Revista Brasileira de Paleontologia 8(1):83-98, Janeiro/Abril 2005

PALYNOLOGY AND PALAEOBOTANY IN THE RECONSTRUCTION OF LANDSCAPE UNITS FROM THE CANDIOTA COALFIELD, PERMIAN OF PARANÁ BASIN, BRAZIL

MIRIAM CAZZULO-KLEPZIG, RUALDO MENEGAT & MARGOT GUERRA-SOMMER
Departamento de Paleontologia e Estratigrafia, IG, UFRGS, Cx. P. 15001, 91501-970,
Porto Alegre, RS, Brasil. *miriam.klepzig@ufrgs.br*

ABSTRACT – Previous palynological studies on coals from Candiota coalfield in southern Paraná Basin have recognized palynofloras produced by herbaceous and shrub-like vegetation, with predominance of Lycophyta, Filicophyta and Sphenophyta, subordinate spores of arborescent Lycophyta as well as gymnospermic pollen grains (Cordaitophyta, Glossopteridophyta and Coniferophyta). Other components of the palynofloras, were considered restrictively as freshwater markers, indicating presence of limnic conditions for paleoenvironment. A discordance was observed between this palynological interpretation and the sequence stratigraphy models established for the Candiota coals that have indicated for the coal-forming environment a lagoon/barrier system, related to coastal plain, where episodic marine flooding influenced the peat accumulation. A palaeoecological revaluation of the microfloristic content of these coals recognized a dominance of spores derived from arborescent Lycophyta, an enlarged spectrum of tolerance to salinity variation of the microplankton elements and significant compositional changes between the different coal seams. These floristic changes were supposed to have been controlled by different palaeoenvironmental conditions, pointing out to a reinterpretation of the ancient plant-communities and the prevailing scenario. Aiming to establish a better calibration between the contradictory interpretations, many palaeobotanical, taphonomic and stratigraphic data were considered for a new conception about the coal accumulation process. Two landscape units were reconstructed, corresponding to the lower and upper Candiota coal seam.

Key words: coal palynology, peat-forming floras, palaeoecology, landscape units, Paraná Basin, Permian.

RESUMO – Estudos palinológicos anteriores sobre os carvões de Candiota no sul da bacia do Paraná reconheceram palinofloras derivadas de vegetação herbácea e arbustiva, com predomínio de esporos de Lycophyta, Filicophyta e Sphenophyta, onde esporos de Lycophyta arborescente, grãos de pólen de Cordaitophyta, Glossopteridophyta e Coniferophyta aparecem como formas subordinadas. Alguns palinomorfos têm sido considerados, restritivamente, como indicadores de água doce, indicando a presença de condições límnicas para o paleoambiente. Uma discordância é observada entre a interpretação palinológica e os modelos de estratigrafia de seqüências definidos para esses carvões, que relacionam o ambiente deposicional a uma planície costeira, em sistema barreira/laguna, onde ingressões marinhas episódicas teriam influenciado a acumulação da turfa. Uma reavaliação paleoecológica do conteúdo microflorístico desses carvões permitiu reconhecer a dominância de esporos produzidos por Lycophyta arborescente e um espectro mais amplo de tolerância a variações de salinidade por parte dos elementos do microplancton, além de significativas variações composicionais da microflora entre as diferentes camadas da jazida. Estas variações, controladas provavelmente por diferenças nas condições paleoambientais, apontam para uma nova interpretação da composição da vegetação ancestral formadora da turfa e do cenário dominante. Para estabelecer uma melhor calibração entre as interpretações discordantes, foram considerados dados paleobotânicos, tafonômicos e estratigráficos que reforçaram a nova concepção. As diferentes unidades de paisagem reconstruídas correspondem às camadas Candiota inferior e superior.

Palavras-chave: palinologia de carvão, megafloras, paleoecologia, unidades de paisagem, bacia do Paraná, Permiano.

INTRODUCTION

Among the most important features controlling the distinctive facies of south Brazilian Permian coals are the type and relative abundance of the constituent coal-forming plants, spores, pollen and other plant-remains such as cuticles and woody fragments. According to Stach *et al*. (1982), the peats, that represent the precursor coal-forming material, and the vegetation developed in the mires and surrounding areas, can be affected by climate, geographical area and geological setting, producing distinct coal-types. Taking into account that vegetation is very sensitive to environmental variations, plant-remains could provide important data on the palaeoecology of the different peat forming plant groups. Furthermore, the composition of the original vegetation is reflected, in general, by the palynological record.

Studies of the origin and composition of Permian coals from different coalfields in the southernmost Paraná Basin, integrating palynology, palaeobotany, coal petrography and organic geochemistry have been continuing since 1968, at the Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Brazil. These studies have provided important insights into the recognition of the origin and organic composition of coals (Nahuys *et al*., 1968; Ybert, 1975; Marques-Toigo *et al*., 1975, 1984; Burjack, 1978; Bortoluzzi *et al*., 1980; Dias-Fabrício, 1981; Araújo *et al*., 1985; Corrêa da Silva *et al*., 1984; Marques-Toigo & Corrêa da Silva, 1984; Corrêa da Silva & Marques-Toigo, 1985; Guerra-Sommer *et al*., 1991; Kalkreuth *et al*., 1999; Holz & Kalkreuth, 2002).

The most important studies of the peat-forming vegetation responsible for the original biomass of south Brazilian coals are those of Marques-Toigo & Corrêa da Silva (1984) and Guerra-Sommer *et al.* (1991). In these studies palaeobotanical, palynological and coal petrography data were integrated, aiming to define the main organic constituents of the coals. The authors suggested that the coal originated in limno-telmatic moors, in which pteridophytic herbaceous and arborescent plant-material accumulated after some transport, forming hypauthocthonous coals.

Based on some outstanding palynological and palaeobotanical differences observed in distinct coals in Rio Grande do Sul, Cazzulo-Klepzig (2002) presented a reconstruction of some landscape units and dynamic processes in the peats supposed to be the controlling factors responsible for differences in the floristic composition of the coals. Palynological and palaeoecological reappraisal of these coal-related palynofloras, allowed for identify some important changes in the floristic composition pattern that could be related to stages in a palaeoecological succession. According concepts presented by Cairncross & Cadle (1998) and Glasspool (2003), these changes could be caused by topological features of the different coal seams.

Whenever the problem of dispersed spores and pollen is considered, fossil plant-community tends to be undervaluated in the palynological record (Traverse, 1988; Nichols, 1995). These authors describe the complex relationship between the proportion of spores and pollens relative to the abundance of their parent plants. It is important to note that the palynological record may not provide a true representation of the types and relative abundance of plants within coal-forming vegetation (Shearer *et al.,* 1995). Distinct factors such as differential spore and pollen production, introduction into the mires of extraneous regional pollen grains, and oxidation of the palynological material, can lead to a misrepresentation of the original mire vegetation. Organic-walled palynomorphs commonly found in southern Brazilian coals, such as algae-like forms and acritarchs, are often undervalued due to different preparation methods (a large mesh size allows small microfossils to be lost), transport and potential of preservation.

Taking into account significant discrepancies between palynological and stratigraphic models previously presented for the depositional environment of the Candiota coal sequence, the present study was developed, aiming to obtain, through a careful revaluation of the ancient peat-forming plant-communities responsible for the original biomass of lower and upper Candiota coal seams. The recognition of important changes in the palaeoenvironmental conditions related to peat-accumulation phases, as well as a better calibration between the different results, lead to a more appropriate depositional model. Other available data, such as macrofossils, organic petrography, cuticles, taphonomic process, organic geochemistry and sequence stratigraphy supported the palaeoecological interpretation.

GEOLOGICAL SETTING

The Paraná Basin is a large intracratonic basin, located in the central-east part of the South American Platform, covering a surface area about 1.700.000 km^2. According to Milani *et al.* (1998) and Milani (2001), the Paraná Basin comprises six stratigraphic megasequences bounded by interregional unconformities. The Carboniferous-Early Triassic megasequence includes the major southern coal-bearing strata related to isolated coal fields outcropping from the southernmost part of Rio Grande do Sul State, through Santa Catarina State, to the northern portion of Paraná State (Figure 1).

