UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE GEOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ

ISABELA DEGANI SCHMIDT

ORIENTADORA – Profª. Drª. Margot Guerra Sommer

Porto Alegre – 2016

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE GEOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ

ISABELA DEGANI SCHMIDT

ORIENTADORA – Profª. Drª. Margot Guerra Sommer

BANCA EXAMINADORA
Profª. Drª. Etiene Fabbrin Pires - Curso de Ciências Biológicas, Universidade Federal do Tocantins
Profª. Drª. Mary Elizabeth C. Bernardes de Oliveira – Instituto de Geociências, Universidade de São Paulo
Prof. Dr. João Graciano Mendonça Filho - Instituto de Geociências, Universidade Federal do Rio de Janeiro

Tese de Doutorado apresentada como requisito parcial para a obtenção do Título de Doutor em Ciências.

Porto Alegre – 2016

CIP - Catalogação na Publicação

Schmidt, Isabela Degani
Múltiplas evidências de perturbações ambientais durante a deposição da turfeira pós-glacial (Sakmariano) da Mina de Faxinal, sul da Bacia do Paraná / Isabela Degani Schmidt. -- 2016.
190 f.

Orientador: Margot Guerra Sommer.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Programa de Pós-Graduação em Geociências, Porto Alegre, BR-RS, 2016.

1. Paleobotânica. 2. Paleoincêndios. 3. carvão vegetal macroscópico. 4. Flora de Glossopteris. 5. Gondwana. I. Sommer, Margot Guerra, orient. II. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

UFRGS
UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

Instituto de Geociências
Programa de Pós-Graduação em Geociências

ATA Nº 003/2016

Às nove horas e vinte minutos horas do dia vinte e oito de janeiro de dois mil e dezesseis no Anfiteatro do Centro de Estudos em Geologia Costeira e Oceânica – CECO, no Campus do Vale, reuniu-se a Comissão Examinadora constituída pelos doutores: Etiene Fabbrin Pires (Universidade Federal do Tocantins - UFT), Mary Elizabeth C. Bernardes de Oliveira (Universidade de São Paulo - USP) e João Graciano Mendonça Filho (Universidade Federal do Rio de Janeiro - UFRJ), para a defesa da tese intitulada: **"MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ"** a que se submete **ISABELA DEGANI SCHMIDT**, depois de haver cumprido as exigências regulamentares do Programa. A Coordenadora do Programa Profa. Dra. Ana Maria Pimentel Mizusaki fez a abertura da sessão e passou a presidência dos trabalhos para orientadora Profa. Dra. Margot Guerra Sommer de acordo com o previsto no artigo 69 do Regimento do Programa. A candidata fez a apresentação do seu trabalho e a seguir foi arguida pelos membros da Comissão Examinadora. Às doze horas e vinte minutos a sessão foi suspensa por quinze minutos para julgamento e atribuição dos conceitos, que foram os seguintes: Etiene Fabbrin Pires **"A" (EXCELENTE)**, Mary Elizabeth C. Bernardes de Oliveira **"A" (EXCELENTE)** e João Graciano Mendonça Filho **"A" (EXCELENTE).** Face aos conceitos atribuídos foi conferido a candidata o grau de **DOUTOR EM CIÊNCIAS** pela Universidade Federal do Rio Grande do Sul. Às doze horas quarenta minutos a sessão foi encerrada, do que para constar, eu, Roberto Martins Pereira, lavrei a presente Ata que é assinada pela Comissão Examinadora.

Profa. Dra. Etiene Fabbrin Pires

Profa. Dra. Mary Elizabeth C. Bernardes de Oliveira

Prof. Dr. João Graciano Mendonça Filho

Profa. Dra. Margot Guerra Sommer
(Presidente)

Homologação pela Comissão de Pós-Graduação,	
Ata nº	Data:
Conceito Final:	
Rubrica:	

ANEXO I

Título da Dissertação/Tese:

"MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ"

Área de Concentração: **PALEONTOLOGIA**

Autora: **ISABELA DEGANI SCHMIDT**

Orientadora: **Profa. Dra. Margot Guerra Sommer**

Examinador: **Prof. Dr. João Graciano Mendonça Filho**

Data: 28/01/2016

Conceito: A

PARECER:

A tese apresenta elevado conceito técnico-científico. Destaca-se a coerência e a clareza dos objetivos e da hipótese de trabalho proposta. Os trabalhos publicados apresentam conteúdos inéditos e de caráter científico diferenciado e conceituado. A aplicação de diferentes técnicas, a coerência metodológica e concatenação das interpretações é outro ponto forte a ser destacado. Soma-se a isso o elevado conhecimento técnico e desenvolvimento científico mostrado, tanto no trabalho escrito quanto na defesa e argumentação demonstrada pela candidata. Sendo assim, não há dúvida que se trata de um trabalho que merece um "voto de louvor".

Assinatura: Data: 28/01/2016

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Dissertação/Tese:

"MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ"

Área de Concentração: **PALEONTOLOGIA**

Autora: **ISABELA DEGANI SCHMIDT**

Orientadora: **Profa. Dra. Margot Guerra Sommer**

Examinadora: **Profa. Dra. Etiene Fabbrin Pires**

Data: 28/01/16

Conceito: A

PARECER:

A tese está muito bem elaborada, os resultados são inéditos com grande importância científica. A organização dos capítulos está clara e facilita a leitura e compreensão. A linguagem utilizada é pertinente e adequada. O referencial teórico é adequado tanto do ponto de vista histórico quanto atual. A hipótese, embasada em trabalhos anteriores está bem elaborada. Os objetivos estão claros e bem distribuídos (2 por artigo). As metodologias, que são diversas, estão bem aplicadas. Os resultados são bem discutidos à luz de modernas técnicas e interpretações. Pontuo adicionalmente a apresentação dos anexos, que demonstram o comprometimento acadêmico da estudante. A apresentação oral foi impecável, com a apresentação de elementos adicionais que contribuíram para o pleno entendimento da tese. Frente a todas estas considerações atribuo VOTO DE LOUVOR, visto que a tese tem grande qualidade científica principalmente relativo às técnicas utilizadas.

Assinatura: Data: 28/01/16

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Dissertação/Tese:

"MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ"

Área de Concentração: **PALEONTOLOGIA**

Autora: **ISABELA DEGANI SCHMIDT**

Orientadora: **Profa. Dra. Margot Guerra Sommer**

Examinadora: **Profa. Dra. Mary Elizabeth C. Bernardes de Oliveira**

Data: Porto Alegre, 28 de janeiro de 2016

Conceito: A (Excelente) com "Louvor" *Observação

PARECER:

O documento ora apresentado pela candidata, para obtenção de seu grau de Doutor em Ciências Paleontológicas, do ponto de vista formal está muito bem desenvolvido em três partes distintas: a) uma introdução ao tema, com boa fundamentação teórica e clara conceituação de cada ítem a ser abordado, bem como definição de hipóteses e objetivos; b) uma segunda parte relacionada com apresentação do material estudado e métodos de estudo, bem como coleta de dados e algumas interpretações parciais de dados apresentados na forma de publicações em periódicos especializados na área, de grande impacto internacional e c) uma terceira parte, onde, numa síntese muito bem elaborada, é feita a integração de dados de diferentes naturezas, interpretando-os e chegando à conclusão final. O Resumo e Abstract são informativos, narrando de forma sucinta todo conteúdo da tese. O texto está bem escrito em linguagem culta e clara, demonstrando que a candidata explorou variados tipos de material paleobotânico e palinológico (lenhos, folhas, cutículas, palinomorfos) preservados por diferentes processos tafonômicos (adpressões, incarbonizações, carvões pirogênicos, etc.). Utilizou-se de diferentes métodos de estudo desde clássicos como observação em estereomicroscópio e preparações químicas palinológicas até mais modernos e sofisticados como exame sob MEV, sob fluorescência, medidas de reflectância. Analisou em detalhe estruturas estomáticas e microestruturas epidermo-cuticulares de folhas, estruturas anatômicas de caules, estruturas sedimentares da rocha matriz. Fez considerações taxonômicas e de estruturas adaptativas genotípicas e fenotípicas de glossopterídeas. Utilizou a literatura pertinente tanto de importância histórica como moderna, com desenvoltura, buscando nela apoio para suas interpretações e integrações de dados.

Observ.* O "Voto de Louvor" é dado considerando o valor científico têm dados relevantes para o conhecimento do Gondwana Brasileiro e para o conhecimento global de paleoincêndios de turfeiras e tonstein. Pela integração e interpretação de dados e sua publicação em periódicos com "Qualis" elevado.

Portanto, buscou evidências e argumentos para embasar cada conclusão feita. Trouxe dados muito relevantes para o conhecimento do Gondwana Brasileiro e, em particular, da área carvoeira sulriograndense. Também contribuiu para o conhecimento global de paleoincêndios de turfeiras e de cinzas vulcânicas associadas às turfas gondvânicas, além de chamar atenção para a grande capacidade adaptativa das glossopterídeas aos ambientes estressantes do Permiano. A contribuição para o conhecimento mais detalhado da anatomia de lenhos de prováveis glossopterídeas (Agathoxylon) e de seu floema secundário também é muito relevante.

A título de sugestão fazemos as seguintes recomendações: 1º) incluir no título a informação da unidade litoestratigráfica, uma vez que há carvões pensilvanianos e eopermianos na área norte da bacia do Paraná, tanto no Grupo Itararé como na Fm. Rio Bonito; 2º) no sumário e no texto, antecipar os subtítulos 1.9 a 1.11 (p.p. 32-42) referentes a conceitos de incêndios e geração de carvão vegetal, para antes do item 1.3. Incêndios em turfeiras do Neodevoniano; 3º) substituir a expressão "carvão vegetal" muito vaga e geral por "carvão pirogênico", muito mais específica e próxima (a nosso ver) do termo inglês "charcoal"; 4º) fazer algumas correções, de ordem mais geral ou específica, apontadas e discutidas oralmente durante a defesa.

Externamos aqui nossos cumprimentos à doutoranda pela grande maturidade científica demonstrada; domínio de diferentes temas e análises paleobotânicas; pela argumentação bem baseada em dados e literatura de ponta na elaboração de brilhante tese. Cumprimentos extensivos à competente orientadora.

Assinatura: Mary Elizabeth C. Bernardes de Oliveira Data: 28/01/2016

Ciente do Orientador:

Ciente do Aluno:

ERRATA

Tese de Doutorado

MÚLTIPLAS EVIDÊNCIAS DE PERTURBAÇÕES AMBIENTAIS DURANTE A DEPOSIÇÃO DA TURFEIRA PÓS-GLACIAL (SAKMARIANO) DA MINA DE FAXINAL, SUL DA BACIA DO PARANÁ

página	parágrafo	linha	onde se lê	leia-se
158	2	10-13	As perturbações relacionam-se com baixa diversidade de espécies no ambiente de turfeira, e extensos intervalos de incêndios poderiam ter reforçado a dominância de ***G. pubescens*** nesse ambiente restrito.	As perturbações relacionam-se com baixa diversidade de espécies no ambiente de turfeira, e extensos intervalos de incêndios, associados à influência regional de vulcanismo, poderiam ter reforçado a dominância de ***Glossopteris pubescens*** nesse ambiente restrito.

Dedico esta tese a três mulheres que
têm para sempre minha mais profunda
gratidão e admiração:
Vera, Patrícia e Margot,
cada uma delas é, ao mesmo tempo,
mãe, irmã, orientadora e amiga.

AGRADECIMENTOS

Expresso, aqui, meu agradecimento às pessoas e instituições que contribuíram para o desenvolvimento da presente pesquisa.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (159690/2012-9) e CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, pelo auxílio financeiro.

Ao Programa de Pós-Graduação em Geociências – PPGGeo/IG-UFRGS, especialmente nas pessoas do Secretário Roberto Martins Pereira e da Auxiliar Administrativa, Letícia Barbosa, pelo apoio institucional, e aos funcionários do Instituto de Geociências nos Laboratórios de Preparação de Amostras, Juliano e Marcelo, do CECO, Gilberto Silveira dos Santos, e Laboratório de Palinologia Marleni Marques Toigo, Bruno Noronha pelo apoio técnico.

Ao Departamento Alemão de Intercâmbio Acadêmico (DAAD) e Instituto Senckenberg em Frankfurt pelo apoio financeiro e acolhimento respectivamente.

À minha orientadora, Margot, pessoa de força inspiradora, pela confiança, amizade e generosidade a mim dedicadas em meio a momentos difíceis de sua vida.

Aos pesquisadores e professores André Jasper, Rualdo Menegat, João Graciano Mendonça Filho, Joalice de Oliveira Mendonça, Miriam Cazzulo-Klepzig, Milton Luiz Laquintinie Formoso, Dieter Uhl, Sybille Roller, Abdalla Abu Hamad, Roberto Iannuzzi, Marion Bamford, Paulo Alves de Souza, Daiana Boardman, Cristina Félix, João Carlos Coimbra, Luiz Drude de Lacerda, Wolfgang Kalkreuth, Gustavo Simão, Volker Wilde, Robert Gastaldo e Felix Gradstein, pela amizade, auxílio, disponibilidade, ensinamentos e incentivo.

Aos colegas e amigos Veri Ribeiro, Gabi Gadens, Esther Pinheiro, Paula Sucerquia, Margarete Simas, Cris Bahi, Wagner Guimarães da Silva, pelo companheirismo e ajuda, e a todos os colegas e professores dos Institutos de Biociências e Geociências desta Universidade, em especial do Departamento de Paleontologia e Estratigrafia e PPGGeo/IG-UFRGS, com quem o contato foi de fundamental importância para minha formação.

Karin Kirchner, Karin Mielack und Carlos Pallarés für die Freundschaft und schöne Momente.

À minha família, esposo, mãe, pai, irmã, irmão, cunhada e primos, Norman, Vera, João, Patrícia, Giovanni e Lisiane, José Eduardo e João Roberto, pelo apoio irrestrito e incondicional, pela acolhida sempre afetuosa e peço desculpas por tantas ausências.

“*Aprendi a ser paciente, a confiar e a entregar-me*
ao tempo, a esse tempo que simultaneamente
nos vai construindo e destruindo para de novo
nos construir e outra vez nos destruir.”
José Saramago

RESUMO

Perturbações ambientais foram detectadas em sistema de turfeira no sul da Bacia do Paraná (Mina de Faxinal, Formação Rio Bonito) durante o Eopermiano (idade radiométrica 291 ± 1.3 Ma, topo do Sakmariano) sob vigência de período climático pós-glacial da Idade do Gelo do Neopaleozoico. Além da detecção de incêndios recorrentes, foi identificado um evento de incêndio autóctone/hipoautóctone em vegetação arbórea em um horizonte no carvão contendo grandes fragmentos de lenhos queimados comprimidos (21,8 x 13.4 cm). A influência de vulcanismo está registrada sob a forma de uma camada de tonstein (cinza vulcânica sedimentada) intercalada ao carvão, onde estão incluídas abundantes compressões de folhas glossopterídeas. A análise do carvão consistiu em determinação de refletância sob óleo de macerais do grupo inertinita em blocos polidos para confirmar a identificação de carvão vegetal macroscópico e ocorrência de incêndios na turfeira. Adicionalmente, a observação da matéria orgânica sob fluorescência nos blocos revelou que os incêndios não afetaram a microflora, mas alteração na fluorescência evidenciou dessecação ambiental, verificada também em lâminas palinofaciológicas. Sob microscopia eletrônica de varredura, o carvão vegetal apresentou paredes celulares homogeneizadas, indicando temperaturas de queima acima de 325ºC, mas não superiores a 400ºC devido aos baixos resultados de refletância e à preservação de tecido vegetal delicado. A preservação de floema secundário, em associação orgânica com xilema tipo *Agathoxylon*, é registrada ineditamente. A observação sob microscopia de luz transmitida das cutículas foliares extraídas do tonstein permitiu descrição detalhada de padrões xeromórficos que ocorrem de forma endêmica nas epidermes de glossopterídeas de Faxinal e foram atribuídos a respostas adaptativas às frequentes perturbações ambientais que afetaram a floresta turfosa, tais como incêndios recorrentes por dessecação ambiental cíclica ou influência de vulcanismo regional. Esses fatores, em conjunto ou alternativamente, garantiram a dominância monotípica de *Glossopteris pubescens* nom. nov. na comunidade. O conjunto de evidências indicou que os incêndios foram de superfície, em baixas temperaturas, o transporte do carvão vegetal foi praticamente inexistente no horizonte de grandes fragmentos de lenhos queimados e que os demais incêndios recorrentes tiveram pouco efeito na comunidade proximal, ocorrendo regularmente nas áreas de entorno da turfeira dado o aporte de carvão vegetal macroscópico fragmentário. Durante a fase de aquecimento pós-glacial no Permiano, os ambientes de turfeira no Gondwana eram altamente suscetíveis à ocorrência de incêndios dos quais as glossopterídeas se beneficiavam para manter sua dominância e abundância nessas comunidades, por possuírem eficiente plasticidade adaptativa para sobreviver a condições extremas em ambientes altamente perturbados.

Palavras-chave: carvão vegetal macroscópico, paleoincêndios, vulcanismo, Flora de *Glossopteris*, Gondwana, paleobotânica

ABSTRACT

MULTIPLE EVIDENCES OF ENVIRONMENTAL DISTURBANCES DURING THE POST-GLACIAL PEAT DEPOSITION OF THE FAXINAL COALFIELD (SAKMARIAN), SOUTHERN PARANÁ BASIN - Environmental disturbances were detected in a peat-forming environment from the southern Brazilian Paraná Basin (Faxinal Coalfield, Rio Bonito Formation) during the lower Permian (radiometric age 291 ± 1.3 Ma, late Sakmarian) under post-glacial conditions in the Late Paleozoic Ice Age. In addition to recurrent wildfires, an autochthonous/hypauthochthonous wildfire event was identified in the woody vegetation from a coal horizon containing compressed, large-sized logs (21,8 x 13.4 cm). Volcanic influence is recorded in a tonstein layer (sedimentary volcanic ash) interbedded in the coal, where abundant compressed glossopterid leaves are entombed. The coal analysis consisted of reflectance measurements in polished blocks under oil of macerals of the inertinite group to confirm the macroscopic charcoal identification and wildfire occurrence in the peatland. Additionally, the observation of the organic matter in the polished block under fluorescence showed that the microflora has not been affected by the wildfires, but altered fluorescence evidenced environmental dryness, verified in palynofacies slides as well. Under scannin electron microscopy, the charcoal showed homogenized cell walls, indicating burning temperatures higher than 325ºC, but not higher than 400ºC given the low reflectance values and the preservation of fragile plant tissue. The preservation of secondary phloem in organic association with *Agathoxylon* wood-type is a first paleobotanical record. Observation under transmitted light of the leaf cuticles extracted from the tonstein allowed for the detailed description of xeromorphic patterns, which have been attributed to adaptative responses to the frequent environmental disturbances affecting the peat forest, such as recurrent wildfires due to environmental dryness or regional volcanic activity. These factors, collectively or in an alternating way, ensured the monotypic dominance of *Glossopteris pubescens* nom. nov. in the plant community. The set of evidences indicated low temperature surface fires, virtually inexistent charcoal transport in the charcoalified log horizon and that the other wildfire events had little effect in the proximal community, occurring regularly in the surrounding areas of the peatland given the fragmentary macroscopic charcoal input. During the postglacial warming in the Permian, the Gondwanan peatlands were highly susceptible to wildfires from which the glossopterids benefited to maintain their dominance and abundance in these communities due to efficient adaptative plasticity to survive under extreme conditions in highly disturbed environments.

Keywords: macroscopic charcoal, paleowilfires, ash-fall, *Glossopteris* Flora; Gondwana, paleobotany

LISTA DE ILUSTRAÇÕES

CAPÍTULO 1

CAPÍTULO 2

CHARCOALFIED LOGS AS EVIDENCE OF HYPAUTOCHTHONOUS/ AUTOCHTHONOUS WILDFIRE EVENTS IN A PEAT-FORMING ENVIRONMENT FROM THE PERMIAN OF SOUTHERN PARANÁ BASIN (BRAZIL)*

CHARCOALFIED *AGATHOXYLON*-TYPE WOOD WITH PRESERVED SECONDARY PHLOEM FROM THE LOWER PERMIAN OF THE BRAZILIAN PARANA BASIN*

EPIDERMAL MORPHOLOGY AND ECOLOGICAL SIGNIFICANCE OF *GLOSSOPTERIS PUBESCENS* NOM. NOV. FROM THE BRAZILIAN PERMIAN (SAKMARIAN)

CAPÍTULO 3

*Numeração entre parêntesis refere-se à paginação do periódico.

LISTA DE TABELAS

CAPÍTULO 2

CHARCOALIFIED LOGS AS EVIDENCE OF HYPAUTOCHTHONOUS/ AUTOCHTHONOUS WILDFIRE EVENTS IN A PEAT-FORMING ENVIRONMENT FROM THE PERMIAN OF SOUTHERN PARANÁ BASIN (BRAZIL)*

EPIDERMAL MORPHOLOGY AND ECOLOGICAL SIGNIFICANCE OF *GLOSSOPTERIS PUBESCENS* NOM. NOV. FROM THE BRAZILIAN PERMIAN (SAKMARIAN)

---

*Numeração entre parêntesis refere-se à paginação do periódico.

SUMÁRIO

CAPÍTULO 1

---

1 INTRODUÇÃO

CAPÍTULO 2

CAPÍTULO 3

ANEXOS

TEXTO EXPLICATIVO SOBRE A ESTRUTURA DA TESE

Sobre a Estrutura desta Tese:

Esta tese de Doutorado está estruturada em torno de artigos publicados em periódicos. Conseqüentemente, sua organização compreende as seguintes partes principais:

a) Introdução sobre o tema e descrição do objeto da pesquisa de Doutorado, onde estão sumarizados os objetivos e a filosofia de pesquisa desenvolvidos e o estado da arte sobre o tema de pesquisa.

b) Artigos publicados em periódicos ou submetidos a periódicos com corpo editorial permanente e revisores independentes escritos pela autora durante o desenvolvimento de seu Doutorado.

c) Anexos, compreendendo: primeira página de artigos e capítulos publicados pela doutoranda em primeira autoria ou coautoria em periódicos e livros e resumos publicados em anais de eventos.

Este documento foi redigido em concordância com a Norma 103 - Submissão de teses e dissertações na forma de artigos do Programa de Pós-Graduação em Geociências/UFRGS.

Foram seguidas as normas ABNT para apresentação de referências e citações em documentos conforme compilação disponibilizada pela Biblioteca de Geociências/UFRGS atualizada em 2015.

CAPÍTULO 1

1 INTRODUÇÃO

1.1 AMBIENTES DE TURFEIRAS ATUAIS

As turfeiras têm sido utilizadas como indicadores de alterações climáticas globais por serem repositórios de dados climáticos pretéritos (JACKSON; CHARMAN, 2010), contribuindo para o sequestro global de carbono, funcionando como reservatórios de água e abrigando biodiversidades endêmicas. As altas taxas de acumulação de material orgânico autóctone ou hipoautóctone e sensibilidade hidroclimática guardam informações relacionadas à dinâmica da matéria orgânica, evolução das paisagens, mudanças climáticas e ciclos de poluição atmosférica locais, regionais e globais. (SILVA et al., 2009). Esses sistemas fornecem um registro de inúmeros indicadores (*proxies*) de origem biótica e abiótica dos quais é possível extrair informações para reconstruções ambientais (*e.g.* VAN HOOF et al., 2008; CHARMAN et al., 2009; COUWENBERG et al., 2011).

Ecossistemas de turfeiras acumulam espessas camadas de matéria orgânica porque a produtividade vegetal ultrapassa a decomposição. Atualmente a quantidade de carbono armazenada sob a forma de turfa excede aquela armazenada na vegetação, sendo similar em magnitude ao reservatório atmosférico de carbono (TURETSKY et al., 2015).

Por possuírem maior densidade de carbono em comparação a outros sistemas, as turfeiras são ambientes-chave para a compreensão dos processos de captura de carbono na Terra, atuando, ao mesmo tempo, como fonte de gases de efeito estufa (metano) (LLOYD et al., 1998; MACDONALD et al., 2006). Elas exercem, portanto, grande influência na composição dos gases atmosféricos, contribuindo significativamente para mudanças climáticas, em grande e em pequena escala (MACDONALD et al., 2006; MARTINI; CORTIZAS; CHESWORTH, 2006). As informações obtidas desses ambientes podem, portanto, ser aplicadas tanto no estudo de problemas de natureza climática e ecológica quanto da dinâmica global do carbono (CHARMAN, 2002).

A variada distribuição geográfica dos sistemas de turfeiras leva a complexos processos de acumulação de turfa nas distintas regiões climáticas e zonas bióticas globais. Não existe um ambiente típico de formação de turfa, e não existem padrões únicos para caracterizá-la (RICH, 2015).

Integrações de estudos em turfeiras atuais de diferentes latitudes permitiram identificar que, mais do que a intensidade, a continuidade de precipitação ao longo do ano é fator decisivo para a ocorrência de turfeiras em faixas tropicais (BUSTIN, 1997). Por outro lado, em regiões temperadas, a estação fria, que coincide com a seca, constitui fator que impede sazonalmente tanto o crescimento vegetal quanto a decomposição da matéria orgânica (LOTTES; ZIEGLER, 1994).

O papel das turfeiras de médias e altas latitudes do Hemisfério Norte no sequestro de carbono durante o Holoceno tem sido amplamente investigado e a contribuição dessas vastas zonas úmidas para o ciclo global do carbono ganha maior reconhecimento em um contexto de mudanças climáticas (*e.g.* VÄLIRANTA; KAAKINEN; KUHRY, 2003, YU; BEILMAN; JONES, 2009; CHAMBERS; DANIELL, 2010; GAŁKA et al., 2014). Análises em turfeiras do permafrost têm levado, por exemplo, à melhor compreensão do fluxo do metano em altas latitudes. As turfeiras da Sibéria ocidental são repositório de cerca de um terço do carbono sequestrado, o equivalente a cerca de metade do carbono atmosférico disponível (MACDONALD et al., 2006). Atualmente as turfeiras das faixas climáticas temperadas a frias correspondem a 70% dos 5 milhões de km^2 de turfeiras no mundo (FIG. 1), e ocorrem entre 40 e 70º norte e sul (JACKSON; CHARMAN, 2010).

As turfeiras tropicais ainda não foram suficientemente estudadas como as do hemisfério norte e boreais. A análise de turfeiras ombrofíticas na Amazônia permitiu caracterizar a sua importância local para o ciclo do carbono e seu potencial como paleoarquivos de clima e dinâmica vegetacional (LÄHTEENOJA; ROUCOUX, 2010; ROUCOUX et al., 2013; KELLY et al., 2014). Page et al. (2002), ao analisar as extensas turfeiras do sudeste da Ásia, demonstraram a severidade dos impactos na atmosfera global quando esses sistemas ricos em carbono são perturbados em decorrência de ação antrópica. Os incêndios nas turfeiras da Indonésia em 1997 liberaram na atmosfera uma quantidade equivalente a até 40% das emissões anuais por queima de combustíveis fósseis, a maior contribuição já registrada de dióxido de carbono aos níveis atmosféricos atuais.

Sob a concentração atual de oxigênio atmosférico, relativamente baixa em comparação ao período glacial do final do Paleozoico, a liberação do carbono sequestrado por queima de turfeiras decorrente de atividades antrópicas, tanto nos trópicos quanto nas regiões temperadas, foge ao padrão dos regimes naturais de incêndios (*e.g.* HIGUERA et al., 2008; GAŁKA et al., 2014).

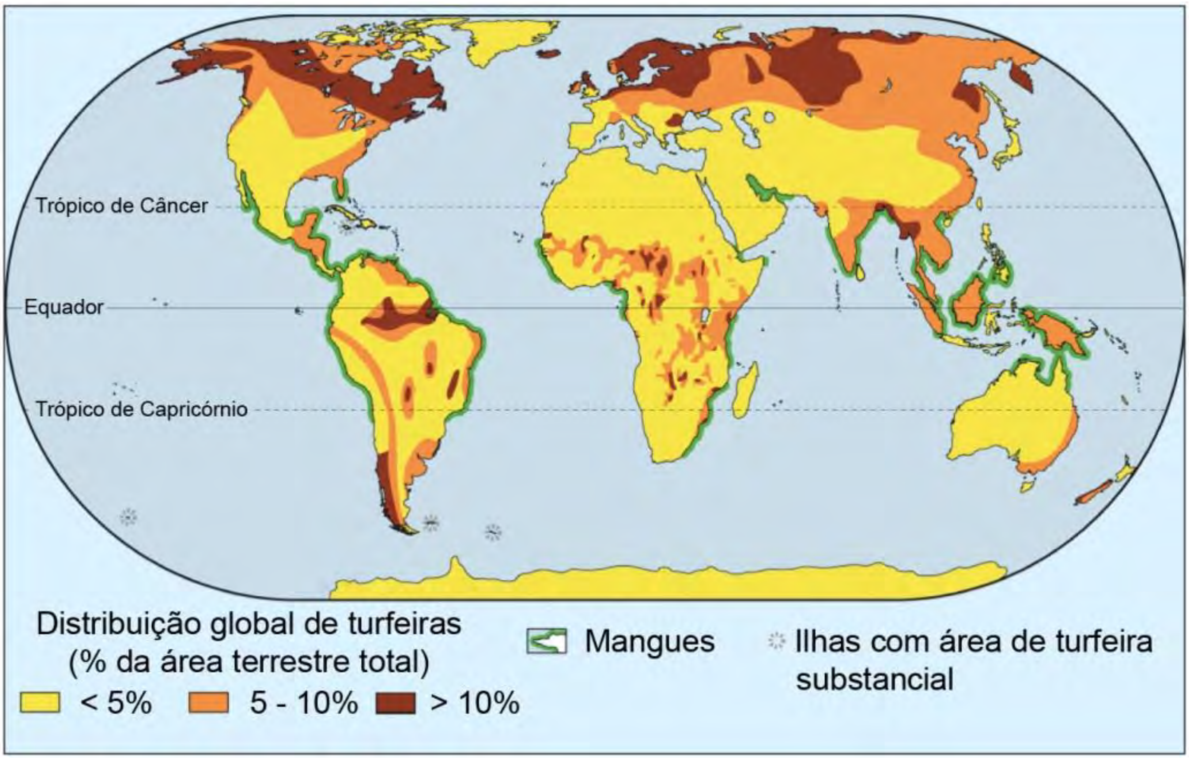


FIGURA 1 - Mapa esquemático das principais áreas de ocorrência atual de turfeiras e percentual de cobertura terrestre.
FONTE: JACKSON; CHARMAN, 2010, p. 3, FIG. 1.

A susceptibilidade a incêndios espontâneos aumenta com a elevação das temperaturas e dessecação ambiental, criando um mecanismo de retroalimentação no sistema climático, que é um processo global que se autoacelera (REIN, 2013). Drenagem, mudanças no uso da terra e consequentes secas são provavelmente as principais causas que levam às condições de alta inflamabilidade da turfa. Eventos de ignição possíveis podem ser de origem natural (descargas elétricas atmosféricas, autoaquecimento, erupções vulcânicas) ou antropogênica (ordenamento do território, ignição acidental, incêndios criminosos) (REIN, 2015).

Interpretações da natureza das turfeiras pretéritas a partir do estudo das camadas de carvão com base na observação de turfeiras atuais têm sido apresentadas por diferentes autores, todavia, a estrutura vegetacional, a composição e a distribuição dos biomas e dos continentes mudaram de maneiras incontáveis desde o Neodevoniano, quando surgiram no registro as primeiras turfeiras terrestres. Evidentemente, portanto, não há análogos modernos perfeitos aos ecossistemas formadores de carvão do passado geológico (MOORE, 1987, 1989).

Diferentemente da concentração geográfica atual de turfeiras, a maioria dos carvões do Neopaleozoico originou-se em faixa climática tropical a subtropical, com exceção dos carvões de Gondwana e Angara, que se originaram em regiões de clima temperado frio (BUSTIN, 1997). Análises integradas de cunho paleobotânico, palinológico, geoquímico e petrográfico têm sido desenvolvidas em jazidas de carvão originadas em turfeiras que se acumularam no Gondwana, especialmente durante o intervalo Carbonifero-Permiano em que vigorou a ―Idade do Gelo do Neopaleozoico" (MONTAÑEZ; POULSEN, 2013), dado que esses estudos permitem observar a evolução de ambientes úmidos em uma escala de tempo inacessível em turfeiras atuais e, consequentemente, fornecem subsídios preditivos relacionados a ciclos completos de congelamento e descongelamento de calotas polares (BUSTIN, 1997).

1.2 A IDADE DO GELO DO NEOPALEOZOICO

Durante o final do Neopaleozoico, a superfície terrestre uniu-se em uma única massa de terras, Pangeia, circundada pelo Oceano Pantalassa. Esse megacontinente foi subdividido em quatro regiões principais de acordo com critérios paleogeográficos, paleoclimáticos e paleoflorísticos (MEYEN, 1987; CHALONER; CREBER, 1988; ZIEGLER, 1990). Angara e Gondwana incluíam-se respectivamente nas latitudes temperadas norte e sul; microcontinentes tropicais orientais contornando o Mar de Tétis compreendiam a Cataísia, constituindo-se a Euramérica na mais expressiva massa de terras no domínio tropical (DIMICHELE, 2014).

A Idade do Gelo do Neopaleozoico envolveu um conjunto dinâmico de eventos físicos e bióticos no intervalo Neocarbonífero-Eopermiano (FIELDING; FRANK; ISBELL, 2008). O acúmulo de grandes volumes de gelo iniciou-se no final do Devoniano e continuou até o Eomissisipiano, seguindo-se um intervalo de seca e aquecimento em latitudes paratropicais e tropicais (BREZINSKI et al., 2008; ISAACSON et al., 2008). A glaciação reaparece no Mesomississipiano, gerando condições de umidade nas regiões equatoriais. As alterações na composição das comunidades de floras terrestres em baixas latitudes foram respostas a ciclos glaciais e interglaciais evidenciados em altas latitudes (MONTAÑEZ et al. 2007; FIELDING; FRANK; ISBELL, 2008; BISHOP et al. 2009; ISBELL et al. 2012; MONTAÑEZ; POULSEN 2013). Nos trópicos, as alterações no volume de gelo refletem-se em uma série de eventos globais de flutuações eustáticas que atingem diferentes magnitudes em ciclos glaciais e interglaciais (BIRGENHEIER et al., 2009; HORTON et al., 2012).

As camadas de carvão, que são sedimentos climaticamente sensitivos, refletem no Carbonífero da América do Norte e Europa os registros da alternância de recuos e avanços no nível do mar representando os eventos glaciais e interglaciais. O padrão de ocorrência das sequências sedimentares é composto por ciclos de camadas de carvão (sequências interglaciais) alternando-se com sequências de arenitos, que são indicativas de períodos secos, frios (glaciais) (DIMICHELE et al., 2009).

Diferentes autores defendem a hipótese de que, durante as fases glaciais, teria havido uma retração para refúgios das floras interglaciais, correspondentes em grande parte à vegetação das turfeiras. Na fase interglacial subsequente ocorreria nova expansão dessa vegetação. As floras glaciais, por sua vez, durante intervalo interglacial, ficariam restritas a possíveis nichos em terras altas (*e.g.* CLEAL; THOMAS, 2005; DIMICHELE; PFEFFERKORN; GASTALDO, 2001; DIMICHELE et al., 2009; GASTALDO; DIMICHELE; PFEFFERKORN, 1996). No final do Eopermiano (Asseliano-Sakmariano), as camadas de gelo retraíram-se dramaticamente, abrindo novos ambientes para que as plantas colonizassem as altas latitudes no hemisfério sul (GASTALDO; DIMICHELE; PFEFFERKORN, 1996).

As rochas sedimentares são chave para a precisão das reconstruções paloclimáticas. Por serem diretamente influenciadas pelo clima, são excelentes indicadores de suas variações (FLUTEAU et al., 2001). Os carvões indicam o desenvolvimento de antigas turfeiras e historicamente foram utilizados como indicadores de um clima permanentemente úmido, com uma forte dependência de subsidência e níveis freáticos regionalmente altos (FALCON-LANG; DIMICHELE, 2010). No entanto, incêndios recorrentes são registrados para esses sistemas, indicando frequentes ciclos de dessecação ambiental com rebaixamento temporário do lençol freático (GLASSPOOL; SCOTT, 2010).

São, portanto, diversas as evidências que apontam para uma Idade do Gelo neopaleozoica dinâmica, que consistia em uma série de glaciações descontínuas no espaço e no tempo de duração entre menos de 1 Ma até 8 Ma, expandindo-se a partir de diversos núcleos (FIG. 2) (FIELDING; FRANK; ISBELL, 2008; ISBELL et al., 2012; MONTAÑEZ; POULSEN, 2013).

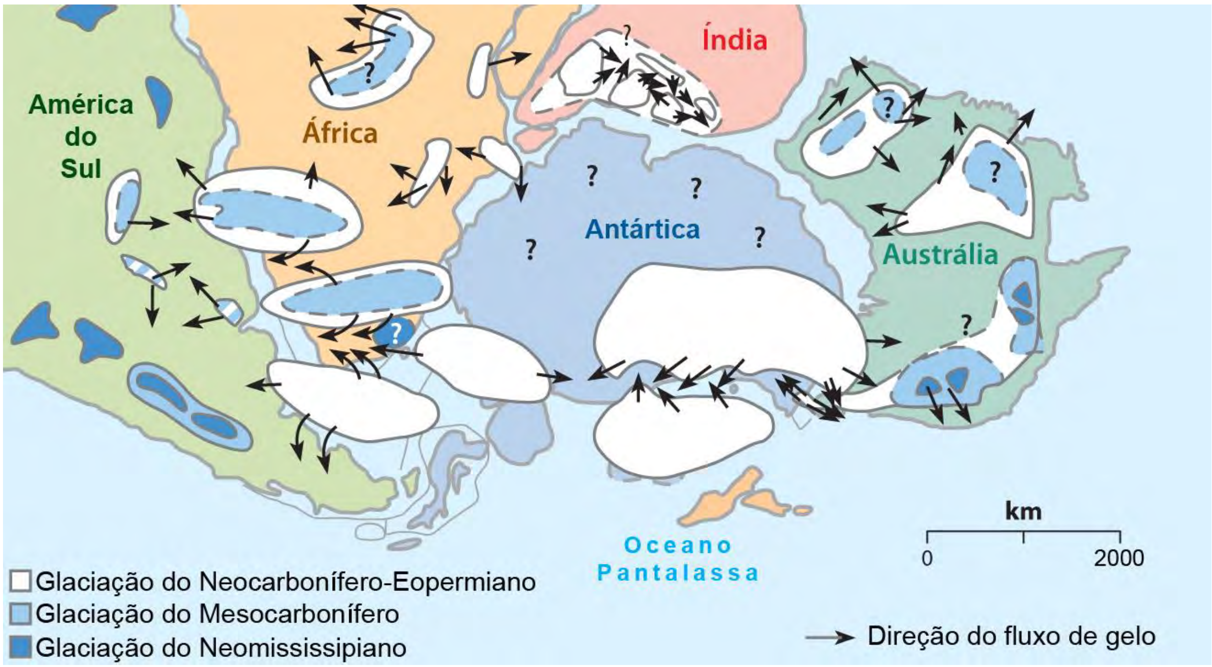


FIGURA 2 – Mapa paleogeográfico e paleoclimático do Gondwana durante a Idade do Gelo do Neopaleozoico. Linhas tracejadas e interrogações indicam as melhores estimativas (porém incertas) para as posições geográficas e extensões das capas de gelo.
FONTE: MONTAÑEZ; POULSEN, 2013, p. 634, FIG. 3.

Processos relacionados à subsidência, alteração nas taxas de sedimentação, paleotopografia, modificações paleoflorísticas, de ambientes deposicionais, de alterações do nível de base e transgressões marinhas, além das alterações expressivas nos níveis de gases atmosféricos, foram os principais fatores atuantes no desaparecimento das extensivas turfeiras que ocorreram nas faixas climáticas úmidas temperadas ao sul (Gondwana) e também ao norte (Angara) de Pangeia durante o Permiano (LANGFORD, 1991).

Para Fielding et al. (2010) é pouco provável que as glaciações neopaleozoicas fossem globalmente síncronas. Ao invés disso, o registro estratigráfico aponta para um mosaico de eventos assíncronos no espaço e no tempo. Isso fez com que a visão do Neopaleozoico evoluísse de um modelo estável em longo termo para um novo modelo de mudanças dinâmicas com respostas biológicas e climáticas a intensas oscilações glaciais-interglaciais de forma análoga à recente transição que marca o início do Holoceno (MONTAÑEZ; POULSEN, 2013).

1.3 INCÊNDIOS EM TURFEIRAS DO NEODEVONIANO

Eventos de incêndios que se intensificaram desde o Siluriano até o Eodevoniano detectados por Scott e Glasspool (2006) correlacionam-se com os elevados níveis de oxigênio paleoatmosférico estimados por Berner (2006) para esse intervalo. A ausência de registros significativos de carvão vegetal no Mesodevoniano durante o desenvolvimento das primeiras florestas caracterizou essa época como um hiato no registro do carvão vegetal (*charcoal gap*), o qual tem sido mais recentemente atribuído a baixos teores paleoatmosféricos de oxigênio do que à ausência de combustível (GLASSPOOL; SCOTT, 2010).

Todavia, analises petrográficas recentes em carvões devonianos euramericanos indicaram que, durante o Neopaleozoico, incêndios eram mais prevalentes do que no presente em ambiente de turfeira (GLASSPOOL et al., 2015). Adicionalmente, a abundância de carvão vegetal (*charcoal*/inertinita) indica um aumento dramático nos teores atmosféricos de oxigênio (pO_2) durante os últimos 10 a 15 milhões de anos do Devoniano, sendo estimados como superiores aos níveis atuais (GLASSPOOL et al., 2015).

A presença de carvão vegetal (inertinita) como elemento alóctone em folhelhos negros marinhos do Devoniano sugere a disseminação de sistemas de incêndios de superfície em vegetação dominada por pteridófitas e licófitas. Com base em resultados de refletância da inertinita, temperaturas moderadamente altas (550ºC) foram estimadas (RIMMER et al., 2015).

1.4 INCÊNDIOS EM TURFEIRAS TROPICAIS DO CARBONÍFERO EURAMERICANO

A ocorrência de incêndios em turfeiras do Carbonífero na Província Euramericana tem sido fartamente registrada em bacias da Europa (*e.g.* SCOTT, 1990; SCOTT; JONES, 1994; FALCON-LANG, 2000; UHL; KERP, 2003; UHL et al., 2004) e América do Norte (*e.g.* SANDER, 1987; SANDER; GEE, 1990; FALCON-LANG, 2000; DIMICHELE et al., 2004). As evidências fornecidas pela presença de carvão vegetal como indicador de incêndios têm sido usadas para inferências de caráter paleoecológico, paleoambiental e paleoclimático (*e.g.* BELCHER et al., 2010a; BOND; SCOTT, 2010; UHL et al., 2010; UHL; JASPER; SCHWEIGERT; 2012).

1.5 INCÊNDIOS EM TURFEIRAS DA CATAÍSIA

Não existem relatos de evidências de incêndios em turfeiras da Cataísia, todavia, Wang e Chen (2001) referiram abundante carvão vegetal ao final do Permiano após o desaparecimento dos sistemas deposicionais de turfeiras no norte da China e relacionaram os incêndios com o desaparecimento das florestas de licófitas que teriam ainda persistido na região até o final do período.

1.6 INCÊNDIOS EM TURFEIRAS DE ANGARA

Lenhos gimnospérmicos atribuídos a cordaiteanas sobressaem-se no registro sob a forma de carvão vegetal (HUDSPITH, 2012a). Apesar de diferenças taxonômicas na composição da vegetação – Flora de *Glossopteris* no sul e Flora de *Rufloria* no norte (*e.g.* DIMICHELE; PFEFFERKORN; GASTALDO, 2001) – a anatomia do carvão vegetal e os altos teores de inertinita nos carvões de Gondwana e Angara nesse período sugerem a ocorrência de tipos de incêndios similares (HUDSPITH, 2012b).

1.7 AS TURFEIRAS TEMPERADAS DO GONDWANA NO PERMIANO

Paralelamente à constituição de Pangeia, os últimos vestígios da Idade do Gelo do Neopaleozoico (335-260 Ma) são evidenciados no hemisfério sul durante o Eopermiano. O supercontinente de Gondwana estendia-se desde o equador até a região polar (FIG. 3) e sofreu influência de extremas oscilações climáticas (MONTAÑEZ; POULSEN, 2013).

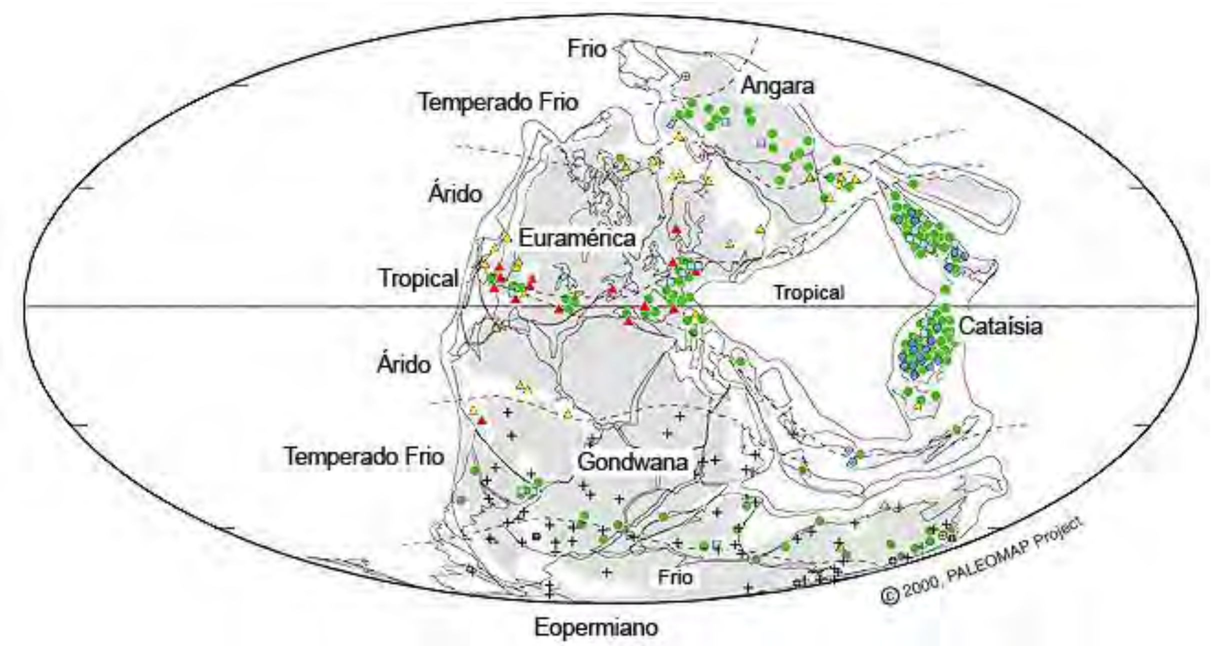


FIGURA 3 – Mapa paleoclimático e paleofitogeográfico do Eopermiano (280 Ma). Chave: Verde= carvão; azul= bauxita/laterita; vermelho= calcrete; amarelo= evaporito
FONTE: SCOTESE, 2000.

Indicadores litológicos, entre eles os carvões, foram utilizados para mapear a localização aproximada de quatro zonas climáticas caracterizadas no Gondwana como 1) tropical úmida, 2) subtropical quente e seca, 3) temperada e 4) polar, de forma análoga aos modernos gradientes latitudinais que ocorrem atualmente no Hemisfério Norte (ARCHANGELSKY, 1996; CÚNEO, 1996; LI; WU, 1996). No entanto, tem-se demonstrado que essas faixas climáticas não permaneceram estáveis e que não havia uma calota polar permanente e única durante a Idade do Gelo do Neopaleozoico (FIG. 2; MONTAÑEZ; POULSEN, 2013; DIMICHELE, 2014; GLASSPOOL et al., 2015).

No Gondwana como um todo no Eopermiano, a composição florística das turfeiras temperadas, onde as gimnospermas, principalmente as glossopterídeas, tornaram-se importantes componentes, é nitidamente distinta daquela da Euramérica no Pensilvaniano e da Cataísia no Eopermiano, que eram dominadas por licófitas arborescentes e pteridófitas. (GREB; DIMICHELE; GASTALDO, 2006). As turfeiras de climas temperados em Angara, embora também eminentemente gimnospérmicas, eram compostas principalmente por plantas cordaiteanas de tipo *Rufloria* (DIMICHELE; PFEFFERKORN; GASTALDO, 2001).

A composição das turfeiras gondwânicas, desenvolvidas em uma grande variedade de tipos de ambientes úmidos, também incluía esfenófitas dominantemente herbáceas, pteridófitas, licófitas herbáceas e semi-arborecentes e briófitas (GREB; DIMICHELE; GASTALDO, 2006) em diversos ambientes fluviais, deltaicos e de laguna-barreira.

1.7.1 Incêndios em turfeiras da Antártica

McLoughlin e Drinnan (1996) relataram a ocorrência comum de carvão vegetal em distintos horizontes de carvão do Permiano Superior na Antártica, indicando períodos de seca no ecossistema gerador de turfa. Tal constatação foi subsequentemente confirmada por presença de carvão vegetal nos estratos das Montanhas Transantárticas e Príncipe Charles (MCLOUGHLIN; DRINNAN, 1997; LINDSTRÖM; MCLOUGHLIN, 2007; SLATER; MCLOUGHLIN; HILTON, 2015).

Slater, McLoughlin e Hilton (2015) relatam que um ambiente marcadamente sazonal influenciou as turfeiras silicificadas da Antártica no Mesopermiano (sílex do Membro Toploje, jazida de carvão Bainmedart, Montanhas Príncipe Charles, Antártica oriental, Roadiano-Wordiano), evidenciado por distintas bandas de carvão vegetal em meio à turfa. Em algumas amostras, a quantidade de inertinita chega a 50%. A queima favoreceu a preservação de delicados órgãos de glossopterídeas e licófitas que aparecem bastante danificados quando não queimados, levando a inferir baixas temperaturas de queima, entre 240 e 370°C. Fragmentos de carvão vegetal tanto macro quanto microscópicos ocorrem em abundância, com fragmentos de lenho acima de 5 centímetros.

1.7.2 Incêndios em turfeiras da Austrália

Para o carvão Whybrow Inferior (Neopermiano da Nova Gales do Sul, Austrália), Glasspool (2000) identificou que o padrão comum a diversas jazidas australianas e gondwânicas (carvão brilhante na base seguido por carvão opaco e, após, aumento na matéria mineral) reflete a ocorrência de incêndios (carvão opaco) e consequente alteração da sedimentação e hidrologia no ambiente de deposição (entrada de matéria mineral), com implicações nas taxas de acumulação dos carvões permianos. Um evento principal de incêndio foi relacionado com uma mudança importante na vegetação, representada pelo desaparecimento de pólen, esporângios e sementes de afinidade glossopterídea no nível de inertinita. Seguindo-se ao evento de incêndio, esporos de afinidade pteridofítica passam a dominar, interpretados como colonização por vegetação pioneira, ocorrendo novamente, também, as sementes do nível inferior. Glasspool (2000) concluiu que os incêndios eram parte integral dos ecossistemas de turfeiras gondwânicos de latitudes médias a altas.

A devastação causada pelo fogo nas glossopterídeas, entretanto, sugeriu que, embora essas pteridospermas fossem tolerantes a tal tipo de perturbação e até mesmo tivessem se beneficiado competitivamente com incêndios sistêmicos, eventos de incêndios de maiores proporções tinham o potencial de causar um impacto negativo na sua prevalência na comunidade

A presença de camadas de carvão no topo do Permiano Superior australiano originada em turfeiras sob condições de clima temperado contrasta com os climas quentes, até áridos, vigentes em outros subcontinentes do Gondwana durante o Wuchiapingiano. Isso é explicado pela rotação do Gondwana sobre o Polo Sul, localizado perto da Austrália durante o Permiano, permitindo a manutenção de condições de clima temperado e desenvolvimento de turfeiras (ROSCHER; STORDAL; SVENSEN, 2011; EMBLETON, 1984; GLASSPOOL, 2000; JASPER et al., 2013).

A presença de carvão vegetal macroscópico em camadas de tufos vulcânicos intercalados em camadas de carvão indicou que atividades vulcânicas poderiam ter atuado como fonte de ignição de paleoincêndios na região leste da bacia de Sydney (GLASSPOOL, 2000).

1.7.3 Incêndios em turfeiras da Índia peninsular

Jasper et al. (2012) descreveram carvão vegetal macroscópico gimnospérmico de níveis ricos em matéria orgânica associados à Sequência VI da Formação Raniganj, Permiano Superior, Bacia do Vale do Damodar, Índia, indicando a ocorrência de paleoincêndios na área durante o Neopermiano (Lopingiano). Para a Formação Raniganj existem relatos de ocorrência de inertinita (de origem pirogênica) em níveis de carvão (MISHRA; CHANDRA; VERMA, 1990; NAVALE; SAXENA, 1989), demostrando que paleoincêndios foram eventos comuns durante a deposição dos carvões também na Índia no Neopermiano.

Cabe ressaltar que a dominância de inertinita (até 48%) em carvões caracterizados como fúsicos para o intervalo Karharbari (NAVALE; SAXENA, 1989), de acordo com os conceitos de Scott (2010), indica alta incidência de incêndios nas terras baixas associadas às turfeiras e deposição hipoautóctone desses fragmentos queimados nos locais de acumulação da turfa.

1.7.4 Incêndios em turfeiras da África do Sul

A alta concentração de macerais do grupo da inertinita em todas as amostras de carvão de diferentes localidades na África do Sul (Bacia Witbank) e Transvaal Oriental (Tanzânia) é relacionada por Glasspool (2003a, 2003b) a incêndios, de acordo com as hipóteses de Scott (2000, 2002) de que fusênio e carvão vegetal seriam equivalentes.

Amostras de carvão da Formação Vryheid (Eopermiano da Bacia do Karoo, África do Sul) contendo entre 48 e 77% de inertinita indicaram que incêndios sazonais desempenharam um papel importante naqueles sistemas de turfeiras. O acúmulo de carvão vegetal ocorreu tanto de forma autóctone quanto hipoautóctone/alóctone, refletindo diferentes condições de inundação e dessecação.

De maneira geral, o aumento de inertinita é seguido por um aumento de matéria mineral, refletindo condições de maior escoamento superficial. A vegetação era dominada por gimnospermas lenhosas e licófitas, sendo que estas eram mais abundantes e diversas onde o conteúdo de vitrinita era maior. Evidências de incêndios de dossel e de sub-superfície (queima da turfa) foram relatadas. A ausência de carvão vegetal de afinidade com licófitas, apesar da abundância de seus megásporos, indicou que essas plantas eram menos suscetíveis à queima e, se queimavam, tinham um baixo potencial de preservação. Mais provavelmente as licófitas ocupariam um nicho permanentemente saturado, escapando, assim, ao fogo (GLASSPOOL, 2003a, 2003b).

A presença de carvão vegetal em sedimentos Permianos associados a níveis de carvão em diferentes localidades do Gondwana confirma, portanto, que esse tipo de evento foi amplamente disseminado no continente nos sistemas de turfeiras.

1.8 CARVÕES DA BACIA DO PARANÁ (BRASIL)

Com a tendência de deglaciação que se estabelece a partir do Eopermiano na porção sul da América do Sul, os diamictitos glaciais não são mais registrados e camadas de carvão ocorrem na porção brasileira da Bacia do Paraná durante o Cisuraliano-Eoguadalupiano, em período climático pós-glacial definido com base em indicadores litológicos, bioestratigráficos e cronoestratigraficos (LIMARINO et al., 2014). A análise integrada dos dados disponíveis concorda com os resultados de Langford (1991), que indicaram que os maiores fatores que controlaram a acumulação, distribuição e preservação das turfeiras permianas gondwânicas (incluindo-se aí as jazidas brasileiras) foram o paleoclima e a tectônica.

Camadas contínuas e exploráveis de carvão de até 2,5 metros de espessura concentram-se na margem direita da Bacia do Paraná e são incluídas em uma sucessão de sedimentos de origem deltaica e marinha (HOLZ et al., 2010) na faixa climática temperada em latitude aproximada de 50° (ZIEGLER et al., 2003) durante período climático pós-glacial (LIMARINO et al., 2014). O conjunto das características faciológicas do pacote sedimentar aponta, segundo Holz (2003), para um sistema estuarino influenciado por ação de ondas que evoluiu para um sistema deposicional laguna-barreira, onde as turfeiras se formaram protegidas das variações eustáticas pelas ilhas de barreira.

As mais significativas jazidas de carvão da Formação Rio Bonito ocorrem no Rio Grande do Sul – jazidas de Candiota, Leão-Butiá e Faxinal (exaurida), Santa Catarina – bacia carbonífera de Santa Catarina e Paraná – região de Figueira – e se depositaram no intervalo pós-glacial do Sakmariano-Artinskiano (HOLZ et al., 2010).

1.8.1 Carvões do Rio Grande do Sul

As maiores jazidas de carvão da porção meridional da Bacia do Paraná são Candiota (a mais extensa de toda a bacia), Faxinal e Leão-Butiá (FIG. 4). As distintas características composicionais da flora identificadas entre essas três jazidas representam condições paleoambientais locais sem conotação estratigráfica significativa (SIMAS et al., 2012). Essas inferências concordam com a carta cronoestratigráfica de Holz et al. (2010), que vincula o carvão no Rio Grande do Sul a uma única sequência estratigráfica de idade sakmariana, com idade média de 291 ± 1,3 Ma obtida com base em datação de zircões em tonsteins das três jazidas (SIMAS et al., 2012).

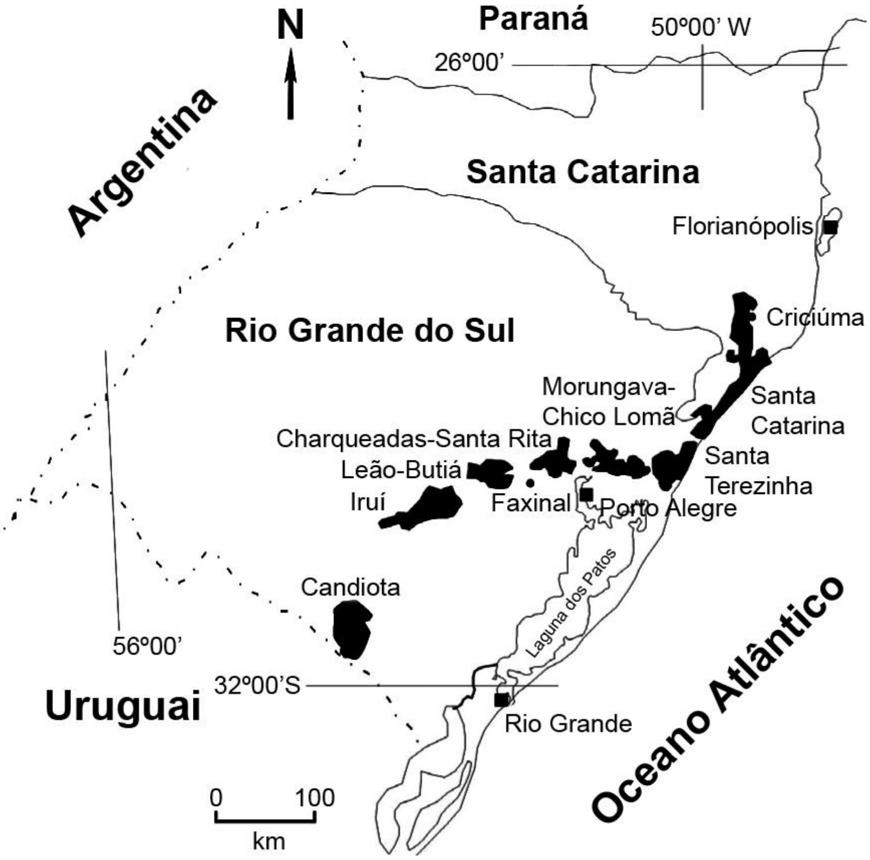


FIGURA 4 – Mapa dos estados Rio Grande do Sul e Santa Catarina e designação das jazidas de carvão do extremo sul brasileiro.
FONTE: KALKREUTH et al., 2013, p. 486, FIG. 1.

1.8.1.1 Carvões de Faxinal

A jazida de Faxinal, localizada a aproximadamente 100 km a oeste de Porto Alegre (RS), foi explorada no período de 1984 a 2009 como uma mina a céu aberto. A jazida inclui 5 camadas de carvão nomeadas desde a base até o topo como I, IM, M, MS, S. Uma camada de tonstein ocorre intercalada à camada superior S com idade média de 291 ± 1.3 Ma (Sakmariano de acordo com COHEN et al., 2013; atualizado em 2015) e é testemunho de deposição de cinza vulcânica sobre a turfeira (SIMAS et al., 2013), um evento geologicamente instantâneo (PROTHERO, 1990; DIMICHELE; FALCON-LANG, 2011). Essa camada, com espessura média de 10 cm, contém uma associação bem preservada de fitofósseis da Flora de *Glossopteris* (Guerra-Sommer, 1988).

A macroflora, preservada como compressões carbonificadas, é predominantemete gimnospérmica (GUERRA-SOMMER, 1992), e as folhas de glossopterídeas correspondem a 78% da associação (BOARDMAN et al., 2012). Morfograficamente, foram reconhecidos os táxons *Sphenopteris* cf. *S. ischanovensis* Zalesky 1934, *Glossopteris communis* Feistmantel 1876, *G. indica* Schimper 1869, *G. leptoneura* Bunbury 1861, *G. occidentalis* White emend. Tybusch and Iannuzzi, 2010, *Glossopteris* spp., *Rufloria gondwanensis* Guerra-Sommer, 1989, *Cordaites* sp., *Plumsteadia semnes* Rigby 1963 e *Cordaicarpus* sp. Com base em análise cuticular, foram identificados os táxons *Glossopteris brasiliensis*, *G. papillosa* e *G. similis-intermittens* Guerra-Sommer (1992). A cordaiteana *R. gondwanensis* e a pteridófita (?) *Sphenopteris* cf. *ischanovensis* são elementos sub-dominantes (GUERRA-SOMMER, 1988).

Frequências estomáticas em cutículas de glossopterídeas procedentes do tonstein de Faxinal e da região de Figueira (PR) calculadas por Degani-Schmidt, Guerra-Sommer e Bernardes-de-Oliveira (2011) indicaram maior teor de CO_2 paleoatmosférico para o clímax do intervalo formador de carvão na jazida de Faxinal, que possivelmente poderia ser atribuído à atividade vulcânica regional representada pela presença do tonstein.

