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THE PALYNOLOGIC CATALOGUE OF THE LOWER PERMIAN (ASSELIAN-?ARTINSKIAN) COPACABANA FORMATION AT APILLAPAMPA, COCHABAMBA, BOLIVIA AND PALEOBIOGEOGRAPHIC APPROACHES

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1 Introduction

The Copacabana Formation at Apillapampa in Bolivia was studied for palynology and from twelve shales samples of marine and transitional paleoenvironments 92 spores, pollen and other taxa recorded and their quantitative stratigraphical distribution published by di Pasquo and Grader (2012). The present palynologic catalogue includes illustration of those taxa and some taxonomic comments for selected species. Two palynozones of Lower Permian age (*Vittatina costabilis* and *Lueckisporites virkkiae*) established by di Pasquo and Grader (2012). The assemblages are composed of gymnosperms (coniferaleans, cordaitaleans, and pteridosperm-like plants), with significant contributions from lower vascular plants (variably pteridophytes, sphenophylls and lycophytes). These palynoassemblages characterized by di Pasquo et al. (2015) based on the appearance of some key taxa and compared and correlated with palynozones of South America and elsewhere. The lower assemblage was correlated with South American *Vittatina costabilis* (VcZ) Souza (2006), *Pakhapites fusus-Vittatina subsaccata* (FSZ) Césari and Gutiérrez (2001), *Cristatisporites inconstans-Vittatina subsaccata* (ISZ) Beri et al. (2011) palynozones due to the presence of species such as *Converrucosporites confluens, Polypodiisporites mutabilis* and, *Lunatisporites pellucidus*. The upper assemblages correlated to the *Lueckisporites virkkiae* (LvZ) Souza (2006), *Lueckisporites-Weylandites* (LWZ) Césari and Gutiérrez (2001), and *Striatoabieites anaverrucosus-Staurosaccites cordubensis* (ACZ) biozones (e.g. *Lueckisporites virkkiae*, *Lunatisporites acutus*, *Protohaploxypinus samoilovichii*, *Thymospora criciumensis*, *T. rugulosa*, *Convolutispora uruguaiensis*). Globally, Early Permian palynoassemblages mostly shared long-ranged taxa and/or those key taxa exhibit diachronic ranges. Five volcanic ash layers isotopically- dated confirmed that the lower Copacabana Formation at this location is Asselian and Sakmarian and the overlying "Coal Member" is Sakmarian through probably Artinskian. Di Pasquo et al. (2015) discussed the disagreement between those older absolute ages of the Bolivian biozones with the ones from Brazil, Uruguay, Argentina and elsewhere in Africa, Australia, Oman and, Saudi Arabia, also constrained with radiometric data. Therefore, Bolivia may be part of older centers of dispersion for some striate-taeniate pollen grains and monolete spores. Despite this disagreement was not refuted or confirmed up to now, it was explained in relation to palynofloral evolution based on near-field glaciation and deglaciation as likely responsible for migration of plants throughout Gondwana (di Pasquo et al., 2015, 2019). An approach on climatic and paleogeographic changes reflected by provincialisms during the Asselian-Sakmarian to Late Permian is addressed herein.

2 Systematic palaeontology

The systematic classification of miospores follows the schemes of Potonié and Kremp (1954), and Playford and Dettmann (1996). Taxonomic remarks and synonymies are included in this section as well as selected literature for geographic and biostratigraphic distribution of taxa summarized in Table 1 along with their botanical affinities mainly based on Balme (1995, see also di Pasquo and Grader, 2012; di Pasquo et al., 2015).

Anteturma PROXIMEGERMINANTES Potonié 1970
Turma TRILETES (Reinsch) Dettmann 1963
Suprasubturma ACAVATRILETES Dettmann 1963
Subturma AZONOTRILETES (Luber) Dettmann 1963
Infraturma LAEVIGATI (Bennie & Kidston) Potonié 1970

Genus *Calamospora* Schopf, Wilson & Bentall 1944
Type species. *Calamospora hartungiana* Schopf in Schopf, Wilson & Bentall 1944.

Calamospora liquida Kosanke 1950, Pl. 1, fig. 1
Calamospora microrugosa (Ibrahim) Schopf, Wilson & Bentall 1944, Pl. 1, fig. 2

Genus *Waltzispora* Staplin 1960
Type species. *W. lobophora* (Waltz in Luber & Waltz) Staplin 1960
Waltzispora sp., Pl. 1, fig. 3

Remarks. Only one specimen has been found showing the same characters (e.g., amb trilobate, laesurae one-half of spore radius with a darkened contact area) defined for *Waltzispora* sp. A Playford & Rigby 2008, except for its larger spore diameter (57 µm) than the one of the latter species (29 µm). Although it is likely they are conspecific, the lack of more specimens prevented a more close comparison. *Waltzispora*? sp. A in Beri et al. (2006, pl. 2, fig. D) is very similar except for having trilete laesura extending up to the equator and bearing narrow lips.

Genus *Punctatisporites* Ibrahim emend. Potonié & Kremp 1954
Type species. *P. punctatus* Ibrahim 1933.

Punctatisporites minutiarcus Cousminer 1965, Pl. 1, fig. 4

Infraturma RETUSOTRILETI Streel 1964

Genus *Retusotriletes* Naumova emend. Streel 1964
Type species. *R. simplex* Naumova 1953.

Retusotriletes nigritellus (Lüber) Foster 1979, Pl. 1, fig. 5

Infraturma APICULATI Bennie & Kidston emend. Potonié 1956
Subinfraturma NODATI Dybová & Jachowicz 1957

Genus *Brevitriletes* Bharadwaj & Srivastava 1969
Type species. *B. communis* Bharadwaj & Srivastava 1969.

Brevitriletes cornutus (Balme & Hennelly) Backhouse 1991, Pl. 1, fig. 6
1965 *Apiculatisporis* cf. *A. cornutus* Balme & Hennelly, Cousminer, p. 1103, pl. 127, fig. 22.

Remarks. The specimen illustrated by Cousminer (1965) shows quite similar features, chiefly the mammoid ornamentation similar to the one here recovered supporting their conspecificy.

Previous records. Widely distributed in the Late Pennsylvanian and Cisuralian of Argentina, Brazil and Uruguay (see di Pasquo, 2003; Vergel, 2008; di Pasquo et al., 2010; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010) and in the Cisuralian of Gondwana (see Doubinger and Marocco, 1981; MacRae, 1988; Millsteed, 1999; Stephenson, 2004; Gutiérrez et al., 2010).

Subinfraturma BACULATI Dybová & Jachowicz 1957

Genus *Horriditriletes* Bharadwaj & Salujha 1964
Type species. *H. curvibaculosus* Bharadwaj & Salujha 1964.

Horriditriletes ramosus (Balme & Hennelly) Bharadwaj & Salujha 1964, Pl. 1, fig. 7

Comparison. *Neoraistrickia* aff. *N. ramosus* Balme & Hennelly illustrated by Cousminer (1965, p. 1103, pl. 127, fig. 21) closely resembles *Horriditriletes* sp. cf. *H. ramosus* described by Bharadwaj and Salujha (1964, p.194, pl. 2, fig. 43) as having blunt bacula more densely distributed on the exine and a more subcircular amb than *H. ramosus.*

Previous records. Widely recorded from the Pennsylvanian and Cisuralian of Gondwana: Antarctica (Lindström, 1995), Argentina (Césari et al., 1995; García, 1995; Vergel, 2008; di Pasquo et al., 2008, 2010), Australia (Foster, 1979; Gilby and Foster, 1988; Backhouse, 1991; Jones and Truswell, 1992), Brazil (Dino and Playford, 2002; Souza and Callegari, 2004; Mori and Souza, 2010), India (Bharadwaj and Salujha, 1964), Iran (Ghavidel-syooki, 1997), Oman and Saudi Arabia (see Stephenson, 2004), Peru (Doubinger and Marocco, 1981), South Africa (MacRae, 1988; Stephenson and McLean, 1999; Millsteed, 1999), Uruguay (see Gutiérrez et al., 2010; Beri et al., 2010). Late Permian to Early Triassic of Antarctica (Lindström and McLoughlin, 2007).

Subinfraturma VARITRILETI Venkatachala & Kar 1965

Genus *Didecitriletes* Venkatachala & Kar 1965

Type species. *D. horridus* Venkatachala & Kar 1965.

Didecitriletes eoericianus (Anderson) Millsteed 1999, Pl. 1, fig. 8

Remarks. This specimen matches very well with all the features of the species except for having a slightly smaller spinae.

Previous records. Cisuralian of South Africa (Anderson, 1977; Millsteed, 1999).

Didecitriletes sp., Pl. 1, fig. 9

Description. Trilete spore triangular with slightly convex sides. Laesurae distinct simple and straight extending ca. ½ of the spore ratio. Exine thin, proximal face laevigate to sparsely granulose, distal face with both grana and bulbous spines less than 1 μm.

Dimensions. Equatorial diameter 45 μm.

Comparison. This specimen closely resembles *Didecitriletes bellus* Venkatachala & Kar 1968 in having subtriangular amb with proximal face laevigate to sparsely granulose, distal face with both grana and bulbous spines less than 1 μm. Although the latter species is larger (65-85 μm) and has a thick exine and a trilete associated with folds.

Infraturma MURORNATI Potonié & Kremp 1954

Genus *Convolutispora* Hoffmeister, Staplin & Malloy 1955
Type species. *Convolutispora florida* Hoffmeister, Staplin & Malloy 1955.

Convolutispora ordonensis Archangelsky & Gamerro 1979, Pl. 1, fig. 10

Previous records. It is a very well known species from the Pennsylvanian of Bolivia (di Pasquo, 2009) to Cisuralian of Argentina, Brazil and Uruguay (see di Pasquo, 2003; di Pasquo et al., 2003a, 2010; Vergel, 2008; Gutiérrez et al., 2010; Beri et al., 2010), and Permian of Paraguay (Muff et al., 1999).

Convolutispora uruguaiensis Mautino, Vergel & Anzótegui 1998b, Pl. 1, fig. 11, 12

1977 *Cyclogranisporites intrareticulatus* Anderson, p. 72, pl. 70, figs. 4, 12, 21-23 [partim].

Comparisons. Very similar specimens illustrated as *Cyclogranisporites intrareticulatus* Anderson (1977, p. 72, pl. 70, figs. 4, 12, 21-23) are here transferred to *C. uruguaiensis* on the grounds of a slightly coarser vermiculate sculpture with visible discrete verrucae rather than completely rugulate pattern as described by Millsteed (1999), who validly combined *C. intrareticulatus* to *Convolutispora*.

Previous records. Cisuralian of Uruguay (Mautino et al., 1998b) and South Africa (Anderson, 1977).
Genus *Dictyotriletes* Naumova emend. Potonié & Kremp 1954
Type species. *Dictyotriletes bireticulatus* (Ibrahim) Potonié & Kremp 1955

Dictyotriletes cousmineri di Pasquo & Grader 2012, Pl. 1, figs. 13–16

Remark. This species only occurs in one sample and mainly in the 525 mm fraction.

Comparison. *Dictyotriletes aules* Rigby in Rigby & Heckel 1977 differs from *Dictyotriletes cousmineri* by having laesurae-bearing lips and a different reticulate ornamentation.

Infraturma CINGULATI Potonié & Klaus emend. Dettmann 1963

Genus *Iraquispora* Singh 1964
Type species. *I. labrata* Singh 1964

Iraquispora sp., Pl. 1, fig. 12

Remarks. The single specimen recorded is not well preserved enough to be assigned confidently to *Iraquispora labrata* Singh 1964 from the Kungurian to Upper Permian of Iraq. It is also recognized in the Permian of Pakistan (Balme, 1970) and West Papua, New Guinea (Playford and Rigby, 2008). Although it shows similar features such as a subtriangular amb, trilete almost extended to the equator, conctact area with kyrtomate interradial thickening, cingulum ca. 5 μm slightly widen in radial extremes.

Subturma ZONOTRILETES Waltz 1935
Infraturma AURICULATI Schopf emend. Dettmann 1963

Genus *Triquitrites* Wilson & Coe emend. Potonié & Kremp 1954
Type species*. T. arculatus* Wilson & Coe 1940

Triquitrites sp. cf. *T. kaiseri* Playford & Rigby 2008, Pl. 2, fig. 1

Remarks. The single specimen recorded is not well preserved but displays all morphological characteristics of *Triquitrites kaiseri* Playford & Rigby 2008 from the Kungurian-Roadian of West Papua, New Guinea.

Suprasubturma LAMINATITRILETES Smith & Butterworth 1967
Subturma ZONOLAMINATITRILETES Smith & Butterworth 1967
Infraturma CINGULICAVATI Smith & Butterworth 1967

Genus *Cirratriradites* Wilson & Coe 1940
Type species*. C. saturni* (Ibrahim) Schopf, Wilson & Bentall 1944.

Cirratriradites africanensis Hart 1963, Pl. 2, fig. 2

Previous records. Cisuralian of South Africa (MacRae, 1988).

Genus *Cristatisporites* Potonié & Kremp emend. Butterworth, Jansonius, Smith & Staplin 1964
Type species. *Cristatisporites indignabundus* (Loose) Potonié & Kremp 1954.

Cristatisporites morungavensis (Días Fabricio) Picarelli & Días Fabricio 1990, Pl. 2, fig. 3

Previous records. Recorded from Cisuralian deposits of Brazil and Uruguay (see di Pasquo et al., 2003a; Souza and Callegari, 2004; Beri et al., 2006, 2010; Gutiérrez et al., 2006).

Genus *Gondisporites* Bharadwaj 1962
Type species. *Gondisporites raniganjensis* Bharadwaj 1962

Gondisporites sp. cf. *G. imbricatus* Segroves 1970, Pl. 2, fig. 4

Remarks and comparisons. The specimen recorded is closely similar to *G. imbricatus* although as it is a single, not so well preserved specimen it is left in comparison. A very similar species is *Gondisporites serrulatus* Césari, Archangelsky & Seoane 1995 yet it differs by having the proximal face smooth and ornamentation of two or three small warts somewhat fused. Rayner (1986) recorded spores *in situ* in the fructification of *Azaniadendron* Rayner (Lepidodendrales); these are similar to this species although they differ in having a cingulizona and by being less ornamented, with grana confined to the distal central body surface.

Previous records. Artinskian – Late Permian of the Perth Basin, Western Australia (Segroves, 1970), West Papua, New Guinea (Playford and Rigby, 2008).

Genus *Lundbladispora* Balme emend. Playford 1965
Type species. *L. wilmottii* (Balme) Playford 1965.

Lundbladispora braziliensis (Pant & Srivastava) Marques-Toigo & Pons emend. Marques-Toigo & Picarelli 1984, Pl. 2, fig. 5

1965 *Densosporites braziliensis* Pant & Srivastava, p. 469-470, pl. 1, figs. 1-6 [published in october].

1965 *Kraeuselisporites chamotii* Cousminer, p. 1104, pl. 127, figs. 15-19 [published in november].
1977 *Gondisporites braziliensis* (Pant & Srivastava) Anderson, p. 23, pl. 23, figs 1-27.

For description and further synonymy see Marques-Toigo and Picarelli (1984) and Stephenson (2004, and references therein).

Remarks. The recovery of many specimens of "*Kraeuselisporites chamotii*" so defined by Cousminer (1965) in the Coal Member of this locality (see Table 1) support conspecificy with *L. braziliensis* as both share the same morphological characters. On the other hand, the combination proposed by Anderson (1977) to *Gondisporites* is not sustainable mainly because of this genus is zonate and not cingulate/cingulizonate like *Lundbladispora*.

Previous records. Widely registered in the Pennsylvanian and Cisuralian of Argentina (see di Pasquo, 2003; Vergel, 2008; Gutiérrez et al., 2010), Brazil (see di Pasquo et al., 2003a; Souza et al., 2003; Souza and Callegari, 2004; Souza and Marques-Toigo, 2005; Mori and Souza, 2010), and the Cisuralian of Uruguay (see Mautino et al., 1998a; Gutiérrez et al., 2010; Beri et al., 2010), Oman and Saudi Arabia (see Stephenson, 2004), Paraguay (Muff et al., 1999) and South Africa (Anderson, 1977).

Lundbladispora riobonitensis Marques-Toigo & Picarelli 1984, Pl. 2, fig. 6

Previous records. Widely registered in the Pennsylvanian and Cisuralian of Argentina (see di Pasquo, 2003; Vergel, 2008; di Pasquo et al., 2010), Brazil (see di Pasquo et al., 2003a; Souza et al., 2003; Souza and Callegari, 2004; Mori and Souza, 2010), and Cisuralian of Uruguay (see Mautino et al., 1998a; Gutiérrez et al., 2010; Beri et al., 2010), Oman and Saudi Arabia (Stephenson and Filatoff, 2000a) and Paraguay (Muff et al., 1999).

Genus *Lycospora* Schopf, Wilson & Bentall emend. Somers 1972
Type species. *L. pusilla* (Ibrahim) Schopf, Wilson & Bentall emend. Somers 1972

Lycospora variabila Cousminer 1965, Pl. 2, fig. 7-9

1981 *Lundbladispora variabila* (Cousminer) Doubinger and Marocco, p. 1094, pl. 1, figs. 6, 7, 11.

Remarks. This species has been abundantly recorded by Cousminer (1965) especially in the BOGOC 6-2560 (see di Pasquo and Grader, 2012) and likewise in this study (see Table 1) where variable arrangements of grains (i.e., single grains, half tetrads, tetrads and groups of spores) are found (see Pl. 2, figs. 7-9). Somers (1972) proposed the synonymization of Cousminer´s species with *L. pusilla*, which is not confirmed in this study. Although the emended diagnosis of the latter includes the description of the former, the analysis of the present population is in agreement with Cousminer´s opinion on the variably folded character of the spore wall as a distinguishing specific character.

Turma MONOLETES Ibrahim 1933
Suprasubturma ACAVATOMONOLETES Dettmann 1963
Subturma AZONOMONOLETES Luber 1935
Infraturma LAEVIGATOMONOLETI Dybová & Jachowicz 1957

Genus *Laevigatosporites* Ibrahim emend. Alpern & Doubinger 1973
Type species. *Laevigatosporites vulgaris* (Ibrahim) Ibrahim emend. Alpern &

Doubinger 1973 (by original designation).

Laevigatosporites vulgaris (Ibrahim) Ibrahim emend. Alpern & Doubinger 1973, Pl. 2, fig. 10

Remarks. Cousminer (1965) has found this species as dominant in the sample BOGOC 6-2557 although here we found it fairly well- represented at one level. It is rare or absent in the others (see Table 1).

Infraturma SCULPTATOMONOLETI Dybová & Jachowicz 1957

Genus *Leschikisporis* Potonié 1958
Type species. *Leschikisporis aduncus* (Leschik) Potonié 1958

Leschikisporis chacoparanaensis Vergel 1990, Pl. 2, figs. 11, 12

Previous records. Cisuralian of Argentina, Brazil and Uruguay (Vergel, 1990, 1993; Mautino et al., 1998 a; Neregato et al., 2008; di Pasquo et al., 2010).

Genus *Polypodiisporites* Potonié in Potonié & Gelletich emend. Khan & Martin 1971
Type species. *Polypodiisporites favus* (Potonié) Potonié 1956.

Polypodiisporites mutabilis Balme 1970, Pl. 2, fig. 13-15

1965 *Verrucososporites* aff. *V. leopardus* Balme & Hennelly, Cousminer, p. 1104, pl. 128, figs. 6 a 11.
1977 *Polypodiiporites detritus* (Leschik) Anderson, pl. 79, figs. 6-16, 26-29 [partim]

Dimensions (55 specimens). Maximum diameter 25-50 µm.

Remarks and comparisons. The numerous specimens here recovered showed that both asymmetric trilete and monolete marks are present. A very rough rugulate (with more verrucae intersperse) to a more comprehensive rugulate pattern (with well- defined negative reticulum) is developed on the exine. Cousminer (1965) assigned with doubts his illustrated specimens to *Verrucososporites* aff. *V. leopardus* Balme & Hennelly, which are better assigned to this taxon from those pictures. On the other hand, *V. leopardus* was combined to *Polipodiisporites* by Foster (1975) and characterized as having densely distributed small and low verrucae (1-2 µm wide, 0.5 µm high) with reduced sculpture on the contact areas (see also Alpern and Doubinger, 1973 and Foster, 1979). Although Anderson (1977) has also recorded *P. mutabilis* in such assemblages from the Ecca Group of South Africa (Pl. 79, figs. 42-49), some specimens illustrated as *P. detritus* are morphologically so close to *P. mutabilis* that are here considered conspecific with this species.

