

Epidermal morphology of the cordaitalean leaf *Noeggerathiopsis brasiliensis* nom. nov. from the southern Paraná Basin (Lower Permian, Rio Bonito Formation) and paleoenvironmental considerations

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Abstract

A Brazilian cordaitalean leaf is reassigned and redescribed based on cuticular analysis. The new name *Noeggerathiopsis brasiliensis* is erected as a replacement for *Rufloria gondwanensis* Guerra-Sommer. The leaf adpressions come from a tonstein layer within a Sakmarian coal seam of the Faxinal Coalfield, southern Paraná Basin, Brazil (U–Pb SHRIMP mean age 291 ± 1.3 Ma, Rio Bonito Formation). The leaf micromorphological pattern, observed under optical transmitted light and field emission gun — scanning electron microscopy, is distinct from the Euramerian *Cordaites* Unger and very similar to the Angaran *Rufloria* Meyen. The lower epidermis has conspicuous longitudinal stomatiferous furrows typical of *Noeggerathiopsis* (Feistmantel) McLoughlin & Drinnan covered by tightly interwoven trichomes, epidermal and probably also hypodermal highly cutinized sheaths at the borders of furrows, and haplocheilic stomatal apparatus surrounded by long conical trichomes. The xeromorphic cuticle structures are similar to those of *Glossopteris pubescens* (Guerra-Sommer) Degani-Schmidt & Guerra-Sommer, the dominant leaf species preserved in the tonstein layer, indicating convergent ecological adaptations to abiotic stress factors in distinct plant groups in the peat-forming paleoenvironment.

KEYWORDS: Gondwana; Cordaitales; Cuticular analysis; Trichomes; Paleozoic; Fossil plants.

INTRODUCTION

Cordaitalean plants, represented by leaves, woods and reproductive structures have been recorded from plant assemblages in various geological provinces from the Mississippian to the Permian. These plants were important components of floristic associations in late Paleozoic mires and are very well documented in paleotropical Europe and North America whence several cordaitaleans have been reconstructed as whole plants. Although most examples have been reported from upland and lowland peat mires, others have been linked to mineral soils and even coastal settings (Taylor *et al.* 2009, and citations therein).

Cordaitaleans were less common in sub-tropical Cathaysia, but some diagnostic features found in whole reconstructed plants (*e.g.*, *Shanxiioxylon*) have provided important milestones in understanding their phylogenetic and evolutionary history (Shi-Jun *et al.* 2003, Hilton & Bateman 2006, Hilton *et al.* 2009).

The habit and paleoecology of cordaitaleans in Angaran and Gondwanan Paleotemperate Realm remain poorly understood, mainly due to the absence of direct linkages between

the diagnostic reproductive structures and vegetative organs. This also hampers an understanding of their phylogenetic relationships with Euroamerian forms.

Since leaves are the most common cordaitalean fossils, various analyses based on gross morphology, venation, epidermal and anatomical characters have been undertaken to determine shared characters between the morphogenera identified in different paleogeographic provinces.

The characteristics of Euramerian *Cordaites* Unger leaves are generally well known based on anatomical details of material from coal balls and on epidermal patterns identified in compressions (Harms & Leisman 1961, Good & Taylor 1970, Rothwell & Warner 1984) and more recently, on Fourier-transform infrared spectroscopy (FTIR) and elemental analyses (Zodrow *et al.* 2000a, 2000b, and citations therein). The epidermis of *Cordaites* is characterized by stomata arranged in stomatiferous bands between the veins, and sclerenchymatous strands on the lower surface. Papillae are very rare, and trichomes have not been found (Šimůnek 2007, Šimůnek *et al.* 2009). This set of leaf characteristics differs from those recognized in many Gondwanan and Angaran leaves.

The present study deals with *Noeggerathiopsis* (Feistmantel) McLoughlin & Drinnan, a leaf morphogenus of uncertain although presumed cordaitalean affinities owing to the absence of associated fertile organs (McLoughlin & Drinnan 1996). *Noeggerathiopsis* has been recorded from the Mississippian to late Permian of the Southern Hemisphere, albeit sometimes placed under *Cordaites*. Leaves are linear to spatulate, elongate

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and with sub-parallel venation (Feistmantel 1879, McLoughlin 1992). Maithy (1964) emended the generic diagnosis adding epidermal patterns, which were not included in the original description based on impressions.

The diagnostic characteristics of *Noeggerathiopsis* distinguishing it from *Cordaites* were, according to Pant & Verma (1964), simple veins of uniform thickness throughout the lamina, ill-defined files of stomata along the stomatiferous bands and absence of interstitial fibers. Anatomical analysis was decisive in understanding the leaf organization, confirming the lack of fiber bundles in the leaf structure, leading McLoughlin & Drinnan (1996) to propose an emended diagnosis for the morphogenus so far characterized by discernible stomatiferous furrows in the lower epidermis, protected by densely arranged trichomes.

The probable presence of northern cordaitalean elements in the Gondwanan floras was supported by the identification of *Cordaites bifolius* Césari & Hünicken (2013), which shares features with *Cordaites* (e.g., heterophylly, needle-like leaves, leaf scars similar to *Cordaicladus* Grand'Eury, fertile organs similar to *Cordaitanthus* Feistmantel bearing *Cordaicarpus*-type of seeds). The occurrence of Gondwanan *Cordaites* was previously reported by Archangelsky & Leguizamón (1980), Archangelsky & Cúneo (1991), Chandra & Srivastava (1991) and Srivastava (1996) based only on leaf gross morphology and venation patterns. The absence of anatomic and epidermal features in the Gondwanan type material of both *Cordaites* and *Noeggerathiopsis* preserved as impressions precludes close comparisons.

The epidermal patterns of Gondwanan *Noeggerathiopsis* compressions are very similar to those of the Angaran *Ruffloria* Meyen. Morphological similarities were attributed to homoplasy by Meyen (1970, 1979, 1984), though a floristic interchange via disjunct landmasses in the Tethyan — East Asian region during the Carboniferous — was suggested by McLoughlin & Drinnan (1996).