The overall transgressive trend of the top of Itararé Group, the basal sedimentary unit in the study area that is essentially represented by marine deposits, points to a relative sea-level rise that was later interrupted during the Rio Bonito deposition. Coal occurrences are traditionally assigned to the Rio Bonito Formation, a fluvial to marine sandstones and shale-prone lithostratigraphic unit of Early

Permian age, approximately deposited between 262 and 258 Ma (Artinskian/Kungurian), using the time scale of Harland *et al*. (1989), as refered by Holz (1998). Cazzulo- Klepzig *et al.* (2002), based on radiometric age determination for tonsteins interbedded in some coal seams (267 ± 3.4 Ma., Matos, 1999), and compositional similarity of the palynofloras identified in the tonsteins as well in some coals, ascribed the uppermost coals deposition to the top of Kungurian/base of Roadian (chronostratigrahic framework of Jin *et al*., 1997).

The Candiota coal field, located in Rio Grande do Sul State, is the largest Brazilian coalfield, covering an area of 3.500 km² (Figure 1). Alves & Ade (1996), Chaves *et al.* (1994), Holz *et al.* (2000), Kalkreuth *et al*. (1999) and Holz & Kalkreuth (2002), applying sequence stratigraphy methods to the Candiota coal-bearing strata, suggested lateral facies changes and a model for the palaeoenvironmental evolution. They ascribed the Candiota coal deposition to a barrier/lagoon palaeoenvironment, in which several coal seams were formed. The most important coals (e.g. Candiota) occur within the transgressive system tract of sequence S2 of Holz (1998).

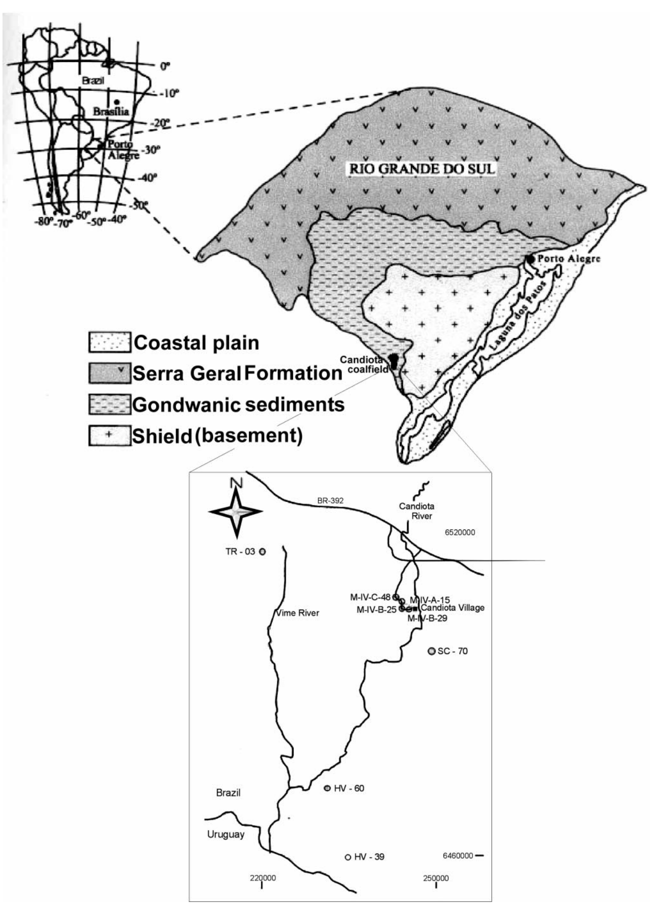

Figure 1. Location map of the Candiota coal field and studied cores.

MATERIAL AND METHODS

Sampling for the palynological study were taken from the following coal seams in selected boreholes in the Candiota coalfield (HV-39, HV 60, M-IV-C48, M-IV-B-25, M-IV-B29 and SC-70) (Figure 1).

A stratigraphic section of M-IV-C48 borehole was established as a standard section, showing all the main coal beds identified in the studied boreholes (Figure 2). Standard processing methods (HCl, HF and HNO_3), and Schulze's solution to oxidize the organic matter, were used to make

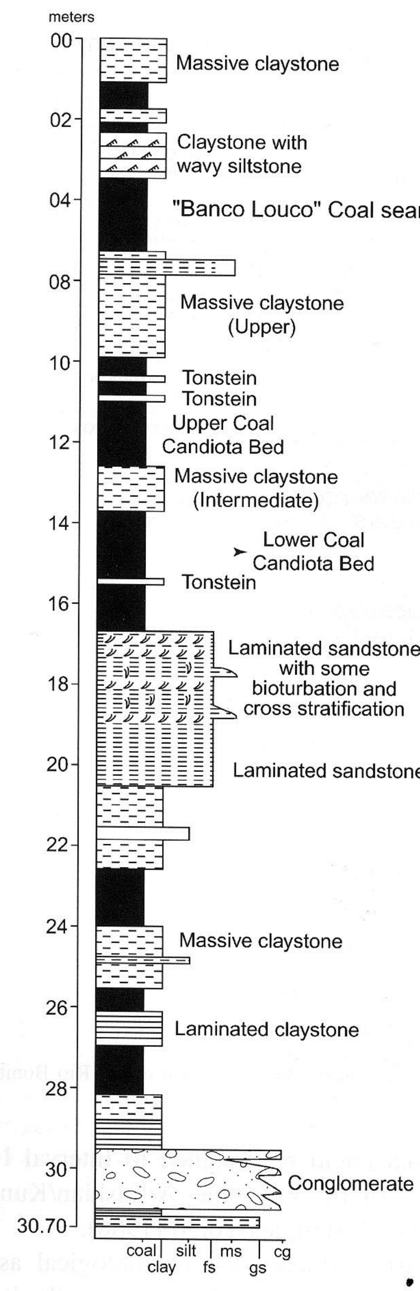

Figure 2 . The M-IV-48-RS reference section.

palynological preparations. Qualitative and quantitative analyses of the lower and upper Candiota coal seams are presented in Figures 3-6. Representative spores, pollen and other palynomorphs identified in both coalseams are illustrated in Figures 7 and 8.

The permanent repository of slides is the Laboratório de Palinologia, Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul.

Taking into account that the palynological material are not *in situ,* concepts of Potonié & Kremp (1956), Gould & Delevoryas (1977), Azcuy (1978), Balme (1995) and Servais (1996) were adopted for interpret the botanical affinity of spores and pollens.

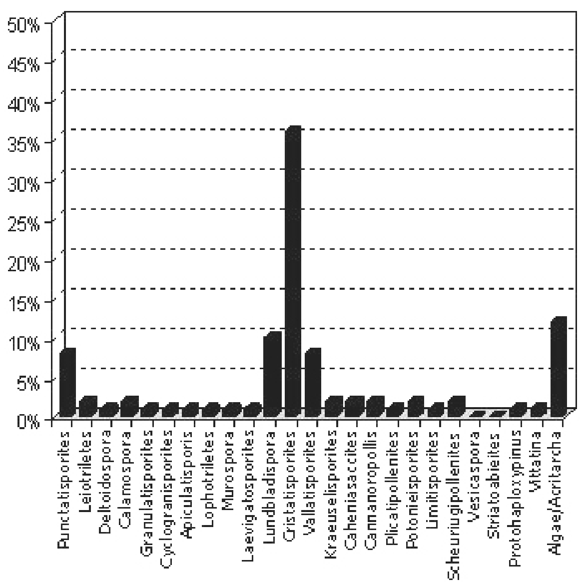

Figure 3. Histogram showing percents of major genera of palynomorphs recorded in the lower Candiota coal seam, borehole M-IV-48-RS.

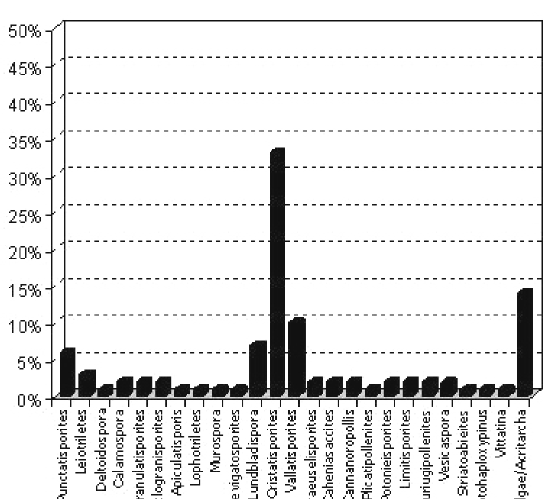

Figure 4. Histogram showing percents of major group of palynomorphs recorded in the lower Candiota coal seam, borehole HV-60-RS.

