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Syndesmorion stellatum (Fijałkowska) Foster et Afonin chlorophycean algae and associated microphytoplankton from lacustrine successions of the La Veteada Formation (late Permian), Paganzo Basin, Argentina. Paleoenvironmental interpretations and stratigraphic implications

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ABSTRACT

A diverse microphytoplankton assemblage recovered from terrestrial deposits of the La Veteada Formation, north of the La Rioja Province, Paganzo Basin, Argentina, is described and illustrated. The ~180 m thick sedimentary type section of the unit in the Los Colorados anticline is composed of a basal gray silcrete covered by gypsum beds and a thick succession of purple mudstones inter-layered with varicolored fine sandstone sheets and laminated yellowish dolomites. The aquatic assemblage is mainly characterized by a great variety of *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin coenobia, recorded for the first time in the late Permian Gondwanic realm. All the previous morphotypes described for this chlorophycean alga are recognized in this assemblage, and new polymorph-coenobia are described and illustrated. The diversity of coenobia morphotypes of this alga is likely to reflect response to stress conditions. The genera *Maculatasporites* and *Mehlisphaeridium* are commonly present, and their algal origin is discussed. *Maculatasporites gondwanensis*, *Maculatasporites amplus*, *Mehlisphaeridium parvum*, and *Mehlisphaeridium regulare* and *Mehlisphaeridium* sp. are also described and illustrated. Representatives of the zygnematacean algae, *Brazilea scissa*, *Brazilea plurigenus*, *Brazilea* sp. A, *Tetraporina tetragona*, ?*Lecaniella* sp., as well as large clusters of sphaeromorphs *incertae sedis* chlorophyta algae, are described. In addition, planar colonial chlorococcalean *Pediastrum*-like forms suggesting hydrodictyaceaen algae are recorded for the first time in late Paleozoic strata of Argentina, and the zygnematalean affinity of *Reduviasporonites chalastus* as green algae is discussed. The highly diverse La Veteada microphytoplanktonic assemblage is composed by algae that grew in hypersaline lacustrine environment together with species commonly associated with either fresh or brackish water conditions; presumably these taxa were washed in after heavy rainfall and/or flooding events. In general terms, the land-derived palynological composition of the La Veteada assemblage at Central Famatina Range reflects parent vegetation adapted to arid or semi-arid climate as reported from late Guadalupian to late Lopingian in the Paganzo Basin. The whole palynological composition suggests a Lopingian age for the La Veteada Formation at its stratotype, based on the stratigraphic range of all the land-derived miospore species recognized, resulting younger than assemblages assigned to the *Lueckisporites–Weylandites* Biozone (*LW*: Wordian–Capitanian). Therefore, it is the youngest Permian palynofloral assemblage recorded up to now in Argentina and South America.

1. Introduction

The upper Paleozoic basins of southern South America were grouped by Limarino et al. (2014) into two major types: the eastern intraplate basins and those located along the western active margin of Gondwana, separated by the Pampean Arch composed by crystalline upper Precambrian and lower Paleozoic rocks. According to these authors, to the west of this large upland area the discontinuous orogenic belt, the

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"Protoprecordillera", acted as a barrier separating a large foreland area (Paganzo Basin) from a more tectonically and magmatically active region located in the Andean Cordillera (Río Blanco and Calingasta–Uspallata basins) (Fig. 1). Other authors proposed a more complex account for the region during the late Paleozoic, interpreting an extensional tectonic setting during the Mississippian–Pennsylvanian, mainly expressed in the western region, and a shrinkage period linked to a back-arc basin for the Permian (Ezpeleta, 2009; Astini et al., 2009; Martina et al., 2011).

The Paganzo Basin (Limarino and Spalletti, 2006) is located in northwestern and central Argentina and contains one of the most complete late Paleozoic continental sedimentary records (Fig. 1). Its sedimentary infilling comprises the Guandacol, Tupe and Patquía supersequences (López Gamundí et al., 1990, 1992; Fernández Seveso et al., 1993; Gutiérrez et al., 2014) ranging from Late Mississippian to Permian (Limarino and Césari, 1985; Limarino et al., 2006, 2014; Limarino and Spalletti, 2006; Spalletti et al., 2010). In the eastern part of the Paganzo Basin, in the Famatina Range, the Paganzo Group encompasses four main intervals of sedimentation: (1) at the base, the Agua Colorada Formation, which represents the Bashkirian glacial event; (2) the Las Pircas Formation, a Late Pennsylvanian alluvial succession (Ezpeleta et al., 2008); (3) the Permian eolian–fluvial red beds of the De La Cuesta Formation, and (4) a relatively thin but regionally tabular shallow lacustrine interval named the La Veteada Formation by Dávila et al. (2005).

The Carboniferous–Permian palynological record from central-western Argentina includes the following biozones: *Reticulatisporites magnidictyus–Verrucosisporites quasigobbetti* (*MQ* Biozone), *Raistrickia densa–Convolutispora muriornata* (*DM* Biozone), *Pakhapites fusus–Vittatina subsaccatta* (*FS* Biozone) and *Lueckisporites–Weylandites* (*LW* Biozone) (see Césari and Gutiérrez, 2001; Pérez Loinaze, 2007). In the eastern part of the Paganzo Basin in the Famatina Range, palynological assemblages have been recorded only in the De La Cuesta Formation (Aceñolaza and Vergel, 1987; *LW* Biozone) and in the Agua Colorada Formation (Vergel et al., 1993; Vergel and Lech, 2001; Césari et al., 2008; *DM* Biozone). A diverse palynoflora from the lower part of the La Veteada Formation found in shallow lacustrine and playa lake deposits at Sierra de Narváez, Famatina Range, has been assigned to *LW* Biozone, suggesting a middle Permian (Guadalupian) age (Gutiérrez et al., 2011) based on previously published Permian palynological studies on South American strata (Césari and Gutiérrez, 2001).

In addition, the diverse and well-preserved palynoflora of the upper La Veteada Formation in its type section in Central Famatina is still being studied. It has already been assigned to the upper Permian (Lopingian) based on the stratigraphic range of all the recognized species (Zavattieri and Gutiérrez, 2012; Gutiérrez et al., 2014). Consequently, the palynological association of the upper La Veteada Formation is considered the youngest Permian palynoflora recorded hitherto in Argentina and South America completing the Permian biostratigraphical scheme from central-western Argentina.

In the present study, we aim to describe and illustrate the diverse chlorophycean algae and other organic-walled microphytoplankton (most of which are also considered of algal affinity) recorded within the diverse land-derived spores and pollen grains assemblages of the La Veteada Formation at its type locality (Table 1). An interpretation of the sedimentary environment suggests a shallow lacustrine deposition and a hypersaline/brackish water depositional environment, also indicated by the different coenobia shapes of *Syndesmorion stellatum* alga as complement of the palynoflora (Table 2).

2. Geological setting

Outcrops of the La Veteada Formation (Dávila et al., 2005) have been regionally recognized in different areas of the Famatina Range (Paganzo Basin) (Figs. 1, 2) and their age is late Guadalupian to late Lopingian (Zavattieri and Gutiérrez, 2012; Gutiérrez et al., 2014). The lower section of the unit is exposed in the Sierra de Narváez, Catamarca Province, and its sedimentary sequence and diverse palynological content were studied by Gutiérrez et al. (2011).

The palynoflora from the stratotype of the upper part of the La Veteada Formation (Fig. 2B) is a diverse assemblage of spores and pollen

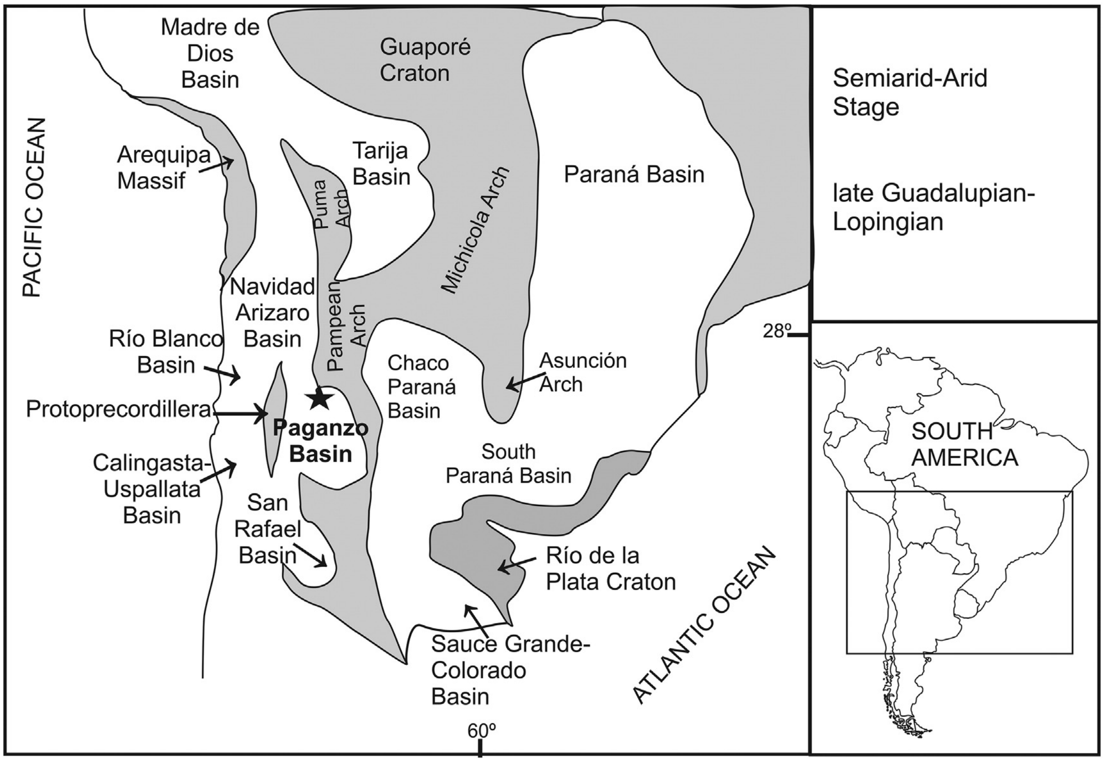


Fig. 1. Paleogeography of the Late Paleozoic basins of southern South America and location of the study area (star) in the Paganzo Basin. Shaded areas indicate positive regions. (Modified from Limarino et al., 2014.)

Table 1
Composition and distribution (in % per samples) of the palynological groups of spores, pollen grains (PG) and microphytoplankton recorded in the La Veteada Formation at its type locality.

	Samples					
Palynomorphs	MPLP 8248	MPLP 8249	MPLPB 8250	MPLP 8251	MPLP 8252	MPLP 8253
Taeniate bisaccate PG	18.9	25.6	23.6	53.5	36.6	46.5
Plicate and monocolpate PG	0.8	1.4	1.6	1.3	1.8	3.6
Non-taeniate bisaccate PG	10.7	14.4	12.7	11.0	11.4	10.9
Polysaccate PG	0	0	0	0.2	0	0
Non-taeniate monosaccate PG	30.9	24.8	32.7	5.1	14.0	8.5
Taeniate monosaccate PG	0.2	0.4	0.6	1.6	1.1	0.6
Spores	32.6	28.5	25.4	16.7	25.0	14.5
Microphytoplankton	5.9	4.9	3.4	10.6	10.1	15.4

with only a small amount of, mainly algal, microphytoplankton (Gutiérrez et al., 2014) (Table 1). In this locality, the La Veteada succession para-conformably overlies the fluvio-eolian Permian deposits of De La Cuesta Formation and unconformably underlies the lower Miocene sequence of the Del Crestón Formation (Dávila et al., 2005) (Fig. 2B). This section begins with a basal gray silcrete, which is recognized regionally and has been used as marker bed (Ezpeleta, 2009; Dávila et al., 2005) (Fig. 3.1). Above this chert-level, the succession continues with medium- to coarse-grained tabular sandstones and fine conglomerate lenses, hardly silicified and calcretized with subrounded clasts associated with a fluctuation in the phreatic level and pedogenic processes. This facies association suggests the formation of immature soil near river channels, mounted on a substrate with sandy parent material favoring vertical drainage. Upwards, La Veteada Formation consists of a rhythmic interbedding of tabular fine sandstones, with fine to very fine dark-gray laminated siltstones and claystones, and locally gypsum levels (Fig. 3, 2–3). Laminar mudstone indicates that for some intervals these plains could have been covered by water. However, the red-purple color and frequent interbedding levels with mud cracks, raindrop marks and ripple marks indicate marginal sedimentation in very shallow lakes where settling intervals are interrupted by subaerial exposure and sporadic low-flow regimes in a relatively arid environment. Bioturbation at some levels indicates a certain biological activity in some intervals. The nodular to prismatic gypsum banks are distributed irregularly, forming locally thick lenticular banks of rhythmic evaporites and stromatolitic laminated limestones. The development of nodular and prismatic gypsum in the basal part of the succession suggests the precipitation of evaporites in floodplains under high-evaporation conditions, in which the fluctuation of the phreatic-ground water table has been periodical, either in nearby lacustrine hypersaline bodies and/or in saline sheedloads (Ezpeleta, 2009). Towards the top, the presence of carbonate-cemented sandstones, laminated mudstones and stromatolitic dolomites (Fig. 3, 3–5) is interpreted as having formed at the edge of a lake in continuous expansion and shrinkage, which allows the interaction of subaqueous and subaerial processes. Interbedding dolomitic banks with algal structures characterized by low detrital content, show shallow conditions and probably reflect entrapment of clastic material in the margins of the lake where calcareous sandstones develop. The different facies associations and their vertical organization led to interpret the development of lakes after a discontinuity, represented by silcretes associated with low-sedimentation condensed intervals favoring the formation of paleosoils. These lakes were mainly hypersaline, semiperennial, with periodic expansions and retractions, suggesting low-relief settings.