In the Brazilian Permian, cordaitalean leaves are known from interglacial, periglacial and post-glacial deposits from the late Carboniferous (Pennsylvanian) to the early Permian (Sakmarian — Artinskian) in the Paraná Basin. Impressions of isolated leaf fragments were identified either as *Noeggerathiopsis* (e.g., Millan 1972, 1987, Millan *et al.* 1982, Zampiroli 2001, Bernardes-de-Oliveira *et al.* 2016) or *Cordaites* (Millan & Dolianiti 1981, Millan *et al.*, 1982, Guerra-Sommer & Cazzulo-Klepzig 2000) or even as *Ruffloria* (Christiano-de-Souza & Ricardi-Branco 2015), lacking taxonomic justification.

Iannuzzi (2010), in an overview of post-glacial floras of the coal-bearing Rio Bonito Formation in the Paraná Basin, recorded the presence of leaf impressions attributed to *Cordaites hislopii* (Bunbury) Seward & Leslie in paleoenvironments adjacent to peatlands within estuarine, deltaic, backshore, foreshore and shoreface siliciclastic sedimentary facies. However, there was no mention of the paleoflora preserved in the tonstein layer within the upper coal seam S of the Faxinal Coalfield — the object of the present study. Several researchers have studied this ash-fall layer for taxonomic, biostratigraphic, paleoecological, paleoclimatic, petrographic and radiometric dating

purposes (Guerra-Sommer 1988, 1989, 1992, Cazzulo-Klepzig *et al.* 2007, 2009, Guerra-Sommer *et al.* 2008, Simas *et al.* 2013, Degani-Schmidt *et al.* 2011, Degani-Schmidt & Guerra-Sommer 2016a, 2016b, Jasper *et al.* 2011, Boardman *et al.* 2012, Degani-Schmidt *et al.* 2015).

This study aims to correct, by means of cuticular analysis, the taxonomic identity of the cordaitalean leaf species from the tonstein layer of the Faxinal Coalfield previously described by Guerra-Sommer (1989) as *Ruffloria gondwanensis* Guerra-Sommer, renaming it and contributing to the understanding of leaf micromorphology and diversity of cordaitalean plants from Gondwana.

GEOLOGICAL AND PALEONTOLOGICAL CONTEXT

The Paraná Basin is a large (1,500,000 km²) intracratonic sag basin covering part of southern Brazil, Paraguay, Uruguay and Argentina (Fig. 1). Basin subsidence, in addition to Paleozoic sea-level changes, created six second-order sequences deposited from the Ordovician to the late Cretaceous, separated by regional unconformities (Milani *et al.* 2007). The coal-bearing Rio Bonito Formation, which is the subject of this study, occurs at the base of the second order Carboniferous — Lower Triassic sequence (Gondwana I Supersequence). Extensive peat swamps developed during the deposition of Rio Bonito Formation in Paraná Basin at a paleolatitude of approximately 50°S, included in the cool temperate biome (Rees 2002). Most of the peat-forming areas have been identified as part of a back-barrier lagoonal paleoenvironment (Holz 2003).

The study area comprises the Faxinal Coalfield, a former opencast coal mine closed in 2009, in the southeastern outcrop belt of Rio Bonito Formation in southern Brazil, Rio Grande do Sul State. This coalfield overlies the Precambrian basement rock (Fig. 1).

The present study focuses on a fossiliferous argillite 7–12 cm thick, interbedded in the upper coal seam S. Petrographic studies revealed that this layer represents a tonstein (Simas *et al.* 2013). U–Pb SHRIMP dating of zircons from the tonstein by Simas *et al.* (2012) yielded a mean age of 291 ± 1.3 Ma (Sakmarian), corresponding to the *Protohaploxypinus goraiensis* Subzone within the palynostratigraphic framework defined by Souza & Marques-Toigo (2005) and to the phytostratigraphic *Glossopteris* — *Brasilodendron* Zone of Iannuzzi & Souza (2005).

Analysis of the compression taphoflora preserved within the tonstein revealed a predominantly gymnospermous association (Guerra-Sommer 1992, Boardman *et al.* 2012) and a dominance of glossopterid leaves (up to 70%) followed by cordaitalean leaves (up to 17%), reproductive axes (2%), pteridophyte fronds (about 1%) and seeds (1%).

Micromorphological analysis identified the following taxa: *Glossopteris brasiliensis* Guerra-Sommer; *G. pubescens* (Guerra-Sommer) Degani-Schmidt & Guerra-Sommer, *G. similis-intermittens* Guerra-Sommer; *Ruffloria gondwanensis* Guerra-Sommer, *Sphenopteris* sp. cf. *S. ischanovensis* Zalessky, *Plumsteadia semnes* Rigby and *Platycardia* sp. (Guerra-Sommer 1988, Degani-Schmidt & Guerra-Sommer 2016b).

MATERIALS AND METHODS

The adpressions of spathulate cordaitalean leaves occur haphazardly in horizontal disposition, stacked in several planes along the tonstein layer. Fossils occur as compressions and impressions of isolated, incomplete leaves and rarely disposed in clusters. The association is dominated by *Glossopteris* spp. interspersed with cordaitalean leaves, which are never restricted to monotypic horizons within the tonstein bed (Figs. 2A, 2B and 2C).

Cuticle samples from 14 unattached leaves were individually macerated according to the process described by Degani-Schmidt & Guerra-Sommer (2016b) for the material of the Faxinal Coalfield, consisting of treatment with hydrofluoric acid (HF), Schulze's solution and potassium hydroxide (KOH). After dehydration with glycerin, cuticles were mounted on glass slides in glycerin jelly.

Slides were examined using a Zeiss Axioplan 2 transmitted light microscope and photographed with an AxioCam MRc camera. The images were analyzed, and measurements taken with Zeiss Axio Vision 4.8.1 software. Figures were composed with Adobe Photoshop CS3 Extended. Transformations made

to the images consist of cropping, rotation, contrast adjustment and focus stacking.

Analysis of the epidermal tissue via optical microscopy was greatly hampered by the fact that the cuticles readily disintegrated during the chemical preparation as a consequence of the micromorphological characters — notably the occurrence of longitudinal U-shaped furrows that represent lines of weakness in the epidermis.

For Scanning Electron Microscopy, leaf fragments were processed in HF only, rinsed with distilled water, air dried, placed on standard stubs with double-sided carbon tape and gold coated. Analysis was carried out with an Inspect F50 FEI microscope.

Part of the original material prepared and described by Guerra-Sommer (1989) was re-examined and re-illustrated. Since the material was described based on features present in diverse fragmentary specimens, a holotype was originally not designated. The remaining lectotype and paratype received new numbers since the original description.