PREVIOUS STUDIES

Previous palynological studies on Candiota coals have indicated moderately diverse and well-preserved palynofloras, from which the original source-plant community were determined (Marques-Toigo *et al*., 1975; Corrêa da Silva & Marques-Toigo, 1985; Marques-Toigo & Corrêa da Silva, 1984; Guerra-Sommer *et al*., 1991; Meyer, 1999). According to these authors, the peat-forming flora was composed of pteridophytic vegetation (with dominant shrub-like Lycophyta), as well as spores of Filicophyta and Sphenophyta. Subordinate Gymnospermae pollen are less frequent, while algae (*Botryococcus*) or alga-like elements (*incertae sedis*), probably of fresh-water origin, occur in different proportions for in the different coal seams.

Although these papers have detailed the palynological composition of the most important Candiota coal seams, more recent palaeobotanical and palaeoecological data about the peat-forming vegetation indicated the presence of other palaeoenvironmental conditions prevailing during the process of coal formation (Cazzulo-Klepzig, 2002).

On the other hand, taking into account important discordances between the palaeoecology previously related to the common palynomorphs found in the coals, restrictively considered as fresh-water markers, as *Portalites, Tetraporina, Brazilea, Quadrisporites*, *Maculatasporites*, *Circulisporites* and *Pilasporites*, and the stratigraphic interpretations presented for the precursor mires, that have linked the Candiota coal accumulation to a barrier/lagoon palaeoenvironment (Lavina & Lopes,1987; Alves & Ade, 1996; Chaves *et al.,* 1994; Holz *et al*., 2000), a palaeoecological revaluation about these microfossils was performed by Cazzulo-Klepzig (2001). Ecological conditions tolerated by these microfossils and their true significance as fresh-water markers were discussed. The improved knowledge on their enlarged tolerance to different palaeoenvironmental conditions, ranging from fresh to brackish or marine waters, contributed for a better understanding of the peat-accumulation environment. Considering their palaeoecological characteristics and the recognition of an enlarged spectrum of tolerance to changeable water salinity conditions, these microfossils are herein included in the Acritarcha group, considered by the majority of authors as representing algal elements from brackish or marine microplanckton (Evitt, 1963; Hemmer & Nygreen, 1967; Venkatachala & Tiwari, 1987; Traverse, 1988). Colbath & Grenfell (1995) related most of the similar Palaeozoic microfossils to green algae or phytoplankton cysts, although the exact affinities of these palynomorphs are still disputed.

Elsik (1996), assigned *Portalites* and *Maculatasporites* to Fungi, but some authors regard them as fresh-water algae (Cazzulo-Klepzig & Marques-Toigo, 1998). *Portalites* is the most abundant palynomorph found in south Brazilian coals. In this paper, both genera were considered as Acritarcha, following criteria presented in their original diagnosis.

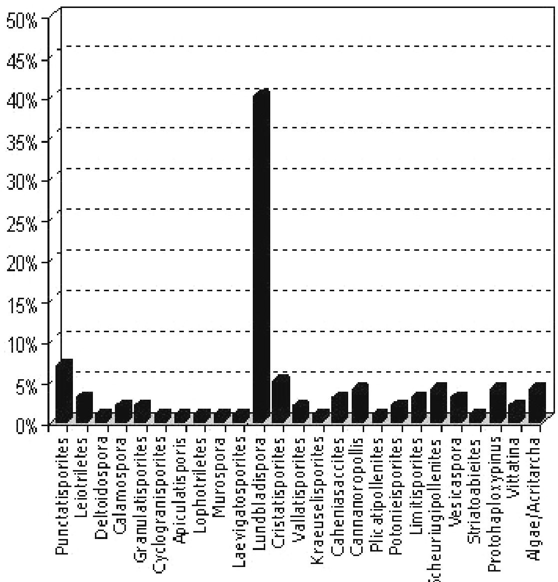

Figure 5. Histogram showing percents of major group of palynomorphs recorded in the upper Candiota coal seam, borehole M-IV-48-RS.

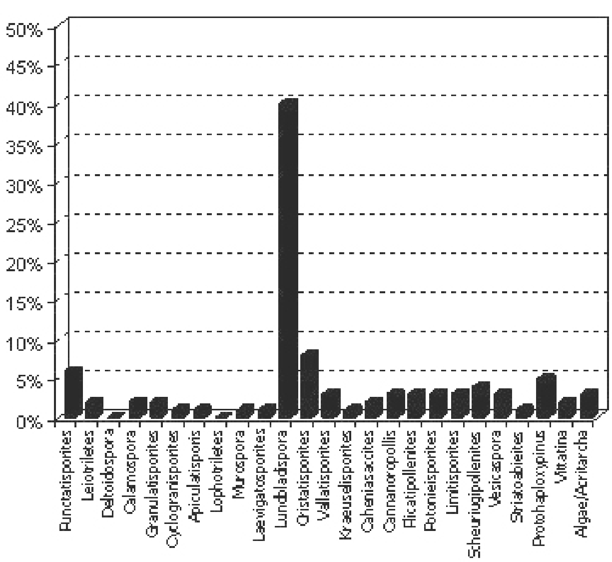

Figure 6. Histogram showing percents of major group of palynomorphs recorded in the upper Candiota coal seam, borehole HV-60-RS.

The most abundant spores recorded in southern Brazilian coal palynofloras, included in the *Lundbladispora* genus, have been traditionally related to herbaceous or shrub-like Lycophyta (Dias-Fabrício, 1981; Marques-Toigo & Corrêa da Silva, 1984; Corrêa da Silva *et al*., 1984; Guerra-Sommer *et al*., 1991; Meyer, 1999).

Marques-Toigo & Picarelli (1984), based on morphological analyses of this genus, established a close botanical affinity with herbaceous Lycophyta (Sellaginelales), suggesting that a shrub-like vegetation was common in peat-forming floras. The authors also describe compositional differences between Brazilian and Northern Hemisphere coals, which are dominated by a forest-tree palaeoecology. Archangelsky & Césari (1990), based on structural analysis of the exine of Brazilian species of *Lundbladispora* (*Lundbladispora braziliensis*, *Lundbladispora riobonitensis*), established a close affinity with arborescent Lycophyta. In addition, the recent record of arborescent Lycophyta trees, found *in situ* in other similar coal seams in the Paraná Basin, contribute to confirm the role of these plants as important components in the peat forming plant-communities of south Brazilian coals.

Holz *et al*. (2001) mentioned that the focus of coal research in the 1960s and 1970s was on the role of depositional environment on peat formation and the main goals of the coal geologists were to understand aspects such as facies studies and plant community reconstitution (Murchison & Westoll, 1968). Concerning the Eo-permian coal seams of the Paraná Basin in south Brazil, Holz (1998) presented an analysis of the depositional conditions using sequence stratigraphic concepts. This paper included a palaeoenvironmental interpretation about the Candiota coal seams.

Alves & Ade (1996) considered that the barrier must have been high enough to prevent seawater ingressions into the peat forming areas.

Holz (1999) focused on the geologic evolution of the entire Early Permian interval through a sequence stratigraphy approach, and concluded that the Rio Bonito Formation coal bearing-strata were mostly deposited within a barrier/lagoon palaeoenvironment. Depositional sequences were interpreted following criteria of Diessel (1992) and Bohacs & Sutter (1997) as a third-order transgressive system tract, subdivided into four parasequence sets, each representing a major transgressive pulse in the sedimentary history of the basin.

Holz *et al.* (2002) and Holz & Kalkreuth (2002), applying sequence stratigraphy methods to the Early Permian coal-bearing of the Rio Bonito formation in Rio Grande do Sul State, recognized four main depositional systems for the coal-bearing succession: alluvial fan, delta, lagoonal estuary and barrier/shoreface. According the authors, the Candiota coals are linked to swamps and marshes in a lagoonal estuary setting (paralic environment). Taking into account the palynological, palaeoecological and stratigraphic interpretations, a significant discordance can be observed between these models.

CANDIOTA COAL PALYNOFLORAS

Lower Candiota coal palynoflora

The present review of the lower Candiota coal palynoflora confirmed the dominance of trilete spores, mainly assignable to the Cingulicavati group (*Vallatisporites*, *Cristatisporites, Lundbladispora, Kraeuselisporites*), Laevigati (*Punctatisporites,* *Leiotriletes, Deltoidospora, Calamospora, Retusotriletes*), Apiculati (*Apiculatisporis, Granulatisporites, Cyclogranisporites, Lophotriletes, Verrucosisporites, Horriditriletes*), Cingulati (*Murospora*) and Murornati (*Convolutispora*) (Figure 7). These groups of spores are related to herbaceous and arborescent lycopsids, flourishing in hygrophilous to mesophylous environments. According to Rothwell (1988) and DiMichele & Phillips (1985, 1994), these plants might tolerate flooded environments due to their specialized growth and reproductive strategies *Punctatisporites, Leiotriletes, Deltoidospora, Verrucosisporites, Convolutispora* and *Murospora* are also important components of the palynofloras. Some trilete and monolete spores such as *Calamospora, Retusotriletes* and *Laevigatosporites* are also present ancient plant-communities of this type have been interpreted as swamp margin colonists flourishing on flooded swamp or surrounding areas (Pryor, 1996).