Table 2
Distribution per level of the microphytoplankton taxa content.

	Samples					
Microphytoplankton	MPLP 8248	MPLP 8249	MPLPB 8250	MPLP 8251	MPLP 8252	MPLP 8253
Syndesmorion stellatum	✓	✓	✓	✓	✓	✓
Maculatasporites amplus	✓	✓	✓	✓	✓	✓
Maculatasporites gondwanensis	✓	✓	✓	✓	✓	✓
Mehlisphaeridium parvus		✓	✓	✓	✓	✓
Mehlisphaeridium regulare			✓		✓	
Mehlisphaeridium sp.						✓
Pediastrum-like forms	✓		✓	✓		✓
Sphaeromorph clusters	✓	✓	✓	✓		✓
Brazilea plurigenus						✓
Brazilea scissa		✓	✓	✓		✓
Brazilea sp. A			✓	✓		✓
Tetraporina tetragona		✓	✓			
Leiosphaeridia sp.	✓	✓		✓		✓
?*Lecaniella* sp.			✓	✓		✓
Reduviasporonites chalastus	✓	✓	✓	✓	✓	✓

3. Material and methods

Six outcrop samples from pelitic levels were available for palynological study, yielding abundant and diverse spore-pollen, algae and other organic-walled microphytoplankton from the type section of the La Veteada Formation (Table 1). The samples were processed using standard palynological HCl–HF–CHl acid maceration techniques, 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 examined using a light microscope (Olympus BX 50), and the photomicrographs were taken with an Olympus digital camera from the Paleopalynology Unit, Argentinian Institute of Nivology, Glaciology and Environmental Sciences (IANIGLA), CCT-CONICET, Mendoza, and with a Nikon H550S optical microscope as well as an adapted DS-U2-Fil-U2 digital camera from the Paleopalynology Laboratory, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires. The studied slides are identified by the catalog numbers 8248–8253 followed by the abbreviation MPLP (Mendoza-Paleopalinoteca-Laboratorio de Paleopalinología). Specimen locations are referred to England Finder coordinates (E.F.co.). Residues for a Scanning Electron Microscope (SEM) were mounted on aluminum stubs and coated with a gold–palladium alloy. A Phillips XL 30 TMP from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, was used for detailed examination and imaging of selected specimens. For the nomenclature, definition and discussion for organic-walled algal microfossils we follow Colbath and Grenfell (1995). Some size measures are presented in the format N1(N2)N3, where N1 and N3 represent the minimum and maximum values measured respectively, and N2 the mean for all the specimens evaluated. A complete list of marine and continental Permian acritarchs (along stages distribution) and organic-walled microphytoplankton (OWM) (including representatives of possible fungi and green algae) taxa reported worldwide (including southern South American continental basins) have been compiled and analyzed by Lei et al. (2013). In supplementary material (Appendix) we add "Previous records" only for those taxa herein recorded omitted or posterior to Lei et al. (2013) compilation, and the worldwide distribution of the Chlorococcalean planar colonial algae which were not considered by those authors.

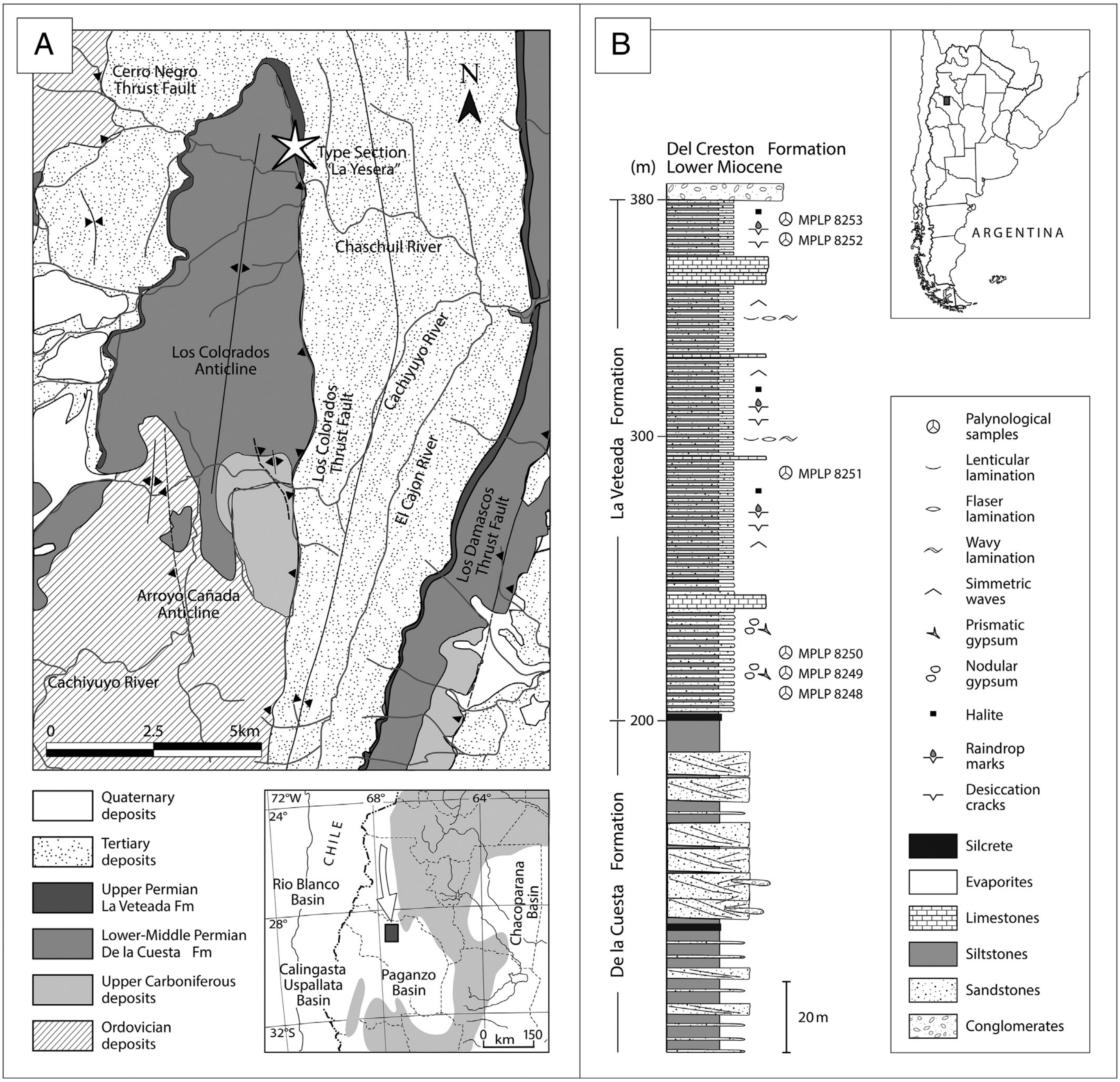


Fig. 2. A. Geological map of the study area, showing the location of the studied type section profile (star). B. Stratigraphic type section of the La Veteada Formation at Famatina Range and location of the palynological samples.
(Modified from Dávila et al., 2005.)

4. Systematic paleontology

Division Chlorophyta Pascher, 1914
Class Chlorophyceae Kützing, 1843
Order CHLOROCOCCALES Marchand, 1895
Genus ***Syndesmorion*** Ecke *ex* Foster et Afonin, 2006

Type species: *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin, 2006, pl. I, 1–12; pl. II, 1–6.

Syndesmorion stellatum (Fijałkowska) Foster et Afonin, 2006
Plate I, 1–27; Plate II, 1–21

Remarks: All morphotypes described by Foster and Afonin (2006) for *Syndesmorion stellatum* are recognized in the material from La Veteada. However, remarks on the already described morphotypes are given according to the Argentinean specimens. Conversely, new morphotypes and morphotype combinations are also described herein (Plates I and II). Frequently, some show "internal bodies" in most of their cells that are not mentioned in the original descriptions. Range sizes are given for most of the morphological parameters, and the dimensions between brackets are the dominant values (usually more than 75% of the measurements). Based on morphological criteria, Foster and Afonin (2006) suggested a phylogenetic relationship with both fossil and extant members of the Chlorococcales. Besides, they considered that reticulate forms of *Syndesmorion* are reminiscent coenobia of recent *Hydrodictyon*, and the single-star bilaterally symmetrical 16-celled coenobia could be

Fig. 3. 1. Silcretes at the basis of the La Veteada Formation overlying paracomformably on the red beds of the La Cuesta Formation. 2. Multicolored and massive sandstones interpreted as flood-flows in a playa-lake environment covered by yellowish dolomites and mudstones suggesting a lacustrine environment. 3. Red mudstones interbedded with nodular gypsum. 4. Laminated dolomites interbedded with fine calcareous sandstones. 5. Heterolytic succession formed by an alternation of fine sandstones and thinly laminated green mudstones interpreted as rhythmites (possible lake varves).

compared with those of extant representatives of the genus *Scenedesmus*, as they are planar and linear coenobia with two rows of cells of equal number.

Descriptions:

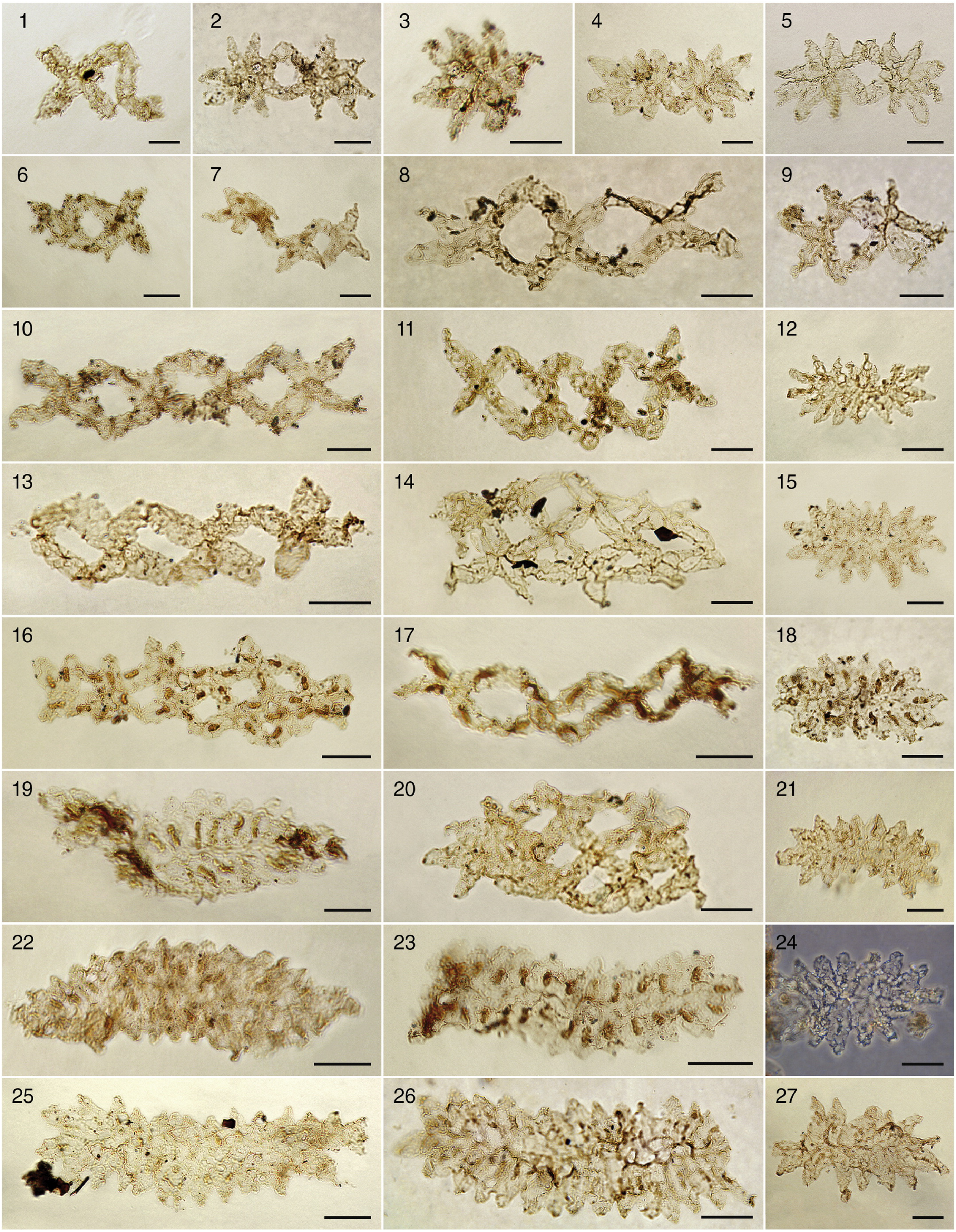
(1) *Single star-shaped coenobia* (rare) (Plate I, 3). Isolated flat coenobia, usually folded and corroded. Each coenobium usually consists of 6 to 8 cells, arranged radially. Single cell fusiform to elliptical, slightly rhomboidal particularly in the bases of the cells (zigzag joint bases), 3–15 μm wide, 8–29 μm long. Cell walls laevigate, very fine (*c.* 0.5 μm thick). Some cells show ovoidal-shape internal bodies (Plate I, 3). Total diameter of coenobia: 43–59 μm (6 specimens measured).

Remarks: In this material, we recognize dispersed single coenobia of 4 to 5 cells (Plate I, 1) that form a new morphotype described below as "*Single chain (one row) coenobia*".

