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The Pennsylvanian palynoflora of the Pando X-1 Borehole, northern Bolivia

Mercedes di Pasquo

CONICET, National Research Council of Argentina, UBA, Department of Geological Sciences, Faculty of Pure and Natural Sciences, University of Buenos Aires, Ciudad Universitaria, Pabellón II (1428), Capital Federal, Argentina

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ABSTRACT

Palynological analysis of ten core samples obtained from 867–729 m depth in the Pando X-1 Borehole (11° 36′07″ S, 67° 56′45″ W), northern Bolivia, is presented. Palynomorphs are fairly well-preserved although many contain abundant pyrite. The whole assemblage is composed of 48 species of which six are spores. Among the pollen grains, 21 are monosaccate and 19 bisaccate (11 striate species). Scarce scolecodonts, microforaminifera and algae are also present. Two assemblages are recognized on the basis of the stratigraphic distribution of species, mainly of the striate pollen grains. The lower assemblage (A1) is dominated by amorphous organic matter and scarce monosaccate pollen grains, trilete spores and microforaminifera. The upper assemblage (A2) is dominated by tracheids and brown and black phytoclasts and characterized by more diverse palynomorphs, mainly striate and non-striate pollen grains. The geographical and stratigraphic distribution of taxa reveals that many species are recorded from Pennsylvanian and Permian palynofloras elsewhere in Gondwana and Euramerica. The presence of *Lahirites segmentatus*, *Limitisporites scitulus*, *Lunatisporites onerosus* and *Vittatina* species, common with Brazilian palynofloras, supports a Moscovian age for the assemblage 2. This age is also supported by calcareous microfossils previously found in the same interval of this borehole. Twenty two species are first records in the Pennsylvanian of Bolivia (e.g., *Florinites eremus*, *Protohaploxypinus varius*, *Striatopodocarpites antiquus*, *S. gondwanensis*, *S. solitus*, *Vittatina* sp.). Palynofacies features of both assemblages are indicative of a shallow marine palaeoenvironment. Qualitative changes on the floral composition between A1 and A2 may reflect broadly local palaeoclimatical changes. The dominance of Cordaitales and Coniferales in A1 indicates a relatively more humid local condition than during A2 time, which is characterized by the appearance of abundant and diverse striate pollen grains related to new groups of Pteridosperms. These features are in agreement with a lower humidity or seasonally arid conditions prevailing in the terrestrial landscape near to the Copacabana marine palaeoenvironment.

1. Introduction

The palynological analysis of ten core samples obtained from the Copacabana Formation between 867 and 729 m depth of the Pando X-1 Borehole (11° 36′07″ S, 67° 56′45″ W) from northern Bolivia is presented (Fig. 1A–B). The age of this palynoflora is discussed on the basis of comparison with similar assemblages and stratigraphic range of the species recorded mainly from South America. The Copacabana Formation was deposited over a span of ~45 Ma. from Bashkirian to Artinskian time. Especially thick, locally continuous assemblages of Moscovian (Atokan) rocks occur with geographically more widespread Sakmarian to Artinskian rocks (see Grader et al., 2000). According to Isaacson et al. (1995), the carbonates and evaporites in this borehole correspond to the Copacabana Formation and were interpreted as restricted warm-water marine deposits under semiarid condition (see also, Grader et al., 2008). The contact with the underlying Yaurichambi Formation occurs at the first appearance of carbonate beds. The upper contact is represented by an unconformity marked by a coarse sandstone bed of the Jurassic/Cretaceous Beu Formation (Fig. 1C). Mamet (1996a,b) and Mamet and Isaacson (1997) have studied diverse microfossils related to foraminifera and algae recovered from the same section here analyzed for the first time for palynology. These microfossils were attributed to the Bashkirian–Moscovian; hence, they considered that the Permian deposits were eroded. Previous Pennsylvanian palynological studies are not known from northern Bolivia. Instead, Mississippian and Pennsylvanian palynofloras of the Macharetí and Mandiyutí Groups were documented by di Pasquo (2003, 2007a,b,c, 2009). Other palynological information from Bolivia is referenced to the Permian Vitiacua (Sempere et al., 1992, 2002) and Copacabana Formations (Cousminer, 1965; Ottone et al., 1998) and the late Viséan–Serpukhovian Kaka Formation (Azcuy and Ottone, 1987; Fasolo et al., 2006). Correlations of the Carboniferous and Permian stratigraphic and palynostratigraphic units of South America, here summarized in Figs. 2 and 3, are slightly modified from Azcuy et al. (2007) on the basis of more recent information.

E-mail address: medipa@gl.fcen.uba.ar.

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2. Brief geological setting

The Titicaca Group in the Madre de Dios Basin (Fig. 1A) includes the Pennsylvanian–Permian Tarma and Copacabana Formations from southern Peru and the Yaurichambi, Copacabana and Chutani Formations from northern Bolivia following the stratigraphic correlation proposed by Díaz-Martínez (1999) (see Fig. 2). Of these stratigraphic units, the Copacabana Formation is well-known by its fossiliferous carbonates interbedded with different lithologies such as evaporites, cherts, sandstones, shales and tuffs ranging from 200 to 800 m in thickness throughout this entire region in surface and subsurface sections (see Isaacson et al., 1993; Suárez-Soruco and Díaz-Martínez, 1996). Currently, Grader et al. (2000, 2008) analyzed the geological and palaeontological information of the Titicaca Group to conclude that Western Gondwana underwent a steady drift from mid-latitudes (~50°S, Mississippian) to lower latitudes (<40°S) by Pennsylvanian time. Therefore, glacial deposition would have ended in Bolivia by the early Pennsylvanian. During the rest of this time and throughout the Permian, the Titicaca Group is represented by an Andean transgressive marine to restricted carbonate platform and regressive red bed megasequence across the Peru–Bolivia Basin.

3. Materials and methods

The Pluspetrol Oil Company S.A. allowed sampling the Pando X-1 Core, (housed in Santa Cruz de la Sierra until 2000), between 1932 and 729 m depth. Ten of the sixty core samples collected are here studied (see Fig. 1C) after being processed using standard palynological methods

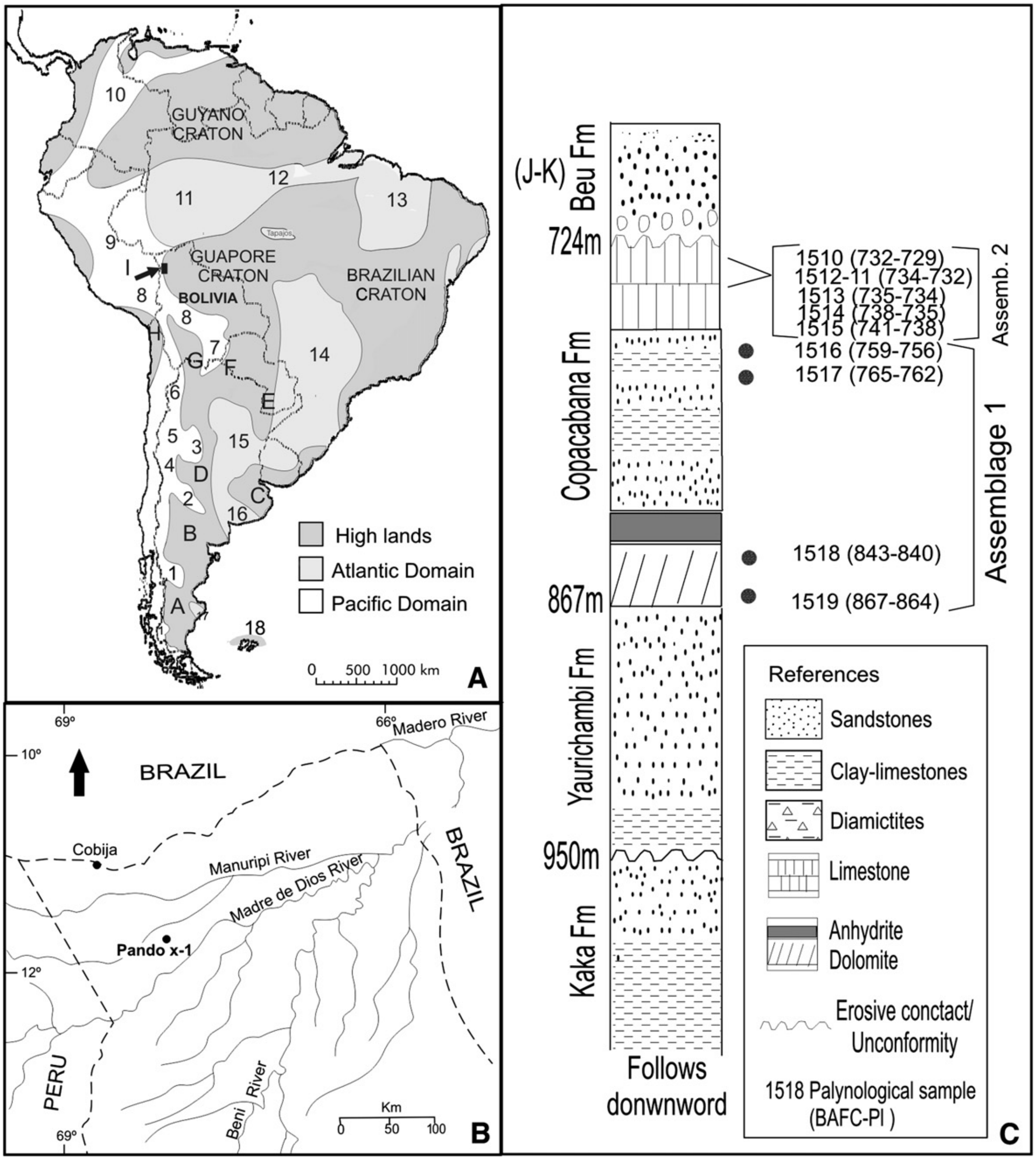


Fig. 1. A. Main Carboniferous basins of South America (modified from Azcuy et al., 2007): 1. Tepuel–Genoa. 2. San Rafael. 3. Paganzo. 4. Uspallata–Iglesia. 5. Río Blanco. 6. Arizaro. 7. Tarija. 8. Madre de Dios. 9. Ucayali–Marañón–Acre. 10. Los Llanos Orientales. 11. Solimões. 12. Amazonas. 13. Parnaiba. 14. Paraná. 15. Chaco–Paranense. 16. Sauce Grande–Claromecó–Colorado. 17. Golondrina. 18. Falklands Islands. High lands: A. Deseado Massif. B. Somuncurá Massif. C. Río de la Plata Craton. D. Pampean Arch. E. Asunción Arch. F. Michicola Arch. G. Puna Arch. H. Arequipa Massif. I. Fitzcarrald Arch. B. Location of the Pando X-1 Borehole in northwestern Bolivia. C. Lithostratigraphy (after Isaacson et al., 1995), samples location and assemblages defined in the studied section of the borehole.

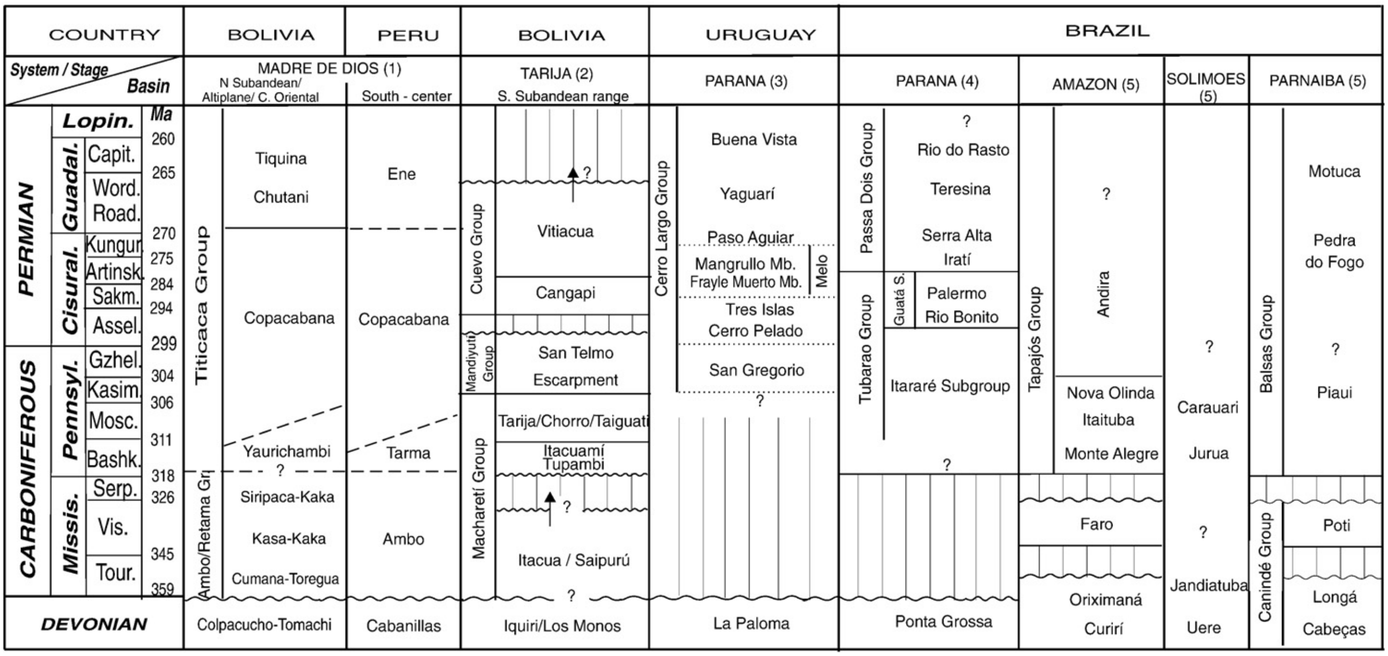


Fig. 2. Correlation of the Carboniferous and Permian stratigraphic units of Bolivia, Brazil, Peru and Uruguay, South America (after Azcuy et al., 2007). Selected references: 1-Díaz-Martínez (1999), `Suárez-Soruco (2000), Sempere et al. (2002); 2-di Pasquo (2002, 2003, 2007a,b); 3-de Santa Ana et al. (2006); 4-Melo and Loboziak (2003), Souza (2006); 5-Melo and Loboziak (2003). For more references see Azcuy et al. (2007). The Carboniferous–Permian limit is considered here at 299 Ma after Gradstein et al. (2004).