Less frequent monosaccate and bisaccate pollen such as *Plicatipollenites*, *Caheniasaccites*, *Cannanoropollis*, *Vesicaspora*, *Scheuringipollenites*, *Limitisporites* and *Alisporites* of botanical affinity with gymnospermic plants growing in more distant areas from the swamp, were probably transported to the accumulation where they are bad preserved.

Knoll & Nicklas (1987) suggest that Glossopteridophyta and Cordaitophyta, growing in mesophylous and xerophylous palaeoenvironments, flourished on lowlands, which could to explain their presence in lowland peats. Coniferophyta were also probably carried out from more distant areas to the mires, being represented by scarce and fragmented taeniate pollen (e.g. *Vittatina*, *Protohaploxypinus, Striadopocarpites*).

A reappraisal of favourable conditions for the development of the algae-like group (*Portalites, Tetraporina*, *Quadrisporites, Maculatasporites, Brazilea, Pilasporites, Circulisporites*), presented by Cazzulo-Klepzig (2001, 2002), pointed out to their enlarged tolerance to different aquatic environments, from fresh to brackish or marine waters, based on other similar palynoassemblages (Downie *et al*., 1963; Sinha, 1969; Bakker & Van Smeerdjik, 1982; Tiwari *et al*., 1994; Colbath & Grenfell, 1995; Strother, 1996; Tripathi, 1997; Srivastava & Bhattacharyya, 1996). Previous papers on the original biomass of these coals regarded them as indicative of fresh-water mires (Marques-Toigo & Corrêa da Silva, 1984; Guerra-Sommer *et al*., 1991). However, specimens of prasinophycean algae (*Cymatiosphaera, Navifusa*), together with abundant land-derived spores, pollen and other palynomorphs in these lower coals contributed to support this new palaeoecological assumption (Meyer, 1999). According to Downie *et al*. (1963), the majority of acritarchs, which cannot be attributed to modern algal groups, represent cysts of marine phytoplankton, occurring frequently together with forms of Prasinophyceae.

In addition, the record of some fragmentary colonies of *Botryococcus* (Chlorophyceae), developing in fresh to brackish or marine waters, together with other organic-walled palynomorphs, suggested that this taxon was more tolerant of a range of salinities (Guy-Ohlson, 1992; Batten, 1996).

Upper Candiota coal palynoflora

Cingulicavati and Laevigati spores derived from arborescent Lycophyta (*Lundbladispora)* as well as Sphenophyta (e.g. *Leiotriletes, Calamospora, Retusotriletes, Murospora*) are the dominant components in the microfloras (Figure 8). Species of *Vallatisporites, Cristatisporites* and *Kraeuselisporite*s genera, probably produced by shrub-like Lycophyta, are less common than in the lower coal seam, whereas forms of gymnospermous saccate pollen, very similar to those found in the lower coal seam, occur in higher proportion (e.g. *Cannanoropollis, Potonieisporites, Caheniasaccites, Plicatipollenites, Protohaploxypinus, Vittatina*). Other trilete spores, related to Filicophyta, common in the lower Candiota coals, are also commonly found in the upper coal palynofloras (e.g. *Granulatisporites, Cyclogranisporites, Apiculatisporis, Lophotriletes, Convolutispora, Verrucosisporites, Horriditriletes*, *Convolutispora*). The arborescent Lycophyta are dominant in the upper coal seam; this is suggested by the abundance of *Lundbladispora*. The dominance of tree-lycophytes in these coals in opposition to previous interpretations (e.g. Marques-Toigo & Corrêa da Silva, 1984), points out to a similarity with the source-plant community of Carboniferous Northern Hemisphere coals, which are dominated by tree forest plants.

Habib (1966) and Habib & Growth (1967) interpreted *Densosporites* (Cingulicavati), derived from arborescent Lycophyta, as representing a specialized saliferous flora that could develop in lowlands with sea transgressions. Marques-Toigo & Pons (1974) synonymized in prior papers the Brazilian species of *Lundbladispora* with *Densosporites*. Thus, a new concept about the habitat of the dominant plant-communites in the coals must be considered.

The record of palynomorphs herein included in the Acritarcha group (*Brazilea*, *Portalites, Tetraporina*, *Quadrisporites, Pilasporites*, *Maculatasporites*, *Circulisporites*), shows a decrease in the upper Candiota coal palynofloras. *Botryococcus* is also rare and *Cymatiosphaera* and *Navifusa* are not recorded.

Discussion of Candiota coal seams

The floristic differences between the lower and the upper Candiota coal palynofloras suggest that they were deposited in different palaeoenvironments.

Marques-Toigo & Corrêa da Silva (1984), taking into account the peat-forming vegetation, palynomorph botanical affinities, and types of ancient moors defined four moor facies. In their scheme, the *Cristatisporites-Vallatisporites* association, compositionally very similar to the lower Candiota coal palynoflora, was related to limno-telmatic reed-moor, characterized by a shrub-like plant-community, living between the high and low watermark, at the transition to open-water conditions. Pteridophytic arborescent and herbaceous plant material accumulated after some transport, promoting hypauthoctonous coal seam.

The *Lundbladispora-Punctatisporites-Portalites* association was related to open-water moor and appears very similar to that identified for the upper Candiota coals. The organic matter of this facies was also supposedly derived from herbaceous plants, growing around swamps and fresh-water bodies. This interpretation is different from that of Archangelsky & Césari (1990), who established a close affinity of *Lundbladispora braziliensis* with arborescent Lycophyta. This affinity was also noted by Cazzulo-Klepzig (2001). Furthermore, Holz & Kalkreuth (2002) mentioned the presence of arborescent Lycophyta in south Brazilian coals, attested to by the abundance of well-preserved botanical structures derived from this type of trees. For Marques-Toigo & Corrêa da Silva (1984), coal accumulation process in south Brazil must be always related to fresh water conditions, without marine influence. Otherwise, considering different habitat indicated for Lycophyta as mentioned above and the enlarged tolerance of palynomorphs to different palaeoecological conditions, as referred to hereby, a new palaeoenvironmental interpretation for the coal formation process is now supposed.

According to Gastaldo *et al*. (1996) and Pryor (1996), that developed studies on dynamic processes of peat-accumulation, these important palynological and floristic compositional changes between the lower and upper Candiota coal seams could be explained by the development of an ecological succession of topological or edaphic differences, that occurred between the upper and lower coal seams. Taking into account these floristic changes, different scenarios or landscape units (*sensu* Gastaldo *et al*., 1996) could to be the controlling factors for these palaeoenvironmental changes.

PALEOENVIRONMENTAL INTERPRETATION

The recognition of different plant-communities in the two Candiota coal seams, based on the palaeobotanical affinity of the identified microflora and their preferential environment, suggest different palaeoecological conditions. Furthermore, the recognition that organic-walled palynomorphs of doubtful origin, commonly found in the coals such as *Tetraporina, Portalites, Quadrisporites, Maculatasporites, Brazilea, Pilasporites, Circulisporites*, *Cymatiosphaera* and *Navifusa*, tolerated brackish or moderate salinity water suggest that the peat-forming palaeoenvironment may have been brackish rather than freshwater as supposed previously.

The remarkable abundance of *Cristatisporites*, *Vallatisporites* and *Kraeuselisporites* in the lower coal palynoflora, as well as the dominance, by the other hand, in the upper coals, of *Lundbladispora*, indicates that these palynofloras were originated by plant-communities flourishing in different conditions. For the lower coal seam, the peat plant-community reflected through the palynological content, shows the dominance of a shrub-like vegetation (spores of herbaceous and/or shrub-like lycopsids, herbaceous ferns and small articulates) that flourished around the mire. Other palynomorphs (algae and acritarchs), representing hygrophylous environment, found together with *Botryococcus* and land-derived spores and pollen (Figures 9, 10), could be carried from their original environment into the mire during episodic marine ingressions.