A palinoflora do carvão de Faxinal é distinta da composição palinológica de outros carvões brasileiros de domínio de vegetação pteridofítica em relação a gimnospérmica. O predomínio de grãos de pólen bissacados e estriados, (*Alisporites*, *Limitisporites*, *Scheuringipollenites*, *Vesicaspora* e *Protohaploxypinus)* em Faxinal reflete a presença de uma vegetação formadora das turfeiras constituída principalmente por glossopterídeas, cordaitaleanas e coníferas (FIG. 5). Esporos triletes derivados de licófitas, esfenófitas e pteridófitas (*sensu* TAYLOR; TAYLOR; KRINGS, 2009), abundantes na maioria das palinofloras dos carvões sul-brasileiros, como *Lundbladispora*, *Punctatisporites*, *Granulatisporites*, *Leiotriletes*, *Calamospora*, *Deltoidospora*, *Cristatisporites* e *Vallatisporites* ocorrem em baixa proporção (CAZZULO-KLEPZIG et al., 2007).

O conjunto de informações tanto de caráter biótico quanto abiótico da jazida de Faxinal remete a uma comunidade vegetal de tipo floresta turfosa em um cenário que se distingue dos demais descritos para as turfeiras brasileiras do Eopermiano (CAZZULO-KLEPZIG et al., 2007).

Figura 5 - Reconstrução da comunidade vegetal geradora do depósito de carvão da Mina de Faxinal com base em palinologia e paleobotânica:
1. Elementos algálicos (associação hidrófila)
2. Plantas herbáceas e arbustivas (licófitas, pteridófitas e esfenófitas (associação higrófila)
3. Licófitas arborescentes (associação higro-mesófila)
4. Cordaiteanas e glossopterídeas (associação higro-mesófila)
5. Coníferas (associação xerófila)

FONTE: CAZZULO-KLEPZIG et al., 2007, p. 125, FIG. 6.

1.8.2 Incêndios em turfeiras gondwânicas brasileiras

A presença de carvão vegetal macroscópico em sedimentos clásticos associados a camadas de carvão tem sido registrada na grande maioria das jazidas, desde a porção norte, na região de Figueira (PR) até a porção sul da Bacia do Paraná (JASPER et al. 2008, 2011a, 2011b, 2011c) durante o intervalo Sakmariano-Artinskiano.

Os padrões anatômicos preservados nos fragmentos de carvão vegetal, identificados por observação em microscópio eletrônico de varredura, revelaram a dominância de xilema secundário relacionado ao tipo *Agathoxylon* Hartig, o qual é comum em glossopterideas, não sendo, porém, exclusivo desse grupo vegetal no Permiano. Os dados indicaram, portanto, que a vegetação queimada nas áreas de geração de turfa corresponde a gimnospermas arborescentes. Glasspool (2003b), ao registrar paleoincêndios em áreas de turfeira na Bacia do Karoo (Formação Vryheid), identificou situação similar e considerou a possibilidade de tendenciamento tafonômico, dado que esporos de licófitas são identificados como elementos importantes na composição palinológica, enquanto que a evidência fornecida pela presença de grãos de pólen gimnospérmicos é mais modesta. Possibilidades que justifiquem essas evidências de queima seletiva seriam a baixa susceptibilidade das licófitas ao fogo ou, então, baixo potencial de preservação, dada a estrutura delicada de seus tecidos. A preservação de megásporos associada a fragmentos queimados de gimnospermas poderia indicar que as licófitas não ocorrem como carvão vegetal por ocuparem ambientes permanentemente saturados, enquanto que as gimnospermas ocupavam nichos suscetíveis a seca cíclica ou sazonal onde incêndios ocorreriam mais facilmente (GLASSPOOL, 2003b).

Na Bacia do Paraná, evidências de incêndios em turfeiras que envolveram a comunidade de licófitas arborescentes restringem-se a caules horizontalizados e comprimidos de *Brasilodendro*n (Carruthers) Chaloner, Leistikow et Hill que ocorrem no teto da camada de carvão Bonito, na mina subterrânea Bonito (jazida carbonífera de Santa Catarina) onde se observou queima parcial e superficial de tecido parenquimático das almofadas foliares na totalidade dos fragmentos analisados. Essa evidência sugeriu a ocorrência de incêndios em densas associações de licófitas subarborescentes, pouco intensos, durante estágios finais da deposição de turfa, em fase de exaustão da turfeira, provavelmente por seca ambiental. Fragmentos de carvão vegetal macroscópico de gimnospermas ocorrem também na base da mesma camada, detectados pela análise palinológica que caracterizou a dominância de elementos gimnospérmicos na composição da biomassa da turfeira (MENDONÇA FILHO et al., 2013).

A presença de carvão vegetal macroscópico relacionado a tecido condutor de licófitas subarborescentes é registrada também no afloramento Quitéria (RS), em uma sucessão de níveis de conglomerado associados a centimétricas camadas de carvão e a um paleossolo onde se preservaram as bases de caules e radicelas *de Brasilodendron pedroanum* (Carruthers) Chaloner, Leistikow et Hill em posição de crescimento (JASPER et al, 2008).

Elevado conteúdo de inertinita detectado em análises petrográficas de diversas camadas de carvões da Bacia do Paraná (KALKREUTH et al., 2006; SILVA et al., 2008; COSTA et al.; 2014) também foi considerado por Jasper et al. (2013) como evidência de paleoincêndios na área de deposição da turfa e em terras baixas circundantes. Para o tonstein intercalado à camada S da mina de Faxinal, Jasper et al. (2011a) observaram que a presença de inertinita no carvão acima e abaixo do tonstein poderia indicar que os incêndios não estariam unicamente relacionados ao evento gerador da cinza vulcânica.

As evidências fornecidas pela presença de carvão vegetal macro e microscópico em ambientes de geração de turfa na Bacia do Paraná indicam que incêndios eram eventos sistêmicos e comuns nesses ambientes ao final de período climático glacial de longa duração em intervalo pós-glacial. Tais resultados sugeriram a ocorrência de incêndios nas terras baixas muito próximas à área de deposição da turfa.

Incêndios seriam potencializados pela ocorrência de perturbações ambientais que se traduziam em fases de seca periódica em regiões de terras baixas costeiras, sob condições climáticas transicionais entre climas úmidos e sazonalmente secos. A instalação e intensificação desse regime climático culminaria com o desaparecimento das extensivas turfeiras gondwânicas e não gondwânicas de latitudes temperadas em Pangeia, com condições ambientais muito secas no final do Permiano.

Considerando a importância dos dados indicadores de incêndios em turfeiras que afetaram todo o Gondwana (JASPER et al., 2013), é possível correlacionar a ocorrência de incêndios a crises recorrentes de aquecimento global durante o declínio do período glacial permiano conforme detectado por Retallack (2013) (FIG. 6). Muito embora os eventos glaciais-interglaciais neopaleozoicos tenham sido provavelmente assíncronos (FIELDING; FRANK.; ISBELL, 2008), Retallack (2013) considerou que picos paleoatmosféricos de dióxido de carbono em escala global, estabelecidos através de múltiplos indicadores, teriam afetado o clima em todo o planeta (FIG. X). Um importante evento de aquecimento detectado durante o Sakmariano no Gondwana (GASTALDO; DIMICHELE; PFEFFERKORN, 1996; MONTAÑEZ et al. 2007), indicado também por Retallack (2013) (FIG. 6), marca uma grande mudança florística, refletida pelo domínio das glossopterídeas (IANNUZZI, 2010).

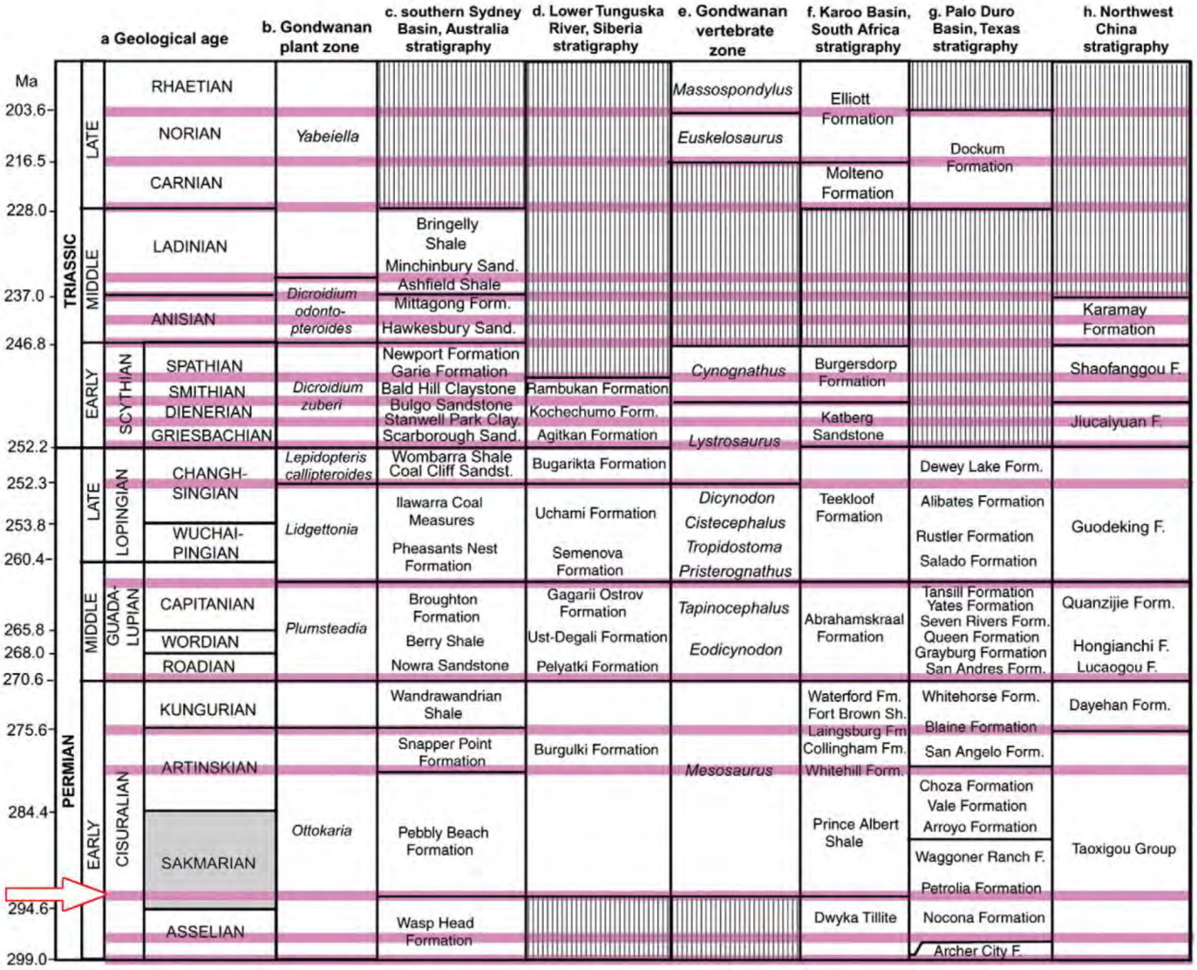


FIGURA 6 – Correlações globais de crises de efeito estufa (*greenhouse*) durante o Permiano e Triássico. Destaque feito para o Sakmariano (seta). Idades baseadas em Gradstein et al. (2004).

FONTE: RETALLACK, 2013, p. 100, FIG. 9.

1.9 INCÊNDIOS E GERAÇÃO DE CARVÃO VEGETAL

O fogo é um dos elementos de perturbação inerentes às comunidades vegetais, com papel na renovação e evolução de indivíduos, espécies e populações (RAUP, 1981). Enquanto perturbação ecológica, o fogo envolve fatores físicos e biológicos. A disponibilidade de material combustível depende da produtividade biológica de uma comunidade vegetal. As variáveis que influenciam a ocorrência de incêndios na vegetação abrangem o acúmulo de combustível na forma de material vegetal produzido por fixação fotossintética de carbono, clima favorável à dessecação ao menos sazonal para que haja ignição do material, composição atmosférica propícia à combustão (abundância de oxigênio) e mecanismo de ignição (COPE; CHALONER, 1985).

Entretanto, observou-se uma correlação entre alta frequência de carvão vegetal no registro geológico em ambientes permanentemente alagados (turfeiras) e picos de teores estimados de oxigênio atmosférico nos períodos Permo-Cabonífero e Cretáceo (SCOTT, 2000, 2002; SCOTT; GLASSPOOL 2006, 2007; SCOTT et al. 2000; BELCHER et al., 2010b; DIESSEL, 2010; GLASSPOOL; SCOTT, 2010; BELCHER; COLLINSON; SCOTT, 2013; GLASSPOOL et al., 2015). Em comparação com os níveis atuais de oxigênio na atmosfera (21% pO_2), teores de 25-30% aumentariam a combustibilidade de material vegetal mesmo úmido (SCOTT et al., 2014).

Com base em dados experimentais, Scott e Glasspool (2006) estabeleceram limites que definem a ―janela de incêndios” (FIG. 7), confirmando as estimativas feitas anteriormente por Jones e Chaloner (1991). Sob pO_2 abaixo de 13%, geralmente não há ignição e propagação de incêndios, mesmo que o combustível esteja seco. Entre 13% e 16%, incêndios seriam raros, ocorrendo somente com combustível muito seco. Entre 18% e 23% a ocorrência de incêndios é semelhante ao que ocorre atualmente sob 21% pO_2, facilitada por estações secas. Acima de 25%, incêndios tornam-se amplamente disseminados, principalmente em regiões de clima mais úmido devido à prevalência de descargas elétricas atmosféricas. Acima de 30% pO_2, a atividade de incêndios ocorreria globalmente e, a partir de 35%, não seria possível extinguir os incêndios (SCOTT; GLASSPOOL, 2006; BELCHER; COLLINSON; SCOTT, 2013). Watson e Lovelock (2013) demonstraram que, sob 25% pO_2, ocorre queima de matéria vegetal contendo até

72% de umidade e, sob 30% pO_2, até mesmo material coberto por água pode queimar. Isso significa que em períodos de pO_2 muito alta, a dessecação ambiental é praticamente irrelevante para a ocorrência de incêndios (HE et al., 2015).

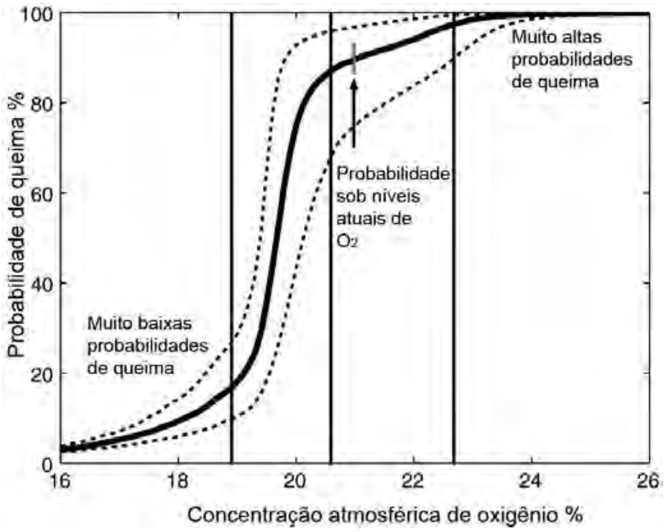


FIGURA 7 – A “janela de incêndios”. Probabilidades de queima estimadas em função da concentração atmosférica de oxigênio.
FONTE: BELCHER; COLLINSON; SCOTT, 2013, p. 232, FIG. 12.3.

Entre as inúmeras variáveis que influenciam o início e propagação do fogo, três são essenciais, denominadas como “triângulo do fogo” (FIG. 8): 1) energia suficiente para ignição e manutenção do calor, 2) combustível em quantidade suficiente para propagação do fogo e 3) pronta disponibilidade de oxigênio (SCOTT et al., 2014).

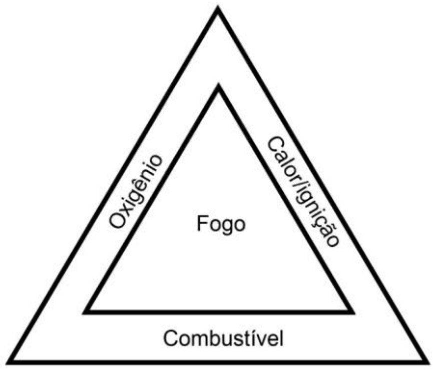


FIGURA 8 – O “triângulo do fogo”: elementos necessários para ignição e manutenção do fogo.
FONTE: BELCHER; COLLINSON; SCOTT, 2013, 2013, p. 232, FIG. 12.2.

Cope e Chaloner (1985) relacionaram as seguintes cinco principais fontes naturais de ignição de incêndios: descargas elétricas atmosféricas (raios), atividades vulcânicas, faíscas por atrito de deslizamento de rochas, combustão espontânea e impactos de meteoritos. A alta frequência de raios era o principal fator que controlava a ocorrência de incêndios no passado geológico, tendo sido suplantada pela ação antrópica no Holoceno (SCOTT, 2000).

Os tipos de incêndios podem ser de superfície, de dossel e de sub-superfície (FIG. 9). Frequentemente os incêndios naturais iniciam-se pela superfície, onde há grande quantidade de material depositado (serapilheira). De maneira geral, a temperatura desse tipo de incêndio é de até 400ºC. Se o nível do lençol freático estiver muito baixo, o fogo pode atingir a sub-superfície que, no caso de turfeiras, é a turfa propriamente dita. Estando a turfa suficientemente seca, ela queimará muito lentamente em um incêndio sem chamas e com pouca fumaça, pois a disponibilidade de oxigênio ali é baixa. O fogo de sub-superfície também pode se propagar para a superfície, gerando chamas e aumento de temperatura. Se houver suficiente acúmulo de matéria combustível em um ambiente de floresta, o fogo pode alcançar os caules e a copa das árvores, propagando-se como incêndio de dossel. A temperatura do fogo de dossel pode atingir 800-900ºC e, se houver vento alimentando o fogo com oxigênio, até 1200ºC (SCOTT et al., 2014).

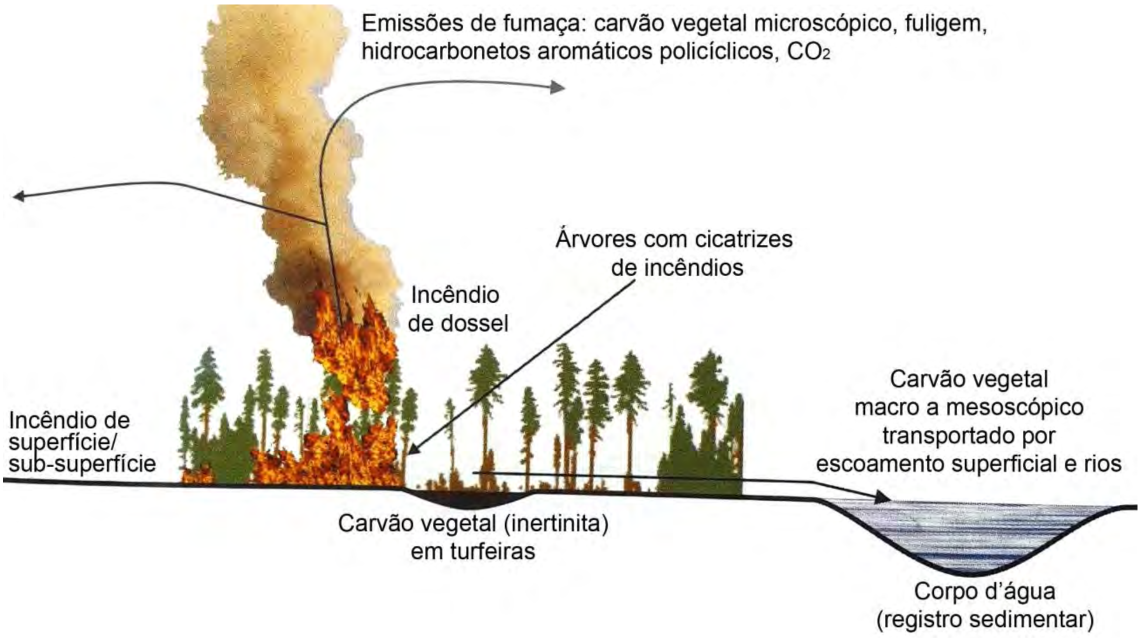


FIGURA 9 – Tipos de incêndio e transporte de carvão vegetal.
FONTE: SCOTT et al., 2014, p. 59, FIG. 2.13.

O carvão vegetal é gerado por meio de pirólise (aquecimento na ausência de ar) na escassez de oxigênio, não sendo, portanto, um produto de oxidação (SCOTT; GLASSPOOL, 2007). Esse processo consiste em combustão incompleta de material vegetal cujos compostos são volatilizados, remanescendo um resíduo de alto conteúdo de carbono, tornando o material vegetal menos biodegradável e promovendo sua preservação durante a diagênese (COPE; CHALONER, 1985). O carvão vegetal, por ser inerte, caracteristicamente apresenta boa preservabilidade no registro geológico e a preservação da anatomia vegetal permite identificação taxonômica do material (SCOTT, 2010).

Scott (2010) definiu três tipos de carvão vegetal com base nas dimensões dos fragmentos. São eles:

1) carvão vegetal macroscópico - maiores do que 1 mm
2) carvão vegetal mesoscópico - 180 µm até 1 mm
3) carvão vegetal microscópico - menores do que 180 µm

A maior parte de carvão vegetal macroscópico é produzida por incêndios de superfície. Geralmente, partículas menores de carvão vegetal são resultado de incêndios que atingem maiores temperaturas (incêndios de dossel) ou de material queimado alóctone.

A identificação de carvão vegetal deve atender os seguintes requisitos (SCOTT, 2010): sujar as mãos ao toque, coloração preta, brilho acetinado, textura quebradiça ou de pó, fraturamento de material lenhoso em cubos (macroscópico), farpas/fibras alongadas ou pulverizado (microscópico), apresentar anatomia preservada (observação sob lupa de mão ou microscópio estereoscópico) e homogeneização da lamela média com as paredes celulares (sob microscopia eletrônica de varredura) (FIG. 10).

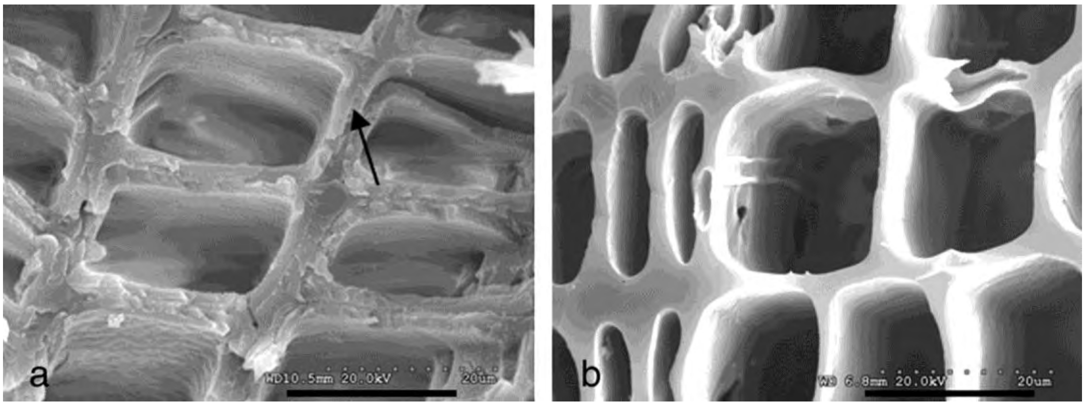


Figura 10 – Micrografias de lenho de *Sequoia* queimado em experimento controlado.
a) Lamela média ainda presente entre as células (seta) após queima a 300ºC por 1 hora
b) Paredes celulares e lamela média homogeneizadas após queima a 500ºC por 1 hora
FONTE: SCOTT, 2010, p.18, FIG. 8.

Através da observação de incêndios naturais e de experimentos, verificou-se que grande parte do carvão vegetal microscópico desloca-se por ação do vento, mas o principal agente de transporte é a água. Chuvas podem transportar o material junto com sedimento por escoamento superficial, que poderá chegar a sistemas fluviais e sofrer transporte também por esse meio e, por apresentar flutuabilidade, pode percorrer grandes distâncias e ser depositado em sedimentos marinhos (FIG. 9). Dessa forma, o achado de fragmentos macro e mesoscópicos não significa necessariamente autoctonia ou hipoautoctonia do material no local de deposição (SCOTT, 2010).

Experimentos de combustão inicialmente conduzidos pela indústria de carvão vegetal (*e.g*. MCGINNES; KANDEEL; SZOPA, 1971) permitiram estabelecer que a homogeneização das paredes celulares em lenhos ocorre sob temperaturas de queima acima de 300-325ºC. Observou-se também que o carvão vegetal gerado sob temperaturas mais altas resultou mais frágil e quebradiço, consequentemente com menor resistência a processos de transporte e soterramento. Em experimentos subsequentes, constatou-se que maiores temperaturas de queima estavam relacionadas a maiores índices de refletância do material queimado (SCOTT, 2010).

Portanto, a observação de características dos fragmentos de carvão vegetal, tais como tamanho, formato, integridade anatômica, revela informações a respeito da temperatura de queima, intensidade de dessecação ambiental, tipo de incêndio, história de transporte, composição e afinidade taxonômica de espécies e comunidades.

Troncos caídos parcialmente queimados, por exemplo, são encontrados com frequência em locais onde ocorrem incêndios naturais. De maneira geral, eles ocorrem parcialmente soterrados no solo, apresentando a superfície superior queimada e a inferior, não queimada. Em caules ou ramos queimados em posição de crescimento, todo o perímetro externo apresenta-se queimado, enquanto que o centro permanece não queimado. A proporção de espécimes com todo o perímetro queimado indica a proporção de indivíduos queimados em posição de crescimento na associação, e pode oferecer informações a respeito da comunidade vegetal e ecossistema onde ocorreu o incêndio. Jones, Scott e Mattey (1993) designaram como ―fósseis de fusênio transicional" tal configuração de lenhos parcialmente queimados, em que os processos de queima se restringiram à superfície externa (microscopicamente observável como fusinita/semifusinita) com porções internas do xilema e medula carbonificados (vitrinita, não queimada) (FIG. 11).

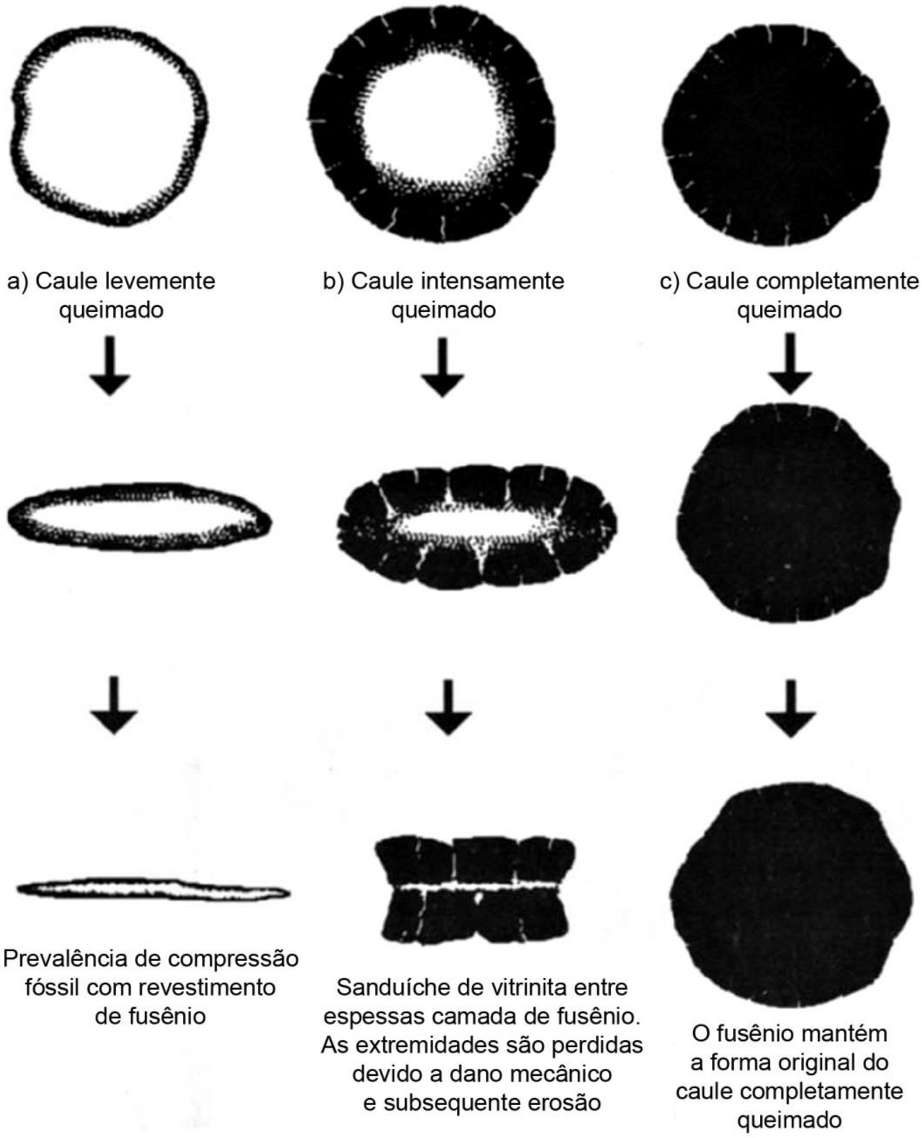


FIGURA 11 – Diagrama esquemático demonstrando diferentes processos tafonômicos em caules queimados. As imagens da linha superior representam caules anteriormente ao soterramento e, as das linhas inferiores, os processos de compressão e carbonificação subsequentes.
Fonte: JONES, SCOTT; MATTEY, 1993, Fig. 4, p. 48.

1.10 CARVÃO VEGETAL COMO SINÔNIMO DE INERTINITA

Stopes (1919) descreveu o fusênio como um dos elementos constituintes do carvão. Esse elemento macroscópico foi definido como porções de material preto, fibroso e opaco, apresentando estrutura celular de madeira, com lumens celulares geralmente vazios. Bastante frágil e inerte, esse macrolitotipo está presente em rochas de diversas litologias (SCOTT, 1989).

Em contrapartida à composição parcial do carvão por minerais, Stopes (1935) estabeleceu o termo ―maceral” para designar sua porção orgânica, que, em última instância, consiste em fragmentos macerados de vegetação acumulados sob água. Esse conceito, ao mesmo tempo em que diferenciou os componentes não minerais dos minerais do carvão, prestou-se também a descrever e classificar as diversas unidades orgânicas que compõem o carvão como um todo.

Subsequentes análises de blocos polidos sob microscopia de luz refletida revelaram que o fusênio é composto predominantemente por dois macerais, fusinita e semifusinita, incluídos no grupo de macerais inertinita, com valores geralmente altos de refletância quando comparados aos grupos da vitrinita e liptinita. A longa controvérsia que cerca a determinação da origem do fusênio por incêndios ou alterações bioquímicas foi sumarizada por Scott (1989, 2002) Guo e Bustin (1998) e Scott e Glasspool (2007).

A homologia das características físicas e químicas entre fusênio fóssil e carvão vegetal atual levou ao reconhecimento de que ambos são equivalentes. No entanto, a aceitação dessa afinidade tem ocorrido gradualmente (SCOTT; GLASSPOOL, 2007). A presença de grandes quantidades de inertinita em carvões do Neopaleozoico já foi atribuída a diferentes fatores, tais como exposição subaérea, deposição em clima frio e atividade fúngica (GLASSPOOL, 2003a).

Atualmente, é amplamente aceito que a toda a inertinita representa carvão vegetal originado por paleoincêndios (SCOTT; GLASSPOOL, 2007; DIESSEL, 2010; GLASSPOOL; SCOTT, 2010; SCOTT, 2010; HUDSPITH, 2012a, 2012b; GLASSPOOL et al., 2015), embora para alguns autores, como Hower et al. (2011, 2013) e O'Keefe et al. (2013), interações bióticas (atividade bacteriana, fúngica ou de invertebrados) ou abióticas (exposição aeróbica ou alterações químicas) possam ter sido relevantes para a formação de macerais no grupo da inertinita, particularmente da macrinita.

A quantidade de inertinita no carvão pode ser utilizada para interpretar a história de paleoincêndios em escala local. Horizontes de fragmentos macroscópicos de fusinita e semifusinita provavelmente representam incêndios de superfície localmente dentro do ambiente gerador da turfa, com história de curto transporte (hipoautóctone/autóctone), enquanto que carvão vegetal microscópico disperso geralmente representa material alóctone de incêndios regionais transportado pelo ar (HUDSPITH et al., 2012b).

Segundo McParland et al. (2009), existe uma correlação positiva entre temperatura de formação do carvão vegetal e valor de refletância da parede celular (inertinita) que permite estimar a temperatura de queima (FIG. 12). Essa correlação foi demonstrada experimentalmente por Guo e Bustin (1998) e Scott e Glasspool (2007). A determinação da temperatura de queima, em conjunto com as demais características do carvão vegetal, possibilita inferir informações relacionadas ao tipo predominante de queima e demais informações ecológicas associadas, como grau de dessecação ambiental e órgãos vegetais preferencialmente queimados.

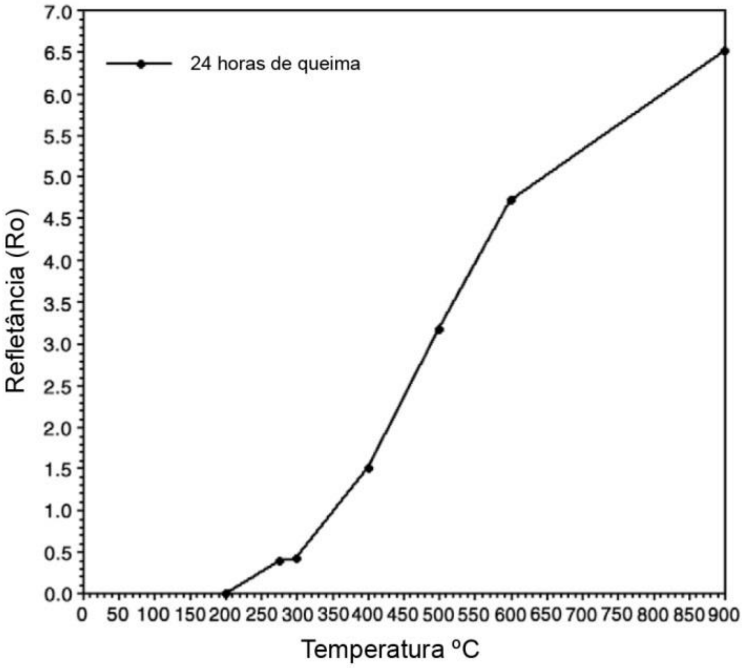


FIGURA 12 – Relação entre temperatura de queima e refletância. Resultados obtidos em experimento controlado das relações entre valores de refletância (em óleo) e temperatura na formação de carvão vegetal em queima de 24 horas.
FONTE: SCOTT, 2010, p. 18, FIG. 7.

Carvões vegetais com valores de refletância maiores do que 5% Ro requerem altas temperaturas de queima ou tempo de exposição prolongado ao calor. Carvões com refletâncias abaixo de 1% Ro podem ter sido formados sob temperaturas entre 300 e 400ºC. A temperatura de muitos tipos de incêndios cai nesse intervalo, concluindo-se que os carvões produzidos por temperaturas mais baixas terão valores de refletância menores, no intervalo da semifusinita. Logo, a refletância da fusinita é adquirida antes do processo de carbonificação e, portanto, independe da idade, litologia ou diagênese/ambiente geológico (SCOTT, 1989).

1.11 INCÊNDIOS NO NEOPALEOZOICO E TEORES DE OXIGÊNIO ATMOSFÉRICO

Os argumentos aqui sintetizados basearam-se em evidências de que expressivos incêndios de caráter global ocorreram em áreas de deposição de turfa nas diferentes fases da Idade do Gelo do Neopaleozoico. Esses incêndios são identificados pela ocorrência de carvão vegetal macro e microscópico em sedimentos associados a carvões e, também, pela presença abundante de fusênio na composição dos carvões. Os incêndios ocorreram tanto em sistemas climáticos peri e pós-glaciais quanto em sistemas tropicais ao longo do intervalo Neodevoniano-Neopermiano durante a fase de agregação do supercontinente Pangeia.

Especificamente para o Gondwana, Jasper et al. (2013) integraram registros de carvão vegetal, inertinita e hidrocarbonetos aromáticos policíclicos e concluíram que a grande maioria do carvão vegetal macroscópico do Permiano gondwânico é de afinidade gimnospérmica e proveniente de estratos de carvões ou a eles associados. As principais ocorrências estendem-se por diferentes sequências e intervalos estratigráficos tais como Bacia do Paraná (Sakmariano-Artinskian do Brazil), Bacia do Karoo (Artinskiano da África do Sul), Bacia de Damodar (Lopingiano da Índia), Lopingiano da Antártica oriental e bacias neopaleozoicas da Austrália e Nova Zelândia, abrangendo sistemas climáticos desde peri e pós-glaciais até temperado ao longo de todo o Permiano.

Através do levantamento de dados referentes ao percentual de inertinita por volume (Inert%) em carvões de todo o Fanerozoico, Glasspool e Scott (2010) demonstraram que a abundância de carvão vegetal/inertinita em ambientes de turfeira é controlada pela pO_2, e que a quantidade de carvão vegetal pode ser utilizada como indicador (*proxy*) para estimar a pO_2. Para turfeiras do Pleistoceno, observou-se uma média de 4,3% de carvão vegetal (máximo de 11%). Para os períodos do Carbonífero e Permiano, para os quais há uma ocorrência de carvão vegetal de até 83% (média de 44% para o Eopermiano em 280 Ma), Glasspool e Scott (2010), estimaram que a pO_2 permaneceu invariavelmente acima de 26%.

Glasspool et al. (2015) analisaram os dados de volume de carvão vegetal/inertinita em carvões do mundo inteiro depositados durante o Neopaleozoico e compararam com turfas atuais, linhitos e carvões do Cenozoico e argumentaram que os dados de petrografia de carvão indicam que o elemento que determinou altos índices de incêndios durante o Neopaleozoico foi a concentração atmosférica de oxigênio (pO_2), e não clima ou temperaturas globais (FIG. 13).

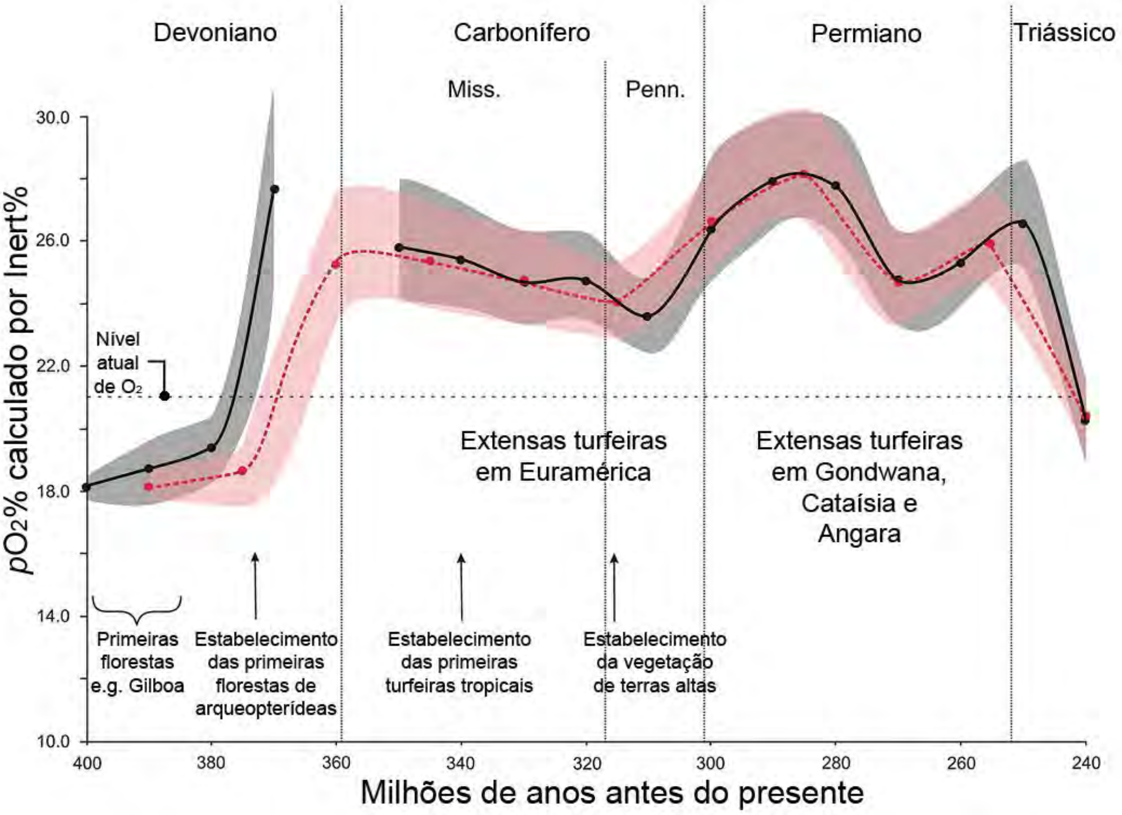


FIGURA 13 – Evolução dos sistemas de incêndios do Neopaleozoico. O cálculo das curvas de oxigênio foi baseado em teores de inertinita em carvões agrupados a cada 10 milhões (linha preta) e 15 milhões (tracejado vermelho) de anos.
FONTE: GLASSPOOL et al. 2015, p. 6, FIG. 3.

Para Diessel (2010), o padrão da distribuição estratigráfica da inertinita indica que a combustão incompleta da matéria vegetal teria sido a principal origem desse maceral. Com relação à maior proporção de inertinita em carvões do Neopermiano e do limite Cretáceo-Paleogeno, Diessel (2010) reconheceu que uma influência global se sobrepujou à variabilidade local em sistemas geradores de carvões, destacando-se a elevação da concentração de oxigênio atmosférico (pO_2) entre as variáveis analisadas.

O intervalo de tempo de quase 70 milhões de anos desde o Eopensilvaniano até o final do Neopermiano evidencia uma diversificação ímpar no reino vegetal, ocupando uma variedade imensa de biótopos. O padrão universal de aumento e diminuição na proporção de inertinita observado nos carvões paleozoicos em diferentes continentes sugere que a formação de inertinita respondeu a influências globais, muito além de uma resposta a influências ambientais locais e de suas floras especificas (DIESSEL, 2010).

Análises em ambientes de turfeira para obter estimativas de pO_2 são especialmente interessantes porque esses são sistemas permanentemente inundados, com o lençol freático sempre acima ou próximo da superfície. Tais ambientes, portanto, minimizam a influência de variações climáticas sobre o acúmulo de carvão vegetal em longo prazo (GLASSPOOL; SCOTT, 2010).

Cope e Chaloner (1985) identificaram que incêndios na vegetação ocorreram com frequência no passado geológico e que esse longo histórico estimulou respostas adaptativas em plantas e comunidades vegetais. Incêndios assumiram um papel ambiental importante ao mesmo tempo em que as plantas terrestres enriqueceram a atmosfera com oxigênio a partir do Carbonífero (SCOTT, 1989, 2000; SLATER et al., 2015)

A pressão parcial atmosférica de dióxido de carbono (pCO_2) tem sido considerada a principal forçante de mudanças climáticas no Fanerozoico, sendo os períodos quentes correlacionados com alta pCO_2 e os frios, com baixa pCO_2. Entretanto, os modelamentos paleoclimáticos falham em conciliar os dados de diversos indicadores ambientais se não forem alimentados com valores irreais de pCO_2 (PEPPE; ROYER, 2015).

Modelamentos baseados em variações da pO_2 mostraram que, mesmo o oxigênio não sendo um gás-estufa, através de sua influência significativa (e subestimada) na densidade atmosférica e dispersão da luz solar, a pO_2 amplifica os efeitos da pCO_2 (PEPPE; ROYER, 2015; POULSEN et al., 2015). Alta pO_2 intensifica a dispersão da radiação ultravioleta, enfraquecendo o efeito estufa e reduzindo o vapor d'água atmosférico, a precipitação global e a temperatura superficial. O inverso é observado em modelamentos com baixa pO_2. Esse novo modelo poderá explicar, ao menos em parte, os resultados de diversos indicadores paleoambientais que detectam baixas temperaturas durante as glaciações do final do Carbonífero e início do Permiano, bem como altas temperaturas durante o Cenomaniano e início do Paleogeno (PEPPE; ROYER, 2015).

Estudos de perturbações ambientais durante o final do Paleozoico têm especial relevância porque, nesse intervalo, vigoravam condições ambientais análogas àquelas ocorrentes na atualidade nas diferentes paleolatitudes, relacionadas principalmente à alternância de períodos glaciais e interglaciais (DiMICHELE et al., 2009).

2 ESTABELECIMENTO DA HIPÓTESE E OBJETIVOS

Evidências bióticas e abióticas de perturbações no ambiente de deposição de turfa registradas na jazida de Faxinal compõem as premissas para a delimitação da hipótese. São elas:

- detecção de perturbações vulcânicas através da presença de camada de tonstein (cinza vulcânica);
- ocorrência de macroflora preservada em uma camada de tonstein intercalada ao carvão com especializações epidérmicas xeromórficas;
- registro de carvão vegetal macroscópico no tonstein e de conteúdo de inertinita no carvão adjacente.

O seguinte conjunto de referenciais bio e geocientíficos serviu como embasamento da hipótese:

- amplas evidências de paleoincêndios nos ambientes geradores de carvões durante a Idade do Gelo do Neopaleozoico;
- alta plasticidade fenotípica de plantas como resposta a estímulos ambientais, especialmente dos órgãos foliares;
- correlação estabelecida entre a frequência de incêndios e elevada concentração de oxigênio paleoatmosférico durante o Neopaleozoico.

2.1 HIPÓTESE

Os principais fatores ambientais responsáveis pelas variações composicionais da comunidade geradora da turfa de Faxinal e pelas especializações cuticulares endêmicas na glossopterídea dominante seriam paleoincêndios sistêmicos e influência de atividades vulcânicas, traduzidos pelas ocorrências de carvão vegetal e de cinza vulcânica sedimentada associados ao carvão.

2.2 OBJETIVO GERAL

Verificar a recorrência de incêndios na área de deposição da turfa e identificar, em nível de espécie e de comunidade, respostas a perturbações ambientais através de diferentes técnicas de microscopia.

2.3 OBJETIVOS ESPECÍFICOS

- Identificar a ocorrência de incêndios por meio de microscopia eletrônica de varredura em amostras metalizadas de fragmentos orgânicos procedentes da camada de carvão e por meio microscopia petrográfica de luz refletida e fluorescência em blocos polidos de carvão;
- determinar a refletância sob óleo de macerais do grupo da inertinita (fusinita/semifusinita) em blocos polidos de carvão para confirmar a presença de carvão vegetal macroscópico, precisar temperatura de queima e tipos de incêndios na turfeira;
- identificar o padrão anatômico e estabelecer a afinidade taxonômica do carvão vegetal através de microscopia eletrônica de varredura;
- identificar grupos de palinomorfos em lâminas palinofaciológicas sob luz transmitida e fluorescência refletida;
- retificar a denominação e a descrição da espécie glossopterídea dominante na orictocenose por meio de análise cuticular em microscopia de luz transmitida;
- identificar as possíveis funções das especializações epidérmicas através de comparações com material similar na literatura.

REFERÊNCIAS

ARCHANGELSKY, S. Aspects of Gondwana paleobotany: gymnosperms of the Paleozoic—Mesozoic transition. **Review of Palaeobotany and Palynology**, Amsterdam, v. 90, n. 3-4, p. 287–302, 1996.

BELCHER, C. M. et al. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. **Nature Geoscience**, New York, v. 3, n. 6, p. 426–429, 2010a.

______..; COLLINSON, M. E.; SCOTT, A. C. A 450-Million-Year History of Fire. In: BELCHER, C. M. (Ed.). **Fire Phenomena and the Earth System**. Chichester: Wiley-Blackwell, 2013. p. 229–249.

______. et al. Baseline intrinsic flammability of Earth ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. **Proceedings of the National Academy of Sciences**, Washington, v. 107, n. 52, p. 22448–22453, 2010b.

BERNER, R. A. GEOCARBSULF: A combined model for Phanerozoic atmospheric O_2 and CO_2. **Geochimica et Cosmochimica Acta**, New York, v. 70, n. 23, p. 5653–5664, 2006.

BIRGENHEIER, L. P. et al. Evidence for dynamic climate change on sub-10^6-year scales from the late Paleozoic glacial record, Tamworth Belt, New South Wales, Australia. **Journal of Sedimentary Research**, Tulsa, v. 79, n. 2, p. 56–82, 2009.

BISHOP, J. W. et al. The onset of mid-Carboniferous glacio-eustasy: Sedimentologic and diagenetic constraints, Arrow Canyon, Nevada. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 276, n. 1-4, p. 217–243, 2009.

BOARDMAN, D. R. et al. Paleobotanical and palynological analysis of Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Paraná Basin), Rio Grande Do Sul, Brazil. **International Journal of Coal Geology**, Amsterdam, v. 102, p. 12–25, 2012.

BOND, W. J.; SCOTT, A. C. Fire and the spread of flowering plants in the Cretaceous. **New Phytologist**, London, v. 188, n. 4, p. 1137–1150, 2010.

BREZINSKI, D. K. et al. Late Devonian glacial deposits from the eastern United States signal an end of the mid-Paleozoic warm period. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 268, n. 3-4, p. 143–151, 2008.

BUSTIN, R. M. Cold temperate peats and coals: their sedimentology and composition. In: MARTINI, I. P. (Ed.). **Late Glacial and Postglacial Environmental Changes: Quaternary, Carboniferous-Permian, and Proterozoic**. New York: Oxford University Press, 1997. p. 294–310.

CAZZULO-KLEPZIG, M. et al. Peat-forming environment of Permian coal seams from the Faxinal coalfield (Paraná Basin) in southern Brazil, based on palynology and palaeobotany. **Revista brasileira de paleontologia**, Porto Alegre, v. 10, n. 2, p. 117–127, 2007.

CHALONER, W. G.; CREBER, G. T. Fossil plants as indicators of late Palaeozoic plate positions. **Geological Society Special Publications**, London, v. 37, n. 1, p. 201–210, 1988.

CHAMBERS, F. M.; DANIELL, J.; OTHERS. Peatland archives of late-Holocene climate change in northern Europe. **PAGES Newsletter**, v. 18, n. 1, p. 4–6, 2010.

CHARMAN, D. J. Peatlands and environmental change. **Land Degradation & Development**, Chichester, v. 13, n. 6, p. 527–528, 2002.

______. et al. Climate drivers for peatland palaeoclimate records. **Quaternary Science Reviews**, Amsterdam, v. 28, n. 19-20, p. 1811–1819, 2009.

CLEAL, C. J.; THOMAS, B. A. Palaeozoic tropical rainforests and their effect on global climates: is the past the key to the present? **Geobiology**, Oxford, v. 3, n. 1, p. 13–31, 2005.

COHEN, K. et al. The ICS International Chronostratigraphic Chart. **Episodes**, London, v. 36, n. 3, p. 199–204, 2013.

COPE, M. J.; CHALONER, W. G. Wildfire: an interaction of biological and physical processes. In: TIFFNEY, B. H. (Ed.). **Geological Factors and the Evolution of Plants**. New York: Yale University Press, 1985. p. 257–277.

COSTA, J. B. et al. A petrological and organic geochemical study of Permian coal seams east of Maracajá, South Santa Catarina, Paraná Basin, Brazil. **International Journal of Coal Geology**, Amsterdam, v. 132, p. 51–59, 2014.

COUWENBERG, J. et al. Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. **Hydrobiologia**, Den Haag, v. 674, n. 1, p. 67–89, 2011.

CÚNEO, N. . Permian phytogeography in Gondwana. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 125, n. 1-4, p. 75–104, 1996.

DEGANI-SCHMIDT, I.; GUERRA-SOMMER, M.; BERNARDES-DE-OLIVEIRA, M. E. C. Variation in stomatal numbers of *Glossopteris* leaves from the lower Permian of Paraná Basin, Brazil. **Revista Brasileira de Paleontologia**, Porto Alegre, v. 14, n. 2, p. 137–148, 2011.

DIESSEL, C. F. K. The stratigraphic distribution of inertinite. **International Journal of Coal Geology**, Amsterdam, v. 81, n. 4, p. 251–268, 2010.

DIMICHELE, W. A. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. **International Journal of Plant Sciences**, Chicago, v. 175, n. 2, p. 123-164, 2014.

______.; FALCON-LANG, H. J. Pennsylvanian ―fossil forests” in growth position (T0 assemblages): origin, taphonomic bias and palaeoecological insights. **Journal of the Geological Society**, London, v. 168, n. 2, p. 585–605, 2011.

______.; PFEFFERKORN, H. W.; GASTALDO, R. A. Response of late Carboniferous and early Permian plant communities to climate change. **Annual Review of Earth and Planetary Sciences**, Palo Alto, v. 29, p. 461–487, 2001.

______. et al. An unusual middle permian flora from the Blaine formation (Pease River group: Leonardian-Guadalupian series) of King County, West Texas. **Journal of Paleontology**, Tulsa, v. 78, n. 4, p. 765–782, 2004.

______. et al. Climate and vegetational regime shifts in the late Paleozoic ice age earth. **Geobiology**, Oxford, v. 7, n. 2, p. 200–226, 2009.

EMBLETON, B. J. J. Australia global setting: past global settings. In: VEEVERS, J. J. (Ed.). **Phanerozoic Earth History of Australia**. Oxford: Clarendon Press, 1984. p. 11-17. (Oxford Geology Series)

FALCON-LANG, H. J. Fire ecology of the Carboniferous tropical zone. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 164, n. 1-4, p. 339–355, 2000.

______.; DIMICHELE, W. A. What happened to the coal forests during Pennsylvanian glacial phases?. **Palaios**, Tulsa, v. 25, n. 9, p. 611-617, 2010.

FIELDING, C. R.; FRANK, T. D.; ISBELL, J. L. The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. **Geological Society of America Special Papers**, Boulder, v. 441, p. 343–354, 2008.

FIELDING, C. R. et al. Stratigraphic signature of the late Palaeozoic Ice Age in the Parmeener Supergroup of Tasmania, SE Australia, and inter-regional comparisons. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 298, n. 1-2, p. 70–90, 2010.

FLUTEAU, F. et al. The Late Permian climate. What can be inferred from climate modelling concerning Pangea scenarios and Hercynian range altitude? **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 167, n. 1-2, p. 39–71, 2001.

GAŁKA, M. et al. Palaeoenvironmental changes in Central Europe (NE Poland) during the last 6200 years reconstructed from a high-resolution multi-proxy peat archive. **The Holocene**, London, v. 25, n. 3, p. 421–434, 2014.

GASTALDO, R.; DIMICHELE, W.; PFEFFERKORN, H. Out of the Icehouse into the Greenhouse-a Late Paleozoic analog for modern global vegetational change. **GSA Today**, Washington, v. 6, n. 10, p. 1–7, 1996.

GLASSPOOL, I. A major fire event recorded in the mesofossils and petrology of the Late Permian, Lower Whybrow coal seam, Sydney Basin, Australia. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 164, n. 1-4, p. 357–380, 2000.

______. Palaeoecology of selected South African export coals from the Vryheid Formation, with emphasis on the role of heterosporous lycopods and wildfire derived inertinite. **Fuel**, Oxford, v. 82, n. 8, p. 959–970, 2003a.

______. Hypautochthonous–allochthonous coal deposition in the Permian, South African, Witbank Basin No. 2 seam; a combined approach using sedimentology, coal petrology and palaeontology. **International Journal of Coal Geology**, Amsterdam, v. 53, n. 2, p. 81–135, 2003b.

______.; SCOTT, A. C. Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. **Nature Geoscience**, New York, v. 3, n. 9, p. 627–630, 2010.

______. et al. The impact of fire on the Late Paleozoic Earth system. **Frontiers in Plant Science**, Lausanne, v. 6, article 756, 2015.

GRADSTEIN, F. M.; OGG, J. G.; SMITH, A. G. **A geologic time scale 2004**. Cambridge: University Press, 2004. 588 p.

GREB, S. F.; DIMICHELE, W. A.; GASTALDO, R. A. Evolution and importance of wetlands in earth history. **Geological Society of America Special Papers**, Washington, v. 399, p. 1–40, 2006.

GUERRA-SOMMER, M. **Padrões epidérmicos da Flora *Glossopteris* na Jazida do Faxinal (Formação Rio Bonito, Kunguriano, RS):** implicações taxonômicas, bioestratigráficas, paleoecológicas e paleogeográficas. Tese de Doutorado (Programa de Pós-Graduação em Geociências) - Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, 1988.

______. Padrões Epidérmicos de Glossopteridales da Tafoflora do Faxinal (Formação Rio Bonito - Artinskiano-Kunguriano, Bacia do Paraná, Brasil). **Pesquisas em Geociências**, Porto Alegre, v. 19, p. 26–40, 1992.

GUO, Y.; BUSTIN, R. M. FTIR spectroscopy and reflectance of modern charcoals and fungal decayed woods: implications for studies of inertinite in coals. **International Journal of Coal Geology**, Amsterdam, v. 37, n. 1-2, p. 29–53, 1998.

HE, T. et al. A 350-million-year legacy of fire adaptation among conifers. **Journal of Ecology**, London, 2015.

HIGUERA, P. E. et al. Frequent Fires in Ancient Shrub Tundra: Implications of Paleorecords for Arctic Environmental Change. **PLoS ONE**, San Francisco, v. 3, n. 3, p. e0001744, 2008.

HOLZ, M. Sequence stratigraphy of a lagoonal estuarine system-an example from the lower Permian Rio Bonito Formation, Parana Basin, Brazil. **Sedimentary geology**, Amsterdam, v. 162, n. 3, p. 305, 2003.

______. et al. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. **Journal of South American Earth Sciences**, Amsterdam, v. 29, n. 2, p. 381–399, 2010.

HORTON, D. E. et al. Eccentricity-paced late Paleozoic climate change. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 331, p. 150-161, 2012.

HOWER, J. C. et al. Notes on the origin of inertinite macerals in coal: Evidence for fungal and arthropod transformations of degraded macerals. **International Journal of Coal Geology**, Amsterdam, v. 86, n. 2-3, p. 231–240, 2011.

______. et al. An investigation of Wulantuga coal (Cretaceous, Inner Mongolia) macerals: Paleopathology of faunal and fungal invasions into wood and the recognizable clues for their activity. **International Journal of Coal Geology**, Amsterdam, v. 114, p. 44–53, 2013.

HUDSPITH, V. et al. Evaluating the extent to which wildfire history can be interpreted from inertinite distribution in coal pillars: An example from the Late Permian, Kuznetsk Basin, Russia. **International Journal of Coal Geology**, Amsterdam, v. 89, p. 13–25, 2012a.

______. **The Palaeoecological and Industrial Significance of Inertinite (Charcoal) in Late Permian Coals from the Kuznetsk Basin, Russia**. PhD Thesis—London: Royal Holloway, University of London, 2012b.

IANNUZZI, R. The flora of Early Permian coal measures from the Paraná Basin in Brazil: A review. **International Journal of Coal Geology**, Amsterdam, v. 83, n. 2-3, p. 229–247, 2010.

ISAACSON, P. E. et al. Late Devonian–earliest Mississippian glaciation in Gondwanaland and its biogeographic consequences. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 268, n. 3-4, p. 126–142, 2008.

ISBELL, J. L. et al. Glacial paradoxes during the late Paleozoic ice age: evaluating the equilibrium line altitude as a control on glaciation. **Gondwana Research**, Amsterdam, v. 22, n. 1, p. 1-19, 2012.

JACKSON, S. T.; CHARMAN, D. J. Peatlands: Paleoenvironments and carbon dynamics. **PAGES Newsletter**, v. 18, n. 1, 2010.

JASPER, A. et al. Palaeobotanical evidence of wildfires in the Late Palaeozoic of South America – Early Permian, Rio Bonito Formation, Paraná Basin, Rio Grande do Sul, Brazil. **Journal of South American Earth Sciences**, Amsterdam, v. 26, n. 4, p. 435–444, 2008.

______. Evidências Paleobotânicas de incêndios vegetacionais no afloramento Morro Papaléo, Paleozóico superior do Rio Grande do Sul, Brasil. **Revista Geonomos**, Belo Horizonte, v. 19, n. 1, p. 18–27, 2011a.

______. Charcoal remains from a tonstein layer in the Faxinal Coalfield, Lower Permian, southern Paraná Basin, Brazil. **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, v. 83, n. 2, p. 471–481, 2011b.

______. Upper Paleozoic charcoal remains from South America: Multiple evidences of fire events in the coal bearing strata of the Paraná Basin, Brazil. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 306, n. 3-4, p. 205–218, 2011c.

______. Palaeobotanical evidence of wildfire in the Upper Permian of India: Macroscopic charcoal remains from the Raniganj Formation, Damodar Basin. **Palaeobotanist**, Lucknow, v. 61, p. 75–82, 2012.

______. The burning of Gondwana: Permian fires on the southern continent—a palaeobotanical approach. **Gondwana Research**, Amsterdam, v. 24, n. 1, p. 148–160, 2013.

JONES, T. P.; CHALONER, W. G. Fossil charcoal, its recognition and palaeoatmospheric significance. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 97, n. 1-2, p. 39–50, 1991.

JONES, T. P.; SCOTT, A. C.; MATTEY, D. P. Investigations of “fusain transition fossils” from the Lower Carboniferous: comparisons with modern partially charred wood. **International Journal of Coal Geology**, Amsterdam, v. 22, n. 1, p. 37–59, 1993.

KALKREUTH, W. et al. Petrology and chemistry of Permian coals from the Paraná Basin: 1. Santa Terezinha, Leão-Butiá and Candiota Coalfields, Rio Grande do Sul, Brazil. **International Journal of Coal Geology**, Amsterdam, v. 68, n. 1-2, p. 79–116, 2006.

______. The coalbed methane (CBM) potential and CO 2 storage capacity of the Santa Terezinha Coalfield, Paraná Basin, Brazil - 3D modelling, and coal and carbonaceous shale characteristics and related desorption and adsorption capacities in samples from exploration borehole CBM001-ST-RS. **Energy, Exploration & Exploitation**, London, v. 31, n. 4, p. 485–528, 2013.

KELLY, T. J. et al. The high hydraulic conductivity of three wooded tropical peat swamps in northeast Peru: measurements and implications for hydrological function. **Hydrological Processes**, Chichester, v. 28, n. 9, p. 3373–3387, 2013.

LÄHTEENOJA, O.; ROUCOUX, K. H. Inception, history and development of peatlands in the Amazon Basin. **PAGES Newsletter**, v. 18, n. 1, p. 140–145, 2010.

LANGFORD, R. **Permian coal and palaeogeography of Gondwana**. Canberra: Bureau of Mineral Resources/Australian Petroleum Industries Research Association. Palaeogeographic Maps Project, BMR Record, 1991. v. 95.