Previous records. Cisuralian of Uruguay (Mautino et al., 1998a; Gutiérrez et al., 2010) and Israel (Eshet, 1990a, 1990b); Late Permian of Pakistan (Balme, 1970), South Africa (Anderson, 1977). Early Triassic of Antarctica (Lindström and McLoughlin, 2007).

Genus *Polypodiites* Potonié & Gelletich 1931
Type species. *P. favus* (Potonié) Potonié 1934.

Polypodiites secoensis Mautino, Vergel & Anzótegui 1998 b, Pl. 2, fig. 16-17

1960 *Verrucososporites* aff. *V. ambylogonus* Imgrund Cousminer, 1965, p. 1104, Pl. 128, figs. 15, 16.

1977 *Polypodiiporites detritus* (Leschik) Anderson, pl. 79, figs. 21-25, 34-41 [partim]

Remarks and comparisons. Cousminer (1965) assigned with doubts two specimens to *Verrucosoporites ambylogonus* Imgrund 1960. However, from the pictures and with help fom the specimens recorded in this study, they are better attributed to the present species. On the other hand, *V. ambylogonus* is considered a junior synonym of *Thymospora thiessenii* (Kosanke) Wilson & Venkatachala by Alpern and Doubinger (1973), which is differentiated from the present species because of having verrucae, rugulae to cristae that are generally serrate (i.e. with small coni on the top, and not smooth like in *P. secoensis*), loosely to sharply distributed and small grains intermingled. Anderson (1977) illustrated some specimens as *Polypodiisporites detritus* that are morphologically close to *Polypodiites secoensis*, so they are here considered conspecific with this species.

Previous records. Cisuralian of Uruguay (Mautino et al., 1998b) and Africa (Anderson, 1977).

Genus *Reticuloidosporites* Pflug 1953
Type species. *R. dentatus* Pflug 1953

Reticuloidosporites warchianus Balme 1970, Pl. 3, fig. 1, 2

Comparisons. This species looks similar to *Polypodiisporites mutabilis* Balme 1970. Although, it differs by having more varied elements like coni, grana, and verrucae intermingle with rugulae.

Previous records. Permian of Pakistan (Balme, 1970); Cisuralian of Israel (Eshet, 1990a, 1990b), Peru (Doubinger and Marocco, 1981), and Uruguay (Mautino et al., 1998a).

Genus *Thymospora* Wilson & Venkatachala emend. Alpern & Doubinger 1973
Type species. *Thymospora thiessenii* (Kosanke) Wilson & Venkatachala 1963.

Thymospora criciumensis Quadros, Marques-Toigo & Cazzulo-Klepzig 1996, Pl. 3, fig. 3, 4

1965 *Pericutosporites* aff. *P. potoniei* Imgrund, Cousminer, p. 1105, pl. 128, figs. 12, 13.

Remarks and comparisons. Cousminer (1965) assigned with doubts two illustrated specimens to *Pericutosporites potoniei* Imgrund because they were larger. From the pictures and with help of the specimens recorded in this study, they are better attributed to *T. criciumensis*. On the other hand, *P. potoniei* is considered a junior synonym of *Thymospora pseudothiessenii* (Kosanke) Wilson & Venkatachala emend Alpern & Doubinger 1973. The latter is differentiated from the present species because of having verrucae and intermingled grains with the rugulate-cristate pattern.

Previous records. Permian of Brazil (Quadros et al., 1996; Souza and Marques-Toigo, 2005; Neregato et al., 2008).

Thymospora rugulosa Mautino, Vergel & Anzótegui 1998b, Pl. 3, fig. 5, 6

1965 *Pectosporites*? sp. Cousminer, p. 1105, pl. 128, fig. 14.
1977 *Polypodiiporites detritus* (Leschik) Anderson, pl. 79, figs. 17-20, 30-33 [partim].

Remarks and comparisons. Cousminer (1965) assigned with doubts a single specimen to *Pectosporites?* sp., although from the picture and with help of the specimens recorded in this study, it is better attributed to *T. rugulosa*. Anderson (1977) illustrated some specimens as *Polypodiisporites detritus* that are morphologically very close to *T. rugulosa*. Hence, they are here considered conspecific with this species.

Previous records. Cisuralian of Uruguay (Mautino et al., 1998b; Neregato et al., 2008); Permian of South Africa (Anderson, 1977).

Genus *Striatosporites* Bhardwaj emend. Playford & Dino 2000 a
Type species. *S. major* Bhardwaj 1954.

Striatosporites heyleri (Doubinger) emend. Playford & Dino 2000 a, Pl. 3, fig. 7-10

For synonymy see Foster (1979), Playford and Dino (2000 a) and Playford and Rigby (2008).

Remarks. We registered specimens with different kind of preservations, including well preserved ones with complete sculpture (Pl. 3, figs. 8, 9), incomplete ones (without secondary muri, Pl. 3, fig. 7), and also laevigate forms with a wrinkle pattern corresponding to the inner body (Pl. 3, fig. 10) (see also Playford and Dino, 2000 a).

Previous records. Widespread geographic distribution from Westphalian to Permian in Gondwana (see Doubinger and Marocco, 1981; Playford and Dino, 2000 a; Dino and Playford, 2002; Playford and Rigby, 2008). Pennsylvanian of Euramerica and Mid-Permian of Cathaysia (see Foster, 1979).

Turma SACCITES Erdtman 1947
Subturma MONOSACCITES Chitaley emend. Potonié & Kremp 1954
Infraturma DIPOLSACCITI Hart emend. Dibner 1971

Genus *Caheniasaccites* Bose & Kar emend. Azcuy & di Pasquo 2000
Type species. *Caheniasaccites flavatus* Bose & Kar, 1966.

Caheniasaccites flavatus Bose & Kar emend. Azcuy & di Pasquo 2000, Pl. 4, fig. 1

Genus *Cannanoropollis* Potonié & Sah 1960
Type species. *Cannanoropollis janakii* Potonié & Sah, 1960.

Cannanoropollis densus (Lele) Bose & Maheshwari 1968, Pl. 4, fig. 2
Cannanoropollis janakii Potonié & Sah 1960, Pl. 4, fig. 3

Genus *Latusipollenites* Marques-Toigo 1974
Type species. *L. quadrisaccatus* Marques-Toigo 1974.

Latusipollenites quadrisaccatus Marques-Toigo 1974, Pl. 4, fig. 4

Previous records. This species is known mainly from the Pennsylvanian to Permian deposits of South America (Argentina, Brazil, Uruguay; see Gutiérrez et al., 2010; Beri et al., 2010).

Genus *Peppersites* Ravn 1979
Type species. *P. ellipticus* Ravn 1979.

Peppersites ellipticus Ravn 1979, Pl. 4, fig. 5

Previous records. Late Pennsylvanian of Brazil, USA, Saudi Arabia (see Playford and Dino, 2000a; Dino and Playford, 2002).

Genus *Plicatipollenites* Lele 1964
Type species. *Plicatipollenites indicus* Lele 1964 (= *Plicatipollenites malabarensis* (Potonié & Sah) Foster 1975).

Plicatipollenites malabarensis (Potonié & Sah) Foster 1975, Pl. 4, fig. 6
Plicatipollenites trigonalis Lele 1964, Pl. 4, fig. 7

Genus *Potonieisporites* (Bhardwaj) Bharadwaj 1964 a
Type species. *Potonieisporites novicus* Bhardwaj emend. Poort & Veld 1997.

Potonieisporites barrelis Tiwari 1965, Pl. 4, fig. 8

1997 *Caheniasaccites ellipticus* Maheshwari & Bose (*auct. non*), Ghavidel-syooki, p. 248, pl. 2, fig. 1.

Potonieisporites congoensis Bose & Maheshwari 1968, Pl. 4, fig. 9
Potonieisporites densus Maheshwari 1967, Pl. 4, fig. 10
Potonieisporites lelei Maheshwari 1967, Pl. 4, fig. 11
Potonieisporites magnus Lele & Karim 1971, Pl. 4, fig. 13
Potonieisporites marleniae Playford & Dino 2000 a, PL. 4, fig. 12
Potonieisporites neglectus Potonié & Lele 1961, Pl. 4, fig. 14
Potonieisporites novicus Bhardwaj emend. Poort & Veld 1997, Pl. 4, fig. 15

Infraturma STRIASACCITI Bharadwaj 1962

Genus *Crustaesporites* Leschik emend. Cousminer 1965
Type species*. C. globosus* Leschik 1956.

Crustaesaccites hessii Cousminer 1965, Pl. 5, fig. 3, 4

Genus *Mabuitasaccites Bose & Kar 1966*
Type species*. M. ovatus* Bose & Kar 1966.

Mabuitasaccites crucistriatus (Ybert) Playford & Dino 2000b, Pl. 5, fig. 2

Previous records. It is well- known from Cisuralian of Argentina, Brazil and Uruguay (see Souza et al., 2003; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Genus *Striomonosaccites* Bharadwaj 1962
Type species. *S. ovatus* Bharadwaj 1962.

Striomonosaccites cicatricosus Archangelsky & Gamerro 1979, Pl. 5, fig. 1

Previous records. Permian of Argentina, Brazil, Iran, Paraguay and Uruguay (see Ghavidel-syooki, 1997; Muff et al., 1999; Premaor et al., 2006; Gutiérrez et al., 2010; Beri et al., 2010).

Subturma DISACCITES Cookson 1947
Infraturma DISACCITRILETI Leschik emend. Potonié 1958

Genus *Alisporites* Daugherty emend. Jansonius 1971
Type species. *A.opii* Daugherty 1941.

Alisporites ovatus (Balme & Hennelly) Jansonius 1962, Pl. 5, fig. 5, 6

1965 ?Bisaccate indet. Cousminer, p. 1108, Pl. 129, fig. 12.
1979 *Alisporites splendens* (Lesckik) Foster, p. 73, pl. 25, figs. 9-10.
1991 *Scheuringipollenites ovatus* (Balme & Hennelly) Foster (*auct. non*), Backhouse, pl. 16, fig. 9.
1999 *Scheuringipollenites ovatus* (Balme & Hennelly) Foster (*auct. non*), Millsteed, pl. 12, figs. 2, 3.
2008 *Alisporites nuthallensis* Clarke, Stephenson, p. 170, pl. 5, figs. 7-9.
2010 *Falcisporites nuthallensis* (Clarke) Balme, Gutiérrez et al., p. 469, figs. 11L, 12A.

For further synonymy see MacRae (1988), Raine et al. (2006), and Gutiérrez et al. (2010).

Description. Pollen disaccate, sulcate. Haploxylonoid to slightly diploxilonoid. Amb oval to subrectangular. Corpus quite distinctive mostly vertically oval to rhomboidal. Cappa exoexine thin. Frequently the cappula is delimited by folds at the distal roots of the sacci, and inside a narrow leptoma (sulcus) is sometimes visible. Sacci crescentic to semi-circular in outline, the offlap is greater than the overlap.

Remarks. *Alisporites nuthallensis* Clarke 1965 is accepted here as junior synonym of this species considering both the synonymy list proposed by Foster (1979) for *Alisporites splendes* and MacRae´s (1988) for *Alisporites ovatus* (Balme & Hennelly) Jansonius. Hence, all the species listed above are here included in this taxon as they exhibit the same morphological characters of the present species. The specimen illustrated by Cousminer (1965) as Bisaccate indet. is badly preserved but very likely conspecific with this species. A third specimen illustrated as *Scheuringipollenites ovatus* (Balme & Hennelly) Foster by Millsteed (1999, pl. 12, fig. 1) is better assigned to *Scheuringipollenites medius* (Burjack) Dias-Fabricio. *Alisporites nuthallensis* Clarke illustrated by Souza and Marques-Toigo (2005, Fig. 3, b) is better assigned to *Pteruchipollenites gracilis* (Segroves) Foster 1979.

Previous records. Late Pennsylvanian?-Cisuralian to Triassic of Euramerica and Gondwana (see Foster, 1979; Doubinger and Marocco, 1981; MacRae, 1988; Lindström, 1996; Millsteed, 1999; Raine et al., 2006; Stephenson, 2008; Gutiérrez et al., 2010).

Genus *Chordasporites* Klaus 1960
Type species. *Chordasporites singulichorda* Klaus 1960.

Chordasporites endroedi MacRae 1988, Pl. 5, fig. 7

1979 *Chordasporites*? Sp. A in Foster, p. 78, pl. 26, figs. 9-12.
Remarks. The specimens described and illustrated by Foster (1979) are in agreement with the diagnosis of the present species.

Previous records. Pennsylvanian of Bolivia (di Pasquo, 2009) and Cisuralian of Argentina (see di Pasquo, 2009), Australia (Foster, 1979) and South Africa (MacRae, 1988).

Genus *Klausipollenites* Jansonius 1962
Type species. *K. schaubergeri* (Potonié & Klaus) Jansonius 1962

Klausipollenites sp. cf. *K. vestitus* Jansonius 1962, Pl. 5, fig. 8

Remarks and comparisons. The specimen recorded seems to be conspecific with the species, although it is left in comparison as it is not well preserved. Some specimens of *Vestigisporites ventrisaccatus* Anderson (1977, p. 92, pl. 83, figs. 6-13) are also similar to this species in having non-connected sacci smaller than the central body, with very slight intramarginal overlap. Instead, other specimens like the holotype defined by Anderson (1977, pl. 82, fig. 14) differ in having both sacci apparently interconnected.

Previous records. Lower Triassic of Canada (Jansonius, 1962).

Genus *Limitisporites* Leschik emend. Schaarschmidt 1963
Type species. *L. rectus* Leschik 1956.

Limitisporites sp. cf. *L. luandensis* Bose & Maheshwari 1968, Pl. 5, fig. 9

Remarks. This specimen is very similar, however due to its poor preservation distal sacci attachments comprising two well-defined longitudinal crescentic folds are not clearly seen. Hence, a more precise designation is prevented.
Previous records. *L. luandensis* is recorded in the Permian of Africa (Bose and Maheshwari, 1968) and Brazil (Longhim et al., 2003) and with doubts in Uruguay (Gutiérrez et al., 2010).

Genus *Pteruchipollenites* Couper 1958
Type species. *P. thomasii* Couper 1958.

Pteruchipollenites indarraensis (Segroves) Foster 1979, Pl. 5, figs. 10, 11

2005 *Alisporites nuthallensis* Clarke (*auct. non*), Souza & Marques-Toigo, pl. 3, fig. b.
2008 *Alisporites nuthallensis* Clarke (*auct. non*), Neregato et al., pl. 4, fig. H.

For description see Segroves (1969) and further synonymies see Foster (1979).

Comparison. *Alisporites nuthallensis* Clarke 1965 and *Alisporites splendens* (Leschik) Foster 1979 are here accepted as junior synonyms of *Alisporites ovatus* (Balme & Hennelly) Jansonius 1962. This species is distinguished from *Pteruchipollenites indarraensis* mainly due to the presence of the t-a oval central body amb, a smaller oval cappula (1-9 µm) with a sulcus (tenuitas), longitudinal folds associated to the distal roots of sacci, and its larger overall maximum size (see Foster, 1979).

Previous records. Cisuralian-Guadalupian of Australia, Africa, Brazil, Oman, Pakistan, Paraguay and Saudi Arabia (see Foster, 1979; Muff et al., 1999; Stephenson and Filatoff, 2000b; Stephenson and Osterloff, 2002; Stephenson et al., 2003; Souza and Callegari, 2004; Neregato et al., 2008).

Genus *Scheuringipollenites* Tiwari 1973
Type species. *S. maximus* (Hart) Tiwari 1973.

Scheuringipollenites circularis Césari, Archangelsky & Seoane 1995, Pl. 5, fig. 12
Previous records. Cisuralian of Argentina and Uruguay (see Gutiérrez et al., 2010; Beri et al., 2010).

Scheuringipollenites maximus (Hart) Tiwari 1973, Pl. 5, figs. 13, 14

Genus *Vitreisporites* Leschik emend Jansonius 1962
Type species. *Vitreisporites pallidus* (Reissinger) Nilsson 1958 (= *V. signatus* Leschik 1955).

Vitreisporites pallidus (Reissinger) Nilsson 1958, Pl. 5, fig. 15

Infraturma STRIATITI Pant 1954

Genus *Corisaccites* Venkatachala & Kar 1966
Type species. *Corisaccites alutas* Venkatachala & Kar 1966.

Corisaccites alutas Venkatachala & Kar 1966, Pl. 6, fig. 1

For description, synonymy and comments see Balme (1970), Playford and Dino (2000b), Stephenson (2008) and Gutiérrez et al. (2010).

Previous records. Wide geographic distribution in the Permian of Gondwana and Euramerica (see Balme, 1970; Lindström, 1996; Ghavidel-syooki, 1997; Playford and Dino, 2000b; Stephenson and Filatoff, 2000b; Stephenson and Osterloff, 2002; Stephenson et al., 2003; Diéguez and Barrón, 2005; Lindström and McLoughlin, 2007; Stephenson, 2008; Gutiérrez et al., 2010).

Genus *Hamiapollenites* Wilson emend. Tshudy & Kosanke 1966
Type species. *Hamiapollenites saccatus* Wilson 1962.

Hamiapollenites dettmannae Segroves 1969, Pl. 6, figs. 2, 3

For description, synonymy and comparisons see Playford and Dino (2000b as *H. andiraensis*) and Stephenson (2008).

Comparisons. A very similar specimen was illustrated as *Hamiapollenites* cf. *gabonensis* by Doubinger and Marocco (1981) from the Artinskian Copacabana Formation of Peru.

Previous records. Permian of Australia, Brazil, Iraq, Oman and Saudi Arabia (see Dino et al., 2002; Stephenson, 2008).

Hamiapollenites karrooensis (Hart) Hart 1964, Pl. 6, fig. 5, Pl. 9, figs. 5-7

For description, synonymy and comparisons see Playford and Dino (2000b) and Stephenson (2008).

Previous records. Permian of northern Gondwana (see Doubinger and Marocco, 1981; Ghavidel-syooki, 1997; Playford and Dino, 2000b; Dino et al., 2002; Souza and Marques-Toigo, 2005; Stephenson, 2008).

Genus *Lueckisporites* Potonié & Klaus emend. Klaus 1963
Type species. *Lueckisporites virkkiae* (Potonié & Klaus) Klaus 1963.

Lueckisporites nyakapendensis Hart 1960, Pl. 6, fig. 6

1996 *Lueckisporites latisaccus* Archangelsky & Gamerro (*auct. non*), Césari et al., p. 55, pl. 1, fig. 23.

2010 *Lueckisporites latisaccus* Archangelsky & Gamerro (*auct. non*), Gutiérrez et al., p. 510, fig. 14, A, C.

For further synonymy see Premaor et al. (2006, p. 226).

Remarks and comparisons. Considering the effect of harmomegathy explained by Foster (1979), we agree with the criteria and synonymy list proposed by Premaor et al. (2006) for this taxon. The specimens illustrated as *L. latisaccus* by Gutiérrez et al. (2010) show a subcircular to l-a ovally elongated central body that is not characteristic of this species and are reassigned to the present taxon.

Previous records. Permian of Africa (Hart, 1960; Millsteed, 1999), Argentina (Archangelsky and Gamerro, 1979; Césari et al., 1996), Brazil (Premaor et al., 2006; Neregato et al., 2008).

Lueckisporites singhii Balme 1970, Pl. 6, fig. 7

Previous records. Permian of Pakistan (Balme, 1970) and Saudi Arabia (Stephenson and Filatoff, 2000b) and Triassic of Israel (Eshet, 1990a, 1990b).