(HCl, HF). Several slides were prepared with sieved residues (+25 µm) and glycerin jelly. Slides and residues are housed at the Palynostratigraphy and Palaeobotany Laboratory of the Department of Geology of the Natural and Pure Sciences Faculty (University of Buenos Aires). Identification of palynomorphs was undertaken using a *Nikon Eclipse 80i* binocular transmitted light microscope with DIC objectives (×400 and

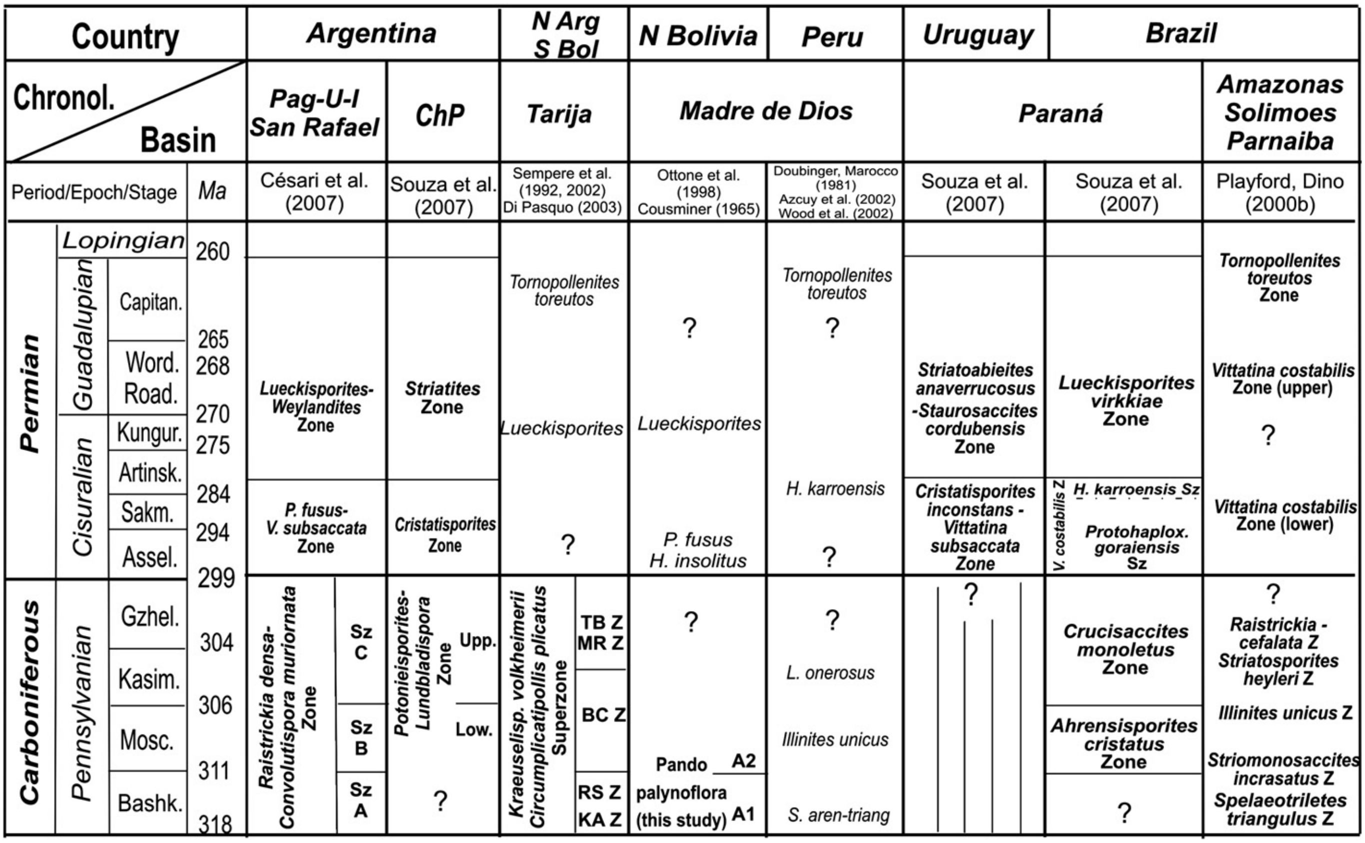


Fig. 3. Correlation of the Carboniferous and Permian palynostratigraphic units of Argentina, Bolivia, Brazil, Peru and Uruguay. Some diagnostic species are mentioned for some basins when biozones formally defined are not available (slightly modified from Azcuy et al., 2007). Biozone abbreviations: *Crassispora kosankei–Cystoptychus azcuyi* (*KA*), *Raistrickia radiosa–Apiculatasporites spinulistratus* (*RS*), *Dictyotriletes bireticulatus–Cristatisporites chacoparanensis* (*BC*), *Converrucosisporites micronodosus–Reticulatisporites reticulatus* (*MR*), *Marsupipollenites triradiatus–Lundbladispora braziliensis* (*TB*).

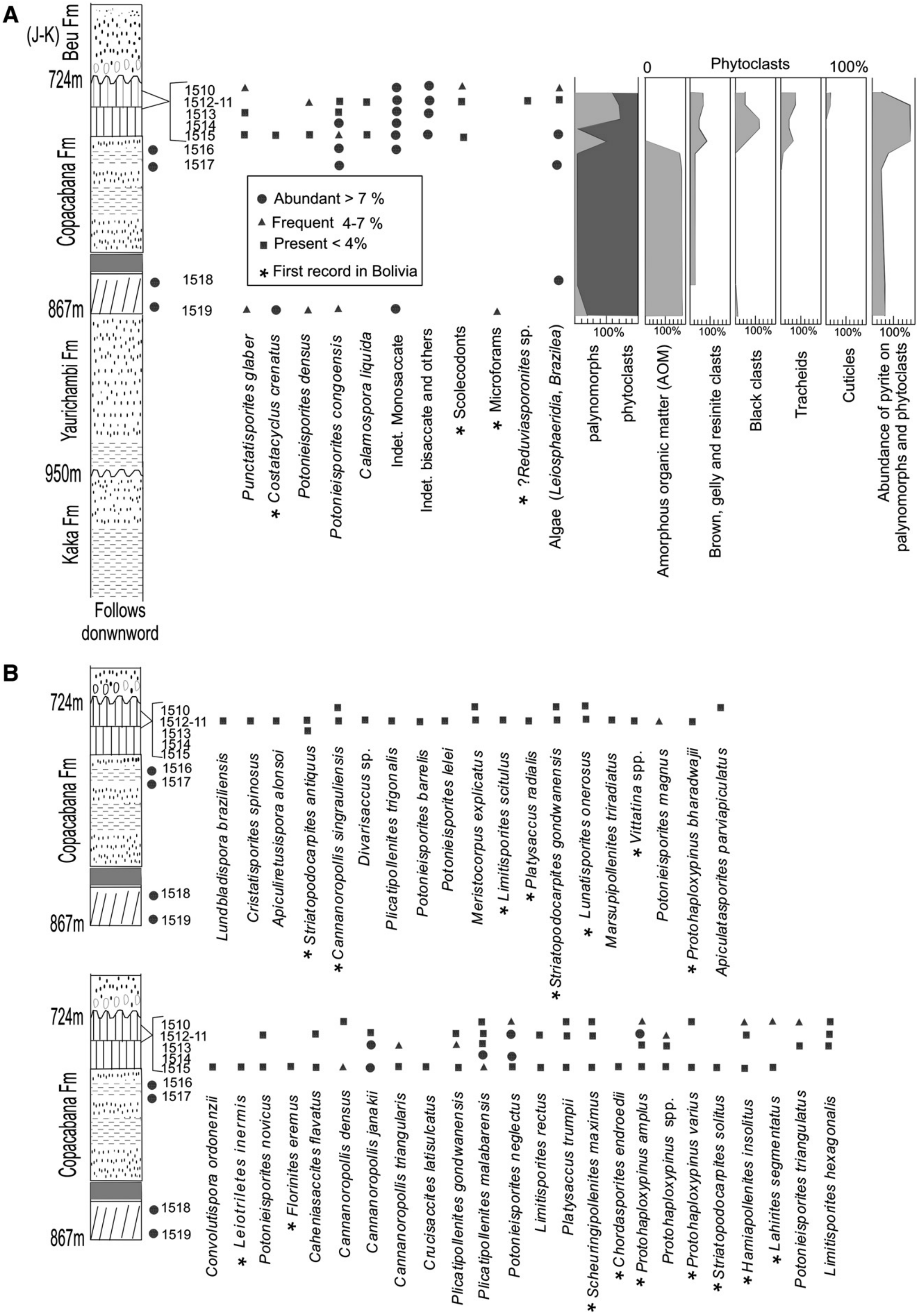


Fig. 4. Relative abundance of phytoclasts and palynomorphs taxa recorded in the Pando X-1 Borehole. For other references see Fig. 1C.

1000 magnifications). The photomicrographs were obtained with a *Pax-it* (3.1 megapixels) video camera and the position of illustrated specimens in the respective slides quoted with the BAFC-Pl acronym, are based on England-Finder coordinates.

4. Palynology

4.1. Composition of the assemblages

In the assemblages here recovered from the Pando X-1, 48 species are recorded, six of which are trilete spores. Among the pollen grains, 21 are monosaccate and 19 bisaccate (11 striate species); scarce scolecodonts, microforaminifera and algae are also present (see Fig. 4 and Plates I–V). Palynomorphs are fairly well-preserved, light yellow to light orange in colour corresponding to a thermal alteration index (TAI) between 1 and 2 according to the scale of Utting et al. (1989). However, many specimens are crushed or quite pyritized thus, their taxonomical designations were prevented. Major groups of palynomorphs and phytoclasts showed an uneven distribution throughout the studied interval in terms of both relative abundance and diversity but the appearance of striate pollen grains enables the distinction of two assemblages (see Figs. 1C, 3, 4). The lower assemblage (A1) is dominated by amorphous organic matter (Pl. 5 H) and less frequent palynomorphs represented by monosaccate pollen grains and spores. The upper assemblage (A2) is characterized by a more diverse palynoflora (mainly striate and non-striate pollen grains) and a dominance of tracheids and brown and black phytoclasts. Trilete spores, scolecodonts, microforaminifera and algae are less frequently recorded.

Most of the species recognized in both assemblages are well-known in several Pennsylvanian and/or Cisuralian palynofloras of South America and elsewhere (see Fig. 5 and Appendix A). Hence, descriptions, range of measures, previous synonymy lists and occurrences of these taxa are here avoided, so readers should consult Playford and Dino (2000a,b), Azcuy and di Pasquo (2000), Azcuy et al. (2002), di Pasquo et al. (2003a,b), Souza et al. (2003) and Félix

Plate I. Magnification of all specimens: 500x (Scale bar: 20 μm).