LI, X.; WU, X. Late paleozoic phytogeographic provinces in China and its adjacent regions. **Review of Palaeobotany and Palynology**, Amsterdam, v. 90, n. 1-2, p. 41–62, 1996.

LIMARINO, C. O. et al. A paleoclimatic review of southern South America during the late Paleozoic: A record from icehouse to extreme greenhouse conditions. **Gondwana Research**, Amsterdam, v. 25, n. 4, p. 1396–1421, 2014.

LINDSTRÖM, S.; MCLOUGHLIN, S.. Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains, Antarctica: implications for palynofloristic turnover across Gondwana. **Review of Palaeobotany and Palynology**, Amsterdam, v. 145, n. 1, p. 89-122, 2007.

LLOYD, D. et al. Methanogenesis and CO_2 exchange in an ombrotrophic peat bog. **Atmospheric Environment**, Oxford, v. 32, n. 19, p. 3229–3238, 1998.

LOTTES, A. L.; ZIEGLER, A. M. World peat occurrence and the seasonality of climate and vegetation. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 106, n. 1-4, p. 23–37, 1994.

MACDONALD, G. M. et al. Rapid Early Development of Circumarctic Peatlands and Atmospheric CH_4 and CO_2 Variations. **Science**, Washington, v. 314, n. 5797, p. 285–288, 2006.

MARTINI, I. P.; CORTIZAS, A. M.; CHESWORTH, W. (Ed.). **Peatlands: evolution and records of environmental and climate changes**. Amsterdam: Elsevier, 2007. 587 p. v. 9

MCGINNES, E.; KANDEEL, S.; SZOPA, P. Some structural changes observed in the transformation of wood into charcoal. **Wood Fiber**, Lawrence, v. 3, p. 77–83, 1971.

MCLOUGHLIN, S.; DRINNAN, A. N. Anatomically preserved Permian *Noeggerathiopsis* leaves from east Antarctica. **Review of Palaeobotany and Palynology**, Amsterdam, v. 92, n. 3, p. 207-227, 1996.

______. Revised stratigraphy of the Permian Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica. **Geological Magazine**, New York, v. 134, n. 03, p. 335-353, 1997.

MCPARLAND, L. C. et al. The use of reflectance values for the interpretation of natural and anthropogenic charcoal assemblages. **Archaeological and Anthropological Sciences**, Berlin, v. 1, n. 4, p. 249–261, 2009.

MENDONÇA FILHO, J. G. et al. Permian carbonaceous rocks from the Bonito Coalfield, Santa Catarina, Brazil: Organic facies approaches. **International Journal of Coal Geology**, Amsterdam, v. 111, p. 23–36, 2013.

MEYEN, S. V. **Fundamentals of palaeobotany**. London: Chapman and Hall, 1987. 432 p.

MISHRA, H. K.; CHANDRA, T. K.; VERMA, R. P. Petrology of some Permian coals of India. **International Journal of Coal Geology**, Amsterdam, v. 16, n. 1-3, p. 47–71, 1990.

MONTAÑEZ, I. P.; POULSEN, C. J. The Late Paleozoic Ice Age: an evolving paradigm. **Annual Review of Earth and Planetary Sciences**, Palo Alto, v. 41, p. 629–656, 2013.

MONTAÑEZ, I. P. et al. CO_2-forced climate and vegetation instability during late Paleozoic deglaciation. **Science**, Washington, v. 314, n. 5808, p. 87, 2007.

MOORE, P. D. Ecological and hydrological aspects of peat formation. In: SCOTT, A. C. (Ed.). Coal and coal-bearing strata: recent advances and future prospects. **Geological Society Special Publications**, London, v. 32, p. 1–6.1987.

______. The ecology of peat-forming processes: a review. **International Journal of Coal Geology**, Amsterdam, v. 12, n. 1-4, p. 89–103, 1989.

NAVALE, G. K. B.; SAXENA, R. An appraisal of coal petrographic facies in Lower Gondwana (Permian) coal seams of India. **International Journal of Coal Geology**, Amsterdam, v. 12, n. 1-4, p. 553–588, 1989.

O’KEEFE, J. M. K. et al. On the fundamental difference between coal rank and coal type. **International Journal of Coal Geology**, Amsterdam, v. 118, p. 58–87, 2013.

PAGE, S. E. et al. The amount of carbon released from peat and forest fires in Indonesia during 1997. **Nature**, London, v. 420, n. 6911, p. 61–65, 2002.

PEPPE, D. J.; ROYER, D. L. Can climate feel the pressure? **Science**, Washington, v. 348, n. 6240, p. 1210–1211, 2015.

POULSEN, C. J.; TABOR, C.; WHITE, J. D. Long-term climate forcing by atmospheric oxygen concentrations. **Science**, Washington, v. 348, n. 6240, p. 1238-1241, 2015.

PROTHERO, D. R. **Interpreting the Stratigraphic Record**. New York: W. H. Freeman, 1989. 410 p.

RAUP, H. M. Physical disturbance in the life of plants. In: NITECKI, M. H. (Ed.). **Biotic Crises in Ecological and Evolutionary Time**. New York: Academic Press, 1981. p. 39–52.

REIN, G. Smouldering fires and natural fuels. In: BELCHER, C. M. (Ed.). **Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science**. Oxford: Wiley-Blackwell, 2013. p. 15–33.

______. Peat megafires. In: STRACHER, G. B.; PRAKASH, A.; REIN, G. (Ed.). **Coal and Peat Fires: A Global Perspective**. Amsterdam: Elsevier, 2015. p. 2–11.

RETALLACK, G. J. Permian and Triassic greenhouse crises. **Gondwana Research**, Amsterdam, v. 24, n. 1, p. 90-103, 2013.

RICH, F. J. Peat: Its origins, characteristics, and transformations. In: STRACHER, G. B.; PRAKASH, A.; REIN, G. (Ed.). **Coal and Peat Fires: A Global Perspective**. Amsterdam: Elsevier, 2015. p. 14–38.

RIMMER, S. M. et al. The rise of fire: Fossil charcoal in late Devonian marine shales as an indicator of expanding terrestrial ecosystems, fire, and atmospheric change. **American Journal of Science**, Washington, v. 315, n. 8, p. 713–733, 2015.

ROSCHER, M.; STORDAL, F.; SVENSEN, H. The effect of global warming and global cooling on the distribution of the latest Permian climate zones. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam v. 309, n. 3, p. 186-200, 2011.

ROUCOUX, K. H. et al. Vegetation development in an Amazonian peatland. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 374, p. 242–255, 2013.

SANDER, P. M. Taphonomy of the Lower Permian Geraldine Bonebed in Archer County, Texas. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 61, p. 221–236, 1987.

______.; GEE, C. T. Fossil charcoal: techniques and applications. **Review of Palaeobotany and Palynology**, Amsterdam, v. 63, n. 3-4, p. 269–279, 1990.

SCOTESE, C. R. **Paleomap Project**. Disponível em: <http://www.scotese.com/permian.htm>. Acesso em: 18 set. 2015.

SCOTT, A. C. Observations on the nature and origin of fusain. **International Journal of Coal Geology**, Amsterdam, v. 12, n. 1-4, p. 443–475, 1989.

______. Preservation, evolution, and extinction of plants in Lower Carboniferous volcanic sequences in Scotland. **Geological Society of America Special Papers**. Boulder, v. 244, p. 25–38, 1990.

______. The Pre-Quaternary history of fire. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 164, n. 1-4, p. 281–329, 2000.

______. Coal petrology and the origin of coal macerals: a way ahead? **International Journal of Coal Geology**, Amsterdam, v. 50, n. 1-4, p. 119–134, 2002.

______. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 291, n. 1-2, p. 11–39, 2010.

______.; GLASSPOOL, I. J. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. **Proceedings of the National Academy of Sciences**, Washington, v. 103, n. 29, p. 10861–10865, 2006.

______.; GLASSPOOL, I. J. Observations and experiments on the origin and formation of inertinite group macerals. **International Journal of Coal Geology**, Amsterdam, v. 70, n. 1-3, p. 53–66, 2007.

______.; JONES, T. P. The nature and influence of fire in Carboniferous ecosystems. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 106, n. 1-4, p. 91–112, 1994.

______. et al. The taphonomy of charcoal following a recent heathland fire and some implications for the interpretation of fossil charcoal deposits. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 164, p. 1–31, 2000.

______. et al. **Fire on earth: an introduction**. Chichester: Wiley-Blackwell, 2014. 413 p.

SILVA, A. C. et al. Turfeiras da Serra do Espinhaço Meridional - MG: I - caracterização e classificação. **Revista Brasileira de Ciência do Solo**, Viçosa, v. 33, n. 5, p. 1385–1398, 2009.

SILVA, M. B.; KALKREUTH, W.; HOLZ, M. Coal petrology of coal seams from the Leão-Butiá Coalfield, Lower Permian of the Paraná Basin, Brazil — Implications for coal facies interpretations. **International Journal of Coal Geology**, Amsterdam, v. 73, n. 3-4, p. 331–358, 2008.

SIMAS, M. W. et al. Geochronological correlation of the main coal interval in Brazilian Lower Permian: Radiometric dating of tonstein and calibration of biostratigraphic framework. **Journal of South American Earth Sciences**, Amsterdam, v. 39, p. 1–15, 2012.

______. An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a Lower Permian tonstein bed (Faxinal Coalfield, Paraná Basin, Brazil). **Geologica acta**, Barcelona, v. 11, n. 1, p. 47–57, 2013.

SLATER, B. J.; MCLOUGHLIN, S.; HILTON, J. A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. **Gondwana Research**, Amsterdam, v. 27, n. 4, p. 1446–1473, 2015.

STOPES, M. C. On the Four Visible Ingredients in Banded Bituminous Coal: Studies in the Composition of Coal, No. 1. **Proceedings of the Royal Society B**, London, v. 90, n. 633, p. 470–487, 1919.

______. On the petrology of banded bituminous coal. **Fuel**, London v. 14, p. 4-13, 1935.

TAYLOR, E. L.; TAYLOR, T. N.; KRINGS, M. **Paleobotany: the biology and evolution of fossil plants**. 2. ed. New York: Academic Press, 2009. 1230 p.

TURETSKY, M. R. et al. Global vulnerability of peatlands to fire and carbon loss. **Nature Geoscience**, London, v. 8, n. 1, p. 11–14, 2015.

UHL, D.; JASPER, A.; SCHWEIGERT, G. Charcoal in the Late Jurassic (Kimmeridgian) of Western and Central Europe—palaeoclimatic and palaeoenvironmental significance. **Palaeobiodiversity and Palaeoenvironments**, Berlin, v. 92, n. 3, p. 329–341, 2012.

UHL, D.; KERP, H. Wildfires in the Late Palaeozoic of Central Europe – The Zechstein (Upper Permian) of NW-Hesse (Germany). **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 199, n. 1-2, p. 1–15, 2003.

UHL, D. et al. Wildfires in the Late Palaeozoic of Central Europe—an overview of the Rotliegend (Upper Carboniferous–Lower Permian) of the Saar–Nahe Basin (SW-Germany). **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 207, n. 1-2, p. 23–35, 2004.

______. Evidence of palaeo-wildfire in the early Middle Triassic (early Anisian) Voltzia Sandstone Fossil-Lagerstätte — the oldest post-Permian macroscopic evidence of wildfire discovered so far. **Palaios**, Tulsa, v. 25, n. 12, p. 837–842, 2010.

VÄLIRANTA, M.; KAAKINEN, A.; KUHRY, P. Holocene climate and landscape evolution East of the Pechora Delta, East-European Russian Arctic. **Quaternary Research**, New York, v. 59, n. 3, p. 335–344, 2003.

VAN HOOF, T. B. et al. A role for atmospheric CO_2 in preindustrial climate forcing. **Proceedings of the National Academy of Sciences**, Washington, v. 105, n. 41, p. 15815–15818, 2008.

WANG, Z.; CHEN, A. Traces of arborescent lycopsids and dieback of the forest vegetation in relation to the terminal Permian mass extinction in North China. **Review of Palaeobotany and Palynology**, Amsterdam, v. 117, n. 4, p. 217–243, 2001.

WATSON, A. J.; LOVELOCK, J. E. The Dependence of Flame Spread and Probability of Ignition on Atmospheric Oxygen. In: BELCHER, C. M. (Ed.). **Fire Phenomena and the Earth System**. Oxford: Wiley-Blackwell, 2013. p. 273–287.

YU, Z.; BEILMAN, D. W.; JONES, M. C. Sensitivity of northern peatland carbon dynamics to Holocene climate change. In: BAIRD, A. J. et al. (Ed.). **Northern peatlands and carbon cycling**. Washington: American Geophysical Union, 2009. p. 55–69. Monograph Series.

ZIEGLER, A. M. Phytogeographic patterns and continental configurations during the Permian Period. **Geological Society Memoirs**, London, v. 12, n. 1, p. 363–379, 1990.

ZIEGLER, A. et al. Tracing the tropics across land and sea: Permian to present. **Lethaia**, Oxford, v. 36, n. 3, p. 227–254, 2003.

CAPÍTULO 2

International Journal of Coal Geology 146 (2015) 55–67

Contents lists available at ScienceDirect

International Journal of Coal Geology

journal homepage: www.elsevier.com/locate/ijcoalgeo

Charcoalified logs as evidence of hypautochthonous/autochthonous wildfire events in a peat-forming environment from the Permian of southern Paraná Basin (Brazil)

Isabela Degani-Schmidt [a,*], Margot Guerra-Sommer [b], Joalice de Oliveira Mendonça [c], João Graciano Mendonça Filho [c], André Jasper [d], Miriam Cazzulo-Klepzig [b], Roberto Iannuzzi [b]

[a] Programa de Pós-Graduação em Geociências/UFRGS, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil
[b] Instituto de Geociências/UFRGS, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil
[c] Laboratório de Palinofácies e Fácies Orgânica LAFO/DEGL/IGEO/CCMN/UFRJ, Av. Athos da Silveira Ramos, 274, Bloco J1, Sala 20, 21941-916 Rio de Janeiro, RJ, Brazil
[d] Setor de Botânica e Paleobotânica, Museu de Ciências Naturais, Centro Universitário UNIVATES, Avenida Avelino Tallini, 171, 95900-000 Lajeado, RS, Brazil

ARTICLE INFO

Article history:
Received 31 March 2015
Received in revised form 6 May 2015
Accepted 7 May 2015
Available online 15 May 2015

Keywords:
Charcoal
Fossil plants
Glossopteris Flora
Rio Bonito Formation
Sakmarian
Gondwanaland

ABSTRACT

Evidences of paleowildfires from the upper coal seam S from the Faxinal Coalfield have been analyzed through petrographic, fluorescence, and scanning electron microscopy (SEM) specifically at the base (1) and top (2) boundaries of an interlayered tonstein bed and revealed recurrent charcoal deposition in the peat-forming environment. An unusual accumulation of adjacent, large-sized (21.8 × 13.4 cm and larger) charred logs occurs throughout the coal seam area (1.6 km^2) beneath the tonstein bed (boundary 1) reflecting an extensive wildfire event in hypautochthonous/autochthonous conditions. The logs display a semifusinite–vitrinite–semifusinite sandwich-like structure (*sensu* Jones et al., 1993) indicating burning in growth position, and reflectance measurements below 1%Ro suggest that this was a low-temperature fire. Dryness in the peatland during the fire event was clearly detected by altered fluorescence of spores and algae. Corroborating previous studies, the paleoecological setting can be characterized as a swamp forest based on the presence of pollen clusters and organs observed under fluorescent light and on the identification under SEM of the morphogenus *Agathoxylon* Hartig as a single wood type, reflecting the dominance of arborescent gymnosperms (glossopterids) in the peatland. Homogenized cell walls observed under SEM ratified the recognition of the material as charcoal. The reestablishment of regular conditions of peat deposition following the major fire episode is represented by alternate bands of vitrinite and semifusinite in both boundaries 1 and 2, suggesting an oscillation from dry to wet conditions in the climate pattern and the occurrence of wildfires as common and systemic events. Fire ignition, activity, and spread in the peat-forming environment resulted from a combination of lightning strikes, dryness, fuel abundance, and high atmospheric oxygen levels.

1. Introduction

Wildfire events play important roles in different terrestrial environments (Belcher, 2013; Scott, 1989 and references therein; Scott and Glasspool, 2006; Scott et al., 2014) and charcoal fragments are present in the fossil record since the Silurian in different settings, from terrestrial to marine (e.g. Glasspool et al., 2004; Scott, 2010).

In addition to reflectance measurements of coal macerals and scanning electron microscopy (SEM) in extant and fossil material, charring experiments lead to the confirmation of fusain (inertinite) as charcoal, a product of wildfire (Scott, 1989; Scott and Glasspool, 2007). However, according to Hower et al. (2013) and O'Keefe et al. (2013), biotic (bacterial, fungal, or invertebrate) or abiotic interactions (aerobic exposure or biochemical alteration) may have been relevant for the maceral formation in the inertinite group, in particular macrinite.

In Recent peat-forming swamps, fires have affected extensive areas, as observed by Hudspith et al. (2014); Page et al. (2002), Prat et al. (2015), Rein et al. (2008), and Turetsky et al. (2015). According to Scott et al. (2014), while charcoal corresponds to roughly 4% of the total volume in modern peat, in the Late Paleozoic it could reach 70%. Based on fossil evidence and experimental observations, several authors (Belcher et al., 2013; Bergman et al., 2004; Chaloner, 1989; Cope and Chaloner, 1985; Glasspool and Scott, 2010) concluded that the percentage of charcoal in coals through the geologic record can be considered as a proxy for atmospheric oxygen levels.

---

* Corresponding author at: PPG-Geo/UFRGS, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil. Tel.: +55 51 3308 63 78.
E-mail addresses: degani.schmidt@ufrgs.br (I. Degani-Schmidt), margot.sommer@ufrgs.br (M. Guerra-Sommer), joalice@lafo.geologia.ufrj.br (J.O. Mendonça), graciano@geologia.ufrj.br (J.G. Mendonça Filho), ajasper@univates.br (A. Jasper), miriam.klepzig@ufrgs.br (M. Cazzulo-Klepzig), roberto.iannuzzi@ufrgs.br (R. Iannuzzi).

http://dx.doi.org/10.1016/j.coal.2015.05.002
0166-5162/

In the Early Permian, atmospheric oxygen levels were estimated to have reached a peak of 35% (Scott and Glasspool, 2006). Therefore, if the percentage of charcoal in coal (inertinite) is indeed a proxy for atmospheric oxygen content, then Early Permian coals should have high inertinite contents. In coals from the southern Paraná Basin, inertinite contents can be larger than 50% (Kalkreuth et al., 2006). In addition, Jasper et al. (2011a) reported the occurrence of macroscopic charcoal (*sensu* Jones and Chaloner, 1991; Scott, 2010) in clastic sediments associated with hypautochthonous coal seams in Brazilian coalfields. The study therefore demonstrated that fires were relatively common events in and around peat-forming environments in the Early Permian Paraná Basin.

Along the five coal seams of the Faxinal Coalfield inertinite contents range from 6 to 15% (Henz and Corrêa-da-Silva, 1987). For the interlayered tonstein bed in the coal seam S, Jasper et al. (2011b) reported macroscopic charcoal fragments of gymnospermous affinities. Unabraded edges and dimensions up to 3.5 cm indicated low-energy transport, pointing to a hypautochthonous deposition. It was observed that the presence of fusain in the coal both overlying and underlying the tonstein bed could indicate that fire events were not restricted to the ash-fall interval.

For the present study, a reassessment of the upper coal seam S (Fig. 1A) from the Faxinal Coalfield (Fig. 2) is carried out, specifically at the base (1) and top (2) boundaries of the interbedded tonstein ply (Fig. 1B). Aiming to investigate wildfire events in the peat-forming environment, analyses were conducted through petrographic, fluorescence, and scanning electron microscopy in inertinite-rich levels associated with the tonstein ply. Logs, branch, and twig fragments occurring in the coal at the tonstein contacts had previously been considered as coalified in nature by Guerra-Sommer (1992). Here they are recognized as an impressive charcoalified wood assemblage of unusually large dimensions (Fig. 1C–G) occurring continuously over the entire exploitation area of the Faxinal open cast mine (ca. 1.6 km^2).

To support paleoenvironmental inferences, the present study investigates fire temperature, type, and ignition sources and identifies charcoalified and coalified biomass components, complementing previous studies on paleowildfires in various Permian ecosystems.

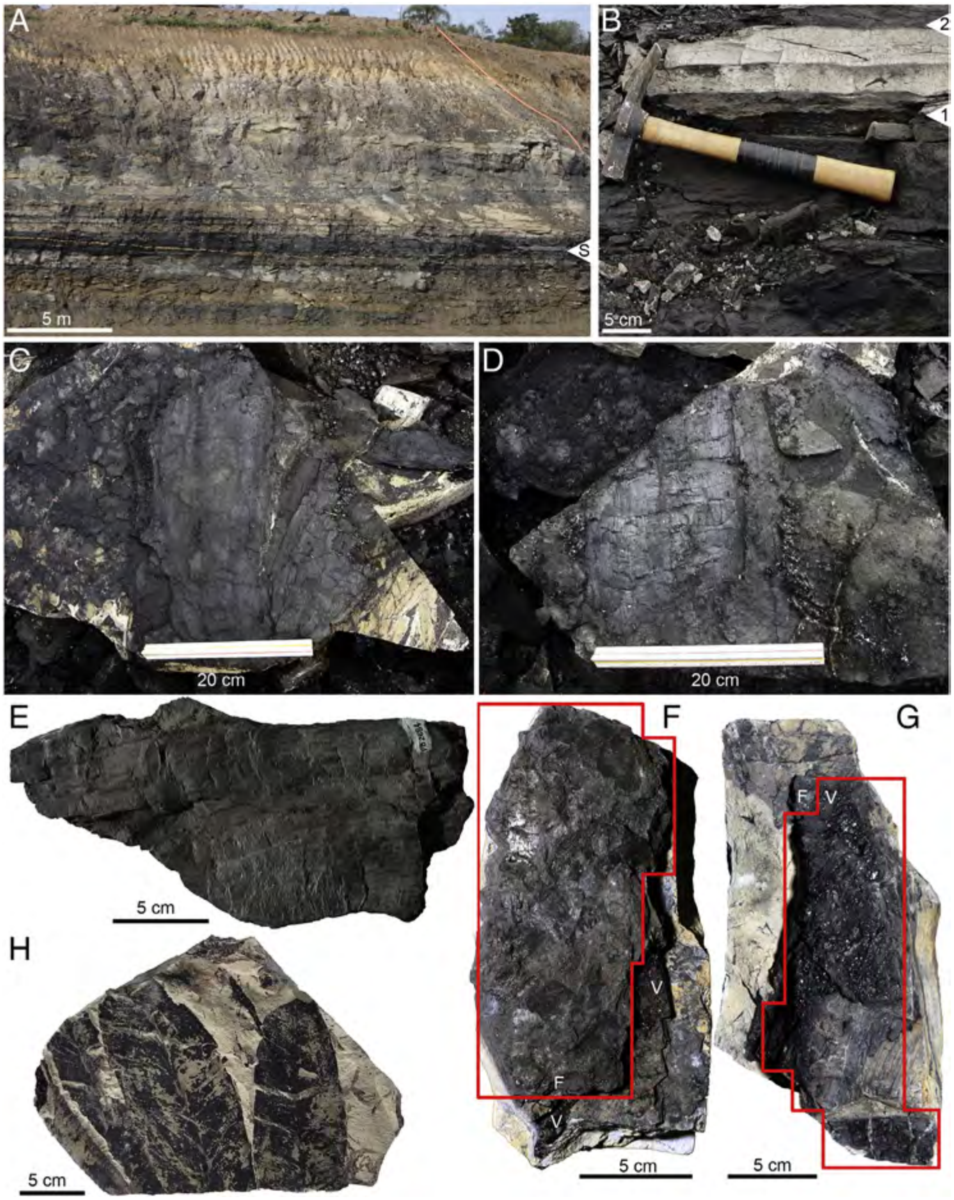


Fig. 1. Field and hand sample photographs. A) Pit bench exposure of coal seam S; B) close up of the interbedded tonstein ply in upper coal seam S; arrows indicate the coal-tonstein boundaries 1 and 2 here analyzed; C, D) large fragments of charred logs from boundary 1; E) charred stem fragment from the boundary 1 (PB2684); F) charcoal clasts from the boundary 2 (Pb4629); G) sample from boundary 2 showing high vitrain content (Pb4618); H) coalified leaves of the *Glossopteris* Flora preserved in the tonstein bed (Pb4762a).

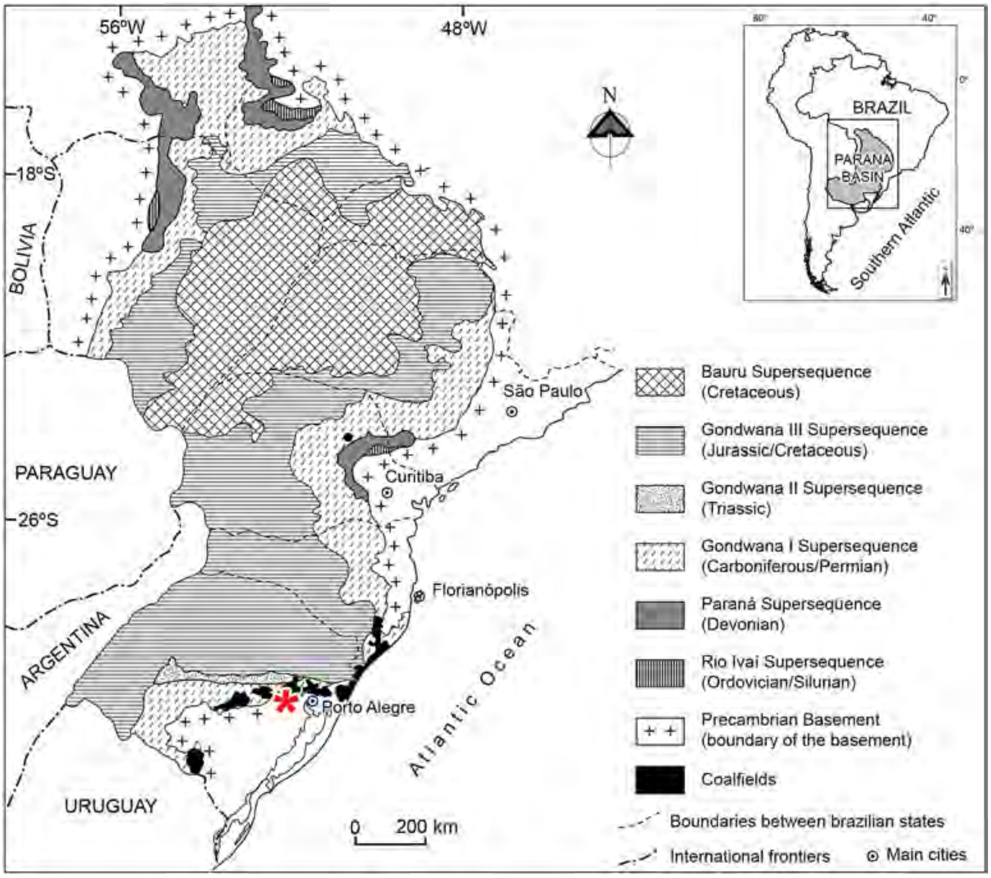


Fig. 2. Map of the Brazilian Paraná Basin with stratigraphic framework, geographic references (after Santos et al., 2006), and location of the Faxinal Coalfield.

2. Geological and paleontological context

In the Paraná Basin, the Gondwana I Supersequence (Fig. 2), with sediments spanning from the Upper Pennsylvannian through the Lower Triassic, represents a second-order transgressive/regressive cycle and includes the coal-bearing strata of the Rio Bonito Formation (Milani et al., 2007). These strata are related to a paralic setting, i.e., adjacent to estuarine, deltaic, backshore, foreshore, and shoreface siliciclastic depositional environments (Holz et al., 2010). Strata deposition occurred in the cool temperate climatic belt at a paleolatitude of approximately 50° (Ziegler et al., 2003).

The study area comprises the Faxinal Coalfield, an opencast mine located at the southeastern outcrop belt of the Rio Bonito Formation of the Paraná Basin, southern Brazil (Fig. 2, 30°15′52.6″S, 51°41′53.8″W). The area is situated in an elongated structure trending SE–NW, referred by Guerra-Sommer et al. (2008) as a graben. The mine closure took place in 2009 after the coal was exhausted, and the site has been rehabilitated.

The Faxinal succession includes five coal seams, named from base to top I, IM, M, MS, and S (Fig. 3). A tonstein ply dated at 291 ± 1.3 Ma (Simas et al., 2012) corresponding to the late Sakmarian (Cohen et al., 2013; updated 2015) is interbedded in the upper coal seam (S) and contains abundant compressed fossil leaves of the *Glossopteris* Flora (Fig. 1H). The prevalent lithotype composition in this coal seam is of banded and thin-banded coal, with predominance of dull coal (Henz and Corrêa-da-Silva, 1987).

Petrographic analysis under both reflected and transmitted light conducted by Henz and Corrêa-da-Silva (1987) in the Faxinal coal seams showed a high vitrinite/mineral matter ratio and a predominance of mono and bimaceral microlithotypes (vitrite, vitrinertite and inertite) over trimacerite. The upper coal seam (S) subject of the present study has a mean vitrinite content of 57%, inertinite 13.75%, liptinite 2.25%, and 27% mineral matter.

Paleobotanical data from the tonstein bed was originally obtained by Guerra-Sommer (1992) from an abundant compressed hypautochthonous taphoflora, predominantly gymnospermous. Boardman et al. (2012) reported relative abundances of 78% of glossopterid leaves, followed by 17.6% of coradaitalean leaves, 2% of reproductive axes, 1.4% of pteridophyte fronds and 1% of seeds. In spite of the occurrence of paleosols at the base of the coal seam, stems in growth position have not been found. The presence of cordaitalean plants and the dominance of glossopterid leaves occurring in horizontal layers occasionally still attached to short shoots with well-preserved epidermal patterns (Degani-Schmidt et al., 2011; Guerra-Sommer, 1992) point to a forested association (Simas et al., 2013).

Previous palynological and palynofaciological analyses inferred changes in the microfloristic relative frequencies along the coal seam S, i.e. a decrease in lycopsids and filicopsids spores and an increase from 56% to 80% in the frequency of gymnosperm pollen grains from base to top (Cazzulo-Klepzig et al., 2009). However, Boardman et al. (2012) reported a relative frequency of 24% of Zygnemaphyceae algae for the coal underlying the tonstein. Additionally, Simas et al. (2013) observed well-preserved pollen clusters (mainly bisaccates) along the profile of the tonstein bed, especially at its base, and *Botryococcus* algae at the top.

The studied interval is included in the *Protohaploxypinus goraiensis* Subzone within the palynostratigraphic framework for the Lower Permian of Brazilian Paraná Basin and in the phytostratigraphic *Glossopteris–Rhodeopteridium* Zone (Boardman et al., 2012; Simas et al., 2012).

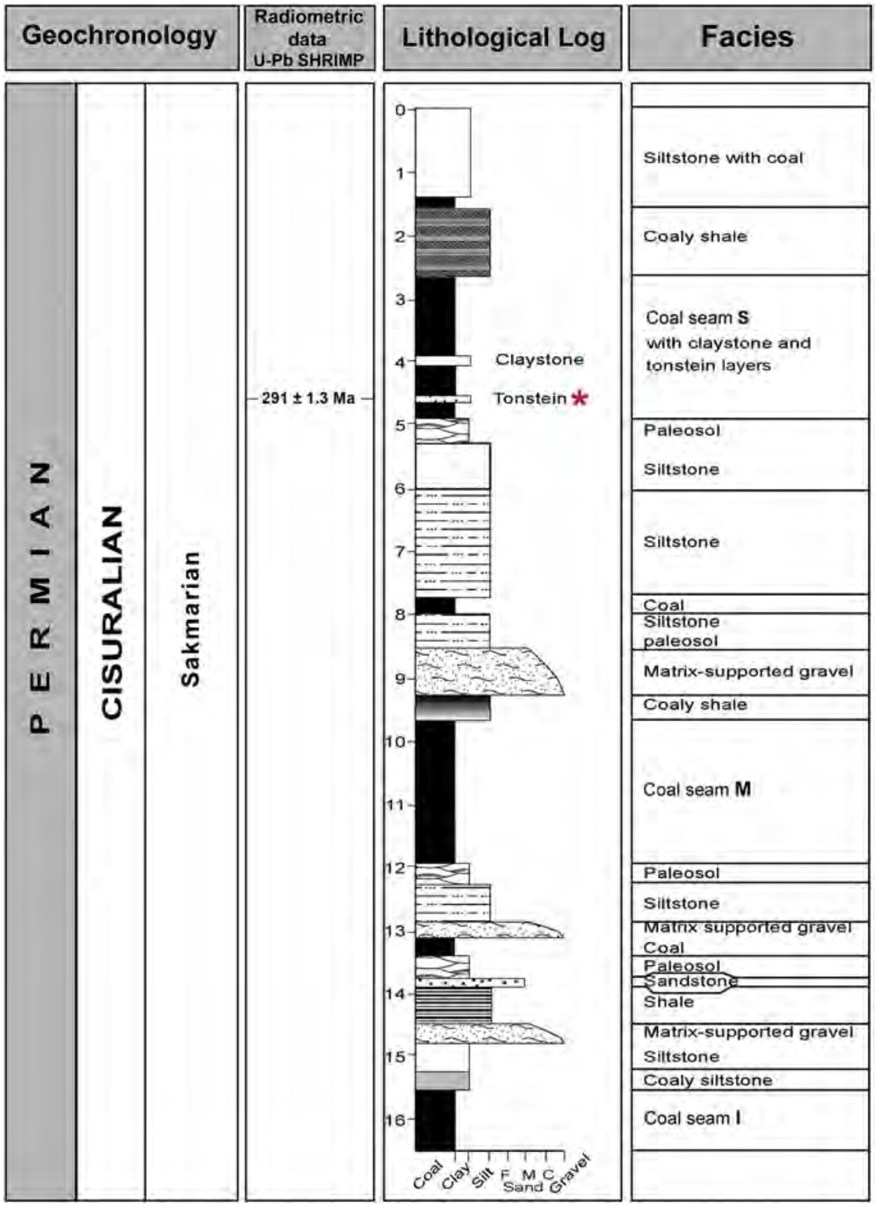


Fig. 3. Geochronology, radiometric age, lithological log, and facies of the Faxinal Coalfield (after Simas et al., 2012).

3. Material and methods

Tonstein samples were collected between 1984 and 2009 (Boardman et al., 2012; Degani-Schmidt et al., 2011; Guerra-Sommer, 1992; Jasper et al., 2011b; Simas et al., 2012). Slabs were removed from the coal seam with pickaxe or hammer and chisel. Large-sized charcoalified specimens of brittle nature could have only been retrieved because they were attached to the highly silicified tonstein rock, which held the specimens together (Fig. 1C–G).

Twenty coal samples were analyzed in this study. All samples show constant attributes for either the tonstein base (boundary 1) or top (boundary 2) surfaces. At the base of boundary 1, a dense concentration of highly compressed, partially charred logs can be observed (Fig. 1C–E), followed by banded coal and the tonstein rock. At boundary 2, vitrain predominates at the contact with the underlying tonstein, with subsequent alternation of mineral matter and thin-banded coal. Branch and twig fragments (charcoal clasts) are abundant and occur together with coalified stem fragments and leaves (Fig. 1F–G).

3.1. Polished block preparation

To make the blocks, the slabs were broken down to smaller, manageable sizes, surface embedded in epoxy resin followed by vacuum treatment to prevent fragmentation (Jones and Rowe, 1999), sawn perpendicular to bedding into slices of appropriated size for reflectance analysis, and then polished using aluminum oxide powder to obtain a highly reflective surface (Collinson et al., 2007).

3.1.1. Petrographic analysis

To interpret the microscopic appearance of the specimens and to obtain reflectance data as a proxy for estimating charring temperature (e.g. McParland et al., 2009), petrographic analysis was carried out in polished blocks under oil (Immersol 518 F) using microscope Axioskop 2 Plus Zeiss equipped with spectrophotometer J&M (MSP 200) through a × 50 objective. The microscope was calibrated with a Sapphire standard (0.595%Ro).

3.2. Slide preparation

The preparation technique employed was the non-oxidative procedure for sedimentary organic matter according to Mendonça Filho et al. (2010). Coal samples have been fragmented and first treated with HCl and HF, followed by heavy liquid ($ZnCl_2$) in order to concentrate the organic matter, which was then mounted on 12 slides.

3.2.1. Fluorescence observation

The analysis of the dispersed organic matter involved the identification of morphogroups, their relative abundances and preservation state of selected particulate components (palynomorphs and phytoclasts) under fluorescence. Due to the goal constraints of the present study, palynomorph relative abundances were based on broad morphological groups (algae, spores, and saccate pollen grains), enough to allow a gross reconstruction of the parent vegetation and comparison with previous studies of the coal seam S from the Faxinal Coalfield. A total of 100 palynomorphs were counted per slide for frequency determination.

3.3. Scanning electron microscopy

For observation of the homogenization status of cell walls and anatomy of the wood types, the material was examined under scanning electron microscopy (Collinson, 1999; Figueiral, 1999; Scott, 2001). Small pieces, often fragmented into elongated laths, were sampled from the compressed, charred wood specimens with aid of dissecting needles under a Leica S8 APO stereoscopic microscope. The fragments were then mounted on standard stubs with double-sided tape, gold coated, and subsequently examined and photographed with a JEOL JSM 6060 Scanning Electron Microscope (SEM).

4. Results

All features described by Jones and Chaloner (1991) and Scott (1989, 2000, 2010) as typical of macroscopic charcoal (black color, silky luster, well preserved anatomical details and homogenized cell walls) are present.

4.1. Appearance in hand specimen

At the base of boundary 1, the opaque and fibrous appearance of the partially charred logs is perceptible to the naked eye, in an obvious sandwich-like organization (*sensu* Jones et al., 1993) of vitrain cores surrounded by an outer layer composed by fusain (Fig. 4), with aspects of lustrous sheen and brittle surface, with a black streak (Scott, 2010). As a rule, the surface of the logs shows a splitting pattern (Fig. 1C–E) similar to modern charred stems (Cope and Chaloner, 1985; Scott, 1989). The logs are overlain by 8 mm of alternate bands of vitrain and fusain, with a dominance of vitrain, and followed by the tonstein bed (Fig. 4).

The boundary 2 above the tonstein consists of bands of fusain and vitrain just like the top sequence of boundary 1. The charcoal fragments are generally smaller, narrower, thinner, and more loosely spaced, corresponding to dispersed branch fragments (Fig. 1F, G), without vitrain cores.

The minimum and maximum measurements of the studied fragments in each boundary are shown in Table 1.

4.2. Petrographic analysis

Analysis on polished blocks of the boundary 1 showed that the compressed logs up to 8-mm thickness at the base are composed of a clear inertinite–vitrinite–inertinite transition (Fig. 5). In the inertinite zones, the cell lumina are generally not well defined. “Bogen-struktur” produced by shattering of the cell walls are present, indicating high compaction of the tissues. Reflectance measurements characterize the maceral as semifusinite. The transition between the structured semifusinite and the homogeneous vitrinite is sharp (Fig. 5). Reflectance values across the transition decreased from the basal outermost semifusinite (0.84–0.61%Ro) to the

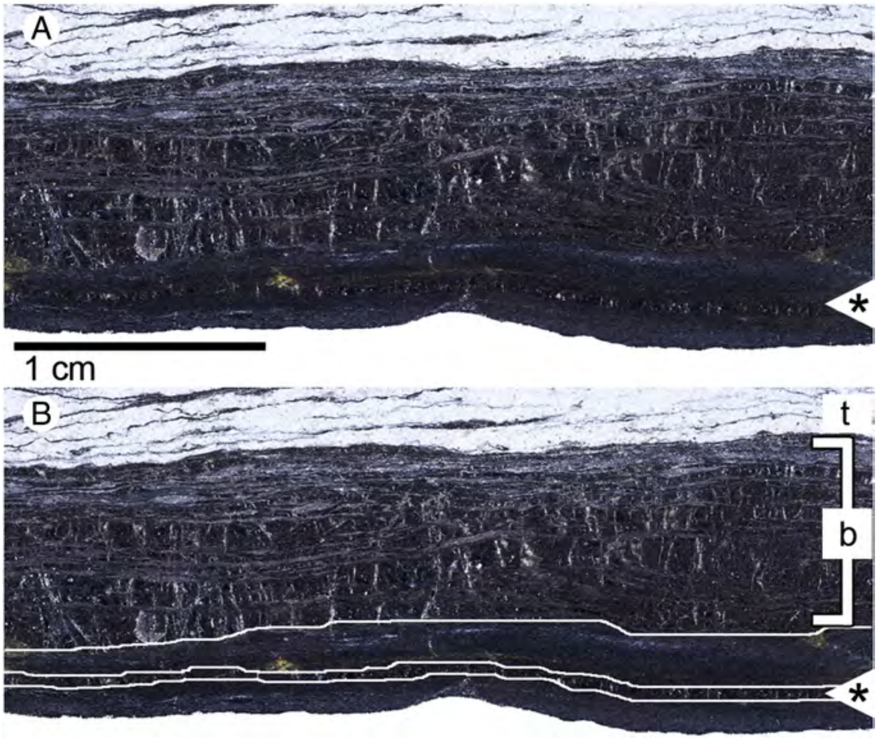


Fig. 4. Visual aspects of a sample. A) Polished block from the boundary 1 with the horizon of charred logs (*) at the base; B) “sandwich-like” sequence of inertinite–vitrinite–inertinite (*) visible by naked eye (outlined); followed by thinner coal bands (b) and tonstein (t), arrowhead = vitrain core (Pb4587a).

Table 1
Maximum and minimum dimensions of the charcoal fragments. Number of samples (slabs) = 20. Measurements in cm.

	Max length	Max width	Min length	Min width	Mean thickness
Boundary 2	16.4	5.7	0.3	0.3	0.3
Boundary 1	21.8	13.4	3.5	0.3	0.8

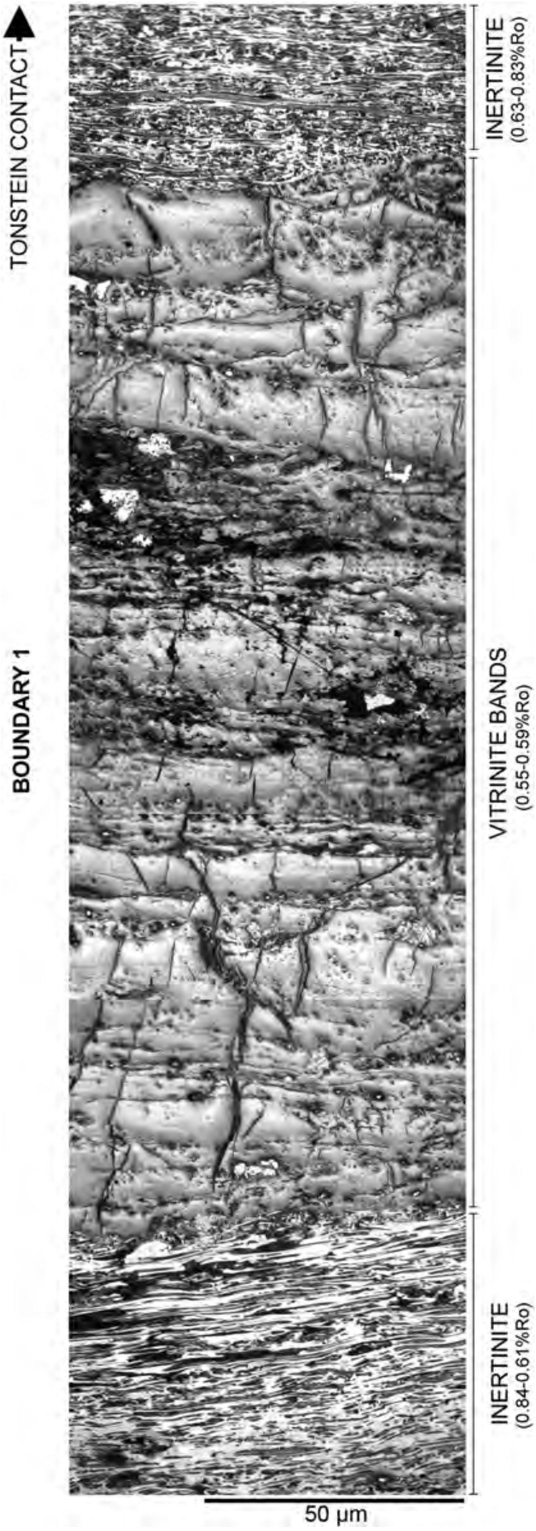


Fig. 5. Composite image of the inertinite–vitrinite–inertinite transition of a compressed log from the boundary 1 and corresponding reflectance results (Pb4587a).

innermost vitrinite (0.55–0.59%Ro), increasing in the top outermost semifusinite (0.63–0.83%Ro). At the top of boundary 1, vitrinite is the dominant maceral at the contact with the overlying tonstein, alternating with inertinite bands between the charred log horizon and the mineral matter (tonstein). In the top section of boundary 1, the inertinite bands are also composed of semifusinite, and the organization of the cellular structure is clear.

A coal section of 15-mm thickness perpendicular to the bedding in the boundary 2 showed an alternation of thin bands of inertinite and vitrinite interlayered by bands of mineral matter (Fig. 6). From the contact with the massive tonstein at the base of the section towards the top the following reflectance readings have been obtained: Vitrinite 0.36–0.43%Ro; inertinite 0.82–0.99%Ro; vitrinite 0.42–0.48%Ro; inertinite 0.68–0.85%Ro; and vitrinite 0.37–0.59%Ro. Thicker bands of vitrinite predominate at the contact with the underlying tonstein bed.

Liptinite is also present in both boundaries and has been observed in high detail under fluorescent light (Fig. 7).

4.3. Fluorescence observation of dispersed organic matter

In the polished blocks from both boundaries 1 and 2 liptinite is represented by dispersed palynomorphs and fragments of sporangia/pollen organs and cuticle (Fig. 7). Dense sporinite masses composed by both mature (pollen clusters) and immature (sporangial content?) unidentifiable bisaccate pollen grains can be observed in discrete areas under fluorescence microscopy. At boundary 1, cutin and pollen clusters (Fig. 7B, E) showed altered pattern of fluorescence color and intensity in relation to the sporangial (?) content (Fig. 7C, D).

Slide observation under fluorescent light showed differences between the two associations. At the boundary 1, a relative deviation from the normal pattern in fluorescence color and intensity was observed in the dispersed algal and pteridophytic spores which showed color change and weaker fluorescence in comparison to the pollen grains. At the boundary 2, all palynomorphs showed the same pattern of unaltered fluorescence color and intensity (Fig. 8).

Bisaccate pollen grains predominate in both boundaries and an increase from base to top was detected along with a corresponding decrease in the abundance of algae and spores. Zygnemaphyceae was the major group in the observed algae (Table 2).

4.4. SEM observation

Homogenized cell walls can be observed in axial and cross-section views in all samples (Fig. 9A, B, G) and confirmed the categorization of the material as charcoal (Jones, 1993; Scott and Jones, 1991). Due to the high compression after burial (Fig. 9C), the integrity of the xylem cell walls is not always preserved. Cell walls are fractured, both perpendicularly across the weakest or thinnest part of the wall and lengthwise (Fig. 9D). Nevertheless, the SEM observation revealed gymnospermous secondary anatomy in tangential (Fig. 9E) and radial (Fig. 9F) views, and in rarely preserved cross-sections (Fig. 9G). The organization of both secondary xylem and phloem is evident, which are equally preserved in both boundaries.

Tracheids exhibit a mixed type of pitting in single specimens (Fig. 9H–K). Uniseriate, biseriate, and triseriate pitting were frequently observed in a single tracheid as well (Fig. 9H). Cross-field pitting (Fig. 9L) is rarely preserved but cross-fields are frequently present and are of the Araucarian type with numerous, contiguous, unordered cupressoid to taxodioid oculipores (*sensu* Philippe and Bamford, 2008).

Secondary phloem (Fig. 9M–O) was identified by the presence of well-preserved sieve areas in tangential view and thick-walled fibers in cross-section. A detailed study of wood anatomy is under preparation.

Fig. 6. Composite image of petrographic observation and reflectance values of boundary 2 (Pb467T). \\ = content of mineral matter has been omitted from the image composition due to space constraints.

5. Discussion

5.1. Physical and petrographic analyses

Physical analysis of the charred logs from the base of boundary 1 revealed specimens charred all around with a vitrain core (Figs. 1C–E, 4), indicating burning in growth position (*sensu* Jones et al., 1993) prior to their collapse. The dominance of vitrain following this horizon indicates the return to regular conditions of peat formation, while thin bands of interlayered inertinite (Fig. 4) attest that fire events were recurrent.

In the charcoal assemblage from boundary 2, a persistence of smaller and thinner fragments of charred wood associated with abundant coalified material (Fig. 1F, G) can be observed. This indicates a different transport history, suggesting that in situ events as the one recorded at the base of boundary 1 were infrequent.

The distinct maceral organization (Figs. 4, 5, 6) observed after the log horizon reflects the dominance of coalification process of the organic matter over charcoalification, showing that the conditions of peat-deposition have not been altered by the fire regime.

Organic petrography of the transition from structured semifusinite to the inner core of unstructured, homogenous vitrinite in a single log (Fig. 5) reflects a process where the outer portion of the wood stem is burnt and the uncharred inner portion was later coalified to vitrinite Jones et al. (1993).

The low reflectance values below 1%Ro found for the semifusinite in both boundaries (Figs. 5 and 6) are an indication that the wood burned in cool temperature fires (330 to 460 °C according to Jones et al., 1991). Additionally, the partially charred logs from boundary 1 with vitrinite cores point to a short fire duration (Jones et al., 1993) and a surface type of fire within a forested ecosystem (Scott et al., 2014).

In Jasper et al. (2011b), the occurrence of charcoalified remains in the tonstein bed suggested that fire ignition was generated under the influence of volcanic activities. The gradual decrease of charcoal content observed towards the top of the tonstein has been correlated with a reduction in fuel quantity and in fire ignition source at the end of the ash deposition. Likewise, Glasspool (2000) observed in Permian Australian coals that a general correlation between tonsteins and inertinite-rich coal layers indicates a possible fire ignition provided by the proximity to explosive volcanic activity. Nevertheless, the low fire temperature detected here by quantitative reflectance and the presence of vitrinite inside the superficially charred stems point to potential ignition sources such as lightning strikes, which are the most common cause of ignition (Cope and Chaloner, 1985; Glasspool and Scott, 2013). Moreover, for the tonstein ply interbedded in the coal seam S, Simas et al. (2013) concluded that the ash has been deposited on the peat surface at a cool temperature, and no evidence of thermal-induced alteration has been observed through leaf cuticle analyses (Degani-Schmidt et al., 2011; Guerra-Sommer, 1992).

The continuous presence of charcoal before, during, and after the ash fall indicates that fire ignition occurred independently of volcanic activity and constituted a cyclical mechanism in this peat-forming environment.

5.2. Fluorescence observation of dispersed organic matter

Uncharred dispersed structures are preserved as cutinite and sporinite, and can be observed in both boundaries 1 and 2 (Fig. 7). Some sporinite masses, showing a very homogenous pattern and displaying a characteristic shape of sporangia (Fig. 7C, F), are probable pollen organs/sporangial content. The relative integrity of reproductive structures indicates the growth of parent vegetation close to the site of peat accumulation (Glasspool, 2003; Scott and King, 1981). Their presence in inertinite rich levels implies the occurrence of a fire type with little effect on the crown. This hypothesis accounts for the presence of sporangial content in the coal, and also of coalified reproductive axes and abundant leaf whorls preserved in the tonstein bed.

The dispersed palynomorph count indicated a co-dominance of pollen grains and spores in the boundary 1, revealing the proximity of both gymnospermous and pteridophytic groups to the peat accumulation site. The weak fluorescence shown by spores in comparison to pollen grains (Fig. 8B, D) can be related to prolonged oxidation of organic

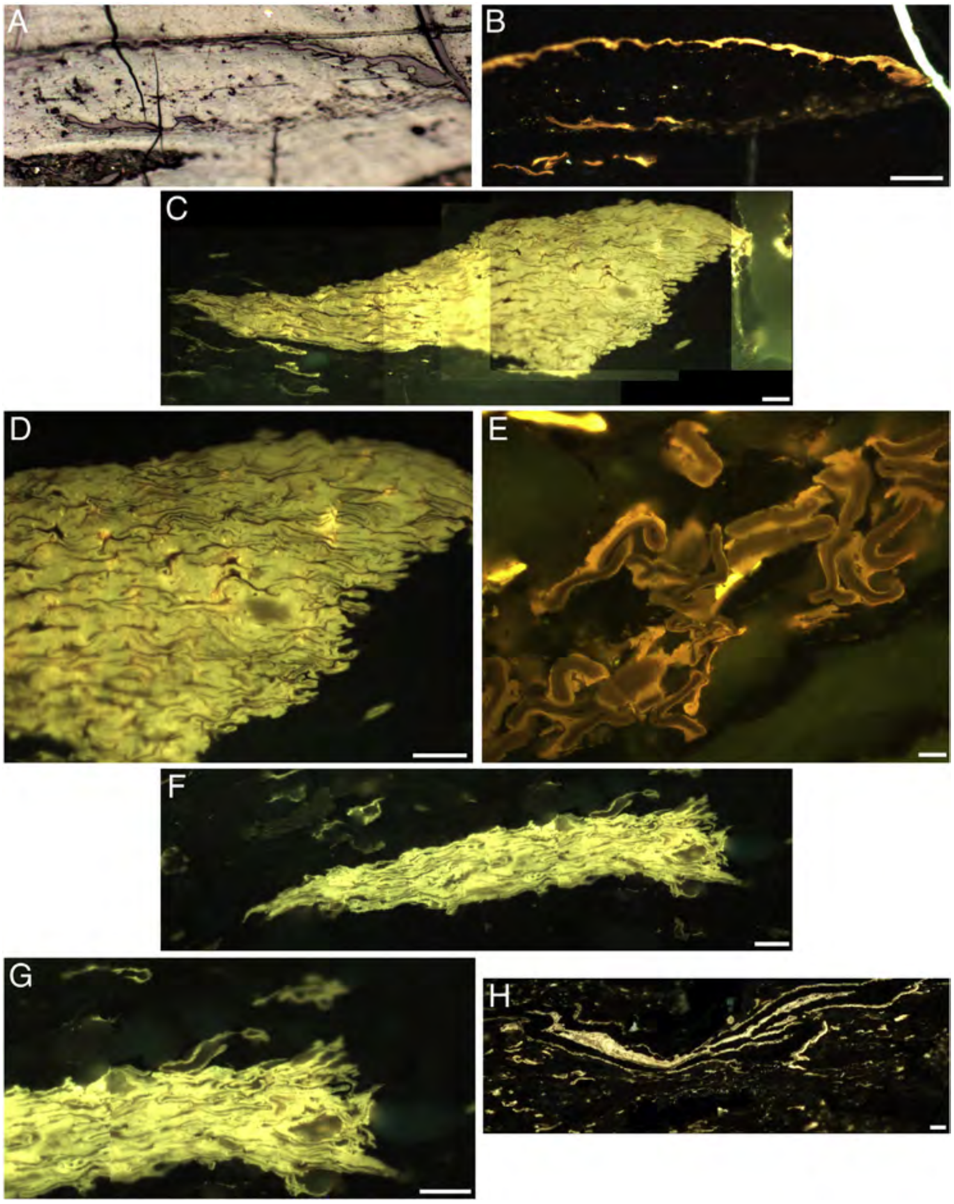


Fig. 7. Polished blocks seen through fluorescence microscopy under oil. A–E) Sample from boundary 1 (Pb4587a); F–H) sample from boundary 2 (Pb467T). A and B) cutinite under reflected and fluorescent light; C) composite image of pollen organ (?) fragment; D) detail from (C); E) pollen cluster; F) composite image of pollen organ (?) fragment; G) detail from (F); H) cutinite. Scale bars = 10 μm.

matter. The presence of zygospores (zygnematacean algae) is an indicator of conditions related to lacustrine shallow margins, sloughs, and tree islands in swamp environments (Chmura et al., 2006; Grenfell, 1995; Yi, 1997). The oxidation observed for both spores and zygospores points to lowering of the water table (Hutton et al., 1980; Livingstone and Melack, 1984) and a drought event (Fig. 10A).

At the boundary 2, the unaltered fluorescence (Fig. 8F, H, J) observed in all palynomorphs (pollen grains, spores, and algal elements) indicates the reestablishment of moisture and peat-forming conditions, even though episodes of wildfires occurred. The severe decrease in the number of dispersed trilete spores in relation to the lower level suggests a change in the proportion of the main vegetation groups immediately following ash fall, and is in agreement with previous palynological and palynofaciological analyses of the coal seam S (Cazzulo-Klepzig et al., 2009; Simas et al., 2013). The increased dominance of bissacate pollen grains over pteridophytic spores after the ash fall indicates that the glossopterid vegetation was not suppressed by the fire, and a new niche was not opened for recolonization. Furthermore, the increased dominance of mesophylous seed-bearing over hygrophilous pteridophytic vegetation could be a response to changes in the peat-deposition environment.

5.3. SEM observation

The homogenization of cell walls (Fig. 9A, B, G) confirms that the wood has been charred to a minimum temperature of 300–325°C (Scott, 2010).

Anatomical parameters of the wood assemblage are those of the fossil-genus *Agathoxylon* Hartig (Philippe and Bamford, 2008; Rößler et al., 2014), pointing to a predominantly monotypical association (Fig. 9). This wood pattern is often found in Late Paleozoic gymnosperms from both northern and southern hemispheres, having been formerly identified as *Dadoxylon* Endlicher, which is an illegitimate name (Philippe, 1993; Vogellehner, 1964). According to Philippe (2011), the name *Agathoxylon* seems to be the most appropriate for the corresponding morphogenus. This pattern is known from several gymnosperm

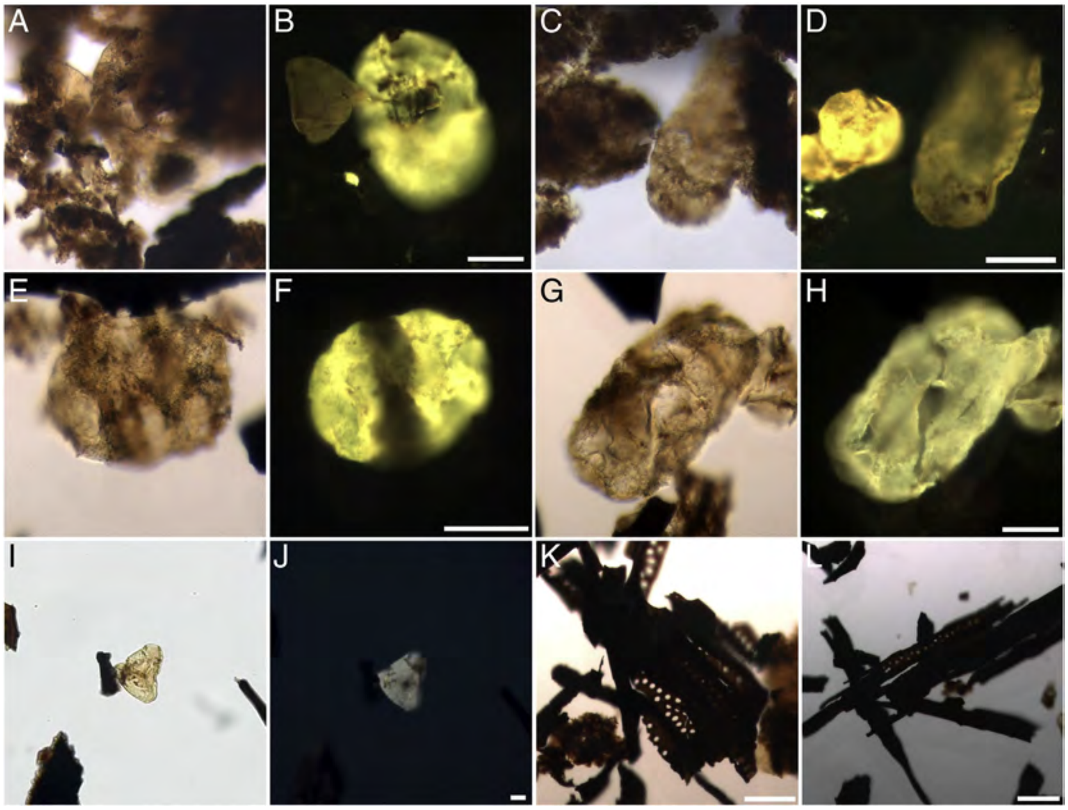


Fig. 8. Slides seen under white and fluorescent light. A-D) Palynomorphs from boundary 1 (Pb4587a); E-K) palynomorphs and phytoclasts from boundary 2 (Pb467T). A, B) trilete spore and bisaccate pollen grain; C, D) bisaccate pollen grains and zygospore; E, F) bisaccate pollen grain; G, H) zygospore; I, J) trilete spore; K, L) opaque and non-opaque phytoclasts composed of tracheid fragments. Scale bars = 10 μm.

groups of different phylogenetic affinities and has been assigned to taxa with different stratigraphic age ranges, including the Glossopteridales (Prevec et al., 2009). Its occurrence in both boundaries and the dominance of glossopterid leaves in the interbedded tonstein ply testify to the proximity of these plants to the accumulation site.

Considering that upon charring the resultant material, although resilient, is highly friable, the anatomical integrity of the charred logs and branches attests to a short or almost non-existent transport distance (Ohlson and Tryterud, 2000) and low-temperature fires (Scott, 2010). The outstanding preservation of the extremely delicate phloem tissue (Fig. 9M–O) in the stems and branches from both boundaries also supports these inferences. The phloem very rarely survives the charring process, and would not resist transportation, nor high-temperature fire, given its superficial position in the wood underneath the bark. According to Hather (2000), during wildfire the phloem tissue either deteriorates, or solidifies leaving a formless mass of glassy charred tissue. However, good preservation occurs if it has been slowly dried prior to charring.

5.4. Environmental factors

The wildfire history emerging from the evidences gathered here involves hypautochthonous to autochthonous charcoal input and a surface type of fire that burned at low temperature (325–400 °C), supported by low reflectance readings <1%Ro and exceptional integrity of fragile plant tissues (Scott, 2010) along the whole studied profile.

Table 2
Relative abundances of the gross palynomorph morphogroups are given in %. A total of 100 palynomorphs were counted on each slide.

	Pollen grains	Spores	Algae
Boundary 2	71	18	9
Boundary 1	49	27	24

In the basal level of boundary 1, even though no stems in growth position, stumps, or roots are present, the size and preservation state of the logs point to proximity of the trees and the deposition site. This event is maybe related to a more extended drought episode and consequent lowering of the water table, which allowed the fire to get closer to the catchment basin (Fig. 10A).