(2) *Star-shaped coenobia, connected in "chains"* (rare) (Plate I, 2, 4–7, 9; Plate II, 1–5). Each chain consists of 2 or rarely 3 single star-shaped coenobia, usually joined together in planar arrangement, although sometimes not linearly folded. Single coenobia show weak bilateral symmetry of five to eight (rarely 10) cells-radially arranged, laevigate, fusiform, thin-walled, slightly rhomboidal mainly at their bases, 12(22)39 μm long and 5(9)22 μm wide. Each coenobium is joined to another one by the tips (horns) of the lateral cells, forming a free space, commonly rhomboidal (Plate I, 2, 5, 9; Plate II, 1), between connected colonies. The dimensions of each star-shaped coenobium are *c.* 31 × 28–68 × 44 μm (length × width); two cell coenobia: total length 50(89)135 μm, breadth 29(43)60 μm (38 specimens). Some coenobia show internal bodies inside the cells, 4–9 μm long; 2–4 μm wide (Plate II, 1–3, 5).

(3) *Elongated (elliptical) coenobia* (common) (Plate I, 12, 15, 18, 21, 24, 27). Coenobium flat, usually single, rarely joined in pairs. Each coenobium consists of 16 (rarely 12, 14, 17) cells radially disposed and arranged in two parallel rows. Cell bases form a distinct zigzag "axis" resulting in a bilateral symmetry appearance of the coenobium; at least one end of this "axis" ends in single or double cells. Termini of cells may bear a short "spine" or "horn" when the cells are compressed and small, or are pointed to rounded when the cells and the coenobium are "expanded". Single cells are laevigate, fusiform, slightly rhomboidal; each cell: 11(22)38 μm long, 4(9)18 μm wide. Dimensions of the most common of 16-celled coenobia: 50(80)105 μm in total length, 32(41)58 μm wide (29 specimens). Commonly coenobia show cells with distinct internal bodies 4(6)7 μm long and 2–3 μm wide (Plate I, 12, 18, 21).

(4) *Elongated multicellular coenobia*, new morphotype (rare) (Plate I, 19, 22–23, 25–26). Single, elongate, fusiform (Plate I, 19, 22) and/or rectangular (Plate I, 23, 25–26) planar coenobia. Each coenobium usually consists of 22(26–28)34 cells, arranged in two parallel rows, resulting in a longitudinal bilateral symmetry. Cell bases form distinct zigzag "axes" which form the mid-line of the coenobium, which is not clearly seen in poorly preserved specimens; each coenobium may end in a single cell (Plate I, 19, 22) or in double or three radial cells in both ends (Plate I, 25–26) of the coenobium. The termini of the cells are rounded, truncated or pointed, sometimes bearing a short "spine". Single cells are laevigate, variable in shape, slightly rhomboidal,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quadrangular, fusiform or broadly oval of 11(29)32 μm long, 4(8)13 μm wide. The cells of the coenobia may show internal bodies of 6–7 × 2–3 μm (Plate I, 19, 23). Coenobia total length: 60(113)146 μm, width: 30(44)59 μm (20 specimens).

Remarks: This morphotype is distinguished from "elongated (elliptical) coenobia", as described by Foster and Afonin by the external shape (longer and narrower) and by the size and the multicellular (more than 16 cells) feature of the coenobia. The specimens with multicellular coenobia assigned by Fijałkowska (1995, p. 319–320, pl. III, 12) to *Actinastrum pauli* (Ecke, 1986) Brenner and Foster (1994) closely resemble this morphotype. Foster and Afonin (2006, p.7), considered this nomenclature *nomen nudum* therefore Fijałkowska's illustrated specimens are conspecific with *stellatum*.

(5) *Reticulate coenobia* (abundant) (Plate I, 14, 16, 20; Plate II, 8–9, 11–15, 17–18, 21). Planar coenobia, complete specimens rectangular in shape, in a characteristic reticulate pattern formed usually by three alternating rows of cells; coenobia variable in size in relatively complete and well-preserved specimens; some specimens are fragmented, showing one or both extremes broken or truncated. Some more complete coenobia end in "single star" coenobia, at least in one of the termini (see "transitional coenobia") (Plate I, 20; Plate II, 15). Well-preserved colonies comprise between 26 and more than 65 cells in planar arrangement. The basic unit of these coenobia consists of four (very rarely five) cells in cross-like (X shape) arrangement (see "single-star" coenobia); single cells of 9(20)38 μm long, 4(9)17 μm wide, laevigate, rectangular to slightly rhomboidal in shape. Cell wall thin (*c.* 0.5 μm). As in previously described morphotypes, some reticulate coenobia show internal bodies inside the each cells, 3–12 × 2–4 μm (Plate I, 16; Plate II, 11, 17, 18). More complete rectangular coenobia 65(121)205 μm long and 36(55)93 μm wide (65 specimens measured).

(6) *Single chain (one row) coenobia*, new morphotype (rare) (Plate I, 6–7, 8, 10–11, 13, 17). Chain-like coenobia, flat and formed by one row of cells. The basic unit of these coenobia consists of four cells in a planar cross-shape (X-like) arrangement (Plate I, 1, 6–7). The basic unit can be found dispersed as single X-like coenobia or even in chain of two individuals (see "single-star" star coenobia) (Plate I, 6–7, 9). The more complete coenobia consist of four X-shaped cells in one plane and row (Plate I, 10, 11, 13). Cells laevigate, thin-wall (*c.* 0.5 μm), fusiform or slightly rhomboidal, 13(21)30 μm long and 5(9)12 μm wide. As in other morphotypes, the cells of the coenobia show internal bodies, 5–7 × 2–3 μm (Plate I, 17). The termini of the coenobia sometimes end in a 5-celled "single-star" coenobium. Rarely observed, this morphotype shows a transition to "reticulate coenobia" (Plate I, 16). Dimensions of complete coenobia: 95–150 μm long, 25–45 μm wide (5 specimens measured).

(7) *Transitional coenobia* (rare) (Plate I, 16, 20; Plate II, 6–7, 8, 10, 15, 18). Reticulate and single star-shaped coenobia occur in organic connection coenobia on one end of the reticulate coenobia (Plate I, 20; Plate II, 8,13, 15, 18) but lateral connection is also observed forming coenobial "clusters" (Plate II, 6–7, 10). Dimensions as those indicated for each morphotype.

Remarks: As pointed out by Foster and Afonin (2006) the occurrence of "transitional" or "mixed" coenobial types in organic connection demonstrates that all described morphotypes belong to the same species. They suggested also that the different types of coenobia possibly represent stages in coenobial development, or responses to external environmental conditions.

(8) *Undetermined type coenobia* (Plate II, 16, 19, 20). This group contains few specimens, which do not share the characteristic of the other morphotypes described or they show combination of them.

Comparisons: Similar and comparable algae reported previously in the literature from different parts of the world have been detailed by Foster and Afonin (2006, p. 6–7) (Fig. 4).

Discussion: As noted by Foster and Afonin (2006) the diversity of coenobial morphotypes, including organic connections between reticulate, elongate, and star-shaped forms and/or combinations of two or more morphotypes, undoubtedly indicates that all these different shaped coenobia belong to one natural species. Afonin et al. (2003) suggested a possible ontogenetic pathway to explain the development of these morphotypes (see Foster and Afonin, 2006, p. 8).

Class Zygnemaphyceae Round, 1971
Order ZYGNEMATALES Borge, 1931
Family ZYGNEMATACEAE Kutzing, 1898
Genus ***Brazilea*** Tiwari et Navale, 1967

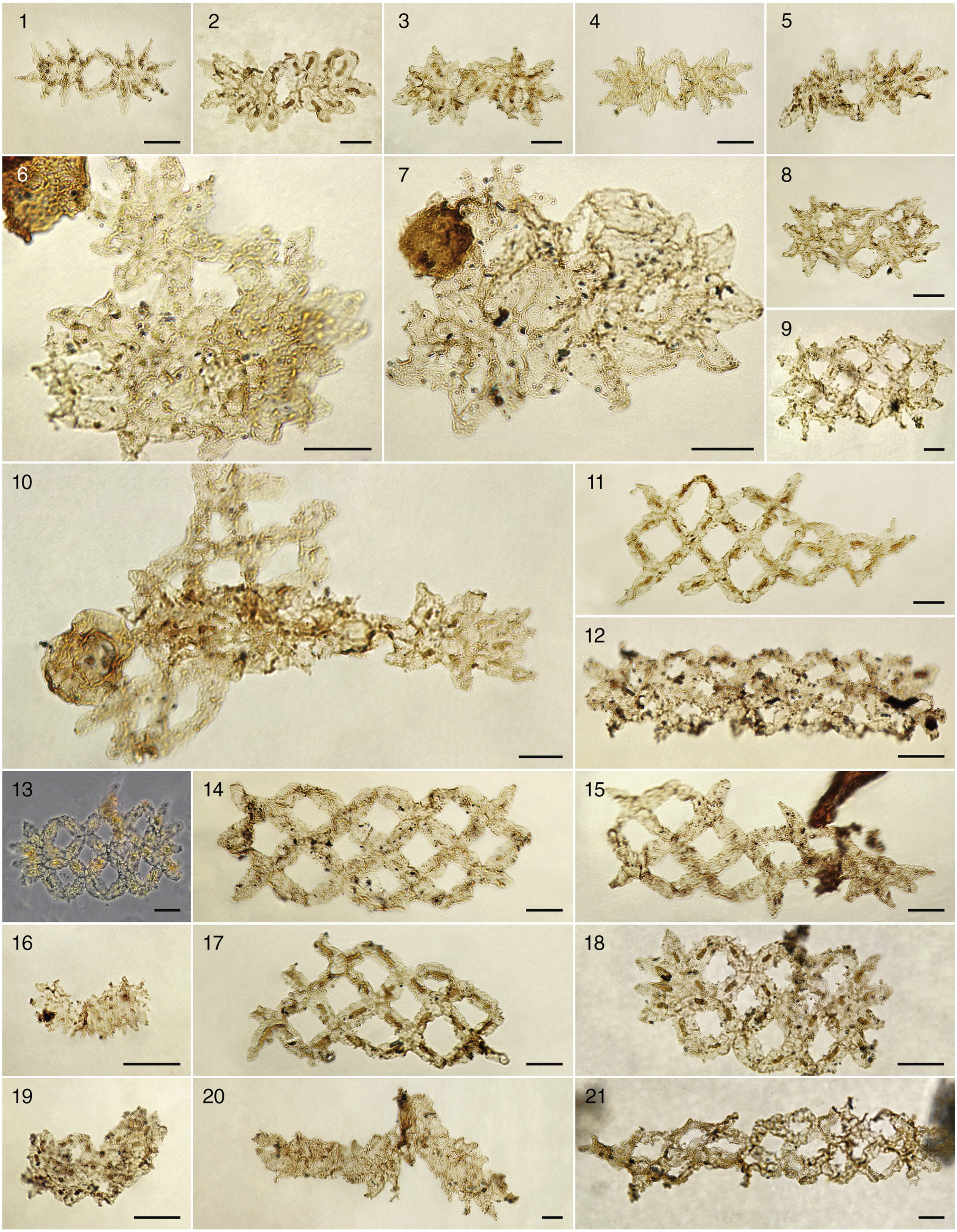
Type species: *Brazilea punctata* Tiwari et Navale, 1967.

For synonymy and discussion on the genus, see Foster (1979) and Grenfell (1995).

Remarks: In the Upper Paleozoic strata of Gondwana forms characterized by smooth to scabrate wall, originally ovoid to sub-spherical in shape that may rupture along the equatorial dehiscence line splitting

Plate I. *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin, 2006.

1. Single cross-shape coenobium of 4 cells, MPLP 8251(G) F49/0.
2. Star-shaped coenobia connected in chain of 8 and 7 cells each coenobium, MPLP 8250(B) T31/4.
3. Single star-shaped coenobium, showing cylindrical inner bodies in cells (chloroplast), MPLP 8251(G) E48/1.
4-5. Star-shaped coenobia connected in chain, showing different morphologies, (4) MPLP 8251(I) S49/3; (5) MPLP 8250(G) R43/3.
6-7. Coenobium of 4 cross-shape cells connected in chain, (6) MPLP 8251(G) P40/0; (7) cells showing inner bodies, MPLP 8251(H) C46/1.
8. Single chain (one row) coenobia, MPLP 8252(B) E32/3.
9. Coenobium of 4 cells cross-shape connected in chain, MPLP 8250(B) P32/0.
10-11. Single chain (one row) coenobia, (10) MPLP 8251(G) S34/3; (11) MPLP 8251(H) K40/0.
12. Elongated (elliptical) coenobia, MPLP 8251(I) S55/0.
13. Single chain (one row) coenobia, MPLP 8251(I) Q55/4.
14. Reticulate coenobia, MPLP 8251(K) A42/1.
15. Elongated (elliptical) coenobia, MPLP 8250(H) L54/0.
16. Transitional coenobia of two reticulate types, showing cylindrical inner bodies (chloroplasts) in each cell, MPLP 8251(J) R40/4.
17. Single chain one row coenobia, showing chloroplasts inside the cells, MPLP 8251(G) H43/1.
18. Elongated (elliptical) coenobia, with cylindrical inner bodies (chloroplasts) in each cell, MPLP 8251B F27/3.
19. Elongated (fusiform) multicellular coenobia, MPLP 8251(H) B39/0.
20. Transitional coenobia, MPLP 8252(I) J44/3.
21. Elongated (elliptical) coenobia, MPLP 8248(E) U32/0.
22. Elongated multicellular (fusiform) coenobia, MPLP 8250(H) P43/3.
23. Elongated (multicellular fusiform) coenobia, showing inner cylindrical bodies in each cells, MPLP 8251(K) S37/4.
24. Elongated (elliptical) coenobia, phase contrast illumination, MPLP 8250(B) W26/4.
25. Elongated multicellular coenobia, MPLP 8250(G) T46/3.
26. Elongated multicellular coenobia, MPLP 8249(E) U31/3.
27. Elongated (elliptical) coenobia, MPLP 8248(E) K44/3. Scale bars = 20 μm.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into similar halves have been assigned alternatively to the genus *Brazilea* Tiwari et Navale, 1967 and/or *Schizosporis* Cookson et Dettmann *emend.* Pierce, 1976. Grenfell (1995, p. 209), Zippi (1998, p. 35–36) and Zavattieri and Prámparo (2006, p. 1198) analyzed the validity for the use of *Ovoidites spriggi* (Cookson et Dettmann) Zippi, 1998 instead of *Brazilea scissa* (Balme et Hennelly) Foster, 1975 and they gave their synonymy listing. However, the genus *Brazilea* is recorded in the Paleozoic as common component of Carboniferous and Permian assemblages. Therefore, herein, we maintain the last genus although both genera refer the same zygnemaphycean type of algae.