The upper coal seam palynoflora reflects a significant increase in arborescent lycopsids and tree ferns from a hygrophylous to mesophylous environment. Pollen grains of Glossopteridophyta and Cordaitophyta are more frequent in relation to the lower coal palynoflora, as well as pollen derived from Coniferophyta. Furthermore, a decrease in *Botryococcus* and Acritarcha indicates a significant water-table fluctuation in relation to the lower coals (lower sea level) (Figure 11).

Previous stratigraphy sequence studies performed in the same study area have linked Candiota coal deposition to a lagoon-barrier system, in which parasequences sets are bounded by flooding surfaces. Although the lowland coastal mires could to be sporadically flooded by coastal sea water, they were isolated from direct marine influence by a barrier island, precluding major marine ingressions. Stagnant conditions in the coastal bays or lagoons could propitiate the development of the peats.

Data presented here could be interpreted as representing different stages of an ecological succession, with remarkable changes in the scenario (topography, distance of shoreline and plant-communities), that could to originate base level change in the mires. In view of these aspects, two different landscape units, distinctively related to the lower and upper Candiota coal seams, were tentatively reconstructed, based on revaluated palynological and palaeobotanical data and previous stratigraphic models (Figures 9-12).

The landscape unit corresponding to the lower Candiota coal seam was interpreted as composed by distinct plant-communities, with dominance of shrub-like plants, flourishing in adjacent areas to the ancient mire. This mire, located in coastal plain, was linked to a lagoon/barrier system, in relative high sea level conditions, in which sporadic sea water flooding have occurred (Figures 7, 8). For the upper Candiota coal seam, the landscape unit can be characterized by the presence of arborescent plants that developed in adjacent areas to the mire, the shrub-like vegetation being less significant. Algae and acritarchs are very scarce. The ancient mire, placed in lowland coastal plain, was linked also to a lagoon/barrier system, however the probable relative low sea level conditions in this landscape unit did not allow significant sea water flooding (Figures 11, 12).

In opposite to previous palynological models, that indicated limnic conditions for the south Brazilian coal environment, new

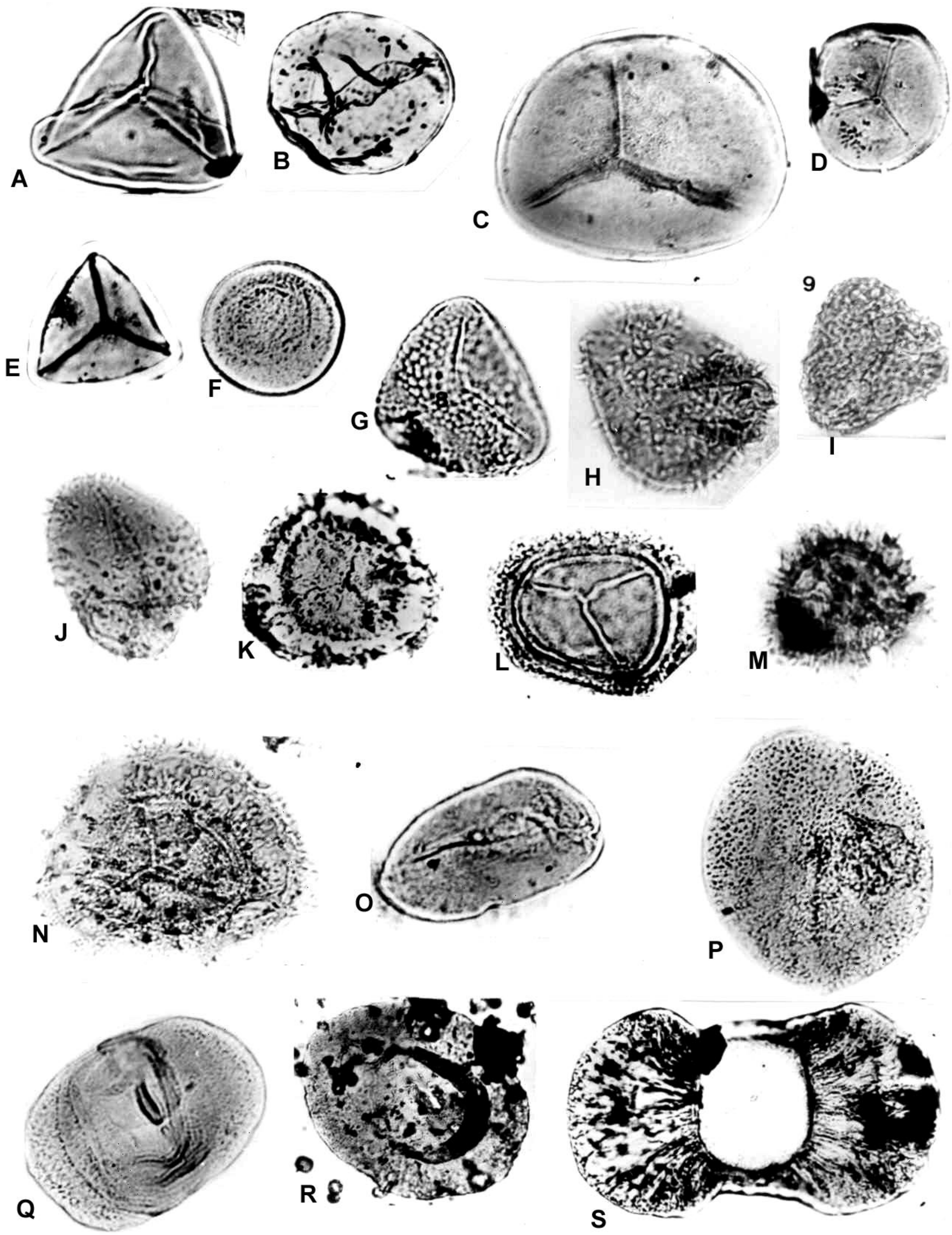

Figure 7. A, *Deltoidospora directa* (Balme & Hennelly) Hart, 1965; **B,** *Calamospora sahariana* Bharadwaj, 1957; **C,** *Punctatisporites gretensis* forma *minor* Hart, 1965; **D,** *Retusotriletes simplex* Naumova, 1953; **E,** *Murospora bicingulata* Ybert, 1975; **F,** *Cyclogranisporites gondwanensis* Bharadwaj & Salujha, 1963; **G,** *Granulatisporites micronodosus* Balme & Hennelly, 1956; **H,** *Horriditriletes ramosus* (Balme & Hennelly) Bharadwaj & Salujha, 1964; **I,** *Convolutispora candiotensis* Ybert, 1975; **J,** *Lophotriletes pseudoaculeatus* Potonié & Kremp, 1955; **K,** *Vallatisporites arcuatus* (Marques-Toigo) Archangelsky & Gamerro, 1979; **L,** *Lundbladispora* braziliensis (Pant & Srivastava) Marques-Toigo & Picarelli, 1984; **M,** *Cristatisporites crassilabratus* Archangelsky & Gamerro, 1979; **N,** *Kraeuselisporites spinosus* Jansonius, 1962; **O,** *Laevigatosporites vulgaris* (Ibrahim) Alpern & Doubinger, 1973; **P,** *Scheuringipollenites medius* (Burjack) Dias-Fabrício, 1981; **Q,** *Limitisporites rectus* Leschik, 1956; **R,** *Plicatipollenites malabarensis* (Potonié & Sah) Foster, 1975; **S,** *Caheniasaccites ovatus* (Bose & Kar) Archangelsky & Gamerro, 1979. Magnification of all illustrated specimens = 500 x;

