamentation (4–7 µm high and 4–10 µm wide). It is exclusively composed of verrucae and does not exhibit/present foldings and/or a peripheral thickening of the intexine. Specimens whose ornamentation appears tight and fused give a false negative aspect of the sculpture (fosules). Therefore, these specimens could be compared with the only species of *Lundbladispora* with negative ornamentation, *L. foveota* Qu and Wang (1986), although it has conspicuous and larger foveolae.

Lundbladispora? sp. A (Foster, 1979, pl. 13, fig. 8) has a similar ornamentation to that of the La Veteada specimens, which mainly consists of verrucae and granules of similar dimensions, laesurae with sinuous lips and an inner body slightly thickened at the equator. All of these features enable its inclusion within *L. verrucosa* sp. nov.

The material assigned by Zavattieri (1990a) as *Cirratriradites* sp. 1, *Densoisporites* sp. 1 and *Cirratriradites* sp. cf. *C. splendens* Balme and Hennelly, 1956 also has a similar morphology and sculptural features (dimensions, amb and, mainly, an ornamentation composed of verrucae and granulae) allowing to consider them as *Lundbladispora verrucosa* sp. nov.

Probably, some of the species illustrated by Ouyang and Norris (1988), such as *L.* sp. A (pl. 3, fig. 11), *L.* sp. B (pl. 3, fig. 12) and *L.* sp. C (pl. 3, figs. 19–20), are superficially similar to *L. verrucosa* sp. nov. However, they have not been described and their comparison is thus purely speculative.

Lundbladispora wilmotti Balme emend. Playford, 1965

Figure 5.10–11

Dimensions (120 specimens). Exoexine maximum diameter, 55(65–80)90 µm; intexine maximum diameter, 40(44–65)75 µm; ED/id ratio, 1.1(1.2–1.4)1.8; thickness of the

Figure 5. 1, ***Lundbladispora*** **sp. cf.** ***L. gracilis*****, MPLP** 8250(G) O45/0. **2,** ***Lundbladispora obsoleta*****, MPLP** 8252(J) M45/0. **3–5,** ***Lundbladispora riobonitensis*****; 3, MPLP** MEB 8249(T6) 0273; **4, MPLP** 8249(F) R38/1; **5, MPLP** 8248(D) R42/1. **6, 8–9, 12,** ***Lundbladispora verrucosa*** **sp. nov.; 6, MPLP** MEB 8249(T7) 0339; **8,** Holotype, **MPLP** 8251(I) R51/3; **9,** Paratype, **MPLP** 8248(F) E44/3; **12,** Paratype, **MPLP** 8249(G) H54/3. **7,** ***Lundbladispora*** **sp. cf.** ***L. springsurensis*****, MPLP** 8253(H) P36/3. **10–11,** ***Lundbladispora wilmotti*****; 10, MPLP** 8250(H) J36/0; **11, MPLP** MEB 8253(T3) 0102. Scale bars= 20 µm.

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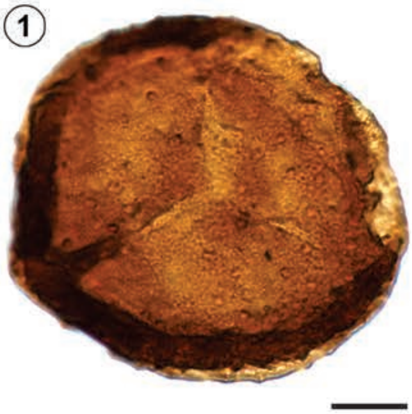

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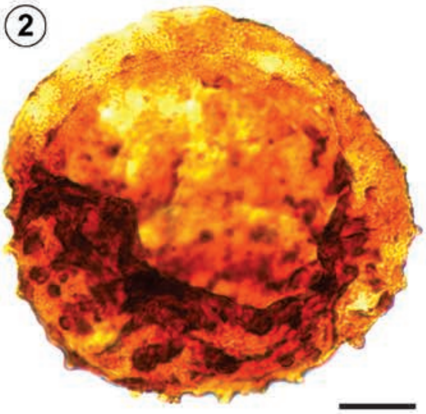

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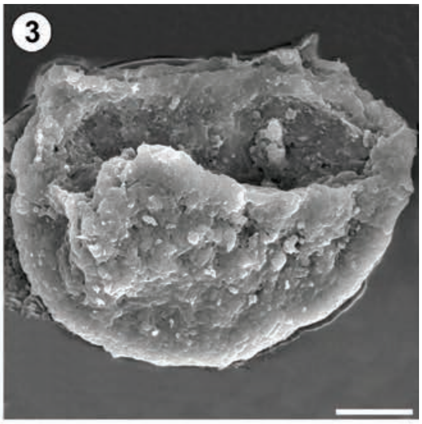

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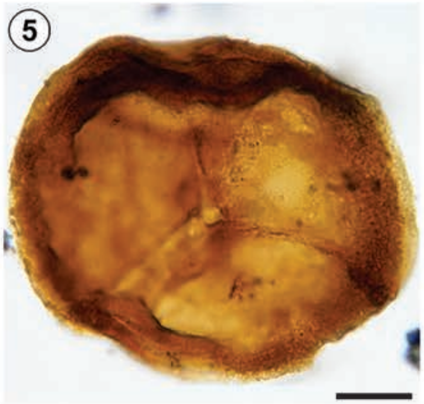

