

## Depositional cyclicity and paleoecological variability in an outcrop of Rio Bonito formation, Early Permian, Paraná Basin, Rio Grande do Sul, Brazil

André Jasper<sup>a,\*</sup>, Rualdo Menegat<sup>b</sup>, Margot Guerra-Sommer<sup>b</sup>,  
Miriam Cazzulo-Klepzig<sup>b</sup>, Paulo Alves de Souza<sup>b</sup>

<sup>a</sup> Setor de Botânica e Paleobotânica, Museu de Ciências Naturais, UNIVATES (SBP/MCN/UNIVATES), Avelino Tallini, 171, CEP 95.900-000 Lajeado, RS, Brazil

<sup>b</sup> Instituto de Geociências, Universidade Federal do Rio Grande do Sul (IG/UFRGS), Avenida Bento Gonçalves, 9.500, CEP 91.540-000 Porto Alegre, RS, Brazil

Received 1 December 2004; accepted 1 January 2006

### Abstract

This article integrates faciological, paleobotanical, and palynological analyses to establish the relationship between depositional cyclicity and paleoecological patterns for the (Early Permian) Quitéria outcrop, Rio Bonito Formation, southern Paraná Basin, Rio Grande do Sul state. The basal section of this outcrop represents a coastal lagoon depositional system protected by barriers in microtide conditions, where peat-forming conditions developed in lowlands with ingression of distal alluvial fan deposits. The upper clastic section represents different environmental conditions, originated by the barrier sectioning brought by washover fans. The palynoflora identified in the basal section present a dominance of spores produced by arborescent and herbaceous lycophytes, as well as by sphenophytes and filicophytes, complementary forms of gymnosperm pollen grains. Algae or algae-elements, indicative of fresh, brackish, or marine water, are recorded together with terrestrial spores and pollen grains. The palynological content of matrix-supported conglomerates suggests a close, qualitative similarity with the coaly facies; however, the increase in gymnosperm pollen grains accompanied by a decrease in spores produced by pteridophyte vegetation is remarkable. The autochthonous roof-shale flora related to the clastic upper section is composed of basal stumps of arborescent cormose lycophytes (*Brasilodendron pedroanum*), understory vegetation (*Botrychiopsis valida*, *Lycopodites* sp.), small trees (*Coriocladius quiteriensis*), undetermined filicoid rodheopterid fronds, and parautochthonous elements (*Rubidgea* sp., *Cordaites* sp.). Palynofloras point to floristic similarity between the roof-shale floras and the subjacent coal-forming parautochthonous floras. Correlations between the floristic data and those from high-resolution sequence stratigraphic methods indicate that this interval is associated with the final parasequences of the transgressive tract of Rio Bonito Formation, where coal levels are thin. The record in some coal palynofloras of *Striadopodocarpites fusus*, a component of the *Hamiapollenites karrooensis* subzone, as defined in the palynostratigraphic framework for the Paraná Basin, indicates a Kungurian age for the palynoflora.

© 2006 Elsevier Ltd. All rights reserved.

**Keywords:** Early permian; Gondwana; Paraná basin; Faciological analysis; Roof-shale floras; Palynology; Paleoecology

### Resumo

O presente trabalho apresenta análises faciológicas, paleobotânicas e palinológicas, em que são estabelecidas relações entre ciclicidade deposicional e padrões paleoecológicos para as duas seções deposicionais definidas no afloramento Quitéria (Permiano Inferior/Médio), Formação Rio Bonito, sudeste da Bacia do Paraná, no estado do Rio Grande do Sul. A seção basal representa um sistema deposicional de laguna costeira protegida por barreiras em condições de micro-maré, onde se desenvolveram turfeiras em terras baixas assoreadas por depósitos distais de leques aluviais. A seção clástica sobreposta representa o mesmo sistema, porém em condições distintas, originadas pelo seccionamento da barreira provocada por leques de washover. A palinoflora identificada nos folhelhos carbonosos e nos carvões do intervalo

\* Corresponding author.

E-mail address: [ajasper@univates.br](mailto:ajasper@univates.br) (A. Jasper).

URL: <http://www.univates.br/mcn> (A. Jasper).

basal mostra o predomínio de esporos de licófitas arborescentes e herbáceas e abundância de esporos de esfenófitas e flicófitas, constituindo os grãos de polens de gimnospermas formas complementares. Palinomorfos de afinidade botânica indeterminada, representando elementos do microplankton de água doce, salobra ou marinho, são identificados em associação com esporos e grãos de polens derivados de vegetação terrestre. Nos conglomerados, as análises palinológicas mostram forte similaridade de composição em relação à palinoflora das fácies carbonosas, ficando, entretanto, evidenciado aumento expressivo na quantidade de grãos de pólen gimnospérmicos e diminuição dos esporos de Pteridophyta. A flora identificada no nível de *roof-shale*, vinculado à seção superior, é caracterizada como uma flora autóctone composta por bases cormofíticas de licófitas arborescentes (*Brasilodendron pedroanum*), vegetação de soto-bosque (*Botrychiopsis valida*, *Lycopodites* sp.), arbustos (*Cori cladus quiteriensis*), frondes indeterminadas de filicópsidas e rodeopterídeas, elementos paraúctones (*Rubidgea* sp. e *Cordaites* sp.). Evidências palinológicas comprovam similaridade composicional entre as floras relacionadas ao *roof-shale* e à vegetação formadora dos carvões paraúctones subjacentes. A correlação dos dados paleobotânicos e palinológicos, associados aos resultados obtidos através de estratigrafia de seqüências de alta resolução, demonstra que o intervalo analisado está relacionado com as paraseqüências finais do trato transgressivo da Formação Rio Bonito, onde os níveis de carvão se apresentam bastante delgados. A identificação de *Striadopodocarpites fusus*, componente da Subzona palinoestratigráfica *Hamiapollenites karrooensis* definida para a Bacia do Paraná, indica para a palinoflora idade correspondente ao Kunguriano.

© 2006 Elsevier Ltd. All rights reserved.

Palavras-chave: Permiano Inferior; Gondwana; Bacia do Paraná; Análise faciológica; *Roof-shale* floras; Palinologia; Paleocologia

1. Introduction

The Quitéria outcrop (Pantano Grande County, Rio Grande do Sul; Figs. 1 and 2) corresponds to a 6.4 m sedimentary exposure and represents an isolated fragment of the Rio Bonito Formation overlying the basement. This peculiarity and the absence of evident contact with overlying and underlying sedimentary sequences complicate the correlation with other exposures of the Rio Bonito Formation in the southern portion of the Paraná Basin, Brazil.

At this outcrop, two depositional sections are observed. In the light to dark grayish basal section, palynological analyses performed in different facies enable the identification of well-preserved palynoflora (Piccoli et al., 1991; Cazzulo-Klepzig et al., 2002). The basal facies of the yellowish, clastic upper section (Fig. 5) is considered a roof-shale level, according to

the criteria of Gastaldo et al. (1995). The roof-shale flora is characterized by in situ basal stumps of arborescent, cormose lycophytes identified as *Brasilodendrum pedroanum* (Jasper and Guerra-Sommer, 1998).

Evidence of volcanism is detected in both sections by petrographic analysis on matrix-supported conglomerate facies, where vitreous vesicular and laminar-shaped fragments are important elements.

At western Gondwana, the presence of dense thickets of lycophyte cormose stumps with similar morphology and habitats has been recorded in the Mid-Carboniferous of the Paracas Floral Belt (Alleman and Pfefferkorn, 1991; Pfefferkorn, 1997), in the Late Carboniferous/Early Permian of western Argentinean basins (Azcuay et al., 1987; Cerro Agua Negra Formation, Calingasta Uspallata Basin, San Juan Province), and in southern Argentinean basins (Cúneo and

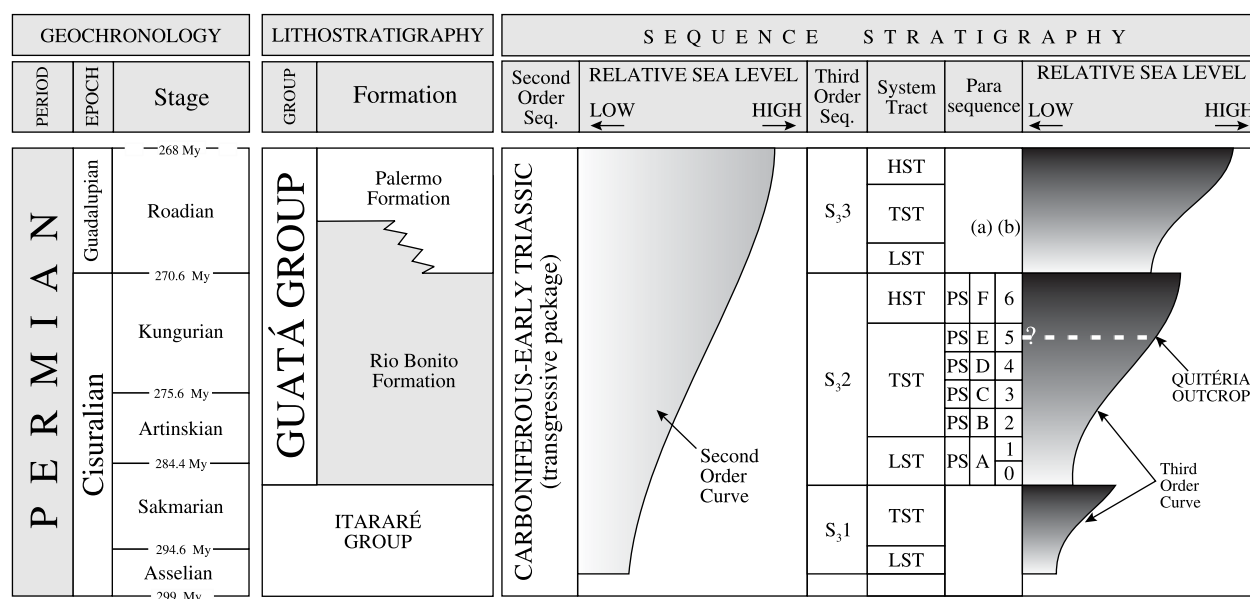


Fig. 1. Stratigraphic setting of Rio Bonito Formation and sequence stratigraphy framework of the basal succession of Paraná Basin (geochronology, Gradstein et al., 2004; second-order sequence, Milani et al., 1998; third-order sequence, Alves and Ade, 1996; Holz et al., 2000). HST, highstand system tract; TST, transgressive system tract; LST, lowstand system tract; PS, parasequence *sensu* (a) Alves and Ade (1996) and (b) Holz et al. (2000).

