Terræ

Early Permian conifers *Paranocladus* and *Buriadia* of Southern Brazil

As coniferas eopermianas *Paranocladus* e *Buriadia* do sul do brasil

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ABSTRACT : A study of compressed plant remains in sedimentary rocks associated with coal strata related to a deltaic and coastal marine system during the Early Permian has resulted in important contributions to our knowledge about two gondwanic genera of conifers. The fossils were collected in the Figueira region, in the state of Paraná, in southern Brazil. Coniferous shoots constitute some of the most abundant fossils in these coals seams. Morphological and cuticular analyses of some of these specimens have revealed the presence of a new species of *Buriadia* (*Buriadia figueirensis sp. nov*), as well as the existence of heterophyllous branches and terminal female cones of *Paranocladus dusenii* Florin emend. nov., associates with bisaccate pollen grains located both within the cone and seeds and on leaf cuticles thus providing a link to platispermic seeds. Cuticular features of the species suggest that the area was still subject to severe winters at the time these plants flourished.

Introduction

Numerous compressed plant remains, including those of gondwanic conifers, are found in the sediments associated with the coal strata of the Figueira region in the state of Paraná in southern Brazil (Ricardi-Branco 1998, Ricardi-Branco et al. 2002, Ricardi-Branco & Torres 2003). The fossils described here were formed in the Early Permian period after the retreat of the glaciers at the end of the Carboniferous period when the climate had become milder and vegetation again proliferated on the recently exposed land (Rösler & Rohn 1987, Scotese & Mckerrow 1990). The fossils were located in the Rio Bonito Formation (Soares & Cava 1982, Aboarrage & Yamamoto 1982, Morrone & Daemon 1985, Della Favera & Chaves 1998), which consists of post-glacial sediments in the eastern portion of the Paraná Basin, an enormous Paleozoic basin extending from Brazil south to Paraguay, Uruguay and Argentina, and possibly linked to the Karoo basin of South Africa (Zalán et al. 1990). The horizontal layers of sediment and coal have not been affected by post-depositional faults and present thin alternating layers of coal and carboniferous siltstone with extensive lateral development. This formation has been interpreted as the depositional response to the elevation of the eastern border of the basin as a consequence of the Tardhercinian Orogenisis (Santos et al. 1996). The coal layers in these Permian sedimentary rocks have preserved a rich fossil record of the vegetation flourishing in the area at the end of the neopaleozoic glaciation which covered much of present-day southern Brazil, when it was still part of Gondwanaland and located near what is now the South Pole.

Source of samples

The fossils of conifers investigated here were collected in the coalfields of the Companhia Carbonifera do Cambuí (Fig. 1A), from the Amando Simões mine (AS, wells 01 and 06) and the Slope Plain mine 115 (SP-115), as well as from the general waste deposit of the Amando Simões mine. The specimens were found in the grey siltstone located at the top of the coal seam (Fig. 1B), in conjunction with numerous isolated megaspores (Ricardi-Branco et al. 2002) and microphylls, along with lycophyte shoots (Ricardi-Branco & Torres 2003), glossopterid leaves and the scales of paleoniscid fish.