At the return of peat accumulation after the autochthonous wildfire event there is a change in the charcoal characteristics from large charred logs to smaller charcoal clasts accumulated in thin inertinite bands, which can be related to an increased distance between the fire and the depositional site (Fig. 10B–D). Even large logs can be transported because they are buoyant (Glasspool and Scott, 2013). Yet the preservation of vascular tissue, the integrity of associated coalified sporangia/pollen organs, and the presence of palynomorph clusters and oxidized but not burned pteridophytic and algal spores indicate that the crown and the peat itself have not been significantly affected by the fire and transport was very limited for all plant parts. All evidences assembled here suggest the dominance of surface fire events at the margin and short distances from the peat depositional site.

According to Diessel (1992), the growth of a swamp forest composed by gymnosperms as the main element of the peat-forming vegetation under the influence of systemic wildfires is typical of Gondwana coals. The lack of macroscopic fragments of the pteridophytic components could be attributed to their occurrence in distal plant communities dependent on wetness and less liable to combustion (Glasspool, 2003), or preservational bias.

Wildfires in modern peat-forming environments (Bowman et al., 2009; Flannigan et al., 2009; Glasspool and Scott, 2010; Hudspith et al., 2014; Page et al., 2002; Pierce et al., 2004; Prat et al., 2015; Rein et al., 2008; Turetsky et al., 2015) are an important source of disturbance

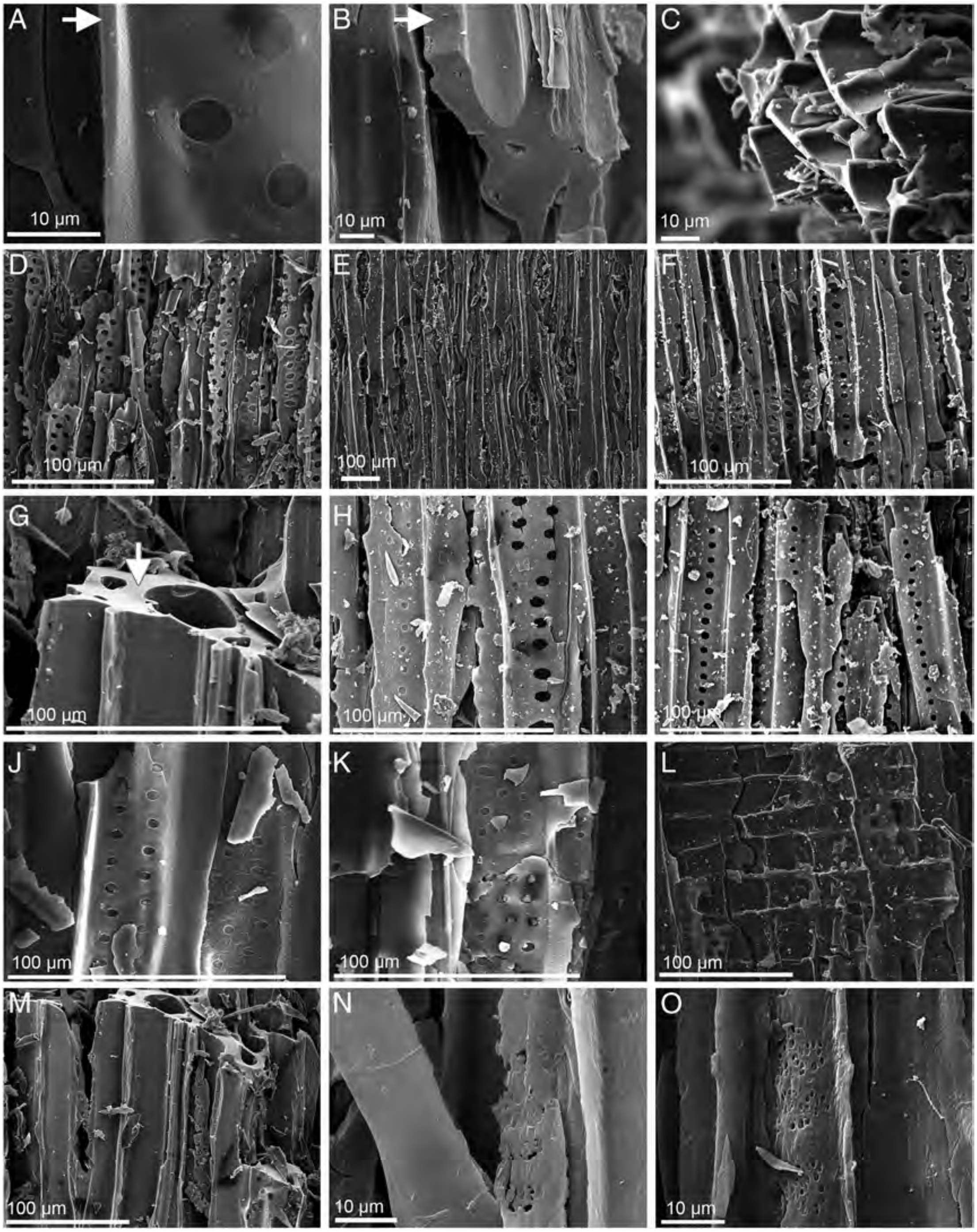


Fig. 9. SEM micrographs of gymnospermous secondary wood anatomy preserved as charcoal. A, B) Homogenized cell walls (arrows): A) in axial view (4587a-04-04); B) in B) in axial and oblique section (4587b-56-09); C) wood cross-section showing compression (5128-71-009); D) common fracturing pattern of tracheid radial walls (5126-27-08); E) wood pattern in tangential view (4639-45-04); F) radial view of tracheids (5126-27-04); G) homogenized cell walls (arrow) of secondary phloem in cross-section (4587b-56-02); H, I) single specimen 5126–26: H) uniseriate and biseriate mixed type of tracheid pitting (5126-26-56); I) uniseriate pitting (5126-26-34). J, K) single specimen 4587a-04: J) biseriate pitting (4587a-04-15); K) triseriate pitting (4587a-04-14); L) cross-field with poorly preserved pitting (5126-26-13); M–O) secondary phloem in tangential view (4629-01-04; 4629-01-03; 4587b-56-03).

for renewal of plant cover. However, a delay in the disturbance recurrence leads to a reduction in diversity (Attiwill, 1994), and extended intervals between fires with prolonged dryness could be one of the reasons to the long lasting dominance exerted by the glossopterid woody species in this restrict setting.

The Sakmarian global warming previously detected by Gastaldo et al. (1996) and Montañez et al. (2007) after the end of the earliest Permian glacial phase in Gondwana has been correlated for the Paraná Basin by Iannuzzi (2010). With atmospheric oxygen levels at >25%, the widespread occurrence of fires in wet environments can be reconciled by the prevalence of lightning strikes and abundant fuel (Scott and Glasspool, 2006). Nevertheless, the peat-forming conditions continued further in the Faxinal Coalfield after the first fire horizon here analyzed, indicating a persistence of a humid trend in climate.

6. Conclusions

The occurrence of in situ charred stems deposited in a coal layer, followed by multiple horizons of charcoal supports the view that

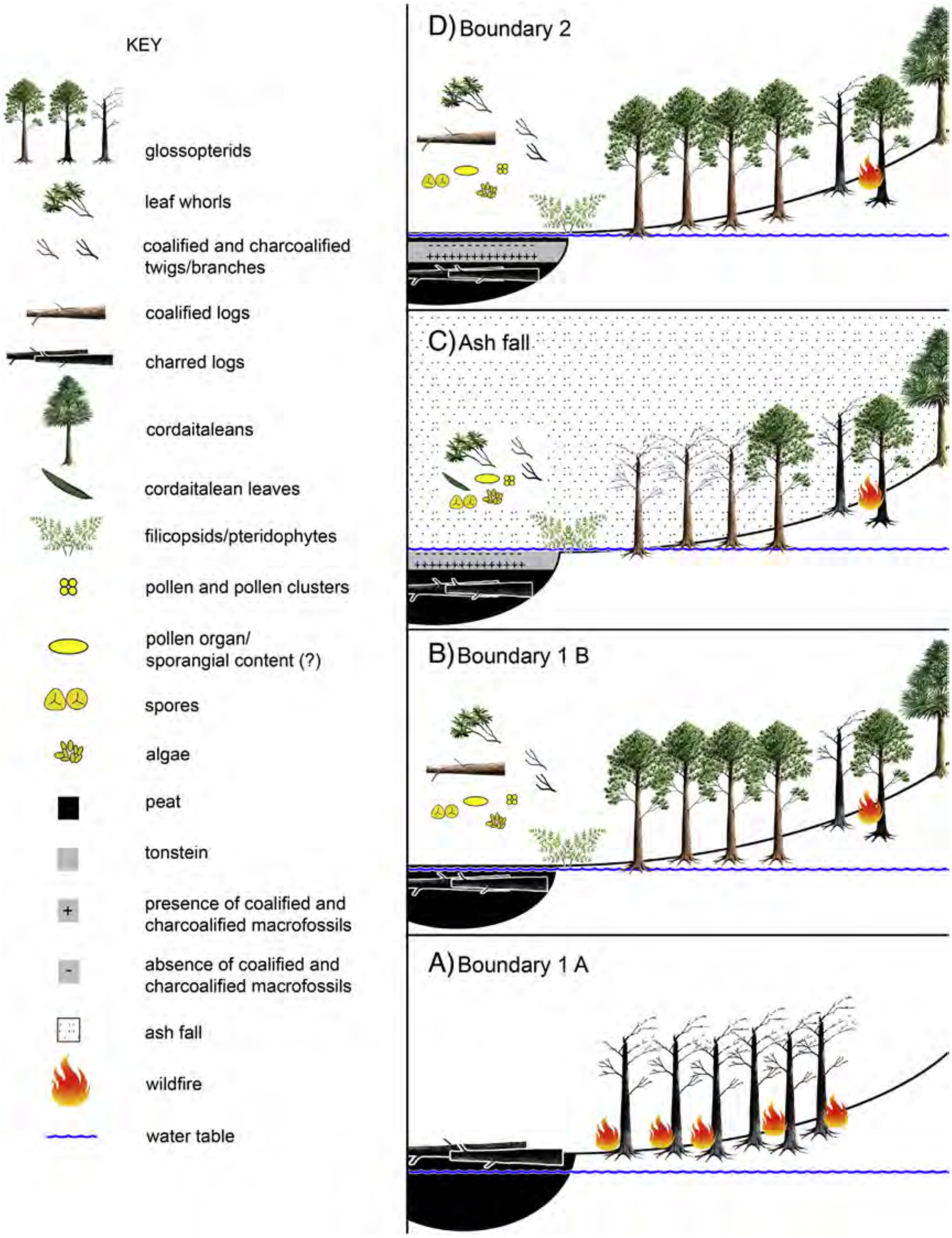


Fig. 10. Schematic paleoecological reconstruction of the Faxinal Coalfield. A) Major wildfire event; B) regular conditions of peat deposition; C) ash fall event; and D) like (B).

wildfires were common and systemic events in this Early Permian peat-forming environment in Gondwanaland. The charred logs indicate that woody gymnosperms, probably of glossopterid affinity, were important elements of the hypautochthonous/autochthonous peat-forming vegetation. The woody vegetation burned in growth position during superficial, extensive, low temperature wildfires most likely ignited by lightning strikes. The increased dominance of gymnospermous vegetation after the ash fall indicates that a climate regime with extreme oscillations between humidity and dryness with wildfires was favorable to the seed-bearing plants.

Acknowledgments

This study is submitted by IDS in partial fulfillment of the requirements for the PhD degree at the Programa de Pós-Graduação em Geociências/UFRGS, Porto Alegre, Rio Grande do Sul under the tenure of a scholarship funded by the Brazilian National Council of Technological and Scientific Development CNPq (159690/2012-9). The authors thankfully acknowledge Margarete Wagner Simas for the field photographs, Gustavo Simão and the Thin Section and Polishing Laboratory CPGQ/UFRGS for the technical support with the preparation of the polished blocks, and are grateful to James Hower and an anonymous reviewer for the comments which significantly improved the manuscript.

References

Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manag. 63 (2–3), 247–300. http://dx.doi.org/10.1016/0378-1127(94)90114-7.

Belcher, C.M. (Ed.), 2013. Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science. John Wiley & Sons, Oxford http://dx.doi.org/10.1002/9781118529539 (333 p).

Belcher, C.M., Collinson, M.E., Scott, A.C., 2013. A 450-million-year history of fire. In: Belcher, C.M. (Ed.), Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science. John Wiley & Sons, Oxford, pp. 229–249. http://dx.doi.org/10.1002/9781118529539.ch12.

Bergman, N.M., Lenton, T.M., Watson, A.J., 2004. COPSE: a new model of biogeochemical cycling over Phanerozoic time. Am. J. Sci. 304 (5), 397–437. http://dx.doi.org/10.2475/ajs.304.5.397.

Boardman, D.R., Iannuzzi, R., de Souza, P.A., da Cunha Lopes, R., 2012. Paleobotanical and palynological analysis of Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Paraná Basin), Rio Grande Do Sul, Brazil. Int. J. Coal Geol. 102, 12–25. http://dx.doi.org/10.1016/j.coal.2012.07.007.

Bowman, D.M., Balch, J.K., Artaxo, P., et al., 2009. Fire in the Earth system. Science 324 (5926), 481–484. http://dx.doi.org/10.1126/science.1163886.

Cazzulo-Klepzig, M., Mendonça Filho, J.G., Guerra-Sommer, M., Menezes, T.R., Simas, M.W., Mendonca, J.O., Degani-Schmidt, I., 2009. Effect of volcanic ash-fall on a Permian peat-forming environment, on the basis of palynology, palynofacies and paleobotany (Faxinal Coalfield, Brazil). Rev. Bras. Paleontol. 12 (3), 179–194. http://dx.doi.org/10.4072/rbp.2009.3.02.

Chaloner, W.G., 1989. Fossil charcoal as an indicator of paleoatmospheric oxygen level. J. Geol. Soc. 146 (1), 171–174. http://dx.doi.org/10.1144/gsjgs.146.1.0171.

Chmura, G.L., Stone, P.A., Ross, M.S., 2006. Non-pollen microfossils in Everglades sediments. Rev. Palaeobot. Palynol. 141 (1), 103–119. http://dx.doi.org/10.1016/j.revpalbo.2006.03.019.

Cohen, K.M., Finney, S.M., Gibbard, P.L., Fan, J.-X., 2013. The ICS International Chronostratigraphic Chart. Episodes 36 (3), 199–204.

Collinson, M.E., 1999. Scanning electron microscopy of megafossils and mesofossils. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 57–64.

Collinson, M.E., Steart, D.C., Scott, A.C., Glasspool, I.J., Hooker, J.J., 2007. Episodic fire, runoff and deposition at the Palaeocene–Eocene boundary. J. Geol. Soc. Lond. 164, 87–97. http://dx.doi.org/10.1144/0016-76492005-185.

Cope, M.J., Chaloner, W.G., 1985. Wildfire: an interaction of biological and physical processes. In: Tiffney, B.H. (Ed.), Geological Factors and the Evolution of Plants. Yale University Press, New York, pp. 257–277.

Degani-Schmidt, I., Sommer, M.G., Bernardes-de-Oliveira, M.E.C., 2011. Variation in stomatal numbers of Glossopteris leaves from the Lower Permian of Paraná Basin, Brazil. Rev. Bras. Paleontol. 14 (2), 137–148. http://dx.doi.org/10.4072/rbp.2011.2.02.

Diessel, C.F.K., 1992. Coal-Bearing Depositional Systems. Springer, Berlin (721 p).

Figueiral, I., 1999. Lignified and charcoalified wood. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 92–96.

Flannigan, M., Stocks, B., Turetsky, M., Wotton, M., 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob. Chang. Biol. 15 (3), 549–560. http://dx.doi.org/10.1111/j.1365-2486.2008.01660.x.

Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1996. Out of the icehouse into the greenhouse: a Late Paleozoic analog for modern global vegetation change. GSA Today 6 (10), 1–7.

Glasspool, I., 2000. A major fire event recorded in the mesofossils and petrology of the Late Permian, Lower Whybrow coal seam, Sydney Basin, Australia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 164 (1–4), 357–380. http://dx.doi.org/10.1016/S0031-0182(00)00194-2.

Glasspool, I., 2003. Hypautochthonous–allochthonous coal deposition in the Permian, South African, Witbank Basin No. 2 seam; a combined approach using sedimentology, coal petrology and palaeontology. Int. J. Coal Geol. 53 (2), 81–135. http://dx.doi.org/10.1016/S0166-5162(02)00193-3.

Glasspool, I.J., Scott, A.C., 2010. Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. Nat. Geosci. 3 (9), 627–630. http://dx.doi.org/10.1038/NGEO923.

Glasspool, I.J., Scott, A.C., 2013. Identifying past fire events. In: Belcher, C.M. (Ed.), Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science. John Wiley & Sons, Oxford, pp. 177–206. http://dx.doi.org/10.1002/9781118529539.ch10.

Glasspool, I.J., Edwards, D., Axe, L., 2004. Charcoal in the Silurian as evidence for the earliest wildfire. Geology 32 (5), 381–383. http://dx.doi.org/10.1130/G02363.1.

Grenfell, H.R., 1995. Probable fossil zygnematacean algal spore genera. Rev. Palaeobot. Palynol. 84 (3–4), 201–220. http://dx.doi.org/10.1016/0034-6667(94)00134-6.

Guerra-Sommer, M., 1992. Padrões epidérmicos de Glossopteridales da tafoflora do Faxinal (Formação Rio Bonito—Artinskiano-Kunguriano, Bacia do Paraná, Brasil). Pesqui. Geosci. 19 (1), 26–40.

Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., Formoso, M.L.L., Basei, M.Â.S., Barboza, E.G., Simas, M.W., 2008. Geochronological data from the Faxinal coal succession, southern Paraná Basin, Brazil: a preliminary approach combining radiometric U–Pb dating and palynostratigraphy. J. S. Am. Earth Sci. 25 (2), 246–256. http://dx.doi.org/10.1016/j.jsames.2007.06.007.

Hather, J.G., 2000. Archaeological Parenchyma. Archetype, London (97 p).

Henz, G.I., Corrêa-da-Silva, Z.C., 1987. Organo-petrologia dos carvões da Jazida do Faxinal, Município de Arroio dos Ratos, RS. I Congresso Brasileiro de Geoquímica 2. Anais, Porto Alegre, pp. 521–546.

Holz, M., França, A.B., Souza, P.A., Iannuzzi, R., Rohn, R., 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Parana Basin, Brazil, South America. J. S. Am. Earth Sci. 29 (2), 381–399. http://dx.doi.org/10.1016/j.jsames.2009.04.004.

Hower, J.C., O'Keefe, J.M., Wagner, N.J., Dai, S., Wang, X., Xue, W., 2013. An investigation of Wulantuga coal (Cretaceous, Inner Mongolia) macerals: paleopathology of faunal and fungal invasions into wood and the recognizable clues for their activity. Int. J. Coal Geol. 114, 44–53. http://dx.doi.org/10.1016/j.coal.2013.04.005.

Hudspith, V.A., Belcher, C.M., Yearsley, J.M., 2014. Charring temperatures are driven by the fuel types burned in a peatland wildfire. Front. Plant Sci. 5, 714. http://dx.doi.org/10.3389/fpls.2014.00714.

Hutton, A.C., Kantsler, A.J., Cook, A.C., 1980. Organic matter in oil shales. J. Aust. Petrol. Explor. Assoc. 20, 44–67.

Iannuzzi, R., 2010. The flora of Early Permian coal measures from the Paraná Basin in Brazil: a review. Int. J. Coal Geol. 83 (2), 229–247. http://dx.doi.org/10.1016/j.coal.2010.05.009.

Jasper, A., Uhl, D., Guerra-Sommer, M., Bernardes-de-Oliveira, M.E.C., Machado, N.T.G., 2011a. The Late Paleozoic charcoal remains from South America: multiple evidence of fire events in the coal bearing strata of the Paraná Basin, Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 306 (3–4), 205–218. http://dx.doi.org/10.1016/j.palaeo.2011.04.022.

Jasper, A., Uhl, D., Guerra-Sommer, M., Hamad, A.A., Machado, N.T., 2011b. Charcoal remains from a tonstein layer in the Faxinal Coalfield, Lower Permian, southern Paraná Basin, Brazil. An. Acad. Bras. Cienc. 83 (2), 471–481.

Jones, T.P., 1993. New morphological and chemical evidence for a wildfire origin for fusain from comparisons with modern charcoal. Spec. Pap. Palaeontol. 49, 113–123.

Jones, T.P., Chaloner, W.G., 1991. Fossil charcoal, its recognition and palaeoatmospheric significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 97 (1–2), 39–50. http://dx.doi.org/10.1016/0031-0182(91)90180-Y.

Jones, T.P., Rowe, N.P., 1999. Embedding techniques: adhesive and resins. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 71–75.

Jones, T.P., Scott, A.C., Cope, M., 1991. Reflectance measurements against temperature of formation for modern charcoals and their implications for the study of fusain. Bull. Soc. Geol. Fr. 162, 193–200.

Jones, T.P., Scott, A.C., Mattey, D.P., 1993. Investigations of fusain transition fossils from the Lower Carboniferous: comparisons with modern partially charred wood. Int. J. Coal Geol. 22, 37–59. http://dx.doi.org/10.1016/0166-5162(93)90037-B.

Kalkreuth, W., Holz, M., Kern, M., Machado, G., Mexias, A., Silva, M.B., Burger, H., 2006. Petrology and chemistry of Permian coals from the Paraná Basin: 1. Santa Terezinha, Leão-Butiá and Candiota Coalfields, Rio Grande do Sul, Brazil. Int. J. Coal Geol. 68 (1–2), 79–116. http://dx.doi.org/10.1016/j.coal.2005.10.006.

Livingstone, J.A., Melack, D.M., 1984. Some lakes of sub-Saharan Africa. In: Taub, F.B. (Ed.), Lake and reservoir ecosystems 23. Elsevier Science, Amsterdam, pp. 467–497.

McParland, L.C., Collinson, M.E., Scott, A.C., Campbell, G., 2009. The use of reflectance values for the interpretation of natural and anthropogenic charcoal assemblages. Archaeol. Anthropol. Sci. 1 (4), 249–261. http://dx.doi.org/10.1007/s12520-009-0018-z.

Mendonça Filho, J.G., Mendonca, J.O., Menezes, T.R., Oliveira, A.D., Carvalho, M.A., Santanna, A.J., Souza, J.T., 2010. Palinofácies. In: Carvalho, I.S. (Ed.), 3rd ed. Paleontologia 1. Interciência, Rio de Janeiro, pp. 379–413.

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. Boletim de Geociências da Petrobras, Rio de Janeiro 15 (2), 265–287.

Montañez, I.S., Tabor, J.N., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.P., Rygel, M.C., 2007. CO_2-forced climate and vegetation instability during Late Paleozoic deglaciation. Science 315 (5808), 87–91. http://dx.doi.org/10.1126/science.1134207.

Ohlson, M., Tryterud, E., 2000. Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. The Holocene 10 (4), 519–525.

O'Keefe, J.M., Bechtel, A., Christanis, K., et al., 2013. On the fundamental difference between coal rank and coal type. Int. J. Coal Geol. 118, 58–87. http://dx.doi.org/10.1016/j.coal.2013.08.007.

Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.-D.V., Jaya, A., Limin, S., 2002. The amount of carbon released from peat and forest fires in Indonesia during 1997. Nature 420, 61–65. http://dx.doi.org/10.1038/nature01131.

Philippe, M., 1993. Nomenclature générique des trachéidoxyles mésozoïques à champs araucarioïdes. Taxon 42, 74–80. (http://dx.doi.org/10.2307/1223305).

Philippe, M., 2011. How many species of Araucarioxylon? C. R. Palevol 10 (2), 201–208. http://dx.doi.org/10.1016/j.crpv.2010.10.010.

Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. Rev. Palaeobot. Palynol. 148 (2), 184–207. http://dx.doi.org/10.1016/j.revpalbo.2007.09.004.

Pierce, J.L., Meyer, G.A., Jull, A.T., 2004. Fire-induced erosion and millennial-scale climate change in northern ponderosa pine forests. Nature 432 (7013), 87–90. http://dx.doi.org/10.1016/S0378-1127(03)00055-0.

Prat, N., Belcher, C.M., Hadden, R.M., Rein, G., Yearsley, J.M., 2015. A laboratory study of the effect of moisture content on the spread of smouldering peat fires. FLAMMA 6 (1), 35–38.

Prevec, R., Labandeira, C.C., Neveling, J., Gastaldo, R.A., Looy, C.V., Bamford, M., 2009. Portrait of a Gondwanan ecosystem: a new late Permian fossil locality from KwaZulu-Natal, South Africa. Rev. Palaeobot. Palynol. 156 (3–4), 454–493. http://dx.doi.org/10.1016/j.revpalbo.2009.04.012.

Rein, G., Cleaver, N., Ashton, C., Pironi, P., Torero, J.L., 2008. The severity of smouldering peat fires and damage to the forest soil. CATENA 74 (3), 304–309. http://dx.doi.org/10.1016/j.catena.2008.05.008.

Rößler, R., Philippe, M., van Konijnenburg-van, Cittert, et al., 2014. Which name (s) should be used for Araucaria-like fossil wood?—Results of a poll. Taxon 63 (1), 177–184.

Santos, R.V., Souza, P.A., Alvarenga, C.J.S., Dantas, E.L., Pimentel, M.M., Oliveira, C.G., Araújo, L.M., 2006. Shrimp U–Pb zircon dating and palynology of bentonitic layers from the Permian Irati Formation, Paraná Basin, Brazil. Gondwana Res. 9 (4), 456–463. http://dx.doi.org/10.1016/j.gr.2005.12.001.

Scott, A.C., 1989. Observations on the nature and origin of fusain. Int. J. Coal Geol. 12 (1–4), 443–475. http://dx.doi.org/10.1016/0166-5162(89)90061-X.

Scott, A.C., 2000. The Pre-Quaternary history of fire. Palaeogeogr. Palaeoclimatol. Palaeoecol. 164, 281–329. http://dx.doi.org/10.1016/S0031-0182(00)00192-9.

Scott, A.C., 2001. Preservation by fire. In: Briggs, D.E.G., Crowther, P.J. (Eds.), Palaeobiology II. Blackwell, Oxford, pp. 277–280.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291 (1–2), 11–39. http://dx.doi.org/10.1016/j.palaeo.2009.12.012.

Scott, A.C., Glasspool, I.J., 2006. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. Proc. Natl. Acad. Sci. U. S. A. 103 (29), 10861–10865. http://dx.doi.org/10.1073/pnas.0604090103.

Scott, A.C., Glasspool, I.J., 2007. Observations and experiments on the origin and formation of Inertinite group macerals. Int. J. Coal Geol. 70 (1–3), 55–66. http://dx.doi.org/10.1016/j.coal.2006.02.009.

Scott, A.C., Jones, T.P., 1991. Fossil charcoal: a plant fossil record preserved by fire. Geol. Today 7, 214–216.

Scott, A.C., King, G.R., 1981. Megaspores and coal facies; and example from the Westphalian A of Leicestershire, England. Rev. Palaeobot. Palynol. 34, 107–113. http://dx.doi.org/10.1016/0034-6667(81)90068-3.

Scott, A., Bowman, D.M.J.S., Bond, W.J., Pyne, S.J., Alexander, M.E., 2014. Fire on Earth: An Introduction. Wiley-Blackwell, Oxford (434 p).

Simas, M.W., Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., Santos, J.O.S., Ferreira, J.A.F., Degani-Schmidt, I., 2012. Geochronological correlation of the main coal interval in Brazilian Lower Permian: radiometric dating of tonstein and calibration of biostratigraphic framework. J. S. Am. Earth Sci. 39, 1–15. http://dx.doi.org/10.1016/j.jsames.2012.06.001.

Simas, M.W., Guerra-Sommer, M., Mendoça Filho, J.G., Cazzulo-Klepzig, M., Formoso, M.L.L., Degani-Schmidt, I., 2013. An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a Lower Permian tonstein bed (Faxinal Coalfield, Paraná Basin, Brazil). Geol. Acta 11 (1), 47–57. http://dx.doi.org/10.1344/105.000001835.

Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R., Watts, A., 2015. Global vulnerability of peatlands to fire and carbon loss. Nat. Geosci. 8, 11–14. http://dx.doi.org/10.1038/ngeo2325.

Vogellehner, D., 1964. Zur Nomenklatur der fossilen Holzgattung Dadoxylon Endlicher 1847. Taxon 13, 233–237. http://dx.doi.org/10.2307/1216692.

Yi, S., 1997. Zygnematacean zygospores and other freshwater algae from the Upper Cretaceous of the Yellow Sea Basin, southwest coast of Korea. Cretac. Res. 18 (4), 515–544. http://dx.doi.org/10.1006/cres.1996.0072.

Ziegler, A.M., Eshel, G., Rees, P.M., Rothfus, T., Rowley, D., Sunderlin, D., 2003. Tracing the tropics across land and sea: Permian to present. Lethaia 36 (3), 227–254. http://dx.doi.org/10.1080/00241160310004657.

Review of Palaeobotany and Palynology 226 (2016) 20–29

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Charcoalified *Agathoxylon*-type wood with preserved secondary phloem from the lower Permian of the Brazilian Parana Basin

Isabela Degani-Schmidt [a,*], Margot Guerra-Sommer [b]

[a] Programa de Pós-Graduação em Geociências/UFRGS, Porto Alegre, Brazil
[b] Instituto de Geociências/UFRGS, Porto Alegre, Brazil

ARTICLE INFO

Article history:
Received 2 July 2015
Received in revised form 10 December 2015
Accepted 13 December 2015
Available online 19 December 2015

Keywords:
Secondary phloem
Fossil wood anatomy
Glossopteris Flora
Gondwanaland
Paleozoic
Charcoal

ABSTRACT

For the first time, secondary phloem tissue of *Agathoxylon* Hartig (sensu Rößler et al. 2014) is described from Permian charcoalified wood remains. Large (up to 13.4 × 21.8 cm), highly compressed, charred logs and branches were collected from the lower and upper boundaries of a tonstein bed (U/Pb age 291 ± 1.3 Ma) interlayered in a Sakmarian coal seam in the Faxinal Coalfield, Rio Grande do Sul, Brazil (Rio Bonito Formation). Small pieces were sampled with a dissecting knife and needles, mounted on standard stubs, gold-coated, and photographed under a scanning electron microscope. The phloem tissue is composed of thin-walled sieve cells, thick-walled fibers, and axial and radial uniseriate parenchyma. The extraordinary preservation shows sieve cells with pores grouped in conspicuous sieve areas occurring on lateral cell walls. Sieve cells are inferred to be arranged in tangential layers alternating with mixed rows of fibers and scarce parenchyma. Conclusions are drawn about preservation conditions involving cyclic environmental dryness and possible affinities with pteridosperms and cordaitaleans.

1. Introduction

Land plants underwent a rapid diversification after the emergence of conductive tissue approximately 400 million years ago (Niklas, 1997), and the knowledge of the evolution of the vascular tissue through geologic time comes predominantly from secondary xylem (Taylor, 1990). Even though bifacial vascular cambium yielding both secondary xylem and secondary phloem is already present in the Devonian (Raven and Andrews, 2010), for a long time, contributions to phloem phylogeny were mainly based on inferences from extant groups due to its rarity in the fossil record (Van Bel, 1999).

The preservation of phloem tissue is influenced by its generally insubstantial production by the cambium, the thin-walled structure of the conducting cells, and physical instability on account of the functional hydrostatic pressure to which they are subjected, favoring the collapse of the sieve cells following damage (Esau et al., 1953; Smoot and Taylor, 1978; Taylor, 1990; Beck, 2005). Furthermore, Paleozoic stems are in most cases decorticated, precluding secondary phloem observation (Decombeix et al., 2014).

The charcoalification process can potentially preserve most cellular structures three-dimensionally (Lupia, 1995), but the resultant material is brittle and susceptible to breakage from transport and compression; additionally, the fire temperature can either preserve or destroy delicate tissues (Scott, 2010). According to Hather (2000), during a wildfire, the phloem tissue can deteriorate or solidify, generating a formless mass of glassy charred tissue. However, good preservation occurs if the plant tissues have been slowly dried prior to charring. Specific environmental conditions are thus required to yield informative charcoalified plant material.

The present study documents the occurrence of charcoalified *Agathoxylon*-type wood and describes the organically associated secondary phloem tissue from large, exceptionally well-preserved specimens resulting from autochthonous/hypautochthonous charcoal input to Permian peat (Degani-Schmidt et al., 2015). Conclusions about the preservation conditions are drawn and anatomical affinities are briefly discussed based on xylem and phloem features.

2. Geologic and paleontological context

The study area comprises the Faxinal Coalfield, an opencast coal mine located at the southeastern outcrop belt of the Rio Bonito Formation of the Paraná Basin, southern Brazil (Fig. 1A, 30°15′52.6″S, 51°41′53.8″W).

The top coal seam S interlayers with a tonstein bed (Plate I, 1, 2) dated at 291 ± 1.3 Ma (radiometric age after Simas et al., 2012) thus being of late Sakmarian age (Cohen et al., 2013; updated 2015) (Fig. 1B, C). The tonstein occurs throughout the coal seam area (1.6 km^2) and contains abundant compressed plant organs of the *Glossopteris* Flora (Plate I, 3).

---

[*] Corresponding author at: PPG-Geo/UFRGS, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil. Tel.: +55 51 3308 63 78.

E-mail addresses: degani.schmidt@ufrgs.br (I. Degani-Schmidt), margot.sommer@ufrgs.br (M. Guerra-Sommer).

http://dx.doi.org/10.1016/j.revpalbo.2015.12.003

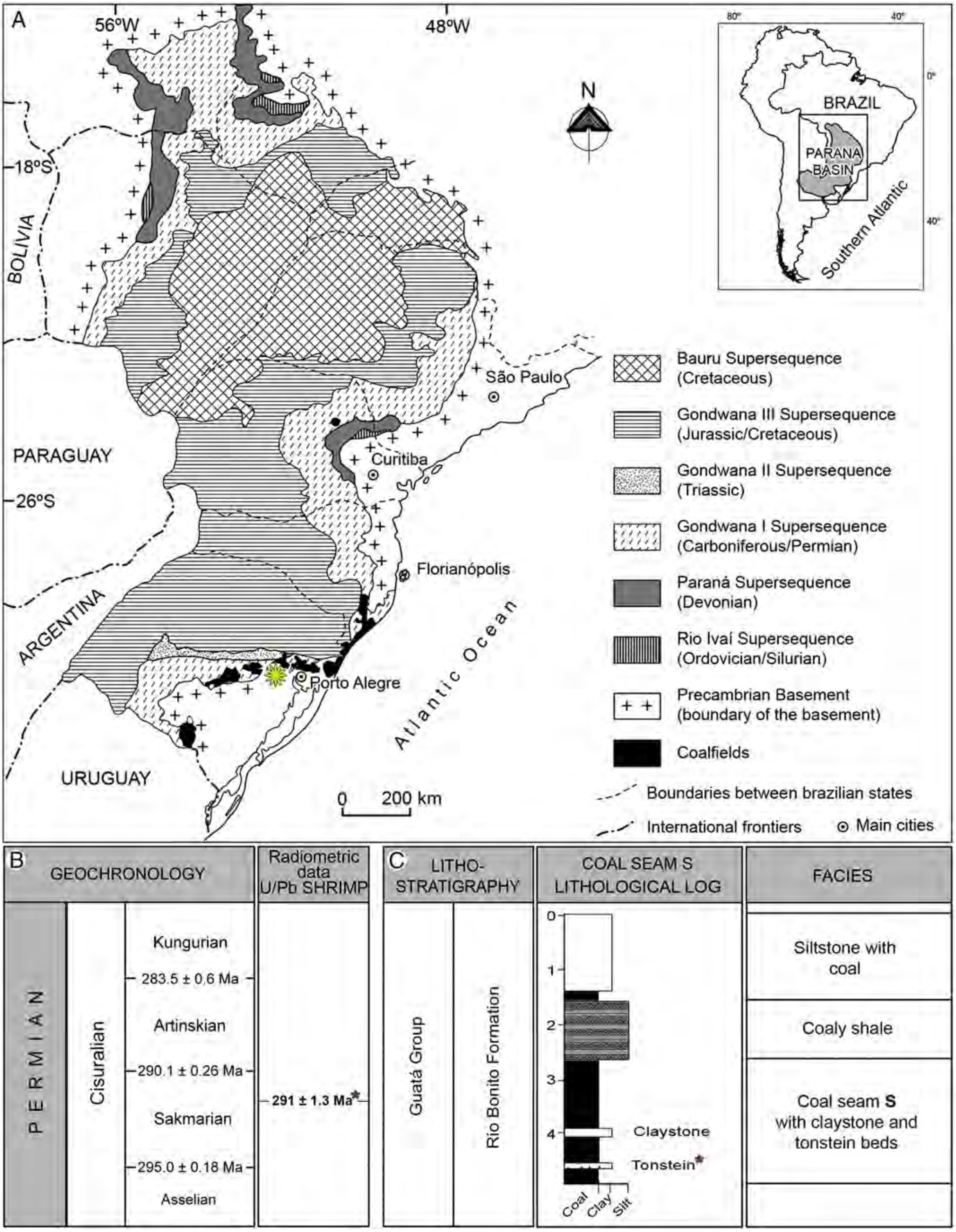


Fig. 1. Map and stratigraphic framework. A) Location map (modified from Santos et al., 2006); B) geochronology (after Cohen et al., 2013; updated 2015), and radiometric age (Simas et al., 2012); C) lithostratigraphy of the coal seam S and overlying layers (after Guerra-Sommer et al., 2008). *Radiometric age obtained through SHRIMP (Sensitive High Resolution Ion Microprobe) in zircons from the tonstein bed.

In their most recent revision of the tonstein coalified macroflora, Boardman et al. (2012) reported relative abundances in glossopterid leaves of 78%, followed by cordaitalean leaves 17.6%, reproductive axes 2%, pteridophyte fronds 1.4%, and seeds 1%, and confirmed the low plant diversity previously reported by Cazzulo-Klepzig et al. (2007). It is important to highlight that there is no record of conifer macrofossils in the Faxinal Coalfield.

Palynological and palynofacies analyses conducted by Cazzulo-Klepzig et al. (2009) found that bisaccate pollen grains are the most abundant components (41%) in the palynoassemblage from the coal beneath the tonstein and include *Protohaploxypinus*, *Vittatina*, and *Fusacolpites* (according to Boardman et al., 2012), providing strong evidence of glossopterid proximity to the catchment basin. Monosaccate pollen grains of cordaitaleans (9%) and striate pollen grains (6%) indicate that conifers were less significant constituents of the original peat-forming community. In the coal above the tonstein a frequency of 57% glossopterid-related palynomorphs has been found (Cazzulo-Klepzig et al., 2009).

3. Material and methods

Charcoalified wood fragments come from the coal associated with the base and the top of the tonstein bed (Plate I, 2). Large, highly compressed, brittle specimens (Plate I, 4–6) could be retrieved because they were attached to the tonstein, which held the specimens together.

The lower charcoal horizon contains highly compressed charred logs up to 21.8 × 13.4 cm in size (Plate I, 4, 6). The upper charcoalified material is mostly composed of branch and twig fragments up to 16.4 × 5.7 cm in size (Plate I, 5).

Small pieces were collected with a dissecting knife and needles from tonstein slabs under a Leica S8 APO stereoscopic microscope. The unprepared material, often fragmented into elongated laths, was then mounted on standard stubs with double-sided tape, gold coated and subsequently examined and photographed with a JEOL JSM 6060 Scanning Electron Microscope (Collinson, 1999; Figueiral, 1999; Scott, 2001). Measurements were taken with the Zeiss Axio Vision 4.8.1 software. Plates were composed with Adobe Photoshop CS3 Extended.

Ten stubs have been analyzed from a total of six specimens, all of which are deposited at the Paleobotanical Collection of the Universidade Federal do Rio Grande do Sul (UFRGS), Brazil. The phloem tissue is described from the specimens Pb4587B, Pb4629, and Pb5122A, and the xylem tissue from Pb4587A, Pb4626A, Pb4629, Pb5122A, Pb5126, and Pb5128.

4. Description

Attributes like black color, silky luster, well-preserved anatomical details, and homogenized cell walls (Plate II, 1; Plate III; 1–3) are present in the xylem and phloem tissues of the analyzed material and are according to Jones and Chaloner (1991) and Scott (1989, 2000, 2010) diagnostic of macroscopic charcoal.

Cell measurements are not given because longitudinal cell walls are mostly inconspicuous due to homogenization and cell ends can only rarely be seen in ?parenchyma cells of the phloem tissue. General cell proportions can, however, be observed on the present images.

4.1. Secondary xylem anatomy

The secondary xylem is composed of tracheids and parenchymatous rays. Tracheids exhibit a mixed pattern of pitting in a single specimen (Plate II, 2). When uniseriate, the disposition of the areolate pitting is rounded, separated, rarely contiguous but not flattened, with distances between neighboring pitting from uniform to irregular (Plate II, 2, 3). Biseriate pitting is arranged from sub-opposite to alternate, flattened when crowded (Plate II, 4, 5, 7), and when triseriate, they are opposite to sub-opposite, sometimes flattened (Plate II, 6). Cell walls are

Plate I. Field and hand sample photographs. Scale bars 1) 5 m; 2–6) 5 cm.

1. Pit bench exposure of coal seam S (arrowhead).
2. Close up of the interbedded tonstein ply in upper coal seam S.
3. Coalified leaves of the *Glossopteris* Flora preserved in the tonstein bed (Pb4762A).
4. Large fragments of a probably branched log associated to the tonstein rock.
5. Charcoalified branch fragments (Pb5122A).
6. Charred log fragment (Pb2684).

Plate II. Xylem tissue. Scale bars 1) 10 μm; 2–14) 20 μm. (see on page 6)

1. Homogenized cell wall (Pb4587A-05-07).
2. Mixed type of pitting in a single specimen. *Uniseriate contiguous; **biseriate (Pb4587A-84-04).
3. Uniseriate, separated pitting (Pb4587A-05-04).
4. Biseriate, alternate pitting (Pb4587A-04-04).
5. Biseriate, alternate, crowded and flattened pitting (Pb5128-54-21).
6. Triseriate type of pitting (Pb4587A-04-14).

7, 8. *Wall corrugation on the inside of tracheids (Pb4587A-04-15; Pb4587A-04-03).

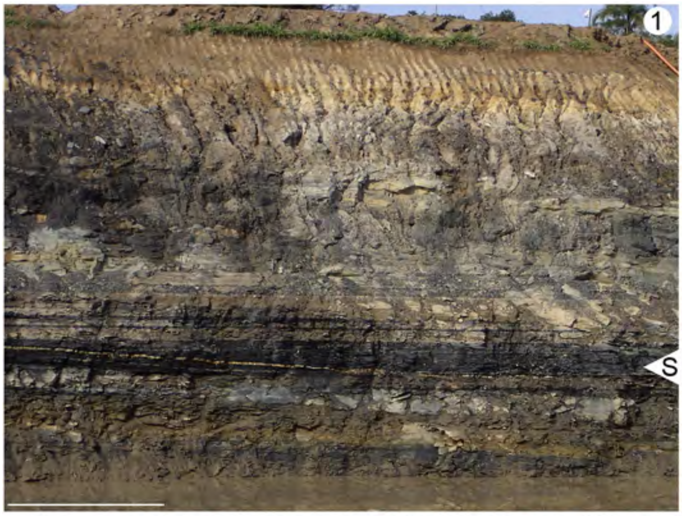
9, 10. Cross-fields with unordered oculipores (arrows) (Pb5126-26-19; Pb5126-26-13).

11. Uniseriate rays of varying heights (arrows) (Pb5128-54-16; Pb5128-71-08).
12. Crushed tracheids in tangential/cross-section (Pb5128-72-13). *Ray; **tracheid radial wall broken along the pitting due to compression.
13. Fungal hypha (Pb4587A-04-06).

Plate III. Phloem tissue. Scale bars 20 μm. (see on page 7)

1. Composite image of tangential and cross-section featuring all phloem elements, i.e. sieve cells, axial fibers and parenchyma and parenchymatous ray; *homogenized cell walls; probable bundle of fibers (white arrow) (Pb4587B-56-03).
2. Colorized version of image 1 (see color key below).
3. Homogenized cell wall of thick-walled fiber in axial and oblique section; fiber lumen (black arrow); probable intercellular space (white arrow) (Pb4587B-56-09).
4. Detail of sieve areas; fungal hypha (white arrow). Axial wall of sieve cell is inconspicuous due to homogenization (Pb4587B-56-14).
5. Transverse end walls of parenchyma cells (white arrow); row of simple pits on the inner side of the sieve cell at the place where it attaches to a fiber (black arrow); highlighted fungal hypha (Pb4587B-56-53).
6. Composite image featuring long strands of sieve cells and ray in tangential view (Pb4587B-57-08).
7. Tangential tearing pattern of sieve cells and vesicles on the parenchymatous walls (arrow) (Pb4587B-57-03).
8. Branching and anastomosing fungal hyphae (black arrow); sieve area (white arrow) (Pb4587B-56-32).
9. Probable fungal haustorium (Pb5122A-08-21).
10. Probable fungal sclerotia (white arrow) located between transverse end walls of parenchymatous cells (Pb4587B-56-01).

Color key: yellow = sieve cells; red = fibers; blue = axial parenchyma; green = parenchymatous ray; orange = fungal hyphae.


1
S


4


2


5


3


6
PB 2684

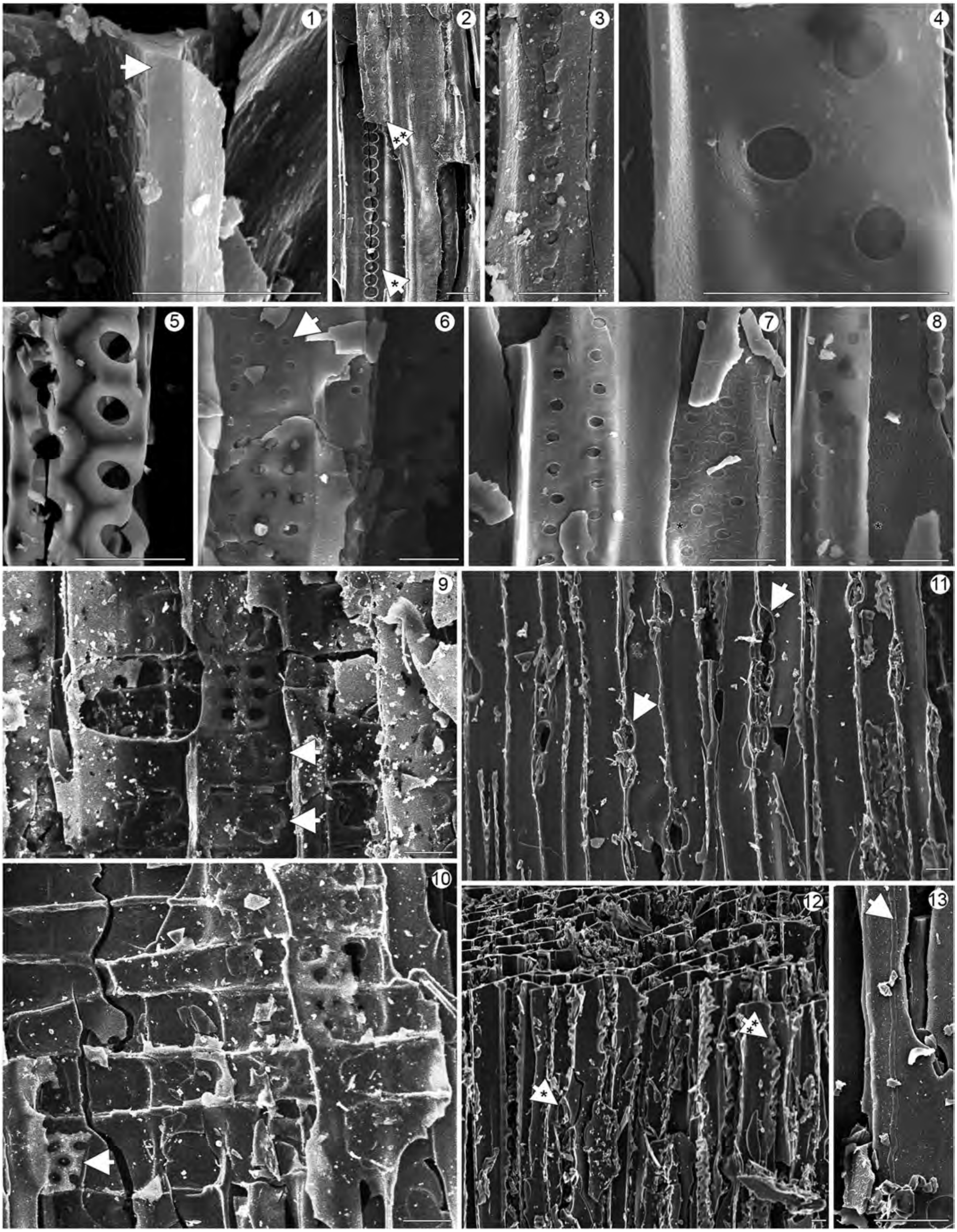


Plate III (*caption on page 22*).

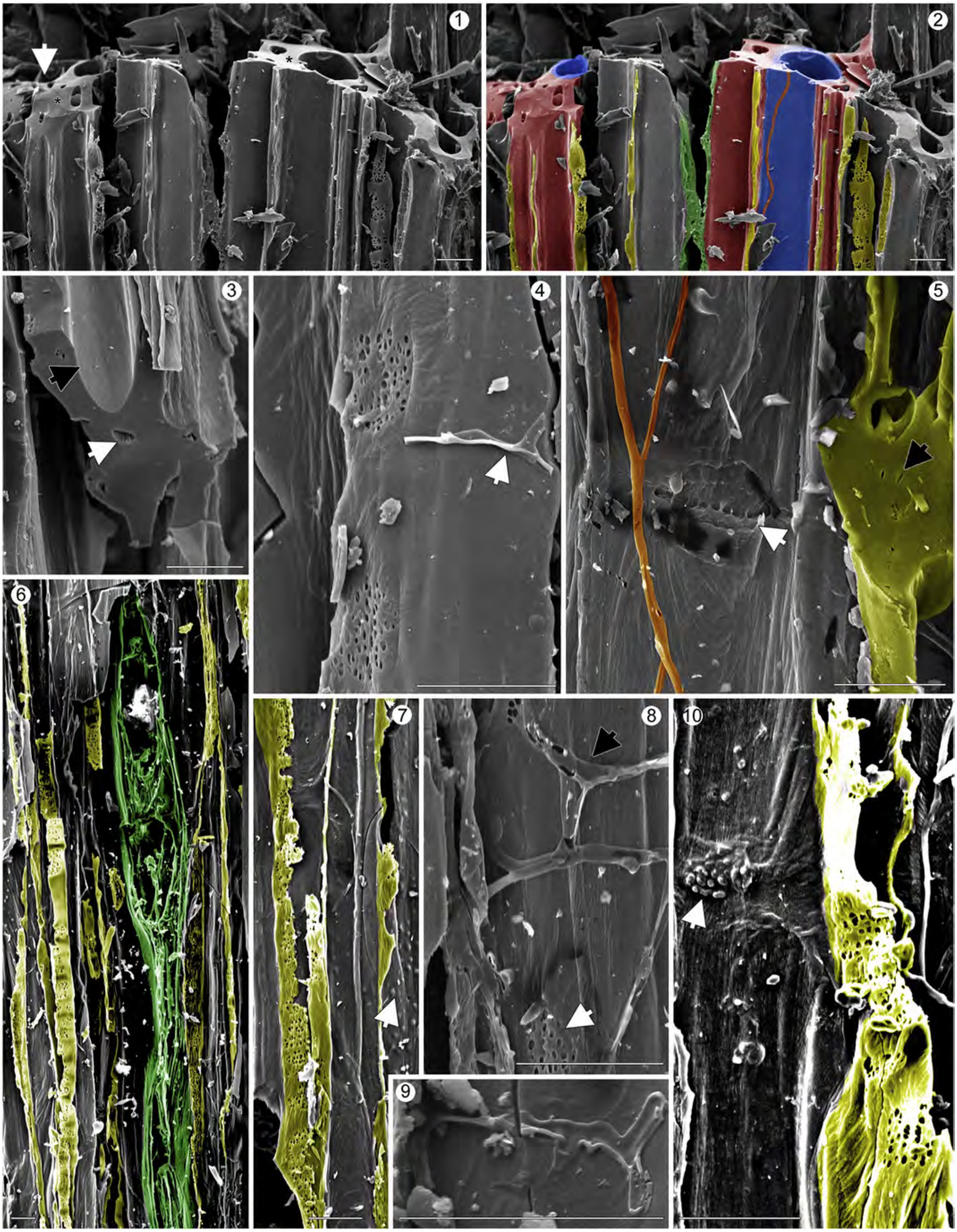


Plate III (*caption on page 22*).

sometimes corrugated on the inside (Plate II, 7, 8). Cross-fields are frequently present but cross-field pitting is rarely preserved, being of the araucarian type with numerous contiguous unordered cupressoid to taxodioid oculipores (Plate II, 9, 10). Tangential views show uniseriate parenchymatous rays 1–11 cells high, more frequently 1–8 (Plate II, 11). Cross-section views are not informative because specimens are compressed and tracheids are crushed (Plate II, 12).

4.2. Secondary phloem anatomy

Phloem tissue is preserved in very superficial areas of the charred wood fragments. It is similar in all observed specimens, organized in axial and transversal cell systems, which are composed by thin-walled sieve cells, axial parenchyma, fibers, and uniseriate parenchymatous rays. While thick-walled cells of the phloem tissue are homogenized (Plate III, 1–3), the sieve cells are found more often detached or adhered to the secondary walls of the adjacent cells, but sometimes also homogenized (Plate III, 1, 2, 4, 6, 7). Probable intercellular spaces can be observed in the homogenized walls in cross-section view (Plate III, 3).

Limited cross-section and tangential views suggest that sieve cells are arranged in continuous tangential layers alternating with mixed rows of parenchyma and fibers (Plate III, 1, 2, 6). The sieve cells are elongated, contiguous, noticeably composed of thin primary wall only, shrunk, and collapsed so that the radial sieve areas are seen in tangential view, being narrower than the rectangular molds formed by a matrix of adjacent and homogenized secondary walls of axial parenchyma and fibers (Plate III, 1, 2). Sometimes, the sieve cells are attached to the secondary wall matrix by one side and torn longitudinally (Plate III, 5, 7). Simple pits can be observed inside the sieve cells at the site where they attach to the fibers (Plate III, 5).

Sieve areas occur on lateral (radial) walls, are sub-elliptical to sub-rectangular in shape, range from 4.9 to 13.3 μm high, with a mean width of 17.2 μm (60 sieve areas measured; Plate III, 4), and are nearly as wide as the sieve cell. Distances between sieve areas range from 0.4 to 12.7 μm. Sieve pores are round to elliptical, occasionally septate or coalesced (Plate III, 4), with sizes ranging from 0.5 to 1.9 μm high and 0.4 to 1.0 μm wide. The number of pores per area ranges from 34 to 70. Generally, the pores seem to spread centrifugally from several origin centers in a single sieve area.

In cross-section, thick-walled cells can be observed and are interpreted as fibers. They have sub-triangular to oval lumen, and their thick walls are homogenized with adjacent parenchyma and other fiber walls (Plate III, 1, 2, 3). They sometimes occur in bundles.

Cells of the axial parenchyma are identified by having a round, larger lumen than the fibers (Plate III, 1, 2), and transverse cell ends (Plate III, 5). Vesicles can be frequently observed in the parenchyma walls (Plate III, 7).

Parenchymatous rays are frequent, uniseriate and from 1 to 10 cells high, mostly 1–6 (Plate III, 6).

4.3. Fungal hyphae

Fungal hyphae are rare in the xylem and frequent in the phloem tissue, where they are associated with the sieve cells and parenchymatous rays (Plate II, 13; Plate III, 2, 4, 5, 8, 9). Filaments are collapsed (flat) and adhered to the cell walls, anastomosing and branching, and their width ranges from 0.84 to 2.41 μm. Occasional groupings of subspherical bodies could correspond to fungal sclerotia (Plate III, 10).

5. Discussion

5.1. Paleoenvironmental context

The studied material comes from an environment where peat accumulated in a wet woodland setting with understory shrubs. Previous palynological, palynofacies, and organic petrographic analyses showed that woody gymnosperms (mainly glossopterids) in a forested environment were the main producers of the original coal biomass in the Faxinal Coalfield (Henz and Corrêa-da-Silva, 1987; Cazzulo-Klepzig et al., 2007, 2009; Boardman et al., 2012; Simas et al., 2013). This particular scenario differs from other Brazilian coalfields, which are characterized by a herbaceous and shrub-like vegetation, with a predominance of sub-arborescent and herbaceous lycophytes, subordinate filicophytes and sphenophytes, and less abundant gymnospermous groups of glossopterids, cordaitaleans, and conifers from the hinterland (e.g. Cazzulo-Klepzig et al., 1993, 2005; Ricardi-Branco and Rösler, 2004; Mendonça Filho et al., 2013).

Evidences of wildfires have been reported from Gondwanan coal-bearing strata based on the presence of macroscopic charcoal (Jasper et al., 2013; Slater et al., 2015) and occur in different Permian sequences, e.g., the Sakmarian–Artinskian of the Paraná Basin (Brazil), the Artinskian of the Karoo Basin (South Africa), the Lopingian of the Damodar Basin (India), the Roadian–Wordian of East Antarctic Toploje Member. Macroscopic charcoal fragments, mostly of gymnospermous anatomy, are generally found as small pieces (up to about 5 cm long), with abraded edges. In the material here analyzed, the extremely delicate primary walls of the sieve cells (Evert, 1977, 2006), preserved in the large charred logs and branches, indicate particular autochthonous/hypautochthonous depositional conditions in the peat-forming environment, such as low-temperature wildfires following cyclic environmental dryness. This is confirmed by low values of inertinite reflectance measurements (Degani-Schmidt et al., 2015). Fire susceptibility in this swamp forest of temperate southern latitude was explained by the combination of dry events, large fuel supply, and atmospheric oxygen levels higher than in present. Fires were probably ignited by lightning strikes.

5.2. General anatomical aspects

Given the naturally fragile constitution of charcoalified tissue, the radial walls in the secondary phloem are frequently folded over the tangential walls due to high compression from the sedimentation process and have been preferentially preserved (Plates II, 12; III, 1, 2).

A study conducted by Lupia (1995) showed that fire introduces preservational bias, and structures undergo differential shrinkage during charcoalification, which is reflected in the observed longitudinal tearing pattern of the thin-walled sieve cells (Plate III, 2, 7). Despite the shrinkage, the distribution of sieve areas and sieve pores do not appear to be artifacts of the preservation process and seem to have held sizes and distances proportionally. Marked fluctuations in sieve pore size, as well as in the spacing between sieve areas are observed in single specimens and could be attributed to distinct maturation status of the sieve cell. Sieve cell ends are not discernible in the analyzed material, but it is possible that the crowding of sieve areas occurs at sites of overlapping ends (Plate III, 6, 7).

The absence of callose structures suggests that either the phloem was still active at the moment of the fire or, due to its polysaccharidic composition (Boureau, 1954), the callose has been selectively destroyed by the fire. The presence of few axial parenchyma cells could mean that the observed sections belong to old phloem, where thin-walled cells are mostly collapsed and compressed against fibers towards the cortex region, as sometimes observed by Decombeix et al., 2014. On the other hand, Decombeix et al. (2015) reported a proliferation of axial parenchyma in the old (outer) phloem of glossopterid wood, associated with bark shedding. Considering the good preservation of the here described material and absence of bark, it is more likely that the observed sections belong to the inner part of the (active) phloem tissue and that the outer part would have probably been damaged by the fire. However, not enough layer repetitions have been observed in order to ascertain this.

The occurrence of corrugated walls in the xylem (Plate II, 7, 8) and vesicles in the secondary walls of phloem cells (Plate III, 7) could be attributed to thermal deformation rather than being actual anatomical features.

Fungal hyphae are more abundant in the phloem than in the xylem, and scarce signs of tissue decay suggest that the fungal infestation may have been interrupted early on by the fire. Hyphae are preferentially adhered to the walls of axial and radial parenchyma and sieve cells (Plate III, 2, 4, 5, 8). Petrographic analysis indicated that the plants burned in growth position (Degani-Schmidt et al., 2015), and the fungi probably colonized the plants shortly before the fire event. Fungal hyphae and spores associated to charcoals in the fossil record have also been mentioned by Harris (1958), Scott (2000), and Uhl et al. (2007). Harris (1958) observed chlamydospores on mixed charred and uncharred fossil remains, concluding that the plant shoots begun to rot before the fire, while Uhl et al. (2007) could not be certain if the wood infestation began in living or dead tissue.

5.3. Secondary xylem

The mixed type of araucarian pitting occurring in single specimens corresponds to the fossil genus *Agathoxylon* Hartig (sensu Bamford and Philippe, 2001; Philippe, 2011; Rößler et al., 2014). This anatomical wood pattern is characterized by the occurrence in the tracheids of bordered pits both contiguous uniseriate and alternate multiseriate, cross-field pitting of araucarian type showing contiguous cupressoid to taxodioid oculipores, uniseriate rays, and absence of axial parenchyma. This wood pattern is widespread among late Paleozoic and Mesozoic gymnosperms of different phylogenetic affinities (Prevec et al., 2009; Taylor et al., 2009) from both the northern and southern hemispheres, most of which had previously been identified as *Dadoxylon* Endlicher (according to Gothan, 1905; Vogellehner, 1964; Philippe, 1993). After analyzing more than 400 morphospecies designated as *Araucarioxylon*-type of wood, Philippe (2011) concluded that *Agathoxylon* seems to be the most appropriate name for the corresponding fossil genus. Rößler et al. (2014) advocate the use of *Agathoxylon* rather than *Dadoxylon* or *Araucarioxylon* Kraus.

The main differences between *Agathoxylon* and *Australoxylon* Marguerier, defined for Permian Gondwanan woods (Marguerier, 1973), are the co-occurrence in the latter of three types of radial pitting on the tracheids, namely, araucarioid, abietinean, and the conspicuous arrangements in groups of 2–5 pits. Such a pattern is frequently attributed to glossopterid pteridosperms (e.g., Gulbranson et al., 2014). Charcoal fragments identified as *Agathoxylon* have been reported several times from the Permian of Gondwanaland associated with the *Glossopteris* Flora (Jasper et al., 2013 and citations therein), and the dominance of glossopterid pollen grains both in the coal and the tonstein of Faxinal Coalfield, and abundant coalified glossopterid leaves found in the interlayered tonstein bed are indirect evidences of a possible glossopterid affinity for the studied charred woods. However, other affinities with cordaitaleans, which occur in the assemblage in lower frequency, cannot be excluded.