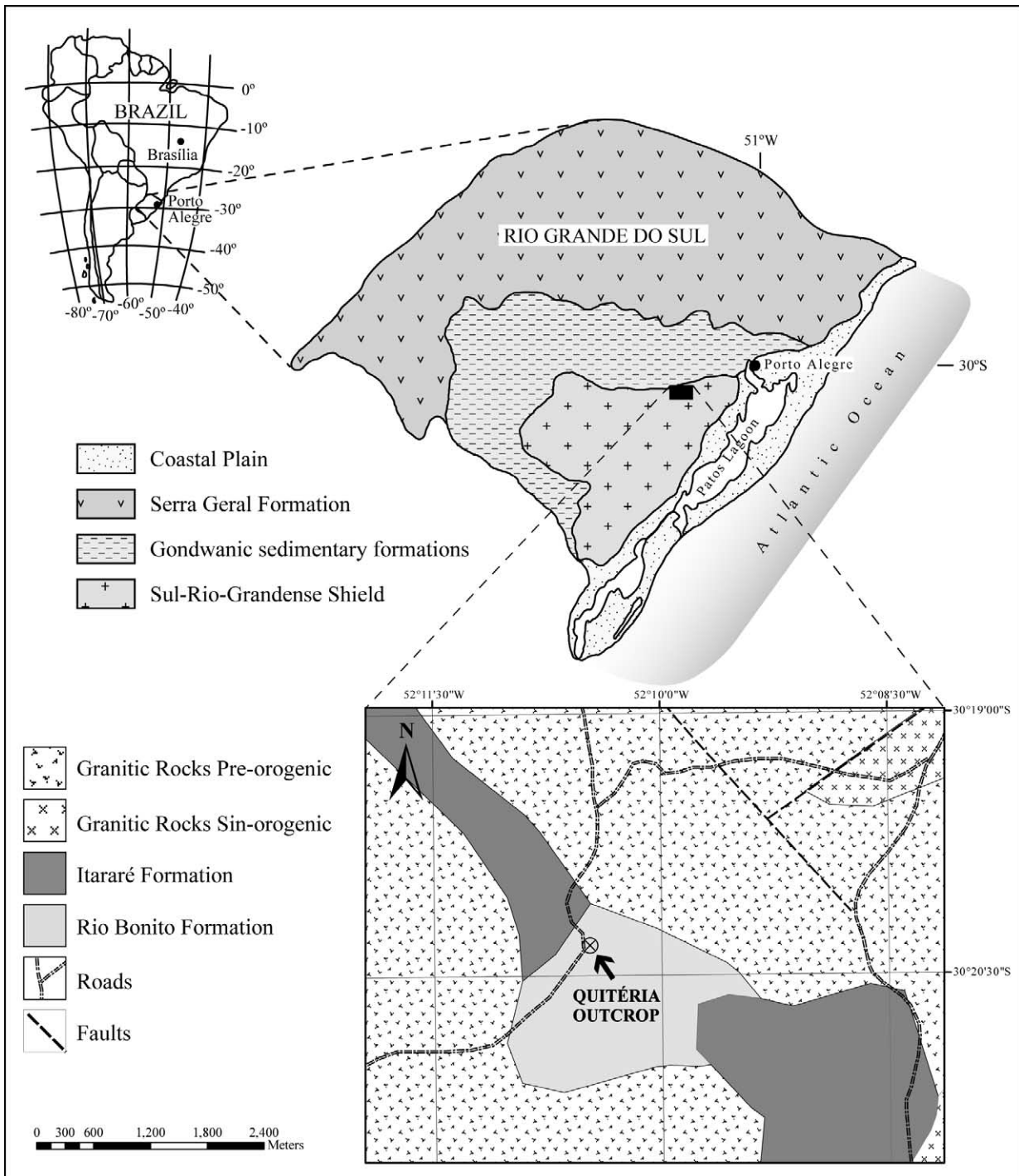


Fig. 2. Location map and geological map of the Quitéria outcrop area (Menegat et al., 1995).

Andreis, 1983; Rio Genoa Group, Nueva Lubecka Formation, Chubut Province), as well as in the Early Permian of the Brazilian southern Paraná Basin (Jasper and Guerra-Sommer, 1998). These data support a hypothesis about relationships between the spatial and temporal distribution of the arborescent, cormose lycophyte with climatic and tectonic events during the Carboniferous/Early Permian interval in western Gondwanaland. The cormophytic complex adapted to coastal, clastic swamps and silty/sandy soils, with poor nutrient

conditions, a stressful habitat for most land plants (Guerra-Sommer et al., 2001).

At the Quitéria outcrop, prostrate, subhorizontal, and horizontal plant fragments, including large sterile shoots, fertile shoots, and fronds, occur among the erect lycophyte casts (Jasper et al., 2003). The presence of *Botrychiopsis valida* in this megafloora enlarged the biochron of the genus. A phytos-tratigraphic zonation for southern Paraná Basin, based on the stratigraphic distribution of different species of *Botrychiopsis*,

is proposed by Jasper et al. (2003), who considered this *taxon* to have a broader climate tolerance than previously supposed, with different species ranging from cool-temperate to warm-temperate climates closely related to an icehouse stage (Jasper et al., 2005a). Herbaceous lycophytes (*Lycopodites* sp.) were also described as components of the understory flora (Ricardi-Branco et al., unpublished). Dense associations of fertile and sterile shoots of conifers (*Corielladus quiteriensis*; Jasper et al., 2005b) also were identified as components of the roof-shale flora.

Previous palynological, petrographic, and paleobotanical studies have interpreted the original biomass of south Brazilian coals (Marques-Toigo and Corrêa da Silva, 1984; Guerra-Sommer et al., 1991) as composed of herbaceous lycophytes, sphenophytes, and filicophytes. Cazzulo-Klepzig (unpublished) reevaluates the palynological content of these coals in an attempt to define the dominant vegetation and landscape units related to coal formation. The author concludes that the plant communities responsible for the peat-forming biomass, reflected by spores, pollen, and other plant remains, generally were dominated by arborescent lycophytes, and herbaceous vegetation was less significant than previous interpretations suggested.

In Brazilian Gondwana coal-bearing strata, roof-shales are commonly sterile in fitomegafossils, making the reconstruction of the structure of communities and palaeoecology of Early Permian lowland vegetation difficult. In exclusive parautochthonous plant assemblages, selective decay and transport change the rates of different parts of diverse plant species preserved in fossiliferous sites. Nevertheless, studies on some roof-shale floras in southern Brazilian Gondwana reveal vegetational heterogeneity in the lowland floras in the different coal deposits (Guerra-Sommer et al., 1991, 2001). At the Quitéria outcrop, the exceptional record of palynofloras in coaly facies and in situ well-preserved megaflora in the roof-shale, with the presence of standing stumps, support advances in the recognition of floristic successions in the coal-bearing strata.

This article reports detailed paleobotanical, palynological, petrographical, and faciological studies along the outcropping sequence to establish the probable relationships between depositional cyclicity and changes in paleoecological patterns. Integration of the floristic data with application of high-resolution sequence stratigraphy methods may lead to a correlation between the Quitéria outcrop and the southern Brazilian stratigraphic framework.

## 2. Stratigraphical framework of Rio Bonito Formation, Paraná Basin

The 1,700,000 km<sup>2</sup> Paraná Basin, located in central-south-east South America, comprises an interval of six depositional megasequences (cf. Milani et al., 1998), originated by second-order eustatic and tectonic events. These megasequences are known from the base to the top as follows: (1) Ordovician/Silurian; (2) Devonian; (3) Carboniferous/Early Triassic, which is the thickest at approximately 2800 m; (4) Late Triassic; (5) Jurassic/Early Cretaceous; and (6) Late Cretaceous.

The Carboniferous/Early Triassic megasequence, which includes the Rio Bonito Formation, represents a second-order transgressive–regressive cycle (Fig. 1). It comprises a basal transgressive package superimposed by a regressive package. The basal package corresponds to lithostratigraphic units formerly known as the Itararé and Guatá groups, represented by the Rio Bonito and Palermo formations. The latter represents the maximum flooding event, whereas the upper package comprises the Irati, Serra Alta, Teresina, Rio do Rasto, and Sanga do Cabral formations.

Tectonic and eustatic events at the southernmost part of Paraná Basin led to several third-order sea level cycles during the long-term Carboniferous/Early Triassic sea level cycle. According to Alves and Ade (1996) and Holz et al. (2000), the second-order Carboniferous/Early Triassic sequence can be subdivided into four third-order sequences: S<sub>3</sub>1, S<sub>3</sub>2, S<sub>3</sub>3, and S<sub>3</sub>4. The Rio Bonito Formation corresponds to subsequence S<sub>3</sub>2 and the lower part of S<sub>3</sub>3 (Fig. 1). In addition, the stratigraphic framework of these subsequences establishes smaller hierarchic units, such as system tracts, and parasequences. Thus, S<sub>3</sub>2 corresponds at its base to lowstand system tract (LST), followed by a transgressive system tract (TST) and a highstand system tract (HST) at the top. Following it, the lower part of S<sub>3</sub>3 is identified as a LST. The top interval of S<sub>3</sub>3 belongs to the Palermo Formation and identifies a TST and HST (Fig. 1).

Lavina and Lopes (1987) interpret the depositional models of the Rio Bonito Formation in terms of a transgressive–regressive sequence. Although they had not established a stratigraphic framework *sensu* sequence stratigraphy (Posamentier et al., 1988; Van Wagoner et al., 1990), they anticipated close results with that theory. Alves and Ade (1996) first defined a third- and fourth-order framework according to sequence stratigraphy theory and methods. Then, based on the correlation of drilling cores in the Candiota region, Holz et al. (2002) confirmed a third-order stratigraphic framework for the Rio Bonito interval (Fig. 1). In both papers, the third-order sequence was divided in system tracts and parasequences. According to Alves and Ade (1996), the LST (Fig. 1, S<sub>3</sub>2-LST) is composed of one parasequence (Fig. 1, PS A); according to Holz et al. (2002), it consists of two parasequences (Fig. 1, PS 0 and 1). These parasequences, or fourth-order sequences, identify prograding fluviodeltaic depositional paleoenvironments, with important sedimentary support and few coal beds. The LST is superimposed by a TST that comprises four parasequences (PS B–E *sensu* Alves and Ade, 1996; PS 2–5 *sensu* Holz et al., 2002), which record swamp paleoenvironments associated with barriers/lagoons. From the second to the fourth parasequences (PS 2–4) occur thick, continuous coal beds, whereas in the uppermost parasequence (PS 5), the coal beds are thin and discontinuous. The HST comprises a single parasequence of marine facies (PS F *sensu* Alves and Ade, 1996; PS 6 *sensu* Holz et al., 2002).

## 3. Geological setting of the Quitéria outcrop

The Rio Bonito Formation, a thick sandstone-siltstone interval, is exposed in both continuous beds of the



southernmost part of Paraná Basin and fragmented exposures on the Sul-Rio-Grandense Shield (Fig. 2). Until the early 1990s, these fragmented outcrops were thought to belong to the Devonian Caneleiras Formation. However, detailed mapping has revealed that some belong to the Paraná Basin (Menegat and Scherer, 1993).

The Quitéria outcrop is preserved as a normal dip-slip faulted block with a NW trend in the Encruzilhada do Sul region (Fig. 3), first described by Silva and Menegat (1988). Piccoli et al. (1991) also present a composed stratigraphic section of the Rio Bonito Formation exposed in the region (Quitéria and Pantano sheet map). A framework based on lithofacies and biofacies data identified 10 lithofacies (I–X) and 10 biofacies (A–J). The Quitéria outcrop interval corresponds to lithofacies VII, interpreted as a deltaic depositional environment. Therefore, Jasper and Guerra-Sommer (1999) propose a lagoon/barrier depositional model (*sensu* Reinson, 1992), as defined by Menezes (1994), Chaves et al. (1994) and Della Fávera et al. (1994), Holz (unpublished, 1997, 1998), and Lopes and Lavina (1995) for coal-bearing strata in the southernmost part of the Paraná Basin.

#### 4. Materials and methods

This study is based on detailed facies analyses that integrate textural, structural, petrographic, and paleofloristic parameters, in line with Walker's concepts (Walker and James, 1992). These concepts postulate the subdivision of a sedimentary section into basic units (facies) that can be grouped into upper hierarchic units, such as facies successions, depositional models, and depositional systems (Fig. 1).

Criteria such as geometry, lithology, structures, fossil content, and paleocurrent patterns were used to identify the facies. The facies were recognized at the outcrop through vertical and lateral variations considered at a columnar profile scale of 6.4 m (Fig. 4) and identified in a photomosaic of the 30 m outcropping section (Fig. 3). Subsequently, the facies were grouped into facies successions, based on textural and typology variation, as well as a hierarchy of contact surfaces. The identification of depositional models and systems was based on facies and cyclicity patterns.

Megafloral assemblages are contained in some facies and occur as impressions and casts, identified by hand specimens. The megafossil taxa are distributed into autochthonous remains, such as stumps of arborescent lycophytes with corm-like rooted systems, and parautochthonous (*sensu* Gastaldo et al., 1995; Martín-Closas and Gomez, 2004, considered a synonym of hypoautochthonous) plant material represented by leaves, sterile and fertile shoots, and fronds. On the basis of statistical data (Clark and Evans, 1954), a distribution index of in situ arborescent lycophytes was produced. The obtained index corresponds to  $R=1.69$ , which indicates a random distribution on the surface.

Regarding the parautochthonous material, different horizons across the outcropping area were set on a quadrate surface measuring  $1 \times 1$  m. In each horizon, the distribution of fossil taxa is studied qualitatively with data recorded in terms of its presence or absence. Quantitative parameters are represented by size and relative abundance. For characterizing the size, the following equivalence was established: small fragments up to 3 cm; medium fragments 3–10 cm; and large fragments more than 10 cm. The relative abundance



Fig. 3. Photomosaic of Quitéria outcrop. Black lines indicate the roof-shale level. Detailed picture shows in situ basal stump.