Lueckisporites virkkiae (Potonié & Klaus) Klaus 1963, Pl. 6, figs. 4, 8

Previous records. Late Permian of Africa, China, Europe, Iran, Oman and Saudi Arabia, Pakistan, and USA (see Balme, 1970; Ghavidel-syooki, 1997; Playford and Dino, 2000b; Stephenson and Filatoff, 2000b; Stephenson et al., 2003; Zhu et al., 2005), late Cisuralian to Late Permian of Argentina (see Césari and Gutiérrez, 2001), Brazil and Uruguay (see Playford and Dino, 2000b; Souza and Marques-Toigo, 2005; Premaor et al., 2006; Neregato et al., 2008; Gutiérrez et al., 2010; Mori and Souza, 2010) and Paraguay (Muff et al., 1999). Late Permian to Early Triassic of Antarctica (Lindström and McLoughlin, 2007), Spain (Diéguez and Barrón, 2005), and Israel (Eshet, 1990a, 1990b). Utting et al. (2004) noted the near global distribution of *Lueckisporites virkkiae* cited in approximately 350 localities in the Permian, whereas Triassic records account for approximately 30. The latter are mainly Lower, and less commonly Middle and Upper, Triassic occurrences that could also be reworked.

Genus *Lunatisporites* Lesckik emend. Scheuring 1970
Type species*.* *L. acutus* Leschik 1955.

Lunatisporites acutus Leschik 1955, Pl. 6, fig. 9
Lunatisporites noviaulensis (Leschik) Foster 1979, Pl. 6, fig. 10
Lunatisporites pellucidus (Goubin) Helby emend. de Jersey 1972, Pl. 6, fig. 11

Lunatisporites variesectus Archangelsky & Gamerro 1979, Pl. 6, figs. 12-14

1965 *Lueckisporites* ? sp. Cousminer, p. 1105, Pl. 129, figs. 1, 2.
1965 *Strotersporites apillapampaensis* Cousminer, p. 1105, pl. 129, figs. 4, 8, ?9, 10.

Remarks. The specimens illustrated by Cousminer (1965) show a diploxylonoid to slightly diploxilonoid amb with an ovally l-a central body, the cappa dissected by 6 or more striae some running the full length of the body, others incomplete. Hence, they are better assigned to *L. variesectus*, which is a frequent component of this microflora (see Table 1).

Previous records. Late Pennsylvanian to mostly Permian of Argentina, Brazil, Paraguay and Uruguay (see Muff et al., 1999; Souza and Marques-Toigo, 2005; Premaor et al., 2006; di Pasquo et al., 2010; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Genus *Protohaploxypinus* Samoilovich emend. Morbey 1975
Type species. *Protohaploxypinus latissimus* (Luber in Luber & Waltz) Samoilovich 1953.

Protohaploxypinus amplus (Balme & Hennelly) Hart 1964, Pl. 6, fig. 15

Protohaploxypinus haigii Foster 1979, Pl. 7, fig. 1

Previous records. Permian of Australia (Foster, 1979).

Protohaploxypinus samoilovichii (Jansonius) Hart 1964, Pl. 7, figs. 2, 4

1965 *Strotersporites apillapampaensis* Cousminer, p. 1105, pl. 129, figs. 5, 6 (holotype), 7.

Remarks. The holotype of *Strotersporites apillapampaensis* Cousminer is included in this taxon due to its similarity with *P. samoilovichii*, as having a slightly diploxylonoid amb, a slightly t-a oval central body, six to ten longitudinal ribs on the cappa, sacci semi-circular or greater than semi-circular, an offlap slightly greater than the onlap, and the distal zone is 1/3 or less l-a of the central body.

Previous records. Cisuralian of Brazil (Quadros et al., 1996; Mori and Souza, 2010), Permian to Early Triassic of Antarctica (Lindström and McLoughlin, 2007), Australia and Europe (see Foster, 1979) and Triassic of Canada (Jansonius, 1962).

Protohaploxypinus rugatus Segroves 1969, Pl. 7, figs. 3, 5

For synonymy see Gutiérrez et al. (2006).

Previous records. Permian of Australia (see Foster, 1979; Backhouse, 1991), Argentina, Brazil, Oman, Saudi Arabia and Uruguay (see Gutiérrez et al., 2006; di Pasquo et al., 2010; Beri et al., 2010) and Antarctica and West Papua (see Playford and Rigby, 2008).

Genus *Striatoabieites* Zoricheva & Sedova *ex* Sedova emend. Hart 1964
Type species. *S. bricki* Sedova 1956.

Striatoabieites multistriatus (Balme & Hennelly) Hart 1964, Pl. 7, fig. 6

1965 *Protosacculina* aff. *P. multistriatus* (Balme & Hennelly) Jansonius, Cousminer, p. 1106, Pl. 129, fig. 11.

For further synonymy see Foster (1979) and Millsteed (1999).

Genus *Striatopodocarpites* Zoricheva & Sedova *ex* Sedova emend. Hart 1964
Type species. *S. tojmensis* Sedova 1956.

Striatopodocarpites cancellatus (Balme & Hennelly) Hart 1965, Pl. 7, fig. 7
Striatopodocarpites solitus (Bharadwaj & Salhuja) Foster 1979, Pl. 7, fig. 8
Striatopodocarpites phaleratus (Balme & Hennelly) Hart 1964, Pl. 7, fig. 9

Previous records. Permian (Artinskian and younger) of Antarctica, Australia and India (see Foster, 1979; Lindström, 1996).

Infraturma CIRCUMSTRIATITI Lele & Makada 1972

Genus *Illinites* Kosanke emend. Azcuy, di Pasquo & Ampuero 2002
Type species. *I. unicus* Kosanke emend. Jansonius & Hills 1976

Illinites unicus Kosanke emend. Jansonius & Hills 1976, Pl. 7, fig. 10

2002 *Limitisporites rotundus* Stapleton (*auct. non*), Stephenson and Osterloff, p. 35, pl. 7, fig. 6.
1997 *Complexisporites polymorphus* Jizba, Ghavidel-syooki, p. 254, pl. 6, fig. 1, 12.

For description and further synonymy see Playford and Dino (2000b) and Azcuy et al. (2002).
Previous records. Pennsylvanian and Cisuralian of Euramerica and Gondwana (see Playford and Dino, 2000b; Azcuy et al., 2002; Dino and Playford, 2002; Souza and Callegari, 2004; Souza and Marques-Toigo, 2005; di Pasquo et al., 2010; Gutiérrez et al., 2010; Mori and Souza, 2010).

Subturma MONOCOLPATES Wodehouse emend. Iversen & Tröels-Smith 1950

Genus *Pakhapites* Hart 1965
Type species. *Pakhapites fasciolatus* (Balme & Hennelly) Hart 1965.

Remarks. In agreement with Menéndez (1971), García (1996) and Playford and Dino (2000b), and others, we accept that *Fusacolpites* Bose and Kar 1966 and *Striasulcites* Venkatachala and Kar 1968 are junior synonyms of *Pakhapites*. However, other authors have not agreed with this synonymy (Césari et al., 1995; Quadros et al., 1996; Gutiérrez and Césari, 2000; Césari and Gutiérrez, 2001), have maintained the genus *Fusacolpites* for *Pakhapites fusus* (Bose and Kar) Menéndez and *Pakhapites ovatus* (Bose and Kar) García.

Pakhapites fasciolatus (Balme & Hennelly) Hart 1965, Pl. 7, fig. 11

1965 *Vittatina* aff. *fasciolata* (Balme & Hennelly) Bharadwaj, Cousminer, p. 1106, Pl. 129, figs. 13, 14.

Previous records. Widely recorded from the Permian of Gondwana (see Souza and Marques-Toigo, 2005; Playford and Rigby, 2008; Beri et al., 2010).

Pakhapites fusus (Bose & Kar) Menéndez 1971, Pl. 8, fig. 1
For synonymy see Gutiérrez et al. (2006).

Previous records. From the Permian of Gondwana (see Ghavidel-syooki, 1997; Souza and Marques-Toigo, 2005; Vergel, 2008; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Pakhapites ovatus (Bose & Kar) García 1996, Pl. 8, fig. 2

Previous records. From the Permian of Gondwana (see Ghavidel-syooki, 1997; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Infraturma DIPTYCHES Naumova emend. Potonié 1958

Genus *Cycadopites* Wodehouse *ex* Wilson & Webster 1946
Type species. *C. follicularis* Wilson & Webster, 1946.

Cycadopites cymbatus (Bame & Hennelly) Hart 1965, Pl. 9, fig. 4

Comparisons. *Cycadopites follicularis* Wilson & Webster is similar but the exine is fairly smooth (see Balme, 1970).

Previous records. From the Permian of Gondwana (see MacRae, 1988; Lindström, 1996; Ghavidel-syooki, 1997; Playford and Dino, 2000b; Stephenson and Filatoff, 2000a; Playford and Rigby, 2008; Vergel, 2008).

Subturma PRAECOLPATES Potonié & Kremp 1954

Genus *Marsupipollenites* Balme & Hennelly emend. Balme 1970
Type species. *M. triradiatus* Balme & Hennelly 1956.

Marsupipollenites striatus (Balme & Hennelly) Hart 1965, Pl. 8, fig. 3

For synonymy see Gutiérrez et al. (2006).

Turma PLICATES Naumova emend. Potonié 1960

Subturma POLYPLICATES Erdtman 1952

Genus *Vittatina* Lüber *ex* Samoilovich emend. Wilson 1962
Type species. *V. subsaccata* Samoilovich 1953 (designated by Wilson 1962).

Vittatina corrugata Marques-Toigo 1974, Pl. 8, fig. 4

Previous records. Cisuralian of Brazil and Uruguay (see Souza and Marques-Toigo, 2005; Gutiérrez et al., 2010; Beri et al., 2010).

Vittatina costabilis Wilson 1962, Pl. 8, figs. 5, 6

For synonymy see Gutiérrez et al. (2006).

Previous records. Widely recorded from the Permian of the world (see Eshet, 1990a, 1990b; Ghavidel-syooki, 1997; Playford and Dino, 2000b; Stephenson and Filatoff, 2000a, 2000b; Souza and Callegari, 2004; Souza and Marques-Toigo, 2005; Zhu et al., 2005; Premaor et al., 2006; Gutiérrez et al., 2006, 2010; Vergel, 2008; di Pasquo et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Vittatina saccata (Hart) Playford & Dino 2000b, Pl. 8, figs. 7, 8

Previous records. From the Permian of Argentina, Brazil, Tanzania (see Playford and Dino, 2000b; Souza and Callegari, 2004; Souza and Marques-Toigo, 2005; Vergel, 2008; Mori and Souza, 2010; Beri et al., 2010).

Vittatina sp. cf. *V. simplex* Jansonius 1962, Pl. 8, fig. 13

Previous records. Permian of Canada (Jansonius, 1962).
Vittatina subsaccata Samoilovich 1953, Pl. 8, figs. 9, 10

1965 *Vittatina* aff. *fasciolata* (Balme & Hennelly) Bharadwaj, Cousminer, p. 1106, Pl. 129, figs. 15.

Remarks. The Cousminer (1965)'s specimen is reassigned to this species due to the presence of small sacci and less than 9 striae.

Previous records. From the Permian of Gondwana, China and Russia (see Ghavidel-syooki, 1997; Playford and Dino, 2000b; Stephenson and Filatoff, 2000a, 2000b; Souza and Marques-Toigo, 2005; Zhu et al., 2005; Vergel, 2008; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Vittatina vittifera (Luber &Waltz) Samoilovich 1953, Pl. 8, figs. 11, 12

Previous records. Permian of Brazil, Canada, China, Russia and Uruguay (see Playford and Dino, 2000b; Souza and Marques-Toigo, 2005; Zhu et al., 2005; Neregato et al., 2008; Beri et al., 2010).

Genus *Weylandites* Bharadwaj & Srivastava 1969
Type species. *W. lucifer* (Bharadwaj & Srivastava) Foster 1975.

Weylandites lucifer (Bharadwaj & Srivastava) Foster 1975, Pl. 9, figs. 1, 2

For synonymy see Foster (1979), Premaor et al. (2006) and Gutiérrez et al. (2006).

Previous records. Widely recorded in the Permian of Gondwana and Russia (see Foster, 1979; Lindström, 1996; Millsteed, 1999; Stephenson and Filatoff, 2000b; Gutiérrez et al., 2010). This species is frequent in the *Lueckisporites virkkiae* Zone in Brazil (see Souza and Marques-Toigo, 2005; Premaor et al., 2006; Neregato et al., 2008; Mori and Souza, 2010), Argentina (see Césari and Gutiérrez, 2001) and Uruguay (see Gutiérrez et al., 2010; Beri et al., 2010). Late Permian to Early Triassic of Antarctica (Lindström and McLoughlin, 2007).

Weylandites magmus (Bose & Kar) Bharadwaj & Dwivedi 1981, Pl. 9, fig. 3

For synonymy see Gutiérrez et al. (2006).

Previous records. Permian of Gondwana (see Lindström, 1996; Ghavidel-syooki, 1997; Backhouse, 1991; Lindström and McLoughlin, 2007; Gutiérrez et al., 2010; Beri et al., 2010).

Algae
Division CHLOROPHYTA
Class CHLOROPHYCEAE
Order CHLOROCOCCALES
Family: BOTRYOCOCCACEAE Wille 1909

Genus *Botryococcus* Kützing 1849
Type species. *B. braunii* Kützing 1849.

Botryococcus braunii Kützing 1849, Pl. 9, figs. 9-11, Pl. 10, fig. 9

Previous records. Widely recorded from the Middle Devonian to Quaternary of the fresh water to brackish environments of the world (see MacRae, 1988; Millsteed, 1999; di Pasquo et al., 2003a; Amenábar et al., 2006).

Class SYGNEMAPHYCEAE
Order ZYGNEMATALES
Family: ZYGNEMATACEAE Kützing 1898

Genus *Brazilea* Tiwari & Navale 1967
Type species. *B. punctata* Tiwari & Navale 1967.

For synonymy see Foster (1979) and Grenfell (1995).

Brazilea scissa (Balme & Hennelly) Foster 1975, Pl. 9, fig. 8

1970 *Schizosporis scissus* (Balme & Hennelly) Balme, p. 416, lám. 22, figs. 1-2.
1975 *Pilasporites calculus* Balme & Hennelly emend. Tiwari & Navale (*auct. non*), Ybert, p. 203, pl. 8, figs. 147-149.

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

Previous records. Widely recorded from the Pennsylvanian and/or Cisuralian of Gondwana (see Cousminer, 1965; Doubinger and Marocco, 1981; Backhouse, 1991; Lindström, 1995, 1996; Dino and Playford, 2002; di Pasquo et al., 2003a; Gutiérrez et al., 2006; Vergel, 2008; Mori and Souza, 2010; Beri et al., 2010) and Permian to Triassic of Canadá (Jansonius, 1962) and Pakistán (Balme, 1970) and Oman and Saudi Arabia (Stephenson and Filatoff, 2000b).

Genus *Tetraporina* Naumova *ex* Naumova emend. Lindgren 1980
Type species. *T. antiqua* Naumova 1950 (designated by Potonié, 1960, p. 130).

Tetraporina punctata (Tiwari & Navale) Kar & Bose 1976, Pl. 10, fig. 2

Previous records. Pennsylvanian of Argentina (see Gutiérrez et al., 2010) and Cisuralian of Africa, Argentina, Brazil and Australia (see Playford and Dino, 2000b; Longhim et al., 2003; Vergel, 2008; Gutiérrez et al., 2010; Mori and Souza, 2010; Beri et al., 2010).

Genus *Reduviasporonites* Wilson emend. Foster, Stephenson, Marshall, Logan & Greenwood 2002

For botanical affinity see Foster et al (2002), of algal affinity based on its geochemistry, and discussion in Mays et al. (2021).

Type species. *Reduviasporonites catenulatus* Wilson 1962.

Reduviasporonites chalastus (Foster) Elsik 1999, Pl. 10, figs. 1, 3, 4, 6, 7, 10

For description and synonymy and comparisons see see Foster et al. (2002).

Dimensions. Maximum length 260 µm of chains; maximum width 70 µm; discrete units maximum length 130 µm; maximum width 70 µm; minimum length 70 µm; minimum width 33 µm.

Remarks. After Foster et al. (2002) the size of the constituent cells present in *R. chalastus* appears to be related to paleolatitude, with large examples occurring in the paleotemperate Permian of China, Russia, Sverdrup and Australia, and smaller cells occurring in the paleotropical and paleoequatorial Permian of northern Australia, Saudi Arabia, United Kingdom and Austria. The maximum length 220 µm; maximum width 127 µm; minimum length 18 µm; minimum width 9 µm; mean length to width ratio 2.2 (230 specimens measured by Foster et al., 2002). This trend may indicate a paleoenvironmental control on the growth and development of the organism that produced *R. chalastus*.

Previous records. Foster et al. (2002) documented that this species occurs in Late Permian and Early Triassic

(Capitanian to Griesbachian) rocks spanning at least 10 m.y., and ranging beyond the Permian–Triassic boundary. Stephenson et al. (2003) registered this species in the Roadian to Capitanian of Oman and Saudi Arabia.

Group ACRITARCHA Evitt 1963

Genus *Deusilites* Hemer & Nygreen 1967
Type species. *D. tentus* Hemer & Nygreen 1967.

Deusilites tenuistriatus Gutiérrez, Césari & Archangelsky 1997, Pl. 10, fig. 8

For further synonymy see Gutiérrez et al. (1997) and Souza (1998).

Previous records. Pennsylvanian to Cisuralian of Argentina and Brazil (see di Pasquo et al., 2003a; Longhim et al., 2003; Souza and Callegari, 2004; Gutiérrez et al., 2006; Beri et al., 2010).

Acritarch undetermined, Pl. 10, fig. 5

Remarks. Only one specimen was recovered so it could not be designated.

Scolecodonts
Phylum ANNELIDA Lamarck 1809
Class POLYCHAETA Grube 1850
Order EUNICIDA Dales 1963

Genus *Menogenys* Jansonius and Craig 1971
Type species. *Leodicites summus* Eller 1942.

Menogenys sp., Pl. 10, figs. 11, 12

Comparisons. It is very close to *Menogenys curvus* Ottone 1988 from the Late Pennsylvanian-Cisuralian of Argentina, differing only in the form of the anterior part.

Scolecodont form A, Pl. 10, fig. 13

Comparisons. It is similar to *Nereigenys* sp. in García 1991 from the Late Pennsylvanian- Cisuralian of Argentina, although it differs in having a large hook on the anterior part and being dorsally more convex.

3 Approaches on paleogeography and paleoclimatology

Pangaea was in an advanced state of assembly in the Cisuralian, as the result of a number of Late Carboniferous collisions, including Gondwana and Laurussia (North America and Europe) along the equator, and Laurussia, Kazakhstania and Siberia in the northern hemisphere), with the exception of a number of independent south Asian microcontinents which existed along an equatorial Tethyan seaway (Vai, 2003). On the other hand**,** the Permian Period records a considerable climatic transition from a major glaciation during the early Cisuralian to a fully ice-free state since the Guadalupian. For example, Laurussia moved across the equator during the Late Paleozoic, and a succession of climates, arid-humid-arid, was recorded. At the same time continent size was increasing as a result of continental collision and marine regression (Ziegler, 1990). Ziegler et al. (1998) referred that the Pangea moved about 15° latitude to the North during the Permian, so that its southern portions rotated off the South Pole, while the northern portions approached the North Pole.

