Gymnosperm pollen grains from the La Veteada Formation (Lopingian), Paganzo Basin, Argentina: biostratigraphic and palaeoecological implications

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This work forms the concluding part of a series of systematic studies of typical Gondwanan Permian palynofloras from the type section of the La Veteada Formation in the Paganzo Basin, central-western Argentina. It deals with the description and/or illustration of the non-taeniate monosaccate, bisaccate and polysaccate gymnosperm pollen species that are richly represented in the La Veteada Formation and are attributed to 25 genera. These taxa are allied to, or derived from, a diverse range pteridosperms (corystosperms, peltasperms), conifers (including Voltziales) and cordaites; Ginkgoales, Cycadales and Gnetales also have some representation. The new species, *Jugasporites vellicoites*, is instituted and the new combination, *Alisporites angustus* (Ouyang & Norris) comb. nov. et emend., is proposed. New evidence to support a Lopingian age for the palynoflora, considered to be the youngest Permian palynoflora recorded hitherto in South America, is based on a summary of the published information about its composition, together with an assessment of previous records of the diversity of gymnosperm taxa analysed in this contribution. The co-occurrence of several species of taeniate pollen (described in a previously published part of our work) and the gymnosperm taxa documented here, which have not been reported before from South America, differentiates the palynoflora of the upper La Veteada Formation from all others so far described from this continent. The high ratio of pollen versus spores, plus the botanical and palaeoecological inferences of the gymnospermous component of the formation's palynoflora, reflects a parent vegetation adapted to relatively dry conditions. Such a low-humidity environment is consistent with the sedimentological evidence, which suggests that, through the Lopingian, semi-arid to arid climates dominated the southern South American basins.

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THE PALYNOFLORA of the upper La Veteada Formation, which crops out at its type section in the Paganzo Basin, Argentina, is dominated by pollen derived from higher vascular plants (gymnosperms) but also includes a rich representation of spores derived from lower vascular plants (bryophytes, lycophytes, sphenophytes, fern spores: Gutiérrez *et al*. 2017) together with organic-walled microphytoplankton (mainly chlorophycean freshwater algae) and fungi (Zavattieri *et al*. 2017).

The gymnospermous component of the palynoflora is diverse. Zavattieri & Gutiérrez (2012) studied the monosaccate (cordaitalean) pollen abundantly represented in this palynoflora, and Gutiérrez *et al*. (2014) documented the association of striate bisaccate, striate monosaccate, plicate and colpate grains. In this concluding part of our systematic study of the palynoflora of the La Veteada Formation, we describe and illustrate

the non-striate (monosaccate, bisaccate and polysaccate) gymnospermous pollen content.

Outcrops of the La Veteada Formation (Dávila *et al*. 2005) have been recognized in various parts of the Famatina Range (Paganzo Basin; Fig. 1) and have been dated to late Guadalupian to late Lopingian (Zavattieri & Gutiérrez 2012, Gutiérrez *et al*. 2014). The lower section of the unit is exposed in the Sierra de Narváez, Catamarca Province; its sedimentary succession and diverse palynological content were studied by Gutiérrez *et al*. (2011). The upper part of the La Veteada Formation crops out at its type section where it encompasses a 180-m-thick succession of red–purple, laminated siltstones, mudstones and sandstones, with interbedded, lenticular evaporitic strata and laminated dolomites, which were deposited in fluvio-lacustrine environments under semi-arid to arid climates (Limarino *et al*. 2014, Zavattieri *et al*. 2017). The type locality of the unit (La Yesera section; 28°38′S, 67°46′W; Dávila *et al*. 2005) is situated on the eastern edge of the central Famatina
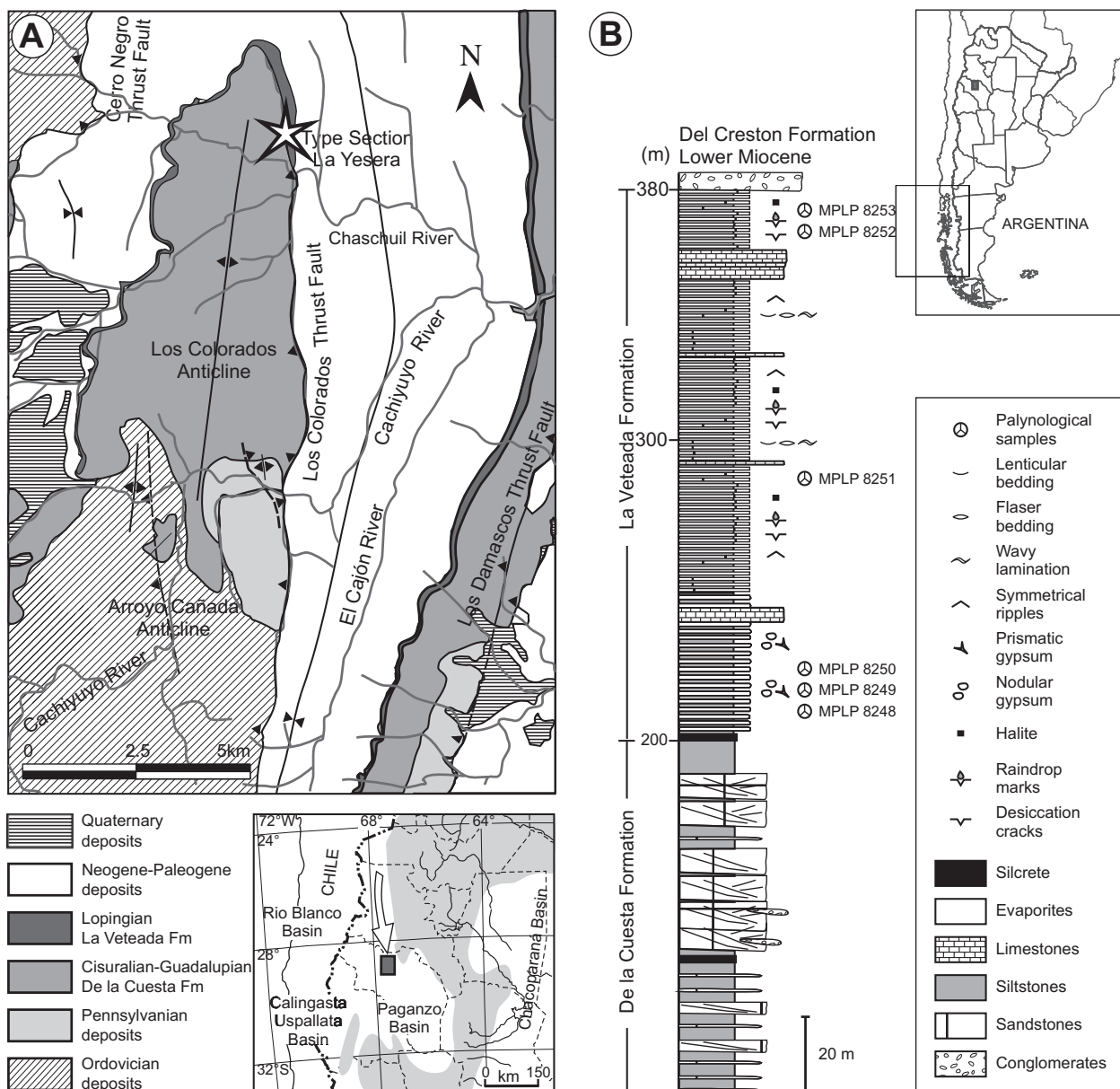
Fig. 1. **A,** Geological map of the study area, showing the location of the studied type section (star). **B,** Type section of the La Veteada Formation at Famatina Range and source of the palynological samples (modified from Dávila *et al.* 2005).

Range, northern part of La Rioja Province, central-western Argentina (Fig. 1A). At this locality, the La Veteada Formation overlies Permian fluvio-eolian deposits of the De La Cuesta Formation with a paraconformity and is overlain un-conformably by strata of the lower Miocene Del Crestón Formation (Dávila *et al.* 2005; Fig. 1B). The type section of the unit begins with a basal grey silcrete (a siliceous duricrust) that is recognized regionally and used as marker bed (Dávila *et al.* 2005, Ezpeleta 2009). Above this silcrete, the succession continues with medium- to coarse-grained tabular sandstones and fine conglomerate lenses that are silicified and calcretized with sub-rounded clasts associated with a fluctuation in groundwaters and pedogenic processes. This facies association suggests the development of an immature soil on a substrate with sandy parent

material favouring vertical drainage. Upwards, the La Veteada Formation consists of rhythmically interbedded tabular fine-grained sandstones, with fine to very fine, dark grey, laminated siltstones and claystones, and locally, some layers with gypsum. Laminar mudstones present at some intervals suggest these plains may have been covered by water. However, the generally red–purple colour of the strata and common interbedded levels with mud cracks, raindrop prints and ripple marks indicate deposition along the margins of very shallow lakes where sedimentation was interrupted by subaerial exposure and sporadic low-flow regimes in a dry environment. Bioturbation points to biological activity in some intervals. The nodular to prismatic gypsum banks are distributed irregularly, forming locally thick lenticular deposits of rhythmic evaporites and stromatolitic

laminated limestones. This development of nodular and prismatic gypsum in the basal part of the succession suggests the precipitation of evaporites on floodplains under highly evaporative conditions, in which the fluctuation of the phreatic-ground water-table was periodic, either in lacustrine hypersaline bodies and/or in saline sheet-loads (Ezpeleta 2009). Towards the top, the presence of carbonate-cemented sandstones, laminated mudstones and stromatolitic dolomites is interpreted as having formed at the edge of a lake that was undergoing continuous expansion and contraction, allowing the interaction of subaqueous and subaerial processes. Dolomitic banks interbedded with algal structures characterized by low detrital content, indicate shallow-water conditions and probably reflect entrapment of clastic material at the margins of the lake where calcareous sandstones developed. The different facies associations and their vertical arrangement have led to the interpretation of lake development following a discontinuity that is represented by silcretes associated with condensed, low-sedimentation intervals that favoured the formation of palaeosols. These lakes were mainly hypersaline, semi-perennial, with periodic expansion and retraction, suggesting low-relief settings (cf. Zavattieri *et al.* 2017).

The palynological assemblages recovered from the upper part of the La Veteada Formation are unique both in composition and age, as they constitute the youngest Permian palynoflora hitherto recorded from South America. A Lopingian age has been suggested from biostratigraphic analysis of the associated taeniate pollen grains (Gutiérrez *et al.* 2014), spores (Gutiérrez *et al.* 2017) and the diversity of microphytoplankton (Zavattieri *et al.* 2017).

Material and methods

Six outcrop samples of pelitic strata from the type section of the La Veteada Formation were processed using standard palynological techniques (Volkheimer & Melendi 1976). Some organic residues were subjected to slight oxidation using concentrated nitric acid (HNO_3) for 2 minutes and briefly washed (*ca* 45 s) in 5% ammonium hydroxide, to remove the oxidation products. All residues were sieved through 10 µm mesh and then were finally mounted in glycerine jelly. The slides were examined with an Olympus BX 50 light microscope, and photomicrographs were taken with an adapted Olympus digital camera of the Paleopalynology Unit of the Argentinian Institute of Nivology, Glaciology and Environmental Sciences (IANIGLA), CCT-CONICET, Mendoza. A Nikon H550S light microscope and an adapted Nikon DS-U2-Fil-U2 digital camera from the Paleopalynologic Laboratory, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, were also used. The studied slides are identified by the acronym MPLP (Mendoza-Paleopalinoteca-Laboratorio de Paleopalinología); the

corresponding catalogue numbers range from 8248 to 8253. Specimens are located by England Finder coordinates (E.F.co.). Residues for scanning electron microscopy (SEM) were mounted on aluminium stubs and coated with gold-palladium. A Phillips XL 30 TMP at the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires was used for detailed examination and imaging of selected specimens. Size measurements are given in the format N1(N2)N3, where N1 and N3 represent, respectively, the minimum and maximum dimensions, and N2 represents the mean dimension.

Well-known gymnosperm pollen species identified in the present study are listed and illustrated, with full descriptions being provided only for the new species or for those species where taxonomic or morphological clarification is needed. The suprageneric classification follows that of Potonié & Kremp (1954), with modifications introduced by Playford & Dettmann (1996). For the morphometric terminology and measurements quoted, we follow Playford & Dino (2000a, 2002). Poorly preserved and other specimens that do not permit a clear specific identification are assigned to 'spp.'. The assessments of biostratigraphy and age are based on the known worldwide stratigraphic distribution of the mono- and bisaccate pollen species identified in this study, together with previous records from South America, especially Argentina (see Supplementary Data File 1 and summarized in Fig. 7).