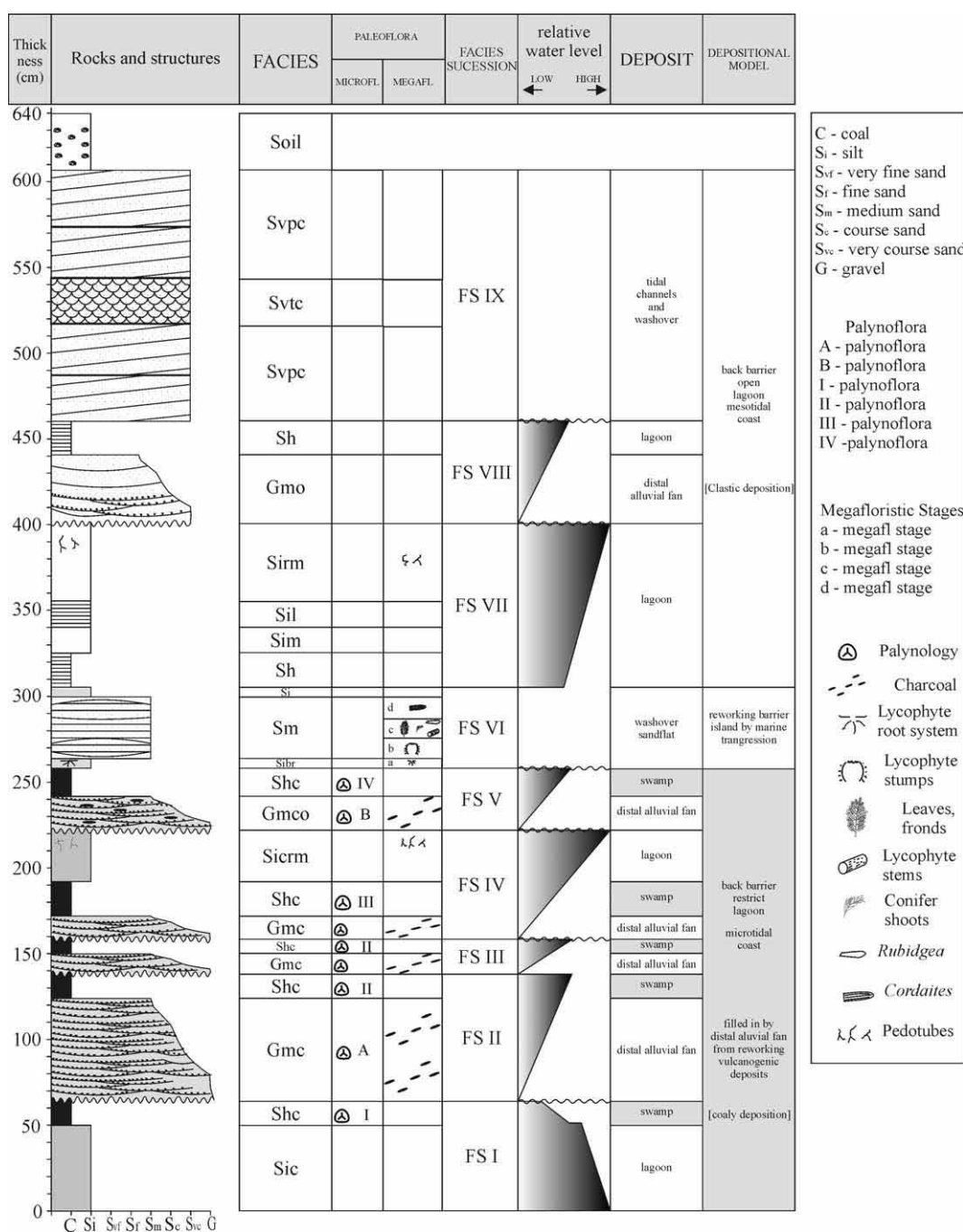


Fig. 4. Columnar section of the Quitéria outcrop.

takes into consideration the following rates: rare forms 1–3 fragments per sample, common forms 4–7 fragments per sample, and abundant forms more than 7 fragments per sample. In a linear east–west 30 m transect of the outcropping facies Sm (medium sandstone, see description in Section 5.7), a concentration of conifer assemblages was observed, concentrated exclusively in a narrow 6 m area at the western limit. Thus, considering the heterogeneity of megafloristic remains in different areas of the same horizon, quantitative analysis of parautochthonous material was established at two sites.

For the palynological study, standard extraction of paly-nomorphs using HCl and HF acids, Schulze’s solution, and NaOH was carried out on samples collected from different facies in the studied succession, including coaly shale and interbedded coal lenses, matrix-supported conglomerates, and paleosoils (Fig. 4). The analytical process followed procedures outlined by Phipps and Playford (1984) with minor modifications to achieve the best result fraction. From Entelan preparation of each sample residue, qualitative and quantitative determination was conducted on seven samples of coaly shales and conglomerates; the remaining

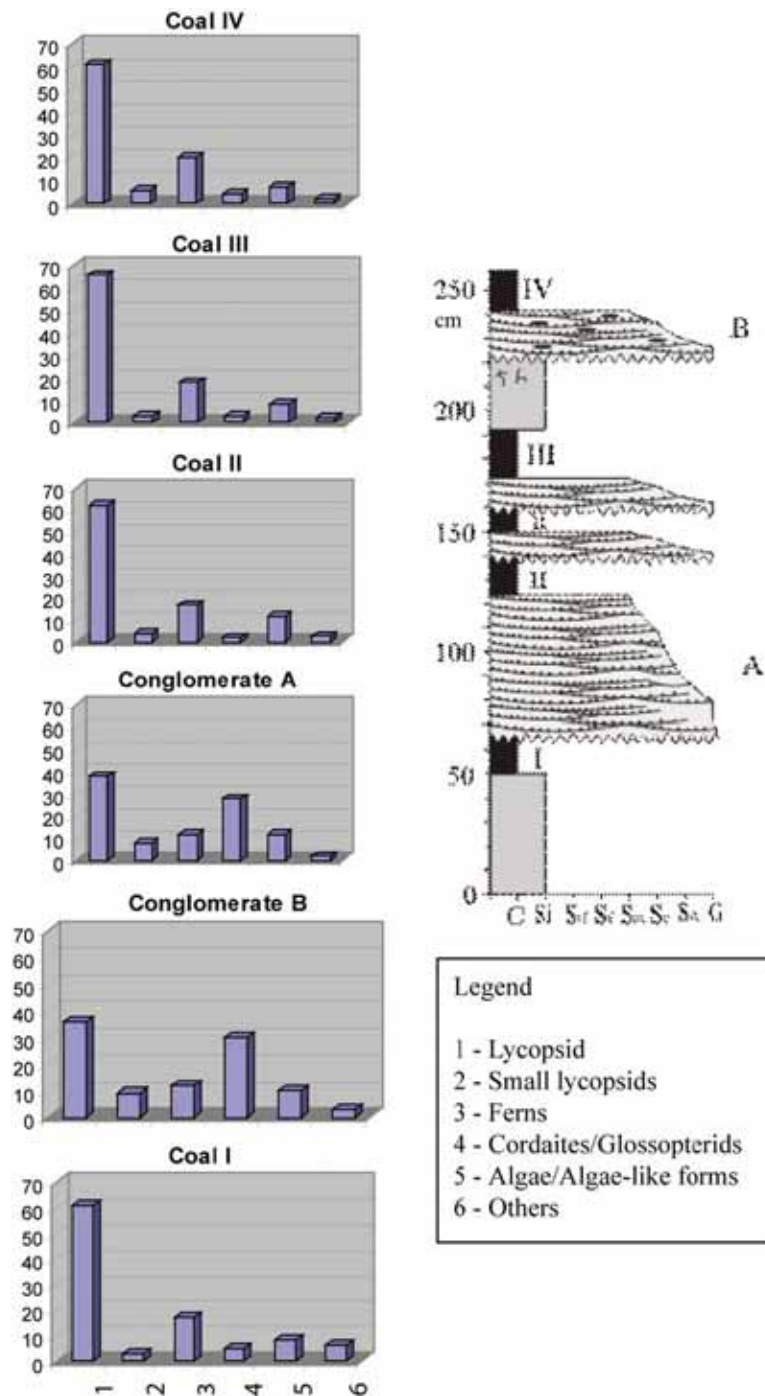


Fig. 5. Distribution of relative abundances of plant groups between coals and conglomerates (reflected in palynofloras).

samples contained poorly preserved palynomorphs. The frequency of each palynological group was considered abundant (>60%), frequent (30–60%), less frequent (30–10%), or scarce or rare (<10%, Fig. 5).

Taxonomic determination of dispersed spores and pollen grains was based on morphology criteria indicated by Potonié and Kremp (1956). Concepts provided by Gould and Delevoryas (1963), Staplin et al. (1967), Taylor and Taylor (1993) and Balme (1995) were adopted for botanical affinity inferences. In relation to the algae and algae-like elements,

taxonomic determinations and paleoecology were based mainly on Hemmer and Nygreen (1967), Loeblich and Tappan (1976), Tiwari et al. (1994), Guy-Ohlson (1992), Elsik (1996), Batten (1996) and Servais (1996). For characterization and identification of paleosoils, megascopic and nomenclatural criteria outlined by Andreis (1981) were adopted.

The studied specimens are stored at the Setor de Botânica e Paleobotânica do Museu de Ciências Naturais da UNIVATES, under PbU, and the Departamento de Paleontologia, Instituto

de Geociências, Universidade Federal do Rio Grande do Sul, under PB (palaeobotany). Palynological slides are stored at the Departamento de Paleontologia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, under MP-P.

## 5. Facies analysis

Facies analysis enabled the identification of 16 facies in the outcropping section, characterized as follows.

### 5.1. Coaly siltstone (Sic)

Tabular beds up to 50 cm thick of dark grey, coaly siltstone, sterile for palynomorphs and plant megafossils.

### 5.2. Coaly shale and coal (Shc)

Coaly shale with coal lenses up to 4 mm. The palynological content is dominated by a diversified, well-preserved palynological material. Trilete spores derived from arborescent lycophytes are the predominant elements, represented mainly by *Lundbladispora braziliensis* and *Lundbladispora riobonitensis*. Many tetrads of these two species are also recorded. Spores produced by herbaceous lycophytes (e.g. *Cristatisporites* spp., *Vallatisporites arcuatus*, *Kraeuselisporites* sp.) are less frequent. Other common elements recorded in the palynofloras are spores of filicophytes (e.g. *Punctatisporites gretensis*, *Leiotriletes virkii*, *Brevitriletes cornutus*, *Cyclogranisporites* sp., *Granulatisporites angularis*, *Granulatisporites austroamericanus*, *Lophotriletes rectus*, *Convolutispora candiotensis*, *Horriditriletes* sp.) and sphenophytes, such as *Calamospora plicata*, *Calamospora sahariana*, *Retusotriletes simplex*, *Retusotriletes nigrifellus*, and *Laevigatosporites vulgaris*. Pollen grains produced probably by conifers (*Potonieisporites methoris*, *Protohaploxylinus limpidus*, *Striadopodocarpites fusus*), glossopterids (*Scheuringipollenites medius*, *L. rectus*, *Vesicaspora* sp.), and cordaitophytes (*Cannanoropollis*, *Plicatipollenites*,) are scarce. Organic-walled palynomorphs of uncertain botanical affinity, related to the algae group, such as *Portalites gondwanensis* (the most abundant palynomorph identified in the coals and considered by some authors as fungal spore), *Tetraporina punctata*, and *Brazilea scissa*, as well as fragmentary colonies of the planktonic algae *Botryococcus*, were found together with the spores, pollen grains, and other palynomorphs of terrestrial environment (selected palynomorphs are illustrated in Fig. 7). This facies is sterile for plant megafossils.