Thus, the major Permo-Carboniferous Gondwana glaciations disappeared (especially western Gondwana), while indications of local mountain glaciers appeared for example, in the Verkhoyansk and Omolon regions of the Russian northeast toward the end of the period. While the change in latitude probably triggered the deglaciation in Gondwana, portions of the supercontinent remained between 40° to 80°, a latitudinal range occupied by the earlier ice sheets (Vai, 2003). Hence, the latitudinal temperature gradient in the southern hemisphere decreased during the Early Permian, and mechanisms, such as the development of warm polar currents or increases in atmospheric carbon dioxide, are proposed to explain this climate shift (Ziegler et al., 1998). Changes observed in equatorial to subtropical regions during the Permian relate to the northward drift of Pangea rather than to any global change. Schefler et al. (2003) stated that the clockwise drift of the southern Gondwana continent shifted the Karoo Basin into polar cold regions and can be regarded as the primary trigger for glaciation processes. This mechanism is, however, insufficient to explain the cyclic climate variations as well as the terminal and abrupt breakdown of the ice shields. Warm currents along the eastern coast of Pangea (Kutzbach et al., 1990) transported moist air to Polar region. In combination with high albedo rates and low $p\mathrm{CO}_2$, icehouse conditions were established and glaciers started to accumulate in high latitudes. High temperature gradients between equatorial and polar region favored the development of a psychrosphere where deep ocean cold-water currents reached equatorial regions. Feedback mechanisms intensified the cooling rates and favored the fixation of water as glaciers on southern continents. This in turn caused a global fall in sea level. During regression phases, CO_2 fixing carbonate-complexes were exposed above sea level and carbonate weathering led to increasing $p\mathrm{CO}_2$. In concert with phases of enhanced tectonic activity (Stollhofen et al., 2000), elevated atmospheric CO_2 release initiated greenhouse conditions. Elevated temperatures established new air-ocean circulation pathways and possibly a retreat of the CO_2-fixing psychrosphere. Most importantly, the Pangean closure of the equatorial seaway (Saltzman, 2003) decoupled the evolution of the Panthalassian and Paleotethys Oceans. As a result of reduced equatorial to polar temperature gradients, glaciers retreated and sea level rose. The processes of CO_2 release and temperature increase, linked in a positive feedback, caused global warming. The final termination of the Carboniferous–Permian glaciation phase in southern Africa must be viewed to have resulted from the interaction of different climate-controlling factors, including variations in $p\mathrm{CO}_2$ values, the continent ocean configuration, and continental topography, as well as changing atmospheric and oceanic circulation pathways (Stollhofen et al., 2000).

As the solar system passes through one of the four galactic spiral arms, the cosmic ray flux increases, which may trigger global glaciation. The poor correlation between the cosmic ray flux maximum and the timing of the Pennsylvanian glaciation excludes this external forcing mechanism and underlines the need for further investigation (Schefler et al., 2003). Stephenson et al. (2007) found that in the early Cisuralian of Oman the sedimentary organic matter of the associated clastic rocks shows a decreasing $\delta^{13}C$ trend believed to reflect palaeoatmospheric change due to post-glacial global warming. Early Permian farfield isotope studies, compiled by other workers, from brachiopods from the southern Urals, show a $\delta\ ^{18}O$ decline of 2.5‰ in the Early Permian (Asselian to Artinskian) and stable $\delta^{13}C$ values of around +4.3‰ in the same period. This farfield evidence is in part consistent with palaeontological data since the most likely cause for the decline in $\delta^{18}O$ is the return of isotopically light waters to the oceans from melting of glaciers at high latitudes (Stephenson et al, 2007 and its references).

Korte et al. (2006) noticed that the Early Permian decrease in the strontium isotope curve commences in the early Sakmarian in coincidence with the advancing deglaciation of the Gondwana and with the increased aridity in large parts of the Pangaea. These factors may have led to a reduced continental weathering of Rb-rich silicate rocks, and thus to the decline in seawater $^{87}Sr/^{86}Sr$. The opening of the Neotethys in the Artinskian, and the associated widespread basaltic volcanism supplied low radiogenic strontium to seawater from an enhanced hydrothermal flux. In the Capitanian, basaltic volcanism in the entire Palaeotethys ceased and this may have been the reason for a slightly more radiogenic seawater isotopic composition during the Lopingian. Higher input of riverine Sr due to expansion of humid areas may have been a contributory factor.

The Permo - Carboniferous glaciation on Gondwana culminated in the Asselian and early Sakmarian (Frakes et al., 1992; Fielding et al., 2008) with glaciers covering large parts of the late Palaeozoic Southern Hemisphere continents. Tillites were documented in Antarctica, South America, South Africa, Western Australia, India and Pakistan (e.g., Isbell et al., 2003; López-Gamundí and Buatois, 2010). For the Australian continent, it was shown that glaciers waned and vanished by the late Sakmarian. The same Asselian and early Sakmarian time span was also characterised by a comparatively higher worldwide humidity, with coals close to and immediately above the glacial deposits in Gondwana (e.g., India) and with moderately wet climate prevailing in the Euramerican province. In contrast, the Artinskian–Late Permian interval was dominated mostly by dry climate across the entire Euramerican province (Red Beds), but in the Gondwana both coals and red beds were deposited. Overall, therefore, the climate became progressively more arid (e.g., "White Band" of South Africa; de Wit et al., 2007) particularly during the Artinskian and Kungurian, and aridity persisted throughout the Capitanian and most of the Lopingian. This is documented by Red Beds and salt deposits, including potash salts, in the Euramerian Province of North America (Delaware Basin and surroundings), Europe (Zechstein Basin), North Africa, and western margin of the Angaride province (Kungurian salt deposits of the Fore-Urals). Red Beds occur also in the Middle and Late Permian of parts of Gondwana (Rio do Rasto Formation of the Paraná Basin in South America). Only the latest Permian witnessed again more humid conditions. Nevertheless, parts of Gondwana, Angara and Cathaysia remained humid during all this time, as indicated by the large Middle-Late Permian coal deposits in Australia, India and South Africa (Ziegler, 1990).

3.1 Bolivia

The Titicaca Group of Bolivia reflects the significant displacement experienced by Gondwana during the Carboniferous. During this time, the area pertaining to Bolivia went from high latitudes (sub-polar) during the Late Devonian, to low latitudes (tropical), starting at the Late Carboniferous and Permian (e.g., Díaz et al., 1993; Isaacson and Díaz-Martínez, 1995; Iannuzzi and Rösler, 2000; Grader et al., 2008). Grader et al. (2000, 2008) analyzed geological and palaeontological information of the Titicaca Group to conclude that the Western Gondwana underwent a steady drift from mid-latitudes (~50°S, Early Carboniferous) to lower latitudes (<40°S) by Late Carboniferous time. Further, Iannuzzi and Pfefferkorn (2002) highlighted through sedimentary sequences and the floral record that during this period the entire Gondwanan continent experienced a large clockwise rotation in which the western Gondwana (South America and Africa) moved from higher to lower latitudes while the eastern Gondwana (Australia, India, Antarctica) was moving from lower to higher latitudes simultaneously.

The glacial deposition ended in Bolivia by the Early Pennsylvanian (Morrowan). During the rest of the Pennsylvanian and the Permian, the Titicaca Group represented an Andean transgressive marine to restricted carbonate platform and regressive red bed megasequence across the Peru-Bolivia Basin (di Pasquo et al., 2019). This transgressive-regressive Cisuralian marine shale/carbonate and transitional heterolithic succession was deposited in a sub-basin unaffected by direct ice-proximal sedimentation during glaciation/ deglaciation of the Gondwana Glacial III ice age (Grader et al., 2008). Palynology of the Tarabuco/ Santa Rosa Formation below the Titicaca Group at Apillapampa defines a major hiatus between Silurian-Early Devonian and Early Permian strata (e.g., Limachi et al., 1996; di Pasquo et al., 2009). Permo-Carboniferous uplands, basin inversion, and near-field seaway carbonate sedimentation occurred in concert with ice-proximal deposition and climate change in the Peru-Bolivia Basin (Grader et al., 2008; di Pasquo, 2009) and Argentinean Tarija Basin (di Pasquo, 2003). Stratigraphic data show evidence of Early Permian 2nd-order transgression and regression with 3rd-order subtidal sequences in a Gondwana back-arc environment (Grader et al., 2003, 2008). About 1 Ma Asselian Copacabana shale/carbonate sequences with turbidite facies reflect a partitioned basin inversion, near-field climate change, and glacioeustasy proximal to "coeval" South American glacigene depocenters. Steady early Sakmarian basin restriction and transition to the heterolithic Coal Member (*sensu* Chamot, 1965) culminates in a sequence boundary zone with plant-bearing lagoonal carbonaceous shale and paleosols. These facies and transitional mudstones, lagoonal carbonates, and lithic sandstones of the Coal Member reflect regional relative sea level fall and the end of open marine sedimentation. Second-order regression may occur in conjunction with mid Sakmarian deglaciation and global sea level rise near the end of Glacial III/Australian P1 ice ages (Isbell et al., 2003). Although the entire Coal Member may eventually be recognized as mostly Sakmarian, it should be noted that marine carbonates equivalent to units below the Coal Member both to the northeast and southwest occur with corresponding *Eoparafusulina* sp. and the *Frontinodosaria-Robuloides* foraminifera assemblage previously identified as Artinskian (Mamet and Pinard, 1998). This will require further analysis for a better resolution (cf. Cisterna et al., 2022).

As discussed herein, Pennsylvanian – Cisuralian warm sedimentation in the Peru-Bolivia Basin occurred "coevally" with glacigenic deposits in the Tarija and Paraná basins to the south and east, but dissimilar biostratigraphic schemes and divergent correlation schemes still do not offer a good resolution of late Paleozoic geohistory. Mississippian through Permian cold water siliciclastic sedimentation (Ambo, Macharetí, Mandiyutí groups) and warm water Pennsylvanian–Permian carbonate sequences (Titicaca and Cuevo groups) occurred in relative proximity to mid-latitude ice centers. Accumulation of glacigenic sediments in southeastern Bolivia, and fossiliferous carbonates in central and northern Bolivia probably occurred in divided subbasins and seaways during staggered glacial/interglacial climate switching. Third-order carbonate sedimentation may have been encouraged by warmer currents and climate, but may also have been retarded by regional cold/warm cycles in siliciclastic denudation and transport. Earth's climates warmed in the early Sakmarian following glaciation (e.g. Isbell et al., 2003; Montañez et al., 2007; Stephenson et al., 2007, 2008), and they continued during the Artinskian, since it contains fusulinids in paleotropical regions including Bolivia. Pangea moved steadily northward about 0° of latitude between the Asselian and the Middle Permian (Ziegler et al., 1998), so the movement during the rapid deposition of the Copacabana Formation itself was likely very small. Hence, temperature increase due to combined post glacial warming and northward movement yielded a combination of increasing aridity and warming. New data show that volcaniclastics, sandy carbonates, silicified mudstones of the Chutani Formation overlie the Coal Member. Accommodation of these upper Permian rocks across Bolivia (beginning in the late Cisuralian?) suggests a return to restricted marine environments in lower latitudes, during onset of proximal volcanism (see di Pasquo et al., 2019). Though post-glacial global warming and northward movement of Gondwana may have contributed to temperature increase, aridity was also likely caused by the onset of Permian monsoons with dominant offshore winds and the influence of rift shoulders to the east and south (cf. Scotese et al., 2021).

4 Provincialism

Great floral realms of the Permian were subequal in extent and comprised the south temperate Gondwanan Realm of central Gondwana, the tropical Cathaysian - Euramerican Realms of equatorial Gondwana, Laurussia, and the south Asian microcontinents, and the north temperate Angaran Realm of Siberia and Kazakhstan (Ziegler, 1990; Figure 1). Ziegler (1990) indicated the existence two tropical realms, the Euramerican and the Cathaysian. The former was characterized by seasonal tropical climates. The gymnosperms were major components of Euramerican floras (Scott, 1980), and these plants are known to have been associated with seasonally dry climates. The Euramerican floras covered most of the USA, Europe, and western Russia, and similar floras occurred on the Gondwanan part of Pangaea in Saudi Arabia and Sibumasu. The Euramerican Realm was extensive during the Sakmarian but contracted dramatically by the Kazanian (e.g., Utting and Piazecki, 1995).

These realms became distinct in the Carboniferous as a result of increasing equator-to-pole temperature gradients, and the major barriers to floral interchange were the two great subtropical deserts. The southern desert may have extended across Gondwana and is represented by evaporites in Brazil and Arabia, and the northern desert is known from the evaporites of the western United States and northern Europe. Ziegler (1990) considered that true geographic barriers to floral migrations, such as wide seaways, evidently did not play a major role in floral provinciality as there seems to be just one realm per broad latitudinal zone. Moreover, the major floral discontinuities in the Permian, like the Recent, are affected by the subtropical deserts and these separate three major realms, the tropical Cathaysian Realm from both the north temperate Angaran Realm and the south temperate Gondwanan Realm. Boundary areas like Siberia and Kazakhstan, and to a lesser extent the northern rim of Gondwana may repeatedly change provincial affinity.

Wnuk (1996) stated that there are two tropical to sub-tropical Realms: Euramerica including the USA, Europe, North Africa, northern South America, Ukraine, Georgia, and parts of Kazakhstan; Cathaysia was scattered across the various micro-continents of South China, Indochina, Sino-Korea, Tarim, and Sibumasu. More recently, Zhou et al. (2005) presented a comparison of Permian palynological assemblages from Junggar and Tarim Basins being the former part of the Angaran realm (Subangara area) during the Cisuralian whereas the latter is related to the Euramerican realm mixed with Angaran floras especially from the Artinskian. Climates within these provinces are presumed to have been uniform and equable. The absence of growth rings in petrified Euramerican woods indicates a climate without marked seasonality. The newly formed mountain chains altered atmospheric circulation patterns (Rowley et al., 1985) and, from observed changes in major vegetation types from wetland communities to the mesophytes and xerophytes earlier associated with the uplands, atmospheric humidity. Considering the plant record during this interval, in Europe at least, interpretation of data from the late Stephanian and Early Permian are complicated by imprecise correlation between small basins, stratigraphic hiatuses, and facies biases of certain taxa. During the Stephanian however, the conifers became more abundant and callipterid pteridosperms diversified. These trends continued into the Rotliegend (Cisuralian) with increasing numbers of plants adapted to drier conditions, although peat-forming communities still persisted and dominate concepts of Lower Rotliegend vegetation (e.g., Utting and Piasecki, 1995). In contrast, in the Late Permian Zechstein, meso- and xerophilous vegetation types dominated, marked by a proliferation of gymnosperms (particularly conifers and to a lesser extent pteridosperms), with adaptations typical of a warm and dry climate. Such differences in assemblages have led to the concept of a Palaeophytic-Mesophytic boundary within the Permian (e.g., di Michele et al., 2008), which might be related to the cessation of glaciations in Gondwana (Kerp, 1996).

4.1 Gondwana

The Gondwanan Realm (as defined by the occurrence of a diverse cool to cold temperate glossopterid flora) can be divided into a number of biomes composed of plant associations that have developed in response to regional environmental/ climatic controls. For example, the *Glossopteris* Biome occurs in cool temperate latitudes and is characterized by a very diverse *Glossopteris* dominated flora. The subjacent *Gangamopteris* Biome occupies cold temperate latitudes. It is also characterized by the occurrence of abundant glossopterids, but the *Gangamopteris* Biome floras are much less diverse and are dominated by different taxa than the floras of the *Glossopteris* Biome (Ziegler, 1990).

Occurrences of the southern warm temperate province designated by Wnuk (1996) as the Austroafroamerican Region were scattered across the Gondwanan landmass. During the Sakmarian, these cool temperate floras, i.e. the traditional *Glossopteris* floras, were found in India, Madagascar, Argentina and Antarctica (Ziegler, 1990). The continued persistence of continental glaciers at this time significantly disrupted the geographic continuity of this floral zone. Different ages of glacial deposits in South America were consequences of tectonic and climatic factors. The latter were controlled by orbital forcing that triggered the major global changes. The timing of these changes is not completely correlated to Milankovitch periodicities or intervals (Izart et al., 2003).

The northward drift of South America and Arabia in this period (Torsvik and Cocks, 2004) brought about a more abrupt postglacial change than that experienced in higher latitude Gondwana areas (Stephenson et al., 2008), where cool, wet coal-forming environments directly after deglaciation developed (Isbell et al., 2003). The relatively low palaeolatitude northern Brazilian Solimões, Amazonas and Parnaíba basins experienced very little glacial activity, with Carboniferous–Permian rocks being characterized by aeolian sandstones and evaporites (Milani and Zalán, 1999). The Oman Basin, which during the Sakmarian was positioned at a latitude approximately halfway between the northern Brazilian (~20°S) and the southwestern Australian basins (~60°S; Ziegler et al., 1998), illustrates characteristics between these two extremes. In northern to central Bolivia, the Pennsylvanian palynofloras reflected changes from a probably related to uplands glacial monosaccate pollen-producing flora (Cordaitales and Coniferales) into a warmer climate bisaccate striate pollen-producing flora (Pteridosperms) and lowlands generally associated with pteridophytes and cordaitaleans (di Pasquo, 2009).

During the early Cisuralian, in the terrestrial lowlands, a parallel change occurred from a glacial fern flora to a warmer climate colpate pollen-producing and lycopsid lowland flora. As a contrast, warm temperate floras were found in New Guinea (or West Papua), and Brazil (Wnuk, 1996). The southern warm temperate floras are sometimes called "mixed floras" and are distinctive because they contained arborescent lycopods or tree ferns mixed with glossopterid floral elements (Lacey, 1975; Ziegler, 1990).

The parent plant composition of palynological assemblages in the Lower Member of the Copacabana Formation is dominated by varied gymnosperm groups with some algae and minor, yet significant contributions from lower vascular plants, notably pteridophytes, sphenophylls and lycopods. Taeniate-striate pollen grains are increasingly prominent in the basal samples with lower vascular plants especially pteridophytes and lycophytes becaming dominant in the overlying Coal Member (Table 1). The palynofacies and sedimentological analysis presented by di Pasquo and Grader (2012) suggest that Lycophytes, Pteridophytes and Sphenophytes probably together with Cordaitales and some Coniferales would have occupied more humid restricted areas of swamps or mangrove-like, lakes and rivers near the Copacabana`s sea. However, the Pteridospermaphyta, probably represented by Glossopteridales, and also Corystospermaceae and Peltaspermaceae, bearing mainly striate pollen grains, indicate relatively low humidity or seasonally arid conditions. These groups of plants prevailed in open lowlands along seaway margins under a paleotemperate climate during the early Cisuralian and, despite the macroremains of glossopterids not occurring at Apillapampa, the presence of these pollen grains confirms the widespread distribution of the *Glossopteris* flora during the Permian in Gondwanaland. Among the megafossils, the remanents of seed-producing plants are quite scarce in this section, corresponding to small fragments of leaves tentatively assigned to *Psigmophyllum* (?) sp. and *Cordaites* (?) sp. (in Iannuzzi et al., 2008). Additional collections are necessary.

Analysis of the geographic distribution of Bolivian taxa (di Pasquo and Grader, 2012), shows that in the Apillapampa palynoflora species from Gondwana (Figure 2A and Table 1) and particularly from South America (Figure 2B) are dominant, several species are also recorded in Cathaysia, Angara and Euramerica realms (Figure 2A). Those from South America are *Convolutispora ordonensis*, *Cristatisporites morungavensis*, *Leschikisporis chacoparanaensis*, *Thymospora* *criciumensis*, *Mabuitasaccites crucistriatus*, *Scheuringipollenites circularis*, *Lunatisporites variesectus*, *Vittatina corrugata*, while others are only present in Africa (*Didecitriletes eoericianus*, *Cirratriradites africanensis*) or in both continents (*Convolutispora uruguaiensis*, *Thymospora rugulosa*, *Polypodiites secoensis*, *Limitisporites luandensis*, *Lueckisporites nyakapendensis*, *Vittatina saccata*). *Striomonosaccites cicatricosus* has been recorded in South America and Iran (Ghavidel-syooki, 1997).

Outside South America, *Lueckisporites singhii* is the single species known only from the Arabian Plate and related areas, *Gondisporites imbricatus* and *Protohaploxypinus haigii* from Australia and related areas while *Striatopodocarpites phaleratus* is registered in Australia and India. Few species remain endemic in Bolivia (e.g., *Crustaesporites hessi* and *Punctatisporites minutiarcus*, *Dictyotriletes cousmineri*) and 52 species are recorded for the first time in this country. The remaining species occur in Gondwana or they are cosmopolitan (Figure 2 and Table 1).

Therefore, the presence of numerous cosmopolitan species with others found in Cathaysia (e.g., *Striatosporites heyleri*), Angara (e.g., *Vittatina subsaccata*, *Weylandites lucifer*) and Euramerica (e.g., *Klausipollenites vestitus*, *Vittatina simplex*) realms allow the inclusion of the Apillapampa assemblages in the category of "mixed floras". As stated by several authors (e.g., Lacey, 1975; Ziegler, 1990; Broutin et al., 1995), these floras are mainly recognized around the Paleoequator extended between subtropical southern and northern latitudes (Figure 1). Although, intermingling of floras are recorded along boundaries of the floral realms (Lacey, 1975; Broutin et al., 1990).