1. *Calamospora liquida* Kosanke. BAFC-Pl 1515(5) W38/3.
2. *Punctatisporites glaber* (Naumova) Playford. BAFC-Pl 1515(5) S19/2.
3. *Apiculiretusispora alonsoi* Ottone. BAFC-Pl 1511(4) G30/2.
4. *Leiotriletes sphaerotriangularis* (Loose) Potonié and Kremp. BAFC-Pl 1515(5) M43/2.
5. *Apiculatasporites parviapiculatus* Azcuy. BAFC-Pl 1510(5) D64/2.
6. *Convolutispora ordonensis* Archangelsky and Gamerro. BAFC-Pl 1515(5) P53/3.
7. *Cristatisporites spinosus* (Menéndez and Azcuy) Playford. BAFC-Pl 1512(5) Z27/4.
8. *Lundbladispora braziliensis* (Pant and Srivastava) Marques Toigo and Pons emend. Toigo and Picarelli. BAFC-Pl 1512(5) D34/4.
9. *Caheniasaccites flavatus* Bose and Kar emend. Azcuy and di Pasquo. BAFC-Pl 1515(5) O56.
10. *Cannanoropollis triangularis* (Mehta) Bose and Maheshwari. BAFC-Pl 1515(5) G50.
11. *Florinites eremus* Balme and Hennelly. BAFC-Pl 1515(5) Y16.
12. *Cannanoropollis janakii* Potonié and Sah. BAFC-Pl 1512(5) P57.
13. *Cannanoropollis singrauliensis* (Sinha) Foster. BAFC-Pl 1510(5) L45.
14. *Divarisaccus* sp. BAFC-Pl 1512(5) D33/2.
15. *Crucisaccites latisulcatus* Lele and Maithy. BAFC-Pl 1515(5) D52.
16. *Cannanoropollis densus* (Lele) Bose and Maheshwari. BAFC-Pl 1515(5) S17/4.
17. *Costatacyclus crenatus* Felix and Burbridge. BAFC-Pl 1515(5) Z62/3.

Plate II. Magnification of all specimens: 500× (Scale bar: 20 μm). (see on page 272)

1. *Plicatipollenites gondwanensis* (Balme and Hennelly) Lele. BAFC-Pl 1515(5) Q63/2.
2, 4. *Potonieisporites lelei* Maheshwari. 2. BAFC-Pl 1512(5) S33/3. 4. BAFC-Pl 1512(5) S65/3.
3. *Potonieisporites densus* Maheshwari. BAFC-Pl 1515(5) G17/4.
5. *Potonieisporites congoensis* Bose and Maheshwari. BAFC-Pl 1515(5) P51.
6. *Potonieisporites magnus* Lele and Karim. BAFC-Pl 1511(4) R16/4.
7. *Plicatipollenites malabarensis* (Potonié and Sah) Foster. BAFC-Pl 1515(5) G56.
8. *Potonieisporites neglectus* Potonié and Lele. BAFC-Pl 1515(5) C44.
9. *Potonieisporites barrelis* Tiwari. BAFC-Pl 1512(5) D51.
10. *Plicatipollenites trigonalis* Lele. BAFC-Pl 1512(5) Z26/4.

Plate III. Magnification of all specimens: 500× (Scale bar: 20 μm). (see on page 273)

1. *Potonieisporites novicus* Bhardwaj emend. Poort and Veld. BAFC-Pl 1515(5) J39/4.
2. *Potonieisporites triangulatus* Tiwari. BAFC-Pl 1513(5) Q52/3.
3, 4. *Meristocorpus explicatus* Playford and Dino. 3. BAFC-Pl 1511(4) V55/3. 4. BAFC-Pl 1512(5) R109.
5. *Limitisporites hexagonalis* Bose and Maheshwari. BAFC-Pl 1512(5) E21/3.
6. *Limitisporites rectus* Leschik. BAFC-Pl 1515(5) W49/3-4.
7. *Limitisporites scitulus* Playford and Dino. BAFC-Pl 1512(5) T60/4.
8. *Chordasporites endroedii* MacRae. BAFC-Pl 1515(5) U44.
9. *Platysaccus trumpii* Ottone. BAFC-Pl 1512(5) H54/4.
10. *Platysaccus radialis* (Leschik) Clarke. BAFC-Pl 1512(5) B36/4.

Plate IV. Magnification of all specimens: 500× (Scale bar: 20 μm). (see on page 274)

1. *Scheuringipollenites maximus* (Hart) Tiwari. BAFC-Pl 1512(5) C43/3.
2, 3. *Marsupipollenites triradiatus* (Balme and Hennelly) Balme. 2. BAFC-Pl 1512(5) E52. 3. BAFC-Pl 1512(5) D63/2.
4, 15, 16. *Protohaploxypinus amplus* (Balme and Hennelly) Hart. 4. BAFC-Pl 1512(5) H36. 15. BAFC-Pl 1510(5) J29/2.16. BAFC-Pl 1511(4) P50.
5. *Protohaploxypinus varius* (Bharadwaj) Balme. BAFC-Pl 1510(5) D56/4.
6. *Lunatisporites onerosus* Playford and Dino. BAFC-Pl 1510(5) N34/4.
7, 10. *Hamiapollenites insolitus* (Bharadwaj and Salujha) Balme. 7. BAFC-Pl 1512(5) B65/1. 10. BAFC-Pl 1511(4) U38/2.
8. *Striatopodocarpites antiquus* (Leschik) Potonié. BAFC-Pl 1512(5) C53/2.
9. *Protohaploxypinus bharadwajii* Foster. BAFC-Pl 1511(4) U46/2.
11. *Lahirites segmentatus* Dino and Playford. BAFC-Pl 1510(5) C46.
12, 14. *Vittatina* spp. 12. BAFC-Pl 1512(5) U61/3. 14. BAFC-Pl 1512(5) B65.
13. *Striatopodocarpites gondwanensis* Lakhanpal, Sah and Dube emend. Hart. BAFC-Pl 1510(5) Y18/4.
17. *Striatopodocarpites solitus* (Bharadwaj and Salujha) Foster. BAFC-Pl 1515(5) D56/2.

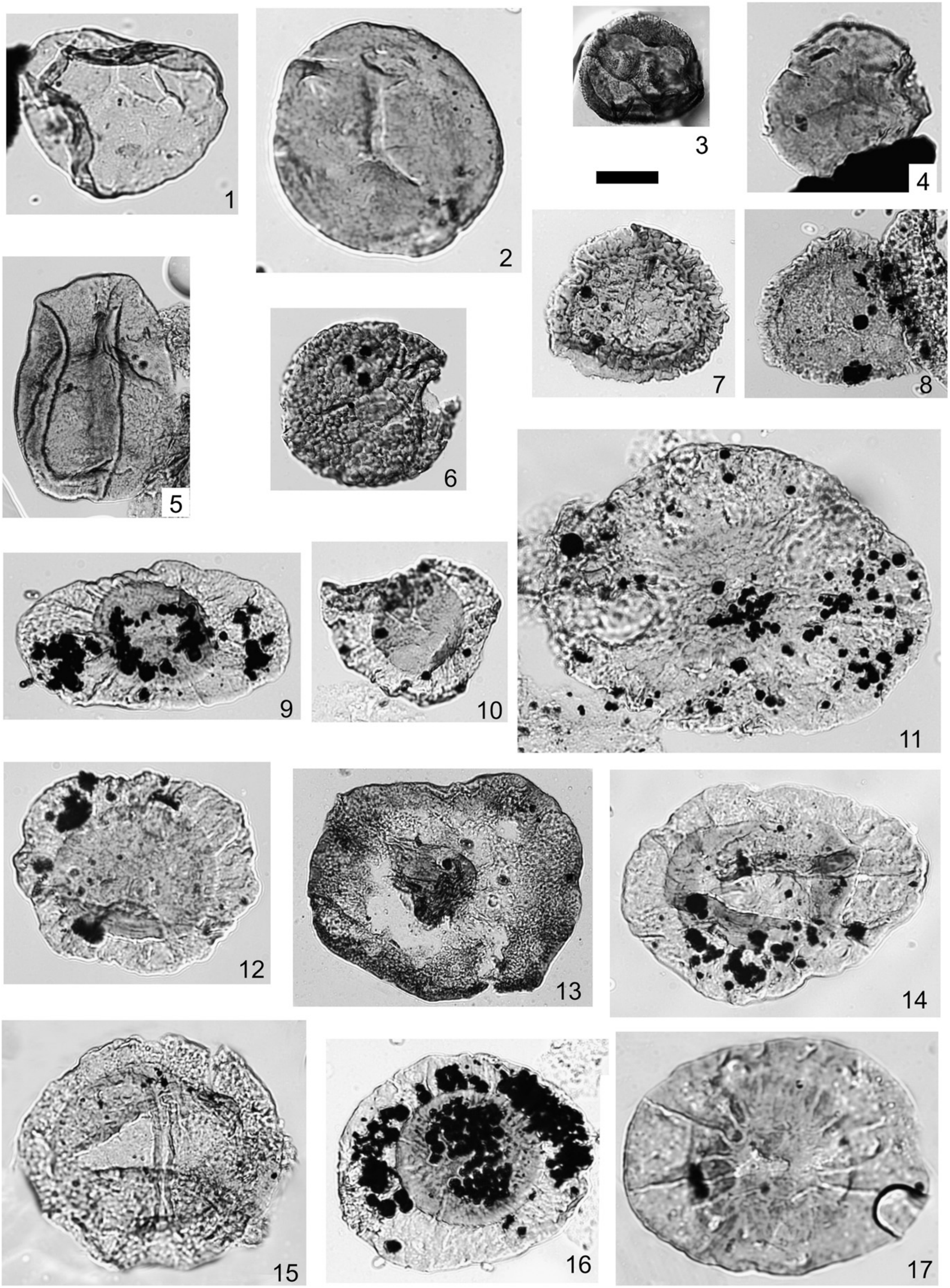


Plate I.

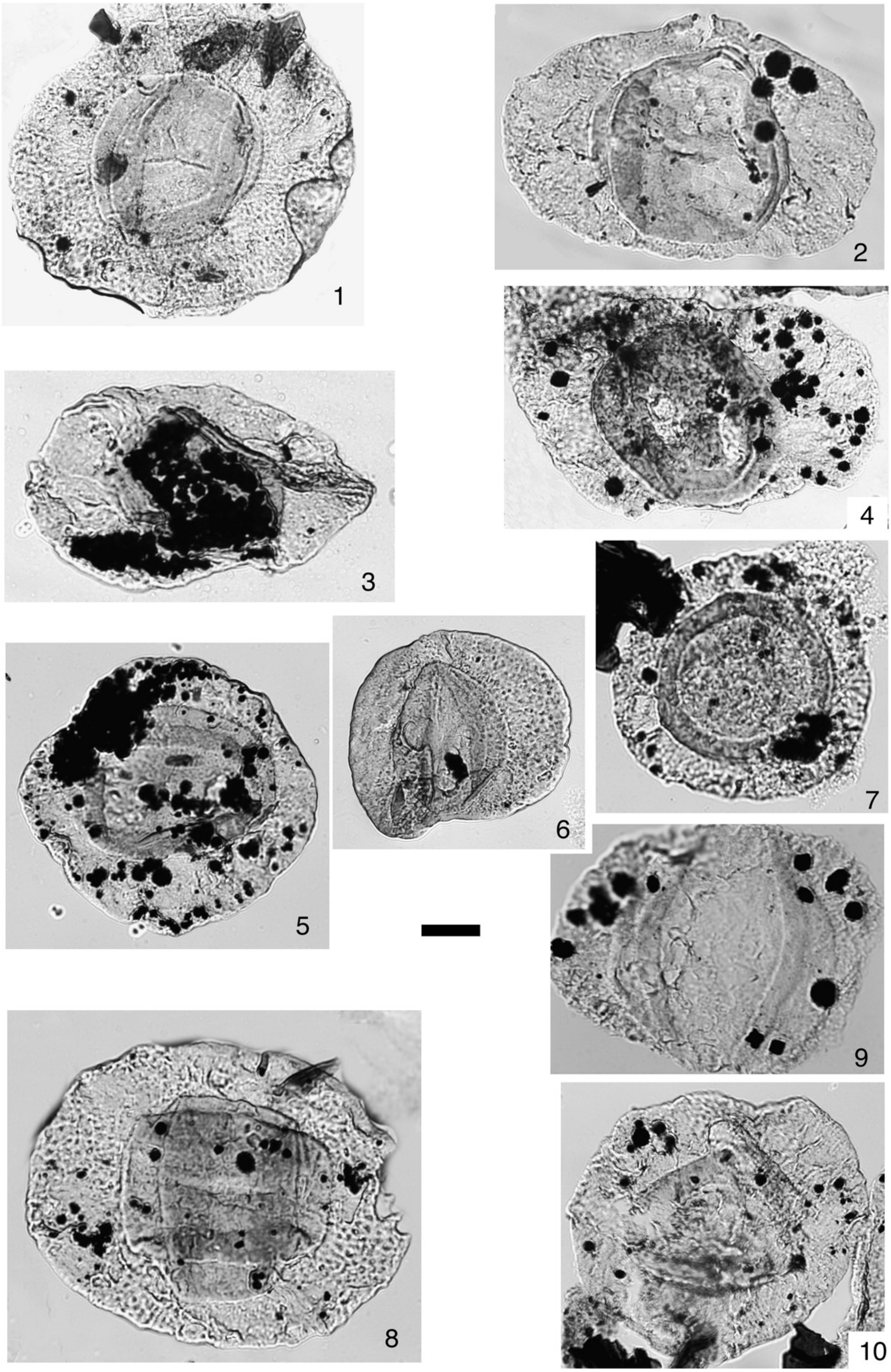


Plate II (*caption on page 270*).