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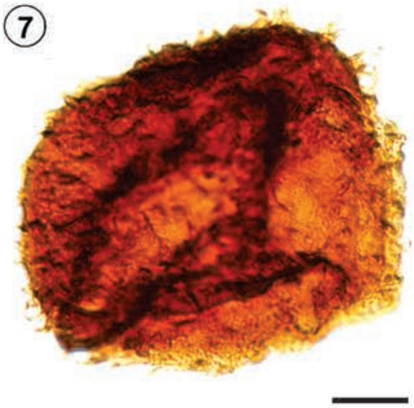

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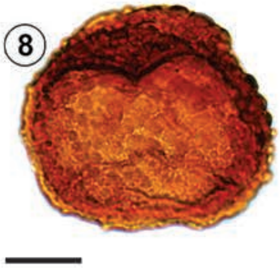

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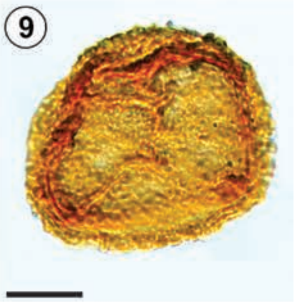

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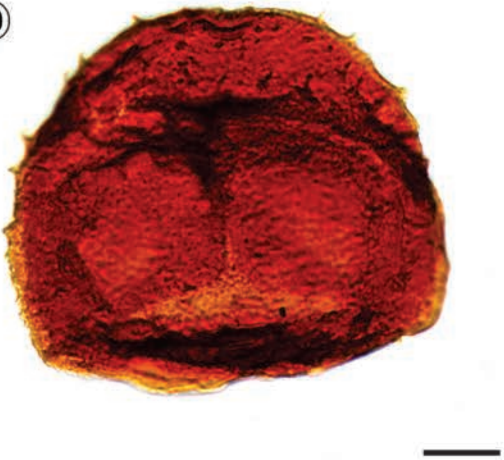

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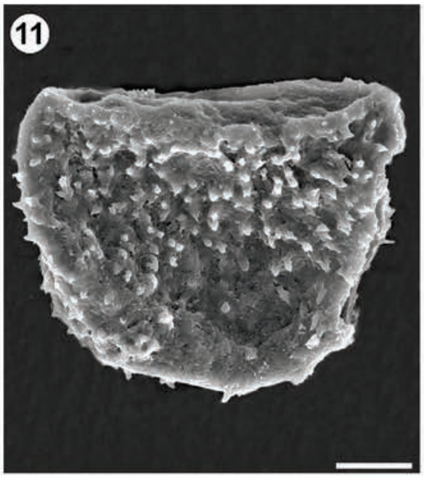

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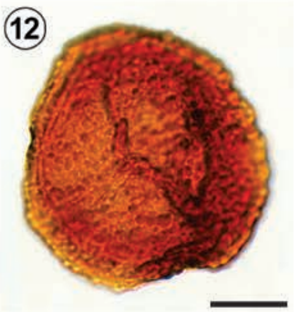

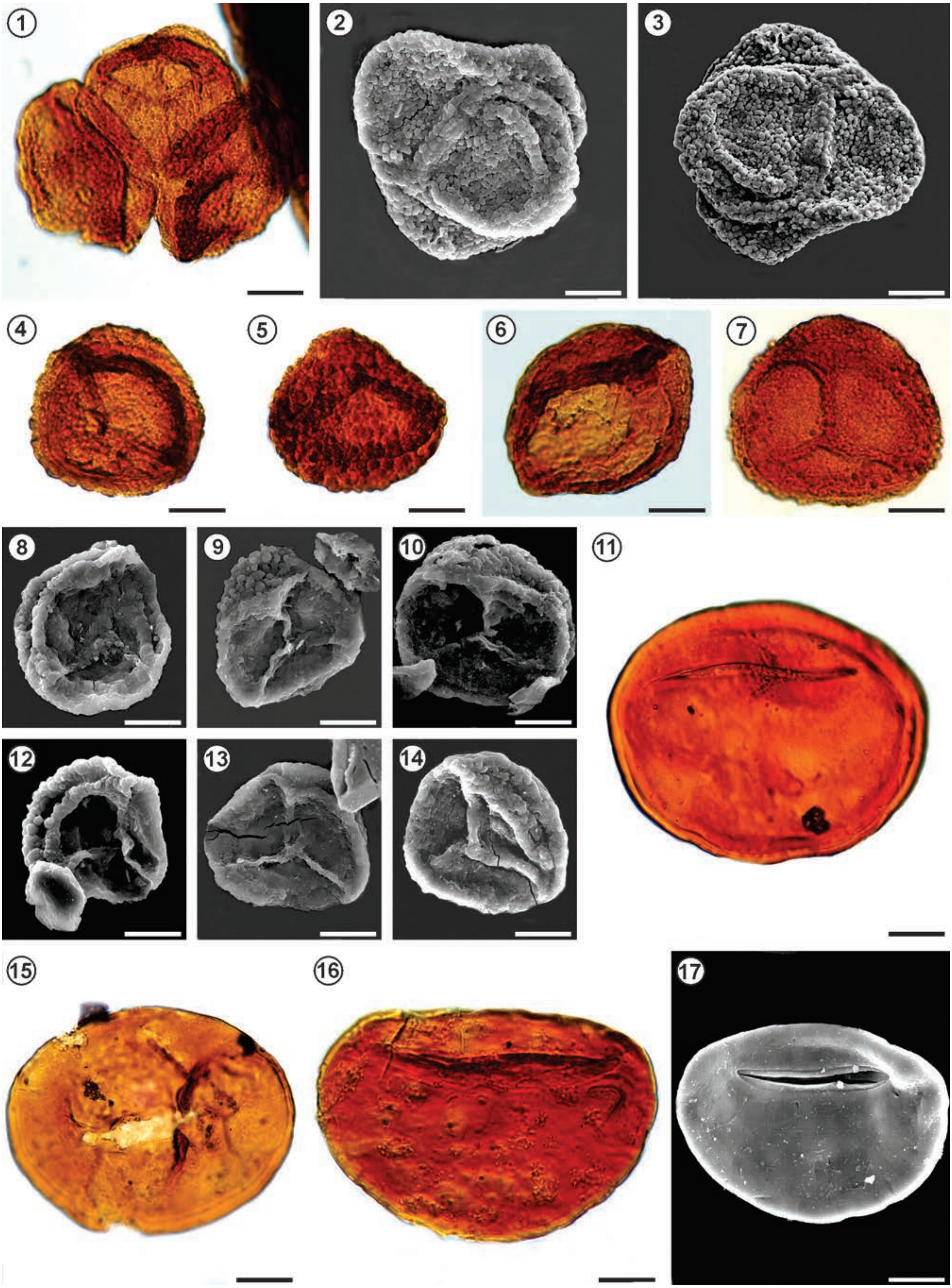
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cingulum, 3(4)6 μm. Sculptural elements: spinae, (1–2)2.5 μm in basal width (2.2–4), 5 μm high; coni and bulbous elements, 1.2(1.5–3)4.5 μm in basal diameter and 1(2–4)5 in hight.