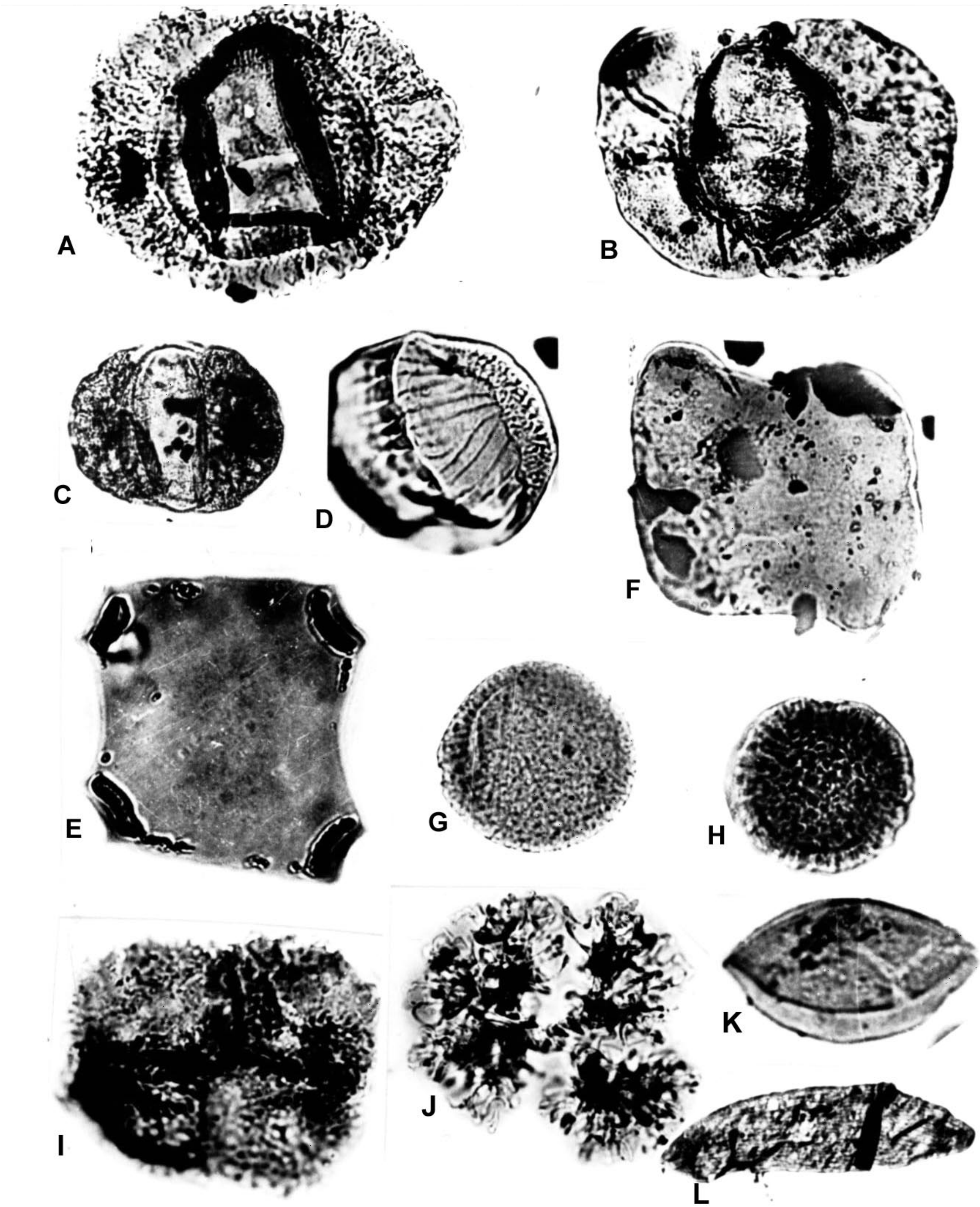

Figure 8. A; *Potonieisporites neglectus* Potonié & Lele 1961*;* **B,** *Potonieisporites braziliensis (*Nahuys, Alpern & Ybert) Archangelsky & Gamerro, 1979; **C,** *Protohaploxypinus amplus* (Balme & Hennelly) Hart, 1964; **D,** *Vittatina saccata* (Hart) Jansonius, 1962; **E,** *Tetraporina punctata* (Tiwari & Navale) Kar & Bose, 1976; **F,** *Tetraporina horologia* (Staplin) Playford, 1963; **G,** *Portalites gondwanensis* Nahuys, Alpern& Ybert, 1968; **H,** *Maculatasporites gondwanensis* Tiwari, 1965; **I,** *Quadrisporites horridus* (Hennelly) Potonié & Lele, 1961; **J,** *Botryococcus braunii* Kutzing, 1849; **K,** *Brazilea scissa* Foster, 1975; **L***,* *Navifusa* sp. Magnification of all illustrated specimens = 500 x.

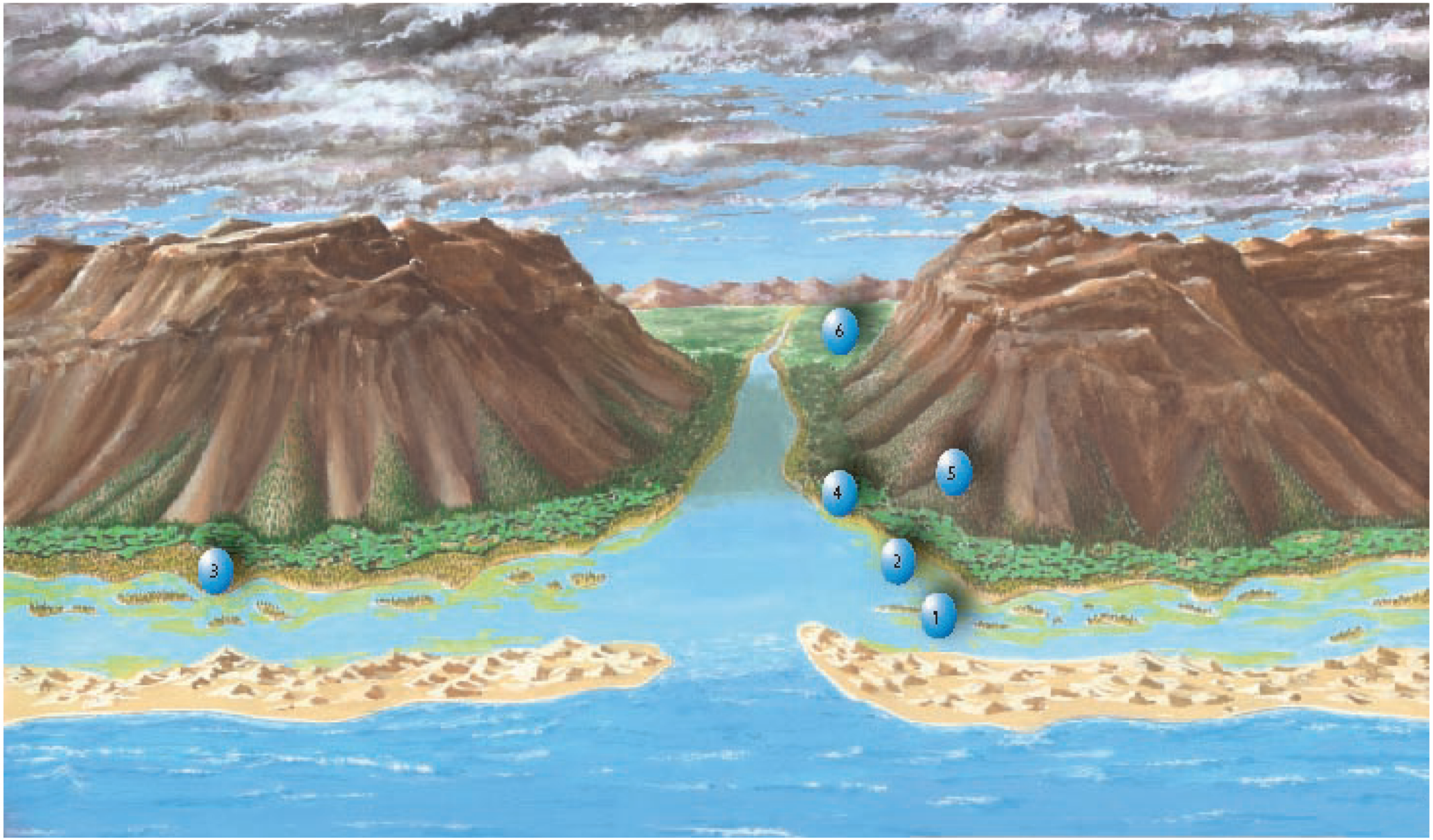

Figure 9. Reconstruction of landscape unit of peat-forming coals at high relative sea level (lower Candiota coal seam); **1,** hydrophylous plant-community (aquatic elements); **2,** hygrophylous plant-community (at the borders of coastal mires); **3,** hygrophylous/mesophylous plant-community (at the borders of mires or flooding lowlands close to mires); **4, 6,** mesophylous plant-community (in better drained lowlands surrounding the mires); **5,** xerophylous plant-community (in distant and poorly drained areas).