### 5.3. Coaly matrix-supported conglomerate with dispersed organic matter (Gmc)

Lenticular beds of dark grey, coaly, matrix-supported conglomerate; normal grading and clasts ranging from sand to silt. Most clasts are very angular, whitish feldspar, with 4 mm maximum diameter. Other frequent clasts are quartz, muscovite, and burned organic material. Dark to medium

gray silt-sand matrix, with vitreous vesicular and laminar fragments, whose parallel orientation to the bedding originates an incipient fissility. Lenses are 1 m long and reach up to 20 cm in thickness. The palynoflora is marked by the predominance of spores mainly derived from arborescent and herbaceous lycophytes (e.g. *Lundbladispora*, *Cristatisporites*, *Vallatisporites*). Spores of filicophytes such as *Punctatisporites*, *Leiotriletes*, and *Granulatisporites* and sphenophytes (*Calamospora*) are less frequent. Frequent monosaccate pollen grains are recorded (*Cannanoropollis*, *Potonieisporites*, *Caheniasaccites*, *Plicatipollenites*), as are bisaccate pollen grains (*Scheuringipollenites*, *Limitisporites*), whereas Striatiti forms are scarce. Algae and algae-like elements are less frequent. The palynological content identified in this facies indicates a microfloristic composition similar to that recognized in facies Shc; however, the palynological material is not as well preserved (selected palynomorphs are illustrated in Fig. 7).

### 5.4. Coaly siltstone with root marks (Sicrm)

Tabular beds up to 50 cm thick of dark grey, coaly siltstone, with root marks of undetermined taxonomic affinity and characterized by elongated pedotubes densely ramified, with a carbonified inner part. Palynological material identified in this facies, characterized by the presence of paleosoils, is scarce and poorly preserved.

### 5.5. Coaly matrix-supported conglomerate (Gmco)

Lenticular beds of reddish, normally grading, coaly matrix-supported conglomerate. Most clasts are very angular whitish feldspar with 4 mm maximum diameter. Other frequent clasts are quartz, muscovite, and charcoal, identified as fragments of gymnosperm wood. Reddish silt-sand matrix, with vitreous vesicular and laminar-shaped fragments. The palynoflora is marked by the predominance of spores derived from arborescent lycophytes mainly attributed to the *Lundbladispora* genus, whereas spores from herbaceous lycophytes are less frequent (*Vallatisporites*, *Cristatisporites*). Spores of filicophytes, such as *Punctatisporites*, *Leiotriletes* and *Granulatisporites*, as well as of sphenophytes (*Calamospora*, *Retusotriletes*) are less common. Although the palynological material is not well preserved, it is possible to observe a marked increase in pollen grains derived from cordaitophytes (*Plicatipollenites*, *Cannanoropollis*). Striated pollen grains are scarce, occurring only in forms of *Protohaploxylinus* and *Vittatina* (Fig. 7).

### 5.6. Siltstone with *B. pedroanum* roots (Sibr)

Tabular beds up to 4 cm thick of massive, whitish to reddish siltstone. Exclusive presence of impressions of fragments of the radial rooting system of *B. pedroanum*, with individual diameters between 0.4 and 0.6 mm, parallel to or sometimes outcrossing the tabular lamination.



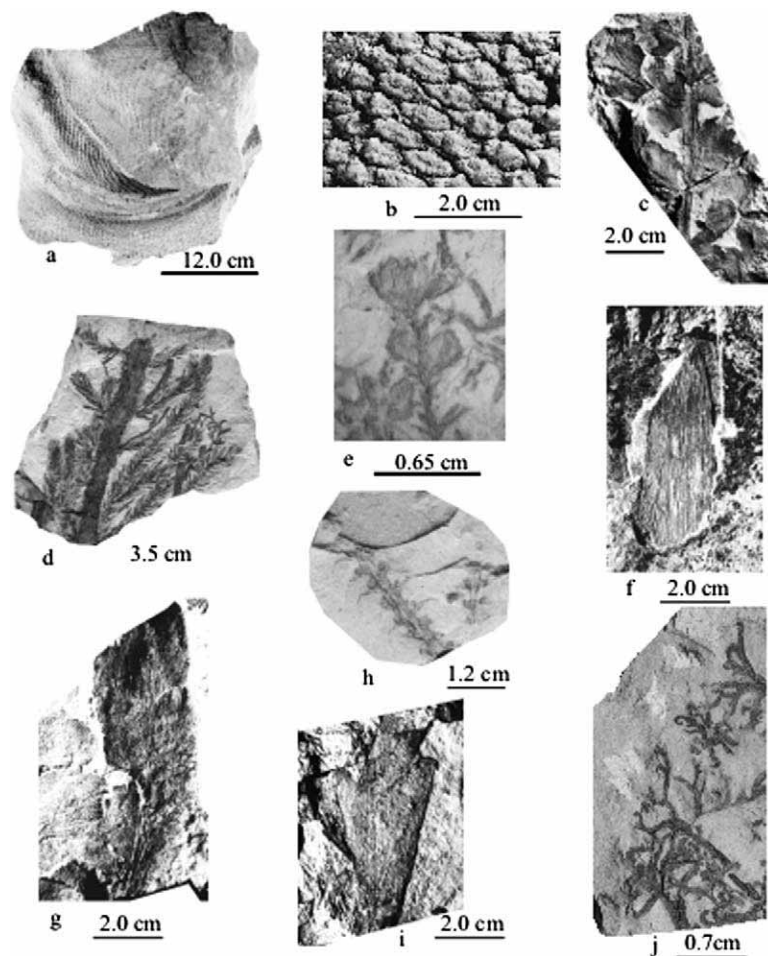


Fig. 6. Megafloristic elements from the roof-shale level of the Quitéria outcrop: (a) *Brasilodendron pedroanum* cormose base; (b) leaf cushions from *B. pedroanum*; (c) *Botrychiopsis valida*; (d) *Cori cladus quiteriensis* shoot; (e) cone of *C. quiteriensis* with ovuliferous scales and elliptically elongated seeds; (f) fragment of *Rubidgea* sp. leaf; (g) fragment of *Cordaites* sp.; (h) *Lycopodites?* sp. presenting sporanges; (i) undetermined leaf; and (j) filicoid undetermined fronds.

### 5.7. Medium sandstone with planar bedding (Sm)

Amalgamated beds of very coarse reddish and yellowish sandstone interlain with lenses and lamina of coarse to very coarse sandstone. At the bottom, this facies presents basal stumps of arborescent lycophytes (*Brasilodendron pedroanum*), closely spaced, cross-cutting the depositional sequence, and with basal flared rings (Fig. 6(a)). The extreme basal portions are depicted as a rounded corm-like structure associated with thin, elongated, acicular roots. These stumps are, in rare cases, attached to fallen trunks represented by compressed casts that cross-cut the sediments at angles from 45 to 20° and also are related to *B. pedroanum* through the morphology of the leaf cushion. Elongated thin and narrow leaves, horizontally dispersed, are indirectly associated with the *Brasilodendron* stems. Fragmented plant material without preferential orientation and unsorted by size was recorded from the base to the upper section of this facies, comprising basal and median basal fragments of *B. valida* fronds (Fig. 6(c)), as well as rare impressions of sterile and fertile shoots of herbaceous lycophytes (*Lycopodites* sp.) (Fig. 6(h)). Dispersed

and rare fragments of leaves of *Rubidgea* sp. (Fig. 6(f)) were recovered from the upper part (10 cm) of this section. Basal segments of leaves with undetermined taxonomic affinity (Fig. 6(i)) are rare at this level. Ramified conifer fragments, sometimes in organic connection, representing sterile and fertile branches of *C. quiteriensis* (Fig. 6(d and e)) are distributed in restricted portions of this facies, in a 6 m transect of the 30 m outcropping area, associated with basal stumps of *B. pedroanum*. Small, sterile, filicoid rhodheopterid fronds (Fig. 6(j)) are also common, associated with *C. quiteriensis*. No detectable change in the lithology accompanied the floristic change. At the top of the roof-shale nonoriented fragments, scattered strap-like leaves, identified as *Cordaites* sp. (Fig. 6(g)) are observed exclusively in sandstones lenses. Morphological details of the plant material are described in Table 1. Palynomorphs are not recorded in this facies.

### 5.8. Siltstone (Si)

Tabular bed up to 4 cm thick of whitish to reddish massive siltstone; sterile for palynomorphs and plant megafossils.

Table 1

Detailed description of the plant material from facies Sm.

<i>B. pedroanum</i> (stems)	Fragments 0.5–6 cm in diameter, 4.0–10.0 cm long, and 3.0–20.0 cm wide, with fusiform, heliptical, or sigmoid leaf cushions (0.5–0.9, 0.2–0.3 cm long) and lepidodendroid phyllotaxis. Parichnos and ligule not visible. Detailed description in Jasper and Guerra-Sommer (1998).
<i>B. pedroanum</i> (basal casts)	Basal clindric casts 1.5–25.0 cm long and 9.0–20.0 cm in diameter with basal flared rings. Basal portions with elongated acicular roots (0.4 cm diameter). At the top, rhombic-helicoidal leaf cushions (0.3–0.4, 0.5–0.7 cm long) and lepidodendroid phyllotaxis. Parichnos and ligule not visible. Detailed description in Jasper and Guerra-Sommer (1998). (Fig. 6(e))
<i>Lycopodites</i> sp.	Shoots 0.5–2.3 cm long and 0.4 cm wide presenting acicular leaves (0.1–0.2 cm long) with a spiral and alternate-opposite disposition. Ovoid sporanges (0.2 long, 0.1 cm wide) adpressed at the basal portion of leaves. (Fig. 6(h))
<i>B. valida</i>	Fragments of fronds (3.8–9.0 cm long, 0.6–7.9 wide) with a robust main rachis presenting strong longitudinal nervures. Pines rhomboidal-ovoid to rhomboidal-elongated (0.8–1.8 cm long, 1.3–1.8 cm wide) presenting an open venation derived from the rachis nervures. Detailed description in Jasper et al. (2003). (Fig. 6(c))
Rhodeopterid fronds	Delicately dichotomized fronds (0.5–5.6 cm long, 0.1–0.2 cm wide), presenting parallel venation. (Fig. 6(j))
<i>C. quiteriensis</i>	Ramified vegetative and fertile branches (6.1–84.3 cm long, 2.4–6.5 cm wide), leafless, other with homomorphic, acicular, and sessil leaves (0.1–0.5 cm long, 0.1 cm wide) with parallel venation. Ovuliferous scales and seeds adpressed to the main axis. Detailed description by Jasper et al. (2005b). (Fig. 6(d and e))
<i>Rubidgea</i> sp.	Medial and rounded apical parts of leaves with parallel veination at the central part of the lamina, recurved in the peripheral region, rarely dichotomized at the base. (Fig. 6(f))
<i>Cordaites</i> sp.	Strap-like leaves (5.2–23.0 cm long, 3.8–4.1 cm wide), with pronounced parallel venation, not anastomosed. (Fig. 6(g))
Unidentified leaves	Incomplete basal portion of leaves (12.0 cm long, 6.0 cm wide), tripartite at the top, with parallel dicotomized venation. (Fig. 6(i))
Charcoal gymnospermic woods	Fusinised wood fragments with secondary xylem represented by multiseriate araucarioid pitting in radial walls of tracheids.

### 5.9. Shale to coaly shale (Sh)

Reddish shale to laterally coaly shale (Shc), sterile for palynomorphs and plant megafossils.

### 5.10. Massive siltstone (Sim)

Tabular beds of reddish massive siltstone; sterile for palynomorphs and plant megafossils.

### 5.11. Siltstone with lamination (Sil)

Tabular beds of reddish laminated siltstone; sterile for palynomorphs and plant megafossils.

### 5.12. Siltstone with root marks (Sirm)

Light-brown siltstone bed, with root marks without defined taxonomic affinity, characterized by elongated pedotubes densely ramified, with yellowish–reddish inner part; sterile for palynomorphs.

### 5.13. Matrix-supported conglomerate (Gmo)

Lenticular beds of light-brown, matrix-supported conglomerate with sand normally grading to silt. Most clasts are very angular whitish feldspar, with 3 mm maximum diameter. Other frequent clasts are quartz and muscovite, with a light-brown silty/sandy matrix. This facies is sterile for palynomorphs and plant megafossils.

### 5.14. Very coarse sandstone with planar cross-bedding (Svpc)

Lenticular beds of yellowish, very coarse sandstone, with low-angle cross-bedding and normal grading; facies is sterile for palynomorphs and plant megafossils.

### 5.15. Very coarse sandstone with through cross bedding (Svtc)

Lenticular beds of very coarse, yellowish sandstones, with trough cross-bedding and normal grading.