Lundbladispora-Densoisporites *tetrads significance*

According to Looy *et al.* (2001), in the terrestrial ecosystems of the northern hemisphere at the end of the Permian, vegetation reflects a gradual conversion from closed forests dominated by conifers to stable open herbaceous vegetation mainly composed of seed ferns and heterosporous lycopsids strongly dominated by Selaginellales and Isoetales. This change appears in the palynological record evidenced by the replacement of assemblages dominated by gymnosperm pollen palynological assemblages dominated by lycopsid spores (*Lunbladispora*, *Densoisporites*, *Kraeuselisporites*, *Secarisporites*, *Limatulasporites=Ringosporites*, etc.). These "new" lycopsid-dominant microfloras present a considerable number of tetrads. Microfloras containing a high proportion of lycopsid-tetrads are commonly recorded in Lopingian to Early Triassic strata mainly in the extra Gondwanic realm (see Fig. 7) of Canada (Utting, 1994; Looy *et al.*, 2005), Barents Sea (Mangerud, 1994), the Pechora Basin/Urals in Russia (Tuzhiakova, 1985), East Greenland (Looy *et al.,* 2001; Visscher *et al.*, 2004), the Moscow Basin in Russia (Afonin, 2000), Italy (Massari *et al.*, 1994; Looy *et al.*, 2005), Hungary (Góczán *et al.,* 1986; Haas *et al.,* 1986, 1988), the Jungar Basin of Xinjian in North China (Qu and Wang, 1986; Ouyang and Norris, 1999; Looy *et al.*, 2005) and Meishan in South China (Ouyang and Utting, 1990), among others. Gondwanic records of the Permian/Triassic boundary are restricted to India and south-eastern Africa: Auranga Basin, India (Banerji and Maheswari, 1975); Raniganj Basin, India (Tiwari and Tripati, 1987; Tiwari and Meena, 1988); Madagascar (Wright and Askin, 1987; Looy *et al.,* 2005); Sri Lanka (Dahanayake *et al.*, 1989); and Mombassa Basin, Kenya (Hankel, 1992).

These spore-tetrads are known to occur among a variety of lycopsids and this is a feature usually found in the genera *Densoisporites* Weyland and Krieger 1953, *Lundbladispora* Balme, 1963, *Secarisporites* Neves, 1961, *Kraeuselisporites* Leschik, 1956 and *Decisporis* Kar, 1970. On the other hand, the genus *Lapposisporites* Visscher, 1966 is used to nominate spore-tetrads. Some megaspores have also retained their status as tetrads (see Fuglewicz, 1977).

In particular, in the microflora of the upper section of the La Veteada Formation, the spore-tetrads are referred to the most common lycopsid genera, such as *Densoisporites, Lundbladispora* and *Secarisporites*, reaching striking proportions of up to 4.94% of the total spectra (Supplementary Online Information 1).

According to Looy *et al.* (2001) and Visscher *et al.* (2004), this high-occurrence of tetrads phenomenon would be the result of opportunistic herbs (lycopsids) which, due to their capacity to expand rapidly into stressed environments, proliferated and colonized the vacant ecosystems dominated by woody elements.