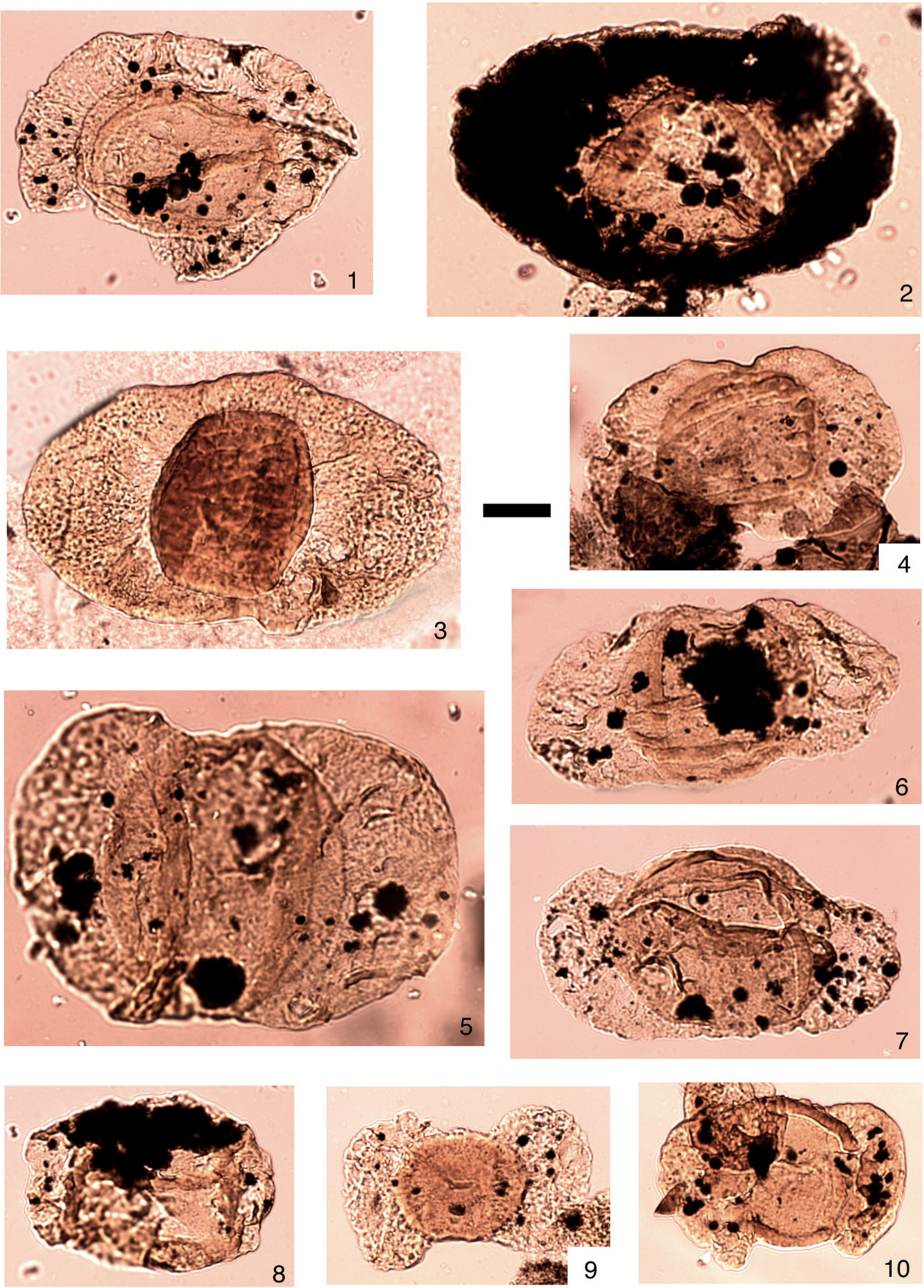


Plate III (*caption on page 270*).

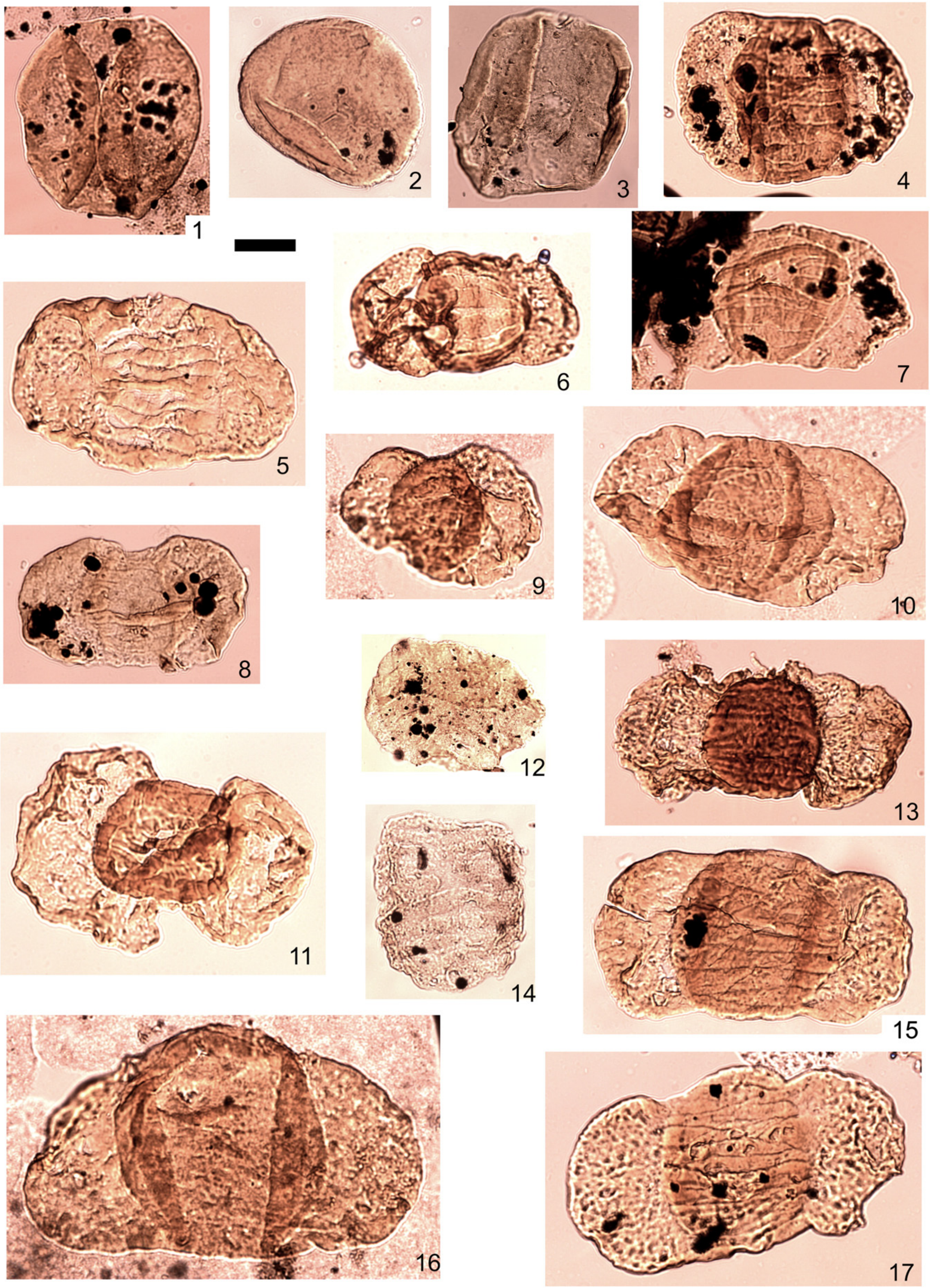


Plate IV (*caption on page 270*).

et al. (2006) and references therein. Only additional taxonomical considerations (remarks and more synonymies) are reported when necessary in the list of recorded taxa presented below following the systematical order of Potonié (1970) and others. Orientation terms for general and central body ambs of bilateral pollen grains are after Hart (1965) where l-a and t-a elongations are equivalent to length and height respectively. Other terms are accorded to Punt et al. (2007).

4.2. Systematic list

Anteturma PROXIMEGERMINANTES Potonié, 1970

Turma TRILETES (Reinsch) Dettmann, 1963

Suprasubturma ACAVATRILETES Dettmann, 1963

Subturma AZONOTRILETES (Luber) Dettmann, 1963

Infraturma LAEVIGATI (Bennie and Kidston) Potonié, 1970

Genus *Calamospora* Schopf, Wilson and Bentall, 1944

Type species: *Calamospora hartungiana* Schopf *in* Schopf, Wilson and Bentall, 1944.

Calamospora liquida Kosanke, 1950 (Plate I, 1)

Genus *Leiotriletes* Naumova emend. Potonié and Kremp, 1954

Type species: *Leiotriletes sphaerotriangulus* (Loose) Potonié and Kremp, 1954.

Leiotriletes inermis (Waltz) Ischenko, 1952 (Plate I, 4)

Genus *Punctatisporites* Ibrahim emend. Potonié and Kremp, 1954

Type species: *Punctatisporites punctatus* Ibrahim, 1933.

Punctatisporites glaber (Naumova) Playford, 1962 (Plate I, 2)

Infraturma RETUSOTRILETI Streel, 1964

Genus *Apiculiretusispora* Streel, 1964

Type species: *Apiculiretusispora brandtii* Streel, 1964.

Apiculiretusispora alonsoi Ottone, 1989 (Plate I, 3)

Infraturma APICULATI (Bennie and Kidston) Potonié, 1956

Subinfraturma NODATI Dybová and Jachowicz, 1957

Genus *Apiculatasporites* Ibrahim emend. Smith and Butherworth, 1967

Type species: *Apiculatasporites spinulistratus* (Loose) Ibrahim, 1933.

Apiculatasporites parviapiculatus Azcuy, 1975 (Plate I, 5)

Infraturma MURORNATI Potonié and Kremp, 1954

Genus *Convolutispora* Hoffmeister, Staplin, and Malloy, 1955

Type species: *Convolutispora florida* Hoffmeister, Staplin, and Malloy, 1955

Convolutispora ordonensis Archangelsky and Gamerro, 1979 (Plate I, 6)

Suprasubturma LAMINATITRILETES Smith and Butherworth, 1967

Subturma ZONOLAMINATITRILETES Smith and Butherworth, 1967

Infraturma CINGULICAVATI Smith and Butherworth, 1967

Genus *Cristatisporites* Potonié and Kremp emend. Butterworth, Jansonius, Smith, and Staplin, 1964

Type species: *Cristatisporites indignabundus* (Loose) Potonié and Kremp, 1954.

Cristatisporites spinosus (Menéndez and Azcuy) Playford emend. Césari, 1985 (Plate I, 7)

2002 *Cristatisporites* sp. A Stephenson and Osterloff, p. 16, pl. 3, fig. 7.

Remarks: Both the description and illustration of this specimen presented by Stephenson and Osterloff (2002) are in agreement with the diagnosis and later emendation of this species (see Césari, 1985).

Genus *Lundbladispora* Balme emend. Playford, 1965

Type species: *Lundbladispora wilmottii* (Balme) Playford, 1965.

Lundbladispora braziliensis (Pant and Srivastava) Marques Toigo and Pons emend. Marques Toigo and Picarelli, 1984 (Plate I, 8)

Anteturma VARIEGERMINANTES Potonié, 1970

Turma SACCITES Erdtman, 1947

Subturma MONOSACCITES (Chitaley) Potonié and Kremp, 1954

Infraturma DIPOLSACCITI Hart emend. Dibner, 1971

Genus *Caheniasaccites* Bose and Kar emend. Azcuy and di Pasquo, 2000

Type species: *Caheniasaccites flavatus* Bose and Kar emend. Azcuy and di Pasquo, 2000.

Caheniasaccites flavatus Bose and Kar emend. Azcuy and di Pasquo, 2000 (Plate I, 9)

1968 *Vestigisporites* cf. *gondwanensis* (Mehta) Hart; Nahuys, Alpern and Ybert, p. 32, 55, 56.

1988 *Limitisporites* sp. MacRae, p. 51, pl. 20, figs. 13–18.

1988 *Caheniasaccites ovatus* Bose and Kar; MacRae, p. 79, pl. 37, figs. 8–13, pl. 38, figs. 1–5.

1988 *Potonieisporites* sp. Gilby and Foster, p.189, pl. 4, fig. 1.

1988 *Caheniasaccites ovatus* Bose and Kar; Gilby and Foster, p. 190, pl. 5, fig. 1.

1988 *Potonieisporites* sp. Coquel, Doubinger and Massa, p.13, pl. 2, fig. 16.

1989 *Potonieisporites brasiliensis* (auct. non) (Nahuys, Alpern and Ybert) Archangelsky and Gamerro; Ottone, p. 123, pl. 10, fig. 4.

2002 *Caheniasaccites ovatus* Bose and Kar; Playford and Dino, p. 263, pl. 7, figs. 7, 8.

2002 *Caheniasaccites densus* Lele and Karim; Playford and Dino, p. 263, pl. 7, fig. 6.