Results

The following alphabetical lists of monosaccate, bisaccate and polysaccate gymnosperm pollen encompass the non-taeniate (non-striate) species that have been identified in this study of the La Veteada palynoflora from the formation's type section. That these gymnosperm species constitute the palynoflora's dominant component has been detailed by Gutiérrez *et al.* (2014, table 1). Other pollen have been identified here but, because of their poor preservation and mature colour (brown to dark brown), which suggest allochthony and reworking, they are neither listed nor illustrated. They are mostly non-striate monosaccate pollen comprising: *Cannanoropollis* sp. cf. *C. densus* (Lele) Bose & Maheshwari, 1968, *C. janakii* Potonié & Sah, 1960, *C. mehtae* (Lele) Bose & Maheshwari, 1968, *Cannanoropollis* sp., *Circumplicatipollis* sp., *Divarisaccus* sp. cf. *D. stringoplicatus* Ottone, 1991, *Limitisporites rectus* Leschik, 1956, *Potonieisporites triangulates* Tiwari, 1965, *P. novicus* Bharadwaj, 1954, *Potonieisporites* sp., *Plicatipollenites malabarensis* (Potonié & Sah) Foster, 1975 and *Tuberisaccites varius* Lele & Makada, 1972.

Monosaccate pollen

Accinctisporites ligatus Leschik, 1955 (Fig. 2A)
Crucisaccites monoletus Maithy, 1965 (Fig. 2C)

Genus	MPLP 8248	MPLP 8249	MPLP 8250	MPLP 8251	MPLP 8252	MPLP 8253
Accinctisporites				0.15		
Crucisaccites					0.20	
Gondwanapollis			0.29			
Potonieisporites		0.38			0.20	
Cladaitina	30.9	24.00	31.84	4.95	13.59	8.5
Vesicaspora			0.57			
Alisporites	2.40	3.46	3.59	2.91	2.60	2.68
Colpisaccites					0.40	0.24
Cuneatisporites	0.22		0.14			0.24
Falcisporites	0.65	2.11	1.72	1.53	1.60	0.97
Granisaccus		0.19				
Jugasporites	2.62	2.11	2.01	1.84	0.60	1.95
Klausipollenites	0.65	0.58	1.01	0.46	0.20	0.24
Limitisporites		0.96	0.29	1.07	1.20	1.46
Minutosaccus	0.22	1.35	1.15	0.77	1.60	
Pinuspollenites	0.22	0.96	0.29			
Platysaccus	1.53	1.73	1.01	0.92	1.20	0.73
Protodiploxypinus	0.87	0.58	0.29	0.31	0.20	0.49
Pteruchipollenites	0.22	0.19	0.57	0.31	0.20	0.73
Scheuringipollenites	0.44	0.19		0.15	0.20	0.24
Sulcosaccispora		0.19		0.15		
Triadispora			0.14	0.15	0.40	
Valialasaccites						0.24
Vitreisporites	0.65	0.58	0.57	0.46	0.40	0.24
Polarisaccites				0.2		

Table 1. Distribution of non-taeniate gymnosperm pollen genera recorded in the La Veteada Formation at its type locality, Paganzo Basin. Numbers are expressed in percentages of the total recorded taxa per level.

Gondwanapollis frenguelli (Césari) Gutiérrez, 1993 (Fig. 2F)

Potonieisporites brasiliensis (Nahuys *et al.*) Archangelsky & Gamerro, 1979 (Fig. 2E)

Potonieisporites lelei Maheshwari, 1967 (Fig. 2D)

Vesicaspora magnalis (Andreeva) Hart, 1965 (Fig. 2B).

Remarks. The main diagnostic features of this species are its transversely oval corpus and the degree of distal inclination of its sacci. The latter feature gives rise to a characteristic development of an apparent thickening around the margins of the corpus. This 'thickening' or 'equatorial cingulum' (*sensu* Hart 1965), which is wider on the lateral margins of the corpus, is associated with folding of the distally inclined sacci at their bases. It distinguishes *Vesicaspora magnalis* from other species of the genus. The distal roots of the sacci are convex and do not extend to the lateral margins of the corpus; and the distal zone of the corpus is fusiform, extending over about one-third of the corpus. The La Veteada specimens attributed to *V. magnalis* resemble the specimen illustrated under the same name by Ouyang & Norris (1999, pl. 5, Fig. 13), who considered this species to partially overlap in characteristics with *V. acrifera* (Andreeva) Hart, 1965, and that both species differed from *V. wilsonii* (Schemel) Wilson & Venkatachala, 1963 in having more distinct and broader sulci. The La Veteada specimens also have distally inclined sacci giving rise to the characteristic thicker area of folding at their distal roots.

Vesicaspora spp.

Bisaccate pollen

Alisporites angustus (Ouyang & Norris, 1999) comb. nov. et emend. (Fig. 2I–J)

Alisporites australis de Jersey, 1962 (Fig. 2G–H)

Alisporites lowoodensis de Jersey, 1963 (Fig. 2K)

Alisporites rioclarensis Menéndez, 1976 (Fig. 2L–M)

Alisporites spp.

Colpisaccites granulosus Archangelsky & Gamerro, 1979 (Fig. 2N)

Cuneatisporites radialis Leschik, 1956 in Kräusel & Leschik, 1955 (Fig. 2O).

Remarks. Jain (1968, p. 26) discussed the distinction between *Cuneatisporites* Leschik, 1956 and *Platysaccus* Naumova ex Potonié & Klaus, 1954 on the basis of the differences established by Bharadwaj (1962), who pointed out that *Cuneatisporites* has a corpus that is distinctly elongated vertically in polar view, an intra-microreticulate exine, and it lacks a germinal aperture. Furthermore, in its type species, *C. radialis*, the attachments of the sacci appear to be sub-equatorial and the infra-reticulation of the sacci characteristically tends to be radial towards their bases, with the brochi being of different shapes and size. Usually, the sacci are not strongly inclined distally. The La Veteada specimens of the species are closely similar to those illustrated by Jain (pl. 7, Figs 96–99), from the Argentinian Triassic. *Cuneatisporites radialis* of the La Veteada palynoflora is slightly smaller (75–105 × 42–60 μm) than Jain's specimens (87–140 × 51–80 μm).

Falcisporites nuthallensis (Clarke) Balme, 1970 (Fig. 2P–Q)

Gymnosperm species	MPLP 8248	MPLP 8249	MPLP 8250	MPLP 8251	MPLP 8252	MPLP 8253
Alisporites angustus	X	X	X	X	X	X
Alisporites rioclarensis	X	X	X	X	X	X
Alisporites/Falcisporites spp.	X	X	X	X	X	X
Falcisporites nuthallensis	X	X	X	X	X	X
Falcisporites stabilis	X	X	X	X	X	X
Jugasporites delasaucei	X	X	X	X	X	X
Jugasporites nubilus	X	X	X	X	X	X
Jugasporites vellicoites	X	X	X	X	X	X
Jugasporites spp.	X	X	X	X	X	X
Klausipollenites spp.	X	X	X	X	X	X
Minutosaccus spp.	X	X	X	X	X	X
Pinuspollenites thoracatus	X	X	X	X	X	X
Protodiploxypinus americus	X	X	X	X	X	X
Scheuringipollenites ovatus	X	X	X	X	X	X
Scheuringipollenites spp.	X	X	X	X	X	X
Triadispora crassa	X	X	X	X	X	X
Vitreisporites spp.	X	X	X	X	X	X
Klausipollenites devolvens	X	X	X	X	X	
Klausipollenites schaubergerii	X	X	X	X		X
Klausipollenites staplinii	X	X	X	X	X	
Minutosaccus acutus	X	X	X	X	X	
Protodiploxypinus spp.	X	X		X	X	X
Cuneatisporites radialis	X		X	X	X	X
Jugasporites lueckoides	X		X	X	X	X
Jugasporites sp. A	X		X	X	X	X
Platysaccus alatus	X		X	X	X	X
Pteruchipollenites gondwanensis	X		X	X	X	X
Scheuringipollenites medius	X		X	X	X	X
Scheuringipollenites tentulus	X		X	X	X	X
Vitreisporites microsaccus	X		X	X	X	X
Vitreisporites pallidus	X		X	X	X	X
Platysaccus queenslandii		X	X	X	X	X
Platysaccus spp.		X	X	X	X	X
Limitisporites hexagonalis		X	X	X	X	X
Jugasporites gamsi		X	X	X	X	X
Jugasporites perspicuus		X	X	X	X	X
Klausipollenites decipiens		X	X	X	X	X
Pteruchipollenites gracilis		X	X	X	X	X
Vitreisporites subtilis	X			X	X	X
Pinuspollenites spp.	X	X	X	X		
Limitisporites spp.	X		X		X	X
Minutosaccus potoniei		X	X	X	X	
Minutosaccus schizeatus	X		X	X	X	
Protodiploxypinus fastidiosus	X		X	X		X
Scheuringipollenites circularis	X		X	X	X	
Sulcosaccispora alaticonformis		X	X	X		X
Colpisaccites granulosus			X	X	X	X
Potonieisporites spp.		X		X	X	X
Alisporites australis		X	X	X	X	
Scheuringipollenites barakarensis		X	X	X		X
Gondwanapollis frenguelli	X		X	X		
Jugasporites purus	X		X	X		
Jugasporites schaubergeroides	X				X	X
Platysaccus sp. cf. *P. papilionis*			X	X		X
Jugasporites parvus			X	X		X
Vitreisporites signatus	X			X		
Granisaccus sp.	X	X				
Triadispora muelleri	X		X			
Limitisporites fuscus			X	X		
Vesicaspora magnalis			X	X		
Polarisaccites bilateralis		X		X		
Platysaccus sp. cf. *P. trumpii*			X			X
Accinctisporites ligatus				X		X
Potonieisporites brasiliensis				X		X

(Continued)

Table 2.   (Continued).

Gymnosperm species	MPLP 8248	MPLP 8249	MPLP 8250	MPLP 8251	MPLP 8252	MPLP 8253
Potonieisporites lelei				X		
Vesicaspora spp.				X		
Crucisaccites monoletus					X	
Alisporites lowoodensis			X			
Valialasaccites sp.						X

Table 2. Distribution per sample of the gymnosperm species of the La Veteada Formation at its type section, Paganzo Basin.

Falcisporites stabilis Balme, 1970 (Fig. 2R)

Falcisporites spp.

Granisaccus sp. A (Fig. 2S–T).

Remarks. Pautsch (1973, pp. 138–139), in his emendation of *Granisaccus* Mädler, 1964, pointed out that Scheuring (1970) had included this genus in the synonymy of *Protodiploxypinus* Samoilovich, but the latter embraces forms having smooth or striate corpi, whereas *Granisaccus* has a variable corpus sculpture (mainly on the cappa) of grana, verrucae, gemmae, rugulae or cristae. Retention of *Granisaccus* was advised by Pautsch (1973) for bisaccate pollen with such ornament. The La Veteada specimens assigned to *Granisaccus* sp. A have distally pendant sacci that are smaller than the corpus, and a cappa that is seemingly sculptured.

Dimensions (two specimens). Saccus height × distal length: 32–36 μm × 22–27 μm; corpus height × width: 40–42 μm × 38 μm; total length: 55–60 μm.

Jugasporites delasaucei (Potonié & Klaus) Leschik, 1956 (Fig. 3A)

Jugasporites gamsi (Klaus) Foster, 1983 (Fig. 3B)

Jugasporites lueckoides Klaus, 1963 (Fig. 3C–D)

Jugasporites nubilus Leschik, 1956 (Fig. 3E–F)

Jugasporites parvus (Klaus) Foster, 1983 (Fig. 3G–H)

Jugasporites perspicuus Leschik, 1956 (Fig. 3I–J)

Jugasporites purus (Leschik) Tiwari & Singh, 1984 (Fig. 3K)

Jugasporites schaubergeroides Klaus, 1963 (Fig. 3L–M)

Jugasporites vellicoites sp. nov. (Figs 3Q–R, 4A–O)

Jugasporites sp. A (Fig. 3N–P)

Jugasporites spp.

Klausipollenites decipiens Jansonius, 1962 (Fig. 4P–Q)

Klausipollenites devolvens (Leschik) Clarke, 1965 (Fig. 4R).

Remarks. This species is similar to *K. schaubergerii* (which is rare in the present material), but differs in having a more prolate corpus, and sacci that are less pointed.

Klausipollenites schaubergerii (Potonié & Klaus) Jansonius, 1962 (Figs 4S, 5A)

Klausipollenites staplinii Jansonius, 1962 (Fig. 5B–C)

Klausipollenites spp.

Limitisporites fuscus Schaarschmidt, 1963 (Fig. 5D)

Limitisporites hexagonalis Bose & Maheshwari, 1968 (Fig. 5F)

Limitisporites spp.

Minutosaccus acutus Mädler, 1964 (Fig. 5E)

Minutosaccus potoniei Mädler, 1964 (Fig. 5G–H)

Minutosaccus schizeatus Mädler, 1964 (Fig. 5J–K)

Minutosaccus spp.

Pinuspollenites thoracatus Balme, 1970 (Fig. 5L–N)

Pinuspollenites spp.