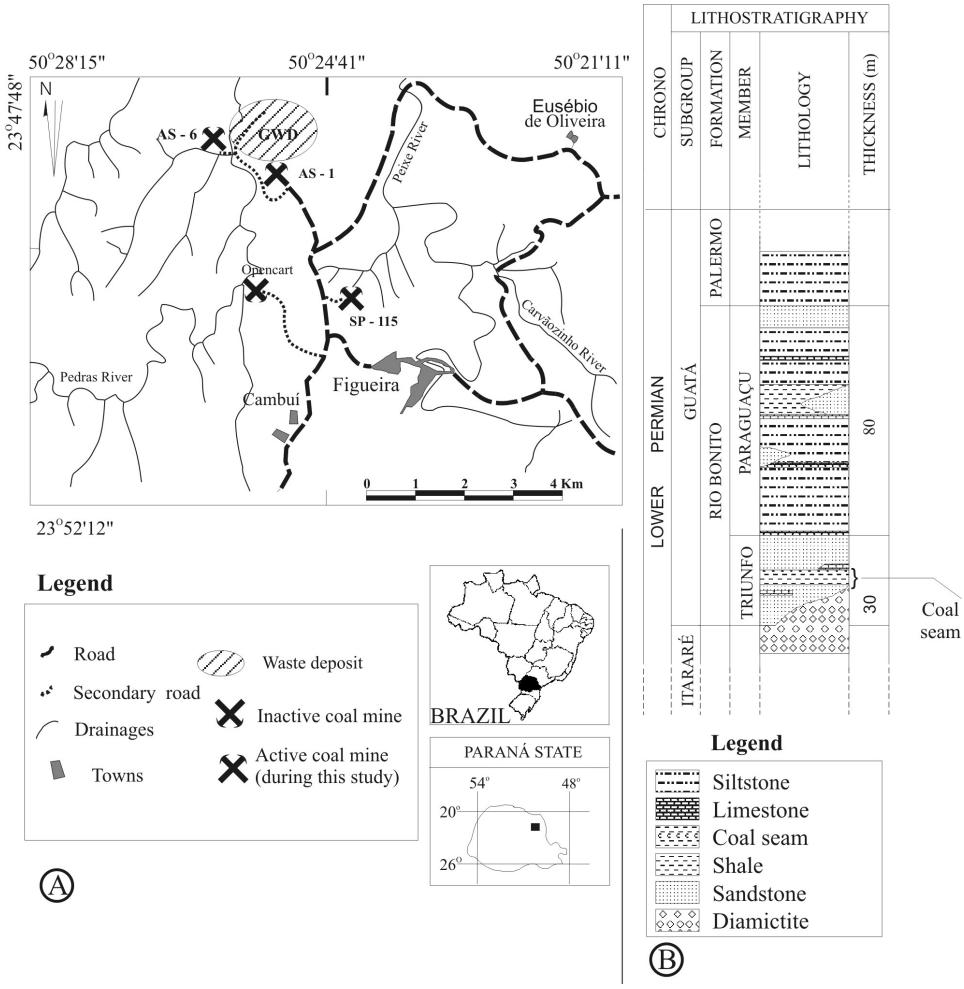

FIGURE 1: Map locating the Figueira region in the state of Paraná and the Amando Simões Mine, with indication of the mining fronts AS-1 and AS-6, the Slope Plain Mine 115 and the general waste deposit. (Source: IBGE – Folha Figueira, PR.). Lithostratigraphic column of the Rio Bonito Formation of the Figueira region (Modified from Morrone & Daemon 1985).

Material and Techniques

The fossils investigated here were preserved as compressed specimens, and the presence of cuticles made detailed anatomical and morphological studies possible. The specimens, numbered GP/3T 2137 to 2205, are housed in the Paleontological Collection of the Institute of Geosciences of the University of São Paulo, S. Paulo in the state of São Paulo, Brazil.

Some samples with well-preserved cuticles were selected for detailed study via bulk maceration in a 50% Schulze solution, followed by the removal of amorphous organic material from the internal portion by rapid immersion in KOH. A total of 45 samples were processed. Once the cuticles of both leaves and seeds were separated, they were mounted on slides using celosize and Entellan.

Systematic Study

The fossil material collected for this study included the fossilized remains of various early conifers, including specimens of the genera *Buriadia* Seward *et* Sahni and *Paranocladus* Florin, as well as numerous coniferous seeds. The presence of the cuticles in these compressed specimens made detailed anatomical and morphological studies possible.

Buriadia Seward *et* Sahni

Although previous reports of *Buriadia* exist in Brazil (Monte Mor, Paraná, and Rio Grande do Sul, as well as the Figueira region), these specimens are the first from the Figueira region to be subjected to anatomical analysis. They were included in the following classification.

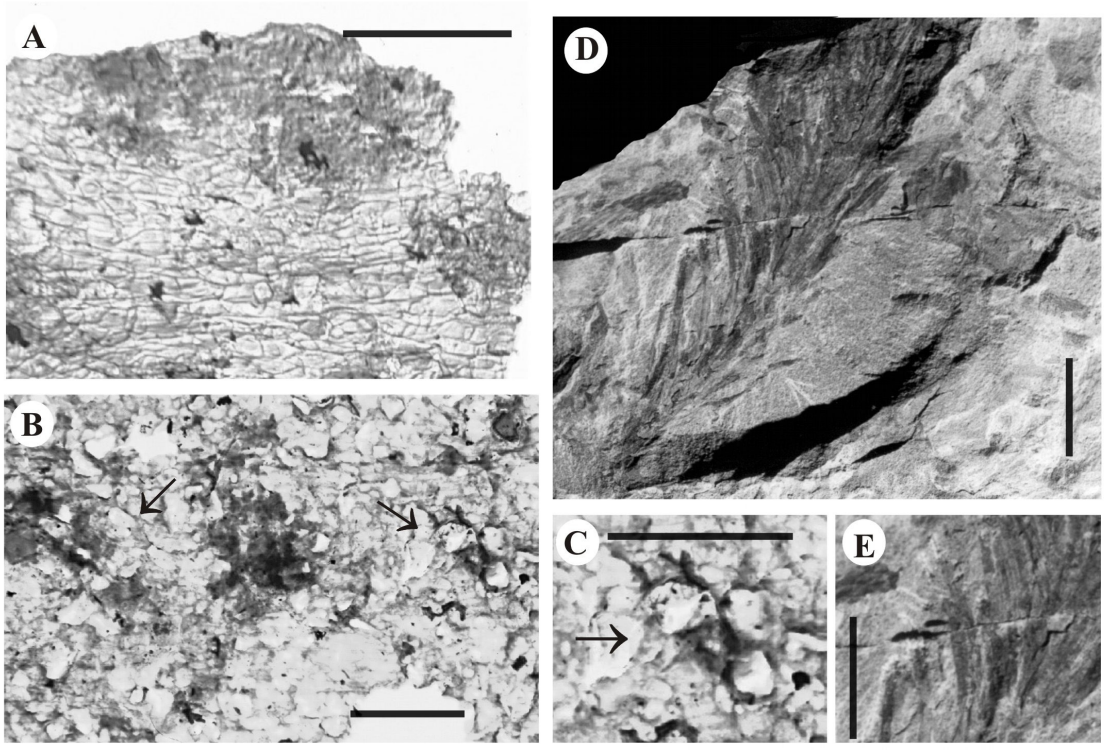

FIGURE 2. *Buriadia figueirensis* sp. nov. A. Costal zone of abaxial epidermis showing pores and hairs (GP/3T 2146b – Slide 453). Scale bar = 200 μm. B. Paraderaml view of adaxial epidermis with stomata indicated by arrows (GP/3T 2146b – Slide 454). Scale bar = 100 μm. C. Magnified detail of stoma. Scale bar = 100 μm. D. Steril branch shows upper order branching (GP/3T 2146a). Scale bar = 20 mm. E. Detail of leaf branch (GP/3T 2146a). Scale bar = 2 mm

GYMNOSPERMOPSIDA Stewart *et* Rotwell 2001

Buriadia Seward *et* Sahni, 1927

Buriadia figueirensis nov. sp.