Remarks: The following synonymy list is in agreement with the criteria presented by Azcuy and di Pasquo (2000) for this taxon. For additional synonymies see also di Pasquo et al. (2003b) and Souza et al. (2003).

Genus *Cannanoropollis* Potonié and Sah, 1960

Type species: *Cannanoropollis janakii* Potonié and Sah, 1960.

Cannanoropollis densus (Lele) Bose and Maheshwari, 1968 (Plate I, 16)

1987 *Parasaccites* sp. Besems and Schuurman, p. 45, pl. 3, fig. 11.

Remarks: The specimen illustrated by Besems and Schuurman (1987) shows a more or less circular amb conformable with a thick corpus, and radial folds in the saccus. These features suggest its assignment to *Cannanoropollis densus*. For additional synonymies see Azcuy and di Pasquo (2000) and Souza et al. (2003).

Cannanoropollis janakii Potonié and Sah, 1960 (Plate I, 12)

2002 *Cannanoropollis korbaensis* (Bharadwaj and Tiwari) Foster; Wood, Groves, Wahlman, Breckle and Alemán, p. 660, pl. 10, fig. 1.

2002 *Parasaccites difussus* Tiwari; Pittau, Barca, Cocherie, Del Rio, Fanning and Rossi, p. 569, fig. 6.1.

2002 *Parasaccites distinctus* Tiwari; Pittau, Barca, Cocherie, Del Rio, Fanning and Rossi, p. 569, fig. 6.2.

Remarks: The specimens illustrated by Wood et al. (2002) and Pittau et al. (2002) are considered conspecific with *Cannanoropollis janakii* as they show a more or less circular or slightly oval amb conformable with the corpus, and radial folds in the saccus. For additional synonymies see Foster (1979), MacRae (1988), Millsteed (1999), Azcuy and di Pasquo (2000), Playford and Dino (2000b) and Souza et al. (2003).

Cannanoropollis singrauliensis (Sinha) Foster, 1979 (Plate I, 13)

Cannanoropollis triangularis (Mehta) Bose and Maheshwari, 1968 (Plate I, 10)

Genus *Costatacyclus* Felix and Burbridge emend. Urban, 1971

Type species: *Costatacyclus crenatus* Felix and Burbridge emend. Urban, 1971. *Costatacyclus crenatus* Felix and Burbridge emend. Urban, 1971 (Plate I, 17)

1968 *Katangaites ovatus* Bose and Maheshwari, p. 53, pl. 12, figs. 4, 5.

Remarks and comparisons: *Katangaites ovatus* Bose and Maheshwari is indistinguishable from this taxon and thus, considered to be a junior synonym. A similar specimen was illustrated as *Gondwanopollis* sp. by Pittau et al. (2002, p. 569, fig. 6.8) from the earliest Cisuralian palynoflora in Italy.

Genus *Crucisaccites* Lele and Maithy, 1964

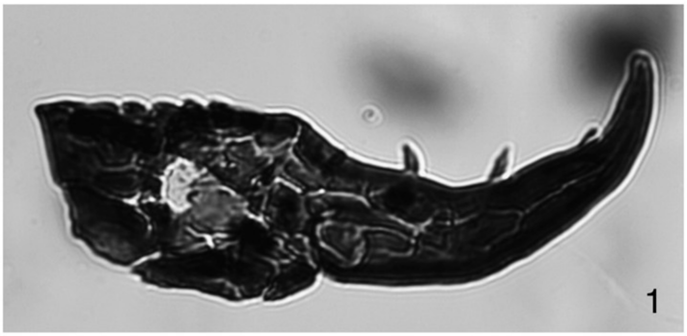
Type species: *Crucisaccites latisulcatus* Lele and Maithy, 1964.

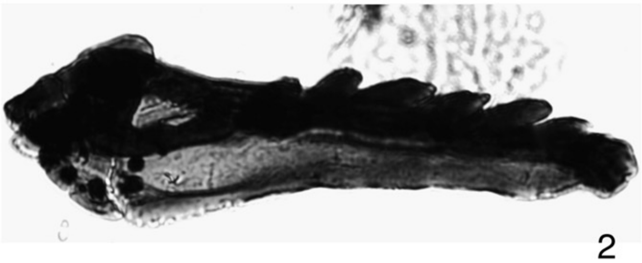
Crucisaccites latisulcatus Lele and Maithy, 1964 (Plate I, 15)

Genus *Divarisaccus* Venkatachala and Kar, 1966

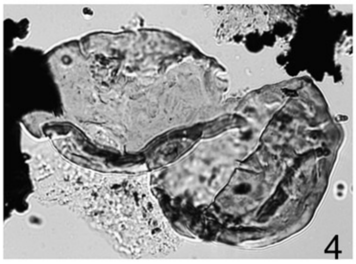
Type species: *Divarisaccus lelei* Venkatachala and Kar, 1966.

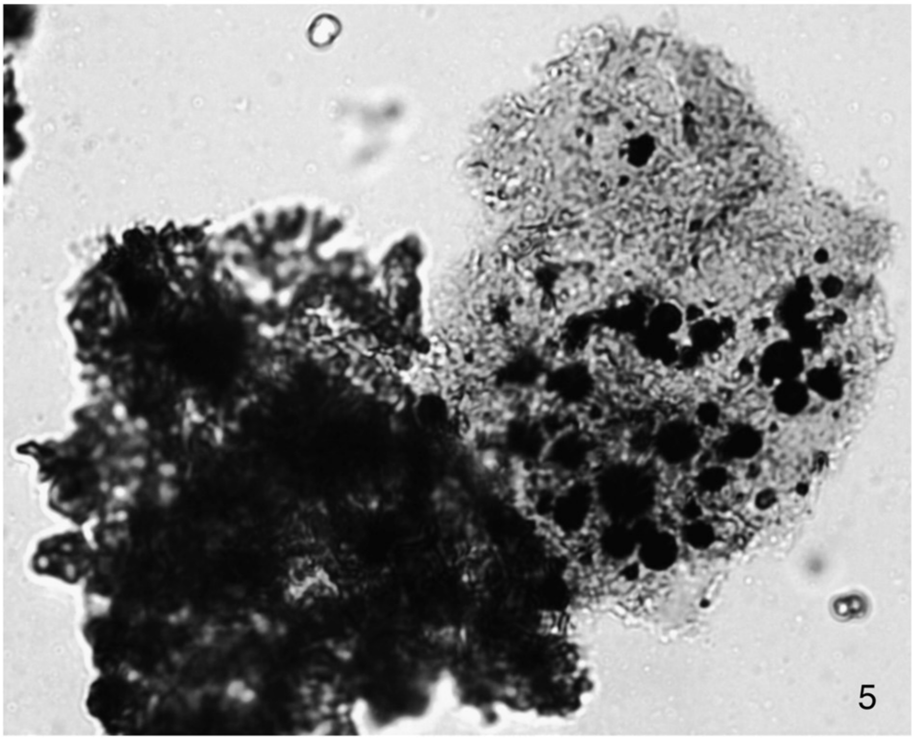
Divarisaccus sp. (Plate I, 14)


1


2


3


4


5


6


7


8

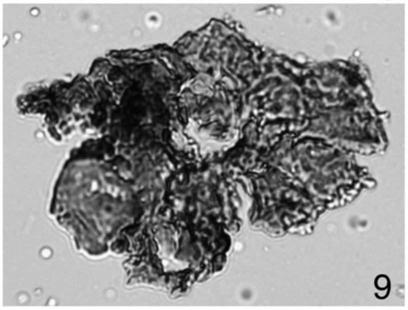

9

Plate V. Magnification of all specimens: 500× (Scale bar: 20 μm) except Fig. 4 (Scale bar: 40 μm).

1, 7.	Indeterminate Scolecodonts. 1. BAFC-Pl 1512(5) Z65/1. 7. BAFC-Pl 1512(5) X57/2.
2.	*Menogenys* sp. in García. BAFC-Pl 1515(5) P50.
3.	*Nereigenys* sp. in García. BAFC-Pl 1512(5) D39/3.
4.	*Leiosphaeiridia* sp. BAFC-Pl 1515(5) Y18/3.
5.	Amorphous organic matter (AOM) and pyrite. BAFC-Pl 1516(5) K40.
6.	*Hemiruptia* sp. BAFC-Pl1515(5) K40/3.
8.	?*Reduviasporonites* sp. BAFC-Pl 1512(5) S59/4.
9.	Microforaminifera. BAFC-Pl 1519(5) W32/2.

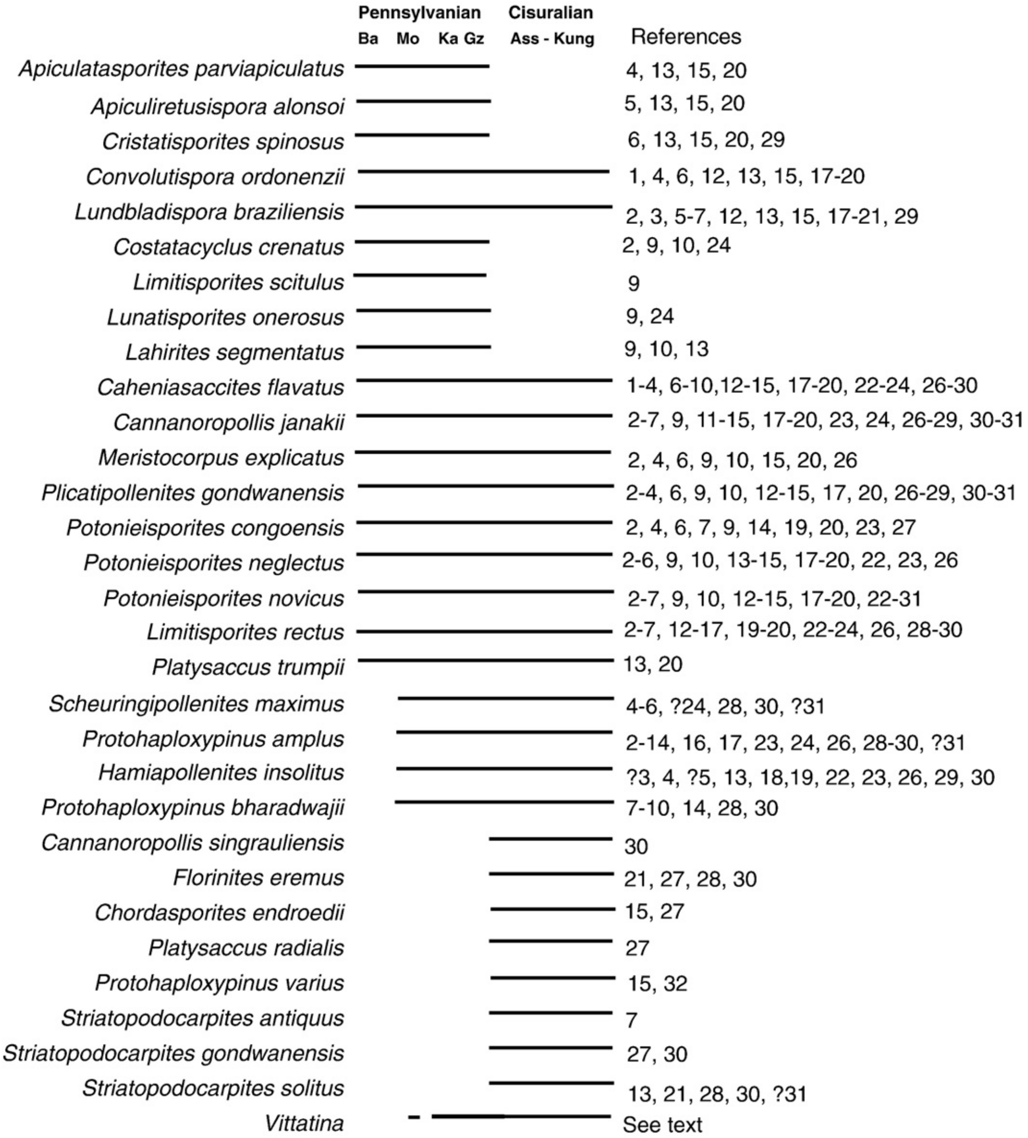


Fig. 5. Global Pennsylvanian and Cisuralian stratigraphic distribution of selected species recorded in the Pando X-1 Borehole. References: 1-Souza (2003), 2-Souza et al. (2003), 3-Souza et al. (2006, *Ac* Zone), 4-di Pasquo et al. (2003a,b *Cm* Zone), 5-Longhim et al. (2003), 6-Souza and Marques-Toigo (2005), Souza (2006), 7-Souza and Callegari (2004, *Vit* Zone), 8-Premoar et al. (2006, *Lv* Zone), 9-Playford and Dino (2000a,b), 10-Dino and Playford (2002), 11-Melo et al. (1999), 12-Beri and Pecoits (2001, *Lv* Zone), 13-Césari and Gutiérrez (2001), 14-Vergel and Lech (2001), 15-García (1995, 1996), 16-Césari et al. (1996, *LW* Zone), 17-Césari et al. (1995), 18-Archangelsky and Vergel (1996), 19-Playford and Dino (2002), 20-di Pasquo (2003), 21-Cousminer (1965, *Lv* Zone in Azcuy et al., 2007), 22-Ottone et al. (1998), 23-Azcuy et al. (2002), 24-Wood et al. (2002), 25-Dunn (2001), 26-Besems and Schuurman (1987), Coquel et al. (1988), Attar et al. (1980), Loboziak and Clayton (1988), 27-MacRae (1988), 28-Lindström (1995), Semkiwa et al. (1998), Stephenson and McLean (1999), Lindström and McLoughlin (2007), 29-Stephenson and Filatoff (2000), Stephenson and Osterloff (2002), Stephenson et al. (2003), 30-Foster (1979, 1982), Gilby and Foster (1988), Backhouse (1991), 31-Pittau et al. (2002), 32-Balme (1970). See also Fig. 3.