Platysaccus alatus (Luber) Ouyang & Norris, 1999 (Fig. 5I)

Platysaccus papilionis Potonié & Klaus, 1954 (Fig. 5O)

Platysaccus queenslandii de Jersey, 1962 (Fig. 5R–S)

Platysaccus trumpii Ottone, 1989 (Fig. 5P)

Platysaccus spp.

Protodiploxypinus americus Dunay & Fisher, 1979 (Figs 5Q–U)

Protodiploxypinus fastidiosus (Jansonius) Warrington, 1974 (Figs 5T, X)

Protodiploxypinus spp.

Pteruchipollenites gracilis (Segroves) Foster, 1979 (Fig. 5W)

Pteruchipollenites gondwanensis (Jain) Ottone & García, 1991 (Fig. 5V)

Scheuringipollenites barakarensis (Tiwari) Tiwari, 1973 (Fig. 6A–B)

Scheuringipollenites circularis Césari *et al.*, 1995 (Fig. 5Y)

Scheuringipollenites medius (Burjack) Dias-Fabrício, 1981 (Fig. 6C–D)

Scheuringipollenites ovatus (Balme & Hennelly) Foster, 1975 (Fig. 6E–F)

Scheuringipollenites tentulus (Tiwari) Tiwari, 1973 (Fig. 6G–H)

Scheuringipollenites spp.

Sulcosaccispora alaticonformis (Malyavkina) de Jersey, 1968 (Fig. 6I)

Triadispora crassa Klaus, 1964 (Figs 6K, L, U).

Generic remarks. Visscher (1966), in discussing *Triadispora* Klaus, 1964 and its comparison with similar disaccitriletes pollen genera as well as the variations among the most common species, indicated that the diagnostic feature of the genus is the presence, on the proximal surface of the corpus, of a small tri-radiate mark devoid of any area of exoexinal structure. In the La Veteada palynoflora, most forms belong to *T. crassa* Klaus, 1964 and its numerous transitional variants with *T. muelleri* (Reinhardt & Schmitz *in* Reinhardt, 1964) Visscher, 1966. The La Veteada specimens exhibit all the morphological variations described and illustrated by Visscher, (1966), ranging from
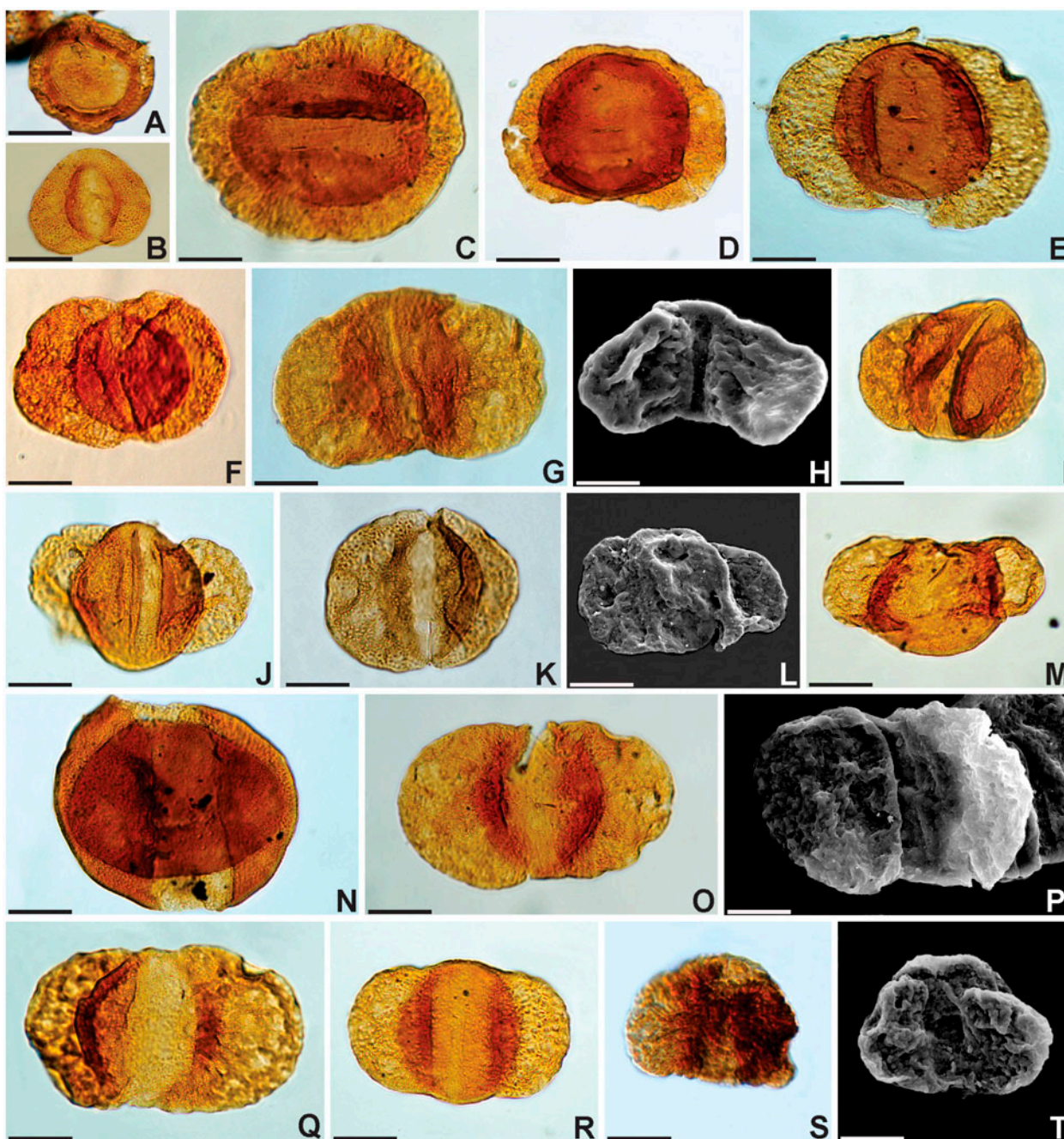
Fig. 2. **A,** *Accinctisporites ligatus* Leschik, 1955; MPLP 8251(I) M46/0. **B,** *Vesicaspora magnalis* (Andreeva) Hart, 1965; MPLP 8251(H) D53/0. **C,** *Crucisaccites monoletus* Maithy, 1965; MPLP 8252(J) W53/1. **D,** *Potonieisporites lelei* Maheshwari, 1967; MPLP 8251(I) X51/0. **E,** *Potonieisporites brasiliensis* (Nahuys *et al.*) Archangelsky & Gamerro, 1979; MPLP 8251(J) G54/0. **F,** *Gondwanapollis frenguelli* (Césari) Gutiérrez, 1993; MPLP 8248(G) N47/4. **G–H,** *Alisporites australis* de Jersey, 1962; **G,** MPLP 8250(G) H47/4; **H,** MPLP 8253 MEB T1 F036. **I–J,** *Alisporites angustus* (Ouyang & Norris, 1999) comb. nov. et emend. **I,** MPLP 8251(I) E51/2; **J,** MPLP 8251(H) K47/0. **K,** *Alisporites lowoodensis* de Jersey, 1963; MPLP 8250(G) L46/0. **L–M,** *Alisporites rioclarensis* Menéndez, 1976; **L,** MPLP 8249 MEB T8 393; **M,** MPLP 8252(I) E39/2. **N,** *Colpisaccites granulosus* Archangelsky & Gamerro, 1979; MPLP 8251(I) G40/1. **O,** *Cuneatisporites radialis* Leschik, 1956, in Kräusel & Leschik, 1955; MPLP 8252(I) S53/0. **P–Q,** *Falcisporites nuthallensis* (Clarke) Balme, 1970; **P,** MPLP 8253 MEB T3 123; **Q,** MPLP 8250(I) U54/0. **R,** *Falcisporites stabilis* Balme, 1970; MPLP 8251(H) M52/3. **S–T,** *Granisaccus* sp. A, **S,** MPLP 8248(G) P45/0; **T,** MPLP 8249 MEB T7 295. Scale bar = 20 μm.

sub-monosaccate/monosaccate (Fig. 6L), sub-trisaccate (Fig. 6K) to trisaccate (Fig. 6U) forms.

Triadispora muelleri (Reinhardt & Schmitz *in* Reinhardt, 1964) Visscher, 1966 (Fig. 6M)

Valialasaccites sp. A (Fig. 6P).

Remarks. Only two poorly preserved specimens were recorded in the present study and, accordingly, their specific identification is problematic. Of the formally described species assigned to the genus, they are very similar to the type species, *Valiasaccites validus* Bose
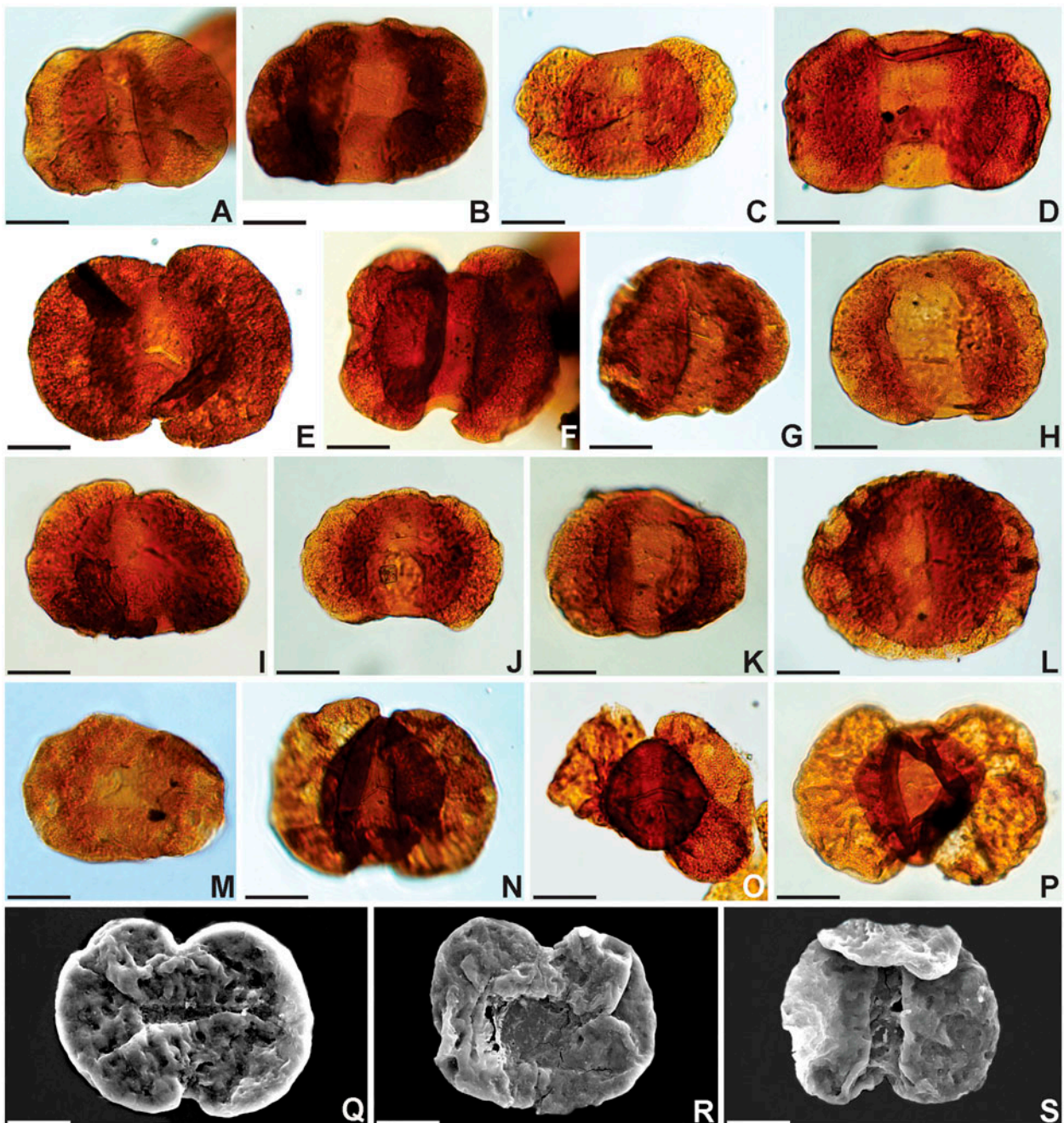
Fig. 3. **A,** *Jugasporites delasaucei* (Potonié & Klaus) Leschik, 1956; MPLP 8250(I) M54/0. **B,** *Jugasporites gamsi* (Klaus) Foster, 1983; MPLP 8249(I) T41/3. **C–D,** *Jugasporites lueckoides* Klaus, 1963; **C,** MPLP 8252(I) S50/0; **D,** MPLP 8251(I) G44/0. **E–F,** *Jugasporites nubilus* Leschik, 1956; **E,** MPLP 8251(J) T38/2; **F,** MPLP 8250(H) F38/1. **G–H,** *Jugasporites parvus* (Klaus) Foster, 1983; **G,** MPLP 8250(I) H34/4; **H,** MPLP 8251(K) C44/0. **I–J,** *Jugasporites perspicuus* Leschik, 1956; **I,** MPLP 8251(K) W44/4; **J,** MPLP 8252(I) F52/0. **K,** *Jugasporites purus* (Leschik) Tiwari & Singh, 1981; MPLP 8251(J) D51/1. **L–M,** *Jugasporites schaubergeroides* Klaus, 1963; **L,** MPLP 8248(E) M42/1; **M,** MPLP 8252(I) V41/2. **N–P,** *Jugasporites* sp. A; **N,** MPLP 8250(J) R47/4; **O,** MPLP 8251(I) T55/0; **P,** MPLP 8252(I) H38/0. **Q–S,** *Jugasporites vellicoites* sp. nov. **Q,** MPLP 8253 MEB T1 F054, paratype; **R,** MPLP 8249 MEB T7 292; **S,** MPLP 8249 MEB T6 F254. Scale bar = 20 μm.