Brazilea scissa (Balme et Hennelly) Foster, 1975

Plate III, 1; Plate IV, 21

1970 *Schizosporis scissus* (Balme et Hennelly) Balme, p. 416, pl. 22, 1–2.

1975 *Pilasporites calculus* Balme et Hennelly emend. Tiwari et Navale *auct. non*, Ybert, p. 203, pl. 8, 147–149.

For further synonymy see Foster (1979) and Archangelsky and Gamerro (1979).

Dimensions: Diameter, longitudinal axis: 35–58 μm (16 specimens).

Brazilea plurigenus (Balme et Hennelly) Foster, 1979

Plate III, 2

For synonymy see Foster (1979).

Dimensions: Diameter, longitudinal axis: 35–45 μm (5 specimens).

Remarks: The specimens here assigned to *Brazilea plurigenus* comprise oval, thick and two-layered wall and split in halves with faintly infra-structured inner layer and smooth outer layer.

Brazilea sp. A in Backhouse, 1991

Plate III, 3

Dimensions: Diameter, longitudinal axis: *c.* 40–72 μm (9 specimens).

Remarks: The specimens herein assigned to *Brazilea* sp. A described and illustrated by Backhouse (1991) show similar morphological characteristics and dimensions as those assigned to *Brazilea* sp. A by Playford and Dino (2000), even when these last authors remark that differences only refer to the thickness of the wall. The La Veteada specimens show transitional shapes and dimensions to that assigned as *Brazilea* sp. A of both mentioned records. Therefore, we considered that all of these forms could be an intraspecific transition.

Genus ***Maculatasporites*** Tiwari, 1964

Type species (by original designation): *Maculatasporites indicus* Tiwari, 1964, p. 257, pl.1, 11–12; text-fig. 7.

Remarks: Tiwari (1964) placed this genus in the infraturma Reticulonapiti (Erdtman) Vilmal, 1952. Bose and Kar (1967) emended this infraturma to accommodate alete, azonate spores with sub-circular-circular shape and reticulation on both surfaces. Sinha (1969) regarded *Maculatasporites* Tiwari, 1964 and *Greinvillites* Bose et Kar, 1967 in the group Acritarcha Evitt (1963) and in which a new subgroup named “Reticulosphaeromorphitae” for these reticulate and “alete” microfossils was proposed. Evitt (1963) defined the acritarchs as: “small microfossils of unknown and probably varied biological affinities, consisting of a central cavity enclosed by a wall of single or multiple layers and or chiefly organic composition; symmetry, shape, structure and ornamentation varied; central cavity closed or communicating with exterior by varied means, for example: pores, a slit-like or irregular rupture, a circular opening (the pylome)”. Subsequently Kar and Bose (1976, p. 63) placed *Maculatasporites* in the Turma Aletes Ibrahim (1933).

In turn, Tappan (1980, p. 811, 818, tab. 10.1, figs 10.8.3–7) associated *Maculatasporites* Tiwari with Prasinophyta. Backhouse (1991) transferred organic microfossils without any apparent opening or split, originally spherical in shape and with narrow membranous muri, to the genus *Cymatiosphaera* Wetzel, 1933 *emend.* Deflandre, 1954. He retained those with quite distinctively wide and large wavy muri within *Maculatasporites gondwanensis* Tiwari. Playford and Rigby (2008, p. 45) assigned the aquatic green-algal microphytoplankton *Cymatiosphaera* to the Prasinophyceae. Specimens of the La Veteada Formation clearly display a circular pore and/or split-like rupture. Otherwise, some specimens of this assemblage are clearly two-layered, with the inner wall (endospore?) thin and smooth, which is sometimes observed in the Australian Permian material as pointed out by Grenfell (1995, p. 210). Accordingly, we follow the criteria of Balme and Segroves (1966), Segroves (1967), Foster (1979) and Grenfell (1995), who considered the genera *Maculatasporites* and *Mehlisphaeridium* of probably algal derivation (fresh or brackish water). Grenfell (1995) considers the genus *Maculatasporites* as spores of probably zygnematalean zygospore algae.

The genera *Maculatasporites* and *Mehlisphaeridium* share a densely ornamented outer wall, remarkably spherical in shape, sometimes showing a small circular pore or pylome. However, *Mehlisphaeridium* is ornamented with small to large, hollow conical processes on the outer layer of the wall. As pointed out by Backhouse (1991, p. 303) for *Mehlisphaeridium regulare*, the forms with a pylome are indistinguishable from those without. It is not easy to determine whether a pylome is absent because it did not develop or because it is obscured by the dense sculpture and/or by the orientation of the microfossil. Thus, according to Backhouse's considerations, until the taxonomic significance of a pylome is demonstrated, we maintain both genera (herein extensive to *Maculatasporites*) with or without a pylome. The display of a clear pore in most of the specimens of these last two genera recorded in the La Veteada Assemblage allows assigning them to the zygnematacean algal spore genera (cf. Grenfell, 1995).

Maculatasporites gondwanensis Tiwari, 1965

Plate III, 6–9; Plate IV, 20, 24–27, 29

1965. *Maculatasporites irregularis* Tiwari, p. 205, pl. 8, 188, 190 (except pl. 8, 189).

For further synonymy see Foster, 1979, p.105.

Remarks: In the La Veteada assemblage we have observed all transitional features concerning the variations in shape and size for the reticulum, and the marginal projection of the muri on the periphery and of the overall range-size dimensions of the species erected and described

Plate II. *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin, 2006.

1-5.	Different types coenobia and cell-shapes of star-shaped coenobia connected in chains, most of them showing inner bodies (chloroplasts); (1) MPLP 8251(H) M32/0, (2) MPLP 8252(B) D29/0, (3) MPLP 8251(H) G46/0, (4) MPLP 8251(I) H48/3, (5) MPLP 8251(K) J42/0.
6-7.	Transitional coenobium of star-shaped and incipient development of reticulate morphotype, also showing coenobium-shape diversity, (6) MPLP 8251(I) M44/3, (7) MPLP 8251(H) D49/0.
8.	Transitional coenobium of reticulate type and star-shaped on one end, MPLP 8251(J) D42/0,
9.	Reticulate coenobium, showing inner chloroplasts inside the cells, MPLP 8251(E) S25/2.
10.	Transitional coenobium of three of reticulate, star-shape and multicellular (fusiform) morphotypes, MPLP 8251(I) K44/3.
11.	Transitional coenobium of reticulate to single chain (one row) morphotypes, MPLP 8249(I) T48/1.
12.	Reticulate coenobium, remarkably elongated and narrow, MPLP 8251(G) V43/1.
13.	Reticulate coenobium, taken under phase contrast illumination, MPLP 8251(B) N31/0.
14.	Reticulate coenobium, MPLP 8251(J) R49/0.
15.	Transitional coenobium formed by reticulate and single star morphotypes, MPLP 8251(G) E40/2.
16.	Undetermined type coenobia connected in chain, MPLP 8250(F) G52/4.
17.	Fragment of reticulate coenobium, showing inner elongated chloroplasts inside the cells, MPLP 8251(G) W38/3.
18.	Reticulate coenobium ending transitionally to single-star 8-cell coenobium, MPLP 8251(B) N31/0.
19-20.	Undetermined type coenobia, showing diversity of forms, (19) MPLP 8251(G) F48/0, (20) connected in chain, MPLP 8250(F) G50/0.
21.	Reticulate coenobia, MPLP 8250(B) L35/0. All scale bars = 20 μm.

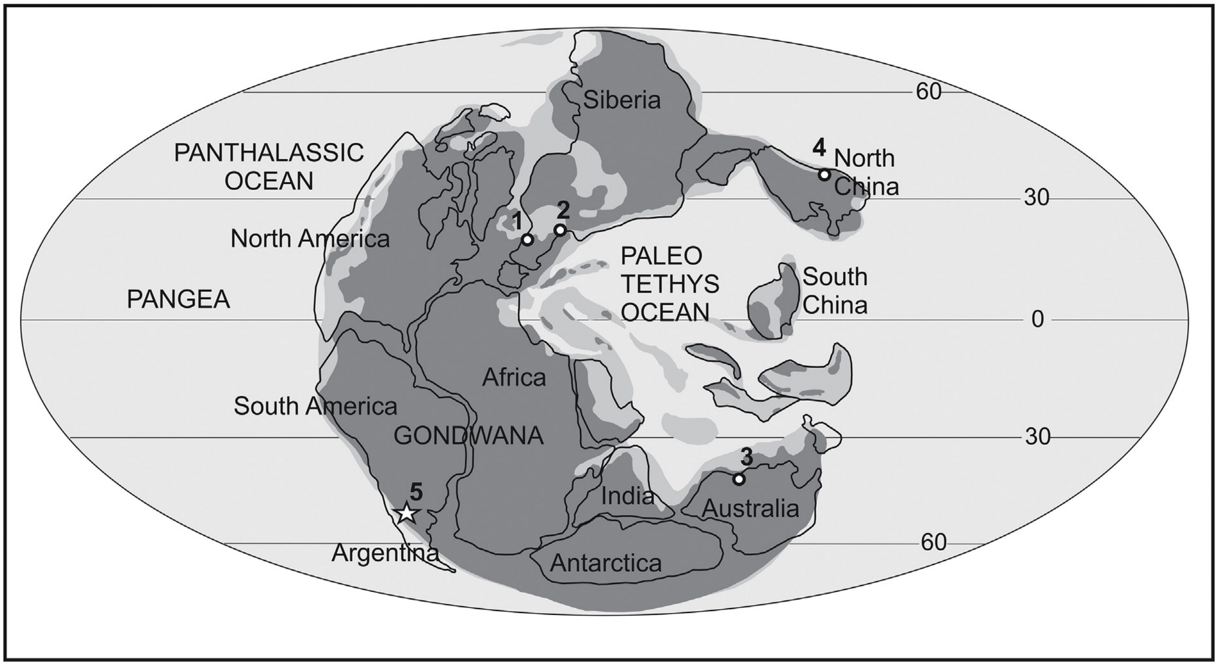


Fig. 4. Generalized Late Permian paleogeographic map showing known localities of *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin 2006: 1. Germany (Ecke, 1986; 2. Poland (Fijałkowska, 1995); 3. Western Australia (Brenner and Foster, 1994); 4. North China (Foster and Afonin, 2006); 5. Central-western Argentina, Paganzo Basin (this paper). (Modified from Foster and Afonin, 2006.)

by Tiwari (1965) as *Maculatasporites gondwanensis* and *Maculatasporites irregularis*. Even the type species *Maculatasporites indicus* of Tiwari (1964) shows similar morphological characteristics and size within reasonable ranges of intra-specific variation, mainly considering the advanced technology in microscopy. Closer comparisons of these species are difficult due to the low quality of Tiwari's (1964, pl.1, figs. 11, 12 for *M. indicus*, 1965, pl.8, fig. 187 for *M. irregularis*) photomicrographs.

Description: Vesicle originally spherical, outline subcircular or rarely oval. Eylima (wall) composed by two layers. Inner layer smooth, 1–2 μm thick; outer layer comprehensively reticulate and probably detached from the inner layer. Muri sinuous 0.5(1.1)2.8 μm wide and 1.2–2.5 μm high, slightly projecting at the periphery enclosing usually polygonal lumina, 1.0(3.1)8.3 μm in diameter. The connecting muri appear as a thin (1–2 μm) and low membranous extension, giving an undulant appearance to the periphery. Most of the specimens display a small circular opening (pylome) on both layers of unknown position ranging in size 2.0(3.4)6.0 μm in diameter; rarely a thickened border of the pylome is observed; other specimens show a probable split or ruptured line almost parallel to the equator, but not entirely ruptured along it.

Dimensions: Equatorial diameter: 32 (47.5) 67 μm (80 specimens).

Remarks and comparisons: The presence of a circular opening (pylome?) is a structural feature not described previously for the genus, although some specimens illustrated by Anderson (1977) as *Mehlisphaeridium gondwanensis* (pl. 2, figs. 12, 23), *Maculatasporites eraduensis* (pl. 3, figs. 2, 6) and *Maculatasporites indicus* (pl. 3, figs. 15–16) show this circular aperture. Tiwari (1965, p. 205) noted that *M. gondwanensis* differs from the type species in having thinner muri, regular polygonal and larger lumina with a thin extension of the connecting muri at the periphery. The specimens illustrated by Tiwari (1965) as *Maculatasporites irregularis* Tiwari (1965, pl. 8, fig. 189) seem to be *Mehlisphaeridium regulare* regarding the presence of dense muri, projecting prominently as closely set bacula at the equator as described by the author; such characteristic falls out of the regular reticulate pattern of this species. However, close comparisons are hard to make due to the poor quality of that figure.