The stratigraphic section of the Quitéria outcrop can be divided into nine facies successions (Table 2), identified upward by roman numbers from I to IX. Facies successions are recognized on the basis of facies textural pattern variation and boundary surface type. Some facies successions are characterized by fining-upward sequences and bounded by erosional flat surfaces.

## 6. Depositional models and facies cyclicity pattern

The stratigraphy of the Quitéria outcrop is divided in two depositional sections: a light to dark gray basal section and a yellowish–reddish top section. The basal section comprises five facies succession (FS I–V) and represents mire deposits associated with back barrier-restricted lagoons in a microtidal coast (Leeder, 1999; Reinson, 1992). This mire deposit is interlaid with alluvial fan distal deposits. The top section comprises four facies successions (FS VI–IX) and identifies a reworking of the barrier by a washover sandflat due to marine transgression (FS VI) and a back barrier open lagoon (Leeder, 1999; Reinson, 1992) without organic matter deposition (FS VII–IX) and with significant incidence of washover deposits (Fig. 8).

Nine facies successions (superimposition of sedimentary record) and five cyclicity patterns (depositional dynamic of an environmental system due to climatic and topographic conditions) were recognized in the Quitéria outcrop (Fig. 4). Pattern A, identified by siltstones superimposed by shales, indicates a restricted lagoon without currents and sediment transportation. The mire prograded toward the lagoon, recording a relative water-level fall. This pattern is represented

Table 2  
Facies and facies successions in the Quitéria outcrop

Facies succession	Facies	Description
FS IX	Svpc Svtc Svpc	Composed of facies Svpc (55 cm thick) at the base, superimposed by Svtc (30 cm), followed by Svpc (62 cm)
FS VIII	Sh	Fining-upward succession of tabular beds. From base to top, facies are Gmo (45 cm thick), superimposed by Sh (15 cm), bounded with next succession by an erosional surface
FS VII	Gmo Sirm  Sil Sim Sh Si Sm	Fining-upward succession of tabular beds. From base to top, facies are Sh (12 cm thick), Sim (15 cm), Sil (15 cm), and Sirm (55 cm); bounded with next succession by an erosional surface
FS VI	Sibr	Fining-upward succession of tabular beds. From base to top, facies are Sibr (4 cm thick), Sm (37 cm), and Si (4 cm); bounded with next succession by sharp surface
FS V	Shc	Fining-upward succession of tabular beds. From base to top, facies are Gmco (20 cm thick), flat contact with Shc (20 cm); bounded with next succession by an erosional surface
FS IV	Gmco Sicrm Shc	Fining-upward succession of tabular beds. From base to top, facies are Gmc (13 cm thick), flat contact with Shc (20 cm), flat contact with Sicrm (30 cm); bounded with next succession by an erosional surface
FS III	Gmc Shc	Fining-upward succession of tabular beds. From base to top, facies are Gmc (12 cm thick), flat contact with Shc (8 cm); bounded with next succession by an erosional surface
FS II	Gmc Shc	Fining-upward succession of tabular beds. From base to top, facies are Gmc (60 cm thick), flat contact with Shc (15 cm); bounded with next succession by an erosional surface
FS I	Gmc Shc  Sic	Fining-upward succession of tabular beds. From base to top, facies are Sic (50 cm thick), flat contact with Shc (15 cm). The lowermost contact is covered, and the contact with next succession is an erosional flat surface

by the coaly facies of FS I and occurs only once at the base of the outcropping section.

Pattern B is characterized by a siltstone superimposed by shale. This aspect records a relative water-level rise, bringing about the transgression of the distal lagoon facies over the proximal ones. This pattern, represented only as FS VII, occurred in an open lagoon; however, there was no deposition of organic matter, probably due to the occurrence of currents of an open lagoon.

Pattern C is identified as matrix-supported gravel facies superimposed by shale. It records the filling of a perilagoon mire by progradation of distal alluvial fans, succeeded by a relative water-level rise. Distal alluvial fan deposits, poorly selected, originated near highlands on which volcanogenic material had been deposited. Low-weathering glass fragments indicate the proximity to the source. The fan deposits recovered lowlands with very dense flows, partially eroding the mire area, as is indicated by intraclasts and carbonified material fragments. This pattern recurs three times, sequentially, as recorded by FS II, FS III, and FS IV in a back barrier lagoon system in the microtidal coast and in FS VIII, probably in a mesotidal coast, without organic material. These cycles show that the relative water level rises higher than the filling of the lagoon by fan deposits. This dynamic process allows sufficient accommodation space to keep similar patterns of facies variation throughout most intervals.

Pattern D, identified by matrix-supported conglomerate facies superimposed by shales and siltstones and indicated by FS IV, evinces that the flooded lowlands were covered by distal alluvial fan deposits, succeeded by more proximal facies and then distal deposits of the lagoon. This pattern records a relative water-level rise.

Pattern E is identified as sandstone facies and records reworked events of the sand barrier by washover sandflat deposits. In FS VI, distal washover deposits filled the lagoon, characterizing an occasionally well-drained sandflat. In FS IX, washover deposits were more proximal.

## 7. Floristic changes and paleoecological variability

At the coaly basal section, compositional changes observed in palynofloras of the different facies (Shc, Gmc, and Gmco) comprising the facies succession FS I–V (Figs. 4 and 8) provide important paleoecological data.

The palynological content of the Shc facies indicates the presence of pteridophyte vegetation, in which the dominant presence of arborescent lycophytes is reflected by the remarkable abundance of species of *Lundbladispota* (Archangelsky and Césari, 1990; Cazzulo-Klepzig, unpublished). The abundance of tetrads of *L. braziliensis* and *L. riobonitensis*, significant presence of spores derived from filicophytes, sphenophytes, and herbaceous lycophytes, and the remains of

algae and algae-like elements found together with spores and pollen grains derived from terrestrial vegetation points to the proximity of the parent plants to the peat-forming environment. Aquatic elements, probably carried by occasional sea flooding to the mires, were deposited with the terrestrial palynological material, transported through short distances to the peat-forming environment. Regarding the presence of lycophytes developing in transitional environments, [Habib and Growth \(1967\)](#) state that arborescent or herbaceous lycophytes could flourish in a salinized environment in response to small marine incursions. This coal palynoflora is very similar to the *Lundbladispora/Punctatisporites/Portalites* association, defined by [Marques-Toigo and Corrêa da Silva \(1984\)](#) for the southern Brazilian coals, which was linked to limnotelmatic conditions.

The presence of pollen grains derived from cordaitophytes (*Cannanoropollis*, *Plicatipollenites*) flourishing in lowland substrates and mangrove areas, together with scarce and fragmented pollen grains of glossopteridophytes

(*Limitisporites*, *Scheuringipollenites*), indicate the possibility that these plants coexisted in the same habitat ([Glasspool, 2003](#)). Their complementary presence in the fossil assemblage could be related to biostratigraphic processes related to hydrodynamic factors, which transported the grains from the original habitat to the mires. Studies on south Brazilian coal-forming plants ([Cazzulo-Klepzig, unpublished](#)) conclude that coal palynofloras, dominated by spores of arborescent and shrub-like vegetation and with complementary forms of gymnospermic pollen grains, found together with palynomorphs of aquatic environment such as *Botryococcus* and algae-like forms, indicate plant communities developed under autochthonous or hypautochthonous peat-forming conditions.

The dominant peat-forming plant communities flourished in lowlands surrounding the mires in a coastal environment as the subordinate forms related to vegetation typical of more drained, higher, distant areas from the depositional site. In this scenario, some episodic marine incursions could have

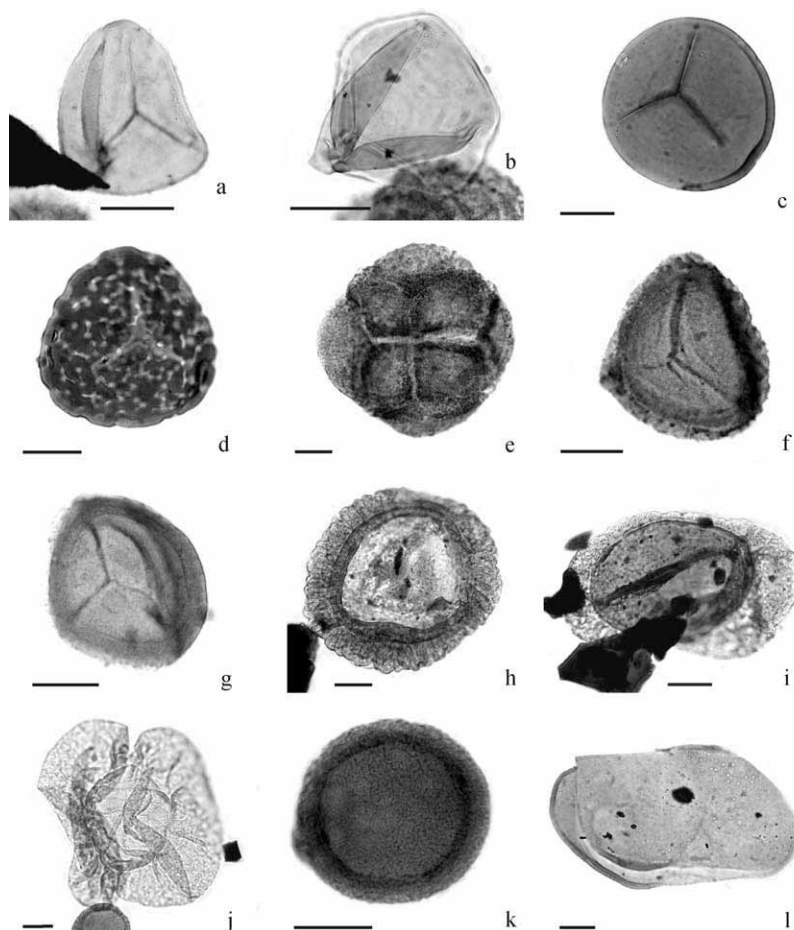


Fig. 7. Photomicrographs of selected palynomorphs; scale-bar corresponds to 20  $\mu\text{m}$ . (a) *Leiotriletes virkii* Tiwari, 1965 (MP-P 4446, England Finder coordinates: J 45/2); (b) *Calamospora plicata* (Luber and Waltz) Hart, 1965 (MP-P 4446, EF: G44/1); (c) *Punctatisporites gretensis* Hart, 1965 (MP-P 4446, EF: B36/1); (d) *Convolutispora candiotensis* Ybert, 1975 (MP-P 4446, EF: Q 53); (e) Tetrad of *Lundbladispora braziliensis* (Pant and Srivastava) Marques-Toigo and Pons emend. Marques-Toigo and Picarelli, 1984 (MP-P 4448, EF: B 34/1); (f) *L. braziliensis* (Pant and Srivastava) Marques-Toigo and Pons emend. Marques-Toigo and Picarelli, 1984 (MP-P 4448 EF: L33/4); (g) *Lundbladispora riobonitensis* Marques-Toigo and Picarelli 1984 (MP-P 4448, EF R 38/1); (h) *Cannanoropollis korbaensis* (Bharadwaj and Tiwari) Foster, 1975 (MP-P 4446, EF: D35/4); (i) *Caheniasaccites flavatus* Bose and Kar emend. Azcuy and DiPasquo, 2000 (MP-P 4446, EF: P39/3); (j) *Striatopodocarpites fusus* (Balme and Hennelly) Potonié, 1958 (MP-P4446, EF: H/41); (k) *Portalites gondwanensis* Nahuys, Alpern and Ybert, 1969 (MP-P 4448, EF: 34/3); and (l) *Tetraporina punctata* (Tiwari and Navale) Kar and Bose, 1976 (MP-P 4448, EF: P/49).



carried minor elements from marine microplankton (*Navifusa*) to the mire. In the mire, chlorococcalean algae such as *Botryococcus braunii* flourished. For De Deckker (1988), fossil colonies of *Botryococcus*, developing in fresh or brackish waters, occurred periodically in small and shallow lagoons, where saline fluctuations were common.

The significant content of vitrinite in these coals and coaly shales, previously identified by coal petrographic analysis (Cazzulo-Klepzig et al., 1999), reflects the presence of arborescent plants according to Holz et al. (2002). According to Corrêa da Silva (1984), the southern Brazilian coals, formed under subaquatic conditions, are mainly parautochthonous, which enhanced the deposition of inorganic matter along with plant tissues. These conditions differ from those of autochthonous coals originated on the Euramerican Pennsylvanian peat swamps (Gastaldo, 1984).