Figure 2A, 2B, 2C, 2D and 2E.

Holotype: GP3T 2146a - b, GP/L - 3T 454

Derivatio nominis: specific epithet derived from the Figueira region.

Diagnosis

Morphological features. Sterile shoots covered with homophyllous leaves, ranging from 19 to 95 mm long and from 3 to19 mm wide (average of 6 mm), concentrated mainly at the apex. Leaves spiraled, with divergence angles acute, bifacial, falcate and slightly imbricated, ranging from 7 to 54 mm long and 0.5 to 2 mm wide, with apexes acute, bases decurrent, margins entire; midvein well defined, with long, thick hairs; second order veins parallel to midvein.

Paradermal view. Adaxial epidermis constituted by elongated polyhedral and angular cells with 4-5 sides, measuring 63 μm long and 20 μm wide. Periclinal walls with papillae and pores. Stomata sunken, monocyclic, and arranged in bands. Subsidiary cells papillate, in number of 4-6, larger than the rest of the epidermal cells. Abaxial epidermis constituted by isodiametric and polyhedral cells (32 μm long and 25 μm wide) of 4-6 sides. Anticlinal walls thin and slightly wavy. Periclinal walls with papillae and pores. No stomata observed.

Discussion

The situation of this genus is rather confused. Numerous specimens found in India were described as *B. heterophylla* (Feistmantel 1879, Seward & Sahni 1927), and later included in a newly characterized family (Buriadiaceae) on the basis of the presence of attached ovules of seeds conserved among the branches (Pant & Nautiyal 1967). Various species of *Buradia* have also been identified in Brazil, including some from the Figueira region (Read 1941). Florin (1940) included various Brazilian specimens in the species *Buradia heterophylla*, including those of White (1908), Lundquist (1919

in Rösler 1972) and Oliveira (1927), and further specimens of this species have been found in the Itararé Subgroup (Upper Carboniferous) in the state of São Paulo (Millan 1972, 1974). Moreover, specimens of similar species have been found in the coal strata of the Rio Bonito Formation in the Southern part of the country, including *B. mendesi* (Bernardes-de-Oliveira and Yoshida 1981) and *Buradia isophylla* (Guerra-Sommer & Bortoluzzi 1982). Similar samples found in Argentina were classified as a new genus in the same family (Table 1).

Then, in 2003, a re-analysis of the Indian samples revealed that the seeds used for the original identification could not be linked to the samples, and the family name was eliminated (Signh et al. 2003). The known specimens in Brazil, including those reported here from the Figueira region, however, should still be maintained in the original genus of *Buriadia*. The present specimens have been identified as a new species on the basis of two main characteristics. Individuals in this new species differ from those of *Buriadia heterophylla* in relation to the size and number of subsidiary stomatal cells (Fig. 2 B and C), which are 50-100% larger than the other epidermal cells and number 5-6 cells, rather than the 5-7 described by Florin (1940). The epidermal cells are also smaller than those of *Buriadia isophylla*, with more subsidiary cells (5-6 rather than the 4-5 described by Guerra-Sommer & Bortoluzzi 1982). As with all the other *Buriadia*, stomata are present on only one side of the leaves (Fig. 2 A).

Paranocladus Florin 1940

Paranocladus dusenii (Florin) emend. nov.

Figures 3A, 3B, 3C, 3D, 3E, 3F, 4A, 4B, 4C, 4D, 4E, 4F, G, 5D, 5E, 6A and 6B

Simonime:

Lepidendron. Oliveira 1927, p. 58, Plate s/n, figs. s/n

Brachyphullum cf. *B.* ? *australe* Feistmantel. Read 1941, p. 94, Plate 6, figs. 6-8.

Paranocladus ? *fallax* Florin. Rösler 1972, p. 81, Plate 2, figs. 10 and 11.

Paranocladus ? *fallax* Florin. Millan 1972, p. 80, Plate 10, figs. 3, 4 and 5.

Paranocladus ? *fallax* Florin. Millan 1974, p. 128, Plate 1, figs. 3, 4 and 5.

Paranocladus ? *fallax* Florin. Fittipaldi & Rösler, 1978, p. 111, Plate 1, figs. 1- 5 and 7.

Paranocladus ? *fallax* Florin. Castro 1985, p. 551.

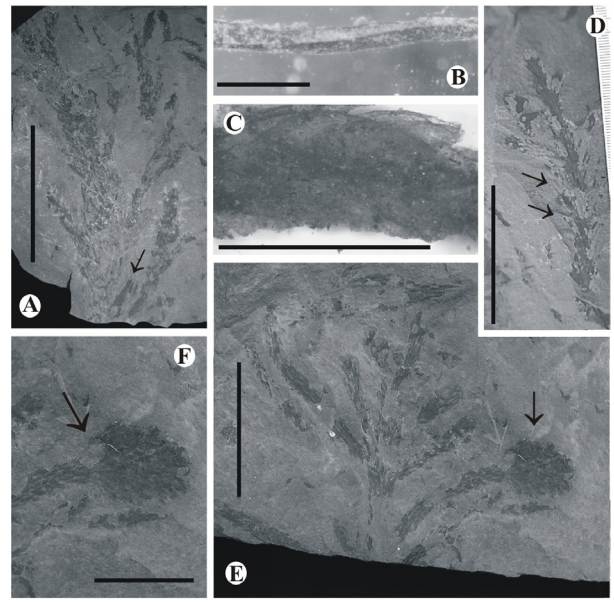

FIGURE 3. *Paranocladus dusenii* (Florin) emend. nov. A. Heterophyllous branch with arrow inticating linear leaf. As setas indicam folhas lineares (GP/3E 5923a). Scale bar = 5 mm. B. Cuticle of linear leaf (GP/3T 2160a). Scale bar = 5 mm. C. Branch showing cuticle of scale leaves. Scale bar = 2 mm. D. Heterophyllous branch, with arrows indicating linear leaf. (GP/3T 2143a). Scale bar = 30 mm. E. Feminine cone, with arrow indicating organic attachment to branch (GP/3T 2171a/b). Scale bar = 50 mm. F. Detail of feminine cone, with arrow indicating area of removal tissue for cuticular studies. (GP/3T 2171a/b). Scale bar = 25 mm