The specimens of the La Veteada assemblage are comparable to those illustrated by Backhouse (1991) as *Cymatiosphaera gondwanensis* in the similar pattern of the reticulum, although the muri are higher (2–5 μm) and the lumina bigger (5–10 μm) than in the Argentinean material. *Mehlisphaeridium delicatus* described by Foster (1975) is smaller than *M. gondwanensis*, being 23–39 μm in diameter and having a much thinner wall with a delicate reticulum (muri 0.5 μm wide). Playford (in Playford and Rigby, 2008) erected *Maculatasporites gravidus* from the Permian of West Papua (western New Guinea) for spherical vesicles bearing a broad ± regularly reticulum enclosing subcircular to roundly polygonal lumina. Utting (1994) illustrated regular reticulate specimens as *Maculatasporites* sp. (pl. 10, figs. 21, 25) similar to the La Veteada specimens, but he did not provide descriptions or dimensions. Lindström and McLoughlin (2007) illustrated as *M.* sp. (pl. II, fig. n) a specimen that could be assigned to *M. gondwanensis* from Ritchie Member, Flagstone Formation of Earliest Triassic (Induan) the Prince Charles Mountains, Antarctica.

Maculatasporites amplus Segroves, 1967
Plate III, 10, 15, 20–23; Plate IV, 22–23, 28.
1976. *Maculatasporites zairensis* Kar and Bose, p. 64, pl. VII, 2–3.
1976. *Maculatasporites* sp. Kar and Bose, p. 64, pl. VII, 4.

Description: Vesicle originally spherical, outline subcircular. Eylima (wall) composed of two layers. Inner layer smooth, thickness difficult to measure due to the density of the ornamentation; outer layer comprehensively foveo-reticulate. Thick muri 0.8(1.2)2.3 μm, enclosing small subcircular to irregular lumina 0.2(1.2)2.6 μm, giving a foveolate aspect to the vesicle. Small, originally circular opening (pylome?) of 2.2–5.2 μm in diameter with a thickened margin usually discernible.

Dimensions: Equatorial diameter: 38(50)85 μm (49 specimens).

Remarks and comparisons: *Maculatasporites amplus* is distinguished from the type species *Maculatasporites indicus* Tiwari by its characteristic smaller, denser and conspicuous reticulate outer layer, which may be transitional to a "foveolate" pattern, as those illustrated by Segroves (1967) and Backhouse (1991) for the species. *Maculatasporites gondwanensis* differs in having thinner muri, irregular to almost polygonal to subcircular and bigger lumina, and a thin extension of the connecting muri at the periphery. *Maculatasporites zairensis* and *Maculatasporites* sp. created by Kar and Bose (1976) have flat meshes and small foveo-like lumina, being smaller and larger respectively, in comparison to *M. indicus*, *M. gondwanensis* and *M. amplus* as suggested by the authors (they do not mention the number of specimens studied). However, taking into account newer records, these species fall within the range-size of *M. amplus* as explained below. Even when the illustrations of the African specimens are deficient, they show a real foveo-like pattern. *Maculatasporites minimus* Segroves (1967) is smaller (24–33–40 μm), with the outer layer presenting remarkably thicker muri and fewer circular to oval lumina. The specimens from the La Veteada Assemblage have similar dimensions as mentioned by Foster (1979, p. 105: 29(43)66 μm) and Segroves (1967) for the species: 52(68)86 μm.

Genus ***Mehlisphaeridium*** Segroves, 1967

Type species (by original designation): *Mehlisphaeridium fibratum* Segroves, 1967, p. 295. pl. II, 8–14.

Remarks: Specimens from the La Veteada assemblage bear conical and baculate processes that vary in length and density among specimens.

Mehlisphaeridium regulare Anderson, 1977

Plate III, 11–12, 14; Plate IV, 30

1988. *Portalites baculatus* Gutiérrez and Césari (1988, p.92, pl. II, 5)

For further synonymy see Backhouse (1991, p. 303).

Dimensions: Equatorial diameter (excluding sculpture): 43–50 μm. Baculae: 2.4(3.6)4.4 μm high; 2.8(3.4)4.0 μm wide (5 specimens).

Remarks and comparisons: The specimens recorded in the La Veteada Formation assemblage as *Mehlisphaeridium regulare* concur broadly with the material illustrated by Anderson (1977), and with the specimens illustrated by Backhouse (1991), having mainly baculate processes (1991, plate 13, figs. 9, 10, 11a–b). Anderson mentioned that the processes are hollow, not fibrous as described by Segroves (1967) and Backhouse (1991) for the genus. A small circular pylome 3–4 μm in diameter is clearly observed in many of our specimens, a feature also mentioned and illustrated by Backhouse (1991) and by Playford and Rigby (2008) for the species, and observed in Anderson's illustrations (1977; pl. 1, figs. 6, 10, 25). Backhouse (1991) pointed out that the presence of a pylome was not mentioned by Anderson in the generic diagnosis for the genus, although specimens with or without pylome are morphologically indistinguishable and could probably be obscured by dense sculpture and/or inappropriate orientation. Gutiérrez and Césari (1988) created *Portalites baculatus* from the Carboniferous of Argentina to include circular forms with a thick wall, ornamented by closely distributed conspicuous baculae, and scattered coni. They also mentioned the presence of a pore in some specimens. The genus *Portalites* Hemmer et Nygreen 1967 is characterized by a circular to oval amb, thick wall with a pore from which a canal extends inwardly. In the type species (*Portalites confertus*) the exine is microgranulate with occasional larger granules. Therefore, the Carboniferous specimens previously assigned to *P. baculatus* should be considered synonym of *M. regulare*. The Argentinean specimens are within the size range originally mentioned by Anderson for the two species (*M. regulare*: 36–64 μm; *Mehlisphaeridium irregulare*: 30–50 μm).

Mehlisphaeridium parvum Anderson, 1977

Plate III, figs. 13, 16–17, 19

Description: Microfossil, spherical to subspherical, wall *c.* 1–3 μm thick. Extensively ornamented by diverse elements on the surface of each specimen: slender pilae [height 0.7(1.8)3.8 μm; apical width 0.5(0.9)1.7 μm], spines [1.1(2.4)5.5 μm high, base width 0.5(1.1)2.2 μm], coni (0.6–1.3 μm high, wide at the base), verrucae [(0.6(1.0)1.7 μm high; base width 0.6(1.4)2.2 μm], saeta and bacula (1.4–1.5 μm high; base 1.6 μm); some specimens show hollow conical and truncated processes. Sometimes, sculptural elements are too close to form an irregular reticulum (Plate III, 17). A circular pylome without thickened rim of 2.3 to 6.2 μm is clearly observed in the majority of the studied specimens depending on their position.

Remarks: Anderson (1977) created the species *Mehlisphaeridium parvum* to include circular forms ornamented with hollow, saetate to baculate processes (1 μm high), smaller in overall size (28–38 μm) in comparison to the dimensions of *Mehlisphaeridium regulare* (36–64 μm). Backhouse (1991) included all forms previously identified by Anderson (1977) as *M. parvum* and *Mehlisphaeridium irregulare* in *M. regulare*, because he considered that the evidence in favor of retaining both species is not conclusive. We do not agree with Backhouse's (1991) proposal because the processes of *M. irregulare* are remarkably larger than those of *M. parvum*. Anderson (p. 1, Section 9.3) compared *M. parvum* with *Spongocystia eraduica* Segroves, 1967 alluding to the density and size of the ornament, but we consider that both genera are quite different according to the original description and illustrations of *S. eraduica* by Segroves. Therefore, we prefer to maintain the species *M. parvum*, considering the emendation of the original diagnosis to include forms with a range-size wider (31–50 μm) than that suggested by Anderson (1977: 28–33–38 μm; 8 specimens), ornamented by slender pilae, spines, coni, verrucae, saeta and bacula of *c.* 2.5 μm in maximum height. It is worth mentioning that the ornamentation in *M. parvum* is smaller, more diverse and more closely disposed than in *M. regulare*, which has a more conspicuous, typically baculate ornamentation. A circular pylome is observed in a few specimens, depending on their orientation and preservation state.

Dimensions: Equatorial diameter (excluding sculpture): 31(40)50 μm (16 specimens).

Mehlisphaeridium sp.

Plate III, 18

Dimensions: Overall diameter (excluding ornamentation): 45 × 46 μm; inner body diameter: 30 × 42 μm: wall thickness: 1–2 μm; spines and/or coni: 1.7–2.5 high; 1.8–2.5 wide at bases; diameter of processes: 1.5–1.9 × 1.9–2.5 μm (1 specimen).

Remarks: Small and spherical microfossil. Wall two-layered; the inner and outer layers are widely separated; hence, the specimen looks hollow around the inner and thinner body. Outer layer sculptured with short and pointed conical processes, blunt spinae are also frequent. The outer layer also shows a granulate?/foveolate surface between the processes.

Genus ***Tetraporina*** Naumova ex Naumova *emend.* Lindgren, 1980

Type species (designated by Potonié, 1960, p. 130): *Tetraporina antiqua* Naumova, 1950.

For the synonymy of the genus see Grenfell (1995, p. 205).

Remarks: Grenfell (1995, p. 204–206) pointed out that the genus *Tetraporina* has a rather complex unresolved taxonomic history, and he discussed its validity. We follow Grenfell's concept of *Tetraporina* who includes simple, quadrate, pillow-like forms with or without modified corners. Based on comparison with modern similar forms Balme (1963) suggested that closely similar forms are considered as aplanospores of a member of the Cyanophyceae. The zygnematacean affinity of *Tetraporina* has been discussed by many authors (see Grenfell, 1995). Brenner and Foster (1994) also compared spores of the recent Zygnematales assigned to the genus *Mougeotia* Agardh with fossil forms assigned to *Tetraporina* (see Grenfell, 1995). Zippi (1998) also considered that the genus has several features in common with genera of the modern Zygnemataceae, including size, wall thickness, quadrangular morphology, longitudinal dehiscence slit, wall layers composed of sporopollenin, and freshwater paleoecology.

Tetraporina tetragona (Pant et Mehtra) Anderson, 1977

Plate III, 4

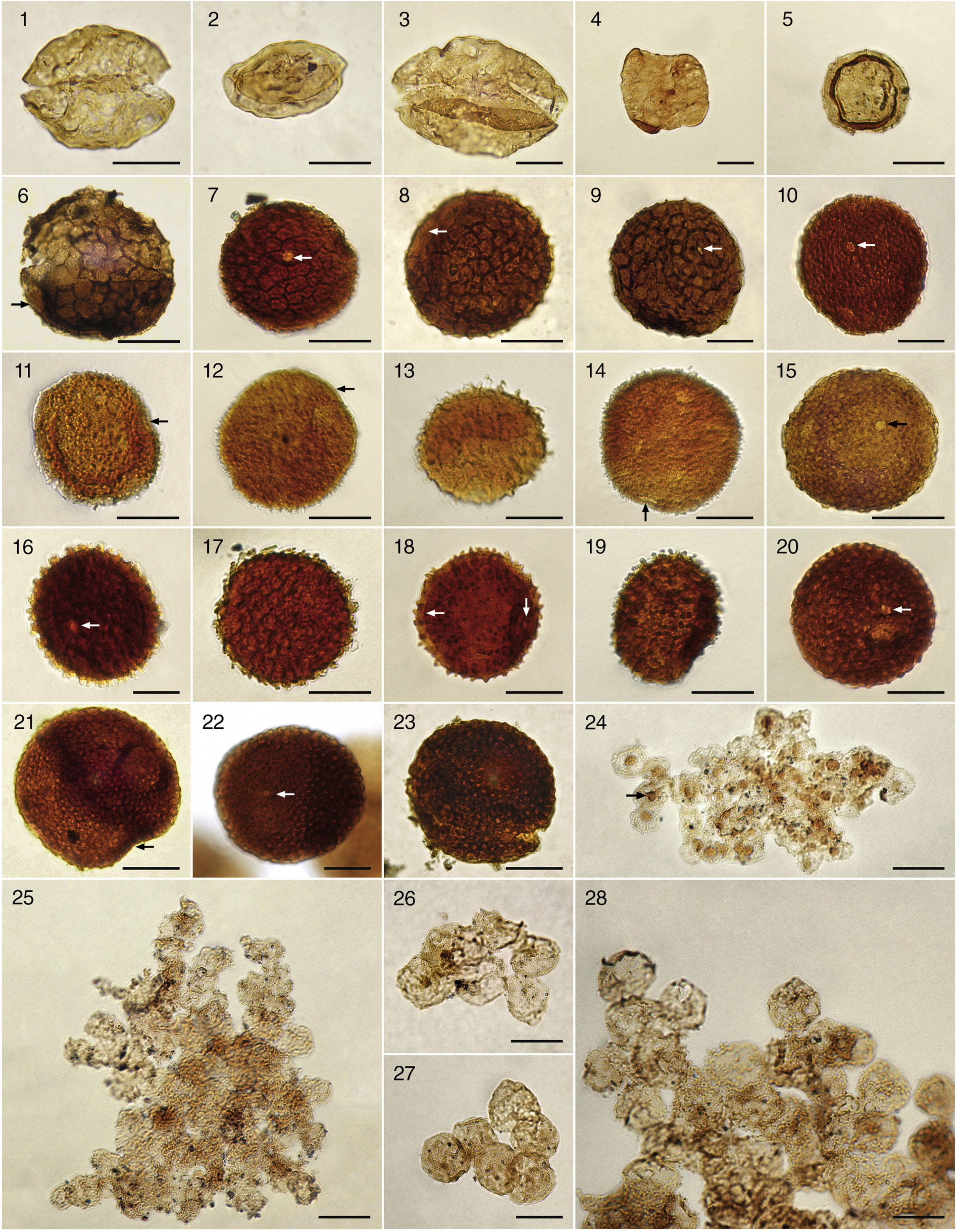
Remarks and comparisons: The outline of *Tetraporina tetragona* is characteristically quadrangular to slightly rectangular with arcuate folds at angles, rounded angles and straight, or slightly convex to concave sides. Exine, laevigate to psilate, thin, *c.* 0.5 μm thick and apparently thicker at the angles.