Comparison: Divarisaccus stringoplicatus Ottone (1991) differs from this species in having a slightly large oval central body.

Genus *Florinites* Schopf, Wilson and Bentall, 1944

Type species: *Florinites pellucidus* (Wilson and Coe) Wilson, 1958.

Florinites eremus Balme and Hennelly, 1955 (Plate I, 11)

Occurrence: This is the only one species in common with the Permian palynoflora of the Copacabana Formation in Peru described by Doubinger and Marocco (1981) (see Fig. 3).

Genus *Plicatipollenites* Lele, 1964

Type species: *Plicatipollenites malabarensis* (Potonié and Sah) Foster, 1975.

Plicatipollenites gondwanensis (Balme and Hennelly) Lele, 1964 (Plate II, 1)

1964 *Nuskoisporites* sp. Singh, p. 253, pl. 45, fig. 12.

1988 *Plicatipollenites malabarensis* (Potonié and Sah) Foster; Loboziak and Clayton, p. 149, pl. 24, fig. 5.

1988 *Plicatipollenites gondwanensis* (Balme and Hennelly) Lele; MacRae (pars.), p. 71, pl. 28, figs. 2, 3, 6.

Remarks: MacRae (1988) has found in his assemblages from the Pennsylvanian–Permian of South Africa, a morphological transition between *Plicatipollenites gondwanensis* and *P. malabarensis*, and all the specimens were attributed to *P. gondwanensis*. It appears elsewhere that these taxa are not strictly recorded together every time. Hence, both taxa are here maintained and those specimens illustrated by MacRae (1988) that present the peripheral continuous fold on the central body are here transferred to *Plicatipollenites malabarensis*. For additional synonymy see Playford and Dino (2000b) and Souza et al. (2003) and references therein.

Plicatipollenites malabarensis (Potonié and Sah) Foster, 1975 (Plate II, 7)

1988 *Plicatipollenites gondwanensis* (Balme and Hennelly) Lele; MacRae (pars.), p. 71, pl. 28, figs. 1, 5, 7.

Plicatipollenites trigonalis Lele, 1964 (Plate II, 10)

1988 *Wilsonites ephemerus* (auct. non) Tschudy and Kosanke; Coquel, Doubinger and Massa, p.13, pl. 2, fig. 14.

Remarks: The specimen illustrated by Coquel et al. (1988) has a more or less circular amb and a subtriangular central body with three intexinal folds on its distal face defining a subtriangular cappula. These features support its assignment to *Plicatipollenites trigonalis*. For additional synonymy see Playford and Dino (2000b) and Souza et al. (2003).

Genus *Potonieisporites* Bhardwaj emend. Bharadwaj, 1964

Type species: *Potonieisporites novicus* Bhardwaj emend. Poort and Veld, 1997.

Potonieisporites barrelis Tiwari, 1965 (Plate II, 9)

1988 *Potonieisporites novicus* (auct. non) Bhardwaj emend. Poort and Veld; MacRae (pars.), p. 76, pl. 36, figs. 9, 12.

1988 *Limitisporites* sp. Gilby and Foster, p. 190, pl. 6, fig. 19.

Remarks: The specimens illustrated by MacRae (1988) and Gilby and Foster (1988) show an oval to subcircular amb, a barrel to subhexagonal shaped central body and two distal intexinal folds delimiting a subrectangular cappula. Hence, they are attributed to *Potonieisporites barrelis* in agreement with Azcuy and di Pasquo (2000).

Potonieisporites congoensis Bose and Maheshwari, 1968 (Plate II, 5)

1988 *Potonieisporites novicus* (auct. non) Bhardwaj emend. Poort and Veld; MacRae (pars), p. 76, pl. 37, fig. 4.

1988 *Potonieisporites* sp. Gilby and Foster, p. 190, pl. 5, fig. 8.

2002 *Potonieisporites lemniscatus* Shwartsman in Inossova, Shwartsman and Krusina; Pittau, Barca, Cocherie, Del Rio, Fanning, Rossi, p. 570, fig. 7.10.

Remarks: The specimens illustrated by MacRae (1988), Gilby and Foster (1988) and Pittau et al. (2002) show an amb subquadrangular to subcircular more or less conforming with its central body, which presents an intexinal distal fold system more or less peripheral composed of four elements. Therefore, they are considered junior synonym of *Potonieisporites congoensis* in agreement with Azcuy and di Pasquo (2000).

Potonieisporites densus Maheshwari, 1967 (Plate II, 3)

For synonymy see Souza et al. (2003).

Potonieisporites lelei Maheshwari, 1967 (Plate II, 2, 4)

1988 *Potonieisporites novicus* (auct. non) Bhardwaj emend. Poort and Veld; MacRae (pars.), p. 76, pl. 36, fig. 10.

1988 *Florinites diversiformis* (auct. non) Kosanke; Coquel, Doubinger and Massa, p. 11, pl. 1, fig. 11.

1995 *Potonieisporites balmei* (auct. non) (Hart) Segroves; Lindström, p. 399, pl. 10, figs. 3, 4.

2000 *Potonieisporites brasiliensis* (?auct. non) (Nahuys, Alpern and Ybert) Archangelsky and Gamerro; Stephenson and Filatoff, p. 184, pl. 3, fig. i.

2002 *Potonieisporites solidus* (?auct. non) Shwartsman *in* Inossova, Shwartsman and Krusina; Pittau, Barca, Cocherie, Del Rio, Fanning, Rossi, p. 570, fig. 7.3.

2008 *Potonieisporites* spp. Stephenson, Rawahi, Casey, p. 20, pl. 1, figs. n, o.

Remarks: The specimens illustrated by MacRae (1988), Coquel et al. (1988), Lindström (1995), Stephenson and Filatoff (2000), Pittau et al. (2002) and Stephenson et al. (2008) are considered to be attributed to *Potonieisporites lelei* as they present its main diagnostic features (i.e., amb transversely oval to elliptical, central body circular to subcircular, saccus relatively narrow laterally with distal attachment associated to more or less circular body infold system and frequent radial folds). This species was recorded from the Early Permian of Congo (Bose and Maheshwari, 1968) and India (Maheshwari, 1967). Many specimens attributed to *Potonieisporites brasiliensis*, figured in the literature of South American palynofloras, are neither included here nor in the Appendix A as they will be re-examined and included in a specific contribution on this genus (see Félix et al., 2008).

Potonieisporites magnus Lele and Karim, 1971 (Plate II, 6)

1988 *Jugasporites delasaucei* (auct. non) (Potonié and Klaus) Klaus; MacRae, p. 53, pl. 21, figs. 17–18.

1988 *Potonieisporites novicus* (auct. non) Bhardwaj emend. Poort and Veld; MacRae (pars.), p. 76, pl. 37, fig. 3.

1988 *Rugasaccites* sp. A Gilby and Foster, p. 190, pl. 4, fig. 12.

1993 *Gondwanopollis lenticulatus* Gutiérrez, p. 196, pl. 4, fig. 4, pl. 5, fig. 7.

non 1999 *Potonieisporites magnus* Lele and Karim; Melo, Loboziak and Streel, p. 32, pl. 3, fig. 15.

Remarks: The specimens illustrated by MacRae (1988), Gilby and Foster (1988) and Gutiérrez (1993) show an amb suboval, a central body t-a oval and one more or less peripheral distal fold or two t-a semilunar folds associated with the vertically elongated cappula. Hence, they are considered junior synonyms of *Potonieisporites magnus*, except for the specimen illustrated by Melo et al. (1999), which is considered to be *Potonieisporites methoris* (Hart) Foster. For additional synonymy see Azcuy and di Pasquo (2000) and Souza et al. (2003).

Potonieisporites neglectus Potonié and Lele, 1961 (Plate II, 8)

1980 *Potonieisporites elegans* (auct. non) (Wilson and Coe) Wilson and Venkatachala; Attar, Fournier, Candilier, Coquel, p. 616, pl. 4, fig. 11.

Remarks: The specimen illustrated by Attar et al. (1980) shows an amb oval to subrectangular, a central body slightly l-a oval to subcircular with a well-defined distal intexinal fold system delimiting a cappula t-a subrectangular in shape. These features support its attribution to *Potonieisporites neglectus*. For additional synonymy see Azcuy and di Pasquo (2000) and Souza et al. (2003).

Potonieisporites novicus Bhardwaj emend. Poort and Veld, 1997 (Plate III, 1)

1964 *Potonieisporites* sp. Singh, p. 253, pl. 45, fig. 18.

1988 *Vestigisporites* sp. Coquel, Doubinger and Massa, p.13, pl. 2, fig. 13.

(*auct. non*) 1988 *Potonieisporites novicus* Bhardwaj emend. Poort and Veld; MacRae (pars.), p. 76, pl. 36, figs. 8, 11, 13, 14.

2000a *Potonieisporites brasiliensis* (auct. non) (Nahuys, Alpern and Ybert) Archangelsky and Gamerro; Playford and Dino, p. 26, pl. 8, fig. 6.

2002 *Potonieisporites* sp. Wood, Groves, Wahlman, Breckle and Alemán, p. 660, pl. 10, fig. 10.

Remarks: The specimens illustrated by Singh (1964), Coquel et al. (1988), Playford and Dino (2000a) and Wood et al. (2002) show an amb smooth elliptical to subcircular, a corpus l-a elliptical to subcircular, one more or less peripheral and discontinuous distal fold, associated or not with two t-a semilunar-shaped folds, broadly oval cappula and slightly marked radial folds on the saccus. These features characterize *Potonieisporites novicus* supporting this synonymy list. Therefore, the selected specimens illustrated as *Potonieisporites novicus* by MacRae (1988) are better assigned to *Potonieisporites methoris* (Hart) Foster. For additional synonymy see Playford and Dino (2000a), Azcuy and di Pasquo (2000) and Souza et al. (2003) and its references.

Potonieisporites triangulatus Tiwari, 1965 (Plate III, 2)

1964 *Potonieisporites* cf. *neglectus* Potonié and Lele; Singh, p. 253, pl. 45, fig. 17.

1988 *Nuskoisporites dulhuntyi* (auct. non) Potonié and Klaus; Coquel, Doubinger and Massa, p.13, pl. 2, fig. 18.

1991 *Potonieisporites novicus* (auct. non) Bhardwaj emend. Poort and Veld; Backhouse, p. 287, pl. 15, fig. 5.

Remarks: The specimens illustrated by Singh (1964), Coquel et al. (1988) and Backhouse (1991) show an amb oval, a central body subtriangular and a distal infold system composed of three peripheral elements delimiting a subtriangular cappula. These features are present in the diagnosis of *Potonieisporites triangulatus* and support this synonymy list. For additional synonymy see Playford and Dino (2000a) and its references.

Infraturma STRIASACCITI Bharadwaj, 1962

Genus *Meristocorpus* Playford and Dino, 2000

Type species: *Meristocorpus explicatus* Playford and Dino, 2000b.

Meristocorpus explicatus Playford and Dino, 2000b (Plate III, 3, 4)

1987 *Protohaploxypinus* spp. Besems and Schuurman, p. 45, pl. 3, fig. 4.

1996 Genus and species indet. García, p. 12, pl. 3, fig. 10.

Remarks: The monosaccate specimens illustrated by Besems and Schuurman and García (1996) show an amb l-a oval to subrectangular and its central body more or less conformable; the proximal face bears 6 to 10 taeniae l-a arranged and more or less parallel and continuous or somewhat bifurcant; two distal semilunar folds are associated to the attachment zone of the saccus delimiting a subrectangular cappula. These features are present in the diagnosis and illustrations of *Meristocorpus explicatus* and support this synonymy list. For additional comparisons and synonymies see Playford and Dino (2000b) and Souza et al. (2003).

Subturma DISACCITES Cookson, 1947

Infraturma DISACCITRILETES Leschik, 1956

Genus *Chordasporites* Klaus, 1960

Type species: *Chordasporites singulichorda* Klaus, 1960.