Age and correlation

The upper section of the La Veteada Formation, at its type locality "La Yesera", was assigned to the Lopingian Stage (Zavattieri *et al.*, 2008; Zavattieri and Gutiérrez, 2012; Gutiérrez *et al.*, 2014; Zavattieri *et al.*, 2017) based on the stratigraphic range of all the land-derived miospore species therein recognized. The spores described and/or illustrated herein are widely distributed in Lopingian strata; *e.g. Densoisporites complicatus*, *D. nejburgii, D. playfordii, D. solidus, Leptolepidites jonkeri, Lundbladispora brevicula, L. obsoleta, L. springsurensis, L. wilmotti, Ringosporites fossulatus, Secarisporites bullatus, S. imperialis* and *S. lacunatus*, which were recorded in these assemblages together with several pollen grain species belonging to the genera *Striatopodocarpites, Protohaploxypinus, Lueckisporites, Hamiapollenites, Lunatisporites, Vittatina, Weylandites, Marsupipollenites, Corisaccites,*

Figure 6. 1–10, 12–14, ***Lundbladispora verrucosa*** sp. nov.; **1, MPLP** 8248(H) J45/0; **2, MPLP** MEB 8249(T7) 0333; **3, MPLP** MEB 8249(T6) 0350; **4, MPLP** 8250(I) L42/0; **5, MPLP** 8251(I) M51/0; **6, MPLP** 8250(J) G54/0; **7, MPLP** 8249(I) J40/0; **8,** Paratype, **MPLP** MEB 8249(T6) 0232; **9, MPLP** MEB 8249(T6) 0234; **10,** Paratype, **MPLP** MEB 8253(T3) 0126; **12, MPLP** MEB 8249(T6) 0283; **13,** Paratype, **MPLP** MEB 8249(T6) 0259; **14**, **MPLP** MEB 8249(T7) 0337. **11, 15,** ***Laevigatosporites*** sp. cf. ***L. vulgaris*****; 11, MPLP** 8251(I) E37/0; **15, MPLP** 8252(B) E39/4. **16–17,** ***Laevigatosporites callosus*****; 16, MPLP** 8249(F) S37/4; **17, MPLP** MEB 8249(T6) 0256. Scale bars= 20 μm.

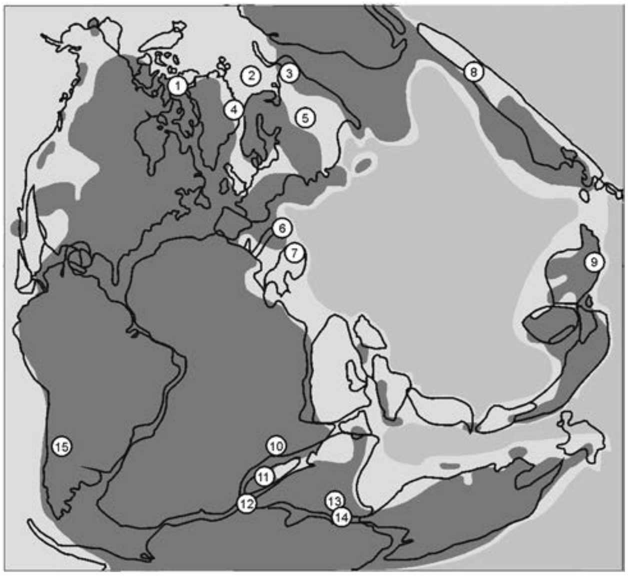

Figure 7. Records of lycopsid tetrads in Permian-Triassic transitional sequences (modified from Looy *et al.,* 2005). **1,** Sverdrup Basin, Arctic Canada; **2,** Barents Sea; **3,** Pechora Basin/Urals, Russia; **4,** East Greenland; **5,** Moscow Basin, Russia; **6,** Italy; **7,** Hungary; **8,** Jungar Basin, Xinjian, North China; **9,** Meishan, South China; **10,** Mombassa Basin, Kenya; **11,** Madagascar; **12,** Sri Lanka; **13,** Auranga Basin, India; **14,** Raniganj Basin, India; **15,** Paganzo Basin Argentina (this paper).

Staurosaccites, Pakhapites and *Gouvinispora*, among others (Gutiérrez *et al.*, 2014), widely omnipresent in Late Paleozoic microfloral assemblages. The occurrence of the lycopsid spore tetrads (up to 4.94% of the total palynological spectra, see Supplementary Online Information 1) mainly pertains to the genera *Densoisporites, Lundbladispora* and *Secarisporites* and constitutes another common feature observed in palynological assemblages of the Lopingian strata (Looy *et al.*, 2001, 2005; Visscher *et al.*, 2004) from the Northern Hemisphere and part of Gondwana (see Fig. 7).

The aquatic components of the La Veteada assemblage are also characterized by the occurrence of widely distributed continental Lopingian microphytoplankton and fungi such as the chlorophycean algae *Syndesmorion stellatum* (Fijałkowska) Foster and Afonin, the genera *Maculatasporites* and *Melhisphaeridium* of likely algal derivation, and representatives of zygnematacean algae, *Brazilea scissa*, *B. plurigenus*, *B.* sp. A and *Tetraporina tetragona*, among others, together with *Reduviasporonites chalastus* (Zavattieri *et al.*, 2017).