Emended diagnosis

Morphological features. Shoots densely covered by heterophyllous leaves; those of inferior orders linear (10-27 mm long and 8-38 mm wide) and of superior orders scale-like (3-8 mm long and 2-7 mm wide). Both linear and scale-like leaves in spiral insertion, with constant 1.5 mm width in medial portion; symmetrical, decurrent, acute, mucronate. Midvein well defined; unicellular hairs on margin and midvein. Female cones adherent to ultimate shoots, with the youngest measuring 23.5-26 x 18.3-20 mm and the oldest 63.9 mm x 50.6 mm; rhomboidal bracts arranged in spirals.

Anatomical features

Paradermal view. All leaves amphistomatic. Abaxial epidermis with cells polymorphic; polyhedric with 4-6 sides, oriented in various directions; anticlinal walls wavy. Linear leaves 38 x 18 μm and scale-like leaves 26 x 17 μm. Stomata monocyclic,

Table 1: Comparison of *Buriadia* species subjected to cuticular studies.

Country	BRASIL			INDIA
Species Synonymy	*Buriadia figueirensis* sp nov	*Buriadia heterophylla* (Feist.) Seward *et* Sahni (=? *Voltzia heterophylla*)	*Buriadia isophylla* Guerra-Sommer *et* Bortoluzzi	*Buriadia heterophylla* (Feist.) Seward *et* Sahni
Localization	Figueira, Paraná State	Candiota, Rio G. do Sul State and other localities.	Candiota, Rio G. do Sul State	Girdih coal layers
Lithostratigraphy	Rio Bonito Formation	Rio Bonito Formation	Rio Bonito Formation	Karhabari System
Author	Present study	Florin (1940)	Guerra-Sommer & Bortoluzzi (1982)	Pant & Nautiyal (1967) Singh et al. (2003)
Nº order shoots Dimensions (width mm)	2 3,0 - 8,0	2 1, 4 - 4,0	2 1,0 - 3,0	several orders inferior orders over 27,0
Leaves 1- Physionomy	- Homophyllous, linear leaves spirally arranged, bifacial, decurrent, apexes acute and margins entire. - Midvein straight, well defined and covered by hairs.	- Leaves lanceolate, wider above the base, slimmer towards the apex. Apexes divided one or more times, acute or obtuse. - Single-nerved, possibly dimorphic,with upper leaves elongated.	- Leaves spirally arranged, quite imbricate, simple, straight lanceolated, decurrent. Apexes obtuse and acute. - Small leaves ate apex of branches. - Bifacial and trifacial.	- Leaves of three types: simple undivided, apex with two or more divisions. - Leaves cuneate and decurrent, bifacial and trifacial. - Simple leaves more common.
Dimensions (mm)	7,0 - 54,0 x 1,5 - 2,0	Inferior order: 35,0 x 3,0 – 7,0 Superior order: 10,0 – 25,0 x 1,5 – 2,5	1,0 - 5,0	Bifid more than 15,0 x 0,5 Multidivided more than 26,0
2- Epidermis	- Adaxial surface: cells elongated, angled, polyhedric. Anticlinal walls thin with pits. Periclinal walls with papillae. - Stomata sunken, arranged in rows, with 5-6 subsidiary cells, larger than the remaining epidermic cells and with terminal papillae. - Abaxial surface.: polyhedric cells, isodiametric. Anticlinal walls straight and thin. Periclinall walls with papillae and pores. - No stomata observed.	- Epidermic cells moderatly elongated, with straight and flat anticlinal walls, sometimes with cuticular papillae. - Stomata haplocheilic with 5 - 6 subsidiary cells. Stomata arranged in irregular rows, subsidiary cells with rounded papillae.	-Adaxial surface: stomata in irregular rows; costal zones of rectangular cells with papillae. - Haplocheilic stomata of 4 - 5, monocyclic subsidiary cells with converging papillae. - Abaxial surface: elongated cells. Anticlinal walls straight, with pits and hairs on margins. - No stomata observed.	- Adaxial surface: poligonal cells diposed irregularly. Papillae present, decreasing towards apex. - Haplocheilic stomata, monocyclic or amphicyclic of 5 - 7 subsidiary cells with dense papillae. -Abaxial surface: elongated cells arranged in longitudinal rows, ocasional papillae. Anticlinal walls straight and irregular. - No stomata observed.