Figure 10. Dominant plant-communities developed in the landscape unit related to the lower Candiota coal seam (high sea level); **1,** algae, alga-like elements and acritarchs (hydrophylous plant community); **2,** herbaceous and/or shrub-like plants: Lycophyta, Filicophyta, Sphenophyta (hygrophylous plant-community); **3,** arborescent Lycophyta (hygrophylous/mesophylous plant-community); **4,** arborescent Cordaitophyta and Glossopteridophyta (mesophylous plant-community); **5,** arborescent Coniferophyta (xerophylous plant-community).

Figure 11. Reconstruction of the landscape unit and plant-communities related to peat-forming coal in low relative sea level (upper Candiota coal seam). Plant-communities are detailed in Figure 10; **1,** hydrophylous plant-community (aquatic elements); **2,** hygrophylous plant-community (at the borders of coastal mires); **3,** hygrophylous/mesophylous plant-community (in flooding lowlands close to the mires); **4,** mesophylous plant-community (in more drained areas surrounding the mires); **5,** xerophylous plant-community (in more distant and poorly drained

Figure 12. Dominant plant-communities developed in the landscape unit related to the upper Candiota coal seam (lower sea level). **1,** algae, alga-like elements and acritarchs (hydrophylous plant-community); **2,** herbaceous and/or shrub-like plants: Lycophyta, Filicophyta, Sphenophyta (hygrophylous plant-community); **3,** herbaceous and arborescent Lycophyta (hygrophylous/mesophylous plant-community); **4,** Cordaitophyta and Glossopteridophyta (mesophylous plant-community); **5,** Coniferophyta (xerophylous plant-community).

palaeoecological patterns and unit landscapes reconstruction support for the Candiota coal seams the presence of paralic conditions, in lowland coastal plains, where episodic marine flooding influenced the coal accumulation. This depositional model, based mainly on palynological and palaeobotanical data, allowed for corroborate the sequence stratigraphy model established for the Candiota coals.

ACKNOWLEDGEMENTS

The authors express gratitude to Jorge Herrmann for his important contribution in the figures of the landscape reconstructions and to Dani Genz Uszacki for assistance in the field. This research was carried out with the finantial support of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa no Rio Grande do Sul (FAPERGS).

REFERENCES

Alves, R. G. & Ade, M.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.

Archangelsky, S. & Césari, S. 1990. Ultra-estrutura de la exina en ejemplares carboniferos de *Lundbladispora* (Licofita), La Rioja, Argentina. *Ameghiniana,* **27**:131-139.

Azcuy, C.L.1978. Posible significado paleoecologico de microfloras gondwanicas del Paleozóico Superior, especialmente argentinas. *Ameghiniana*, **15**:85-95.

Bakker, M. & Van Smeerdjik, D.C. 1982. A paleoecological study of Late Holocene Section from Het llper Verd. Western Netherlands. *Review of Palaeobotany and Palynology,* **36**:95-163.

Balme, B.E. 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology,* **87**:81-323.

Batten, D. J. 1996. Green and blue-green algae - Colonial chlorococcales *In*: J. Jansonius & D.C. McGregor (eds.) *Palynology: principles and applications*. American Association of Stratigraphic Palynologist Foundation, v. 1**,** p. 191-203.

Bharadwaj, D.C. 1957. The palynological investigation in the Saar Coals, Part I: morphology of *sporae dispersae. Palaeontographica* Abt. B, **10**:73-125.

Bohacs, K. & Sutter, J. 1997. Sequence stratigraphy distribution of coaly rocks: fundamental controls and paralic examples. *AAPG Bulletin*, **81**:1612-1637.

Bortoluzzi, C.A.; Piccoli, A.E.M.; Corrêa da Silva, Z.C.; Cazzulo-Klepzig, M.; Dias-Fabrício; M.E; Guerra-Sommer, M.; Marques-Toigo, M.; Bossi, G.E. & Andreis, R.R. 1980. Estudo Geológico da Bacia Carbonífera de Gravataí- Morungava, RS. *In*: CONGRESSO BRASILEIRO DE GEOLOGIA, 31, 1980. *Anais,* Balneário Camboriú, SBG, 1:266-282.

Burjack, M.I.A. 1978. Estudo palinológico da jazida carbonífera de Charqueadas, Rio Grande do Sul, Brasil. Goiânia, Editora da Universidade Federal de Goiás, 204 p.

Cairncross, B. & Cadle, A.B. 1998. Depositional palaeoenvironment of the coal-bearing Permian Vryheid Formation in the east Witbank Coalfield, South África. *International Journal of Coal Geology*, **91**:1-17.

Cazzulo-Klepzig, M. & Marques-Toigo, M. 1998. Considerações taxonômicas e paleoecológicas sobre o gênero *Portalite*s no Gondwana sul-americano. *Pesquisas*, **25**(2):59-65.

Cazzulo-Klepzig, M. 2001. Significado paleoecológico de alguns palinomorfos ocorrentes nos carvões eopermianos do Rio Grande do Sul, sul do Brasil. *Pesquisas,* **22**:81-97.

Cazzulo-Klepzig, M. 2002. *Palinologia aplicada à reconstituição das unidades de paisagem e dinâmica das turfeiras formadoras dos carvões permianos do Rio Grande do Sul, sul do Brasil.* Programa de Pós-graduação em Geociências, Universidade Federal do Rio Grande do Sul, Tese de Doutorado, 300 p.

Cazzulo-Klepzig, M.; Guerra-Sommer, M.; Formoso, M.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**:375-380.

Chaloner, W.G. 1962. A sporangiostrobus with *Densosporites* microspores. *Palaeontology,* **5**:73-85.

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.

Colbath, G.K. & Grenfell, H.R. 1995. Review of biological affinities of palaeozoic acid-resistant, organic walled eukaryotic algal microfossils, including "acritarchs". *Review of Palaeobotany and Palynology,* **86**:287-314.

Corrêa da Silva**,** Z.C. & Marques-Toigo, M. 1985. Considerações petrológicas e palinológicas sobre a camada Candiota, jazida carbonífera de Candiota. *In*: SIMPÓSIO SUL-BRASILEIRO DE GEOLOGIA, 2, 1985. *Actas,* Florianópolis, SBG, p. 432-488.

Corrêa da Silva, Z.C.; Bortoluzzi, C.A.; Cazzulo-Klepzig, M.; Dias-Fabrício, M.E.; Guerra-Sommer, M.; Marques-Toigo, M.; Paim, P.S.G.; Piccoli, A.E.M. & Silva Filho, B. 1984. Geology of Santa Rita Coal basin, Rio Grande do Sul, Brazil. *International Journal of Coal Geology*, **3:**383-400.

DiMichele,W.A. & Phillips, T.L. 1985. Arborescent lycopod reproduction and palaeoecology in a coal-swamp environment of Late Middle Pennsylvanian age (Herrin Coal, Illinois, USA). *Review of Palaeobotany and Palynology*, **44**:1-26.

DiMichele,W.A. & Phillips,T.L. 1994. Palaeobotanical and paleoecological constrains on models of peat-formation in the Late Carboniferous in Euramerica*. Palaeogeography, Palaeoclimatology, Palaeoecology***, 106**:39-90.

Dias-Fabrício, M.E. 1981. Palinologia da Formação Rio Bonito na área de Gravataí-Morungava, RS. *Pesquisas,* **14**:69-129.

Downie, C; Evit, W. & Sarjeant, W.A.S. 1963. Dinoflagellates, hystricospheres and the classification of the acritarchs*. Publications of Geological Sciences,* **7**(3):13-16.

Elsik, W.C. 1996. Fungi. *In*: J. Jansonius & F. MacGregor (eds.) *Palynology: principles and applications*, American Association of Stratigraphic Palynologist Foundation, p. 207-210.

Evitt, W. R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystricospheres and acritarchs. *Proceedings of the National Academy of Science of USA,* **49**(2):158-164.

Gastaldo,K.A.; DiMichele, N.A. & Pffeferkorn, H.W. 1996. Out of icehouse into greenhouse:a Late Paleozoic analog for modern global vegetational change. *GSA Today*, **6**(10):1-7.

Glasspool, I.J. 2003. Hypauthocthonous-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 Coal Geology*, **53**:81-135.

Gould, R.E. & Delevoryas, J. 1977. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organes. *Alcheringa,* **1**:1387-99.

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 Societé Géologique de France,* **62**(2):227-237.

Guy-Ohlson, D. 1992. *Botryococcus* as an aid in the interpretation of paleoenvironment and depositional processes. *Review of Palaeobotany and Palynology*, **71**(1/4):1-16.

Habib, D. & Growth, P.H.K. 1967. Palaeoecology of migrating Carboniferous peat-environments. *Paleogeography, Paleoclimatology, Paleoecology,* **3**:185-195.