Among the species recorded so far in the upper La Veteada assemblage (Zavattieri and Gutiérrez, 2012; Gutiérrez *et al.*, 2014; Zavattieri *et al.*, 2017), two groups of miospores are distinguished (Tab. 2). The first one comprises records from the Permian and the Triassic of central-western Argentina, which enable a comparison with the *LW* Biozone (*Lueckisporites-Weylandites*), as defined by Césari and Gutiérrez (2001) for the west of the country. The second group comprises species recorded for the first time in Argentina, including though not limited to *Cladaitina veteadensis* Zavattieri and Gutiérrez, *Syndesmorion stellatum* (Fijałkowska) Foster and Afonin, *Meristocorpus veteadensis* Gutiérrez, Zavattieri and Ezpeleta, *Striomonosaccites circularis* Bharadwaj and Salujha, *Guttulapollenites hannonicus* Goubin, *Lahirites segmentatus* Dino and Playford, *Lueckisporites crassus* Sinha, *Lueckisporites biformis* Gutiérrez *et al.*, *Lunatisporites arluki* Utting, *L. globus* Hart, *L. lenticularis* Gutiérrez *et al.*, *L. transversundatus* (Jansonius) Dunay and Fisher, *Protohaploxypinus chaloneri* Clarke, *P. panaki* Utting, *Striatopodocarpites renisaccatus* (Lakhanpal, Sah and Dubé) Hart, *Striatisaccus goswicensis* Mädler, *Vittatina simplex* Jansonius and *Weylandites circularis* Bharadwaj and Srivastava.

This last group indicates that the upper La Veteada Assemblage could be separated from the *LW* Biozone. Such separation is reinforced by the fact that among the 36 species of spores identified in this assemblage (Tab. 2), half have no records in the Permian/Triassic of central-western Argentina (*i.e.*, *Densoisporites solidus*, *Indotriradites apiculatus*, *Leptolepidites jonkeri*, *Lundbladispora brevicula*, *L.* cf. *gracilis, L. obsoleta*, *L.* cf. *springsurensis*, *L. wilmotti*, *Ringosporites fossulatus*, *Secarisporites bullatus*, *S. imperialis*, *S. lacunatus* and *S. triangularis*).

All of these features provide supporting evidence for the age of the upper La Veteada assemblage, which is the youngest Permian palynofloral assemblage recorded up to now in Argentina and South America.

Remarks on the composition and diversity

More than 90 palynomorph genera of spores, pollen grains, algae and fungi were described, listed and illustrated from the upper La Veteada Formation microflora (Zavattieri *et al.*, 2008, 2017; Zavattieri and Gutiérrez, 2012; Gutiérrez *et al.*, 2014). The La Veteada Assemblage is significantly dominated by bisaccate pollen grains (~78%) [taeniate

TABLE 1 – Distribution of the species of spores in the La Veteada type section assemblages.

Taxa	*MPLP 8248*	*MPLP 8249*	*MPLPB 8250*	*MPLP 8251*	*MPLP 8252*	*MPLP 8253*
Brevitriletes cornutus	*X*	*X*	*X*	*X*	*X*	*X*
Brevitriletes levis	*X*	*X*	*X*	*X*	*X*	*X*
Brevitriletes *sp. A*	*X*	*X*	*X*	*X*	*X*	*X*
Densoisporites complicatus	*X*	*X*	*X*	*X*	*X*	*X*
Densoisporites nejburgii	*X*	*X*	*X*	*X*	*X*	*X*
Densoisporites playfordii	*X*	*X*	*X*	*X*	*X*	*X*
Densoisporites solidus	*X*	*X*	*X*	*X*	*X*	*X*
Densoisporites *spp.*	*X*	*X*	*X*	*X*	*X*	*X*
Indotriradites apiculatus	*X*	*X*	*X*	*X*	*X*	*X*
Lundbladispora brevicula	*X*	*X*	*X*	*X*	*X*	*X*
Lundbladispora verrucosa	*X*	*X*	*X*	*X*	*X*	*X*
Lundbladispora wilmotii	*X*	*X*	*X*	*X*	*X*	*X*
Punctatisporites gretensis	*X*	*X*	*X*	*X*	*X*	*X*
Punctatisporites lucidulus	*X*	*X*	*X*	*X*	*X*	*X*
Punctatisporites *spp.*	*X*	*X*	*X*	*X*	*X*	*X*
Secarisporites imperialis	*X*	*X*	*X*	*X*	*X*	*X*
Secarisporites lacunatus	*X*	*X*	*X*	*X*	*X*	*X*
Tetrads cingulati/apiculati spores	*X*	*X*	*X*	*X*	*X*	*X*
Convolutispora *spp.*	*X*	*X*	*X*	*X*		*X*
Kraeuselisporites punctatus	*X*	*X*	*X*	*X*		*X*
Anapiculatisporites *spp.*	*X*		*X*	*X*	*X*	*X*
Leiotriletes *spp.*	*X*		*X*	*X*	*X*	*X*
Retusotriletes *spp.*	*X*		*X*	*X*	*X*	*X*
Cyclogranisporites *sp. A*	*X*		*X*		*X*	*X*
Ringosporites fossulatus	*X*			*X*	*X*	*X*
Calamospora tener	*X*	*X*	*X*	*X*	*X*	
Lundbladispora riobonitensis	*X*	*X*	*X*	*X*	*X*	
Lundbladispora *spp.*	*X*	*X*	*X*	*X*	*X*	
Secarisporites triangularis	*X*	*X*	*X*	*X*	*X*	
Verrucosisporites *spp.*	*X*	*X*	*X*	*X*	*X*	
Indotriradites *spp.*	*X*	*X*	*X*		*X*	
Leiotriletes *sp. cf.* **L. adnatus**	*X*	*X*	*X*		*X*	
Lundbladispora obsoleta	*X*	*X*	*X*		*X*	
Lundbladispora *sp. cf.* **L. gracilis**	*X*		*X*	*X*	*X*	
Laevigatosporites *spp.*	*X*		*X*	*X*	*X*	
Cyclogranisporites *spp.*	*X*			*X*	*X*	
Leiotriletes directus	*X*				*X*	
Osmundacidites wellmanii	*X*	*X*	*X*	*X*		
Grumosisporites *sp. A*	*X*	*X*	*X*	*X*		
Calamospora breviradiata_	*X*		*X*	*X*		
Converrocosisporites *sp. A*	*X*		*X*	*X*		
Punctatisporites priscus	*X*		*X*	*X*		
Cristatisporites *spp.*	*X*			*X*		
Stereisporites psilatus	*X*			*X*		
Granulatisporites *spp.*	*X*		*X*			
Laevigatosporites callosus	*X*		*X*			
Osmundacidites senectus	*X*		*X*			
Dictyotriletes *spp.*	*X*					
Horriditriletes ramosus		*X*				
Brevitriletes *spp.*		*X*	*X*	*X*	*X*	*X*
Secarisporites bullatus		*X*	*X*	*X*	*X*	*X*
Lundbladispora *sp. cf.* **L. springsurensis**		*X*	*X*			*X*
Leptolepidites jonkerii		*X*	*X*		*X*	
Lophotriletes lentiginosus			*X*			
Stereisporites *spp.*			*X*	*X*		
Laevigatosporites *sp. cf.* **L. vulgaris**					*X*	