& Kar, 1966, which has well-developed longitudinal 'lateral ridges' on the oval corpus that may be continuous with the sacci and without constrictions; ridges infra-microreticulate; and the exine of the remaining part of the corpus is vermiculate to pseudo-reticulate; a monolete mark is present. *Valiasaccites elilaensis* Bose & Kar, 1966 differs as it has 'lateral ridges' that are not as well developed.

Vitreisporites microsaccus de Jersey, 1964 (Fig. 6N–O).

Remarks. The main diagnostic features are the small size of the sacci, which frequently do not project far beyond the corpus, and which are distally inclined (de Jersey 1964, p. 10, pl. 2, figs 3, 4).

Vitreisporites pallidus (Reissinger) Nilsson, 1958 (Fig. 6Q–R).

Remarks. Transitional morphological features are shared between *V. signatus*, *V. pallidus* and *V. subtilis*. Several authors have treated these species as synonyms (e.g.,
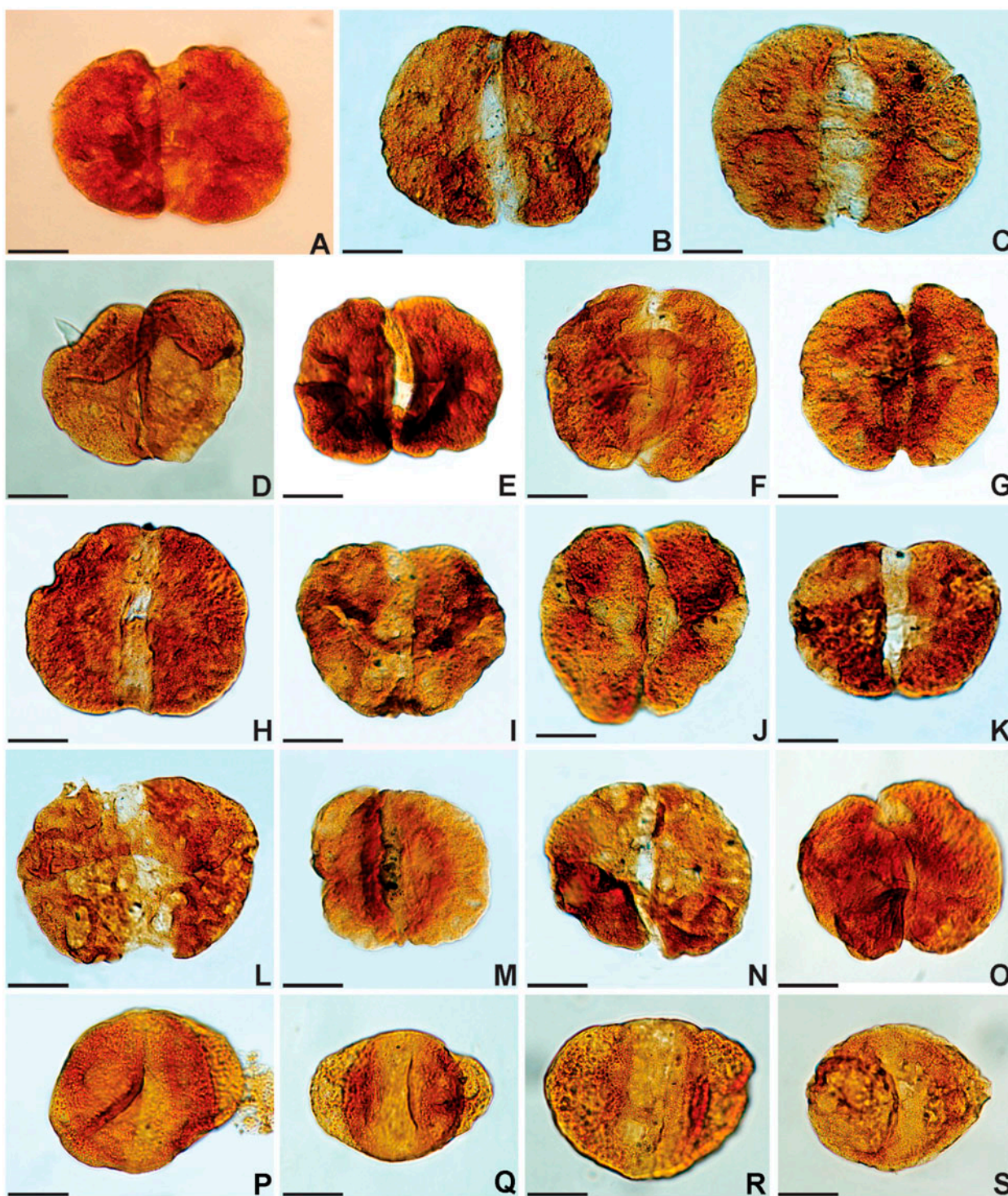
Fig. 4. **A–O,** *Jugasporites vellicoites* sp. nov. **A,** MPLP 8248(G) F39/3, paratype; **G,** MPLP 8252(H) U44/3, holotype; **D,** MPLP 8251(I) N53/2; **C,** MPLP 8250(J) N43/3, paratype; **E,** MPLP 8250(H) W51/4, paratype; **I,** MPLP 8248(H) M42/0; **B,** MPLP 8251(H) H39/3, paratype; **F,** MPLP 8251(H) M52/1; **J,** MPLP 8250(I) N54/0; **H,** MPLP 8251(I) E46/3; **L,** MPLP 8250(G) F37/4, paratype; **K,** MPLP 8248(H) X42/0, paratype; **M,** MPLP 8248(H) W42/3; **N,** MPLP 8248(H) M43/0; **O,** MPLP 8249(F) K49/3. **P–Q,** *Klausipollenites decipiens* Jansonius, 1962; **P,** MPLP 8251(H) N47/0; **Q,** MPLP 8251(H) R46/3. **R,** *Klausipollenites devolvens* (Leschik) Clarke, 1965; MPLP 8251(K) O41/0. **S,** *Klausipollenites schaubergerii* (Potonié & Klaus) Jansonius, 1962; MPLP 8251(K) D36/1. Scale bar = 20 µm.

Balme 1970), but examination of their original material is necessary to determine this, and, until then, it seems advisable to regard them as being distinct. In the La Veteada palynoflora, transitional forms between the three species are also difficult to separate. However, specimens assigned in the present study to *V. pallidus*, based not only on our observations of them, but also on Balme′s (1963) and Haskell′s (1968) descriptions of the
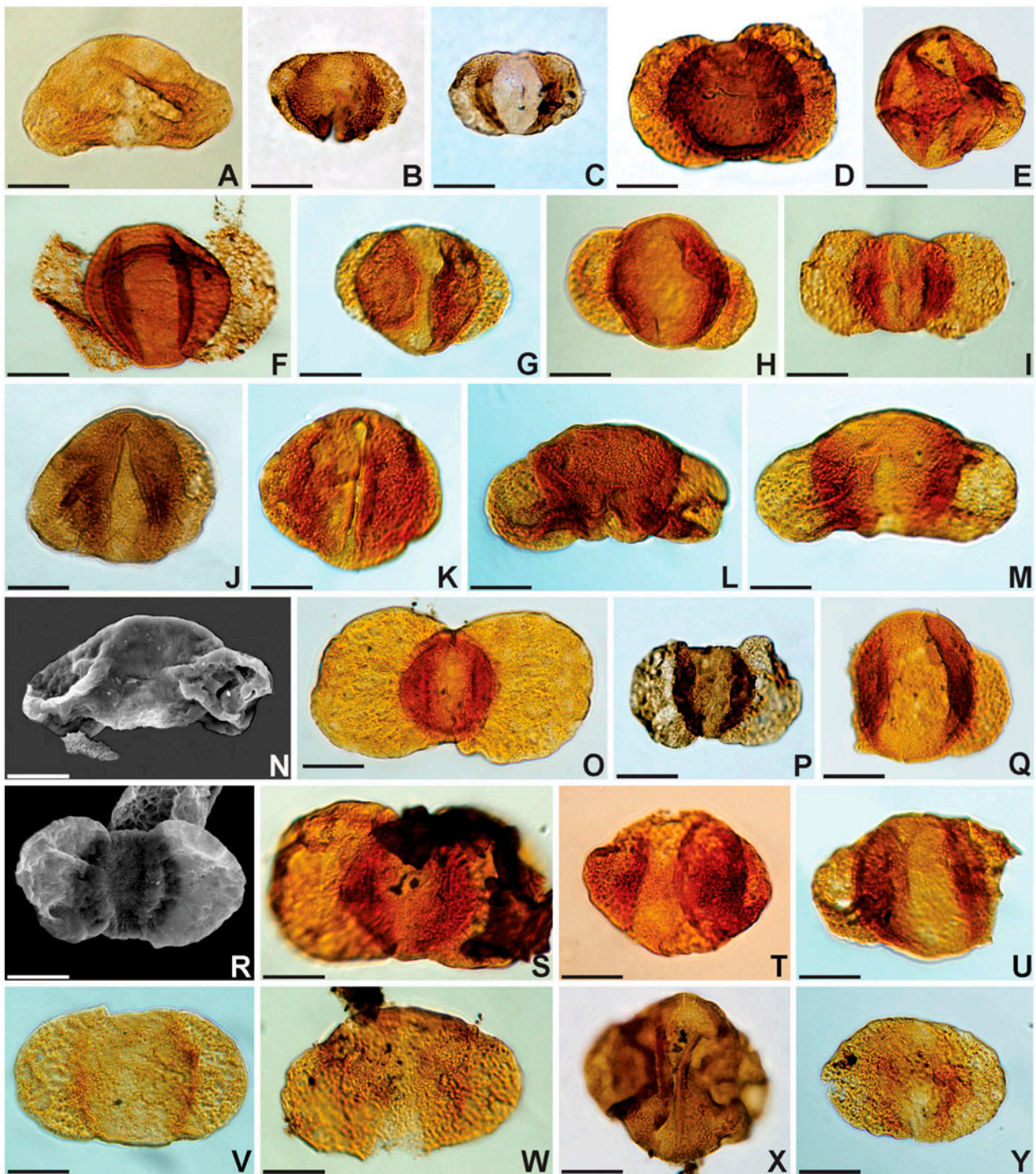
Fig. 5. **A,** *Klausipollenites schaubergerii* (Potonié & Klaus) Jansonius, 1962; MPLP 8249(G) P47/0. **B–C,** *Klausipollenites staplinii* Jansonius, 1962; **B,** MPLP 8249(C) O25/0; **C,** MPLP 8252(C) H29/1. **D,** *Limitisporites fuscus* Schaarschmidt, 1963; MPLP 8251(H) E42/0. **E,** *Minutosaccus acutus* Mädler, 1964; MPLP 8251(H) G36/4. **F,** *Limitisporites hexagonalis* Bose & Maheshwari, 1968; MPLP 8253(I) E36/1. **G–H,** *Minutosaccus potoniei* Mädler, 1964; **G,** MPLP 8251 (H) E46/0; **H,** MPLP 8251(H) J50/0. **I,** *Platysaccus alatus* (Luber) Ouyang & Norris, 1999; MPLP 8250 (H) S53/2. **J–K,** *Minutosaccus schizeatus* Mädler, 1964; **J,** MPLP 8250(G) Q48/1, **K,** MPLP 8250(I) P44/3. **L–M,** *Pinuspollenites thoracatus* Balme, 1970; **L,** MPLP 8250(H) N37/2; **M,** MPLP 8250(I) M38/1; **N,** MPLP 8249 MEB T7 F280. **O,** *Platysaccus papilionis* Potonié & Klaus, 1954; MPLP 8251(I) X54/1. **P,** *Platysaccus trumpii* Ottone, 1989; MPLP 8250(G) N45/0. **Q,** *Protodiploxypinus americus* Dunay & Fisher, 1979; MPLP 8251(H) S47/0. **R–S,** *Platysaccus queenslandii* de Jersey, 1962; **R,** MPLP 8253 MEB T3 F118; **S,** MPLP 8250(H) J46/0. **U,** *Protodiploxypinus americus* Dunay & Fisher, 1979 MPLP 8248(H) H40/2. **T, X,** *Protodiploxypinus fastidiosus* (Jansonius) (Klaus) Dunay & Fisher, 1979; **T,** MPLP 8248(G) V34/0; **X,** MPLP 8249 MEB T7 F371. **V,** *Pteruchipollenites gondwanensis* (Jain) Ottone & García, 1999; MPLP 8251(K) V37/0. **W,** *Pteruchipollenites gracilis* (Segroves) Foster, 1979; MPLP 8250(F) E45/1. **Y,** *Scheuringipollenites circularis* Césari, Archangelsky & Seoane 1995; MPLP 8251(I) M37/0. Scale bar = 20 μm.