The palynological content from the Gmc and Gmco facies shows less frequent spores of arborescent lycophytes (*Lundbladispora*, *Vallatisporites*), filicophytes (*Granulatisporites*, *Apiculatisporis*, *Cyclogranisporites*, *Lophotriletes*, *Convolvatispora*), or sphenophytes (*Punctatisporites*, *Calamospora*). These facies can be characterized by a significant increase in pollen grains produced by cordaitophytes (*Scheuringipollenites*, *Limitisporites*) living in mesophilous environments near the mire. Pollen grains from glossopteridophytes and conifers are rare. Taking into account the lower occurrence of aquatic elements and acritarchs, development for this palynoflora can be inferred to have taken place in different paleoenvironmental conditions than the palynoflora from Shc facies, which shows changes in the vegetation dynamic. According to Moore (1995), hydrological characteristics, particularly the source of water entering the peat system, differ and cause compositional variations in the plant communities.

In Fig. 5, the distribution of different groups of plants reflected by quantitative changes in palynofloras between coals (and coaly shales) and conglomerates is represented.

The abundance of typically charred woods of gymnosperms (charcoal) in Gmc facies, composed of secondary xylem with uni- to multiseriate pitting, supports the hypothesis that woody gymnosperms (*Cordaites*?) were important elements in the original floras of the surrounding areas and transported to the depositional site from nearby, well-drained environments (*sensu* Pfefferkorn, 1980). Forest fires occurring during the deposition of the Gmc with volcanic influence could be responsible for the presence of fusinized fragments.

Compositional changes in Shc, Gmc, and Gmco facies enable the inference of cyclic paleoecological patterns along the sequence. This cyclicity is supported by changeable proportions among the different palynological groups, which reflect the presence of different plant communities and the abundance or scarcity of elements from marine microplankton in relation to terrestrial palynological elements (Fig. 7). Cyclic microfloristic changes among Shc, Gmc, and Gmco facies in FS I–V support the interpretation of a mire depositional system associated with a restricted lagoon, protected by barrier islands in a microtide shore, and interbedded with distal alluvial fan deposits.

The palynoassemblages are assigned to the upper part of the *Vittatina costabilis* zone (Souza and Marques-Toigo, 2003), included in the *Hamiapollenites karrooensis* interval subzone, which is characterized by the appearance of the eponymous, as well as *Staurosaccites cordubensis* and *S. fusus*. This subzone relates to the Early Permian. Among its index taxa, *S. fusus* is found in the coaly shales (Shc, Fig. 4). Diagnostic species of the subsequent *Lueckisporites virkkiae* interval zone (e.g. *L. virkkiae*, *Lueckisporites stenotaeniatus*, *Weylandites lucifer*) are absent (Fig. 8).

Basal facies of the yellowish upper section (Sibr and Sm, FS V–IX) correspond to episodic sediment from the coastal land, which changes the morphology of depositional systems. Autochthonous and parautochthonous plant debris of roof-shale flora distinguish the relationships between the peat-forming flora and the overlying clastic sediments.

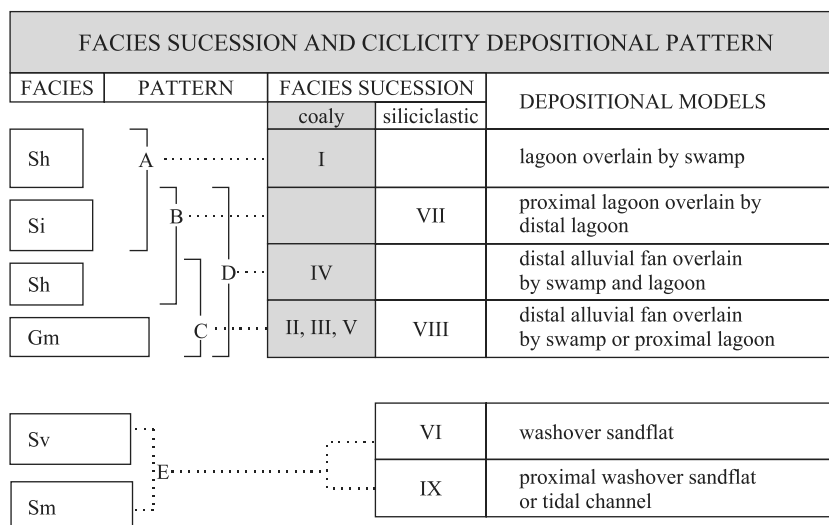


Fig. 8. Facies succession and cyclicity depositional pattern in Quitéria outcrop (adapted from Leeder, 1999; Reinson, 1992).

The more impressive assemblage of the roof-shale corresponds to arborescent in situ lycophyte remains, characterized by (1) concentration in a single stratigraphic horizon, defined by a linear transect; (2) random distribution; (3) occasional attachment of the basal cormophytic bases to compressed stumps; (4) presence of basal flared rings in caulinar systems; and (5) root system structured by radial disposition of filaments.

The paleosuccession in this interval is recorded in four stages (see Fig. 4). At Stage A (Sibr facies), the exclusive presence of filaments of the radial rooting system from the cormose lycophytes, preserved in this facies underlying the Sm facies whence the basal casts were recovered, confirms the hypothesis that the arborescent lycophytes composed a pioneer community established in a sandy permeable paleosol, originated by the ingression of sediments on the peat surface.

In Stage B, at the bottom of the roof-shale (Sm facies), second depositional level, the compositional index variation ( $R=1.69$ ) of in situ upright stems casts provides information about the composition and spatial arrangement of the original plant communities, with minimal taxonomic bias (Pfefferkorn et al., 2000).

The random distribution of basal stumps is not unexpected in a group of plants that had clonal reproduction and appear to have been opportunistic. According to DiMichele and DeMaris (1987), opportunistic species invading an open site would establish initially more or less randomly if the substrate and microhabitat were uniform. Pfefferkorn et al. (2000), using actualistic data, show that environments characterized by very high rates of sedimentation, or episodic sedimentation events, have an unusually high potential to preserve standing forests. Pigg and Taylor (1985) indicate that the presence of lycophytes with cormose growth forms is important paleoecological evidence of growth in dry, rather than swamp-like, environments. Using actualistic data, Lepage and Pfefferkorn (2000) conclude that the most important factors to determine the dominance of an assemblage in a given environment are the hydric and nutrient availability and the absence of a faster growing competitor. At the Quiteria roof-shale, stumps, visible in longitudinal sections across cuts, show that these trees were established on a sandy/silty surface but not on the peat itself and indicate a span of time between the last phase of coal swamp plant deposition and the beginning of the colonization in silty soil. The pioneer arborescent lycophytes (*Brasilodendron*) and forms related to *Botrychiopsis* and *Lycopodites* developed on the new mineral substrate originated in the lagoon surface after the cessation of peat formation.

The prostrate, horizontal, and subhorizontal plant parts, including shoots, leaves, fronds, aerial branches, and reproductive structures, preserved at the site among the erect vegetation at Stage C of the roof-shale (10 cm) indicate autochthonous/parautochthonous deposition, probably representing groundcover forms (DiMichele and DeMaris, 1987; DiMichele and Nelson, 1989; Gastaldo, 1990; Gastaldo et al., 1995; Martín-Closas and Gomez, 2004). Thus, the presence of forms identifiable with groundcover, associated with the upright arborescent lycophyte stumps, indicates periods of

the absence of standing water in the area, sufficient to permit the growth of groundcover vegetation.

The record of *B. valida* as an element of the understory vegetation confirms the hypothesis of Jasper et al. (2005a) that *Botrychiopsis* (with *B. valida* species) became a common element in floral assemblages related to coal-forming environments under a cool/warm temperate climate in Kungurian in southern Paraná Basin.

In this stage, the lateral contact (traceable for approximately 6 m) between the understory forms and vegetation dominated by conifers (*C. quiteriensis*), also associated with *B. pedroanum* stumps, indicates that the two vegetational types were segregated. This small-scale patchiness of the megafloora shows that the vegetation could have been heterogeneous, with assemblages of different predominance and diversity structure coexisting in small areas. According to DiMichele and Nelson (1989), zones of contact probably reflect abiotic conditions, related to slightly different microhabitat preferences. These microhabitats, typically of wash fan morphology, were too slight to be reflected in the sediment deposit. The vegetational patchiness (lycophyte community, *B. pedroanum*; conifer community, *C. quiteriensis*) observed in short distance probably was a response to microtopographic variation. Large fragments of *C. quiteriensis* with branches and female cones in organic connection suggest a local deposition or minimal transport. The exceptional preservation indicates that these forms were included in biostratigraphic phases as fresh fragments, not as litter. Their association with stumps of arborescent lycophytes, *B. valida*, herbaceous lycophytes (*Lycopodites*), and filicopsids agrees with the inferences of Archangelsky and Cúneo (1987), suggesting that Ferrugliocladaceae in the Gondwana Early Permian lived in temperate, humid conditions and had a wider range of habitats than the conifers found in the equatorial belt, which are mainly xerophyllous.

At the top of Stage C, the scarce occurrence of badly preserved leaves of *Rubidgea*, a protoglossopterid with arborescent habit, may indicate transport from surrounding dry lands related to washover flat area.

At Stage D, restricted to the top of the Sm facies, a monotypic association of *Cordaites* leaves scattered exclusively in lenses of coarse sandstones represents a significant paleoecological marker. Many studies of coal-forming floras in Euramerica show that *Cordaites* trees constituted a diverse group that included mangrove-like plants (Cridland, 1964; Scott, 1977; Raymond, 1988; Raymond and Phillips, 1983; Constanza, 1985) and understory shrubs (Rothwell and Warner, 1984; Constanza, 1985). Paleoecological studies indicate that cordaites trees inhabited well-drained, clastic, lowland substrates (Trivett and Rothwell, 1985; Taylor and Taylor, 1993), whereas the shrubs and mangrove-like forms inhabited the peat-forming swamps (Raymond and Phillips, 1983; Taylor and Taylor, 1993). In contrast, Falcon-Lang (2003) characterizes, from the Upper Carboniferous, successions of New Scotia (Canada) as a *Cordaites*-dominated dry land unit from the seasonal continental interior.

In some roof-shale of south Paraná Basin (Rio Bonito Formation, Faxinal mine) *Cordaites*-compressed leaves associated with glossopterids were dominant elements in an assemblage characterized as a ‘forest swamp’ (Guerra-Sommer, 1988). The simultaneous occurrence of these forms in the same sedimentary horizon suggests that *Cordaites* leaves were produced by plants that cohabited with glossopterids in the southern Brazilian Gondwana ecosystem.

Evidence provided by the present study leads to the hypothesis that in Gondwana, different stocks of cordaites could adapt to specific environments. Their rare and fragmentary presence in roof-shale flora of the Quitéria outcrop suggests the ingression of remains of a parautochthonous seasonal dryland flora in the depositional system. According to Falcon-Lang and Scott (2000) and Falcon-Lang (2003), this succession of humid, coastal, coal-forming wetlands to seasonally dry lands probably reflects the proximity of the ocean. However, Scott et al. (1997) mention that megafloreal remains in some transgressive deposits in Euramerican Paleozoic sequences are cordaites dominated.

Comparing the data obtained by palynological analyses of the basal coaly interval with megaflorestic studies of the overlying roof-shale flora from the clastic interval, it can be inferred that the roof-shale community reflects the same compositional spectrum represented in the peat-forming plant community, confirming the genetic relationship between the peat and clastic swamp flora.

Small diameter (0.1–0.5 cm), tubular root traces are locally very dense in tabular-laminated facies (Sicrm and Sirm) in both the organic-rich basal interval (FS I–V) and the overlying clastic interval (FS VI–IX), which implies dense cover by small, herbaceous plants (Lepage and Pfefferkorn, 2000). Their morphology differs from those of the arborescent cormose lycophyte in facies Sibr and indicates that tabular siltstone deposits were generated in shallow water conditions. Evidence presented here agrees with the inference that in the outcropping sequence, lagoons developed in periods with high water tables and intense deposition of organic matter, which produced coaly shales and coals (Shc), followed by periods of development of shallow-water lagoons, which produced siltstones with paleo-soils (Sicrm and Sirm) with root marks of herbaceous/shrub-like vegetation.