Chordasporites endroedii MacRae, 1988 (Plate III, 8)

Remarks: The specimen illustrated as *Vestigisporites* sp. B by García (1996, p. 14, pl. 4, fig. 2) resembles *Chordasporites endroedii* although the former seems to be distinct in having a poorly defined chorda, and in being slightly larger.

Genus *Limitisporites* Leschik emend. Schaarschmidt, 1963

Synonymy: See Playford and Dino (2000b).

Type species: *Limitisporites rectus* Leschik, 1956.

Limitisporites hexagonalis Bose and Maheshwari, 1968 (Plate III, 5)

1991 *Sahnites* sp. Backhouse, p. 287, pl. 15, figs. 1, 2.

2002 *Limitisporites* sp. Wood, Groves, Wahlman, Breckle and Alemán, p. 660, pl. 10, fig. 8.

Remarks: The specimens illustrated by Backhouse (1991) and Wood et al. (2002), show the general features of *Limitisporites hexagonalis* (i.e. diploxylonoid amb, t-a elongated hexagonal to oval central body, and two lunate folds associated with distal sacci attachment zone). Hence, they are assigned to this taxon.

Limitisporites rectus Leschik, 1956 (Plate III, 6)

1970 *Vestigisporites gondwanensis* Cauduro, pl. 19, figs. 132–134.

1988 *Vitreisporites signatus* (auct. non) Leschik; Coquel, Doubinger and Massa, p. 13, pl. 2, fig. 9.

2000 *Sahnites gondwanensis* (auct. non) (Mehta) Pant; Stephenson and Filatoff, p. 180, pl. 2, fig. l.

2002 *Limitisporites* sp. Wood, Groves, Wahlman, Breckle and Alemán, p. 660, pl. 10, fig. 9.

Remarks: *Vestigisporites gondwanensis* Cauduro and the three specimens illustrated by Coquel et al. (1988), Stephenson and Filatoff (2000) and Wood et al. (2002) are considered synonyms of *Limitisporites rectus* because they show its diagnostic features (i.e. haploxylonoid to slightly diploxylonoid amb, corpus subcircular to slightly l-a or t-a oval amb, semilunar folds associated with distal sacci attachment, lateral sacci slightly developed). Analysis of the illustration and description of *Sahnites gondwanensis* (Mehta) Pant (1955, p. 759), suggest that it is distinct from *Limitisporites rectus* in having wider lateral sacci (a more monosaccate form) and lacking of lunate folds associated to t-a distal attachment zones of sacci (see also Hart, 1965). *Vitreisporites signatus* Leschik (1955) is distinct in having a narrow, t-a oval corpus, in lacking folds associated with distal sacci attachment and being small in size. See additional synonymy in Foster (1979), García (1996) and Souza et al. (2003).

Limitisporites scitulus Playford and Dino, 2000b (Plate III, 7)

Genus *Platysaccus* Naumova *ex* Potonié and Klaus, 1954

Type species: *Platysaccus papilionis* Potonié and Klaus, 1954.

Platysaccus trumpii Ottone, 1989 (Plate III, 9)

Platysaccus radialis (Leschik) Clarke, 1965 (Plate III, 10)

Genus *Scheuringipollenites* Tiwari, 1973

Type species: *Scheuringipollenites maximus* (Hart) Tiwari, 1973.

Scheuringipollenites maximus (Hart) Tiwari, 1973 (Plate IV, 1)

Comparisons: Pittau et al. (2002, p. 571, fig. 8.3) illustrated a specimen of *Vesicaspora wilsonii* Schemel from the earliest Cisuralian in Italy, which is very similar to *Scheuringipollenites maximus*. See additional synonymy in Tiwari (1973) and Foster (1979).

Turma PLICATES Naumova emend. Potonié, 1960

Subturma PRAECOLPATES Potonié and Kremp, 1954

Genus *Marsupipollenites* Balme and Hennelly emend. Balme, 1970

Type species: *Marsupipollenites triradiatus* Balme and Hennelly, 1956.

Marsupipollenites triradiatus Balme and Hennelly, 1956 (Plate IV, 2, 3)

Infraturma STRIATITI Pant, 1954

Genus *Hamiapollenites* Wilson emend. Tschudy and Kosanke, 1966

Type species: *Hamiapollenites saccatus* Wilson, 1962.

Hamiapollenites insolitus (Bharadwaj and Salujha) Balme, 1970 (Plate IV, 7, 10)

Remarks: For synonymy and other remarks see Azcuy et al. (2002).

Genus *Lahirites* Bharadwaj, 1962

Type species: Lahirites raniganjensis Bharadwaj, 1962.

Lahirites segmentatus Dino and Playford, 2002 (Plate IV, 11)

2000b *Verticipollenites* sp. A Playford and Dino, p. 111, pl. 13, fig. 1.

2001 *Protohaploxypinus* sp. Césari and Gutiérrez, p. 118, pl. 2, fig. 3.

Remarks: The specimens illustrated by Playford and Dino (2000b) and Césari and Gutiérrez (2001) show a diploxylonoid amb, a subcircular to slightly oval corpus, and a cappa divided into 8–12 taeniae. The taeniae have l-a subparallel arrangement, which is more or less dissected by a t-a discontinuous fine clefts to produce a brickwork-like pattern, and a rectangular, relatively narrow cappula bordered by two folds. Therefore, they are assigned to *Lahirites segmentatus.*

Genus *Lunatisporites* Lesckik emend. Scheuring, 1970

Type species: *Lunatisporites acutus* Leschik, 1955.

Lunatisporites onerosus Playford and Dino, 2000b (Plate IV, 6)

Occurrence: This species is recorded exclusively in the Pennsylvanian of the Amazonas and Madre de Dios Basins (see Figs. 1A, 5 and Appendix A).

Genus *Protohaploxypinus* Samoilovich emend. Morbey, 1975

Type species: *Protohaploxypinus latissimus* (Luber and Waltz) Samoilovich, 1953.

Protohaploxypinus amplus (Bharadwaj and Hennelly) Hart, 1965 (Plate IV, 4, 15, 16)

1965 *Strotersporites indicus* Tiwari, p. 199–200, pl. 6, figs. 139–141.

1987 *Protohaploxypinus* spp. Besems and Schuurman, p. 45, pl. 3, fig. 1.

1988 *Strotersporites indicus* Tiwari; Loboziak and Clayton, p. 149, pl. 24, fig. 12.

1999 *Strotersporites indicus* Tiwari; Melo, Loboziak and Streel, p. 32, pl. 3, fig. 14.

2000 *Strotersporites indicus* Tiwari; Stephenson and Filatoff, p. 180, pl. 2, fig. c.

Remarks and comparisons: Foster (1979) included the species *Strotersporites indicus* Tiwari (1965) as a doubtful junior synonym of *Protohaploxypinus amplus*, but without justification. Nevertheless, from the analysis of the diagnosis and illustrations of both taxa it seems that the only one subtle morphological difference is that *P. amplus* has a few more striae (7–10) than *S. indicus* (4–8). Hence, it is considered not enough to maintain both taxa in agreement with Foster (1979). The specimens attributed to *S. indicus* illustrated by Melo et al. (1999) and Stephenson and Filatoff (2000) are morphologically consistent with *Protohaploxypinus amplus*. Pittau et al. (2002, p. 571, fig. 8.11) illustrated a specimen of *Striatopodocarpites concinnus* Krusina *in* Inossova et al. from the earliest Cisuralian in Italy, which is very similar to *Protohaploxypinus amplus*. For previous synonymy see also Foster (1979), Playford and Dino (2000b) and di Pasquo et al. (2003b).

Protohaploxypinus bharadwajii Foster, 1979 (Plate IV, 9)

Protohaploxypinus varius (Bharadwaj) Balme, 1970 (Plate IV, 5)

1996 *Protohaploxypinus* sp. García, p. 18, pl. 4, fig. 11.

Remarks: The specimen illustrated by García (1996) shows a haploxylonoid amb, a subcircular to slightly oval corpus, a cappa divided into 7 taeniae subparallel to wedge-shaped l-a arrangement, and a wide more or less rectangular cappula. These features fit very well with the description of *Protohaploxypinus varius* in agreement with Balme (1970). For other synonymy see the latter author.

Occurrence: This species is the only one shared with the Cisuralian palynoflora of the Vitiacua Formation in southern Bolivia (Sempere et al., 1992; see Figs. 1A, 2 and 3).

Genus *Striatopodocarpites* Zoricheva and Sedova *ex* Sedova emend. Hart, 1964

Type species: *Striatopodocarpites tojmensis* Sedova, 1956.

Striatopodocarpites antiquus (Leschik) Potonié, 1958 (Plate IV, 8)

Striatopodocarpites gondwanensis Lakhanpal, Sah and Dube emend. Hart, 1964 (Plate IV, 13)

Striatopodocarpites solitus (Bharadwaj and Salujha) Foster, 1979 (Plate IV, 17)

1965 *Striatites* sp. Cousminer, p. 1106, pl. 129, fig. 3.

Remarks and comparisons: The specimen illustrated by Cousminer (1965) shows a diploxylonoid amb, a t-a oval corpus, a cappa divided into 8–9 taeniae with an l-a subparallel arrangement, and a narrow cappula more or less rectangular in shape. These features are in agreement with the description of *Striatopodocarpites solitus* (see Foster, 1979). Pittau et al. (2002, p. 571, fig. 8.2, 5) illustrated specimens of *Striatohaplopinites latissimus* (Luber) Efremova from the earliest Cisuralian in Italy, which are very similar to *Striatopodocarpites solitus*.

Turma PLICATES Naumova emend. Potonié, 1960

Subturma POLYPLICATES Erdtman, 1952

Genus *Vittatina* Luber *ex* Samoilovich emend. Wilson, 1962

Type species: *Vittatina subsaccata* Samoilovich, 1953.

Vitattina spp. (Plate IV, 12, 14)

Remarks: Two morphotypes are recovered, one with l-a elongated amb that presents slightly developed sacci and 4 or 5 striae; the other, t-a elongated, without sacci and 7 or 8 striae.

Acritarch/algae

Genus *Hemiruptia* Ottone, 1996

Type species: *Hemiruptia legaultii* Ottone, 1996.

Hemiruptia sp. (Plate V, 6)

Remarks: Scarce specimens prevented a more accurate assignment.

Genus *Leiosphaeridia* Eisenack emend. Downie and Sarjeant, 1963

Leiosphaeiridia sp. (Plate V, 4)

Fungus/algae (see Foster et al., 2002)

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

Type species: *Reduviasporonites catenulatus* Wilson, 1962.

?*Reduviasporonites* sp. (Plate V, 8)

Comparisons: This species differs from *Reduviasporonites chalastus* (see Foster et al., 2002) in having oval cells with quite long and taper ends that are connected one to each other to form a chain. *R. chalastus* is mainly distinguished from *R. catenulatus* by a greater size of its rectangular cells (up to 10 times greater in most cases), and by the presence of terminal rims allowing regular articulation of cells into chains (Foster et al., 2002).

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. García, 1991 (Plate V, 2)

Comparisons: A very similar form was illustrated as Scolecodont by Coquel et al. (1988, pl. 1, 10) from the Visean/Serpukhovian of Libya.

Genus *Nereigenys* Jansonius and Craig, 1971

Type species: *Nereidavus disjunctus* Eller, 1963.

Nereigenys sp. García, 1991 (Plate V, 3)

1988 *Staurocephalites* sp. A Ottone, p. 423, pl. 1, figs. 8, 9.

Comparisons: *Staurocephalites* sp. A Ottone (1988, pl. 1, figs. 8, 9) from the Uppermost Pennsylvanian of Mendoza, Argentina (Sub-zone C in *DM* Zone Césari and Gutiérrez, 2001; see Fig. 3 and Appendix A) is considered conspecific with this species, and is better assigned to the genus *Nereigenys* mainly due to the presence of a strong falcate anterior hook.

Scolecodonts, Indeterminate forms (Plate V, 1, 7)

Microforaminifera (Plate V, 9)

5. Age assessment and correlation

Knowledge of Pennsylvanian and Permian South American microfloras has been expanded significantly during the past 5 yr, especially as a result of detailed investigations in Argentina (Tarija, Paganzo, Uspallata–Iglesia, San Rafael, Chacoparaná, Colorado and Tepuel–Genoa Basins), Brazil (Paraná, Amazon and Parnaíba Basins), Uruguay (Paraná/Chacoparaná Basin), Bolivia (Tarija and Madre de Dios Basins) and Peru (Madre de Dios Basin) as summarised by Azcuy et al. (2007) (see Figs. 1A, 5 and Appendix A). Several Pennsylvanian palynostratigraphic units covering most of these basins contain variable frequencies of spores and pollen grains (monosaccate, bisaccate and asaccate striate and non-striate pollen); common species supported its correlation (see Azcuy et al., 2007; Figs. 3, 5 and Appendix A). Among these palynomorphs, *Protohaploxypinus*–*Striatoabieites*–*Striatopodocarpites* pollen genera represent predominantly gymnospermous (mainly Coniferales and Pteridosperms) vegetation but with significant contributions of spores derived from lower vascular plants (notably Pteridophytes, Sphenophytes and Lycophytes) and also other Pteridosperms. More diverse bisaccate and asaccate striate taxa including the above cited genera and others such as *Vittatina*, *Lueckisporites*, *Hamiapollenites*, *Lunatisporites*, *Pakhapites* and *Illinites* mainly of glossopterid and coniferous origin (for botanical affinities see Balme, 1995), become increasingly prominent in the Cisuralian palynofloras (e.g., Playford and Dino, 2000b; Souza and Marques-Toigo, 2005).