4.2 Floral Migration and Diachroneity

Bolivia during the Permian (earliest Cisuralian) received migrating plants, as well as sent plants to new territories in Pangea. Our information herein demonstrates this (di Pasquo and Grader, 2012). Wnuk (1996) remarked that the general cool to cold temperate Gondwanan flora is the realm that shows potentially the greatest range of climatic variation, especially the low-latitude peri-Gondwanan areas, which are generally intermingled with some northern floras, and thus, called "mixed-floras." These climatic differences inside Gondwana are related to the floral/palynofloral dissimilarities between northern and southern regions (Utting and Piasecki, 1995). Ziegler (1990) discussed the confusion that results when a region moved from low to higher latitudes. Some floras changed in response to climate by migration rather than evolution. The migration of floras controlled by the northward movement of the South American plate towards the equator during the Carboniferous was shown by Iannuzzi and Rösler (2000). In this case, three distinct floras adapted to cold, warm temperate and tropical climatic conditions respectively. They were dislocated as the continent moved into different climatic zones during this period.

In this context, plant migrations are accelerated by local paleoenvironmental changes triggered mainly by global paleoclimatic changes (glacial and interglacial conditions). Tectonics and eustasy were other factors also, but they may have had a more local influence. These migrations would produce intermittent appearances and re-appearances of taxa in such a region (equivalent to cyclicity of paleoenvironmental conditions), or simply appearance and disappearance from it (e.g., suitable conditions for plants changed and they could not return nor readapt to the area). An explanation for such diachronous appearances of species was addressed by Meyen (1977), who suggested that the majority of shared species of mixed floras are attributed to parallel evolution in the absence of megafloral evidence (e.g., fructifications). On the other hand, Foster et al. (1994) noted that sporomorph assemblages from quite different paleobotanical provinces would appear more taxonomically similar than would be expected from the megafossil records from the same areas. Meyen (1977) also suggested that there was probable parallel evolution of sporomorphs in different groups of plants. Foster et al. (1994) observed, however, that detailed study of at least some of the superficially identical sporomorph taxa showed that they actually could be distinguished. Although, it is true that spores and pollen are not easily separated below the level of genera of whole plants. An example of this is the appearance of *Lueckisporites-Scuttasporites* group in the Carboniferous – Permian boundary in Kazakhstan (Dunn, 2001). The specimens illustrated from this morphologic group show resemblance to *Lueckisporites stenotaeniatus* recorded in the middle-late Cisuralian in Argentina, Brazil and Uruguay (Gutiérrez et al., 2010), although this species is more diploxylonoid with larger sacci. Stephenson et al. (2008) recorded during the late Sakmarian (Early Permian) Haushi limestone of Oman and Saudi Arabia, moderately diverse palynofloras with bitaeniate pollen *Corisaccites alutas* and other bisaccates together with colpate pollen *K. subcircularis* and acritarchs. The overall dominance of bisaccate gymnosperm pollen, rarity of fern spores, as well as the upward increase of *K. subcircularis* and *C. alutas* therefore suggest~~s~~ a dry climate for the terrestrial hinterland of the Haushi Sea. The thick exine of *Corisaccites alutas* is likely to be a protection against dry conditions reinforced by its association with plants of likely xerophytic aspect that probably grew in arid conditions. This taxon is also known to be common from unequivocally arid settings in the overlying middle Gharif Member (Stephenson, 2008). Hence, the interpretation of convergence (parallelism) proposed by Meyen (1977) to explain the appearance of similar plant groups and/or dispersed palynomorphs in quite separated regions such as Gondwana and Angara realms, could also be explained by means of migration and evolution during the Permian (*cf.* Huntley, 1991). As discussed by di Pasquo et al. (2015), the first appearances of selected taxa like the cosmopolitan *Lueckisporites virkkiae* that originated earlier in the mid Asselian of Bolivia and from there it was dispersed through Gondwana during the Cisuralian to the North Hemisphere during the Guadalupian and Lopingian.

Early Pennsylvanian (Moscovian) appearance of striate pollen grains was reported by di Pasquo (2009) from the Copacabana Formation from the Pando X-1 borehole in northern Bolivia (e.g., *Protohaploxypinus varius*, *Striatopodocarpites antiquus, S. gondwanensis, S. solitus*), and especially scarce undetermined species of *Vittatina* came in Bolivia (di Pasquo, 2009). Other records of this genus (di Pasquo, 2009) were reported from the latest Pennsylvanian of the Chacoparaná Basin in Argentina (Archangelsky and Vergel, 1996), the Kasimovian of the Donetz Basin (Inossova et al. in Utting et al., 2004), the Moscovian (Westphalian D) of Arabia (Owens and Turner, 1995), the early Moscovian (Westphalian C) marine strata in northeastern Greenland (Thomsen, 1999), subsurface deposits of Moscovian–Kasimovian (Westphalian C–D and Stephanian) age dated with macroflora in the German North Sea (Josten, 1995; Lund, 2001) and below the Carboniferous– Permian boundary stratotype at Aidaralash creek in

Kazakhstan (Dunn, 2001). Hence, these quite geographically dispersed records reflect parallel evolution probably related to different Pteridospermaphyta more than migration of same parent plant (Figure 1; *cf*. Meyen, 1977).

Hence, it should be noted as a caution here that paleobotanical provinces based on megafossil plants and data from paleopalynology are sometimes difficult to integrate. The above reasons help to explain such diachronism in the stratigraphic range of taxa among different regions globally (cf. di Pasquo et al., 2015, their supplementary online material), and this is very important at the time to strengthen or establish long distance correlations without other information (i.e., radiometric data, other fossils). So, more information we have, better possibilities of reliable correlations and definition of centers of dispersion of taxa may be established. The information provided by di Pasquo and Grader (2012) allowed di Pasquo et al. (2015) to propose the possible dispersion of some taxa from Apillapampa, based on their previous records in South America and globally. The mentioned information shows that *L. virkkiae* is appearing in different moments during the mid-Asselian and the mid Artinskian in South America, South Africa, Pakistan, Australia and India whereas later in other regions. So, it is a very useful key taxa but with local importance. Other diachronous appearances involve selected taxa such as *Corisaccites alutas* (and similar species), *Lunatisporites*, *Hamiapollenites karroensis*, *H. dettmanae*, and *Polypodiisporites mutabilis* (see di Pasquo et al., 2015). Several species (discarding some uncertain taxonomic assignments) in the Apillapampa section are radiometrically dated, and they show older appearances than their known stratigraphic record (e.g., *Protohaploxypinus haigii, Striatopodocarpites phaleratus, Lueckisporites nyakapendensis, L. virkkiae, L. singhii, Lunatisporites noviaulensis, L. acutus, L. pellucidus, Reduviasporonites chalastus*).

Broutin et al. (1995) referred to the increasing proportion of taeniate-striate and non-taeniate pollen grains in the microfloras of the Arabian Peninsula from the Asselian-Sakmarian to the Artinskian that showed paleoclimatologic amelioration. In the Apillapampa section this trend occurs in the lower member. In the Coal Member of the Copacabana Formation an increase in abundance of spores of pteridophytes and lycophytes occurs. This change documents a warmer and more humid climate during the Sakmarian.

Another interesting case of migration is recognized from the analysis of the stratigraphic record of *Polypodiisporites mutabilis* present in Apillapampa, as it was recorded in the Cisuralian of South America (Mautino et al., 1998a; Gutiérrez et al., 2010; di Pasquo and Grader, 2012) and Israel (Eshet, 1990a, 1990b); the Late Permian of Pakistan (Balme, 1970), South Africa (Anderson, 1977) and the Early Triassic of Antarctica (Lindström and McLoughlin, 2007). This fern required temperate and humid conditions and migrated, looking for these favorable conditions through time around Gondwana. Another case is *Lycospora pusilla* that represents the arborescent group of Lepidodendrales (Lycophyta) generally associated with swamp areas forming coal deposits and thus, widely distributed from the Carboniferous to the Cisuralian in Euramerica and northern Gondwana (Somers, 1972; Stephenson and Filatoff, 2000a). In Bolivia a very morphologically similar *Lycospora variabila* occurs (Table 1).

Continued northward drift of Pangaea involved Stephanian-Cisuralian wrench faulting, which produced a number of intramontane basins across the former hinterland and caused fragmentation of the wetland zone (Grader et al., 2008). Changes in topography and drainage again drastically reduced the number of habitats available to the mire plants and particularly the arborescent lycopods that comprise the most conservative of communities, and associated changes in sedimentation patterns produced new edaphic conditions, e.g. an increase in the production of sandy soils.

The Pteridospermaphyta represented by Glossopteridales, Corystospermaceae, and Peltaspermaceae bearing mainly striate pollen grains (Table 1) indicates relatively low humidity or seasonally arid conditions. This open lowland vegetation would have prevailed in a paleotemperate climate during the Cisuralian in Bolivia. However, the presence of few species of disaccate striate pollen grains in the Pennsylvanian Copacabana Formation in the Pando X- Borehole (northern Bolivia) as mentioned above (e.g., *Vittatina*) was explained by di Pasquo (2009) as a consequence of climatic and paleogeographic changes produced by northern movement or rotation of Gondwana during the Late Pennsylvanian to the Cisuralian (Figure 1). Hence, more or less coeval Pennsylvanian assemblages in Peru and northern Bolivia, containing scarce to moderately frequent striate pollen grains imply seasonally drier climates close to the Copacabana`s sea. Mostly striate pollen-barren assemblages in northern Argentina and southern Bolivia developed under more humid conditions (di Pasquo, 2003, 2009). During the Permian, the ever-present striate taxa attest to seasonally warmer climates, supporting both northward rotation of Gondwana into lower paleolatitudes and expanding diversification trends of Copacabana invertebrates (Grader, 2003). The mixed character of the faunas and floras of the Central Andes suggest the influence of cold waters from the Gondwanan environments and the warmer currents connected to tropical to equatorial environments in North America and elsewhere in Europe and northern Africa (Newell et al., 1953; Iannuzzi and Rösler, 2000; Scotese, 2003, 2013).

Another interesting species is *Reduviasporonites chalastus,* whose constituent cell size indicates a paleoenvironmental control on its growth and development of the organism related to paleolatitude. di Pasquo and Grader (2012) published the size of this taxon (i.e. maximum length 260 µm of chains; maximum width 70 µm; discrete units maximum length 130 µm; maximum width 70 µm; minimum length 70 µm; minimum width 33 µm), and compared this trend with large examples (maximum length 220 µm; maximum width 127 µm; minimum length 18 µm; minimum width 9 µm; mean length to width ratio 2.2 on 230 specimens measured by Foster et al., 2002) occurred in the paleotemperate Permian of China, Russia, Sverdrup Basin and Australia, whereas smaller cells appeared in the paleotropical and paleoequatorial Permian of northern Australia, Saudi Arabia, United Kingdom and Austria. Considering the large size of the cells recovered in Apillapampa, di Pasquo and Grader (2012) interpreted this assemblage occurred in a subtropical paleotemperate climate. This is in agreement with the above comments and paleogeographic and paleoclimatic reconstructions presented by Scotese et al. (1999) and Scotese (2003, 2013) and Boucot et al. (2013) (see Figure 1).

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Plate 1. The scale bar represents 10 µm.

1. *Calamospora liquida* Kosanke, MP-P-6027-c, U38/1. 2. *Calamospora microrugosa* (Ibrahim) Schopf, Wilson & Bentall, MP-P-6032-b, T40. 3. *Waltzispora* sp., MP-P-6032-b, N39. 4. *Punctatisporites minutiarcus* Cousminer, MP-P-6027-b, Q65/3. 5. *Retusotriletes nigritellus* (Lüber) Foster, MP-P6026-a, M46. 6. *Brevitriletes cornutus* (Balme & Hennelly) Backhouse, MP-P6032-d, Q47/3. 7. *Horriditriletes ramosus* (Balme & Hennelly) Bharadwaj & Salujha, MP-P-6032-b, V39/2. 8. *Didecitriletes eoericianus* (Anderson) Millsteed, MP-P6026-a, U41/1. 9. *Didecitriletes* sp. MP-P6029-c, N38/1. 10. *Convolutispora ordonensis* Archangelsky & Gamerro, MP-P-6033-a, K41/1. 11. *Convolutispora uruguaiensis* Mautino, Vergel & Anzótegui, MP-P-6031-b, K49. 12. *Iraquispora* sp., CICYTTP-Pl 2 (+25), O37/3. 13-16. *Dictyotriletes cousmineri* di Pasquo & Grader, Fig. 13, holotype (proximal face), Fig. 14 (distal face), CICYTTP-Pl 3 (+10), Q28/4. Fig. 15, CICYTTP-Pl 3 (+10), R27/1. Fig. 16 (fluorescence light), CICYTTP-Pl 3 (+10), V62/2.

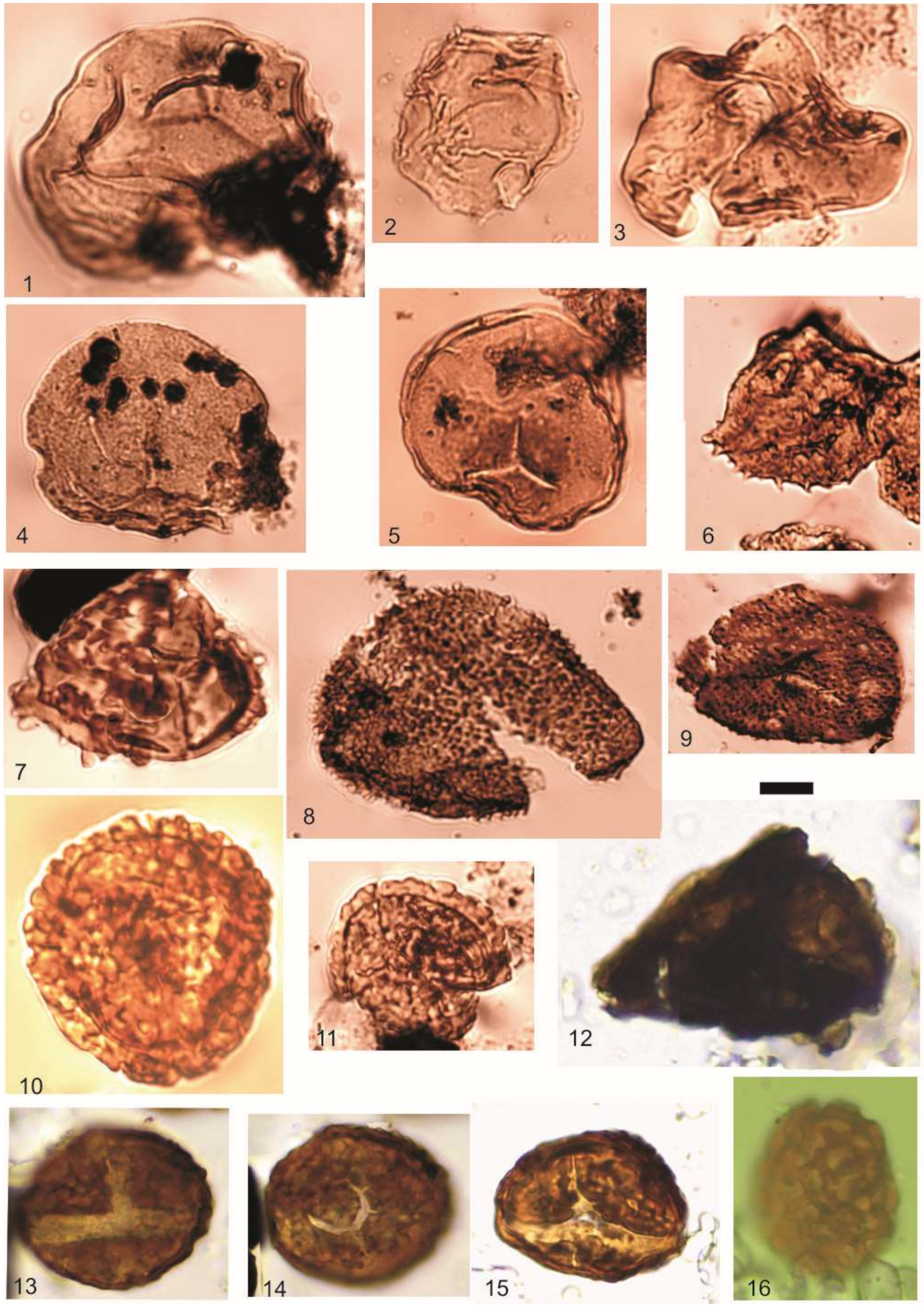


Plate 2. Scale bar 10 µm.

1. *Triquitrites* sp. cf. *T. kaiseri* Playford & Rigby, CICYTTP-Pl 2(+25), U50/3. 2. *Cirratriradites africanensis* Hart, MP-P-6032-b, R34/2. 3. *Cristatisporites morungavensis* (Días Fabricio) Picarelli & Días Fabricio, MP-P-6032-b, Y48/2. 4. *Gondisporites* sp. cf. *G. imbricatus* Segroves, CICYTTP-Pl 2(+25), L45/1. 5. *Lundbladispora braziliensis* (Pant & Srivastava) Marques-Toigo & Pons emend. Marques-Toigo & Picarelli, CICYTTP-Pl 1(1), E49/3. 6. *Lundbladispora riobonitensis* Marques-Toigo & Picarelli, MP-P-6032-b, M41/2. 7-9. *Lycospora variabila* Cousminer, 7 - MP-P-6030-b, G43/3, 8 - MP-P-6030-b, L49/4, 9 - MP-P-6030-b, N47/4. 10. *Laevigatosporites vulgaris* (Ibrahim) Ibrahim emend. Alpern & Doubinger, MP-P6033-a, P37/1. 11-12. *Leschikisporis chacoparanaense* Vergel, 11 - MP-P6032-b, G33/3, 12 - MP-P-6031-b, L50/3. 13-15. *Polypodiisporites mutabilis* Balme, 13 - MP-P-6032-b, J41/2, 14 – 15 - MP-P-6030-b, K46/2. 16-17. *Polypodiites secoensis* Mautino, Vergel & Anzótegui, 16 - MP-P-6031-b, L55/1, 17 – MP-P6033-a, P41/3.