The fragmentation of the specimens was not a consequence of taphonomic processes but was related to the nature of the

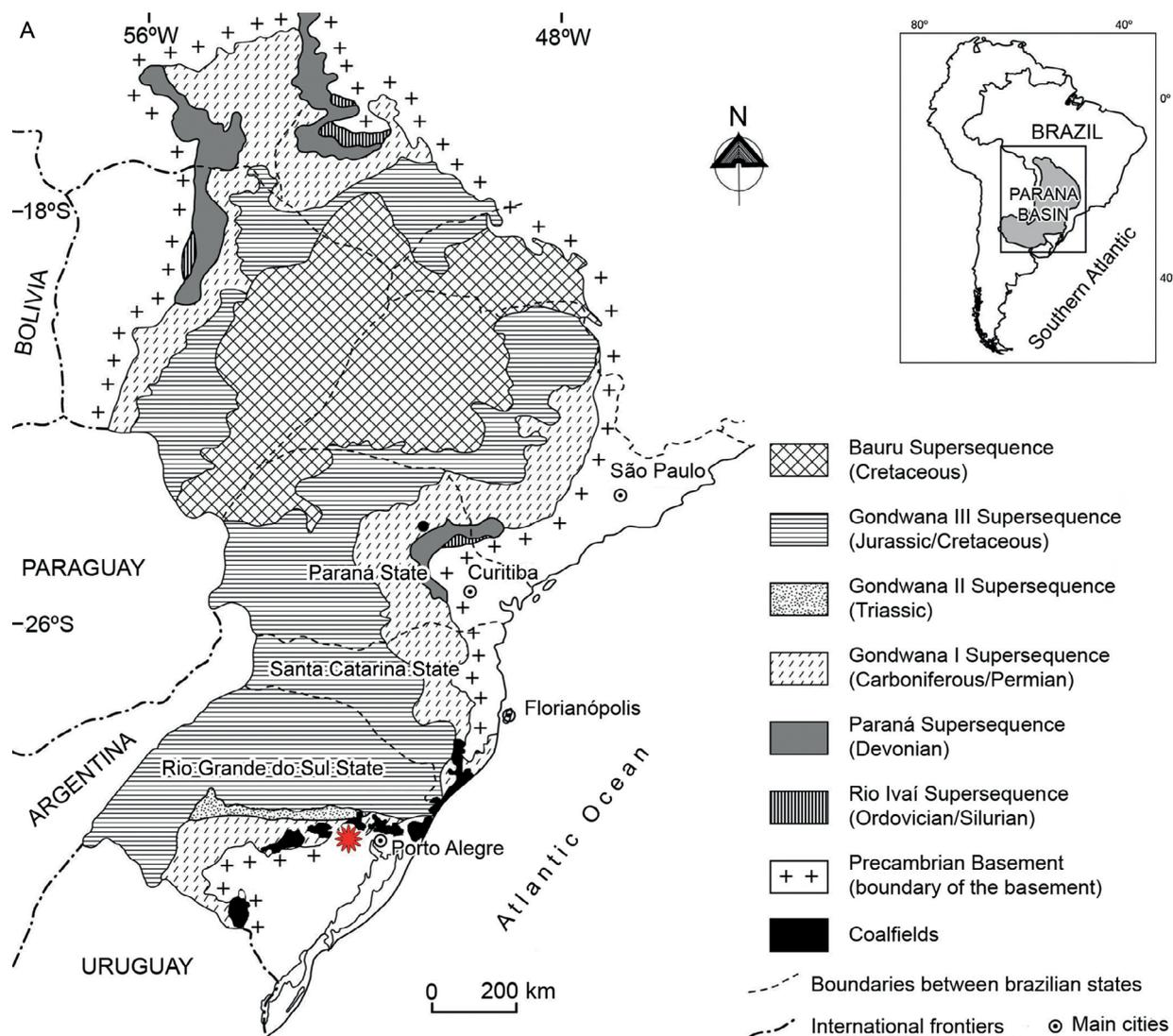


Figure 1. Location map and stratigraphic framework (modified from Degani-Schmidt *et al.* 2016b). Coalfield coordinates 30°15'52.6"S, 51°41'53.8"W.

host rock (massive ash-fall sediment). Thus, the absence of bedding planes and the highly silicified state of the host rock led to the recovery of only fragmentary material.

The fossils from the Faxinal Coalfield and the corresponding slides and stubs are housed in the collection of the Paleobotanical Section of the Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul (DPE-IG/UFRGS), Porto Alegre, Brazil, under the numbers Pb 2622, 2644, 2688, 2694, 2796-b, 2792, 2799, 2802, 2803, 2806, 3538 (former 2693), 3545, 4792, 4789, 4774, 5277 (former 2806).

SYSTEMATIC PALEOBOTANY

Order Cordaitales (*sensu* Taylor *et al.* 2009)

Genus *Noeggerathiopsis* (Feistmantel) McLoughlin & Drinnan 1996

Noeggerathiopsis brasiliensis (Guerra-Sommer) Guerra-Sommer & Degani-Schmidt nom. nov.

Basionym: *Rusfloria gondwanensis* Guerra-Sommer 1989

Holotype: not designated

Lectotype: Pb 5277 (former Pb 2806); Pb 1696 lost.

Paratype: Pb 3538 (former Pb 2693)

Type locality: Faxinal Coalfield, Arroio dos Ratos, RS, Brazil

Type stratum: Rio Bonito Formation, Guatá Group, Gondwana I Supersequence, Paraná Basin

Etymology: Latin, from Brazil

Emended diagnosis, based on Guerra-Sommer (1989): Leaf simple, spatulate, margins entire, apex acute round, base truncated, midvein absent. The veins run parallel between furrows. Upper epidermis banded, cells elongated in the direction of the leaf axis, non-papillate. Ordinary cells of non-stomatiferous bands thin-walled, thick-walled in stomatiferous bands.