5.4. Secondary phloem

Descriptions of secondary phloem tissue in fossil stems are rare and illustrations showing details at cellular level are usually not possible due to poor preservation or impaired by preparation techniques. The record of phloem tissue in charcoalified material which yields exquisite details is especially rare.

Little attention has been paid to phloem tissue in most descriptions of fossil wood, but the information it contains can contribute to elucidate diversification at species level and growth strategies, while xylem yields more generic information. In a review of the phloem tissue in Paleozoic and Mesozoic plants, Taylor (1990) pointed out that the presence of fibers and the layered arrangement of phloem cells can be of taxonomic value for both fossil and extant plant groups. Decombeix et al. (2014) observed that the arrangement in successive tangential layers was already present in Devonian–Carboniferous lignophytes and created four categories for the different structural types of secondary phloem tissue found in Paleozoic plants. Their “Model C” includes gymnospermous phloem types featuring regular alternation of tangential layers of the different cell types, fibers in generally continuous tangential layers of 1–2 cell thickness, and axial parenchyma. The apparent regular arrangement of the secondary phloem here described for *Agathoxylon*-type wood, inferred as an alternation of uniseriate tangential rows of sieve cells and mixed rows of fibers and scarce axial parenchyma, with uniseriate radial parenchyma, could be a variation of this model. The taxa listed by Decombeix et al. (2014) under this category, which also include most extant gymnosperms, are Devonian–Mississippian progymnosperms and seed ferns, Pennsylvanian arborescent medullosalean seed ferns, and a species of Permian cordaitaleans. In addition to considering phloem patterns, in the following discussion the co-occurrence of araucarian pitting in the secondary xylem tissue is also taken into account for establishing comparisons.

5.5. Anatomical comparisons

The general rhythmicity in the production of different secondary phloem cells is less conspicuous in the older Devonian progymnosperms and Mississippian seed ferns included by Decombeix et al. (2014) in the “Model C,” but it is clearly seen in the gymnosperms, i.e. the arborescent medullosaleans and one cordaitalean species, characterized by continuous rows of sieve cells.

The secondary phloem tissues of the arborescent medullosaleans from the tropical Pennsylvanian peat swamps of Euramerica described by Smoot (1984) for *Medullosa anglica* Scott, *M. endocentrica* Baxter, and *M. noei* Steidtmann feature distinctive multiseriate rays and uniseriate tangential layers of sieve cells (with elliptical sieve areas nearly as wide as the cell on the lateral walls, like the ones observed here), alternating with fibers and thin-walled cells. This phloem tissue organization has been referred by Decombeix et al. (2014) as a repetition of continuous layers of fibers, axial parenchyma, and one-cell-thick tangential layers of sieve cells. In the secondary xylem tissue, tracheids are characterized by multisseriate, alternate, frequently flattened areolate pitting. Unlike other Carboniferous seed ferns, the pitting pattern in the medullosalean tracheids presents up to 12 rows of bordered pits on the radial walls and shows araucarioid affinity (sensu Stewart and Rothwell, 1993) and could be an ancestral form of *Agathoxylon*-type wood. In the secondary phloem, the uninterrupted layer of sieve cells with wide sieve areas supported by adjacent fibers is the most evident similarity between the medullosaleans and *Agathoxylon*.

Due to their similar composition and organization of the phloem tissue, the medullosaleans have been compared to Mesozoic cycadophytes (*Cycadeoidea* Buckland) by Smoot (1984) and Ryberg et al. (2007). The main difference at cellular level is the extended length of the medullosalean sieve cells, reflecting the leaning tendency in the growth habit in some of the pteridosperm species. The *Cycadeoidea* xylem tissue, however, in addition to being manoxylic like the medullosaleans, is characterized by scalariform tracheids and uni- to biseriate rays, and in this regard, these plant groups are extremely dissimilar from *Agathoxylon*.

For the secondary xylem of the cordaitalean included in the “Model C,” *Shanxioxylon sinense* Wang et al. from early Permian strata of China, Cathaysia, tracheids with a mixed type of araucarian pitting (*Agathoxylon*-type of wood) have been described, and for the secondary phloem tissue, the presence of thick-walled, nearly isodiametric fiber cells, thin-walled parenchyma cells, and moderately thick-walled sieve cells is reported (Wang et al., 2003). As referred by Decombeix et al. (2014), the cross-section of the inner part of the secondary phloem of *S. sinense* reveals one-cell thick tangential layers of fibers, alternating with two to four thick layers of thin-walled cells and sieve cells. Even though the repetition pattern in the phloem organization of *S. sinense* is not the same as the one inferred for *Agathoxylon*, the secondary xylem and phloem patterns of the here described *Agathoxylon*-type wood from wet peatland environments of the Permian of Gondwana points to a comparable organization as in cordaitalean-like plants from analogous environments of Cathaysia because they reflect adaptations of these woods to peat-forming environments.

It should be emphasized, however, that *Agathoxylon* is a xylem-based fossil genus encompassing distinct groups of gymnosperms, while *Shanxioxylon sinense* is reconstructed as a nearly complete plant with well-established cordaitalean affinities. Interestingly, Taylor et al. (2009) refer to *S. sinense* as a cordaitalean with shared traits with conifers, such as the helical arrangement of the secondary fertile shoots (*Cathayanthus*) and small needle-like leaves. The compositional and organizational similarity between the vascular tissue of *S. sinensis* and *Agathoxylon* seems to point to a probable common ancestor, but such observations are rather speculative as other associated plant organs from the Faxinal Coalfield have not been investigated yet.

From the upper Permian of Antarctica (Skaar Ridge), Decombeix et al. (2015) reported preserved bark of glossopterid specimens from silicified peat. Just like in the specimens described here, the fiber layers are discontinuous, but only one cell thick. The presence of successive periderms in the older (outer) phloem with proliferation of axial parenchyma, retained as an insulating layer with a spongy aspect, suggests that the glossopterids shed the oldest bark as large scales and is an evidence of the adaptation of these plants to the strong environmental oscillations (e.g., dry/wet fire and flooding conditions) to which they were widely subjected throughout Gondwanaland.

The Gondwanan Mesozoic seed fern *Cuneumxylon spallettii* Artabe et Brea (Middle Triassic), with araucarian pitting and a polyxylic wood type, shows a poorly preserved phloem in which sieve cells, abundant parenchymatous cells, and fibers have been recognized, but the cell organization has neither been described nor figured (Artabe and Brea, 2003), impeding a more detailed comparison, although from the sample fragments here described it is possible to affirm that it differs quantitatively in the parenchyma abundance.

In the phloem of the Upper Cretaceous conifer *Taxodioxylon* Ramanujam and Stewart, 1969, all the cell types occurring in *Agathoxylon* have been observed, and the phloem pattern is arranged in alternating, tangential uniseriate layers (fiber/sieve cell/axial parenchyma/sieve cell/fiber). Taylor et al. (2009) included this taxon in the Cupressaceae based on the tracheid pitting of abietinian type in the secondary xylem.

Taking into account the general evolutionary trend in modern conifers, the secondary phloem pattern found in the studied material can be considered as typical for most extant conifers other than Pinaceae (sensu Esau, 1969). In more complex groups such as Cupressaceae, Taxodiaceae, and parts of Podocarpaceae and Taxaceae, fibers are consistently present, and the typical pattern is based on a regular sequence of alternating tangential uniseriate bands of fibers, parenchyma, and sieve cells (Evert, 2006). Nevertheless, in those groups, the patterns of secondary xylem, which have been considered of phylogenetic value, are of the mixed, mainly abietinian type, contrasting with the typical araucarian type found in *Agathoxylon*. However, a close conifer affinity is unlikely because conifer macrofossils have not been reported from the Faxinal Coalfield.

The features here described from a Gondwanan gymnosperm correspond to a tissue with well differentiated cell functions, ratifying the conservatism observed by Taylor (1990) and Decombeix et al. (2014) for the phloem tissue during the Paleozoic. The remarkable structural uniformity of mature sieve cells in fossil and extant gymnosperms from different plant groups contrasts with the varied patterns found in the tracheids of secondary xylem. Cell characteristics are mainly attributed to genetic factors but can also be influenced by ecological constraints (Bosshard, 1974; Schweingruber, 2007). While the new data presented here do not allow definitive phylogenetic or taxonomic inferences, they suggest that diversity in phloem architecture could reflect adaptations to environmental pressures, allowing the plants of *Agathoxylon*-type of wood to thrive in an environment marked by extreme oscillations from flooded to dry and prone to wildfires.

6. Final considerations

For the first time, secondary phloem tissue in organic connection with *Agathoxylon*-type wood is described from charcoalified specimens from a Permian peat-forming environment in western Gondwana. The preservation of such delicate tissue occurred under cyclic, low-temperature wildfires following environmental dryness and hypautochthonous/autochthonous depositional conditions.

The xylem pattern here described is characterized by the occurrence in the tracheids of bordered pits of both the contiguous uniseriate and alternate multiseriate, cross-field pitting of araucarian type showing contiguous cupressoid to taxodioid oculipores, uniseriate rays, and the absence of axial parenchyma.

The phloem pattern is defined as having uniseriate parenchymatous rays and alternating unicellular tangential layers of thin-walled sieve cells featuring clearly defined sieve areas and sieve pores with mixed layers of thick-walled axial fibers and scarce parenchyma.

Possible affinities for the charred logs established through previous palynological and paleobotanical data from the same coal seam are probably with glossopterids or cordaitaleans.

Despite *Agathoxylon* being a fossil genus related with different gymnospermous groups and even though the fragmentary preservation does not allow a formal diagnosis, the results here reported about the secondary phloem constitution and its organization provide new data for Permian gymnosperm forms from Gondwanaland.

The compositional similarity between the secondary phloem and xylem patterns of the Cathaysian species *Shanxioxylon sinensis* and the here described gymnosperm genus *Agathoxylon* from western Gondwana seems to point to probable adaptative convergence to similar environmental conditions.

Even though direct correlation with extant gymnosperm groups cannot be established from the fragmentary observations made here, there is no doubt that the building blocks of vascular tissue carry conservative attributes since the late Paleozoic.

Should the vascular tissue from other plant organs from the Faxinal Coalfield be investigated in the future, a progress could be made in completing the description and establishing affinities for the tissues reported here.

Acknowledgments

This study is submitted by I. D. S. in partial fulfillment of the requirements for the PhD degree at the Programa de Pós-Graduação em Geociências/UFRGS, Porto Alegre, Rio Grande do Sul, under the tenure of a scholarship funded by the Brazilian National Council of Technological and Scientific Development CNPq (159690/2012-9). M. G. S. is thankful to CNPq for a research grant. The authors gratefully acknowledge Margarete Wagner Simas for the field photographs and André Jasper for the technical support. Two anonymous reviewers are gratefully acknowledged for the helpful comments and suggestions which much helped to improve the text.

References

Artabe, A., Brea, M., 2003. A new approach to Corystospermales based on Triassic permineralized stems from Argentina. Alcheringa 27, 209–229. http://dx.doi.org/10.1080/03115510308619353.

Bamford, M.K., Philippe, M., 2001. Jurassic-Early Cretaceous Gondwanan homoxylous woods: a nomenclatural revision of the genera with taxonomic notes. Rev. Palaeobot. Palynol. 113, 287–297. http://dx.doi.org/10.1016/S0034-6667(00)00065-8.

Beck, C.B., 2005. An Introduction to Plant Structure and Development: Plant Anatomy for the Twenty-First Century. University Press, Cambridge.

Boardman, D.R., Iannuzzi, R., de Souza, P.A., Lopes, R.D.C., 2012. Paleobotanical and palynological analysis of Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Parana Basin), Rio Grande do Sul, Brazil. Int. J. Coal Geol. 102, 12–25. http://dx.doi.org/10.1016/j.coal.2012.07.007.

Bosshard, H.H., 1974. Holzkunde zur Biologie, Physik und Chemie des Holzes. Birkhäuser, Basel.

Boureau, E., 1954. Anatomie Végétale: l'Appareil Végétatif des Phanérogames. Presses Universitaires de France, Paris.

Cazzulo-Klepzig, M., Corrêa-da-Silva, Z., Marques-Toigo, M., 1993. Peat-Forming Environment of the Permian Gondwanic South Brazilian Coals. Abstracts 45 Annual Meeting of International Comission of Coal and Organic Petrology. ICCP, Athens, p. 17.

Cazzulo-Klepzig, M., Guerra-Sommer, M., Menegat, R., 2005. Palynology and Palaeobotany in the reconstruction of landscape units from the Candiota Coalfield, Permian of Paraná Basin, Brazil. Rev. Bras. Paleontol. 81, 83–98.

Cazzulo-Klepzig, M., Guerra-Sommer, M., Menegat, R., Simas, M.W., Mendonça Filho, J.G., 2007. Peat-forming environment of Permian coal seams from the Faxinal coalfield (Paraná Basin) in southern Brazil, based on palynology and palaeobotany. Rev. Bras. Paleontol. 10, 117–127. http://dx.doi.org/10.4072/rbp.2007.2.05.

Cazzulo-Klepzig, M., Mendonça Filho, J.G., Guerra-Sommer, M., Menezes, T., Simas, M., Mendonça, J., Degani-Schmidt, I., 2009. Effect of volcanic ash-fall on a Permian peat-forming environment, on the basis of palynology, palynofacies and paleobotany (Faxinal Coalfield, Brazil). Rev. Bras. Paleontol. 12, 179–194. http://dx.doi.org/10.4072/rbp.2009.3.02.

Cohen, K.M., Finney, S.M., Gibbard, P.L., Fan, J.-X., 2013. The ICS international chronostratigraphic chart. Episodes 36, 199–204.

Collinson, M.E., 1999. Scanning electron microscopy of megafossils and mesofossils. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 57–64.

Decombeix, A.-L., Galtier, J., Meyer-Berthaud, B., 2014. Secondary phloem in Early Carboniferous seed plants: anatomical diversity and evolutionary implications. Int. J. Plant Sci. 175, 891–910. http://dx.doi.org/10.1086/677650.

Decombeix, A.-L., Taylor, E.L., Taylor, T.N., 2015. Bark Anatomy of Glossopteridalean Trees from the Late Permian of Antarctica. Abstracts Agora Paleobotanica, Autun, p. 7.

Degani-Schmidt, I., Guerra-Sommer, M., Mendonça, J.D.O., Mendonça Filho, J.G., Jasper, A., Cazzulo-Klepzig, M., Iannuzzi, R., 2015. Charcoalified logs as evidence of hypautochthonous/autochthonous wildfire events in a peat-forming environment from the Permian of southern Paraná Basin (Brazil). Int. J. Coal Geol. 146, 55–67. http://dx.doi.org/10.1016/j.coal.2015.05.002.

Esau, K., 1969. The Phloem. Encyclopedia of Plant Anatomy. Gebrüder Borntraeger, Berlin.

Esau, K., Cheadle, V.I., Gifford, E.M., 1953. Comparative structure and possible trends of specialization of the phloem. Am. J. Bot. 40, 9–19. http://dx.doi.org/10.2307/2438486.

Evert, R.F., 1977. Phloem structure and histochemistry. Annu. Rev. Plant Physiol. 28, 199–222. http://dx.doi.org/10.1146/annurev.pp.28.060177.001215.

Evert, R.F., 2006. Esau's Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development. John Wiley & Sons, New Jersey.

Figueiral, I., 1999. Lignified and charcoalified wood. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 92–96.

Gothan, W., 1905. Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. Abh. Preuss. Geol. Landesanst. 44, 1–108.

Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., Formoso, M.L.L., Basei, M.A.S., Barboza, E.G., Simas, M.W., 2008. Geochronological data from the Faxinal coal succession, southern Paraná Basin, Brazil: A preliminary approach combining radiometric U-Pb dating and palynostratigraphy. J. S. Am. Earth Sci. 25, 246–256. http://dx.doi.org/10.1016/j.jsames.2007.06.007.

Gulbranson, E.L., Ryberg, P.E., Decombeix, A.-L., Taylor, E.L., Taylor, T.N., Isbell, J.L., 2014. Leaf habit of Late Permian Glossopteris trees from high-palaeolatitude forests. J. Geol. Soc. 171, 493–507. http://dx.doi.org/10.1144/jgs2013-127.

Harris, T.M., 1958. Forest fire in the Mesozoic. J. Ecol. 46, 447–453. http://dx.doi.org/10.2307/2257405.

Hather, J.G., 2000. Archaeological Parenchyma. Archetype, London.

Henz, G.I., Corrêa-da-Silva, Z.C., 1987. Organo-Petrologia dos Carvões da Jazida do Faxinal, Município de Arroio dos Ratos, RS. Proc. I Congresso Brasileiro de Geoquímica. SBG, Porto Alegre, pp. 521–546.

Jasper, A., Guerra-Sommer, M., Abu Hamad, A.M.B., Bamford, M., Bernardes-de-Oliveira, M.E.C., Tewari, R., Uhl, D., 2013. The burning of Gondwana: Permian fires on the southern continent—a palaeobotanical approach. Gondwana Res. 24, 148–160. http://dx.doi.org/10.1016/j.gr.2012.08.017.

Jones, T.P., Chaloner, W.G., 1991. Fossil charcoal, its recognition and palaeoatmospheric significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 97, 39–50. http://dx.doi.org/10.1016/0031-0182(91)90180-Y.

Lupia, R., 1995. Paleobotanical data from fossil charcoal: an actualistic study of seed plant reproductive structures. PALAIOS 10, 465–477. http://dx.doi.org/10.2307/3515048.

Marguerier, J., 1973. Paléoxylologie du Gondwanan africain: étude et affinités du genre *australoxylon*. Palaeontol. Afr. 16, 37–58.

Mendonça Filho, J.G., Guerra-Sommer, M., Klepzig, M.C., Mendonça, J.O., Silva, T.F., Kern, M.L., Menezes, T.R., Jasper, A., Silva, M.C., Santos, L.G.C., 2013. Permian carbonaceous rocks from the Bonito Coalfield, Santa Catarina, Brazil: Organic facies approaches. Int. J. Coal Geol. 111, 23–36. http://dx.doi.org/10.1016/j.coal.2012.07.008.

Niklas, K.J., 1997. The Evolutionary Biology of Plants. The University of Chicago Press, Chicago.

Scott, A.C., 2000. The Pre-Quaternary history of fire. Palaeogeogr. Palaeoclimatol. Palaeoecol. 164, 281–329. http://dx.doi.org/10.1016/S0031-0182(00)00192-9.

Philippe, M., 1993. Nomenclature générique des trachéidoxyles fossiles mésozoïques à champs araucarioïdes. Taxon 42, 74–80. http://dx.doi.org/10.2307/1223305.

Philippe, M., 2011. How many species of Araucarioxylon? C.R. Palevol. 10, 201–208. http://dx.doi.org/10.1016/j.crpv.2010.10.010.

Wang, S.-J., Hilton, J., Baolin, T., Galtier, J., 2003. Cordaitalean seed plants from the Early Permian of North China. I. Delimitation and reconstruction of the *Shanxioxylon sinense* plant. Int. J. Plant Sci. 164, 89–112. http://dx.doi.org/10.1086/344558.

Prevec, R., Labandeira, C.C., Neveling, J., Gastaldo, R.A., Looy, C.V., Bamford, M., 2009. Portrait of a Gondwanan ecosystem: a new late Permian fossil locality from KwaZulu-Natal, South Africa. Rev. Palaeobot. Palynol. 156, 454–493. http://dx.doi.org/10.1016/j.revpalbo.2009.04.012.

Ramanujam, C.G.K., Stewart, W.N., 1969. Taxodiaceous bark from the Upper Cretaceous of Alberta. Am. J. Bot. 56, 101–107.

Raven, J.A., Andrews, M., 2010. Evolution of tree nutrition. Tree Physiol. 30, 1050–1071. http://dx.doi.org/10.1093/treephys/tpq056.

Ricardi-Branco, F., Rösler, O., 2004. The paleoflora of Figueira in the context of the Neopaleozoic of the Paraná Basin, Brazil. Terrae 2, 44–51.

Rößler, R., Philippe, M., Van Konijnenburg-van Cittert, J.H.A., McLoughlin, S., Sakala, J., Zijlstra, G., Bamford, M., Booi, M., Brea, M., Crisafulli, A., Decombeix, A.L., Dolezych, M., Dutra, T., Esteban, L.G., Falaschi, P., Feng, Z., Gnaedinger, S., Sommer, M.G., Harland, M., Herbst, R., Iamandei, E., Iamandei, S., Jiang, H., Kunzmann, L., Kurzawe, F., Merlotti, S., Naugolnykh, S., Nishida, H., Noll, R., Oh, C., Orlova, O., de Palacios, P.D.P., Poole, I., Pujana, R.R., Rajanikanth, A., Ryberg, P., Terada, K., Thévenard, F., Torres, T., Vera, E., Zhang, W., Zheng, S., 2014. Which name(s) should be used for *Araucaria*-like fossil wood?—Results of a poll. Taxon 63, 177–184. http://dx.doi.org/10.12705/631.7.

Ryberg, P.E., Taylor, E.L., Taylor, T.N., 2007. Secondary phloem anatomy of *Cycadeoidea* (Bennettitales). Am. J. Bot. 94, 791–798. http://dx.doi.org/10.3732/ajb.94.5.791.

Santos, R.V., Souza, P.A., de Alvarenga, C.J.S., Dantas, E.L., Pimentel, M.M., de Oliveira, C.G., de Araújo, L.M., 2006. Shrimp U-Pb zircon dating and palynology of bentonitic layers from the Permian Irati Formation, Paraná Basin, Brazil. Gondwana Res. 9, 456–463. http://dx.doi.org/10.1016/j.gr.2005.12.001.

Schweingruber, F.H., 2007. Wood Structure and Environment. Springer, Berlin.

Scott, A.C., 1989. Observations on the nature and origin of fusain. Int. J. Coal Geol. 12, 443–475. http://dx.doi.org/10.1016/0166-5162(89)90061-X.

Scott, A.C., 2001. Preservation by fire. In: Briggs, D.E.G., Crowther, P.J. (Eds.), Palaeobiology II. Blackwell, Oxford, pp. 277–280.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 11–39. http://dx.doi.org/10.1016/j.palaeo.2009.12.012.

Simas, M.W., Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., Schneider Santos, J.O., Fonseca Ferreira, J.A., Degani-Schmidt, I., 2012. Geochronological correlation of the main coal interval in Brazilian Lower Permian: radiometric dating of tonstein and calibration of biostratigraphic framework. J. S. Am. Earth Sci. 39, 1–15. http://dx.doi.org/10.1016/j.jsames.2012.06.001.

Simas, M.W., Guerra-Sommer, M., Mendonça Filho, J.G., Cazzulo-Klepzig, M., Formoso, M.L.L., Degani-Schmidt, I., 2013. An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a lower Permian tonstein layer (Faxinal Coalfield, Paraná Basin, Brazil). Geol. Acta 11, 45–57. http://dx.doi.org/10.1344/105.000001835.

Slater, B.J., McLoughlin, S., Hilton, J., 2015. A high-latitude Gondwanan lagerstätte: the Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. Gondwana Res. 27, 1446–1473. http://dx.doi.org/10.1016/j.gr.2014.01.004.

Smoot, E.L., 1984. Phloem anatomy of the Carboniferous pteridosperm *Medullosa* and evolutionary trends in gymnosperm phloem. Bot. Gaz. 145, 550. http://dx.doi.org/10.1086/337490.

Smoot, E.L., Taylor, T.N., 1978. Sieve areas in fossil phloem. Science 202, 1081–1083. http://dx.doi.org/10.1126/science.202.4372.1081.

Stewart, W.N., Rothwell, G.W., 1993. Paleobotany and the Evolution of Plants. University Press, Cambridge.

Taylor, E.L., 1990. Phloem evolution: an appraisal from the fossil record. In: Behnke, H.-D., Sjolund, R.S. (Eds.), Sieve Elements - Comparative Structure, Induction, and Development. Springer-Verlag, Berlin, pp. 285–298.

Taylor, E.L., Taylor, T.N., Krings, M., 2009. Paleobotany: The Biology and Evolution of Fossil Plants. Academic Press, New York.

Uhl, D., Abu Hamad, A., Kerp, H., Bandel, K., 2007. Evidence for palaeo-wildfire in the Late Permian palaeotropics—charcoalified wood from the Um Irna Formation of Jordan. Rev. Palaeobot. Palynol. 144, 221–230. http://dx.doi.org/10.1016/j.revpalbo.2006.08.003.

Van Bel, A.J.E., 1999. Evolution, polymorphology and multifunctionality of the phloem system. Perspect. Plant Ecol. Evol. Syst. 2, 163–184. http://dx.doi.org/10.1078/1433-8319-00069.

Vogellehner, D., 1964. Zur Nomenklatur der fossilen Holzgattung *Dadoxylon* Endlicher 1847. Taxon 13, 233–237. http://dx.doi.org/10.2307/1216692.

Gmail by Google

Isabela Degani-Schmidt <degani.schmidt@gmail.com>

Your manuscript PALBO_2015_58 has been sent for review

1 message

(Evise) <EviseSupport@elsevier.com>　　Mon, Dec 21, 2015 at 9:16 AM
Reply-To: EviseSupport@elsevier.com
To: degani.schmidt@gmail.com

This message was sent automatically. Please do not reply.

Reference: PALBO_2015_58
Title: Epidermal morphology and ecological significance of Glossopteris pubescens nom. nov. from the Brazilian Permian (Sakmarian)
Journal: Review of Palaeobotany and Palynology

Dear Mrs. Degani-Schmidt,

I am currently identifying and contacting reviewers who are acknowledged experts in the field. Since peer review is a voluntary service it can take time to find reviewers who are both qualified and available. While reviewers are being contacted, the status of your manuscript will appear in EVISE® as 'Reviewer Invited'.

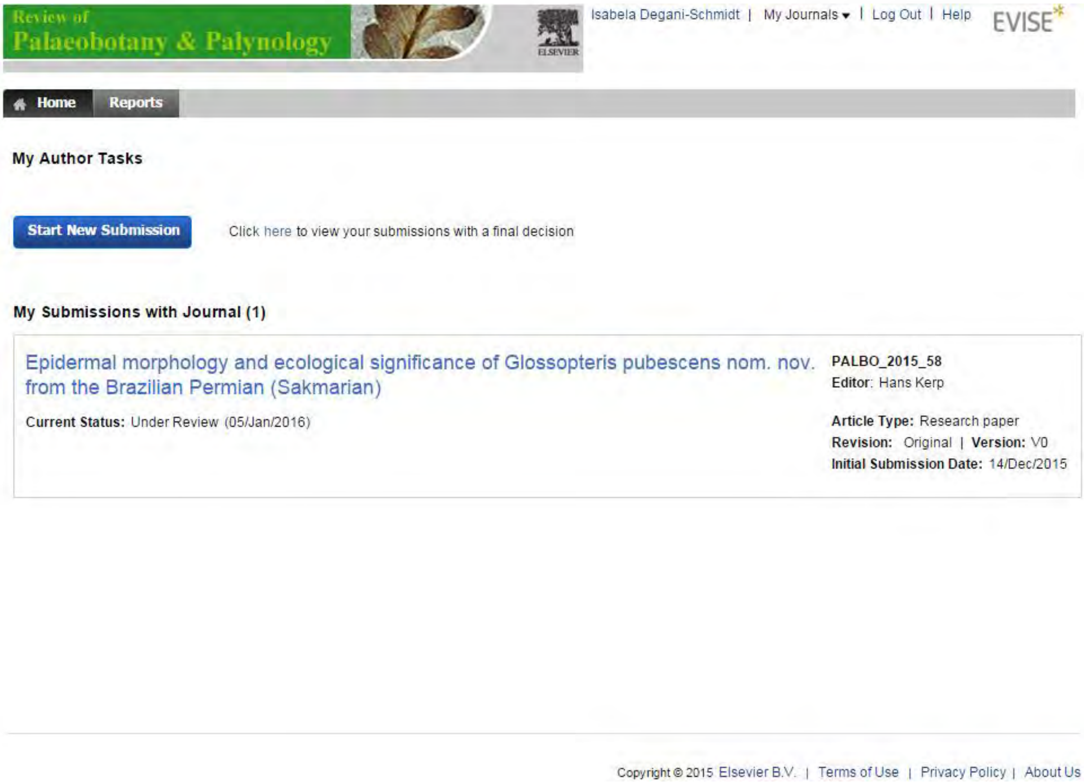
Once a reviewer agrees to review your manuscript, the status will change to 'Under Review'. When I have received the required number of expert reviews, the status will change to 'Ready for Decision' while I evaluate the reviews before making a decision on your manuscript.

To track the status of your manuscript, please log into EVISE® and go to 'My Submissions' via:
http://www.evise.com/evise/faces/pages/navigation/NavController.jspx?JRNL_ACR=PALBO

Kind regards,

Review of Palaeobotany and Palynology

Have questions or need assistance?
For further assistance, please visit our Customer Support site. Here you can search for solutions on a range of topics, find answers to frequently asked questions, and learn more about EVISE® via interactive tutorials. You can also talk 24/5 to our customer support team by phone and 24/7 by live chat and email.



My Author Tasks

Click here to view your submissions with a final decision

My Submissions with Journal (1)

Epidermal morphology and ecological significance of Glossopteris pubescens nom. nov. from the Brazilian Permian (Sakmarian)

Current Status: Under Review (05/Jan/2016)

PALBO_2015_58
Editor: Hans Kerp

Article Type: Research paper
Revision: Original | **Version:** V0
Initial Submission Date: 14/Dec/2015

Epidermal morphology and ecological significance of *Glossopteris pubescens* nom. nov. from the Brazilian Permian (Sakmarian)

Isabela Degani-Schmidt [a,*], Margot Guerra-Sommer [b]

a Programa de Pós-Graduação em Geociências/UFRGS, Porto Alegre, Brazil, degani.schmidt@ufrgs.br

b Instituto de Geociências/UFRGS, Porto Alegre, Brazil, margot.sommer@ufrgs.br

*Corresponding author at (present address): PPG-Geo/UFRGS, Av. Bento Gonçalves 9500, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil. Tel.: +55 (51) 3308 63 78

E-mail address: degani.schmidt@ufrgs.br (I. Degani-Schmidt)

Abstract

Redescription of a Brazilian glossopterid species is done based on cuticular analysis. The original description (Guerra-Sommer, 1992) is illegitimate because it is a later homonym of *Glossopteris papillosa* Srivastava (1969). The material comes from a tonstein layer interbedded in a Sakmarian coal seam (U/Pb age 291 ± 1.3 Ma) of the Faxinal Coalfield, southern Paraná Basin, Brazil (Rio Bonito Formation). Cuticle fragments have been macerated in Schulze‟s solution yielding larger cuticle fragments than those previously described, totalizing over 100 analyzed specimens. The new species name *Glossopteris pubescens* is erected as a replacement name and refers to the hairy lower epidermis. The unique set of characters of the elaborate indumentum of the abaxial lamina comprises subsidiary cells with papillae overarching the stomatal pore, papillate epidermal cells, simple trichomes and trichome base complexes apparently homologous to stomatal apparati densely concentrated on the venation system. The epidermal structures are compared to that of fossil and extant plants and interpreted under the light of new paleoecological data for the Faxinal

Coalfield which include humidity oscillations with wildfire occurrences and influence of volcanic activity.

Keywords

trichome base complex, fossil cuticles, pteridosperms, Permian, *Glossopteris* Flora, Gondwana

Highlights

- Redescription of a glossopterid species based on cuticular analysis
- Cuticular analysis has been performed in over 100 leaves from a single locality
- The lower epidermis features elaborate indumentum
- Trichome base complexes are apparently homologous to stomatal apparati
- Environmental cyclicity is inferred to have influenced epidermal plasticity

1. Introduction

The Gondwana Realm is essentially identified based on the presence of the *Glossopteris* Flora of which the leaf genus *Glossopteris* Brogniart is the main constituent, being the dominant fossil in Permian sediments (e.g., Gould and Delevoryas, 1977; Pigg, 1990; Taylor et al., 1992; Cúneo, 1996; Tewari et al. 2015).

Based on its various organs, the affinities of glossopterids have been suggested to be with varied groups such as cordaitaleans (Schopf, 1973), Gnetales (Schopf, 1976), ,„,cycadophytes‘“‘ (Rigby, 1978), and Pinophyta (Meyen, 1987). Pant and Singh (1974) and Pigg and Nishida (2006) recognize similarities of the *Glossopteris* plant with the extant *Ginkgo*. Some authors have suggested a separate class or order (Archangelsky, 1970; Surange and Chandra, 1975), the Glossopteridopsida or Glossopteridales, at the same rank as the Pteridospermopsida or Pteridospermales. Others are inclined to relate them to the seed ferns as Glossopteridales, at the same rank as the Medullosales or Lyginopteridales (Gould and Delevoryas, 1977; Taylor and Taylor, 1993); for Boureau (1967) they constituted the phyllum Glossopteridophyta. A glossopterid ancestry has been suggested for the flowering plants (e.g., Plumstead, 1956; Krassilov, 1977; Retallack and Dilcher, 1981; Melville, 1983), and phylogenetic analyses considering ovule-bearing structures of fossil and extant plants placed the group at the base of Angiosperm origins (Doyle, 2006).

The form genus *Glossopteris* occurs abundantly, but not exclusively, in clastic levels directly associated with coal seams, which are considered to be climate-sensitive sediments (Gibbs et al., 2002). The taxon is important in wetlands and swampy habitats (Anderson and Anderson, 1985; Pigg, 1990; Guerra-Sommer et al., 1991; Pigg and McLoughlin, 1997; Banerjee, 2005) in cool temperate biomes (Rees, 2002).

In the Brazilian Gondwana, assemblages with abundant specimens and well preserved compressions of glossopterid leaves have been described from mud and silty-sandy layers interbedded with coal seams in coalfields in the northeastern and southern areas of the coal-bearing Rio Bonito Formation from the Lower Permian of the Paraná Basin (Fittipaldi and Rösler, 1985 for Paraná State; Guerra-Sommer, 1992 for Rio Grande do Sul State) (Fig. 1A).

In addition to its presence in the coal-bearing Rio Bonito Formation, *Glossopteris* leaves are also known from gangampoterid-glossopterid leaf assemblages collected from older periglacial environments of the Itararé Group from the lower Permian (Asselian to Sakmarian). The leaves are also present in fluvial and lacustrine deposits from younger strata of Irati, Teresina and Rio do Rasto formations (Fig. 1B) throughout the Middle and Late Permian (Late Artinskian to Wuchiapingian), during the transitional icehouse-hot house conditions, suggesting that these plants could also occur at wetter areas of seasonally dry environments. However, such specimens are preserved as impressions only (e.g., Rösler, 1975, 1978; Corrêa-da-Silva and Arrondo, 1977; Bernardes-de-Oliveira et al., 1978; Perinotto and Rösler, 1984; Rohn, 1984; Rohn and Rösler, 1989, 2000; Rohn et al., 1997; Ricardi-Branco et al., 1999; Guerra-Sommer and Cazzulo-Klepzig, 2000; Iannuzzi, 2000; Boardman et al., 2006; Tybusch and Iannuzzi, 2008, 2010; Tybusch et al., 2012).

About 200 species of the genus *Glossopteris* have been described from the lower Permian to the lower Triassic rocks of the Gondwanan continents, viz. Africa, Antarctica, Australia, South America, peninsular India (Pigg, 1990 and references therein; Srivastava and Agnihotri, 2010; Goswami and Singh, 2013) and even from the Arabian plate (Archangelsky and Wagner, 1983; Berthelin et al., 2006), most frequently based on the morphography of the impression leaves. The main difficulty posed by leaf morphography consists in delimiting species based on the variation of venation patterns and shape, which frequently intergrade subtly from one fossil to the next (Bernardes-de-Oliveira, 1978; Kovács-Endrödy, 1979; Srivastava, 1991; McLaughlin, 1994; Pigg and Nishida, 2006).

Epidermal micromorphology of leaf adpressions has been used to distinguish a number of *Glossopteris* species in material recovered mainly from roof shale levels (e.g., Zeiller, 1896; Sahni, 1923; Srivastava, 1956; Surange and Srivastava, 1956; Pant, 1958; Høeg and Bose, 1960; Surange, 1966; Pant and Gupta, 1968, 1971; Srivastava, 1969; Pant and Singh, 1971, 1974; Pant and Choudhury, 1977; Chandra and Srivastava, 1981; Fittipaldi and Rösler, 1985; Bajpai, 1986; Pant and Pant, 1987; Guerra-Sommer, 1992; Maheshwari and Tewari, 1992; Singh and Maheshwari, 2000; Srivastava et al., 2010), however, some descriptions are based on a limited number of specimens and/or small-sized cuticle fragments and led to a proliferation of species.

The interpretation of anatomically preserved leaves has influenced the understanding of this group by providing information that would be unknowable from compressions alone (e.g., Gould and Delevoryas, 1977; Pigg, 1990; Pigg and Taylor, 1990, 1993; Taylor, 1996; Pigg and McLaughlin, 1997). Upon review of anatomical features described for petrified glossopterids of Late Permian silicified cherts from Antarctica and Australia, Pigg and Trivett (1994) reported distinctive variation in leaf-stem attachment among glossopterids with similar venation patterns. Nevertheless, this kind of preservation for glossopterid leaves seems to be very rare in the geological record.

A well preserved assemblage of compressed *Glossopteris* leaves, collected from an ash fall level (tonstein) interbedded in a coal seam from the Faxinal Coalfield, southern Brazil, lead Guerra-Sommer (1992) to identify a predominantly monotypic cuticular pattern. Based on the epidermal architecture, the leaf assemblage was considered as mostly composed by a single biological entity identified as *Glossopteris papillosa* (illegitimate name). Its lower cuticle pattern is characterized by haplocheilic stomata with papillate subsidiary cells overarching sunken guard cells, dispersed epidermal papillae and single elongated unicellular trichomes, presenting also peculiar cuticular appendages densely concentrated mainly in the costal fields. Such pattern is unique to the glossopterids preserved in the tonstein of the Faxinal Coalfield.

The aims of the present study are to rectify the taxonomic identity of the glossopterid species previously described by Guerra-Sommer (1992) by means of cuticular analysis as *Glossopteris papillosa* (illegitimate), renaming it and emending the original description, and to discuss the micromorphological features, comparing them to those of fossil and extant plants, and interpreting their meaning under the light of new paleoecological data for the Faxinal Coalfield.

2. Geologic and paleontological context

The study area comprises the Faxinal Coalfield, a former opencast coal mine located at the southeastern outcrop belt of the coal-bearing Rio Bonito Formation of the Paraná Basin, southern Brazil (Fig. 1A). The mine closure took place in 2009 after the coal has been exhausted and the mine site has been rehabilitated.

The top coal seam S is interlayered with a 10 cm thick (mean) fossiliferous tonstein ply (Fig. 1C; Plate I, 1, 2) dated at 291 ± 1.3 Ma (radiometric age after Simas et al., 2012) corresponding to the late Sakmarian (Cohen et al., 2013; updated 2015) (Fig. 1B, C). The tonstein occurs throughout the coalfield area (ca. 1.6 km^2) and contains abundant plant organ adpressions of the *Glossopteris* Flora (Plate I, 3-7).

FIGURE 1 - PLATE I

Autochthonous/parautochthonous adpression floras in peat-forming environments are uncommon (Gastaldo et al., 1995). However, the ash-fall layer (tonstein) is considered a typical entombing facies (DiMichele and Falcon-Lang, 2011) yielding excellent fossil preservation (e.g., Wang et al., 2012). The presence of the tonstein reflects an instantaneous geological event (sensu Prothero, 1990) and played an important role in the plant preservation in the Faxinal Coalfield due to the rapid inclusion of the plant organs in the falling ash. This kind of process also favors the obtaining of paleoecological data because it can be considered as a snapshot of minutes to days of the plant assemblage (DiMichele and Falcon-Lang, 2011).

According to sequence stratigraphy, the coal deposition in the southern Paraná Basin is inferred to have occurred in a lagoon-barrier depositional system, where the mires were formed behind a barrier island (Holz, 2003; Holz et al., 2010).

Palynological data from the coal seams and the tonstein rock (Cazzulo-Klepzig et al., 2007, 2009) supported the occurrence of paralic conditions in lowland coastal plains and corroborated the sequence stratigraphy model established by Holz (2003). Monosaccate and bisaccate pollen grains (*Cannanoropollis* and *Scheuringipollenites*) comprise approximately 33% of the whole palynological assemblage in the tonstein layer, followed by *Protohaploxypinus* 8% (Cazzulo-Klepzig et al., 2009). Abundance of trilete spores of lycopsid and filicopsid affinities is 9%. Fragments of the colonial alga *Botryococcus* were identified (less than 2%), as well as scarce algae-like elements belonging to the genus *Portalites* (less than 2%). The palynoassemblage reflects a plant community dominated by gymnosperms (glossopterids, cordaitaleans and conifers) in a forest swamp habitat with periods of standing water.

Palynofacies analyses showed the presence of amalgamated sporomorphs at the base level of the tonstein layer and algal colonies of *Botryococcus* at the top. Environmental conditions have been associated with a subaqueous deposition of the ash-fall layer, pointing to a rapid burial process (Cazzulo-Klepzig et al., 2009). Zygospores of zygnematacean algae from the contacts of the coal with the tonstein were observed under fluorescence microscopy and have been reported by Degani-Schmidt et al. (2015), suggesting conditions related to lacustrine shallow margins, sloughs, and tree islands in swamp environments (Grenfell, 1995; Yi, 1997; Chmura et al., 2006).

Petrographic analysis of polished blocks under fluorescent light revealed probable pollen organs and abundant pollen clusters at the lower and the upper coal boundaries with the tonstein, suggesting autochthonous/hypautochthonous deposition of gymnosperm organs (Degani-Schmidt et al., 2015).

Simas et al. (2013) inferred a rapid and intense leaf deposition process during the ash-fall, mostly corresponding to leaves organically attached to short shoots in apparent whorls. Analysis of dispersed organic matter along the tonstein layer showed that the organic matter succession reflects the composition of different plant strata (herbaceous pteridophytes and arboreal glossopterids/cordaitaleans) around the deposition site (Simas et al., 2013).

In their most recent revision of the tonstein coalified macroflora, Boardman et al. (2012) reported a dominance of glossopterid leaves at 78%, followed by cordaitalean leaves 17.6%, reproductive axes 2%, pteridophyte fronds 1.4% and seeds 1%.

Stomatal counts found lower numbers in the glossopterid leaves from the tonstein of the Faxinal Coalfield when compared to the results from the northern of the Paraná Basin (Cambuí coal mines in Paraná State) pointing to higher atmospheric CO_2 levels, perhaps due to the influence of volcanic activities and revealing probable atmospheric fluctuations within the Sakmarian–Artinskian interval during the development of peat-forming systems in Brazilian sequences (Degani-Schmidt et al., 2011). However, the compared glossopterid leaves probably do not belong to the same species as will be discussed herein.

Charcoal analyses in the tonstein layer (Jasper et al., 2011) showed a progressive reduction of gymnosperm macroscopic charcoal towards to the layer top, indicating a reduction in fire activity. Volcanic events were suggested as ignition source for wildfires in this peat-forming environment. Subsequent studies, however, indicated that the ash has been deposited at a cool temperature on the peat surface (Simas et al., 2013). Additionally, no evidence of thermal-induced alteration has been observed in the cuticles included in the tonstein (Guerra-Sommer, 1992; Degani-Schmidt et al., 2011).

Analysis of large autochthonous/hypautochthonous charcoalified logs included in the lower and upper coal boundaries with the tonstein considered that fire ignition, activity and spread were more often related to extreme wet-dry recurrent climatic oscillations (Degani-Schmidt et al., 2015).

4. Material and Methods

Abundant *Glossopteris* leaves occur haphazardly in horizontal disposition, frequently stacked in several planes along the tonstein layer. Most of the compressions are fragments of isolated leaves; however, leaves organically attached to short shoots in apparent whorls are also present (Plate I, 4-7).

Tonstein samples were collected between 1984 and 2009 (Guerra-Sommer, 1992; Degani-Schmidt et al., 2011; Jasper et al., 2011; Boardman et al., 2012; Simas et al., 2012). Slabs were removed from the coal seam with pickaxe or hammer and chisel and also with the help of a mechanical excavator where the tonstein was at ground level (Plate I, 1).

Cuticle samples from 9 whorls/short shoots containing 4 to several leaves in organic or inferred connection and 20 unattached leaves have been collected and individually macerated. At least 2 leaves from each whorl had their cuticles prepared individually to ascertain they carried the same cuticular pattern Additional 59 fragmented leaves, whose morphography is sometimes indiscernible, had their cuticles collected and macerated in bulk. The number of analyzed leaves exceeds 100 individual specimens.

Cuticles are firmly adhered to the rock matrix and are cracked (Plate X, 3). Small chips were broken off and treated with hydrofluoric acid (HF) 45% for 24-48 hours according to Kerp (1990). After rinsing with distilled water, cuticles have been immersed for two hours in a saturated dry Schulze"s solution in a concentration similar to that proposed by Gray (1965) for palynology of coals (70% HNO_3 and $KClO_3$ 4 : 1). Next, the cuticles were repeatedly washed and put in 5% KOH solution for 5-10 minutes and washed again with distilled water (Kerp, 1990; Krings and Kerp, 1997; Kerp and Krings, 1999). All cuticles were dehydrated in glycerin (Krings and Kerp, 1997) and mounted in glycerin jelly slides with the help of a Leica S8 APO stereoscopic microscope.

It is important to emphasize that differently from the methods described in the literature to prepare the glossopterid cuticles from the northern Paraná Basin and from India, and pteridosperm cuticles from the northern hemisphere, long maceration times in a low concentrated Schulze"s solution resulted in excessively eroded cuticles.

A few cuticle fragments have been prepared for observation under fluorescent light by maceration in HF only for 24-48h for freeing the adhered sediments.

Trichomes, which are mostly trapped in the rock matrix, have been extracted by dissolving small chips in HF for 24 hours. After decanting and rinsing in water, the plant material was filtered and picked with a dropper and put on glass slides with a drop of cellosize and then covered with glycerin jelly and cover slips.

Slides were examined under transmitted light using a Zeiss Axioplan 2 microscope with Plan-Neofluar objectives, H/DIC II differential interference contrast filter and dark-field microscopy. The same equipment has been used for fluorescence observation with blue (DAPI) and green (AF488) filters. Pictures were taken using an AxioCam MRc camera, and the images were analyzed and measurements taken with Zeiss Axio Vision 4.8.1 software.

Plates were composed with Adobe Photoshop CS3 Extended. Transformations made to the images consist of cropping, rotation, contrast adjustment, focus stacking and image composition.

The fossils from the Faxinal Coalfield and the corresponding slides are housed at 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) in Porto Alegre, Brazil.

Whorl codes PB-4694, 4760-67; individual leaves PB-4770-72, 4775-78, 4780-85, 4789, 4791, 4793-95, 4797, 4800-01, 4804, 4807, 4809-10, 4812, 4814, 4816-18, 4820-22, 4825, 4828, 4830-31, 4833, 4835, 4839.

The original material prepared (published and unpublished) and described by Guerra-Sommer (1992) has been reexamined and new pictures were taken. Codes of 16 hand specimens are PB2703, 2767, 2768-71, 2776, 2777, 2779, 2789-91, 2793, 2794, 2800, 2802.

5. Systematic paleobotany

Phylum Pteridospermophyta (sensu Taylor et al., 2009)

Order Glossopteridales

Genus *Glossopteris* Brogniart

Glossopteris pubescens nom. nov.

Homonym: 1992 *Glossopteris papillosa* Guerra-Sommer 1992 (illegitimate)

Lectotype: PB-2777 (Plate II)

Paratypes: PB-4764-E (Plate III); PB-4765-G (Plate IV)

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

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

Etymology: Latin, hairy.

Emended diagnosis: Leaf shape from lanceolate, oblanceolate to obovate in whorls/short shoots, elliptic to oblong in single leaves; apex from acute to obtuse, sometimes rounded; base tapers gradually; margins entire. Midvein narrow, conspicuous, persistent and tapering. Lateral venation narrow and gently arched. Hypostomatic epidermis with glabrate upper and pubescent lower cuticle. On lower cuticle single central, hollow, domed papillae present on most costal and all intercostal cells and lacking from midvein. Stomata crowded, haplocheilic, monocyclic, stephanocytic to actinocytic with sunken guard cells and 4-8 subsidiary cells with papillae overarching the stomatal pore. Single simple, short trichomes sometimes bordering costal fields, borne centrally on epidermal cells; long trichomes emerging from intercellular spaces on venation. Complex, thick, 4 to 8-celled papillate trichome bases abundant on costal fields, scattered on intercostal fields; non-papillate abundant over midvein; thin, non-papillate on petiole.

5.1 Description

Leaves are frequently borne in apparent whorls, with lanceolate, oblanceolate to obovate shape, elliptic to oblong when isolated, margins entire. Specimens are mostly fragmentary and apex and base are rarely present in the same leaf. Whole leaf dimensions range from 11 cm to 32 cm long and 3.8 cm to 7.2 cm wide. Apex varies from acute to obtuse, sometimes rounded (Plate II, 1, 2, 5). Leaf tapers gradually towards base when in whorls, acute when isolated. Midvein narrow (mean width 0.4 cm), conspicuous and persistent, tapering slightly towards the apex. Departing angle of the lateral veins from midvein varies along the leaf being narrower at the base and top than in the middle, from 12-45º, continuing in arches, reaching the margins at an angle of 50-80º, generally at wider angles at mid-length of leaf. Mean venation density is 19/cm between midvein and margin and 24/cm at the margin. Dichotomies and anastomoses of veins are mostly obscured by the coalified nature of the cuticles on unprepared material, but appear to be infrequent.

Epidermis is hypostomatic. The upper cuticle is thick, glabrate while the lower one is pubescent and less cutinized, being profusely covered by papillae, simple hairs and complex trichome bases (Plate V).

The margins of the lamina in both upper and lower cuticles feature a border composed of undifferentiated, glabrous, 3-4 cell wide (78.6 µm mean total width) with more or less isodiametric, squarish, triangular or polygonal cells, with straight, thick anticlinal walls (Plate V, 4).

The midvein of upper lamina is several cells wide, with straight-walled, squarish cells arranged end to end, vertically oriented along the vascular system and features some vertical folds (Plate XI, 1). Very sparse trichome bases (35-53 µm in diameter) (type 1b, Table 1) and apparently structured apertures (105 µm mean diameter) with an occasional bordering hollow papilla can be observed in the upper midvein area (Plate XI, 1-3).

The secondary venation of the upper cuticle is generally indistinct, epidermal cells are mostly elongated in the venation direction, arranged end to end, sub-rectangular, with straight, oblique or curved end walls (Plate II, 6; Plate III, 3; Plate V, 1,4; Plate XI, 6, 7), rarely sinuous (Plate XI, 7). Sometimes cells show short filamentous projections from the corners (Plate XI, 4, 5). Sparse round flat cells (mean diameter 50 µm) with dark content can be observed on the area of lateral venation. Their surrounding cells show no special features or arrangement (Plate V, 1; Plate XI, 5).

In the lower cuticle the midvein is several cells wide, with heavier cutinization in the central area than close to lateral venation (Plate V, 3). Cells are arranged end to end in rows, with straight walls, square to rectangular (mean 29 µm length x 14.8 µm width), non papillate and profusely covered with heavily cutinized, non-papillate trichome bases (Plate III, 5; Plate IV, 4; Plate VIII, 1-7; Plate XI, 8-11). Very narrow intercostal fields have been observed containing uniseriate stomata rows with heavily cutinized papillae in the subsidiary cells overarching the stomatal pore. Occasionally a few costal cells present papillae adjacent to the intercostal fields of the midvein (Plate III, 4; Plate IV, 5). Cells of lower midvein are frequently observed in what appears to be interrupted cell divisions (Plate III, 6,7; Plate 11, 8-11).

Secondary venation is organized in costal and thin stomatiferous intercostal fields (Plate III, 9; Plate V, 2, 5, 6; Plate VI, 10). Costal fields are mostly 6-11 cells wide (69-230 µm in width) composed of elongated cells with straight or oblique end walls, medium cutinization, frequently bordered by simple short to elongated papillae/ (Plate IX, 10, 11). Cells of costal fields are frequently covered by single, centralized, domed papillae (Plate V, 2, 5, 6, Plate VII, 1), or glabrous (Plate III, 9). Simple, long trichomes frequently emerge from intercellular contacts on costal fields (Plate X, 5, 9, 10).

Intercostal fields are 217-288 µm wide with generally isodiametric cells, being most of them subsidiary cells, sometimes subtriangular, subquadrangular, oval or irregular in shape (Plate VI). Non-specialized epidermal cells are very rare (Plate VI, 9). Anticlinal walls are straight or curved.

Stomata are crowded, haplocheilic, monocyclic, stephanocytic to actinocytic (sensu Carpenter, 2005), sometimes loosely oriented parallel to venation (Plate VI, 7) to irregularly oriented, with 4-8 (generally 5-7) subsidiary cells arranged in irregular rings, each bearing a prominent hollow, hood-shaped papilla arching over the stomatal pore in the center (mean papillae length 11.1 µm; mean width 11.8 µm). Subsidiary cells are frequently shared between adjacent stomata (Plate VI, 5). Guard cells are sunken and not seen. Stomatal density is 234.7 mm^{-2} and stomatal index is 15.7. Stomatal pore mean length 25.6 µm, stomatal apparatus mean diameter 74 µm.

Trichome bases and trichomes

Multicellular trichome bases are of three types: (1a) heavily cutinized with papillae occurring on costal (density 77 mm^{-2}) and intercostal (density 26 mm^{-2}) fields of the secondary venation (Plate VII); (1b) heavily cutinized without papillae on the midvein (density from 103 mm^{-2} at the borders to 296 mm^{-2} in the center) (Plate VIII, 1-7) and (1c) thin without papillae on the stalk/petiole (density 177 mm^{-2}) (Plate VIII, 8). Very rare unicellular trichomes remain attached to such bases after treatment with Schulze‟s solution

(Plate VII, 8, 9). In the material treated with HF only, the basal part of the broken off trichomes is still attached to the bases (Plate VII, 12-15).

Type 1a heavily cutinized, multicellular trichome bases with protruding papillae (46.2 µm mean diameter) occur on the lower cuticle randomly distributed and irregularly concentrated, sometimes clustered, exclusively on costal (abundant) and intercostal (sparse) fields where the cells are papillate (Plate VII). Bases of various shapes (distinct ?developmental stages), similar to stomata, can be observed on a single cuticle fragment (Plate VII, 1-7, Plate XI, 12-14). They are composed by 4-8 adjacent cells over which a thick ring-shaped pedestal (sensu Payne, 1978) or foot cell (sensu Carpenter, 2006) develops and fuses with the centripetally elongating and then centrifugally, outward protruding central papillae of each cell composing the base (Plate VII, 2-7). Sometimes papillae fuse with only half of the ring-shaped pedestal (Plate XI, 13). In profile view, the papillae appear to hold some type of content (Plate VII, 10-11). A heavier cutinization of the intercellular spaces in the center of the base (at the place where the stomatal pore would be) can frequently be observed. Sometimes trichome bases appear to be connected to each other by thickened strands of cuticle (?canals) (Plate V, 5, Plate VI, 10). Occasionally stomata are arranged radially around an isolated trichome base on the intercostal field (Plate VI, 3).

Type 1b trichome bases of the lower midvein seem to be composed and to develop like the ones from the secondary venation, except that there are no papillae protruding from the bulging, heavily cutinized foot cell (Plate VIII). Mean diameter of bases is 54 µm, being larger at the leaf base (38-60 µm at the leaf top; 47-88 µm at the leaf base). Like with type 1a, bases type 1b of distinct shapes (?developmental stages) can be observed on a single cuticle fragment, usually with a small round cell in the center that could be the foot cell meristematic precursor (sensu Carpenter, 2006) (Plate III, 7, Plate XI, 9, 10). The bases appear to hold a small globule or vesicle with content that should have been protected by the hair when it was in place (Plate VIII, 1-3, Plate XI, 14).

Type 1c thin-walled trichome bases without papillae occurring on the stalk/petiole are very similar to the ones described above, but without the bulging foot cell or papillae (57.7 µm mean diameter). The cutinization of these bases is weaker, forming a modest pedestal (Plate VIII, 8).

Abundant trichomes both with and without complex bases occur on the surface of the lower cuticle, however they are mostly adhered to the tonstein matrix and could only be retrieved separately from the cuticle (Plate X, 1,2).

Trichomes without complex bases are of two types: (2a) resembles an elongate papilla emerging from the center of the periclinal wall of a single epidermal cell, usually bordering the costal fields (43.4-135.2 µm long, mean length 85.2 µm) (Plate IX, 3-11). This type of trichome, although not belonging to subsidiary cells, has frequently been observed at extending towards a stomatal pore (Plate IX, 7, 8-10). The abaxial lamina bears numerous type 2a short trichomes/elongated papillae close to the leaf margin (Plate IX, 1, 2).

Type 2b seems to emerge from the contact between anticlinal walls of two adjacent epidermal cells, and its occurrence is ubiquitous on the costal fields of secondary venation, midvein of lower lamina and petiole areas (Plate VIII, 8; Plate X).

Cuticles observed under fluorescence microscopy after treatment with HF only showed a larger number of trichomes still attached to bases, which are opaque, contrasting markedly with the highly fluorescing bases (Plate VII, 8, 9, 12-15). Trichomes are fragmented and damaged, and their possible celullarization or septation could not be ascertained.

In their disposition, trichomes seem to point towards midvein and petiole and measure mostly between 400-500 µm (Plate X, 2, 4). Trichome apices unknown.

The trichome and trichome base types are summarized in Table 1.

TABLE 1- PLATES II - XI

5.2. Description remarks

The specific epithet *Glossopteris papillosa* was already erected to designate a glossopterid species from India by Srivastava (1969), consequently the designation by Guerra-Sommer (1992) remained illegitimate. The holotype (PB-2779) is missing and had not been originally illustrated; therefore a lectotype has been selected. The hand specimen PB-2777 has been chosen because, although the leaf bases are missing, the two different apices illustrate well how the morphography variation corresponds to a single cuticle pattern; additionally, it had been intended to be the holotype in Guerra-Sommer (1988). New paratypes have been selected because the newly prepared material yielded larger cuticle fragments which better represent the many cuticular features from single specimens.

5.3. Comparisons

Regarding cuticular patterns, Barclay et al. (2007) emphasize on distinguishing between anatomically conservative (genetically determined) and environmentally controlled (ecophenotypic plasticity) characters. The distinguishing features of *Glossopteris pubescens* are straight to arched anticlinal walls (rarely sinuous, never undulate), stomatal complex with subsidiary cells bearing papillae overarching the stomatal pore and trichome occurrence with complex bases. The common occurrence of papillae on subsidiary cells or also occurring on the ordinary epidermal cells has been assigned to several *Glossopteris* species, however, a large part of them have undulate/sinuous anticlinal walls. Other leaf characters such as amphistomy or hypostomy should not be considered for comparison because they have been shown to be environmentally influenced (Barclay et al., 2007). Attention will be given to species described with trichome occurrence.

The previous descriptions of the present material (Guerra-Sommer; 1992; Degani-Schmidt et al., 2011) have identified the morphographic set of characteristics as predominantly being that of *Glossopteris communis* Feistmantel (= *G. pseudocommunis* P. Srivastava in Maheshwari and Tewari, 1992) from the Early Permian of India (base of Barakar Formation).

For the upper cuticle of *G. communis*, Srivastava (1956) described a well differentiated secondary venation into costal and intercostal fields with elongated and polygonal cells respectively. For the lower cuticle, probably papillate stomata occur in groups of four to five, sometimes partly dicyclic, traits that have not been observed in *G. pubescens*, in which practically all epidermal cells of the intercostal fields have a subsidiary function. Describing a different specimen from a different locality, Singh and Maheshwari (2000) defined the cells of the upper cuticle as having "a dense central region". The lower cuticle is thin and cells have a more conspicuous “dense central region”. It is not clear if the cells are papillate or not. The stomatal apparatus is like the one described for *G. pubescens*, with papillae overhanging the stomatal pore. There is no evidence of trichome occurrence. The papillate nature of the subsidiary cells, their orientation and crowding are similar to *G. pubescens*.

Upon re-examination, the material described by Fittipaldi and Rösler (1985) from the Sakmarian-Artinskian of northern Paraná Basin (Cambuí coal mines, Paraná State, Brazil) identified as *G. communis* indicates an overall similarity with *G. pubescens* in regard to the epidermal micromorphology, particularly the crowded stomatal apparati with overarching papillae and the clear delimitation of costal and intercostal zones on one of the leaf faces. However, the stomatal pattern remained insufficiently known due to the misinterpretation of upper and lower cuticles and stomatal description was based on the sparse stomata from the adaxial leaf surface (described as lower lamina) and no stomatal counts were carried out. The intercostal fields from the actual abaxial surface should have been recognized as having stomatiferous intercostal fields, rather than papillate ones. Microscopic observation of slides of this material confirmed the photograph interpretation and revealed crowded stomata oriented in rows parallel to venation. An additional marked difference between that material and *G. pubescens* is the absence of papillae on the costal fields from the secondary venation in the lower lamina.

Although *G. papillosa* S. Srivastava (from the Lower Triassic of India - Nidpur, Sidhi District, Madhya Pradesh) does not bear trichomes, it will also be mentioned here for the disambiguation of the previous description of *G. pubescens* as *G. papillosa* by Guerra-Sommer (1992). Differently from *G. pubescens*, this species is heavily papillate on both surfaces. Papillae are solid and dome-shaped, occurring on most cells from both costal and intercostal fields; stomata sparse. Anticlinal walls are straight to curved like in *G. pubescens* and subsidiary cells have overarching papillae (Srivastava, 1969).

For *G. subtilis* Pant et Gupta (Early Permian of India, Raniganj Coalfield - Raniganj Stage) sparse hair pedestals have been described in the lower cuticle on intercostal fields (Pant and Gupta, 1971). This species differs from *G. pubescens* in having sinuous anticlinal walls in the cells of intercostal fields and no papillae at all.

G. kusumiae Maheshwari et Tewari (Early Permian of India, Barakar Formation, Churulia area, Raniganj Coalfield), with papillae from subsidiary cells overarching the stomatal pore, has undulate anticlinal walls (Maheshwari and Tewari, 1992). This species presents multicellular circular hair bases on the midvein which are very similar to the type 1c described for the petiole of *G. pubescens*.

G. hispida Pant (Early Permian of Tanzania, Mhukuru Coalfield) bears the most striking similarity with *G. pubescens* in relation to trichome occurrence in the lower epidermis. Non-papillate, multicellular ring-shaped trichome bases (foot cell/pedestal) are observed on the midvein and well-preserved hairs have been recovered from the matrix in contact with the lower side of the leaf (Pant, 1958, Fig. 4A, B, pp.137; Fig. 5 pp. 138; Fig. 6

pp.140). Trichomes occur on lateral venation (like in *G. pubescens*) and are simple, three- to six-celled, tapering, cells short or long, apex of end cell acutely pointed. Trichomes point in different directions but usually outwards and backwards on the midvein and backwards on the lamina. The main differences to *G. Pubescens* are mottling or occurrence of several small papillae on cells of upper cuticle, sinuous anticlinal walls on the lower cuticle with non-papillate ordinary cells and occurrence of trichomes with simple, non-papillate bases only.