Dimensions: Length × width: 43 × 36–43 μm; 73 × 52–54 μm (2 specimens).

Genus ***Lecaniella*** Cookson et Eisenack, 1962

For synonymy, see Zippi (1998).

Type species: *Lecaniella margostriata* Cookson et Eisenack, 1962.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Remarks: Zavattieri and Prámparo (2006, p. 1193) discussed the taxonomic status of the fossil zygospores of *Lecaniella* Cookson et Eisenack, 1962 *vs. Peltacystia* Balme et Segroves, 1966 on the bases of Head's arguments (1992, p. 246). In this contribution, we follow the same criteria.

?*Lecaniella* sp.

Plate III, 5

Description: Outline almost circular in polar view. The wall surface is smooth to faintly irregularly granulate and pitted, probably by corrosion; wall *c.* 0.5 μm thick. In polar view, it bears an irregularly indented subequatorial laevigate/smooth ridge, 1.0–2.7 μm wide. Central area diameter, 23 × 24 μm; width of the equatorial area 2–5 μm.

Dimensions: Equatorial diameter: 37 × 32 μm (3 specimens).

Remarks and comparisons: Closely similar forms have been described from the Permian–Triassic of Canada by Jansonius (1962, pl. 16, figs. 2–4, *non* pl. 16, fig. 1) as *Grebespora concentrica*. Grenfell (1995, p. 212) pointed out that it has not been demonstrated that *Grebespora* is produced by the equatorial rupture of a spherical or sub-spherical vesicle. DeJersey (1979, p. 25, pl. 11, fig. 5) and Hankel (1992, pl. 2, fig. 2) interpreted *G. concentrica* as "alete" pollen grains, but Grenfell (1995) noted that the Triassic material of Australia described by de Jersey (1970, 1972) may belong to a *Brazilea*-like taxon, although he did not describe the presence of joined "pairs" of *Grebespora*. This form is also comparable to those described and illustrated by Segroves (1967) as *Peltacystia galeoides* (pl. 3, figs. 3–5), but it is remarkably more oval in outline and seems to have a thinner wall in the equatorial zone. As mentioned by Backhouse (1991), *P. galeoides* does not show the regular circumpolar structures that characterize the other three species described within this genus (*Peltacystia venosa*, *Peltacystia monile*, *Peltacystia calvitum*). The specimen recorded herein as *Lecaniella* is circular in polar view, but the equatorial suture along which both halves split into is not observed. More specimens are needed to confirm the assignation.

Family HIDRODICTYACEAE (Gray, 1821) Dumortier, 1829

Remarks: Batten (1996, p. 191–193) referred the coenobia of *Pediastrum* as a flat colony, commonly comprising between 4 and 128 cells arranged in concentric rings. The individual cells may be triangular, quadratic and/or polygonal in shape, which can be contiguous, forming a compact colony or a perforate colony with spaces between the individual cells. The outer cells are commonly extended into one or more lobes or pointed, truncated and/or sometimes divided projections. Batten stated that the most important diagnostic characters of fossil specimens are the morphology of the marginal cells and the sculpture, comparing them with the structure and morphology of the extant taxa. The compact feature of such characteristic coenobia of *Pediastrum* is frequently recorded in Cretaceous and Cenozoic deposits. Planar compact coenobia consisting of (usually 16) spherical to subspherical cells that may become angular in contact areas, without ornamentation or obvious dehiscence structures, referred to hydrodictyaceaen algae, have been reported from pre-Carboniferous strata (Wood and Miller, 1997); the earliest reports of Hydrodictyaceae are from the Middle Ordovician (Miller and Wood, 2001). Colbath and Grenfell (1995) mentioned that the oldest *Pediastrum*-like form was recorded from the Middle Triassic. In Argentina, the oldest records of *Pediastrum* are from continental deposits of the early Late Triassic Los Rastros Formation from central western part of the country (Ottone et al., 2005) and from the coastal sequence of the Nestares Formation, Lower Jurassic of Pagatonia (Zavattieri et al., 2008).

cf. ***Pediastrum*** Type Form 1

Plate IV, 4–5, 8–9

Description: Circular, planar coenobia composed of 12 to 18 concentrically arranged cells, without holes or spaces between central cells. Cell wall thin, smooth or slightly granulate, subcircular, quadrangular to polygonal in outline due to the compact arrangement of the cells. The outer cells of the coenobium may project into rounded or polygonal contours, sometimes divided or with truncated or pointed projections giving the colony a fenestrate outline. Some cells have accumulation bodies (chloroplasts?).

Dimensions: Diameter of coenobia: 44–65 μm; cell diameter: 4–18 μm (3 × 2–18 × 10 μm) (7 specimens).

Comparisons: Geometrically regular or irregular aggregations of cells that form coenobia often occur in Paleozoic and Mesozoic associations. Miller and Wood (2001) erected *Tapetisphaerites formale* for planar coenobia from the Middle Ordovician to Upper Devonian. The main difference with the La Veteada coenobia is the basic arrangement of the cells in the coenobium. In *T. formale* the ontogenetic development begins with a cruciform four-celled coenobium followed by 8- and 16-celled coenobia. Moreover, cells are ornamented with granulate to spinose elements; the cells in the specimens from La Veteada are concentrically arranged.

cf. ***Pediastrum*** Type Form 2

Plate IV, figs. 3, 7, 9–10

Description: Planar coenobium, circular to subcircular in overall shape, compact but showing some internal spaces between the central cells. Coenobium of 16 to 32 cells in concentric and/or spiral disposition. Inner cells mainly polygonal due to the compact arrangement of the coenobium and similar in size. The outer cells may project into a

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Plate III. 1. *Brazilea scissa* (Balme and Hennelly) Foster, 1975, specimen split into two similar halves, MPLP 8253(I) P50/0.

2. *Brazilea plurigenus* (Balme and Hennelly) Foster, 1979, MPLP 8253(I) D31/0.

3. *Brazilea* sp. A *in* Backhouse, 1991, MPLP 8251(I) O41/0.

4. *Tetraporina tetragona* (Pant and Mehtra) Anderson, 1977, MPLP 8249(G) C46/0.

5. ?*Lecaniella* sp., MPLP 8251(G) J52/0.

6-9. *Maculatasporites gondwanensis* Tiwari, 1965 showing different size of the reticulate pattern, (6) MPLP 8252(E) J43/2, (7) showing circular opening (pyloma?) (arrow), MPLP 8248(H) T34/0, (8) showing the inner laevigate layer (arrow), MPLP 8249(H) O42/3, (9) the arrow shows the circular opening MPLP 8248(H) P49/4.

10. *Maculatasporites amplus* Segroves, 1967, the specimen shows the circular opening (pyloma?) bordered by an annular thickening (arrow), MPLP 8248G P52/4.

11-12. *Mehlisphaeridium regulare* Anderson, 1977 showing different sculptural elements, (11) specimen slightly folded, that shows the circular opening (pyloma?) (arrow), MPLP 8250(G) L50/0, (12) the (black) arrow shows the laevigate inner layer, MPLP 8249(G) K49/4.

13. *Mehlisphaeridium parvum* Anderson, 1977, specimen slightly folded showing processes projecting in the equator, MPLP 8249(I) N31/0.

14. *Mehlisphaeridium regulare* Anderson, 1977, the arrow shows the circular opening (pyloma?), MPLP 8250(I) Q52/0.

15. *Maculatasporites amplus* Segroves, 1967, the arrow shows circular opening (pyloma?) bordered by an annular thickening, MPLP 8248(G) U51/3.

16. *Mehlisphaeridium parvum* Anderson, 1977, specimen slightly folded and extensively ornamented by thick baculate processes, the arrow shows circular opening (pyloma?) bordered by annular thickening, MPLP 8250(H) O51/0.

17. *Mehlisphaeridium parvum* Anderson, 1977 showing diverse sculptural elements which are too close to form an irregular reticulum, MPLP 8251(I) S55/0.

18. *Mehlisphaeridium* sp., (left) arrow shows the inner layer and the right arrow showing the circular opening bordered by annular thickening, MPLP 8252(I) M45/0.

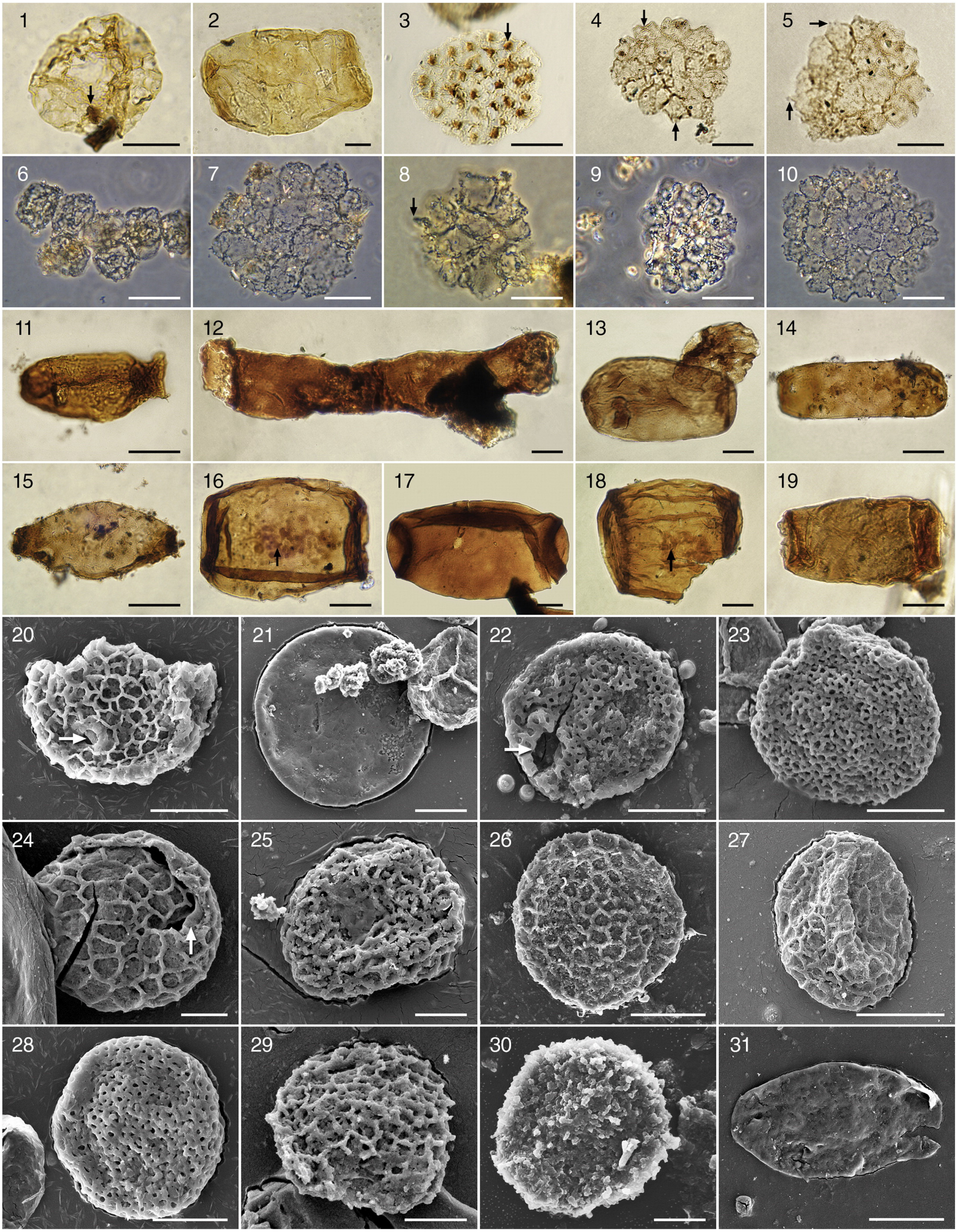
19. *Mehlisphaeridium parvum* Anderson, 1977, specimen partially folded given oval shape, coarse baculate sculptural processes projecting on the equator, MPLP 8250(J) H54/4.

20-23. *Maculatasporites amplus* Segroves, 1967, showing small, dense and conspicuous "foveolate" pattern, (20) MPLP 8248 (G) V52/3, (21) MPLP 8250(B) D25/2, (22) the arrow shows circular opening (pyloma?) bordered by an annular thickening MPLP 8250(G) L40/0; (23) specimen partially split into two halves, MPLP 8248(G) V52/0.

24-25. Sphaeromorph cluster in large masses of several crowded individuals, (24) the arrow shows inner circular bodies (chloroplast?), MPLP 8251(J) F35/2, (25) MPLP 8251(G) R50/3.

26-27. Sphaeromorph clusters of few spherical individuals, (26) shows inner chloroplast bodies, MPLP 8251(B) N31/0, (27) MPLP 8251(G) K48/0.

28. Part of a large mass of crowded spherical to subspherical small bodies (= sphaeromorphs), MPLP 8248(G) F45/0. Scale bars = 20 μm.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rounded, polygonal and slightly pointed external contour, giving a fenestrate aspect to the colony. Surface of cells granulate and also showing very small and very thin spinae (less than 0.5 μm).