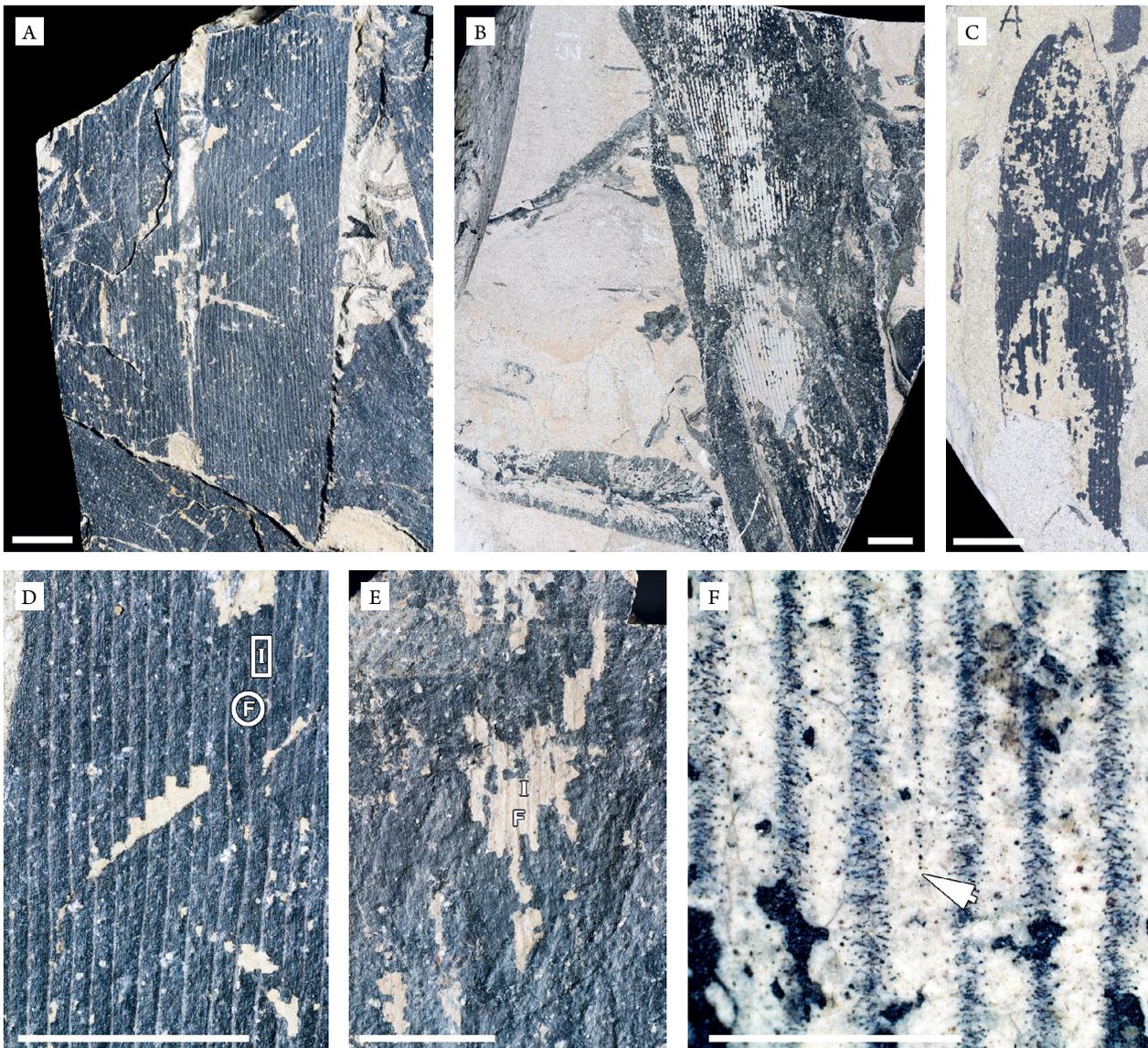


Figure 2. Morphologic patterns of compressions/impressions of *Noeggerathiopsis brasiliensis*. Scale bars (A–E) = 1 cm; (F) = 500 μ m. (A) specimen Pb 4789; (B) specimen Pb 3538, paratype, isolated leaf with associated glossopterid leaf fragment; (C) specimen Pb 5277, lectotype; (D) Specimen Pb 4789, lower surface of a compression showing alternating bands of furrows (circle outline) and inter-furrows (square outline); (E) specimen Pb 4792, upper surface of a compression showing inconspicuous epidermal pattern and partially visible impression of the opposite lower epidermis on the rock; (F) specimen Pb 2796-b, impression of the lower epidermis featuring the superficial trichomes adhered to the host rock; detail of a furrow end (arrow).

Stomata haplocheilic, monocyclic in longitudinal files, 4–6 subsidiary cells slightly differentiated in shape and size from the ordinary cells. On lower epidermis ribbing pattern corresponds to longitudinal, unbranched stomatiferous furrows alternating with wide non-stomatiferous bands. Cells of the non-stomatiferous bands rectanguloid, longitudinally elongated, non-papillatae and papillatae. Epidermal and hypodermal highly cutinized sheaths border the furrows. Stomata haplocheilic, monocyclic, in ill-defined longitudinal files, in the trough and on the lateral walls of the furrows. Guard cells protected by protruding, densely arranged trichomes. Gradual evolution from papillae to elongate papillae and trichomes at furrow borders.

Taxonomic remarks

The name *Noeggerathiopsis gondwanensis* Lele & Maithy is already in use, thus preventing the maintenance of the specific epithet. No holotype was originally established and one of the lectotypes is missing, therefore the remaining lectotype and paratype are maintained as the type specimens.

General morphology

Specimens are fragmentary, longitudinally elongated, showing coarse parallel ribbing, lacking a midrib, margins entire, corresponding to the morphology of associated impressions and compressions. The specimens are 10–28 cm long and 2.5–9 cm wide. The dominance of leaf fragments over 7 cm across their widest part indicates that mainly larger leaves were preserved. The leaf surfaces are marked by ribbing running almost parallel to the margins that is evident in both compressions and impressions (Fig. 2).

The features of the upper surface are inconspicuous. Impressions left by the lower surface on the rock show continuous, non-dichotomous ridges which correspond to furrows bordered with elongate trichomes in the compressions (Figs. 2D, 2E and 2F). Between the grooves (inter-furrow area), wider bands with very thin striations presumably cover the veins (Fig. 2D). A few discontinuous grooves start/end with very narrow furrows (mean 25 μm wide), probably related to areas of vein dichotomies (Fig. 2F), and expand up to 300 μm wide.