It is worth mentioning that a few gangamopterid species feature similar cuticular structures as the ones here described for *Glossopteris pubescens*, for instance *Gangamopteris cyclopteroides* Feistmantel, *G. papillosa*, *G. media* and *G. hispida* Pant et Singh (from Madhya Pradesh and Bihar, India), which present elongated papillae and trichomes similar to the types 2a and 2b here described (Pant and Singh, 1968).

6. Discussion

The distinctive architecture of the indumentum of the lower cuticle of *G. pubescens* comprises haplocheilic, monocyclic, stephanocytic to actinocytic stomata with sunken guard cells and subsidiary cells with papillae overarching the stomatal pore, anticlinal walls straight or curved, sometimes sinuous, never undulated, epidermal cells frequently papillate, some elongated papillae, and trichomes with and without complex bases concentrated mainly on venation areas. This set of characters has not been reported before, warranting the creation of a new specific epithet, *Glosspteris pubescens*.

Based on these micromorphological features, Guerra-Sommer (1992) erected a new glossopterid species from the Faxinal Coalfield, *G. papillosa* (illegitimate name, now rectified). However, very small cuticle fragments obtained through chemical preparation led to a limited understanding of the newly described structures, which had been hypothesized to be complete secretory complexes, and no trichomes had been observed.

6.1. Morphography

Shape and venation are mostly similar to *G. communis*. Variations in morphography of incomplete specimens which yielded one and the same cuticular pattern possibly reflect phenotypic plasticity and might correspond to leaves from different positions in the canopy or on the branches. The varied apex shapes from acute to obtuse, sometimes rounded, occur commonly in the Lower Permian of India and Africa (Karoo Basin), and do not seem to be a species specific character but rather a leaf polymorphism. According to Stewart and Rothwell (1993), where many specimens are available, possibly much of the variability observed from specimen to specimen represents stages in development of a single species.

The morphographic pattern of *G. communis* is typical from the Karharbari/Barakar Stages in India and its abundance decreases in the later periods (Chandra and Surange, 1979), but it is also widespread in Gondwana (e.g., Bernardes-de-Oliveira and Pons, 1975; Fittipaldi and Rösler 1985; Guerra-Sommer, 1992).

Leaves with acute bases when in whorls and elliptic when isolated as in the material studied here could be attributed to the occurrence of leaves borne in tight helices on short shoots, and single leaves on long shoots (Pant and Singh, 1974). Pigg and Trivett (1994) consider that variations in internodal length could simply represent the expected variation in a temperate plant.

6.2. Micromorphology

Cuticles have been collected from practically all available hand specimens from the most recent field gatherings and the bulk maceration yielded meager 5.8% of cuticle fragments with different cuticular patterns, such as the ones described by Guerra-Sommer (1992).

Genotypic traits (Barclay et al., 2007) like occurrence of papillae and a fairly homogenous stomatal architecture have been described for a large group of glossopterids, and thus have not been useful to assess the species diversity (Chandra and Singh, 1992). The common occurrence of papillae on subsidiary cells and on the ordinary epidermal cells of the lower epidermis has been assigned to about 60% of *Glossopteris* species from India (Pant and Singh, 1971). Differences in papillae length here observed are attributed to probable continuous growth in older leaves rather than different species bearing short or long papillae. The trichome type 2a (Table 1), for instance, seems to originate from continuous growth (Cleal and Shute, 1992) of selected papillae (Plate IX).

According to Barclay et al. (2007), a larger suite of epidermal characters, including trichome type and arrangement, in addition to stomatal complex attributes and presence or absence of papillae, provide a more robust approach for constraining the taxonomy of modern and fossil cuticle specimens.

As observed by Pigg and Nishida (2006), cuticular analysis lead to the proliferation of new names for leaves and increased the taxonomic indistinctness, making it difficult to get an accurate idea of the diversity within glossopterid leaf forms. Probable causes to such fragmentary descriptions are the organic maturation or desiccation of the cuticles leading to material disintegration during the oxidation treatment (Kerp and Barthel, 1993; McLaughlin, 1994), generating cuticular fragments too small to detect natural pattern variations on a single leaf. Additionally, ornamentation can be lost also due to preservational and/or preparation factors. For instance, prolonged maceration in diluted alkali solution might yield larger fragments but with eroded structures and obscure cell outlines. In the present study, skipping the oxidation treatment allowed for the observation of trichome fragments still attached to the bases on the thin abaxial surface using florescence microscopy (Plate VII, 12-15).

The upper cuticle of *G. pubescens* features sparse dark round structures (Plate V, 1; Plate XI, 5) which resemble the secretory cavities identified through chemical analysis for neuropterid pteridosperms (D‟Angelo and Zodrow, 2016, Fig. 8, pp. 24). The short filamentous projections from the cell corners (Plate XI, 4, 5) have also been observed by Kerp and Barthel (1993) on the cuticles of the pteridosperm *Alethopteris zeilleri* (Ragot) Wagner. These characters could be part of a pattern trend in some Paleozoic pteridosperm groups.

Trichome bases

The lower cuticle of *G. pubescens* shows heavy ornamentation with profuse papillae and outstanding, elaborate trichome bases. Cuticles bearing abundant papillae, trichomes and specialized structures with probable glandular function have been described for numerous Paleozoic pteridosperms (e.g., Cleal and Zodrow, 1989; Poort and Kerp, 1990; Cleal and Shute, 1992; Kerp and Barthel, 1993; Krings and Kerp, 1997a, 1997b, 1998, 1999; Krings et al., 2003; Hamad et al., 2008; Zodrow et al., 2014).

Kerp (1990) observed that the hair bases of late Paleozoic conifers and many pteridosperms resemble stomatal complexes lacking guard cells, and illustrated a trichome base (Fig. 4A, pp. 562) similar to the multicellular non-papillate types described here (Table 1, types 1b and 1c).

Carpenter (2006) investigated epidermal structures in the basal angiosperms and hypothesized that a number of “specialized leaf epidermal complexes are homologous with and evolutionarily derived from stomatal complexes, with a portion of the specialized structure itself (e.g., [...] the trichome foot cell) possibly homologous to the guard cell pair or guard mother cell”. In fact, the trichome foot cell in *G. pubescens* (Table 1, types 1a and 1b), seems to originate from a “poorly developed pair of guard cells” (as per Carpenter, 2006).

Cleal and Zodrow (1989) and Cleal and Shute (1992) described the presence of trichomes for some neuropterid pteridosperms. Like in *G. pubescens*, they are frequent on the abaxial surface, concentrate mostly on the costal fields and are sparser on the intercostal fields. Some very long trichome fragments have been reported (up to 550 µm). Papillae are not always present. *Neuropteris flexuosa* Sternberg showed numerous trichome bases close to the edge of the lower cuticle (Cleal and Zodrow, 1989, Plate 102, 4, pp. 859) which is an aspect similarly present in *G. pubescens* (Plate IX, 1, 2).

Hamad et al. (2008) pointed out that in the *Dicroidium* species from the Upper Permian of Jordan the presence and density of trichomes is apparently related to the presence and density of papillae, thick anticlinal walls and highly cutinized subsidiary cells, similarly to the papillate trichome bases of *G. pubescens* (Table 1, type 1a).

In the late Paleozoic seed fern from Central France *Barthelopteris germarii* (Giebel 1857) Zodrow et Cleal, rosette-like structures occur associated to the secondary venation and are interpreted as peltate glandular trichomes, i.e., as having a secretory function (Krings and Kerp, 1998). It is possible that the trichome types here described for *G. pubescens* also had a chemical/physiological function in addition to a mechanical one considering their high concentration on vascular areas. Due to the poor preservation of the long trichomes in the tonstein matrix, no evidence has been found for multicellular trichomes with specialized glandular or secretory tips. Similarly, among the structures homologous to stomata observed by Carpenter (2006) in the basal angiosperms, there are secretory oil cells, meaning that a developmental homology for such structures could also be possible.

The absence of fluorescence of the trichomes contrasts with the high fluorescence of the bases, indicating a non-lipidic, subcuticular origin for the trichome (Plate 7, 12-15).

The interaction observed between the papillae and the trichome foot cell (?originated from the guard cell pair) could mean that the guard cell would have some secretory function considering that the papillae appear to hold some type of content. It is interesting to note that, in extant conifers, the guard cells have a function of secreting stomatal plugs (Jeffree et al., 1971), which act as water repellant devices in species from environments with high precipitation (Haworth and McElwain, 2008). It cannot be discarded that the bases themselves could have been secretory structures that would expel their contents upon breakage of the trichome, especially the ones from the lower midvein which frequently bear a vesicle (Plate VIII, 1-3).

6.3. Ecological factors

Considering the limitations inherent to an analysis based on morphotaxonomy, the large leaf assemblage here identified as mostly belonging to a single species raises hypotheses involving a peculiar set of ecological conditions occurring in the peat-forming environment of the Faxinal Coalfield in comparison with other habitats with glossopterid assemblages in the Gondwana. The type of indumentum produced by the plant is genotipically determined (DiMichele et al., 1987; Barclay et al., 2007; Haworth and McElwain, 2008), and the phenotypic identity of a taxon is flexible to a certain degree, allowing the plants to react to different site conditions and short-term environmental changes (DiMichele et al., 1987). According to Johnson (1975), strong selection forces are operative in the development of leaf indumenta and the elaborate ornamentation of *G. pubescens* suggests an ecologic adaptation to specific environmental factors.

Alternative or additional functions to the most obvious transpiration reduction and herbivory repellence conferred by heavy pubescence include decreased leaf wettability, reduction of pathogen germination, improvement of freezing resistance in a highly seasonal environment (Cordell et al., 1998; Roy et al., 1999), and even as waste repositories (Payne,1978).

The possible ecological significance of overarching stomatal papillae and great density of papillae and trichomes in fossil and extant plants has been mainly related to stressful conditions such as phytophagy. Pant and Singh (1971), recognizing the difficulties of linking any particular ecological condition with the papillate cuticles, considered a number of functions, among them protection against insects and other harmful animals. However, glossopterid leaves are associated with low indices of phytophagy (Cleal and Zodrow, 1989; Slater et al., 2012, 2015 and references therein), be it due to low incidence of herbivores or efficient chemical defense.

Further possible explanations for the frequent occurrence of papillate cuticles among the glossopterids (e.g., Pant, 1958; Pant and Singh, 1971) include environmental draught or physiological water stress (e.g., Kerp, 1990; Haworth and McElwain, 2008;). However, the large leaf size of *G. pubescens* (up to 32 cm in length) indicates otherwise. Leaf size is a genetic factor that is also strongly environmentally controlled (Roy et al., 1999). In extant plants, responses to water limitation are often characterized by development of small leaves (Haworth and McElwain, 2008). Thus, the exuberance of the glossopterid foliage preserved in the Faxinal tonstein points to water and nutrient availability rather than to physiologically stressful conditions.

Nevertheless, charcoal occurrence associated to the sediments bearing the *Glossopteris* Flora suggests that the glossopterids were indeed under generally environmental pressures of cyclical environmental disturbance. Charcoal studies carried out in recent decades established a wildfire origin for fusain (Scott, 1989; 2010), allowing for the recognition of regular fire events in Permian peatlands at high latitudes as systemic events in western and eastern Gondwana during Permian (Jasper et al., 2013; Slater et al., 2015). Degani-Schmidt et al. (2015) analyzed charcoalified logs occurring in the upper coal seam S from the Faxinal Coalfield at the base and top boundaries of the interbedded tonstein ply and identified autochthonous/hypautochthonous charcoal input from wildfire events in which fire intensity was apparently controlled by humidity oscillations. The apparent conflicting occurrence of fire events in peat-forming environments, which require a permanent moist setting, was explained through evidences of cyclical conditions from wet to drying intervals with a possible lower water table along the coal seam S, in addition to the high paleoatmospheric O_2

levels estimated for the Early Permian (Berner, 2009) that allowed for the burning of plant matter with high moisture (He et al., in press).

These wildfires were relevant in the Gondwana continent during the Sakmarian global warming event previously detected by Gastaldo et al. (1996) and Montañez et al. (2007) after the end of the earliest Permian glacial phase in Gondwana. Considering the importance of the fire data, there could be a correlation of these events with the recurrent Permian global greenhouse crises during the waning of the ice house age, more specifically with the one signaled for the Sakmarian by Retallack (2013).

The one specific environmental factor distinguishing the Faxinal Coalfield from other coeval Gondwanan peatlands is the ash-fall event recorded by the tonstein interbedded in the top coalseam S. The proximity of the south Brazilian Sakmarian peatlands to a hypothesized source of volcanic activity close to the southern margin of the Paraná Basin (Rocha Campos et al., 2011) could be associated with an increase in atmospheric aerosols and gases. An environmental disturbance like this could have stimulated the development of the trichome complex to carry out functions such as protection of the stomata against dust and toxic gases (Haworth and McElwain, 2008); the ongoing multiplication of the trichome bases here observed (Plate III, 6, 7; Plate XI, 8-14) could be a response triggered by the ash-fall itself. However, even though there are multiple interbedded ash-fall layers in other nearby coal deposits from the southern Paraná Basin (Guerra-Sommer et al., 2008; Rocha Campos et al., 2011; Simas et al., 2012), in the Faxinal Coalfield there is only one tonstein layer, leaving a hypothesis of ash-fall recurrence unsupported.

These hypotheses seem to conciliate the development of an elaborate epidermal indumentum with multiple functions of protection against seasonal herbivory, cyclical desiccation and moisture excess, dust and gas pollution.

Ultimately, the indumentum is a primary recipient of environmental stimuli and forces, and it can be influential on the development of organs upon which they mature (Payne, 1978; Roy et al., 1999). The trichome bases reveal extraordinary plasticity of the stomata initial cells, comparable to that of the Angiosperm cuticle evolution documented by Upchurch (1984) and extant basal angiosperms (Carpenter, 2006). Structures like these occurring in Paleozoic pteridosperms can bring new supporting insights to the discussion about an ancestral affinity of the Glossopteridales with the flowering plants.

Like in a few extant plants from disturbed environments (e.g., Cordell et al., 1998), the ability of *Glossopteris pubescens* to dominate its habitat probably derived from a combination of genetic factors with an environmentally driven plasticity (e.g., Barthélémy and Caraglio, 2007).

7. Final considerations

The remarkable adaptative plasticity of *Glossopteris pubescens* is represented by the elaborate indumentum preserved in the leaf cuticles and resulted in the dominance of this species in the swamp forest that generated the Faxinal Coalfied, where it thrived and dominated in an environment heavily disturbed by extreme climate oscillations.

The lower leaf surface of *G. pubescens* bears an indumentum composed of overarching stomatal papillae, papillate epidermal cells, simple trichomes and complex trichome bases densely concentrated under the vascular system of the leaf. This epidermal architecture is unique to *G. pubescens* and apparently endemic to the locality of Faxinal Coalfield, southern Paraná Basin.

The varying morphology of trichome bases here observed is considered to reflect the developmental stages of this genetically determined structure. Trichome base development is strikingly similar to that of extant basal angiosperms.

The dominance of one micromorphological pattern in a large leaf assemblage suggests that there is a great level of so far undetected leaf polymorphism among glossopterids.

Such elaborate indumentum is inferred to be a response triggered by environmental cyclicity from dry to wet conditions detected through wildfire evidences (charcoal analyses) as common and systemic events in the peat-forming environment during climate oscillations at the waning of the Permian icehouse stage.

These evidences seem to conciliate the presence of the epidermal indumentum with multiple functions of protection essentially against cyclical environmental disturbance. The occurrence of the peculiar trichome complexes mainly under the venation system implies that they were most likely connected with the vascular physiology or having a secretory function.

Additionally, the peculiar entombment in ash-fall suggests an influence of regional volcanic processes in the swamp forest, and the development of the trichome complexes could be linked to protection against air pollution.

Acknowledgments

This study is submitted by I.D.S. in partial fulfillment of the requirements for the PhD degree at the Programa de Pós-Graduação em Geociências/UFRGS, Porto Alegre, Rio Grande do Sul under the tenure of a scholarship funded by the Brazilian National Council of Technological and Scientific Development CNPq (159690/2012-9). M.G.S. is thankful to CNPq for a research grant. The authors gratefully acknowledge Rajni Tewari for kindly providing literature, João Carlos Coimbra for a discussion on taxonomy, the Marleni Marques-Toigo Palynology Laboratory/UFRGS headed by Paulo Alves de Souza and CECO/UFRGS for making available their facilities for the preparation of the fossil material, and Luiz Flávio Lopes (DEP-IG/UFRGS) for the photographs of the hand specimens. COPELMI mining company is thanked for facilitating the fossil collections from the Faxinal Coalfield between 1984 and 2009 even after the mine closure. I.D.S. is grateful to Dieter Uhl for the welcome at the Senckenberg Institute, to DAAD for the financial help (PKZ A/12/72459), and to Abdalla Abu Hamad for a discussion on preparation of microscopic slides.

References

Anderson, J.M., Anderson, H.M., 1985. The Palaeoflora of southern Africa. Prodromous of South African megafloras: Devonian to Lower Cretaceous. AA Balkema, Rotterdam.

Archangelsky, S., 1970. Fundamentos de Paleobotánica, Serie Técnica y Didáctica 11. Universidad Nacional, La Plata.

Archangelsky, S., Wagner, R.H., 1983. *Glossopteris anatolica* sp. nov. from uppermost Permian strata in south-east Turkey. Bull. Br. Mus. Nat. Hist. Geol. 37, 81–91.

Bajpai, U., 1986. *Glossopteris shailae*, a new fossil leaf from Upper Permian (Raniganj Formation) of India. Palaeobotanist 35, 159-164.

Banerjee, M., 2005. Autochthonous deposition of Indian coal beds with palaeobotanical evidences of in-situ plants from Saharjuri Basin, Jharkhand. Curr. Sci. India 88, 1487-1490.

Barclay, R., McElwain, J., Dilcher, D., Sageman, B., 2007. The Cuticle Database: Developing an interactive tool for taxonomic and paleoenvironmental study of the fossil cuticle record. Cour. Forsch.-Inst. Senckenberg 258, 39-55.

Barthelemy, D., Caraglio, Y., 2007. Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Ann. Bot.-London 99, 375-407. doi:10.1093/aob/mcl260

Bernardes-de-Oliveira, M.E.C., Pons, D., 1975. Tafoflora of Karroo in the Zambesi Basin (Tefe Region, Mozambique). Bol. IG-USP 6, 33-53. doi:10.11606/issn.2316-8978.v6i0p33-53

Bernardes-de-Oliveira, M.E.C., 1978. Ensaio sobre a utilização de caracteres biométricos das Glossopteridófitas em Estratigrafia. Bol. IG-USP 9, 91-95. doi:10.11606/issn.2316-8978.v9i0p91-95

Berner, R.A., 2009. Phanerozoic atmospheric oxygen: New results using the GEOCARBSULF model. Am. J. Sci. 309, 603–606. doi:10.2475/07.2009.03

Berthelin, M., Stolle, E., Kerp, H., Broutin, J., 2006. *Glossopteris anatolica* Archangelsky and Wagner 1983, in a mixed middle Permian flora from the Sultanate of Oman: Comments on the geographical and stratigraphical distribution. Rev. Palaeobot. Palynol. 141, 313-317. doi:10.1016/j.revpalbo.2006.02.004

Boardman, D.R., Tybusch, G.P., Iannuzzi, R., Dutra, T.L., Lima, L., 2006. Presença de *Glossopteris browniana* Brongniart em níveis do topo do afloramento Quitéria (Formação Rio Bonito), Rio Grande do Sul, Brasil (Permiano Inferior). Gaea-Journal of Geoscience 2, 9-17.

Boardman, D.R., Iannuzzi, R., Souza, P.A., Lopes, R.C., 2012. Paleobotanical and palynological analysis of Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Paraná Basin), Rio Grande Do Sul, Brazil. Int. J. Coal Geol. 102, 12–25. doi:10.1016/j.coal.2012.07.007

Boureau, E., 1967. Traité de Paléobotanique, Tome 2, Bryophyta, Psilophyta, Lycophyta. Masson et Cie., Paris.

Carpenter, K.J., 2005. Stomatal architecture and evolution in basal angiosperms. Am. J. Bot. 92, 1595-1615. doi: 10.3732/ajb.92.10.1595

Carpenter, K.J., 2006. Specialized structures in the leaf epidermis of basal angiosperms: morphology, distribution, and homology. Am. J. Bot. 93, 665-681. doi: 10.3732/ajb.93.5.665

Cazzulo-Klepzig, M., Guerra-Sommer, M., Menegat, R., Simas, M.W., Mendonça Filho J. G., 2007. Peat-forming environment of Permian coal seams from the Faxinal Coalfield (Paraná Basin) in Southern Brazil, based on palynology and palaeobotany. Rev. Bras. Paleontol. 10, 117-127. doi:10.4072/rbp.2007.2.05

Cazzulo-Klepzig, M., Mendonça Filho, J.G., Guerra-Sommer, M., Menezes, T.R., Simas, M.W., Mendonça, J.O., Degani-Schmidt, I., 2009. Effect of volcanic ash-fall on a permian peat-forming environment, on the basis of palynology, palynofacies and paleobotany (Faxinal Coalfield, Brazil). Rev. Bras. Paleontol. 12, 179-194. doi:10.4072/rbp.2009.3.02

Chandra, S., Singh, K.J., 1992. The genus *Glossopteris* from the late Permian beds of Handapa, Orissa, India. Rev. Palaeobot. Palynol. 75, 183-218. doi:10.1016/0034-6667(92)90016-A

Chandra, S., Srivastava, A.K., 1981. A new species of *Glossopteris* from the Barakar Formation or Lower Gondwana of India. Palaeobotanist 27, 166-73.

Chandra, S., Surange, K.R., 1979. Revision of the Indian species of *Glossopteris*. Birbal Sahni Institute of Palaeobotany, Lucknow.

Chmura, G.L., Stone, P.A., Ross, M.S., 2006. Non-pollen microfossils in Everglades sediments. Rev. Palaeobot. Palynol. 141, 103-119. doi:10.1016/j.revpalbo.2006.03.019

Cleal, C.J., Shute, C.H., 1992. Epidermal features of some Carboniferous neuropteroid fronds. Rev. Palaeobot. Palynol. 71, 191-206. doi:10.1016/0034-6667(92)90162-A

Cleal, C.J., Zodrow, E.L., 1989. Epidermal structure of some medullosan *Neuropteris* foliage from the Middle and Upper Carboniferous of Canada and Germany. Palaeontology 32, 837-882.

Cohen, K.M., Finney, S.M., Gibbard, P.L., Fan, J.X., 2013. The ICS International Chronostratigraphic Chart. Episodes 36, 199-204.

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D., Vitousek, P.M., 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia, 113, 188-196. doi:10.1007/s004420050367

Corrêa-da-Silva, Z.C., Arrondo, O.G., 1977. Tafoflora Permiana de Mariana Pimentel, Município de Guaíba, Rio Grande do Sul, Brasil. Pesquisas UFRGS 7, 27-44.

Cúneo, N.R., 1996. Permian phytogeography in Gondwana. Palaeogeogr. Palaeocl. 125, 75-104. doi:10.1016/S0899-5362(97)83529-4

D'Angelo J.A., Zodrow E.L., 2016. 3D chemical map and a theoretical life model for *Neuropteris ovata* var. *simonii* (index fossil, Asturian, Late Pennsylvanian, Canada). Int. J. Coal Geol. 153, 12-27. doi:10.1016/j.coal.2015.11.007

Degani-Schmidt, I., Guerra-Sommer, M., Mendonça, J.O., Mendonça Filho, J.G., Jasper, A., Cazzulo-Klepzig, M., Iannuzzi, R., 2015. Charcoalified logs as evidence of hypautochthonous/autochthonous wildfire events in a peat-forming environment from the Permian of southern Paraná Basin (Brazil). Int. J. Coal Geol. 146, 55–67. doi:10.1016/j.coal.2015.05.002

Degani-Schmidt, I., Guerra-Sommer, M., Bernardes-de-Oliveira, M.E.C., 2011. Variation in stomatal numbers of *Glossopteris* leaves from the Lower Permian of Paraná Basin, Brazil. Rev. Bras. Paleontol. 14, 137-148. doi: 10.4072/rbp.2011.2.02

DiMichele, W.A., Falcon-Lang, H.J., 2011. Pennsylvanian „fossil forests' in growth position (T0 assemblages): origin, taphonomic bias and palaeoecological insights. J Geol. Soc. London 168, 585-605. doi:10.1144/0016-76492010-103

DiMichele, W.A., Phillips, T.L., Olmstead, R.G., 1987. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. Rev. Palaeobot. Palynol. 50, 151-178. doi:10.1016/0034-6667(87)90044-3

Doyle, J. A., 2006. Seed ferns and the origin of angiosperms. J. Torrey. Bot. Soc. 133, 169-209. doi:10.3159/1095-5674(2006)133[169:sfatoo]2.0.co;2.

Fittipaldi, F.C., Rösler, O. 1985. A cutícula de *Glossopteris communis* da Formação Rio Bonito no Estado do Paraná. Geologia 27, 579-595.

Gastaldo, R.A., Pfefferkorn, H.W., DiMichele, W.A., 1995. Taphonomic and sedimentologic characterization of „roof-shale" floras. In: Lyons, P., Wagner, R.H., Morey, E. (Eds.), Historical Perspective of Early Twentieth Century Carboniferous Paleobotany in North America. Geol. Soc. Am. Mem. 185, 341-352. doi: 10.1130/MEM185-p341

Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1996. Out of the Icehouse into the Greenhouse: A late Paleozoic analog for modern global vegetational change. GSA Today 6, 1-7.

Gibbs, M.T., Rees, P.M., Kutzbach, J.E., Ziegler, A.M., Behling, P.J., Rowley, D.B., 2002. Simulations of Permian climate and comparisons with climate-sensitive sediments. J. Geol. 110, 33-55. doi: 10.1086/324204

Goswami, S., Singh, K.J., 2013. Floral biodiversity and geology of the Talcher Basin, Orissa, India during the Permian-Triassic interval. Geological Journal 48, 39-56.

Gould, R.E., Delevoryas, T., 1977. The biology of *Glossopteris*: Evidence from petrified seed-bearing and pollen-bearing organs. Alcheringa 1, 387-99.

Gray, J., 1965. Extraction techniques. In: Kummel, B., Raup, D. (Eds.), Handbook of paleontological techniques. W.H. Freeman, San Francisco, pp. 530-586.

Grenfell, H. R., 1995. Probable fossil zygnematacean algal spore genera. Rev. Palaeobot. Palynol. 84, 201-220. doi: 10.1016/0034-6667(94)00134-6

Guerra-Sommer, M. 1988. Padrões epidérmicos da Flora *Glossopteris* na Jazida do Faxinal (Formação Rio Bonito, Kunguriano, RS): implicações taxonômicas, bioestratigráficas, paleoecológicas e paleogeográficas. Ph.D. Thesis, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Brasil, pp. 372.

Guerra-Sommer, M., 1992. Padrões epidérmicos de Glossopteridales da tafoflora do Faxinal (Formação Rio Bonito, Artinskiano-Kunguriano, Bacia do Paraná, Brasil). Pesquisas em Geociências 19, 26-40.

Guerra-Sommer, M.; Marques-Toigo, M., Corrêa-da-Silva, Z.C., 1991. Original biomass and coal deposition in Southern Brazil (Lower Permian, Paraná Basin). Bull. Soc. Géol. France 162, 227-237.

Guerra-Sommer, M., Cazzulo-Klepzig, M., 2000. Permian Palaeofloras from Southern Brazilian Gondwana: A palaeoclimatic approach. Rev. Bras. de Geoc. 30, 486-491.

Guerra-Sommer, M., Cazzulo-Klepzig, M., Formoso, M.L.L., Menegat, R., Mendonça Filho, J.G., 2008. U-Pb dating of tonstein layers from a coal succession of the southern Paraná Basin (Brazil): A new geochronological approach. Gondwana Res. 14, 474-482. doi:10.1016/j.gr.2008.03.003

Hamad, A.A., Kerp, H., Vörding, B., Bandel, K., 2008. A Late Permian flora with *Dicroidium* from the Dead Sea region, Jordan. Rev. Palaeobot. Palynol. 149, 85–130. doi:10.1016/j.revpalbo.2007.10.006

Haworth, M., McElwain, J., 2008. Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. Palaeogeogr. Palaeocl. 262, 79-90. doi:10.1016/j.palaeo.2008.02.009

He, T., Belcher, C.M., Lamont, B.B., Lim, S.L., 2015. A 350-million-year legacy of fire adaptation among conifers. J. Ecol. in press. doi:10.1111/1365-2745.12513

Høeg, O.A., Bose, M.N., 1960. The *Glossopteris* Flora of the Belgian Congo: Annales du Musée Royal du Congo Belge 32, 1-107.

Holz, M., 2003. Sequence stratigraphy of a lagoonal estuarine system-an example from the lower Permian Rio Bonito Formation, Paraná Basin, Brazil. Sediment. Geol. 162, 305-331. doi:10.1016/S0037-0738(03)00156-8

Holz, M., França, A.B., Souza, P.A., Iannuzzi, R., Rohn, R., 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Parana Basin, Brazil, South America. J. S. Am. Earth Sci. 29, 381-399.

Iannuzzi, R., 2000. Bainha outcrop, Criciúma, Santa Catarina State (Permian *Glossopteris* flora). Flora *Glossopteris* do Permiano Inferior. In: Schobbenhaus, C., Campos, D.A.; Queiroz, E.T., Winge, M., Berbert-Born, M. (Eds.), Sítios Geológicos e Paleontológicos do Brasil v. 1, DNPM/CPRM-Comissão Brasileira de Sítios Geológicos e Paleobiológicos (SIGEP), Brasília, pp 23-31. http://sigep.cprm.gov.br/sitio082/sitio082english.htm

Jasper, A., Uhl, D., Guerra-Sommer, M., Hamad, A.A., Machado, N.T., 2011. Charcoal remains from a tonstein layer in the Faxinal Coalfield, Lower Permian, southern Paraná Basin, Brazil. An. Acad. Bras. Cien. 83, 471-481. doi:10.1590/s0001-37652011000200009

Jasper, A., Guerra-Sommer, M., Hamad, A.A., Bamford, M., Bernardes-de-Oliveira, M.E.C., Tewari, R., Uhl, D., 2013. The burning of Gondwana: Permian fires on the southern continent - A palaeobotanical approach. Gondwana Res. 24, 148-160. doi:10.1016/j.gr.2012.08.017

Jeffree, C.E., Johnson, R.P.C., Jarvis, P.G., 1971. Epicuticular wax in the stomatal antechamber of Sitka Spruce and its effects on the diffusion of water vapour and carbon dioxide. Planta 98, 1–10. doi:10.1007/bf00387018

Johnson, H.B., 1975. Plant pubescence: an ecological perspective. Bot. Rev. 41, 233-258. doi:10.1007/bf02860838

Kerp, H., 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios 5, 548-569. doi:10.2307/3514861

Kerp, H., Barthel, M., 1993. Problems of cuticular analysis of pteridosperms. Rev. Palaeobot. Palynol. 78, 1-18. doi:10.1016/0034-6667(93)90014-l

Kerp, H., Krings, M., 1999. Light microscopy of cuticles. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern techniques. Geological Society, London, pp. 52-56.

Kovács-Endrödy, E., 1979. A re-evaluation of the venation structure of *Glossopteris*. Ann. Geolog. Surv. S. Afr, 12, 107-141.

Krassilov, V. A., 1977. The origin of angiosperms. Bot. Rev. 43, 143-176.

Krings, M., Kerp, H., 1997a. An improved method for obtaining large pteridosperm cuticles. Rev. Palaeobot. Palynol. 96, 453-456. doi:10.1016/s0034-6667(96)00059-0

Krings, M., Kerp, H., 1997b. Cuticles of *Lescuropteris genuina* from the Stephanian (Upper Carboniferous) of Central France: evidence for a climbing growth habit. Bot. J. Linn. Soc. 123, 73-89. doi:10.1111/j.1095-8339.1997.tb01405.x

Krings, M., Kerp, H., 1998. Epidermal anatomy of *Barthelopteris germarii* from the Upper Carboniferous and Lower Permian of France and Germany. Am. J. Bot. 85, 553-553. doi:10.2307/2446440

Krings, M., Kerp, H., 1999. Morphology, growth habit, and ecology of *Blanzyopteris praedentata* (Gothan) nov. comb., a climbing neuropteroid seed fern from the Stephanian of central France. Int. J. Plant Sci. 160, 603-619. doi:10.1086/314154

Krings, M., Kerp, H., Taylor, T. N., Taylor, E. L., 2003. How Paleozoic vines and lianas got off the ground: on scrambling and climbing Carboniferous-Early Permian pteridosperms. Bot. Rev. 69, 204-224. doi:10.1663/0006-8101(2003)069[0204:hpvalg]2.0.co;2

Maheshwari, H.K., Tiwari, R., 1992. Epidermal morphology of some Indian species of the genus *Glossopteris* Brongniart. Palaeobotanist 39, 338-380.

McLoughlin, S., 1994. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: part 2. Palaeontogr. Abt. B 231, 1-29.

Melville, R., 1983. Glossopteridae, Angiospermidae and the evidence for angiosperm origin. Bot. J. Linn. Soc. 86, 279-323. doi:10.1111/j.1095-8339.1983.tb00975.x.

Meyen, S.V., 1987. Fundamentals of Palaeobotany. Chapman and Hall, London.

Montañez, I.S., Tabor, J.N., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C. R., Isbell, J.L., Birgenheier, L.P., Rygel, M.C., 2007. CO_2-forced climate and vegetation instability during Late Paleozoic deglaciation. Science 315(5808), 87-91. doi: 10.1126/science.1134207

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. Bol. de Geoc. Petrobras 15, 265-287.

Pant, D.D., 1958. The structure of some leaves and fructifications of the *Glossopteris* flora of Tanganyika. Bull. Br. Mus. Nat. Hist. Geol. 3, 127-175.

Pant, D.D., Choudhury. A., 1977. On the genus *Belemnopteris* Feistmantel. Palaeontogr. Abt. B 164, 153-166.

Pant, D.D., Gupta, K.L., 1968. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart: Part 1. Palaeontogr. Abt. B 124, 45-81.

Pant, D.D., Gupta, K.L., 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart: Part 2. Palaeontogr. Abt. B 132, 130-152.

Pant, D.D., Pant, R., 1987. Some *Glossopteris* leaves from Indian Triassic beds. Palaeontogr. Abt. B 205, 165-178.

Pant, D.D., Singh, K.B., 1968. On the genus *Gangamopteris* McCoy. Palaeontogr. Abt. B 124, 83-101.

Pant, D.D., Singh, K.B., 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopleris* Brongniart. Part 3. Palaeontogr. Abt. B 135, 1-40.

Pant, D.D., Singh, K.B., 1974. On the stem and attachment of *Glossopteris* and *Gangamopteris* leaves. Part II. Structural features. Palaeontogr. Abt. B 147, 42-73.

Payne, W. W., 1978. A glossary of plant hair terminology. Brittonia, 30, 239-255.

Perinotto, J.A.J., Rösler, O., 1984. Glossopterídeas de Fluviópolis (Permiano superior) do sul do Estado do Paraná. Bol. IG-USP Série Científica 15, 90-96. doi:10.11606/issn.2316-8986.v15i0p90-96

Pigg, K.B., 1990. Anatomically preserved *Glossopteris* foliage from the central Transantarctic Mountains. Rev. Palaeobot. Palynol. 66, 105-127. doi:10.1016/0034-6667(90)90030-m

Pigg, K.B., McLoughlin, S., 1997. Anatomically preserved *Glossopteris* leaves from the Bowen and Sydney basins, Australia. Rev. Palaeobot. Palynol. 97, 339-359. doi:10.1016/s0899-5362(98)90640-6

Pigg, K.B., Nishida, H., 2006. The significance of silicified plant remains to the understanding of Glossopteris-bearing plants: a historical review. J. Torrey. Bot. Soc. 133, 46-61. doi:10.3159/1095-5674(2006)133[46:tsospr]2.0.co;2

Pigg, K.B., Taylor, T.N., 1990. Permineralized *Glossopteris* and *Dicroidium* from Antarctica. In: Taylor, T.N, Taylor, E.L. (Eds.), Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana. Springer, New York, pp.164-172.

Pigg, K.B., Taylor, T.N., 1993. Anatomically preserved *Glossopteris* stems with attached leaves from the central Transantarctic Mountains, Antarctica. Am. J. Bot. 80, 500-516. doi:10.2307/2445365

Pigg, K.B., Trivett, M.L., 1994. Evolution of the glossopterid gymnosperms from Permian Gondwana. J. Plant Res. 107, 461-477. doi:10.1007/bf02344068

Plumstead, E. P., 1956. Bisexual fructifications borne on *Glossopteris* leaves from South America. Palaeontogr. Abt. B 100, 1-25.

Poort, R.J., Kerp, J.H.F., 1990. Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of West and Central Europe and a reclassification of the species formerly assigned to *Peltaspermum* Harris. Rev. Palaeobot. Palynol, 63, 197-225. doi:10.1016/0034-6667(90)90100-w

Prothero, D.R., 1990. Interpreting the stratigraphic record. W.H. Freeman & Co., New York, pp. 410.

Rees, P.M., 2002. Land plant diversity and the end-Permian mass extinction. Geology 30:827–830. doi:10.1130/0091-7613(2002)030<0827:lpdate>2.0.co;2

Retallack, G.J., 2013. Permian and Triassic greenhouse crises. Gondwana Res. 24, 90-103. doi:10.1016/j.gr.2012.03.003

Retallack, G., Dilcher, D.L., 1981. Arguments for a glossopterid ancestry of angiosperms. Paleobiology 7(1), 54-67.

Ricardi-Branco, F., Bernardes-de-Oliveira, M.E.C., Garcia, M.J.,1999. Novos elementos tafoflorísticos da Formação Assistência, Subgrupo Irati, Grupo Passa Dois, bacia do Paraná, provenientes de Angatuba (SP), Brasil. Revista Universidade Guarulhos 6, 85-95.

Rigby, J.F., 1978. Permian glossopterid and other cycadopsid fructifications from Queensland. Geol. Surv. Queensl. Publ., 367 Palaeontol. Pap. 41, 1-21.

Rocha-Campos, A.C., Basei, M.A., Nutman, A.P., Kleiman, L.E., Varela, R., Llambias, E., Canile, F.M., Rosa, O.C.R., 2011. 30 million years of Permian volcanism recorded in the Choiyoi igneous province (W Argentina) and their source for younger ash fall deposits in the Paraná Basin: SHRIMP U-Pb zircon geochronology evidence. Gondwana Res. 19, 509-523. doi:10.1016/j.gr.2010.07.003.

Rohn, R., 1984. *Glossopteris* da Formação Rio do Rasto no sul do estado do Paraná. Anais do XXXIII Congresso Brasileiro de Geologia, Rio de Janeiro, Brasil, pp. 1047-1061.

Rohn, R., Rösler, O., 1989. Folhas denteadas da Formação Rio do Rasto (Bacia do Paraná, Permiano Superior) e seu possível significado paleoclimático. Bol. IG-USP 7, 127-137.

Rohn, R., Rösler, O., 2000. Middle to Upper Permian phytostratigraphy of the eastern Paraná Basin. Revista Universidade Guarulhos 5, 69-73.

Rohn, R., Rösler, O., Pennatti, J.-R.R., Czajkowski, S., Iannuzzi, R., Mendonça, E., Ferreira, A.R., Pereira, S.C.A., Quitério, L., 1997. Plant megafossil occurrences in the Teresina and Rio do Rasto Formations (Upper Permian of the Paraná Basin) in the southern region of the Paraná state, Brazil. Revista Universidade Guarulhos - Geociências II special number, 58–68.

Rösler, O., 1975. Tafoflórulas eogondwânicas do Brasil II: ocorrência de Rio da Estiva (Permiano, Formação Rio Bonito, Santa Catarina). Bol. IG-USP 6, 1–11. doi:10.11606/issn.2316-8978.v6i0p01-11.

Rösler, O., 1978. The Brazilian Eogondwanic floral succession. Bol. IG-USP 9, 85–91.

Roy, B.A., Stanton, M.L., Eppley, S.M., 1999. Effects of environmental stress on leaf hair density and consequences for selection. J. Evolution. Biol. 12, 1089-1103. doi:10.1046/j.1420-9101.1999.00107.x

Sahni, B., 1923. On the structure of the cuticle in *Glossopteris angustifolia* Brongn. Records of Geological Survey of India 54, 277-281.

Santos, R.V., Souza, P.A., Alvarenga, C.J.S., Dantas, E.L., Pimentel, M.M., Oliveira, C.G., Araújo, L.M., 2006. Shrimp U-Pb zircon dating and palynology of bentonitic layers from the Permian Irati Formation, Paraná Basin, Brazil. Gondwana Res. 9, 456-463. doi: 10.1016/j.gr.2005.12.001

Schopf, J.M., 1973. The contrasting plant assemblages from Permian and Triassic deposits in southern continents. In: Logan, A., Hills, L. (Eds.), The Permian and Triassic Systems and their Mutual Boundary. Alberta Soc. Pet. Geol. Mem. 2, pp. 379-397.

Schopf, J.M., 1976. Morphologic interpretation of fertile structures in glossopterid gymnosperms. Rev. Palaeobot. Palynol. 21, 25-64. doi:10.1016/0034-6667(76)90021-x

Scott, A.C., 1989. Observations on the nature and origin of fusain. Int. J. Coal Geol. 12, 443-475. doi: 10.1016/0166-5162(89)90061-X

Scott, A. C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeocl. 291, 11-39. doi: 10.1016/j.palaeo.2009.12.012

Simas, M.W., Guerra-Sommer, M., Cazzulo-Klepzig, M., Menegat, R., Santos, J.O.S., Ferreira, J.A.F., Degani-Schmidt, I., 2012. Geochronological correlation of the main coal interval in Brazilian Lower Permian: radiometric dating of tonstein and calibration of biostratigraphic framework. J. S. Am. Earth Sci. 39, 1-15. doi: 10.1016/j.jsames.2012.06.001

Simas, M.W., Guerra-Sommer, M., Mendoça Filho, J.G., Cazzulo-Klepzig, M., Formoso, M.L.L., Degani-Schmidt, I., 2013. An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a Lower Permian tonstein bed (Faxinal Coalfield, Paraná Basin, Brazil). Geologica Acta, 11, 47-57. doi: 10.1344/105.000001835

Singh, S.M., Maheshwari, H.K., 2000. On the species of genus *Glossopteris* from Barakar Formation of Karanpura and Bokaro coalfields, India. Palaeobotanist 49, 409-441.

Slater, B.J., McLoughlin, S., Hilton, J., 2012. Animal-plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Palaeogeogr. Palaeocl. 363–364, 109–126. doi:10.1016/j.palaeo.2012.08.018

Slater, B.J., McLoughlin, S., Hilton, J., 2015. A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. Gondwana Res. 27, 1446-1473. doi: 10.1016/j.gr.2014.01.004

Srivastava, S.C., 1969. Two new species of *Glossopteris* from the Triassic of Nidpur, Madhya Pradesh, India. In: Santapau, H. (Ed.), J. Sen Memorial Volume. J. Sen Memorial Committee and Botanical Society of Bengal, Calcutta, pp. 299-303.

Srivastava, P.N., 1956. Studies in the *Glossopteris* flora of India - 4. *Glossopteris*, *Gangamopteris* and *Palaeovittaria* from the Raniganj Coalfield. Palaeobotanist 5, 1-45.

Srivastava, A.K., 1991. Evolutionary tendency in the venation pattern of Glossopteridales. Geobios 24, 383-386. doi:10.1016/s0016-6995(06)80235-4

Srivastava, A.K., Agnihotri, D., 2010. Upper Permian plant fossil assemblage of Bijori Formation: A case study of *Glossopteris* flora beyond the limit of Raniganj Formation. J. Geol. Soc. India 76, 47-62. doi:10.1007/s12594-010-0082-0

Srivastava, A.K., Tewari, R., Agnihotri, D., 2010. Morpho-cuticular study of *Glossopteris stenoneura* Feistmantel from the Barakar Formation of Raniganj Coalfield, West Bengal. Palaeobotanist 59, 139-144.

Stewart, W.N., Rothwell, G.W., 1993. Paleobotany and the evolution of plants. Cambridge Univ. Press, New York. 2nd ed.

Surange, K.R.,1966. The present position of the genus *Glossopteris*. Proceedings of the Autumn School of Botany, Mahabaleshwar, pp. 316-327.

Surange, K.R., Chandra, S., 1975. Morphology of the gymnospermous fructifications of the *Glossopteris* Flora and their relationships. Palaeontogr. Abt. B 149, 153-180.

Surange, K.R., Srivastava, P.N., 1956. Studies in the *Glossopteris* Flora of India - 5. Generic status of *Glossopteris*, *Gangamopteris*, and *Palaeovittaria*. Palaeobotanist 5, 46-49.

Taylor, E.L., 1996. Enigmatic gymnosperms? Structurally preserved Permian and Triassic seed ferns from Antarctica. Rev. Palaeobot. Palynol. 90, 303-318. doi:10.1016/s0034-6667(96)00089-9

Taylor, T.N., Taylor, E.L., 1993. The Biology and Evolution of Fossil Plants. Prentice Hall, New Jersey.

Taylor, E.L., Taylor, T.N., Cuneo, N.R., 1992. The present is not the key to the past: A polar forest from the Permian of Antarctica. Science 257, 1675-1675. doi:10.1126/science.257.5077.1675

Taylor, T.N., Taylor, E.L., Krings, M., 2009. Paleobotany: The Biology and Evolution of Fossil Plants. Academic Press, Burlington. 2nd ed.

Tewari, R., Chatterjee, S., Agnihotri, D., Pandita, S.K., 2015. *Glossopteris* Flora in the Permian Weller Formation of Allan Hills, South Victoria Land, Antarctica: Implications for paleogeography, paleoclimatology, and biostratigraphic correlation. Gondwana Res. 28, 905-932. doi:10.1016/j.gr.2015.02.003

Tybusch, G.P., Iannuzzi, R., 2008. Reavaliação taxonômica dos gêneros *Gangamopteris* e *Rubidgea*, Permiano inferior da Bacia do Paraná, Brasil. Rev. Bras. Paleontol. 11, 73-86. doi:10.4072/rbp.2008.2.01

Tybusch, G.P., Iannuzzi, R., 2010. *Glossopteris occidentalis* White emended: geographic and biostratigraphic implications. Rev. Bras. Paleontol. 13, 33-40. doi:10.4072/rbp.2010.1.04

Tybusch, G.P., Iannuzzi, R., Rösler, O., 2012. Estudo das glossopterídeas do afloramento de Rio da Estiva, estado de Santa Catarina (Permiano Inferior da Bacia do Paraná). Pesquisas em Geociências 39, 23-33.

Upchurch Jr, G.R., 1984. Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. Ann. Mo. Bot. Gard. 71, 522-550. doi:10.2307/2399036

Wang, J., Pfefferkorn, H.W., Zhang, Y., Feng, Z., 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. P. Natl. Acad. Sci. USA 109, 4927-4932. doi:10.1073/pnas.1115076109

Yi, S., 1997. Zygnematacean zygospores and other freshwater algae from the Upper Cretaceous of the Yellow Sea Basin, southwest coast of Korea. Cretaceous Res. 18, 515-544. doi: 10.1006/cres.1996.0072

Zeiller, M.R., 1896. Etude sur quelques plantes fossiles en particulier *Vertebraria* et *Glossopteris* des environs de Johannesburg (Transvaal). B. Soc. Geol. Fr. 24, 349–378.

Zodrow, E.L., D'Angelo, J.A., Werner-Zwanziger, U., Chen, B., 2014. Hair-trichomes-files, and spectrochemistry of *Macroneuropteris scheuchzeri* (Basal Cantabrian, Sydney Coalfield, Canada). Palaeontogr. Abt. B, 141-153.

Legends

Table 1.

Types of trichome bases and their distribution on the lower cuticle of *Glossopteris pubescens*. The multicellular bases are composed of 4-8 cells.

Figure 1. Map and stratigraphic framework.

A) Location map (modified from Santos et al., 2006), coalfield coordinates 30°15'52.6" S, 51°41'53.8" W; B) geochronology (after Cohen et al., 2013; updated 2015), lithostratigraphy of the Paraná Basin (after Milani et al., 2007) and *radiometric age of the tonstein from the Faxinal Coalfield (after Simas et al., 2012); C) lithological log of the coal seam S and overlying layers (after Guerra-Sommer et al., 2008). *Radiometric age obtained through SHRIMP (Sensitive High Resolution Ion Microprobe) in zircons from the tonstein bed.

Plate I. Field and hand sample photographs. Scale bars 5 cm.

1. Pit bench exposure of coal seam S with the tonstein at ground level. The samples have frequently been sampled after breakage with the mechanical excavator.

2. Close up of the interbedded tonstein ply in upper coal seam S (photo courtesy of M.W. Simas).

3. *Ottokaria* sp. adpression (PB-4820a).

4. *Glossopteris* leaves in organic connection (PB-4694F-a).

5. Leaves with inferred organic connection (PB-4762C-a).

6, 7. Isolated leaves (PB-2769; PB-2790-I).

Plate II. Lectotype PB-2777. Scale bars 5 cm (hand specimens), 50 µm (cuticle fragments).

1. Hand specimen bearing leaves with different apices (specimens a and b).

2. Detail of specimen PB-2777-a.

3, 4. Cuticle fragments from lower epidermis of specimen PB-2777-a. Intercostal fields with stomata with papillate subsidiary cells and scattered papillate, heavily cutinized trichome base complexes (type 1a) (slides 2777-a-1, 2777-a-2).

5. Detail of specimen PB-2777-b.

6. Glabrate upper epidermis of specimen PB-2777-b (slide 2777-b-2).

7. Clustered, heavily cutinized trichome base complexes (type 1a) on costal field from lower epidermis, and one isolated base of the same type on intercostal field where stomata can also be seen (slide 2777-b-1).

Plate III. Paratype PB-4764-E. Scale bars 5 cm (hand specimen), 50 µm (cuticle fragments).

1. Leaves in whorl/short shoot.

2. Leaf detail.

3. Cuticle from upper epidermis, lateral venation area (slide 4764E-10).

4. Midvein of lower epidermis with non-papillate trichome bases (type 1b) showing a very narrow intercostal field with uniseriate row of stomata (slide 4764E-16).

5. Possibly immature trichome base complex from the midvein region of lower epidermis (type 1b) (slide 4764E-5).

6. Cell divisions in the midvein area of lower epidermis (slide 4764E-6).

7. Possible trichome foot mother cell in the midvein area of lower epidermis (slide 4764E-17).

8. Intercostal field of lower epidermis showing subsidiary cells with upright papillae (slide 4764E-8).

9. Costal and intercostal fields of lower epidermis. Stomatiferous intercostal field showing two clustered immature trichome bases and adjacent non-papillate costal field with trichome bases in different developmental stages with cutinized extensions (?canals) (slide 4764E-21).

Plate IV. Paratype PB-4765G. Scale bars 5 cm (hand specimens), 50 µm (cuticle fragments).

1. Leaves in whorl/short shoot.

2. Leaf detail.

3. Cuticle from upper epidermis, lateral venation area (slide 4765G-8).

4. Non-papillate trichome bases (type 1b) from the midvein of lower epidermis (slide 4765G-8).

5. Narrow stomatiferous, papillate intercostal zone in the lower midvein with stomata arranged in an uniseriate row (slide 4765G-3).

6. Intercostal field of lower epidermis showing scattered trichome bases type 1a (slide 4765G-5).

7. Intercostal field of lower epidermis showing scattered trichome bases type 1a and costal field with elongate bordering trichome type 2a.

Plate V. General cuticular features. Scale bars 100 µm.

1. Cuticle from upper epidermis, lateral venation area showing a round cell with dark content (?secretory cavity) (slide 4797-9).

2. General view of alternation between costal and intercostal fields with scattered trichome bases (slide 4775-4).

3. Midvein area from lower epidermis profusely covered with trichome bases type 1b. Note the heavier cutinization towards the center of the leaf (slide 4765G-6).

4. Attachment of upper and lower cuticles showing the border with thick-walled geometric cells (slide 4766H-2).

5-6. Papillate costal field showing connected and clustered trichome bases (type 1a) (slides FXB-37, FXB-84-1).

7. View of midvein-lateral venation transition (slide 4775-3).

8. Detail of trichome bases (type 1a) under DIC filter (slide FXB-70-1).

9. Typical papillate trichome base on intercostal field with the papillae fused to the foot cell (type 1a) (slide FXB-72-1).

Plate VI. General aspect of the stomatiferous intercostal fields of the abaxial surface of the leaves. Note that many stomata share one or several subsidiary cells. Scale bars 50 µm.

1. Intercostal and adjacent costal field (slide FXB-55).

2. Dark-field view of (2).

3. Stomata radially arranged around an isolated trichome base (type 1a) (slide FXB-37).

4. Intercostal and adjacent papillate costal field bearing trichome bases in different developmental stages (slide FXB-61).

5. Detail of (4) showing stomata sharing multiple subsidiary cells.

6. Intercostal field under DIC filter (slide FXB-78-1).

7. Intercostal field with clustered trichome bases (type 1a) (slide FXB-66).

8. Intercostal field showing subsidiary cells with long upright papillae and connected trichome bases (slide FXB-55).

9. Intercostal field showing rare epidermal cells which do not belong to stomatal apparati (slide FXB-12).

10. General view of alternation between papillate costal and intercostal fields. Intercostal fields show scattered trichome bases and costal fields are papillate with connected (?canals) trichome bases (slide FXB-7).

Plate VII. Trichome bases type 1a (see Table 1). Scale bars 50 µm.

1. Composite image of a cuticle fragment from the lower epidermis showing trichome bases in different developmental stages. The center of the fragment shows a papillate intercostal field (slide FXB-72-1).

2-7. Details of (1).

8, 9. Complete trichome base with attached trichome on intercostal field under white and fluorescent light showing lower fluorescence of the trichome in comparison to the base (slide FXB-16).

10, 11. Composite image (stacked focus) of trichome bases in profile view (slide FXA-19).

12-15. Cuticle fragments macerated in hydrofluoric acid and observed under fluorescence. Cutine of trichome bases is highly fluorescent, while trichomes are opaque (PB-4830; photo courtesy of J.O. Mendonça).

PlateVIII. Trichome bases type 1b and 1c (see Table 1). Scale bars 50 µm.

1-3. Trichome bases of the midvein from lower epidermis under DIC filter (slides 4694F-5, -4, -3). Note the vesicles inside the bases.

4, 5. General aspect of the midvein from lower epidermis (slides FXB-6, 4765G-5).

6. Detail of (5).

7. A few trichomes type 2a can be seen interspersed with the base complexes (type 1b) (slide FXB31-1).

8. Trichome bases type 1c from leaf attachment (slide 4763-c). Note trichome type 2b (circle) emerging from intercellular contact between two epidermal cells.

Plate IX. Trichomes type 2a (see Table 1). Scale bars 50 µm.

1. Leaf margin showing several empty unicelullar trichome bases (slide 4766H-2).
2. Trichomes type 2a close to the leaf margin (slide FXA-3).
3. Trichome type 2a bordering costal field under DIC filter (slide FXB78-1).
4. Trichome type 2a on costal field (slide 4765G-7).
5. Trichome type 2a bordering costal field (slide 4765G-3).
6. Broken off trichome type 2a under DIC filter (slide FXB70-1).

7, 8. Trichome type 2a extending from costal field to a stomatal pore (slides FXB31-3, 4781-1).

9. Two trichomes extendingtowards a stomatal pore and another one in upright position (type 2a) under DIC filter (slide FXB-59).
10. Trichomes type 2a bordering costal field (slide FXB35-2).
11. Dark-field view of (10).

Plate X. Trichomes type 2b (see Table 1). Scale bars (1) 1cm; (2, 3) 1 mm; (4-9) 50 µm.

1. Hand specimen PB-4830.
2. Detail of (1) showing trichomes adhered to the rock matrix.
3. Cuticle after maceration in hydrofluoric acid (HF) (PB-4813).
4. Trichomes extracted from the rock matrix with HF (PB-4830).
5. Creased, broken trichome type 2b. Its simple base emerges from intercelullar contact on costal area (slide FXB-66).
6. Dark-field view of (5).
7. Trichome base emerging from intercelullar contact on midvein area from lower epidermis (slide FXB-58).
8. Cuticle fragment with long papillae and trichomes type 2a and 2b (slide FXB-31-3).

9. Multiple trichomes type 2b wrapped around a trichome base type 1a under DIC filter (slide FXB-83-3).

10. Trichome type 2b on the left and type 2a on the right costal field (slide 4818-2). Several pollen grains remained adhered to the cuticle fragment.

Plate XI. 1-7 Features of upper epidermis; 8-14 celullar divisions and maturating trichome bases from lower epidermis. Scale bars 50 µm.

1. General view of midvein area of upper epidermis (slide 4694E-2).

2. Detail of (1) showing a trichome base type 1b with a vesicle inside (under DIC filter).

3. Detail of (1) showing a ?secretory canal bordered by a ?papilla (under DIC filter).

4. Detail of (1) showing short filamentous projections from the cell corners (under DIC filter).

5. Round ?secretory cavity with dark content under DIC filter (slide 4694E-1). Note short filamentous projections from the cell corners.

6. Secondary venation area of upper epidermis showing folds (slide 4775-2).

7. Secondary venation area of upper epidermis showing sinuous anticlinal walls and a cell with ?ruptured anticlinal wall with dark content (slide 4694E-17).

8. Maturating trichome bases from lower midvein type 1b (slide 4694E-16).

9. Dividing cells and ?trichome foot mother cell in the center (slide 4818-12).

10. Detail from (9).

11. Early formation stages of trichome bases type 1b (slide 4818-4). Note vesicles and a base of trichome type 2a.

12. Trichome bases in different developmental stages (slide FXB-61).

13, 14. Details of (12). Note the base at the bottom bears a vesicle.