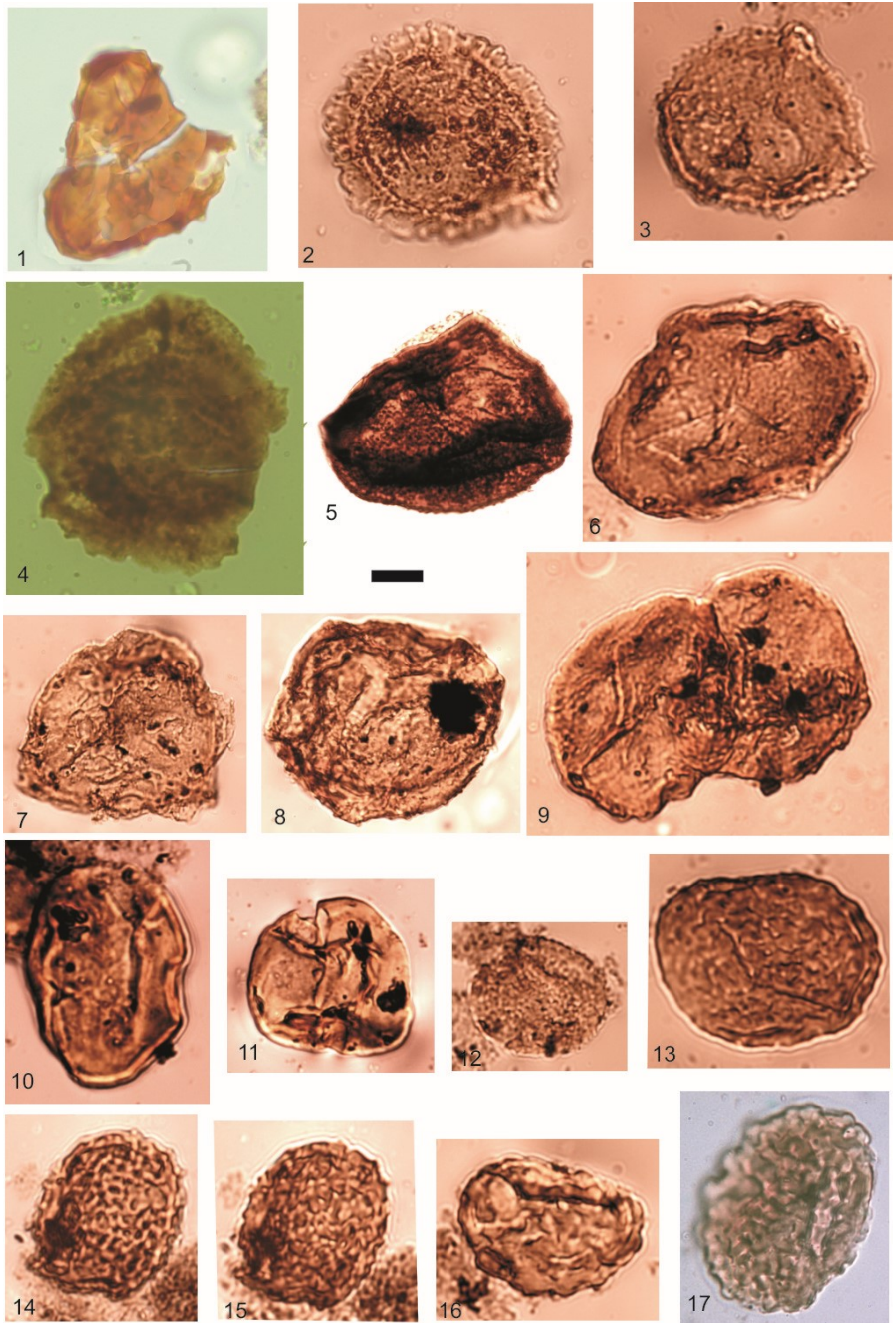


Plate 3. Scale bar 10 µm.
1-2. *Reticuloidosporites warchianus* Balme, 1 – MP-P6033-a, K53, 2 - CICYTTP-Pl 1(1), F49/1. 3-4. *Thymospora criciumensis* Quadros, Marques-Toigo & Cazzulo-Klepzig, 3 - CICYTTP-Pl 1(1), Z38/3, 4 - MP-P-6032-b, E44/1. 5-6. *Thymospora rugulosa* Mautino, Vergel & Anzótegui, 5 – MP-P6033-a, L51/1, 6 – CICYTTP-Pl 5(Mer1), Y41/4. 7-10. *Striatosporites heyleri* (Doubinger) emend. Playford & Dino, 7 -MP-P-6030-b, N50/3, 8 – 9 - MP-P6034-b, S44/2, 10 - MP-P-6032-b, W39/4.

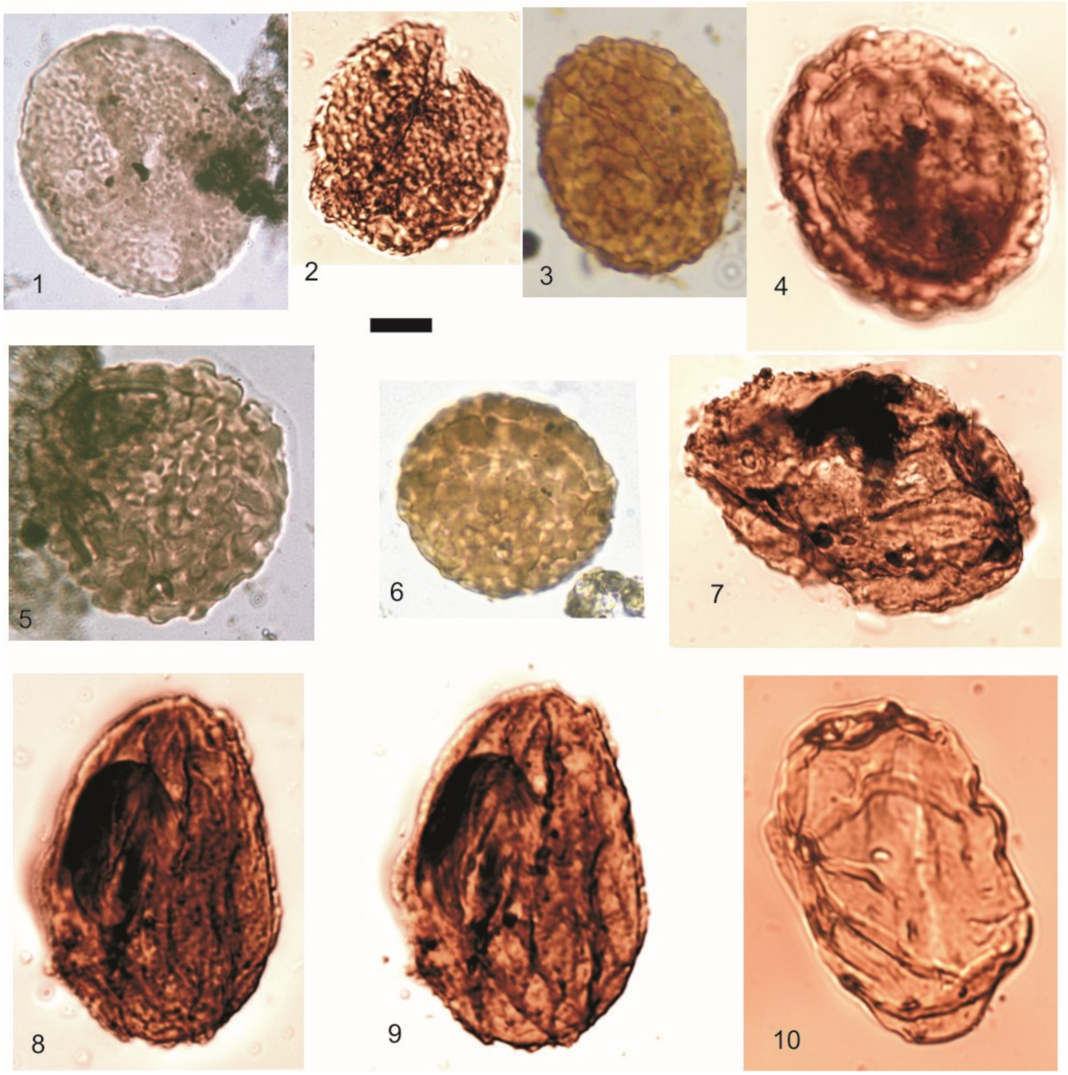


Plate 4. Scale bar 20 µm.
1. *Caheniasaccites flavatus* Bose & Kar emend. Azcuy & di Pasquo, MP-P6026-a, S57. 2. *Cannanoropollis densus* (Lele) Bose & Maheshwari, MP-P-6027-b, J51/2. 3. *Cannanoropollis janakii* Potonié & Sah, MP-P6032-b, S35/1. 4. *Latusipollenites quadrisaccatus* Marques-Toigo, MP-P-6027-b, U39/1. 5. *Peppersites ellipticus* Ravn, MP-P-6032-b-A39/3. 6. *Plicatipollenites malabarensis* (Potonié & Sah) Foster, MP-P6034-c, R46/3. 7. *Plicatipollenites trigonalis* Lele, MP-P6026-a, F42. 8. *Potonieisporites barrelis* Tiwari, MP-P6026-a, N45/1. 9. *Potonieisporites congoensis* Bose & Maheshwari, MP-P6026-a, X61. 10. *Potonieisporites densus* Maheshwari, MP-P6029-c, G54. 11. *Potonieisporites lelei* Maheshwari, MP-P6026-a, P50. 12. *Potonieisporites marleniae* Playford & Dino, MP-P-6027-b, Q57/2. 13. *Potonieisporites magnus* Lele & Karim, MP-P6026-a, S56/2. 14. *Potonieisporites neglectus* Potonié & Lele, MP-P6029-c, P39/4. 15. *Potonieisporites novicus* Bhardwaj emend. Poort & Veld, MP-P6026-c, M57.

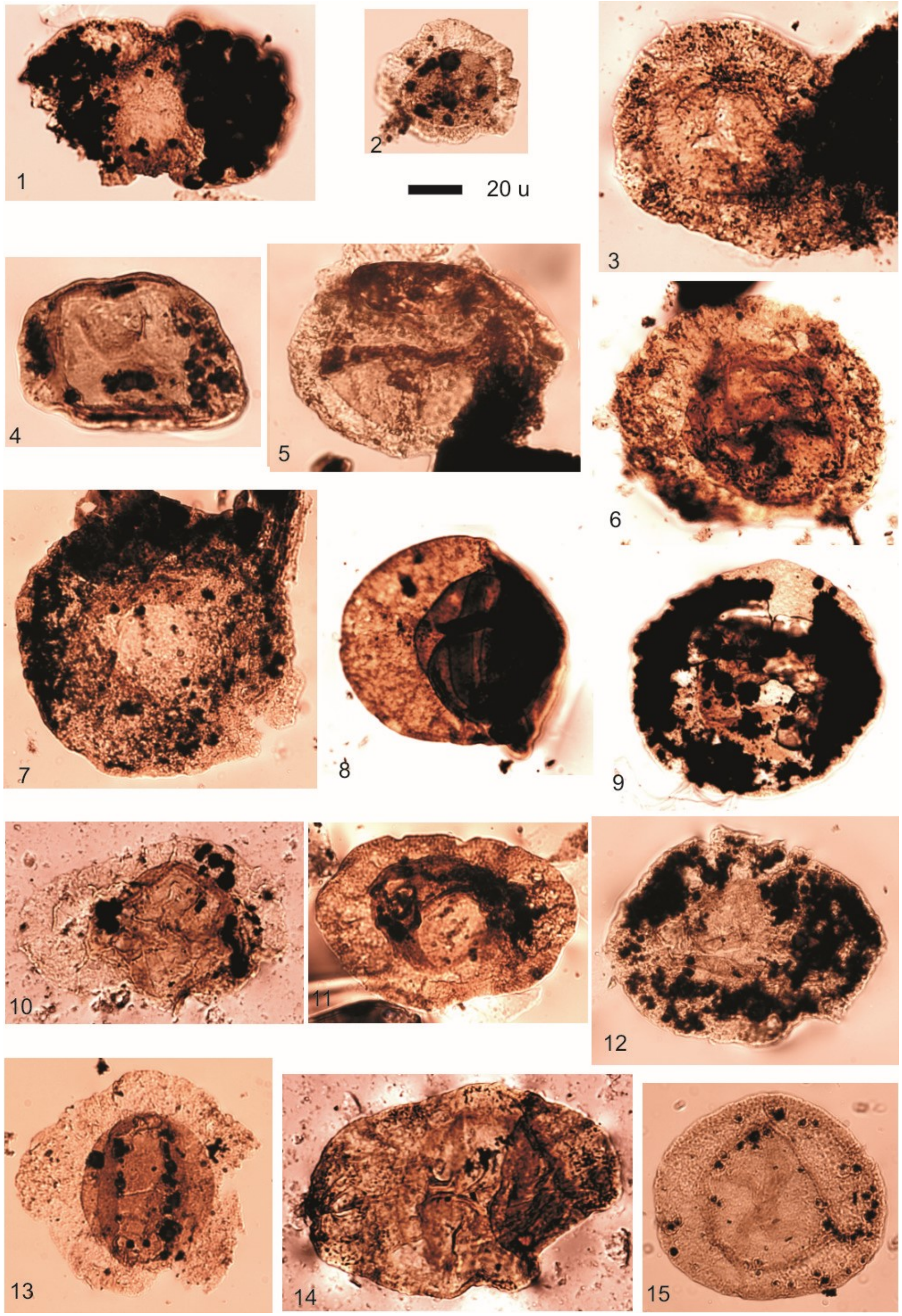


Plate 5. Figures 1-5, 7, 10 Scale bar = 15 µm, Figures 6, 9, 14 Scale bar = 20 µm, Figures 8, 11-13, 15 Scale bar = 10 µm.

1. *Striomonosaccites cicatricosus* Archangelsky & Gamerro, MP-P6026-a, N42. 2. *Mabuitasaccites crucistriatus* (Ybert) Playford & Dino, MP-P6032-b- X42/1. 3, 4. *Crustaesaccites hessii* Cousminer, MP-P6026-a, L52/1. 5-6. *Alisporites ovatus* (Balme & Hennelly) Jansonius, MP-P-6027-b, P59/2, 6 - MP-P6026-a, G49. 7. *Chordasporites endroedi* MacRae, MP-P6026-a, O39/4. 8. *Klausipollenites* sp. cf. *K. vestitus* Jansonius, MP-P6029-c, T55/1. 9. *Limitisporites* sp. cf. *L. luandensis* Bose & Maheshwari, MP-P6027-b, L60/3. 10-11. *Pteruchipollenites indarraensis* (Segroves) Foster, 10 - MP-P-6032-b, X41/2, 11 - CICYTTP-Pl 1(1+25), R27/4. 12. *Scheuringipollenites circularis* Césari, Archangelsky & Seoane, CICYTTP-Pl 5(Mer2), S43. 13. *Scheuringipollenites maximus* (Hart) Tiwari, CICYTTP-Pl 1(1+25), Q29. 14. *Scheuringipollenites maximus* (Hart) Tiwari, MP-P6026-a, P46/4. 15. *Vitreisporites pallidus* (Reissinger) Nilsson, MP-P-6031-b, T49/3.

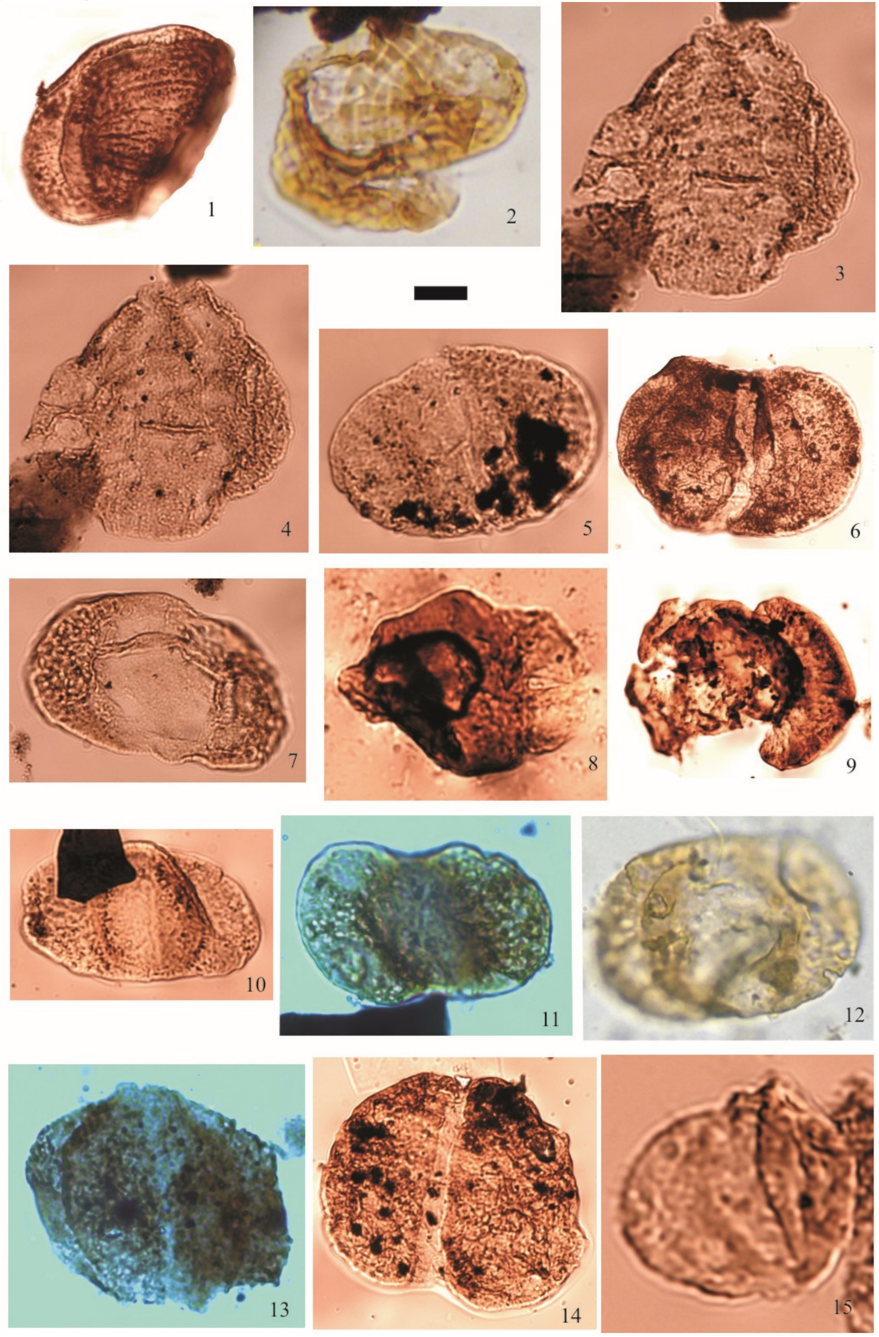


Plate 6. Figures 1-6, 8-10, 14 Scale bar = 15 µm, Figures 7, 11-13, 15 Scale bar = 20 µm.
1. *Corisaccites alutas* Venkatachala & Kar, MP-P6032-b, K39/3. 2-3. *Hamiapollenites dettmanae* Segroves, 2 - CICYTTP-Pl 1(1+25), M41/4, 3 - CICYTTP-Pl 1(2+10), F41. 4, 8. *Lueckisporites virkkiae* (Potonié & Klaus) Klaus, 4 - MP-P-6027-b-L51/4, 8 - MP-P6026-a, O43/0-1. 5. *Hamiapollenites karrooensis* (Hart) Hart, CICYTTP-Pl 1(2+10), Q41. 6. *Lueckisporites nyakapendensis* Hart, MP-P6028-a, R48/3. 7. *Lueckisporites singhii* Balme, MP-P6026-c, Q42/1. 9. *Lunatisporites acutus* Leschik, MP-P6028-a, J55/4. 10. *Lunatisporites noviaulensis* (Leschik) Foster, MP-P6026-c, U51. 11. *Lunatisporites pellucidus* (Goubin) Helby emend. de Jersey, MP-P-6027-b, D57. 12-14. *Lunatisporites variesectus* Archangelsky & Gamerro, 12 - MP-P6026-a, N59, 13 - MP-P6026-a, N60/1, 14 - MP-P6026-c, O43/2. 15. *Protohaploxypinus amplus* (Balme & Hennelly) Hart, MP-P6026-a, G46/3.