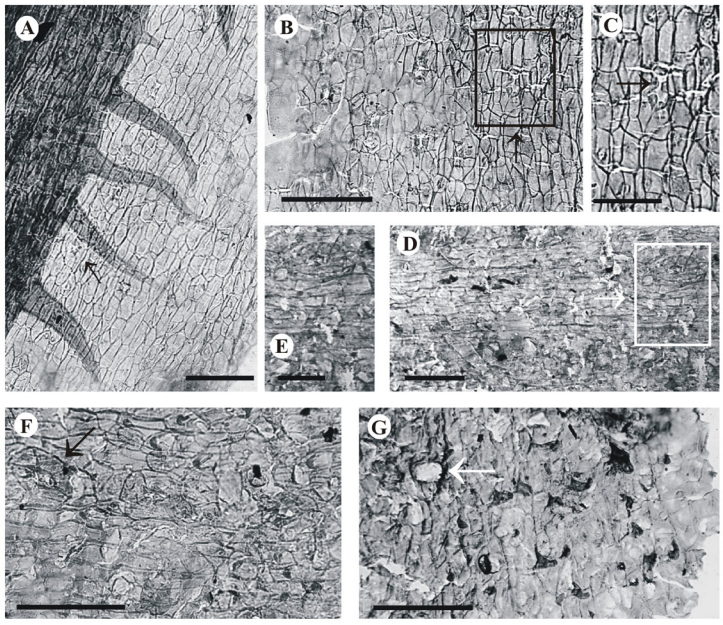

FIGURE 4. *Paranocladus dusenii* (Florin) emend. nov. A. Paradermal view of adaxial epidermis and marginal hairs on a scale leaf (GP/3T 2171a –Slide 437). Scale bar = 100 μm. B. Paradermal view of abaxial epidermis with intercostal zone of scale leaf (GP/3T 2171c – Slide 439). Scale bar = 100 μm. C. Detail of stoma of intercostal zone (enlargement of área in B), with arrow indicating guard cell with papilla (GP/3T 2171c – Slide 439). Scale bar = 200 μm. D. Stomata arranged in row on abaxial epidermis of linear leaf (GP/3T 2171c – Slide 427). Scale bar = 100 μm. E. Detail of stoma of abaxial epidermis (enlargement of area in D) (GP/3T 2171c – Slide 427). Scale bar = 200 μm. F. Stomata arranged in row of adaxial epidermis of linear leaf, with arrow indicating one of them (GP/3T 2160b – Slide 428). Scale bar = 100 μm. G. Paradermal view of adaxial epidermis of linear leaf, showing pores and papillae, with arrow indicating small pore, possibly the base of a papilla (GP/3T 2160 – Slide 426). Scale bar = 100 μm

sunken, with 4-6 subsidiary cells, surrounded by papillae protecting the occlusive cells. Stomata distributed in the intercostal zones in single, occasionally discontinuous, bands, longitudinally oriented or slightly oblique.

Linear leaves. Adaxial epidermis with costal and intercostal zones well defined, with bands of rectangular cells (65 x 23 μm). Anticlinal walls slightly wavy, thickened (2-2.5 μm), with pits. Terminal walls slightly slanted, with abundant pits. Intercostal zones with cells of irregular arrangement, polymorphous, polyhedric of 4-7 sides, isodiametric (40 x 30 μm), with thin, wavy walls and pits. Both zones present cuticular papillae, rounded or elongated, of irregular distribution, more abundant towards the base of the leaf, with numerous pores, possibly associated with hair bases.

Scale-like leaves. Adaxial epidermis of relatively even structure more even, with rectangular cells (63 x 23 μm) with pits, cuticular papillae and pores present. Wavy anticlinal walls slightly thickened (3-3.5 μm).

Discussion

The material of *Paranocladus* available was quite extensive, and made more complete anatomical and morphological study possible. Although the characteristics of the leaf cuticles suggest that the specimens should be classified as *P. dusenii*, the nature of the sample makes it possible to emend the original description of Florin to include heterophylly (Fig. 3A, 3B, 3C and 3D) and the presence of female cones (Fig. 3E and 3F), as well as the presence of hairs and papillae on the cuticles (Fig. 4A, 4F and 4G).

Material from the genus of *Paranocladus* has been reported from various other locations in Gondwanaland (Table 2), including India (Surange & Lele 1956) and Argentina (Feruglio 1934, 1951, Archangelsky & Arrondo 1973), but the material available has consisted mainly of impressions, making extensive anatomical studies impossible. The initial specimens used as the basis for the description of Florin did, however, include well-preserved cuticles, and their characteristics were included in the original description. Although previous descriptions of *Paranocladus* were based on sterile shoots, the specimens studied here were much more complete and revealed the presence of female cones.

The initial specimens of *Paranocladus* were identified as primitive conifers (Florin 1940), and consequently included in the same order as the other primitive conifers found not only throughout Gondwanaland, but also in the Northern Hemisphere, Siberia, and Europe. Due to certain primitive characteristics (Meyen 1987), all have been designated as Voltziales. This diagnosis has never been reconsidered, and given the lack of information about the orientation of the ovules in the female cones, it seems better to leave the material without an established family.

The genus *Paranocladus* was apparently wide-

TABLE 2. Comparison of *Paranocladus* species with similar *taxa* found in Argentina and India.