Table 1

Trichome bases	Description	Size	Location	Illustration
1. multicellular	a) Heavily cutinized foot cell with protruding papillae	46.2 µm	both costal and intercostal areas of secondary venation	Plate VII
	b) Heavily cutinized foot cell without papillae	54 µm	midvein	Plate VIII
	c) Thin foot cell without papillae	57.7 µm	petiole	Plate VIII
2. unicellular	a) Centralized on the periclinal wall of a single epidermal cell, bearing a trichome resembling an elongated papilla sometimes with ?content	85.2 µm	usually bordering costal areas, and at leaf margin	Plate IX
	b) Emerges from the contact between cells, usually bearing a well-developed trichome	450 µm and longer	costal areas, midvein and petiole	Plate X

Figure 1

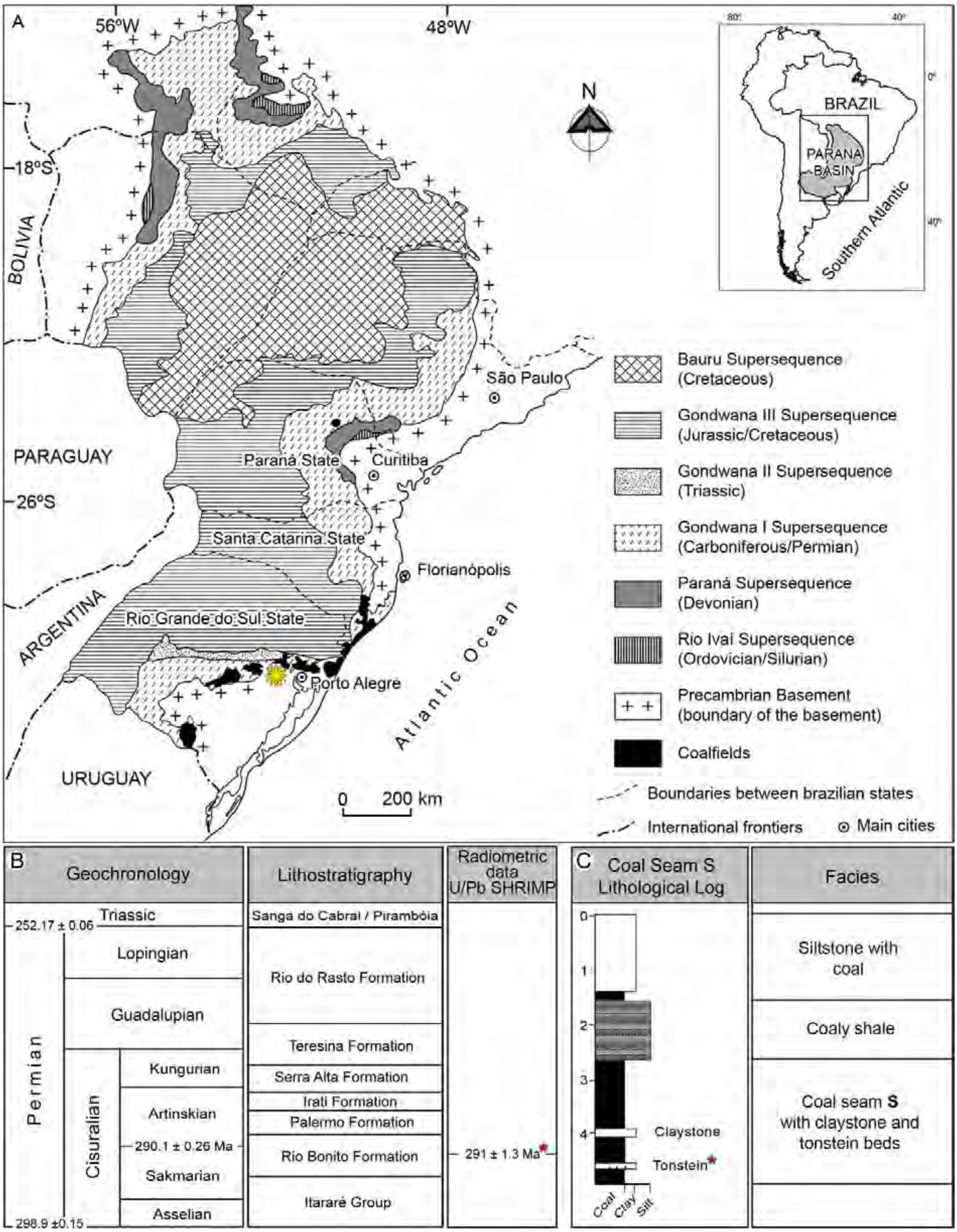

A
56°W
48°W
N
18°S
26°S
BOLIVIA
PARAGUAY
ARGENTINA
URUGUAY
São Paulo
Paraná State
Curitiba
Santa Catarina State
Florianópolis
Rio Grande do Sul State
Porto Alegre
Atlantic Ocean
0 200 km
80°
40°
0°
40°
BRAZIL
PARANÁ BASIN
Southern Atlantic
Bauru Supersequence (Cretaceous)
Gondwana III Supersequence (Jurassic/Cretaceous)
Gondwana II Supersequence (Triassic)
Gondwana I Supersequence (Carboniferous/Permian)
Paraná Supersequence (Devonian)
Rio Ivaí Supersequence (Ordovician/Silurian)
Precambrian Basement (boundary of the basement)
Coalfields
Boundaries between brazilian states
International frontiers
Main cities
B
Geochronology
Lithostratigraphy
Radiometric data U/Pb SHRIMP
Triassic
252.17 ± 0.06
Lopingian
Guadalupian
Permian
Cisuralian
Kungurian
Artinskian
290.1 ± 0.26 Ma
Sakmarian
Asselian
298.9 ±0.15
Sanga do Cabral / Piramboia
Rio do Rasto Formation
Teresina Formation
Serra Alta Formation
Irati Formation
Palermo Formation
Rio Bonito Formation
Itararé Group
291 ± 1.3 Ma*
C
Coal Seam S Lithological Log
Facies
0
1
2
3
4
Claystone
Tonstein*
Coal
Clay
Silt
Siltstone with coal
Coaly shale
Coal seam S with claystone and tonstein beds

Plate I

Plate II

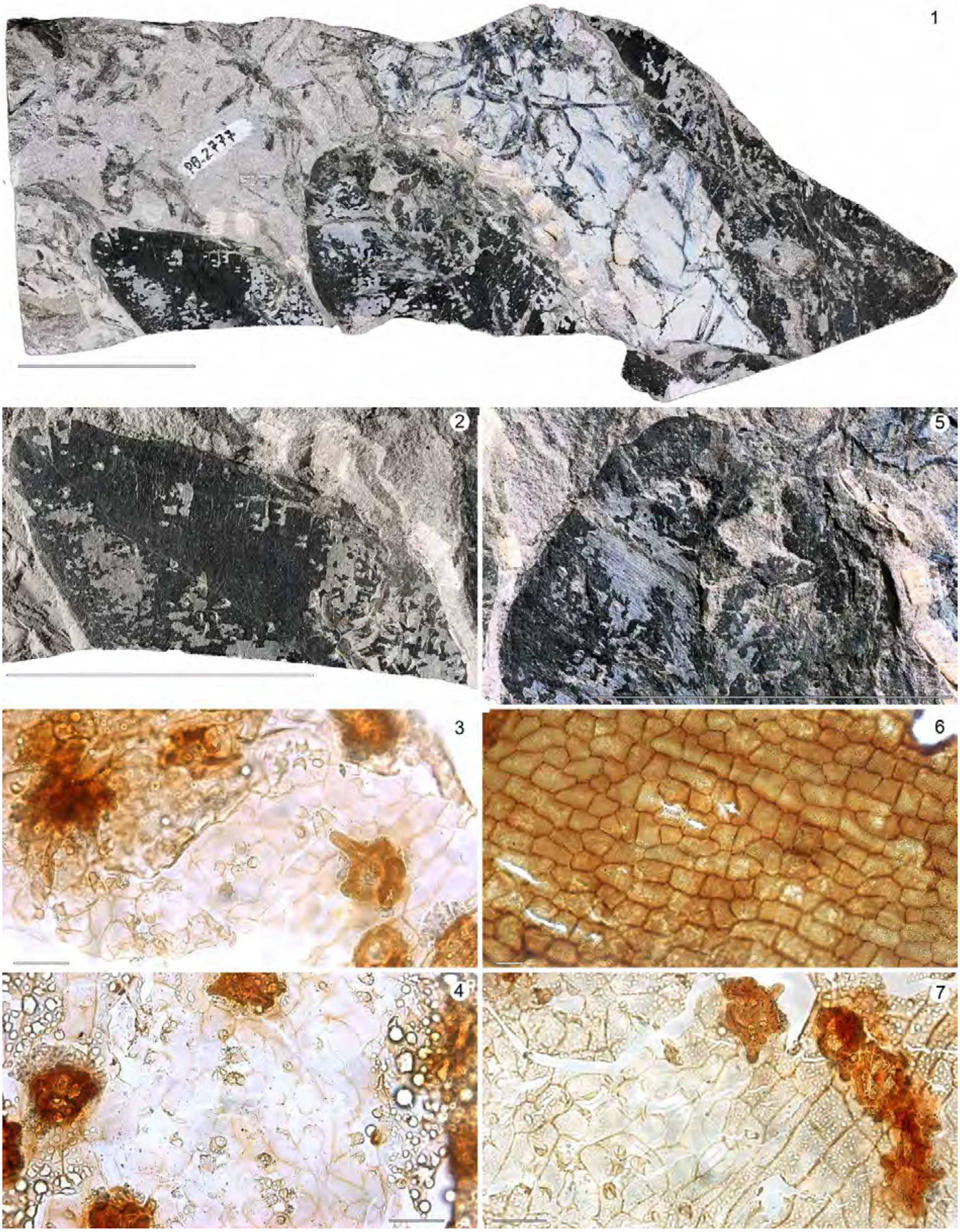


Plate III

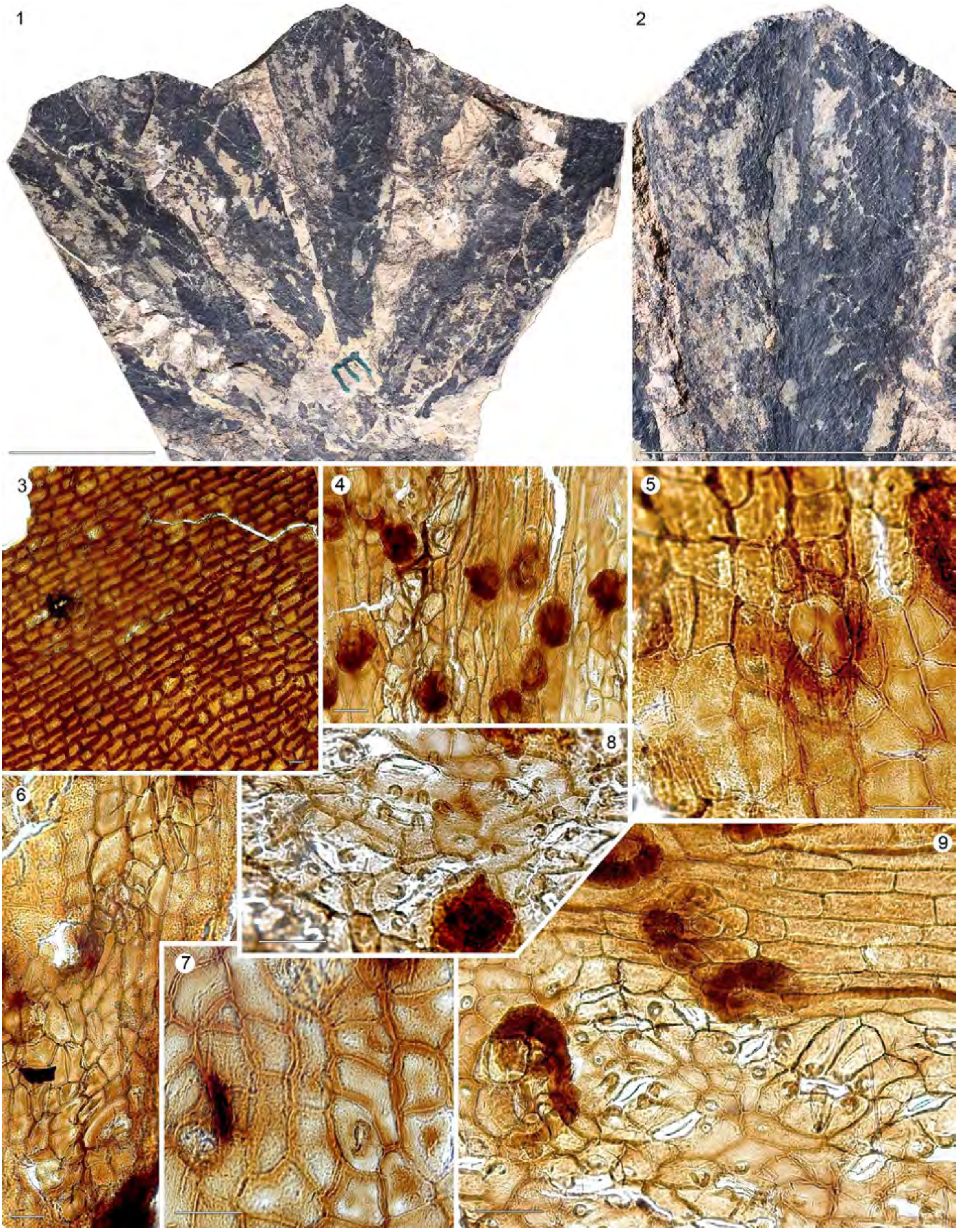


Plate IV

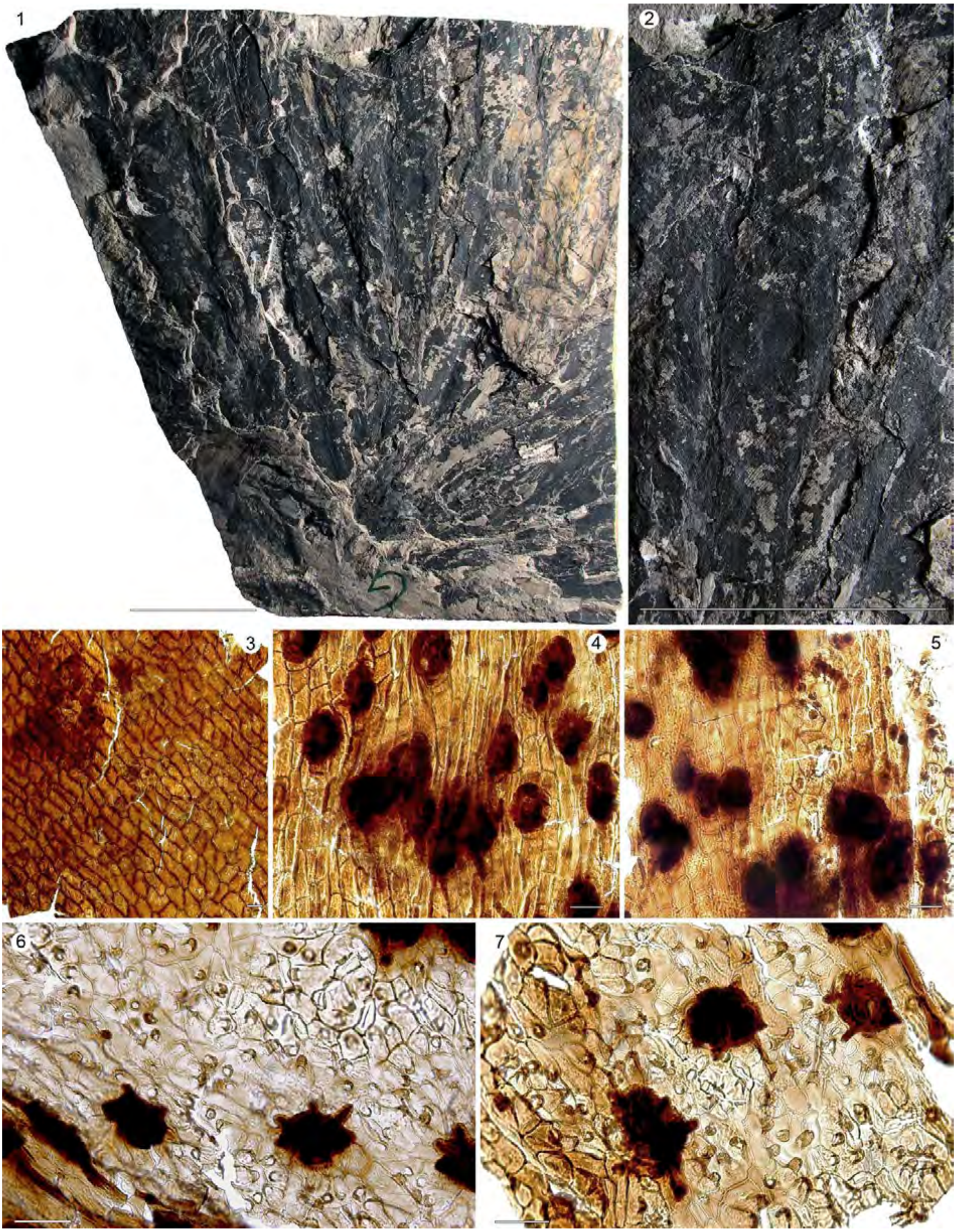
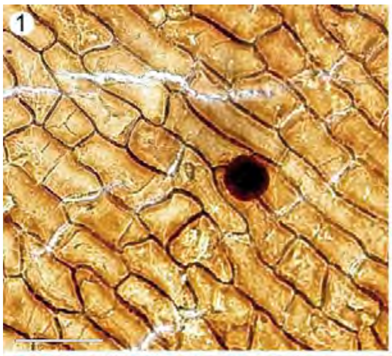
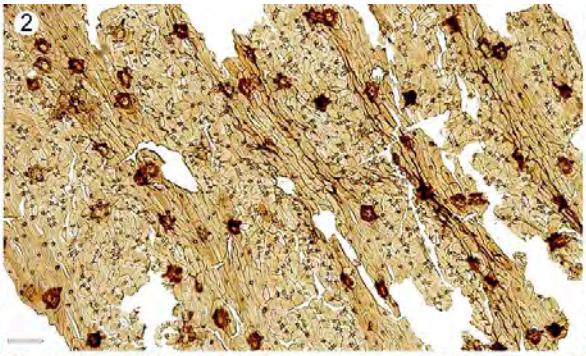
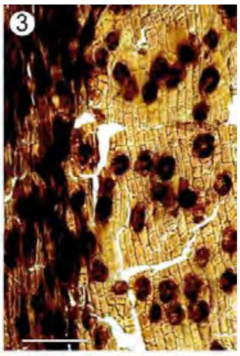
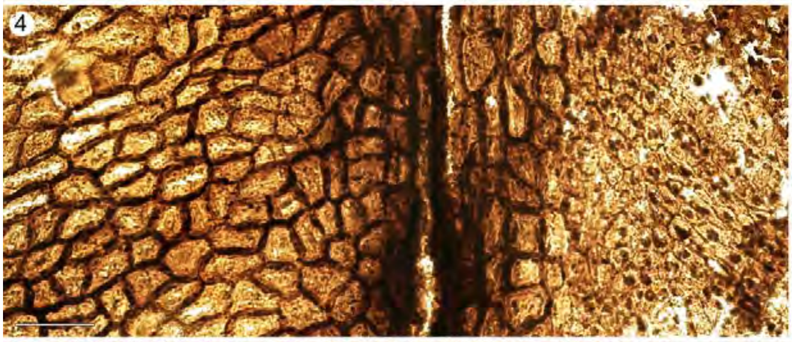


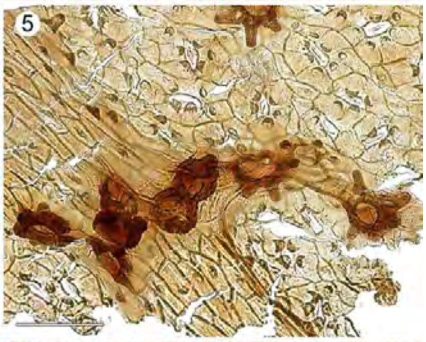
Plate V

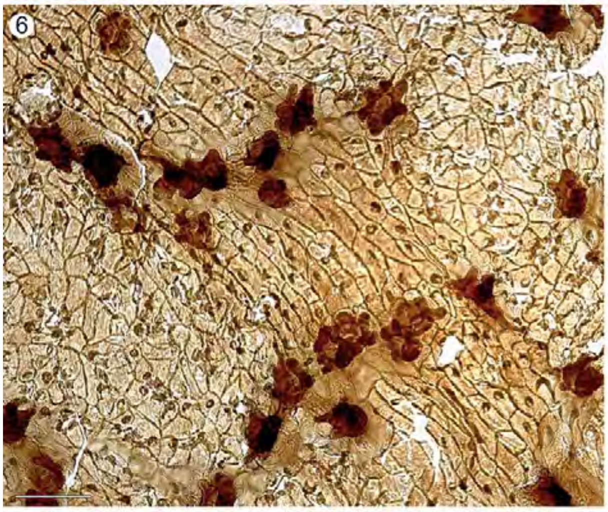

1

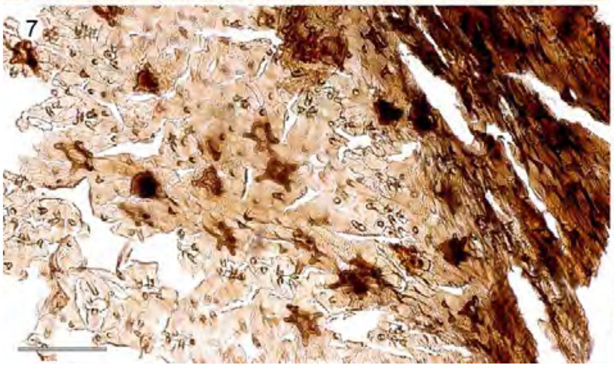

2


3


4


5

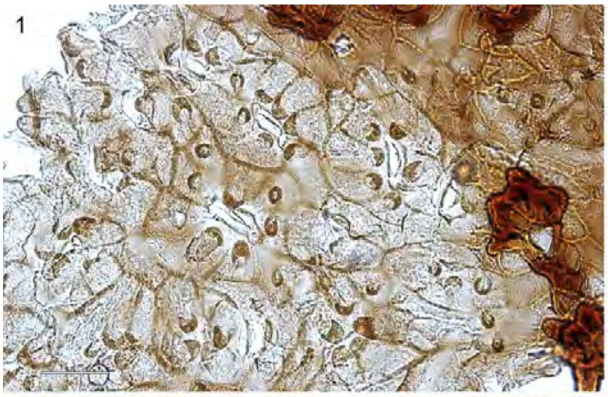

6

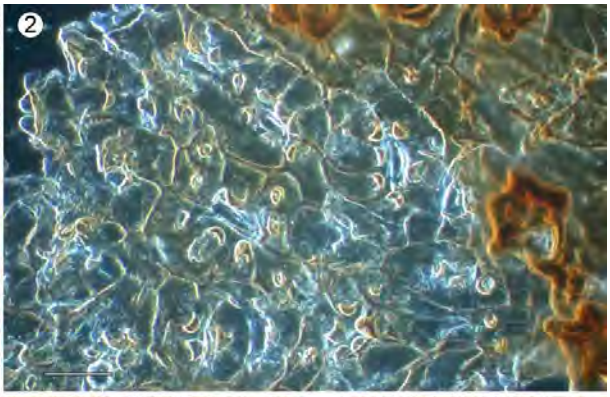

7


8

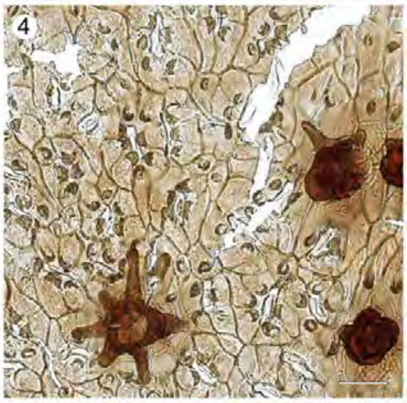

9

Plate VI


1


2

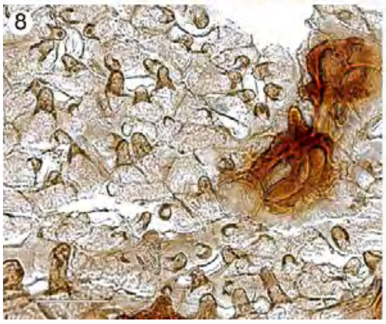

3

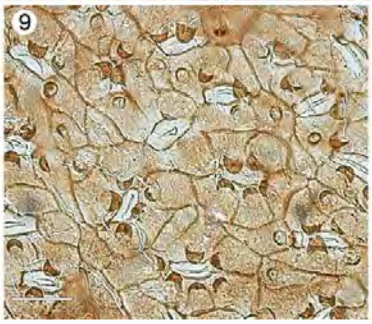

4


5


6


7


8


9

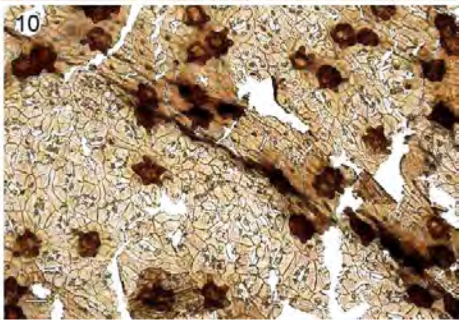

10

Plate VII

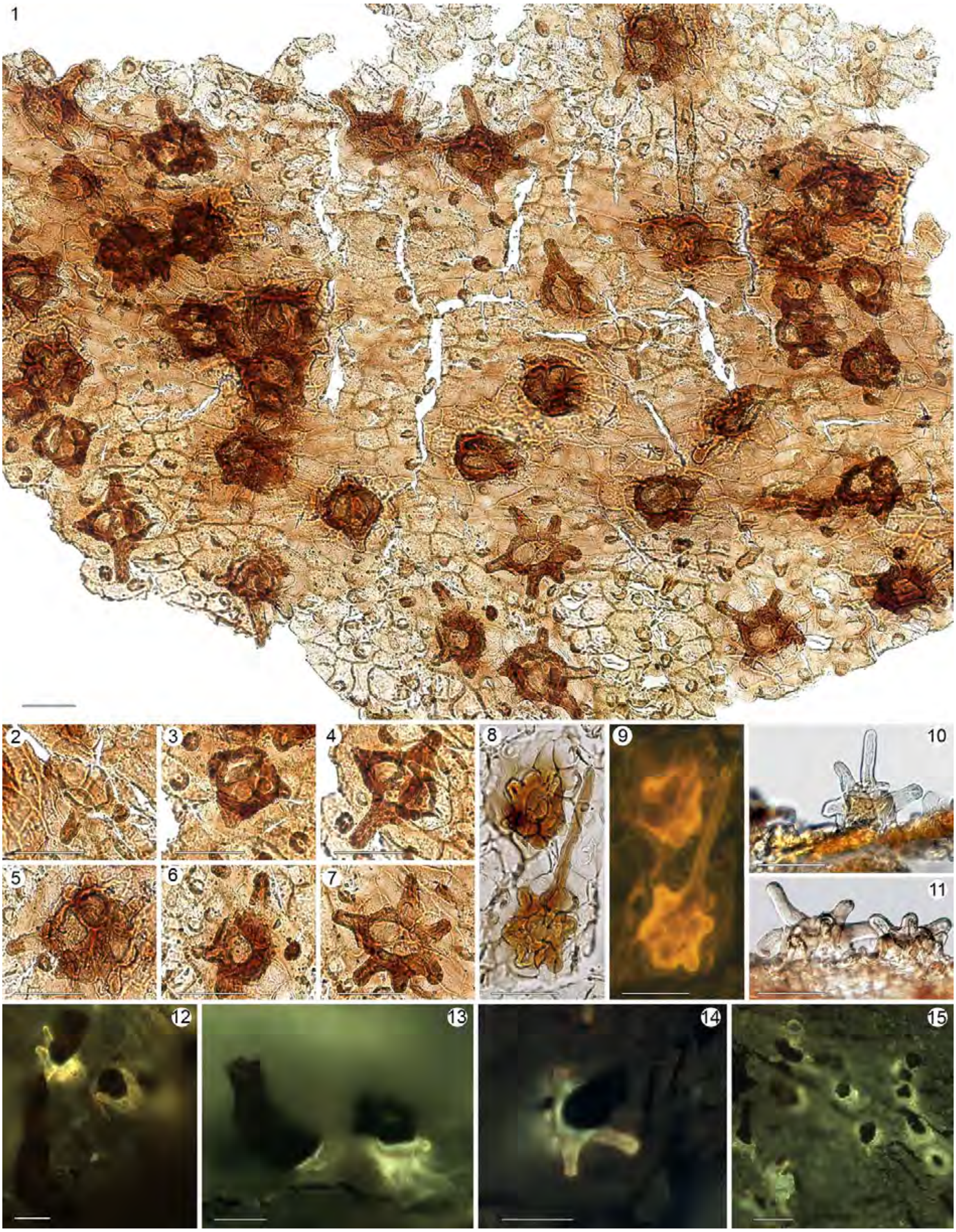


Plate VIII

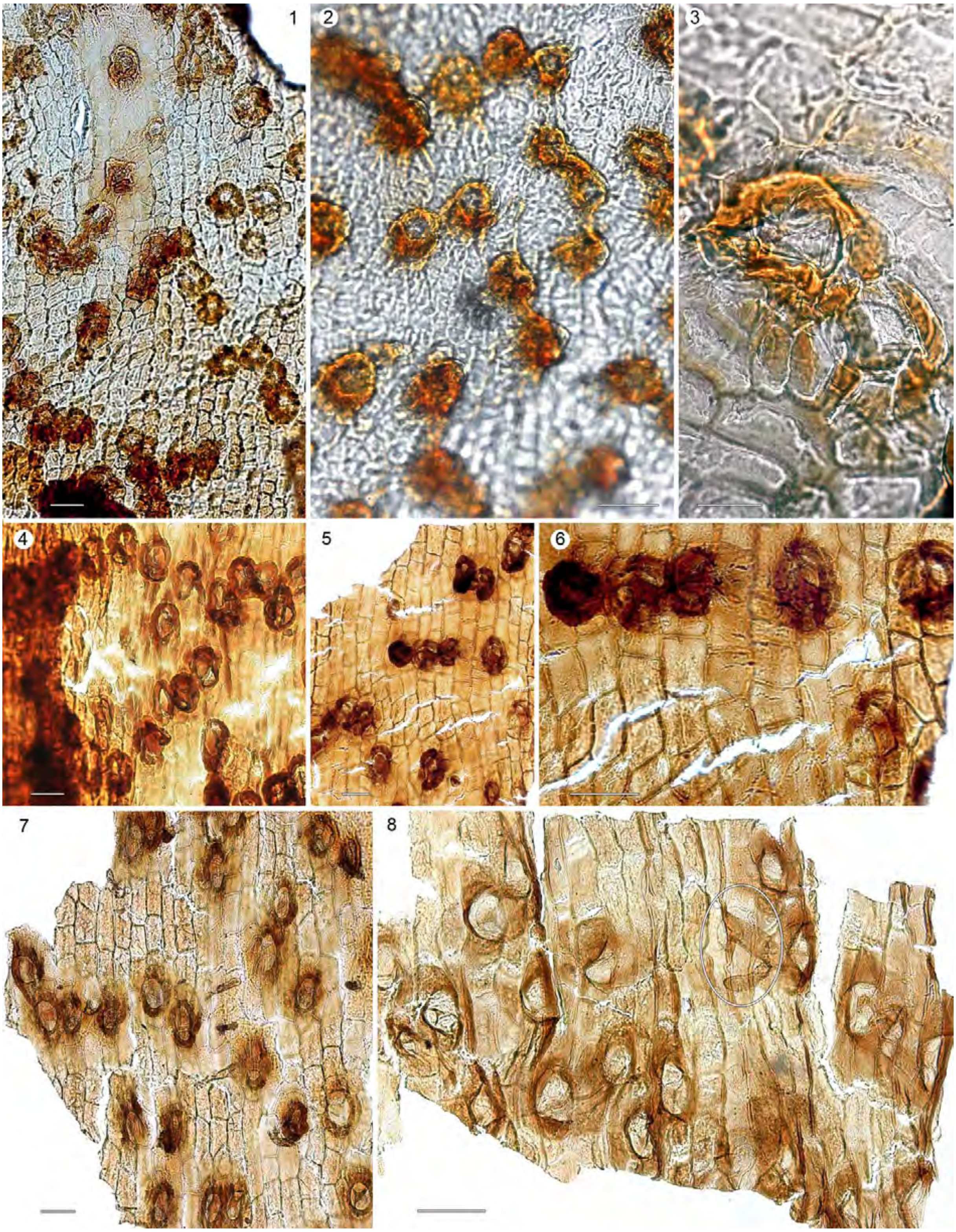


Plate IX

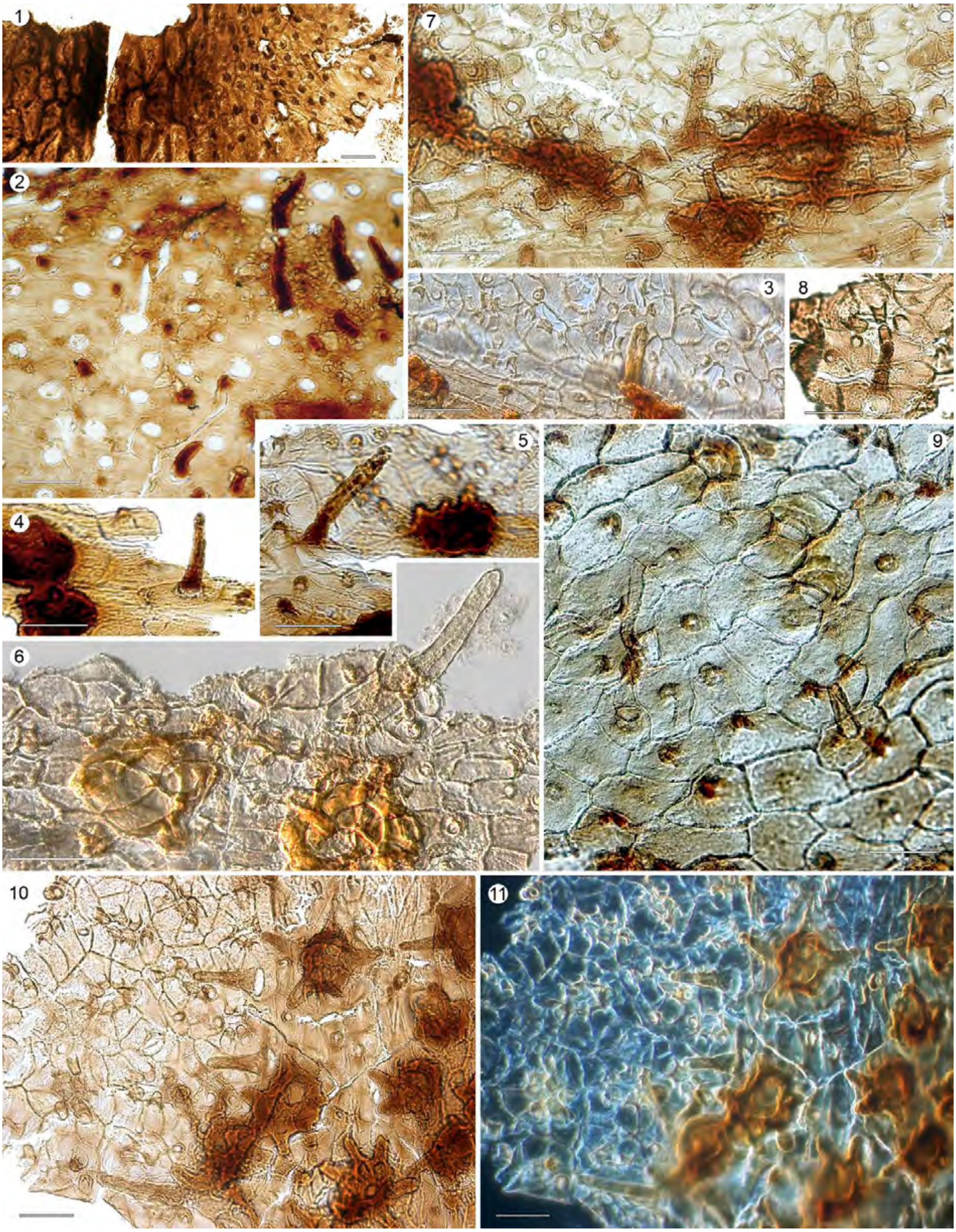


Plate X

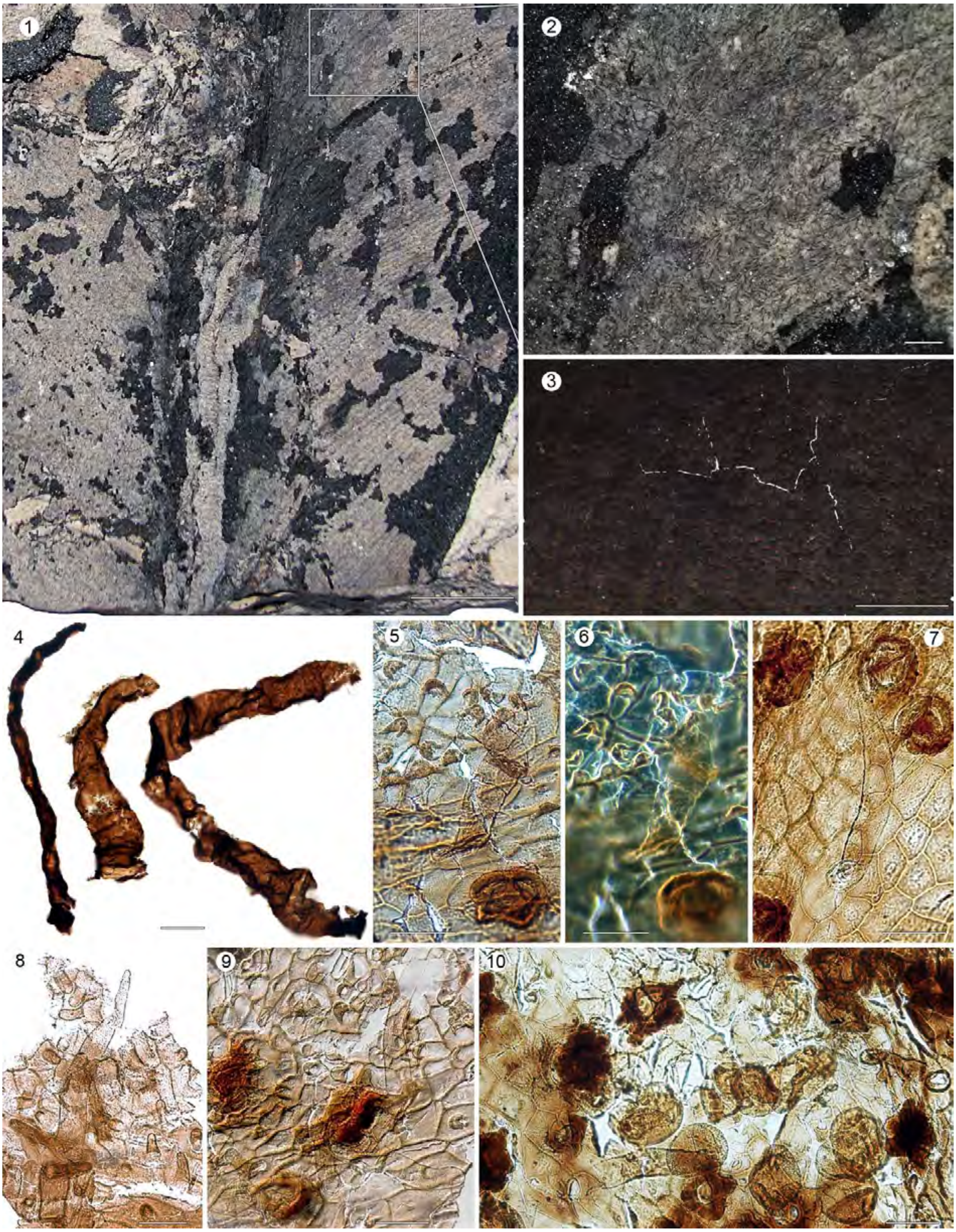
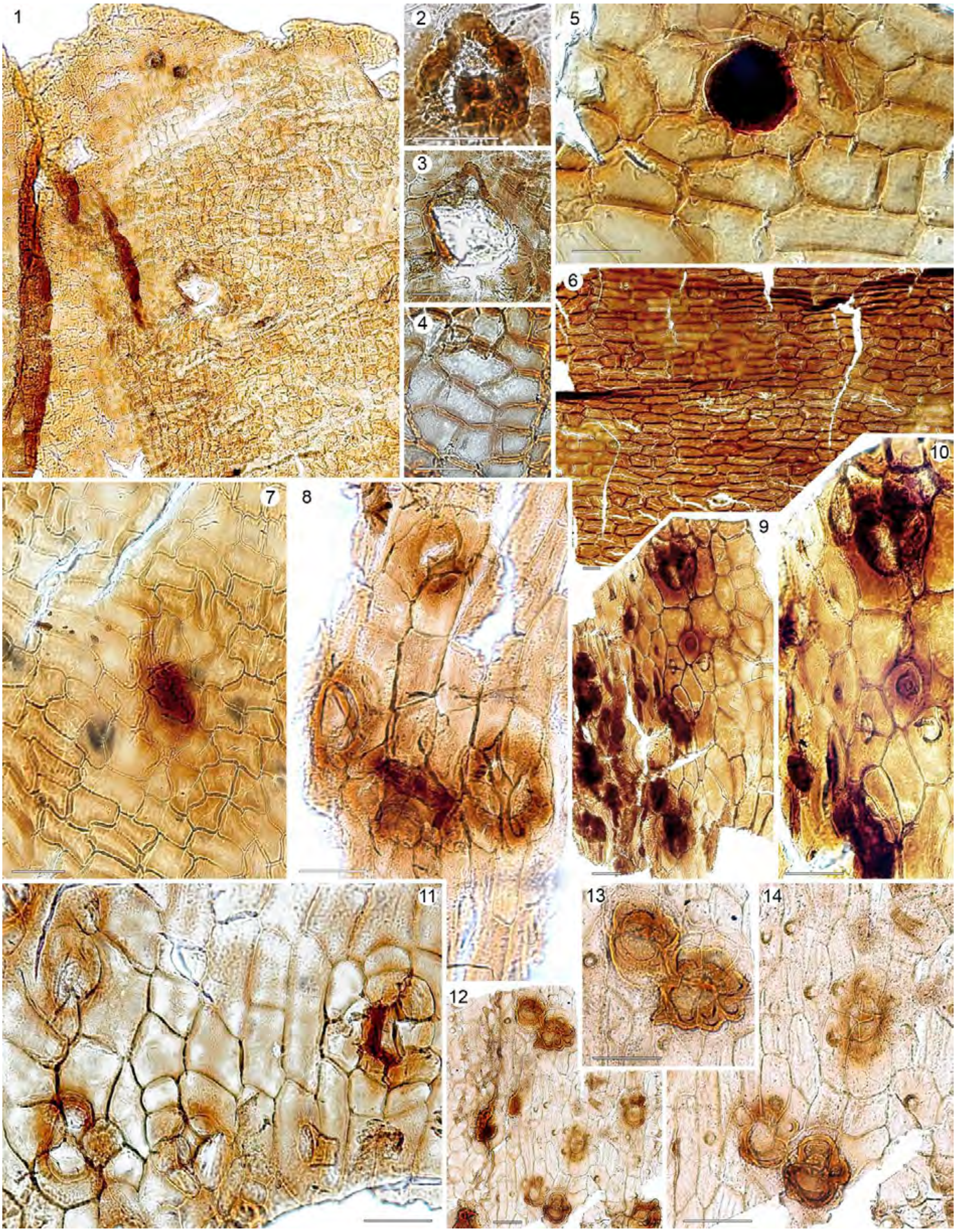


Plate XI



CAPÍTULO 3

6 INTEGRAÇÃO DE RESULTADOS

Análises na camada de carvão S e no nível de tonstein intercalado foram conduzidas com a finalidade de investigar respostas, em nível de espécie e de comunidade formadora da turfeira, a perturbações ambientais relacionadas à ocorrência de incêndios e vulcanismo durante o Sakmariano na jazida de Faxinal, sul da Bacia do Paraná.

Na seção analisada foram detectadas evidências de incêndios sistêmicos de baixa temperatura, controlados essencialmente por mudanças no padrão de umidade, que poderiam estar localmente relacionadas a variações do nível do lençol freático. Altos teores de oxigênio atmosférico estimados para o período e descargas elétricas atmosféricas (GLASSPOOL et al., 2015) contribuíram para a combustão do abundante material vegetal ainda úmido. Adicionalmente, o nível de tonstein é um registro de perturbação vulcânica na comunidade em estudo (SIMAS, 2008) que introduz, de forma pontual ou frequente, partículas e aerossóis na atmosfera, afetando regiões próximas ou mesmo distantes da fonte (SIMAS et al., 2013).

A análise petrográfica em blocos polidos sob óleo demonstrou que grandes fragmentos comprimidos de lenhos queimados dispostos horizontalmente no limite inferior do carvão com o tonstein apresentam uma organização em “sanduíche” em seção transversal (fusênio transicional *sensu* JONES; SCOTT; MATTEY, 1993), sendo compostos por uma clara sequência de inertinita-vitrinita-inertinita (FIG. 14). A transição entre a semifusinita estruturada e a vitrinita homogênea é brusca, e os valores de refletância na transição decrescem desde a porção inferior de semifusinita (%Ro= 0.840-0.609) até a vitrinita interna (%Ro= 0.554-0.596), aumentando novamente na transição para semifusinita superior (%Ro= 0.632-0.834). Foram analisados espécimes de até 13,4 cm de diâmetro antes da fragmentação em blocos e espessura média 8 mm.

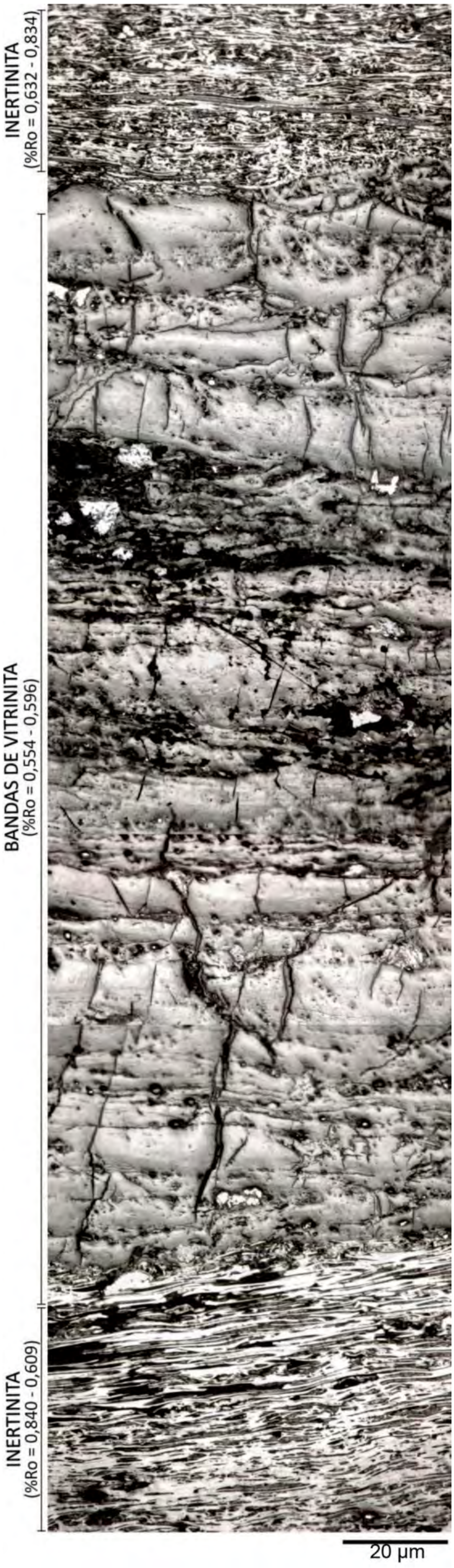


FIGURA 14 – Perfil de lenho comprimido em bloco polido sob observação petrográfica com objetiva de 10x. Imagem montada com 9 fotos, correspondendo a 1,8 cm da seção em luz branca refletida (PB4587A).

O refinamento do quadro paleoambiental com atividade de incêndios na turfeira incluiu observação em fluorescência da matéria orgânica dispersa em blocos polidos e lâminas palinofaciológicas.

Os blocos polidos revelaram fluorescência inalterada em fragmentos de cutinita, aglomerados de polens maduros e mássulas de esporinita (prováveis polens imaturos em microesporângios (GLASSPOOL, 2003) para ambos os horizontes abaixo e acima do tonstein (FIG. 15). O testemunho oferecido pela presença dessas mássulas é muito mais contundente do que o dos grãos dispersos para inferências de parâmetros tafonômicos e ecológicos, e a sua relativa integridade e abundância indicam proximidade das plantas-mãe gimnospérmicas ao local de acumulação da turfa. Além disso, a preservação dessas estruturas como compressões não queimadas indica a ocorrência de incêndios que não teriam afetado o dossel ou a turfa.

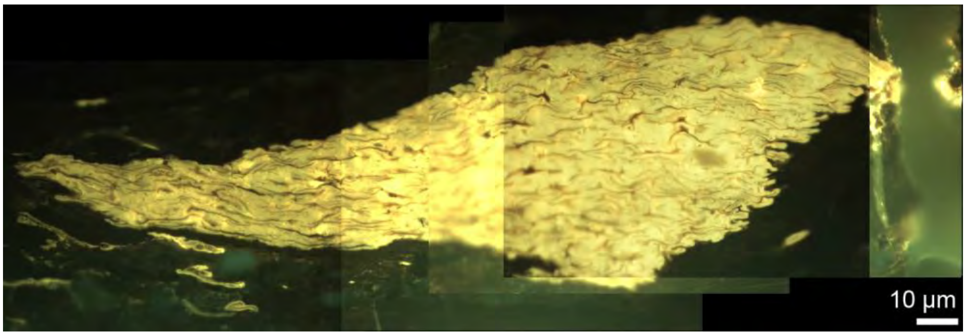


FIGURA 15 – Imagem composta de provável órgão polínico (PB4587A).

Dadas as características do material analisado, composto por fragmentos de lenho queimado e fragmentos de possíveis estruturas reprodutivas não queimadas, as projeções de temperatura de queima (325-400°C) obtidas a partir de baixos valores de refletância da inertinita são típicas de queima superficial (*sensu* SCOTT, 2010), indicando a ocorrência de incêndios autóctones, de superfície, em baixa temperatura.

Em ambos os limites inferior e superior do carvão com o tonstein, a baixa fluorescência observada nos esporos em comparação aos grãos de pólen dispersos (FIG. 16) foi relacionada a um rebaixamento do lençol freático e consequente oxidação dos esporos (que requerem elevada umidade para dispersão) devido a condições de dessecação ambiental. Os grãos de pólen gimnospérmicos, adaptados à dispersão pelo ar, não foram afetados pela oxidação.

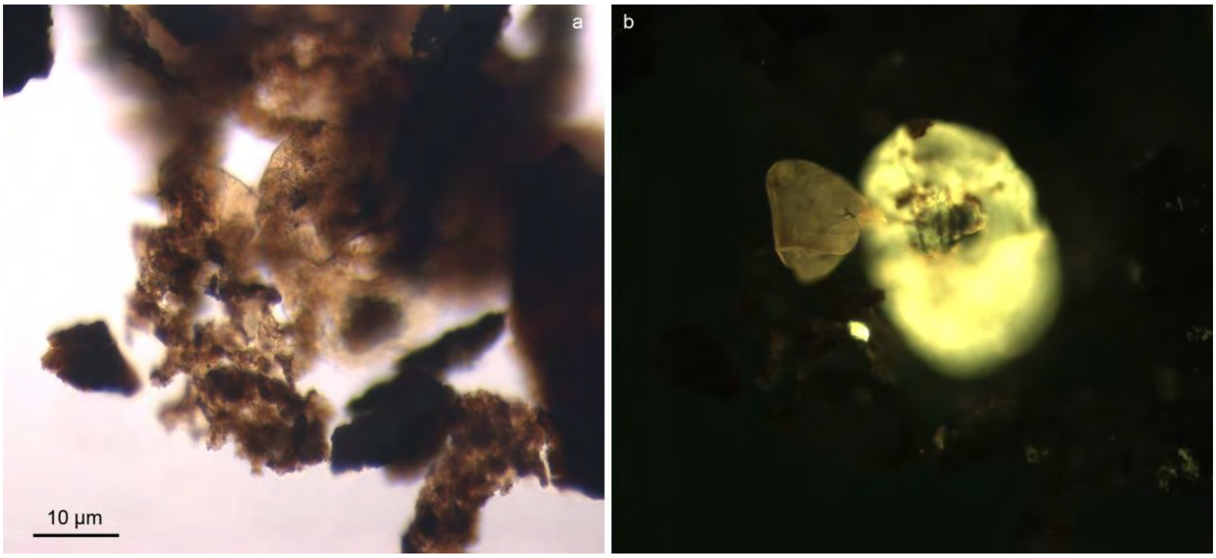


FIGURA 16 – Esporo e pólen do carvão do limite inferior com o tonstein (PB4587A):
a) Em luz branca transmitida
b) Sob fluorescência. A baixa fluorescência do esporo revelou dessecação no seu ambiente de dispersão.

No nível de carvão abaixo do tonstein foi detectada fluorescência de intensidade reduzida em zigósporos de algas zignematáceas (FIG. 17), que são indicadoras ambientais de margens de corpos lacustres rasos e “ilhas” de vegetação arbórea em pântanos (GRENFELL, 1995; YI, 1997; CHMURA; STONE; ROSS, 2006). Esse resultado é compatível com as evidências de maior severidade na dessecação ambiental no nível inferior onde foi inferido incêndio de maior impacto e raseamento do nível de água superficial, que posteriormente retornou a condições de maior umidade. Os resultados quantitativos permitiram concluir que houve um aumento na dominância de grãos de pólen bissacados em relação a esporos pteridofíticos após a queda da cinza vulcânica, sugerindo que a vegetação gimnospérmica foi revigorada pela ação do fogo e pela perturbação vulcânica e não se abriu um novo nicho para recolonização. O reestabelecimento, ou continuidade, das comunidades de plantas após a ocorrência de expressivo incêndio autóctone e após o evento de queda da cinza vulcânica indica a ocorrência de impacto de curto alcance das perturbações ambientais.

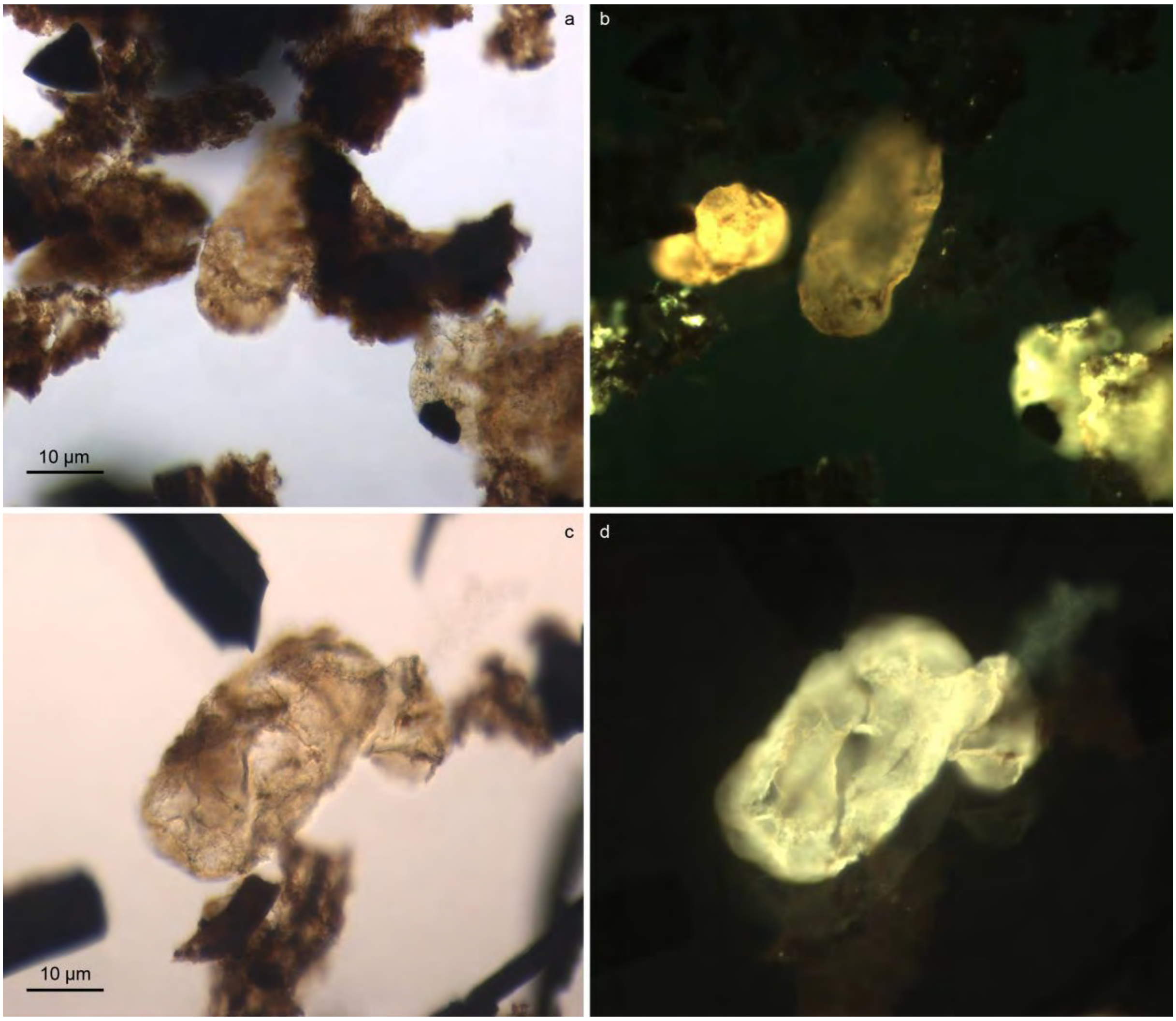


FIGURA 17 – Zigósporos dos níveis inferior e superior do carvão com o tonstein:
a, b) Oxidação de zigósporo no nível inferior ao tonstein, vistas em luz branca transmitida e fluorescência (PB4587A)
c, d) Zigósporo do nível superior ao tonstein com fluorescência inalterada (PB467-T)

A observação sob microscopia eletrônica de varredura (MEV) evidenciou paredes celulares homogeneizadas em todos os espécimes (FIG. 18, a), confirmando a categorização do material como carvão vegetal (*charcoal*) de acordo com os critérios de Scott (2010). A preservação de delicadas estruturas celulares como células crivadas do floema secundário ratifica a conclusão de que as temperaturas de queima mantiveram-se brandas, apenas altas o suficiente para promover a homogeneização da lamela média com as paredes celulares (SCOTT, 2010).

Os detalhes anatômicos preservados nos fragmentos de lenhos queimados (FIG. 18) permitiram a identificação de uma associação monotípica com afinidade taxonômica ao gênero *Agathoxylon*, que corresponde a um padrão encontrado em diferentes grupos gimnospérmicos tais como Cordaitales, Glossopteridales e Coniferales.

Todavia, o domínio de polens com afinidade glossopterídea nas associações palinológicas (CAZZULO-KLEPZIG et al., 2007, 2009) e a presença dominante de folhas de *Glossopteris* spp. na associação paleobotânica procedente do tonstein da Mina do Faxinal (BOARDMAN et al., 2012) constituem evidências indiretas de que os lenhos parcialmente queimados, identificados como de tipo *Agathoxylon*, corresponderiam com maior probabilidade a fragmentos de caules e ramos de glossopterídeas e, secundariamente, de cordaitaleanas. Nesse caso, o padrão anatômico comum a todos os espécimes analisados está indicando a presença de uma associação predominantemente monotípica de plantas.

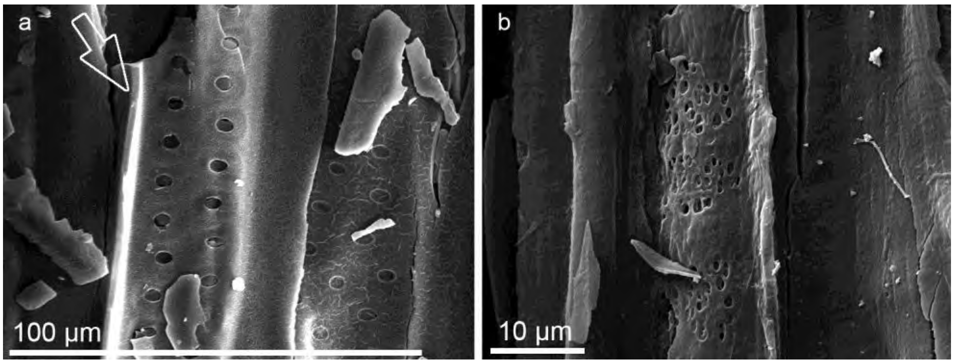


FIGURA 18 – Tecido vascular secundário queimado:
a) Xilema secundário evidenciando parede celular homogeneizada (seta) (PB4587A-04-15)
b) Floema secundário (PB4629-01-04)

A preservação de floema constitui-se em uma relevante evidência paleoecológica. As delgadas paredes celulares das células crivadas estão constantemente sujeitas a pressões hidrostáticas ao longo da vida da planta, favorecendo seu colapso instantâneo mediante injúria (VAN BEL, 1999). Portanto, a preservação de tecido tão delicado ratifica as inferências relacionadas a baixas temperaturas de queima em condições de relativa seca ambiental (HATHER, 2000) e deposição relacionada a pouco ou nenhum transporte (SCOTT, 2010).

A similaridade composicional entre o tecido vascular secundário de *Shanxioxylon sinense* Wang et al. (2003), uma cordaitaleana da província de Cataísia, e o material gondwânico procedente de Faxinal, identificado como *Agathoxylon*, parece apontar para uma provável convergência adaptativa a condições ambientais semelhantes, uma vez que ambos os táxons são procedentes de sequências portadoras de carvões no hemisfério norte e sul respectivamente. Os padrões celulares encontrados no tecido vascular atestam que o conservadorismo anatômico gimnospérmico já estava presente nas pteridospermas paleozoicas (TAYLOR, 1990).

Os padrões epidérmicos da associação de folhas glossopterídeas comprimidas no tonstein da Mina de Faxinal corroboram as inferências de uma comunidade arbórea predominantemente monotípica (GUERRA-SOMMER, 1992). O processo tafonômico que gerou as compressões foliares é considerado um “evento geológico instantâneo” (*sensu* PROTHERO, 1990) capaz refletir as condições ambientais vigentes na turfeira no exato momento em que a cinza precipitou (DIMICHELE; FALCON-LANG, 2011).

O padrão cuticular dominante (95% da associação foliar) caracteriza a espécie *Glossopteris pubescens* nom. nov. como endêmica da Mina de Faxinal, portando um conjunto exclusivo de características. Na face abaxial, ocorrem estômatos com células subsidiárias portadoras de papilas que se encurvam em direção ao poro estomático, papilas nas células epidérmicas não especializadas, pelos com base unicelular (também comuns a outras glossopterídeas) e multicelular (FIG. 19, a) concentrados na região vascular. A face adaxial apresenta cavidades secretoras.

Tais atributos são resultado de interação entre fatores genéticos e ambientais e têm sido identificados em plantas atuais que vivem em condições estressantes, frequentemente vinculados a aridez e perturbações ambientais, tendo sido tradicionalmente utilizados como indicadores de aridez em plantas fósseis (HAWORTH; MCELWAIN, 2008).

A presença de tão elaborado indumento poderia estar relacionada com múltiplas funções, desde defesa mecânica contra dessecação cíclica e herbivoria sazonal por artrópodes que, entre outros, tinham por hábito alimentar a sucção de seiva diretamente do sistema de venação, até proteção dos estômatos contra dessecação ou umidade excessiva, poeira e gases tóxicos oriundos da própria turfeira ou de influência vulcânica próxima ou distante. Adicionalmente, haveria a possibilidade de função secretora dada a ocorrência de possíveis canais interligando as bases (FIG. 19, b) e de cavidades secretoras na face adaxial. Em especial, o aumento de gases, partículas e aerossóis atmosféricos em regiões próximas a vulcanismo poderia ser um fator potencializador do desenvolvimento de tais tricomas complexos conforme referido por Haworth e McElwain (2008) para plantas atuais que, por exemplo, passam por fumigação com gases tóxicos. O grande número de divisões celulares e bases imaturas de tricomas observados nas cutículas de *G.*

pubescens sugere que a queda de cinzas teria sido um fator que promoveu a necessidade de multiplicação das estruturas de proteção (FIG. 19, c, d).