Micromorphology

The glabrous upper epidermal pattern consists of bands with 15–18 longitudinal files of elongate, rectangular cells (63–95 μm long; 20–28 μm wide) with thin anticlinal walls (mean 2.5 μm) alternating with 4–6 files of rectanguloid, quadranguloid to pentagonal cells (28–56 μm long), showing thicker (up to 5 μm), highly cutinized anticlinal walls (Fig. 3A). In these thick-walled bands, there are sparse haplocheilic, monocyclic superficial stomata, longitudinally oriented, arranged in poorly defined longitudinal files (Fig. 3B). They are irregularly ringed by 4–6 subsidiary cells, similar in shape and size to the ordinary epidermal cells (60–70 μm long; 21–24 μm wide), in some cases highly cutinized. Guard cells are concealed.

The lower epidermis features different appendages. It is impossible to precisely define the appendage type without ontogenetic studies (Werker 2000); however, Barthlott & Ehler

(1977) proposed to distinguish between papillae and trichomes based on the ratio between their width and height. For single central appendages exhibiting a gradual length increase, they defined three types based on the appendage height:

- D2: papilla;
- D3: elongate papilla;
- D4: trichome.

These types match the gradient observed from both sides of each furrow toward the furrow borders (Figs. 3C and 3D).

The lower epidermis consists of alternating wide non-stomatiferous and stomatiferous bands typically organized in longitudinal furrows (Figs. 3C, 3D and 3E). Non-stomatiferous bands are 1 mm wide (mean) and composed of 10–18 files of longitudinally oriented cells with thin anticlinal walls (1.5 μm mean thickness). In the center of the bands, the cells are non-papillate (70–82 μm long; 21–28 μm wide; Fig. 3D), whereas, in the areas proximal to the furrows, random cells bear thickly cutinized hollow papillae with rounded apices (mean 40 μm long; mean diameter 13 μm). There is a gradual elongation of these structures toward the stomatal furrows (mean diameter 30 μm ; Fig. 3E).

The borders of the furrows are composed of thick-walled, elongate epidermal cells probably stacked upon hypodermal cells (Fig. 3E), forming highly cutinized sheaths which give rise to linear and robust trichomes (up to 100 μm long; 10 μm wide) with usually rounded, rarely acute apices. They are transversally oriented, lining the borders and the walls of the stomatiferous furrows (Fig. 3E).

Narrow furrows (25–50 μm wide) are bordered by elongate, sparsely papillate cells, but the highly cutinized sheath is still present (Fig. 3F). The stomatiferous area is composed of a single or double file of stomata transversally disposed in the trough of the U-shaped furrow (Fig. 3F and Fig. 4D).

Wider furrows (up to 300 μm) have a dense and diverse ornamentation of epidermal tissue comprising single and elongate papillae and long trichomes protecting the mouth of the furrows like a palisade (Figs. 3E, 3G and 3H). Stomata are arranged in two to several ill-defined longitudinal files occurring both in the trough and in the lateral walls of the furrows (Fig. 4A, arrows).

Stomata are haplocheilic and monocyclic. Each stomatal apparatus consists of a pair of sunken guard cells (Fig. 4B), surrounded by 5–7 subsidiary cells. The presence of dense trichome complexes overarching the stomatal pore hampered the detailed observation of the stomatal apparatus (Figs. 4C, 4D, 4E and 4F). The trichomes are hollow, elongate (up to 50 μm long), with broad bases (mean 30 μm) and in some cases constricted, cutinized apices (Fig. 4C).