Country	BRAZIL	ARGEN	TINA	INDIA
Species Synonymy	*Paranocladus dusenii* Florin emend. nov.	*Ugartecladus genoensis* Archangelsky *et*_ Cúneo (=*Paranocladus* ? *hallei* Feruglio and *Paranocladus* ?*fallax* Florin)	*Feruglíocladus patagonicus* Archangelsky *et* Cúneo (=*Paranocladus patagonicus* Feruglio)	*Paranocladus* ? *indica* Surange *et* Lele
Localization	Figueira, Paraná State	Chubut Province La Rioja Province	Chubut Province	Johilla River
Lithostratigraphy	Rio Bonito Formation	Río Genoa and A. Totoral formations	Río Genoa Formation	Talchir System
Author	Present study	Feruglio (1934, 1951) Archangelsky & Arondo (1973) Archangelsky & Cúneo (1987)	Feruglio (1934, 1951) Archangelsky & Cúneo (1987)	Surange & Lele (1956)
Nº order shoots Dimensions (width mm)	6 Inferior 8,0 - 38,0 Superior 2,0 - 7,0	4 Inferior 6,0 - 12,0 Superior 3,0 - 4,0	5 Inferior 7,0 - 15,0 Superior 3,0 - 6,0	? ?
Leaves 1 - Physionomy	- Heterophyllous, linear and scale-like. - Spiral insertion, decurrent, apex acute, with hairs. - Midvein well defined and nervure pattern parallel.	- Homophyllous, lanceolat curved towards the axis. - Spiral insertion, apex acute, adpressed, margin entire, longitudinally striated and without trichomes.	- Homophyllous (?), linear, lanceolate. - Spiral insertion, adpressed, apex acute. - Nervure pattern probably single-nerved.	- Homophyllous, bifatial cuneate-lanceolate. - Spiral insertion, adpressed, entire, decurrent and with acute or acuminated apexes. - Nervure pattern single-nerved.
Dimensions (mm)	Linear: 10,0 - 27,0 x 1,5 - 2,5. Scale-like: 3,0 - 8,0 x 1,5 - 2,1	8,0 x 2,4	18,0 x 3,0	?
2.- Epidermis	- Amphistomatic. Stomata sunken, monocyclic, arranged in rows and papillous subsidiary cells. - Adaxial surface: polymorphic cells, anticlinal walls thickened, abundant papillae. - Abaxial surface: zones well defined, elongated cells with thick walls with pits and frequent papillae.		- Stomata oval-shaped, with 6 subsidiary cells, dispersed and without specific direction.	
Female cones	- Terminal, ovoid and situated on the last order branches. - Bracts mucronated.	- Situated on branched of last two orders. - Subrombic base. Bracts lanceolate and apex curved.	- Ovoid. Situated on branches of the last two orders. - Bracts curved, ovuliferous group of subcircular shape.	
Dimensions (mm)	Mature: 63,0 x 50,3 Immature: 26,0 x 19,0	Mature: 40,0 x 12,0	Mature: 20,0 x 10,0	

-spread in what is now Brazil, with two species having been reported in the states of Paraná and São Paulo, especially in the Figueira region. The first report was of material found in the regions of Figueira and Texeira Soares in the state of Paraná (Oliveira 1927), and this was the material that later studied by Florin (1940), who described the genus and separated it into two species: *P. dusenii* (based on epidermal studies) and *P.? fallax* (for similar specimens without preserved cuticles). Various other reports of the presence of the genus in the Figueira region have also been made (Read 1941, Rösler 1972, Castro 1985). Further material has been reported from the north of the state of São Paulo, near Monte Mor, in the layers of the Itararé Subgroup (Upper Carboniferous) (Millan 1972, 1974, Mune & Bernardes de Oliveira 2007), although this has never been submitted to cuticular analysis. Another species (*P. indica*, described by Surange & Lele 1956) has also been reported from the coal layers of the Talchir System in India. All of these species have the stomata located on the abaxial side of the leaves, rather than above, although the specimens from India are limited to a single axial shoot with homomorphic scalar leaves.

When Florin (1940) identified the original material as belonging to the genus *Paranocladus*, a reexamination of some of the Argentinian material persuaded Feruglio (1954) that his specimens belonged in this same genus, and he identified two more species: *P. hallei* and *P.patagonicus*. Working on the Argentinian material originally identified as *Paranocladus* on the basis of external characteristics of the impressions, Archangelsky & Cúneo (1987, 1991) later reclassified the Argentinian samples of *Paranocladus* into two new genera, *Ugartecladus* and *Feruglіocladus*, on the basis of leaf bract size, and they suggested that the Brazilian samples should be subjected to a similar modification. An examination of the extensive Brazilian material, complete with cuticles, however, refutes such a course. Although the scale-like leaves of *P. dusenii* are similar to those of *Ugartecladus* (= *P. hallei*) and *Feruglіocladus* (Archangelsky & Cúneo 1987), the *P. dusenii* is heterophyllous; moreover the mature female cones of *Paranocladus* are larger, and the bracts are mucronate. Furthermore, no cuticules have been preserved in Argentina to enable morphological/anatomical comparisons.

The *Paranocladus* specimens bear certain similarities to the Paleozoic conifers of the Euroamerican Province, especially *Lebachia* and *Ernestiodendron*, as all three genera are amphistomatic, with longitudinally oriented, monocyclic stomata (haplocheilic), which contrast with the dicyclic stomata of the genus Ortiseia (Stewart & Rothwell 2001), but there are important differences: *Lebachia* has homophyllous bifid leaves, and the stomata are grouped into two intercoastal zones (Taylor & Taylor 1993, Stewart & Rothwell 2001), whereas *Ernestiodendron* has a single intercostal zone (Taylor & Taylor 1993, Stewart & Rothwell 2001). *Paranocladus*, on the other hand, has heterophyllus entire leaves with stomata distributed in various scattered bands.

In contrast with *Paranocladus*, other well-known conifer genera of Gondwanaland, such as *Walkomiella* (Florin 1944, Høeg & Bose 1960, Le Roux 1963, White 1981, Anderson & Anderson, 1985), reveal the presence of stomata only on the papillous epidermis of the adaxial surface of the leaves. The work here has made possible the first reconstruction of this Brazilian neopaleozoic conifer (Fig. 6).