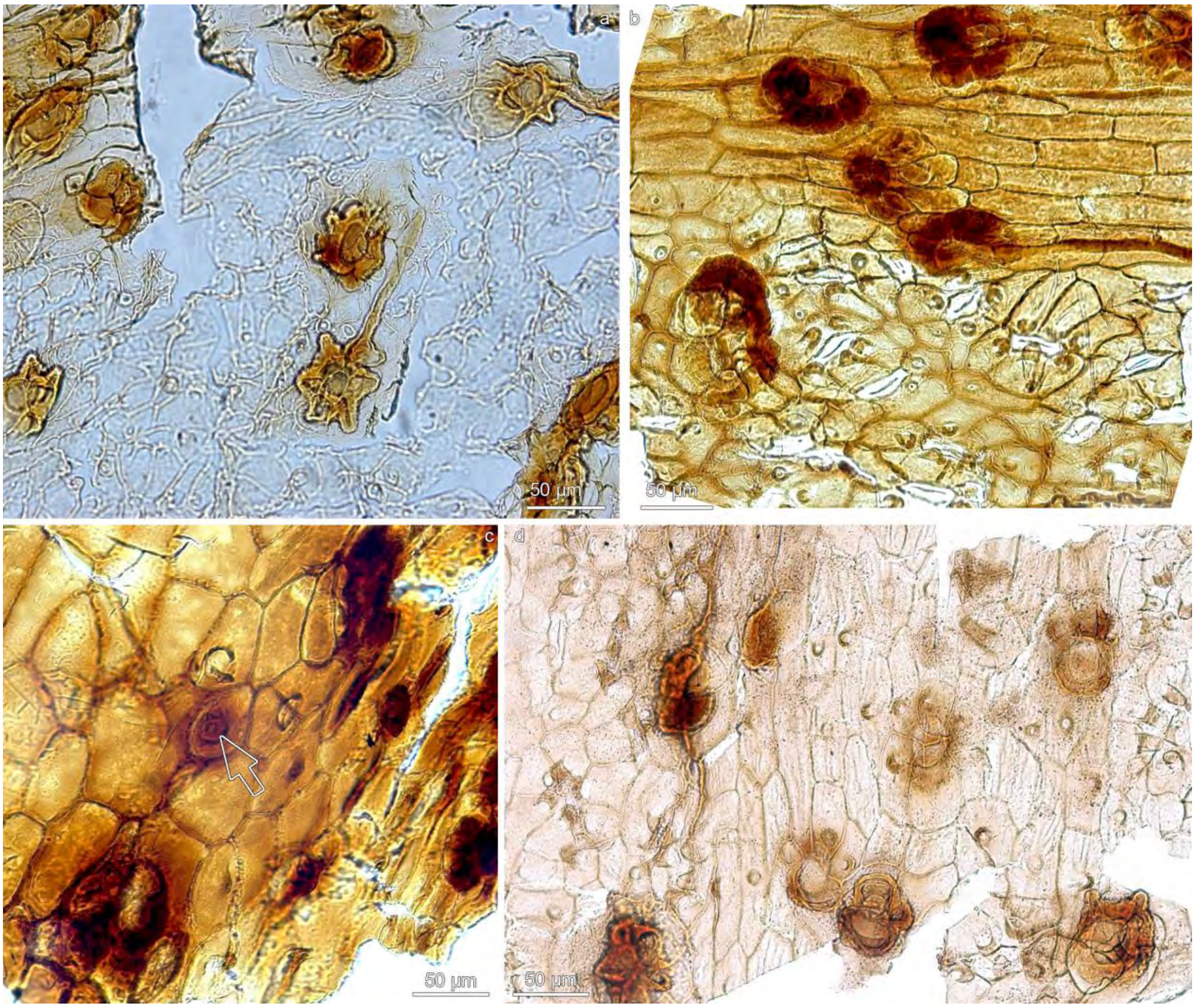


FIGURA 19 – Bases complexas de tricomas:
a) Base no campo intercostal com tricoma conectado (FXB-16)
b) Base com prolongamento cutinizado (?canal) no campo costal (4764E-21)
c) Células iniciais de base de tricoma em divisão na venação média e célula-mãe do pedestal do tricoma (seta) (4818-12)
d) Bases de tricomas em maturação no campo costal (FXB-61)

Essa ornamentada arquitetura epidérmica teria sido mais provavelmente uma adaptação a fatores predominantemente abióticos que distinguem as turfeiras permianas do sul do Brasil de outras turfeiras contemporâneas do norte da Bacia do Paraná e do Gondwana como um todo. Para o sul da Bacia do Paraná, há evidências da ocorrência de processos vulcânicos contemporaneamente em diversas jazidas pela presença de camadas de tonstein associadas às camadas de carvão (GUERRA-SOMMER et al., 2008; ROCHA CAMPOS et al., 2011; SIMAS et al., 2012). Essa peculiaridade ambiental poderia ter estimulado a plasticidade adaptativa de *G. pubescens* a uma resposta fenotípica para marcadas oscilações no padrão de umidade durante a fase interglacial no Sakmariano (MONTAÑEZ; POULSEN, 2013).

Glasspool et al. (2015) relacionam algumas características desenvolvidas pelas plantas que podem ser consideradas vantajosas em sistemas onde incêndios são frequentemente registrados. O sistema clonal de propagação através de rizomas subterrâneos existente desde o Devoniano (BATEMAN et al., 1998) propicia a regeneração rápida em ambientes de turfeira onde incêndios de superfície ocorriam frequentemente (ROBINSON, 1989; SCOTT, 2010). Pteridófitas com esse sistema radicular recuperam-se mais rapidamente após incêndios mesmo que a folhagem tenha sido destruída pelo fogo (SCOTT et al., 2000). As pequenas e espessas acículas de coníferas são particularmente inflamáveis, e a perda dos ramos mais baixos em alguns grupos também pode ter sido uma resposta a incêndios frequentes (BELCHER et al., 2010; LOOY, 2013). Similarmente, a grande distância entre a base do caule e a copa ramificada em licófitas arborescentes impediria a expansão do fogo até o topo da planta onde se concentravam os órgãos reprodutivos (GLASSPOOL et al., 2015). Por outro lado, as grandes frondes pinadas com cutículas espessas de pteridospermas que se depositavam profusamente na superfície das turfeiras (DIMICHELE et al., 2006; DIMICHELE, 2014) facilitavam a propagação de incêndios de superfície (SCOTT, 1978, 1984, 2000, 2010; DIMICHELE; PHILLIPS; PFEFFERKORN, 2006; GLASSPOOL et al., 2015) e provavelmente teriam como função inibir o estabelecimento de espécies competidoras.

Os incêndios seriam regulados pelas oscilações no regime de umidade (evaporação/precipitação/nível do lençol freático), dado que as condições de deposição de turfa permaneceram inalteradas, indicando a persistência de clima predominantemente úmido, correlacionada com a tendência de aquecimento global detectada por Gastaldo, DiMichele e Pfefferkorn (1996) e Montañez et al. (2007) no declínio da glaciação permiana.

Evidências de incêndios em terras baixas associadas a turfeiras gondwânicas foram detectadas de forma geral no Sakmariano em latitudes semelhantes (aprox. 50º). Considerando que carvões são rochas marcadoras de condições climáticas úmidas, pode-se inferir que oscilações climáticas ocorreram durante esse intervalo de forma ampla no Gondwana. Desse modo, tomando-se como referência as evidências de incêndios autóctones e hipoautóctones no local de deposição da turfa, fica constatado que os ambientes de turfeira eram altamente suscetíveis à ocorrência de incêndios.

Ficou evidenciado, também, que as glossopterídeas possuíam grande plasticidade adaptativa para sobreviver a condições extremas em ambientes altamente perturbados e que os incêndios teriam servido como fator de dispersão do grupo (GLASSPOOL et al., 2015).

6.1 CONCLUSÕES

A integração dos resultados das diferentes análises realizadas permitiu investigar a ocorrência de perturbações ambientais durante o intervalo de deposição dos carvões na jazida do Faxinal e sua influência na comunidade vegetal. As perturbações relacionam-se com baixa diversidade de espécies no ambiente de turfeira, e extensos intervalos de incêndios poderiam ter reforçado a dominância de *G. pubescens* nesse ambiente restrito.

A história de incêndios sistêmicos, de baixas temperaturas (325-400°C), em ambiente úmido, que emerge das evidências levantadas, envolve aporte de carvão vegetal macroscópico na turfeira de origem autóctone/hipoautóctone. Após o episódio de incêndio mais intenso registrado no carvão abaixo do tonstein pelos caules comprimidos, as características do carvão vegetal mudam para fragmentos menores, restritos principalmente a porções de floema secundário que correspondem a finas bandas de inertinita. Essas características foram interpretadas como condições hipoautóctones, indicando alguma distância entre os incêndios e o local de deposição dos fragmentos queimados e como tendo baixo impacto na comunidade vegetal de predominância gimnospérmica, dado que não foram observados palinomorfos ou outros órgãos queimados (DEGANI-SCHMIDT et al., 2015).

A preservação de tecido floemático muito delicado (DEGANI-SCHMIDT; GUERRA-SOMMER, 2016), a presença de mássulas de palinomorfos imaturos e a ocorrência de zigósporos algálicos e esporos pteridofíticos oxidados, mas não queimados, indicam que nem a turfeira propriamente dita nem o dossel entraram em combustão (DEGANI-SCHMIDT et al., 2015).

A elaborada arquitetura epidérmica, com bases de tricomas complexas homólogas a estômatos distinguem as folhas de *Glossopteris pubescens* nom. nov. de todas as demais glossopterídeas e sugerem que sua grande plasticidade fenotípica desempenhou um papel importante no domínio e manutenção da espécie na comunidade do Faxinal sob as extremas oscilações ambientais às quais estava sujeita (DEGANI-SCHMIDT; GUERRA-SOMMER, submetido).

O conjunto dessas evidências indicou que os incêndios foram de superfície, em baixas temperaturas, o transporte do carvão vegetal foi praticamente inexistente no grande incêndio registrado na base do tonstein e que os demais incêndios tiveram pouco efeito na comunidade proximal, ocorrendo regularmente nas áreas de entorno da turfeira, dado o aporte de carvão vegetal de menores dimensões (FIG. 20).

Generalizações que podem ser feitas para o Gondwana são de que, sob os altos teores de O_2 vigentes durante o final do Paleozoico, os ambientes de turfeira eram altamente suscetíveis à ocorrência de incêndios dos quais as glossopterídeas se beneficiavam para manter sua dominância e/ou abundância nessas comunidades, por possuírem grande plasticidade adaptativa para sobreviver a condições extremas em ambientes altamente perturbados.

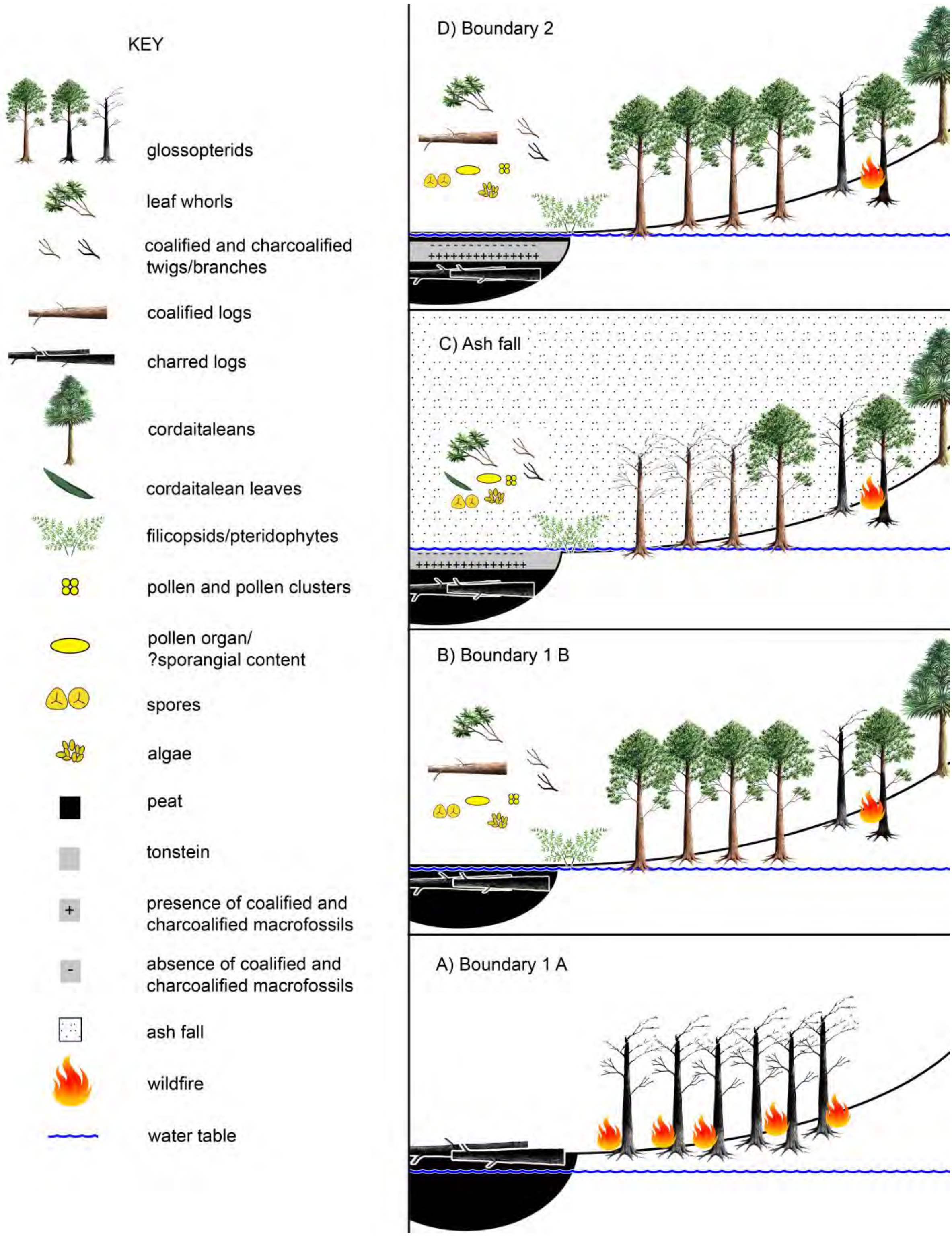


FIGURA 20 – Reconstituição esquemática das perturbações ambientais analisadas na Mina de Faxinal:
a) Incêndio de maior impacto na comunidade
b) Condições regulared de acumulação de turfa
c) Queda de cinza vulcânica
d) Igual a (b)

REFERÊNCIAS

BATEMAN, R. M. et al. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. **Annual Review of Ecology and Systematics**, Palo Alto, p. 263-292, 1998.

BELCHER, C. M. et al. Increased fire activity at the Triassic/Jurassic boundary in Greenland due to climate-driven floral change. **Nature Geoscience**, New York, v. 3, n. 6, p. 426–429, 2010.

BOARDMAN, D. R. et al. Paleobotanical and palynological analysis of Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Paraná Basin), Rio Grande Do Sul, Brazil. **International Journal of Coal Geology**, Amsterdam, v. 102, p. 12–25, 2012.

CAZZULO-KLEPZIG, M. et al. Peat-forming environment of Permian coal seams from the Faxinal coalfield (Paraná Basin) in southern Brazil, based on palynology and palaeobotany. **Revista brasileira de paleontologia**, Porto Alegre, v. 10, n. 2, p. 117–127, 2007.

______. Effect of volcanic ash-fall on a Permian peat-forming environment, on the basis of palynology, palynofacies and paleobotany (Faxinal Coalfield, Brazil). **Revista Brasileira de Paleontologia**, Porto Alegre, v. 12, n. 3, p. 179–194, 2009.

CHMURA, G. L.; STONE, P. A.; ROSS, M. S. Non-pollen microfossils in Everglades sediments. **Review of Palaeobotany and Palynology**, Amsterdam, v. 141, n. 1-2, p. 103–119, 2006.

DEGANI-SCHMIDT, I. et al. Charcoalified logs as evidence of hypautochthonous/ autochthonous wildfire events in a peat-forming environment from the Permian of southern Parana Basin (Brazil). **International Journal of Coal Geology**, Amsterdam, v. 146, p. 55–67, 2015.

DEGANI-SCHMIDT, I.; GUERRA-SOMMER, M. Charcoalified *Agathoxylon*-type wood with preserved secondary phloem from the lower Permian of the Brazilian Parana Basin. **Review of Palaeobotany and Palynology**, Amsterdam, v. 226, p. 20-29, 2016.

______. Epidermal morphology and ecological significance of *Glossopteris pubescens* nom. nov. from the Brazilian Permian (Sakmarian) (submetido).

DIMICHELE, W. A. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. **International Journal of Plant Sciences**, Chicago, v. 175, n. 2, p. 123-164, 2014.

______.; FALCON-LANG, H. J. Pennsylvanian “fossil forests” in growth position (T_0 assemblages): origin, taphonomic bias and palaeoecological insights. **Journal of the Geological Society**, London, v. 168, n. 2, p. 585–605, 2011.

______.; PHILLIPS, T. L.; PFEFFERKORN, H. W. Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica 1. The **Journal of the Torrey Botanical Society**, Lawrence, v. 133, n. 1, p. 83-118, 2006.

GASTALDO, R.; DIMICHELE, W.; PFEFFERKORN, H. Out of the Icehouse into the Greenhouse-a Late Paleozoic analog for modern global vegetational change. **GSA Today**, Washington, v. 6, n. 10, p. 1–7, 1996.

GLASSPOOL, I. J. Hypautochthonous–allochthonous coal deposition in the Permian, South African, Witbank Basin No. 2 seam; a combined approach using sedimentology, coal petrology and palaeontology. **International Journal of Coal Geology**, Amsterdam, v. 53, n. 2, p. 81–135, 2003.

______. et al. The impact of fire on the Late Paleozoic Earth system. **Frontiers in Plant Science**, Lausanne, v. 6, article 756, 2015.

GRENFELL, H. R. Probable fossil zygnematacean algal spore genera. **Review of Palaeobotany and Palynology**, Amsterdam, v. 84, n. 3, p. 201–220, 1995.

GUERRA-SOMMER, M. Padrões Epidérmicos de Glossopteridales da Tafoflora do Faxinal (Formação Rio Bonito - Artinskiano-Kunguriano, Bacia do Paraná, Brasil). **Pesquisas em Geociências**, Porto Alegre, v. 19, p. 26–40, 1992.

______. et al. U-Pb dating of tonstein layers from a coal succession of the southern Paraná Basin (Brazil): A new geochronological approach. **Gondwana Research**, Amsterdam, v. 14, n. 3, p. 474–482, 2008.

HATHER, J. G. **Archaeological parenchyma**. London: Archetype Publications, 2000. 112 p.

HAWORTH, M.; MCELWAIN, J. Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 262, n. 1-2, p. 79–90, 2008.

JONES, T. P.; SCOTT, A. C.; MATTEY, D. P. Investigations of “fusain transition fossils” from the Lower Carboniferous: comparisons with modern partially charred wood. **International Journal of Coal Geology**, Amsterdam, v. 22, n. 1, p. 37–59, 1993.

LOOY, C. V. Natural history of a plant trait: branch-system abscission in Paleozoic conifers and its environmental, autecological, and ecosystem implications in a fire-prone world. **Paleobiology**, Lawrence, v. 39, n. 2, p. 235-252, 2013.

MONTAÑEZ, I. P.; POULSEN, C. J. The Late Paleozoic Ice Age: an evolving paradigm. **Annual Review of Earth and Planetary Sciences**, v. 41, p. 629–656, 2013.

MONTAÑEZ, I. P. et al. CO_2-forced climate and vegetation instability during late Paleozoic deglaciation. **Science**, Washington, v. 314, n. 5808, p. 87, 2007.

PROTHERO, D. R. **Interpreting the Stratigraphic Record**. New York: W. H. Freeman, 1989. 410 p.

ROBINSON, J. M. Phanerozoic O_2 variation, fire, and terrestrial ecology. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 75, n. 3, p. 223-240, 1989.

ROCHA-CAMPOS, A. C. et al. 30 million years of Permian volcanism recorded in the Choiyoi igneous province (W Argentina) and their source for younger ash fall deposits in the Paraná Basin: SHRIMP U-Pb zircon geochronology evidence. **Gondwana Research**, v. 19, n. 2, p. 509–523, 2011.

SCOTT, A. C. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 291, n. 1-2, p. 11–39, 2010.

______. The Pre-Quaternary history of fire. **Palaeogeography, Palaeoclimatology, Palaeoecology**, Amsterdam, v. 164, n. 1-4, p. 281–329, 2000.

SIMAS, M. W. **Origem vulcânica para o tonstein da jazida do Faxinal (RS):** estudos mineralógicos, petrográficos e de palinofácies. Dissertação (Mestrado em Geociências) – Porto Alegre, Instituto de Geociências, Curso de Pós-Graduação em Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, 2008.

______. Geochronological correlation of the main coal interval in Brazilian Lower Permian: Radiometric dating of tonstein and calibration of biostratigraphic framework. **Journal of South American Earth Sciences**, Amsterdam, v. 39, p. 1–15, 2012.

______. et al. An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a Lower Permian tonstein bed (Faxinal Coalfield, Paraná Basin, Brazil). **Geologica Acta**, Barcelona, v. 11, n. 1, p. 47–57, 2013.

TAYLOR, E. L. Phloem evolution: An appraisal from the fossil record. In: BEHNKE, H. D.; SJOLUND, R. S. (Ed.). **Sieve Elements - Comparative Structure, Induction, and Development**. Berlin: Springer-Verlag, 1990. p. 285–298.

VAN BEL, A. J. Evolution, polymorphology and multifunctionality of the phloem system. **Perspectives in Plant Ecology, Evolution and Systematics**, Jena, v. 2, n. 2, p. 163–184, 1999.

WANG, S.-J. et al. Cordaitalean seed plants from the Early Permian of North China. I. Delimitation and reconstruction of the *Shanxioxylon sinense* plant. **International Journal of Plant Sciences**, Chicago, v. 170, n. 3, p. 400–418, 2003.

YI, S. Zygnematacean zygospores and other freshwater algae from the Upper Cretaceous of the Yellow Sea Basin, southwest coast of Korea. **Cretaceous Research**, London, v. 18, n. 4, p. 515–544, 1997.

ANEXOS

ANEXO A – Artigo publicado (2011)

Variation in stomatal numbers of Glossopteris *leaves from the lower Permian of Paraná Basin, Brazil*

Disponível em < http://www.sbpbrasil.org >

Rev. bras. paleontol. 14(2):137-148, Maio/Agosto 2011

doi:10.4072/rbp.2011.2.02

VARIATION IN STOMATAL NUMBERS OF *GLOSSOPTERIS* LEAVES FROM THE LOWER PERMIAN OF PARANÁ BASIN, BRAZIL

ISABELA DEGANI SCHMIDT & MARGOT GUERRA SOMMER
Instituto de Geociências, UFRGS, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91501-970, Porto Alegre, RS, Brasil.
degani.schmidt@ufrgs.br, *margot.sommer@ufrgs.br*

MARY ELIZABETH C. BERNARDES DE OLIVEIRA
Programa de Pos-graduação em Geoquímica e Geotectônica, IGc, USP, Cidade Universitária, 05508-080,
São Paulo, SP, Brasil. *maryliz@usp.br*

ABSTRACT – The stomatal density and index in compressed leaves of *Glossopteris communis* from two different roof shales from the Lower Permian in Paraná Basin, Brazil (Western Gondwana) have been investigated to test the possible relationship with modeled global changes in atmospheric CO_2 during the Phanerozoic. The obtained parameters show that the genus *Glossopteris* from the Cool Temperate biome can be used as CO_2-proxy, despite the impossibility of being compared with living relatives or equivalents. When confronted with already published data for the Tropical Summer Wet biome, the present results confirm the detection of low levels of atmospheric CO_2 during the Early Permian, as predicted by the modeled curve. Nevertheless, the lower stomatal numbers detected at the climax of the coal interval (Faxinal Coalfield, Sakmarian) when compared to the higher ones obtained in leaves from a younger interval (Figueira Coalfield, Artinskian) could be attributed to temporarily high levels of atmospheric CO_2. Therefore, the occurrence of an extensive peat generating event at the southern part of the basin and subsequent greenhouse gases emissions from this environment may have been enough to reverse regionally and temporarily the reduction trend in atmospheric CO_2. Additionally, the Faxinal flora is preserved in a tonstein layer, which is a record of volcanic activity that could also cause a rise in atmospheric CO_2. During the Artinskian, the scarce generation of peat mires, as revealed by the occurrence of thin and discontinuous coal layers, and the lack of volcanism evidence would be insufficient to affect the general low CO_2 trend.

Key words: paleo-CO_2 proxy, pteridosperms, fossil cuticles, Rio Bonito Formation, peat-forming floras, Gondwana.

RESUMO – Frequências estomáticas foram calculadas em cutículas de *Glossopteris communis*, procedentes de dois afloramentos do Permiano Inferior na bacia do Paraná, com o objetivo de relacioná-las com variações na concentração atmosférica de CO_2 modeladas para o Fanerozoico. Os resultados indicam que as glossopterídeas do bioma Temperado Frio podem ser utilizadas como equivalentes climáticos para inferência de níveis de CO_2 paleoatmosférico, apesar da impossibilidade de estabelecer um equivalente ecológico atual. Quando confrontados com dados obtidos para o bioma Tropical de Verão Úmido, os resultados aqui apresentados confirmam a detecção de baixos níveis de CO_2 na atmosfera durante o período, de acordo com o modelamento da curva. Porém, as frequências estomáticas mais baixas detectadas no clímax do intervalo formador de carvão (jazida de Faxinal, Sakmariano), quando comparadas às frequências mais altas obtidas nas folhas de intervalo mais jovem (jazida de Figueira, Artinskiano), poderiam ser atribuídas a níveis temporariamente altos de CO_2 na atmosfera. A ocorrência de extenso evento gerador de turfa na parte sul da bacia, com a consequente emissão de gases-estufa deste ambiente, poderia ter sido suficiente para reverter a tendência de queda de CO_2 atmosférico em âmbito regional ainda que de forma temporária. Além disso, a flora de Faxinal está preservada em uma camada de *tonstein*, registro de atividade vulcânica que poderia ter afetado os níveis de CO_2. No Artinskiano, a formação de turfeiras em menor escala, evidenciada por camadas de carvão descontínuas e delgadas, sem registro de vulcanismo, teria sido insuficiente para afetar a tendência de baixo CO_2.

Palavras-chave: equivalente paleoclimático para CO_2, pteridospermas, cutículas fósseis, Formação Rio Bonito, floras formadoras de turfa, Gondwana.

INTRODUCTION

The applicability of fossil plant leaves as biosensors of Earth's paleoatmospheric CO_2 fluctuations is being increasingly ratified through the comparisons between the stomatal numbers (stomatal density and index) of fossil, living and herbarium material (McElwain, 1998; Kouwenberg *et al*., 2003; Wagner *et al*., 2005) since Woodward (1987) observed an inverse correlation between stomatal frequency in extant plants and the concentration of atmospheric CO_2. Even

ANEXO B – Artigo publicado em coautoria (2011)
Lenhos de coníferas do Mesocretáceo do norte do Maranhão, Brasil
Disponível em < http://www.sbpbrasil.org >

Rev. bras. paleontol. 14(1):29-38, Janeiro/Abril 2011

doi:10.4072/rbp.2011.1.03

LENHOS DE CONÍFERAS DO MESOCRETÁCEO DO NORTE DO MARANHÃO, BRASIL

KIRLEY CRISTINA DE OLIVEIRA ARAÚJO
Departamento de Biologia, UFMA, Av. dos Portugueses, s/n, 65085-580, São Luís, MA, Brasil.
kirleycristina-araujo@hotmail.com

MARGOT GUERRA SOMMER
Programa de Pós-Graduação em Geociências, UFRGS, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91540-970,
Porto Alegre, RS, Brasil. *margot.sommer@ufrgs.br*

MANUEL ALFREDO MEDEIROS, EMÍLIA CRISTINA GIRNOS
Departamento de Biologia, UFMA, Av. dos Portugueses, s/n, 65085-580, São Luís, MA, Brasil. *alf@ufma.br*

ISABELA DEGANI SCHMIDT
Programa de Pós-Graduação em Geociências, UFRGS, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91540-970,
Porto Alegre, RS, Brasil. *degani.schmidt@ufrgs.br*

ABSTRACT – CONIFER WOODS FROM THE MIDDLE CRETACEOUS OF NORTHERN MARANHÃO STATE, BRAZIL. In the present work, 13 silicified logs collected in the fossiliferous levels of the Alcântara Formation (Upper Albian-Lower Cenomanian estuarine deposits in northern Maranhão State, NE Brazil) were analyzed through petrographic slides applying parataxonomic approach. The gymnospermous araucarioid pattern is the prevailing pattern observed in the wood association, suggesting a possible relation to the Araucariaceae. Considering that pollen grains of *Araucariacites australis* were previously reported from the same sedimentary deposits where the sample came from, the presence of Araucariacea is assumed, mainly in the estuarine environment inferred for the region of Alcântara and São Luís. Conifers with abietoid wood pattern may be related to Taxaceae and probably throve in inland areas. The absence of angiospermous woods in the assemblage, opposed to the expressive representation in palynological analyses, can be attributed to a combination of taphonomic factors or, alternatively, to the development of conifer and angiosperm plants in distinct paleoenvironment during the middle Createaceous. The predominance of uninterrupted wood growth and rare evidences of partially interrupted wood growth patterns and the presence of radial desiccation cracks led to the inference of a stable paleoclimate, but with sporadic drought episodes during growing season, included in global scale in the equatorial humid belt in the boundary with the northern hot arid belt.

Key words: xylotypes, araucarioid, abietoid, Alcântara Formation, Upper Albian-Lower Cenomanian.

RESUMO – No presente trabalho, 13 fragmentos de lenhos silicificados coletados nos níveis fossilíferos da Formação Alcântara (Albiano superior-Cenomaniano inferior do norte do Estado do Maranhão, NE Brasil) foram estudados a partir da análise de lâminas petrográficas, utilizando critérios parataxonômicos. O padrão gimnospérmico é exclusivo nas amostras, com dominância de xilema de coníferas de tipo araucarioide, sugerindo, de forma ampla, uma possível relação com a família Araucariaceae. Considerando que *Araucariacites australis* é um grão de pólen abundantemente reportado nesses mesmos depósitos sedimentares de onde provém a amostra, a presença de Araucariaceae é assumida no ambiente estuarino que existiu na região de Alcântara e São Luís. Coníferas representadas por formas com padrão abietóide, talvez relacionado à Taxaceae, medravam provavelmente em áreas mais interiores. A ausência de lenho de Angiospermae, que se contrapõe à sua expressiva diversidade nos registros fósseis palinológicos, é atribuída a uma combinação de circunstâncias tafonômicas ou, alternativamente, ao desenvolvimento de coníferas e angiospermas em paleoambientes diferenciados no intervalo estudado. A dominância de padrões de crescimento ininterrupto do lenho, com registro de padrões de crescimento parcialmente interrompido em raros espécimes, associado à presença de lacunas de ressecamento no xilema, levou à inferência de um paleoclima estável com ocorrência esporádica de secas na fase de crescimento, incluído em escala global no cinturão equatorial úmido na área limítrofe com o cinturão quente e árido do Norte.

Palavras-chave: xilotipos, araucarioide, abietoide, Formação Alcântara, Albiano superior-Cenomaniano inferior.

INTRODUÇÃO

No norte do Estado do Maranhão, nordeste do Brasil, rochas cretáceas afloram nas falésias litorâneas revelando uma associação de fácies sedimentares depositadas por um sistema estuarino datado como Eocenomaniano. Todo o conjunto pós-Aptiano do norte maranhense originalmente era incluído na então chamada Formação Itapecuru, mas posteriormente essa designação passou a definir um grupo de formações (Grupo Itapecuru) e as rochas aflorantes nas praias

ANEXO C – Capítulo de livro publicado em coautoria (2011) in: CARVALHO, I. S. et al. (Org.). Paleontologia: Cenários de Vida. Rio de Janeiro: Interciência, v.4, p. 95-107.
Mesophytic Gondwanan paleofloras from Brazil and India: composition and paleoclimatical approach

MESOPHYTIC GONDWANAN PALEOFLORAS FROM BRAZIL AND INDIA: COMPOSITION AND PALEOCLIMATICAL APPROACH

PALEOFLORAS MESOFÍTICAS GONDVÂNICAS DO BRASIL E ÍNDIA: COMPOSIÇÃO E CONSIDERAÇÕES PALEOCLIMÁTICAS

[1,2]Mary E.C. Bernardes de Oliveira, [2]Sandra Mune, [2]Paula Sucerquia, [1]Maria Judite Garcia, [3]Margot Guerra-Sommer, [3]Isabella Degani Schimidt & [4]Rajni Tewari

E-mails: maryeliz@usp.br, smune@hotmail.com, psucerquia@gmail.com, mgarcia@ung.br, margot.sommer@ufrgs.br, degani.schmidt@gmail.com, rajni.tewari@gmail.com

[1] Universidade Guarulhos - Mestrado em Análise Geoambiental, Guarulhos – SP, Brasil;[2] Universidade de São Paulo – Instituto de Geociências. Programa de Pós-Graduação em Geoquímica e Geotectônica. São Paulo;

[3]Universidade Federal do Rio Grande do Sul -Instituto de Geociências - Porto Alegre, RS, Brasil;

[4]Birbal Sahni Institute of Palaeobotany/BSIP- Lucknow, India

RESUMO

Apresenta-se aqui uma síntese da composição geral de floras mesofíticas das bacias gondvânicas brasileiras e indianas. Dados paleobotânicos evidenciaram que o mesofítico indiano tem implicações paleoclimáticas e bioestratigráficas. A presença de importantes marcadores paleoflorísticos como Flora de *Ptilophyllum* não é observada na bacia do Paraná, Brasil. Associações de plantas mesofíticas no Brasil não estão bem preservadas, são homogêneas na composição e principalmente representadas por lenhos fósseis. A presença de floras de *Dicroidium* no Gondwana oriental e ocidental permanece como uma única e forte feição, comum entre as floras dos dois países. Considerando os recentes dados sobre a ancestralidade da flora de *Dicroidium* no Eopermiano gondvânico indiano e sua ocorrência em províncias extra-gondvânicas neopermianas, estudos mais detalhados nesta flora poderiam dar informações importantes envolvendo filogenias, paleobiogeografia e paleoclimatologia vegetais.

Palavras-chave: Mesozóico, Fitofósseis, Índia, Brasil, Floras de *Ptilophyllum* e de *Dicroidium*

ABSTRACT

A synthesis from the general composition of mesophytic floras from the Brazilian and Indian Gondwana basins here is presented. Paleobotanical data evidenced that the Indian mesophytic have biostratigraphic and paleoclimatic significance. The presence of important paleofloristic markers as the *Ptilophyllum Flora* it is not represented in Brazilian Paraná Basin. Plant associations from Brazil are poorly preserved, homogeneous in composition and mainly represented by fossil woods. The presence of *Dicroidium* floras in Eastern and Western Gondwana remains, as a unique strong, and a common character between Indian and Brazilian Gondwana floras. Considering the recent data about the ancestry of *Dicroidium* Flora in Early Permian Gondwana, and its occurrence in extra Gondwanian provinces at Late Permian,

ANEXO D – Capítulo de livro publicado em coautoria (2012)

Integration of geochronologic, paleobotanical and organic matter studies in Gondwanan tonstein (Sakmarian, Paraná Basin, Brazil)”
Disponível em < http://www.uc.pt/congressos/GeoCPLP2012 >

PARA CONHECER A TERRA

MEMÓRIAS E NOTÍCIAS
DE GEOCIÊNCIAS
NO ESPAÇO LUSÓFONO

VOLUME I

Lopes, F. C., Andrade, A. I.,
Henriques, M. H., Quinta-Ferreira, M.,
Barata, M. T. & Pena dos Reis, R.
Coordenação

IMPRENSA DA UNIVERSIDADE DE COIMBRA
2012

12

INTEGRATION OF GEOCHRONOLOGIC, PALEOBOTANICAL AND ORGANIC MATTER STUDIES IN GONDWANAN TONSTEIN (SAKMARIAN, PARANÁ BASIN, BRAZIL)

INTEGRAÇÃO DE ESTUDOS GEOCRONOLÓGICOS, PALEOBOTÂNICOS E DE MATÉRIA ORGÂNICA DISPERSA EM TONSTEIN GONDWÂNICO (SAKMARIANO, BACIA DO PARANÁ, BRASIL)

M. Guerra-Sommer[1], M. Cazzulo-Klepzig[2], J. G. Mendonça Filho[3],
I. Degani-Schmidt[4], A. Jasper[5], R. Menegat[6] & M. W. Simas[7]

Abstract *– Integration of petrographic, paleobotanic and dispersed organic matter studies, associated to radiometric data (Tuffzir age of 290.15 + 2.45/-0.85 Ma) in a tonstein bed interbedded in a coal seam in Faxinal Coalfield (Sakmarian) in Brazilian Southern Paraná Basin (Brazil), evidenced that the rapid volcanic ash fall deposition must be taken into account to interpret the composition, taphonomic process and consequently, preservation of the organic matter which is identified in different stages of deposition of a forested plant-association.*

---

[1] UFRGS, Instituto de Geociências, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91501-970, Porto Alegre, RS, Brasil; margot.sommer@ufrgs.br

[2] UFRGS, Instituto de Geociências, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91501-970, Porto Alegre, RS, Brasil; miriam.klepzig@ufrgs.br

[3] UFRJ, Instituto de Geociências, Av. Athos da Silveira Ramos, 274, 21949-900, Rio de Janeiro, RJ, Brasil; graciano@geologia.ufrj.br

[4] UFRGS, Instituto de Geociências, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91501-970, Porto Alegre, RS, Brasil; degani.schmidt@ufrgs.br

[5] UNIVATES, Rua Avelino Tallini, 171, Cx.P. 155, 95900-000, Lajeado, RS, Brasil; ajasper@univates.br

[6] UFRGS, Instituto de Geociências, Av. Bento Gonçalves, 9500, Cx.P. 15001, 91501-970, Porto Alegre, RS, Brasil; rualdo.menegat@ufrgs.br

[7] Companhia de Pesquisa de Recursos Minerais, Av. Dr. Freitas, 3645, 66095-110, Belém, PA, Brasil. margaws@yahoo.com.br

ANEXO E – Resumo publicado XV Simposio Argentino de Paleobotánica y Palinología, Corrientes, 2012

Stomatal numbers of Glossopteris communis respond to variations in CO2 levels of the Permiam paleoatmosphere

Stomatal numbers of *Glossopteris communis* respond to variations in CO_2 levels of the Permiam paleoatmosphere

I. DEGANI-SCHMIDT[1]; M. GUERRA-SOMMER[1]y M. E. C. BERNARDES-DE-OLIVEIRA[2]

The use of fossil plant cuticles for estimating levels of CO_2 in the paleoatmosphere is based on an observed inverse correlation between atmospheric CO_2 and stomatal density (number of stomata per mm^2 leaf area) of vascular plant leaves. The stomatal density in compressed leaves of the pteridosperm *Glossopteris communis* from two different roof shales from the Lower Permian Paraná Basin, Brazil (Rio Bonito Formation) were investigated to test the possible relationship with global changes in atmospheric CO_2 during the late Paleozoic in the western Gondwana. Samples from Figueira coal mines, Paraná state (Artinskian according to sequence stratigraphy relative dating), yielded a mean stomatal density of 284 mm^{-2} and from Faxinal Coalfield, Rio Grande do Sul state, 235 mm^{-2} (290.6 ± 1.5 Ma, middle Sakmarian, based on radiometric absolute dating). The statistically significant difference (P= 0,0018) is consistent with the hypothesis of changing atmospheric CO_2 concentrations during the Permian due to glaciation-deglaciation cycles. Despite the impossibility of comparing pteridosperms with living relatives or equivalents, the obtained results could help to refine global paleoclimate reconstructions based on modeling and other proxies of lower resolution. The present results support the use of pteridosperms as a proxy for CO_2 in the paleoatmosphere of Gondwana, as already shown for Euramerica. Stomatal parameters of Permian conifers from the Paraná Basin are being currently investigated to estimate CO_2 levels in the paleoatmosphere using the nearest living equivalent comparison method.

[1]Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil
[2]Universidade de São Paulo (USP), São Paulo, SP, Brazil
*degani.schmidt@ufrgs.br; margot.sommer@ufrgs.br; maryeliz@usp.br

ANEXO F – Artigo publicado em coautoria (2012)

Geochronological correlation of the main coal interval in Brazilian Lower Permian: Radiometric dating of tonstein and calibration of biostratigraphic framework

Disponível em < http://dx.doi.org/10.1016/j.jsames.2012.06.001 >

Journal of South American Earth Sciences 39 (2012) 1–15

Contents lists available at SciVerse ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

Geochronological correlation of the main coal interval in Brazilian Lower Permian: Radiometric dating of tonstein and calibration of biostratigraphic framework

Margarete Wagner Simas[a], Margot Guerra-Sommer[b,*], Miriam Cazzulo-Klepzig[b], Rualdo Menegat[b], João Orestes Schneider Santos[c], José Alcides Fonseca Ferreira[d], Isabela Degani-Schmidt[b]

[a] *CPRM – Serviço Geológico do Brasil, Avenida Dr. Freitas, 3645, 66095-110 Belém, PA, Brazil*
[b] *Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Cx.P. 15001, 91501-970 Porto Alegre, RS, Brazil*
[c] *Centre for Global Targeting, University of Western Australia, Crawley, Perth 6009, WA, Australia*
[d] *CPRM – Serviço Geológico do Brasil, Rua Banco da Província 105, CEP 90840-030, Porto Alegre, RS, Brazil*

ARTICLE INFO

Article history:
Received 26 July 2011
Accepted 5 June 2012

Keywords:
Ash fall
SHRIMP U–Pb
Biostratigraphic framework
Gondwana coals

ABSTRACT

The radiometric age of 291 ± 1.2 Ma obtained through single-crystal zircon U–Pb ages (Sensitive High Resolution Ion MicroProbe – SHRIMP II) of tonsteins from the Leão-Butiá Coalfield, southern Paraná Basin (Rio Grande do Sul state), associated with previous SHRIMP II radiometric data obtained from tonsteins from the western (Candiota Coalfield) and eastern (Faxinal and Leão-Butiá coalfields) borders of the basin indicate that the mean age of the main peat-forming interval is 291.0 ± 1.3 Ma. In a regional context, the mean age represents a consistent geochronological correlation for the uppermost and more important coal seams in southern Brazilian coalfields, but this assumption does not establish an ash fall origin from a single volcanic event. According to the International Stratigraphic Chart, the interval is dated as middle Sakmarian. The coal palynofloras are included in the *Protohaploxypinus goraiensis* Subzone within the palynostratigraphic framework for the Brazilian Paraná Basin. Formal relationships are also established with the *Glossopteris–Rhodeopteridium* Zone within the phytostratigraphic chart for the Lower Permian of southern Brazilian Paraná Basin.

1. Introduction

Tonsteins are volcanic ash falls in coal-bearing sequences that have altered to kaolinite (Spears, 2012) and are recognized as reliable marker beds for stratigraphic analysis (Bouroz, 1972; Lyons et al., 2006). These clay beds can extend over large distances and usually contain relict volcanic minerals that can be dated by radiometric analyses. As the geographical distribution of the marker beds is restricted to sites with favorable preservation potential (such as lacustrine and swamp environments), their occurrence in coal sequences reflects particular sedimentary conditions in peat-forming areas and constitutes possible target of reliable geochronological data (Way et al., 1986; Saylor et al., 2005). Air fall volcanic ash deposited during a short-term eruptive event helps identify tonstein beds as chronostratigraphic markers and, consequently, as useful stratigraphic tools in both regional and global correlations (Huff et al., 1992).

Evidence of Early Permian explosive volcanic activity (Formoso et al., 1999), represented by tonstein beds, is widespread in various coal successions in the Cisuralian of the southern Brazilian Paraná Basin (Fig. 1). These coal-bearing rocks are related to a paralic setting (assigned to the Rio Bonito Formation), that is, adjacent to estuarine, deltaic, backshore, foreshore and shoreface siliciclastic sedimentary facies and most of the peat-forming areas in the basin have been identified as part of a back-barrier lagoonal paleoenvironment (Alves and Ade, 1996; Holz, 1998; Milani et al., 2007).

The resolution of a stratigraphic framework for the coal-bearing interval in southernmost Paraná Basin has presented difficulties due to the discontinuity of strata and the apparently isolated, discontinuous coalfields placed at different tectonic blocks and the distance of approximately 300 km between the coalfields located at the western and eastern borders of the basin (Fig. 1).

Nevertheless, in the last decade, tonstein beds have been used as a geochronological correlation tool for the coal-bearing strata in the southern Paraná Basin (Guerra-Sommer et al., 2008a,b,c; Rocha-Campos et al., 2007; Mori et al., 2012) because they enable high resolution calibration with other paleontological and stratigraphic tools for the study interval.

---

* Corresponding author. Tel.: +55 51 33086378; fax: +55 51 33313590.
E-mail address: margot.sommer@ufrgs.br (M. Guerra-Sommer).

0895-9811/$ – see front matter © 2012 Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.jsames.2012.06.001

ANEXO G - Resumo publicado XIV Simpósio Brasileiro de Paleobotânica e Palinologia, Rio de Janeiro, 2013
Concepções tafonômicas para a Flora Glossopteris *preservada em leito de tonstein na jazida de carvão de Faxinal (Formação Rio Bonito, Bacia do Paraná, RS, Brasil)*

Série Livros 49

Conservação do Patrimônio Paleobotânico e Palinológico

ANAIS
XIV SIMPÓSIO BRASILEIRO DE PALEOBOTÂNICA E PALINOLOGIA
5º ENCONTRO LATINOAMERICANO DE FITÓLITOS
13 A 16 de maio de 2013

Organizadores
Claudia Barbieri Ferreira Mendonça
Vania Gonçalves Lourenço Esteves
Marcelo de Araujo Carvalho
Rita Scheel-Ybert

Rio de Janeiro-RJ, Brasil
Museu Nacional
2013

CONCEPÇÕES TAFONÔMICAS PARA A FLORA *GLOSSOPTERIS* PRESERVADA EM LEITO DE TONSTEIN NA JAZIDA DE CARVÃO DE FAXINAL (FORMAÇÃO RIO BONITO, BACIA DO PARANÁ, RS, BRASIL)

Taphonomy of the Glossopteris flora preserved in the Tonstein Bed Of Faxinal Coalfield (Rio Bonito Formation, Paraná Basin, RS, Brazil)

Isabela DEGANI-SCHMIDT[1]; Margot GUERRA-SOMMER[2]; André JASPER[3]& João Graciano MENDONÇA FILHO[4]

[1]Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil (degani.schmidt@ufrgs.br)
[2]Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil (margot.sommer@ufrgs.br)
[3]Centro Universitário UNIVATES, Lajeado, Brasil (ajasper@univates.br)
[4]Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil (graciano@geologia.ufrj.br)

The paleoflora preserved in a 10 cm thick claystone level interbedded with coal seams in the Faxinal Coalfield, Arroio dos Ratos, RS (Lower Permian, Paraná Basin) is composed mainly by glossopterid leaves, reproductive axes and isolated seeds and cordaitalean leaves. Fragments of filicoid fronds occur in low frequency. Early studies inferred a detrital origin for this claystone, which was denominated stratotonstein. Based on this assumption, the origin of the dense and horizontally layered leaf assemblage had been interpreted as slow deposition in limnic environment. However, later recent studies established a volcanic origin for the tonstein, changing radically the conception of the taphonomic process that yielded the good preservation of the paleoflora. The plant composition and paleosuccession in this fossil assemblage can therefore be explained by a catastrophic episode which interrupted the peat deposition , considered geologically instantaneous, , , related to volcanic ash deposition as evidenced by geochemical studies. The depositional process through volcanic ash-fall is a peculiar sedimentary event generating an immediate horizontally-layered compression-impression record of the vegetation. Results of paleobotanical, palynofacies and charcoal analyses of the taphocenose in meter-square plots show that leaves of the arboreal canopy (*Glossopteris* spp. and *Rufloria* sp.) are concentrated mainly at the base of the tonstein layer. Conversely, at the top of the tonstein, rare and delicate filicoid fronds (*Sphenopteris* spp.) occur, which could be interpreted as the subcanopy layer of the same plant community, reflecting thus a single-event deposit rather than a succession of assemblages through time. A similar megafossil distribution was reported for a taphoflora preserved in a volcanic tuff layer interbedded with coal seams in the Early Permian of Mongolia, also comparable to the recent preservation of plant remains in ash derived from volcanic activity in Mexico (El Chichón). Additional paleoecological interpretations include (1) a rapid drop of megascopic charcoalified gymnosperm fragments with non abraded edges towards the top of the tonstein correlated with a reduction in the intensity of fire at the end of ash deposition based on previous charcoal analysis, corroborating the single-event hypothesis or, alternatively, (2) a multiple-event of ash-fall yielding the record of plant succession in which the filicoid fronds represent the pioneer vegetation.

Financiamento: CAPES; CNPq (470315/2010-5; 474857/2011-5); FAPERGS.

ANEXO H - Resumo publicado XXIII Congresso Brasileiro de Paleontologia, Gramado, 2013
Epidermal structures of Glossopteris communis *from the Faxinal Coalfield (Lower Permian, Rio Bonito Formation, Paraná Basin)*
Disponível em < http://www.sbpbrasil.org >

ISSN 1516-1811

Paleontologia em Destaque

Boletim Informativo da Sociedade Brasileira de Paleontologia

Edição Especial

XXIII Congresso Brasileiro de Paleontologia

Gramado - Outubro/2013

que representa o substrato para o processo fotossintético de autótrofos. Registros confirmam que folhas fósseis do Quaternário demonstram que o decréscimo de CO_2 aumenta a densidade estomática. Tal adaptação é creditada à tentativa da planta em evitar a perda d´água, já que sob elevados índices de CO_2 atmosférico é possível alcançar altas taxas fotossintéticas com menor condutância estomática, portanto, menor transpiração. Evidências de alterações climáticas são reveladas na análise de amostras de fragmentos vegetais fósseis coletados nas Formações Ramon e Solimões, pelo alto índice de densidade estomática, indicando prováveis condições ambientais xerofíticas, ou ainda podendo ser associado a condições climáticas de período frio com menor índice de CO_2 atmosférico, ou seja épocas frias denunciadas pelo elevado número de estômatos. As análises seguem focadas em mais coletas nas regiões da Serra do Divisor e Vale do Juruá para elucidação de possíveis alterações climáticas durante o Paleógeno e Neógeno através do registro de fitofósseis em afloramentos das Formações Ramon e Solimões. [Projeto MCTI – 01200.001631/2010-32]

EPIDERMAL STRUCTURES OF GLOSSOPTERIS COMMUNIS FROM THE FAXINAL COALFIELD (LOWER PERMIAN, RIO BONITO FORMATION, PARANÁ BASIN)

ISABELA DEGANI-SCHMIDT & MARGOT GUERRA-SOMMER

Laboratório de Paleobotânica, UFRGS, Porto Alegre, RS, Brasil. degani.schmidt@ufrgs.br, margot.sommer@ufrgs.br

Cuticular analysis conducted in leaf fragments identified as *Glossopteris communis* Feistmantel evidenced the presence of complex, highly cutinized, crown-shaped trichome bases dispersed on the abaxial (lower) leaf surface. Leaf compressions were recovered from an ash-fall level of late Sakmarian age (290.6 ± 1.5 Ma) interbedded in a coal seam in the Faxinal Coalfield (Rio Bonito Formation, southern Paraná Basin). Leaf fragments were mechanically lifted from the matrix rock, macerated in hydrofluoric acid and bleached in Schulze's solution. Cuticles were then mounted on glass slides with glycerin jelly and observed in transmitted light microscopy. Considering that cuticle coverage carries unique information regarding physiological responses of plants to paleoclimate changes, leaf epidermal analysis has been one of the most widely used techniques in paleobotanical and paleoclimatological research. *Glossopteris* leaves, which are the most abundant macrofossils in the Permian of Gondwana, became important to the discussion of past high latitude climates. Their cuticle descriptions comprise presence or absence of epidermal papillae, simple trichomes, stomatal papillae and sunken or superficial stomata. The fragments here analyzed differ from specimens described from wet, peat-forming habitats from the same coal-prone interval in the northern part of the basin (coalfields in the Figueira region, Paraná state) with papillate stomata but lacking dispersed multicellular trichomes. Furthermore, trichomes are poorly documented in glossopterids, and their abundance is apparently endemic to the paleoflora preserved in the tonstein of the Faxinal Coalfield. This suggests that they are a functional trait and their presence is most probably an ecological adaptation giving a selective advantage in certain environmental conditions as in many modern plants. [CAPES, CNPq 159690/2012-9, 470315/2010-5]

ANEXO I – Artigo publicado em coautoria (2013)

An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a lower Permian tonstein layer (Faxinal Coalfield, Paraná Basin, Brazil)

Disponível em < http://www.geologica-acta.com >

Geologica Acta, Vol.11, Nº 1, March 2013, 45-57
DOI: 10.1344/105.000001835
Available online at www.geologica-acta.com

An accurate record of volcanic ash fall deposition as characterized by dispersed organic matter in a lower Permian tonstein layer (Faxinal Coalfield, Paraná Basin, Brazil)

M.W. SIMAS[1] **M. GUERRA-SOMMER**[1,*] **J.G. MENDONÇA FILHO**[2] **M. CAZZULO-KLEPZIG**[1]
M.L.L. FORMOSO[1] **I. DEGANI-SCHMIDT**[1]

[1] **Instituto de Geociências, Universidade Federal do Rio Grande do Sul (UFRGS)**
Av. Bento Gonçalves, 9500 -91501.970, Porto Alegre, RS, Brazil. Guerra-Sommer E-mail: margot.sommer@ufrgs.br

[2] **Instituto de Geociências, Universidade Federal do Rio de Janeiro (UFRJ)**
Ilha do Fundão - 21949-900, Río de Janeiro, RJ, Brazil

*Corresponding author

ABSTRACT

For the first time, the dispersed organic matter in the tonstein layer interbedded with a coal seam in the Faxinal Coalfield (Sakmarian, Southern Paraná Basin, Brazil) is characterized. The deposition of clusters of pollen grains was highly influenced by the intense ash fall process that probably occurred during seasonal dehiscence of reproductive structures. The well-preserved phytoclasts with their upper and lower leaf cuticles stuck together indicate that the rapid fall of ash on this material hindered organic biodegradation. The preservation of seemingly autochthonous *Botryococcus* colonies at the top of the tonstein layer is evidence of the subaqueous deposition of this layer. The darkening in cuticles and xylem phytoclasts can be attributed to different causes: the thermal influence of ash fall during deposition, chemical effects of the ash, prolonged oxidation of organic matter in low water level conditions or the burning of plant organs by wildfires. Analyses of dispersed organic matter along the tonstein layer showed that the organic matter succession reflects the composition of different plant strata (herbaceous pteridophytes and arboreal glossopterids-cordaitaleans) around the deposition site.

KEYWORDS **Tonstein. Organic matter. Volcanic ash fall. Southern Paraná Basin.**

INTRODUCTION

Tonsteins are altered volcanic ash layers (Bohor and Triplehorn, 1993) that extend over large distances and usually contain minerals that can be dated by isotopic analyses. Their occurrence is limited to coal-bearing sequences.

Evidence of volcanic activity is widespread in different coal successions of southern Brazil, which are historically assigned to the Río Bonito Formation, a fluvial-marine lithostratigraphic unit constituted by sandstones and shales. This unit contains discrete and continuous clay bed horizons, identified as tonsteins, interbedded within the coal seams from the western to the eastern portion of the southern Brazilian coal basins (Fig. 1; 2) (Formoso *et al.*, 1999; Guerra-Sommer *et al.*, 2008a).

Corrêa da Silva (1973) suggested, on the basis of field relationships and preliminary mineralogical and chemical analyses,

ANEXO J – Artigo publicado em coautoria (2014)
The stratigraphic significance of the Solenoid Complex in the Permian of Gondwana
Disponível em < http://www.revistas.usp.br >

Geologia Série Científica USP

DOI: 10.5327/Z1519-874X201400020008

Revista do Instituto de Geociências - USP
Geol. USP, Sér. cient., São Paulo, v. 14, n. 2, p. 139-148, Junho 2014

The stratigraphic significance of the Solenoid Complex in the Permian of Gondwana

O significado estratigráfico do Complexo Solenoide no Permiano do Gondwana

Margot Guerra-Sommer[1], Isabela Degani-Schmidt[1], Diana Mussa (in memoriam)[2], Pauline Sabina Kavali[3], Mahesh Shivanna[3]

[1]Programa de Pós-graduação em Geociências, Instituto de Geociências, Universidade Federal do Rio Grande do Sul - UFRGS, Avenida Bento Gonçalves 9500, Caixa Postal 15001, CEP 91501-970, Porto Alegre, RS, BR (margot.sommer@ufrgs.br; degani.schmidt@gmail.com)
[2]Museu Nacional, Universidade Federal do Rio de Janeiro - UFRJ, Rio de Janeiro, RJ, BR
[3]Birbal Sahni Institute of Palaeobotany, Lucknow, IN (paulinesabina@gmail.com; paulinemaxwell7@gmail.com)

Received 24 September 2013; accepted 14 April 2014

Abstract

The Solenoid Complex comprises a fossil wood assemblage with stratigraphic distribution restricted to the middle-late Kungurian, present in Western (Irati Formation, Paraná Basin, Brazil) and Eastern (Upper Barakar Interval of the Indian basins) Gondwana. Its occurrence seems to be related to the adaptation of certain plant groups to paleoenvironmental stress in lowland niches of coastal areas subject to salinity variation. The disappearance of these forms in the latest Kungurian is probably linked to the cessation of these conditions, which is confirmed by the sedimentary record. The here designated "Solenoid Complex Zone" correlates with the acme in diversification of striate and taeniate patterns especially in bisacatte pollen grains, but also in monosacatte ones, reflecting important tectonically and climatically driven changes in the vegetational pattern. The waning icehouse stage during the Permian was an important factor to the development of similar vegetation patterns in Western and Eastern Gondwana in the latitudinal belt of 40° – 55°.

Keywords: Stratigraphic correlation; Biostratigraphy; Fossil wood; Kungurian; India; Brazil.

Resumo

O Complexo Solenoide compreende um conjunto de lenhos fósseis com distribuição estratigráfica restrita ao Kunguriano médio-superior, presente no Gondwana Ocidental (Formação Irati, Bacia do Paraná, Brasil) e Oriental (Intervalo Barakar Superior de bacias da Índia). A sua ocorrência parece estar relacionada à adaptação de determinados grupos vegetais ao estresse paleoambiental em terras baixas de áreas costeiras sujeitas a variações de salinidade. O desaparecimento dessas formas no topo do Kunguriano está provavelmente relacionado à cessação de tais condições, o que é confirmado pelo registro sedimentar. A "Zona do Complexo Solenoide" aqui designada correlaciona-se com o clímax na diversificação de padrões estriados e teniados principalmente em polens bissacados, mas também em monossacados, refletindo importantes modificações no padrão vegetacional relacionadas à evolução climática e a processos tectônicos. O declínio do estágio *icehouse* durante o Permiano foi um fator importante para o desenvolvimento de padrões florísticos similares no leste e oeste do Gondwana em uma faixa latitudinal entre 40° – 55°.

Palavras-chave: Correlação estratigráfica; Bioestratigrafia; Lenhos fósseis; Kunguriano; Índia; Brasil.

ANEXO K – Reportagem em revista de divulgação científica (2015)
A floresta da água e do fogo
Disponível em < http://revistapesquisa.fapesp.br >

A floresta da água e do fogo

Fósseis em mina de carvão no Rio Grande do Sul revelam paisagem pantanosa sujeita a incêndios frequentes há 290 milhões de anos

Maria Guimarães


1


2

Muito mudou na paisagem da região Sul do Brasil nos últimos 290 milhões de anos. A América do Sul se separou da África e ergueu-se a serra Geral, cujas montanhas acompanham de perto o que hoje é a costa dos estados do Paraná, de Santa Catarina e do Rio Grande do Sul. Registros preservados nas rochas sugerem que, antes disso, a região tinha áreas alagadas onde brotavam árvores de cerca de 15 metros de altura do grupo das pteridospermas, coníferas ancestrais que dominavam o que hoje são ambientes geradores de carvão no hemisfério Sul. O grupo da paleobotânica Margot Guerra-Sommer, da Universidade Federal do Rio Grande do Sul (UFRGS), obteve mais do que fósseis em expedições à mina de carvão de Faxinal, no município gaúcho de Arroio dos Ratos. As rochas dali preservaram informações paleoecológicas que contam uma história de incêndios recorrentes em um ambiente onde se imaginava uma umidade constante.

"No meio do carvão mineral encontramos fragmentos de troncos com cerca de 20 centímetros de diâmetro", conta a bióloga Isabela Degani-Schmidt, doutoranda no laboratório de Margot. O achado é incomum porque a matéria orgânica vegetal queimada é extremamente delicada e costuma quebrar-se em fragmentos de no máximo 4 a 5 centímetros no caminho até o local no qual fica acumulada e encontra condições de ser preservada para a posteridade. Não foi


3


4

1 Possível estrutura produtora de pólen ao microscópio de fluorescência

2 Brilho indica que pólen não foi queimado

3 e 4 Vistas a olho nu: folhas carbonificadas

FOTOS 1 E 2 JOALICE DE OLIVEIRA MENDONÇA UFRJ/CCMN/IGEO/LAFO 3 E 4 ISABELA DEGANI-SCHMIDT

o que aconteceu na região estudada pelo grupo de Margot. Os fósseis de dimensões incomuns indicam que as árvores da região foram queimadas em pé. Os troncos, depois de caídos, permaneceram no mesmo lugar em que seriam encontrados bem mais tarde por mineradores e pesquisadores.

O material guarda registros importantes do ambiente da época (início do período geológico conhecido como Permiano) naquela região, que agora podem ser interpretados. A fossilização dos troncos e das folhas indica que eram florestas em ambiente pantanoso. “São condições propícias à fossilização porque o material vegetal que cai na água acumula-se em um ambiente ácido inóspito para as bactérias e fungos responsáveis pela decomposição”, explica Isabela. Por isso, a ideia até agora era de um pântano permanente na região. “Nessa turfeira alagada em todas as estações, não se imaginaria que ocorressem incêndios.”

Os achados recentes, publicados na edição de julho da revista *International Journal of Coal Geology*, pintam, porém, um quadro mais complexo. “O ambiente provavelmente nunca ficava seco”, propõe a pesquisadora, “mas haveria um período suficientemente seco para permitir incêndios naturais, que indicam nessas ocasiões uma atmosfera muito mais rica em oxigênio do que a atual”.

O estudo de amostras de troncos e pólen por microscopia de fluorescência e eletrônica de varredura revelou também que não eram incêndios avassaladores. A medula dos troncos e os pólens não foram carbonizados, revelando temperaturas relativamente baixas. Isabela interpreta o achado como indicação de que as estações secas nunca eliminavam por completo a umidade e o solo provavelmente ficava sempre recoberto por um filme d’água, favorecendo a fossilização no próprio local e pela queima incompleta.

FLORA ESPECIALIZADA

A hipótese mais plausível para a origem dos incêndios, segundo Isabela, é que seriam causados por raios. Outra possibilidade aventada seria vulcanismo, reforçada pela presença de uma camada de rocha de cor branca, rica em folhas fossilizadas, em meio ao carvão, interpretada como cinza vulcânica. Examinando essa camada de rocha, o grupo de Margot concluiu que as cinzas já teriam caído frias sobre a região e devem ter vindo de longe. Ainda não se sabe de onde. “Não há indícios de fontes de atividade vulcânica por ali”, afirma Isabela.

Mais do que uma flora carbonizada, os achados revelam uma dinâmica ecológica. A pesquisadora defende que a mata era adaptada ao fogo. “Encontramos a deposição de fósseis de pteridospermas em camadas diferentes, indicando que essas plantas permaneciam ali ao longo do tempo”, explica. Falta determinar se tinham recursos para subsistir nessas condições. “Estamos analisando estruturas nas folhas para ver se tinham especializações nesse sentido.”

Os fósseis encontrados, assim como as condições ambientais que eles permitem inferir, podem ser uma pista de que a diversidade vegetal era um tanto limitada por ali, determinada pela capacidade de resistir aos incêndios constantes. São estudos curiosos porque revelam uma paisagem da qual já não há vestígios vivos, com protagonistas completamente extintos. Antes vistas como um elo evolutivo entre as samambaias e as coníferas, as pteridospermas pertenciam a um grupo de gimnospermas ancestrais cujos parentes mais próximos atuais são, provavelmente, as cicas e o ginkgo. “Não há nada parecido hoje no local”, conta a pesquisadora, que não conhece nenhuma paisagem como a que vê desenhar-se a partir dos fósseis. “Só analisando as rochas para extrair o que está preservado.” ■

Artigo científico

DEGANI-SCHMIDT, I., *et al.* Charcoalified logs as evidence of hypautochthonous/autochthonous wildfire events in a peat-forming environment from the Permian of southern Paraná Basin (Brazil). **International Journal of Coal Geology**, v. 146, p. 55-67. 1º jul. 2015.