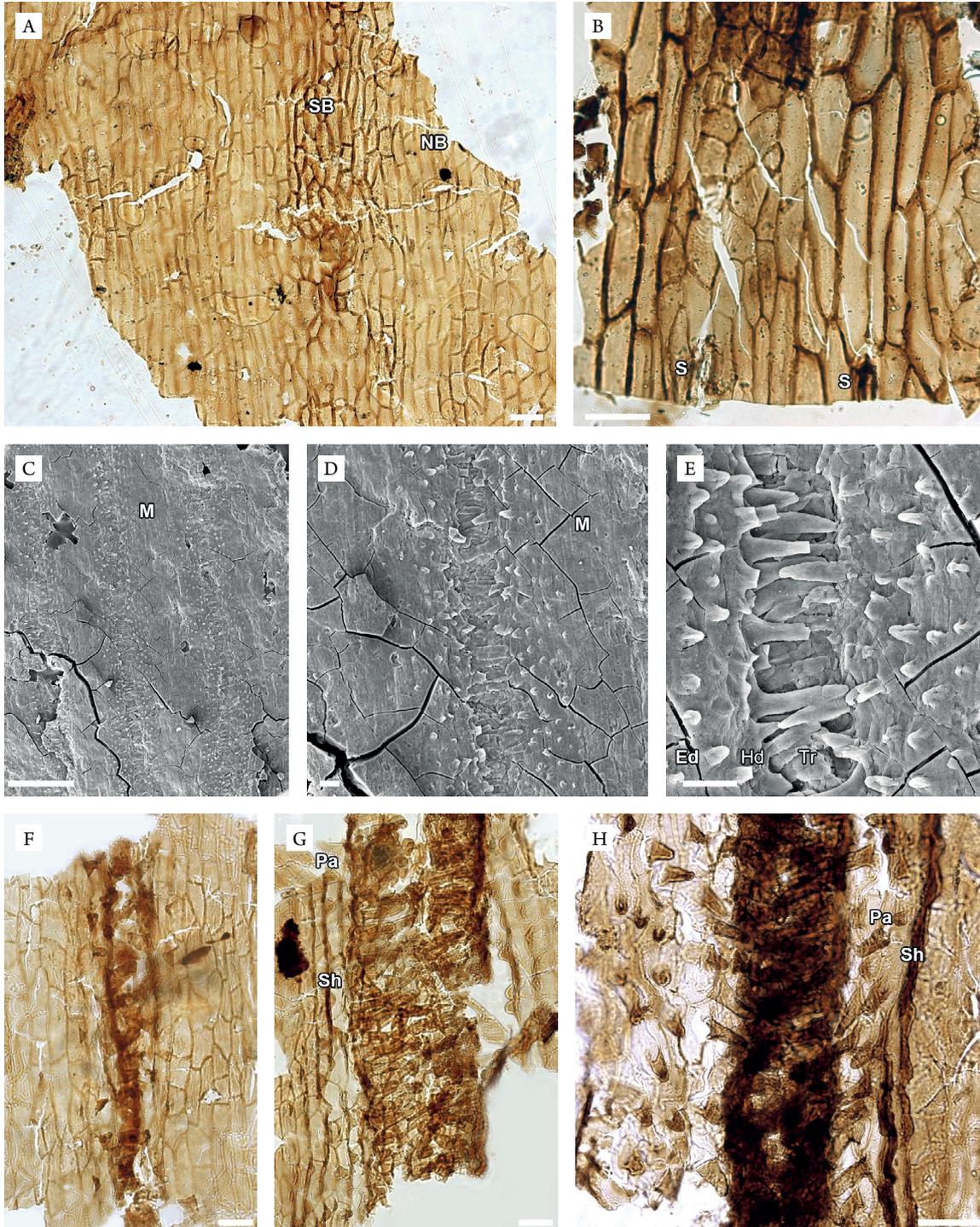
DISCUSSION

Generic and specific status

The suite of epidermal characteristics of these spatulate leaves contrasts markedly with that of *Cordaites* leaves from the Carboniferous–Permian of paleotropical Euramerica. Comparisons with *Rufloria*, the most common cordaitalean

foliage from the Pennsylvanian to the Permian of Angara, were partially impaired because significant diagnostic features were not clearly documented by Meyen (1963, 1964, 1984, 1987). However, the thickened hypodermal cells bordering the mouth of the furrows, described as an exclusive pattern of

Ruffloria, probably correspond to the highly cutinized sheaths described here (Figs. 3E, 3F, 3G and 3H). Additionally, the epidermal hairs that are entirely confined to the border of the furrows referred by Meyen are also a feature in common with *Noeggerathiopsis brasiliensis* (Fig. 3F).



SB: stomatiferous band; NB: non-stomatiferous band; S: stoma; M: median area of non-stomatiferous band; Ed: epidermal cells; Hd: hypodermal cells; Tr: trough, Pa: papillate cells; Sh: sheath.

Figure 3. Micromorphologic patterns of *Noeggerathiopsis brasiliensis*. (A, B, F–H) under transmitted light; (C–E) under FEG-SEM. Scale bars (A, B, D – H) = 50 μm ; (C) = 500 μm . (A, B) Upper epidermal surface. (A) Slide Pb 2688a-1; (B) slide Pb 2622-8, stomatiferous band showing highly cutinized cell walls and files of haplocheilic, non-papillate stomata; (C–H) lower epidermal surface; (C) specimen Pb 4789, general epidermal pattern with alternating stomatiferous and non stomatiferous bands; (D) detail of (C), stomatiferous band in the center; non stomatiferous bands show non papillate and papillate cells; (E) detail of (D), stomatiferous band showing horizontally disposed trichomes and bordering papillae, furrow bordered by a sheath of highly cutinized epidermal and hypodermal cells, cells of the trough show round to elongate papillae; (F) slide Pb 4789-2, uniseriate file of stomata in a narrow furrow bordered by scarcely papillate cells; (G, H) slides Pb 4789-1 and Pb 4792-2, wide furrows densely bordered by papillate cells and epidermal sheath.

To explain the morphological similarities in different stocks of Cordaitales, Meyen (1987) presented the hypothesis of an early migration (before Serpukhovian) of ancestral cordaitalean forms from the Euroamerian province to Angara and an independent development of the Cordaitanthales in the Northern Temperate Realm as an isolated plant group.

Considering the striking similarities between *Ruflorea* and *Noeggerathiopsis*, we agree with the suggestion by McLoughlin

& Drinnan (1996) that, besides morphological and anatomical criteria, geographic provincialism should be considered in the definition of different groups in Cordaitales while there is no definition of reproductive patterns for most Gondwanan forms.

In addition to *Noeggerathiopsis* and *Cordaites*, McLoughlin & Drinnan (1996) include, among the Gondwanan cordaitalean genera, *Cheirophyllum* Pant & Singh and possibly *Metreophyllum* Anderson & Anderson. Singh (2000), Singh *et al.* (2007), Césari