species, are circumscribed as follows: pollen bisaccate, small; corpus smaller than the sacci, and, in shape, elongate-oval, biconvex; proximal face infra-granulate; distal area smooth and very thin. Sacci micro-reticulate, slightly inclined distally; proximal roots equatorial or slightly distal; distal roots sub-polar, straight to concave,
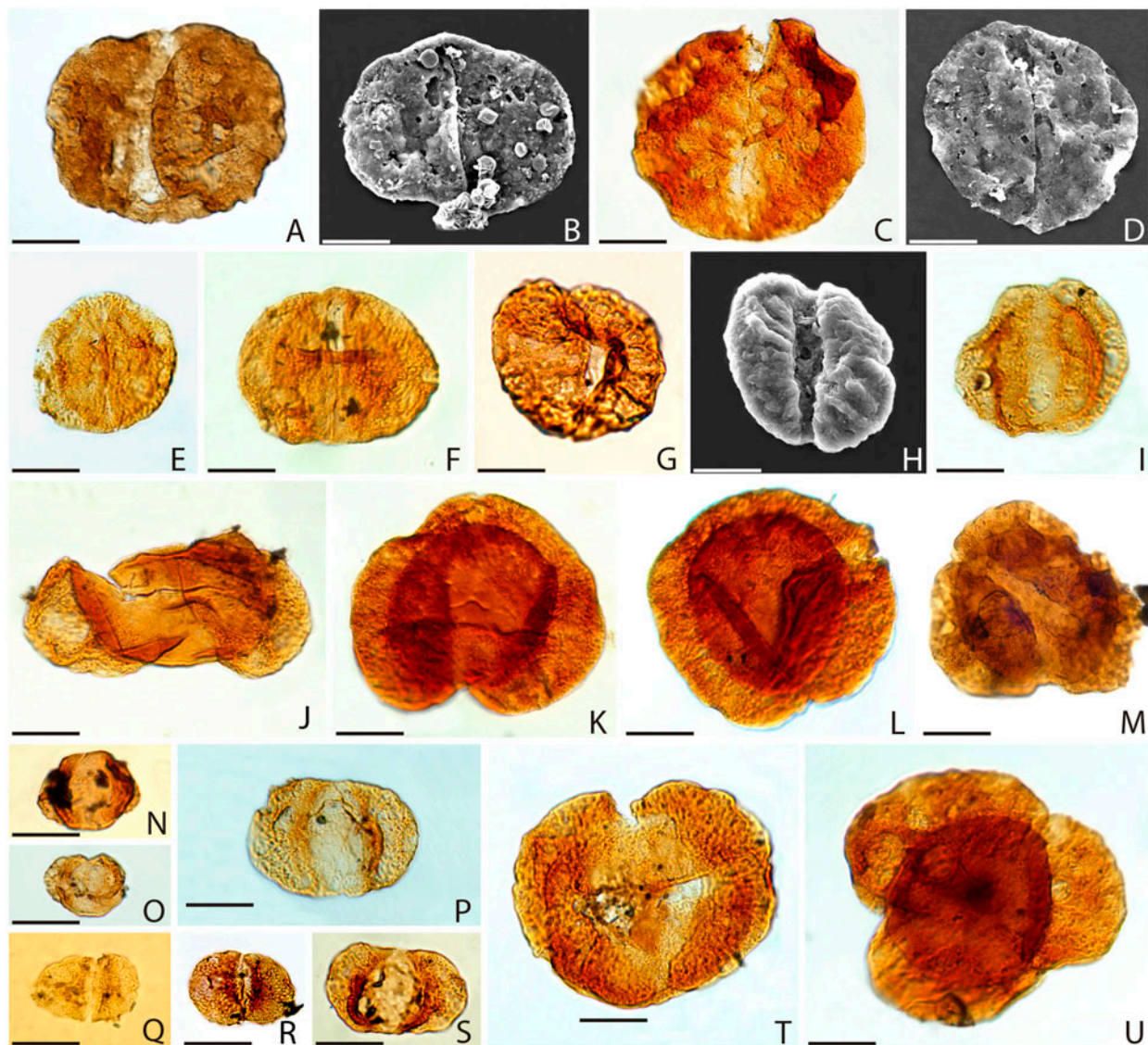
Fig. 6. **A–B,** *Scheuringipollenites barakarensis* (Tiwari) Tiwari, 1973; **A,** MPLP 8250(G) O36/0; **B,** MPLP 8253 MEB T1 F010. **C–D,** *Scheuringipollenites medius* (Burjack) Dias-Fabrício, 1981; **C,** MPLP 8250(G) P46/3; **D,** MPLP 8253 MEB T1 F003. **E–F,** *Scheuringipollenites ovatus* (Balme & Hennelly) Foster, 1975; **E,** MPLP 8251(H) H40/0; **F,** MPLP 8252(I) Y50/1. **G–H,** *Scheuringipollenites tentulus* (Tiwari) Tiwari, 1973; **G,** MPLP 8248(G) Q41/0; **H,** MPLP 8253 MEB T1 F006. **I,** *Sulcosaccispora alaticonformis* (Malyavkina) de Jersey, 1968; MPLP 8251 (H) H47/3. **J,** *Valialasaccites* sp. A, MPLP 8253(I) R45/0. **K–L, U,** *Triadispora crassa* Klaus, 1964; **K,** MPLP 8249(I) T35/1; **L,** MPLP 8251(H) E52/0; **U,** MPLP 8253(I) H35/3. **M,** *Triadispora muelleri* (Reinhardt & Schmitz in Reinhardt, 1964) Visscher, 1966 MPLP 8248(C) J32/0. **N–O,** *Vitreisporites microsaccus* de Jersey, 1964; **N,** MPLP 8252(G) M54/0; **O,** MPLP 8252(G) V53/0. **P,** *Vitreisporites signatus* Leschik, 1955; MPLP 8251(J) R51/0. **Q–R,** *Vitreisporites pallidus* (Reissinger) Nilsson, 1958; **Q,** MPLP 8252(B) V23/4; **R,** MPLP 8250(B) V30/4. **S,** *Vitreisporites subtilis* (de Jersey) de Jersey, 1962; MPLP 8252(G) G40/0. **T,** *Polarisaccites bilateralis* Ybert & Marques-Toigo, 1970 MPLP 8251(H) T52/0. Scale bar = 20 μm.

giving rise to a narrow, commonly indistinct cappula; bases of sacci with radial structuring. This species is known from the Pennsylvanian to the Lower Cretaceous (see Supplementary Data File 1).

Vitreisporites signatus Leschik, 1955 (Fig. 6P).

Remarks. The main features followed here for separation of this species from *V. pallidus* are: corpus transversely oval to sub-circular; exine weakly granulate; sacci almost equal to the corpus in size, proximally attached at equator, distally attached at equator or extending onto sub-equatorial to sub-polar regions of corpus, characteristically thickened at their (distal) bases, leaving a narrow distal area embracing a leptoma; saccus intrareticulum coarser at saccus base.

Vitreisporites subtilis (de Jersey) de Jersey, 1962 (Fig. 6S).

Remarks. The main diagnostic features followed here for distinguishing this species from *V. signatus* and *V. pallidus* are: corpus oval in polar view, longer than broad; length 14–30 μm, breath 12–28 μm; average ratio of length:breadth = 1:2; sacci about same size as corpus, attached equatorially or sub-equatorially, with slight distal inclination, distal roots clearly thickened and distal area broad, leaving a wide leptoma.

Transitional forms between specimens assigned here to *V. subtilis*, *V. pallidus* and *V. signatus* are present in the La Veteada palynoflora.

Polysaccate pollen
Polarisaccites bilateralis Ybert & Marques-Toigo, 1970 (Fig. 6T)

Systematic descriptions

Subturma DISACCITES Cookson, 1947
Infraturma DISACCIATRILETES (Leschik 1956) Potonié, 1958
Alisporites Daugherty, 1941

Type species. Alisporites opii Daugherty, 1941.
Alisporites angustus (Ouyang & Norris 1999) comb. nov. et emend. (Fig. 2I–J)
Basionym. Klausipollenites angustus Ouyang & Norris, 1999, pp. 38–41; pl. 6, Figs 10–13; pl. 7, Figs 4–5; text-Fig. 8.

Emended diagnosis. Pollen bisaccate, diploxylonoid. Corpus transversally oval to broadly oval. Sacci semi-circular to more than semi-circular, smaller than the corpus, clearly discernible and strongly inclined distally; roots poorly defined straight or slightly concave to convex, usually folded or thickened, of various widths; distance between roots 8–15 μm. Cappula narrow, rectangular to fusiform, usually having a narrow sulcus (2–3 μm). Saccus wall irregularly infra-microreticulate to punctate-reticulate with muri and lumina *ca* 0.5 μm across; some lumina are enlarged owing to coalescence. Sacci merge from the corpus at a slight angle. Cappa finely infra-reticulate; cappula smooth.

Dimensions (96 specimens). Overall breadth × length: 45(61)75 × 30(45)58 μm; corpus breadth × length: 25 (35)46 × 30(45)58 μm; ratio corpus breadth × length: 0.6(0.8)1.0; saccus breadth × length: 9(18)27 μm (proximal face), 16(28)39 μm (distal face) × 23(36)53 μm; sacci projecting 9(13)18 μm beyond the corpus.

Comparisons and remarks. Originally, this species was referred to *Klausipollenites* by Ouyang & Norris (1999). However, based on the characteristic features observed in the La Veteada specimens assigned to the species, it is attributed here to *Alisporites* Daugherty. *Alisporites angustus* (Ouyang & Norris) comb. nov. et emend. is very similar to *Falcisporites snopkovae* Visscher (1966, p. 347), but the main difference is that the latter species is larger (80–92 μm). Visscher's (1966) species also should be assigned to *Alisporites*, as its sacci are usually strongly inclined distally, and laterally, they are not inter-connected.

Infraturma DISACCITRILETES Leschik, 1956

Jugasporites Leschik 1956 emend. Klaus, 1963

Type species (by original designation). *Pityosporites delasaucei* Potonié & Klaus, 1954, p. 536, pl. 10, Fig. 6 (re-described by Klaus 1955, p. 782).

Remarks. The emendation by Klaus (1964) is followed here. *Jugasporites* is separated from *Limitisporites* (Leschik) Schaarschmidt, 1963 by the presence of two clearly distinguishable lateral exinal bands on the proximal side of its corpus, in sub-equatorial position. This feature is clearly visible in the original material described and illustrated by Leschik (1956), Klaus (1963), Foster (1983), Tiwari & Singh (1984, 1985) and, especially, by Draxler (2010). *Lueckisporites* (Potonié & Klaus) Jansonius, 1962 differs by the presence of two well-developed, expanded and well-defined taeniae. *Illinites* (Kosanke) Potonié & Kremp 1954 is distinguished by its corpus divided into segments by two or more well-marked ridges; in some cases, ridges are subdivided by bifurcated grooves.

Jugasporites delasaucei (Potonié & Klaus) Leschik, 1956 (Fig. 3A)
1954 *Pityosporites delasaucei* Potonié & Klaus, p. 536, pl. 10, Fig. 6.
1956 *Jugasporites delasaucei* (Potonié & Klaus) Leschik, p. 132, pl. 21, Figs 9–11.
1962 *Illinites delasaucei* (Potonié & Klaus) Grebe & Schweitzer, pp. 212–214, pl. 7, Figs 1–2, 4, 6, 10–11, 13; pl. 8, Figs 1, 3, 5, 7, 10, 12.
2010 *Limitisporites delasaucei* (Potonié & Klaus) Schaarschmidt; Gutiérrez *et al.*, p. 467, Fig. 10G.
Remarks. Specimens recorded here from the La Veteada palynoflora are predominantly haploxylonoid to slightly diploxylonoid in outline. Their corpus, is usually oval and transversely elongated, and in some cases polygonal to lenticular owing to folding. Two lateral folds are present at the bases of the sacci; these folds are wedge-shaped on both sides of the corpus, and they have a maximum width of 2–8 μm (usually 2–3 μm). On the proximal face, exinal bands on the sides of the corpus have variable widths, 7–20 μm (mainly 12 μm), widening towards the ends of the grain where their boundaries are not discernible on the sacci. The centre of the proximal face has an asymmetrical dilete or trilete scar, with laesurae of varying length: 2(7)14 μm.