Dimensions: Diameter of coenobia: 57 × 70 μm–56 × 68–79 × 88 μm; cell diameter: 8(10.6)18 μm (8 × 12–14 × 18 μm) (3 specimens).

Remarks: The main differences between the two forms here described are the larger dimensions of the cells and the coenobia, and the ornamented surfaces of the cells/coenobium.

Chlorophycean algae *incertae sedis*

Sphaeromorph clusters

Plate III, 24–28; Plate IV, 6

Remarks: The informal term "sphaeromorphs" is used here in the same sense as defined previously by Zavattieri and Prámparo (2006, p. 1199) for inaperturate, spherical to subspherical small bodies or cells, each 5 to 25 μm in diameter, with a smooth or faintly ornamented wall, and no accumulation bodies (chloroplasts) in the cells. In this assemblage they are common in short chains, clusters of few bodies but more frequently in large masses of several crowded individuals, the clusters ranging from 60 μm to more than 350 μm (22 clusters measured). An algal origin is possible for these forms based on the nature of the rest of the association. Batten et al. (1994) compared small, inaperturate, subspherical bodies commonly found as isolated specimens and in clusters of varying size (sometimes consisting of more than 100 individuals) with sphaeromorphs and closely comparable or identical to species of the pollen genus *Sphaeripollenites* Couper, 1958. They considered an algal origin as a possibility for some of such small rounded forms, particularly when they occur abundantly in clusters. Van Geel (1976) suggested that *Schizosporis*, *Ovoidites* and *Sphaeripollenites* probably represent spores of Zygnemataceae related to the recent genus *Spirogyra*. Such forms, frequently reported from pre-Quaternary strata, down to the Upper Paleozoic, are erroneously compared with pollen grains (cf. Van Geel, 1979 and references therein). This palynomorph type includes forms that have also been assigned to the Sphaeromorphitae Downie, Evitt et Sarjeant and the Herkomorphitae Downie, Evitt et Sarjeant (*sensu* Backhouse, 1991). From Permian strata, Foster (1979) and Foster et al. (2002) illustrated spherical forms linked in chains, which they assigned to *Brazilea helbyi* forma *gregata* Foster, 1979. The La Veteada material is similar in appearance to that illustrated by Foster (1979) but the spherical bodies are remarkably smaller than the Australian specimens (individual cells? 120 to 132 μm). The Australian specimens are arranged in chains of two to six individuals, while the clusters of the La Veteada assemblage consist of six to more than 20 spherical bodies. The presence of single or similar colonial fossil forms, supposedly of algal origin, has also been recorded for the Permian in the southern hemisphere (Balme and Hennelly, 1956; Balme and Segroves, 1966, Segroves, 1967, among others).

Algae *incertae sedis*

Genus ***Leiosphaeridia*** Eisenack, 1958

Leiosphaeridia sp.

Plate IV, 1

Dimensions: Equatorial diameter, 32–60 μm (6 specimens).

Remarks: In this taxon we include simple leiosphere-like forms, with a smooth and very thin wall *c.* 0.5 μm thick. They are rare in the assemblage. The specimens are folded and/or corroded but the original body is almost spherical or subspherical in shape. The specimens have a small darker inner accumulation body (choloroplast?). The problems regarding the morphology, the controversy on the taxonomy, and the possible affinities of the genus *Leiosphaeridia* Eisenack, 1958 have been discussed by Colbath and Grenfell (1995). Specimens of the La Veteada Assemblage are too poorly preserved to observe any dehiscence rupture/excystment or a circular pylome. According to the latter authors, Prasinophyte affinities are plausible for some species of *Leiosphaeridia* but, in general terms, the genus may be polyphyletic. Here, we consider the few specimens assigned to *Leiosphaeridia* sp. as algae *incertae sedis*.

Genus ***Reduviasporonites*** Wilson, 1962 *emend.* Foster et al., 2002

1962. *Reduviasporonites* Wilson, p. 91–93, pl. 1, 1–6.

1979. *Chordecystia* Foster, p. 109–110, pl. 41, 3–9, text-fig. 22.

1980. *Tympanicysta* Balme, p. 22–24, pl. 1, 3–7.

Type species: *Reduviasporonites catenulatus* Wilson, 1962, by original designation.

Remarks: The fossil genus *Reduviasporonites* is commonly described in the literature as *Tympanicysta* and *Chordecystia*, although Elsik (1999) regarded these genera as synonyms of *Reduviasporonites*. Foster et al. (2002) examined the type material of *Reduviasporonites catenulatus* Wilson, 1962, *Reduviasporonites chalastus* (Foster) Elsik, 1999 and *Tympanicysta stoschianus* (Balme) Elsik, 1999 as well as well-preserved specimens of these taxa recorded previously from the northern hemisphere. They proposed an emended generic diagnosis and description. In this contribution we follow the taxonomy and the morphological terminology of Foster et al. (2002, p. 36-38). These

Plate IV. 1.	*Leiosphaeridia* sp., the arrow shows small darker inner accumulation body (choloroplast?), MPLP 8253(I) L25/4.
2.	*Reduviasporonites chalastus* (Foster) Elsik, 1999 flask shaped specimen, MPLP 8250(H) P40/3, scale bar = 10 μm.
3.	cf. *Pediastrum*-Type Form 2, coenobium of 32 cells having inner bodies (arrow) and fenestrate contour of the external cells, MPLP 8248(H) D34/0.
4-5.	cf. *Pediastrum*-Type Form 1, (4) coenobium of ca. 16 cells, the arrows show outer cells divided in two lobe and pointed projections, MPLP 8248(H) V37/1, (5) coenobium of ca. 18 cells, the outer cells of the coenobium showing polygonal contours and truncated or pointed projections (arrows), MPLP 8253(H) L34/0.
6.	Sphaeromorph clusters of few spherical individuals, taken under contrast interference phase illumination, MPLP 8251(B) N26/0.
7.	cf. *Pediastrum*-Type Form 2, coenobium of 16 cells, taken with contrast illumination phase showing a infragranulate surface of the cells, MPLP 8251(B) E41/4.
8-9.	cf. *Pediastrum*-Type Form 1, (8) Coenobium of polygonal cells, some outer cells with pointed projection (arrow), MPLP 8250(E) Q42/3, (9) coenobium partially folded, phase contrast illumination, MPLP 8248(D) P41/0.
10.	cf. *Pediastrum*-Type Form 2, coenobium of 32 cells, phase contrast illumination showing an infragranulate surface of the cells, MPLP 8251(B) O41/0.
11-19.	*Reduviasporonites chalastus* (Foster) Elsik, 1999, showing different forms; (11) flask-shape specimen, MPLP 8249(H) K45/3, (12) specimens in chain, MPLP 8253(H) K43/4, (13) flask-shape specimen, MPLP 8250(G) O39/3, (14) tube-shape specimen, MPLP 8251(F) D28/3, (15) spindle-shaped specimen, MPLP 8251(B) V29/1, (16) cylinder-shape, with inner content (arrow) MPLP 8251(B) F36/4, (17) cylinder-shape with constricted terminal rims on both extremes, MPLP 8251(I) N49/3, (18) cylinder-shape, the arrow shows inner content MPLP 8251(I) T53/3, (19) cylinder-shape MPLP 8253(H) B48/0.
20.	*Maculatasporites gondwanensis* Tiwari, 1965 showing a broad reticulate pattern, the arrow show circular opening (pyloma?) having annular thickening, MEB 8249 (T7).
21.	*Brazilea scissa* (Balme and Hennelly) Foster, 1975, complete specimen, circular in polar view, dehiscence line is extended along the equator MEB 8249 (T5).
22.	*Maculatasporites amplus* Segroves, 1967 showing small "foveolate" sculpture, the arrow shows circular opening (pyloma?) bordered by an annular thickening MEB 8249 (T6).
23.	*Maculatasporites amplus* Segroves, 1967, MEB 8249 (T5).
24-27.	*Maculatasporites gondwanensis* Tiwari, 1965 showing a different size and forms of the reticulate pattern, (24) broad lumina and low meshes of the reticulum, the arrow shows the inner smooth layer, MEB 8249(T7), scale bar = 10 μm, (25) dented specimen showing small, close and prominent reticulum, MEB 8249 (T7), scale bar = 10 μm, (26) MEB 8253 (T2), (27) dented specimen, MEB 8249 (T8).
28.	*Maculatasporites amplus* Segroves, 1967, showing small foveolate sculpture MEB 8249 (T7).
29.	*Maculatasporites gondwanensis* Tiwari, 1965, showing small reticulum, the junctions of the reticulum project as short baculate elements, MEB 8249 (T7), scale bar = 10 μm.
30.	*Mehlisphaeridium regulare* Anderson, 1977 showing different sculptural elements, MEB 8253 (T1), scale bar = 10 μm.
31.	*Reduviasporonites chalastus* (Foster) Elsik, 1999, specimen of cylinder-shape showing smooth external surface, MEB 8249 (T5). Scale bars = 20 μm, otherwise as indicated.

authors discussed (p. 35) the fungal or algal origin of *Chordecystia* Foster, 1979 and *Tympanicysta* Balme, 1980 being junior synonyms of *Reduviasporonites* Wilson, 1962. Based on geochemical analysis, they suggested that *R. chalastus* has an algal rather than a fungal affinity. They used a new morphological terminology, independent of that used in mycology and/or phycology, for the description of these fossils, as the natural affinities of the specimens assigned to the genus *Reduviasporonites* are still uncertain. Earlier, Utting (1994), Visscher et al. (1996) and Yaroshenko and Gomankov (1998) interpreted these forms as hyphae and conidia of ascomycetes, fungal cysts or fungal spores, respectively. Elsik (1999) considered that the gross morphology of *Reduviasporonites* could be a Paleozoic analogue of modern basidiomycete *Rhizoctonia*, *i.e.* conidiophores (branched) and/or conidia (unbranched). Afonin et al. (2001) gave arguments for a green algal, zygnematalean affinity of *Tympanicysta* and the related (congeneric) forms. Recently, Spina et al. (2015) discussed the synonymy of *R. chalastus*, its distribution close to the P/T boundary and its affinity. They concluded that *R. chalastus* is a chlorophycean alga that probably lived in brackish water, although it shares some morphological features with Trentepohliales algae and shows also similarity to Zygnematalean algae, displaying additional typical characteristics of other green algae. Otherwise, Sephton et al. (2009) suggested that *Reduviasporonites* is of fungal origin, according to results of organic chemistry analysis, and more recently Visscher et al. (2011) confirmed this conclusion based on the interpretation of the morphology of this fossil forms.

Reduviasporonites chalastus (Foster) Elsik, 1999

Plate IV, 2, 11–19, 31

Remarks: All morphotypes described for *Reduviasporonites chalastus* by Foster et al. (2002) are recorded in the La Veteada Assemblage, including specimens occurring in chains (Plate IV, 12), flask-shaped (Plate IV, 2, 11), ovoid (Plate IV, 13, 17), spindle-shaped (Plate IV, 15), cylindrical (Plate IV, 16, 18), tube-shape (Plate IV, 14, 19) specimens with constricted terminal rims on both end (Plate IV, 11, 17–19). The main unit has smooth thin-walled, hollow cells with or without internal cell material (Plate IV, 16, 18). Cylindrical forms with the terminal rim on one or both ends are darker. They closely resemble those illustrated by Elsik (1999, pl. 1) as dispersed individual cells (= conidiosphores) and short chains (two to three individuals) of *Reduviasporonites stoschianus* (Balme) Elsik, 1999.

Dimensions: Maximum length of chain: 100–370 μm; discrete units: maximum length: 52–138 μm; maximum width: 23–75 μm (25 measured specimens).

5. Paleoecological and paleoenvironmental implications

According to Limarino et al. (2014) a progressive climatic amelioration took place during the Permian (postglacial stage) in South America, and the late Guadalupian–Lopingian sediments were predominantly deposited in arid or semiarid climates throughout most southern South America (Fig. 1). These climatic conditions are reflected in the Paganzo Basin by a widespread record of eolian deposits, evaporites, large playa-lake successions, interbedded with fluvial sequences, and a concomitant absence of coal beds (McLoughlin et al., 1997; Limarino et al., 2014).

As interpreted by Dávila et al. (2005) the upper part of the La Veteada Formation, at its type locality in Central Famatina, suggests sedimentation in shallow lakes probably formed by the action of strong, periodically fluctuating groundwater levels in the periphery of hypersaline lacustrine bodies and/or in saline playa-lake deposits within low-relief environments subjected to intense evaporation and arid–semiarid conditions. In such semi-permanent lacustrine environments, there were occasionally favorable conditions for the preservation of the organic matter, containing diverse land-plant-derived pollen grains and spores as well as microphytoplankton.

On the basis of palynological data, the La Veteada Formation as a whole is considered as Guadalupian–Lopingian in age. In the lower part of the unit, exposed in the Sierra de Narváez section (Gutiérrez et al., 2011), as well as in the upper part (Zavattieri and Gutiérrez, 2012; Gutiérrez et al., 2014) abundant palynofloras are broadly dominated by a diverse group of striate (mono- and bisaccate) and non-taeniate (mono- and bisaccate) pollen grains with less significant proportions of spores (Appendix 1.A).