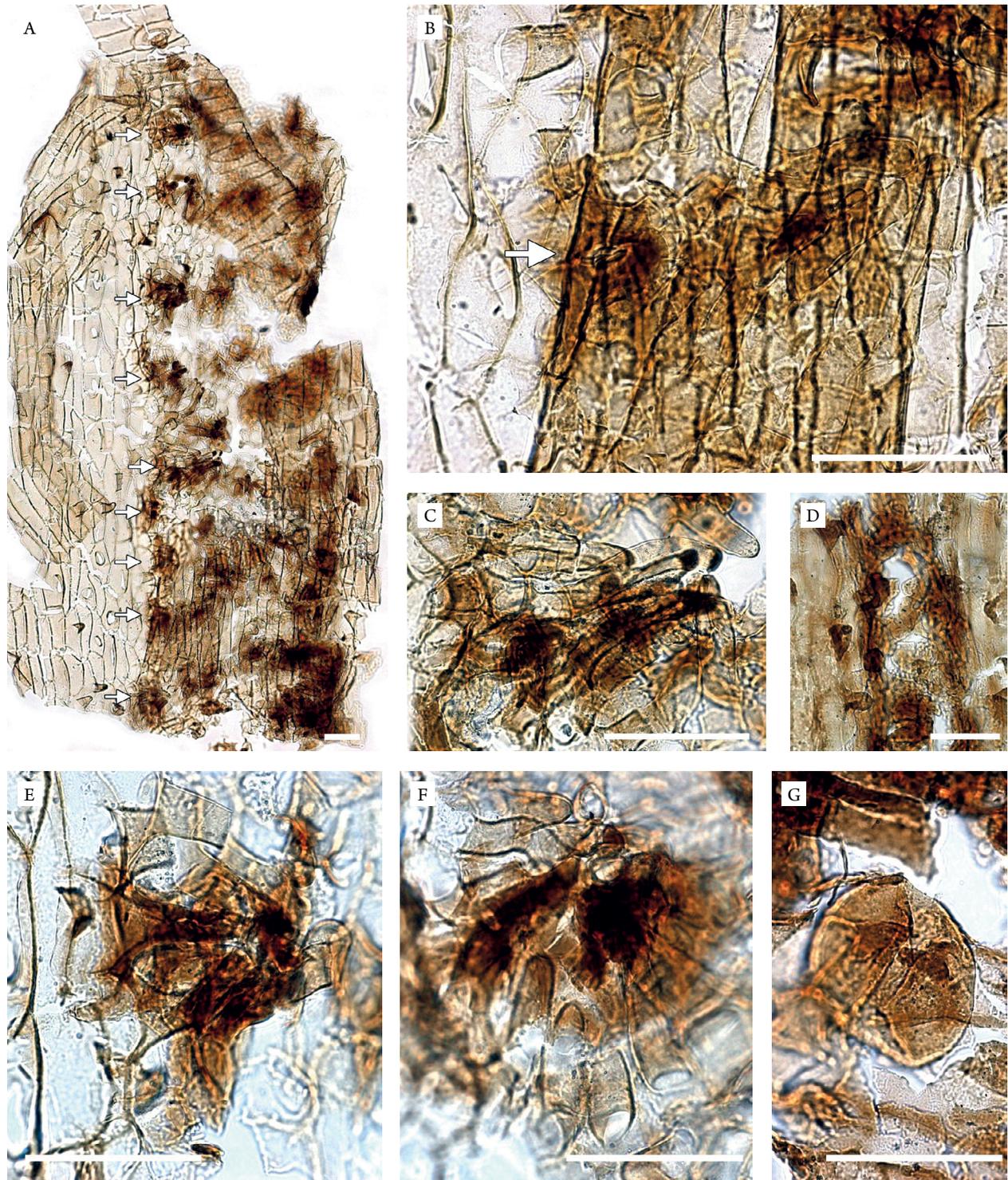


Figure 4. Details of stomata under transmitted light. Scale bars = 50 μ m. (A) Slide Pb 2806-1, wide furrow with several ill-defined stomatal files, arrows point to stomata in the lateral walls of the furrows; (B) detail of (A), stoma showing possible kidney-shaped guard cells; (C) detail of (A), cone-shaped trichomes with round, cutinized apices overarched over the stoma; (D) detail of (Fig. 3F), stoma from narrow furrow protected by papillae; (E, F) detail of (A), stomata densely covered by cone-shaped trichomes; (G) slide Pb 4792-2, saccate pollen grain trapped in a furrow.

& Hünicken (2013) and Saxena *et al.* (2013) also consider the genera *Euryphyllum* Feistmantel, *Kawizophyllum* Kapoor and, with some disagreement, *Panthophyllum* Rigby in the group, even though they are all very close variations of *Noeggerathiopsis* and were erected on the basis of characters that are not preserved in the type specimen (McLoughlin & Drinnan 1996).

The main diagnostic feature of *Euryphyllum* consists of secondary veins in the lateral portion of the lamina arching toward the margins (Saxena *et al.* 2013). *Kawizophyllum* presents a distinguished fold along the median region (Kapoor 1979, Singh 2000). The genus *Panthophyllum* was erected by Rigby (1984) for Gondwanan cordaitalean leaves with preserved cuticle. Maheshwari & Singh (1999) specifically instituted the genus *Panthophyllum* for early Permian leaves with preserved cuticle, albeit with low agreement (*e.g.*, McLoughlin & Drinnan 1996, Srivastava & Tewari 2004, Singh *et al.* 2007, Saxena *et al.* 2013).

In our material, the prominent trichomes in the stomatiferous furrows of the lower leaf surface are consistent with the Gondwanan morphogenus *Noeggerathiopsis* according to the emended diagnosis proposed by McLoughlin & Drinnan (1996). Nevertheless, as a consequence of compression taphonomic bias in the Brazilian specimens, it is not possible to observe the internal leaf anatomy of venation and mesophyll which are important distinctive features between *Cordaites* and *Noeggerathiopsis* leaves.

Since the establishment of *Noeggerathiopsis* by Feistmantel (1879) for the Permian of Gondwana of India, several species have been erected based on venation patterns. After the emended diagnosis by Maithy (1964), several morphospecies were erected based on epidermal patterns associated with venation: *Noeggerathiopsis indica* Lele & Maithy, *N. gondwanensis* Lele & Maithy and *N. zeilleri* Lele & Maithy; *N. fibrosa* Pant & Verma, *N. bunburyana* Pant & Verma and *N. papillosa* Pant & Verma; *N. conspicua* Lele & Makada; *N. saharjuriensis* Bajpai and *N. bihariensis* Bajpai (Singh *et al.* 2007).

The common characteristic of *Noeggerathiopsis* species from India is the clearly outlined non-stomatiferous/stomatiferous bands. However, distinguishing characters are very subtle, being centered on densities rather than on their absence/presence. Surface papillae are a common feature of ordinary epidermal cells, more abundant in lower than in upper epidermis and are also present in subsidiary cells of stomata. The gross morphology of almost all leaves defined by epidermal characters is very similar. As observed by Srivastava & Tewari (2004), *N. bunburyana* and *N. indica* have essentially the same epidermal pattern as *N. papillosa* and *N. gondwanensis*.

The most strikingly distinctive feature in the *Noeggerathiopsis* leaves is the occurrence of stomatiferous furrows bordered by continuous cutinized sheaths in the south Brazilian and Antarctic material and absent in the Indian material described by Lele & Maithy (1963) and Pant & Verma (1964).

The features that distinguish the epidermal pattern described here from the Antarctic material described by McLoughlin & Drinnan (1996) are:

- the occurrence of stomata not only restricted to the trough but also in the lateral walls of the furrows;
- the presence of long trichomes surrounding the stomatal pore;

- the absence of trichomes on epidermal cells in the inter-furrow regions of the lower surface;
- the gradual elongation of papillae from the sides of the inter-furrow areas towards the borders of stomatal furrows.

For these reasons, we decided to establish the new specific epithet *Noeggerathiopsis brasiliensis* to replace *Rufflora gondwanensis*.

Floristic association and paleoenvironmental significance

The dispersed fragments of *Noeggerathiopsis brasiliensis* are accessory fossils in the paleofloristic association of the Faxinal tonstein layer (southernmost Brazilian Gondwana), which was largely dominated by *Glossopteris* leaves as previously described by Guerra-Sommer (1992), Boardman *et al.* (2012), Degani-Schmidt *et al.* (2015) and Degani-Schmidt & Guerra-Sommer (2016b). However, the cordaitalean pollens are well represented in the underlying coalbeds, supporting their contribution to the original coal biomass (Cazzulo-Klepzig *et al.* 2009). Additionally, unlike the glossopterids, which were restricted to the southern megacontinent of Gondwana, the cordaitalean paleobiogeography has worldwide significance.