Many species in common with Pennsylvanian and Permian palynofloras from South America and others selected from elsewhere are recorded along the studied section of the Pando X-1 (see Figs. 4, 5 and Appendix A). Among them, *Apiculiretusispora alonsoi*, *Cristatisporites spinosus*, *Apiculatasporites parviapiculatus*, *Costatacyclus crenatus*, *Lunatisporites onerosus*, *Lahirites segmentatus* and *Limitisporites scitulus* are restricted to the Pennsylvanian on the basis of comparison of several Pennsylvanian palynofloras mainly from Peru, Brazil and Argentina in South America (see Figs. 1A, 3, 5 and Appendix A). Diverse Pennsylvanian assemblages described by Playford and Dino (2000a,b) from the Amazon Basin, enabled the authors to define five zones spanning the late Bashkirian to Moscovian in age and two more akin to the Permian. The beginning of the regional joint epibole of *Spelaeotriletes triangulus* and *S. arenaceus*, and inception of saccate pollen grains (predominance of non-striate monosaccate genera like *Caheniasaccites*, *Cannanoropollis*, *Plicatipollenites*, *Potonieisporites* over less frequent striate pollen like *Protohaploxypinus*, *Striatoabieites*, *Striatopodocarpites*, *Striomonosaccites* and non-striate bisaccates such as *Limitisporites* and *Pityosporites*) characterize the first *Spelaeotriletes triangulus* (*Tri*) Biozone in this basin. The *Mag* (*Magnidictyus* Biozone Melo and Loboziak, 2003)/*Tri* boundary is erosional and coincides with the regional pre-Monte Alegre unconformity, traceable all over the basin. The late Bashkirian (early Westphalian) age attributed to this zone is faunally calibrated and correlated with Euramerican reference sections (see discussions in Loboziak et al., 1997; Melo et al., 1999; Playford and Dino, 2000b; Melo and Loboziak, 2003). In this basin, the shared species *Costatacyclus crenatus* and *Protohaploxypinus amplus* appear in the oldest *Spelaeotriletes triangulus* (*Tri*) Biozone and follow up to the next *Striomonosaccites incrassatus* Biozone where the former disappears. *Meristocorpus explicatus* and *Limitisporites scitulus* appear in the latter zone and disappear in the last *Raistrickia cephalata* Biozone where *Lunatisporites onerosus* appears. Species of *Striatopodocarpites* appears in the upper *Striatosporites heyleri* Biozone and follows in the next *Raistrickia cephalata* Biozone up to the Permian. Melo and Loboziak (2003) established that partial correlation with the early Bashkirian (Late Namurian) palynozones of Western Europe (Clayton et al., 1977, *C. kosankei–G. varioreticulatus* (*KV*)–*F. fulva-R. reticulatus* (*FR*) Biozones) is conceivable for the lowest part of the *Tri* Biozone in the Solimões Basin (see Fig. 3), where striate bisaccates are seemingly absent (see also Melo et al., 1999). Same features are recorded in the A Sub-zone of the *DM* Biozone, western basins of Argentina (see Césari and Gutiérrez, 2001) and in the oldest *C. kosankei-C. azcuyi* Biozone in the Tarija Basin (see Figs. 2, 3). The latter is characterized by abundant non-striate monosaccate pollen grains and spores; only one striate species (*Meristocorpus explicatus*) is found (di Pasquo, 2002, 2003).

On the other hand, *Apiculiretusispora alonsoi*, *Cristatisporites spinosus* and *Apiculatasporites parviapiculatus* are long-ranged species recorded through the Pennsylvanian rocks of the western basins of Argentina (Césari and Gutiérrez, 2001), the Macharetí and Mandiyutí Groups of the Tarija Basin (di Pasquo, 2003, 2009) and the Paraná Basin (Souza, 2006). Other species recorded in assemblage 2 showed longer stratigraphic ranges from Moscovian to Cisuralian, corresponding to *Protohaploxypinus*, *Striatopodocarpites* and *Hamiapollenites* genera (see Figs. 4, 5 and Appendix A). Among them, *Protohaploxypinus varius* is recorded from the Cisuralian Vitiacua Formation of southern Bolivia (Sempere et al., 1992), *Striatopodocarpites solitus* is present in the Cisuralian part of the Copacabana Formation in western Bolivia (Cousminer, 1965) and *Florinites eremus* in the same unit in Peru (Doubinger and Marocco, 1981).

Such disparities among the appearance–disappearance of the above mentioned species prevented a close correlation with a specific zone of those basins. Although, the presence of *Lunatisporites onerosus* in the *Protohaploxypinus*/*Lunatisporites onerosus* horizon (Bashkirian–Moscovian) defined by Wood et al. (2002) in the Copacabana Formation at the Pongo de Mainique in Peru, would suggest a closer correlation with the A2 of this borehole. Moreover, the absence of *Illinites unicus* in the Pando assemblages, abundantly recorded in the Tarma Formation at the Pongo de Mainique by Azcuy et al. (2002), supports this correlation. Hence, a Bashkirian age is given to A1 while A2 is attributed to the Moscovian. This age is in agreement with Isaacson et al. (1995), who interpreted that the Permian in this borehole has been eroded or not deposited, due to the record of microfossils attributed to the Bashkirian–Moscovian in this same interval (see Fig. 1C; Mamet, 1996a,b; Mamet and Isaacson, 1997). Nevertheless, it deserves to be mentioned that the presence of some Permian species in A2 like *Florinites eremus*, *Striatopodocarpites solitus*, *S. antiquus*, *S. gondwanensis*, *Protohaploxypinus varius*, *Chordasporites endroedii* and *Cannanoropollis singrauliensis* among others (see Figs. 4, 5 and Appendix A), could have been used many years ago to attribute this assemblage to the Early Cisuralian. Currently, their ranges are here extended to the Pennsylvanian.

Finally, it is interesting to note the appearance of scarce specimens of *Vittatina* in A2 (see Fig. 4). This genus has been registered in the latest Pennsylvanian of the Chacoparaná Basin (e.g., Archangelsky and Vergel, 1996). Outside of South America, Inossova et al. (in Utting et al., 2004) have recorded well-calibrated *Vittatina* species in the Kasimovian of the Donetz Basin. A few more records are known from: 1) the Moscovian (Westphalian D) of Arabia (Owens and Turner, 1995), 2) little below the Carboniferous–Permian boundary stratotype at Aidaralash creek in Kazakhstan (Dunn, 2001), 3) the early Moscovian (Westphalian C) marine strata in northeastern Greenland (Thomsen, 1999), 4) subsurface deposits of Moscovian–Kasimovian (Westphalian C–D and Stephanian) age dated with macroflora in the German North Sea (see Josten, 1995; Lund, 2001). Hence, this record is the oldest one in Bolivia (see all first Pennsylvanian records in Fig. 4).

6. Palaeoclimatical and palaeoenvironment considerations

Three members of the Copacabana Formation ranging from Bashkirian up to Artinskian were documented by Grader et al. (2000, 2008) throughout its outcrop area in Bolivia (mainly in the Titicaca Lake area) and Peru. They interpreted its palaeoclimatical evolution related to several glaciation–deglaciation events during the Pennsylvanian and the Permian on the basis of cyclicity analysis into a sequence-stratigraphic model. The studied section of the Pando X-1 is in agreement with the lower Copacabana Member (Bashkirian and Moscovian), which is spatially limited and 0–300 m thick. Middle and outer ramp limestone overlie evaporitic lagoon and coastal plain siliciclastics due to differential subsidence controls and filling of previous palaeotopography. A transgressive carbonate cycle occurs near the top of this member, which ends with a significant time gap and unconformity. As a whole, these terrigenous–calcareous and evaporitic deposits were interpreted as being settled under restricted marine warm-waters and semiarid conditions according to Isaacson et al. (1995) and Grader et al. (2008). This interpretation was supported by diverse small foraminifera and calcareous algae documented from the same studied section of the Pando X-1 by Mamet (1996a,b) and Mamet and Isaacson (1997). A shallow marine palaeoenvironment is here confirmed with palynology (i.e., abundant AOM and scarce spores, monosaccate pollen grains and microforaminifera in the A1; a high amount of pyrite on palynomorphs, abundance of striate pollen grains and terrestrial phytoclasts and presence of scolecodonts in the A2; see Fig. 4).

On the other hand, the uneven distribution of striate pollen grains around the World during the Pennsylvanian may be related to differing palaeoclimatical and palaeoenvironmental conditions. In particular, striate pollen grains bearing assemblages of the Pennsylvanian of South America seem to have developed under seasonal climates with drier conditions in northern Bolivia, Peru, Brazil and eastern Argentina. In contrast, other nearly striate-barren assemblages of Tarija (southern Bolivia and northern Argentina; see di Pasquo, 2009 and references therein) and western basins of Argentina (see Césari and Gutiérrez, 2001) probably reflect more humid conditions during the early Pennsylvanian. During the Cisuralian, an evident increase of striate pollen grains is recorded in all these basins attesting broad seasonal warmer climates that are related to the movement of Gondwana to a lower palaeolatitude (see di Pasquo and Azcuy, 1999; Playford and Dino, 2000b; Césari and Gutiérrez, 2001; di Pasquo, 2003; di Pasquo and Souza, 2004; di Pasquo, 2007c). In northern Bolivia, a variable terrestrial input and varying composition of pollen grains through Pando X-1 (see Fig. 4), attest to the evolution of the palaeofloras between A1 and A2, which were probably related to palaeoclimatic and palaeoenvironmental changes during the Pennsylvanian. Cordaitales and Coniferales, which appeared in the early Pennsylvanian A1, flourished in a temperate to warm and humid post-glacial landscape. The A2 is characterized by a more diverse flora with the inception of new Pteridosperms producing striate species like *Vittatina* that became common later in Cisuralian assemblages (see Balme, 1995; Playford and Dino, 2000b). This new paleofloristic assemblage would have been adapted to arid or seasonal lowlands around the Copacabana shallow marine palaeoenvironment.

7. Conclusions

Ten core samples obtained from 867–729 m depth in the Pando X-1 Borehole, northern Bolivia, were investigated for palynology. The assemblages yielded 48 species, fairly well-preserved, of which six are trilete spores and among the pollen grains, 21 are monosaccate and 19 bisaccate (11 striate species). Scarce scolecodonts, microforaminifera and algae are also present. Two assemblages are mainly recognized on the basis of its stratigraphic distribution. The lower assemblage (A1, 867 m to 756 m depth) is dominated by amorphous organic matter and scarce monosaccate pollen grains, trilete spores and microforaminifera. The upper assemblage (A2, 741 m to 729 m depth) is dominated by tracheids and brown and black phytoclasts, and characterized by abundant and diverse palynomorphs, mainly striate and non-striate pollen grains and scarce spores and scolecodonts.

The stratigraphic range of selected species based on close comparisons chiefly with Argentinean and Brazilian palynofloras supports an early Pennsylvanian age for both assemblages. Regarding the stratigraphic distribution of pollen grains, it is likely that A1, characterized only by monosaccate pollen grains, is Bashkirian in age whereas A2 is Moscovian mainly due to the appearance of many striate pollen grains (e.g., *Lunatisporites onerosus*, *Lahirites segmentatus* and other species of the genera *Protohaploxypinus*, *Striatopodocarpites*, *Hamiapollenites* and asaccate species of *Vittatina*). This age is in agreement with the Bashkirian to Moscovian age attributed on the basis of calcareous microfossils obtained from the same interval in this borehole. Hence, twenty two species of trilete spores, pollen grains, scolecodonts and microforaminifera, are here recorded for the first time in the Pennsylvanian of Bolivia (see Fig. 4).

Scolecodonts and microforaminifera together with the abundant pyritization of palynomorphs and phytoclasts are in agreement with previous interpretations suggesting a shallow marine palaeoenvironment. The qualitative difference between A1 and A2 appears to be controlled by broadly palaeoclimatical conditions. In the first assemblage, the Serpukhovian glacial event followed a deglaciation phase in the early Pennsylvanian favouring the appearance of a new flora composed mainly of Cordaitales and Coniferales. The appearance of striate pollen grains in A2 is related to a diversification of the flora with the inception of new pteridosperms, and to a relative decrease of humidity with the establishment of seasonally arid conditions in the terrestrial landscape near the Copacabana marine palaeoenvironment. In this framework, the appearance of striate species like *Vittatina* was favoured earlier in the Pennsylvanian of Bolivia, but only later, in Cisuralian palynoassemblages, do striate pollen grains became abundant.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.revpalbo.2009.05.006.

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