Habib, D. 1966. Distribution of spore and pollen assemblages in the Lower Kittaning coal of western Pennsylvanian. *Palaeontology,* **9**:629-666.

Hemer, D.O. & Nygreen, P.W. 1967. Algae, acritarchs and other microfossils *incertae sedis* from the Lower Carboniferous of Saudi Arabia. *Micropalaeontology,* **13**(2):183-194.

Holz, M. 1998. The Eopermian coalseams of the Paraná Basin in southernmost Brazil: an analysis of the depositional conditions using sequence stratigraphy concepts. *International Journal of Coal Geology,* **36**:141-163.

Holz, M. & Kalkreuth, W. 2002. Sequence Stratigraphy and Coal Petrology applied to the Early Permian coal-bearing Rio Bonito Formation, Paraná Basin, Brazil. *American Association of Petroleum Geology*, *Special Publication*, 45-56.

Holz, M.; Kalkreuth,W. & Banerjee, I. 2002. Sequence stratigraphy of paralic coal-bearing strata: an overview. *International Journal of Coal Geology*, **48**:147-179.

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 Geociência*s, **30**:420-422.

Jin, Yu-Gan; Wardlaw, B.R.; Glenister, B.F. & Kotlyar, G.V. 1997. Permian chronostratigraphic subdivisions. *Episodes*, **20**(10):10-20.

Kalkreuth, W.; Holz, M.; Cazzulo-Klepzig, M.; Marques-Toigo, M.; Utting J. & Semkiwa, P. 1999. A comparative study of the geology, petrology and palynology of Permian coals in Tanzania and southern Brazil. *Journal of African Earth Sciences*, **29**(1):91-104.

Knoll, J. & Nicklas, E. 1987. Adaptation and fossil record of plants. *American Journal of Botany*, **72**:886-887.

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.

Marques-Toigo, M. & Corrêa da Silva, Z.C. 1984. On the origin of gondwanic south Brazilian coal measures. *Comunicações dos Serviços Geológicos de Portugal*, **7**:151-160.

Marques-Toigo, M. & Picarelli, A.T. 1984. On the morphology and botanical affinities of *Lundbladispora* Balme, 1963, in the Permian of the Paraná Basin, Brazil. *Boletim do Instituto de Geociências da USP*, **15**:46-52.

Marques-Toigo, M. & Pons, E. 1974. Estudo palinológico do furo de sondagem P_7 - malha oeste da Bacia Carbonífera do Iruí. *In*: CONGRESSO BRASILEIRO DE GEOLOGIA, 28, 1974. *Anais*, Porto Alegre, SBG, 2:277-88.

Marques-Toigo, M.; Corrêa da Silva, Z.C. & Herter, G. 1975. Geology and palynology of Candiota Coal Mine, RS, Brazil. *In*: CONGRESO ARGENTINO DE PALEONTOLOGIA Y BIOESTRATIGRAFIA, 1, 1975. *Actas,*Tucumán*,* APA, p. 401-427.

Marques-Toigo, M.; Dias-Fabrício, M.E. & Cazzulo-Klepzig, M. 1984. A sucessão da microflora nas camadas de carvão da Bacia Carbonífera de Charqueadas, Formação Rio Bonito, RS, Brasil. *Boletim do Instituto de Geociências da USP*, **15**: 65 -72.

Matos, S.L.F. 1999. *História deposicional e idade do intervalo portador de carvão da Formação Rio Bonito, Permiano da Bacia do Paraná no depósito de carvão Candiota, RS.* Programa de Pós-graduação em Geologia Sedimentar, Universidade de São Paulo, Tese de Doutorado, 158 p.

McCabe, P.S. 1984. Facies studies of coal and coal-bearing strata: recent advances. *Special Publication of Geological Society,* **32:**51-66.

Meyer K.B. 1999. *Caracterização palinológica das camadas de carvão da Malha IV, Candiota, RS, Permiano da Bacia do Paraná, Brasil*. Programa de Pós-graduação em Geociências, Universidade Federal do Rio Grande do Sul, Dissertação de Mestrado, 112 p.

Milani, E.J.; Faccini, U.F.; Scherer, C.M.; Araújo, L.M. & Cupertino, J.A. 1998. Sequences and stratigraphic hierarchy of the Paraná basin (Ordovincian to Cretaceous), Southern Brazil. *Boletim do Instituto de Geociências da USP,* Série Científica, **29**:125-173.

Milani, E.J. 2001. Geodinâmica fanerozóica do Gondwana sul-ocidental e a evolução geológica da Bacia do Paraná. *In*: L.F. De Ros, & M. Holz (eds*.) Geologia do Rio Grande do Sul*, CIGO/UFRGS, p. 275-302.

Murchison, D.G. & Westoll, T.S. 1968. *Coal and coal-bearing strata.* Edinburgh, Oliver and Boyd, 307 p.

Nahuys J.; Alpern B. & Ybert J.P. 1968. Estudo palinológico e petrográfico de alguns carvões do sul do Brasil. *Boletim Técnico do Instituto Tecnológico do Rio Grande do Sul*, **6**:3-61.

Nichols, D.J. 1995. The role of palynology in palaeoecological analyses of Tertiary coals. *International Journal of Coal Geology,* **28**:139-160.

Nowak,G. J. & Gorecka-Nowak, A. 1999. Peat-forming environments of Westphalian coal seams from the Lower Silesian Coal basin of SW Poland based on petrographic and palynologic data. *International Journal of Coal Geology*, **40:**327-351.

Piccoli, A.E.M.; Lopes, R.C. & Camozzato, E. 1986. Análise paleoambiental das jazidas de carvão do Rio Grande do Sul. *Acta Geologica Leopoldensia*, **22**(10):15-54.

Potonié, R. & Kremp, G. 1956. Die sporae dispersae der Ruhrkarbons, ihre morphographie und stratigraphie mit Auslicken auf Arten anderer Gebiete und Zeitabschnitte – Teil III. *Palaeontographica, Abt. B.,* **100**:85-191.

Pryor, J.S. 1996. The Upper Pennsylvanian Duquesne coal of Ohio (USA): evidence for a dynamic peat accumulation swamp community. *International Journal of Coal Geology,* **29**:119-146.

Rothwell, G.W. 1988. *Cordaitales. In*: C.B. Beck (ed.) *Origin and evolution of Gymnosperms*. Columbia University Press, p. 273-297.

Servais, T. 1996. Some considerations on Acritarcha classification. *Review of Palaeobotany and Palynology,* **93**:9-22.

Sinha, S. 1969. Some acritarchs and other microfossils from the Barakar stage of Lower Gondwana, India. *The Palaeobotanist,* **17:**326-331.

Srivastava, C. & Battacharya, A.P. 1996. Early plant microfossils in faunal coalballs from Arunachal Pradesh, India - phytogeographic and paleoenvironmental significance. *Geophytology*, **26**:75-82.

Stach, E.; Mackowski, M T.; Teichmuller, M.; Taylor, G.; Chandra, D. & Teichmuller, R. 1882. *Stach's Textbook of Coal Petrology*. 3ª ed., Berlin, Gebrüder Borntraeger, 535 p.

Staplin, F.L.; Pocock, S.J. & Jansonius, J. 1967. Relationship among the gymnospermous pollen. *Review of Palaeobotany and Palynology,* **3**(1**)**:297-310.

Strother, P.K. 1996. Acritarchs. *In*: J. Jansonius & F. MacGregor (eds.) *Palynology: principles and applications*, American Association of Stratigraphic Palynologists Foundation, p. 81-106.

Tiwari, R.S.; Tripathi, A. & Vijaya Awatar, R. 1994. Organic-walled microfossils of doubtful origin in Permian and Triassic sequences on peninsular India. *The Palaeobotanist,* **43**:1-58.

Traverse, A. 1988. *Paleopalynology*. London, Academic Division of Unwin Hyman Ltd. Editors, 600 p.

Tripathi, A. 1997. Representation of acritarchs across the Permian-Triassic boundary in India. *The Palaeobotanist*, **46**:79-81.

Venkatachala, B.S. & Tiwari, R.S. 1987. Lower Gondwana marine incursion: periods and pathways. *The Palaeobotanist*, **36**:24-29.

Ybert, J.P. 1975. Étude des miospores du Bassin Houiller de Candiota-Hulha Negra, Rio Grande do Sul, Brésil. *Pesquisas*, **5**:181-226.

Received August, 2004; accepted March, 2005.