Isolated platyspermic seeds occur in dense and monotypic concentrations (*Platycardia* sp.) within the tonstein layer (Guerra-Sommer 1988). This type of seed has been linked to Cordaitales in the Gondwanan Realm (*e.g.*, Bernardes-de-Oliveira & Pontes 1977, Archangelsky & Leguizamón 1980, García 1990), but as previously referred by McLoughlin & Drinnan (1996), physical connection between those seeds and *Noeggerathiopsis* has not yet been established.

Palynological and palynofacies analyses of the tonstein layer (Cazzulo-Klepzig *et al.* 2009, Degani-Schmidt *et al.* 2015) revealed the dominance of phytoclasts and poorly preserved sporomorphs. Monosaccate and bisaccate pollen grains were dominant (*e.g.*, *Cannanoropollis* Potonié and Sah and *Scheuringipollenites* Tiwari), occurring together with *Protohaploxypinus* (Samoilovich) Morbey. Their probable botanical affinity is with cordaitaleans, glossopterids and conifers.

Although no sporangia have been found attached to *Noeggerathiopsis* leaves, we observed the common occurrence of saccate pollen grains trapped within the longitudinal furrows (Fig. 4G). They are very similar to *Cladaitina* Maheshwari & Meyen, which was found associated to *Cladostrobus* Zalessky, a putative reproductive organ of the Angaran Rufloiriaceae (Maheshwari & Meyen 1975) and was also reported from palynological assemblages in Permian strata of Argentina and attributed to Cordaitales (Zavattieri & Gutiérrez 2012).

As a general rule, *Noeggerathiopsis* is associated with a peat-forming environment all over Gondwana. The co-fossilization of *Glossopteris* interspersed with *Noeggerathiopsis* leaves in a single ash-fall bed (Figs. 2A and 2B) within a coal seam and deposited in a very limited span of time (days or months according to DiMichele & Falcon-Lang 2011) indicates that both genera were contemporaneous components of a single peat-forming plant association. A similar association

showing glossopterid dominance occurs in the Bainmedart Coal Measures of East Antarctica (Holdgate *et al.* 2005) where McLoughlin & Drinnan (1996) obtained the silicified and fusainized *Noeggerathiopsis* leaves with preserved anatomy. Both Brazilian and Antarctic assemblages are thus known to have been influenced by autochthonous wildfire events (Jasper *et al.* 2011, Slater *et al.* 2015, Degani-Schmidt *et al.* 2015).

The typical epidermal pattern of *Noeggerathiopsis* leaves from both peat-forming environments in Antarctica and Brazil, showing extreme protection of the stomatal apparatus, indicates an ecological adaptation to specific environmental factors. In extant plants, there is a most obvious response to stressful conditions related to transpiration reduction in a xeromorphic environment (Haworth & McElwain 2008). However, stomata occurring in furrows strongly protected by trichomes are present in *Noeggerathiopsis* leaves from swampy, peat-forming environments subjected to physiological drought in both Antarctic and Brazilian settings. McLoughlin & Drinnan (1996) considered that swamp plants clearly somehow benefit for regulating the uptake of water in environments of very low nutrients, especially in raised peat mires, which could also be the case for the plant association under study. Degani-Schmidt *et al.* (2015) and Degani-Schmidt & Guerra-Sommer (2016b) also considered that the recurrent wildfire events represented by several thin inertinite layers in the coal, in addition to the macrocharcoal present in the tonstein layer itself (Jasper *et al.* 2011), could have played a role similar to environmental aridity, even in a wet setting such as a swamp forest.

The occurrence of only incipient papillae in some of the material described from India could reflect different climate conditions probably derived from higher humidity. Saxena *et al.* (2013) observed that during the Permian of India the genus *Euryphyllum* showed a marked decrease in epidermal papillae until their complete absence in the leaves of later age, probably reflecting a climate change from cool and dry in the early Permian to warm and humid in the late Permian.

The absence of furrows in the Indian material was considered by McLoughlin & Drinnan (1996) as an artificial flattening resulted from preservation or chemical degradation during preparation. However, like the trichomes, the development of such furrows was probably another adaptation to high stress environments, and the specific ecological and/or climate conditions requiring such responses were absent from the Indian settings.

Johnson (1975) observed that some species develop (or suppress) trichomes as an environmental response and the different forms of a single species will be expressed according to the habitat variations. Consequently, the phenotypic identity

of a taxon is flexible to a certain degree, allowing the plants to react to different site conditions (DiMichele *et al.* 1987). Trichome morphology and basic distribution are genotypically determined, whereas trichome density and size are known to be affected by environmental influences (Stace 1966, DiMichele *et al.* 1987, Barclay *et al.* 2007, Haworth & McElwain 2008).

The epidermal architecture of *Glossopteris pubescens*, the dominant species in the plant association studied here, also incorporates long trichomes and is unique and endemic to the Faxinal Coalfield (Degani-Schmidt & Guerra-Sommer 2016b). The epidermal cells of the lower surface carry papillae, in some cases elongate ones, simple and complex trichomes. The sets of epidermal features presented by both *Noeggerathiopsis brasiliensis* and *G. pubescens* from the Faxinal ash-fall layer probably developed to provide protection against environmental disturbances such as seasonal cyclicity from wet to dry conditions, marked by frequent, recurrent and possibly cyclical wildfires related with the lowering of the water table during climate oscillations at the waning of the Permian icehouse stage (Degani-Schmidt *et al.* 2015).

CONCLUSIONS

The micromorphological patterns of the *Noeggerathiopsis brasiliensis* samples from the Faxinal Coalfield, mainly characterized by the presence of stomatal furrows strongly protected by trichomes, are very similar to those described for the Antarctic genus, but differ from those described for India, which occasionally bear only incipient papillae. This difference could reflect intrageneric adaptations to environmental stress, remaining the possibility of water regulation on mineral-poor, acidic, and episodically dry raised mires. The new specific epithet *Noeggerathiopsis brasiliensis* replaces *Rufloria gondwanensis* on the basis of morphological and anatomical criteria and geographic provincialism.

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