Seeds

Numerous preserved conifer seeds were found throughout the material investigated. Although most of them were detached, the removal of a scale from a female cone of *Paranocladus* revealed the presence of the wing of a seed, complete with cuticle, with the cells and stomata identical to those of *Paranocladus*, as well as to the wings of the isolated seeds found nearby. It thus seems probable that the loose seeds belong to *Paranocladus*, but since this is not certain, a special genus for these seeds has been created on the basis of anatomical and morphological data.

Paranospermum gen. nov.

Diagnosis

Morphological features. Platispermic seed, cuneiform, symmetrical; apex cordiform, ending in one or two triangular appendices. Base cuneate. Wing enveloping the nucellus, narrower at the base, and with margin entire.

Anatomical features. Wing cells elongated and polyhedric with 4-6 sides, narrower at margins. Each cell has a single pore in the external periclinal wall.

Type species: *Paranospermum cambuiense*

Paranospermum cambuiense nov. sp.

Figures 5A, 5B, 5C, 5F and 6C

Holotypes: GP/3T 2191 a, GP/3T 2146 aA and

Lam. GP/L - 3T 443

Derivatio nominis: specific epithet derived from the region of Cambuí, ancient name of Figueira region.

Synonymy:

Cordaicarpus nitens (Feruglio) Millan. Millan 1972; p. 98, Plate 12, figs. 1 to 7.

Cordaicarpus nitens (Feruglio) Rösler 1972; p. 88.

Cordaicarpus nitens (Feruglio) Millan. Millan 1977; p. 34.

Cordaicarpus nitens (Feruglio) Millan. Castro 1985; p. 551, figs. 1 and 2.

Diagnosis

Morphological features. Platispermic seed, cuneiform, symmetrical, 7-12 mm long and 7-12 mm wide in the medial portion. Apex cuneiform, ending in one or two triangular appendices, straight or curved, of 1-2 mm x 1-2 mm. Base acute to rounded. Seeds present a continuous groove from base to apex in the medial region. Nucellus ovulate, 3.5 – 7 mm x 3.5-6 mm.. Wing enveloping central body narrower at the base, with margin entire.

Anatomical features. Wing cells elongated and polyhedric with 4-6 sides, 70 μm x 30 μm, longer and narrower at margin. Anticlinal walls wavy and somewhat thickened. Each cell with a single pore in the external periclinal wall. Unicellular and pluricellular hairs present. Stomata monocyclic, arranged in scattered groups.

Discussion

Other Platispermic seeds similar to those studied here have also been collected in the Figueira region by Rösler (1972) and Castro (1985), and dispersed cuticle tissue reported by Fittipaldi & Rösler (1978) was similar to that found for the wings of the seeds investigated here. Impressions of similar seeds were also found in the Rio Genoa Formation in the south of Argentina (Early Permian) by Feruglio (1934, 1946) and Arrondo (1972), among others. These were classified as belonging to *Eucerospermum nitens* Feruglio and *Eucerospermum patagonicum*, Feruglio on the basis of the size of the seeds (Feruglio 1946). Millan (1972, 1977) found similar seeds in the Itararé Subgroup (Late Carboniferous) in Brazil and, after morphological study, decided that the two species of *Eucerospermum* described by Feruglio (1946) were the same, uniting them in a new genus, the *Cordaicarpus* (with this new species identified as *C. nitens*); the seeds of this new genus present two short bifid spines, in contrast to the single thin micropilar appendix of *Eucerospermum opimum*. Independent work by Archangelsky & Cúneo (1987) established the synonymity of *E. nitens* with the vegetative shoot impressions they had identified as *Feruglіocladus patagonicus*, with *E. patagonicum* reserved for the isolated large seeds in general

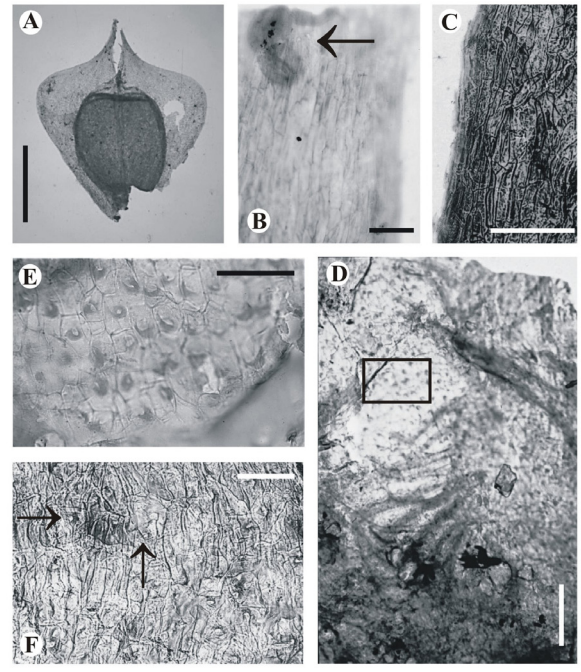

FIGURE 5. *Paranospermum cambuiense* gen. et sp. nov. A. Seed separated from the rock matrix (GP/3T 2167). Scale bar = 3 mm. B. Bissaccate pollen found inside micropile of Paranospermum cambuiense (GP/3T 2146aA – Slide 443). Scale bar = 100 μm. C. Wind cells of seed (GP/3T 2152aA – Slide 44). Scale bar = 100 μm. D. Epidermis of seed wing observed inside tissues removed for cuticular studies of feminine cone (Fig. 3F); seed protected by two bracts with marginal papillae (GP/3T 2171b – Slide 435). Scale bar = 200 μm. E. Detail of epidermis of wing of Paranospermum cambuiense of feminine cone showing stomata of wing cells identical to those of Paranocladus dusenii (GP/3T 2171b – Slide 435). Scale bar = 200 μm. F. Epidermis of seed wing with arrows indicating stoma and pore (GP/3T 2152aA – Slide 44). Scale bar = 100 μm