The extended and thick lacustrine systems that developed in the stratotype of the La Veteada Formation at Central Famatina are evidenced by low, though persistent proportion of aquatic (fresh and/or brackish) palynomorphs (ranging from 3.4 to15.4% of the total assemblages). This microphytoplankton consists mostly of green algae (mainly Zygnemataceae), together with other organic-walled microfossils, most of which are of likely algal affinity. Table 2 shows the distribution of different components integrating the studied microphytoplankton assemblage per sample. This algal assemblage is mainly dominated by polymorph coenobia of the chlorophycean alga *Syndesmorion stellatum* Foster et Afonin, 2006. Foster and Afonin (2006) pointed out that “different types of coenobial shapes may represent either different stages of their development or, as seems more likely, the response to various environmental stresses relating to changes in pH, salinity, nutrient supply, and light levels”. The diversity of *S. stellatum* morphotypes is likely to reflect response to stress conditions. Thus we conclude that it grew in the highly saline lacustrine environment of the La Veteada succession.

Samples of the uppermost levels of the type section of the La Veteada Formation also record *Reduviasporonites chalastus* (= *Tympanicysta stoschiana* Balme, 1979 = *Reduviasporonites stoschianus* (Balme) Elsik, 1999), their frequency ranges from 2.8 to 6.2% of the total assemblages. Many authors explained the common worldwide occurrence of this organic-walled microfossil as a spike-fungal event linked to saprophytic fungal activity resulting from the ecological crisis in woody forests at the Permian–Triassic boundary (Wood and Mangerud, 1993; Wood, 1994, 1995; Eshet et al., 1995; Visscher et al., 1996, 2011; Elsik, 1999; Steiner et al., 2003; Sandler et al., 2006; Sephton et al., 2009). Such a “fungal spike” is expressed by the high abundance of the genus *Reduviasporonites*, or when it is a dominant component (up to 95%) in palynological assemblages (Vajda and McLoughlin, 2004; Lei et al., 2013, and references therein). Several other authors reported *Reduviasporonites* and/or *Tympanicysta* as a minor constituent of diverse plant-derived assemblages (*e.g.*, Balme, 1970; Foster, 1979; Backhouse, 1991; Looy et al., 2001; Lei et al., 2013) as occurred in the La Veteada microflora. Other authors, *e.g.*, Ouyang and Utting (1990), Afonin et al. (2001), Foster et al. (2002), Lei et al. (2013) and Spina et al. (2015), suggested that these microfossils are most likely of algal origin. In this sense, Krassilov et al. (1999), and Afonin et al. (2001) considered *Tympanicysta* (synonym of *Reduviasporonites*) as a green algae of zygnematalean affinity, particularly because of the inner chloroplast content present in some forms. As such it occurs in fresh-water or brackish environments. McElwain and Punyasena (2007) also suggested the development of worldwide PTB anoxia, generally stressed environments and a widespread algal pulse, rather than a fungal spike. The algal origin of *R. chalastus* recorded in the La Veteada Assemblage is also suggested by their inner chloroplast bodies, which are clearly visible in many specimens, confirming that they represent green algae comparable to extant zygnematalean green algae, as asserted by Wood and Elsik (1999). However, some other forms lacking these features could represent fungal remains.

Representatives of zygnematacean algae are also recorded in these assemblages by the genera *Brazilea*, *Tetraporina*, ?*Lecaniella*, *Maculatasporites* and *Mehlisphaeridium* (Balme and Segroves, 1966; Segroves, 1967; Grenfell, 1995; Playford and Rigby, 2008) as well as large clusters of sphaeromorphs *incertae sedis*, probably representing spores of Zygnemataceae (van Geel, 1976). Colbath and Grenfell (1995) pointed out that from a palynological perspective, the zygnematacean zygospores are frequently recovered in association with land-plant miospores, indicating freshwater deposition. Zygnematacean algae inhabit a great variety of freshwater habitats

(Colbath and Grenfell, 1995) or even tolerate high salinity levels (Brenner and Foster, 1994; Grenfell, 1995). Head (1992) noted that the presence of fossil zygnematacean zygospores has been linked with seasonal warming and rising water temperatures causing desiccation of the habitat (Ellis and Van Geel, 1978; Van Geel and Van der Hammen, 1978). Hammer et al. (1983) also demonstrated that some extant chlorophyte algae (e.g. *Pediastrum* and *Scenedesmus*) tolerate high salt concentration levels (between 50 and 100 g/l^{-1}).

Planar colonial *Pediastrum*-like forms as representatives of the hydrodictyaceaen algae inhabit freshwater environments (Colbath and Grenfell, 1995; Batten, 1996), although these chlorophycean algae may also be found in low-salinity environments (*e.g.*, Tyson, 1995; Batten, 1996; Batten and Grenfell, 1996).

In general, the palynoflora derives mainly from diverse gymnosperm vegetation, composed of conifers, peltasperms, corystosperms and Caytoniales, but taeniate bisaccate pollen mostly of glossopterids are dominant (Table 1) (Gutiérrez et al., 2011, 2014). Playford and Rigby (2008) described the glossopterids as opportunistic, well-rooted deciduous trees that spread progressively over post-glacial Gondwana Permian landscapes, growing in humid lowland, mire-type settings under conditions of ameliorating climates. This mesophyllous gymnosperm forest would have developed in the distant upland – and probably dryer – surrounding areas, providing most of the allochthonous elements. Low proportions of spores (Table 1) derived mostly from lycophytes (cingulate-cavate spores) and ferns (smooth and ornamented trilete spores) with hygro-mesophyllous requirements locally inhabited moist terrestrial environments surrounding the depositional area (para-autochthonous elements). Fine red-bed siliciclastic sediments containing several thick layers of marls, gypsum, and chert (silcrete-type paleosoils) indicate an extended episode of continental sedimentation, which clearly implies accentuated aridity accompanied by intense oxidation during the deposition of La Veteada Formation, presumably reflecting increasingly adverse conditions. The palynological evidence also reflects a parental vegetation adapted to arid, perhaps even desert-like conditions, certainly of low humidity, thus consonant with the sedimentological evidence. The highly diverse La Veteada microphytoplanktonic assemblage is composed by algae that grew in hypersaline lacustrine environment (*Syndesmorion*) associated with usually fresh-water/brackish (*Maculatasporites*, *Mehlisphaeridium*, *Brazilea*, *Tetraporina*, *Lecaniella*, *Reduviasporonites*) or even tolerant to certain salinity taxa (*Pediastrum*-like forms). These last groups of taxa probably were transported by streams, rivers or floodings into the stressed depositional site.

6. Composition and age of the La Veteada Assemblage — phytogeographic and paleofloristic implications

The late Paleozoic paleogeographic situation of the Paganzo Basin (see Limarino et al., 2014) evidences the northwest Gondwanan floristic affiliation for the La Veteada palynoflora (Fig. 1). Gutiérrez et al. (2011) described 81 species of spores and pollen grains, together with rare algae and fungal remains recovered from the shallow lacustrine successions of the lower part of the La Veteada Formation, at Sierra de Narváez, Catamarca Province, Famatina Range. This palynoflora has been dated as Middle Permian (Guadalupian) and represents the uppermost limit of the *LW* (*Lueckisporites*–*Weylandites*) Biozone, the age of which is considered as Wordian to Capitanian (Césari and Gutiérrez, 2001; Césari, 2007). Zavattieri and Gutiérrez (2012) and Gutiérrez et al. (2014) considered that the composition of the upper La Veteada palynofloristic assemblage indicates that it differs from other known early–Middle Permian or Middle Triassic microfloras of Argentina. Therefore, we concluded that the composition of the upper La Veteada palynoflora in its stratotype, suggests a Lopingian age. It is thus considered to be the youngest Permian palynofloral assemblage recorded up to now in Argentina and South America.

The green algae genus *Syndesmorion* has only been recorded from Late Permian–Early Triassic continental deposits in the Northern Hemisphere (Fig. 4 and Supplementary material, Appendix). This is the first find of *Syndesmorion stellatum* for the latest Permian in the western Gondwana realm (Fig. 4). Moreover, in this assemblage we report the first record of coenobia of *Pediastrum*-like hydrodictyaceaen algae in the hypersaline environment of the upper La Veteada Formation, together with various Zygnematacean algae including *Brazilea scissa*, *Brazilea plurigenus*, *Brazilea* sp. A, *Tetraporina tetragona*, ?*Lecaniella* sp., Sphaeromorph clusters *incertae sedis*, *Maculatasporites gondwanensis*, *Maculatasporites amplus*, *Mehlisphaeridium regulare*, *Mehlisphaeridium parvum* and *Mehlisphaeridium* sp. *Reduviasporonites chalastus*, also of likely algal affinity. It is possible that the usually fresh-water to brackish water taxa inhabited in fresh water lenses and probably they came in to the lake after heavy rainfall and/or floodings. This is the first record of Lopingian age in Argentina, southern South America and elsewhere in northwestern Gondwana in which *S. stellatum* and *Pediastrum*-like forms are associated with a diverse assemblage of green algae that are commonly recorded worldwide in late Permian–early Triassic strata. This assemblage characterizes a stressed hypersaline lacustrine environment that developed in arid to semiarid climates. Table 1 shows the upper Permian distribution of microphytoplankton taxa recorded in the La Veteada Assemblage. Thus, the microphytoplankton recorded in this assemblage has potential as an age diagnostic and environmental indicator for Lopingian continental deposits as well as for paleogeographic and paleoclimatic reconstructions.

7. Discussion and conclusions

As previously mentioned, the shallow lacustrine successions of the La Veteada Formation were initially deposited in Sierra de Narváez, where the palynological associations are consistent with a Guadalupian age for that section (Gutiérrez et al., 2011). In contrast, the Central Famatina deposition of this unit begins with paleosols of undefined age (<5 m), underlying a lacustrine succession deposited during the Lopingian (Zavattieri and Gutiérrez, 2012; Gutiérrez et al., 2015). The absence of records of the younger palynological association in the north may be due fact that to top of the sequence is eroded. The difference in rates of sedimentation and lateral facies changes during the Guadalupian suggests a slightly higher subsidence in the north, constituting the main depocenter. In Central Famatina base-line paleosols could represent a condensed sedimentation stage for that interval. Due to profuse erosion at the top of the La Veteada Formation in the northern region, it is not possible to determine whether there was a shift of the main depocenter to the south, or an expansion of lake systems during the Lopingian.

Wide-spread records of eolian deposits, evaporites, large playa-lake successions, and interbedded eolian and fluvial deposits are all indicators of arid to semiarid climates throughout most of southern South America during the late Guadalupian–Lopingian (Limarino et al., 2014). As pointed out by Dávila et al. (2005) and Limarino et al. (2014), the La Veteada Formation was deposited when global atmospheric conditions deteriorated caused by extensive volcanic activity.

The deposition in the Permian Paganzo Basin is commonly considered to have been caused by regional subsidence. However, the diachronic lacustrine depositional sequences of the La Veteada Formation indicates the existence of a low topographic relief, though pronounced enough to generate independent depocenters with different subsidence and sedimentation rates.

On the western slope of the Famatina Range, the Paganzo Basin is unconformably covered by red beds of the Talampaya Formation, which marks the beginning of the deposition of the extensional Ischigualasto Basin (*e.g.* Milana and Alcober, 1994). In contrast to the Paganzo Basin, Ischigualasto is a halfgraben basin, which has a restricted areal distribution with high sedimentation rates. A volcanic tuff near the top of the Talampaya Formation yielded late Permian ages of 252.4 ± 0.07 Ma (Gulbranson et al., 2015). This minimum deposition age of the Talampaya Formation suggests an almost continuous transition from the final stages of a foreland basin, dominating the Central Andes during the Permian represented for the La Veteada Formation, to an extensional context, which extends to the upper Triassic. Therefore, the palynological association defined in this paper is a useful tool to restrict the interval of change in the regional subsidence regime.

The upper La Veteada palynological assemblage contains an abundant, well-preserved diverse palynoflora, mainly composed of pollen grains, spores, chlorococcalean algae and other organic-walled microphytoplankton of likely algal affinities (Gutiérrez et al., 2014).

The diverse microphytoplankton assemblage recorded from the hypersaline lacustrine environment of the upper part of the La Veteada assemblage is dominated mainly by Chlorophycean algae:

1) Well-preserved planar coenobia of *Syndesmorion stellatum* showing diverse coenobial morphotypes are recorded for the first time in the Permian strata of Gondwanan realm. Two new morphotypes are described. Most of these coenobia show "internal cylindrical bodies" (chloroplasts) that are herein mentioned for the first time for this green alga.
2) Chlorophyta algae belonging to the Hydrodictyaceae *Pediastrum*-like planar coenobia are for the first time recorded from upper Permian sequences.
3) Various groups of green algae belonging to the Zygnemataceae are also recorded as part of the microphytoplankton assemblage: *Brazilea scissa*, *Brazilea plurigenus*, *Brazilea* sp. A, *Tetraporina tetragona*, ?*Lecaniella* sp., large clusters of sphaeromorphs as well as common *Maculatasporites gondwanensis*, *Maculatasporites amplus*, *Mehlisphaeridium parvum*, *Mehlisphaeridium regulare*, *Mehlisphaeridium* sp. and few specimens of *Leiosphaeridia* sp.
4) *Reduviasporonites chalastus* is recorded from this assemblage showing a high morphology, many forms having internal chloroplasts resembling zygnematalean green algae *sensu* Afonin et al. (2001) and Spina et al. (2015). Although, some specimens recorded here could be assigned to fungal remains based on morphological characteristics, according to Visscher et al. (1996) and Elsik (1999). These organic microfossils are present in low frequency in the assemblage.
5) The overall palynological composition suggests a Lopingian age for the La Veteada Formation in its strato-type, based on the stratigraphic ranges of all the recognized land-derived miospore species. Therefore, it is considered as the youngest Permian palynofloral assemblage recorded up to now from Argentina and South America (Gutiérrez et al., 2014).

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