(~68%) and non-taeniate (~32%)]. Quantitatively less important components are trilete and monolete spores (~20%) while the remaining groups (plicates, monosaccates and inaperturates) are relatively rare (~2%).

Diverse gymnosperms (conifers and pteridosperms-glossopterids, peltasperms and corystosperms) are abundantly represented in the La Veteada assemblage, with different pollen types being the prevalent components both quantitatively and qualitatively. The taeniate bisaccate pollen grains comprise very conspicuous elements (derived from voltzials and glossopterids) of this palynoflora mainly represented by the genera *Protohaploxypinus, Lunatisporites, Lueckisporites*, *Guttulapollenites*, *Corisaccites*, *Staurosaccites*, *Striatiabieites*, *Striatopodocarpites, Limitisporites* and *Hamiapollenites,* among others (Gutiérrez *et al.,* 2014). Pteridosperm bisaccate non-striate pollen grains (peltasperms, corystosperms, caytonialean) are common components mainly represented by *Alisporites-Falcisporites, Scheuringipollenites, Klausipollenites, Vitreisporites, Minutosaccus* and *Protodiploxypinus.* Other pteridosperm (Peltaspermaceae) contributions most likely include plicate or polyplicate pollen grains including the genera *Vittatina*, *Weylandites, Marsupipollenites Praecolpatites* and *Cycadopites* (Cycadophyte) (Gutiérrez *et al.,* 2014). Cordaitalean and coniferalean monosaccate pollen grains (stratiate and non-striate) are scarcely represented by *Potoniesporites*, *Cannanoropollis*, *Goubinispora, Gondwanapollenites* and *Striomonosaccites.*

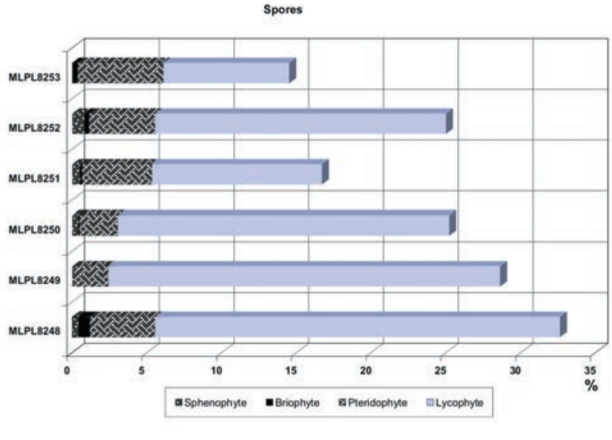

Figure 8. Composition according to botanical affinity of spores identified in the La Veteada Formation assemblages at its type section.

Derived from lower vascular plants, the trilete spores (Fig. 8; Supplementary Online Information 1) represented in this palynoflora are prominently dominated by the lycopsid cingulate-cavate group represented by species of the genera *Densoisporites*, *Densosporites-Lundbladispora, Secarisporites* and, in less proportion, by the complex *Cristatisporites-Kraeuselisporites.* Smooth and apiculate trilete spores (derived from Pteridophyte, Sphenophyte and Bryophyte) are represented by the genera *Calamospora, Punctatisporites, Granulatisporites, Brevitriletes*, *Cyclogranisporites*, *Osmundacidites*, *Verrucosisporites, Raistrickia* and *Foveosporites,* among others.

Trilete spores are one of the dominant groups in the palynological assemblage of the upper section of the La Veteada Formation at its type locality (see tab. 1 in Gutiérrez *et al.*, 2014) and decrease their proportion towards the top of the sampled section (from 32.2% to 14.5%), while monolete spores appear in very low proportions (less than 0.4%) throughout the section.