Dimensions (18 specimens). Total breadth, 60(72) 90 μm; corpus breadth, 28(34)42 μm; corpus length, 36 (45)62 μm; breadth/length ratio of the corpus, 0.7(0.8) 0.9 μm; saccus height × length, 39(48)71 μm × 26(31) 41 μm; width of cappula, 4(8–9)19 μm. Thickness of corpus wall, 0.7(0.8)1.2 μm; thickness of saccus wall, 0.5(0.7)1.1 μm.

Discussion. The revision of the material, described as *Limitisporites delasausei* by Gutiérrez *et al.* (2010, p. 467, Fig. 10G) from the Permian of Uruguay, confirmed the presence of the exinal bands on the proximal face between the sacci. The La Veteada specimens

[assigned to *Jugasporites delasaucei* (Potonié & Klaus) Leschik] also bear these features and are considered to accord with the species diagnosis. The specimen figured by Visscher (1968, pl. 4, fig. G), from the Thuringian of France, is regarded here as not being conspecific, as it has a sub-circular corpus and sacci that are smaller than or equal to the corpus. Also, as the exinal bands can not be seen clearly, provisional exclusion from the present species is also here applied to the material described and/or illustrated as *Jugasporites delasausei* form *minor* by Ybert (1975, p. 200, pl. 7, Figs 122, 123), and as *Limitisporites delasausei* by Schaarschmidt (1963, p. 47, taf. 11, Figs 14–17) and Dino *et al.* (2002, pl. 2, Fig. 19).

Jugasporites vellicoites sp. nov. (Figs 3Q–S, 4 A–O)

Diagnosis. Pollen bisaccate, diploxylonoid, bilaterally symmetrical; equatorial contour transversely sub-rectangular to sub-circular; corpus poorly defined, transversely elongate, sub-rhomboidal, sub-lenticular to oval. Trilete mark asymmetrical, not visible in all cases. Intexine fine (*ca* 0.5 µm thick), usually poorly discernible. Sacci semi-circular to cresentic, strongly pendant distally and defining a narrow cappula with continuous edges. Roots of sacci sub-equatorial on the proximal face and sub-polar on the distal face. Proximally, the corpus bears two exinal bands that extend on to the full width of the sacci as pinched/folded exine.

Holotype. MPLP 8252(H) U44/3 (Fig. 4G).

Paratypes. MPLP 8248(G) F39/3 (Fig. 4A); MPLP 8251(H) H39/3 (Fig. 4B); MPLP 8250(J) N43/3 (Fig. 4C); MPLP 8250(H) W51/4 (Fig. 4E); MPLP 8248(H) X42/0 (Fig. 4K); MPLP 8250(G) F37/4 (Fig. 4L); MPLP 8253 MEB T1 F054 (Fig. 3Q).

Etymology. Latin *vellico*: 'pinching', referring to the proximal pinchs/folds on the sacci that represent extension of the lateral bands of the corpus on to the sacci.

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

Stratigraphic provenance. Upper part of the La Veteada Formation in its type section; Lopingian.

Description. Pollen bisaccate, diploxylonoid, transversely sub-rectangular to sub-circular in equatorial outline. Corpus poorly defined, with transversely elongated contour, being sub-rhomboidal to sub-lenticular or oval. Trilete mark asymmetrical, not visible in all cases. Corpus intexine fine, usually poorly discernible. Sacci strongly inclined towards the distal face where they cover a large proportion of the central corpus; finely infra-reticulate with very small lumina and comparatively thicker muri. Sacci cresentic to sub-circular in outline; attached equatorially to the proximal face, and

distal attachments are sub-equatorial, poorly defined and in some cases thickened (Figs 4D–G, M–O), defining a narrow cappula (about 1/3–1/10 width of corpus), the sides of which are straight (Figs 3S, 4A, D, G, H, K–O) to biconcave (Fig. 4C) or sporadically somewhat convex—at least on one side (Figs 4E, J, O). On the proximal face, the corpus has two lateral exinal bands that extend on to the full width of the sacci as pinched/folded exine (Figs 3Q–S, 4A–O). The ornamentation and/or the structure of the cappa is difficult to observe, but appears to be laevigate to infra-microreticulate, similar to the structure of the sacci.

Dimensions (130 specimens). Overall width, 52(71) 102 µm; width of the corpus, 25(36)56 µm; corpus length, 38(54)77 µm; saccus width × length, 20(32) 50 µm × 40(58)82 µm; cappula width, 1(7)20 µm, equivalent to 1/20(1/8)1/2 of the width of the corpus. Exinal bands 13(24)44 µm wide; width of the space between the two exinal bands varies between 2 and 20 µm, usually 7 µm, being 1/3–1/2 of the corpus length.

Remarks and comparisons. Jugasporites vellicoites sp. nov. is characteristically transversely sub-rectangular to sub-circular in equatorial outline, has a narrow cappula, poorly defined corpus that is sub-rhomboidal, sub-lenticular to longitudinally oval, and bears, on the proximal face of the corpus, two lateral exinal bands that extend on to the full width of the sacci as pinched/folded exine. The presence of exinal bands on the lateral side of the corpus has been described not only in *Jugasporites* but also in *Latusipollenites* Marques-Toigo, 1974 and in *Valialasaccites* Bose & Kar, 1966.
Latusipollenites was described for tetra-saccate pollen with lateral symmetry—and the exinal bands between the sacci were interpreted as sub-sacci of sub-equatorial to proximal position (Marques-Toigo 1974, p. 614). This genus also has, as diagnostic features, not only a sub-rectangular contour (in overall outline and in the outline of its corpus), with the longer measurement being transverse, but also a wide cappula and a monolete to dilete mark. We interprete *Latusipollenites* as clearly a monosaccate pollen.
Valialasaccites has a similar structure: a bisaccate pollen with bilateral symmetry and two infra-microreticulate ridges (taeniae, according to Jansonius & Hills 1976, card 3153) on the lateral sides of the corpus. Based on our interpretation, such structures could be considered exinal bands between the two sacci, similar to those borne by *Jugasporites vellicoites* sp. nov. *Valialasaccites* is distinguished by its transversely oval outline (both in its overall shape and the shape of its corpus) smaller sacci (compared with the corpus); sacci with distal insertion (attachment) sub-equatorial, associated with exinal folds and the presence of a small monolete mark.

Jugasporites sp. A (Fig. 3N–P)

Description. Bisaccate pollen with bilateral symmetry, strongly diploxylonoid. Corpus well defined, transversely oval to sub-triangular in outline. Trilete mark asymmetrical. Intexine thick (1.5–2 μm), usually darker than the rest of the grain. Sacci semilunar in contour, larger than the corpus, distally inclined. Insertion of sacci sub-equatorial on the proximal face and sub-polar on the distal face. Distal roots of sacci straight, usually associated with exine folds defining a narrow cappula. On the proximal face of the corpus, two exinal bands (9–35 μm, mean 22 μm) connect both sacci to the margins of the corpus and delimit a sub-rectangular area surrounding the laesurae.

Dimensions (20 specimens). Total breadth, 63(76) 100 μm; corpus breadth, 30(42)64 μm; corpus length, 35(47)66 μm, ratio corpus breadth/corpus length, 0.7 (0.9)1.2; sacci: breadth, 22(34)55 μm; length 37(57) 75 μm; width of cappula, 1(6)15 μm; exinal fold width, 2(4.5)10 μm.

Remarks. Jugasporites sp. A differs from *J. nubilus* Leschik by the dimensions, shape and wall thickness of the corpus and by the presence of folds at the bases of the sacci on the distal side.

Age and biostratigraphy

Most of the palynomorph taxa from the upper part of the La Veteada Formation (Upper La Veteada Formation Assemblage) suggest a Lopingian age (Zavattieri & Gutiérrez 2012, Gutiérrez *et al.* 2014, 2017, Zavattieri *et al.* 2017; Fig. 7; Supplementary Data File 1). Of the 46 species that have cosmopolitan records, 41 are represented in the Lopingian. Especially important is the co-occurrence of *Accinctisporites ligatus, Alisporites angustus, Crucisaccites monoletus, Jugasporites delasaucei, J. purus, J. lueckoides, Limitisporites fuscus, L. hexagonalis, Minutosaccus acutus, M. potoniei, M. schizeatus, Potonieisporites lelei, Pteruchipollenites gracilis, Triadispora muelleri, T. crassa* and *Vesicaspora magnalis*. Only one species (*Potonieisporites brasiliensis*) has been recorded from the Pennsylvanian to the Guadalupian. *Alisporites lowoodensis* has been recorded previously from the late Cisuralian–early Guadalupian of the central-western basins of Argentina (*LW* Biozone, Gutiérrez *et al.* 2011). Three species (*Protodiploxypinus americus, Sulcosaccispora alaticonformis* and *Vitreisporites subtilis*) have documented first appearances in the Early Triassic.

On the other hand, a group of South American endemic species ranging from the Carboniferous to Permian (*Alisporites rioclarensis, Colpisaccites granulosus, Gondwanapollis frenguelli, Platysaccus trumpii, Polarisaccites bilaterales, Scheuringipollenites circularis, S. medius*) and to the Triassic (*Pteruchipollenites gondwanensis*), are common elements in the La Veteada Formation palynoflora. The following gymnosperm species recorded herein are new Permian components for South American basins: *Alisporites angustus, Jugasporites lueckoides, J. nubilus, J. perspicuus, Klausipollenites devolvens, Limitisporites fuscus, Minutosaccus potoniei, Pinuspollenites thoracatus, Protodiploxypinus fastidiosus, Triadispora muelleri* and *Vesicaspora magnalis*.

Comparing the gymnosperm saccate-pollen content with other late Palaeozoic assemblages and biozones established for other basins in South America (Fig. 7), the upper La Veteada Formation (ULV Fm) assemblage is similar to the *LW* Zone defined for central-western Argentina (César & Gutiérrez 2001), sharing *Accinctisporites ligatus, Alisporites lowoodensis, Falcisporites nuthallensis, F. stabilis, Klausipollenites decipiens, K. schaubergeri, K. staplinii, Minutosaccus acutus, Platysaccus queenslandii, Vitreisporites microsaccus* and *V. signatus*. Cosmopolitan species that are confined in South America to the La Veteada Formation assemblages include *Alisporites angustus, Cuneatisporites radialis, Jugasporites gamsi, J. lueckoides, J. nubilus, J. parvus, J. perspicuus, J. purus, J. schaubergeroides, Klausipollenites devolvens, Limitisporites fuscus, Minutosaccus potoniei, M. schizeatus, Pinuspollenites thoracatus, Protodiploxypinus americus, P. fastidiosus, Pteruchipollenites gondwanensis, Scheuringipollenites tentulus, Sulcosaccispora alaticonformis, Triadispora crassa, T. muelleri, Vesicaspora magnalis, Vitreisporites pallidus* and *V. subtilis*. This denotes clear compositional differences from Permian palynofloras previously recorded from this continent.

Alisporites angustus and *Limitisporites fuscus* are here reported for the first time in Lopingian strata of southwestern Gondwana (Fig. 7; Supplementary Data File 1). Most of the non-taeniate pollen taxa have long-ranging Gondwanan records.

The ULV Formation Assemblage differs significantly from other South American Permian palynofloras by containing *Cladaitina veteadensis, Goubinispora morondavensis, Guttulapollenites hannonicus, Lahirites raniganjensis, Lueckisporites biformis, Lunatisporites arluki, L. globus, L. lenticulatus, L. transversundatus, Protohaploxypinus panaki, Striatoabieites rugosus, Striatopodocarpites varius, Vittatina simplex, Syndesmorion stellatum, Mehlisphaeridium parvum, Densoisporites complicatus, D. nejburgii, D. playfordii, D. solidus, Leptolepidites jonkerii, Lundbladispora brevicula, L. obsoleta, L. springsurensis, L. verrucosa, L. wilmottii, Ringosporites fossulatus, Secarisporites imperialis, S. lacunatus, S. triangularis* that constitute new records for the continent (see Zavattieri & Gutiérrez 2012, Gutiérrez *et al.* 2014, 2017, Zavattieri *et al.* 2017).