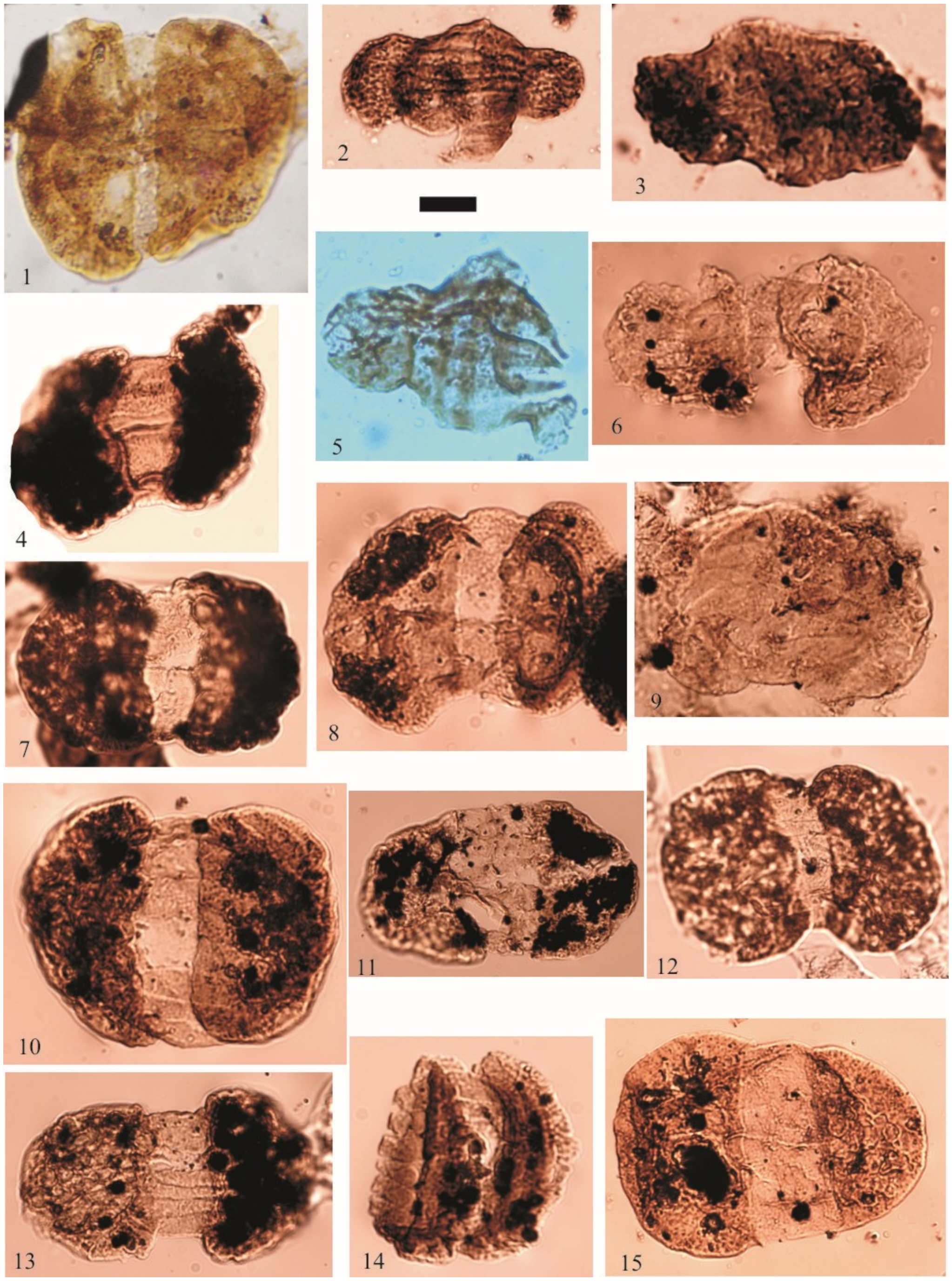


Plate 7. Figures 1, 2, 4 Scale bar = 20 µm, Figures 3, 5, 7, 8 Scale bar = 10 µm, Figures 6, 9-11 Scale bar = 15 µm.

1. *Protohaploxypinus haigii* Foster, MP-P-6027-c, S44/4. 2, 4. *Protohaploxypinus samoilovichii* (Jansonius) Hart, 2 - MP-P6032-b, Q38/3, 4 - MP-P6026-a, K43/1. 3, 5. *Protohaploxypinus rugatus* Segroves, 3 - MP-P6032-b, Q34, 5- MP-P6026-c, M60/1. 6. *Striatoabieites multistriatus* (Balme & Hennelly) Hart, MP-P6026-a, L44/1. 7. *Striatopodocarpidites cancellatus* (Balme & Hennelly) Hart, MP-P6026-a, R47/1. 8. *Striatopodocarpidites solitus* (Bharadwaj & Salhuja) Foster, CICYTTP-Pl 1(1+25), S27/2. 9. *Striatopodocarpites phaleratus* (Balme & Hennelly) Hart, MP-P6026-c, V58. 10. *Illinites unicus* Kosanke emend. Jansonius & Hills, MP-P6027-c, R49/2. 11. *Pakhapites fasciolatus* (Balme & Hennelly) Hart, MP-P6032-b, M33.

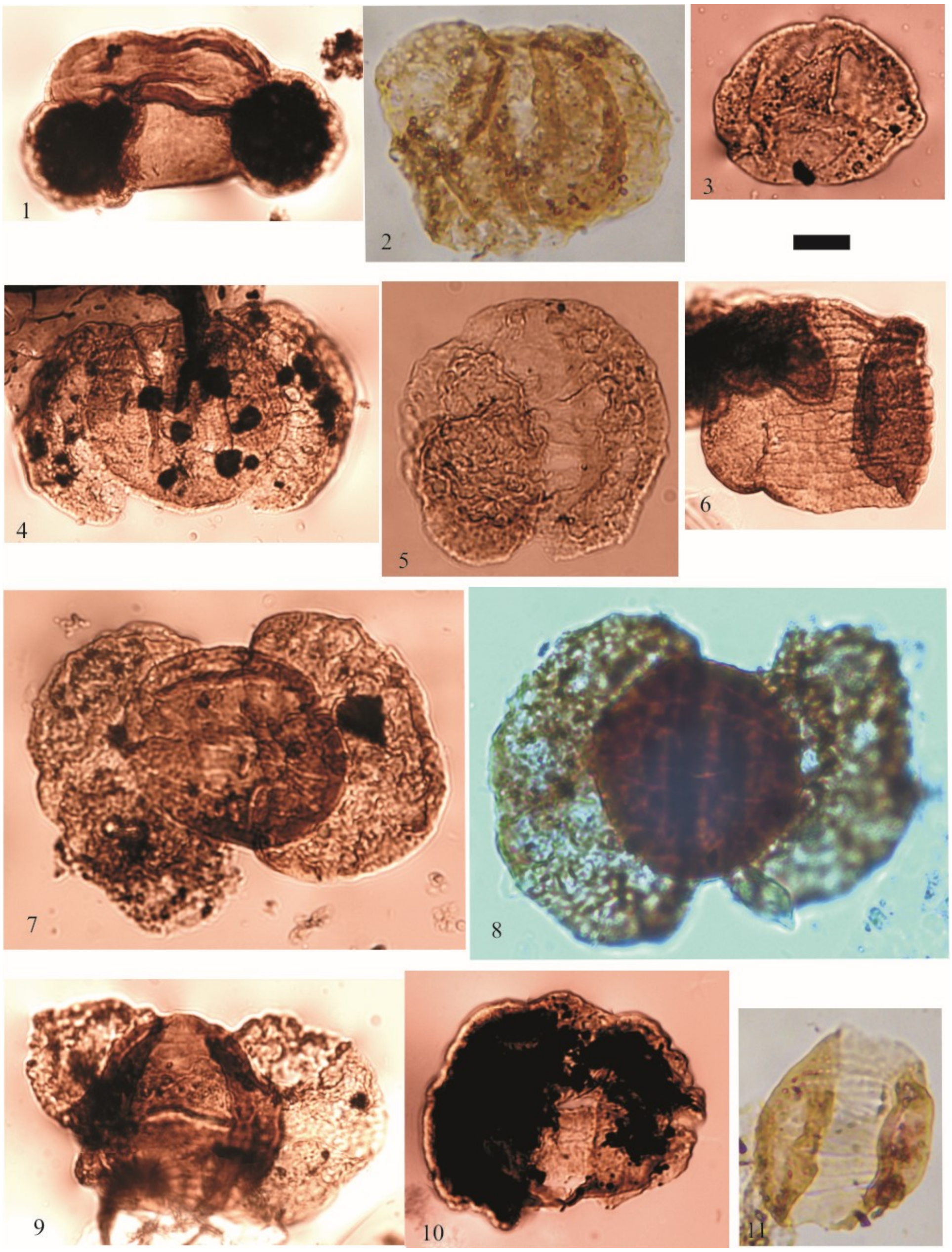


Plate 8. Figures 1, 3, 4, 6, 8, 9, 12 Scale bar = 15 µm, Figures 2, 5, 7, 10, 11, 13 Scale bar = 10 µm. 1. *Pakhapites fusus* (Bose & Kar) Menéndez, MP-P6028-c, W44/1. 2. *Pakhapites ovatus (*Bose & Kar) García, MP-P6028-a, F50/3. 3. *Marsupipollenites striatus* (Balme & Hennelly) Hart, MP-P6028-a, F60/4. 4. *Vittatina corrugata* Marques-Toigo, MP-P6028-c, P47/3. 5, 6. *Vittatina costabilis* Wilson, 5 - MP-P6026-a, K46/4, 6 - MP-P6029-c, D44/0-3. 7, 8. *Vittatina saccata* (Hart) Jansonius, 7 - MP-P6032-b, K39/3, 8 - MP-P-6032-b, M37/1. 9, 10. *Vittatina subsaccata* Samoilovich, 9 - MP-P6028-d, Y48/1, 10 - MP-P6026-c, J59/4. 11, 12. *Vittatina vittifera* (Luber &Waltz) Samoilovich, 11 - MP-P-6032-b, F41, 12 - MP-P6032-b, K43/2-4. 13. *Vittatina* sp. cf. V. *simplex* Jansonius, MP-P-6032-b, B42/3.

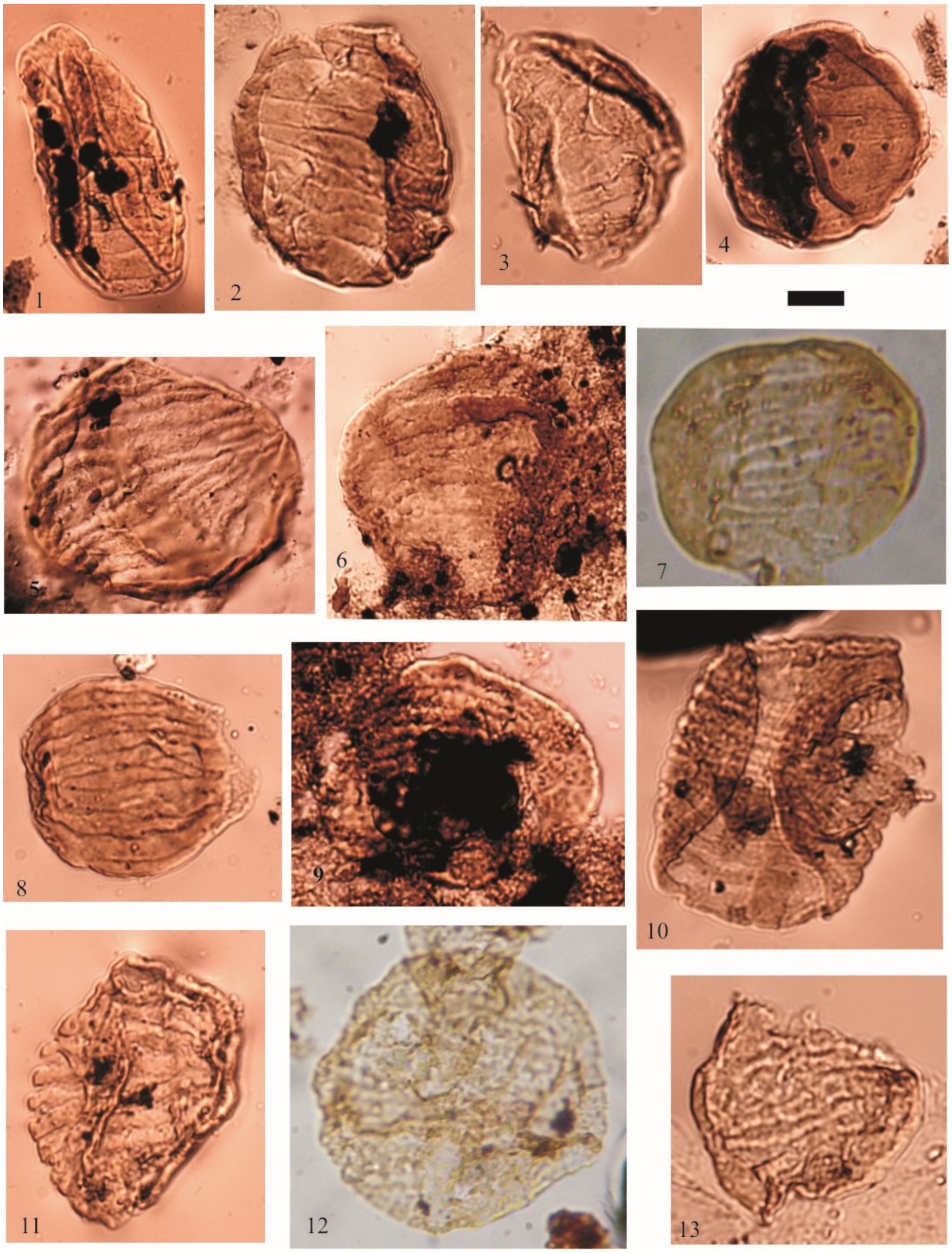


Plate 9. Figures 1-3, 5-8 Scale bar = 10 µm, Figure 4, Scale bar = 15 µm, Figures 9-11 Scale bar = 20 µm.

1, 2. *Weylandites lucifer* (Bharadwaj & Srivastava) Foster, 1 - MP-P6027-c, S42/1, 2 - MP-P-6032-b, L36. 3. *Weylandites magmus* Bose & Kar, MP-P6028-d, V44/2. 4. *Cycadopites cymbatus* (Bame & Hennelly) Segroves, MP-P6026-c, O41/4. 5-7. *Hamiapollenites karrooensis* (Hart) Hart, CICYTTP-Pl 1(1+25), C24. 5 - proximal face, 6 – distal face, 7 – specimen under fluorescence. 8. *Brazilea scissa* (Balme & Hennelly) Foster, MP-P6032-b, H41/3. 9-11. *Botryococcus braunii* Kützing, 9 - MP-P6032-b, Q38/0-4, 10, 11 -CICYTTP-Pl 2(1+25), H28/4, 11 – specimen under fluorescence.

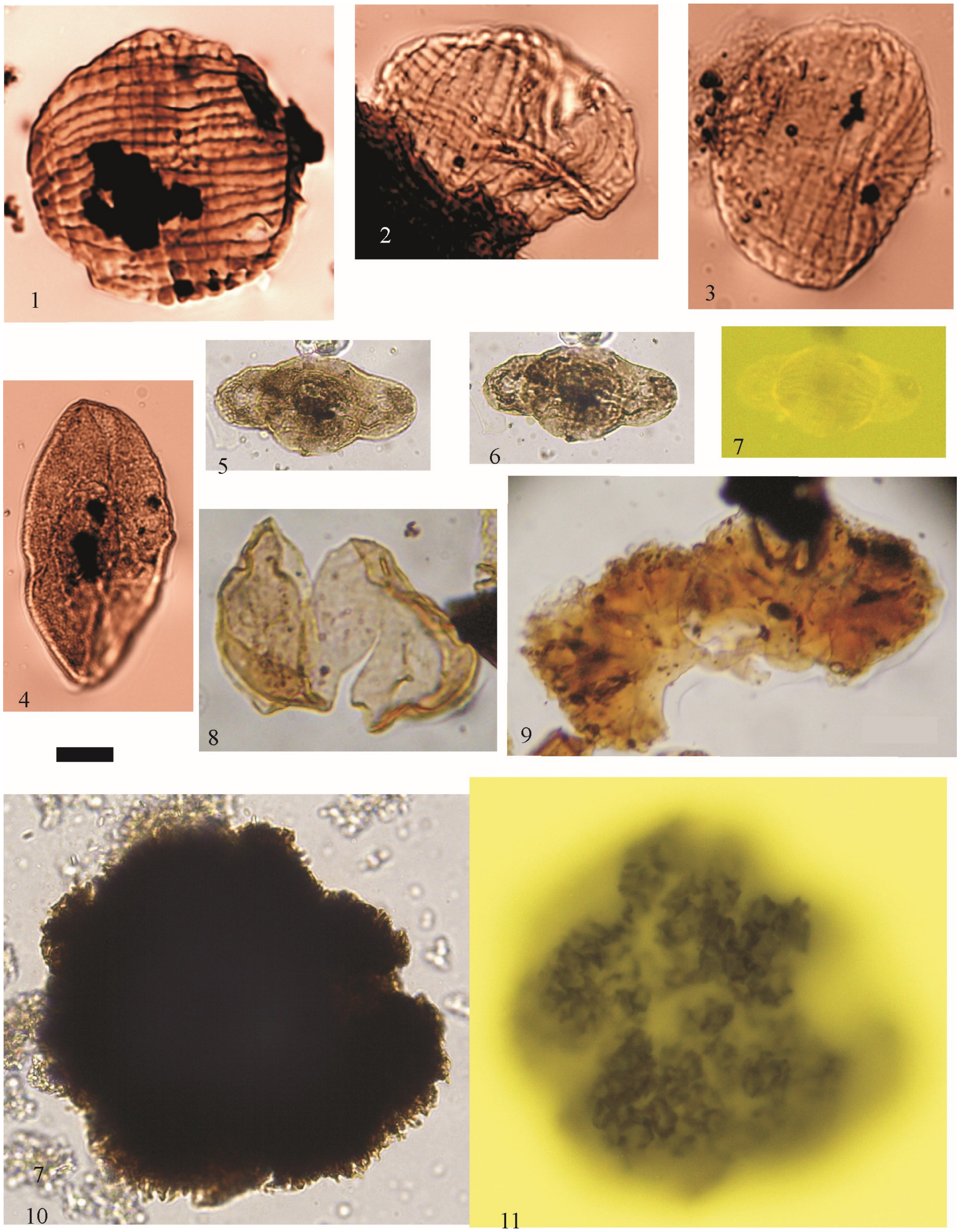
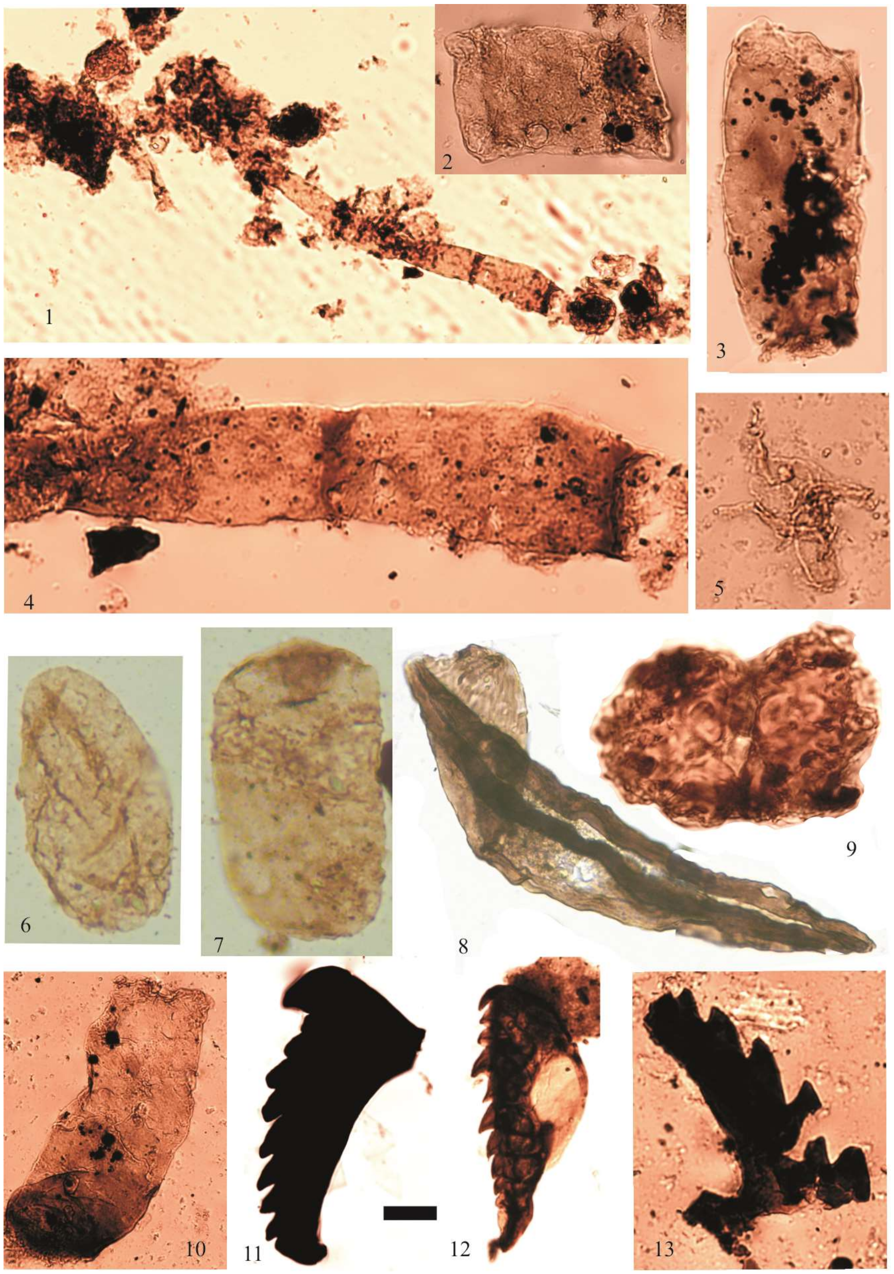


Plate 10. Figures 1, 8, 10, 11 Scale bar = 30 µm, Figures 3, 4, 9, 12, 13 Scale bar = 20 µm, Figure 2, 5 Scale bar = 10 µm.
1, 3, 4, 6, 7, 10. *Reduviasporonites chalastus* (Foster) Elsik, 1, 4 - MP-P-6031-b, S42/0-4, 3 - MP-P6028-a, U65, 6 - CICYTTP-Pl 1(1+25), U31, 7 - CICYTTP-Pl 1(1+25), U31/0-2, 10 - MP-P6029-c, T52/3. 2. *Tetraporina punctata* (Tiwari & Navale) Kar & Bose, MP-P6028-a, P52/1-3. 5. Acritarch undetermined, MP-P6029-c, U45. 8. *Deusilites tenuistriatus* Gutiérrez, Césari & Archangelsky, CICYTTP-Pl 2(1+25), X32/1. 9. *Botryococcus braunii* Kützing, MP-P-6032-b, X39. 11, 12. *Menogenys* sp., 11 - MP-P6026-a, U52/1, 12 - MP-P6029-c, R54/0-2. 13. Scolecodont form A, MP-P6026-a, O47/1.