PALEOECOLOGICAL IMPLICATIONS

This section describes the ecological preferences of spore-producing plant groups (bryophytes, lycophytes, sphenophytes and fern spores) that contributed to the composition of the palynological assemblages in the type section of the La Veteada Formation (Fig. 8). The botanical affinities of the taxa identified in this work are summarized in Supplementary Online Information 2. The relative abundances of the identified genera are expressed as percentages based on a count of at least 300 palynomorphs (Supplementary Online Information 1).

Based on the botanical affinities of the miospores and the habitats of the parent-plants, we use the concept of Sporomorph EcoGroups (SEG), introduced by Abbink (1998) and Abbink *et al.* (2004), which refers to taxa with broadly similar ecological preferences that characterize distinctive habitats or plant paleocommunity types. Applying this term to the continental environments recognized in the La Veteada type section, we identify four SEGs: upland, lowland, coastal (or lacustrine-influenced) and riverside.

Bryophyta

Bryophytes including mosses, hornworts and liverworts (Taylor and Taylor, 1993; Balme, 1995) are represented in

Table 2 – Biostratigraphic/lithostratigraphic distribution of the species of spores identified in the palynological assemblages of the upper La Veteada Formation.

Biostratigraphic/Lithostratigraphic units		*FS*	*LW*	*LV Fm (us)*	*QdLF Fm*	*CdLC FM*	*Po Fm*	*Ca Fm*
Taxa	*Source*	*1*	*1*	*2*	*3*	*4*	*5*	*6*
Kraeuselisporites punctatus		X		X				X
Brevitriletes levis		X	X	X	X	X		
Brevitriletes cornutus		X		X		X		
Horriditriletes ramosus		X	X	X	X			
Leiotriletes directus		X	X	X	X		X	
Punctatisporites gretensis		X	X	X	X			
Calamospora breviradiata		X	X	X				
Lundbladispora riobonitensis		X	X	X				
Laevigatosporites vulgaris		X	X	?				
Lophotriletes lentiginosus		X		X				
Densoisporites complicatus				X	X	X	X	X
Calamospora tener				X	X	X	X	
Stereisporites psilatus				X		X	X	
Densoisporites playfordii				X			X	
Osmundacidites senectus				X			X	
Densoisporites nejburgii				X	X	X	X	
Osmundacidites wellmanii				X			X	
Lundbladispora verrucosa				X		X		
Densoisporites solidus				X				
Indotriradites apiculatus				X				
Leiotriletes adnatus				?				
Leptolepidites jonkerii				X				
Lundbladispora brevicula				X				
Lundbladispora gracilis				?				
Lundbladispora obsoleta				X				
Lundbladispora springsurensis				?				
Lundbladispora wilmotii				X				
Punctatisporites lucidulus				X				
Punctatisporites priscus				X				
Ringosporites fossulatus				X				
Secarisporites bullatus				X				
Secarisporites imperialis				X				
Secarisporites lacunatus				X				
Secarisporites triangularis				X				
Laevigatosporites callosus				X				
Tetrads cingulati/apiculati spores				X				

FS *(***Pakhapites fusus-Vittatina subsacata*** *Biozone);* ***LW*** *(***Lueckisporites-Weylandites*** *Biozone);* ***LV Fm-us*** *(La Veteada Formation, upper section);* ***QdLF Fm*** *(Quebrada de Los Fósiles Formation);* ***CdLC Fm*** *(Cerro de Las Cabras Formation);* ***Po Fm*** *(Potrerillos Formation);* ***Ca Fm*** *(Cacheuta Formation).* ***1,*** *Césari and Gutiérrez (2001);* ***2,*** *this paper;* ***3,*** *Ottone and García, 1991; Zavattieri, 2002; Zavattieri* et al., *2003; Vázquez* et al., *2012; Vázquez, 2013;* ***4,*** *Zavattieri, 1990a, b, 2002;* ***5,*** *Zavattieri, 1986, 2002; Rojo and Zavattieri, 2005; Zavattieri and Rojo, 2005;* ***6,*** *Zavattieri, 2002; Rojo and Zavattieri, 2005; Zavattieri and Rojo, 2005.*

the La Veteada assemblage by *Ringosporites* and *Strereisporites*. Both genera appear in very low proportions (less than 0.45%, see Supplementary Online Information 1; Fig. 8). Bryophytes prefer wet or humid environments, but most can tolerate long periods of drought (Abbink *et al.*, 2004). They were assigned to the river-side and/or lowland bryophytes SEGs by Abbink *et al.* (2004).

Sphenophytes

Calamospora is the only dispersed morphogenus identified in this microflora whose parent-plant refers to articulate Equisetales. According to Abbink *et al.* (2004), Sphenophytes (horsetails) require a wet habitat (river bank). Thus, it would represent riverside SEG.