## 8. Conclusions

The integration of paleontological and high-resolution sequence stratigraphy in the Quitéria outcrop led to the conclusion that distinguishable coastal dynamics conditions are indicated by particular characteristics of two sections, the basal characterized by a high content of organic matter and the upper by clastic sedimentation.

The basal interval (FS I–V) represents a coastal lagoon depositional system protected by a barrier, probably under microtide conditions. In this peat-forming system in lowlands, the ingression of sediments by distal alluvial fans reworked debris of volcanic origin, previously deposited in very close higher lands. The overlying clastic interval represents different

conditions due to the sectioning of the barrier brought about by washover fans (FS VI–IX), which generated a washover plain.

The facies succession pattern reveals that deposition occurred in conditions of a large supply of sediments from distal alluvial fans and with continued increases of accommodation space in transgressive conditions. The facies successions represent seven cycles of relative water level variation in the lagoon; the basal one (FS I) is marked by a relative water level fall, and the others represent the relative water level rise.

An episodic deposit, reflected in FS VI, from coastal land changed the morphology of the depositional system, generating sandy soil poor in nutrients, which became a substrate for a floristic succession process, in which arborescent, cormose lycophytes developed as the colonizing group. In the pioneer community preserved in the roof-shale level at the Quitéria outcrop, the absence of standing water, at least in some periods, is inferred by the presence of understory forms, which represent groundcover vegetation developed under the canopy. The development of distinct vegetation patterns in a small area (arborescent lycophyte community versus conifer community) was made possible by the presence of different microhabitats originated by microtopographic variation. This exposure provides a rare look at short-term spatial heterogeneity and reveals an unexpected degree of patchiness not observed in most outcrops in Brazilian Gondwana.

Paleoenvironmental changes, indicated by the exclusive presence of fragmentary *Cordaites* leaves in sandstone lenses at the top of the roof-shale level, point to an important event, identified as distal washover fans that caused the ingression of dryland communities, which likely represent the vegetation of the seasonal continental interior.

The roof-shale flora represents an Early Permian (Kungurian) autochthonous floristic association, adapted to warm climates and developed in lowland coastal sandy soils in the Early Permian. The arborescent, cormophytic lycophytes can be considered paleoecological and paleoclimatic markers in environments related to clastic lowlands in a coastal plain.

Palynological data from subjacent coaly facies reflect a strong floristic compositional similarity with the plant communities preserved in the roof-shale. Considering this paleobotanical evidence, it is possible to infer that at the Quitéria outcrop, the origin of the roof-shale flora was related to plant communities that also generated the underlying peat. These data confirm the genetic relationships between the peat-forming flora and the overlying clastic flora.

The deposition interval of the outcropping sedimentary package can be correlated with the final parasequences of the Rio Bonito Formation transgressive tract, where coal levels are thin. This correlation is confirmed by *S. fusus* in the palynological association in the shale underlying the roof-shale, which indicates the *H. karrooensis* palynostratigraphic subzone that corresponds to the Kungurian.

## Acknowledgements

The study was supported by the Brazilian agencies FUNA-DESP, FAPERGS, CAPES and CNPq (personal research and

study grants). The manuscript benefited from helpful comments by Dr Volker Mosbrugger and the anonymous reviewer, as well as suggestions by Dr Reinhardt A. Fuck, Regional Editor.

## References

- Allemán, V., Pfefferkorn, H.W., 1991. Bosques en posición de vida en el Carbonífero de Paracas. In: VII Congreso Peruano de Geología, Lima, Resúmenes Expandidos, pp. 395–398.
- Alves, R.G., Ade, M.V.B., 1996. Sequence stratigraphy and coal petrography applied to the Candiota coalfield, Rio Grande do Sul, Brazil: a depositional model. *International Journal of Coal Geology* 30, 231–248.
- Andreis, R.R., 1981. Identificación e importancia geológica de los paleosuelos. Editora da UFRGS. Universidade Federal Rio Grande do Sul, Porto Alegre, 67 p.
- Archangel'sky, S., Césari, S., 1990. Ultraestructura de la exina en ejemplares carboníferos de *Lundbladispora* (Licófitas), la Rioja, Argentina. *Ameghiniana* 27 (1–2), 131–139.
- Archangel'sky, S., Cúneo, R., 1987. Ferugliocladaeae, a new conifer family from the Permian of Gondwana. *Review of Palaeobotany and Palynology* 51, 3–30 (text-fig.).
- Azcuy, C.L., Longobucco, M., Alvarez, L., Strelkov, E., 1987. Licofitas arborescentes de la Formación Cerro Agua Negra (Provincia de San Juan). *Ameghiniana* 24 (3–4), 257–261.
- Azcuy, C.L., Di Pasquo, M., 2000. Palynology of the Late Carboniferous from the Tarija Basin, Argentina: a systematic review of monosaccate pollen genera. *Palaeontographica B*, Stuttgart 253, 107–137.
- Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology* 87 (2–4), 1–323.
- Batten, D.J., 1996. Colonial chlorococcales. In: *Palynology-principles and applications*. Jansonius & MacGregor (Eds.), American Association of Stratigraphic Palynologists Foundation, 1, pp. 191–203.
- Cazzulo-Klepzig, M., unpublished. Palinología aplicada à reconstrução das unidades de paisagem e dinâmica das turfeiras formadoras dos carvões permianos do Rio Grande do Sul, Brasil. PhD Thesis, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil, 2 v. 250p.
- Cazzulo-Klepzig, M., Mendonça-Filho, J.G., Peralba, M.C.R., Jasper, A., 1999. Caracterização do carvão da localidade de Quitéria, Encruzilhada do Sul, RS através de métodos palinológicos, petrográficos e organogeoquímicos. *Anais da Academia Brasileira de Ciências* 71 (4–1), 812–813.
- Cazzulo-Klepzig, M., Guerra-Sommer, M., Formoso, N.L., Calarge, L.M., 2002. Geochemical and Palynological evidence for the age determination of Permian coals, Southern Brazil. *Journal of South American Earth Sciences* 15 (2), 375–380.
- Chaves, H.A.F., Della Fávera, J.C., Pereira, E., Medeiros, M.A.M., Câmara Filho, L.M., 1994. Eventos cíclicos na seqüência Permiana da região de Candiota-RS-Brasil. *Acta Geologica Leopoldensia* 39 (1), 221–234.
- Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 33, 445–453.
- Constanza, S.H., 1985. *Pennsylvanioxylon* of Middle and Upper Pennsylvanian coals from the Illinois Basin and its comparison with *Mesoxylon*. *Palaeontographica Abt. B* 197, 81–121.
- Corrêa da Silva, Z.C., 1984. Petrography and facies analyses of Santa Rita coal measures, Southern Brazil. In: *Anais XXXIII Congresso Brasileiro Geologia, Rio de Janeiro, RJ*, vol. 3, pp. 1326–1333.
- Cridland, A.A., 1964. *Amyelon* in American coals balls. *Palaeontology* 7, 189–209.
- Cúneo, R., Andreis, R.R., 1983. Estudio de un bosque de Licofitas en la Formación Nueva Lubecka, Permiano de Chubut, Argentina. *Implicancias Paleoclimáticas y Paleogeográficas*. *Ameghiniana* 20 (1–2), 132–140.
- De Deckker, P., 1988. Biological and sedimentary facies of Australian salt lakes. *Palaeogeography Palaeoclimatology Palaeoecology* 62, 237–270.
- Della Fávera, J.C., Chaves, H.A.F., Pereira, E., Medeiros, M.A.M., Câmara Filho, L.M., 1994. Evolução geológica da seqüência permiana da região de Candiota-RS-Brasil. *Acta Geologica Leopoldensia* 39 (1), 235–246.
- DiMichele, W.A., DeMaris, P.J., 1987. Structure and Dynamics of a Pennsylvanian-age *Lepidodendron* Forest: Colonizers of a Disturbed Swamp Habitat in the Herrin (n° 6) Coal of Illinois. *Palaios* 2, 146–157.
- DiMichele, W.A., Nelson, W.J., 1989. Stratigraphic inter-regional changes in Pennsylvanian coal-swamp vegetation environmental inferences. *International Journal of Coal Geology* 5, 43–109.
- Elsik, W.C., 1996. Fungi. In: *Palynology—principles and applications*. Jansonius & MacGregor (Eds.), American Association of Stratigraphic and Palynology Foundation, vol. 1, pp. 207–210.
- Falcon-Lang, H.J., 2003. Late Carboniferous Tropical Dryland Vegetation in an Alluvial-plain Setting, Joggins, Nova Scotia, Canada. *Palaios* 18, 197–211.
- Falcon-Lang, H.J., Scott, A.C., 2000. Upland ecology of some Late Carboniferous cordaitalean trees from Nova Scotia and England. *Palaeogeography Palaeoclimatology Palaeoecology* 156, 225–242.
- Foster, C.B., 1975. Permian plant microfossils from the Blair Athol Coal Measures, Central Queensland, Australia. *Geological Survey of Queensland, Brisbane* 45, 1–154.
- Gastaldo, R.A., 1984. A case against pelagochthony: the untenability of Carboniferous arborescent Lycopod-dominated floating mats. In: Walker, K.R. (Ed.), *The Evolution—Creation Controversy, Perspectives on Religion, Philosophy, Science and Education*, The Paleontological Society Special Publication, vol. 1, pp. 97–116.
- Gastaldo, R.A., 1990. Early Pennsylvanian swamp forest in the Mary Lee coal zone, Warrior Basin, Alabama. In: Gastaldo, R.A., Demko, T.M., Liu, Yuejin. (Eds.), *Carboniferous coastal environments and paleocommunities of the Mary Lee coal zone, Marion and Walker Counties, Alabama: Southeastern Section of the Geological Society of America, 39th Annual Meeting, Guidebook for Field Trip 6, Tuscaloosa, Alabama: Tuscaloosa, Geological Survey of Alabama*, pp. 41–54.
- Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1995. Taphonomic and sedimentological characterization of roof shale floras. *Geological Society of America Memoir* 185, 341–352.
- Glasspool, I.J., 2003. Hypautochthonous—allochthonous coal deposition in the Permian, South African, Witbank Basin No. 2 seam; a combined approach using sedimentology, coal petrology and palaeontology. *International Journal of Geology* 53, 81–135.
- Gould, R.E., Delevoryas, T., 1963. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringa* 1, 387–399.
- Gradstein, F.M., et al., 2004. A geological time scale 2004. *Geological survey of Canada, Miscellaneous Report* 86, 1 poster.
- Guerra-Sommer, M., 1988. Padrões epidérmicos da Flora *Glossopteris* na Jazida da Faxinal (Formação Rio Bonito, Kunguriano, RS): implicações taxonômicas, bioestratigráficas e paleogeográficas. PhD. Thesis (unpublished), Inst. Geociências, Univ. Federal Rio Grande do Sul, Porto Alegre, = 716pp.
- Guerra-Sommer, M., Marques-Toigo, M., Corrêa da Silva, Z.C., 1991. Original biomass and coal deposition in Southern Brazil (Lower Permian, Paraná Basin). *Bulletin de la Société Géologique de France, Paris* 162, 227–237.
- Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., 2001. Roof-shale floras in Early Permian southern Brazilian Gondwana: evidences of the icehouse waning. *Contributions to Geology and Palaeontology of Gondwana in honour of Helmut Wopfner*. In: Weiss, R.H. (Ed.), pp. 231–251 (3 figs., 5 pls).
- Guy-Ohlson, D., 1992. *Botryococcus* as an aid in the interpretation of palaeoenvironment and depositional processes. *Review of Palaeobotany and Palynology* 71, 1–15.
- Habib, D., Growth, P.H.K., 1967. Palaeoecology of migrating Carboniferous peat-environments. *Paleogeography Paleoclimatology Paleoecology* 3, 185–195.
- Hart, G.F., 1965. The systematics and distribution of Permian miospores, Johannesburg, Witwatersrand University Press, 252p.