Epidermal studies of the tissue of the wing of the seeds found here reveal tissue identical to that found in the female cone (GP/3T 2171 b, Fig. 5D and 5E) of *Paranocladus dusenii* Florin. Supported by these findings, it is suggested that the seeds likely belong to *P. dusenii*. This conclusion is corroborated by the presence of stomata similar to those found in *P. dusenii* (distributed in scattered groups) as well as by the shape of the epidermal cells of the

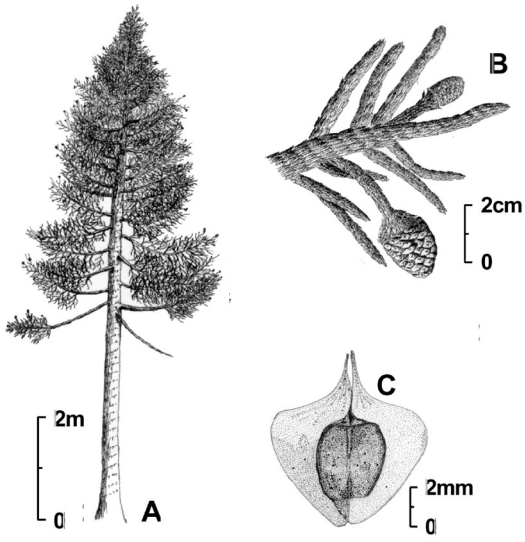

FIGURE 6. Reconstruction of *Paranocladus dusenii*. A. Tree. B. Branch showing femal cones. C. Seed *Paranospermum cambuiense*.

wing (Fig. 5F). The shape of these epidermal cells may indicate that the seed originated in the abaxial epidermis of the ovuliferous scale.

Since the morphological and epidermal characteristics of the seeds found here have been established and a possible relationship to *P. dusenii* determined, we believe that the species name should be changed, although the failure to find any organic connection led to the decision to create a new genus, designated as *Paranospermum*, with *P. cambuiense* representing the species type.

Discusion and Conclusions

This study of *P. dusenii* and *Buriadia figueirenses* has revealed the presence of characteristics also present in the angiosperms of temperate climates (Torres 1995, 1998), including the presence of imbricate leaves, an abundance of hair and papillae on the epidermis, the presence of thickened anticlinal walls with abundant pits, sunken stomata surrounded by strongly cutinized papillous subsidiary cells, and stomata restricted to the adaxial surface (only *B. figuerensis*). These characteristics have been interpreted as protective mechanisms to prevent the loss of water through transpiration. Their presence has thus been interpreted as an indication of an at least periodic water shortage, and has led to the suggestion that they may have lived in a temperate climatic regime with well-defined seasons (Ricardi-Branco et al. 2003), a conclusion corroborated by the latitude of the Brazilian portion of the Paraná basin (between 40º and 50º) during the Early Permian (Scotese & McKerrow, 1990) and the affirmations of other authors (Rigby1970, Rösler 1972, 1976, 1993, Rigby 1970, Rohn & Rösler 1987, Guerra-Sommer 1989, Guerra-Sommer & Cazzulo-Klepzig 1993, Ricardi-Branco et al. 2002, 2003).

These plants (Fig. 6) flourished after the retreat of the glaciers of Gondwanaland. The oldest samples of these genera were found in interglacial coal further north, near Monte Mor (in the Itararé Subgroup) in the state of São Paulo (Millan 1972). This suggests that these genera may have survived the period of glaciation and later colonized the space left by the melting ice in the interior of Gondwanaland.

Although fossils of *Paranocladus* are quite abundant, they have usually consisted of terminal branches. The abundance of seeds linked to deltaic depositions (Scheihing & Pfefferkorn 1984, Greenwood 1991), and now linked to *Paranocladus*, however, suggests that *Paranocladus* may have inhabited the flood plain (Cúneo 1983, Ricardi-Branco et al. 2003), along with the glossopterids, although they could have inhabited higher terrains at a certain distance from the coast, since the external morphology of the seeds would have permitted wide-spread wind or water dispersion.

Since the fossils of *Buriadia* are less common and are limited to the apical portions of branches, these conifers probably inhabited areas located at a certain distance from the coast, although a few individuals probably grew close enough to steams for occasional small branches to have fallen into the water and been transported to the place of their deposition.

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RESUMO: O estudo de fósseis vegetais coletados em rochas sedimentares associadas com níveis de carvão depositados em um sistema costeiro deltaico de idade eopermiana permitiu ampliar os conhecimentos acerca de dois gêneros gonwanicos de coníferas. Os fósseis foram coletados na região de Figueira, estado do Paraná, porção sul do Brasil. Os ramos de coníferas representam os fósseis mais abundantes nas camadas estudadas. A sua análise morfológica e anatômica permitiu descrever uma nova espécie de *Buriadia* (*Buriadia figuirensis*), e também completar a descrição de *Paranocladus dusenii* (Florin) emend. nov, do qual foram encontrados ramos heterofilos e estróbilos femininos terminais conectados organicamente. Esses órgãos se encontram associados com grãos de polens bissacados observados nas cutículas removidas do estróbilo e das sementes platispermicas conectadas ao estróbilo e isoladas, fornecendo dessa forma uma relação natural entre os ramos, estróbilos e sementes paltispermicas descritas. As características das cutículas estudadas permitem sugerir que a região de Figueira esteve durante o início do Permiano baixo a influência de invernos severos.

PALAVRAS CHAVE: Coníferas, Gondwana, Permiano, Bacia do Paraná, Formação Rio Bonito