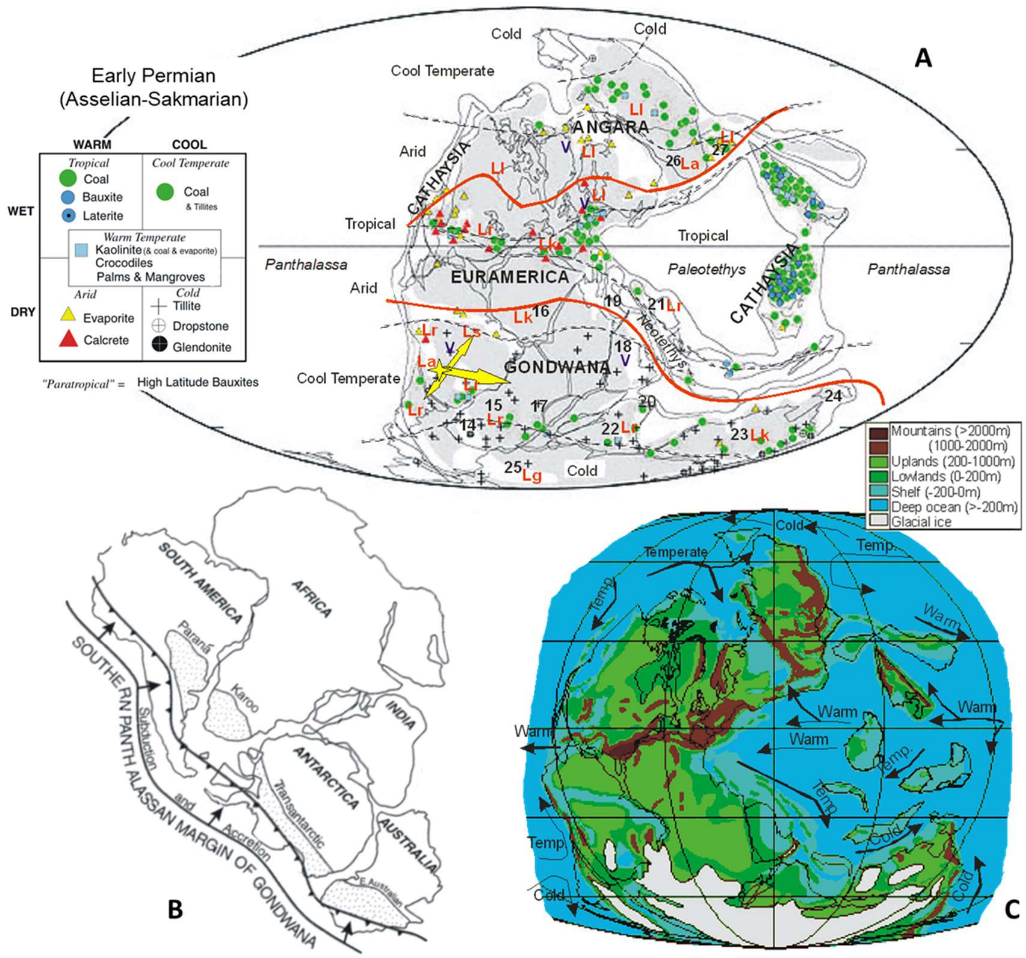


Figure 1.A. Floral provinces after Broutin et al. (1990) and Utting and Piasecki (1995; and others) shown demarcated by red lines on an Early Permian (Asselian-Sakmarian) paleogeographic and paleoclimatic (dashed line) reconstruction taken from Scotese (2003, 2013, see also Boucot et al., 2013). An aborted Pangaea break-up stage during the Early Permian separating Laurussia from Gondwanaland was interpreted to have occurred as a shallow sea from Tunisia to Cuba. Abbreviations: V= Moscovian occurrences of *Vittatina* - Parallel evolution or incomplete fossil record?. L= *Lueckisporites* appearances (La=mid Asselian; Ls= Sakmarian; Lr=Artinskian; Lk= Kungurian; Lg=Guadalupian; Ll=Lopingian). Possible route of migration (see arrows in yellow color) except for Kazakhstan that should be parallel evolution (?). For locations (basins and countries) and biostratigraphic records of taxa in South America see di Pasquo et al. (2015) and taxonomic section in this work (e.g. Doubinger and Marocco, 1981; Sempere et al., 1992, 2002; Archangelsky and Vergel, 1996; Ottone et al., 1998; Beig et al., 1998; Muff et al., 1999; Césari and Gutiérrez, 2001; Playford and Dino, 2000b; Dino et al., 2002; Iannuzzi et al., 2004; Souza and Marques Toigo, 2005; Iannuzzi and Souza, 2005; Césari et al., 2007; Souza et al., 2007; Holtz et al., 2008; Gutiérrez et al., 2010; Beri et al., 2010; di Pasquo et al., 2010; Pérez Loinaze et al., 2010). Further records from Euramerica and Angara are from Balme (1970), Foster (1979), Broutin et al. (1990), Utting and Piasecki (1995). References indicated for Gondwana: 14- South Africa, Anderson (1977), Prevec et al. (2010), 15- Namibia, Stephenson (2009), 16- Tanzania, Semkiwa et al. (2003), 17- Nigeria, Broutin et al. (1990), 18- Oman and Saudi Arabia, Stephenson et al. (2003), Stephenson (2006, 2008), 20- Pakistan, Balme (1970), 22- India, Tiwari and Tripathi (1992), 23- Australia, Foster (1979, 1982), Backhouse (1991), 24- West Papua, Playford and Rigby (2008), 25- Antarctica, Lindström (1995, 1996), Lindström and McLoughlin (2007). Other regions elsewhere: 19- Israel, Eshet (1990 a, 1990b), 21- Iran, Ghavidel-syooki (1997), 26- Kazakhstan, Dunn (2001), 27- China, Zhou et al. (2005). **B** and **C** are

complementary figures. **B**. Gondwanan configuration after Turner (1999, see also Milani and de Wit, 2008). **C**. Topographic map after Ziegler et al. (1997, 1998) with surface global ocean circulation pattern after Shi and Archbold (1998, line arrows).

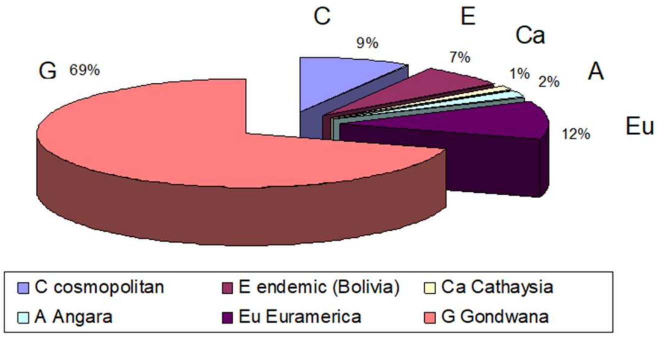


Figure 2.A

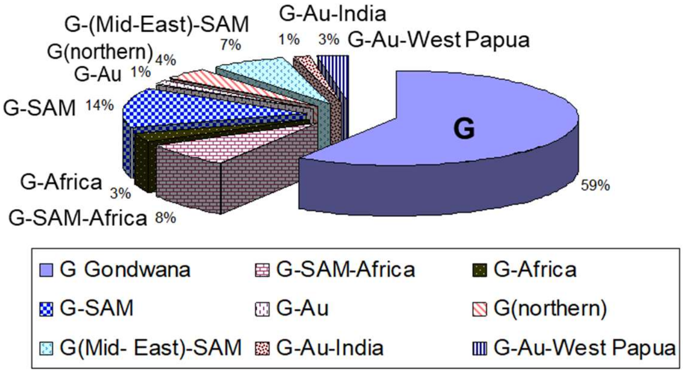


Figure 2.B

Figure 2. Paleogeographic distribution of taxa (see Table 1) documented in the Copacabana Formation at Apillapampa.

Table 1. Botanical affinities, geographic and biostratigraphic distribution of taxa of the Copacabana Formation at Apillapampa, based on the revision done by di Pasquo and Grader (2012). Synonyms of taxa cited by Cousminer (1965) marked with (a) in Lv (Coal Mb) column. Global range of taxa based on supplementary online material published by di Pasquo et al. (2015). For botanical affinity of *Lueckisporites* see Clement-Westerhof (1987) and Looy (2007). Abbreviations under botanical affinities: G- Gymnosperm. Abbreviations under geographic distribution: G-Gondwana, E- Endemic (Bolivia), C- Cosmopolitan, Ca-Cathaysia, A- Angara, Eu- Euramerica, SAM- South America. Abbreviations under Global range: Cisural-Cisuralian, Guadal-Guadalupian, Wuchiap-Wuchiapingian, Pennsylv-Pennsylvanian, Assel-Asselian.

TAXA / BIOSTRATIGRAPHY	Vc	Lv	Lv (Coal Mb)	GEOGRAPHIC DISTRIBUTION	BOTANICAL AFFINITIES	GLOBAL RANGE
Alisporites ovatus		X	X(a)	Eu, G	G: Corystospermaceae, Peltaspermaceae	*Permian-Triassic*
Brevitriletes cornutus			X(a)	G	Pteridophyte	*late Pennsylv-Permian*
Caheniasaccites flavatus		X	X	G	G: Cordaitales, Coniferales	*Pennsylv-Permian*
Calamospora liquida		X		C	Sphenophyte	*Pennsylv-Permian*
Calamospora microrugosa			X	C	Sphenophyte	*Pennsylv-Permian*
Cannanoropollis densus		X		G	G: Cordaitales, Coniferales	*Pennsylv-Permian*
Cannanoropollis janakii		X	X	G	G: Cordaitales, Coniferales	*Pennsylv-Permian*
Chordasporites endroedi	X	X	X	G	G: Corystospermaceae, Peltaspermaceae	*Pennsylv-Cisural*
Cirratriradites africanensis			X	G-Africa	Lycophyte	*Cisural*
Convolutispora ordonensis			X	G-SAM	Pteridophyte, Lycophyte	*Pennsylv-Cisural*
Convolutispora uruguaiensis			X	G-SAM-Africa	Pteridophyte, Lycophyte	*Cisural*
Corisaccites alutas		X	X	G, Eu	Gymnosperm	*latest Asselian-early Triassic*
Cristatisporites morungavensis		X	X	G-SAM	Lycophyte	*Pennsylv-Cisural*
Crustaesporites hessii		X	X(a)	E	G: Cordaitales, Coniferales, Glosspteridales	*Cisural*
Cycadopites cymbatus		X	X	G	G: Pteridospermaphyta (Peltaspermaceae); Cycadophyte; Ginkgophyte	*late Pennsylv-Permian*
Didecitriletes eoericianus		X		G-Africa	Pteridophyte	*Cisural*
Gondisporites sp. cf. G. imbricatus			X	G-Au-West Papua	Lycophyte: Lepidodendrales	*Artinsk-Lopingian*
Hamiapollenites dettmannae			X	G(northern)	G: Coniferales	*mid Assel-Wuchiap*
Hamiapollenites karrooensis			X	G(northern)	G: Coniferales	*mid Assel-Wuchiap*
Horriditriletes ramosus			X(a)	G	Pteridophyte	*Pennsylv-early Triassic*
Illinites unicus		X		Eu, G	Gymnosperm	*Pennsylv-Cisural*
Klausipollenites sp. cf. K. vestitus	X	X	X	Eu-NAM	G: Pinopsida	*early Triassic*
Laevigatosporites vulgaris		X	X(a)	C	Pteridophyte, Sphenophyte	*Carboniferous-Recent*
Latusipollenites quadrisaccatus		X		G-SAM	Gymnosperm	*Pennsylv-Guadal*
Leschikisporis chacoparanensis			X	G-SAM	Pteridophyte	*Cisural*
Limitisporites sp. cf. L. luandensis		X		G-SAM-Af	G: Pterydospermaphyta, Glossopteridales, Coniferophyta	*Cisural*
Lueckisporites nyakapendensis		X		G-SAM-Af	G: Pinopsida Majonicaceae	*mid Artinskian-Lopingian*
Lueckisporites singhii		X	X	G-Arabian Plate	G: Pinopsida Majonicaceae	*Kungurian-early Triassic*
Lueckisporites virkkiae		X	X	C	G: Pinopsida Majonicaceae	*Sakmarian/mid Artinskian-Lopingian*
Lunatisporites acutus		X		Eu, G	G: Coniferales	*Lopingian-Triassic*
Lunatisporites noviaulensis		X		Eu, G	G: Coniferales	*mid Artinskian-Triassic*
Lunatisporites pellucidus		X		G	G: Coniferales	*mid Artinskian-Triassic*
Lunatisporites variesectus		X	X(a)	G-SAM	G: Coniferales	*latest Penssylv-Capitanian*
Lundbladispora braziliensis			X(a)	G-SAM-Africa-Arabian Plate	Lycophyte: Sellaginelales	*Pennsylv-Guadal*
Lundbladispora riobonitensis	X	X	X	G-SAM-Arabian Pl	Lycophyte: Sellaginelales	*Pennsylv-Guadal*
Lycospora variabila			X(a)	E	Lycophyte: Lepidodendrales	*Cisural*
Mabuitasaccites crucistriatus		X	X	G-SAM	G: Cordaitales, Coniferales, Glosspteridales	*Cisural-Guadal*
Marsupipollenites striatus	X	X	X	G	G: Pterydospermaphyta, Glossopteridales	*Permian-Triassic*
Pakhapites fasciolatus			X(a)	G	G: Pterydospermaphyta, Glossopteridales	*Permian*
Pakhapites fusus		X		G	G: Pterydospermaphyta, Glossopteridales	*Asselian-Wuchiap*
Pakhapites ovatus	X	X		G	G: Pterydospermaphyta, Glossopteridales	*Asselian-Wuchiap*
Peppersites ellipticus			X	Eu-USA, G-Brazil, Saudi Arabia	Gymnosperm	*late Pennsylv*
Plicatipollenites malabarensis		X		G	G: Coniferales	*Pennsylv-Permian*
Plicatipollenites trigonalis		X		G	G: Coniferales	*Pennsylv-Cisural*
Polypodiisporites mutabilis			X(a)	G	Pteridophyte	*mid Asselian?-Triassic*
Polypodites secoensis			X(a)	G-SAM-Africa	Pteridophyte	*Artinsk-Kungur*
Potonieisporites barrelis	X	X	X	G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites congoensis		X	X	G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites densus	X	X		G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites lelei		X		G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites magnus	X	X		G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites marleniae		X		G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv*
Potonieisporites neglectus	X			G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Potonieisporites novicus		X	X	G	G: Pteridospermaphyta, Cordaitales, Coniferales	*Pennsylv-Permian*
Protohaploxypinus amplus		X		G	G: Pterydospermaphyta, Glossopteridales	*Pennsylv-Permian*
Protohaploxypinus haigii		X		G-Au	G: Pterydospermaphyta, Glossopteridales	*Cisural*
Protohaploxypinus rugatus		X	X	G	G: Pterydospermaphyta, Glossopteridales	*Asselian-?Capitan*
Protohaploxypinus samoilovichii		X	X(a)	Eu, G	G: Pterydospermaphyta, Glossopteridales	*late Asselian-Triassic*
Pteruchipollenites indarraensis	X	X	X	G	G: Corystospermaceae, Peltaspermaceae	*laPennsylv-Guadal*
Punctatisporites minutiarcus		X	X(a)	E	Pteridophyte	*Artinskian*
Reticuloidosporites warchianus			X	G(northern, Mid- East)-SAM	Pteridophyte	*mid Asselian?-Lopingian*
Retusotriletes nigritellus		X		G	Sphenophyte	*Pennsylv-Cisural*
Scheurigipollenites circularis			X	G-SAM	G: Cordaitales, Coniferales, Glosspteridales	*Cisural*
Scheuringipollenites maximus		X	X	G	G: Cordaitales, Coniferales, Glosspteridales	*Pennsylv-Permian*
Striatoabieites multistriatus		X	X(a)	G	G: Pterydospermaphyta, Glossopteridales	*laPennsylv-Triassic*
Striatopodocarpites cancellatus		X	X(a)	G	G: Pterydospermaphyta, Glossopteridales	*Permian-early Triassic*
Striatopodocarpites solitus			X(a)	G	G: Pterydospermaphyta, Glossopteridales	*Pennsylv-Triassic*
Striatopodocarpites phaleratus		X		G-Au-India	G: Pterydospermaphyta, Glossopteridales	*Arthinsk-?Capitan*
Striatosporites heyleri			X	Eu, G, Ca	Sphenophyte: Sphenophyllales	*Pennsylv-Permian*
Striomonosaccites cicatricosus		X		G-SAM-Iran	G: Cordaitales, Coniferales, Glosspteridales	*Cisural-Guadal*
Thymospora criciumensis			X(a)	G-SAM	Pteridophyte: Marattiales	*late Asselian-Kungur*
Thymospora rugulosa			X(a)	G-SAM-Africa	Pteridophyte: Marattiales	*late Asselian-Lopingian*
Triquitrites sp. cf. T. kaiseri			X	G-West Papua	Pteridophyte	*Kungur-Roadian*
Vitreisporites pallidus			X	C	G: Corystospermaceae, Peltaspermaceae	*?Pennsylv-Cretac.*
Vittatina corrugata		X	X	G-SAM	G: Peltaspermaceae	*Cisural*
Vittatina costabilis	X	X	X	C	G: Peltaspermaceae	*Permian*
Vittatina saccata		X	X	G-SAM-Af	G: Peltaspermaceae	*Permian*
Vittatina sp. cf. V. simplex		X	X	Eu-NAM	G: Peltaspermaceae	*Permian*
Vittatina subsaccata		X	X(a)	G, Eu, A-China-Russia	G: Peltaspermaceae	*Permian*
Vittatina vittifera	X	X	X	C	G: Peltaspermaceae	*Permian*
Weylandites lucifer		X	X	G, A-Russia	G: Pterydospermaphyta, Glossopteridales	*Asselian-Triassic*
Weylandites magmus		X		G	G: Pterydospermaphyta, Glossopteridales	*Permian*
Botryococcus braunii	X		X	C	Chlorophyceae	*late Devon-Present*
Brazilea scissa			X(a)	Eu, G	Chlorophyte-Zygnemataceae	*Pennsylv-Permian*
Reduviasporonites chalastus	X	X	X	C	Algae	*Artinskian-Early Triassic*
Tetraporina punctata		X		G	Chlorophyte-Zygnemataceae	*Pennsylv-Permian*
Deusilites tenuistriatus	X		X	G-SAM	Acritarch	*late Pennsylv-Cisural*
Number of species	15	59	62			