- Hemmer, D.O., Nygreen, P.W., 1967. Algae, acritarchs and other microfossils *incertae sedis* from the Lower Carboniferous of Saudi Arabia. *Micro-palaeontology* 13 (2), 183–194.
- Holz, M., 1997. Early Permian sequence stratigraphy and paleophysiology of the Paraná Basin in northeastern Rio Grande do Sul State, Brazil. *Anais da Academia Brasileira de Ciências* 69 (4), 521–543.
- Holz, M., 1998. The Eopermian coal seams of the Paraná basin in southernmost Brazil: an analysis of the depositional conditions using sequence stratigraphy concepts. *International Journal of Coal Geology* 36 (1–2), 141–164.
- Holz, M., unpublished. O intervalo gondwânico basal (Eo-permiano) da Bacia do Paraná na região nordeste do Rio Grande do Sul—um exercício de estratigrafia. PhD Thesis, Universidade federal do Rio Grande do Sul, UFRGS, Porto Alegre, 2v, 246 pp.
- Holz, M., Vieira, P.E., Kalkreuth, W., 2000. The Early Permian coal-bearing succession of the Paraná Basin in southernmost Brazil: depositional model and sequence stratigraphy. *Revista Brasileira de Geociências* 30 (3), 420–422.
- Holz, M., Kalkreuth, W., Banerjee, A., 2002. Sequence stratigraphy of paralic coal-bearing strata: an overview. *International Journal of Coal Geology* 48, 147–179.
- Jasper, A., Guerra-Sommer, M., 1998. Licófitas cormofíticas arborescentes do afloramento Quitéria—Formação Rio Bonito (Bacia do Paraná), RS. *Pesquisas* 25 (1), 43–60 (text-fig.).
- Jasper, A., Guerra-Sommer, M., 1999. Licófitas arborescentes in situ como elementos importantes na definição de modelos deposicionais (Formação Rio Bonito-Bacia do Paraná-Brasil). *Pesquisas* 26, 49–58.
- Jasper, A., Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., 2003. The *Botrychiopsis* genus and its biostratigraphic implication in Southern Paraná Basin. *Anais da Academia Brasileira de Ciências* 75 (4), 513–535.
- Jasper, A., Guerra-Sommer, M., Cazzulo-Klepzig, M., Iannuzzi, R., 2005. Biostratigraphic and palaeoclimatic significance of *Botrychiopsis* fronds in Gondwana realm. *Proceedings of XV ICCP (GE 03-10.291): MS ICCP-XV-21* (accepted for publication, in press).
- Jasper, A., Ricardi-Branco, F., Guerra-Sommer, M., 2005b. *Cori cladus quiteriensis* gen. & sp. nov., a new conifer in Southern-Brazil Gondwana (Lower Permian, Paraná Basin). *Anais da Academia Brasileira de Ciências* 77 (1), 157–168.
- Kar, R.K., Bose, M.N., 1976. Palaeozoic *spora dispersae* from Congo. III—Assise des schistes noirs de la Lukuga. *Musé Royal de L'Afrique Centrale, Tervuren, Belgique, Annales* 77, 21–33.
- Lavina, E.L., Lopes, R.C., 1987. A transgressão marinha do Permiano Inferior e a evolução paleogeográfica do Supergrupo Tubarão no estado do Rio Grande do Sul. *Paula-Coutiana* 1, 51–103.
- Leeder, M., 1999. *Sedimentology and Sedimentary Basins; from Turbulence to Tectonics*. Blackwell Science, London p. 592.
- Lepage, B.A., Pfefferkorn, H.W., 2000. Did ground cover change over geologic time? In: Gastaldo, R.A., DiMichele, D.A. (Eds.), *Phanerozoic Terrestrial Ecosystems*. Paleontological Society Special Paper, 6, pp. 171–182.
- Loeblich, A.R., Tappan, H., 1976. Some new revised organic-walled phytoplankton microfossil genera. *Journal of Palaeontology* 50, 301–308.
- Lopes, R.D.A.C., Lavina, E.L., 1995. Arcabouço aloestratigráfico para o intervalo 'Rio Bonito-Palermo' (Eo-permiano), entre Butiá e São Sepé, RS. In: *Boletim de Resumos Expandidos do II Simpósio sobre Cronoestratigrafia da Bacia do Paraná*, Porto Alegre, pp. 51–56.
- Marques-Toigo, M., Corrêa da Silva, Z.C., 1984. On the origin of gondwanic south Brazilian coal measures. *Comunicações Serviços Geológicos de Portugal* 70 (2), 151–160.
- Marques-Toigo, M., Picarelli, A.T., 1984. On the morphology and botanical affinities of *Lundbladispora* Balme (1963) in the Permian of Paraná Basin. *Boletim do Instituto de Geociências, USP, São Paulo* 15, 46–52.
- Martín-Closas, C., Gomez, B., 2004. Taphonomie des plantes et interprétations paléocologiques: Une synthèse. *Geobios* 37, 65–88.
- Menegat, R., Scherer, C.M.S., 1993. Formação Caneleiras (RS): devoniana ou permo-triássica?—Critérios para o enquadramento estratigráfico de seqüências isoladas sobre o Escudo Sul-Rio-Grandense. In: *Simpósio sobre Cronoestratigrafia da Bacia do Paraná*, 1, 1993, Rio Claro. *Resumos Expandidos*. Rio Claro (SP): IG/UNESP, pp. 90–93.
- Menegat, R., Scherer, C.M.S., Ketzer, J.M.M., Caravaca, G., 1995. Discordância entre a Formação Rio Bonito e a seqüência Rio do Rasto/Sanga do Cabral da Bacia do Paraná na região de Encruzilhada do Sul, RS: implicações tectônicas. In: *Simpósio sobre Cronoestratigrafia da Bacia do Paraná*, 2, 1995, Porto Alegre. *Boletim de Resumos*. Porto Alegre: CIGO-UFRGS, pp. 42–44.
- Menezes, J.R.C., 1994. Seqüências de segunda e terceira ordens (0.5–50 ma) do Permiano da Bacia do Paraná na região de Candiota (RS). In: *Boletim de Resumos Expandidos do Congresso Brasileiro de Geologia*, 01, pp. 119–142.
- Milani, E.J., Faccini, U.F., Scherer, C.M., Araújo, L.M., Cupertino, J.A., 1998. Sequences and Stratigraphy hierarchy of the Paraná Basin (Ordovician to Cretaceous), Southern Brazil. *Bol. IG. USP, Série Científica*, 29, pp. 125–173.
- Moore, P.D., 1995. Biological processes controlling the development of modern ecosystems. *International Journal of Coal Geology* 28, 99–110.
- Nauhys, J., Alpern, B., Ybert, J.P., 1969. Estudo palinológico e petrográfico de alguns carvões do sul do Brasil. *Boletim Técnico do Instituto Tecnológico do Rio Grande do Sul*, Porto Alegre 6, 3–61.
- Pfefferkorn, H.W., 1980. A note on the term 'upland flora'. *Review of Palaeobotany and Palynology* 30, 157–158.
- Pfefferkorn, H.W., 1997. Paleoclimates of Peru during the late Paleozoic-fossil plants and moving continents. *Sociedad Geológica del Perú, Lima, Volumen Especial* 1, pp. 671–673.
- Pfefferkorn, H.W., Gastaldo, R.A., DiMichele, W.A., 2000. Ecological stability during the Late Palaeozoic cold interval. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), *Phanerozoic terrestrial Ecosystems*. Paleontological Society Special Papers 6, pp. 63–78.
- Phipps, D., Playford, G., 1984. Laboratory techniques for extraction of palynomorphs from sediments. *Papers of the Department of Geology, University of Queensland*, vol. 11, pp. 1–23.
- Piccoli, A.E.M., Menegat, R., Guerra-Sommer, M., Marques-Toigo, M., Porcher, C.C., 1991. Faciologia da seqüência sedimentar nas folhas de Quitéria e Várzea do Capivarita, Rio Grande do Sul. *Pesquisas* 18, 31–43.
- Pigg, K.B., Taylor, T.N., 1985. *Cormophyton* gen. nov., a cormose lycophyte from the Middle Pennsylvanian Mazon Creek Flora. *Review of Palaeobotany and Palynology* 44, 165–181.
- Posamentier, H.W., Jervy, M., Vail, P.R., 1988. Eustatic controls on clastic deposition I—conceptual framework. In: Wilgus, C.K., Hastings, B.S., Kendall, C.G.St.C., Posamentier, H.W. (Eds.), *Economic Paleontologist and Mineralogists, Special Publication* 42, pp. 125–154.
- Potonié, R., Kremp, G.O.W., 1956. Die spora dispersae des Ruhrkarbons—ihre morphographie und stratigraphie mit ausblicken auf den arten anderer gebiet und Zeitabschnitte. *Teil III. Palaeontographica abt. B, Stuttgart* 100 (4–6), 85–191.
- Potonié, R., 1958. Synopsis der Gattungen der *Spore dispersae*. III Teil -1 Sporites, Saccites, Aletes, Precolpates, Polyplicates, Monocolpates. *Geologisches Jahrbuch, Hannover* 52, 1–172.
- Raymond, A., 1988. The palaeoecology of a coal-ball deposit from the Middle Pennsylvanian of Iowa dominated by cordaitalean gymnosperms. *Review of Palaeobotany and Palynology* 3, 233–250.
- Raymond, A., Phillips, T.L., 1983. Evidence for an Upper Carboniferous mangrove community. In: Teas, H. (Ed.), *Biology and Ecology of Mangroves*. *Tasks Veg. Sci*, vol. 8, pp. 19–30.
- Reinson, G.E., 1992. Transgressive barrier island and estuarine systems. In: *Facies models, response to sea level change*. Ontario, Canada, Love Printing Service Ltd, pp. 179–194.
- Rothwell, G.W., Warner, S., 1984. *Cordaixylon dumusum* n. sp. (Cordaitales): I. Vegetative structure. *Bot. Gaz.*, vol. 145, pp. 275–291.
- Scott, A.C., 1977. A review of the ecology of Carboniferous plant assemblages with new data. *Paleontology* 20, 447–473.
- Scott, A.C., Galtier, J., Mapes, R.H., Mapes, G., 1997. Palaeoecological and evolutionary significance of anatomically preserved terrestrial plants in Upper Carboniferous marine goniatite bullions. *Journal of the Geological Society London* 154, 61–68.
- Servais, T., 1996. Some considerations on the acritarch classification. *Review of Palaeobotany and Palynology* 93, 9–22.

- Silva, O., Menegat, R., 1988. Geologia da Faixa IV. Projeto Quitéria-Várzea do Capivarita. Porto Alegre: Instituto de Geociências da UFRGS. Trabalho de Graduação (inédito). v.1, 198 pp.; v.2, 68 pp.
- Souza, P.A., Marques-Toigo, M., 2003. An overview on the palynostratigraphy of the Upper Palaeozoic strata of the Brazilian Paraná Basin. *Revista del Museo Argentino de Ciencias Naturales* 5 (2), 205–214.
- Staplin, F.L., Pocock, S.J., Jansonius, J., 1967. Relationship among gymnospermous pollen. *Review of Palaeobotany and Palynology Amsterdam* 3 (1–4), 297–310.
- Taylor, T.N., Taylor, E.L., 1993. *The Biology and Evolution of Fossil Plants*. Prentice-Hall Inc., New Jersey, USA. 982 pp. (illustr).
- Tiwari, R.S., Tripathi, A., Vijaya, A., 1994. Organic-walled microfossils of doubtful origin in Permian and Triassic sequences on Peninsular India. *The Palaeobotanist* 43 (1), 1–58.
- Tiwari, R.S., 1965. Miospore assemblage in some coals of Barakar Stage (lower Gondwana) of India. *The Palaeobotanist, Lucknow*, 13 168–214.
- Trivett, M.L., Rothwell, G.W., 1985. Morphology, systematics, and paleoecology of Paleozoic fossil plants: *Mesoxylon priapi* sp. nov. (Cordaitales). *System Bot.* 10, 203–223.
- Van Wagoner, J.C., Mitchum, R.M., Campion, K.M., Rhamanian, V.D., 1990. Siliciclastic sequence stratigraphy in well logs, cores, and outcrops. *American Association of Petroleum Geologists, Methods in Exploration Series*, 7, 55 pp.
- Walker, R.G., James, N.P., 1992. Facies models—response to sea level change. *St. John Newfoundland, Geological Association of Canada* 409 pp.
- Ybert, J.P., 1975. Étude des miospores du Bassin Houiller de Candiota-Hulha Negra, Rio Grande do Sul, Brésil. *Pesquisas, Porto Alegre* 5, 181–226.