Representation of gymnosperm pollen

The palynoflora from the type section of the La Veteada Formation is dominated (*ca* 78%) by pollen of several gymnosperm groups, mostly saccate grains (Voltziales,

	South America																			World						
ARGEN-TINE	CHILE	URU-GUAY	BRAZIL					ARGENTINA									PERIOD		CARBONIFEROUS	PERMIAN				TRIASSIC		
TRIASSIC			Paraná Basin					Chaco-paraná Basin			Claromecó Basin		Central western basins			EPOCH			Pennsylvanian	Cisuralian	Guadalupian	Lopingian		Early	Middle	Late
Late	Middle	Late	Middle	AC	IS	Lv	Vc	Cm	Ac	S	Cr	PL	TC	CV	LW	FS	DM	SPECIES									

Potonieisporites brasiliensis
Jugasporites delasaucei
Jugasporites purus
Limitisporites hexagonalis
Potonieisporites lelei
Pteruchipollenites gracilis
Crucisaccites monoletus
Vesicaspora magnalis
Alisporites angustus
Limitisporites fuscus
Jugasporites lueckoides
Accinctisporites ligatus
Minutosaccus acutus
Minutosaccus potoniei
Minutosaccus schizeatus
Triadispora muelleri
Triadispora crassa
Klausipollenites decipiens
Falcisporites nuthallensis
Falcisporites stabilis
Jugasporites schaubergeroides
Pinuspollenites thoracatus
Klausipollenites staplinii
Vitreisporites microsaccus
Cuneatisporites radialis
Jugasporites nubilus
Jugasporites perspicuus
Klausipollenites devolvens
Klausipollenites schaubergeri
Platysaccus alatus
Jugasporites gamsi
Jugasporites parvus
Scheuringipollenites barakarensis
Alisporites australis
Platysaccus papilionis
Scheuringipollenites ovatus
Vitreisporites pallidus
Vitreisporites signatus
Platysaccus queenslandii
Protodiploxypinus fastidiosus
Scheuringipollenites tentulus
Alisporites lowoodensis
Sulcosaccispora alaticonformis
Vitreisporites subtilis
Protodiploxypinus americus
Alisporites rioclarensis
Colpisaccites granulosus
Gondwanapollis frenguelli
Platysaccus trumpii
Polarisaccites bilateralis
Pteruchipollenites gondwanensis
Scheuringipollenites circularis
Scheuringipollenites medius

Fig. 7. Stratigraphic distribution of the identified species from the upper section of the La Veteada Formation. Abbreviations: AC (*Striatoabieites anaverrucosus* Zone) and IC (*Cristatisporites inconstans-Staurosaccites cordubensis* Zone) of the Paraná Basin, Uruguay (Gutiérrez *et al.* 2010, Beri *et al.* 2011); Ac (*Arhesisporites cristatus* Zone), Cm (*Crucisaccites monoletus* Zone), Vc (*Vittatina costabilis* Zone), Lv (*Lueckisporites virkkiae* Zone), Paraná Basin, Brazil (Souza & Marques-Toigo 2005). PL (*Potonieisporites-Lundbladispora* Zone); Cr, *Cristatisporites* Zone; S, Striatites Zone of the Chacoparaná Basin (Russo *et al.* 1980, Vergel 1993, Archangelsky & Vergel 1996). TC (*Tornopollenites toreutos–Reduvias-poronites chalastus* Zone) and CV (*Converrucosisporites confluens–Vittatina vittifera*) of the Colorado-Claromecó Basin (Balarino 2014). DM (*Raistrickia densa–Convolutispora muriornata* Zone), FS (*Pakhapites fusus–Vittatina subsaccata* Zone), LW (*Lueckisporites–Weylandites* Zone) of the western basins of Argentina (Césari & Gutiérrez 2001). Dotted lines refer to species assigned as 'cf.'. The abbreviation 'Carbon' refers to 'Carboniferous'. The ages of the biozones and their bibliographic references are included in Supplementary Data File 1.

other conifers, cordaites and pteridosperms—glossopterids, peltasperms and corystosperms), although some other genera of monosulcate (cycadophytes, ginkgophytes), and polyplicate pollen (gnetales) are also present in low proportions (Table 3).

Taeniate pollen grains are the most conspicuous elements (*ca* 68%) comprising 23 genera and 72 species, of which the taeniate bisaccates (18.9–53.5%) are characterized by the dominance and rich diversity of *Striatopodocarpites* (11 species), *Protohaploxypinus* (nine species), *Lueckisporites* (nine species), *Lunatisporites* (eight species), *Vittatina* (four species) and *Hamiapollenites* (three species), together with other species belonging to *Corisaccites*, *Guttulapollenites*, *Illinites*, *Staurosaccites*, *Striatoabieites*, *Striatisaccus* and *Laharites* (Gutiérrez *et al.* 2014). Sulcate, plicate or polyplicate pollen grains are scarce (0.8–3.6%), and are attributed to *Weylandites* (three species), *Marsupipollenites*, *Pakhapites*, *Praecolpatites*, *Cycadopites* and *Equisetosporites*, together with a few taxa of striate monosaccate grains (0.2–1.6%), represented by *Goubinispora*, *Meristocorpus* and *Striomonosaccites* (Gutiérrez *et al.* 2014, table 1).

Non-taeniate monosaccate (5.1–32.7%) and non-taeniate bisaccate (10.5–15.2%) pollen grains are common components of the palynoflora (Tables 1, 2). Within the first group, *Cladaitina veteadensis* is the dominant species (5.0–31.9%). The bisaccate pollen genera with greatest relative abundance are (Table 1): *Alisporites* (four species, with 2.4–3.6% of the total spectrum), *Jugasporites* (10 species, 0.6–2.9%), *Falcisporites* (two species, 0.7–2.1%), *Platysaccus* (four species, 0.7–1.7%) and *Limitisporites* (two species, 0.9–1.5%). Other genera with high species diversity are: *Scheuringipollenites* (five species), *Klausipollenites* (four species), *Vitreisporites* (four species) and *Minutosaccus* (three species).

Palaeobotanical and palaeoecological interpretations

Several authors have pointed out the uncertain botanical affinities of the majority of dispersed palynotaxa (de Jersey & Raine 1990, Balme 1995, Taylor *et al.* 1996, 2009, Playford & Dino 2000b, Playford & Rigby 2008, among others). Furthermore, different systematic classifications of fossil gymnosperms adopted in palaeobotanical studies are based on contrasting phylogenetic studies (Hilton & Bateman 2006, and references therein). The inferred botanical affinities of all gymnosperm pollen grains recorded in the ULV Formation palynoflora in this contribution, and those previously described by Gutiérrez *et al.* (2014), are summarized in Table 3. The palaeobotanical classification adopted herein follows that of Taylor *et al.* (2009). Some taxa represent more than one major natural group (e.g., the polyphyletic *Cycadopites*, *Alisporites*, *Lunatisporites*, *Protohaploxypinus*), whereas, for other taxa, only very

generalized relationships can be inferred. The genera recorded here whose natural alliance is unknown have been categorized as 'gymnosperms *incertae sedis*'.

The botanical affinities of the Palaeozoic gymnosperm pollen genera have been determined mainly from palaeobotanical studies of *in situ* pollen; this has allowed dispersed grains to be indirectly related to fossil plants, most of which have been found in strata in the Northern Hemisphere (Meyen 1987, Traverse 1988, Balme 1995, Taylor *et al.* 1996, 2009, among others). Playford & Dino (2000b, pp. 133–134) discussed the difficulties in attempting to meet palaeofloristic (and palaeobiogeographic/phytogeographic) objectives from a purely palynological standpoint. There are also certain risks inherent in attempting to extrapolate for palaeoecological and palaeoclimatic patterns on the basis of the dispersed (spore-)pollen taxa found in hemispherically opposite palaeolatitudinal locations. The Angaran and Gondwanan phytoprovinces were located respectively in the northern and southern regions of Pangea during the Permian, and diverse communities of gymnosperms characterized each: cordaitaleans were dominant in Angara and glossopterids in Gondwana. Such palaeogeographic locations and climates influenced floristic composition and distribution and, hence, the same form-taxa can reflect different habitats.

Archangelsky (1996) summarized most of our knowledge of the gymnosperm vegetation across the Palaeozoic–Mesozoic transition in Gondwana, analysing palaeogeographic relationships and plant dispersal. He also remarked on differences between the plant records of the Northern and Southern hemispheres and on past studies of the botanical affinities of dispersed fossils (Table 3).

Clearly, the vegetation at the time of deposition of the La Veteada Formation was dominated by pollen producers. As a typical Gondwanan Permian palynoflora, it was over-represented by dispersed pollen of glossopterid gymnosperms, with significant contributions from pteridosperms (corystosperms and peltasperms), conifers (including Voltziales) and cordaites, together with a few representatives of Ginkgoales, Cycadales and Gnetales (Table 3). Other plant groups, including ferns, complete the spectrum of the vegetation that inhabited the La Veteada palaeoenvironments (Gutiérrez *et al.* 2014).

Glossopterids

The glossopterid gymnosperms that characterized the flora of the Southern Hemisphere produced taeniate pollen (Taylor *et al.* 2009). This diverse group is represented in the La Veteada palynoflora by *Hamiapollenites*, *Protohaploxypinus*, *Lueckisporites*, *Lunatisporites*, *Striomonosaccites*, *Striatopodocarpites*, *Illinites* and *Striatoabieites*; and possibly by the non-saccate *Vittatina*, *Weylandites* and *Pakhapites* (Tables 1–3).

DIVISION	ORDER	GENERA	Remarks
PTERIDOSPERMOPHYTA	**Callistophytales** (Pennsylvanian–Permian)	*Vesicaspora*[1][2][3]	(=*Scheuringipollenites*)[13]
	Glossopteridales (Permian)	*Hamiapollenites, Protohaploxypinus**[1][2][18][+20], *Lueckisporites*[1], *Lunatisporites*[18][+20], *Striomonosaccites*[16], *Striatopodocarpites*[1][11][14][16][18][20], *Striatoabieites*[22]*Vittatina*[1], *Weylandites*[1], *Marsupipollenites*[1], *Pakhapites*[13]	*Polyphyletic origin [1][2][18]. Striate/taeniate bisaccate and monosaccate pollen grains. (+20) consider *Lunatisporites, Guttulapollenites* and some species of *Protodiploxypinus* as non-glossopterids Non-saccate taeniate/striate pollen grains
	Corystospermales (Upper Permian–Cretaceous)	*Alisporites* (s.l.)*, *Falcisporites** (s.l.), *Peruchipollenites*[1][2], *Platysaccus* (pars)[4][8], *Vesicaspora*-type[2], *Vitreisporites*[11]	*Polyphyletic origin (1)(2)
	Peltaspermales (Pennsylvanian–Triassic)	*Alisporites* (s.l.)*, *Falcisporites*[1], *Peruchipollenites*[1], *Lueckisporites*[1], *Illinites, Protohaploxypinus*[1][2][7], *Cycadopites**[1][2][7][18], *Vitreisporites*[1][11], *Vittatina*[1][7][18][24], *Vesicaspora*-type[1][2][7], *Pakhapites*[18]	*Polyphyletic origin (1)(2)
CYCADOPHYTES	**Cycadales** (Pennsylvanian–Recent)	*Cycadopites**[1][2], *Praecolpatites*[9][10]	*Polyphyletic origin (1)(2)(7). Includes also putative pollen of Benettitales, Czekanowskiales and Pentoxylales, which occur in Mesozoic strata[1]
GINKGOPHYTES	**Ginkgoales** (Carboniferous–present)	*Cycadopites*, *Alisporites** (s.l.), *Praecolpatites* [9][10], *Weylandites*[1]	*Polyphyletic origin (1)(2)(7)
CONIFEROPHYTES	**Cordaitales** (Mississippian–Upper Permian)[12]*	**Ruffloriaceae:** *Cladaitina* [1][2][4][12][21], *Potonieisporites* [1][5], *Limitisporites*[18], *Marsupipollenites*[1], *Scheuringipollenites*[13], *Vesicaspora*[3]	*New record for uppermost Permian (12)
	Voltziales (Pennsylvanian–Triassic)	*Cladaitina*[1][2], *Triadispora*[1][2][19], *Illinites*[1][2], *Potonieisporites*[2], *Lueckisporites*[2], *Lunatisporites*[2][15][19], *Protohaploxypinus*[2], *Striatoabieites*[2] [19]**Ullmaniaceae** (Upper Permian): *Jugasporites*[1][2][18][19][23], *Limitisporites*[1][2], *Alisporites* (s.l.) (pars)[1], *Triadispora*[1][8][23], *Lueckisporites*[8] [23]**Majonicaceae** (Upper Permian): *Lueckisporites*[1] [19]**Utrechtiaceae** (=Lebachiaceae)/Emporiaceae: *Potonieisporites*[1][2]	
	Coniferales (Pennsylvanian–present)	*Lunatisporites, Lueckisporites*[1], *Pteruchipollenites*[1], *Platysaccus*[1], *Limitisporites*[18], *Potonieisporites*[5], *Illinites*[4], *Alisporites* (s.l.)[1], *Corisaccites*[6], *Guttulapollenites*[2]**?Podocarpaceae** (?Permian/Triassic–present): *Lunatisporites*[1], *Taeniaesporites*[1], *Protohaploxypinus* (pars)[1], *Platysaccus, Cycadopites*[1], *Limitisporites*[1]**Pinaceae** (?Permian/Triassic–present): *Platysaccus, Limitisporites*[1], ? *Pinuspollenites*[1]	
	Conifers *Insertae sedis* (Pennsylvanian–present)	*Hamiapollenites*[14], *Lueckisporites*[5], *Alisporites* (s.l.)[1][2], *Triadispora*[1][2], *Klausipollenites*[4], *Minutosaccus*[7][22], *Striatoabieites*[7][8],	