Lycophytes

Lycopsids (microspores and megaspores) comprise Lycopodiaceae, Selaginellaceae and Isoetaceae, and, since the Lopingian, their dispersed spores generally constitute minor but persistent components of fossil microfloras (Balme, 1995). The lycopsid species recorded in the La Veteada assemblage are: *Densoisporites, Lunbladispora, Secarisporites, Kraeuselisporites, Indotriradites, Leptolepidites* and *Cristatisporites. Densoisporites, Lunbladispora* and *Secarisporites* show the higher percentages within this group (Supplementary Online Information 1). *Densoisporites* are supposed to adapt to water dispersal and may belong to a tidally-influenced ecosystem (Abbink *et al.*, 2004). Balme (1995) remarked that the dispersed genera *Densoisporites* and *Lunbladispora*, pertaining to the Pleuromeiaceae, are particularly abundant in Early Triassic shallow marine strata, indicating that at least some species were halophytes colonizers of broad tidal flats. The Lycopsid spores recorded in this microflora suggest that their parent-plants grew in lowland, riverside and/or coastal hypersaline lacustrine ecosystems within the La Veteada environments according to the SEG concept of Abbink *et al.* (2004).

Ferns

The fern spores are represented in low proportions (2.28 to 5.73%) by the form-genera *Brevitriletes, Punctatisporites, Verrucosisporites, Osmundacidites, Leiotriletes, Cyclogranisporites, Retusotriletes, Convolutispora, Anapiculatisporites, Laevigatosporites, Grumosisporites, Granulatisporites, Horriditriletes* and *Dictyotriletes*. Most of these forms are rare elements (see Supplementary Online Information 1) in the La Veteada Assemblage.

Most ferns grow in warm and humid conditions, in protected places, such as swamps, river banks or understory in forests (Van Konijnenburg-Van Cittert, 2002). In the ecological system of Abbink *et al.* (2004), most of the fern spores are considered as characteristic of the lowlands (swamps) or river-side SEGs.

Spore-producing plants (bryophytes, lycophytes and ferns) require optimal humidity conditions to grow. Thus, microfloras recovered from lithologies indicating humid environments usually the contents of spores appear in high relative abundance (see Schrank, 2010).

The sedimentology of the upper section of the La Veteada Formation at its type locality evidences that it was deposited in fluvial-lacustrine environments, mainly semi-perennial hypersaline/brackish lakes with periodic expansion and retraction episodes, suggesting a low-relief setting (see Gutiérrez *et al.,* 2014; Zavattieri *et al.,* 2017). In the vicinity of these flood-prone environments, herbaceous vegetation mainly composed of herbaceous lycophytes (Isoetales, Selaginellales, Lycopodiales) and ferns developed. On the flood-plain, the areas bordering rivers draining into the water bodies, vegetation included pteridophytes (Filicales, Zygopteridales), bryophytes and herbaceous sphenophytes, whose spores were washed away by the water-courses towards the places of deposition. The lacustrine hypersaline/brackish depositional environments evidenced in the La Veteada type section were colonized by coenobia of the authochthonous chlorophycean algae *Syndesmorion stellatum* (Fijałkowska) Foster and Afonin, which grew in these stressed hypersaline lacustrine environments. Representatives of zygnematacean algae were also recorded within the La Veteada micro-phytoplantkton, including species of *Brazilea*, *Tetraporina,* ?*Lecaniella*, *Maculatasporites, Mehlisphaeridium* and planar colonial chlorococcal hydrodictyaceaen *Pediastrum*-like forms, as well as *Reduviasporonites chalastus*, also of a probable zygnematacean afinity (Zavattieri *et al.,* 2017). It was interpreted that the Zygnematacean algae were probably dragged from close freshwater habitats and/or from other low salininity water bodies to the site of deposition (Zavattieri *et al.*, 2017). Dávila *et al.* (2005) and Limarino *et al.* (2014) pointed out that the La Veteada Formation was deposited, during the Lopingian, under arid to semiarid climates. The relative low proportion of spores in relation to the high abundance of coniferous, voltzialean and cordaitalean pollen grains also reflects parental vegetation adapted to arid, perhaps even desert conditions, of certainly low humidity, as reflected by the sedimentological evidence.

CONCLUSIONS

Two new species were recorded in the Permian of Argentina: *Lundbladispora verrucosa* nov. sp. and *Secarisporites triangularis* nov. sp., and the new combination was proposed for *Secarisporites imperialis* (Jansonius) nov. comb.

On the other hand, the spores identified in the palynological assemblages of the upper La Vetedada Formation support a Lopingian age for the type locality of the unit (La Yesera) as discussed previously on the basis of the characteristic features showed by the striate pollen grains (Gutiérrez *et al.*, 2014) and the microphytoplankton diversity (Zavattieri *et al.*, 2017).

The composition of the upper La Veteada assemblage can be clearly differentiated from that of the Permian as well as the Triassic Argentinian palynological assemblages. This assemblage is thus the youngest Permian microflora hitherto recorded in Argentina and South America.

The upper section of the La Veteada Formation at its type locality was deposited in fluvial-lacustrine environments under arid to semiarid climatic conditions. Semi-perennial hypersaline/brackish lakes dominate the sedimentation, with periodic expansion and retraction episodes suggesting a low-relief setting. In the surrounding areas of these stressed evaporate-dominated water-bodies, herbaceous vegetation mainly composed of herbaceous lycophytes (Isoetales, Selaginellales, Lycopodiales) and ferns grew. Conversely, in the flood-plain, herbaceous vegetation of pteridophytes (Filicales, Zygopteridales), bryophytes and herbaceous sphenophytes developed along the river courses and in the surrounding areas of the freshwater bodies. In higher and far away areas, forests of conifers, voltzialean and cordaitalean that could also tolerate drought periods provided the allochthonous components of the La Veteada assemblage.

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