GNETOPHYTES	**Gnetales** (Permian–present)	*Protodiploxypinus*[7][22], *Marsupipollenites*[1][15], *Striasulcites*[10], *Falcisporites*-type[2], *Illinites*[4], *Vittatina*[4], *Scheuringipollenites*[6][13], *Lunatisporites*-type[7]
		Equisetosporites (=*Ephedripites*)[1], *Cycadopites*[1], *Vittatina*[4]
GYMNOSPERMS *INSERTAE SEDIS*	Unknown	*Meristocorpus, Laharites, Staurosaccites, Striatisaccus, Goubinispora, Cuneatisporites, Sulcosaccispora, Colpisaccites, Protodiploxypinus, Gondwanapollis, Granisaccus, Polarisaccites, Accinctisporites, Crucisaccites, Vialialasaccites*

Table 3. Known botanical affinities of the non-taeniate gymnosperm pollen recorded in the La Veteada Formation palynoflora at its type locality. The palaeobotanical classification adopted herein follows that of Taylor *et al.* (2009). References: (1) Balme 1995; (2) Taylor *et al.,* 2009; (3) Millay & Taylor 1974; (4) Traverse 1988; (5) Gomankov 2009; (6) Visscher 1980; (7) Ouyang & Norris 1999; (8) Playford *et al.* 1982; (9) Raine *et al.* 2011; (10) Tripathi *et al.* 2012; (11) McLoughlin *et al.* 1997; (12) Zavattieri & Gutiérrez 2012; (13) Tiwari 1973; (14) Quadros *et al.* 1996; (15) Mishra & Joshi 2015; (16) Lindström *et al.* 1997; (17) Playford & Dino 2000b; (18) Foster 1983; (19) Looy *et al.* 1999; (20) Lindström & McLoughlin 2007; (21) Zavialova & Gomankov 2009; (22) Scheuring 1970; (23) Scheuring 1979; (24) Traverse 2007; for additional botanical affinities of the various gymnosperm pollen genera recorded herein see Kustatscher *et al.* (2010).

Archangelsky (1996) considered that the vast palaeogeographical extent of Gondwana denoted the adaptive power of glossopterid vegetation during the Permian. Given their broad distribution, it is reasonable to assume that glossopterids were adapted to various climates and ecological conditions (Cúneo *et al.* 1993). Therefore, some may have been able to adapt to arid or semi-arid environments, possibly alternating with moist periods (strongly seasonal conditions). In the more arid phases, the glossosperids could have taken refuge in environments with available water (Simon *et al.* 2016).

Cazzulo-Klepzig *et al.* (2007) admitted that the cordaites, glossopterids and some conifers have been linked to various mesophytic-xerophytic environments, and they considered it important to recognize that some of their palaeoecological features explain their presence in areas adjacent to mires. Knoll & Niklas (1987) concluded that xeromorphic structures shown by some glossopterids, as identified in the Faxinal coal seam (Guerra-Sommer *et al.* 1991), may indicate that they originally grew in elevated habitats.

Lindström & McLoughlin (2007) indicated that the glossopterids proliferated markedly in the humid, temperate climatic conditions that existed in several Lopingian Gondwanan basins where they were dominated peat-forming mires and produced the accumulation of vast coal resources in the Permian of Australia (McLoughlin & Hill 1996), even under conditions of ameliorating climates (Playford & Rigby 2008). However, Foster (1979) noted that the parent plants of the dispersed striate pollen could have been derived from a diverse floodplain flora of which some constituents may have occupied drier, better-drained and slightly elevated areas. Several southeastern Gondwanan basins have extensive uppermost Permian coals (Australia, Antarctica, South Africa and India), but most coals disappeared slightly below the P–T boundary. Lindström & McLoughlin (2007) noted that the disappearance of the peat-forming mires that hosted the glossopterids is a conspicuous feature of many Permian–Triassic transitions in southeastern Gondwana. McLoughlin *et al.* (1997) inferred that, across Gondwana, the diachronous disappearance of coal deposits and appearance of redbeds is suggestive of a response to shifting climatic belts, resulting in progressively drier seasonal conditions at successively higher palaeolatitudes during the Late Permian. Climates of the Lopingian in South America were typically hot and locally very dry (Fluteau *et al.* 2001). For the Lopingian, the Paganzo Basin was located between 30° and 40° of latitude (Isbell *et al.* 2003, Tomezzoli 2009). Recently, Limarino *et al.* (2014) also reported a gradual climatic amelioration and (warming) throughout the Permian in South America (southwestern Gondwana). The progressive aridity observed in all southern South American basins from the late Guadalupian to Lopingian indicates continental-scale environmental deterioration (Limarino *et al.* 2014, p. 1416).

Non-glossopterid gymnosperms

Pteridospermous bisaccate non-striate pollen grains are sub-dominant components in the La Veteada palynoflora. They were derived from peltasperms and corystosperms, and are represented mainly by *Alisporites-Falcisporites*, *Pteruchipollenites*, *Platysaccus*, *Lueckisporites*, *Klausipollenites*, *Vitreisporites* and *?Illinites* (Table 3). In particular, the corystosperms appeared in the Late Permian, being small to large woody shrubs and trees (Artabe *et al.* 2001; Taylor *et al.* 2009) adapted to a wide range of environments.

Diverse types of pollen grains have also been assigned to peltasperms ranging from *Vesicaspora (=Scheuringipollenites)*-type bisaccate to *Cycadopites*-type monosulcate (Taylor *et al.* 2009; Table 3). Pteridosperms presumably preferred upland habitats, peripheral to the depositional sites. Therefore, bisaccate pollen grains may have been incorporated as allochthonous elements to depositional sites. Small bisaccate pollen derived from the Umkomasiales (=Corystospermales) or Peltaspermales are also common components in the studied assemblages, represented by diverse species of *Vitreisporites* and *Klausipollenites*, and probably also by small, dispersed, bisaccate pollen grains assigned to *Alisporites*. Taylor *et al.* (2009) indicated that there is no confident record of caytonialean foliage (*Sagenopteris*) before the Middle Triassic and, therefore, it is unlikely that Permian pollen assigned to *Vitreisporites* is associated with that order. *Vitreisporites*-type pollen has been found in reproductive structures, such as *Salpingocarpus*, which may be corystospermaean or peltaspermalean. *Vitreisporites* is known from the Early Permian to the early Cenozoic (Foster 1979).

Dispersed saccate pollen of cordaitaleans is abundant in the La Veteada palynoflora and belongs predominantly to *Cladaitina* (Zavattieri & Gutiérrez 2012, see also Gomankov 2009). The specialized epidermal morphology of cordaitalean leaves identified from the Faxinal coals in the Permian of the Paraná Basin (Cazzulo-Klepzig *et al.* 2007) might represent an adaptation to prevent desiccation or a response to changes in compositional features of the soil, and such physiological and morphological features might have permitted these plants to adapt to various ecological conditions, this being supported by Guerra-Sommer's (1988) interpretation. Cridland & Morris (1963) and Falcon-Lang (2005) also noted that cordaitaleans probably encompassed a very large ecological spectrum and may have occasionally tolerated brackish incursions by modification of the root system and leaves. These authors demonstrated that some species grew in coastal plains adapted to periodically submerged conditions. According to Raymond (1988), some cordaitaleans could also live in lowland hygrophylous–mesophylous environments. Archangelsky (1996) suggested that cordaitaleans may have grown in, or immediately adjacent to shallow lacustrine environments, indicating probable

(seasonal?) flooding episodes and/or that they also could have probably formed part of upland communities.

Voltzialean conifers are particularly well represented in the La Veteada assemblages by *Jugasporites*, *Lueckisporites*, *Limitisporites*, *Triadispora*, *Illinites*, *Scheuringipollenites*, *Potoniesporites* and other striate pollen (Table 3). The families Ullmaniaceae and Majoniaceae are restricted to the Late Permian (Taylor *et al.* 2009), whereas the remaining families have their earliest appearances before the Early Permian. Voltziales were woody shrubs or small to large trees that inhabited lowland peat mires where they formed part of mixed vegetation types.

Other saccate pollen derived from conifers are also well represented in the studied assemblages, mainly by *Minutosaccus*, *Protodiploxypinus*, *Platysaccus*, *Pinuspollenites*, *Klausipollenites*, *Limitisporites*, and *Scheuringipollenites* (Table 3). Diverse Permian taeniate pollen grains have also been referred to conifers (Balme 1995, Quadros *et al.* 1996, Playford & Dino 2000b, Traverse 2007, among others). In the La Veteada assemblages they are represented by *Guttulapollenites*, *Corisaccites*, *Hamiapollenites*, *Illinites*, *Lunatisporites*, *Taeniaesporites* and the non-saccate *Marsupipollenites*. The monosaccate pollen, *Potoniesporites*, is also considered to be the dispersed pollen of conifers. Permian conifers had arborescent habits, although a few were also shrub-like plants (Taylor *et al.* 2009). Permian conifers especially colonized highlands and well-drained environments, although some probably inhabited a range of lowland settings (Archangelsky & Cúneo 1987, Archangelsky 1990, McLoughlin 1993, Taylor *et al.* 2007).

A few of the simple monocolpate/monosulcate pollen types may also belong to cycadalean and/or ginkgoalean gymnosperms, represented in the La Veteada assemblages by the genera, *Cycadopites* and *Praecolpatites*. Pollen grains assigned to *Cycadopites* are undoubtedly of polyphyletic origin (some linked to peltasperms) and occur in sediments of late Palaeozoic to Holocene age (Taylor *et al.* 2009).

A few polyplicate gymnosperm pollen are recorded in the studied assemblages by forms assigned to *Equisetosporites*. This genus and other polyplicate pollen genera have probable gnetalean (ephedraceous) affinities (de Jersey & Raine 1990, Balme 1995). Taylor *et al.* (2009, p. 777) considered that numerous polyplicate (or ephedroid) pollen grains have been reported as putative gnetophyte pollen, the earliest record being in Permian strata. They also remarked that many of the Permian putative gnetophyte pollen grains similar to *Ephedra* grains have been 'unfortunately' called *Equisetosporites*. Ephedralean pollen, distinguished by numerous ridges extending along the grain, are placed in the dispersed-pollen form genera *Gnetaceaepollenites*, *Steevesipollenites*, *Ephedripites* and *Equisetosporites*, most of which are common components of Mesozoic palynofloras.

Lindstrom & McLoughlin (2007) observed that, from the palynological data, it is evident that many gymnospermous taxa that increased in abundance in Early Triassic assemblages were already present in low numbers in the Permian (e.g., *Alisporites/Falcisporites*, *Klausipollenites*, *Vitreisporites*, *Scheuringipollenites*, among others). They appear to have played a subordinate role in the glossopterid-dominated plant communities, perhaps occupying drier sites. In fact, many of the gymnosperms that played a minor role in the Permian of Gondwana may have been adapted to better-drained and perhaps more elevated areas and probably inhabited environments adjacent to the site of deposition (Gutiérrez *et al.* 2011, 2017).

Conclusions

(1) The sedimentology of this unit in its type section (Dávila *et al.* 2005, Gutiérrez *et al.* 2014) suggests the development of floodplains under high-evaporative conditions with fluctuation of the ground water-table associated with mainly hypersaline, periodically expanding and contracting semi-perennial lakes (Zavattieri *et al.* 2017). This sequence suggests the prevalence of a semi-arid climate that could have been interrupted by brief humid episodes (but remaining strongly seasonal). During humid periods, plant fossils probably reflect persistent water bodies on a relatively dry alluvial plain, where riparian plants experienced periodic water-stress, but had access to groundwater almost all year round (Simon *et al.* 2016).

(2) The La Veteada Formation palynoflora derives mainly from a diverse gymnosperm vegetation that was dominanted by glossopterids with sub-dominant conifers (Voltziales), Cordaitales, peltasperms and corystosperms (Gutiérrez *et al.* 2011 2014). Its composition and diversity are typical of Lopingian palynofloras from southwestern Gondwana (Gutiérrez *et al.* 2017).

(3) Woody and/or shrub-sized gymnosperms represented by the La Veteada Formation palynoflora suggest a parent vegetation that was adapted to semi-arid to arid climates, which prevailed throughout an extensive part of southern South America during the late Guadalupian to Lopingian (Limarino *et al.* 2014, p. 1411).

(4) The La Veteada Formation would have been deposited during a predominantly warm or even hot period, but that does not exclude the possibility of brief cold intervals. The high ratio of pollen versus spores suggests that the La Veteada Formation palynoassemblages were clearly deposited under deteriorating continental-scale environments.

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Supplemental material

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